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Richmond & Strait (2000) have attracted much attention with a recent morphometric analysis of distal radii of anthropoids and hominid fossils, suggesting some of the latter share knuckle-walking traits. Several aspects of their treatment deserve comment.

These authors show A.L. 288-1q,v and the putative hominid fossil KNM-ER 20419 falling near chimpanzees and gorillas in a canonical analysis of four angles and indices [Richmond & Strait, 2000: Figure 2(b)], hence their conclusions. However those fossils are also clearly in the near morphometric vicinity of *Pongo* and A.L. 288-1q,v seems actually to fall in that suspensory ape's statistical scatter. The orang-utan is not a knuckle-walker and should in many ways represent the opposite morphological extreme, but Richmond & Strait's analysis does not afford much separation. On the other hand, two other (later) hominids, from Sterkfontein and Swartkrans, cluster far away from the previous taxa, near modern *Homo sapiens*, and these hominids/humans are well separated from the great apes. In fact Richmond's & Strait's analysis seems to function more to cluster nonhuman hominoids in distinction to humans (and quadrupedal monkeys), rather than reflecting knuckle-walking function. We question the knuckle-walking functional significance of morphometric results that, after clustering some (but not all) hominids with African apes, next join those with the suspensory Asian apes, the orang-utan and gibbon,

while humans and other hominids (which must also have all shared the putative knuckle-walking ancestry) are quite distinct [Richmond & Strait, 2000: Figure 2(c)].

Richmond & Strait choose not to cite an earlier intensive morphometric treatment of knuckle-walking features from this *Journal* (Corruccini, 1978) which shared several similar measures. Corruccini used 30 wrist features and found maximum separation between African apes and *Pongo*, clearly delineating a knuckle-walking functional complex, and modern *H. sapiens* was quite a bit more similar to knuckle-walkers than to *Pongo* or macaques. Later McHenry & Corruccini (1983) figured these dimensions and showed *Proconsul* to be quite unlike extant knuckle-walkers. Humans still retain features from a probable knuckle-walking heritage, particularly the developmentally early os centrale-scapoid fusion. Therefore the claim (Collard & Aiello, 2000) that Richmond & Strait provide the "first good" evidence for knuckle-walking in human ancestry is curious, because humans themselves retain a fair amount of such evidence. This then would require that hominid sister groups no more remote than *Pan/Gorilla* should demonstrate this complex as well. Also overlooked is the evidence for knuckle-walking in the metacarpal of the Miocene *Kenyapithecus* (Benefit & McCrossin, 1995:247–248).

Corruccini's (1978) measurements include 11 of the distal radius, allowing

Table 1 Distal radius measurements (mm) for hominid fossils and a sample of 16 *Pan paniscus*

Measurement no. (see text)	KNM-ER 20419	Stw 46	A.L. 288-1 (q,v)	<i>P. paniscus</i>
1	5.5	4.0	2.5	9.5
2	3.3	3.5	2.1	2.7
3	14.1	11.5	10.4	15.9
4	2.5	1.5	1.1	3.1
5	27.8	22.5	17.0	25.2
6	4.7	6.0	3.5	5.7
7 (5+6 - 11)	3.0	3.7	2.1	3.4
8 (9-10)	0.0	4.7	5.3	8.2
9	13.5	13.5	10.3	17.0
10	13.5	8.8	5.0	8.8
11	29.5	24.8	18.4	27.6

Measurements 1-8 correspond to numbers 18-25 respectively in [Corruccini, 1978, Table 1](#).

examination of the evident affinities of the hominid fossils. Therefore we decided to apply our old data to the new question of similarities of hominid fossils.

The applicable measurements are the distal projection from the volar rim to the dorsal rim of the distal radius parallel to the radial long axis (measurement no. 1 in [Table 1](#)), the breadth between those ridges across the scaphoid facet (no. 3), depths (concavity) of the scaphoid articular facet perpendicular to the dorso-volar (no. 2) and of the carpal articulation perpendicular to the medio-lateral (no. 4) planes, breadth of that latter plane (no. 5), proximo-distal height of the ulnar facet (no. 6), ulnar-carpal articular angle (no. 7) expressed as the sum of the previous two measures (no. 5+no. 6) minus the diameter between their most distant endpoint (- no. 11), and medio-lateral scaphoid (no. 9) and lunate (no. 10) facet diameters as well as (no. 8) their difference (no. 9 - no. 10) expressing scaphoid pre-dominance in weight transmission.

These traits incorporate specific aspects of similarity to measures figured by [Richmond & Strait \[2000: Figure 2\(a\)\]](#). Our no. 1 resembles their DP (distal projection of the dorsal ridge) and our no. 5 resembles their

MRB (maximum radial breadth), while our no. 3 and no. 4 more tenuously relate respectively to their NB (scaphoid notch breadth) and SLA (scaphoid-lunate angle).

The samples consist of 13 *Gorilla gorilla*, 16 *Pan paniscus* (pygmy chimp or bonobo), 16 *P. troglodytes*, 20 *H. sapiens* (these latter two samples coming down to us only as means since individual data have been misplaced over these decades), and 19 *Pongo*. Means for 20 *Hylobates* and 16 *Macaca* are also available but more individual cases (for intrasample variation) and phyletic relationship to humans reside in the aforementioned samples.

The measurements from KNM-ER 20419 (ostensibly *Australopithecus anamensis*) were taken on the original specimen after reconstructing part of the dorsal rim and styloid process in plasticine. As the original describers of that fossil point out ([Heinrich et al., 1993](#)), it has a large area for the lunate articulation that calls to mind the condition seen in *Pongo*. The measurements from Stw 46 (probably *A. africanus*) were taken on the original specimen after reconstruction of the damaged styloid process. Although the original specimens of A.L. 288-1q,v (*A. afarensis*) were examined, the measurements are

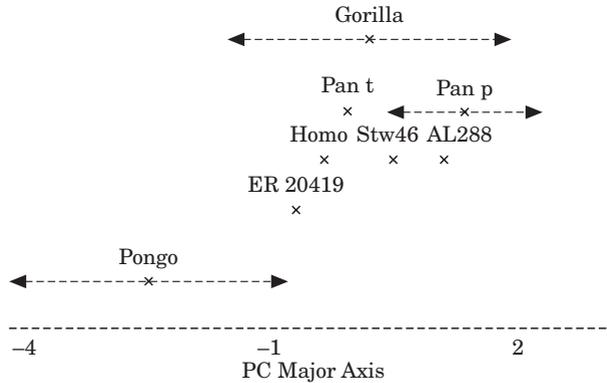


Figure 1. Averaged PC position of cases, of sample 95% two-tailed confidence limits, and of sample means for two different shape PC 1s and the raw data PC 2.

from casts. Table 1 gives all the new data not contained in Corruccini (1978: Table 1).

We subjected these 11 measures (including two approaches to adjusting for or estimating missing data) to a wide variety of analyses: principal components (PC) analysis and discriminant (Mahalanobis) analysis of raw measurements with attention to seeming size and residual (shape) axes of maximum variation, C score (Howells, 1989) transformation of raw measures and shape vector transformations (Corruccini, 1987) to equalize size followed by PC, generalized and Euclidian distance and WPGM clustering of individual specimens and sample means, and repeating all steps with shape vectors adjusted for the within-African ape regression on size variables as in Corruccini’s (1978) original approach (which heuristically pretends knuckle-walking is a monophyletic phenomenon with similar morphological outcomes but for size, contra Dainton & Macho, 1999). Results are sufficiently consistent over all modes of analysis as to allow summarization of key aspects by arithmetic averaging of homologous PC axes. Documentation shall be provided upon request to individuals wishing the fully detailed treatment.

The second component for raw measurements and the primary axes for C-score

and regression adjusted shape vectors were especially similar. Figure 1 provides averaged PC positions of cases and samples and estimated dispersions for this axis over those three analyses. It serves to separate African apes from Asian apes, and the axis correlations with variables also logically demonstrate knuckle-walking function. The positive PC scores for knuckle-walkers correlate with relatively large dorsal rim projection distally, scaphoid facet depth, medio-lateral scaphoid facet diameter; especially large scaphoid-minus-lunate imbalance; relatively small dorso-volar and medio-lateral breadths and ulnar facet; and especially small ulnar-carpal angle (expressing more forced adduction), lunate facet diameter, and total distal carpal articulation medio-laterally. There is fairly detailed functional anatomical correspondence between this pattern and demonstrated knuckle-walking tendencies in the earlier classic literature (see Corruccini, 1978) especially as regards to dorsal resistance to compressive forces transmitted along the third metacarpal.

In this regard, all humans and all hominid fossils are somewhat intermediate, but closer to knuckle-walkers (particularly *P. troglodytes*). KNM-ER 20419 is somewhat of an exception as it is slightly but consistently

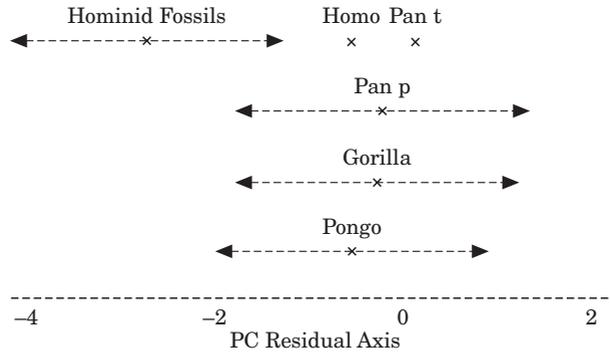


Figure 2. Averaged positions for a homologous PC axis which was the third for raw data, fourth for C-scores and second for size-regressed geometric shape variables (the latter arbitrarily ascribing all *Pan*–*Gorilla* difference to size).

more similar to *Pongo*, which does not conflict too sharply with Richmond & Strait's (2000) placement and is consistent with aspects of the treatment and description by Heinrich *et al.* (1993: Figure 6). The Stw 46 and KNM-ER 20419 fossils are anatomical knuckle-walkers only roughly to the extent that *H. sapiens* is, while A.L. 288-1q,v is more completely chimpanzee-like. We feel this axis (and its functional interpretation) is much more consistent with some (perhaps incipient) knuckle-walking adaptation in hominids that is largely retained in modern humans, than the evidence provided by Richmond & Strait.

A subsidiary axis of PC results always is evident, whether second, third or fourth axes according to different analyses, and this seems also quite homologous according to interpretation afforded by the correlations of variables with the axis. This factor separates all hominid fossils from all other hominoids (Figure 2). Consistent with a broad range of australopithecine postcranial morphometric analyses (e.g., McHenry, 1975, 1986; Oxnard, 1979; Bacon, 2000) there is shared uniqueness, not merely intermediacy in australopithecine distal radial as well as many other postcranial patterns such as their talus, distal humerus, proximal femur, etc. The three fossil hominids are united in distinction to all other hominoids on subsidiary

axes primarily through very large values for relatively deeply concave scaphoid facet, but also through relatively large medio-lateral breadth and lunate facet breadth, and relatively smaller ulnar facet height and total medio-lateral carpal articulation.

Therefore there is actually a roughly triangular disposition of morphometric distances between hominids, African apes and *Pongo* that is also seen when employing generalized (covariance adjusted) distance as opposed to the simple linear distance reflected in these PC dispersions. However, humans and hominids, when projected on to the axis of knuckle-walking *vs Pongo* discrimination, are closer to the knuckle-walkers, while KNM-ER 20419 falls a bit toward *Pongo*.

We feel Richmond & Strait's (2000) results serve mainly to demonstrate general apelike affinities of KNM-ER 20419 and A.L. 288-1q,v, while demonstrating more human morphology in the later Sterkfontein and Swartkrans fossils. Obviously their conclusion about knuckle-walking as an ancestral condition requires that the two former specimens are in fact correctly identified as belonging to taxa that are direct human ancestors. It is argued here that adequate morphological evidence has long been understood for the retention in modern humans of some of the morphopattern

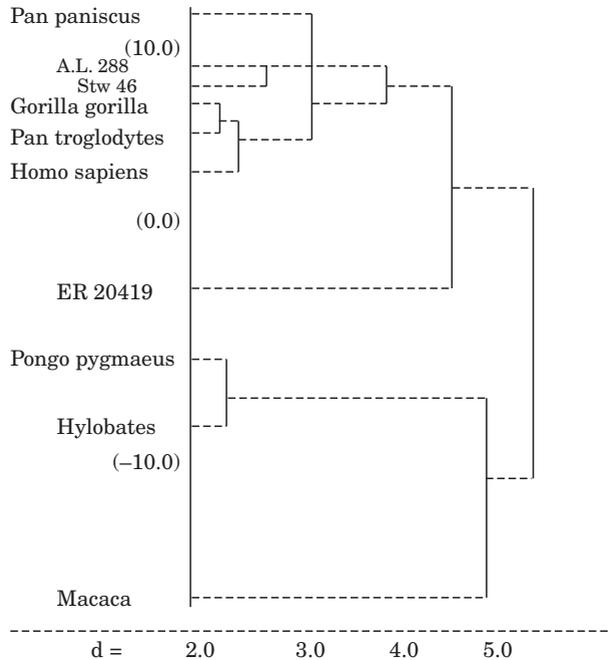


Figure 3. Placement of sample means and individual fossils along the first PC of geometric shape plotted vertically, with WPGM clustering sequence according to the linear Euclidian distance depicted horizontally. With variables more numerous than cases, subroutine ITER (Cooley & Lohnes, 1971) was used to estimate the first eight PC axes. The African clade is faithfully reconstructed from the distal radius when using these variables.

signaling knuckle-walking as a synapomorphy of the African clade. Such diverse anthropoids as orang-utans, gibbons and macaques then would share the plesiomorphous pattern. This is reflected in the PCA of means only for all available taxa and their clustering, as indicated in Figure 3.

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