



Side steps: the erratic pattern of hominin postcranial change through time

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ABSTRACT

The hominin fossil record reveals brain-size expansion, canine reduction, premolar metaconid development, and numerous other craniodental features that become more human-like through time. In general, the postcranial skeleton also gets more human-like through time, but in some respects it does not. This is particularly apparent in the overall morphology of one of the most frequently preserved elements, the distal humerus. Some of the earliest hominins display quite human-like morphologies, whereas later specimens are quite unusual among extant species of Hominoidea: when described metrically and subjected to multivariate discriminant analyses in the context of large samples of extant hominoid humeri, the shapes of the earliest hominin fossils are more human-like than many of the later specimens. The Mahalanobis distances between many of the 1.5–2 Ma hominin humeri and *Homo sapiens* are remarkably large. Many of the less well-represented postcranial specimens do not follow a linear path through time of increasing hominization either. This is particularly noticeable in the fore-to-hind limb joint-size proportions, ulnar morphology, and pelvic architecture. The hominin postcranial fossil record reveals many side-steps: there appears to be no simple march toward our human bodies, but a pattern better explained as adaptations to proximate conditions and constrained by ontogeny and history.

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Introduction

Two observations shape this study. The first derives from formal phylogenetic analyses of hominin craniodental fossils that reveal the accumulation of synapomorphies with later species of hominins through time (Skelton and McHenry, 1992; Strait et al., 1997; Wood and Collard, 1999; McHenry, 2002; Strait and Grine, 2004; White et al., 2006). Although differing in detail, these studies reveal a consistent pattern: the geological age of each species is closely associated with the number of derived traits shared with later species. White et al. (2006) demonstrate this in their analyses of dental change from late Miocene hominoids (7–6 Ma) to *Ardipithecus ramidus* (4.4 Ma) to *Australopithecus anamensis* (3.9–4.2 Ma) to *Au. afarensis* (3–3.4 Ma), where the upper canine became more incisiform with a short crown and higher shoulders; the P₃ became less asymmetric with the protoconid reduced in height and the transverse crest changed to be more transverse; canine size decreased relative to the molars; dm₁ became broader with a relatively smaller protoconid, larger and more mesially placed metaconid, developed anterior fovea, and a larger and higher talonid; the articular eminence of the temporomandibular joint (TMJ) became more defined; canine and molar

enamel thickened; P₃ became less asymmetric with a less dominant buccal cusp; and the postcanine teeth became more megadont.

Although *Kenyanthropus* (3.5–3.3 Ma) appears to have a derived face linking it to a later species that has been assigned to *Homo rudolfensis* (Leakey et al., 2001), it still retains many primitive traits befitting its early date (e.g., indistinct articular eminence, shallow TMJ, narrow external auditory meatus, lack of megadontia). White (2003) suggests that its flat face may be due to distortion and not to an untimely appearance of a derived trait.

Au. africanus (3–2.4 Ma) shares a host of derived features linking it to later hominin species relative to *Au. afarensis* (52 such traits are listed in Table 1 of McHenry, 1985). Although KNM-WT 17000 (2.6 Ma) shares many apparent traits with *Paranthropus boisei* (Walker et al., 1986; Walker and Leakey, 1988), it still retains the numerous primitive features of a 2.6 Ma old hominin (e.g., facial prognathism, small brain, shallow TMJ, posterior position of the main part of the temporalis muscle attachment). Its resemblance to *P. boisei* may be due to parallel evolutionary adaptations to heavy chewing (Skelton et al., 1986; Skelton and McHenry, 1992; Skelton and McHenry, 1998), but this alternative has been challenged (Strait et al., 1997; Strait and Grine, 1998; Strait and Grine, 2004; Strait et al., 2007). Whatever it is, it retains the primitive craniodental morphology that fits its geological age. *Au. garhi* (2.5 Ma) retains numerous primitive features relative to later hominin species (e.g., pronounced prognathism, shallow TMJ), although it has more

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Table 1
Sample sizes, means, and standard deviations of the comparative sample

Measurement	<i>Homo</i>		<i>Pan</i>		<i>Gorilla</i>		<i>Pongo</i>	
	n = 64		n = 42		n = 66		n = 34	
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
1. trochwd	21.9	2.61	21.6	1.86	30.7	3.99	22.5	2.69
2. trochap	15.0	2.03	16.1	1.91	22.2	3.61	15.2	2.54
3. lattroch	22.3	2.11	26.8	1.92	33.0	5.30	27.0	3.98
4. capwd	15.7	1.55	18.2	1.40	21.5	2.56	17.6	2.14
5. capht	19.0	2.05	21.4	1.82	28.2	4.34	23.8	3.39
6. artwd	38.8	4.35	44.6	2.90	59.8	8.49	45.5	5.28
7. biepi	55.7	6.15	62.1	4.55	88.4	13.2	64.2	7.44
8. tmedepi	38.6	4.48	43.7	3.26	64.3	9.92	48.1	6.21
9. tsupcon	36.6	4.10	40.4	2.56	60.5	8.77	47.2	5.69
10. clatepi	26.5	2.34	30.8	2.65	43.7	6.01	34.6	4.27
11. wdolec	25.0	2.47	25.2	2.05	35.7	5.77	25.4	3.46
12. dolec	6.7	0.90	9.3	1.12	12.7	2.30	8.1	1.40
13. medolec	9.3	2.51	11.9	1.69	15.2	3.07	15.0	2.36
14. latolec	14.8	2.04	19.3	2.18	26.3	4.06	19.5	3.06
15. apshaft	14.7	1.82	17.4	1.42	22.3	2.85	15.9	2.57
16. wdmedepi	12.0	1.74	12.6	1.31	16.5	2.48	13.8	2.46

derived features shared with later hominins than does *Au. afarensis* (Asfaw et al., 1999).

The phylogenetic placement of the late “robust” australopithecines fits surprisingly well in this view of hominin craniodental evolution through time. Both *P. robustus* (ca. 2–1 Ma) and *P. boisei* (2.3–1.4 Ma) share numerous derived features with early *Homo* relative to earlier hominin species. Many studies have pointed this out, but Skelton et al. (1986), Skelton and McHenry (1992), Strait et al. (1999), and Strait and Grine (2004) tried to objectively assess as many craniodental features as possible and their results revealed the close phylogenetic relationship between late “robust” australopithecines and early *Homo*. Reduced facial prognathism, tucked cerebellum, flexion of the cranial base, depth of the mandibular fossa, increased size of the postglenoid process, petrous orientation, inclination of the nuchal plane, vertical orientation of the mandibular symphysis, lateral direction of the mental foramen, loss of hollowing above and behind the mental foramen, increased frequency of a well-developed P₃ metaconid, mesiodistal protrusion of the P₃ base, dental arcade shape, weakening of the parietomastoid angle, reduction of the arching of the supraorbital contour, and smoothing of the nasal cavity entrance are some of the derived character states shared by *Homo*, *P. robustus*, and *P. boisei* relative to earlier hominin species. Some of these resemblances may be due to homoplasy and there are certainly many autapomorphies, but it is presently apparent that the craniodental synapomorphies accumulated in successively younger species.

The second observation is that although in many respects the postcranial morphology changes through time so that older species are more primitive and younger species share derived features with later hominin species, this is demonstrably untrue of many other aspects of the postcranium. Unlike the pattern in craniodental remains, in some respects, older fossil hominins have more modern looking postcrania than younger ones. For example, the 3.0 Ma *Au. afarensis* ulna, A.L. 438-1m, is more like *H. sapiens* than are the later Omo L40-19 (2.3 Ma) and OH 36 (1.1–1.3 Ma) specimens (Drapeau et al., 2005; McHenry et al., 2007). The relative mediolateral width of the femoral shaft that appears to be related to pelvic width and activity patterns (Ruff, 1995) is moderate in the earliest hominins, expanded in archaic *Homo*, and moderate again in *H. sapiens*. Forelimb joint size relative to hind limb joint size is more human-like in the earlier species, *Au. afarensis*, than it is in the later species, *Au. africanus*, despite the fact that the craniodental morphology of the latter species shares numerous derived traits with *Homo* relative to the former species (McHenry and Berger, 1998a; Richmond

et al., 2002; Berger, 2006; Green et al., 2007, but see Dobson, 2005; Reno et al., 2005).

The purpose of this study is to examine the pattern of morphological change through time of one of the most frequently-preserved postcranial elements in the hominin fossil record, the distal humerus. Well-preserved specimens span four million years and represent species that accumulate craniodental synapomorphies with *H. sapiens* through time from the primitive *Au. anamensis* (3.9–4.2 Ma) to *Au. afarensis* (3.0–3.7 Ma) to *Au. africanus* (2.4–3.0 Ma) to early *Homo* (1.5–1.9 Ma) to *Paranthropus boisei* (1.4–2.2 Ma) and *P. robustus* (1–2 Ma). A reasonable prediction would be that progressively younger species should display more human-like morphology that reflects greater similarity in behavior and function to later species of *Homo*.

Materials and methods

The oldest available fossil hominin distal humerus is that of KNM-KP 271 attributed to *Au. anamensis* and securely dated to 4.12–4.07 Ma (Leakey et al., 1995; Leakey et al., 1998). Hadar humeri are part of the *Au. afarensis* sample and consist of A.L. 137-48 (Sidi Hakoma Member, 3.3 Ma), A.L. 322-1 (Sidi Hakoma/Denen Dora Members, 3.2 Ma), and the right and left sides of A.L. 288-1 (m and s, respectively; Kada Hadar Member, 3.2 Ma; Johanson et al., 1982a; Johanson et al., 1982b; Lovejoy et al., 1982; Walter, 1994; Lockwood et al., 2000). *Australopithecus africanus* is represented by STW 431 (Toussaint et al., 2003). It is part of the partial skeleton from Member 4 of Sterkfontein that is biostratigraphically dated to between 2.4 and 2.8 Ma (Vrba, 1985; Delson, 1988; McKee et al., 1995), but may be older (Partridge et al., 2003) or younger (Berger et al., 2002).

There are four well-preserved distal humeri from the Koobi Fora formation including KNM-ER 1504 and 3735 (upper Burgi Member, 1.9 Ma), 6020 (upper KBS member, 1.8 Ma), and 739 (Okote Member, 1.5 Ma; Feibel et al., 1989). KNM-ER 1504 and 739 have been tentatively assigned to *P. boisei* (Leakey, 1971; Leakey, 1973; Senut, 1980; Senut, 1981). However, a quantitative analysis by Lague and Jungers (1996) showed that these two fossils were very distinct from TM 1517 (the type specimen of *P. robustus*), thus suggesting that they may not belong to the same genus. Although KNM-ER 3735 was too fragmentary to be included in the analysis, it has been noted by multiple researchers that its morphology is extremely close to that of KNM-ER 1504 and 739 (Leakey et al., 1989; Lague and Jungers, 1996). KNM-ER 3735 is associated with cranial remains that have been attributed to *H. habilis* (Leakey et al., 1989). Lague and Jungers (1996) suggest that KNM-ER 1504, 739, and 3735 may all belong to some type of early *Homo*. They note that the sheer size and geologic position of KNM-ER 739 make it unlikely to belong to *H. habilis* with KNM-ER 1504 and 3735, and that it should instead be attributed to *H. rudolfensis*. KNM-ER 6020 is still enigmatic and its taxonomic position is undetermined (Leakey and Walker, 1985; Feibel et al., 1989).

From the Nachuki Formation (Nariokotome, West Turkana) is KNM-WT 15000F, part of the adolescent partial skeleton dated to 1.54 Ma and attributed to *H. erectus/ergaster* (Brown and McDougall, 1993; Walker and Leakey, 1993a; Walker and Leakey, 1993b). The first discovered Plio-Pleistocene distal humerus is part of the type specimen of *Paranthropus robustus* from Kromdraai, South Africa, TM 1517 (Broom, 1938). By associated fauna, Vrba (1985) estimated its age as about 2 Ma. Another specimen attributed to *P. robustus* is SK 24600 from Member 1 of Swartkrans (Susman et al., 2001) that Vrba (1985) puts at between 1.6–1.8 Ma through biostratigraphical analysis. The most recent fossil is SKX 10924 from Member 3 of Swartkrans that may be as young as 1 Ma (Brain, 1993). Since Grine (1993, 2005) attributes all craniodental specimens from Member 3 to *P. robustus*, it is likely that SKX 10924 also

belongs to that taxon, although [Susman et al. \(2001\)](#) assigns SKX 10924 to *Homo*.

[Table 1](#) gives means and standard deviations of the 16 measurements originally used in [McHenry \(1972; McHenry and Corruccini, 1975a; McHenry, 1976\)](#). [Figure 1](#) illustrates each dimension. The measurements are 1) TROCHWD (trochlear width): the distance between the crest of the ridge marking the medial border of the trochlear surface and the crest marking the lateral border, taken on the posterior aspect. The caliper arms are held parallel to the crests whenever possible. This measurement is the breadth of the auricular surface that joins the humerus and the ulna. It is taken in the posterior aspect because in some primates the lateral crest does not extend all the way around the auricular surface but is only present on the posterior side. The posterior aspect has the added advantage of having the two crests approximately the same height, whereas distally and anteriorly the medial ridge is much higher and projecting. 2) TROCHAP (a-p diameter of the trochlea): the distance

between the anterior and posterior surfaces of the trochlea taken perpendicularly to the axis of the shaft. Calipers with sharp edges are used so that the deepest point of the trochlea can be reached. This measurement indicates, among other things, the depth of the trochlear groove. A deep trochlea is possibly associated with greater side-to-side stability. 3) LATTROCH (a-p diameter of the lateral trochlear ridge): the distance between the anterior-most point on the groove between the capitulum and trochlea and the posterior-most point on the lateral trochlear ridge. This is taken perpendicularly to the shaft with flat-armed calipers. It measures the extent to which the lateral wall of the olecranon fossa is built up. 4) CAPWD (capitular width): the distance between the lateral border of the capitulum on the anterior aspect and the groove that separates the capitulum from the trochlea. This is identical to the measurement in [Straus \(1948\)](#). It measures the width of the articular surface associated with the head of the radius. 5) CAPHT (capitular height): the distance from the anterioproximal border of the capitulum to the distoposterior border along the midline. This dimension is related to the posterior extent of the articular surface of the capitulum. One subtle difference between the human and chimpanzee humerus is the greater posterior extent of the capitulum in the latter. When the capitulum height measurement is compared with the capitular width, it gives an indication of the proximo-distal flatness of the capitulum. 6) ARTWD (width of the articular surface): the width across the anterior aspect of the articular surface from the lateral border of the capitulum to the edge of the articular surface medially. This is identical to [Straus' \(1948\)](#) width measurement of the distal articular surface ([Martin and Saller, 1957; Martin 12a](#)). 7) BIEPI (biepicondylar): the greatest distance between the most projecting points on the epicondyles ([Martin and Saller, 1957; Martin 4a](#)). 8) TMEDEPI (lateral trochlear ridge to proximal border of medial epicondyles): the direct distance between the distal-most point on the ridge forming the lateral border of the trochlea and the proximal border of the medial epicondyle. This measurement proved to be one of the seven measurements that effectively separated the human and chimpanzee humeri in the study by [Patterson and Howells \(1967\)](#). In combination with the width of the trochlea it gives an index of the relative projection of the medial epicondyle. 9) TSUPCON (lateral trochlear ridge to medial supracondylar ridge): the minimum distance between the distal-most point on the ridge between the capitulum and the trochlea and the medial supracondylar ridge. This is also from [Patterson and Howells \(1967\)](#), and in combination with the previous measurement (TMEDEPI), gives an indication of the extent to which the medial epicondyle is turned up. 10) CLATEPI (proximal border of the lateral epicondyle to the groove between the capitulum and the trochlea in the distal aspect): another measurement defined by [Patterson and Howells \(1967\)](#). It gives a measure of the position of the lateral epicondyle. 11) WDOLEC (width of the olecranon fossa): the maximum distance between the medial and lateral borders of the olecranon fossa. This was taken as described by [Straus \(1948\)](#), only not necessarily perpendicular to the axis of the shaft. 12) DOLEC (depth of the olecranon fossa): the distance between the deepest point in the olecranon fossa and the line connecting the trochlear groove and the proximal border of the olecranon fossa. A straight-edge is placed across the olecranon fossa and the depth is measured from the straight-edge to the floor of the fossa with the back end of the Helios Caliper. 13) MEDOLEC (medial border of the shaft to the olecranon fossa): the minimum distance between the medial border of the shaft and the medial border of the olecranon fossa. This measurement, combined with the width of the olecranon fossa and the next measurement (LATOLEC), gives an indication of the transverse diameter of the shaft above the epicondyles. Measuring the transverse diameter of the shaft directly depends on the position in which it is measured so much that it becomes inaccurate and unrepeatable. 14) LATOLEC

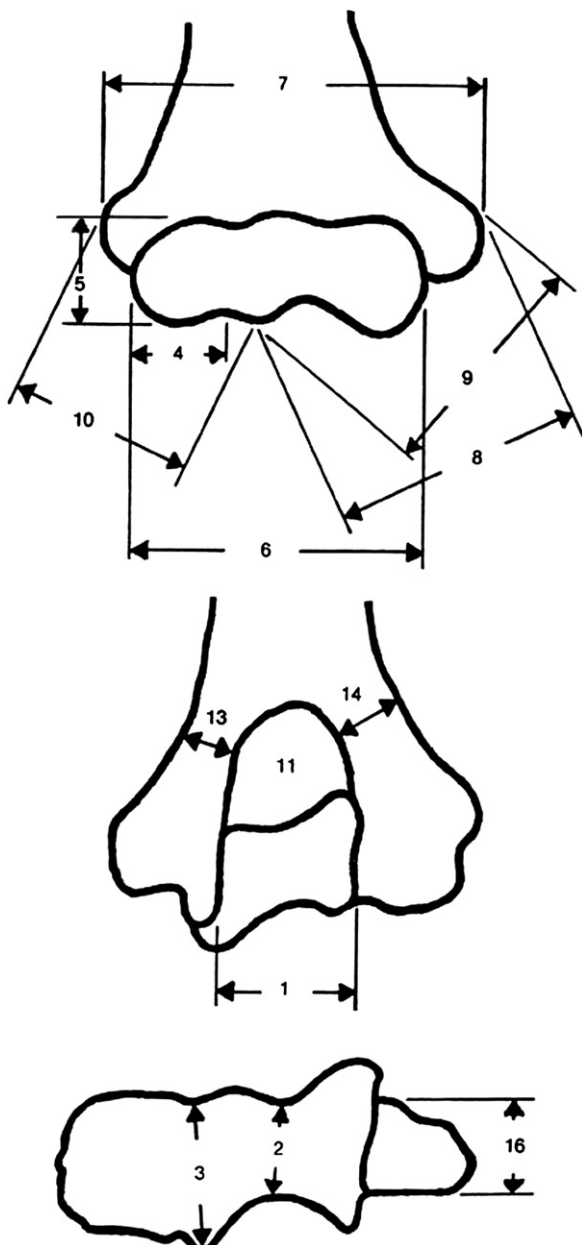


Fig. 1. Diagram of the 16 measurements used in this study. Measurements #12 and #15 not shown ([McHenry, 1976](#)).

(lateral border of the shaft to the olecranon fossa): the minimum distance between the lateral border of the shaft and the lateral border of the olecranon fossa. 15) APSHAFT (a–p diameter of the shaft): the shaft diameter at the proximal border of the olecranon fossa. 16) WDMEDIPI (width of the medial epicondyle): the anterior–posterior diameter of the medial epicondyle taken parallel to the long axis of the epicondyle.

Table 2 provides fossil measurements. The senior author used plasticine to reconstruct missing parts on the original fossils guided by the morphology of similar and more complete fossils; all reconstructed fossils are marked in Table 2. The measurements describe aspects of the shape of the distal humerus without particular regard to possible redundancy because the multivariate discriminant analysis takes into account inter-correlations. Highly correlated measurements (e.g., #6 [ARTWD], width of the articular surface and # 7, [BIEPI] biepicondylar width, with the $r = 0.95$) are not weighted equally in the discriminant functions (i.e., if one has a high coefficient, the other will be low). The method produces orthogonal axes that maximally separate known groups. We transform the raw measurements into size-adjusted variables by dividing each measurement of each specimen by its geometric mean (Jungers et al., 1995). The resulting shape variables appear in Table 3. The comparative samples define the multidimensional discriminant space and the fossils were projected onto this space.

When fossils are entered indirectly after the space is already defined, the assumption of the analysis is that the fossils actually do belong to one of the four comparative samples, which is untrue and has the effect of disregarding unique properties of the fossils. Oxnard (1972) noted that although the shoulder girdle of *Daubentonia* is visually markedly different from that of other primates, when entered after the space is defined, the *Daubentonia* genus belongs to the main group of primate superfamilies. If instead it is

used in creating the discriminant space, *Daubentonia* lies far outside of the space created by the others, reflecting the unique characters obvious to those who are familiar with their anatomy (Oxnard, 1972). One cannot conclude that the unknown specimens belong to any of the known groups because, as Bronowski and Long (1951:794) pointed out long ago, “...the measurements might, for example, be matched by a pebble or a fake.”

However, entering the fossils as their own group has its own disadvantages. Unlike a biological group, such as the genus *Daubentonia*, the fossil specimens are quite variable, violating the assumption of group homogeneity. There are also very few fossil specimens, although there are many measurements. As shown in McHenry et al. (2007), a random sample test indicates that when there are many measurements but few specimens, multiple discriminant analysis artificially defines an axis that separates the fossil group from the others. This means that the uniqueness registered by the axis may not be meaningful biologically (please refer to McHenry et al., 2007, for more discussion of this particular problem and results of this random sample test).

Entering the fossils without allowing them to help define the discriminant spaces avoids the problem of heterogeneity among the fossil group, but does not register their uniqueness. This approach is conservative in the sense that fossils are placed in a multidimensional space defined by extant species without reference to their possible uniqueness. We also performed analyses in which the fossils were entered into the calculation of the discriminant scores and it had little effect on the first three functions and the Mahalanobis distances from the human centroid.

Although multivariate discriminant analysis adjusts for possible redundancy among the measurements, there is also the potential problem of bias in calculating the shape variables. We explored the effects of this by determining shape variables derived by dividing

Table 2
Fossil values in mm^a

	trochwd	trochap	lattroch	capwd	capht	artwd	biepi	tmedepi
A.L. 137-48A	17.3	11.7	16.8	12.8	14.6	36.0	49.6	33.5
A.L. 322-1	18.9	14.1	18.9	11.7 ^b	16.4	32.7	45.9	31.8
A.L. 288-1m	16.1	12.1	16.5	11.5	14.5	29.0	41.0	29.3
A.L. 288-1s	15.8	11.8	15.8	11.1	14.0	29.5	41.1	30.2
KNM-KP 271	24.6	13.2	22.2	16.3	19.4	44.8	60.2	41.5
STW 431	19.5	15.6	21.2	15.8	19.0	40.5 ^b	59.5	42.0
KNM-ER 3735A	18.6 ^b	12.0	19.8 ^b	11.8 ^b	16.4 ^b	32.3 ^b	57.4 ^b	38.7 ^b
KNM-ER 1504	20.4	10.4 ^b	20.1	14.0	17.9	39.5	59.9	40.1
KNM-ER 6020	24.6 ^b	16.7 ^b	26.6 ^b	17.0	23.8	44.7	75.3 ^b	53.0 ^b
KNM-WT 15000	22.0 ^b	15.8	21.1	15.2	16.5	39.0	58.0 ^b	42.2 ^b
KNM-ER 739	24.7	14.6	24.4	17.3	25.6	43.6	71.2	49.7
TM 1517	20.0	12.6	20.6	16.5	16.9	40.1	53.8	34.1
SKX 10924	17.6	10.7	16.7	13.6	15.3	31.0	43.6	30.7
SK 24600	16.0 ^b	11.2 ^b	16.9 ^b	12.7	16.5	30.5 ^b	44.6	31.7
	tsupcon	clatepi	wdolec	dolec	medolec	latolec	apshaft	wdmedepi
A.L. 137-48A	31.9	20.0	23.1	6.5	8.8	13.7	13.5	11.6
A.L. 322-1	32.2	21.0	20.8	6.7	8.6	11.8	15.1	11.8
A.L. 288-1m	30.5	19.3	19.7	7.4	8.3	11.2	12.6	8.5
A.L. 288-1s	30.9	17.8	21.0	6.6	7.9	10.8	13.0	8.5
KNM-KP 271	39.3	27.6	28.6	8.2	10.7	15.2	15.7	13.5
STW 431	38.6 ^b	26.4	20.6	8.0 ^b	9.6 ^b	15.5	14.6 ^b	11.8
KNM-ER 3735A	38.6 ^b	25.1 ^b	25.4	7.8	10.2	15.0	13.7	12.3
KNM-ER 1504	37.5	26.2	21.5	6.9 ^b	14.0	17.5	15.8	12.2
KNM-ER 6020	51.2 ^b	34.5 ^b	27.5 ^b	8.2	14.3 ^b	20.8 ^b	21.2	13.5 ^b
KNM-WT 15000	39.2	26.8	23.3	6.3 ^b	9.8	18.2	16.2	12.0 ^b
KNM-ER 739	47.1	34.3	29.9	8.1	13.3	18.6	17.3	13.3
TM 1517	31.8	24.9	19.1	6.4	8.8	14.3	13.1	10.4
SKX 10924	30.0	21.4	21.3	6.0	6.5 ^b	9.9	11.3	8.0 ^b
SK 24600	30.3	20.0 ^b	21.4	5.5	8.2	9.9	11.8	7.5

^a The measurements from left to right are: trochlear width, trochlear anterior–posterior (a–p) diameter, lateral trochlear ridge a–p diameter, capitular width, capitular height, articular surface width, biepicondylar width, trochlea to medial epicondyle, trochlea to supracondylar ridge, capitata to lateral epicondyle, olecranon fossa width, olecranon fossa depth, width of medial wall of olecranon fossa, width of lateral wall of olecranon fossa, a–p shaft diameter, and width of medial epicondyle.

^b Reconstructed.

Table 3
Group shape means and fossil values

	trochwd	trochap	lattroch	capwd	capht	artwd	biepi	tmedepi
<i>Homo</i>	1.096	0.745	1.118	0.792	0.949	1.932	2.781	1.920
<i>Pan</i>	0.938	0.699	1.163	0.789	0.930	1.938	2.697	1.897
<i>Gorilla</i>	0.987	0.713	1.057	0.693	0.903	1.916	2.837	2.058
<i>Pongo</i>	0.945	0.637	1.130	0.738	0.996	1.908	2.689	2.012
A.L. 137–48A	0.996	0.674	0.967	0.737	0.840	2.072	2.855	1.928
A.L. 322–1	1.079	0.805	1.079	0.668	0.936	1.867	2.620	1.815
A.L. 288–1m	1.015	0.763	1.041	0.725	0.915	1.829	2.586	1.848
A.L. 288–1s	1.014	0.757	1.014	0.712	0.899	1.894	2.638	1.938
KNM-KP 271	1.139	0.611	1.028	0.755	0.898	2.075	2.788	1.922
STW 431	0.960	0.768	1.043	0.778	0.935	1.993	2.928	2.067
KNM-ER 3735A	0.976	0.630	1.039	0.619	0.861	1.692	3.012	2.031
KNM-ER 1504	1.016	0.518	1.001	0.697	0.891	1.967	2.983	1.997
KNM-ER 6020	0.976	0.662	1.055	0.674	0.944	1.773	2.986	2.102
KNM-WT 15000	1.075	0.772	1.032	0.743	0.807	1.907	2.836	2.063
KNM-ER 739	1.023	0.605	1.010	0.716	1.060	1.805	2.948	2.058
TM 1517	1.085	0.684	1.118	0.895	0.917	2.176	2.920	1.851
SKX 10924	1.125	0.684	1.067	0.869	0.978	1.981	2.786	1.962
SK 24600	1.017	0.712	1.075	0.807	1.049	1.939	2.836	2.015
	tsupcon	clatepi	wdolec	dolec	medolec	latolec	apshaft	wdmedepi
<i>Homo</i>	1.824	1.335	1.263	0.341	0.443	0.732	0.732	0.596
<i>Pan</i>	1.757	1.338	1.095	0.403	0.518	0.839	0.757	0.547
<i>Gorilla</i>	1.940	1.403	1.147	0.409	0.487	0.844	0.717	0.530
<i>Pongo</i>	1.976	1.450	1.062	0.337	0.630	0.816	0.665	0.577
A.L. 137–48A	1.836	1.151	1.330	0.374	0.507	0.789	0.777	0.668
A.L. 322–1	1.838	1.199	1.187	0.382	0.491	0.674	0.862	0.674
A.L. 288–1m	1.924	1.217	1.242	0.467	0.523	0.706	0.795	0.536
A.L. 288–1s	1.983	1.143	1.348	0.424	0.507	0.693	0.834	0.546
KNM-KP 271	1.820	1.278	1.324	0.380	0.495	0.704	0.727	0.625
STW 431	1.900	1.299	1.014	0.394	0.472	0.763	0.719	0.581
KNM-ER 3735A	2.026	1.317	1.333	0.409	0.535	0.785	0.719	0.645
KNM-ER 1504	1.868	1.305	1.071	0.344	0.697	0.872	0.787	0.608
KNM-ER 6020	2.030	1.368	1.091	0.325	0.567	0.825	0.841	0.535
KNM-WT 15000	1.917	1.310	1.139	0.308	0.479	0.890	0.792	0.587
KNM-ER 739	1.950	1.420	1.238	0.335	0.551	0.770	0.716	0.551
TM 1517	1.726	1.351	1.037	0.347	0.478	0.776	0.711	0.564
SKX 10924	1.917	1.367	1.361	0.383	0.415	0.633	0.722	0.511
SK 24600	1.926	1.272	1.361	0.350	0.521	0.629	0.750	0.477

each variable by the square root of the articular width multiplied by caputular height. The resulting discriminant analysis was very similar to that produced by the shape variables derived from dividing by the geometric mean, and so is not shown.

We used SPSS 14.0 to perform the discriminant analyses. We divided the comparative sample into four groups: *Homo*, *Pan*, *Gorilla*, and *Pongo* with both sexes represented for each comparative species. *Pan* did not include *Pan paniscus* because the sample size was too small. We conducted two analyses, one on raw variables and one using size-standardized variables (or “shape” variables) as described above. Discriminant scores were used to calculate Mahalanobis distances between the fossils and the centroid of each extant species distribution. We then wrote a statistical program (described more fully in McHenry et al., 2007) that calculates the proportion of 1,000 randomly-selected intraspecific pairs from each of the four comparative species that have a greater distance than the distance between each fossil and the proportion of pairs that have a greater distance than that between each fossil and each species centroid. The purpose of this analysis was to more fully evaluate the morphological similarity among fossils. We then used the Mahalanobis distances to the human centroid and geologic dates of the fossils to graph the change in morphology through time. For specimens without exact ages, we used the midpoint of the range.

Results

The means and standard deviations of the comparative samples appear in Table 1. Table 2 gives the measurements for each fossil. Table 3 provides the size-standardized measurements for the

comparative samples and fossils. Figures 2 and 3 plot the discriminant functions based on 16 raw measurements, and Table 4 gives the correlations between each function and each measurement. Function one accounts for 61.9% of the variation and is dominated by size variation. This function maximizes the projections of the largest distal humeri (i.e., *Gorilla*), and all the measurements are positively correlated with the discriminant scores derived from this function. Function two explains 22.6% of the variance, maximizes the projection of *Pongo*, and is most highly correlated with measurement #13 (medial border of the shaft to the olecranon fossa). Function three explains only 15.5% of the variance and maximizes the projection of *Pan* from the other groups on the basis of the chimpanzee’s relatively-deep olecranon fossa (#12), wide shaft a-p diameter (#15), and wide lateral pillar (#14).

As visible in Fig. 2, the fossils cluster tightly around the *Homo* and *Pan* distributions for functions one and two. The only exceptions are KNM-ER 6020 and 739. KNM-ER 6020 falls within the distribution of *Gorilla*, and KNM-ER 739 somewhere in-between the *Homo* and *Gorilla* distributions. This placement is related to their scores on function one and the fact that both specimens are quite large.

Table 5 reports the Mahalanobis distances among the centroids and fossils based on the discriminant scores. The values above the diagonal line formed by the zero-values are from the raw-variable discriminant analysis, those below are size-adjusted. Distances are marked that exceed all but 5% of the 1,000 randomly selected pairs within each comparative species. The oldest fossil, KNM-KP 271, is very close to the human centroid as are all other fossil hominins, except three specimens from Koobi Fora, KNM-ER 739, 1504, and 6020.

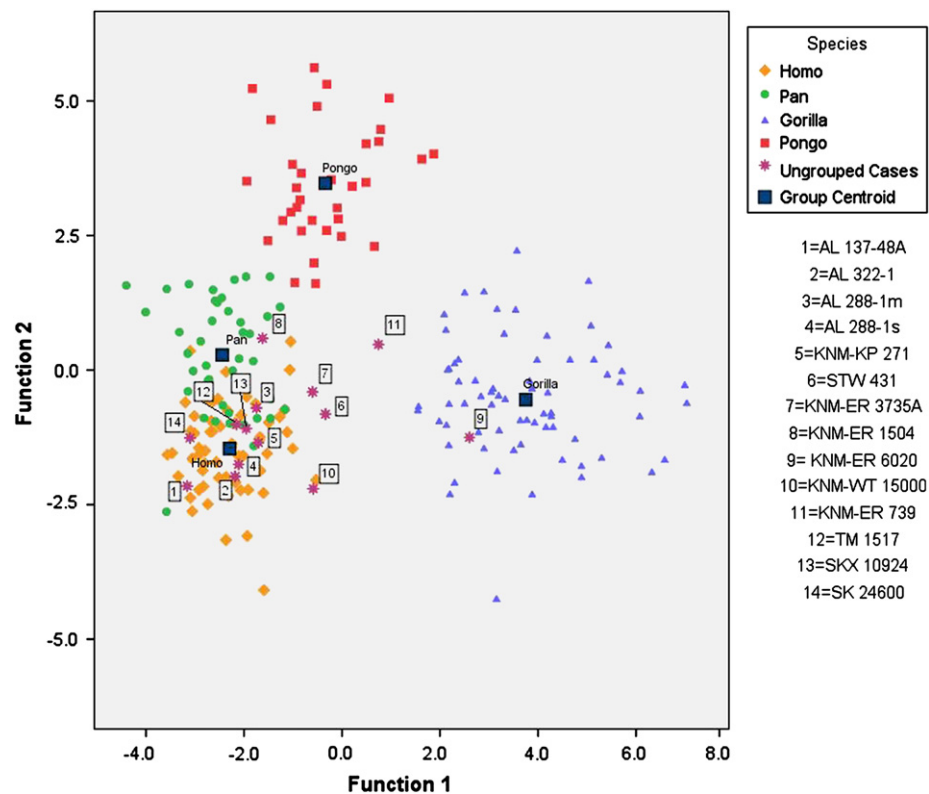


Fig. 2. Scatter plot of discriminant functions 1 and 2 based on 16 raw measurements of the distal humerus.

Table 5 also shows the Mahalanobis distances between each fossil. Among the fossils, the largest distances are seen between the Hadar and Koobi Fora fossils. The distances between A.L. 137 and KNM-ER 6020 and 739, for example, exceed all pairs drawn at random, except 4% within the gorilla sample.

Figures 4 and 5 show the discriminant functions based on 16 size-corrected measurements. Function one minimizes the projections of *Homo* and *Pan* and maximizes *Gorilla* and *Pongo*. It accounts for 45.9% of the variance. Table 4 shows that the most highly and positively correlated measurements with this function are #8

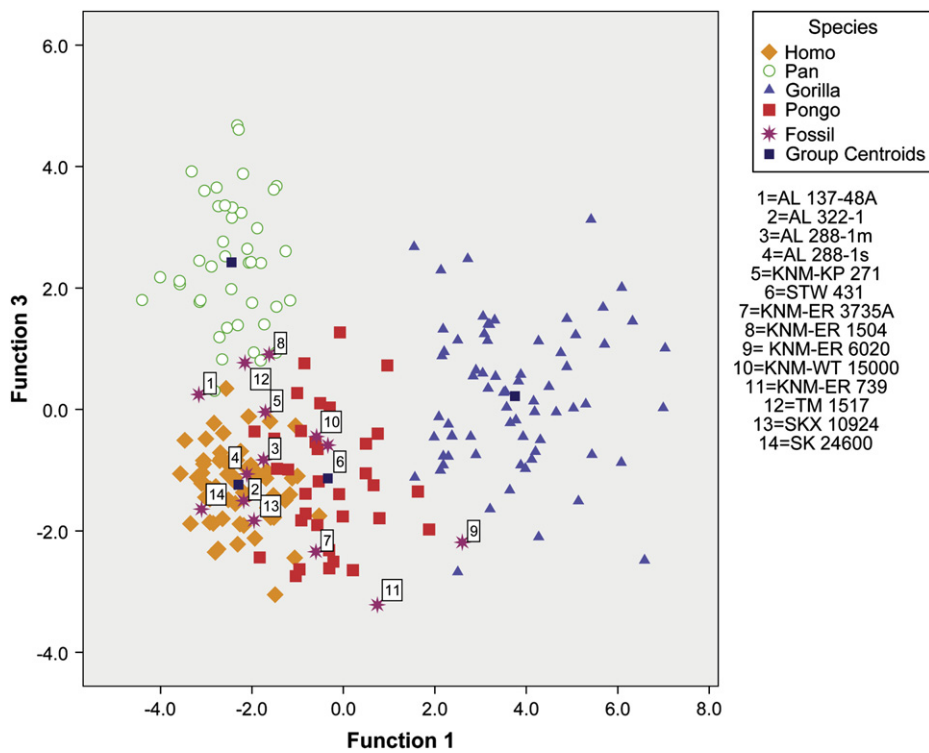


Fig. 3. Scatter plot of discriminant functions 1 and 3 based on 16 raw measurements of the distal humerus.

Table 4
Variable correlations with discriminant functions

	Raw			Shape		
	Function 1	Function 2	Function 3	Function 1	Function 2	Function 3
9.tsupcon	0.618	0.144	0.178	0.475	−0.008	0.353
10.clatepi	0.605	0.172	0.260	−0.466	0.185	0.006
8.tmedepi	0.581	0.083	0.236	0.380	−0.134	0.091
7.biepi	0.561	−0.005	0.264	0.264	0.113	0.117
14.latolec	0.534	0.127	0.417	−0.076	−0.011	−0.050
6.artwd	0.525	0.053	0.314	0.191	0.407	0.029
12.dolec	0.517	−0.031	0.492	−0.256	−0.356	0.246
1.trochwd	0.497	−0.123	0.096	0.083	−0.320	0.045
15.apshaft	0.487	−0.055	0.426	−0.215	0.301	−0.087
11.wdolec	0.460	−0.144	0.129	−0.065	0.283	0.236
5.capht	0.429	0.167	0.188	−0.148	−0.272	−0.004
2.trochap	0.421	−0.123	0.229	0.160	−0.161	−0.420
4.capwd	0.405	0.051	0.368	−0.232	−0.287	0.313
3.lattroch	0.396	0.120	0.323	0.247	0.069	−0.298
16.wdmedepi	0.347	0.074	0.104	−0.193	0.085	0.263
13.medolec	0.325	0.383	0.185	−0.180	−0.137	−0.251

and #9 (the distance between the lateral trochlear ridge and the medial epicondyle and supracondylar ridge, respectively), which are relatively large in *Gorilla* and *Pongo*. Capitular width (measurement #4) is strongly negatively correlated and is relatively small in *Gorilla* and *Pongo*. Function two (29.2% of the variance) maximally separates *Pongo*, based on the orangutans' relatively larger column medial to the olecranon fossa (measurement #13), in combination with a relatively-smaller olecranon fossa width (measurement #11) and biepicondylar distance (measurement #7). Function three, accounting for 24.9% of the variance, maximally separates *Pan* from the others' based on *Pan*'s relatively-deep olecranon fossa (measurement #12) and small trochlear width (measurement #1). Also correlated (negatively) with this is the lateral olecranon fossa width (measurement #13), which is larger in *Pan*.

The placement of the fossils in the discriminant analysis using size-adjusted variables appears in Figs. 4 and 5 and below the diagonal line defined by the zero-values in Table 5. As in the analysis using raw measurements, the earliest fossils (i.e., KNM-KP 271; A.L. 137-48, 322-1, and 288-1) are closest to the human centroid. Many of the later fossils are also close to the human centroid (i.e., KNM-WT 15000; SK 24600; SKX 10924). The middle, however, is

muddled: many of the fossils occurring after 3 Ma and before 1.5 Ma are quite unlike *H. sapiens*. *Au. africanus* (Stw 431) is closest to the gorilla centroid as are KNM-ER 3735A, 1504, 6020, and 739. The *P. robustus* type specimen, TM 1517, is about midway between the human and chimp centroids.

Figures 6 and 7 plot the Mahalanobis distance from the human centroid of these fossils against geological age. By either raw-measurements or size-adjusted variables, the general pattern is clearly not one of progressive approach to modern human form through time.

Discussion

Australopithecus anamensis

The results of this study confirm what the original describers of KNM-KP 271 found: that is, it is quite human-like (Patterson and Howells, 1967). They noted that the Kromdraai specimen (TM 1517; *P. robustus*) was less human-like despite its later age. They attributed this paradox to lineage: *P. robustus* was, as its genus name implies, a distant side branch to the lineage leading from *Australopithecus* to *Homo*. But in 1994 came the discovery of craniodental material from Kanapoi revealing the remarkably primitive morphology of *Au. anamensis* relative to the numerous human-like features of *P. robustus* (Skelton and McHenry, 1992; Leakey et al., 1995; Leakey et al., 1998; Strait and Grine, 2004). Formal cladistic analyses consistently place *Paranthropus* as a sister group to *Homo*, whereas *Au. anamensis* is a distant cousin (Strait and Grine, 2004). However, there are many autapomorphies within the “robust” australopithecine clade that lead some investigators to conclude that the many derived traits shared by *P. robustus*/*P. boisei* with *Homo* are due to parallel evolution (for a discussion of this issue see McHenry, 1996a).

Many other studies emphasize the human-like qualities of KNM-KP 271. McHenry's metrical analyses found it to be the most human-like of the three Plio-Pleistocene humeri known by 1972 (McHenry, 1972, 1976; McHenry and Corruccini, 1975a). Senut noted its human-like qualities, especially its apparently weak development of its lateral trochlear crest, and proposed that, along with IB 7594 and A.L. 333w-29, it should be placed in the genus *Homo* (Senut, 1980; Senut, 1981; Senut and Tardieu, 1985).

Table 5
Mahalanobis distances of fossils and comparative species^a

	<i>Homo</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>	KNM-KP 271	A.L. 137-48A	A.L. 322-1	A.L. 288-1M	A.L. 288-1S	Stw 431	KNM-ER 3735A	KNM-ER 1504	KNM-ER 6020	KNM-ER 739	KNM-WT 15000	TM 1517	SK 24600	SKX 10924
<i>Homo</i>	0.00	4.06	6.28 ^b	5.30 ^b	1.34	1.86	0.59	1.02	0.39	2.16	2.28	3.04	4.99 ^b	4.11	2.02	2.06	0.93	0.78
<i>Pan</i>	4.84 ^b	0.00	6.63 ^b	5.22 ^b	3.04	3.34	4.54	3.47	4.05	3.84	5.15 ^b	1.75	7.00 ^b	6.48 ^b	4.23	2.12	4.40	4.49
<i>Gorilla</i>	5.31 ^b	5.46 ^b	0.00	5.89 ^b	5.52 ^b	7.10 ^b	6.34 ^b	5.60 ^b	6.12 ^b	4.78	5.05 ^b	5.53 ^b	2.76	4.68	4.69	5.95 ^b	7.14 ^b	6.09 ^b
<i>Pongo</i>	6.09 ^b	5.98 ^b	5.29 ^b	0.00	5.13 ^b	6.44 ^b	5.76 ^b	4.42	5.52 ^b	4.32	4.07	3.76	5.66 ^b	3.80	5.72 ^b	5.20 ^b	5.50 ^b	4.88
271	1.97	3.50	3.96 ^b	5.88 ^b	0.00	1.69	1.66	1.02	1.17	1.57	2.72	2.16	4.81	4.41	1.47	1.00	2.13	1.83
137-48	2.91	4.24 ^b	4.87 ^b	7.62 ^b	1.76	0.00	2.01	2.29	1.73	3.23	4.04	3.22	6.32 ^b	5.85 ^b	2.67	1.61	2.09	2.63
322	2.14	5.92 ^b	4.36 ^b	6.70 ^b	2.43	2.86	0.00	1.51	0.50	2.36	2.38	3.57	4.89 ^b	4.19	1.93	2.47	1.18	0.98
288M	2.79	4.49 ^b	2.53	5.10 ^b	1.75	3.04	2.20	0.00	1.13	1.43	1.92	2.17	4.59	3.65	1.93	1.68	1.68	1.09
288S	2.35	5.28 ^b	3.74	6.57 ^b	1.84	2.23	0.92	1.64	0.00	2.06	2.39	3.10	4.87 ^b	4.21	1.70	1.98	1.25	1.03
431	4.70 ^b	5.58 ^b	1.43	6.25 ^b	3.37	3.89 ^b	3.37	2.09	2.70	0.00	1.82	2.42	3.37	3.12	1.42	2.28	2.99	2.06
3735A	4.69 ^b	6.83 ^b	2.60	5.05 ^b	4.33 ^b	5.44 ^b	3.46	2.63	3.42	2.66	0.00	3.55	3.32	1.83	2.61	3.53	2.73	1.60
1504	4.61 ^b	3.35	2.55	3.84 ^b	3.23	4.62 ^b	4.78 ^b	2.61	4.16 ^b	3.31	3.99 ^b	0.00	5.55 ^b	4.76 ^b	3.27	1.69	3.48	3.23
6020	5.10 ^b	7.03 ^b	2.28	5.85 ^b	4.50 ^b	5.33 ^b	3.57	2.81	3.40	2.09	1.00	4.23 ^b	0.00	2.74	3.76	5.60 ^b	5.73 ^b	4.57
739	4.18 ^b	6.55 ^b	3.39	4.07 ^b	4.21 ^b	5.61 ^b	3.53	2.72	3.65	3.60	1.38	3.87 ^b	2.36	0.00	4.08	5.15 ^b	4.50	3.41
15000	2.58	5.09 ^b	3.65	6.73 ^b	1.74	1.93	1.33	1.70	0.43	2.55	3.63	4.08 ^b	3.52	3.94 ^b	0.00	2.31	2.94	2.25
1517	2.90	2.79	4.39 ^b	6.52 ^b	1.18	1.51	3.44	2.66	2.74	3.82	5.28 ^b	3.44	5.33 ^b	5.26 ^b	2.49	0.00	2.60	2.61
24600	0.30	4.98 ^b	5.17 ^b	6.18 ^b	1.93	2.80	1.84	2.65	2.08	4.50 ^b	4.51 ^b	4.62 ^b	4.89 ^b	4.06 ^b	2.33	2.91	0.00	1.18
10924	1.21	5.71 ^b	5.01 ^b	5.90 ^b	2.57	3.56	1.57	2.60	2.14	4.38 ^b	3.85 ^b	4.56 ^b	4.33 ^b	3.32	2.51	3.69	1.04	0.00

^a The fossil names in the left column have been abbreviated; they are in the same order as those in the top row. Values above the diagonal line defined by the zero-values are from the raw-variable analysis, those below from the size-adjusted.

^b Greater than 95% of intra-*Gorilla* pairs. *Gorilla* was selected as a comparator because it was the most variable of the species.

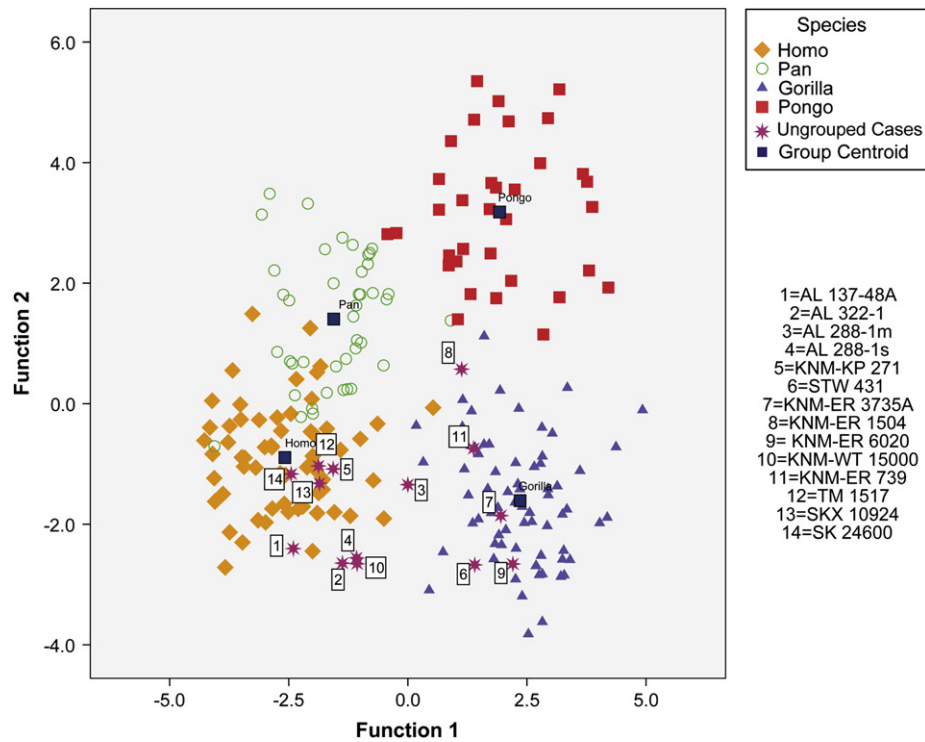


Fig. 4. Scatter plot of discriminant functions 1 and 2 based on 16 size-adjusted variables describing the distal humerus.

Although Hill and Ward (1988) argued that the lateral trochlear crest was too variable to support an attribution to *Homo*, they did note its many human qualities. Ward et al. (2001) noted that the lateral trochlear crest is abraded in KNM-KP 271 and may have been more prominent. But even adding considerable amounts of clay to

compensate for this abrasion to KNM-KP 271 does not change the measurement intended to quantify this feature (measurement #3: anteroposterior diameter of the lateral trochlear ridge) enough to make it chimp-like. The original fossil is 22.2 mm for this measurement compared to the human mean of 22.3 mm and the chimp

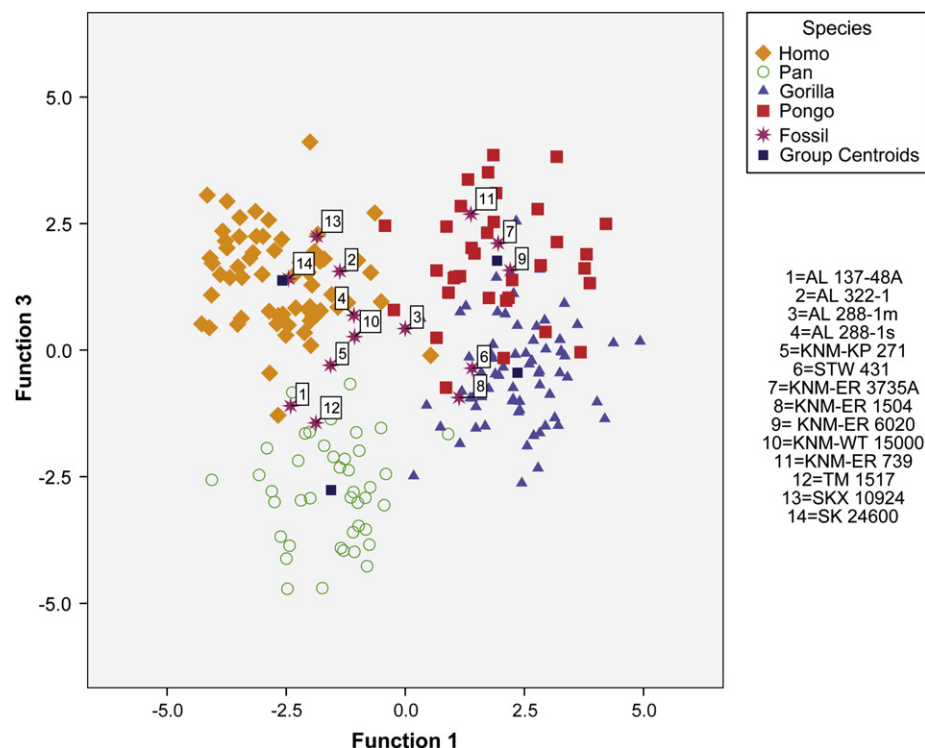


Fig. 5. Scatter plot of discriminant functions 1 and 3 based on 16 size-adjusted variables describing the distal humerus.

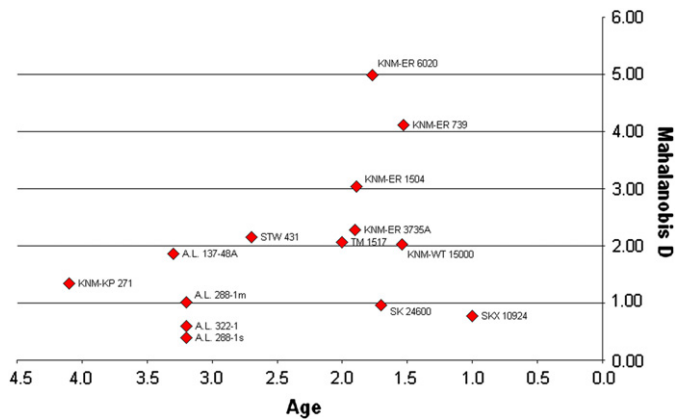


Fig. 6. Plot of the relationship between geological time in Ma and the Mahalanobis distance of each fossil humerus from the human centroid in the discriminant analysis based on 16 raw measurements. Mid-points of date ranges for each fossil are used.

mean of 26.8 mm. *Lague and Jungers (1996)* agree with *Hill and Ward (1988)* that the traits *Senut and Tardieu (1985)* used are too variable to be used in sorting specimens taxonomically. *Lague and Jungers' (1996)* thorough quantitative analysis found KNM-KP 271 not particularly more human-like than other Plio-Pleistocene humeri, and they argue that KNM-KP 271 should continue to be attributed to *Au. anamensis*. *Bacon (2000)* noted the high level of variability in the distal humerus of *H. sapiens* and pointed out that KNM-KP 271 cannot securely be separated from either *Homo* or *Australopithecus*.

Australopithecus afarensis

The results agree with what the original describers observed about the distal humeri of *Au. afarensis*: humeri are generally similar to each other and are more human-like than ape-like in shape (*Johanson et al., 1982a,b; Lovejoy et al., 1982*). In the discriminant analysis using shape variables, A.L. 288-1 was equally distant from the *Homo* and *Pan* centroids, but over 20% of the human pairs drawn at random exceeded the distance between A.L. 288-1 and the human centroid. The A.L. 333w-29 specimen is too fragmentary to include in this analysis so there is no test of *Senut's* findings that this specimen is morphologically close to the human centroid in contrast to other *Au. afarensis* specimens.

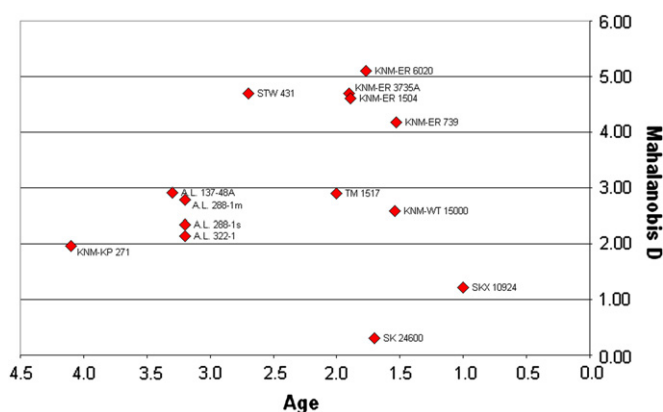


Fig. 7. Plot of the relationship between geological time in Ma and the Mahalanobis distance of each fossil humerus from the human centroid in the discriminant analysis based on 16 size-standardized variables. Mid-points of the date ranges for each fossil are used.

Australopithecus africanus

The placement of Stw 431 in our analysis is unique, and its relationships to other fossils enigmatic. In our shape analysis, Stw 431 projected very close to the *Gorilla* centroid, as close as 77.6% intraspecific pairs of *Gorillas*. The next closest centroid was *Homo*, but fewer than 2% of *Gorilla* pairs have a distance so large. This contrasts with *Menter (2002)* who found that when size was controlled, Stw 431 projected within the human distribution (or fossil distribution depending on whether fossils were used to create the discriminant space or not). *Menter (2002)* also found that the closest fossils to Stw 431 were A.L. 288-1 and KNM-ER 1504. *Lague and Jungers' (1996)* reduced shape data set also found Stw 431 to be similar to the *Au. afarensis* sample. Our analyses agree: Stw 431 is the least distant from A.L. 288-1. The next closest relative is KNM-ER 6020. Interestingly, *Lague and Jungers (1996)* found Stw 431 to be directly in-between the two most distant fossils in their study (IB 7594 and KNM-ER 1504). Our plot of the change in distance from the human centroid through time also finds that Stw 431 is an outlier. A large part of the reason it appears to be an outlier however, derives from the fact that it is the only fossil in the study between 2–3 Ma.

Koobi Fora

At least three (*P. boisei*, *H. habilis*, and *H. ergaster/erectus*), and probably more (*H. rudolfensis*), species are represented by cranio-dental remains in the Lake Turkana collection of hominins between 2 and 1.5 Ma (*Wood, 1991*). Isolated postcranial fossils have proven to be difficult to attribute to species, except for associated partial skeletons (*McHenry, 1992, 1994*). These partial skeletons include, in order of taxonomic certainty, KMM-WT 15000 (*H. ergaster/erectus*), KNM-ER 3735 (*H. habilis*), KNM-ER 803 (*H. ergaster/erectus*), and KNM-ER 1500 (*P. boisei*). The latter is quite uncertain (*Wood, 1991*). The frustration involved in attributing isolated postcrania is intense because specimens are precisely dated (*Feibel et al., 1989*) and well-preserved (*Leakey and Leakey, 1978*). Without taxonomic attribution one might despair that these beautiful specimens are of little use to understanding human evolution. But even without names, they do show an unexpected twist to the pattern of human evolution: hominin forelimbs became more diverse and more distant from the human centroid between 2 and 1.5 Ma than before. One could attribute this to the increase of species diversity at this time, but it is still surprising that the craniodental synapomorphies track time but the postcranial fossils become more diverse.

The results reported here show the heterogeneity of the 2–1.5 Ma Turkana hominin humeri. One is as close to the human centroid as 30% of human pairs drawn at random using size-adjusted variables (KNM-WT 15000), but several are as close to the *Gorilla* centroid (also using shape variables) as many of *Gorilla* pairs drawn at random (KNM-ER 3735, 1504, 1605, 739). These specimens are more distant from the human centroid than over 95% of human pairs drawn at random are from each other.

As reported in *Table 5*, the oddest distal humerus is KNM-ER 1504. Its distance from the other 2–1.5 Ma Turkana humeri exceeds that seen among more than 95% of human or chimp pairs drawn at random. This heterogeneity contrasts with the results of *Lague and Jungers (1996)* who found enough homogeneity to lump the Koobi Fora humeri into one group, although KNM-ER 6020 was not included in their analysis. Perhaps the inclusion of KNM-ER 6020 in this study partially explains the difference in our results.

Swartkrans: *Paranthropus* or *Homo*?

Both *Paranthropus* and *Homo* are present in the large hominin sample from Swartkrans (*Brain, 1993; Grine, 2005*). The 16 variables describing humeral shape variation make it clear that the two

most complete Swartkrans humeri, SK 24600 of Member 1 and SKX 10924 of Member 3, are extraordinarily similar to each other and to modern humans. The original describers of these specimens (Susman et al., 2001) noted that the Member 3 specimen, SKX 10924, had a less distinct demarcation of the capitulo-trochlear sulcus (*zona conoidea*), which is more typical of *Homo*. They attributed SKX 10924 to *H. erectus* and SK 24600 to *P. robustus* on the basis of this observation. Their observations that the anterior-posterior diameter of the distal humerus is large in *Homo*, and that the position of the lateral epicondyle relative to the capitulum is more distal in *Homo*, also contributed to their attributions of the specimens to different species.

Although our study did not include a measurement of the capitulo-trochlear sulcus, previous studies have examined the distribution and functional morphology of the superior articular facet of the radial head, which articulates with the capitulo-trochlear sulcus (Grine and Susman, 1991; Rose, 1993; Menter, 2002; Patel, 2005). Consensus is that African ape radii have a larger superior articular surface medially and anteriorly as well as a distinct bevel between the proximal and distal articular surfaces on the radial head (Grine and Susman, 1991; Patel, 2005). This translates to a larger articular area in the capitulo-trochlear sulcus during full pronation in the African apes, which Rose (1988, 1993) has suggested allows for better distribution of force placed on the forearm during the load-bearing phase of locomotion and increased joint stability. Patel (2005) included all genera of the Hominoidea in a discriminant analysis of the morphology of the radius and concluded that the superior articular surface of the radial head is not only larger in African apes, but also in *Hylobates*, in distinct contrast to the radial morphology exhibited by *Pongo* and *Homo* (Patel, 2005). Based on this, Patel suggested that the increased elbow stability given by the anterior expansion of the proximal surface would also be important in withstanding peak vertical reaction forces during fast ricochet brachiation (Patel, 2005). Although *Pongo* is also adapted to forelimb suspension, Patel argues that the extra elbow stability may not be needed because it is slow-moving (Patel, 2005). In addition to differences between hominoids, Patel (2005) also found that australopithecines and paranthropines have a radial morphology similar to that of African apes and Hylobatidae, while early *Homo* has a morphology more similar to that of modern humans, in agreement with Grine and Susman (1991). Despite the understanding of variation among Hominoidea in radial head morphology, the variation in the capitulo-trochlear sulcus of the distal humerus was not quantitatively assessed until Menter's (2002) study. That study found that the two Swartkrans humeri were not significantly different enough to warrant taxonomic separation (Menter, 2002). In addition to our results, this suggests that the Swartkrans humeri should be attributed to the same species. Other than their similarity to each other, they are not more similar to either KNM-WT 15000 (*H. ergaster/erectus*) or TM 1517 (part of the type specimen of *P. robustus*). The Mahalanobis distances of SKX 10924 and SK 24600 to KNM-WT 15000 are 2.5 and 2.2, and to TM 1517 are 3.3 and 2.9, respectively.

Morphological change through time

In many respects postcranial features of the earliest hominin species are less like *H. sapiens* than are later species. Stern (2000) lists 36 traits of *Au. afarensis* (Jungers and Stern, 1983; Stern and Susman, 1983; Susman et al., 1984) that distinguish it from modern humans, for example. The metacarpal II facet on the capitate is more laterally facing in *Pan* and *Au. anamensis*, intermediate in *Au. afarensis* and *Au. africanus*, and more distally facing in *H. sapiens* (McHenry, 1983; Leakey et al., 1998; Ward et al., 1999). The femoral diaphysis is short relative to other dimensions of the postcrania in

Au. afarensis (Jungers, 1982), intermediate in the hominin postcranial remains from Bouri Hata that may be associated with *Au. garhi* (Asfaw et al., 1999), and long in *H. ergaster/erectus* (Ruff and Walker, 1993; Walker and Leakey, 1993a) and *H. sapiens*. When 86 postcranial characters are treated to formal cladistic analysis (Coffing and McHenry, 2000), the resulting cladogram correlates with chronology in general, but not among *H. habilis sensu stricto*, *P. robustus*, and *Au. africanus*.

As Figs. 6 and 7 show, the morphology of the distal humerus does not become more human-like through time, suggesting that it is not accumulating synapomorphies. The Mahalanobis distances from the human centroid are larger in many later specimens relative to earlier ones. The three best preserved ulnae show a similar relationship with time. The earliest, A.L. 438-1, is more human-like than the later ones (Omo L40-19 and OH 36; Aiello et al., 1999; Drapeau, 2004; McHenry et al., 2007). The forelimb joints are small relative to hind limb joints in humans and *Au. afarensis*, but less human-like in *Au. africanus* and possibly *H. habilis* (McHenry and Berger, 1998a; Haeusler and McHenry, 2007).

Pelvic architecture also has a complex relationship to time. The earliest pelvic remains are fundamentally human-like, but have peculiarities (Häusler, 2001; Lovejoy, 2005). By 1.9 Ma the pelvic bone becomes strikingly more human-like as shown by KNM-ER 3228 (Rose, 1984), but the later specimen discovered in Member 1 of Swartkrans SK 3155 (Brain et al., 1974), is very odd (McHenry, 1975b; McHenry and Corruccini, 1975b). SK 3155 is clearly adapted to bipedality (McHenry, 1975a), but it has numerous unusual characteristics for a hominid (McHenry, in press).

As Reno et al. (2005) point out, one cannot assume phyletic diversity necessarily unless one can falsify an anagenic pattern. Their argument holds well in some respects: proportions of fore-to-hind limb lengths should be based on complete specimens. Uncertainty of reconstruction undermines current attempts to demonstrate reversals in limb length proportions, but the findings reported here and many other studies (McHenry and Berger, 1998a,b; Green et al., 2007; Haeusler and McHenry, 2007) support a more complex view of hominin postcranial evolution.

There are multiple explanations for the non-linear trend seen in the distal humerus and other aspects of the postcrania. One explanation for the apparent erratic pattern of postcranial change might be phylogenetic. Robinson (1972), for example, attributed the unusual qualities of *P. robustus* to its ancient phylogenetic separation from the lineage leading to *Homo*. Patterson and Howells (1967) invoked this argument to explain why the Kanapoi humerus (KNM-KP 271) was so much more like *H. sapiens* than the *P. robustus* humerus, TM 1517. Napier (1964) was one of the first to call attention to the unusual nature of *P. robustus* postcrania and its implications for phylogeny. From this point of view, the *Paranthropus* clade separated early (as the name "*Paranthropus*" implies) and its unique postcranial morphology persisted right up through Swartkrans Member 3 times that might be as young as 1 Ma (Brain, 1993). The unusual craniodental specializations of *Paranthropus* certainly make it appear to be a distant cousin of the lineage leading to *Homo*, but phylogenetic analyses of its craniodental morphology consistently place it as a sister clade to *Homo* relative to all non-*Homo* species (Strait and Grine, 2004). *P. robustus* and *P. boisei* share with *Homo* a long list of unique traits not seen in *Au. africanus* or any other non-*Homo* species (Skelton and McHenry, 1992; Strait and Grine, 2004). However, *Paranthropus* does have a large number of uniquely-derived craniofacial characteristics, and it is possible that its distal humerus also evolved uniquely after its split from the *Homo* lineage. This would explain some of the variability seen from 1–2 Ma around Lake Turkana. It would not, however, explain why *Au. anamensis* appears to have more human-like characteristics than all of the other represented species at Lake Turkana around 1–

2 Ma, as *H. ergaster/erectus* is much closer on the hominin lineage to modern humans than is *Au. anamensis*.

Another explanation for the apparent diversity in the morphology of the distal humerus in later species might be that this metrical characterization of biological form is meaningless in terms of function. From this point of view the unique qualities of many of the later humeri are registering uninteresting noise without significance. Early hominids were bipedal with forelimbs liberated from locomotor duty, and therefore patterns of variability not seen in the modern species can be ignored. As summarized by the original describers of *Au. afarensis*, "...the anatomical picture that emerges from this collection is one of a powerful upper limb, but not primarily involved in locomotor behavior" (Johanson et al., 1982b:385).

In contrast to this view is the interpretation that the forelimbs of *Australopithecus* were adapted to greater arboreality than is true of later species of *Homo* (summarized by Stern, 2000). The invocation of greater or lesser degrees of arboreality may help to explain many ape-like features of some species of early hominids, but in the study reported here the most divergent forelimbs are from environmental contexts characterized by fewer trees and more xeric conditions (Vrba et al., 1995; Reed, 1997; Fernández and Vrba, 2006). Another functional explanation is given in Larson et al. (2007) who find differences in the degree of humeral torsion between archaic hominins (including *H. floresiensis*) and modern humans resulting in a lateral set to the elbow that might be related to tool making ability.

There are also multiple explanations that invoke functional constraints. One of these explanations for the increase in forelimb diversity in the early Pleistocene might be found in Darwin's (1872) feed-back theory involving bipedalism, free hands, and canine reduction. As often quoted, he speculated that

The free use of the arms and hands, partly the cause and partly the result of man's erect position, appears to have led in an indirect manner to other modifications of structure. The early male forefathers of man were, as previously stated, probably furnished with great canine teeth; but as they gradually acquired the habit of using stones, clubs, or other weapons, for fighting with their enemies or rivals, they would use their jaws and teeth less and less. In this case, the jaws, together with the teeth, would become reduced in size, as we may feel almost sure from innumerable analogous cases.

(Darwin, 1872, pp. 53)

From this point of view, the diversity in forelimbs reflects differences in the degree of sexual selection (McHenry, 1996b; Carrier, 2004). In some species it may have had a strong effect causing forelimbs to become exceptionally powerful in males. The small and very human-like distal humeri from Swartkrans, from this point of view, are *Paranthropus* females. By this argument the pattern of sexual selection changed sharply in *H. ergaster/erectus*, as registered in the relatively gracile forelimbs of the young man, KNM-WT 15000 (Walker and Leakey, 1993b). However, new discoveries of small bodied (and brained) hominins in the Republic of Georgia and Kenya that may be attributed to *H. erectus/ergaster* complicate the picture of sexual dimorphism within this species (Lordkipanidze et al., 2007; Spoor et al., 2007). Although differences in sexual selection might be related to the high diversity of later distal humeri, it is also possible that the differences are due to overall body size or skeletal size dimorphism which itself may represent pressures shaping both males and females that may or may not have operated directly on the forelimb.

The phylogenetic diversity seen between 1–2 Ma may also be affecting our results. During this period of human evolution, there were multiple species and even genera co-existing at the same time and place. It is possible that these very similar hominin species may

have been forced to occupy slightly different niches in order to co-exist successfully, and the diversity of distal humeri from this time is a reflection of adaptation to different ecological niches.

The results supplement the evidence for complexity and uniqueness in the evolution of hominin postcranial morphology noted long ago (Napier, 1964; Robinson, 1972; Oxnard, 1975) and highlighted by the unusual fore-to-hind limb proportions of Stw 431 (McHenry and Berger, 1998a,b). The discovery of associated partial skeletons of *H. habilis* with remarkably odd fore-to-hind limb proportions add to the evidence that hominin postcranial evolution did not happen in a linear progression but was marked by patterns that are difficult to interpret in the context of extant Hominoidea (Johanson et al., 1987; Leakey et al., 1989; Hartwig-Scherer and Martin, 1991; Richmond et al., 2002; Reno et al., 2005; Haeusler and McHenry, 2007).

Conclusion

The hominin fossil record is dense enough now to probe many interesting questions. Here we examine the nature of cranial and postcranial morphology in relationship to geological time. Although there are many autapomorphies, there is a pattern of accumulating craniodental synapomorphies with successively younger species of hominin. In many respects the postcranial anatomy follows a similar pattern where the earliest species have more primitive bodies than later species, but in some features this appears not to be the case. In this study we describe the morphology of the distal humerus using 16 size-standardized measurements in a large comparative sample of Hominoidea and 14 of the best preserved hominin species. The results of multiple discriminant analyses reveal some of the earliest fossils (especially the 4.2 Ma *Au. anamensis*) project close to *H. sapiens* in the discriminant space defined by the extant species. The later fossil humeri are more diverse and many are far removed from the human centroid. When plotted against time, the Mahalanobis distance from the human centroid shows a pattern of increasing diversity with decreasing geological age. This pattern appears to be true of many postcranial features including fore-to-hind limb joint proportions and the morphology of the ulna, femur diaphysis, and pelvis.

The pattern of morphological change in the evolution of the human body appears not to be a linear accumulation of human-like traits through time. Bipedalism was established early (by at least 4 Ma and probably before) and there appears to have been a great deal of diversity in how these bipeds used their bodies. The extant species of Hominoidea present a very limited view of what is possible.

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