



Clavicle length, throwing performance and the reconstruction of the *Homo erectus* shoulder



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ABSTRACT

Powerful, accurate throwing may have been an important mode of early hunting and defense. Previous work has shown that throwing performance is functionally linked to several anatomical shifts in the upper body that occurred during human evolution. The final shift to occur is the inferior reorientation of the shoulder. Fossil scapulae show the earliest evidence of a more inferior glenoid in *Homo erectus*. However, where the scapula rests on the thorax is uncertain. The relative length of the clavicle, the only skeletal attachment of the scapula to the torso, is quite variable. Depending on which fossils or skeletal measures are used to reconstruct the *H. erectus* shoulder, either a novel, anteriorly facing shoulder configuration or a modern human-like lateral orientation is possible. These competing hypotheses have led to very different conclusions regarding the throwing ability and hunting behavior of early *Homo*. Here, we evaluate competing models of *H. erectus* shoulder morphology and examine how these models relate to throwing performance. To address these questions, we collected skeletal measures from fossil and extant taxa, as well as anthropometric ($N = 36$) and kinematic ($N = 27$) data from Daasanach throwers from northwestern Kenya. Our data show that all *H. erectus* fossil clavicles fall within the normal range of modern human variation. We find that a commonly used metric for normalizing clavicle length, the claviculohumeral ratio, poorly predicts shoulder position on the torso. Furthermore, no significant relationship between clavicle length and any measure of throwing performance was found. These data support reconstructing the *H. erectus* shoulder as modern human-like, with a laterally facing glenoid, and suggest that the capacity for high speed throwing dates back nearly two million years.

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Introduction

The evolution and functional anatomy of the hominin upper limb are relatively understudied. This is due in part to an understandable focus on adaptations in the lower limb for bipedalism, but also to the difficulty of accurately reconstructing the morphology of the hominin shoulder. Delicate bones, such as the scapula and clavicle, are often missing or poorly preserved in the fossil record, leaving long gaps in our understanding of shoulder evolution. Furthermore, reconstructing shoulder position and function from scant fossil material is made more difficult by the fact that this joint is highly mobile and changes position on the thorax. Fossils preserving associated and nearly intact shoulder and upper thorax elements raise new questions about the evolution of this region and the behaviors that may have driven morphological

changes at this crucial joint (Walker and Leakey, 1993; Alemseged et al., 2006; Lordkipanidze et al., 2007; Haile-Selassie et al., 2010; Green and Alemseged, 2012; Churchill et al., 2013).

High speed throwing is one potentially important behavior enabled by shifts in shoulder anatomy. While a number of primate species throw (e.g., Goodall, 1964, 1986; Galdikas, 1982; Jordan, 1982; Nakamichi, 1999; Cleveland et al., 2003; Leca et al., 2008; Hopkins et al., 2012), humans are unique in our ability to throw objects with both tremendous accuracy and velocity. Even *Pan troglodytes*, which are prolific and accurate throwers (Sugiyama and Koman, 1979; Goodall, 1986; Whiten et al., 1999) with considerable strength advantages (Bauman, 1923; Finch, 1943; Walker, 2009), only reach projectile velocities that are about one-third the speed of the average human male's throw (Roach et al., 2013). Recent work has shown that modern humans' remarkable throwing ability is linked to anatomical shifts that enable elastic energy to be stored and released at the shoulder (Roach, 2012; Roach et al., 2013; Roach and Lieberman, 2014). Furthermore, it has been hypothesized that the requisite anatomy for high speed throwing was first fully present

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two million years ago in *Homo erectus* and may have been critical for the advent of intensive carnivory and early migration out of Africa (Roach et al., 2013). However, reconstructing the *H. erectus* shoulder and attributing throwing proficiency to this taxon remain subjects of debate (Larson, 2007, 2009; Roach, 2012; Roach et al., 2013).

Much of the debate centers on the analysis of a single fossil: KNM-WT 15000, a juvenile *H. erectus* skeleton from Nariokotome, Kenya (Walker and Leakey, 1993). Despite this fossil being nearly complete, varying interpretations of age at death, developmental status and Nariokotome's health have complicated reconstructions of normal, adult morphology in this taxon (e.g., Walker and Leakey, 1993; Dean et al., 2001; Latimer and Ohman, 2001; Simpson et al., 2008; Graves et al., 2010; Haeusler et al., 2011; Schiess and Haeusler, 2013). Initial descriptions of KNM-WT 15000 detailed a modern human-like shoulder and torso (Walker and Leakey, 1993). However, a comprehensive survey of the hominin shoulder by Larson noted that the Nariokotome specimen has a short clavicle relative to the length of its humerus (Larson, 2007, 2009).

Given that the clavicle is the only skeletal anchor of the shoulder complex to the torso, clavicle length is an important measure for reconstructions of scapular position. Based on Nariokotome's relatively short clavicle (and similar proportions in the *Homo floresiensis* LB1 fossil; Larson, 2007; Larson et al., 2007), Larson proposes that the *H. erectus* shoulder faced anteriorly, a unique configuration among apes and humans (Fig. 1A). Larson further hypothesizes that this novel, anteriorly-placed shoulder was necessary to allow early *H. erectus* to overcome deficits in internal shoulder rotation caused by very low humeral torsion and still engage in manipulative tasks. However, she suggests that this anterior position would have restricted external shoulder rotation

and thus compromised throwing performance (Larson, 2007). This assessment of diminished throwing ability is based on reports of poor throwing ability in individuals suffering from pathologically short clavicles (Milgram, 1942; Guidera et al., 1991).

This anteriorly placed reconstruction has recently been called into question (Roach et al., 2013). Roach and colleagues argued that KNM-WT 15000's short relative clavicle length could be found in a population of modern humans living at comparable latitude. Furthermore, they note that early *H. erectus* fossils from Dmanisi, Georgia have relative clavicle lengths firmly in the modern human range. They hypothesized that *H. erectus* had a more modern human-like, laterally oriented shoulder (Fig. 1B) and were likely proficient throwers. Nariokotome's relatively short clavicles may thus simply reflect a tall, lean, heat-adapted body form as seen in the Nilotic peoples that inhabit the northern Kenyan rift today.

Additionally, Roach and colleagues (2013) questioned the utility of using the claviculohumeral ratio alone, clavicle length standardized by humeral length, for reconstructing shoulder position. While standardizing the clavicle by some measure of body size is necessary for both inter- and intraspecific comparison, they argued that the claviculohumeral ratio does not accurately represent scapular position because the shape and size of the ribcage around which the clavicle wraps cannot be extrapolated from humeral or clavicular lengths (see also Trinkaus et al., 2014). A potential solution to this problem is to use upper rib area as a means of standardizing clavicle length. Previous research has shown that normalizing clavicle length by thorax width accurately predicts apes to have relatively elongated clavicles compared with monkeys (Kagaya et al., 2010). Such a measure would include information about body mass, but also the size of the upper thorax.

Here, we address four primary research questions:

1. Do relative clavicle length values for *H. erectus* fall within the modern human range (supporting a human-like shoulder morphology) or are they unique (indicating a novel shoulder form)?
2. Does relative clavicle length affect throwing performance?
3. Does standardizing clavicle length by humerus length accurately recover shoulder position on the torso?
4. Does using upper rib area to standardize clavicle length more accurately recover shoulder position information?

We examine these questions using comparative primate and human skeletal measures, as well as shoulder morphology and throwing performance data from a population of modern humans from northwestern Kenya. We then use these data to evaluate the competing reconstructions of the *H. erectus* shoulder and address throwing ability in this species.

Materials and methods

Anthropometric ($N = 36$) and throwing performance ($N = 27$) data were collected from Daasanach males (Table 1). The Daasanach

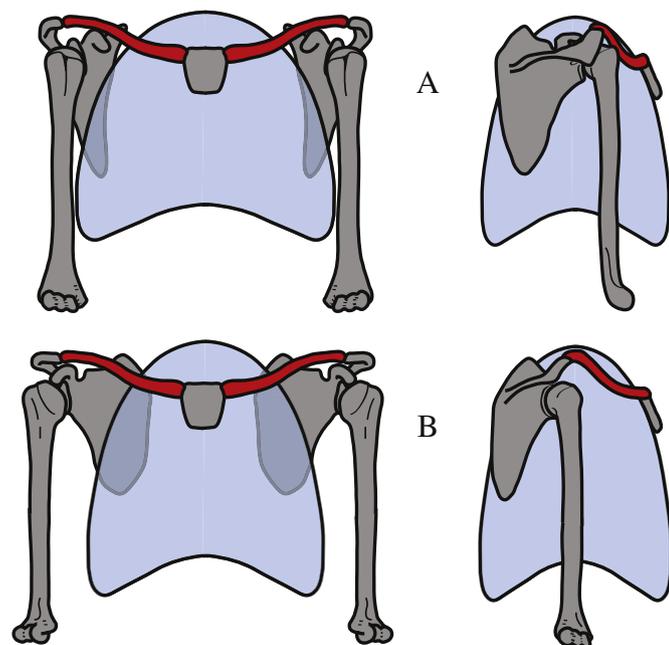


Figure 1. Competing reconstructions of the KNM-WT 15000 shoulder. Larson (2007) proposes that Nariokotome's short clavicle indicates that *H. erectus* had a shoulder that faced anteriorly (A). She further hypothesizes that this anterior shoulder orientation was necessary to accommodate low humeral torsion and maintain overlapping ranges of motion for the hands. Roach et al. (2013) argue that *H. erectus* had a laterally oriented shoulder, much like modern humans, and that KNM-WT 15000 simply had a lean, heat adapted torso (B). They propose that humeral torsion is largely a result of functional demands and not shoulder position, and that low torsion would not hinder bimanual overlap (Roach et al., 2012, 2013). In both illustrations, clavicle length and humeral torsion are held constant and rib cage size and scapular position are varied. Modified after Larson (2007).

Table 1
Demographic profile of all subjects ($N = 36$).

Age	# of subjects
10–15	9
16–20	6
21–25	5
26–30	7
31–35	5
36–40	2
41–45	2

are a group of contemporary agro-pastoralists living along the east and north sides of Lake Turkana in northwestern Kenya and southwestern Ethiopia. This group was chosen for study as they are tall and lean, and occupy a similar landscape at the same latitude as that occupied by the Nariokotome boy. Daasanach boys are also prolific throwers, using bent throwing sticks (called 'shar'; Fig. 2) to hunt small game and herd livestock.

We recorded body mass using a digital scale, rotational range of motion at the shoulder using a goniometer, and height, clavicle length, humerus length, forearm length, and arm and chest circumference using hard and soft measuring tapes. The claviculohumeral ratio (Larson, 2007) was calculated as:

$$\text{Claviculohumeral ratio} = 100 \times \left(\frac{\text{clavicle length}}{\text{humeral length}} \right)$$

While clavicle length was easily measured in our subjects, humeral length was estimated from the distance from the acromion to the lateral humeral epicondyle. This proxy measure accounts for the added length of the distal articulation by including the comparable length of the sub-acromial space. Humeral torsion was calculated from shoulder rotational range of motion (Roach et al., 2012). Twenty-seven of the measured subjects then threw a throwing stick as far as they could across a dry river bed with stone cairns placed every 10 m to mark the distance. These throwing sticks are carved from *Commiphora africana* wood, using the branches' natural bends to create aerodynamic projectiles. The preferred throwing stick used in this experiment weighed 350.0 g and measured 59.5 cm along its long axis. Throwing speed was measured using two Bushnell Velocity Speed radar guns. Digital video of each throw was collected at 60 Hz using a Canon ZR50MC video camera. All data were statistically analyzed using JMP software (v. 11).

For the comparative skeletal data, claviculohumeral ratios for apes, modern humans and fossil hominins were taken from the literature (Lordkipanidze et al., 2007; Larson, 2007, 2009; Churchill et al., 2013). To assess whether rib size is a more appropriate measure for standardizing clavicle length, associated ape, monkey and modern human clavicles and ribs were also measured (Table 2).



Figure 2. Daasanach man throwing his shar. Throwing speed was recorded using radar guns. Photo credit: Fernando Ortiz.

Table 2

Claviculocostal skeletal sample ($N = 189$).

Taxon	# of females	# of males
<i>Ateles</i>	5	7
<i>Colobus guereza</i>	10	10
<i>Macaca mulatta</i>	10	12
<i>Chlorocebus aethiops</i>	10	10
<i>Papio anubis</i>	9	9
<i>Hylobates lar</i>	10	9
<i>Pongo</i>	11	9
<i>Gorilla</i>	7	11
<i>Pan troglodytes</i>	10	10
<i>Homo sapiens</i>	10	10

Clavicle lengths were collected using digital calipers, and second rib area was calculated from digital photographs using ImageJ and defined as the area within the full medial curvature of the rib shaft (Appendix A, Supplementary Online Material [SOM] Fig. S1). From these data, a claviculocostal ratio was calculated as:

$$\text{Claviculocostal ratio} = \frac{\text{clavicle length}}{\sqrt{\text{second rib area}}}$$

Nariokotome clavicular measurements were taken from the literature (Walker and Leakey, 1993) and rib area measured from a first generation cast of the intact right second rib. Museum specimens were measured at the Smithsonian Institution's National Museum of Natural History, American Museum of Natural History, Harvard Museum of Comparative Zoology and the Cleveland Museum of Natural History.

Results

Daasanach claviculohumeral ratios are highly variable (Table 3). These values are indistinguishable from other modern human skeletal populations (Fig. 3). It should be noted that this variation may be inflated by the inclusion of juveniles with incomplete bone growth. However, we found no relationship between age and claviculohumeral ratio in our subjects ($R^2 = 0.006$, $P = 0.66$). Furthermore, any resulting skew due to the inclusion of juveniles should overestimate the adult claviculohumeral ratio as the clavicle grows with negative allometry and the humerus grows nearly isometrically (Jungers and Hartman, 1988). Accordingly, the low claviculohumeral values reported here and used to assess the validity of the competing shoulder reconstructions should be unaffected.

Daasanach maximum throwing velocity is comparable to that of skilled, Western athletes (Table 4; Fleisig et al., 1996, 1999). All of these throws traveled more than 60 m, with multiple individuals throwing over 100 m. Claviculohumeral ratios were not significantly correlated with maximum throwing speed (Fig. 4; $R^2 = 0.09$; $P = 0.13$). No age effects on throwing speed ($R^2 = 0.04$; $P = 0.32$) or distance ($R^2 = 0.003$; $P = 0.76$) were found.

Table 3

Daasanach anthropometry summary statistics ($N = 36$).

Measure	Mean	St. dev.	Range
Body mass (kg)	53.3	7.0	28.0–59.7
Height (cm)	175.1	8.2	147.5–188.5
Clavicle length (cm)	16.6	1.5	11.5–18.0
Humerus length (cm)	34.7	2.5	29.3–39.5
Forearm length (cm)	29.2	2.4	23.5–34.0
Chest circumference (cm)	82.1	5.0	65.5–89.0
Arm circumference (cm)	22.9	2.1	17.0–26.0
Humeral torsion (deg)	137.8	7.7	122.5–149.0

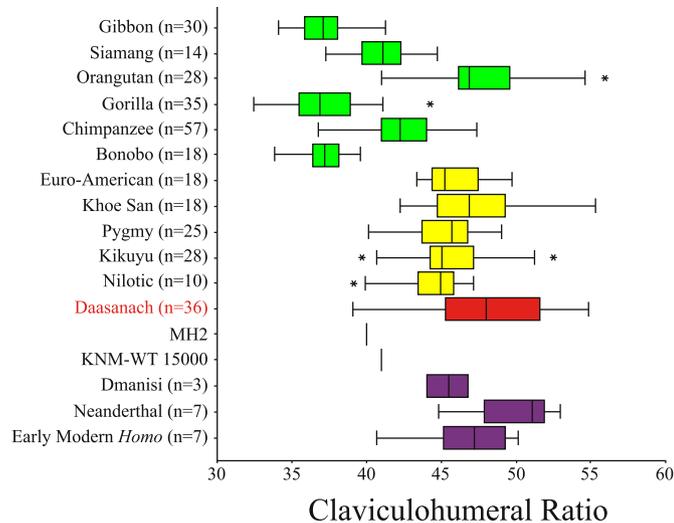


Figure 3. Comparative claviculohumeral ratios. Box and whisker plots show minimum, maximum, quartile and mean values. Apes are shown in green, modern humans in yellow, Daasanach values are in red and fossil taxa are shown in purple. Statistical outliers are shown using asterisk. Dmanisi values are shown as minimum, maximum and mean. Daasanach claviculohumeral ratios are quite variable and indistinguishable from other modern human groups. Note that all hominin values are encompassed by the Daasanach range. Modified after Larson (2009). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4
Daasanach stick throwing performance summary statistics ($N = 27$).

Measure	Mean	St. dev.	Range
Maximum velocity (m/s)	29.1	3.5	23.7–36.2
Distance (m)	77.4	13.0	60.0–110.0

Claviculocostal ratios calculated from skeletal data show mean human values are lower than other primates (Student's t -test, $t = 4.68$, $P < 0.0001$). As expected, ape claviculocostal ratios are higher than those of monkeys (Student's t -test, $t = 2.76$, $P = 0.006$).

Discussion

Functional implications of Daasanach shoulder morphology

The range of Daasanach claviculohumeral ratios fully encompasses all available fossil hominin values, including KNM-WT 15000 (40.9). Dmanisi values (mean: 45.4) are similar to the central tendency of the Daasanach. No shoulder position pathologies or confounding evidence of prior bone breakage were found in any of our subjects. This suggests that the short relative clavicle lengths (<42) present in approximately 7% of modern Daasanach males simply represent normal human variation. Given that the Nariokotome relative clavicle lengths can reasonably be sampled from the modern human data and that the Dmanisi values are incompatible with an anteriorly oriented shoulder, the most parsimonious reconstruction of *H. erectus* clavicular proportions is modern human-like. More associated postcranial fossils will be needed to test this further.

The lack of a significant relationship between claviculohumeral ratio and throwing speed (Fig. 4) suggests that this metric is not useful for functional assessments of throwing behavior. Further, it is worth noting that the one subject, a 12 year-old boy, with a claviculohumeral ratio (39) lower than Nariokotome's managed to throw 25 m/s (55 mph). This is comparable to maximum throwing

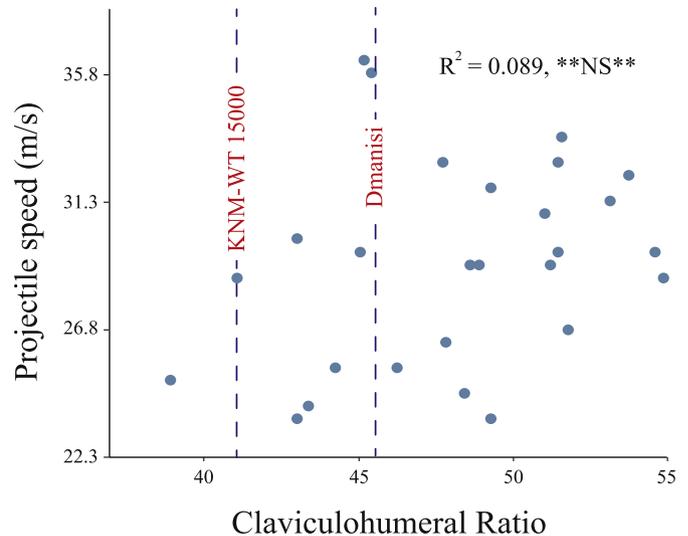


Figure 4. Throwing stick speed and relative clavicle length. The claviculohumeral ratio does not significantly predict throwing performance. Nariokotome and Dmanisi ratios are plotted for comparison. Projectile speeds (in meters per second) correspond to 10 mph increments from 50 to 80 mph.

speed for a proficient little league baseball thrower of the same age (Fleisig et al., 1999) and suggests that, even at extremes, a relatively short clavicle is not necessarily a hindrance to throwing performance.

While the hypothesis that a relatively short clavicle results in an anteriorly positioned shoulder and reduced throwing performance is not supported by our data, the functional implications for other behaviors such as stone tool manufacture and use are worth considering further. Larson hypothesized that these bimanual manipulative behaviors, requiring overlapping hand positions, are achieved primarily through internal rotation of the humerus (Larson, 2007). Very low humeral torsion found in early *Homo* should result in an externally shifted rotational range of motion at the shoulder and a deficit to internal rotation (Pieper, 1998; Osbahr et al., 2002; Reagan et al., 2002; Roach et al., 2012). Given this low torsion, Larson argues that the Nariokotome boy's short clavicles and anterior shoulder position are necessary to maintain overlapping spheres of hand motion. Contrary to Larson's hypothesis, there was no significant relationship between relative clavicle length and humeral torsion in the Daasanach ($R^2 = 0.08$; $P = 0.09$). Furthermore, there are reasons to question this hypothesis as it relates to manipulative behaviors. First, the shoulder is highly mobile. While internal rotation of the humerus can lead to overlapping hand positions, the same positions can be achieved through either protraction at the scapulothoracic joint or horizontal flexion at the glenohumeral joint. Such a solution is presumably employed by throwing athletes today that have very low humeral torsion (Pieper, 1998; Roach et al., 2012), and yet remain capable of manipulative tasks such as extracting a baseball from a glove. Thus, a deficit in internal rotation at the shoulder need not result in a deficit in manipulative ability.

Additionally, humeral torsion is known to be highly plastic and to change throughout ontogeny (Cowgill, 2007). Accordingly, it seems an unlikely solution for selection to act to reduce clavicle length solely to accommodate low torsion when we know torsion is quite responsive to functional demands and activity patterns during growth. For example, in later hominins asymmetries in torsion appear with the dominant arm maintaining lower, juvenile levels of torsion into adulthood while the non-dominant arm develops higher torsion (Churchill, 1994; Larson, 2007). This is consistent

with competing biomechanical regimens influencing upper limb development, with manipulative demands driving the development of higher torsion and other actions such as throwing driving the retention of low torsion on the dominant side.

Claviculohumeral ratio and shoulder position

Humeral length is correlated with body mass (Jungers, 1994) and is thus potentially appropriate for standardizing clavicle length. However, our data show the resulting measure does not accurately recover shoulder position on the torso. This problem with using the claviculohumeral ratio is well illustrated in the apes, which have a lower claviculohumeral ratio than modern humans and the fossil hominins. Using this metric alone for shoulder reconstructions would falsely predict that species such as chimpanzees and gibbons had anteriorly positioned shoulders (Fig. 6). While the claviculohumeral ratio may accurately describe the relative size of the clavicle to the body overall, it does not account for independent changes in the relative size of the upper thorax. This is critical to the validity of shoulder reconstructions as it is the size of the superior rib cage in conjunction with clavicle length, and not overall body mass, that influences shoulder position. Given that changes in thorax shape and size occur within the hominin lineage (Trinkaus, 1983; Bramble and Lieberman, 2004; Haile-Selassie et al., 2010), the claviculohumeral ratio is a poor proxy for shoulder position even within this closely related group.

The claviculocostal ratio more accurately recovers shoulder position information. The higher claviculocostal ratio observed in apes is largely driven by suspensory taxa, such as *Hylobates* and *Pongo* (as well as *Ateles*), with very long relative clavicle lengths and dorsally positioned shoulders, in comparison to arboreal and terrestrial quadrupeds (Student’s *t*-test, $t = 8.64$, $P < 0.0001$). However, although the low claviculocostal ratio in humans suggests a relatively short clavicle, the observed ratio is not driven by a shortened clavicle but rather by a larger upper thorax than predicted for a primate of a comparable body mass (Fig. 7). The KNM-WT 15000 skeleton falls at the edge of the human range, indicating a short clavicle overall, but not abnormally so. How the juvenile status of Nariokotome affects this ratio is unknown at this time, as rib ontogeny is poorly understood. Additional limitations of this

Homo sapiens Pan troglodytes

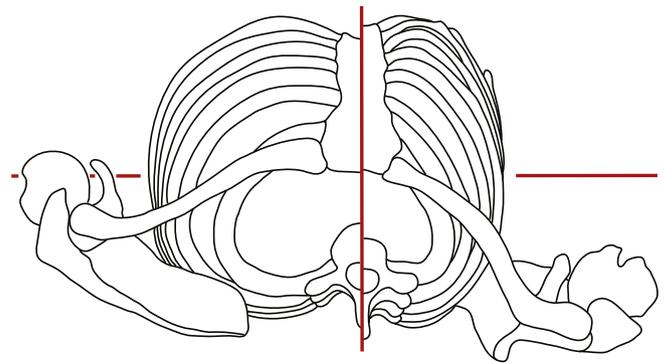


Figure 6. Relative shoulder position in humans and chimpanzees. The claviculohumeral ratio alone is a poor predictor of shoulder position. Claviculohumeral data would incorrectly suggest that *Pan* has a more anteriorly positioned shoulder than *Homo*. These superior views of the shoulder complex and rib cage (size standardized to the same clavicle length) illustrate that this is not the case, likely as a result of differences in thorax size and shape.

metric include the fact that it accounts for rib cage size well, but rib cage shape less so. Furthermore, the complete preservation of associated second ribs and clavicles is exceedingly rare in the hominin fossil record.

Shoulder position and throwing ability in Homo erectus

The balance of the current evidence suggests that *H. erectus* had laterally oriented, modern human-like shoulders. Both the claviculohumeral and claviculocostal metrics show the KNM-WT 15000 clavicles to be relatively short, but within the range of normal human variation. Recent work by Trinkaus et al. (2014) indicates that clavicle length is likely conserved in Pleistocene and recent *Homo*. It remains possible that ecogeographic factors may help to explain

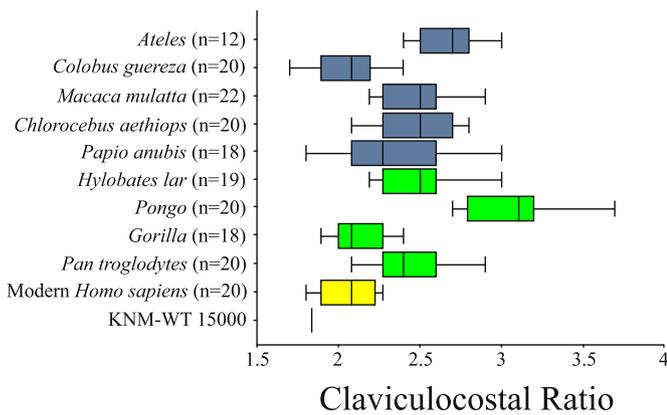


Figure 5. Comparative claviculocostal ratios. Box and whisker plots show minimum, maximum, quartile and mean values. Monkeys are shown in blue, apes in green and modern humans are in yellow. While significant overlap exists between taxa, suspensory species show higher values relative to non-suspensory species, indicative of relatively long clavicles and dorsally positioned shoulders. Modern human values are significantly lower than most apes and monkeys. KNM-WT 15000 has a low value, but falls within the human range. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

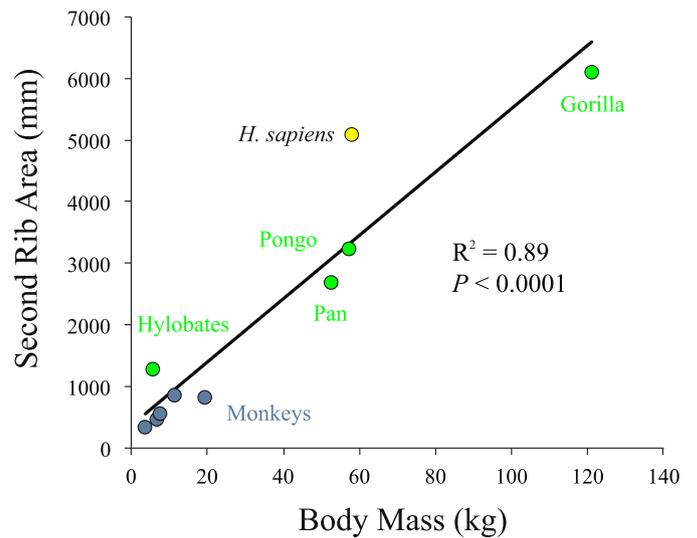


Figure 7. Primate second rib area by body mass. Points reflect mean costal area across all measured individuals. Monkeys are shown in blue, apes in green and modern humans are in yellow. Body mass estimates were taken from the literature (Ruff et al., 1997; Fleagle, 1999). Second rib area closely tracks body mass, making this measure a useful means of standardizing clavicle length. Note that modern human values fall significantly above the regression line, suggesting that an expansion in upper thorax volumes occurred during human evolution. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the variation in clavicle length seen in the Nariokotome and Dmanisi fossils. However, it is also possible that Nariokotome's proportions simply represent a lag between the expansion of the superior rib cage and the retention of an ancestrally short clavicle, and little is currently known about how rib cage shape changes during development. Regardless, the fact that Nariokotome's clavicular proportions exist within modern humans, who show no pathology in shoulder orientation or reduction in throwing performance, suggests that an anterior shoulder model is unnecessary. That the anterior shoulder model is also inconsistent with the morphology of the Dmanisi fossils lends further support to this conclusion.

Most scapular and clavicular shape variables also support *H. erectus* having a modern human-like shoulder. Both the Nariokotome and Dmanisi scapulae have bar-glenoid angles within the modern human range, consistent with a human-like inferiorly rotated glenoid (Jashashvili, 2005; Larson, 2007, 2009). The more complete Nariokotome scapula also shows a human-like lateral scapular spine orientation and supra- and infraspinatus fossae proportions consistent with or beyond those of modern humans (Jashashvili, 2005; Larson, 2007; Green and Alemseged, 2012). Clavicle shape and curvature in *H. erectus* are also consistent with a modern-human like form (Walker and Leakey, 1993; Jashashvili, 2005; Larson, 2007, 2009; Voisin, 2008). The single exception to this is Nariokotome's increased superior clavicular curvature, which could result in a slightly more superiorly placed acromial facet and a scapula that sits higher on the thorax (Voisin, 2006a, b). It is possible that this minor elevation of the shoulder complex may explain the diminutive clavicle lengths found in both the Nariokotome fossil and some modern Daasanach, due to the rapid constriction of the superior rib cage. However, there are no data to suggest that such a modest superior shift affects glenoid orientation or throwing performance in any way.

In sum, the overall similarity in shape between modern humans and all currently available early *H. erectus* fossils strongly support the presence of modern human-like shoulders by two million years ago. The lack of any relationship between relative clavicle length and throwing performance further suggests that relative clavicle length is not useful for functional assessments of throwing behavior in the fossil record. The combination of inferiorly rotated, human-like shoulders with a tall, mobile waist and low humeral torsion, support *H. erectus* as the first known hominin possessing the full anatomical complex associated with proficient throwing (Roach et al., 2013). While direct evidence of early throwing behavior remains elusive, evidence for the intensification of hominin carnivory and hunting behavior dating back two million years is increasing (e.g., Dominguez-Rodrigo, 1997; Braun et al., 2010; Ferraro et al., 2013). We propose that this increased carnivory was facilitated by a flexible, situation-dependent hunting and scavenging strategy that included high-speed throwing.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.jhevol.2014.09.004>.

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