The upper limb of *Homo naledi*

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Abstract

The evolutionary transition from an ape-like to human-like upper extremity occurred in the context of a behavioral shift from an upper limb predominantly involved in locomotion to one adapted for manipulation. Selection for overarm throwing and endurance running is thought to have further shaped modern human shoulder girdle morphology and its position about the thorax. *Homo naledi* (Dinaledi Chamber, Rising Star Cave, Cradle of Humankind, South Africa) combines an australopith-like cranial capacity with dental characteristics akin to early *Homo*. Although the hand, foot, and lower limb display many derived morphologies, the upper limb retains many primitive traits. Here, we describe the *H. naledi* upper extremity (excluding the hand) in detail and in a comparative context to evaluate the diversity of clavicular, scapular, humeral, radial, and ulnar morphology among early hominins and later *Homo*.

Homo naledi had a scapula with a markedly cranially-oriented glenoid, a humerus with extremely low torsion, and an australopith-like clavicle. These traits indicate that the *H. naledi* scapula was situated superiorly and laterally on the thorax. This shoulder girdle configuration is more similar to that of *Australopithecus* and distinct from that of modern humans, whose scapulae are positioned low and dorsally about the thorax. Although early *Homo erectus* maintains many primitive clavicular and humeral features, its derived scapular morphology suggests a loss of climbing adaptations. In contrast, the *H. naledi* upper limb is markedly primitive, retaining morphology conducive to climbing while lacking many of the derived features related to effective throwing or running purported to characterize other members of early *Homo*.

Introduction

The modern human upper limb reflects a history of selection for proficiency with manipulative tasks (Harmand et al., 2015; Key and Dunmore, 2015; Skinner et al., 2015), improved throwing performance (Roach et al., 2013), and, potentially, enhanced stabilization of the trunk during long-distance bipedal running (Bramble and Lieberman, 2004). Recently recovered skeletal remains from the Dinaledi Chamber (Rising Star cave system, Gauteng Province, South Africa) represent at least 15 individuals of *Homo naledi* (Berger et al., 2015). The morphology of the lower limb and foot (Harcourt-Smith et al., 2015; Marchi et al., 2016) suggests that *H. naledi* was a proficient biped, but the morphology of the hand and wrist suggests that climbing was of continued importance to this extinct species of *Homo* (Kivell et al., 2015). Accordingly, detailed assessment of the *H. naledi* upper limb material provides an opportunity to better understand the mosaic nature of the evolution of hominin locomotor anatomy.

The Dinaledi collection includes 90 identifiable fragments of clavicaulae, scapulae, humeri, radii, and ulnae, of which 20 preserve diagnostic anatomy (Figs. 1–9, Tables 1–7). Remains of the shoulder girdle include fragments representing at least six scapulae and five clavicaulae. The length and morphology of the *H. naledi* clavicle, as well as the shape and orientation of the scapula and glenohumeral joint, permit investigation of shoulder position and mobility (Larson, 2007; Voisin, 2001, 2004, 2006a, b, 2008), and in turn, the locomotor and manipulative capabilities of the upper limb of this species.

Current interpretations of shoulder morphology in hominins prior to the appearance of the genus *Homo* are based largely on isolated remains that are not associated with craniodental or other postcranial evidence (Larson, 2007). In fact, the shoulder girdle configuration of *Australopithecus*—characterized by short, obliquely-oriented clavicaulae, scapulae with cranially-oriented glenohumeral joints, and humeri displaying low to moderate

torsion—is all that is available to approximate the primitive hominin condition; pectoral girdle remains for early *Homo* are scarce (Larson, 2007). With a narrower upper thorax, the shoulder was likely to have been situated superiorly, as in African apes, which enables the scapula to rest dorsally upon the thorax, despite a shorter clavicle and low to moderate humeral torsion. In contrast, the modern human shoulder girdle is situated lower on a mediolaterally broad thorax with longer clavicles that lie predominately in the transverse plane, dorsally-positioned scapulae with laterally-oriented glenoid fossae, and humeri with high torsion (Larson, 2007).

The cranial and dental morphology of *H. naledi* compare most favorably with early species of *Homo* including *Homo habilis*, *Homo rudolfensis*, and *Homo erectus* (Berger et al., 2015). Nothing is known of the shoulder girdle of *H. rudolfensis* and only a single morphologically informative clavicle (OH 48) has been attributed to *H. habilis* (Leakey et al., 1964; Napier, 1965), meaning that the transition from the “primitive” hominin shoulder condition to that found in *H. erectus* is essentially unknown. Representatives of early *H. erectus*¹—namely KNM-WT 15000 and the Dmanisi material—display relatively shorter clavicles than modern humans (Lordkipanidze et al., 2007) and humeri with even lower torsion values than the australopiths (Larson, 2007). This raises several questions regarding scapular position about the thorax, clavicular length, humeral torsion, and the interplay of all of these traits with regard to upper limb function at this stage of hominin evolution. These issues directly relate to debates about purported climbing activities in early hominins (Stern and Susman, 1983; Susman et al., 1984; Rein et al., 2011; Green and Alemseged, 2012; Venkataraman et al., 2013), and the evolution of proficient throwing (Larson, 2015; Roach

¹Recent work by Dembo and colleagues (2015) highlighted problems in referring to KNM-WT 15000, fossils from Dmanisi, and Asian *Homo* fossil material collectively as *H. erectus*. As the debate is ongoing and exact taxonomic positions have yet to be clarified, we refer to KNM-WT 15000 and the Dmanisi material as “early *H. erectus*” as this taxonomic assignment has been most commonly used in discussion of the evolution of the early *Homo* shoulder girdle.

and Richmond, 2015a, b) and endurance running (Bramble and Lieberman, 2004) in our lineage. Though the date of the Dinaledi hominins is as yet unknown (Dirks et al., 2015; see also Dembo et al., 2016), knowledge of the upper limb morphology of *H. naledi* should improve our understanding of pectoral girdle evolution in the hominin lineage (Table 2).

Anatomical descriptions of diagnostic fossils

The following section describes each clavicular, scapular, humeral, radial, and ulnar element with diagnostic morphology, including its preservation (Figs. 1–9, Tables 1–5). Descriptions of remains lacking functionally relevant morphology can be found in the Supplementary Online Material (SOM) 1. All measurements are in millimeters (mm).

U.W. 101-1301: right partial scapula (Fig. 1)

U.W. 101-1301 is a right scapular fragment refitted from two primary pieces. The superior portion consists of the glenoid fossa and lateral scapular spine, while the inferior portion consists of the proximal aspect of the axillary border, broken via transverse fracture originating at the distal infraglenoid tubercle. Much of the glenoid fossa is preserved, excluding the superior and inferior-most portions, some of the infraglenoid tubercle, and ~60 mm of the axillary border. The spinoglenoid notch and the lateral-most extent of the base of the spine are preserved, along with a small portion of the spinal crest that would have been continuous with the acromion. The spine projects dorsally from the scapular body at an approximate angle of 87° relative to the long axis of the glenoid fossa. The superoinferior thickness of the base of the spine is 7.5 mm. On the costal surface, the ventral bar is prominent, with a proximal origin at the mid-point of the infraglenoid tubercle, and is oriented obliquely in line with the long axis of the axillary border. There is a sulcus between the ventral bar and median crest. True depth of this sulcus is difficult to determine as a result

of damage to the median crest of the axillary border. When viewed laterally, the axillary morphology is lacking a dorsal sulcus and strongly developed dorsal pillar. The dorsal surface of the axillary border is strongly concave, as in other specimens from this assemblage. The orientation of the glenoid fossa is markedly cranial (see below). There is slight costal notching to the costal margin of the glenoid fossa. While the dorsal margin is damaged, enough remains to allow an estimated greatest absolute breadth of the glenoid at 18.8 mm. The greatest articular breadth of the glenoid (without the rim of the glenoid labrum) is 12.3 mm. The remaining fragment of the supraspinous fossa, superior to the lateral root of the spine, appears broad. There are two foramina on the supraspinous surface of the spine. The larger lateral foramen is located ~12 mm from the superior point of breakage, while the medial foramen is located ~11 mm from the medial point of breakage. Medially, the spine narrows to the crest of the scapular spine, though this is not preserved. The dorsomedial margin of the fragment inflects superiorly before flaring to the base of the acromion process.

U.W. 101-258: right clavicle midshaft (Fig. 2)

U.W. 101-258 is a right clavicular shaft totaling 63.3 mm in length. This specimen is missing both the sternal and acromial ends. The edges of the breaks are not rounded by taphonomic processes and there is no observable distortion to the shaft of the clavicle. At the medial point of breakage (the approximate midshaft), shaft dimensions are 9.8 mm superoinferior (SI) and 9.0 mm anteroposterior (AP). In cross-section medially, the clavicle is rounded inferiorly with a slightly flattened superior surface. Laterally, the cross-sectional shape is slightly flattened inferiorly and anteriorly, and rounded superiorly. As both articular ends are absent, it is impossible to accurately determine the degree of clavicular torsion, however, based on visual assessment, some degree of torsion is present. The sigmoid curvature of the clavicle is moderate. Overall the appearance of the clavicle is notably smooth

with only a few weakly developed entheses. The deltoid crest is present as a sharpened ridge located on the anterior surface of the lateral curvature and extending approximately 8.8 mm from the lateral breakage point. The conoid tubercle is very well-developed, centrally-placed, and flanges posteriorly to form a pronounced border to a deep subclavian sulcus. Continuous with the tubercle medially is a strongly developed crest separating the inferior from the posterior surfaces. Moving superiorly from the conoid tubercle, the transition is smooth and rounded. In cranial view, there is a more pronounced internal than external curvature.

U.W. 101-1229: right medial clavicle (Fig. 2)

U.W. 101-1229 is a partial right clavicle consisting of three refitted fragments that, when reassembled, measure 73.1 mm in length. A segment of the sternal metaphysis is preserved, measuring 8.8 mm AP by 5.4 mm SI, but the metaphysis is otherwise absent. While this element is unfused, the size of the shaft is comparable to mature elements from this assemblage and may be indicative of a nearly-mature or even young adult individual since this epiphysis may not fuse in modern humans until the mid-to-late twenties (Langley, 2016).

The cross-sectional shape of the medial end is ovoid and rounds along the posterior aspect. Laterally, the superoanterior profile is rounded, however, on the posterior margin there is a distinct angular margin separating the posterior and superior surfaces. The inferior margin of the lateral end is also angular, which is attributable to the crest leading to the conoid tubercle. The subclavian groove is present as a distinct sulcus on the inferoposterior aspect. The inferred position of the conoid tubercle, based on the orientation of the crest leading to the tubercle, is central to the shaft of the clavicle, similar to U.W. 101-258. With the exception of some exfoliation, the superior surface of this specimen is smooth and relatively featureless. There are two nutrient foramina on the posterior surface 10.0 mm from

the lateral point of breakage superior to the crest of the conoid tubercle. Medially, the sternal articulation is badly damaged, particularly on the anteroinferior aspect, exposing the trabecular bone. Some infilling with sediment has occurred.

U.W. 101-1347: left lateral clavicle (Fig. 2)

U.W. 101-1347 is a well-preserved lateral portion of a left clavicle, 53.6 mm in length, and broken just lateral to the conoid tubercle. The acromial end is missing, exposing trabecular bone. The deltoid scar is present on the anterior margin of the clavicle and as a marked rugosity on the lateral curve of the shaft. On the inferior surface of the fragment, the origin of m. deltoideus is largely smooth. The clavicular insertion for m. trapezius on the superoposterior surface is a marked ridge. There is a nutrient foramen on the posterior surface 14.4 mm from the medial point of breakage. On the inferomedial surface there is a prominent ridge leading to the conoid tubercle. As with other clavicular specimens from this assemblage, the conoid tubercle is centrally located on the shaft. The shaft dimensions at the medial point of breakage are 7.5 mm AP and 8.2 mm SI (including the crest to the tubercle). In cross-section, the diaphysis is strongly ovoid with a transverse tilt. On the posterior aspect, there is a rugosity 5.2 mm from the lateral point of breakage that represents the medial-most attachment for the acromioclavicular ligament on this surface. The lateral extent of the subclavian groove is marked by the crest leading to the conoid tubercle and presents as a slight sulcus on the inferior surface. The lateral end of the specimen has an inferior inflection.

U.W. 101-283: largely complete right humerus (Fig. 3, Tables 3–5)

U.W. 101-283 is a largely complete right humerus refitted from five fragments: the first includes the humeral head missing the articular surface; the second is a section preserving the distal halves of the mm. pectoralis major and latissimus dorsi insertions

proximally and the proximal section of the deltoid tuberosity; the third section preserves the midshaft and the distal segment of the deltoid tuberosity proximally on the anterior surface; the fourth segment preserves the lower midshaft with the proximal lateral supracondylar crest; the fifth segment is the distal extremity of the humerus including a portion of the distal articular surfaces. While the humerus has been reconstructed from pieces, there is no distortion and all pieces are congruent with each other, with only minor bone loss at the break margins that is attributable to erosion of the cortical surfaces. Missing from this specimen are both medial and lateral epicondyles, the medial trochlear margin, and the capitulum. The articular surface of the humeral head is absent. The greater tubercle is eroded on its anterior and lateral aspects, although part of the insertion for m. supraspinatus, the heavily eroded insertion for m. infraspinatus, and the non-articular intracapsular area remain. The lesser tubercle is intact, save for the anterior lip bounding the bicipital groove. The insertion for m. subscapularis is also intact. The floor of the bicipital groove is largely intact with only minor flaking. The distal articular surface overall is poorly preserved.

The refitted humerus is 256.0 mm long and extremely gracile, with a shaft that is transversely thin. Observing the humerus cranially, the humeral head appears to be directed entirely posteriorly, indicating very little torsion. While the articular surface of the humeral head is absent, the intra-capsular non-articular area is intact up to the margin of the articular surface, allowing the head diameters to be estimated. The mediolateral (ML) head diameter (measured transversely across the width of the anatomical neck from greater to lesser tubercle) is estimated at 26.4 mm, and the SI diameter (measured from the superior-most midpoint of the articular margin to most projecting point on the anatomical neck inferior of the articular surface) is estimated as 30.2 mm. The greater tubercle appears large. On the superior surface of the greater tubercle, the insertions for mm. supraspinatus and infraspinatus are relatively smooth, with an angular margin separating the insertion facets. Greater tubercle

length is estimated at 24 mm. While there is damage to the greater tubercle superiorly and on the shaft inferiorly, the lateral lip of the bicipital groove in the remaining section is rounded and only moderately developed. The lesser tubercle is prominent and projects medially. The length of the lesser tubercle (taken from laterosuperior-medioinferior along the insertion area of *m. subscapularis*) is 15.6 mm. The maximum dorsal projection cannot be determined due to damage to the medial lip of the bicipital groove. The attachment area of *m. subscapularis* has mineralized sediment adhering to it, but it is mostly smooth with a slight depression inferomedially. The lateral margin of the lesser tubercle and, thus, the medial lip of the bicipital groove, is absent. Distally, the medial edge of the bicipital groove is present as a moderately developed crest that intersects the lesser tubercle proximally at the center line. The bicipital groove is very narrow proximally. Distally, the medial lip of the sulcus (formed by the lesser tubercle) deflects medially, such that the sulcus widens markedly. The ML breadth between the points of greatest projection of the lesser and greater tubercles (and perpendicular to the shaft axis) is 32.5 mm.

The maximum neck diameter is 19.3 mm and the minimum neck diameter is 18.8 mm. The circumference of the surgical neck is 49.7 mm. The insertion site for *m. pectoralis major* is too damaged to assess rugosity, though the proximal section of the crest of the greater tubercle suggests that it was not very well-developed. On the medial margin of the distal part of the bicipital groove, an area of moderate rugosity marks the insertion site for *m. latissimus dorsi*. The insertion of *m. teres major*, if present at all, has been obliterated by erosion; it is represented by a prominent ridge on the lateral margin of the greater tubercle. The origin of the lateral head of *m. triceps brachii* can be discerned on the posterolateral shaft as a slight tuberosity. The deltoid tuberosity is only very weakly developed and more anteriorly positioned than normally found in modern humans.

Insertions for mm. coracobrachialis and brachialis are both smooth and featureless. On the medial aspect of the fourth shaft fragment is a longitudinal ridge 33.4 mm in length that continues proximally on the third fragment for 18.3 mm, and is low and thin representing the medial humeral origin of m. triceps brachii medius. Distally, there is a very well-developed depression on the medial epicondyle, 19.6 mm length, representing the humeral origin of m. flexor carpi ulnaris. The origin for m. pronator teres is so weakly developed as to be absent superiorly and missing inferiorly due to damage. As a result of the strong development of m. flexor carpi ulnaris, the medial margin of the distal humerus is more posteriorly placed and rounded.

The lateral supracondylar ridge extends proximally from the superior-most point of breakage on the lateral aspect as a relatively sharp border between the anterior and posterior surfaces of the shaft. The origin of m. brachioradialis is partially obliterated by the damage to the lateral supracondylar ridge. There is a weakly developed ridge adjacent to the origin site. The origin of m. extensor carpi radialis longus presents as a sulcus adjacent the lateral supracondylar ridge, 16.4 mm SI by 2.1 mm ML. Projection of the lateral and medial epicondyles cannot be determined.

The shape of the olecranon fossa is ovoid and medially offset. The lateral pillar is well-developed, contributing to the medially offset olecranon fossa. Within the olecranon fossa there is a moderately sized septal aperture, 3.8 mm SI by 7.0 mm ML. The margins of this feature are rounded with intact cortical bone, suggesting that this is a true feature and not the result of taphonomic or preparatory damage. The proximal edge of the olecranon fossa is marked by a rounded apex. On the anterolateral aspect, the radial fossa is a marked ovoid depression that is ML elongated (12.5 mm in this dimension) compared to its SI dimension (5.6 mm). The coronoid fossa is taller and wider than the radial fossa (15.1 mm ML, 11.7 mm SI). The radial fossa is shallow compared to the coronoid fossa.

Distal articular and biepicondylar breadth cannot be determined. The gentleness of the slope on the remaining lateral edge of the trochlea suggests that trochlear/capitular keel is likely to be minimal; the sulcus between the trochlea and the capitulum appears very shallow. The trochlea has a relatively deep waist, resulting in a pronounced groove between the medial and lateral margins of the trochlea. Posteriorly, the lateral trochlear margin has a SI orientation. Trochlear breadth is estimated at 15.5 mm. The AP diameter of the medial trochlea is approximately 16.7 mm and 11.5 mm for the lateral trochlea.

U.W. 101-466: right distal humerus (Fig. 4, Table 3)

U.W. 101-466 is a well-preserved right distal humerus, 128.5 mm in length. The shaft is gracile, broken just inferior to the deltoid tuberosity, and has an ovoid diaphyseal shape at the proximal point of breakage. There is a nutrient foramen on the medial aspect of the shaft, 32.9 mm distal to the proximal point of breakage. The crest for the lateral epicondyle is sharp, moderately developed, with a marked tuberosity at the proximal-most extremity, and is approximately 23.7 mm in length and 5.5 mm in breadth. The medial epicondyle is fused and complete with damage only to the posterior surface and slight abrasion to the superior margin. It projects medially 12.5 mm from the medial border of the trochlea, achieving its greatest projection superiorly. The medial epicondyle is 9.7 mm in AP breadth and the enthesal surface is oriented slightly inferiorly. While the medial epicondylar crest is weakly developed and interrupted by pitting, there is a slight depression parallel to it, forming a tuberosity on the anteromedial aspect similar to that found on U.W. 101-744. The septal aperture has an SI height of 5.0 mm and a ML breadth of 7.8 mm. The radial fossa is present as a slight concavity adjacent the septal aperture before terminating distally with the break. There is a slight projection of bone medially that is suggestive of the continuation of the fossa to the (absent) capitulum.

U.W. 101-744: left distal humerus (Fig. 4, Table 3)

U.W. 101-744 is a left distal humerus, 117.9 mm in length and broken at the coronoid fossa. The distal articular surfaces are absent and the medullary cavity is infilled with sediment, with only traces of trabecular bone present. What remains of the septal aperture is elliptical and approximately 8 mm in breadth. The olecranon fossa is broad and medially offset. Posteriorly, the shaft flattens to a slight concavity just superior and lateral to the olecranon fossa. Mid-distal shaft diameter is difficult to establish with certainty due to the significant damage to the anterior shaft. The lateral epicondylar crest is preserved only at its proximal extremity as a ridge approximately 15.5 mm in length; the remainder is absent due to damage. There is a slight depression on the medial aspect of the distal humerus parallel to the medial supracondylar crest, forming a tuberosity on the anteromedial aspect.

U.W. 101-1240: right distal humerus (Fig. 4, Table 3)

U.W. 101-1240 is a right distal humerus, 70.4 mm in length, and broken at the level of the radial and coronoid fossae. Both epicondyles and the articular surfaces are missing in this specimen. The lateral supracondylar crest is damaged somewhat along its length. The origin of *m. flexor carpi ulnaris* on the medial epicondyle appears as a slight depression on the posteromedial aspect. The margins of the olecranon fossa at the distal breakage point appear rounded when examined under the microscope. The lateral distodorsal pillar of the olecranon fossa is well-developed, offsetting the fossa medially. The lateral supracondylar crest is extremely well-developed, displaying marked attachment sites for the *m. brachioradialis* proximally and *m. flexor carpi ulnaris longus* distally.

U.W. 101-499: right ulna diaphysis (Fig. 5, Table 6)

U.W. 101-499 is a right ulnar shaft refitted from two fragments, together 169.0 mm in length, though missing its proximal extremity. The distal fragment preserves the distal portion of the diaphysis and distal articular surface. The articular surface is heavily abraded and missing the styloid process. The ulna is gracile and the shaft, when viewed anteriorly, is curved laterally along its length. The interosseous crest is weakly developed; it is low and is expressed proximally as a slightly sharpened ridge on the proximal fragment. In the coronal plane, the distal articular surface and neck are laterally deflected. This specimen is one of the larger ulnae in the assemblage. At the proximal point of breakage, the cross-section is tear-drop shaped; the lateral aspect is flatter and more dorsolaterally deflected than the medial aspect. The posterior margin of the lateral aspect is rounded with no noticeable rugosity for the attachments of mm. abductor pollicis longus, extensor pollicis longus, and extensor indicis.

The ridge for m. pronator quadratus is strongly expressed (3.7 mm thick), beginning on the anteromedial aspect of the distal shaft and spiralling to the posterior surface, where it meets the superior extremity of the styloid process. The length of the crest is 30.6 mm. The shaft deviates laterally at the level of the pronator ridge, such that the neck and head sit slightly lateral to the long axis of the shaft. The AP width of the distal head (excluding the styloid) is 12.2 mm. Mediolateral diameter is difficult to determine due to damage to the distal surface. Although the styloid is missing, the shape and contours of the area of the point of breakage indicate that it was reduced and quite thin mediolaterally and it is not possible to determine the degree of projection. Anteromedially, there is a distinct foramen adjacent to the styloid. The m. extensor carpi ulnaris groove is poorly preserved but can be seen as a shallow concavity on the posterolateral surface adjacent to the broken surface of the absent styloid process. There are a number of small foramina on the anterior surface.

U.W. 101-560: right proximal ulna (Fig. 6, Table 6)

U.W. 101-560 is a right olecranon process of the ulna, 34.4 mm in length, preserving the articular surfaces of the semilunar and radial notches, as well as the coronoid process. It is missing its posterior and most of the cranial surface. A section of the insertion for *m. triceps brachii* is preserved and quite smooth in appearance. The olecranon process is mediolaterally narrow, though exact breadth cannot be accurately determined due to damage. The coronoid process has an estimated maximum ML diameter (measured from the proximal margin of the radial notch to the medial margin on the coronoid process) of 13.9 mm. The guiding ridge at the central line of the semilunar notch is weakly developed, dividing the notch into medial and lateral sections. The medial region has a maximum ML diameter of 8.5 mm and the lateral region has a maximum diameter of 10.5 mm in the same dimension. The semilunar (trochlear) notch appears to have a proximoanterior orientation, though the absence of the ulnar diaphysis and damage to the proximal and posterior surfaces of the specimen makes this difficult to estimate with accuracy. There is also pronounced waisting of the semilunar notch with some development of the non-articular surface on the medial margin of the notch. Minimum breadth at this point is 11.0 mm ML. Maximum ML breadth of the articular surface is estimated at 15 mm. The radial notch is shallow. The proximal margin of the radial notch is straight, while the distal margin is round; both the anterior and posterior margins are gently convex and straighter as they move towards their junction with the proximal margin. The radial notch is slightly anteriorly deflected along its AP axis. A weakly developed, somewhat rounded proximal margin separates the radial notch from the adjacent semilunar notch.

U.W. 101-831: right distal ulna (Fig. 7, Table 6)

U.W. 101-831 is a right distal ulna comprising three refitted pieces preserving the distal articular surface and distal diaphysis, altogether 102.6 mm in length (taken from the proximal point of breakage to the head of the ulna, excluding the styloid). The distal articular surface is missing its medial and lateral margins, exposing trabecular bone. The styloid process has been refitted to the ulna, though it appears that some minor crushing has occurred, possibly resulting in some minor loss of length. The surface of the tip of the styloid is damaged exposing trabecular bone. A large foramen can be found centrally on the distal articular surface in the non-articular area. The m. pronator quadratus crest is strongly developed, 4.2 mm thick, and spirals 23.6 mm distally from the anteromedial aspect of the distal shaft to meet the medial margin of the styloid process. The m. extensor carpi ulnaris groove is shallow and broad.

U.W. 101-1480: right ulnar diaphysis (Fig. 8)

U.W. 101-1480 is a right ulna fragment preserving midshaft and the insertion for m. brachialis, measuring 187.0 mm in length. It comprises two refitted fragments and is broken proximally, just inferior to the coronoid process and missing the distal articular surface and styloid process. The distal portion of the ulna is missing a large portion of its posteromedial aspect. The diaphysis of this specimen in posterior view is straight without any noticeable lateral curvature of the posterior border. The insertion for m. anconeus is present as a small tuberosity on the posterior border, 31.9 mm from the proximal point of breakage, with a slight crest moving proximolaterally from this point. The ulnar attachment for m. supinator is heavily abraded though still observable as a slight projection at the proximal point of breakage and as a rounded ridge 14.1 mm from the break. The m. brachialis insertion is a marked depression on the anterior aspect. Distally, a nutrient foramen is located on the

anterior aspect of the specimen 98.0 mm from the proximal point of breakage adjacent the interosseous crest.

U.W. 101-070: right radial diaphysis (Fig. 9, Table 7)

U.W. 101-070 is a fragment of a right radial shaft, 125.0 mm in length, with a poorly preserved radial tuberosity. This specimen is refitted from three fragments. The radial head and neck are absent, and there is no noticeable distortion of the specimen. The diaphyseal cross-sectional shape at the distal point of breakage is D-shaped. A nutrient foramen is located 47.5 mm from the distal point of breakage on the anterior surface of the specimen. The interosseous crest is present as an angular margin on the medial aspect of the shaft. On the lateral aspect of the shaft, 20.7 mm from the distal point of breakage, is a rugosity for the insertion of m. pronator teres that is 21.9 mm long and 2.7 mm wide. While damage obscures much of the surface morphology, it is clear that the radial tuberosity is similar to those of other radii from this assemblage in being well-developed. Exact dimensions of the tuberosity cannot be determined.

U.W. 101-935: left proximal radius (Fig. 9, Table 7)

U.W. 101-935 is a mostly complete left proximal radius preserving the articular surface and three-quarters of the shaft. This specimen is comprised of two congruent pieces, broken transversely, and is 192.5 mm in length. The fracture points join cleanly, but minor bone loss has occurred near the point of refit (no more than 1.0–3.0 mm), resulting in a slight anteromedial displacement of the distal fragment. The surface of the shaft is otherwise complete and marred only by minor defects. The most striking feature of this radius is its large size relative to other radii in the assemblage. U.W. 101-935 is robust and straight through the midshaft. The minimal flaring of the distal point of breakage suggests that the

shaft would continue for a distance before reaching the distal extremity. In proximal view, the radial head appears rounded and the radial neck is mediolaterally narrow. The radial tuberosity is extremely well-developed and globular. Anteriorly, the tuberosity is relatively smooth and projects from the posterior margin by a slight sulcus 1.7 mm in breadth and 7.2 mm in length. The posterior margin of the tuberosity and attachment for m. biceps brachii is smooth. The proximolateral margin of m. supinator attachment is slightly rugose along the lateral margin of the radial tuberosity and inferiorly adjacent to the interosseous crest; the medial margin is smooth. Proximally, the shaft has a rounded cross-section. The oblique line of the radius and attachment for m. flexor digitorum superficialis is relatively low and round, with a sulcus just anterior to this (possibly the attachment for m. flexor pollicis longus). The interosseous crest is well-developed, but the insertion for m. pronator teres is absent. Just posterior to this is a low ridge that may mark the radial origin of m. abductor pollicis longus. At the distal point of breakage, the shaft cross-section is ovoid.

U.W. 101-1346: right partial radius (Fig. 9, Table 7)

U.W. 101-1346 is a partial right radius, totalling 133.8 mm in length, refitted from two fragments. It is possible that this specimen is the antimer of U.W. 101-935 based on overall size and morphology. It preserves an eroded segment of radial head and midshaft with a heavily damaged interosseous crest. The radial tuberosity is similar to other radii from the assemblage in being extremely well-developed and globular. Anteriorly, the tuberosity surface is somewhat abraded making surface development difficult to determine accurately. The tuberosity is strongly projecting with distinct flanging to the medial and lateral borders, possibly indicating development of mm. biceps brachii and supinator (with the attachment of the latter on the anterior surface of the shaft presenting as a deep sulcus adjacent to the radial

tuberosity, contributing to the projecting appearance of the tuberosity). The medial margin of the tuberosity and attachment for m. biceps brachii is smooth.

There is noticeable curvature along the lateral aspect of the shaft. The interosseous crest is damaged distally, but easily identifiable as a sharp angulation to the anteromedial margin of the shaft. A distinct sulcus is present on the posterior aspect of the interosseous crest that is deeper proximally than distally where it begins to flatten. Proximally, diaphyseal shape is mediolaterally ovoid. The posterior surface is angulated distally and distinctly flattened proximally.

U.W. 101-1712: right radial diaphysis (Fig. 9)

U.W. 101-1712 is a poorly preserved fragment of right radial shaft refitted from three pieces, totalling 84.1 mm in length. It preserves the proximal-most part of the radial shaft, absent the radial head and neck. The radial tuberosity morphology is typical for this assemblage: large and globular with a distinct sulcus adjacent to it on the anterior aspect for the m. supinator attachment. Moving distally, there are two distinct crests on the medial aspect of the shaft with a SI oriented sulcus separating them both. The proximal crest is 41.1 mm in length; the second (distal) crest is 21.6 mm in length, but has been artificially shortened by both damage to the subperiosteal bone and the distal breakage. The proximal crest represents the radial attachment of m. flexor digitorum superficialis and the distal crest represents the radial origin of m. flexor pollicis longus. Enveloped within the second crest are two nutrient foramina, the first beginning 7.3 mm from the distal point of breakage.

Comparative anatomy

Materials and methods

The *H. naledi* upper limb sample. To assess the minimum number of individuals (MNI) and number of individual specimens (NISP; Table 1) in the upper limb (excluding the hand) sample of the Dinaledi assemblage, we examined element morphology, side, size, and state of epiphyseal fusion. Individuals were determined using bone siding and morphological variation between elements of similar size (though morphological differentiation was used infrequently due to the remarkable homogeneity of the assemblage and was considered only in cases of extreme variation). Only elements capable of being sided were used to calculate MNI. Maturity of the remains was assessed primarily using state of epiphyseal fusion and, secondarily, using element size for more fragmentary elements with unpreserved epiphyses or metaphyses. Remains were grouped broadly into two categories: mature (complete epiphyseal fusion) and immature (unfused or partially-fused epiphyses). For purposes of classification, elements within or above the size range for known mature specimens with fused epiphyses were deemed mature; specimens markedly smaller than the mature sample were tentatively designated immature. Specimens lacking epiphyses or metaphyses and of indeterminate or intermediate size were not categorized.

Scapular angle measures. Comparative data were taken on original fossil hominin shoulder material from *Australopithecus africanus* and early *H. erectus* housed at the Ditsong National Museum of Natural History (Pretoria, South Africa), the University of the Witwatersrand (University of Witwatersrand; Johannesburg, South Africa), and the National Museums of Kenya (Nairobi). Measurements were taken on a first generation cast of the A.L. 288-1 (*Australopithecus afarensis*) partial skeleton housed at the University of Witwatersrand. Comparative metrics of MH2 (*Australopithecus sediba*) were also taken at the University of Witwatersrand on a three-dimensional (3D) printout, as the scapula is a composite of right and left scapular fragments (Churchill et al., 2013). These individuals were studied in

conjunction with samples of *Homo sapiens*, *Pongo pygmaeus*, *Gorilla gorilla*, *Pan troglodytes*, and *Hylobates* spp. from skeletal collections housed at the National Museum of Natural History (Washington, DC), the American Museum of Natural History (New York, NY), the Cleveland Museum of Natural History (Cleveland, Ohio), the Museum of Comparative Zoology (Cambridge, MA), and the Powell-Cotton Museum (Birchington, UK; Table 8). An Immersion MicroScribe G2 digitizer was used to capture 3D landmark points for estimating both glenoid fossa and spine orientation.

For a specimen like A.L. 288-1, which preserves the entire glenoid fossa and much of the lateral border, two points were placed on the bar of bone along the inferior aspect of the subscapularis fossa (the “ventral” bar) to form a line representing this feature. Points were also collected at the superior and inferior margins of the glenoid fossa. The ventral bar/glenoid angle was then derived using code written for R (Ihaka and Gentleman, 1996) by Dr. Adam Gordon: this program calculated the angle of any two lines (i.e., four points) in space by defining a plane represented by three points (in this case, three of the four previously described points, which are roughly coplanar) and four points representing the two lines. The lines were then projected against the previously determined plane so that they might intersect to calculate the angle of interest. For U.W. 101-1301, a comparable amount of the ventral bar is present to that of A.L. 288-1, but the superior and inferior aspects of the glenoid are missing. However, enough of the central aspect of the glenoid is preserved to appreciate that the fossa orientation would not be dramatically altered if it were complete (see also Fig. 10c). Several different points were estimated in the light of the missing landmarks, and the angle presented in Table 8 and Figure 10 represents the average value of multiple trials; most of the estimated values ranged between 119° and 122°. To further validate this estimate, and given the overall similarity in size and shape of the A.L. 288-1 and U.W. 101-1301 scapulae, we overlaid the complete glenoid of the former atop the fragmentary glenoid

of the latter, aligning the curvatures of the intact portions of the two fossae to better establish the position of the superior and inferior margins of the U.W. 101-1301 glenoid. This procedure was performed in Photoshop (Adobe CS4) by rotating the A.L. 288-1 glenoid to fit the contour of the U.W. 101-1301 fragment; no resizing was necessary (Fig. 10c). The ventral bar/glenoid angle of this “composite” scapula was calculated with ImageJ (Rasband, 1997–2014) to be 121.2° , leaving us confident in our reported estimate of 121.1° .

Estimating spine orientation in these specimens was further complicated by fossil preservation. In a complete specimen, the axillary border/spine (ABS; axillospinal) angle is formed by two line segments, each formed by two discrete landmarks: 1) base of the spine – a. the spinoglenoid notch and b. the point where the spine meets the vertebral border, and 2) axillary border – a. the infraglenoid tubercle and b. the inferior angle. In both A.L. 288-1 and U.W. 101-1301, only points 1a and 2a are present. The placement of point 1b followed the principal that the base of the spine forms a straight line, regardless of any curvature that might occur as it approaches the medial border (e.g., in our comparative sample, the point that completed an imaginary straight line was selected as point 1b, even if the spine tapered or curved inferiorly). As such, picking an intermediate spinal point along the broken edge should approximate this straight line. In choosing point 2b, it is important to note that the axillary border often curves and the inferior angle lies inferior to a straight line representing that border (in large part due to the morphology of the m. teres major origin). Accordingly, a point that would represent an intermediate point along line 2 must be estimated in space, inferior to the broken edge. Owing to this, several different points were selected to determine a reasonable range of estimates. These four points were used to calculate the axillospinal angle in R, the mean of which represents a conservative estimate of spinal orientation with regard to the comparative sample.

Determination of humeral torsion and robusticity index. Humeral torsion refers to the orientation of the humeral head relative to the long axis of the distal articular surface. Humeri with posteriorly orientated humeral heads (i.e., low torsion) have torsion values between 90–120°, with 90° being equivalent to 0° retroversion as generally reported in the clinical literature (e.g., Pieper, 1998; Reagan et al., 2002). The higher the torsion value, the more medially directed the humeral head: a torsion value of 180° indicates a humeral head orientated directly medially. Comparative data on humeral torsion for fossil specimens were drawn from the literature. Modern human and non-human primate humeral torsion data were collected from specimens at the Raymond A. Dart Collection at the University of Witwatersrand (Johannesburg, South Africa), American Museum of Natural History (New York, U.S.A.), Cleveland Museum of Natural History (Cleveland, U.S.A.), and Anthropological Institute and Museum, University of Zürich (Zürich, Switzerland). See Table 3 for further details.

The U.W. 101-283 mature humerus is missing much of the head proximal to the anatomical neck and part of the superoanterior surface of the greater tubercle as a result of taphonomic damage. As such, it was necessary to use landmarks on the anatomical neck and proximal shaft to determine the position of the long axis of the humeral head. The landmarks included the most projecting point on the anatomical neck inferior to the articular surface and the most projecting part of the base of the greater tubercle, in line with the approximate margin between the insertion facets for the supra- and infraspinatus muscles on the superior surface of the greater tubercle (Fig. 11). The axis of the humeral head was determined by projecting a line through these two landmarks. Larson's (1996) bisector of the bicipital sulcus and assumed humeral head position at 120° did not align with the inferior projection of the humeral head (arguably the more definitive landmark for humeral head axis position in this

specimen) and, as a result, tended to over-estimate humeral head position. The axis of the elbow is defined as a line that passes through the center of the capitulum and trochlea (Krahl and Evans, 1945). As these features are absent in U.W. 101-283, a digital image of a complete modern human distal humerus was overlaid and aligned with a digital image of U.W. 101-283. The transverse axis of the elbow was then projected onto U.W. 101-283 using both the complete distal humerus and the preserved morphology in the fossil specimen as a guide.

Alternate landmarks were used for the immature specimen, U.W. 101-948, which is missing its secondary ossification centers at the distal extremity for both the medial and lateral epicondyles and proximal epiphysis. The distal axis was therefore defined as the axis through the most laterally and medially projecting points of the distal diaphysis in the coronal plane where the secondary ossification centers for the epicondyles would ultimately fuse. The long axis of the humeral head in U.W. 101-948 was defined as in U.W. 101-283: the axis through the most projecting anterior point of the greater tubercle to the most projecting point on the anatomical neck.

Torsion was determined by measuring the angle between the long axis of the humeral head and elbow as per Larson (1996, 2007) using 3D renderings of the U.W. 101-283 humerus created by a NextEngine desktop 3D scanner from NextEngine, Inc. and photographic superimposition. Scans were prepared using the ScanStudio software suite (NextEngine, Inc., 2006) and imported into MeshLab (Cignoni et al., 2008) for further rendering. In both methods, Viewbox 4 cephalometric software was used to define the axes of the distal and proximal articular surfaces by drawing and aligning the axes using the Curves function of the Viewbox templates. The Protractor tool was then used to measure the torsion angle between the axes.

To ensure the reliability of the measures, the two methods were tested against each other statistically by taking repeated measures of torsion on a sample of modern human humeri ($n = 5$, measured torsion four times on each for both methods at one hour intervals), as well as U.W. 101-283. A repeated measures t -test was conducted and no significant difference was found between the mean humeral torsion values for the two methods ($p = 0.3$). The torsion values presented for U.W. 101-283 and U.W. 101-948 are the average of the values produced during testing.

The robusticity index (RI) was determined for fossil hominin humeri from two measurements: humeral minimum circumference (HMinC) and humeral maximum length (HML). HMinC was measured as the minimum possible diaphyseal circumference, generally taken distal of the midshaft; HML was measured as the maximum length of the bone, taken from the superior most point of the humeral head to the most distal extremity of the distal humerus, using an osteometric board. RI was calculated as HMinC/HML.

Radial neck angle. Radial neck angle was measured as a proxy for diaphyseal curvature following Rodríguez et al. (2016) and Trinkaus (1983). In order to calculate radial neck angle, three axes were determined according to the procedure outlined by Rodríguez et al. (2016) following Martin and Saller (1957; measurement no. 7): the long axis of the neck (a), the long axis of the proximal portion of the diaphysis (b), and the horizontal intersection between the latter two axes where the proximal diaphysis meets the radial neck (c; Fig. 12). Only two *H. naledi* radii were sufficiently intact to analyze this way: U.W. 101-935 and U.W. 101-1346. The right radius for MH2 (U.W. 88-85) was also measured. Digital images of these specimens in anterior view were imported into Viewbox 4 cephalometric software and the axes were determined by drawing them onto the images using the Curves function of the Viewbox templates and the neck angle measured using the protractor tool. Neck angle is

defined as the angle formed by the intersection of the long axes of the radial neck and proximal diaphysis, with larger values indicating a straighter radial diaphysis (that is, with less lateral deviation) relative to the neck. Smaller neck angle values are therefore indicative of a radial diaphysis that projects more laterally, as in specimens with greater diaphyseal curvature. Measurements were repeated four times and the average value taken for each specimen.

Results

Scapula. The overall size and morphology of U.W. 101-1301 is remarkably similar to that of A.L. 288-1 (*A. afarensis*; Fig. 10c, Table 8). The orientation of the glenohumeral (GH) joint was estimated by the angle formed between the vertical axis of the glenoid fossa and an anterior projection of bone subparallel to the axillary border, commonly referred to as the ‘ventral bar’ (e.g., Stern and Susman, 1983). Highly obtuse ventral bar/glenoid (VBG) angles represent more laterally orientated GH joints, as in *Homo*, while *Hylobates* joints are cranially-oriented with more acute VBG angles (Fig. 10, Table 8). *Pan*, *Gorilla*, and *Pongo* were all similar to one another and significantly more cranially-oriented than *Homo*. The ventral bar/glenoid angle of U.W. 101-1301 is estimated to be 121.1°, indicative of a more cranially orientated glenoid fossa than *A. africanus* (Sts 7: 128.0°), *A. afarensis* (A.L. 288-1: 132.2°; KSD-VP-1/1: 134°), *A. sediba* (MH2: 131.2°), and even modern great apes (Fig. 10b; see Methods; Green and Alemseged, 2012).

The mean modern human axillary border/spine angle is ca. 45° and represents a transversely (horizontally) oriented spine (Table 8). The ABS angle is more acute in the apes (particularly *Hylobates* and *Pan*), representing more obliquely (superiorly) oriented spines. Given the limited preservation, the ABS angle is tentatively estimated to be 26.8°, which

suggests a markedly oblique orientation of the spine, similar to Sts 7 and intermediate between *Pan* and *Gorilla* (Table 8).

Clavicle. Both the U.W. 101-258 and U.W. 101-1347 fragments present well-developed conoid tubercles, implying a similar degree of development at the dorsolateral tubercle of the coracoid process of the scapula. Vrba (1979) hypothesized that dorsolateral tubercle development might correspond with a superiorly orientated clavicle and a high scapular position. The Dinaledi clavicular remains also bear a strong overall similarity in gross morphology to the clavicular specimens attributed to *A. sediba* (MH2; Churchill et al., 2013), *H. habilis* (OH 48; Ohman, 1986; Oxnard, 1969; Voisin, 2001), and *Pan*, suggests that the *H. naledi* shoulder position was more superior than in modern humans or KNM-WT 15000. In the lateral clavicular fragment, U.W. 101-1347, the remainder of the shaft appears to have an inferomedial inflection when the acromial extremity of the specimen is held horizontally, indicating a clavicular position higher than is typical for modern humans (Ohman, 1986). While fragmentary, the clavicular evidence coupled with the primitive, australopith-like scapula morphology further supports an interpretation of the clavicle in *H. naledi* as being obliquely oriented.

Humerus, radius, and ulna. The head of the U.W. 101-283 humerus faces posteriorly with a torsion angle of 91.0° (Fig. 13; Table 4). A nearly complete immature humerus (U.W. 101-948; SOM section 1.3) likewise displays low torsion (105.0 °; Table 4). Fossil hominins have more posteriorly directed humeral heads (i.e., lower torsion) than observed for modern humans and great apes. *Homo naledi* fits this pattern but is exceptional in that U.W. 101-283 has the lowest humeral torsion value of any mature fossil hominin to date. The mature Dinaledi hominins also appear to have less torsion than the immature individuals, further

distinguishing this species from other fossil assemblages containing both mature and immature individuals (*A. sediba* from Malapa and *H. erectus* from Dmanisi) and extant hominoids where the opposite tendency is observed (Table 4).

All of the clavicular, humeral, radial, and ulnar diaphyses are noteworthy in their overall gracility, while also displaying prominent enthesal markings. The robusticity index of the U.W. 101-283 humerus is 0.18, which is similar to that of MH2 (0.19–0.20) and more gracile than A.L. 288-1 (0.24), modern human males (0.21 ± 0.02 , $n = 52$), and modern human females (0.20 ± 0.02 , $n = 52$; Fig. 14, Table 5). The deltoid tuberosity and m. brachioradialis crest of U.W. 101-283 are not very well-developed, but both the greater and lesser tubercles are prominent and bound a deep bicipital groove. Distally, this humerus and others (U.W. 101-466, -744, and -1240; Fig. 15, Table 3) display relatively narrow medial and lateral distodorsal pillars with septal apertures (Churchill, 1994). Medial distodorsal pillar breadth tends to be narrow relative to olecranon fossa breadth, with at least two of the *H. naledi* distal humeri (U.W. 101-283 and -466) falling just outside the range of variation for modern humans, and Dinaledi specimens all falling within the ranges of variation exhibited for the *A. sediba* specimens included in the analysis (Fig. 15). The Dinaledi humeral specimens differ in distal humeral proportions from other African *Homo* specimens, including KNM-WT 15000, Kabwe (Pycraft et al., 1928), Gombore (Gombore IB-7594; Chavallion et al., 1977), and Omo Kibish (KHS 1-30 and 1-31; Day et al., 1991).

Several radial fragments have also been recovered, including two proximal radii with at least half of the diaphysis preserved (U.W. 101-935 and -1346) and another that preserves most of the radial tuberosity (U.W. 101-070; Table 7). All of these radii display prominent, globular radial tuberosities, possibly suggestive of strong development of m. biceps brachii, as posited for *A. afarensis* (Drapeau et al., 2005) and *H. habilis sensu stricto* (OH 62 [Johanson et al., 1987] and KNM-ER 3735 [Leakey et al., 1989]). Two immature proximal

radii (U.W. 101-259 and -703) exhibit similar morphology (SOM section 1.3). Using radial neck angle as an indirect measure of radial diaphyseal curvature, the radial diaphysis of *H. naledi* appears to be straighter compared to modern humans, Neandertals, and the Sima de los Huesos hominins (Rodríguez et al., 2016), averaging 9° of angulation (Table 7). The diminished degree of diaphyseal curvature may indicate that the complex for forearm rotational precision is not present in *H. naledi* (Ibáñez-Gimeno et al., 2014). The ulnae are more fragmentary, but appear to possess straight shafts with exaggerated m. pronator quadratus crests and less pronounced styloid processes compared to modern humans, the latter suggesting enhanced ability for ulnar deviation of the hand at the wrist that is important for overhead reaching and climbing behaviors (Ward, 2007). The semilunar notch appears to be orientated more anteriorly than proximally, potentially indicating an enhanced ability for forearm flexion (Knussmann, 1967), however more complete specimens are necessary to confirm this hypothesis. The brachial index was not estimated due to the lack of complete forearm elements and no clear association of these elements with the U.W. 101-283 humerus.

Discussion and conclusions

The Dinaledi hominins display a cranially directed glenohumeral joint—much as is inferred for *Australopithecus* (Green and Alemseged, 2012; Schmid, 1983; Stern and Susman, 1983)—but with substantially lower humeral torsion than seen in *A. afarensis* (Larson, 1996), *A. africanus* (Larson, 1996), and *A. sediba* (Churchill et al., 2013).

The distal humeral proportions of *H. naledi* along with *A. sediba* appear to fall on a line with other African and two Eurasian (Skhul IV and Cro-Magnon) humeral specimens attributed to *Homo*, suggesting a positive association between olecranon fossa breadth and medial pillar thickness in these specimens (Fig. 16). The significance of this is unclear

relative to Neandertals and the Sima de los Huesos hominins. The African humeral specimens (KNM-WT 15000, Gombore IB-7594, and Kabwe, excluding *H. naledi* and *A. sediba*) plus the Skhul IV and Cro-Magnon specimens display olecranon fossa and distodorsal pillar proportions more similar to modern humans (narrower olecranon fossae and wider medial and lateral distodorsal pillars; Yokley and Churchill, 2006; Carretero et al., 2009). The *H. naledi* and *A. sediba* specimens (MH1 and MH2) fall together either outside or at the lower end of the range for modern humans, indicating relatively narrow medial pillars relative to olecranon fossa breadth (Fig. 15) and relatively thin pillars (pillar index, Table 3). Two of the Dinaledi specimens, U.W. 101-283 and U.W. 101-466, cluster with MH2, while the third Dinaledi specimen, U.W. 101-1240, falls with MH1. MH2 has been attributed to an adult female individual, while MH1 has been attributed to an immature male individual (Berger et al., 2010), raising the possibility that the observed clustering in distal humeral proportions is indicative of sexual dimorphism in the Dinaledi hominins.

While absolutely smaller, the *H. naledi* specimens appear to fit the same pattern of smaller pillar indices and wider olecranon fossae seen for Middle and Late Pleistocene African and European hominid samples (Carretero et al., 1997, 2009). The morphological and phylogenetic significance of this pattern is unclear. Carretero et al. (1997) suggest that a wide olecranon fossa in the Sima de los Huesos hominins may be related to a large olecranon process or perhaps a low cubital angle, however the Dinaledi assemblage lacks a complete and associated humerus and ulna with which to evaluate this hypothesis. MH2 (*A. sediba*) preserves both a complete humerus and ulna, and it is noteworthy that the olecranon process of MH2 is mediolaterally narrow (with a breadth of 17.3 mm; pers. obs.). The variability of relative olecranon fossa breadth in African fossil hominin populations might then suggest that these populations varied in their expression of this feature, or a wide olecranon fossa may represent a primitive retention wherein species fitting a more human-like pattern are either

closely related or ancestral to modern humans. Nevertheless, the similarity of the *H. naledi* distal humeral morphology to *A. sediba* and limited similarity with modern humans suggests a more australopith-like distal humeral morphology to match the primitive proximal humeral morphology.

The combination of extremely low humeral torsion and primitive clavicular morphology suggests that the Dinaledi scapula was positioned superiorly and laterally about a narrow upper thorax (Williams et al., 2016). Larson (2007) proposed a similar configuration for KNM-WT 15000 and the Dmanisi hominins, implying that the glenoid fossa would have to face anteriorly to meet the humeral head, while also enabling a humeroulnar joint axis of rotation in the coronal plane (Larson, 1988). Furthermore, Larson (2015) contended that such an orientation was required to maintain the sufficient amount of internal rotation required for tool use, a behavior that undoubtedly characterized this group based on manual characteristics (Kivell et al., 2015). *Homo naledi* is thus akin to early *H. erectus* in traits relating to scapular position about the thorax, but maintains primitive scapular and clavicular morphologies found in australopiths and OH 48 (*H. habilis*). With potentially short clavulae, cranially-directed glenoid fossae, and superiorly positioned scapulae, *H. naledi* closely resembles the configuration seen in *A. sediba* (Churchill et al., 2013).

Since no absolute date is currently available (but see Dembo et al., [2016] for an appraisal of the morphological date for *H. naledi* using dated Bayesian phylogenetic methods), the upper limb morphology of the Dinaledi hominins leaves open several plausible evolutionary scenarios. 1) Should the fossils date to the late Pliocene/early Pleistocene, they could represent a transitional form between the primitive shoulder girdle morphologies of more recent australopiths (as represented by *A. sediba*) and the more derived condition seen in KNM-WT 15000 and the Dmanisi hominins. 2) A more recent age for Dinaledi might indicate long term stasis of *H. erectus*-like shoulder characters, or a relatively recent

evolutionary reversal (from a modern human-like to a *H. erectus*-like shoulder configuration). 3) Alternatively, an early to mid-Pliocene date might suggest that *H. naledi* represents an early—and possibly homoplastic—departure from the ancestral shoulder condition proposed by Larson (2007), coupled with very early evidence of derived (again perhaps homoplastically) lower limb morphologies (Berger et al., 2015; Harcourt-Smith et al., 2015; Marchi et al., 2016).

In her reconstruction, Larson (2007) proposed that the dorsal position of the modern human scapula evolved from the more lateral position hypothesized for early *H. erectus* through clavicular elongation, an increase in humeral torsion, and a concomitant shift of the scapula to a more dorsal position. Larson (2007) also suggested that anterior-facing glenoid fossae would limit external rotation, and as a result, throwing capabilities. Roach and Richmond (2015a, b) contend that the early *H. erectus* (and by extension, *H. naledi*) scapula could have still been dorsally positioned, if it were situated more superiorly about the upper thorax (Williams et al., 2016), thereby allowing for development of high speed throwing proficiency. However, these positional similarities are coupled with important differences that might preclude throwing competency in *H. naledi*. Even if clavicular length is a poor predictor of throwing abilities in modern humans (Roach and Richmond, 2015a), *H. naledi* still combines a cranially-oriented glenoid fossa with primitive thoracic features, such that they did not possess the full suite of features indicated by Roach et al. (2013) that would enable a competent overarm throwing motion (Guidera et al., 1991; Ledger et al., 2005; Larson, 2007; Patel et al., 2012). Moreover, resolving with certainty the age of the Dinaledi material relative to both australopiths and early *Homo* will help clarify the importance of overarm throwing as a selective pressure influencing the evolution of the modern human shoulder.

Despite its highly derived lower limbs (Berger et al., 2015; Harcourt-Smith et al., 2015), the primitive nature of the *H. naledi* upper limb is also inconsistent with the configuration in early *H. erectus* suggested as being adapted to endurance running (Bramble and Lieberman, 2004). Modern humans are effective distance runners through a combination of derived lower limb and pelvic girdle traits, as well as low and wide shoulders, shortened forearms, narrow trunks, and a narrow and tall waist, which promotes dynamic stabilization of the trunk (via counter-rotation) to oppose the large rotational torques generated during running (Bramble and Lieberman, 2004). A high position of the Dinaledi pectoral girdle would not have facilitated counter-swinging of the upper limb and a human-like counter-rotation of the trunk or head during endurance running as suggested by Bramble and Lieberman (2004) for *H. erectus*. The combination of primitive upper limb and derived lower limb features displayed by *H. naledi* implies that the lower limb evolved without concordant selection for the upper limb and trunk features thought to support endurance running.

The morphology of the *H. naledi* lower limb is consistent with capable bipedal walking, but does not preclude climbing abilities. As described here and by Kivell et al. (2015), the *H. naledi* upper limb maintained many apelike characteristics indicative of a high degree of competency in climbing. The mosaic nature of the Dinaledi postcranial fossils provides further evidence for the hypothesis that the upper and lower portions of the modern human body plan did not evolve in concert (Sylvester, 2006; Young et al., 2010). Alternative scenarios for the course of these changes may include stabilizing selection for climbing adaptations or “phylogenetic lag” between the upper and lower limbs contributing to the retention of primitive features in this species. Nevertheless, *H. naledi* represents a hominin species where derived lower limb locomotor morphology evolved in the context of a primitive upper body plan, highlighting the necessity for further analyses of the Dinaledi fossil assemblage to clarify its place in the human lineage.

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Figure legends

Figure 1. U.W. 101-1301 partial scapula: a) dorsal aspect, b) ventral aspect, c) lateral margin, d) superior aspect (glenoid fossa on right of the image), and e) inferolateral view (glenoid fossa on right).

Figure 2. Diagnostic clavicle fragments of *H. naledi* in a) superior, b) anterior, c) inferior, and d) posterior view. U.W. 101-258 right clavicle midshaft, U.W. 101-1229 right sternal clavicle, U.W. 101-1347 left acromial clavicle.

Figure 3. U.W. 101-283 largely complete right humerus in a) anterior, b) medial, c) posterior, and d) lateral views.

Figure 4. Distal humeral specimens attributed to *H. naledi*. U.W. 101-466 right, U.W. 101-744 left, and U.W. 101-1240 right distal humeri in a) anterior, b) medial, c) posterior, and d) lateral views.

Figure 5. U.W. 101-499 right ulna diaphysis in a) anterior, b) medial, c) posterior, and d) lateral views.

Figure 6. U.W. 101-560 right proximal ulna in a) anterior, b) medial, c) posterior, and d) lateral views.

Figure 7. U.W. 101-831 right distal ulna in a) anterior, b) medial, c) posterior, and d) lateral views.

Figure 8. U.W. 101-1480 right ulna diaphysis in a) anterior, b) medial, c) posterior, and d) lateral views.

Figure 9. Radial material attributed to *H. naledi*. U.W. 101-070 right radial diaphysis, U.W. 101-935 left proximal radius, U.W. 101-1346 right proximal radius, and U.W. 101-1712 right radial diaphysis in a) anterior, b) medial, c) posterior, and d) lateral views.

Figure 10. Scapular morphology in *H. naledi*. a) Comparison of right scapulae in ventral view, from left: *Pan*, *H. naledi* (U.W. 101-1301), *A. afarensis* (A.L. 288-1 cast), *A. sediba* (MH2 3D printed scapula reconstruction including the U.W. 88-56 scapula body with the U.W. 88-103 acromion mirrored), *H. erectus* (KNM-WT 15000), and *H. sapiens*. The infraglenoid tubercles of all the specimens are aligned horizontally and the ventral “bars” are oriented at the same angle to highlight differences in glenoid fossa orientation. b) Ventral bar/glenoid angle in U.W. 101-1301 compared with fossil specimens and extant hominoids. The value used here (121.1°) is an average of multiple trials. Boxplots depict the lower quartile, median, and upper quartile, as well as minimum and maximum values, for data collected from extant species. c) Comparison of U.W. 101-1301 and A.L. 288-1 illustrating their overall similarity in size and shape. As the U.W. 101-1301 glenoid fossa is missing both its superior and inferior margins, the glenoid of A.L. 288-1 is superimposed to highlight that only small portions are missing.

Figure 11. Measurement of humeral torsion in modern humans and fossil humeri. The horizontal dashed line represents the mediolateral axis of the distal articular surface; the solid line represents the long axis of the proximal epiphysis. Humeral torsion is measured as the angle (marked in gray) between these two axes. a) Proximal view of a right modern human humerus with ends superimposed; b) Proximal view of U.W. 101-283 with ends superimposed, traced from a 3D surface scan.

Figure 12. Outline of a right radius in anterior view with neck and diaphyseal long axes illustrated. The horizontal axis indicates the point of intersection between these two axes. Radial neck angle is measured as the angle marked in gray between the neck and diaphyseal axes. Axis (a) is the long axis of the neck, (b) the long axis of the diaphysis, and (c) is the intersection of these two axes. Diagram after Martin and Saller (1957).

Figure 13. Mature humeral torsion values (degrees) in U.W. 101-283 and other fossil hominins plotted against comparative samples. Bars represent minimum and maximum values and circles the mean value for data collected from extant species.

Figure 14. Robusticity index of the U.W. 101-283 *H. naledi* humerus compared with selected fossil hominins and modern human comparative sample. Bars represent minimum and maximum values and circles the mean value for data collected from extant species.

Figure 15. Medial distodorsal pillar thickness plotted against olecranon fossa breadth in fossil and modern human specimens. Measurements in mm. Neandertal specimens are indicated by triangle markers and Sima de los Huesos specimens by square markers. The dotted ellipse represents 90% equiprobability for a pooled modern human sample comprising Aranda, San Pablo, and Hamann-Todd individuals ($n = 275$). Modified from Carretero et al. (2009).

Table 1. NISP and MNI calculations for the *H. naledi* upper limb material.

	No. individual specimens (NISP)				Minimum no. individuals (MNI)			
	Mature	Immature	Indet	Total	Mature	Immature	Indet	Total
Scapulae	8	-	3	11	4	-	2	6
Claviculae	3	1	5	9	3	1	2	6
Humeri	11	4	3	18	7	2	-	9
Ulnae	17	2	5	24	8	-	2	10
Radii	13	2	3	18	5	1	1	7
	Total NISP			80	Final MNI			10

Table 2. Comparison of selected upper limb and pectoral girdle traits in *Australopithecus* and *Homo*.

Trait	<i>A. sediba</i> ^a	<i>A. africanus</i> ^b	<i>A. afarensis</i> ^c	<i>H. floresiensis</i> ^d	<i>H. habilis</i> ^e	<i>H. naledi</i>	<i>H. erectus</i> ^f	Additional references
Scapula								
Axillary border ventral bar	Strongly developed	Strongly developed	Strongly developed	Strongly developed	NA	Strongly developed	Moderately developed	Larson et al. (2007)
Axillary sulcus position	Ventral	Ventral	Ventral	Ventral	NA	Predominantly ventral (85.8%)	Ventral	Toussaint et al. (2003); Melillo (2016)
Axillospinal angle (°)	44.4	29.8	43.1 (<i>n</i> = 2)	45.0	NA	26.8	69.6	
Ventral bar/glenoid angle (°)	131.2	126.2 (<i>n</i> = 2)	133.1 (<i>n</i> = 2)	157.0	NA	121.1	137.5	
Clavicle								
Relative length	Short	NA	NA	Short	Short	Short?	Short?	Larson et al. (2007)
Conoid tubercle morphology	Angular margin	Angular margin	Angular margin	Angular margin	Weak/absent	Prominent tubercle	Weak/absent	Drapeau et al. (2005); Larson (2007, 2013)
Mid-lateral shaft x-sectional shape	Dorsoventrally elongated oval	Dorsoventrally elongated oval	Dorsoventrally elongated oval	Rounded	Rounded	Rounded	Variably dorsoventrally elongated oval or rounded	Lovejoy et al. (1982)
Humerus								
Lesser tubercle	Prominent, more medially projecting	Prominent	Prominent, more medially projecting	NA	NA	Projecting and narrow	NA	
Deltoid tuberosity	Anterolateral position, wide with two crests	NA	Anterolateral position, wide	More lateral position	NA	Anterior position, narrow with two crests	More lateral	Hunt (1998)
Bicipital groove	Shallow and wide	Shallow and wide	Shallow and wide	Shallow and wide	NA	Narrow and deep	Shallow and wide	
Septal aperture	Present	Absent	Present	Absent	Present	Present	Absent	

Olecranon fossa	Wider and deep	Narrower and deep	Wider and deep	Wider and deep	Wider and deep	Wider and deep	Narrower and shallow	
Supracapitular fossa	Moderate to deep	Moderate	Moderate	NA	Moderate to deep	Moderate to deep	Shallow	
Humeral torsion (°)	117.0	126.0	124.0	115.0	NA	91.0	110.0	
Ulna								
Supinator crest	Moderate	Moderate	Weak	Moderate	NA	Rounded, length indet.	Pronounced	
Interosseous crest shape	Weak	Weak	Moderate	Weak	Weak	Rounded		Johanson et al. (1987); Larson et al. (2009)
Radius								
Neck angle (°)	10.4	14.9	12.4	7.7	NA	9.0 ($n = 2$)	NA	
Radial tuberosity position	Medial	Medial	Medial	Medial	Medial	Medial	Medial?	Drapeau et al. (2005); Larson et al. (2009)
^a As represented by MH1 and MH2. ^b As represented by Sts 7, Sts 14, StW 25, StW 88, StW 99, StW 102, StW 181, StW 311, StW 347, StW 358, StW 363, StW 389, StW 392, StW 403, StW 431, StW 443, StW 479, StW 486, StW 501, StW514, StW 522, StW 527, StW 573, and StW 598. ^c As represented by A.L. 288-1, A.L. 333-6, A.L. 333-9a, A.L. 333-9b, A.L. 333X-6/9, and KSD-VP-1/1. ^d As represented by LB1/5, LB1/50, LB1/51, LB1/52, LB2/1, LB3, LB4/1, LB6/2, and LB6/4. ^e As represented by OH 48 and OH 62. ^f Early <i>H. erectus</i> (<i>ergaster</i>) represented by KNM-WT 15000 and D4166, D4161, D4162, D4507, D2715, D2680, D3160, and D2724.								

Table 3. Humeral dimensions (mm) in *Homo naledi* and comparative material.^a

	U.W. 101-283	U.W. 101-466	U.W. 101-744	U.W. 101-1240	MH1	MH2	A.L. 288-1	KNM- WT 15000	<i>H. sapiens</i> (female, <i>n</i> = 52) ^g	<i>H. sapiens</i> (male, <i>n</i> = 52) ^g	<i>Gorilla</i> (<i>n</i> = 20)	<i>Pan</i> (<i>n</i> = 23)
Humeral maximum length	256.0	-	-	-	248.0	269.0	236.8 ^e	319.0	294.2 (12.9)	323.5 (16.8)	420.4 (41.2)	283.5 (14.7)
Humeral head SI diameter	30.2	-	-	-	34.5	32.3	26.8 ^e	29.2	37.9 (2.1)	43.3 (2.7)	57.17 (7.8)	39.5 (2.49)
Humeral head ML diameter	26.4	-	-	-	28.4	28.1	31.1 ^e	34.1	36.5 (1.7)	40.9 (1.9)	50.5 (8.8)	32.3 (2.1)
Humeral head index ^b	114.6	-	-	-	121.5	115.1	116.0	85.6	103.9 (4.5)	105.7 (4.2)	113.8 (5.3)	122.6 (7.5)
Humeral midshaft circumference	48.4	-	-	-	55.5	55.0	-	55.0 ^f	-	-	97.4 (18.3)	74.8 (5.8)
Humeral minimum circumference	47.5	-	-	-	50.0	51.0	57.0	-	59.5 (4.3)	66.4 (4.6)	-	-
Maximum midshaft diameter	16.8	-	-	-	19.0	15.5	-	-	19.7 (1.4)	22.0 (1.7)	-	-
Minimum midshaft diameter	13.3	-	-	-	13.7	15.9	-	-	15.1 (1.6)	17.4 (1.4)	-	-
Medial pillar breadth	6.9	7.3	-	8.6	9.6	7.7	-	11.8	-	-	-	-
Lateral pillar breadth	12.9	13.6	-	11.6	14.9	14.1	-	17.3	-	-	-	-
Olecranon fossa breadth	19.2	19.6	22.0	22.7	23.6	19.6	-	21.0	-	-	-	-
Pillar index ^c	53.5	53.4	-	74.2	64.4	54.6	-	68.2	-	-	-	-
MPB/OFB ^d	36.0	37.1	-	38.0	40.7	39.3	-	56.2	-	-	-	-

^a Standard deviation values are presented in parentheses for the extant groups.^b Humeral head index calculated as (humeral head SI diameter/humeral head ML diameter)*100^c Pillar index calculated as medial pillar breadth/lateral pillar breadth^d MPB/OFB = Medial pillar breadth/olecranon fossa breadth^e Data from Johanson et al. (1982)^f Data from Richmond et al. (2002)^g Collected from the Raymond A. Dart Collection, University of Witwatersrand, South Africa.

Table 4. Humeral torsion values (degrees) in fossil hominins and extant hominoids.^a

Species	Mature	Immature
<i>Homo naledi</i> (U.W. 101-283)	91.0°	-
<i>Homo naledi</i> (U.W. 101-948)	-	105.0°
<i>H. erectus</i> (KNM WT15000) ^b	-	111.5°
<i>H. erectus</i> (D4167) ^c	110.0°	-
<i>H. erectus</i> (D2680) ^c	-	104.0°
<i>H. floresiensis</i> (LB1) ^b	115.0°	-
<i>A. sediba</i> (MH1) ^d	-	112.0°
<i>A. sediba</i> (MH2) ^d	117.0°	-
<i>A. afarensis</i> (A.L. 288-1)	124.0°	-
<i>A. africanus</i> (STS7) ^c	126.0°	-
<i>A. boisei</i> (KNM-ER 739) ^c	111.0°	-
<i>H. sapiens</i> ^f	144.1° (SD 6.5°, <i>n</i> = 20)	137.1° (SD 8.5°, <i>n</i> = 50)
<i>P. troglodytes</i> ^g	139.0° (SD 6.7°, <i>n</i> = 7)	136.4° (SD 13.3°, <i>n</i> = 44)
<i>G. gorilla</i> ^g	150.0° (SD 9.8°, <i>n</i> = 5)	152.3° (SD 12.1°, <i>n</i> = 44)
<i>P. pygmaeus/abelii</i> ^d	135.0° (SD 6.5°, <i>n</i> = 5)	138.4° (SD 7.5°, <i>n</i> = 9)
<i>H. lar</i> ^d	116.6° (SD 8.1°, <i>n</i> = 11)	118.0° (SD 6.9°, <i>n</i> = 10)
^a Standard deviation values are presented in parentheses for the extant groups. ^b Data from Larson et al. (2007) ^c Data from Lordkipanidze et al. (2007) ^d Data from Churchill et al. (2013) ^e Data from Larson (1996) ^f Collected from specimens at the Raymond A. Dart Collection, University of Witwatersrand, South Africa. ^g Collected from specimens at the American Museum of Natural History, Cleveland Museum of Natural History, and Anthropological Institute and Museum, University of Zürich.		

Table 5. Relative humeral shaft size as measured by the robusticity index.^a

Species	HML ^b	HMinC ^c	RI ^d
<i>Homo naledi</i> (U.W. 101-283)	256	47	0.1835
<i>A. sediba</i> (MH1)	248	50	0.2016
<i>A. sediba</i> (MH2)	269	51	0.1895
<i>A. afarensis</i> (AL 288-1)	236.8 ^e	57	0.2405
<i>H. sapiens</i> (female, $n = 52$) ^f	294.2 (12.9)	59.5 (4.3)	0.2027 (0.2)
<i>H. sapiens</i> (male, $n = 52$) ^f	323.5 (16.8)	66.4 (4.6)	0.2055 (0.2)
^a Standard deviation values are presented in parentheses for the extant groups. ^b HML: Humeral maximum length ^c HMinC: Humeral minimum circumference ^d RI = Robusticity index calculated as (HMinC/HML) ^e Data from Johanson et al. (1982); ^f Collected from the Raymond A. Dart Collection, University of Witwatersrand, South Africa.			

Table 6. Dimensions of ulnar specimens attributed to *H. naledi*.^a

	U.W. 101-831	U.W. 101-560	U.W. 101-499
Coronoid process maximum ML diameter ^b	-	13.9	-
Semilunar notch height ^c	-	16.1	-
Olecranon length ^d	-	13.0	-
Radial notch SI breadth	-	9.4	-
Radial notch AP breadth	-	11.2	-
Midshaft ML diameter	-	-	10.8
Midshaft AP diameter	-	-	11.2
Ulna midshaft circumference	-	-	34.8
Distal minimum circumference ^e	28.0	-	29.0
Maximum diameter ^f	9.7	-	9.3
Distal AP diameter ^g	14.7	-	12.2
Ulna head depth ^h	7.2	-	-
Styloid ML breadth ⁱ	4.0	-	-
Styloid projection ^j	2.0	-	-
^a All measurements are in millimeters (mm). ^b Coronoid process maximum mediolateral diameter, measured from the proximal margin of the radial notch to the medial margin on the coronoid process ^c Semilunar notch height or the minimum distance between the anterior projections of the coronoid and olecranon processes ^d Olecranon length, as measured from the midpoint of the semilunar notch to the proximal olecranon ^e Distal minimum circumference measured inferior to the pronator quadratus crest ^f Maximum diameter measured at the level of maximum development for the pronator quadratus crest ^g Anteroposterior diameter of the distal epiphysis including the styloid process ^h The depth of the head of the ulna anteroposteriorly and excluding the styloid process and non-articular area ⁱ Breadth of the styloid process measured mediolaterally at the tip ^j Projection of the styloid process beyond the articular surface of the ulnar head			

Table 7. Dimensions of radial specimens attributed to *H. naledi*.^a

	U.W. 101-070	U.W. 101-935	U.W. 101-1346	U.W. 101-703	U.W. 101-259
Radial head-neck length	-	19.1	17.7	-	-
Anteroposterior (AP) head diameter	-	19.3	-	-	-
Mediolateral (ML) head diameter	-	17.6 (approx.)	17.4	-	-
Capitular fossa AP breadth	-	13.8	-	-	-
Capitular fossa ML breadth	-	14.1	-	-	-
Capitular fossa depth	-	2.0	-	-	-
Radial tuberosity length ^b	-	20.1	21.6	17.3	17.6
Radial tuberosity breadth ^c	-	12.4	13.2	8.3	8.9
Radial neck AP diameter	-	12.0	17.7	8.0	8.2
Radial neck ML diameter	-	10.6	10.6	7.7	7.6
Neck circumference	-	36.0	35.0	26.0	26.0
Minimum shaft diameter ^d		10.5	9.5	7.1	7.2
Minimum shaft circumference ^e	35.0	-	30.5	-	-
Neck angle	-	12.3	7.3	-	-
AP midshaft diameter	-	10.5	-	-	-
ML midshaft diameter	-	12.0	-	-	-
^a All measurements are in millimeters (mm). ^b Radial tuberosity length measured proximodistally. ^c Radial tuberosity breadth measured mediolaterally. ^d Minimum shaft diameter measured inferior to the radial tuberosity. ^e Minimum shaft circumference measured inferior to the radial tuberosity.					

Table 8. Mean scapular angle values in extant hominoids and fossil hominins.^a

Species	Ventral bar / glenoid angle	Axillospinal angle
<i>Homo naledi</i> (U.W. 101-1301)	121.1°	26.8°
<i>H. erectus</i> (KNM-WT 15000)	137.5°	69.6°
<i>H. floresiensis</i> (LB1) ^b	157.0°	45.0°
<i>A. sediba</i> (MH2) ^c	131.2°	44.4°
<i>A. afarensis</i> (A.L. 288-1)	132.2°	38.2°
<i>A. afarensis</i> (KSD VP-1/1) ^d	132.7°	48.0°
<i>A. africanus</i> (Sts 7)	128.0°	29.8°
<i>A. africanus</i> (StW 162)	124.3°	-
<i>H. sapiens</i> (<i>n</i> = 109)	142.4° (5.5°)	45.6° (5.3°)
<i>P. troglodytes</i> (<i>n</i> = 110)	127.9° (4.5°)	22.8° (4.3°)
<i>G. gorilla</i> (<i>n</i> = 140)	130.2° (5.5°)	30.1° (4.2°)
<i>P. pygmaeus/abelii</i> (<i>n</i> = 55)	131.4° (6.4°)	35.0° (5.9°)
<i>Hylobates</i> sp. (<i>n</i> = 194)	121.1° (5.2°)	10.1° (4.2°)
^a Standard deviation values are presented in parentheses for the extant groups.		
^b Data from Larson et al. (2009)		
^c Measured from a 3D digital printout of the MH2 scapula, following methods reported in Green and Alemseged (2012) and Green (2013), which slightly differs from the approach taken in Churchill et al. (2013).		
^d Data from Melillo (2011). All other comparative and fossil data collected by D.J.G.		

Figure 1. U.W. 101-1301 scapula

Figure 2. Clavicle fragments

Figure 3. U.W. 101-283 humerus

Figure 4. Humeral specimens

Figure 5. U.W. 101-499

Figure 6. U.W. 101-560 ulna

Figure 7. U.W. 101-831 ulna

Figure 8. U.W. 101-1480 ulna

Figure 9. radial fragments

Figure 10. Scapula angles

a

b

c

Figure 11. Humeral torsion angles

Figure 12. Radial neck angle

Figure 13. Humeral torsion comparison

Figure 14. Robusticity index

Figure 15. Medial pillar thickness