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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*.

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1. 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 claviculae, 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

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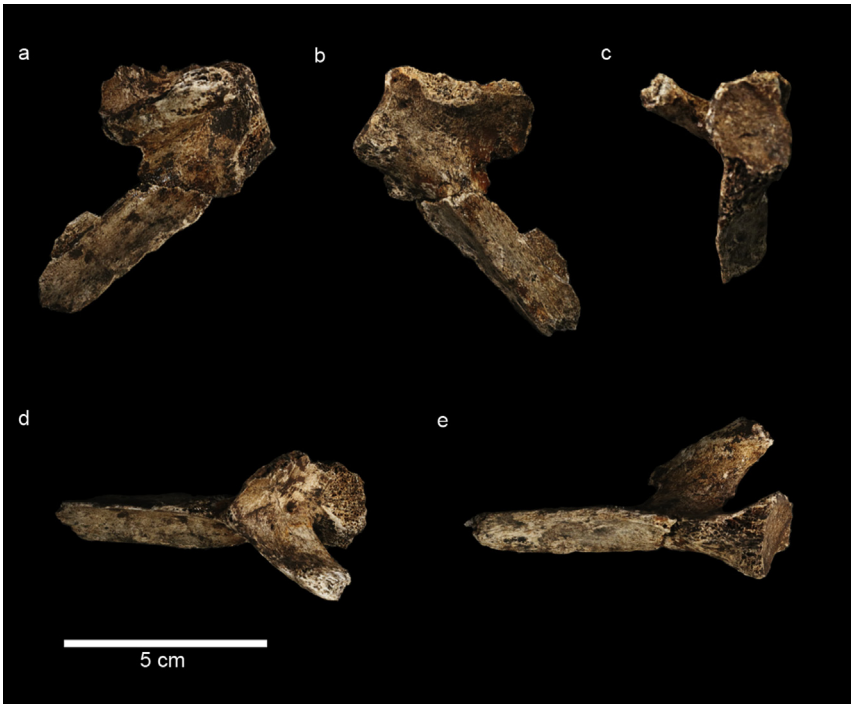

Figure 1. U.W. 101-1301 partial scapula: a) dorsal aspect, b) ventral aspect, c) lateral margin, d) superior aspect (glenoid fossa on right of the image), and e) inferolateral view (glenoid fossa on right).

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.

claviculae. The 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 (Voisin, 2001, 2004, 2006a, b, 2008; Larson, 2007), 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 claviculae, 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 claviculae that lie predominately in the transverse plane, dorsally-positioned scapulae with laterally-oriented glenoid fossae, and humeri with high torsion (Larson, 2007).