

The shoulder girdle of *Homo naledi*

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Introduction

Since the discovery of *H. naledi* in South Africa more than 2000 specimens have been recovered from two chambers (Dinaledi and Lesedi) in the Rising Star system (Berger et al., 2015; Hawks et al., 2017). *H. naledi* is an enigmatic species mostly because of its unusual distribution of derived and archaic traits but also because of its young geological age (236 - 335 ka; Dirks et al., 2017).

Thus far 12 clavicles and 15 scapulae have been recovered from the two chambers. Of the 15 scapulae unearthed none are complete and most are limited to the lateral border. The clavicles are better preserved, and one is nearly complete. This work focuses on the two best preserved remains (Fig. 1), U.W. 101-1301 and U.W. 102a-021, to better place *H. naledi* in its comparative context and shed more light on its locomotor repertoire.

Materials and methods

Ventral bar / glenoid angle (VbG angle) was measured to determine the orientation of the scapular glenoid cavity. An acute angle, or cranial orientation of the glenoid cavity, indicates a shoulder adapted to overhead reaching and climbing (Voisin, 2015 for a review). Clavicular length, robusticity and curvatures (in dorsal and superior views) were measured using Olivier's method as these metrics are linked to upper limb movements and shoulder architecture (Voisin, 2006). Clavicle length is correlated to both stature and upper thorax breadth and thus scapula position.

Results

***VbG Angle:** U.W. 101-1301 falls within the *Hylobates* distributions, indicating that these species display the most cranial glenoid cavity (Fig. 2).

***Clavicle Length:** U.W. 102a-021 clavicle is absolutely short (no associated complete humerus was present to determine relative length), corresponding to the lowest *P. paniscus* values and the MH2 (*A. sediba*) right clavicle (Fig. 3). This indicates that the upper thorax of *H. naledi* is likely narrow and the scapula positioned higher than human and similar to the conditions in apes (Voisin, 2010).

***Clavicle Curvatures:** In superior view, curvatures fall within the Hominoid distribution, indicating that U.W. 102a-021 displays a classical S-shaped morphology. This morphology increases muscle power during arm elevation (Voisin, 2006). Contrastingly U.W. 102a-021 also displays two curvatures in dorsal view falling within the ranges of the two *Pan* species (Fig. 4). This morphology is associated to a high scapula relative to the thorax (Voisin, 2006).

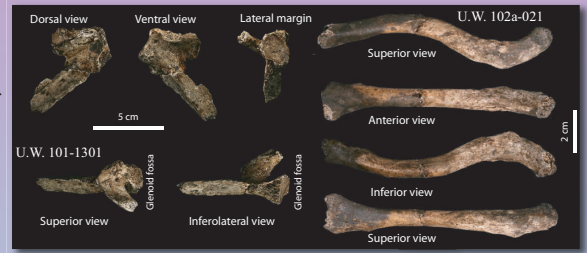


Figure 1 : *Homo naledi* right scapula and clavicle, after Feuerriegel et al. (2017, in prep)

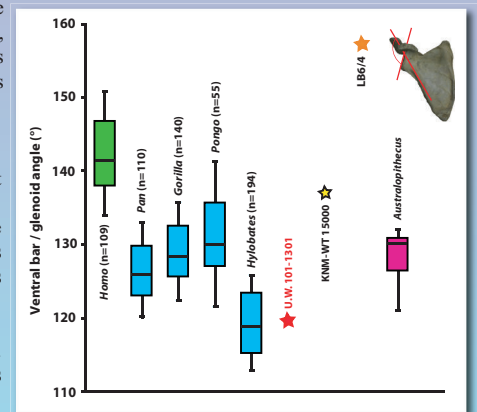


Figure 2: Variation of the VbG angle. *Australopithecus* includes *A. africanus* (Sts 7; Stw 162), *A. afarensis* (A.L. 288-1; KSD VP-1/1) and *A. sediba* (MH2). *Homo* corresponds to current humans. (after Feuerriegel et al., 2017).

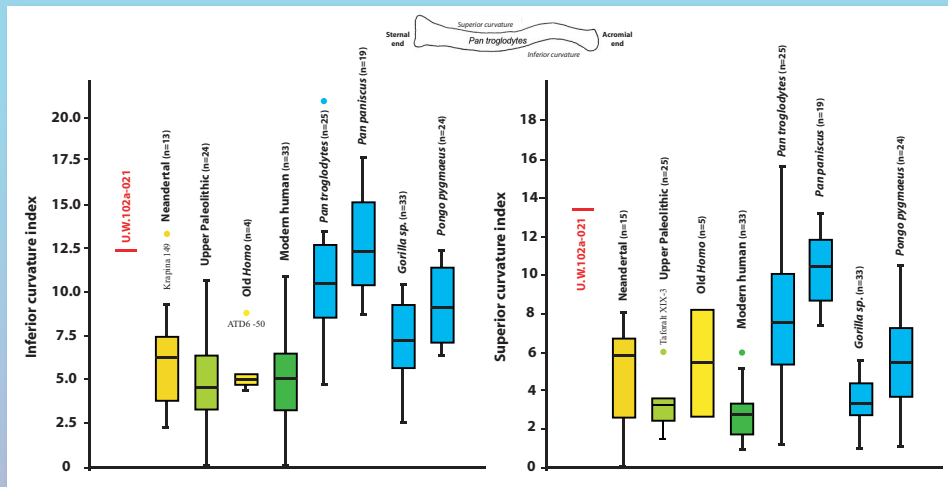


Figure 4: Clavicle curvatures in dorsal view. Within modern humans, only individuals displaying a superior curvature are taken into account (35%). This curvature includes type II and III, the last one exhibited only by *Homo* species (Voisin, 2006).

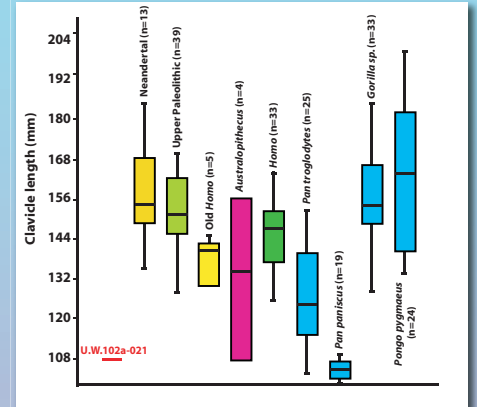


Figure 3 : Absolute length of the clavicle within extant Hominoids and different *Homo* species. *Australopithecus* includes *A. afarensis* (AL333x-6/9, KSD-VP-1-1F, STW 431) and *A. sediba* (MH2). *Homo* corresponds to current humans.

Discussion and conclusion

Table 1: Clavicle morphologies and shoulder architectures within genus *Homo*. **Lateral:** the scapula is more laterally placed than in modern human. **Dorsal:** the scapula is dorsally placed like in modern human.

Clavicular curvatures (Posterior view)	Group 1		Group 2
	Two curvatures		One curvature (or two but slightly pronounced)
Clavicle length	Group 1a	Group 1b	Long
Scapula position (in regard to the thorax)	Short	long	Long
	High	High	Low
	Lateral	Dorsal	Dorsal
<i>Homo</i> species	<i>Homo habilis</i> , <i>Homo ergaster</i> <i>Homo georgicus</i> <i>Homo naledi</i>	Neanderthal <i>Homo antecessor</i>	Modern human (including Upper Paleolithic remains)

A high scapula is associated with a cranial orientation of the glenoid cavity and is necessary for habitual use of the upper limbs in overhead positions (Voisin, 2006; Voisin et al., 2014). The narrow upper thorax and the less dorsal scapula of *H. naledi* fit well with extant apes and early Pleistocene *Homo* shoulder architectures (Voisin, 2010, Table 1), though the latter group display a glenoid cavity that is more laterally than cranially oriented revealing another peculiarity of *H. naledi* (Feuerriegel et al., in prep).

The shoulder girdle remains of *H. naledi* demonstrate continued relevance of climbing behaviours in the locomotion of this species contrasting with other, presumably more terrestrial, members of the genus *Homo* (Berger et al., 2015). Given that *H. naledi* was discovered in a cave system, rock climbing may have comprised a significant portion of this behaviour. The similarity of the *H. naledi* elbow and shoulder morphology to several species of australopithecines implies stabilising selection for traits favouring climbing behaviours for at least one lineage within the genus *Homo* (Feuerriegel et al., in prep).

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