Evolutionary development of the *Homo antecessor* scapulae (Gran Dolina site, Atapuerca) from a 3D geometric morphometrics approach

Daniel García-Martínez[1,2,3], **David Green**[4], **José María Bermúdez de Castro**[1]

1 - Centro Nacional para el Estudio de la Evolución Humana (CENIEH), Burgos, Spain · 2 - Departamento de Paleobiología, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain · 3 - Centro de Estudios del Campo de Montiel (CECM), Castilla - La Mancha, Spain · 4 - Department of Anatomy, Campbell University School of Osteopathic Medicine, Buies Creek, USA.

The study of scapular morphology has had an important impact on the study of human evolution from both functional and phylogenetic perspectives [1]. Moreover, it is critical to understand scapular ontogeny (growth and development), since evolution occurs via genetically conserved developmental variations. This issue has been well-documented in the scapular morphology of extant primates, but the scarcity of the scapular fossil record poses a serious challenge to understanding the scapular ontogeny of extinct hominins. Recently, two well-preserved, 800ky scapulae from Atapuerca attributed to Homo antecessor were described: ATD6-116 is purported to have been a young child, whereas ATD6-118 is thought to have been an adolescent [2]. This material provides a unique opportunity to investigate shoulder girdle evolution and address growth and development trajectories in a Lower Pleistocene human species. To evaluate the ontogenetic trend of *H. antecessor*, we investigated scapular morphology in a sample of 98 *Pan troglodytes* and 108 *Homo sapiens* from ontogenetic stage 1 (deciduous teeth not fully erupted) to stage 7 (full permanent dentition). We also compared the ATD6 scapulae with the scapulae from Dikika [3, 4](*Australopithecus afarensis*; similar in age to ATD6-116), Nariokotome (*H. ergaster*; close in age to ATD6-118), and Malapa [5](MH2, A. sediba; adult female). Missing data estimation, when necessary, was carried out through a partial least squares approach following previously suggested protocols. We performed a Procrustes analysis to derive novel shape variables, which were regressed against centroid size to derive the slope of the different ontogenetic shape trajectories. ATD6-116 is slightly larger than the Dikika scapula, and both are between developmental groups 2 and 3 of *Homo* and *Pan*. ATD6-118 is about the same size as MH2 and slightly smaller than Nariokotome. Developmentally, *P. troglodytes* and *H. sapiens* differed in both their regression scores and slope of their trajectories. *P. troglodytes* had the highest positive regression scores, relating to relatively narrow scapulae with a more cranial orientation of the glenoid fossa and the acromion. Alternatively, *H. sapiens* had more negative regression scores, with mediolaterally broader scapulae and laterally oriented glenoid fossae. Both *H. antecessor* and *Australopithecus* trajectories present slightly more positive values than modern humans, but are distinct from *P. troglodytes* of the same size with an ontogenetic trajectory closer to that of humans, both in terms of distance and slope (*P. troglodytes*=0.0013; *H. sapiens*=0.0018; *Australopithecus*=0.0021; *H. antecessor*=0.0021). The fact that both fossil hominin taxa share a similar ontogenetic trajectory to one another and modern humans suggests that scapular development in *Australopithecus* and *H. antecessor* was already modern human-like – though, importantly, there are several morphological features that distinguish them from modern humans along the entire trajectory. We also note that the *Australopithecus* specimens studied here (DIK-1-1 and MH2) are assigned to different species and span an expansive range of chronology and geography. Accordingly, validation of this trajectory will require the inclusion of additional specimens (e.g., the adult *A. afarensis*, KSD-VP-1/1 or the juvenile MH1 *A. sediba*). All told, the preservation of two fairly complete, subadult scapulae, likely belonging to the same Lower Pleistocene population, provides a unique opportunity to study evolutionary development of the hominin shoulder girdle. We purport that by ~800ky, archaic hominin shoulder development was already trending towards that of modern humans.

Acknowledgments: Ministerio de Ciencia, Innovación y Universidades funded this research through the project PGC2018-093925-B-C31 and "Juan de la Cierva Formación" program FJCI-2017-32157. Field seasons are supported by the Consejería de Cultura y Turismo of the Junta de Castilla y León and the Fundación Atapuerca.

References: [1] Young, N. M. Function, ontogeny and canalization of shape variance in the primate scapula. J. Anat. 209, 623–636 (2006). [2] de Castro, J. M. B. et al. A descriptive and comparative study of two Early Pleistocene immature scapulae from the TD6. 2 level of the Gran Dolina cave site (Sierra de Atapuerca, Spain). J. Hum. Evol. 139, 102689 (2020). [3] Melillo, S. M. An alternative interpretation of the Australopithecus scapula. Proc. Natl. Acad. Sci. 112, E7159–E7159 (2015). [4] Green, D. J. & Alemseged, Z. Scapular Ontogeny, Function, and the Australopithecus afarensis. Proc. Natl. Acad. Sci. USA 109, 11746 (2012). [5] Churchill, S. E. et al. The Upper Limb of Australopithecus sediba. Science. 340, (2013).