Adult Neandertal clavicles from the El Sidrón site (Asturias, Spain) in the context of *Homo* pectoral girdle evolution

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ABSTRACT

We undertook a three-dimensional geometric morphometric (3DGM) analysis on 12 new Neandertal clavicle specimens from the El Sidrón site (Spain), dated to 49,000 years ago. The 3DGM methods were applied in a comparative framework in order to improve our understanding of trait polarity in features related to *Homo* pectoral girdle evolution, using other Neandertals, *Homo sapiens*, *Pan*, ATD6-50 (*Homo antecessor*), and KNM-WT 15000 (*Homo ergaster/erectus*) in the reference collection. Twenty-nine homologous landmarks were measured for each clavicle. Variation and morphological similarities were assessed through principal component analysis, conducted separately for the complete clavicle and the diaphysis. On average, Neandertal clavicles had significantly larger muscular entheses, double dorsal curvature, clavicle torsion, and cranial orientation of the acromial end than non-Neandertal clavicles; the El Sidrón clavicles fit this pattern. Variation within the samples was large, with extensive overlap between *Homo* species; only chimpanzee specimens clearly differed from the other specimens in morphometric terms. Taken together, our morphometric analyses are consistent with the following phylogenetic sequence. The primitive condition of the clavicle is manifest in the cranial orientation of both the acromial and sternal ends. The derived condition expressed in the *H. sapiens* + Neandertal clade is defined by caudal rotation of both the sternal and acromial ends, but with variation in the number of acromia remaining in a certain cranial orientation. Finally, the autapomorphic Neandertal condition is defined by secondarily acquired primitive cranial re-orientation of the acromial end, which varies from individual to individual. These results suggest that the pace of phylogenetic change in the pectoral girdle does not seem to follow that of other postcranial skeletal features.

Key words: *H. neanderthalensis*, clavicle morphology, geometric morphometrics, trait polarity.

Introduction

Clarifying whether the features frequently observed in Neandertal populations originated in the last common ancestor of Neandertals and *Homo sapiens* or only in the lineage leading to Neandertals (since divergence) may provide insight into morphofunctional evolution in Pleistocene hominins. Many derived features in the postcranial skeleton may be morphological consequences of body-form divergences; pelvis breadth, thorax shape, and the pectoral girdle seem to be involved in these divergences in one way or another. The Neandertal torso is large and deep (Bastir et al., 2015), traditionally perceived as a body form specialized for cold weather (Vandermeersch and Trinkaus, 1995; Churchill, 1996). The upper thorax of modern humans differs in shape from that of Neandertals, which shows more anteriorly projecting upper ribs during inspiration (Bastir et al. 2015). This in turn implies a reconfigured spatial arrangement of the pectoral girdle. In this context, analysis of the 3D configuration of the clavicle through three-dimensional geometric morphometric (3DGM) analysis may help characterize variations in form and elucidate its potential covariation with other elements of the pectoral girdle.

Clavicle length is one of the characteristics that originally enabled researchers to distinguish Neandertal anatomy from that of anatomically modern humans (Boule, 1911; Churchill, 1994; Holliday, 1997; Larson, 2013; see Trinkaus et al., 2014 for a complete review). Supposedly, a long clavicle allows for a broad thorax. As a consequence of an enlarged chest, Vandermeersch and Trinkaus (1995) and Churchill (1996) suggested that Neandertal scapulae were positioned more laterally, with a horizontal scapular spine and a distinctive axillary-border morphology, and with their tall and narrow glenoid fossae (Churchill and Trinkaus, 1990) more anteriorly directed. Later, Larson (2007) suggested that the relatively long clavicles of Neandertals were also products of large chest size, as they were needed to bridge the longer distance from the sternum to the acromion. A distinctive scapulo-humeral joint shape has also been reported (Carretero et al., 1997; Lari et al., 2015). Nonetheless, Trinkaus et al. (2014) recently downplayed this evidence on the basis that relative clavicle length, appropriately scaled to body mass, maintains a constant relationship across species of the genus *Homo (sensu stricto)*, and thus paleobiological inferences based on the study of clavicle length should be avoided.

In contrast, other experts have determined that in addition to the size of the clavicle, its shape discriminates among groups of *Homo*. Independent of length, clavicle morphology potentially yields insight into *Homo* paleobiology and evolution. For instance, Voisin (2004) stated that the

Neandertal clavicle reflects the special architecture of the Neandertal shoulder, which is characterized by a high scapula in relation to the thorax. In a broader context, clavicular curvature on the dorsal view is related to shoulder position (Voisin, 2001, 2004, 2006, 2008, 2010). The vast majority of hominin species (except *H. sapiens*) normally exhibit clavicles with two curvatures on the dorsal view: one inferior, at the lateral extremity, and one superior, at the medial extremity. The morphology of these type-II clavicles is related to a scapula that is positioned high relative to the rib cage. By contrast, most modern humans harbor clavicles with a single curvature (type I) due to the low position of the scapula in relation to the thorax (Voisin, 2001, 2004, 2008, 2010); 75% of Neandertal clavicles are type II, but this morphology appears in only 15% of modern human clavicles (Voisin, 2001).

The collarbone also displays a morphological characteristic that is rarely mentioned in the literature: clavicular twist (Ashton and Oxnard, 1964; Oxnard, 1984; Aiello and Dean, 1990). This twist is defined by the line of the anterior border and is related to the orientation of the acromial end (Oxnard, 1984). Generally, modern humans exhibit low torsion, while non-human hominoids and other primates present a cranially oriented acromial end (Oxnard, 1984; Aiello and Dean, 1990). Such torsion is also evident in the hominin fossil record (Oxnard, 1984; Carretero et al., 1999; Churchill, 2013), together with a diaphysis twist that is marked in some Neandertals (Vandermeersch and Trinkaus, 1995; Carretero et al., 1997).

The shape of the midshaft cross section is also relevant to the morphological evolution of the human clavicle. Hominin species preceding *H. sapiens* exhibit an elliptical midshaft cross section with a low midshaft index (<80 ; $\text{minimum diameter}/\text{maximum diameter} \times 100$); these clavicles have been designated as platycleidic (Carretero et al., 1997, 1999). In contrast, in modern humans, the cross section at midshaft is circular, with mesocleidic morphology and a midshaft index of 80 – 120 (McCown and Keith, 1939; Trinkaus, 1983; Carretero et al., 1997, 1999). It has been reported that 88% of *Homo neanderthalensis* clavicle fossils present a flattened diaphysis. In most cases, this flattening is dorsoventral (Vandermeersch and Trinkaus, 1995; Carretero et al., 1997, 1999), but some craniocaudal examples have been described that are consistent with the elliptical cross section reported for Neandertals (Trinkaus, 1983; Vandermeersch and Trinkaus, 1995; Carretero et al., 1997, 1999; Mersey et al., 2013).

Despite large variations in clavicle dimensions, the anatomy of isolated clavicles seems to indicate systematic differences among *Homo* species. However, the phylogenetic pattern of this variation remains largely unexplored. Three-dimensional (3D) geometric morphometric

analysis of the clavicle as part of the pectoral girdle may shed new light onto this problem. Discovery of new, well-preserved clavicle remains from the ~49 ka (thousands of years old) El Sidrón site (Northern Spain) (Rosas et al., 2006, 2012) encouraged us to use a comparative framework to explore several questions. Do the new El Sidrón clavicle remains fit the characteristic form of Neandertal clavicles? Are there significant differences in clavicle size and shape between Neandertals and modern humans? If so, which features provide information about classification and what is the phylogenetic trait polarity of these features? Although we recognize the difficulty in establishing functional relationships through the study of isolated anatomical elements, we sought to evaluate these features in the context of the evolution of the *Homo* pectoral girdle. Thus, this investigation evaluated the new Neandertal clavicles from El Sidrón site in comparison with samples of Neandertal, modern human, and chimpanzee clavicles and ATD6-50 (*Homo antecessor*) and KNM-WT 15000 (*Homo ergaster/erectus*) specimens. Using 3DGM methods complemented with classic measurements, we sought to determine the main form differences among clavicles from human species in order to improve our understanding of trait polarity in features related to *Homo* pectoral girdle evolution. Identification of so-called “Neandertal features” in European Lower Pleistocene populations, particularly those attributed to *H. antecessor* from TD6 (Atapuerca), has renewed interest in trait polarity (Martínón et al., 2007; Bermúdez de Castro et al., 2015; Gómez-Robles et al., 2015). Determining which of these features are uniquely derived (autapomorphies) and which are inherited from previous ancestors (Bermúdez de Castro et al., 2012, 2015; Rosas et al., 2015) is a key issue in the resolution of the *Homo* evolutionary model.

Material and methods

The El Sidrón site

El Sidrón is a karst system located in Asturias, Spain (Fortea et al., 2003; Rosas et al., 2006; de la Rasilla et al., 2011). Since 2000, samples ~49 ka have been recovered from this site (Wood et al., 2013), constituting the most complete Neandertal sample from the Iberian Peninsula (Rosas et al., 2006, 2012). The remains were in a secondary position; the original deposit, worn out by erosion, is thought to have been either on the surface or in an upper karst level (Fortea et al., 2003). All skeletal parts are preserved, and there is a moderate occurrence of Middle Paleolithic stone tools at the site (Rosas et al., 2006; Santamaría et al., 2010). The remains of at least 13 individuals were present at the site: one infant, two juveniles, three adolescents, and seven adults (Rosas et al., 2012, 2013).

Conservation and inventory of the clavicle material

A total of 12 clavicle fragments have been recovered from the El Sidrón site, representing eight clavicles: five left and one right adult clavicles, one indeterminate fragment and two clavicles from juvenile 1 (Rosas et al., 2013) which were not included in the current analysis (Table 1), as only the adult specimens were considered. The diaphysis, together with the acromial end, is the most represented component.

Comparative sample

Our comparative sample included a *H. sapiens* collection with known ages and sexes from Palencia (Spain) (see Rosas et al., 2015 for further details) (Table 2). The comparative sample also included *Pan troglodytes* clavicles housed at the University of Valladolid (Spain), the National Museum of Natural Sciences (Madrid, Spain) and the Digital Morphology Museum, KUPRI (Table 2). Fossil specimens included original Krapina fossils (142, 143, 146, right; 153 and 154 left), scientific-quality casts of Neandertals from Feldhofer (right) and La Ferrassie 1 (right and left) as well as ATD6-50 (*H. antecessor*, right) and KNM-WT 15000 (*H. ergaster/erectus*, right). Virtual reconstructions of Regourdou 1 (right and left, from NESPOS), Shanidar 1 (left, from casts), and Kebara 2 (right and left, from casts) clavicles were also studied.

Linear measurements

Data on classic collarbone measurements were taken from the published literature (Heim, 1974; Trinkaus, 1983; Vandermeersch and Trinkaus, 1995; Carretero et al., 1997, 1999). These measurements included maximum length, midshaft circumference (for estimation of the robusticity index as $[\text{midshaft circumference}/\text{maximum length}] \times 100$), and maximum and minimum midshaft diameters (for calculation of the midshaft index as $[\text{minimum midshaft diameter}/\text{maximum midshaft diameter}] \times 100$).

Morphometric analyses

Three dimensional geometric morphometric techniques were employed for most analyses. For each complete clavicle, 29 homologous landmarks were recorded (Table 3 and Figure 1) with a MicroScribe device on modern species, original fossils, and fossil casts. Amira software (Stalling et al., 2005) was used for landmark acquisition on virtual specimens. Intra-observer error was determined for the two digitization techniques by measuring *H. sapiens* clavicle EV-4 five times with the MicroScribe tool and five additional times with Amira. These digitizations were compared with other modern human collarbones by means of Procrustes distances. The

largest Procrustes distance between repetitions (0.0636) was smaller than the smallest Procrustes distance between non-repeated specimens (0.0818), indicating acceptable intra-observer error.

Due to the fragmentary state of fossil specimens and in order to increase our sample size, we conducted mean size and shape comparisons and explored morphological variability (via multivariate principal component analysis [PCA] in form and shape space) separately for the complete clavicle and for the diaphysis. Partial Procrustes superimposition was performed for comparisons, allowing rotation, scaling, and translation of landmark coordinates (Bookstein, 1991; O'Higgins, 2000; Slice, 2007; Mitteroecker and Gunz, 2009). Mean centroid sizes of Neandertal and modern human clavicles were compared with a Student's *t* test using SPSS v.20 (IBM Corp. 2011). Mean shape comparisons were carried out with Procrustes distances, and a permutation test was executed with MorphoJ software (Klingenberg, 2011).

Morphological variability among samples was examined with PCA, which was performed with Morphologika2 v2.5 (O'Higgins and Jones, 2006). In order to investigate further the morphological affinities among specimens, a Procrustes distance minimum spanning tree (the graph linking all dataset specimens using the smallest sum of distances) was created using NTSys (Applied Biostatistics Inc., 1986-2000) and plotted in principal component space (Harvati et al., 2007; Bastir et al., 2008; Rosas et al., 2015). To simplify tree visualization, male and female means were included for chimpanzee and modern human samples.

Results and preliminary discussion

Brief description of the El Sidrón clavicles

Photographs of the adult El Sidrón clavicle specimens included in this study can be found in Figures 2 – 5, with a brief description in Table 1; SD 695g is a very small fragment of the sternal end, and is not described further below.

SD 2100 is a nearly complete adult left clavicle that lacks only part of the sternal end and the costoclavicular ligament-attachment area. This clavicle is strongly twisted and dorsoventrally flattened toward the midshaft, with an elliptical cross section. Muscle attachments for the deltoid and pectoralis major are visible. A nutrient foramen can be observed in the posterior side of the shaft, clearly displaced toward the acromial third. A shallow subclavian sulcus is perceptible. The medial epiphysis is not completely fused, corresponding to an individual aged 22 – 30 years (Scheuer and Black, 2000). Due to its length and overall size, this specimen could

be considered to be male in accordance with the pattern of sexual dimorphism in modern humans (Olivier, 1951-1956; Genovés, 1962; Krogman and Isçan, 1986; Rodriguez-Perez, 2014). Cut marks are also visible on the shaft surfaces. Linear dimensions are given in Table 4.

SDR 016+ is the diaphysis of a left clavicle. The midshaft is superoinferiorly flattened, with a perimeter value (38 mm) well within the range of adult modern humans (Olivier, 1951-1956; Akhlaghi et al., 2012; Papaioannou et al., 2012). A nutrient foramen is visible on the posterior-inferior side of the shaft and located toward the acromial end, close to a shallow subclavian sulcus. The deltoid crest is present, and the pectoralis and trapezius entheses are also evident. Strong torque is conspicuous at the acromial end, yielding a cranial orientation. Linear dimensions are given in Table 4.

SD 2011 is a nearly complete left clavicle diaphysis lacking its lateral and medial ends. The midshaft is dorsoventrally flattened and twisted, and its perimeter (35 mm) is within the range of adult modern human clavicles. The nutrient foramen is located on the posterior surface of the shaft, displaced toward the acromial third. A subclavian sulcus is not appreciable. The deltoid tubercle is well developed. Cut marks are visible on the posterior surface as well as on the deltoid and pectoralis major entheses. Linear dimensions are given in Table 4.

SD 593 is a small fragment of the acromial end of a right clavicle. Its inferior and posterior surfaces are badly eroded. The deltoid tubercle is apparent in the superior view.

SDR 017 is a fragment of the sternal end of a left clavicle; the sternal facet is absent. The costoclavicular insertion and the subclavian groove are visible on the inferior surface.

SDR 156+ is a nearly complete acromial third of a left clavicle. The inferior surface is badly eroded and partly absent. A nutrient foramen is located in the posterior surface of the lateral shaft end, near to the acromial third. The conoid tubercle is perceptible, and although the deltoid tubercle is well preserved, the end of the deltoid entheses is not clear. The acromial facet suggests a cranial orientation at the end of the lateral third.

Morphological characteristics of the El Sidrón clavicles

The length of SD 2100 falls well within the Neandertal range and is a bit larger than that the modern human clavicles (Table 5; Fig. 6). The midshaft index for three El Sidrón specimens (SD-2100, SDR-016+, and SD-2011) are all <80, which is not consistent with the index of *H. sapiens* who ranges from 79.1-97.0 (Table 5; Fig. 6) but is in agreement with the platycleidic condition of most Neandertal clavicles (Carretero et al., 1997).

Geometric morphometric comparison of samples from Neandertals and modern humans

The centroid size from Neandertal samples was significantly greater than that from modern humans for both the complete clavicle ($t(160)=-4.403, p<0.01$), and the diaphysis ($t(170)=-4.998, p<0.01$). Mean shape measurements also differed significantly (complete clavicle $p=0.04$; diaphysis, $p=0.013$; Fig. 7). We detected morphological differences that were consistent with previous studies, including a larger extension of the muscular entheses in Neandertals (e.g., costoclavicular ligament, trapezoid line, and deltoid attachments [Vandermeersch and Trinkaus, 1995]) and double dorsal curvature in the Neandertal clavicle (Voisin, 2010), superior at the sternal end and inferior at the acromial end relative to the position of the epiphysis.

Our comparison of mean shapes indicated that the acromial half of the Neandertal clavicle is twisted toward a cranial orientation (clavicle torsion; Fig. 7), an observation that has not been made previously. From a ventral view, the anterior border of the clavicle is horizontally maintained all along the bone in modern humans, whereas in Neandertals, the anterior border rises toward the acromial end. As a consequence, in Neandertals the deltoid attachment is located in a superior position relative to the anterior border, and the conoid tubercle changes its orientation. The conoid tubercle is largely posteriorly-oriented in modern humans, while its orientation is mainly inferior in Neandertals. The El Sidrón clavicles fit this pattern; cranial orientation of the acromial end is conspicuous in SD-2100 and SDR-016+, with a superiorly located deltoid attachment and a strong and inferiorly oriented conoid tubercle (Fig. 4).

Multivariate analyses

In the form space analysis of the complete clavicle (which takes size into account and allows variation to be assessed in a broad comparative context) (Fig. 8), up to 49.2% of the shape variation was size-related, with a clear separation between sexes in modern humans (males were larger than females; Fig. 8A). Measurements from the Nariokotome specimen fell well within the distribution of data from modern human females (Fig. 8A). Note, however, that this is a juvenile who has not finished his growth, which may influence location in the form space.

At the other extreme, most of the Neandertal specimens, with the exception of Krapina 142, which, as indicated by Voisin (2006b) is small, were associated with the highest values in the entire hominid sample, and the *H. antecessor* clavicle had an elevated score for principal component (PC)1. A neat division between chimpanzee and hominin clavicles was established on PC2 (Fig. 8A), which at the positive end showed clavicles with both ends elevated and closed acromial curvature, whereas clavicles at the negative end exhibited lowered epiphyses, with opened curvature of the acromial third. The TD6 specimen had a high score for PC2, while Krapina 142 and La Ferrassie 1 (right side) are located in the upper limit of the modern human plus Neandertals distribution.

In the shape space analysis (Fig. 8B), clavicles at the positive end of PC1 (*Pan* plus Atapuerca-TD6) displayed more acromial curvature, a deltoid attachment located on the superior border, and a sternal end that is superiorly orientated and slightly elevated. Clavicle thickness and epiphyses elevation relative to the diaphysis was represented on PC2. There was no separation between modern human and Neandertal clavicles in this subspace (Fig. 8B). However, considering PC1 and PC2 together yielded morphological polarity: measurements from most Neandertals and modern humans localized to a region opposite that occupied by data from chimpanzees, *H. antecessor*, and *H. ergaster/erectus* (Fig. 8B). In this latter group, the acromial third was relatively small and slightly cranially elevated and the acromial curvature was more pronounced, but the sternal curvature was more open, and also cranially elevated. This difference was also apparent from a dorsal view (Fig. 8B). However, Atapuerca TD-6 displayed a more *Pan*-like morphology (notable cranial orientation of the acromial third and a very close acromial curvature), while KNM-WT 15000 presented a less striking expression of this morphology. A note of caution must be expressed here, nevertheless, as data from TD6-50 clavicle derive from a high quality cast, but a slight reconstruction of the original fossil was performed (Carretero et al., 1999). On the other hand, the Neandertal clavicles La Ferrassie 1 (right) and Krapina 142 showed a position closer to the *Pan*/TD-6/ KNM-WT 15000 group. In modern humans and most of the Neandertals, both ends of the clavicle were inferiorly located with regard to the midshaft, while in the other specimens the extremes of the clavicle were more or less aligned with the diaphysis (Fig. 8B). Consequently, we hypothesize that the group comprising *Pan* + *H. ergaster/erectus* + *H. antecessor* shows primitive-state morphology.

The shape PCA of the diaphysis, excluding the epiphyses, enabled us to include a larger number of fossil specimens in our analysis (Fig. 9). Principal component 1 explained 39.6 % of the variation and separated *Pan* from *Homo* specimens. In PC1, some Neandertal specimens tended to fall closer to data from chimpanzees, with a large and superiorly located deltoid

attachment, despite the large variation in these data (Fig. 9). However, Atapuerca TD-6 and KNM-WT 15000 fell away from the *Pan* sample, plotting within the modern human distribution. Principal component 2 is mostly associated with diaphysis thickness and curvature. Data from the Neandertal sample mainly occupied a more negative position on PC2 (Fig. 9), reflecting relatively thinner and more curved diaphyses that contrast with the thicker and more linear diaphyses found more frequently in modern humans. For these features, *H. antecessor* data appeared at the lower limit of the Neandertal data, and *H. ergaster/erectus* data fell in the middle of this distribution (Fig. 9).

Discussion and conclusions

This study places new fossil clavicles recovered from El Sidrón into a comparative framework using 3D geometric morphometric methods. We reassessed the form and variation of the *Homo* clavicle via new samples and new methods that have rarely been used to study this bone. We also revisited the phylogenetic polarity of previously considered Neandertal features due to renewed interest in these features in samples from the Lower Pleistocene (e.g., Atapuerca TD6 *H. antecessor*; Bermúdez de Castro et al., 2015).

We found that the size and shape of the El Sidrón clavicles fit into previously known clavicle variation in Neandertals. We also uncovered statistically significant differences in shape between Neandertal and modern human clavicles after adding data from the new El Sidrón specimens to an enlarged set of Neandertal data. Consistent with previous studies by Vandermeersch and Trinkaus (1995) and Voisin (2004), we observed that the Neandertal clavicle is, on average, larger than that of modern humans, with double dorsal curvature and a flatter diaphysis. Three dimensional shape analyses confirmed a degree of torsion in this bone, with some cranial orientation at the acromial end.

Phylogenetic relevance

Morphometric analyses of the complete clavicle established a polarity between the “primitive” pattern evident in *Pan*, *H. ergaster/erectus* and *H. antecessor* and a derived pattern exhibited by the Neandertal-modern human clade. However, Neandertal clavicles displayed a larger degree of rotation that is related to the cranial orientation of the acromial end, which is obvious in individual diaphyses. Taken together, our morphometric analyses may be congruent with the following phylogenetic sequence. The primitive condition is expressed by the cranial orientation of both the acromial and sternal ends. The derived condition arises in the *H. sapiens* + Neandertal clade; it is defined by caudal rotation of both the sternal and acromial

ends, but with a varying amount of remaining cranial orientation in the acromial end. Finally, we detected an autapomorphic Neandertal condition that is defined by a secondarily acquired primitive cranial re-orientation of the acromial end, to a degree that varies among individuals.

Consistent with these observations, Neandertals have a long clavicle that was possibly inherited from ancestors as old as *H. antecessor*. Both the complete clavicles of *H. antecessor* (the adult TD6-50 [Carretero et al., 1999] and the subadult TD6-37 [García-González et al., 2009]) were longer than clavicles in age-matched *H. sapiens*, sharing with Neandertals a relatively longer clavicle (García-González et al., 2009) probably related to a primitive body plan of wide and heavy bodies (Arsuaga et al., 1999; 2015; Carretero et al., 2004). A remarkable reduction in clavicle length may have occurred in late *H. sapiens* populations, being associated with a derived morphology of thin bodies (Arsuaga et al., 1999, 2015; Carretero et al., 2004). The apomorphic condition of caudal rotation of both the sternal and acromial ends of the clavicle, mentioned above and shared by some Neandertals and all modern humans, may have been acquired by a post-*H. antecessor* ancestor; such apomorphy is consistent with the classic notion of a mid-Pleistocene last common ancestor for the Neandertal + *H. sapiens* clade. Finally, autapomorphic modifications may have occurred independently in the Neandertal and *H. sapiens* lineages: the cranial orientation of the acromion is partially increased in Neandertal specimens, whereas *H. sapiens* specimens lack the double curvature but contain a diaphysis that is rounded in cross section.

In the light of these results, the pace of phylogenetic change in the pectoral girdle does not seem to follow that of other skeletal features, as Voisin (2010) has already proposed. For instance, an initial “post-*H. ergaster* and pre-*H. antecessor*” change in the organization of the body has been suggested, involving several “Neandertal clade” derived features such as a large olecranon fossa and very thin medial and lateral pillars at al humerus (Bermúdez de Castro et al., 2012; Rosas et al., 2015) and other features affecting the cranial (e.g. minimally projecting mastoid process and presence of a medial pterygoid tubercle) and dental skeleton (e.g. reduced occlusal polygon in the permanent lower fourth premolars) (Martínón et al., 2007; Bermúdez de Castro et al., 2015; Gómez-Robles et al., 2015). Thus, while the distal humerus may have changed, the anatomy of the clavicle would have remained primitive in this “post-*H. ergaster* and pre-*H. antecessor*” ancestor, consistent with Arsuaga et al.’s (2015) recent proposition of mosaic evolution in the postcranium of the Neandertal lineage.

Morphofunctional meaning

From a morphofunctional viewpoint, the primitive state of a clavicle with cranially oriented ends may be related to an oblique position of the clavicle relative to the thorax (Ohman, 1986; Aiello and Dean, 1990; Voisin, 2001; Larson, 2007; Churchill et al., 2013). Cranial orientation of the acromial end is a feature of the great apes (Ashton and Oxnard, 1964; Oxnard, 1984; Aiello and Dean, 1990) that distinguishes them from modern humans. This acromial cranialization is directly related to functional inferomedial inclination of the clavicle (Ohman, 1986). More recently, Churchill et al. (2013) described this inferomedial inclination in *Australopithecus sediba* (MH-2). Similarly, specimen ATD6-50 displays a rising of the anterior border from the sternal end (Carretero et al., 1999), a marked acromial cranial orientation. This characteristic has not been identified in the Neandertal fossil record (Heim, 1974; Trinkaus, 1983; Vandermeersch and Trinkaus, 1995), although diaphysis torsion is evident in some cases (Vandermeersch and Trinkaus, 1995; Carretero et al., 1997). Such torsion may be related to a primitive configuration of the acromial end, supposedly inherited from a primitive *Homo* (Voisin, 2001, 2004, 2008). However, in our opinion, the distinct Neandertal upper thorax configuration, which is mediolaterally narrower and anteroposteriorly projected (Bastir et al., 2015), may involve relocation of the scapular girdle elements, with the scapulae somehow becoming more lateral than in *H. sapiens*. This relocation modifies the position of the scapular acromion and affects the acromial third of the Neandertal clavicle, which may explain its secondarily primitive condition.

Our results show that the hypothetically primitive cranial orientation of the sternal end has great phylogenetic relevance, although it has not been considered extensively (Lovejoy et al., 1982; Carretero et al., 1997, 1999; Lordkipanidze et al., 2007; Haile-Selassie et al., 2010; Churchill et al., 2013). From a functional viewpoint, a relationship between the contact surfaces of the sternal end and the manubrium has been identified, intended to constrain the elongation of the costoclavicular ligament (Inman and Saunders, 1946; Abbott and Lucas, 1954; Grant, 1971). More recently, Voisin (2001, 2006a) emphasized that the functional relationship related to clavicular stability, and Churchill et al. (2013) pointed out that the morphology of the sternoclavicular articular surface may indicate oblique clavicle orientation in *Au. sediba*. In-depth study of the sternal end in the context of the complete pectoral girdle and upper thorax is needed to obtain a better understanding of the functional and phylogenetic relevance of these features.

Two current models address the evolution of the pectoral girdle and shoulder in *Homo*. In one model, Roach et al. (2013) and Roach and Richmond (2015) reported that although the relative

length of the clavicle is quite variable, the shoulder configuration of modern humans may have originated more than 2 million years ago, with the emergence of *H. erectus*. A similar position can be inferred from the study of Trinkaus et al. (2014), who detected stable clavicle length when the data were scaled to body mass. In a second model based on the short KNM-WT 15000 clavicle, Larson (2007) identified a singular transitional shoulder configuration in *H. erectus*, with scapulae located in a more lateral location than in the hypothetical ancestors of *H. erectus*. Recently, Roach and Richmond (2015) criticized this transitional stage, pointing to high variability in the relative length of the clavicle in early *Homo* samples. However, Larson (2015) updated her model, arguing that a transitional shoulder configuration in *H. erectus* should be inferred not so much based on short clavicle length (accepting the criticism from Roach and Richmond [2015]) but based on the especially low humeral torsion in these samples, which is not present in a modern configuration, with scapulae more dorsally located and glenoid fossa laterally oriented. According to Larson (2007), the modern configuration may have originated in *H. antecessor* populations and remained more or less stable until *H. sapiens*, despite interspecific variation.

The pattern of phylogenetic variation detected in our study does not seem to coincide with any of these models, as we have demonstrated significant differences in the clavicle among distinct *Homo* species. By inference, our observations do not support the hypothesis of evolutionary stability of the shoulder/pectoral girdle configuration over the last 2 million years. On the other hand, our results suggest that *H. antecessor* maintained a primitive clavicle shape and size, as Carretero et al. (1999) and García-González et al. (2009) have noted, which seems to indicate, in contrast to the model of Larson (2007), that their scapulae may have maintained a relatively elevated position, as discussed by Voisin (2010). Nonetheless, our results are in agreement with Larson (2007, 2015) in terms of detecting evolutionary changes in this body region, even in situations that can be considered to constitute evolutionary “reversals”, e.g., more-lateral scapulae in *H. erectus* and an apparent cranial reorientation of the acromial end in Neandertals. In addition to a modern pectoral girdle configuration shared with *H. sapiens*, Neandertals achieved a hypothetical secondarily primitive condition in the acromial end. The potential influences of this condition on the shoulder/pectoral girdle of the deep upper thorax in Neandertals (Bastir et al., 2015) remain to be explored. Further studies should consider integration analyses of the elements composing the pectoral girdle and shoulder, together with those of the thorax. Overall, it is becoming clear that various elements of the postcranial skeleton have an unequal cadence of change. Whereas certain features of the thorax and arm (e.g. enlarged first ribs and wide humerus olecranon fossa) seem to have evolved in a “post-*H.*

ergaster and pre-*H. antecessor*” ancestor (Gómez-Olivencia et al., 2009; Bermúdez de Castro et al., 2012; Rosas et al., 2015), others (e.g., the pectoral girdle) seem to have changed after *H. antecessor*, with later autapomorphies independently evolving in the *H. sapiens* and Neandertal lineages.

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Figure Captions

Figure 1. Anatomical location of the 29 homologous landmarks used in our analyses. These landmarks are projected on the inferior and anterior views of a digital model of a modern human clavicle. Descriptions of numbered landmarks are given in Table 3.

Figure 2. Inferior view of the adult Neandertal clavicles from El Sidrón (Asturias, Spain).

Figure 3. Superior view of the adult Neandertal clavicles from El Sidrón (Asturias, Spain).

Figure 4. Anterior view of the adult Neandertal clavicles from El Sidrón (Asturias, Spain).

Figure 5. Posterior view of the adult Neandertal clavicles from El Sidrón (Asturias, Spain).

Figure 6. Box and whisker diagrams of clavicle midshaft index and maximum length from hominin samples.

Figure 7. Comparison of mean shape, Neandertals versus modern humans.

Figure 8. Multivariate comparisons of size and shape variation. A) Form space (PCA of shape coordinates plus centroid size) for the complete clavicle. Principal component 1 and PC2 explain 49.2% and 9.5% of variation respectively. B) Shape space (PCA of shape coordinates) for the complete clavicle. Principal component 1 explains 18.6% of morphological variation, PC2 explains 8.4% of the variability. Extreme clavicular shapes for PC1 – PC2 combinations are located in the superior left and inferior right corners

Figure9. Shape space (PCA of Procrustes shape coordinates) for the diaphysis of the clavicle, excluding the epiphyses. Principal component 1 and PC2 explain 39.6% and 11.4% of the morphological variation respectively.