

A geometric morphometrics comparative analysis of the neandertal humeri (epiphyses-fused) from the El Sidrón cave site (Asturias, Spain).

Antonio Rosas¹, Laura Pérez-Criado¹, Markus Bastir¹, Almudena Estalrich¹, Rosa Huguet², Antonio García-Taberner¹, Juan Francisco Pastor³ and Marco de la Rasilla⁴.

1 - Group of Paleoanthropology MNCN-CSIC, Department of Paleobiology; Museo Nacional de Ciencias Naturales-CSIC. Calle José Gutiérrez Abascal 2, 28006 Madrid, Spain.

2 - Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Àrea de Prehistòria, Universitat Rovira i Virgili, Zona Educacional 4 - Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain. Unidad Asociada al CSIC.

3 - Museo Anatómico, departamento de Anatomía Humana, Universidad de Valladolid, Calle Ramón y Cajal 7, 47005 Valladolid, Spain.

4 - Área de Prehistoria, Department of History; Universidad de Oviedo. Calle Teniente Alfonso Martínez s/n, 33011 Oviedo, Spain.

Corresponding author: Dr. Antonio Rosas. Group of Paleoanthropology MNCN-CSIC. Department of Paleobiology. Museo Nacional de Ciencias Naturales (CSIC). C/ José Gutiérrez Abascal 2, 28006 Madrid (Spain). Phone +34 915668973. Fax +34 91564 50 78. e-mail: arosas@mncn.csic.es

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ABSTRACT

Here, we report on the comparative analyses conducted on the 49,000 year-old humeral fossil neandertal remains discovered at the El Sidrón site (Spain). We present a new collection of neandertal fossil humeri from the El Sidrón cave site (Asturias, Spain). A total of 49 humeral remains were recovered, representing 10 left and 8 right humeri. Adult, adolescent, and juvenile (not included in the analyses) individuals are represented within the sample.

Aspects related to within-sample variation and the phylogenetic significance of some taxonomically meaningful features are addressed. Comparisons between neandertal and modern humans received more specific attention. A broad comparative analysis of classic anthropological variables using three-dimensional (3D) geometric morphometric (GM) methods. Mean centroid size and shape comparison, principal components analysis, and cluster studies were conducted. Due to the fragmentary nature of the fossils, comparisons were organized in independent analyses according to different humeral portions: distal epiphysis, diaphysis, proximal epiphysis, and the complete humerus.

From a multivariate viewpoint, 3D-GM analyses revealed major differences among taxonomic groups, supporting the value of the humerus in taxonomic and systematic classification. Notably, the *Au. anamensis* (KP-271) and Nariokotome distal humerus consistently clusters close to modern humans. This may imply that *H. sapiens* displays a primitive morphology and *Australopithecus* specimens show a high degree of dispersion, with no *Australopithecus* humeri falling within the modern human distribution.

Previous studies have demonstrated that a relatively wide olecranon fossa, as well as thin lateral and medial distodorsal pillars, was very common in neandertals and the El Sidrón cave sample fits perfectly into this morphological pattern. These characteristics were also typical of the Sima de los Huesos sample (Atapuerca), African mid-Pleistocene Bodo specimen, and Lower Pleistocene TD6-Atapuerca remains and may be considered as a derived state. , Finally, we hypothesize that most of the features thought to be different between neandertal and modern humans might be associated with structural differences in the pectoral girdle and shoulder joint.

Introduction

Understanding the phylogeny of the genus *Homo* is becoming more complicated due to recent discoveries. In fact, based on the deme variation associated with new fossils discovered in Dmanisi (Georgia), an extreme simplification in the number of species at the base of the lineage has been proposed (Lordkipanidze et al., 2013). On the other hand, genetic data have unraveled a new hominin lineage (i.e. Denisovans) (Reich et al., 2010) and verified the occurrence of restricted but regular interbreeding among later *Homo* species (Green et al., 2010; Prüfer et al., 2014). Collectively, these findings suggest that characterization based on variation in fossil sample patterns and the morphological basis for phylogenetic reconstruction should be reconsidered. From this perspective, there is great interest in understanding the evolutionary pathways related to humeral anatomy, as these skeletal elements are often

found in the paleoanthropological record (McHenry and Brown, 2008; Trinkaus, 2012; Lague, 2014).

The morphology of the humerus is thought to differ in numerous ways among later *Homo* species: neandertals, modern humans, and other Pleistocene hominin groups (Yokley and Chrurchill, 2006; Trinkaus, 2012). Significant size and shape variations have also been observed in Plio-Pleistocene hominins (McHenry and Corruccini, 1975; Senut, 1981; Senut and Tardieu, 1985; Lague and Jungers, 1996). Indeed, evolutionary variation has been identified in the projection/location of the epicondyles, degree of humeral torsion, shape of the deltoid tuberosity, olecranon fossa size, as well as relative size of the lateral and medial pillars (among other features) when comparing modern humans and classic neandertals (Vandermeersch and Trinkaus, 1995; Carretero et al., 1997; Yokley and Chrurchill, 2006). In the absence of further fossil evidence, it could be expected that the difference between these two human forms could have emerged in the evolutionary differentiation of the two human evolutionary lineages, since modern humans and neandertals shared a recent common ancestor.

In this regards, neandertal distal humerus morphology has been proposed to represent a derived or specialized form, and hence a few of these traits have been traditionally included in the category of “neandertal features” (e.g. narrow pillars/broad olecranon fossa) (Arsuaga y Bermúdez de Castro, 1984; Carretero et al., 1997). For its part, shape of humeri from modern humans is thought to be the unchanged or primitive state. For example, Yokley and Chrurchill (2006) concluded that “Australopiths (...) are morphologically more similar to modern humans than to neandertals, which suggests that modern human distal humeral morphology is primitive and that of the neandertals is derived” (p. 614) (see also McHenry and Brown, 2008). Accordingly, Trinkaus (2012) reported that modern humans (from late Middle Pleistocene to recent) display a pattern similar to Early Pleistocene specimens (e.g., Dmanisi, Nariokotome), suggesting that the modern human distal humeral shape may be primitive (but see Lague, 2014). Therefore, the simplest model would state that the derived expression (e.g. narrow pillars/broad olecranon fossa) emerged in the course of the neandertal evolutionary lineage after the divergence from the last common ancestor (LCA) with modern humans, while modern human lineage remains primitive. In this scenario, distal humerus traits would be properly labeled as “neandertal features” as emerged along the neandertal evolutionary lineage.

This was partially supported by Carretero et al. (1997) when they reported that the Atapuerca-SH Middle Pleistocene sample, representing the putative direct ancestor of neandertals, already displayed the “neandertal features”. However, an improved fossil record has failed to validate this model. “Neandertal morphology” has also been recognized in the Lower Pleistocene TD6-Atapuerca remains (Bermúdez de Castro et al., 2012), which corresponds to a time that predates the hypothetical last common ancestor for neandertals and modern humans (Bermúdez de Castro et al., 2012). Consequently, and discarding for the moment the hypothesis that TD6 *H. antecessor* fossils may really correspond to the LCA of neandertals and modern humans ((as previously proposed by Bermudez de Castro et al., (1996)), the TD6 evidence reveals that “neandertal features” from the distal humerus were already present in hominins predating neandertal evolutionary lineage differentiation. This finding has raised the possibility that the so called “neandertal features” may actually

represent retained features that were inherited from a still unknown ancestor (as previously hypothesized by Carretero et al. 1997). And, consequently, these features have been maintained for at least a million years.

However, chronologically intermediate African fossils between *H. ergaster erectus* and modern humans show, however, a more confusing pattern. Broken Hill E.898 displays a modern morphology (Yokley and Chrurchill, 2006; Trinkaus, 2012) (although a recent study by Trinkaus (2012) recommended the exclusion of the Broken Hill specimen from analyses until a better chronological framework is available) By contrast, a neandertal-like set of features was also present in the African mid-Pleistocene Bodo specimen (Carretero et al., 2009), and similar morphology has been inferred from the olecranon form of other African samples (Churchill et al., 1996). Yokley and Chrurchill (2006) have suggested that Middle Pleistocene specimen from Baringo, as well as specimens from the Klasies River Mouth and Border Cave sites (i.e., early modern humans from South Africa) would show neandertal-like distal humerus morphology. To further complicate the matter, that also happen in later populations from Dolni Vestonice (Europe) and Tianyuan (China) (Shang and Trinkaus, 2010), weakening the hypothesis of neandertal specificity.

In this scenario, we would see early *Homo* (Nariokotome, Dmanisi) displaying primitive expression, chronologically intermediate populations showing the derived condition in varying frequency, and modern humans showing the primitive condition again. This behavior faithfully fits the pattern described by McHenry and Brown (2008), whereby “older fossil hominins have more modern looking postcrania than younger ones” (but see Lague, 2014).

Possible explanations for this evolutionary pattern have come from several sources. To reconcile the evidence Yokley and Chrurchill (2006) have considered the possibility of homoplasy, which results from similar behavioral practices and is epigenetically induced rather than genetically determined, could be responsible of this erratic pattern. It has also been suggested the possibility of an evolutionary reversals, affecting the postcranial skeleton and specifically to humerus (McHenry and Brown, 2008; Trinakus, 2012). Alternatively, Bermúdez de Castro et al. (2012) set up a frequency-based model related to the polymorphic nature of features. Based on this, the derived condition (e.g., “neandertal features”) would have appeared in a pre-*Homo antecessor* population (but posterior to *H. ergaster*), who should have maintained a relatively high frequency of the plesiomorphic state for the feature. Subsequently, descendant populations would have differentially inherited the distinct “morphological alleles”. In particular, late Early Pleistocene European populations would have received a much larger amount of these alleles. In Africa, descendant populations should have maintained both primitive and derived states at different frequencies, becoming relatively fixed only late in *Homo sapiens* evolution.

In view of these uneven interpretations, one may conclude that the polarity and phylogenetic meaning of some taxonomically useful humeral characteristics remains unsolved, and the present study aims to add on this matter. Previous investigations using landmark-based techniques have proved to be useful for the clarification of humeral morphological determinants (Lague and Junguers, 1999; Bacon, 2000; Arias-Martorell et al., 2012; Holliday and Friedl, 2013), whereas more traditional studies have found it difficult to quantify complex

anatomy regions (e.g., proximal humerus head) (Carretero et al., 1997). We combine classic anthropological methods with standard three-dimensional (3D) geometric methods to perform a broad comparative analysis of the unpublished fossil neandertal humeri (epiphyses-fused) collection discovered at the El Sidrón site (Asturias, Spain) to further question whether the so called “neandertal features” correspond to derived, primitive or homoplastic states. Related to this, the question whether the humerus features behave as independent traits or may be part of a more general anatomical system is also considered.

Accordingly, we organize analytical procedures to assess the following topics. One, we explore the magnitude of intra-sample neandertal variation, and question whether this morphological pattern referred as neandertal is fixed at the population/species level or if it varies with respect to size, sexual, genetic, or functional characteristics. If fixed, we expect a low variability within the El Sidron sample. Two, we aim to better define the polarity of humerus traits. In particular, we approach the hypothesis of modern human distal humerus primitive condition vs a postergaster-but-not-modern-human derived condition (previously referred as neandertal-features). A larger similarity of modern humans and early hominins might be expected as well as a distinctive occupation of the morphospace by the neandertal-like specimens. Three, an initial approach to the variation and covariation pattern is made by PCA of shape variables in order to explore whether humerus features might be considered isolated or as a part of a more integrated system. These questions seem to be appropriated if we are to understand the phylogenetic fate of the *Homo* lineages.

Materials and methods

El Sidrón site

The El Sidrón karst system is located in the municipality of Piloña (Asturias, Spain) (Fortea et al., 2003; Rosas, 2006; de la Rasilla et al., 2011). Since 2000, more than 2,300 human fossils dated to 49ky by 14C (Wood et al., 2013) have been recovered, representing the most complete neandertal sample of the Iberian Peninsula (Rosas et al., 2006; 2012). At least 13 individuals have been identified: one infantile, two juveniles, three adolescents, and seven adults (Rosas et al., 2012; 2013). All skeletal regions have been preserved, and Middle Paleolithic stone tools have also been discovered at the site (Santamaría et al., 2010). Notably, all remains were found in a taphonomically secondary position (Fortea et al., 2003). In addition, some macro-faunal materials have been identified (Rosas et al., 2011).

Conservation and inventory of the humeri material

A total of 49 humeral remains were recovered from the El Sidrón site. Several fragments have been glued together, representing 10 left and 8 right humeri (Table 1). The sample is made up of adult, adolescent, and juvenile (not included in the analyses) individuals (see Table 1). Antimere identification was difficult due to the fragmentary state of the specimens, differences in preservation between right (distal fragments) and left (diaphyses) specimens, as well as mixed preservation. In this regard, the only exception concerns Juvenile 1, whose right and left humeri were identified based on common developmental stage (Scheuer and Black, 2000) and overall similarity. The distal epiphysis proved to be the best represented humeral

part in the El Sidrón sample, in agreement with previously studies indicating the superior taphonomic durability of this anatomical region (McHenry and Brown, 2008; Trinkaus, 2012).

Comparative sample

Two *H. sapiens* collections have been used as a basis for our comparative analyses. The first is from an age and sex known twentieth century population from Palencia (Spain), which belongs to the Paleoanthropology Group of Museo Nacional de Ciencias Naturales (MNCN-CSIC) (Madrid) and the Anatomical Museum of the Valladolid University (Spain), (N=88 right humeri; 45 males and 43 females). The second sample is of unknown age and sex, but represents a seventeenth century population found at the Plaza de Ramales (Madrid, Spain) (N=15 right humeri; housed at MNCN-CSIC). This living species comparative sample is complemented using humeri from chimpanzees (N=20; 10 males and 10 females) from the Anatomical Museum of the Valladolid University (UVa, Valladolid, Spain). In order to avoid the potential effects of laterality, only right side humeri were included in our analyses.

The neandertal comparative sample is comprised of high-quality casts of Feldhofer, La Ferrassie 1, and Lezetxiki specimens as well as virtual reconstruction from Régourdou 1, Spy, and Krapina (MNCN-CSIC) remains. Additionally, casts of AT-25 (*H. heidelbergensis*), KNP-KP 271 (*Australopithecus anamensis*), A.L. 288-1s (*Au. afarensis*), STW 431 (*Au. africanus*), KNM-ER 739 (*P. boisei* or *H. habilis*), and KNM-WT 15000 (*H. ergaster*) were also added to the sample.

Morphometric analyses

Here, 3D geometric morphometric techniques based on landmark configurations were employed for most of the analyses. For each complete humerus, we measured 43 homologous landmarks (Table 2 and Figure 1), which were taken with a MicroScribe device in living species humeri, original fossils, and casts. Amira software (Stalling et al., 2005) was used for virtual specimens.

In order to test for intra-observer error between the two digitization methods, the most complete humerus from the El Sidrón site was measured five times using the MicroScribe device and repeated five additional times with Amira. These digitizations were compared with other neandertal humeri via Procrustes distances. The largest Procrustes distance between repetitions (0.038) was less than the smallest Procrustes distance measured (0.049). Therefore, we considered the intra-observer error admissible.

Sexual differences among El Sidrón humeri were explored by means of published criteria of sexual differences in living human populations (Carretero et al., 1995; Alemán-Aguilera et al., 1997; Iscan et al., 1998; Steyn and Iscan, 1999; Rios Frutos, 2005; Kranioti et al., 2009) along with a mean sex 3D shape comparison based on the modern human sample from Palencia (Spain). In this regard, mean shape comparison analyses were performed to determine the foremost dimorphic features of humeri from modern human males and females. Specifically, the average shapes from female and male bones were superimposed and sexual dimorphism criteria were extracted (see later).

Due to the fragmentary nature of the fossils and to maximize the number of specimens involved in our study, evolutionary morphological comparisons were independently conducted for different humeral portions, including the distal epiphysis, diaphysis, proximal epiphysis, and the complete humerus. Missing landmarks varied by number, position, and analysis. Therefore, they were estimated by regression or spline (Gunz et al., 2009), as presented in Tables 3 and 4.

For comparative analysis, a partial Procrustes superimposition was performed, allowing rotation, scaling, and translation of the landmark coordinates (Bookstein, 1991; O'Higgins 2000; Slice, 2007; Mitteroecker and Gunz 2009). The mean centroid sizes (CS) of neandertal and modern human were compared by Student's t-test using SPSS v.20 software (IBM Corp. 2011). Mean shape comparisons were subsequently carried out based on Procrustes distances and a permutation test was performed using MorphoJ software (Klingenberg 2011).

Principal component analysis (PCA) was conducted with Morphologika2 v2.5 software (O'Higgins and Jones, 2006) in order to explore the within and between variability and distribution of the samples in the morphospace. Later, Procrustes distances were employed to evaluate the morphological similarity among recent and fossil samples. Similar to Harvati et al. (2007) and Bastir et al. (2008), a minimum spanning tree (MST) (i.e., the graph linking all dataset specimens using the smallest sum of distances) was created using the NTSys program (Applied Biostatistics Inc., 1986e2000) and plotted in principal components space in order to better visualize relationships between individual specimens/samples upon which to later discuss polarity trait hypotheses. In the case of chimpanzees, only male and female means were used in the trees. For modern humans, the Ramales sample mean as well as the male and female means for the Valladolid sample were employed in order to simplify the visualization. Procrustes distances were also used for sample clustering using the complete-linkage clustering agglomerative method.

In order to make comparisons with other studies, we also determined traditional measurements (i.e., biepicondylar breadth, olecranon fossa breadth, medial and lateral pillar thicknesses) of the distal epiphysis, which is the most frequently studied humerus structure, the comparative data were collected mostly from Carretero et al. (1997) and Bermúdez de Castro et al. (2012). The torsion/retroversion angle (i.e., the angle between the distal articular axis and proximal midhumeral axis) was also measured with a torsionmeter, following the methods of Rhodes and Churchill (2009). Moreover, similar to studies by Trinkaus et al. (1994) and Bermúdez de Castro et al. (2012), several measurements and morphological indications were used to identify specific locations from the distal end of the diaphysis, as established by mean percentage distances.

The El Sidrón humeri

Here, we first provide a description of the major anatomical features of the individual humeri and then consider the relevant features in more detail.

Humerus 1 (SDR-036+SDR-042) (Figures 2 and 3) is a large adult right distal humerus with elevated cortical thickness (7.7 mm at the medial wall) measured at 25% of the diaphyses. The specimen shows large but non-perforated olecranon fossa. Both epicondyles are highly

projecting and there is a wide lateral pillar. Moreover, the capitulum and coronoid fossa are relatively large. Also, several cut marks can be appreciated on the medial pillar (Rosas et al., 2012).

Humerus 2 (SD-929 + SD-356a) (Figures 2 and 3) is a large adult right distal humerus, representing the largest of the El Sidrón sample (both centroid size and linear measurements). Both epicondyles are highly projected, with a marked trochlear groove and an extremely large medial trochlea. The specimen also has a wide olecranon fossa with a perforated septum and a relatively shallow radial fossa. In addition, a well-marked lateral supracondylar ridge ascends high in the diaphysis (Figure 2).

Humerus 3 (SDR-035 + SDR-041) (Figures 4 and 5) is a nearly complete left humerus. It belongs to an adolescent with fused distal epiphyses, but incomplete fusion of the proximal one. It displays both projecting epicondyles, a marked trochlear groove, and perforated olecranon fossa. It also displays a slim shaft and marked muscle insertions, including the most prominent point of the lateral supracondylar ridge, which remains located low in the diaphysis. Deltoid tuberosity crests are slightly divergent. Notably, Humerus 3 presents a proportionally large humeral head and small greater tubercle.

Humerus 4 (SDR-037) (Figures 2 and 3) is a medium-sized right distal humerus that has relatively thick cortical bone (6.5 mm). Humerus 4 shows less projection of the epicondyles, with the proximal point of the medial trochlea projecting anteriorly and distally. Also, it presents a perforated olecranon fossa. The most prominent point of the lateral supracondylar ridge is the most proximal within the sample. Humerus 4 displays an obvious flaring lateral supracondylar crest.

Humerus 5 (SDR-038 + SDR-048) (Figures 4 and 5) is a left humerus that has a mostly preserved diaphysis. The lateral epicondyle is less projecting when compared to Humeri 1 and 2. Moreover, it shows well-marked muscle insertions in the shaft, and its deltoid tuberosity crests are more divergent than in Humerus 3. An acute and well-marked supracondylar ridge can be distinguished, but does not stand out very much from the diaphyseal profile.

Humerus 6 (SD-736a + SDR-040 + SDR-039) (Figures 4 and 5) is a robust left humeral diaphysis with prominent muscle insertions that give rise to a square cross-section shape. Deltoid tuberosity crests are slightly divergent (see Figure 6), and the torsion canal is visually appreciable.

Humerus 7 (SD-1438) (Figures 4 and 5) corresponds to an adolescent left distal humerus, which displays an unfused medial epicondylar epiphysis (not conserved). It shows a wide and flaring most prominent point of lateral supracondylar ridge low in the diaphysis. The capitulum is relatively small. Additionally, the specimen presents a projecting lateral epicondyle, not very marked trochlear groove, anteriorly projecting proximal point of the medial trochlear, and perforated olecranon fossa. Also, there is secondary remodeling of the small fossa of the olecranon fossa (see Figure 7).

Humerus 8 (SD-1208a + SD-1208c + SD-1433 + SD-1329 + SDR-201 + SDR-207) (Figures 2 and 3) represents a right specimen and is composed of several fragments found during different

excavation seasons. It has a highly projecting medial epicondyle, which displays deep fossa for tendinous attachment. The proximal point of the medial trochlea projects anteriorly and distally, whereas the olecranon fossa is non-perforated. Muscle insertions are slightly marked in the diaphysis, and cortical thickness is moderate.

Humerus 9 (SD-2143) (Figures 4 and 5) is a small and gracile left specimen. Its deltoid tuberosity crests are slightly divergent (almost parallel).

Humerus 10 (SDR-046 + SDR-243) (Figures 4 and 5) corresponds to a left distal humeral diaphysis fragment; however, the distal epiphysis is missing. Cortical wall development is moderate (5.5mm thick). A flaring, but low positioned, lateral supracondylar ridge can be observed in the diaphysis.

SD-1618 (Figures 4 and 5) is a proximal left humeral end from an adolescent. Thus, the distal epiphysis displays an active fusion process. Also, a wide and well-defined bicipital groove is present.

SD-1322 (Figures 2 and 3) is a small portion of a right proximal diaphysis with well-marked muscular attachments and a thick cortical.

Age at death and minimum number of individuals (MNI)

The MNI represented by humeral remains including J juvenile 1 are 10 for the left humeri and 8 for the right humeri. Among the specimens, 6 correspond to adults and 3 present some degree of incomplete epiphyses fusion. In addition, both the right and left humeri from the juvenile individual (Juvenile 1; Rosas et al., 2013) present distal and proximal unfused epiphyses (not conserved). Within the adolescents, complete distal epiphyses are fused at the distal end in Humerus 3 and Humerus 7; however, the medial epicondyle epiphysis was completely unfused in the latter at the time of death. According to Scheuer and Black (2000), distal epiphyses fuse on average earlier than proximal ones, establishing a younger age for the Humerus 7.

Size variation and sexual dimorphism

Our mean sex shape comparison revealed significant differences ($p < 0.0001$) in the modern human sample from Valladolid (Spain). Based on this analysis, the criteria used for sex assessment included a higher biepipicondylar/articular breadth in males. Moreover, males displayed greater projection of both epicondyles, with the medial end of the lateral pillar projecting posteriorly as well as a capitulum that is higher than it is wide. In females, the most prominent point of the supracondylar ridge is more proximal, and the junction line of the anteroproximal trochlea is more distally inclined. Analysis of the main dimorphic traits in the proximal region revealed a more posterior orientation of the humeral head in males and more open intertubercular grooves in females. Results related to the application of these criteria to the El Sidrón humeri can be found in Table 1.

Assignment of humeral remains to the El Sidrón individuals

Considering size, sex and age at death, the humeral remains have been tentatively attributed to previously dentally-identified individuals (Rosas et al., 2012; 2013), some of which have a

genetically-established sex (Lalueza-Fox et al., 2012). Although we have not found criteria for the adult individuals within the sex subsets, a hypothesis for assignation to adolescent individuals has been reached (see Table 1).

Morphological characteristics of the El Sidrón humeri

Distal epiphysis

El Sidrón humeri display a wide and high olecranon fossa with thin distodorsal pillars, especially the medial one, mimicking the pattern found in both classic neandertals and Atapuerca-SH samples. Notably, there was a narrow range of intra sample variation detected for El Sidrón humeri (Figure 8A). The lateral pillar index indicated a similar but less extreme position (Figure 8B). Modern humans show a different pattern, with relatively small olecranon fossa and wide distodorsal pillars (with some exceptions).

Study of Procrustes-based mean comparisons of centroid size and 3D shape also revealed significant differences between neandertals and modern humans ($p < 0.0001$ in both cases). PCA showed that the aforementioned traits could be considered to be a partial aspect of a more general morphological factor affecting the distal epiphysis as a whole. The first two PCs explained 47.15% of the variability and clearly separated the taxonomic groups. PC1 showed a discrete polarity between modern humans and chimpanzees, while neandertals occupied an intermediate position (Figure 9). Fossils from El Sidrón are distributed in the middle of the neanderthal sample.

Next, the MST based on Procrustes distances was overlaid onto the PC1–PC2 plot (Figure 10). The links between specimens using the minimum spanning distances closely mirrored the distribution of samples in the PC plot. The first two PCs could be taken to represent the overall pattern of variation. This is also consistent with the association found in a phenetic tree based on Procrustes distances (Figure 11). Several associations could be detected. Firstly, chimpanzee cases occupied a distinctive branch (and area) in the morphospace, together with *A. africanus* and ER739. Secondly, modern humans, WT-15000, and *A. anamensis* were grouped at the other end of the cluster. In the central region of the diagram, neandertals formed a consistent cluster, without any grouping apparent in the El Sidrón specimens. Finally, the *Australopithecus* specimens showed a high degree of dispersion and were distributed across the different branches. Taken together, distal humerus morphology revealed an obvious and consistent pattern of differences between the distinct hominin samples, which was reflected by a well-delimited distribution in the morphospace (Figure 9, 10 and 11).

In addition, the features of taxonomic value (olecranon fossa-lateral pillars complex) vary as part of a spatial configuration affecting the complete distal humerus (see analyses of the complete humerus). Firstly, in neandertals, the medial half of the distal humerus is located more proximally and posteriorly, also there is a relative increment of the medial trochlear articular surface and it is located in a more distal and anterior position. Secondly, the lateral half is relatively larger in neandertals, and the location of the lateral epicondyle is located in a more proximal position in relation to the capitulum. Also, the most prominent point of the lateral supracondylar ridge is located in a higher position.

Proximal region: morphology of the lesser tubercle

This anatomical region is badly represented in the El Sidrón sample, The Humerus 3 conserves the lateral end of the lesser tubercle, which is anteriorly projecting, contributing to the formation of a deep bicipital or intertubercular groove. In contrast, SD-1618 solely conserves the distal end of the tubercle swellings, but it was possible to deduce that this anatomical region was also projecting.

Our 3D geometric morphometric analyses of the El Sidrón Humerus 3 and Sima de los Huesos AT-25 specimen were based solely on shared anatomical portions (described by Lm22, 24-31, 33, 39, 41, 43: head, lesser, and greater tubercles ridges). Centroid size comparison did not indicate significant differences ($p=0.13$) between neandertals (including AT-25) and modern humans, but the mean shape comparison revealed significant differences ($p=0.01$). Corroborating previous findings, the principal differences were related to the projection of the lesser tubercle. Further analysis of the complete proximal Humerus 3 (conserved region represented by Lm27-31, 33, 39-41, 43: head and greater tubercle) indicated that there was a difference in size ($p=0.022$), but not shape ($p=0.14$), with the neandertal proximal epiphysis larger than in modern humans. However, additional anatomical differences can be observed, including a larger greater tubercle and posterior orientation of the humeral head in neandertals (see also the analysis of the complete humeri).

Diaphysis

Muscular entheses. Certain variation in muscular entheses can be found in the El Sidrón sample. For instance, while Humerus 6 displays strong muscular relieves, some other cases of very weak muscular marks are found in the sample (e.g., Humerus 9). Overall, in the El Sidrón sample we do not observe a different pattern of muscular impressions as compared to modern humans.

Deltoid tuberosity. Shape of the deltoid tuberosity in the El Sidrón specimens (Figure 6) conforms to the “closed” tuberosity morphology, as defined by Carretero et al. (1997) (i.e., “the lateral crest of the tuberosity is parallel to the shaft axis and either does not reach the lateral border of the diaphysis, or reaches that border close to the surgical neck” p. 398). All of the El Sidrón humeri present two crests on the deltoid tuberosity.

However, in our 3D multivariate analyses we did not find evidence to support this notion. When comparing only the diaphysis data subset, we found that there were no significant differences in mean size ($p=0.61$). However, mean shape comparison revealed significant differences between the two human groups ($p<0.0001$).

Shape space PC1 (Figure 12) explains 34% of the sample variability and showed that the most notable differences were related to the position of coracobrachialis muscle attachment, which is located in a lower position in neandertals. This muscle insertion is slightly marked in the El Sidrón humeri. Moreover, the proximal point of the supracondylar ridge is higher in

neandertals. In addition, the distal portion of the neandertal shaft is characterized by a more distal location of the maximum inflection point of the medial supracondylar ridge and a more proximal position of the most prominent point in the lateral supracondylar ridge (already noted in the distal epiphysis section). PC2 (22.87%) showed muscle attachment length variability (e.g., deltoid, pectoral major, and teres major). The muscles are larger in chimpanzees leading to differential spatial positioning in relation to the lateral supracondylar ridge.

The PC1–PC2 subspace fully separated neandertals from the other groups, with the El Sidrón sample positioned in the middle of neandertal distribution. WT-15000 was located within *H. sapiens* variation. No clear separation between *Australopithecus* and modern humans was observed, which is in sharp contrast to findings of humeral ends analyses.

The torsion angle

The torsion angle could be estimated only on Humerus 3 from El Sidrón, yielding a value of 150°, with 30° of retroversion based on the Rhodes and Churchill (2009) method. These values position Humerus 3 at an extreme end of the neandertal distribution: respective means ranging from 138.5° ± 6.3° to 144° ± 4.5° according to Carretero et al. (1997) and 52.2° as described by Rhodes and Churchill (2009). Thus, Humerus 3 fits better into modern human sample distributions, with mean population averages ranging from 135° to 164° (see Carretero et al., 1997; Shah et al., 2006 and citations therein).

Aside from the directly recording angles, humeral torsion was also indirectly documented in some of our multivariate analyses of the complete humerus (Figure 13).

Complete humerus

Maximum length was only preserved in Humerus 3 (306 mm). The neandertal mean length is reported to be 310±12 mm (Carretero et al., 1997), where as recent humans range from 265.5 to 330 mm (Delsaux, 1977). Given the ample margin of overlap, the Humerus 3 from El Sidrón fell within several samples/species ranges. Nevertheless, the length of Humerus 3 suggests a relatively short arm for a neandertal male. In addition, mean centroid size comparison did not show significant differences ($p=0.35$) between *H. sapiens* and neandertals, while mean shape comparison indicated significant differences between these groups ($p<0.0001$).

PCAs were calculated to include the preserved region of Humerus 3 from El Sidrón (Lm1, 7-31, 33, 39-41, 43) (Figure 13). The first PC explained 28.74% of the variability and clearly separated taxonomic groups, while at the same time incorporating the patterns of variation described in the previous sections in a more integrated way. When observed along the longitudinal axis, it was found that the neandertal humerus shows a different spatial position of the head and distal epiphysis. The head was retroverted, facing more posteriorly. At the same time, the lateral epicondyle was more posteriorly located at the distal end, contributing to less humeral torsion.

Discussion and Conclusions

Here, we report on the comparative analyses conducted on the 49,000 year-old humeral fossil remains discovered at the El Sidrón site (Spain). Aspects related to within-sample variation and the phylogenetic significance of some taxonomically meaningful features are addressed. Comparisons between neandertal and modern humans received more specific attention. Indeed, in agreement with previous studies, centroid size comparisons confirmed that major differences between these two groups could be found at both epiphyses. In addition, conspicuous shape differences have been detected at the different regions of the humerus.

Variability and Sexual dimorphism

From a 3D morphometrics viewpoint, El Sidrón humeri samples fell well within the neandertal cloud, occupying only a limited area of the morphospace. Also, discrete features indicated low phenotypic variation, possibly suggesting close genetic links among these individuals. This appears to be in accordance with mtDNA data (Lalueza-Fox et al., 2012) and dental development alterations (Dean et al., 2013). Thus, there are solid grounds for considering that El Sidrón neandertal individuals are derived from a single biological population. Also, In spite of the chrono-geographical dispersion of neandertal samples, the level of variation observed is even lower than that found in local modern human samples. So far, humerus evidence has reinforced this notion of low species variation among neandertals (Castellano et al., 2014).

Although sex assessment of the El Sidrón humeri has been attempted, high levels of uncertainty persist. On average, sex-related size and shape differences have been found in modern human populations. Nevertheless, high overlap has been found between sexes, making individual sex diagnosis challenging. In a similar way, PCAs of shape coordinates do not show a clear distinction between the El Sidrón humeri from estimated males and females. This is also true for other previously sex-estimated neandertal specimens. These findings may suggest that a moderate/low structural sexual dimorphism is present in neandertal humeri, which would be similar in magnitude to that found in modern humans. Indeed, this is in agreement with conclusions reported by Trinkaus (1980) and Heim (1983). In contrast, a high degree of sex variation has been proposed with regard to left–right differences in cortical thickness (Ben-Itzhak et al., 1988; Aiello and Dean, 1990), indicating greater weight and/or functional variability between the sexes in neandertals than in *H. sapiens* (Ben-Itzhak et al., 1988). This structure–function dimorphism between the sexes could be controlled largely by genetic factors or develop epigenetically along the individual life. For example, greater use of the right arm in males may result in greater development of morphological aspects that are then intensified with further exercise and use. Notably, functional sexual dimorphism cannot be evaluated directly based on the El Sidrón sample, as we lack certainty as to whether taphonomically disconnected humeral specimens (right and left) belong to the same individual.

Phylogenetic meaning of the humerus features

Taken together, humeral shape presents a conspicuous and consistent pattern of differences among hominid samples, with dispersion in the morphospace closely matching standard taxonomic categories (Figures 9-11), with the exception to Australopithecines. For example, chimpanzees occupy a restricted and distinctive area within the different PC1–PC2 subspaces, which is in agreement with Arias-Martorell et al. (2012) and Holliday and Friedl (2013), defining clearly differentiated shapes. In contrast, *Australopithecus* humeri display a high degree of dispersion, as already found by Senut (1980), Aiello and Dean (1990), and McHenry and Brown (2008). However, Bacon (2000) and Lague (2014) reported a contrary finding. Also, all shape multivariate analyses revealed discrete and consistent differences between modern humans and neandertals, with very limited overlap. Thus, results of this study reinforce the idea that the humerus represents a useful tool for phylogenetic reconstruction (Lague and Jungers, 1996; McHenry and Brown, 2008; Lague, 2014).

Due to its superior preservation, a more accurate picture can be extracted from analysis of the distal humerus region. Modern humans present relatively small olecranon fossa and wide lateral pillars. Interestingly, our analyses revealed the WT-15000 Early Pleistocene African humerus distal epiphysis fell within the middle of the modern human sample (also with regard to the diaphysis), which may imply a primitive morphology for *H. sapiens*. Similar scoring in multivariate analyses of primitive species (e.g., *Australopithecus anamensis* and early *H. erectus/ergaster* represented by Nariokotome) indicated wide distodorsal pillars and relatively narrow olecranon fossa in the plesiomorphic state. In addition, according to Bermúdez de Castro et al. (2012), the 1.9 Ma old Dmanisi humeri displayed a similar pattern, reinforcing this hypothesis. However, in this regard, we do not detect a common pattern for australopithecines, which show a wide range of variation. For instance, ER 739 and *A. anamensis* (KP 271) occupied opposite locations in the morphospace.

In contrast, relatively wide olecranon fossa and thin lateral and medial distodorsal pillars have been commonly found in neandertals, as well as in the SH-Atapuerca sample (Arsuaga y Bermúdez de Castro, 1984; Carretero et al., 1997). When observed in multivariate analyses, neandertals score systematically at different positions of the distribution when compared to modern humans (see Figures 9, 10 and 12), which indicates that this morphology might be considered as an apomorphic state.

From a historical perspective, the conspicuous differences detected when comparing modern human and neandertal morphology allowed the use of the so called “neandertal features”. Currently, comparison of these two human groups with new 3D methodologies certainly confirms the hypothesis of a neat shape difference between them. However, enlarging the analyses focus, looking at the evolution of *Homo* scale, the use of the so called “neandertal features” has become extremely misleading. Two factors impact on this. On the one hand, the current perception that modern humans and neandertals shared a relatively recent last common ancestor (LCA) during the mid-Middle Pleistocene (Endicott et al., 2010) (against the hypothesis of an earlier Lower Pleistocene LCA, characterized by *H. antecessor*, Bermúdez de Castro et al., 1997). And, on the other hand, the fact that “neandertal morphology” has also been detected in the Lower Pleistocene TD6-Atapuerca remains, which corresponds to a time that predates the hypothetical LCA for neandertals and modern humans (Bermúdez de Castro et al., 2012), as well as in Middle and Upper Pleistocene samples (supposedly outside the

phylogenetic neandertal lineage). Therefore, at least for some features, the use of “neandertal features” is certainly incorrect as these traits are not exclusive of its evolutionary line. But, in the case of the distal humerus, we found that the morphological pattern recording those classic “neandertal features” is certainly stable and well defined. Consequently, a phylogenetic signal can be recognized in the humerus morphology. How can we interpret the corochronological pattern of variation in *Homo* samples?

As stated in the introduction, Bermúdez de Castro et al., (2012) set up a frequency-based model related to the polymorphic nature of features. Based on this, the derived condition (e.g., “neandertal features”) would have appeared in a pre-*Homo antecessor* population (but posterior to *H. ergaster*), who should have maintained a relatively high frequency of the plesiomorphic state for the feature. Certainly, this model uses a population genetic rationale in which shape features can be equivalent to “morphological alleles”. Thus, descendant populations from this pre-*Homo antecessor* population would have differentially inherited the primitive and derived allele. In particular, late Early Pleistocene European populations would have received a much larger amount of these alleles. In Africa, descendant populations should have maintained both primitive and derived states at different frequencies, becoming relatively fixed only late in *Homo sapiens* evolution.

In this context, it might be speculated that fixation of these traits in different populations could stem from the existence of local bottlenecks. Therefore, the communality of features in European Early and Middle-Late Pleistocene populations may not imply phyletic continuity. Nevertheless, the low variation detected in the large sample from Atapuerca-SH suggests that this pattern was already fixed in Middle Pleistocene populations. Neandertal samples show a similar pattern, and the El Sidrón intra-sample variability appears to confirm that these features were fixed at the population level.

An alternative hypothesis to the frequency model states that the primitive condition found in *H. sapiens* represents an evolutionary reversal, as indirectly suggested by Trinakus (2012). This possibility was considered in the more general framework of the hominin postcranial skeletal evolution when McHenry and Brown (2008) hinted at the possibility of reversal. However, methodological difficulties at the time of their study did not allow for testing of the hypothesis. Finally, homoplastic plasticity cannot be discarded as a possible contributing factor.

In addition to the distal epiphyseal features that were considered above, neandertal and modern humans also present differences in other anatomical areas of the humerus. Among them, morphometric analyses revealed a greater projection of the lesser tubercle, the neandertals and Atapuerca-SH humeri show a massive and anteriorly projecting lesser tubercle and a closer position to the surgical neck (Vandermeersch and Trinkaus, 1995; Carretero et al., 1997). A so-called “close” deltoid tuberosity (*sensu* Carretero et al., 1997) with a double crest being the most frequent for the Middle Pleistocene and classic neandertal fossils (Carretero et al., 1997). In combination with other muscular markings in the diaphysis, indeed, the same was reported by Carretero et al. (1997) for the SH-Atapuerca sample. Also the variation could be indicating an age-related factor (Wilczak, 1998; Alves Cardoso and Henderson, 2010; Milella et al., 2012; Villote and Knüsel, 2013; among others) Also, the coracobrachialis muscle attachment site is located in a lower position in neandertals. PCA, which incorporated

landmark recording of these regions, seemed to indicate a consistent pattern of feature covariation and taxonomic distribution in the morphospace (Figures 12 and 13).

Furthermore, independently of the size, neandertals and Atapuerca-SH hominins display a transversally-expanded humeral head (Basabe, 1966; Carretero et al., 1997), giving rise to a transversally oval shape. On the other hand, modern humans show an oval shape in the vertical dimension. This vertical oval morphology is also present in *Australopithecus*, suggesting that modern humans may represent a plesiomorphic condition, whereas the transversal oval humeral head may be derived from the European *Homo* clade (Carretero et al., 1997).

Functional/Structural meaning of the anatomical features

Previously, it was proposed that several anatomical features of the humerus might collectively vary as part of a single biological factor. For example, shape of the deltoid tuberosity has been related to humeral torsion angle (Carretero et al., 1997) in such a way that a “close” morphology of the deltoid tuberosity (independent of the metrical width) corresponds to a low humeral torsion. Our results support this conclusion even though Churchill and Smith (2000) did not find a significant correlation between humeral torsion and deltoid tuberosity width.

Explaining the variation in humeral torsion angle and integrated features has been approached from distinct lines of evidence. Evans and Krahl (1945) reported that humeral torsion is the result of an interaction of two factors. The first one suggests that primary torsion is determined by genetic or evolutionary factors without much variation in different populations. However, there is also a secondary or ontogenetic torsion that is produced by muscular forces, and it is this torsion that produces the greatest differences among populations and individuals.

In modern human populations, humeral torsion displays large intra- and inter-population variability. This feature changes as a function of sex, age, and activity. Indeed, it is higher in females, adults, and on the non-dominant side (Rhodes and Churchill, 2009). The Humerus 3 from El Sidrón has a torsion angle of 150°, which represents an elevated value for neandertal humeral torsion. Nevertheless, it must be noted that the torsion angle was mostly measured in right humeri, and most neandertals are right-handed (Uomini, 2011), including the El Sidrón sample (Estalrich and Rosas, 2013). Thus, one might expect that the humeral torsion on the left side would be greater than the right. For example, La Chapelle-aux-Saints has a lower humeral torsion in the right humerus (142°) than in the left (156°) (Heim, 1982). Considering these data, the humeral torsion in Humerus 3 is within of the neandertal range. On the other hand, La Ferrasie 1 has a similar humeral torsion in both humeri (135° in right and 134° in left, Heim, 1982). Thus, neandertal humeral torsion shows a range of variability similar to that of modern humans.

Several studies (Rhodes 2005; 2006; Crockett, 2002; Pieper, 1998; Roach 2012) have analyzed the relationship among humeral torsion and activity patterns in modern human populations. All of them have observed that lower torsion is correlated with higher activity levels. This explains the variability in current populations and differences related to sex and side. However, humeral torsion differences in modern human samples are also present in early development, so it is important that genetic factors are not ignored (Cowgill, 2007).

From a structural viewpoint, humeral torsion is related to a greater anteroposterior depth of the upper thorax in neandertals (Churchill 1994; 1996; Rhodes and Churchill 2009). In a broader comparative and anatomical framework, humeral torsion is also related to the glenoid fossa orientation and the position of the scapula (Martin, 1933; Aiello and Dean, 1990; Larson, 2007b). In this regard, a different position of the neandertal scapula is likely due to their apparently narrow upper thorax morphology, which is suggested by the small size of upper neandertal ribs in relation to the lower ones (Carretero et al., 1997; Gómez-Olivencia et al., 2009, Bastir et al., 2013; García-Martínez et al., 2014; Bastir et al., accepted). Such rib cage morphology would indirectly affect the connections with the shoulder girdle and upper limbs.

Humerus shape and body form

Based on these findings, one may posit that the origin of some of the so called “neandertal features” of the humerus might be associated with a common anatomical evolutionary phenomenon (e.g., body shape). In this respect, neandertal thorax features have been interpreted in the context of a “primitive body plan” (Gómez-Olivencia, et al. 2009), rather than a neandertal autoapomorphy. In the case of the humerus, its morphology may be related to body shape and the way the forelimb is connected to the trunk (Churchill, 1994; 1996; Larson, 2009). As a direct consequence, the aforementioned features of the distal epiphysis have to be seen in the context of a more far-reaching anatomical complex that would affect the relative position of both head and distal humeral ends.

Evidence resulting from analysis of the distal humerus, however, may fit well with Ruff’s (1991) body shape evolution model. Indeed, a post-*ergaster* and pre-*antecessor* population may have shifted to heavier bodies, which are shared by most of the late Early and Middle Pleistocene, with *H. sapiens* shifting back to a slim body shape. In this regard, there is discussion as to whether *H. ergaster* showed a wide body or not (Arsuaga et al., 1999; Carretero et al., 2004). Nevertheless, even though body breadth might have increased (contra Ruff and Walker, 1993), shoulder articulation, pectoral girdle (Larson, 2009), and the possible retention of an elongated upper limbs (Holliday, 2012) has led to the idea that there were structural differences between early *Homo ergaster/erectus* and later *Homo*. In that case, the “primitive body plan” described by Gómez-Olivencia et al., (2009) cannot be used as a reference any more. In fact, what we are inferring is that the new body shape might have emerged in a post-*ergaster* and pre-*antecessor* population, upon which derived postcranial features developed. Indeed, our humerus evidence may support a model in which some of the historically called “neandertal features” (shared by post-*ergaster* samples) might be associated with a, in fact, “derived body plan” (similar to other postcranial features [e.g., large chest]). For its part, the relatively narrow bi-iliac breadth of *H. sapiens* would be considered as an autoapomorphy (Holliday, 2012). By extension, the similarity between early *H. ergaster/erectus* and *H. sapiens* distal humerus would be the result of homoplasy. In other words, the appearance of *H. sapiens* morphology would only be secondarily primitive.

Although this study cannot provide a conclusive answer with regard to this topic, geometric morphometric analyses point to a consistent pattern of covariation between different parts of the humerus bone: head, diaphysis and distal epiphysis. Whatever the final cause of this intra and interspecific variation, common determinants appear to be the basis for a certain amount

of it. Nevertheless, further studies could be performed to address specific hypotheses related to this covariation (e.g., using PLS methods). However, until confirmation can be achieved via the analysis of more fossils or through a better understanding of these functional and integration patterns, we hypothesize that most of the variable features identified between neandertal and modern humans are associated with differences in the pectoral girdle and shoulder joint structures.

From a functional viewpoint, rather than interpreting the so called “neandertal features” of the humerus in an isolated way, we have related them to a more fundamental anatomical complex that involves variations in the glenoid-humeral and dorso-medial orientation linked to a barrel-shaped thorax (Churchill, 1994; 1996; Carretero et al., 1997; Larson, 2007b; Larson, 2009). This interpretation is further framed in the more general context of quadruped and ortograde body habit, scapula position, and glenoid orientation (Aiello and Dean, 1990). If this hypothesis is true, then a general change in the basic body architecture took place at some point in the *Homo* lineage to give rise to neandertals.

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FIGURES AND TABLES

Figure 1: Anatomical location of the landmarks in anterior (A) and posterior (B) humerus view. (C) Proximal epiphysis in superior view. Numbers indicate the anatomical position of the landmarks, and red lines are the wireframes used for visualization.

Figure 2. Anterior view of the right humeri from the El Sidrón site (Asturias, Spain) (scale in cm).

Figure 3. Posterior view of the right humeri from the El Sidrón site (Asturias, Spain) (scale in cm).

Figure 4. Anterior view of the left humeri from the El Sidrón site (Asturias, Spain) (scale in cm).

Figure 5. Posterior view of the left humeri from the El Sidrón site (Asturias, Spain) (scale in cm).

Figure 6. Detail of the deltoid tuberosity morphology in the Humerus 5 and Humerus 6 from the El Sidrón site (Asturias, Spain) in lateral view (scale in cm).

Figure 7. Olecranon fossa detail of the 2 and 4 right humeri, and 3 and 7 left humeri from the El Sidrón site (Asturias, Spain). Note the elevated remodeling activity.

Figure 8. Box and whisker plot for some relative dimensions of the distal humeri. (A) Medial pillar index (medial pillar thickness/olecranon fossa breadth)*100 calculated for El Sidrón sample. (B) Lateral pillar index (lateral pillar thickness/biepicondylar breadth)*100 calculated for El Sidrón sample. Comparative data from Bermúdez de Castro et al. (2012; Table 3, p. 609). Numbers in parentheses indicate samples sizes.

Figure 9. Scatter plots of the PCA shape space in distal humerus, representation the first two PCs (PC1-PC2). Green rhomboids represents the modern humans populations, orange rhomboids the neandertal sample (Feldhofer r,l; La Ferrassie1l; Regourdou 1 r,l; Spy 1 r; Spy 2 r, l; Krapina 159, 160, 162, 166, 169, 170, 171, 174 and Lezetxiki), red rhomboids the El Sidrón fossils (Humeri 1, 2, 3 and 7), black rhomboids is KNM-WT 15000, blue rhomboids is Australopithecus sample (KNM-ER 739; STW 431; A.L. 288-1s and KNM-KP 271) and red cross is the chimpanzee sample. A picture with the wireframes laid is presented on top.

Figure 10. Minimum spanning tree (MST) projected onto principal components space of distal humeri sample.

Figure 11. Complete-linkage clustering of distal humeri sample. (MH: modern human, Ch: chimpanzee)

Figure 12. Scatter plots of the PCA shape space in the diaphysis, representation the first two PCs (PC1-PC2). Green rhomboids represents the modern humans populations, orange rhomboids the neandertal sample (Feldhofer r, l; La Ferrassie1 r, l; Regourdou 1 r; Spy 1 r, l; Spy 2 r, l; Krapina 165, 167, 168, 177 and Lezetxiki), red rhomboids the El Sidrón fossils (Humeri 3, 5, 6 and SD-2143), black rhomboids is KNM-WT 15000, blue rhomboids is Australopithecus sample (KNM-ER 739 and A.L. 288-1m) and red cross is the chimpanzee sample. A picture with the wireframes laid is presented on top.

Figure 13. Scatter plots of the PCA shape space in complete humerus, representation the first two PCs (PC1-PC2). Green rhomboids represent the modern human populations, orange rhomboids the neandertal sample (Feldhofer r, Regourdou1r and Lezetxiki), red rhomboids the El Sidrón Humerus 3 and red cross is the chimpanzee sample. A picture with the wireframes laid is presented on top.

Table 1. El Sidrón fossil humeri collection. Inventory number, side and ontogenetic period of each fragment are shown.

Catalog number of the specimens	Humerus number	Side	Age and individual attribution	Sex estimation	Preserved region
SDR-036 + SDR-042	Humerus 1	Right	Adult 1, 2 or 6	Male	Distal fragment.
SD-929 + SD-356a	Humerus 2	Right	Adult 1, 2 or 6	Male	Distal fragment.
SDR-035 + SDR-041	Humerus 3	Left	Adolescent 3	Male	The most complete humeri, the distal region of the distal join and the anterior part of the proximal epiphysis are absent.
SDR-037	Humerus 4	Right	Adult 3, 4 or 5	Female	Distal fragment.
SDR-038 + SDR-048	Humerus 5	Left	Adult 3, 4 or 5	Female	Diaphysis and distal fragment.
SDR-039 + SDR-040+ SD-736a	Humerus 6	Left	Adult 1, 2 or 6	Male	Diaphysis.
SD-1438	Humerus 7	Left	Adolescent 1	Male	Distal fragment without medial epicondyle (unfused).
SD-1208a + SD-1208c + SD-1329 SD-1433 + SDR-201 + SDR-207	Humerus 8	Right	Adult 3, 4 or 5	Female	Fragment of diaphysis and distal epiphysis.
SD-2143	Humerus 9	Left	Adolescent 2	Female	Diaphysis
SDR-046+ SDR-243	Humerus 10	Left	Adult		Distal shaft and lateral epicondyle.
SD-334a	Humerus 11	Right			Shaft fragment.
SD-1437+ SD-1511	Humerus 12	Right	Adult		Distal shaft fragment.
SD-695h	Humerus 13	Right	Adult		Distal shaft fragment.
SDR-047	Humerus 14	Left	Adult		Shaft fragment.
SD-1313 + SD-710	Humerus 15	Left	Adult		Shaft fragment.
SDR-218b + SDR-218f + SD-1343c	Humerus 16	Left	Adult		Shaft fragment.
SD-2180	Humerus17	Right	Juvenile 1		Proximal diaphysis (unfused).
SD-1717	Humerus18	Left	Juvenile 1		Distal diaphysis (unfused).
SD-1306		Right	Adult		Coronoid fossa.
SD-1322		Right	Adult		Proximal diaphysis.
SD-1656		Right	Adult		Shaft fragment. <i>Pectoralis major</i> attachment.
SD-1157		Right	Adult		Capitulum
SD-1122a		Left			Coronoid fossa.
SD-253		Left	Adult		Medial trochlea.
SD-1100 +SD-1163b		Left			Lateral trochlea.
SD-1332		Left			Shaft fragment. Deltoid attachment.
SD-1618		Left	Adolescent		Proximal epiphysis.
SD-1432		Left			Shaft fragment.
SD-362					Shaft fragment.
SD-1417					Shaft fragment.
SD-1163a					Trochlea fragment
SD-1425					Shaft fragment.

Landmark	Type	Description
1	2	Most projection of the lateral epicondyle
2	1	Proximal junction point between lateral epicondyle and capitulum
3	1	Distal junction point between lateral epicondyle and capitulum
4	3	Middle curvature point of the lateral trochlea
5	3	Middle curvature point of the trochlear groove
6	3	Middle curvature point of the medial trochlea
7	2	Proximal junction point between medial trochlea and medial epicondyle
8	2	Most projection of the medial epicondyle
9	1	Proximal anterior point of the lateral trochlea
10	1	Proximal anterior point of the medial trochlea
11	1	Proximal posterior point of the lateral trochlea
12	1	Proximal posterior point of the medial trochlea
13	2	Proximal point of the olecranon fossa
14	2	Distal point of the olecranon fossa
15	2	Lateral point of the olecranon fossa
16	2	Medial point of the olecranon fossa
17	2	Most inflexión between medial epicondyle and shaft
18	2	Most prominence of the lateral supracondylar ridge
19	1	Proximal point of the lateral supracondylar ridge
20	2	Middle point of the coracobraquial insertion
21	1	Distal point of the lateral crest of the deltoid tuberosity
22	1	Proximal point of the lateral crest of the deltoid tuberosity
23	1	Distal point of the medial crest of the deltoid tuberosity
24	1	Proximal point of the medial crest of the deltoid tuberosity
25	1	Distal point of the greater tubercle crest
26	1	Distal point of the lesser tubercle crest
27	2	Posterior point of the greater tubercle surface
28	2	Lateral point of the greater tubercle surface
29	2	Proximal point of the greater tubercle surface
30	2	Medial point of the greater tubercle surface
31	2	Most proximal point projected of the medial surface of the greater tubercle
32	2	Proximal anterior point where intertubercular groove is between both tubercles
33	2	Most projection of the lateral surface of the lesser tubercle
34	2	Proximal point of the lesser tubercle surface
35	2	Anterior point of the lesser tubercle surface
36	2	Distal point of the lesser tubercle surface
37	2	Posterior point of the lesser tubercle surface
38	1	Junction point between the humeral head perimeter and long head of the biceps brachii
39	2	Proximal point of the humeral head perimeter
40	2	Posterior point of the humeral head perimeter
41	2	Distal point of the humeral head perimeter
42	2	Anterior point of the humeral head perimeter
43	3	Middle point of the humeral head

Table 2: Landmarks list, categorization and description.

Distal epiphysis (Lm: 1-18) N=22			
Complete	Incomplete	Estimating Lm	Estimating method
Feldhofer (r, l)	Ferrasia (r, l)	13	Spline
Sidrón H.2 (r)	Sidrón H.1	8	Spline
Sidrón H.4 (r)	Spy 1(r)	8	Spline
Regourdou 1 (r, l)	Spy 2 (r)	1-3	Regression
Spy 2(l)	Krapina 169(r)	8	Spline
Krapina 160 (l)	Krapina 171 (r)	2-3, 6, 8	Regression
Krapina 162 (l)	Krapina 174 (r)	8, 13, 17	Regression
Krapina 170 (r)	Sidrón H.7 (l)	8	Spline
Lezetxiki (r)	Krapina 159 (l)	8	Spline
	Krapina 166 (l)	18	Spline

Table 3: List of fossils employed in distal epiphysis analysis. With estimation method and estimated landmarks used in incomplete fossils (r: right, l: left).

Diaphysis (Lm: 13, 17-26) N=18			
Complete	Incomplete	Estimating Lm	Estimating method
Feldhofer (r, l)	Krapina 177 (r)	17	Spline
Ferrassie (r, l)	Sidrón H.6 (l)	17	Spline
Sidrón H.3 (l)	Sidrón H.9 (l)	13, 18, 26	Spline
Sidrón H.5 (l)	Spy 2 (r)	26	Spline
Regourdou 1 (r)	Spy1 (r)	22	Spline
Spy 2(l)	Spy1 (l)	13, 17-18	Spline
Lezetxiki (r)	Krapina 165 (l)	22, 24-26	Spline
	Krapina 167 (l)	13, 17-18	Spline
	Krapina 168 (l)	17	Spline

Table 4: List of fossils employed in diaphysis analysis. With estimation method and estimated landmarks used in incomplete fossils (r: right, l: left).