

TITLE PAGE

Updated study of adult and subadult pectoral girdle bones from Sima de los Huesos site (Sierra de Atapuerca, Burgos, Spain). Anatomical and age estimation keys

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MAIN TEXT

Abstract

Here we present an updated inventory and a study of the pectoral girdle remains recovered from Sima de los Huesos (SH) site up to the present. We describe the morphological key traits of the adult and, for the first time, subadult specimens. Since morphological traits can change with age, we also discuss some of the shortcomings related to age estimation in postcranial fossil specimens. Adult clavicles from SH are absolutely long, with low robusticity index and marked curvatures in superior view. Among these traits, only the extreme clavicular length seems characterize the subadult individuals. All these traits are shared with Neandertals. In the case of the scapula, the SH specimens share with the Neandertals a relatively long and narrow glenoid fossa. This trait is also present in subadult individuals. Additionally, most specimens from SH, adults or subadults, show a dorsal axillary sulcus on the scapular lateral border, a trait also present in most adult and subadult Neandertals. The presence of these traits in adult and subadult specimens, supports a strong genetic control for many of them in both human species.

Key Words: clavicle, scapula, Sima de los Huesos, growth, age at death.

1. Introduction and objectives

The numerous studies about shoulder morphology in genus *Homo* have shown that this skeletal region underwent major structural changes over the course of evolution (Churchill and Trinkaus, 1990; Bramble and Lieberman, 2004; Voisin, 2006; Larson, 2007; Voisin, 2008; Di Vincenzo et al., 2012; Roach et al., 2013; Macias and Churchill, 2015; Roach and Richmond, 2015; Rosas et al., 2016; Feuerriegel et al., 2017; Rodriguez-Perez et al., 2018). These structural changes have been inferred from morphology of each of the bones forming the pectoral girdle (clavicle and scapula) along with the humerus. While some authors propose that modern human shoulder morphology appeared around 1.8 million years ago (Ma) with the species *Homo ergaster* species (Roach and Richmond, 2015), others proposed that the special configuration of the modern human (MH) pectoral girdle evolved later, possibly with *Homo antecessor* dated around 1 Ma (Larson, 2007). These different shoulder morphologies have been suggested to relate to different adaptations, such as throwing performance (Roach et al., 2013), manipulative capabilities (Larson, 2007), or endurance running (Bramble and Lieberman, 2004). Thus, much of the debate over evolution of the pectoral girdle is associated with the evolution of human behaviors. However, besides the changes in some traits of pectoral girdle that may have postural and/or biomechanical implications, they can also present a phylogenetic signal that can help us understand the tempo and mode of evolution in our genus.

Unfortunately, our knowledge on the evolution of the pectoral girdle in the genus *Homo* is hampered by a geographically and chronologically scattered fossil record. For example, prior to work at the Sima de los Huesos (SH) site, the Middle Pleistocene postcranial fossil record in Europe was very incomplete. Even less material is known from Africa and Asia. Thus, the Middle Pleistocene SH fossil collection provides the rare opportunity to thoroughly characterize the postcranial skeleton in a fossil population, only comparable to that obtained in the study of the Neandertal hypodigm and recent (and fossil) modern humans.

In this paper, we will describe and illustrate the main morphological characters and their variation within the SH sample, comparing, when possible, to other fossil hominines and recent humans. From these descriptions and comparisons, we will try to infer some paleobiological aspects, such as sexual dimorphism or body proportions, mechanical or functional aspects of the pectoral girdle, individual or ontogenetic variation and phylogenetic clues, when it is possible for each bone and feature.

For our purposes here, we consider it more useful to combine the description and discussion of each mentioned anatomical trait.

2. Material and methods

2.1. SH sample

The material objects of this study are the pectoral girdle remains recovered from SH between 1976 to the present day. Some of these remains have been previously studied and described elsewhere (Carretero et al., 1997). Systematic excavations in SH have allowed us to recover more human fossils and to reconstruct some complete bones of the scapular girdle. A brief update of some of these new remains was presented by Arsuaga et al. (2015). Here, we provide more detailed anatomical descriptions and metric analysis of the most complete bones of the scapular girdle, mainly based on adult specimens. In cases where it was possible, morphological characteristics of subadults were reported for the first time.

All human remains recovered from SH are labelled as AT followed by Arabic numeral. When a clavicle preserved the acromial one-third and a scapula the glenoid fossa, the label of these remains is represented by the letters Cl (in the case of the clavicle) or Esc (in the case of scapula) and a Roman numeral. These labels indicate that these remains represent at least one bone.

Among the clavicular remains, there are two complete adult clavicles (Table 1, Figure 1 and Figure 2) and three belonging to three different subadult individuals (Table 1, Figures 3, 4 and 5). In addition to these complete clavicles, there are three adult clavicles in which maximum length can be estimated with some precision (Table 1, Figure 6, 7 and 8).

[INSERT TABLE 1 HERE]
[INSERT FIGURES 1,2,3,4,5,6 AND HERE]

Among the scapular remains, 20 belong to adult individuals and 13 to subadult individuals (Table 2). None of the scapular remains are complete. The most complete are depicted in Figures 9, 10, 11, 12, 13, 14 and 15. Due to the incompleteness of the scapular remains, anatomical details will be explored in the glenoid fossa (SGF) and axillary border.

[INSERT TABLE 2 HERE]
[INSERT FIGURES 9,10,11,12,13,14 and 15]

2.2 Comparative samples

For comparative purposes, we have also studied the following original fossil specimens: those of the TD6 level from Gran Dolina site (Atapuerca), the Roc de Marsal child (Musée National de Préhistoire, Les Eyzies de Tayac, France) and La Ferrassie 1 (Musée de l'Homme, Paris) and the casts of Amud 7, KNM-WT-15000 and Kebara 2, also housed in the Musée de l'Homme de Paris. For other fossils, we have derived data from different bibliographic sources. Mainly, data from the main dimensions of adult clavicles were derived from McCown and Keith (1939a), Trinkaus (1983a, 2016), Vandermeersch and Trinkaus (1995), Lordkipanidze et al. (2007), Walker et al. (2011), Trinkaus et al. (2014) and Rosas et al. (2016). Those for clavicular curvatures were derived from Voisin (2006; 2008), and those for scapular dimensions were taken from Di Vincenzo et al. (2019)

In addition to these original or bibliographic data, we have also studied several MH samples. The modern comparative samples employed in this study comprise adult and subadult specimens. The first comparative sample is called “Portuguese sample” which was drawn from the individuals belonging to the collections housed in the Bocage Museum (National Museum of Natural History, Lisbon, Portugal) and in the Department of Life Sciences at Coimbra University (Coimbra, Portugal). Both collections come from modern cemetery sources and consist of Portuguese people who lived in the nineteenth and twentieth centuries representing the middle-to-low social class of the cities of Lisbon and Coimbra (Cardoso, 2006; Coqueugniot and Weaver, 2007). The second sample is composed of individuals of known age at death from the Hamann-Todd collection (HTH) housed in the Cleveland Museum of Natural History in Ohio (USA). This sample was divided into two subsamples based on whether these individuals were African American or with a European ancestry. The third sample is composed of individuals from the archaeological collection from San Pablo (Burgos) housed in the Laboratory of Human Evolution. These individuals were classified as adult or subadults. In the adults, sex was estimated based on non-metric traits of the skull and pelvis using the standard described in Buikstra and Ubelaker (1994). In the case of subadults, age at death was estimated based on the calcification and formation of dental crowns and roots. The mineralization stages of each tooth class were obtained analyzing 3D volume renderings from CT-scans. The developmental stages of the permanent dentition were scored using the method of Demirjian et al. (1973), and they were converted into age following the adjusted data for prediction proposed by Liversidge et al. (2006). For deciduous dentition, we used the method developed by Liversidge and Molleson (2004)

2.3 Measurements

To take all measurements in SH specimens and in our comparative samples, we used standard anthropological techniques and instruments (caliper and osteometry board). The exception were the measurements of clavicle curvatures, which were measured digitally.

To do that, we took photographs in superior and posterior view to characterize clavicular curvatures in the transverse and coronal planes, respectively. We drew the outline of each of these photographs using the AUTOCAD software. From these outlines, we established the midline curve in both, superior and posterior view. To do that, we draw several thickness measurements across the length of the clavicles. From

these measurements we establish the midline point and then, we draw a curve united them. Lastly, we established in each of these curves the length of the chord and the height of the curvature (subtense). These measurements were used to calculate the middle arc of curvature according to Olivier's method (1951). In the transverse plane, we calculated two curvatures: one acromial (external) and one sternal (internal). The external or acromial curvature was calculated as the ratio between external subtense and external chord. The internal or sternal curvature was calculated as the ratio between internal subtense and internal chord. Figure 16 depicts the steps followed to measure these curvatures digitally.

[INSERT FIGURE 16 HERE]

The coronal plane exhibits more subtle curvatures, and modern human clavicles can be classified into three groups. Type I clavicles possess only an inferior curvature. Type II and Type III display two curvatures in dorsal view. While in Type II clavicles, the superior curvature is at the sternal end and the inferior curvature at the acromial end, in Type III the reversal condition is presented. Thus, we classified the different clavicles into these groups, and, in each group, we measured the correspondent chords and heights (Figure 17).

[INSERT FIGURE 17 HERE]

2.4 Estimations of maximum clavicular length

Given the importance of maximum clavicular length in comparative analysis, we decided to estimate this dimension in the three adult specimens CI-I, CI-II and CI-III. To accomplish that, we used CT-scan images and 3D models to virtually reconstruct these clavicles. To do that, we took into consideration the shaft dimensions (diameters and perimeters) and anatomical landmarks, such as conoid tubercle and costal impression, and employed as reference the complete CI-V.

2.5. Age at death estimations

Due to the fact that metric and morphological traits change with age, for correct comparisons of subadult specimens a precise determination of age at death is important to avoid misinterpretations. In the majority of SH specimens only the adult or subadult status could be assessed, but for the most complete subadult ones, we used the pattern of growth and development of modern clavicles and scapulae to estimate the most probable age at death.

Regarding the clavicle, clavicular length is the best variable to estimate age at death in subadult individuals. In contrast to other long bones, there are not many standards or methods for estimating age from clavicular length. However, there is the growth standard proposed by Black and Scheuer (1996) and the classical calibration model proposed by Cardoso et al. (2017). The Black and Scheuer's standard cannot be used to estimate age, since it provides the range of variation of clavicular length by age and not the variation in age per clavicular length (Cardoso et al., 2014; Stull et al., 2014). Thus, age estimation was based on the method proposed by Cardoso et al. (2017). These authors provide two models: one model for individuals younger than 2 years and another model for individuals 2 years of age or older. Given the size of the three complete subadult clavicles from SH, we discard the possibility that it belonged to

individuals younger than 2 years old. Moreover, three different models are given for each of these two age groups: one for females, one for males and one for both sexes combined. We employed the model for individuals for both sexes 2 years of age and older.

We are aware that these estimations can suffer of some shortcomings when applying it to fossil specimens. Probably, the most important issues are related to differences in body size and proportions and in the pattern of skeletal growth and development between fossil species and MH. Thus, in order to test the consistency of our estimations, we compared the age of five Neandertals of known dental age and that of KNM-WT-15000 with the age predicted with this method.

Regarding age estimation for scapular remains, it is important to note that none of the scapulae from SH are complete. Although Cardoso et al. (2017) proposed models for age estimation from scapular measurements such as scapular glenoid fossa height and breadth, they should not be applied to the SH subadult scapulae. The SH adult scapulae show a glenoid fossa that is relatively longer and narrower than MH (Carretero et al., 1997; Arsuaga et al., 2015). This trait is already present in all subadult scapulae from this site (Salazar et al., 2021). Thus, ages can be over- and under- estimated from scapula glenoid fossa (SGF) height and breadth respectively. In contrast, the timing of union of these epiphyses have been extensively studied (Cardoso, 2008; Kothary et al., 2014), and several standards will be used in this study. However, these standards show some shortcoming since their utility is limited to adolescents. This is the developmental state for most subadult specimens from SH and thus, with these standards only an upper limit for the age interval could be estimated for many of them.

To perform most appropriate comparative analyses, it is more reasonably to try to estimate the age with more precision. In clinical contexts, maturity changes are frequently defined based on radiographic changes of epiphyses prior to their fusion. In the case of scapular development, these maturity indicators are related to the development of the bipolar growth plate and the appearance of the subcoracoid secondary centers of ossification. In this way, Kothary et al. (2014) asserted that the establishment of the bipolar growth plate occurred as early as 1 year and as late as 2 years. The next change in maturation in the glenoid-coracoid interface is the appearance of the subcoracoid center. The youngest age of appearance of this center is 9 years old and the oldest age of appearance is 12 years old (Kothary et al., 2014). Fusion of the subcoracoid center begins at about age 14-15 and completes by age 16-17 (Cardoso, 2008; Kothary et al., 2014). Thus, from 1 year old to 9-12 years old, we can only detect the formation of the bipolar growth plate in subadult scapulae. In the same way, we will detect the subcoracoid center from the age of its appearance (9-12 years old) to its fusion (14-17 years). If we could detect these changes in the skeletal remains, we would get a narrower age range before adolescence.

One of the problems with these maturity indicators is that they are defined based changes in the epiphyses prior to their fusion, which are usually difficult to duplicate using dry bone observations (Krogman and Iscan, 1987). For example, the small and relatively undifferentiated subcoracoid center may not be recovered or even identified. Thus, it is difficult to assess whether this secondary center of ossification has appeared. Fortunately, the appearance and developmental changes of secondary centers of ossification could be marked in the corresponding metaphysis of the primary centers of

ossification. This is the case in the development of the scapular glenoid fossa and glenoid-coracoid interface. When the formation of the bipolar growth has not yet occurred, the glenoid surface extends onto superior and ventral aspects for the place of fusion of the coracoid process forming both a contiguous and smooth surface (Figure 18).

[INSERT FIGURE 18 HERE]

The establishment of the bipolar growth can be recognized in two ways. First, the future site for the coracoid forms an angle with the glenoid fossa. Second, there are some furrows indicatives of the onset of vascular activity (Figure 18). With skeletal maturity, the bipolar growth plate becomes progressively thinner as the coracoid and scapula grow towards each other (Kothary et al., 2014). This leads to the future site of coracoid fusion mirroring the morphology of the base of coracoid. Thus, we can detect a billowed surface in this site (Figure 18).

The appearance of subcoracoid center is marked by a noticeable groove located supero-posteriorly in the glenoid fossa. This groove increases in size and depth as the secondary ossification center further develops (Figure 18). We use these morphological changes in the SGF to infer an age at death of SH scapulae with a narrower interval than if we only used the state of fusion. But it is important to note that we do not pretend to establish a method for age estimation based on maturity changes of the scapular glenoid fossa. Our intention is to find some developmental markers which help us to perform appropriate comparisons of subadult individuals. Thus, we have sorted the subadult scapulae in the documented comparative samples (see above) in the maturity stages described above. These age-ranges are compared to those derived from radiological studies about fusion of scapular epiphyses in order to test their congruence.

3. Results and discussion on the clavicle

3.1. MNI, MNE and age at death of the SH specimens

Within the SH sample, 14 is the minimum number of individuals (MNI) represented by right clavicles based on the insertion of deltoid muscle in the acromial one-third of the bone. Four of them are adults and ten subadults (Table 1). The minimum number of elements (MNE) is 22, 14 from the right side and 8 from the left side (Table 1).

Regarding age at death estimation of subadult clavicular remains, the model proposed by Cardoso et al. (2017) provides a mean age of 13, 14 and 15 years old for CI-IV, CI-VI and CI-XII, respectively. The prediction intervals are the following: 10.4-15.5 years for CI-IV, 11.4-16.6 years for CI-VI and 12.4 -17.6 years for CI-XII.

In Table 3, we show the estimated ages from clavicular length and from dental development for juvenile Neandertals and KNM-WT-15000. In the Neandertals, with the sole exception of Amud 7, the estimated age from clavicular length exceeds those estimated from dental age by 1.5 to 3 years. Indeed, dental age is closer to the lower limit of the prediction interval from clavicular length. The most notable difference between clavicular age and dental age is that shown by KNM-WT-15000, in which dental age exceeds by more than eight years the age estimated from clavicular length (Table 3).

[INSERT TABLE 3 HERE]

The lack of agreement between skeletal and dental age in these fossil specimens could be due to different reasons, such as For example, the relationship between dental and skeletal indicators of maturity and age, the differences in the response of dental and skeletal growth to environmental factors, the differences in the pattern of growth and development and/or the interspecific differences in body sizes and shapes among Neandertals, *Homo ergaster* and modern humans.

The relationship between dental and skeletal indicators and age have been intensively studied in the field of human biology. Several studies noted that differences between dental and skeletal age estimation can be as large as 3 years (Lewis, 1991; Clegg and Aiello, 1999; Smith, 2004). Dental age vs skeletal age differences in subadult Neandertals fall well inside of this range. However, it is important to note that in modern individuals, skeletal age exceeding dental age is relatively unusual: only 2.6% of boys and 0.8% of girls had dental ages 2 years or more below their skeletal ages (Lewis, 1991; Smith, 2004). Thus, it is difficult to assume that all Neandertals studied here show this unusual pattern of differences between skeletal and dental ages. Moreover, an important point is that differences between clavicular and dental age estimates are maintained when the dental age is inferred from histological methods (Table 3), which are species-specific and independent of both modern standards and the error associated with their applications. The ages calculated from histological methods are younger than those derived from modern schedules of dental development in all Neandertals, but the difference between histological age and skeletal age increase with age (Smith et al., 2007, 2010). Thus, this difference can be even greater in Neandertals such as Teshik-Tash. Based on this, we can discard the possibility that differences between skeletal and dental ages in Neandertals are due to different maturational processes.

The same is true if we consider the effect of environmental factors in dental and skeletal development. It has been confirmed by numerous scholars that subadult individuals of low socioeconomic status are frequently delayed in dental development but much more delayed in skeletal growth relative to children of higher socioeconomic status (Saunders et al., 2000; Cardoso, 2007; Conceição and Cardoso, 2011). But, again, in these cases is also common that dental ages exceed skeletal ones. However, it is important to note that the formula used here to estimate age from clavicular length is suitable for populations living under adverse conditions (Cardoso et al., 2017). This leads to an overestimation of age when this formula is applied to individuals/populations with a normal growth. Studies on enamel hypoplasia in Neandertals argued that they experienced nutritional stress during the development (Skinner, 1996; Guatelli-Steinberg et al., 2004). Moreover, some evidence points to a slower growth rate in Neandertals during infancy and early childhood compared to MH, probably due to ontogenetic constraints or to metabolic stress (Martín-González et al., 2012). Based on this, it is reasonable to assume that in the case of Neandertals, the overestimation of age from clavicular length is not the cause of differences between the dental and skeletal age estimates.

Thus, the most plausible explanation for the differences between clavicular and dental ages is a difference in the pattern of growth and development and/or in body size and shapes among these human species. Regarding KNM-WT-15000, Dean et al. (2001) asserted that the dental development in *Homo ergaster* is faster than in *Homo sapiens*. Moreover, the somatic growth curve of this human species may be unique, with no

adolescent growth spurt or with an early growth spurt with less duration than ours (Smith, 1993; Dean and Smith, 2009; Graves et al., 2010). For this reason, this specimen shows a difference of more than 8 years between dental and clavicular ages when modern standards are applied.

In the case of Neandertals, most studies have focused on dental development inferring an accelerated pace of general growth (Smith et al., 2007, 2010). In modern humans, dental development and skeletal growth show a moderate correlation, and individuals that are dentally advanced for their age also tend to be skeletally advanced (Šešelj, 2013). If we assume the same relationship between dental and skeletal development in Neandertals and MH, it is reasonable to infer that Neandertals showed an advanced skeletal development.

Several findings support an advanced skeletal development in Neandertals. First, clavicular growth and development in Neandertals is faster than in modern humans, a trait shared with *H. ergaster* (García-González et al., 2009). Second, Neandertals had relatively long femora for their age (Šešelj, 2017). In contrast, Rosas et al. (2017) have showed that maturation of most skeletal elements in a Neandertal juvenile from El Sidrón fell within the expected range of MH at this age. The exceptions were the development of the atlas and mid-thoracic vertebrae and brain growth. However, these authors also show that the length of clavicles of several Neandertal juveniles is longer than MH of the same ages, which they related to differences in body shape (shoulder breadth) between these two human species from early in ontogeny. Thus, it is reasonable to assume that the difference between clavicular age and dental age in Neandertals is due to differences in the skeletal growth patterns along with differences in body shape relative to MH.

Evidence from the relative development of the teeth and the time of formation of dental tissues support that SH hominins had a shorter period of dental development (Modesto-Mata et al., 2020; 2022). Moreover, SH hominins share with Neandertals the “wide *Homo*” body *bauplan* characterized by a large thorax with broad shoulders and pelvises and great body mass (Arsuaga et al, 1997; Carretero et al, 2012, 2018; Gómez-Olivencia et al., 2009, 2018; García-Martínez et al., 2014; Arsuaga et al., 2015). Thus, it is reasonable to assume that, as in the case of KNM-WT-15000 and Neandertals, age estimated in SH hominins from clavicular length is overestimated. Based on this, we can assume that the most probable age estimations for subadult clavicles from SH are those that are closer to the lower limit of the prediction interval. In this case, the most probable ages would be around 10, 11 and 12 years-old for CI-IV, CI-VI and CI-XII, respectively.

3.2 Clavicular maximum length

In Table 4 presents the main dimensions of the most complete clavicles from SH. Table 5 and Table 6 show the measurements and indices used for comparisons of recent and fossil samples of adult and subadult individuals respectively.

[INSERT TABLES 4, 5 AND 6 HERE]

The maximum lengths of the two complete adult clavicles from SH (CI-V and CI-VII) are higher than mean values for all MH samples, close to the top of the range of

variation for many of comparative samples used in this study (Table 4 and Table 5). However, these values are closer, although slightly below, the Neandertals (Table 5). This is because of they are shorter than some Neandertal clavicles, such as La Ferrassie 1 (179.0 mm and 178 mm), Kebara 2 (165.2 mm), Shanidar 3 (163 mm), Krapina 153 (185 mm) and SD 2100 (162.6 mm) (Vandermeersch and Trinkaus, 1995; Trinkaus et al., 2014; Rosas et al., 2016). Thus, although these two clavicles are long for a recent human, they are not especially long compared to Neandertals and ATD6-50.

The estimated maximum lengths of Cl-I, CL-II and Cl-III are 171, 176 and 170 mm, respectively. If we consider these estimates, the mean of clavicular lengths for the five adult clavicles from SH is 165 mm, which is well above the mean of all modern human samples and even the Neandertal mean (Table 6). Results of Mann-Whitney pairwise comparisons revealed that both Neandertals and SH clavicles are statistically significantly longer than MH clavicles.

Based on these results, we can assert than Neandertals and SH hominins possessed absolutely long clavicles. These long clavicles could be related to broad shoulders, since clavicle length is a significant predictor of shoulder breadth (Melillo et al., 2019). These broad shoulders would also be characteristic of the species *Homo antecessor* and *Homo ergaster*, based on the unusual clavicular length of KNM-WT-15000 for its age and the very large clavicle ATD6-50 (Carretero et al., 1997; García-González et al., 2009). These broad shoulders fit well within the “wide-body *Homo*” bauplan which is largely present in early and middle Pleistocene individuals and in Neandertals (Arsuaga et al., 2015). This bauplan is characterized by a medio-laterally (ML) wide biotype consisting of a large thorax with broad shoulders and pelvises.

However, the nearly complete clavicle OH-48 has an estimated length which falls well inside MH variation (Day and Scheuer, 1989). The range of variation of clavicles from Dmanisi are close to the bottom of the range of variation of MH samples (Lordkipanidze et al, 2007). Thus, it seems that these small-brained and small-bodied hominins did not possess a broad shoulder like MH. Arsuaga et al. (2015) proposed as the most parsimonious interpretation that the ML wide biotype was likely present in *H. habilis*. However, the clavicular lengths of OH-48 and Dmanisi specimens create some doubts about this hypothesis. One possible explanation is that the earliest members of *Homo* possessed a largely primitive shoulder configuration, like the earlier hominins (Larson, 2007), with different proportions between shoulder and pelvis breadth than later *Homo*.

In addition to the absolute length, another important trait is clavicular proportions relative to body size or other postcranial dimensions. Traditionally, clavicle length has been compared with humeral length using the claviculohumeral index. Based on this index, it has been claimed that Neandertals possessed clavicles that are relatively longer than MH. However, Trinkaus et al.(2014) cautioned about the use of this index, because humeral length is a poor proxy for body size within *Homo*. Instead, he proposed using body mass for assessing the relative sizes of clavicles and humeri. Following this approach, he established that relative to body size, the Neandertals did not have long clavicles, but rather they had short humeri.

Although we cannot yet calculate any of these indices for the SH individuals, we can still explore this issue.

The pooled sex-weighted mean body mass estimated from five adult SH femoral heads is 69.1 kg, which is only 6.3 kg below the Neandertal mean (75.4 kg) (Arsuaga et al.,

2015). The present sample of humeri from SH indicates that probably, on average, they were above the values that characterized the later Neandertals (Carretero et al. this issue, 2022). Thus, based on these data, the most parsimonious hypothesis is that SH hominins did not share short humeri with Neandertals. As we mentioned above, there are not statistically significant differences in clavicular length between SH hominins and Neandertals. Based on this finding and the fact that the large body mass characteristic of SH hominins was largely maintained in Neandertals, it seems reasonable to suggest that, as Neandertals, SH hominins did not possess relatively longer clavicles scaled to their body masses. Thus, the longer lengths of clavicles of Neandertals and SH hominins may simply be reflecting their body shape and high body masses.

Ideally, stature is a better proxy of body size than body mass for assessing the relative sizes of humeri or clavicles (Auerbach and Sylvester, 2011). Trinkaus et al. (2014) did not use stature due to the problems inherent in its estimation. Several studies suggest that stature estimations for fossil hominins should be based on equations derived from modern populations with similar body proportions and, in the case of fossil hominins (such as the SH sample), there is no way of knowing if the reference sample is representative of the population from which target specimen is drawn. However, Carretero et al. (2012) estimated stature in the SH sample and several Neandertals based on mixed sex and multi-racial regression formulae. In this way, these authors solve many of the methodological issues on the stature estimation in fossil specimens. Their results point out that the overall stature of the SH hominins (163.6 cm) is 3.0 cm taller than the mean stature in Neandertals (160.6 cm). Thus, SH humans were likely a slightly taller population than the Neandertals, who probably reduced their stature compared with their ancestors.

In our opinion, the evolution of stature in humans seems to have been characterized by a long period of stasis during which different *Homo* species varied little in stature throughout the Pleistocene, until the appearance 200ka of *Homo sapiens*. Because all large-bodied archaic human species are characterized by absolutely longer clavicles, the most parsimonious hypothesis is that all of them possessed relatively longer clavicles than MH when scaled to their statures.

3.3. Clavicular midshaft index

In all adult SH specimens, the shape of the clavicle midshaft cross sections is elliptical (flat), usually dorsoventrally compressed and never circular, thus the midshaft index (minimum/maximum diameter) is low. This is described as a “platycleidic” condition (Olivier, 1951a,b,c; Olivier, 1954a, 1954b, 1955a, 1955b; Olivier et al., 1954), where the midshaft index is usually below 80.

The five adult clavicles show a low midshaft index (<80) which is consistent with a platycleidic condition, *i.e.*, an elliptical cross-section at midshaft.

The MH samples used in this study show mean values also in agreement with this platycleidic condition. However, the midshaft index is variable among different modern human samples. For example, Olivier (1951-1956) reported a range for 25 sample means between 79.1 and 97.0. MH samples used in the present study show values in the lower limit of these means. Nevertheless, SH clavicles show a lower midshaft index than MH samples used here.

Most Neandertals show the platycleidic condition (77%, n=17) (Carretero et al., 1999), a mean value closer to the mean value of SH clavicles.

A low clavicular midshaft index was also common among the primitive populations of the genus *Homo*. This trait is present in the Zhoukoudian clavicle (76.3), the Olduvai clavicle OH-48 (70.3) and in the *H. antecessor* clavicle ATD6-50 (75.6) (Carretero et al., 1999). However, these values are higher than those shown by Neandertal and SH clavicles.

As in the case of adult specimens, the different age groups of subadult of our comparative samples show a platycleidic condition. The three complete clavicles from SH show a midshaft index with a lower value than all of these age groups.

3.4. Clavicular robusticity index

The midshaft circumferences of clavicles from SH are very close to both the Neandertal and the MH means. These midshaft circumferences produce robusticity indices ranging from 22.2 to 24.3. These values are at the lower end of the range of variation of the means of our MH samples. Interestingly, robusticity indices of SH clavicles are closer to the range of variation of the female means than to the male means (Tables 4 and 5). Neandertal clavicles also show a robusticity index towards the bottom of the MH range. Trinkaus (1983a) asserted that the low robusticity index of Neandertals is due to the extreme length of their clavicles. This could also be the case for SH clavicles.

We have discussed above that both Neandertals and SH subadults are also characterized by longer clavicles than is the norm for the modern children of the same age. However, in both cases, the robusticity index falls well inside of the range of variation of the four age groups depicted in Table 6. Thus, a low robusticity index would be attained in the latter stages of ontogeny, maybe as result of a great growth of the clavicular length in SH hominins.

3.5. Clavicular curvatures in cranial view

In cranial view, SH clavicles show the morphological pattern typical of modern humans and most of Neandertals: their external curvatures are more pronounced than their internal ones (Tables 4 and 5). However, SH clavicles exhibit some peculiarities with respect to this pattern. The external curvatures of Cl-V and Cl-VII are very high and well above the mean of MH (Tables 4 and 5). These values are comparable, although slightly higher than those shown by Taf XVI (20.8), Taf XIX-3 (20.5) and Taf XXVc (20.2) Late Upper Paleolithic (LUP) clavicles (Voisin, 2008). Cl-VII shows a lower value than Cl-V from SH, but still above the Neandertal mean. Its external curvature is comparable, although higher, than those exhibited for the left clavicle of Kebara 2 (16.5), the right clavicle of Neanderthal 1 (16.7) and Krapina 142 (16.7) (Voisin, 2008). Voisin (2001) explains the pronounced sternal curvatures in Neandertals as an effect of their extreme clavicular lengths. This may be the case in SH clavicles.

In contrast, values for the internal curvature of the two clavicles from SH fall well outside the range of variation of LUP and the lower extreme of Neandertals. Voisin (2001) asserted that both MH and fossils of the genus *Homo* are characterized by pronounced internal curvatures, which he related to the effectiveness of the muscle *pectoralis major*. The development of the internal curvature of the clavicle helps the elevation of the arm since it facilitates orientation of the glenoid fossa upwards. Following from this assertion, Neandertals and SH could show a different development of this muscle. However, it is important to note that the curvatures shown here were

derived from indices, and it is not clear whether the pattern of variation of these indices results from variance in the denominator (chord of the curvature), the numerator (subtense of curvature), or both. Although a more detailed analysis is needed to clarify this question, the most plausible hypothesis is that the lesser pronounced internal curvatures in Neandertals and SH hominins could be due to their clavicles show a longer sternal third than MH. In agreement to this hypothesis is the fact that subadult clavicles from SH show curvatures (both external and internal) falling in the range of variation of individuals of the different age groups used in this study (Tables 4 and 6). Thus, the lower values of internal curvatures could be attained due to a great growth of the length of the sternal one-third latter in ontogeny.

3.6. Clavicular curvatures in posterior view

SH clavicles display two curvatures in dorsal view: an inferior curvature at their acromial end and a superior curvature at their sternal end (Table 4). This corresponds with Type II, as is the case in all Neandertals that we have studied and the few known early Pleistocene specimens. In contrast, MH specimens show three curvature types.

Voisin (2001) proposed that curvatures in dorsal view affect shoulder height by mediating the relative positions of the acromial and sternal ends. Based on this, Type I clavicles are expected to co-occur with a descended configuration of shoulder, in which the medial and lateral articulations are positions in adjacent transverse planes. In contrast, Type II clavicles co-occur with a higher position of the shoulder. Based on this, SH individuals presented a high position of the scapula on the thorax. However, Melillo et al.(2019) asserted that the position of the scapula on the thorax is only minimally affected by clavicle curvature in dorsal view. Rather, the position of the scapula on the thorax is governed by clavicle orientation and rib declination (Melillo et al., 2019). Thus, based only in the curvatures in dorsal view, we cannot predict the position of the scapula on the thorax in SH hominins.

4. Results and discussion of scapulae

4.1 MNI, MNE and age at death of the SH specimens

Among the scapular remains, the MNI represented by right adult scapulae based on scapular glenoid fossa (SGF) is 9. The MNI represented by left subadult scapulae is also nine. Thus, we have a total MNI of 18 (Table 2). The MNE is 30, 13 for the right side and 17 for the left side.

Regarding age at death estimation, there are four subadult scapulae in which we can apply criteria about fusion of the secondary centers: Esc-VIII, Esc-XI, Esc-XII and Esc-XXX (Figure 19). Among these, the youngest individual is that represented by Esc-XXX. In this scapula, the subcoracoid center was fusing, but the fusion of the inferior centers has not yet begun. It also shows an unfused angle of the coracoid. This leads to an age interval between 11 and 13 years old (Cardoso, 2008; Kothary et al., 2014).

[INSERT FIGURE 19 HERE]

The next maturity stage is the one shown by Esc-VIII and Esc-XII. In those scapulae fusion of the subcoracoid center has already occurred, but the inferior ossification centers are fusing (Figure 19). The age interval for individuals represented by these two

scapulae is between 14 and 16 years old (Cardoso, 2008; Kothary et al., 2014). Finally, in Esc-XI, all secondary centers of glenoid fossa are fused, but the fusion of acromial epiphyses had not yet begun. The age interval for this scapula is between 16 and 17 years old (Cardoso, 2008; Kothary et al., 2014).

For the rest of scapulae, we must apply the maturity criteria based on the establishment of the bipolar growth plate and the appearance of the subcoracoid secondary center of ossification. But, as we have mentioned above, first we must test the congruence between the age ranges obtained with developmental markers defined in this study with those obtained in radiographic studies.

In our modern skeletal sample, we detect the presence of the bipolar growth plate as early as 1.5 years. The youngest age for the appearance of the subcoracoid center is 8 years old. Based on this, we detect only the bipolar growth plate from 1.5 years to 8 years. This age range is compatible with that provided by Kothary et al. (2014). The age of youngest fusion of subcoracoid center in our skeletal sample is 14 years old. Thus, in this sample we detected the subcoracoid center from 8 years to 14 years. Again, this age range is compatible with that derived from Cardoso (2008) and Kothary et al. (2014).

These results reveal that changes in the SGF can provide a good proxy for age estimation in subadult scapulae. Thus, we applied these morphological changes in those subadult scapulae from SH in which fusion of secondary centers has not yet begun.

Figure 20 depicts subadult SGF in which fusion of the different secondary centers of ossification not yet begun. In Esc-XXIX, Esc-XIII and Esc-XXV, the bipolar growth plate has already established. We observe some furrows in the site of fusion of coracoid. The age range for this stage is between 1.5 and 8 years old. Due to the growth of the coracoid fusion site, we think that the most probably age at death for these individuals is approximately eight years old. In Esc-XXIV, Esc, XXVII, Esc-IX and Esc-X, we detect that the subcoracoid center has already appeared, since they all show a marked groove in the supero-posterior part of the glenoid fossa. This leads to an age range between 8 and 14 years.

[INSERT FIGURE 20 HERE]

4.2 *The scapular glenoid fossa*

Table 7 presents the main dimensions of the SGF of the scapulae. Table 8 and Table 9 show the measurements and indices used as comparative data for adult and subadult individuals respectively.

[INSERT TABLES 7, 8 AND 9 HERE]

There are no significant differences among the SH scapulae, Neandertals, and MH samples means in absolute values of glenoid height and glenoid breadth. However, differences between the SH sample and MH sample glenoid index means are highly significant (Carretero et al, 1997). The same result was found in the comparison between Neandertals and MH. Although some variability in the relative width of the glenoid fossa is shown in modern human samples, most tend to have relatively wide glenoid fossae. The Middle Paleolithic modern humans from Skhul and Qafzeh appear to be the exception. These two specimens show a relatively narrow SGF similar to that

of Neandertals, but also the early modern European specimens from Romania, Muierii 1 (Trinkaus, 2008a).

These results agree with previous findings that both Neandertals and SH hominins are characterized by scapular glenoid fossae that are narrow relative to their height, which is reflected in a low glenoid index (breadth/height) (Carretero et al, 1997).

Despite differences in technique for recording glenoid diameters, all workers agree that the australopithecines have a long and narrow glenoid cavity (Vallois, 1977; Vrba, 1979; Senut, 1981; Johanson et al., 1982). Walker et al. (1993) report a low index for the african *Homo ergaster* scapula of KNM-WT 15000, and although influenced by their subadult status, the glenoid index of the *Homo antecessor* scapulae ATD6-116 and ATD6-118 measured by us on the original specimens is also low, following the trend of the rest of fossil hominines. Thus, the long and narrow glenoid cavity exhibited by the Middle Pleistocene hominids from SH and the Late Pleistocene Neandertals is shared with the australopithecines ($n=2$) and early *Homo* ($n=3$) specimens. This trait distinguishes all of them from the most common condition of modern human populations. A relatively narrow and long glenoid fossa (low glenoid index) is the primitive condition for our genus, and even for the hominids, this hypothesis is consistent with the present evidence (Carretero et al., 1997; Di Vincenzo et al., 2012; Rodríguez-Pérez et al., 2018).

Traditionally, differences in the shape of the glenoid fossa have been argued to relate to evolutionary changes in function (Churchill and Trinkaus, 1990; Macias and Churchill, 2015). According to these hypotheses, the progressive increase in the width of the glenoid fossa, as well as other aspects of the morphology of the shoulder, could be related to changes in hunting strategies and/or the introduction of throwing-based hunting projectiles in the late Pleistocene (Churchill and Trinkaus, 1990; Churchill and Rhodes, 2009; Macias and Churchill, 2015; Roach and Richmond, 2015). Individuals with a wider glenoid fossa and with a throwing-based hunting technology were more resistant to osteoarthritis at shoulder (Churchill, 2014).

However, Di Vincenzo et al. (2012) pointed out that it is very unlikely that the evolutionary continuum from very narrow glenoid fossa in australopithecines to very wide fossa in MH is explained by a gradual increase in the importance of throwing. These authors proposed that differences in the relative width of the glenoid fossa is related to differing degrees of development of the inferior component of glenoid fossa (the scapular portion) and the coracoid component (superior portion). We cannot test this hypothesis here. However, it is important to note that all subadult scapulae from SH show a lower glenoid index than all age groups of modern humans studied here (Table 7 and Table 9). Thus, it seems that SGF that are narrow relative to their height also characterize subadult scapulae from SH.

Another important issue regarding SGF is that several authors have demonstrated that dimensions of glenoid cavity in MH are sufficiently sexual dimorphic to provide an effective method for discriminating between sexes (Di Vella et al., 1994; Murphy, 1994; Frutos, 2002; Özer et al., 2006; Macaluso, 2011). As mentioned above, there are no significant differences between the SH scapulae and MH samples means in absolute values of glenoid height and glenoid breadth. Thus, it would be interesting to explore the possibility to assign sex in SH scapulae based on SGF height and breadth.

The glenoid height in the SH sample ranged from 32.3 mm (Esc-IV) to 41.2 mm (Esc-VI), well inside the range of variation of all MH samples (Table 8). This range of variation of scapulae from SH seems to be accommodated within the range of when two sexes are represented: while the glenoid height of Esc-VI is practically equal to the mean of modern human males when all populations are considered, that of Esc-IV is close, although lower than the mean of female samples (Table 8). In contrast, the values of glenoid breadth indicate a clear trend in the SH fossils: its range of size variation overlaps widely with that of recent females. It has been demonstrated elsewhere that Neandertals and the SH humans had the same degree of size variation (interpreted as pattern of sexual dimorphism) as modern humans (Trinkaus, 1980; Lorenzo et al., 1998; Arsuaga et al., 2015). This is the case in glenoid breadth, but the degree of size variation is offset towards lower values. Thus, while some specimens could be sexed with some accuracy based on glenoid fossa height, it would be difficult to decide a sexual determination based on glenoid breadth alone. In those cases, relative proportions can help to estimate sex in fossil specimens. In this sense, Churchill and Trinkaus (1990a) asserted that sexual dimorphism in both MH and Neandertals is expressed in the size of the glenoid fossa relative to stature, which they related to sexual dimorphism in muscularity and skeletal robusticity. These authors used the maximum humeral length as a surrogate of stature and found that Neandertals and MH exhibit a different relationship between glenoid articular dimensions and humeral length. In general, Neandertals have relatively long SGF, but they do not differ in relative glenoid breadth.

In SH three complete adult humeri have been recovered that are sexed as males (Carretero et al., 2012). The maximum length is quite variable among these three complete SH specimens, ranging from 318 mm (H-X) to 345 mm (H-II and H-XV) (Carretero et al., 2022 this special issue). As it has been mentioned above, the range of variation in SGF height can be interpreted as pattern of sexual dimorphism. Thus, we can consider the three scapulae from SH with the longest SGF to be males (Esc-I, Esc-VI and Esc-XVII; Table 7). The indices (SGF height/humeral length) calculated from SGF height, and maximum humeral lengths ranged from 11.6 to 12.9, which is closer to the mean values of MH males (11.4) and Neandertal males (12.3) than the mean of females (10.7 and 11.0, for MH and Neandertals, respectively).

4.3 The axillary border of the scapula

In the SH collection (and see Carretero et al., 1997), we can now determine the sulcus position in nine adult specimens and three subadults. In 8 of the adult specimens the sulcus is dorsally placed. and in 1 specimen (Esc-IV) it is ventrally located (Figure 21). The three subadult specimens show a dorsally placed sulcus.

[INSERT FIGURE 21 HERE]

This condition is also dominant in Neandertals, among whom there is a high frequency of an axillary sulcus dorsally placed along the lateral margin of the scapula: only the scapula from Altamura (Italy) displays a ventral sulcus (Boule, 1911, 1912, 1913; McCown and Keith, 1939b; Stewart, 1962, 1963; Endo, and Kimura, , 1970; Trinkaus, 1977, 1983b, 1983a; Heim, 1982; Churchill, 1996; Carretero et al., 1997; Di Vincenzo et al., 2019) Early anatomically modern humans (Skhul-Qafzeh sample), Upper Palaeolithic people and modern populations tend to have either a ventrally positioned sulcus (ventral sulcus) or one of intermediate morphology (bisulcate pattern).

In contrast to SH and Neandertal scapulae, in those of specimens prior to the Late Pleistocene there is a high frequency of a ventrally placed axillary sulcus. This is the case

in Sts 7 (*A. africanus*), AL-288-11 (*A. afarensis*), KNM-WT-15000 (*H. ergaster*) and D4166 (*H. georgicus*) (Carretero et al., 1997; Leakey and Walker, 1985; Lordkipanidze et al., 2007, Walker et al., 1993). Only the scapula of KMN-ER 1808 displays the axillary sulcus in a dorsal position.

The two complete subadult scapulae of *H. antecessor* (ATD6-116 and ATD-118) also show a ventrally positioned sulcus (author's personal observation on originals).

This polymorphic condition and frequential character of the position of the axillary sulcus obscures its phylogenetical meaning. In our opinion, a ventrally positioned axillary sulcus is the primitive condition for hominins. Considering that the limited available fossil evidence for *Homo ergaster* display both morphotypes, and it is ventral in the two subadult specimens of *Homo antecessor*, it is possible that in the European lineage leading to Neandertals this variability was reduced in one direction, i.e., a much higher frequency of dorsal axillary sulcus, while in the modern human lineage, reduction has occurred towards fixation of a much higher frequency of ventral sulcus.

Another important issue with the axillary sulcus position is its relationship to relative muscle development for synergistic stabilization of the scapulohumeral joint during activity (Trinkaus, 1977; 1983a, b; Heim, 1982). In this sense, in the SH sample, the dorsal sulcus appears in robust and gracile scapulae as well as in immature individuals (Esc-VIII, Figure 13), so in this population the dorsal sulcus is not specific to adult age or high muscular development or skeletal robusticity. Also, the infant Neandertal from Kiik-Koba shows a dorsal sulcus (Trinkaus, 2008b) which points to some type of genetic control for this trait in this species, since muscular activity seems unlikely as a causal factor at such young age.

Churchill and Trinkaus (1990) have asserted that the dorsal sulcus is a consequence of structural buttressing to resist dorsoventral bending stresses in the lateral scapular body in response to yet undetermined loading patterns. Associated with the dorsal sulcus, the SH scapulae and those of Neandertals present a well-developed dorsoaxillary pillar and a complete absence of the ventral bar. The purpose of the ventral bar (a real bone reinforcement) is to ensure that the axillary border neither buckles nor breaks when *m. serratus anterior* is steadying the inferior angle of the scapula or pulling it anteriorly against resistance (protraction of the scapula, as in punching or stretching forwards, essential movements during the anteversion (flexion) of the arm. The axillary border is the strongest border of the scapula, and as such, the mechanical reinforcement of the lateral border of the scapula occupies a dorsal position in Neandertals and the SH hominids. For these reasons, we believe that the dorsal sulcus is very likely linked with the different morphological complex of the SH and Neandertal shoulder, thorax, and body bauplan, and that it is somewhat genetically encoded.

4.4 The infraglenoid tuberosity of the scapula

[INSERT FIGURE 22 HERE]

The infraglenoid tubercle (attachment for the long head of *m. triceps brachii*) is very well developed and forms a long, strong crest (for the attachment of the inferior part of the origin of this muscle) that is limited inferiorly by the groove housing the circumflex artery of the scapula. The crest runs from dorsal to ventral leaving a deep proximal and ventral fossa for the attachment of *m. subscapularis*. In Esc-XIV and Esc-VIII, the infraglenoid tubercle is prolonged becoming the medioaxillary crest of the lateral border of the scapula (Figure 22). In Esc-II and Esc-VII, the border is broken just immediately inferior to this infraglenoid crest (Figure 22). This morphology is quite

similar to that of the Vindija 209 Neandertal, but in the SH specimens the ventral fossa and infraglenoid tubercle are much more developed.

5. General Conclusions

The detailed study of complete and fragmentary shoulder girdle specimens from SH indicates that all clavicles are long, highly curved and relatively gracile, that the scapular glenoid fossa is relatively long and narrow, and that most of scapulae display a dorsal axillary sulcus. All these traits are shared with the Neandertals and, beyond their clear phylogenetic significance, their presence in adult and subadult individuals indicates that they are likely not related only to strong physical activity during adult life. In our view, all these traits are related to the primitive body “*bauplan*” of the archaic *Homo* representatives characterized by a large thorax with broad shoulders and pelvis and great body mass. Broad shoulders also characterized the subadult individuals of the SH population.

6. References

- Arsuaga JL, Lorenzo C, Carretero JM, Gracia A, Martínez I, García N, Bermúdez de Castro JM, Carbonell E, 1999. A complete human pelvis from the Middle Pleistocene of Spain. *Nature* 399: 255-258
- Arsuaga, J.L., Carretero, J.-M., Lorenzo, C., Gómez-Olivencia, A., Pablos, A., Rodríguez, L., García-González, R., Bonmatí, A., Quam, R.M., Pantoja-Pérez, A., 2015. Postcranial morphology of the middle Pleistocene humans from Sima de los Huesos, Spain. *Proc. Natl. Acad. Sci.* 112, 11524–11529.
- Auerbach, B.M., Sylvester, A.D., 2011. Allometry and apparent paradoxes in human limb proportions: Implications for scaling factors. *Am. J. Phys. Anthropol.* 144, 382–391.
- Bermúdez de Castro, J.M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martínez, I., Mosquera, M., 1997. A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. *Science*. 276, 1392–1395.
- Black, S., Scheuer, L., 1996. Age changes in the clavicle: from the early neonatal period to skeletal maturity. *International Journal of Osteoarchaeology*. 6, 425–434.
- Boule, M., 1911. L’homme fossile de La Chapelle-aux-Saints. Presented at the *Annales de paléontologie*, pp. 111–172.
- Boule, M., 1912. L’homme fossile de La Chapelle-aux-Saints. Presented at the *Annales de paléontologie*, pp. 85–192.
- Boule, M., 1913. L’homme fossile de La Chapelle-aux-Saints. Presented at the *Annales de paléontologie*, pp. 1–70.
- Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of Homo. *Nature*. 432, 345.
- Buikstra, J., Ubelaker, D.H., 1994. Standards for data collection from human skeletal remains.
- Cardoso, H.F., 2006. Brief communication: the collection of identified human skeletons housed at the Bocage Museum (National Museum of Natural History), Lisbon, Portugal. *Am. J. Phys. Anthropol.* 129, 173–176.
- Cardoso, H.F., 2007. Environmental effects on skeletal versus dental development: using a documented subadult skeletal sample to test a basic assumption in human osteological research. *Am. J. Phys. Anthropol.* 132, 223–233.

- Cardoso, H.F., 2008. Age estimation of adolescent and young adult male and female skeletons II, epiphyseal union at the upper limb and scapular girdle in a modern Portuguese skeletal sample. *Am. J. Phys. Anthropol.* 137, 97–105.
- Cardoso, H.F., Abrantes, J., Humphrey, L.T., 2014. Age estimation of immature human skeletal remains from the diaphyseal length of the long bones in the postnatal period. *Int. J. Leg. Med.* 128, 809–824.
- Cardoso, H.F., Spake, L., Humphrey, L.T., 2017. Age estimation of immature human skeletal remains from the dimensions of the girdle bones in the postnatal period. *Am. J. Phys. Anthropol.* 163, 772–783.
- Carretero, J.M., Arsuaga, J.L., Lorenzo, C., 1997. Clavicles, scapulae and humeri from the Sima de los Huesos site (Sierra de Atapuerca, Spain). *J. Hum. Evol.* 33, 357–408.
- Carretero, J.M., Lorenzo, C., Arsuaga, J.L., 1999. Axial and appendicular skeleton of *Homo antecessor*. *J. Hum. Evol.* 37, 459–499.
- Carretero, J.M., Rodríguez, L., García-González, R., Arsuaga, J.-L., Gómez-Olivencia, A., Lorenzo, C., Bonmatí, A., Gracia, A., Martínez, I., Quam, R., 2012. Stature estimation from complete long bones in the Middle Pleistocene humans from the Sima de los Huesos, Sierra de Atapuerca (Spain). *J. Hum. Evol.* 62, 242–255.
- Carretero, J.M., Rodríguez, L., García-González, R., Quam, R., Arsuaga, J.L., 2018. Exploring bone volume and skeletal weight in the Middle Pleistocene humans from the Sima de los Huesos site (Sierra de Atapuerca, Spain). *J. Anat.*
- Carretero, J.M., García-González, R., Rodríguez, L., Arsuaga, J.L. this volume. Updating of the main anatomical characteristics of the fossil humeri from Sima de los Huesos Middle Pleistocene site, Sierra de Atapuerca, Burgos, Spain.
- Churchill, S.E., 1996. Particulate versus integrated evolution of the upper body in late Pleistocene humans: a test of two models. *Am. J. Phys. Anthropol.* 100, 559–583.
- Churchill, S.E., 2014. *Thin on the ground: Neandertal biology, archeology, and ecology.* John Wiley & Sons.
- Churchill, S.E., Rhodes, J.A., 2009. The evolution of the human capacity for “killing at a distance”: the human fossil evidence for the evolution of projectile weaponry. In: *The Evolution of Hominin Diets.* Springer, pp. 201–210.
- Churchill, S.E., Trinkaus, E., 1990. Neandertal scapular glenoid morphology. *Am. J. Phys. Anthropol.* 83, 147–160.
- Clegg, M., Aiello, L.C., 1999. A comparison of the Nariokotome *Homo erectus* with juveniles from a modern human population. *Am. J. Phys. Anthropol.* 110, 81–93.
- Conceição, E., Cardoso, H., 2011. Environmental effects on skeletal versus dental development II: further testing of a basic assumption in human osteological research. *Am. J. Phys. Anthropol.* 144, 463–470.
- Coqueugniot, H., Weaver, T.D., 2007. Brief communication: infracranial maturation in the skeletal collection from Coimbra, Portugal: new aging standards for epiphyseal union. *Am. J. Phys. Anthropol.* 134, 424–437.
- Day, M. H., & Scheuer, J. L. 1989. Olduvai Hominid 48: a clavicle. *Human Biology Budapest*, 19, 9-14.
- Dean, C., Leakey, M.G., Reid, D., Schrenk, F., Schwartz, G.T., Stringer, C., Walker, A., 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature.* 414, 628–631.

- Dean, M.C., Smith, B.H., 2009. Growth and development of the Nariokotome youth, KNM-WT 15000. In: *The First Humans—Origin and Early Evolution of the Genus Homo*. Springer, pp. 101–120.
- Demirjian, A., Goldstein, H., Tanner, J.M., 1973. A new system of dental age assessment. *Hum. Biol.* 211–227.
- Di Vella, G., Campobasso, C.P., Dragone, M., Introna Jr, F., 1994. Skeletal sex determination by scapular measurements. *Bollettino della Società Italiana di Biologia Sperimentale.* 70, 299–305.
- Di Vincenzo, F., Churchill, S., Buzi, C., Profico, A., Tafuri, M., Micheli, M., Caramelli, D., Manzi, G., 2019. Distinct among Neanderthals: The scapula of the skeleton from Altamura, Italy. *Quat. Sci. Rev.* 217, 76–88.
- Di Vincenzo, F., Churchill, S.E., Manzi, G., 2012. The Vindija Neanderthal scapular glenoid fossa: Comparative shape analysis suggests evo-devo changes among Neanderthals. *J. Hum. Evol.* 62, 274–285.
- Endo, B., Kimura, T., 1970. Postcranial skeleton of the Amud man. In: *The Amud Man and His Cave Site*. Academic Press of Japan., Tokyo, pp. 231–406.
- Feuerriegel, E.M., Green, D.J., Walker, C.S., Schmid, P., Hawks, J., Berger, L.R., Churchill, S.E., 2017. The upper limb of *Homo naledi*. *J. Hum. Evol.* 104, 155–173.
- Frutos, L.R., 2002. Determination of sex from the clavicle and scapula in a Guatemalan contemporary rural indigenous population. *Am. J. For. Med. Pathol.* 23, 284–288.
- García-González, R., Carretero, J.M., Rodríguez, L., Gómez-Olivencia, A., Arsuaga, J.L., de Castro, J.M.B., Carbonell, E., Martínez, I., Lorenzo, C., 2009. Étude analytique d'une clavicule complète de subadulte d'*Homo* antecessor (site de Gran Dolina, Sierra d'Atapuerca, Burgos, Espagne). *L'Anthropologie.* 113, 222–232.
- García-Martínez, D., Barash, A., Recheis, W., Utrilla, C., Sánchez, I.T., Río, F.G., Bastir, M., 2014. On the chest size of Kebara 2. *J. Hum. Evol.* 70, 69–72.
- Gómez-Olivencia, A., Barash, A., García-Martínez, D., Arlegi, M., Kramer, P., Bastir, M., Been, E., 2018. 3D virtual reconstruction of the Kebara 2 Neandertal thorax. *Nature communications.* 9, 1–8.
- Gómez-Olivencia, A., Eaves-Johnson, K.L., Franciscus, R.G., Carretero, J.M., Arsuaga, J.L., 2009. Kebara 2: new insights regarding the most complete Neandertal thorax. *J. Hum. Evol.* 57, 75–90.
- Graves, R.R., Lupo, A.C., McCarthy, R.C., Wescott, D.J., Cunningham, D.L., 2010. Just how strapping was KNM-WT 15000? *J. Hum. Evol.* 59, 542–554.
- Guatelli-Steinberg, D., Larsen, C.S., Hutchinson, D.L., 2004. Prevalence and the duration of linear enamel hypoplasia: a comparative study of Neandertals and Inuit foragers. *J. Hum. Evol.* 47, 65–84.
- Heim, J.L., 1982. Les hommes fossiles de la Ferrassie. Tome II. Les squelettes adultes (squelettes des membres). *Arch.Inst. Paleont. Hum.* 38, 1–272.
- Johanson, D.C., Lovejoy, C.O., Kimbel, W.H., White, T.D., Ward, S.C., Bush, M.E., Latimer, B.M., Coppens, Y., 1982. Morphology of the Pliocene partial hominid skeleton (AL 288-1) from the Hadar formation, Ethiopia. *Am. J. Phys. Anthropol.* 57, 403–451.
- Kothary, S., Rosenberg, Z.S., Poncinelli, L.L., Kwong, S., 2014. Skeletal development of the glenoid and glenoid–coracoid interface in the pediatric population: MRI features. *Skeletal radiology.* 43, 1281–1288.
- Krogman, W., Iscan, M., 1987. *The human skeleton in forensic medicine.*

- Larson, S.G., 2007. Evolutionary transformation of the hominin shoulder. *Evol. Anthropol.* 16, 172–187.
- Leakey, R., Walker, A.C., 1985. Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. *Am. J. Phys. Anthropol.* 67, 135–163.
- Lewis, A.B., 1991. Comparisons between dental and skeletal ages. *Ang. Othod.* 61, 87–92.
- Liversidge, H., Chaillet, N., Mörnstad, H., Nyström, M., Rowlings, K., Taylor, J., Willems, G., 2006. Timing of Demirjian's tooth formation stages. *Ann. Hum. Biol.* 33, 454–470.
- Liversidge, H.M., Molleson, T., 2004. Variation in crown and root formation and eruption of human deciduous teeth. *Am. J. Phys. Anthropol.* 123, 172–180.
- Lordkipanidze, D., Jashashvili, T., Vekua, A., De León, M.S.P., Zollikofer, C.P., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., 2007. Postcranial evidence from early Homo from Dmanisi, Georgia. *Nature.* 449, 305–310.
- Lorenzo, C., Carretero, J.M., Arsuaga, J.L., Gracia, A., Martínez, I., 1998. Intrapopulational body size variation and cranial capacity variation in Middle Pleistocene humans: the Sima de los Huesos sample (Sierra de Atapuerca, Spain). *Am. J. Phys. Anthropol.* 106, 19–33.
- Macaluso, P.J., 2011. Sex discrimination from the glenoid cavity in black South Africans: morphometric analysis of digital photographs. *Int. J. Leg. Med.* 125, 773–778.
- Macias, M.E., Churchill, S.E., 2015. Functional morphology of the Neandertal scapular glenoid fossa. *Anat. Rec.* 298, 168–179.
- Martín-González, J.A., Mateos, A., Goikoetxea, I., Leonard, W.R., Rodríguez, J., 2012. Differences between Neandertal and modern human infant and child growth models. *J. Hum. Evol.* 63, 140–149.
- McCown, Th.D., Keith, A., 1939a. *The Stone Age of Mount Carmel. Vol II.* Clarendon Press, Oxford.
- McCown, Th.D., Keith, A., 1939b. *The Stone Age of Mount Carmel.* Clarendon Press., Oxford.
- Melillo, S., Gunz, P., Coqueugnot, H., Reske, S., Hublin, J., 2019. Structural effects of variation in the human clavicle. *Am. J. Phys. Anthropol.* 168, 687–704.
- Modesto-Mata, M., Dean, M.C., Lacruz, R.S., Bromage, T.G., García-Campos, C., Martínez de Pinillos, M., Martín-Francés, L., Martín-Torres, M., Carbonell, E., Arsuaga, J.L., Bermúdez de Castro, J.M. 2020. Short and long period growth markers of enamel formation distinguish European Pleistocene hominins. *Scientific reports*, 10: 1–12
- Modesto-Mata, M., García-González, R., Quintino, Y., García-Campos, C., Martínez de Pinillos, M., Martín-Francés, L., Martín-Torres, M., Heuzé, Y., Carbonell, E., Arsuaga, J.L., Dean, M.C., Bermúdez de Castro, J.M. 2020. Early and Middle Pleistocene hominins from Atapuerca (Spain) show differences in dental development pattern. *Am. J. Biol. Anthropol.* 178: 273–285.
- Murphy, A., 1994. Sex determination of prehistoric New Zealand Polynesian clavicles. *New Zealand Journal of Archaeology.* 16, 85–91.
- Odwak, H., 2006. Scapular axillary border morphology in modern humans and Neandertals. *Period. Biol.* 108, 353–364.

- Olivier, G. 1951a. Anthropologie de la clavicule. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*. 2, 121–157.
- Olivier, G. 1951b. Anthropologie de la clavicule. I.—La clavicule de l'Australien. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*. 2, 67–85.
- Olivier, G., 1951. Technique de mesure des courbures de la clavicule. *Comptes Rendus de l'Association des Anatomistes, XXXIXe Réunion (Nancy)*. 69, 753–764.
- Olivier, G., 1954a. Anthropologie de la clavicule. VII. La clavicule des japonais. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*. 5, 47–56.
- Olivier, G., 1954b. Anthropologie de la clavicule. VIII. La clavicule des amérindiens. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*. 5, 144–153.
- Olivier, G., 1955a. Anthropologie de la clavicule; IX. La clavicule des Nord-Africains. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*. 6, 282–289.
- Olivier, G., 1955b. Anthropologie de la clavicule; X, La clavicule des Hommes néolithiques; le problème de la différence sexuelle. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*. 6, 290–302.
- Olivier, G., Chabeuf, M., Lalueze, P., 1954. Anthropologie de la clavicule. VI. La clavicule des Mélando-Africains. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*. 5, 35–46.
- Özer, I., Katayama, K., Sahgir, M., Güleç, E., 2006. Sex determination using the scapula in medieval skeletons from East Anatolia. *Collegium antropologicum*. 30, 415–419.
- Roach, N.T., Richmond, B.G., 2015. Clavicle length, throwing performance and the reconstruction of the *Homo erectus* shoulder. *J. Hum. Evol.* 80, 107–113.
- Roach, N.T., Venkadesan, M., Rainbow, M.J., Lieberman, D.E., 2013. Elastic energy storage in the shoulder and the evolution of high-speed throwing in *Homo*. *Nature*. 498, 483–486.
- Rodriguez-Perez, F.J., Rosas, A., García-Martínez, D., Bastir, M., García-Tabernero, A., Estalrich, A., Huguet, R., Pastor, J.F., 2018. A 3D form comparative analysis of the Neandertal glenoid fossa in the context of the genus *Homo*. *Quat. Int.* 481, 91–100.
- Rosas, A., Ríos, L., Estalrich, A., Liversidge, H., García-Tabernero, A., Huguet, R., Cardoso, H., Bastir, M., Lalueze-Fox, C., de la Rasilla, M., 2017. The growth pattern of Neandertals, reconstructed from a juvenile skeleton from El Sidrón (Spain). *Science*. 357, 1282–1287.
- Rosas, A., Rodriguez-Perez, F.J., Bastir, M., Estalrich, A., Huguet, R., García-Tabernero, A., Pastor, J.F., de la Rasilla, M., 2016. Adult Neandertal clavicles from the El Sidrón site (Asturias, Spain) in the context of *Homo* pectoral girdle evolution. *J. Hum. Evol.* 95, 55–67.
- Salazar, A., García-González, R., Rodríguez L., Quintino Y., Arsuaga J. L., Carretero J. M. (2021). A 3D geometric morphometric analysis of the scapular glenoid fossa of subadult scapulae from Sima de los Huesos (Sierra de Atapuerca, Burgos, Spain). *Proceedings of European Society for the Study of Human Evolution (ESHE)*. 243
- Saunders, S.R., Hoppa, R.D., Macchiarelli, R., Bondioli, L., 2000. Investigating variability in human dental development in the past. *Anthropologie*. 38, 101–107.
- Senut, B., 1981. L'humérus et ses articulations chez les Hominidés plio-pléistocènes. *FeniXX*.
- Šešelj, M., 2013. Relationship between dental development and skeletal growth in modern humans and its implications for interpreting ontogeny in fossil hominins. *Am. J. Phys. Anthropol.* 150, 38–47.

- Šešelj, M., 2017. Brief communication: An analysis of dental development in Pleistocene Homo using skeletal growth and chronological age. *Am. J. Phys. Anthropol.* 163, 531–541.
- Skinner, M., 1996. Developmental stress in immature hominines from Late Pleistocene Eurasia: evidence from enamel hypoplasia. *J. Archaeol. Sci.* 23, 833–852.
- Smith, B.H., 1993. The physiological age of KNM-WT 15000. The Nariokotome Homo erectus skeleton. 195–220.
- Smith, S.L., 2004. Skeletal age, dental age, and the maturation of KNM-WT 15000. *Am. J. Phys. Anthropol.* The Official Publication of the American Association of Physical Anthropologists. 125, 105–120.
- Smith, T.M., Tafforeau, P., Reid, D.J., Pouech, J., Lazzari, V., Zermeno, J.P., Guatelli-Steinberg, D., Olejniczak, A.J., Hoffman, A., Radovčić, J., 2010. Dental evidence for ontogenetic differences between modern humans and Neanderthals. *Proc. Natl. Acad. Sci.* 107, 20923–20928.
- Smith, T.M., Toussaint, M., Reid, D.J., Olejniczak, A.J., Hublin, J.-J., 2007. Rapid dental development in a middle Paleolithic Belgian Neanderthal. *Proc. Natl. Acad. Sci.* 104, 20220–20225.
- Stewart, T., 1963. Shanidar skeletons IV and VI. *Sumer.* 19, 8–26.
- Stewart, T.D., 1962. Neanderthal scapulae with special attention to the Shanidar Neanderthals from Iraq. *Anthropos.* 779–800.
- Stull, K.E., L'Abbé, E.N., Ousley, S.D., 2014. Using multivariate adaptive regression splines to estimate subadult age from diaphyseal dimensions. *Am. J. Phys. Anthropol.* 154, 376–386.
- Trinkaus, E., 1977. A functional interpretation of the axillary border of the Neandertal scapula. *J. Hum. Evol.* 6, 231–234.
- Trinkaus, E., 1980. Sexual differences in Neanderthal limb bones. *J. Hum. Evol.* 9, 377–397.
- Trinkaus, E., 1983a. The shanidar neandertals. Academic Press.
- Trinkaus, E., 1983b. Neandertal postcrania and the adaptive shift to modern humans. *The Mousterian Legacy: Human Biocultural Change in the Upper Pleistocene.* 164, 165–200.
- Trinkaus, E., 2008a. Behavioral implications of the Muierii 1 early modern human scapula. *Annuaire Roumain d'Anthropologie.* 45, 27–41.
- Trinkaus, E., 2008b. Kiik-Koba 2 and Neandertal axillary border ontogeny. *Anthropol. Sci.* 116, 231–236.
- Trinkaus, E., 2016. The Krapina human postcranial remains: morphology, morphometrics and paleopathology. Faculty of Humanities and Social Sciences, University of Zagreb.
- Trinkaus, E., Holliday, T.W., Auerbach, B.M., 2014. Neandertal clavicle length. *Proc. Natl. Acad. Sci.* 111, 4438–4442.
- Vallois, H., 1977. Interpretation of the Scapula of Plesianthropus transvaalensis. *J. Hum. Evol.* 6, 675–679.
- Vandermeersch, B., Trinkaus, E., 1995. The postcranial remains of the Régourdou 1 Neandertal: the shoulder and arm remains. *J. Hum. Evol.* 28, 439–476.
- Voisin, J., 2006. Clavicle, a neglected bone: morphology and relation to arm movements and shoulder architecture in primates. *Anat. Rec. Part A.* 288, 944–953.
- Voisin, J.-L., 2001. Évolution de la morphologie claviculaire au sein du genre Homo. Conséquences architecturales et fonctionnelles sur la ceinture scapulaire. *L'anthropologie.* 105, 449–468.

- Voisin, J.-L., 2006. Krapina and other Neanderthal clavicles: A peculiar morphology? *Period. Biol.* 108, 331–339.
- Voisin, J.-L., 2008. The Omo I hominin clavicle: Archaic or modern? *J. Hum. Evol.* 55, 438–443.
- Vrba, E., 1979. A new study of the scapula of *Australopithecus africanus* from Sterkfontein. *Am. J. Phys. Anthropol.* 51, 117–129.
- Walker, A., Leakey, R.E., Leakey, R., 1993. *The nariokotome Homo erectus skeleton.* Harvard University Press.
- Walker, M.J., Ortega, J., Parmová, K., López, M.V., Trinkaus, E., 2011. Morphology, body proportions, and postcranial hypertrophy of a female Neandertal from the Sima de las Palomas, southeastern Spain. *Proc. Natl. Acad. Sci.* 108, 10087–10091.