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The costal skeleton of the Regourdou 1 Neandertal

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Abstract

The morphology and size of the Neandertal thorax is a subject of growing interest due to its link to general aspects of body size and shape, including physiological aspects related to bioenergetics and activity budgets. However, the number of well-preserved adult Neandertal costal remains is still scarce. The recent finding of new additional costal remains from the Regourdou 1 (R1) skeleton has rendered this skeleton as one of the most complete Neandertal costal skeletons with a minimum of 18 ribs represented, five of which are complete or virtually complete. Here we describe for the first time all the rib remains from R1 and compare them to a large modern Euroamerican male sample as well as to other published Neandertal individuals. The costal skeleton of this individual shows significant metric and morphological differences with our modern human male comparative sample. The perceived differences include: dorsoventrally large 1st and 2nd ribs, 3rd ribs with a very closed dorsal curvature and large maximum diameters at the posterior angle, a large tubercle-iliocostal line distance in the 4th rib, thick shafts at the dorsal end of its 6th ribs, thick mid-shafts of the 8th ribs, large articular tubercles at the 9th ribs, and thick shafts of the 11th and 12th ribs. Here we also describe a new mesosternal fragment: the left lateral half of sternbral segments 4 and 5. This portion reveals that the mesosternum of R1 had a sternal foramen in its inferiormost preserved sternal segment and supports previous estimation of the total length of this mesosternum.

The new costal remains from R1 support the view that Neandertals, when compared with modern humans, show a significantly different thorax, consistent with differences found in other anatomical regions such as the vertebral column and pelvis.

1. Introduction

The morphology and size of the Neandertal thorax is a subject of growing interest due to its link to general aspects of body size and shape, including physiological aspects related to bioenergetics and activity budgets (Franciscus and Churchill, 2002; Churchill, 2006; Weinstein, 2008; Gómez-Olivencia et al., 2009; Bastir et al., 2013, 2017). The review of “classical” skeletons such as Shanidar 3 (Shan.3; Franciscus and Churchill, 2002), Kebara 2 (K2; Gómez-Olivencia et al., 2009), La Chapelle-aux-Saints 1 (LC1; Gómez-Olivencia, 2015) and the description of new fossil remains, such as that of El Sidrón (Bastir et al., 2015; García-Martínez et al., 2017), the application of geometric morphometric techniques (e.g., García-Martínez et al., 2014, 2016) and a more integrative view of the thorax, taking into account the morphology of the thoracic spine (e.g., Bastir et al., 2013, 2017; Gómez-Olivencia et al., 2015) are providing new insights into the Neandertal thorax.

However, well-preserved adult Neandertal costal remains are still scarce and limited to a handful of individuals, only a few of which preserve complete or nearly complete ribs. In this context, the description of new Neandertal costal remains provides the opportunity to gain additional insights into Neandertal thorax size and morphological variation.

In recent years, considerable effort has been invested in identifying new Neandertal fossil remains that had been mixed in with the faunal remains from the site of Regourdou (Montignac-sur-Vézère, Dordogne, France) and also reorganizing the collections housed at the Musée d'Art et Archéologie du Périgord (MAAP). This effort has resulted in finding more than 50 new fossil remains (Madelaine et al., 2008;

Maureille et al., 2015a; this study). Thanks to this effort, the Regourdou 1 Neandertal individual is now one of the most complete Neandertal skeletons from Western Europe. Regarding the thorax, 25 new costal fragments have been identified (Maureille et al., 2015a). These new finds have allowed the reconstruction of new ribs, such that now Regourdou 1 preserves the second most complete Neandertal costal skeleton (after that of Kebara 2) with a minimum of 18 ribs represented, five of which are complete or virtually complete.

1.1. The Neandertal costal skeleton

Fuhlrett (1859) provided the first inventory of the ribs from the Neandertal 1 individual found at Feldhofer and noted their rounded cross-section and lack of curvature. Similar qualitative assessments were provided in the first descriptions of the ribs found in Spy (Fraipont and Lohest, 1887), Krapina (Gorjanović-Kramberger, 1906), La Chapelle-aux-Saints 1 (Boule, 1911-13), and La Ferrassie 1 (Heim, 1976). Gorjanović-Kramberger (1906) also described a series of (incomplete) first ribs and noted that they were less curved than in modern humans, suggesting that the Krapina individuals would show a dorso-ventrally expanded thorax. The first quantitative analysis was that of the costal skeleton of the Neandertal woman Tabun I (or Tabun C1), which showed a large, barrel-shaped chest (among other features) and more horizontal and thick ribs (McCown and Keith, 1939). While a quantitative description was provided for Shanidar 1, 3, 4, and 5 ribs (Trinkaus, 1983) and those of Kebara 2 (Arensburg, 1991), no statistical analyses were performed. It was suggested that the Shanidar ribs were robust, but for Trinkaus (1983) it was not possible to conclude

whether they showed a larger thorax than in modern humans. Arensburg (1991) concluded that the ribs of Kebara 2 were metrically and morphologically very similar to modern populations. Franciscus and Churchill (2002) re-evaluated the anatomical position of the ribs of Shanidar 3 and provided the first modern comparative study using statistics, which confirmed the presence of significant differences between this individual and their modern comparative sample. Significant differences were also found between Neandertals and modern humans in other individuals/collections such as Kebara 2, La Chapelle-aux-Saints 1 and El Sidrón (Gómez-Olivencia et al., 2009; García-Martínez et al., 2014, 2017; Bastir et al., 2015; Gómez-Olivencia, 2015).

The most recent works provide a more accurate picture of the differences between Neandertals and modern humans. Based on Kebara 2, Neandertals show significantly longer ribs in the mid-thorax (Gómez-Olivencia et al., 2009; García-Martínez et al., 2014). These ribs also show larger maximum diameters of the sternal end (Gómez-Olivencia et al., 2009; Gómez-Olivencia, 2015). These larger mid-ribs have been related to a larger thorax (especially in the medio-lateral dimension) in order to be anatomically consistent with the wide pelvis present in Neandertals (Gómez-Olivencia et al., 2009, 2015; García-Martínez et al., 2017). In fact, the long mesosternum present in some of the individuals (Regourdou 1, Tabun C1; McCown and Keith, 1939; Vallois, 1965) has also been related to the hypothesized large size of the Neandertal thorax (Gómez-Olivencia et al., 2012). Moreover, the vertebral column would be more invaginated into this thorax, which is consistent with more dorsally-oriented transverse processes of the thoracic vertebrae (Gómez-Olivencia et al., 2015; Bastir et al., 2017). The first ribs are less curved than those of modern humans, even in immature individuals (Gómez-Olivencia et al., 2010; Bastir et al., 2015). The

twelfth rib shows a distinct pattern on its cranial surface with two crests for the intercostal muscles and a clear sulcus between them (Franciscus and Churchill, 2002). There are also significant differences in the shaft between Neandertals and modern humans: larger distances between the articular tubercle and the posterior angle in mid-thoracic ribs (4th to 9th); larger cranio-caudal diameters of the shaft at the posterior angle in the upper half of the thorax (ribs 3 to 7); and they tend to show thick mid-shafts in ribs 7-9 (although this is variable and can extend to other ribs) (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; Gómez-Olivencia, 2015).

1.2. Objectives

The main objective of this paper is to present a detailed study of all the costal remains of the Regourdou 1 (R1) Neandertal and a new mesosternal fragment. The specific objectives include to provide: a) a complete inventory of all the costal remains including their anatomical determination, and a description of the detected anomalies and/or potential pathologies; and b) a comparative metric study. In the comparative metric study, the null hypothesis (H0) of morphological similarity between the costal skeletons of Neandertals and modern humans (Trinkaus, 1983; Arensburg, 1991) is tested. The alternative hypothesis (H1) is that there are indeed differences in the costal skeleton between Neandertals and modern humans (Franciscus and Churchill, 2002; Gómez-Olivencia, 2009, 2015; Gómez-Olivencia et al., 2009; Bastir et al., 2015; García-Martínez et al., 2017). A new small mesosternal fragment was also identified by Maureille et al. (2015a), which completes the mesosternum of Regourdou 1 (Vallois, 1965), and thus allows us to test the

hypothesis regarding the total length of this bone as proposed by Gómez-Olivencia et al. (2012). Finally, these new results are discussed in the context of the postcranial (and more specifically, thoracic) evolution of genus *Homo*, especially in the Neandertal lineage.

2. Materials

2.1. The Regourdou 1 skeleton

Regourdou 1 is a well-known Neandertal skeleton found in 1957 and further excavated in 1961-1964 in the site of Regourdou (Montignac-sur-Vézère, Dordogne, France; Maureille et al., 2015b). It represents a very complete skeleton of a young adult, preserving most of the skeleton, except for the cranium (see Maureille et al., submitted). The skeleton was found within layer 4 (Bonifay, 1964), which also yielded a large number of brown bear bones and, to a lesser extent, other macrofaunal remains (Delpech, 1996; Cavanhié, 2009-2010). Recently, the stratigraphic integrity of layer 4 has been questioned (Madelaine et al., 2008; Cavanhié, 2009-2010), which could be the result of post-depositional mixing by rabbit activity (Pelletier et al., 2017). Additionally, rabbits were likely responsible for the scattering of some of the bones of R1 outside the main concentration of bones (in squares G2 and G3; Maureille et al., 2015b; Pelletier et al., 2017). On the other hand, the bear bones, once thought to represent the result of Neandertal anthropogenic accumulation (Bonifay, 2002), are the result of natural accumulation due to use of the cave as a den by these

animals (Cavanhié, 2009-2010).

2.2. The costal remains of Regourdou 1

While Piveteau (1963-1966) only mentioned the presence of rib fragments, Vandermeersch and Trinkaus (1995) provided the first inventory of the ribs, and they mentioned the presence of the two 1st ribs and 13 rib fragments. Madelaine et al. (2008) report the presence of seven rib fragments including both 1st ribs in the collections of the MAAP. The lower number of rib fragments mentioned by Madelaine et al. (2008) likely stems from the fact that the MAAP did not have all of the Regourdou 1 ribs on display, as some were kept separately in a curation room (Gómez-Olivencia, personal observation) and were not available when Madelaine et al. (2008) did their inventory. Madelaine et al. (2008) also described new human remains belonging to Regourdou 1 and mentioned that they identified some potentially human ribs, the status of which were still being determined. Maureille et al. (2015a) continued this work and published 25 new rib fragments. Some of these fragments were refitted together and/or to the “original” collection, and also listed 16 fragments that may or may not be attributed to Regourdou 1.

For this study, we have studied all of the original costal and sternal remains of the R1 Neandertal. These include all the remains kept at the MAAP, plus new fragments listed in Maureille et al. (2015a), and finally, two new costal remains (R#ar and R#as) recently identified (at the end of 2016) among undifferentiated bone fragments at the MAAP from the site of Regourdou as belonging to the R1 individual. This study does not include the potential human costal remains listed in Maureille et

al. (2015a: their Figure 11), as we have not been able to further assess their taxonomic status and/or refit them to the current skeleton.

In terms of rib completeness, R1 has the second most complete adult Neandertal costal skeleton, after that of Kebara 2. R1 preserves a minimum of 18 ribs (MNE = 18; 10 from the right side and 8 from the left), among which five are complete or virtually complete (1R, 1L, 2L, 11R, 12L). A visual inventory can be found in Figure 1, and general photos of the rib collection are presented in Figures 2-5; a general inventory can be found in Table 1 and in the Supplementary Online [Material (SOM) Table S1.

[INSERT FIGURES 1-5 HERE]

[INSERT TABLE 1 HERE]

Similar to what we have argued in the past with regard to the vertebrae, we regard all of the costal remains as belonging to R1. We regard this as the most parsimonious working hypothesis for several reasons: 1) a large part of the rib remains were discovered and identified when this individual was found in 1957; 2) many of the new fragments found among the faunal remains either refit with the original ribs, or show either size or articular congruence with them; 3) more importantly, none of the new fragments duplicates previous remains; 4) so far, the second Neandertal individual (R2) is only represented by a calcaneus which was found in a different part of the site (Maureille et al., 2015a, b; Coutinho Nogueira et al., submitted; Maureille et al., submitted; Pablos et al., submitted). This same reasoning applies to the sternal remains.

2.3. Comparative samples

The modern human comparative sample is composed of 32 male individuals of Euroamerican ancestry: 26 from the Hamann-Todd collection (Cleveland Museum of Natural History, Cleveland, USA) and six from the collection housed at the University of Iowa (Iowa City, USA). This population and Neandertals inhabited similar latitudes. Regourdou 1 has been regarded as a male (e.g., Vallois, 1965; Gómez-Olivencia et al., 2007; Carretero et al., 2012; Volpato et al., 2012) or as of undetermined sex (Vandermeersch and Trinkaus, 1995; Meyer et al., 2011). Thus, in the general metric comparison we used only male modern humans that are similar in size to the studied sample, in order to avoid confounding issues of sexual dimorphism and general size. Indeed, the Euroamerican sample studied here has a similar or slightly larger stature (using humerus maximum length as a proxy) than the Regourdou 1 individual (see Gómez-Olivencia et al., 2017 for more information about this sample).

The fossil comparative sample (Neandertals, modern humans and other fossil *Homo* specimens) includes both individuals studied by us (Krapina, Amud 1, Kebara 2, La Chapelle-aux-Saints 1, Ohalo 2, Sima de los Huesos; Gómez-Olivencia et al., 2009, 2010; Arsuaga et al., 2015; Gómez-Olivencia, 2015) as well as data from the literature (Arensburg, 1991; Franciscus and Churchill, 2002; Bastir et al., 2015; García-Martínez et al., 2017).

2.4. Metric variables and statistical analysis

We used standard anthropometric techniques and instruments to take all measurements. The metric variables have been previously defined and described by Gómez-Olivencia et al. (2010; see also SOM Figure S1). R1 and the other Neandertal individuals were compared to a modern human male sample using z-scores. Significant values, i.e. z-score values beyond 1.96 ($p < 0.05$) and 2.576 ($p < 0.01$) standard deviations (Sokal and Rohlf, 1981) and/or beyond the range of our modern comparative sample were highlighted. Univariate and bivariate plots were used to illustrate and characterize rib size and shape. Statistical analyses and graphics were performed in the R statistical environment (R Core Team, 2016).

2.5. Anatomical determination of rib remains

The seriation of costal remains in complete skeletons is a relatively simple task. However, the fragmentary nature of ribs in the fossil record renders this task more difficult. The anatomical determination of certain ribs is fairly straightforward (1st, 2nd, 11th, 12th) (White and Folkens, 2005). For the rest of the elements we followed a double procedure:

- the relative seriation of the ribs follows the criteria by Mann (1993), Dudar (1993), and Jellema et al. (1993), which have been summarized by Franciscus and Churchill (2002).
- the comparison of the R1 fossils to casts and 3D models of the Kebara 2 Neandertal ribs (Arensburg, 1991), taking into account the anatomical errors detected by Gómez-Olivencia et al. (2009, manuscript in preparation).

2.6. Description of the pathological lesions

We have described all the anomalies and pathological lesions that we have found in the costal remains of R1. These are basically limited to the 1st and 7th ribs from the right side. The ribs from R1 were scanned at the AST-RX platform (“Accès Scientifique à la Tomographie à Rayons X”) using the microfocus tube of the micro-CT scanner “v|tome|x L 240” (GE Sensing & Inspection Technologies Phoenix X|ray). The 1st rib was scanned at a resolution of 72.32 μm and the 7th rib at a resolution of 87.67 μm .

3. Anatomical and metric description of the costal skeleton of Regourdou 1

A synthetic (visual) inventory of the costal remains can be found in Figure 1. The costal remains are shown in Figures 2-6. The measurements for all the ribs can be found in SOM Table S2. The metric study allows the rejection of H_0 (i.e., there are not significant differences between the R1 costal skeleton and that of modern humans). The differences found are consistent with the differences found in previous studies on Neandertals (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014, 2017; Bastir et al., 2015; Gómez-Olivencia, 2015).

[INSERT FIGURES 2-6 HERE]

3.1. Vertebrosteral ribs

Rib 1 The 1st rib from the right side (R#a) is composed of two different fragments glued together at mid-shaft. It is virtually complete and lacks only the head and neck. A large tubercle for the attachment of the first digitation of the serratus anterior muscle is evident on the cranial surface of the rib ca. 36 mm from its preserved vertebral end (Figure 7). The left 1st rib lacks this tubercle. The micro-CT image shows that it is formed by trabecular bone and has thus created an asymmetry between the two sides, not only on the external surface, but also with regard to the internal structure (Figure 7).

The 1st rib from the left side (R#b) also presents a break at the same position as that of the right side. It is missing a bone chip in the medial part of the mid-shaft, just alongside the fracture. The cranial surface of the sternal end is eroded. Unlike the right side it preserves 12 mm of the neck but still lacks the head. The more vertebral half of its shaft is craniocaudally much thicker along its external margin than on the right, and it also shows a more prominent attachment for the scalenus anterior muscle. On both the left and right 1st ribs the grooves for the subclavian artery and vein are present but shallow.

From a metric point of view the 1st ribs of R1 stand out as being dorsoventrally long (tuberculo-ventral chord - TVC) compared to both modern humans, Kebara 2, and two individuals from El Sidrón (see Table 2). Arensburg (1991) previously noticed the difference in shape between R1 and K2. There is, however, the possibility that the 1st rib from Amud 1 could have been dorsoventrally

even longer than R1 (see Figure 8; and Gómez-Olivencia et al., 2009 for a complete discussion). The complete middle Pleistocene rib from Sima de los Huesos (Gómez-Olivencia, 2009; Arsuaga et al., 2015) is even longer than that of Regourdou. Figure 9 shows the 95% confidence ellipses for modern Euroamerican males for 1st rib tuberculo-ventral arc (TVA) regressed against the tuberculo-ventral chord (TVC). Note that both Kebara 2 and R1 show less curved 1st ribs on average than either the modern males or the two individuals from El Sidrón. The differences evident between El Sidrón and the other Neandertals are likely due to differences in either how the measurements were taken, and/or a certain degree of uncertainty with regard to SD-1699+, for which these measures were estimated (see Bastir et al., 2015: their Table 3).

[INSERT TABLE 2 AND FIGURES 7-9 HERE]

Rib 2 The right 2nd rib is composed of three specimens that do not refit. The most vertebral one (R#y) preserves part of the neck, the articular and non-articular tubercles, and a fragment of the shaft. It shows erosion on the most prominent parts of the tubercle and on the external surface of the shaft that has exposed trabecular bone. The second specimen (R#f+R#e) represents two-fifths of the shaft slightly more vertebral to the fragment R#t+R#al from the left side (see below) and is composed of three fragments. Small bone chips have been lost along the break lines. The third specimen (R#ae) represents the sternal end of the rib and shows mild erosion on its most prominent edges.

The left 2nd rib is composed of three specimens that refit but that have not

actually been refitted due to the small contact surface between them. The most vertebral specimen (R#c) preserves the head, neck and articular tubercle and displays mild erosion on the most prominent parts of the head. The second specimen (R#d) is composed of two fragments that perfectly refit (and are therefore glued together) and represents three-fifths of the shaft, including well-marked attachments for the scalenus posterior and the first digitation of the serratus anterior muscle. It has lost bone matter in the contact area between the fragments that compose it and has suffered mild erosion on the most prominent edge of the crest for the attachment of the scalenus posterior that has exposed trabecular bone. This ridge, as well as that for the attachment of the M. serratus anterior, is clearly visible. The third specimen (R#t+R#a1) is composed of four refitted fragments that represent approximately the sternal-most two-fifths of the shaft, but the sternal end is not preserved. It has lost some bone matter along the break lines, but otherwise its preservation is good.

The three fragments of the left 2nd rib represent a nearly complete bone, allowing estimation of its general dimensions. This rib is dorsoventrally (TVC) longer than both the modern human comparative sample and the 2nd rib of Kebara 2 for this measure. However, its arc (TVA) is not significantly longer than the modern human male mean, signifying that the rib is relatively less curved than those of our modern human sample, paralleling what one observes with the 1st rib (Figure 8). When compared to our modern human comparative sample (and K2), the 2nd ribs of R1 also stand out for their smaller cranio-caudal diameter of the head and the greater width of the shaft at the tubercle (THD) (Table 3).

[INSERT TABLE 3 HERE]

Rib 3 The right 3rd rib is preserved in two pieces. The first (R#an+R#am) is comprised of two fragments and represents a section of the mid-shaft. There has been very minor bone loss in the contact between the two fragments and mild erosion along the caudal edge of the rib. The second specimen (R#z) is preserved in two fragments and represents the sternal-most part of the shaft, including the sternal end. It shows slight erosion on the most prominent parts of the sternal end and on the caudal edge of the shaft.

The left 3rd rib (R#g+R#s) is comprised of two fragments and preserves the neck, the articular and non-articular portions of the tubercle and a shaft fragment of around 65 mm in length which includes the posterior angle. Some bone has been lost along the caudal aspect of the contact between the fragments that compose this specimen. There is also some erosion on the caudal aspect of the posterior angle that has exposed the trabecular bone. On the cranial margin of the shaft it is possible to see the attachments for the intercostal muscles.

The metric analysis shows that the 3rd ribs of R1 are significantly different from modern humans for certain variables (Table 4). First the curvature of 3L is more closed (i.e., acute) at the posterior angle. Second, they show significantly larger shaft maximum (craniocaudal) diameters at the posterior angle (SMxD), and in the case of 3L, also at the dorsal end (DSMxD), something also present in other Neandertal individuals such as K2 and Shan.3.

[INSERT TABLE 4 HERE]

Rib 4 The right 4th rib is composed of two fragments (R#ab+R#ac) and represents the tubercle and a shaft fragment including the posterior angle. The articular tubercle is only partially preserved and eroded on its caudal edge. The non-articular portion of the tubercle is eroded on its most prominent part, and the caudal edge of the posterior angle is also eroded, exposing trabecular bone. There has also been a loss of bone in the break between the two fragments that compose this specimen.

The left 4th rib (R#j+R#i) is composed of three fragments and represents around a third of the 4th rib, including the non-articular portion of the tubercle, the posterior angle, and a portion of the shaft. The caudal aspect of the posterior angle is not well preserved as it includes the break point (with associated bone loss) between the two largest fragments that compose this specimen. It has also suffered mild erosion along the caudal surface of the rib, along the crest, that has exposed trabecular bone.

Metric analysis shows that the 4th ribs of R1 are significantly different from modern humans for certain variables (Table 4). First, the distance between the tubercle and the iliocostalis line (TID2) is similar to that of Kebara 2, and both Neandertals are significantly larger than the modern human males for this measurement. The maximum (craniocaudal) diameter of the posterior angle, like that of the 3rd rib, and like that of other Neandertals, is significantly larger than that of the modern human males.

Rib 5 For R1, there are no clear 5th rib remains from either side.

Rib 6 The right 6th rib is represented by a specimen which is composed of two

fragments (R#ap+R#aq) that represent the external half of the posterior angle. The costal groove is well marked, but its crest has been eroded and trabecular bone is exposed.

The left 6th rib (R#ag) preserves part of the articular tubercle, the non-articular tubercle and the shaft vertebral to the posterior angle. The preserved part of the articular tubercle is eroded. Its shaft thickness vertebral (i.e., more proximal) to the posterior angle lies significantly above (and outside the range of) the modern human comparative sample.

The metric analysis of these specimens is restricted by their limited preservation. Nonetheless, the rib shaft portions vertebral to the posterior angle are similar to La Chapelle-aux-Saints 1, and significantly thicker than our modern human comparative sample (Table 5).

[INSERT TABLE 5 HERE]

Rib 7 The right 7th rib (R#ad+R#ah+R#ak) preserves approximately half of the shaft and is composed of four fragments. It has lost small bone chips at the union of the different fragments that comprise it. It also shows erosion along the caudal aspect of the rib, especially at the posterior angle, exposing trabecular bone. This specimen shows mild porosity and remodeling at its sternal-most end, likely due to a pathological lesion. Figure 10 shows a cross-sectional CT scan of the rib at this point, revealing a porosity in the external table of the cortical bone, perhaps due to a healed fracture, although we cannot rule out that it is some other type of pathological lesion. With regard to the position of this rib, the preserved length of TID2 (which cannot be

accurately measured due to the fact that this rib does not preserve the articular tubercle) is similar to the 7th rib from K2, and thus, would be too long to be a 5th or 6th rib. It is not an 8th rib, because sections of it overlap with the right 8th rib. From a metric point of view, the measurements taken on this fragment (shaft maximum and minimum diameters at different points) are not significantly different from the modern human comparative sample. Due to the incompleteness of this rib it is not possible to assess whether the tuberculo-ventral arc of this rib is similar to that of Kebara 2, and thus significantly longer than modern humans (Gómez-Olivencia et al., 2009; García-Martínez et al., 2014). This rib's mid-shaft is narrower than K2, LC1 and Shan.3 (Table 5).

There are no remains of the left 7th rib.

[INSERT FIGURE 10 HERE]

3.2. Vertebrochondral ribs

Rib 8 The right 8th rib is represented by two pieces. The first (R#l) preserves the posterior angle. In caudal view it shows a well-developed costal groove. The second (R#k) is composed of two fragments that represent the sternal half of the 8th rib. It has lost some bone matter where the two fragments that make it up have been refitted. The caudal-internal margin of the sternal end has not been preserved and trabecular bone is exposed here. In terms of size and shape (i.e., shaft craniocaudal and internal-external diameters and the size and extent of the costal groove), this rib is very similar to the 8th rib of K2. Metrically, its mid-shaft is thicker (MMnD) than the other

Neandertal individuals (K2, Shan.3), and significantly thicker than the modern human comparative sample (see Table 6).

There are no remains of the left 8th rib.

[INSERT TABLE 6 HERE]

Rib 9 The right 9th rib is represented by two pieces. The first (R#m) is a vertebral-end fragment of a right rib that preserves the head, neck, articular tubercle and a small portion (~13 mm) of the shaft. The lack of a clear non-articular tubercle points toward this rib being a 9th rib and comparisons with Kebara 2 (Table 6; Figure 11), support this view. The second piece (R#n+R#o) is a shaft fragment immediately sternal to the posterior angle. The feeble development of the costal groove (especially in comparison with R#k), and comparisons with Kebara 2, suggest that this specimen is a 9th rib. It shows mild erosion along the cranial border, slightly vertebral to mid-shaft, which has exposed trabecular bone.

The left 9th rib is represented by two pieces. The first (R#aa) is a shaft fragment that preserves the posterior angle. It has suffered mild erosion along its caudal surface, exposing trabecular bone. The second (R#h) is a shaft fragment on which the costal groove ends. Although rather uninformative, its shape is similar to R#n+R#o, and thus its anatomical determination is based on this.

Metrically, the preserved portion of the 9th rib of R1 follows the Neandertal pattern of showing larger articular tubercles (Figure 11) and thicker shafts than the modern human sample used in this study (Table 6).

[INSERT FIGURE 11 HERE]

Rib 10 There are no remains of the 10th rib.

3.3. Vertebral ribs

Rib 11 The right 11th rib (R#p+R#q+R#w) is composed of four refitted fragments that represent a complete rib. A few bone chips have been lost in the break lines between the different fragments that make up this rib. The head is eroded along its cranial and most vertebral edges, exposing trabecular bone. The caudal edge of the rib has also suffered erosion at some points, exposing trabecular bone.

The left 11th rib is represented by two specimens that do not refit. The largest and most vertebral (R#r) represents a portion of the shaft including the posterior angle. The second (R#af) is composed of two fragments which represent a portion of the shaft more sternal to R#r.

From a metric point of view (Table 7), Regourdou 1 (and Neandertals in general) displays a thick shaft along its vertebral third when compared to modern humans. It is possible to assess the degree of curvature of the complete right 11th rib comparing its arc (HVA) and chord (HVC) (Figure 8). Both Regourdou 1 and Kebara 2 show curvatures that are within modern human variation.

[INSERT TABLE 7 HERE]

Rib 12 The right 12th rib is represented by a fragment of the mid-shaft (R#u). It has

suffered mild erosion on its cranial and caudal edges, but especially the former. In cranial view it is possible to distinguish the double crest for the attachments of the intercostal muscles although they are not as marked as in Kebara 2. This double-crest pattern was first described by Franciscus and Churchill (2002).

The left 12th rib is represented by two specimens. R#as represents approximately the vertebral-most 40% of the rib, preserving the intact head, neck and shaft until approximately the posterior angle. R#ar is comprised of three refitted pieces representing the distal half of the shaft. While not as marked as in the right 12th rib, the left 12th rib also shows the double crest morphology along its cranial margin.

From a metric point of view (Table 7), the 12th ribs of Regourdou 1 (and the rest of the studied Neandertals) show thicker shafts than modern humans, especially at the posterior angle (SMnD).

3.4. Additional rib elements

R#v and R#x

There are two costal fragments from the right side that preserve the head and neck: R#v and R#x. The former is less complete and preserves only the cranial two-thirds or so of the head and half of the neck. It has suffered some erosion along its most vertebral edge, exposing trabecular bone. R#x is better preserved but suffers some erosion along the external part of the neck and mild erosion on its cranial surface. The cranial crest of R#x is around 1 mm longer than R#v, which would mean a longer neck, and would therefore be slightly more cranially located. Thus, R#x

would be a 5th to 7th rib, while by exclusion, R#v would be a 6th to 8th rib.

R#ai

This is a shaft fragment with a well-marked costal groove. It is from the left side and from a mid-thorax rib (5th-6th?). The costal crest that runs parallel to the costal groove has been eroded and trabecular bone is exposed.

R#aj

This is a shaft fragment (probably a right) with a costal groove, but one not as developed as that of R#ai. Nearly the entire caudal border is badly eroded with trabecular bone exposed. It is not possible to ascertain its anatomical position.

R#ao

This is a shaft fragment with a well-marked costal groove. It is probably from the left side and from a mid-thoracic rib (4th-7th). It shows mild erosion along its caudal crest that has exposed trabecular bone.

3.5. The sternal ends of the Regourdou 1 Neandertal

The preserved sternal ends of the ribs of Regourdou 1 are restricted to the uppermost (1-3) and lowermost ribs (11-12). The measured values are similar to other Neandertals and are not significantly different from our modern human comparative sample (Tables 2, 3, 4 and 7). Neandertals show significantly larger sternal end maximum diameters (SEMxD) in the mid-thoracic ribs, while they are similar to modern humans in the uppermost and lowermost ribs (Gómez-Olivencia et al., 2009;

Gómez-Olivencia, 2015). The R1 individual preserves only the uppermost and lowermost sternal ends which, as is the case in other Neandertals, are similar to modern humans (Figure 12).

[INSERT FIGURE 12 HERE]

4. A new mesosternal fragment

The recent reassessment of the Regourdou collection (Maureille et al., 2015) revealed the presence of the left lateral half of sternebraal segments 4 and 5 (mesosternal segments 3 and 4; Figure 13) that had been previously undescribed. This portion reveals that the mesosternum of Regourdou 1 had a sternal foramen in its inferiormost preserved sternal segment. Medially the fifth sternebraal segment evinces anteroposterior thinning. It remains unclear as to whether there were two lateral halves of this portion of the sternum, due to erosion along the cranialmost medial margin of the specimen. The current total length of the R1 mesosternum is 118.5 mm. A very conservative estimation of its mesosternal length is 120 mm. This figure is consistent with the preferred estimate of 124.1 mm of Gómez-Olivencia et al. (2012).

[INSERT FIGURE 13 HERE]

5. Discussion

The Regourdou 1 Neandertal costal remains provide new insights into

Neandertal thoracic variation but also on the paleobiology of this individual.

5.1. Asymmetries and pathological lesions in the Regourdou 1 Neandertal

In this work we present additional evidence of lesions on two ribs from the right side. The etiology of the 1R from R1 is unknown, but we hypothesize that the remodeling in 7R could be related to either trauma and/or infection. While there is not a clear disruption of the cortical bone of the internal part of the rib, we cannot rule out the possibility of a fissure, implying the breakage of only the external part of the rib, in a very specific area.

There is growing evidence for several lesions and/or asymmetries on the Regourdou 1 Neandertal (Maureille et al., submitted). First, the right 1st rib shows a bump on the rib body, which is both slightly larger and slightly different from the right side. Second, the sacrum shows a marked asymmetry with an underdevelopment of the right side ala (Meyer et al., 2011; Rmoutilová et al., submitted). Third, both femora show portions of their cortical bone with secondary vascularization (Maureille et al., submitted). Fourth, the second thoracic vertebra (T2) (Gómez-Olivencia et al., 2013) shows a marked asymmetry of its upper facets. Finally, the tali are also asymmetrical in the orientation of their heads (Maureille et al., submitted; Pablos et al., submitted). We hypothesize that some of these asymmetries could be functionally related to each other. Future work should provide additional, more complete descriptions of these lesions, as well as their differential diagnosis and etiologies. Additionally, the asymmetry in the pectoral girdle and upper limb (Vandermeersch and Trinkaus, 1995) are related to the right-handedness of this individual (Volpato et al., 2012).

5.2. Neandertal thoracic variation: new information provided by Regourdou 1

Most of the metric and morphological information regarding the Neandertal thorax comes from direct evidence: i.e., costal and sternal remains, or indirect evidence (morphology of the thoracic vertebrae). Current knowledge of the Neandertal costal skeleton is built upon Kebara 2, Shanidar 3, La Chapelle-aux-Saints 1, Tabun C1 (although there are some reconstruction problems in this individual; Gómez-Olivencia, personal observation) and the El Sidrón collection (Franciscus and Churchill, 2002; Weinstein, 2008; Gómez-Olivencia et al., 2009, 2012, 2015; García-Martínez et al., 2014, 2017; Bastir et al., 2015). The costal skeleton of Regourdou 1(R1) provides new evidence which helps to improve our understanding of the Neandertal costal skeleton and provides new insights.

Uppermost thorax (Ribs 1-2) Regarding the uppermost thorax (ribs 1-2), R1 provides new complete to nearly-complete specimens. Specifically, R1 provides the antero-posteriorly longest complete Neandertal 1st ribs, using the tuberculo-ventral chord (TVC) as a proxy. The 1st ribs of R1 are less curved than those of Kebara 2 (K2), although the incomplete 1st rib of Amud 1 could have been even longer. However, all of the Neandertal specimens for which we have the TVC of the 1st rib (K2, R1, El Sidrón; Gómez-Olivencia et al., 2009; Bastir et al., 2015) are smaller than the only complete rib recovered from the Sima de los Huesos Middle Pleistocene site (Arsuaga et al., 2015). The complete Pelvis 1 and less complete Pelvis 2 from Sima de los Huesos are wider than those of Neandertals (Arsuaga et al., 1999, 2015; Bonmatí et

al., 2010; Holliday, 2012). Thus, Arsuaga et al. (2015) propose a process of a relative narrowing of the body in the Neandertal lineage from the middle to late Pleistocene. The current evidence for the 1st rib would be consistent with this hypothesis. Regarding the 2nd rib, the nearly complete 2nd left rib of R1 falls outside of the 95% confidence limits of our modern human comparative sample due to its significantly longer tuberculo-ventral chord (TVC). The straightness of this rib may cast doubts on the reconstruction of the mid-shaft of the complete (right) 2nd rib, which is at the limits of variation of our modern human comparative sample. However, there seems to be a parallelism between 1st and 2nd ribs, which are more curved in K2 and more straight in R1. Future studies should address the covariation between ribs in order to gain new insights into this matter.

Bastir et al. (2017) found significant morphological differences between Neandertals and modern humans at all the thoracic vertebral levels and they mention differences in the orientation of the transverse processes (TPs) (i.e., more dorsally oriented TPs, among other differences) starting in T3-T4. Our assessment of the horizontal orientation of the transverse processes of the first (T1) and second (T2) thoracic vertebrae results in no significant differences between Neandertals and modern humans (Gómez-Olivencia et al., 2015, unpublished data; Been et al., 2016). Thus, the observed differences in the TVC dimensions of the R1 Neandertal 1st and 2nd ribs would have impacted their skeletal antero-posterior dimensions. There is a consensus that Neandertals show significantly less curved 1st ribs (Gómez-Olivencia, 2009; Gómez-Olivencia et al., 2010; Bastir et al., 2015) although there are not many complete specimens in which the TVC dimension can be securely measured. In the case of the 2nd rib, while a pattern towards less curved ribs is demonstrated here (and

outside of the limits of variation in the case of R1, although, within the limits of modern human variation in the case of K2, which is reconstructed in the mid-part and for which the curvature of this individual should be regarded as the minimum; Gómez-Olivencia, personal observation), additional complete elements are needed in order to fully understand the morphological variation of this bone and whether it is also shows TVCs significantly larger than modern humans. In fact, if differences in the uppermost thorax (ribs 1-2) exist, they may not be maintained in the middle thorax: the 3D reconstruction of the K2 individual does not show significant metric differences in the maximum antero-posterior dimension of the thorax; it instead shows significant metric differences in the maximum medio-lateral (transverse) dimensions of the thorax. In summary, additional complete uppermost Neandertal ribs are needed in order to understand the geometric relationship between the uppermost thorax and the positioning of the clavicle and scapula.

Articular tubercle Neandertals show consistently larger articular tubercles in ribs 7-9 (Figure 10). Whether this difference actually begins at the level of the 6th rib is unknown due to the dearth of Neandertal remains preserving this region. The origin of this difference is currently unknown. Neandertal mid-thoracic ribs are known to be longer in terms of arc (tuberculo-ventral arc [TVA]; Gómez-Olivencia et al., 2009) and are also thicker (e.g., Gorjanović-Kramberger, 1906; Franciscus and Churchill, 2002; Gómez-Olivencia, 2015) which would result in heavier ribs. Thus, we hypothesize that larger articular tubercles would facilitate the articulation between these ribs and the vertebrae, decreasing the pressure per surface unit that the articulation would have to withstand. In modern humans, males tend to show larger

articular tubercles in ribs 1-8, while they are more similar in size in ribs 9-10 (García-Martínez et al., 2017: their Table S6).

Shaft dimensions (cranio-caudal dimensions and thickness) The R1 costal skeleton provides new rib specimens which enable one to assess the pattern of shaft dimensions in the Neandertal costal skeleton. First, R1 is consistent with the pattern of Neandertals showing shaft maximum diameters at the posterior angle (SMxD) which are significant larger than modern humans in ribs 3 and 4.

Neandertal shaft dimensions have been compared to a modern industrial population. Thus, we should be cautious as to whether the perceived differences could be of taxonomic significance, related to other perceived differences in both costal and general body size and shape between Neandertals and modern humans, because they could also stem from differences in mobility between hunter-gatherer groups and industrial groups. Unfortunately, data on Upper Paleolithic costal skeletons are sparse and we lack a good characterization of the potential differences in the costal skeleton between industrial vs hunter-gatherer populations. We have compared the data published by Sládek et al. (2000) for the Dolní Věstonice skeletons and compared the shaft values to our modern comparative sample. We found significant differences in DV13 (Ribs 4-7, and 10; mid-shaft maximum and minimum diameters [MMxD, MMnD]), DV14 (ribs 8 and 9 from the left side; mid-shaft maximum diameter [MMxD]), and DV15 (rib 12 from the right side, shaft minimum diameter at the posterior angle [SMnD]). Our own assessment of the Abri Pataud 11th ribs (1311 and 1535) found significant differences for the shaft dorsal end (both maximum and minimum dimensions; DSMxD, DSMnD) and at the posterior angle (SMxD and

SMnD). Carretero et al. (2012) found only a few significant differences at the 10th and 11th ribs in the El Mirón 1 Magdalenian female individual, and also noted the well-marked attachments of the intercostal muscles and the very well-marked posterior angle of the 11th rib. Based on this meager sample, we can hypothesize that, while it is clear that hunter-gatherer populations (regardless of their species) show more robust ribs than industrial populations, it seems that some of the differences perceived between Neandertals and modern humans in the rib shaft are not related to differences in activity. Additional work in extant and past *Homo sapiens* hunter-gatherer populations should help to better characterize the potential differences in the costal skeleton due to activity levels.

Relationship between the 11th rib and the width of the pelvis R1 has provided the second complete 11th rib after that of K2. These two ribs show a curvature (using the relationship between the head-ventral arc and chord [HVA and HVC] as a proxy) which is similar to that of modern humans. The relationship of the ribs at this level with the pelvis depends on its articulation with the eleventh thoracic vertebra (T11). While this rib does not articulate with the transverse processes (TPs) of the T11, the orientation of these TPs may provide some insights on the orientation of this rib regarding this vertebra. The T11 of R1 (Gómez-Olivencia et al., 2013) shows the same TP orientation as K2, i.e., more dorsally oriented than modern humans (see Williams et al., 2017, their Figure 7 for a comparison). Neandertal 11th ribs likely would look externally rotated when compared to modern humans. This would likely result in larger transverse diameters of the thorax at this level, which would, in turn, be useful in maintaining anatomical congruence with the wider pelvis of Neandertals.

6. Summary and conclusions

The recent finding of new costal remains ($n = 25$) from the Regourdou 1 (R1) skeleton has rendered this skeleton the second most complete Neandertal costal skeleton (after that of Kebara 2) with a minimum of 18 ribs represented, five of which are complete or virtually complete. The thorax of this individual shows significant metric and morphological differences with our modern human male comparative sample and provides new insights into Neandertal thoracic variation. When compared to our modern comparative sample, the main characteristics of the R1 preserved costal skeleton are the presence of:

- dorsoventrally large 1st and 2nd ribs (when compared to both modern humans, and to the Kebara 2 Neandertal).
- 3rd ribs with a very closed dorsal curvature and large maximum diameters at the posterior angle.
- a large tubercle-iliocostal line distance in the 4th rib
- thick shafts at the dorsal end of the 6th ribs
- thick mid-shafts of the 8th ribs
- large articular tubercles at the 9th ribs
- thick shaft of the 11th and 12th ribs

Additionally, the new mesosternal piece recently identified by Maureille et al. (2015a) refits with the mesosternal specimen originally described by Vallois (1965) and provides evidence of the presence of a sternal foramen in this individual. The

current total length of the R1 mesosternum is 118.5 mm, and a very conservative estimate of its mesosternal length is 120 mm, which would be consistent with the preferred estimate of Gómez-Olivencia et al. (2012).

The large articular tubercle in the lower ribs of Neandertals (for which R1 preserves only the 9th rib), could be related to the longer arc and thicker ribs, which would result in heavier ribs, necessitating larger articular surfaces to articulate with the thoracic vertebrae. While the 11th rib is similar to that of modern humans in general size and curvature, it is likely that these ribs were more outwardly rotated, which would be consistent with more dorsally-oriented transverse processes in the eleventh thoracic vertebra. Thus, at this level of the thorax, the transverse diameters would be larger, which would allow the maintenance of anatomical congruence with the wider pelvis of Neandertals. Finally, the differences found in the shaft are consistent with those found in other Neandertal individuals.

In summary, the costal skeleton of Regourdou 1 supports the view that Neandertals, when compared to modern humans, show a significantly different costal skeleton, consistent with differences found in other Neandertal skeletal parts which directly articulate and/or are related to the thorax, such as the scapular girdle, the vertebral column and the pelvis (Rak and Arensburg, 1987; Carretero et al., 1997; Gómez-Olivencia et al., 2013a, b, 2017).

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Supplementary Online Material

Supplementary online material related to this article can be found at

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Figure legends

Figure 1. Synthetic inventory of the costal remains of Regourdou 1. Note that the fragments may not follow exactly the same scale. For information about the preserved size of each of the fragments see SOM Table S1.

Figure 2. Cranial view of the ribs from the right side of the Regourdou 1 Neandertal.

Figure 3. Caudal view of the ribs from the right side of the Regourdou 1 Neandertal.

Figure 4. Cranial view of the ribs from the left side of the Regourdou 1 Neandertal.

Figure 5. Caudal view of the ribs from the left side of the Regourdou 1 Neandertal.

Figure 6. Head and/or neck portions preserved in the Regourdou 1 Neandertal. Note the relatively longer and cranio-caudally narrower necks in the upper ribs (2-3) compared to the relatively shorter and cranio-caudally expanded necks in the lower ribs. Note the absence of a non-articular tubercle in R#m (9R), a character also present in Kebara 2's 9th ribs.

Figure 7. Cranial, caudal, lateral and cross-sectional views of the 1st ribs from Regourdou 1 individual. The 1st rib from the right side shows a distinct “bump” which is also different in cross-section.

Figure 8. Comparison of the 1st rib of Regourdou 1 with those of Amud 1 and Kebara 2. These three 1st ribs were aligned using the insertion for *M. scalenus anterior*. In the case of Amud, even though it is broken, it is still possible to align it using the groove which is present on the caudal surface of this insertion. Note that despite being broken, Amud 1 seems to have a longer 1st rib than that of Regourdou 1, which would be consistent with the higher stature of the former.

Figure 9. Bivariate plots representing the curvature of the 1st, 2nd and 11th ribs of Regourdou1 (R1; red triangles) compared to other Neandertals (black triangles), other fossil specimens (black squares or circles) and modern humans (represented by gray open circles and 95% equiprobability ellipses). ATD6 represents the ATD6-108 1st right rib from Gran Dolina-TD6 level belonging to *Homo antecessor*. OH represents the Ohalo 2-H2 Upper Paleolithic modern human. Individuals closer to the straight ($x=y$) line represent straighter ribs. In the case of the 1st rib, Kebara 2 and R1 are close to the limit or outside the 95% equiprobability ellipse of the modern human 1st ribs. The Sidrón (SD-) individuals are more similar to modern humans, likely due to differences in measuring techniques. In the case of the 2nd ribs, K2 is close to the limit of variation of modern humans, while Regourdou 1 falls outside of the 95% equiprobability ellipse of modern humans, being antero-posteriorly (based on the Tuberculo-ventral chord) larger. In the case of the 11th ribs, both R1 and K2 lie within the modern human scatter.

Figure 10. Caudal (top), cranial (middle) and external (bottom) views of the right 7th rib of Regourdou 1 (R#ad+R#ah+R#ak). From the external view, the shaft portion

close to the sternal end of the preserved fragment is thicker. The cross-section in this area (shown at the very bottom) shows a more vascularized external cortical bone and more density of the trabecular bone (the two cross-sections on the right), when compared to other portions of the shaft that show more regular morphology (the two cross-sections on the left).

Figure 11. Articular tubercle height (ATH) and articular tubercle width (ATW) of ribs 3-9 of Regourdou 1 (R1; red triangles), other Neandertals (black triangles; K2: Kebara 2; LC1: La Chapelle-aux-Saints 1; Shan.3: Shanidar 3; labels starting with SD/SDR refer to the El Sidrón sample; Block also refers to another Sidrón specimen; the anatomical position of the El Sidrón specimens represented by a gray triangle is currently unknown (6th or 7th rib); R refers to ribs from the right side and L to ribs from the left side) and our modern male comparative sample (mean \pm 1 standard deviation). Data for K2 from Arensburg (1991). Data for LC1 from Gómez-Olivencia (2015). Data for the modern human comparative sample and for Shan.3 from Franciscus and Churchill (2002). Data for Sidrón from García-Martínez et al. (2017). Note that for the available uppermost ribs (3-5) there is no clear pattern, while for the lowermost ribs (7-9) Neandertals are in general larger than the modern Euroamerican male sample. The asymmetry present in K2 could be related to the pathology present in the right side of the costal skeleton of this individual in ribs 5-7 (Duday and Arensburg, 1991).

Figure 12. Comparison of the sternal end maximum diameter (SEMxD) of the Regourdou 1 Neandertal to other Neandertals (Amud 1, Kebara 2 and La Chapelle-

aux-Saints 2) and to the recent modern male sample used in this study.

Figure 13. New fragment of the mesosternum, preserving the left lateral part of sternebraal segments 4 and 5 (mesosternal segments 3 and 4). This preserved portion indicates that the sternum had a foramen in its fifth segment (arrow).

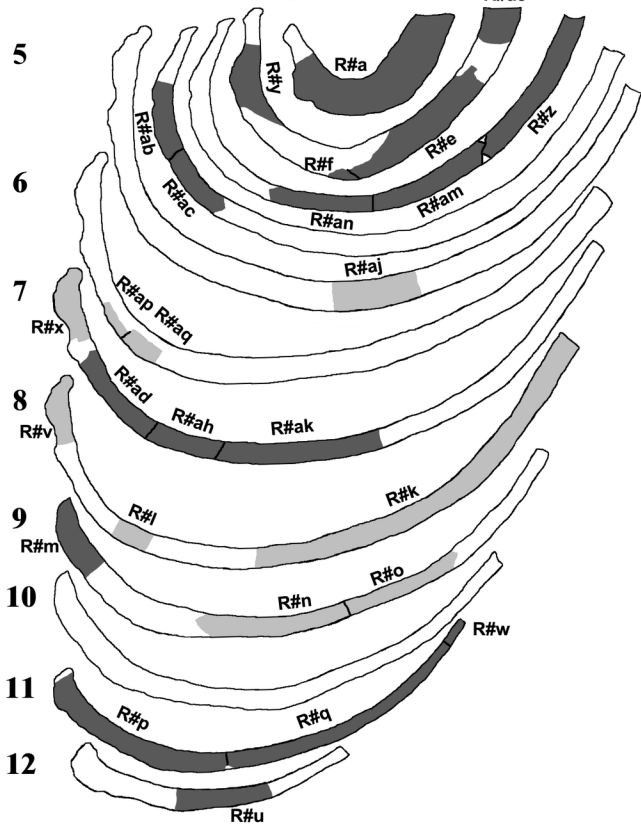
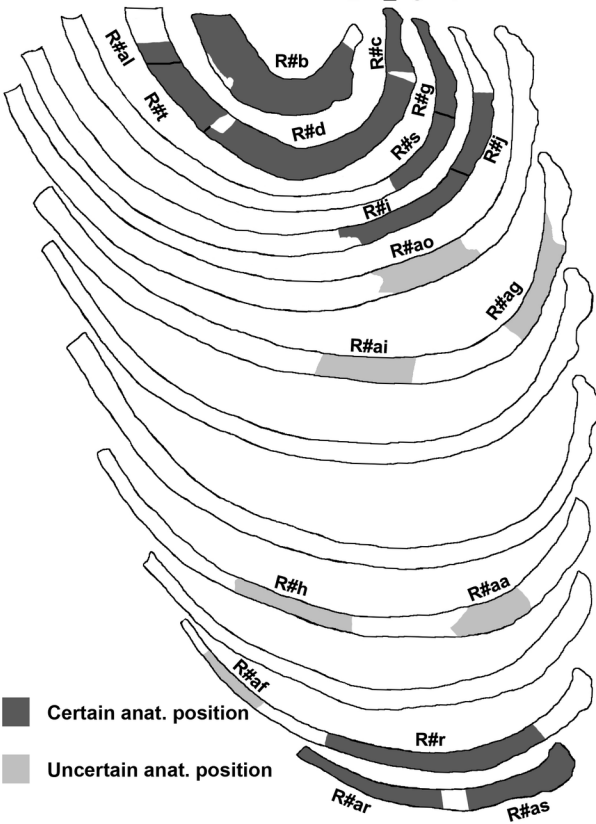
Left side

Right side

1 2 3 4

4 3 2 1

R#ae

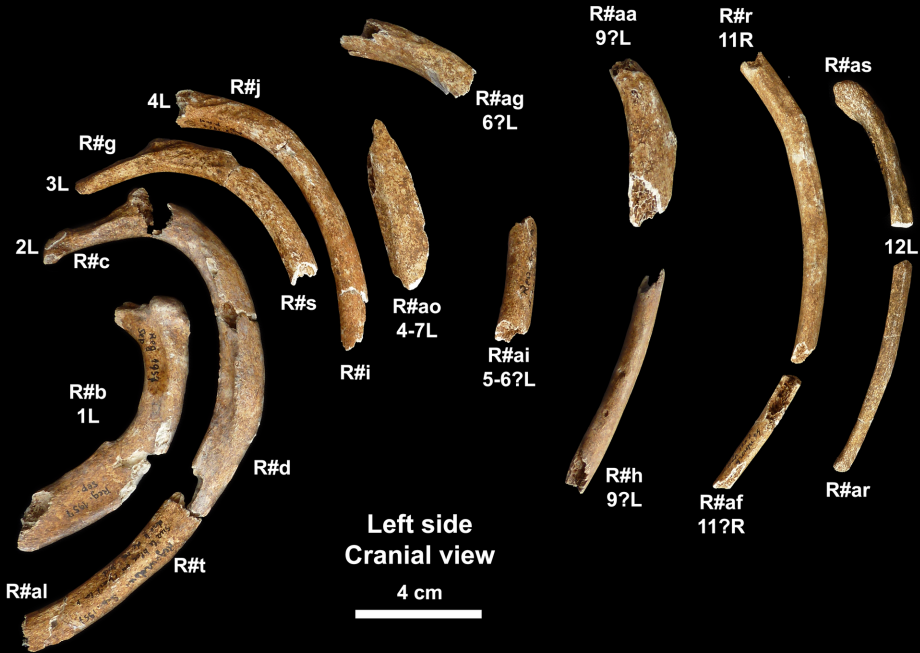


■ Certain anat. position
■ Uncertain anat. position

Right side
Caudal view

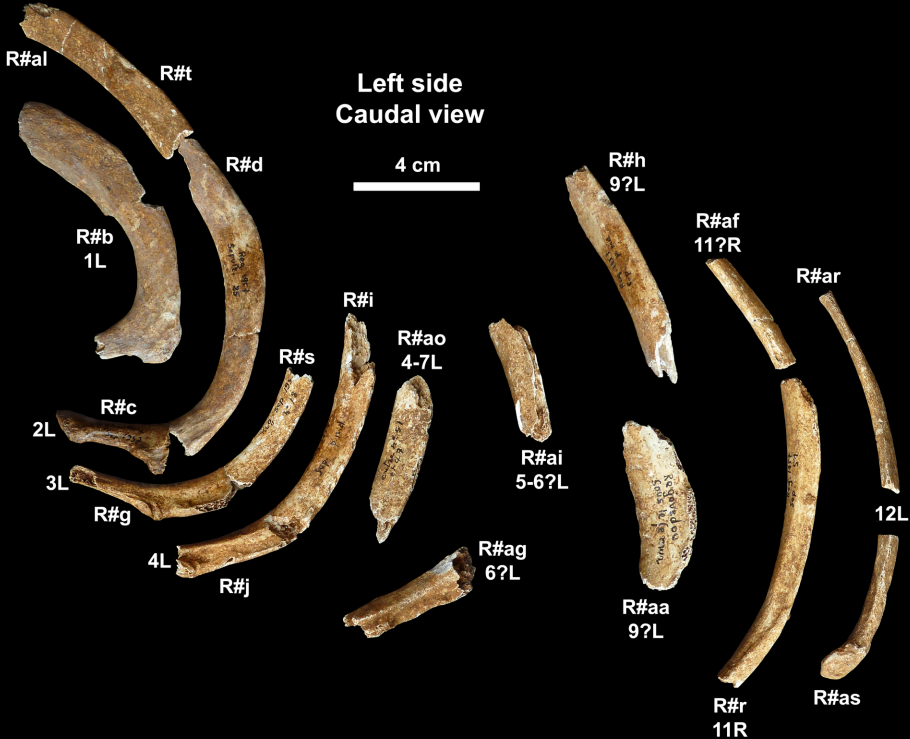
4 cm





Left side
Caudal view

4 cm



Left side

Right side

R#c (2L)



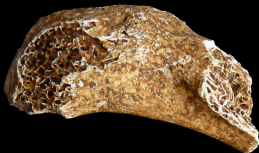
R#g (3L)



2 cm



R#x (5-7R)



R#v (6-8R)



R#m (9R)





Kebara 2

2 cm

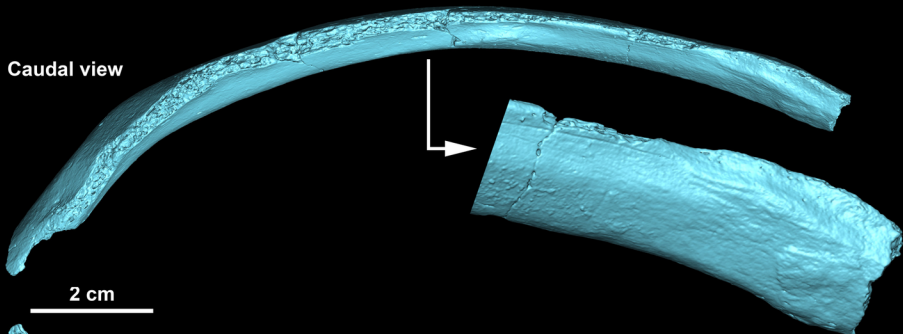


Amud 1

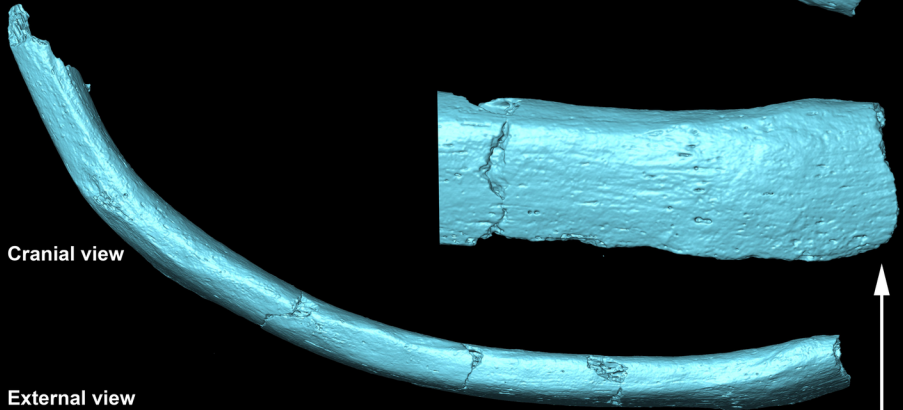


Reg. 1

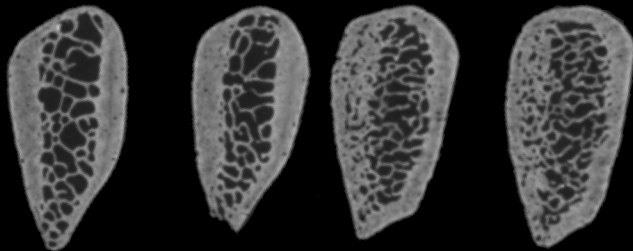
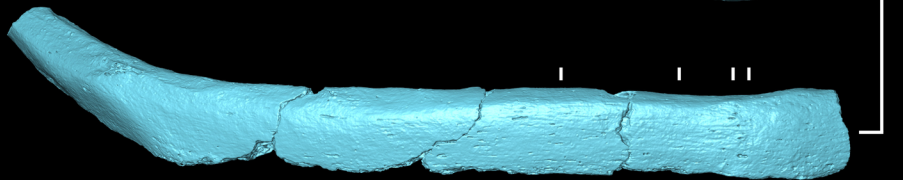
Caudal view



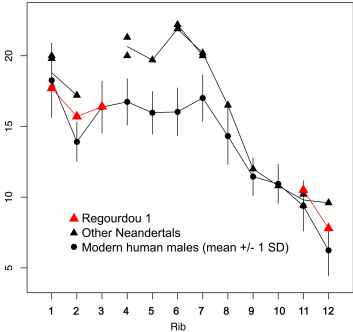
Cranial view



External view



Sternal end maximum diameter (SEMxD) (in mm)

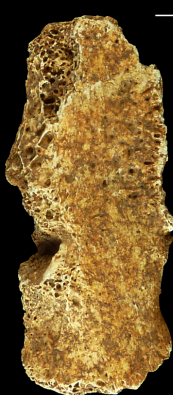


Medial

Ventral

Lateral

Dorsal



ST4

ST5

2 cm



ST2

ST3

Ventral view



ST4

ST5

2 cm

Table 1

General inventory of the costal remains of the Regourdou 1 Neandertal individual.

Anatomical position	Side	Labels	Number of fragments	Head	Neck	Tubercle	Shaft	Posterior angle	Shaft	Sternal end
1	R	R#a	2			C	N/A	N/A	C	C
	L	R#b	2		P	C	N/A	N/A	C	C
2	R	R#y, R#f+R#e, R#ae	5		P	C	N/A	N/A	P	C
	L	R#c, R#d, R#t+R#al	7		C	P	N/A	N/A	C	
3	R	R#an+R#am, R#z	4						P	C
	L	R#g+R#s	2		C	C	C	P	P	
4	R	R#ab+R#ac	2			P	C	C	P	
	L	R#j+R#i	3			P	C	C	P	
5	R									
	L									
6	R	R#ap+R#aq					P	P		
	L	R#ag	1			P	C			
7	R	R#ad+R#ah+R#ak	4				C	C	P	
	L									
8	R	R#l, R#k	3					C	P	P
	L									
9	R	R#m, R#n+R#o	3	C	C	C	P		P	
	L	R#aa, R#h	1					C	P	
10	R									
	L									
11	R	R#p+R#q+R#w	4	P	C	N/A	C	C	C	C
	L	R#r, R#af	3			N/A	P	C	P	
12	R	R#u	1			N/A			P	
	L	R#ar, R#s	4	C	C	N/A	C	P	P	C
5-7	R	R#x	1	C	C					
6-8	R	R#v	1	P	P					
5-6?	L	R#ai	1						P	
4-6?	R?	R#aj	1						P	
4-7	L	R#ao	1						P	
6-8	L	R#ag	1			P	C			

Table 2

Raw dimensions (in mm) of the Regourdou 1 and other Neandertal 1st ribs, summary statistics of the recent human sample, and results of the z-score analysis between Neandertals and recent modern humans.^a

Variable ^b		Regourdou 1		Amud 1	Kebara 2	Kebara 2	Sidrón SD-1767	Sidrón SD-1699+	Krapina 117.2	Krapina 117.3	Krapina 118.2	Krapina 117.1	Krapina 118.4	Sima de los Huesos-Col	Euroamerican males ^c	
		1R (R#a)	1L (R#b)	1L	1R	1L	1R	1L	1R	1R	1R	1L	1L	1L	1R	1L
1a	Tuberculo-ventral chord (TVC)	94.2	92.8*		85.7	82.7	79.05	(83.0)						97.5**	84.68 ± 5.42 (74.8-94.5)	83.87 ± 4.52 (73.9-91.4)
2a	Tuberculo-ventral arc (TVA)	103	103.5		99.0	(96.0)	105.0	(115.0)							104.24 ± 9.35 (85.0-126.0)	104.38 ± 8.34 (86-120)
6	Neck minimum cranio-caudal diameter (NMnCCD)		4.9			4.7										4.88 ± 0.61 (3.8-6.1) <i>n</i> = 32
14	Tubercle horizontal diameter (THD)	18.4	19.0		19.8	19.4	16.05	17.9	17.1	(16.5)	15.2	15.4			17.08 ± 1.63 (12.9-19.8) <i>n</i> = 33	17.01 ± 1.62 (13.9-19.6) <i>n</i> = 32
19	Mid-shaft maximum diameter (MMxD)	16.3		> 19.0	(20.7)	(20.5)	16.05	17.9	14.0*	13.8*	13.2*		15.6		19.55 ± 2.70 (14.4-23.9) <i>n</i> = 32	19.23 ± 2.82 (14.2-24.3) <i>n</i> = 32
20	Mid-shaft minimum diameter (MMnD)	4.1	4.1	4.2	3.3	3.5	4.55	5.75	3.5	4.3	4.0		3.4		4.21 ± 0.67 (2.9-5.3) <i>n</i> = 32	4.06 ± 0.63 (2.9-5.4) <i>n</i> = 32
23	Sternal end maximum diameter (SEMxD)	17.7		(20.0)	19.8	17.8	19.0	(17.3)							18.26 ± 2.63 (14.0-24.1)	
24	Sternal end minimum diameter (SEMnD)	9.9	8.8	8.9	8.4	9.3	6.15	5.95							9.44 ± 1.53 (7.3-12.7)	9.47 ± 0.90 (7.9-10.9)

^a Data for Kebara 2 from Gómez-Olivencia et al. (2009). Data for Sidrón from Bastir et al. (2015). Data for Amud 1 and Krapina from Gómez-Olivencia et al. (2010). Data for Sima de los Huesos from Arsuaga et al. (2015). Values in parentheses are estimated. Values underlined are outside the range of the modern human comparative sample. The z-score analyses values with a * or ** are significantly different from the modern male comparative sample (* = $p < 0.05$, ** = $p < 0.01$). Values in bold indicate those values that are significantly different from, and/or outside the range of, the modern human sample.

^b Variable number following Gómez-Olivencia et al., 2010.

^c Mean ± Standard deviation (SD); (Minimum-Maximum). For the Euroamerican sample $n = 30$, unless otherwise stated.

Table 3

Raw dimensions (in mm) of the Regourdou 1 and other Neandertal 2nd ribs, summary statistics of the recent human sample, and results of the z-score analysis between Neandertals and recent modern humans.^a

Variable ^b		Regourdou 1		Kebara 2		Euroamerican males ^c	
		2R (R#y, R#ae)	2L (R#c, R#d, R#t+al)	2R	2L	2R	2L
1a	Tuberculo-ventral chord (TVC)		<u>(155)**</u>	(137.2)		129.44 ± 9.16 (110.7-148.0) <i>n</i> = 27	130.01 ± 9.57 (108.4-149.0) <i>n</i> = 29
2a	Tuberculo-ventral arc (TVA)		(195-200)	184		188.33 ± 16.40 (150.5-221.0) <i>n</i> = 26	189.68 ± 14.94 (154.0-220.5) <i>n</i> = 28
3	Tuberculo-ventral subtense (TVS)		(54.5)	(56.0)		57.49 ± 6.30 (44.2-69.5) <i>n</i> = 27	57.36 ± 5.34 (46.9-67.0) <i>n</i> = 29
4a	Head cranio-caudal diameter (HCCD)		<u>8.1*</u>	10.8		10.91 ± 1.29 (8.5-13.6) <i>n</i> = 30	11.04 ± 1.26 (8.6-14.1) <i>n</i> = 31
5a	Total neck length (TNL)		37.9	35.5		35.35 ± 1.86 (30.0-40.2) <i>n</i> = 30	35.43 ± 1.73 (30.4-39.0) <i>n</i> = 31
6	Neck minimum cranio-caudal diameter (NMnCCD)		5.9	6.7	6.1	6.41 ± 0.98 (4.8-8.6) <i>n</i> = 30	6.44 ± 0.94 (5.1-8.5) <i>n</i> = 31
7	Neck thickness (NTh)		7.5	7.2	6.7	6.84 ± 1.19 (4.5-9.5) <i>n</i> = 30	7.07 ± 1.49 (4.6-11.5) <i>n</i> = 31
14	Tubercle horizontal diameter (THD)	<u>16.6**</u>	<u>>16.1**</u>	14.3		12.12 ± 1.59 (8.5-15.2) <i>n</i> = 30	12.05 ± 1.44 (8.0-14.1) <i>n</i> = 31
19	Mid-shaft maximum diameter (MMxD) (internal-external)		14.6	14.7	17.2	15.87 ± 1.90 (11.6-20.0) <i>n</i> = 29	15.24 ± 1.56 (12.7-19.1) <i>n</i> = 31
20	Mid-shaft minimum diameter (MMnD) (cranio-caudal)		8.3	4.8	4.8	6.18 ± 1.45 (3.7-9.3) <i>n</i> = 29	6.25 ± 1.48 (3.2-9.0) <i>n</i> = 31
23	Sternal end maximum diameter (SEMxD)	15.7		<u>17.2*</u>		13.91 ± 1.39 (11.3-16.8) <i>n</i> = 27	13.60 ± 1.21 (10.7-16.1) <i>n</i> = 29
24	Sternal end minimum diameter (SEMnD)	8.4		7.8		7.38 ± 1.09 (5.2-9.2) <i>n</i> = 27	7.46 ± 1.04 (5.9-10.0) <i>n</i> = 29

^a Data for Kebara 2 from Gómez-Olivencia et al. (2009). Values in parentheses are estimated. Values underlined are outside the range of the modern human comparative sample. The z-score analyses values with a * or ** are significantly different from the modern male comparative sample (* = $p < 0.05$, ** = $p < 0.01$). Values in bold indicate those values that are significantly different from, and/or outside the range of, the modern human sample.

^b Variable number following Gómez-Olivencia et al., 2010.

^c Mean ± Standard deviation (SD); (Minimum-Maximum); number of individuals (*n*).

Table 4

Raw dimensions (in mm) of the Regourdou 1 and other Neandertal 3rd and 4th ribs, summary statistics of the recent human sample, and results of the z-score analysis between Neandertals and recent modern humans.^a

Variable ^b	Regourdou 1		Kebara 2		Shanidar 3	Euroamerican males	Regourdou 1		Kebara 2		Shanidar 3	Euroamerican males	
	3R (R#an+R#am, R#z)	3L (R#g+R#s)	3R	3L	3R	3R	4R (R#ab+R#ac)	4L (R#j+R#i)	4R	4L	4R	4R	
5a	Total neck length (TNL)		[28.9]	32.9		34.24 ± 1.79 (29.2-38.5)							
6	Neck minimum cranio-caudal diameter (NMnCCD)		8.3	9.1		8.61 ± 1.34 (6.3-11.2)							
7	Neck thickness (NTh)		5.6	5.0	4.9	4.95 ± 0.83 (3.4-6.3)							
8	Articular tubercle height (ATH)		5.6	6.0	8.6	7.0 ± 1.8							
9	Articular tubercle width (ATW)		9.6	9.4	9.4	7.6 ± 1.3							
10b	Tubercle-iliocostal line distance 2 (TID2)		(34.0)	32.1		29.74 ± 3.03 (22.7-33.8)	(45.0)**		44.8**			35.29 ± 2.91 (29.5-40.5)	
11b	Posterior angle chord 2 (PAC2)		(62.0)	61.7		55.85 ± 5.34 (43.3-61.7)							
12b	Posterior angle subtense 2 (PAS2)		(14.0)	12.7		10.12 ± 2.01 (6.8-15.0)							
13	Posterior angle (PA)		(131°)*			140.42 ± 4.80 (130.6-148.8)							
15	Shaft maximum diameter at dorsal end (DSMxD)		9.3	11.8**		8.71 ± 1.03 (6.2-11.3)		9.5	9.2	8.7		8.90 ± 0.92 (6.9-11.3)	
16	Shaft minimum diameter at dorsal end (DSMnD)		9.3	9.4	9.7	7.2	7.83 ± 1.03 (5.4-10.4)		9.1	8.1	8.2	7.78 ± 1.42 (5.9-13.1)	
17	Shaft maximum diameter at posterior angle (SMxD)		14.9 (16.0)**	13.3 (15.0)**	(15.5)**		14.9**	10.26 ± 1.14 (7.3-12.2)	[13.5]		16.7**	(17.0)**	10.83 ± 1.54 (7.6-13.8)
18	Shaft minimum diameter at posterior angle (SMnD)		9.9	8.5	7.9	7.8	7.4	8.37 ± 1.04 (6.1-10.4) n = 28	9.3	9.5	7.6	9.6	8.74 ± 1.52 (5.9-12.0)
19	Mid-shaft maximum diameter (MMxD)		15.8						14.5			12.06 ± 1.85 (6.0-15.8)	
20	Mid-shaft minimum diameter (MMnD)		6.7						6.4			5.99 ± 0.79 (4.5-7.8) n = 28	
23	Sternal end maximum diameter (SEMxD)		16.4										
24	Sternal end minimum diameter (SEMnD)		7.1										

^a Data for Kebara 2 from Gómez-Olivencia et al. (2009). Values in parentheses are estimated. Values underlined are outside the range of the modern human comparative sample. The z-score analyses values with a * or ** are significantly different from the modern male comparative sample (* = $p < 0.05$, ** = $p < 0.01$). Values in bold indicate those values that are significantly different from, and/or outside the range of, the modern human sample.

^b Variable number following Gómez-Olivencia et al., 2010.

° Mean ± Standard deviation (SD); (Minimum-Maximum). For the Euroamerican sample, $n = 29$ unless otherwise stated. Articular tubercle height (ATH) and articular tubercle width (ATW) of the Euroamerican male sample from Franciscus and Churchill (2002).

Table 5

Raw dimensions (in mm) of the Regourdou 1 and other Neandertal 6th and 7th ribs, summary statistics of the recent human sample, and results of the z-score analysis between Neandertals and recent modern humans.^a

Variable ^b	Regourdou 1		Kebara 2	LC1		Shanidar 3	Euroamerican males ^c	Regourdou 1	Kebara 2		LC1		Shanidar 3	Euroamerican males ^c	
	6?R (R#ap+R#aq)	6L (R#ag)	6R	6R	6L	6R	6R	7R (R#ad+R#ah+R#ak)	7R	7L	7R	7L	7R	7R	
15	Shaft maximum diameter at dorsal end (DSMxD)	10.1		10.8			10.14 1.06 (7.8-12.3)	10.4		9.6	10.4		11.0	10.57 ± 1.21 (8.8-13.4)	
16	Shaft minimum diameter at dorsal end (DSMnD)	<u>10.1**</u>		<u>10.1**</u>			7.82 0.88 (5.9-9.3)	8.4		8.2	<u>10.7**</u>		<u>10.1*</u>	8.04 ± 0.85 (6.6-10.0)	
17	Shaft maximum diameter at posterior angle (SMxD)	[14.5] (15.0)		(18.2)*		(17.5)*	14.3	13.35 ± 2.04 (9.9-18.3)	[15.3] (16.5)	16.4	15.1	(18.0)*	(17.0)	16.4	13.88 ± 2.08 (9.0-18.3)
18	Shaft minimum diameter at posterior angle (SMnD)							8.2	11.8	9.3	11.0	11.5	9.9	9.64 ± 1.24 (7.7-12.4)	
19	Mid-shaft maximum diameter (MMxD)							(13.9)	14.5	(12.5)			17.0*	13.32 ± 1.70 (10.3-17.0)	
20	Mid-shaft minimum diameter (MMnD)							(6.2)	<u>9.3*</u>	<u>9.2*</u>		<u>(10.0)**</u>	8.1	7.13 ± 0.92 (5.3-9.0)	

^a Data for Kebara 2 from Gómez-Olivencia et al. (2009). Data for La Chapelle-aux-Saints 1 (LC1) from Gómez-Olivencia (2015). Values in parentheses are estimated. Values underlined are outside the range of the modern human comparative sample. The z- score analyses values with a * or ** are significantly different from the modern male comparative sample (* = $p < 0.05$, ** = $p < 0.01$). Values in bold indicate those values that are significantly different from, and/or outside the range of, the modern human sample.

^b Variable number following Gómez-Olivencia et al., 2010.

^c Mean ± Standard deviation (SD); (Minimum-Maximum). For the Euroamerican sample, $n = 29$ unless otherwise stated.

Table 6

Raw dimensions (in mm) of the Regourdou 1 and other Neandertal 8th and 9th ribs, summary statistics of the recent human sample, and results of the z-score analysis between Neandertals and recent modern humans.^a

Variable ^b		Regourdou 1	Kebara 2		LC1		Shanidar 3		Euroamerican males ^c		Regourdou 1		Kebara 2		LC1		Shanidar 3		Euroamerican males ^c	
		8?R (R#l, R#k)	8R	8L	8R	8L	8R	8L	8R (n=29)	8L	9R (R#m)	9?L (R#aa)	9R	9L	9R	9L	9R	9L		
5a	Total neck length (TNL)									35.2									31.56 ± 2.58 (26.1-36.0)	
6	Neck minimum cranio-caudal diameter (NMnCCD)									16.8									16.06 ± 1.83 (13.0-19.8) n=24	
7	Neck thickness (NTh)									7.3							6.8		6.06 ± 0.90 (4.7-8.7)	
8	Articular tubercle height (ATH)									10.7**		11.1**	9.0**	12.9**			6.3		6.0 ± 1.5	
9	Articular tubercle width (ATW)									12.6*		9.6	9.0	10.9**			7.6		7.0 ± 1.8	
15	Shaft maximum diameter at dorsal end (DSMxD)									(11.4)		10.6	10.2	10.1	10.8	12.5	9.7		10.38 ± 1.23 (8.4-13.4)	
16	Shaft minimum diameter at dorsal end (DSMnD)									(9.8)**		9.0**	8.7*	10.8**	10.3**	9.6**	9.0**		7.12 ± 0.69 (5.7-8.6)	
17	Shaft maximum diameter at posterior angle (SMxD)	(17.5)	16.8	15.8	(17.5)	(17.0)	16.9	18.4	15.01 ± 2.32 (9.8-18.7)	15.47 ± 2.32 (11.6-20.4) n = 27		19.5	17.2	18.1			17.1	18.1	15.0	16.33 ± 2.01 (12.9-20.3)
18	Shaft minimum diameter at posterior angle (SMnD)	10.1	10.1	10.0	10.4	11.3*	9.8	9.3	8.72 ± 1.22 (5.9-11.9)	8.67 ± 1.33 (4.9-10.9) n = 27		10.5*	8.8	8.8	10.5*	10.1*	9.8	9.2	7.94 ± 1.00 (5.5-9.9)	
19	Mid-shaft maximum diameter (MMxD)	(16.3)	(16.1)			8.7*	16.3		14.64 ± 1.93 (11.8-18.3)	14.87 ± 2.18 (11.3-19.9) n = 27	(15.3)		16.1		13.5			15.3	15.28 ± 1.79 (12.4-19.7)	
20	Mid-shaft minimum diameter (MMnD)	(8.9)*	(8.3)				8.2		6.14 ± 1.16 (3.8-9.0)	6.14 ± 1.02 (4.0-8.0) n = 26	(7.3)		7.4		8.3**			8.5**	5.60 ± 0.93 (3.9-7.3)	

^a Data for Kebara 2 from Gómez-Olivencia et al. (2009). Data for La Chapelle-aux-Saints 1 (LC1) from Gómez-Olivencia (2015). Values in parentheses are estimated. Values underlined are outside the range of the modern human comparative sample. The z-score analyses values with a * or ** are significantly different from the modern male comparative sample (* = $p < 0.05$, ** = $p < 0.01$). Values in bold indicate those values that are significantly different from, and/or outside the range of, the modern human sample.

^b Variable number following Gómez-Olivencia et al., 2010.

^c Mean ± Standard deviation (SD); (Minimum-Maximum). For the Euroamerican sample, $n = 29$ unless otherwise stated. Articular tubercle height (ATH) and articular tubercle width (ATW) of the Euroamerican male sample and of Shanidar 3 from Franciscus and Churchill (2002). ATH and ATW values of Kebara 2 from Arensburg (1991).

Table 7

Raw dimensions (in mm) of the Regourdou 1 and other Neandertal 11th and 12th ribs, summary statistics of the recent human sample, and results of the z-score analysis between Neandertals and recent modern humans.^a

Variable ^b		Regourdou 1		Kebara 2		LC1	Shanidar 3		Euroamerican males ^c	Regourdou 1		Kebara 2		Shanidar 3		Euroamerican males ^c
		11R	11L	11R	11L	11R	11R	11L	11R	12R	12L	12R	12L	12R	12L	12R
1b	Head-ventral chord (HVC)	170			189				159.02 ± 17.56 (127-193)							
2b	Head-ventral arc (HVA)	210			220				197.86 ± 24.92 (144-235)							
15	Shaft maximum diameter at dorsal end (DSMxD)	8.2	8.9	9.2	8.4	9.0		9.4	9.76 ± 1.26 (8.3-13.4) <i>n</i> = 28		10.4	8.8	12.9*	8.6		9.62 ± 1.42 (6.6-12.3) <i>n</i> = 24
16	Shaft minimum diameter at dorsal end (DSMnD)	7.8**	7.7**	6.7	6.4	6.3		7.3	5.63 ± 0.75 (4.3-7.6) <i>n</i> = 28		6.4	6.3	5.6	5.6		5.14 ± 0.73 (4.0-6.8) <i>n</i> = 24
17	Shaft maximum diameter at posterior angle (SMxD)	12.8	11.3	14.5	14.2	(11.0)	12.4		12.84 ± 1.67 (10.2-18.1)	11.2	(11.3)	14.3	11.3	10.9	(13.8)	12.67 ± 2.10 (9.0-17.2) <i>n</i> = 24
18	Shaft minimum diameter at posterior angle (SMnD)	8.3*	8.2	7.2	8.2	8.8*	8.0		6.16 ± 1.08 (4.6-8.5)	6.6**	(6.0)*	7.1**	8.3**	7.1**	7.1**	4.23 ± 0.83 (3.1-5.9) <i>n</i> = 24
19	Mid-shaft maximum diameter (MMxD)	12.2	(13.8)	12.1	13.3				12.7 ± 1.8							
20	Mid-shaft minimum diameter (MMnD)	7.3*	6.9	6.5	6.7				5.2 ± 1.0							
23	Sternal end maximum diameter (SEMxD)	10.5		10.2	9.4				9.38 ± 1.78 (5.0-12.8) <i>n</i> = 25		7.8		9.6			6.24 ± 1.81 (3.8-9.4) <i>n</i> = 18
24	Sternal end minimum diameter (SEMnD)	6.6		6.1					5.27 ± 0.90 (3.1-7.1) <i>n</i> = 25		4.9		6.5*			3.69 ± 1.15 (1.7-5.6) <i>n</i> = 18

^a Data for Kebara 2 from Gómez-Olivencia et al. (2009). Data for La Chapelle-aux-Saints 1 (LC1) from Gómez-Olivencia (2015). Values in parentheses are estimated. Values underlined are outside the range of the modern human comparative sample. The 11R of Kebara 2 is wrongly reconstructed as it has a head and neck fragment from another rib attached to the most vertebral part of this rib. Thus, we have avoided providing the HVA value published by Gómez-Olivencia et al. (2009). This error in the reconstruction was noticed after the publication by Gómez-Olivencia et al. (2009). The z-score analyses values with a * or ** are significantly different from the modern male comparative sample (* = $p < 0.05$, ** = $p < 0.01$). Values in bold indicate those values that are significantly different from, and/or outside the range of, the modern human sample.

^b Variable number following Gómez-Olivencia et al., 2010.

^c Mean ± Standard deviation (SD); (Minimum-Maximum). For the Euroamerican sample, $n = 29$ unless otherwise stated. Mid-shaft maximum diameter (MMxD) and Mid-shaft minimum diameter (MMnD) of the Euroamerican male sample from Franciscus and Churchill (2002).