The costal remains of the El Sidrón Neanderthal site (Asturias, northern Spain) and their importance for understanding Neanderthal thorax morphology.

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Abstract

The study of the Neanderthal thorax has attracted the attention of the scientific community for more than a century. It is agreed that Neanderthals have a more capacious thorax than modern humans, but whether this was caused by a medio-lateral or an antero-posterior expansion of the thorax is still debated, and is key to understanding breathing biomechanics and body shape in Neanderthals. The fragile nature of ribs, the metameric structure of the thorax and difficulties in quantifying thorax morphology all contribute to uncertainty regarding precise aspects of Neanderthal thoracic shape. The El Sidrón site has yielded costal remains from the upper to the lower thorax, as well as several proximal rib ends (frequently missing in the Neanderthal record), which help to shed light on Neanderthal thorax shape. We compared the El Sidrón costal elements with ribs from recent modern humans as well as with fossil modern humans and other Neanderthals through traditional morphometric methods and 3D geometric morphometrics, combined with missing data estimation and virtual reconstruction (at the 1st, 5th and 11th costal levels). Our results show that Neanderthals have larger rib heads and articular tubercles than their modern human counterparts. Neanderthal 1st ribs are smaller than in modern humans, whereas 5th and 11th ribs are considerably larger. When we articulated mean ribs (size and shape) with their corresponding vertebral elements, we observed that compared to modern humans the Neanderthal thorax is medio-laterally expanded at every level, especially at T5 and T11. Therefore, in the light of evidence from the El Sidrón costal remains, we hypothesize that the volumetric expansion of the Neanderthal thorax proposed by previous authors would mainly be produced by a medio-lateral expansion of the thorax.

Resumen

El estudio del tórax Neandertal ha atraído el interés de la comunidad científica por más de un siglo. Existe acuerdo acerca de la mayor capacidad torácica en Neandertales en comparación con humanos modernos. Sin embargo, si esto es causado por una expansión antero-posterior o medio-lateral del tórax es debatido a día de hoy y es clave para el entendimiento de la biomecánica respiratoria y la morfología corporal en Neandertales. La frágil naturaleza de las costillas, la estructura metamérica del tórax y las dificultades en la cuantificación morfológica contribuyen a la incertidumbre en referencia a aspectos de la morfología torácica Neandertal. El yacimiento de El Sidrón ha proporcionado elementos costales que comprenden desde el tórax superior hasta el inferior, así como diferentes restos costales proximales (frecuentemente ausentes en el registro fósil Neandertal), los cuales pueden arrojar luz sobre esta incertidumbre. Nosotros comparamos las costillas de El Sidrón con costillas de humanos modernos actuales, así como con humanos modernos fósiles y otros Neandertales, a través de técnicas de morfometría clásica y morfometría geométrica 3D, combinadas con técnicas de estimación de datos perdidos y de reconstrucción virtual (a nivel de 1ª, 5ª y 11ª costilla). Nuestros resultados muestran que los Neandertales presentan cabezas costales y tubérculos articulares más grandes que humanos modernos. A nivel de tamaño global de las costillas, las 1ª costillas Neandertales son más pequeñas que las de humanos modernos, mientras que las 5ª y 11ª son considerablemente más grandes. Cuando articulamos costillas medias (forma y tamaño) con sus correspondientes elementos vertebrales, nosotros observamos que el tórax Neandertal presenta una expansión medio-lateral en los diferentes niveles estudiados con respecto a humanos modernos, aunque esto es más evidente a nivel T5 y T11. Por lo tanto, a la luz de la evidencia proporcionada por los restos costales de El Sidrón, nosotros hipotetizamos que la expansión volumétrica Neandertal propuesta por

autores previos, debería ser fundamentalmente producida por una expansión medio-lateral del tórax.

Introduction

Studying rib cage morphology provides much important information about the biology of extinct hominin species, as thoracic morphology is directly tied to respiratory dynamics. Expansion of the lungs during breathing and consequent oxygen intake is facilitated by the action of the intercostal muscles, the diaphragm and other accessory muscles (Spalteholz, 1970; De Troyer et al., 2005). Therefore, oxygen availability, basal metabolic rate (BMR) and physical activity are also dependent on various aspects of rib cage morphology (Franciscus and Churchill, 2002; Churchill, 2006; Froehle and Churchill, 2009; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014, 2016a; Bastir et al., 2017a). In addition, the rib cage contributes to the configuration of gross trunk shape in hominins due to its morphological integration caudally with the pelvis (Jellema et al., 1993; Bastir et al., 2014a) and cranially with the upper limb (Churchill, 1994; Bastir et al., 2013; Schmid et al., 2013). Specifically, wide trunks consisting of a wide lower thorax linked to a wide pelvis have been proposed to be the characteristic bauplan of several fossil hominin species such as Neanderthals (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014; Bastir et al., 2015a), Middle Pleistocene hominins (Arsuaga et al., 1999; Carretero et al., 2004), *Homo erectus* (Arsuaga et al., 1999; Carretero et al., 2004; Graves et al., 2010; Holliday, 2012; García-Martínez et al., 2016b; but see Walker and Leakey, 1993) and even the recently discovered species of *Homo naledi* (Berger et al., 2015; Van Sickle et al., submitted; Williams et al., 2017). Further, it is possible that factors such as gut size or function could account for morphological differences in the lower part of the rib cage (Aiello and Weeler, 1995; Ben-Dor et al., 2016).

Notwithstanding the importance of rib cage anatomy, morphological variation in the thorax has received much less attention than other cranial and postcranial regions (Gómez-Olivencia et al., 2009). Thus, thoracic variation in fossil hominin species and its

paleobiological implications are still not clear. This is mainly the result of: 1) the fragile nature of thoracic elements (ribs and vertebrae), which means that they usually appear broken or taphonomically distorted in the hominin fossil record; 2) the metameric structure of the rib cage and the fact that the whole thorax (ribs and vertebrae) is rarely found, usually requiring that thorax morphology to be inferred from a small number of anatomically isolated and distorted elements; and 3) quantifying the complex three-dimensional (3D) curvature of the costal elements with linear measurements such as chords, angles or diameters potentially complicates interpretation of fossil thorax morphology.

Historic perspective on the study of the Neanderthal ribcage

The first studies of fossil hominin thoracic morphology were undertaken in the late 19th and early 20th centuries on Neanderthal ribs from Feldhofer Grotte (Fuhlrott, 1859), Krapina (Gorjanović-Kramberger, 1906), La Chapelle-aux-Saints (Boule, 1911-1913) and Tabun 1 (McCown and Keith, 1939). Although Fuhlrott (1859) and Boule (1911-1913) mainly provided inventories of costal remains, Gorjanović-Kramberger (1906) and McCown and Keith (1939) carried out metric analyses drawing attention to interesting features of the ribs such as their marked robusticity, their rounded cross section, and the straightness of the 1st ribs. These morphological features were linked by McCown and Keith (1939) to a greater respiratory capacity in Neanderthals compared to modern humans. Later, at the end of the 20th century, monographs on the Shanidar Neanderthals (Trinkaus, 1983), La Ferrassie (Heim, 1976) and Kebara 2 individual (Arensburg, 1991; Bar-Yosef et al., 1991) also included study of the ribs. The work carried out by Heim (1976) was mainly a summary of the remains of La Ferrassie individuals and no differences were found between La Ferrassie costal morphology and that of modern humans. Trinkaus (1983) concluded that the ribs of Shanidar 3 were thicker and more robust than in modern humans, but the incompleteness of the remains did not allow for an overall reconstruction of their thoracic configuration.

Arensburg (1991) concluded that the morphology of the Kebara 2 Neanderthal rib cage did not differ from the thoraces of modern populations.

Even though some of the previously cited studies undertook metric analyses on the fossils, comparative samples (when present) were always very small, so differences between Neanderthals and modern humans were assessed without statistics. This changed with the monograph on *Homo ergaster* or *Homo erectus* KNM-WT 15000 (Walker and Leakey, 1993), the first complete and detailed comparative study carried out on thoracic fossils (ribs and vertebrae) using statistical analyses and large comparative samples (Jellema et al., 1993; Latimer and Ward, 1993). Walker and Leakey (1993) pointed out that modern human rib cage morphology arose with the emergence of *H. erectus*, with features such as the volumetric expansion of the upper rib cage, the invagination of the spine and the declination of the ribs, although the modernity of the KNM-WT 15000 rib cage has recently been questioned (García-Martínez et al., 2016b).

Similar quantitative studies using traditional measurements such as arcs, chords or angles have subsequently been performed, resulting in very complete and detailed comparative studies of Neanderthal ribs, improving the understanding of Neanderthal rib cage morphology greatly (Franciscus and Churchill, 2002; Weinstein, 2008; Gómez-Olivencia et al., 2009; Gómez-Olivencia, 2015). Franciscus and Churchill (2002) carried out an exhaustive and comprehensive metric analysis on the Shanidar 3 Neanderthal ribs, comparing them with a wide range of Neanderthals (from Western European to Levantine individuals) as well as with early and modern European *Homo sapiens*. Based on analysis of the upper ribs, they observed that the Neanderthal upper thorax (although variable) could be more antero-posteriorly expanded than in modern humans. They stated that this feature was more evident in Western European Neanderthals than in the Levantine ones. These observations are consistent with the straightness of the 1st ribs observed in the Krapina

sample by Gorjanović-Kramberger (1906) or the straightness in the 2nd rib of Tabun 1 observed by McCown and Keith (1939), which would be consistent with the elongated clavicles observed by other authors (Churchill, 1994; Rosas et al., 2016). However, a later reassessment of the 2nd rib of La Chapelle-aux-Saints by Gómez-Olivencia et al. (2009) challenged this idea, who proposed that the rib was less straight than previously thought.

In addition, Franciscus and Churchill (2002) concluded that although there is some degree of variation in the Neanderthal thorax (perhaps caused by factors such as sexual dimorphism and possibly eco-geographical variation), their rib cages were more voluminous (mainly at the caudal part), with a hypothesized greater vital capacity, than in modern humans. They stated that the larger volume of the Neanderthal thorax was produced by a medio-lateral expansion of the lower thorax in Tabun 1, by a medio-lateral and an antero-posterior expansion of the thorax in Kebara 2, and by an antero-posterior expansion of the overall thorax in Shanidar 3. The larger inspiratory volume of Neanderthals is consistent with their larger nasal cavities (Bastir and Rosas, 2016), which could be linked to a higher oxygen demand due to greater physical activity compared to modern humans (Churchill, 2006; Froehle and Churchill, 2009). However, other explanations such as cold adaptation and/or genetic drift as causal mechanisms for generating this thorax morphology were not excluded by Franciscus and Churchill (2002). The results of Franciscus and Churchill (2002) were later confirmed by Weinstein (2008), who measured Shanidar 3 and Tabun 1 ribs and compared them to Andean populations, which are known to present enlarged thoraces in response to a higher oxygen demand because of their hypoxic living conditions. She observed that both Neanderthals' rib cages were slightly larger than their Andean counterparts, concluding that the large Neanderthal thorax may reflect an adaptation to both high oxygen intake and high activity levels. Subsequently, Gómez-Olivencia et al. (2009) carried out a very detailed analysis of the Kebara 2 Neanderthal ribs in comparison to populations inhabiting moderate

and cold climates. They found that the central (4, 5 and 7) and lower ribs (8 and 10) were larger than in modern humans (ribs 6 and 9 were not complete, possibly explaining the lack of differences in those ribs), and inferred a large thorax capacity for Kebara 2. However, they could not definitively conclude whether these differences were caused by a medio-lateral expansion of the thorax, an antero-posterior expansion, or both. Clarifying this issue would contribute not only to the understanding of the breathing kinematics in Neanderthals (which is dependent on thorax shape), but also to the understanding of their body shape.

Previous research has improved understanding of the differences between thorax morphology in Neanderthals and modern humans, and associated paleobiological implication, but several issues should be noted. First, linear measurements (chords, arcs, angles) do not accurately quantify the complex three-dimensional morphology of ribs. Missing costal ends are very difficult to estimate using such methods. For example, Shanidar 3 does not preserve any of the distal or proximal ends of the ribs in connection with the rib shaft, as noticed by Trinkaus (1983). Therefore, the estimation of the rib ends and the evaluation of the overall curvature of the rib present a serious challenge in some cases. Second, inferences about thorax morphology based solely on rib size and shape, regardless of its anatomical connection with the thoracic vertebrae, might lead to misinterpretations of antero-posterior or medio-lateral expansion of the thorax. It has recently been observed that a different orientation of the transverse processes of the thoracic vertebrae could significantly alter thorax breadth (Bastir et al., 2014b, 2015a; 2017b, submitted; García-Martínez et al., 2016c). Therefore, the same rib morphology could produce a different thoracic configuration depending on the degree of dorsal orientation of the transverse processes of the thoracic vertebra. This fact reinforces the need to combine knowledge of ribs and vertebrae to make inferences about features such as the antero-posterior or the medio-lateral expansion of the thorax, which are emergent from the anatomical composite and can seldom be inferred from individual elements.

More recent perspectives on the study of the Neanderthal ribcage

Methodological advances in virtual anthropology (Recheis et al., 1999; Weaver et al., 2015) and improvements of 3D quantification of sliding semilandmark within geometric morphometrics have allowed for more accurate quantification of the thorax and individual ribs, even when the record is fragmentary (Bastir et al., 2013, 2015a; García-Martínez et al., 2014, 2016b, c; Shi et al., 2014; Weaver et al., 2014; Williams et al., 2017). Virtual reconstruction and virtual estimation of missing elements or distorted parts has allowed for analyses of fossils previously regarded as uninformative, and re-analyses of fossils that were previously reconstructed wrongly (Zollikofer et al., 2005; Gunz et al., 2009; Bastir et al., 2010; García-Martínez et al., 2014; Gómez-Olivencia et al., 2015). García-Martínez et al. (2014) quantified the size of individual ribs of the Kebara 2 Neanderthal from the 1st to the 10th using 3D geometric morphometrics techniques, conducting a virtual reconstruction of the 6th and 7th ribs from the left side following the reassessment made by Gómez-Olivencia et al. (2009). In accordance with previous research using traditional morphometrics, the ribs belonging to the lower thorax (from 7th onwards) had larger centroid sizes than the corresponding ribs in modern humans (García-Martínez et al., 2014). Since these are the ribs functionally linked to diaphragmatic action, a greater diaphragmatic contribution to Neanderthal breathing than is found in modern humans was suggested, consistent with previous research (Franciscus and Churchill, 2002; Weinstein, 2008; Gómez-Olivencia et al., 2009) and with the hypothesis of high oxygen demand because of high levels of physical activity (Churchill, 2006; Rosas et al., 2006a; Bastir, 2008; Froehle and Churchill, 2009; Bastir and Rosas, 2016). The 1st ribs of the Neanderthal sample from El Sidrón have been studied in an ontogenetic and comparative framework, with a divergent ontogenetic trajectory found in the El Sidrón specimens compared to modern humans, helping to explain why Neanderthal 1st ribs on average show less curvature in cranial view (Bastir et al., 2015a).

Additionally, it has been suggested that straighter 1st ribs in Neanderthals should be correlated with antero-posterior projection of the entire ribcage (Gorjanović-Kramberger, 1906), but with modern virtual anthropology methods this was found to be the case only in the upper thorax, with the lower rib cage more medio-laterally expanded in Neanderthals compared to modern humans. This correlation between ribs and thorax morphology is based on modern human data and assumed for Neanderthals in our study (following Bastir et al. 2015a). Although we expect the correlation to be conserved, it is possible that correlation patterns are different in the two hominin groups. In addition, the proposal from Bastir et al. (2015a) is consistent with an earlier physical reconstruction of a Neanderthal rib cage (mainly based on Kebara 2 but, unusually, using both ribs and vertebrae), which indicated a medio-lateral expansion of the lower thorax (Sawyer and Maley, 2005).

The El Sidrón site

The El Sidrón site is a karstic cave located in Asturias in northern Spain, in the “Surco Oviedo-Infiesto” – a band of Mesozoic and Cenozoic sediments limited to the north and south by Paleozoic reliefs (Forteza et al., 2003; Rosas et al., 2006b). Archaeological excavations in the cave were conducted from 2000 to 2014. They uncovered 415 lithic tools (Santamaría et al., 2010), 51 macro-mammal remains (Rosas et al., 2011), and more than 2500 Neanderthal bone fragments (Rosas et al., 2013), all from the same archaeological unit (Unit III; Cañaveras et al., 2011), representing the most complete Neanderthal sample of the Iberian Peninsula (Rosas et al., 2006b, 2012, 2015). These remains were found in a secondary position; the original deposit, worn out by erosion, is thought to have been either on the surface or in an upper karst level (Forteza et al., 2003). Several dating methods applied to the Neanderthal bones and teeth give a consistent date of around 49,000 BP (before present; de Torres et al., 2010; Wood et al., 2013), with environmental conditions similar to those of the

area today (Forteza et al., 2003; Badal-García, 2011; Rosas et al., 2011; Sanchíz and Martín, 2011).

All skeletal regions have been preserved in the El Sidrón sample, with some (thorax, arms, feet and hand bones) recovered in anatomical articulation (Rosas et al., 2006b, 2013). A total of 13 Neanderthal individuals have been identified from El Sidrón (Rosas et al., 2013, 2015), including seven adults (four females, three males), three adolescents (one female, two males), two juveniles (one male, one for whom sex determination is still in progress), and one infant (whose sex is indeterminate). The site has yielded a large number of costal remains, ranging from remains of the 1st ribs to the 12th ribs (García-Martínez et al., 2016d). Although the costal sample is fragmentary, every part of the rib anatomy is represented: head, neck, rib shaft and distal end. Importantly, the costal sample includes several well preserved proximal ends (head and articular tubercle) that are rare and scarce in the Neanderthal fossil record – articular tubercles are preserved in several Neanderthals but only Kebara 2 presents two partially complete rib heads from true ribs and four almost complete ones from floating ribs.

Aims of this study

Previous work on Neanderthal costal morphology has been based mainly on four individuals (Kebara 2, Shanidar 3, La Chapelle-aux-Saints and Tabun 1), so study of the El Sidrón remains enlarges the sample considerably. The main aim of this paper is to describe and analyze in a comparative context the costal material from the El Sidrón site, undertaking an in-depth analysis of all the costal material except that probably belonging to juveniles 1 and 2 (according to Rosas et al., 2013). Specifically, because of the good preservation of several rib heads in the El Sidrón sample, we address the previous paucity of information about differences between rib heads in Neanderthals and modern humans, and test the hypothesis (H1) that Neanderthals and modern humans share similar dimensions at the

proximal rib end. In addition, although there is a consensus about the more capacious rib cage in Neanderthals, it is still unknown if this is because of differences to the antero-posterior, the medio-lateral dimensions, or a combination. Since ribs from the upper, middle and lower thorax are preserved in the El Sidrón sample, we investigate this and test the hypothesis (H2) that the Neanderthal thorax is more antero-posteriorly expanded in the upper thorax and more medio-laterally expanded in the lower thorax than in modern humans.

Materials and methods

The El Sidrón costal sample

The Neanderthal costal remains of the El Sidrón site are temporarily housed at the Department of Paleobiology of the Museo Nacional de Ciencias Naturales (MNCN-CSIC) in Madrid, Spain. The most informative costal remains, and those included in this study, are shown in Figures 1–3 and number of individual specimens (NISP), minimum number of elements (MNE) and minimum number of individuals (MNI) are given in Table 1. A complete list of specimens used in this study is in Supplementary Online Material (SOM) Table S1.

Comparative sample for traditional measurements

The comparative sample comprised ribs from each level belonging to contemporary European human adults (Spain, $n=120$ ribs; Portugal, $n=120$ ribs; Austria, $n=48$ ribs; 12 males and 12 females in total). Individual ribs from the Spanish and Austrian populations were segmented from CT scans of healthy subjects using semiautomatic methods in Mimics software (<http://www.materialise.com/en/medical/software/mimics>) to get measurable 3D models of individual ribs. (These data were obtained from subjects scanned previously as a healthy control group in order to compare with pathological individuals as part of a different research project at the Hospital Universitario La Paz [Madrid, Spain] and Medizinischen Universität Innsbruck [Innsbruck, Austria].) Individual ribs from the Portuguese population

(21st century Identified Skeletal Collection, housed at the Laboratory of Forensic Anthropology, University Of Coimbra, Portugal; Ferreira et al., 2014) were scanned using a Next Engine HD 3D (high definition three dimensional) laser scanner in ‘wide mode’ (with a resolution 0.38 mm and an accuracy of 6 points per mm). In no case could any pathologies affecting skeletal thorax form be identified. Detailed information on the comparative sample can be found in SOM Table S2.

Comparative sample for geometric morphometric analyses

Only the 1st, 5th and 11th ribs from the El Sidrón site were included in 3D geometric morphometric analysis, so the modern comparative sample comprised the corresponding ribs from the dataset described above (see SOM Table S2). The comparative fossil sample comprised HD surface 3D models of ribs from these levels obtained using a Next Engine 3D laser scanner (SOM Table S2). The Neanderthal sample included both 1st ribs, one 5th and one 11th rib from the Kebara 2 individual (Arensburg, 1991; Gómez-Olivencia et al., 2009) that were scanned at the Sackler Faculty of Medicine (Tel Aviv, Israel) plus two Neanderthal 1st ribs from Krapina (117.2 and 118.2; Gorjanović-Kramberger, 1906) scanned at the Croatian Natural History Museum (Zagreb, Croacia). The modern human fossil sample comprised 1st ribs from Mladeč (Trinkaus et al., 2006), Cueva de la Paloma (Hernández-Pacheco, 1923), and Oetrange (Meiklejohn et al., 2014). In addition, we included the two 1st ribs from a ~19 year old female *H. sapiens* named “La Femme de Tigermoyen”, discovered in the d’Arlit region (Nigeria) by Henri Lothe in 1974 and dated to 5,420 BP. Housed at the MNHN (Paris, France), it has not been properly published to date. Neither 5th nor 11th ribs from modern human fossil were preserved, so only the 1st ribs listed above are included in the comparative sample.

Position and side assessment of the costal remains

The El Sidrón costal remains were sided using anatomical features such as the costal groove or the rib axis orientation. To determine anatomical position we used morphological features together with specific diagnostic features for atypical ribs (1st, 2nd, 11th and 12th). These features include the presence of specific muscle insertions for the 1st and 2nd ribs (scalene and serratus insertions), the absence of the articular tubercle for the 11th and 12th ribs and the presence of a single facet at the rib head on the 1st, 11th and 12th ribs. Even though these features are common (Spalteholz, 1970), there may be some variation in the traits, such as the presence of a double facet at the rib head (Ohman, 1986; Tawane et al., 2016) or the lack of the articular tubercle in the 10th rib (such as in the case of Kebara 2 individual; see Gómez-Olivencia et al., 2009). For the typical ribs (3rd to 10th) we used comparative anatomy to estimate the positional range when the proximal end (and thus the rib head) was missing. When the rib head was preserved (five specimens in the sample), we determined level via an index of rib head shape. To devise this index, which quantified changes in the rib head shape along the costal sequence, we divided rib head height by rib head width for each of the 1st to 10th ribs in our comparative sample of contemporary humans. Head height was represented by head cranio-caudal diameter (HCCD) following the definition of Gómez-Olivencia et al. (2010) and head width (HW) was the maximum length of the articular surface of the rib head perpendicular to the cranio-caudal axis (coinciding with the length of the inter-articular crest, when applicable). Cirillo and Henneberg (2005: 185) measured HW as the “distance between the most lateral aspects of the rib head when the articular facet of the rib head and articular facet of the tubercle are aligned in a straight line (180°) on a surface situated on a horizontal plane.” Although this is similar to the method we use, ours is more straightforward since measuring the inter-articular crest of the rib head is based on an anatomical feature and is not a geometric construction. Both HCCD and HW

were measured on the 3D virtual models using Artec v11 software (www.artec3d.com). To validate the modern human index as a proxy for positioning Neanderthal ribs we measured Neanderthal rib heads of known anatomical position: the 1st and 2nd from Kebara 2 (again, measured on a virtual model) and an 8th from the El Sidrón (in anatomical connection within a partial thorax, measured using calipers, as were the other El Sidrón rib heads). The position of the 3rd rib from the El Sidrón site was evaluated because of its anatomy and measured and validated using calipers.

Morphological descriptions, metrics and qualitative analyses of the more diagnostic remains

A full morphological description, seriation, qualitative observations, state of preservation as well as standard measurements (following Franciscus and Churchill, 2002 and Gómez-Olivencia et al., 2010) and assessment of developmental age (following Ríos and Cardoso, 2009) was undertaken for the best preserved and most informative costal specimens from the El Sidrón sample ($n=18$; see Results). Fragments preserving information about anatomical position but lacking diagnostic morphology are listed with approximate identification and preservation in SOM Table S1. For the best preserved proximal rib remains, measurements of the articular tubercle (maximum cranio-caudal diameter of the articular tubercle with the rib positioned in approximate anatomical position [ATH] and maximum width of the articular tubercle with the rib positioned in approximate anatomical position [ATW], following Franciscus and Churchill, 2002) and neck (straight line distance between the lateral (sternal)-most margin of the articular tubercle to the medial-most point of the head [TNL], following Gómez-Olivencia et al., 2010) were made, alongside the head dimensions mentioned above. Metric dimensions for La Chapelle-aux-Saints 1 were taken from Gómez-Olivencia (2015), and measurements for Kebara 2 and Shanidar 3 were taken on 3D models using Artec v11 software. Fossil and modern human dimensions were compared

with 95% confidence intervals for the mean (Sokal and Rohlf, 1973) using SPSS software (SPSS Inc., 1995).

Virtual reconstruction methods

The preservation of some remains necessitated virtual reconstruction of a 5th and an 11th rib from the El Sidrón sample to reconstruct their probable morphologies. Virtual reconstruction was undertaken if the rib shaft was almost complete but the proximal and distal ends were missing. We created parsimonious hypothetical anatomical composites using virtual techniques such as mirror imaging, fusing and smoothing (similar to the methods used by Gómez-Olivencia et al., 2015). The final 3D models allowed us to measure variables such as the TVC (straight line distance between the dorsal-most margin of the articular tubercle to the ventral-most point of the sternal end of the rib), TVA (arc length measured along the greater curvature of the rib from the lateral end of the articular surface of the tubercle to the sternal end of the rib) and TID2 (straight line distance from the medial end of the articular tubercle to the furthest extent of the iliocostal line) for the 5th rib, and the HVC (straight line distance between the lateral margin of the articular surface of the head to the ventral-most point of the sternal end of the rib) and HVA (arc length measured along the greater curvature of the rib from the lateral margin of the articular surface of the head to the sternal end of the rib) for the 11th rib. These measurements could not be estimated in individual remains. These linear measurements provide an overall idea of the curvature in cranial view of the rib (Gómez-Olivencia et al., 2009, 2010). Virtual reconstructions were also analyzed using 3D geometric morphometrics.

SD-1450 (5th rib from the right side; see Results for details of siding and attributions for all material mentioned in this section) and SD-2187 (11th rib from the left side) were virtually reconstructed. To reconstruct the proximal part of SD-1450, we used the proximal

shaft SD-965a as a proxy, which was assessed as a 5th rib. To align them, we superimposed SD-1450 and SD-695a on the 5th right rib of Kebara 2. We used the tubercle-angle distance of the Kebara 2 5th rib to set the distance between SD-1450 and SD-695a. Once the proximal part was correctly aligned, we superimposed, at a posterior angle, SD-1450 and the 5th right rib of Kebara 2 to estimate the missing part of the distal end of SD-1450 (we estimated that 98.9 mm were lacking). Then, we virtually dissected the necessary section from the Kebara 2 rib and fused it virtually to SD-1450+SD-695a to create a virtual reconstruction of a complete 5th rib from the El Sidrón sample, the anatomy of which was consistent with the anatomy of 5th ribs (Figure 4a). For reconstruction of the proximal part of SD-2187, we used the mirror image of SDR-131, a complete proximal end of an 11th rib from El Sidrón. Mirror imaging was necessary in SDR-131, since the two elements were from different sides. To align them, we used the 11th left rib of Kebara 2 to superimpose SD-2187 and the mirror image of SDR-131, to estimate its relative position. In order to confirm the alignment, we applied the rib head-posterior angle distance of the Kebara 2 11th right rib to set the distance between SD-2187 and SDR-131. Once the proximal part was correctly aligned, we followed the protocol detailed above to create a virtual reconstruction of an 11th rib from El Sidrón, whose anatomy was consistent with the anatomy of 11th ribs (Figure 4b).

3D geometric morphometrics of individual ribs

Three dimensional geometric morphometric analyses were undertaken on material from the 1st, 5th and 11th thoracic levels, which were the best preserved components of the El Sidrón costal sample. Landmarks were placed using Viewbox4 software (www.dhal.com) in order to quantify rib head morphology, 3D rib curvature, shaft height and shaft thickness for geometric morphometric analyses. Missing data estimation was carried out in Viewbox 4 through Thin Plate Spline and following the bending energy approach (Gunz, 2005; Gunz et al., 2009). Semilandmarks were first slid between each specimen and the template (first

specimen), then they were slid a second time along their curves to minimize bending energy between each specimen and the sample average (Gunz et al., 2005, 2009; Mitteroecker and Gunz, 2009); such sliding adjusts the relative locations of semilandmarks along the curve.

1st ribs For the 1st rib (total $n=35$) we placed 55 3D landmarks and semilandmarks (SOM Fig. S1). When estimation of missing data at the proximal or distal ends was required for the *H. sapiens* ribs (both early and modern) the mean coordinates of their respective sample were used as a reference. For missing landmarks at the proximal ends of Neanderthal 1st ribs (SD-1767; SD-1699+SD-1685; Krapina 117.2; Krapina 118.2), we used the Kebara 2 1st rib as a reference. When missing landmarks were at the distal end of 1st ribs (SD-1699+SD-1685; Krapina 117.2; Krapina 118.2), we used the average coordinates of the 1st ribs of the Neanderthal specimens preserving this region (SD-1767; both antimeres of Kebara 2) as a reference.

5th ribs For the 5th rib (total $n=27$), we placed 61 3D landmarks and semilandmarks (SOM Fig. S2). No missing data estimation was needed in the virtual reconstruction of the El Sidrón 5th rib and we used the average coordinates of SD virtual reconstruction as a reference for estimating missing points at the missing ends of the Kebara 2 ribs.

11th ribs For the 11th rib (total $n=27$), we placed 44 3D landmarks and semilandmarks (SOM Fig. S3). No missing data estimation was needed in the virtual reconstruction of the El Sidrón site 11th rib and we used the coordinates of SD virtual reconstruction for estimating missing points at the rib heads of the Kebara 2 11th left (rib head taphonomically damaged) and right ribs (rib head wrongly glued to the rib shaft; Asier Gómez-Olivencia, personal communication).

Geometric morphometrics analyses Shape data were obtained by Generalized Procrustes Analysis (GPA). Size was quantified as centroid size (i.e., the square root of the summed

squared distances of each landmark to the centroid; O'Higgins, 2000; Mitteroecker and Gunz, 2009) and 95% confidence intervals for the mean were used to compare and explore the size relations between the El Sidrón ribs and the rest of the sample in SPSS (SPSS Inc., 1995). Shape data were subjected to Principal Components Analysis (PCA) to reduce the dimensionality of data and to visualize the main axes of variation (O'Higgins, 2000) using MorphoJ software (Klingenberg, 2011). Shapes associated with variations along PC axes were visualized as warps of the sample mean shape into shapes corresponding to the observed maximum and minimum ranges of principal component (PC) scores for the 1st and 11th ribs, allowing comparison of Neanderthals and the rest of the sample. This was done using the EVAN Toolkit version 1.71 (<http://www.evan3society.org/>). Moreover, in order to reaffirm differences in shape between Neanderthals and modern humans at the 1st, 5th and 11th costal levels, mean shape analyses were undertaken in MorphoJ. Differences were assessed through Procrustes distance between means and a permutation test ($n=10,000$) for testing equal group means. Group means were also warped and illustrated using the EVAN Toolkit when differences were statistically significant.

3D virtual reconstruction of costo-vertebral articulation at the 1st, 5th and 11th levels

Once the individual rib morphology at the aforementioned levels was studied, we explored the interaction between rib shape and thorax morphology, articulating the mean ribs obtained from the results of this study with their corresponding vertebrae for Neanderthals and modern humans. We used the vertebrae from Kebara 2 for Neanderthals, and vertebrae from the Santarém Collection (Coimbra, Portugal) for modern humans.

Results

Position and side assessment of the costal remains

Assessment of anatomical position and side was possible in 94 costal remains. Because of the preservation of some remains, a precise side and position assessment was not possible for 82 of them. The analyses of atypical ribs identified five 1st rib remains (two from the left side and three from the right side), three 2nd rib remains (all of them from the left side), seven 11th rib remains (four from the left side and three from the right side) and six 12th rib remains (three from each side). Additionally, 16 remains were attributed to a range from 2nd to 4th ribs (eight from each side), 35 remains to a range from 4th to 8th ribs (20 from the left side and 15 from the right side) and 22 remains to a range from 8th to 12th ribs (11 from the left side and 10 from the right side). Figure 5 shows that the HCCD/HW index increases along the costal sequence from the 1st (index around 1) to the 10th (index between 2 and 2.5). This indicates that upper ribs present similar dimensions of HCCD and HW (more square-shaped rib heads) whereas lower ribs present larger HCCD compared to HW (taller and narrower rib heads). Neanderthal ribs of known position fall within their correspondent modern human ranges (Fig. 5). This indicates that the modern human index calculated in this study is useful for anatomically assessing Neanderthal rib heads of unknown anatomical position. Following this method, SDR-161+ was evaluated as a 4th rib, SD-695a and SD-448 as 5th ribs and SD-666 and SD-788 as 6th or 7th ribs.

Morphological descriptions, metrics and qualitative analysis of the more diagnostic remains

Morphological descriptions, metrical and qualitative analyses were undertaken for 18 costal elements (24 specimens in total), ranging from the upper (1st ribs) to the lower thorax (12th ribs).

SD-1767 and SD-1699+ (Fig. 1): These are 1st ribs from the left and right side respectively, probably belonging to different individuals. A full morphological description and metric comparison of these elements can be found in Bastir et al. (2015a).

SD-1534 (Fig. 1): This is a proximal part of a 1st rib from the right side. It is flattened in its cranio-caudal direction and preserves the articular tubercle and the area adjacent to it. It also preserves part of the rib neck but lacks the rib shaft almost entirely. Measurements available for this element can be found in Table 2.

SD-695b (Fig. 1, Table 2): This is a proximal part of a 2nd rib from the left side that preserves part of the neck, the articular and non-articular tubercles and part of the rib shaft, including the posterior angle and part of the insertion of the posterior scalene muscle. This insertion is very pronounced, being more marked than in every other adult Neanderthal 2nd rib known (SOM Fig. S4). The epiphysis at the articular tubercle is completely fused, so a minimum age of 11 or 14 years old (depending on the sex, with females maturing earlier than males, and based on modern human reference samples) is estimated for this individual.

SDR-159 (Fig. 1, Table 2): This is a distal fragment of a left 2nd rib, preserved from the distal part of the serratus anterior muscle insertion (which is not very pronounced) to the distal end, which is complete and not damaged. The shaft is cranio-caudally flattened and presents a lack of curvature in cranial view, similar to that proposed for Tabun 1 by McCown and Keith (1939), and is much straighter than both antimeres of the Kebara 2 individual. Although SD-695b and SDR-159 do not refit together, we cannot exclude the fact that both remains may belong to the same element because both belong to the left side and there is no anatomical overlap between them.

SDR-026+SDR-166 (SDR-026+ onwards; Fig. 2, Table 2): This is a proximal-medium part of a 3rd rib from the left side of the rib cage. It is preserved from the rib head to beyond the costal angle, almost reaching the midshaft. The insertions for the intercostal muscles are pronounced, both at the costal groove and at the superior border of the rib. The posterior angle is not fully apparent as it is eroded, but the articular tubercle and the rib head are

complete and not taphonomically damaged in this individual. The epiphysis at the articular tubercle is completely fused, so a minimum age of 11 to 14 years old (depending on the sex) is estimated.

SDR-161+SDR-196+SDR-192 (SDR-161+ onwards; Fig. 2, Table 2): This is a proximal part of a 4th rib from the left side of the thorax. It is well preserved from the rib head to the costal tubercle, which presents some taphonomical erosion at the bottom of it. This element comes from the refitting of three fragments. The epiphysis at the articular tubercle is completely fused but the one at the rib head is not, so an age range of 14 to 21 years old is estimated.

SD-695a (Fig. 2, Table 2): This is a proximal part of a 5th rib from the right side, preserved from the rib head to beyond the articular tubercle. The rib head and the articular and non-articular tubercles are well preserved, although the head has slight erosion in the superior part. The epiphysis at the articular rib head is completely fused, so a minimum age of 18 years old is estimated.

SD-448 (Fig. 2, Table 2): This is a proximal part of a 5th rib from the left side, which is preserved from the rib head to the articular tubercle. The superior part of the rib head is missing but the articular tubercle is well preserved. The epiphysis at the rib head is in active fusion, so an age range of 15 to 22 years old is estimated.

SD-1450 (Fig. 1, Table 2): This is a medial-distal part of what is probably a 5th rib, which is preserved from the posterior angle almost to the distal end. It is one of the most complete rib shafts from the central thorax of the El Sidrón costal sample. The posterior angle, which is complete and well preserved, is very pronounced (as observed in Kebara 2 Neanderthal; Fig. S5) so a strong iliocostalis muscle can be inferred from this rib. Both proximal and distal ends are missing.

SD-666 (Fig. 2, Table 2): This is a proximal part of a 6th or 7th rib from the right side of the thorax. It is preserved from the rib head to beyond the articular tubercle. The rib head and the articular and non-articular tubercles are well preserved, although the head is eroded superiorly. The epiphysis at the rib head is in active fusion, so an age range from 15 to 22 years old is estimated.

SD-788 (Fig. 2, Table 2): This is a proximal part of a 6th-7th rib from the right side. It is preserved from the rib head to the articular tubercle. The rib head and the articular tubercle are well preserved, although the head is eroded inferiorly. The epiphysis at the rib head is in active fusion, so an age range from 15 to 22 years old is estimated.

False ribs

SD-2001+SD-1834+SD-1771 (2001+ onwards; Fig. 1, Table 2): This is a rib shaft (preserved from the posterior angle to beyond the midshaft) probably belonging to a 9th or 10th rib from the right side. The shaft is expanded in the superior-inferior plane at the midshaft, which is characteristic of 9th and 10th ribs. The shaft at the inferior part of the posterior angle is eroded. The element is composed of three fragments.

SD-2187 (Fig. 1, Table 2): This is a partially complete 11th rib shaft from the left side, which lacks only the very proximal and distal parts. It is one of the most complete rib shafts from the lower thorax of the El Sidrón costal sample.

SDR-131 (Fig. 1, Table 2): This is a proximal part of an 11th rib of the right side of the thorax, which preserves the rib head (complete) and part of the proximal shaft. The rib head presents a single facet.

SD-695c (Table 2): This is a rib head of an 11th rib from the left side. It clearly presents a single facet. The epiphysis at the rib head is in active fusion, so an age range from 15 to 23 years old (depending on the sex) is estimated for this individual.

SD-573c (Table 2): This is a rib head of a 12th rib from the right side. It has only a single facet and the epiphysis at the rib head is in active fusion, so an age range from 15 to 21 years old is estimated for this individual.

SD-653a (Table 2): This is a rib head of a 12th rib from the left side. It has only a single facet and the epiphysis at the rib head is in active fusion, so an age range from 15 to 21 years old is estimated.

SD-56 (SOM Fig. S6, Table 2): This is a proximal-medial part of a 12th rib which showing the insertion of the diaphragm in the cranial part. This insertion is very similar to the ones observed on the 12th ribs of Kebara 2 or Shanidar 3 (SOM Fig. S6).

Metrics Metrical data (mean, standard deviation and 95% confidence interval for the mean) for the modern human sample and the El Sidrón and comparative fossil samples (ATH, ATW, HCCD, HW, TNL) are given in SOM Tables S4–S9. Rib heads are larger in the cranio-caudal (HCCD) and medio-lateral (HW) dimension in the El Sidrón sample at almost every level. The Kebara 2 non-floating rib heads are within the modern human range but floating ribs In Kebara 2 are larger than in modern humans (except for the HW of the 11th left rib). Articular tubercle height is close to the modern human range for upper ribs in Kebara 2 and El Sidrón Neanderthals but is much larger in the lower Neanderthal ribs (SOM Table S5). Articular tubercle width is more variable in Neanderthals but we also observed that this measurement at the lower thorax is larger overall in Neanderthals (SOM Table S7). We observed that tubercle neck length in Neanderthals fell within the modern human range (SOM Table S9).

Virtual reconstructions: metrics

Based on the virtually reconstructed ribs, the following dimensions were obtained: TVA (329.50 mm), TVC (226.85 mm) and TID2 (46.23 mm) for the 5th rib, as along with

HVA (249.62 mm) and HVC (180.74 mm) for the 11th rib (SOM Table S3). Kebara 2 and the reconstructed ribs from the El Sidrón site had values outside the 95% confidence interval for the mean of modern humans in every value, except for the TID2 of the Kebara 2 right rib, which was close to the upper part of the confidence interval for modern human males. It should be noted that the larger values observed in the El Sidrón virtually reconstructed ribs and in the Kebara 2 11th right rib must be treated with some caution since the estimation methods could introduce some error.

3D geometric morphometrics of individual ribs

1st ribs Results of the 95% confidence interval for the mean of the CS showed that ribs of modern human males are larger (based on centroid size) than those of females (Fig. 6a). Early modern human ribs were highly variable for centroid size, ranging from the small right rib of the Nigerian individual “La Femme de Tigmoyen” (168.36) to the large 1st rib from Cueva de la Paloma site (205.66). All of these individuals were below the confidence interval of both male and female modern humans (Fig. 6a). The centroid size distribution of Neanderthal 1st ribs was less dispersed than that of modern human fossils, ranging from 202.81 in SD-1767 to 222.18 in Krapina 117.2. Most Neanderthal 1st ribs, even those from Kebara 2 that are known to belong to a male, fell below the modern male range. Krapina 117.2 was the only exception to this, but was found within the lowest part of the confidence interval of modern males (Fig. 6a). Every Neanderthal 1st rib fell near the confidence interval of modern females.

Neanderthal 1st rib shapes were distributed more towards the negative values of PC1 than were their modern human counterparts, while fossil *H. sapiens* fell within the center of the distribution of modern humans (PC1 and PC2 together account for 61.67% of sample variance; Fig. 7a). In the associated warps, the positive values of PC1 were characterized by

1st ribs presenting a stronger curvature in cranial view than those at the negative values. Additionally, different orientations of both proximal and distal ends were explained by PC1. At the proximal end, positive values presented a more closed angle between the neck and the proximal part of the shaft, whereas negative values had a more opened angle between the neck and the proximal shaft. A more medial orientation of the distal end was observed in the warps associated with positive PC1 scores, whereas the other pole of the axis was characterized by a more lateral orientation of the distal end (Fig. 7a).

Results of mean comparisons (Table 3) showed statistical differences ($p < 0.01$) between the Neanderthal group and modern humans, both fossil and current. The largest Procrustes distance (0.09) was found between Neanderthals and current modern humans. Warps associated with means are shown in Figure 8a, and indicate that the differences between Neanderthals and modern human groups are the same as observed in the warps associated with PC1: less curvature in cranial view, more opened angle at the tubercle between the neck and the proximal shaft, and a more lateral orientation of the distal end in Neanderthals.

5th ribs Modern human male 5th ribs were larger than female ones (Fig. 6b). The Kebara 2 left rib fell within the highest part of the interval for modern males but the Kebara 2 right rib and the reconstructed 5th rib from El Sidrón were above this range (Fig. 6b). For shape, Neanderthal 5th ribs overlapped with modern humans in every PC projection, a result confirmed by mean comparisons (Table 4), as there were no statistical differences between the groups.

11th ribs Males in the modern human sample were larger than females (Fig. 6c). Neanderthal 11th rib centroid sizes ranged from 462.36 in Kebara 2 to 469.18 in the reconstructed El

Sidrón specimen. Every Neanderthal 11th rib was located clearly above the modern human range (Fig. 6c).

Neanderthal 11th ribs were more polarized towards the negative values of PC1 than those of their modern human counterparts (PC1 and PC2 together accounted for 81.81% of variance; Fig. 7b). As can be observed in the associated warps, negative values of PC1 characterize 11th ribs with a stronger curvature in cranial view than the 11th ribs located at the positive values. Additionally, the relative head-posterior angle distance was shorter in the negative values of the PC1 and, therefore, the posterior angle-distal end distance was relatively larger in the ribs at the negative values than in the ones at the positive values (Fig. 7b). Results of mean comparisons show that there are statistically significant differences between the groups studied (Table 5). Warps associated with means are observed in Figure 8b. The same differences observed in the PC1 scores warps were observed in the means: stronger curvature in cranial view and a shorter relative head-posterior angle distance in Neanderthals compared to modern humans.

3D virtual reconstruction of costo-vertebral articulation at the 1st, 5th and 11th levels

When mean (size and shape) Neanderthal and modern human 1st ribs are articulated with their corresponding vertebrae (T1), Neanderthal upper thoraces appear relatively more medio-laterally expanded than those of modern humans. When 5th ribs are articulated with their corresponding vertebral levels (T4-T5), we observe that the Neanderthal thorax at this level is more medio-laterally expanded but also slightly more antero-posteriorly projected (Figs. 9a, c). Finally, when mean (size and shape) Neanderthal and male modern human 11th ribs are articulated with their corresponding vertebrae, we observe that the Neanderthal thorax at this level is notably more medio-laterally expanded but also slightly more antero-posteriorly projected than in modern humans (Fig. 9a, d).

Discussion

This study presents new thoracic costal remains of the El Sidrón Neanderthal site and uses traditional morphometrics and 3D geometric morphometrics, alongside with virtual reconstruction methods to compare the morphology of the Neanderthal rib cage with the anatomically modern human rib cage. Importantly, we considered the morphology of the proximal part of the ribs to reconstruct the thorax morphology. Even though this part articulates with the thoracic vertebrae, contributing therefore to the morphology of the anatomically composed rib cage, these parts are usually not preserved in the Neanderthal record, which challenges the reconstruction of their rib cage.

The proximal rib ends and its potential role for understanding breathing kinematics in Neanderthals

Only a few Neanderthal proximal rib ends have been preserved in the fossil record and those that have been preserved have never been measured in a comparative context, hence the importance of the El Sidrón sample. Previous studies based on quantitative analyses have been used extensively and usefully to examine traditional measurements of the proximal segment of the rib (Hoppa and Saunders, 1998; Owers and Pastor, 2004; Cirillo and Henneberg, 2005). However, none of them has ever combined HCCD and HW for costal position assessment as we do in this study. We advocate the use of this method for ribs 1-10, since specific features of the 11th and 12th ribs, such as the presence of a single facet at the head or the absence of the articular tubercle, are diagnostic enough.

Our results show that Neanderthal head index is comparable to that of modern humans (Fig. 5), so this method is here demonstrated to be useful to assess the position of Neanderthal proximal costal ends of unknown position. However, there are remarkable differences when looking at some individual measurements (HCCD, HW, ATH and ATW)

between the two groups. This allows us to reject H1, which predicts that “Neanderthals and modern humans present the same dimensions at the proximal rib end.” However, we specify that differences in head measurements are more pronounced in the lower than in the upper thorax.

In our study, the articular tubercles of Neanderthal ribs in the lower thorax are taller and wider than in modern humans (Table S7a, b). Franciscus and Churchill (2002) observed that the larger size of Neanderthal tubercles could be caused by in-vivo remodeling due to a more frequent or greater degree of joint excursion during breathing. The Neanderthal individuals addressed in Franciscus and Churchill (2002) were mainly old adults (Heim, 1976; Trinkaus, 1983; Bar-Yosef et al., 1991) and results from documented collections show that age is an important factor for articulation remodeling (Cardoso and Henderson, 2010; Cardoso et al., 2016). However, although this is consistent with acquisition of larger articular tubercles over a lifetime, it is also possible that Neanderthals have inherently large tubercles, and the El Sidrón data help to shed light on this. The El Sidrón costal sample contains two specimens, SD-666 and SD-788 (assessed here as 6th or 7th ribs), that clearly belong to young adults (as the epiphysis of the head is in active fusion), which do not show remodeling of the articular tubercle, and do have values of ATH and ATW larger than those of modern humans. This suggests that larger articular tubercles could be an inherent feature of Neanderthal lower ribs, although this assertion does not exclude the hypothetical remodeling of the tubercle as a factor that also underlies the size of the tubercle. Therefore, the large articular tubercles observed in older Neanderthals (Kebara 2 and Shanidar 3) by Franciscus and Churchill (2002) could be the result of both the aging process and an inherited feature. Larger tubercles, together with larger rib heads, could reflect strong breathing kinematics in the lower thorax, perhaps caused by an intense diaphragmatic action, as described in previous

studies (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014; Bastir et al., 2015a).

Hypothetic Neanderthal thorax morphology at 1st, 5th and 10th levels

The El Sidrón site costal remains, also allowed us to hypothesize about Neanderthal thorax morphology. Due to the preservation of the El Sidrón costal sample, we addressed the thorax morphology at only three levels: 1st, 5th and 11th. It is demonstrated in Figure 9 that the three levels together provide an excellent indication of overall morphology of the Neanderthal rib cage.

Regarding the upper thorax, according to our results, the lesser curvature in Neanderthal 1st ribs observed in our analyses occurs through features at both ends of the rib, a more open angle at the proximal end and a more lateral orientation at the distal end compared to modern humans. This straighter Neanderthal 1st rib is consistent with a more antero-posterior expansion of the upper thorax. SDR-159 (a distal shaft of a 2nd rib preserving the distal end) also shows a low degree of curvature in cranial view. Curvature in cranial view is controversial in 2nd ribs. McCown and Keith (1939) described the 2nd rib of Tabun 1 as presenting a low degree of curvature in cranial view, but Franciscus and Churchill (2002) questioned the morphology of this rib since its proximal part is missing and the overall morphology was uncertain. Second ribs from Kebara 2 are described as curved by Franciscus and Churchill (2002) and Gómez-Olivencia et al. (2009). However, it must be noted that the left 2nd rib of Kebara 2 is incomplete and heavily reconstructed, and the right has some degree of reconstruction in the middle of the shaft, which could alter the degree of curvature in cranial view and, thus, its interpretation. Our observation of antero-posteriorly straight ribs in the upper thorax of the Neanderthals (as seen in both the 1st and 2nd ribs) is consistent with those of previous authors (Gorjanović-Kramberger, 1906; McCown and

Keith, 1939; Bastir et al., 2015a). Study of other complete Western European Neanderthal upper ribs, such as the ones from the Regourdou site (Maureille et al., 2015) or the Sima de Las Palomas site (Walker et al., 2011) will be helpful in confirming our results.

However, even though individual elements (1st and 2nd ribs) points to a more antero-posterior expansion of the Neanderthal rib cage, when mean Neanderthal and modern human 1st ribs are articulated with their corresponding vertebrae (T1), Neanderthal upper thoraces appear relatively more medio-laterally expanded than those of modern humans. This is because the transverse processes of the T1 vertebra of Neanderthals are more dorsally oriented than in the T1 of modern humans (Bastir et al., 2015b, 2017b; Fig. 9a, b). Therefore, the orientation of the transverse processes, coupled with the more opened angle at the proximal end and the more lateral orientation of the distal end, would generate a wider thoracic aperture in cranial view at T1 level, which would also leave a wide space for the manubrium. There are some studies on the Neanderthal manubrium (Vallois and Félice, 1976; Pap et al., 1995), but they do not provide information about inter-specific differences. However, a recent studies on the Regourdou material (Gómez-Olivencia et al., 2012) proposed a larger mesosternum for Neanderthals compared to modern humans, a morphology that Demonet (1905), looking at living humans, had earlier linked to a large vital capacity. However, since sternal morphology and its relation with the upper thorax are not the focus of our study, this should be addressed in future research.

Finally, it has been proposed by some authors a hypothetic morpho-functional link of the upper rib cage and the shoulder girdle (Churchill, 1994; Schmid et al., 2013; Feuerriegel et al., 2017). Specifically, Churchill (1994) proposed a correlation between the clavicle morphology and the 1st rib, concluding that the elongation of Neanderthal clavicles would be linked to ribs with less curvature in cranial view and, thus, an antero-posterior expansion of the rib cage. Even though there could be a correlation between 1st rib and clavicle

morphology, our results show that less curvature in cranial view of the 1st rib would produce a different thoracic configuration depending on the orientation of the transverse process of the adjacent vertebra (Bastir et al., 2015b, 2017b).

Regarding the central thorax, a large size of the Neanderthal central thorax has been found in previous research (Gómez-Olivencia et al., 2009), which proposed a volumetric expansion in this area. These results are confirmed by our 3D analyses on the 5th rib size (even though 5th rib shape does not differ between species; Table 4). In addition, the differences between Neanderthals and anatomically modern humans become even more apparent when mean 5th ribs are articulated with their corresponding vertebral levels (T4-T5), since we observe that the Neanderthal thorax at this level would be more medio-laterally expanded but also more antero-posteriorly projected (Figs. 9a, c).

Because of the preservation of the El Sidrón costal sample, other central thorax levels such as the 6th or the 7th, which are understood to be very informative of thorax shape and breathing kinematics (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014), are preserved and they should be studied in the future to complement and confirm the results obtained here, if and when enough fossils become available.

Finally, regarding the lower thorax, it has been proposed by previous research (Gómez-Olivencia et al., 2009) that the 11th ribs of Neanderthals could be similar in size to those of modern humans. However, both our linear measurements and the CS analysis show that the Neanderthal ribs present considerably larger dimensions compared to our modern human sample. The differences between previous research and our results might be produced by differences in sample composition. In addition, Neanderthal 11th ribs present more curvature in cranial view than their modern human counterparts according to our results. It has also been hypothesised that other Lower Pleistocene hominins (such as the ones from

Gran Dolina TD6 or *H. ergaster* KNM-WT 15000) show a stronger curvature in cranial view in some lower ribs (Jellema et al., 1993; García-Martínez et al., 2016b). This greater curvature, producing an expansion of the lower thorax, could be a character inherited and shared with Lower Pleistocene hominins.

Alongside the results of individual elements, when mean Neanderthal and male modern human 11th ribs are articulated with their corresponding vertebrae (T11), we observe that the Neanderthal thorax at this level is notably more medio-laterally expanded than in modern humans (Fig. 9a, d). Therefore, a more volumetric expansion in this area is expected for Neanderthals compared to modern humans at the T11 level, which is consistent with results obtained by authors at other lower levels, such as the 8th and the 10th (Franciscus and Churchill, 2002; Sawyer and Maley, 2005; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014).

This expansion at the lower thorax could be linked to a higher diaphragmatic action, since the lower ribs (7-12) are the ones that present a direct anatomical link to the diaphragm. In this regard, has been proposed by recent research (Bastir et al., 2017a) that the size increase in lower ribs increases considerably the capacity of volumetric and size change during respiratory kinematics. Therefore, the larger lower thorax ribs observed in Neanderthals would be linked to a more efficient thorax kinematics, producing larger differential of size during breathing than modern humans. The stronger diaphragmatic action is confirmed by the proximal part of a 12th rib (SD-56) from the El Sidrón site. Although short, it shows a strongly pronounced insertion for the diaphragm as do Kebara 2 and Shanidar 3 12th ribs (SOM Fig. S6).

The evidence of the upper, central and lower thorax of our study allows us to accept H2, based on the hypothesis from Bastir et al. (2015a) only partially: this is because the

Neanderthal thorax morphology is more medio-laterally expanded in the lower thorax than in modern humans [as proposed by Bastir et al. (2015a)] but it is also more slightly medio-laterally expanded in the upper part thorax. It is important to note that Bastir et al. (2015a) used patterns of covariation of modern human rib cages in articulation in order to hypothesize about Neanderthal morphology. However, the orientation of the transverse processes in thoracic vertebrae of Neanderthals differ from that of modern humans (Bastir et al., 2017b), which could explain the differences of the present findings from the model proposed by Bastir et al. (2015a;).

Our study shows that it is highly beneficial to study ribs and vertebrae together to accurately interpret the morphological information obtained from individual elements. However, we do not mean to discredit studies of individual bones. Studying both ribs and vertebrae together is usually not possible due to bias in the fossil record. In these cases, the study of individual elements also provides valuable information about thorax morphology, as shown by previous research (Jellema et al., 1993; Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009, 2010; Schmid et al., 2013; Bastir et al., 2015a; Latimer et al., 2016; Williams et al., 2017). This notwithstanding, the costal remains from the El Sidrón site, ranging from the 1st to 12th ribs and comprising every part of rib anatomy, provide an important perspective on Neanderthal thorax morphology.

Conclusions

The presence of rib heads is especially relevant since there is an overall lack of this part of the rib in the Neanderthal fossil record, and we hope that the method we developed and validated in this paper to assess position of Neanderthal rib heads out of their anatomical context, is valuable in future research. In addition, as well as supporting previous work identifying lack of curvature in cranial view of the Neanderthal 1st rib and the larger costal

size of the Neanderthal 5th ribs, we also show that Neanderthal 11th ribs – often poorly preserved in the fossil record – are much larger and more curved than in modern humans.

Our results based on the El Sidrón and Kebara 1st, 5th and 11th ribs allow us to hypothesize that the Neanderthal thorax was slightly more medio-laterally expanded in the upper part, more medio-laterally and antero-posteriorly expanded in the central part and remarkably more medio-laterally expanded in the inferior part.

This thoracic morphology would be consistent with a higher level of diaphragmatic action and greater oxygen intake in Neanderthals than in modern humans, which is linked to a higher energetic demand and BMR (Franciscus and Churchill, 2002; Churchill, 2006; Weinstein et al., 2008; Froehle and Churchill, 2009; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014; Bastir et al., 2015a; Gómez-Olivencia, 2015). This greater diaphragmatic action would also be supported by costal evidence such as the insertion of the diaphragm on the 12th ribs or the larger articular tubercles at diaphragmatic ribs, which, according the evidence from El Sidrón, would be inherently larger. However, we do not exclude that other factors could cause the differences observed in the Neanderthal thorax, such as cold adaptation or a plesiomorphic condition like previous members of the genus *Homo*. However, this should be tested in future studies.

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Figure captions

Figure 1: The most diagnostic ribs studied in the El Sidrón costal sample. Ribs are shown in cranial view.

Figure 2: The most diagnostic proximal rib remains studied in the El Sidrón costal sample. Ribs are shown in cranial view in the top of the figure and in external view in the bottom of the figure.

Figure 3: The most diagnostic proximal ends of floating ribs in the El Sidrón costal sample. A detail of the articular facet in external view is shown.

Figure 4: Virtual reconstruction of the 5th (a) and 11th (b) ribs from the El Sidrón site. The 5th rib was reconstructed based on SD-695a, SD-1450 and the distal end of the Kebara 2 5th rib. The 11th rib was reconstructed based on SD-2187, SDR-131 (mirror image) and the distal end of the Kebara 2 11th rib.

Figure 5: HCCD/HW index with 95% confidence interval (IC) for the mean of modern human ribs from 1st to 10th. Kebara 2 (orange circles) and El Sidrón (blue squares) are shown. Neanderthal proximal ends of known position (Kebara 2, 1st; Kebara 2, 2nd; El Sidrón, 3rd; El Sidrón, 8th) fall into the confidence interval of their modern human counterparts. Head cranio-caudal diameter (HCCD) follows the definition of Gómez-Olivencia et al. (2010) and head width (HW) is defined in this study as the maximum length of the articular surface of the rib head perpendicular to the cranio-caudal axis (coinciding with the length of the inter-articular crest, when applicable).

Figure 6: Centroid size (CS) distribution with 95% confidence interval for the mean of modern human 1st (a), 5th (b) and 11th (c) ribs separated by sex. Early modern humans (orange circles) and Neanderthals (blue squares) are compared.

Figure 7: PC-shape analysis of 1st (a) and 11th (b) ribs. Scatterplot of principal component (PC) 1 and PC 2 (see percentage of total variance explained in parenthesis in each axis), and warped 3D models of PC-scores of 1st and 11th ribs in cranial view. For 1st ribs note that Neanderthal specimens (blue) are located in the negative values of the axis, whereas early modern humans (green) are located in the center of the distribution of current modern humans. For 11th ribs note that Neanderthal specimens (blue) are located in the negative values of the axis.

Figure 8: Mean shapes of 1st (a) and 11th ribs (b) of Neanderthals (blue, left) and current European modern humans (green, right).

Figure 9: Mean 1st, 5th and 11th ribs (size and shape) of Neanderthals (blue) and European modern humans (red) obtained from our results in articulation with their corresponding vertebral levels. For those vertebral models, we used the vertebrae from Kebara 2 for articulating mean Neanderthal ribs and a modern human from the Santarém Collection (Coimbra, Portugal) for articulating mean modern human ribs. A frontal view of the whole hypothetical model (a) as well as a cranial view of each level studied (1st – b; 5th – c; 11th – d) are shown. The most remarkable features are the slight mediolateral expansion of the thorax at T1 level and the medio-lateral expansion of the rib cage at the T5 and T11 levels.