The relevance of the first ribs of the El Sidrón site (Asturias, Spain) for the understanding of the Neanderthal thorax

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Abstract

The paleobiological significance of the rib cage in Neanderthal ranges from functional anatomy, energetics to the general evolution of human body shape. However, despite this importance there is still debate as to the nature and extent of variations in size and shape of the Neanderthal thorax. The El Sidrón Neanderthals can contribute to this debate providing new thoracic remains (N=245) ranging from fully preserved and undistorted ribs to highly fragmented elements. Five first ribs are particularly well preserved and offer the opportunity to analyze their potential contribution to overall thorax morphology in Neanderthals. The aims of this paper are to present this new material, to compare the ontogenetic trajectories of the first ribs between Neanderthals and modern humans, and to test the hypothesis of morphological integration between the first rib and the remaining thorax morphology. The first ribs of El Sidrón adult Neanderthals are smaller and tend to be less curved when compared to that of anatomically modern humans, but those features are similar to Kebara 2 first ribs. Our results show further that the straightening of the first ribs is significantly correlated with a straightening of the ribs 2-5 of the upper thorax (R=0.66; p<0.0001), supporting a developmental differentiation in the upper and lower thorax units. This supports the hypothesis that the upper thorax of Neanderthals differs in shape from modern humans with more forwards projecting upper ribs during inspiration. This could have biomechanical consequences and account for stronger muscle marks in Neanderthals than in modern humans, a hypothesis that requires testing. The results also suggest a different spatial arrangement of the shoulder girdle and articulation with the humerus (torsion) and its connection to the upper thorax. Future research should address these questions in the context of Neanderthal overall body morphology.

Introduction

Hypotheses about the paleobiological significance of Neanderthal thorax morphology have referred to different factors ranging from cold adaptations, energetics and activity levels, increased body mass (Franciscus and Churchill, 2002; Churchill, 2006) to questions related to the evolution of overall body shape (Jellema et al., 1993; Ruff, 2002; Gómez-Olivencia et al., 2009; Ruff, 2010; García-Martínez et al., 2012; Bastir et al., 2013a; Bastir et al., 2013b; Bastir et al., 2013c).

However, despite its importance the extent of differences in size and shape of the Neandertal thorax is still not entirely clear (Franciscus and Churchill, 2002; Churchill, 2006; Gómez-Olivencia et al., 2009). The question of size and shape differences is also important in the light of recent evidence that supports a division of the thorax into an upper and a lower part for functional, developmental and evolutionary reasons (Arensburg, 1991; Bastir et al., 2013c; Schmid et al., 2013). While the upper part (ribs 1 to 5) has been related to thoracic breathing and to upper limb locomotion the lower part (rib 6-12) reflect features related to diaphragmatic breathing and posture and body shape as well as subt-horacic organ content.

In a pioneering quantitative analysis and by introducing arcs and chords to the measurement of isolated ribs of the Shanidar 3 Neanderthal, Franciscus and Churchill (2002) suggested that the lower Neanderthal thorax is larger in volume, with more rounded cross sections of the lower ribs than in modern humans. Other researcher has suggested that the ribs of the lower thorax in Kebara are relatively large (Gómez-Olivencia et al., 2009; García Martínez et al., accepted). This evidence, together with a complete reconstruction of a Neanderthal skeleton (Sawyer and Maley, 2005) suggests a wider lower thorax in Neanderthals than in modern humans.

The morphology of the upper thorax in Neanderthals is considerably less well known. Sizes of the upper ribs of Kebara seem to be all within or at the lower end of the range of modern humans (Gómez-Olivencia et al., 2009; García Martínez et al., accepted). But there is also evidence suggesting that the shape might be different. More than hundred years ago Karl Gorjanovic-Kramberger (Gorjanovic Kramberger, 1906) described the first ribs of the Krapina Neanderthals as particularly straight, much less curved than those of modern humans. Based on these observations he speculated further that the ribcage of the Krapina Neanderthals was likely projecting more forwards than in modern humans [*wodurch auch der Brustkorb mehr vorgewölbt war"* (Gorjanovic Kramberger, 1906): 212.]. Thus, by predicting that the morphology of the first rib is significantly related to the morphology of the remaining thorax, Gorjanovic-Kramberger proposed an important hypothesis that is relevant to the previously mentioned studies on general thorax morphology and evolution (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009).

However, this hypothesis has not yet been tested. The scantiness of upper thorax elements (for example, first ribs) in the Neanderthal fossil record as well as the difficulty to quantify properly the curved morphology of the outer rib circumference have hampered so far a thorough analysis of this important problem.

The El Sidrón Neanderthal site in Asturias, Northern Spain, (Fortea et al., 2003; Rosas et al., 2006; Rosas et al., 2012) provides a significant contribution to the fossil record of thoracic elements. In addition, recent methodological developments can be used for rigorous quantification of rib curvature, which is a key-factor of overall thoracic morphology and variation (García-Martínez et al., 2012; Bastir et al., 2013b; Bastir et al., 2013c; García-Martínez et al., 2013).

The aim of the present study is to describe and analyze a set of first ribs of the El Sidrón Neanderthals within the framework of Gorjanovic-Kramberger's (1906) hypothesis that the

morphology of the first rib morphology is significantly related to the shape of the remaining skeletal thorax.

Material and Methods

The fossil site of El Sidrón (Asturias, Spain) has produced a considerable sample of thoracic elements (N=245). Six first ribs (SD-2148, SD-2172, SD-1767, SD-417, SD-1225, SD-1699+SD-1685 – called SD-1699+ onwards) are particularly well preserved (Fig. 1; Table 1). Morphological descriptions and linear measurements (Table 2, 3) were carried out on the original fossils and casts (KNM WT 15-000) whereas for 3D geometric morphometrics we used high resolution laser scans of the El Sidrón fossils and 3D reconstructions of CT scans of the first ribs of Kebara 2 (Arensburg, 1991) and of La Ferrassie VI (Heim, 1982).

These data were compared with measurements on 3D reconstructions of CT scans of a growth series of isolated first ribs of twenty-seven modern humans ranging from newborns to adults of both sexes (Bastir et al., 2013b; Bastir et al., 2013c). This data set was also used to study covariation between the first ribs and the remaining ones in anatomical connection with the spine in order to quantify thorax shape covariation.

Linear measurements

Arcs, cords and diameters were measured with standard anthropometric instruments following the definitions used in previous studies (Gómez-Olivencia et al., 2009; Gómez-Olivencia et al., 2010; Franciscus and Churchill, 2002) and are listed in Table 2. Each measurement was calculated from the average of three measurements in order to reduce intra-observer error (Gómez-Olivencia et al., 2009; Gómez-Olivencia et al., 2010; Franciscus and Churchill, 2002).

Moreover, in order to evaluate the symmetry pattern in antimeric ribs we calculated the following index: (size difference between antimeres / by the smaller antimere size) x 100 (Franciscus and Churchill (2002).

Ontogenetic state assessment

The maturation state of the first ribs was evaluated using the scoring system proposed by Ríos and Cardoso (2009) based on the epiphyseal fusion of the articular tubercle of the rib (preserved in most cases of our sample). According to this protocol, three ranges of maturation can be differentiated: 1- no fusion; 2- partial fusion; 3- complete fusion, but it should be noted that the maturation rate of Neanderthal epiphyses fusion could differ from that of *H. sapiens*. When the articular tubercle of the rib was missing, an ontogenetic assessment was carried out throughout a comparison with size (see Fig. 3).

Morphological analysis

A detailed description of the surface morphology, such as the marks of the scalene and serratus muscles attachments and the subclavian artery, as well as the preservation status was carried out in the costal elements SD-2148, SD-2172, SD-1699+, SD-1767, SD-1225, SD-417 based on the principal anatomical features of this rib (Spalteholz, 1970; Aiello and Dean, 1990; Gómez-Olivencia et al., 2009; Gómez-Olivencia et al., 2010; White et al., 2011).

Geometric morphometric analyses

Twenty 3D-landmarks and semilandmarks were measured on each rib (García-Martínez et al., 2012; Bastir et al., 2013b; Bastir et al., 2013c; García-Martínez et al., 2013). Semilandmarks were slid to the GPA average to minimize bending energy between each specimen and the GPA-consensus. Missing data were few and estimated using the thin-plates spline approach available to

3D semilandmark techniques (Gunz et al., 2009; Bastir et al., 2011; Bastir et al., 2013c). Size was measured as centroid size and shape as Procrustes shape coordinates (O'Higgins, 2000).

Centroid size of first ribs was tested for normality (Kolmogorow-Smirnov, K-S) and analyzed by ANOVA and ages in comparative sample were grouped into infant (0-5 yrs.; N=11), juvenile (6-10 yrs.; N=6), adolescent (11-15 yrs.; N=3) and adults (> 16yrs.; N=8). Shape data was analyzed in two ways: First, a principal components analysis (PCA) in Procrustes Form space was performed to explore shape variation and allometric growth trajectories (Mitteroecker et al., 2004; Bastir et al., 2007). Then, to assess non-growth dependent shape covariation, data were corrected for ontogenetic growth allometry by multivariate regression of shape on CS size. After that, shape variation of the first rib was correlated with that of the remaining ribs 2-10 of the twenty-seven thoraces in anatomical connection in modern humans. This was done by using Two-Block Partial Least Squares (2B-PLS) (Rohlf and Corti, 2000; Bastir et al., 2005). This analysis aimed at testing the hypothesis of Gorjanovic-Kramberger (1906) which predicts that elongation of the first rib is associated with elongation of the remaining ribs of the thorax.

Results

Anatomical description and traditional measurements

The results of the traditional measurements of the individuals of our sample are listed in Table 3. The values of tuberculo-ventral cord (TVC), tuberculo-ventral arc (TVA), and tuberculo-horizontal diameter (THD) could not be measured in the ribs SD-2172 and SD-417. Likewise, sternal end minimum diameter (SEMnD) and sternal end maximum diameter (SEMxD) could not be assessed in SD-417. The values SEMxD, TVA and TVC were estimated on morphological criteria in the ribs SD-1225 and SD-1699+ (Table 1). The comparative data were taken from Gómez-Olivencia et al. (2009) and Gómez-Olivencia et al. (2010).

The element SD-2148 (Fig. 1b) is a first rib of the right side that preserves half of the neck, the articular tubercle and the shaft of the rib including the complete sternal end. The groove of the subclavian artery, the anterior scalene tubercle, the insertion of the medium scalene and the insertion of the anterior serrate are slightly marked in this individual. Regarding the ontogenetic state, SD-2148 does not preserve the rib head, but the epiphysis of the articular tubercle is not fused in this individual (stage 1), which suggests a maximum age of 18 years at the time of death (Ríos and Cardoso, 2009).

SD-2172 (Fig. 1c) is a first rib of the left side. It preserves the shaft of the rib from the half of the insertion of the medium scalene and anterior serrate muscles to the sternal end and lacks the costal tubercle, the neck and head of the rib. The groove of the subclavian artery and the anterior scalene tubercle are very slightly marked. In this rib, the ontogenetic state cannot be assessed at the epiphyseal fusion of the head nor at the articular tubercle because these parts are not preserved.

Overall morphology and MMxD, MMnD, SEMnD and SEMxD of SD-2448 and SD-2172 are very similar in both elements and very different from the rest ribs of the sample. This fact, together with the low symmetric percentage (5.77), suggests that these ribs are probablly antimeres belonging to one individual [probably Juvenile 1 following Rosas et al., (2013)].

SD-1225 (Fig. 1i) is a first rib of the left side that preserves the rib shaft from half of the neck to the sternal extremity. The groove of the subclavian artery presents a smoother surface and is clearly identified, as are the insertions of the anterior and medium scalene muscles and the anterior serrate. The epiphyseal surface of the articular tubercle is not fused (stage 1) suggesting a maximum age of 18 years at the time of death (Ríos and Cardoso, 2009).

SD-417 (Fig. 1h) is a fragment of the medial part of the rib shaft (43 mm) of a right rib. The groove of the subclavian artery is preserved, the anterior scalene tubercle is eroded and the insertion of the medium scalene muscle is marked only at its distal half. The features of this rib do not allow any direct association to an ontogenetic state, but the linear measurements (MMxD and MMnD) and the low asymmetry obtained in comparison with SD-1225 (2.11), suggest that SD-417 and SD-1225 are antimeres belonging to the same individual [probably Juvenile 2, according to Rosas et al., (2013)].

SD-1767 (Fig. 1g) is a first rib of the right side that preserves the shaft from the distal part of the articular tubercle to the sternal end. The fossil has lost the neck and the head of the rib and the upper surface of the vertebral extreme is eroded. Thus, neither the proximal part of the articular tubercle nor of the anterior serrate insertion muscle can be appreciated. The subclavian groove is present and the anterior scalene tubercle is very marked. The insertion mark of the medium scalene muscle is missing at its vertebral part due to the aforementioned taphonomical damage. As in SD-2172 epiphyseal fusion could not be assessed.

SD-1699+ (Fig. 1j) is a first rib from the left side which lacks the rib neck, the head of the rib and a fragment of the interior border of the rib shaft at the sternal end. The rib presents small cracks (4 millimeters) along the axis of the shaft, which, however, do not alter its morphology. One such fracture is located at the upper part, at the vertebral extreme above the insertion of the anterior serrate and the other fracture is situated at the lower border, near the anterior scalene tubercle. The insertions of the anterior and medium scalene muscle are very marked. The groove of the subclavian artery is present. The articular tubercle is well preserved and the epiphysis is not fused with the metaphysis (state 1), suggesting a maximum age of 18 years at the time of death (Ríos and Cardoso, 2009).

The similarity of linear measurements (TVC, TVA, THD, MMxD, MMnD, SEMnD and SEMxD) of SD-1767 and SD-1699+ with the Kebara 2 suggest an adult Neanderthal size. However, whether these ribs belong to the same individual cannot be determined because the symmetric value is the highest of our sample (10.85) and because there are seven adult individuals represented in the site (Rosas et al., 2013).

Geometric morphometric analysis

K-S test indicated normality (d=0.08, n.s.) and ANOVA showed significant ontogenetic increases of size across the age classes [F (3.24) = 59.63, P<0.0001]. Despite our small comparative sample of modern humans, it is evident that the first ribs in adult Neanderthals tend to be smaller. Figure 2 shows the 95% CI intervals of the modern human sample and the individual values of the Neanderthal fossils. The adult El Sidrón ribs are comparable with those of Kebara 2 and all are closer to the adolescent than to the adult modern human values. The ribs of El Sidrón juvenile 1 are within the 95% confidence intervals of the modern human juvenile sizes.

Figure 3 shows the results of the comparative growth analysis. PC1 (92.3% of total variance) displays common growth variation with the small and younger individuals plotting towards the negative scores and the larger and adult ones towards the positive PC1 scores (Fig. 3a). Along PC2 (4.9% of total variance) a different trend between adult Neandertals and modern humans can be seen. General growth allometry is shown along PC1 (Fig. 3b). Shapes associated to PC2 (Fig. 3c) are relevant to the hypothesis tested here. They confirm a trend towards a straight shaft in Neandertal first ribs compared to a more rounded outline in modern humans. The adult Neandertals plot also at the lower range of the adult modern humans reflecting again their decreased sizes.

The Partial Least Squares analysis reveals highly statistically significant correlations between the first ribs and the remaining ribcage with different morphological patterns. The first pattern (PLS1, r=0.79; p<0.0001, 79% of covariation), reflects covariation related to upwards and downwards inclination of the lateral part of the rib-shaft relative to the vertebral end. However, while this is an important part of covariance, it is not relevant to the hypothesis addressed here. PLS2, nevertheless, is very relevant (r=0.66; p<0.0001; 13.7% of covariation) as it reflects shape correlations between the first ribs and the remaining rib-cage related to straightening such as indicated by Gorjanovic-Kramberger (1906). Figure 4 shows that straightened first ribs are accompanied by a similar straightening of the remaining ribs of the upper thorax. In addition, Figure 4c,d shows that this straightening is stronger from rib 2 to rib 5, while in the lower ribs there is a medium-lateral widening and an elevation of the sternal end of the shaft (Fig.4e,f). In sum these effects produce an increase in depth in Neanderthals respect modern humans, which could support part of the hypothesis of Gorjanovic-Kramberger (1906).

Discussion

The first ribs of the El Sidrón Neanderthals clearly show typical Neanderthal features: strong muscle marks and decreased curvature particularly in the distal 1/3 of the shaft. This is not only evident from Figure 1 but also from quantitative analysis (Fig. 3; Table 3).

When compared with Kebara 2, the adult El Sidrón ribs show a similar TVC and a greater TVA, which together with the 3D semilandmarks analysis (Fig. 3) clearly demonstrate the straight shaft profile in the first ribs of Neanderthals (Gorjanovic Kramberger, 1906; McCown and Keith, 1939; Arensburg, 1991; Franciscus and Churchill, 2002). This straightness pattern can be also observed, although not as markedly, in ATD6-108 of *H. antecessor* (Gómez-Olivencia et al., 2010).

No comparative Neanderthal data exist yet for immature individuals. However, the data of the El Sidrón site presented here will provide a reference for juvenile measurement onwards.

The analysis of centroid size also confirms reduced dimensions in Neanderthals compared adult modern humans. Gómez-Olivencia et al. (2009) has shown that the first ribs of the Kebara 2 Neanderthal are within the range of modern humans. Our results suggest they are smaller, possibly even below the modern human range [erroneously reported in preliminary findings of Bastir et al. (2013a)]. Smaller ribs could also fit with reduced size of the thoracic vertebrae in Neanderthals (Gorjanovic Kramberger, 1906; Arensburg, 1991; Gómez-Olivencia et al., 2013a; Gómez-Olivencia et al., 2013b) accounting for their shared developmental background (Aoyama et al., 2005) and common function in the costo-vertebral joints (De Troyer et al., 2005).

However, less curved and smaller first ribs, together with greater lower thorax capacities (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García Martínez et al., accepted) necessarily imply differences in the shape of the overall rib cage configuration. This could also be inferred from our PLS-analysis of morphological covariation in modern humans between the first ribs and the remaining rib cage (ribs in anatomical connection). As suggested by Gorjanovic-Kramberger (1906) increased forwards projection of the first ribs, due to their decreased curvature would accompany a similar forwards projection of the remaining ribs. Extending this argument one would expect that, if the first ribs are different and if their shapes correlated with the rest of the ribs, the entire thorax would be different in Neanderthals.

SD-1225 has been assessed as a juvenile rib on the basis of traditional measurements. However, the CS of this rib is similar with adults, such as SD-1767 and SD-1699+. This is likely due to our template which collects morphological information at the outer rib curvature. However, the main differences between juvenile and adults first ribs seem to increase the width. This information is

thus not captured by measuring the outer curvature. Future research should thus also include interior curve measurement of the rib.

PLS analysis (Fig. 4) demonstrates indeed a strong correlation between the first rib and the remaining rib cage, although at the intra-specific level of our modern human sample. If details of our reference model of modern humans were extrapolated to Neanderthals, only the first five ribs (upper thorax) would be more projecting due to a straightening. This is because from the fifth rib onwards no further forwards straightening can be observed (Figs. 4 e,f). Forwards projection is still there but this is produced by an upwards flexion of the sternal extremes for which all segments of the ribs are in the same axial plane. Thus, the upper and lower parts of the ribcage show different morphological covariation patterns with the first ribs.

A separation of the entire ribcage into upper and lower thorax units makes also sense from a growth perspective. We have shown elsewhere that diverging growth trajectories of the upper and lower thorax likely reflects a different integration of these body parts within the entire skeletal system and body plan (Bastir, 2008; Bastir et al., 2013c) in that the upper thorax relates to respiration (in thoracic mode) and the upper limbs, while the lower thorax relates more to diaphragmatic respiration, sub-thoracic organ content and locomotion. Both parts together have thus important morphological and functional implications but more functional research is necessary in this direction.

A smaller upper thorax may reflect a developmental trade-off between necessities of the respiratory apparatus and its relation to the shoulder girdle, the upper limbs and their muscles. Differences in humeral torsion of Neanderthals and modern humans may be one feature of this different arrangement (Carretero et al., 1997; Rosas et al., submitted). Theoretically, a straighter

shape of the first rib could affect the leverage of the scalene muscles and relate to differences in robustness of the insertion marks in modern humans and Neanderthals.

In turn, a larger lower thorax might relate to climatic adaptations, body-mass related energetics and/or retention of archaic body plan (Franciscus and Churchill, 2002; Carretero et al., 2004; Churchill, 2006; Gómez-Olivencia et al., 2009). In any case, from a functional point of view, a wider lower thorax likely reflects an increased diaphragmatic contribution to respiration. Future study on the lower ribs of a larger comparative sample will shed more light on the biological significance of this important part of the human axial skeleton and trunk.

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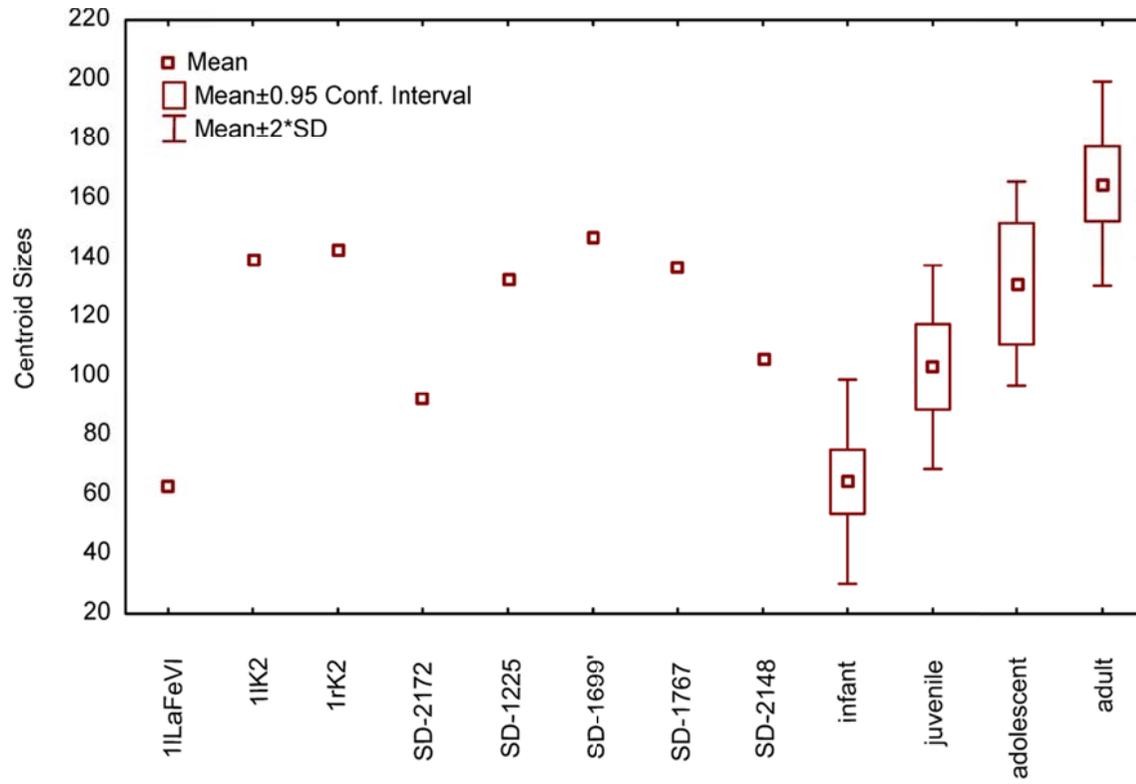White, T.D., Black, M.T., Folkens, P.A., 2011. Human Osteology, 3rd ed. Academic Press.
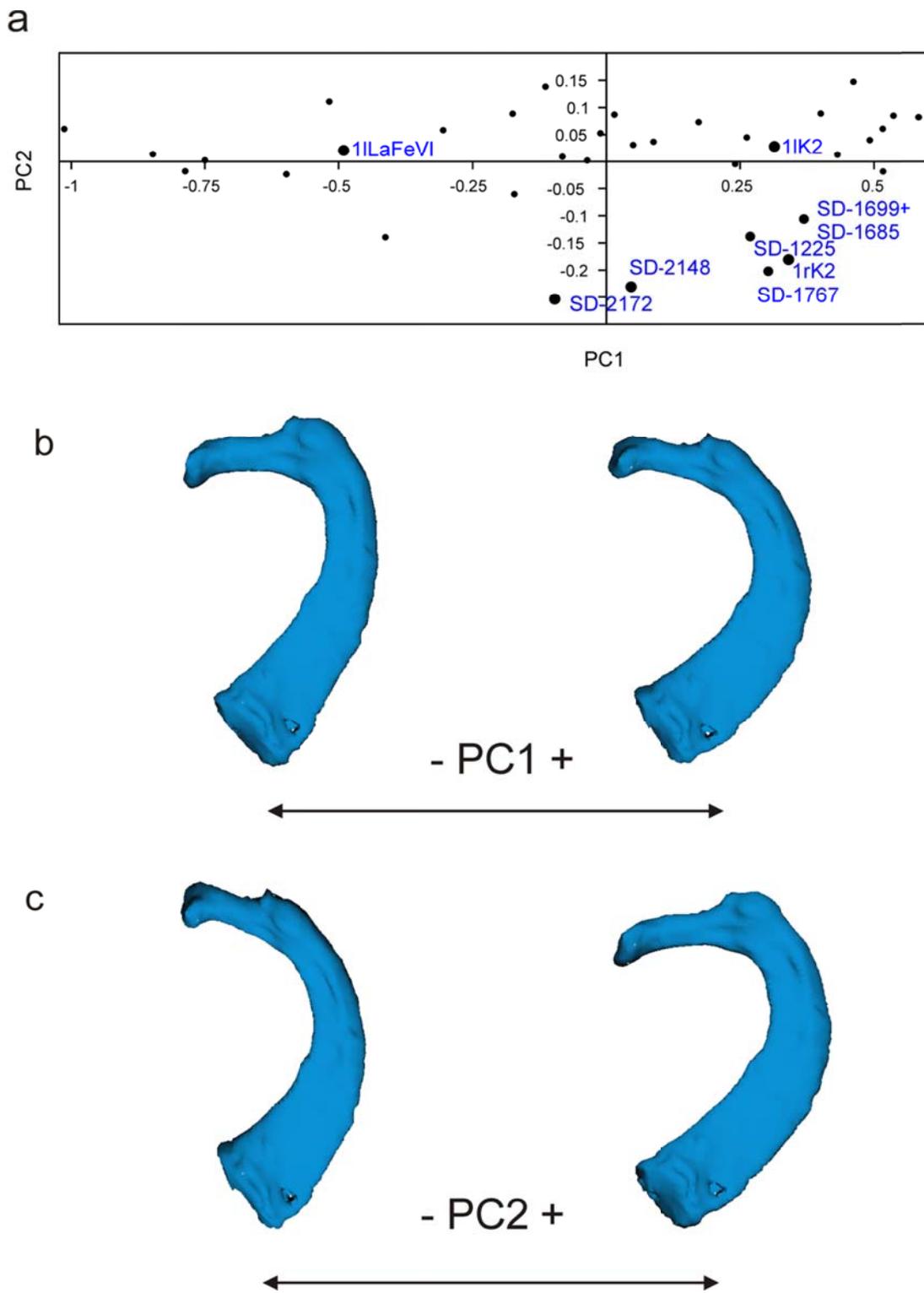
Figure 1

Figure 2

a

PC2

1lLaFeVl

1lK2

SD-1699+
SD-1685
SD-1225
SD-2148
1rK2
SD-1767
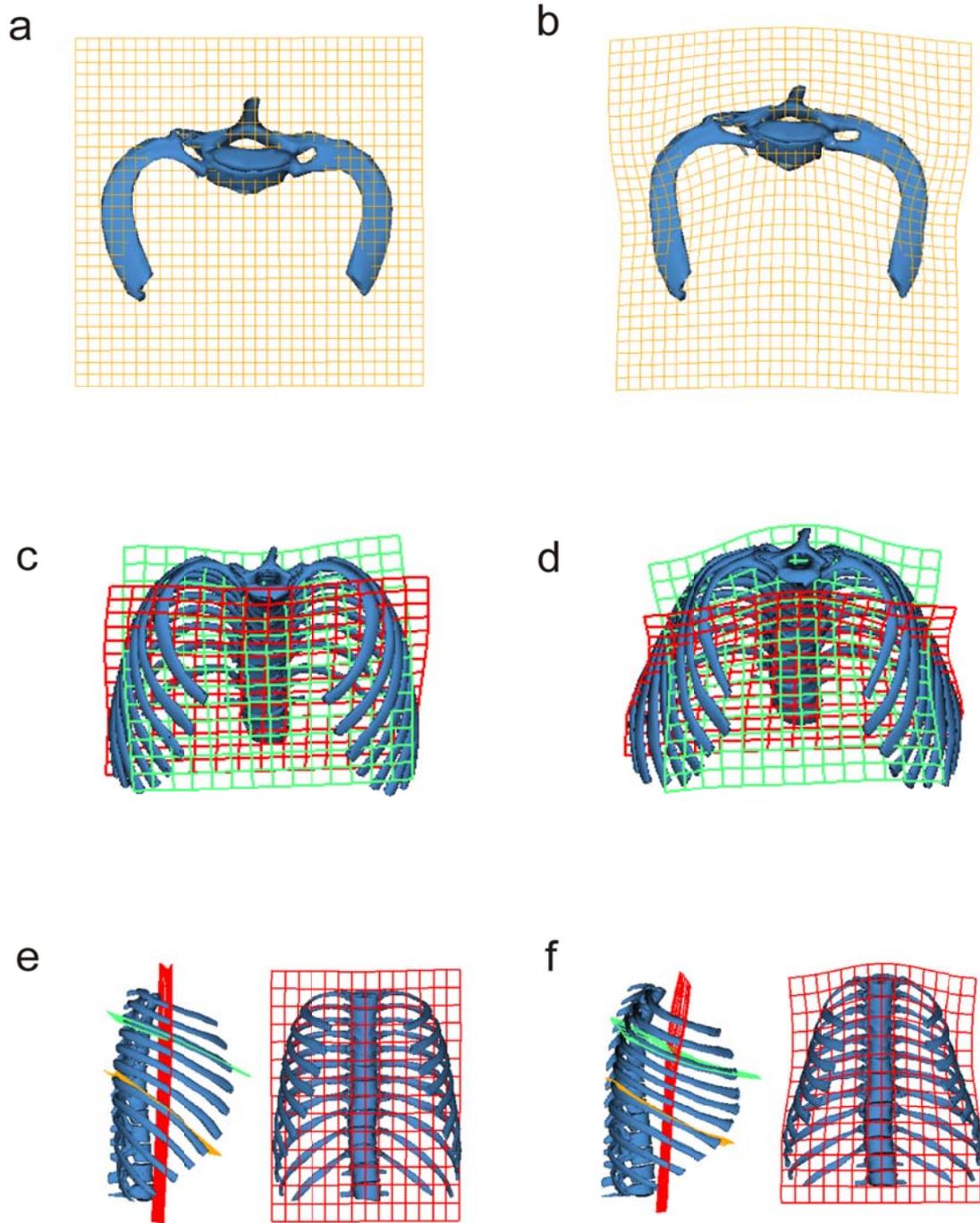SD-2172

PC1

b

- PC1 +

c

- PC2 +

Figure 3

Figure 4

Figure captions

Figure 1. Cranial views of Neandertals from El Sidrón compared with modern humans. Juvenile (a, e) and adults (f, k) modern humans are shown to illustrate the greater curvature than that of Neandertals (b) SD-2148, c) D-2172, g) SD-1767, h) SD-417, i) SD-1225, j) SD-1699+.

Figure 2. Comparative size analysis of the first ribs. Note that Neandertals first ribs tend to be smaller, that is, at the lower margin of the modern human range.

Figure 3. Form space growth trajectories. a) distributions along PC1 and PC2 axes. Small dots: modern humans, Large dots: Neandertals (labelled) 1lLaFEVI: first left rib of La Ferrassie 6; 1lK2: first left rib Kebara 2, 1rK2 (first right ribe Kebara 2) and El Sidron (SD) first ribs, b) shape changes related to growth allometry along negative and positive PC1 scores, c) shapes associated to negative and positive PC2 scores contrasting modern humans and Neandertals. Note also the smaller sizes of adult Neandertals compared to adult modern humans along PC1.

Figure 4. PLS analysis of first ribs and the remaining ribs of the thorax in anatomical connection. Morphological covariation patterns show that curved first ribs a) are correlated with thorax shapes c) and e) with rounded and barrel shaped outlines while straight first ribs b) are correlated with thorax shapes d) and f) reflecting straightened ribs in the upper thorax (ribs 2-5) and widening at the lower thorax (ribs 6-10) in modern humans.

Table 1. Inventory of the first ribs of the El Sidrón site and its position in Figure 1.

Label	Side	Ontogenetic assessment	Head	Neck	Articular tubercle	Shaft	Sternal end	Figure 1
SD-2148	Right	Juvenile 1	No	Half	Yes	Yes	Yes	1b
SD-2172	Left	Juvenile 1	No	No	No	Yes	Yes	1c
SD-1767	Left	Adult	No	No	Half	Yes	Yes	1g
SD-417	Left	Juvenile 2	No	No	No	Half	No	1h
SD-1225	Right	Juvenile 2	No	Half	Yes	Yes	Half	1i
SD-1699+	Right	Adult	No	No	Yes	Yes	Half	1j

Table 2. Measurement definitions based on previous articles (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; Gómez-Olivencia et al., 2010).

Variable	Name	Description
TVC	Tuberculo-Ventral Chord	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	Tuberculo-Ventral Arc	Straight line distance between the dorsal-most margin of the articular tubercle to the ventral-most point of the sternal end of the rib.
THD	Tubercle Horizontal Diameter	Maximum diameter from the internal surface of the rib to the further extent of the articular tubercle.
MMxD	Mid-shaft Maximum Diameter	Measured at the midshaft, maximum diameter from the internal to external surface, at the groove for the subclavian artery.
MMnD	Mid-shaft Minimum Diameter	Measured at the midshaft, minimum diameter from the internal to external surface, at the groove for the subclavian artery.
SEMxD	Sternal End Maximum Diameter	Measured at the sternal end. Maximum diameter, approximately horizontal.
SEMnD	Sternal End Minimum Diameter	Measured at the sternal end. Minimum diameter, approximately vertical.

Table 3. Traditional measurements (mm). Estimated data in parenthesis.

	SD-2148 1R	SD-2172 1L	SD- 1225 1L	SD-417 1R	SD-1767 1R	SD-1699+ 1L	K2 1R	K2 1L	Amud 1 1L	Krapina 117.2 1R	Krapina 117.3 1R	Krapina 118.2 1R	Krapina 118.4 1L	Krapina 117.1 1L	KNM-WT 15.000 1R	KNM-WT 15.000 1L	ATD6-108 1R
TVC	55.84	-	(75.16)	-	79.05	(83.00)	85.7	82.7							(81.0)	(80.5)	(90.0)
TVA	70.10	-	(104.50)	-	105.0	(115.0)	99.0	(96.0)							(116.0)	(115.0)	(107.0)
THD	11.18	-	13.76	-	16.95	15.35	19.8	19.4		17.1	(16.5)	15.2		15.4	14.8	14.6	17.9
MMxD	9.95	9.25	11.31	10.90	16.05	17.90	(20.7)	20.5	> 19.0	14.0	13.8	13.2	15.6		19.0	17.1	15.4
MMnD	3.57	3.35	4.27	4.25	4.55	5.75	3.3	3.5	4.2	3.5	4.3	4.0	3.4		3.0	2.8	3.3
SEMnD	4.78	4.75	4.43	-	6.15	5.95	8.4	9.3	8.9						5.1	5.2	5.9
SEMxD	11.97	11.05	(15.17)	-	19.0	(17.30)	19.8	17.8							20.5	20.5	-

Table 4. Asymmetric percentage calculated in each possible antimere of the El Sidrón site and in Kebara 2 Neanderthals.

	SD-2148/SD-2172	SD-1225/SD-417	SD-1767/SD-1699	Kebara 2 L/R	KNM-WT 15.000 L/R
TVC	-	-	4.99	3.62	0.62
TVA	-	-	9.52	3.12	0.87
THD	-	-	10.42	2.06	1.37
MMxD	7.56	3.76	11.52	0.97	11.11
MMnD	6.57	0.47	26.37	6.06	7.14
SEMnD	0.63	-	3.36	10.71	1.96
SEMxD	8.32	-	(9.82)	11.24	0.00
Asymmetry average	**5.77**	**2.11**	**10.85**	**5.39**	**3.30**