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How different are the Kebara 2 ribs to modern humans?

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Summary - *This study analyses rib geometric parameters of individual ribs of 14 modern human subjects (7 males and 7 females) in comparison to the reconstructed ribs of the Kebara 2 skeleton which was taken from the reconstruction of a Neandertal thorax by Sawyer & Maley (2005). Three-dimensional (3D) models were segmented from CT scans and each rib vertex cloud was placed into a local coordinate system defined from the rib principal axes. Rib clouds were then analysed using best fitting ellipses of the external contours of the cross-section areas. The centroid of each ellipse was then used to measure the centroidal pathway between each slice (rib midline). Curvature of the ribs was measured from the mid-line of the ribs as the sum of angles between successive centroids in adjacent cross sections. Distinct common patterns were noted in all rib geometric parameters for modern humans. The Kebara 2 reconstructed ribs also followed the same patterns. This study demonstrated that there are differences between the sexes in rib geometrical parameters, with females showing smaller rib width, chord length and arc length, but greater curvature (rib torsion, rib axial curvature, rib anterior-posterior bending) than males. The Kebara 2 reconstructed ribs were within the modern human range for the majority of geometrical parameters.*

Keywords - *Rib, Curvature, Thorax, Neandertal, Ellipse.*

Introduction

Ribs have rarely been studied in palaeoanthropology due to the fact that they are fragile with complex curvatures, difficult to identify and are rarely found complete. However, in recent years there has been a growing interest in Neandertal rib remains. This is due to more complete Neandertal rib remains, recent discoveries, availability of collections and re-analysis of existing collections (Franciscus & Churchill, 2002; Weinstein, 2008; Gomez-Olivencia *et al.*, 2009; Garcia-Martinez *et al.*, 2014a; Bastir *et al.*, 2015; Gómez-Olivencia, 2015). The study

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of Neandertal ribs has given rise to different hypotheses on the overall morphology of the Neandertal thorax. There has been much debate on Neandertal thoracic shape and size and there still remains a lack of consensus on how different the Neandertal thorax is in comparison to modern humans (Arensburg, 1991; Franciscus & Churchill, 2002; Weinstein, 2008; Gomez-Olivencia *et al.,* 2009; Bastir *et al.,* 2012; Garcia-Martinez *et al.,* 2014a; Bastir *et al.,* 2015).

The thorax has variously been described as dome shaped (McCown & Keith, 1939), barrel shaped (Boule, 1911, 1912, 1913; Weinstein, 2008), hyper barrel shaped (Heim, 1976) and Sawyer & Maley (2005) reconstructed a Neandertal bell shaped thorax with a flaring lower thorax area. Neandertal thoraces have been described as either in the range of modern humans, within the extreme limits or with an increased thoracic capacity, either from anterior-posterior or medio-lateral expansion or both (Boule, 1911, 1912, 1913; McCown & Keith, 1939; Arensburg, 1991; Franciscus & Churchill, 2002; Sawyer & Maley, 2005; Weinstein, 2008; Gomez-Olivencia *et al.,* 2009; Bastir *et al.,* 2012; Garcia-Martinez *et al.,* 2014a; Bastir *et al.,* 2015; Gómez-Olivencia, 2015). Gomez Olivenica *et al.,* (2009) stated that rib arc length 1-3 in Kebara 2 were similar to a modern human Euro-american male sample, although ribs then become significantly larger caudally. There have been several other recent studies based on individual ribs which have further suggested that the Neandertals would have had a different organisation of the ribcage, such as an expanded thoracic volume in the lower rib cage (Gomez-Olivencia *et al.,* 2009; Garcia-Martinez *et al.,* 2014a; Bastir *et al.,* 2015; Franciscus & Churchill, 2002).

The analysis of Neandertal ribs and thoracic capacity has been previously performed using various different techniques such as morphological descriptions, varying linear measurements and geometric morphometrics (Boule, 1911, 1912, 1913; McCown & Keith, 1939; Heim, 1976; Arensburg, 1991; Franciscus & Churchill, 2002; Weinstein, 2008; Bastir *et al.,* 2012; Garcia-Martinez *et al.,* 2014a; Bastir *et al.,* 2015). The analysis of rib curvature is useful in how it contributes to overall thoracic shape, although has been relatively little studied in Neandertals due to the difficulties in analysing curvature. Franciscus & Churchill (2012) stated that early studies on Neandertal rib curvature suggested that Neandertals had more open (i.e. less curved) posterior angles in comparison to modern humans, although this was due to the fact that studies were largely based on qualitative analysis. Recent studies have shown that Neandertals had either similar or more curved posterior angles than modern humans (Franciscus & Churchill, 2002; Gómez-Olivencia, 2015). Bastir *et al.* (2015) recently found that the Neandertal first rib was less curved than in modern humans. They further suggested that less curved and smaller first ribs, combined with greater lower thorax capacities, could imply differences in the overall shape of the rib cage, although see Franciscus & Churchill (2002) who stated that there was a wide variation in curvature in Neandertal ribs, ranging from relatively straight to quite curved, with contralateral ribs from the same individual showing different curvatures.

There has also been a growing interest in rib curvature in modern humans and how this relates to thoracic shape. García-Martínez *et al.* (2016) analysed sagitall and axial rib curvature and torsion and found that they were important factors that modified the thoracic configuration during ontogeny. Mohr *et al.* (2007) analysed rib curvature and found that it changed along the lengths of individual ribs and between ribs of different anatomical levels. Kindig & Kent (2013) analysed the rib centroidal path from CT data. Curvature was analysed by the radius of a best fit circle at different positions along the rib, which was a method adapted from Mohr *et al.* (2007). Studies on modern humans have recently quantified specific rib geometry, including rib curvature, using the medium of computed tomography (CT) (Roberts & Chen, 1972; Dansereau & Stokes, 1988; Bertrand *et al.,* 2008; Mitton *et al.,* 2008; Kindig & Kent, 2013; Sandoz *et al.,* 2013; Weaver *et al.,* 2014). Geometric parameters such as rib arc length, chord, subtense and angles of curvature can all be quantified by taking measurements on the CT scans themselves or from 3D models created from CT scans.

This study aims to analyse rib geometric morphology using surface vertices. Three dimensional (3D) models were created from thoracic CT scans from modern humans and were compared to 3D models of previously reconstructed Neandertal ribs taken from the Neandertal thorax constructed by Sawyer & Maley (2005). Female ribs have previously been described as being more curved, shorter, more delicate and with costal arches longer than males (Karmaker, 2010). However, there are relatively few studies which have quantitatively analysed this, with the notable exceptions of Bellemare *et al.* (2006), Cirillo & Henneberg (2012) and Weaver *et al.* (2014). Bellemare *et al.* (2006) analysed the lengths of the third, sixth and ninth ribs between males and females and found that they were not significantly different. Cirillo & Henneberg (2012) found significant differences when examining all the ribs together between males and females, although at individual levels male ribs were not significantly different from females. This study also aimed to analyse the difference between the sexes in all geometrical parameters and to examine where the Kebara 2 specimen more closely fits. The methods of Sandoz *et al.* (2013) and Kindig & Kent (2013) were used to define the centroidal path from the surface vertices. This method enabled rib geometry to be analysed. Curvature of the ribs was measured from the mid-line of the ribs as the sum of angles between successive centroids in adjacent cross sections along the length of the rib.

Materials and methods

The Kebara 2 skeleton was found in 1983 at the Kebara Cave, Mt Carmel, Israel (Rak & Arensburg, 1987). The skeleton has been referenced as a mature male individual with an estimated age of 50 – 55,000 year BP (Rak & Arensburg, 1987), although remains have also been dated to be 59900 (±3500 years) and 64300 (± 5500) years, from flint materials found in association with the skeleton at the site (Valladas *et al.,* 1987). The height and weight of Kebara 2 has been calculated as 166 cm and 75.6 kg respectively (Ruff *et al.,* 1997). The set of ribs are complete but only a few of them are whole ribs and deformation is present. Rib geometrical parameters were therefore analysed from the ribs of the reconstructed Neandertal thorax based on the Kebara 2 remains from Sawyer & Maley (2005). A CT scan (Siemens SOMATOM, helical mode, slice thickness = 0.5 mm, inter-slice spacing = 1 mm, image data format: DICOM 3.0) was taken of the cast of the reconstructed thorax and a 3D model was obtained using AMIRA software (Amira 4.0, San Diego, CA, USA). Ribs were cut from the model at the vertebral and sternal end using the software programme 'MeshLab'. The right ribs 3-9 were analysed. The left ribs were not analysed as minor realignment was done on left ribs 4, 7, and 8 (Sawyer & Maley, 2005). Left rib 6 was also found to be a composite of left ribs 6 and 7 (Gómez-Olivencia *et al.,* 2009). Heads on the vertebral end were missing on original Kebara 2 right ribs 3-9 and had to be remodelled. Sternal ends were also missing and were remodelled on right ribs 6, 7, 8 and 9 (Sawyer & Maley, 2005). Sawyer (personal communication) stated that the right ribs were quite intact and were not modified in any way with the exception of ribs 1 and 2, which were not analysed in this study.

The sample of modern humans analysed in this study were 14 randomly chosen healthy adults from Belgium (mean age 30±6 years). Data were obtained from CT scans (Siemens SOMATOM, helical mode, slice thickness = 0.5 mm, inter-slice spacing = 1 mm, image data format: DICOM 3.0) and the AMIRA software was used to manually segment each rib (1 to 10) and vertebra to obtain accurate 3D models of the thorax (Beyer *et al.,* 2014; Beyer *et al.,* 2015). This set of data were previously used to analyse costovertebral joint motion in modern humans when breathing (Beyer *et al.,* 2014; Beyer *et al.,* 2015, 2016).

Geometrical parameters

All 3D models obtained were then transformed into AVS UCD ascii (Advanced Visual Systems Unstructured Cell Data) file formats (.inp). A protocol was developed and implemented in Matlab®

to determine geometric characteristics of all ribs. The method followed Kindig & Kent (2013) and Sandoz *et al.* (2013). In order to compare rib geometry from all subjects, each rib vertex cloud (presented in the original CT scan coordinate system) was analysed using a rigid transformation into the local coordinate system (LCS), which was defined by the principal axes of the rib (Fig. 1). Each rib vertex cloud was then processed using rib slices (Kindig & Kent, 2013) obtained from "a rescanning" process within MATLAB in order to get cross-section shape, size and area using best fitting ellipses of the external contour of the cross-section area (Fig. 1). The centroid of each ellipse was used to measure the centroidal pathway between each slice (the rib midline) (Fig. 1) This 'rescanning' then enabled specific geometrical parameters to be obtained from: a) rib midline: arc length, chord length, rib width, rib curvature in the XZ plane which was measured in an axial plane (rib curvature), rib curvature in the YZ plane (rib torsion), rib curvature in the XY plane, (anterior-posterior bending, which is the difference in mm between the sternal and head ends of the rib) and b) from fitted ellipses: rib torsion was measured as the sum of the long axes (Fig. 1).

Analysis of measurements

All measurements were made on the 3D models. Manual measurements on physical bones have previously shown no statistical differences when compared with virtual models from CT scans of the same bones (Chapman *et al.,* 2014). The following parameters were analysed: rib chord (distance between costo-chondral joint to costo-vertebral joint), rib width (or head/ventral subtense), rib arc length (length of the complete rib along the body) and rib curvature (which was in the axial plane), rib torsion and rib anterior-posterior bending (Appendix, Fig. 1). Data were tested for normality. Parameters were all normal with the exception of rib curvature in rib 9 (Appendix). A paired t-test was calculated and no statistically significant differences were found between left and right ribs of the same subject in all geometrical parameters. Therefore, all ribs were used in analyses and the average between each side was calculated.

Results

Absolute rib geometric parameters

Mean modern human rib arc lengths increased from rib 3 (mean = 248.5±14.3mm) to rib 6 (mean = 296.4 ±18.5mm) and decreased to rib 9 (mean = 262.3±24.5mm). Kebara 2 ribs showed a similar pattern in rib arc lengths, increasing from rib 3 (246.3mm) to rib 6 (335.6mm), then decreasing to rib 9 (276.8mm) (Appendix). Mean modern human rib arc lengths were greatest between rib 6 and 8 and the largest variations in range were present in ribs 8 (247.0 to 324.7mm) and 9 (230.7 to 336.9mm). Mean modern human chord lengths increased from rib 3 (mean = 136.6±11.3mm) to rib 7 (mean = 202.9 ±17.1mm) and decreased slightly to rib 9 (mean = 191.0±13.4mm) (Appendix). The Kebara 2 ribs were similar, although there was an increase from rib 3 (141.3mm) to rib 8 (232.2 mm) and then a slight decrease to rib 9 (222.4 mm). Chord lengths in the Kebara 2 ribs were also greatest between ribs 6 and 8 (Appendix). Mean modern human rib widths increased from rib 3 (mean = 80.6±5.3mm) to rib 5 (mean = 87.4 ±5.9mm) and decreased to rib 9 (mean = 70.1±6.8mm) (Appendix). The Kebara 2 ribs also showed a similar pattern to the mean of modern humans, increasing from rib 3 (77.4 mm) to rib 5 (100.7mm), then decreasing to rib 9 (67.7mm) (Appendix).

The means of modern human rib curvatures (in the axial plane) demonstrated decreases between adjacent descending ribs from rib 3 (mean = 204.4±10.8°) to rib 9 (mean = 152.5 ±20.4°) (Appendix). The Kebara 2 speciman shows a similar decrease in rib curvature from rib 3 (183.8°) to rib 4 (178.0°), then a slight increase to rib 6 (186.1°), and a descending decrease to rib 9 (139.1°). The modern human mean for rib torsion also showed a large variability with small differences in the pattern. The patttern of the Kebara 2 ribs in rib torsion was also present in individual human subjects (Appendix).The modern human mean demonstrated an increase in anterior-posterior (AP) bending from rib 3 (mean = 6.2±3.3mm) to rib 8 (mean = 21.1±3.4mm) and

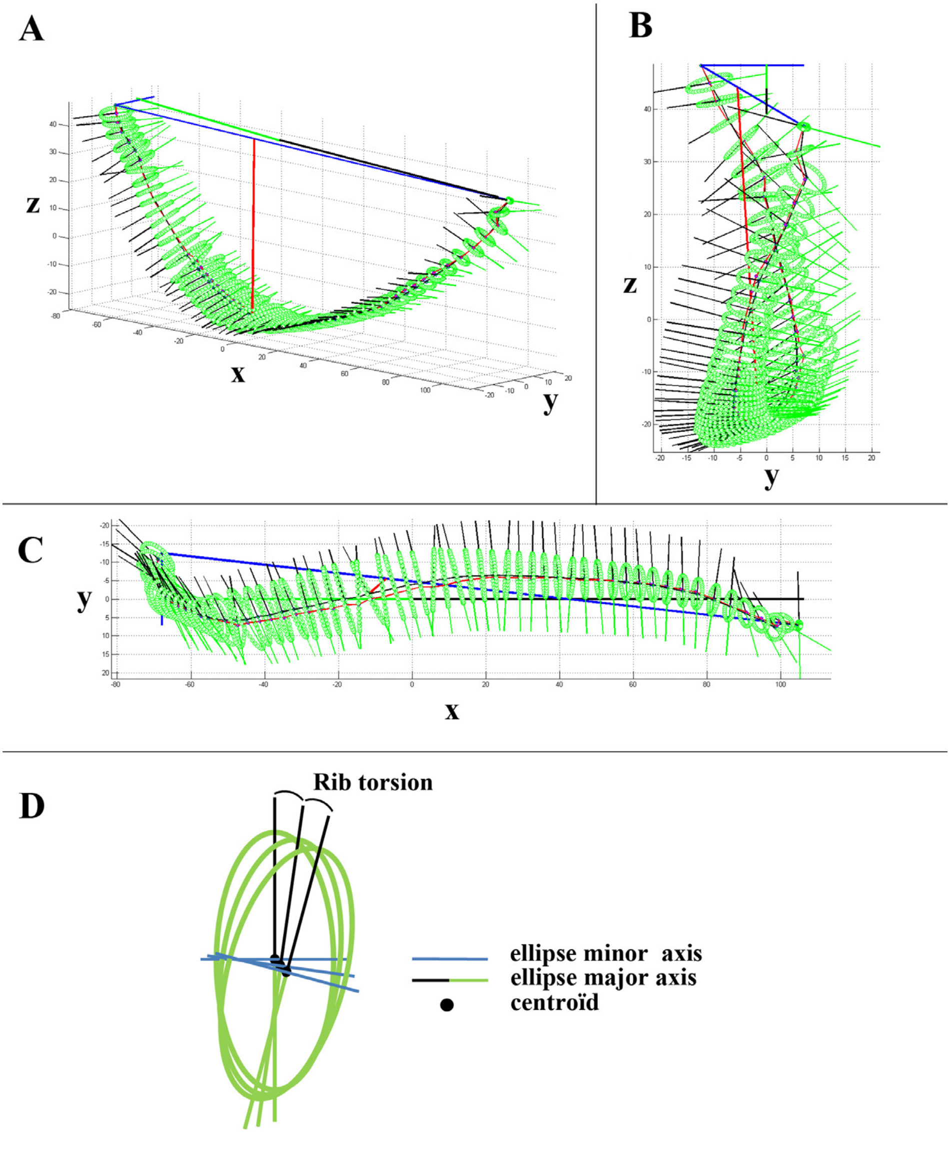

Fig. 1 - New axis origin and orientations after scanning. Each rib cloud was analysed using best fitting ellipses of the external contour of the cross-section area. The long ellipse axis orientations (black to green lines) are depicted in different views. The centroid of each ellipse was used to measure the centroidal pathway between each slice (rib midline). A) view from the axial plane from the posterior to the inferior part of the rib from left to right. Arc length is measured as the length of the rib mid-line. The blue line indicates the chord length and the red line indicates rib width. Rib curvature was measured as the sum of angles between centroids in adjacent cross sections in the longitudinal axis (X). B) view in the anterior plane rotated by 90 degrees which depicts the anterior-posterior bending. C) lateral view from the sagittal plane from the posterior to the anterior part of the rib from left to right. The difference between the sternal and rib head (anterior-posterior bending) were measured in mm (blue line along y axis) D) rib torsion was measured as the sum of the long axes rotation of the ellipses. The colour version of this figure is available at the JASs website.

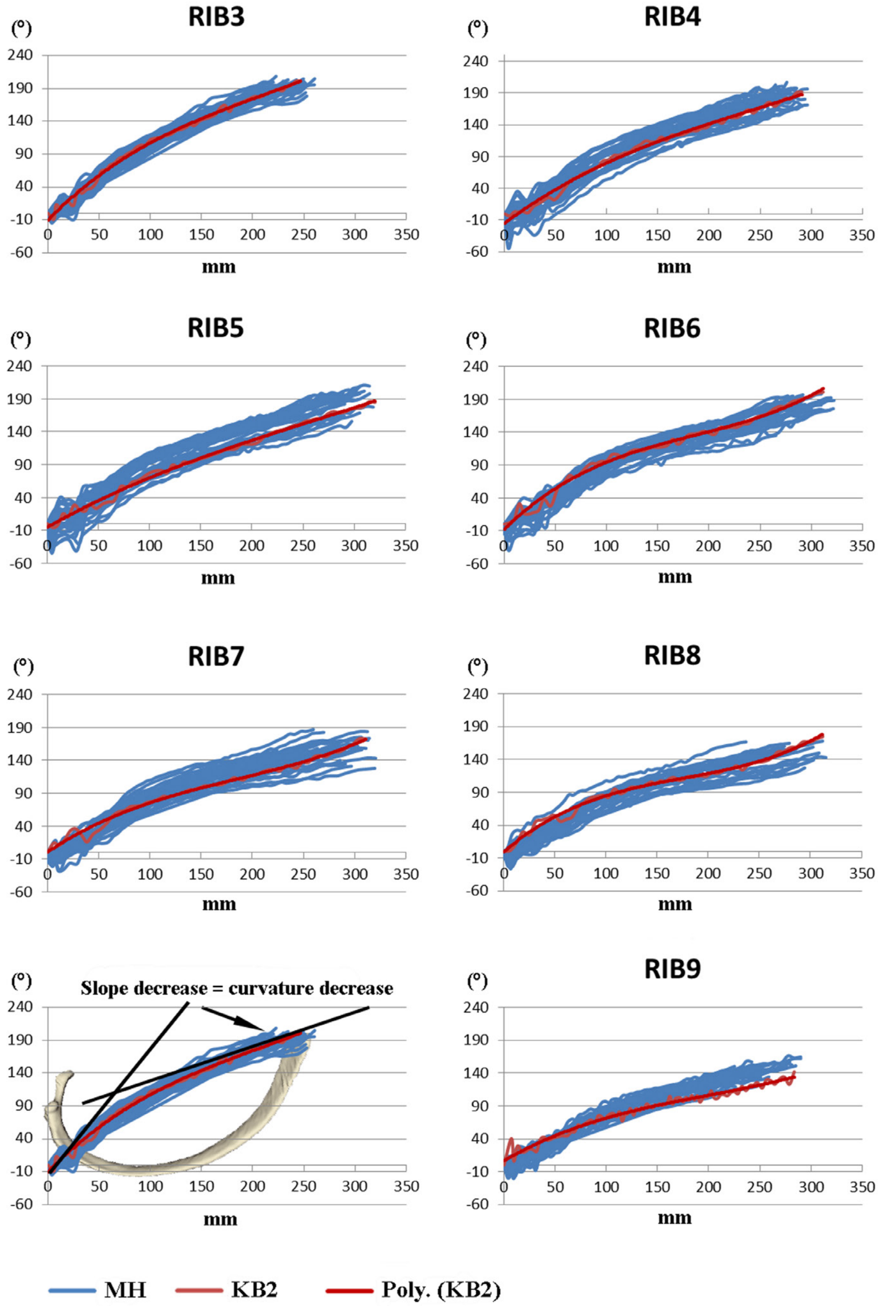

Fig. 2 - Rib curvature/ rib arc length for all modern human samples and each Kebara 2 reconstructed rib. The more the slope increases the more the rib is curved. Curvature decreases as the slope decreases at the sternal part of the rib. The slope of the curvature/arc length curve becomes stable around 100mm and then the curve declines gradually. The colour version of this figure is available at the JASs website.

Tab. 1 - Results of the Mann Whitney U test between the sexes for all geometrical parameters.

	ARC LENGTH	CHORD LENGTH	AP BENDING	MAX WIDTH	TWIST ANGLE	RIB CURVATURE	TOTAL RIB INDEX
RIB 3	**0.000**	**0.000**	0.098	**0.000**	**0.017**	1.000	0.440
RIB 4	**0.000**	**0.000**	0.168	**0.001**	**0.013**	**0.039**	0.181
RIB 5	**0.000**	**0.000**	0.154	**0.002**	**0.035**	**0.022**	**0.045**
RIB 6	**0.000**	**0.000**	**0.003**	**0.003**	0.089	0.291	0.217
RIB 7	**0.000**	**0.000**	**0.081**	**0.008**	**0.000**	**0.048**	0.304
RIB 8	**0.000**	**0.000**	0.435	**0.013**	**0.001**	0.098	0.411
RIB 9	**0.000**	**0.000**	0.270	**0.004**	**0.004**	0.783	0.681

then a decrease in AP bending to rib 9 (mean = 16.8±2.7mm). The Kebara 2 individual ribs showed an increase in AP bending from rib 3 (8.6mm) to rib 5 (17.3mm) then a decrease in AP bending to rib 6 (13.7mm) and a relatively even distribution of AP bending in rib 7-9 from (15.4-15.6mm) (Appendix).

Analysis of rib curvature

Franciscus & Churchill (2002) previously analysed total rib curvature index (TRC) (width/chord) and stated that relatively larger values for this index reflect a less open curvature with less mediolateral expansion in the thorax. The Kebara 2 individual ribs were shown to have TRC within the standard deviation from the modern human mean of all ribs, except for rib 9 where Kebara 2 was below the standard deviation from the modern human mean (Appendix).

Rib curvature was further analysed with rib arc length to examine the distribution of curvature in different parts of the shaft (Fig. 2). There is a progressive curvature along the rib from the posterior to the inferior part of the rib (Fig. 2). At the posterior extremity, around the first 50mm, jumps in the curve can be observed (Fig. 2). This is due to the orientation of the rib midline in the neck and tubercula region. It is possible to smooth the data although we preferred to display raw data (Fig. 2). In summary, all Kebara 2 ribs appear to demonstrate a rib curvature which was within the range of modern humans over the entire arc of the rib (Fig. 2).

Data analysed by sex

The 95% confidence interval of the male and female mean was analysed in comparison to the Kebara 2 ribs (Fig. 3). A Mann Whitney U test was performed between the sexes. There were statistically significant differences between the sexes for arc, length and chord, with the male mean showing greater values than the female mean (Appendix and Tab. 1, Fig. 3). Rib curvature showed that there were some significant differences between rib curvature, AP bending or rib torsion between the sexes with the female mean either being equal to (rib curvature – rib 3) or showing greater values than the male mean (Appendix and Tab. 1, Fig. 3). The Kebara 2 ribs were largely within the male range for all geometrical parameters (Appendix, Fig. 3).

A principal components analysis (PCA) was carried out using all values for all geometric parameters to determine if the ribs of Kebara 2 were within the modern human range (Appendix, Fig. 4). Fig. 4 shows that the Kebara 2 specimen is within the modern human range (Fig. 4.). PC1 is 78.4% of the variance and PC2 is 12.1% of the variance. PC1 is largely explained by arc length, followed by chord length for the

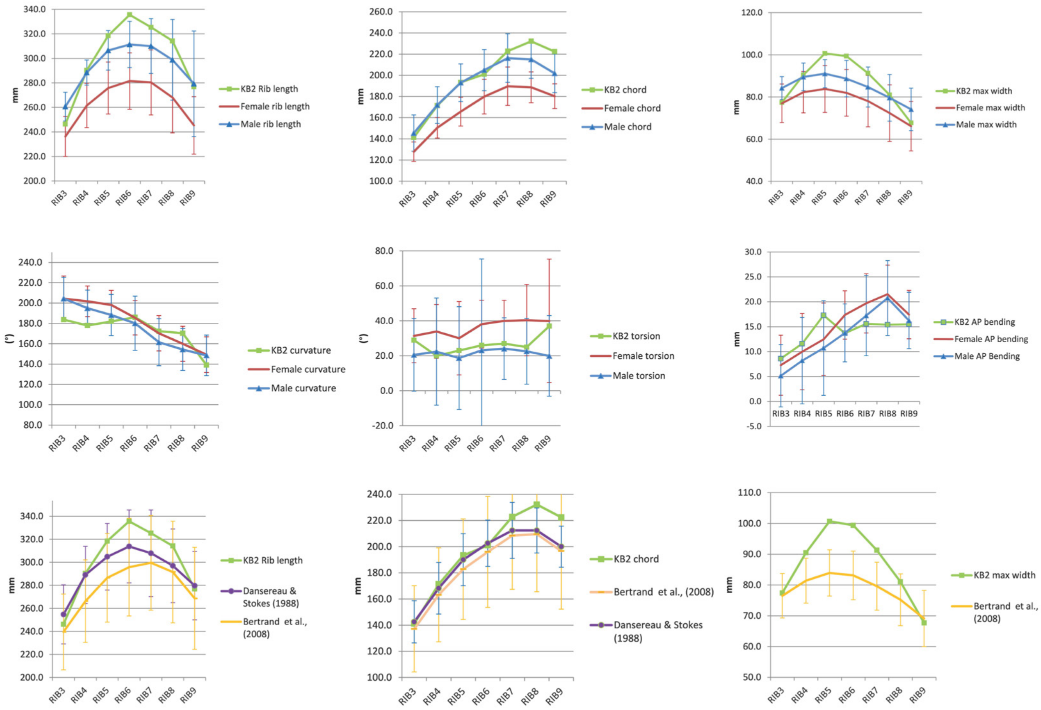

Fig. 3 - Line graphs showing rib length, chord length, rib width, rib curvature, rib torsion and anterior-posterior bending for the Kebara 2 reconstructed ribs in comparison to the male and female mean. The error bars for the male and female mean show standard deviation (Appendix) x 1.96 to express the 95% confidence interval of the mean. Comparative means and standard deviation are also depicted from the studies of Bertrand* et al. *(2008) and Dansereau & Stokes (1988). The colour version of this figure is available at the JASs website.

positive value and rib curvature for the negative value. PC2 is largely explained by chord length. Please also note the close position of the left and right ribs of each individual (Fig. 4). A paired samples t-test also showed that there were no statistical differences between left and right ribs.

Global shape of Kebara 2 reconstructed ribs

The overall global shape of all individual Kebara 2 reconstructed ribs together were compared with a modern human by using a biomechanical model of a modern human breathing. Individual reconstructed Kebara 2 ribs were registered onto each individual rib of the modern human thorax using iterative closest point (ICP) registration, which is available from lhpFusionBox. LhpFusionBox is a freely available musculo-skeletal software, developed at the Université de Bruxelles, that has recently been adapted for paleoanthropological analysis (Chapman *et al.,* 2013). The ribs were fused onto the modern human specimen using a rigid transformation (where form and size were not changed) (Fig. 5).

Discussion

Geometrical parameters in this study of modern human rib chord length, rib width and rib arc length were found to be similar to results from other studies in the literature on modern humans (Dansereau & Stokes, 1988; Cirillo & Henneberg, 2012), indicating that the method

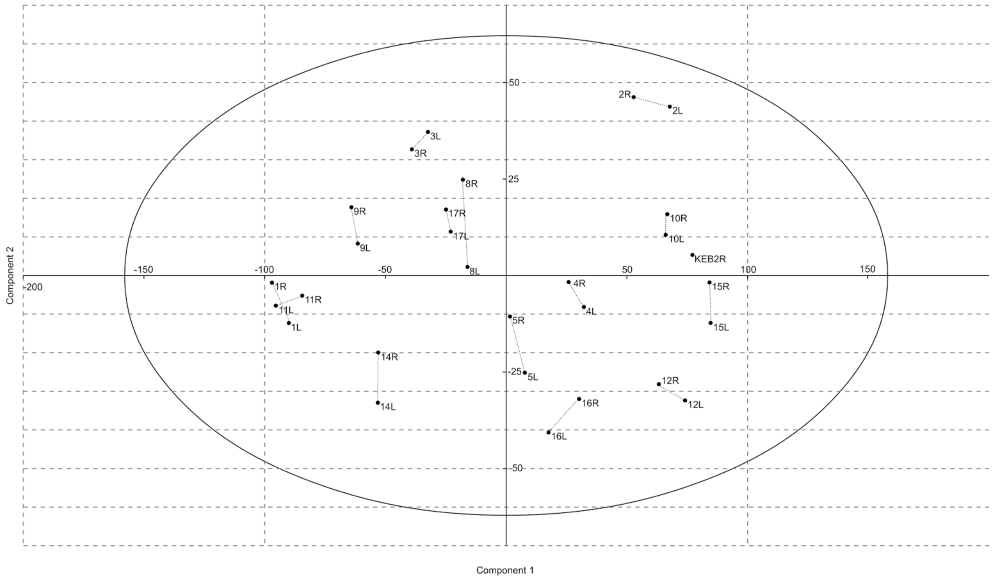

Fig. 4 - Principal components analysis using all geometric parameters

is in line with other contemporary research. Distinct patterns between human rib levels were demonstrated across all human subjects used in this study (Appendix, Figs. 3, 5). The same distinct patterns were also noted in the Kebara 2 reconstructed ribs (Appendix, Fig. 3).

Arensburg (1991) examined the Neandertal Kebara 2 original ribs and vertebrae and stated that all measurements were within the limits of anatomically modern humans. Garcia-Martinez *et al.,* (2014a) examined the centroid sizes of the Kebara 2 ribs and found that the total thorax size was within the mean size of modern humans in the original reconstructions of the ribs (manual reconstruction) by Arensburg (1991). However, Gómez-Olivencia *et al.,* (2009), found that the Kebara 2 left rib 6 was actually a composite of 6L and 7L and Garcia-Martinez *et al.,* (2014a) virtually reconstructed these ribs. When Garcia-Martinez *et al.* (2014a) included the new reconstructions of the left rib 6 and 7 in their analyses, they found that the Kebara 2 lower thorax and total thorax size was statistically larger than the modern human mean. Gómez-Olivencia *et al.* (2009) later analysed arc length in the original ribs of Kebara 2 and found that that the upper ribs of Kebara 2 were within the range of modern humans (1-3) but the middle (4, 5, 7) and lower (8, 10) thoracic ribs exceeded the range of human variation. Comparisons are difficult as, in contrast to this study, both Gomez-Olivencia *et al.* (2009) and Garcia-Martinez *et al.* (2014a) did not measure certain ribs or measured only the left side. They also used different methods to analyse the ribs, geometric morphometrics (Garcia-Martinez *et al.,* 2014a) and traditional measurements (Gomez-Olivencia *et al.,* 2009). Gomez-Olivencia *et al.* (2009) further measured the tuberculo-ventral arc and the lateral edge of the rib (as opposed to the head-ventral arc and the mid-line of the rib as in this study and the study by Dansereau & Stokes (1988) and Bertrand *et al.* (2008)). Similar to Gomez-Olivencia *et al.* (2009), the present study found that the arc length of rib 3 was within the range of standard deviation of the modern human range (males and females). The Kebara 2 ribs were also relatively longer in arc length than the mean of modern

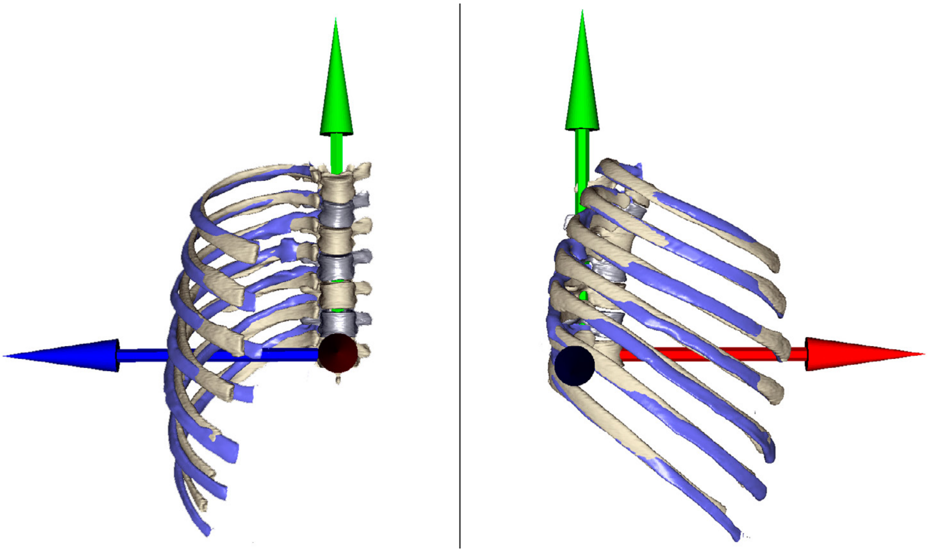

Fig. 5 - Results of ICP registration of KB2 ribs on to a model of a modern human breathing. The model was created by taking CT scans of three respiratory poses (total lung capacity (TLC), middle inspiratory capacity (MIC) and functional residual capacity (FRC) and interloping the positions between these poses. For full details see (Beyer et al., 2014). The modern human thorax is in bone colour and the Kebara 2 ribs are blue. The animated colour version of this figure is available at the JASs website.

humans and there was a sharp increase in arc length from rib 3-4 (Fig 3, Appendix). However, in contrast to the study by Gomez-Olivencia *et al.* (2009), the present study found that all rib arc lengths, with the exception of rib 6, were within the 95% confidence interval of the modern human male mean (S.D. * 1.96: Appendix, Fig.3). Arc lengths for the Kebara 2 ribs 3-9 were also within the range of standard deviation in the study by Dansereau & Stokes (1988) for all ribs and for rib 3, 8 and 9 in the study by Betrand *et al.* (2008). Arc lengths for modern humans and the Kebara 2 ribs were shown to increase in adjacent ribs from rib 3 to rib 6 and then decrease to rib 9, forming a distinctive curve (Appendix), which was also seen in the studies by Cirillo & Henneberg (2012), Dansereau & Stokes (1988) and Bertrand *et al.* (2008).

Franciscus & Churchill (2002) previously suggested that the Neandertal Tabun C1 would have had a greater medio-lateral expansion of the thorax, measured by the tuberculo ventral-subtense, whilst Shanidar 3 demonstrated a greater anterior-posterior expansion, which was measured by the tuberculo-ventral chord. The same authors reported that Kebara 2 was a mix of anterior-posterior and medio-lateral expansion (Franciscus & Churchill, 2002). Chord length in this study was measured from the head ventral-chord, similar to Dansereau & Stokes, (1988) and Bertrand *et al.* (2008). The Kebara 2 individual ribs were within the 95% confidence interval of the modern human mean (both males and females) (S.D. * 1.96: Appendix, Fig. 3) for ribs 3-7. These ribs were also within the limits of standard deviation from the mean of modern humans for ribs 3-7 according to Dansereau & Stokes, (1988) and for ribs 3-6 in the study by Bertrand *et al.* (2008) (Appendix, Fig. 3). The Kebara 2 ribs were therefore outside of the limits of modern humans for ribs 8-9 in this and all comparative studies (Appendix). The Shanidar 3 Neandertal was also found to be outside of the limits of the modern human mean for rib 8 (Shanidar 3 = 248.3, modern human mean = 227.9, SD: 16.1) (Franciscus & Churchill, 2002). Chord length in modern humans showed an increase in size from rib 3 to either rib 7 (Appendix) and Cirillo & Henneberg (2012), or to rib 8, Dansereau and Stokes, (1988) and Bertrand *et al.* (2008), followed by a decrease to rib 9 (Appendix). However, Cirillo & Henneberg (2012) analysed the difference between descending adjacent rib pairs, which were all found to be significantly different except for ribs 7-8. This could explain the differences between rib patterns in the different studies. The Kebara 2 individual ribs showed an increase from ribs 3 - 8 (Appendix).

The reconstructed Kebara 2 rib widths were shown to be within the 95% confidence interval of the modern human mean (males and females) (S.D. * 1.96: Appendix, Fig. 3) for ribs 3-4 and ribs 7-9. They were also within the 95% confidence interval of the modern human mean for rib 3 and ribs 8-9 in the study by Bertrand *et al.* (2008) (Appendix, Fig. 3). Mean rib width was found to increase from rib 3 to rib 5 and then decrease to rib 9 in both modern humans and the Kebara 2 ribs (Appendix) and showed an even variation between all ribs. The Shanidar 3 rib 8 was similarly found to have rib width within the human mean (Shanidar 3 = 67.3, modern human mean = 63.6, SD: 8.1) (Franciscus & Churchill, 2002).

Total rib curvature index (TRC) (width/chord) has previously been analysed in hominid specimens as a means to reflect the curvature of the ribs. Relatively smaller values for this index have been reported to reflect less curved ribs (Schmid *et al.,* 2013) with more medio-lateral expansion (Franciscus & Churchill, 2002). The reconstructed Kebara 2 ribs were shown to have TRC at the lower end of the modern human mean, although were within the standard deviation of the mean of all ribs except for rib 9 (Appendix). Franciscus & Churchill (2002) previously analysed the 8th rib of Shanidar 3 using TRC and similarly found that the 8th rib of Shanidar 3 had a TRC at the lower end of the modern human mean (Shanidar 3 = 27.1, modern human mean = 28.1).

Rib curvature

Comparisons on curvature of the ribs in modern humans and Neandertals are problematic due to the differing methodologies used in the few studies that have analysed ribs. However, this newly developed method enabled us to analyse the angles of curvature of individual ribs in exactly the same way, both overall and at different intervals along the ribs.

The sum of rib curvature only gives an indication of overall curvature and not how curvature differs in different parts of the ribs. Curvature in the axial plane was therefore plotted against rib arc length to examine how curvature differs from the posterior part of the rib to the inferior part of the rib (Fig. 2). Similar to the results of the study by Mohr *et al.* (2007), this study found that rib curvature changed considerably along the lengths of individual ribs and between ribs of different anatomical levels (Fig. 2). Kindig & Kent, (2013) similar to Mohr *et al.* (2007), found a greater curvature at the posterior part of the rib, around the area of the posterior angle, with a gradual decrease towards the sternal end. This is similar to our study where the slope of the bending/length curve demonstrates the same phenomenon for both modern humans and the Kebara 2 reconstructed ribs, with the curve declining gradually and becoming stable at around 100mm in length (Fig. 2). Mohr *et al.* (2007) found that rib 3 demonstrated the highest curvature, similar to this study (Appendix). Dansereau & Stokes (1988) also found that the means of rib maximum curvatures were greatest in the upper ribs. Kebara 2 ribs 3-9 demonstrated a curvature by arc length at the lower end of human variation (Fig. 2). This also corroborates the finding of TRC, with Kebara 2 being at the lower end (Appendix). However, ribs 6-9 show that the Kebara 2 ribs demonstrate a relatively greater curvature around the area of the posterior angle, which is at approximately 40-50% of the overall arc length (Fig. 2), similar to the study by Franciscus & Churchill (2002), who found that the Shanidar 3 Neandertal had high values of the posterior angle index ((posterior angle subtense / posterior angle chord) x 100), which was slightly above the human mean for ribs 5-9. Gómez-Olivencia (2015) equally found that the ribs of Shanidar 3 had a high posterior angle index, the La Chapelle-Aux-Saints ribs were within modern human limits and the Kebara 2 ribs were within modern human limits for rib 7, although rib 8 was less curved in this area (which Gómez-Olivencia (2015) states may be related to a pathological lesion in ribs 5-6).

There is a large cross over of the 95% confidence interval between males and females in all rib curvatures. The Kebara 2 ribs were closer to the modern human male mean, however, they were within the 95% confidence interval of the modern human mean for all male and female ribs (S.D. * 1.96: Appendix), with the exception of being below the mean for rib 4 for rib curvature for males and ribs 3-5 for rib curvature for females (Fig. 3). The modern human mean demonstrated a decrease in rib curvature between adjacent descending ribs from rib 3 to rib 9. The Kebara 2 specimen shows a decrease from rib 3 to rib 4, then a slight increase to rib 6 and a descending decrease to rib 9, although this demonstrates a similar pattern to other modern humans with decreases seen from ribs 3-4 and then slight increases between ribs 4-6 in some subjects, followed by a descending decrease in adjacent ribs until rib 9. The pattern of descent in rib curvature in Kebara 2 is therefore similar to modern humans, although it is notable that that there is a sharp decrease in rib curvature from rib 8-9 (Appendix, Fig. 3).

Roberts & Chen (1972) analysed rib torsion using semi-ellipses and found a range between 20 and 30°, similar to the results of this study, with the exception of rib 9. Rib torsion was however, found to be highly variable in modern humans. The Kebara 2 ribs were within the 95% confidence interval of the modern human mean for all male and female ribs (Appendix, Fig. 3). The degree of anterior-posterior bending in the sagital plane was within the 95% confidence interval of the modern human mean, with the exception of being below the modern human female mean for rib 8 (Appendix, Fig. 3). However, this specific parameter only represents the difference in height between rib head and sternal extremity.

Limitations of the study

A limitation of this study is that the reconstructed ribs of Kebara 2 were used. Sawyer, (personal communication), stated that the original ribs 3-9 were not changed in the reconstruction, although rib heads and sternal ends were estimated based on modern human anatomy. This means that for certain parameters, rib arc length, chord and width, there is a portion of the rib which is estimated and it is based on modern human anatomy. This is relevant as Arensburg (1991), and the present study found that the Kebara 2 ribs were within the limits of modern humans for the large majority of geometrical parameters. However, the inclusion of a reconstructed portion of the rib could introduce slight unknown artefacts in certain measurements. Rib curvatures will be affected in that the head and neck and sternal end of the rib are estimated based on the trajectory of curvature on the rib. However, this does not affect the rest of the curvature of the rib, (see Arensburg (1991) for detailed photographs of each individual rib). Previous authors have analysed Neandertal rib chord from the tubercle to the distal end, which circumvents the problem of missing sternal and vertebral ends (Franciscus & Churchill, 2002; Gomez-Olivencia *et al.,* 2009). However, the analysis of the entire rib is important in that it enables the quantification, in three-dimensions, of many more geometrical parameters of the ribs than have previously been analysed and also allows the comparative analysis of the ribs with other similar studies, such as Dansereau & Stokes (1988), Bertrand *et al.* (2008) and Cirillo & Henneberg (2012). Neandertal rib heads and necks are scarce but do exist (García-Martinez *et al.,* 2014b; Gomez-Olivencia, in press). A future study could therefore include a detailed analysis of existing rib heads and necks of Neandertals to examine potential differences with modern human anatomy.

Bastir *et al.* (2012) previously examined the reconstructed Neandertal thorax based on the Kebara 2 remains by Gary Sawyer. They also confirmed the findings of Arensburg (1991) in that there was no evidence of an enlarged chest size (Bastir *et al.,* 2012). However, Garcia-Martinez *et al.* (2014a) stated that when incorporating a new virtual rib reconstruction of the left rib 6 and rib 7, which were incorrectly fitted by Arensburg (Gomez-Olivencia *et al.,* 2009), into the rib centroid size of Kebara 2, this would give a significantly bigger ribcage with a significant size increase of the lower thorax. However, in this study we analysed only the right side of the ribs.

In this study, the 3D models were 'rescanned' in MATLAB. The computation of the rib midline is sensitive to this 'rescanning process' and the line connecting two successive centroids is altered when the angle between two successive cross-sections increases. The shape of the contours obtained close to the extremities (i.e. rib head and sternal end) can make it difficult to fit ellipses. The 'recanning' therefore starts with the first possible ellipse fitting, which as a result means that the rib midlines are slightly underestimated by a few millimeters in comparison with the exact length. This underestimation could explain the discrepencies between the results obtained in this study and previous measurements on the Kebara 2 specimen by Gomez *et al.* (2009). However, the same 'rescanning' steps were used for both modern humans and the Kebara 2 reconstructed ribs. We are therefore confident that this systematic underestimation does not dramatically alter the results, and enables the opportunity to compare samples using exactly the same method. The size of the sample used in this study (7 males and 7 females) could also impact the results as 95 % confidence intervals become closer to the mean when larger samples are considered. However, this method allowed the comparison of the Kebara 2 reconstructed ribs with other published studies (Dansereau & Stokes 1988; Bertrand *et al.,* 2008), that also demonstrated that Kebara 2 was within the 95% confidence interval of modern humans for chord and arc length (Fig. 3).

Differences between the sexes

The Kebara 2 reconstructed ribs were shown to have curvature within the range of modern humans, albeit at the lower end, and larger than average traditional rib geometric parameters, rib arc length, chord and width, that were nevertheless largely within the 95 % confidence interval of the modern human male mean (Appendix, Fig. 3). Female ribs have previously been described as being more curved, shorter, more delicate and with costal arches longer than males (Karmaker, 2010). An analysis between the sexes demonstrated that males have ribs with less curvature and greater arc length, chord and width (Appendix and Tab. 1). In this study, the characteristics of the Kebara 2 reconstructed ribs therefore fit within the modern human sample in the range of modern human males (Appendix, Fig. 3). Bellemare *et al.* (2006) found no difference between male and female arc lengths in ribs 3, 6 and 9 using absolute data in their sample of 46 subjects. They also found that males had a significantly greater height than females in their study and that the ratio of rib arc length to body length was significantly greater in females (Bellemare *et al.,* 2006). The finding in this study on arc length differences between males and females is in contrast to the study by Bellemare *et al.* (2006), as males were significantly greater than females when analysing absolute data. In future studies on sex differences, it could be interesting to normalise data between males and females by height or thoracic spine height for example, similar to Bellemare *et al.* (2006). The difference in the studies may also be related to the significant variability in thoracic shape and size in modern humans, sample sizes as noted above, or to differing methodologies. Bellemare *et al.* (2006) detailed that as arc length was measured by a lead wire on the internal aspect of the rib, this may introduce a bias in favour of females in their study. This is due to the fact that if ribs are thicker in males (as males are generally sturdier than males) then lengths measured along the inside of the rib would be smaller than lengths measured along the central axis, which was the method used in the present study. The present study also found that chord length was greater in males in all ribs. Cirillo & Henneberg (2012) found no significant difference between chord length when analysing all ribs together in males and females. However, they found that male values for chord length were greater in all individual ribs and that chord length was significantly greater in males in ribs 8-10.

Implications of thorax shape

Bastir *et al.* (2015) analysed the first rib in Neandertals through geometric morphometrics and stated that the first ribs of Neandertals were straighter than modern humans. They also found that the first rib is correlated with the straightening of all ribs in the upper thorax and hypothesised that the upper thorax of Neandertals would have differed in shape from modern humans with more anteriorly projecting upper ribs during inspiration (Bastir *et al.,* 2015). As female ribs were shown to be more curved than males in this study (Appendix, Fig. 3), it may be the case that Neandertal male ribs were straighter and female ribs were more curved, similar to modern humans. The La Ferrassie VI and El Sidrón ribs in the analysis of Bastir *et al.* (2015) are of unknown sex. The Kebara 2 specimen is thought to be a male based on the analysis of the pelvis by Rak & Arensburg (1987), although a study on the pelvis by DSP analysis (Tillier *et al.,* 2008), demonstrated that there are both male and female characteristics in the pelvis and it was therefore difficult to sex this specimen using the pelvis. The Kebara 2 specimen is placed largely within the males in this study (Appendix, Fig. 3). However, as Neandertals are more robust generally, it may be that we cannot use the same criteria as modern humans to sex the Neandertals. It is therefore only possible to say that in this study the Kebara 2 specimen is closer to the modern human males.

The distinctive patterns of rib width, chord and arc length form parabolic curves which could be said to contribute to the so called 'barrel' shape of the human thorax. The same distinct patterns were also noted in the Kebara 2 individual ribs (Appendix, Fig. 3). The maximum rib width of ribs 5-7 of the Kebara 2 skeleton were shown to be slightly outside modern human limits, which could lead to a slightly medio-laterally wider thorax in the middle (Appendix). However, the rib width of the middle ribs (4-7) are generally high (Appendix), which could again partially account for the typical barrel shape as depicted by numerous authors in modern humans or account for the Neandertals being depicted as having a barrel or hyper-barrel shape (Boule, 1911, 1912, 1913; Heim, 1976; Weinstein, 2008). The analysis of all variables in the PCA analysis also firmly places the Kebara 2 specimen within the range of modern humans (Fig. 4).

Previous authors have suggested that the Neandertals would have had an expanded thoracic volume in the lower rib cage (Gomez-Olivencia *et al.,* 2009; Garcia-Martinez *et al.,* 2014a; Bastir *et al.,* 2015; Franciscus & Churchill, 2002). Bastir *et al.* (2015) states that evidence of larger sizes in the lower ribs coupled with the reconstruction by Sawyer & Maley (2005) may suggest a wider lower thorax in Neandertals. The Kebara 2 reconstructed ribs was shown to be within modern human limits for chord length for ribs 1-7, but ribs 8-9 were outside modern human limits which could be said to lead to a larger antero-posterior thorax in the lower part, similar to the result for Shanidar 3 (Franciscus & Churchill, 2002) (Appendix). Significant size differences have also been found in the Kebara 2 10**th** rib (Gómez-Olivencia *et al.,* 2009; García-Martínez *et al.,* 2014a), although this rib was not analysed in this study. However, caution needs to be attributed when looking at one single geometrical parameter accounting for thoracic shape, as all parameters play a role in global thoracic shape. We are also unable to account for taphonomy and distortion in the ribs which may inadvertently affect measurements (Gomez-Olivencia *et al.,* 2009). The same ribs could produce very different results in thoracic reconstruction, as thorax shape and size also depends on the orientation of both joints and transverse processes (Bastir *et al.,* 2014, Bastir *et al.,* 2015, García-Martinez *et al.,* 2016).

The Kebara 2 ribs were fused onto a modern human thorax model of breathing kinematics obtained from a previous study (Beyer *et al.,* 2014, 2015, 2016) to visualise the differences at each rib individual level (Fig. 5, Supplementary information). This fusion demonstrated that globally there were few differences between the Kebara 2 reconstructed ribs and modern human ribs (Fig. 5). Based on the visualisation of this model and the results of the geometrical parameters we cannot say that the Kebara 2 reconstructed ribs would have had a similar thoracic structure, but from this analysis alone, we equally cannot say they would have had a very different thoracic structure to modern humans. Males have been shown to have more dorsally orientated transverse processes than females (Bastir *et al.,* 2014). A more dorsal orientation of the transverse processes could rotate the attached ribs in a way that would increase thoracic width and Neandertals (including Kebara 2) have demonstrated a clear trend towards more dorsally flexed transverse processes in the lower thoracic vertebrae (Bastir *et al.,* 2014, Bastir *et al.,* 2015). This is also in line with the reconstruction of the Kebara 2 thorax by Sawyer & Maley (2005) with a wide flaring lower thoracic region. However, the orientation of the transverse processes are not enough to estimate thoracic shape on their own. In future studies it could also be interesting to consider the breathing motion of the ribs in relation to lung volumes, as detailed in Beyer *et al.* (2015, 2016) and the neutral position of the orientation of the ribs at the costotransverse joint. The motion of the ribs at this joint is currently little understood (i.e. the ribs glide at the costotransverse joint) and this could lead to significant changes in thorax diameters.

Concluding comments

The analysis of the Kebara 2 reconstructed individual ribs has demonstrated that the majority of rib geometrical parameters were within the norms of the modern humans in this study. Many previous papers have suggested that Neandertals would have had larger chests than anatomically modern humans (Franciscus & Churchill, 2002; Gomez-Olivencia *et al.,* 2009; Garcia-Martinez *et al.,* 2014a). In absolute measurements, Neandertals are above the average of modern humans for traditional rib geometric parameters (rib width, rib chord, rib length), although largely remain within the 95% confidence interval of the modern human mean. This study also analysed rib curvatures (rib curvature in the axial plane, rib torsion and rib anterior-posterior bending) and found that the Kebara 2 reconstructed ribs were within the 95% confidence interval of the modern human mean for almost all parameters of curvature. The additional information received from all parameters, including the analysis of rib curvatures, has allowed us to place the Kebara 2 ribs in context with other modern humans. The study has further demonstrated that sex can have a significant influence on geometrical parameters. As Neandertals are more robust than modern humans, we cannot state that the Kebara 2 is a male. However, we can state that all rib measurements, including rib curvature, for the Kebara 2 reconstructed ribs, fit closely within modern human male parameters. It should be noted that there is some debate on whether the western 'classical' Neandertals should be grouped with the near Eastern Neandertals. Arensburg & Belfer-Cohen (1998) have suggested that Kebara 2 and other individuals from the Levantine sample were not in fact Neandertal, although this is in opposition of the majority of other authors who regard the Kebara 2 to be Neandertal (i.e. Gomez-Olivencia *et al.,* 2009; Garcia-Martinez *et al.,* 2014a; Bastir *et al.,* 2015). It is only possible to say therefore that the Kebara 2 reconstructed ribs were very similar to modern human rib geometrical parameters. More analysis should be undertaken on complete Neandertal ribs and a greater modern human sample using the same methodology. A limitation of this study is that reconstructed ribs were used, as ribs are required to be complete in order to be analysed using this method. However, in this era of virtual anthropology, more and more teams are working on reconstruction of fossil remains and a distinctive advantage of virtual anthropology is that fragile specimens are not damaged in reconstructions and even different versions of the same ribs can be reconstructed and analysed using the same methodology.

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Appendix - Rib measurements in mm and degrees for the reconstructed Kebara 2 ribs (KB2) with mean and standard deviation for all modern humans (MH), mean and standard deviation for males and females with the maximum and minimum. Comparative means and standard deviation are also listed from the studies of Bertrand* et al. *(2008) and Dansereau & Stokes (1988). Bertrand* et al. *(2008) examined 15 subjects (5 males and 10 females). Dansereau & Stokes (1988) examined 10 subjects (6 males and 4 females).

		KB2	MH	STDEV	FEMALE	STDEV	MALE	STDEV	MIN	MAX	BER[1]	STDEV	DAN[2]	STDEV
RIB LENGTH	RRIB3	246.3	248.5	14.3	236.3	8.3	260.6	6.0	227.0	274.0	239.6	16.8	254.8	25.6
	RRIB4	290.3	275.1	15.6	261.6	9.2	288.5	5.2	246.8	297.4	266.3	18.3	289.1	24.8
	RRIB5	318.5	291.2	18.3	275.8	10.8	306.5	8.2	261.6	320.6	286.5	19.6	304.8	28.9
	RRIB6	335.6	296.4	18.5	281.5	11.8	311.4	9.6	266.4	326.8	295.8	21.6	313.8	31.7
	RRIB7	325.3	295.2	19.5	280.4	13.6	310.0	11.4	262.1	326.2	299.6	21.0	307.9	37.6
	RRIB8	314.2	283.4	22.0	268.1	14.7	298.8	16.8	247.0	324.7	291.6	22.5	297.0	32.0
	RRIB9	276.8	262.3	24.5	245.3	12.0	279.3	21.9	230.7	336.9	268.7	22.6	279.7	29.6
CHORD LENGTH	RRIB3	141.3	136.6	11.3	127.8	4.7	145.4	8.7	120.7	155.7	137.2	6.8	142.6	16.1
	RRIB4	171.3	161.1	13.0	150.4	4.9	171.9	8.9	143.7	180.9	163.2	10.0	168.2	19.7
	RRIB5	193.3	179.3	16.0	165.6	7.0	193.0	9.1	156.0	200.7	182.8	11.1	190.0	19.9
	RRIB6	201.0	192.4	15.6	179.9	8.4	204.9	9.9	170.3	215.6	196.0	12.6	202.6	17.7
	RRIB7	222.8	202.9	17.1	189.7	9.3	216.2	11.7	179.0	234.9	208.5	13.1	212.4	21.4
	RRIB8	232.2	201.8	15.7	188.6	7.4	215.0	9.1	177.9	229.6	209.6	13.0	212.4	17.2
	RRIB9	222.4	191.0	13.4	180.2	5.9	201.8	9.4	172.3	210.3	196.6	13.1	200.0	15.7
MAX WIDTH	RRIB3	77.4	80.6	5.3	77.0	4.7	84.2	2.8	73.1	89.7	76.5	7.2		
	RRIB4	90.5	85.9	5.6	82.3	5.0	89.5	3.4	77.2	95.4	81.4	7.3		
	RRIB5	100.7	87.4	5.9	83.8	5.7	91.1	3.4	77.9	95.5	83.9	7.5		
	RRIB6	99.4	85.3	6.0	82.0	5.6	88.7	4.4	75.4	95.9	83.1	7.9		
	RRIB7	91.3	81.4	6.4	78.0	6.2	84.7	4.8	72.2	92.7	79.6	7.8		
	RRIB8	81.0	76.0	7.2	72.4	6.8	79.6	5.7	64.3	90.1	75.2	8.4		
	RRIB9	67.7	70.1	6.8	66.2	6.0	74.1	5.2	58.8	83.0	69.1	9.1		
RIB CURVATURE (°)	RRIB3	183.8	204.4	10.8	204.4	11.4	204.4	10.7	184.2	222.0				
	RRIB4	178.0	198.3	9.0	201.8	7.7	194.9	9.1	183.8	215.3				
	RRIB5	182.1	193.2	10.1	198.1	7.4	188.3	10.3	169.8	216.3				
	RRIB6	186.1	182.9	11.5	185.6	8.6	180.2	13.6	158.0	204.2				
	RRIB7	172.4	165.9	11.2	170.3	8.8	161.5	11.8	141.9	183.0				
	RRIB8	170.4	157.2	10.0	160.0	8.8	154.4	10.6	142.9	175.4				
	RRIB9	139.1	152.5	20.4	149.2	9.0	148.6	10.2	137.0	169.8				

Appendix - continued.

		KB2	MH	STDEV	FEMALE	STDEV	MALE	STDEV	MIN	MAX	BER[1]	STDEV	DAN[2]	STDEV
RIB TORSION (°)	**RRIB3**	29.0	26.0	10.7	31.4	7.9	20.5	10.6	49.2	7.4				
	RRIB4	20.0	28.2	13.5	33.9	7.8	22.4	15.6	56.2	3.5				
	RRIB5	23.0	24.4	14.0	30.0	10.7	18.7	15.0	47.3	9.4				
	RRIB6	26.0	30.6	20.6	38.1	7.0	23.1	26.7	51.9	11.7				
	RRIB7	27.0	32.1	11.1	40.0	6.0	24.1	9.0	52.7	15.0				
	RRIB8	25.0	31.5	13.4	40.4	10.4	22.5	9.6	56.6	7.3				
	RRIB9	37.0	29.9	18.1	40.0	18.0	19.9	11.8	76.9	6.9				
AP BENDING (MM)	**RRIB3**	8.6	6.2	3.3	7.3	3.1	5.2	3.2	2.0	12.5				
	RRIB4	11.6	9.1	4.2	10.0	3.9	8.2	4.4	2.1	18.2				
	RRIB5	17.3	11.6	4.3	12.5	3.7	10.7	4.9	4.9	22.3				
	RRIB6	13.7	15.6	3.2	17.4	2.5	13.7	3.0	9.4	20.7				
	RRIB7	15.6	18.5	3.8	19.7	3.0	17.2	4.1	10.8	25.6				
	RRIB8	15.4	21.1	3.4	21.5	3.0	20.7	3.8	15.5	29.7				
	RRIB9	15.5	16.8	2.7	17.4	2.5	16.2	2.9	11.8	21.5				
TOTAL RIB CURVATURE INDEX	RRIB3	54.8	59.6	5.1	60.4	5.2	58.8	5.1	52.5	71.3				
	RRIB4	52.8	53.9	4.4	54.8	4.5	52.9	4.3	46.8	63.1				
	RRIB5	52.1	49.4	4.1	50.7	4.5	47.9	3.1	41.8	59.2				
	RRIB6	49.4	45.0	3.8	45.7	4.2	44.1	3.4	37.3	53.5				
	RRIB7	41.0	40.6	3.8	41.3	4.0	39.9	3.6	32.8	48.1				
	RRIB8	34.9	37.9	3.1	38.4	3.7	37.4	2.3	32.5	42.8				
	RRIB9	30.4	36.9	2.9	36.7	3.2	37.2	2.5	31.6	41.6				

[1] Bertrand *et al.,* (2008)

[2] Dansereau& Stokes (1988)