Three-dimensional morphometrics of thoracic vertebrae in Neandertals and the fossil evidence from El Sidrón (Asturias, Northern Spain)

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Abstract

Well-preserved thoracic vertebrae of Neandertals are rare. However, such fossils are important as their three-dimensional (3D) spatial configuration can contribute to the understanding of the size and shape of the thoracic spine and the entire thorax. This is because the vertebral body and transverse processes provide the articulation and attachment sites for the ribs. Dorsal orientation of the transverse processes relative to the vertebral body also rotates the attached ribs in a way that could affect thorax width. Previous research indicates possible evidence for greater dorsal orientation of the transverse processes and small vertebral body heights in Neandertals, but their 3D vertebral structure has not yet been addressed. Here we present 15 new vertebral remains from the El Sidrón Neandertals (Asturias, Northern Spain) and used 3D geometric morphometrics to address the above issues by comparing two particularly well-preserved El Sidrón remains (SD-1619, SD-1641) with thoracic vertebrae from other Neandertals and a sample of anatomically modern humans. Centroid sizes of El Sidrón vertebrae are within the human range. Neandertals have larger T1 and probably also T2. The El Sidrón vertebrae are similar in 3D shape to those of other Neandertals, which differ from *Homo sapiens* particularly in central-lower regions (T6-T10) of the thoracic spine. Differences include more dorsally and cranially oriented transverse processes, less caudally oriented spinous processes, and vertebral bodies that are anteroposteriorly and craniocaudally short. The results fit with current reconstructions of Neandertal thorax morphology.

Introduction

Recent research on fossil ribs has provided solid evidence for capacious dimensions of the Neandertal thorax (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014a, in revision; Bastir et al., 2015a). A recent three-dimensional (3D) assessment of rib size in Kebara 2 has shown that the ribs close to the diaphragm (ribs at levels 6–9) are larger than in modern humans, which is valid both absolutely as well as relative to body size (e.g., estimates of stature, García-Martínez et al., 2014a). Also, Neandertal rib shape differs from that of modern humans in a way that contributes to larger thorax capacity. Several researchers have observed an elongated midshaft of the ribs and also reduced torsion, suggesting a deep and wide chest in Neandertals (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; Bastir et al., 2012; Bastir et al., 2015a; García-Martínez et al., in revision).

The large chest is a characteristic feature of the short and wide shape of the stocky Neandertal body (Sawyer and Maley, 2005). Estimated average stature in Neandertals is low (165.9 cm) relative to their body mass estimates, which are comparatively high (72 kg) and associated with an estimated daily energy expenditure that is almost twice as high as in anatomically modern humans adapted to cold environments (Neandertal males: 5500 kcal d^{-1}; Inuit males: just below 3000 kcal d^{-1}; Churchill, 2014). In relation to this, the large thorax of Neandertals has been associated functionally with elevated oxygen consumption (Steegman et al., 2002; Churchill, 2006, 2014; Bastir, 2008).

In this sense, the large Neandertal thorax is the postcranial part of an overall large respiratory system, which is also reflected by the dimensions of their nasal and pharyngeal airways (Franciscus 1999; Rosas et al., 2006; Bastir, 2008, 2017; Bastir and Rosas, 2011, 2013, 2016). Thus, the craniofacial and postcranial parts together reflect the functional anatomy of a respiratory apparatus expected for a high-energy consuming and heavy-bodied hominin (Rosas et al., 2006a; Bastir, 2008; Churchill, 2014). However, hypotheses on the size and shape of the Neandertal chest (i.e., thorax capacity) cannot be addressed on the basis of rib morphology alone. This is because the rib cage is an anatomical complex, composed by ribs that are dorsally connected with the thoracic vertebrae at the costo -vertebral and -transverse joints, and ventrally with the sternum by the costosternal cartilages. Consequently, the size and shape of the thorax as well as its capacity depend on the size and shape of the ribs (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014a; Bastir et al., 2015a), the sternum (Gómez-Olivencia et al. 2012), and on the morphology of the thoracic vertebrae (Bastir et al., 2015b).

It has been suggested that greater dorsal orientation of the transverse processes together with proximal rib curvature increase the invagination of the thoracic spine within the ribcage in relation to evolutionary changes in locomotor function in early hominins (Jellema et al., 1993; Latimer and Ward, 1993; Ward et al., 2012). However, transverse process orientation could also be important for respiratory function. In *Homo sapiens*, the thoracic capacity of males is greater than in females, both absolutely and relative to stature (Silbernagl and Despopoulos, 1991; Bellemare et al., 2003, 2006; García-Martínez et al., 2016a). It has been shown recently that the larger male thoracic capacity can be related to a greater dorsal orientation of the transverse processes of their thoracic vertebrae, particularly the lower ones (T6-T9; Bastir et al., 2014). A more dorsal orientation of the rib attachment at the transverse processes rotates a given pair of ribs into a position that increases the medio-lateral diameters of the rib cage (Jellema et al., 1993; Latimer and Ward, 1993; Ward et al., 2012; Bastir et al., 2014), and when combined with longer ribs, greater dorsal orientation of the transverse process also increases the capacity of the thorax. Small angular variations could thus have large effects on thorax morphology. This geometric effect, together with the fact that Neandertal ribs are longer, particularly in the middle and lower thorax (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014a), allows us to establish the hypothesis that the greater thorax capacity in Neandertals is not only the result of rib elongation (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014a), but also of a greater dorsal orientation of the rib attachments at the transverse processes of thoracic vertebrae (Bastir et al., 2015b).

Arensburg (1991) and Been et al. (2010, their Fig. 3) already show illustrations and data suggesting strongly dorsally oriented transverse processes in thoracic vertebrae of the Kebara 2 Neandertal. Similar features can be observed in illustrations of other recent descriptions of thoracic vertebrae in Neandertals of Regourdou 1, La Chapelle-aux-Saints 1, or La Ferrassie 1 (Gómez-Olivencia, 2013a, b; Gómez-Olivencia et al., 2013a). These studies suggested further subtle and variable differences, such as greater laminae heights in the first and second thoracic vertebrae in La Ferrassie 1, shorter spinous processes in La Ferrassie 1 and Kebara 2 (Gómez-Olivencia, 2013a), and smaller median heights in some vertebral bodies (T7, T10, T11) of Regourdou 1 (Gómez-Olivencia et al., 2013a). Interestingly, median vertebral body height of T7 is similarly low in La-Chapelle-aux-Saints

1 and Kebara 2, and outside the minimum of the human reference sample as reported by Gómez-Olivencia et al. (2013a, their Table 5).

On the basis of this previous work, it has been proposed that “the overall vertebral size of the modern comparative samples are similar to that of the Neandertal male sample and that the differences found in only some of the variables suggest true morphological difference” (Gómez-Olivencia et al., 2013a:603). There is thus reason to expect differences between anatomically modern humans and Neandertals in their 3D vertebral architecture, that is, shape but not in size. However, 3D variation in thoracic vertebrae of other Neandertals has yet only been addressed in a preliminary way (Bastir et al., 2015b).

The Neandertal site from El Sidrón (Asturias, Northern Spain) dated to 49 ka (Rosas et al., 2006b, 2012) can potentially contribute to these questions. Over the past years, 15 fossil thoracic vertebral elements (Figs. 1 and 2) have been recovered at this site. These remains provide information that is relevant in the context outlined above, and some of these fossils (SD-1619, SD-1641, and Fig. 1) are complete enough to include them in comparative 3D geometric morphometric (3D-GM) analysis.

There are two aims to this study. First, we present and describe thoracic fossil remains of the El Sidrón Neandertal site. Second, a 3D-GM analysis is carried out addressing the hypothesis that the orientation of the transverse processes and vertebral body heights are involved in overall differences of 3D shape in Neandertal thoracic vertebrae when compared with modern humans.

Material and methods

The thoracic vertebral fossils from the El Sidrón site (Asturias, Spain) constitute a sample that ranges from fairly well preserved and undistorted vertebrae (Fig. 1) to more fragmented elements (Fig. 2). Following previous work on the Neandertal spine (Gómez-Olivencia, 2013a, b; Gómez-Olivencia et al., 2013a), the anatomical determination of the El Sidrón thoracic vertebrae relied on comparisons with complete modern human thoracic spines. Specifically, determination was based on observations of changes in shape, orientation, and size of different vertebral structures (e.g., transverse processes, articular facets, and demifacets) along the spine. We also followed previously used terminology for descriptions and anatomical determination of the Neandertal spine (Gómez-Olivencia, 2013a, b; Gómez-Olivencia et al., 2013a).

The first step in the determination process was to divide the vertebral remains into four groups based on degree of completeness: almost complete vertebrae (including parts of the arches, processes, and body of the same element), fragments including transverse process, fragments including laminae, and fragments of vertebral body. Each group was described separately.

The metric description followed measurements used and described by Gómez-Olivencia et al. (2013a). The age at death was only estimated through assessment of the degree of maturation of the thoracic vertebral epiphyses, following data for modern humans provided by Cardoso and Ríos (2011).

For the 3D-GM analysis, the comparative human data were obtained from 239 vertebrae from complete vertebral columns of 24 identified individuals (12 males and 12 females, one female lacked a third thoracic vertebra), ranging in age from 20 to 42 years. The bones belong to the identified skeletal collection curated at the School of Legal Medicine, Universidad Complutense de Madrid. The completeness and preservation of the skeletons from this collection is excellent and only the youngest skeletons were selected for study in order to avoid vertebral degenerative joint disease. Cases with other pathological conditions affecting the spine were also excluded. Only the first 10 thoracic vertebrae were selected for comparative study (Jellema et al., 1993; Latimer and Ward, 1993), as well as in order to collect the same landmarks in all vertebrae, including those located at the transverse costal facets, the presence of which at T11 and T12 is highly variable (Ríos and Cardoso, 2009; Cardoso and Ríos, 2011).

Landmark measurements

Forty-six 3D landmarks were measured per vertebra with a Microscribe G2 digitizer following the definitions of Bastir et al. (2014) that are depicted in Figure 3. Despite the excellent quality and preservation state of this osteological collection, a few landmarks were missing and estimated using multivariate regression methods as described in Bastir et al. (2014).

Measurements of the Neandertal vertebrae sample were obtained from 3D reconstructions of computed tomography (CT) scans of the original fossils. Medical CT-scans of the Kebara 2 male Neandertal were produced at the Sackler Faculty of Medicine of Tel Aviv University (General Electric, Discovery CT750 HD, 120kV, 1.25mm slice thickness, 1mm overlap) and that of La Chapelle-aux-Saints 1 and La Ferrassie 1 were provided by the Muséum National d'Histoire Naturelle (Paris; Philips iCT128; 120 kV; 0.625 mm slice thickness). Three-dimensional landmarks of the El Sidrón SD-1619 and SD-1641 vertebrae (Fig. 1) were measured on virtual models obtained by high-resolution surface scans. While Kebara 2, La Chapelle-aux-Saints 1, and La Ferrassie 1 individuals are assumed to be males (Arensburg, 1991; Gómez-Olivencia, 2013a, b), the El Sidrón vertebrae were not assigned to a given sex.

Viewbox 4.0 software (http://www.dhal.com) was used to digitize 3D landmarks on virtual models of the Neandertal thoracic vertebrae. The modern human reference sample was measured on real bones and the associated intra-observer error is reported in Bastir et al. (2014). The fossil samples were measured using virtual 3D models obtained from CT and surface scans. Landmarks measurements on real bone and 3D models based on clinical CT scans are comparable in geometric morphometrics as shown previously (Rosas et al., 2016). The comparability of landmark measurements taken on real bones and on 3D models obtained from surface scans was assessed here by producing a surface scan of one of the modern human vertebrae (T8 of individual Acc-62) that was physically digitized using a Microscribe G2 digitizer in Bastir et al. (2014) and by re-measuring the same 3D landmarks repeatedly on the virtual model of this bone.

Although nine out of 12 thoracic vertebrae are preserved in La Chapelle-aux-Saints 1 (Gómez-Olivencia, 2013b) only at levels T1, T2, and T8-T10, the overall geometry was considered complete enough, preserving parts of the body, neural arches, and processes, allowing for reasonable reconstructions of missing landmarks and 3D-GM analysis (see Supplementary Online Material [SOM] Table S1). Also in La Ferrassie 1, only vertebrae of the cranial part of the thoracic spine (T1-T3) could be analysed by 3D-GM despite preserving remains from T1-T4, T12, and five elements between T5 and T9 (Gómez-Olivencia, 2013a). Thus, most fossils required estimation of some missing landmarks except T7 and T9 of Kebara 2, which provided all structures for landmark measurements. The missing structures and landmarks of the fossil vertebrae and the methods of their estimations are listed in SOM Table S1. Following Gunz et al. (2009), we first exploited the symmetry of the object to estimate missing symmetric structures when one of the antimeres was preserved (transverse processes, demifacets, articular processes, or parts of the vertebral body). Specifically, we used reflected relabelling in order to estimate these missing symmetric structures by data of the same specimen (Mardia et al., 2000; Gunz et al., 2009). Reflected relabelling required all vertebrae of the entire sample to be symmetrized. For the estimation of unilateral missing landmarks at the mid-sagittal plane (e.g., spinous process and landmarks at the mid-sagittal plane of the vertebral body), we used a reference-based approach (Gunz et al., 2009). Thin plate spline (TPS) interpolations were applied to estimate missing landmarks with the most similar Neandertal vertebra (of the same level of another individual) as a source whenever possible. In absence of conspecific specimens from the same level, we used the mean shape of the corresponding modern human vertebral level as a source for the TPS estimation. This leads to statistically conservative reconstructions when compared with anatomically modern human data.

To address potential uncertainty in the positional assignment on the basis of morphological criteria of SD-1619 (T6 or T7) and SD-1641 (T3 or T4), these vertebrae were reconstructed twice. In the first reconstruction the fossils were reconstructed as if they belonged to level 3 for SD-1641 (labelled SD-1641-T3) and to level 6 for SD-1619 (labelled SD-1619-T6). In a second set of reconstructions we assumed level 4 for SD-1641 (labelled SD-1641-T4) and level 7 for SD-1619 (labelled SD-1619-T7; SOM Table S1).

Statistical analyses

Shape data were extracted as shape coordinates after generalized Procrustes registration and size was obtained as centroid size, the square root of the summed squared distances between the landmarks and their centroid (O'Higgins, 2000; Zelditch et al., 2012). Intra-observer error was tested by repeated landmark measurements on virtual models in a principal components analysis (PCA) and further analyzed by comparisons of Procrustes distances among these repeated measurements.

The Neandertal centroid sizes were compared with the 95% confidence intervals of the modern human males and of females separately. Shape data were analyzed first by a PCA of levels T3-T4 for comparisons with SD-1641-T3 and SD-1641-T4 and of levels T6-T7 for analysis of SD-1619-T6 and of SD-1619-T7. Then a PCA was performed on all levels between T3 and T7 to investigate the El Sidrón vertebrae with respect to changes in seriality. All PCAs were also subjected to regression analysis to statistically address the amount of variance explained by seriality (1000 permutations). Both quantitative reconstructions (SD-1619-T6 and SD-1619-T7; SD-1641-T3 and SD-1641-T4) were included simultaneously in all analyses.

Finally, we used permutation tests (N = 1000) to assess mean shape differences between thoracic levels T1 and T10 in Neandertals and in modern human males. Mean shape differences were quantified as Procrustes distances, defined as the square root of the summed square interlandmark distances after Procrustes registration (O'Higgins, 2000; Zelditch et al., 2012), at each vertebral level from T1 to T10. All shape analyses were carried out in MorphoJ-software (Klingenberg, 2011). EVAN Toolkit software (EVAN-Society, 2010) was used for 3D visualizations.

Results

Descriptive morphology and comparative analysis of the thoracic vertebral remains of El Sidrón.

The 15 thoracic vertebral specimens from El Sidrón represent 10 different vertebrae. This number was estimated by considering those specimens with preservation of overlapping regions from the right transverse process, pedicle, and dorsolateral corner of the body (SD-022, SD-719, SD-1050b, SD-1228, SD-1619, SD-1641, SD-1657, SD-1679, SD-1697, SD-1932). The estimation of the number of individuals represented by these vertebrae was based on the maturation state of the epiphyseal rings from the vertebral bodies and of the epiphyses from the tip of the transverse processes (Cardoso and Ríos, 2011). Complete fusion of the epiphyses from the transverse process was observed in five cases (SD-719, SD-1228, SD-022, SD-1050b, SD-1619), while absence of that epiphysis was observed in two cases (SD-1641, SD-1697), an incompatible maturation state within a single spine resulting in a minimum number of two individuals. Almost complete vertebrae are shown in Figure 1. Fragments including transverse process, fragments including lamina, and fragments of vertebral body are depicted in Figure 2. A metric study of the two most complete vertebrae (SD-1619, SD-1679) and of the rest of the vertebral fragments is presented in Tables 1 and 2, alongside age-at-death estimations based on thoracic epiphyses.

Vertebrae preserving body, neural arches, and processes

SD-1619 (Fig. 1) Almost complete vertebra, with postmortem absence of the upper left articular facet, the spinous process, and the caudal third of both lower articular facets. Both transverse processes are horizontal (their longitudinal axes are located in the transverse plane) and their cranial edges are located below the caudal edges of the upper right articular facets. The cranio-caudal diameter of both transverse processes is similar along their lengths. The outline of the cranial edges of both laminae presents a U shape with a horizontal plateau at the midline. In the vertebral body, both cranial demifacets are almost completely separated from the cranial body surface and are located on the lateral surface of the pedicles. Their shape is dorso-ventrally elongated. Both lower costal demifacets are almost completely separated from the caudal body surface. The vertebral body and endplate surfaces are intermediate in size, considering size variation within a modern human thoracic spine from T1 to T12. In cranial view, on the left side of the body, a clear aortic impression is present. Comparison of these features with modern human spines suggests an identification of this vertebra as T6-T7. The epiphyses from the transverse and spinous processes are completely fused, but the cranial and caudal epiphyseal rings are in active fusion. The cranial vertebral endplate presents a semicircular defect in its dorsal third.

SD-1641 (Fig. 1) Almost complete vertebra, with postmortem absence of the ventral half of the vertebral body and the tip of the spinous process. Both transverse processes are cranially oriented (especially the right one), with their cranial edges above the caudal edges of the upper articular facets. The cranio-caudal diameter of both transverse processes is larger at the lateral extreme than at the base. The outline of the cranial edges of both laminae presents a U shape. Both superior demifacets are lateral extensions of the cranial body surface and do not reach the pedicles in their most dorsal projection. Both inferior demifacets are cranio-lateral extensions of the caudal body surface. Comparison of these features with modern human spines suggests an identification of this vertebra as T3-T4. There is absence of fusion of the epiphyses from the transverse processes and cranial and caudal epiphyseal rings.

Fragments including transverse process

SD-719 (Fig. 2) Fragment consisting of the caudal part of the root and complete dorsal half of the spinous process, the right lamina with the lower articular facet, and most of the right transverse process. The transverse process is cranially oriented, as can be observed by the obtuse angle formed by its caudal edge and the lateral edge of the lamina (higher than in SD-1228). The lower articular facet is horizontally elongated. The spinous process projects horizontally with very limited caudal projection. There is almost no caudal extension of the lamina beyond the caudal edge of the lower articular facet. Comparison of these features with modern human spines suggests an identification of this vertebra as T1. The epiphyses of the right transverse process and the spinous process are completely fused.

SD-1228 (Fig. 2) Fragment consisting of the base of the spinous process, the right lamina and complete lower articular facet, caudal portion of the upper articular facet, right transverse process, and the base of the right pedicle. The transverse process is cranially oriented and above the caudal edge of the upper articular facet. The transverse process is projected more ventrally in comparison, for instance, with SD-1619. The cranio-caudal diameter of the transverse process is larger in the lateral extreme than at its base. The outline of the cranial edge of the left lamina presents a U shape. Comparison of these features with modern human spines suggests an identification of this vertebra as T2-T3. The epiphysis of the right transverse process is completely fused.

SD-1697 (Fig. 2) Fragment consisting of the right transverse process, right lamina, right upper and lower articular facets, dorsal half of the right pedicle, root of the spinous process, and medial portion of the left lamina. The transverse process is horizontal and its cranial edge is above the caudal edge of the upper articular facet. The cranio-caudal diameter of the transverse process is larger at the lateral extreme than at the base. The outline of the cranial edges of both laminae presents a U shape, with a horizontal plateau at the midline. Comparison of these features with modern human spines suggests an identification of this vertebra as T3-T4. There is lack of fusion of the epiphysis of the right transverse process.

SD-022 (Fig. 2) Fragment consisting of a complete right transverse process, right upper articular facet, most of the right pedicle, and the right dorso-lateral corner of the cranial vertebral body surface. The transverse process is cranially oriented, with its cranial edge above the caudal edge of the upper articular facet. The cranio-caudal diameter of the transverse process is larger at the extreme than at the base. The upper articular facet is horizontally elongated. The upper demifacet is a lateral extension of the cranial vertebral body surface with a clear dorsal projection, positioning the demifacet in the pedicle. Comparison of these features with modern human spines suggests an identification of this vertebra as T4-T6.The epiphysis of the right transverse process is completely fused, while the fragment of cranial epiphyseal ring is scored as active fusion/recent fusion.

SD-1050b (Fig. 2) Fragment consisting of an almost complete right transverse process, right upper articular facet, most of the right pedicle, and the right dorso-lateral corner of the cranial vertebral body surface. The orientation of the transverse process cannot be precisely described, but a horizontal projection above the level of the caudal edge of the upper articular facet is suggested. The cranio-caudal diameter of the transverse process is similar along its length. The upper demifacet is a lateral extension of the cranial vertebral body surface with a clear dorsal projection, positioning the demifacet in the pedicle. Comparison of these features with modern human spines suggests an identification of this vertebra as T5-T7. The epiphysis of the right transverse process is completely fused, while the fragment of epiphyseal ring is in active fusion. The dorso-ventral diameter or thickness of the transverse process is clearly smaller in comparison with the dimensions of the transverse processes of the other vertebrae from El Sidrón.

Fragments including lamina

SD-1446 (Fig. 2) Fragment consisting of the lateral part of the left lamina and the left lower articular facet. The preserved cranial edge of the lamina indicates a clear U shape outline. The shape of the articular facet is horizontally elongated with triangular shape. Comparison of these features with modern human spines suggests an identification of this vertebra as T1-T2, possibly T1.

SD-2222 (Fig. 2) Fragment consisting of the upper and lower left articular facets, the base of both the left lamina and pedicle, and the ventral half of the left transverse process. The cranial edge of the transverse process contacts the upper articular facet in its cranial third. The shape of both preserved upper and lower articular facets is horizontally elongated with triangular shape. Comparison of these features with modern human spines suggests an identification of this vertebra as T1-T2, possibly T1.The costal facet of the left transverse process is partially preserved.

SD-456 (Fig. 2) Fragment consisting of the root of the spinous process and the right lamina, with the medial third of the lower articular facet. The spinous process is horizontally oriented, with limited caudal extension of the lamina beyond the caudal border of the lower articular facet. Comparison of these features with modern human spines suggests a position of this fragment within the upper third of the thoracic spine (T1-T4).

SD-147 (Fig. 2) Fragment consisting of the left upper articular facet and most of the left pedicle. The cranial edge of the transverse process is inserted below the caudal edge of the upper articular facet. The preserved portion of the left upper demifacet is located on the lateral surface of the pedicle. Comparison of these features with modern human spines suggests a position of this fragment as middle thoracic, T4-T9.

SD-1657 (Fig. 2) Partially preserved neural arch consisting of the medial part of the left lamina, root of the spinous process, complete right lamina with upper and lower articular facets, base of the right transverse process, and part of the right pedicle. At its base, the cranial edge of the right transverse process is located below the caudal-most edge of the upper articular facet, suggesting a horizontal orientation of the transverse process. The transverse process is projected more dorsally in comparison, for instance, with SD-1619. The outline of the cranial edges of both laminae presents a V shape. The upper demifacet connects with the cranial vertebral body surface but it is located dorsally, on the lateral surface of the pedicle, and its shape is cranio-caudally elongated. Comparison of these features with modern human spines suggests an identification of this vertebra as T8-T9.

Fragments of vertebral body

SD-1932 (Fig. 2) Fragment consisting of the right dorso-caudal corner of the vertebral body with the base of the right pedicle. The lower demifacet is completely preserved and it is separated from the caudal vertebral body surface. Only the caudal half of the upper demifacet is preserved, but it can be said that it is well developed on the lateral surface of the body. There is a short distance between the edges of both demifacets (6.8 mm). Comparison of these features with modern human spines suggests an identification of this vertebra as T1. The cranial epiphyseal ring preserved at the dorso-caudal corner of the vertebral body is fused (postmortem breakage allows observing a sharply defined vertebral body border and empty space between the epiphyseal ring and the vertebral body surface).

SD-1428 (Fig. 2) Fragment consisting of the right ventro-lateral third of the vertebral body, with the ventral half of the upper right demifacet. At least the ventral half of the demifacet is located in the lateral surface of the vertebral body and its cranial border is slightly below the level of the cranial vertebral body surface. The vertebral body seems to present a transverse elongated shape. Comparison of these features with modern human spines suggests an identification of this vertebra as T1.The preserved fragments of the cranial and caudal epiphyseal rings are fused.

SD-1679 (Fig. 2) Fragment consisting of complete right pedicle, partial upper right articular facet, and ventral and right halves of the vertebral body. The preserved upper demifacet is a lateral extension of the cranial vertebral body surface, and the main feature is an almost vertical wall shared by both the body surface and the demifacet that creates a well-defined step just ventral to the proper pedicle. Comparison of these features with modern human spines suggests an identification of this vertebra as T2-T4. The caudal epiphyseal ring is in active fusion, while the cranial epiphyseal ring is absent, possibly postmortem.

Centroid size analysis

Centroid size of the El Sidrón and other Neandertals is shown in Table 3, while Table 4 shows the 95% range of modern human males and females. Figure 4 plots these data together for visual comparisons of the fossil and recent samples. In the first two thoracic segments, Neandertal vertebrae are mostly outside the 95% range of modern human males (except T2 of Kebara 2). T3 of Kebara 2 falls at the upper size limit of the modern male sample. The first thoracic vertebra in all Neandertals is particularly large compared with the human reference sample. At more caudal levels, centroid size is comparable to that of human males with La Chapelle-aux-Saints 1 being outside the human male range at T9 and T10. The El Sidrón vertebrae are within the male ranges of the modern human sample. SD-1641-T4 is smaller than modern males at this level. The modern human females are all considerably smaller than the males and the Neandertals.

Shape analysis: intra-observer error

Shape variation related to repeated measurement on the virtual model measured as Procrustes distance (PD) was very low (average PD = 0.009) and the largest difference due to measurement error between the data obtained from the real bone and from its virtual model was 0.048, which was almost 50% smaller than the smallest distance between two different real vertebrae (PD = 0.092). In correspondence with these small Procrustes distances, in a PCA (not shown) the virtual models plotted very closely to its physical counterpart indicating that different methods of landmark measurement produce very similar results. These results demonstrate quantitatively that methodological error is acceptable.

Shape analysis of the El Sidrón vertebrae

Figure 5a shows the principal components analysis of levels T3 and T4 to assess both reconstructions of SD-1641-T3 and SD-1641-T4 in a comparative context. Principal component (PC) 1 accounts for 19.9% of total variance, PC2 for 12.7%. The scatterplot indicates that the El Sidrón SD-1641-T3 reconstruction is close to the modern human T4 range and the SD-1641-T4 plots outside the corresponding modern human range. Also, La Ferrassie T3 is within the human T4 distribution and T3 of Kebara 2 at the limit of modern human T3 scores along PC1 and in the center of the human T4 range. Regression analysis of PC1 on serial position indicates that 28.2% of total variance is significantly ($p < 0.001$) related to seriality (no significant signal along PC2, $p < 0.09$, 5.75%). This PCA illustrates that the Neandertal vertebrae tend to plot one level inferiorly to the shape of the corresponding human level. Their shape differences follow the serial pattern. The warps associated with PC1 show relatively longer bodies, more dorsally and cranially oriented transverse processes, and slightly longer spinous processes towards positive PC1 scores.

Figure 5b shows the PCA of levels T6 and T7 to assess both reconstructions of SD-1619-T6 and SD-1619-T7 in a comparative context. Principal component 1 accounts for 21.7% of total variance, PC2 for 12.5%. In this analysis there is no statistical signal of seriality at all (regression of PC1 on serial position: 1.6% of total variance, $p < 0.38$; PC2: 0.01% of total variance, $p < 0.92$). Both reconstructions of El Sidrón and both Kebara 2 vertebrae fall outside the human PC1 range. Morphologically, PC1 shows relatively shorter (both antero-posteriorly and cranio-caudally) and medio-laterally wider vertebral bodies, more dorsally and more cranially oriented transverse processes, and more horizontally (less caudally) oriented spinous processes towards positive scores. At level T6-T7, interspecific differences are not associated with serial variation (Fig. 5b).

Figure 6 shows a similar picture but visualizing more directly the interaction between seriality and non-serial interspecific features between levels T3 and T7. Principal component 1 accounts for 24.1% of total variance, PC2 for 14.7% (Fig. 6a). Principal component 1 polarizes serial levels, with T3 plotting towards negative PC1 scores and T7 towards positive PC1 scores (95% confidence intervals of seriality are shown in SOM Fig. S1). Regression analysis reveals that serial shape change accounts for 67.46% of total variance ($p < 0.0001$) of PC1. No serial signal is detected along PC2 (0.83% of total variance, $p < 0.31$). On PC2, there is overlap between both species within more cranial vertebral levels and differences towards more caudal thoracic levels. Thus non-serial species-specific differences increase caudally.

Morphological features of serial shape change of the thoracic vertebrae are shown in Figure 6b. The relative antero-posterior length of the vertebral body increases from T3 approaching T7 and the spinous processes change from a more horizontal orientation to more caudal one. Cranio-caudally the transverse processes get relatively shorter and very slightly more dorsally oriented. The transverse costal facets are oriented laterally towards more superior levels of the thoracic spine and slightly more cranially at inferior levels of the spine (Fig 6b). Non-serial species-specific differences show up more clearly towards negative PC2 scores and caudal levels of the thoracic spine (i.e., positive PC1 scores) as a greater dorsal orientation of the transverse processes, relatively larger transverse costal facets, and more horizontally aligned spinal processes (Fig. 6c). The diverging serial trajectories in Figure 6a indicate also that patterns of serial shape change may differ in modern humans and Neandertals.

Differences in mean shape of thoracic levels 1–10 between Neandertals and modern human males

Mean shape comparisons (Table 5, Fig. 7) show interspecific differences in standardized anatomic views at each level. Table 5 further indicates an increase of shape differences towards more caudal vertebral levels of the thoracic spine. All shape differences (except at T5) are statistically significant at least at $p < 0.05$ (Table 5).

At T1, Neandertals show more sagittally oriented transverse costal facets, a relatively longer spinous process, and a relatively shorter (antero-posteriorly) vertebral body. The central part of the body is slightly higher in modern humans. At the T2 of Neandertals, both the spinous process and the body (antero-posteriorly) are relatively longer. From T3-T4 onwards, the transverse processes are oriented slightly cranially and they also become progressively more dorsally oriented. Also, the relative size of the transverse costal facets is larger than in modern humans. Central vertebral body heights are relatively reduced between T7 and T10 and the shape of these vertebral bodies, particularly between T8-T10, displays a more oval outline that is relatively wider than long when compared with the modern human means. Spinous processes between T6 and T10 are more horizontally oriented in Neandertals than in modern human males.

Discussion

This study presents new thoracic vertebral remains of the El Sidrón Neandertal site and uses geometric morphometric methods to compare the 3D spatial architecture of some of these vertebrae with those of other Neandertals and with a sample of anatomically modern humans. Recent comparative work has indicated growing evidence for differences in the morphological structure of the Neandertal vertebral column, not only in the morphology of cervical (Gómez-Olivencia et al., 2013b) and lumbar regions (Been et al., 2010), but also in thoracic vertebrae (Gómez-Olivencia, 2013a, b; Gómez-Olivencia et al., 2013a, Bastir et al., 2015b; Been et al., 2017a). For example, linear measurements could indicate greater cranio-caudal diameters of the laminae in upper thoracic vertebrae of La Ferrassie 1 (Gómez-Olivencia , 2013a) and slightly shorter spinous process lengths in mid and lower thoracic vertebrae in La Ferrassie 1 and Kebara 2 (Gómez-Olivencia , 2013a). However, such features were not observed in La Chapelle-aux-Saints 1 (Gómez-Olivencia, 2013b). In addition, slightly smaller vertebral body heights were found in some vertebrae of Regourdou 1 (T3, T7, T11) but not in other vertebrae of this individual, although at T7 the vertebral body heights are also small in Kebara 2 and La-Chapelle-aux-Saints 1 (Gómez-Olivencia et al, 2013a).

No clear general idea emerges from these previous comparisons, and also the linear measurements from the El Sidrón vertebrae do not contribute much to clarify this situation. Tables 1 and 2 show that measurements of specimens from the El Sidrón site are all within the ranges of other Neandertals, but also overlap with modern humans, as already shown by Gómez-Olivencia et al. (2013a) for the majority of measurements of their Neandertal sample. However, a classic metric comparative assessment with vertebrae from other Neandertals and from modern humans is beyond our objective; rather, metric data from El Sidrón are presented here to increase the available Neandertal vertebral record.

This situation gets a bit clearer when analyzing size and shape data obtained by the 3D landmark data collected here. In terms of centroid size, Table 3 shows that in most Neandertals (except Kebara 2) the upper thoracic vertebrae within T1-T2 are larger. Clearly, all first thoracic vertebrae are outside the modern human male range (). This could reflect developmental effects between thoracic and adjacent cervical segments

(McIntyre et al., 2007), because in Neandertals cervical vertebrae have been shown recently to be “mediolaterally wider and dorsoventally longer” (Gómez-Olivencia et al., 2013b:608). Such differences should translate into greater overall centroid sizes of Neandertal vertebrae in the cervico-thoracic transition, although cervical vertebrae still need to be investigated with 3D-GM.

At the cranial part of the thoracic spine (T1, T2) there may be reason to reject the hypothesis of similar sizes, whereas between T3 and T8 the Neandertal centroid sizes are within the human male range and thus in agreement with previous hypotheses of similar sizes (Gómez-Olivencia et al., 2013a). Also, in more caudal thoracic vertebrae, i.e., between T9-T10, Kebara is close to the upper 95% confidence interval and within the distribution of modern males (K2; Fig. 4). Only La-Chapelle-aux-Saints 1 plots outside. However, taphonomic and pathological alterations may influence these results, as noted already by Gómez-Olivencia (2013: 21b), although the “amount of pathological lesions in the thoracic spine” of La-Chapelle-aux-Saints 1 may be lower than previously assumed.

In terms of centroid size, we find evidence that upper thoracic vertebrae (T1-T2; might be larger in Neandertals than in anatomically modern humans, while in more central and caudal regions the hypothesis of similar overall sizes is supported. However, caution is necessary until more fossils and wider geographic ranges of *H. sapiens* are analyzed. With respect to the El Sidrón fossils, the analysis of centroid size (Fig. 4) supports an assignment of SD-1619 to a young (and not so large) adult and of SD-1641 to an adolescent individual. All reconstructions of vertebrae of El Sidrón are within the human range of centroid size. Interestingly, while vertebral body height SD-1619

(18.39mm) is within the modern human range of a published T7 sample (18.71 mm mean, ranging from 16.8–20.7mm; Gómez-Olivencia et al., 2013a, their Table 5), two other thoracic vertebrae from El Sidrón, SD-1641 (estimate: 15.29 mm) and SD-1679 (16.49 mm), are below and more similar to Regourdou 1, Kebara 2, and La Chapelle-aux-Saints 1 (Gómez-Olivencia et al., 2013a). This supports suggestions of these authors that low vertebral body height might be a Neandertal specific feature (Gómez-Olivencia et al., 2013a). Lateral views of the mean shapes in Figure 7 also indicate variable, but reduced, relative vertebral body heights between T6 and T10 and support their suggestions. The data on vertebral body height from the El Sidrón fossils, together with the geometric morphometric analyses presented here, also statistically support a recent virtual reconstruction of the lumbar and thoracic part of the Kebara 2 spine (Been et al., 2017a), which is considerably shorter in vertical height, at least in comparison with a modern human individual.

In a more general morphological framework, the current study addressed the hypothesis that the enlarged thorax of Neandertals is not only the result of larger ribs (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014a, Bastir et al., 2015a), but also of a more dorsal orientation of the transverse processes of the thoracic vertebrae (Bastir et al., 2015b). A similar kind of influence of vertebral shape on rib cage morphology has been proposed in *Australopithecus* (Ward et al., 2012) and *Homo ergaster/erectus* (Jellema et al., 1993; Latimer and Ward, 1993), and more recently also identified as a geometric feature of modern human sexual dimorphism (Bastir et al., 2014; García-Martínez et al., 2016a). Shape data of both El Sidrón (SD-1641-

T3, -T4; SD-1619-T6, -T7) vertebral reconstructions available for 3D analysis (Figs. 5 and 6), together with the morphological descriptions of the more fragmentary El Sidrón thoracic sample described above and shown in Figure 2, shed more light on this issue. Our results clearly suggest that Neandertal thoracic vertebrae, including specimens SD-1619 and SD-1641 (Figs. 1, 5, 6), but also SD-719, SD-1050b, and SD-1657 (Fig. 2) from the El Sidrón sample, are characterized by strongly posteriorly oriented transverse processes. This is particularly evident in the geometric morphometric comparisons with the modern human reference sample and fits with images of T10 of Regourdou 1 (Gómez-Olivencia et al., 2013a) and T12 of Kebara 2 (Been et al., 2010), and images presented in Gómez-Olivencia (2013a, b) as well as images presented by Arensburg (1991).

Clearly, dorsal orientation is also a feature of seriality that increases cranio-caudally, as shown in Figures 5 and 6 and previously in other studies (Jellema et al., 1993; Latimer and Ward, 1993; Ward et al., 2012, Bastir et al., 2014), and could potentially contribute to confusing serial and interspecific differences. However, in our analyses, serial variation has been quantitatively controlled for (Figs. 5 and 6) and is a priori absent in the mean shape comparisons (Table 5, Fig. 7), assuming correct serial assignments in the fossils. Thus, we propose that difference in transverse process orientation between Neandertals and the modern human reference sample likely reflects true species differences. These species-specific differences may have a serial developmental genetic signal in more cranial levels T3-T5 (McIntyre et al., 2007), and may involve features less related to seriality in central-lower parts of the thoracic spine. Although more research is necessary in this respect, differences in transverse process orientation may add to the reduced vertebral body heights shown already in other studies (Gómez-Olivencia et al. 2013a; Been et al., 2017a).

All mean shape analyses indicate statistically significant differences (except T5) in the sum of their geometric features, not only regarding the orientation of the transverse processes. Figure 7 shows also slightly greater relative antero-posterior vertebral body lengths in Neandertals along levels T2-T7. Gómez-Olivencia et al. (2013a) found greater dorso-ventral length at the body of T2 in Regourdou 1. On the other hand, between levels T8 and T10 these lengths become relatively shorter again in Neandertals (Fig. 7), which contribute to differences in general vertebral shape (Table 5).

Also, the relative sizes of the transverse costal facets seem to differ between Neandertals and humans (Fig. 6c). These features are compatible either with greater rib size in Neandertals in general (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014a) or with particularly larger articular rib tubercles (Franciscus and Churchill, 2002). García-Martínez et al. (2014b, 2016b; in revision) have observed greater articular tubercles in the El Sidrón costal skeleton and discussed this in a biomechanical context. Furthermore, the more sagittal and slightly cranial orientation of the transverse costal facets (Figs. 1, 2, 6c) might indicate subtle biomechanical differences in breathing kinematics in Neandertals. Sagittal-cranial orientation of these facets facilitate vertical and oblique gliding movements, allowing for greater medio-lateral expansions (Bastir et al., 2017), particularly in combination with longer ribs possibly in response to greater diaphragmatic action on central and lower parts of the thorax (T7-T10; Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014a; Bastir et al., 2015a). All these aspects are compatible with bio-energetic arguments related to greater muscle and body mass estimates in Neandertals.

The more horizontally oriented spinous processes could indicate a thicker layer of epaxial muscles, particularly those of the transverso-spinalis and longissimus group in Neandertals, and possibly differences in muscle morphology and biomechanics. A similar feature was observed in the spinous processes of KNM-WT 15.000, where Jellema et al. (1993) discussed these differences in terms of muscle morphology and biomechanical changes. “More horizontally oriented spinous processes have the effect of deepening the vertebral gutter,” which “would also increase the moment arm of the associated musculature” (Jellema et al., 1993:286–287). Again, thicker muscle layers would fit with greater estimated body and muscle mass and the associated bioenergetic aspects (Churchill, 2014).

The less caudal orientation of the spinous processes in the thoracic vertebrae fits with findings reported by Gómez-Olivencia et al. (2013b), who observed longer and more horizontally oriented spinous processes in cervical vertebrae. These authors discussed spinous process length and orientation in relation to biomechanics of cranial posture and cranial morphology. Occipital morphology differs considerably between Neandertals and modern humans (Bastir et al., 2010) and parts of these differences relate to the head-neck muscles. It seems therefore that a common axial muscular factor links the orientations of the spinous processes of lower cervical vertebrae and thoracic vertebrae with specific functional implications in the cervical areas, associated with head-neck relations, and in the thoracic areas, associated with postural stability.

Similar to Jellema et al. (1993) and Ward et al. (2012), spinous process orientation was linked with biomechanical implications in lumbar vertebrae with respect to spine leverage (Been et al., 2010) because greater horizontal projection increases the moment arms of erector spinae muscles attaching to them. These authors suggest further that greater horizontal orientation implies less “imbrication” and thus greater mobility. Interestingly, Been et al. (2010, 2017a) also find a more cranial orientation of the transverse processes of lumbar vertebrae in Neandertals similar to the cranial orientation of the transverse processes of the thoracic vertebrae (Fig. 7). This coincidence might suggest systemic effects of erector spinae musculature between thoracic and lumbar segments similar to the shared horizontal orientations of the spinous processes in lower cervical (Gómez-Olivencia et al., 2013b) and thoracic vertebrae.

From a structural point of view, the greater dorsal orientation of transverse processes at the thoracic spine may indicate its greater overall invagination within the ribcage. Similar propositions were made in the context of early hominins, although in the context of changing features in locomotor evolution (Jellema et al., 1993; Latimer and Ward, 1993; Ward et al, 2012). Morphologically, these arguments would also apply to Neandertals, possibly in relation to posture. A more anterior position of the thoracic part of the spine within the ribcage should be accompanied by corresponding adjustments of lumbar parts of the Neandertal spino-pelvic alignment (Been et al., 2014, 2017b). Positional variations of the spine affect the demands on the global muscles to provide postural stability (Wagner et al., 2012) and the altered spinous processes of the thoracic vertebrae contribute to this stability as mentioned above. It has been proposed that the sacrum of Neandertals is more vertically oriented within the pelvis and possibly located more anteriorly (Been et al., 2014, 2017a, b). These differences in position may influence indirectly the position of the thoracic part of the spine within the ribcage, and thus contribute to increased invagination and different spine biomechanics. These factors likely account for the covariation between the orientations of the transverse and spinous processes reported here. Future studies should address these questions in the context of the entire spine and cannot be addressed using the data from the current study.

While the present study provides findings important for understanding Neandertal thorax form and function, caution is also necessary because of several limitations. One limitation relates to the modern human reference sample. Because intraspecific variation in 3D thoracic vertebral shape of *H. sapiens* is not well known, the hypothesis that reported differences in vertebral structure are taxonomically relevant will need further comparison with heterogeneous comparative samples. Gómez-Olivencia et al. (2013a: 596) propose that "Neandertals are significantly different in having small ventral and median heights of the vertebral body", specifically at T11. This implies taxonomic differences. Because differences in vertebral body heights are also present in other thoracic levels and accompanied by differences in overall body morphology and the orientations of transverse and spinous processes, potential taxonomic relevance of the shape differences can be assumed.

A further important limitation is the very small sample and fragmentary nature of thoracic vertebrae. We excluded badly preserved vertebrae of La Ferrassie 1 and La-Chapelle-aux-Saints 1, following detailed descriptions of Gómez-Olivencia (2013a, b), but pathology, taphonomy, and uncertainty in serial assignments could influence aspects of shape variations interpreted here. Most fossils required at least some landmark estimations and reconstructions (SOM Table S1). Because Kebara 2 is one of the most complete individuals, using these data for reference-based reconstructions (Gunz et al., 2009) might bias our interpretations by disregarding Neandertal intraspecific variability. Ideally, less fragmented or less deformed thoracic vertebrae should be analyzed. Fortunately, some of the new thoracic vertebral fossils from the El Sidrón site provide further evidence for potential Neandertal features, including a more dorsal orientation of the transverse processes, a sagittal orientation of larger transverse costal facets (SD-1619, SD-1641, Fig. 1; SD-1657, Fig. 2), and reduced body height at T7 in two out of three fossils.

Future studies should expand the comparative samples both at intraspecific adult and subadult levels to enhance our understanding of geographic, ontogenetic, and interspecific variation of thoracic vertebral structure. This will produce a better idea of the taxonomic relevance of the 3D morphological characteristics of the thoracic vertebrae in human evolution.

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Table 1. Raw dimensions (in mm) from the two most complete vertebrae from El Sidrón, following the measurements described by Gómez-Olivencia et al. (2013a).[a]

Measurement	**SD-1619**	**SD-1641**
Identification	T6-T7	T3-T4
Age estimation (years)	14-27	≤ 17
Maximum transverse diameter (MaxTrDi)	58.53	55.99
Superior transverse diameter (SupTrDI)	27.52	31.19
Inferior transverse diameter (ITrDi)	32.14	30.79
Canal dorsoventral diameter (M10)	14.96	14.41
Canal transverse diameter (M11)	14.86	14.31
Body ventral craniocaudal diameter (M1)	20.88	-
Body dorsal craniocaudal diameter (M2)	21.91	17.66
Body median craniocaudal diameter (M3)	18.39	(15.29)
Body superior dorsoventral diameter (M4)	25.36	-
Body inferior dorsoventral diameter (M5)	26.69	-
Body superior transverse diameter (M7)	29.57	-
Body inferior transverse diameter (M8)	32.53	(29.5)
Pedicle craniocaudal diameter (PedCrCdDi)	11.25/11.04	11.03/11.37
Pedicle transverse diameter (PedTrDi)	5.80/6.79	6.26/5.89
Articular pillar bi-articular diameter (BiArtDi)	-/-	31.25/30.25
Transverse process maximum length (TrPrMaxLe)	29.25/30.74	26.28/25.74
Upper articular facet sagittal diameter (UFaSgDi)	13.97/-	11.05/-
Upper articular facet transverse diameter (UFaTrDi)	8.12/-	10.63/10.45
Lower articular facet sagittal diameter (LwFaTrDi)	-/-	9.1/10.14
Lower articular facet transverse diameter (LwFaTrDi)	9.26/9.78	10.45/11.18
Laminae craniocaudal diameter (LamCrCdDi)	-/-	18.19/17.22
Laminea thickness (LamTh)	7.3/7.27	6.4/6.59

[a] For age estimation, the degree of fusion of the vertebral epiphyses from Cardoso and Ríos (2011) was used. Note that SD-1641 is an immature vertebra lacking fusion of cranial and caudal epiphyseal rings, and the epiphyses of both transverse processes. In comparison with values from fully mature vertebrae, measurements from these vertebrae (especially those including the body and transverse processes) can be considered an

underestimation of their respective adult values. Values between parentheses are estimates. Cells that contain two entries are for the right and left sides (right/left). M = Martin number.

Table 2. Raw dimensions (in mm) from the vertebral fragments from El Sidrón, following the measurements described by Gómez-Olivencia et al. (2013a).[a]

Measurement	SD-1428	SD-1932	SD-719	SD-2222	SD-1446	SD-456	SD-1228	SD-1679	SD-1697	SD-022	SD-147	SD-1050b	SD-1657
Identification	T1	T1	T1	T1-T2	T1-T2	T1-T4	T2-T3	T2-T4	T3-T4	T4-T6	T4-T9	T5-T7	T8-T9
Age (years)	≥18	14–21	≥17	≤21	-	-	≥15	15–24	≤ 17	≥ 15	-	14–27	-
M1	-	-	-	-	-	-	-	18.37[b]	-	-	-	-	-
M3	-	-	-	-	-	-	-	16.49	-	-	-	-	-
PedCrCdDi	-/-	-/-	-/-	-/-	-/-	-/-	-/-	11.22/-	-	11.94/-	-/-	11.8/-	14.73/-
PedTrDi	-/-	-/-	-/-	-/-	-/-	-/-	-/-	7/-	6.5/-	7.07/-	-/-	6.6/-	7.6/-
BiArtDi	-/-	-/-	-/-	-/29.97	-/-	-/-	-/-	-/-	32.94/-	-/-	-/-	-/-	38.13/-
TrPrMaxLe	-/-	-/-	-/-	-/-	-/-	-/-	26.63/-	-/-	26.82/-	30.72/-	-/-	(31.8)/-	-/-
UFaSgDi	-/-	-/-	-/-	-/13	-/-	-/-	-/-	-/-	13.9/-	12.78/-	-/-	11.85/-	13.27/-
UFaTrDi	-/-	-/-	-/-	-/14	-/-	-/-	-/-	(9.34)/-	12.81/-	11.19/-	-/-	10.47/-	9.33/-
LwFaTrDi	-/-	-/-	11.41/-	-/13.83	-/14.19	-/-	11.18/-	-/-	12.39/-	-/-	-/-	-/-	13.28/-
LwFaTrDi	-/-	-/-	11.84/-	-/13.46	-/15.17	-/-	10.59/-	-/-	12.27/-	-/-	-/-	-/-	12.08/-
LamCrCdDi	-/-	-/-	-/-	-/-	18.63	17.69	18.9	-/-	17.23	-/-	-/-	-/-	19.63
LamTh	-/-	-/-	7.05	-/-	6.72	5.69	5.56	-/-	5.83/5.71	-/-	-/-	-/-	5.86

[a] For age estimation, information from Cardoso and Ríos (2011) was used. Values between parentheses are estimates. Cells that contain two entries are for the right and left sides (right/left).

[b] The caudal epiphyseal ring presents active fusion, while the cranial epiphyseal ring is absent. Abbreviations defined in Table 1.

Table 3. Centroid sizes of Neandertal vertebrae.[a]

Level	**El Sidrón**	**Kebara 2**	**La Chapelle-aux-Saints 1**	**La Ferrassie 1**
T1		173.53	174.07	168.46
T2		158.26	166.33	165.27
T3	148.36[b]	154.48		150.61
T4	145.18[c]	154.53		
T5		155.74		
T6	158.88[d]	158.88		
T7	159.17[e]	163.68		
T8		162.29	162.56	
T9		165.00	183.20	
T10		167.52	179.07	

[a] Underlined values indicate Neandertal centroid sizes outside the range of the human male reference sample (shown in Table 4).

[b] SD-1641 estimated as T3

[c] SD-1641 estimated as T4

[d] SD-1619 estimated as T6

[e] SD-1619 estimated as T7

Table 4. Mean centroid sizes and 95% confidence intervals of modern human male and female vertebrae.

Level	**Male mean**	**95%-**	**95%+**	**Female mean**	**95%-**	**95%+**
T1	160.77	157.38	164.15	146.49	143.90	149.09
T2	155.50	152.12	158.89	140.58	137.99	143.18
T3	150.97	147.58	154.36	135.74	133.03	138.45
T4	150.36	146.97	153.74	136.53	133.94	139.13
T5	153.05	149.66	156.43	138.58	135.99	141.18
T6	157.49	154.11	160.88	142.43	139.84	145.03
T7	159.51	156.13	162.90	143.85	141.26	146.45
T8	161.22	157.84	164.61	145.15	142.55	147.74
T9	162.33	158.94	165.71	146.11	143.52	148.71
T10	165.35	161.96	168.74	150.16	147.56	152.75

Table 5. Mean shape differences between modern human and Neandertal male vertebrae in Procrustes distance (Pd; *p*-values calculated from 1000 permutations).

Level	**Pd**	***p*-value**	***n***
T1	0.124	0.002	3
T2	0.094	0.011	3
T3	0.106	<0.001	3
T4	0.123	0.006	2
T5	0.131	0.090	1
T6	0.126	0.010	2
T7	0.141	0.010	2
T8	0.134	<0.001	2
T9	0.145	0.004	2
T10	0.175	0.005	2

Figure legends

Figure 1. The two most complete thoracic vertebrae from El Sidrón. On the left, cranial (top) and lateral left (bottom) views of SD-1619 are presented. In this vertebra, identified as T6-T7, the dorsal orientation of the transverse processes, together with the sagittal orientation of the facets for the rib tubercle, can be observed (see text for discussion of these features). On the right, cranial (top) and lateral right (bottom) views of SD-1641 are presented. In this vertebra, identified as T3-T4, there is lack of fusion of the epiphyses of the transverse processes, but a sagittal orientation of the immature surfaces on the tip of the transverse processes can be observed (especially on the right side). Scale bar equals 10 mm.

Figure 2. Vertebral fragments from El Sidrón; see Tables 1 and 2 for vertebral number identification. Top: Fragments with transverse process. The five fragments correspond to the right side and are presented in cranial view, ordered from T1 (SD-719) on the left to T5-T7 (SD-1050b) on the right. The dorsal orientation of the transverse processes and the sagittal orientation of the transverse costal facets can be observed. Middle: Fragments including lamina. The five fragments are presented in ventral view, ordered from T1 (SD-1446) on the left to T8-T9 (SD-1657) on the right. Bottom: Fragments of vertebral body. The three fragments are presented in two views, cranial and lateral right, ordered from T1 (SD-1932) on the left to T2-T4 (SD-1679) on the right. Scale bar equals 10 mm.

Figure 3.Thoracic vertebra and 3D landmarks as per Bastir et al. (2014). a) Cranial view, b) caudal view, c) frontal view, and d) left lateral view.

Figure 4. Centroid size comparisons. X-axis shows different vertebral levels from T1 to T10; y-axis shows means and 95% confidence intervals of vertebrae of modern human males (solid lines) and females (dashed lines) and Neandertals. K = Kebara 2, C = La-Chapelle-aux-Saints 1, F = La Ferrassie 1, S = El Sidrón (SD-1641 in comparison of T3, T4; SD-1619, in comparison of T6, T7).

Figure 5. Principal components analyses of El Sidrón reconstructions. a) Comparisons of SD-1641-T3 and SD-1641-T4. The scatterplot of PC1 (19.9% total variance) and PC2 (12.7% total variance) illustrates shape distributions of T3 and T4 along PC1 and relations to other Neandertal vertebrae and *Homo sapiens*. LaFe_3 = T3 of La Ferrassie 1, K2_3 = T3 of Kebara 2, K2_4 = T4 of Kebara 2. Note that the Neandertal vertebrae belonging to level T3 fall within the human T4 range and the Neandertal T4 vertebrae fall outside the human T4 range. Three-dimensional models show associated shapes. b) Comparisons of El Sidrón SD-1619-T6 and SD-1619-T7. The scatterplot of PC1 (21.7% total variance) and PC2 (12.5% total variance) illustrates shape distributions of T6 and T7 along PC1 and relations to other Neandertals and *H. sapiens* K2_6 = T6 of Kebara 2, K2_7 = T7 of Kebara 2. There is no statistical signal of shape variation related to serial position in these PCs. The Neandertals fall outside the modern human ranges of T6 and T7, which overlap to a great extent. 3D models show shapes associated to PC1. The scale factor of 3D warps in both PCA visualizations is the magnitude of the shape change as a Procrustes distance corresponding to Procrustes distances of -0.1 and +0.1 along PC1.

Figure 6. Principal components analysis of the thoracic spine between levels T3-T7. a) The scatterplot of PC1 (24.1% total variance) and PC2 (14.7% total variance) illustrates

diverging trajectories of serial shape change in modern humans and Neandertals. Polygon marks the Neandertal range. Principal component 1 carries a strong serial signal (indicated by regression analysis, see also SOM Fig. S1). Principal component 2 shows interspecific trends that increase towards positive PC1 scores. Shape changes associated with PC1 (b) and PC2 (c) are depicted in (b) and (c). Serial shape changes along PC1 include increase in vertebral body length, increasingly caudally oriented spinous processes and transverse processes that become slightly shorter, and slightly more dorsally oriented and cranially oriented transverse costal facets. Interspecific shape changes along PC2 include transverse processes that are markedly more dorsally and cranially oriented, with more cranially facing and slightly larger transverse costal facets, slightly less caudally oriented spinous processes and relatively shorter vertebral bodies with very slightly decreased central body height towards negative PC2 scores, a range that is occupied by Neandertals.

Figure 7. Mean shape differences at each vertebral level between the modern human males (blue) and the Neandertal (green) samples in standardized anatomical views. Note that the Neandertal sample sizes varied among the different levels. At T5, Neandertal shape is from one individual only (Kebara 2), while between levels T1 and T3 mean shapes are composed of three individuals and between T6 and T10 of two individuals.