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

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ABSTRACT

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

RESUMEN

El estudio del tórax Neandertal ha atraído el interés de la comunidad científica por más de un siglo. Existe acuerdo acerca de la mayor capacidad torácica en Neandertales en comparación con humanos modernos. Sin embargo, si esto es causado por una expansión antero-posterior o medio-lateral del tórax es debatido a día de hoy y es clave para el entendimiento de la biomecánica respiratoria y la morfología corporal en Neandertales. La frágil naturaleza de las costillas, la estructura metamérica del tórax y las dificultades en la cuantificación morfológica contribuyen a la incertidumbre en referencia a aspectos de la morfología torácica Neandertal. El yacimiento de El Sidrón ha proporcionado elementos costales que comprenden desde el tórax superior hasta el inferior, así como diferentes restos costales proximales (frecuentemente ausentes en el registro fósil Neandertal), los cuales pueden arrojar luz sobre esta incertidumbre. Nosotros

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comparamos las costillas de El Sidrón con costillas de humanos modernos actuales, así como con humanos modernos fósiles y otros Neandertales, a través de técnicas de morfometría clásica y morfometría geométrica 3D, combinadas con técnicas de estimación de datos perdidos y de reconstrucción virtual (a nivel de 1ª, 5ª y 11ª costilla). Nuestros resultados muestran que los Neandertales presentan cabezas costales y tubérculos articulares más grandes que humanos modernos. A nivel de tamaño global de las costillas, las 1ª costillas Neandertales son más pequeñas que las de humanos modernos, mientras que las 5ª y 11ª son considerablemente más grandes. Cuando articulamos costillas medias (forma y tamaño) con sus correspondientes elementos vertebrales, nosotros observamos que el tórax Neandertal presenta una expansión medio-lateral en los diferentes niveles estudiados con respecto a humanos modernos, aunque esto es más evidente a nivel T5 y T11. Por lo tanto, a la luz de la evidencia proporcionada por los restos costales de El Sidrón, nosotros hipotetizamos que la expansión volumétrica Neandertal propuesta por autores previos, debería ser fundamentalmente producida por una expansión medio-lateral del tórax.

1. Introduction

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

Notwithstanding the importance of rib cage anatomy, morphological variation in the thorax has received much less attention than other cranial and postcranial regions (Gómez-Olivencia et al., 2009). Thus, thoracic variation in fossil hominin species and its paleobiological implications are still not clear. This is mainly the result of: 1) the fragile nature of thoracic elements (ribs and vertebrae), which means that they usually appear broken or taphonomically distorted in the hominin fossil record; 2) the metameric structure of the rib cage and the fact that the whole thorax (ribs and vertebrae) is rarely found, usually requiring thorax morphology to be inferred from a small number of anatomically isolated and distorted elements; and 3) quantifying the complex three-dimensional (3D) curvature of the costal elements with linear measurements such as chords, angles or diameters potentially complicates interpretation of fossil thorax morphology.

1.1. Historic perspective on the study of the Neanderthal ribcage

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

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

Similar quantitative studies using traditional measurements such as arcs, chords or angles have subsequently been performed, resulting in very complete and detailed comparative studies of Neanderthal ribs, improving the understanding of Neanderthal rib cage morphology greatly (Franciscus and Churchill, 2002;