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Comparison of the rib bone density in *Homo sapiens* and *Pan troglodytes*: implications for the interpretation of the *Australopithecus africanus* ribcage

Comparación de la densidad ósea en costillas de *Homo sapiens* y *Pan troglodytes*: implicaciones para la interpretación de la caja torácica de *Australopithecus africanus*

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Abstract

Like many other anatomical structures, the rib cage has changed its morphology and configuration throughout primate evolutionary history. The evaluation of the bone density at an intraspecific level is informative about the function of the upper and lower thorax, whereas the variation of the midshaft rib bone section at an interspecific level could also explain potential biomechanical changes during evolution. We assessed this issue through the study of the internal rib microstructure via microCT of three ribs from *Australopithecus africanus* Sts-14 and the complete set of ribs of ten modern humans and ten chimpanzees. Our results show that the rib bone section differs both at intraspecific and interspecific levels. Thus, the most robust ribs (1 and 11-12) have strong muscle insertions in the three studied taxa, which could give them resistance to mechanical stress. In addition, the ribs with the highest mineral percentage are those belonging to *Pan troglodytes* and *Australopithecus africanus*, which are very similar to each other. This similarity could hypothetically imply strong loadings on their ribs, but also similar rib or even thorax morphologies. Future research should study the covariation between costal bone density and rib morphology.

Keywords: Biomechanics, rib cross section, thorax morphology, compartmentalization index, microCT.

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1. Introduction

From an evolutionary perspective, the rib cage has changed largely in morphology and number of metamers within the order Primates (Hofer *et al.*, 1961). The rib cage in African great apes has been defined as “funnel-shaped”, narrow in the cranial part and wide in the caudal part. On the contrary, the so-called “barrel-shaped” ribcage of *Homo sapiens* is more globular (Thompson *et al.*, 2015; Latimer *et al.*, 2016; Bastir *et al.*, 2017a), being relatively expanded in the cranial part and narrower in the caudal one. More specifically, the chimpanzee ribs do not demonstrate

a torsion along the rib corpus and have more circular cross sections than those of modern humans (Latimer *et al.*, 2016).

Even though these features have been studied for a long time for living species, less evident aspects are known from an evolutionary perspective. The issues are that fossil costal elements tend to be broken and a whole set of ribs is rarely preserved in the fossil record (Carretero *et al.*, 1999). Both reasons imply that the methodology to be used must be as minimally invasive as possible, so that the scarce material found is not damaged, and sufficiently reliable to obtain

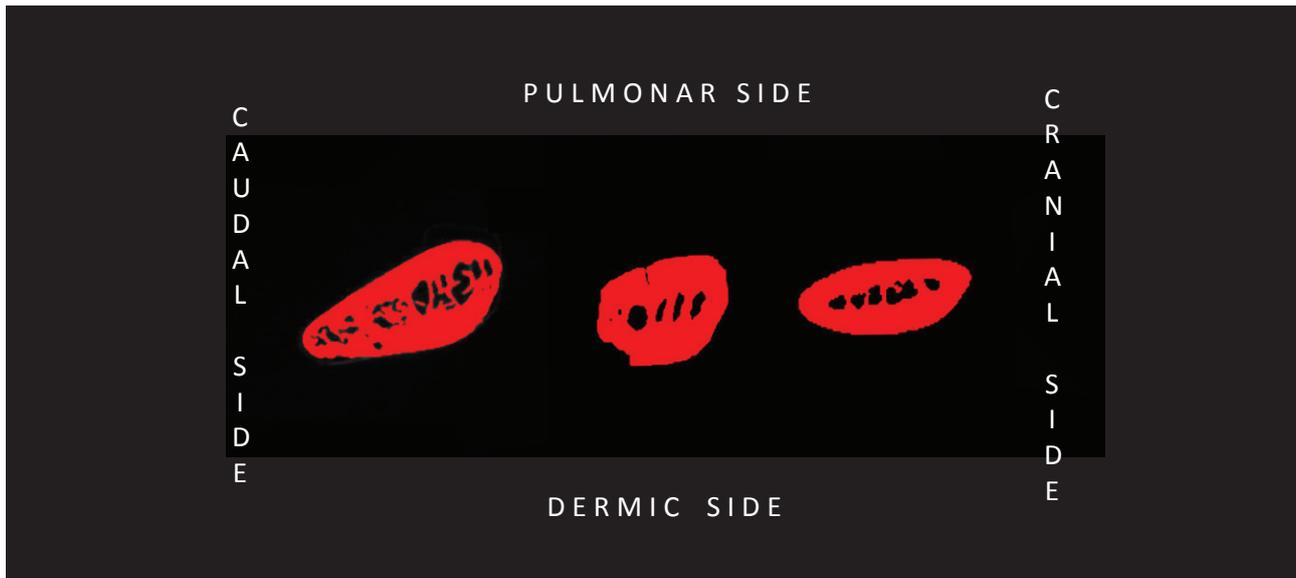


Fig. 1. -Mid-cross-sectional morphology of *Homo sapiens* twelfth rib (left) compared to *Pan troglodytes* twelfth rib (right) and *Australopithecus africanus* Sts-14 lower thorax rib (middle). Differences are clearly appreciated regarding the mineral content (bone = red). *Pan troglodytes* and *Australopithecus africanus* ribs present a larger mineral composition than their *Homo sapiens* counterparts.

representative results in fragmentary assemblages.

These premises have made micro computed tomography (microCT) scanners and geometric morphometrics the best tools for the analysis of complex costal variations for extant modern humans (Beresheim *et al.*, 2019; Holcombe *et al.*, 2019), but its use in human evolution is yet unexplored.

The study of rib curvature and its degree of torsion using the above-mentioned techniques could provide relevant information about morpho-functional changes in hominid species related to ventilatory mechanics (Bastir *et al.*, 2017b). In addition, recent research also points out an interesting evolutionary and ontogenetic covariation between mineralized area percentage (% Md.Ar) at the rib midshaft and the entire rib morphology in hominins (García-Martínez *et al.*, 2017, 2018). This fact might be a mechanic response to a relationship between ribs and muscles forces, as well as metabolic needs at evolutionary and ontogenetic levels (Beresheim *et al.*, 2019).

In this framework, it has been hypothesized that circular rib cross sections, such as those observed in chimpanzees and probably *Australopithecus*, have larger % Md.Ar than ribs with medio-laterally flattened cross sections, which are typical of modern humans (Latimer *et al.*, 2016). However, to the best of our knowledge, this hypothesis has never been tested before.

Therefore, the aim of this study is to analyze if there is any variation in the % Md.Ar in the ribs mid-section of *P. troglodytes* and *H. sapiens* and, if so, what kind of biomechanical implications it may have.

In this comparative framework, we also analyze ribs of the genus *Australopithecus* to check whether the % Md.Ar of the middle section of its ribs is closer to that of chimpanzees or anatomically modern humans, and infer its morphology and biomechanical properties.

2. Material and methodology

To carry out this study, the complete set of ribs of twenty adult individuals lacking of macroscopic evidence of alteration or pathological change was selected: ten *Homo sapiens* (120 ribs) and ten *Pan troglodytes* (130 ribs). We also included three ribs of *Australopithecus africanus* Sts-14 (Thackeray *et al.*, 2002), whose costal level was not found in all the available literature and it is tentatively assessed in this work.

All ribs were scanned by means of high-resolution micro-focus X-ray tomography (microCT). The ribs of modern humans and chimpanzees were imaged at the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH) and the American Museum of Natural History (AMNH) facilities, respectively, using a V|Tome|X s 240 equipment (by GE Sensing & Inspections Technologies), with a resolution 100 microns and a voltage of 140V. The fossil ribs of *A. africanus* Sts-14 were scanned at the South African Nuclear Energy Corporation (NECSA) by a Nikon XTH 225 ST equipment. The final volumes were reconstructed and saved in DICOM.

Using Amira 5.4.0 software (Stalling *et al.*, 2005), we extracted from the 3D digital rib models the cross

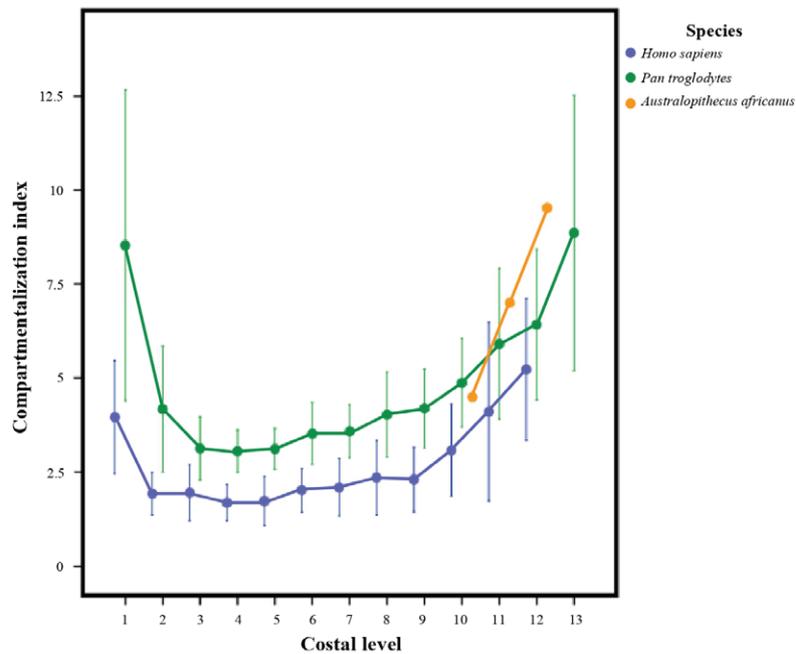


Fig. 2. -Comparison of average midshaft rib compartmentalization index between *Homo sapiens*, *Pan troglodytes* and *Australopithecus africanus* Sts-14 costal levels with corresponding standard deviation. As expected, *Homo sapiens* is the species with less mineral content in its ribs, which is much higher in *Pan troglodytes* and *Australopithecus africanus* Sts-14.

section positioned at the rib midshaft and perpendicular to the main axis of the rib corpus. This image was then saved in TIFF format to be analyzed using the Fiji software (Schindelin *et al.*, 2012), as it can be observed in Figure 1. We obtained the compartmentalization index (Comp. Index) at the rib midsection (Cambra-Moo *et al.*, 2012), which consists on the ratio between the mineral and non-mineral area of each rib midshaft cross section.

Before the analyses, we tested the normality of the Comp. Index by costal level using the Kolmogorov-Smirnov test in SPSS software (IBM Corp., 2017). The p-value obtained for each sample was over 0.05, so did not have statistical support to reject the normal distribution of the indexes by level. Then we applied a parametric test (Student's t) in PAST software (Hammer *et al.*, 2001) to check if there were statistical differences between each costal level of in *H. sapiens* and *P. troglodytes*.

3. Results

As it can be observed in Figure 2, the expected (Latimer *et al.*, 2016) % Md.Ar for each species matches with what was experimentally observed. Firstly, *H. sapiens* ribs have a much lower average Comp. Index than *P. troglodytes* ribs, both following a similar trend. In addition, the three studied ribs from *A. africanus* Sts-14 have a Comp. Index higher than chimpanzees and far from modern humans. Even

though the costal level was uncertain, we assumed that these are the last three ribs in the australopithecine rib cage (10-12) (Williams, 2012) due to the obtained values and their morphology. Recent research suggest that the *Australopithecus* thorax had 12 ribs and the corresponding number of thoracic vertebrae (Williams *et al.*, 2018). However, this issue should be further investigated.

These results were supported by the statistics analyses (Tab. 1). According to Student's t test, we found statistically significant differences for costal levels 1 to 10 of *H. sapiens* and *P. troglodytes* Comp. Index ($p < 0.05$). Nevertheless, for costal levels 11 and 12 the averages values of Comp. Index of both species are similar and there is no statistical difference between them ($p > 0.05$). The 13th costal level was not tested because it is unique of chimpanzees (Hofer *et al.*, 1961).

4. Discussion and conclusions

Results depicted in Figure 2 show a clear difference between the Comp. Index of *Homo sapiens* and *Pan troglodytes* ribs at the midshaft. However, it is interesting to remark that the compartmentalization trend for both species, from the first to the last rib, remains largely parallel between both types of rib cage, except for the first ribs, which present a much larger mineral component in *P. troglodytes* than in *H. sapiens*. This trend has a concave shape with two maximum average

<i>Homo sapiens</i> N = 10			<i>Pan troglodytes</i> N = 10		
Costal level	Average compart. index	Standard deviation	Costal level	Average compart. index	Standard deviation
1	3,96	2,11	1	8,53	5,78
2	1,93	0,79	2	4,18	2,35
3	1,95	1,04	3	3,13	1,19
4	1,69	0,68	4	3,06	0,79
5	1,73	0,92	5	3,12	0,76
6	2,02	0,82	6	3,53	1,16
7	2,09	1,06	7	3,58	0,99
8	2,35	1,39	8	4,03	1,59
9	2,30	1,20	9	4,19	1,47
10	3,08	1,71	10	4,88	1,65
11	4,11	3,33	11	5,91	2,80
12	5,23	2,63	12	6,42	2,80
			13	8,87	5,11

Tab. 1. -Average mid-cross-sectional rib compartmentalization index and standard deviation per costal level of *Homo sapiens* and *Pan troglodytes*.

values at the first and last rib and a minimum average value at the fourth rib in both species.

It is already known that upper and lower thorax have different biomechanical functions due to the link that exists between the lower thorax and the diaphragm (García-Martínez *et al.*, 2016; Bastir *et al.*, 2017b). Therefore, the increment in their mineral percentage could be associated with greater exposure to mechanical stress of the lower ribs due to the diaphragmatic excursion. This reasoning would also explain the large compartmentalization index obtained for the first rib, a small but robust bone that has strong insertions with muscles such as the interior and middle scalene (Spalteholtz, 2013; García-Martínez *et al.*, 2017).

It is interesting to point out that compartmentalization index varies not only between species, but also with ontogeny (García-Martínez *et al.*, 2017). To eliminate the possible bias this might create, all the *Homo sapiens* and *Pan troglodytes* samples analyzed in this study belong to adult individuals.

Unfortunately, our sample of *Australopithecus* ribs is incomplete, thereby it is not possible to make inferences about the entire morphological trend for ribs 1-12. However, if we assume that there is a correlation between rib mineral composition and its shape and middle cross section, we can at least suggest some inferences about the *Australopithecus* ribcage. Given that *Australopithecus* ribs have a Comp. Index closer to chimpanzees than to modern humans, it could be expected that their ribs have a similar morphological structure. Thus, the *Australopithecus*' thorax, as that of chimpanzees, might potentially be broader in its lower part due to the slight torsion of its ribs (Schmid, 1983; Schmid, 1991; Latimer *et al.*, 2016). Nevertheless, it is suggested that *Australopithecus africanus* Sts-14 is a subadult individual (Bonmatí *et al.*, 2008),

which could explain its apparently circular midshaft rib cross section (Fig. 1) as well as its higher Comp. Index compared to the other two tested species (Fig. 2), since subadults present more dense ribs than adults. Although fossil record is very limited, future studies comparing ribs should check how ontogenetic changes in australopithecines could affect these two variables.

In conclusion, the similarity between the mineral content of chimpanzee and *Australopithecus* ribs could mean a similar construction of their thorax, as previously proposed (Latimer *et al.*, 2016). This could be linked to the mechanical stress of ribs or the fact that Sts-14 was not fully adult, but further comparative studies are needed to understand the biomechanical implications of these results.

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