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A hominin first rib discovered at the Sterkfontein Caves, South Africa

First ribs – the first or most superior ribs in the thorax – are rare in the hominin fossil record, and when found, have the potential to provide information regarding the upper thorax shape of extinct hominins. Here, we describe a partial first rib from Member 4 of the Sterkfontein Caves, South Africa. The rib shaft is broken away, so only the head and neck are preserved. The rib is small, falling closest to small-bodied *Australopithecus* first ribs (AL 288-1 and MH1). Given that it was recovered near the StW 318 femur excavation, which also represents a small individual, we suggest that the two may be associated. Three-dimensional geometric morphometric analyses were used to quantify the rib fragment morphology and compare it to extant hominoid and other fossil hominin ribs. While only the proximal end is preserved, our analyses show that South African *Australopithecus* share derived features of the proximal first rib more closely resembling *A. afarensis* and later hominins than great apes.

Introduction

Ribs are rare in the human fossil record because of their delicate structure; this scarcity is particularly pronounced in the early hominin fossil record. Moreover, those that have been discovered are usually fragmentary and distorted, and their interpretation is difficult because of the complicated morphological quantification of their 3D curvature.[1-5] In spite of the scarcity of these remains, it is important to note that, among ribs, the first rib is generally the best preserved in the fossil record as a result of its unique morphology relative to the rest of the ribs in the thorax.[6,7] The first rib is also important because it bears diagnostic features informative of upper thorax morphology.[7-9] For example, the modern human first rib usually has a univertebral articulation (with the T1 vertebra), as do those of early hominins, whereas the other great apes have a bivertebral articulation (with the C7 and T1 vertebrae).[10]

In early hominins, first ribs are known from *Australopithecus afarensis* (AL 288-1ax)[11], *Homo erectus* (KNM-WT 15000 AG and AY&AZ)[12], *A. sediba* (MH1, UW88-148; MH2, UW88-198 and UW88-187)[8] and *H. naledi* (UW101-83)[13]. *A. afarensis* AL 288-1 and *A. sediba* (MH1 and MH2) were hypothesised as presenting a narrow upper thorax, as extant apes do, and this thoracic shape is probably related to suspensory locomotor behaviour.[8,11,14,15] This narrow upper thorax has also been observed in the recently published small-bodied species *H. naledi.*[13] In contrast, other early hominin specimens, such as *H. erectus* (KNM-WT 15000) and the large-bodied *A. afarensis* (KSD-VP-1/1), have been proposed to have modern human-like, expanded upper thoraces.[12,16]

Sterkfontein Caves (located 40 km from Johannesburg) – one of the most important South African sites regarding the quantity and quality of the fossils discovered[17-20] – has yielded several costal remains, but a first rib has not been reported from this site to date. The *A. africanus* partial skeleton Sts 14, discovered at Sterkfontein in 1947, is associated with a number of ribs.[21] Robinson's analysis positioned the preserved ribs toward the lower thorax. According to Robinson[21], these ribs are smaller than those of modern *H. sapiens* but are characterised by a similar degree of curvature. The features observed on the ribs suggested a modern human-like lower thorax shape, but there is still some degree of uncertainty about the upper thorax shape of *A. africanus*.

In 1987, another partial skeleton, StW 431, this time of a larger-bodied, presumed male *A. africanus* was discovered at Sterkfontein in Bed B of Member 4.[22] StW 431 preserves a right rib with the head, neck and tubercle, which was assessed as a probable third rib.[22] However, the preservation of this fragment was not sufficient to discuss upper thorax morphology in *A. africanus* from an evolutionary point of view.

Here we report, present and discuss, in a comparative anatomical context, a well-preserved proximal part of a first rib previously recovered at Sterkfontein but neither identified nor published, as well as its provenance and its relation to the previously discovered remains from the Sterkfontein Caves.

Materials and methods

The new fossil, a proximal fragment of a first rib from the right side (StW 670; Figure 1) was discovered at Sterkfontein site (Cradle of Humankind, Gauteng, South Africa) in grid square V 46, at 21 feet 1 inches to 22 feet 4 inches (27'2–28'2), Member 4[23] (Figure 2). The date of the discovery of the rib is unknown. The collection from Sterkfontein Caves housed at the University of the Witwatersrand dates from 1966 to present excavations. Material collected from Sterkfontein prior to 1966 is housed at Ditsong Museum (formerly known as the Transvaal Museum).

Preservation, morphology and ontogenetic assessment of StW 670

A detailed description of the preservation status as well as the morphology was carried out on StW 670 based on the principal anatomical features of the first rib. Frequencies of single/double articular facet/s of rib head in the comparative sample were also studied (Supplementary table 1 of the supplementary material).

The maturation state of the first rib was evaluated based on the epiphyseal fusion of the articular tubercle of the rib and the articular facet of the rib head.[24] However, it should be noted that the maturation rate of *Australopithecus* epiphyseal fusion could differ from that of *H. sapiens*.

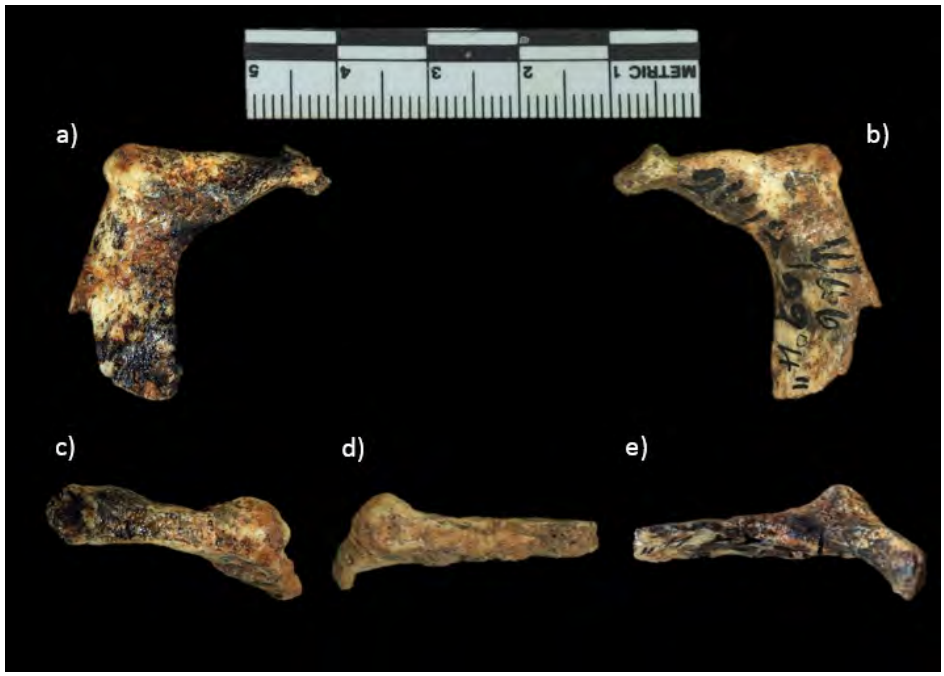


Figure 1: Rib StW 670 in different views: (a) superior, (b) inferior, (c) posterior, (d) exterior and (e) interior.

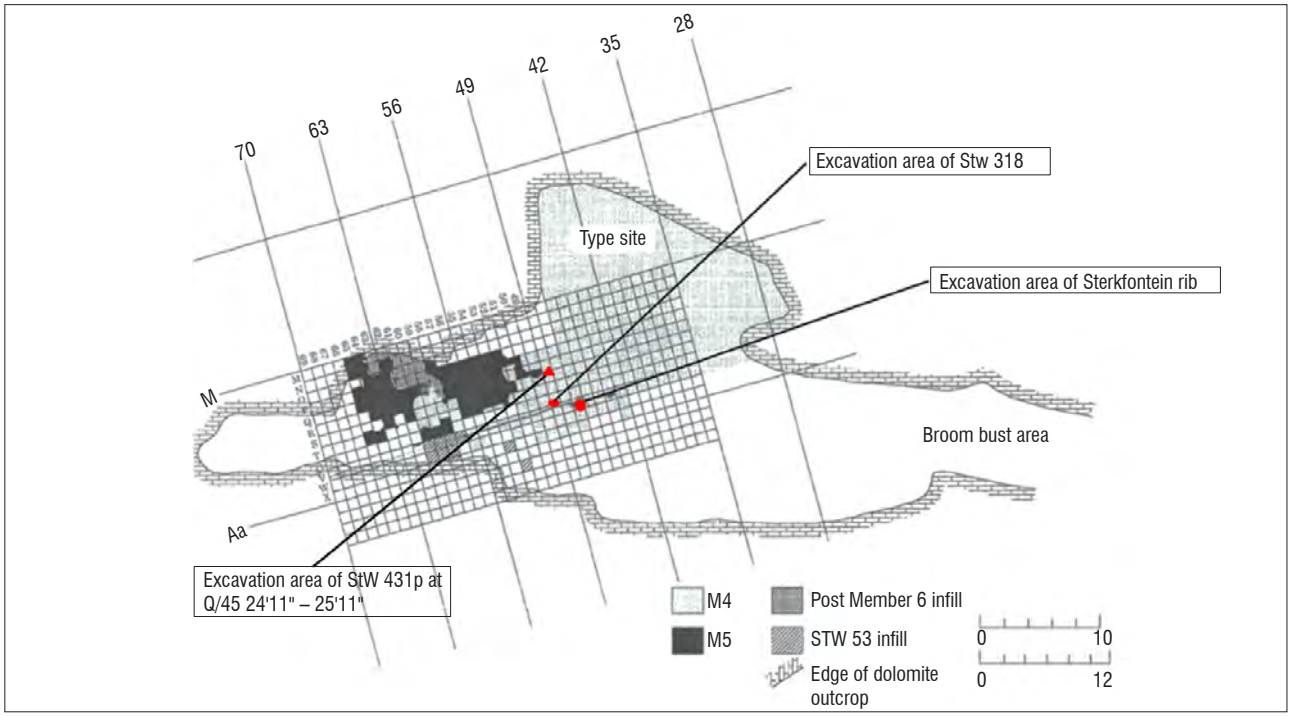


Figure 2: Stratigraphy of Sterkfontein Members 4 and 5, indicating the locality of excavation of StW 670 and StW 318.

Linear measurements

Linear measurements taken on StW 670 were carried out on the original remains. The linear measurements taken were: head height (superoinferior diameter of the rib head), head width (anteroposterior diameter of the rib head), neck length (distance from the medial-most point on the rib head to the medial-most point on the articular facet of the tubercle) and neck width (taken midway between the rib head and articular tubercle in anteroposterior dimension).[2,9,25] Each measurement was calculated from the average of three measurements in order to reduce intra-observer error.[1,2,25] The measurements are given in Table 1.

Table 1: Linear measurements taken on StW 670

	Head height (mm)	Head width (mm)	Neck length (mm)	Neck width (mm)
StW 670	6.4	6.7	18.8	5.5

Measurements on StW 670 were made with standard anthropometric instruments following the definitions used in previous studies.[2,9,25]

Geometric morphometric analyses

For 3D geometric morphometrics, 3D high-resolution laser scans of original fossils – StW 670, *A. sediba* MH1 (UW88-148) and MH2 (UW88-198) – and of a high-quality cast of AL 288-1ax *(A. afarensis)* were used. These scans were obtained using a NextEngine 3D laser scanner in 'wide mode' (with a resolution of 0.38 mm and an accuracy of 6 points per mm). Additionally, computerised tomography (CT) scans of the original remains of *H. erectus* KNM-WT 15000 (AG and AY&AZ) were employed for the analyses (Supplementary table 1).

For the 3D geometric morphometrics analyses, remains of 33 *H. sapiens* (20 Europeans, 10 sub-Saharan Africans, 1 small-bodied member of the San population and 2 small-bodied individuals from the Andaman Islands) were analysed (Supplementary table 1). These scans were also obtained through a NextEngine 3D laser scanner in 'wide mode' (with a resolution of 0.38 mm and an accuracy of 6 points per mm). Additionally, 8 ribs of *Pan troglodytes* (chimpanzee), 3 ribs of *Gorilla gorilla* (gorilla), 3 ribs of *Pongo* sp. (orangutan) and 3 ribs of *Hylobates* sp. (gibbon) from Kyoto University Primate Research Institute (www.pri.kyoto-u.ac.jp) were used to represent non-hominin morphological pattern (Supplementary table 1). Technical specifications of CT scanning can be obtained from www.pri.kyoto-u.ac.jp.

Six 3D type 1 landmarks were collected on each rib, quantifying morphological information of the rib head and the articular tubercle as well as the thickness of the rib neck (Figure 3). Landmarks were collected at the rib head on the most lateral, most medial, most caudal and most cranial points of the articular facet/s of the rib head and at the most lateral point of the articular tubercle. Additionally, one landmark was located at the point defined by the shortest distance from the most lateral point of the articular tubercle to the internal margin of the rib curvature ('d' distance in Figure 3). Because StW 670 is missing a large part of the body of the rib and the sternal end, no landmarks were taken on this area of the comparative sample.

Size was measured as centroid size.[26,27] The size relations between the Sterkfontein first rib and the rest of the individuals in our sample were explored using a box plot. These analyses were carried out in PAST software version 3.[28] In order to study the shape relations along the variability of the sample, we superimposed the landmark configurations using generalised Procrustes analysis.[26,27] The superimposed coordinates were then submitted to principal component analysis (PCA) in shape space in order to reduce the dimensionality of data and to visualise the main axes of variation.

Ordinations were computed into MorphoJ 1.05f software[29] and the shape differences of the surface associated with PC1 and PC2 axes were warped and visualised using the EVAN Toolkit software version 1.62 (www.evan-society.org/). A box plot of Procrustes distances was used to compare and explore shape relations from the individual under study (StW 670) to the different groups of the sample. These analyses were carried out in the Virtual Morphology Lab of the National Museum of Natural Sciences (Madrid, Spain).

Results

Preservation, morphology and ontogenetic assessment of StW 670

There is sufficient preservation of features in the first rib fragment (StW 670) to make description, comparison and analysis possible, even though the fossil is incomplete. The fragment has a well-preserved head, neck, tubercle and most of the proximal part of the body, although the rest of the body is lacking distally.

The rib fragment StW 670 was determined as a first rib from the right side. Siding was determined because the head is positioned at an angle caudal to the tubercle and shaft which produces a mediolateral slope of the neck. Moreover, as the caudal surface of the shaft is smoother than the cranial surface, this feature also confirms the side of the rib as a first rib from the right side.

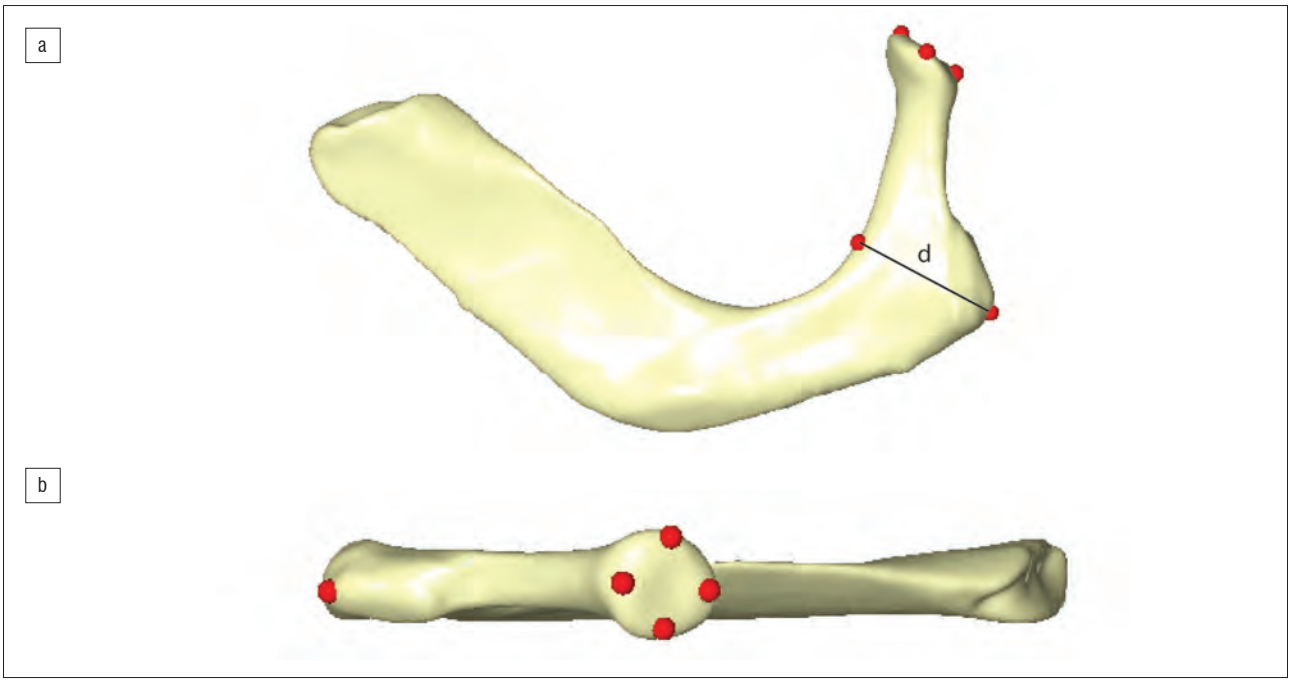


Figure 3: Anatomical location of the six landmarks type 1 taken on the sample. In (a), landmarks at the rib head on the most lateral, most medial and most cranial points of the articular facet/s of the rib head as well as at the most lateral point of the articular tubercle and the landmark defined by the distance 'd' are observed. In (b), the four landmarks at the rib head as well as the one at the tubercle are observed. Measurement 'd' is defined by the shortest distance from the most lateral point of the articular tubercle to the internal margin, which is important to calculate the landmark defined by this measurement.

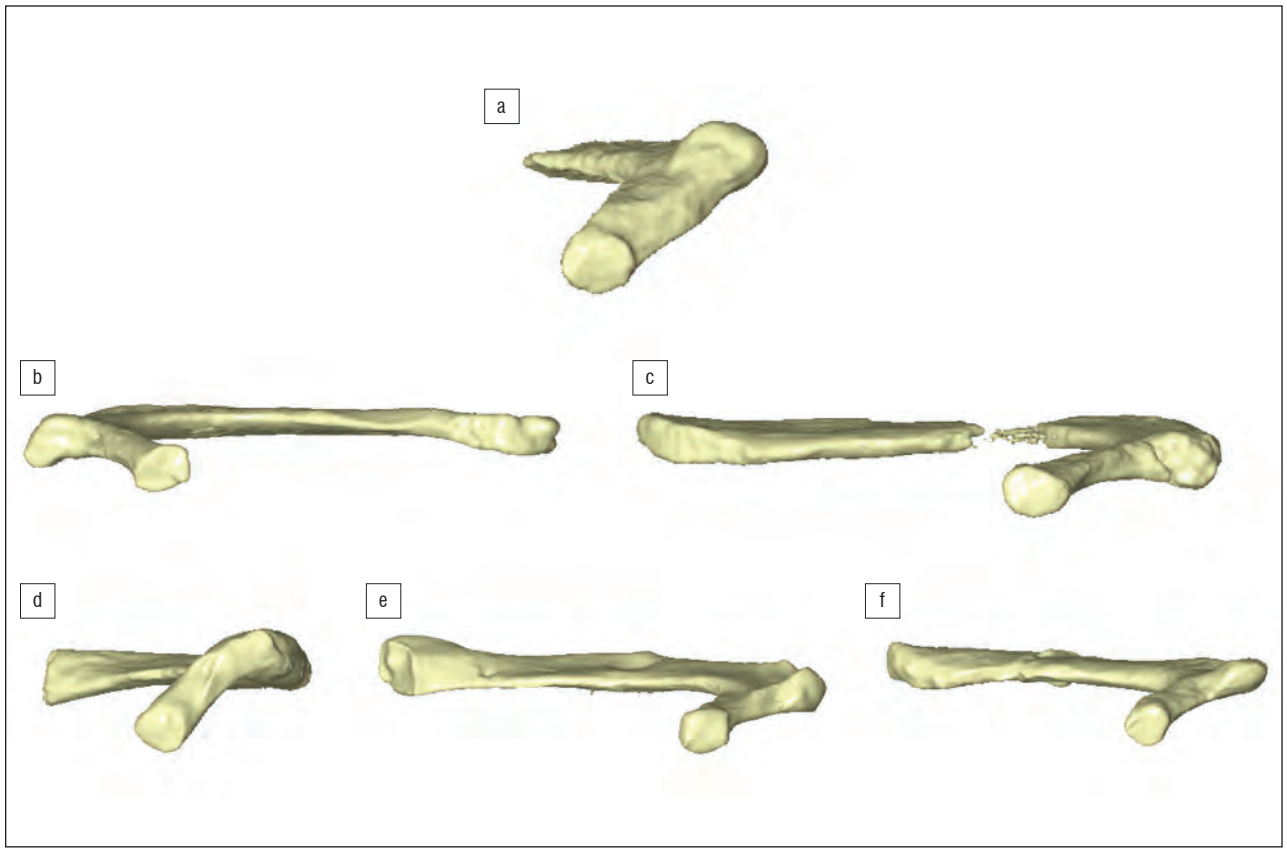


Figure 4: Detail of the single articular facet at the rib head of every fossil specimen studied in the sample: (a) StW 670, (b) KNM-WT 15000 left, (c) KNM-WT 15000 right, (d) AL 288-1, (e) MH1 and (f) MH2. As the goal of this image is to display the single facets, every specimen has been scaled to the same size.

The head has a rim that is thickened for the attachment of the costovertebral ligament. The angle and the tubercle coincide – a feature that is presented in extant and fossilised primate first ribs. The neck is narrow proximally and widens distally as the tubercle is approached. The neck is also rounded proximally and flattened distally. The tubercle is well developed and has a well-defined, smooth and rounded articular facet. The non-articular part of the tubercle for the attachment of the lateral costotransverse ligament is present.

The head has a single articular facet, which is rounded – a morphology that most closely resembles modern humans. The rest of the fossil specimens studied also presented a single articular facet (Figure 4). Regarding the comparative sample, 95% of the European modern humans presented a single articular facet at the rib head for articulation with T1, while 100% of the African modern humans presented this feature. In contrast, all of the non-hominin hominoids (*Pan*, *Gorilla*, *Pongo* and *Hylobates*) presented a double facet for articulation with C7 and T1.

The preservation of the fragment does not allow for the finer detail of anterior scalene and anterior serrate muscle insertions elevations, but it does allow us to study the scalene medium muscle insertion, which is only slightly marked in StW 670. The epiphysis at the articular tubercle and the rib head are well preserved and totally fused with the metaphysis, suggesting that the individual was adult at the time of death.[24]

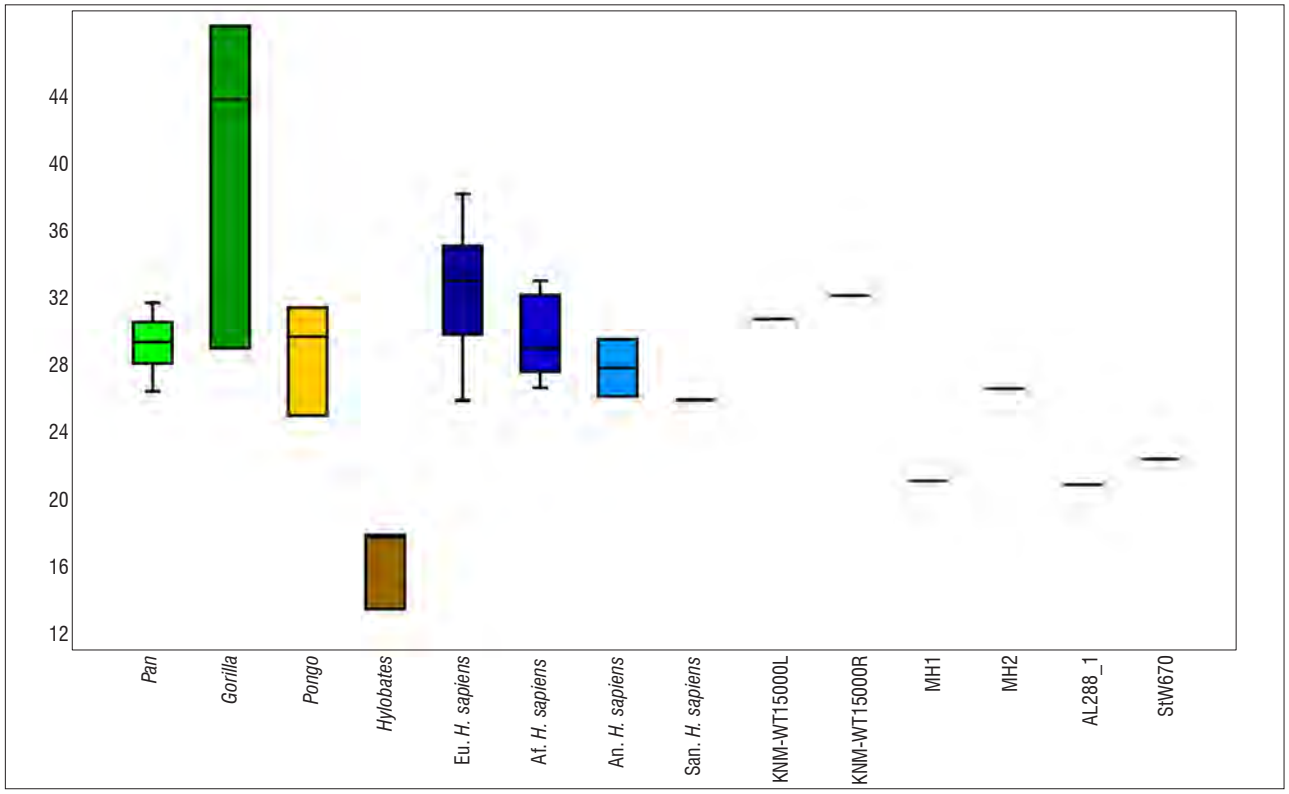
Geometric morphometric analyses

Figure 5 shows a box plot of centroid size distribution of the different groups included in the sample. The centroid size of the StW 670 fossil is smaller than that of *H. erectus* (KNM-WT 15000, both antimeres), *A. sediba* (MH2), the great apes (*Pan, Gorilla* and *Pongo*) and *H. sapiens* (including the small-bodied individuals), and larger than that of *Hylobates*, and is located closest to the centroid size of *A. afarensis* AL 288-1 and *A. sediba* MH1.

Regarding shape, in Figure 6, we can observe that PC1 (44.3% of the total variation) polarises most of the non-hominin hominoids on the positive side of the axis, whereas the scatter of *H. sapiens* of different populations is located mostly towards the negative values of the PC1 axis. As it can be observed on the associated warps (Figure 6), the positive values of PC1 (associated with great apes) correspond to first ribs with a shorter relative distance between the head and the articular tubercle and a larger neck width at the articular tubercle. The negative values of PC1 (mainly associated with hominins) correspond to first ribs with a larger relative distance between the head and the articular tubercle and a shorter neck width at the articular tubercle. Moreover, PC1 polarisation differentiates between different rib head orientations. That is, in the positive values of PC1 (associated with non-hominin hominoids), the plane of the rib head is more oblique to the plane of the neck, while in the negative values of PC1 (mainly associated with modern humans and fossil specimens – so hominins), the plane of the rib head is more parallel to the plane of the neck.

As PC2 (16.7% of the total variation), which explains intraspecific variation, does not polarise between groups observed in PC1, as is observed in Figure 6, we will not discuss PC2. The rest of the principal components explain little of the variation so they also will not be discussed here.

Finally, looking at shape similarities according to the Procrustes distances, it is observed in the box plot (Figure 7) that the closest groups to StW 670 are *A. sediba* (mean distance=0.09), small-bodied Andaman *H. sapiens* (mean distance=0.09), European *H. sapiens* (mean distance=0.11), *H. erectus* (mean distance=0.11), small-bodied San *H. sapiens* (distance=0.12), *A. afarensis* (distance=0.12) and the sub-Saharan African *H. sapiens* (mean distance=0.13). The farthest groups are *P. troglodytes* (mean distance=0.16), *Hylobates* sp. (mean distance=0.21), *G. gorilla* (mean distance=0.22) and *Pongo* sp. (mean distance=0.28).



Eu, European; Af, African; An, Andaman

Figure 5: Centroid size distribution of StW 670 compared to first ribs in the comparative sample. StW 670 centroid size is smaller than that of *Homo erectus* (KNM-WT 15000, both antimeres), the great apes (*Pan, Pongo* and *Gorilla)* and *H. sapiens* (including small-bodied ones); bigger than that of *Hylobates;* and is located between the centroid sizes of the two *Australopithecus* species (*A. afarensis* AL 288-1 and *A. sediba* MH1). Comparative extant sample sizes are listed in Supplementary table 1.

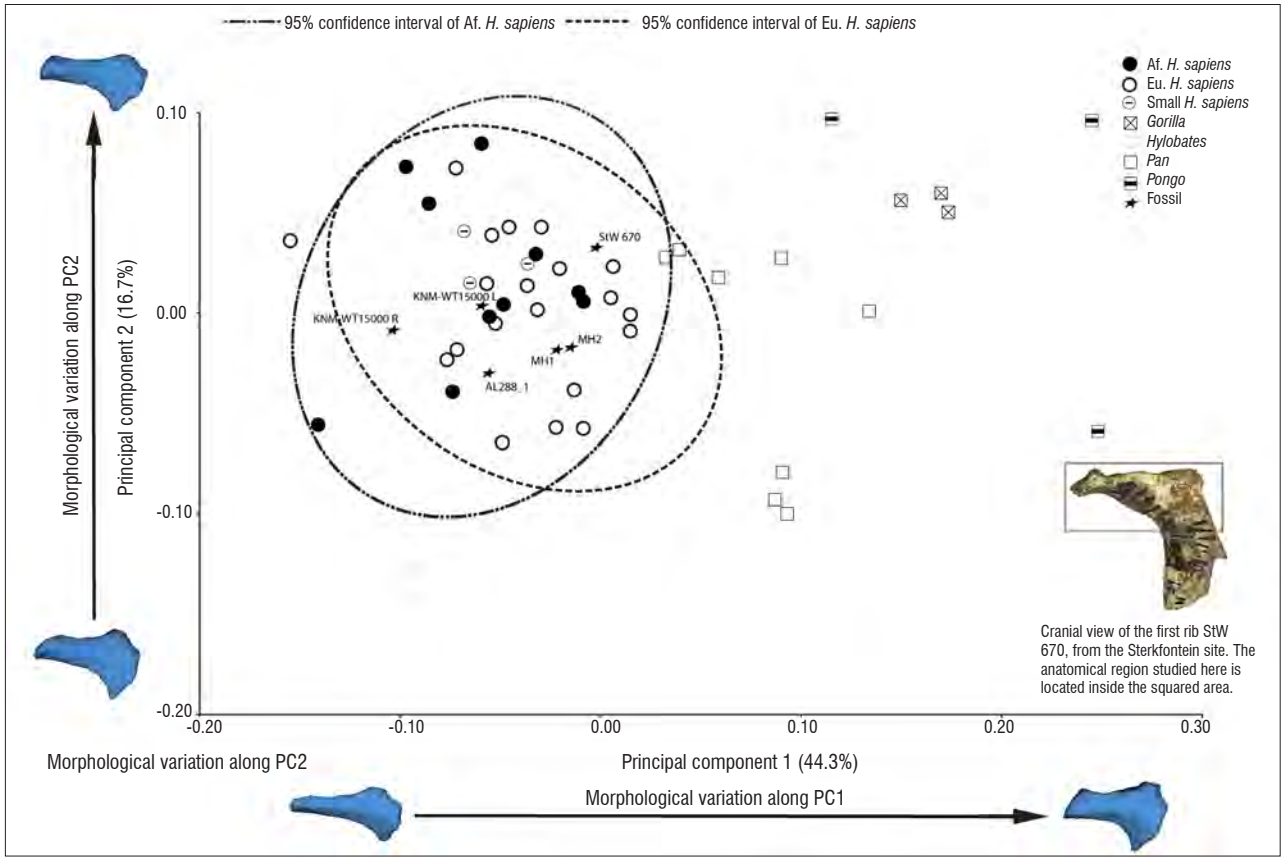


Figure 6: Principal component (PC)-shape analysis of first ribs of all specimens. Scatterplot of PC1 (44.3% of total variance) and PC2 (16.7% of total variance), and warped 3D models of proximal parts of first ribs in axial view. Note that fossil specimens (stars) are within the 95% confidence ellipse of European (Eu) and African (Af) *Homo sapiens*.

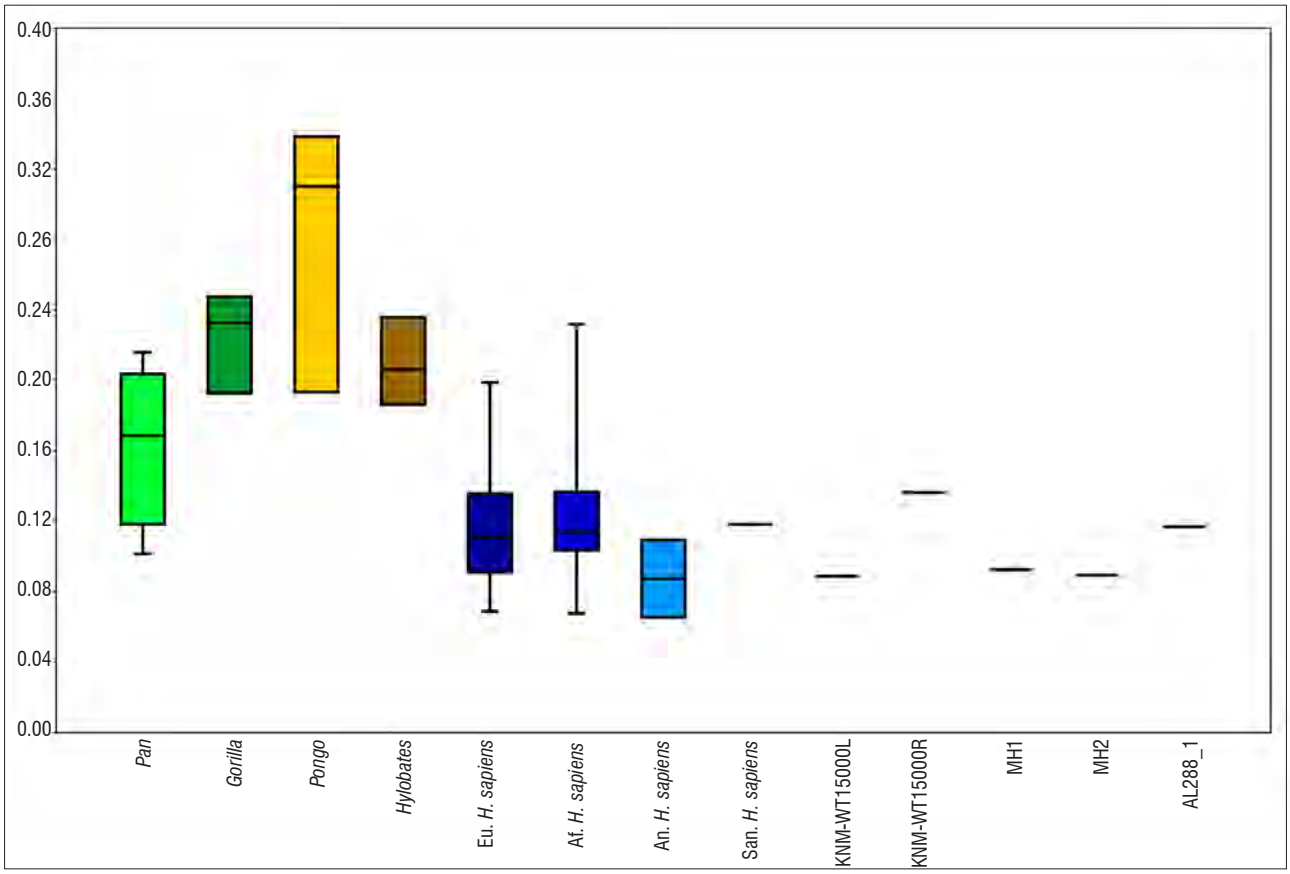


Figure 7: Box plot comparing the Procrustes distances between StW 670 (distance: 0.00) and the comparative sample. The closest groups to StW 670 are *Australopithecus sediba* (mean distance=0.09), small-bodied Andaman (An) *Homo sapiens* (mean distance=0.09), European (Eu) *H. sapiens* (mean distance=0.11), *H. erectus* (mean distance=0.11), small-bodied San *H. sapiens* (distance=0.12), *A. afarensis* (0.12) and sub-Saharan African (Af) *H. sapiens* (mean distance=0.13). The farthest groups are *Pan* (mean distance=0.16), *Hylobates* (mean distance=0.21), *Gorilla* (mean distance=0.22) and *Pongo* (mean distance=0.28).

Discussion and conclusion

Sterkfontein Member 4 has yielded quite a number of hominin remains, with Sts 14 and StW 431 (both *A. africanus*) among the best-known and well-studied hominins from this locality.[21,22] Four beds are recognised within Member 4 – labelled A, B, C and D.[23] StW 431 was excavated in Member 4 Bed B. The excavation beds of Sts 14 and StW 670 were apparently never recorded, so we do not know for certain from which bed StW 670 was excavated. However, StW 670 was excavated close to the excavation area of StW 318, a femur found at U/49 24'0"–25'0". Berger and McHenry[30] surmised the femur to be from an individual of small stature, weighing about 45–50 kg. The small size of the StW 670 rib may mean it is associated with this femur.

Three-dimensional geometrics morphometric analyses, which take into account the 3D spatial relationship between rib head and tubercle, show that the morphology of the preserved portion of StW 670 first rib is quite similar to *A. sediba* as it is close to this taxon in the box plot of the Procrustes distances. Regarding the morphological similarities with the rest of the groups, we can see that, besides *A. sediba*, the morphology of StW 670 is more similar to the *H. sapiens* groups, *H. erectus* and *A. afarensis* than it is to non-hominin hominoids (*Pan*, *Pongo, Gorilla* and *Hylobates).* In fact, in the PCA analyses, every fossil specimen (StW 670, MH1, MH2, AL 288-1 and KNM-WT 15000) falls inside the 95% confidence interval ellipse of *H. sapiens* (Figure 6).

Morphologically, the similarity of the fossils to modern humans observed in this PCA is because these groups are characterised by a larger relative distance between the head and the articular tubercle, and a shorter neck width at the articular tubercle, and because the plane of the rib head is more parallel to the plane of the neck in modern humans and the fossils than in the non-human hominoids. This latter feature observed at the rib head should probably be reflected in the orientation of the transverse processes of the T1 vertebrae, thus future studies should investigate this possibility.

Additionally, the presence of a single facet observed in every early hominin studied (*Australopithecus* and *H. erectus*) also supports the modern-like pattern of this fragment. This observation contrasts strongly with the pattern observed in the great apes (*Pan*, *Pongo*, *Gorilla* and *Hylobates*) as all of them present two articular facets at the rib head. Although we are conscious of the limitations of our sample size, we think that the observations made here are relevant to discuss the modernity of this character in StW 670. So, in the light of these observations, we conclude that the single facet of the rib head of the first rib is a feature unique to the hominin lineage, which emerged, at least, with the genus *Australopithecus.*[10] Moreover, aspects observed in the rib head should be reflected in the adjacent vertebrae as well, but because an associated vertebra does not exist and an assessment of vertebral morphology is not the goal of this work, it should be addressed in future studies.

The similarity of the proximal rib morphology observed in *Australopithecus* and *H. sapiens* first ribs is interesting because it has traditionally been thought that the upper thorax morphology of *Australopithecus* is characterised by a great ape-like form.[6,7] So, another hypothesis to be tested in future studies is that if we accept the derived morphology of the proximal part of the first rib in *Australopithecus* (*A. afarensis*, *A. sediba* and *A. africanus*), we can infer that the archaic pattern of the upper *Australopithecus* thorax should be found at the distal part of the ribs. This would suggest that the proximal part of the rib became derived in the direction of the *H. sapiens* morphology earlier than did the distal part of the first rib. This suggestion is consistent with the fact that the proximal and distal parts of the first rib belong to different morphogenetic modules in ontogeny,[31] which allows both units to evolve at different rates according to different requirements.

Great apes are often described as having a narrow upper thorax, while humans have a more expanded one.[32] It would be useful to be able to use fragmentary ribs in the hominin fossil record to determine when the transition between the two morphologies took place. The 2D analyses performed in previous studies do not make this goal look promising because of the complex morphology of ribs and the ribcage more broadly; however, the 3D analyses performed here show that the spatial configuration of the rib head and articular tubercle could be informative about the archaic or derived morphology, at least of the proximal part of the first rib. This fact, together with features such as the single facet of the rib head[10], could be informative in finding evolutionary traits in the upper thorax of early hominins. More research employing 3D techniques is needed on complete first ribs as well as the rest of the ribs in the costal sequence (from first to twelfth) in order to better quantify and understand *Australopithecus* rib morphology and the role of the thorax in hominin evolution more broadly.

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Authors' contributions

G.T. identified the rib fragment as hominin and described it. D.G-M. and J.E. analysed the 3D and linear data, respectively. G.T., D.G-M., J.E., S.N. and S.A.W. wrote the paper. M.B., P.S. and L.B. provided data and supervisory support, respectively.

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Note: This article includes supplementary material