Variation in human 3D trunk shape and its functional implications in hominin evolution

Markus Bastir1, José Maria González Ruiz2, Javier Rueda2, Gonzalo Garrido López2, Marta Gómez-Recio1, Benoit Beyer3, Alejandro F. San Juan2,4 & Enrique Navarro2,4

This study investigates the contribution of external trunk morphology and posture to running performance in an evolutionary framework. It has been proposed that the evolution from primitive to derived features of torso shape involved changes from a mediolaterally wider into a narrower, and antero-posteriorly deeper into a shallower, more lightly built external trunk configuration, possibly in relation to habitat-related changes in locomotor and running behaviour. In this context we produced experimental data to address the hypothesis that medio-laterally narrow and antero-posteriorly shallow torso morphologies favour endurance running capacities. We used 3D geometric morphometrics to relate external 3D trunk shape of trained, young male volunteers (N = 27) to variation in running velocities during different workloads determined at 45–50%, 70% and 85% of heart rate reserve (HRR) and maximum velocity. Below 85% HRR no relationship existed between torso shape and running velocity. However, at 85% HRR and, more clearly, at maximum velocity, we found highly statistically significant relations between external torso shape and running performance. Among all trained subjects those with a relatively narrow, flat torso, a small thoracic kyphosis and a more pronounced lumbar lordosis achieved significantly higher running velocities. These results support the hypothesis that external trunk morphology relates to running performance. Low thoracic kyphosis with a flatter ribcage may affect positively respiratory biomechanics, while increased lordosis affects trunk posture and may be beneficial for lower limb biomechanics related to leg return. Assuming that running workload at 45–50% HRR occurs within aerobic metabolism, our results may imply that external torso shape is unrelated to the evolution of endurance running performance.

Evolutionary anatomical changes. The trunk consists of the ribcage, the spine and the pelvis. During human body shape evolution, each of these elements experienced specific morphological changes. For example, the ribcages of Homo erectus and Neandertals were not only wider at the level of the central and lower thorax, but also antero-posteriorly deeper than most modern human populations1–4. Also the pelvis shows a systemic evolutionary trend towards reduction of its bi-iliac width, when comparing modern humans with H. erectus and members of the Neandertal lineage5–8. Evolutionary changes in the spine of the genus Homo show changes in overall height, its position within the ribcage and possibly spine curvatures. Within Homo, the overall spine length has increased, as a consequence of larger body size. Greater dorsal orientation of the transverse processes in non-modern humans likely positioned the thoracic vertebral bodies more within the ribcage, producing a greater spine invagination10,11. Also, in Neandertals a smaller lumbar lordosis (hypolordosis) is discussed and could be particularly relevant with respect to trunk morphology as it directly affects the position and orientation of the sacrum and, thus, the pelvis12,13. The potential adaptive significance and functional implications of these features in hominin trunk evolution are not well understood and have been discussed in the context of thermo-regulatory15, digestive16, respiratory3, and locomotor functions17. Here, we focus on the latter two aspects.

Trunks with a narrow lower thorax and a narrow, tall waist have been associated with emerging endurance running capacities, possibly appearing with African H. erectus and together with elongated lower limbs18. Yet, a recent reconstruction of the KNM-WT 15,000 African H. erectus ribcage seems more similar to Neandertals in

1Paleoanthropology Group, Museo Nacional de Ciencias Naturales, CSIC, J.G. Abascal 2, 28006 Madrid, Spain. 2Department of Health and Human Performance, Faculty of Physical Activity and Sports Sciences-INEF, Universidad Politécnica de Madrid, 28040 Madrid, Spain. 3Laboratory of Functional Anatomy (LAF), Faculty of Motor Skills Sciences, Université Libre de Bruxelles, Brussels, Belgium. *These authors jointly supervised this work: Alejandro F. San Juan and Enrique Navarro. *email: mbastir@mncn.csic.es
terms of width and depth than to modern human populations. Nevertheless, Neandertals are thought to show adaptations for sprinting based on the anatomy of their foot skeleton, and for power locomotion, as paleo-
ecological and genetic evidence indicates, which is interpreted in the context of ambush hunting in a forested ecosystem.

Thus, given the new evidence for greater similarities of trunk shape in primitive Homo and Neandertals, together with known differences in the lower limb anatomy, it is interesting to investigate the implications of variation in trunk morphology in the context of locomotor capacities.

**Trunk anatomy and running capacities.** The trunk contributes to locomotor performance and energetics in two different ways: (1) the effect of trunk morphology on limb biomechanics, and (2) the effect of thorax morphology on breathing mechanics. Grossly speaking, sprinting and endurance running differ at energetic and locomotor (limb) biomechanics in the context of stride lengths, frequency and energetics. It has been shown that runners with relative longer lower limbs have lower locomotor costs. Effective sprinting requires greater stride length and powerful lumbar muscles, specifically erector spinae and quadratus lumborum. Endurance running, nevertheless, does not require longer strides. Higher frequency is more important to running performance during long distances and time, especially in longer trails, where the loss of stride length typically appeared due to fatigue. Generally, a more upright trunk posture is observed among runners who perform efficiently in comparison with those less efficient, whose trunks were increasingly flexed during endurance running.

Besides a positive effect of overall trunk muscularity on running performance, it has been shown that several other specific trunk morphological aspects relate to running performance, including the width of the pelvis, the trunk flexion angle, lumbar lordosis, and associated hip flexion angle, and thorax breathing mechanics. Within modern humans, the relationship between the widths of the thorax and the pelvis are important parameters of human variability in form and function. The narrower pelvis relative to the wider thorax in males is associated with a gait pattern that differs biomechanically from that of females, who are characterized by a wider pelvis and narrower thorax dimensions. The width of the pelvis influences the biomechanics of the psoas major affecting its hip rotator and flexor capacities. Trunk flexion also affects significantly stride kinematics and kinetics. Although the factors of trunk flexion are unclear, higher trunk flexion angle correlates with shorter stride length, higher stride frequency, greater reaction forces and increased locomotion costs.

Lumbar lordosis varies considerably in human populations and affects locomotor capacities. It has been shown that greater lordosis facilitates shock absorption, for example, when running, while weaker lordosis produces a more forwards orientation of the pelvis, which is beneficial for leg return during sprinting. Weak lordosis is also related to greater trunk muscle strength. Overall trunk muscularity (e.g. erector spinae, quadratus lumborum, psoas major, transverse abdominal, etc.) has been correlated positively with sprinting capacities. Differences in the tonus of the erector spinae and quadratus lumborum muscles have been related to greater lumbar lordosis.

The contribution of thorax shape to trunk morphology is further interesting in the context of respiratory biomechanics. It has been suggested that morphological features of the rib joints are relevant for ventilatory capacity during running. These authors showed that Homo erectus has similar rib joint morphologies as modern humans that differed from Australopithecus and chimpanzees. But also overall thorax morphology is important: antero-posteriorly flatter ribcages with more inferiorly declined ribs were suggested to show different thoraco-diaphragmatic and abdominal muscle recruitment during ventilatory movement than antero-posteriorly deeper thoraces with more horizontally aligned ribs. Although pump- and bucket-handle patterns of rib motion seem more uniformly distributed along the ribs than originally assumed, variation in thorax-shape related breathing biomechanics indirectly affect the locomotor capacities due to energetic competition and demands between the locomotor and the respiratory systems. Thus, several studies have so far addressed the implication of specific elements of trunk morphology in isolation on locomotor performance. This study explores the relationship between entire 3D trunk shape and running performance based on virtual and geometric morphometric methods. In the light of the functional anatomical evidence reviewed above, we address the hypothesis that trunks with an antero-posteriorly flat ribcage, a medio-laterally narrow pelvis and a lower lumbar lordosis are associated to a better running performance.

**Materials and methods**

**Functional analyses, variables and experimental set up, ethics.** Twenty-seven healthy trained young male students of the Degree in Sciences of Physical Activity and Sports (Table 1) were voluntarily recruited. Twelve of them were trained in endurance (ER) disciplines and fifteen were team sport players (non-ER). The inclusion criteria were the following: (1) Age between 18 and 30 years; (2) volunteers athletes had to be long distance runners or team sports players (e.g., rugby, soccer, basketball); (3) not having suffered a musculoskeletal injury one month prior to the date of the protocol (i.e., checked through a previous exclusion questionnaire). And exclusion criteria were: (1) Age younger than 18 years; (2) having consumed any narcotic and/or psychotropic agents or drugs during the test; (3) any cardiovascular, metabolic, neurologic, pulmonary, or orthopaedic disorder that could limit performance in the different tests. Informed consent was obtained by all volunteers. The study protocol adhered to the declaration of Helsinki and was approved by the Ethics Committee of the Technical University of Madrid (Spain).

All the participants performed a physiological (ramp) protocol on a treadmill (Telju JT4100-Liton -035, Toledo, Spain) in three different phases of exercise intensities: 45–50%, 70%, and 85% of the heart rate reserve (HRR). These three intensities correspond with the cardiorespiratory phase 1 (i.e., Light intensity, below the...
ventilatory threshold (VT), phase 2 [i.e., Moderate intensity, between the VT and the respiratory compensation threshold (RCT)], and phase 3 [i.e., High intensity, above the RCT]27. The rate of perceived exertion (RPE) was introduced as a complement of the HRR to help the control of the adequate intensity in each of the three submaximal workloads (i.e., For a HRR of 45–50% the RPE should be 2–4/10, HRR of 70% the RPE 5–6/10, and for HRR 85% the RPE ≥ 8/10). Before warm-up, rest heart rate was measured in sitting position until it was stable. After a general warm-up, the test started between 6 and 7 km h⁻¹ and 1% of slope to mimic effects of air resistance53,54. Then, running velocity was increased by 0.5 km h⁻¹ every 30 s until the achievement of HRR ≥ 85%, RPE ≥ 8 and volitional exhaustion. The following variables were recorded at these instances: time, running velocity, and RPE. Heart rate (beats·min⁻¹) was continuously monitored during the test using a telemeter (Polar Ceinture H10+; Polar Electro OY, Kempele, Finland). Changes in velocity during the different work load phases were analysed by repeated measures ANOVA carried out in PAST55. Anthropometrical and running performance data were collected and summarized in Table 1 and Table 2.

Table 1. Descriptives of the sample showing age, body size, and weight.

|          | Age (yr) | Stature (m) | Body weight (kg) | BMI   |
|----------|----------|-------------|------------------|-------|
| N        | 27       | 27          | 27               | 27    |
| Min      | 18       | 1.62        | 53.50            | 19.97 |
| Max      | 29       | 1.90        | 83.00            | 25.76 |
| Mean     | 20.78    | 1.77        | 69.06            | 22.06 |
| SD       | 2.53     | 0.07        | 7.20             | 1.34  |

Figure 1. Frontal, lateral and posterior views of the 3D landmarks on the trunk surface. Red dots are fixed landmarks (Supplementary Table 1) and anatomically homologous between subjects, blue dots are curve semilandmarks, and green dots are surface semilandmarks. After resliding the semilandmarks are mathematically homologous among subjects.

Table 2. Descriptive statistics of the running velocities at different experimental steps.

|          | V_initial (km/h) | V1 (km/h) | V2 (km/h) | V3 (km/h) | Vmax (km/h) |
|----------|-----------------|-----------|-----------|-----------|-------------|
| N        | 27              | 26        | 26        | 27        | 27          |
| Min      | 6               | 6         | 8         | 12        | 12          |
| Max      | 8               | 9         | 14        | 20        | 20          |
| Mean     | 6.85            | 7.35      | 10.33     | 14.42     | 15.07       |
| SD       | 0.43            | 0.75      | 1.35      | 2.09      | 1.81        |

3D shape data collection and geometric morphometric analyses. 3D body surface data were manually recorded by an Artec MHT 3D (www.artec3d.com) surface scanner in standardized positions, standing upright on a turning table, with quiet breathing and the arms slightly raised over the head to leave the 360° of
The analyses were carried out using MorphoJ software, PAST v3.2555, STATISTICA v.858, geomorph package weight on running performance using GLM. We set the significance level for the regression analyses on \( p < 0.05 \).

and pectoralis major muscles were removed. Finally, we explored the data for a possible impact of stature and landmark set (N = 142 lms), where those landmarks that covered the skin surface related to the latissimus dorsi athletes, we performed a pooled-within group regression. We also tested the hypotheses with a reduced torso landmark set (N = 142 lms), where those landmarks that covered the skin surface related to the latissimus dorsi and pectoralis major muscles were removed. Finally, we explored the data for a possible impact of stature and weight on running performance using GLM. We set the significance level for the regression analyses on \( p < 0.05 \). The analyses were carried out using MorphoJ software, PAST v3.2555, STATISTICA v.858, geomorph package for R and Evan toolkit following the workflows outlined in Bastir et al. (Table 2).

Results
Repeated-measures ANOVA (Table 3) shows that mean velocity increased significantly during incremental HRR phases (Fig. 2).

The regression analyses of torso shape on velocity phases indicated no significant relations during the first two stages (V1, V2) of workload. However, statistically significant relations were found between torso shape and velocity during phase 3 (V3) and maximum velocity (Vmax) (Table 4). Comparison of slopes in the ER and non-ER groups in the pooled within group regression models revealed no evidence for differences in the full torso shape data (P = 0.19; F = 1.833), nor in the non-muscular torso shape data (P = 0.18; F = 0.187) in relation Vmax. The GLM model revealed a significant influence of both, full and non-muscular torso shapes on running performance but no such effect of stature or weight (Table 5).

The associated 3D shapes (Fig. 2) show that the following morphological features of the trunk are positively associated with increased running performance: smaller antero-posterior diameter at the central-lower rib cage (flat thorax), narrower lower trunk (narrow pelvis), taller trunk, reduced thoracic kyphosis and more pronounced lumbar lordosis.

Discussion
Modern humans are characterized by a relatively flat and narrow ribcage and pelvis when compared to fossil representatives of the genus Homo that are characterised by more stocky, wider and antero-posteriorly deeper torso configurations. While more and more evidence seems to document this morphological trend, possible functional implications of reduced widths and depths of the trunk remain poorly understood. Because the trunk comprises elements of the respiratory and locomotor systems, the interaction of trunk shape with respiratory and locomotor performance is of specific interest.

In the present study, we address possible relations between torso shape and locomotor function in an experimental setting relating 3D external trunk surface shape with running velocity at different levels of intensity. The results showed no relationship between trunk shape and running performance at lower levels of exercise (V1, V2) below the anaerobic (respiratory) threshold, and just above it, indicating no relations between external torso shape and endurance running speeds between 7 and 10 km/h. However, at higher intensities and velocities above the anaerobic (respiratory) threshold (V3; average 14.4 km/h) a statistical relation between torso shape and running speed emerged. According to our results, subjects with a flatter and slightly narrower thorax, lower thoracic kyphosis, more pronounced lumbar lordosis, and slightly narrower pelvis can achieve such higher velocities such as indicated by the higher variances of 3D trunk shape shown at V3 and maximum velocity. It has been suggested that an endurance running velocity of about (5 ms\(^{-1}\) = 18 km/h) can be sustained by many amateurs without special training, which is considerably faster than in our sample. At moderate intensity (V2), presumably within the aerobic metabolic domain, the average speed was about 10 km/h (Table 2). This may be related to the slight inclination of the treadmill (1%) during the incremental experiment (and the thereby simulated air resistance), but it could also reflect the fact that not all the volunteers were specialized endurance runners. Likewise, the average speed of 14 km/h at V3, which is likely already beyond the anaerobic threshold, is still lower than the published one and, again, could be related to the factors mentioned before. However, at and beyond this velocity, 3D torso shape was statistically related to running capacity.

The most visible features related to higher running capacities were a low degree of thoracic kyphosis, with a flatter, slightly narrower central thorax and a greater degree of lumbar spine curvature with a relatively slightly narrower pelvis. Covariation in depths was more clearly recognisable than in widths (Fig. 2). While the thoracic part suggests interpretation within a respiratory biomechanical perspective, the lumbo-pelvic part of the torso shape was positively associated with increased running velocities.

| Sum of sqrs | df | Mean square | F | p (same) |
|-------------|----|-------------|---|---------|
| Between groups | 1526.05 | 4 | 381.51 | 393.5 | < 0.001 |
| Within groups | 251.161 | 125 | 2.01 | | |
| Error | 96.954 | 100 | 0.96 | | |
| Between subjects | 154.207 | 25 | 6.17 | | |
| Total | 1777.21 | 129 | | | |

Table 3. ANOVA of velocities during the three different phases (V1, V2, V3).
also requires consideration within functions of the locomotor system, although both are clearly related with each other. For example, the role of the posterior lumbar muscles is essential, as they act keeping an upright posture of the lower trunk during running and giving stability to the diaphragm and psoas major lumbar insertions. So, trunk extensors have the ability to reduce the kyphosis angle.\textsuperscript{64,65} Links between breathing biomechanics and lumbar stability have been found in Kang et al.\textsuperscript{66} who showed that spinal posture was improved by specific breathing exercises in a clinical context.

The combination of a reduced thoracic kyphosis and a flat ribcage, with anteriorly declined ribs, in which the anterior rib ends are more caudally located than the posterior rib ends, could point to the importance of ventilatory biomechanics in higher intensity running. Bellemare et al.\textsuperscript{44,45} suggested that declined ribs can be elevated more during inspiration than horizontally aligned ones accentuating potentially the costal contribution to thorax movement during lung ventilation. Also, anteriorly declined ribs may have better biomechanical leverage during forced expiration, which crucially increases the tidal volume during heavy exercise breathing.\textsuperscript{45} Because the declination of the ribs is morphologically related to a flatter rib cage configuration, the hypothesis that a flat thorax is positively related to running performance finds support. Physiologically, a less curved thoracic spine increases further the vertical space potentially available for lung expansion through enhancing of rib mobility. For example, negative consequences for lung ventilation due to kyphotic thoracic spine deformations, which compress thoracic space and affect rib biomechanics, have been reported.\textsuperscript{46,67}

The implication of lumbar lordosis for locomotor biomechanics consists of its effect on the forwards orientation of the anterior superior iliac spine, which is an advantageous position for efficient leg return.\textsuperscript{31} However, while these authors have not found a significant relation between lumbar lordosis angle and hip flexion capacity,
our results in Fig. 2 clearly show that more pronounced lumbar curvature, to which also the lower thoracic kyphosis contributes, produces forwards tilt of the pelvis. Warrener et al.\(^{32}\) have found a significant reduction of length and an increment of frequency of strides associated with higher trunk flexion posture during running. This finding is supported by Castillo and Liebermann\(^{34}\), who pointed out that higher lumbar lordosis (trunk extension) is linked with longer stride length in runners, a key factor in speed running as we have observed in our sample. Additionally, upright posture have been associated with better economy and running performance in the context mechanically interactions between trunk kinetics, reaction forces and spatiotemporal patterns of strides\(^{29}\).

### Table 4. Multivariate regressions of full torso shape (160 lms) and non-muscular torso shape (142 lms) on running performance at different workloads (V1, V2, V3 and Vmax). (Note that sample size is N = 27 for Vmax, but N = 26 for V1, V2 and V3). Significant values are in bold.

|     | Df | SS     | MS       | R² | F      | Z     | p Value |
|-----|----|--------|----------|----|--------|-------|---------|
| 160 lms |    |        |          |    |        |       |         |
| V1  | 1  | 0.003868 | 0.003868 | 0.04589 | 1.1543 | 0.54784 | 0.3 |
| Residuals | 24 | 0.080422 | 0.003351 | 0.95411 |       |       |         |
| Total | 25 | 0.08429  |          |        |        |       |         |
| V2  | 1  | 0.003358 | 0.003358 | 0.04248 | 1.0646 | 0.30142 | 0.387 |
| Residuals | 24 | 0.08071  | 0.003363 | 0.95752 |       |       |         |
| Total | 25 | 0.08429  |          |        |        |       |         |
| V3  | 1  | 0.005871 | 0.005871 | 0.06965 | 1.7968 | 1.8401  | 0.034 |
| Residuals | 24 | 0.078419 | 0.003267 | 0.93035 |       |       |         |
| Total | 25 | 0.08429  |          |        |        |       |         |
| Vmax | 1  | 0.007102 | 0.007102 | 0.08071 | 2.1948 | 2.4653  | 0.009 |
| Residuals | 25 | 0.08089  | 0.003236 | 0.91929 |       |       |         |
| Total | 26 | 0.087991 |          |        |        |       |         |

|     | Df | SS     | MS       | R² | F      | Z     | p Value |
|-----|----|--------|----------|----|--------|-------|---------|
| 142 lms |    |        |          |    |        |       |         |
| V1  | 1  | 0.003644 | 0.003645 | 0.04369 | 1.0965 | 0.39524 | 0.359 |
| Residuals | 24 | 0.079767 | 0.003324 | 0.95631 |       |       |         |
| Total | 25 | 0.083412 |          |        |        |       |         |
| V2  | 1  | 0.003291 | 0.003291 | 0.03945 | 0.9857 | 0.082949 | 0.458 |
| Residuals | 24 | 0.080121 | 0.003338 | 0.96055 |       |       |         |
| Total | 25 | 0.083412 |          |        |        |       |         |
| V3  | 1  | 0.005547 | 0.005547 | 0.06665 | 1.7096 | 1.728   | 0.044 |
| Residuals | 24 | 0.077865 | 0.003244 | 0.9335  |       |       |         |
| Total | 25 | 0.083412 |          |        |        |       |         |
| Vmax | 1  | 0.006828 | 0.006828 | 0.07836 | 2.1256 | 2.2905  | 0.01  |
| Residuals | 25 | 0.080303 | 0.003212 | 0.92164 |       |       |         |
| Total | 26 | 0.08713  |          |        |        |       |         |

### Table 5. Generalized Linear Models assessing the effects of stature, weight, torso shape (160 lms, 142 lms) on running performance. Significant values are in bold.

|     | SS | df | MS | F  | p  |
|-----|----|----|----|----|----|
| 160 lms |    |    |    |    |    |
| Intercept | 7.93 | 1 | 7.93 | 5.38 | 0.030 |
| Stature | 0.51 | 1 | 0.51 | 0.35 | 0.562 |
| Weight | 0.88 | 1 | 0.88 | 0.60 | 0.447 |
| Torso shape | 46.85 | 1 | 46.85 | 31.79 | 0.000 |
| Error | 33.90 | 23 | 1.47 |    |    |

|     | SS | df | MS | F  | p  |
|-----|----|----|----|----|----|
| 142 lms |    |    |    |    |    |
| Intercept | 6.43 | 1 | 6.43 | 4.33 | 0.048 |
| Stature | 0.19 | 1 | 0.19 | 0.13 | 0.720 |
| Weight | 46.59 | 1 | 46.59 | 31.36 | 0.519 |
| Torso shape | 0.64 | 1 | 0.64 | 0.43 | 0.000 |
| Error | 34.16 | 23 | 1.49 |    |    |
Therefore, the empirical evidence reported in the present study seems to indicate that trunk evolution as a whole may have brought about the appearance of some features that are more clearly related to long distance running, along with others that are more related to power locomotion with higher workloads. However, these features lead to a mosaic notion, which reflects a complex picture of potential adaptations to running economy. In Neandertals, some adaptations to power locomotion were proposed on anatomical, genetic, and ecological grounds.\textsuperscript{19,20} Our results suggest that the relatively straight thoracic column along with their high level of trunk muscularity, possibly reflected by wide, deep thorax shape and associated high body mass estimates, would fit with the power locomotion hypothesis.\textsuperscript{6,8,9} On the other hand, their supposed hypo-lordosis would argue against such interpretation as the relatively uncurved reconstruction of the thoracic and lumbar spine in the Kebara 2 Neandertal\textsuperscript{13,69} would indicate reduced pelvic tilt and thus a reduced capacity of leg return, hip flexion and sprinting capacity. Yet, the most recent reconstruction of the La Chapelle aux Saints Neandertal suggests vertebral curvatures similar to modern humans\textsuperscript{14} and this indicates that a better fossil documentation of lumbar spine anatomy in Neandertals is needed. Importantly, a recent study accounting for a wide range of population variability in modern humans, identified consistently and significantly more pronounced lordotic wedging in Neandertal L5 of Kebara 2, Shanidar 3, and La Chapelle aux Saints\textsuperscript{41} together with a more hypo-lordotic wedging in upper lumbar vertebra. Accordingly, this could suggest a completely different position of the lumbar spine within the trunk, with yet unclear biomechanical implications. Therefore, further fossil reconstructions of Neandertal torso skeletons together with experimental testing are necessary.

In African \textit{H. erectus}, as reconstructed on the remains of KNM-WT 15,000, the straight thoracic\textsuperscript{3} and curved lumbar spine morphology\textsuperscript{23} would be more in line with effective power-locomotion. This, together with greater torso width and depth would be also compatible with higher muscularity and body mass\textsuperscript{13,15,71,72}. However, clearly, the elongated limbs favour an interpretation of long-distance locomotion and, possibly, running\textsuperscript{17,21}. Altogether, the present evidence and reviews suggest that our interpretations relate to a great extent on the reliability of the fossil body reconstructions.

However, it is important to bear in mind the limitations of our experimental evidence in the evolutionary context of endurance running. Obviously, the fossil record does not contain information about soft tissue anatomy, while the present data was exclusively collected on the external surface of the torso and so the relations between skeletal and soft tissue anatomy are unknown. Yet, bony features are considered. The curvature of the spine is assessed by the tips of the spinous processes which are variable in terms of sagittal orientations and thus do not directly inform about the curvature as assessable on the basis of the vertebral bodies. Also, the ribcage anatomy is only indirectly reflected by the skin surface landmarks and closer to skeletal thorax shape only at the central and lower parts of the rib cage. These data can thus only give a general idea about thorax shape. The pelvic landmarks are clearer in this respect as the iliac spines can be identified without problems. However, the reduced landmark set, which excluded shape information related to the latissimus dorsi and major pectoralis muscles may be less influenced by muscularity, and the fact that the results of the full and the reduced data are similar suggests little soft tissue effects on the results.

Further limitations are related to the proper running experiment. Endurance running in the evolutionary context appeared in the context of specific climatic conditions that were not considered in the present experiment. Also, actual endurance running is defined as running at intermediate velocities and aerobic conditions for longer time than considered in our experiment, where we only tested for potential relations between velocity and aerobic running conditions during the early stages of the incremental exercise. In this perspective, our data are only informative about shape-function relation during high intensity running. Future studies should relate torso shape to running performance data on velocity and distance during longer trials and in hot weather conditions. Such analysis will provide further insight into the important relationships between torso shape, body shape and locomotor performance relevant for human evolution.

Received: 22 December 2021; Accepted: 22 June 2022
Published online: 11 July 2022

References

1. Franciscus, R. G. & Churchill, S. E. The costal skeleton of Shanidar 3 and a reappraisal of Neandertal thoracic morphology. \textit{J. Hum. Evol.} \textbf{42}, 303–356 (2002).
2. Gómez-Olivencia, A. et al. 3D virtual reconstruction of the Kebara 2 Neandertal thorax. \textit{Nat. Commun.} \textbf{9}, 4387 (2018).
3. Bastir, M. et al. Rib cage anatomy in \textit{Homo erectus} suggests a recent evolutionary origin of modern human body shape. \textit{Nat. Ecol. Evol.} \textbf{4}, 1178–1187 (2020).
4. García-Martínez, D. et al. Early development of the Neanderthal ribcage reveals a different body shape at birth compared to modern humans. \textit{Sci. Adv.} \textbf{6}, eabb4377 (2020).
5. Arsuaga, J. L. et al. A complete human pelvis from the middle pleistocene of Spain. \textit{Nature} \textbf{399}, 255–258 (1999).
6. Simpson, S. W. et al. A female \textit{Homo erectus} pelvis from Gona, Ethiopia. \textit{Science} \textbf{322}, 1089–1092 (2008).
7. Torres-Tamayo, N. et al. Three-dimensional geometric morphometrics of thorax-pelvis covariation and its potential for predicting the thorax morphology: A case study on Kebara 2 Neandertal. \textit{J. Hum. Evol.} \textbf{147}, 102854 (2020).
8. Stansfield, E., Fischer, B., Grunstra, N. D. S., Pouca, M. V. & Mitteroecker, P. The evolution of pelvic canal shape and rotational birth in humans. \textit{BMC Biol.} \textbf{19}, 1–11 (2021).
9. Meyer, M. R. & Williams, S. A. The Spine of Early Pleistocene Homo. In \textit{The Human Spine} (eds Been, E. et al.) 153–1845 (Springer, 2019).
10. Gómez-Olivencia, A., Couture-Veschambre, C., Madelaine, S. & Maurelle, B. The vertebral column of the Regourdou 1 Neandertal. \textit{J. Hum. Evol.} \textbf{64}, 582–607 (2013).
11. Bastir, M. et al. Three-dimensional morphometrics of thoracic vertebrae in Neandertals and the fossil evidence from El Sidrón (Asturias, Northern Spain). \textit{J. Hum. Evol.} \textbf{108}, 47–61 (2017).
12. Been, E., Gómez-Olivencia, A. & Kramer, P. A. Lumbar lordosis of extinct hominins. \textit{Am. J. Phys. Anthropol.} \textbf{147}, 64–77 (2012).
13. Been, E. et al. Evolution of spinopelvic alignment in hominins. *Anat. Rec.* **300**, 900–911 (2017).
14. Hauser, M. et al. Morphology, pathology, and the vertebral posture of the La Chapelle-aux-Saints Neandertal. *Proc. Natl. Acad. Sci. USA* **116**, 4923–4927 (2019).
15. Ruff, C. Body size and body shape in early hominins—implications of the Gona Pelvis. *J. Hum. Evol.* **58**, 166–178 (2010).
16. Aiello, A. & Wheeler, P. The expensive tissue hypothesis: The brain and digestive system in human and primate evolution. *Curr. Anthropol.* **36**, 199–221 (1995).
17. Bramble, D. M. & Lieberman, D. E. Endurance running and the evolution of Homo. *Nature* **432**, 345–352 (2004).
18. Lieberman, D. E., Bramble, D. M., Raichlen, D. A. & Shea, J. J. Brains, brawn and the evolution of human endurance running capabilities. In *The first humans: origin and early evolution of the genus Homo*. 77–92 (Springer, 2009).
19. Raichlen, D. A., Armstrong, H. & Lieberman, D. E. Calcaneus length determines running economy: Implications for endurance running performance in modern humans and Neandertals. *J. Hum. Evol.* **60**, 299–308 (2011).
20. Stewart, J. R. et al. Palaeoecological and genetic evidence for Neandertal power locomotion as a adaptation to a woodland environment. *Quat. Sci. Rev.* **217**, 310–315 (2019).
21. Lordkipanidze, D. et al. Postcrania1 evidence from early Homo from Dmanisi, Georgia. *Nature* **449**, 305–310 (2007).
22. Pontzer, H. Economy and endurance in human evolution. *Curr. Biol.* **27**, R613–R621 (2017).
23. Weaver, T. D. The meaning of Neandertal skeletal morphology. *Proc. Natl. Acad. Sci. USA* **106**, 16028–16033 (2009).
24. Steudel-Numbers, K. L., Weaver, T. D. & Wall-Scheffler, C. M. The evolution of human running: Effects of changes in lower-limb length on locomotor economy. *J. Hum. Evol.* **53**, 191–196 (2007).
25. Mattes, K., Schaffert, N., Habermann, N. & Mühlbach, T. A longitudinal study of kinematic stride characteristics in maximal sprint running. *J. Hum. Physiol. 9*, 686–699 (2014).
26. Kubo, T. Contribution of trunk muscularity on sprint run. *Int. J. Sports Med.* **32**, 223–228 (2011).
27. Esteve-Lanao, J., Sanjuan, A. F., Earnest, C., Foster, C. & Lucia, A. How do endurance runners actually train? Relationship with competition performance. *Med. Sci. Sports Exerc.* **37**, 496–504 (2005).
28. Esteve-Lanao, J., Rhea, M. R., Fleck, S. J. & Lucia, A. Running-specific, periodized strength training attenuates loss of stride length during intense endurance running. *J. Strength Cond. Res.* **22**, 1176–1183 (2008).
29. van Oeveren, B. T., de Ruiter, C. J., Beek, P. J. & van Dieën, J. H. The biomechanics of running and running styles: a synthesis. *Sports Biomech.* **1**, 39–63 (2021).
30. Fujita, S. A 100-m sprint time is associated with deep trunk muscle thickness in collegiate male sprinters. *Front. Sports Act. Living* **1**, 32 (2019).
31. Copaver, K., Hertogh, C. & Hue, O. The effects of psoas major and lumbar lordosis on hip flexion and sprint performance. *Res. Q. Exerc. Sport* **83**, 160–167 (2012).
32. Warren, A., Tamai, R. & Lieberman, D. E. The effect of trunk flexion angle on lower limb mechanics during running. *Hum. Mov. Sci.* **78**, 102817 (2021).
33. Castillo, E. R., Hsu, C., Mair, R. W. & Lieberman, D. E. Testing biomechanical models of human lumbar lordosis variability. *Am. J. Phys. Anthropol.* **163**, 110–121 (2017).
34. Castillo, E. R. & Lieberman, D. E. Shock attenuation in the human lumbar spine during walking and running. *J. Exp. Biol.* **221**, 16799–16800 (2018).
35. Aliverti, A. et al. Human respiratory muscle actions and control during exercise. *J. Appl. Physiol.* **83**, 1256–1269 (1997).
36. Kenyon, C. M. et al. Rib cage mechanics during quiet breathing and exercise in humans. *J. Appl. Physiol.* **83**, 1242–1255 (1997).
37. Torres-Tamayo, N. The torso integration hypothesis revisited in Homo sapiens: Contributions to the understanding of hominin body shape evolution. *Am. J. Phys. Anthropol.* **167**, 777–790 (2018).
38. Waldock, C., Milne, N., Rubenson, J. & Donnelly, C. J. The use of geometric morphometric techniques to identify sexual dimorphism in Gait. *J. Appl. Biomech.* **32**, 441–448 (2016).
39. Vialle, R. et al. Radiographic analysis of the sagittal alignment and balance of the spine in asymptomatic subjects. *J. Bone Jt. Surg.* **87**, 260–267 (2005).
40. Ložiniski, L. et al. 3D geometric morphometric analysis of variation in the human lumbar spine. *Am. J. Phys. Anthropol.* **170**, 361–372 (2019).
41. García-Martínez, D. et al. Sexual dimorphism in the vertebral wedging of the human lumbar vertebrae and its importance as a comparative framework for understanding the wedging pattern of Neanderthals. *Quat. Int.* **566–567**, 224–232 (2020).
42. Hsu, C., Castillo, E. R. & Lieberman, D. The relationship between trunk muscle strength and flexibility, intervertebral disc wedging, and human lumbar lordosis. *Harvard Undergrad. Res. J.* **8**, 35–41 (2015).
43. Callison, W. E., Holowka, N. B. & Lieberman, D. E. Thoracic adaptations for ventilation during locomotion in humans and other mammals. *J. Exp. Biol.* **222**, 16793577 (2019).
44. Bellemare, F., Jeanneret, A. & Couture, J. Sex differences in thoracic dimensions and configuration. *Am. J. Respir. Crit. Care Med.* **168**, 305–312 (2003).
45. Bellemare, F., Fuamba, T. & Bourgea, A. Sexual dimorphism of human ribs. *Respir. Physiol. Neurobiol.* **150**, 233–239 (2006).
46. Sanchez-Gimeno, J. A. et al. Association between ribs shape and pulmonary function in patients with Osteogenesis Imperfecta. *J. Adv. Res.* **21**, 177–185 (2020).
47. Beyer, B. et al. In vivo thorax 3D modelling from costovertebral joint complex kinematics. *Clin. Biomech.* **29**, 434–438 (2014).
48. Beyer, B., Van Sint Jan, S., Chêze, L., Sholukha, V. & Feipel, V. Relationship between costovertebral joint kinematics and lung volume in supine humans. *Respir. Physiol. Neurobiol.* **232**, 57–65 (2016).
49. Dominelli, P. R. et al. Effects of respiratory muscle work on respiratory and locomotor blood flow during exercise. *Exp. Physiol.* **102**, 1535–1547 (2017).
50. Horiiuchi, M., Kirihara, Y., Fukuoka, Y. & Pontzer, H. Sex differences in respiratory and circulatory cost during hypoxic walking: potential impact on oxygen saturation. *Sci. Rep.* **9**, 9550 (2019).
51. Bastir, M. et al. Workflows in a Virtual Morphology Lab: 3D scanning, measuring, and printing. *J. Anthropol. Sci.* **97**, 1–28 (2019).
52. González-Ruiz, J. M., Pérez-Núñez, M. I., García-Alfaro, M. D. & Bastir, M. Geographic morphometrics of adolescent idiopathic scoliosis: a prospective observational study. *Eur. Spine J.* **30**, 612–619 (2021).
53. Pugh, L. G. Oxygen intake in track and treadmill running with observations on the effect of air resistance. *J. Physiol.* **207**, 823–835 (1970).
54. Lucia, A. et al. Physiological characteristics of the best Eritrean runners—exceptional running economy. *Appl. Physiol. Nutr. Metab.* **31**, 530–540 (2006).
55. Hammer, O. PAST: Palaeontological Statistics, version 3.25. (2019)
56. Gunk, P. & Mitteroecker, P. Semilandmarks: A method for quantifying curves and surfaces. *Hystrix* **24**, 103–109 (2013).
57. Klingenberg, C. P. MorphoJ: An integrated software package for geometric morphometrics. *Mol. Ecol. Resour.* **11**, 353–357 (2011).
58. StatSoft. *Statistica 8.0*. StatSoft, Inc., Tulsa, OK, USA. (1984–2007).
59. Adams, D. C. & Otárola-Castillo, E. Geomorph: An R package for the collection and analysis of geometric morphometric shape data. *Methods Ecol. Evol.* **4**, 393–399 (2013).
60. R Core Team. R: A language and environment for statistical computing (2017).
61. EVAN-Society. ET, Toolkit for geometric morphometric analysis (2010).
62. Rosenberg, K. R., Zuné, L. & Ruff, C. B. Body size, body proportions, and encephalization in a Middle Pleistocene archaic human from northern China. *Proc. Natl. Acad. Sci. USA* **103**, 3552–3556 (2006).

63. Ruff, C. B., Burgess, M. L., Squyres, N., Junno, J.-A. & Trinkaus, E. Lower limb articular scaling and body mass estimation in Pliocene and Pleistocene hominins. *J. Hum. Evol.* **103**, 85–111 (2018).

64. Ball, J. M., Cagle, P., Johnson, B. E., Lucasey, C. & Lukert, B. P. Spinal extension exercises prevent natural progression of kyphosis. *Osteoporos. Int.* **20**, 481–489 (2009).

65. Feng, Q., Wang, M., Zhang, Y. & Zhou, Y. The effect of a corrective functional exercise program on postural thoracic kyphosis in teenagers: A randomized controlled trial. *Clin. Rehabil.* **32**, 48–56 (2018).

66. Kang, J.-Y., Seo, D.-K., Cho, J.-C. & Lee, B.-K. Effectiveness of breathing exercises on spinal posture, mobility and stabilization in patients with lumbar instability. *J. Korean Soc. Phys. Med.* **13**, 81–89 (2018).

67. LoMauro, A. *et al.* Rib cage deformities alter respiratory muscle action and chest wall function in patients with severe osteogenesis imperfecta. *PLoS ONE* **7**, e35965 (2012).

68. Ruff, C. B., Trinkaus, E. & Holliday, T. W. Body mass and encephalization in Pleistocene *Homo*. *Nature* **387**, 173–176 (1997).

69. Been, E., Gómez-Olivencia, A., Kramer, P. A. & Barash, A. 3D Reconstruction of the spinal posture in the Kebara 2 Neanderthal. In *Human Paleontology and Prehistory* (eds Marom, A. & Hovers, E.) 239–251 (Springer, 2017).

70. Latimer, B. & Ward, C.V. The thoracic and lumbar vertebrae, in *The Nariokotome Homo erectus Skeleton*. 266–293 (Harvard University Press, 1993).

71. Ruff, C. B. & Burgess, M. L. How much more would KNM-WT 15000 have grown?. *J. Hum. Evol.* **80**, 74–82 (2015).

72. Torres-Tamayo, N. *et al.* New reconstruction of the pelvis of KNM-WT 15000 supports a wide body shape for Early African *H. erectus*. *Proc. Eur. Soc. Stud. Hum. Evol. Hum. Evol.* (2021).

**Acknowledgements**

We thank the volunteers for participating in this study. Funding: Grant PID2020-115854GB-I00 to MB is funded by MCIN/AEI/10.13039/501100011033 of the Spanish Ministry of Science and Innovation and the European Union. We thank Prof. Mitteroecker and one anonymous reviewer for their helpful comments.

**Author contributions**

M.B. designed the associated research project, collected 3D surface data, analysed the geometric morphometrics data, wrote the main manuscript and prepared the Figures. J.M.G.R. collected and postprocessed the 3D-landmark data, prepared Figures and wrote parts of the paper. M.G.R programmed code and analysed additional data. M.B., B.B., A.S.J. and E.N worked on the development of the experimental procedures. M.B., J.R., G.G.L., A.S.J. and E.N. carried out the experiments and A.S.J and E.N supervised all steps of the experiment at the laboratory. All authors reviewed the manuscript.

**Competing interests**

The authors declare no competing interests.

**Additional information**

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-022-15344-x.

Correspondence and requests for materials should be addressed to M.B.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher’s note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2022