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Geometric morphometrics of 4D motion data: a proof of concept for applications in palaeoanthropology

Morfometría geométrica de movimiento 4D: una prueba de concepto para aplicaciones en paleoantropología

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Abstract: This paper presents a proof of concept in the study of human respiratory motion from a palaeoanthropological approach. The hybrid methodology proposed merges Motion Capture techniques (optoelectronic plethysmography) with 3D geometric morphometrics of the superior torso surface during incremental running exercise. Results reveal the importance of the expiratory phase during high-intensity exercise breathing and arouse a discussion about the structure and function of the respiratory system in human evolution.

Resumen: Este artículo presenta una *prueba de concepto* (test de método) en el estudio del movimiento respiratorio humano desde un enfoque paleoantropológico. La metodología híbrida propuesta fusiona técnicas de captura de movimiento (pletismografía optoelectrónica) con morfometría geométrica 3D del torso superior durante el ejercicio incremental en la carrera. Los resultados revelan la importancia de la fase espiratoria durante la respiración en ejercicio de alta intensidad y sugieren una discusión acerca de la estructura y función del sistema respiratorio en la evolución humana.

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Palabras-clave:
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INTRODUCTION

Virtual morphology, geometric morphometrics, and optoelectronic plethysmography for motion capture

How structure and function are related to each other is one of the main questions of evolutionary biology (Olson & Miller, 1958; Rudwick, 1964; Bock & Wahlert, 1965; Gould, 1970; Nachtigall, 1991; Foote, 1997; Erwin, 2007; Cooke & Terhune, 2014). Consequently, this also attracts attention from the palaeontological perspective. Virtual morphological methods (Elewa, 2011; Rahman & Smith, 2014; Sutton *et al.*, 2016) have contributed considerably over the last decades to the reconstruction of fossil anatomical structures (Gunz *et al.*, 2009), but more recently, these methods have also been used for the reconstruction of behavioural aspects of extinct organisms and their relationship with their environment, defining their ecological roles in systems, hence, their biology (Rahman, 2017; Godinho *et al.*, 2018; Gómez-Olivencia *et al.*, 2018; Bastir *et al.*, 2020).

The ecology of animals is driven by motion, an essential component for the manifestation of all kinds of behavior, which can be studied through the biomechanics of mobile structures. In palaeontology, many aspects of ethology can be inferred through the study and reconstruction of the shape of organisms and their comparison with recent animals, extrapolating observed links between structure and function. However, few works from this field introduce the multivariate analysis of experimental quantitative data regarding the movement of biological structures as the central objective of their research, which is why quantifying *in vivo* movement is of high interest in evolutionary biology. In this work, we present a proof of concept for a new method in the quantification of motion (4D) in the context of human palaeontology, subdividing it into structure (measured by 3D-form) and function (measured by motion along 1D-time) and discussing it from the framework of the evolution of the respiratory system.

One structure that is starting to arouse palaeoanthropological interest is the torso (Torres-Tamayo *et al.*, 2018; Bastir *et al.*, 2022). As the principal axial structure of the body, its form and function (including motion) are highly interesting in the context of the locomotor, respiratory and energetic points of view (Franciscus & Churchill, 2002; Bastir, 2004, 2008; Froehle & Churchill, 2009; Beyer, 2016; Chapman *et al.,* 2017). The thorax has been in the spotlight of the study of the hominin torso since the first contributions made by Arensburg (1991) on the Neanderthal remains of Kebara 2, and by Jellema (1993) on *Homo ergaster* KNM-WT 15000. These authors proposed a modern anatomy for the *Bauplan* of these species, while posterior works suggested a different, wider thoracic morphotype in relation to body size (Franciscus & Churchill, 2002; Gómez-Olivencia *et al.,* 2009). Contemplating the torso as one key element determining body shape, the integration of the thorax with the pelvis, an equally important element that shapes torso form, must be considered (Schmid *et al.*, 2013; Torres-Tamayo *et al.*, 2018). Recently, as a result of the development of new computational techniques, the latest virtual tridimensional reconstructions of hominin ribcages (Gómez-Olivencia *et al.*, 2018; Bastir *et al.*, 2020; García-Martínez *et al.,* 2020a) have shed some light on the scientific knowledge about the evolution of the thoracic form. According to these latest contributions, modern humans would probably express a derived anatomy, due to their flat and narrow thoraces.

As a consequence of different torso morphotypes spanning probably in a mosaic pattern (Holliday, 2012; Schmid *et al.*, 2013; Gruss & Schmitt, 2015), we hypothesize that throughout human evolution the respiratory function (in particular ventilatory biomechanics) varied accordingly to these different *Baupläne*, entailing palaeophysiological and palaeoecological implications (Bastir *et al.*, 2022). This work presents the first steps towards a quantitative link between the human respiratory structure and function as a proxy that can be potentially extrapolated to a palaeontological context. Hominin ventilatory mechanics depend on the biomechanics and three-dimensional shape of the principal structures that conform the upper and mid torso. These are the thorax (Openshaw *et al.*, 1984; Bastir *et al.*, 2017), the main respiratory skeletal structure, which hosts the main muscles involved in the respiratory process, such as the diaphragm and ribcage muscles; and the abdomen, which holds accessory expiratory muscles (Aliverti & Pedotti, 2002; Flynn & Vickerton, 2019).

One of the main morphological thoracic features that seems to have changed during hominin evolution is the anteroposterior depth of the thorax, a consequence of the individual morphologies of the ribs (García-Martínez *et al.*, 2016; Gómez-Olivencia *et al.*, 2018; Bastir *et al.*, 2020; García-Martínez *et al.*, 2020b).

Recently, Bastir *et al.* (2020) proposed that in *Homo* a deep thorax with low rib torsion is a primitive condition in contrast to modern humans' flat thorax and a high degree of rib torsion, which implies potential differences in thorax motion and biomechanics (Openshaw *et al.*, 1984; LoMauro & Aliverti, 2018; García-Martínez *et al.*, 2019). These authors proposed mechanical differences between deep and wide torsos and flat and narrow torsos, which would allow the use of these deep/flat phenotypes as a palaeontological proxy.

To deal with these aspects from the perspective of mechanics, specifically breathing kinematics, we combine geometric morphometrics (**GMM**; Bookstein, 1991), widely used in palaeontology (Elewa, 2004; Zelditch *et al.*, 2004), with motion capture data obtained through Optoelectronic Plethysmography (**OEP**; Ferrigno & Pedotti, 1985; Cala *et al.,* 1996; Aliverti & Pedotti, 2002), more recently used in respiratory physiology and sports sciences (Vogiatzis *et al.*, 2005; Layton *et al.,* 2011, 2013). GMM is the quantitative analysis of biological shape variation based on anatomical landmark data that consist of 3D Cartesian coordinates (Bookstein, 1991). OEP is a method for the quantification of chest wall motion based on the analysis of motion trajectories of a series of marker points, defined by variations of their 3D Cartesian coordinates along time (Cala *et al.,* 1996). The variation of these coordinates communicates directly with the concepts and toolkit of GMM.

Therefore, the aim of this study is to present a preliminary, hybrid-methodological approach to understanding the quantitative links between torso form and its respiratory function as motion patterns in the context of hominin evolution.

MATERIAL AND METHODS

The quantitative integration of motion and shape analyses enables the development of a methodology that, applied to a recent, living sample, brings together structure and function. Applied to palaeontology, this allows identifying proxies to infer functionality from its relationship to biological form. The present proof of concept is a first approach to testing this hybrid methodology through the study of ventilation during incremental exercise. Incremental exercise places torso motion (changes in form through time) close to its mechanical and physiological limits. Therefore, it can be used to explore the respiratory movement from the point of view of functional anatomy and its potential consequences in hominin palaeoecology related to endurance exercise (Carrier *et al.,* 1984; Bramble & Lieberman, 2004).

GMM is a mathematical tool for the measurement of biological shape through the placement of anatomically homologous points, or landmarks, that are characterised by two or three-dimensional Cartesian coordinates (Zelditch *et al.*, 2004). The use of this tool made possible the breaking down of form into shape and size, a relevant achievement for biological studies. GMM not only enables the statistical quantification of shape and its variation, but also a detailed description of differences in shape in an intuitive graphic method based on the consistency and repeatability of the mathematical analysis of geometric variation.

In this study, GMM is used as a method of measuring and comparing the respiratory movement of two individuals, one with a flat torso and the other with a deep torso. With this purpose, the shape of the respiratory trajectories reflected by a Principal Component Analysis (**PCA**) derived from torso morphometrics at different instants of an average respiratory cycle is analysed. In this case, homologous anatomical structures are not directly analysed, but rather the respiratory cycle is interpreted as a trajectory of shapes, a biological event (structure), from the beginning to the end of a cyclical ventilatory movement that relates the respiratory function to the torso form. This functional anatomy analysis provides a new tool in the field of palaeomechanics that, applied to three-dimensional reconstructions of fossils such as the rib cages of KNM-WT 15000 (Bastir *et al.*, 2020) or Kebara 2 (Gómez-Olivencia *et al.*, 2018) could shed light on the evolution of the human respiratory system.

Sample, analyses and data sources

A sample of 27 young male student volunteers (18–29 years of age) from the Degree in Sciences of Physical Activity and Sports formed part of this experimental test (Bastir *et al.*, 2022). The selected students were young athletes, trained either in endurance or team sports. The form of their torsos was captured through 3D surface scanning using Artec MHT 3D (www.artec3d.com), in standardized upright position (González-Ruiz *et al.*, 2021; *Bastir et al.*, 2022). The complete torso morphological variation was studied through these 3D surface models. 160 landmarks and semilandmarks (Fig. 1; González-Ruiz *et al.*, 2021) were used to measure torso form and standard GMM procedures (Gunz & Mitteroecker, 2013) were carried out through Morphologika2 v2.5 (O'Higgins & Jones, 2006) and R environment (R v4.2.0 and RStudio v1.4.1717; R Core Team, 2022), specifically through geomorph (Adams & Otárola-Castillo, 2013) and Morpho (Schlager *et al.*, 2021) packages.

GMM data collection and analysis. For the statistical treatment of form, a Generalized Procrustes Analysis (**GPA**; Gower, 1975) was performed, through the rotation, scaling, and translation of the torso configurations, minimizing variances among the Cartesian coordinates of homologue 3D landmarks (GPA1). This yielded a set of Procrustes shape coordinates. Posteriorly, on these shape coordinates we performed a Principal Component Analysis (PCA; PCA1) in Procrustes form space (*i.e.*, including size and shape variation) (Mitteroecker *et al.*, 2004; Bastir *et al.*, 2007). Considering form variation rather than shape introduces the importance of size as an expression of the air volume inspired in the study of ventilatory motion, which allows us to make mechanical and physiological interpretations (Aliverti *et al.*, 1997). The purpose of this PCA1 is to describe principal morphological variations that define the torso sample and to extract torso shape features potentially relevant to the context of human evolution that could be analysed in relation to motion in the following step.

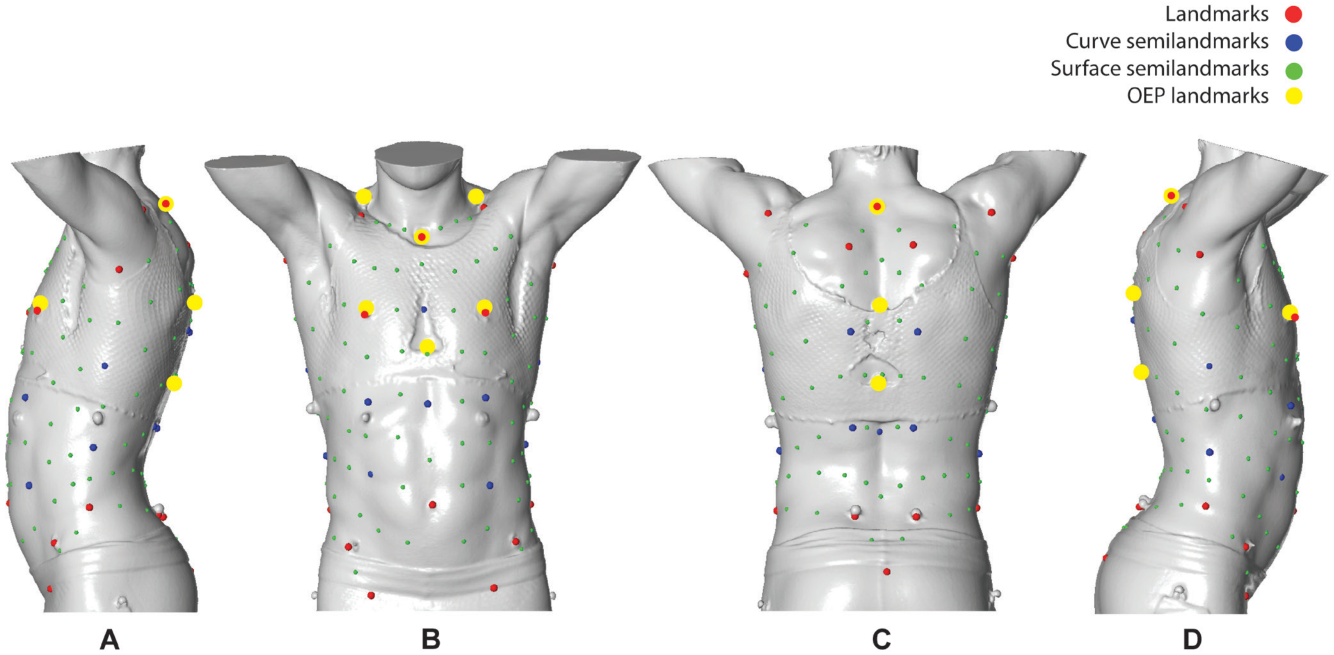

Figure 1. Complete torso landmark template. Template described in González-Ruiz *et al.* (2021) and with the addition of OEP landmarks (described in Tab.1). **A,** Left lateral view; **B,** Anterior view; **C,** Right lateral view; **D,** Posterior view.

Motion Capture data collection and analysis. Once the torso form was collected, the students faced an incremental running test (Bastir *et al.*, 2022). In this work, we use the high-intensity phase of the exercise (85% of heart rate reserve) to push respiratory mechanics to their limits. Seven individuals from the sample were selected for preliminary analyses of shape motion. Thereby, a new, reduced landmark template was used to explore movement variation through OEP (Fig. 1, OEP landmarks; Tab. 1), a motion capture technique used to measure chest wall motion (Aliverti & Pedotti, 2002). Infrared reflective markers, used here as motion landmarks, were placed directly on specific anatomical regions at the superior chest wall of the athletes and their motion patterns were recorded during the incremental running test. This was achieved by six infrared cameras at the INEF (Vicon System; Bastir *et al.*, 2022) capable of tracking the movements of these markers during the high-intensity phase of the exercise (heavy exercise breathing).

Table 1. Anatomical description and numeration of the OEP landmark template.

Landmark No.	Anatomical correspondence
1	Prominence of the first thoracic vertebra
2	Prominence of the fifth thoracic vertebra
3	Prominence of the tenth thoracic vertebra
4	Sternal notch
5	Xiphoid process of the sternum
6	Anterior prominence of the left first rib
7	Anterior prominence of the right first rib
8	Anterior prominence of the left fifth rib
9	Anterior prominence of the right fifth rib

We collected the respiratory motion of the chest wall during five complete respiratory cycles, from the end-expiratory status (**endEX**) to the end-inspiratory status (**endIN**). This motion coordinate data was post-processed in Mokka software (Barre & Armand, 2014) to extract the three-dimensional position of the OEP landmarks during 20 equidistant instants (in time, per individual) of a complete average respiratory cycle to minimize measuring error and breathing irregularities. Each of these 20 instants corresponds to a 3D configuration sequentially captured in an average respiratory cycle, and therefore corresponding with different torso geometries captured during heavy exercise breathing. This way, ventilatory movement during locomotion was translated to kinematic variation in torso form during time. This allowed us to merge OEP methodology with GMM and develop a standard analysis of form in motion.

Consequently, 20 instants of torso form, captured per each of the seven individuals, resulted in 140 form configurations, which were subjected to the analysis. GPA2 was performed over these and processed through a new PCA2 analysis into a Procrustes form space. This form space revealed a series of circular respiratory trajectories in a 2D projection (PC1 and PC2), orientated in the inspiratory-expiratory direction (the direction of principal size variation). In this form space, the trajectories resulted in different circular shapes, which reflected the biological cyclicity of ventilation consisting of two biomechanically and physiologically distinct expiratory and inspiratory phases. These phases can be geometrically compared considering their similar orientation in the projection to tangent space (see Results). The endEX and the endIN can be treated as functionally homologous physiological instants. Here, we merge structure and function from the boundaries of motion that result from an incremental exercise test in the high-intensity phase of heavy exercise breathing. The trajectories of two individuals were selected to compare their breathing shapes. These individuals were selected as morphological extremes, as proxies of anteroposteriorly deep and flat torsos. Each respiratory trajectory in the PCA is composed of 20 configurations (PC scores), defined by its x and y position in the space defined by PC1 and PC2. This way, the deep and flat torsos respiratory trajectories were defined by 20 2D coordinates that were translated to 2D landmarks in a third GMM analysis (this time analysing trajectories). This way, the shape of trajectories becomes a new set of variables which were preliminarily analysed using a different GMM superimposition method: Bookstein baseline superimposition (**BBS**; Bookstein, 1991), through the software CoordGen8 (Zelditch *et al.*, 2004). This geometrical fit consists of the superimposition of landmark configurations in a Cartesian plane, with the configurations being defined by two anatomically homologous points. However, in this case of study, the object of comparison were not biological structures, but their function, expressed in terms of the shape of their motion trajectory. These two points are endEX and endIN. They can be considered functionally homologous (Wagner, 1989) because they reflect the configurations of maximum change in form linked to the biomechanical and physiological limits of heavy exercise breathing in both individuals. This kind of superimposition allows for the physiological comparison of respiratory cycles during the high-intensity phase of the exercise. Through BBS, the configurations of a deep torso trajectory and a flat torso trajectory were translated, rotated, and rescaled. To do so, the landmark endEX was situated in the plane over (0,0), while the landmark endIN was situated over (0,1), defining the baseline (abscissa). This fit allowed the geometrical description and comparison of the trajectories and the exploration of differences in ventilatory kinematics.

RESULTS

PCA1 on torso form revealed the principal component of its morphological variation (Fig. 2A). PC1 explained 40.30% of form variance (including size and shape variation). The 3D models that show the morphological extremes of PC1 (Fig. 2A) separate the torso configurations by size and shape, finding shorter and smaller torsos with more lordotic backs towards the negative values of PC1, and relatively flatter, narrower, taller and larger torsos with straighter backs towards positive PC1 scores.

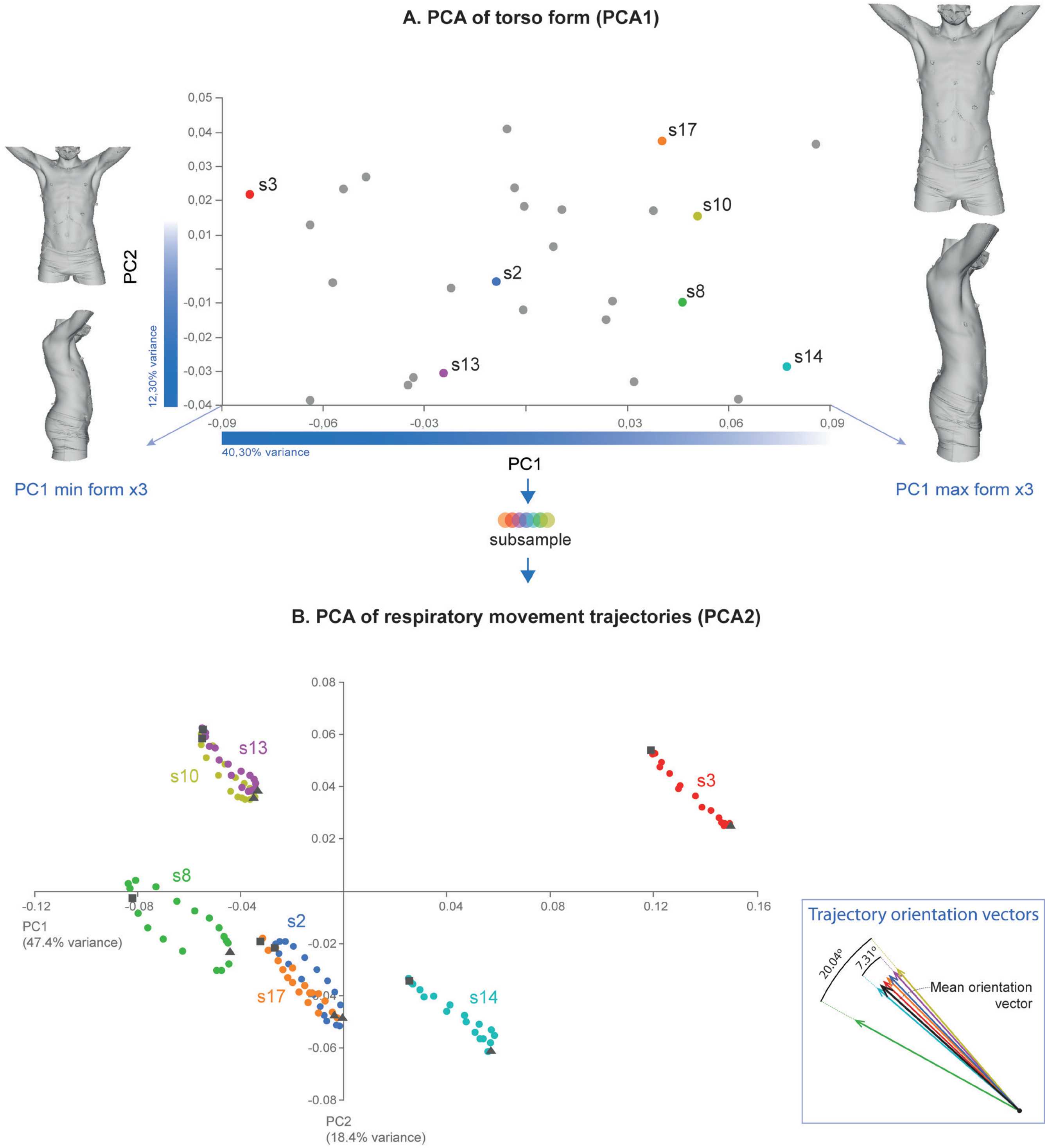

Figure 2. A, PCA of torso form of the student sample; **B,** PCA of 7 respiratory trajectories obtained from the student subsample. Note that the trajectory orientation vectors are very similar, presenting a maximum difference in orientation of 20.04**º**. The difference in the orientation of the trajectories of the proxies for deep (s13) and flat (s14) torsos is of 7.31º, allowing their posterior superimposition through BBS without losing information about the morphospace they belong to.

Through this form space, a subsample of seven individuals was selected for the motion capture analysis during the high-intensity phase of exercise (Fig. 2B). The selected individuals express the morphological variation contained in PC1 (PCA1) ranging from deep to flat torsos. However, PCA2 (Fig. 2B) is a new morphospace showing the principal components (65.8% of total variance) of respiratory motion common to all individuals.

PCA2 shows seven circular trajectories, reflecting cyclical average respiratory movements. As this is a form space analysis, the trajectories are orientated in the direction of changes in size (measured as Centroid Size). They correspond to the endEX and endIN instants of the respiratory trajectory. The orientation of the circular trajectories is quite similar between individuals, finding an average difference of 7.38**º** (Fig. 2B; trajectory orientation vectors range from 0.51º to 20.04º). Therefore, they are comparable by superimposition, maintaining the meaning of the axes that define that morphospace (PCA2).

The first approach towards the geometric comparison of cyclical respiratory movement trajectories was carried out between two subjects (Fig. 3). The selected subjects share similar PC2 values (Fig. 2A) and their principal differences in form can be expressed by PC1. Thus, subject s13 displays a wider and deeper torso (and therefore, thorax) than s14, which can be observed in the lateral view of the torsos in Figure 3. On the contrary, s14 presents a flatter, more gracile torso, which results in a flat chest wall. These subjects can thus be considered as proxies for torso shapes that are relevant to human evolution.

Apart from their morphological differences, these individuals present also a series of differences in their respiratory trajectories. The trajectories can be divided into two phases with different physiological and biomechanical meanings. The inspiratory phase elapses from the endEX to the endIN, and the expiratory phase elapses from the endIN to the endEX, following the direction of the arrows (Fig. 3). In both individuals the kinematic component explained by the ordinate is larger in the expiratory phase. This is indicative of differential motion patterns and magnitude between phases during forced respiratory movement of the superior torso. Importantly, during the inspiratory phase the magnitude of morphological change (motion) defined by the ordinate is slightly larger in the deep torso configuration.

This kind of geometric fit reveals potentially differential respiratory movements in subjects with deep and flat torso forms. It shows, more specifically, that the principal motion difference during the high-intensity phase of incremental exercise occurs during the expiratory phase, which can be observed through the superimposition of both trajectories (Fig. 3). While inspiratory movement seems to be similar in both deep and flat forms, expiratory movement follows a different trajectory during this phase of the exercise.

DISCUSSION

This proof of concept presents a new tool for the study of the statistical link between structure and function in a palaeoanthropological framework. Quantifying respiratory movement through GMM and motion capture techniques enables the translation of function to measurable data that can be used to address evolutionary questions, a method that can be extended into other palaeontological studies.

Specifically, this study has found evidence for biomechanical differences in the respiratory movement of two individuals used as palaeontological proxies of deep and flat torso configurations. The expiratory function stands out as the determining phase of the respiratory cycle during heavy exercise breathing in an incremental exercise test. This may be indicative of the physiological role of exhalation to increment the subsequent inspiratory cycle and, thus, enhance respiratory efficiency. Actually, a study by Aliverti (2016) revealed that expiratory requirements gained relevance during intense exercise demands, where an increase of VO_2 max (maximal oxygen uptake) is needed to maintain exercise performance. Thus, in healthy subjects, differences in the forced expiratory phase could be observed. This fact is opposite to the one observed in non-healthy subjects (*i.e.*, osteogenesis imperfecta), where the significant differences were present during the inspiratory phase rather than the expiratory phase (González-Ruiz *et al.*, 2021). These differences were found in *in vivo* individuals, evidencing a relationship between torso form and respiratory function. Following this rationale, the different thoracic phenotypes of fossil hominin specimens could lead to differences in respiratory function. Therefore, we propose that during high-intensity breathing, differences in inspired air volume and respiratory efficiency are determined by torso form and by the expiratory movement, rather than the inspiratory one, which would reach its biomechanical limit before this phase**.** This hypothesis, however, needs to be tested with the necessary detail. Through the present work, we tested the workflow and methodology, based on a small sample size and very small number of markers (OEP landmarks). In the future, this method needs to be reinforced through a larger sample and marker number, such as using the "full marker protocol" (89 marker template) typical of OEP analyses (Aliverti & Pedotti, 2002). Only in such an experimental setting the anatomical detail can be revealed and analysed with statistical robustness. However, for the moment, the data do serve perfectly as methodological proof of concept.

From a palaeontological and evolutionary perspective, the modern human anatomy of the trunk and thorax is derived. The modern human trunk is characterized by a flat and narrow thorax and a tall, large torso, while the latest fossil hominin thorax reconstructions are described as anteroposteriorly deeper, wider, and stockier than actual forms (Gómez-Olivencia *et* *al.*, 2018; Bastir *et al.*, 2020; García-Martínez *et al.*, 2020a). This would imply respiratory biomechanical differences in the derived anatomy, compared to other fossil hominins. Bastir *et al.* (2022) proposed that a flat thorax (smaller anteroposterior diameter) would be related to increased running performance during high-intensity exercise. This could be linked to the kinematic differences observed here, specifically regarding the expiratory motion of the torso surface.

Fossil hominin thorax reconstructions, such as *Homo ergaster* KNM-WT 15000 (Bastir *et al.*, 2020) or *Homo neanderthalensis* Kebara 2 (Gómez-Olivencia *et al.*, 2018; García-Martínez *et al.*, 2020a) can be considered analogous to the deep torso modern human proxy

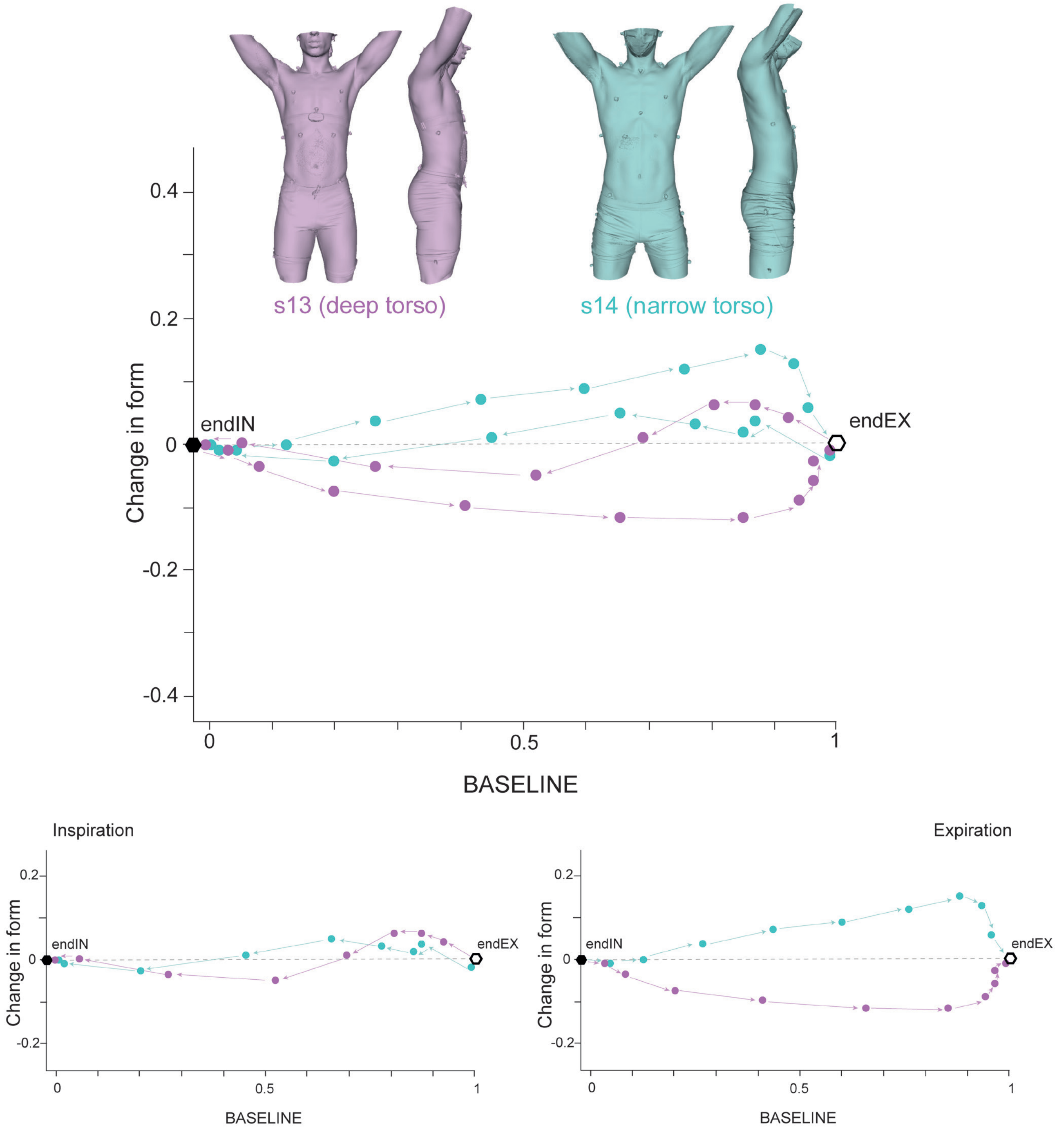

Figure 3. Bookstein baseline superimposition of respiratory cycle motion trajectories in the high-intensity phase of two individuals: s13 (deep torso configuration) and s14 (flat torso configuration). The direction of the arrows indicates the temporality of movement. **endEX**, end-expiratory status; **endIN**, end-inspiratory status. Note the differences in shape change particularly during expiration.

selected for the respiratory trajectory comparison. Here lies the potential palaeontological importance of the present study. Future analyses of *in vivo* torso kinematics could shed light on the relationship between deep and flat torso configurations and respiratory function. However, to infer significant evolutionary aspects about respiratory mechanics we must bear in mind other important aspects that could shape breathing motion in different hominin species. These range from morphological variability to sexual dimorphism and ontogenetic stages. In modern humans, different morphologies and/or kinematic patterns have been observed related to sex (Bellemare *et al.*, 2003; Torres-Tamayo *et al.*, 2017; LoMauro & Aliverti, 2018; García-Martínez *et al.*, 2019) and age (García-Martínez *et al.*, 2020b). Therefore, before inferring hominin species breathing patterns from their reconstructed thoracic morphologies we must understand if the kinematics of respiratory cycles are comparable between subadults (such as *H. ergaster* KNM-WT 15000) and adults (Kebara 2), and if kinematics can be inferred from the study of shape and form. One study addressed functional differences between different ontogenetic stages and suggested that the "mature" pattern of thoraco-diaphragmatic breathing occurs early in human ontogeny, when the pyramidal rib cage of the newborn changes into the cylindrical thorax shape of the adults (Openshaw *et al.,* 1984; Bastir *et al.,* 2013). Based on these results on modern humans we can assume that subadult (but not newborn) and adult fossil hominins would show similar breathing kinematics.

Neandertals adaptations were related to power-locomotion patterns, rather than endurance running (Raichlen *et al.*, 2011; Stewart *et al.*, 2019) and their wide, deep thorax may point in this direction (Bastir *et al.,* 2022). Similarly, the thoracic anatomy of *H. ergaster* subadults would be related to power locomotion as well, even though its appendicular anatomy and, particularly, longer legs may also suggest palaeoecological behavioral aspects related to endurance locomotion (Bramble & Lieberman, 2004; Lordkipanidze *et al.*, 2007).

However, considering the mosaic evolution of hominin anatomy, it is possible that kinematic differences in the respiratory function were not necessarily related to a more efficient respiratory functionality or to "better adapted" structures. On the contrary, this could be revealing how through different motion patterns an equivalent functional state could be achieved, regarding the implication of the role of the complete body anatomy in the running function. Therefore, to explore the topic of efficiency, morpho-kinematic analyses should be complemented with studies of the energetics underlying physiological and biomechanical limits of the motion of respiratory structures, to shed light on the evolution of the respiratory function.

CONCLUSIONS

Our study demonstrated that geometric morphometric methods can be successfully combined with motion capture data for the statistical and quantitative comparison of body functions such as motion. Applied to breathing motion, our analysis may suggest differences in expiratory motion in subjects with anteroposteriorly deeper and flatter torso configurations.

Authors' contributions. MGR analysed torso form and motion capture data using geometric morphometrics, designed the figures, and wrote the manuscript. JMGR measured the torso form of GMM1 analyses. JR, AFSJ, and EN carried out the MOCAP experiments. JR extracted and post-processed MOCAP data for GMM2. BB and MB designed the experiments and developed the Research Project and co-supervised MGR's MSc Thesis leading to this paper.

Competing interests. The authors declare no competing interests.

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