

The evolution, form and function of the human respiratory system

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Summary - This paper presents an updated view on the morphological and functional significance of the human respiratory system in the context of human evolutionary anatomy. While usually the respiratory system is treated either from a craniofacial perspective, mostly in the context of nasal evolution and air-conditioning, or from a postcranial perspective featuring on overall thoracic shape changes, here we pursue a holistic perspective on the form, function, integration, and evolutionary change of the entire organismal system in hominins. We first present a brief review of the most important morphological structures, their function, and its potential integration and interaction with the nasal cavity and thoracic skeleton. This is followed by an overview of the most important improvements in methods for the comparative study in recent humans and fossil hominins. We then overview and list a compendium of hominin fossil material currently available for the study. We propose four functional categories of hominin respiratory system configurations that differ potentially with respect to size, shape, biomechanics and/or bioenergetics. Finally, we discuss these and speculate on possible ways for future research into an anatomical system that, despite its under-investigated status, is central to the understanding of the form and functions of the hominin organism and its paleobiology.

Keywords - Paleanthropology, Human evolution, Respiratory system, Paleophysiology, 3D Virtual morphology, Morphometrics.

Introduction

At a given level of anatomical observation, humans, as any other kind of living organisms, consist of an integrated set of major organ systems, apparatus, or otherwise-termed functional units, such as the central nervous, masticatory, digestive, reproductive, locomotor, and respiratory systems (Bastir 2018). These different units

interact with each other during ontogeny and evolution and at functional and structural levels, giving rise to a specific phenotype (Riedl 1975; Callebaut et al. 2007). Interactions between these organismic systems is controlled by genetic, epigenetic and environmental factors and the study of these factors in recent organisms can be used to contribute to our understanding of evolutionary processes (Laland et al. 2015), responsible for

the morphological and functional variation of the hominin fossil record.

In palaeoanthropology, different questions are related to the morphological approach to fossil remains that are all based on the scientific assessment of similarity or differences in ranges of variation among anatomical structures and/or their reconstructions: phylogenetic relations and ancestry, morphological and functional reconstructions, paleophysiology, paleoecology, etc. (Holliday 1997; Ruff 1991; Trinkaus 1981; Rosas et al. 2006; Bastir et al. 2020b). Although many of these questions are increasingly addressed by including molecular and genetic approaches, most of them also require the assessment of morphology, that is, the substrate, by which an organism interacts physically with its environment (Wagner and Laubichler 2000). This is a reason why biologically meaningful interpretations of adaptive processes need to account for the morphological evidence of the fossil record (Callebaut et al. 2007; Laland et al. 2015; Bastir 2018).

Yet, the theoretical background of proposed morphological explanations usually differs substantially. In a simple morphological model, a given morphology is the result of either adaptive selection, when morphological aspects fit into functional models, or of random genetic drift (Null hypothesis), when morphology does not fit a model prediction. However, importantly, Weaver (2009) indicated that exclusively adaptive approaches to studying fossil morphology could be limited unless accounting also for the morphological integration of structures. This is because integration introduces covariation between structures that can bias a simple interpretation of morphological evidence (Olson and Miller 1999; Rosas and Bastir 2004; Klingenberg 2008; Bastir and Rosas 2005). The morphology of a given structure may be the result of functional adaptations as well as their morphogenetic *limits*, due to constraints on morphological development that may result from the interaction during growth, development and function of the given structure with otherwise biologically related anatomical systems of the organism

(Alberch 1982; Maynard-Smith et al. 1985; Alberch 1990). Yet, incorporating such information into testable models of functional adaptation and selection is difficult (Churchill 1996). It requires the development and testing of more complex morphological models.

The size and shape of the hominin face provides good examples for the difficulties of functional interpretations in craniofacial hominin evolution. For example, prognathism in Neanderthals and Middle Pleistocene hominins has often been interpreted in terms of masticatory biomechanics and efficiency (Spencer and Demes 1993; O'Connor et al. 2005). Indeed, experimental data shows that prognathic faces withstand better bite-force induced deformation than orthognathic faces. However, on the other hand, the orthognathic modern human face is capable of producing higher bite forces than the prognathic face (Godinho et al. 2018), leaving us with the question of what is more important in the context of adaptation: capability of bite force generation or skeletal resistance to bite force?

Godinho et al. (2018) suggested that prognathism in these hominins could be an evolutionary spandrel (Gould and Lewontin 1979), a non-adaptive morphological side product of other evolutionary factors. In this latter line of reasoning, facial prognathism can be considered in terms of integrated craniofacial growth and allometric patterns (Rosas 1997; Bastir and Rosas 2005; Rosas and Bastir 2004), characterised by the spatio-temporal order of the ontogenetic maturation of the central nervous system, the cranial base and the attached facial skeleton (Bastir et al. 2006; Bastir and Rosas 2016). Evolutionary and basicranial factors would contribute to facial prognathism (Trinkaus 1987, Bastir and Rosas 2016), while body (=organism) energetics and associated demands for large cranial airways could account for facial size (Franciscus and Churchill 2002; Bastir 2004; Rosas et al. 2006, Bastir 2008; Yokley et al. 2009; Froehle et al. 2013; Wroe et al. 2018; Bastir 2019).

Yet, contrasting functional or structural models in the same, complex, numerical morphological model is difficult. Thus, we are still far

away from implementing complex morphological models into testing evolutionary scenarios of adaptation. However, theoretically, a systems approach, pursuing a holistic view on the morphology of the fossil evidence can prove useful.

The aim of this paper is thus to review the potential of the respiratory system as “organism integrator” of cranial and post-cranial systems for a future development of models that account for functional *and* structural explanations of human evolutionary variation. To achieve this goal we will address the functional and evolutionary anatomy of the craniofacial and postcranial skeleton of the respiratory apparatus and review its fossil record, addressing the following major evolutionary questions: How did craniofacial airways and the thorax change during hominin evolution? What are the most recently developed methodologies to study any functional implications? Is there evidence for an integrated evolutionary change in human evolution?

Functional morphology of the cranial respiratory system: the cranial airways

For more than a century, numerous works have collected evidence to document the possible association between midfacial and nasal morphology and environmental conditions, particularly in the light of interpreting modern human variation and respiratory function (e.g. Thomson 1913; Thomson and Buxton 1923; Weiner 1954; Hiernaux and Froment 1976; Carey and Steegmann 1981; Franciscus and Long 1991; Yokley 2009; Maddux et al. 2017; Zaidi et al. 2017). The cranial airways are in direct contact with the external environment and are involved in several body activities. Besides chemoreception, respiration is of central importance and it can be divided into two separate physiological functions: the control of the quality of inspired air (air conditioning) (Elad et al. 2008), and the amount of air for gas exchange (energy metabolism) (Enlow and Hans 1996; Rosas and Bastir 2002). The inhaled air must reach the lungs at body temperature and maximum saturation with water vapour to avoid damage in the pulmonary respiratory epithelium, as well as to facilitate

a rapid exchange of gases (O_2 ; CO_2) (Proctor 1982). Mlynski et al. (2001) suggested dividing the cranial airways into several functional tracts (Fig. 1): the air enters the nose through the nostrils, vestibulum, isthmus and anterior cavum. These airway zones comprise the *inflow tract*, which is mostly built of soft tissue and responsible for mechanical filtering and the shaping of the airstream before the air passes into the *functional tract* within the bony nasal cavity. There, the most of the proper air conditioning process takes place, thanks to the highly vascularized mucosa that covers the internal surfaces (Elad et al. 2008). This internal surface of the nasal cavity is amplified and divided into the superior, intermediate and inferior meatus, i.e. vertically organised airflow channels formed by three equally named bony turbinates (Cole 1982; Keck et al. 2000; Churchill et al. 2004; Naftali et al. 2005; Elad et al. 2008; Yokley 2009; Maddux et al. 2017). Posterior to the functional tract there is the *outflow tract* that consists of the choanae and the epipharynx, which redirects the airflow towards the lower airways of the lungs. The choanae are important regarding the energy demands of the body metabolism, since together with the anterior nasal openings, the choanae determine the amount of inhaled air that passes into the lungs (Hall 2005; Froehle et al. 2013; Bastir 2019). Both air-conditioning and metabolic respiratory functions are affected by climatic factors in modern humans. Cold and/or dry environments are the most stressful from a physiological point of view (Maddux et al. 2016), as these environmental conditions are farthest from the internal conditions of the body. Thus, some studies have found that human populations in those climatic zones tend to have relatively taller and narrower nasal cavities, increasing the contact surface between the air and the respiratory mucosa (e.g. Lindemann et al. 2009). As well, antero-posteriorly longer nasal cavities increase the contact surface between the air and the respiratory mucosa (Yokley 2009) and lengthen the residence time of the airflow inside the nasal passage (Noback et al. 2011). Taller cavities also allow more air to pass through. Higher energy

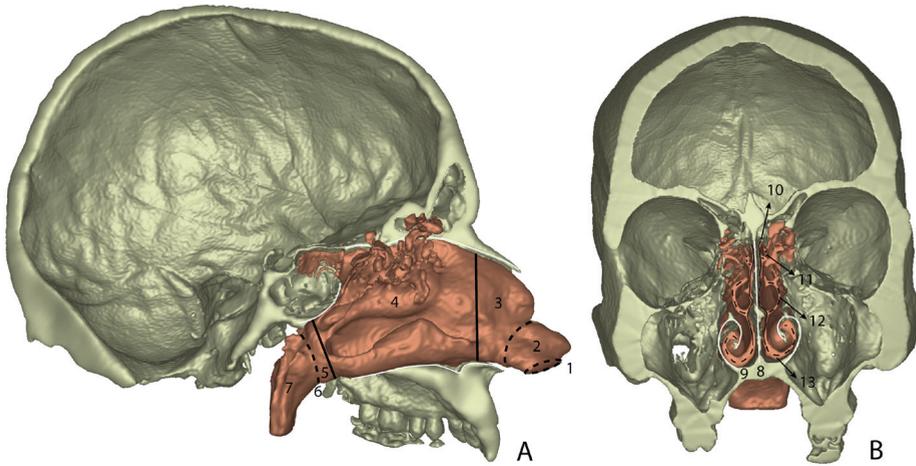


Fig. 1 - Hard and soft tissue relations between the cranial airways and the skull. The lateral view with a midsagittal cutting plane on the cranium (A) shows the inflow tract (1: nostrils, 2: vestibulum, 3: anterior cavum), the functional tract (4: area of the meatus), and the outflow tract (5: posterior cavum, 6: choanae, 7: epipharynx) delimited by black solid lines. The frontal view with a coronal cutting plane on both hard and soft elements (B) shows the nasal septum and inferior turbinates (8 and 9 respectively, white solid lines), the common nasal meatus (10, black solid lines) and the superior, intermediate and inferior meatus (11, 12 and 13 respectively, black dashed lines).

demands have been linked not only to higher body mass and/or physical activity, but also to more demanding climatic environmental conditions (Bastir et al. 2011; Bastir and Rosas 2016; Holton et al. 2016; Maddux et al. 2016), as historically hypothesised regarding the greater dimensions of Neanderthal cranial airways (Rae et al. 2011a,b; Holton et al. 2011; Wroe et al. 2018). Yet, distinguishing morphological features related to either climatic, activity, or lean-body mass related energetic demands is difficult due to equifinality (Churchill 2006).

However, the role of air-conditioning and adaptation in fossil hominins other than Neanderthals is relatively unknown although there is evidence that cranial airways and nasal shape and size may not only be the result of simple adaptations to eco-geographic or energetic factors. Evolutionary factors related to craniofacial integration and architecture in the context of brain and masticatory system evolution, sexual selection, genetic drift, and others may have influenced to variable degree evolutionary trends in midfacial morphology in hominins. To

start with, a forward projecting nose in the face is a trait that appeared late during human evolution (Franciscus and Trinkaus 1988; Nishimura et al. 2016). Early hominins, such as Australopithecines and their ancestors were characterised by a flat midfacial morphology and no nasal protrusion, and were likely more similar to the midfacial morphology of chimpanzees. Anatomically, this midfacial flatness is a combination of small, flat nasal bones that lack any kind of curvatures (transversal convexity, sagittal concavity) and of frontal maxillary processes that lack any kind of eversion. In this primitive face, the planes of the nasal aperture and the zygomatic bones and infraorbital planes are roughly at the same level, when viewed laterally. Their midface is strongly prognathic (Bilsborough and Wood 1988) and the vertical distance between nasion and the nasal floor and palate (midfacial height) is short (Rak 1983; Bastir et al. 2010).

Only with the appearance of transitional hominins (early *Homo* such as *H. habilis*, *H. rudolfensis*) (Wood and Boyle 2016) and clearly with *Homo ergaster*, a dissociation occurred

between these planes in lateral view, with an anterior nasal opening projecting beyond the level of the zygomatic, infraorbital regions and planes. This anterior projection is morphologically caused by anteriorly everted maxillary frontal processes and both, sagittally and transversally, curved nasal bones. In addition to these topological changes there is a reduction in lower facial prognathism (Bilsborough and Wood 1988; Arsuaga et al. 1995) and the vertical midfacial height increases (Bastir et al. 2010). *H. ergaster* specimens and later hominins, particularly in the Middle Pleistocene, show large and wide piriform apertures (and choanae) housed within large faces (Bodo, Kabwe, Petralona, Arago) (Franciscus 1995; Franciscus and Churchill 2002; Bastir and Rosas 2011; Froehle et al. 2013; Bastir 2019). A particular, derived morphology is observed in the origins of Neanderthal lineage (Arsuaga et al. 2014) and consists of an everted projection of the superior region of the piriform aperture, associated with the Neanderthal midfacial prognathism, a combination of large facial size and a specific midfacial topology of the nasal bones, and maxillary frontal processes (Trinkaus 1987). This facial configuration is associated with increased antero-posterior length of the midface and differs from the orthognathic, reduced face of anatomically modern humans and (Trinkaus 1987, 2003; Bastir and Rosas 2016).

The degree to which these facial changes influenced the functional morphology of the enclosed (internal) cranial airways and interacted with their paleo-ecologically adaptive background is a field with a wide spectrum of potential research. A common view holds that the origin of the nose is linked to the Early Pleistocene paleo-ecological habitat transition between the genus *Australopithecus* and the earliest representatives of the genus *Homo* (Franciscus and Trinkaus 1988). Australopithecines inhabited humid arboreal forested environments, where air-conditioning would be physiologically less relevant than in first representatives of early *Homo*, who populated the newly emerging, open areas of dry and hot savannah (Antón et al. 2014). In early *Homo* respiratory physiology, retention of

humidity during expiration related to regulation of air temperature may have been an important evolutionary factor (Franciscus and Trinkaus 1988). In addition, it is likely that changes in the subsistence patterns had their influence on the respiratory system. It is assumed that the genus *Homo* was characterised by an increased ranging activity in the savannah, a new ecological niche that was also possibly exploited by a new, persistence hunting strategy combined with endurance running at relatively low speeds drawing on aerobic respiratory energy supply (Lieberman et al. 2009). These changes likely challenged respiratory, locomotor and thermoregulatory systems during foraging (Carrier et al. 1984; Bramble and Lieberman 2004; Lieberman 2019; Hora et al. 2022).

Functional morphology of the post-cranial respiratory system: the thorax

The ribcage is an osteo-cartilaginous network that consists of twelve thoracic vertebrae and intervertebral discs (the thoracic spine), twelve rib pairs with their costal cartilages and the sternum. The thorax holds and protects vital organs (e.g. heart, lungs, liver) and great vessels (e.g. aorta, vena cava) and articulates the shoulder girdle with the axial skeleton (Schultz 1961) (Fig. 2). It thus contributes to locomotion and body movement by providing attachments to skeletal muscles of the neck, back, upper limbs and abdomen within the trunk (Thompson et al. 2015). However, the main biomechanical roles of the ribcage are a structural support for respiratory function (Cappello and de Troyer 2002) and spinal stiffness (Oda et al. 1996, 2002; Takeuchi et al. 1999). The respiratory movement consists in expanding and contracting the thoracic cavity in order to facilitate pulmonary ventilation (Cappello and de Troyer 2002; Beyer 2016). This is predominantly driven by the activity of the diaphragm and intercostal muscles (de Troyer et al. 2005), which are supported by other muscles such as the scalenes, sternocleidomastoid, pectorals and abdominals (Gray 1918).

Expansion of the rib cage during inspiration is produced by the external intercostals in the dorsal

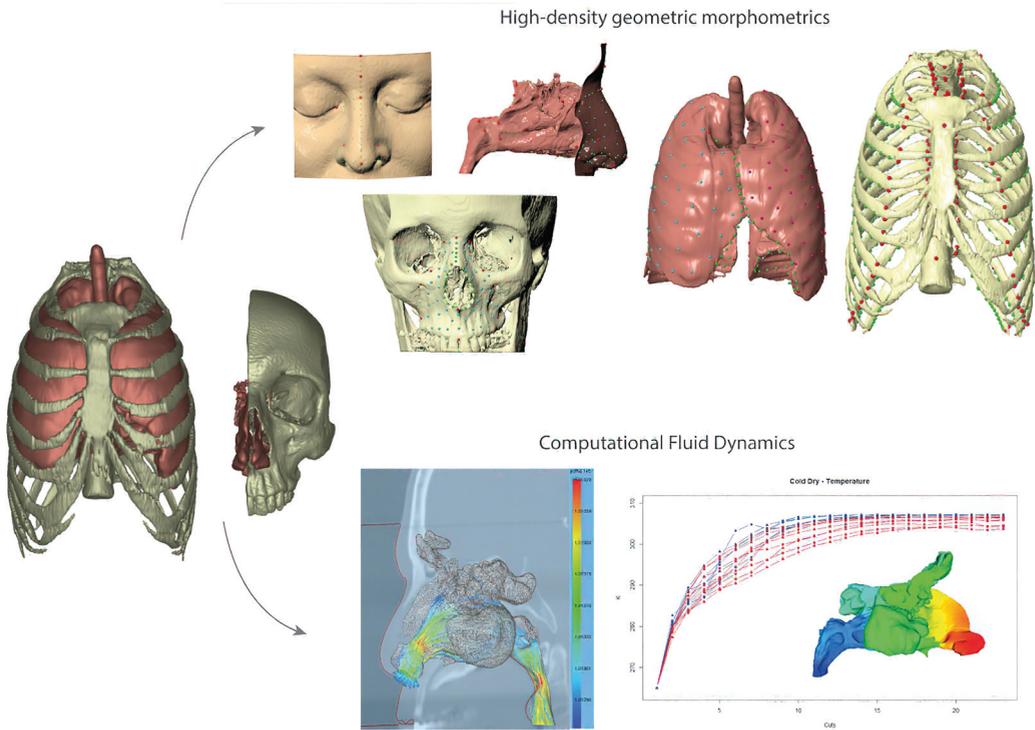


Fig. 2 - Analyses on hard and/or soft tissue reconstructions of the respiratory system: High Density Geometric Morphometrics (superior) and Computational Fluid Dynamics (inferior). Superior: HD-GMM templates of landmarks and semilandmarks in the cranial airways and skull (left), and in the lungs and thorax (right). Inferior: airflow streamlines characterising the pressure within the cranial airways (left) and a graph depicting air conditioning in terms of temperature along the cranial airways in two different human groups (right).

portion of the rostral interspaces, the intercartilaginous portion of the internal intercostals (the so-called parasternal intercostals), and, in humans, the scalenes. In contrast, during expiratory efforts, a concomitant activation of the abdominal muscles, the internal interosseous intercostals in the caudal interspaces and the triangularis sterni enable for contracting the rib cage helping to deflate the lungs (De Troyer and Boriek 2011)

Functionally, the different contributions of these respiratory muscles lead to three types of rib movements in modern humans: 'pump-handle', 'bucket-handle' and 'spreading-calliper' (Osmond 1995; Beyer et al. 2014; Beyer 2015; Bastir et al. 2017a). Generally, the 'pump handle' movement is more marked in the upper

thorax. It is mostly driven by the external intercostals and involves the anteroposterior expansion of the ribcage. The 'bucket-handle' and the 'spreading-calliper' movements are more marked in the lower thorax because of the diaphragmatic action, allowing for the mediolateral and transversal expansion of the ribcage (Aiello and Dean 1990; Beyer et al. 2014; Beyer 2016; Bastir et al. 2017a; Torres-Tamayo et al. 2018a). However, Beyer et al. (2016) have found that pump and bucket-handle motions are actually similar in the first 10 rib pairs.

During quiet breathing mode, expiration is largely passive due to the recoil of the lungs, the elasticity of the muscles and cartilages, and the effect of gravity, while active contraction of the

abdominal muscles support forced expiration during exercise (Aliverti et al. 1997). The elastic recoil of the ribcage is also contributing to expiration when increasing lung volumes. This recoil is due to both sternocostal (through costal cartilages) and manubriosternal joints that are able to store energy as torsion springs to help the mainly passive mechanism of expiration (Beyer et al. 2017). These movements determine the capacity of volumetric change of the thorax, possibly in relation to its three-dimensional (3D) shape (Openshaw et al. 1984; Bellemare et al. 2003; García-Martínez et al. 2016b; Bastir et al. 2017a). Therefore, there is an increasing interest in studying the evolution of ribcage anatomy in hominins not only to reconstruct the evolution of their torso and overall body shape, but also to estimate their functional capacities and breathing biomechanics (Jellema et al. 1993; Gea 2008; Latimer et al. 2016; García-Martínez et al. 2014; Chapman et al. 2017; García-Martínez et al. 2018; Bastir et al. 2020b). However, the metameric and fragile nature of fossil ribs and thoracic vertebrae mean that reconstructing ribcage morphology in hominin evolution is challenging and there is little agreement among scholars (García-Martínez 2017). Thus, reconstruction attempts are often complemented and influenced either by inferences based on anatomically related structures, such as the pelvis (Torres-Tamayo et al. 2018b; Schmid et al. 2013), inferences based on the interpretation of partial structures (rib or vertebral features) and their potential covariation with the entire ribcage (Bastir et al. 2015, 2016b; García-Martínez et al. 2017), often together with considerations of paleo-environmental factors (Schmid et al. 2013; Latimer et al. 2016).

Early hominins like *Australopithecus* and possibly early- or morphologically primitive representatives of the genus *Homo* (e.g. *H. habilis*, *H. naledi*) likely had a combined bipedal and arboreal locomotion repertoire, whose adaptive pressure on the ribcage was probably greater than that of breathing. First morphological assessments of ribs and thorax reconstructions of AL 288-1 (Lucy, *A. afarensis*) by Schmid (1983) indicated a small size of the first rib and less torsion and declination

of more central and inferior ribs. This implied a thorax that is constricted at its superior aperture, antero-posteriorly deeper in the central region, and medio-laterally wider at its inferior part to fit with the everted iliac blades (Schmid 1991). The costal remains of *A. sediba* point towards a similar, superiorly narrow and inferiorly divergent

thorax reconstruction, although the lower thorax morphology was also inferred based on iliac blade morphology (Schmid et al. 2013). Later discoveries of scarce fragmentary material of KSD-VP-1/1 (Kadanuumuu), a large-bodied partial *A. afarensis* skeleton, may document a slightly wider superior aperture, also possibly true for *A. sediba* (Bastir et al. 2016), and a slightly narrower lower thorax than previous reconstructions of Australopithecine ribcages (Latimer et al. 2016). This discrepancy illustrates the methodological and conceptual difficulties of thorax reconstructions and the disagreement that exists on thoracic evolution and the functional adaptations of these earliest hominins. The small size of a first rib and shape features on lower rib levels of *H. naledi* remains could also point towards smaller, constricted upper thoracic proportions relative to a wider lower ribcage (Bastir et al. 2016b; Williams et al. 2017, 2018).

Abandoning arboreal activity in favour of exclusive bipedalism had implications on the shape of the *Homo* ribcage (Jellema et al. 1993; García-Martínez 2017). Although the lower thorax was probably still wide and deep, hominins like *H. ergaster*, *H. erectus* and *H. antecessor* (Gómez-Olivencia et al. 2010; García-Martínez et al. 2018a) showed a more expanded upper and central thorax than previous species due to the necessity of accommodating their horizontally-oriented shoulder girdles (Jellema et al. 1993; Ruff 2008; Been and Bailey 2019). Expansion of the upper thorax is related to greater lengths and curvatures of the more superiorly situated ribs (Jellema et al. 1993).

In Middle Pleistocene hominins, no thorax reconstructions are yet available but comparisons of isolated thoracic material may suggest a ribcage configuration similar to Neanderthals that were reconstructed with large, deeper and

inferiorly wide proportions in relation to their wider pelvis (Franciscus and Churchill 2002; Churchill 2006; Gómez-Olivencia et al. 2009, 2018; García-Martínez et al. 2014, 2017, 2020). Explanatory models of Neanderthal ribcage morphology proposed adaptations to cold climatic conditions and high oxygen demand, also due to their larger body mass, possibly inherited (Franciscus and Churchill 2002; Bastir et al. 2020b), to higher physical activity (Franciscus and Churchill 2002), a high protein diet (Bendor et al. 2016), ambush hunting (Stewart et al. 2019), or due to equifinality of different factors (Churchill 1998, 2006).

Modern human thoracic structure is different. A recent geometric morphometric comparison of reconstructed ribcages from the Kebara 2 Neanderthal, the KNM WT 15000 *H. ergaster* reconstruction and an ontogenetic sample of modern humans suggests that *H. sapiens* is derived by showing a medio-laterally narrower and antero-posteriorly flatter thorax (Bastir et al. 2020b). Flatness of the ribcage is the result of their marked rib torsion and associated inferior declination (Schmid 1991; Jellema et al. 1993; García-Martínez et al. 2016a). Fossil discoveries of ribs belonging to early *H. sapiens* are also relatively scarce and do not often count with well-preserved costal and vertebral material to make inferences about their thoracic shape. The few 3D comparisons carried out so far suggest that fossil and modern *H. sapiens* shared torsion and associated declination (García-Martínez et al. 2018b).

In spite of the disagreement about different ribcage configurations in the aforementioned fossil hominins, and in very general terms, it can be stated that the evolutionary trend of medio-laterally wider and antero-posteriorly deeper lower thorax configurations towards narrower and flatter thoraces may have had biomechanical implications. This evolutionary trend may document a functional change from greater diaphragmatic contributions in non modern humans to more thoracic biomechanical contributions in modern humans (Franciscus and Churchill 2002; Gomez-Olivencia et al. 2009; García-Martínez et al. 2014; Bastir et al. 2020b).

Methods

High-density geometric morphometrics, virtual and quantitative fossil reconstructions

The morphological and geometrical properties of the respiratory system are extremely difficult to measure, analyse and represent. In the cranial part, the nasal cavity and the soft tissue airways consist of complexly curved cavities and surface boundaries, both externally and within the face. But also the geometry of the post-cranial part is difficult to measure. The pulmonary lobes and diaphragm offer few easily definable measurement points. The ribs are curved in three dimensions and arcs, angles or lengths may only roughly describe rib features that are biologically relevant. Because appropriate quantification of the 3D form is the first step of a biologically meaningful anatomical analysis, traditional measurements are of limited value when geometry is of interest. Therefore, while size is easier to capture, geometric morphometrics is the preferred method of choice for quantification of shape.

Geometric morphometrics (GMM) is the statistical analysis of Cartesian coordinates of biological landmarks and has been used widely in anthropology for more than 30 years (Bookstein 1991; O'Higgins 2000; Zelditch et al. 2012; Mitteroecker and Schaefer 2022). In these methods biologically corresponding, that is, homologous landmarks (Oxnard and O'Higgins 2009) are collected on a sample of different objects and defined to represent the geometry of the biological structures that are relevant to the testing of the hypotheses. During analysis the landmark coordinates are subjected to a superimposition (Bookstein 1991), most often a Procrustes Registration or Generalised Procrustes Analysis (GPA), when applied to samples, producing shape and size variables (Gower 1975; Rohlf and Slice 1990). These data can be used in many different aspects including pure analysis of respiratory system components (Fig. 2), to quantify biomechanics and motion (Fig. 3) and for entire fossil reconstructions (Fig. 4).

GPA removes all the variation in the landmarks that is related to the orientation, position and

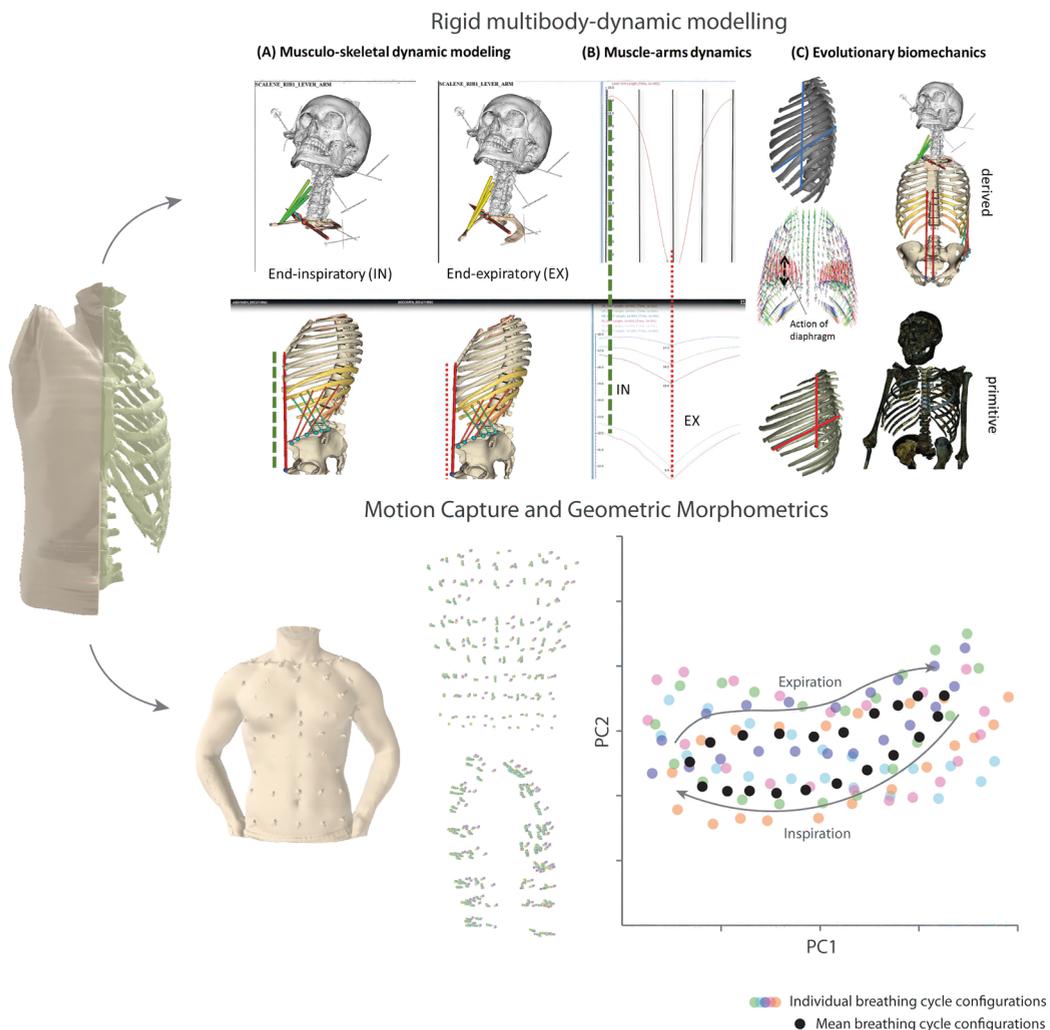


Fig. 3 - Analyses of thorax breathing motion: Rigid multibody-dynamic modelling (superior) and Motion Capture together with GMM (inferior). Superior: A) an example of the musculo skeletal modelling performed on scalene (superior) and abdominal (inferior) muscles both at the end-inspiratory and end-expiratory levels; B) dynamic trajectories of their lever arms lengths during breathing; C) Extrapolation of biomechanical modelling to fossil reconstructions. Inferior: workflow showing an analysis of motion through GMM. First, thorax breathing motion is captured through different landmarks via OEP. Secondly, these landmarks are analysed via GMM and standardised via GPA. Finally, each step of the breathing motion is analysed as a point of a trajectory configuration that represents the motion and can be compared.

scale of the objects. During several iterations, GPA applies rotation, translation and re-scaling to the landmark configurations. First, all configurations are superimposed onto the first configuration of the sample and an overall mean is calculated.

Then, all configurations are superimposed onto this mean shape (“consensus”) during several iterations until the distances amongst homologous landmarks (called “Procrustes distances”) converge on a minimum (Rohlf and Slice 1990;

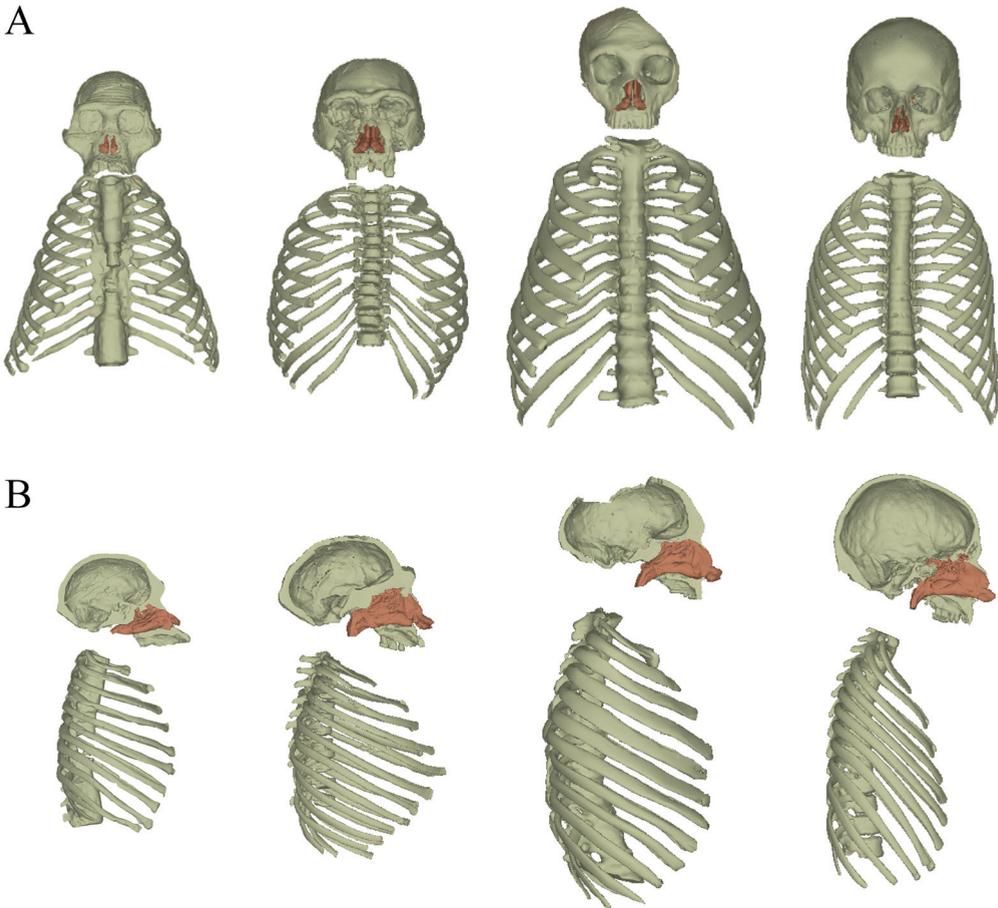


Fig. 4 - Virtual reconstructions of the skull and cranial airways, and the ribcage belonging to the 4 morpho-functional groups in frontal (A) and lateral (B) view. From left to right: Group 1: Cranium from Sts 5 and ribcage from AL 288-1; Group 2: Cranium from KNM-ER 3733 and ribcage from KNM-WT 15000; Group 3: Cranium from Gibraltar 1 and ribcage from Kebara 2; and Group 4: Cranium and ribcage a from Caucasian current human. Images from Group 3 are mirrored.

Zelditch et al. 2012). That way, a standardised set of shape variables is obtained (Procrustes shape coordinates) that can be analysed by multivariate statistical methods and visualised by powerful 3D interactive graphs. Independent on the shape data, a size value (the scaling factor, “centroid size”) is obtained, that only in the case of allometry shares a relation to shape. However, while formally practical, the biological meaning of centroid size depends on the structure and on the question and should be complemented with other, more question-specific size measurements. For example,

while centroid size gives a good estimate of overall nasal cavity size, it is not useful when referring to the rate of airflow passing through the cavity in the context of energetic considerations. Indicators of height and width are more informative in this respect (Heuzé 2019; Megia et al. 2018).

Geometric morphometric approaches to the study of the respiratory system have been applied in 2D and 3D in ontogenetic, comparative and evolutionary context (Rosas and Bastir 2002; Bastir et al. 2009; Yokley 2009; Holton et al. 2014; Pagano and Laitman 2015; Bastir

2019; Heuze 2019; Pagano et al. 2022; etc). However, these applications gained considerably from a more recent improvement in GMM: the use of semilandmarks on curves and surfaces. Introduced already early to GMM by Bookstein (1991), the extension to 3D data (Gunz et al. 2005; Gunz and Mitteroecker 2013) have led to what more recently is being termed high density geometric morphometrics (HD-GMM) (Mitteroecker and Schaefer 2022). HD-GMM and their extension to virtual morphological methods (Bastir et al. 2019b) have greatly contributed to a better understanding of the variation of the respiratory system in recent and fossil humans, particularly at the postcranial levels.

Application of HD-GMM techniques to study the respiratory system has been successfully applied to the study of basic features of recent variation in the skeletal thorax (Bastir et al. 2013), the lungs (Torres-Tamayo et al. 2018a) and the nasal (Megía et al. 2018; Bastir et al. 2020a) (Fig. 2). However, the potential for quantitative 3D reconstructions in hominin fossils is extraordinary and offers promising roads towards respiratory paleophysiology. The first quantitative 3D reconstruction of the fossil thorax was carried out using HD-GMM, computer-tomographic and surface scans of fossils from the Nariokotome *H. ergaster* skeleton. The term “quantitative” reconstruction aims at indicating full reproducibility of the reconstruction results due to statistically validated, and standardised methods for aligning thoracic vertebrae and fitting ribs (Bastir et al. 2019a), as well as for the estimation of missing data of either parts of vertebrae or ribs or of entirely missing serial elements (García Martínez et al. 2018c). These methods minimise potential subjective perspectives that could underlie the process of assembling virtually vertebrae and ribs (parts) to get the thorax (whole).

Sanz-Prieto (2021) used HD-GMM for preliminary statistical and geometric reconstructions to generate the first quantitative approximations towards soft-tissue airway geometries of early hominins (Sts 5, KNM-ER 3733) (Fig. 4). Based on a reference sample of recent chimpanzees and modern humans, Thin Plate

Spline (TPS) methods (Gunz et al. 2009) were used to interpolate airway geometries of recent species and to fit them into the fossil hard tissue structure. Similar methods were also used for the generation of the cranial airways of the Gibraltar 1 Neanderthal (Forbe’s Quarry) that was further reconstructed manually by virtual morphological methods (Perez-Ramos et al. 2022) (Fig. 4).

The advances of 3D quantification and visualisation by using geometric morphometric analysis in the study of the respiratory system become particularly evident in the combination with other, computer-based methods for the functional research of breathing functions, such as computational fluid dynamics, the modelling of musculoskeletal biomechanics and or chest wall motion capture.

Computational Fluid Dynamics

While HD-GMM turns out to be a powerful tool to study the shape of the respiratory system, complementary methodologies are necessary to study in depth the biological function of breathing. One of those is Computational Fluid Dynamics (CFD), a branch of fluid mechanics that covers the numerical simulation of flows and subsequent study of their parameters (Burgos et al. 2017). CFD is based on three laws of conservation of physics: conservation of mass (continuity equation), energy, and momentum (Newton’s second law). Generally, but not exclusively, the simulation and resolution of flows in the literature are performed considering steady, laminar and compressible flows. Thus, these laws can be formulated as a system of differential equations, which along with the equation of state of the fluid (a constitutive equation that relates the state variables that describes a system in thermodynamic equilibrium), the boundary conditions and the initial conditions (pressure, volume, temperature, etc...), constitute as a whole the Navier–Stokes equations. A general solution to the Navier–Stokes equations employing analytical methods is not yet available, so CFD obtains the results for the Navier–Stokes equations by numerical simulations employing the power of computing software and allowing the prediction

of the fluid flow (e.g. Ansys Fluent, <https://www.ansys.com>; OpenFOAM, <https://www.openfoam.com>). The results of these analyses can provide important information on fluid dynamics and other variables such as velocity, resistance, temperature, humidity, and a large number of further parameters that cannot be obtained by other methods (Elad et al. 2008) (Fig. 2, lower panel).

Common steps of typical studies based on CFD (Nishimura et al. 2016; Burgos et al. 2017; Bastir et al. 2022a) have been reviewed comprehensively by Rahman (2017) and are briefly summarised here. The first step is to define the computational domain, which in the present context is usually a 3D model (=geometry) of computed-tomography (CT) reconstruction (segmentation) of some part of the airways (external nose, nasal cavity, pharynx, larynx, or lungs). Then, the material properties of the air (density, viscosity) and a flow model needs to be defined, which in the cranial airways is usually a constant pressure drop between the atmosphere and nostrils (inlet) and the nasopharynx (outlet), in order to mimic the natural respiration induced by the lungs (Burgos et al. 2013). Furthermore, the volumetric flow rate Q was kept below 15 L/min in order to ensure laminar flow (Taylor et al. 2010). The model was set to rigid body dynamics to omit the effect of respiratory-related soft-tissue deformation, which often involves fluid flow and structural solid coupling, particularly at the outer region of the nose, which are typically negligible (Kim et al. 2013). The outer (atmosphere) temperature was set to 20°C, and the nasal inner wall was set to 37°C. This is followed by discretization of the geometry, where the 3D shape of the nasal cavity is divided into a large number of discrete 3D cells so that the governing equations of fluid flow can be discretized and solved on each of the mesh cells. That is how the 3D morphology of the anatomical structures enters into the CFD system. Then, the discretized equations are solved for each cell and the fluid flow is simulated, which is a time consuming process according to the complexity of the 3D model. Finally, post-processing includes the

extraction of the airflow parameters for quantitative analysis, the visualisation, and/or simulation of stream lines, particle movement, etc.

Current study of human respiratory evolution draws on sophisticated quantitative soft and hard tissue reconstructions of fossil hominins (Laitman et al. 2010; Sanz-Prieto 2021) of different geological periods and their combination with CFD in different evolutionary scenarios. De Azevedo et al. (2017) and Wroe et al. (2018) carried out the first virtual reconstructions of the nasal soft tissue of hominin fossils, specifically of Neanderthals. They used the geo-morphometric data of the cranial skeleton of human individuals and fossils, to deform a reference 3D model of human nostrils using thin plate spline to the estimated theoretical space that soft tissue would occupy in fossil individuals. Subsequently, they simulated the airflow in the estimated models using CFD techniques. Their results showed subtle adaptations to cold environments by Neanderthals (de Azevedo et al. 2017), and also suggested higher energy demands (Wroe et al. 2018). However, these reconstructions have been criticised for using only a single human reference 3D model (Evteev and Heuzé 2018) and also because there are indications that the association between bone and soft tissue in the nasal cavity may be too weak to predict nasal morphology from the skeletal morphology (Heuzé 2019).

Thus, this novel line of research has a great potential to provide important information for solving physiological questions about human respiratory system evolution, as long as progress includes the validation of methods, and the analyses of larger and more geographically diverse modern human samples as references in soft tissue reconstructions.

Rigid multibody-dynamic modelling

While airflow is also interesting in the post-cranial part of the respiratory system, functional reconstructions in thorax evolution in this region require further some modelling of motion (Fig. 3, upper panel). Virtually reconstructed ribcages of fossil hominins like Kebara 2 (Gómez Olivencia et al. 2018) or KNM-WT 15000

(Bastir et al. 2020b) can be used to gain paleo-physiologically relevant information, applying virtual biomechanical experiments, for example, using an in vivo sample of *H. sapiens* as a reference. This procedure, developed by Beyer et al. (2016) with lhpFusionbox software (<http://lhp-fusionbox.org/>), provides precise information about the ranges of motion in the rib joints and other biomechanical features associated with differently shaped ribcages.

Callison et al. (2019) compared rib joint morphologies of *Australopithecus* and *H. ergaster* with chimpanzees and modern humans and found similarities between modern and fossil Homo, a similarity, also recently confirmed statistically by San Román (2021). Based on the morphological joint similarities, Callison et al. (2019) proposed then similar ranges of rib motions in modern humans and *H. ergaster*. Thus, assuming such functional similarity, rigid multibody-dynamic modelling methods can be used to simulate breathing kinematics in a fossil thorax reconstruction. To create a virtual dynamic model, it is necessary to first define the orientation of axes of rotation at each costovertebral joint and then, to apply a range of motion from a neutral ribs position equivalent to functional residual capacity (Beyer 2016). In addition to rib level-specific motion ranges, the associated muscle arms related to these rib motions can be calculated and compared. The calculation of muscle arms, however, requires adjustment of the methods (Beyer 2016). This is because the origins and insertions of the respiratory ribcage muscles are located not only on the proper thorax and thoracic part of the vertebral column (intercostal muscles, diaphragm) but also on the external cranial base (sternocleidomastoid muscles), the cervical spine (scalene muscles), and the iliac blades and symphysis of the pelvic girdle (abdominal muscles). These muscles must be “attached”, virtually (Fig. 3), to the existing thorax models of biomechanical analyses and allow for modelling and calculating muscle arms of inspiratory and expiratory ribcage muscles in the fossil. First steps in this work modelled respiratory rib movement in the thorax of

the Nariokotome Boy (Bastir et al. 2020b) but reconstructions of entire torso models are necessary for biomechanical more complete simulations of breathing.

Another important aspect in the study of respiration is the morphological and functional analysis of the diaphragm in current *H. sapiens* and its estimation in fossil specimens. Even though the diaphragm is the most important breathing muscle in hominins, its action in modern humans is complemented by other respiratory muscles (e.g. scalenes, intercostals, abdominals). It is speculated that ancient hominins such as *H. ergaster*, *H. neanderthalensis* or even members of the genus *Australopithecus* may have differed biomechanically from modern humans and may have counted with a more powerful and differently shaped diaphragm than that of *H. sapiens* according to the differences in their thoracic morphotypes (Jellema et al. 1993; Gea 2008; Latimer et al. 2016; García-Martínez et al. 2018b).

Using the virtual morphological methods and HD-GMM, the anatomy and biomechanics of the modern human diaphragm could be studied and the results could be used for understanding the paleophysiology of the diaphragm of fossil specimens. Preliminary steps in that direction (López-Rey et al. 2021) may confirm previous suggestions of increased diaphragm size in Neanderthals and *H. ergaster* (Franciscus and Churchill 2002; Gomez-Olivencia et al. 2009, 2018).

Opto-electronic motion capture

The functionality of fossil respiratory structures studied using rigid multibody-dynamic modelling is informative but limited to musculo-skeletal biomechanics of the thorax; yet, respiratory motion also includes soft-tissues that are not preserved in the fossil record, such as abdominal structures of the torso (Aliverti et al. 1997). To complement musculo-skeletal biomechanics, in vivo functionality observations can also be used to address questions related to respiratory system evolution (Callison et al. 2019; Bastir et al. 2022b). Such in vivo techniques usually consist of measuring pulmonary volume displacements through invasive methods, such as facemasks or spirometers, which

introduce a subject/instrument-dependent measuring bias (Aliverti and Pedotti 2002). Alternatively, the introduction of Motion Capture (MoCap) techniques like Opto-electronic Plethysmography (OEP) in 1990 (Ferrigno and Pedotti 1985; Cala et al. 1996) allowed a non-invasive method to measure torso surface and, therefore, to estimate lung volume variations (Aliverti and Pedotti 2002). OEP is a motion analysis system applied to the study of the respiratory system that consists of quantifying the movement of the chest wall during breathing by capturing the dynamic change of positions of photo-reflective markers placed on its surface. In these methods 3D infrared-reflective markers are used and their 3D trajectories during motion are captured by special infrared cameras (Aliverti et al. 2001).

The chest wall surface is reconstructed through a geometrical model applied to the position of the markers and this allows measuring different volumes and movement patterns during different instants of ventilation. Calculating volume displacements between end-expiratory and end-inspiratory lung volumes through OEP is particularly useful during incremental exercise tests, as it shows the progressive change in volumes until reaching biomechanical or physiological limits, which are interesting in the context of energetics and locomotor performance of ancient hominins, such as potential adaptations to endurance running and sprint capacities (Bramble and Lieberman 2004; Raichlen et al. 2011; Pontzer 2017; Callison et al. 2019; Bastir et al. 2022b).

The combination of in vivo kinematic analysis with shape analysis (HD-GMM) allows blending shape, size and movement information with physiological parameters and uncovers possible covariation between these variables (Gómez-Recio 2022) (Fig. 3, lower panel). Many studies have used MoCap techniques to analyse locomotion patterns using multivariate approaches (Troje 2002) and through GMM in the form of “Procrustes motion analysis” (Adams and Cerney 2007). In this approach movement is quantified as shape changes during time that can be projected to a tangent space through PCA. Applied to breathing kinematics, respiratory cycles are

mapped as circular (=repeated) trajectories in this space. Multiple methods can be used to compare this motion trajectories, such as measuring their shape with GMM and applying GPA and PCA a second time (Adams and Cerney 2007; Waldock et al. 2016), or using Fourier analysis (Slice 2000). Recently, Bookstein’s Baseline Superimposition on physiologically relevant instances of the respiratory cycle along the kinematic trajectories was used for the comparisons of kinematic trajectories (Gómez-Recio et al. 2022). If applied to a palaeoanthropological context, OEP could shed light on fossil hominin breathing kinematics in the context of endurance capacities (Bramble and Lieberman 2004; Pontzer 2017), which is also dependent on the biomechanics of the locomotor system (Isbell and Young 1996; Sockol et al. 2007), and relies on the capacities of the respiratory system (Bastir et al. 2022b), a context, in which future developments can be expected.

Results and Discussion

Table 1 lists the most important fossil remains that preserve craniofacial (particularly midfacial) morphology and axial and thoracic fossils, relevant for the study of the hominin respiratory system evolution and its paleophysiology. These are assigned to four “potentially” different functional groups, which are not taxonomic groupings, but rather based on currently available thorax and nasal cavity reconstructions that can be considered in terms of size, shape and the functional aspects of the associated elements and/or their reconstructions.

Group 1: Early hominins (Australopithecus, Paranthropus and primitive Homo).

Group 1 characterizes early hominins and other small-brained and relatively small-bodied hominins with a flat, small midface and overall facial prognathism that are not exclusively committed to fully bipedal locomotion. The cranium TM 266-01-060-1 (*Sahelanthropus tchadensis*, approx. 6-7 mya) (Brunet et al. 2002) has long

been considered the holotype of the last common ancestor between hominins and chimpanzees, but recently published evidence of a potentially associated femur casts increasingly doubt on the hominin status of this fossil (Macchiarelli et al. 2020). It is not until specimen ARA-VP-6/500 (*Ardipithecus ramidus*, approx. 4.4 mya) (White et al. 1994) that the hominin fossil record counts with both craniofacial and very fragmentary costo-vertebral material. Its craniofacial skeleton is characterized by a weak subnasal prognathism compared to *Pan*, with a short but primitive protruding snout, slightly smaller cranial capacity than that of *Australopithecus* and lacking the masticatory derived specialisations, with emphasis on an omnivore/frugivore diet (Suwa et al. 2009).

There is no research about ribcage morphology and/or function of the basal hominins as shown in Table 1. Although *Ardipithecus* preserves small fragments of ribs and vertebrae, these are not studied or published in a comparative framework, to the best of our knowledge. However, because of the high levels of arboreal behavior inferred from the limbs it is reasonable to assume that they might have been similar to that of great apes like *Pan* or *Pongo*, or even to *Australopithecus* (Schmid et al. 2013; Latimer et al. 2016; Bastir et al. 2017b; García-Martínez 2017).

Thoracic morphology of *Australopithecus* has been proposed, although there is some debate. Most authors hypothesize a narrow upper thorax, and a wide (and likely deep) lower thorax. Such kind of configuration would not only characterize the 3.2 mya *A. afarensis* AL 288-1, known as “Lucy” (Johanson et al. 1982; Schmid 1983) but also the 1.8 mya *A. sediba* specimens MH1 and MH2 (Berger et al. 2010; Schmid et al. 2013; Bastir et al. 2016a). However, descriptions of the 3.6 mya *A. afarensis* KSD-VP-1/1 proposed a more modern-human like thoracic morphology due to some evidence of upper thoracic widening (Haile-Selassie 2016; Latimer et al. 2016). Clearly, more research, particularly using HD-GMM for quantitative assessment of rib curvature and torsion should focus on the costal and thoracic morphology of those individuals in order to clarify this discrepancy. Ideally, they

would including also other specimens such as the 3.3 mya *A. africanus* StW 573 (Clarke 1998), or Sts 14 (*A. africanus*, approx. 2.5 mya) (Broom et al. 1950) for a common comparison.

The midfacial morphology in Group 1 hominins is particularly well preserved in StW 573 and MH1. Other individuals without costo-vertebral material but whose cranio-facial skeleton is suitable for study are *A. africanus* specimens Sts 71 (approx. 2.4-2.8 mya) (Broom et al. 1950), StW 13 (approx. 2.4-2.8 mya) (Tobias 1972) and Sts 5, recently re-dated to 3.4-3.7 mya (Granger et al. 2022).

Among the best preserved crania of *Paranthropus* are the specimens KNM-WT 17000 (*P. aethiopicus*, approx. 2.5 mya) (Walker et al. 1986), DNH 7 (*P. robustus*, approx. 2 mya) (Keyser 2000) and KNM-WT 17400 (*P. boisei*, approx. 1.77 mya) (Leakey and Walker 1988). No costo vertebral material has been published yet to make inferences about the configuration of the thorax in this species. Early and/or primitive *Homo* specimens are those hominins that may still show adaptations to both bipedal and arboreal locomotion. Although little costo-vertebral remains belonging to these species are preserved, the thoracic skeleton *H. naledi* (approx. 0.2-0.3 mya, Berger et al. 2015; Hawks et al. 2017) may have been relatively similar to that of pre-*Homo* individuals (Bastir et al. 2015; Williams et al. 2017; Hawks et al. 2017). Cranio-facial evidence of respiratory system evolution suggests a small, relatively flat midface with none or very little eversion of nasal bones and as seen in OH 24 (*H. habilis*, approx. 1.8 mya) (Johanson et al. 1987), KNM-ER 1470 (*H. rudolfensis*, approx. 1.78-1.9 mya) (Leakey 1973), KNM ER 1813; and LES1 (*H. naledi*, approx. 0.4 mya) (Hawks et al. 2017).

Group 2: First obligatory bipedal Homo
(*H. ergaster*, *H. erectus*, *H. georgicus*, *H. antecessor*, *H. floresiensis*)

Group 2 encloses morphotypes of early hominins that are obligatory bipeds, with increased ranging behavior (mostly attributed to *H. ergaster*, *H. erectus s.l.*, *H. georgicus*), and with intermediate but also variable body size and with

brain sizes larger than in Group 1. Midfacial morphology shows a clearly recognizable eversion of nasal bones and frontal maxillary processes indicating the presence of a small *cavum nasi*. Facial size ranges from small to intermediate. The ribs are somehow larger than in Group 1, rounded (=pencil shaped) in cross section, and with little rib torsion (García-Martínez et al. 2018b). The only ribcage reconstructed so far comes from a subadult skeleton KNM-WT 15000 (Bastir et al. 2020b) and shows clear widening at the upper ribcage and wider and particularly deep proportions both in central and lower parts of the thorax. As the size of the faces in Group 2 hominins, the overall size of the thorax could be variable ranging from small to intermediate. KNM-WT 15000 (*H. ergaster*, approx. 1.45 mya) (Walker and Leakey 1993) is one of the most completely preserved hominin fossil skeletons ever discovered. Analysis of isolated ribs suggest a new thoracic bauplan, overall large and with a considerable increase in upper thoracic width (Jellema et al. 1993; Franciscus and Churchill 2002; Gomez-Olivencia et al. 2009), in relation to obligatory bipedalism and the necessity of accommodating their horizontally-oriented shoulder girdles (Jellema et al. 1993).

This morphotype was also potentially present in some of the ATD6 hominins (*H. antecessor*, approx. 0.9 mya) (Gómez-Olivencia et al. 2010; García-Martínez et al. 2018a). Both KNM-WT 15000 and ATD6 (ATD6-15 and ATD6-69) (Bermúdez de Castro et al. 1997) have a preserved cranium suitable for study, such as the *H. ergaster* remains of KNM-ER 3733 (approx. 1.7 mya) (Leakey 1976) and Buia UA31 (approx. 1 mya) (Macchiarelli et al. 2004). Also the Dmanisi hominins (*H. georgicus*, approx. 1.77 mya; Vekua et al. 2002; Lordkipanidze et al. 2013) preserve craniofacial remains with airways morphology and some thoracic vertebrae and rib remains (Lordkipanidze et al. 2007) that, at the vertebral level, are comparable to KNM-WT 15000 (Williams et al. 2017). No comparative research on the ribs has yet been published. The skeletal anatomy of *H. erectus sensu strictu*, has been classically attributed as being close to that of *H. ergaster*. However, we are not aware

of any costo-vertebral material to make inferences about their thoracic shape and just few specimens like Sangiran 4 or 17 (approx. 0.8 mya) (Jacob 1973) allow a study of their cranio-facial airways. Additionally, cranio-facial remains of LB1 (*H. floresiensis*, approx. 60 ky) (Brown et al. 2004) also fit architectonically in this group.

Group 3: Heavy-bodied Homo (*H. heidelbergensis*, *H. rhodesiensis*, *H. neanderthalensis*)

Group 3 are large, robust, heavy-bodied hominins with a larger brain and massive midfacial dimensions with a wide and large piriform apertures and a strongly everted, projecting and wider *cavum nasi* presumably reflecting high ventilatory demands. These faces are further related to large, inferiorly wide and deep ribcages, built by large and robust ribs with low curvatures and torsion with powerful diaphragms although rib material from the Midpleistocene is not yet published. We propose that both Midpleistocene hominins s.l. and the Neanderthal lineage belong to this 3rd functional group.

Cranial airways are preserved in Arago 21, (de Lumley and de Lumley 1971) AT 700 (*H. heidelbergensis*, approx. 0.43 mya: Arsuaga et al. 1993), Petralona 1 (*H. heidelbergensis*, approx. 0.25 mya: Kokkoros and Kanellis 1960), Broken Hill 1 (*H. rhodesiensis*, approx. 0.15 mya: Woodward 1921); Bodo (*H. rhodesiensis*: Conroy et al. 1978) and most Neanderthals, e.g. from Saccopastore (Sergi 1944); Gibraltar 1 (Forbes Quarry; *H. neanderthalensis*, approx. 60 ky: Busk 1864); La Chapelle aux Saints 1 (*H. neanderthalensis*, approx. 60 ky: Bouyssonie and Bardon 1908) and, regarding the costal skeleton Kebara 2 (approx. 58 ky: Arensburg et al. 1983; Gomez-Olivencia et al. 2018). Further costal and thoracic remains are preserved of La Chapelle aux Saint 1, La Ferrassie 1, 2, and La Regourdou (Gómez Olivencia 2013a,b, 2015; García-Martínez 2017; Gómez Olivencia et al. 2012).

Group 4: Homo sapiens

Group 4 is represented by modern humans with relatively tall, but slender and more gracile body configurations, large brains and small

orthognathic midfaces that show great variation of anterior nasal morphology in relation to climatic adaptations. The ribcages are narrower and shallower than in Group 3 and the ribs generally present a high degree of torsion.

Up to now, the first remains catalogued as *H. sapiens* correspond to the cranium Jebel Irhoud 1 (approx. 0.3 mya) (Ennouchi 1962) that, together with the cranium of Omo 1 (approx. 0.2 mya) (Leakey 1969) and BOU-VP-16/1 (approx. 0.16 mya) (White 2003), represent what is called ‘early *H. sapiens*’. The first evidence of a relatively complete fossil *H. sapiens* ribcage is from Skhul 4 and Qafzeh 9 (approx. 0.1 mya) (Garrod et al. 1937). However, no studies have yet been carried out on this thoracic material. Cranium and ribcage remains are well preserved in the archaeological sites of Cro-Magnon (approx. 28 ky: Lartet 1868; Broca 1868), Abri Pataud (approx. 22 ky: Movius and Vallois 1959) and Oberkassel (approx. 14 ky: Verworn and Bonnet 1914). Eventually, Holocene hunter gatherers like those from Nataruk (approx. 11 ky: Lahr et al. 2016) or neolithic Ötzi (approx. 5 ky: Seidler et al. 1992) are of interest due to their particularities.

Closing remarks and speculations for the future research

Paleoanthropological research into respiratory function has addressed craniofacial and postcranial parts from different viewpoints and analysed empirical evidence in the light of rather simple functional models attempting to explain evolutionary variation.

The study of cranial airways and nasal variations has been dominated by investigations into climatic adaptations mostly in modern human variation (e.g. Maddux et al. 2017) and cold adaptation in Neanderthals (e.g. Churchill 1998; Franciscus 1999; Steegman et al. 2002; Wroe et al. 2018). In this context, the nasal structure has been linked with one function (air conditioning) and in modern humans statistical links between both are commonly accepted (Franciscus and

Long 1991; Noback et al. 2011; Maddux et al. 2017). However, in fossil hominins, these links are less clear and possibly more complex models may be needed to address them (Weaver 2009; Rae et al. 2011a,b; Holton et al. 2011; Bastir 2018, 2019; Wroe et al. 2018).

On the other hand, research into the configuration of the thorax showed a greater focus on the evolution of body shape and locomotor patterns (Schmid 1983; Jellema et al. 1993; Schmid et al. 2013; Gómez-Olivencia et al. 2018; Bastir et al. 2020b) and breathing function only rarely played a role in these considerations. Only few researchers have sometimes attempted a more holistic view on respiratory system evolution unifying –conceptually– fossil remains from both parts of this functionally integrated system (Franciscus 1995; Churchill 1998; Franciscus and Churchill 2002; Bastir 2004, 2008; Rosas et al. 2006; Bastir 2018).

The present work aimed to continue this research line by associating craniofacial and postcranial fossil remains of the respiratory system. Because rarely cranial and postcranial material of the same individual is discovered, we attempted to propose groups that are somehow similar in facial and postcranial anatomy of the respiratory system. Therefore, taxonomy does not fit well with these functional, paleophysiological group assignments (Supplementary Tab. 1).

Morphological features of rib remains, such as cross-sectional shape or lack of torsion or overall size of *H. naledi* and possibly *H. habilis* (OH-50) seem not too different from rib fragments attributed to *A. afarensis* (Lucy, Kadanuumuu: Schmid 1983; Haile-Selassie et al. 2010) or *A. sediba* (Schmid et al. 2013). This is related to many difficulties, including morphometrics, the uncertainties of thoracic reconstructions and problems due to incomplete preservation, metamerism, and individual-specific assignments (e.g. MH1, MH2: Schmid et al. 2013; Williams et al. 2018). However, it may also be possible that respiratory physiological requirements of Australopithecines and early and morphologically transitional hominins were probably not so different from each other. It may suggest that

selection pressure on locomotor behaviour in Group 1 hominins was more pronounced than that on the respiratory system configuration.

Thus, it is difficult to interpret, in a respiratory context, the associated variations of facial morphologies ranging from totally flat faces (OH-24) to midfacial morphologies with some evidence for eversion of the nasals bones and the upper part of the piriform aperture (*A. sediba*, *Paranthropus*, KNM-ER 1813 and even Dmanisi). One of the major reasons to pool them together functionally in Group 1 is related to body size and basic links between size and energetics (Froehle et al. 2013), although clearly, more research is needed to address these putative respiratory similarities. For example, because this group comprises midfacial morphologies ranging from flat to slightly everted anterior nasal openings one of the most important future lines of research is to address a possible functional significance of these midfacial variations in the light of respiratory physiology and its integration with masticatory system size and function.

First steps in this direction seem to point also towards reduced selection pressure on respiratory function: Assuming that differences in cranial airways morphologies of living chimpanzees and humans can serve as proxies for *Australopithecus* and early *Homo* (Sanz Prieto 2021), airflow simulations did not support different capacities of air conditioning in terms of temperature and humidity adjustments (Nishimura et al. 2016; Bastir et al. 2022a). This may indicate that the midfacial variations in Group 1 hominins are related to interactions between the relative sizes of the airways and masticatory systems. It could be speculated that reduced gnathic dimensions with stable midfacial dimensions could lead to projection of the latter. However, such a hypothesis has yet to be tested. To perform the necessary analyses, robust and quantitatively validated soft-tissue airway reconstructions are needed. These should be based on the skeletal variations of 3D midfacial shapes encountered in Group 1 and Group 2, as well as testing the impact of midfacial size, such as reflected by Group 3, on respiratory physiology.

The combination of HD-GMM methods, virtual morphological modifications and experiments subjected to CFD analysis with robust comparative samples can provide better insight into the possible functional implications of external and/or internal midfacial fossil variations. Preliminary work of Sanz-Prieto (2021) has provided a successful proof of concepts and methods (Fig. 2, upper panel), but better fossil reconstructions and more robust reference samples are necessary to test these functional models. Experimental work *in silico* is necessary to sharpen our functional understanding of the skeletal morphological features related to the emerging nose, such as mentioned by Franciscus and Trinkaus (1988) in Group 1 and Group 2 hominins, or with respect to the convexity and eversion of upper nasal aperture morphology, nasal sills and nasal floor variations (Franciscus 2003), medial projections of lateral piriform aperture walls (Schwartz and Tattersal 1996) in Group 3 hominins. Computer experiments could complement the pioneering physical experiments carried out by Churchill et al. (2004).

Some airways of Midpleistocene humans (Kabwe) and Neanderthals (La Chapelle aux Saints 1) were recently analysed with similar methods and produce important insights into Group 3 hominin paleophysiology (Wroe et al. 2018). Their Figure 3 shows different airflow direction in Kabwe and in La Chapelle aux Saints, suggesting that the spatial arrangement of the intermediate and inferior meatus affects airflow geometry close to the anterior cavum at the posterior part of the inflow tract (*sensu* Mlynski et al. 2002), but not necessarily the effect of air-conditioning. Clearly, the CFD simulations of Wroe et al. (2018) indicated that midfacial size influences flow rates, which supports quantitatively the idea that energetic parameters are important aspects of cranial airway function in Group 3 hominins (Franciscus and Churchill 2002; Bastir 2004, 2008; Yokley et al. 2009; Froehle et al. 2013).

Virtual morphology and HD-GMM methods can improve the anatomical models subjected to CFD analyses and can be used systematically to

assess physiological questions such as: How do the externally recognised (and sometimes taxonomically relevant) skeletal features affect internal airway features of the inflow, the functional and the outflow tracts relate to airflow dynamics, air conditioning capacities, laminar and turbulent flow generation and flow rates? Also, one could use CFD to address the hypothesis that residence time of air in orthognathic modern humans (Group 4) (Noback et al. 2011) is shorter than in hominins belonging to Groups 1-3, and that the physical factors of air-flow and air-conditioning in modern humans is not necessarily similar to those of ancient *Homo* (Wroe et al. 2018).

Finally, airflow analyses can be extended to the lungs and connected with the biomechanics and motion of the postcranial respiratory system. Do differences in CFD parameters detected in cranial airways relate to the size, 3D shape and biomechanics of the musculoskeletal system and diaphragm of the thorax? López-Rey et al. (2021) provided preliminary size and shape estimates of the diaphragm in fossil hominins: a quantitatively reconstructed diaphragmatic surface of the Kebara 2 Neanderthal male was significantly larger and the Nariokotome juvenile was within the range of adult human males sizes published by Cluzel et al. (2000). While relations between diaphragmatic shape and respiratory function are not yet clear, size differences point towards more powerful respiratory systems in hominins belonging to Group 2 and certainly Group 3 (García-Martínez et al. 2018a). They further indicate that the need of oxygen is a driving factor that links piriform aperture and choanae size with rib geometry in the sense discussed by Franciscus and Churchill (2002).

Diaphragmatic size and shape differences also communicate with HD-GMM analysis of thoracic in vivo musculo-skeletal biomechanics. Bastir et al. (2017a) has shown that the lower thorax produces much greater size differences during breathing kinematics than the upper part of the rib-cage. Thus, evolutionary changes at the lower thorax, related to the diaphragm, should affect respiratory physiology and capacity.

However, links between thoracic shape and energetics and the potentially differential

contribution of ribcage muscles and the diaphragm in these thorax configurations are not clear. One could speculate that while large diaphragms may be capable to move greater air volumes for lung ventilation, increasing oxygen supply of the organism, larger diaphragm per se may also be more costly in energetic terms, which would then off-set the net effect of increased oxygen uptake due to increased work of breathing (Dominelli et al. 2017). Experimental analysis should address these questions of energetics and oxygen consumption. These could be used to test paleobiological interpretations such as explosive sprinting during ambush hunting in heavy-bodied Neanderthals and/or other Group 3 hominins (Stewart et al. 2019; Raichlen et al. 2011) or the hypothesis of aerobic long-distance running, suggested for Group 2 hominins (Bramble and Lieberman 2004; Lordkipanidze et al. 2007).

A recent study combined HD-GMM of torso shape and running performance to relate torso shape with aerobic and non-aerobic running performance in young athletes (Bastir et al. 2022b). This study found that running at low speeds within aerobic metabolism was not related to torso shape. However, during aerobic running performance higher velocity was significantly related to narrower and, particularly, flatter thorax configurations (Bastir et al. 2022b). Interestingly, however, the mean velocity during this anaerobic running performance was far lower than the one proposed for typically anaerobic endurance running (Lieberman et al. 2009). So, running at the speeds proposed by Lieberman et al. (2009) would be highly related to torso shape, but not aerobic. Clearly, better experiments are necessary. These would need also improvements in terms of control for temperature and humidity conditions to approximate the assumed paleoecological conditions. In addition, rather than static torso shape, the kinematic changes of respiratory chest wall motion should be analysed during exercise in order to infer biomechanical differences that could be related to thorax variations and breathing modes. Once the work of breathing is quantified, HD-GMM could be used to disentangle pulmonary, diaphragmatic and abdominal portions of chest wall motion that

may vary across subjects with different thorax and overall torso geometries. It can be speculated that different torso geometries pre-determine to some degree preferred breathing motions and exercise efficiencies Gómez-Recio et al. (2022). These could be studied through the compartmentalization of torso motion (Ward et al. 1992; Ferrigno et al. 1994; Cala et al. 1996; Aliverti et al. 2001) and the statistical treatment of form and motion of these compartments through HD-GMM in relation to hominin torso shape variation.

All these questions link paleoanthropology directly with physiology, sports sciences and bio engineering and highlight the need for interdisciplinary collaborations in order to progress in hominin respiratory paleophysiology. However, at the basis of such functional evolutionary research is the quality of our fossil hard and soft tissue reconstructions. This, nevertheless, is not only a question of methods, but also of fieldwork, which is necessary to improve the fossil record that could be integrated into morphological and functional reconstructions. Since the first suggestions by Franciscus and Churchill (2002) who indicated the need for linking the cranial and postcranial parts of the respiratory systems, some progress has been made in this research avenue. The methods for reconstructions, analysis and experiments outlined here can be used to advance in this important field of hominin paleophysiology.

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Author Contributions

MB and DGM designed the associated projects. MB wrote major parts of the manuscript. DSP, JMLPP, CAP, MGR, MLC, and JMGR added specific parts of text to the manuscript and produced artwork. APR worked on manual reconstructions of the Gibraltar 1 Neanderthal and contributed to artwork. MAB, BB and DGM wrote specific technical sections of the manuscript. All authors critically discussed and reviewed the manuscript.

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