Big choanae, larger face: scaling patterns of cranial airways in modern humans and African apes and its significance for Mid- and Late Pleistocene hominin facial evolution

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Summary

This study aims at understanding the ontogenetic and allometric scaling relations between anterior and posterior openings of the cranial airways and facial size to shed light on the mechanisms that might underlie the evolution of a large face and airways in Middle Pleistocene hominins and Neandertals. Size is calculated from 3D-landmarks measured at the facial skeleton and airways structures of 403 skulls of two ontogenetic series of *H. sapiens* and *P. troglodytes*, an adult sample of gorillas and 11 Middle Pleistocene hominins and Neandertals. RMA regression models were used to compare scaling patterns of anterior and posterior airways with overall facial size. Results show that anterior airways scale with a significantly greater slope with facial size than the posterior airways. This ontogenetic mechanism could explain the large faces and noses in the Neandertal lineage despite suboptimal effects for respiratory air-conditioning in cold climate. Large facial size could be a developmentally constrained consequence of generating airways, large enough, to provide the necessary oxygen for elevated energetic demands in this large-brained and heavy bodied hominin lineage.

Introduction

Neanderthals are specific with respect to the size and shape of their bodies. Many anatomical features of the craniofacial and postcranial skeleton are morphologically derived. Neandertal characters include midfacial prognathism and projection, a large, wide nasal aperture and an elongated overall cranial shape, at the craniofacial level, and a wide shorter torso (that is, thorax and pelvis), as well as generally short limb proportions at postcranial levels [1-8]. Midfacial morphology and body shape of Neandertals have been interpreted as functional adaptations to cold climate [5]. However, more detailed work on nasal functional anatomy has challenged climatic interpretations [4, 9, 10]. This is because modern humans, adapted to extreme cold, show tall and narrow nasal apertures, while in Neandertals these structures are large and wide (Holton and Franciscus, 2008). In this respect, their noses are more comparable to modern humans adapted to hot and humid climates [4, 11-13].

Also the stocky body shape and high body mass estimates of Neandertals are thought to reflect cold adaptations [5] although they inherited a basic body configuration from heavy bodied Early and Midpleistocene ancestors [14-16]. This lineage of hominins likely had elevated energetic demands and a body economy different from that of anatomically modern *H. sapiens* [16-19]. The bioenergetic heritage of Neandertals probably had functional implications for different anatomical systems, some of which affected directly or indirectly the position and morphology of the cranial airways. This is why investigating the integration and function of respiratory apparatus is important in human evolutionary anatomy [20].

The cranial airways connect the outer environment with the inner organs of the body. They support directly a series of functions such as respiration, olfaction, thermoregulation, phonation, deglutition and speech [21]. At the skeletal level the cranial airways consist of the nasal cavity, which is located in the center of the facial skeleton (midface) and of the external part of the posterior cranial base as the skeletal roof of the nasopharynx [22, 23]. The nasal cavity is delimited anteriorly by the piriform aperture of the maxilla and the nasal bones. The

posterior airways are demarcated by the choanae, formed cranially by the sphenoid, laterally by the pterygoid processes, interiorly by the palates and by the external part of the sphenoccipital clivus and pharyngeal tubercle, the roof of the nasopharynx. The internal roof of the nasal cavity is delimited anteriorly by the cribriform plate of the ethmoid and more posteriorly by the sphenoid body. The internal floor of the airways is formed by the palatine processes of the maxilla and the horizontal laminae of the palate. The lateral walls are provided by the maxilla, the lacrimal bone, the superior and medial turbinates of the ethmoid and the vertical parts of the palate. In the midsagittal plane, the nasal cavity is divided by the nasal septum, which is an osseocartilaginous structure formed by the perpendicular lamina of the ethmoid and the vomer.

Because of this anatomical context, the cranial airways are a central functional space around which adjacent craniofacial structures are organized. For their central position the airways are important in both, an ontogenetic and evolutionary context (Enlow, 1990). Integration analyses in modern humans have shown differences in the patterns of covariation between facial morphology and the openings of the nasal cavity [24]. These studies indicate that the choanae and posterior areas of the airways are morphologically more independent from the face than the anterior nasal opening, which correlates more tightly with facial morphology.

Such differences in correlation patterns reflect an important aspect of posterior airway function. The choanae are the last skeletal diameter that determines the caliber of the soft-tissue components of the airways within the nasopharynx: the larger the posterior airways, the greater the amount of respiratory air that passes to the lungs available for skeletal muscle work and body activity.

Variation of cranial airway space and its importance for craniofacial morphology has been proposed by Enlow [25]. Internal spatial differences are reflected morphologically in sex-specific differences of human faces [26]. Actually, in many different human populations both

absolutely and relatively larger airway proportions are a constant feature of sexual dimorphism in males [22, 27, 28]. Because males have greater energetic and oxygen demands than females, greater cranial airways have been interpreted as skeletal evidence for physiological components of sexual dimorphism and body function [28, 29]. This evidence supports the view that the size of the choanae might act as a constraint on respiratory function and could thus be potentially important in the context of human evolution in a similar physiological and respiratory-energetic context. But how do anterior and posterior airways interact with the face during growth and across different hominins and non-human primates?

The aim of this paper is to study the ontogenetic and allometric scaling relations between the anterior and posterior cranial airway openings and the size of the face in a wider comparative data set. I address the null hypothesis that no differences exist in the scaling patterns of the sizes of the anterior and posterior cranial airway openings and the face.

Material and Methods

A total of 403 skulls of two ontogenetic series of geographically variable *H. sapiens* (N=263) and *P. troglodytes* (N=83) and an adult sample of Gorilla (N=46) was analysed. Data were collected at the Anthropological Institute of the University of Coimbra, University of Cambridge, and the Natural History Museum (London) (Table 1). The fossil hominin sample consisted of Neandertals (N=6) and Midpleistocene hominins (N=5).

In the present analysis 3D landmarks were measured on external craniofacial structures related to the airways and the peripheral face by a Microscribe G2 digitizer. Data collection and landmarks were described in detail in Bastir and Rosas [24]. In the fossil hominins, the landmarks data were digitized on original fossils (Kabwe, Forbes Quarry), on high quality casts (SH5) and on high resolution 3D reconstructions of CT scans of La Chapelle aux Saints, La Ferrassie 1, Saccopastore 1, Saccopastore 2, Guattari 1, Petralona, Bodo, and a virtual reconstruction of Arago 21 by Gunz et al. [30]. Missing landmarks due to fragmentary

preservation in the fossils were reconstructed using a multiple multivariate regression approach by Morpheus et al. [30, 31].

The entire craniofacial landmarks were divided into subsets quantifying overall facial size (20lms), anterior airways (11lms) and posterior airways (11 lms) (Table 2, Fig. 1) and based on previous studies on the nasopharynx and associated skeletal structures [12, 22-24]. Centroid sizes were calculated for these compartments for comparative scaling analysis. The anterior airway opening consisted of landmarks of the piriform aperture and the anterior part of the ethmoid while the posterior opening consisted of the choanae and the associated nasopharyngeal landmarks at the spheno-occipital clivus (Table 2).

Scaling patterns of anterior and the posterior cranial airway opening against overall facial size were compared using RMA regression models [32]. To test the null hypothesis of no differences between these airway compartments and overall facial size 95% confidence intervals of the slopes were compared using PAST permutation analysis [33]. Scaling patterns were analyzed in different groups, including human and chimpanzee growth series, the entire sample of *Homo*, and the full hominin and great apes data set.

Results

Table 3 shows the slopes of the regression models and the 95% confidence intervals of their slopes. All RMA models were statistically significant at $P=0.001$ or higher. In all comparisons the anterior openings of the airways scaled more positively than the posterior openings. This trend was more markedly in chimpanzees, where the slopes of the posterior airways were completely outside the 95% of the range of the anterior slope. In the human data set the slope of the posterior airways was close to the lower range of the anterior airways and the anterior close to the upper range of the lower. In the full *Homo* data set the anterior slope was fully outside the range of the posterior and vice versa. Figure 2 shows the data of the full

sample. All these results show that the size of the anterior facial opening increases more with facial size than the size of the posterior cranial airways.

Discussion

This study aimed at investigating the ontogenetic and evolutionary interaction of the sizes of the anterior and posterior cranial airways and the face. Specifically, ontogenetic and allometric scaling relations between the anterior and posterior airways in humans, fossil hominins and great apes were studied. The null hypothesis predicted no differences in the scaling of the anterior and posterior airways with facial size. Our results suggest, however, that the anterior airway openings increase more strongly relative to the face than the posterior airways. Consequently, the null hypothesis is rejected.

The results of the ontogenetic analyses suggest that growth mechanisms of the anterior and posterior openings of the cranial airways have similar effects in African great apes and hominins. This is surprising because postcranial changes in the nasopharyngeal area differ substantially in great apes and hominins due to different ontogenetic trends of the posterior cranial base. In humans the base flexes antero-inferiorly, while in apes the base retro-flexes [34-37]. Theoretically, this should diminish nasopharyngeal size in humans and increase this region in great apes. Yet, the posterior airways scale similarly with facial size in both groups. Such a result could be explained by the fact that while retro-flexion produces antero-posterior expansion of the nasopharyngeal space in apes, in humans, ontogenetic flexion is accompanied by a lowering of the posterior base and face expanding posterior airway size in a vertical direction. Importantly, both in human and in chimpanzee ontogeny the posterior airways scale with a significantly lesser slope with facial size than the anterior airways. This is found in all group comparisons (Table 3, Fig. 2).

These systematic differences between anterior and posterior airway scaling patterns can explain facial morphology and size in a functional context that could be important for

Midpleistocene hominins and Neandertals. As expected, due to their large faces, these hominins plot at the upper part of the modern human range (Fig. 2). Different comparative studies have shown that facial size scales positively with body size, not only in primates, but also more generally in mammals [34, 38-40]. However, scaling patterns are based on biological processes and should be discussed also within a functional context. The size of the airways is one functional factor that might underlie this general face-body scaling patterns [20, 41, 42]. This can be assumed because, for physiological reasons, body mass and the size of the respiratory organs scale isometrically and are correlated tightly across mammals [43]. The present results could explain large facial sizes by linking energetic factors and associated respiratory constraints with general facial growth and scaling patterns. The very large nasal apertures in Midpleistocene hominins and the Neandertal lineage seem to be related to this. Body mass estimates in these hominins are higher in anatomically modern humans [19, 44]. Following Stahl [43] larger body masses require (and correlate with) larger respiratory organ sizes. Although represented only by skeletal anatomy, the large cranial airways of Neandertals correspond to their large thoracic capacities [8, 45-48] and likely larger lungs [49]. These relations could drive the size of the face via functional constraints on airway size.

The airway-facial growth pattern could also have reduced its morpho-functional evolvability and possible climatic adaptations of the piriform apertures of Neandertals [4] explaining the different strategies of air-conditioning in Neandertals and modern humans [10]. Cold adapted modern humans show narrow and tall anterior nasal openings [11-13], which are achieved by specific patterns of integration of the nasal cavity and the maxillary sinuses [50-52]. These narrow anterior airway openings are thought to increase turbulence, which should favor heating and moistening of the inspired air [11]. Thus, while cold-adapted modern humans show such narrow tall narrow apertures, those of cold-adapted Neandertals are large and wide [4]. Neandertals might not have been able to evolve (and grow) narrow anterior nasal openings, as these might simply not have provided the necessary airway space [16, 20,

53] despite its possible advantages for airflow dynamics and turbulence induction. Instead, air-conditioning in Neandertals might have been taken over by increased resilient time [10]. This situation illustrates how similar functional problems are resolved by different mechanisms, and might shed light on evolutionary process and the importance of tinkering [54].

Increased resilient time of air within the nasal cavity is likely related to the greater length of the cranial airways as part of their prognathic and projecting midface, suggesting that the entire nasofacial functional system should be considered embedded within a specific cerebro-basicranial configuration. In Neandertals, the nasofacial functional system is related to their typical overall skull morphology. Recent analysis of basicranial and facial integration has shown that modifications at the basicranium shift the nasal cavity (and face) into a more anterior position contributing thereby to midfacial projection and prognathism [7]. This shift could be related to encephalisation and its impact on basicranial evolution, which in Neandertals is different than in anatomically modern humans [55-57]. So, rather than a localized, independent functional adaptation to cold climate by evolution of a narrow piriform aperture (through selective pressure), slight modifications among interrelated parts of systems (brain, base, face, and airways interactions) of the organism, linked by ontogenetic scaling relations (such as the link between body mass and facial size via the respiratory organs), could have provided effective air conditioning *despite* naso-facial differences in the Neandertal lineage and modern humans [4, 10]. Such longer and wider airways and faces may further have offered a structural solution that guarantees sufficient oxygen supply to the high-energy demanding Neandertal bodies, and so, altogether contributing to their cold “exaptation” by an integrated set of organism-related anatomical features.

This could illustrate how slight modifications of integrated systems (thorax and airways in relation to body mass and encephalisation) change the form and position of structures (airways, face) in which functional needs (air-conditioning) are taken over by new functional

principles (resilience time due to prognathism rather than turbulence). If confirmed in future studies, this kind of tinkering could prove as important factor in later hominin facial evolution.

Acknowledgments

I am grateful to the Société d'Anthropologie de Paris, in particular to François Marchal and Guillaume Daver, for their kind invitation to participate in the meeting of Poitiers 2018. Data and data access were provided by Chris Stringer, Fred Spoor, Rob Kruszynski and Loise Humphrey, Maggie Bellatti, Giorgio Manzi, Roberto Machiarelli, Luca Bondioli, Alain Froment, Philippe Menecier, and Antoine Balzeau. Funding: CGL2015-63648-P (MINECO, Spain)

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TABLES

Table 1. Comparative data sets, origins and ages.

Recent data	Adults N	Subadults N	Data source
Europeans (Coimbra)	50	42	dry skulls
Europeans (Spitalfields, NHM)		88	dry skulls
Africans (NHM)	36		dry skulls
Inuit (Cambridge)	12		dry skulls
Australians (NHM)	30		dry skulls
Fueguians (NHM)	5		dry skulls
	133	130	dry skulls
Pan troglodytes (NHM, Cambridge)	50	33	dry skulls
Gorilla gorilla (NHM)	46		dry skulls
Fossil hominins			
Kabwe			CT-reconstruction
Bodo			CT-reconstruction
Arago 21			Cast
SH5			Cast
Petralona			Cast
Forbes Quarry			CT-reconstruction
Guattari 1			CT-reconstruction
Ferrassie 1			CT-reconstruction
La Chapelle aux Saints 1			CT-reconstruction
Saccopastore 1			CT-reconstruction
Saccopastore 2			CT-reconstruction

Table 2. Landmarks and assignation to different facial and airway regions

nasion	ant. airways
rhinion	ant. airways
anterior nasal spine	ant. airways
left anterior ethmoid fm	ant. airways
left lacrimal	ant. airways
left distal nasomaxillary junction (at the distal suture)	ant. airways
left alare	ant. airways
right anterior ethmoid fm	ant. airways
right lacrimal	ant. airways
right distal nasomaxillary junction (at the distal suture)	ant. airways
right alare	ant. airways
left optic canal (most medial, inferior point)	post. airways
left choana roof (most superior point)	post. airways
left midturbinate base (most posterior point at choanae level)	post. airways
left choana base (most lateral intranasal point at the palate)	post. airways
right optic canal (most medial, inferior point)	post. airways
right choana roof (most superior point)	post. airways
right midturbinate base (most posterior point at choanae level)	post. airways
right choana base (most lateral intranasal point at the palate)	post. airways
staphylion	post. airways
vomero-sphenoid junction [26]	post. airways
pharyngeal tubercle (maximal projection)	post. airways
glabella	peripheral face
nasion	peripheral face
A-point [26]	peripheral face
prosthion	peripheral face
left posterior alveolar point (post. alveolar tubercle)	peripheral face
right posterior alveolar point (post. alveolar tubercle)	peripheral face
left frontomolare orbitale	peripheral face
left zygomaxillary superior	peripheral face
left infra-orbital foramen (most lateral point)	peripheral face
left zygomaxillary inferior	peripheral face
left zygomatic root (most inferior point)	peripheral face
left zygotemporale	peripheral face
right frontomolare orbitale	peripheral face
right zygomaxillary superior	peripheral face
right infra-orbital foramen (most lateral point)	peripheral face
right zygomaxillary inferior	peripheral face
right zygomatic root (most inferior point)	peripheral face
right zygotemporale	peripheral face
right canine alveolus (most posterior point)	peripheral face
left canine alveolus (most posterior point)	peripheral face

Table 3. RMA regressions, slopes plus 95% confidence intervals of different groups

	human growth	chimpanzee growth	all hominins	hominin and apes
anterior airways	0.49 (0.47-0.53)	0.55 (0.52-0.57)	0.48 (0.45-0.52)	0.66 (0.63-0.69)
posterior airways	0.46 (0.43-0.49)	0.48 (0.46-0.51)	0.42 (0.39-0.46)	0.4 (0.38-0.42)

Captions to the figures:

Figure 1. Landmark sets of the different anatomical units. a, b) show anterior airways in is general context and details; c, d) show posterior airways and e, f) show the peripheral landmarks of the face. For definitions see Table 2.

Figure 2. Scatterplot of centroid sizes of the anterior and posterior airways (y-axis) against the centroid size of the face (x-axis). Note the divergence of the sizes of the anterior airways along facial size compared to the posterior airways. Because of these scaling relations the differences between anterior and posterior airways is greater in larger faces.

Figure 1

Figure 2