

Big Choanae, Larger Face: Scaling Patterns Between Cranial Airways in Modern Humans and African Apes and Their Significance in Middle and Late Pleistocene Hominin Facial Evolution

Taille des choanes et de la face : modèles d'échelles des voies aériennes crâniennes chez les hommes modernes et les grands singes africains. Signification pour l'évolution du massif facial chez les hominines du milieu et de la fin du Pléistocène

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Abstract This study aimed to understand the ontogenetic and allometric relationships in scaling between the anterior and posterior openings of the cranial airways and facial size, in order to shed light on the mechanisms that might underlie the evolution of a large face and large airways in Middle Pleistocene hominins and Neandertals. Sizes were calculated from 3D landmarks measured on the facial skeleton and airway structures of 403 skulls from 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 the patterns in scaling between the anterior and posterior airways in relation to overall facial size. Our results show that the size of the anterior airways correlates more positively with facial size than the size of the posterior airways. This ontogenetic mechanism could explain the large faces and noses in the Neandertal lineage despite the adverse effects of such a phenotype for respiratory air-conditioning in cold climates. A large facial size could be a developmentally constrained consequence of generating airways large enough to provide the necessary oxygen for high energy demand in this large-brained and heavy-bodied hominin lineage.

Keywords Facial integration · Scaling constraints · Nasal cavity

Résumé Cette étude étudie les relations d'échelles ontogénique et allométrique entre les ouvertures antérieures et postérieures des voies aériennes crâniennes et la taille du massif

facial. L'objectif est de mettre en évidence les mécanismes qui peuvent expliquer l'apparition d'un massif facial et de voies aériennes de grande taille chez les hominines du Pléistocène moyen et chez les Néandertaliens. La taille est calculée à partir de point-repères 3D positionnés sur la face et les ouvertures liées aux voies aériennes de 403 crânes provenant de deux séries ontogénétiques d'*H. sapiens* et de *P. troglodytes*, d'une série de gorilles adultes et de 11 Néandertaliens et hominines du Pléistocène moyen. Des modèles de régressions RMA sont utilisés pour comparer les modèles d'échelles des voies aériennes antérieures et postérieures avec la taille générale de la face. Les résultats montrent que la taille des voies aériennes antérieures est corrélée avec la taille de la face, de façon plus positive que celle des voies aériennes postérieures. Ce mécanisme ontogénique pourrait expliquer la taille importante des faces et ouvertures nasales au sien de la lignée néandertalienne malgré l'effet négatif que ce phénotype peut avoir sur le système respiratoire dans des conditions climatiques froides. Une taille faciale importante pourrait être une contrainte développementale, conséquence de l'apparition de voies aériennes suffisamment grandes pour obtenir l'oxygène nécessaire à une demande énergétique élevée dans cette lignée d'hominines aux cerveaux de grandes tailles.

Mots clés Intégration faciale · Contraintes d'échelle · Cavité nasale

Introduction

Neandertals have specific characteristics in body size and shape. Many anatomical features of the craniofacial and postcranial skeleton are morphologically derived. Neandertal

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characters include midfacial prognathism and projection, a large, wide nasal aperture and an elongated overall cranial shape at the craniofacial level, a short, wide torso (thorax and pelvis) and generally short postcranial limb proportions [1–8]. The midfacial morphology and body shape of Neandertals have been interpreted as functional adaptations to cold climates [5]. However, more detailed work on functional nasal anatomy has challenged these climatic interpretations [4,9,10], because modern humans adapted to extreme cold have tall, narrow nasal apertures, whereas these structures are large and wide in Neandertals [4]. In this respect, Neandertal noses are more comparable to those of modern humans adapted to hot and humid climates [4,11–13].

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

The cranial airways connect the outer environment with the inner organs of the body. They directly support a series of functions such as respiration, olfaction, thermoregulation, phonation, deglutition and speech [21]. In the skeleton, the cranial airways consist of the nasal cavity, which is located in the centre 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 delimited by the choanae, formed cranially by the sphenoid, laterally by the pterygoid processes, and inferiorly by the palates and by the external part of the sphenoid-occipital clivus and pharyngeal tubercle, forming 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 formed 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 form a central functional space around which adjacent craniofacial structures are organized. The central position of the

airways is important in both the ontogenetic and evolutionary contexts (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 closely with facial morphology.

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

Variations in cranial airway space and their importance for craniofacial morphology have been proposed by Enlow [25]. Internal spatial differences are reflected morphologically in gender-specific differences between human faces [26]. In many different human populations, both absolutely and relatively larger airway proportions in males are a constant feature of sexual dimorphism [22,27,28]. Because males have greater energetic and oxygen demands than females, larger 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 therefore be important in the context of human evolution in a similar physiological and respiratory–energetic context. But how do the anterior and posterior airways interact with the face during growth and across different hominins and non-human primates?

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

Material and methods

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

For this analysis, 3D landmarks were measured on external craniofacial structures related to the airways and the

Table 1 Comparative data sets, provenances and ages / <i>Description de l'échantillon de comparaison, origine géographique et âge</i>			
Recent data	Adults <i>N</i>	Subadults <i>N</i>	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
Petalona			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

peripheral face, using a MicroScribe G2 digitizer. Data collection and landmarks are described in detail in Bastir and Rosas [24]. In the fossil hominins, the landmark data were digitized from original fossils (Kabwe, Forbes Quarry), high-quality casts (SH5) and high-resolution 3D reconstructions of CT scans from La Chapelle aux Saints, La Ferrassie 1, Saccopastore 1, Saccopastore 2, Guattari 1, Petralona and Bodo, and a virtual reconstruction of Arago 21 by Gunz et al. [30]. Landmarks that were missing due to fragmentary preservation of the fossils were reconstructed by Morpheus et al. using a multiple multivariate regression approach [30,31].

All the craniofacial landmarks were divided into subsets quantifying overall facial size (20 lms), anterior airways (11 lms) and posterior airways (11 lms) (Table 2, Fig. 1), based on previous studies on the nasopharynx and associated skeletal structures [12,22–24]. Centroid sizes were calculated for these compartments for the comparative scaling analysis. The anterior airway opening consisted of landmarks on 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 sphenoccipital clivus (Table 2).

Scaling patterns between the anterior and the posterior cranial airway openings in relation to overall facial size were compared using RMA regression models [32]. To test the null hypothesis postulating no scaling 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 analysed in different groups, including human and chimpanzee growth series, the entire *Homo* sample, and the full hominin and great apes data sets.

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 size of the anterior openings of the airways correlated more positively with facial size than the posterior openings. This tendency was more marked 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 slope of the anterior airways was close to the upper range of the posterior airways. In the full *Homo* data set, the anterior slope was entirely outside the range of the posterior slope and vice versa. Figure 2 shows the data for 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.

Name of landmarks	Position on the cranium
Nasion	Ant. airways
Rhinion	Ant. airways
Anterior nasal spine	Ant. airways
Left anterior ethmoid fm	Ant. airways
Left lachrymal	Ant. airways
Left distal nasomaxillary junction (at the distal suture)	Ant. airways
Left alare	Ant. airways
Right anterior ethmoid fm	Ant. airways
Right lachrymal	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

Discussion

This study aimed to investigate the ontogenetic and evolutionary interactions between the sizes of the anterior and posterior cranial airways and the face. Specifically, I studied

ontogenetic and allometric correlations in scaling between anterior and posterior airway sizes in humans, fossil hominins and great apes. The null hypothesis predicted no differences in the sizes of the anterior and posterior airways in relation to facial size. However, the results suggest a greater

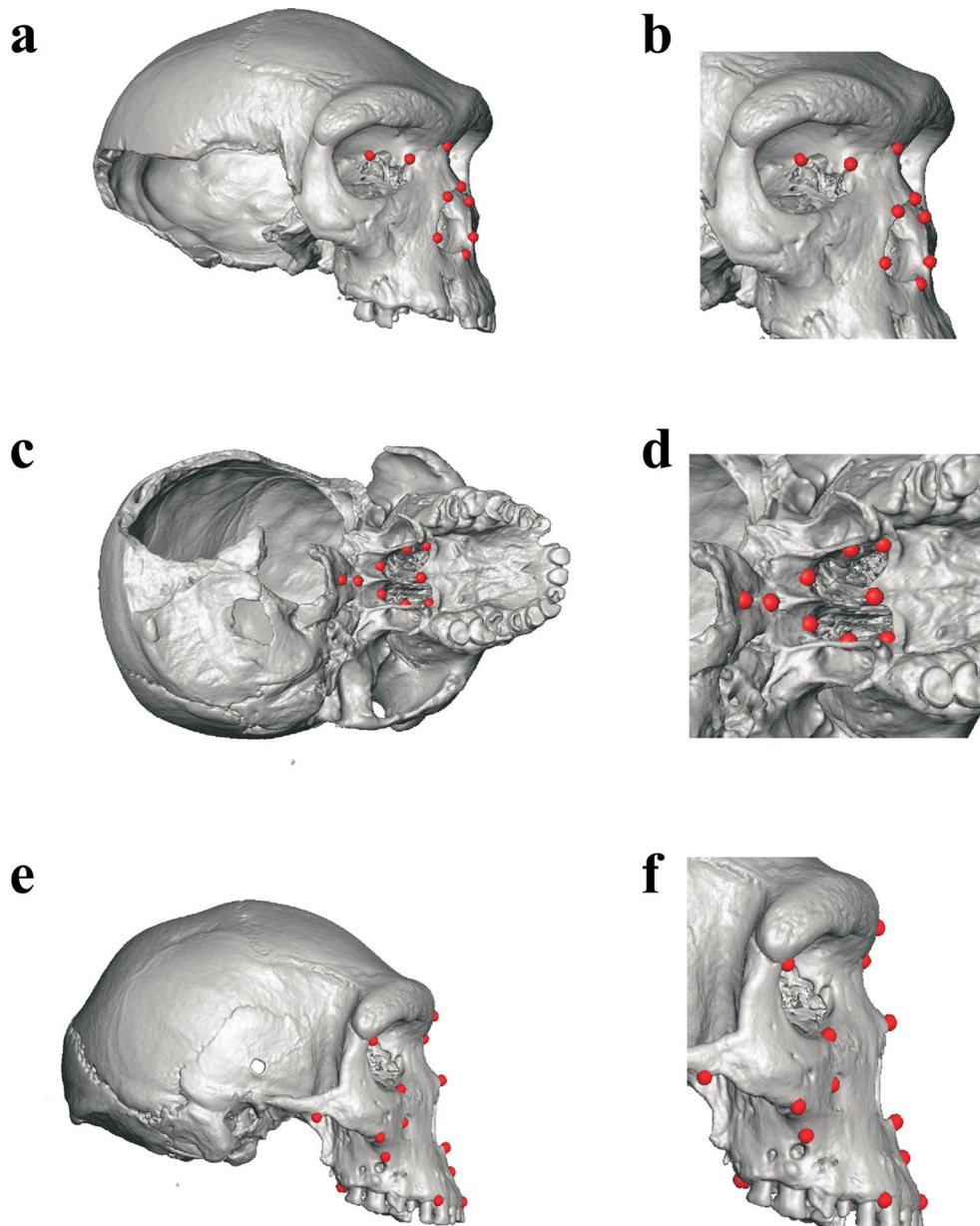


Fig. 1 Landmark sets of the different anatomical units. (a, b) show anterior airways in general context and details; (c, d) show posterior airways and (e, f) show the peripheral landmarks of the face. For definitions, see Table 2 / *Position des points-repères pour les différentes zones anatomiques. a, b : voies aériennes antérieures, contexte général et détails ; c, d : voies aériennes postérieures ; e, f : points-repères périphériques de la face. Les points-repères sont définis dans le tableau 2*

Table 3 RMA regressions, slopes plus 95% confidence intervals for the different groups / *Régression RM, pente et intervalle de confiance 95 % pour les différents groups*

	Human growth	Chimpanzee growth	All hominins	Hominins 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)

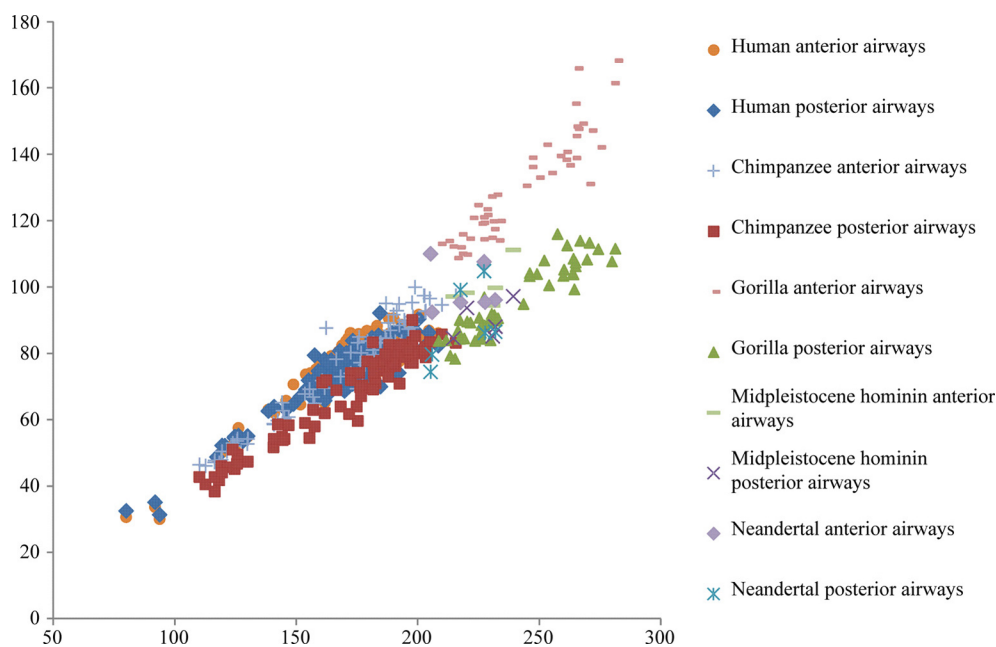


Fig. 2 Scatterplot of centroid sizes of the anterior and posterior airways (y -axis) against the centroid size of the face (x -axis). Note the divergence of the sizes of the anterior airways along facial size compared to the posterior airways. Because of these scaling relations, the differences between anterior and posterior airways is greater in larger faces / *Nuage de points des tailles centroïdes des voies aériennes antérieures et postérieures (axe y), comparé à la taille centroïde du massif facial (axe x). Nous pouvons observer la différence entre la taille des voies antérieures par rapport à la taille du massif facial, comparés à la taille des voies postérieures par rapport à la taille du massif facial. Du fait de ces corrélations d'échelles, les différences entre les voies aériennes antérieure et postérieure sont plus importantes pour les massifs faciaux de plus grande taille*

increase in the anterior airway openings relative to the face than in the posterior airways. Consequently, the null hypothesis is rejected.

The results of the ontogenetic analyses suggest that the 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 in the posterior cranial base. In humans, the base flexes antero-inferiorly, while in apes the base retroflexes [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. This could be explained by the fact that while retroflexion produces anteroposterior expansion of the nasopharyngeal space in apes, ontogenetic flexion in humans is accompanied by a lowering of the posterior base and face, which vertically expands posterior airway size. 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 may explain facial morphology

and size in a functional context that could be important in Mid-Pleistocene 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 pattern [20,41,42]. This can be assumed because, for physiological reasons, body mass and the size of the respiratory organs scale isometrically and are closely correlated across mammals [43]. The results of this study could explain large facial sizes by linking energy-related factors and associated respiratory constraints with general facial growth and scaling patterns. The very large nasal apertures in Mid-Pleistocene hominins and the Neandertal lineage seem to be related to this. Body mass estimates for these hominins are higher than for anatomically modern humans [19,44]. According to 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 probably larger lungs [49]. These

correlations 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], thus accounting for the different air-conditioning strategies in Neandertals and modern humans [10]. Cold-adapted modern humans have tall, narrow 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 favour heating and moistening of the inspired air [11]. Thus, while cold-adapted modern humans have these high, narrow apertures, those of cold-adapted Neandertals are large and wide [4]. Neandertals may 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 their possible advantages for air-flow dynamics and turbulence induction. Instead, air-conditioning in Neandertals might have been taken over by increased air resilience 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 air resilience time within the nasal cavity is probably related to the greater length of the cranial airways as part of the prognathic and projecting midface, suggesting that the entire nasofacial functional system should be considered as embedded in a specific cerebro-basiscranial 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, thereby contributing to midfacial projection and prognathism [7]. This shift could be related to encephalization and its impact on basicranial evolution, which in Neandertals differs from that of anatomically modern humans [55–57]. So, rather than a localized, independent functional adaptation to a cold climate achieved by evolving a narrow piriform aperture (through selective pressure), slight modifications among interrelated parts of systems in the organism (brain, base, face and interactions between airways), linked by ontogenetic scaling relationships (such as the link between body mass and facial size *via* the respiratory organs), could have provided effective air-conditioning *despite* nasofacial differences between the Neandertal lineage and modern humans [4,10]. Such longer and wider airways and faces may also have provided a structural solution guaranteeing a sufficient supply of oxygen to cover the high energy demands of Neandertal bodies, thus contributing to their “exaptation” to cold *via* 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 encephalization) 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 to be an important factor in later hominin facial evolution.

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