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What Does Nasal Cavity Size Tell us about Functional Nasal Airways?

Qu'est-ce que la taille de la cavité nasale nous dit sur les voies aériennes nasales ?

Y. Heuzé

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Abstract Studies on dry human skulls have shown that nasal cavity (NC) morphology varies with eco-geographic factors. These findings have been used by some authors to interpret the facial morphology of Neanderthals. However, respiratory and air-conditioning functions are primarily carried out by the nasal airways (NA), which are delimited by mucosa. The aims of this study were to test whether: (1) NC volume (V) and surface-area-to-volume ratio (SA/V) are proportional to NA counterparts; (2) measurements for male NC and NA are larger than in females; (3) the centroid size (CS) of a set of landmarks measured on NC provides a reliable proxy for NC V. Head CT (computed tomography) images of adult patients ($N = 30$) at the University Hospital of Bordeaux were selected retrospectively. NA were defined by segmenting the lumen corresponding to the functional volume. NC was defined by adding to NA the soft tissues delimited by the bones forming the NC. The coordinates of 16 landmarks measured on NC bones were recorded. A rather low correlation was found between NA and NC V while NA SA/V and NC SA/V were not correlated. No significant differences were found between male and female NA and NC measurements. A rather low correlation was found between NC V and NC CS. If these preliminary results were to be confirmed by future studies, results using NC as a proxy for NA focusing on air-conditioning and respiratory energetics might need to be re-interpreted.

Keywords Air conditioning · Respiratory energetics · Computed tomography · *in vivo*

Résumé Plusieurs études sur des crânes secs humains ont révélé que la morphologie de la cavité nasale (NC) varie selon des facteurs écogéographiques. Ces résultats ont été utilisés par certains auteurs pour interpréter la morphologie faciale des Néandertaliens. Cependant, les fonctions respiratoires et le conditionnement de l'air sont assurés en premier lieu par les voies aériennes nasales (NA) qui sont délimitées par une muqueuse. Les buts de cette étude étaient de tester si : 1) le volume (V) et le rapport de l'aire surfacique sur le volume (NA/V) de NC sont proportionnels à ceux de NA ; 2) NC et NA sont plus grandes chez les hommes ; 3) la taille centroïde (CS) représente un indicateur fiable du V de NC. Des images tomographiques d'individus adultes (N = 30) du CHU de Bordeaux ont été sélectionnées de manière rétrospective. NA étaient définies par la segmentation du lumen correspondant au volume fonctionnel. NC était définie en ajoutant à NA les tissus mous délimités par les os formant NC. Les coordonnées de 16 landmarks mesurés sur les os de NC ont été enregistrées. Une faible corrélation a été trouvée entre les V de NA et NC tandis qu'aucune n'a été identifiée entre NA SA/V et NC SA/V. Aucune différence significative entre hommes et femmes n'a été trouvée. Une corrélation relativement faible a été identifiée entre NC V et NC CS. Si ces résultats préliminaires venaient à être confirmés par de futures études, les résultats utilisant NC comme un proxy pour NA pour l'étude des capacités respiratoires et du conditionnement de l'air devraient être réinterprétés.

Mots clés Conditionnement de l'air · Dimension énergétique de la respiration · Tomographie · *in vivo*

Y. Heuzé (✉)
CNRS, Univ. Bordeaux,MCC, PACEA, UMR 5199, Bordeaux archaeological sciences cluster of excellence, Pessac, France
e-mail : yann.heuze@u-bordeaux.fr, yannheuze@gmail.com

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Introduction

Several studies on dry skull materials of different human populations from different latitudes have shown that nasal cavity (NC) morphology varies with eco-geographic factors such as temperature and humidity. Historically, the relationship between climate and NC size and proportions was

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established by studies focusing primarily on the dimensions of the nose and the nasal aperture [1–7]. Later on, studies taking the entire NC into account confirmed this relationship, particularly for populations living in extremely cold climates [8–11]. Populations living in cold climates tend to display a narrower nasal aperture, a sagittally enlarged NC and a larger surface-area-to-volume ratio (SA/V) of the NC, resulting in greater air-conditioning capacity [9,12–16]. On the other hand, a recent paper by Maddux et al. [17] indicates that the internal nasal fossa is the only component of the nasal complex (i.e., external pyramid, nasal aperture, internal nasal fossa, and nasopharynx) that displays an eco-geographic pattern of variation consistent with adaptation to climatic conditions. Because European Neanderthals lived during periods characterized by glacial conditions, many aspects of their morphology, including facial skeletal traits (e.g., nasal cavity and paranasal sinuses), have been interpreted as adaptations to a cold climate [18]. However, it has been shown that genetic drift can account for several of these traits [19]. Consequently, the significance of Neanderthal skeletal morphology is still debated.

The NC is a negative space delimited by bones housing the nasal airways (NA). As such, the NC is the gateway to the respiratory system [20] and indirectly participates in inspired and expired air conditioning. The NC displays a variable and complex morphology based on the shape and size of the aspects of the bones forming that negative space – the maxilla, nasal, palatine, vomer, sphenoid, frontal, ethmoid and lachrymal bones. The upper, middle and lower nasal turbinates or conchae contribute to the complexity of the NC morphology. The quantity of inspired air depends on NC size, shape and particularly on its height and width, especially at its entrance and exit points (i.e., piriform aperture and the choanae, respectively) [21,22]. Consequently, it is likely that NC morphology influences respiratory energetics. The effectiveness of air conditioning is also related, at least partially, to NC morphology, and particularly to NC length (e.g., [8]) and SA/V (e.g., [9]).

However, the functional negative space primarily responsible for air conditioning is represented by the NA. The NA are delimited by mucosa and housed within the NC. Because of its dense vascularization, NA mucosa vary in thickness depending on several possibly interrelated factors, including blood pressure, temperature, humidity and the nasal cycle [9,23,24]. This results in fluctuations in the level of congestion (reduced volume), or the opposite, i.e,. decongestion, exhibited by the NA. Obviously, only studies based on living individuals allow NA morphology to be analyzed and quantified; computed tomography (CT) images offer appropriate material for that purpose. Very few studies quantifying NA morphology have been published to date. One such study is that of Yokley [9], in which the author uses a two-dimensional approach for *in vivo* CT images to compute the ratio between the perimeter and the area of one coronal section through the nasal passages. These measurements were done twice per specimen, one with NA partially congested by the nasal mucosa and another with nasal airways fully decongested after virtually removing the nasal mucosa. Only the measurements of the fully decongested NA were found to correlate with eco-geographic variables. However, the results obtained with fully decongested NA are somewhat artificial since they are based on the hypothesis that the thickness of the mucosa is null, which effectively produces a measurement of NC.

The following question therefore remains: what does NC size (i.e., volume, V) tell us about functional NA? In other words, what are the differences between NC and NA size when the mucosa is taken into account? The aim of the present study is to quantify NC size and air-conditioning potential (i.e., SA/V) and compare them with those of NA. Since NC volume is often approximated by the centroid size (square root of the sum of squared distances of a set of landmarks from their centroid, CS) of a set of anatomical landmarks measured on the bones forming the NC, we also explore whether CS is a reliable proxy for NC volume. Three working hypotheses were tested throughout the present study: (H1) NC V, surface area (SA) and SA/V are proportional to NA counterparts; (H2) because of larger body and lean mass, males display larger NC and NA than females; (H3) the CS of a set of anatomical landmarks measured on the bones forming the NC provides a reliable proxy for NC volume.

Materials and methods

For the purposes of this study, head CT angiogram images (slice thickness: 0.625 mm) of adult patients examined at the emergency ward of the University Hospital of Bordeaux were selected. The following patients were systematically excluded: those less than 18 and more than 59 years of age and those with major facial skeletal dysmorphology, under respiratory assistance, or with obstructed nasal airways. Patients imaged with their mouth open were also excluded to avoid potential bias linked to mouth breathing. Fifteen men and fifteen women were included in the sample (mean age = 31.8 years; SD = 11.0 years). There were no significant age differences between males and females (t = -0.0652, p = 0.9502). All images were collected retrospectively and anonymized. Only the sex and exact age on examination were kept. This study has been reviewed and approved by the Univ. of Bordeaux IRB (*Comité de Protection des Personnes Sud-Ouest et Outre Mer III*).

First, the NA were defined by segmenting the lumen corresponding to the airways' functional volume and delimited anteriorly by the nasal aperture and posteriorly by the

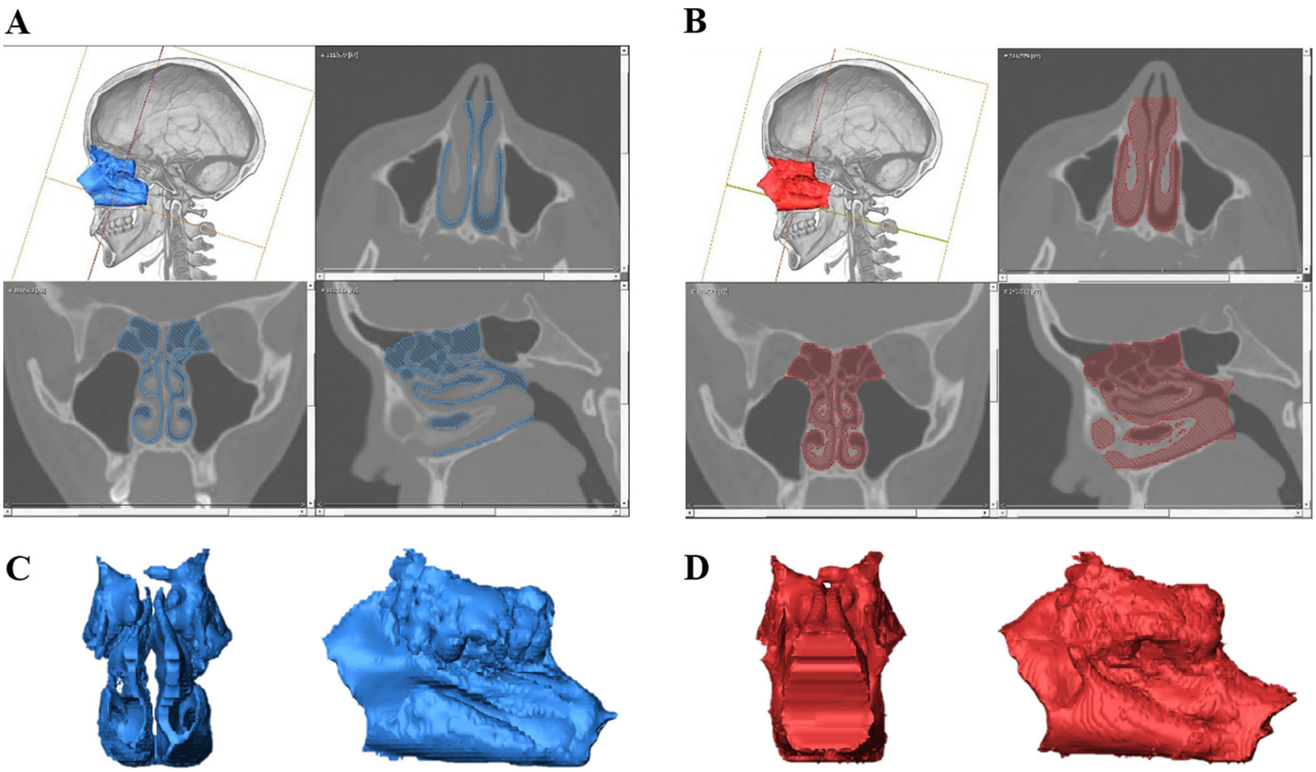

Fig. 1 Segmentation of the nasal airways (NA) (A) and nasal cavity (NC) (B). NA and NC are delimited anteriorly by the nasal aperture and posteriorly by the choanae. They were segmented in the transverse plane (upper right) and inspected in the coronal and sagittal planes (lower left and lower right, respectively). Anterior and lateral views of three-dimensional reconstructions of NA (C) and NC (D). / *Segmentation des voies aériennes nasales (NA, A) et de la cavité nasale (NC, B). NA et NC sont délimitées antérieurement par l'ouverture nasale et postérieurement par les choanes, et ont été segmentées dans le plan transverse (en haut à droite) et inspectées dans les plans coronal et sagittal (respectivement en bas à gauche et en bas à droite). Vues antérieure et latérale des reconstructions 3D de NA (C) et NC (D)*

choanae (Figs 1A, 1C). Because of the difficulty of objectively determining where the NA end and where the ethmoidal cells begin, the latter were included in what is defined as NA in the present study. Then, the NC was defined by segmenting both the lumen (i.e. NA) and the soft tissues covering the bones forming the NC (from anterior nasal aperture to choanae) (Figs 1B, 1D). Though segmenting nasal conchae can sometimes be challenging (e.g., [25]), they were segmented as bone and not included in the computation of NC measurements. NA and NC were segmented in the transverse plane and inspected in the coronal and sagittal planes (Fig. 1). Both NC and NA were closed on each transverse slice anteriorly by a line joining the two aspects of the maxilla or the nasal bones forming the nasal aperture, and posteriorly by a line joining the distal walls of the choanae formed by the sphenoid and passing through the most posterior aspect of the vomer (Fig. 1). For NA and NC, both left and right sides were considered to avoid potential nasal cycle effects. The nasal cycle is characterized by a recurrent variation in air mass flow partitioning between the right and left airways, which alternatively display different degrees of mucosa congestion, enabling the passageways to alternate between predominantly fulfilling their air-conditioning and mucus clearance roles [24]. Because of the central aspect of the segmentation process in the present study, the repeatability of the protocol was quantified by measuring five individuals twice (one set of measurements at the start of data collection, one set at the end). The results are given in Table 1 and show that intra-observer error is negligible.

In addition, 16 three-dimensional landmarks were measured on bone (Fig. 2). The three-dimensional coordinates of the landmarks were then analyzed by geometric morphometrics using generalized Procrustes superimposition [26,27]. Centroid size (CS, the square root of the summed squared distances of each landmark to the centroid) was used as a proxy for NC size.

Next, because it has been shown that airflow in the lower and middle meatus account for over 80% (50% and 30% respectively) of the total nasal airflow [28], the hormion and the most anterior point on the left and right nasomaxillary sutures were selected to define a plane that was subsequently used to separate the upper meatus from the middle

Table 1 Repeatability of the segmentation process of the nasal airways including ethmoidal cells (NA) and nasal cavity (NC) with corresponding volume and surface area[a]; each individual was segmented twice / *Répétabilité de la segmentation des voies aériennes nasales incluant les cellules ethmoïdales (NA) et de la cavité nasale (NC) avec les volumes et aires surfaciques correspondants. Chaque individu a été segmenté deux fois*

	NA V	NC V	NA SA	NC SA
Ind. A_round#1	22.95	59.79	22.83	18.35
Ind. B_round#1	29.10	58.57	27.04	23.63
Ind. C_round#1	28.32	54.32	23.77	18.34
Ind. D_round#1	29.13	48.76	20.60	14.59
Ind. E_round#1	18.28	61.48	25.12	21.46
Ind. A_round#2	23.03	59.48	23.20	18.65
Ind. B_round#2	29.08	57.92	26.93	21.84
Ind. C_round#2	28.31	53.97	23.63	17.94
Ind. D_round#2	29.38	48.52	20.78	14.38
Ind. E_round#2	18.95	60.96	25.82	21.17
% diff. Ind. A	0.34%	0.51%	1.62%	1.68%
% diff. Ind. B	0.07%	1.11%	0.40%	7.58%
% diff. Ind. C	0.02%	0.65%	0.56%	2.14%
% diff. Ind. D	0.85%	0.49%	0.87%	1.46%
% diff. Ind. E	3.66%	0.84%	2.78%	1.35%

[a] Values are in cm^3 for volumes and mm^2 for surface areas / *Les valeurs sont exprimées en cm^3 pour les volumes et en mm^2 pour les aires surfaciques*.

and lower meatus. Only the latter portion was then studied. Though this plane might not be ideal, among the several planes tested passing through the measured landmarks, this was the one that produced the most satisfactory results for the separation of the upper meatus from the middle and lower meatus.

The SA/V ratio was computed for both the NC and NA as it is a relevant proxy for air-conditioning potential.

Finally, to broadly describe relative NC dimensions, linear measurements of NC length (from nasomaxillary suture, left to choanal roof, left) and NC width (mean between inter-lower turbinate base and inter-alare distances) were recorded (Fig. 2). NC height was measured from, superiorly, the most anterior point of the lower surface of the cribriform plate taken on a slice parallel to the mid-sagittal plane (passing through the nasal, anterior nasal spine and posterior nasal spine), and inferiorly to the perpendicular projection of the uppermost point onto the nasal surface of the maxilla. This slice was the closest to the mid-sagittal plane, on which the vomer was no longer visible, to avoid any artificial reduction of NC height (Fig. 2). Greater NC height and width were expected to facilitate volumetric air intake, while NC length has no influence. However a longer NC was expected to facilitate air conditioning by increasing air residence time.

T-tests with Monte Carlo permutations ($n = 9999$) and Pearson's correlation coefficients with Monte Carlo permutations ($n = 9999$) were used to test the hypotheses. For these tasks, the PAST software package was used [29].

Results

H1: NC V, SA and SA/V are proportional to NA counterparts

When considering the entire NC and NA, including the ethmoidal cells, there was no significant correlation between NA V and NC V ($R^2 = 0.0445$, $p = 0.2625$), although there was a significant correlation between NA SA and NC SA ($R^2 = 0.2305$, $p = 0.0075$) (Table 2). There was no significant correlation between NA SA/V and NC SA/V ($R^2 = 0.0065$, $p = 0.7066$) (Table 2). NA SA/V was characterized by greater dispersion (coefficient of variation: $c_v = 0.223$) than NC SA/V ($c_v = 0.144$). When considering only the lower two-thirds of NA and NC, a significant though relatively low correlation was found between NA V and NC V ($R^2 = 0.1408$, $p = 0.0349$) and another between NA SA and NC SA ($R^2 = 0.7066$, $p = 0.0001$) (Table 2). There was no significant correlation between NA SA/V and NC SA/V ($R^2 = 0.0078$, $p = 0.6234$) (Table 2). NA SA/V was characterized by greater dispersion ($c_v = 0.313$) than NC SA/V ($c_v = 0.131$).

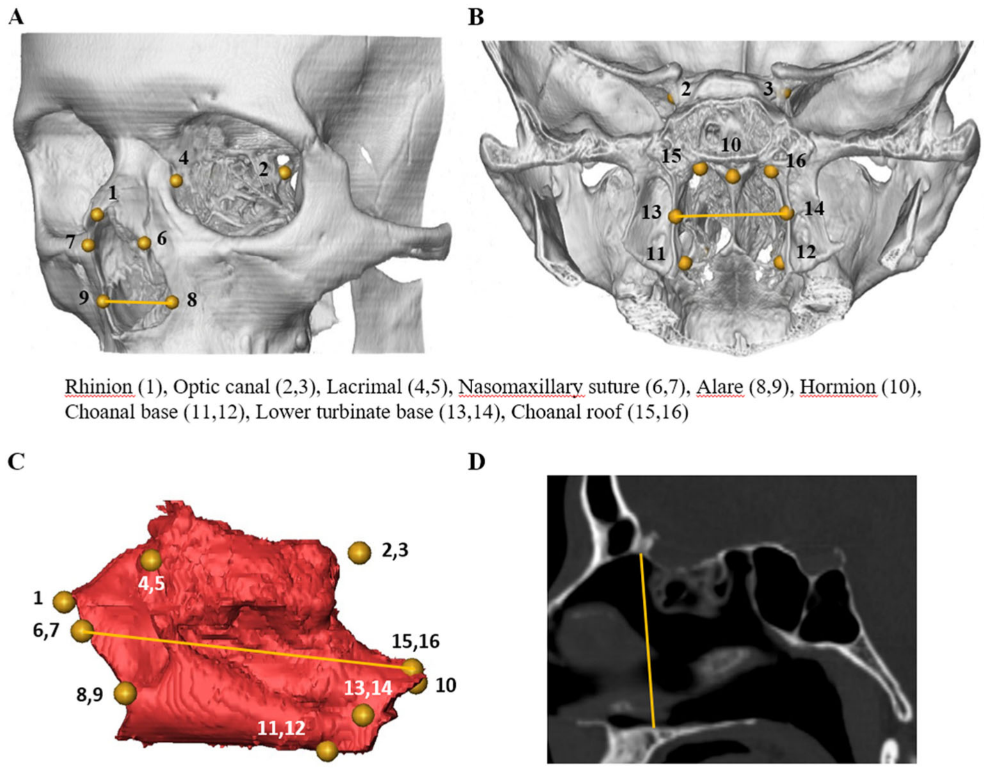

Fig. 2 Landmarks (n = 16) were measured on bone to compute the centroid size of the nasal cavity (NC) (anterior–lateral view, A; posterior–inferior view, B). Lateral view of the reconstructed NC with projected landmarks (C). Sagittal slice used to measure NC height, from, superiorly, the most anterior point of the lower surface of the cribriform plate to, inferiorly, the perpendicular projection of the uppermost point onto the nasal surface of the maxilla (D). The four linear distances measured are represented on the corresponding images / *Les landmarks ont été mesurés sur les os afin de calculer la taille centroïde de la cavité nasale (NC) (vue antéro-latérale, A ; vue postéro-inférieure, B). Vue latérale de NC une fois reconstruite avec les landmarks projetés (C). Coupe sagittale utilisée pour mesurer la hauteur de NC, du point le plus antérieur de la surface inférieure de la plaque cribriforme (point supérieur) au point correspondant à la projection orthogonale du point supérieur sur le maxillaire (point inférieur) (D). Les quatre distances linéaires mesurées sont représentées sur les vues correspondantes*

H2: Males display larger NC and NA than females

When considering the entire NA and NC, no significant differences were found between males and females for NA V (t = 1.2721, p = 0.2144), NA SA (t = –0.1336, p = 0.8982), NA SA/V (t = –2.0569, p = 0.0510), NC V (t = –1.8106, p = 0.0792), NC SA (t = –0.1429, p = 0.2599) or NC SA/V (t = 0.1149, p = 0.9613) (Table 3). When considering only the lower two-thirds of NA and NC, there were no significant differences between male and female NA V (t = 1.1018, p = 0.2736), NA SA (t = –0.1778, p = 0.8584), NA SA/V (t = –1.4302, p = 0.1575), NC V (t = –1.4307, p = 0.1656), NC SA (t = –0.5453, p = 0.5925) or NC SA/V (t = 0.9974, p = 0.3319) (Table 3). While measurements taken on males were larger overall than on females, the latter displayed larger NA V, both for the entire NA and for only the lower two-thirds.

Although males displayed larger NC linear measurements overall, no significant differences between male and female NC height (t = 1.2981, p = 0.2024), NC width (t = 0.8589, p = 0.3950) and NC length (t = 0.9827, p = 0.3301) were found (Table 4).

H3: CS of NC provides a reliable proxy for NC volume

There was a significant though rather low correlation between NC V and NC CS, both when considering the entire NC (R^2 = 0.3597, p = 0.0005) or only the lower two-thirds of the NC (R^2 = 0.1944, p = 0.0147). Male NC CS was significantly larger than female NC CS only when considering the entire NC (t = 2.5138, p = 0.0180). When considering the lower two-thirds of NC, there were no significant differences between male and female NC CS (t = 1.9556, p = 0.0606).

Table 2 Comparison of volume (V), surface area (SA) and surface-area-to-volume ratio (SA/V) between nasal airways (NA) and nasal cavity (NC)[a] / *Comparaison des volumes (V), aire surfacique (SA) et ratio aire surfacique sur volume (SA/V) entre les voies aériennes nasales (NA) et la cavité nasale (NC)*

	NA V *vs.* NC V	**NA SA *vs.* NC SA**	**NA SA/V *vs.* NC SA/V**
NC and NA with ethmoidal cells	0.0445 (0.2625)	0.2305 (0.0075)	0.0065 (0.7066)
NC and NA lower two-thirds	0.1408 (0.0349)	0.7066 (0.0001)	0.0078 (0.6234)

[a] Values are coefficients of determination (R^2) and significance after Monte Carlo permutations (p, in parenthesis) / *Les valeurs correspondent à des coefficients de détermination (R^2) et à la significativité après simulations de Monte Carlo (*p*, entre parenthèses)*

Table 3 Nasal airways (NA) and nasal cavity (NC) volume (V), surface area (SA), and surface-area-to-volume ratio (SA/V) by sex[a,b] / *Volume (V), aire surfacique (SA) et ratio aire surfacique sur volume (SA/V) des voies aériennes nasales (NA) et de la cavité nasale (NC) selon le sexe*

	NA V	**NC V**	**NA SA**	**NC SA**	**NA SA/V**	**NC SA/V**
Entire nasal airways (NA) and nasal cavity (NC)						
M	22.55	63.38	24.86	21.5	1.17E-03	3.40E-04
F	25.37	59.21	24.70	20.20	9.98E-04	3.42E-04
M *vs*. F	1.27 (0.2144)	-1.81 (0.0792)	-0.13 (0.8982)	-0.14 (0.2599)	-2.06 (0.0510)	0.11 (0.9613)
Lower two-thirds of nasal *airways (NA) and nasal cavity (NC)*						
M	9.90	32.85	10.82	10.69	1.20E-03	3.27E-04
F	11.33	30.39	10.69	10.36	1.02E-03	3.43E-04
M *vs*. F	1.10 (0.2736)	-1.4307 (0.1656)	-0.18 (0.8584)	-0.55 (0.5925)	-1.43 (0.1575)	1.00 (0.3319)

[a] Values are means in cm^3 for volumes and mm^2 for surface areas / *Les valeurs correspondent à des moyennes en cm^3 pour les volumes et en mm^2 pour les aires surfaciques*.
[b] Values are Student *t*-values (t) and significance after Monte Carlo permutations (p, in parenthesis) / *Les valeurs correspondent à des valeurs de test t de Student (*t*) et à leur significativité après simulations de Monte Carlo (*p*, entre parenthèses)*.

Table 4 Nasal cavity linear measurements by sex[a,b] / *Mesures linéaires de la cavité nasale selon le sexe*

	NC height	**NC width**	**NC length**
M	49.2	25.8	71.2
F	47.8	25.3	69.8
M *vs*. F	1.2981 (0.2024)	0.8589 (0.3950)	0.9827 (0.3301)

[a] Values are means in mm / *Les valeurs correspondent à des moyennes exprimées en mm*.
[b] Values are Student *t*-values (t) and significance after Monte Carlo permutations (p, in parenthesis) / *Les valeurs correspondent à des valeurs de test t de Student (*t*) et à leur significativité après simulations de Monte Carlo (*p*, entre parenthèses)*.

Discussion

Based on our results, H1, stating that NC V, SA and SA/V are proportional to NA counterparts, can only be supported with some limitations, since only the volume of the lower two-thirds of NC was significantly correlated with that of NA. However, this correlation seemed relatively low ($R^2 = 0.1408$). Although the correlation was high for SA between NA and NC, this was not the case for SA/V, which is commonly used as a proxy for air-conditioning potential. Consequently, it might be more appropriate to consider only the lower and middle meatus when measuring NC. This is consistent with the fact that the lower two-thirds of NA account for over 80% of the total nasal airflow [28]. However, it appeared that interpolation made on air-conditioning potential on the basis of NC SA/V could be problematic.

This study revealed no significant differences between male and female NA V, NC V, NA SA, NC SA, NA SA/V, or NC SA/V, either considered as a whole or for only the lower two-thirds. Consequently, H2, stating that males display larger NC and NA than females, should be rejected. Because NC height and width primarily constrain volumetric air intake, both were expected to be significantly larger in males. However, neither was significantly larger in males than in females. Overall, these results offer little support to the hypothesis that, due to larger body size and lean mass, male NC and NA are larger than female NC and NA. However, these results are based on a rather small sample size ($n = 30$) and it is expected that with a larger sample, some of these differences might exceed the significance threshold.

The 16 anatomical landmarks measured in this study on NC correspond to the measurable landmarks on CT images from a list of landmarks conventionally measured on dry skulls in comparable studies [e.g., 8,10,11,22]. Based on our results, the CS of such a landmark configuration appears to be a relatively poor proxy for NC volume, especially when considering the lower two-thirds of NC ($R^2 = 0.1944$). Thus, H3, stating that the CS of NC provides a reliable proxy for NC volume, should be rejected. It is unlikely that the rather complex geometry of NC could be captured in an optimal manner by these external landmarks that might over-simplify NC complex geometric properties. Consequently, measuring NC volume might be the only reliable way of quantifying NC size.

NA appears to be much more variable than NC. One obvious explanatory factor of this inter- and intra-individual variation is the mucosa itself, which varies in volume and consequently contributes to variation in NA volume as well. In contrast, for the same individual, the NC volume remains constant. This study attempted to control for a maximum of factors influencing mucosa congestion/decongestion. First, only patients breathing through the nose, without respiratory assistance and with their mouth closed during the CT exam were selected. Second, a relative rest state was assumed at the time of imaging (i.e., no engagement in significant physical activities), as well as relatively homogeneous environmental conditions, as temperature and humidity levels were controlled by air conditioning. Third, the nasal cycle was taken into account by measuring the right and left NA rather than just one side. Since this study focused on the state of rest, considering a fully decongested NA did not seem relevant. Note that during physical exercise, the nasal mucosa decongests almost to the same level as after using a topical decongestant [30], although a significant part of respiration occurs through the mouth. The level of stress experienced by the patients could not be controlled for, however. Despite all these precautions, NA SA/V was twice to three times more variable than NC SA/V. This result agrees with that obtained by Yokley [9] in two dimensions and showing that, when the mucosa was taken into account (i.e., not fully decongested), variation in SA/V was too substantial to observe any significant difference in SA/V between individuals of European and African descent.

Another explanatory factor for the overall low correlation between NA and NC measurements is the anatomical complexity of the nasal conchae and the acknowledged difficulty of segmenting them on CT images. This difficulty is linked to the complex geometry of the nasal conchae and the surrounding soft tissues and fluids [25]. While the nasal conchae were segmented as bone and consequently not taken into consideration when computing NC measurements, it is possible that for some individuals, imperfect segmentation resulted in the inclusion of small parts of the nasal conchae in NC measurements. The fact that males displayed larger mean NC volumes but smaller mean NA volumes compared to females (Table 3) could suggest that males have larger nasal conchae potentially associated with larger mucosa volumes.

The results of this preliminary study seem to challenge the validity of the often assumed or implied correlation between NA and NC size/volume. Because of our relatively small sample size and methodological limitations (e.g., segmentation of the conchae, variation in mucosa thickness), these preliminary results should still be validated by future studies that could provide a more robust description of the relationship between NA and NC. If these preliminary results were to be confirmed by future studies, results produced by studies based on dry skull materials focusing on air-conditioning and respiratory energetics using NC as a proxy for NA might need to be re-interpreted. This would also apply to studies on these topics involving fossils such as Neanderthals, for which the NC is rarely fully preserved. Such future studies would need to use larger *in vivo* samples, as well as possibly samples from different regions of the world, to provide more in-depth results on the nature of the relationship between NA and NC morphological variation and co-variation and their implications for air-conditioning and respiratory energetics. One key aspect for future work will be to use imaging parameters optimized for nasal conchae visualization and segmentation in order to investigate the potential role of the nasal conchae and the overlying mucosa in the differences observed between NC and NA measurements.

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