

Para além da Idade da Pedra: a evolução nasal do Neandertal ao Homem moderno

Artigo Original

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Resumo

Introdução: Os Neandertais, nossos parentes extintos, exibiam uma morfologia nasal distinta em comparação com o Homo sapiens.

Objetivos: Este estudo explora essas diferenças através de uma análise comparativa de medidas nasocranianas.

Material e Métodos: Dados sobre as características nasais do Homo Neanderthalensis e Homo Heilderbergensis foram obtidos a partir da literatura paleoantropológica existente, com foco em 16 fósseis. Uma amostra paralela de 38 de crânios de Homo Sapiens foi analisada retrospectivamente mediante tomografia computadorizada (TC), com obtenção de medições relativas à região nasal.

Resultados: Os Hominídeos exibiram cavidades nasais significativamente maiores, com distâncias *basion-nasion* e *basion-prosthion* aumentadas, dimensões intercaninas maiores e maior largura e altura nasal em comparação com os humanos modernos. A largura coanal e o índice nasal não diferiram significativamente.

Conclusões: Esses achados sugerem adaptações funcionais na morfologia nasal neandertal, potencialmente auxiliando na termorregulação em ambientes frios. Pesquisas adicionais são necessárias para compreender totalmente o significado evolutivo dessas adaptações.

Palavras-chave: Hominídeos; Fósseis; Nariz; Anatomia Comparada; Sistema Respiratório; Evolução Biológica; Adaptação ao Frio; Termorregulação; Neandertal; Homo Sapiens

Introduction

The evolutionary trajectory of the human lineage is a complex narrative marked by both successful adaptations and episodes of extinction. Neanderthals, a close relative of Homo sapiens, thrived for hundreds of thousands of years before bafflingly disappearing around 40,000 years ago¹⁻³. Their legacy continues to captivate researchers, with their distinctive physical features sparking numerous inquiries. One intriguing aspect of Neanderthal anatomy lies in their nasal

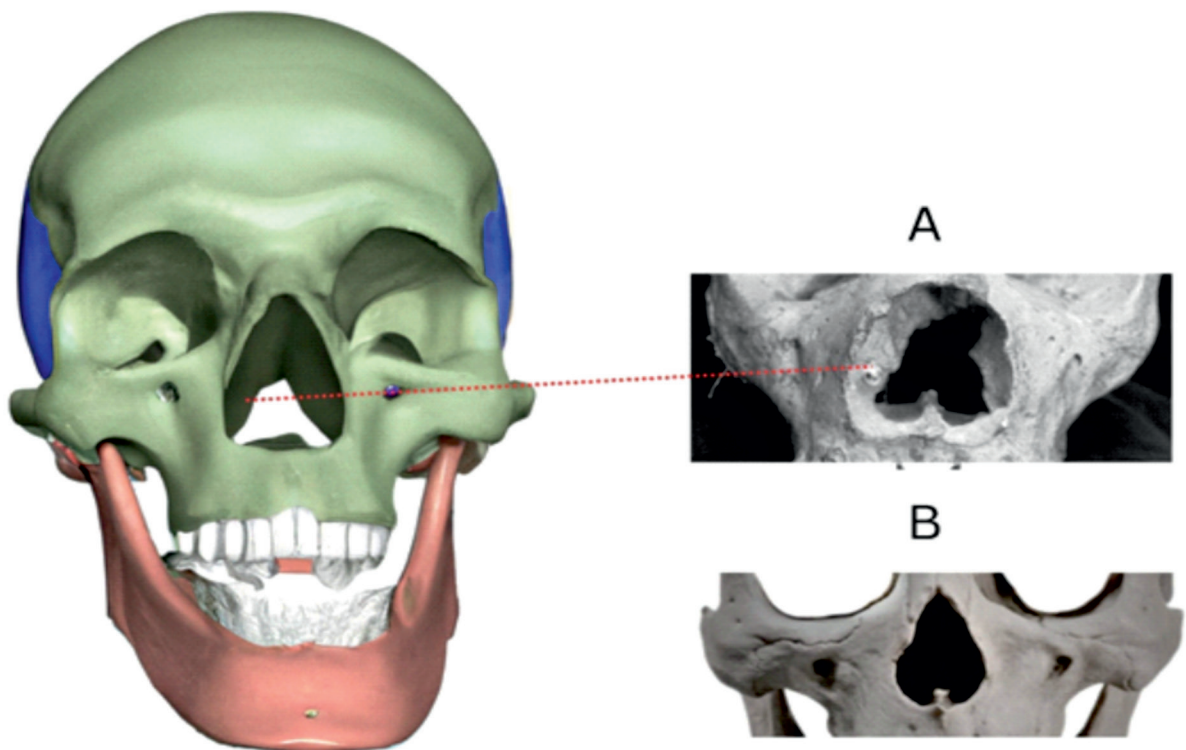
structure⁴⁻⁸. These includes a well-developed, vertically oriented medial projection on the internal nasal margin (Figure 1), a pronounced medial swelling of the lateral nasal wall projecting posteriorly, and the absence of an ossified roof over the lacrimal fossa. This peculiar morphology has powered scientific curiosity, prompting questions about its potential adaptive significance⁴⁻⁹.

Neanderthals inhabited glacial Europe and western Asia, facing harsh climatic conditions characterized by cold temperatures and dry environments. Many argue that these environmental pressures likely played a significant role in shaping their nasal morphology^{6,7}. Adaptations to the nasal morphology and function could have been critical for survival. These adaptations possibly aimed to improve air conditioning, facilitating the warming and humidification of inhaled air¹⁰. Higher nitric oxide mixing with pulmonary

oxygen diffusion facilitation is another noted possibility⁷. Another potential adaptive explanation lies in the need for a higher airflow capacity through the nasal cavity. Increased nasal volume could have facilitated greater air intake, potentially addressing higher metabolic demands⁵. Nevertheless, some dispute this idea pointing to genetic drift as the most likely explanation for anatomical differences¹¹⁻¹³. Understanding the evolutionary trajectory of craniofacial features in hominids holds significant value for various medical fields, including Otorhinolaryngology. This knowledge illuminates the functional adaptations that shaped humans' facial anatomy over time. The primary objective of this study was to compare craniofacial morphology in hominid fossils and modern *Homo sapiens*. Selective pressures that may have influenced form and function are discussed.

Figure 1

Medial crest (also known as crista turbinalis). A - Prominent bony projection (marked with red line) flank the inner opening of the nasal cavity in a *Homo Neanderthalensis* fossil. These structures extend upwards along the nasal walls for a variable distance (one-third to halfway) before expanding into broad, rounded formations that project medially into the nasal cavity. B - comparison with a *Homo Sapiens* skull specimen. (copyright©, Francisco Sousa).



Material and Methods

Sample enrollment

A multifaceted approach was employed, utilizing data from both paleoanthropological literature and modern medical imaging (Figure 2). Data collection and analysis involved three main steps. Firstly, a paleoanthropological literature review was performed, allowing for identification and data collection on hominid craniofacial features. Fossil specimens of *Homo heidelbergensis* and *Homo neanderthalensis* that were identified as adults by expert paleontologists were included (Figure 2). This determination was based on established criteria for age estimation in hominid fossils such as dental eruption and wear, cranial suture closure and pelvic morphology. The inclusion of *Homo Heidelbergensis* in the sample stemmed from evidence placing *Homo heidelbergensis* as the last common ancestor of modern humans and Neanderthals¹⁴. The species classification of the Hominid fossils was defined based on

the Smithsonian National Museum of Natural History classification for each specimen (available at: <https://humanorigins.si.edu/evidence/human-fossils/fossils>).

Secondly, to set a reference point for *Homo Sapiens* morphology, a database of paranasal sinus computed tomography (CT) scans from living adults was utilized. This database included only scans from individuals with no history of facial trauma or sinonasal disease. The exams were obtained by GE® or SIEMENS® tomographs and measurements were performed by SECTRA® software using axial, coronal and sagittal sections.

The measurements obtained on hominid fossil and modern human CT scans were then pooled in a common dataset. For each specimen, data included nasofrontal angle, nasal height, nasal breadth, basion-nasion and basion-prosthion distances, maxillary intercanine distance, choanal width, biorbital length and calculated nasal index. Lastly, statistical analysis allowed for comparison

Figure 2
Multifaceted research approach. CT stands for “Computed Tomography”.

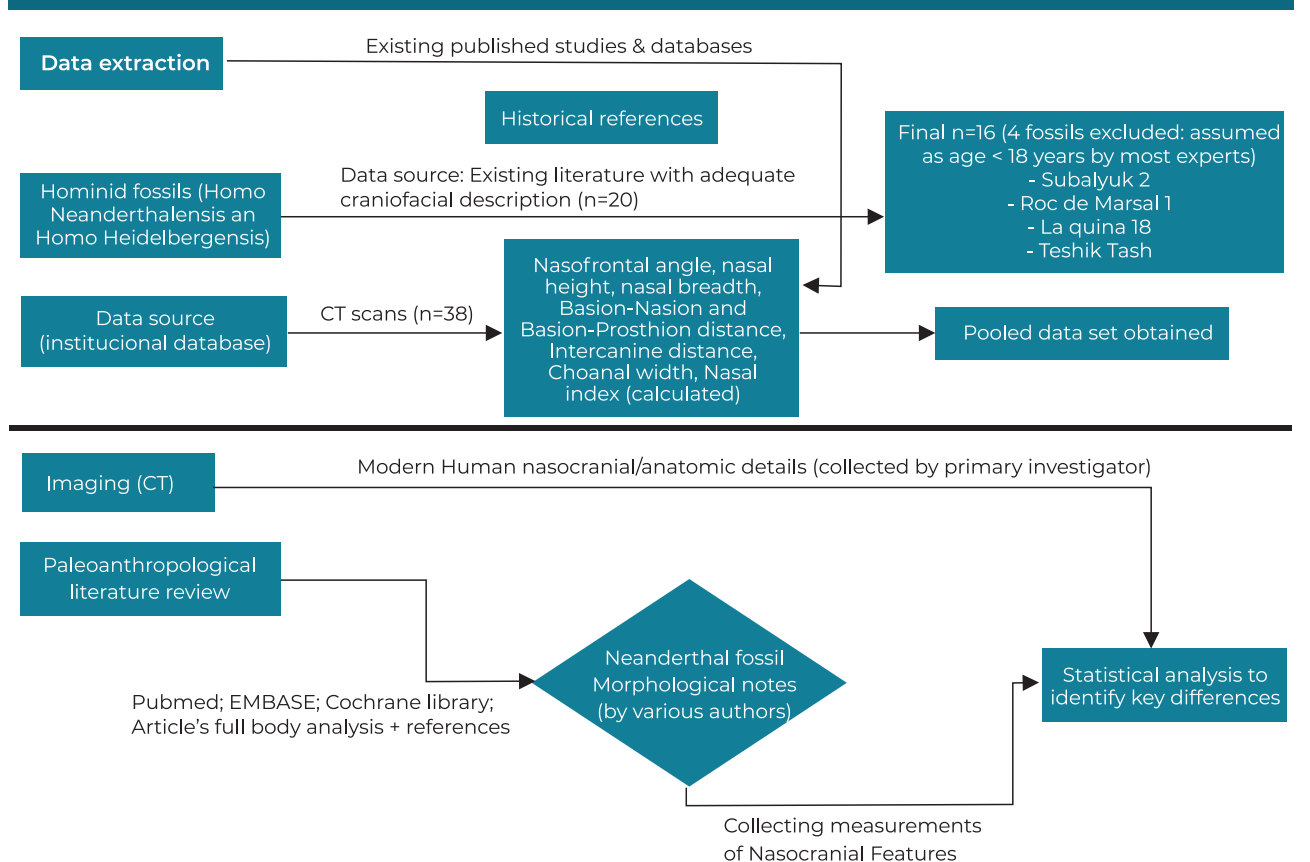
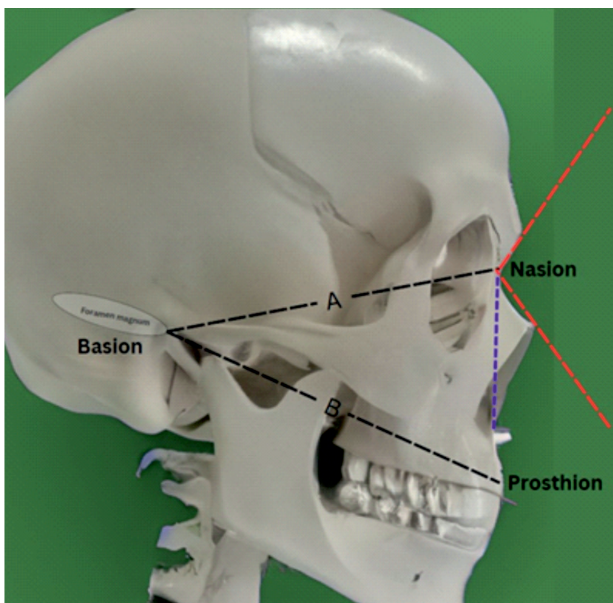


Figure 3

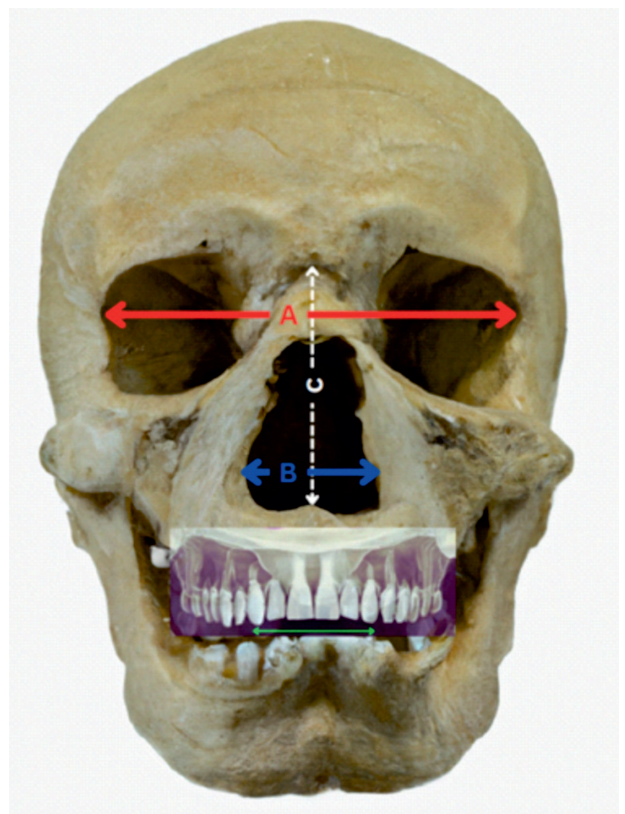
Sagittal section landmarks and measurements. Black line A – Basion-Nasion distance; black line B – Basion-Prosthion distance; red lines – delimitate nasofrontal angle; purple line – nasal height. Definitions - Nasion: the most anterior point of the frontonasal suture that joins the nasal part of the frontal bone and the nasal bones. It marks the midpoint at the intersection of the frontonasal suture with the internasal suture joining the nasal bones. Nasofrontal angle: The angle formed at the juncture where the line from the glabella to the nasion crosses the line from the nasion to the tip. In modern man should be between 115-130 degrees and is usually greater in females than males. Basion: midpoint on the anterior border of the foramen magnum. Prosthion definition: the most forward projecting point of the anterior surface of the upper jaw, in the midsagittal plane. Nasal height: the height of the nose from the nasion to the nasospinale (midline anatomical point where midsagittal plane intersects inferior margin of nasal aperture). (copyright©, Francisco Sousa).



between groups. Figure 3 and Figure 4 depict relevant anatomical landmarks and measurements, excepting choanal width. Choanal width measurement was done at the reference level between both pterygoid plates in the axial plane. Nasal index was obtained by dividing the width to the height of the nose and multiplying by 100 to be expressed in percentage.

Figure 4

Coronal section landmarks and measurements. Red line (A) – biorbital length; Blue line (B) – nasal breadth; white line (C) – nasal height; Green line: intercanine width; Definitions - Biorbital length: a measure taken between the outer borders of the bony orbits. Nasal breadth: the distance between the two most lateral points on the rim of the nasal opening. Nasal height: the height of the nose from the nasion to the nasospinale; Intercanine width: The distance between cusp of the right and left permanent canines. (copyright©, Francisco Sousa).



Ethics

The design complies with the Declaration of Helsinki's ethical standards. De-identified data from a prior institutional study with informed consent was utilized for this analysis.

Statistical analysis

Statistical analyses were conducted using IBM SPSS Statistics 29 software. Descriptive statistics were employed, presenting categorical variables as percentages and continuous variables as means and standard deviations. The Shapiro-Wilk test confirmed

normal distribution for continuous variables. Bivariate analysis explored asymmetries in measurements between groups by means of independent t-test. Pearson Chi-square/Fisher's tests (95% confidence intervals) were used for categories and Spearman's test for continuous variables. To address potential confounding variables in the subsequent multivariate analysis, a multiple imputation regression technique was implemented. This facilitated the application of both binomial logistic regression and multinomial logistic regression (MLR). MLR was chosen as the dependent variable, "group" (categorized as *Homo sapiens*, *Homo neanderthalensis*, and *Homo heidelbergensis*), had three unordered categories. Additionally, the test of parallel lines indicated a violation of the proportional odds assumption, making MLR the most suitable method. All reported p-values are two-tailed, with a significance level set at $p \leq 0.05$.

Results

Population

A total of 54 patients were enrolled, 25 males and 28. 16 hominid fossils (HF) were included: 10 *Homo Neanderthalensis* (HN) and 6 *Homo Heidelbergensis* (HH) - accounting for 29,6 %

of the sample. According to literature, 10 fossils were assumed as male (62,5 %) and 6 fossils as female (37,5 %). 38 alive human CT scans were included [*Homo sapiens* (HS)] – accounting for 71,4 % of the sample. 16 were male (42,1 %) and 22 female (67,9%). A general description of the main variables is displayed on Table 1, comparing hominids as a whole class against modern humans. Detailed description and analysis for each groups of Homo species (HH, HN and HS) is found on Figure 5.

Craniofacial Features in Hominids Compared to Modern Humans

Further analysis was performed to adjust for the effect of sex and explore morphological differences between hominids and modern humans (Table 2). By using a Binary logistic regression adjusting for sex, it was found that the odds of being a Hominid increased by 14 % for each unit increase in nasofrontal angle (95% CI (1.115, 20.403)), 23,5 % for each unit increase in biorbital length and 29,7 % for each unit increase in nasal height. When integrated in this model, no other variables sustained significant associations (Table 2).

Table 1
Main variables description and bivariate analysis: hominids versus modern

Feature	Hominids	Modern Humans	p-value
Sample Size (n)	16	38	-
Sex Distribution	10 M / 6 F	16 M / 22 F	0.171
Basion-Nasion Distance (mm)	112.6 ± 5.4	102.1 ± 5.2	< 0.001
Basion-Prosthion Distance (mm)	119.6 ± 6.7	95.3 ± 6.1	< 0.001
Nasofrontal Angle (degrees)	139.8 ± 10.8	127.3 ± 8.0	0.022
Inter canine Dimension (mm)	31.8 ± 4.2	23.1 ± 2.1	< 0.001
Biorbital Length (mm)	111.1 ± 2.9	90.9 ± 4.1	< 0.001
Nasal Breadth (mm)	34.9 ± 3.7	23.4 ± 2.3	< 0.001
Nasal Height (mm)	59.4 ± 5.7	42.8 ± 3.7	< 0.001
Choanal Width (mm)	29.6 ± 3.4	27.1 ± 2.3	0.109
Nasal Index (%)	58.3 ± 7.9	54.8 ± 6.4	0.307

M = Male, F = Female; Values are presented as Mean ± Standard Deviation; p-value indicates statistical significance between Neanderthal and Modern Human values. A value of less than 0.05 is considered statistically significant.

Figure 5
Main variables description and bivariate analysis between Homo species

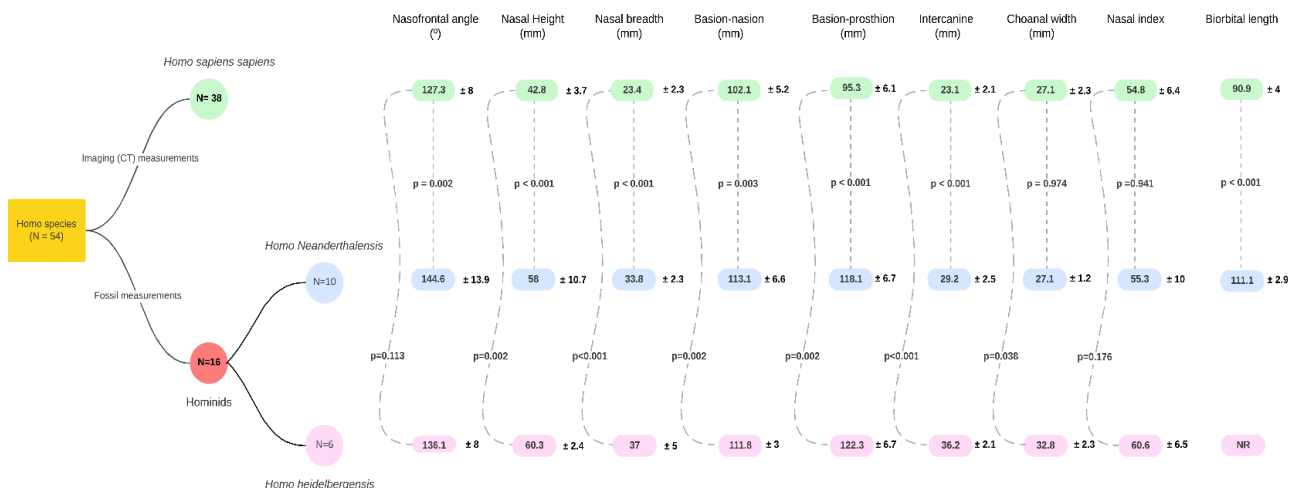


Table 2
Results of binary logistic regression taking “Hominid” as the outcome of interest

Craniofacial measurements	β 1	S.E β ²	Wald	OR (Exp(B))	[95% CI] for OR		p-value
					Lower	Upper	
Basion-Nasion	-0.091	0.078	1.348	0.913	0.783	1.064	0.246
Basion-Prosthion	0.128	0.084	2.311	1.137	0.964	1.342	0.128
Nasofrontal angle	0.131	0.042	9.677	1.140	1.050	1.238	0.002
Inter canine distance	0.144	0.150	0.924	1.155	0.861	1.548	0.336
Biorbital length	0.211	0.103	4.185	1.235	1.009	1.512	0.041
Nasal breadth	0.031	0.128	0.057	1.031	0.803	1.324	0.811
Nasal height	0.260	0.099	6.918	1.297	1.068	1.574	0.009
Sex	1.562	0.742	4.437	4.769	1.115	20.403	0.035
Constant	-59.637	10.901	29.928	0.000			<0.001

OR – Odds Ratio, [95% CI] – lower and upper bound of 95% confidence interval; 1 - β stands for unstandardized regression coefficient; 2) Standard error for unstandardized regression coefficient; 3) Exp(β), or the odds ratio, is the predicted change in odds for a unit increase in the predictor. The “exp” refers to the exponential value of β; Bold for p values translating statistical significance

Species membership: craniofacial measurement analysis

A multinomial logistic regression was performed to model the relationship between predictor variables (various craniofacial measurements and sex) and membership in the three groups (HH, HN and HS). With the addition of the predictor variables, the fit between the model including only the intercept and data improved, $\chi^2 (16, N = 148) = 681.9$, Nagelkerke R² = 0.883, $p < .001$. HN was the reference group. As a result, each predictor

contains two parameters: one for predicting HH membership and one for predicting HS group membership. This model successfully classified 91.1% of the HN patients, 99.8 % of the HS patients and 61.7 % of HH patients. The overall correct classification rate was 94.2%. Table 3 displays the parameter estimates. When comparing HN group to HH, 2 predictors showed significance (see Table 3). The odds of being in HN group rather than the HH group were 20 % higher for each standard deviation (SD) increase in basion-nasion (OR: 0.787,

Table 3

Parameter Estimates Contrasting Homo Neanderthalensis versus each of the other groups

Predictor	Neanderthalensis vs.	B	OR	p-value
Basion-Nasion	Heidelbergensis	- 0.239	0.787	0.006
	Sapiens	- 0.019	0.982	0.841
Basion-Prosthion	Heidelbergensis	- 0.101	0.904	0.127
	Sapiens	- 0.213	0.808	0.025
Nasofrontal angle	Heidelbergensis	0.030	1.031	0.231
	Sapiens	-0.102	0.903	0.028
Intercanine distance	Heidelbergensis	0.477	1.612	< 0.001
	Sapiens	0.150	1.162	0.365
Biorbital length	Heidelbergensis	-0.068	0.935	0.282
	Sapiens	-0.222	0.801	0.041
Nasal breadth	Heidelbergensis	-0.039	0.962	0.692
	Sapiens	-0.089	0.914	0.527
Nasal height	Heidelbergensis	-0.026	0.974	0.566
	Sapiens	-0.289	0.749	0.006

OR = odds ratio associated with the effect of a one standard deviation increase in the predictor.
 Orange for statistical significance between Homo Neanderthalensis and Homo Heidelbergensis.
 Green for statistical significance between Homo Neanderthalensis and Homo Sapiens.

$p = 0.006$). Conversely, the odds of being in HN group were 60 % decreased for each SD increase in intercanine distance (OR: 1.612, $p < 0.001$). When comparing the HN to HS, 4 predictors exhibited significant parameters (see Table 3). The odds of being in the HN group rather than HS group were around 10 % higher for each SD increase in nasofrontal angle (OR: 0.903, $p = 0.028$), 20 % higher for each SD increase in basion-prosthion (OR: 0.808, $p = 0.025$) and biorbital length (OR: 0.801, $p = 0.041$) and about 25 % for a SD increase in nasal height.

Discussion

The investigation of human evolution is enriched by examining the anatomical variations across hominid lineages. As such, the primary objective of this study was to analyze craniofacial morphology to identify differences between hominids and modern humans, particularly those involving the nasal cavity. Secondly, a comparison within hominid species was also achieved (HH vs

HN), allowing for an extended chronological perspective of anatomical evolution.

The craniofacial analyses revealed distinct morphological differences between groups. Notably, individuals classified as *Homo heidelbergensis* and *Homo neanderthalensis* exhibited significantly larger nasofrontal angles, biorbital lengths, and nasal heights compared to modern humans (*Homo sapiens*). Basion-Prosthion distance was also significantly higher in HN. Results confirmed that such traits may be particularly useful for distinguishing between ancestral and modern human groups.

The multinomial logistic regression model also pinpointed specific morphological differences within ancestral groups, allowing for a broader time prospection. Compared to *Homo heidelbergensis*, *Homo neanderthalensis* exhibited a larger basion-nasion distance and a smaller intercanine distance. Since HH preceded HN in extinction taxa, such findings suggest a trend towards prognathism, midfacial projection and higher vertical

dimensioning in later pre-modern *Homo*¹⁵. Supporting the discriminatory power of these measurements, the classification model achieved a high success rate in assigning individuals to their respective hominid groups (HH, HN, HS). This reaffirms the legitimacy of craniofacial methods to differentiate between *Homo* species¹⁶.

Craniofacial variations may translate distinct selective pressures occurring throughout millions of years¹⁷. Not only encephalization and bipedalism¹⁸, but also breathing, diet and vocalization needs may have shaped human face^{15,17,19}. Anatomical changes associated with the evolution of language undoubtedly facilitated speech production in *Homo Sapiens* compared to other species. In fact, some evidence suggests limited vocal repertoire in Neanderthals compared to modern humans^{20,21}. However, the retracted jaw, smaller upper airway and higher hyoid with subsequent positioning of the pharynx, while potentially facilitating the production of a wider range of vocalizations, may have presented new challenges in modern humans^{20,22,23}: two of the most significant being obstructive sleep apnea^{19,24} and choking/aspiration²³. This observed trade-off underscores the dynamic nature of craniofacial evolution, where adaptations for one function can have consequences for others.

Recent studies challenged the ideas that biomechanics and adaptive selection fully explain the unique facial structure of Neanderthals. Instead, some suggest that random evolutionary processes, such as genetic drift, may be more important factors in shaping craniofacial form¹⁵. Alternatively, others propose that facial evolution resulted from integrated changes in brain development and cranial base shape during evolution. This perspective emphasizes the influence of brain size on the cranial base, which in turn would have affected facial conformation¹⁵.

A noteworthy finding of this study is the absence of statistically significant differences in nasal index and choanal width between Hominid specimens and modern humans.

This observation bolsters the notion that morphological asymmetries within the nasal cavity may be more directly linked to thermoregulatory requirements, such as air conditioning of inspired air, rather than serving to optimize airflow patterns. In fact, the medial projection within the Neanderthal nasal cavity (Figure 1) is theorized to play a role in air temperature regulation⁷. It has been suggested as an autapomorphic feature in HN⁸. Nevertheless, *Franciscus*⁹ argues against its diagnostic value in HN claiming that the bony rim in question, termed the crista turbinalis, has been documented in both modern humans and fossil *Homo*.

Additionally, some supported that Neanderthals have relatively larger paranasal sinuses¹¹. Increased craniofacial pneumatization was proposed as an adaptation to lower ambient temperatures. Nevertheless, a recent work evaluated HN volumes compared to its scaled craniofacial dimensions and refused this hypothesis¹¹. Although the lack of soft tissue in fossils hinders direct comparisons of breathing ability, researchers reconstructed HN and HS nasal cavities, including mucosal distribution. A computerized virtual model revealed more efficient air conditioning (warming and humidification) in HN, suggesting specific climate adaptation²⁵.

Another interesting avenue for exploration concerns the potential link between nasal morphology and olfactory function. Recent studies suggest nasal airflow patterns play a significant role in olfactory function. A narrower vestibule and a stronger airflow vortex within the nasal cavity may enhance odor detection, particularly for highly soluble odorants²⁶. This finding compels further investigation into the potential link between nasal anatomy, airflow dynamics, and olfactory sensitivity in Neanderthals, particularly considering the presence of the medial projection (Figure 1). Modern humans possess larger olfactory bulbs and wider orbitofrontal cortex, suggesting a potential evolutionary link to enhanced learning, social skills, and possibly roles for olfaction in cognition and behavior¹⁸. Beyond

the established focus on respiratory function, the evolving nasal morphology in hominids might also be linked to olfactory adaptations. One unconventional hypothesis proposes that the emergence of the external nose in early *Homo* facilitated stereo olfaction, enhancing their ability to navigate vast distances through improved odor detection²⁷. Future studies could investigate whether the observed differences in nasal cavity size or structure translate into variations in olfactory capabilities, potentially lending support to this intriguing theory. There are limitations in this study, beginning in the nature of the evidence. The scarcity of well-preserved fossil specimens restricted sample size. Furthermore, inconsistencies in measurement protocols across different studies introduce the possibility of bias. Adding to this complexity, analysis of modern humans relied on CT scans instead of skull specimens, which may have influenced measurements. While the same landmark points were utilized to minimize this discrepancy, methodological differences remain. Additionally, focus on specific measurements, while informative, offers a limited perspective. Incorporating a wider range of anatomical features could yield richer insights. Finally, the study design does not account for potential environmental variations across sample populations, a factor that likely influenced nasal adaptations.

Conclusion

This investigation into *Homo* craniofacial morphology, specifically nasal cavity structure, adds a narrative to human evolution. By comparing fossil specimens with modern humans, the study reveals distinct features linked to a fascinating shift in nasal function. Neanderthal nasal morphology stands out for its unique characteristics. Unlike the smaller, narrower noses of modern humans, Neanderthals possessed a larger, broader nose with a prominent medial crest. This finding suggests a significant environmental influence on facial anatomy. However, various explanations exist for such observations, and no single theory has yet garnered

universal acceptance. This lack of consensus underscores the ongoing debate in this field. Further exploration of the hominid nasal morphology holds promise for not only deepening understanding of human evolution but also for potential applications in paleoenvironmental reconstruction and species identification.

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Conflict of Interests

The authors declare that they have no conflict of interest regarding this article.

Data Confidentiality

The authors declare that they followed the protocols of their work in publishing patient data.

Human and animal protection

The authors declare that the procedures followed are in accordance with the regulations established by the directors of the Commission for Clinical Research and Ethics and in accordance with the Declaration of Helsinki of the World Medical Association.

Privacy policy, informed consent and Ethics committee authorization

All the processed data were based in published reports that fulfilled privacy policy and ethical considerations.

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Scientific data availability

There are no publicly available datasets related to this work.

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