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Research Article

Discrete Cranial Traits in Neanderthals and Modern Humans Show Convergent Responses to Environment

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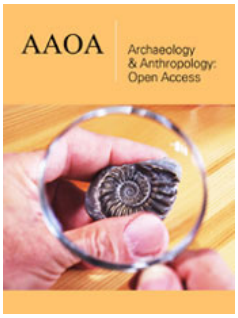

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Abstract

Discrete or epigenetic cranial traits, which exhibit heritable morphological variation influenced by environmental and developmental factors, are crucial for understanding human evolution. Despite genetic differences, Neanderthals and anatomically modern Homo sapiens inhabited diverse Eurasian environments, yet the impact of these environments on cranial trait variability remains underexplored. Here we analyzed discrete cranial traits in individual Neanderthals and modern humans using the Simple Matching Coefficient to assess phenotypic variability across species and environments. Our results reveal similar patterns of trait expression, indicating convergent phenotypic responses to environmental pressures. These findings suggest that environmental factors significantly influence the expression of epigenetic cranial traits, reflecting adaptive plasticity in hominin populations. This study highlights the complex interplay between genetics and environment in shaping cranial morphology during human evolution.

Keywords: Discrete cranial traits; Phenotypic variability; Adaptive plasticity; Convergent evolution; Environmental selective pressures

Introduction

Human populations have the potential to respond relatively rapidly to climatic and environmental stresses. This occurs through culturally mediated behaviors (e.g., technology, subsistence, settlement strategies, and especially spatial knowledge) developed within systems that can evolve over time. This potential can be expressed in multiple forms at variable speeds [1]. Middle Pleistocene populations in Eurasia responded to climate and environmental changes in ways that varied over time and across regions. Recent research has shown that Neanderthals implemented this survival strategy effectively, suggesting it was not limited to anatomically modern humans [2]. However, little attention has been paid to Neanderthals in terms of the ecological niches they occupied, nor how these niches and adaptations may have evolved biologically in response to pronounced environmental changes. The evolutionary history of Neanderthal populations spans the last 400,000 years of the Pleistocene and is significant for understanding human evolution across Eurasia.

The slow emergence and diversification of this species may exemplify how climatic fluctuations, including three major glacial-interglacial cycles, shaped their development and adaptation. Neanderthals inhabited a vast range, from the coasts near Morocco (Gibraltar) to the Altai Mountains in Siberia, and although their populations were not large, they were evidently well adapted and possessed a deep knowledge of the territories they occupied.

It is now clear that different human lineages coexisted with Neanderthals during the Middle and Late Pleistocene [3,4]. These extinct hominins include H. heidelbergensis/H. rhodesiensis, Homo naledi, Homo floresiensis, H. luzonensis, Denisovans, Homo erectus, and most recently Homo sapiens [5,6]. Paleogenomic research has shown that modern humans, Neanderthals, and their most recent common ancestor exhibited lower genetic diversity than living great apes [7]. While low levels of genetic diversity in modern humans are often attributed to a relatively recent demographic bottleneck [8], this explanation does not account for the similarly low genetic diversity observed in Middle Pleistocene hominins.

An alternative, more conservative hypothesis suggests that hominin effective population sizes remained very low for over 500,000 years; however, the mechanisms underlying genetic variability in Pleistocene hominin populations, and why these mechanisms did not similarly affect their contemporaries, remain unclear [7]. Additionally, genetic differentiation between individuals is greater among Neanderthals than among modern humans, implying that Neanderthals lived in small, relatively isolated populations, which led to greater divergence among groups due to varying environmental selective pressures [9]. In light of these factors, we investigated the potential phenotypic variability among Neanderthals and some Anatomically Modern Sapiens (AMH) living in Eurasia, taking into account that spatial barriers in this region may not have significantly restricted their movements [1].

Material and Methods

The study sample was drawn from the literature, casts, and direct observations (Table 1). We selected morphological variants commonly referred to as discrete, discontinuous, non-metric, or epigenetic traits- due to their demonstrated genetic heritability [10-14] and their reliability in both intra- and inter-population studies [15-19]. These traits are heritable characteristics or changes in gene expression that occur without alterations to the underlying DNA sequence, often resulting from environmental factors and behaviors that add chemical tags (such as DNA methylation or histone modification) to DNA or its associated proteins. In genetics, the traits we examine are considered threshold traits: polygenic characteristics that do not follow simple inheritance patterns but instead display a bimodal or multimodal distribution, where only some individuals express the trait. The threshold effect means that a certain combination of genetic and/or environmental factors is necessary for the trait to be phenotypically expressed. According to Falconer's model, the predisposition to develop such a trait is polygenic and follows a Gaussian (bell-shaped) distribution, but only individuals whose predisposition exceeds a certain threshold will actually express the trait. Both genetic and environmental factors contribute to pushing the predisposition past this threshold. Because our sample comprised individual specimens rather than statistically significant population groups, we employed an individual comparison approach. By analyzing Neanderthals and Anatomically Modern Homo Sapiens (AMH) together as a single comparative group, we aimed to identify potential affinities between these individuals, despite the limited sample sizes. The recorded morphological traits were transformed into binary dichotomies that evaluate their presence (1) or absence (0), in order to calculate a Simple Matching Coefficient according to the formula:

$$dij = (N10 + N01)/(N10 + N01 + N11 + N00)$$

Dummy variables (i.e., traits always present or always absent in all cases) were excluded [20]. The distance between the two samples (dij) is calculated by dividing the number of variables present in the ith individual and absent in the jth and vice versa (scored as 10 or 01), by the total number of variables, including those present or absent in both (11 and 00) [19,21]. A spreadsheet containing binary scores and formulas was used to organize the results into a matrix, which was used for cluster analysis using the WPGMA and Euclidean range squared methods. The traits used are shown in Table 2. The geographic locations of the samples are identified in Figure 1.

Table 1: list of the traits. r=right; l=left.

1	metopism
2	preauricular sulcus r
3	preauricular sulcus l
4	supratrochlear notch r
5	supratrochlear notch l
6	supraorbital notch r
7	supraorbital notch l
8	supraorbital canal r
9	supraorbital canal l
10	pteric bone r
11	pteric bone l
12	asterion bone r
13	asterion bone l
14	mastoid foramen r
15	mastoid foramen l
16	extrasutural mastoid foramen r
17	extrasutural mastoid foramen l
18	bregma bone
19	parietal foramen r
20	parietal foramen l
21	sagittal ossicles
22	coronal ossicles r
23	coronal ossicles l

Table 2: Specimens, dating and geographic location. Am - anatomically modern. Ya- years ago. E- Early.

Specimen	Age	Location	Species	
Qafzeh 5, 6, 9	~92.000 Ya	Galilee Israel	*Am Homo sapiens*	De Stefano, Hauser 1991
Shanidar 1	~45-35.000 Ya	Kurdistan Iraq	*Homo neanderthalensis*	Cast

Neander 1	~40.000 Ya	Germany	*Homo neanderthalensis*	De Stefano, Hauser 1991
Teshik-Tash 1	~70.000 Ya	Uzbekistan	*Homo neanderthalensis*	Cast
La Chapelle aux Saints 1	~60.000 Ya	France	*Homo neanderthalensis*	De Stefano, Hauser 1991 and cast
La Ferrassie 1	~70-50.000 Ya	France	*Homo neanderthalensis*	De Stefano, Hauser 1991and cast
Amud 1	~60-50.000 Ya	Galilee Israel	*Homo neanderthalensis*	De Stefano, Hauser 1991
Monte Carmelo (Skhul 5)	120-80.000 Ya	Israel	*Am Homo sapiens*	De Stefano, Hauser 1991
Krapina 3	~125.000 Ya	Croatia	*Homo neanderthalensis*	De Stefano, Hauser 1991
Gibraltar 1	~70-45.000 Ya	Gibraltar	*Homo neanderthalensis*	De Stefano, Hauser 1991 and cast
Saint-Cesaire	~36.000 Ya	France	*Homo neanderthalensis*	Cast
Saccopastore 1	~250.000 Ya	Italy	*E Homo neanderthalensis*	De Stefano, Hauser 1991 and cast
Swanscombe	~400.000 Ya	England	*E Homo neanderthalensis*	De Stefano, Hauser 1991
La Quina 5	~65.000 Ya	France	*Homo neanderthalensis*	De Stefano, Hauser 1991
Guattari 1, 4, 5	~60-50.000 Ya	Italy	*Homo neanderthalensis*	Original

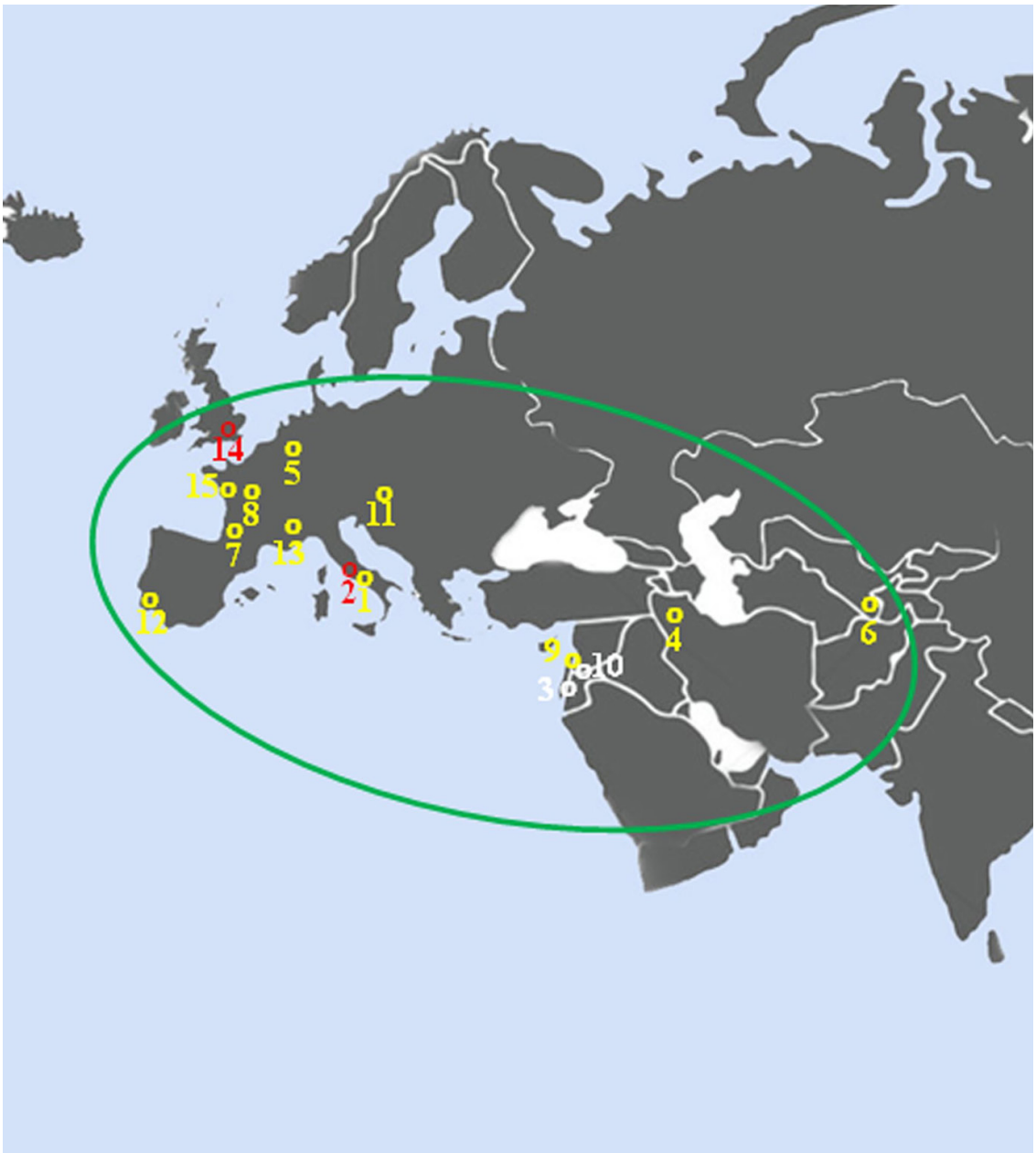

Figure 1: Geographic location of the specimens.

Results and Discussion

The results of the test are presented in Figure 2 and, given the nature of the sample, warrant several observations. The chronological progression from ancient Neanderthals to classical Neanderthals and Anatomically Modern Homo Sapiens (AMH) can be viewed as a temporal continuum. Within a 10% similarity threshold, three clusters-A, B, and C-emerge. Cluster C comprises the ancient Neanderthals from Swanscombe and Saccopastore 1, which is consistent with expectations given their temporal proximity. The high, though not exact, correspondence between them may reflect evolutionary changes over the interval separating these specimens. Clusters A and B are particularly noteworthy. Cluster B, the largest, contains several subclusters that include nearly all classical Neanderthals, except for the three AMH individuals from Qafzeh 5, 6, and Skhul 5. Qafzeh 6 and Skhul 5 form a subcluster with strong similarities, and their inclusion within a larger cluster of classical Neanderthals may reflect phenotypic similarity. This phenomenon could also explain the strong correspondence between Qafzeh 5, Krapina 3, and Guattari 5, as well as the substantial, though less pronounced, similarities with Guattari 4, Gibraltar 1, and Saint-Cesaire.

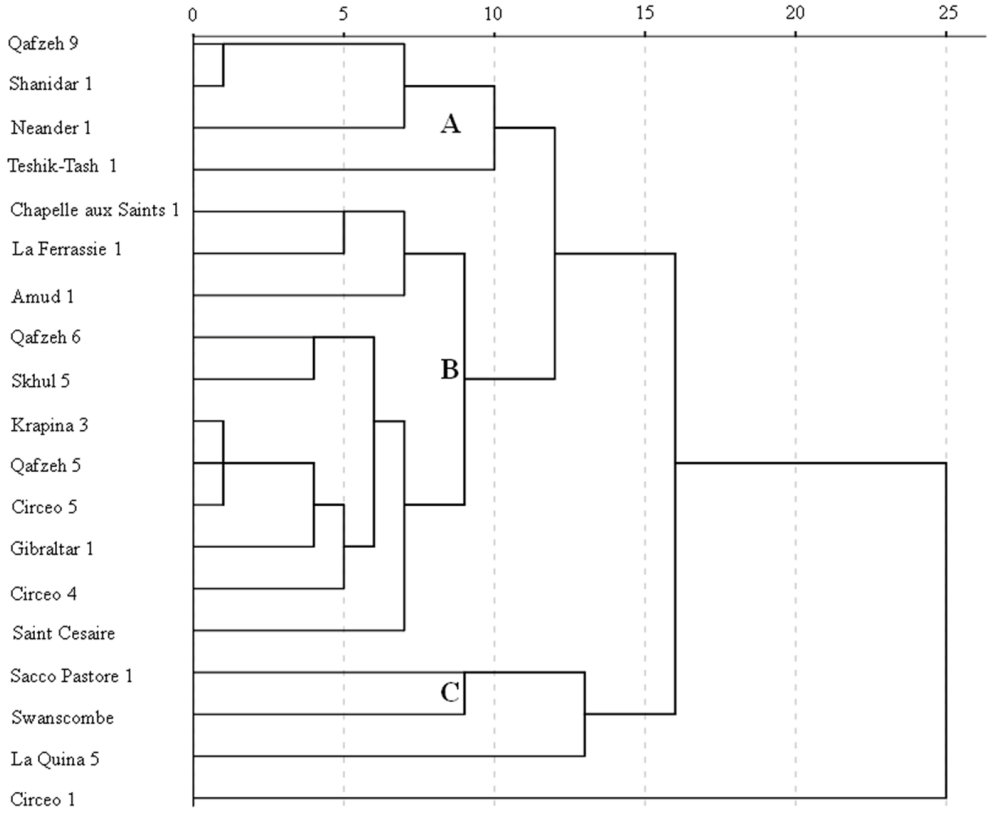

Figure 2: Dendrogram of the SMC.

The grouping of Chapelle aux Saints 1, La Ferrassie 1, and Amud 1 aligns with previous morphometric analyses [22]. In Cluster A, the close association of Qafzeh 9 and Shanidar 1 may be attributed to their shared Middle Eastern environment, which could also account for the presence of Neanderthals 1 and Teshik-Tash 1 in this cluster. Overall, the dendrogram reveals a complex mosaic of interrelationships both within Neanderthals and between Neanderthals and sapiens, indicating that patterns of similarity are not straightforward. Notably, Neanderthals do not form a single, low-variability cluster; some individuals, such as La Quina 5 and especially Guattari 1, are positioned at the periphery of the dendrogram, distant from other specimens. Because the traits analyzed are expressed only when certain genetic and environmental thresholds are met, they are particularly susceptible to environmental influences.

While genetic factors play a role, environmental selective pressures may influence trait expression past the threshold. Our sample spans a broad chronological range (Table 2), from MIS 10 to MIS 4, encompassing multiple glacial and interglacial cycles. Although geographically limited to Eurasia, this region experienced significant climatic fluctuations and diverse microclimates, leading to a variety of environmental adaptations that likely contribute to the complex mosaic of trait expression observed in our analysis. According to some geneticists, the Neanderthal genome exhibits low variability attributable to an equally low population density and an evidently high level of inbreeding [23,24]. The situation is different

for sapiens, who, according to some authors, exhibit significantly greater variability [24]. The morphology of fossil skeletons, like every aspect of the phenotype, is the product of genetic and environmental influences, and often interactions between the two [25,26]. Genetic influences on skeletal morphology are ultimately the result of adaptive (natural selection) or neutral (mutation, gene flow, genetic drift) evolutionary forces that have shaped allele frequencies in a population or species over the course of multiple generations.

Analyses that combine between-group and within-group variation within a species can identify patterns of covariance not immediately apparent from analyses of individual groups, but these associations must be interpreted with caution, as they may be due to population history or phylogeny rather than genetic, evolutionary, or functional links [26]. The fossil record shows a certain degree of independence for cranial features typically found in Neanderthals. For example, European fossils dating back 130,000 years exhibit some, but not all, Neanderthal features, which is not what would be expected if all Neanderthal features were part of an integrated assemblage. This is illustrated by the Sima de los Huesos fossils from Spain, which display Neanderthal-like prognathic midfaces and some associated features, but lack basal cranial features such as a mastoid tubercle or a large juxtamastoid eminence, and some cranial vault features, while exhibiting others like an incipient supranuchal fossa [27]. Groups of individuals sharing genetic similarities are not the same as those sharing morphological similarities. Neanderthals may have been a highly dynamic population, with the potential for rapid migration and long-distance dispersal, rather than a unitary group that evolved in isolated glacial conditions.

Neanderthal features appear to have appeared among the hominids of Sima de los Huesos around 400,000-350,000 years ago [27-29], while it is widely believed that a coherent morphological pattern defining Neanderthals emerged around 300-250,000 years ago and that the so-called "classical" Neanderthal morphology evolved around 70,000 years ago [30,31]. In parallel, AMH evolved more or less simultaneously in Africa. The earliest evidence for AMH is debated, but fossils from Jebel Iroud, Morocco, dating to 315kya [32,33], Omo Kibish, Ethiopia, dating to approximately 230kya [34], and Florisbad, South Africa, dating to approximately 259kya, all show AMH traits, although the tendency toward skeletal gracilization and globularization of the cranial vault is evident much later in the evolution of our species [35,36]. The first significant European occupations by AMH migrating from Africa date back to approximately 43,000 years ago [37-39] although earlier intermittent occupations are known, e.g., in Mandrin, France: Slimak et al., [40].

Neanderthals became extinct between approximately 40,000–30,000 years ago [41], leading some to argue for a link between these events [42-45]. This contrast between the early evolutionary environments of Neanderthals (cold/temperate environments) and AMH (subtropical/tropical Africa) likely resulted in fundamental differences in the morphology, physiology and adaptive behaviour of these groups, with geographic isolation and neutral evolutionary processes likely playing a key role [26,30,46]. The phenotypic similarities observed between Neanderthals and Homo sapiens are consistent with the possibility that species can develop similar traits in response to comparable environmental pressures. This pattern also suggests that local populations-referred to as paleodemes, or distinct ancient population groups—may have evolved and diverged more frequently than previously recognized, raising the possibility that some groups (such as the Krapina individuals) may not have a direct phyletic relationship with later Neanderthal populations [8].

Conclusion

The low genetic variability observed in Neanderthal mtDNA studies [24] may reflect a small effective population size throughout much of their evolutionary history, spanning approximately 400,000 years, or it may be characteristic only of late Neanderthals who experienced demographic reductions, possibly due to interactions with Homo sapiens outside Africa. Briggs et al. [24] suggest that Neanderthals maintained small effective population sizes for an extended period. Despite this low genetic variability, the morphological traits we examined showed considerable variability in their expression, similar to the pattern seen in Homo sapiens. This phenotypic variability likely results from multiple factors, including the diverse environments inhabited by different groups. Environmental selective pressures may have influenced trait expression in a geographically uneven and diverse manner. Moreover, the traits analyzed-referred to as epigenetic traits [47,48] are heritable phenotypic changes that do not involve alterations to the underlying DNA sequence, but instead often result from mechanisms such as DNA methylation or chromatin modification. These epigenetic mechanisms allow for reversible phenotypic variability in response to environmental stressors, facilitating short-term adaptation. Our analysis indicates that such epigenetic changes may have played a significant role in enabling both Neanderthals and Homo sapiens to adapt to diverse environmental pressures.

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