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RESEARCH ARTICLE

Eco-Geographical Variation in Craniofacial Size and Shape, With Emphasis in Cold Adaptation, Through a 3D Approach

Manuel Domingo D'Angelo del Campo[1,2,3,4] | Gülkan Gökdoğan Aktepe[5] | Markus Bastir[6] | Daniel García Martínez[5,7,8]

[1]Consejo Nacional de Investigaciones Científicas y Técnicas, Centro Científico Tecnológico-Tandil (CONICET, CCT Tandil), Tandil, Argentina | [2]Laboratorio de Ecología Evolutiva Humana (LEEH), Unidad de Enseñanza Universitaria Quequén (UEUQ), Facultad de Ciencias Sociales (FACSO), Universidad Nacional del Centro de la Provincia de Buenos Aires (UNCPBA), Quequén, Argentina | [3]Laboratorio de Poblaciones de Pasado (LAPP), Departamento de Biología, Universidad Autónoma de Madrid (UAM), Madrid, Spain | [4]Museo de Antropología, Instituto de Investigación Arqueológica y Antropológica (INIAA), Universidad Mayor, Real y Pontificia de San Francisco Xavier de Chuquisaca (UMRPSFXCH), Sucre, Bolivia | [5]Unidad de Antropología Física, Departamento de Biodiversidad, Ecología y Evolución, Universidad Complutense de Madrid (UCM), Madrid, Spain | [6]Departamento de Paleobiología, Grupo de Paleoantropología, Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain | [7]Center for Functional Ecology-Science for People and the Planet (CFE), Universidade de Coimbra (UC), Coimbra, Portugal | [8]Centro Nacional de Investigación Sobre la Evolución Humana (CENIEH), Burgos, Spain

Correspondence: Manuel Domingo D'Angelo del Campo (manueldomingodangelo@gmail.com)

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ABSTRACT

Introduction: This study examines cranial morphological variations across populations adapted to different climates, with a focus on cold adaptation. Using a 3D geometric morphometric approach, the study analyzes skull variability between populations from various latitudes and climates. Two null hypotheses are tested: (1) differences in skull size and shape are unrelated to climate, and (2) no differences exist between populations with recent versus ancient cold adaptation.

Material and Methods: Skulls from five populations across different climates were analyzed using 3D geometric morphometrics. Landmarks were digitized, and statistical analyses were performed to evaluate size and shape variations among the populations.

Results: One-way ANOVA Bonferroni post hoc analysis revealed significant size differences. Norsemen differed significantly from all other samples, except Sub-Saharan Africans. Cold-adapted populations exhibited larger skull sizes, whereas populations from mild and hot climates had smaller skulls. However, Norsemen exhibited unexpectedly smaller sizes. Notable anatomical disparities are observed along both PCs. PC1+ showed increased prognathism and wider faces in Southern Patagonia and Greenland Thule. PC2+ highlighted larger faces and sloping foreheads in Southern Patagonia and European populations. Median shape analysis reveals pronounced prognathism and wider skulls in Southern Patagonia, with Greenland Thule showing similar traits but with a more globular braincase.

Conclusion: Notable craniofacial similarities associated with extreme cold adaptation, including increased prognathism, prominent glabellar and supraciliary regions, lateral zygomatic expansion, enlarged nasal cavity and orbits, and elongated, flattened braincase, despite genetic differences. However, the Norse sample presents a deviation from expected patterns, exhibiting smaller sizes despite inhabiting a cold region.

1 | Introduction

The human skull stands as the primary focus of analysis for biological anthropologists (Hefner et al. 2016; Slice 2007). Cranial studies offer insights into hominin phylogenies, population histories, and inter- and intra-group human affinities (Harvati and Weaver 2006). Furthermore, they offer avenues for inferring characteristics related to sex, climate, and environmental adaptations (Slice 2007). Human cranial diversity results from a combination of genetic and environmental influences, with morphological studies revealing these differences (Beguelín and Barrientos 2006).

Environmental factors commonly shape the adaptive conditions necessary for distinct human groups; varying climates often correlate with different human populations (Beguelín and Barrientos 2006). The human skull undergoes macro- and micro-evolutionary adaptations in response to environmental influences, particularly climatic conditions (von Cramon-Taubadel 2014). However, different aspects of cranial morphology retain distinct types of information, with some cranial regions believed to be more sensitive to environmental pressures, such as the facial shape (Harvati and Weaver 2006; Hubbe et al. 2009; Menéndez 2018). The shape of the vault and cranial base, by contrast, appears to show less correlation. Fundamentally, the cranial base is considered one of the most evolutionary conservative areas of the skull (Harvati and Weaver 2006; Menéndez 2018).

Facial structures such as the nasal cavity, external and internal nose, maxillary sinuses, orbital structure, glabellar region, maxilla, and zygomatic bones are especially sensitive to environmental pressure. These differences are more notable in populations living in extreme cold and dry climates (Harvati and Weaver 2006; Noback et al. 2011; Stansfield et al. 2021). Individuals in such environments tend to have larger and more robust skulls (Beals et al. 1983; Roseman 2004; Harvati and Weaver 2006; Pérez and Monteiro 2009; Menéndez 2018). However, as certain authors (Beals et al. 1983; Harvati and Weaver 2006; Hubbe et al. 2009; Stansfield et al. 2021) noted, the potential influence of cold climates on skull size and shape remains an ongoing subject of discussion.

Despite uncertainties surrounding the environmental impact on skull morphology, variations in human body size and shape appear to be influenced by environmental factors according to ecogeographical principles. Bergmann's rule (1847) posits that endothermic mammals in warmer climates tend to exhibit smaller body sizes, facilitating heat dissipation through a higher surface-to-volume ratio. In contrast, animals adapted to colder climates typically display larger dimensions, minimizing heat loss with a lower surface area-to-volume ratio. While Bergmann's rule is often associated with latitude, implying colder conditions at higher latitudes, this correlation is not absolute. Allen's rule (1877) suggests that endothermic mammals in warmer climates possess longer limbs relative to their body size compared to those in colder climates, aiding in heat dissipation.

1.1 | Populations Inhabiting Cold Regions

Body proportions of humans adapted to cold regions differ from those of individuals from other latitudes, often featuring longer and broader bodies with shorter extremities (Holliday and Ruff 2001; Katzmarzyk and Leonard 1998; Ruff 1994). In addition to sharing body proportions, climatic and environmental hypotheses regarding skull traits among Southern Patagonian (SP) human groups suggest that adaptation to cold conditions may explain craniofacial morphological traits shared with northern American Inuit populations. These similarities include notable craniofacial robustness, such as great frontal and basal dimensions, enlarged orbit and nasal cavities, prominent mastoids and glabellar regions, and a marked occipital ridge (Hernández et al. 1997; Lahr 1995; Lalueza et al. 1997). In recent decades, further insights have indicated that despite genetic distance between Inuit and SP human groups (Chiaroni et al. 2009; de la Fuente et al. 2015; de Saint Pierre et al. 2008, 2012), they share morphological traits such as nasal cavity structure (Noback et al. 2011), *os* coxae (Betti 2014; Betti et al. 2014), pelvic canal (Betti and Manica 2018; Kurki 2013), and ribs (García-Martínez et al. 2018). Additionally, they exhibit similar metabolism characteristics, height, weight, and robustness (Hernández et al. 1997; Leonard 2018; Pearson and Millones 2005). A recent geometric morphometric study on craniofacial morphology of different SP human groups inhabiting various ecogeographical SP areas has confirmed the environmental cold influence on skull morphology (D'Angelo del Campo 2020).

However, despite the possible environmental influence and application of ecogeographical rules to humans, some authors have highlighted the role of culture and technological adaptations in facilitating biological adaptations to different climate conditions (Irving 1957; Scholander 1955, 1956). Opportunities to evaluate this situation among human populations are, however, scarce. Perhaps an example lies in the Norse settlement in Greenland, established in AD 985 and lasting approximately 500 years before their disappearance, possibly due to sea-level rise (Borregine et al. 2023). According to Nordic Sagas, it was the renowned Eric the Red who founded the first settlement after being banished from Iceland (Arneborg et al. 1999; Lynnerup 1991; Lynnerup and Von Wovern 1997). Thus, this human group could be considered Vikings of European origin, with a different cultural adaptation to cold learned in a "warmer" region and genetically distinct from Greenland Thule culture (Margaryan et al. 2020; Sailard et al. 2000). Regarding Norse people, it is important to note that during Greenland settlement, the diet shifted drastically from predominantly terrestrial to marine around AD 1000 (Arneborg et al. 1999), particularly in the latter period of occupation (Nelson et al. 2012). Recent studies, including nuclear and mitochondrial genomic (Margaryan et al. 2020) and morphogeometrical (Plomp et al. 2023) analyses, have shown that Norse ancestry is geographically diverse, mixing between Scandinavia, Britain and Ireland.

To date, few studies had analyzed the Norse from a morphological perspective with an ecogeographical outlook (García-Martínez et al. 2018; López-Rey, D'Angelo del Campo, et al. 2024; López-Rey, García-Martínez, et al. 2024a). García-Martínez et al. (2018) observed no similarities in rib size or shape between Greenland Thule and Norse. These authors noted smaller values than their Inuit counterparts inhabiting the same regions. However, López-Rey, D'Angelo del Campo, et al. 2024 and López-Rey, García-Martínez, et al. (2024a) indicated that the ribcage of Norse people is similar to that of Inuit populations (Point Hope and, Thule culture) and Southern Patagonian groups, characterized by "bell-shaped" ribcage with medium rib declination and variable width and depth. Cold-adapted populations show significant statistical differences in shape with temperate and tropical populations.

Further evidence is required to confirm the potential buffering effect of human culture on biological adaptations. Assuming the existence of an ecogeographical environmental influence that cannot be buffered by human culture, the question arises: how much time or how many generations are needed to begin appreciating changes?

1.2 | Aims of This Study

This study aims to investigate cranial morphological variations among populations adapted to different climates, with a particular focus on cold adaptation. The findings are expected to contribute to a deeper understanding of how environmental pressures shape human cranial morphology, which could, in turn, inform the fields of biological anthropology and evolutionary biology. We will assess 3D skull morphological variability using a Geometric Morphometric (GM) approach across five populations adapted to various climates: hot (Sub-Saharan Africans), warm (Iberian Peninsula populations), and cold (Thule and Norse from Greenland, and Southern Patagonians). Two hypotheses will be tested:

H1. *There are differences in skull size and shape among populations depending on climate, with populations adapted to cold environments exhibiting larger dimensions. According to Bergmann's rule, we would expect larger forms in cold regions and smaller forms in warm and hot areas. It's worth noting that this is one of the first applications of 3D GM to compare characters derived from potential cold adaptation in humans.*

H2. López-Rey, D'Angelo del Campo, et al. (2024) *suggest that the Norse ribcage resembles that of populations adapted to extreme cold, consistent with Bergmann's rule. In contrast,* Plomp et al. (2023) *argue that Norse skull shape and size are more similar to Scandinavian and British populations. Based on this, we expect the Norse cranial size and shape to be intermediate, between the extreme cold and mild/hot populations. Specifically, we anticipate similarities in shape and size among individuals form extreme cold regions, following the Bergman's rule.*

The potential variability among populations may be attributed to environmental impact and ecogeographical adaptation. However, we cannot discount the influence of genetic and cultural factors. As Roseman (2016) emphasized, human skull variation is a complex process in which no single factor predominates.

2 | Materials and Methods

GM and Virtual Anthropology (VA) have greatly expanded the potential for morphological studies (Weber 2015; Weber et al. 1998). GM involves analyzing the geometry of structures using Cartesian coordinates and landmarks in a 2D or 3D space, enabling the capture of the specific spatial configuration of the underlying structure and analyzing shape and size independently (Bookstein 1991).

2.1 | Sample Analyzed

The study examined 85 skulls obtained from five populations residing in various latitudes and climates across both hemispheres (Table 1). These populations include three from cold climates: (1) Southern Patagonian terrestrial hunter-gatherers from the north of *Isla Grande de Tierra del Fuego* ($n = 14$), housed at the *Naturhistorisches* Museum (Vienna, Austria) and the *Laboratorio de Ecología Evolutiva Humana* (LEEH-CONICET, Necochea-Quequén, Argentina); (2) Greenland Norse/Vikings from the west settlements ($n = 10$), housed at the Panum Institute (Copenhagen, Denmark); and (3) Greenland Thule Culture ($n = 29$), also from the Panum Institute (Copenhagen, Denmark). Additionally, one population from a mild climate ($n = 26$) was included, consisting of European Portuguese individuals from the *Colecção de Esqueletos Identificados do Século XXI*, housed at the Laboratory of Forensic Anthropology of the University of Coimbra (Portugal). Finally, a population from a hot climate was represented by a Sub-Saharan African sample ($n = 6$) from the Guinea Gulf, housed at *Dryas Octopetala* (Coimbra, Portugal). All samples are archaeological and date from the 11th to 21st centuries (see Table S1). The populations analyzed were of ancestral origin corresponding to the regions where their remains were exhumed. Exceptions included the Sub-Saharan and Norse groups, whose origins were determined based on literature (Martiniano et al. 2014; Ferreira et al. 2019; Margaryan et al. 2020). Regarding Norse people, as Dugmore et al. (2007) indicate, it seems that there were no other cultural groups in south-west Greenland at this time; therefore, Viking ancestry of the individuals is assumed.

Only complete and well-preserved skulls devoid of noticeable pathological signs or taphonomic alterations, as well as individuals lacking cultural skull deformations, were included in the analysis. The sex ratio within each population was balanced as much as possible, and only adult individuals were studied. Adult age status was determined based on the eruption of the third molars (Ubelaker 1978), as well as the fusion of epiphyses and skull base (Scheuer and Black 2004).

2.2 | Landmarks Digitalization Template

3D geometric morphometric methods were employed to capture the morphological information of the skulls. Throughout the history of typological analysis, the skull has remained a focal point of anatomical study, garnering considerable attention (Hefner et al. 2016; Slice 2007). As a result, a vast array of templates has been proposed and utilized for analyzing

TABLE 1 | Samples analyzed.

Sample	Institution	*n* ♂	♀	Σ	Chronology (centuries)	Latitude (approx.)	Annual temp. (approx.) (°C)	Climate	Subsistence strategy	References
Southern Patagonia	LEEH/NM	10	4	14	19th–20th	50°–55° S	5	Cold	Hunter-gatherer	D'Angelo del Campo et al. 2020
Thule culture (Greenland)	PI	13	16	29	13th–15th	67°–69° N	≤ −2	Cold	Hunter-gatherer	
Norse (Greenland)	PI	4	6	10	13th–15th	64° N	≤7	Cold	Preindustrial	Arneborg et al. 1999
Europeans (Iberian Peninsula)	CEI	12	14	26	20th–21th	40° N	16	Mild	Postindustrial	Ferreira et al. 2014
Sub-Saharan Africa	DO	3	3	6	15th–17th	15° N–20° S	≥25	Hot	Preindustrial	Martiniano et al. 2014; Ferreira et al. 2019

Abbreviations: CEI, Coleção de Esqueletos Identificados do século XXI (Coimbra. Portugal); DO, Dryas Octopetala (Coimbra. Portugal); LEEH, Laboratorio de Ecología Evolutiva Humana (Necochea. Argentina); NM, Naturhistorisches Museum (Wien. Austria); PI, Panum Institute (Copenhague. Denmark).

its morphology. In this study, we utilized a template comprising 65 landmarks and 723 semilandmarks (Figure 1; see Supporting Information; Table S2), previously developed by Peña-López et al. (2018).

2.3 | Data Acquisition

The cranial data were acquired following the standard virtual morphological workflow outlined by Bastir et al. (2019). Initially, skulls were digitized using two methods: (1) a high-resolution Artec Space Spider 3D surface scanner with blue light technology and (2) clinical CT scans performed on a Philips Brilliance CT 64, with one scanner located at *Allgemeines Krankenhaus-Wien* (AKH, Vienna, Austria) and the other at *Instituto Radiológico* (IR, Mar del Plata, Argentina).

Subsequently, post-processing procedures including cleaning, smoothing, and alignment were conducted using specialized software tailored to each digitized data source: (1) Artec Studio software version 12 for processing Artec scans; and (2) the 3D Slicer image computing platform (https://slicer.org) for processing CT scans. Finally, to obtain the coordinates of the landmarks and semilandmarks, 3D surface models were imported into Viewbox software version 4.0 (www.dhal.com, Kiffisia, Greece).

2.4 | Statistical Analyses

The configurations of skull landmarks and semilandmarks underwent generalized procrustes analysis (GPA, Bookstein 1991), in which they were translated to a common origin, scaled to unit centroid size, and rotated to minimize the Procrustes distance between homologous points. The resulting GPA data were then analyzed following standard procedures for size and shape analysis (Zelditch et al. 2012) using EVAN Toolbox (version 1.71; http://www.evan-society.org/) and MorphoJ (Klingenberg 2011).

A Kolmogorov–Smirnov test was initially performed to assess the normality of the centroid size data. Once normal distribution was confirmed, a one-way ANOVA followed by a Bonferroni post hoc analysis was performed on the means of the different groups. This was done to identify and compare homogeneous mean subsets and detect any significant difference at a 0.05 significance level.

Subsequently, Principal Component Analysis (PCA) was applied to the shape data to reduce the dimensionality of the data, visualize the variation and distribution of the sample in the morphospace (O'Higgins 2000; Zelditch et al. 2012), and explore potential morphological affinities between different groups, such as cold-adapted populations.

Finally, a mean shape comparison was performed in MorphoJ software to simplify the description of group differences and statistically assess any significant differences between them, carrying out a cluster analysis to observe morphological affinities between groups.

3 | Results

Summary statistics of the centroid size analysis by group can be observed in Table 2. The Kolmogorov–Smirnov test conducted did not provide statistical evidence to reject the hypothesis of sample normality in the size analysis ($Z = 0.61$; $p = 0.85$). The one-way ANOVA Bonferroni post hoc analysis revealed significant size differences between Norse and all other samples, except for Africans (Table 3). Upon examining Figure 2, the data reveal that the average size is larger for populations inhabiting cold regions and smaller for those in mild and hot regions. However, the Norse sample exhibits a lower size compared to the others.

The projection of PC1 versus PC2 accounts for 42% of the sample variability (Figure 3; Supporting Information, Table S3). This percentage indicates that these two principal components capture nearly half of the observed variation in the sample, highlighting their importance in distinguishing population-specific cranial morphological traits. In this projection, distinct differences between populations are evident (Figure 4): along the PC1 axis, a gradient from negative to positive forms is observed, with Norse, Europeans, and sub-Saharan on the left and cold-adapted populations in southern Patagonian and Thule Greenland on the right. Anatomical disparities are apparent along both PCs. Concerning PC1 (Figure 5), PC1+, which encompasses south Patagonia and Thule, exhibits notable differences in the splanchnocranium, characterized by increased prognathism leading to a more projecting midface with prominent glabellar and supraciliary regions, along with a pronounced lateral expansion of the zygomatic arches resulting in a broader and larger face, as well

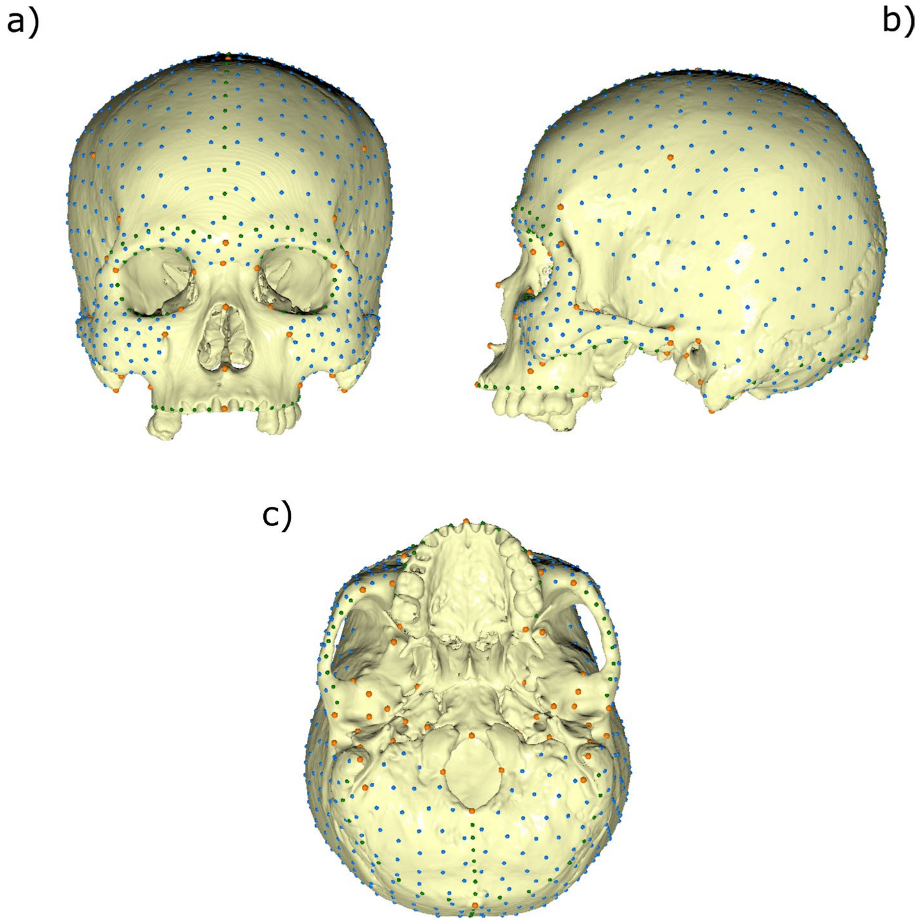

FIGURE 1 | Anatomical localization of 65 landmarks (orange), semilandmarks (blue), and curve semilandmarks (green). (a) Frontal view, (b) Lateral view, (c) basal view.

TABLE 2 | Summary statistics for the distribution of each population studied based on the size results.

	Southern Patagonia	Thule	Sub-saharan	European	Norse
Mean	2372.80	2346.41	2270.90	2318.44	2205.52
Std. Error	19.40	14.87	34.08	18.86	18.24
Variance	5267.32	6411.12	6969.10	9249.39	3327.62
Stand. Dev.	72.58	80.07	83.48	96.17	57.69
Median	2370.86	2355.69	2289.45	2332.01	2197.70

TABLE 3 | Confidence interval to evaluate size differences between populations (1 = sub-Saharan; 2 = Norse; 3 = southern Patagonian; 4 = Thule; 5 = European).

Populations	Mean	Conf. Int. 95% inferior	Conf. Int. 95% superior
1–2	65.38	−57.55	188.32
1–3	−101.89	−218.06	14.26
1–4	−75.51	−182.28	31.26
1–5	−47.54	−155.36	60.28
2–1	−65.38	−188.32	57.55
2–3	**−167.28**[a]	−265.85	−68.71
2–4	**−140.89**[a]	−228.20	−53.59
2–5	**−112.92**[a]	−201.51	−24.34
3–1	101.89	−14.26	218.06
3–2	**167.28**[a]	68.71	265.85
3–4	26.38	−51.09	103.86
3–5	54.35	−24.56	133.27
4–1	75.51	−31.26	182.28
4–2	**140.89**[a]	53.59	228.20
4–3	−26.38	−103.86	51.09
4–5	27.96	−36.32	92.26
5–1	47.54	−60.28	155.36
5–2	**112.92**[a]	24.34	201.51
5–3	−54.35	−133.27	24.56
5–4	−27.96	−92.26	24.56

Note: Bold indicates $p < 0.01$.
[a] Size differences.

as a wider skull. Additionally, a significant enlargement of the nasal cavity and orbits is observed. The neurocranium displays a less globular posterior skullcap, a narrower frontal bone with a sloping forehead, and an elongated, flattened braincase. Positive forms exhibit a face larger than the neurocranium, indicating a more prominent midface and broader zygomatic arches, while the opposite pattern, where the neurocranium is larger relative to the face, is observed in negative forms. This terminology refers to variations in cranial morphology along the PC1 axis, which distinguishes cold-adapted populations from others. The variability observed in PC2 (Figure 6), particularly PC2+, where southern Patagonian and Europeans are situated, entails larger and wider faces, with a notable distinction in the frontal region characterized by a sloping forehead. The PC3 scores contribute to further separating the two cold-adapted populations, with Greenland specimens plotting toward the negative values of the PC, whereas the Southern Patagoninan ones plot toward the positive values (Figures 7 and 8).

The 3D warps associated with the average morphologies of the groups (Figure 9) reveal that the southern Patagonian population occupies the positive quadrant (PC1 and PC2) of the morphospace. This population exhibits pronounced prognathism, a broader and larger face, and a wider skull. Additionally, the posterior skullcap is less globular, the forehead is more sloping, and the braincase is elongated and flattened. Comparatively, Thule exhibits a shape similar to the southern Patagonian population, but with a more lobular braincase, less pronounced sloping forehead, and reduced prognathism. The European samples (Norse and Iberian) exhibit a similar shape, albeit with Greenland Vikings displaying a broader skull. The sub-Saharan sample demonstrates the most globular skull shape and a more differentiated nasal cavity, which is wider than the others. Finally, the cluster analysis based on the Procrustes distances between the average of each group (Table 4, Figure 10) reveals a clear association between the cold adapted populations, as well as affinities between the Norse with the Europeans, and this group with Sub-Saharan.

4 | Discussion

Morphological variation in body traits, including shape, size, and proportions, has long been associated with climatic influence (Ruff 1994). Ecogeographical principles often presume that this relationship results from environmental factors (Allen 1877; Bergmann 1847). Nonetheless, doubts persist about the direct impact of climate on skull morphology, likely due to the complex interplay between intrinsic and extrinsic factors, suggesting a multifactorial origin for craniofacial variation (Beguelín and Barrientos 2006).

Although establishing a direct causal link between craniofacial variation and climate remains challenging, indicative patterns have been observed (D'Angelo del Campo 2020; Harvati and Weaver 2006; Relethford 2010; Roseman 2004). The skull's plastic response to climate appears more pronounced in extreme environments, such as the extreme cold (Roseman 2004; Harvati and Weaver 2006; Relethford 2010; Noback et al. 2011; Menéndez 2018; Stansfield et al. 2021), which is the focus of this study. Notably, craniofacial similarities associated with cold adaptation have been observed between populations from southern and northern America, despite significant genetic distances (Chiaroni et al. 2009; de la Fuente et al. 2015; de Saint Pierre et al. 2012, 2008). These include craniofacial robustness characterized by pronounced frontal dimensions, enlarged orbits and nasal cavities, prominent mastoids and glabellar regions, and a marked occipital ridge (Hernández et al. 1997; Lahr 1995; Lalueza et al. 1997; Noback et al. 2011). Additional features include prognathism, lateral expansion of the zygomatic arches, a sloping forehead, and a non-globular elongated braincase. These traits are especially prominent in the southern Patagonian sample. These observations align with the notion proposed by Harvati and Weaver (2006) that the face and neurocranium are more susceptible to environmental influences. The cranial base presents fewer differences between the samples analyzed, supporting the idea of a conservative evolutionary skull region (Harvati and Weaver 2006; Menéndez 2018).

In terms of size, while prior studies focusing on cranial size (CS) have found limited correlations with climate (Harvati and Weaver 2006), this study reveals notable differences. Populations adapted to extreme cold exhibit larger CS, while individuals from warm and hot climates display a reduction

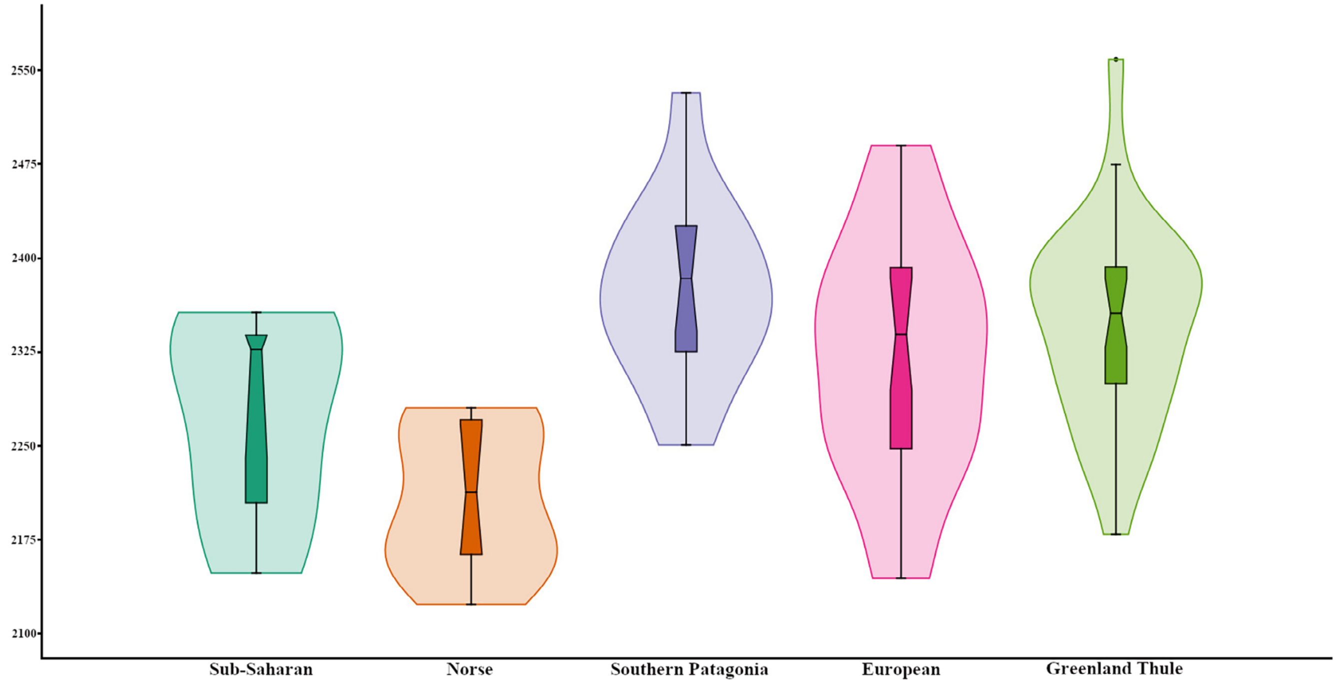

FIGURE 2 | Box-plot distributions of centroid size (CS) in mm.

FIGURE 3 | Screeplot depicting the % of variability explained on each PC of the whole PCA.

in size, consistent with Bergmann's rule (1847). However, the Norse sample presents a significant exception. Despite inhabiting a cold extreme region like Thule individuals, they possess smaller skulls. While craniofacial differences exist between populations related to climate, the Norse sample's deviation from Bergmann's rule highlights the complexity of environmental and genetic interactions. As Serrat et al. (2008) indicate, the degree of these interactions remains an unresolved issue. Furthermore, individuals of northern European origin exhibit smaller skull sizes than those inhabiting milder climates, challenging conventional expectations based exclusively on climatic models. Nevertheless, it is important to consider the potential influence of secular changes in craniofacial morphology when comparing size differences between Norse and European samples. Over the past two centuries, secular trends have been observed in the shape and size of the cranium, with an increase in dimensions reported in some Europeans samples (Weisensee and Jantz 2011; Buretić-Tomljanović et al. 2006; Jonke et al. 2007).

Hypothesis H2 is rejected due to clear differences between the Norse sample and the other two samples from extreme cold regions. Furthermore, Norse cranial size and shape are not intermediate between populations from extreme cold and those form mild or hot climates. Despite some similarities in shape between Norse and Thule Greenland individuals, particularly in facial height, significant differences in both size and shape exist. Distinct cultural and technological adaptations, as

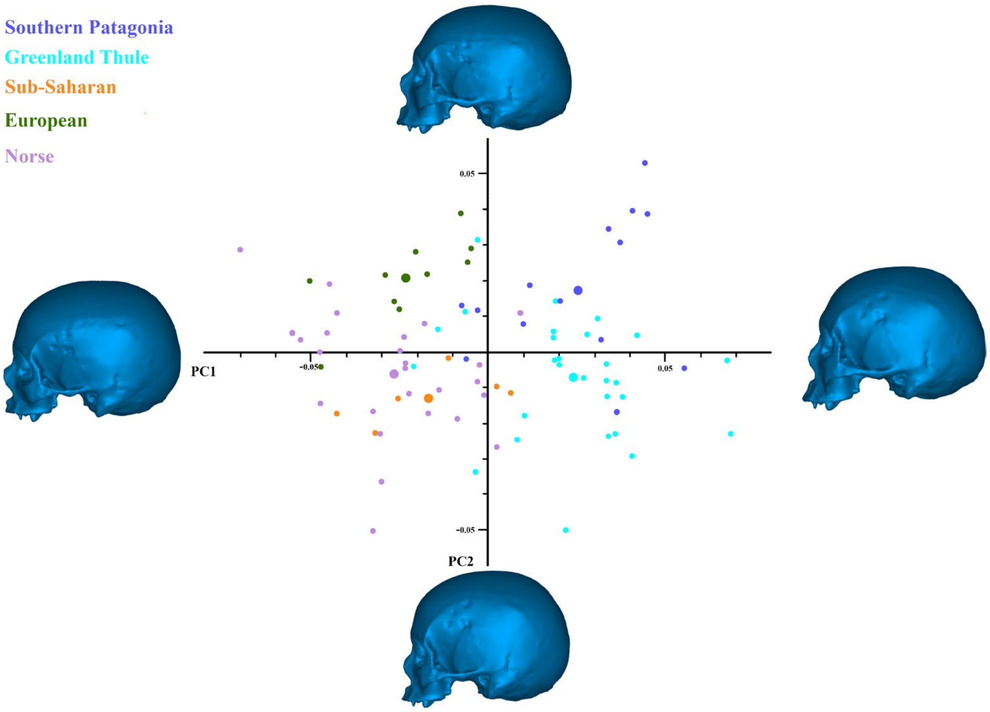

FIGURE 4 | PC1 versus PC2 plot in skull shape space. Surface warps show morphological variation associated with different parts of the morphospace. Big points. One for each sample, indicate the medium shape of each sample (Figure 9).

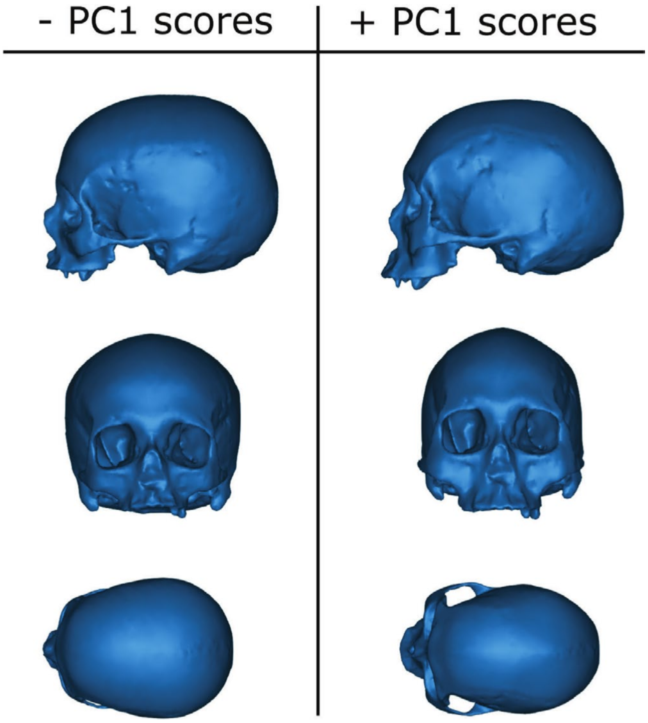

FIGURE 5 | Wireframes of extreme shapes were observed in PC1 in the lateral, frontal, and superior views.

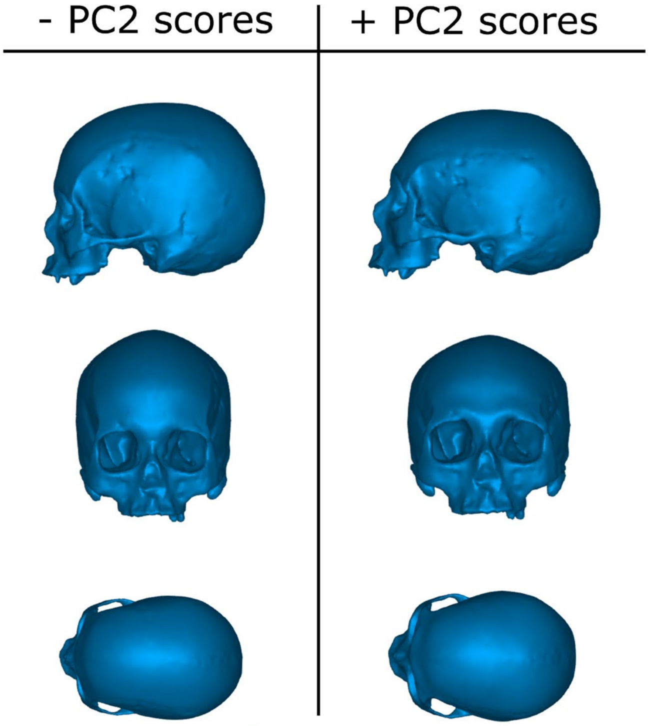

FIGURE 6 | Wireframes of extreme shapes were observed in PC2 in the lateral, frontal, and superior views.

proposed by some authors (Irving 1957; Scholander 1955, 1956), could account for these differences, potentially mitigating or even eliminating the influence of environmental and climatic factors. Among these modifications, the drastic diet change that occurred at the beginning of Greenland settlement period are noteworthy (Arneborg et al. 1999; Nelson et al. 2012). However, the Thule and southern Patagonian populations were culturally and technologically adapted to extreme cold climates with different subsistence strategies. Thule culture is characterized by marine hunter-gather lifestyle, in contrast with the terrestrial hunter-gatherers of Southern Patagonia. Regardless of these differences, they exhibit shape and size variations consistent with Bergmann's rule.

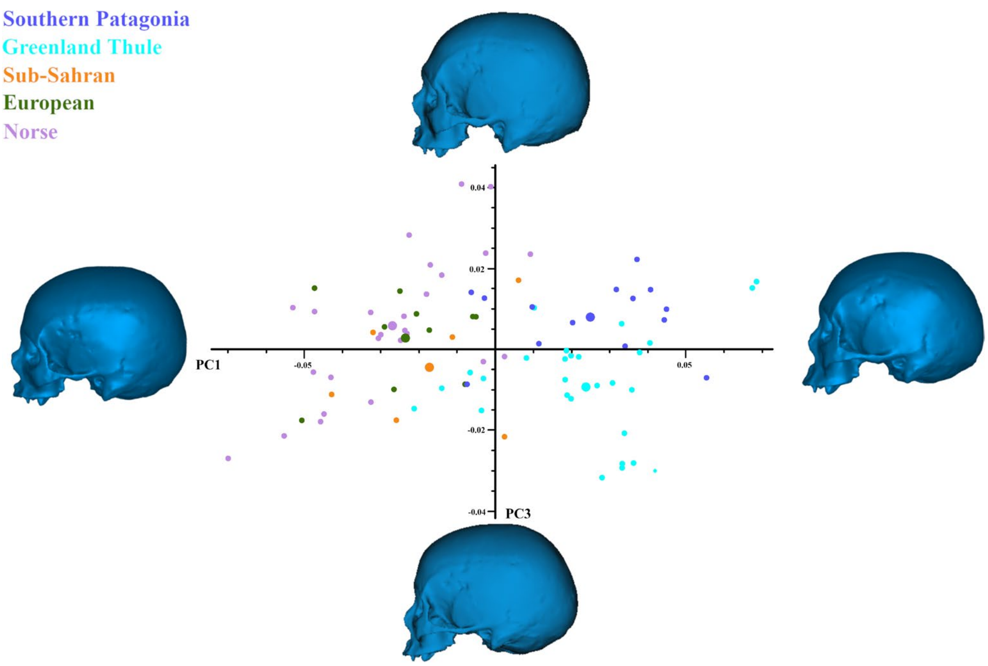

FIGURE 7 | PC1 versus PC3 plot in skull shape space. Surface warps show morphological variation associated with different parts of the morphospace. Big points. One for each sample. Indicate the medium shape of each sample (Figure 9).

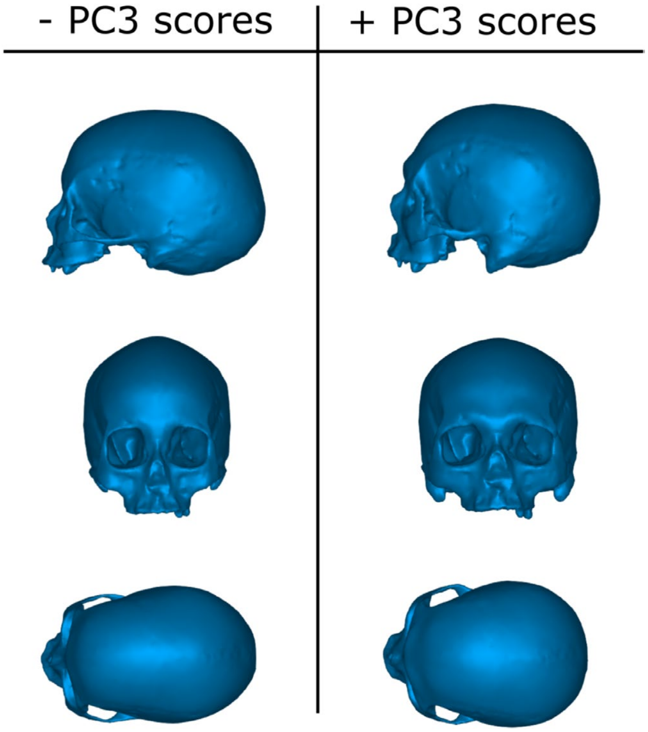

FIGURE 8 | Wireframes of extreme shapes observed in PC3 in lateral, fronta, and superior view.

Differences in Norse cranial size and shape compared to other cold-adapted populations may be explained by the European ancestry of Norse individuals (Margaryan et al. 2020; Plomp et al. 2023) and their proximity to Scandinavian and British populations. Norse individuals also show no similarities in rib size and shape with extreme cold samples (García-Martínez et al. 2018). However, these individuals present a ribcage similar to populations from extreme cold regions, characterized by "bell-shaped" ribcage with medium rib declination and variable width and depth (López-Rey, D'Angelo del Campo, et al. 2024; López-Rey, García-Martínez, et al. 2024a). This situation could be explained by environmental pressures. Extreme cold may induce bone modifications that occur at different rates across skeletal structures. For instance, ribcage might adapt earlier than the skull, suggesting varying sensitivity to environmental pressures. Therefore, it is possible to hypothesize that skeletal variations derived from environmental pressures are not homogeneous. Additionally, there may be chimeric phenotypical plasticity, where certain skeletal structures, such as ribcage, adapt to extreme cold, while others, like skull, retain ancestral characteristics. Despite the potential influence of environmental factors, other considerations must be considered. On one hand, the skull is a highly integrated and constrained anatomical structure (Enlow and Hans 1996; Lieberman et al. 2000), which may hinder adaptation or slow down the adaptation process. On the other hand, the human ribcage reconstruction method proposed by López-Rey, García-Martínez, et al. (2024b) has proven to be an efficient and reliable approach for reconstructing the full ribcage, producing results that closely resemble the originals. However, as the authors have noted, certain limitations exist. These include the skeletal material's preservation state, the researcher's anatomical considerations, and the ribcage's complex metameric composition. This structure consists of numerous interrelated elements, 24 ribs (12 on each side), and 12 dorsal vertebrae that articulate with one another, exhibiting intricate anatomical and functional correlation.

Phenotypic expression of cold adaptation requires a significant number of generations to manifest. While the results of this work do not specify the exact number of generations needed, they allow for a deeper exploration of this issue. In the case of extreme cold adaptation, Norse ribcage adapted to the "bell-shape"

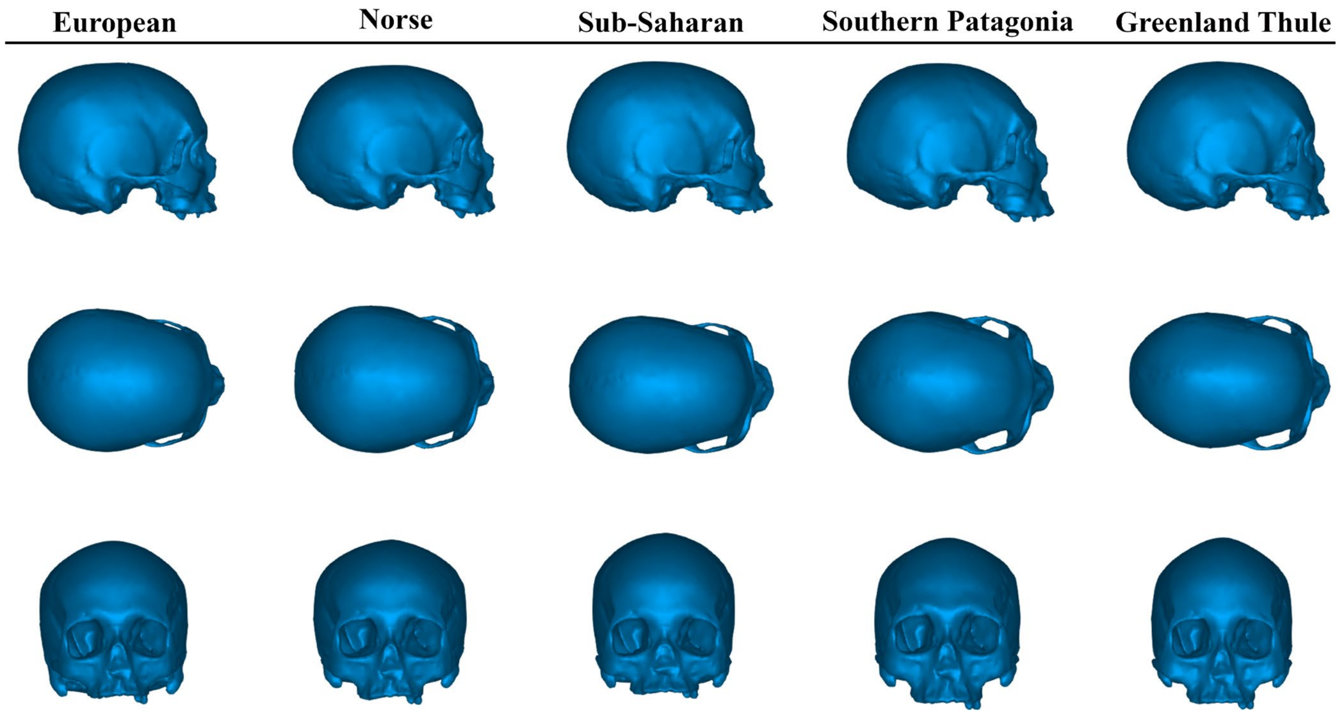

FIGURE 9 | The average shape of each sample in lateral, superior, and frontal view.

TABLE 4 | Procrustes distance between each group analyzed in this study.

	Sub-Saharan	European	Thule	Southern Patagonia	Norse
Sub-saharan	0	0.0379	0.0515	0.0638	0.0498
European	0.0379	0	0.0549	0.0602	0.034
Thule	0.0515	0.0549	0	0.0365	0.0584
Southern patagonia	0.0638	0.0602	0.0365	0	0.0531
Norse	0.0498	0.034	0.0584	0.0531	0

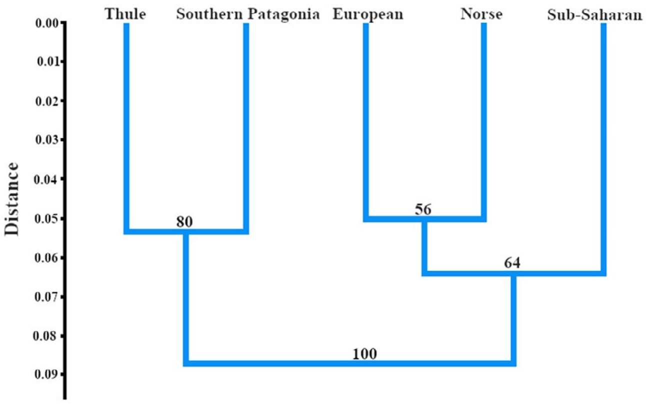

FIGURE 10 | Cluster analysis based on the Procrustes distance between each of the groups analyzed in this study.

characteristic of the extreme cold population in less than 300–400 years. Meanwhile, no appreciable morphological changes occurred in the skull, which preserved ancestral characteristics. We hypothesize that postcranial (at least trunk) structures show greater adaptability than the highly integrated and constrained craniofacial complex. Experimental data on animal models could be used to test this hypothesis. Another possibility involves genetic adaptation associated with the Norse morphological phenotype, akin to alternative strategies for cold adaptation observed in high-altitude and hypoxia environments. For example, Andean, Tibetan, and Ethiopian populations adapted to hypoxia employ different genetic strategies (Leonard 2018). Andean populations exhibit functional adaptations involving increased lung volume and diffusion capacity, as well as more efficient oxygen transport and diffusion to tissues, resulting in chest expansion and modifications in thoracic skeletal morphology, sternal and clavicular proportions, and rib areas and curvatures (Beall 2007; Frisancho 2013; Weinstein 2007). In contrast, Tibetan and Ethiopian populations possess specific genetic traits associated with high altitudes distinct from those found in Andean natives (Beall 2007; Frisancho 2013).

Finally, certain limitations should be acknowledged. Firstly, a larger number of individuals and populations would enhance the robustness of these findings, although this limitation is common in bioanthropological studies. Secondly, to further explore hypothesis H2, a sample spanning 500 years of Norse presence in Greenland would be necessary. Thirdly, future studies investigating environmental pressure should focus on limb bones, but fundamentally on specific facial areas that are sensitive to environmental variations, such as nasal anatomy (Harvati and Weaver 2006; Noback et al. 2011; Stansfield et al. 2021). Bone structure is remarkable because it is directly linked with ribcage and respiratory system. In addition, sexual dimorphism, while not the primary focus of this study, represents a fundamental biological factor that contributes to cranial morphological variability across human populations (Bastir et al. 2011). Previous research has demonstrated that differences in cranial size and shape between males and females can result from a range of factors including genetic and environmental pressures. Among these, climatic conditions have been suggested as a key determinant, with colder climates often associated with increased sexual dimorphism due to selective pressures related to thermoregulation, resource allocation, and survival strategies (Kleisner et al. 2021; Wells 2012). Although the present study does not specifically address sexual dimorphism, the patterns of morphological variation observed in our analyses may partially reflect underlying dimorphic trends, particularly when considering population-level responses to distinct climatic conditions. Future research should aim to disentangle the relative contributions of sexual dimorphism from other factors influencing cranial morphology.

5 | Conclusions

Environmental factors, particularly climate, significantly influence craniofacial morphology. The Thule Greenland and southern Patagonian populations display distinct craniofacial features, including a wider and larger face, a less globular skullcap, a sloping forehead, and a long, flat braincase. Additionally, their overall larger size aligns with Bergmann's rule. However, the Norse sample, while sharing some shape characteristics with the Thule sample, exhibits the smallest overall size, contradicting Bergmann's rule. This discrepancy suggests that Norse adaptation to extreme cold may have followed a different trajectory than other populations. Alternatively, more time or additional generations may be required for these adaptations to become evident. Further research is necessary to explore these possibilities and clarify the factors driving these differences.

Future studies could examine craniofacial morphological differences between Norse individuals who arrived in Greenland during the 10th century and those who left 500 years later. Such comparisons could shed light on potential morphological changes and the factors influencing them over time.

Author Contributions

Manuel Domingo D'Angelo del Campo: investigation (equal), software (equal), validation (equal), writing – original draft (lead), writing – review and editing (equal). **Gülkan Gökdoğan Aktepe:** data curation (lead), formal analysis (equal), investigation (equal), writing – review and editing (equal). **Markus Bastir:** conceptualization (equal), funding acquisition (equal), investigation (equal), methodology (equal), resources (equal), software (equal), supervision (equal), validation (equal), writing – review and editing (equal). **Daniel García Martínez:** conceptualization (equal), formal analysis (equal), funding acquisition (equal), investigation (lead), methodology (equal), project administration (lead), resources (equal), software (equal), supervision (lead), validation (equal), visualization (equal), writing – review and editing (equal).

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Data Availability Statement

The data that support this study are available from the corresponding author upon request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.