



OPEN Intracranial volume variation in Chinchorro mummies: a comparative study with pre-hispanic farmers and contemporary Chilean populations

Gonzalo M. Rojas-Costa^{1,2,3,15}✉, Verónica Silva-Pinto^{4,5,6,15}, Yanis Valenzuela⁷, María de la Iglesia-Vayá^{3,8,9}, José Molina-Mateo¹⁰, Domingo C. Salazar-García^{11,12}, Pedro A. Valdes-Sosa^{13,14} & Marcelo Gálvez^{1,2}

The Chinchorro culture inhabited the coastal Atacama Desert between 7,500 and 3,500 years BP, maintaining a hunter-gatherer-fisher lifestyle and practicing complex mortuary rituals. With the later adoption of agriculture, shifts in subsistence strategies and burial customs emerged. This study investigated long-term biological variation across three diachronic populations from northern Chile: Archaic-period Chinchorro individuals, pre-Hispanic agriculturalists, and contemporary Chileans. Using computed tomography (CT) and 3D reconstruction techniques, we analyzed intracranial volume (ICV) and estimated stature to assess morphological differences. The results show that both ICV and stature are significantly greater in the present-day Chilean population than in the pre-Hispanic groups. The average ICV was 1,321.26 cc in Chinchorro individuals, 1,336.57 cc in pre-Hispanic agriculturalists, and 1,481.22 cc in modern Chileans—representing a 12.05% increase between the earliest and most recent groups. Males and females exhibited 14.62% and 10.81% increases, respectively. Sexual dimorphism in the ICV was lower among agriculturalists (8.97%) than among Chinchorro (10.84%) and modern individuals (13.68%). Notably, the transition to agriculture did not result in significant changes in either ICV or stature. Instead, the marked increases observed in modern individuals have been associated primarily with improved nutrition, healthcare, and overall living conditions since the 20th century.

Keywords Chinchorro culture, Mummification, Intracranial volume, Archaic period, Mediterranean diet, Seafood-based diet, Anthropology

Intracranial volume (ICV) is a key metric for understanding human cranial morphology and its variation across time and populations. It has long been used to assess encephalization trends in human evolution, offering insights into brain growth and cognitive complexity in hominins relative to other species¹. ICV has also played

¹School of Medicine, Finis Terrae University, Santiago 7501015, Chile. ²Department of Radiology, Clínica las Condes, Santiago 7591046, Chile. ³Biomedical Imaging Unit and Artificial Intelligence FISABIO-CIPF, Foundation for the Promotion of Health and Biomedical Research of the Valencia Region, Valencia, Spain. ⁴Escuela de Antropología, Facultad de Ciencias Sociales e Historia, Universidad Diego Portales, Santiago, Chile. ⁵Anthropology Area, Museo Nacional de Historia Natural from Chile, Santiago, Chile. ⁶PhD Programme in Geography and History of the Mediterranean from Prehistory to the Modern Age, University of Valencia, Valencia, Spain. ⁷Volunteer Anthropology Area, Museo Nacional de Historia Natural from Chile, Santiago, Chile. ⁸General Directorate of Research and Innovation, Regional Ministry of Health in Valencia Region, Valencia, Spain. ⁹Biomedical Research Networking Center in Mental Health (CIBERSAM G23), Spanish National Network for Research in Mental Health, Madrid, Spain. ¹⁰Center for Biomaterials and Tissue Engineering, Universitat Politècnica de València, Valencia 46022, Spain. ¹¹Department of Prehistory, Archaeology and Ancient History, University of Valencia, Valencia, Spain. ¹²Department of Geological Sciences, University of Cape Town, Cape Town, South Africa. ¹³MOE Key Lab for Neuroinformation, The Clinical Hospital of Chengdu Brain Science Institute, University of Electronic Science and Technology of China, Chengdu, China. ¹⁴Cuban Center for Neuroscience, Havana, Cuba. ¹⁵These authors contributed equally to this work: Gonzalo M. Rojas-Costa and Verónica Silva-Pinto. ✉email: gonzalo.rojas.costa@gmail.com

an important role in analyzing sexual dimorphism in cranial structures^{2–6} and in identifying correlations between cranial capacity and neurological or developmental pathologies in clinical contexts^{7–11}. However, ICV remains a contested indicator, as its interpretation is affected by multiple biological and environmental factors.

In bioarcheological contexts, direct measurement of brain volume is no longer possible because of decomposition or mummification. ICV serves instead as a proxy to estimate brain size and assess morphological patterns associated with health, the environment, and cultural practices^{12–15}. However, how cranial volume has changed in response to long-term environmental, dietary, or genetic transitions in South America remains poorly understood. This gap is particularly relevant for comparing early coastal populations—such as the Archaic-period Chinchorro—with both later agricultural populations and contemporary mestizo groups in Chile.

The human skull is composed of anatomically and developmentally distinct regions—chiefly the neurocranium and viscerocranium—each with different embryological origins and functional roles^{16,17}. These regions exhibit varying degrees of morphological integration, shaped by functional pressures, genetic regulation, and spatial constraints during development^{18,19}. Such integration occurs in semi-independent modules that respond to both genetic and environmental influences²⁰. Cultural practices such as artificial cranial deformation (ACD), which are widely documented in Andean populations including Chinchorro and later agricultural groups, offer insight into how postnatal mechanical forces can reshape cranial morphology without necessarily altering the ICV^{21,22,22}. ACD was achieved by binding the heads of infants using boards, textiles or bands to produce culturally valued cranial shapes and is often interpreted as a marker of social identity or group affiliation^{23,24}.

The Chinchorro culture developed along the hyperarid Pacific coasts from Ilo in southern Peru to Antofagasta in northern Chile between 7,500 and 3,500 cal BP^{25–31} (Fig. 1). These groups practiced a complex form of hunter-gatherer-fisher subsistence and demonstrated a remarkable degree of technological and social innovation. Archaeological evidence reveals semisedentary settlements, specialized fishing equipment, and highly elaborate

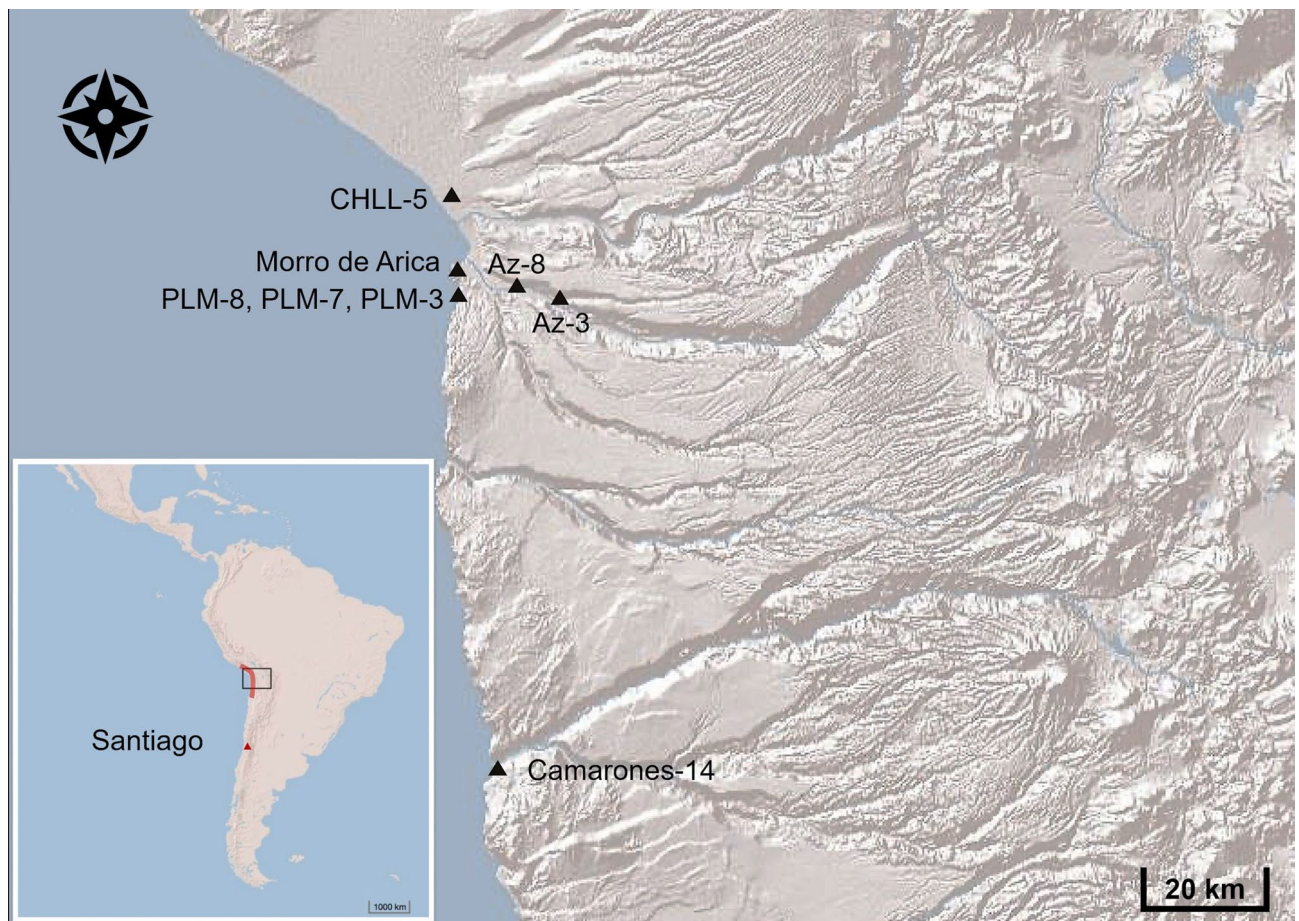


Fig. 1. Map showing the locations of archaeological sites associated with the Chinchorro culture (Morro de Arica, PLM-8, Camarones 14) and pre-Hispanic agricultural populations (CHLL-5, PLM-7, PLM-3, AZ-8, AZ-3) situated along the coast and lowland valleys of the Arica and Parinacota region, northern Chile. The inset on the left displays a map of South America highlighting the broader territorial extent of the Chinchorro culture (in red), with a zoom box indicating the enlarged area shown on the main map. The red triangle marks the location of Santiago, Chile. Maps were created using public domain sources provided by the Geological Mining Service of Argentina (SEGEMAR; <https://sigam.segemar.gov.ar/visor/>; <https://sigam.segemar.gov.ar/>; <https://creativecommons.org/licenses/by-nc-nd/4.0/>) and later modified using Adobe Photoshop (Adobe Systems Incorporated, CA, USA).

mortuary traditions. Most notably, Chinchorro is recognized for having developed the earliest known artificial mummification techniques, involving complete bodily disassembly and reassembly, anatomical reconstruction, and detailed external treatments using clay, pigments, and other materials^{32–37}. Their subsistence economy relies primarily on marine resources such as fish, mollusks, and marine mammals, which provide stable and nutrient-rich dietary inputs.

Beginning around 4,000 cal BP, archaeological and isotopic data indicate that these coastal populations underwent gradual but significant transformations through sustained interactions with agricultural groups from adjacent inland valleys^{38–41}. These contacts led to changes in subsistence strategies, with increasing incorporation of cultivated C₃ and C₄ plants and domesticated animals. This dietary shift—from protein-rich marine sources to more carbohydrate-dense agricultural products—was accompanied by broader changes in social organization, mortuary customs, and patterns of mobility. The decline of Chinchorro mummification practices and the emergence of new ideological expressions in funerary contexts mark this cultural transition.

The adoption of agriculture during the Holocene has been widely associated with reductions in dietary protein intake, decreases in adult stature, greater disease burdens, and notable changes in cranial morphology^{42–44}. In South America, the forager-to-farmer transition between ~ 10,000 and 6,000 years ago led to significant morphological differentiation among human populations over relatively short timescales⁴⁵. This evidence underscores the role of developmental plasticity in shaping biological forms in response to changing environmental and dietary conditions, supporting a model of rapid and context-dependent morphological evolution rather than one driven solely by neutral genetic drift⁴⁶.

In parallel with these biological changes, archaeological evidence indicates that the practice of intentional cranial modification intensified following the adoption of agriculture. While annular (circular) forms of cranial deformation were already present among Chinchorro individuals, later agricultural populations exhibited an increasing diversity of modification styles, including various annular and tabular forms^{47–49,49}. These practices likely served as visual markers of social identity, group affiliation, and status, reflecting the growing cultural complexity during this period of economic and ideological transformation⁵⁰.

The present-day Chilean population is predominantly mestizo, reflecting centuries of admixture between Indigenous American, European (primarily Spanish), and African ancestries^{51–53}. Over time, modern populations have undergone substantial changes in diet, urbanization, healthcare access, education, and mobility—factors that collectively shape biological development through epigenetic mechanisms and developmental plasticity. These transformations have been accompanied by a marked positive secular trend in adult stature, particularly over the last five decades, reflecting improvements in nutrition, disease control, and overall living conditions.

The objective of this study is to investigate differences in cranial volume and morphology among individuals from three temporally and culturally distinct populations¹: the Chinchorro of the Middle (7,500–6,000 cal BP) and Late Archaic periods (6,000–4,000 cal BP)²; pre-Hispanic agricultural groups from the Formative (4,000–1,500 cal BP), Middle (1,500–900 cal BP), and Late Intermediate periods (900–600 cal BP) in the Arica region; and³ the contemporary Chilean mestizo population. The goal of this study is to assess the impact of long-term historical, environmental, and dietary changes on cranial size and shape.

By evaluating the relationships among ICV, sex, and stature, we aim to understand how these factors may influence cranial development across different ecological and cultural settings. Advanced computed tomography (CT) imaging was employed to measure and compare ICVs in a nondestructive manner, enabling high-resolution volumetric analysis of both mummified and skeletal remains.

We propose the working hypothesis that ICV is directly associated with both sex and body height, with the latter being modulated by dietary and genetic factors. This implies that nutritional conditions may indirectly influence cranial volume through their impact on overall somatic growth. By comparing individuals from the Chinchorro, agricultural, and modern Chilean populations, we aim to evaluate whether diachronic variation in diet and environment contributed to measurable differences in ICV and cranial morphology.

Understanding the variation in ICV across these populations and periods is essential for interpreting how biological and environmental factors interact to shape the human cranial form. This study presents a systematic approach for quantifying and comparing ICVs via high-resolution CT imaging, contributing to broader discussions of morphological diversity and population history. By integrating data from Archaic hunter-gatherer-fisher populations, later pre-Hispanic agricultural societies, and present-day Chileans, this study contributes to broader discussions on morphological diversity, biocultural adaptation, and the long-term consequences of dietary, environmental, and sociocultural transformation in the South Central Andes.

Materials and methods

CT scans were performed on 68 Chinchorro skulls from the Max Uhle ($n = 62$)⁵⁴, Camarones 14 Schiappacasse and Niemeyer ($n = 5$)³¹, and Blanco Encalada ($n = 1$) collections housed at the National Museum of Natural History of Chile. The individuals were between 19 and 52.5 years of age (mean age 38.0 years); 33 skulls were from females, and 35 skulls were from males (Fig. 2a; Table 1). Additionally, nine pre-Hispanic agricultural individuals were scanned (Blanco Encalada collection, mean age 31.78 years, 21.00–37.50.00.50 years) (Fig. 2b; Table 2). The scans were acquired with a Siemens SOMATOM Definition AS CT device (voxel size: $0.6 \times 0.6 \times 0.6$ mm, H70h). As part of the applied methodology, the biological age and sex of the individuals whose skulls were scanned were determined according to standard anthropological indicators^{55–57}.

The state of preservation of the Chinchorro skulls was defined in terms of whether the remains were skeletonized, mummified, or semiskeletonized, along with the degree of completeness according to Buikstra and Ubelaker (1994, 57) as follows: Grade 1 indicates that the piece (bone or tissue) was complete and stable and showed no alterations; Grade 2 means that the piece was complete but had localized areas of erosion at the ends or edges; Grade 3 describes a piece that was fragile or fragmented, with initial cracking of the cortical tissue,

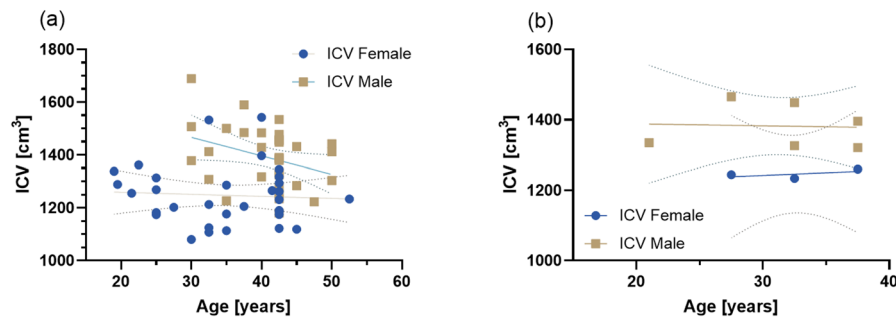


Fig. 2. (a) Intracranial volumes of the skulls of Chinchorro individuals, (b) Intracranial volumes of Agricultural individuals.

extensive areas of erosion, and exposure of the spongy bone; and Grade 4 signifies that the piece was highly fragmented and friable, with the cortical tissue extensively cracked and tending to powder.

Some Chinchorro skulls exhibited fractures, discontinuities, or openings on the internal surface, mainly in the frontal, frontotemporal, and temporal regions. To generate the intracranial meshes, we used the Wrap Solidify module, setting an appropriate threshold that automatically seals the foramen magnum, orbital cavities, and fracture gaps in some skulls. This process facilitated accurate calculation of the ICV (Fig. 3⁵⁸). Given the application of this method, we consider that any errors in the ICV estimation were minimal. Furthermore, the CT acquisitions were performed with a voxel size of $0.6 \times 0.6 \times 0.6$ mm, providing high resolution and ensuring that potential inaccuracies in the reconstruction of the mummified skulls were negligible⁵⁹.

The Chinchorro Max Uhle and Blanco Encalada samples consisted solely of skulls; therefore, sex was determined on the basis of an analysis of cranial sexual dimorphism (the sexes of all Chinchorro individuals could be determined definitively with the exception of one, a possible female), whereas age was estimated according to the palatine sutures^{60–62}. In contrast, the Camarones 14 collection includes complete skeletons, allowing age and sex to be determined through multiple methods^{55,63–69} (Table 1).

Chinchorro and pre-Hispanic agricultural individuals were compared with current Chilean individuals. These individuals were Chilean patients of both sexes (46 females and 37 males) aged between 18 and 85 years (average 40.3 years); none of these 83 individuals had pathological findings, and all underwent brain computed tomography (Toshiba Aquilion Prime, Siemens SOMATOM Definition Flash, $0.5 \times 0.5 \times 0.5$ mm, $0.5 \times 0.5 \times 0.7$ mm). The data associated with the explanatory variables were obtained from the data from each scan (Fig. 4; Table 3).

This study was conducted in accordance with relevant ethical regulations for research involving both modern and archaeological human remains. For the archaeological human remains (Chinchorro and agricultural populations), the research project was approved and funded by the Servicio Nacional del Patrimonio Cultural de Chile (National Heritage Service of Chile) after formal evaluation by its Comité de Ética en la Investigación (Ethics Committee for Research; <https://www.investigacion.patrimoniocultural.gob.cl/comite-de-etica-en-la-investigacion>). This committee ensures that projects involving human remains from museum collections and archaeological sites meet ethical and legal standards, especially in collaboration with other public institutions.

In this study, noninvasive methods, such as CT scanning and image analysis, were prioritized to minimize the impact on the integrity of the remains. Additionally, the research team maintains ongoing engagement with local communities through scientific outreach activities and transparency regarding the research process. In particular, we acknowledge the collaboration and support of Fundación Chinchorro Marka (Chinchorro Marka Cultural Corporation), the organization responsible for the UNESCO World Heritage Chinchorro sites.

The Clínica las Condes institutional review board (Comité de Ética de la Investigación de Clínica las Condes) approved this retrospective study and waived the requirement for written informed consent. No surveys were performed that could compromise the identity or personal information of the included Chilean individuals. The 83 sets of CT images of the current Chileans were anonymized; only information on age and sex was retained. All methods were performed in accordance with the relevant guidelines and regulations.

The inclusion criteria were as follows:

- The presence of brain CT scans and a diagnosis of “without pathological findings”;
- Male or female sex; and.
- Chilean patients.

The exclusion criteria were as follows:

- Age younger than 18 years or older than 85 years;
- Pathologies and/or traumas significantly altering the cranial vault; and.
- Cranial surgeries that altered the original bone structure and/or brain tissue.

To calculate the ICVs of the skulls of the Chinchorro and pre-Hispanic agricultural individuals, 3D Slicer version 4.11.0–2020.0-04–27 was used⁷⁰; (www.slicer.org). The skull was segmented using the “Segment Editor” module with a threshold of 700 to 2000 Hounsfield units. The cranial cavity was subsequently analyzed with the “Wrap

Code MNHN	Site	Collection	Period	Mean age (± 3 years)	Sex	State of conservation	ICV [cm ³]
2016.2.116	Morro de Arica	Chinchorro Max Uhle	Late Archaic	52.5	F	Skeletonized, grade 2	1233.92
2016.2.122	Morro de Arica	Chinchorro Max Uhle	Late Archaic	45.0	M	Skeletonized, grade 2	1431.51
2016.2.126	Morro de Arica	Chinchorro Max Uhle	Late Archaic	40.0	M	Skeletonized, grade 2	1428.23
2016.2.127	Morro de Arica	Chinchorro Max Uhle	Late Archaic	32.5	F	Skeletonized, grade 2	1532.05
2016.2.128	Morro de Arica	Chinchorro Max Uhle	Late Archaic	45.0	F	Skeletonized, grade 2	1118.83
2016.2.120	Morro de Arica	Chinchorro Max Uhle	Late Archaic	50.0	M	Semimummified, grade 2	1303.7
2016.2.129	Morro de Arica	Chinchorro Max Uhle	Late Archaic	50.0	M	Semimummified, grade 2	1442.43
2016.2.130	Morro de Arica	Chinchorro Max Uhle	Late Archaic	35.0	M	Skeletonized, grade 2	1500.06
2016.2.132	Morro de Arica	Chinchorro Max Uhle	Late Archaic	32.5	M	Skeletonized, grade 2	1308.03
2016.2.133	Morro de Arica	Chinchorro Max Uhle	Late Archaic	32.5	F	Skeletonized, grade 3	1107.66
2016.2.134	Morro de Arica	Chinchorro Max Uhle	Late Archaic	37.5	M	Semimummified, grade 1	1589.44
2016.2.135	Morro de Arica	Chinchorro Max Uhle	Late Archaic	37.5	F	Skeletonized, grade 3	1205.95
2016.2.136	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	F	Skeletonized, grade 2	1231.96
2016.2.137	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	F	Skeletonized, grade 2	1262.51
2016.2.140	Morro de Arica	Chinchorro Max Uhle	Late Archaic	47.5	M	Skeletonized, grade 2	1223.11
2016.2.141	Morro de Arica	Chinchorro Max Uhle	Late Archaic	32.5	F	Skeletonized, grade 2	1212.87
2016.2.142	Morro de Arica	Chinchorro Max Uhle	Late Archaic	45.0	M	Skeletonized, grade 2	1284
2016.2.143	Morro de Arica	Chinchorro Max Uhle	Late Archaic	37.5	M	Skeletonized, grade 2	1484.2
2016.2.144	Morro de Arica	Chinchorro Max Uhle	Late Archaic	32.5	F	Skeletonized, grade 2	1124.74
2016.2.145	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	F	Skeletonized, grade 3	1190.37
2016.2.148	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 3	1335.13
2016.2.150	Morro de Arica	Chinchorro Max Uhle	Late Archaic	30.0	F	Skeletonized, grade 3	1080.1
2016.2.152	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 1	1534.33
2016.2.155	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 3	1325.31
2016.2.156	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 2	1390.14
2016.2.157	Morro de Arica	Chinchorro Max Uhle	Late Archaic	25.0	F	Skeletonized, grade 2	1313.44
2016.2.159	Morro de Arica	Chinchorro Max Uhle	Late Archaic	40.0	M	Skeletonized, grade 2	1317.43
2016.2.160	Morro de Arica	Chinchorro Max Uhle	Late Archaic	35.0	M	Semimummified, grade 2	1227.02
2016.2.162	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 3	1386.69
2016.2.163	Morro de Arica	Chinchorro Max Uhle	Late Archaic	25.0	F	Semimummified, grade 3	1174.52
2016.2.165	Morro de Arica	Chinchorro Max Uhle	Late Archaic	27.5	F	Skeletonized, grade 3	1202.33
2016.2.167	Morro de Arica	Chinchorro Max Uhle	Late Archaic	50.0	M	Skeletonized, grade 2	1411.37
2016.2.168	Morro de Arica	Chinchorro Max Uhle	Late Archaic	25.0	F	Skeletonized, grade 2	1182.19
2016.2.171	Morro de Arica	Chinchorro Max Uhle	Late Archaic	22.5	F	Skeletonized, grade 3	1362.53
2016.2.173	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 2	1180.55
2016.2.174	Morro de Arica	Chinchorro Max Uhle	Late Archaic	25.0	F	Skeletonized, grade 2	1268.91
2016.2.175	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	F	Semimummified, grade 2	1317.73
2016.2.176	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 2	1253.33
2016.2.177	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	F	Skeletonized, grade 3	1122.13
2016.2.178	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 2	1458.04
2016.2.179	Morro de Arica	Chinchorro Max Uhle	Late Archaic	35.0	F	Skeletonized, grade 2	1286.13
2016.2.180	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 2	1379.33
2016.2.181	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 3	1455.56
2016.2.183	Morro de Arica	Chinchorro Max Uhle	Late Archaic	35.0	F	Skeletonized, grade 1	1113.36
2016.2.184	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 2	1277.74
2016.2.186	Morro de Arica	Chinchorro Max Uhle	Late Archaic	30.0	M	Skeletonized, grade 2	1378.16
2016.2.187	Morro de Arica	Chinchorro Max Uhle	Late Archaic	30.0	M	Skeletonized, grade 2	1506.78
2016.2.188	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	F	Skeletonized, grade 2	1175.16
2016.2.189	Morro de Arica	Chinchorro Max Uhle	Late Archaic	35.0	F	Skeletonized, grade 2	1177.1
2016.2.190	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	F	Skeletonized, grade 2	1294.3
2016.2.192	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	F	Skeletonized, grade 2	1186.47
2016.2.193	Morro de Arica	Chinchorro Max Uhle	Late Archaic	40.0	M	Skeletonized, grade 2	1483.82
2016.2.194	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 3	1383.56
2016.2.195	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 2	1477.52
2016.2.196	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 3	1277.67
2016.2.199	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Semimummified, grade 3	1447.72
Continued							

Code MNHN	Site	Collection	Period	Mean age (± 3 years)	Sex	State of conservation	ICV [cm ³]
2016.2.201	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Skeletonized, grade 2	1235.28
2016.2.204	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	F	Semimummified, grade 2	1345.29
2016.2.205	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	F	Skeletonized, grade 3	1262.08
2016.2.206	Morro de Arica	Chinchorro Max Uhle	Late Archaic	19.0	F	Semimummified, grade 2	1338.03
2016.2.207	Morro de Arica	Chinchorro Max Uhle	Late Archaic	40.0	F	Skeletonized, grade 3	1396.88
2016.2.209	Morro de Arica	Chinchorro Max Uhle	Late Archaic	42.5	M	Semimummified, grade 2	1454.05
2016.2.253	Camarones 14	Schiappacasse and Niemeyer	Middle Archaic	21.5	F	Skeletonized, grade 2	1255.89
2016.2.254	Camarones 14	Schiappacasse and Niemeyer	Middle Archaic	41.5	F	Skeletonized, grade 2	1265.99
2016.2.258	Camarones 14	Schiappacasse and Niemeyer	Middle Archaic	32.5	M	Semimummified, grade 2	1412.53
2016.2.267	Camarones 14	Schiappacasse and Niemeyer	Middle Archaic	40.0	F	Skeletonized, grade 3	1542.11
2017.2.670	PLM-8	Blanco Encalada	Middle Archaic	19.5	F	Semi mummified, grade 3	1289.03
2017.2.676	Camarones 14	Schiappacasse and Niemeyer	Middle Archaic	30.0	M	Semimummified, grade 2	1689.14

Table 1. Chinchorro skulls from the Museo Nacional de historia natural (MNHN), including code, site of origin, name of collection, chronological period, mean age, sex, state of conservation, and intracranial volume (ICV).

Code MNHN	Site	Collection	Period	Mean age (± 3 years)	Sex	State of conservation	ICV [cm ³]
2017.2.661	AZ-3	Blanco Encalada	Middle Period	32.5	M	Skeletonized, grade 2	1448.61
2017.2.662	AZ-3	Blanco Encalada	Middle Period	37.5	F	Skeletonized, grade 2	1259.58
2017.2.663	AZ-3	Blanco Encalada	Middle Period	32.5	F	Skeletonized, grade 2	1233.65
2017.2.664	PLM-3	Blanco Encalada	Late intermediate period	32.5	M	Skeletonized, grade 2	1326.43
2017.2.665	PLM-3	Blanco Encalada	Late intermediate period	27.5	M	Skeletonized, grade 2	1465.10
2017.2.668	PLM-7	Blanco Encalada	Formative period	27.5	F	Skeletonized, grade 2	1244.48
2017.2.669	PLM-7	Blanco Encalada	Formative period	37.5	M	Skeletonized, grade 2	1395.76
2017.2.673	CHLL-5	Blanco Encalada	Late intermediate period	37.5	M	Skeletonized, grade 2	1320.88
2017.2.882	AZ-8	Blanco Encalada	Late intermediate period	21.0	M	Mummified, grade 1	1334.68

Table 2. Agricultural individuals skulls from the Museo Nacional de historia natural (MNHN), including code, site of origin, name of collection, chronological period, mean age, sex, state of conservation, and intracranial volume (ICV).

Solidify” segment editor tool⁵⁸; (<https://github.com/sebastianandress/Slicer-SurfaceWrapSolidify>) using the options “largest cavity” and “split cavities” and setting the cavity size to 30 mm to prevent the segmentation from “leaking” to other regions through small discontinuities in the bone. The default values were used for advanced parameters: “Smoothing factor”, 0.20; “Oversampling”, 1.50x; and “Number of iterations”, 6. Using a similar algorithm, the ICVs of the skulls of contemporary Chilean individuals were obtained using the bone window of the acquired CT.

“Wrap Solidify” is a 3D Slicer module that can fill in internal holes in a segmented image region or retrieve the largest cavity inside a segmentation automatically. To determine the ICV of the skull, “Wrap Solidify” automatically closes the meshes of the cranial cavity in the foramen magnum; orbital cavity bones; and frontal, temporal, parietal, or occipital bones⁵⁸; (<https://github.com/sebastianandress/Slicer-SurfaceWrapSolidify>; <https://lassoan.github.io/SlicerSegmentationRecipes/CTSkullStripping>).

To calculate the brain volume of the skulls of the current Chilean individuals, the CT soft tissue window (J30s) was used to segment the skull in the “Segment Editor” module, with a threshold ranging from 70 to 2000 Hounsfield units in 3D Slicer software⁷⁰; (www.slicer.org). The “WrapSolidify” segment editor tool⁵⁸; (<https://github.com/sebastianandress/Slicer-SurfaceWrapSolidify>) was subsequently used with the same parameters and options as above. The brain was then segmented using a cranial cavity mask. To increase the signal-to-noise ratio, a $3 \times 3 \times 3$ pixel median filter was applied. By setting the threshold to between 15 and 80, the brain (including the white matter, cortex, cerebellum and brainstem but excluding the cerebrospinal fluid) was subsequently obtained.

Since the remains of the individuals from the Morro de Arica site and Blanco Encalada collection site included only the skulls and to complement the information obtained from the Camarones-14 (CAM14) site, individuals from the Camarones 15 (CAM15) and Morro 1/6 (Mo1/6) sites, which also correspond to the Chinchorro population, were assessed. In total, 50 individuals from Chinchorro contexts were included, comprising 28 females and 22 males (see Supplementary Table 1S). Additionally, for comparative purposes, individuals from agricultural populations were included, specifically from the AZ-70, AZ-14, and AZ-75 archaeological sites (Fig. 1), totaling 47 individuals—24 females and 23 males (see Supplementary Table 2S). To estimate stature,

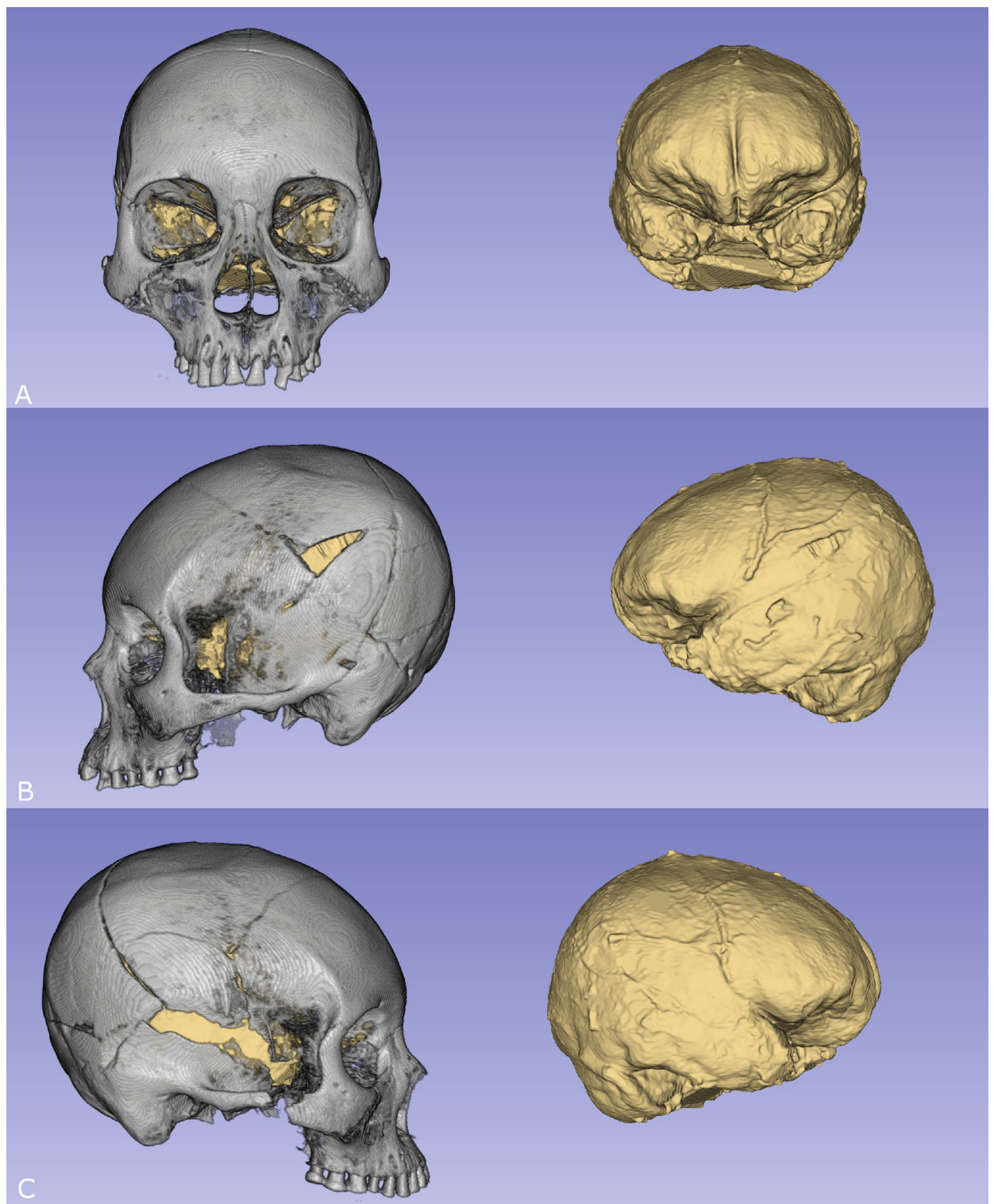


Fig. 3. Some Chinchorro skulls had fractures, discontinuities, or holes in the interior, mainly in the frontal, frontotemporal, and temporal regions (see the Supplementary Video).

the physiological lengths of the femurs and tibiae were measured, and the Genovés regression formulas were applied⁷¹.

According to Hasgall et al.^{72–75}, the average density of the brain is 1.046 gr/cc. Since we were analyzing the same species, the anatomically modern human (*Homo sapiens sapiens*), the same brain density value formula was used for the Chinchorro samples and agricultural populations.

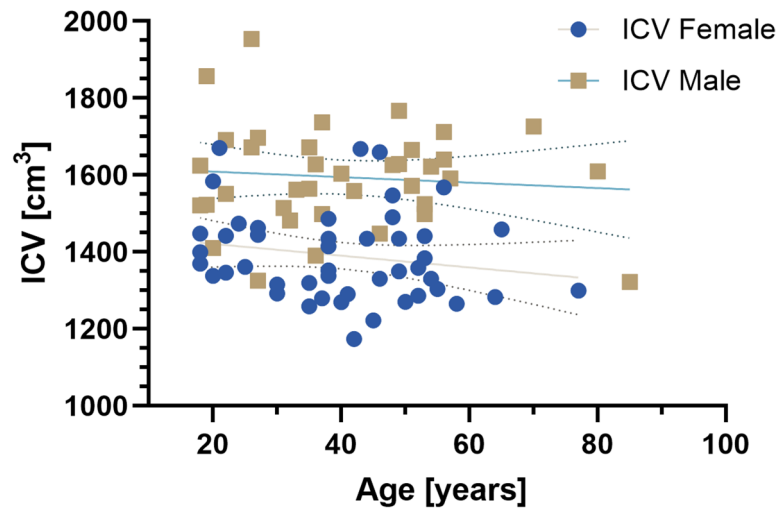


Fig. 4. Intracranial volumes of current Chilean individuals.

To reconstruct the dietary patterns in both the Chinchorro and agricultural populations, we used stable isotope data compiled in the South American Archaeological Isotopic Database (SAAID; 78). This database includes contributions from various authors who have conducted isotopic analyses in the Arica region, covering key archaeological sites located along the coast and valleys. The dataset incorporates samples from different cultural periods recognized in the prehistoric sequence of Arica. For this study, we selected individuals for whom both $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}_{\text{collagen}}$ values were available. These data (see Dataset S1) provided a comparative isotopic framework to assess dietary differences between marine-based and mixed terrestrial subsistence strategies across time and ecological zones.

Results

The ICVs of the Chinchorro skulls, agricultural populations, and Chilean individuals are shown in Tables 1, 2 and 3 and are visualized in Figs. 2a and b and 4, and the brain volumes (BVs; including the white matter, cortex, brainstem, and cerebellum) of the Chilean individuals are shown in Table 3 and are visualized in Fig. 5a and b. ANOVA revealed a significant main effect of group on the ICV, indicating that the ICVs of the Chinchorro individuals and agricultural populations significantly differed from those of the Chilean individuals. Similar results were found when the ICVs of Chinchorro individuals, agricultural populations and Chilean individuals were compared according to sex (Fig. 6a, b and c).

Using linear regression (GraphPad Prism 10.5.0 software), the ICVs of the female and male Chinchorro individuals were calculated as follows:

$$ICV_F = -0.7754 * Age + 1274.83; R^2 = 0.0038, \text{ Age in years} \quad (1)$$

$$ICV_M = -6.9957 * Age + 1676.48; R^2 = 0.1098, \text{ Age in years} \quad (2)$$

The age used in Eqs. (1) and (2) corresponds to the average of the estimated age range for each Chinchorro individual ("Mean Age" column in Table 1).

Additionally, via linear regression, the ICVs of the female and male agricultural individuals were calculated as follows:

$$ICV_F = 1.5100 * Age + 1196.83; R^2 = 0.3361, \text{ Age in years} \quad (3)$$

$$ICV_M = -0.5430 * Age + 1398.97.48; R^2 = 0.0029, \text{ Age in years} \quad (4)$$

Using linear regression, the ICVs of the Chilean individuals were calculated as follows:

$$ICV_F = -1.5344 * Age + 1451.86; R^2 = 0.0348, \text{ Age in years} \quad (5)$$

$$ICV_M = -0.7120 * Age + 1623.20; R^2 = 0.0083, \text{ Age in years} \quad (6)$$

Similarly, the BVs of the Chilean individuals were calculated as follows:

$$BV_F = -2.1735 * Age + 1329.98; R^2 = 0.0858, \text{ Age in years} \quad (7)$$

$$BV_M = -2.0754 * Age + 1498.19; R^2 = 0.0753, \text{ Age in years} \quad (8)$$

Patient	Sex	Age	ICV [cm ³]	BV [cm ³]
P1	F	77	1299.97	1114.73
P2	F	58	1265.12	1161.93
P3	F	53	1441.61	1219.3
P4	F	35	1258.47	1150.99
P5	F	18	1399.40	1272.25
P6	F	18	1447.85	1327.41
P7	F	38	1351.68	1172.2
P8	F	48	1547.12	1413.05
P9	F	18	1369.27	1246.84
P10	F	45	1221.84	1114.2
P11	F	40	1269.95	1122.86
P12	F	24	1473.43	1331.44
P13	F	52	1358.39	1241.23
P14	F	65	1458.97	1303.58
P15	F	42	1174.07	1040.88
P16	F	35	1319.90	1181.69
P17	F	22	1346.27	1237.36
P18	F	49	1349.65	1166.96
P19	F	25	1360.98	1220.39
P20	F	27	1444.82	1299.63
P21	F	43	1667.78	1510.6
P22	F	46	1659.67	1409.36
P23	F	37	1279.43	1140.25
P24	F	46	1330.57	1202.28
P25	F	30	1315.47	1195.51
P26	F	38	1414.97	1242.95
P27	F	55	1304.10	1149.62
P28	F	22	1442.40	1323.01
P29	F	38	1485.89	1345.54
P30	F	56	1567.83	1385.71
P31	F	21	1670.27	1476.34
P32	F	27	1462.53	1315.35
P33	F	20	1583.59	1411.82
P34	F	48	1490.56	1329.32
P35	F	44	1434.77	1262.94
P36	F	53	1383.48	1229.26
P37	F	54	1330.62	1211.1
P38	F	49	1434.36	1280.56
P39	F	64	1282.50	1101.13
P40	F	38	1434.22	1308.23
P41	F	52	1286.11	1120.09
P42	F	30	1292.06	1122.76
P43	F	41	1290.39	1171.47
P44	F	50	1270.66	1143.89
P45	F	38	1337.81	1217.63
P46	F	20	1337.88	1214.51
P47	M	56	1711.82	1510.9
P48	M	18	1521.41	1374.59
P49	M	53	1498.53	1359.21
P50	M	26	1672.26	1525.48
P51	M	27	1325.14	1204.03
P52	M	53	1524.86	1343.51
P53	M	27	1697.25	1525.2
P54	M	49	1767.07	1622.06
P55	M	70	1726.49	1519.16
P56	M	35	1671.70	1510.89
Continued				

Patient	Sex	Age	ICV [cm ³]	BV [cm ³]
P57	M	54	1622.49	1462.29
P58	M	37	1736.91	1568.58
P59	M	20	1410.74	1304.33
P60	M	56	1640.79	1410.2
P61	M	36	1627.57	1476.18
P62	M	40	1603.93	1415.34
P63	M	48	1626.21	1403.84
P64	M	49	1628.68	1348.26
P65	M	46	1447.76	1289.87
P66	M	36	1390.36	1233.78
P67	M	33	1561.70	1416.24
P68	M	80	1609.80	1352.47
P69	M	31	1514.64	1395.31
P70	M	51	1572.02	1407.77
P71	M	26	1953.89	1715.87
P72	M	57	1591.56	1411.52
P73	M	19	1523.08	1373.51
P74	M	35	1564.27	1409.99
P75	M	37	1498.72	1315.43
P76	M	32	1481.89	1309.28
P77	M	42	1558.41	1387.57
P78	M	22	1551.04	1352.19
P79	M	22	1690.91	1544.85
P80	M	19	1857.11	1668.75
P81	M	85	1322.24	1042.42
P82	M	18	1624.68	1403.9
P83	M	51	1665.39	1413.46

Table 3. Data from current Chilean individuals: sex (M: male, F: female); age; and intracranial volume (ICV) and intracerebral volume (BV), both in cm³.

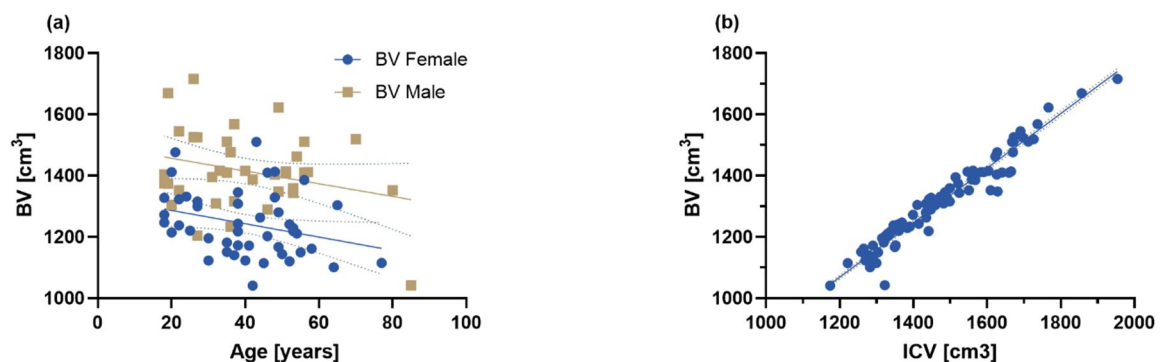


Fig. 5. (a) Brain volumes of current Chilean individuals, (b) Intracranial volume versus brain volume for Chilean individuals.

Using linear regression (GraphPad Prism 10.5.0 software), the following relationship between the BV and ICV was obtained:

$$BV = 0.8904 * ICV; R^2 = 0.9993 \quad (9)$$

with an intercept of 0.

Using Eq. (9) and the brain density value, the brain volume and weight of each Chinchorro and agricultural individual were estimated (Tables 4 and 5).

As shown in the formulas above, the BV and ICV were linearly correlated ($R^2 = 0.9993$; see Fig. 5a), allowing the estimation of the volume and brain weight (BW) of each body. According to Student's t test, the ICVs of

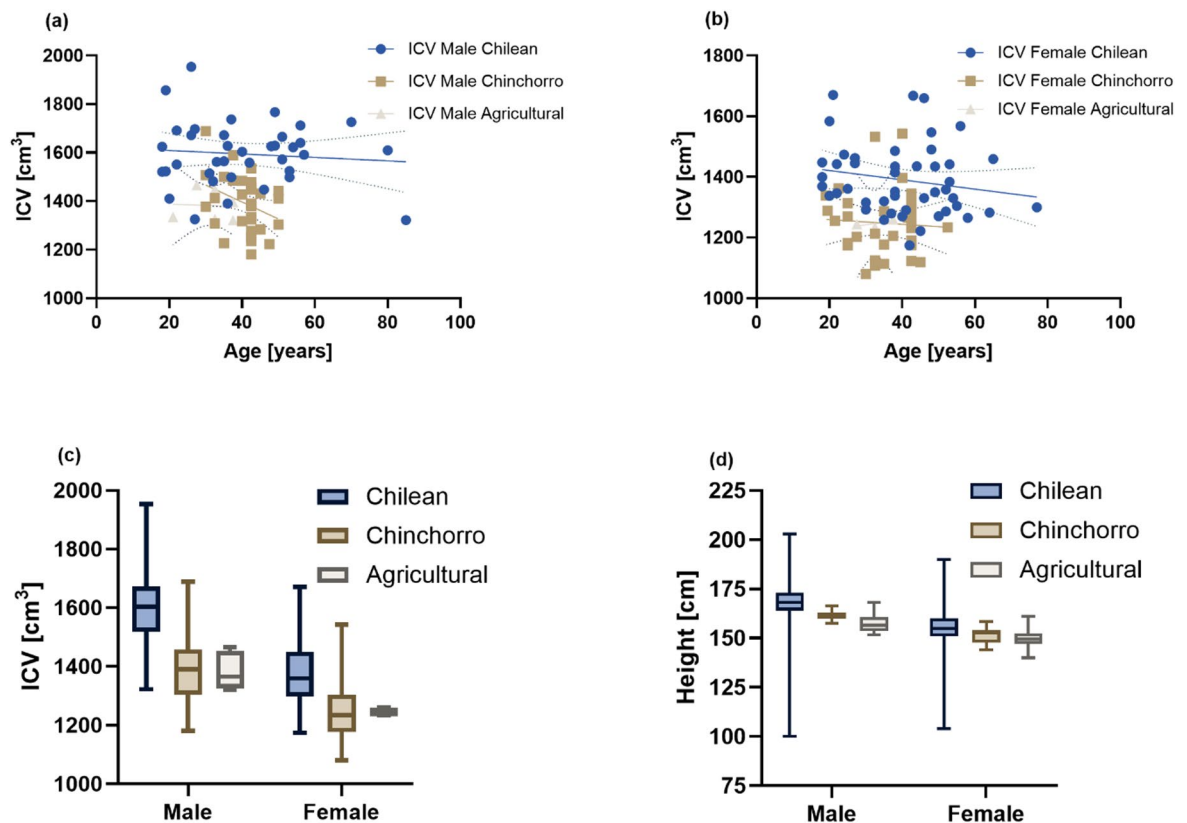


Fig. 6. (a) Male intracranial volumes (mean of Chinchorro individuals: 1390.65 cc; mean of current Chilean individuals: 1594.41 cc). The ICVs of the skulls of Chinchorro individuals were 14.62% smaller than those of current Chilean individuals (mean of Chinchorro individuals (men and women): 1321.74 cc; mean of Chilean individuals (men and women): 1481.23 cc). (b) Female intracranial volumes (mean values of Chinchorro individuals: 1246.36 cc and Chilean individuals: 1390). The ICVs of the skulls of female Chinchorro individuals were 11.52% lower than those of the current female Chilean individuals. (c) ICVs of Chinchorro, Agricultural and current Chilean males and females. (d) Heights of Chinchorro, Agricultural and current Chilean males and females.

the skulls of the male and female Chinchorro individuals were significantly different ($t = 1.34449 \times 10^{-6}$); those of the agricultural individuals were also significantly different ($t = 0.00976$); similarly, the differences between the male and female Chilean individuals ($t = 7.96312 \times 10^{-11}$), the female Chinchorro samples and current female Chilean individuals ($t = 4.862 \times 10^{-7}$), and the male Chinchorro individuals and current male Chilean individuals ($t = 1.05284 \times 10^{-9}$) were also significant. Similarly, the differences between the female agricultural individuals and current female Chilean individuals and between the male agricultural individuals and current male Chilean individuals were also significant ($t = 0.0393$ and $t = 0.000412$, respectively).

The average height of the female Chinchorro individuals, as determined by measuring the lengths of the tibiae and femurs, was 151.448 cm, with a standard deviation of 4.109 cm, a minimum value of 144.018 cm and a maximum value of 158.437 cm, whereas the average height of the males was 161.220 cm, with a standard deviation of 2.445 cm, a minimum value of 157.457 cm and a maximum value of 166.272 cm (Fig. 6d). According to Student's *t* test, the heights of the male and female Chinchorro individuals were significantly different ($t = 1.27202 \times 10^{-13}$). Additionally, the average height of the female pre-Hispanic agricultural individuals was 150.165 cm (standard deviation of 4.709 cm, minimum value of 140.133 cm, and maximum value of 161.021 cm), whereas the average height of the males was 158.034 cm (standard deviation of 4.874 cm, minimum value of 151.694 cm, maximum value of 168.305 cm; Fig. 6d).

The carbon and nitrogen isotope analyses of the Chinchorro individuals confirmed a predominantly marine-based diet. This is evidenced by the high enrichment in both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, with average $\delta^{13}\text{C}$ values of -12.38 and $\delta^{15}\text{N}$ values of 24.48 at the Archaic sites. In contrast, individuals from different agricultural periods present isotopic signatures indicative of a more diverse dietary composition. These values are consistent with the incorporation of both C_3 and C_4 plants, as well as protein from domesticated animals. Additionally, marine-derived resources continued to contribute to the diets of these populations⁸⁰ (Figs. 7 and 8, Dataset S1).

Discussion

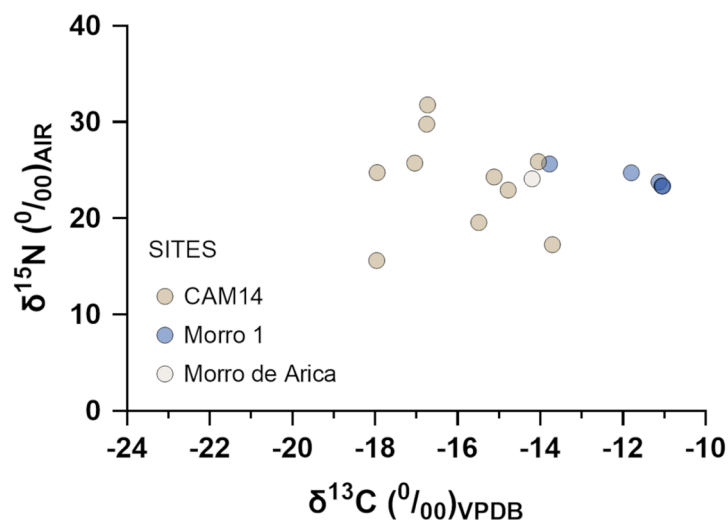
The average ICV of the Chinchorro individuals was 1321.26 cc, that of the pre-Hispanic agricultural individuals was 1336.57 cc, and that of the present-day Chilean population was 1481.22 cc (absolute difference 159.96 cc,

Code MNHN	BV [cm ³]	BW [gr]
2016.2.116	1098.68	1149.22
2016.2.122	1274.62	1333.25
2016.2.126	1271.70	1330.19
2016.2.127	1364.14	1426.89
2016.2.128	996.21	1042.03
2016.2.120	1160.81	1214.21
2016.2.129	1284.34	1343.42
2016.2.130	1335.65	1397.09
2016.2.132	1164.67	1218.24
2016.2.133	986.26	1031.63
2016.2.134	1415.24	1480.34
2016.2.135	1073.78	1123.17
2016.2.136	1096.94	1147.40
2016.2.137	1124.14	1175.85
2016.2.140	1089.06	1139.15
2016.2.141	1079.94	1129.62
2016.2.142	1143.27	1195.86
2016.2.143	1321.53	1382.32
2016.2.144	1001.47	1047.54
2016.2.145	1059.91	1108.66
2016.2.148	1188.80	1243.48
2016.2.150	961.72	1005.96
2016.2.152	1366.17	1429.01
2016.2.155	1180.06	1234.34
2016.2.156	1237.78	1294.72
2016.2.157	1169.49	1223.28
2016.2.159	1173.04	1227.00
2016.2.160	1092.54	1142.80
2016.2.162	1234.71	1291.51
2016.2.163	1045.79	1093.90
2016.2.165	1070.55	1119.80
2016.2.167	1256.68	1314.49
2016.2.168	1052.62	1101.04
2016.2.171	1213.20	1269.00
2016.2.173	1051.16	1099.52
2016.2.174	1129.84	1181.81
2016.2.175	1173.31	1227.28
2016.2.176	1115.97	1167.30
2016.2.177	999.14	1045.11
2016.2.178	1298.24	1357.96
2016.2.179	1145.17	1197.85
2016.2.180	1228.16	1284.65
2016.2.181	1296.03	1355.65
2016.2.183	991.34	1036.94
2016.2.184	1137.70	1190.03
2016.2.186	1227.11	1283.56
2016.2.187	1341.64	1403.35
2016.2.188	1046.36	1094.50
2016.2.189	1048.09	1096.30
2016.2.190	1152.44	1205.46
2016.2.192	1056.43	1105.03
2016.2.193	1321.19	1381.97
2016.2.194	1231.92	1288.59
2016.2.195	1315.58	1376.10
2016.2.196	1137.64	1189.97
2016.2.199	1289.05	1348.35
Continued		

Code MNHN	BV [cm ³]	BW [gr]
2016.2.201	1099.89	1150.49
2016.2.204	1197.85	1252.95
2016.2.205	1123.76	1175.45
2016.2.206	1191.38	1246.19
2016.2.207	1243.78	1301.00
2016.2.209	1294.69	1354.24
2016.2.253	1118.24	1169.68
2016.2.254	1127.24	1179.09
2016.2.258	1257.72	1315.57
2016.2.267	1373.09	1436.26
2017.2.676	1504.01	1573.19

Table 4. Brain volume and weight of each Chinchorro individual.

Code MNHN	BV [cm ³]	BW [gr]
2017.2.661	1289.84	1349.18
2017.2.662	1121.53	1173.12
2017.2.663	1098.44	1148.97
2017.2.664	1181.05	1235.38
2017.2.665	1304.53	1364.53
2017.2.668	1108.08	1159.06
2017.2.669	1242.78	1299.95
2017.2.673	1176.11	1230.21
2017.2.882	1188.40	1243.07

Table 5. Brain volume and weight of each agricultural individual.**Fig. 7.** Paleodietary results for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in bone collagen from Chinchorro samples.

percentage difference 12.05%). The average ICV of the male Chinchorro individuals was 1390.65 cc, that of the male pre-Hispanic agricultural individuals was 1349.44 cc, and that of the skulls of the male present-day Chilean individuals was 1594.41 cc (absolute difference of 203.76 cc, percentage difference of 14.62%). The ICV of the female Chinchorro individuals was 1247.65 cc, that of the female pre-Hispanic agricultural individuals was 1233.65 cc, and that of the skulls of the female Chilean individuals was 1390.19 cc (absolute difference 142.54 cc, percentage difference 10.81%). The percentage difference in the ICV of the Chinchorro between the two sexes (sexual dimorphism) was 10.84% (within the 10–12% range described in the Introduction), with an absolute difference of 143.00 cc, whereas that of the skulls of the Chilean individuals was 13.68% (greater than the 10–12% range previously described), with an absolute difference of 204.22 cc, and the skulls of the

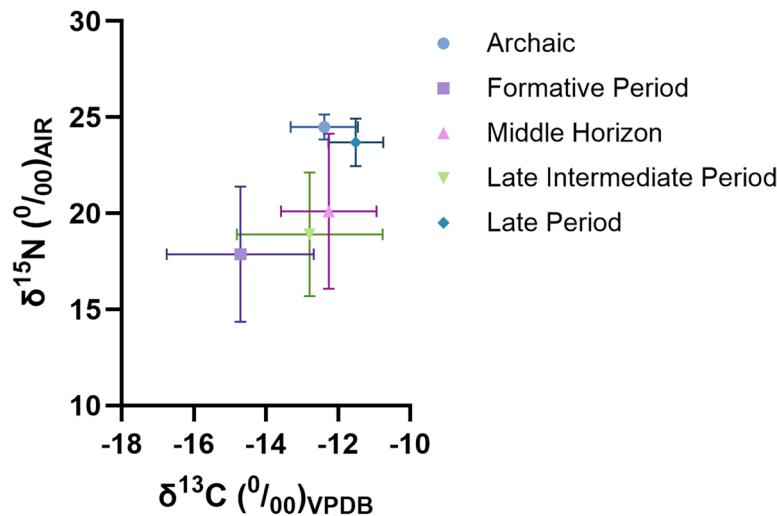


Fig. 8. Biplot of the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\pm$ standard deviation) from bone collagen across different pre-Hispanic periods. Error bars represent standard deviations and reflect variation in dietary intake and subsistence practices over time.

pre-Hispanic agricultural individuals were 8.97% (less than the 10–12% range previously described), with an absolute difference of 115.79 cc. The degree of sexual dimorphism in the ICV was lower in pre-Hispanic agricultural individuals than in the Chinchorro and Chilean individuals.

A significant correlation has been reported between stature and ICV ($r \approx 0.5$)¹⁵, indicating that factors influencing stature—such as sex, genetics, nutrition, and social context—indirectly affect brain volume. Adverse conditions such as war or poverty are known to reduce stature^{77–82}, whereas modern societies with improved access to healthcare, education, and diverse nutrition have shown positive secular trends in both stature and ICV^{83,84}. Early-life malnutrition has been consistently associated with reduced brain volume and cognitive impairments, highlighting the critical importance of adequate energy and nutrient intake during neurodevelopmental windows¹. In contrast, better dietary quality in contemporary populations has been positively associated with brain volume. For example, Croll et al.⁸⁵ found that diets rich in vegetables, fruits, whole grains, dairy, fish, and nuts—typical of the Mediterranean pattern—were linked to larger brain volumes. Similar associations have been reported by Zamroziewicz⁸⁶, and others have noted that lower red meat intake is correlated with greater brain volume⁸⁷. These findings emphasize the potential of nutritional environments to influence cranial development and brain morphology.

Previous studies have shown that the ICV is positively associated with height as well as other factors, such as sex, weight and body mass index^{13,15,88}. This relationship is explained under the concept of allometry, which refers to changes in the relative dimension of body parts with respect to changes in total size^{89,90}. A classic example of an allometric relationship is the ratio between the length of the arm and the height of the individual, which is commonly illustrated in the Vitruvian Man¹⁵. For the ICV and/or total brain volume, an allometric relationship is observed with respect to an individual's body size^{88–94}. O'Brien¹⁵ reported a significant correlation (approximately 0.5) between the ICV and the height of an individual; i.e., the greater the height is, the greater the ICV.

Given the established allometric relationship between height and the ICV, it is reasonable to expect that factors influencing stature similarly affect ICV. Height reflects the composition of the sizes of four skeletal components, i.e., the skull, vertebral column, coxal bones and lower extremities, for which there are known correlations that allow an estimation of height, typically with the long bones, provided that they do not demonstrate pathological alterations^{77,78}. The height of an individual is determined by both intrinsic factors (e.g., sex, age, and genetic predisposition) and extrinsic factors (including nutrition, climate, geographical location, and social context). These factors contribute to differences in height due to differences in growth rates and predominant body proportions^{77–80}.

Historical trends in adult stature in Chile provide valuable context for interpreting long-term patterns of biological development. Adult female height increased from approximately 156.5 cm in the 1860–1870 s to 161.5 cm between the 1970s and 1990 s, representing a gain of approximately 5 cm over more than a century⁹⁶. Most of this increase occurred during two key periods, the late 19th century and the second half of the 20th century, mirroring the pattern observed in men. Although the increase in women's height was slightly smaller than the 5.5 cm gain observed among men, this difference aligns with international trends⁹⁷. In both developed and developing countries, male stature has tended to increase more than female stature over the course of the 20th century. In the Chilean context, the sustained increase in adult height—especially among women—constitutes the greatest improvement in biological welfare in the country's history. These secular trends reflect broader improvements in living conditions, including better nutrition, expanded access to healthcare, improved sanitation, lower child mortality, and increased educational attainment. Importantly, ethnic and regional

Sex	Height ratio (Chilean/Agricultural)	Height ratio (Chilean/Chinchorro)	ICV ratio (Chilean/Agricultural)	ICV ratio (Chilean/ Chinchorro)	Agricultural ICV/height (cm ²)	Chinchorro ICV/height (cm ²)	Chilean ICV/ height (cm ²)	Variation ratio (Chilean/ Agricultural)	Variation ratio (Chilean/ Chinchorro)
Female	1.04	1.03	1.13	1.12	8.2	8.2	8.9	108.4	108.3
Male	1.07	1.05	1.18	1.15	8.5	8.6	9.4	110.1	109.0

Table 6. Height and intracranial volume (ICV) of the current Chilean and Chinchorro individuals and the height-ICV relationship in both populations.

disparities in height remained relatively limited, suggesting that these biological gains were broadly distributed across the population^{96,97}.

Current data from the Chilean Ministry of Health (MINSAL, www.minsal.cl, 94) indicate that the average height of the adult population is 169.6 cm for men (95% CI: 169.0–170.2) and 156.1 cm for women (95% CI: 155.5–156.7), representing a sex difference of 13.5 cm (8.29%). This marked sexual dimorphism may be partly attributable to historical demographic processes. During the European conquest, the arrival of predominantly male Spanish settlers and the subsequent early miscegenation with Indigenous women likely contributed to the persistence of a pronounced male–female height differential in the Chilean population⁹⁵. The overall positive secular trend in height observed over the past 50 years is strongly associated with improvements in health, nutrition, and quality of life, particularly among socioeconomically disadvantaged groups⁹⁶. Additionally, increased internal migration and population mobility may have contributed to greater genetic diversity, further supporting gains in stature. Given the well-established allometric relationship between body size and brain size, this general increase in height is expected to be accompanied by a corresponding increase in cranial and cerebral volumes (86, 100, Fig. 6d).

Our study revealed that although modern Chilean populations exhibit a marked absolute increase in ICV, no statistically significant differences were found between individuals from the Chinchorro culture and those from later pre-Hispanic agricultural populations. This pattern suggests that the transition from foraging to farming subsistence strategies did not substantially impact the ICV. In contrast, the dramatic socioenvironmental transformations of the 20th century—characterized by rapid technological development, improved living standards, and increased human mobility—have been accompanied by measurable improvements in biological indicators such as adult stature. Notably, average male and female height increased considerably during this period, particularly in the latter half of the 20th century, reflecting enhanced nutritional and health conditions^{92,93}. These changes, occurring within a relatively short time span, highlight the potential impact of modern developmental environments on somatic growth. Consequently, variation in the ICV appears to be more strongly associated with allometric, metabolic, and developmental factors than with specific cultural or technological transitions in preindustrial contexts.

In general, the average ICV is significantly greater in men than in women^{98–100}, and the brains of men are approximately 10–12% larger¹⁰¹, although normalized brain volume values are similar between sexes¹⁰⁰. This sexual dimorphism in the ICV has been attributed, in part, to differences in average height between men and women^{102,103}. Spann and Dustmann¹⁰⁴ estimated the brain mass per centimeter of stature, supporting the proportional relationship between height and ICV. In this study, the modern Chilean population presented a greater ICV-to-height ratio than the Chinchorro population did (Table 6), especially among males, suggesting a more pronounced increase in cranial volume relative to body size. Indeed, the percentage and absolute differences in the ICV between the Chinchorro, pre-Hispanic agricultural individuals, and the current Chilean population were greater in men than in women. This outcome is related to height: Chilean men are, on average, taller than Chinchorro men were (169.6 cm vs. 161.2 cm), whereas the difference is smaller among women (156.1 cm vs. 151.5 cm).

The relationship between ICV and age has generated some debate. While several authors report that ICV tends to decrease with age^{15,105,106}, others suggest no significant correlation^{98,100}. In our study, age-related ICV variation generally aligns with previous findings. Among modern Chileans, ICV has declined at a rate of 1.53 cc/year in females and 0.71 cc/year in males—values that fall within the expected ranges. Among the Chinchorro individuals, the decline was 0.78 cc/year in females and 7.00 cc/year in males, although the latter may reflect sampling biases, small sample sizes, or taphonomic alterations rather than true biological trends.

Cranial morphology is also influenced by environmental, geographic, and selective pressures, as reflected in population history^{107–109}. According to Hubbe et al.¹⁰⁸, human groups living in extreme climates exhibit more pronounced morphological adaptations, such as broader neurocrania in cold environments, which is consistent with Bergmann’s and Allen’s rules¹¹⁰. However, the Chinchorro and agricultural populations in this study inhabited the hyperarid Atacama Desert, where thermal pressures were mild and stable; thus, climate likely played a limited role in their cranial variation.

Nevertheless, dietary and functional demands may explain some of the observed morphological differences. The Chinchorro subsisted on a marine-based diet composed of structurally tough resources, in contrast to the softer and more processed foods of modern Chileans. This may have contributed to their distinctive cranial morphology, particularly in masticatory structures⁴². Furthermore, long-term subsistence strategies in arid environments shaped skeletal development. The Chinchorro exemplify adaptation to one of the world’s most extreme ecosystems, relying on marine resources for stability¹¹¹. Over time, agricultural transitions introduced C₃ and C₄ plants, domesticated animals, and continued marine use⁷⁶. This dietary diversification marked a fundamental economic transformation from foraging to food production^{112,113}. In later pre-Hispanic contexts,

elevated $\delta^{15}\text{N}$ values may reflect not only animal protein intake but also the use of nitrogen-rich fertilizers (e.g., seabird guano), which enriched crops and altered isotopic signatures^{114,115}. Thus, agricultural practices must be considered when interpreting isotopic data from desert populations.

Additionally, migratory processes and gene flow influenced cranial variation via developmental plasticity and local adaptation^{109,116}. In South America, miscegenation and changes in diet have resulted in morphological transformations in the cranial vault, face, and teeth¹¹⁷, with allometric shape changes linked to diet⁴⁶. Although significant morphological differences have been documented in association with artificial cranial deformation—particularly regarding facial structure, head posture, and cranial base morphology^{118–120}—several studies have shown that when deformation is successfully performed during early childhood, it does not appear to significantly affect ICV¹²¹. In such cases, the plasticity of the infant cranium allows for a compensatory redistribution of space, maintaining endocranial capacity within normal ranges. This finding suggests that, despite external modifications, brain development is not structurally compromised in terms of volume, which aligns with our findings.

In conclusion, the differences observed in ICV across Chinchorro, pre-Hispanic agricultural, and modern Chilean populations are closely related to stature and sex, supporting our initial hypothesis. While transitions in prehistoric subsistence strategies did not produce significant changes in either height or ICV, the 20th century marked an inflection point. The notable increase in stature observed during this period—approximately 5 cm in women and 5.5 cm in men^{92,93}—coincides with improvements in nutrition, particularly increased intake of dairy and animal proteins, as well as broader gains in public health, sanitation, and education^{83,84,96}. These positive environmental and developmental changes appear to have driven the observed increase in ICV, which was greater in men than in women, in line with documented sexual dimorphism and stature differences^{51,53,108–127}. Although Chilean populations retain a strong Indigenous genetic base, European admixture—particularly through male lineages—also contributed to increased male height⁹⁵. Therefore, the increase in ICV among modern Chileans reflects recent environmental, nutritional, and demographic changes rather than deep evolutionary divergence.

In summary, our results unequivocally demonstrate that both ICV and stature have significantly increased in modern Chilean populations. However, given that the increase in stature is a well-documented and relatively recent phenomenon—emerging primarily during the 20th century—these anatomical changes cannot be attributed to prehistoric developments. Notably, the transition from hunter-gatherer to agricultural lifestyles during the Chinchorro and later pre-Hispanic periods did not result in substantial shifts in either ICV or stature. These findings suggest that long-term changes in subsistence strategies were not the primary drivers of cranial or height variation. Instead, the increases observed in contemporary populations are more plausibly associated with improvements in early childhood nutrition—particularly greater consumption of dairy products and animal protein—as well as broader advances in public health, hygiene, and living conditions that have occurred since the early 20th century.

This study provides the first diachronic quantification of ICV variation in Chile using 3D reconstructions derived from both archaeological and modern CT data. While some limitations remain—such as taphonomic damage in certain Middle Archaic skulls from Camarones-14—these limitations were mitigated through meticulous digital reconstruction. Most archaeological specimens, particularly those from Morro de Arica and Blanco Encalada, were exceptionally well preserved due to the hyperarid conditions of the Atacama Desert. Overall, these findings challenge traditional assumptions about biological change during prehistoric agricultural transitions, laying the groundwork for future research into how recent sociocultural transformations can directly influence and help us better understand ongoing changes in human biology and morphology.

Data availability

The datasets generated and/or analyzed during the current study are included in the paper and in a supplementary section.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to G.M.R.-C.

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