

# The antiquity and ancestral origin of humans in the Americas: a five hundred year inquiry from a biological anthropology perspective

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**Summary** - *The questions – When did humans arrive in the Americas? Who were they, or from where did they come from? – are enduring and fascinating inquiries that have been approached from different perspectives, thanks to the contributions of archaeology, biological anthropology, and linguistics, among other disciplines. As a result, and after several centuries of studies, this body of research inspired several proposed models on the peopling of the Americas. These models are not only equally unique from each other but also distinct from the current themes in recent literature. However, there is a limited and occasionally inaccurate reference to the knowledge produced in the peripheral countries. This may be attributed to differences in language, academic traditions, as well as the consequences of geopolitics and neocolonialism in science. By reviewing both the old and recent literature, my aim is to present a historical account of how biological evidence has contributed to supporting and discussing some of the broad models that were proposed to explain the peopling of the Americas. Instead of providing an exhaustive account on the models, herein I focus on critically linking evidence and discussions ranging from the early skeletal discoveries at Lagoa Santa in Brazil in the 1830s to the current challenges of integrating a large amount of disparate data and collaborating with indigenous communities in the “omics” era. Far from being fully understood, investigations into the antiquity and the ancestral origin of Native Americans are revealing that these complex questions should be addressed by combining diverse data, articulating information at finer and larger grain scales, and adopting a sensitive and respectful approach by engaging with the views of indigenous communities.*

**Keywords** - *Human expansions, Human evolution, Peopling of the Americas, History of Biological Anthropology.*

## Introduction

The peopling of the Americas has been a subject of intense debate over the last centuries (Acosta 1590; Lund 1842; Hrdlička 1912a; Neves and Pucciarelli 1991; Goebel et al. 2008; Böeda et al. 2014; Borrero 2016; Politis et al. 2016; Meltzer 2021). During that time, several inquiries have arisen, some of them were answered with the growing evidence obtained, while others remain unsolved and are a matter of current research. Over the decades, a large number of research projects have aimed to answer questions related

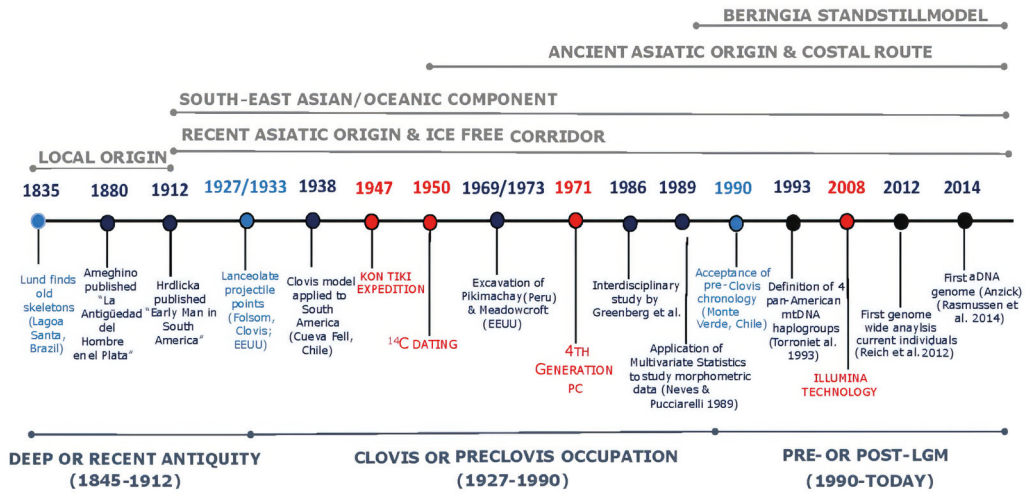
to the timing, migration routes, and biological affinities of the first Americans. Most of these have been approached by discussing the diverse existing evidence: chronological information of the earliest proofs of humans in the continent (i.e. reliable radiocarbon dates of remains recovered in archaeological sites), the presence of technology associated with the extinct Pleistocene megafauna (i.e. fluted and stemmed projectile points such as Clovis and fishtail), linguistic variation (i.e., lexicon) (Nichols 2015; Weitzel et al. 2018; Politis et al. 2019; Prates et al. 2020; Waters et al. 2020;), and bioanthropological data such as

cranial, dental, and genetic variation (Neves and Pucciarelli 1991; O'Rourke and Raff 2010; Scott et al. 2021). As a result, there are plenty of models on the peopling of the Americas, although recently, very few of them discuss the previous literature (Dillehay 2019).

Of special interest are the research questions aimed at unraveling the antiquity and the ancestral origins of the first humans arriving in the Americas by using biological data. The biological evidence analyzed to address this is based on skeletal and molecular data. Most of the skeletal data generated comes from the study of skull and dental variation of individuals recovered from archaeological sites (Turner II 1971; Neves and Pucciarelli 1989; Turner II 1990; Scott et al. 2016; Hubbe et al. 2020), while the molecular data were formerly based on serologic and blood group frequencies, and later on mtDNA, Y chromosome, and autosomal markers from ancient and contemporary individuals (Szathmáry 1979; Baillet et al. 1994; Bianchi et al. 1998; Estrada-Mena et al. 2010). In the last decade, thanks to the development of new technologies (e.g., NGS techniques applied to genome-wide aDNA data, UDG treatment for removing aDNA damage, DNA capture for enriching target sequences; Liu et al. 2022), aDNA has been recovered from ancient skeletons to a greater extent, and full genomes have been sequenced to discuss the biological affinities of Native Americans in relation to the peopling of the continent (Moreno-Mayar et al. 2018; Posth et al. 2018; Nägele et al. 2021; Lindo et al. 2022). Meanwhile, genetic analysis on contemporary populations keeps delivering interesting data for discussing ancient dynamics (Luisi et al. 2020; García et al. 2021; Figueiro et al. 2022; Mendoza-Revilla et al. 2022). Moreover, thanks to the advances in computer science and imagining technologies from the last decades, morphological studies have benefited from using 3D data and geometric morphometric methods. These not only provide a larger quantity and quality of biological information but also allow data sharing and comparative analysis of large datasets (Zollikofer et al. 1998; Weber and Bookstein 2011; Mitteroecker and Schaefer 2022). This enabled the virtual reconstruction and inclusion in the comparative analysis

of some early/middle Holocene skulls that are fragmented (Menéndez et al. 2020; Davis et al. 2021; Menéndez et al. 2023). Additionally, it allows the analysis of endocranial variation of ancient skulls (López-Sosa 2017; Eisová et al. 2022) and expands the modalities of data collection for cranial and dental morphology studies (Hubbe et al. 2020; Vlemincq-Mendieta et al. 2022).

Overall, these advances in biological anthropology have been applied to the study of the peopling of the Americas, and the results obtained have been used to either propose new models or, to a lesser extent, discuss existing ones that have been suggested throughout decades of research. Concerning the ancestral origins of Native Americans, most current evidence indicated that they all diverge from an ancestral population in East Asia ~40,000-25,000 years BP (Fu et al. 2013; Yang et al. 2017; Moreno-Mayar et al. 2018). However, certain aspects that could aid in a deeper understanding of this process remain unknown, such as the magnitude of biological variation in the ancestral population(s), the number of lineages and/or expansions, and possible connections that some Native Americans may have with groups from Oceania. For example, regarding the magnitude of variation, it is anticipated that Native Americans would be the least differentiated, i.e., the least heterogeneous in terms of biological variation, when compared to populations from other continents (Howells 1989). This assumption is based on the expected global pattern of human variation associated with geographic distance from Africa, following an isolation by distance model used to describe the Out-of-Africa (OA) migratory process for humans as a result of genetic drift (Cavalli-Sforza et al. 1994; Betti et al. 2009; Nielsen et al. 2017). A similar correlation is expected for the peopling of the Americas, with Beringia and Panama's Isthmus acting as geographic bottlenecks for expanding populations from Asia to North and South America, encountering new regions with high ecological diversity and environmental challenges. However, dental and cranial data contradict this expectation, showing that Native American populations are widely diverse, exhibiting higher variation



**Fig. 1 - Timeline showing the milestones in the history of the peopling of the Americas research that are mentioned in this article (below, in blue and red), as well as the lifespan of the explanatory models and the debates on the antiquity of humans in the Americas (above, in light grey).**

than anticipated under an isolation by distance model (von Humboldt 1810; Retzius 1850; Lahr 1995; Sardi et al. 2005; Sutter 2005; Pucciarelli et al. 2008; Perez et al. 2009; Hubbe et al. 2014, 2015). This high degree of morphological variation is comparable to the variation among populations from different continents (González-José et al. 2001; Sardi et al. 2005; González-José et al. 2008; Ponce de León et al. 2018). Consequently, a central question in the debate has been whether several ancestral lineages could explain most of the variation among different populations, or if populations have differentiated *in situ* due to the action of different evolutionary processes. Finally, there is a long-standing debate on the antiquity of the first Americans. Some researchers support an early entry based on archaeological evidence from a few sites, while others find this evidence challenging and instead advocate for a more recent arrival, ~15,000 years BP (Martin 1973; Meltzer 1989; Lynch 1990; Boëda et al. 2014; Meltzer 2015; Holen et al. 2017; Prates et al. 2020; Bennett et al. 2021).

Hereby I assert that a comprehensive and historical revision of the models proposed thus far is necessary to fully understand several aspects of the current debate on human diversification in

the Americas (O'Rourke 2011). Unfortunately, in the era of “fast science”, this has become an uncommon practice (Dillehay 2019; Menéndez et al. 2022). Additionally, the knowledge produced in the peripheral countries (*sensu* Yañez et al. 2023) has not been successfully incorporated into the international debates. This might be due to differences in language and academic traditions; for instance, researchers from Latin America sometimes publish articles in Spanish and/or Portuguese and in “local” journals (Ardila Calderón and Politis 1989). It may also be related to the geopolitics of academic science, reproducing the coloniality of power (Dussel 1973; Quijano 2000). In any case, there is a large amount of solid evidence that has allowed proposing distinctive models to discuss different aspects of such a complex process. In this review, I present some of those models, particularly those discussed based on anatomical and genetic data, taking into account archaeological and linguistic evidence relevant to the biological anthropology debate. Through this, I aim to contribute conceptual tools and critical reflections to discussing both past and currently valid models that explain the biological variation of humans in the Americas. Fig. 1 provides a timeline offering a visual summary of milestones

in the history of research on the peopling of the Americas, including key discoveries, meaningful results, and the development of new technologies. It also highlights the lifespan of explanatory models and debates on the antiquity of humans in the Americas, which will be explored further in this article. The two main anthropological questions guiding this review pertain to the antiquity and ancestral origin of the first Native Americans: (a) When did the first humans arrive in the Americas? and (b) Who were the migrant populations or where did the founding population split? The models proposed to answer these questions will be organized into two sections, presented in chronological order where possible. Each section develops an argument independently, discussing some evidence (e.g., cranial shape) in different contexts – contributing to the themes of the main two sections of the paper and/or to the different models. Finally, the archaeological sites and models selected here are carefully chosen to construct a narrative illustrating how biological evidence contributed to supporting and discussing broad models explaining the peopling of the Americas. Therefore, readers should be aware that this critical review is written from a biological anthropological perspective.

### **The question on antiquity: When did the first humans arrive to the Americas?**

The question of the antiquity of humans in the Americas emerged early, during the first encounters between Europeans and Native Americans. Over the ensuing centuries, Europeans sought answers within the context of their knowledge at the time, initially connecting these inquiries to more recent historical groups such as the Lost Tribes of Israel – a prevailing notion until the mid-19<sup>th</sup> century (Meltzer 2021). Among the early proponents of acknowledging the vast linguistic, cultural, and physical diversity among Native Americans was Thomas Jefferson, the former governor of Virginia and later U.S. president. He recognized that such diversity could only be

the result of “an immense course of time”. As the 19<sup>th</sup> century progressed, the previously accepted biblical timeline of 6000 years for life on earth began to be questioned. This shift occurred as human skeletons were discovered in stratigraphic association with extinct megafauna at numerous archaeological sites worldwide (Lyell 1863; Lubbock 1865). It was not until 1859, following a meeting of London’s Royal Society, which included figures like Lyell and Huxley, that the concept of deep human antiquity gained global academic acceptance (Meltzer 2021). This new interpretation had a direct impact on the understanding of the Native American history.

At that time, the primary evidence presented by advocates of deep human antiquity in the Americas stemmed from the identification of primitive features in artifacts or human skeletons and the stratigraphic association between these findings and bones from extinct megafauna (Lund 1845; Burmeister 1864; Abbott 1889). These prehistoric human skeletons were discovered during amateur expeditions conducted primarily from the second half of the 19<sup>th</sup> century to the first decades of the 20<sup>th</sup> century in the USA, Brazil, Cuba, and Argentina. The interpretation of these human skeletons as very old immediately drew South American evidence into the international archaeological and paleontological debates for the first time. However, some archaeologists and anthropologists reacted against these interpretations, sparking heated discussions on the coexistence of humans and megafauna. Since the mid-20<sup>th</sup> century, when radiocarbon dating became a routine procedure in archaeological sciences, many of these presumed ancient human skeletons from the archaeological locality Lagoa Santa in Brazil and several sites in the Argentinean Pampas have been confirmed as among the earliest in the Americas (Fig. 2; Neves et al. 1998; Politis and Bonomo 2011; Politis et al. 2011; Moreno-Mayar et al. 2018). Nevertheless, certain individuals, such as those from the archaeological sites Fontezuelas in Argentina, and Sancti Spiritus in Cuba, have been determined to date back to the late Holocene (Fig. 2; Politis and Bonomo 2011; Rangel 2019). Additionally, in many cases,



**Fig. 2 - Map showing the geographical location of the archaeological sites and archaeological localities from Asia, North America, Central America, and South America mentioned throughout the text. The archaeological sites from Europe are not depicted in this figure. The dark grey circles indicate archaeological sites in which human remains were recovered, the light grey circle indicates a site where human coprolites were recovered (Paisley Caves).**

the re-dating of presumed ancient butchering sites confirmed the coexistence of humans and megafauna (Hubbe et al. 2013; Deviese et al. 2018). Today, the debate continues, focusing on whether the arrival of humans in the Americas occurred before or after the Last Glacial Maximum (LGM) (LGM: 28,000-18,000 years BP).

*Deep antiquity assessed by the coexistence of humans with extinct megafauna and the dolichocephalic skull shape*

In South America, reports describing the association of extinct megafauna with cultural evidence within Pleistocene-age deposits date back to the mid-19<sup>th</sup> century, sparking discussions

among both local and international scholars (Lund 1842, 1845; Burmeister 1864). In North America, the recurring discovery of human fossils or cultural evidence linked to Pleistocene-age deposits faced repeated challenges from geologist William H. Holmes and later from physical anthropologist Aleš F. Hrdlička. Hrdlička corresponded with archaeologists through post communication and/or visited archaeological sites presumed to be ancient (Hrdlička 1907). Hrdlička also offered rebuttals for every claim of antiquity for sites in South America (Hrdlička et al. 1912). However, in the 1920s, the discovery of human artifacts (Folsom and Clovis projectile points in the archaeological sites with the

same names; Fig. 2) associated with the bones of extinct bison and mammoth, led to the widespread acceptance of deep human antiquity. This acceptance was later corroborated when radiocarbon dating of these samples took place during the late 1950s (Meltzer 1983).

The uneven record and discoveries of Pleistocene megafauna in South America, coupled with the diverse histories of investigations in each country, introduce a bias in the available information about the coexistence of humans and megafauna (Borrero 2009; Podgorny 2017). In Argentina, the German zoologist Hermann Burmeister (1807-1892), recommended by Alexander von Humboldt to travel to South America, conducted extensive paleontological work in the La Plata River basin region. He advocated for the deep antiquity of ancient humans and extinct megafauna coexisting in this region (Burmeister 1964). Subsequently, the Italo-Argentinean naturalist Florentino Ameghino (1854-1911), investigated the geology and co-occurrence of humans and animal fossils in various locations in the Argentinean Patagonia and Pampa since the 1870s (e.g., Fontezuelas, La Tirgra, Necochea; Ameghino 1880; Fig. 2). Ameghino discovered stone tools associated with human bones and extinct animal fossils, interpreting the coexistence of humans and megafauna in the region as very ancient, presumably linked to the Pliocene strata (Ameghino 1909, 1910a,b). In Brazil, the Danish naturalist Peter Lund (1801-1880) collected more than 12,000 fossils representing various species. Among them, he reported the stratigraphic association of human and extinct animal bones in archaeological sites that remain relevant today, such as those in Sumidouro cave from the archaeological locality Lagoa Santa, Brazil (Fig. 2; Lund 1842, 1845).

The significance of the human skeletons from Lagoa Santa, Brazil, extends beyond their contribution to the question of the peopling of the Americas; they hold a crucial place in the history of research on human evolution. After over a decade of exploring more than 800 caves in the Lagoa Santa karst region, in 1843, Peter Lund excavated a chamber in Sumidouro Cave where

he described a series of thirty human skeletons attributed to individuals from very ancient times (Fig. 2; Lund 1845). Consequently, the skeletons from Lagoa Santa became the first fossils in the world to be ascribed to the human species while being considered chronologically very ancient. They were discovered and described even before the oldest *Neanderthal* fossils found in 1856 in the Neander Valley, Germany (Schaaffhausen 1858), and *Homo erectus*, discovered in 1891 in Java, Indonesia (Dubois 1894). Despite Peter Lund being a pioneer in recognizing the deep antiquity of humans in South America, his ideas gained international discussion only towards the end of the 19<sup>th</sup> century (Pilo et al. 2004). While his investigations aimed to find evidence supporting the catastrophism theory formulated by George Cuvier (i.e., biological species became extinct due to the periodic flooding and other catastrophic events, and new species originated and evolved afterward), the interpretation of his findings played a crucial role in paving the way for the paradigm shift leading to the rise of evolutionary theory (Luna Filho 2007).

By the end of the 19<sup>th</sup> century, some naturalists supported the deep antiquity of humans in South America based on the dolichocephalic skull shape, a trait also observed in Neanderthal specimens (Lund 1842; Moreno 1874; Burmeister 1879; Moreno 1882; Ameghino 1909). The Swedish anatomist Anders Retzius introduced the cephalic index, which measures the ratio of the breadth to the length of the skull, with the aim of classifying human variation based on cranial morphology (i.e., dolichocephalic, mesocephalic, brachycephalic) (Retzius 1843). This classification was later interpreted in terms of hierarchy and chronology. Despite the discovery of Neanderthal bones in 1829 (Engis, Belgium) and 1848 (Forbes' Quarry, Gibraltar), it was not until the Neander Valley specimen (Düsseldorf, Germany) was found in 1856, that those fossils were recognized as belonging to an early human species (Schaaffhausen 1858; Balter 2009; Green et al. 2010), although others, like Rudolf Virchow interpreted them as human pathological bones. Among other features, Neanderthals were

depicted as having a dolichocephalic skull shape, characterized by larger anteroposterior dimensions in relation to cranial width. This dolichocephalic form was considered older compared to the brachycephalic one, characterized by a large skull width in relation to anteroposterior dimensions, which was present among the most recent human groups (Topinard 1876; but see Retzius 1864). These interpretations, linking skull morphology to more ancient times, and evolutionary stages in the history of humankind, influenced the understanding of skull shape variation and biological evolution among human populations globally for several decades. Questions related to the meaning of such morphology persist to this day (Schaaffhausen 1868; Windle 1905; Abbie 1947; Lieberman et al. 2000; Zollikofer and Ponce de León 2002; Bastir and Rosas 2004; Goodrum 2016).

Both the dolichocephalic and brachycephalic skull shape variants were observed among recent populations in the Americas, and the assignment of certain groups to one type or the other was a topic of ongoing discussion (Burmeister 1879; Moreno 1882). Some researchers suggested that the South American dolichocephalic individuals were comparable in terms of antiquity (and phylogenetic position) to the Euroasiatic Neanderthals (Moreno 1882). For example, in South America's southern cone, Mapuche individuals were described as having a brachycephalic skull shape, Fuegians a dolichocephalic one, while Tehuelche individuals were described as having an intermediate skull shape, interpreted as the result of gene flow between the ancient autochthonous dolichocephalic inhabitants and the more recent brachycephalic migrating groups from Asia into the Americas (Burmeister 1879; Moreno 1879). In this context, the Fuegian groups were considered relicts of the earliest human populations and surviving evidence of the primitive stages of human evolution. European researchers such as Paul Broca in Paris and Rudolf Virchow in Berlin supported these ideas, using the morphometric descriptions of South American skulls to reinforce their concepts of human evolution (Broca 1861; Virchow 1892). Nowadays, biological

anthropologists are aware that the biological variation within a population can be significant. Therefore, characterizing populations based on specific cranial shapes derived from cranial indexes is considered pointless.

Throughout his entire career, Florentino Ameghino dedicated himself to finding fossils that could demonstrate not only the deep antiquity of humans in South America but also the origin of humanity in that continent (Ameghino 1880, 1907, 1909, 1910a,b). Leveraging his extensive knowledge of comparative mammal anatomy and his ideas on transmutation (i.e., the altering of one species into another), he constructed a primate phylogeny by establishing morphological connections between primate fossils and specimens from extinct and contemporary species found worldwide. Employing mathematical calculations, he proposed species names for missing links and assigned the specimens he studied to these hypothetical taxa within the phylogeny he had constructed earlier (Ameghino 1884b). Notably, within this framework, Ameghino posited that *Homo sapiens* originated in the Argentinean Pampas and argued that the dolichocephalic skull shape belonged to an extinct human group later replaced by humans with a brachycephalic skull shape. He suggested that individuals from the Lagoa Santa series retained an antero-posteriorly enlarged skull with short height, representing the ancestors of recent Native Americans (Ameghino 1910). Thus, while Lund interpreted the Lagoa Santa human skeletons as phenotypically very similar to contemporary humans, Ameghino described them with both primitive and more recent features. Additionally, while Ameghino strongly supported autochthonism, Lund believed that humans arrived in the Americas by migrating from the "Old World".

The coexistence of humans and megafauna in South America during the late Pleistocene was later confirmed, thanks to methodological advances and theoretical shifts that began in the 1960s archaeological science. Archaeologists, starting from that period, began to analyse taphonomy and assess the anthropic origin of cut

marks (Binford 1981). They also selected samples to be sent to specialized labs that applied modern radiocarbon dating techniques (MacNeish et al. 1970; Martin 1973; Politis and Messineo 2008; Borrero 2009). The application of these new methods allowed a re-evaluation of previous results and consequently advanced interpretations of the evidence, shedding light on the human past. However, the application of new methods has not completely unravelled some of the oldest enigmas. For example, the association of certain cranial shapes with specific chronologies remains poorly understood. The assignment of the dolichocephalic skull shape to ancient humans in South America has been a subject of debate for decades, with no current consensus on its meaning and its potential association with an earlier chronology. Indeed, it continues to be a topic that is actively discussed (Neves and Pucciarelli 1989, 1991; Hubbe et al. 2015; Kuzminsky et al. 2017; von Cramon Taubadel et al. 2017).

#### *A postglacial arrival: from Aleš Hrdlička to Clovis First*

The interpretations made by Lund and Ameghino, particularly the latter's views on the origin of humanity in South America, had a profound impact not only in Academia but also in society at large. Communications of the findings and a substantial part of the debate was published as newspaper articles, capturing the attention of both the general public and the academic community. The findings faced criticism not only from anthropologists in South America (Burmeister 1891; Lehmann-Nitsche 1907, 1909; Outes 1909; Boman 1919) but also by international scholars (Virchow 1883; Kate 1885; Rivet 1908; Mochi 1910; Schwalbe 1910; Hrdlička 1912a; Boule 1921). Furthermore, their ideas were employed to support other hypotheses, such as the polygenic origin of humanity (Morton 1844; Sergi 1910). The interpretations generated a strong reaction from scholars like William H. Holmes, who later became the Head Curator of the Department of Anthropology at the Smithsonian Institution. Holmes was tasked

by the director of the Smithsonian's Bureau of Ethnology, John Wesley Powell, to critically analyse all the evidence suggesting the idea of a Glacial Man (Adovasio and Page 2002). Holmes argued that artifacts interpreted as belonging to the American Paleolithic and Pleistocene times (Abbott 1977) actually represented early stages of manufacture (or manufacture failures) and should therefore be considered of recent origin. He stressed that the chronology of an artifact should be determined solely by its geological context (Holmes 1890). This interpretation persisted, largely owing to Aleš Hrdlička's support and promotion.

Aleš F. Hrdlička (1869-1943) was a Czech physical anthropologist who relocated to the United States with his family in 1881. In 1904, he assumed the position of head of the newly established Division of Physical Anthropology at the Smithsonian Institution (National Museum of Natural History in Washington D.C.), a prestigious role he held for the next forty years. While serving as the curator of Anthropology at the Smithsonian Institution, Hrdlička meticulously analysed all the human bones that were interpreted as ancient fossils at the time (Podgorny and Politis 2000). Hrdlička thoroughly examined and refuted the earlier chronological assignments of every human skeleton recovered from presumed Pleistocene-age deposits in North America. The femur of Trenton, USA, was the first human bone discovered and initially interpreted as ancient challenging its chronology (Fig. 2; Hrdlička 1902). After identifying this femur as belonging to a recent Native American, Hrdlička continued his scrutiny of other bones over the next twenty-five years, originating from archaeological sites in Lansing-Kansas, Rancho La Brea-California, among others (Fig. 2; Meltzer 2005). He categorized them as *Homo sapiens* and deemed them chronologically very recent, based on the anatomical similarities to contemporary Native groups (Hrdlička 1907).

In 1910, Hrdlička, alongside geologist Bailey Willis, organized a visit to Argentina and Brazil, supported by the Smithsonian Institution. While their primary objective was to participate in the



17th International Congress of Americanists in Buenos Aires their main focus was to scrutinize the locations of contentious ancient human findings and assess the original samples housed in local museums (Podgorny and Politis 2000). Hrdlička extended his analytical approach and interpretations of North American fossils to the South American samples and archaeological sites during his visit (Hrdlička 1912a). In Brazil, he examined the specimens from Lagoa Santa at the National Museum of Rio de Janeiro and explored various archaeological/paleontological sites in Argentina to inspect human fossils and their contextual information. Following a meticulous examination, he identified taphonomic disturbances and inconsistent associations between age and geological strata. He argued that previously described bone alterations presumed to indicate fossilization were more indicative of past environmental conditions than deep antiquity (Hrdlička 1907, 1912a). Concerning morphology, he contended that the presence of the dolichocephalic skull shape among recent native groups was insufficient evidence of ancient chronology. Hrdlička asserted that humans of deeper geological antiquity should exhibit larger morphological differences compared to contemporaneous ones, similar to the distinctions between *Homo sapiens* and Neanderthals (Hrdlička 1907, 1912a). Essentially, he anticipated that if the bones were ancient, they would resemble Neanderthal bones rather than those of Native Americans. He argued that misleading morphological descriptions and orientation of specimens led previous researchers to erroneous interpretations (Hrdlička 1912a). Overall, he criticized previous reports as incomplete, unsatisfactory, and riddle with defects and uncertainties (Hrdlička 1912a). Consequently, he refuted the presence of humans during early times in North and South America, concluding that people arrived on both continents through a recent migration from Northeast Asia via Beringia during post-glacial times (Hrdlička 1907, 1912b). Given that, at that time, the oldest archaeological evidence in the source area (i.e., Asia) was from the Neolithic period, he proposed that the migration commenced after the

Neolithic era, i.e., 10,000 years ago (Hrdlička 1912b). Subsequently, a majority of the international scientific community abandoned the notion of humans having great antiquity in the Americas, now understood as part of recent human history. Notably, contemporaneous such as Hooton disagreed with Hrdlička, considering his stance on the recent date of the peopling of the Americas as outdated (Giles 2010). The post-glacial model proposed by Holmes and Hrdlička wielded significant influence within the international archaeological community establishing itself as the predominant framework in the first half of the 20<sup>th</sup> century. However, its impact was not as pronounced among South American scholars, with some exceptions (Podgorny and Politis 2000; but see Schobinger 1988, for a different argument). From the 1920s to the 1960s, systematic excavations took place in North America, revealing fluted projectile points known as Folsom and Clovis, named after the sites where they were discovered (Fig. 2). These artifacts were consistently found in close proximity to extinct Pleistocene fauna across numerous archaeological sites throughout different regions of North America, providing evidence of human-mega-fauna coexistence during the Ice Age (Figgins and Hook 1927; Hester 1972). The sudden appearance of these artifacts in the archaeological record, with no preceding culture or human evidence in the lower strata, led to the interpretation that they represented the material culture of the first humans arriving in the continent. This interpretation gained strength in the 1960s when the first radiocarbon dating supported the correlation between the appearance of these cultural complexes, the retreat of the largest continental glaciers of North America, and the subsequent opening of an “ice-free” corridor (Meltzer 2021). Subsequently, a new model, known as Clovis First, emerged to explain the peopling of the Americas, representing a revisited and updated version of the earlier “postglacial model”. Clovis First depicted the first Native Americans as possessing a specialized culture characterized by big-game hunting and meat processing, constrained to a narrow time range of 11,500 to 11,000

radiocarbon years BP (Howard 1936; Haynes 1969). The successful hunters during this period were labelled “Paleoindians” (Roberts 1940), a term that has persisted in scientific literature to refer to the earliest Americans. For some scholars, the brief time range suggested a rapid and successful colonization of diverse landscapes (Martin 1973). In fact, a computer simulation study even hypothesized that humans could have reached the Magellan Strait in just 1000 years (Mosimann and Martin 1975).

The Clovis First model and its assumptions were applied to South America, interpreting its archaeological record in a manner similar to the discoveries in North America. The empirical foundation for this was derived from the 1930s excavations by Junius Bird at Cueva Fell in the Chilean Patagonia, where fishtail projectile points were found in association with extinct megafauna (Fig. 2; Bird 1938, 1969). Due to the parallels between this archaeological context and the Clovis discoveries, as well as the resemblance between Clovis and fishtail projectile points, Cueva Fell became identified as the South American equivalent of Clovis, earning the designation of the ancient “Clovis type site” in South America. Subsequent re-evaluation of the site yielded dates contemporaneous with Clovis, ranging from  $10,080 \pm 160$  to  $11,000 \pm 170$  (Waters and Stafford 2007; Waters et al. 2015). The idea of the presence of humans in South America concurrent with Clovis received support from the rapid migration model mentioned earlier (Mosimann and Martin 1975). Consequently, from the 1930s for several decades, South American prehistory was interpreted based on the model proposed for North America, assuming identical historical processes in both continents, and overlooking environmental differences, as well as concurrent technological and socio-economic adaptations (Dillehay et al. 1992). Ironically, after dismantling the Holmes-Hrdlička dogma, it was replaced with an equivalent model, with 10,000 years considered as the new “allowed antiquity” (Krieger 1964), while South American evidence and interpretations by South American scholars were not given

due consideration (Ardila Calderón and Politis 1989). Despite South American archaeological studies being less influenced by the Clovis model paradigm, a substantial North American influence persisted in research funding (e.g., National Geographic Society), networking (Annual Conference of the Society of American Archaeology), and publications (e.g., *Antiquity*) from the last few decades of the 20th century to the present day.

Within the Clovis First model, the term “Paleoindian” was coined to designate the first Americans, being applied to any discovery associated with extinct megafauna or Clovis projectile points (Roberts 1940; Wormington 1939). The limited emphasis on craniometric studies in the early 20<sup>th</sup> century regarding the peopling of the Americas could be attributed to the influence of Hrdlička, who consistently argued that the morphology of early American bones fell within the range of variation of contemporary Native Americans (Owsley and Jantz 1999; Jantz and Owsley 2001). Consequently, after Hrdlička’s publications on North America and South American fossil evidence, discussing the antiquity of early humans in the Americas became a taboo in Anthropology (Schobinger 1988). Currently, the only human burial associated with the Clovis complex is the Anzick skeleton from Montana, USA, discovered in 1968. Described as an infant male aged 1 to 2 years old, the skull shape is identified as dolichocephalic (Fig. 2; Lahren and Bonnischen 1974; Owsley and Hunt 2001). Some archaeologists argue that the association of this individual with Clovis is not sufficiently clear due to site being disturbed by a bulldozer, and the evidence was not recovered *in situ* (Taylor 1969; Steeves 2023). Recently, it became the first Native American genome to be fully sequenced, revealing connections with contemporary Native Americans, along with Asian ancestry (Rasmussen et al. 2015). This skeleton also holds significance in repatriation and provenance studies, as, after a thorough multi-disciplinary analysis, it was restituted to Native American communities, who reburied it in accordance with NAGPRA regulations.

*Back to a deep past: The early sites and the pre/post Last Glacial Maximum debate*

The Ameghino-Hrdlička debate on the early or late presence of humans in the Americas shaped the archaeological and bioanthropological research agenda for much of the 20<sup>th</sup> century (Politis and Bonomo 2011). However, in the 1960s, a paradigm shift began to emerge after several decades in which the “Clovis First” model dominated archaeological explanations on who were the first Native Americans. Critical evidence from South American archaeological sites such as Taima-Taima in Venezuela (Fig. 2; Cruxent 1967) and Lauricocha in Peru (Fig. 2; Cardich 1964) demonstrated the coexistence of humans and megafauna contemporaneously or even at earlier times than Clovis sites. Systematic excavations and the establishment of radiocarbon dating within the discipline led archaeologists like Osvaldo Menghin, Alex Krieger, and Alan Bryan to argue that evidence from certain sites in North and South America supported an earlier arrival of humans to the continent than suggested by Clovis evidence and the Clovis First model (Krieger 1964; Bryan 1973; Menghin 1975; Brzan 1978).

An intense debate unfolded at that time as these premises challenged the rigidly maintained Clovis First model by some North American archaeologists for decades (Lynch 1990). The controversy highlighted the inflexibility within the archaeological community, especially when compared to the more rapid acceptance of an earlier settlement in Australia during the 1960s (Gruhn 1997). Notable advocates of the Clovis First model included C. Vance Haynes and Paul Martin. Martin proposed a hypothesis for the rapid colonization of the continent and megafauna overkill (Martin 1973), while Haynes expressed scepticism about findings interpreted as Pleistocene age only if it showed undeniable traces of humans in undisturbed geological deposits, coupled with reliable radiometric ages as significant chronological proof (Haynes 1969).

Among the most significant archaeological sites with reliable Pleistocene dating that contributed to pushing back the chronologies (or at least

the discussion on human antiquity) to the late Pleistocene, there are several in North America, such as Meadowcroft in Pennsylvania (Adovasio et al. 1975), Paisley Cave in Oregon (Cressman et al. 1940), Cactus Hill in Virginia (McAvoy 1997), Manis Mastadon site (Gustafson et al. 1979), and Valsequillo in southeastern Mexico (Irwin-Williams 1967, 1969, 1978). In South America, relevant sites include Cerro La China, Cerro El Sombrero (Flegenheimer and Zárate 1997), Piedra Museo (Miotti et al. 1995), Los Toldos Cueva 3 (Cardich et al. 1973; Cardich and Flegenheimer 1978), and Arroyo Seco 2 (Steele and Politis 2009) in Argentina; Quebrada Jaguay (Sandweiss et al. 1998), Pikimachay (MacNeish 1979) and Pachamachay (Rick 1980) in Peru; Taima-Taima (Bryan et al. 1978) in Venezuela; Cueva del Medio (Nami 1987) and Monte Verde II (Dillehay 1984, 1989) in Chile; Pedra Pintada (Roosvelt et al. 1996), Alice Boer (Beltrão et al. 1983) and Toca do Boqueirão da Pedra Furada (Guidon and Delibrias 1986) in Brazil; El Abra (Correal 1986) and Tibitó (Correal 1990) in Colombia; and El Inga (Mayer-Oakes 1986) in Ecuador, among others (Fig. 2).

Despite the large number of sites predating the Clovis chronology, Monte Verde was the first to break the “Clovis barrier” (Meltzer et al. 1997). Monte Verde is an open-air site with two components associated with different occupations (MV-I, MV-II) and it has excellent preservation of archaeological evidence (Fig. 2; Dillehay et al. 2015). The site was interpreted as a campsite associated with the remains of long tent-like dwellings, human footprints, stone artifacts, animals, plants, and wood remains (Dillehay and Collins 1988; Dillehay et al. 2015). Thus, owing to its excellent preservation, it depicts a culturally diversified lifeway, contrary to what was proposed by the Clovis model. The higher number of sites dating to the late Pleistocene and early Holocene times in South America compared to North America could be due to differences in paleoclimate conditions and archaeological visibility. For instance, ice sheets were more extensive in North America’s lands (covering 80% vs. only 20% in South America),

which could have greatly altered the landscape in a way that destroyed or reburied archaeological sites (Dillehay 1999). Additionally, since Holocene environments were configured earlier in South America than in North America (14–12,000 years BP vs. 11–10,000 years BP), there was a longer time and more stable environmental conditions allowing for the preservation of archaeological materials (Dillehay 2000).

Johanna Nichols presented the pre-LGM hypothesis for human dispersals to the Americas in the early 90s, a position she has continued to develop and maintain (Nichols 1990, 2000, 2008, 2015). Her hypothesis challenges the Clovis chronology and suggests a more prolonged and complex dispersion with considerable linguistic diversity among Native Americans (Nichols 1990, p. 496). Nichols argues that the extensive linguistic diversity among Native American languages, estimated at 140 language stocks, indicates a lengthy and complex dispersion that is not feasible within the Clovis chronology (Nichols 1990, p. 496). She questions the three language stocks proposed by Greenberg and collaborators (1986), proposing instead that each of them represents different waves of dispersion (Nichols 1990, p. 501–502). According to her calculations, it would take around 50,000 years for the 140 language stocks to diverge, assuming conservative divergence rates. This divergence timeframe aligns better with the dating of pre-Clovis sites. Additionally, Nichols argues that if the Amerind language family entered the Americas as a single language, there would be no possibility for foreign contact in the initial millennia, and all contacts would have been between closely related languages (Nichols 1990, p. 509). Considering the depth of 50,000 years as a very conservative estimate and the possibility of multiple dispersion events, she proposes that the first human dispersion to the Americas occurred ~35,000 years BP (Nichols 1990, p. 511). In her overall model, Nichols suggests a continuous stream of occasional coastal immigrants moving gradually around the Pacific Rim, originating as far south as Southeast Asia and eventually reaching Tierra del Fuego (Nichols 2015, p.

122). Despite proposing several separate arrivals, she emphasizes that this does not contradict the evidence of one or very few genetic ancestral lineages for all Native Americans, as a single diverse genetic population can encompass multiple languages (Nichols 2008).

In contemporary archaeological understanding, the presence of humans in the Americas before Clovis period is widely accepted. The debate that lasted for decades, involving professional visits to controversial sites and meticulous radiometric dating, has contributed to recognizing a pre-Clovis presence. The earliest Native Americans are now seen as engaging in a more generalized forager lifestyle, which does not exclusively rely on hunting, particularly in South America (Krieger 1964; Ardila Calderón and Politis 1989; Gruhn and Bryan 1991; Dillehay 1999). Clovis is interpreted as a subsequent, specialized lifestyle that developed during the early Holocene, lasting for almost five centuries in North America, primarily on the Great Plains (Waters and Stafford 2014; O'Brien and Buchanan 2017). Additionally, there are now tens of sites with reliable Pleistocene evidence that surpasses the previously mentioned list, presenting dates contemporaneous or even earlier than those associated with Clovis. Some of these sites feature stemmed fishtail points, considered by some as the South American equivalent of Clovis points, although this analogy is debated (Bird 1969; Fiedel 1987; Lynch 1990; Nami 2020). However, certain sites and evidence, including the earliest occupations of some sites (e.g., Monte Verde I, Toca do Boqueirão da Pedra Furada in Serra da Capivara; Mastodon Cerutti in California; Chiquihuite cave in Mexico; Fig. 2) remain controversial. The dates associated with these sites are currently under debate, and their interpretations continue to be subjects of discussion (Guidon and Delibrias 1986; Meltzer et al. 1994; Dillehay et al. 2015; Holen et al. 2017; Gruhn 2018; Holen et al. 2018; Prates and Politis 2018; Dillehay et al. 2021). Presently, archaeological evidence from North and South America is interpreted separately, without

necessarily projecting ideas from one region to interpret data from the other.

Claims of hominin in the Americas beyond the expected distribution of *Homo sapiens* have been proposed, suggesting the arrival of another hominin species. Early dating of some archaeological sites, such as the Cerruti Mastodon site in California (~130,000 years BP) and sites in eastern Brazil (Serra da Capivara locality, ~30,000 years BP), along with the characteristics of lithic artifacts, led some authors to suggest that *Homo erectus* was the species that arrived first in South America (Beltrão et al. 1986; Dreier 1986; Lumley et al. 1987; Schobinger 1988). This conclusion emerged in the 1980s, combining two ideas: the increasing evidence for archaeological sites older than 30,000 years BP, and the prevailing notion at the time that *Homo sapiens* originated around 40,000 years BP. Within this context, if earlier sites are accepted in the Americas, then it was proposed that another hominid arrived before than *Homo sapiens*. As *Homo erectus* was interpreted to be the widespread across Asia in the 1980s, it became the leading candidate. More recently, the Cerruti Mastodon site reported mastodon bones with presumed anthropic cut marks and breakage patterns, raising the question of which hominids might have arrived in the Americas 130,000 years ago, with Denisovans suggested as a possibility due to their presence in Asia during the middle to late Pleistocene (Fig. 2; Holen et al. 2017; Xia et al. 2020; Brown et al. 2021). However, these explanations face strong criticism within the archaeological community, with rebuttals challenging the interpretations of the Cerruti Mastodon site (Braje et al. 2017). As of now, there is no consensus regarding these claims, and they remain topics of debate and further investigation.

The current debate on the antiquity of the first humans in the Americas focuses primarily on archaeological studies providing cultural evidence, paleoclimatic studies delivering environmental data from the ancient past, and genomic studies offering insights into the diversification events of the founding populations. The key chronological aspect under discussion in

whether the first migrations occurred before or after the LGM (Madsen 2004; Becerra-Valdivia and Higham 2020; Meltzer 2021). Two main migration routes are considered: one suggests a departure from Alaska before the LGM, following the interior ice-free corridor while it was still open, and the other proposes a migration path across Beringia following a coastal Pacific route to the south. Recent radiocarbon dating of seeds associated with human footprints from the White Sands National Park in New Mexico (23–21,000 years BP) supports the idea of a pre-LGM date for the arrival of the first humans to North America (Fig. 2; Bennett et al. 2021; but see Haynes 2022; Madsen et al. 2022). A recent study modeling paleoclimate records and climate models, suggests that 24,500–22,000 and 16,400–14,800-years BP were the most environmentally favourable periods for migration along the coast (Praetorius et al. 2023). Additionally, the Santa Elina evidence in Brazil, featuring lithic artifacts associated with remains of the extinct giant ground sloth *Glossotherium phoenesis*, supports the notion of human arrival at least during the LGM (28,000–18,000 years BP) (Fig. 2; Pansani et al. 2023). Researchers advocating for a very early arrival (pre-LGM) are more inclined to consider the coastal route as the most plausible one, as it aligns with the evidence of the earliest sites in South America. In contrast, the ice-free corridor model is still debated, particularly regarding whether the crossing occurred before or immediately after the LGM. Therefore, the antiquity debate is intricately connected to discussions on the mode of expansion and migration routes.

Some indigenous archaeologists argue that many scholars underestimate the number of archaeological sites associated with Pleistocene times, neglecting indigenous knowledge on the antiquity of humans in the Americas and downplaying the significant relationship that indigenous people have with their land (Steeves 2023). From this perspective, the denial of late Pleistocene sites by the archaeological community is seen as a political construct that perpetuates colonial power and control over indigenous

heritage, material remains, and history. Steeves asserts that there is evidence suggesting the availability of the Beringian landmass for most of the last 100,000 years BP. She also points to evidence of human voyaging trips dating back at least 60,000 years BP. According to this viewpoint, the ecological diversity of the Americas requires a much longer time frame for people to move across and adapt to new environments (Steeves 2023). Steeves has created an online database (<https://www.tipdba.ca/>) that reports hundreds of archaeological sites older than 14,000 years, supporting her argument that the Pleistocene archaeological signal is more extensive than commonly acknowledged.

### **The question on the ancestral origins: Who were the migrant populations or where did the founding population split?**

By the time of the encounter between the European explorers and Native Americans, various speculations emerged regarding the origins of the indigenous peoples. Some suggested that Native Americans might be descendants of Noah, one of the lost tribes of Israel, survivors of the submerged continent Atlantis, or “immigrants” coming from Egypt or Asia (Dillehay 2000; Lavallée 2000; Adovasio and Page 2002; Meltzer 2021; Raff 2022). However, these were largely speculative claims without scientific evidence. In the 16<sup>th</sup> century, the Spanish priest Fray Bartolomé de las Casas considered the possibility that Native Americans had a very ancient presence in the Americas and viewed them as “very civilized” people, comparable to the Greeks and Romans (Bartolomé de Las Casas 1527-66). In the late 16<sup>th</sup> century, the Jesuit José de Acosta anticipated the idea that the first Americans came from Asia (northern Asia) following a land bridge (Beringia). Acosta proposed that they expanded from Northwestern North America to the rest of the continent, including Central and South America (Acosta 1590). This perspective gained prominence and was championed by

figures like Thomas Jefferson, the former governor of Virginia and later U.S. president, in the late 18<sup>th</sup> century (Jefferson 1788). It continued to be a dominant view for centuries and was strongly supported by Hrdlička in the early 20<sup>th</sup> century (1907, 1912).

In the 19<sup>th</sup> century, influenced by polygenist models explaining human origins on various continents, the conventional idea of a single Asiatic origin through Beringia began to be challenged. With the discovery of early evidence from different archaeological sites, especially those in South America, the focus of the debate on the antiquity of the first Americans shifted to exploring alternative migratory paths within the Americas. The recognition that some of the earliest archaeological sites in South America predated Clovis evidence (the oldest accepted evidence on the “first Americans” at the time), raised questions about the routes taken by the first humans to reach the southern tip of the continent. Alternative models emerged as a response to the mainstream view that migration occurred through Alaska, Beringia, and North America to South America. These alternative models included considerations of expansions originating from other continents such as Europe, Africa, or Oceania. Additionally, alternative routes within Northeastern Asia were proposed, including not only the ice-free interior corridor that opened after the LGM but also the Pacific coastal route before the LGM. The exploration of these alternative scenarios aimed to provide a more nuanced understanding of the complex pathways that early humans might have taken when arriving to the Americas.

#### *A South American origin for humanity: the skeletons of the Pampean plains*

During the second half of the nineteenth century, some naturalists proposed an independent origin for South Americans, aligning with the polygenic view of the origin of humanity (Ameghino 1880; Moreno 1882; Ameghino 1906). Their claims were based on anatomical descriptions, interpreting phenotypic variation as indicative of an independent and lengthy evolutionary history. The skull morphotypes found in

the Americas were a key focus of these anatomical descriptions (Morton 1839; Retzius 1850). In addition to studying skull morphologies, scientists evaluated cranial variation among Native Americans. Some argued that this variation was low when compared to groups from the same continent but high when compared to groups from other continents (Morton 1839; Broca 1861; but see von Humboldt 1810 for descriptions on high heterogeneity). This interpretation resonated with polygenist ideas prevailing at the time, which posited that each continental human group (Americans, Europeans, Asians, Africans, Oceanics) had an independent origin and diversified within each continent over time (Morton 1839; Retzius 1844; Broca 1861). There were also dissenting voices, for example, those who favoured the idea of a single origin of humanity followed by dispersal across the world acknowledged considerable differences in cranial shape between contemporaneous populations and more ancient skeletons (Foster 1873). The scientific discourse of the time reflected a complex interplay of ideas about human origins, influenced by prevailing anthropological and racial ideas.

In the late 19<sup>th</sup> century, Francisco Moreno proposed a unique model regarding the origins of humans in the Americas. Observing that dolichocephalic individuals were predominantly found in South America and Oceania, and that Native Americans exhibited “all the biological and cultural evolutionary stages from humanity”, Moreno postulated the existence of an ancient and now partially submerged meridional continent. According to his model, the continent served as the cradle of the first humans (Moreno 1882). Moreno suggested that the initial inhabitants of this continent, characterized by a dolichocephalic skull shape, might have interbred with more recent brachycephalic populations. Alternatively, some of these populations might have remained geographically isolated, such as the Australians and Fuegians, who he considered as relicts of the first human populations. In a rather speculative extension of his model, Moreno even proposed that Neanderthals could be viewed as an Euro Asiatic variant that descended from the first

humans originating in South America and later migrated to Europe (Podgorny 2009). These ideas aligned with prevalent explanations of the time, suggesting that the dolichocephalic skull morphology, associated with the most ancient groups, underwent transformations over time, eventually giving rise to the more recent brachycephalic shape (Virchow 1892). Others, like Morton (1839) stressed the unity of all American populations which would have descended from a single common ancestor. The debate over the unity or diversity of American populations and their origins remained a complex and evolving discourse.

Decades later, Ameghino expanded on the idea of an independent origin for humans in the Americas, proposing that South America was not only the origin of Native Americans but the cradle of all humanity (Ameghino 1880, 1889; Podgorny 2009). To support these bold claims, he presented evidence such as the presence of primate fossils in South America in older geological layers compared to other continents (i.e., Cretaceous vs. Eocene). Ameghino argued that this allowed for the complete evolution of most primate phylogeny in South America from the Oligocene (when Old World monkeys migrated through the land bridge that connected Africa and South America) until recent times (Ameghino 1909). In his book “Phylogeny” (Ameghino 1884), he posited that the Order Primates originated and diversified in Patagonia. According to his theory, different groups of Hominidis then expanded across the world in three consecutive waves: 1) During the Eocene, Hominidis migrated to Africa and Asia, giving rise to the Asian and African Apes, as well as specimens found in Heidelberg, Germany and Java, Indonesia (assigned today to *Homo neanderthalensis* and *Homo erectus* respectively; Fig. 2); 2) At the beginning of the Pliocene, some Hominidis migrated through an ancient natural bridge, presumably existing between Guaiana and Senegal. This migration gave rise to several populations of *Homo afer* settling in the tropics, including native Australians, Philippine Negritos, Hottentots, and San. Simultaneously, *Homo sapiens* originated in South America

during the middle Pliocene, resulting from morphological changes occurring in a chronologically linear fashion: the *Tetraprothomo* found in the site Monte Hermoso (Upper Miocene; Fig. 2) descended from the Hominidis, followed by *Tritrothomo*, the *Diprothomo* found in Buenos Aires harbor (Lower Pliocene; Fig. 2), and *Prothomo/Homo pampaeus* found at several locations of the Atlantic coast, such as Arroyo La Tigra and Necochea (Ameghino 1909, 1910b, 1913; Fig. 2). *Homo pampaeus* was considered the direct ancestor of *Homo sapiens*. While fossils for all of this species were found in the Argentinean Pampas, *Tritrothomo* remained a theoretically defined species without associated fossils; 3) Finally, during the Quaternary (at that time: upper Pliocene and lower Pleistocene) *Homo sapiens* migrated into Asia through North America, giving rise to Mongols, and through a natural bridge from Canada towards Europe, gradually evolving into Caucasians. Meanwhile, others regressed into Neanderthals (e.g., Spy-Belgium, Krapina-Greece, Chapelle-aux-Saints-France). Additionally, Ameghino considered some South American fossils as parallel branches between the clades *Prothomo* to *Homo Sapiens* (Fontezuelas site, Fig. 2), while others were assigned to species equivalent to *Homo pampaeus* that went extinct over time (*Homo sinemento*, *Homo caputinclinatus*).

Regarding contemporary Native South Americans, Ameghino proposed that they all descend from the Lagoa Santa individuals found in Brazil by Peter Lund, who, in turn, descend from the hominid species that evolved in the Argentine Pampas (Ameghino 1917; Lund 1845; Fig. 2). He identified two main groups inhabiting different geographical settings, interpreting them as descendants of the earliest Americans: a more robust one in Patagonia and a more gracile one in the Argentinean Northwest (Ameghino 1917). Despite variations in the interpretation of the morphological characteristics of the ancient skeletons, both Lund and Ameghino independently concluded that these findings did not chronologically align with the European Stone Age or contemporary Native Americans. Instead,

they believed that these skeletons represented an independent evolutionary lineage that originated separately from the European ones, evolving locally and giving rise to the contemporaneous Native Americans (Achim 2010).

Despite some scholars immediately expressing disapproval of the idea of the origin of humanity in South America (Burmeister 1891; Zeballos 1879; Virchow 1892; Outes 1909; Mochi 1910; Schwalbe 1910; Hrdlička 1912a), other researchers continued to support it even after Ameghino passed away (Zeballos 1920; Vignati 1922; Castellanos 1937; Rusconi 1959; Sergi 1910). As mentioned earlier, Hrdlička was the one who debunked the debate at the international level, but the discussion on the antiquity of humans in South America persisted locally until the end of the 1970s (Schobinger 1961; Vignati 1963; Parodi Bustos 1978; Daino 1979; Tonni et al. 2001; Bonomo 2002). Overall, Ameghino's interpretations have faced strong criticism for several reasons: the age of the sediments where the materials were found was Quaternary rather than Tertiary (Outes et al. 1909; Frenguelli 1920; Frenguelli and Outes 1924), the evidence was not found *in situ*, either due to stratigraphic disturbances or intentional fraud (Bonarelli 1918; Boman 1919; Boule 1921), and the anatomic identification of bones was incorrect. Most of the bones are now recognized as belonging either to *Homo sapiens* skeletons, fossil Platyrrhines, or other mammal species (Bordas 1942; Forasiepi et al. 2007; Tejedor and Rosenberger 2008; Pucciarelli et al. 2010).

In contemporary times, recent radiocarbon dating results, coupled with archaeological findings from systematic excavations, and more detailed stratigraphic and geoarchaeological studies, indicate that the oldest human evidence in South America could be traced back to the late Pleistocene (Politis and Bonomo 2011; Dillehay et al. 2012; Bueno et al. 2013; Rademaker et al. 2014; Dillehay et al. 2015). Interestingly, despite the local origin and the Pliocene antiquity of humans in the Americas turning out to be incorrect, most of the skeletons recovered by Ameghino and Lund have been radiocarbon



dated with modern techniques and are still considered among the oldest in the continent (Neves et al. 2007a; Taylor 2009; Feathers et al. 2010; Politis and Bonomo 2011; Politis et al. 2011; Fontugne 2013; Moreno-Mayar et al. 2018).

*East Asian origin and the North American ice-free interior corridor*

The proposal of an Asiatic origin for all Native Americans, as a result of individuals migrating through Beringia, is a very old idea that was first posed by Friar José de Acosta (Acosta 1590). It was based on the phenotypic similarities between Native Americans and the contemporaneous populations from North Asia. This idea persisted over the centuries, but only in the 19<sup>th</sup> century was it scientifically presented by some scholars (von Humboldt 1810; McIntosh 1843; Quatrefages 1887; Virchow 1892), despite the prevalence of polygenism among the most popular anatomists of the nineteenth century (Morton 1839; Retzius 1844; Broca 1861). The Asiatic origin of Native Americans was revisited when polygenism was questioned after the publication of Darwin's *The descent of Man* (Darwin 1872). The work of Darwin represented a powerful monogenist claim suggesting that all human groups have a common origin from an Ape-like ancestor. Subsequently, Hrdlička, based on the analysis of fossil evidence indicating that "Primates of the higher forms" were only found in Africa, Europe, and Asia, and the established fact at the time by which *Homo sapiens* descended from Neanderthals, interpreted that humans originated in the continent where the oldest Anthropoid fossils were found: Asia (Hrdlička 1907, 1912b). Interestingly, other researchers like Lehmann-Nitsche independently proposed an Asiatic origin and a very early migration based on the similarities that he found between South American fossils, such as the Monte Hermoso atlas assigned to the species *Homo neogenus* (considered by Ameghino as the oldest Hominidae, i.e. *Tetraprothomo argentinus*; Fig. 2) and Asiatic ones belonging to the species *Homo erectus* (then known as *Pithecanthropus erectus*). Lehmann-Nitsche interpreted that Asia and Central

America were previously geographically united, allowing the migration of fossil species from Asia to the Americas (Lehmann-Nitsche 1910).

As previously described, following the publication of Ales Hrdlička's monographic works describing early skeletons from North and South America, the idea of an Asian ancestry for all Native Americans became consolidated (Hrdlička 1907, 1912). This notion gained strength when Hrdlička advocated for the strong phenotypic similarities among all Native Americans (i.e., "the unity of Indians", an idea first proposed by Morton 1842), as well as the geographic proximity between both continents (Hrdlička 1912b). Despite the similarities among Native Americans, Hrdlička recognized some differences ("subtypes") that could be attributed to different groups departing from Asia at successive times. He identified groups with a prevalence of dolichocephalic skull shape (which he considered were represented today by Algonquian, Iroquois, Piman-Aztecs, among others), followed by groups with brachycephalic skull shape (represented by Eastern North American mounds, Antilles, Mexico, Peru), and finally the Inuit and Athapascan (Hrdlička 1912b).

In the 1930s and 1940s, the proposal of an Asiatic migration via the Bering strait became a perfect fit for the "Clovis First" model, which was increasingly becoming the hegemonic explanation for the peopling of the Americas. As described in the section relative to a postglacial arrival, the prevailing interpretation suggested that successful hunting groups rapidly expanded, following their prey, i.e., the Pleistocene megafauna (Martin 1973). The initial independent support for the "Clovis First" model came from paleoenvironmental evidence showing the retreat of glaciers and the creation of an ice-free corridor, through which the first settlers could have migrated into North America via Beringia (Johnston 1933). The concentration of most "Clovis" sites in the North American Great Plains lent significant support to this model (Mandryk et al. 2001). Although the ice-free corridor route of migration lacked sufficient archaeological evidence at the time (MacNeish

1959; Rouse 1976), it quickly became a “myth” widely accepted by several scholars, as described by Fladmark (1986).

The “Clovis First” model gained consolidation with the advancement of radiocarbon techniques and their immediate application in archaeology. In the 1960s, C. Vance Haynes published the first radiocarbon dates on the Clovis and Folsom archaeological sites (Haynes 1964; Fig. 2). Subsequent to this, equivalent South American sites, such as Cueva Fell or Fell’s Cave in southern Chile, were also dated (Bird 1938, 1988; Fig. 2). Currently, despite the wide acceptance of archaeological sites associated with a chronology before “Clovis”, research on the ice-free corridor is ongoing but from a different perspective. Most studies are based on paleoenvironmental and archaeological evidence, suggesting that “Clovis people” migrated to the Americas through the corridor, though they may not represent the oldest human arrivals to the continent (Ives et al. 2014; Pedersen et al. 2016; Lesnek et al. 2018). According to the latest analysis, the Laurentide and Cordilleran glaciers began retreating approximately 17,000 years BP, but it was only around 14,000 years BP that the ice-free corridor became a viable passage (Dyke 2004; Potter et al. 2017; Margold et al. 2018). There are still some gaps in the archaeological record, such as the absence of lithic points resembling the Clovis ones in the archaeological sites in Beringia. Instead, they reveal alternative lithic technologies like the Nenana Complex from the Broken Mammoth site, with the earliest sites preceding Clovis by about 14,000 years (Fig. 2; Dixon 2001; Meltzer 2013).

*East Asian origin and the three-migrations model: the first interdisciplinary attempt*

Additional evidence for the Asian origin and rapid spread through the ice-free corridor was presented in the 1980s in a multidisciplinary paper written by Greenberg, Turner II, and Zegura (Greenberg et al. 1986). This model represents the first interdisciplinary effort to combine different kinds of biological and cultural data to explain the peopling of the Americas

based on the biocultural variation. It also served as the second independent support for the mainstream archaeological interpretations, suggesting that humans arrived in the Americas recently, spread quickly, and most of them descend from the same ancestral population of Asiatic origin. Consequently, it provided support for the “Clovis First” model. This multidisciplinary initiative was triggered after the publication of a series of papers by Greenberg in which he proposed the hypothesis that all the languages from South and North America fall into three groups, Amerind (the largest linguistic family), Na-Dene, and Eskimo-Aleut (Greenberg 1956, 1960). This idea was complemented by previous work by Turner II on dental variation, showing that Native Americans’ dental variation matches the North Asian “sinodont dental pattern” (Turner II 1983a, 1983b). Those three language clusters were also identified when analysing dental and genetic data, interpreted as standing for three separate migrations.

Greenberg, Turner II, and Zegura combined linguistic, dental, and genetic evidence to propose that the Americas were settled by three independent migrations at different moments of the Holocene. This tripartite model, resonating with the one proposed before by Hrdlička (Hrdlička 1912b), was built on the independent analysis of different types of evidence by experts in each field (linguistic, dental, genetic). Later, these findings were combined to generate a unified model for explaining the peopling of the continent. Based on the linguistic classification of Native American languages into three stocks, genetic and dental resemblances found between Native American and Asian populations, the low human dental variation in the Americas compared to Asia, and the absence of human skeletons earlier than the late Pleistocene, they argued for a recent and Asiatic origin characterized by three subsequent migrations (Greenberg et al. 1986). The first migration is represented by the Amerind language family, the more extensive, diverse, and ancient one. The second is represented by the Na-Dene family, associated with the Athabaskan languages, geographically

corresponding to groups from the North-West of North America. The third and last migration is represented by the “Eskimo-Aleut” family, as their languages are considered less differentiated (Greenberg 1987). Additionally, Greenberg dated the arrival of these groups, associating the Amerind family/migration with Clovis approximately 12,000 years ago, Na-Dene 7,000 years ago, and the “Eskimo-Aleut” arrival 6,000 years ago (Greenberg 1987). Complementarily, since dental variation was described as higher in the North than in the South of the continent, they supported the idea that migrating populations entered through Alaska. The absence of sharper linguistic differentiation supported the rapid expansion model proposed by Martin and Klein (1984). Molecular methods were in their infancy in 1986, but Zegura attempted to find genetic patterns that matched the dental and linguistic data found by Greenberg and Turner II. Despite his efforts, the genetic evidence did not align with the dental or linguistic data (Meltzer 2021). Therefore, the authors argued that the genetic results provide secondary support to the model (Greenberg et al. 1986, p. 486).

A separate discussion is warranted for the model proposed by Christy G. Turner II (1933–2013) based on the non-metric dental variation of Native Americans. Turner II likely drew inspiration from Hrdlička’s assessment of shovel-shaped upper incisors as one of the features characterizing all Native Americans and supporting their biological unity (Hrdlička, 1920), as well as Hanihara’s proposal of biological distances between human groups based on dental morphology complexes (Hanihara 1967). Turner II expanded upon these ideas and defined a comprehensive protocol of non-metric dental traits present in populations from different continents, albeit at different frequencies. This allowed for reconstructing population histories through a method he named “dento-chronology” (Turner II 1971, 1983b, 1986, 1990). Based on the frequency of non-metric dental features, Turner II divided the dental variation of Asian groups into two: those presenting a derived sinodont pattern (i.e., Northeast Asians: China, Mongolia, Japan,

Korea), and those from Southeast Asia characterized by the basal “sundadont dental pattern” (i.e., Southeast Asians and Pacific populations from Polynesia and Melanesia, including ancient groups such as Jomon and Ainu) (Turner II 1983a). These dental patterns could be distinguished based on the frequencies of eight out of 29 discrete dental features (Turner II 1990). Sinodont populations were characterized by high frequencies of upper first incisor shoveling, upper first incisor double shoveling, one-rooted upper first premolar, upper first molar enamel extensions, pegged/reduced/missing upper third molar, lower first molar deflecting wrinkle, and 3-rooted lower first molar; whereas sundadont populations have significantly lower frequencies of these traits and a higher frequency of four-cusped lower second molar (Scott and Turner II 1997; Turner II 1983a, 1990; Scott et al. 2016). According to the model, the generalized sundadont dental complex originated in Southeast Asia during the late Pleistocene (25,000–40,000 years BP). Sundadont populations spread southwards to the Pacific islands and also northwards, as the pattern was observed in the oldest skeletons from Japan (Turner II 1990), specifically the Minatogawa individuals dating to approximately 18,000 years BP (Fig. 2; Matsu’ura and Kondo 2010). Since the sundadont pattern has been observed in both mainland and island Southeast Asian samples, Turner II concluded that individuals presenting this dental complex were present when these areas were connected by the Sunda shelf during the Pleistocene (Turner II 1990). He considered that the more specialized sinodont complex evolved in Northeast Asia from the sundadont during the Late Pleistocene (Turner II 2006).

According to Turner II, since all Native Americans, past and present, fall within the sinodont pattern (Turner II 1990), they descend from the same ancestral sinodont population originating in Northeast Asia. Additionally, he divided the sinodont variation in the Americas into three groups, perfectly matching Greenberg’s language families. By assuming that the dental features change at a constant rate (Turner II

1986), he calculated the MMD (Mean Measure of Divergence) to estimate the time elapsed since these groups split. From this, he concluded that the Amerind groups split 14,000 years ago from Northeast Asian populations, followed by the Na-Dene and the Inuit, in line with the expectations of the “Clovis First” model. However, Turner II faced criticisms, including those from geneticist Emőke Szathmáry who argued that Turner II was aligning his results with those of Greenberg (Greenberg et al. 1986:490). Other scholars contended that dental variation is more complex among Native Americans, and that the sundadont pattern is indeed present in individuals from Brazil, Mesoamerica, Patagonia, and the Andes (Lahr 1995; Haydenblit 1996; Powell 1997; Sutter 2005). A controversy also surrounds the dental pattern described for the Zhoukoudian Upper Cave individuals from North China dating to approximately 35,000 years BP (Fig. 2; Li et al. 2018). While Turner II consistently interpreted these fossils as presenting the sinodont pattern (Turner II 1986; Turner II et al. 2000), others interpret them as sundadont (Brown 1998; Delgado 2007). Delgado (2007) points out that despite reliable biological affinities being established when at least 7 dental features are present (Scott and Turner II 1997), only 4 out of 9 of the sinodont features could be registered in the Zhoukoudian Upper Cave individuals. Moreover, only 2 of those features’ present similar frequencies to the ones expected by sinodonts (Delgado 2007). Overall, Turner II and collaborators (2000) suggest that the Zhoukoudian Upper Cave individuals, as well as some Native Americans, may exhibit some sundadont features, but testing this is challenging due to the low sample size of ancient samples. This conclusion has direct implications for explanatory models since Asian fossils are crucial for interpreting human diversification in the Americas (Neves and Pucciarelli 1989).

Almost forty years after its publication, the three-migration model remains embedded in many of the studies focused on the peopling of the Americas. As Bolnick and collaborators argued (Bolnick et al. 2004), it serves as the null

hypothesis for many geneticists, against which new genetic data is tested, and is also used as the classificatory scheme in interdisciplinary studies comparing genetic and linguistic variation. However, various aspects of the model have faced strong criticism, such as the multilateral comparison method that assembled superficial similarities without distinguishing affinities among languages due to common origin (Campbell 1988; Goddard and Campbell 1994; Bolnick et al. 2004). The conclusions on the unity of the Amerind family, have also been criticized as an oversimplification, both linguistically (Campbell 1988; Gruhn 1988; Nichols and Peterson 1996) and biologically (Neves et al. 2007a). Despite these criticisms, one of the first studies based on whole-genome sequencing analysis of present-day populations supports the tripartite model proposed by Greenberg and collaborators (1986). It postulates a unique ancestral population and a post-LGM divergence of the Native American founder population, followed by subsequent migrations of Na-Dene and Inuit groups (Reich et al. 2012; Reich 2018). Similarly, in line with the three-migration model, Kitchen and colleagues (2008) proposed that several waves of migration occurred from a single source population, which initially diverged from northeast Asia approximately 40,000 years ago. The authors further suggested that the initial entry by an early Amerind group of approximately 1,000-5,400 individuals occurred around 15,000 years ago.

Concerning the contribution of dental studies to investigate the peopling of the Americas, Christy Turner II has left an enormous research legacy on dental anthropology, continued by his former students, such as G. Richard Scott, as well as other scholars up to the present day. Recent studies support sinodont dental patterns in some early Holocene skeletons (Owsley et al. 2010; Chatters et al. 2014; Delgado 2015; but see Powell 1995; Haydenblit 1996; Powell 1997; Sutter 2005; Rodriguez Flores and Colantonio 2015). Geographical substructure matching linguistic diversity has been observed when studying the dental variation among late Holocene

Native Americans (Bollini et al. 2005; Scott and Turner II 2008; Delgado-Burbano 2012; Stojanowski and Johnson 2015). In a recent reanalysis of Turner's dataset, Scott and collaborators confirmed the unique contribution of the sinodont component to explain the origin of Native Americans. They even coined the term "Super-Sinodont" to refer to the very specialized dental pattern of Native Americans, presenting higher frequencies and more pronounced expressions than their sinodont Northeast Asian counterparts (Scott et al. 2016). However, the three-wave model was successfully replaced as an explanatory framework by the Beringia Standstill Model (as described later) (Hoffecker et al. 2016; Scott et al. 2016; Scott 2018). Contrary to the dental homogeneity described by Turner II for all Native Americans (Turner 1986, 1990), more regionalized patterns have been fully described in the last decades (e.g. Sutter 2005; Bollini et al. 2009, 2012; Delgado 2015). Moreover, new dental patterns have been detected, such as the geographical extension of the Uto-Aztecan premolar, present in individuals not necessarily associated with the Uto-Aztecan language stock (i.e., eastern North America), including individuals from present-day Mexico (i.e., southern North America), as well as others from the Northwest of South America (Delgado et al. 2010).

Postcranial studies have been also conducted to address questions regarding the biological diversification of Native Americans. Some of the results indicate a large variation in the postcranial skeleton of the earliest individuals, although they overlap with the range of variation present among recent Native American populations (Auerbach 2012). As North American early Holocene and late Holocene skeletons have demonstrated a wider body and higher body mass than Old World skeletons, these results suggest that more recent Native Americans appear to have descended from the same source population as the earliest Native Americans (Auerbach 2012). A study comparing femur variation as a proxy for body size among southern South American populations showed that divergence in body size could be the result of directional

selection associated with cold temperatures (Béguelin 2010). Overall, postcranial variation is highly influenced by ecological factors, so it should be studied complementarily with craniometric or genetic analysis.

#### *Asian origin and the coastal or kelp highway along the Pacific*

The Pacific coastal route has emerged as a robust reaction and a more viable alternative to the ice-free corridor model for explaining the initial arrival of humans in the Americas. Though initially proposed during the 1960s (Heusser 1960; Krieger 1961; Macgowan and Hester 1962), it gained significant traction as an alternative model for human migration routes between Asia and North America when revived by Knut R. Fladmark (Fladmark 1979), and more recently by Dixon (2001). According to the coastal route model, the initial migration route for humans into the Americas involved a series of sea-level refugia around the North Pacific coast of North America (Fladmark 1979). Within this model, Clovis evidence could be interpreted as the result of a more recent migration. A fundamental critique offered by proponents of this model against the ice-free corridor hypothesis was that the corridor was not available until the beginning of the Younger Dryas interval (13,000 cal BP), which postdates the earliest evidence from well-accepted late Pleistocene archaeological sites in North and South America such as Monte Verde and Meadowcroft Rockshelter (Fig. 2; Adovasio and Carlisle 1988; Dillehay and Collins 1988; Adovasio and Pedler 2017). Additionally, paleoenvironmental evidence highlights the absence of biotic communities providing essential resources for human survival in the ice-free corridor (Mandryk et al. 2001), along with the lack of archaeological sites in Beringia associated with Clovis and predating Clovis times (Raff 2022).

When the Pacific coastal route model was initially proposed, it relied on several premises grounded in paleoenvironmental and archaeological data (Fladmark 1979). Among the former, the existence of a significant biotic refugium

along the North Pacific coast, encompassing land mammals such like caribou (Heusser 1960). The model also considered evidence indicating that most of the coastal strip was free of ice, influenced by the Japanese current repeatedly bringing warm subtropical water masses (Pewe et al. 1965; Karlstrom and Ball 1969; Prest 1969; Reid 1970), as well as data showing sea levels 130 meters lower compared to present times (Tiffin 1976). Additionally, Fladmark presented cultural evidence for supporting the coastal route model, such as similarities between the Dyuktai culture of northeastern Asia and the early assemblages of the early north Pacific coast (Powers 1975). There was also archaeological evidence suggesting early maritime adaptations rather than a focus on big-game hunting (Aigner 1976). Despite this, Fladmark proposed that some groups spent most of their time along the coast, while others were primarily oriented towards the interior (Fladmark 1979, p. 63). He claimed that the lack of ancient cultural evidence on the coast was due to sites being overridden and reworked by the rising sea level (Fladmark 1979, p. 62). The description of kelp (seaweed) forests from Alaska to Baja California in Mexico as a rich ecosystem providing resources such as fish, shellfish, seabird, waterfowl, and large and small sea mammals (Erlandson et al. 2007, 2011; Erlandson 2013; Erlandson et al. 2015) provides support to the coastal model in terms of availability of resources along the coast. However, it remains unknown whether these resources available today were also present during the late Pleistocene when the sea was 130 meters lower, and the coastline was several kilometres away from its current location (Meltzer 2021). Additionally, geological evidence shows that some areas of coastal Alaska and British Columbia were higher than sea level, and nowadays those shorelines are well above sea level, which enables the search for ancient sites (Clark et al. 2014).

The coastal model found support from various disciplines, including linguistic, archaeological, genetic, and morphological studies. Archaeologist Ruth Gruhn argued that the distribution of language groups in the Americas

provides independent support for the coastal model (Rogers 1985; Gruhn 1988). She based her ideas on the assumption that areas with greater language diversity serve as a marker of a longer period of settlement, considering the extended time that languages take to differentiate (Rogers et al. 1992). Since the greatest linguistic diversity in North America is found on the Pacific coast (e.g., the largest concentration of language isolates), it follows that the coast has been settled for a longer time than the interior of the continent. Although Nichols (1990, 2008) also supports a coastal route for the initial entry, she considers that the existence of high diversity is independent of migration routes (Nichols 1990, p. 493). According to Gruhn, an advantage of the coastal model is that it allows incorporating data from the Pleistocene sites that present technologies not necessarily indicative of specialization in hunting (Gruhn 1988). She argues that during the final Pleistocene, coastlines were much more appealing in terms of resources than inland environments. Gruhn extended the coastal model, originally proposed to explain the initial route from Asia to North America, to explain human dispersals in South America (Gruhn 1988, 2005; Gruhn and Bryan 2011). Gruhn suggests that the first humans were adaptively oriented towards the coast, entering along the Pacific coast around 50,000 years ago by following the southern edge of the Bering land bridge. While some groups moved to the interior following the main rivers, others continued moving farther south (Gruhn 1998). In lower Central America, human groups split into three dispersal routes, one following the Caribbean and Atlantic coastlines, the other following the Pacific coast, and a third along the eastern slopes of the Andes into Patagonia (Gruhn 1988).

Much of the genetic research conducted on extant and ancient human skeletons has revealed genetic variation patterns supporting the Pacific coastal migration route (e.g. Bonatto and Salzano 1997; Fagundes et al. 2008; Kemp and Schurr 2010; Fehren-Schmitz et al. 2011). Schurr and Sherry (2004) suggested that a single initial source population was responsible for colonizing the New

World along the coast during the LGM. Fagundes et al. (2008) argued that a wave of pre-Clovis people migrated along the Pacific Coast, expanding from Beringia around 18,000 years BP and completing their movements to the south by 15,000 years ago. Molecular research points to a possible genetic relationship between the ancient and extant coastal inhabitants of North and South America. Johnson and Lorenz (2006) provided strong evidence by identifying similar high frequencies of haplogroup D in living and prehistoric human remains sampled from various areas along the Pacific Coast of the Americas. Specifically, a variant of haplogroup D (D4h3) has been described as geographically restricted to the Pacific Coast of North and South America (O'Rourke 2009). The distribution of D4h3, as suggested by Perego et al. (2010), is mostly found among South Americans from Peru, Chile, and Ecuador. Perego and colleagues also reported this same D4h3 variant in Californians, as well as in an East Asian sample from China. The presence of haplogroup D4h3 along the coast of North and South America suggests that a coastal migration occurred at an early time, possibly during the initial expansions to the Americas (Moraga et al. 2010; de Saint Pierre et al. 2012; Sala and Corach 2014; Lindo et al. 2017; Delgado et al. 2021). D4h3 is considered one of the founding haplogroups (Tamm et al. 2007), and recent research has traced Native American ancestry with this haplogroup to northern coastal China (Li et al. 2023).

Morphological studies have shown biological affinities among individuals from the Pacific coasts of North and South America, providing support to the coastal route. Jantz and Owsley (2005) found that early Holocene individuals from California exhibit craniofacial similarities, such as large cranial vault size, with modern Pacific populations, like Polynesians. These individuals also show craniofacial differences compared to recent Native Americans and Asians (e.g., smaller cranial vaults). Susan Kuzminsky (2013) conducted a comprehensive study testing the coastal route model by analysing cranial variation in a skeletal series from western North and South America spanning from the early to

the late Holocene. Similar to Jantz and Owsley (2005), Kuzminsky found craniofacial affinities among East and West Pacific Rim populations from the Late Pleistocene and early Holocene periods. Additionally, she observed close biological affinities between the Peruvian groups and Paleoamericans (Johnson and Lorenz 2006, 2010; Perego et al. 2010; Cui et al. 2013; Kuzminsky 2013). The study also highlighted the biological similarities between individuals from the California Channel Island and Peru (e.g. Neves et al. 2005; Kuzminsky 2013). The close association between individuals from Peru and California was reinforced by genetic studies led by Posth et al. (2018). These studies proposed a late Holocene migration of populations from the California Channel Islands to the Central Andes. Overall, these morphological and genetic findings contribute to the growing body of evidence supporting the coastal migration model for the peopling of the Americas.

The coastal route along North America's west coast is widely accepted as a more viable route for early migrations than the interior ice-free corridor (Dixon 2015; Lesnek et al. 2018; Hoffecker et al. 2023). The Pacific Coast offered a more hospitable environment with a complex and diverse ecology, leading to high population densities in regions like the Pacific Northwest and California, contributing to significant pre-contact language diversity (Gruhn 1988; Golla 2011). The debate continues over whether these early groups travelled by foot or by boat (Meltzer 2021). Archaeological evidence from sites along the North Pacific, dating to pre-Clovis times, such as Paisley Cave in Oregon (Fig. 2; Gilbert et al. 2008), and Manis Mastodon in Washington (Fig. 2; Gustafson et al. 1979) supports the coastal route. However, the absence of sites associated with this chronology is often attributed to many of them being underwater and challenging to locate (Erlandson 1994; Erlandson et al. 2008; Watts et al. 2011), suggesting the need for underwater archaeological exploration. In terms of biological anthropology, significant findings include the human skull and brain discovered in Warm Mineral Springs, Florida, USA (Fig. 2)

dating to ~7500 years BP (Royal and Clark 1960; Clausen et al. 2013). Additionally, the human skeletal series from Quintana Roo, Mexico, dated to ~11,000 years BP, represents some of the earliest human skeletons on the continent (Fig. 2; González et al. 2008, 2013; Chatters et al. 2014). These discoveries contribute valuable insights into the early human populations that inhabited the Americas and further support the importance of the Pacific coastal route in the peopling of the continent.

#### *The distinctive biological contribution from Southeast Asia and/or Oceania*

The coastal route model, as described in the previous section, resurfaced at the end of the 20<sup>th</sup> century, rekindling the hypothesis that human expansions along the Pacific Rim could have played a significant role in the diversification of humans in the Americas. This, coupled with the ease of conducting multivariate analysis due to advancements in computer technology, prompted the reintroduction of some old ideas concerning the deep biological affinities and ancient connections between Native Americans and Austro-Melanesians. I will elaborate on the development of this thesis in detail, as the ancient connections between South America and Oceania currently stand as one of the most intriguing hypotheses. Not only has it inspired several of the most influential papers on the field, but it also, after almost 150 years, continues to be tested with different kinds of evidence.

As previously outlined, at the end of the 19<sup>th</sup> century, an international debate unfolded concerning the interpretation of dolichocephalic skulls found in southern South America, specifically in the Rio Negro valley, Lagoa Santa, and Argentinean Pampas (Navarro Floria et al. 2004). In his comprehensive monograph on the Patagonian groups, Verneau drew parallels among the dolichocephalic Tehuelche, Pampean, Fuegian, Botocudo, and Lagoa Santa individuals, interpreting them as representatives of the oldest lineages in South America (Verneau 1904). On the opposite side of the Atlantic, Burmeister, Moreno, and Ameghino characterized the

dolichocephalic skulls found in South America (e.g., Pampa, Patagonia, Lagoa Santa) as highly ancient (Burmeister 1879; Moreno 1882; Ameghino 1913). Local naturalists in Argentina went even further, contending that the Lagoa Santa, Pampean, and Patagonian skeletons were representatives of an ancestral autochthonous group (Burmeister 1879; Moreno 1882; Ameghino 1913). However, disagreements arose on several aspects; while Moreno argued that contemporaneous groups like the Tehuelche, Inuit, Botocudo, and Fuegians were also dolichocephalic, thus representing relics and survivors of the original autochthonous group, Ameghino interpreted them as brachycephalic. According to Ameghino, the ancient dolichocephalic individuals had been completely replaced by more recent brachycephalic ones (Ameghino 1880; Moreno 1882). These interpretations were influenced by their differing ideas on the main evolutionary processes involved; while Moreno proposed that brachycephalic individuals arrived as a result of an expansion of more recent brachycephalic groups from the north, Ameghino suggested an evolution *in situ*, positing that the “transformation” occurred within the original individuals (Moreno 1882; Ameghino 1884b).

The expansionist model proposed by Moreno also accounted for the similarities in skull shape between South Americans and Polynesians, attributing these resemblances to the existence of a primitive southern continent that facilitated connections among individuals from meridional regions across the world (Moreno 1880). This hypothesis found support in paleontological evidence (Hermann von Ihering 1907). Moreno suggested that the ancient continent was initially inhabited by primitive dolichocephalic groups and later experienced expansions from other dolichocephalic and more recently brachycephalic groups (Moreno 1882, 1901). In addition, Moreno referenced archaeological artifacts in Peru that he believed could have been produced in New Zealand. His study of equatorial marine currents (e.g. Humboldt), led him to the conclusion that all available evidence indicated the arrival of Polynesian groups in South America



in ancient times (Moreno 1880, 1882). Locally, Moreno's ideas received partial or full support from Burmeister (1879) and Outes (1905), as well as international backing from Merejkowsky (1882), Puccioni (1912), and Topinard (1876), as comprehensively reviewed by Navarro Floria and collaborators (2004b) and Podgorny (2009).

In reference to Native North Americans, Ten Kate characterized ancient Californians as dolichocephalic, possessing cranial and dental features akin to the Lagoa Santa series, and both showing affinities with Melanesians (Ten Kate 1884). The Lagoa Santa series from Copenhagen underwent study by several individuals at the end of the 19<sup>th</sup> century, including Hansen and Quatrefages. Their collective conclusion was that these skulls exhibited a high degree of homogeneity in terms of intra-group variation, being uniformly dolichocephalic and prognathic. Additionally, both cranial and postcranial features, such as limb bones indicating small to medium stature, showed marked similarities with the Papuans (Hansen 1888; Quatrefages 1889). Similarly, others highlighted the notable cultural parallels between Native Americans and Melanesio-Polynesians. Examples included the presence of the panpipe, potlach ceremony, and skull trophy, among other shared practices, serving as supplementary evidence supporting these ancient connections (Graebner 1909; Nordenskiöld, 1912; Schmidt 1912).

Several decades later, two European anthropologists significantly advanced these ideas, building upon Moreno's expansionist model and the affinities between South Americans and Oceanic groups highlighted by Quatrefages and others. The Portuguese anthropologist António Mendes Correia and the French anthropologist Paul Rivet contributed influential books and papers, proposing that humans reached the Americas by traversing from Oceania (Mendes Correia 1926; Rivet 1943). While they did not dismiss Asia as the potential origin of some Native American groups, they posited Oceania as an additional and more ancient source of population. Paul Rivet, the founder of *Musée de l'Homme*, was a dedicated diffusionist with

a keen interest in linguistic diversity. He studied human origins and migrations by employing a historical-comparative method (Rival 2010). Rivet described morphological affinities between the Lagoa Santa skeletal series recovered by Peter Lund and indigenous people from New Guinea (i.e. Papuans), as well as Baja Californians and Melanesians (Rivet 1908, 1909). In the early stages of his career, he interpreted these similarities as the outcome of either Oceanic and South Americans descending from a common ancestral population or as a result of a migration of humans from Oceania to South America (Rivet 1908). However, he later consistently argued in favour of the latter scenario (Rivet 1909).

Rivet's central thesis, initially formulated several decades later (Rivet 1924) and further developed in his book *Les origines de l'homme américain* (Rivet 1943), posited that the American continent not only received human migrants from Asia through the Bering Strait but also witnessed the arrival of Australian and then Malayo-Polynesian groups by sea navigation along the Pacific islands (Rivet 1924, 1943; Rivet and Labadie 1956). To support this, he presented linguistic evidence of affinities between Native Americans and Polynesians (e.g., Hoka/Melanesio-Polynesian) and Australians (e.g., Selk'nam/Australians) citing similarities in words for "sweet potato" and "ax" found in Quechua and Polynesian languages. Additionally, he offered diverse evidence to establish ancient connections between South America and Polynesia, such as the presence of a frog from the family *Leptodactylidae* and its parasite *Zelleriella* on both continents (Rivet 1921).

Anthropologist Mendes Correia not only rejected Ameghino's notion that humans originated in South America and spread globally but also disputed Hrdlička's arguments suggesting that similarities between ancient South American skeletons and contemporaneous groups indicated recent human arrival in the Americas (Mendes Correia 1925, 1926). Instead, based on the available fossil evidence at the time, he proposed a transformative process in the continental area surrounding the Indian Ocean, asserting

that both primates and humans evolved there before expanding worldwide (Mendes Correia 1925, 1926). In his book *Homo* (Mendes Correia 1926) and in a series of papers (Mendes Correia 1923, 1925), he further developed his model, suggesting that humans reached South America following a route through Australia-Tasmania-Antarctica-South America. This idea, according to him, aligned with Wegener's model of continental movement and was supported by similarities between Australasian and South American fauna (Wegener 1912). The proposed route involved humans traveling in rafts or small boats from Australia to Tasmania, passing through the Auckland Islands, reaching Antarctica during a milder climate period, and finally arriving in South America (Matos 2011). Mendes Correia cited physical evidence (dolichocephalic skulls, blood groups frequencies), linguistic evidence (similar words between both regions such as "sweet potato"), and ethnographic similarities (use of boomerang) between the populations in Argentina (Patagonia and Tierra del Fuego) and Australia to support his model (Mendes Correia 1926). In subsequent decades, Mendes Correia abandoned these hypotheses, shifting his focus to Portuguese biological and forensic anthropology (Martins 2011).

By the mid-twentieth century, Thomas Gladwin proposed at least six transoceanic migrations to the Americas, including at least two by Australasian groups, based on biological and archaeological features (Gladwin 1947). Concurrently, Rivet published some articles further reflecting on ancient connections between Polynesia and America, providing a more consolidated perspective that suggested regular contact between Polynesians and South Americans. This proposition was based on increasingly recovered cultural and biological evidence (Rivet 1953, 1956). These hypotheses found additional support in archaeological evidence indicating Inka exploration of Pacific islands by raft (Benzoni 1572; Cabello Valboa 1951), as well as the Kon-Tiki expedition by Thor Heyerdahl from South America to the Polynesian islands by raft in 1947 (Heyerdahl 1950). One of the earliest genetic

studies based on the analysis of blood groups, pointed out that the high frequency of blood type O among South Americans made them more similar to Polynesians than to Asiatic groups (Matson et al. 1967). However, after Paul Rivet's death in 1958, the ideas on ancient connections between South America and Oceania, as well as the origin of South Americans, faded from the international anthropology debate. It was only in the 1980s that these scientific questions regained prominence, thanks to the collaboration of two of the greatest South American biological anthropologists of all time.

By the mid-1980s, the Latin American dictatorships came to an end, and democratic governments were restored, enabling Latin American biological anthropologists to establish connections with each other. This newfound collaboration resulted in flourishing international partnerships. One noteworthy collaboration emerged between the Argentinian Héctor Pucciarelli and the Brazilian Walter Neves. They joined efforts to investigate the ancient skeletal variation of South American samples and their affinities to populations from other continents, rekindling the question of the origin of Native Americans in the international debate. Their collaboration yielded two influential papers in quick succession (Neves and Pucciarelli 1989, 1991), reintroducing the idea of ancient connections between South America and Oceania. However, they presented a new model that sparked a scientific debate that continues to the present day. This model has inspired most morphological, linguistic, and genetic studies conducted since then, with researchers consistently testing their data against this hypothesis and obtaining diverse results.

Walter Neves and Héctor Pucciarelli proposed the two biological components model (or four biological components when considering the three migrations proposed in the tripartite model, the main framework at the time) to explain human diversification in the Americas. According to this model, the biological diversity of Native Americans results from two migratory waves: an earlier pre-Mongoloid

expansion and a more recent Mongoloid one (Neves and Pucciarelli 1991). In their comparison of morphological variation among early South American series, represented by individuals from Tequendama and several sites from the archaeological locality Lagoa Santa (Fig. 2) to 20 human populations worldwide, and with late Pleistocene/early Holocene fossils from Europe, Africa, and Asia, they identified distinct characteristics in early Holocene South Americans. These included a long and narrow cranial vault, a low and projecting face, low orbits and nasal aperture, and a sundadont dental pattern (Turner II 1983a; Neves and Pucciarelli 1991). Notably, this ancestral morphological pattern not only differentiated early South Americans from recent populations but also grouped them with individuals from Oceania (Neves and Pucciarelli 1989, 1991). According to the two biological components model, these similarities could result from a common ancestral population located somewhere in Northern China. During the late Pleistocene, this population diverged into two branches, with one expanding southwards to Oceania and the other northwards to Siberia and the Americas, arriving to the latter ~15,000 years BP (Neves and Pucciarelli 1991; Pucciarelli 2004). The distinctive morphology of early South Americans was then interpreted as the retention of the morphological pattern present in humans that left Africa between 135,000-35,000 years BP, estimated now to be ~180,000-200,000 years BP (Rasmussen et al. 2011; Hershkovitz et al. 2018; Harvati et al. 2019). Consequently, most extant Native American populations would have derived from a second expansion. These recent individuals exhibit short and wide cranial vaults, high and retracted faces, high orbits and nasal apertures, and a sinodont dental pattern. They likely descended from a population characterized by derived Mongolian features that expanded from Northeast Asia during the early to mid-Holocene (ca. 10,000-8,000 years BP; Lahr 1995; Neves and Pucciarelli 1991; Neves and Hubbe 2005; Sutter 2005; Hubbe et al. 2010; Pucciarelli et al. 2010; Galland and Friess 2016; Hubbe et al. 2015; von Cramon-Taubadel

et al. 2017). These results were subsequently replicated by Neves and Pucciarelli, along with their teams, incorporating early Holocene individuals from other series such as Tequendama in Colombia (Neves et al. 2007b), Santana do Riacho in Brazil (Neves et al. 2003), Serra da Capivara (Bernardo and Neves 2009), and the Pampean region in Argentina (Pucciarelli et al. 2010; Menéndez et al. 2015) (Fig. 2).

A noteworthy aspect is the reintroduction of the concept “Paleoamerican”, initially formulated by Deniker (1889) to designate all ancient dolichocephalic individuals with upright noses and small cranial sizes from the Americas. In the context of Neves and Pucciarelli’s model, the term is employed to differentiate individuals with distinct cranial shape variations not directly related to recent Asians as “Amerindians” are. According to this model, these shape differences represent different ancestral lineages corresponding to two separate human expansions at different times (Neves and Pucciarelli 1991). Previously, the term “Paleoindian” was associated with the “Clovis First” model, depicting post-glacial human groups specialized in big game hunting, along with other features linked to the “Clovis First” model (Gruhn 2005). In an effort to distinguish their model from the ideas associated with “Clovis First”, Pucciarelli and Neves, proposed the term “Paleoamerican” to designate an older human group with ancestral morphological features, specifically from the early Holocene. Support for this concept was found in some mtDNA studies, which suggested that “Paleoamerican” diversity was compatible with a pre-Clovis entry (Schurr and Wallace 1999). However, more recent interpretations have questioned the notion that the Paleoamerican/Amerindian craniofacial distinctive pattern corresponds to chronological differences (Kuzminsky et al. 2017), and this aspect is currently under debate.

During the 1990s and 2000s, there was a surge in multivariate craniometric studies conducted by the successors of Neves and Pucciarelli in South America, as well as by biological anthropologists from North America. These studies

aimed to test and replicate the two biological components model, using both ancient and contemporary human samples. Additionally, linguistic analyses provided support for the source lineages diverging from Southeast Asia (Nichols 2015). The main findings of these studies revealed that the “Paleoamerican” morphology was consistently present when comparing various ancient and recent samples from South America (Gonzalez-José et al. 2005; Hubbe et al. 2010, 2015; von Cramon-Taubadel et al. 2017), and North America (Powell and Neves 1999; Owsley and Jantz 2001; Jantz and Owsley 2005; Powell 2005; Nelson 2006). This included recent groups considered as relicts of the ancient population, such as Botocudo and Pericú (Gonzalez-José et al. 2003; Strauss et al. 2015). When temporal series were studied, “Paleoamericans” exhibited closer affinities to mid-Holocene populations than to recent and living Native American populations (Steele and Powell 2002). However, it is important to note that “Paleoamerican” crania also display considerable variation in their own cranial shapes. Powell and Neves (1999) demonstrated that while South American ancient skeletons clustered with African and Australian crania, the North American ones showed more similarity to Ainu-Jomon and Polynesian groups (Steele and Powell 1992, 1993).

As extensive studies of ancient skeletons from various geographic areas progressed, the improved representation of samples enabled a more nuanced understanding of morphological variation. This, in turn, prompted discussions about the evolutionary processes that might have contributed to the previously described dichotomous morphological pattern. While some researchers advocated for the involvement of different ancestral lineages in past and present variation among Native Americans (Neves and Pucciarelli 1991; Neves and Hubbe 2005), others supported the emerging idea that a single migration, combined with evolutionary processes *in situ*, might be sufficient to explain the morphological diversification of humans in the Americas and the Paleoamerican/Amerindian craniofacial pattern (Powell 2005; Perez et al. 2009;

Menéndez et al. 2015; Kuzminsky et al. 2018). In addition, some researchers have proposed that small founding populations, likely representing the initial arrivals in the Americas, would have been especially susceptible to genetic drift. This susceptibility could have led to changes in skeletal morphology after their arrival, providing a plausible explanation for the shifts in cranial shape from the late Pleistocene/early Holocene to later periods in the Americas (Roseman and Weaver 2007; Menéndez et al. 2015).

Dental data did not provide a definitive answer either; while some studies supported Turner II’s work, revealing a homogeneous sinodont dental pattern across the Americas, showing similarities to North Asiatic populations (Turner 1983, 1986, 1990; Owsley et al. 2010; Chatters et al. 2014; Stojanowski and Johnson 2015), other studies argued the opposite. There appears to be a large variation in Native American’s dentition (Powell 1995), as well as significant differences between the dental pattern of ancient and recent individuals (Powell et al. 1999). Some researchers described the sundadont pattern among individuals from Brazil, Mesoamerica, Tierra del Fuego, and Southern Andes (Lahr 1995; Powell 1995; Haydenblit 1996; Powell 1997; Sutter 2005; Rodriguez Flores and Colantonio 2015), while others identified an intermediate pattern between the sinodont and the sundadont one (Powell 2005). As a result, some researchers argued that dental evidence supported the two biological components model (Powell 1997; Sutter 2005) by associating Paleoamerican cranial morphology to the sundadont dental pattern that can be traced back to Southeast Asia, and a more recent sinodont pattern associated with Northeast Asian populations.

While the majority of genetic studies indicate strong similarities and shared North Asian ancestry among Native Americans, some studies present alternative explanations and describe the presence of Australasian ancestral lineages in Native South Americans. In 2015, Skoglund and collaborators argued that certain contemporary populations from Brazilian Amazonia (i.e., Surui, Karitiana) exhibit affinities to those of

Australasia (Skoglund et al. 2015). More recently, Castro e Silva and collaborators identified this signal in present-day populations from North Peru and Central-West Brazil (Castro e Silva et al. 2021). This signal was interpreted to derive from an unsampled population, referred to as “Population Y”, named after “Ypikuéra”, which means “ancestor” in the Tupi language. Initially, the existence of connections between Polynesia and South America by ~800 years BP (Ioannidis et al. 2020), suggested that this signal resulted from recent migrations through the Pacific. However, alternative explanations gained traction when this signal was also found in ancient individuals from Lagoa Santa, Brazil (Sumidouro 5, ~10,400 years BP; Fig. 2) (Moreno-Mayar et al. 2018), and Panama (PAPV173, 520-650 years BP; Fig. 2) (Campelo dos Santos et al. 2022). Consequently, it is plausible that the source population from which Native Americans diverged was more diverse than previously considered, encompassing lineages from not only North East Asia and Beringia but also from South East Asia. Nevertheless, the Australasian signal varies with different outgroups and is generally low both in contemporary populations and ancient individuals (approximately 2%), which could be the result of methodological or sampling bias, as some authors have argued (Posth et al. 2018).

#### *African Origin and the Atlantic route*

According to some authors (Guidon 2008; Funari et al. 2018), the proposal of humans arriving in the Americas by navigating through the Atlantic was first suggested by Paul Rivet in his book on the origins of Native Americans, originally published in French in 1943 and then translated to other languages such as Spanish and Portuguese in 1943 and 1960 respectively (Rivet 1943). However, as discussed earlier, while Rivet argues for Asian, Australian, and Melanesian expansions to explain the large cultural and biological variation of humans in the Americas, he does not mention any African component concerning the origin of Native Americans. Instead, some Brazilian archaeologists developed this model further. Based on the antiquity

of archaeological sites from Serra da Capivara in the state of Piauí (Fig. 2), Niède Guidon considered that humans travelled from Africa to the Caribbean and then they entered South America through the Parnaíba river (Guidon 2008). Some researchers even proposed that it might not have been *Homo sapiens*, but instead another more ancient hominid, the first arrived in the Americas. This interpretation stemmed from the evidence found at old sites such as Calico Hills (Simpson 1982; Fig. 2) and Pedra Furada in the Serra da Capivara locality (Fig. 2; Guidon and Delibrias 1986). Since those sites were interpreted as being 70,000 years BP and 50,000 years BP, and at the time *Homo sapiens* was believed to have originated only 35,000 years BP, the rationale was that it should have been *Homo neanderthalensis* or *Homo erectus* the first humans to arrive in the Americas (Dreier 1986; Schobinger 1988; Beltrão 1989; Martin 1992; Pinheiro de Melo 2000; Guidon 2008).

The main evidence supporting the Atlantic route from Africa has been the description of craniometric similarities between the skeletons from Luzia and Zuzu, from the archaeological localities Lagoa Santa and Serra da Capivara to human skeletons from Africa (Guidon 2008; Funari et al. 2018). These morphological features were repeatedly interpreted as the retention of plesiomorphic characteristics resulting from human expansions predating the development of more specialized features (Howells 1973, 1989; Lahr 1995, 1996; Neves et al. 1999; Neves 2006). Additional support for this model was provided by the description of craniometric features of the Yuki individuals from California with *Homo erectus* (Dreier 1986), as well as the presence of the parasite *Anciloma duodenalis*, a tropical parasite found in an ancient individual from Serra da Capivara that could not have survived cold temperatures, i.e., if humans have brought it through Beringia (Ferreira et al. 1987; Araújo et al. 1988; Fig. 2). The maritime currents also provided independent support for navigation (Pinheiro de Melo 2000), considering the sea level was at least 100 meters lower (Guidon 2008), and even the “Atlantis expedition” conducted in 1984 by

five persons traveling by raft from the Canary Islands to Venezuela demonstrated the feasibility of this journey (Barragán 2016). Currently, due to the lack of more compelling evidence supporting ancient maritime connections between Africa and the Americas, this model is not considered among the most plausible alternatives for explaining the origin of humans in the Americas.

#### *European Origin and the Atlantic route*

Centuries ago, Spanish papal scholars Acosta and Garcia anticipated the idea that early European peoples could have crossed the Atlantic Ocean into the Americas (Powell 2005). More consistently, the proposal for ancient connections between Native Americans and Pleistocene Europeans goes back to the beginnings of North American archaeology when Charles Abbott suggested that the development of the North American palaeolithic was the result of European influences (Abbott 1878). Later, the idea of European origins for Native Americans gained support from the description of technological similarities between the Solutrean and Clovis cultures, such as the use of red ochre, the production of bifacial stone tools, and especially the use of the specific overshot technique for thinning lithic bifaces (Bradley and Stanford 2004). These similar features were initially pointed out by Hibben (1941) when studying the evidence and the antiquity of Sandia cave (Fig. 2), and more recently, a model was developed by Dennis Stanford and Bruce Bradley (Stanford and Bradley 2002; Bradley and Stanford 2004; Stanford and Bradley 2012). It was the lack of evidence for Clovis' "progenitors" in Siberia and Beringia, together with the complexity and sophistication of Clovis technology, that led these authors to seek connections elsewhere (Bradley and Stanford 2004).

The transatlantic model suggests that the first human groups that arrived in North America during the LGM may have originated in southwestern Europe and travelled to the Americas through the Atlantic (Stanford and Bradley 2002; Bradley and Stanford 2004). During the LGM the polar front was pushed southwards

to latitudes as far south as Portugal, turning the Iberian peninsula into a steppe-tundra environment with lowered temperatures (Bradley and Stanford 2004). Thus, the perennial Arctic ice formed covered major portions of the North Atlantic and connected Europe and North America with an ice bridge that also pushed the active young ice-edge margin, and the animals adapted to sub-Arctic waters southward (Webb et al. 1993). This model integrates the "pre-Clovis" artefactual evidence by considering them as transitional technology between the Solutrean and Clovis, not necessarily filling the archaeological time gap (e.g. Meadowcroft), or the geographical one since sites such as Cactus Hill and Page-Ladson are located near the Atlantic Coasts of North America (Fig. 2).

The transatlantic model, proposing ancient connections between Native Americans and Pleistocene Europeans, received criticism and is not considered a viable alternative today (reviewed by Powell 2005; Raff and Bolnick 2015; Meltzer 2021). Despite this, some biological evidence provided independent support to it. Classic craniometric analyses conducted by Howells' showed Peruvians and Californians clustering with Europeans (Howells 1989). Early Holocene skeletons from North America have also been described as presenting similarities with Europeans, as well as South Asians (Steele and Powell 1992). Additionally, mtDNA studies identified haplogroup X (now called X2a) in Native Americans (Baillet et al. 1994). This haplogroup has been previously described in contemporaneous Europeans and Southwest Asians but not in those of Central Siberia (Brown et al. 1998; Smith et al. 1999). While some initially interpreted the distribution of the X2a haplogroup as originating in the Near East and spreading into Europe and Asia and becoming extinct in the latter (Brown et al. 1998; Smith et al. 1999), others saw it as evidence for ancient trans-Atlantic gene flow from Europe or the Middle East into North America (Stanford and Bradley 2012; Oppenheimer et al. 2014). However, more recent research has clarified that the distinct X lineage present in North America is not the same as the

one present in Europe (Reidla et al. 2003; Goebel et al. 2008; Raghavan et al. 2014; Southerton 2014). Current genetic evidence shows that this haplogroup descended from peoples in eastern Siberia who were related to the ancestors of both contemporary East Asians and West Eurasians (Kemp and Schurr 2010; O'Rourke and Raff 2010; Raghavan et al. 2014b). It is considered a uniquely North American haplogroup, found at the highest frequencies in Great Lakes populations and lower frequencies in the Plains and the Pacific Northwest (Raff and Bolnick 2015).

The case of Kennewick Man/The Ancient One was initially presented as potentially supporting the transatlantic model. Kennewick Man, recovered from the archaeological site with the same name (8700 cal years BP; Fig. 2), was initially described in forensic terms as “Caucasoid” due to morphological features such as dolichocephalic skull and narrow face, leading to suggested affinities with pre-modern Europeans (Chatters 2000). However, subsequent genetic studies revealed that his mitochondrial DNA exhibits one of the most basal X2a lineages (Rasmussen et al. 2015), and his origins can be traced back to native groups from the North West of North America (Raff and Bolnick 2015; Rasmussen et al. 2015). Current genetic data supports the model that the population ancestral to Native Americans was derived from ancient North Eurasian and East Asian sources. On the other hand, contemporary Europeans were derived from ancient North Eurasian and West Eurasian sources (Lazaridis et al. 2014). There is no evidence of Pleistocene gene flow directly from West Eurasians into Native Americans based on the available genetic data. This contradicts the initial morphological assessment of Kennewick Man and highlights the importance of combining multiple lines of evidence, to reconstruct the history of human populations.

*Beringian Standstill Model: reconciling old ideas of an Asian origin, high diversity of ancestral groups, and multiple expansion waves*

The Beringian Incubation or Standstill model proposes that Beringia, the landmass

bridging Siberia in Asia and Alaska in North America, played a crucial role in human migration during the Pleistocene. This area, including both land and submerged parts, was traversable between approximately 30,000 and 12,000 years BP (Lambeck et al. 2014; Pico et al. 2020). The model suggests that rather than being just a corridor or bridge, Beringia served as a habitat for human populations and other forms of life during the Last Glacial Maximum (LGM) (Hoffecker et al. 1993; Merriwether et al. 1995; Bonatto and Salzano 1997; Raff 2022). The support for this model has come from paleoenvironmental, genetic, and archaeological studies. During the 1930s, ecological studies in various Arctic locations revealed that the submerged Bering Strait served as a refuge for people, animals, and plants during the LGM (Johnston 1933; Hultén 1937; Hopkins 1959). Combining this knowledge of environmental conditions with systematic archaeological studies, late Pleistocene human occupation in areas like the Kamchatka Peninsula was observed around 14,000 years BP, southeastern Beringia around 12,000 years BP, and both the Siberian and North American sides around 13,000 to 15,000 years BP (Powers and Hoffecker 1989; Hoffecker et al. 1993). The idea is that Beringia, with its stable and habitable environment, allowed for a consistent occupation by human populations over long periods. This extended habitation in Beringia gave rise to the hypothesis that the peopling of the Americas should be viewed as an “Out of Beringia” phenomenon (Bonatto and Salzano 1997). Genetic studies have examined the genetic diversity and divergence among Native American populations, and some mitochondrial DNA studies have pointed to a Beringian origin. Archaeological evidence, such as the presence of distinctive tool technologies and cultural adaptations in the Beringian region, also supports the idea that populations inhabited Beringia before moving further into the Americas.

Rogers and his collaborators were pioneers in introducing the notion that the Americas were inhabited by “growing populations settling adjacent territory”, challenging the prevailing

view of independent migrations (Rogers et al. 1992). According to this model, the glacial barrier served as an isolating mechanism, fostering both biological and cultural differentiation. Szathmáry (1993) further refined this concept based on mtDNA data, proposing that the crossing of Beringia was not rapid. Instead, this region was occupied for 3,000 to 12,000 years before human populations migrated southwards, following a leaping-frog model involving small and incremental migrations (Szathmáry 1993). This model found support in evidence showing biological similarities between Na-Dene and Inuit individuals, suggesting that all populations in the Americas belonged to a single migration (Bonatto and Salzano 1997). An updated version of this model was presented by Tamm and collaborators in a highly influential paper in which they sequenced mtDNA genomes. They argued that the initial founders of the Americas descended from a single ancestral population that departed from Asia ~30,000 years BP and evolved during 15,000 years of isolation in Beringia (Tamm et al. 2007). The term “Beringian Incubation Model” was coined to emphasize that during the pause in Beringia, there was sufficient time for differentiation through an accumulation of mutations, leading to the distinctiveness of Native American founder lineages compared to the Asian sister clades. Genetic evidence supporting this model includes the autochthonous pattern of variation of Native American mtDNA haplotypes, as well as their uniform distribution across space (Tamm et al. 2007). Similar results have been replicated with Y-chromosome data, indicating a shorter Beringian standstill lasting between 2,700-4,600 years (Pinotti et al. 2018). Some studies suggest a Beringian standstill lasting 8,000 years (Raghavan et al. 2015). In general, studies agree that there was bidirectional gene flow between Siberia and the North American Arctic, and after the pause in Beringia, there was a swift migration southwards (Tamm et al. 2007; Pinotti et al. 2019).

Various analyses of craniometric and non-metric dental traits have lent support to this model (Gonzalez-José et al. 2001, 2008; de

Azevedo et al. 2011; Scott et al. 2016; de Azevedo et al. 2017). Craniofacial studies have demonstrated that the phenotypic variation among Native Americans is continuously distributed, providing a counterargument to the two components model and suggesting a single migration as the plausible explanation (González-José et al. 2001, 2008). A comprehensive model that integrates genetic, craniofacial, and archaeological evidence was presented by González-José and collaborators (2008), termed the “Recurrent Gene Flow Model”. According to this model, between 26,000 to 18,000 years BP, a reduction in sea levels exposed the Beringia landmass, facilitating the expansion of populations from East Asia characterized by a generalized and heterogenous craniofacial morphology. This migration may have represented a diverse array of Asian lineages, with some lost due to drift, while the remaining ones accumulated mutations over millennia, giving rise to the Native American founding lineages (González-José et al. 2008). As Beringia’s landmass diminished from 18,000 and 12,000 years BP due to rising sea levels, new routes began to emerge. During this period, humans with a generalized morphology expanded throughout the entire continent. In the middle to late Holocene, populations from NE Asia, characterized by a derived craniofacial morphology, expanded to North America.

The “Beringian Standstill” model diverges from the tripartite model (Turner II 1983; Greenberg et al. 1986) and provides an alternative perspective to the “Two Biological Components” model (Neves and Pucciarelli 1991) by expanding and reinterpreting the evidence. This model proposes a more continuous pattern of contacts among circumarctic groups, offering a parsimonious explanation that reconciles genetic and dental evidence supporting a single major Asiatic origin, archaeological findings from pre-Clovis sites, and the high craniofacial and linguistic heterogeneity observed in Native Americans. The “Beringia Standstill” model suggests that the morphological evolution of Native Americans is primarily explained by *in situ* evolutionary mechanisms rather than multiple migrations. The wide



craniometric variation is interpreted as descendants from an ancestral population with a high degree of craniofacial diversity (González-José et al. 2008). Recent studies, such as the analysis conducted by Scott and collaborators, support the “Beringia Standstill” model by indicating that all Native Americans can be considered as Sinodonts, deriving from an East Asian ancestral population (Scott et al. 2016). Furthermore, additional evidence from Hlusko and collaborators (2018), demonstrates that over ~9,000 years of geographic and genetic isolation, the Beringian population underwent selection in the FADS gene cluster and the EDAR V370A allele. This selection was advantageous for transmitting nutrients from the mother to the infant during breastfeeding in response to the low UV environment. Interestingly, the EDAR V370A allele, associated with mammary gland ductal branching and incisor shovelling, has been retained in human populations from Central and South America (being part of the “Super-Sinodont” complex defined by Scott et al. 2016), suggesting a common ancestor for these groups (Hlusko et al. 2018).

Based on current evidence and following the Beringia Standstill model, the formation of the gene pool that gave rise to Native Americans is estimated to have occurred between 43-25,000 years BP (Raff 2022). The earliest archaeological evidence of humans in NE Asia is found at the Yana RHS site in Siberia, dating back to 31,600 years BP, where lithic and non-lithic artifacts were discovered in association with fauna such as artich bison, hare, and mammoth (Pitulko et al. 2013; Fig. 2). The two individuals from the Yana RHS site represent the Ancient North Siberian population (ANS), which diversified ~38,000 years BP, shortly after the basal split between Western and Eastern Eurasians (Sikora et al. 2019; Willerslev and Meltzer 2021). The individual from Mal'ta (~24,000 years BP; Fig. 2) is considered a descendant of that ANS population (Raghavan et al. 2014). Other early archaeological sites in East Asia, such as Tianyuan cave in Northeast China (~40,000 years BP; Fig. 2) and Salkhit in the East of Mongolia (~34,000 years BP; Fig. 2), are believed to have been occupied

by the earliest representatives of the Ancestral East Asian Lineage, i.e., (Hoffecker et al. 2016, 2023). The gene flow between ANS and the East Asian group gave rise to two lineages that split ~25,000-20,000 years BP: the ancient Paleo-Siberians, represented by the Kolyma individual (~9,800 years BP; Fig. 2) from which current NE Siberian groups descend; and the basal American branch that isolated in Beringia (Sikora et al. 2019; Willerslev and Meltzer 2021). Despite a 15,000-year gap in the archaeological record, with Dyuktai cave in Siberia being occupied ~16,800 years BP and Swan Point in Alaska ~14,500 years BP (Willerslev and Meltzer 2021; Fig. 2), there is clear evidence of the human dispersals after 15,000 years BP, driven by factors as the inundation of continental areas, glacier retreat, opening new accessible routes, and rapid population growth (Hoffecker et al. 2023).

The isolated Beringian population underwent differentiation into three lineages: (a) “Unsampled Population A”, which exhibits connections to certain Mesoamerican individuals (Mixe population), (b) the Ancient Beringians, genetically represented by the Upward Sun River site (USR1) in Alaska, displaying equal genetic affinity to all Native American populations (Fig. 2), and (c) the Ancestral Native Americans lineage (ANA) (Moreno-Mayar et al. 2018a,b; Posth et al. 2018). From ANA, an early divergence ~21-16,000 years BP, represented by the Big Bar lake individual, gave rise to groups in the Pacific Northwest (Fig. 2). Later, ~16,000 years BP, a split likely occurred south of Beringia (but alternative proposals suggest a split in Beringia, see Waters 2019; Capodifierro et al. 2021), resulting in two lineages: (c1) North Native Americans (NNA) (or ANC-B) represented exclusively by individuals from North America (with some debate, see Scheib et al. 2018), and (c2) South Native Americans (SNA) or ANC-A, represented in North America by Anzick-1 (Clovis) ~12,000 years BP and Spirit Cave (Western Stemmed Tradition) ~11,000 years BP. Their ancestors migrated to South America in different pulses (Moreno Mayar et al. 2018a; Posth et al. 2018; Willerslev and Meltzer 2021; Fig. 2). The SNA

lineage further split into two additional lineages: (c2.1) SNA1, represented by Anzick-1 and most South American individuals on the Atlantic side, such as Lagoa Santa ~10,400 years BP (Fig. 2), and (c2.2) SNA2, represented by the individual from Spirit Cave (Fig. 2), and the majority of South Americans from the Pacific, like those represented by the individual from Los Rieles ~10,900 years BP (Capodiferro et al. 2021; Fig. 2). It is crucial to note that these models are preliminary, and based on a limited number of individuals. Biological affinities between samples can change as new samples are added to the analysis. So far, two unsampled lineages (UPopA, and UPopI in Central America) have been identified, highlighting our limited understanding of ancient dynamics in the Americas.

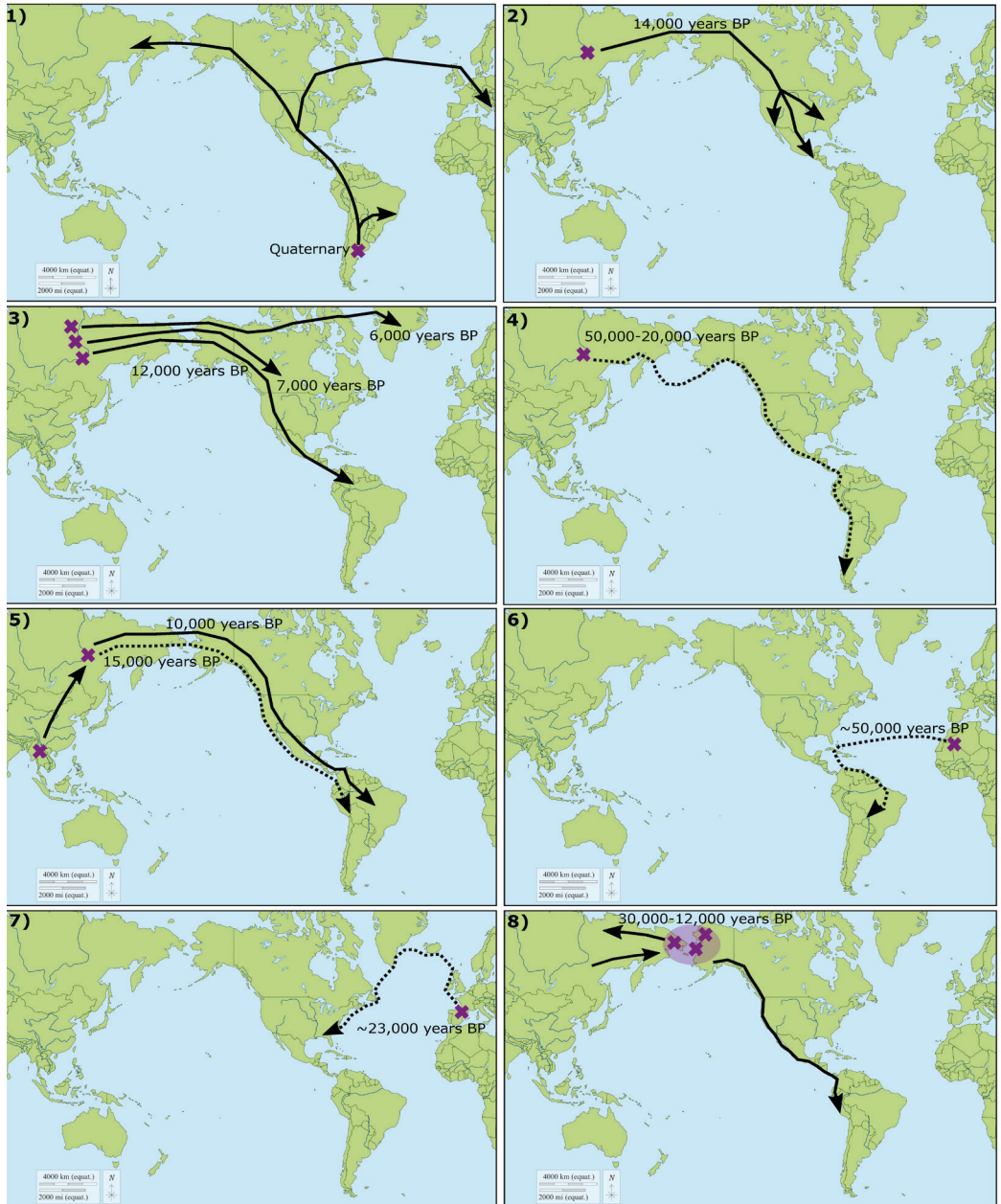
### Current limitations and future prospects on the peopling of the Americas research

In this review, I have presented the main broad models proposed over the centuries to explain when and who were the first humans that arrived in the Americas (Fig. 3). While many of these models are no longer supported by the scientific community, understanding them is crucial for appreciating the history of the investigations and comprehending the origins of current models. Importantly, this review aims to highlight the connections between models and ideas, providing historical context to reveal how seemingly recent or novel models can be traced back to previous centuries. Unfortunately, there has been a recent lack of acknowledgement of previous research, models, and ideas. This review seeks to address this gap and serve as a starting point for changing this trend. Recognizing and acknowledging previous work is essential, especially given the current attempts to improve the interface of paleogenetics and archaeology. To build a sustainable present and future, scientists should engage in more dialogues and open debates not only with the current academic and

indigenous communities but also with the work done by scholars before our time.

A substantial amount of work has been conducted on the peopling of the Americas, and recent reviews effectively summarize investigations performed over the last decades, presenting updated models based on the combination of archaeological and genetic data (Skoglund and Reich 2016; De la Fuente et al. 2021; Meltzer 2021; Willerslev and Meltzer 2021; Nägele et al. 2022; Raff 2022; Strauss 2022). Classic books provide insights into the state of the art at the moment in when they were published (Dillehay 2000; Lavallée 2000; Adovasio and Page 2002; Powell 2005; Politis et al. 2009). It is essential to acknowledge that the results we have today are not without bias and may not fully represent the past. Some biases are intrinsic due to the preservation of old samples, while others are methodological, associated with different methods used, and there are geographic and geopolitical biases. Disciplinary bias arises when, for example, only cultural evidence is discussed without incorporating human biological data (and *vice-versa*). Geographic sampling bias occurs when, despite continental coverage in some studies, samples from South America and Central America are typically underrepresented. Studies often include a few early Holocene individuals to infer biological relationships among populations or test dispersion models (Hubbe et al. 2009; Galland and Friess 2016; von Cramon-Taubadel et al. 2017). Due to this geographical bias, archaeological sites from Latin American countries are not frequently mentioned in the literature (or the same few ones are cited over and over), perpetuating geopolitical imbalances between researchers coming from central and peripheral countries (Yañez et al. 2023). Moreover, early Holocene individuals in these studies often derive from the same few archaeological localities, potentially underestimating the wide regional variation during that period. This sample bias may impact the perception of early Holocene variation due to incomplete sampling of a highly structured population across time.

After the surge of aDNA studies, some misconceptions have emerged, such as the



**Fig. 3 - Graphic summary of models presented in this review: (1) South American origin of humanity; (2) East Asian origin and the North American Ice-free corridor; (3) East Asian origin and three-migrations; (4) Asian origin and the coastal or kelp highway; (5) The distinctive biological contribution from South East Asia; (6) African origin and Atlantic route; (7) European origin and Atlantic route; and (8) Beringian Standstill. The violet cross indicates departure location, dotted lines indicate navigation routes, and the sold lines signify land routes. The numbers reflect the suggested time of arrival to the Americas, as presented in text above.**

expectation that genetic results can answer more questions about human history than realistically possible. Contrary to common belief, interpretations based on genetic results should be approached cautiously. These interpretations often rely on a small number of poorly preserved samples (i.e., aDNA molecules being usually short and damaged), constituting less than 1% of Native Americans' variation. Additionally, various decisions made during the workflow, including molecular clock calibration, reference genomes used for sequence alignment, genotype imputation, and the selection of outgroups, significantly impact the obtained results (Axelsson et al. 2008; Orlando et al. 2021). While genetic data, in combination with other information sources like archaeology can contribute to models determining approximate population divergence (Raff 2022), it is crucial to recognize that genetic results can be misleading (Steeves 2023), and should not be considered ultimate truths. Similarly, studies based on dental and craniometric studies are neither. However, the evidence and interpretations based on dental and cranial variation, despite their historical relevance for understanding Native American origins and variation, have not received full consideration in recent decades (but see Powell 2005). This neglect arises concerns for interdisciplinary research agenda on this topic (Dillehay 2021; Menéndez et al. 2022). An interdisciplinary approach, such as investigating interactions between self-perception of ethnicity, genomic ancestry, and phenotypic data from an evolutionary perspective, holds promise for reconstructing population history and improving health policies (Quinto-Sánchez et al. 2017; Chacón-Duque et al. 2018; Ruderman et al. 2020; Paschetta et al. 2021). However, interdisciplinarity comes with challenges, including defining the unit of analysis. Questions like whether “culture”, “ethnicity”, “linguistic family”, “population”, and “lineage” can be considered equivalent must be thoroughly discussed among archaeologists, biological anthropologists, linguists, and paleogeneticists to advance the study of the human past from

an interdisciplinary perspective (Shennan 2011; Riede et al. 2019).

Several researchers emphasize studying the peopling of the Americas as the culmination of the last continental human journey, positing the arrival of humans in the Americas as the final expansion across the world (Goebel et al. 2008; Hoffecker et al. 2016). This approach allows for integrating North American and Asian evidence to discuss the origin of ancestral lineages. However, an increasing number of researchers argue that South American, Central American, and North American archaeological records should be independently explained and combined or compared at a later stage (Dillehay et al. 1992; Goebel 2022). Furthermore, combining different geographic scales of analysis might be relevant for a better understanding of some processes. Current projects focusing on the peopling of the Americas are moving away from the ambition to build broad models and are instead concentrating on extensive sampling on smaller scales. While broad models provide a useful framework, they are limited as “the peopling” was not a singular population movement but a complex process involving stepping-stone migrations and expansions in various directions. Changes in the focus of researchers in the ancient DNA field illustrate this complexity: in the previous decade (~2010-2020), geneticists analysed few samples from many different regions to build broad models (Reich et al. 2012; Skoglund et al. 2015; Moreno Mayar et al. 2018a; Posth et al. 2018), while in recent years (~2020-now) research has shifted towards discussing regional dynamics in-depth, including recent migrations such as the peopling of the Caribbean (Schroeder et al. 2018; Nägele et al. 2020; Fernandes et al. 2021), the peopling of Patagonia (de la Fuente et al. 2018; Nakatsuka et al. 2020; Postillone et al. 2020; Figueiro et al. 2022;), and South to North population movements (Pinotti et al. 2019; Campelo Santos et al. 2022; Kennett et al. 2022). This shift demonstrates how researchers are now exploring local dynamics to articulate or contrast them with the broad picture. The broad models presented here are being re-evaluated in

light of new and finer-grain evidence from narrower regions. However, disagreements persist regarding the number of founding lineages and migrations, and the geographic and temporal bias of genetic analysis will likely persist due to underrepresented areas in terms of sample preservation and indigenous groups that may be hesitant to share their genetic stories.

Lastly, but not least, much of the research on the peopling of the Americas over the last decade takes seriously the engagement with contemporary indigenous communities and their interests in research. In countries like the USA or Canada, there are strict national laws regulating the consent of indigenous communities before conducting any kind of research on ancient skeletons (e.g., NAGPRA). Initiatives such as SING (Claw et al. 2018) have promoted the training of indigenous people who are now conducting investigations to reconstruct their own history. However, relations between indigenous communities, modern governments, and researchers vary widely across the Americas. In some peripheral countries, measures to protect biocultural heritage are easier to elude, enabling more frequent instances of “helicopter science” and allowing the persistence of colonial practices by researchers from central countries (Tsoie et al. 2020; Ávila-Arcos et al. 2022). Fortunately, there is a recent effort toward building long-term collaborative work between indigenous communities and researchers to answer questions about the past. Some scholars are adopting a more respectful and sensitive approach when studying human remains. The ethical debate has been ongoing for decades, but it recently gained more attention, emphasizing the need not only to build long-term relations with indigenous communities for knowledge sharing and capacity building (Claw et al. 2018; Rocca et al. 2021; Ávila-Arcos et al. 2022; Kowal et al. 2023) but also to establish more equitable and diverse research teams where researchers from the periphery play a leading role in projects conducted in their countries of origin. Finally, a debate is emerging concerning the vocabulary, assumptions, and theoretical perspectives used to narrate the arrival/presence and history of humans in the Americas (Steeves

2015; Furrholt 2017; Crellin and Harris 2020; Rocca et al. 2021). It becomes clear that a full understanding of this process requires not only an interdisciplinary perspective but also a sensitive and respectful approach. Future investigations should aim to integrate disparate evidence and improve dialogues between researchers from different disciplines along with indigenous people and their knowledge in order to overcome what Luigi Cavalli-Sforza described more as a battleground than a research topic when talking about the peopling of the Americas investigations (Churchill 2005).

### Closing statement

The present review does not aim to be exhaustive; rather, it focuses on analyzing the contribution of studies on the biological variation of humans in the Americas to the main proposed models from an academic perspective during the 19<sup>th</sup> to the early 21<sup>st</sup> centuries. The approach involves a historical account and analysis of selected publications, addressing two fundamental questions that guided most research projects within the covered time frame: who were the first Native Americans, and when did they arrive to the continent? This approach leaves out some relevant archaeological sites and alternative explanations and models that do not consider biological variation, such as those from indigenous oral histories. Moreover, socio-political aspects at the time of model development are not extensively covered, which could provide contextual information to better understand certain interpretations in this review. As the focus is on presenting the main broad models, there is a strong bias towards highlighting migration as the most significant evolutionary process contributing to the biological variation of Native Americans. Future work should delve into presenting the main evolutionary mechanisms, beyond migrations and gene flow, proposed to explain the diversification of humans in the Americas throughout the history of research on this captivating topic.

## Acknowledgements

*I express my gratitude to the associated editor and editor-in-chief of the Journal of Anthropological Sciences, Emiliano Bruner and Giovanni Destro-Bisol, for inviting me to write this review paper. Special thanks to the KLI (Konrad Lorenz Institute for Evolution and Cognition Research) for hosting me as a Visiting Fellow during the early stages of this project. The bibliographic research conducted for preparing this review is part of the project "Human morphological diversification in the Argentinean Pampas: Implications for the Peopling of South America", which is funded by the DFG (Deutsche Forschungsgemeinschaft, Project Number 415489479). I extend my appreciation to Sergio Bogan, María Laura Ciampagna, Ruth Gruhn, Mónica Hidalgo, and the staff from the "Florentino Ameghino" Library (Biblioteca Florentino Ameghino, Universidad Nacional de La Plata) for their assistance in scanning and/or sharing some old publications crucial for this research. I acknowledge the ideas presented in this paper, which were partially discussed in lectures at Escuela Nacional de Antropología e Historia (Mexico), DAF-Museo Nacional de Antropología (Mexico), University of Zurich (Switzerland), Liverpool John Moores University (United Kingdom), University of Chile (Chile), and Pasteur Institute (France). I thank the colleagues who invited me to give those lectures and the participants for contributing to enriching the discussions: Bernardo Yañez, Juan Manuel Argüelles, Blanca Martínez de León, Victor Acuña Alonzo, Miguel Angel Contreras Sieck, Chiara Barbieri, Marcelo Sánchez-Villagra, Laura Buck, Kornelius Kupczick, Pierre Luisi, and Nicolás Rascován. A special acknowledgement goes to Stephanie Schnorr for proofreading the article. I emphasize that views and opinions expressed in this article belong solely to the author.*

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Editor, Giovanni Destro Bisol



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