Revista Argentina de Antropología Biológica

DOSSIER-REVIEW ARTICLE

Craniofacial morphological diversity of North, Central, and South America: Implications for discussions about oral biology and health

Diversidad de la morfología craneofacial en América del Norte, Central y del Sur: Implicaciones para las discusiones sobre biología y salud oral

Mark Hubbe[1*]

1) Department of Anthropology, The Ohio State University, United States of America.

Abstract

Craniofacial morphology plays an important role in many aspects of the masticatory function and the oral health of individuals, and as such should be considered a baseline for studies that aim to integrate anthropological and dentistry practices that can improve oral health, dental hygiene, and care practices in populations from different biological and cultural backgrounds. This article presents a synthesis of our current understanding of the craniofacial and dental variation among native populations of North, Central, and South America, as part of the special volume on "Anthropology meets Dentistry in Central America: Research and education in oral biology". The article presents an overview of the history of the human occupation of the American continents, with special focus on how early and recent past events have contributed to the craniofacial morphological diversity observed in these continents. However, there is limited information about native Central American populations, and current inferences about them depend largely on extrapolating from what is known about North and South America. Given the current state of knowledge, this article argues that modern Central Americans share a facial morphological pattern distinct from other populations worldwide, which means that applying models developed for other groups may not be appropriate in this context. Therefore, understanding regional variation in craniofacial morphological patterns is an important priority of study, which must consider the different cumulative factors (genetics, developmen-

REVISTA ARGENTINA DE ANTROPOLOGÍA BIOLÓGICA

Volumen 26, Número 2, Artículo 082
Julio -Diciembre 2024

Editado y aceptado por el editor asociado Miguel Delgado, División Antropología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina; Ministry of Education Key Laboratory of Contemporary Anthropology, Collaborative Innovation Center of Genetics and Development, School of Life Sciences and Human Phenome Institute Fudan University, China.

*Corresponding author: Mark Hubbe. 4020 Smith Labs, 174W 18th Avenue, Columbus, OH 43214. USA. E-mail: hubbe.1@osu.edu

RECIBIDO: 29 de Agosto de 2023

ACEPTADO: 20 de Junio de 2024

PUBLICADO: 27 de Septiembre de 2024

https://doi.org/10.24215/18536387e082

Funding:
FOSEC SS/IMSS/ISSSTE # A3-S-38681.

e-ISSN 1853-6387

https://revistas.unlp.edu.ar/raab

Entidad Editora
Asociación de Antropología Biológica Argentina

tal, cultural, and historical) that have differently influenced the biological and cultural history of the populations in the region. Rev Arg Antrop Biol 26(2), 082, 2024. https://doi.org/10.24215/18536387e082

Keywords: biological diversity; human dispersion; morphology

Resumen
La morfología craneofacial tiene un importante rol en varios aspectos de las funciones masticatorias y de la salud oral de individuos y, por lo tanto, debe ser considerada un aspecto básico de investigaciones dedicadas a la integración de prácticas antropológicas y ortodónticas, dirigidas a mejorar las condiciones de salud oral e higiene bucal en poblaciones de distintos contextos bioculturales. Este artículo presenta una síntesis del conocimiento actual sobre la diversidad craneofacial en poblaciones nativas de las Américas del Norte, Central, y del Sur, sumándose al volumen especial sobre "La antropología se une a la odontología en América Central: Investigación y educación en biología oral". El artículo resume la historia de ocupación humana de los continentes americanos, con especial énfasis en cómo eventos tempranos y recientes contribuyeron a la diversidad morfológica observada en los continentes. Sin embargo, existe poca información sobre poblaciones nativas de la América Central, e inferencias sobre la región dependen en gran parte de extrapolaciones de lo que se conoce desde las Américas del Norte y del Sur. Considerándose el estado de conocimiento actual, este artículo propone que grupos actuales de América Central presentan características morfológicas únicas a la región, lo que significa que la aplicación de modelos construidos usando como referencia otras poblaciones del planeta pueden ser de poca validez. Por lo tanto, comprender la variación regional en la morfología craneofacial es una prioridad, y debe ser abordada considerando los distintos factores cumulativos (genéticos, de desarrollo, culturales, e históricos) que han influenciado la historia biológica y cultural de las poblaciones de América Central. Rev Arg Antrop Biol 26(2), 082, 2024. https://doi.org/10.24215/18536387e082

Palabras Clave: diversidad biológica; dispersión humana; morfología

Improving oral health is one of the main challenges faced by modern human societies, not only because of the impact that oral health has on overall well-being worldwide, but also because of its disparity within and between countries (Petersen *et al.*, 2005; World Health Organization, 2022). Health is a concept that is largely hard to define (Reitsema & McIlvaine, 2014; World Health Organization, 1999), as it encompasses a myriad of factors that disrupt the homeostasis of the body, as well as cultural practices that affect the perception of health itself. Oral health is similarly complex, as it is affected by the complex interaction between several different factors, including developmental and functional aspects of the mouth, pathologies and infections that can severely compromise the well-being and health of a person, cultural perspectives about the definition of "being healthy", and behaviors and cultural practices that change the way individuals interact with their oral biology. This article is part of the Dossier "Anthropology meets Dentistry in Central America: Research and education in oral biology", which addresses several aspects of this complex interaction, drawing on anthropological knowledge to help integrate practices that can improve oral health, dental hygiene, and care practices in populations from different biological and cultural backgrounds in Central America. The present article aims to contribute to this broader discussion by presenting a synthesis of our current understanding of the craniofacial and dental variation among native populations of North, Central, and South America, as this can be considered a fundamental baseline to understand the anatomy of the chewing apparatus, which plays a major role in a person's oral health.

Craniofacial variation and masticatory function

While several different factors ultimately contribute to oral health and masticatory function, one of the most fundamental ones is the bone structure that defines the maxillary region and therefore shapes the morphology of the masticatory apparatus. As explored in detail in other articles in this volume, the shape of the masticatory complex has significant impact on the chewing cycle, and differences in the growth and development of the face can have severely negative effects on oral health and masticatory efficiency over a person's life (e.g., Cevidanes *et al.*, 2005). Moreover, the interplay between dental development and maxillary growth are extremely impactful to overall oral health, as it can result in dental overcrowding and malocclusion. While a vast orthodontic literature is dedicated to the study of the impact of growth and development in the chewing cycle (e.g., Enlow & Hans, 1996; Kiliaridis, 2006), the vast majority of these studies are based on urban populations from affluent countries, and therefore may be of limited applicability when brought to different biological and cultural contexts. Similarly, there is a vast anthropological discussion about the changes in oral health in the past, including the origins of malocclusion (e.g., Pinhasi *et al.*, 2015; Rose & Roblee, 2009), but this discussion is not easily translated to current orthodontic practices. As the goal of the articles in this special volume is to consider how current orthodontic practices can improve oral health in Central American contexts, the understanding of the biological variation of American populations becomes an important informative prior to these endeavors.

There is no doubt that the biological and morphological background of native American populations is different from that of the European descendant populations that inform most of the current models connecting the morphology of the masticatory apparatus and the chewing cycle. However, little is known about how these differences impact the function of the masticatory apparatus and how they can affect the efficacy of orthodontic treatments developed for other contexts. This is an important aspect to consider in the development of orthodontic practices, as craniofacial morphology can have significant impact in the successful outcome of orthodontic treatments (e.g., Nishio & Huynh, 2016; Tahmina *et al.*, 2000). In this review article, I argue that we still know little about the morphological variation in Central America, and that the study of the association between facial morphology, chewing pattern, and oral health is an important area of focus to implement population-wide practices that will improve quality of life and oral health. Moreover, I argue that the large biological and cultural variation observed among native North, Central, and South American populations makes it hard, if not impossible, to establish generalizations about a *typical* Native American morphological pattern. Therefore, it is of tantamount importance that regional variation is considered in any studies designed to understand the craniofacial variation of Central American populations. In other words, effort must be made to avoid *one-size-fits-all* descriptions of Native American biological characteristics.

Early craniofacial variation in the American continents

To support the argument that there is significant craniofacial morphological diversity among native Central American populations, it is necessary to build a larger context of reference, starting with the discussions about the initial occupation of the American continents. Unfortunately, there is limited information about the craniofacial variation of native Central American populations, as a consequence of relatively poor preservation of skeletal remains in tropical environments and of limited research projects that have focused on this region. As such, the study of the craniofacial variation of Central Americans must be extrapolated from the broader context of North and South America, where significant work has been done to characterize the biological and morphological variation of populations across space and time. Since Central America acts as the natural corridor connecting the larger masses of North and South America, its human history is invariably tied to the processes of human dispersion on and between these continents.

The American continents were the last large landmasses to be occupied by modern human groups. The initial occupation of North America is currently thought to date to between 25 and 15 thousand years BP (Bennett *et al.*, 2021; Meltzer, 2010; Waters, 2019), and South America was probably occupied around 15 thousand years ago (Dillehay, 2009; Dillehay *et al.*, 2017; but see Pansani *et al.*, 2023 for possible earlier dates). There is still debate about the routes that early human groups took to occupy the continents, with both terrestrial and coastal routes proposed recently (Erlandson *et al.*, 2007; Farmer *et al.*, 2023). It is likely that humans spread relatively fast along the coastal regions of North and South America, following initially the pacific rim (Erlandson *et al.*, 2007), and splitting along the Atlantic coast once Central and South America was reached (Dillehay, 2009). There is clear evidence that all native American populations can trace their ancestry back to Northeast Asian groups (Goebel *et al.*, 2008; Raff, 2022; Skoglund & Reich, 2016) and, from both genetic and morphological perspectives, Native American populations form a cohesive cluster with Asian populations (Hubbe *et al.*, 2010; Moreno-Mayar *et al.*, 2018; Posth *et al.*, 2018; Reich *et al.*, 2012; Von Cramon-Taubadel *et al.*, 2017). However, despite their closer ancestry with Asian populations, native American populations are biologically and morphologically distinct from the former. Genetic evidence suggests that American ancestral populations have been isolated from Asian groups for long periods of time (Mulligan *et al.*, 2008; Sikora *et al.*, 2019; Tamm *et al.*, 2007), and craniofacial and dental morphologies show that native North and South Americans have phenotypic characteristics that differentiate them from east Asian and other worldwide populations (Hubbe *et al.*, 2010, 2011; Scott *et al.*, 2018).

The occupation of North and South America represents the last of a series of genetic bottlenecks that modern humans went through as they expanded out of Africa during the Late Pleistocene. As such, native American populations show relatively less genetic and phenotypic variance than populations from other continents (Betti *et al.*, 2009; Manica *et al.*, 2007). However, while overall diversity is relatively low, the American continents show remarkable apportionment of variance among populations (Posth *et al.*, 2018; Sardi *et al.*, 2005; Wang *et al.*, 2007), showing that native American populations are far from homogeneous. This higher diversity between populations is true when considering the entire American population, and also when only samples of Central America are considered (Wang *et al.*, 2007)

The diversity of native American populations is already observed early on the history of human presence in the continents. While the genetic evidence points to a common ancestor to modern native North and South American groups (Moreno-Mayar *et al.*, 2018; Posth *et al.*, 2018), the study of the earliest human remains found in the continent supports higher biological diversity in the past. Several studies have shown that the earliest human remains on the continent share craniofacial characteristics that differ from the morphological pattern seen among recent native North, Central, and South American populations (González-José *et al.*, 2008; Hubbe *et al.*, 2010, 2011; Menéndez *et al.*, 2019; Von Cramon-Taubadel *et al.*, 2017). Indeed, early South American populations show higher affinities with groups from Australo-Melanesia than with modern Native Americans (Hubbe *et al.*, 2011; Neves & Hubbe, 2005), which suggests that early South American populations (and some early North American populations as well) share a craniofacial morphology that is less derived than what is observed among modern east Asians and Native Americans (Hubbe *et al.*, 2011; Von Cramon-Taubadel *et al.*, 2017). The differences are of such magnitude that it has fueled long debates about whether they are the result of multiple migrations into North America (Neves & Hubbe, 2005), the result of convergent evolution on the continent (Perez *et al.*, 2011), or the result of progressive gene-flow from Asia into the American continents (González-José *et al.*, 2008). Recent ancient DNA data recovered from a few early South American skeletal remains suggest that South and Central America may have been occupied through multiple waves of migration, even if multiple waves of dispersion from Asia into North America are not supported (Posth *et al.*, 2018).

The morphological diversity at the end of the Pleistocene/beginning of the Holocene varies across continents. In South America, all known skeletal remains older than around eight thousand years BP share a similar morphological pattern, usually referred to as "Paleoamerican" (Neves *et al.*, 2007; Neves & Hubbe, 2005, but see Kuzminsky *et al.*, 2018 for exceptions to this pattern in Chile), suggesting relative biological homogeneity for the first millennia of human presence in the continent. In North America, the scenario is less clear, since there are very few preserved skeletons dated to the early moments of human occupation of the continent. However, among the few skeletons available there is a remarkable diversity of morphological patterns (Hubbe *et al.*, 2020; Jantz & Owsley, 2001), which suggests that in North America there was much more biological diversity in this period when compared to South America. If this is the case, some of the biological diversity was filtered out as populations moved south from North America to occupy South America, resulting in the southern continent sharing only a portion of the variance observed in the northern continent. However, with the lack of well-preserved early skeletons in Central America, it is currently unknown if Central American populations had diversity levels more similar to the northern or to the southern continent.

This discussion assumes special relevance for the topic of this special volume, given that if multiple waves of migration came from North America into South America, they must have crossed Central America, contributing genetic and phenotypic diversity to local populations already during the earliest moments of human presence in the region. As a consequence, the discussion about the morphological and biological diversity during the first millennia of human presence in the continent is important for two reasons. First, it demonstrates that the degree of differences among populations has been significant since early moments of human presence in the continents. Second, it shows that the biological diversity of Native Americans is not homogeneous and has changed over time. Moreover, there is evidence of a few surviving populations that share similar morphological pattern as the early North and South Americans in Central Brazil (Strauss *et al.*, 2015), Patagonia (Lahr, 1995), and Baja California (González-José *et al.*, 2003), which reinforces the point that morphological diversity in Central America, and in North America and

South America as a whole, is the result of long-lasting events of population movement and admixture, some of them possibly extending back for several thousand years.

Craniofacial phenotypic plasticity

Given that craniofacial morphology is the base layer for the growth and development of the chewing apparatus, and therefore has direct implications on oral health (see the other articles in this Dossier), it is important to briefly review the different degrees of phenotypic plasticity observed in different regions of the skull, before further contextualizing the sources of variation in the craniofacial morphology of native North, Central, and South American populations. Craniofacial morphology is the result of the interaction between complex polygenic and hierarchical genes that regulate the growth trajectory of several different functional models in the head, with different levels of integration between them (Bastir & Rosas, 2009; Collard & Wood, 2007; Klingenberg, 2008, 2013; Lieberman *et al.*, 2000; Paschetta *et al.*, 2010). The degree to which the different modules respond to environmental stimuli during growth and development is variable and, as a consequence, different regions of the skull and face have higher plasticity and also higher evolvability. A comprehensive review of the process has been published by Lieberman (2011), but briefly it is possible to divide the skull into three macro anatomical regions that will show different degrees of plasticity associated with their development timing. The first region encompasses all the bones and tissues surrounding the brain, i.e., the neurocranium. The neurocranium develops faster than the rest of the skeleton, as brain development follows an accelerated growth trajectory compared to the rest of the body. This results in a smaller window of time for environmental stimuli to pressure changes in the final shape of the skull, resulting in a relatively high genetic contribution to the final shape of the skull. In other words, the neurocranium shows moderate to high heritability (Carson, 2006; Martínez-Abadías *et al.*, 2009). This does not mean that the region is not inherently plastic, however, as can be demonstrated by the practice of intentional cranial vault deformation in many societies worldwide until recently (Torres-Rouff, 2020).

The second macro anatomical region is the face, particularly its infra-orbital region. Distinct from the neurocranium, facial growth follows the same growth trajectory as the rest of the body, and only finishes growing when individuals reach adulthood. All else remaining the same, the longer window of growth means that environmental stimuli have more time to impact the growth of the facial skeletal structure, compared to neurocranium (Lieberman, 2011). Moreover, the bones of the face interact with most of the major muscles related to mastication, swallowing, and facial expressions, which create a very dynamic environment for their development as they respond to the different forces that act upon it. As a consequence, the facial region's morphology shows a larger contribution of the environmental context of the individual's growth, reflected in higher plasticity and overall lower heritability than the neurocranium (Carson, 2006).

The final region of relevance to the discussion presented here are the teeth. While not strictly part of the skeletal system, teeth play an evident role in the masticatory system and are often associated with aspects of oral health. Teeth are relevant as well in that they show a development progress that is much shorter than what is observed in the rest of the skeleton, with most of the key features of dental crown morphology fully developed in the first years of life of a person. Teeth are considered to be highly non-responsive to environmental stimuli and tend to show high heritability values (Dempsey & Townsend, 2001; Paul *et al.*, 2021; but see discussions about different factors affecting tooth morphology in Hlusko *et al.*, 2018). Despite their high heritability, teeth show considerable morphological variation, with many different genetically controlled phenotypes known in humans, including accessory cusps, variations in crown and root shapes, tissue thickness, among others. This variation has been studied through the evaluation of the frequency of traits and specific morphological patterns have been linked with specific regions of the planet (Scott & Turner, 1997). For instance, most Native American populations show derived dental phenotypes that are quite distinct from what is observed in other continents (Scott *et al.*, 2018).

By themselves, the different degrees of response to environmental factors during growth and development can impair oral health, which merits consideration. For example: changes in diet associated with cooking food and access to processed food items results in significant reduction in the chewing demands on people, which translates itself to under-development of the masticatory muscles. This, in turn, results in a reduced stimulation of the bone tissue of the lower face, causing overall smaller maxillary and mandibular arches. While a smaller face is not by itself a significant problem, it becomes so when teeth are not responding similarly to these pressures, and continue to grow on trajectories that are defined by genes shaped in an evolutionary context prior to food processing. As a result, modern populations see significantly more cases of dental overcrowding and malocclusion and all oral health and masticatory function issues that derive from it. Archaeological evidence suggests this is directly tied to changes in life-style, as the adoption of agriculture between 12,000 and 8,000 thousand years BP correlates with increased frequency of malocclusion (Pinhasi *et al.*, 2015).

Therefore, the different factors that shape the craniofacial variation in a population, from those that contribute to making them different from other populations worldwide to the ones that contribute to the variance accumulated within the population can be important aspects of the masticatory function and oral health of a group. For this reason, I argue that taking them into consideration becomes important in the development of practices that will maximize the effectiveness of dental treatment among Central American populations.

Factors contributing to craniofacial morphological diversity in North, Central, and South America

Besides the morphological diversity that derives directly from the biological variation of the first populations that occupied the American continents, several factors helped to shape and structure the morphological characteristics of Native American populations across space and time. As mentioned previously, it is hard to define a homogeneous morphological type for native populations in North, Central, or South America (despite the common practice of grouping these populations together; see Menéndez *et al.*, 2022, for a discussion about this topic). Besides the genetic background of native populations, environmental and cultural factors also shape significant portions of the morphological diversity of these populations. As a consequence, the amount of diversity observed across the continents varies depending on local contexts.

Starting with a broad overview, there is more morphological homogeneity in the central parts of North America and the Andean region of South America, due to the shared biocultural background of populations in each of these regions and the facilitated gene flow that resulted from these historical processes (e.g., Hanihara, 2008; Howells, 1990; Kuzminsky *et al.*, 2018). However, in regions like the mainland of Mexico (Herrera *et al.*,

2017) and the eastern side of South America (Fidalgo *et al*., 2021; Hubbe *et al*., 2014) there are considerable morphological differences among populations. This is probably the result of the increased isolation among these populations over time, reflected also in some cultural traits such as linguistic diversity (e.g., Nettle, 1999; Nichols, 1990). Once again, given this diversity across the continents, it is hard to describe the level of morphological diversity in Central America until more regional comparative studies are published. However, it is expected that the Native American component of local morphology is already quite diverse in the region, and therefore should be considered carefully in studies of craniofacial morphology of Central American populations.

Given the different levels of plasticity and responses to environmental stimuli in different parts of the skull, environmental factors are important to consider in the characterization of native American morphology. This is especially true if the focus is on facial morphology, given its relatively higher plasticity. Indeed, several different cultural and environmental factors have been shown to impact craniofacial morphology in the American continents. Adaptation to cold environments, for example, have been described in populations living in higher latitudes in North America (Hubbe *et al*., 2009), causing these populations to show high morphological similarities with each other, despite the geographic distance that separates them. On the face, adaptations to cold environments are most pronounced around the nasal cavity, and have been hypothesized as being the result of responses to increase thermoregulation of air flow into the lungs (Hubbe *et al*., 2009).

While adaptations to cold are not a relevant factor in Central America, they illustrate well the impact that environmental pressures can have on the craniofacial morphological pattern of Native American populations over time. Much more relevant to the morphological diversity of Central American populations is the impact that changes in subsistence practices have on facial morphology. Indeed, studies have shown that the transition from foraging to agriculture has had a significant impact on the morphology of Native American populations (González-José *et al*., 2005; Perez *et al*., 2011), especially in the lower face. Most these changes are not just about the adoption of agriculture, but of the overall properties of the food consumed and how it is engaged with the masticatory musculature and skeletal tissue (but see Menéndez *et al*., 2014). As such, it is expected that agricultural populations with different diets of food preparation practices would accumulate significant morphological differences as well. However, while this prediction is supported by some studies, this topic has not been explored in detail among Native Americans.

Ecological diversity also seems to play a role in how differentiated populations are from the perspective of craniofacial morphology. Higher ecological diversity in the Americas seems to be correlated with increased morphological diversity, especially when comparing west (relatively low diversity) and east (relatively high diversity) South America (Menéndez *et al*., 2019; Pucciarelli *et al*., 2006). The expectation in this case is that higher ecological diversity can support more autonomous populations that can adapt to specific environments and limit their gene flow with neighboring groups, accelerating the process of biological and cultural differentiation over time. This topic has been only superficially studied in modern human populations from the American continents, however it is potentially relevant for discussions about Central America craniofacial characteristics given the very high ecological diversity in the region.

As it is clear by now, there is little data available of craniofacial diversity for Central American populations, but this brief review demonstrates that the expectations derived from studies of North and South America are of high morphological diversity across native Central American populations. This is true even before the colonial history of admixture with European and African populations is taken into account. As recent genetic studies show (Melton *et al.*, 2013), there is a significant level of genetic contribution of non-native American genes to many native Central American populations, which will invariably affect the morphological patterns of modern populations. Again, this contribution of admixture to Central American populations has not been explored enough, but it has the potential to inflate the variability seen in craniofacial morphology among and within local populations, and becomes of relevance to discussions of oral health interventions inasmuch as craniofacial morphology plays a significant role in the growth and development of the masticatory complex.

Final considerations

As this article and others in the Dossier "Anthropology meets Dentistry in Central America: Research and education in oral biology" have argued, the morphology of the masticatory apparatus has a very significant impact on masticatory function, oral health, and overall well-being. However, the connections between morphology and function are not fully understood and most available models do not take into account the morphological characteristics of Central America populations. In this article, I briefly reviewed the current knowledge about morphological diversity in North, Central, and South America, and argued that not enough is known about the craniofacial morphology of Central American populations

The challenges with understanding the origins of craniofacial morphological variation in Central America stem from the lack of known past skeletal collections, limited preservation, and relatively little investment in the research of current human groups. While it is possible to infer some of the biological background of Central America from the studies of North and South American populations, these inferences are limited by the fact that Central America may have had multiple distinct roles in the population movements that happened between the northern and southern continents. What is clear, however, is that high morphological diversity should be expected in Central America, as a result of the different factors (genetic, environmental, cultural, historical) that contributed to Native American phenotypic variance. Therefore, even though much study is still needed about the craniofacial morphological background of Central Americans, it is evident that 1) modern Central Americans share a facial morphological pattern distinct from other populations, which means that applying models developed for other groups may not be appropriate in this context; and 2) understanding regional variation in craniofacial morphological patterns is an important priority of study, as there is no *typical* Central American morphology. It is important to start from the framework that many different cumulative factors have differently influenced the biological and cultural history of the populations in the region, which generate diverse and complex craniofacial morphological characteristics. Therefore, initiatives aimed at improving the oral health of Central American native populations must be careful when applying concepts or models developed on other populations on those aspects of orthodontic treatments that are affected by the facial morphology of the individual.

AUTHORS' CONTRIBUTIONS

Mark Hubbe: Conceptualization and writing of article.

ACKNOWLEDGMENTS

I am especially thankful to Cinzia Fornai and Karol Ramirez for inviting me to participate in the workshop "Anthropology meets Dentistry in Central America: Research and education in oral biology". I am also thankful to all participants of the symposium, who generated innumerous fruitful discussions about how anthropology and dentistry can complement each other in the study of oral biology.

CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

LITERATURE CITED

Bastir, M. & Rosas, A. (2009). Mosaic evolution of the basicranium in Homo and its relation to modular development. *Evolutionary Biology*, *36*(1), 57-70. https://doi.org/10.1007/s11692-008-9037-4

Bennett, M. R., Bustos, D., Pigati, J. S., Springer, K. B., Urban, T. M., Holliday, V. T., Reynolds, S. C., Budka, M., Honke, J. S., Hudson, A. M., Fenerty, B., Connelly, C., Martinez, P. J., Santucci, V. L. & Odess, D. (2021). Evidence of humans in North America during the Last Glacial Maximum. *Science*, *373*(6562), 1528-1531. https://doi.org/10.1126/science.abg7586

Betti, L., Balloux, F., Amos, W., Hanihara, T. & Manica, A. (2009). Distance from Africa, not climate, explains within-population phenotypic diversity in humans. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1658), 809-814. https://doi.org/10.1098/rspb.2008.1563

Carson, E. A. (2006). Maximum likelihood estimation of human craniometric heritabilities. *American Journal of Physical Anthropology*, *131*(2), 169-180. https://doi.org/10.1002/ajpa.20424

Cevidanes, L. H. S., Franco, A. A., Gerig, G., Proffit, W. R., Slice, D. E., Enlow, D. H., Yamashita, H. K., Kim, Y.-J., Scanavini, M. A. & Vigorito, J. W. (2005). Assessment of mandibular growth and response to orthopedic treatment with 3-dimensional magnetic resonance images. *American Journal of Orthodontics and Dentofacial Orthopedics*, *128*(1), 16-26.

Collard, M. & Wood, B. (2007). Hominin homoiology: An assessment of the impact of phenotypic plasticity on phylogenetic analyses of humans and their fossil relatives. *Journal of Human Evolution*, *52*(5), 573-584. https://doi.org/10.1016/j.jhevol.2006.11.018

Dempsey, P. J. & Townsend, G. C. (2001). Genetic and environmental contributions to variation in human tooth size. *Heredity*, *86*(6), 685-693. https://doi.org/10.1046/j.1365-2540.2001.00878.x

Dillehay, T. D. (2009). Probing deeper into first American studies. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(4), 971-978. https://doi.org/10.1073/pnas.0808424106

Dillehay, T. D., Goodbred, S., Pino, M., Vásquez Sánchez, V. F., Tham, T. R., Adovasio, J., Collins, M. B., Netherly, P. J., Hastorf, C. A., Chiou, K. L., Piperno, D., Rey, I. & Velchoff, N. (2017). Simple technologies and diverse food strategies of the Late Pleistocene and Early Holocene at Huaca Prieta, Coastal Peru. *Science Advances*, *3*(5), e1602778. https://doi.org/10.1126/sciadv.1602778

Enlow, D. H. & Hans, M. G. (1996). *Essentials of facial growth*. Saunder.

Erlandson, J. M., Graham, M. H., Bourque, B. J., Corbett, D., Estes, J. A. & Steneck, R. S. (2007). The kelp highway hypothesis: Marine ecology, the coastal migration theory, and the peopling of the Americas. *The Journal of Island and Coastal Archaeology*, *2*(2), 161-174. https://doi.org/10.1080/15564890701628612

Farmer, J. R., Pico, T., Underwood, O. M., Cleveland Stout, R., Granger, J., Cronin, T. M., Fripiat, F., Martínez-García, A., Haug, G. H. & Sigman, D. M. (2023). The Bering Strait was flooded 10,000 years before the Last Glacial Maximum. *Proceedings of the National Academy of Sciences*, *120*(1), e2206742119. https://doi.org/10.1073/pnas.2206742119

Fidalgo, D., Hubbe, M. & Wesolowski, V. (2021). Population history of Brazilian south and southeast shellmound builders inferred through dental morphology. *American Journal of Physical Anthropology*, *176*(2), 192-207. https://doi.org/10.1002/ajpa.24342

Goebel, T., Waters, M. R. & O'Rourke, D. H. (2008). The Late Pleistocene dispersal of modern humans in the Americas. *Science*, *319*(5869), 1497-1502. https://doi.org/10.1126/science.1153569

González-José, R., Bortolini, M. C., Santos, F. R. & Bonatto, S. L. (2008). The peopling of America: Craniofacial shape variation on a continental scale and its interpretation from an interdisciplinary view. *American Journal of Physical Anthropology*, *137*(2), 175-187. https://doi.org/10.1002/ajpa.20854

González-José, R., González-Martín, A., Hernández, M., Pucciarelli, H. M., Sardi, M., Rosales, A. & Van Der Molen, S. (2003). Craniometric evidence for Palaeoamerican survival in Baja California. *Nature*, *425*(6953), 62-65. https://doi.org/10.1038/nature01816

González-José, R., Ramírez-Rozzi, F., Sardi, M., Martínez-Abadías, N., Hernández, M. & Pucciarelli, H. M. (2005). Functional-cranial approach to the influence of economic strategy on skull morphology. *American Journal of Physical Anthropology*, *128*(4), 757-771. https://doi.org/10.1002/ajpa.20161

Hanihara, T. (2008). Morphological variation of major human populations based on nonmetric dental traits. *American Journal of Physical Anthropology*, *136*(2), 169-182. https://doi.org/10.1002/ajpa.20792

Herrera, B., Peart, D., Hernandez, N., Spradley, K. & Hubbe, M. (2017). Morphological variation among Late Holocene Mexicans: Implications for discussions about the human occupation of the Americas. *American Journal of Physical Anthropology*, *163*(1), 75-84. https://doi.org/10.1002/ajpa.23186

Hlusko, L. J., Carlson, J. P., Chaplin, G., Elias, S. A., Hoffecker, J. F., Huffman, M., Jablonski, N. G., Monson, T. A., O'Rourke, D. H., Pilloud, M. A. & Scott, G. R. (2018). Environmental selection during the Last Ice Age on the mother-to-infant transmission of vitamin D and fatty acids through breast milk. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(19), E4426–E4432. https://doi.org/10.1073/pnas.1711788115

Howells, W. W. (1990). *Skull shapes and the map: Craniometric analyses in the dispersion of modern Homo*. Peabody Museum Press.

Hubbe, M., Hanihara, T. & Harvati, K. (2009). Climate signatures in the morphological differentiation of worldwide modern human populations. *The Anatomical Record*, *292*(11), 1720-1733. https://doi.org/10.1002/ar.20976

Hubbe, M., Harvati, K. & Neves, W. (2011). Paleoamerican morphology in the context of European and East Asian Late Pleistocene variation: Implications for human dispersion into the new world. *American Journal of Physical Anthropology*, *144*(3), 442-453. https://doi.org/10.1002/ajpa.21425

Hubbe, M., Mata, A. T., Herrera, B., Sanvicente, M. E. B., González, A. G., Sandoval, C. R., Olguín, J. A., Núñez, E. A. & Cramon-Taubadel, N. V. (2020). Morphological variation of the early human remains from Quintana Roo, Yucatán Peninsula, Mexico: Contributions to the discussions about the settlement of the Americas. *PLOS ONE*, *15*(1), e0227444. https://doi.org/10.1371/journal.pone.0227444

Hubbe, M., Neves, W. A. & Harvati, K. (2010). Testing evolutionary and dispersion scenarios for the settlement of the New World. *PLOS ONE*, *5*(6), e11105. https://doi.org/10.1371/journal.pone.0011105

Hubbe, M., Okumura, M., Bernardo, D. V. & Neves, W. A. (2014). Cranial morphological diversity of early, middle, and Late Holocene Brazilian groups: Implications for human dispersion in Brazil: Cranial morphology of Holocene Brazilian groups. *American Journal of Physical Anthropology*, *155*(4), 546-558. https://doi.org/10.1002/ajpa.22607

Jantz, R. l. & Owsley, D. W. (2001). Variation among early North American Crania. *American Journal of Physical Anthropology*, *114*(2), 146-155. https://onlinelibrary.wiley.com/doi/10.1002/1096-8644(200102)114:2%3C146::AID-AJPA1014%3E3.0.CO;2-E

Kiliaridis, S. (2006). The importance of masticatory muscle function in dentofacial growth. *Seminars in Orthodontics*, *12*(2), 110-119. https://doi.org/10.1053/j.sodo.2006.01.004

Klingenberg, C. P. (2008). Morphological integration and developmental modularity. *Annual Review of Ecology, Evolution, and Systematics*, *39*(1), 115-132. https://doi.org/10.1146/annurev.ecolsys.37.091305.110054

Klingenberg, C. P. (2013). Cranial integration and modularity: Insights into evolution and development from morphometric data. *Hystrix, the Italian Journal of Mammalogy*, *24*(1), 43-58. https://doi.org/10.4404/hystrix-24.1-6367

Kuzminsky, S. C., Reyes Báez, O., Arriaza, B., Méndez, C., Standen, V. G., San Román, M., Muñoz, I., Durán Herrera, Á. & Hubbe, M. (2018). Investigating cranial morphological variation of early human skeletal remains from Chile: A 3D geometric morphometric approach. *American Journal of Physical Anthropology*, *165*(2), 223-237. https://doi.org/10.1002/ajpa.23344

Lahr, M. M. (1995). Patterns of modern human diversification: Implications for Amerindian origins. *American Journal of Physical Anthropology*, *38*(S21), 163-198. https://doi.org/10.1002/ajpa.1330380609

Lieberman, D. (2011). *The evolution of the human head*. Belknap Press of Harvard University Press.

Lieberman, D. E., Ross, C. F. & Ravosa, M. J. (2000). The primate cranial base: Ontogeny, function, and integration. *American Journal of Physical Anthropology*, *113*(S31), 117-169. https://doi.org/10.1002/1096-8644(2000)43:31+<117::AID-AJPA5>3.0.CO;2-I

Manica, A., Amos, W., Balloux, F. & Hanihara, T. (2007). The effect of ancient population bottlenecks on human phenotypic variation. *Nature*, *448*(7151), 346-348. https://doi.org/10.1038/nature05951

Martínez-Abadías, N., Esparza, M., Sjøvold, T., González-José, R., Santos, M. & Hernández, M. (2009). Heritability of human cranial dimensions: Comparing the evolvability of different cranial regions. *Journal of Anatomy*, *214*(1), 19-35. https://doi.org/10.1111/j.1469-7580.2008.01015.x

Melton, P. E., Baldi, N. F., Barrantes, R. & Crawford, M. H. (2013). Microevolution, migration, and the population structure of five Amerindian populations from Nicaragua and Costa Rica. *American Journal of Human Biology*, *25*(4), 480-490. https://doi.org/10.1002/ajhb.22382

Meltzer, D. J. (2010). *First peoples in a new world: Colonizing Ice Age America*. University of California Press.

Menéndez, L., Bernal, V., Novellino, P. & Perez, S. I. (2014). Effect of bite force and diet composition on craniofacial diversification of Southern South American human populations. *American Journal of Physical Anthropology*, *155*(1), 114-127. https://doi.org/10.1002/ajpa.22560

Menéndez, L. P., Paul, K. S., de la Fuente, C., Almeida, T., Delgado, M., Figueiro, G., Jorgensen, K., Kuzminsky, S., López-Sosa, M. C., Nichols, J., Roksandic, M., Scott, G. R., O'Rourke, D. & Hubbe, M. (2022). Towards an interdisciplinary perspective for the study of human expansions and biocultural diversity in the Americas. *Evolutionary Anthropology: Issues, News, and Reviews*, *31*(2), 62-68. https://doi.org/10.1002/evan.21937

Menéndez, L. P., Rademaker, K., & Harvati, K. (2019). Revisiting east–west skull patterns and the role of random factors in South America: Cranial reconstruction and morphometric analysis of the facial skeleton from Cuncaicha Rockshelter (Southern Peru). *PaleoAmerica*, *5*(4), 315-334. https://doi.org/10.1080/20555563.2019.1703167

Moreno-Mayar, J. V., Vinner, L., De Barros Damgaard, P., de la Fuente, C., Chan, J., Spence, J. P., Allentoft, M. E., Vimala, T., Racimo, F., Pinotti, T., Rasmussen, S., Margaryan, A., Iraeta Orbegozo, M., Mylopotamitaki, D., Wooller, M., Bataille, C., Becerra-Valdivia, L., Chivall, D., Comeskey, D., … & Willerslev, E. (2018). Early human dispersals within the Americas. *Science*, *362*(6419), eaav2621. https://doi.org/10.1126/science.aav2621

Mulligan, C. J., Kitchen, A. & Miyamoto, M. M. (2008). Updated three-stage model for the peopling of the Americas. *PLOS ONE*, *3*(9), e3199. https://doi.org/10.1371/journal.pone.0003199

Nettle, D. (1999). Linguistic diversity of the Americas can be reconciled with a recent colonization. *Proceedings of the National Academy of Sciences of the United States of America, 96*(6), 3325–3329. https://doi.org/10.1073/pnas.96.6.3325

Neves, W. A., & Hubbe, M. (2005). Cranial morphology of early Americans from Lagoa Santa, Brazil: Implications for the settlement of the New World. *Proceedings of the National Academy of Sciences of the United States of*, *102*(51), 18309-18314. https://doi.org/10.1073/pnas.0507185102

Neves, W. A., Hubbe, M. & Correal, G. (2007). Human skeletal remains from Sabana de Bogotá, Colombia: A case of Paleoamerican morphology late survival in South America? *American Journal of Physical Anthropology*, *133*(4), 1080-1098. https://doi.org/10.1002/ajpa.20637

Nichols, J. (1990). Linguistic diversity and the first settlement of the New World. *Language*, *66*(3), 475-521. https://doi.org/10.2307/414609

Nishio, C. & Huynh, N. (2016). Skeletal malocclusion and genetic expression: An evidence-based review. *Journal of Dental Sleep Medicine*, *3*(2), 57-63.

Pansani, T. R., Pobiner, B., Gueriau, P., Thoury, M., Tafforeau, P., Baranger, E., Vialou, Á. V., Vialou, D., McSparron, C., De Castro, M. C., Dantas, M. A. T., Bertrand, L. & Pacheco, M. L. A. F. (2023). Evidence of artefacts made of giant sloth bones in central Brazil around the last glacial maximum. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2002), 20230316. https://doi.org/10.1098/rspb.2023.0316

Paschetta, C., de Azevedo, S., Castillo, L., Martínez-Abadías, N., Hernández, M., Lieberman, D. E. & González-José, R. (2010). The influence of masticatory loading on craniofacial morphology: A test case across technological transitions in the Ohio valley. *American Journal of Physical Anthropology*, *141*(2), 297-314. https://doi.org/10.1002/ajpa.21151

Paul, K. S., Stojanowski, C. M., Hughes, T., Brook, A. & Townsend, G. C. (2021). The genetic architecture of anterior tooth morphology in a longitudinal sample of Australian twins and families. *Archives of Oral Biology*, *129*, 105168. https://doi.org/10.1016/j.archoralbio.2021.105168

Perez, S. I., Lema, V., Diniz-Filho, J. A. F., Bernal, V., Gonzalez, P. N., Gobbo, D. & Pucciarelli, H. M. (2011). The role of diet and temperature in shaping cranial diversification of South American human populations: An approach based on spatial regression and divergence rate tests. *Journal of Biogeography*, *38*(1), 148-163. https://doi.org/10.1111/j.1365-2699.2010.02392.x

Petersen, P. E., Bourgeois, D., Ogawa, H., Estupinan-Day, S. & Ndiaye, C. (2005). The global burden of oral diseases and risks to oral health. *Bulletin of the World Health Organization*, *83*(9), 661-669.

Pinhasi, R., Eshed, V. & von Cramon-Taubadel, N. (2015). Incongruity between affinity patterns based on mandibular and lower dental dimensions following the transition to agriculture in the near east, Anatolia and Europe. *PLOS ONE, 10*(2), e0117301. https://doi.org/10.1371/journal.pone.0117301

Posth, C., Nakatsuka, N., Lazaridis, I., Skoglund, P., Mallick, S., Lamnidis, T. C., Rohland, N., Nägele, K., Adamski, N., Bertolini, E., Broomandkhoshbacht, N., Cooper, A., Culleton, B. J., Ferraz, T., Ferry, M., Furtwängler, A., Haak, W., Harkins, K., Harper, T. K., …& Reich, D. (2018). Reconstructing the deep population history of Central and South America. *Cell*, *175*(5), 1185-1197.e22. https://doi.org/10.1016/j.cell.2018.10.027

Pucciarelli, H. M., Neves, W. A., González-José, R., Sardi, M. L., Rozzi, F. R., Struck, A. & Bonilla, M. Y. (2006). East-West cranial differentiation in pre-Columbian human populations of South America. *Homo: Internationale Zeitschrift Fur Die Vergleichende Forschung Am Menschen*, *57*(2), 133-150. https://doi.org/10.1016/j.jchb.2005.12.003

Raff, J. (2022). *Origin: A genetic history of the Americas (1st ed.)*. Twelve, Hachette Book Group.

Reich, D., Patterson, N., Campbell, D., Tandon, A., Mazieres, S., Ray, N., Parra, M. V., Rojas, W., Duque, C., Mesa, N., García, L. F., Triana, O., Blair, S., Maestre, A., Dib, J. C., Bravi, C. M., Bailliet, G., Corach, D., Hünemeier, T. … & Ruiz-Linares, A. (2012). Reconstructing Native American population history. *Nature*, *488*(7411), 370-374. https://doi.org/10.1038/nature11258

Reitsema, L. J. & McIlvaine, B. K. (2014). Reconciling "stress" and "health" in physical anthropology: What can bioarchaeologists learn from the other subdisciplines? *American Journal of Physical Anthropology*, *155*(2), 181-185. https://doi.org/10.1002/ajpa.22596

Rose, J. C. & Roblee, R. D. (2009). Origins of dental crowding and malocclusions: An anthropological perspective. *Compendium of Continuing Education in Dentistry*, *30*(5), 292-300.

Sardi, M. L., Ramírez Rozzi, F., González-José, R. & Pucciarelli, H. M. (2005). South Amerindian craniofacial morphology: Diversity and implications for Amerindian evolution. *American Journal of Physical Anthropology*, *128*(4), 747-756. https://doi.org/10.1002/ajpa.20235

Scott, G. R., Schmitz, K., Heim, K. N., Paul, K. S., Schomberg, R. & Pilloud, M. A. (2018). Sinodonty, Sundadonty, and the Beringian Standstill model: Issues of timing and migrations into the New World. *Quaternary International*, *466* (B), 233-246. https://doi.org/10.1016/j.quaint.2016.04.027

Scott, G. R. & Turner, C. G. (1997). *The nnthropology of modern human teeth: Dental morphology and its variation in recent human populations*. Cambridge University Press.

Sikora, M., Pitulko, V. V., Sousa, V. C., Allentoft, M. E., Vinner, L., Rasmussen, S., Margaryan, A., de Barros Damgaard, P., de la Fuente, C., Renaud, G., Yang, M. A., Fu, Q., Dupanloup, I., Giampoudakis, K., Nogués-Bravo, D., Rahbek, C., Kroonen, G., Peyrot, M., McColl, H., … & Willerslev, E. (2019). The population history of northeastern Siberia since the Pleistocene. *Nature, 570,* 182-188. https://doi.org/10.1038/s41586-019-1279-z

Skoglund, P. & Reich, D. (2016). A genomic view of the peopling of the Americas. *Current Opinion in Genetics & Development*, *41*, 27-35. https://doi.org/10.1016/j.gde.2016.06.016

Strauss, A., Hubbe, M., Neves, W. A., Bernardo, D. V. & Atuí, J. P. V. (2015). The cranial morphology of the Botocudo Indians, Brazil. *American Journal of Physical Anthropology*, *157*(2), 202-216. https://doi.org/10.1002/ajpa.22703

Tahmina, K., Tanaka, E. & Tanne, K. (2000). Craniofacial morphology in orthodontically treated patients of Class III malocclusion with stable and unstable treatment outcomes. *American Journal of Orthodontics and Dentofacial Orthopedics*, *117*(6), 681-690. https://doi.org/10.1016/S0889-5406(00)70177-6

Tamm, E., Kivisild, T., Reidla, M., Metspalu, M., Smith, D. G., Mulligan, C. J., Bravi, C. M., Rickards, O., Martinez-Labarga, C., Khusnutdinova, E. K., Fedorova, S. A., Golubenko, M. V., Stepanov, V. A., Gubina, M. A., Zhadanov, S. I., Ossipova, L. P., Damba, L., Voevoda, M. I., Dipierri, J. E., … & Malhi, R. S. (2007). Beringian standstill and spread of Native American founders. *PLOS ONE*, *2*(9), e829. https://doi.org/10.1371/journal.pone.0000829

Torres-Rouff, C. (2020). Cranial modification and the shapes of heads across the Andes. *International Journal of Paleopathology*, *29*, 94-101. https://doi.org/10.1016/j.ijpp.2019.06.007

Von Cramon-Taubadel, N., Strauss, A. & Hubbe, M. (2017). Evolutionary population history of early Paleoamerican cranial morphology. *Science Advances*, *3*(2), e1602289. https://doi.org/10.1126/sciadv.1602289

Wang, S., Lewis, C. M., Jakobsson, M., Ramachandran, S., Ray, N., Bedoya, G., Rojas, W., Parra, M. V., Molina, J. A., Gallo, C., Mazzotti, G., Poletti, G., Hill, K., Hurtado, A. M., Labuda, D., Klitz, W., Barrantes, R., Bortolini, M. C., Salzano, F. M., … & Ruiz-Linares, A. (2007). Genetic variation and population structure in native Americans. *PLOS Genetics*, *3*(11), e185. https://doi.org/10.1371/journal.pgen.0030185

Waters, M. R. (2019). Late Pleistocene exploration and settlement of the Americas by modern humans. *Science*, *365*(6449), eaat5447. https://doi.org/10.1126/science.aat5447

World Health Organization. (2001). *Men ageing and health: Achieving health across the life span*. https://iris.who.int/handle/10665/66941

World Health Organization. (2022). *Global oral health status report: Towards universal health coverage for oral health by 2030*. https://www.who.int/publications/i/item/9789240061484