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Mandibular gracilization through time: a 3D comparison of ancient and contemporary populations *

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Abstract

Understanding the evolution of mandibular morphology provides key insights into the interplay between diet, technology, and oral health. When human populations made the subsistence transition from hunter-gathering to agriculture, the diet softened, and mandibles became more gracile. In this study, we compare the mandibular morphology of agricultural populations from ancient Sudan (350 BCE-350 CE) to contemporary Floridian populations to explore how jaw shape differs across geographic and temporal ranges beyond the agricultural revolution. We hypothesized that contemporary Floridian mandibles would differ significantly in shape from those of ancient agricultural populations, reflecting a continued trend of mandibular gracilization. Specifically, we predicted that the ancient mandibles would be more robust, with wider rami, shorter vertical height, and more acute body-ramus angles consistent with greater masticatory muscle use. To test this hypothesis, 39 contemporary mandibles were 3D surface scanned and compared to 38 ancient mandibles using 3D geometric morphometric quantitative methods, including a Procrustes ANOVA. Our predictions were met, and our hypothesis was supported ($p = 0.001$). Contemporary mandibles are characterized as being more gracile with taller and narrower rami and more obtuse gonial angles. This is likely due to the softness of the contemporary diet, perhaps driven by the recent rise in ultra-processed foods. Our findings demonstrate that mandibular shape can undergo significant change over a 2,000-year span, even between geographically distinct populations, and that contemporary gracilization parallels the morphological shifts associated with the earlier transition from hunter-gathering to agriculture.

Keywords: mandible; gracilization; geometric morphometrics; agriculturalist; diet

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Introduction

In comparison to other primates, the hominin lineage has undergone extremely rapid mandibular shape change (1). The australopiths are characterized by robust mandibles with thick cortical bone and large postcanine teeth for processing tough plant diets. Within *Homo*, mandibular gracilization occurred from the Early to Late Pleistocene, marked by reduced prognathism, smaller teeth, and thinner symphyses (2,3). In the Late Pleistocene, *Homo sapiens* fossils varied in their mosaic of ancestral and derived traits and were variable in overall size (4). During the Holocene, the human mandible experienced a major morphological shift alongside the rise of agriculture, becoming even more gracile due to reduced mechanical loading associated with agrarian diets (5–7). Agricultural diets, typically softer and processed, reduce the need for strong masticatory muscles, leading to less robust mandibles and anatomical restructuring. For example, Galland et al. (6) examined changes in mandibular shape from 13,000 to 2,000 years ago in Lower Nubia (modern Egypt and Sudan) as they underwent the dietary transition from hunter-gathering to agriculture, finding that hunter-gatherer mandibles had a shorter, wider, and more upright ramus and coronoid process, a longer condylar process, and a deeper, wider, and more upright corpus. Similarly, in Upper Nubia (modern Sudan), Brown (8) found that the transition from hunter-gathering to agriculture was marked by size decreases in the mandible, particularly in overall length, body height in the molar region, and width of the ramus. This anatomical transition accompanying the agricultural transition has been documented worldwide (9), including in Africa (6,8,10), and the Levant (7). Contemporary mandibles show considerable shape variation, explained largely by height and width proportions, mandibular angle, coronoid process height, and inclination of the symphysis (11).

The muscles of mastication include the masseter, temporalis, and the medial and lateral pterygoid muscles. The temporalis muscle inserts on the coronoid process and anterior aspect of the mandibular ramus, while the masseter muscle inserts on the mandibular angle and lateral aspect of the ramus (12). The masseter muscle's size is correlated to the mandibular angle (or gonial angle) of the mandible. Thicker, and therefore larger, masseter muscles are associated with lower (more acute) gonial angles (13). Across mammals, the relative size of the temporalis muscle dictates the relative size of its attachment, the coronoid process (14). In human samples, larger masticatory muscles were found to correlate with specific mandibular shapes. Larger temporalis and masseter muscles are associated with a wider ramus, more massive coronoid, and a more rectangular body (14,15). Larger masticatory muscles are associated with the tougher diet of hunter-gatherers, so that the transition to agriculture is accompanied by a decrease in muscle size and corresponding changes in mandibular shape.

The transition from hunter-gathering to full reliance on agriculture likely took thousands of years (16). In a recent study by De Angelis et al. (3), mandible shape was compared over a 2,000-year time frame from the Roman Imperial Age to the present day in Italy. They found a significant reduction in robusticity through time and significant differences in the mandibular angle, which they attribute to dietary and cultural shifts. Changes in the mandible have been shown to occur on a shorter timescale in relatively recent populations as well. Mandibular shape differences have been documented in populations separated by as little as 300 years, with changes attributed to the softening of diets that accompanied major cultural changes, like the Industrial Revolution (17,18). Other cultural changes, like territorial invasion, can result in morphological fluctuations in the mandible for a limited period of time. For example, the Roman occupation of Britain is associated with significant changes in British male mandibular shape (19). While these studies assessed populations from the same geographical area, a recent comparison of cortical bone cross-section morphology found significant shape differences in populations from geographically disparate Sudan (3600-3500 BP) and France (3915-3865 BP) separated by several hundred years (20). In the United States, a comparison of populations between the beginning and end of the 20th century found significant shape changes in the mandible, characterized by decreased bicondylar and bigonial breadth, as well as increases in body length (21). In other words, the American mandible has become narrower, longer, and more gracile in just the past century. As such, morphological changes have been documented both over thousands of years and in recent populations over relatively short time spans, but regional variation and comparisons are understudied.

Comparative morphological studies are essential to help refine the timeline, mechanisms, and variability of gracilization. It has been established that global patterns of archaeological mandibular morphology strongly reflect dietary differences along the hunter-gatherer/agriculture dichotomy rather than climate or geography (9). In contemporary global samples, linear measurements have shown clear distinctions between European and Asian populations, and Asian and African populations (22). Geographic differences between modern populations' mandibular morphology are upheld when using 3D measurements as well (23). Very few comparative studies focus on geographic comparisons, and even fewer examine 3D morphology through time (though see (20)). None, to our best knowledge, compare ancient agricultural populations in Africa to contemporary groups within the United States. This limits our ability to generalize patterns and rates of mandibular change in different ecological and cultural contexts.

This study aims to address this gap and establish a benchmark to connect work focused on differences through time and work focused on differences in geography. Here, we compare 3D mandibular morphology between two temporally and geographically distinct populations: ~2ka agriculturalists from Sudan and contemporary Floridians. We test whether these two groups differ in their overall mandibular shape and whether these differences align with patterns of gracilization established across major cultural transitions, like hunter-gathering to agriculture. We hypothesize that the mandibular shape of contemporary Floridian mandibles will exhibit significant differences in comparison to ancient agricultural populations, following a continuum of shape gracilization that mirrors the transition from hunter-gathering to agriculture and decreased masticatory muscle size. We predict that agriculturalist populations will have more robust mandibles characterized by wider rami (anteroposteriorly), shorter overall height, and more acute body-ramus angles due to the presence of stronger jaw muscles like the temporalis and masseter required for chewing tougher food (15). Through this work, we aim to contribute important data to a well-established body of research while exploring the variability of mandibular evolution and morphology in underrepresented contexts.

Materials and Methods

This study included 77 mandibles: 38 ancient Nubian mandibles downloaded from Morphosource.org (Project ID: 000776197) and 39 contemporary Floridian mandibles from the USF Donated Skeletal Collection, Florida Institute of Forensic Anthropology and Applied Science at the University of South Florida (USF). The ancient mandibles were originally buried in a cemetery at Semna South, in what was once Ancient Nubia and what is now Sudan. These individuals were irrigation agriculturalists from the Meroitic period (350 BCE-350 CE). The Meroitic subsistence economy relied on floodplain cultivation, which restricted crops to wheat, barley, sorghum, and millet (8). Meroitic wealth was tied to iron and copper-alloy industries and their funerary traditions included wooden coffins and burial pyramids (8). Archaeological remains from Sudan are particularly well studied, as they capture the transition of subsistence strategy from hunter-gathering to transitional hunting-gathering-agricultural, to fully agricultural. Gracilization occurred over the course of 10,000 years alongside the adoption of agriculture, with the masticatory apparatus moving inferoposteriorly relative to the cranial vault, the cranial vault becoming more globular, and the teeth reducing in overall size (6,8,10,19). The Meroitic period sample from Semna South represents agriculturalists with the most gracile morphology of the Ancient Nubia populations. Compared to the Neolithic (~4500 BCE), Kerma Ancien (2500-2050 BCE), and Kerma Classique (c. 1750-1500 BCE), the Meroitic period is characterized by the lowest rates of dental caries, the smallest percentage of teeth with severe calculus, and the smallest percentage of teeth with linear enamel hypoplasia banding (8). Because this group's morphology is known, it serves as our baseline or control. In the sample presented here, nineteen of the 38 ancient individuals are female, 18 are male, and one individual is of unknown sex. All individuals have either erupted third molars or a fused sphenoccipital suture. The contemporary Floridian mandibles are from a collection of skeletons donated between 2016-2022. Our subsample includes 19 females and 20 males, ranging in age from 44 to 101 years old. All individuals self-reported as Caucasian, with the exception of one individual reporting as Mixed White. Mandibles were selected based on completeness, with evidence of breaks or fractures precluding inclusion. Individuals averaged ~7 caries. While dental shape was beyond the scope of this project, mandibles with complete dentition and limited bony decay were prioritized. No edentulous mandibles were included in the sample.

While the ancient mandibles in this study were sourced from Morphosource.org in 3D format, the contemporary mandibles were 3D scanned with a Transcan-C structured light scanner (Shining 3D), resulting in PLY format files. Using the proprietary EXscan software, scan resolution was set to "medium" with Turntable mode enabled and set to 14 steps per scan. After scanning, watertight mesh models were exported as PLY files. All digitized mandibles were then landmarked for 3D geometric morphometric analysis (Figure 1).
Geometric morphometrics is a toolkit that allows for the comparison of biological shape variation, or the information left over after location, rotation, and position are removed from an object (24–29). Twenty-four Type 2 (30) fixed 3D landmarks were placed on each mandible in the software Checkpoint (Stratovan Corp.), generally following the landmarks outlined in Bosman et al. (18) (Table 1 and Fig. 1). A limited number of landmarks were chosen to maximize statistical power of comparative analyses (31). The limitations of using only 24 landmarks include the possibility of not capturing the full extent of shape differences between groups, particularly related to robusticity. All landmarks were placed by a single individual (CM) to eliminate interobserver error. The first ten mandibles that were landmarked were deleted and re-landmarked at the end of the process to reduce intraobserver error. Landmark data were exported and collated into a Morphologika format text file and imported into R v4.4.2 (32) for analysis.
The packages geomorph (33,34) and ggplot2 (35) were used for analysis and graphing, respectively. Within geomorph, a general Procrustes alignment was performed (36) using the gpagen function and eight outliers were identified using the plotOutliers command and removed. Six of the outliers were ancient: 3 males and 3 females with no other remarkable grouping element. Two of the outliers were contemporary: 1 male (age 79) and 1 female (age 72) with no other distinguishing or unifying traits. Although not included in any analyses, it is possible that the removed outliers represent the extreme ends of the morphological spectrum separating the ancient and contemporary samples, as abnormal taphonomic alteration and digitization errors were not noted. After outliers were removed, a subsample of 69 individuals (32 ancient [17 Female, 14 Male, 1 Unknown sex] and 37 contemporary [18 Female, 19 Male]) remained. With this subsample, a general Procrustes alignment was performed using the gpagen function, and a principal component analysis (PCA) was generated using the pg.prcomp command in geomorph to visualize group differences (Figure 2). Next, Goodall's F-test (37), or Procrustes ANOVA, was carried out using the procD.lm function to test for significant group differences in shape (ancient versus contemporary). Shape differences were visualized throughout the PCA morphospace by warping the most average mandible mesh into the landmark configurations of the PC axes' minima and maxima using the plotRefToTarget function in geomorph (Fig. 2).

Results

The plot of the sample in shape space is shown in Figure 2. The first two principal components (PC) describe 24.67% of the shape variance, with PC1 accounting for 12.46% and PC2 accounting for 12.21%. PC1 describes the symphysis height (superoinferiorly), and ramus width (anteroposteriorly). PC2 describes the ramus width (anteroposteriorly) and height, body length (anteroposteriorly) and height, and gonial angle. The two populations, ancient and contemporary, showed similar spread along PC1, but showed slight distinction along PC2. Ancient mandibles are characterized by shorter overall height, wider rami, slightly larger coronoid processes, more acute gonial angles, and greater anteroposterior length, primarily driven by differences between ancient and contemporary females. In contrast, contemporary mandibles are characterized by taller overall height and chins, shorter anteroposterior length, and more obtuse gonial angles, primarily driven by differences between ancient and contemporary males. The Procrustes ANOVA indicated significant differences in shape between the ancient and contemporary mandibles ($p<0.05$) (Table 2). Our predictions of ancient mandibles having wider (anteroposterior) rami, shorter overall height, and more acute gonial angles were supported. Though not addressed directly in our hypotheses or predictions, males and females also differed significantly in shape space ($p<0.05$) (Table 3), as demonstrated in several previous studies (11,18,38,39).

Discussion

The contemporary mandibles in this study conform to an anatomical pattern of gracilization (6,8) in comparison to the ancient agricultural mandibles, supporting our hypothesis. This was shown in the areas of the mandible associated with masticatory muscle use, including the ramus and gonial angle, in line with work by Anthwal et al. (14) and Sella-Tunis et al. (15). By comparing populations separated by only ~2,000 years, this study also supports work documenting significant morphological change in the mandible over a relatively short amount of time (17,18,20).

Though not included in our predictions, other morphological trends that characterize the gracilization from hunter-gatherers to agriculturalists were seen here. For example, hunter-gatherer populations and groups with larger masticatory muscles have been noted to have a more upright symphysis, creating an overall rectangular body shape in comparison to agriculturalists or those with small muscles (6,13,18). Here, the larger-muscled agriculturalists were distinguished by a more upright, versus inferiorly tilted, symphysis in comparison to the contemporary sample, as reflected along PC2. Interestingly, the greater PC2 values that pull the ancient sample from the contemporary group are largely female mandibles. The distinctly robust ancient females may indicate stronger sexual dimorphism in ancient populations.

That being said, our results conflict with some morphological patterns seen in contemporary mandibles around the world. For example, late 20th-century American mandibles were shown to be narrower than early 20th-century mandibles (21). Our contemporary Floridian sample did not stand out as narrower than our ancient population, and, in fact, there were several very narrow agricultural mandibles. That this pattern was not replicated in our study may stem from the difference in time periods being compared. While the 20th-century comparison study is able to extract subtle differences in shape, those differences may become muted when compared to mandibles from thousands of years ago. In the Netherlands, contemporary mandibles are characterized by being short overall and mediolaterally wide in comparison to archaeological remains (18). In contrast, our analysis showed contemporary mandibles as being relatively tall. This difference in findings may be attributed to the limited differences between contemporary and archaeological populations in the Netherlands due to shared population history, cultural/dietary differences between the United States and the Netherlands, or methodological differences in landmark choice. Additional contemporary global comparisons are needed to further explore this difference.

The likely driver of the mandibular shape differences between our two populations is a change in diet, which impacts masticatory muscle use, which then impacts bone resorption and remodelling (40,41). American diet quality has changed significantly post-World War II, which accelerated the creation and distribution of shelf-stable foods (42). By the 1980s, the term ‘ultra-processed food’ (UPF) was introduced, referring to the plethora of products whose ingredient lists were often indecipherable with enhancers, additives, and emulsifiers (42,43). Examples of these foods include carbonated soft drinks, ‘energy’ food items, ‘instant’ food products, mass-produced bread products, and packaged snacks. The manufacturing of the processed ingredients in UPF often relies on breaking down the innate structure of an ingredient, which typically results in softer textures and smaller particles in the final food product (44). In the United States, the average American’s caloric intake is made up of more than 50% UPF (45), with over 70% of the US food supply categorized as UPF (46). Diets with a higher caloric share of UPF are significantly cheaper, which means that UPFs tend to be selected by groups with lower socioeconomic status (47,48). The health consequences of a diet high in UPF have been extensively studied globally in the last decade. Positive associations have been made between UPF and obesity, cardiovascular disease, breast cancer, depression, irritable bowel syndrome, and mortality (see (43) for review). In relation to the skeletal system, diets high in UPF may negatively impact bone development, resulting in more porous long bones with lower bone mineral density (49). This extreme softening of the American diet in the last ~80 years is documented in the mandibles of this study and likely contributes to the shape differences shown here.

Another contributing factor to the more gracile shape of contemporary mandibles may be changes in medical care. This aspect is a limitation of the current study. Medical records with detailed dental history were not available for our contemporary Floridian sample, so we were unable to screen or analyze our data by orthodontic history, medical procedure, or other dental categories. Though we were able to assess caries rates in the contemporary Floridian sample, taphonomic processes and 3D model quality limited our ability to probe the impact of caries, periodontal disease, or attrition. For example, several ancient individuals are missing their incisors, however, it is unclear if the teeth

were lost due to disease or taphonomic processes. Having only surface models of the ancient sample also precluded comparison of internal structures, like cortical bone distribution analysis. A further limitation is a lack of dietary information. While agricultural populations two thousand years ago had a diet dictated by factors like environment and climate patterns, contemporary Floridians are able to choose their diet based on preference (though see above concerning the socioeconomic predictors of diet and health). We did not have information concerning dietary choices for our contemporary population, so we were not able to screen the sample accordingly. That being said, the majority of contemporary Americans have a very soft diet, as discussed above. Beyond dental health and environmental factors, differences in behavior or overall lifestyle may influence mandibular shape. We have no ethnographic accounts of the Ancient Nubian lifestyle in the context of the mandible (e.g., chewing smokeless tobacco) and can only assume what the behaviors were of the contemporary Floridian sample. These limitations impact the range of conclusions available to us.
As we gain more understanding concerning contemporary mandibular shape and how it has changed since the advent of agriculture, future work expanding the sample to include other sites in the United States would be useful to corroborate the patterns found here. This study compared populations that differ in both time and place, so comparing populations that are more environmentally similar would help reduce the many limitations of this study. Future work should also focus on filling the time gaps between the introduction of agriculture and contemporary populations with the goal of fully illustrating global trends in mandibular shape in the last ~twelve thousand years. Doing so will put recent dietary changes, like a reliance on UPF, into evolutionary context and inform our understanding of modern oral health trends and medical treatment. Though not in the scope of this research group, future anatomical work would benefit from additional inquiry into the impact of UPF on skeletal formation and adult bone shape. Lastly, collecting dietary isotopes from both the ancient and contemporary samples in this study would allow for a more direct comparison of diet to mandibular shape in the future.

Conclusion

The work presented here identified mandibular shape differences in geographically and temporally disparate groups: ancient Nubian agriculturalists from ~2ka and a contemporary Floridian population. The contemporary Floridian mandibles were distinguished as being taller, thinner, and more gracile, likely due to the softness of the contemporary Floridian diet. This study confirms that mandible shape can change significantly over the course of two thousand years, and that this change may be seen globally or across geographic groups, not just when comparing mandibles from the same region. The findings also demonstrate that the process of contemporary gracilization mirrors the mandibular changes that occurred during the transition from hunter-gathering to agriculture.

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Declaration of Interest

None

Author Contributions

AR: Supervision, Methodology, Writing – Original Draft; MB: Research Question, 3D scanning, Data Interpretation, Writing – Review & Editing; CM: Research Question, 3D Scanning, Model Landmarking, Writing – Review & Editing.

Statement on the use of artificial intelligence in manuscript preparation

Artificial intelligence was not used in the writing of this manuscript.

Table 1. Landmark definitions and Bookstein type (30). 10 landmarks are bilateral, while 4 are in midline (9-12).

Number	Bookstein Type	Description
1 (L), 15 (R)	2	Most superior point of the coronoid process from lateral view
2 (L), 16 (R)	2	Point of maximum curvature on the posterior-inferior border where the posterior ramus and the corpus meet
3 (L), 17 (R)	2	Most inferior point on the mandibular notch
4 (L), 18 (R)	2	Most posterior point on the ascending ramus in line with the alveolus
5 (L), 19 (R)	2	Most anterior point on the ascending ramus in line with the alveolus
6 (L), 20 (R)	2	Most anterior point on the margin of the mental foramen
7 (R), 21 (L)	2	Most superior point of the lingula
8 (R), 22 (L)	2	The point directly inferior to the M2 midline along the mylohyoid line
9	2	Most posterior point of the alveolar process along the anterior midline
10	2	Most anterior midline point on the mental protuberance
11	2	Most posterior point of the lingual cortical plate along the midline, superior to the mental spines
12	2	Most superior point of the digastric fossa along the midline
13 (L), 23 (R)	2	Most medial projection of the condylar head
14 (L), 24 (R)	2	Most lateral projection of the condylar head

Table 2. Procrustes ANOVA results testing the effect of time period on 3D shape using Goodall's F test (1,000 permutations). Significant value (*p*<0.05) in bold.

	df	Sum of Squares	Mean Square	F	p-value
Ancient v. Contemporary	1	0.3248	0.32476	5.4337	**0.001**
Residuals	67	0.40044	0.005977		
Total	68	0.43292			

Table 3. Procrustes ANOVA results testing the effect of sex on 3D shape using Goodall's F test (1,000 permutations). Significant value (*p*<0.05) in bold.

	df	Sum of Squares	Mean Square	F	p-value
Sex	2	0.2497	0.0124831	2.0196	**0.005**
Residuals	66	0.40795	0.0061811		
Total	68	0.43292			

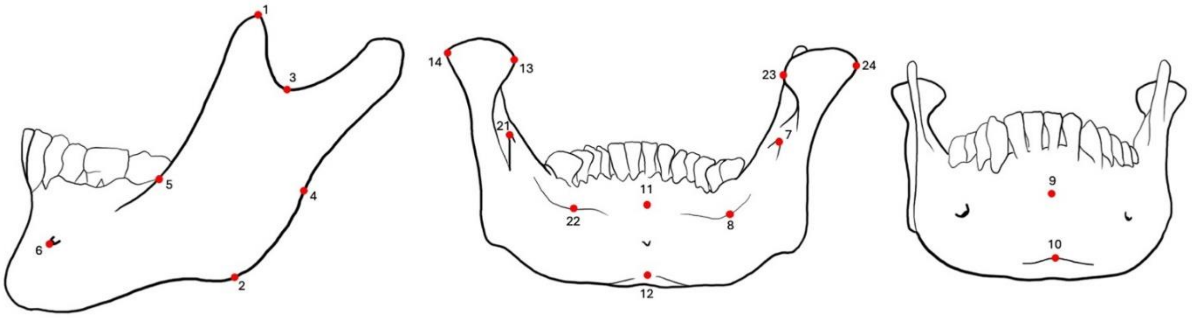

Figure 1. Landmark placement from left (left), posterior (center), and anterior (right) views.

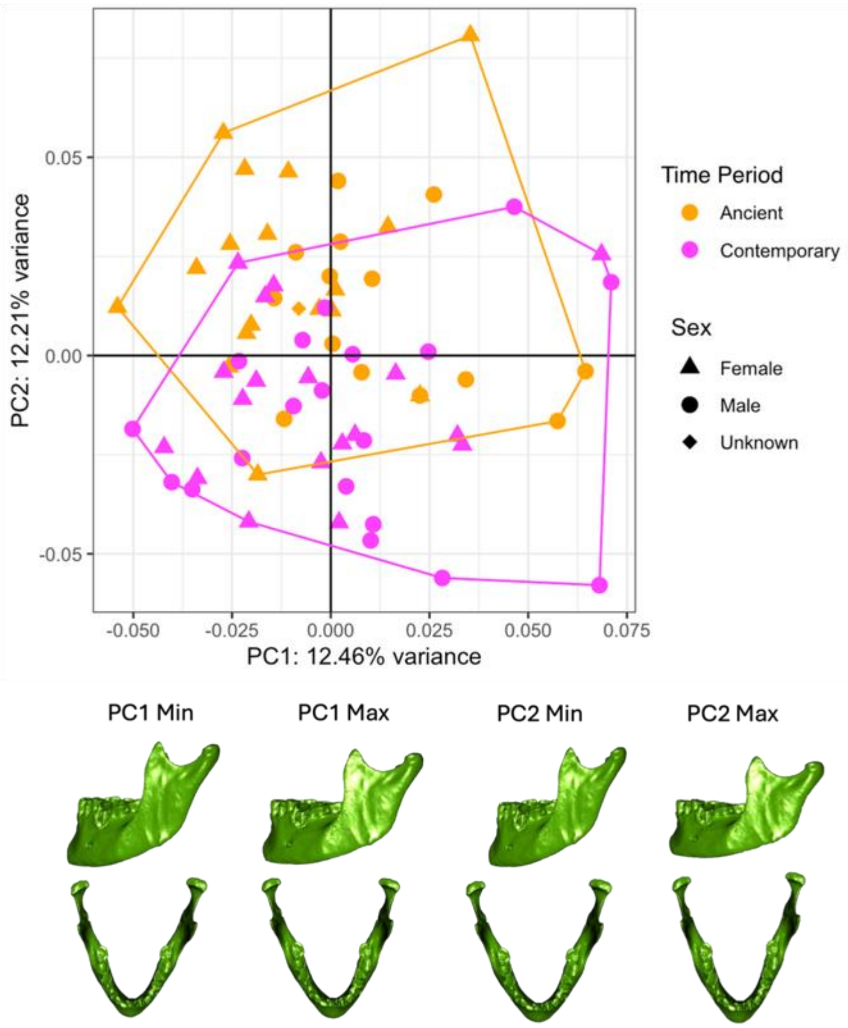

Figure 2. Principal component analysis comparing ancient (orange) and contemporary (pink) mandibles. Shape space extremes are visualized as green mandibles for PC1 minimum (min) and maximum (max) and PC 2 minimum (min) and maximum (max).

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