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Geographic patterns of Early Holocene New World dental morphological variation

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ABSTRACT Dental anthropology played a seminal role in early studies of the peopling of the New World, and was a foundation of the early three wave model proposed by Greenberg, Turner and Zegura. In recent years, however, developments in anthropological genetics, craniometry, and archaeological discoveries have largely omitted dental anthropology from debates regarding Native American origins. Here we consider this situation and reassert dental anthropology's relevance to the topic by presenting an inter-individual analysis of Paleoindian and Paleoamerican dentitions. A small set of dental morphological variables was used to estimate Gower similarity coefficients between individual specimens. The resulting similarity matrix was ordinated using

multidimensional scaling; all analyses were performed in Clustan v. 7.05. While results should be considered preliminary, patterns of variation suggest morphological similarity along both coasts of North and South America with a somewhat distinct grouping of North American Paleoindians deriving from more inland portions of the continent. This pattern is consistent with recent genetic scenarios, notably the bicoastal model presented by O'Rourke and Raff (2010), which indicates that Paleoindians may have taken multiple migration routes from Beringia, moving along both coasts as well as through the ice free corridor. Future studies may build on this work to reintegrate dental data and analysis into research concerning the peopling of the New World.

Dental morphology played a key role in the development of the tripartite model of New World population origins (Greenberg et al., 1985, 1986; Turner, 1971, 1983, 1984, 1985a, b, 1986). While this model still provides a viable explanation for the settlement of the Western Hemisphere (Estrada-Mena et al., 2010; Reich et al., 2012), recent advances in anthropological genetic sampling protocols, amplification techniques, and analytical approaches have provided more nuanced understandings of New World population structure. These include models that propose a single origin from an Asian source population isolated in Beringia prior to colonization of the Americas (Estrada-Mena et al., 2010; Fagundes et al., 2008; Kitchen et al., 2008; Mulligan et al., 2008; Schroeder et al., 2007, 2009; Tamm et al., 2007; Wang et al., 2007), dual origin models (Gilbert et al., 2008; Rasmussen et al., 2010), and more complex scenarios involving one or more migrations from a heterogeneous source population – possibly via different migration routes – followed by bidirectional gene flow between Asia and the Americas that lasted several thousand years (González-José and Bortolini, 2011;

Kumar et al., 2011; Mazières, 2011; O'Rourke and Raff, 2010; Perego et al., 2009, 2010; Ray et al., 2010; Rubicz et al., 2010; Tamm et al., 2007). In addition, recent archaeological discoveries have largely supplanted the "Clovis First" model which dominated Paleoindian research for several decades (e.g., Adovasio and Pedler, 2004; Dillehay, 1997; Goebel et al., 2008; Waters et al., 2011) and which coincided strongly with the predictions of the tripartite model. Discoveries of Early Holocene skeletal material from South America, combined with advances in phenotypic data analysis better grounded in evolutionary processes, have also generated new views on the peopling of the Americas (e.g., de Azevedo et al., 2011; Gonzalez et al., 2010; González-José and Bortolini, 2011; González-

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José et al., 2001, 2008; Mena L. et al., 2003; Neves et al., 2004, 2005; Perez et al., 2007, 2009; Pucciarelli et al., 2003, 2006, 2008, 2010).

Despite the historical importance of dental anthropology in the First Americans debate, recent synthetic surveys of the literature (e.g., Dillehay, 2009; Fiedel, 2004; Goebel et al., 2008; González-José and Bortolini, 2011; Mazières, 2011; O'Rourke, 2011; O'Rourke and Raff, 2010; Pitblado, 2011) indicate that dentition has lost its relevance in these discussions. In fact, the most recent literature review fails to include a single citation for papers using dental morphology as a basis for inferring New World population history (Pitblado, 2011). There are many reasons why this may be. However, one inescapable fact is that genetic, archaeological, and craniometric specialists have adopted new research approaches and methods over the last decade, including more sophisticated types of data capture and analysis, which increase the specificity and nuance of their interpretations. This is evidenced by the incorporation of inferential analyses that access more complex evolutionary models in the analysis of phenotypic size and shape. Dental anthropology on the other hand has largely maintained a focus on population-based frequency analyses and, in particular, the sinodont/sundadont dichotomy (see Turner, 1990).

Our purpose here is not to engage existing debates about the utility of the sinodont/sundadont model or the relationship between specific Paleoindian or Paleoamerican specimens and the morphological complex associated with sinodonty or sundadonty (e.g., Chatters, 2000; Haydenblit, 1996; Lahr and Haydenblit, 1995; Powell, 1993, 1995, 2005; Sutter, 1997, 2005; Turner, 2002). Here, we adopt a more paleontological focus that recognizes the relative dearth of existing Early Holocene material from North and South America and the singleton status of much of the North America Paleoindian record. Our primary goal in this paper is to move the field forward by demonstrating that fragmentary specimens and small data sets can be used to consider hypotheses about the temporal and spatial structure of New World phenotypic variation using a research approach distinct from frequency-based assessments. We make no claims that one approach is necessarily better than the other. We only demonstrate the potential of different approaches for complementing one another

and engaging new models of interpretation that add nuance to the literature.

MATERIALS AND METHODS

Using existing morphological data, our purpose in this paper is to determine whether Early Holocene (Paleoindian and Paleoamerican) inter-individual dental morphological variation is geographically structured. That is, we consider whether inter-individual patterns of affinity reproduce geographic spatial structure, and if so, whether dental variation corresponds with recent hypothesized migration scenarios into the New World, such as the bi-coastal model proposed by O'Rourke and Raff (2010), which accommodates multiple, possibly contemporaneous migration routes from Beringia through the ice-free corridor and along both coasts. We mined published raw dental morphological data from confirmed Paleoindian and Paleoamerican dentitions (see Chatters, 2000; Jenks, 1937; Owsley et al., 2010; Potter et al., 2011; Powell and Rose, 1999; Turner, 1992; Young, 1988) and verified the Early Holocene age of these specimens (> 7500bp). These data are summarized in Table 1. Raw trait scores were used to generate inter-individual similarity statistics using Clustan v. 7.05 (Wishart, 2004). Gower coefficients were used because they allow for missing data (obviating data imputation) and mixed scale data types (ordinal and binary). Similarities were ordinated and visualized using multi-dimensional scaling in two dimensions set at 500 runs and iterations. Variables were removed from the final analysis based on frequency of observation (variables that were too sparse were removed) and if the variable demonstrated insufficient trait score variability among individuals. Those variables that demonstrated no inter-individual variation or were autapomorphic were removed from the raw dataset prior to the calculation of similarities. In addition, traits that were clearly redundant (for example, Carabelli's scores for maxillary M1s and M2s) were reduced, where the trait that was kept was largely decided based upon data density rather than notions of key tooth representation. Individual Paleoindian or Paleoamerican dentitions were omitted if they preserved too few recorded scores, although we note the rarity of North American specimens required more consideration of trait exclusion to maximize the coverage of the

TABLE 1. Early skeletal remains from North and South America^a

Sample/site	Age (¹⁴ C years BP)	N
<u>North American skeletal remains included in the present analysis</u>		
Warm Mineral Springs, FL	10260 +/- 190	1
Arch Lake, NM	10220 +/- 50; 8870 +/- 40	1
Horn Shelter, TX	9875 +/- 110 (average)	2
Gordon Creek, CO	9455 +/- 110 (average)	1
Tehuacán Valley (Tc50), Mexico	ca. 8500-7000	1
Kennewick, WA	8410 +/- 60 (average)	1
Pelican Rapids, MN	7840 +/- 70	1
<u>Additional North American skeletal remains not included in the present analysis</u>		
Upward Sun River, AK	~11500	1
Arlington Springs, CA	10960 +/- 110; 10080 +/- 810; 10000 +/- 310	1
Peñón Woman III, Mexico	10755 +/- 75	1
Anzick, MT	10680 +/- 50 (average)	2
Buhl, ID	10675 +/- 95	1
Wilson-Leonard, TX	10500-10,000	1
Chimalhuacán, Mexico	ca. 10500	1
Mostin, CA	10470 +/- 490	1
Tlapacoya I, Mexico	10200 +/- 65	1
Marnes, WA	10130 +/- 300; 9840 +/- 300; 9820 +/- 300	3
Midland, TX	ca. 10000	1
White Water Draw, AZ	10000-8000	1
J.C. Putnam, TX	_b	1
49-PET-408 (On Your Knees Cave), AK	9730 +/- 40 (average)	1
Grimes Point Burial Shelter, NV	9470 +/- 60	1
Spirit Cave, NV	9415 +/- 25 (average)	1
Wizard's Beach, NV	9225 +/- 60 (average)	1
Browns Valley, MN	9049-8790 +/- 110/82	1
La Brea, CA	9000 +/- 80	1
Metro Balderas, Mexico	ca. 9000	1
Cueva de Tecolote, Mexico	ca. 9000-7000	1
Koster (Horizon 11), IL	ca. 8500	9
Renier, WI	ca. 8500-6000	1 ^c

TABLE 1., Cont'd

Fishbone Cave, NV	8370 +/- 50; 8220 +/- 50	1
La Jolla, CA	8350 +/-90	2
Gore Creek, BC	8250 +/- 115	1
Hourglass Cave, CO	8170 +/-100; 7944 +/-84; 7714 +/-77	1
Stick Man, WA	8125 +/-50 (average)	1
Windover, FL	8120-6990	168
L'Anse Amour, Labrador	7530 +/-140	1
Texcal Cave, Mexico	7480 +/-55	1
Shifting Sands, TX	-	1
<u>South American skeletal remains included in the present analysis</u>		
Cerca Grande 6 and 7, Lagoa Santa, Brazil	ca. 11000-8000	44
Cuchipuy, Chile	8070-6105; ca. 8000-6000	3
<u>Additional South American skeletal remains not included in the present analysis</u>		
Lapa Vermelha IV (Luzia), Brazil	11680 +/-500 – 10200 +/-220; 9330 +/-60 (minimum age)	1
Pampa de Fosiles 13, Peru	10250 +/-180	2
Sueva 1, Colombia	10090 +/-90	1
Quiqche Cave Tomb 1, Peru	9940 +/-200 ^d	1
Toca dos Coqueiros, Brazil	9870 +/-50	1
Tequendama, Colombia	9740 +/-135	9
Toca da Janela da Barra do Antoniao, Brazil	9670 +/-140	1
Santana do Riacho Burial XII, Brazil	9460 +/-110	1
Guavio 1, Colombia	9360 +/-45	1
Piuquenes Cave, Chile	8990 +/-40	3
Acha-2 and Acha-3, Chile	8970 +/-255	5
Baño Nuevo-1 Cave, Chile	8890 +/-90; 8880 +/-50; 8850 +/-50	5
Capelinha Burial II (Luzio), Brazil	8860 +/-60	1
Santo Domingo Tomb 1, Peru	8830 +/-190	1
Pali Aike, Chile	ca. 8800	4
Santana do Riacho, Brazil	8280 +/-40; 8185 +/-110	40
Las Vegas, Ecuador	8250-6600	192
Huentelauquén-2, Chile	8080 +/-70	1
Intihausi, Argentina	8060 +/-100; 7970 +/-100	6

TABLE 1., cont'd

Tres Ventanas Tomb 1, Peru	8030 +/-130	1
Sumidouro Cave, Lagoa Santa, Brazil	>8000	29
Monte Hermoso 1-2, Argentina	7866 +/-75	1
Arroyo Seco, Argentina	7805 +/-85 - 7580 +/-50	5
Checuá, Colombia	7800 +/-60 - 6800 +/-40	4
Santo Domingo Tomb 2, Peru	7740 +/-85	1

a References for early American skeletal remains are listed in Stojanowski et al. (2013).

b Associated with stratum thought to date to the Late Pleistocene (Young 1988).

c The small quantity of calcined bone fragments is suggestive of a single individual (Mason and Irwin 1960).

d Date is from the level underlying the skeletal remains.



Fig. 1. Map of North and South American showing the location of Paleoindian and Paleoamerican specimens used in this analysis: 1. Arch Lake; 2. Gordon Creek; 3. Horn Shelter No. 2; 4. Kennewick; 5. Pelican Rapids; 6. Tehuacán (Tc50-2); 7. Warm Mineral Springs; 8. Cuchipuy; 9. Lagoa Santa.

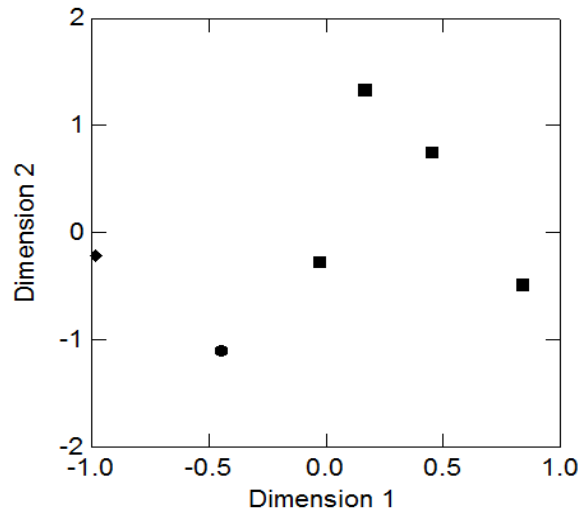


Fig. 2. Multidimensional scaling of Gower similarity coefficients calculated from eight dental morphological traits for confirmed North American Paleoindians. Icons represent geographic divisions: circle = western North America (Kennewick), square = central North America, diamond = eastern North America (Warm Mineral Springs).

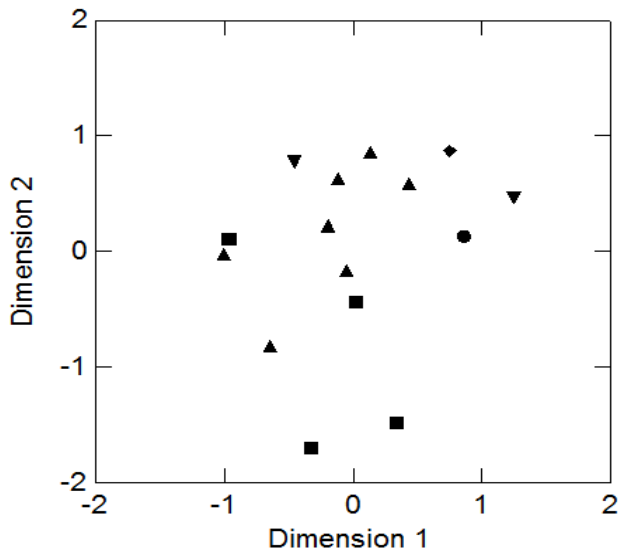


Fig. 3. Multidimensional scaling of Gower similarity coefficients calculated from six maxillary dental morphological traits for confirmed North and South American Paleoindians and Paleoamericans. Icons represent geographic divisions: circle = Mexico, diamond = eastern North America, square = central North America, upward triangle = eastern South America, downward triangle = western South America.

continent so that assessments of geographic structure were possible.

RESULTS

Because the majority of South American dentitions lacked paired maxillae and mandibles we first consider patterns of inter-individual variation among North American Paleoindian specimens. Despite the number of possible Paleoindian specimens (see Table 1) we were only able to include data from six individuals: Pelican Rapids, Gordon Creek, Warm Mineral Springs, Arch Lake, Horn Shelter 2, and Kennewick. These six dentitions range from Washington to Florida with most samples deriving from the middle of the continent (Figure 1). Based on data preservation, we included eight dental morphological traits in the calculation of Gower similarity coefficients (U1 shoveling, UM1 hypocone, UM1 Carabelli, UM1 enamel extension, UP1 root number, UM2 root number, LM2 cusp number, and LM2 root number). Results of the multidimensional scaling are presented in Figure 2. There is some evidence for geographic pat-

tern. For example, the four central North American samples (non-coastal) form a weak cluster in the upper right quadrant while both coastal samples plot in the negative half of both axes. This could be consistent with a single population bifurcating and migrating quickly down the Atlantic and Pacific coasts of North America with a distinct population colonizing the middle of the continent.

Inclusion of South American Paleoamerican dentitions required using only six maxillary traits (U1 shoveling, UM1 hypocone, UM1 Carabelli, UM1 enamel extension, UP1 root number, and UM2 root number). The sample included the same Paleoindian specimens as above (with the exception of Kennewick which had to be excluded), a single individual from Mexico (Tehuacán Tc50-2), two individuals from western South America (Cuchipuy), and seven individuals from eastern South America (Lagoa Santa). Results are presented in Figure 3. Although the clustering tendency was more abstract there does appear to be some geographic patterning evident in this figure. For example, the dentitions from western South America, eastern South America, Mexico, and eastern North America dominate the positive half of the dimension two axis, while dentitions from non-coastal North American Paleoindians dominate the negative half of the dimension two axis. Another way to consider this is that coastal samples from both North and South America cluster in the positive half of the dimension two axis while interior samples (all from North America) plot in the negative half of the dimension two axis. Remarkably, the overall pattern of variation does not change with the addition of South American data. These analyses, therefore, may reflect a possible bi-coastal migration of Early Holocene populations along both the Pacific and Atlantic coasts of North and South America with a somewhat distinct population inhabiting the interior of North America (perhaps involving the ice-free corridor), consistent with O'Rourke and Raff's (2010) model.

CONCLUSION

Recent advances in archaeology, anthropological genetics, and human craniometry have enhanced our understanding of New World population origins and migration dynamics within

the Western Hemisphere. For a variety of reasons, dentition has figured less prominently in recent First American debates to the point that the most recent literature review of this expansive literature ignores dentition entirely (Pitblado, 2011). This is unfortunate. Here we have tried to demonstrate that a specimen-specific approach to Paleoindian and Paleoamerican dental morphology may have some merit. In particular, using a small series of dentitions and morphological traits our results suggest a similar dental phenotype among coastal populations of the Early Holocene New World with a somewhat distinct morphology among central, non-coastal North American dentitions. Here, we have emphasized population structure and evolution as the primary explanatory mechanism; however, differential selection pressures related to distinct coastal/inland diets should also be considered. In closing, we want to stress how preliminary these results are. As indicated in Table 1 there is now an abundance of Paleoindian and Early Archaic period sites and specimens in the Americas and our analyses utilize only a small number of traits for a small number of individuals. Nevertheless, we hope our results show enough promise to justify a more comprehensive survey of dental morphology in these specimens, including the use of recent developments in three-dimensional data capture and incorporation of evolutionary developmental principles in the assessment of evolutionary signatures of human dentition.

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