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 interindividual analysis of Paleoindian and Paleamerican 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-José and Bortolini, 2011;坡者-S.-M.-D.-R.R. Correspondence to: Christopher M. Stojanowski 900 S. Cady Mall School of Human Evolution and Social Change Arizona State University Tempe, AZ 85287 cstojano@asu.edu
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

<table>
<thead>
<tr>
<th>Sample/site</th>
<th>Age (14C years BP)</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>North American skeletal remains included in the present analysis</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Warm Mineral Springs, FL</td>
<td>10260 +/- 190</td>
<td>1</td>
</tr>
<tr>
<td>Arch Lake, NM</td>
<td>10220 +/- 50; 8870 +/- 40</td>
<td>1</td>
</tr>
<tr>
<td>Horn Shelter, TX</td>
<td>9875 +/- 110 (average)</td>
<td>2</td>
</tr>
<tr>
<td>Gordon Creek, CO</td>
<td>9455 +/- 110 (average)</td>
<td>1</td>
</tr>
<tr>
<td>Tehuacán Valley (Tc50), Mexico</td>
<td>ca. 8500-7000</td>
<td>1</td>
</tr>
<tr>
<td>Kennewick, WA</td>
<td>8410 +/- 60 (average)</td>
<td>1</td>
</tr>
<tr>
<td>Pelican Rapids, MN</td>
<td>7840 +/- 70</td>
<td>1</td>
</tr>
<tr>
<td><strong>Additional North American skeletal remains not included in the present analysis</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upward Sun River, AK</td>
<td>~11500</td>
<td>1</td>
</tr>
<tr>
<td>Arlington Springs, CA</td>
<td>10960 +/- 110; 10080 +/- 810; 10000 +/- 310</td>
<td>1</td>
</tr>
<tr>
<td>Peñón Woman III, Mexico</td>
<td>10755 +/- 75</td>
<td>1</td>
</tr>
<tr>
<td>Anzick, MT</td>
<td>10680 +/- 50 (average)</td>
<td>2</td>
</tr>
<tr>
<td>Buhl, ID</td>
<td>10675 +/- 95</td>
<td>1</td>
</tr>
<tr>
<td>Wilson-Leonard, TX</td>
<td>10500-10,000</td>
<td>1</td>
</tr>
<tr>
<td>Chimalhuacán, Mexico</td>
<td>ca. 10500</td>
<td>1</td>
</tr>
<tr>
<td>Mostin, CA</td>
<td>10470 +/- 490</td>
<td>1</td>
</tr>
<tr>
<td>Tlapacoya I, Mexico</td>
<td>10200 +/- 65</td>
<td>1</td>
</tr>
<tr>
<td>Marmes, WA</td>
<td>10130 +/- 300; 9840 +/-300; 9820 +/-300</td>
<td>3</td>
</tr>
<tr>
<td>Midland, TX</td>
<td>ca. 10000</td>
<td>1</td>
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<tr>
<td>White Water Draw, AZ</td>
<td>10000-8000</td>
<td>1</td>
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<tr>
<td>J.C. Putnam, TX</td>
<td></td>
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<tr>
<td>49-PET-408 (On Your Knees Cave), AK</td>
<td>9730 +/- 40 (average)</td>
<td>1</td>
</tr>
<tr>
<td>Grimes Point Burial Shelter, NV</td>
<td>9470 +/- 60</td>
<td>1</td>
</tr>
<tr>
<td>Spirit Cave, NV</td>
<td>9415 +/- 25 (average)</td>
<td>1</td>
</tr>
<tr>
<td>Wizard’s Beach, NV</td>
<td>9225 +/- 60 (average)</td>
<td>1</td>
</tr>
<tr>
<td>Browns Valley, MN</td>
<td>9049-8790 +/- 110/82</td>
<td>1</td>
</tr>
<tr>
<td>La Brea, CA</td>
<td>9000 +/- 80</td>
<td>1</td>
</tr>
<tr>
<td>Metro Balderas, Mexico</td>
<td>ca. 9000</td>
<td>1</td>
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<tr>
<td>Cueva de Tecolote, Mexico</td>
<td>ca. 9000-7000</td>
<td>1</td>
</tr>
<tr>
<td>Koster (Horizon 11), IL</td>
<td>ca. 8500</td>
<td>9</td>
</tr>
<tr>
<td>Renier, WI</td>
<td>ca. 8500-6000</td>
<td>1</td>
</tr>
<tr>
<td>Location</td>
<td>Radiocarbon Age</td>
<td>Notes</td>
</tr>
<tr>
<td>--------------------------------</td>
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<tr>
<td>Fishbone Cave, NV</td>
<td>8370 +/- 50; 8220 +/- 50</td>
<td></td>
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<tr>
<td>La Jolla, CA</td>
<td>8350 +/- 90</td>
<td></td>
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<tr>
<td>Gore Creek, BC</td>
<td>8250 +/- 115</td>
<td></td>
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<tr>
<td>Hourglass Cave, CO</td>
<td>8170 +/- 100; 7944 +/- 84; 7714 +/- 77</td>
<td>1</td>
</tr>
<tr>
<td>Stick Man, WA</td>
<td>8125 +/- 50</td>
<td>(average)</td>
</tr>
<tr>
<td>Windover, FL</td>
<td>8120-6990</td>
<td></td>
</tr>
<tr>
<td>L’Anse Amour, Labrador</td>
<td>7530 +/- 140</td>
<td></td>
</tr>
<tr>
<td>Texcal Cave, Mexico</td>
<td>7480 +/- 55</td>
<td></td>
</tr>
<tr>
<td>Shifting Sands, TX</td>
<td></td>
<td></td>
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<tr>
<td><strong>South American skeletal remains included in the present analysis</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cerca Grande 6 and 7, Lagoa Santa, Brazil</td>
<td>ca. 11000-8000</td>
<td></td>
</tr>
<tr>
<td>Cuchipuy, Chile</td>
<td>8070-6105; ca. 8000-6000</td>
<td></td>
</tr>
<tr>
<td><strong>Additional South American skeletal remains not included in the present analysis</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lapa Vermelha IV (Luzia), Brazil</td>
<td>11680 +/- 500 – 10200 +/- 220; 9330 +/- 60 (minimum age)</td>
<td>1</td>
</tr>
<tr>
<td>Pampa de Fosiles 13, Peru</td>
<td>10250 +/- 180</td>
<td></td>
</tr>
<tr>
<td>Sueva 1, Colombia</td>
<td>10090 +/- 90</td>
<td></td>
</tr>
<tr>
<td>Quiqche Cave Tomb 1, Peru</td>
<td>9940 +/- 200d</td>
<td></td>
</tr>
<tr>
<td>Toca dos Coqueiros, Brazil</td>
<td>9870 +/- 50</td>
<td></td>
</tr>
<tr>
<td>Tequendama, Colombia</td>
<td>9740 +/- 135</td>
<td></td>
</tr>
<tr>
<td>Toca da Janela da Barro do Antonio, Brazil</td>
<td>9670 +/- 140</td>
<td></td>
</tr>
<tr>
<td>Santana do Riacho Burial XII, Brazil</td>
<td>9460 +/- 110</td>
<td></td>
</tr>
<tr>
<td>Guavio 1, Colombia</td>
<td>9360 +/- 45</td>
<td></td>
</tr>
<tr>
<td>Piuquenes Cave, Chile</td>
<td>8990 +/- 40</td>
<td></td>
</tr>
<tr>
<td>Acha-2 and Acha-3, Chile</td>
<td>8970 +/- 255</td>
<td></td>
</tr>
<tr>
<td>Baño Nuevo-I Cave, Chile</td>
<td>8890 +/- 90; 8880 +/- 50; 8850 +/- 50</td>
<td>5</td>
</tr>
<tr>
<td>Capelinha Burial II (Luzio), Brazil</td>
<td>8860 +/- 60</td>
<td></td>
</tr>
<tr>
<td>Santo Domingo Tomb 1, Peru</td>
<td>8830 +/- 190</td>
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</tr>
<tr>
<td>Pali Aike, Chile</td>
<td>ca. 8800</td>
<td></td>
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<tr>
<td>Santana do Riacho, Brazil</td>
<td>8280 +/- 40; 8185 +/- 110</td>
<td></td>
</tr>
<tr>
<td>Las Vegas, Ecuador</td>
<td>8250-6600</td>
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</tr>
<tr>
<td>Huentelauquén-2, Chile</td>
<td>8080 +/- 70</td>
<td></td>
</tr>
<tr>
<td>Intihausi, Argentina</td>
<td>8060 +/- 100; 7970 +/- 100</td>
<td></td>
</tr>
</tbody>
</table>
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).
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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 (UI1 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 patterning. 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 (UI1 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.

LITERATURE CITED


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