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In Memoriam:
Christy G. Turner II
(November 28, 1933 – July 27, 2013)
Personal reflections on his legacy in dental anthropology and beyond

I was an undergraduate at Arizona State University in 1966 when Christy was brought into the Department of Anthropology. I took three of his courses as an undergraduate: World Prehistory, Southwest Archaeology: Anasazi, and Physical Anthropology (Human Biology). I mention this because his courses were both a challenge and an inspiration. He was the most charismatic professor I had encountered and when he discovered I was a fairly good student, he slowly brought me into the 'physical anthropology' fold, redirecting me away for my original goal of becoming a professional archaeologist. He talked Charles Woolf into offering me a graduate fellowship in genetics and that dictated my direction in graduate school, the genetic analysis of dental morphological traits. In retrospect, I got in on the ground floor of something that would eventually become a very significant edifice in the field of physical anthropology and it was Christy who laid much of the foundation.

Christy was all that one could ask for in a mentor. He was encouraging yet demanding. When I was thinking about taking a few extra courses as a graduate student, he said something I tell my students to this day: "When you finish your PhD, you don't stop learning.........that's when you start learning." That was more prophetic than I knew at the time. That stimulated me to finish my PhD in expeditious fashion without taking a lot of extra coursework. When I defended my dissertation in the summer of 1973, I was Christy's first PhD in physical anthropology. Through his Wisconsin contacts, he helped me secure a job at the University of Alaska Fairbanks. Although Alaska was definitely not my first choice to start my career, the doors of academia were closing at that time so I took the job and eventually appreciated the opportunities it provided. As his dissertation was titled *The Dentition of Arctic Peoples* he could not have been happier about where I landed, despite my initial reluctance to go from the fire (Arizona) to the icebox (Alaska).

After leaving for Alaska, Christy and I always stayed in close touch and collaborated on many articles. Neither of us ever thought much about writing books, but in the 1990s, at Gabe Lasker's invitation, we wrote a book published by Cambridge University Press entitled *The Anthropology of Modern Human Teeth: Dental Morphology and Its Variation in Recent Human Populations* (1997). When the book drew near completion, we were talking about titles. I originally suggested only the second half of the title above. It was Christy who thought 'The Anthropology of Modern Human Teeth' had more panache, and was often the case, he was absolutely right. While Christy was not the 'father' of dental anthropology, an honor that should go to Albert A. Dahlberg and P.O. Pedersen, he was definitely the major driving force in the field for the past 40+ years.

In 2010, Joel Irish (PhD, ASU, 1993) and I organized a symposium in Christy's honor at the AAPA meeting in Albuquerque, New Mexico. We had no trouble finding contributors to a full symposium and even had to pull our own papers to keep the number to the maximum allowed of 14. After the symposium, we submitted a book proposal to Cambridge for a festschrift volume entitled *Anthropological Perspectives on Tooth Morphology: Genetics, Evolution, Variation*. Of the 21 papers in the final volume, six authors were former students of his. Thankfully, the volume appeared in March, 2013, so Christy had time to appreciate how others in dental anthropology viewed his monumental contributions. The second chapter, written by Christy, provides an excellent summary of his academic and professional life, along with acknowledging the many students he mentored during his decades of service at ASU.

The traits that best describe Christy are charismatic, driven, productive, imaginative, and far sighted. While others described dental morphological traits, Christy could see their potential in asking questions of population origins and relationships. He travelled the world over and made dental observations on over 30,000 human skeletons. He knew the insides of about every museum in North America and many in South America, Siberia, North Asia, Southeast Asia, and Europe. But he didn't just describe teeth; he developed the methods that are the foundations of modern dental comparative studies (The Arizona State University Dental Anthropology System). Beyond methods, he developed models that addressed long-standing historical issues, including his three-wave model for the peopling of the Americas, and the dental division between North Asians (Sinodonts) and Southeast Asians (Sundadonts). While his ideas may or may not prove to be correct in the long run, he developed models that other researchers had to consider, even if they disagreed with him.

On another front, Christy started what was basically a new field of inquiry when he examined what was presumed to be a secondary burial from Polacca Wash, a site near the abandoned Hopi village of Awatovi. Although his interest, per usual, was in making dental observations, he thought this collection of broken and burned bones could hardly be a secondary burial. After a detailed analysis of cut marks, anvil abrasions, burned bone, etc., he wrote his first paper on Southwest cannibalism entitled "A Massacre at Hopi," co-authored with one of his graduate students, Nancy Tucker Morris. After examining this series, he ran down many more skeletal collections from the Anasazi region that could most parsimoniously be explained by cannibalism. Needless to say, this was not a popular view and he was attacked by Native Americans and professional colleagues who took issue with his interpretation. The culmination of this work came in the volume *Man Corn: Cannibalism and Violence in the Prehistoric American Southwest* (1999), co-authored with Jacqueline, his wife, companion, and collaborator. Always thorough to an admirable fault, he went to central Mexico and examined skeletal series where cannibalism was widely acknowledged. His view was that if you disagreed with his taphonomic signature for cannibalism, provide an alternative explanation for bones that had been bashed, burned, and butchered. Christy had file after file of papers written on the subject and he never felt anyone seriously dented his interpretation of cannibalism, which he always clearly separated from evidence of just violence.

Christy was definitely the hardest working scholar I have ever known. Even with failing health and eyesight greatly diminished by macular degeneration, he just completed another book for Cambridge University Press entitled *Animal Teeth and Human Tools: A Taphonomic Odyssey in Ice Age Siberia*. How he could write and edit a 500 page volume with dozens of tables and photos with all of his physical limitations astounds me to this day. He had a great career and had already made significant marks in dental anthropology and the taphonomy of human cannibalism but he kept pressing on. Thankfully, he finished all the edits and copy proofing of the galleys this past spring and the volume is now in press. Sadly, he will not be around to see this work in book form.

When I was a graduate student, Christy told me his academic idols were William Healy Dall, Franz Boas, and Aleš Hrdlička, who published, respectively 1500, 800, and 600 papers and books. I know Christy's vita is over 50 pages long but I'm not sure if he matched those gentlemen.........of this I am sure though, he gave it 'the old college try.'

For over 40 years, Christy and I (and our families) remained close; we stayed with the Turners on Campo Alegre many times and they stayed with us when they came to Alaska. I could go on and on about the many things we did, crazy and otherwise, but I will save those for private conversations, preferably at a bar during annual meetings of the American Association of Physical Anthropologists. His legacy is substantial, his footprint is large……..he will be missed and remembered by his daughters and grandchildren along with countless former students and colleagues because he was a ‘unique character,’ one whose time on earth made the world a more interesting place.

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2011 Dahlberg Award Winner: Evaluation of the utility of deciduous molar morphological variation in great ape phylogenetic analysis

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Keywords: primate deciduous dentition, non-metric dental traits, *Pan*, *Gorilla*

ABSTRACT Non-metric dental traits are well-established tools for anthropologists investigating population affiliation and movement in humans. Nonetheless, similar traits in the great apes have received considerably less attention. The present study provides data on non-metric trait variability in the deciduous molars of great apes from museum context.Twenty-eight traits are observed in the upper and lower deciduous molars in specimens of *Pan troglodytes, Pan paniscus, Gorilla gorilla,* and *Gorilla beringei*. These groups are compared based on trait frequencies and mean measures of divergence. This study demonstrates the variability of non-metric traits in the deciduous molars of chimpanzees and gorillas. These traits could potentially be used in the same way that non-metric traits are in humans, namely group affiliation and population movements through time. Further, this study establishes scoring guidelines and methodology relevant to deciduous dental morphological characteristics found in the great apes, but not necessarily in humans.

The teeth of the great apes bear an uncanny resemblance to those of humans in terms of their overall morphology. While the permanent teeth of humans and great apes have been studied in depth for several decades, deciduous teeth are often overlooked. Unlike permanent teeth, which are often used in both metric and non-metric studies to trace genetic drift and population variation, deciduous teeth are rarely studied in detail or in large numbers in either humans or primates.

Since non-metric traits in adult primates have been used in many important studies they can serve as an example for work that can be done with deciduous primate teeth. Several studies offer trait frequency data for non-metric traits in great ape adult dentitions (e.g., Bailey 2008, Swindler 2005, Swarts 1988) and Swindler (2005) provides some description of the morphology of great ape deciduous teeth. Human deciduous dental morphology has been described by Jorgensen (1956) and Scott and Turner (1997).

The present study addresses the dearth of information on great ape deciduous dentitions by looking at the variation in tooth crown morphology of subadult chimpanzees and gorillas. Previous research on non-metric traits among humans has revealed that they are useful in assessing population relatedness as well as population movements through time (e.g. Scott and Turner, 1997; Irish, 2006; Hanihara, 2008), and analysis of the deciduous dentition of the great apes may allow for similar assessments. In this study, variations in frequencies and patterns of occurrence for 28 dental traits are examined in five great ape subspecies. The utility of the deciduous dentition is assessed in addressing questions of population affinity and contributing to a set of standards and traits that can be used in further studies.

MATERIALS

Data were collected on the postcanine deciduous teeth from detailed photographs of 179 juvenile great ape dental arcades. The specimens belong to the collections of the Quex Museum of Birchington, UK and the Royal Museum of Central Africa in Tervuren, Belgium. Five of the gorillas came from the collection at the University of Minnesota Department of Anthropology. The samples included specimens identified in the museum catalogs as *Pan troglodytes troglodytes, Pan troglodytes schweinfurthii, Pan paniscus, Gorilla gorilla gorilla,* and *Gorilla beringei graueri* (Table 1).

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TABLE 1. Number of individuals studied in each African ape group

Species	Number of individuals	Number of teeth
Pan troglodytes	99	665
P. t. troglodytes	39	270
P. t. schweinfurthii	60	395
Pan paniscus	48	329
Gorilla gorilla gorilla	28	194
Gorilla beringei graueri	11	81

METHODS

Traits

Upper deciduous molars. Nine traits were observed in the upper deciduous molars. The transverse crest in the upper first deciduous molar (udp3) is an enamel ridge connecting the paracone and protocone (Swindler, 2005). It has been variously labeled the central ridge (Jørgensen, 1956) and the oblique ridge (Kraus et al. 1969) in human deciduous teeth. For the present study it was scored according to a previously used scale from 0 to 3 (Bailey, 2002). Although this scoring was originally for lower adult premolars, it describes the variation in udp3 well.

The lingual cingulum of the two upper deciduous molars (udp3 and udp4) was scored from 0 to 3 (Figure 1). The scores are based on Swindler's observation that the lingual cingulum in *Gorilla* and *Pan* differed in that, "A lingual cingulum is present in *Gorilla* extending mesially from the hypocone to the mesial surface of the protocone. A cingulum is present in *Pan* only on the lingual surface of the protocone." (Swindler, 2005). Due to these distinctions, this trait was scored as absent (0), a raised surface of the lingual side of the protocone (1), an enamel ridge on the lingual side of the protocone (2), or an enamel ridge extending from the protocone to the hypocone (3). On udp3 there is no hypocone, so the scoring of 3 is reserved for a lingual cingulum that extends across the entire lingual surface of the protocone. It is important to note that the smallest lingual cingulum is not considered to be a small Carabelli's trait because these two structures likely derive from separate features (Ortiz et al. , 2010). The buccal cingulum on udp3 and udp4 is scored only as present or absent where presence is considered to be any expression of a cingulum on the buccal surface of the tooth (Figure 2). None of the sources that were used mentioned a buccal cingulum on the great ape upper deciduous dentition, although it is observed in the great apes on lower deciduous molars and upper permanent molars (Swindler, 2005).

The crista obliqua is a ridge connecting the protocone and metacone of udp4 (Swindler, 2005). It has also been referred to as the postprotocrista (Swarts, 1988). It was recorded as absent (0), interrupted (1) or uninterrupted (2). Also on udp4, cusp 5 was scored from 0 to 5 following the Arizona State University Dental Anthropology System (ASUDAS) for cusp 5 on UM1 (Turner et al. 1991). Finally, the anterior and posterior foveae on udp4 were scored as either present or absent. In the ASUDAS, the anterior fovea is scored based on its size, but the present study found that on deciduous teeth both anterior and posterior foveae were generally too small to vary noticeably. Any

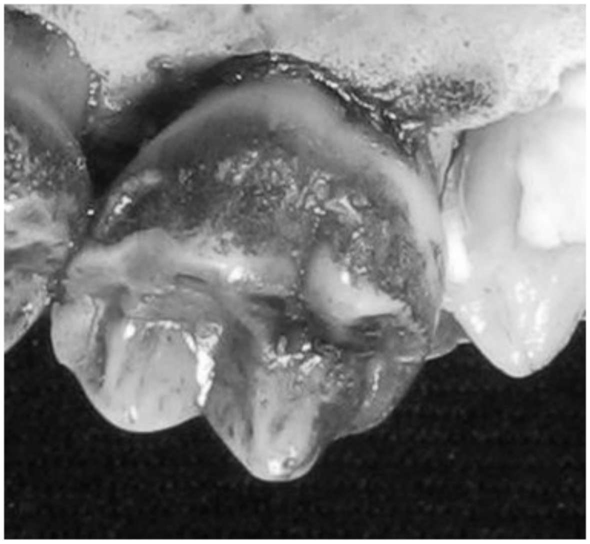

Fig. 1. Complete lingual cingulum on udp4 scored as 3.

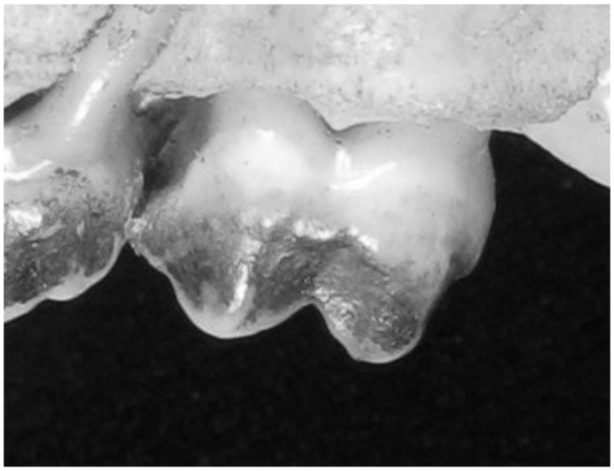

Fig. 2. Buccal cingulum on udp4 scored as present.

visible pit or fovea along the mesial or distal marginal ridge of the tooth was scored as an anterior or posterior fovea respectively.

Lower deciduous molars. Scores for 19 traits on the lower deciduous dentition were recorded for this study. The first takes note of the presence or absence of the metaconid on the lower first deciduous molar (ldp3) and its placement relative to the protoconid. The placement of the metaconid relative to the protoconid has been described both as variable in the permanent lower first and second premolars (LP3 and LP4) of *Pan* (Bailey, 2008) and as distal to the protoconid in ldp3 in the great apes (Swindler, 2005). Jørgensen (1956) also describes the distal metaconid in human deciduous teeth, but mentions that in the great apes the metaconid may be "faint or absent." Based on these reports and early observations, metaconids were scored in this study as absent (0), mesial to the protoconid (1), central to the protoconid (2) or distal to the protoconid (3). Based on Ludwig's (1957) description of the metaconid based on where it sits relative to "the long axis of the median ridge of the buccal cusp," the metaconid is scored as distal if the majority of the metaconid is distal to the median ridge of the protoconid, On the other hand, if the metaconid appears to sit directly on the axis of the median ridge of the protoconid then it is considered central.

The entoconid, hypoconid and hypoconulid are also scored on ldp3 and ldp4. The entoconid and hypoconid were scored as either present or absent and the hypoconulid was scored according to the ASUDAS from 0 to 5 with an additional value denoting a hypoconulid that was clearly present but could not be sized due to heavy wear (7).

The mid-trigonid crest is an enamel ridge on ldp4 that connects the protoconid and metaconid (Figure 3). It is mesial to the distal trigonid crest that connects the same cusps. The mid-trigonid crest may also be called a complete bridge formed by the mesial accessory ridges of the protoconid and metaconid (Hooijer, 1948; Scott and Turner, 1997), or the anterior transverse ridge (Jørgensen, 1956). Although there is an ASUDAS scoring plaque for this trait, the present study used a modified form of a scoring system presented by Bailey (2002) that better fit the variation found in great ape deciduous molars. The mid-trigonid crest was scored based on the absence of a crest (0), the presence of two accessory ridges that did not coalesce to form a crest (1), the presence of a crest interrupted by a mesio-distal groove (2), or the presence of an uninterrupted crest (3). The presence of the anterior fovea on ldp4 was dependent on the presence of the mid-trigonid crest, because without a crest between the anterior fovea and the trigonid basin, the two are indistinguishably joined. The distal trigonid crest sits distal to the mid-trigonid crest, connecting the more distal portions of the protoconid and metaconid (Figure 3). Scott and Turner (1997) call it the distal trigonid crest, but it has also been referred to as an extension of the distal accessory ridges of the protoconid and metaconid (Scott and Turner, 1997), the posterior trigonid crest (Weidenreich, 1937), the oblique crest (Jørgensen, 1956), or the transverse crest (Jørgensen, 1956). When the mid-trigonid crest is absent and there is only one crest connecting the protoconid and metaconid it is still called the distal trigonid crest in the present study, but it may be called the protocristid elsewhere (Swindler, 2005). The distal trigonid crest was scored in the same manner as the mid-trigonid crest.

The deflecting wrinkle in ldp4 is an enamel extension that goes buccally from the metaconid and then curves distally. This trait was ranked according to the ASUDAS as absent (0), weak (1), moderate (2), or marked (3).

There are several traits that involve either the division of existing cusps into multiple elements or the overall number of cusps on the teeth. Both the hypoconulid, following Jørgensen's (1956) ob-

Fig. 3. Mid-trigonid and distal trigonid crests both scored as 3.

servations of ldp4 in humans, and the entoconid were examined for a division in the cusp. These were each scored as either present or absent. The protostylid coming off of the disto-buccal edge of the protoconid on ldp4 was scored from 0 to 7 following the ASUDAS. The expression of cusp 6 on ldp4 appears as a cusp on the distal margin of the tooth between the hypoconulid and the entoconid. This trait was ranked from 0 to 5 with the ASUDAS. It may be important to note that a small cusp 6 may resemble a divided hypoconulid but that a divided cusp should have a single split apex while a cusp 6 will have its own apex distinct from the apex of the hypoconulid. Additionally, cusp 7 appears as a small cusp on the lingual margin of ldp4 between the metaconid and entoconid. It was scored using the ASUDAS from 0 to 5 as well.

Fissure pattern was observed in ldp4 and was scored as Y, + or X according to definitions given by Scott and Turner (1997). As stated previously, the anterior fovea on ldp4 is a depression between the mesial marginal ridge and the mid-trigonid crest. It was scored as either present or absent. The posterior fovea was scored differently, however, because it was often more observable than the anterior or posterior foveae on udp4. This allowed it be scored as absent (0), a pit (1) or a fovea (2), where a pit is a depression bordered by the distal marginal ridge and a fovea is a depression that interrupts the distal marginal ridge.

ANALYSIS

For statistical analysis the traits were dichotomized using threshold values such that all traits were converted to either presence or absence. Table 2 includes the list of traits and their thresholds for presence. Following Turner et al. (1991), any occurrence of a trait in an individual was counted as presence, even if occurrence was unilateral. This way, traits were analyzed according to the number of individuals as opposed to the number of teeth. Metaconid placement and fissure pattern could not be converted to this form for analysis. These two traits were left in their original state and were analyzed by tooth instead of by individual. Frequencies of occurrence for each trait were compared between pairs of groups using Fisher's exact test. Analysis among the groups was conducted using the chi-square test. Both analyses were done using PASW Statistics 18.0. Phenetic distance among the groups was then assessed using Irish's (2010) adaptation of C.A.B. Smith's (1977) mean measure of divergence (MMD) formula.

In order to further study the relatedness of the sample groups, the mean measures of divergence for pair-wise comparisons of the five groups were computed. First Kendall's tau-B test was used to find any correlated traits. Out of the twenty-six dichotomized traits, four (udp3 lingual cingulum with udp4 lingual cingulum and ldp4 anterior fovea with ldp4 mid-trigonid crest) were correlated and four (ldp3 cusp 5, ldp4 entoconid, ldp4 hypoconid, and ldp4 hypoconulid division) were invariable (i.e. fixed as either all present or all absent) and therefore correlated with all of the other traits. All of the invariable traits and half of the correlated traits were removed, since without their related traits the other two would be uncorrelated. The lingual cingulum on udp4 was kept, since it showed greater variation than udp3 lingual cingulum, and ldp4 mid-trigonid crest was chosen instead of the ldp4 anterior fovea, since the presence of an anterior fovea is dependent on the presence of a mid-trigonid crest. Metaconid position on ldp3 and fissure pattern on ldp4 could not be used for the MMD analysis since these traits were not expressed through presence or absence, so metaconid position was converted for analysis and fissure pattern was excluded. The 21 remaining traits were then used for MMD calculations using the Freeman and Tukey transformation for small sample size. The final equation for the mean measure of divergence was (Irish, 2010):

$$\mathrm{MMD}=\sum_{i=1}^{r}\frac{(\Theta_{1i}-\Theta_{2i})^2-(1/(n_{1i}+1/2)+1/(n_{2i}+1/2))}{r}$$

where r represents the number of uncorrelated traits, Θ denotes the angular transformation, which was calculated as:

$$\Theta = (1/2)\sin^{-1}(1-(2k)/(n+1)) + (1/2)\sin^{-1}(1-2(k+1)/(n+1))$$

I represents the trait, n represents the number of individuals examined for the trait, and k represents the number of individuals for whom the trait was present. The MMD was calculated for pair-wise comparisons of each group (Table 3).

In order to test the significance of the MMDs the variance of each pair-wise comparison was calculated using:

$$\mathrm{var(MMD)}= 2\sum_{i=1}^{r}\frac{(1/(n_{1i}+1/2)+1/(n_{2i}+1/2))^2}{r^2}$$

The square root of this var(MMD) value is the equivalent of the standard deviation, and if the MMD > 2 x √var(MMD), the null hypothesis that the proportion of occurrence in sample 1 is equal to the proportion of occurrence in sample 2 is rejected at the 0.025 level (Harris and Sjøvold, 2004; Irish, 2010).

RESULTS

Frequency Analysis

Frequencies of each trait in all groups are listed in Table 2. There was no difference in trait frequencies between males and females in any group, so both sexes were pooled for all analyses. There were several traits that showed statistically significant differences between the various subspecies, species, and genera that were studied.

There are five traits that are significantly different between *P. t. troglodytes* and *P. t. schweinfurthii* (Table 2). This is a surprisingly large number of differences since they are very closely related. Compared to these two subspecies of chimpanzee *G. g. gorilla* and *G. b. graueri*, which belong to two different species, also had five traits with significant differences. However, the low variability in gorilla trait frequencies may be a result of sample size differences. The differences between the two *Gorilla* species are less likely to appear statistically significant because there are so many fewer cases studied. There are six traits that exhibit significant differences in frequency between *P. troglodytes* and *P. paniscus.* Between *Pan* and *Gorilla* eleven traits were found that varied significantly. This is the most variability shown between any of the groups and likely reflects the fact that these genera are the most distantly related of any of the groups studied.

Mean Measure of Divergence

All of the pair-wise comparisons between the primate groups are significant, but the value of these findings is unclear since they demonstrate that *G. g. gorilla* is more similar to *P. paniscus* than to *G. b. graueri* when they are otherwise morphologically dissimilar. The fact that these values show that there is variation between the groups is, at the moment, more important than how much the groups vary and in what ways. The differences show that there is significant variation in the deciduous molars of chimpanzees, bonobos and gorillas that is comparable to variation found in the adult dentition. Therefore, the deciduous dentition does show potential to be used similarly to adult dentition in research of ape population movement and genetic drift.

DISCUSSION AND CONCLUSIONS

The data presented above support several findings of past researchers regarding morphological characteristics, with some exceptions. As observed by Swindler (2005), there were no observable fifth cusps on ldp3 and all observable teeth exhibited the Y fissure pattern. However, lingual and buccal cingula in the upper dentition were present far more often than was described in the past (Swindler, 2005). Additionally, there are similarities seen between traits of primate adult and deciduous dentition. For example, cusp 6 on ldp4 and the lower first adult molar (LM1) seems to be expressed in *P. troglodytes* but not in *P. paniscus* (Bailey, 2008; Swindler, 2005). Cusp 6 is observed on LM1 in 16.2% of *P. t. troglodytes* and 2.3% of *P. t. schweinfurthii,* but none are observed in *P. paniscus* (Bailey, 2008)*,* while on ldp4 cusp 6 was found in 23.5% of *P. t. troglodytes* and 24.2% of *P. t. schweinfurthii* and not at all in *P. paniscus.* Cusp 7 on the same tooth is expressed in 9.1% of adult *P. paniscus* (Bailey, 2008) and in 8.3% of juvenile *P. paniscus* and it is present in *Gorilla*, but it appears in neither adult nor juvenile *P. troglodytes* (Bailey, 2008; Swindler, 2005).

The results of MMD analysis are of particular interest when they are compared with another MMD analysis of similar non-metric dental traits in adult *Pan* (Bailey, 2008). Although the two data sets are quite different, there are some important similarities. Similar to Bailey's findings, we find

TABLE 2.Trait frequencies across species and subspecies withthe number of individuals (or number of teeth for metaconid position and fissure pattern) observed. Columns on the right represent p-values for Fisher's exact test. Abbreviations P Pan; PT P. troglodytes; PTT P. t. troglodytes; PTS P. t. schweinfurthii; PP P.paniscus; G Gorilla; GGG G. gorilla gorilla; GBG G.beringei graueri.

Traits	All PT	PTT	PTS	PP	GGG	GBG	PTT vs. PTS	GGG vs. GBG	PT vs. PP	P vs. G
Transverse crest (udp3) + = 2-3 (present study)	35.3 (51)	43.5 (23)	28.6 (28)	60.0 (30)	22.7 (22)	0.0 (8)	0.378	0.185	**0.027***	**0.005***
Lingual cingulum (udp3) + = 2-3 (present study)	1.5 (68)	3.7 (27)	0.0 (41)	3.1 (32)	4.3 (23)	62.5 (8)	0.397	**0.002***	0.539	**0.002***
Lingual cingulum (udp4) + = 2-3 (present study)	19.0 (84)	34.4 (32)	9.6 (52)	24.2 (33)	44.0 (25)	100 (9)	**0.006***	**0.003***	0.348	**0.000***
Buccal cingulum (udp3) + = any expression	4.0 (75)	10.3 (29)	0.0 (46)	2.6 (39)	0.0 (26)	25.0 (8)	0.054	**0.050***	0.577	0.419
Buccal cingulum (udp4) + = any expression	8.3 (84)	12.5 (32)	5.8 (52)	2.4 (41)	8.0 (25)	72.2 (11)	0.246	**0.000***	0.195	**0.001***
Crista obliqua (udp4) + = uninterrupted	69.8 (86)	50.0 (32)	81.5 (54)	73.3 (30)	87.0 (23)	100 (10)	**0.002***	0.325	0.452	**0.012***
Cusp 5 (udp4) + = ASU 1-5	3.5 (86)	5.7 (35)	2.0 (51)	5.1 (39)	4.2 (24)	9.1 (11)	0.360	0.536	0.498	0.477
Anterior fovea (udp4) + = any expression	68.7 (83)	50.0 (34)	81.6 (49)	29.0 (31)	44.0 (25)	60.0 (10)	**0.002***	0.315	**0.000***	0.218
Posterior fovea (udp4) + = any expression	78.8 (80)	65.7 (35)	88.9 (45)	94.1 (34)	83.3 (24)	100 (11)	**0.013***	0.203	**0.035***	0.325
Metaconid (ldp3) + = any expression	100.0 (72)	100.0 (30)	100.0 (42)	91.9 (37)	87.5 (24)	81.8 (11)	Constant	0.509	**0.037***	**0.021***

TABLE 2 cont'd.

Traits	All PT	PTT	PTS	PP	GGG	GBG	PTT vs. PTS	GGG vs. GBG	PT vs. PP	P vs. G
Metaconid position (ldp3) 1=mesial 2=central 3=distal (P-values for distal)	1=0.8 2=9.5 3=89.7 (126)	1=0 2=16.7 3=83.3 (54)	1=1.4 2=4.2 3=94.4 (72)	1=0.0 2=20.3 3=79.7 (59)	1=0.0 2=25.7 3=74.3 (35)	1=0.0 2=26.7 3=73.3 (15)	**0.042***	0.670	0.063	**0.033***
Entoconid (ldp3) + = any expression	68.1 (47)	56.0 (25)	81.8 (22)	86.7 (30)	85.7 (14)	80.0 (10)	0.056	0.822	0.055	0.303
Entoconid (ldp4) + = any expression	100 (85)	100 (35)	100 (50)	100 (44)	100 (24)	100 (11)	Constant	Constant	Constant	Constant
Hypoconid (ldp3) + = any expression	100 (80)	100 (36)	100 (44)	100 (41)	68.2 (22)	100 (11)	Constant	**0.040***	Constant	**0.000***
Hypoconid (ldp4) + = any expression	100 (89)	100 (36)	100 (53)	100 (45)	100 (24)	100 (11)	Constant	Constant	Constant	Constant
Cusp 5 (ldp3) + = ASU 1-5	0.0 (82)	0.0 (32)	0.0 (47)	0.0 (39)	0.0 (25)	0.0 (11)	Constant	Constant	Constant	Constant
Cusp 5 (ldp4) + = ASU 1-5	98.8 (85)	100 (35)	98.0 (50)	100 (39)	100 (24)	100 (11)	0.588	Constant	0.685	0.780
Deflecting wrinkle (ldp4) + = ASU 2-3	7.5 (53)	9.1 (33)	5.0 (20)	3.3 (30)	4.8 (21)	0.0 (8)	0.537	0.724	0.401	0.510
Mid-trigonid crest (ldp4) + = 2-3 (present study)	48.3 (58)	44.8 (29)	51.7 (29)	66.7 (36)	81.0 (21)	60.0 (10)	0.397	0.208	0.062	**0.048***
Distal trigonid crest (ldp4) + = 2-3 (present study)	100 (76)	100 (33)	100 (43)	97.6 (42)	90.9 (22)	100 (11)	Constant	0.438	0.356	0.120

TABLE 2 cont'd.

Traits	All PT	PTT	PTS	PP	GGG	GBG	PTT vs. PTS	GGG vs. GBG	PT vs. PP	P vs. G
Protostylid (ldp4) + = ASU 3-7	1.3 (79)	0.0 (35)	2.3 (44)	0.0 (39)	78.3 (23)	100 (11)	0.557	0.121	0.669	**0.000***
Division of hypoconulid (ldp4) + = any expression	0.0 (69)	0.0 (35)	0.0 (34)	0.0 (17)	0.0 (21)	0.0 (11)	Constant	Constant	Constant	Constant
Division of entoconid (ldp4) + = any expression	3.8 (78)	5.7 (35)	2.3 (43)	0.0 (36)	0.0 (23)	0.0 (11)	0.422	Constant	0.316	0.454
Cusp 6 (ldp4) + = ASU 1-5	23.9 (67)	23.5 (34)	24.2 (33)	0.0 (18)	4.5 (22)	0.0 (11)	0.639	0.667	**0.014***	**0.021***
Cusp 7 (ldp4) + = ASU 2-4	0.0 (79)	0.0 (35)	0.0 (44)	8.3 (36)	0.0 (24)	9.1 (11)	Constant	0.314	**0.029***	0.768
Anterior fovea (ldp4) + = any expression	55.2 (58)	51.7 (29)	58.6 (29)	60.0 (35)	76.2 (21)	60.0 (10)	0.396	0.302	0.406	0.121
Posterior fovea (ldp4) + = any expression	45.0 (60)	35.3 (34)	57.7 (26)	57.1 (14)	61.9 (21)	40.0 (10)	0.071	0.224	0.301	0.208
Fissure pattern (ldp4) + = Y	100 (127)	100 (64)	100 (63)	100 (60)	100 (45)	100 (22)	Constant	Constant	Constant	Constant

that *P. paniscus* is more similar to *P. t. schweinfurthii* than it is to *P. t. troglodytes*. We also found that the two *P. troglodytes* subspecies are more similar to each other than either is to *P. paniscus*, which fits with Bailey's data (2008) and the substantial genetic and morphological evidence that indicates that the two *P. troglodytes* subspecies are more closely related to each other than to *P. paniscus*. There are also several unexpected similarities between the deciduous teeth of *P. paniscus* and *G. g. gorilla.* MMD analysis indicates that *G..g. gorilla* is more similar to *P. paniscus* than it is to the other *Gorilla* species or *P. troglodytes*. However, since researchers overwhelmingly conclude that *G..g. gorilla* is more closely related to other groups within the *Gorilla* genus than to the *Pan* genus, we assume that these similarities are due primarily to chance and not to a genetic closeness between the two very different species. The point here is that while the data do not give an entirely accurate view of how these subspecies and species are related, they can show that these groups display significant variation in their deciduous dental traits and that future research could perhaps give a more accurate estimation of those differences.

It is important to note the size of the samples used in this study. While our numbers of individuals observed were similar to those of Bailey (2008) for *Pan*, the number of observable samples of each trait is substantially lower, and for many important traits Bailey uses more observable samples. While it would clearly be helpful to have data on more deciduous teeth, it would also be useful to have more data on adult teeth to compare with this study to show more concretely whether deciduous teeth exhibit the same patterns as adult teeth. By using many traits across a larger variety of teeth, studies in the future will be able to produce more reliable data on the deciduous primate dentition.

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LITERATURE CITED

Bailey SE. 2002. A closer look at Neanderthal post canine dental morphology: The mandibular dentition. Anat Rec 269:148-156.

Bailey SE. 2008. Inter- and intra-specific variation in Pan tooth crown morphology: implications for Neandertal taxonomy. In: Irish JD, Nelson GC, editors. Technique and Application in Dental Anthropology Cambridge: Cambridge University Press. p 293-316.

Hanihara T. 2008. Morphological variation of major human populations based on nonmetric dental traits. Am J Phys Anthropol 136:169-182.

Harris EF, Sjøvold T. 2004. Calculation of Smith's mean measure of divergence for intergroup comparisons using nonmetric data. Dent Anthropol 17:83-93.

TABLE 3. Mean measure of divergence values (with variance values) for pair-wise comparison of the five African ape groups. Abbreviations described in Table 2

	PTT	PTS	PP	GGG	GBG
PTT	-	0.074 (0.02)	0.099 (0.02)	0.328 (0.02)	0.806 (0.04)
PTS		-	0.102 (0.02)	0.270 (0.02)	0.935 (0.04)
PP			-	0.243 (0.02)	0.733 (0.04)
GGG				-	0.456 (0.04)
GBG					-

Hooijer DA. 1948. Prehistoric teeth of man and of the orang-utan from Central Sumatra, with notes on the fossil orang-utan from Java and Southern China. Zoologische Mededelingen 29:175-301.

Irish JD. 2006. Who were the ancient Egyptians? Dental affinities among Neolithic through post dynastic peoples. Am J Phys Anthropol 129:529-543.

Irish JD. 2010. The mean measure of divergence: Its utility in model-free and model-bound analyses relative to the Mahalanobis D^2 distance for nonmetric traits. Am J Hum Biol 22:378-395.

Jørgensen KD. 1956. The Deciduous Dentition: A descriptive and comparative anatomical study. Acta Odontol Scand 14:1-235.

Kraus BS, Jordan RE, Abrams L. 1969. Dental anat omy and occlusion; a study of the masticatory system. Baltimore: Williams and Wilkins.

Ludwig FJ. 1957. The Mandibular Second Premolars: Morphologic Variation and Inheritance. Journal of Dental Research 36:263-273.

Ortiz A, Skinner MM, Bailey SE, Hublin JJ. 2010. Carabelli's trait expression at the enamel-dentin junction (EDJ) and outer enamel surface (OES) of *Pan* maxillary molars. Am J Phys Anthropol 141:182-183.

Scott GR, Turner CG II. 1997. The anthropology of modern human teeth: dental morphology and its variation in recent human populations. Cambridge; New York: Cambridge University Press.

Smith CAB. 1977. A note on genetic distance. Ann Hum Genet 40(4):463-479

Swarts JD. 1988. Deciduous dentition: implications for hominoid phylogeny. In: Schwartz JH, editor. Orang-utan Biology. New York: Oxford University Press. p 263-270.

Swindler DR. 2005. Primate dentition: An introduction to the teeth of non human primates. Cambridge: Cambridge University Press.

Turner CG II, Nichol C, Scott GR. 1991. Scoring Procedures for Key Morphological Traits of the Permanent Dentition: the Arizona State University Dental Anthropology System. In: Kelley MA, Larsen CS, editors. Advances in Dental Anthropology. New York: Wiley-Liss. p 13-31.

Weidenreich F. 1937. The dentition of *Sinanthropus pekinensis*: a comparative odontography of the hominids. Palaeontologica Sinica New Series D. No. 1: 1-180.

Brief communication: maxillary lateral incisor morphology and uncommon trait expression: a case study from prehistoric Paa-ko, New Mexico

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Key words: Dental morphology, Upper Central Incisors, Discrete Dental Trait, Prehistory, Iberian Peninsula.

ABSTRACT Prehistoric American Southwest exhibits a high frequency of dental morphological variability. This high variability may be the result of gene flow and subsequent genetic drift occurring in early periods (pre CE 900), though few studies report on dental variability in later periods. Morphological traits of the maxillary lateral incisors were analyzed from the Pueblo IV site of Paa-ko, New Mexico (CE 1300-1425) yielding high frequencies of four traits (shovel, double shovel, tuberculum dentale, interruption groove) and uncommon variants (barrel-shovel, triform, peg-shaped). Lateral incisor morphology is underrepresented in the literature but could be useful in determining population migration and affinity.

Dental morphological traits, such as shoveling, tuberculum dentale, and interruption groove, reflect population affinity and movement (Scott and Turner, 1997). Within the New World, the greatest dental morphological variability is found in the prehistoric American Southwest (Scott et al., 1983; Bailey-Schmidt, 1995; Scott and Turner, 1997; McClelland, 2003; Kuba, 2006).This high variability may be a result of migration and genetic drift, as introduction of new genes and subsequent population isolation changes the expression of dental traits (LeBlanc et al., 2008).Mitochondrial DNA evidence from the prehistoric Southwest region suggests there was migration followed by population isolation in several areas, including the New Mexico Pueblo region (Malhi et al., 2003). Archaeological evidence indicates migration into the Southwest from surrounding areas prior to the Pueblo IV period (CE 900-1500; Wilcox and Haas, 1994; LeBlanc, 1999; Malhi et al., 2003; LeBlanc et al., 2008) was likely a response to resource unpredictability caused by warm droughts and high seasonal resource stress (Dean, 1996; Benson et al., 2007). Unfortunately, few bioarchaeological studies dealing with dental morphology in the later Pueblo IV period have been produced, limiting our ability to address this pre-contact period of population movement. This study interprets dental morphology of one tooth, the maxillary lateral incisor, from the site of Paa-ko, New Mexico in order to add to our understanding of Southwest dental morphological variability.

Expressions of discrete dental traits are used to determine biological distance, population movement, and evolutionary trends (Turner et al., 1991; Scott and Turner, 1997; Irish and Guatelli-Steinberg, 2003). Maxillary lateral incisors, having the highest amount of variation in trait expression of all tooth types, is a key tooth for understanding genetic relationships and population comparisons (Turner et al., 1991; Bailey-Schmidt, 1995; Scott and Turner, 1997). Scott and Turner (1997:32) describe categories of discrete trait variation in maxillary lateral incisors, including barrel-shovel, triform, and peg-shaped or conical incisors, which deviate from the more prevalent morphological forms of shovel and tuberculum dentale.

Studies on dental morphology throughout the prehistoric American Southwest reveal higher variability of maxillary lateral incisor trait expression than any other location worldwide, particularly for shovel, barrel shovel, and full expression of tuberculum dentale and its variants (Sofaer et al. 1972; LeBot and Salmon 1977; Turner and Swindler 1978; Kieser and Preston 1981; Bailey-

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Schmidt, 1995; Scott and Turner 1997; Burnett and Weets 2001; McClelland 2003; Bollini et al., 2008; LeBlanc et al., 2008). This study analyzes the frequency of maxillary lateral incisor traits from the prehistoric site of Paa-ko, New Mexico (CE 1300-1425), adding to the literature on Pueblo IV Southwest dental morphology.

MATERIALS AND METHODS

Skeletal remains analyzed for this study were recovered from Paa-ko, New Mexico between 1935 and 1937 as a joint venture of the Museum of New Mexico, the School of American Research, and the University of New Mexico, with funds allotted by the Works Progress Administration (Lambert, 1954).

Paa-ko is located between Albuquerque and Santa Fe, New Mexico (Lambert, 1954). Occupied from CE 1300-1425, Paa-ko was established through population migration during the Pueblo IV period (Lambert 1954). This study uses a population count of 178 individuals, the majority of which are infants and children (9 years of age and younger). Taphonomic processes affecting the recovered dentition include severe postmortem damage and postmortem loss, both of which impacted observation and recording. For this study, only individuals with intact, fully erupted anterior maxillary dentition were used. Dental morphology was observed and recorded for 53 maxillary lateral incisors associated with 34 individuals; nine subadults (10-17 years), and 25 adults (18 + years). Males and females were not considered separately because of low correlation between sex bias and trait expression (Scott and Turner 1997; Kuba 2006).

Dental morphology of 37 discrete and continuous dental traits were examined and scored following the extensive sequencing of Turner et al's (1991) ASUDAS to ensure accurate recognition. For this study variations of shovel, double shovel, interruption grove, and tuberculum dentale were the focus. In cases where dental attrition or taphonomic processes inhibited scoring of morphological traits, traits were recorded as missing data.

RESULTS

Fifty-three maxillary incisors from 34 individuals were examined. Table 1 shows trait frequencies.

TABLE 1. Frequency of Lateral Incisor Trait

Traits	# of Individuals Scored and Percent Expressed	
	n	%
Shovel	26	0.790
Full Shovel	8	0.235
Marked	5	0.147
Barrel	1	0.290
Double Shovel	12	0.350
Interruption Groove	21	0.610
Tuberculum dentale	22	0.647
Well-developed	13	0.382
Triform	1	0.029
Peg-shaped	4	0.117

The most frequently expressed trait was shoveling, occurring in 26 individuals (79%, n=43 teeth). Of these individuals, 13 (38.2%, n=13 teeth) exhibit either shovel, or marked shovel (Turner et al. 1991). Barrel-shaped incisor was exhibited in one individual (2.9%, n=2 teeth). Double shoveling was exhibited in 12 individuals (35%, n=17 teeth). Interruption groove was expressed in 21 individuals (61%, n=32 teeth). Tuberculum dentale was present in 22 individuals (64.7%, n=35 teeth). Thirteen of the individuals (55.8%, n=19 teeth) with a tuberculum dentale expressed either a weak cuspule with a free apex or a strong cusp with free apex, which are the highest ASUDAS grades (Turner et al 1991:16). One individual (2.9%, n=1 tooth) expressed a triform, bifurcated lateral incisor. This tooth exhibited a developed transverse ridge on the incisal surface originating from the tuberculum dentale dividing two fossae (Lee et al. 1988; Bailey-Schmidt 1995). Mesiodistal and labiolingual dimensions of this tooth were greatly expanded as a result of this morphological arrangement. Four individuals (11.7%, n=4 teeth) expressed a peg-shaped, or conical, lateral incisor. Eight individuals (23.5%, n=11 teeth) expressed some degree of all observed traits (shovel, double shovel, interruption groove, tuberculum dentale). Six individuals (17.6%, n=7 teeth) exhibit maxillary lateral incisor variants which are considered rare in expression (barrel-shovel, peg-incisor, triform; Scott and Turner, 1997).

DISCUSSION

Paa-ko is a quintessential example of prehistoric Southwest dental morphological variation. There is a high prevalence of all four maxillary lateral incisor traits analyzed (shovel, double shovel, tuberculum dentale, and interruption groove) and most correspond with previously reported Native American samples (Sofaer et al., 1972; Scott et al., 1983; Bailey-Schmidt, 1995; Scott and Turner, 1997; McClelland, 2003). Seventeen percent of the Paa-ko sample exhibits uncommon lateral incisor trait variants, barrel-shovel (Figure 1), triform (Figure 2), and peg-shape (Figure 3), a higher frequency than other reported prehistoric Southwest populations (Sofaer et al., 1972; Burnett and Weets, 2001; McClelland, 2003).

An outline of specific migration patterns is beyond the scope of this paper because its focus remains on one population; however, a discussion is necessary to determine the high variability and rare trait expression within the maxillary lateral incisor of Paa-ko. Increased trait prevalence is most likely the result of gene flow into the Southwest followed by period of population isolation (Malhi et al., 2003; LeBlanc et al., 2008). Migration into the region, including into the San Juan Basin (Benson et al., 2007) where Paa-ko is located, occurred prior to the Pueblo IV period. Lambert (1953) argues that Paa-ko was established by communities from the west. High frequencies of morphological variation and prevalence of uncommon traits may be reflective of the broad admixture resulting from eastern migration (Malhi et al., 2003).The Pueblo pattern of large site abandonment followed by isolated community aggregation (Fagan, 2000) likely resulted in short term genetic drift, and contributed to the higher prevalence of rare dental traits observed within Paa-ko.

Fig. 1. Barrel-shovel lateral incisors observed in burial 1971-82-122.

Fig. 2.Triform variant of right lateral incisor observed in burial 1971-82-21.

Adaptive significance can also influence the expression of certain dental traits, as functional demands impact tooth morphology (Hunter and Jernval, 1995). Shoveling and tuberculum dentale may be adapted to strengthen teeth by adding to structural durability with extra enamel (Dahlberg, 1963; Bailey-Schmidt, 1995).However, this explanation is less likely to be the case because traits

Fig. 3. Peg-incisor observed on left maxillary lateral incisor of burial 1971-82-96.

associated with advantageous adaptive changes would be seen in high prevalence throughout the region, not localized to Paa-ko. Additionally, anterior teeth are not used in primary mastication.

CONCLUSION

Prehistoric Native American Southwest exhibits high dental variability in the lateral incisors (Sofaer et al., 1972; Bailey-Schmidt, 1995; Scott and Turner, 1997; McClelland, 2003), especially at Paa-ko, New Mexico (CE 1300-1425). High prevalence of four discreet traits (shovel, double shovel, interruption groove, and tuberculum dentale) and their morphological variants (barrel-shovel, peg-incisors, triform) were observed in Paa-ko, New Mexico. The high observed variability is likely the result of gene flow into the region followed by short term population isolation prior to the Pueblo IV period (CE 900-1500). Even though maxillary lateral incisor traits are good indicators of genetic relationships and population movement (Scott and Turner, 1997),they are underrepresented in the literature. This article provides an additional prehistoric Southwest population for future research on regional behaviors, migration, and population affinity.

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LITERATURE CITED

Bailey-Schmidt S. 1995. Population distribution of the tuberculum dentale complex and anomalies of the maxillary anterior teeth.Masters thesis, Department of Anthropology, Arizona State University.

Benson LV, Berry MS, Jolie EA, Spangler JD, Stahle DW, Hattori E.M., 2007. Possible impacts of early-11th-, middle-12th, and late-13th century droughts on western Native Americans and the Mississippian Cahokians. Quaternary Science Reviews 26: 336-350.

Bollini GA, Rodriguez-Florez CD, Colantonio, SE. 2008. Dental non-metric traits in a pre-conquest sample from Tastil region in Argentina South America. Bulletin of the International Association of Paleodontology 2(1): 1925.

Burnett SE, Weets JD. 2001. Maxillary canine-first premolar transposition in two Native American skeletal samples from New Mexico. Am J Phys Anthropol 16: 45-50.

Dahlberg AA 1963. Dental evolution and culture. Human Biology 35: 237-249.

Dean JS. 1996. Demography, environment, and subsistence stress, In: Tainter JA, Tainter BB (Eds), Evolving Complexity and Environmental Risk in the Prehistoric Southwest.

Fagan BM. 2000. Ancient North America: the archaeology of a continent. New York: Thames and Hudson.

Hunter JP, Jernvall J. 1995. The hypocone as a key innovation in mammalian evolution. Proceedings of the National Academy of Sciences, USA 92: 10718-10722.

Irish JD, Guatelli-Steinberg D. 2003. Ancient teeth and modern human origins: An expanded comparison of African Plio-Pleistocene and recent world dental samples. J Hum Evol 45: 113-144.

Kieser JA, Preston CB. 1981. Dentition of the Lengua Indians of Paraguay. American J Phys Anthropol 55: 485-490.

Kuba CL. 2006. Nonmetric traits and the detection of familial groups in archaeological remains. Dissertation, Department of Anthropology, Arizona State University.

Lambert MF, 1954.Paa-ko, Archaeological chronicle of an Indian village in north central New Mexico. The School of American Research, Monograph 19, Parts I-V, Santa Fe, NM.

LeBlanc SA. 1999. Prehistoric Warfare in the American Southwest. University of Utah Press, Salt Lake City, Utah.

LeBlanc SA, Turner II CG, Morgan ME. 2008. Genetic relationships based on discrete dental traits: Basketmaker II and Mimbres. Intl J Osteoarchaeol 18: 109-130.

Le Bot P, Salmon D. 1977. Congenital defects of the upper lateral incisors (ULI): Condition and measurements of the other teeth, measurements of the superior arch, head and face. Am J

Phys Anthropol 46: 231-244.

Malhi RS, Mortensen HM, Eshleman JA, Kemp BM, Lorenz JG, Kaestle FA, Johnson JR, Gorodezky C, Smith DG. 2003. Native American mtDNA prehistory in the American Southwest. Am J Phys Anthropol 120: 108-124.

McClelland JA. 2003. Refining the resolution of biological distance studies based on the analysis of dental morphology: detecting subpopulations at Grasshopper Pueblo. Dissertation, Department of Anthropology, University of Arizona.

Scott GR, Yap Potter RH, Noss JF, Dahlberg AA, Dahlberg T. 1983. The dental morphology of Pima Indians. Am J Phys Anthropol 61: 13-31.

Scott GR, Turner II CG, 1997. The anthropology of modern human teeth: Dental morphology and its variation in recent human populations. Cambridge University Press, Cambridge, UK..

Sofaer JA, Niswander JD, MacLean CJ, Workman PL. 1972. Population studies on Southwest Indian Tribes. V. Tooth morphology as an indicator of biological distance. Am J Phys Anthropol 37: 357-366.

Turner CG II, Nichol, CR, Scott GR. 1991. Scoring procedures for key morphological traits of the permanent dentition: The Arizona State University Dental Anthropology System, In: Kelly, M.A., Larsen, C.S. (Eds.), Advances in Dental Anthropology. Wiley-Liss, Inc., New York, pp. 13-31.

Turner CG II, Swindler DS. 1978. The dentition of New Britain West Nakanai Melanesians.VIII Peopling of the Pacific. Am J Phys Anthropol 49: 361-372.

Wilcox DR, Haas J. 1994. The scream of the butterfly: Competition and conflict in the prehistoric Southwest, In: Gumerman GJ (Ed.), Themes in Southwest Prehistory. School of American Research Press, Santa Fe, NM, pp. 8-108.

2012 Dahlberg Award Winner: Dental morphological variation among six Pre-Hispanic South American populations with implications for the peopling of the New World

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Keywords: Discrete dental traits, ASUDAS, Dental variation, South American Indians

ABSTRACT The analysis of the human dentition provides important information on the origins and dispersals of the first American inhabitants. However, most of this work has focused on North America, whereas less research has been devoted to variation within Central and South America. This study examines the permanent dentitions of 340 individuals from six pre-Hispanic South American populations and places them in the broader context of the peopling of the New World. Non-metric dental data were collected using the Arizona State University Dental Anthropology System (ASUDAS). Intra- and inter-regional comparisons were assessed using the Mean Measure of Divergence statistical program. All samples are characterized by relatively high frequencies of UM1 enamel extension and LM1 deflecting wrinkle and low frequencies of UM1 cusp 5 and LM2 Y-groove pattern. Although preliminary, results indicate that populations from Chile, Venezuela and Peru-Northern Coast are dentally similar and follow the Sinodont dental pattern. The Peru-Southern Highlands sample is the most divergent of the South American groups examined, showing the closest affinities with Sundadonts. Finally, no clear pattern was found for Bolivia and Peru-Amazonian Andes, as most of their trait frequencies fall within the range of overlap between Sinodont and Sundadont populations.

Since Columbus reached the New World in 1492 and found it already inhabited by humans, one of the most enduring debates among scholars and early natural historians has centered on the origins of the first American inhabitants. Until the 1980s, the predominant view was that one single founding group, represented archaeologically by the Clovis culture, first entered the Americas after the last glacial maximum (LGM) via the Bering land bridge (Martin, 1973; Lynch, 1983). The Clovis-first model hypothesized that around 13,000 years ago people migrated from Siberia to Alaska tracking big game animal herds and that in a few millennia spread rapidly from Beringia to Tierra del Fuego (Dillehay, 1999, 2000, 2009; Meltzer, 2004; Goebel et al., 2008). In accord with this model, Greenberg et al. (1986) published a widely cited, yet highly controversial, three-wave model for the peopling of the New World. Based on the linguistic, dental and genetic evidence available at that time, they argued that the first Americans came from Northeast Asia in three separate waves of migration. Following Greenberg et al. (1986), the first migration would have involved the ancestors of Amerind-speaking populations from South, Central and most of North America. These first settlers would have been associated with the big-game hunting Clovis culture and its rapid spread throughout the American continent. The second migratory wave would have been associated with the ancestors of Na-Dene speakers from the western half of the North American subarctic, including the North Pacific Coast. The third and last migratory wave from Northeast Asia would have involved the ancestors of Aleut-Eskimo populations, occupying territories from western Alaska to eastern Greenland.

Over the past 25 years, several archaeological sites in the Arctic and the Americas have provided compelling evidence for human occupation predating Clovis (e.g., Dillehay, 1997, 2000; Adovasio et al., 1998; Pitulko et al., 2004; Goodyear, 2005). Relatively recent genetic and craniofacial studies have also brought both the Clovis-first and three-wave models into question. For example, molecular data suggest a single and early (i.e., pre-Clovis) migration for the peopling of the New World (Bonatto and Salzano, 1997; Schurr, 2004; Zegura et al., 2004; Tamm et al., 2007; Wang et al., 2007; Fagundes et al., 2008a,b). Mitochondrial DNA (mtDNA) analyses have revealed that the majority of Native Americans (including Na-Dene and Aleut-Eskimo) belong to five distinct mtDNA haplogroups, which have been identified as A-D and

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X (Schurr, 2004). Furthermore, Zegura et al. (2004) demonstrated that these populations exhibit, almost exclusively, Y-chromosome haplogroups Q and C. Although all these lineages can be traced back to modern Northeast Asians, recent genetic data from Native American samples reveal the presence of autochthonous mutations of particular mtDNA and Y-chromosome haplogroups, which cannot be explained by old Clovis paradigms (Tamm et al., 2007; Fagundes et al., 2008a,b). In this regard, and although the exact pre-Clovis timing of migration remains controversial (for reviews see Schurr, 2004), geneticists seem to concur that a population expansion with its roots in Beringia occurred by the end of the LGM, followed by a rapid settlement of the continent along a Pacific coastal route (Bonatto and Salzano, 1997; Tamm et al., 2007; Wang et al., 2007; Fagundes et al., 2008a,b).

Research on craniofacial variation among early American populations also suggests an early date for the peopling of the New World (Powell and Neves, 1999; Pucciarelli et al., 2003; Neves et al., 2003; Neves and Hubbe, 2005; Hubbe et al., 2011). Contrary to interpretations based on molecular markers, these studies have proposed that the New World was initially occupied by two biologically and chronologically distinct human groups. Advocates of this two-wave model argue that the ancestors of a morphologically generalized (or non-specialized Mongoloid) "Paleoamerican" population first migrated to the New World and were later replaced by the ancestors of the "Amerindians," who carried the highly derived Northeast Asian (or Mongoloid-Sinodont) phenotype. Lahr (1995) considers that the high level of diversity observed among Native Americans, including both Paleoamericans and Amerindians, can be explained by a single, albeit not necessarily earlier, migration of non-specialized Mongoloids that entered the Americas before many Mongoloid-Sinodont traits spread throughout Northeast Asia. More recently, González-José et al.'s (2008) analysis of modern human cranial variation also suggests a single origin for all Native Americans. Contrary to Lahr (1995), however, they propose a pre-Clovis occupation of the New World and emphasize the critical role that Beringia played in shaping the Native American pattern of variation.

Although considerable advances have been made since the publication of Greenberg et al.'s (1986) model, our understanding of the real extent of dental morphological variation across the Americas remains elusive. Turner's pioneering research on dental morphology demonstrated the usefulness of non-metric traits for assessing human biological relationships and reconstructing human population history (Turner, 1984, 1986, 1987, 1990, 1993; Scott and Turner, 1997). Based on his work, however, Native Americans have been regarded as a rather biologically and phenotypically homogeneous human group, sharing a strict Sinodont dental pattern (but see Haydenblit, 1996). Nevertheless, the apparent homogeneity of Native American populations, and their close association with modern Northeast Asians, may be attributed to the fact that our characterization of Native American dental morphology has largely been based on North America (Dahlberg, 1951, 1963; Moorrees, 1957; Sofaer et al., 1972; Turner, 1983, 1990, 1993; Scott et al., 1983). In fact, relatively little work has concentrated on Central (Baume and Crawford, 1978; Haydenblit, 1996) and South (Goaz and Miller, 1966; Kieser and Preston, 1981; Turner and Bird, 1981; Sutter and Verano, 2007) America. Furthermore, research in Central and South America has generally focused on a limited number of dental traits in only a few populations. Thus, attempts to assess biological affinities between South Americans and other world populations have been relatively rare (e.g., Turner and Bird, 1981; Turner, 1984, 1986; Sutter, 2005; Hanihara, 2008).

To partially reconcile interpretations derived from dental morphology with those based on relatively recent craniofacial and genetic data, the present study reanalyzes dental affinities in the New World, with special attention to South American populations. Two hypotheses are tested. Hypothesis 1: if South Americans are dentally homogeneous, no significant differences among groups are predicted. Hypothesis 2: if all Native Americans have a relatively recent Northeast Asian origin, a shared Sinodont dental pattern across all samples is predicted. The specific goals of this study are to: (1) describe South American dental morphology; (2) determine biological affinities among South American populations; and (3) compare their morphology with published data from major world populations showing either the Sinodont or Sundadont dental pattern. Ultimately, I analyze dental morphological data to enhance our understanding

TABLE 1. South American samples used in this study

Sample name	Code	n	Time period
Peru - Southern Highlands	PSH	61	pre- or proto-Hispanic
Peru - Northern Coast	PNC	37	from pre-Ceramic Period to Initial Period-Cupisnique times (ca. 3500-200 B.C.)
Peru - Amazonian Andes	PAA	62	from Late Intermediate Period to early Spanish post-contact times (ca. 800 - 1532 A.D.)
Chile	CHI	41	from pre-Ceramic Period to early Spanish post-contact times (ca. 3500 B.C.-1532 A.D.)
Venezuela	VEN	32	pre- or proto-Hispanic
Bolivia	BOL	107	Late Intermediate Period (ca. 1000-1400 A.D.)
TOTAL		340	

n = number of individuals examined

of South American origins and the initial peopling of the New World.

MATERIALS AND METHODS

Study Sample

This study examined the permanent dentitions of 340 individuals from six pre- or proto-Hispanic South American populations. The geographic origin and number of individuals in each sample are presented in Table 1. Figure 1 illustrates the geographical range for each sample. Except for the Peru-Amazonian Andes sample, which is curated at the Instituto Nacional de Cultura (Chachapoyas, Peru), all data were collected on skeletal remains housed at the American Museum of Natural History (New York, USA). In some cases, small collections were pooled to increase the sample size of specific regional populations. Further details of sample composition are provided below.

Peru - Southern Highlands (PSH). This sample includes individuals from Apurimac (n = 53) and Puno (n = 8). Both sites are located in the southern highlands of Peru. All specimens belong to the von Luschan collection. The time period during which these populations lived is not mentioned on museum records. However, some specimens present intentional cranial deformation and/or cranial trephination, suggesting that these populations lived during pre-Hispanic times or had limited Spanish influence.[1]

Peru - Northern Coast (PNC). A total of 37 pre-Hispanic individuals recovered by Junius Bird (1985) during his expedition to the Chicama, Virú and Moche valleys in the northern coast of Peru make up this sample. The majority of specimens (n = 32) came from the Huaca Prieta archaeological site and belong either to the pre-Ceramic Period (*ca.* 3500–1300 B.C.) or the Initial Period-Cupisnique times (*ca.* 1300-200 B.C.). No specific cultural affiliation has been attributed to the remaining five individuals.

Peru - Amazonian Andes (PAA). This sample consists of 62 individuals from the Chachapoya culture, which occupied the territory between the northeastern flank of the Andean Cordillera and the northwestern portion of the Amazonian forest. All individuals were recovered from primary or secondary burials at the archaeological complex of

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[1] Artificial cranial deformation and cranial trephination were regular practices in pre-Hispanic South America (Imbelloni, 1925; Munizaga, 1987). Although these cultural practices have been forbidden since 1585, due to the Spanish influence over the Andean region (Hoshower et al., 1995), a few cases have been reported in relatively isolated post-contact indigenous groups (Bandelier, 1904; Weiss, 1961; Tommaseo and Drusini, 1984).

Kuelap and have been dated to *ca.* 800 – 1532 A.D. (Schjellerup, 1997).

Chile (CHI). This sample consists of 41 individuals from north-central Chile. The majority of the specimens analyzed (n = 24) was recovered by Bird during his expedition to Chile (Bird, 2006). The remaining 17 individuals belong to different museum collections. All specimens date between the pre-Ceramic Period (*ca.* 3500–1300 B.C.) and early Spanish post-contact times (*ca.* 1532 A.D.).

Venezuela (VEN). This sample consists of 32 individuals. Most (n = 26) are from La Mata, an artificial mound situated on the shores of Lake Valencia in the Maracay region (Bennett, 1937). The La Mata site was excavated by archaeologist Wendell Bennett during his 1932 expedition, where several pre-Hispanic burials with no specific cultural affiliation were recovered. The remaining six individuals came from Maracaibo and belong to the von Luschan collection.

Bolivia (BOL). The Bolivian Altiplano is represented by a sample of 107 individuals. They are dated to the Late Intermediate Period, which extends from approximately 1000 to 1400 A.D. (Bandelier, 1910). All specimens were recovered by Adolph Bandelier during his expedition to South America from1894 to 1898.

Scoring Procedures and Statistical Analysis

Dental morphological affinities among samples were assessed using the Arizona State University Dental Anthropology System - ASUDAS (Turner et al., 1991). To avoid misleading results attributed to European admixture, only presumed pre- or proto- Hispanic individuals were included and analyzed. Although data were collected on the complete set of ASUDAS crown and root traits, only 21 tooth-trait combinations were used in this study. These combinations focus on the key tooth *sensu* Dahlberg (1945), as well as traits whose sample sizes consist of at least three individuals in each group. Furthermore, features that were consistently absent across samples (e.g., UC Bushman canine) were removed from analysis. According to Irish (2010), dropping traits that are nondiscriminatory across samples is the standard procedure, as their inclusion does not effectively contribute to group differentiation. Teeth with occlusal wear or *post mortem* damage were analyzed to the extent that the trait observed was not obscured. Previous investigations demonstrated the lack of sexual dimorphism of non-metric dental traits (Turner, 1984; Hanihara, 1992; Irish, 1993, 1997; Scott and Turner, 1997), and thus males and females were combined in this study.

Fig. 1. Map of South America showing the geographical range of the six pre- or proto-Hispanic Andean populations used in this study.

Trait frequencies were estimated using the individual count method of Turner and Scott (1977). This method suggests that the antimere exhibiting the strongest degree of trait expression is used in the analysis, as it is a more accurate indicator of the individual's genotype (Turner and Scott, 1977; Scott and Turner, 1997). Following Sjøvold (1977), trait expression was dichotomized into categories of presence or absence to facilitate multivariate statistical analysis. All traits were dichotomized at the standard breakpoints according to the ASUDAS (see Table 2). Levels of differentiation among samples were calculated using Smith's Mean Measure of Divergence (MMD) multivariate statistic. This method provides a quantitative estimate of biological divergence between two given samples based on the degree of similarity across the entire suite of traits (Berry and Berry, 1967; Sjøvold, 1977; Harris and Sjøvold, 2004; Irish, 2010). Thus, a smaller value indicates greater affinity between comparative groups. Divergence between two samples was considered significant at $p \leq 0.025$, when the MMD value is greater than twice its standard deviation (Sjøvold, 1977). Small sample sizes were corrected using the Freeman and Tukey angular transformation. However, because of the correction factor, this transformation may yield negative MMD values (Berry and Berry, 1967; Sjøvold, 1977; Harris and Sjøvold, 2004). These negative values are statistical artifacts and indicate no meaningful divergence between two samples. Thus, the standard procedure is to set them at zero (Harris and Sjøvold, 2004; Irish, 2010).

Finally, to place the six South American samples examined in a global context, trait frequencies were compared to other populations exhibiting either the Sinodont or Sundadont dental pattern (*sensu* Turner, 1987, 1990). These included samples from North and Southeast Asia (Turner, 1984, 1987, 1990), North America (Turner, 1984, 1986), and Mesoamerica-Mexico (Haydenblit, 1996). All comparative data were scored using the ASUDAS. Special attention was initially given to the eight diagnostic traits of the Sinodont-Sundadont division proposed by Turner (1987, 1990): UI1 shoveling, UI1 double shoveling, UP3 root number, UM1 enamel extension, UM3 peg/reduced/congenital absence, LM1 deflecting wrinkle, LM1 root number and LM2 cusp number. However, the lack of radiographic analysis precluded accurate observations of "present, but unerupted UM3s", so this feature was not included. Trait selection for the inter-regional MMD analysis was based on the availability of published data with similar dichotomized breakpoints.

Intra-observer Error

Intra-observer concordance for the 21 dental traits was assessed by rescoring 30 (five per sample) of the 340 individuals originally examined. Scoring sessions were separated by five months. This analysis was performed by AO according to Nichol and Turner's (1986) recommendations. The percentage of disagreements (of any magnitude) between the two scoring sessions was 4.6%. The percentage of disagreements of two or more grades between the first and second sessions was 0.3%. Finally, the percentage of cases where traits after dichotomization would have been scored as "present" in one session and "absent" in the other was 1.9%. All these values are similar to those reported by Nichol and Tuner (1986).

RESULTS

Trait frequencies of early South Americans: Do they all follow the Sinodont pattern?

Frequency comparisons of 21 discrete dental traits in six South American populations are summarized in Table 2. Examples of these traits in South American upper dentitions are provided in Figure 2. All samples are characterized by relatively high frequencies of UM1 enamel extension, LM1 deflecting wrinkle and LM1 cusp 6 (except for PSH), as well as low frequencies of UP3-UP4 odontome, UM1 cusp 5 and LM2 Y-groove pattern. They also show low to intermediate frequencies of LM1 cusp 7. Frequencies of occurrence of these traits fall within the range of variation of Sinodont populations (Turner, 1987, 1990; Scott and Turner, 1997). Furthermore, in accordance with the Sinodont dental pattern, South Americans exhibit high frequencies of UI1 shoveling, with the exception of PSH and BOL, whose intermediate frequencies of UI1 shoveling more closely approximate those of Jomonese and Ainu populations (Turner, 1987, 1990). While the incidence of UI1 double-shoveling is also high in the PNC, PAA and CHI samples, PSH, BOL and VEN have more Sundadont-like frequencies of occurrence of this trait. Moreover, except for BOL, all samples show high frequencies of four-cusped LM2 (or hypoconulid absence). The absence of the hypoconulid on LM2 is more common in Sundadont than in Sinodont populations (Turner, 1990). In general, there is a broad range of overlap between Sinodonts and Sundadonts regarding the incidence of multi-rooted UP3. The PSH, PNC and BOL samples exhibit intermediate frequencies of this feature, falling within this range of overlap. In contrast, multi-rooted UP3 does not frequently occur in CHI and VEN, and thus they more closely align with Sinodonts.

Except for BOL, all samples show intermediate to high frequencies of UM1 Carabelli's trait. This is surprising not only because trait presence was limited to grades 3-7 (as opposed to Turner's [1987] dichotomizing breakpoint of grades 2-7), but also

TABLE 2. Frequency (in %) and sample size (n) of 21 dental traits in six South American populations

Trait (with expression dichotomy in parentheses)	PSH		PNC		PAA		CHI		VEN		BOL	
	%	n	%	n	%	n	%	n	%	n	%	n
Winging UI1 (+ = ASU 1)	21.4	14	0.0	18	19.4	36	10.0	20	33.3	3	30.0	10
Shoveling UI1 (+ = ASU 2-6)	40.0	10	92.9	14	59.4	32	60.0	10	83.3	6	40.0	5
Double Shoveling UI1 (+ = ASU 2-6)	10.0	10	53.8	13	35.1	37	50.0	12	16.7	6	14.3	7
Interruption Groove UI2 (+ = ASU +)	10.5	19	36.8	19	34.2	38	9.1	22	0.0	5	22.2	18
Tuberculum Dentale UI2 (+ = ASU 2-6)	35.0	20	21.1	19	21.6	37	10.0	20	20.0	5	15.8	19
Distal accessory ridge UC (+ = ASU 2-5)	22.2	18	50.0	10	28.6	28	25.0	8	25.0	4	7.7	26
Odontome UP3-UP4 (+ = ASU 1)	0.0	29	5.9	17	1.9	52	0.0	10	0.0	11	6.3	48
Root number UP3 (+ = ASU 2+)	26.3	19	28.6	14	-[‡]	-[‡]	16.7	6	0.0	6	37.5	48
Hypocone UM2 (+ = ASU 2-5)	91.7	36	90.0	20	79.1	43	100.0	16	88.9	9	93.2	73
Cusp 5 UM1 (+ = ASU 1-5)	0.0	40	6.3	16	3.8	52	7.7	13	0.0	8	7.4	54
Carabelli's trait UM1 (+ = ASU 3-7)	22.6	31	50.0	12	34.0	47	62.5	8	69.2	13	12.5	48
Parastyle UM3 (+ = ASU 1-5)	4.0	25	15.4	13	14.3	21	7.1	14	0.0	6	0.0	38
Enamel extension UM1 (+ = ASU 2-3)	48.7	39	66.7	15	40.0	50	45.0	20	36.4	11	32.4	37
Anterior fovea LM1 (+ = ASU 2-4)	11.1	9	11.1	9	27.3	33	33.3	3	42.9	7	50.0	4
Groove pattern LM2 (+ = ASU Y)	16.7	18	7.1	14	14.6	48	16.7	18	9.1	11	6.3	16
Cusp number LM1 (+ = ASU 6+)	11.8	17	46.7	15	29.5	44	75.0	8	46.7	15	60.0	5
Cusp number LM2 (+ = ASU 4)	57.1	14	30.0	10	35.7	42	23.1	13	44.4	9	0.0	9
Deflecting wrinkle LM1 (+ = ASU 2-3)	22.2	9	30.0	10	41.9	31	25.0	4	42.9	7	50.0	4
C1-C2 crest LM1 (+ = ASU 1)	33.3	12	0.0	10	42.9	35	16.7	6	11.1	9	28.6	7
Protostylid LM1 (+ = ASU 2-6)	0.0	18	0.0	15	11.8	51	0.0	8	6.3	16	0.0	10
Cusp 7 LM1 (+ = ASU 1-4)	6.3	16	6.3	16	13.5	52	12.5	8	22.2	18	14.3	7

[‡] Data not available for study

because similar levels of occurrence have been associated with European and African populations (Scott and Turner, 1997). Moreover, frequencies of LM1 protostylid are remarkably low in all South American groups examined. However, this can be attributed to the fact that, to avoid misleading assessments due to the presence of pit-like caries on the buccal groove, I did not include the ASUDAS grade 1 as part of the protostylid complex. Although Turner (1971) found the high incidence of three-rooted LM1 to be a distinctive Sinodont feature, this trait was invariably absent in all samples studied. These latter results, however, could be biased given that only loose molars or root sockets lacking teeth were recorded (i.e., no radiographic analysis was conducted).

Mean measure of divergence intra-regional analysis

Pair-wise comparisons for the six South American samples using the MMD statistical program are presented in Table 3. MMD values range from 0 to 0.229, with a mean of 0.054. In general, there are significant dental affinities among most of the samples examined, especially in PNC, CHI and VEN. The intra-regional analysis also suggests that, within the South American region, the most divergent group is PSH (and BOL in a lesser degree). The highest dental phenetic divergence was found between PNC vs. BOL (MMD = 0.229). Interestingly, PNC vs. PSH and PNC vs. PAA pair-wise comparisons also show significantly high MMD values (MMD = 0.18 and 0.089, respectively). This was not expected since these three populations (i.e., PSH, PNC and PAA) came from the same country. They were geographically closest to each other relative to the VEN, BOL and CHI samples.

Mean measure of divergence inter-regional analysis

The present study also used the MMD to determine the degree of biological relatedness of early South Americans with several world popula-

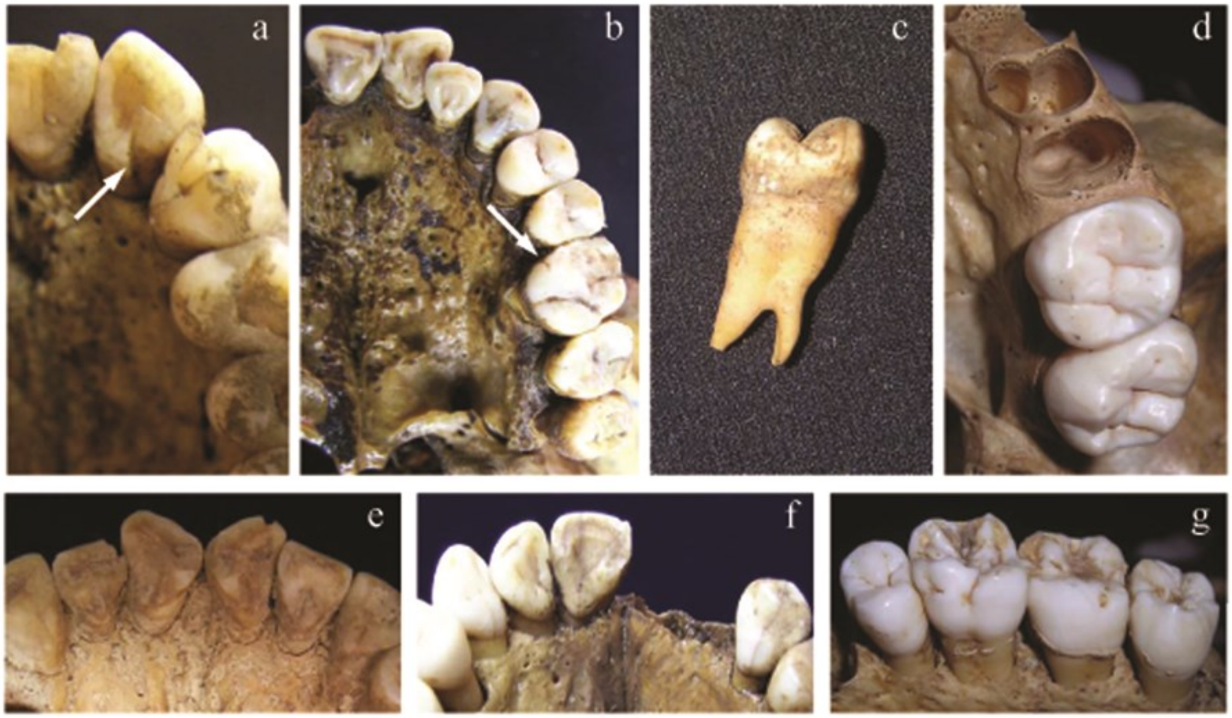

Fig. 2. Examples of morphological traits present in South American upper dentitions. (a) UI2 interruption groove (indicated by a white arrow); (b) UI1-UI2 shoveling, UI1-UC *tuberculum dentale* and UM1 Carabelli's trait (indicated by a white arrow); (c) two-rooted UP3; (d) tooth socket indicating the presence of a two-rooted UP3 (tooth itself is not seen); (e) UI1 winging; (f) UI1 shoveling; (g) UM1 Carabelli's trait. Left side depicted for figures (a-d) and (g).

TABLE 3. Mean Measure of Divergence (MMD) for six South American samples based on 20 dental traits[1]

	PSH	PNC	PAA	CHI	VEN	BOL
PSH	-					
PNC	0.177*	-				
PAA	0.021	0.089	-			
CHI	0.080	0.000	0.012	-		
VEN	0.000	0.035	0.000	0.000	-	
BOL	0.100	0.229	0.055	0.000	0.013	-

* Underlined MMD values are significant at $p \leq 0.025$

ł Root number UP3 not included in MMD analysis as data were not available for PAA (see Table 2)

tions exhibiting either the Sinodont or Sundadont dental pattern. The dental traits and breakpoints are summarized in Table 4. The distance matrix based on MMD values is presented in Table 5. Examination of Table 5, and its comparison with data from Table 3, indicates that trait choice does, in some cases, influence suggested affinities between groups derived from the MMD analysis. Based on the 12 dental traits listed in Table 4, the highest divergence within South American populations is between PSH vs. CHI (MMD = 0.190; the former MMD value based on 20 dental features was 0.080). Likewise, phenetic affinities between PNC vs. PAA, PNC vs. BOL and PAA vs. CHI have become either significantly higher or lower relative to those based on the 20-trait MMD analysis. On the other hand, PNC, CHI and VEN remain dentally closest regardless of the number of traits used for testing relationships among groups.

Comparisons among other world populations reveal that PNC, CHI and VEN exhibit the closest affinities with Northern China. Paradoxically, the PAA sample shows significantly low MMD values with both Northern China and Southeast Asia (MMD = 0.084 and 0.089, respectively). Likewise, although the MMD inter-regional analysis indicates that BOL is dentally closest to Northeast Siberia (MMD = 0.037), it also appears to be dentally similar to Southeast Asia (MMD = 0.063) and, to as lesser extent, to Northern China (MMD = 0.075). All these values are, however, statistically non-significant. Interestingly, PSH is the only of the six South American groups examined in this study that clearly shows the closest relationship with Southeast Asians (MMD = 0.094). Table 5 shows that, except for PSH, the highest divergence between South Americans and the other six world populations included in the MMD analysis is with pre-Hispanic Mexico. The degree of discordance of pre-Hispanic Mexico and South America is particularly high in the case of CHI, VEN and BOL.

This high degree of divergence is greater than would be expected if they share a recent common ancestor. However, it should be noted that relatively similar MMD values were observed for pairwise comparisons between Mexico and the other world populations. Thus, the unusual degree of divergence found between the

TABLE 4. Dental traits used in the inter-regional analysis

Trait	Expression dichotomy
Shoveling UI1	ASU 0-6 / (+) = ASU 2-6
Double Shoveling UI1	ASU 0-6 / (+) = ASU 2-6
Odontome UP3-UP4	ASU 0-1 / (+) = ASU 1
Hypocone UM2	ASU 0-5 / (+) = ASU 2-5
Cusp 5 UM1	ASU 0-5 / (+) = ASU 1-5
Carabelli's trait UM1	ASU 0-7 / (+) = ASU 2-7
Enamel extension UM1	ASU 0-3 / (+) = ASU 2-3
Groove pattern LM2	ASU Y, X, + / (+) = ASU Y
Cusp number LM1	ASU 0-6 / (+) = ASU 6
Cusp number LM2	ASU 0-6 / (+) = ASU 4
Deflecting wrinkle LM1	ASU 0-3 / (+) = ASU 1-3
Cusp 7 LM1	ASU 0-4 / (+) = ASU 1-4

South American and Mesoamerican samples may be an artifact of inter-observer error.

DISCUSSION AND CONCLUSIONS

This study characterized early South American dental morphology through the analysis of six pre- or proto-Hispanic Andean groups. Interestingly, although the importance of discrete dental traits for reconstructing human population history is widely acknowledged, a comprehensive study of dental variation in a broad geographical distribution of South American populations has not yet been undertaken. Most investigations have focused on North America, while research on South America has been scarce and narrow in scope (Goaz and Miller, 1966; Kieser and Preston, 1981; Turner and Bird, 1981; Sutter, 2005; Sutter and Verano, 2007). An accurate reconstruction of early human dispersal to the New World relies on the analysis of archaeological samples without presumed European admixture. This, however, is not an easy task, as the study of archaeological material usually precludes the incorporation of big sample sizes. Bad preservation, *post mortem* damage and excessive dental wear are additional problems faced by dental anthropologists interested in population history reconstructions. Although with these caveats in mind, this study represents an initial step towards the better understanding of the origins and biological affinities of early South Americans.

Examination of the pair-wise comparisons of the South American samples used in this study indicated a mean MMD of 0.054. This value is remarkably similar to that found by Turner (1984) for Native North American populations (mean MMD = 0.051). Turner (1986) argued that dental morphological variation should be greater where human groups have lived the longest period of time. Although bigger sample sizes are needed in order to draw stronger conclusions, the similar levels of variation found within both North and South America would suggest a rapid occupation of the continent by the first American inhabitants. The PNC, CHI and VEN samples appear to be dentally similar, with trait frequencies closely resembling those of major Sinodont populations. The inter-regional analysis indicates that these three samples show greatest affinities with Northern China. On the other hand, PSH is the most divergent of the South American groups examined. Interestingly, trait frequencies of this group more closely approximate those of Sundadont populations from Southeast Asia. Frequencies of occurrence of the majority of BOL and PAA dental traits occupy an intermediate position within the range of overlap of the Sinodonty-Sundadonty dichotomy. In this context, although some dental homogeneity was found among PNC, CHI and VEN, the ambiguous position of BOL and PAA does not provide enough evidence to support or reject hypothesis 1. However, the results of this investigation would falsify hypothesis 2, as South American populations do not necessarily follow the Sinodont dental pattern suggested by Turner (1986) and Greenberg et al. (1986) for all Native Americans and modern Northeast Asians. Although reported data were not big enough to directly contribute to the one-wave vs. multi-wave model conundrum, the results of this study are consistent with those derived from analyses of craniofacial variation among different world human populations (Lahr, 1995; González-José et al., 2008; Hubbe et al., 2011). These studies suggested that the appearance of the derived features present in modern Northeast Asians was a relatively recent event (*ca.* 7000 B.P.) and that the first migrants would have brought with them to the New World a more generalized and heterogeneous set of craniofacial and dental features (*contra* Turner, 1986, 1990; Greenberg et al., 1986). The fact that Native Americans do not necessarily follow a strict Sinodont dental pattern was also found by Haydenblit's (1996) analysis of four pre-Hispanic Mexican populations.

Finally, the greatest similarity of PNC, CHI and VEN dentitions compared to the other South American groups was somewhat unexpected given the relatively ample geographic distances existing among these populations. Interestingly, all three (i.e., PNC, CHI and VEN) are derived from lowland and/or coastal regions. Furthermore, it was surprising to find that some of the highest degrees of dental divergence are between Peruvian-derived populations (PNC vs. PSH and PNCvs. PAA; see Table 3). As noted, the most variable populations (those whose trait frequencies cannot always be accommodated under the Sinodont pattern) are PSH, PAA and BOL. In contrast to PNC, CHI and VEN, the PSH, PAA and BOL samples are from very high altitude regions between ca.

TABLE 5. *Mean Measure of Divergence (MMD) for South American and non-South American samples based on 12 dental traits.*

	PSH	PNC	PAA	CHI	VEN	BOL	MEX[†]	N America[‡]	ESK[‖]	NE Siberia[‡]	N China[₱]	SE Asia[¶]
PSH	-											
PNC	0.177*	-										
PAA	0.022	0.039	-									
CHI	0.190	0.000	0.105	-								
VEN	0.002	0.000	0.000	0.000	-							
BOL	0.141	0.115	0.050	0.000	0.018	-						
MEX	0.243	0.273	0.190	0.456	0.413	0.509	-					
N America	0.410	0.077	0.191	0.176	0.195	0.173	0.576	-				
ESK	0.349	0.143	0.124	0.249	0.238	0.090	0.488	0.057	-			
NE Siberia	0.240	0.215	0.123	0.298	0.178	0.037	0.559	0.165	0.087	-		
N China	0.220	0.037	0.084	0.160	0.088	0.075	0.396	0.102	0.080	0.121	-	
SE Asia	0.094	0.252	0.089	0.203	0.143	0.063	0.370	0.339	0.216	0.209	0.146	-

* Underlined MMD values are significant at $p \leq 0.025$

[†] MEX: pre-Hispanic Mexico. Data from Turner (1984) and Haydenblit (1996)

[†] N America: North American Indians, excluding Na-Dene speakers. Data from Turner (1984, 1986)

[‖] ESK: Eskimo (Inuit populations). Data from Turner (1984, 1986)

[‡] NE Siberia: Northeast Siberia. Data from Turner (1984, 1987, 1990)

[₱] N China: North China-Mongolia. Data from Turner (1984, 1987, 1990)

[¶] SE Asia: Southeast Asia. Data from Turner (1984, 1987, 1990)

3,000 and 3,800 meters above the sea level). This suggests that, regardless of geographic distance, the observed pattern of dental variation may be the result of different rates of gene flow and genetic drift operating in the lowlands and highlands. Thus, while lowland and coastal regions would have favored high rates of gene flow among populations living in those areas, genetic drift would have played an important role in shaping the pattern of diversity present in highland populations. The debate of the initial peopling of the New World is far from being resolved, and many questions remain to be answered. Nevertheless, this study demonstrated that neither the Clovis-first nor the three-wave models for the settlement of the Americas by a highly specialized Sinodont-Mongoloid human group is sufficient to encompass the pattern of dental morphological diversity present across the continent. To move forward past hypotheses need to be reevaluated through systematic and interdisciplinary studies. This study showed that dental morphology is a key area of research towards the accomplishment of these goals.

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LITERATURE CITED

Adovasio JM, Pedler DR, Donahue J, Stuckenrath R. 1998. Two decades of debate on Meadowcroft Rockshelter. North Am Archaeol 19: 317-341.

Bandelier AF. 1904. Trephining in Bolivia. Am Anthropol 6: 440-446.

Bandelier AF. 1910. The islands of Titicaca and Koati. New York: The Hispanic Society of America.

Baume RM, Crawford MH. 1978. Discrete dental traits in four Tlaxcaltecan Mexican populations. Am J Phys Anthropol 49: 351-360.

Bennett WC. 1937. Excavations at La Mata, Maracay, Venezuela. New York: American Museum of Natural History.

Berry AC, Berry RJ. 1967. Epigenetic variation in the human cranium. J Anat 101: 361-379.

Bird JB. 1985. The preceramic excavations at the Huaca Prieta Chicama valley, Peru. New York: American Museum of Natural History.

Bird JB. 2006. Excavaciones en el norte de Chile. Santiago de Chile: Universidad Bolivariana.

Bonatto SL, Salzano FM. 1997. A single and early migration for the peopling of the Americas supported by mitochondrial DNA sequence data. Proc Natl Acad Sci 94: 1866–1871.

Dahlberg AA. 1945. The changing dentition of man. J Am Dent Assoc 32: 676-690.

Dahlberg AA. 1951. The dentition of the American Indian. In: Laughlin T, editor. The physical anthropology of the American Indian. New York: Viking Fund. p 138-176.

Dahlberg AA. 1963. Analysis of the American Indian dentition. In: Brothwell DR, editor. Dental anthropology. New York: Pergamon. p 149-177.

Dillehay TD. 1997. Monte Verde: A late Pleistocene settlement in Chile, vol. 2. The archaeological context and interpretation. Washington, DC: Smithsonian Institution Press.

Dillehay TD. 1999. The late Pleistocene cultures of South America. Evol Anthropol 7: 206-216.

Dillehay TD. 2000. The settlement of the Americas: A new prehistory. New York: Basic Books.

Dillehay TD. 2009. Probing deeper into first American studies. Proc Natl Acad Sci 106: 971-978.

Fagundes NJR, Kanitz R, Eckert R, Valls ACS, Bogo MR, Salzano FM, Smith DG, Silva-Jr WA, Zago MA, Ribeiro-dos-Santos AK, Santos SEB, Petzl-Erler ML, Bonatto SL. 2008a. Mitochondrial population genomics supports a single pre-Clovis origin with a coastal route for the peopling of the Americas. Am J Hum Genet 82: 583-592.

Fagundes NJR, Kanitz R, Bonatto SL. 2008b. A reevaluation of the Native American mtDNA genome diversity and its bearing on the models of early colonization of Beringia. PLoS ONE 3: e3157.

Goaz P, Miller M. 1966. A preliminary description of the dental morphology of the Peruvian Indian. J Dent Res 45: 106-119.

Goodyear AC. 2005. Evidence for pre-Clovis sites in the eastern United States. In: Bonnichsen R, Lepper BT, Stanford D, Waters MR, editors. Paleoamerican origins: Beyond Clovis. Texas: Texas A&M University Press. p 103-112.

Goebel T, Waters MR, O'Rourke DH. 2008. The late Pleistocene dispersal of modern humans in the Americas. Science 319: 1497-1502.

González-José R, Bortolini MC, Santos FR, Bonatto SL. 2008. The peopling of America: Craniofacial shape variation on a continental scale and its interpretation from an interdisciplinary view. Am J Phys Anthropol 137: 175–187.

Greenberg JH, Turner CG II, Zegura S. 1986. The settlement of the Americas: A comparison of the linguistic, dental and genetic evidence. Curr Anthropol 24: 477-497.

Hanihara T. 1992. Dental and cranial affinities among populations of East Asia and the Pacific: the basic populations in East Asia, IV. Am J Phys Anthropol 88: 163-182.

Hanihara T. 2008. Morphological variation of major human populations based on nonmetric dental traits. Am J Phys Anthropol 136: 169-182.

Harris EF, Sjøvold T. 2004. Calculation of Smith's mean measure of divergence for intergroup comparisons using nonmetric data. Dent Anthropol 17: 83-93.

Haydenblit R. 1996. Dental variation among four pre-Hispanic Mexican populations. Am J Phys Anthropol 100: 225-246.

Hoshower LM, Buikstra JE, Goldstein PS, Webster AD. 1995. Artificial cranial deformation at the Omo M10 site: A Tiwanaku complex from Moquegua Valley, Peru. Latin American Antiquity 6: 145-164.

Hubbe M, Harvati K, Neves W. 2011. Paleoamerican morphology in the context of European and East Asian late Pleistocene variation: implica tions for human dispersion into de New World. Am J Phys Anthropol 144: 442–453.

Imbelloni J. 1925. Deformaciones intencionales del craneo en Sud America. Rev Museo de la Plata XXVIII: 329-407.

Irish JD. 1993. Biological affinities of Late Pleistocene through modern African aboriginal populations: the dental evidence. Ph.D. dissertation. Tempe: Arizona State University.

Irish JD. 1997. Characteristic high- and low-frequency dental traits in sub-Saharan African populations. Am J Phys Anthropol 102: 455–467.

Irish JD. 2010. The mean measure of divergence: its utility in model-free and model-bound analyses relative to the Mahalanobis *D2* distance for nonmetric traits. Am J Hum Biol 22: 378-395.

Kieser JA, Preston CB. 1981. The dentition of the Lengua Indians of Paraguay. Am J Phys Anthro pol 55: 485-490.

Lahr MM. 1995. Patterns of human diversification: implication for Amerindian origins. Yrbk Phys Anthropol 38: 163-198.

Lynch TF. 1983. The Paleoindians. In: Jennings J, editor. Ancient South Americans. New York: WH Freeman. p 87–137.

Martin PS. 1973. The discovery of America. Science 179: 969-974.

Meltzer DJ. 2004. Peopling of North America. In: Gillespie A, Porter SC, Atwater B, editors. The Quaternary Period in the United States. New York: Elsevier Science. p 539–563.

Moorrees CFA. 1957. The Aleut dentition. Cambridge: Harvard University Press.

Munizaga JR. 1987. Deformación craneana intencional en América. Rev Chilena de Antropologia 6: 113-147.

Neves WA, Prous A, González-José R, Kipnis R, Powell J. 2003. Early Holocene human skeletal remains from Santana do Riacho, Brazil: implycations for the settlement of the New World. J Hum Evol 45: 759–782.

Neves WA, Hubbe M. 2005. Cranial morphology of early Americans from Lagoa Santa, Brazil: Implications for the settlement of the New World. Proc Natl Acad Sci 102: 18309-18314.

Nichol CR, Turner CG II. 1986. Intra- and interobserver concordance in classifying dental mor phology. Am J Phys Anthropol 69: 299-315.

Pitulko VV, Nikolsky PA, Girya EY, Basilyan AE, TumskoyVE, Koulakov SA, Astakhov SN, Pavlova EY, Anisimov MA. 2004. TheYana RHS site: humans in the Arctic before the last glacial maximum. Science 303: 52–56.

Powell JF, Neves WA. 1999. Craniofacial morphology of the first Americans: pattern and process in the peopling of the New World. Yrbk Phys Anthropol 42: 153–188.

Pucciarelli HM, Sardi ML, Jimenez Lopez JC, Serrano C. 2003. Early peopling and evolutionary diversification in America. Quat Int 109: 123-132.

Schjellerup I. 1997. Incas and Spaniards in the conquest of Chachapoyas. Archaeological and ethnohistorical research in the northeastern Andes of Peru. Goteborg: Goteborg University.

Schurr TG. 2004. The peopling of the New World: Perspectives from molecular anthropology. Ann Rev Anthropol 33: 551-583.

Scott GR, Turner CG II. 1997. The anthropology of modern human teeth: dental morphology and its variation in recent human populations. Cambridge: Cambridge University Press.

Scott GR, Potter RHY, Noss JF, Dahlberg AA, Dahlberg TA. 1983. The dental morphology of Pima Indians. Am J Phys Anthropol 61: 13-31.

Sjøvold T. 1977. Non-metrical divergence between skeletal populations: the theoretical foundation and biological importance of C.A.B. Smith's mean measure of divergence. Ossa Suppl 4: 1-133.

Sofaer JA, Niswander JD, MacLean CJ. 1972. Popu lation studies on the southwestern Indian tribes. V. Tooth morphology as an indicator of biological distance. Am J Phys Anthropol 37: 357-366.

Sutter RC. 2005. The prehistoric peopling of South America as inferred from genetically controlled dental traits. Andean Past 7: 183-217.

Sutter RC, Verano JW. 2007. Biodistance analysis of the Moche sacrificial victims from Huaca de la Luna Plaza 3C: A matrix method test of their origins. Am J Phys Anthropol 132: 193-206.

Tamm E, Kivisild T, Reidla M, Metspalu M, Smith DG, Mulligan CJ, Bravi CM, Rickards O, Martinez-Labarga C, Khusnutdinova EK, Fedorova SA, Golubenko MV, Stepanov VA, Gubina MA, Zhadanov SI, Ossipova LP, Damba L, Voevoda MI, Dipierri JE, Villems R, Malhi RS. 2007. Beringian standstill and spread of Native American founders. PLoS ONE 2: e829.

Tommaseo M, Drusini A. 1984. Physical anthropology of two tribal groups of Amazonic Peru (with reference to artificial cranial deformation). Zeitschrift für Morphologie und Anthropologie 74: 315-333.

Turner CG II. 1971. Three-rooted mandibular first permanent molars and the question of the American Indian origins. Am J Phys Anthropol 34: 229-242.

Turner CG II. 1983. Dental evidence for the peopling of the Americas. In: Shutler R, editor. Early man in the New World. California: Sage Publications. p 147-157.

Turner CG II. 1984. Advances in the dental search for Native American origins. Acta Anthopogenetica 8: 23-78.

Turner CG II. 1986. The first Americans: the dental evidence. Natl Geog Res 2: 37-46.

Turner CG II. 1987. Late Pleistocene and Holocene population history of East Asia based on dental variation. Am J Phys Anthropol 73: 305-321.

Turner CG II. 1990. Major features of sundadonty and sinodonty, including some suggestions about East Asian microevolution, population history, and late Pleistocene relationships with Australian Aboriginals. Am J Phys Anthropol 82: 295-317.

Turner CG II. 1993. Southwest Indians: Prehistory through dentition. Natl Geog Res Expl 9: 32-53.

Turner CG II, Scott GR. 1977. Dentition of the Easter islanders. In: Dahlberg AA, Graber TM, editors. Orofacial Growth and Development. The Hague: Mouton. p 229-249.

Turner CG II, Bird J. 1981. Dentition of Chilean Paleo-Indians and peopling of the Americas. Science 212: 1053-1055.

Turner CG II, Nichol CR, Scout GR. 1991. Scoring procedures for key morphological traits of the permanent dentition. The Arizona State Univer sity Dental Anthropology System. In: Kelley MA, Larsen CS, editors. Advances in Dental Anthropology. New York: Willey Liss. P 13-31.

Wang S, Lewis CM, Jakobsson M, Ramachandran S, Ray N, Bedoya G, Rojas W, Parra MV, Molina JA, Gallo C, Mazzotti G, Poletti G, Hill K, Hurtado AM, Labuda D, Klitz W, Barrantes R, Bortolini MC, Salzano FM, Petzl-Erler ML, Tsuneto LT, Llop E, Rothhammer F, Excoffier L, Feldman MW, Rosenberg NA, Ruiz-Linares A. 2007. Genetic variation and population structure in Native Americans. PLoS Genet 3: 2049-2067.

Weiss P. 1961. Osteologia cultural, practicas cefalicas. Anales de la Facultad de Medicina 2: 133-276.

Zegura SL, Karafet TM, Zhivotovsky LA, Hammer MF. 2004. High-resolution SNPs and microsatellite haplotypes point to a single, recent entry of Native American Y chromosomes into the Americas. Mol Biol Evol 21: 164–175.

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