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## Sinodonty, Sundadonty, and the Beringian Standstill model: Issues of timing and migrations into the New World

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### ABSTRACT

C.G. Turner II made dental morphological observations on thousands of Eskimo-Aleuts and American Indians and concluded they were derived from ancestral populations in northeast Asia during the last stages of the Pleistocene. He further distinguished two dental patterns in Asia. In East Asia, populations exhibit Sinodonty, a specialized dentition with intensified trait expressions. Southeast Asians exhibit Sundadonty, a more generalized dentition for crown and root traits. Turner argued all New World groups were derived from Sinodonts. Recent work has led some researchers to conclude there is evidence for the Sundadont pattern in Native American populations, an observation in accord with craniometric research that argues for an early migration of a generalized Asian population, followed by an influx of more specialized northeast Asians. A reanalysis of Turner's dataset fails to reveal evidence for a Sundadont component in the settlement of the Americas, but it does provide support for the Beringian Standstill model proposed by geneticists.

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### 1. Introduction

Since the European “discovery” of the New World, armchair historians and researchers have addressed the issue of the geographic source and timing of entry for the peopling of the Americas. The overwhelming consensus is that populations from northeast Asia migrated across a landmass that bridged Asia and North America during the late Pleistocene (cf. many papers in [Count, 1950](#); [Hopkins, 1967](#)). During the past three decades, fine-tuned studies of nuclear genetic markers, mtDNA and Y chromosome haplogroups, craniometrics, and tooth morphology arrived at some points of consilience, but there remain a number of disagreements on the who, where, how, when, and number of source populations ancestral to Native Americans.

Tied in part to the discovery of the 30,000 year old Yana RHS site found well above the Arctic Circle (latitude 71°) ([Pitulko et al., 2004](#)), geneticists have developed a model that may help resolve some of the major issues regarding the timing of settlement and

biological variation among Native American populations. First elaborated by [Tamm et al. \(2007\)](#), the “Beringian Standstill Model” proposes Upper Paleolithic hunter–gatherer populations in East Asia dispersed into the far north 30,000+ years ago, with subsequent dispersal across Beringia stalled by formidable ice sheets, coastal glaciers, and other environmental constraints ([Hoffecker et al., 2016](#)). This model provides the geographic and temporal isolation of “proto” Native Americans from the basal ancestral populations from lower latitudes in East Asia. Around the time of the Last Glacial Maximum (ca. 15–20 thousand years ago), environmental conditions improved to the point where elements of the standstill population could finally disperse into the southerly reaches of North America and eventually South America.

Although genetics has contributed significantly to refining models for the initial settlement of the Americas, summarizing the enormous literature in this field is beyond the scope of this paper. Our focus is on how craniometric and tooth morphology data are employed to address, in particular, the source populations for New World groups.

#### 1.1. Craniometrics and the peopling of the New World

Much recent craniometric research (e.g., [Neves et al., 1999a,b](#); [González-José et al., 2001](#)) concerning the peopling of the New

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World has concentrated on refuting the Three-Migration Model (TMM), proposed by Turner (1983a) and refined by Greenberg et al. (1986). The model identifies three migratory waves (Amerind, Na-Dene, and Aleut-Eskimo) that entered the New World from Siberia, through the Bering Sea region. Based in large part on inferences made from population frequencies of dental traits, the model has come under fire from craniometricians who argue it does not account for the morphological diversity in prehistoric and extant New World populations.

The craniometric arguments against the TMM are based on four observations: 1) ancient and recent New World populations differ in cranial morphology; 2) recent east Asian and New World populations resemble each other in cranial morphology; 3) the earliest New World populations resemble modern Australians and Africans in cranial morphology (see Neves et al., 2003); and 4) the shift in morphology appears to have been relatively sudden and may have been accompanied by a shift in material culture associated with subsistence (Neves et al., 1999a,b; Neves and Hubbe, 2005).

Cranial vault form and robusticity are paramount to the argument against the TMM. The generally long, low, dolichocephalic form and robust size ubiquitous among the crania of the earliest known people in the New World differs markedly from the so-called “Mongoloid” cranial complex, with the brachycephalic suite of traits found in late Holocene New World and Northeast Asian populations (Neves et al., 1996). To those who oppose the TMM, the tendency in principal components analyses (PCA) of the earliest known New World crania to cluster with South Pacific populations rather than Northeast Asians and modern Native Americans, is inferred to indicate the existence of an earlier, possibly unrelated group representing the earliest colonists of the Americas (Neves et al., 1999a,b). This group is referred to variously as: Paleoindian (Neves et al., 2003); Paleoamerican (Jantz and Owsley, 1997); proto-Mongoloid (Lahr, 1995); or pre-Mongoloid (Neves et al., 1996). The term “Paleoamerican” is used by some to avoid the implication of an ancestor–descendant relationship between the earliest population and late Holocene and modern populations (Powell and Neves, 1999, pp. 165). Similarly, when referring to extra-continental affinities, Neves et al. (1996, pp. 127) prefer the term “pre-Mongoloid” to “proto-Mongoloid,” as there is no evidence the first inhabitants of the New World were directly related to the group that would give rise to the specialized suite of traits associated with the “Mongoloid” morphological complex.

## 1.2. Paleoindians and Paleoamericans?

The application of PCA to assess population affinity in Paleoindian samples began in earnest in the late 1980s. Neves and Pucciarelli (1989) analyzed 16 craniomorphic variables in three populations of Paleoindian and Early Archaic period individuals from South America. The sample was confined to individuals dated through a mix of radiometric and relative methods to between 12,000 and 6000 BP (presumably cal BP, although this is not specified). When the size and shape data of the samples were compared to those of Old World populations, they clustered closely with the Australo-Melanesian samples in W.W. Howells' dataset. The authors repeated the PCA after correcting for size, reaffirming the similarity between South American samples and populations from the South Pacific. The early samples moved to a position that fell between modern Australians and modern Northeast Asians. The authors pointed out it is unlikely South America was colonized from Australia, and that it is similarly unlikely that New World and Northeast Asian populations evolved on so closely convergent a path (Neves and Pucciarelli, 1989). Rather, they assert the most parsimonious explanation is the existence of a common ancestor

between the populations that colonized Australia and the New World.

Neves and Pucciarelli (1991) expanded on their previous research by incorporating three individuals from Zhoukoudian Upper Cave to their PCA. Their results demonstrated a morphological similarity between early South Americans, early Australians, and the individuals from Zhoukoudian, indicating East Asia as a potential location of a common ancestor between the two populations. More recently, many of these same authors used additional skeletal remains from South America dating to the early Holocene to strengthen these arguments (Neves et al., 2003, 2004; Hubbe et al., 2015).

Small sample sizes and large geographical and temporal ranges have hampered similar analyses in North America. Steele and Powell (1992, 1994) used eight measurements from four North American Paleoindian individuals in univariate and multivariate analyses to assess the degree of similarity with contemporary sample populations (Steele and Powell, 1999). Their analyses, while consisting of fewer measurements and smaller sample sizes than those of Neves and Pucciarelli (1989, 1991), produced a similar result. With the exception of the Browns Valley individual, which most closely resembles modern Native American populations, the North American Paleoindians “...differ from the central tendencies of the northern Asian and North American Indian populations and fall near the southern Asian and European populations” (Steele and Powell, 1992, pp. 324).

Neves et al. (1996) reanalyzed the data from the North American Paleoindian sample. They found the clustering with Southeast Asian and European populations was due to Steele and Powell (1992) using both shape and size data, rather than correcting for size as Neves and Pucciarelli (1989, 1991) had done in their analyses of South American samples. The reanalysis of the female series failed to show any consistent extra-continental affinity. As a potential explanation, the authors cite Howells' (1973, 1989) work showing that females, with their tendency towards gracility, show less geographically patterned affinity than the more robust males (Neves et al., 1996). The male North American Paleoindian series, when corrected for size, clusters with early Holocene populations from South America and the South Pacific. Neves et al. (1996, pp. 126) conclude: “... there is no reason to believe that South America was colonized by human groups that were not represented, contemporaneously, in North America...”

Given the distinctiveness of Paleoindian craniofacial morphology from that of later populations, and the seeming lack of a transitional phase between early dolichocephalic populations and later brachycephalic ones, Neves et al. (1999a,b) propose an alternate model of population movement. In this Two-Components Settlement (TC) model, the idea of a single Amerindian wave populating all of South America and most of North America is replaced by the concept of a brachycephalic component appearing in the New World shortly after the original dolichocephalic colonizing component (Neves et al., 1999a,b, pp. 163; González-José et al., 2001, pp. 159). Subsequent analyses of North American Paleoindian skeletons, including the Spirit Cave mummy (Jantz and Owsley, 1997) and the Wizards Beach individual (Steele and Powell, 1999), highlight the differences between early Holocene samples and populations of modern Native Americans. Furthermore, recent craniometric analysis that includes “Kennewick Man” strengthens the idea of an early, generalized, dolichocephalic form being indicative of a “circumpacific” population that moved along the Pacific Rim into the New World at the end of the Pleistocene (Jantz and Owsley, 2005; Jantz and Spradley, 2014). In South America, there was a significant shift in craniofacial morphology around 8000 cal BP. This shift was contemporaneous with the adoption of horticulture as a subsistence strategy and the associated changes in

material culture. Under the TC model, [Neves et al. \(1999a,b\)](#) explain this shift by invoking population replacement and assimilation.

[Neves et al. \(2007, pp. 1088\)](#) claim there is persistence of the generalized “Paleoamerican” morphology in the Sabana de Bogotá region of Colombia up to 3000 cal BP. The authors claim the exploitation of tubers starting around 5000 cal BP did not significantly alter cranial morphology, nor did the adoption of ceramic technology, an indication of more intensive food production, at 3200 cal BP. While claiming the introduction of tubers into the diet was a significant change in subsistence, it represented only a modest supplement to a predominantly hunter–gatherer diet. Furthermore, the introduction of ceramics at 3200 cal BP may not have accompanied an instant shift in craniofacial morphology, but it was followed soon after (3000 cal BP) by the disappearance of the “Paleoamerican” morphology at Sabana de Bogotá ([Neves et al., 2007, pp. 1088](#)). Rather than representing an argument against the role of adaptive phenotypic plasticity of the craniofacial region as summarized by [Larsen \(2015, pp. 260\)](#) in the conversation about the peopling of the New World, the presence of a morphologically generalized population late into the Holocene, ending shortly after the adoption of ceramic technology contradicts the assumption of population replacement of hunter–gatherers by agriculturalists.

The assumption of purely stochastic mechanisms driving differentiation in New World populations was a large part of the craniometric models with few exceptions (notably [Lahr, 1995](#)), and led to the rejection of an ancestor–descendant relationship between “Paleoamericans” and modern Amerindian populations due to the differences in cranial morphology. [González-José et al. \(2005\)](#) note the retention of plesiomorphic dolichocephaly in modern New World populations is another possibility. [Lahr \(1995\)](#) asserts populations of Patagonia and Tierra del Fuego on the far southern Pacific Coast (Puelche, Tehuelche, Ona, Yahgan, Alacaluf, and Chono) display a robusticity that departs from the typical “Mongoloid” morphology characteristic of Amerindians. Cluster analysis utilizing Howells’ data in comparison with Fuegian data collected by Lahr demonstrates a close similarity between the size and shape of Fuegian crania and that of South Pacific populations ([Lahr, 1995, pp. 185](#)). Similarly, the Pericú of Baja Mexico are located closest to the “Paleoamerican” series from Brazil on a PCA conducted by [González-José et al. \(2003\)](#) and are identified as potential evidence for “the survival of the Paleoamerican stock” ([González-José et al., 2005, pp. 773](#)). Ironically, an initial DNA analysis indicated a genetic relationship between the Pericú and the Maori of New Zealand; however, this result could not be replicated and all further analyses confirmed the relationship between the Pericú and modern New World populations, pointing to laboratory contamination as the cause of the first anomalous result ([Dalton, 2005](#)).

### 1.3. Dental morphology and the peopling of the New World

In 1967, Hanihara proposed the major “races” exhibited distinct dental morphological complexes. For the deciduous dentition, he noted five traits – u1 incisor shoveling, lm2 deflecting wrinkle, lm2<sup>1</sup> protostylid, lm2 cusp 7, and um2 cusp 5 – characterized the “Mongoloid” dental complex. Following the study of dozens of samples across Asia, the Pacific, and the New World, [Turner \(1983b, 1987, 1990\)](#) suggested there were two separate dental

morphological complexes in Asia: (1) Sinodonty, characteristic of Northeast Asian groups, and associated with derived, mass additive traits, and (2) Sundadonty, identified in Southeast Asian and Pacific populations, characterized by retained traits and a less complex dentition. [Turner \(1990\)](#) identified eight morphological features that distinguished the two dental patterns. Sinodont populations were characterized by high frequencies of U11 shoveling, U11 double shoveling, one-rooted UP1, UM1 enamel extensions, pegged/reduced/missing UM3, LM1 deflecting wrinkle, and 3-rooted LM1. Sundadont populations have significantly lower frequencies of these traits and a higher frequency of four-cusped LM2. In general, Sinodonty was characterized by intensification while Sundadonty was characterized by retention or simplification ([Turner, 1983b, 1987, 1990; Scott and Turner, 1997](#)).

[Turner \(1987, 1990, 1992\)](#) proposed the Sundadont dental complex developed *in situ* in Southeast Asia during the late Pleistocene, between 25,000 and 40,000 years BP ([Turner, 2006, pp. 456](#)). Since Sundadonty is less derived and was found at higher latitudes in the late Pleistocene (e.g., Jomon of Japan are Sundadonts), [Turner \(1987, 1990\)](#) suggested Sinodonty evolved out of this more generalized complex. The fact that Sundadonty has been observed in both mainland and island Southeast Asian samples suggests the complex was in place when these areas were connected by the Sunda shelf during the Pleistocene ([Turner, 1990](#)). Other authors suggest Sundadonty is a product of gene flow during the Neolithic between Northeast Asian populations possessing the Sinodont dental pattern and an indigenous Southeast Asian population that exhibited Australo-Melanesian dental characteristics ([Matsumura and Hudson, 2005; Matsumura and Oxenham, 2013](#)). Under this model, Sundadonty would be a recent development, obviating the possibility of any direct contribution to the settlement of the Americas.

For the sake of discussion, we assume Sundadont populations extended back in time to the late Pleistocene, allowing the possibility that early migrants to the New World were Sundadont rather than Sinodont. Assuming the Sundadont dental complex has a long history in Southeast Asia, this led some authors to suggest the complex is evident in Native Americans, including Paleoindians (e.g., [Lahr, 1995; Lahr and Haydenblit, 1995; Powell, 1995; Haydenblit, 1996; Sutter, 1997, 2005; Powell and Neves, 1998; Powell and Rose, 1999; Chatters, 2000](#)). Our primary goals are to evaluate the claim for Sundadonty in the New World and determine if dental morphology is consistent with the Beringian Standstill model.

## 2. Materials and methods

The authors have access to the large database on tooth crown and root morphology collected over three decades by the late C.G. Turner II. With over 100 samples from the New World, Asia, and the Pacific, it is possible to compare regional groups on a trait-by-trait basis and subject samples to multivariate biodistance analyses. The traits used in the analysis are described in detail, along with their breakpoints, in [Turner et al. \(1991\), Scott and Turner \(1997\), Scott \(2008\), and Scott et al. \(2016\)](#).

Four models have been developed that correspond to the contrasting viewpoints on New World source populations, as well as the timing and rate of movement of these populations. Each model generates an assumption of global population relationships based on its unique parameters. These models are presented here in conjunction with their assumptions regarding skeletal sample affinity. The models are: (1) Sinodont only, with all Native Americans exhibiting trait frequencies in line with East Asian populations (e.g., China, recent Japan, Siberia); (2) Beringian Standstill, where Native Americans differ from all Asian populations but exhibit relative uniformity within the New World; (3) Sinodont only plus Beringian

<sup>1</sup> Throughout this text the following abbreviations are used: L (lower), U (upper), I (incisor), C (canine), P (premolar), and M (molar). Molars, incisors, and premolars also have a number designating tooth position. Finally, lower case letters refer to deciduous teeth, whereas upper case letters refer to permanent teeth.

Standstill, where New World populations are distinct from Asians but are closer to East Asians than Southeast Asians; and (4) Sundadont early, followed by Sinodont, where trait frequencies of early New World groups are closer to Southeast Asians with later groups closer to East Asians. Two potential models, Sundadont only (New World populations closer to Southeast Asia than East Asia for all time periods) and Sundadont only plus Beringian Standstill (New World populations internally uniform and different from Asia but closer to Southeast Asia than East Asia) were not observed for any trait. A final possibility is that a dental trait shows no geographic patterning, which is often the case when frequencies are very low.

Because some authors point out specific traits are linked to either Sinodonty or Sundadonty, we constructed two tables with

different emphases. Table 1 shows regional variation for 24 crown and root traits without regard to time period. The mean trait frequencies are based on a total of 135 samples, with regional representation varying from 4 to 25 (note: of the 135 samples, many are composites of multiple samples, e.g., the Arkansas sample for North American Indians is comprised of skeletons from six different archaeological sites). Table 2 focuses on 20 traits in Asian and New World populations, with some areas represented by early and late periods (i.e., Southeast Asia, North America, South America). To characterize samples by region and time period, we used five large samples for each region/time to calculate mean trait frequencies. In four of 12 regions, k (number of samples) deviated from five due to insufficient samples.

**Table 1**  
Regional variation in crown and root trait frequencies (Sinodont/Sundadont traits bold faced).

| No. samples/trait     | k  | WING          | <b>SHOV</b> | <b>DSHOV</b> | INT GR | 3C UM2  | CARA      | CUSP 5 | EN EXT | <b>2RT UP1</b> | 3RT UM2 | UM3         | MLC LP2 |
|-----------------------|----|---------------|-------------|--------------|--------|---------|-----------|--------|--------|----------------|---------|-------------|---------|
| Breakpoint            |    | P             | 3+          | P            | P      | P       | 3+        | P      | P      | P              | P       | PRM         | 2+      |
| Eskimo-Aleut          | 9  | 0.227         | 0.714       | 0.476        | 0.624  | 0.270   | 0.074     | 0.176  | 0.431  | 0.058          | 0.376   | 0.239       | 0.396   |
| NaDene/NW Coast       | 5  | 0.360         | 0.833       | 0.517        | 0.661  | 0.150   | 0.174     | 0.253  | 0.500  | 0.076          | 0.426   | 0.151       | 0.510   |
| North American Indian | 25 | 0.420         | 0.871       | 0.765        | 0.571  | 0.128   | 0.195     | 0.175  | 0.404  | 0.149          | 0.529   | 0.145       | 0.328   |
| Mesoamerica           | 4  | 0.557         | 0.902       | 0.906        | 0.536  | 0.132   | 0.258     | 0.151  | 0.289  | 0.129          | 0.543   | 0.135       | 0.230   |
| South American Indian | 10 | 0.547         | 0.919       | 0.904        | 0.501  | 0.094   | 0.209     | 0.156  | 0.484  | 0.136          | 0.554   | 0.203       | 0.342   |
| Southeast Asia        | 17 | 0.230         | 0.421       | 0.284        | 0.322  | 0.101   | 0.310     | 0.246  | 0.325  | 0.373          | 0.752   | 0.213       | 0.782   |
| East Asia             | 15 | 0.254         | 0.531       | 0.350        | 0.413  | 0.146   | 0.210     | 0.191  | 0.415  | 0.256          | 0.644   | 0.397       | 0.700   |
| Australia             | 15 | 0.104         | 0.387       | 0.063        | 0.200  | 0.042   | 0.341     | 0.613  | 0.083  | 0.448          | 0.811   | 0.054       | 0.745   |
| New Guinea            | 8  | 0.140         | 0.040       | 0.046        | 0.146  | 0.049   | 0.370     | 0.622  | 0.046  | 0.272          | 0.550   | 0.068       | 0.611   |
| Polynesia             | 7  | 0.225         | 0.162       | 0.186        | 0.272  | 0.090   | 0.270     | 0.344  | 0.204  | 0.338          | 0.475   | 0.310       | 0.826   |
| Europe                | 11 | 0.106         | 0.001       | 0.240        | 0.379  | 0.242   | 0.391     | 0.152  | 0.035  | 0.478          | 0.596   | 0.165       | 0.633   |
| Central Asia          | 9  | 0.230         | 0.132       | 0.427        | 0.444  | 0.192   | 0.314     | 0.162  | 0.197  | 0.299          | 0.481   | 0.285       | 0.567   |
| No. samples/trait     | k  | <b>4C LM2</b> | GP LM2      | C6 LM1       | C7 LM1 | PRO LM1 | <b>DW</b> | DTC    | ODONT  | 2RT LC         | TOMES'  | <b>3RM1</b> | 2RT LM2 |
| Breakpoint            |    | 4             | Y           | P            | P      | 2+      | P         | P      | P      | P              | 3+      | P           | P       |
| Eskimo-Aleut          | 9  | 0.057         | 0.279       | 0.475        | 0.038  | 0.030   | 0.574     | 0.097  | 0.047  | 0.001          | 0.015   | 0.309       | 0.686   |
| NaDene/NW Coast       | 5  | 0.047         | 0.192       | 0.447        | 0.039  | 0.102   | 0.547     | 0.076  | 0.071  | 0.001          | 0.097   | 0.151       | 0.586   |
| North American Indian | 25 | 0.140         | 0.256       | 0.463        | 0.052  | 0.060   | 0.565     | 0.037  | 0.049  | 0.003          | 0.160   | 0.059       | 0.672   |
| Mesoamerica           | 4  | 0.065         | 0.284       | 0.562        | 0.101  | 0.037   | 0.560     | 0.006  | 0.053  | 0.017          | 0.239   | 0.047       | 0.693   |
| South American Indian | 10 | 0.088         | 0.183       | 0.568        | 0.057  | 0.039   | 0.691     | 0.05   | 0.059  | 0.008          | 0.091   | 0.055       | 0.602   |
| Southeast Asia        | 17 | 0.311         | 0.310       | 0.369        | 0.077  | 0.046   | 0.429     | 0.074  | 0.024  | 0.009          | 0.219   | 0.111       | 0.751   |
| East Asia             | 15 | 0.303         | 0.250       | 0.367        | 0.055  | 0.087   | 0.362     | 0.061  | 0.058  | 0.012          | 0.158   | 0.197       | 0.700   |
| Australia             | 15 | 0.096         | 0.257       | 0.645        | 0.048  | 0.015   | 0.388     | 0.048  | 0.035  | 0.001          | 0.287   | 0.055       | 0.932   |
| New Guinea            | 8  | 0.556         | 0.389       | 0.133        | 0.045  | 0.049   | 0.104     | 0.003  | 0.001  | 0.004          | 0.038   | 0.001       | 0.813   |
| Polynesia             | 7  | 0.331         | 0.284       | 0.589        | 0.032  | 0.083   | 0.289     | 0.072  | 0.015  | 0.005          | 0.163   | 0.090       | 0.691   |
| Europe                | 11 | 0.734         | 0.261       | 0.077        | 0.041  | 0.008   | 0.137     | 0.038  | 0.016  | 0.059          | 0.108   | 0.005       | 0.741   |
| Central Asia          | 9  | 0.589         | 0.211       | 0.153        | 0.064  | 0.014   | 0.320     | 0.066  | 0.011  | 0.029          | 0.139   | 0.072       | 0.643   |

**Table 2**  
Crown and root trait frequencies in New World and Asia with temporal component (Sinodont/Sundadont traits bold faced).

| No. samples/trait     | k | WING  | <b>SHOV</b> | <b>DSHOV</b> | 3C UM2 | CARA  | C5 UM1 | EN EXT | <b>2RT UP1</b> | 3RT UM2 | <b>PRM UM3</b> |
|-----------------------|---|-------|-------------|--------------|--------|-------|--------|--------|----------------|---------|----------------|
| Breakpoint            |   | P     | 3+          | P            | P      | 3+    | P      | P      | P              | P       | P              |
| Southeast Asia early  | 3 | 0.267 | 0.308       | 0.318        | 0.086  | 0.242 | 0.189  | 0.220  | 0.387          | 0.723   | 0.079          |
| Southeast Asia late   | 5 | 0.198 | 0.391       | 0.201        | 0.088  | 0.371 | 0.240  | 0.367  | 0.337          | 0.744   | 0.193          |
| East Asia             | 5 | 0.249 | 0.572       | 0.362        | 0.129  | 0.192 | 0.290  | 0.385  | 0.299          | 0.675   | 0.322          |
| North America early   | 2 | 0.277 | 0.829       | 0.723        | 0.073  | 0.428 | 0.411  | 0.501  | 0.106          | 0.533   | 0.031          |
| South America early   | 6 | 0.578 | 0.941       | 0.927        | 0.106  | 0.274 | 0.177  | 0.431  | 0.147          | 0.614   | 0.163          |
| Eskimo-Aleut          | 5 | 0.232 | 0.752       | 0.495        | 0.234  | 0.082 | 0.233  | 0.439  | 0.056          | 0.336   | 0.248          |
| NaDene/NW Coast       | 5 | 0.360 | 0.833       | 0.517        | 0.150  | 0.174 | 0.253  | 0.498  | 0.076          | 0.426   | 0.151          |
| North American Indian | 5 | 0.465 | 0.869       | 0.708        | 0.117  | 0.156 | 0.101  | 0.379  | 0.174          | 0.610   | 0.186          |
| Mesoamerican          | 4 | 0.557 | 0.902       | 0.906        | 0.132  | 0.258 | 0.151  | 0.289  | 0.129          | 0.543   | 0.135          |
| South American Indian | 5 | 0.545 | 0.912       | 0.880        | 0.097  | 0.182 | 0.115  | 0.536  | 0.110          | 0.475   | 0.249          |

Table 2 (continued)

| No. samples/trait    | k | WING  | SHOV    | DSHOV  | 3C UM2 | CARA   | C5 UM1 | EN EXT | 2RT UP1 | 3RT UM2 | PRM UM3 |
|----------------------|---|-------|---------|--------|--------|--------|--------|--------|---------|---------|---------|
| Breakpoint           |   | P     | 3+      | P      | P      | 3+     | P      | P      | P       | P       | P       |
| Australia            | 5 | 0.107 | 0.177   | 0.046  | 0.017  | 0.417  | 0.621  | 0.083  | 0.448   | 0.812   | 0.062   |
| New Guinea           | 5 | 0.198 | 0.001   | 0.067  | 0.029  | 0.388  | 0.642  | 0.045  | 0.255   | 0.502   | 0.069   |
| No. samples/trait    | k | ODONT | MLC LP2 | 4C LM2 | GP LM2 | C6 LM1 | C7 LM1 | DW     | TOMES'  | 3RM1    | 2RT LM2 |
| Breakpoint           |   | P     | 2+      | 4      | Y      | P      | P      | 3      | 4+      | P       | P       |
| Southeast Asia early | 3 | 0.027 | 0.810   | 0.314  | 0.298  | 0.408  | 0.067  | 0.443  | 0.212   | 0.081   | 0.753   |
| Southeast Asia late  | 5 | 0.011 | 0.706   | 0.259  | 0.336  | 0.364  | 0.081  | 0.428  | 0.201   | 0.121   | 0.716   |
| East Asia            | 5 | 0.018 | 0.768   | 0.274  | 0.269  | 0.385  | 0.062  | 0.363  | 0.174   | 0.224   | 0.744   |
| North America early  | 2 | 0.079 | 0.171   | 0.042  | 0.059  | 0.326  | 0.006  | 0.877  | 0.218   | 0.178   | 0.695   |
| South America early  | 6 | 0.045 | 0.358   | 0.077  | 0.134  | 0.551  | 0.070  | 0.656  | 0.027   | 0.070   | 0.560   |
| Eskimo-Aleut         | 5 | 0.049 | 0.439   | 0.052  | 0.292  | 0.470  | 0.038  | 0.574  | 0.012   | 0.283   | 0.664   |
| NaDene/NW Coast      | 5 | 0.071 | 0.510   | 0.047  | 0.192  | 0.447  | 0.039  | 0.547  | 0.097   | 0.151   | 0.586   |
| North American       | 5 | 0.039 | 0.460   | 0.101  | 0.323  | 0.525  | 0.054  | 0.557  | 0.202   | 0.064   | 0.700   |
| Indian               |   |       |         |        |        |        |        |        |         |         |         |
| Mesoamerican         | 4 | 0.053 | 0.230   | 0.065  | 0.284  | 0.562  | 0.101  | 0.559  | 0.239   | 0.047   | 0.693   |
| South American       | 5 | 0.048 | 0.312   | 0.091  | 0.195  | 0.546  | 0.076  | 0.677  | 0.119   | 0.041   | 0.591   |
| Indian               |   |       |         |        |        |        |        |        |         |         |         |
| Australia            | 5 | 0.031 | 0.748   | 0.076  | 0.258  | 0.595  | 0.040  | 0.388  | 0.274   | 0.054   | 0.948   |
| New Guinea           | 5 | 0.001 | 0.583   | 0.522  | 0.359  | 0.050  | 0.059  | 0.104  | 0.031   | 0.001   | 0.783   |

Each data set based on regional and temporal variation (see Tables 1 and 2) was subjected to a series of multivariate statistical analyses to explore the relationships among the samples. In XLSTAT v. 2015.1, we generated Bray–Curtis dissimilarity matrices for each data set using the full suite of morphological traits (data set 1 = 24 traits; data set 2 = 20 traits) (Addinsoft, 2014). Euclidean distances and Mean Measures of Divergence (MMD) were also calculated in the R statistical program (R Core Team, 2013). The MMD was calculated using the package “AnthropMMD” and the Anscombe transformation. This package is made freely available by Santos (2015). All three methods yielded highly congruent results. These distances are addressed in the discussion, but dendrograms and ordinations are based on Bray–Curtis values.

To visualize subgrouping within the data sets, we performed agglomerative hierarchical clustering. We generated dendrograms based on each dissimilarity matrix using XLSTAT's Unweighted Pair-Group Mean (or Average Linkage) clustering algorithm, accepting the program's default “best fit” truncation (Addinsoft, 2014). Multidimensional scaling (MDS) was used to ordinate each dissimilarity matrix (500 iterations). Dimensionality and goodness of fit of the MDS were determined with reference to Kruskal stress; results with stress values greater than 0.10 were deemed unacceptable (see Kruskal, 1964). In cases of high stress, dimensionality was increased until adequate fit was attained.

### 3. Results

We first discuss inter-population variation in individual trait frequencies for regional samples based on the data in Table 1. The first eight traits summarized below are those where Turner (1990) found significant differences between East Asians (i.e., Sinodonts) and Southeast Asians (i.e., Sundadont). The remaining traits did not exhibit this dichotomy, but many provide insights on the peopling of the New World. Frequency results for each trait are discussed below with reference to the peopling model that best fits that trait's pattern of variation.

#### 3.1. Shoveling UI1 (3+)

New Guinea shows the least amount of shoveling at 4%, with Southeast Asia and Australia at about 40%. East Asia is higher at 53%, but this frequency is lower than all Native American samples.

Eskimo-Aleuts are toward the low end at 70%, while American Indians have frequencies between 85 and 90%. MODEL: Sinodont only plus Beringian Standstill.

#### 3.2. Double-shoveling UI1

Australia and New Guinea show little double-shoveling (ca. 5%). Southeast Asia is at 28% while East Asia is somewhat higher at 35%. For New World groups, the lowest frequencies are for Eskimo-Aleuts and Na Dene/Northwest Coast at about 50%. American Indians show the highest frequencies, falling between 75 and 90%. MODEL: Sinodont only plus Beringian Standstill.

#### 3.3. Enamel extensions UM1

Australia and New Guinea have few enamel extensions (ca. 6%). Southeast Asia is at 32% with East Asia at 42%. With the exception of Mesoamerica (28.9%), New World groups fall in the 40–50% range. MODEL: Sinodont only.

#### 3.4. 2-Rooted UP1

Australia has the highest frequency at 45%, while Southeast Asia and Polynesia are around 35%. In East Asia, the frequency is somewhat lower at about 25%. In the New World, fused UP1 dominate with two-rooted forms attaining a frequency of only 5–15%. MODEL: Sinodont only plus Beringian Standstill.

#### 3.5. Pegged–reduced–missing UM3

The lowest frequencies are for Australia and New Guinea (6%) and the highest is for East Asia (40%). Southeast Asia and Polynesia fall between 20 and 30%. In the New World, Eskimo-Aleuts have the highest frequencies at 24%, with other groups falling between 15 and 20%. MODEL: Sundadont early, Sinodont late.

#### 3.6. 4-Cusped LM2

Outside of Europe, New Guinea has the highest frequency of 4-cusped LM2 at over 50%. Australians are polar opposites at around 10%. For this trait, Southeast Asia and East Asia have almost identical frequencies (30%). New World groups have the lowest 4-

cusped LM2 frequencies in the world, all falling between 5 and 15%. MODEL: Beringian Standstill.

### 3.7. Deflecting wrinkle LM1

This trait is consistently higher in the New World than in Asia and the Pacific. East Asia, Southeast Asia, and Australia have similar frequencies at around 40%. In New Guinea it is only 10%. In the New World, it falls between 55 and 70%. MODEL: Beringian Standstill.

### 3.8. 3-Rooted LM1 (3RM1)

The highest frequencies of this accessory root are in East Asia (20%) and Eskimo-Aleuts (30%). In Southeast Asia and Polynesia, it falls around 10% with lower frequencies in Australia (6%) and New Guinea (>1%). In the New World, Na Dene/Northwest Coast are around 15% while other Indian groups fall between 5 and 7%. MODEL: Sundadont early, Sinodont late.

### 3.9. Other traits

#### 3.9.1. Winging UI1

In East Asia, Southeast Asia, and Polynesia, winging frequencies are around 25%; it is less common in Australia and New Guinea (ca. 10%). Eskimo-Aleut winging frequencies are similar to those of East and Southeast Asia (23%). The highest frequencies of winging in the world are in American Indians; of these, it is lowest in Na Dene/Northwest Coast at ca. 35%, then North American Indians (45%), and Mesoamerican and South American Indians between 55 and 60% (highest in the world). MODEL: Beringian Standstill.

#### 3.9.2. Interruption grooves UI2

This trait is common in New World populations with all five regions having frequencies above 50%. Southeast Asia and Polynesia fall around 25–30%, with East Asia between these values and New World groups at 40%. Australia and New Guinea have the lowest frequencies (15–20%). MODEL: Sinodont only, Beringian Standstill.

#### 3.9.3. 3-Cusped UM2

Australia and New Guinea show little cusp reduction with low frequencies of 3-cusped UM2 (5%); the trait is more common in Southeast Asia (ca. 10%) and East Asia (15%). In the New World, Eskimo-Aleuts have by far the highest frequency of ca. 27% followed by Na Dene/Northwest Coast (15%). Other North and South American Indians fall between 10 and 15%. MODEL: Sundadont early, Sinodont late.

#### 3.9.4. Cusp 5 UM1

Australia and New Guinea have the highest cusp 5 frequencies at around 60%. Southeast Asia is at 25% while East Asia is at 20%. In the New World, Eskimo-Aleuts and Na Dene/Northwest Coast fall between 18 and 25%. In other New World groups, there is a narrow range between 15 and 18%. MODEL: Undetermined.

#### 3.9.5. Carabelli's trait UM1 (3+)

Australia and New Guinea have the highest frequencies of distinct Carabelli's expressions at about 35%. East Asian frequencies are around 20% with Southeast Asia at 30%. In the New World, Eskimo-Aleuts have the lowest frequency at 8% while Indians fall between 17 and 25%. MODEL: Sinodont only, Beringian Standstill.

#### 3.9.6. 3-Rooted UM2

Australia has the highest frequency at ca. 80% while Southeast Asia falls around 75%. East Asia is a slightly lower at 65%. New World populations show more UM2 root fusion with Eskimo-Aleuts and Na Dene/Northwest Coast Indians having the lowest frequency of 3-rooted UM2 (38–42%). American Indians show a narrow range of variation between 55 and 60%, slightly lower than East and Southeast Asia groups. MODEL: Sinodont only, Beringian Standstill.

#### 3.9.7. Lingual cusp number LP2

Multiple lingual cusps are high in Australia and Asia, where all samples fall between 70 and 80%. New Guinea is slightly lower at 60%. Compared to Asia and the Pacific, this trait is lower in all New World groups. Eskimo-Aleuts and Na Dene/Northwest Coast are in the 40–50% range while other American Indians fall between 25 and 35%. MODEL: Beringian Standstill.

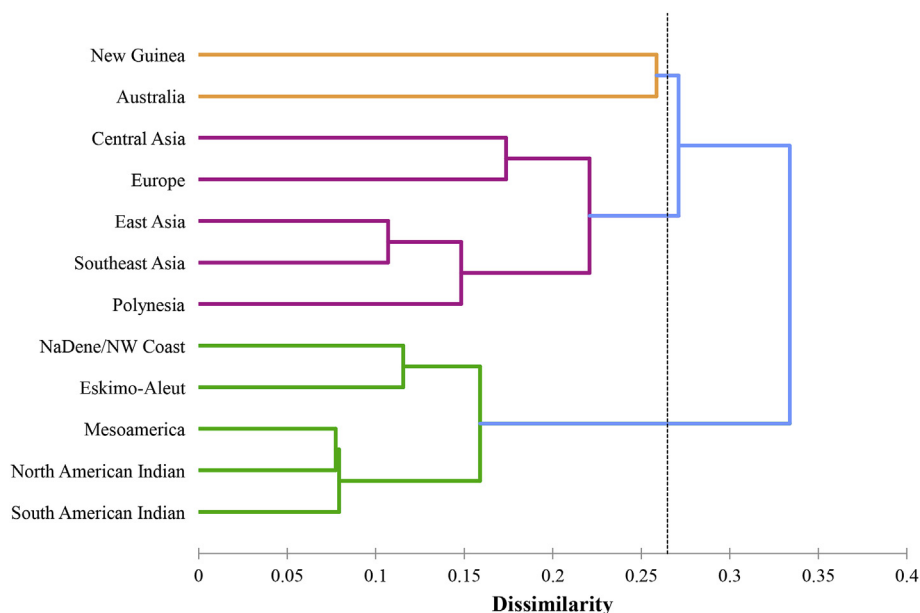
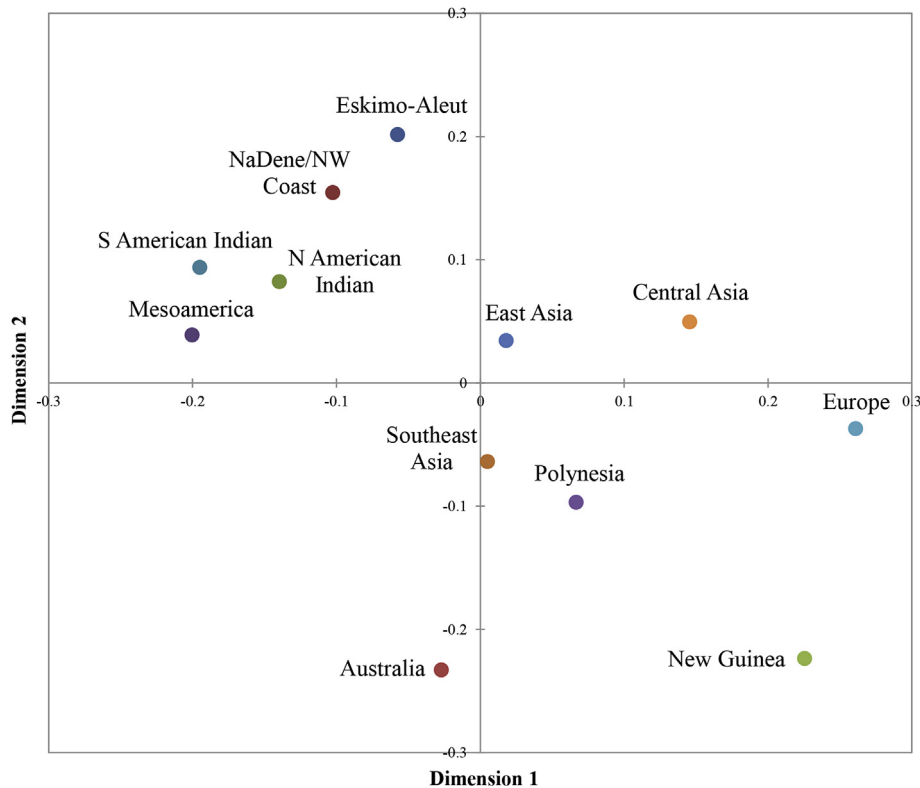


Fig. 1. Dendrogram depicting output of the agglomerative hierarchical cluster analysis of the regional dissimilarity data (clustering algorithm = Average Linkage). Bray–Curtis dissimilarities were calculated using the combined data set of 24 morphological traits.



**Fig. 2.** Two-dimensional MDS based on dissimilarity among the regional samples (Kruskal stress = 0.093). Bray–Curtis dissimilarities were calculated using the combined data set of 24 morphological traits.

### 3.9.8. Y-groove pattern LM2

All Asian and Pacific groups fall between 25 and 35% for Y groove pattern on LM2. This range would include Eskimo-Aleuts, North American Indians, and Mesoamericans. Na Dene/Northwest Coast and South America are a bit lower at around 20%. MODEL: Undetermined.

### 3.9.9. Cusp 6 LM1

In the Pacific, cusp 6 is highest in Australia (65%) and lowest in New Guinea (13%). In Southeast and East Asia, frequencies are similar at around 35%. All five New World groups fall between 45 and 55%. MODEL: Beringian Standstill.

### 3.9.10. Cusp 7 LM1

There is no discernible geographic pattern in this trait as all groups fall between 4 and 10%. MODEL: Undetermined.

### 3.9.11. Tomes' root LP1

Australia and New Guinea are at opposite ends with frequencies of 27% and 3%, respectively. Southeast and East Asians are similar with frequencies around 16–22%. North American and Mesoamerican Indians fall around this frequency (22–24%). Eskimo-Aleuts, Na Dene/Northwest Coast, and South American Indians have notably lower frequencies at between 2 and 10%. MODEL: Undetermined.

### 3.9.12. 2-Rooted LM2

This trait is uniform in Southeast and East Asia, falling between 70 and 75%. New Guinea (80%) and Australia (93%) have the highest frequencies of unfused LM2. In the New World, frequencies for 2-rooted LM2 are slightly lower than in Asia and the Pacific with all

groups falling between 60 and 70%. MODEL: Beringian Standstill/Undetermined.

### 3.9.13. Odontomes

This rare trait is between 2 and 3% in Southeast Asia and Australia and is extremely rare in New Guinea (>1%). The East Asian frequency of almost 6% is in line with New World frequencies where all groups fall between 5 and 7%. MODEL: Sinodont only.

### 3.10. Distance analysis

Table 3 shows the MMD results and Table 4 shows the Bray–Curtis dissimilarity values for the 12 regional groups based on 24 dental traits (see Table 1). The results are very similar; therefore, for visualization, the Bray–Curtis matrix was used to derive a dendrogram (Fig. 1) and a 2-dimensional ordination (Fig. 2). In Fig. 1, there is a fundamental dichotomy between New World populations vs. all Old World populations. Within the New World cluster, Eskimo-Aleut are most closely related to Na Dene/Northwest Coast with North American, South American, and Mesoamerican Indians about equally related to one another (also evident in Bray–Curtis values of 0.077, 0.081, and 0.078). In the Old World cluster, Australia and New Guinea are linked at a high level and separated from all other groups. Europe is closest to Central Asia (largely a European/Asian grouping) while East Asia, Southeast Asia, and Polynesia fall on the final branches of the tree. Somewhat surprisingly, this tree does not produce a clear East Asian/Southeast Asian division but does show that all New World groups are distinctly set apart from Old World groups, including East Asians.

**Table 3**  
Mean measures of divergence for geographic samples.

|                       | ESK AL | ND NW | NAM I | MESO  | SAM I | SEA   | E ASIA | AUST  | NEWG  | POLY  | EUR   | C ASIA |
|-----------------------|--------|-------|-------|-------|-------|-------|--------|-------|-------|-------|-------|--------|
| Eskimo-Aleut          | 0      | 0.030 | 0.083 | 0.166 | 0.130 | 0.207 | 0.106  | 0.396 | 0.534 | 0.258 | 0.541 | 0.257  |
| NaDene/NW Coast       | 0.030  | 0     | 0.032 | 0.102 | 0.066 | 0.177 | 0.087  | 0.370 | 0.549 | 0.249 | 0.578 | 0.269  |
| North American Indian | 0.083  | 0.032 | 0     | 0.015 | 0.009 | 0.181 | 0.108  | 0.392 | 0.558 | 0.287 | 0.542 | 0.249  |
| Mesoamerica           | 0.166  | 0.102 | 0.015 | 0     | 0.016 | 0.284 | 0.212  | 0.484 | 0.697 | 0.404 | 0.673 | 0.356  |
| South American Indian | 0.130  | 0.066 | 0.009 | 0.016 | 0     | 0.269 | 0.183  | 0.504 | 0.712 | 0.385 | 0.694 | 0.353  |
| Southeast Asia        | 0.207  | 0.177 | 0.181 | 0.284 | 0.269 | 0     | 0.012  | 0.108 | 0.206 | 0.041 | 0.207 | 0.084  |
| East Asia             | 0.106  | 0.087 | 0.108 | 0.212 | 0.183 | 0.012 | 0      | 0.188 | 0.284 | 0.071 | 0.269 | 0.090  |
| Australia             | 0.396  | 0.370 | 0.392 | 0.484 | 0.504 | 0.108 | 0.188  | 0     | 0.209 | 0.107 | 0.353 | 0.293  |
| New Guinea            | 0.534  | 0.549 | 0.558 | 0.697 | 0.712 | 0.206 | 0.284  | 0.209 | 0     | 0.143 | 0.119 | 0.165  |
| Polynesia             | 0.258  | 0.249 | 0.287 | 0.404 | 0.385 | 0.041 | 0.071  | 0.107 | 0.143 | 0     | 0.165 | 0.096  |
| Europe                | 0.541  | 0.578 | 0.542 | 0.673 | 0.694 | 0.207 | 0.269  | 0.353 | 0.119 | 0.165 | 0     | 0.061  |
| Central Asia          | 0.257  | 0.269 | 0.249 | 0.356 | 0.353 | 0.084 | 0.090  | 0.293 | 0.165 | 0.096 | 0.061 | 0      |

**Table 4**  
Bray–Curtis dissimilarity values for geographic samples.

|                       | ESK AL | ND NW | NAM I | MESO  | SAM I | SE ASIA | E ASIA | AUST  | NEWG  | POLY  | EUR   | C ASIA |
|-----------------------|--------|-------|-------|-------|-------|---------|--------|-------|-------|-------|-------|--------|
| Eskimo-Aleut          | 0      | 0.116 | 0.147 | 0.200 | 0.187 | 0.261   | 0.200  | 0.389 | 0.496 | 0.309 | 0.421 | 0.288  |
| NaDene/NW Coast       | 0.116  | 0     | 0.111 | 0.172 | 0.137 | 0.249   | 0.193  | 0.367 | 0.475 | 0.297 | 0.422 | 0.281  |
| North American Indian | 0.147  | 0.111 | 0     | 0.077 | 0.081 | 0.237   | 0.188  | 0.347 | 0.454 | 0.292 | 0.395 | 0.275  |
| Mesoamerica           | 0.200  | 0.172 | 0.077 | 0     | 0.078 | 0.263   | 0.248  | 0.349 | 0.481 | 0.316 | 0.423 | 0.312  |
| South American Indian | 0.187  | 0.137 | 0.081 | 0.078 | 0     | 0.279   | 0.234  | 0.375 | 0.498 | 0.326 | 0.438 | 0.310  |
| Southeast Asia        | 0.261  | 0.249 | 0.237 | 0.263 | 0.279 | 0       | 0.107  | 0.183 | 0.299 | 0.132 | 0.248 | 0.191  |
| East Asia             | 0.200  | 0.193 | 0.188 | 0.248 | 0.234 | 0.107   | 0      | 0.266 | 0.348 | 0.164 | 0.277 | 0.176  |
| Australia             | 0.389  | 0.367 | 0.347 | 0.349 | 0.375 | 0.183   | 0.266  | 0     | 0.259 | 0.213 | 0.320 | 0.334  |
| New Guinea            | 0.496  | 0.475 | 0.454 | 0.481 | 0.498 | 0.299   | 0.348  | 0.259 | 0     | 0.270 | 0.210 | 0.267  |
| Polynesia             | 0.309  | 0.297 | 0.292 | 0.316 | 0.326 | 0.132   | 0.164  | 0.213 | 0.270 | 0     | 0.261 | 0.172  |
| Europe                | 0.421  | 0.422 | 0.395 | 0.423 | 0.438 | 0.248   | 0.277  | 0.320 | 0.210 | 0.261 | 0     | 0.174  |
| Central Asia          | 0.288  | 0.281 | 0.275 | 0.312 | 0.310 | 0.191   | 0.176  | 0.334 | 0.267 | 0.172 | 0.174 | 0      |

A 2-dimensional ordination (see Fig. 2) illustrates the relationship among the 12 regional groups in a manner largely analogous to the dendrogram. All New World groups occupy the upper left quadrant, with their greatest distances from Australia, New Guinea, and Europe. Southeast Asia and Polynesia fall below the X-axis, in the direction of Australia and New Guinea, while East Asia falls above this axis, closer to New World groups than any other regional group.

To put time into the equation (using data in Table 2), early and late samples from Southeast Asia, North America, and South

America were contrasted to other regional groups in the New World, Asia, and the Pacific. Under the Sundadont early, Sinodont late model, the presumption would be that the Southeast Asian Sundadonts would be fairly congruent with 'early American Sundadonts' while later New World samples would align with East Asian Sinodonts. The results of the MMD analysis are shown in Table 5 and the Bray–Curtis results derived from these data are shown in Table 6. Again, these results are very similar, and rather than providing a trait by trait description, we focus on the graphical representations from the Bray–Curtis values.

**Table 5**  
Mean measures of divergence for temporal samples.

|                       | SEA E | SEA L | E ASIA | NAM E | SAM E | ESK AL | ND NW | NAM I | MESO  | SAM I | AUST  | NEWG  |
|-----------------------|-------|-------|--------|-------|-------|--------|-------|-------|-------|-------|-------|-------|
| Southeast Asia early  | 0     | 0.016 | 0.046  | 0.360 | 0.356 | 0.249  | 0.203 | 0.181 | 0.316 | 0.341 | 0.140 | 0.277 |
| Southeast Asia late   | 0.016 | 0     | 0.023  | 0.322 | 0.350 | 0.211  | 0.172 | 0.179 | 0.319 | 0.327 | 0.141 | 0.286 |
| East Asia             | 0.046 | 0.023 | 0      | 0.301 | 0.268 | 0.134  | 0.112 | 0.123 | 0.258 | 0.247 | 0.231 | 0.390 |
| North America early   | 0.360 | 0.322 | 0.301  | 0     | 0.136 | 0.187  | 0.112 | 0.157 | 0.140 | 0.138 | 0.537 | 0.810 |
| South America early   | 0.356 | 0.350 | 0.268  | 0.136 | 0     | 0.156  | 0.087 | 0.054 | 0.036 | 0.011 | 0.688 | 0.917 |
| Eskimo-Aleut          | 0.249 | 0.211 | 0.134  | 0.187 | 0.156 | 0      | 0.023 | 0.097 | 0.170 | 0.128 | 0.491 | 0.650 |
| NaDene/NW Coast       | 0.203 | 0.172 | 0.112  | 0.112 | 0.087 | 0.023  | 0     | 0.041 | 0.099 | 0.067 | 0.441 | 0.644 |
| North American Indian | 0.181 | 0.179 | 0.123  | 0.157 | 0.054 | 0.097  | 0.041 | 0     | 0.027 | 0.028 | 0.466 | 0.712 |
| Mesoamerican          | 0.316 | 0.319 | 0.258  | 0.140 | 0.036 | 0.170  | 0.099 | 0.027 | 0     | 0.023 | 0.607 | 0.847 |
| South American Indian | 0.341 | 0.327 | 0.247  | 0.138 | 0.011 | 0.128  | 0.067 | 0.028 | 0.023 | 0     | 0.690 | 0.908 |
| Australia             | 0.140 | 0.141 | 0.231  | 0.537 | 0.688 | 0.491  | 0.441 | 0.466 | 0.607 | 0.690 | 0     | 0.272 |
| New Guinea            | 0.277 | 0.286 | 0.390  | 0.810 | 0.917 | 0.650  | 0.644 | 0.712 | 0.847 | 0.908 | 0.272 | 0     |

**Table 6**  
Bray–Curtis dissimilarity values for temporal samples.

|                      | SEA E | SEA L | E ASIA | NAM E | SAM E | ESK AL | ND NW | NAM I | MESO  | SAM I | AUST  | NEWG  |
|----------------------|-------|-------|--------|-------|-------|--------|-------|-------|-------|-------|-------|-------|
| Southeast Asia early | 0     | 0.092 | 0.114  | 0.320 | 0.295 | 0.286  | 0.260 | 0.220 | 0.262 | 0.316 | 0.196 | 0.306 |
| Southeast Asia late  | 0.092 | 0     | 0.102  | 0.292 | 0.288 | 0.260  | 0.246 | 0.212 | 0.274 | 0.308 | 0.204 | 0.291 |
| East Asia            | 0.114 | 0.102 | 0      | 0.275 | 0.265 | 0.199  | 0.198 | 0.189 | 0.256 | 0.266 | 0.258 | 0.342 |



Table 6 (continued)

|                       | SEA E | SEA L | E ASIA | NAM E | SAM E | ESK AL | ND NW | NAM I | MESO  | SAM I | AUST  | NEWG  |
|-----------------------|-------|-------|--------|-------|-------|--------|-------|-------|-------|-------|-------|-------|
| North America early   | 0.320 | 0.292 | 0.275  | 0     | 0.196 | 0.233  | 0.179 | 0.198 | 0.187 | 0.193 | 0.386 | 0.478 |
| South America early   | 0.295 | 0.288 | 0.265  | 0.196 | 0     | 0.202  | 0.152 | 0.109 | 0.088 | 0.069 | 0.401 | 0.503 |
| Eskimo-Aleut          | 0.286 | 0.260 | 0.199  | 0.233 | 0.202 | 0      | 0.102 | 0.160 | 0.210 | 0.188 | 0.408 | 0.481 |
| NaDene/NW Coast       | 0.260 | 0.246 | 0.198  | 0.179 | 0.152 | 0.102  | 0     | 0.128 | 0.170 | 0.133 | 0.382 | 0.464 |
| North American Indian | 0.220 | 0.212 | 0.189  | 0.198 | 0.109 | 0.160  | 0.128 | 0     | 0.089 | 0.106 | 0.343 | 0.448 |
| Mesoamerican          | 0.262 | 0.274 | 0.256  | 0.187 | 0.088 | 0.210  | 0.170 | 0.089 | 0     | 0.090 | 0.367 | 0.485 |
| South American Indian | 0.316 | 0.308 | 0.266  | 0.193 | 0.069 | 0.188  | 0.133 | 0.106 | 0.090 | 0     | 0.429 | 0.525 |
| Australia             | 0.196 | 0.204 | 0.258  | 0.386 | 0.401 | 0.408  | 0.382 | 0.343 | 0.367 | 0.429 | 0     | 0.271 |
| New Guinea            | 0.306 | 0.291 | 0.342  | 0.478 | 0.503 | 0.481  | 0.464 | 0.448 | 0.485 | 0.525 | 0.271 | 0     |

The dendrogram derived from the proximity matrix is shown as Fig. 3. It shows many parallels and a few differences from the analysis of the regional data set. First, in this tree diagram, New Guinea is set apart at a high level from all groups. Following that division, there is a fundamental division between New World populations and all Asian groups. As to specifics, Eskimo-Aleuts still cluster with Na Dene/Northwest Coast while other Native Americans group together. Early South American samples cluster most closely with recent South American samples, providing support for temporal continuity. Of the New World groups, the early North American sample is the most highly differentiated. This result might be partly a function of sample size because the North American early sample was the smallest of any in the array. Although the most discrepant of New World samples, it still clusters with other New World groups and not Southeast or East Asians.

A 3-dimensional ordination provides another perspective on temporal and regional relationships (Fig. 4). All New World groups are found in the two right quadrants while Old World groups occupy the left quadrants. For the New World, there is a close similarity between Eskimo-Aleut and Na Dene/Northwest Coast (upper right) and between the American Indian groups in the lower right quadrant. In the Old World, New Guinea is the most dramatic outlier while early Southeast Asia shows some affinity to Australia. The later Southeast Asian sample is pulled toward East Asia, likely a product of admixture during the Holocene.

Whether approached from a regional or temporal standpoint, our findings emphasize the distinction between New World and Old World groups. Although there are differences between East Asia and Southeast Asia, as Turner (1987, 1990) proposed, this distinction is not as dramatic as that between the peoples of America and the peoples of Asia.

A final piece of the puzzle based on Euclidean and Mean Measure of Divergence distance values is presented in Table 7. For both the temporal and regional groupings, the average distances of each group from all Native American groups are presented from highest to lowest values. For the temporal groupings, the largest distances are for New Guinea and Australia by a wide margin. The two Southeast Asian samples are similar with values at 0.27–0.28 for the MMD and 0.874 and 0.830 for Euclidean distances. East Asia is, not surprisingly, closer to New World groups with means of 0.206/0.676. When the New World groups are compared among themselves, there are two noteworthy observations. First, the two most distinctive groups are North American early and Eskimo-Aleuts. Second, the remaining five samples show means that are remarkably similar (0.066–0.083 for MMDs/0.302–0.363 for Euclidean distances). The pattern for geographic groupings shows New Guinea and Europe are the most distinct from Native Americans followed by Australians, Polynesians, and Central Asians. Again, Southeast Asians have higher mean distances (0.224/0.757) than East Asians (0.139/0.673). For this set of comparisons, the four American Indian groupings have very similar mean distances

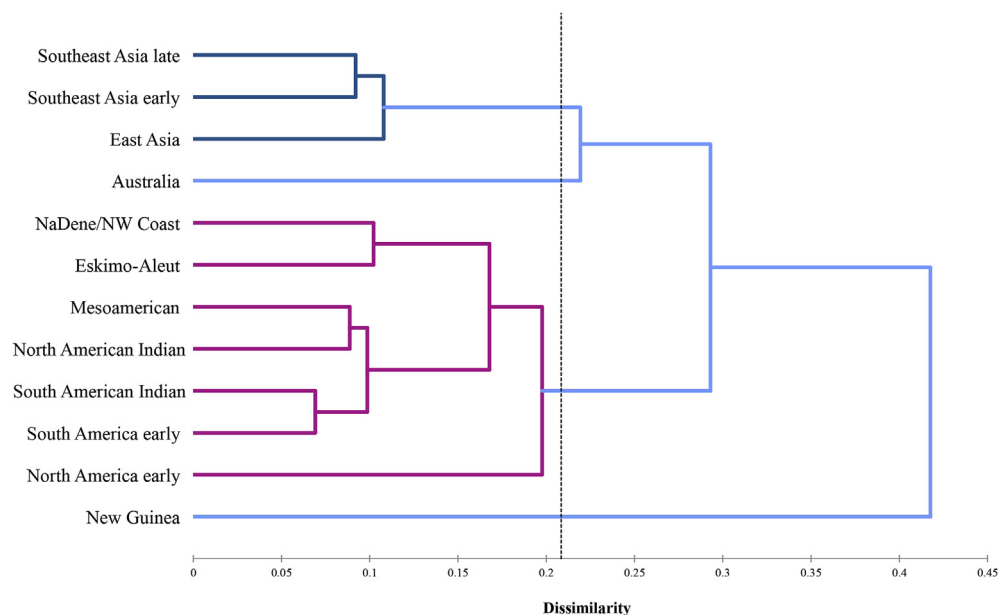
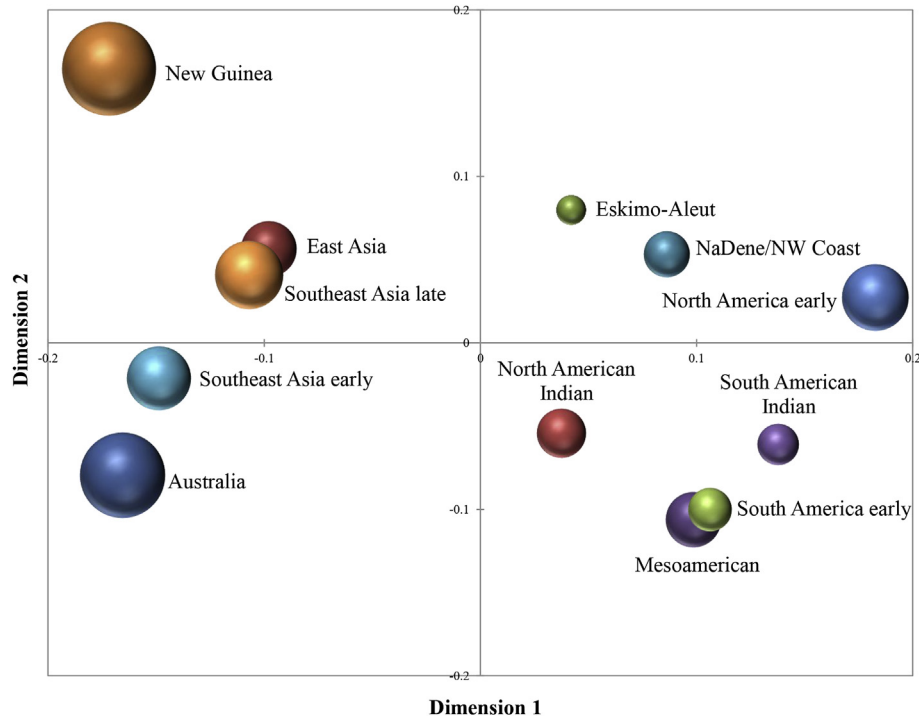


Fig. 3. Dendrogram depicting output of the agglomerative hierarchical cluster analysis of the temporal dissimilarity data (clustering algorithm = Average Linkage). Bray–Curtis dissimilarities were calculated using the combined data set of 20 morphological traits.



**Fig. 4.** Three-dimensional MDS based on dissimilarity among the samples in the temporal data set (Kruskal stress = 0.045). Bray–Curtis dissimilarities were calculated using the combined data set of 20 morphological traits. Dimension 3 is visualized by bubble size (and further by color), such that the largest bubble and smallest bubble correspond to polar ends of the distribution of the samples along the third axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(0.035–0.075 and 0.294–0.370), with Eskimo-Aleuts as an outlier (0.102/0.452).

shoveling, show a pattern corresponding to the Sinodont only plus Beringian Standstill model. Only three traits correspond to the

**Table 7**  
Mean MMD and Euclidean distances of regional groups from Native American groups.

| Temporal grouping       | Mean MMD | S.D.   | Mean Euclidean | S.D.   | Geographic grouping     | Mean MMD | S.D.   | Mean Euclidean | S.D.   |
|-------------------------|----------|--------|----------------|--------|-------------------------|----------|--------|----------------|--------|
| New Guinea              | 0.784    | 0.1158 | 1.388          | 0.1265 | New Guinea              | 0.610    | 0.0869 | 1.342          | 0.1289 |
| Australia               | 0.560    | 0.1031 | 1.144          | 0.1335 | Europe                  | 0.606    | 0.0730 | 1.388          | 0.0955 |
| Southeast Asia early    | 0.287    | 0.0748 | 0.874          | 0.1116 | Australia               | 0.429    | 0.0604 | 0.985          | 0.1401 |
| Southeast Asia late     | 0.269    | 0.0776 | 0.830          | 0.1470 | Polynesia               | 0.317    | 0.0728 | 1.033          | 0.1406 |
| East Asia               | 0.206    | 0.0798 | 0.676          | 0.1490 | Central Asia            | 0.297    | 0.0532 | 1.040          | 0.0924 |
| North America early     | 0.145    | 0.0251 | 0.415          | 0.0397 | Southeast Asia          | 0.224    | 0.0499 | 0.757          | 0.1361 |
| Eskimo-Aleut            | 0.127    | 0.0600 | 0.434          | 0.1339 | East Asia               | 0.139    | 0.0548 | 0.673          | 0.1526 |
| Mesoamerica             | 0.083    | 0.0633 | 0.363          | 0.1438 | Eskimo-Aleut            | 0.102    | 0.0590 | 0.452          | 0.1568 |
| South America early     | 0.080    | 0.0572 | 0.328          | 0.1541 | Mesoamerica             | 0.075    | 0.0732 | 0.370          | 0.1758 |
| Na Dene/Northwest Coast | 0.072    | 0.0345 | 0.370          | 0.1103 | Na Dene/Northwest Coast | 0.058    | 0.0340 | 0.362          | 0.1098 |
| North America late      | 0.067    | 0.0509 | 0.302          | 0.0665 | South America           | 0.055    | 0.0559 | 0.368          | 0.1614 |
| South America late      | 0.066    | 0.0554 | 0.341          | 0.1228 | North America           | 0.035    | 0.0336 | 0.294          | 0.1091 |

**4. Discussion**

A general summary of how dental trait variation corresponds to the four peopling scenarios is provided in Table 8. This table is divided between the eight traits that characterize the Sinodont/Sundadont dichotomy (as per Turner, 1990) and the additional 16 traits that were not part of this regional dichotomy. Exploring population relationships based on univariate trait frequencies and biodistance analyses, the assumptions of the various peopling models can be individually evaluated. Of the 24 traits, only two are consistent with a strict Sinodont only model. Seven traits are consistent with the Beringian Standstill model. Five traits, including

Sundadont early, Sinodont late model, including pegged–reduced–missing UM3, 3-rooted lower first molars, and 3-cusped UM2. It is ironic that 3-rooted lower first molars fall in this group because this was the first trait Turner (1971) used to develop the TMM. Finally, seven of 24 traits do not conform to any of the four models and are placed in an undetermined category. Excluding these seven traits, 12 crown and root traits exhibit a geographic pattern consistent with the Beringian Standstill model, while seven suggest Sinodont ancestry. Overall, findings based on dental morphology are contrary to those of craniometrics that suggest disparate sources for two separate early movements into the New World.

**Table 8**  
How regional trait frequencies conform to different models for peopling the New World.

|                           | Sinodont only | Beringian Standstill  | Sinodont only,<br>Beringian Standstill                                       | Sundadont early,<br>Sinodont late    | Undetermined   |
|---------------------------|---------------|---|--|--------------------------------------|--|
| Sinodont/Sundadont traits | Enamel ext    | 4-cusped LM2  | Shoveling  | Pegged, reduced, missing UM3<br>3RM1 |  |
| Other traits              | Odontomes     | Deflecting wrinkle<br>Winging<br>Carabelli's trait<br>LP2 lingual cusp number<br>Cusp 6<br>2-rooted LM2 | Double shoveling<br>2-rooted UP1<br>UI2 interruption grooves<br>3-rooted UM2 | 3-cusped UM2                         | UM1 Cusp 5<br>Y groove pattern<br>Cusp 7<br>Protostylid<br>Distal trig crest<br>2-rooted LC<br>Tomes' root |
| Total                     | 2             | 7   | 5  | 3                                    | 7  |

#### 4.1. The disparity between craniometrics and dental morphology

The differences in craniometric measurements and overall skull form noted by a number of researchers (e.g., R. Jantz, J. Powell, D. Owsley, W. Neves, M. Hubbe) between early and late Native Americans in North and South America are undeniable. Given that, what might account for the contrasting conclusions provided by skull measurements and dental trait frequencies?

To support the idea of population replacement inherent in the TC model, earlier brachycephalic individuals, unaccompanied by deviations from the forager subsistence pattern must be present in the archaeological record. Presumably the individual from Browns Valley, Minnesota, with a direct date of  $8700 \pm 110$  cal BP, would be significant. However, while Steele and Powell (1992) utilized this cranium in their analysis consisting of eight variables, Powell and Neves (1999, pp. 165) excluded it from their multivariate analyses due to its incomplete nature. Neves and Blum (2000) offered the Buhl burial from Idaho, with a direct date of  $10,675 \pm 95$   $^{14}\text{C}$  BP, as evidence of an early presence of brachycephalic individuals in the New World. Jantz and Owsley (2005, pp. 269) disagreed and pointed to the Buhl individual's strong differentiation from modern Native American populations and its proximity to Polynesian groups in the principal components plot. In their view, there is no uncontested presence of brachycephaly in the New World prior to the late Holocene.

González-José et al. (2005) call attention to the possibility of the retention of plesiomorphic dolichocephaly in modern New World populations. Lahr (1995) asserts Fuegian populations of the far southern Pacific Coast display a robusticity that departs from the typical "Mongoloid" morphology indicative of Amerindians. Cluster analysis utilizing Howells' data in comparison with Fuegian data collected by Lahr, demonstrates a close relationship between the size and shape of Fuegian crania with those of South Pacific populations (Lahr, 1995, pp. 185). Similarly, the Pericú of Baja Mexico are located closest to the "Paleoamerican" series from Brazil on a PCA (González-José et al., 2003).

Given that southern South American populations typically exhibit mtDNA haplogroups C and D (Perez et al., 2007), Perez and Monteiro (2009) examined the diversity of cranial morphology across southern South America using the Generalized Procrustes Superimposition and Relative Warps analysis. From a sample of 12 late Holocene populations from Argentina and Chile, the authors used functional cranial components (*sensu* Pucciarelli et al., 2003) to examine the viability of stochastic mechanisms alone in explaining the differentiation of populations sharing so recent a common ancestor. Relative Warps analyses of the facial component display differentiation between hunter-gatherers and agriculturalists plus horticulturalists. These results indicate the relevance of craniofacial plasticity during ontogeny to the expression of

dolichocephaly. It also shows a correlation between robusticity and height in the face and vault with latitude (Perez and Monteiro, 2009, pp. 984). As a result, they reject that stochastic mechanisms alone sufficiently account for the craniometric diversity in late Holocene New World populations. Furthermore, Menéndez et al. (2015, pp. 261) point out this trend of dolichocephaly can be consistently linked to modern Amerindian haplotypes going back to ca. 8000 cal BP.

In the same spirit as Greenberg et al. (1986), three notable attempts at finding consilience between craniometric models and other data, namely genetic, have been put forth by González-José et al. (2008), De Azevedo et al. (2011), and Galland and Friess (2016). González-José et al. (2008, pp. 177) remark on the "simplistic" morphometric methods driving the conversation on the morphometric affinities of ancient and modern New World populations. Using two-dimensional geometric morphometric analysis, they find that when they plot samples without regard for geographic, or temporal context, rather than forming distinct groups, the plotted variation between late Pleistocene – early Holocene groups and late Holocene groups forms a "continuous spectrum," with substantial areas of overlap in the allometry-free PCA (see Fig. 3 in González-José et al., 2008). These findings dispute those of Neves et al. (1999a,b), who concluded that late-Pleistocene – early-Holocene groups are identifiably distinct from late-Holocene groups, and that they can be confidently assigned to modern craniometric categories.

Under the assumptions that "Paleoamericans" were not as different from modern populations and that modern Amerindians are not as homogenous as previously believed, González-José et al. (2008) integrate genetic data to propose an alternative to the two-component model (Neves et al. (1999a,b)). Their model assumes all modern mtDNA and Y chromosome haplotypes were present in the Bering Sea region prior to the initial settlement of the New World. Gradually, routes of ingress opened up to morphologically generalized populations with high intra-group variability that traveled south along the Pacific coast (ca. 26,000–18,000 cal yr BP). Throughout the Holocene, populations moved into geographically diverse and relatively isolated niches, expediting genetic drift. This pattern of expansion into the interiors of North and South America was accompanied by a constant flow of genetic material back and forth between Arctic populations on both sides of the Bering Strait, to include the period following the rise of sea levels and the subsidence of the land bridge (González-José et al., 2008, pp. 184; see also Tamm et al., 2007).

De Azevedo et al. (2011) use the same 23 series of photographs as González-José et al. (2008) for geometric morphometric analyses and subsequent model construction. They calculate morphological affinity based on Mahalanobis distances matrices, while adding temporal context by multiplying each element of

each matrix by the amount of time elapsed between samples (De Azevedo et al., 2011, pp. 543). The authors then construct four separate models: 1) a null model, reflecting evolutionary expectations of isolation by distance (IBD); 2) a single wave (SW) model, which assumes *in situ* differentiation in the New World, and adds the assumption of a route through Beringia; 3) a two wave (TC) model that assumes two founding populations; and, 4) a recurrent gene flow (RGF) model, where the distances between non-Arctic New World populations are the same as in the IBD and SW models, but reflect the tendency of New World Arctic groups to cluster with Asian Arctic groups (De Azevedo et al., 2011, pp. 540). The authors also add climatic variables (e.g. annual mean temperature, annual precipitation) to these geographical frameworks. Their analysis based on the Mahalanobis distance matrices did not support a significant difference between “Paleoamerican” groups and modern populations. Their findings, based on the closest fitting model, support the idea of a single founding population, as well as *in situ* microevolution, and constant, low-level gene flow to and from Asia, through the Arctic.

Galland and Friess (2016) applied a three-dimensional method of geometric morphometric analysis to a similar range of models. The authors used 39 landmarks and Generalized Procrustes Analysis to assess the similarities between various combinations of Old World and “Paleoamerican” fossils, modern Circumpacific, and New World populations. While they note findings similar to standard craniometric analyses, namely the proximity of “Paleoamericans” to Australo-Melanesians, the most remarkable conclusion they draw is that “the single largest shape contrast is not between Paleoamericans and contemporary Amerindians, but between Circum-Arctic populations and all others” (Galland and Friess, 2016, pp. 9). This conclusion points to the importance of non-stochastic mechanisms in cranial shape. Nevertheless, their findings offer little support to the RGF model, the model that best fit the data of De Azevedo et al. (2011). Rather, they find significant correlation in their SW model, and support for their TC model, but only when the Old World fossil population is considered and when the Pericú of Baja and the Fuegians are considered as relict populations (Galland and Friess, 2016).

Larsen (2015, pp. 257–264) summarizes an extensive body of literature that centers on alterations of craniofacial morphology associated with changes in dietary behavior. That is, decreased robusticity and cranial length along with an overall increase in cranial height results in a shift towards brachycephalization tied to changes in subsistence strategy. Henneberg (1988) demonstrates a statistically significant decrease in overall cranial size through analysis of both internal and external measurements of a series of samples from the Upper Paleolithic to modern times in the Old World. This is a phenomenon seen throughout the species, which Henneberg associates with the overall gracilization of the human skeleton since the end of the Pleistocene. He hypothesizes that, as the overall human form became more gracile, the cranium became smaller to maintain energy efficiency (Henneberg, 1988). As this pattern of brachycephalization is evident throughout the Holocene, it should be considered a possible explanation for the morphological shift from Paleoindians to modern Native American populations.

#### 4.2. Sundadonty in the New World

Scott and Turner (2006) proposed all groups in the Americas possess a Sinodont dental pattern, but several authors find evidence for Sundadonty (e.g. Lahr, 1995; Lahr and Haydenblit, 1995; Powell, 1995; Haydenblit, 1996; Sutter, 1997, 2005; Powell and Neves, 1998; Powell and Rose, 1999; Chatters, 2000). Samples from Washington (Powell and Rose, 1999; Chatters, 2000),

Prehispanic Mexico (Haydenblit, 1996), Tierra del Fuego, Patagonia (Lahr, 1995; Lahr and Haydenblit, 1995), and the South Central Andes (Sutter, 2005) show possible Sundadont dentitions. Some of these authors suggest Turner's Paleoindian (also known as Amerind, Macro-Indian) migration (1971, 1983a, 1985) consisted of two separate waves. The first wave involved people with a Sundadont dentition who were later replaced by people with a Sinodont dentition (Haydenblit 1996; Lahr 1995; Lahr and Haydenblit 1995; Neves et al. (1999a,b); Sutter 2005).

Scott and Turner (2006) feel claims of Sundadonty in the New World are overstated. Turner (2002, 2006; Turner and Scott, 2007) notes extreme dental wear may cause researchers to downgrade key dental morphological features, including shovel-shaped incisors. Stojanowski and Johnson (2015) suggest that, while downgrading due to dental wear may not occur in all samples, there may be unintentionally introduced biases during the recordation process that have influenced claims of Sundadonty in the New World. They further suggest observers may not take into account the simplification that occurs as teeth wear.

To test the notion that dental wear is responsible for claims of Sundadonty in the New World, Stojanowski and Johnson (2015) reanalyzed remains from the Early Archaic Windover site in Florida and compared their observations to those of Powell (1995). In addition to testing the effects of dental wear on the recordation of dental morphological data, they evaluated whether the method of recordation itself introduces bias into the analysis. Biases may include decisions on which teeth are recorded and whether worn teeth should be scored for trait expression. They found that trait downgrading does not appear to have influenced the original assertion that the sample exhibits the Sundadont dental pattern (Powell, 1995). The traits within the Sundadont range that influenced Powell's (1995) final decision were pegged/reduced/missing UM3 and 3-rooted LM1, traits that Stojanowski and Johnson (2015) argue are unlikely to be affected by dental wear. Significantly, the Turner data set shows that pegged/reduced/missing UM3 and 3-rooted lower first molars are two of the three traits consistent with the Sundadont early, Sinodont late model. However, when the 20–24 traits from the present study are taken into account, the majority exhibit a pattern of variation that conforms to the Sinodont only, Beringian Standstill, or Sinodont plus Beringian Standstill models.

In the analyses of Kennewick Man, one of the best known early North American Indian skeletons, Powell and Rose (1999, p. 6) made several interesting observations on the dentition.

“Dental discrete traits were difficult to observe given the considerable attrition of the dentition. Dental discrete traits in Kennewick include no U11 interruption grooves, single-rooted UP3s, no UP3 distosagittal ridge, 3-root LM1s, strong enamel extensions on upper and lower molars, no peg or absent UM3s, no Tome's root, and two-rooted LM1s. Although it is tempting to try to assign Kennewick to either the Sinodont or Sundadont (Turner, 1990) patterns, it is simply not possible to attribute the Kennewick individual's dental discrete traits to either the Sinodont or Sundadont groups based on gross morphological observations. The East Asian Sinodont and Sundadont dental patterns are based on relative frequencies of eight key traits observed in large samples of Asian populations. Any one individual drawn at random from a Sinodont or Sundadont group might exhibit all, some, or none of the characteristics associated with that group's overall pattern of frequencies.”

Most determinations of Sundadonty in New World samples are based on sample frequencies that align more closely with this pattern than with Sinodonty (Lahr and Haydenblit, 1995;

Haydenblit, 1996; Sutter, 1997, 2005). There is no question dental traits show within and between group variation attributable to a variety of factors, including sampling error, microdifferentiation, and/or observational differences. Our analysis shows, however, that the distinction between East Asians and Southeast Asians is not nearly as dramatic as the difference between all Asians and all New World groups. Some researchers (e.g., Stojanowski et al., 2013; Stojanowski and Johnson, 2015) suggest New World groups may be neither Sinodont nor Sundadont and they might be correct. In the Americas, it appears that time, distance, and isolation produced a pattern that, in most regards, could be viewed as super-Sinodont. It is clear dental morphology not only ties New World groups to Asians, particularly northeast Asians, but it also exhibits a pattern largely consistent with the Beringian Standstill model based on a Sinodont source population.

#### 4.3. Dental evidence for the Beringian Standstill

Mean measures of biological distances involving Old World populations and Native Americans (see Table 7) are consistent with the following scenario. Although related to Asian populations, especially Southeast Asians, Australo-Melanesians are distantly related to populations in the New World. At some point after Asians diverged from Australo-Melanesians, a dental dichotomy developed in Asia that separated Southeast from Northeast Asian populations (i.e., Sundadont/Sinodont divergence). One section of the Northeast Asian population that would ultimately be ancestral to all Native Americans drifted into the western reaches of Beringia above the Arctic Circle. They likely dispersed throughout greater Beringia, but could not advance into the southerly reaches of the Americas because of physical and environmental barriers. The remarkably uniform mean distances among the Native American groupings suggest that once dispersal was possible following dramatic environmental changes during the late Pleistocene, the founding population broke down into constituent populations (i.e., Northwest Coast, North America, Mesoamerica, South America) relatively rapidly. Essentially, they diverged quickly from a common ancestor with groups dispersing to every geographic corner of the Americas. This is consistent with the suggestion of many researchers that there was a single founding population that dispersed in relatively short order to eastern North America and Mesoamerica/South America.

Turner (1983a, 1986) held that North and South American Indians were very similar to one another and the likely reason is recent common ancestry. As mean differences attest, they differ but the difference is minor compared to their difference from East Asian populations. In some regards, Eskimo-Aleuts are intermediate to East Asians and American Indians but the reason for this is not altogether resolved. If they were part of the original standstill population, they possibly differentiated within the confines of Beringia before the ancestors of American Indians could disperse further south. Given their residence in the north and more immediate contact with Siberian populations in Chukotka and beyond, their intermediate position may be a product of gene flow.

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Christy G. Turner II. Although he is no longer with us, he would be pleased to know his data are still being used to address big anthropological problems. He loved the Arctic and we suspect he would have been intrigued by the Beringian Standstill model.

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