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A Craniofacial and Postcranial Survey of North and South American Inhabitants from the Perspective of Possible Old World Ancestors

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This study aims to shed light on early migration to the Americas and the population history of inhabitants in the Americas, and evolutionary trends in climatic adaptation using skeletal remains from the American continents, with geographically diverse skeletal samples from East Asia including the Japanese archipelago, Northeast Asia, Southeast Asia, Australia, Oceania, Africa, and Europe. Cluster analysis (the neighbor-joining method) was applied based on biological distances generated by R matrices from craniofacial metric data in order to explore migration to the Americas and investigate population history and structure. We also explored climatic adaptation using body proportions and an index generated from postcranial measurements by principal component analysis and non-parametric regression analysis. The Jōmon of Japan display craniofacial similarity to Paleoindian/Paleoamericans and Archaic Americans. Moreover, the Jōmon and the inhabitants of North and South America display relatively "wider" body breadths as cold-derived adaptation. All results suggest that the ancestors of the Jōmon were the Late Pleistocene inhabitants of the northeastern and the northeastern coast of Asia, with some moving to the Japanese Archipelago and others moving to the New World as "the initial settlers" and they might be biologically related to some of the New World inhabitants.

Este estudio tiene como objetivo enfocar la migración temprana a las Américas y la historia de sus habitantes, además de las tendencias evolutivas en la adaptación climática, utilizando restos esqueléticos de los continentes americanos, con muestras esqueléticas geográficamente diversas del este de Asia, incluido el archipiélago japonés, noreste asiatico, sudeste asiático, Australia, Oceanía, África y Europa. Se aplicó el análisis de conglomerados (el método de unión de vecinos) basado en distancias biológicas generadas por matrices R a partir de datos métricos craneofaciales para explorar la migración a las Américas e investigar la historia y estructura de la población. También exploramos la adaptación climática utilizando proporciones corporales y un índice generado a partir de mediciones poscraneales mediante análisis de componentes principales y análisis de regresión no paramétrica. El individuo Jōmon de Japón muestra *una similitud craneofacial con los paleoindios / paleoamericanos y los pobladores americanos arcaicos. Además, los Jōmon y los habitantes de América del Norte y del Sur muestran una amplitud corporal relativamente "más amplia" como adaptación derivada del frío. Todos los resultados sugieren que los antepasados del Jōmon eran los habitantes del Pleistoceno tardío de las costas norestes, de los cuales algunos se trasladaron al archipiélago japonés y otros al Nuevo Mundo como "los primeros pobladores" y podrían ser biológicamente relacionado con algunos de los habitantes del Nuevo Mundo.*

Introduction

The Peopling of the New World

Human populations began to move from East Asia across Beringia into the New World sometime between 23,000 (Raghavan et al., 2015) and 17,000 years ago (Goebel, 1999). Questions concerning the human settlement of the New World have been long explored and certain topics are particularly discussed:

1. What is the initial date of entry?
2. What are the routes of access? (Quick migration via coastal route or via interior routes)
3. What are the genetic relationships to both living American groups to Asian and Pacific populations and possibly to other Old World peoples?
4. How much time is needed for notable genetic adaptations to occur?
5. What kind of changes in morphology might have taken place during/after the glacial period or migration from the Old World to the New World?

Among these questions, this study aims to shed light on early migration to the Americas and the population history of its inhabitants, and evolutionary trends in climatic adaptation using skeletal remains from the American continents, with geographically diverse skeletal samples from East Asia including the Japanese archipelago, Northeast Asia, Southeast Asia, Australia, Oceania, Africa, and Europe. This paper's focus on understanding the development of morphological diversity in Asia and the Americas will aid in the interpretation of adaptation and patterns of morphological variation throughout the world, including the major human geographic dispersals during the Late Pleistocene and Early Holocene and the peopling of the New World.

We aim to 1) document human cranial and postcranial biodiversity in the New World and further illuminate the population history between the Old and New Worlds; 2) document evolutionary trends using postcranial morphology, ie., climatic adaptation, drift, and gene flow; 3) interpret early New World diversity; and 4) further illuminate the population history between the Old and New Worlds and provide a comparative basis for the morphologies of later populations.

Materials

In this paper, we used craniofacial linear measurements (metric data) from the UMMA (University of Michigan Museum of Anthropology) dataset. There is limited skeletal evidence in Asia that corresponds to Paleoindians/ Paleomericans dated c. 12,000–8,500 years in the New World. In East Asia, the Prehistoric Jōmon of Japan are contemporaries of the Paleoamericans in the New World. Although the Jōmon Era dates from 16,500 to 2,300 BP (uncalibrated radiocarbon dates), our Jōmon sample runs from c. 6,000 to 2,300 years ago. The Neolithic Chinese, dated c. 7,000–5,000 BP, is another sample contemporary to archaic Americans of the New World in our dataset. Our archaic samples of the New World are represented by the Indian Knoll (5,000–4,000 BP), Windover (6,000-5,000 BC), Port au Choix (4,400–3,300 BP), and Tennessee archaic samples, including samples from the Eva Site (Tennessee Archaic 9,000 BP) and the Middle Archaic Period, c. 6,000 BC–3,000 BC. The Mongol Bronze Age Chandman from Western Mongolia, dated around 2,600–2,300 BP, is also included. We also used Paleoamericans of Lagoa Santa from Brazil (9,000-7,000 BP); and historic populations, such as Alaska, Aleut, Blackfoot (Montana and Canada), Chumash (Santa Cruz), Ossossané of the Great Lakes region, Mississippian of 900 BP, Athabascans, Haida, Hopi, Mexico, Peru, Patagonia, and Tierra del Fuego, with geographically diverse skeletal samples from Africa, Europe, Asia--including Yayoi rice agriculturalists of Japan (900 BC-250 AD), modern Siberia, Southeast Asia, Australia, and Polynesia (1,074 female individuals and 1,465 male individuals, totaling 2,539 individuals).

For postcranial data, we used variations in body and limb proportions of samples from Jōmon hunter-gatherers, Yayoi rice agriculturist of Japan; Lagoa Santa, Brazil; Eva Site (Tennessee Archaic 9,000 BP); Windover (6,000-5,000 BC); Indian Knoll (5000–4000 BP); Santa Cruz Islanders, California (Late Prehistoric 1500-1100 AD); and historic Tierra del Fuego with geographically diverse skeletal samples from Africa, Europe, Asia, and Australia. (549 female individuals; 743 male individuals; totaling 1,292 individuals.)

Methods: Craniofacial and postcranial analysis

Reconstruction of population history using craniofacial data

The craniofacial metric traits chosen by biological anthropologists have little adaptive significance and instead provide phylogenetic reconstructions. Craniofacial metric traits--configuration of face and skull--appear to be neutral. Therefore, craniofacial metric traits are useful to investigate population history and structure, and the quantitative treatment of craniofacial form can effectively produce a picture of human population movement (Betti et al., 2010; Brace et al., 2001; 2006; Seguchi and Schmidt, 2016; Relethford, 2005). It is compatible with the picture produced by molecular genetic comparisons of nucleotide haplotypes in modern human populations.

Reconstruction of morphological variation using postcranial data

It is well-known that human body size and shape exhibit considerable global variation. According to Bergmann's and Allen's rules (Bergmann, 1847; Allen, 1877), populations in cold climates exhibit larger body and smaller/shorter extremities than populations in hot climates. Therefore, skeletal limb size proportions may shed light on human evolution and climatic adaptation (Auberbach, 2007; Fukase et al., 2012; Holiday, 1999; Trinkaus, 1981, 2002; Temple et al., 2008, 2011; Ruff, 1991, 1994, 2002; Seguchi et al., 2017). Phenotypes of postcranial traits are influenced by natural selection, gene flow, random genetic drift, relatedness among populations, nutritional adaptation, etc.

Methods: Craniofacial metric analysis

These craniofacial metric analyses follow the methods of our past research (Seguchi et al., 2011; Brace et al., 2014). First, we used pelvic morphology to estimate sex using standard osteological protocols (Buikstra and Ubelaker, 1994). Twenty-one or nineteen craniofacial variables are used in this study. In order to maximize the sample size, all data were standardized to z-scores within each sex to remove sex-related size variation (Williams-Blangero and Blangero, 1989). To compute biological distances and reconstruct biological phylogeny, I employed the R-matrix method on the craniometric data in this study. Using the R-matrix method, overall environmental effects are removed by using an estimate of the overall average of heritability of all variables (Relethford, 2007). Many researchers using the R-matrix method for human craniometric data to average the reported narrow-sense inheritabilities (i.e., h2= 0.55). Then, the biological distances were obtained after an R-matrix analysis (Relethford, 1991; Relethford et al., 1997). The biological distances between samples generated by R-matrix analysis are roughly proportional to Mahalanobis distances (Relethford, 1991). The neighbor-joining method (Saitou and Nei, 1987) was applied based on biological distances generated by R matrices.

Methods: Postcranial metric analysis

These postcranial metric analyses follow the methods of our previous research (Seguchi et al., 2017). The postcranial measurements used in this study are maximum humeral length (abbreviation, HumL), maximum radial length (RadL), maximum femoral length (MaxFemL), bicondylar femoral length (FemL), antero-posterior femoral head breadth (FHB), and maximum tibial length (TibL). We calculated the ratios of FHB to FemL and FHB to lower limb length for an estimation of body mass divided by height that were used in previous studies (Auerbach, 2011b; Auerbach & Ruff, 2004; Fukase et al., 2012b; Ruff, 1994; Ruff et al., 1991, 2012; Temple & Matsumura, 2011). also calculated brachial and crural indices for estimation of upper and lower limb proportions (see Power Point for equations). Body mass was estimated using an equation: 2.3 × FHB-41.72 for combined sex proposed by Ruff et al. (2012). This equation is more suitable for estimating the body mass in European populations. Therefore, we caution that it might be problematic when applied to diverse global populations.

At first, data were subjected to boxplots for indices, ratios, body mass, and principal components analysis and principal components plot to display the distribution of data based on minimum and maximum, median, and 25th and 75th percentiles. We performed Manly's non-parametric regression tests (Manly, 1997) to determine ecogeographic significance (latitude, minimum and maximum temperatures) associated with particular PC scores. Significance was calculated after 10,000 permutations in a two-tail test ($\alpha = 0.05$) distribution. The Relethford-Blangero analysis was also performed using heritability of h2= 0.55 in order to see gene flow and genetic drift.

Results

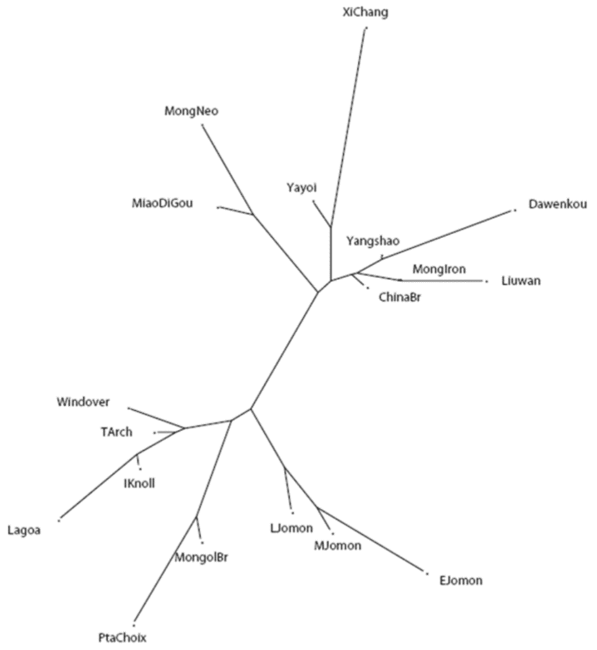
Craniofacial perspective

The neighbor-joining trees which were generated by the R-matrix using 21 variables that include the Jōmon hunter-gatherers of Japan, Chinese Neolithic groups from various areas, the prehistoric Yayoi agriculturalist of Japan, Bronze Age Chinese, Bronze age Mongol Chandman, Neolithic Mongol, Archaic Americans, and Brazilian Lagoa Santa, separated Chinese prehistoric groups, Neolithic Mongol with Yayoi of Japan and Jōmon, archaic Americans and Lagoa Santa (Figure 13.1). When we added the Jōmon, East, Southeast Asia, Africa, Pacific, Europe, and South Asia samples without the New World samples, Lagoa Santa is shown to tie to the Jōmon, Ainu, South Asia, and Europe samples. The tree of previous samples, added to the New World samples, including archaic American samples, and historic and modern native samples of North America, Central America and South America, resulted in showing that samples of the New World tie together, except for

Aleut, Eskimo, and Athabascan samples. The Athabascans, Aleut, and Eskimo samples tie more closely to the Chinese core samples. Lagoa Santa closely ties to the archaic Indian Knoll, and is located at the next branch with the cluster of the Jōmon and Ainu. These samples make a cluster of the historical Central and South American samples and the California coastal group, the Chumash. Other archaic samples such as Windover, Tennessee archaic, Port au Choix, and Mississippians, the historic Great Lakes Ossosone, historic Blackfoot that had migrated from the Great Lakes region, and the Mongol Bronze Age make a sub-cluster. Australian, Melanesian, and African samples form one cluster separated from the New world cluster (See Figure 13.2).

The NJ tree including the Kennewick individual and other Paleoindians in North America using 19 craniofacial variables display that all Paleoindians tie to Archaic American groups (Figure 3). However, the Kennewick individual ties to Ainu and Polynesian groups, and the Jōmon of Japan clustered with a 300 to 1,700 year old sample from Contra Costa county in San Francisco Bay and the Brazilian Paleoamerican Lagoa Santa (Brace et al., 2014). Other branches in the Jōmon clusters are the Haida from the Northwest Coast and other North American groups, Mexico, Peru, and the people of Tierra del Fuego and Patagonia at the southern end of South America.

Figure 13.1.
Craniometric analysis: Prehistoric East Asian samples, Yayoi agriculturalists of Japan and Jōmon of Japan including the Paleoamerican of Lagoa Santa and Archaic New World series.



Postcranial perspective

The box plots of z scores for each index, ratio, and body mass are shown in Figures 4. The box plots of each group are according to latitude from higher to lower, in other words, north to south. First of all, although box plots of brachial index show north to south clines, Jōmon and Kumejima of Japan do not fit this clinal distribution. Jōmon hunter-gatherer of Japan exhibits greater brachial value and similarity to groups from tropical environments at lower latitude as observed in earlier studies (e.g., Fukase et al., 2012b; Seguchi et al., 2017; Temple & Matsumura, 2011; Temple et al., 2008, 2011; Yamaguchi, 1982, 1989, 1994). However, Yayoi agriculturalists of Japan display similarity in brachial index with groups from colder environment at high latitude as observed by Temple et al. (2008). The Kumejima Island (Okinawa) belongs to a subtropical environment; however, the islanders display similarity with groups in higher latitudes and colder climates.

Figure 13.2.

The NJ tree based on craniofacial metric analysis. The prehistoric Jōmon of Japan and the living Ainu, clearly resemble the New World populations (See Seguchi et al., 2011).

Figure 13.3.

The NJ-tree based on craniometric analysis (Brace et al., 2014) including the Jōmon, Paleoamericans-9400 years old Kennewick, and 10,000-9,000 years old Lagoa Santa.

Figure 13.4. (a, b, c, d, e).

Boxplots of Z scores of all regional variation in brachial index, crural index, the ratio of FHB to FemL, the ratio of FHB to lower limb length, and body mass. Upper and lower margin of boxplots represent the 75th and 25th percentiles. The median is the line bisecting the box. Populations are presented in Table 3: From left (north: higher latitude) to right (south: lower latitude).

Figure 13.4a.

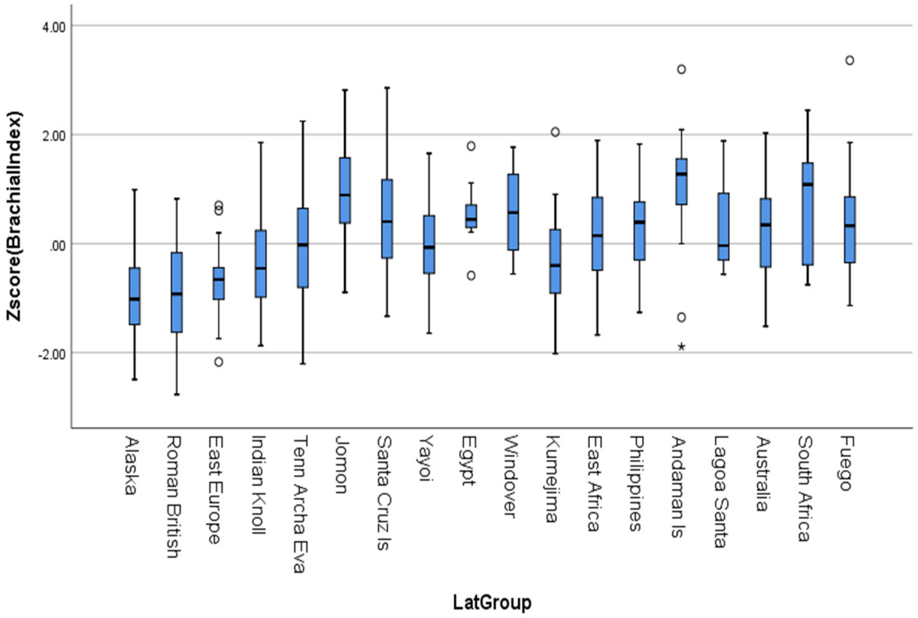


Figure 13.4b.

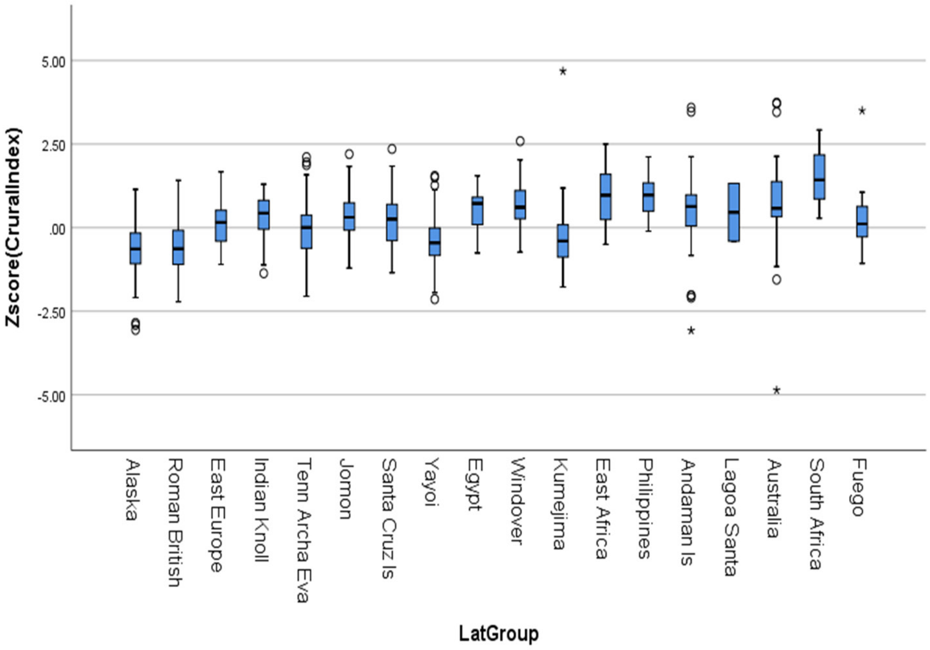


Figure 13.4c.

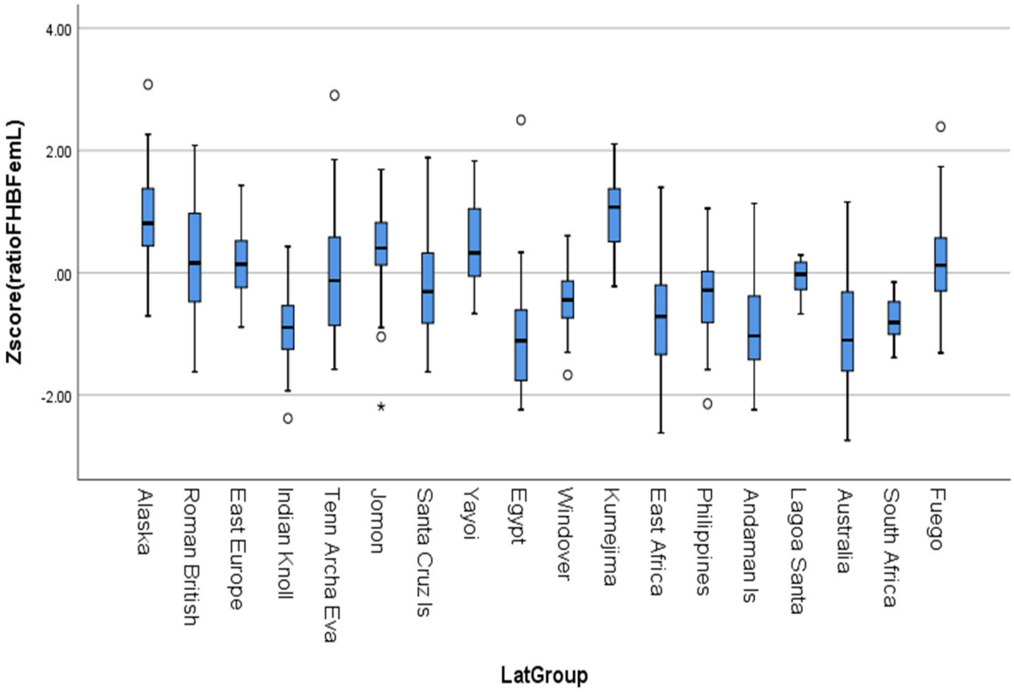


Figure 13.4d.

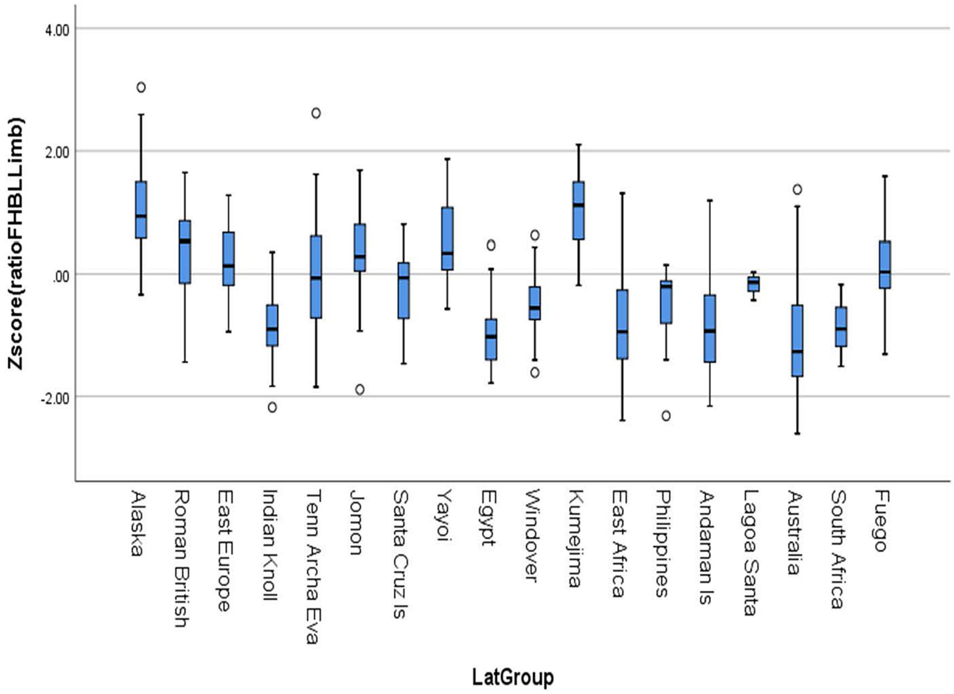


Figure 13.4e.

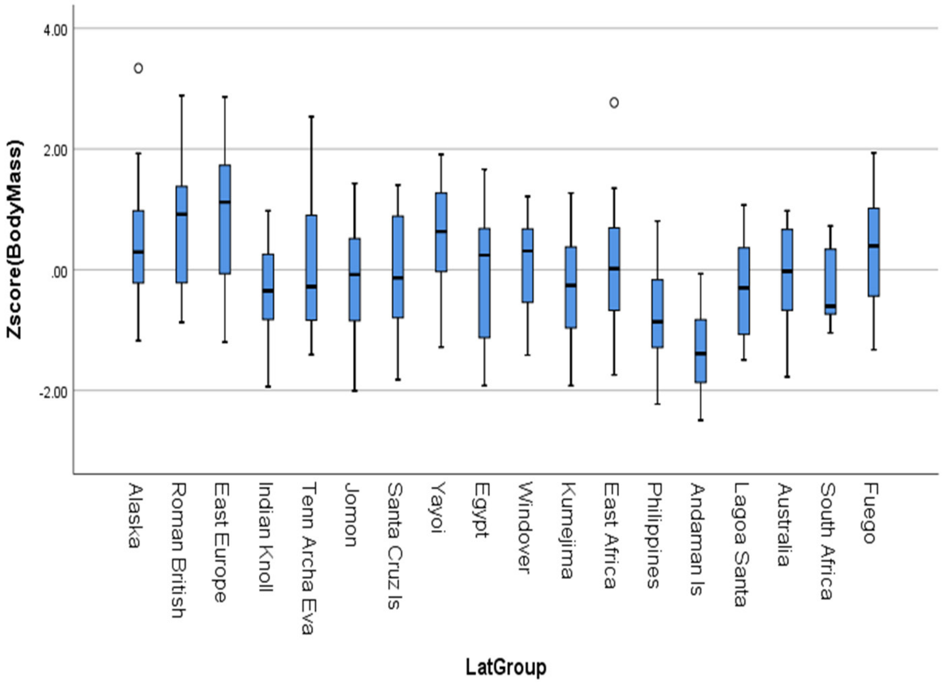
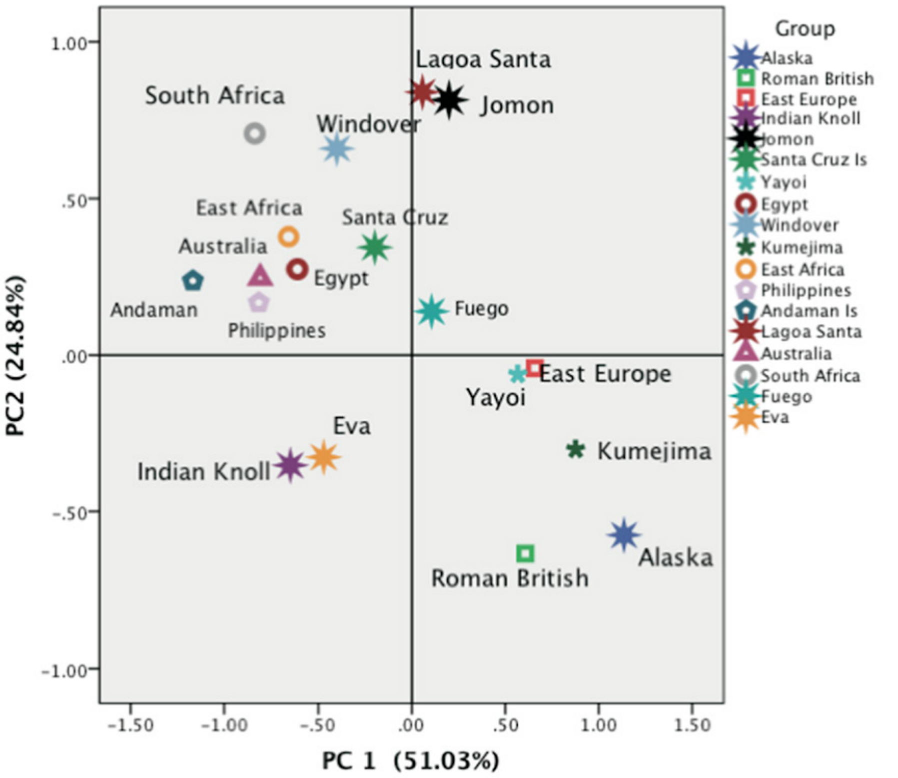


Figure 13.5.

Principal components plot of limb proportions, body proportions, and body mass.



The principal components plot separates well the warm-adapted and cold-adapted groups (Figure 5). For instance, groups that inhabit warmer climates such as East Africa, Egypt, Australia, Philippines Negritos, and Andaman Islanders are plotted in one cluster. Groups that inhabit colder climates such as Alaska, Roman-British, and East Europe are plotted in a separate cluster. Indian Knoll and Santa Cruz Islanders are plotted between the warm climate and cold climate groups. Yayoi is plotted with cold climate groups and, surprisingly, Kumejima is plotted among colder climate groups despite a smaller body mass.

Among those samples, Prehistoric Jōmon hunter-gatherers of Japan and Lagoa Santa Paleoamericans of Brazil are plotted far from either cluster, illustrating wider cold-adapted body proportions and warm adapted limb proportions. Lagoa Santa shows similarity with Jōmon in both body proportion and limb proportion. Alaskans display cold adapted wide-body proportion and cold adapted short-limb proportion. Tierra del Fuego of southernmost South America also displays cold adapted body and limb proportions. In summary, body proportions (relatively wide body; warm-adapted brachial index) of Jōmon, Lagoa Santa, Santa Cruz, Windover, and Tierra del Fuego are relatively similar. Indian Knoll and Eva sites are located close geographically and display similar body and limb proportions (relatively wide body, but warm adapted body mass; cold adapted brachial index). Samples of North America and South America show significant variation in body proportion.

Results of R-matrix-Relethford-Blangero analysis

R-matrix-Relethford-Blangero analysis shows a Fst of 0.3785 among sample groups (data not shown) which assuming average heritability of 0.55—incorporating all samples and assuming all samples have equal effective population size. Lagoa Santa is not included because the sample size is too small.

Furthermore, the results of Relethford-Blangero analysis show that most of the sample groups experienced little gene flow but a few including Kumejima of the Ryukyus may have received some gene flow. Santa Cruz shows statistically significant smaller observed variance than expected variance. On the other hand, Tierra del Fuego show significantly larger observed variance than expected variance. The negative residuals indicate some degree of genetic drift or isolation in these groups and their regions and more restricted gene flow. In other words, Santa Cruz may have experienced genetic drift or isolation or more restricted gene flow, while Tierra del Fuego may have received gene flow from other samples not included in this analysis.

Discussion and conclusions

From these analyses, the period of initial entry could not be concluded. However, the start of the Jōmon Era of Japan has a calibrated date of 16,500 years ago. Considering the craniofacial similarities between Jōmon and Paleoindians/Paleoamericans and the New World populations, a Jōmon Era "common" ancestor could be tied to the initial population that entered the New World in the terminal Pleistocene. They might have used watercraft to migrate via the Pacific Northwest coast to the San Francisco Bay down to Brazil and the southern end of South America (Patagonia) experiencing genetic drift or gene flow, because those coastal groups display craniofacial similarity to the Jōmon of Japan. These data and results suggest that the ancestors of the Jōmon people appear to be important in the peopling of the New World. We (Brace et al., 2001; Seguchi et al., 2011; Brace et al., 2014) have hypothesized that the "common" ancestors of the Jōmon are the Late Pleistocene inhabitants in the northeast coast of Asia and further west and some of them moved to the Japanese Archipelago and others moved to the New World as “the initial settlers.”

This analysis does not support affinities between the Early Brazilians and Australians and Melanesians (Neves et al., 2003; 2005; 2007; Neves and Hubbe, 2005). Rather, it shows they are related to the Late Pleistocene descendants of Northeast Asia, such as the ancestor of Jōmon (Seguchi et al., 2011; Brace et al., 2014). Results show morphological continuity from these Paleoindians/Paleoamericans to the Archaic across the north down to the Windover site in Florida. This indicates that this Jōmon-like morphology has been in place in the New World for at least 9,000 years. Paleoindians/Paleoamericans could be the ancestors of the Archaic people and the Canadian-US border Natives in the New World (Brace et al., 2001, 2014).

All significant correlations between PC 1 score from postcranial proportions and indices, and latitude, minimum and maximum temperatures indicate some trends in the dataset for a potential selective mechanism or adaptive pathway based particularly on body mass/height proportions. The limb proportion elements such as brachial and crural indices did not strongly correlate to the above ecogeographic variables, however the use of all ratios, body mass, and indices might be a good indicator of climatic adaptation as seen in the principal components plots. A mismatch in limb proportions and body proportions of the Jōmon is confirmed again as observed in earlier studies that is having cold-adapted body with tropical-adapted brachial index. Body proportions of the Jōmon and Lagoa Santa display relatively “wide” body breadths which are cold-derived adaptations. Ruff (1994) suggested that body breadth requires more generations to be changed by climatic factors. Groups in North and South America maintained wide bodies, despite living in different environments. This might suggest that initial populations of the New World obtained wider bodies when they were first inhabited and adapted in the colder climate in Northeast Asia before migrating to the American continents or possibly were trapped in a cold environment such as Beringia before they migrated to the New World. Then, they might have dispersed to various climatic environments in the New World at a later time. All results suggest that the ancestors of the Jōmon were the Late Pleistocene inhabitants of the northeastern coast of Asia, with some moving to the Japanese Archipelago and others moving to the New World as “the initial settlers".

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