

Jomon Culture and the peopling of the Japanese archipelago: advancements in the fields of morphometrics and ancient DNA

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ABSTRACT

Archaeological investigation of the Jomon Culture is extensive and well supported among the Japanese public. The distinct pottery that characterizes the Jomon has been well documented and physical anthropological description of skeletal remains in Japan has a long and extensive history. However, questions remain of Jomon peoples origins, biological contribution to modern Japanese and biological relationship to the agriculturalist people associated with the Yayoi culture. Morphological analyses of Jomon skeletal material have suggested ambiguous origins and inter-regional heterogeneity has been observed based on craniofacial variation. Ancient DNA of skeletal remains associated with the Jomon Culture indicates possible distinct genetic lineages associated with various locations throughout greater East and Southeast Asia. Here, we review the relevance of using ancient DNA and morphometrics to answer some of the above questions and challenge models based on the assumption that archaeological culture is equal to a shared biological history. Recent literature is reviewed and summarized in order to give the reader an idea of how basic assumptions of biological ancestry can be questioned using these new data. We end our discussion by suggesting further avenues of study and prospective research questions that could be asked in light of these new technologies.

KEYWORDS: physical anthropology, bioarchaeology, morphology, paleogenetics, Jomon, Yayoi

Introduction

The Jomon Culture of Japan is well known among the Japanese public and archaeologists exploring Japanese prehistory and the origins of the Japanese people. The Jomon people were hunter-gatherers and were named after distinctive pottery sherds first discovered in 1877 by the American zoologist Edward Morse. Japanese archaeologists, anthropologists, and geneticists have extensively studied the Jomon Culture and its people. After years of intense investigation, questions remain about the peoples who composed this culture

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(Adachi *et al.* 2009, 2011; Habu 2004; Hanihara & Ishida 2009). Where did they come from? What is their relationship to ancient peoples and modern groups living in Asia or the Americas? What was the direction of migration into the Japanese archipelago?

The Jomon Culture and period spanned many generations and to characterize the people associated with this culture as homogenous is simplistic at best. Their culture varied through time and space and is not amenable to such general statements. Though Jomon archaeology is a well-established entity in Japan, many Japanese archaeologists, the media, and general public are unaware of recent technological advances in the field of bioarchaeology. Here, we use the term ‘bioarchaeology’ to encompass the varied disciplines employed to study human skeletal remains found in associated Jomon archaeological sites, which includes genetics and morphometrics. In this review, we will prioritize data from morphological studies using a quantitative genetic framework, and newly available data gained from the field of ancient DNA extracted from skeletal remains in an effort to better understand the people associated with the Jomon Culture.

Past studies of the Jomon include geographic origins, their relationship with people’s during the Paleolithic, Bronze and Iron Ages, their possible ancestral relationship to the Ainu and potentially native populations of the Ryukyu Islands, their ecogeographic adaptation to diverse environments, and, finally, their nutrition, health, dietary variation, and environmental stress as evidenced in isotope studies and morphological studies of long bones and teeth (Hammer *et al.* 2006; Hanihara 1991; Hanihara *et al.* 2008; Hanihara & Ishida 2009; Tajima *et al.* 2004; Temple 2010; Yoneda *et al.* 2004). Studies of DNA in living peoples (Jinam *et al.* 2012; Tanaka *et al.* 2004), ancient DNA from skeletal material (Adachi *et al.* 2009; Horai *et al.* 1989; Kanzawa-Kiriyama *et al.* 2013), and craniometric characteristics (Hanihara 1991; Ishida *et al.* 2009) have been used to explore population affinities and movements. Past lifeways and environmental adaptations have been reconstructed through analyses of variation in body proportions, musculoskeletal markers of activity levels, and isotopic dietary markers (Temple 2010; Yoneda *et al.* 2004, 2011). Over more, the geographic area has been expanded in recent studies of Jomon population history to include the Japanese archipelago and East Asia, Southeast Asia, Pacific Islands, Australia, and also the New World (Adachi 2009; Brace *et al.* 2001, 2007, 2014; Omoto & Saitou 1997; Seguchi *et al.* 2011).

This review’s goal is to give the reader a better understanding of these techniques in order to more fully grasp the complexity of the Jomon Period and its people. To this end, we briefly cover advanced methods and summarize recent case studies. This review will summarize topics covering:

- Objectives of our review and frame of argument
- A brief history of physical anthropology in Japan and morphological studies and their implications to Jomon archaeology

- Methodological approaches and studies in Jomon ancient DNA
- Future directions and discussion in the study of Jomon people and bioarchaeology

Objectives and Framework of Argument

The theoretical argument made in many studies that use skeletal samples from an archaeological context is that those peoples who shared a similar cultural tradition (through the analysis of the material record) also shared a biological identity. We can never know if the “Jomon” people all thought of themselves as a singular identity in the same way modern peoples think of ethnic groups as having a shared cultural identity. What the field of ancient DNA can contribute to this argument lies in its ability to differentiate shared biological histories. Using advancements in ancient DNA and morphometric analysis, we now have the ability to resolve this question of biological identity. For example, the people of the Yayoi culture are assumed to be very different from those people who composed the Jomon culture. This is evident in the material record. The Yayoi practiced farming, used iron implements, and there is evidence for stratification not seen in Jomon archaeological sites (Mizoguchi 2013). In morphological appearance, there are significant differences in cranial and dental traits among the Jomon and Yayoi people (Brace & Nagai 1982; Brace *et al.* 1989; Pietrusewsky 2010), as well as cranial differences among Yayoi sites (Nakahashi 1993). Modern morphometric analysis allows us to “see” biological distances between these peoples, while ancient DNA analysis can “show” us exactly how parts of their DNA are different.

Ethnicity can be defined as a culturally constructed identity associated with particular customs and habitus (Bourdieu 1977), often asserting common descent among its members (Jones 1997). Materially defined archaeological cultures do not necessarily “map the extent and boundaries of self-conscious ethnic groups in the past” (Jones 1997 p. 120). Though group differences might exist along lines of descent or ritual, they may share similar styles or artifacts that would define them as a single group. Further, as ethnicity is a concept rather than something that exists biologically, ethnic labels should not be directly equated with biological distinctness or similarity.

These are just some of the difficulties correlating exact ethnic groups in the archaeological record with the material culture produced by those groups. This idea is important in light of Jomon/Yayoi morphological differences. For example, peoples of the Early Yayoi period in the northwest Kyushu region exhibit craniofacial features that are more characteristic Jomon; however, these individuals had clearly adopted rice agriculture and use of pottery closely associated with the Yayoi Culture (Kodaigaku Kyokai 2014; Nakahashi 2005). Also, archaeological data in northwest Kyushu actually indicate a persistent and autonomous Jomon population that persisted into the Yayoi period (Hoover

& Hudson 2013). Therefore, models assuming the people of an archaeological culture are equal to an ethnic group that is equal to a shared biological identity can now be challenged or confirmed using data from bioarchaeology. In this review, we highlight case studies that we hope will bring attention to the fact that these ethnic/biological models are outdated and need to be revised according to new data provided by the field of bioarchaeology, particularly data provided by ancient DNA and morphological studies that include a quantitative genetic framework to guide interpretation.

Our goal in this review is to re-think how we define a population's origins; and to what extent have those origins been clouded through the lens of nationalism, patriotism, historical consequence, racism, and even sexism. Although our target audience is non-East Asian specialists, our conceptual framework for the field of bioarchaeology can be applied to all areas of the world. The question of the peopling of the Japanese archipelago has been asked time and time again throughout the history of Japanese scholarship. The peopling of the Japanese archipelago (or any other part of the world for that matter) was a complex process whereby people moved into either uninhabited places, or encountered people who were already living in those places. What the new bioarchaeology can add to this debate lies in our ability to test these complex hypotheses. Rather than seeing a Jomon "type" or a Yayoi "type" as previous researchers have done, the new methods and data that bioarchaeologists are bringing to the table can potentially answer questions of demography, admixture, or migration that researchers have not heretofore been able to answer.

Humans have always migrated into new environments. Several important questions may be asked about these migrations and how they affected the peopling of the Japanese archipelago. Were the Jomon people a continuation from the Late Pleistocene inhabitants in the Japanese islands? Were Jomon peoples composed of several genetically different human groups? Were there people who continued to migrate from the Asian continent during the Jomon Period? Did those individuals who were representative of the Jomon Culture actively assimilate with the newly migrating Yayoi people? Were they replaced? Did they adopt aspects of Yayoi Culture only with no additional genetic admixture? If genetic admixture occurred, where was it most prevalent?

The dichotomy of indigenous Jomon/migrant Yayoi thinking that has pervaded this debate (and used by archaeologists and physical anthropologists alike) needs to be re-thought of in terms of place, identity, and diversity throughout the history of the peopling of Japan. We can no longer assume old models will account for this complexity.

The most widely held model for the peopling of Japan, i.e. the dual structure model, proposes differential origins for modern Japanese people, and how the ancient peoples of the Japanese archipelago contributed to the peopling of Japan (Hanihara 1991). Although the model has been tested using modern genetic data and a wide array of skeletal samples

with various aspects of the model confirmed, most of the data lack an appropriate time depth. For example, the use of modern genetic data is flawed by only using single marker loci, such as the mitochondrial DNA or Y chromosome (Ding *et al.* 2011), or biased in the genome-wide polymorphisms used to reconstruct Japanese population history (Jinam *et al.* 2012). Skeletal samples using craniometric data may be flawed simply because of a biased sampling scheme, i.e. only those best preserved crania (Brace *et al.* 1989). In addition, the model is too simplistic to account for the observed genetic diversity seen in the Japanese archipelago today.

For example, the Ainu, in the dual structure model, are proposed to be the modern descendants of the Jomon people. This interpretation is based on past study results indicating the Jomon people were morphologically homogenous. The Jomon samples in these studies were treated as a single biological entity. More recent studies suggest Jomon morphological heterogeneity. Therefore, are the Ainu only descended from Jomon peoples who inhabited parts of northern Honshu or Hokkaido? What about groups now living in Siberia? How have they shaped Ainu diversity? Through sophisticated data and analytical methods obtained from ancient DNA or high-resolution data obtained from geometric morphometrics, we can expand on this model to account for these potential complexities.

New data can add to the simplicity of the dual structure model by examining time slices of Japanese history to understand how populations evolved “in real time,” or through technologies that allow us to reconstruct population history based on more fragmented samples. Ancient DNA is one of the most powerful ways to examine these processes. However, the use of ancient DNA is still problematic given the small sample sizes (Kanzawa-Kiriyama *et al.* 2013), focus on only the mitochondrial DNA (Adachi *et al.* 2011; Igawa *et al.* 2009; Oota *et al.* 1995) and difficulties in controlling for modern contamination. Newly acquired morphometric data using explicit evolutionary models can test questions of migration, displacement, or admixture (Hanihara and Ishida 2009; Ishida *et al.* 2009). New technologies, such as CT scanning, have both power and resolution to better understand processes of health and disease (Walker *et al.* 2011) or development (Guntz *et al.* 2014). Combining the approaches of ancient DNA with morphometrics allows us to access population information at an unprecedented scale (Perez *et al.* 2009).

Japanese researchers have understood the complexities of the Jomon Culture through time by observing cultural evolution in the form of material goods. However, Japanese physical anthropologists (and other scholars) in the past have been obsessed with searching for and establishing a national identity for “the Japanese,” as well as defining “Japaneseness” for over 110 years. Consequently, physical anthropology in Japan has strongly influenced the creation of theories of Japanese origins through emphasizing a

unique biological origin for the Japanese people. Though there is no biological validity to the idea that the Japanese consist of one biological entity, racism has encouraged an emphasis on this sort of thought. Such biases have often been inappropriate for understanding biological and social variations and have brought about a world largely seen through the lens of an individual's own bias (Seguchi 1998). Now, it is time for researchers to examine the biological complexity of the Jomon people (and by extension, all modern Japanese peoples) by going beyond archetype descriptions of an “us” versus “them” framework, and view evolution and the peopling of Japan as the complex mixture of peoples and ideas that contributed to the diversity of the Japanese archipelago today.

The Peopling of Japan and Morphometrics

A brief history of Physical Anthropology in Japan

The study of the peopling of Japan from a physical anthropological perspective has a long history, extending back over 100 years (Low 2012). Sakano (1999) has even suggested that interest in archaeology and physical anthropology has its roots during the Tokogawa period (*c.* AD 1603–1868) when the Japanese people showed a regular interest in prehistoric remains. However, this interest did not stem from open-ended curiosity about the past, but rather the quest for old things became evidence for the ancient origin of the imperial line (Tanaka 2004, pp. 33). A key figure in these early years of archaeology was Ninagawa Noritane, part of the Museum Bureau of the Ministry of Education. In the late 1870s, Ninagawa befriended American zoologist Edward S. Morse, whom was educated under Louis Agassiz, a prominent figure in the development of American zoology, archaeology, and physical anthropology in North America.

Though Morse contributed extensively to the founding of anthropology in Japan, most consider Tsuboi Shogoro to be the founder of archaeology in Japan. He is also the founder of what later became known as the Anthropological Society of Nippon in 1884 (Low 2012). In 1893, Tsuboi established the Institute of Anthropology in Tokyo, shifting the focus among archaeologists from antiquarian curiosity to a focused anthropological archaeology akin to today's discipline. A central focus among members of the Nippon Society at this time was the origins of the Japanese people. Rather than the myth of Japanese homogeneity centering on the role of the emperor, many researchers at this time had a diversity of views and opinions on Japanese origins (Low 2012).

A discussion of Jomon archaeology and the origin of the Japanese people must include the Jomon's relationship with the Ainu, an indigenous population now living on Hokkaido, and in the Kuril and Sakhalin islands of Russia. Most researchers now believe the Ainu to be partial descendants of the Jomon people with varying levels of admixture with groups from the Amur River basin in Siberia (Hanihara 1991, 1998; Hanihara *et*

al. 2008; Kaburagi *et al.* 2010; Sato *et al.* 2009a; Shigematsu *et al.* 2004). Although the Ainu's contentious relationship with mainland Japanese is well documented (see Low 2012) in the history of ethnic issues in Japan, most researchers now agree that finding prehistoric cultural and/or biological connections among modern ethnic Japanese, Ainu and Ryukyu Islanders allows for the possibility of a new paradigm of the archaeology of the past to encompass diversity rather than homogeneity, and further provides space for a modern-day acceptance of ethnic diversity within the Japanese archipelago (Habu & Fawcett 1999).

Craniofacial variation: theory & methodology

Much of the research dedicated to uncovering the origins of the Jomon people and to reconstruct their population history has come from morphological studies of craniofacial and dental diversity. The premise for the study of morphological diversity is the same whether one is studying cranial or dental traits. That is, populations that exchange mates over time tend to have similar features and traits. It is these traits that are measured on the human skeleton. The quantification of these traits allows researchers to reconstruct past population structure and population history.

Population structure is primarily concerned with those factors affecting mate choice, the genetic relationships between individuals within a population, or subdivisions within a population. Various cultural, demographic, and ecological factors contribute to mate choice, which in turn invariably affects the genetic distances between individuals and groups. Population history studies generally are those factors that affect the genetic impact of historical circumstance, such as invasion, migration, and other events that might affect the genetic exchange between populations, essentially, historical factors that might affect the biological distance between a pair of populations.

In order to interpret population history and structure, one must calculate some estimate of biological distance. Distances can either be quantitative measurements or discrete traits of the skeleton. Most craniometric studies use an analytical procedure known as biodistance. In the case of craniometrics, craniofacial variation is used as a proxy for genetic variation. This justification, though controversial due to a number of confounding developmental, nutritional, and environmental factors, does have empirical evidence to support such a claim (Buikstra *et al.* 1990; Stojanowski & Schillaci 2006).

Biological distance studies contribute to understanding the pattern of differentiation; however, the interpretation of genetic distance is often complex. Why are populations A and B more similar to each other than either are to population C? For example, why are modern Ainu and Ryukyu Islanders more similar to one another than either are to modern mainland Japanese people? Why is population C more isolated from populations A and B? Is their isolation due to cultural or biological distinctness?

In an effort to answer some of these questions, morphological researchers use a specific model known as the Relethford-Blangero model (Relethford & Blangero 1990), which compares two different measures of variation within populations: the observed and expected levels of heterozygosity, which are similar to levels of phenotypic variation. A comparison can then be made between the observed and expected values of phenotypic variation, which can indicate something about the level of external gene flow into populations. This measure is highly informative for inferring biological diversity of groups that have maintained extensive contact through time but have had diverging histories, such as the Jomon and related groups in Japan.

Morphological studies of the Jomon

Morphological studies of Jomon skeletal remains include traditional craniometric and dental studies of the Jomon in the larger scheme of population history of East Asia, with comparisons to groups in SE Asia, Australo-Melanesia, and Polynesia (Brace *et al.* 1989; Hanihara 1991; Hanihara *et al.* 1993; Hanihara 1993, 2006; Matsumura 2006; Matsumura & Hudson 2005; Pietrusewsky 2006, 2010; Turner 1976); origins of modern Japanese people (Brace & Nagai 1982; Brace *et al.* 1989; Hanihara 1984; Nakahashi 1993); metric and nonmetric investigation of the Japanese people, Ainu and Jomon using the Relethford-Blangero method (Hanihara 2010; Hanihara & Ishida 2009; Hanihara *et al.* 2008; Ishida *et al.* 2009; Nakashima *et al.* 2010); and nonmetric investigations of Jomon and Ainu crania and teeth (Dodo & Kawakubu 2002; Kaburagi *et al.* 2010; Matsumura 2007; Morita *et al.* 2012; Nakashima *et al.* 2010; Ossenberg *et al.* 2006; Shigematsu *et al.* 2004).

Multivariate analyses of Japanese crania go back as early as the mid 1960s (Howells 1966) and continued into the 1980s and early 1990s (Brace *et al.* 1989; Hanihara 1991). These early approaches to population history have formed the basis of questions still being asked among researchers today. For example, Hanihara's seminal article (1991) put forth the "dual structure" model of Japanese population history. He formulated this model using diverse datasets, including multivariate analyses of Jomon crania. The "dual structure" model states that the morphological variation seen in ethnic modern Japanese people is the result of various degrees of admixture between Jomon and rice-farming Yayoi people who migrated to the Japanese islands from mainland East Asia, while the morphological variation seen in modern Ainu and Ryukyu Islanders retained relatively more Jomon derived physical traits, thereby completing the what he termed the "bipolarization" of the Japanese archipelago (Figure 1).

Hanihara (1991) derived this model from several competing models at the time. These include the replacement model, whereby the dominant Yayoi came to completely replace any vestige of Jomon genetic signature after they settled mainland Japan and the

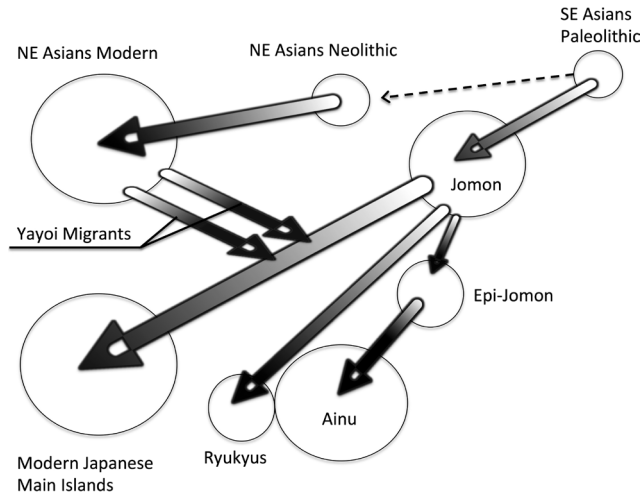


Figure 1. Schematic representing the “dual structure” hypothesis (redrawn from Hanihara, 1991).

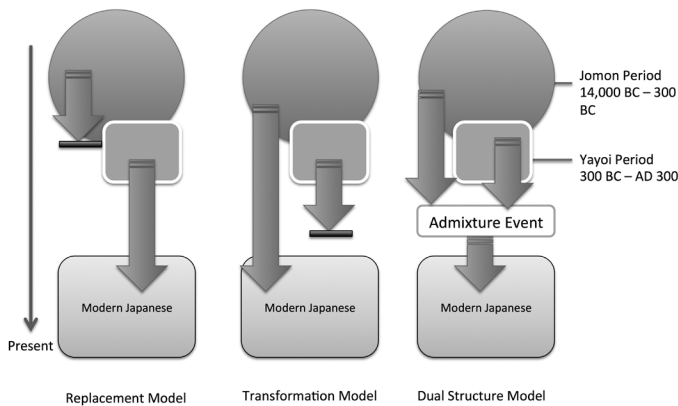


Figure 2. Schematic illustrating three competing hypotheses for the origins of the Japanese people (redrawn from Ding et al. 2011).

Transformation model, which contends the incoming Yayoi people did not extensively admix with the native Jomon, and therefore modern Japanese are an ancestral extension of the Jomon people. Both morphological and genetic evidence are used to support each model; however, most studies now support some aspect of the Admixture, or dual structure model (Figure 2). Even so, the dual structure model is too simple to account for local population structure within the Japanese archipelago. The theoretical underpinnings of the Relethford-Blangero model allow researchers to gain insight into complex admixture scenarios for the peopling of Japan.

For example, Ishida *et al.* (2009) use the Relethford-Blangero approach to reveal additional migration and gene flow into Hokkaido Ainu by the ancient Okhotsk people of the Amur River basin in Russia. Further, the impact of local migrations from Northeast Asian peoples from the Arctic, the Baikal region, or Inland Asian groups must be accounted for when discussing Japanese population history. The authors find the Jomon samples used in their analyses to have higher than expected levels of heterogeneity under the Relethford-Blangero model. These results are consistent with another craniometric study using only Jomon samples (Hanihara & Ishida 2009) and a study of ancient DNA Jomon Hokkaido skeletal remains (Adachi *et al.* 2011). Interestingly, Ishida *et al.* (2009) also find the Jomon people to be more closely related to a Bronze Age people from southern Siberia known to belong to the Tagar culture. Though this result has not been replicated in other studies (with the exception of Hanihara & Ishida 2009), it would prove as additional evidence for the Jomon to have retained archaic features (lack of craniofacial modernization, or gracilization) derived from expanding Upper Paleolithic populations somewhere around the western half of Eurasia, Central Asia, or southern Siberia.

Hanihara and Ishida (2009) make use of biological distance and the Relethford-Blangero model to test hypotheses concerning Jomon origins and pattern of migration into the Japanese archipelago. Intraregional variation was assessed by analyzing craniofacial variation from a number of Jomon sites located across the Japanese islands. Their results suggest a pattern of clinal variation (continuous gradient) emanating from north to south. The Hokkaido Jomon display the greatest levels of variance, followed by regions of eastern Japan, with successfully lower degrees of variance in the southwestern part of Japan. This clinal pattern would suggest a possible migration from the north into Honshu and a possible northern origin for the Jomon. In this respect, the biological identity of the Jomon is heterogeneous, and it may be indicative of diverse peoples who belonged to a common culture, known as the Jomon.

However, this interpretation of Jomon population history is unorthodox, as the prevailing paradigm among researchers is for a southern origin somewhere in SE Asia based largely on dental morphological traits, notably the characteristic sundadont pattern found among Jomon samples and seen in SE Asia and Austro-Melanesian peoples today (Hanihara 1991; Matsumura 2007; Matsumura & Hudson 2005; Turner 1990). Dental morphology of the Jomon indicates a the SE Asian sundadont pattern, however, dental metric evidence is not consistent with a southern origin interpretation since the Jomon possess a smaller dental size relative to SE Asian and Austro-Melanesian peoples, who tend to have larger dental sizes. The reduction in Jomon-Ainu dental size within a period of 12 000 years is not consistent with a SE Asian origin (Brace 1980; Brace & Nagai 1982; Brace *et al.* 1987, 1991).

In addition, a mismatch also exists in Jomon postcranial variation in limb and body proportions. Body proportions of the Jomon display “wide” body breadths and large body mass which are cold-derived adaptations, while their limb proportions are similar to people of a tropical climate (Fukase *et al.* 2012; Temple *et al.* 2008; Temple & Matsumura 2011). Multiple migration processes and possible routes for the peopling of East Asia might explain these results (Jomon affinity to NE Asia peoples and possibly Western Eurasian peoples), rather than a simple northern expansion model generally preferred among researchers (Uinuk-Ool *et al.* 2003).

Research into Jomon population history also includes an assessment of their relationship to skeletal material from the New World in order to answer questions pertaining to the founders of North and South America (Brace *et al.* 2001, 2008; Jantz & Owsley 1998a, 1998b; Lahr 1995; Nelson 1998; Nelson *et al.* 2007; Neves & Pucciarelli 1991; Seguchi *et al.* 2011; Steele & Powell 1992). It has been suggested that the Pleistocene ancestors of Jomon people migrated to the Japanese archipelago from Eurasia, possibly in the Altai Mountains of Siberia. The Altai are also a likely area for the origin of peoples into the New World (Dulik *et al.* 2012). Craniometric similarity between Paleoamericans and the Jomon support a possible link between the two populations, and ancient DNA from Jomon skeletal material suggests close affinities as well (Adachi *et al.* 2009; Brace *et al.* 2001, 2008, 2014; Dulik *et al.* 2012; Nelson *et al.* 2007; Seguchi *et al.* 2011). These data would suggest the ancestors of the Jomon and the Jomon people appear to be an important group in the peopling of the New World.

Ancient DNA

Ancient DNA damage and precautions against contamination

The use of ancient DNA (aDNA) is becoming increasingly popular in archaeological studies due to its ability to address core archaeological questions at a resolution previously unobtainable (Rizzi *et al.* 2012). Since DNA governs the development and functioning of all organisms, aDNA can provide phenotypic, demographic, and functional information invisible to the archaeological record. Another advantage of aDNA is that it provides an additional layer of phylogenetic information and permits the observation of populations evolving in “real time.” These advantages make aDNA a powerful tool to study the past.

However, difficulties do exist within the field of aDNA and one must proceed with caution when attempting to extract DNA from ancient skeletal samples. DNA degrades naturally within an organism’s lifetime, but this damage is repaired via a suite of host repair mechanisms. After death, these repair mechanisms no longer exist. As a result, few intact copies of aDNA tend to survive in older samples, and those that do remain are often highly fragmented and damaged (Fulton 2012). Over time, chemical processes

fragment DNA into short, damaged pieces. Some environmental conditions, such as cold or dry environments, inhibit this activity, potentially reducing the amount of damage. Though most studies of aDNA have focused on these environments, much skeletal material for study come from temperate climates, like Japan.

There are two main barriers to achieving authentic aDNA success from ancient samples: poor preservation of endogenous DNA (DNA inherent in the sample), and the presence of contaminant exogenous DNA (DNA amplified from sources other than the sample under analysis). Contamination is the biggest source of error in aDNA studies. Contamination may occur at multiple stages in the processing of aDNA samples. The sample itself may be contaminated. The most widely used types of samples for aDNA studies are bone and teeth. As bones and teeth are porous, contamination may occur via uptake of exogenous DNA, often in the form of microorganisms residing in the depositional environment. Contamination may also occur during the process of collection, a particular problem for human studies. Lastly, contamination might occur during the extraction and amplification process.

Paleogeneticists attempt to reduce the amount of modern and bacterial contamination by adhering to strict procedures. These procedures include, but are not limited to, physical isolation of the aDNA facility (aka “clean room”) from any post-PCR (polymerase chain reaction) processes and a strict “one-way” rule of movement into the clean room. Negative controls, within-lab replication for amplifications and extractions, a second laboratory to confirm results, and obtaining DNA from other samples, such as animal bones, from the site will lend credence to the results (Cooper & Poinar 2000).

The collection of samples at the archaeological site by trained paleogeneticists or archaeologists also reduces contamination (Allentoft 2013). For example, the excavator should wear protective clothing including a facemask, gloves, and full body suit to prevent contaminating the samples. The sample should be placed into an isolated container directly after removal to reduce potential contamination introduced by humans on-site. The sample should be kept cold and dry after excavation and should never be washed. In addition, if possible, the amount of time between excavation and DNA extraction should be minimized.

In the last several years, there has been a shift away from first generation sequencing technology to new technologies that are collectively known as next generation sequencing, or NGS. This shift has led to improved analytics and a reduction in sequencing costs. NGS uses short reads to sequence samples, and this is particularly useful for ancient DNA since the molecules are already degraded into short strands. NGS also allows researchers to check for contamination, assess whether the DNA reads are from modern or ancient samples, and access DNA from temperate environments, where gaining DNA from fossil material is most challenging.

Ancient DNA studies of Japanese archaeological remains

Ancient DNA studies of human remains from different archaeological periods in Japan have been widespread and include the Jomon Culture, Yayoi and Edo periods, and even studies of the ancient Okhotsk people from Hokkaido (Table 1). Many of these aDNA studies have focused on extracting mitochondrial DNA (mtDNA) from human remains associated with the Jomon in an effort to identify genetic signatures (haplogroups) that may represent modern living peoples from East Asia, SE Asia, or even Siberia. Ancient DNA researchers tend to focus on extracting mtDNA because of the higher copy number of molecules found in each cell as compared to nuclear DNA. Mitochondrial DNA is also useful as it tracks the maternal history of an individual, which tends to be inherited by similar members of a population. Thus, shared mtDNA amongst individuals suggests a similar biological identity.

Early Jomon skeletal remains were some of the first human remains to be sampled for aDNA analysis (Horai *et al.* 1989, 1991). Their results were similar to early morphological studies, suggesting an Early Jomon individual (Urawa I) differed from modern Japanese and were more closely related to populations in Southeast Asia. They also found support for a separate cluster that was the result of the Yayoi expansion. Despite these early results, very few additional studies on Jomon genetic diversity were published with the exception of Shinoda and Kanai (1999) and Shinoda (2003). Shinoda and Kanai (1999) analyzed a Jomon site in the Kanto region. Their results showed a diversity of mitochondrial sequence variation and further; their haplotypes did not segregate from modern Japanese samples, lending possible support to a small Jomon contribution to modern Japanese people, a finding postulated by Jinam *et al.* (2012) using many genetic markers on modern populations.

Much of the recent research into aDNA studies of the Jomon has been centered in Hokkaido, due to its cold climate (Adachi *et al.* 2009, 2011). Adachi *et al.* (2009) examined a small site known as Funadomari dating to 1800–1500 BC. Though the sample size was small (only 14 individuals), the authors observed a high frequency of a mitochondrial DNA lineage known as haplogroup N9b (66%). The coalescence time of this haplogroup (time to most recent common ancestor) is around 14 000 years before the present. This suggests that some of those peoples whom introduced microblades and were a part of the Mikoshiba culture also introduced this haplogroup into the Japanese archipelago. Interestingly, N9b is most common in modern Ainu and Ryukyu Islanders. The haplotype profiles of the Funadomari Jomon also differ from the Kanto Jomon as analyzed by Shinoda and Kanai (1999). Adachi *et al.* (2011) found Hokkaido Jomon to be similar to some modern Amur River Basin Siberian groups, notably the Udegay and Ulchi. However, the haplotypes that are most prevalent among these Siberian groups (A, C, D, and Y) were rare in Hokkaido Jomon, possibly suggesting a spread of these

Table 1. Ancient DNA studies of human remains found in Japanese archaeological sites. Current as of October 2014.

Author(s)	Significance	Location in Japan	Associated Cultural Period	Year Published
Adachi <i>et al.</i>	Ancient mtDNA from Edo period	Honshu	Edo Period	2004
Adachi <i>et al.</i>	Kinship analysis of Jomon site	Hokkaido	Final Jomon	2006
Adachi <i>et al.</i>	14 individuals. Sequencing found evidence for haplogroups D4h2, N9b, and M7a. Over 66% had N9b, considered a pre-Jomon lineage	Hokkaido	Late Jomon	2009
Adachi <i>et al.</i>	101 Late Jomon and Epi-Jomon. Major hgs included N9b, D4h2, G1b and M7a. Family of M7a common in modern Japanese, G1b found in SE Siberia and Ainu but less common in East and SE Asia	Hokkaido	Late Jomon/ Epi-Jomon	2011
Adachi <i>et al.</i>	Sequenced two teeth samples from the same Jomon individual from the Initial Jomon. Both belonged to hg D4b2, widely observed among East Asians	Nagano	Incipient Jomon	2013
Anzai <i>et al.</i>	PCR typing on Jomon (5-6ky BP)	Honshu/ Hokkaido	Late/Final Jomon	1999
Horai <i>et al.</i>	One of the earliest publications for successful DNA amplification and analysis for ancient human bone. Urawa-1, located in central Japan (Honshu) and dated ~6000 BP. Haplogroup later determined to be E1a1a	Kanto region	Early Jomon	1989
Horai <i>et al.</i>	Included 4 Jomon and 6 Ainu remains for analysis. Results showed close affiliation for mtDNA of Jomon and Ainu. Also found some genetic similarity to SE Asian groups	Kanto region	Early Jomon	1990

Table 1. Continued.

Author(s)	Significance	Location in Japan	Associated Cultural Period	Year Published
Igawa <i>et al.</i>	14 individuals from Yayoi Period	Kyushu	Yayoi	2009
Kanzawa-Kiriyama <i>et al.</i>	Sequenced 4 tooth samples from 4 different Tokoku Jomon dating to the Late Jomon period. 2 individuals had N9b (one had N9b12), and two had M7a2, high in Udegey (NE Siberian)	Tohoku	Late/Final Jomon	2013
Kazuta <i>et al.</i>	ABC gene from Jomon/Epi-jomon	Hokkaido	Jomon/ Epi-Jomon	2011
Kurosaki <i>et al.</i>	Two sets of human remains from Kyushu examined via PCR	Kyushu	Yayoi/Kofun	1993
Oota <i>et al.</i>	Ancient remains from the Yayoi period	Kyushu	Yayoi	1995
Sato <i>et al.</i>	ABO gene for Jomon and Okhotsk peoples	Hokkaido	Jomon	2010
Sato <i>et al.</i>	Peoples belonging to the Okhotsk culture	Hokkaido	Okhotsk	2007
Shinoda & Kanai	29 Jomon remains from the Kanto plain were included (~2500 BC, Late Jomon Period). Genetically diverse. Haplotypes were widely distributed among modern Japanese	Kanto region	Middle Jomon	1999
Shinoda & Kumisada	Large sample of individuals from Yayoi period	Kyushu	Yayoi	1994

haplotypes after the initial Jomon period. Indeed, Sato *et al.* (2009a) found a high level of the dominant Y haplotype in ancient Okhotsk people, who were first established in Hokkaido in the 5th century, pointing to the introduction of widely observed Siberian haplotypes before this time.

These results suggest a level of inter-regional heterogeneity not expected among Jomon groups. This observation is further substantiated by the studies of Kanzawa-Kiriyama *et al.* (2013) and Adachi *et al.* (2013). Kanzawa-Kiriyama *et al.* (2013) extracted aDNA from museum samples that came from the Sanganji shell mound site in Fukushima Prefecture dated to the Final Jomon Period. They tested for regional differences and found the Tokoku Jomon (Sanganji) were more similar to Hokkaido Jomon than to geographically adjacent Kanto Jomon. Adachi *et al.* (2013) describe aDNA sequence from a Jomon individual from Nagano (Yugora cave site) dated to the middle of the Initial Jomon Period (7920–7795 cal BP). This individual carried the D4b haplogroup, which is widely distributed among East Asians (Nohira *et al.* 2010; Umetsu *et al.* 2005). These observations, taken together with the Urawa I sample from Horai *et al.* (1989) exhibiting haplogroup E1ala, which originates in SE Asia, seem to indicate a complexity of Jomon population structure that still needs further investigation.

Directions of future research in Jomon bioarchaeology

In this review, we have explored both positive and negative approaches to reconstruct the peopling of the Japanese archipelago. Past physical anthropologists and molecular biologists used data they had available at the time, and they used that data to the best of their ability. In no way were any of these studies “bad” in the sense they were not doing good science. The problem with understanding the origins of the Japanese has been the political and social context in which researchers formulated opinions and interpreted data. Physical anthropologists have been driven to define the Jomon people and the peopling of the Japanese archipelago on the basis of nationalistic overtones of either the homogenization or the superior heterogeneity of the Japanese people. Morphometric and ancient genetic data have been utilized to understand Japanese origins. Those data have helped modern researchers reconstruct Jomon people’s origins and understand how they contributed to modern Japanese people. What we have tried to emphasize in this review is that we can use these questions to re-interpret that data, create new data through advanced technologies, and achieve an objective interpretation of Japanese origins removed from past social conventions. Moving the research in a positive direction means embracing analytical methodologies that may give researchers a greater understanding of how the Japanese archipelago was populated.

Recent theoretical and computational advances have shifted the focus of morphometric

procedure from linear measurements to Cartesian coordinates of anatomical points. This new approach to shape analysis in physical anthropology is called geometric morphometrics (Klingenberg 2010; Slice 2007). Geometric morphometrics is considered the suite of methods for the acquisition, processing, and analysis of shape variables that retain all of the geometric information contained within the data. Importantly, these methods allow for the separation of shape difference from absolute size difference, which might obscure analysis of population history by confounding populations based simply on size measurements. The most widely developed methodological approaches are the so-called Procrustes methods. Geometric morphometrics (GMM) has applications in many areas of skeletal biology, including sexual dimorphism, human evolution and origin studies, biodistance and microevolutionary studies, migration studies, phenotypic plasticity, morphological modularity and integration, growth and developmental studies, secular change, demographic history, selection and adaption of particular morphological traits (McKeown & Schmidt 2013).

Recent technological advancements have made a tremendous impact on the fields of biological anthropology and bioarchaeology. Biological anthropologists and bioarchaeologists are now utilizing many other new forms of technology, including computed tomography (CT) scanning, magnetic resonance imaging (MRI), and 3-dimensional laser scanner imaging. Three-dimensional imaging methods are now enabling biological anthropologists to expand and improve their research (Agathos *et al.* 2010; Emam *et al.* 2014; Katz & Friess 2014). Three-dimensional images are an ideal choice for conservation as they are completely non-destructive to human remains and other organic materials and also allow one to create a more detailed record in order to preserve fragile human remains. Three-dimensional scanning technology is new and therefore has no standard protocol for documenting/creating and analyzing these digital images. However, utilization of these three-dimensional images is just beginning, and we believe it will give tremendous potential to the field of biological anthropology and bioarchaeology in the near future.

Using these new morphometric approaches, researchers can now investigate a larger sample of Jomon remains to expand on the positive results of Ishida *et al.* (2009) and Hanihara and Ishida (2009). For example, these researchers found significant heterogeneity in Jomon remains found throughout the Japanese archipelago. How did Jomon heterogeneity contribute to their survival? Using 3D approaches, researchers now have greater access to uncovering areas of the skull that are most important to distinguish regional variation of Jomon groups. They may also access questions of adaptation that allowed the Jomon people to thrive and adapt to a diverse set of environmental conditions. Were there particular pathologies associated with their diet or living conditions that we might be able to uncover now using new morphometric

approaches?

In the field of ancient DNA, Japanese researchers have gained tremendous insight into Jomon population history. We now have data showing differential Asian maternal history that can apply to understanding where, ultimately, the Jomon originated. More samples are being analyzed from different parts of the Japanese archipelago, and we believe this will open up new questions of admixture analysis and also contribute insight into Jomon people diversity seen in various phenotypic characteristics. However, much work needs to be done. There is only so much information to be gained from the analysis of single marker genetic history. There are now powerful aDNA approaches that allow researchers access to more parts of the genome (Carpenter *et al.* 2013; Gansauge & Meyer 2013). Using these new techniques, researchers will be able to increase the number of samples, investigate remains from different environmental conditions, and achieve greater insight into Jomon population history. We can now start asking questions about how the peoples of the Jomon and Yayoi Cultures interacted in different parts of the Japanese archipelago.

Although we see these new technologies exponentially increasing our power to reconstruct Jomon population history, whole-genome sequencing combined with modern morphometric approaches will be in vain if the cloud of nationalism defines how modern Japanese people see themselves. Colonialism, racism, and nationalism have all driven how scientific researchers define “Japanese origins.” We need to ensure that these new technologies are not used improperly to bolster nationalistic opinions or obscure likeness and difference among modern peoples. Uncovering human history is a messy task with social overtones in the present. The new bioarchaeological approaches to reconstructing our history should be used to open up new avenues of learning and understanding. By showing the public how we are similar, or different, we can acknowledge diversity in the past and use this to build bridges in the present. We hope the fields of physical anthropology and bioarchaeology in the Japanese archipelago continue to uncover new and fascinating insight to better understand the human condition.

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