A Re-examination of the Sinodonty/Sundadonty Dental Complex and the Peopling of Japan

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts in Anthropology

by

Shannon A. Klainer

Dr. G. Richard Scott/Thesis Advisor

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We recommend that the thesis prepared under our supervision by

**SHANNON KLAINER**

Entitled

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G. Richard Scott, Ph.D., Advisor

Marin A. Pilloud, Ph.D., Committee Member

Hugh Shapiro, Ph.D., Graduate School Representative

David W. Zeh, Ph.D., Dean, Graduate School

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Abstract

The primary theory for the peopling of Japan is the dual origin hypothesis that states there were two separate migrations into Japan separated by more than 10,000 years. The early migration involved the ancestors of the Jomon who in turn were ancestral to the Ainu populations in Hokkaido and Sakhalin. A later migration dating to about 2200 BP was comprised of Neolithic farmers known as the Yayoi. There is debate over the origins of both the Jomon and Yayoi, with the dual origin hypothesis positing that the Jomon are Southeast Asian in origin while the Yayoi are East Asian. Others postulate that Jomon origins could lie in Northeast Asia and the Yayoi in Southeast Asia. To re-examine this debate, dental morphological data were analyzed for Jomon (n=643) Ainu (n=285) individuals categorized by island: Honshu, Hokkaido, and Sakhalin. Trait frequencies were compared to East Asian, Southeast Asian, Polynesian, Micronesian, Melanesian, New Guinea, and Australian samples to explore population relationships. Sinodont/Sundadont traits were analyzed through ANOVA for Jomon, Ainu, East Asian, and Southeast Asian populations to determine which traits showed significant differences among the groups. Analysis shows the modern Japanese are quite distinct from, and not related to, the Jomon and Ainu. The most likely geographic origin for the Jomon is Southeast Asia. Gene flow between East and Southeast Asians from the early Holocene on may contribute to some of the problems of interpreting Jomon and Yayoi origins. A lack of significant differences for UI1 double shoveling, UM1 enamel extensions, UP1 root number, LM1 deflecting wrinkle, and cusp number LM2 shows the possibility of Holocene gene flow between East Asia and Southeast Asia. UI1 shoveling most strongly characterizes the migration patterns in the dual origin hypothesis. UI1 shoveling is a trait associated with the EDAR 370A gene variant as well as Sinodonty, meaning that the gene could aid in characterizing migrations into Japan.
I would like to dedicate this thesis to my parents, who have always supported me in all that I do, no matter how many miles away.
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Introduction

The debate over population history in Asia, specifically Japan, extends back to the mid-1800s when American Naval Commodore Matthew C. Perry demanded that Japan open its borders to trade. The exchange of ideas accompanied the exchange of goods as western anthropologists flocked to the country to conduct research in archaeology and physical anthropology. The Ainu people fascinated the western anthropologists who sought to classify them as Mongoloids, Australoids, or Caucasoids and determine how they were related to other Asian groups (Fitzhugh 1999).

The debate over Ainu origins eventually evolved into a discussion of the population history of Japan. The modern Japanese people have long realized they are not related to the Ainu but believed they were affiliated with the prehistoric Jomon, a rich hunter-gatherer culture known for their intricate pottery. As the paradigm shifted, nationalistic Japanese archaeologists saw archaeology as history and studied only the ancestors of modern Japanese peoples, that is the Jomon (Mizoguchi 2002; Habu 2004). Questions of relatedness were considered taboo in the field in the event that it contradicted their presupposition about Jomon-Japanese relationships. This thesis seeks to answer questions about the peopling of Japan through the use of dental morphological evidence to determine “who came from where, and when?” as well as provide additional commentary on traits used in morphological analysis.

Archaeology

In discussing Japanese archaeology, it is important to define the area of the sites. Some texts note site location relative to modern Japanese states, whereas others specify the general location of a site, e.g., western or eastern Japan (Mizoguchi 2002; Kenrick 1995; Habu 2004).
Western Japan refers to the Kinki, Chugoku, Shikoku, and Kyushu regions, while eastern Japan refers to the Hokkaido, Tohoku, Kanto, Chubu, Hokuriku, and Tokai regions (Figure 1.1). The main island of Japan will be referred to as Honshu or Hondo interchangeably depending on the author cited, but Honshu by the thesis author. The Ainu are not located exclusively in Japan but also occupy Sakhalin and the Kurile Islands of Russia. Dates are listed as BP or BC/AD depending on the author.

**Fig. 1.1.** Map of Japan and surrounding islands. Map courtesy of Free Vector Maps, allowed for use with attribution.
The Jomon era extends over ten millennia and is subdivided into several stages (Takahashi et al. 1998): Incipient (12,000-10,000 BP), Earliest (10,000-6000), Early (6000-5000), Middle (5000-4000), Late (4000-3000), and Latest (3000-2500 or 2400). Some also add categories of Late and Final (Kenrick 1995). The Jomon sample for this thesis dates around 2500-300 BC, which is the Middle to Late Jomon period, after later material culture is present in the archaeological record (Mizoguchi 2002).

The origin of the Ainu is shrouded in more ambiguity than the Jomon (Siddle 1999). They are largely considered to be the remains of a proto-Japanese culture that failed to evolve over the past 1500 years (Yamaura and Ushiro 1999; Low 2012; Sleeboom 2004), and are regarded to be directly descended from Satsumon and Okhotsk cultures (Watanabe 1972; Kreiner 1999; Walker 2001) with their relation to the Jomon hotly debated. Written Japanese state records refer to emishi, or barbarians, that appeared in the north between the 7th and 12th centuries (Siddle 1999).

Since both the Ainu and Jomon inhabited the northern island of Hokkaido, similarities can be drawn between their subsistence strategies. Given their many millennia of occupation in Japan and the dramatic temperature changes that occurred within this timeframe (Mizoguchi 2002; Habu 2004; Palmer 2007), there is debate over Jomon subsistence strategies. Their subsistence strategies were not homogenous and varied with region and tribe, and were influenced by climatic factors associated with different time periods (Mizoguchi 2002).

The first of the debated subsistence strategies, the “salmon hypothesis” (Habu 2004), is based off a subsistence pattern practiced by the Hokkaido Ainu as well as Native Americans in California. There is little evidence to suggest this was a primary subsistence strategy. The same can be said for the second “plant cultivation hypothesis” (Habu 2004) that specifically dates to
the Middle Jomon period due to the use of hand axes as aids in planting cultigens; however, there is little physical evidence to suggest this was a primary source of food. Another theory reconciles the two as well as the variation of evidence at Jomonese sites. The Jomon subsistence calendar (Habu 2004) indicates that fish and other seafood were usually hunted in the spring and summer, gathering took place in the fall, and game hunting took place in the winter.

Jomon reliance on river fish has been compared to that of the Ainu. The Ainu are more technologically advanced in their hunting (Watanabe 1972), which enabled them to hunt in mid- to late-November as well as December. The advent of the bow and arrow made their terrestrial hunting method more advanced, as the Jomon used spears (Watanabe 1972; Habu 2004). Regardless of technological differences in hunting, both the Jomon and Ainu held particular reverence for hunting bears (Etter 1949; Akino 1999; Habu 2004).

When wet rice agriculture was introduced into Japan by the Yayoi culture around 2200 BP, the archaeological question becomes one of replacement versus adaptation: did the Jomon adopt new subsistent techniques or were they replaced by an incoming culture from the mainland (Brace et al. 1989)? The similarities between the Ainu and Jomon suggest some level of continuity. Given that the Ainu are primarily located in the north while the Jomon settled all across the Japanese islands, the possibility of replacement in some areas does exist (Watanabe 1972; Habu 2004). The incoming Yayoi are thought to have replaced the Late Jomon due to their sheer numbers. Aoki and Omoto (1980) used blood groups to compute migration and population growth estimates, suggesting a staggering number of 2,800,000 Yayoi individuals to 14,000 Jomon, or a ratio of approximately 200:1. The replacement of the Jomon by the Yayoi is related to relative reproductive success (Brace et al. 1989) as there is no physical or material evidence for violence between the two groups. While material culture cannot answer the question of
Jomon and Ainu relatedness in full, skeletal remains have been analyzed in an attempt to clarify the relationship.

_Cranial Data_

While there are regional variants among the islands, Japan has become increasingly homogenous in terms of cranial morphology over time (Ossenberg et al. 2006). The Jomon population as a whole spans over thirteen thousand years across the Japanese archipelago, so it is natural to assume their skeletal remains will vary with time and geographic area. However, their physical variation is still less than that exhibited by the modern Japanese population (Ossenberg et al. 2006). Howells (1986) claims the Jomon are not uniform and vary between populations.

From craniometric analysis, some researchers concluded the Ainu are the direct descendants of the Jomon (Hanihara T 1992a; Pietrusewsky 1992; Brace et al. 1989; Kaifu 1997). The incoming Yayoi culture matches more closely with mainland populations as well as the modern Japanese (Pietrusewsky 1999; Brace et al. 1989). Pietrusewsky (1992) notes that the modern Japanese show relation to modern Southeast Asia, although he concludes in a more recent article (2010) that the Japanese share a recent common ancestor with China and Korea instead. Cranial nonmetric trait frequencies appear regionally in a clinal pattern due to gene flow that occurs from people immigrating into already occupied lands (Weiss 1988). The Japanese migrated from westward to northeastward. It is in the northeastern-most parts of Japan that the cranial and genetic influence of continental Asia is the weakest (Ossenberg et al. 2006). Nonmetric cranial analysis has also been used in support of the Ainu’s direct relation to the Jomon (Ossenberg et al. 2006; Hanihara T 1992a).
In addition to the question of the Jomon-Ainu relatedness, there is the problem of Jomon origins. Craniometrics and nonmetric cranial traits (Hanihara T 1992b) indicate the Jomon originated from Southeast Asia. There is disagreement on their closest relatives: the Jomon have been stated to be closely related to Polynesia and Micronesia (Brace et al. 1989) while others find the Jomon are most similar to “proto-Malays” (Hanihara T 1992b) or the aboriginal population in Southeast Asia prior to recent Chinese influence.

The Ryukyu Islanders also provide insight on the Jomon/Ainu relationship. Kazuro Hanihara (1991) found the Ryukyu Islanders and the Ainu to be related from a common ancestor. Pietrusewsky (1999) found no biological closeness between the Jomon/Ainu and the Ryukyu Islanders, but viewed them as similar to the Ainu in that they represent a lack of Yayoi admixture. This suggests two early groups on the Japanese archipelago prior to the immigration of the Yayoi.

Another complication is that the Ainu are admixed with the Okhotsk people, most notably the Sakhalin Ainu (Hanihara T. et al 2008). The Okhotsk people originated from northeast continental Asia, and spread from the southernmost point of Sakhalin Island into northern Hokkaido (Hanihara T. et al. 2008). Admixture between peoples of the Okhotsk culture and recent Ainu populations in northeast Hokkaido may have biologically impacted the Ainu so that they look less like the ancient Jomon population (Hanihara T. et al 2008). This hypothesis is in agreement with some genetic studies (Taijima et al. 2004).

**Dental Data**

Similar to cranial data, dental data are typically broken into metrics and nonmetrics. Dental nonmetrics, or dental morphology, refers to crown and root traits that are typically absent
or present and when present, vary from slight to pronounced expressions. Tooth crown and root traits show a positive relationship to population ancestry (Turner et al. 1991; Scott and Irish 2017). The genetic variation in dental morphological trait expression has led to the discovery of several ancestral patterns around the globe (Scott et al. 2018a). Initially K. Hanihara (1968) defined a “Mongoloid dental complex” based on high frequencies of shoveling, cusp 6, the protostylid, and the deflecting wrinkle in Japanese, Native American, and Eskimo populations.

In 1990, Turner found that the Mongoloid dental pattern could be divided into two patterns: Sinodonty and Sundadonty. The Sinodont pattern is shown by populations in East Asia and the New World (Turner 1990; Turner 1992a; Manabe et al. 2003; Scott et al. 2018a). It is characterized by high frequencies of a few select traits. The Sundadont pattern that characterizes Southeast Asian and derived populations (e.g., Polynesians) is characterized by trait retention, wherein most traits have neither a particularly high nor low frequency (Turner 1990; Turner 1992a; Scott et al. 2018a). There are eight traits that define the dichotomy. UI1 double shoveling, three-rooted LM1, pegged-reduced missing UM3, LM1 deflecting wrinkle, UM1 enamel extensions, and UI1 shoveling have higher frequencies in Sinodons. Four-cusped LM2 and two-rooted UP1 have higher frequencies in Sundadonts (Turner 1990; Turner 1992a; Scott et al. 2018a). The Sinodont pattern is considered the derived pattern (Turner 1992a; Scott et al. 2018a) that is more specialized than the ancestral Sundadont pattern that served as the base for the eventual development of Sinodonty (Turner 1990) during the late Pleistocene (Manabe et al. 2003). Basically, the Sundadonty pattern is conserved while Sinodonty reflects a more derived pattern for a suite of variables, highlighted by UI1 shoveling and double-shoveling.

The recognition of two dental patterns has allowed anthropologists to address questions regarding migration and ancestry. The implications of Sundadonty being the base for Sinodonty
means that, at some point, Sundadont populations had to have been more widely distributed in East and Northeast Asia. This is also the primary explanation for the relatedness of the Ainu and Jomon using dental morphology. In 1976, Turner published an article on the relatedness of the Jomon, Ainu, modern Japanese, and An-yang Chinese. Some of the traits he lists fall outside the Sinodont and Sundadont dichotomy, such as Carabelli’s cusp and groove pattern, although most Sinodont and Sundadont traits are represented. Turner (1976) states that the dental data from chi-square analysis supports the archaeological evidence of a mass migration. He found a significant difference between the Jomon and modern Japanese dentition, and concluded the Jomon were not ancestral to the modern Japanese population. He stated that the modern Japanese were related to Neolithic Chinese agriculturalists, while the Ainu were descendants of the Jomon (Turner 1976; Turner 1992a).

Further dental morphological studies support the Ainu as the direct descendants of the Jomonese population, with the modern Japanese derived from Yayoi agriculturalists (Turner and Hanihara K 1977; Turner 1979; Turner 1987; Hanihara T 1990; Hanihara T 1992a; Hanihara T 1992c; Turner 1992a; Matsumura 1995; Higa et al. 2003; Hanihara T 2010). Much like the Jomon and the cranial variation between populations across Honshu, the dental morphology for the Ainu has been described as homogenous regardless of whether the population resides in Hokkaido or Sakhalin (T Hanihara 2010). This means both populations likely come from the same common ancestor.

Dental metric data have also been used to address the Jomon-Ainu question. Much like cranial metrics, cranial nonmetrics, and dental morphology, distance analyses of dental metrics support the Jomon-Ainu link and the Sinodont/Sundadont dichotomy (Hanihara T 1992a; Hanihara T 1992c; Hanihara T 2010). There has been opposition to this conclusion. T. Hanihara
acknowledges in his 2010 article that some of his previous work has indicated the Jomon and Ainu are closely related to Northeast Asia (Hanihara T. et al 2008). T. Hanihara and Ishida (2005) state that the dental metrics do not support the division of East Asian groups into Sinodonts and Sundadonts. Notably, the Jomon are thought to be most like populations from Australia and Papua New Guinea, while the Ainu are most closely related to Northeast Asians. Matsumura (1995) agrees that the Jomon might not be related to Southeast Asians, but cites East Asians as possible ancestors. This view is later reiterated by Hudson and Matsumura (2006).

**Genetic Data**

Mitochondrial DNA sequencing, autosomal single nucleotide polymorphisms (SNPs), genome-wide SNPs, and Y chromosome polymorphisms have been used by scientists to evaluate the relatedness of East and Southeast Asian populations. Admixture makes using “synchronic genetic markers” difficult, particularly between Ainu and Japanese populations (Omoto 1992).

Mitochondrial DNA analysis suggests that while physically the Jomon may seem uniform among their island populations, genetically they are not (Adachi et al. 2009). The Funadomari (Hokkaido) Jomon differ from the Kanto Jomon in haplogroups; the Funadomari Jomon belong to haplogroups N9b and M7a while the Kanto Jomon have D^a and M10 (Adachi et al. 2009). Adachi et al. (2009) note the Jomon are completely different genetically from Southeast Asians; however, shared mtDNA sequences have been found between the Jomon and Southeast Asia. Oota et al. (1999) found connections between the Jomon and Southeast Asia, although they do not call it a strong connection since the Jomon do not cluster with all Southeast Asian groups. Mitochondrial DNA haplogroups differentiate the Hokkaido Ainu from the Hokkaido Jomon (Sato et al. 2009) although it is believed this is due to gene flow between the Okhotsk people and the Ainu (Tajima et al. 2004; Sato et al. 2009). Sequences in Ryukyu Islanders and the Ainu
indicate evidence of northern and southern migrations due to M and N lineages within both populations (Tanaka et al. 2004). Tanaka et al. (2004) suggest that the northern influences acquired by the Ryukyuan Islanders and the Ainu are from recent admixture with mainland Japanese, while their southern genetic lineages suggest a more ancient migration.

Autosomal (non-sex chromosomes) single nucleotide polymorphism analysis has further confounded the source of migrations in and out of Japan. The genetic evidence remains consistent with previous biological data as the Jomon are shown to be unrelated to the modern Japanese (He et al. 2012). None of the Jomon groups analyzed using SNPs suggest South Asian or Southeast Asian origin (He et al. 2012). Classic markers also show that the Ainu and Ryukyu Islanders, who are likely descendants of the Jomon, belong to a Northeast Asian group (Omoto and Saitou 1997). Polymorphisms in easily observed phenotypic traits have pointed to multiple migration events (Yamaguchi-Kabata et al. 2008), and mainland modern Japanese individuals are most likely derived from the Yayoi, while Okinawans and the Ainu are related to the Jomon.

One of two genetic analyses that is particularly relevant to the peopling of Japan is a dichotomy in Y chromosomal polymorphisms. A haplogroup within the Y chromosome, DE, is central to Asia, Africa, Europe, and the Middle East, with the subclade D only existing in East Asia (Karafet et al. 2008). The mutation that defines haplogroup DE is the Y-chromosome Alu polymorphism, or YAP (Hammer and Horai 1995; Hammer et al. 2006; Karafet et al. 2008). All Y chromosomes belonging to DE and subclades are YAP-positive, or YAP+ (Hammer and Horai 1995; Hammer et al. 2006; Karafet et al. 2008). Since East Asians belong to Haplogroup D, this means they should exhibit YAP+ while Southeast Asian and Australo-Melanesian populations should be YAP-. This hypothetically should create a dichotomy like Sinodonty and Sundadonty, where East Asian individuals would be YAP+ and Sinodont, while Southeast Asian individuals
would be YAP- and Sundadont. However, this is not the case. Hammer and Horai (1995) believe that the YAP+ polymorphism was carried to Japan by the Jomon approximately 10,000 years ago, and that YAP- came with the Yayoi around 2,300 years ago. These data have been used to suggest the Jomon are from Central Asia and the Yayoi from Southeast Asia, which the authors acknowledge is the opposite of most genetic or morphometric studies (Hammer et al. 2006). Despite the origins of the Jomon and Yayoi coming into question, both studies (Hammer and Horai 1995; Hammer et al. 2006), agree that the Jomon are ancestral to the Ainu as well as Ryukyuans, and the Yayoi are ancestral to the modern Japanese. Other studies have cited the Jomon and Ainu as YAP+ while agreeing the two are unrelated to the modern Japanese (Tajima et al. 2004; Matsukusa et al. 2010).

The second genetic analysis suggests a biological dichotomy in the single nucleotide polymorphism *ectodysplasin A receptor* gene (EDAR), (Park et al. 2012; Hlusko et al. 2018). There is a strong association for the EDAR 370A allele in Asian populations, and it is rare in African and European populations (Fujimoto et al. 2008; Park et al. 2012; Hlusko et al. 2018). It is traditionally associated with hair thickness (Fujimoto et al. 2008; Park et al. 2012) and was likely selected for approximately 20,000 years ago in Northeast and East Asia due to the variant giving an advantage in nutrient transfer through breast milk in low ultraviolet light environments (Hlusko et al. 2018). The allele is also associated with higher frequencies of at least three Sinodont traits: shoveling, double shoveling, and the hypoconulid (Park et al. 2012; Hlusko et al. 2018). Park et al. (2012) found that while both Korean and Japanese samples had high frequencies of the gene, the Korean sample had a higher frequency indicating that the allele likely arose in continental East Asia. Worldwide genome analysis from the Allele Frequency Database (ALFRED) indicates that East Asians typically have a higher frequency of the EDAR
370A allele (66-95%); Southeast Asians have a lower frequency (20-50%) with Australo-Melanesia populations almost not representing the gene at all with a frequency of approximately 0-0.03% (Kidd et al. 2003; Kidd et al. 2018). This creates a dichotomy similar to that of Sinodonty and Sundadonty.

_Dual Origin Hypothesis_

The theories for the peopling of Japan fall into three main categories: substitution, hybridization, and transformation (Hammer et al. 2006). Substitution theories involve the replacement of a group of people, meaning that the modern population should have no genetic or visible physical characteristics of the original population (Hammer et al. 2006). Hybridization involves admixture or gene flow between two groups. Conversely, transformation theories involve a group gradually evolving from a single ancient population—this is more often referred to as a continuity theory (Hammer et al. 2006).

The original model for the peopling of Japan was the continuity model. Kenji Kiyono was an archaeologist who proposed in the 1930s that the Jomon were the ancestors of the modern Japanese population, who became morphologically altered from the Jomon over time (Nishioka and Schenck 1937; Sato et al. 1983; Hanihara K 1991; Nanta 2008). This theory was in line with the nationalist thoughts at the time, as the beautiful Jomon pottery was thought of as inherently Japanese (Sato et al. 1983; Habu 2004; Nanta 2008).

The way Japanese archaeologists refer to integrated groups of people is lost in the English translation. In English “race” is one word, but in Japan there are two terms that can be defined as such with differing connotations (Low 2012). *Jinshu* means “human breed” or “human race” whereas *minzoku* is defined as “ethnicity,” “nationality,” or “race” (Low 2012).
These 19th century anthropologists most often stated they are interested in the jinshuteki, or physical racial origins, of the Ainu. This explains the historical focus on the physical evidence of the origins of the Ainu. Prior to Kiyono in 1888, Japanese anatomist Yoshikiyo Koganei studied Ainu skeletons and concluded the Jomon were ancestral to them rather than the Japanese (Nishioka and Schenck 1937; Tubbs et al. 2009; Watanabe et al. 2012). Koganei’s interpretation of Ainu skeletons would not be revisited until much later.

The dual structure model for the peopling of Japan, or dual origin hypothesis, was originally proposed by Kazuro Hanihara in 1991. It hypothesizes two different migratory events into Japan: (1) the peopling of the Japanese archipelago by the Jomon, who would later go on to be ancestral to the Ainu as well as Ryukyu Islanders, and (2) a second migration from continental East Asia of Neolithic farmers (the Yayoi) who would become ancestral to the modern Japanese population (Hanihara K 1991). Biological evidence, such as genetics or morphometrics, tends to either give partial support (Matsumura 1995; Omoto and Saitou 1997; Hanihara T and Ishida 2005; Hammer et al. 2006; Hudson and Matsumura 2006; Adachi et al. 2009; He et al. 2012) or mostly full support while noting there are still poorly understood complexities introduced by migration (Turner 1976; Hanihara T 1992a; Hanihara T 1992b; Hanihara T 1992c; Turner 1992a; Oota et al. 1999; Tanaka et al. 2004; Park et al. 2012; Hlusko et al. 2018; Scott et al. 2018a). The primary disagreement is over the specific origins of the Jomon and Yayoi before entering the Japanese archipelago, rather than the relatedness between the Jomon and Ainu or modern Japanese and Yayoi—or more simply put: “who was where and when?”

This thesis seeks to delve further into the complexities of the peopling of the Japanese archipelago by analyzing dental morphological data from different Jomon and Ainu populations,
as well as samples from modern Japan, East Asia, Southeast Asia, and Australo-Melanesia using biodistance analysis. Questions to address include: (1) are Jomon populations uniform throughout Japan?; (2) are Ainu populations uniform throughout Japan?; (3) are the Ainu and Jomon populations more closely related to East Asians or Southeast Asians?; and (4) do the Sinodont/Sundadont traits accurately depict the relationship between the Jomon and Ainu?

**Materials and Methods**

Throughout his career, Christy G. Turner II traveled the world systemically categorizing crown and root morphology on over 25,000 skulls. He initially began his research in the Arctic but expanded the range to include the New World, Asia, Australia, the Pacific, and Europe, with limited research in Africa and India (Scott and Irish 2017). After Turner’s death in 2013, G. Richard Scott salvaged Turner’s data, including 3,000 slides, about 25,000 data sheets, and hundreds of printouts with the full class frequency distributions of Turner’s 29 key crown and root traits (Scott and Irish 2017). These sheets have allowed dental anthropologists to explore geographic variation in crown and root morphology. His printouts of the Jomon, Ainu, and Yayoi are critical in addressing questions surrounding the peopling of Japan.

While Scott and Irish (2017) provide Jomon and Ainu frequency tables, Turner’s printouts allowed the two populations to be further broken down by region: Hokkaido, Honshu, and the island of Sakhalin. To obtain the frequencies for the printouts, the individual count method was used (Turner and Scott 1977; Scott and Irish 2017; Scott et al. 2018a). The individual count method involves scoring both the left and the right antimeres for trait expression, and then tabulating the most pronounced degree of expression for an individual. The reasoning for this being biologically sound is that even if trait scores are different on the left and right antimeres, the individual has the genotype (genetic ability) to express the higher score
(Scott and Irish 2017; Scott et al. 2018a). Individuals who were not adults or expressed NA (not available) for every single tooth were left out of the total count.

After obtaining counts and sample size totals from Turner’s printouts, the Jomon can be broken down by Hokkaido and Honshu samples, and the Ainu can be divided into Hokkaido and Sakhalin samples. While the Honshu, Hokkaido, and Sakhalin groups could be further divided into subgroups, such as northern or southern, it is necessary to keep them in larger “by island” groups due to sample size problems. Trait frequencies from <10 observations cannot be used in quantitative analyses as they are unlikely to be representative of the population (Scott and Irish 2017). For this reason, while Yayoi counts were tabulated, their trait frequencies are not used in any quantitative analyses because of their small sample size.

For geographical regions beyond the Jomon and Ainu samples, frequency tables and group provenance were obtained from Scott and Irish (2017). This method was used for the following groups: East Asia, Southeast Asia, Melanesia, Micronesia, Polynesia, New Guinea, and Australia.

The samples obtained from Scott and Irish (2017) and Turner’s printouts are as follows:

- Jomon: Hokkaido (n = 111), Honshu (n = 532)
- Ainu: Hokkaido (n = 198), Sakhalin (n = 87)
- East Asia: Japan (n = 311), An-Yang (n = 277), South China (n = 63), Urga (n = 190), Yayoi (n = 11)\(^1\)
- Southeast Asia: Borneo (n = 39), Calatagan (n = 61), Malaysia (n = 58), Philippines (n = 154), Taiwan (n = 66)

\(^1\) Sample size is small and so Yayoi not be included in statistical analyses; however, frequencies are mentioned in discussion.
Melanesia: Fiji (n = 92), New Britain (n = 220), New Hebrides (n = 78)

Micronesia: Guam (n = 222)

Polynesia: Mokapu (n = 248), New Zealand (n = 117)

New Guinea: New Guinea (n = 50), New Guinea 94 BP (n = 286), New Guinea Gulf (n = 72), Torres 1 and 2 (n = 36), Torres Strait (n = 26), Solomon Islands (n = 56), Papua Gulf (n = 53), New Guinea Milne (n = 26), New Guinea North (n = 24)

Australia: Lower Murray (n = 74), North Australia (n = 57), Queensland (n = 96), South Australia (n = 133)

The samples are broken down by frequency per trait grade using the Turner-Scott dental scoring system (Turner et al. 1991; Scott and Irish 2017; Scott et al. 2018a), formerly known as the Arizona State University Dental Anthropology System (ASUDAS). In 1991, Turner et al. created these scoring procedures in a widely cited article, which Scott and Irish improved and expanded upon in a guidebook published in 2017. These methods have been standardized so that researchers can minimize observer error when conducting dental morphology analysis. For a trait to be standardized, it required the following: 1) the trait must be easily and readily observed; 2) the morphology (physical structure) of the trait must be able to withstand wear and other harsh conditions; 3) there is little or no sexual dimorphism; 4) the evolution of the traits is slow; and 5) the traits show a positive relationship to population ancestry (Scott and Irish 2017; Scott et al. 2018a).

While total frequencies of trait presence are used for some traits, many dental anthropologists use “breakpoints” to derive frequencies for characterizing a sample (Scott and Irish 2017). Many traits are graded on a scale where values include absence and presence, where presence ranges from slight to pronounced (Scott and Irish 2017; Scott et al. 2018a). Breakpoints
are used to create an overall frequency of the trait in the population by choosing representative grades. The grades can differ for each trait, and can even in different studies. For example, while a breakpoint of 2 is common for shoveling, in areas with pronounced shoveling expression such as North America, 3 may be used to differentiate frequencies between groups (Scott and Irish 2017). More simply put, it is a cut-off value that serves to derive frequencies for nonmetric traits that can be compared among samples.

**ASUDAS Trait Descriptions**

Over 100 different dental traits have been described throughout anthropological history, but only 30-40 are well standardized, and 35 are used within the Turner-Scott Classification System (Turner et al. 1991; Scott and Irish 2017; Scott et al. 2018a). This thesis uses 21 crown traits and 6 root traits. Their properties and the geographical context for the primary groups involved in this thesis are described below:

- **Winging, UI1.** Winging (Fig. 2.1) is differentiated from other crown and root traits in that it is technically neither. Instead, it is defined by the rotation of the upper central incisors (Scott and Irish 2017). Originally it was categorized by bilateral or unilateral rotation with the distal margin of the upper central incisors rotated outward; however, the definition has been updated to include the lower central incisors as well. It is classified by absence and three degrees of presence. The breakpoint is typically 1 as any form is scored as present (Scott and Irish 2017). It is one of the traits associated with Sinodonty (Turner 1990; Scott et al. 2018a). It is most common in American Indians (45-55%), and occurs in an intermediate percentage of 15-30% for East Asians, Southeast Asians, and the Jomon/Ainu (Scott et al. 2018a). Australo-Melanesian populations have lower percentages from around 0-15% (Scott et al. 2018a).
Figure 2.1. UI1 winging in an Ecuadorian individual. Photo courtesy of G. Richard Scott.

- *Shoveling, UI1.* Shoveling (Fig 2.2) is part of the lingual marginal ridge complex on the anterior teeth (Hrdlička 1920; Scott and Turner 1997). Although it is present on all upper and lower anterior teeth, the key tooth for population comparisons is UI1 (Scott and Irish 2017). The most important feature of this trait is “the presence of mesial and distal marginal ridges on the lingual surface of the upper anterior teeth, with a lingual fossa as a secondary reflection of marginal ridge development” (Scott and Irish 2017). The expression of both marginal ridges is crucial to scoring shoveling, as one ridge may be present while the other is absent. The UI1 ranked scale includes grade 0 as absence with grades 1-7 indicating trace to extremely pronounced shoveling (Scott 1973). The breakpoint of shoveling often differs among researchers, as those who study groups with modest shoveling may use a breakpoint of 2, whereas those who study populations with pronounced shoveling often use grade 3. It is in high frequency in Sinodonts; when grade 2 is used a breakpoint, it has a frequency of 90-100% in East Asia (Turner 1990; Scott et al. 2018a). Southeast Asians and the Jomon/Ainu both have intermediate frequencies of around 50-80%, although it occurs slightly more often in recent Southeast Asian groups than early Southeast Asians or the Jomon/Ainu (Scott et al. 2018a).
Fig 2.2. UI1 and UI2 Shoveling in an An-Yang individual. Photo courtesy of G. Richard Scott.

- **Double shoveling, UI1.** Similar to shoveling, the anterior incisors exhibit mesial and distal ridges on the labial surface of the teeth (Fig 2.3). In most cases, the mesial ridge is more developed than the distal (Scott et al. 2018a). It is most pronounced on UI1, although it can be present on UI2. It is scored from grades 0 to 6, with 0 for trait absence, and grades 1-6 from trace to pronounced expressions. The breakpoint is typically grade 2. Scott et al. (2018a) report that it has higher frequencies in East Asia (40-50%) than Southeast Asia (20-35%), with the Jomon and Ainu having an even lower frequency of about 10-20%.

Fig 2.3. UI1 double shoveling. Photo courtesy of G. Richard Scott.

- **Interruption grooves, UI2.** Interruption grooves are manifest as distinct furrows that interrupt the normal course of the mesial and distal marginal ridges on the upper incisors.
They differ from other morphological traits in that the groove may be evident on different parts of the tooth crown and root, which complicates the classification of its expression (Scott and Irish 2017). The original classification by Turner notes the presence and location of grooves rather than numbers. Any groove present on any lingual marginal ridge or on the basal cingulum is scored as present. East Asians and Southeast Asians have moderate frequencies of this trait (30-40%); the Jomon and Ainu have higher frequencies that fall between 45 and 65% (Scott et al. 2018a).

- **Tuberculum dentale.** UI2. Tuberculum dentale are cingular projections on the lingual surface of the upper anterior teeth that take the form of ridges or tubercles (Scott and Irish 2017). Their classification varies among anterior teeth, but the key tooth that is typically scored is UI2. This is because tuberculum dentale can be expressed as either ridges or tubercles on UI2. Grade 0 is noted as absence, with 1-2 representing small to moderate ridges, and 3-6 graded from small tubercles to a pronounced welt at the base of the crown. A breakpoint of 2 and above is typically used to denote trait presence. It is typical in Asian and Asian derived populations. The world range is characterized by low frequencies and limited geographic variation with most groups falling between 20 and 40% (Scott et al. 2018a). East Asia, early Southeast Asia, and the Jomon/Ainu fall in the lower part of that range, whereas recent Southeast Asia, Melanesia, and Micronesia fall in the upper half (Scott et al. 2018a).

- **Bushman canine, UC.** Also known as the canine mesial ridge in Turner’s scoring system, this trait is virtually exclusive to Sub-Saharan Africans, particularly the San and Khoekhoe (Scott and Irish 2017). Canines can have large mesial ridges or tubercles, but the requirement to be scored as a Bushman canine is that the mesial ridge and tuberculum...
dentale coalesce so that the lingual sulcus is distal to the midline of the tooth (Scott and Irish 2017). There are four grades of expression, with 0 indicating that neither the mesial or distal lingual ridges connect to the tuberculum dentale and are the same size. Grades 1-3 vary from a weak attachment to the tuberculum dentale to its full incorporation. The breakpoint is grade 1+. The presence is lower than 5% in East and Southeast Asians as well as Australo-Melanesians (Scott et al. 2018a).

- **Distal accessory ridge, UC.** The lingual lobe on the upper and lower canines can express three different ridges: a medially positioned essential ridge, a mesial marginal ridge, and a distal marginal ridge. Between the essential ridge and the distal ridge an additional ridge can be expressed -- the distal accessory ridge. It is more common and pronounced on the upper canine, which Turner used as the key tooth for this variable. Although less frequent, it can also appear on the lower canine (Scott 1977; Scott and Irish 2017). Grade 0 is noted as trait absence, with grades 1-5 on a scale ranging from faint to pronounced expression. Grade 2 is typically used as the breakpoint as 1 is too subtle. Although its world range is broad enough to be divided into low, moderate, high moderate, and high categories, all Asian groups fall within the high moderate, 45-65%, category (Scott et al. 2018a).

- **Hypocone, UM2.** The hypocone was the last cusp added to the upper molars as primates evolved into their modern forms. In hominoids, the trigon plus the hypocone results in a four-cusped molar (Scott and Irish 2017). The key tooth in hypocone scoring is UM2 since the hypocone is a typical feature of first molars and exhibits less variation in size (Scott and Irish 2017; Scott et al. 2018a). This thesis uses Turner et al.’s (1991) six grades of expression, and grades 2-6 are used as the breakpoint (Scott and Irish 2017).
The frequency of the hypocone is low, 50-65%, in the Jomon and Ainu, while it is intermediate, 70-80%, in East Asia and high, 85-95%, in Southeast Asia and Polynesia (Scott et al. 2018a).

- **Cusp 5 UM1.** The fifth cusp is a conule between the hypocone and the metacone on the upper molars. While it can be expressed on all upper molars, the key tooth is UM1 (Scott and Irish 2017). The breakpoint for presence is 1+. Presence is scored based on whether there are two vertical grooves associated with a cuspule that run parallel to the distal marginal ridge complex (Scott and Irish 2017). Cusp 5 has an exceptionally high frequency of 60% or more in Australia and New Guinea. In Southeast Asia, the frequency is 30-50%; East Asia and the Jomon/Ainu have frequencies of 10-25% (Scott et al. 2018a).

- **Carabelli’s Cusp, UM1.** Also referred to as a tubercle, it is a cingular derivative on the lingual surface of the protocone that exhibits a wide range of variation (Scott and Irish 2017; Scott et al. 2018a). Its frequent usage in dental anthropology has been likened to the often studied ABO blood groups in serology and genetics (Scott et al. 2018a). Grade 0 is characterized by complete absence while grades 1-4 are expressed from a slight eminence to the most pronounced form without a free apex. Grades 5-7 are characterized by a free apex going from a small to large tubercle (Scott and Irish 2017). Since most researchers and observers agree on the expression of free-standing tubercles, grades 5+ can be used as a breakpoint for world variation (Scott and Irish 2017). Grade 2+ can also be used to denote presence due to the difficulty of scoring grade 1 (Scott and Irish 2017). Using a grade 2 breakpoint, the Jomon/Ainu have low percentages of Carabelli’s trait of around 10-20% (Scott et al. 2018a). East Asians exhibit the trait in around 20-30% of the
population, while Southeast Asians have a higher intermediate frequency of 30-40% (Scott et al. 2018a).

- **Parastyle UM3.** The parastyle is expressed on the paracone of the upper molars, and the key tooth varies relative to trait size (Scott and Irish 2017). Typically, it is UM1, but for large paramolar tubercles, UM2 or UM3 may be used. Grade 0 is characterized by absence with grade 1 as a small pit near cusps 2 and 3. Grade 2 is characterized by a cusp with no free apex, where grades 3-6 are medium to large cusps with a free apex. It does not distinguish any modern human population (Scott et al. 2018a).

- **Enamel extensions, UM1.** Enamel extensions (Fig 2.4) refer to contours on the cervical enamel line, distinguished by a line that is directed apically towards the bifurcation of the roots (Scott et al. 2018a). These extensions can range from 1-4 mm, and are scored depending on length, with grade 1 equating to 1 mm and grade 3 as 4 mm or more. They are expressed on both upper and lower molars and premolars and either UM1 or LM1 may be used, but UM1 is the key tooth for this thesis. The breakpoint is grade 2 or higher. It is a trait that is most common in Sinodonts; it has a frequency range of 40-60% in East Asian populations (Turner 1990; Scott et al. 2018a). The Jomon/Ainu and Southeast Asians both display intermediate frequencies of around 20-30% (Scott et al. 2018a).
Root number, UP1. Upper premolars have either two or three root cones, with two being the most common (Fig 2.5). One is below the buccal cusp and the other below the lingual cusp. Root number is determined by whether or not these root cones are bifurcated for \( \frac{1}{4} \) to \( \frac{1}{3} \) the total length of the root (Scott and Irish 2017; Scott et al. 2018a). When they are also bifurcated along the buccal root, this produces a three-rooted upper premolar. UP1 is the key tooth, as UP2 exhibits two roots less commonly. Two-rooted UP1 are more common in Sundadonts (Turner 1990; Scott et al. 2018a). Southeast Asians have a population frequency of 30-40\%, while East Asians and the Jomon/Ainu have a lower intermediate presence of 20-30\% in their respective populations (Scott et al. 2018a).
Root number, UM2. Upper molars have three roots, each associated with a major cusp. UM1 has the most stable cusp number and because of this most have three primary roots. UM3 has some of the most variable cusp numbers and tends to exhibit three root cones but the roots are not separated, giving UM3 often one root. It is because of this that UM2 is the key tooth. Grade 1 is scored as a one-rooted UM2, grade 2 as two-rooted UM2, and grade 3 as three-rooted UM2. The breakpoint is typically the total frequency of three-rooted UM2. East Asians and Southeast Asians have a high intermediate frequency among their populations of around 65-75% (Scott et al. 2018a). The Jomon/Ainu have a slightly lower frequency range of 50-65% (Scott et al. 2018a).

Pegged-reduced-missing UM3. As the most distal tooth in the jaw, the upper third molars have been subject to microevolution associated with a decrease in tooth size (Brook 1984). Agenesis of the third molar refers to complete absence, but this is the extreme range of a continuum that also includes peg-shaped (Fig 2.6) or distinctly reduced UM3 (Scott and Irish 2017; Scott et al. 2018a). It showed patterned geographic variation.
Grade 0 is noted when the third molar is present and normal, with grade 1 a reduction in size, grade 2 peg-shaped, and grade 3 complete congenital agenesis. For population comparisons, grades 1-3 are combined, making 1+ the breakpoint. The trait is most common in Sinodonts (Turner 1990), with frequencies of 25-40% among East Asians, Micronesians, and Polynesians (Scott et al. 2018a). It is less common among the Jomon/Ainu and Southeast Asians who have frequencies of 10-20% (Scott et al. 2018a).

Fig. 2.6. Pegged-reduced-missing UM3. Photo courtesy of G. Richard Scott.

- **Lingual cusp number, LP2.** The lingual cusp(s) of the lower premolars are smaller than the buccal cusps (Scott and Irish 2017), and often have two, three, or even more small cusps with free apexes. Trait presence in this instance is the occurrence of two or more lingual cusps; the second lower premolar is the key tooth for this trait. The grade scale from Scott and Irish (2017) is simplified from Turner and is as follows: grade 0 -- lingual cusp has no free apex; grade 1 – a single lingual cusp; grade 2 -- two lingual cusps; and grade 3 -- three lingual cusps. The breakpoint is grade 2+. It has high frequencies in Polynesian, Micronesian, and Melanesian populations of around 80-90%; East Asia, Southeast Asia, and the Jomon/Ainu have a slightly lower frequency range of 70-80% (Scott et al. 2018a).
• *Groove pattern LM2*. Lower molars have five major cusps with a groove pattern that varies depending on which cusps come into contact at the central occlusal fossa. Most hominoids have lower molars with contact between cusps 2 and 3, resulting in a Y pattern. In recent hominins, cusps 1 and 4 can come into contact producing an X pattern (Scott and Irish 2017; Gregory and Hellman 1926). An X-pattern is rare on LM1 in humans but can happen on LM2, the key tooth for this variable. The classification is not based on grades but by pattern: the Y pattern, X pattern, or a + pattern where there is contact between cusps 1-4. In Scott and Irish’s (2017) appendix for provenance tables, 1 = Y pattern, 2 = X pattern, and 3 = + pattern. The frequency of the Y pattern on LM2 is used for population studies, although there is so little variation it is infrequently used in comparisons (Scott and Irish 2017). East Asians have a relatively low frequency of 20-25%, while the Jomon/Ainu have a slightly higher range of 24-40% (Scott et al. 2018a).

• *Cusp number LM2*. Cusp 5, or the hypoconulid, is typically present on LM1 but is more widely varied in presence on LM2 (Scott and Irish 2017) which is why it is used for population comparisons. It is graded on a scale of 0-5, with 0 marking absence and 1-5 as trace to pronounced expressions; 1+ is the typical breakpoint. However, in the Scott and Irish (2017) frequency tables used for this thesis, 0 = 4 cusps, 1 = 5 cusps, and 2 = 6 cusps. The absence of the hypoconulid (Fig 2.7), or four-cusped lower second molars, is used in world variation studies (Scott et al. 2018a). East Asian, Southeast Asian, and the Jomon/Ainu have low intermediate frequencies of 25-40% (Scott et al. 2018a). Four cusped LM2 is notably higher in Sundadonts than in Sinodonts (Turner 1990).
Fig. 2.7. Four-cusped LM2. Photo courtesy of G. Richard Scott.

- **Cusp 6 LM1.** Cusp 6 is expressed between the entoconid and hypoconulid of the lower molars. Cusp 5 must be present for cusp 6 to be scored; the key tooth is LM1. Grade 0 is the absence of cusp 6, grades 1-2 exhibit a cusp 5 that is more than twice the size of cusp 6, grade 3 is cusps 5 and 6 equal in size, and grades 4-5 are when cusp 6 is slightly larger and much larger than cusp 5. In the Scott and Irish (2017) tables, the grades are as follows: 0 = 4 cusps, 1 = 5 cusps, and 2 = 6 cusps. The breakpoint is 1+, or total trait presence. East Asians and recent Southeast Asians exhibit a lower frequency of 25-35% of cusp 6, while the Jomon/Ainu and early Southeast Asians have a higher frequency of 40-60% (Scott et al. 2018a).

- **Deflecting wrinkle LM1.** The medial occlusal ridge of the metaconid is examined for the direction of the course it follows from the cusp tip to the central occlusal fossa; if the ridge is straight, it is considered normal, with those that are angled about halfway along its length are referred to as “deflecting” (Scott and Turner 1997; Scott and Irish 2017). East Asians, Southeast Asians, and the Jomon/Ainu have frequencies around 25-45% (Scott et al. 2018a). The deflecting wrinkle (Fig 2.8) is more commonly associated with Sinodonts (Turner 1990).
- **Trigonid crest LM1.** The trigonid crest is also known as C1-C2 contact, where the two major cusps of the trigonid exhibit connected distal accessory ridges. If the ridge runs from one cusp tip to another it is classified as a mid-trigonid crest, whereas if the ridges run distally it is known as the distal-trigonid crest. LM1 is considered a key tooth and is listed as such on the provenance tables; however, Scott and Irish (2017) feel that LM2 should be examined as a key tooth. On this tooth, both crests are easier to evaluate compared to LM1 which often has a large essential ridge on the metaconid that often disrupts possible contact between the distal accessory ridges of the metaconid and protoconid. Both the mid-trigonid and the distal-trigonid crests are scored on a grade of 0 marking absence and 1 marking presence. The distal trigonid crest is the one used in this thesis. It has a high frequency of 10% or more in early Southeast Asians (Scott et al. 2018a). The Jomon/Ainu have a low frequency of 0-5% of the trait, while East Asians and recent Southeast Asians have a frequency of 5-10% (Scott et al. 2018a).

- **Protostylid LM1.** The protostylid is like Carabelli’s trait on UM1—it is a cingular derivative (Scott and Irish 2017) and the two traits are linked at a relatively low level of correlation (Scott 1978). Grade 0 marks absence, grade 1 marks a buccal pit formation,
grade 2 a slight swelling and a groove appearing mesially from the buccal groove, and grade 3-7 a slight positive to a distinctive expression on the mesiobuccal cusp. The breakpoint for trait expression is grade 2+. Asians and Asian-derived populations have the highest frequency, although the trait is far more common in Australopithecines than modern *Homo sapiens* (Dahlberg 1950; Hlusko 2004; Skinner et al. 2009). It has low frequencies, less than 10%, in Australo-Melanesians, while East Asians, recent Southeast Asians, and the Jomon/Ainu have frequencies of about 20-30% (Scott et al. 2018a). Early Southeast Asians fall on the lower range at about 10-20% (Scott et al. 2018a).

- **Cusp 7 LM1.** This accessory cusp takes the form of a wedge between cusps 2 and 4 on the lower molars. It is graded on a scale of 0 to 4, with 0 marking absence, 1 a small wedge-shaped cusp and 4 a large cusp. Turner included a 1A for cases where the cusp does not assume the typical wedge shape and there is a groove on the lingual surface of the metaconid. Scott and Irish (2017) suggest that when a 1A is scored, it should not be included in the total frequency of cusp 7. The breakpoint is 1+ minus the frequency of 1A. It is useful in distinguishing African-derived populations where it has a frequency of 20-30%. All other world populations have frequencies between 0-10% (Scott et al. 2018a).

- **Tomes’ root LP1.** Since lower premolars do not have prominent buccal and lingual cusps like upper premolars, their roots are shaped differently as well. Since the lingual cusp on the lower premolars is commonly off center, the lower premolars may exhibit more than one lingual root with one buccal root (Scott and Irish 2017). Tomes’ root occurs when a mesiolingual root exhibits an inter-radicular projection, creating an independent root. To put it simply, it is a single root with a deep groove creating a split at the bottom rather
than a complete bifurcation. Grade 0 is no groove separating the cones, while grade 1-5 marks a slight V-shaped groove to a pronounced inter-radicular projection. Grades 4-5 are considered the only scores that mark the presence of Tomes’ root (Scott and Irish 2017). The trait is moderately common, about 20-25% in Southeast Asia, while it exhibits lower frequencies of 10-20% in East Asia (Scott et al. 2018a).

- **Root Number LC.** Upper and lower canines typically exhibit only one root with two root cones. In some instances, the root cones are bifurcated to produce two roots (Scott and Irish 2017). The pattern of two-rooted lower canines varies geographically. It is scored rather simply, with grade 0 marking one root and grade 1 marking two roots. The trait is most common in Europeans (Lee and Scott 2011), while East Asians, Southeast Asians, and the Jomon/Ainu all exhibit low frequencies of 0-1% (Scott et al. 2018a).

- **Root Number LMI.** Most lower molars have only a mesial and distal root (Scott and Irish 2017). Occasionally, the first lower molar can have an accessory distolingual root (Scott et al. 2018a). This trait is indicated by a presence of a supernumerary root lingual to the distal root (Fig 2.9). The grading scale is as follows: 1 = one-rooted lower first molar, 2 = two-rooted lower first molar, 3 = three-rooted lower first molar. The presence or absence of three-rooted lower molars is used in studies involving population variation. Low frequencies of about 2-5% are found in the Jomon/Ainu as well as Melanesia. As noted in Scott et al. (2018a), Southeast Asians have a lower frequency (10-15%), while East Asians and Eskimo-Aleuts have the highest frequencies of 3RM1 at 20-40%.
Fig. 2.9. Three-rooted LM1 in an Urga individual. Photo courtesy of G. Richard Scott.

- **Root Number LM2.** Similar to LM1, the second lower molars typically exhibit two roots. LM1 is the most conservative of the lower molars and it usually retains the two-rooted form (Scott and Irish 2017). Much like cusp number, LM2 is the key tooth since it is not as conservative as LM1 or as subjected to developmental factors like LM3. One rooted LM2 is what is typically measured worldwide for frequency variation (Scott and Irish 2017; Scott et al. 2018a). For two-rooted LM2, Scott et al. (2018a) state that the frequencies are low for East Asians (60-70%), intermediate for Southeast Asians (70-80%), and high for the Jomon/Ainu (80-90%).

- **Odontome, UP/LP1/LP2.** An odontome is a cone-shaped tubercle expressed in the central sulcus of any upper or lower premolar (Scott and Irish 2017). Grade 0 is absent with 1 as present. Odontomes, which have a dentine component (Scott and Irish 2017), are rare in most populations. Although rare, they ‘pop up’ in Asian populations on a consistent basis but are effectively zero in Europeans and Africans. They are most common in Eskimo-Aleuts, nearly absent in the Jomon and Ainu, and are rare, about 1-3%, in East Asia and Southeast Asia as well as in Australo-Melanesia (Scott et al. 2018a).
Table 2.1 The breakpoints of traits considered present.

Statistical Methods

Once frequencies are obtained, the comparison of group means are measured through an Analysis of Variance, or ANOVA (Fisher 1921). ANOVA measures the variability in a response variable—in this case, trait frequency—of the treatment variables, the populations of East Asia, Southeast Asia, Jomon, and Ainu. It will compare how the groups differ from each other and the variability within each group (Field et al. 2012). The null hypothesis ($H_0$) is that mean group
frequencies do not differ significantly from each other. The alternative hypothesis (H_A) is that at least one of the population groups is significantly different from the rest. When the null is rejected, a post hoc Tukey’s test is used to determine where the differences lie between the groups. Both ANOVA and Tukey’s test will be conducted through the R statistical software using the *stats* package (R Core Team 2017). Although there are samples ranging from East Asia, Southeast Asia, Micronesia, Polynesia, Australo-Melanesia, and New Guinea, comparative results are restricted to the Jomon, Ainu, Japan, East Asia, and Southeast Asia to better focus on the peopling of Japan and the dual origin hypothesis as well as its counterarguments. ANOVA will be performed using each of the key Sinodont and Sundodont traits as the response variable.

For quantitative biodistance analyses, dissimilarity matrices are calculated, where values closer to 0 indicate sameness and values closer to 1 indicate dissimilarity. Two dissimilarity matrices were calculated: Bray-Curtis (Bray and Curtis 1957) using NTSYSpc (Exeter Software 2005) and the mean measure of divergence, or MMD (Constandse-Westermann and Huizinga 1972) using the R GUI anthropMMD (Santos 2018). Although the two tests are similar (Scott and Schomberg 2016), MMD occasionally encounters problems with small sample sizes (Irish 2010). Although small sample sizes can cause distortion within the MMD statistic, each sample is grouped by region to allow for larger sample values to minimize error. Given that the Bray-Curtis and MMD tests are so similar, the two tests will act as the other’s ‘safety net’ should sample size prove problematic for the MMD statistic.

For the Bray-Curtis matrix, Unweighted Pair Group Method with Arithmetic Mean, or UPGMA (Sokal and Michener 1958), and Neighbor Joining trees (Saitou and Nei 1987) were created with NTSYSpc. The MMD matrix was arranged into a dendrogram in R using the
ggdendro package, which utilizes ggplot2 functions to better orient and extract plot data from already created dissimilarity matrices (de Vries and Ripley 2016).

Results

Bray-Curtis and Mean Measure of Differences are distance statistics that use pairwise comparisons among groups using trait frequencies. These comparisons are then input into a matrix, where values closer to 0 indicate similarity, while values closer to 1 indicate the two groups are different. By using Bray-Curtis and Mean Measure of Distance matrices, it is possible to determine which populations differ from each other the most. Trait frequencies were calculated by counting those that had met the ASUDAS breakpoint values for that trait and dividing that number by the total individuals who expressed the trait regardless of grade. Ainu and Jomon values were taken from the Turner data sheets while other frequencies were provided by Scott and Irish (2017). For East Asia, Southeast Asia, Micronesia, Polynesia, Melanesia, New Guinea, and Australia, groups were averaged together to create a trait frequency representative of the region (Table 3.1).
Table 3.1. Average trait frequencies among studied populations.

The difference between Bray-Curtis and Mean Measure of Difference is minimal.

Correlations closer to 1 indicate similarity. However, given that the counts for some traits were smaller in a few populations, MMD did end up having negative values. Those matrix values can be assumed as zero (Irish 2010), but Bray-Curtis has no such issue. Due to this the two matrices (Tables 3.2 and 3.3) provide a sense of checks and balances with each other. The Bray-Curtis matrix and MMD matrices were created using the same 21 crown and 6 root traits as described in the methodology.
Table 3.2. Bray-Curtis matrix derived from population frequencies.

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<tr>
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<td>0.139</td>
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<td>0.251</td>
<td>0.280</td>
<td>0.323</td>
<td>0.240</td>
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</tr>
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<td>0.374</td>
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<td>0.285</td>
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<td>0.210</td>
<td>0.181</td>
<td>0.244</td>
<td>0.000</td>
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<td>JomonHok</td>
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<td>0.211</td>
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<td>0.347</td>
<td>0.367</td>
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<td>0.351</td>
<td>0.342</td>
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<td>0.335</td>
<td>0.258</td>
<td>0.269</td>
<td>0.311</td>
<td>0.244</td>
<td>0.211</td>
<td>0.201</td>
<td>0.290</td>
<td>0.170</td>
<td>0.000</td>
</tr>
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</table>

Table 3.3. Mean Measure of Differences matrix derived from population frequencies.

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<tr>
<th></th>
<th>Japan</th>
<th>JomonHon</th>
<th>JomonHok</th>
<th>AinuH</th>
<th>AinuS</th>
<th>Easia</th>
<th>SEAsia</th>
<th>Mic</th>
<th>Pol</th>
<th>Mel</th>
<th>NewG</th>
<th>Aust</th>
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</thead>
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<td></td>
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<tr>
<td>JomonHon</td>
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<td>0.000</td>
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</tr>
<tr>
<td>AinuS</td>
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<td>0.155</td>
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<td>0.077</td>
<td>0.000</td>
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<td>0.399</td>
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<td>0.328</td>
<td>0.252</td>
<td>0.237</td>
<td>0.072</td>
<td>0.000</td>
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<td></td>
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</tr>
<tr>
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<tr>
<td>Pol</td>
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<td>0.304</td>
<td>0.345</td>
<td>0.293</td>
<td>0.317</td>
<td>0.190</td>
<td>0.078</td>
<td>0.283</td>
<td>0.000</td>
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<tr>
<td>Mel</td>
<td>0.070</td>
<td>0.200</td>
<td>0.357</td>
<td>0.255</td>
<td>0.335</td>
<td>0.318</td>
<td>0.157</td>
<td>0.128</td>
<td>0.179</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>NewG</td>
<td>0.220</td>
<td>0.150</td>
<td>0.360</td>
<td>0.263</td>
<td>0.397</td>
<td>0.437</td>
<td>0.256</td>
<td>0.268</td>
<td>0.243</td>
<td>0.098</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td>Aust</td>
<td>0.497</td>
<td>0.553</td>
<td>0.582</td>
<td>0.569</td>
<td>0.594</td>
<td>0.505</td>
<td>0.313</td>
<td>0.628</td>
<td>0.217</td>
<td>0.456</td>
<td>0.528</td>
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</tr>
</tbody>
</table>

Dendrograms provide a visual representation of each matrix. Branches closer to each other indicate that groups are more related, and the clusters within those branches show the most recent common ancestor for those populations at the point of divergence. The dendrograms are similar with a few key differences, as UPGMA and NJT use different algorithms to create their branches. In both the UPGMA dendrogram (Fig. 3.1) and the NJT dendrogram (Fig. 3.2) derived from the Bray-Curtis matrix the Ainu and Jomon cluster tightly together. In the UPGMA dendrogram, East Asia clusters tightly with Southeast Asia. On the NJT dendrogram, Southeast Asia diverges from East Asia and no longer clusters as closely with them, although they still share a common ancestor, albeit earlier.
Fig. 3.1 UPGMA dendrogram derived from Bray-Curtis matrix.
A by-sample dendrogram was made to better illustrate the possible gene flow between East and Southeast Asia (Fig 3.3). These sample populations are defined in materials, with the Jomon and Ainu samples taken from Turner’s printouts and the rest defined by Scott and Irish (2017). The Southeast Asian and East Asian samples are more distributed across the dendrogram, with a few of the samples clustering together. The Hokkaido Ainu cluster with the Honshu Jomon, while the Hokkaido Jomon and Sakhalin Ainu are separate but still have a common ancestor. This could indicate that the northernmost groups were possibly biologically
different than their southern counterparts.

**Fig. 3.3.** UPGMA dendrogram broken down by sample populations derived from a Bray-Curtis matrix

The dendrogram derived from the MMD matrix is similar (Fig. 3.4). The Ainu and Jomon cluster tightly together again, but unlike the previous two dendrograms the Ainu and Jomon do not each have their own subcluster. Rather, the Sakhalin Ainu cluster with the Hokkaido Jomon and the Hokkaido Ainu cluster with the Honshu Jomon. Much like Fig. 3.1, Japan clusters with East Asia and Southeast Asia. In all three dendrograms, Australo-Melanesia and New Guinea do not cluster with East Asia, Southeast Asia, or the Jomon/Ainu.
Fig. 3.4. Dendrogram derived from Mean Measure of Differences matrix.

The matrices and dendrograms show how groups are different from each other. To determine which traits best separate out the key groups involved in the hypotheses regarding the peopling of Japan, the focus of ANOVA is on Sinodont and Sundadont traits. ANOVA Model I compares sample means to find if there is a significant difference among the groups. When there is a significant difference, the Tukey test determines which groups in the sample array differ significantly from one another. For the Tukey test, a value of 0.05 is used to determine significance; any values equal to or less than are counted as significantly different means.

The frequency data are normal for most chosen traits, with pegged-reduced-missing UM3, deflecting wrinkle LM1, and root LM1 were calculated having some slight abnormality through a Shapiro-Wilk test, meaning that they do not follow a standard normal distribution. Although the data are now broken down into frequencies and are on some level continuous, the
scores were originally ordinal data which are typically not normally distributed. This also could
due to issues within the data sets themselves, for example, since deflecting wrinkle LM1 is a
Sinodont trait it should be within the Japanese population, however the trait was not scored on
the Turner data sheets for that population. Additionally, some of the frequencies actually being 0
likely skewed the distribution. However, in this case, 0 is important if it comes from a scored
trait—it means that a trait is absent in a particular group and this information is very significant.
Although ANOVA was the statistic chosen for this thesis, future tests should take these
distributions into account.

ANOVA was then run for the following populations: East Asia (k = 4), Ainu (k = 4),
Jomon (k = 4), and Southeast Asia (k = 6), where k = the number of samples within a population.
Mean scores and standard deviations were calculated (Table 3.4), and Tukey was used to find
significant differences between groups (Table 3.5). There are also times where the Jomon and
Ainu do not share a relationship with East Asia and Southeast Asia. While the Ainu do not differ
significantly from Southeast Asia or East Asia for UI1 double shoveling, the Jomon are
significantly different from East Asia. A similar phenomenon occurs with UP1 root number as
well. The Jomon are not significantly different from the Ainu, East Asia, or Southeast Asia, but
the Ainu differ significantly from Southeast Asia.
### Table 3.4

ANOVA values for Jomon, Ainu, East Asia, and Southeast Asia of Sinodont and Sundadonty traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Tooth</th>
<th>BP</th>
<th>Mean</th>
<th>S.D</th>
<th>Mean</th>
<th>S.D</th>
<th>Mean</th>
<th>S.D</th>
<th>Mean</th>
<th>S.D</th>
<th>Mean</th>
<th>S.D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ainu = Jomon = SE Asia ≠ E Asia</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Shoveling</td>
<td>UI1</td>
<td>3+</td>
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<td>0.151</td>
<td>0.400</td>
<td>0.166</td>
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<td>0.422</td>
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<tr>
<td>Root number</td>
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<td>0.020</td>
<td>0.028</td>
<td>0.056</td>
<td>0.293</td>
<td>0.111</td>
<td>0.129</td>
<td>0.070</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| E Asia = SE Asia = Ainu; Ainu = Jomon = SE Asia, but Jomon ≠ E Asia |
|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
| Double shoveling | UI1 | 2+ | 0.097 | 0.046 | 0.145 | 0.181 | 0.358 | 0.165 | 0.166 | 0.066 |
| Enamel extensions | UM1 | 2+ | 0.104 | 0.059 | 0.400 | 0.171 | 0.519 | 0.082 | 0.408 | 0.153 |

| E Asia = SE Asia = Jomon; Ainu = Jomon = E Asia, but Ainu ≠ SE Asia |
|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
| Root number | UP1 | 2 | 0.226 | 0.078 | 0.116 | 0.058 | 0.268 | 0.058 | 0.394 | 0.130 |
| Pegged/Reduced/Missing | UM3 | 1+ | 0.000 | 0.000 | 0.000 | 0.000 | 0.383 | 0.075 | 0.225 | 0.157 |

<p>| Ainu = Jomon = E Asia = SE Asia |
|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
| Deflecting Wrinkle | LM1 | 2+ | 0.062 | 0.088 | 0.205 | 0.173 | 0.295 | 0.413 | 0.327 | 0.188 |
| Cusp number | LM2 | 4 | 0.383 | 0.292 | 0.119 | 0.148 | 0.161 | 0.048 | 0.283 | 0.055 |</p>
<table>
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<th>Group Comparison</th>
<th>Mean Difference</th>
<th>P- Value</th>
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<tr>
<td>Jomon/East Asia</td>
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<td>0.002</td>
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<td>Jomon/Southeast Asia</td>
<td>0.165</td>
<td>0.383</td>
</tr>
<tr>
<td>Ainu/East Asia</td>
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<td>0.024</td>
</tr>
<tr>
<td>Ainu/Southeast Asia</td>
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<td>0.996</td>
</tr>
<tr>
<td>East Asia/Southeast Asia</td>
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<td>0.02</td>
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<td><strong>UI1 Double Shoveling</strong></td>
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<td>0.944</td>
</tr>
<tr>
<td>Jomon/East Asia</td>
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<tr>
<td>Jomon/Southeast Asia</td>
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<td>Ainu/East Asia</td>
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<tr>
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<td>0.994</td>
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</tr>
<tr>
<td><strong>UP1 Root Number</strong></td>
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</tr>
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<td>0.383</td>
</tr>
<tr>
<td>Jomon/East Asia</td>
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<tr>
<td>Jomon/Southeast Asia</td>
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<td>0.062</td>
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<td>Ainu/East Asia</td>
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<td>0.147</td>
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<td>Ainu/Southeast Asia</td>
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<tr>
<td>East Asia/Southeast Asia</td>
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<td>0.203</td>
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<td><strong>UM1 Enamel Extensions</strong></td>
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<td>Jomon/Ainu</td>
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<tr>
<td>Jomon/East Asia</td>
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<td>0.013</td>
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<td>0.583</td>
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<tr>
<td>Ainu/Southeast Asia</td>
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<td>1.000</td>
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<td>1.000</td>
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<tr>
<td>Jomon/East Asia</td>
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<td>0.000</td>
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<td>Jomon/Southeast Asia</td>
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<tr>
<td>Ainu/Southeast Asia</td>
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<td>0.017</td>
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<tr>
<td>East Asia/Southeast Asia</td>
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<td>0.113</td>
</tr>
</tbody>
</table>
Table 3.5. Tukey significance values between means of groups.

The significant differences among groups and the contributing traits are broken down as follows:

- **Jomon/Ainu**: The only significant difference between the Jomon and Ainu was for UM1 enamel extensions.
- **Jomon/East Asia**: Five traits differ significantly between the Jomon and East Asia (UI1 shoveling, UI1 double shoveling, LM1 root number, UM1 enamel extensions, and UM3 pegged/reduced/missing).
- **Jomon/Southeast Asia**: Two traits differ significantly between the Jomon and Southeast Asia (UM1 enamel extensions, UM3 pegged/reduced/missing).
• **Ainu/East Asia**: Three traits differ significantly between the Ainu and East Asia (UI1 shoveling, LM1 root number, UM3 pegged/reduced/missing).

• **Ainu/Southeast Asia**: There are two traits that differ significantly between the Ainu and Southeast Asia (UP1 root number, UM3 pegged/reduced/missing).

• **East Asia/Southeast Asia**: Even though these groupings represent the original Sinodont/Sundadont division, only two traits differ significantly (UI1 shoveling, LM1 root number.)

The traits that show the most significant differences between the groups in line with the Sinodont/Sundadont dichotomy complex are UI1 shoveling and LM1 root number. Both are associated with higher frequencies in Sinodonts and show a significant difference between East Asia and Southeast Asia, the Jomon, and the Ainu. Not all traits define the Sinodont/Sundadont dichotomy or the dual origin hypothesis. UM3 Enamel extensions show a significant difference between the Ainu and the Jomon, but it is the only trait to do so. Four-cusped LM2, despite being a trait defined in the Sinodont/Sundadont dichotomy, does not show any significant difference. While UI1 double shoveling shows a significant difference between the Jomon and East Asia, there is no significant difference for UI1 double shoveling between the Japanese and Ainu. The Ainu are the only group significantly different from Southeast Asia for UP1 root number. Additionally, in the case of pegged/reduced/missing UM3, there is support for the Ainu/Jomon relationship but not for one with either East Asia or Southeast Asia.

Since the Yayoi was too small to include in the distance and ANOVA analyses, individuals could be analyzed through rASUDAS. The beta version of rASUDAS utilizes Bayesian statistics to calculate a posterior probability for ancestry based on 21 crown and root traits. rASUDAS (beta) allows for ancestry to be determined per individual rather than per
sample, making it useful analysis for when there are small sample sizes. To have data input into rASUDAS (beta), an individual needed 12 out of the 21 traits needed.

For the analysis, the following number of individuals were used:

- Honshu Jomon, n = 8
- Hokkaido Jomon, n = 7
- Hokkaido Ainu, n = 8
- Sakhalin Ainu, n = 8
- Yayoi, n = 5

The individuals were tested to estimate their probability of being assigned to the four following groups: American Arctic & Northeast Asia, Australo-Melanesia & Micronesia, East Asia, and Southeast Asia & Polynesia.

<table>
<thead>
<tr>
<th>Group</th>
<th>No. of Traits</th>
<th>Am. Arctic &amp; NE. Asia</th>
<th>Australo-Melanesia &amp; Mic.</th>
<th>E. Asia</th>
<th>SE. Asia &amp; Polynesia</th>
<th>Estimated</th>
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<td>16</td>
<td>0.013</td>
<td>0.375</td>
<td>0.069</td>
<td>0.543</td>
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</tr>
<tr>
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<td>0.311</td>
<td>0.241</td>
<td>0.237</td>
<td>AM.M</td>
</tr>
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<td>0.184</td>
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<td>AA &amp; NE.A</td>
</tr>
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<td>0.584</td>
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</tr>
<tr>
<td>Honshu Jomon</td>
<td>13</td>
<td>0.469</td>
<td>0.265</td>
<td>0.034</td>
<td>0.232</td>
<td>AA &amp; NE.A</td>
</tr>
<tr>
<td>Honshu Jomon</td>
<td>15</td>
<td>0.903</td>
<td>0.001</td>
<td>0.074</td>
<td>0.022</td>
<td>AA &amp; NE.A</td>
</tr>
</tbody>
</table>

Table 3.6. Posterior probabilities for estimated ancestry of Honshu Jomon individuals.
Table 3.7. Posterior probabilities for estimated ancestry of Hokkaido Jomon individuals.

The Jomon ancestries vary across different populations, although the population that both the Honshu and Hokkaido Jomon align with the most is Northeast Asia. It is worth noting that there have been misclassification issues for Southeast Asian & Polynesian groups. Scott et al. (2018b) state that individuals that are intermediate between Sinodonts and Sundadonts tend to misclassify as either American Arctic & Northeast Asian or Australo-Melanesia & Micronesia. Two individuals do classify as the expected Southeast Asia.

Table 3.8. Posterior probabilities for estimated ancestry of Hokkaido Ainu individuals.
Both the Hokkaido Ainu (4 of 8) and the Sakhalin Ainu (3 of 8) have individuals who classify as Southeast Asia & Polynesia. The Sakhalin Ainu classify more often into American Arctic & Northeast Asia, although whether this is a misclassification error due to intermediate Sinodont/Sundadont trait grades within individuals or gene flow with Northeast Asian individuals cannot be determined.

### Table 3.9. Posterior probabilities for estimated ancestry of Sakhalin Ainu individuals.

<table>
<thead>
<tr>
<th>Group</th>
<th>No. of Traits</th>
<th>Am. Arctic &amp; NE. Asia</th>
<th>Australo-Melanesia &amp; Mic.</th>
<th>E. Asia</th>
<th>SE. Asia &amp; Polynesia</th>
<th>Estimated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sakhalin Ainu</td>
<td>17</td>
<td>0.452</td>
<td>0.037</td>
<td>0.368</td>
<td>0.144</td>
<td>AA &amp; NE.A</td>
</tr>
<tr>
<td>Sakhalin Ainu</td>
<td>17</td>
<td>0.348</td>
<td>0.154</td>
<td>0.304</td>
<td>0.195</td>
<td>AA &amp; NE.A</td>
</tr>
<tr>
<td>Sakhalin Ainu</td>
<td>17</td>
<td>0.054</td>
<td>0.336</td>
<td>0.209</td>
<td>0.402</td>
<td>SE.A &amp; P</td>
</tr>
<tr>
<td>Sakhalin Ainu</td>
<td>16</td>
<td>0.012</td>
<td>0.385</td>
<td>0.031</td>
<td>0.573</td>
<td>SE.A &amp; P</td>
</tr>
<tr>
<td>Sakhalin Ainu</td>
<td>15</td>
<td>0.009</td>
<td>0.021</td>
<td>0.774</td>
<td>0.196</td>
<td>EA</td>
</tr>
<tr>
<td>Sakhalin Ainu</td>
<td>12</td>
<td>0.183</td>
<td>0.208</td>
<td>0.211</td>
<td>0.398</td>
<td>SE.A &amp; P</td>
</tr>
<tr>
<td>Sakhalin Ainu</td>
<td>14</td>
<td>0.441</td>
<td>0.016</td>
<td>0.322</td>
<td>0.220</td>
<td>AA &amp; NE.A</td>
</tr>
<tr>
<td>Sakhalin Ainu</td>
<td>14</td>
<td>0.500</td>
<td>0.107</td>
<td>0.221</td>
<td>0.173</td>
<td>AA &amp; NE.A</td>
</tr>
</tbody>
</table>

### Table 3.10. Posterior probabilities for estimated ancestry of Yayoi individuals.

Only one of the Yayoi individuals had the highest probability of being East Asian. However, many of the probabilities for East Asia, Southeast Asia & Polynesia, and Australo-Melanesian & Micronesia were relatively close to each other. Yayoi individuals had very low probabilities of belonging to American Arctic & Northeast Asian groups.
Discussion

Hudson and Matsumura (2006) suggest gene flow between Sinodonts and Sundadonts occurred during the early Holocene when Sinodonts moved into Sundaland. The clustering of East Asia and Southeast Asia in the Bray-Curtis UPGMA dendrogram (see Fig. 3.1) and the MMD dendrogram (see Fig. 3.4) supports this position. Additionally, six out of eight traits do not point to any significant difference between East Asia and Southeast Asia. The difference between frequency values for the key crown and root traits for East Asia and Southeast Asia tends to be slight, as in the dissimilarity matrices (see Table 3.1, Table 3.2) the dissimilarity values are close to 0, indicating sameness. Scott et al. (2018a) also note that recent Southeast Asians shift more to East Asia than earlier Southeast Asian samples.

The dendrogram with branches by sample frequencies instead of averaged sample frequencies (Fig. 3.3) better shows the breakdown of East Asian and Southeast Asian gene flow. After the initial divergence of Australians, the next two clusters include both East Asians and Southeast Asians. After that, there are two primary clusters remaining: one that contains the two Jomon and two Ainu groups and a final cluster that has Polynesians splitting off first, followed by Melanesians and New Guinea, with three Southeast Asian groups in the last cluster. Although there is some indication of a dental dichotomy in Asia following Turner’s (1989) Sinodont-Sundadont division, the distinction is not always evident when comparing East and Southeast Asian samples.

The Ainu and Jomon link is evident in both the ANOVA and dendrograms derived from the Bray-Curtis and MMD matrices. The dendrograms show the Ainu and Jomon fall consistently in the same cluster. For both of the Bray-Curtis dendrograms (see Figs. 3.1 and 3.2) the Ainu and Jomon cluster more tightly with themselves. For the MMD dendrogram and the by-
sample Bray-Curtis dendrogram (Fig 3.4; Fig. 3.3) the Hokkaido Jomon are closest to the Sakhalin Ainu, and the Honshu Jomon are closest to the Hokkaido Ainu. It is important to note that those two groups are divided into northernmost and southernmost populations of the samples available in this research. Not only does this suggest a Jomon-Ainu relationship but also possible movement of the Jomon north in response to the Yayoi population moving into Honshu. Omoto and Saitou (1997) and T. Hanihara suggest northeastern influences on Jomon and Ainu DNA, providing another explanation for the MMD cluster. Ossenberg et al. (2006) state that the Jomon are closer to the Japanese than any population within Northeast Asia, a position at odds with influences from the north causing a distinction between groups.

It is possible that Sundadonty itself is what is causing Jomon/Ainu similarities with Northeast Asia. Turner (1990) describes Sundadonty as a long-standing conservative dental complex that characterized Southeast Asia and Northeast Asia until Sinodonty developed during the Pleistocene. The genetic and morphological data might indicate a persistent older remnant of Sundadonty. Regardless of population origin, there is little contention over the fact the Jomon are ancestral to the Ainu. The main issue is the ancestral population of the Jomon and Yayoi.

<table>
<thead>
<tr>
<th></th>
<th>Jomon</th>
<th>Ainu</th>
<th>Modern Japanese</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turner</td>
<td>Southeast Asian</td>
<td>Jomon, Southeast Asian</td>
<td>Yayoi, East Asia</td>
</tr>
<tr>
<td>Scott</td>
<td>Southeast Asian</td>
<td>Jomon, Southeast Asian</td>
<td>Yayoi, East Asia</td>
</tr>
<tr>
<td>Hanihara K.</td>
<td>Southeast Asian</td>
<td>Jomon, Southeast Asian</td>
<td>Yayoi, East Asia</td>
</tr>
<tr>
<td>Hanihara T.</td>
<td>Northeast Asia, Southeast Asia*</td>
<td>Jomon, Northeast Asia</td>
<td>Yayoi, East Asia</td>
</tr>
<tr>
<td>Pietrusewsky</td>
<td>Northeast Asia</td>
<td>Jomon, Northeast Asia</td>
<td>Yayoi, Northeast Asia/East Asia</td>
</tr>
<tr>
<td>Hammer</td>
<td>Central Asia</td>
<td>Jomon, some Northeast Asia</td>
<td>Yayoi, Southeast Asia</td>
</tr>
<tr>
<td>Omoto and Saitou</td>
<td>Northeast Asia</td>
<td>Jomon, pre-Yayoi Northeast Asia</td>
<td>Yayoi, Northeast Asia</td>
</tr>
</tbody>
</table>

*change in author's opinion over different articles

**Table 4.1.** Summarized views of different authors on the relationships of the Jomon, Ainu, and modern Japanese.

The Yayoi are represented by a very small dental sample (n = 11) and could not be included in statistical analyses. Although there is a potential for sampling error, observations can
be noted for those traits best shown to distinguish Sinodonts and Sundadonts: UI1 shoveling and LM1 root number. Of the 11 individuals, four had UI1 shoveling, and all were at or above grade 3. Eight individuals could be observed for the LM1 root number trait, and out of those, only one person had three-rooted LM1 (12.5%). Other Sinodont traits seemed low for this sample. Only four individuals could be measured for UI1 double shoveling, and two expressed 0 and the other two were 1+. With this in mind, it is easy to understand why there is debate over the Yayoi origins as well as the Jomon. There is not enough sufficient data to make a claim about the Yayoi’s origins for this thesis. ANOVA analysis and the dendrograms indicate a possible Southeast Asian origin for the Jomon and subsequently, the Ainu.

The ANOVA values also provide insight to the Sinodont/Sundodont and *ectodysplasin A receptor* gene (EDAR) dichotomies. East Asian populations have a high degree of presence of the *EDAR V370A* gene (Park et al. 2012; Hlusko et al. 2018). Park et al. (2012) found the V370A gene to be associated with UI1 shoveling, UI1 double shoveling, and LM2 hypoconulid (cusp 5). Those three traits are all associated with Sinodonty. Knowing this, it makes sense that out of the Sinodonty and Sundodonty traits tested for most significant among the Jomon, Ainu, East Asia, and Southeast Asia, UI1 shoveling and UI1 double shoveling were significant in showing that the Jomon and Ainu are similar to Southeast Asia.
Fig. 4.2. Moderate UI1 shoveling and reduced UM3 in Japanese maxillary dentition. Photo courtesy of G.R. Scott.

East Asia and Southeast Asia also differ significantly with UI1 shoveling and LM1 root number, but not UI1 double shoveling. It has been debated over whether or not Ryukyu Islanders are related to the Ainu (Hanihara K 1991; Omoto and Saitou 1997) or not (Pietrusewky 1999; Higa et al. 2003); however, if we assume that they are, the presence of the V370A allele as reported by ALFRED (Kidd et al. 2018) is intriguing.

<table>
<thead>
<tr>
<th>Population</th>
<th>EDAR Absence</th>
<th>EDAR Presence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mainland Japanese</td>
<td>0.241</td>
<td>0.759</td>
</tr>
<tr>
<td>American Japanese</td>
<td>0.225</td>
<td>0.775</td>
</tr>
<tr>
<td>Ryukyu Islanders</td>
<td>0.342</td>
<td>0.659</td>
</tr>
</tbody>
</table>

Table 4.2. Average frequencies of EDAR allele V370A values in varying Japanese populations. Data taken from the Allele Frequency Database website (Kidd et al. 2003; Kidd et al. 2018) on November 28th, 2018.

In table 4.2, the Ryukyu Islanders show less of the V370A allele than mainland Japanese. Since EDAR presence is elevated in Sinodonts, it would make sense that the Ryukyu Islanders
and Ainu, who possibly have Southeast Asian origins, have lower levels of gene presence. The reason these traits are connected to the gene is unknown, although it is possibly related to diet (Park et al. 2012; Hlusko et al. 2018). The EDAR dichotomy supports K. Hanihara’s (1991) dual origin hypothesis, as he also stated that the Ryukyu Islanders were related to the Jomon. The dual origin hypothesis remains as the most likely explanation for the peopling of Japan if the possible gene flow between East and Southeast Asia during the Holocene is taken into account. The EDAR-related trait UI1 shoveling is also a likely contributor to the separation of Ainu populations in fig. 3.4 and 3.3, as the Sakhalin Ainu have a higher frequency of shoveling more in line with the Japanese populations than the Jomon or Southeast Asia (Table 3.1). This could be due to gene flow between the Sakhalin Ainu and Sinodont East Asian populations.

The rASUDAS (beta) analysis adds further complexity to the ANOVA and distance measure results. The Honshu Jomon (Table 3.6) had two individuals classify as most likely East Asian, and many fell within the category of American Arctic & Northeast Asia, which the program will occasionally misclassify Sinodont/Sundadont intermediacy as if they tend toward Sinodonty. The Hokkaido Jomon (Table 3.7) had no individuals classify as East Asia, although six classified as American Arctic & Northeast Asian. Two fell into the Southeast Asian & Polynesian group. The Hokkaido Ainu (Table 3.8) and Sakhalin Ainu (Table 3.9) also had three individuals each fall into the Southeast Asian group. It is likely that any individuals within these four groups that classify into Northeast Asian or Australo-Melanesian groups are part of the misclassification errors of rASUDAS associated with Southeast Asian individuals. However, due to the belief that Northeast Asians, especially those belonging to the Okhotsk culture, have biologically impacted the Ainu (Hanihara T. et al. 2008; Taijima et al. 2004), it cannot be entirely ruled out as a classification error. It additionally generates further questions as to the
separation of Honshu Jomon-Hokkaido Ainu and Hokkaido Jomon-Sakhalin Ainu groups within the dendrograms (Fig. 3.3; Fig. 3.4).

Yayoi individuals could also be further analyzed through the rASUDAS method. Most of the probabilities for Australo-Melanesia, East Asia, and Southeast Asia were similar. One individual did distinctly classify as East Asian. None of them classified as American Arctic & Northeast Asia. Northeast Asia can be ruled out as having a biological influence on the Yayoi analyzed within the program. It could be possible both Southeast Asian and some Northeast Asian influences could be causing the Jomon/Ainu to be different from the Japanese, but nothing for certain can be determined at this time. It is unclear whether the Jomon/Ainu are getting classified appropriately, or if it is an issue with the application, or the reflection of persistent remnants of Sundadonty within Northeast Asian Sinodonty.

Through ANOVA analysis, frequency comparisons, and dissimilarity matrices, it is clear that the relationship between East Asia and Southeast Asia is complex. However, there is little debate in regard to the relationship of the Jomon and Ainu. It is most likely that the Jomon are ancestral to the Ainu. Further research needs to be conducted on the differentiation between island populations, particularly regarding possible East Asian or Northeast Asian gene flow into the Jomon/Ainu groups.

Conclusions

The peopling of Japan is a complex topic. Although there is evidence for the Sinodont/Sundadont dichotomy and for the relationship between the Jomon/Ainu and Southeast Asians, there is also evidence for gene flow between East Asia and Southeast Asia, possibly dating back to the early Holocene. The UPGMA dendrogram analyses support Jomon/Ainu and
East Asian/Southeast Asian gene flow, but the MMD dendrogram and the NJT dendrogram analyses do not. This means that if there is Holocene gene flow between the two populations, it is most likely very minimal and does not disrupt the proposed Sinodont/Sundadont dichotomy. The ANOVA values exhibited similar evidence. The comparison of modern populations in a global world could be a primary cause of confusion for the origins of the Jomon and the Yayoi. Despite the conundrum, the following conclusions may be reached:

1. Modern Japanese populations are not related to the Jomon/Ainu. Higher frequencies of Sinodonty traits in the Sakhalin Ainu may indicate some gene flow between the Ainu and East Asians. A lack of significant difference in the ANOVA analysis between the Ainu and modern Japanese for UM1 enamel extensions, LM1 deflecting wrinkle, and LM2 cusp number may also indicate an increase in Sinodonty traits for Ainu populations.

2. The lack of significant differences between East Asia and Southeast Asia in ANOVA analysis and the clustering of the groups in whatever analysis this was – not the figure – suggest Holocene gene flow between the two populations.

3. The lack of significant differences between East Asia and Southeast Asia in the ANOVA results means that the Sinodonty/Sundadonty dichotomy is more complex than originally believed.

4. The data are mostly in line with the dual origin hypothesis. The Jomon/Ainu have less significant differences between traits with Southeast Asia than they do East Asia.

5. The dual origin hypothesis is best illustrated by UI1 shoveling and LM1 root number.

6. The *ectodysplasin A receptor* gene is likely the reason that UI1 shoveling and UI1 double shoveling are the traits that best show a connection between the Jomon/Ainu and Southeast Asia, as Southeast Asians have a lower frequency of the gene. If one accepts
that Ryukyu Islanders are most closely related to the Ainu and Jomon, modern Ryukyu Island populations also show a lower frequency of the EDAR gene. LM2 root number did not show a significant difference among any of the groups despite its linkage to EDAR. 7. Hokkaido Jomon-Sakhalin Ainu and Honshu Jomon-Hokkaido Ainu clusters exist in the MMD dendrograms and the Bray-Curtis by-sample dendrograms. This shows a closer link between the two northernmost island populations and the two southernmost island populations.

From the evidence it is likely the Sundadont Jomon were displaced by the Sinodont Yayoi, who then caused the Jomon to further move upward. The Yayoi are ancestral to the modern Japanese, while the Jomon are the ancestral to the Ainu. This adds to the support of the dual origin hypothesis.
### Appendix

**Appendix 1.** Frequency data for tooth and crown traits of Japanese sample from Scott and Irish (2017).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Sample: Japan</th>
<th>Grade</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n 0 1 2 3 4 5 6 7</td>
<td></td>
</tr>
<tr>
<td>Winging UI1</td>
<td>268 0.227 0.041 0.732 0.000</td>
<td></td>
</tr>
<tr>
<td>Shoveling UI1</td>
<td>280 0.011 0.032 0.293 0.421 0.168 0.064 0.011 0.000</td>
<td></td>
</tr>
<tr>
<td>Double-shoveling UI1</td>
<td>271 0.568 0.240 0.077 0.055 0.026 0.000 0.033</td>
<td></td>
</tr>
<tr>
<td>Interruption grooves UI2</td>
<td>304 0.553 0.447</td>
<td></td>
</tr>
<tr>
<td>Tuberculum dentale UI2</td>
<td>307 0.844 0.000 0.036 0.016 0.003 0.000 0.101</td>
<td></td>
</tr>
<tr>
<td>Bushman canine UC</td>
<td>368 0.967 0.005 0.022 0.005</td>
<td></td>
</tr>
<tr>
<td>Distal acc. Ridge UC</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uto-Aztecan UP1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hypocoone UM2</td>
<td>489 0.100 0.033 0.092 0.225 0.458 0.092</td>
<td></td>
</tr>
<tr>
<td>Cusp 5 UM1</td>
<td>395 0.876 0.043 0.041 0.015 0.013 0.013</td>
<td></td>
</tr>
<tr>
<td>Carabelli’s cusp UM1</td>
<td>462 0.416 0.275 0.035 0.097 0.030 0.084 0.009 0.054</td>
<td></td>
</tr>
<tr>
<td>Parastyle UM3</td>
<td>237 0.983 0.004 0.004 0.008 0.000 0.000</td>
<td></td>
</tr>
<tr>
<td>Enamel extension UM1</td>
<td>529 0.285 0.174 0.064 0.476</td>
<td></td>
</tr>
<tr>
<td>Root number UP1</td>
<td>510 0.747 0.249 0.004</td>
<td></td>
</tr>
<tr>
<td>Root number UM2</td>
<td>500 0.108 0.200 0.688 0.002 0.002</td>
<td></td>
</tr>
<tr>
<td>PRC-Abs UM3</td>
<td>511 0.583 0.014 0.020 0.384</td>
<td></td>
</tr>
<tr>
<td>Lingual cusp no. LP2</td>
<td>345 0.000 0.339 0.583 0.078</td>
<td></td>
</tr>
<tr>
<td>Groove pattern LM2</td>
<td>358 0.302 0.564 0.134</td>
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</tr>
<tr>
<td>Cusp number LM1</td>
<td>319 0.003 0.574 0.423</td>
<td></td>
</tr>
<tr>
<td>Cusp number LM2</td>
<td>351 0.140 0.519 0.151 0.191</td>
<td></td>
</tr>
<tr>
<td>Deflecting wrinkle LM1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trigonid crest LM1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protostylid LM1</td>
<td>360 0.789 0.097 0.000 0.056 0.036 0.006 0.017 0.000</td>
<td></td>
</tr>
<tr>
<td>Cusp 7 LM1</td>
<td>388 0.936 0.008 0.026 0.028 0.003 0.000</td>
<td></td>
</tr>
<tr>
<td>Tome’s root LP1</td>
<td>203 0.054 0.527 0.187 0.128 0.094 0.005 0.000 0.005</td>
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<tr>
<td>Root number LC</td>
<td>343 0.988 0.012</td>
<td></td>
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<tr>
<td>Root number LM1</td>
<td>438 0.000 0.760 0.240</td>
<td></td>
</tr>
<tr>
<td>Root number LM2</td>
<td>414 0.329 0.659 0.012</td>
<td></td>
</tr>
<tr>
<td>Odontome UP/LP P1P2</td>
<td>466 0.951 0.049</td>
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</table>
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