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On the Pleistocene Population History in the Japanese Archipelago

by Yuichi Nakazawa

This paper provides a current understanding of human population history in the Pleistocene Japanese Archipelago, particularly with respect to the routes and timing of hunter-gatherer migrations, by incorporating multiple lines of evidence from the records of archaeology, human paleontology, and genetic studies. The human fossil remains are concentrated on the Ryukyu Islands in southwestern Japan, suggesting that there may have been a northward migration via the Ryukyu Islands. In contrast, studies of ancient mitochondrial DNA demonstrate genetic continuity among Holocene hunter-gatherer populations in the Paleo-Sakhalin-Hokkaido-Kurile Peninsula, whereas the Pleistocene genetic history is little explored. Although it is largely supported, the assumed population continuity from the Pleistocene to the Holocene inside the Japanese Archipelago is also challenged by an examination of the Paleolithic record and a comparison of the short- and long-term chronologies of the Japanese Paleolithic, implying that the Japanese Paleolithic record was created by hunter-gatherer population migrations from the north and south with substantial time lag and endemic technological invention and transformation during the Late Pleistocene.

Since the beginning of paleoanthropology, human population history in East Asia has been critical in assessing the evolution of human lineages. Although the Pleistocene human fossil records are still limited in this large and diverse geographic area, advances in human fossil and genetic studies have revealed that various species and populations in the genus Homo (e.g., Homo erectus, archaic Homo sapiens, modern H. sapiens, Homo floresiensis, and Denisovans) were present during the Pleistocene in eastern Asia (C. Bae 2010; Elder 1996; Reich et al. 2010; Xiao et al. 2014). The geographic location of the Japanese Archipelago, characterized by the eastern end of Eurasia between the extensive Chinese mainland, Siberia, and the northern Pacific Ocean, makes Japan a unique feature in human evolution. In terms of the human migratory record out of Africa, the Japanese Archipelago is, in addition to Australia and the Americas, one of the farthest points along the Eurasian trail. In addition, it is a cul-de-sac in the sense that no more explorations into new terrestrial habitats were achieved until more extensive explorations were conducted of the smaller islands in the surrounding oceans of the northern Pacific.

Unlike in China, where fossil evidence of H. erectus, archaic H. sapiens, and modern H. sapiens is present (C. Bae 2010; Dennell 2010, 2015; Elder 1996; Liu et al. 2010; Xiao et al. 2014), the fossil record in Japan is attributed solely to modern H. sapiens and dated to late marine isotope stage (MIS) 3 and MIS 2 (Kaifu and Fujita 2012; Nakagawa et al. 2010). On the other hand, there is an abundant Upper Paleolithic archaeological record in Japan, mainly due to the intensive excavation projects carried out by various organizations that include local government offices and cultural resource management firms (Barnes 1990; Nakazawa 2010). Despite the accumulation of a rich Paleolithic archaeological record, there is still limited evidence of human occupation before late MIS 3 (>40,000–38,000 BP), unlike in China, where affirmative cultural evidence has been accumulated since at least the late Early Pleistocene (Dennell 2009; Gao 2013; Gao and Norton 2002; Norton et al. 2010a; Wang 2005). Here, I will provide an overview of the current understanding of the Paleolithic archaeological and Late Pleistocene paleoanthropological records in this particular geographic region and propose how they may contribute to future directions in human evolutionary studies in Asia. Given my background, the discussion will be biased toward the archaeological evidence, but recent discussions and contributions about human migration history and genetic studies are incorporated where applicable.

Paleogeography and Human Migrations

The arc-trench system of the Japanese Archipelago was created by complex tectonic activities involving five plates: Eurasia, Amur, Okhotsk, Pacific, and the Philippine Sea (Taira 2001). The topographic characteristics of the islands were formed by the interactions of these plates. This resulted in the formation of four larger islands: Hokkaido, Honshu, Shikoku, and Kyushu from the north to south. There are also thousands of smaller islands in and around the Pacific and the Sea of Japan. The Ryukyu Islands are the long chain of islands situated in the south-
west between Kyushu and Taiwan. Because of continuous tectonic forces, volcanism and earthquakes often happened even during the Pleistocene. The current position of this long chain of the four major islands, stretching between 45°N and 31°N, was eventually established by the onset of the Holocene, when the global sea level rose to its current level (Yonekura et al. 2001). During the Pleistocene, numerous islands, including the four larger islands, were connected to form part of the larger island or peninsula (Iwase et al. 2012; Ota and Yonekura 1987). For instance, between MIS 4 and MIS 2, Honshu, Shikoku, and Kyushu were connected to form a single island, commonly referred to as “Paleo-Honshu,” while Hokkaido formed the southern end of a peninsula in northeastern Siberia, commonly called the “Paleo-Sakhalin/Hokkaido/Kurile Peninsula” (Paleo-SHK; Ono 1990).

The palynological record in Japan allows us to reconstruct vegetation changes and spatial variation across the entire archipelago during the Late Pleistocene. A recent study by Takahara et al. (2015) provides a synthetic picture of MIS 3 vegetation in and around the Japanese Archipelago (i.e., Sakhalin, Paleo-SHK, Paleo-Honshu, Ryukyu, and Taiwan) using 47 locational pollen samples. Species in temperate to cool forests vary according to the latitudes and altitudes in Japan, resulting in a vegetation map that is a mosaic of cold and temperate forests, whereas relatively high occurrences of deciduous broad-leaf forests are observed regardless of vegetation zones. During the Last Glacial Maximum (LGM), on the other hand, the area of deciduous broad-leaf forest shifted to the southwestern coastal margin of the Paleo-Honshu, and cool and temperate forests mostly covered Japan (Iwase et al. 2012, fig. 2).

Given the unique geographic features of the Japanese Archipelago, several different migration routes to the islands are viable. Saitou (2005) proposes six possible routes of human entry (fig. 1). The first route is a migration from the Korean Peninsula to northern Kyushu via the Tsushima Strait (route 1). The second is a route of migration from the Russian Far East in the north to Hokkaido via Sakhalin Island (route 2). The third possible track is also a southward migratory route, from the Kamchatka Peninsula in western Beringia to eastern Hokkaido via the Kurile Islands (route 3). The fourth is a northward route that originates in southern China, extends to Taiwan Island and to the Ryukyu Islands, and crosses over the southern Pacific Ocean, eventually reaching southern Kyushu (route 4). The fifth route goes east from eastern China to Kyushu and crosses the East China Sea (route 5). The sixth route is from the coastal Russian Far East (Primorski) to Honshu and crosses the Sea of Japan (route 6). All of these routes are viable if humans have advanced seafaring skills and the ability to navigate oceans over long distances even when landmarks are no longer visible. Even during the LGM, when sea levels may have dropped by as much as 100 m, Paleo-Honshu Island was not connected to either the Korean Peninsula (Tada 1999) or southern China; small strips of open ocean would have remained between these different landmasses (Li et al. 2014). Although Hokkaido was connected to Sakhalin and eastern Siberia to form the Paleo-SHK, there is no evidence that Hokkaido was connected to Paleo-Honshu at this time (Ono 1990). Given these possible land connections, terrestrial human migrations are only achievable through route 2, the northern entry route from Far Eastern Russia to Hokkaido. The other five routes all require a certain level of seafaring navigation capability, which was clearly present in the region by the advent of the Late Paleolithic, as evidenced by obsidian transportation from the Pacific island of Kozu to Paleo-Honshu (Ikeya 2015; Shimada et al. 2017; Tsutsumi 2010).

Compatibility, Inconsistency, and Biases in the Study of Prehistoric Human Migrations: Human Paleontology, Genetic Studies, and Archaeology

In evaluating the routes and timing of the earliest human migrations into the Japanese Archipelago, employing multiple lines of evidence is a useful approach to reach a synthetic picture. Currently available data are from human paleontology, genetics, and archaeology, which should be combined with our understanding of the geography and paleoenvironment of Pleistocene Japan. The most ubiquitous record comes from archaeology, whereas there are limited human fossil remains. Although studies of DNA have provided a picture of how different human populations contributed to the formation of modern Japanese, sources of data, particularly ancient DNA, are still small in number. Below, I discuss the Japanese records of human fossils, genetic studies, and archaeology to build a more synthetic picture of what the peopling of the Japanese Archipelago likely resembled.

Human Fossil Record

In 1931, the first discovery of a possible Pleistocene human fossil, known as the “Akashi Genjin” (Akashi hominin), from the Nishiyagi Coast in western Japan was made by archaeologist Nobuo Naora (Harunari 1994). Although the original specimen of the Akashi hominin was lost during World War II, a later reexamination of the cast of the innominate bone indicated that the specimen was likely from a Holocene modern Homo sapiens (Endo and Baba 1982). Since the discovery of the Akashi hominin, a number of Pleistocene human fossils have been reported in Japan, with the majority of them found on the Ryukyu Islands in the southern part of the archipelago (table 1). To date, no Pleistocene human remains have been identified in Hokkaido and northern Honshu.

All of the ages established for these Pleistocene human fossils fall in the second half of MIS 3 or MIS 2. The dates for these fossils are usually obtained from analysis of associated charcoal, but the age of the human fossils from the newly discovered Shiraho-Saonetabarû Cave was determined with direct radiocarbon dating (Nakagawa et al. 2010). Despite the scarcity of Pleistocene human remains, paleoanthropologists have discussed the routes of these Late Pleistocene humans on the basis...
of their morphology. For example, it was suggested that the Minatogawa individuals were morphologically different from the Holocene Jomon (Neolithic) population in Japan and may be more closely linked with populations from Southeast Asia (Baba, Narasaki, and Ohyama 1998). Human fossils from the collapsed karstic cave site of Nekata in Hamakita City present a more complicated picture. The human remains from the upper layer of Nekata, known as the Hamakita upper specimen, are morphologically close to Jomon, while the specimen (tibia) from the lower level was not assigned to Jomon (Kondo and Matsu’ura 2005; Suzuki 1966; Suzuki and Endo 1966). Because the associated date is from the Late Pleistocene, the tibia fossil was simply referred to as a “Palaeolithic hominid,” with no specific assignment (Kondo and Matsu’ura 2005:155).

As opposed to the limited number of Pleistocene human remains, there are more Holocene human remains from prehistoric sites in Japan that date to the Jomon (hunter-gatherers) and Yayoi (agriculturalists; Barnes 2015; Habu 2004; Imamura 1996; Mizoguchi 2013). A number of metric and morphometric studies of the human skeletal remains from Jomon and Yayoi sites indicate that they represent different populations (e.g., Dodo and Ishida 1990; Kaifu 1995, 1997; Nakahashi 1993). The physical difference between the Jomon and Yayoi led to the proposal of the admixture model for explaining the formation of “Japanese.” This is referred to as the “dual-structure model” and was proposed by Kazuo Hanihara (1991:25). The dual-structure model proposes that humans first entered the Japanese Archipelago from Southeast Asia with a continual...
<table>
<thead>
<tr>
<th>Region, site</th>
<th>Anatomical parts</th>
<th>Context</th>
<th>Radiocarbon dates (BP)</th>
<th>Dated specimens</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Honshu:</strong></td>
<td></td>
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<tr>
<td>Hamakita (Upper)</td>
<td>Cranial fragments, clavicle, humerus, ulna, innominate</td>
<td>Sediments inside fissure</td>
<td>14,050 ± 50 (Beta-160571), 14,200 ± 50 (Beta-160572), 13,860 ± 50 (Beta-160570)</td>
<td>Human remains (parietal, occipital, humerus)</td>
<td>Kondo and Matsu’ura 2005; Suzuki 1966</td>
</tr>
<tr>
<td>Hamakita (Lower)</td>
<td>Tibia</td>
<td>Sediments inside fissure</td>
<td>17,910 ± 70 (Beta-94983)</td>
<td>Faunal remains (leopard or tiger)</td>
<td>Kondo and Matsu’ura 2005; Suzuki 1966</td>
</tr>
<tr>
<td><strong>Ryukyu:</strong></td>
<td></td>
<td></td>
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<tr>
<td>Yamashita-cho Cave 1</td>
<td>Femur, tibia</td>
<td>Upper layer of the cave</td>
<td>32,100 ± 1000</td>
<td>Charcoal fragments</td>
<td>Suzuki 1983</td>
</tr>
<tr>
<td>Minatogawa Fissure (Minatogawa Man series)</td>
<td>Skeletons (5 individuals)</td>
<td>Clay layer in the lower fissure fillings</td>
<td>18,250 ± 650 (TK-99), 16,600 ± 300 (TK-142)</td>
<td>...</td>
<td>Baba et al. 1998; Matsu’ura and Kondo 2011; Suzuki and Hanihara 1982</td>
</tr>
<tr>
<td>Minatogawa Fissure (Upper Minatogawa series)</td>
<td>Nine postcranial (&gt;3 individuals)</td>
<td>Likely from the upper fissure fillings</td>
<td>...</td>
<td>...</td>
<td>Matsu’ura and Kondo 2011</td>
</tr>
<tr>
<td>Shim-šibaru</td>
<td>Talus, metatarsal, infant skeleton, mandible</td>
<td>Clay layer below travertine</td>
<td>15,200 ± 100</td>
<td>Crab shell</td>
<td>Matsu’ura and Kondo 2000</td>
</tr>
<tr>
<td>Pinza-abu</td>
<td>Right humerus, right femur, parietal, occipital, lumbar vertebra, hand bones, isolated teeth</td>
<td>Clay layer below flowstone</td>
<td>25,800 ± 900 (TK-535), 26,800 ± 1300 (TK-605)</td>
<td>Charcoal fragments</td>
<td>Hamada 1985; Sakura 1985</td>
</tr>
<tr>
<td>Shiraho-Saonetabaru Cave</td>
<td>Right parietal, second metatarsal, right fibula</td>
<td>Unconsolidated muddy sediments likely secondary deposition in a chamber</td>
<td>20,416 ± 113, 18,752 ± 100,  15,751 ± 421</td>
<td>Gelatin from bone collagen</td>
<td>Nakagawa et al. 2010</td>
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</tbody>
</table>

Note. Dates for the Minatogawa Fissure (Minatogawa Man series) are listed for references, because these dates were obtained from charcoals sampled from the clay layer with little certain association with the human remains (Kondo and Matsu’ura 2005).
influx from the Jomon but were later assimilated by the Yayoi peoples, who originated from mainland Northeast Asia some 3,000 years ago. According to this model, populations in the southern lands of Japan (i.e., Honshu, Shikoku, and Kyushu) were the result of admixture between Jomon and Yayoi, whereas Ainu, an indigenous population in Hokkaido, and Ryukyans, an indigenous people living in the Ryukyu Islands, were not assimilated and retained Jomon morphology. The dual-structure model proposes that gene flow occurred from both Southeast and Northeast Asia. Human genetic studies largely support the admixture model for the Ryukuan and Ainu populations and their relations to Jomon populations (e.g., Dodo and Ishida 1990; Hammer et al. 2006; Horai et al. 1996; Omoto and Saitou 1997; Shigematsu et al. 2004; Tanaka et al. 2004). However, the genetic relationship between Southeast Asia and Jomon is less supported (e.g., Jinam, Kanzawa-Kiriyama, and Saitou 2015; Omoto and Saitou 1997), suggesting that Late Pleistocene and Holocene hunter-gatherer population history in Japan is more complex than a simple migration from Southeast Asia. In contrast, Paleo-Atlantic migrations from Southeast Asia, as proposed in the original admixture model, have not been explicitly tested through comparative analyses of the Paleo-Atlantic archaeological records of Japan and adjoining regions.

How Do the DNA Studies Tell Us about the Routes of Human Entry into Japan?

The Holocene human fossil record supports an admixture model in which the Paleo-Atlantic population originated from both southeastern and northeastern Asia (e.g., Hanihara 1991). The mitochondrial DNA (mtDNA) analyses of modern Japanese revealed that non-African superhaplogroups M and N originally derived from modern *H. sapiens* dispersing out of Africa (Forster 2004) that eventually came to be the Japanese indigenous populations of Ainu and Ryukuan (e.g., Tanaka et al. 2004; cf. Mac-Meyer et al. 2001). Because Ainu and Ryukuan are descendants of the original Jomon populations (Hanihara 1991; Horai et al. 1996; Omoto and Saitou 1997) and M and N superhaplogroups represent southern and northern routes of human migrations, respectively (Tanaka et al. 2004), the Holocene Jomon population was founded from both northward and southward gene flows.

Studies of ancient mtDNA from the Jomon skeletal remains of Hokkaido show genetic relations between Jomon and Ainu, because both populations retain high frequencies of the haplogroup N9b (Adachi et al. 2011), whereas N9b is scarce among East Asian populations other than Japanese (Tanaka et al. 2004: 1842) and is likely skewed to northern regions in Japan (Shinnoda 2007). Because the coalescent time of N9b is estimated to be approximately 22,000 year ago (Adachi et al. 2011:355), populations that have this haplogroup emerged around the LGM. In Hokkaido, Epi-Jomon human remains in Hokkaido also have N9b (Adachi et al. 2011), which suggests some degree of gene flow during the LGM to the late Holocene in Hokkaido (22,000–2000 years ago).

As discussed above, both genetic studies based on ancient Jomon mtDNA and those based on modern mtDNA more or less support the “dual-structure model” (Hanihara 1991). This also suggests a complex population history even during the Holocene. Nevertheless, what do these genetic implications tell us about Pleistocene population migrations into Japan? In other words, what does the genetic affinity of the Jomon peoples tell us about Paleo-Atlantic population dynamics? In general, because the descendants of Jomon and Yayoi both contributed to the formation of the current Japanese population, Paleo-Atlantic foragers should be regarded as the founding population of the Jomon (Hanihara 1991). However, the extent to which Pleistocene Paleo-Atlantic populations contributed to modern Japanese is largely unidentified, mainly because there are few genetic and human fossil records, with the exception of some good fossil specimens, notably Minatogawa Man (Baba, Narasaki, and Ohyama 1998; Suzuki 1982). The remaining question is how we understand the complexity in Japanese Paleo-Atlantic population history. A question that will not be addressed here is whether there is clear evidence that the Jomon were the direct descendants of the Japanese Paleo-Atlantic foragers and whether both hunter-gatherer populations were genetically continuous for the past 30,000 years in Japan.

What Does Archaeology Tell Us about Human Entry into Japan?

The Paleo-Atlantic archaeological record provides a basic picture of Pleistocene human population history in Japan. Although the number of Paleo-Atlantic sites during the 1960s was only slightly more than 300 (Ohyi 1968:52), the number of registered sites is now greater than 15,000 (Japan Palaeolithic Research Association 2010). Some clarification is necessary, however, regarding this latter number. The “sites” in the recent database include assemblages and collections of artifacts recorded in various contexts, ranging from extensively excavated sites to a few specimens collected on the surface. Because a single cultural level in a deeply excavated multilayered Paleo-Atlantic open-air site is counted as a single site, a single location was sometimes counted multiple times, and site size and artifact density from a single site are not standardized among the recorded sites. Although some bias is present in the record, the database is still useful to explore to understand general macro- and micro-regional patterns of human occupation across the entire Japanese Archipelago.

Considering the regional geographic features and Paleo-Atlantic culture history, I divided the 47 prefectures into 7 broader regions (fig. 2). From north to south, they are labeled as north (N), northeast (NE), southeast (SE), central (C), southwest (SW), south (S), and far south (FS). N, S, and FS are isolated islands corresponding to Hokkaido, Kyushu, and Ryukyu islands. NE, SE, C, and SW are the divisions of Honshu Island, the main island in the archipelago along with adjacent Shikoku. Divisions of NE, SE, C, and SW are based on the presence of mountain chains, plains, and the Pleistocene paleogeography. For example, C is...
the region characterized by high-altitude mountains and plains mostly above 600–1,000 m asl. SW is the region in the middle of the Pleistocene Paleo-Honshu Island. Using the site location data recorded in the database, the number of archaeological sites is counted according to the microregions (table 2). The microregions are then sorted by site density using the areal extent data announced by the Geospatial Information Authority of Japan (2015). SE is the microregion with the highest density, followed by S, C, SW, NE, N, and FS. The highest density in SE is probably explained by sampling bias, due to the high population density in the Tokyo area. It is also because the deeply excavated sites yielded multiple levels of human occupation on the Musashino and Sagamino Uplands in the southern part of SE (e.g., Yajima and Suzuki 1976; Yamaoaka 2010). Except for the microregions with the highest density (SE) and lowest density (FS), the site density shows a south to north inclination. High site density in SE, followed by a gradual increase from C to SW, NE, and N, is observed. The sites are all attributed to the Pleistocene, whereas the chronological affiliations of these sites vary depending on the region, especially between N (the southern part of Paleo-SHK) and the rest of the microregions (i.e., Paleo-Honshu and Ryukyuan islands). The

### Table 2. Counts, areal extent, and density of Late Pleistocene sites in Japan

<table>
<thead>
<tr>
<th>Microregion</th>
<th>No. sites</th>
<th>Areal extent of microregion (km²)</th>
<th>Site density per 100 km²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southeast</td>
<td>7,484</td>
<td>27,436.64</td>
<td>27.3</td>
</tr>
<tr>
<td>South</td>
<td>2,855</td>
<td>42,232.7</td>
<td>6.8</td>
</tr>
<tr>
<td>Central</td>
<td>1,537</td>
<td>35,019.4</td>
<td>4.4</td>
</tr>
<tr>
<td>Southwest</td>
<td>2,413</td>
<td>89,023.22</td>
<td>2.7</td>
</tr>
<tr>
<td>Northeast</td>
<td>1,612</td>
<td>98,563.63</td>
<td>1.6</td>
</tr>
<tr>
<td>North</td>
<td>862</td>
<td>83,424.22</td>
<td>1.0</td>
</tr>
<tr>
<td>Far south</td>
<td>8</td>
<td>2,281</td>
<td>0.4</td>
</tr>
<tr>
<td>Total</td>
<td>16,771</td>
<td>377,971.81</td>
<td>4.4</td>
</tr>
</tbody>
</table>
Paleolithic in the Paleo-Honshu record started at the beginning of the Upper Paleolithic, around 40,000–37,000 years ago, and ended around 11,500 years ago (Yamaoka 2010; Yoshikawa 2014), whereas the beginning of the Paleolithic record in Hokkaido is not earlier than 30,000 years ago (Izuhu et al. 2012; Naoe and Kudo 2014). Thus, the time depth of the Paleo-Honshu Paleolithic record is approximately 27,000 years, as opposed to 18,500 years for Paleo-SHK, because the reliable dates obtained from the hearths in the Agonki-5 site in Sakhalin are 23,500 years ago (Kuzmin et al. 2004; Vasilevski 2003). Because of the difference in time depths, the south to north inclination of site density implies that the earlier Paleolithic sites are more abundant in southern Japan than in northern Japan. High site density in the S microregion (Kyushu) next to the SE of the southern Kanto region in Honshu suggests that waves of the earlier hunter-gatherers would have migrated into Kyushu and spread to the north along Paleo-Honshu Island. Conversely, the likelihood of earlier human population migrations in the early Upper Paleolithic (EUP) from eastern Siberia via Paleo-SHK is not supported. On the one hand, site density patterns alone do not answer the question of timing and size of northerly migratory populations from Paleo-Honshu to Paleo-SHK. The lowest density of the FS microregion of the Ryuku Islands suggests that human arrivals into the Ryuku Islands were relatively low and that occupations were not necessarily continuous, unlike the situation in the microregions in Paleo-Honshu. Relatively high site density in C (the central region in Paleo-Honshu) suggests that humans occupied high-elevation regions during the Upper Paleolithic. Good examples are represented by the open-air sites located on the Nobeyama Plateau, where Paleolithic hunter-gatherers could have followed seasonal movements between the central highlands and southern Kanto regions in SE (e.g., Tsutsumi 2011), similar to pastoral transhumance (e.g., Chang and Tourtellotte 1993), and where groups of hunter-gatherers seasonally aggregating to kill large herbivores around lakes would have sometimes succeeded (e.g., Norton et al. 2010b). Given the population entry routes (fig. 1), the observed south to north inclination of site density in the Paleo-Honshu suggests that the majority of Paleolithic migratory groups were from the Korean Peninsula and southern China. If so, routes 1 and 5 are the best-supported routes for early hunter-gatherers’ dispersals into the Japanese Archipelago.

Paleolithic Chronologies in Japan: Short- versus Long-Term Chronologies

In the study of population history, an establishment of cultural chronology is one of the major debated areas of research among the other topics in Paleolithic studies in Japan. Below, I give an overview of the long-term and short-term chronologies and discuss how both chronological models are relevant to global models of human population migrations and dispersals in Eurasia.

Clear evidence of the Japanese Paleolithic appears beginning around 40 ka, and blade technology was incorporated since the earliest lithic assemblages appeared in the southern Kanto region in the SE microregion (Yamaoka 2010; but see Nakamura 2012). The gradual but consistent increase in the number of blade tools (e.g., endscrapers, burins, and perforators) and various blade-production technologies, including prismatic blade technology, which certainly spread across Japan during the Upper Paleolithic, suggests that the technology of the Japanese Upper Paleolithic is not dissimilar to that of the Upper Paleolithic in Europe. On the contrary, unique stone tools characterized in the Japanese EUP are principally represented by three classes of stone tools (fig. 3): trapezoids defined as abruptly and/or minimally retouched small flakes (Sato 1988), backed blades (Ono 1988) characterized by abrupt retouches and truncations on elongated flakes and/or blades traditionally described as knife-shaped tools (Serizawa 1960; Sugihara 1965; Tozawa 1990), and edge-ground axes (Tsutsumi 2012). The combination of trapezoids, knife-shaped tools, and edge-ground axes in EUP is unique to the Japanese Paleolithic industry, and they have not been recovered together in neighboring regions, such as South Korea (K. Bae 2010; Lee, Bae, and Lee 2016), which suggests that they were newly innovated in Japan at the beginning of the Upper Paleolithic; however, edge-ground stone axes attributed to MIS 3 have recently been identified at the Galsanri and Yonghodong sites in Korea (Lee, Bae, and Lee 2016). Indeed, knife-shaped tools long persisted as the formal stone tool class in the Japanese lithic industries, and the “knife-shaped tool culture” is the technocomplex that is extensively distributed from Kyushu to southern Hokkaido (e.g., Ambiru 1986; Morisaki 2012; Naganuma 2010; Ono 1988; Yoshikawa 2010). In the Korean Peninsula, the Upper Paleolithic industry has tanged points (Seumbe Chireugae) from its initial stage with the emergence of blade technology (C. Bae 2017, in this issue; K. Bae 2010; Lee 2015, 2016; Seong 2008, 2009; Seong and Bae 2016). Tanged points also appeared in Japan in the late Upper Paleolithic, around 30,000 years ago, mainly in the Kyushu region; however, they occur rather briefly, perhaps in response to small-scale human migrations from Korea or cultural transmission after the collapse of the regional environment in Kyushu, caused by the large explosive event of the Aira Volcano, which occurred some 30,000 years ago (Matsufuji 1987; Morisaki 2015). The traits shared between the retouch technologies used in the Japanese knife-shaped tools and the Korean tanged points make archaeologists hypothesize that an immediate technological transmission of tanged points from Korea to Japan at the beginning of the Upper Paleolithic stimulated the invention of knife-shaped tools (Ambiru 2010), which could be evidence of foraging groups migrating to Kyushu from the Korean peninsula (C. Bae 2017, in this issue; Matsufuji 1987).

Chronometric dates, mostly radiocarbon dates based on associated charcoal, demonstrate that the lithic industry characterized by a composite of trapezoids, knife-shaped tools, and edge-ground axes appeared in Japan at 40,000 to 38,000 years ago (Izuhu and Kaifu 2015; Tsutsumi 2012; Yamaoka 2010). A substantial number of EUP assemblages (~500) dated to 38,000 to 30,000 years ago further indicate that modern H. sapiens mi-
grated into the Japanese Archipelago around 40,000 years ago, bringing the new lithic technological complex (Izuho and Kaifu 2015). Culture-chronological division between the Early and Late Paleolithic to characterize lithic industries in East Asia (Gao and Norton 2002; Ikawa-Smith 1978; Seong and Bae 2016) may also be validly applicable to the current Japanese Paleolithic record, although it is necessary to address the question of whether there was Paleolithic human occupation before 40 ka.
and, if there was, how the earlier Paleolithic record is related to other East Asian Paleolithic records, notably those in China and Korea.

The possibility of an archaeological record before 40 ka was largely dismissed when the Early Paleolithic hoax was exposed in 2000. At that time, it was shown conclusively that the Early and Middle Paleolithic stone tool industries from Miyagi Prefecture were all faked by an amateur archaeologist beginning in the 1980s (Nakazawa 2010; Yamada 2001). Before the fakes were produced, however, the reality of an Early Paleolithic in Japan had been seriously discussed for several sites, such as Sozudai in northern Kyushu and Hoshino in Honshu (Serizawa 1971; Yanagida and Ono 2007). The debate regarding the reality of the Early Paleolithic industry was largely over the issue of whether the fractured flakes were man-made artifacts or not (i.e., geofact). Quaternary geologists suggested that the geological layers of "archaeological artifacts" were derived from alluvial/ colluvial sediments that could have created naturally fractured cobbles to make flake-like geofacts (Arai 1971). In contrast, a systematic examination of the angle between the striking platform and the ventral surface of flakes from the pre-40 ka level in the Sozudai site suggested that they were man-made (Bleed 1977), which was largely supported by the proponents of the long-term chronology in the Japanese Paleolithic (Serizawa 1982). Although debate over these sites was shelved while the sensation was ongoing, many of these sites have subsequently been revisited (e.g., Hagiwara 2006; Ikawa-Smith 2016; Matsufuji 2010; Naruse 2010; Sato 2016; Wada 2016). The candidate assemblages for occupation of the archipelago before the Upper Paleolithic are Kanedori (Tohoku region, NE), Takesa-Nakahara (central Japan, C), Sunabara (southwestern Honshu, SW), and Iriguchi (northern Kyushu, SW; see fig. 2). Multiple criteria have been employed to assign them to the Upper Paleolithic. First, flaking and retouch technologies have been used. Besides mechanical criteria to distinguish flakes from geofacts (Barnes 1939; Bleed 1977), a peculiar flaking technology called "obtuse angle technology" (Nagai 2011) that is often found in spheroids in the "Lower/Middle Paleolithic" industry in South Korea (Lee 2015) is chosen. The second criterion is whether these stone tools are really different from or similar to the earliest Upper Paleolithic assemblages (i.e., edge-ground axes, knife-shaped tools, and trapezoids) with respect to patterns in tool morphology, reductive technology, and raw material use (e.g., Matsufuji 2010; Suto 2006). For example, Matsufuji (2010:196) suggests that crude and large tools with two small flakes recovered from the Kanedori IV layer are different from the EUP industry, and therefore it is attributed to the "broader East Asian core and flake tool tradition." The third criterion is the chronological age of the assemblage. Instead of using chronometric dates associated with tool assemblages from before the Upper Paleolithic, Japanese Paleolithic archaeologists have usually employed tephras to develop culture-stratigraphic sequences.

Based on the above multiple criteria, most of the Japanese assemblages from before the Upper Paleolithic cannot support the arrival of humans before 40 ka. However, some recently excavated sites, notably Sunabara, have been investigated through examination of site integrity (Matsufuji and Uemine 2013; Uemine, Matsufuji, and Shibata 2016) and microscopic analysis of fracture mechanics in rhyolite (a coarse-grained material recovered from the site) to identify the man-made nature of lithic artifacts (Uemine 2014). These efforts may eventually stand up to further scientific scrutiny to support an MIS 5e human arrival in the archipelago, as some researchers propose. However, in a case like Sunabara, researchers will be further required to explain how man-made "artifacts," naturally fractured debris, and naturally transported pebbles were all recovered together in the same alluvial sediments (i.e., layer Vla; Uemine 2014). Only a thorough analysis of the site formation processes may really answer this question.

Among the other artifacts, the lithic assemblages from Kanedori layers IV and III are the most promising lithic artifacts attributable to the Upper Paleolithic in Japan (Kuroda et al. 2005, 2016; Matsufuji 2010). The lower level of Kanedori layer IVb, where the lower assemblage was recovered, has multiple tephras that were secondarily deposited, suggesting that the age of layer IVb is in the time range of 50,000 to 90,000 years ago (Soda 2005; Yagi 2005). Despite the seeming credibility of stratigraphy, lithic artifacts, and tephra-assisted chronometric dates in the Kanedori assemblages from before the Upper Paleolithic, the number of candidates for Japanese lithic assemblages from before the Upper Paleolithic is still small. Even among the 16 so-called assemblages, there are surface collections (e.g., Kaseizawa) that are undateable (Sato 2016:31, table 1). More detailed evaluation of the characteristics and variability in those assemblages requires further systematic comparison through technological and morphological studies (e.g., Bleed 1977; Nagai 2011). Given the sporadic and sparse occurrence of those candidates for sites from before the Upper Paleolithic, categorizing them into the notion of the "Early Paleolithic" and the extent to which they are comparable to the archaeological record in the East Asian mainland (e.g., Gao 2013; Gao and Norton 2002; Wang 2005) will be an important future research avenue.

Discussion

How much do we know about the Pleistocene human population history in Japan, and how much do we not know? With respect to human migratory routes into the Japanese Archipelago, of the six hypothesized routes of human entry (fig. 1), the routes from the Korean Peninsula and southern China to Kyushu (i.e., routes 1 and 5), a southern part of Paleo-Honshu Island, are the most parsimonious based on the Paleolithic site density and technological and morphological comparisons of formal stone tools between Japan and Korea during the EUP. This route was likely, given that hunter-gatherer population density in the adjacent regions would have been higher than Paleo-Honshu at the time of the earliest population entry. For example, researchers have identified an increasing number of
Middle and Late Pleistocene sites in southern China (e.g., Pei et al. 2013; Shen and Keates 2003; Wang 2003, 2005; Wei et al. 2017), suggesting that the Late Pleistocene hunter-gatherer population density in southern China was higher than that in Paleo-Honshu.

In contrast with the extensive Paleolithic record in Japan, the Pleistocene human fossil record is primarily concentrated in the Ryukyus. This implies that Upper Paleolithic hunter-gatherers had already migrated into the far southern Japanese islands by seafaring, although the migratory route to get to the Ryukyus is still not clear. It is possible that the initial foragers to arrive in the Ryukyus came from Taiwan in the south (Kaifu et al. 2015) or from southern Kyushu in the north. The latter route was present at least during the Holocene (Obata, Morimoto, and Kakubuchi 2010; Yamazaki 2012). To further complicate the various migration models, ancient DNA data largely support gene flow from eastern Siberia to Hokkaido, possibly since the LGM. If this was the case, Pleistocene population dynamics were more complex than the admixture model, which assumes population continuity from the Paleolithic to Jomon, followed by the admixture of late Holocene Yayoi peoples, as outlined in the dual-structure model (Hanihara 1991).

A more complex picture of Pleistocene hunter-gatherer migrations into the Japanese Archipelago is legitimately implied from the long- and short-term chronologies of the Japanese Paleolithic record. In the framework of the long-term chronology, the question is the extent to which human populations before the Upper Paleolithic (>40 ka) contributed to the establishment of subsequent hunter-gatherer populations since 40 ka. Regardless of the relationship between populations, given the scarce evidence of credible human occupations before 40 ka, which has so far only been provided from a small number of archaeological sites (e.g., lithic industry from the Kandori before 50 ka), the human population size before 40 ka in Japan was smaller than that of the Upper Paleolithic. In stone tool technology, although it could be an effect of small sample size (n = 40), there seems to have been a change from the unstandardized retouched tools and heavy-duty tools in the industry before 40 ka, as represented by the Kandori III assemblage, to the formal and standardized stone tool inventory consisting of trapezoids, knife-shaped tools, and edge-ground hand axes in the EUP. This change further suggests that the EUP tool inventory and technology were independently invented among hunter-gatherers before the Upper Paleolithic. In contrast, the currently dominant short-term Paleolithic chronology may pose a different explanation for technological change. In the short-term chronology, the EUP hunter-gatherers were the first population to enter into the Japanese Archipelago. In this context, the EUP tool inventory and blade technology were all brought into Japan, and the subsequent proliferation was the result of relatively rapid population expansion across the archipelago (i.e., demic expansion; Cavalli-Sforza, Menozzi, and Piazza 1993). The Upper Paleolithic demic expansion in Japan syncs well with the modern Homo sapiens single-dispersal model out of Africa and rapid dispersal into South Asia (e.g., Forster and Matsumura 2006; Mellars 2006a, 2006b). However, Upper Paleolithic lithic industries that appear after the end of the EUP (>30,000 years ago) exhibit extensive regional variation, particularly in the technological, morphological, and stylistic characteristics of the complexes represented by the knife-shaped tools (e.g., Morisaki 2012; Ohyi 1968; Yoshikawa 2010), bifacial points (e.g., Hashizume 2015), and microblade cores (e.g., Sato and Tsutsumi 2007). The observed variation might have been created by a combination of human migrations from the East Asian mainland and endemic technological invention and transformation among Upper Paleolithic hunter-gatherers between the different microregions in the Japanese Archipelago. The interactions and foraging across the boundaries of microregions are often perceived in archaeological patterns, including the long-distance transportation of obsidian (e.g., Tsutsumi 2010) and isolated occurrences of regionally stylistic weapons outside of their core areas, such as the Kou-type knife-shaped tools (e.g., Kato 1975; Morisaki 2012). Moving forward, it will be critical to evaluate the extent to which indigenous hunter-gatherer population density at the microregional scale and the size of populations dispersing from the East Asian mainland covaried and influenced cultural change and variation on the archipelago. Given the complex nature of the Paleolithic archaeological record, human occupation history in Japan is likely compatible with a multiple-dispersal model of H. sapiens (e.g., Bae and Bae 2012; Boivin et al. 2013; Lahr and Foley 1994; Petraglia et al. 2010).

What makes the population history in Japan complicated is that the migration from the north via Paleo-SHK was significantly later than for Paleo-Honshu. While a small number of trapezoids that are morphologically comparable to those of the EUP in Paleo-Honshu have been identified in some assemblages in eastern Hokkaido, allowing some archaeologists to place them in late MIS 3 (e.g., Izuho and Takahashi 2005; Oda and Morisaki 2016), archaeological assemblages from the sites having secure associations of chronometric dates and stratigraphy in Hokkaido only appear at the onset of the LGM, 25,000 years ago (Izuho et al. 2012). Flake technology, blade, and microblade technologies were incorporated into the LGM technocomplex in Hokkaido (Izuho et al. 2012; Nakazawa and Izuho 2006, Nakazawa et al. 2005), which later converged into the microblade technocomplexes (Nakazawa and Yamada 2015). This development likely resulted from a combination of independent innovation, cultural transmission, and demic expansion from eastern Siberia and Paleo-Honshu in and after the LGM (e.g., Buvit et al. 2016; Graf 2009; Nakazawa et al. 2005; Nakazawa and Yamada 2015). Why the initial occupation of Paleo-SHK lagged behind that of Paleo-Honshu by some 15,000 years is another area that needs to be further investigated.

Although the number of migratory events is difficult to tease out from the current archaeology, human paleontology, and human genetic records, it is likely that it was the result of the admixture of two opposite large migratory events, similar to the Korean Upper Paleolithic (K. Bae 2010; Bae and Bae 2012). This population admixture likely occurred during MIS 2 (30,000 to 11,500 years ago) and involved an influx of hunter-gatherers...
from the north and south. Evident increases in the number of sites and stone tool technological variability during MIS 2 in both Paleo-Honshu and Paleo-SHK (e.g., Nakazawa and Yamada 2015; Ono et al. 2002; Suto 2006) could be explained by demographic increase and an associated cumulative adaptive culture model (e.g., Henrich 2004; Shennan 2001; Powell, Shennan, and Thomas 2009, 2010).

An examination of current evidence in Paleolithic archaeology, human paleontology, and human genetics in Japan necessarily provides a complex picture of Late Pleistocene demographic history. In the vast region of Asia, describing the Pleistocene population history in the Japanese Archipelago will doubtlessly be important in understanding human colonization and evolutionary history. Moreover, the accumulated Paleolithic record in Japan has the potential for improving understanding of the complexity of Pleistocene hunter-gatherer cultural and biological evolution.

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