

Review Article

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Achievements of Yaponesian Genome Project FY2018-2022

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Abstract

We started the five-year project “Deciphering Origin and Establishment of Yaponesian mainly based on Genome Sequences”, or nick-named as “Yaponesia Genome” under MEXT Grant-in-Aid for Scientific Research on Innovative Areas from FY2018. We aimed to establish a new research area by integrating biological studies and humanity and social science studies. I was Leader of this Project. Yaponesian means people on Japanese Archipelago, or Yaponesia. Writer Shimao Toshio proposed “Japonesia” in 1960s. He fused two Latin words, Japo (Japan) and nesia (islands) to create Japonesia. We changed its Alphabetical spelling to Yaponesia. Main questions of this project were origin and formation of people who live on Japanese Archipelago (Yaponesia). Research group A01 (P.I. was Saitou Naruya) determined full genome sequences of more than thousand modern individuals, while research group A02 (P.I. was Shinoda Ken-ichi) determined genome sequences of more than 100 ancient individuals. Research group A03 (P.I. was Suzuki Hitoshi) determined genome sequences of animals and plants moved to Yaponesia with humans. We try to decipher genomic history of people on Yaponesia through analyses of these newly determined genome sequences with other available ones. Research group B01 (P.I. was Fujio Shin-ichiro) conducted archeological studies focused on radiocarbon dating, while research group B02 (P.I. was Endo Mitsuaki) determined linguistic studies involving dialects of Japanese and Ryukyuan languages as well as many languages spoken by people who live near Yaponesia. Research group B03

(P.I. was Osada Naoki) estimated demographic changes through genome data collaborated with A01-A03 groups. These six research groups were established in FY 2018, and 17 small groups, classified into A04 and B04 groups, started from FY 2019 for two years followed by 21 small groups for FY2021-FY2022.

Introduction

Problem of the origin of Japanese was already discussed in Kojiki and Nihon Shoki edited in 712 A.D. and 720 A.D., respectively. Hitachi-no-kuni Fudoki, edited in 713 A.D., mentioned a shell mound found in Ogushi (Terada, 1975). Around 1725, Arai Hakuseki, noted scholar at the Edo Period, discussed stone arrowheads as artifacts, not originated from heaven (Terada, 1975). Philipp Franz Balthasar von Siebold stayed in Dejima of Nagasaki in the late Edo Period, and he published several books about Japan. He suggested that Ainu people were descendants of native people of Japan, by incorporating idea of Kiuchi Sekitei, stone collector (Terada, 1975). After the Meiji Period started, many foreign scholars taught in universities in Japan, and some of them gave important contributions on the origin of Japanese. Edward Morse, an American, discovered Omori Shell Mound in 1877 (Terada, 1975) while Erwin von Bälz (1911) pointed out the similarity between the Ainu people and the Okinawa people.

Until 1960s, studies on human population similarity were almost restricted to examination of morphological characters. Exceptions were blood group allele frequency comparisons, started from the ABO blood group. Probably influenced by Bälz, some researchers examined various blood groups in Ainu people and in Okinawa people (Misawa and Hayashida 1968, 1970; Nakajima and others 1967). Omoto's group also examined polymorphism of red cell enzymes and serum proteins using electrophoresis for Ainu and Okinawa people (Omoto 1972; Omoto and Harada 1972; Omoto and others 1973). In particular, Omoto (1972) presented a phylogenetic tree of eight human populations including Ainu by using the method of Cavalli-Sforza and Edwards (1967) based on allele frequency data of 16 polymorphic loci, and he concluded that the Ainu may be regarded as a peripheral population derived from the Upper Paleolithic or Mesolithic populations of East Asia, from which the so-called Mongoloid peoples were also derived (Omoto 1973).

Meanwhile, researchers of morphological studies proposed somewhat mixed models. Suzuki (1983) classified the models on the origin of Japanese into three; the substitution model, the admixture model, and the transformation model. Suzuki himself supported the transformation model. Yamaguchi (1986) briefly mentioned the possible pattern on the formation of modern

Japanese as “dual composition”. This idea was expanded by Hanihara (1991) as “the dual structure model” on the formation of Japanese, though Hanihara never mentioned about Yamaguchi’s (1986) idea. In any case, the dual structure model clearly assumes admixtures.

Omoto and Saitou (1997) presented various phylogenetic trees of 26 human populations including Ainu and Okinawa

Table 1 Member list of eight research groups of the Yaponesian Genome Project

Research Group A01 (FY2018-2022)

Saitou Naruya*, Inoue Ituro, Yoshiura Koichiro, Timothy A. Jinam, Matsunami Masatoshi, Kamatani Yoichiro**

Research Group A02 (FY2018-2022)

Shinoda Ken-ichi*, Adachi Noboru, Sato Takehiro, Kakuda Tsuneo, and Kanzawa-Kiriyama Hideaki

Research Group A03 (FY2018-2022)

Suzuki Hitoshi*, Masuda Ryuichi, Endo Toshinori, Itoh Tsuyoshi

Research Group B01 (FY2018-2022)

Fujio Shin-ichiro*, Kinoshita Naoko, Seike Akira, Yamada Yasuhiro, Hamada Tatsuhiko, Sakamoto Minoru**, Takigami Mai**

Research Group B02 (FY2018-2022)

Endo Mitsuaki*, Karimata Shigehisa, Kibe Nobuko, Nakagawa Hiroshi, Kazama Shinjiro

Research Group B03 (FY2018-2022)

Osada Naoki*, Fujimoto Akihiro, Gojobori Jun, Kawai Yosuke, Nakagome Shigeki**

Research Group A04 (FY2019-2020)

Hanada Kosuke*, Hosomichi Kazuyoshi*, Imanishi Tadashi*, Kimura Ryosuke*, Nakayama Ichidai*, Naito Ken*, Ohashi Jun*, Oota Hiroki*,

Satomura Kazuhiro*, Terai Yohei*, Sato Yoichi*

Research Group B04 (FY2019-2020)

Kawada Masakado*, Nishiuchi Isamu*, Funabashi Kyoko*, Takenaka Masami*, Aso Reiko*, Hayashi Yuka*

Research Group A04 (FY2021-2022)

Hosomichi Kazuyoshi*, Imanishi Tadashi*, Kimura Ryosuke*, Matsumoto Yuuki*, Miura Fumihito*, Mizuno Fuzuki*, Motohashi Reiko*, Naito

Ken*, Niimura Tsuyoshi*, Ohashi Jun*, Oota Hiroki*, Suga Hiroshi*, Takenaka Masami*, Terai Yohei*, Yamaoka Yoshio*

Research Group B04 (FY2021-2022)

Kato Tetsuhisa*, Kenan Celik*, Nakagawa Natsuko*, Nakazawa Kohei*, Nishiuchi Isamu*

*P.I. **Research Associate

people by using the neighbor-joining method (Saitou and Nei 1987) based on allele frequency data of 20 polymorphic loci. They also compared four populations [Ainu, Okinawa (Ryukyu), Yamato (Hondo Japanese), and Korean] based on allele frequency data of 25 polymorphic loci, and found that Ainu and Okinawa populations were clustered, though the bootstrap supports were up to 85%. Later, we compared genome-wide SNP data of Japanese and surrounding East Asian populations, and Ainu and Okinawa populations were clearly clustered with the 100% bootstrap support (Japanese Archipelago Human Population Genetics Consortium 2012). We finally proved the hypothesis of von Bälz (1911) 101 years later. Of course, the dual composition model (Yamaguchi 1986) or the dual structure model (Hanihara 1991) was also supported by this result.

Study of ancient DNA of Japanese was initiated by Horai and others (1989). They determined a 190bp mitochondrial DNA sequence of a Jomon skull dated 6,000 years BP. They further determined four Jomon (3,000-6,000 years BP) mitochondrial DNA sequences (Horai and others 1991). Later, two research groups reported mitochondrial DNA sequences of Yayoi period people (Shinoda and Kunisada 1994; Oota H. and others 1995). We also started ancient mitochondrial DNA sequence analysis (Kanzawa-Kiriyama and others 2013), and eventually succeeded to determine some nuclear DNA sequences of a late Jomon period people (Kanzawa-Kiriyama and others 2017) thanks to the next-generation sequencing technique.

Japanese language is mysterious. Saitou (2005) presented a phylogenetic network of Japanese, Ryukyuan, Ainu, and Korean based on shared first consonants of basic 100 words, and found that Ainu and Korean share 15 words. This suggests that these two languages might have some shared ancestry in the past. Saitou and Jinam (2017) showed a phylogenetic tree of Japanese and Ryukyuan dialects using the neighbor-joining method (Saitou and Nei 1987), and this tree suggested an ancient origin of the Hachijo Island dialect.

Saitou and Jinam (2017) also presented the genome-wide SNP data of Izumo people, and their location in PCA was similar to that of people in Tohoku. They thus proposed the “inner dual structure” model on the formation of modern Japanese based on the three-wave migration model proposed by Saitou (2015). Two phases of migrations are assumed to form the current Japanese Mainlanders in this model. Phase 1 is the earlier migrants who possibly arrived at the Japanese Archipelago in the late Jomon period (~4000 years ago), while phase 2 is later migrants who came to Northern Kyushu and later spread eastward. Interestingly, haplotype frequency data of mitochondrial DNA for 47 prefectures in Japan shown by Saitou (2017) did fit to this inner dual structure model.

Yaponesian Genome Project

Considering the new trend of genome sequencing by the next generation sequencers, we proposed the “Yaponesian Genome” Project to Ministry of Education, Culture, Sports, Science and Technology of Japan, and it was accepted for FY2018-FY2022. The word “Yaponesia” was proposed by writer Shimao Toshio in 1960s, and this comes from the Latin word for Japanese Archipelago.

Table 1 shows researchers involved in this Yaponesia Genome Project. There were six Planned Research Groups (A01-A03 and B01-B03) that studied for all the five fiscal years. Research Group A01 studied modern Japanese by determining genome-wide SNPs and full genome sequences, while Research Group A02 studied ancient Japanese by determining genome sequences. Research Group A03 studies animals and plants on Yaponesia by determining their full genome sequences. Research Group B01 studied archeology, while Research Group B02 studied linguistics. Finally, Research Group B03 studied methods for analyzing large-scale genome data. We also solicited application based Research Groups (A04 and B04) for two periods (FY2019-2020 and FY2021-2022). In total, 60 researchers were involved in this “Yaponesian Genome” Project.

Our first major publication under this project was determination of Rebun Island Funadomari Jomon genomes (Kanzawa-Kiriyama and others 2019). A high quality DNA was extracted from a molar of F23, and full genome sequence data were obtained from that lady, as well as less abundant genome data from F5 male. If we use the F23 Jomon genome sequence data, modern Ainu, modern Okinawa, and modern Yamato (mainland Japanese) inherited 66%, 25%, and ~10% Jomon genomes, respectively (Kanzawa-Kiriyama and others 2019). Previously, we estimated the Jomon proportion in the modern Yamato and modern Okinawa people using only modern human genome data,

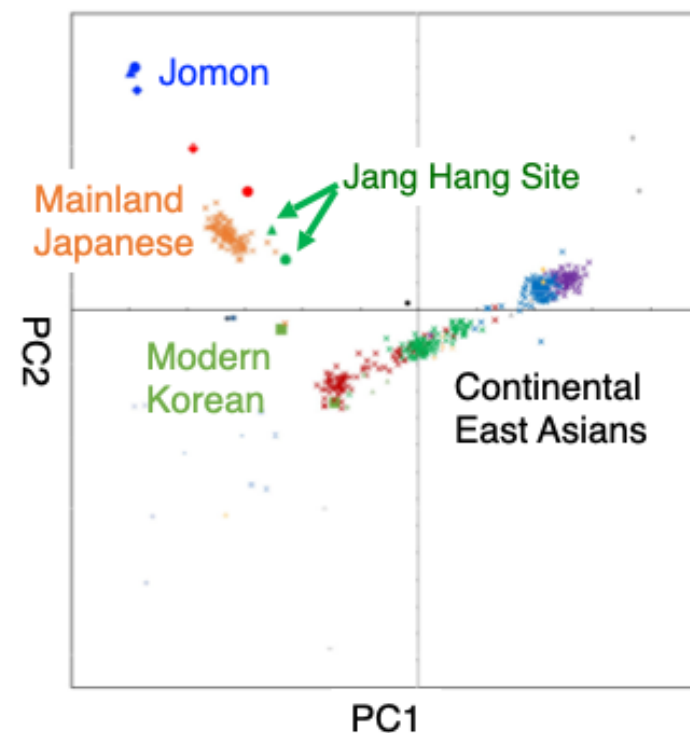


Figure 1. A PCA plot of ancient and modern human genome data. From Shinoda and others (2019).

and they were ~18% and ~27%, respectively (Jinam and others 2015).

Shinoda and others (2019) also reported the ancient genome sequence determined from a human bone discovered at the ~5,000 years old Jang Hang site in Gadeokdo Islands, Korea. Interestingly, that ancient human genome contained a much higher Jomon component than modern Korean. Figure 1 shows a PCA result (modified from Shinoda and others [2019]).

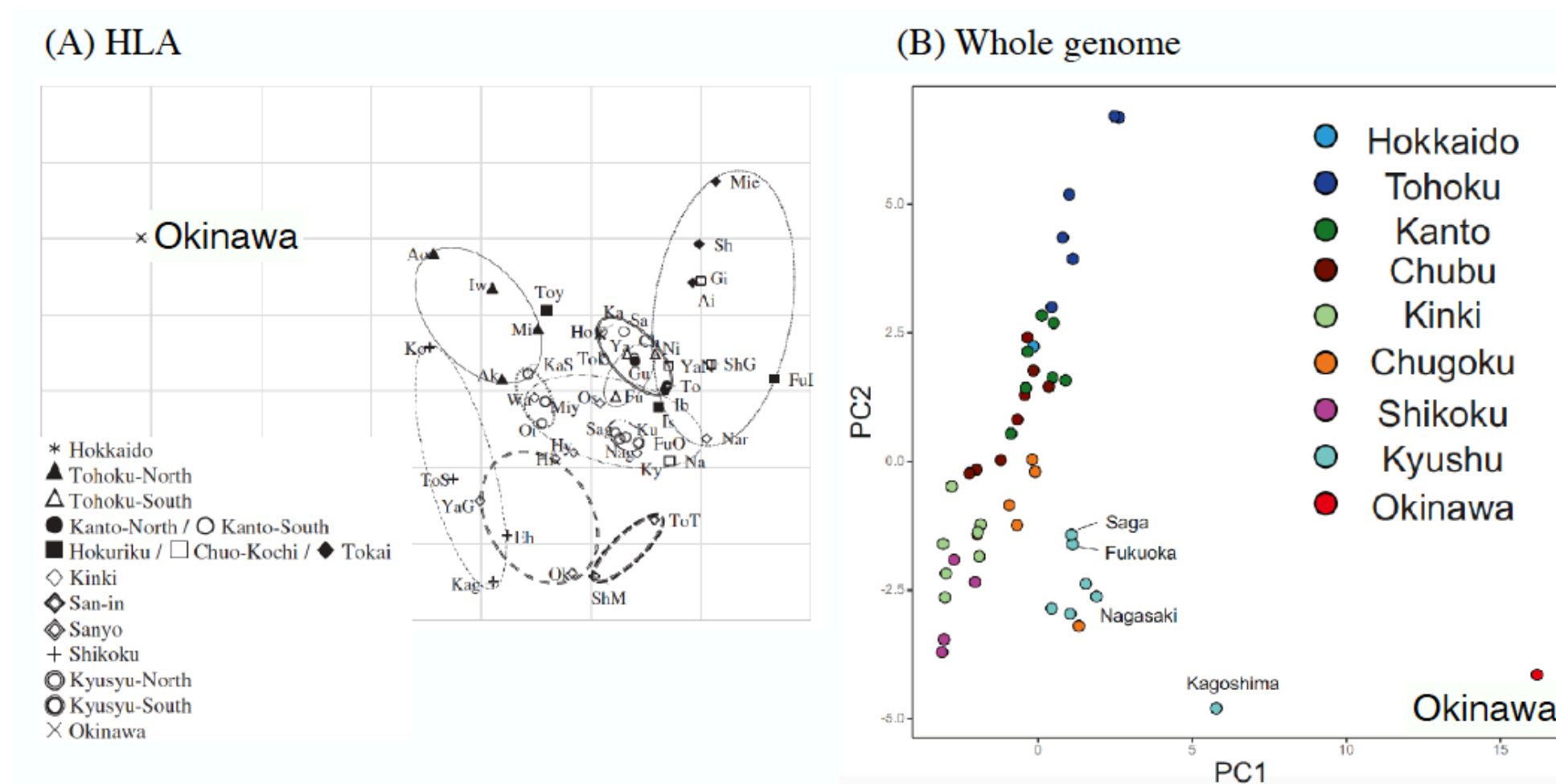


Figure 2. Two PCA plots of 47 prefectures in Japan. (A) PCA based on HLA haplogroup frequency data. From Hashimoto and others (2020). (B) PCA based on whole genome data. From Watanabe and others (2021).

Suzuki's group reported complete mitochondrial DNA sequences of 98 mouse sampled from various parts of East Eurasia (Li and others 2020). They showed that mouse subspecies *Mus musculus castaneus* first reached Yaponesia at around 3,500 years ago, followed by subspecies *M. m. musculus* ~2,700 years ago. These two events may correspond to phases 1 and 2 of the inner dual structure model. Later, whole nuclear genomes of the same 98 mouse individuals were determined and analyzed (Fujiwara and others 2022).

Imanishi's group analyzed HLA gene region haplotypes for 47 prefectures, and found that Tohoku prefectures, that are geographically quite apart from Okinawa, have somewhat similar HLA pattern with Okinawa, followed by Shikoku prefectures (Hashimoto and others 2020; see Figure 2A). Oota's group determined and analyzed human genomic DNA from Ikawazu Shell Mound of the early Yayoi period, and found that it was Jomon type (Gakuhari and others 2020). Ohashi's group analyzed genome-wide SNP data for 47 prefectures, and Kyushu prefectures are the closest to Okinawa, followed by Tohoku and Chugoku prefectures (Watanabe and others 2021; see Figure 2B). Matsunami and others (2021) studied genome-wide SNP data of Miyako Island people, and found a large genetic heterogeneity in this area.

Jinam and others (2021a) generated genome-wide SNP data of Izumo and

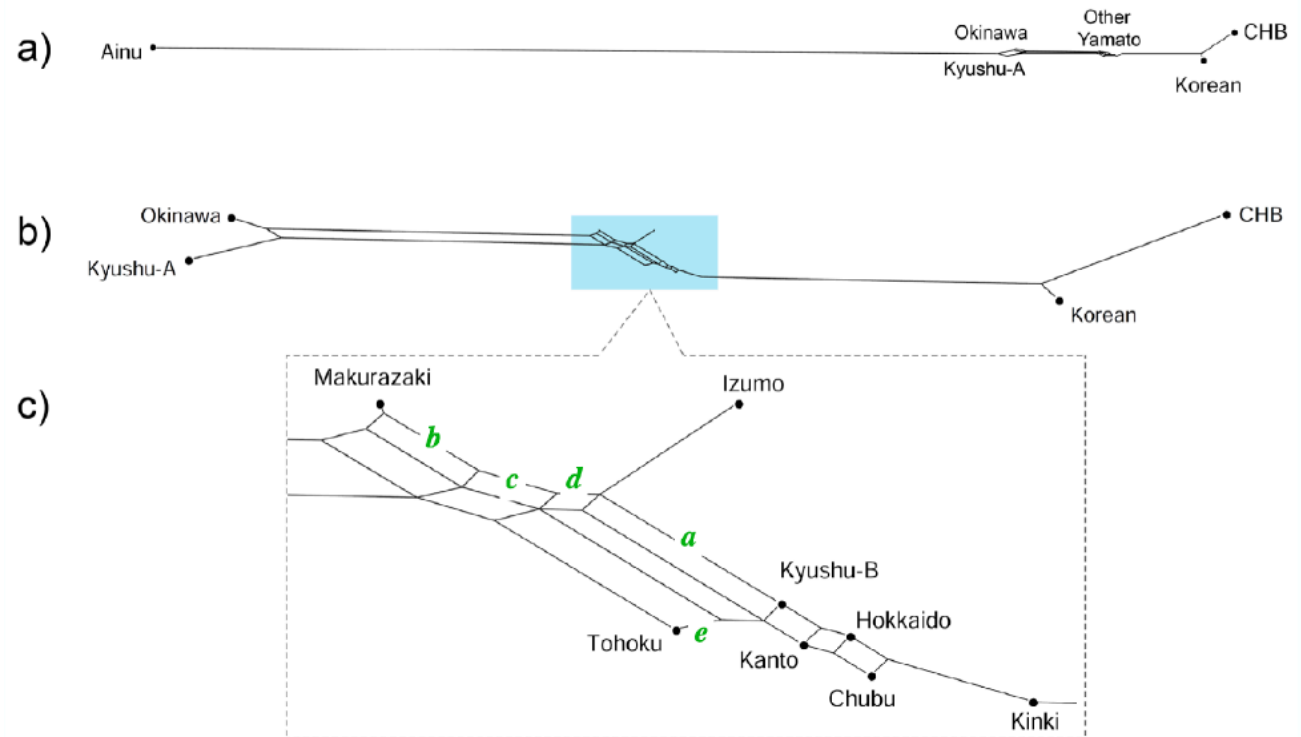


Figure 3. Neighbor-Net networks of various populations in and around Yaponesia. (A) A phylogenetic network of CHB, Korean, Ainu, and other Yaponesian populations. (B) phylogenetic network after eliminating Ainu from network (A). (C) A phylogenetic network of eight Yaponesian populations as expansion of the blue-colored center part of (B). From Jinam and others (2021a).

Makurazaki, and compared them with those reported by RIKEN for seven regions (Hokkaido, Tohoku, Kanto-Koshinetsu, Tokai-Hokuriku, Kinki, Kyushu, and Okinawa), Ainu, and with two continental populations (Korean and Chinese Han in Beijing). They found that the Ainu population is far apart from the remaining populations, and the Yamato population was between Okinawa and continental populations. The Kinki area population was closest to continental populations, while the Makurazaki population was closest to the Okinawa population (Jinam and others 2021a; see Figure 3).

Fujio (2021) examined the introduction of grain cultivation and the processes of development in the Japanese Archipelago. Farmers who came from the southern Korean Peninsula began wet rice cultivation with irrigation systems around 3,000 years ago in cooperation with original inhabitants of the Fukuoka Plain in northern Kyushu. Fujio (2021) also found that the periods between the initiation and dissemination of wet rice cultivation were progressively shortened from northern Kyushu (~250 years), Kinki (~150 years), and southern Kanto (20-30 years).

In 2020, *Anthropological Science*, a journal published by the Anthropological Society of Nippon, asked me to contribute a series of papers from the Yaponesian Genome Project. I asked six researchers, and my preface (Saitou 2021) and the six papers were published in *Anthropological Science* in 2021.

Modern Yaponesians were first analyzed by Jinam and others (2021b), and the mitochondrial DNA haplotype frequency data for 47 prefectures, provided by Genesis Health Care, Co., that were much larger than that used by Saitou (2017), also fit to the inner dual structure model (see Figure 4).

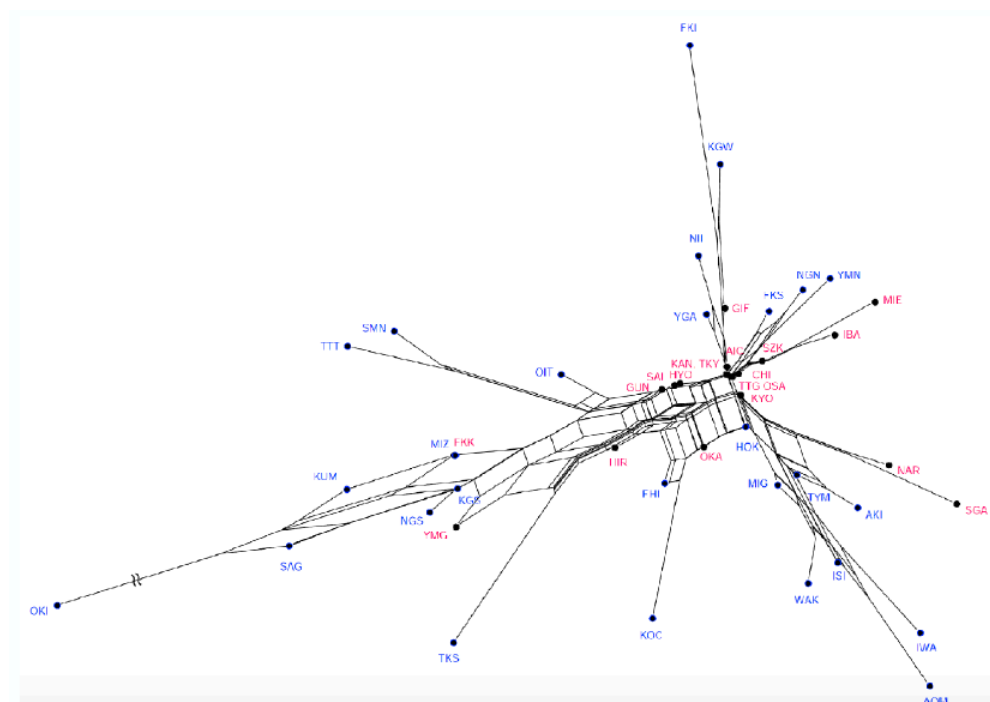


Figure 4. A Neighbor-Net network of 47 prefectures based on mtDNA haplogroup frequencies. From Jinam and others (2021b).

Adachi and others (2021) determined the nuclear genome sequence of early Jomon individual excavated from Higashimyo site in Saga Prefecture, Kyushu. They found that all the five Jomon genomes from early to the final stages of the Jomon period and spanning from Kyushu to Hokkaido were similar with each other, indicating the spacial and temporal homogeneity of the Jomon people.

Suzuki (2021) examined the time-dependent evolutionary rate of mitochondrial DNA in small rodents in the Japanese archipelago, and concluded that the rate varied ca. four times during 120,000 years.

Endo (2021) examined toponyms in a Korean history book “Samguk Sagi”, and found that Japonic-sourced toponyms are typically distributed in the central and northern areas of the Yalu River, primarily in the district of Koguryō. This reveals that Japonic-speaking people still dwelled in the central area of the peninsula and in the northern area of the Yalu River in the 8th century.

Osada and Kawai (2021) summarized recent genome sequencing efforts of present-day and ancient people in Asia, mostly focusing on East Asia. They also conducted meta-analysis by compiling publicly available datasets to clarify the genetic relationships of present-day and ancient Japanese populations with surrounding populations. However, no clear conclusion was made because of paucity of genome data.

Koganebuchi and Oota (2021) discussed the history of ancient DNA analysis leading to paleogenomics, then outlined three sequencing stages (partial, draft, and complete genome sequencing) and capture methods, and discussed the necessity of high-quality sequencing for paleogenomes of Eastern Eurasia.

Shinoda and Kanzawa-Kiriyama coauthored a paper (Wang and others 2021) that reported many ancient human genome data from East Asia including two from the Jomon sites, and authors estimated the Jomons as admixed between Southern Island elements and Northern seashore elements. Shinoda, Kanzawa-Kiriyama, Kimura, and Oota coauthored a paper (Robbeets and others 2021) that discussed the linguistic, archeological, and genomic diversity of East Asian. Although a language group “Trans Eurasian” was used in Robbeets and others (2021), this is just another name for “Altaic” language group that was rejected by many linguists.

Inoue’s group reported ancient virus metagenomes from Jomon people’s coprolites (Nishimura and others 2022). Yamaoka’s group determined many genome sequences of *Helicobacter pylori*, and reported very unique two strains from

Okinawa (Suzuki and others 2022). Finally, Dauyey and Saitou (2022) estimated intelligence of ancient people including Jomon people based on modern human data.

We also published many books and articles in Japanese during the Yaponesian Genome Project period. I will list these chronologically. Yamada published a book (Yamada 2018) about the view of life and death of the Jomon people. Shinoda and others (2019) reported nuclear genome data of Yayoi people from Northwestern Kyushu. Shinoda (2019) published the second edition of “Our ancestors who became Japanese” that was originally published in 2007. Yamada published two books (Yamada 2019a, 2019b) on the Jomon period. Nakagawa (2019) published a book on “Golden Kamui”, a famous cartoon that is related to Ainu culture. Fujio published a book (Fujio 2021) on the prehistoric periods of Japan. Hayashi and others (2021) edited a book on languages in Japan and Ryukyu. Endo and others (2021) edited “Linguistic Atlas of Asia”. Shinoda published a book (Shinoda 2022a) on the origin of humans.

In 2022, Kagaku, published from Iwanami Shoten, asked us about a series of review articles, and we published five review articles in Kagaku. Fujio (2022) discussed the difference between archeological studies and ancient DNA studies. Shinoda (2022b) discussed the genomic diversity of the Yayoi people. Kanzawa-Kiriyama (2022) discussed the Jomon genes found from Korean Peninsula. Yamada (2022) discussed the present status of research on Jomon cemetery systems. Saitou (2022) discussed the dual structure model proposed by Hanihara (1991).

Though the Yaponesian Genome Project formally ended at the end of March 2023, many papers and books will be published in near future on Yaponesians. As the Principal Investigator of the Yaponesian Genome Project, I am very proud of our achievements.

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