

Original Research

# An ancient genome perspective on the dynamic history of the prehistoric Jomon people in and around the Japanese archipelago

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## Abstract

The Jomon people were prehistoric residents of the Japanese archipelago who occupied the region from *ca.* 16,500 to 2,300 years before present (BP). While recent accumulation of ancient genomes and genome-wide data of the Jomons has substantially enhanced our understanding of their genetic profiles and contribution to present-day populations, their genetic history in the Jomon-period archipelago, spanning over 14,000 years in time and 2,000 km in distance, remains scarcely investigated. Here we report multiple findings illuminating the Jomon genetic history based on the analysis of the genetic relationship between published ancient genome-wide data of 23 Jomon and Jomon-like individuals. First, the Initial Jomon individual from Shikoku, dated to *ca.* 9,000 BP, forms a common outgroup to the remaining later Jomon individuals, suggesting a population turnover in western Japan. Second, genetically Jomon-like individuals outside the Jomon archaeological context, found in the Miyako Island in Ryukyu and the Yokjido island in the southern coast of Korea, show the closest genetic affinity with the Late Jomon individual from Shikoku, narrowing down their sources in space and time. This study highlights a dynamic history of the Jomon people in and out of the Japanese archipelago and calls for a large-scale investigation of the ancient Jomon genomes.

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## 1. Introduction

The Jomon people are a group that inhabited the Japanese archipelago from approximately 16,500 to 2,300 years before present (BP) [1]. Although predominantly relied on hunting, gathering, and fishing in their subsistence strategy, the Jomon people developed a sedentary lifestyle and manufactured and utilized pottery, the cord-markings on which gave the name Jomon [1,2]. Based on temporal changes in their pottery style, the Jomon period has been separated into the Incipient (*ca.* 16,500–10,500 BP), Initial (*ca.* 10,500–7,000 BP), Early (*ca.* 7,000–5,500 BP), Middle (*ca.* 5,500–4,500 BP), Late (*ca.* 4,500–3,250 BP), and Final (*ca.* 3,250–2,500 BP) Jomon periods [3,4]. The origins and genetic history of the Jomons have been of keen academic interest not just to understand the Jomons themselves, but also to understand the genetic diversity of present-day populations in the Japanese archipelago. For example, the Ainu from the northernmost region of the archipelago are genetically closer to the Ryukyuans from the southernmost region than to the mainland Japanese in the middle, because they inherited higher proportions of their ancestry from the Jomon-related ancestors than the mainland Japanese did [5–12]. Most archaeogenetic studies on the Jomons mainly targeted mitochondrial haplogroups, finding that distinct haplogroups N9b1 and M7a were representative of the northern and southern Jomons, respectively, thus suggesting an internal population differentiation among the Jomons [13–16]. For the last few years, finally ancient genomes or genome-wide data of the Jomons have been reported, providing a chance to investigate the population structure and the genetic history of the Jomons in a fine resolution [17–21]. Particularly, a recent study reported genomes of nine Jomon individuals covering a time period of five millennia (*ca.* 8,800–3,800 BP) and confirmed a long-standing homogeneous Jomon genetic profile [19].

The recently published Jomon genomes drove substantial progress in major questions about their origins and genetic legacy in present-day populations. For example, the Jomon gene pool is distinct from neighboring populations from the continent because they had a strong genetic link with a deeply branching Eastern Eurasian lineage not well represented by any present-day population [17,22]. The isolation between the Jomon and other East Asian populations was dated to *ca.* 20–25 thousand years ago (kya) with a small effective population size (<1,000) of Jomon [19]. Also, the tripartite model of Japanese origin, an extension of the traditional dual-structure model [23], has been recently proposed based on the genetic comparison of the ancient Jomon, Yayoi, and Kofun-period individuals [19]. Interestingly, archaeogenetic studies have reported ancient individuals genetically related to the Jomons but found outside the range of the Jomon archaeological culture and out of the Jomon archaeological context [15,20]. This includes the southern islands of the Ryukyu (e.g., Miyako and Yaeyama) and the southern

coast of the Korean peninsula. However, these studies have largely focused on the shared common origin of the Jomons and a comparison between the Jomons and the non-Jomons, while leaving the population history within the Jomons largely unexplored.

In this study, we conducted an in-depth re-analysis of the published genome or genome-wide data of the Jomon-related individuals, focusing on the relationship among them. These individuals, 23 in total and ranging between the Initial and Late Jomon periods, provide evidence for rich dynamics within the overall homogeneous Jomon gene pool. Specifically, we found that the Initial Jomon individual from Shikoku forms an outgroup to the later Jomon individuals across the archipelago, suggesting a population turnover in the region. We could also localize the origins of the genetically Jomon-like individuals outside the traditional Jomon area into the Middle/Late Jomon-period western Japan (including Chugoku, Kansai, Shikoku, and Kyushu).

## **2. Materials and Methods**

### **2.1 Processing of the genome-wide data of Jomon-related individuals**

We compiled whole genome or genome-wide sequencing data reported in previous publications, focusing on ancient Jomon and Jomon-related individuals [17–21]. We obtained genome-wide genotype data of these individuals on a set of 1,233,013 ancestry-informative single nucleotide polymorphisms (SNPs) referred to as the “1240K” panel [24,25]. For the studies that made pseudo-haploid pulldown genotype data for the 1240K panel publicly available, we took the published genotype data to guarantee maximum reproducibility. For those that did not release the genotype data, we started from raw sequence data (FASTQ format) or from aligned reads (BAM format), obtained from public sequencing data repositories such as the European Nucleotide Archive (ENA) and the DNA Data Bank of Japan (DDBJ). We provide details of data acquisition information in a separate table (Table S1).

For raw data in the FASTQ format, we first trimmed Illumina adapter sequences from raw reads and merged read pairs for paired-end sequencing data using AdapterRemoval v2.3.0 [26] with a minimum overlap of 1 base pair (bp). We removed trimmed/merged reads shorter than 35 bp and unmerged read pairs from the analysis. We mapped the remaining trimmed/merged reads to the human reference genome with decoy sequences (hs37d5) using the bwa-aln and bwa-samse modules in BWA (Burrows-Wheeler Aligner) v0.7.17 [27]. Then, we removed PCR duplicates using DeDup v0.12.5 [28] and removed reads with the Phred-scaled mapping quality score lower than 30 using SAMtools v1.9 [29].

As ancient DNA has post-mortem DNA damage, we used mapDamage v2.2.1 [30] to check if each individual shows a sufficient level of post-mortem damage matching the pattern expected from the corresponding library preparation method. To minimize the effect of chemical DNA damages in later population genetic analysis, we masked 3 and 10 bps at both ends of reads for partial-UDG and non-UDG treated double-stranded libraries, respectively, using the trimBam function of bamUtil v.1.0.15 [31]. For single-stranded libraries, we did not mask the read ends.

We called pseudo-haploid genotypes using the pileupCaller v1.4.0.5 (<https://github.com/stschiff/sequenceTools>; v1.5.2 last accessed on 19 April 2023) with the randomHaploid option. For double-stranded libraries, we used masked and non-masked BAM files for calling genotypes of transition and transversion SNPs, respectively. For single-stranded libraries, we used non-masked BAM files and the 'singleStrandMode' option implemented in pileupCaller. We estimated relatedness between the Jomon-related individuals based on the pairwise genotype mismatch rate [32] calculated over the autosomal SNPs in the 1240K panel.

## 2.2 Compilation of worldwide genome-wide data

We integrated the 1240K genotype data of ancient Jomon individuals [17–21] with two present-day individual datasets. For the 1240K SNP set, we retrieved genotype data of high-coverage whole genome sequenced individuals included in the Simons Genome Diversity Project [33]. For the "HumanOrigins" data set, we took publicly available genome-wide data of a broader set of present-day individuals genotyped on the Affymetrix Axiom Genome-wide Human Origins 1 array ([34–37]). The HumanOrigins array included 593,124 autosomal SNPs overlapping with the 1240K set. We utilized the HumanOrigins dataset for principal component analysis (PCA). To perform f4 symmetry tests between the Jomon individuals against the world-wide population, we employed 1240K genotype data to utilize the genotype information of the Jomon individuals to the maximum degree. The details of the present-day individuals included in this dataset are provided in Table S2.

## 2.3 Principal component analysis

We performed PCA using the smartpca v18140 from the Eigensoft v8.0.0 package using 2,077 present-day Eurasian individuals genotyped on the HumanOrigins panel [38]. We projected ancient Jomon-related individuals not included in PC calculation using the 'lsqrproject: YES' option. The detailed information of present-day individuals used in PCA are provided in Figure S1–S2 and Table S2. For PCA of ancient Jomon-related individuals only, we first computed covariance between each

pair of individuals using SNPs not missing in both individuals to avoid an issue due to varying level of genotype missingness across individuals. For this, we used 'cov' function and 'use="pairwise.complete.obs"' option implemented in R v4.2.0 and applied the "eigen" function to perform PCA on the calculated covariance matrix.

## 2.4 *f*-statistics

We calculated the *f*-statistics by *qp3pop* and *f<sub>i</sub>* functions from the R library ADMIXTOOLS2 v2.0.0. (<https://github.com/uqrmaie1/admixtools>, publication pending). We calculated outgroup-*f*<sub>3</sub> using the central African rainforest hunter-gatherer population Mbuti in Congo as an outgroup to measure shared genetic drift between two target populations. We also used Mbuti as an outgroup when calculating *f*<sub>4</sub> statistics. To figure out the population structure within the Jomon-related groups, we calculated all pairs of *f*<sub>4</sub>(Mbuti, Jomon 1; Jomon 2, Jomon 3). We calculated *f*<sub>4</sub>(Mbuti, worldwide; Jomon 1, Jomon 2) for testing genetic symmetry between Jomon groups or searching for additional admixture sources over worldwide populations. Present-day worldwide populations used in the analysis are listed in Table S2. We calculated standard error measure (s.e.m.) of *f*<sub>3</sub> and *f*<sub>4</sub> statistics using the default 5 cM block jackknife resampling approach.

## 2.5 Runs of homozygosity

We investigated runs of homozygosity (ROH) segments of Jomon individuals covering more than 400,000 SNPs among the 1240K panel using hapROH [39]. We used pseudo-haploid genotype call of each Jomon genome and the 1000 Genomes Project Phase 3 haplotype data set as the reference panel [40].

# 3. Results

## 3.1 Genome-wide data of published Jomon-related individuals

For our study, we used genome-wide data of 23 published ancient Jomon or Jomon-like individuals (Figure 1, Table 1 and Table S1). Among these 23 individuals, 17 are Jomon individuals from the Honshu or Shikoku islands in Japan directly associated with the Jomon archaeological contexts. The remaining 6 harbor a Jomon-like genetic profile but are from an archaeological context not directly related to the Jomons: five are from the Nagabaka site in the Miyako Island of the Ryukyu ("Nagabaka\_2800BP" and "Nagabaka\_4000BP"), and one is from the Yokjido shell midden site in Tongyeong city, Republic of Korea ("Yokjido\_4000BP"). We detected no close relatives among the 23 individuals and therefore included all of them in the analysis (Figure S3 and Table S3). We split them into 11 analysis groups based on their

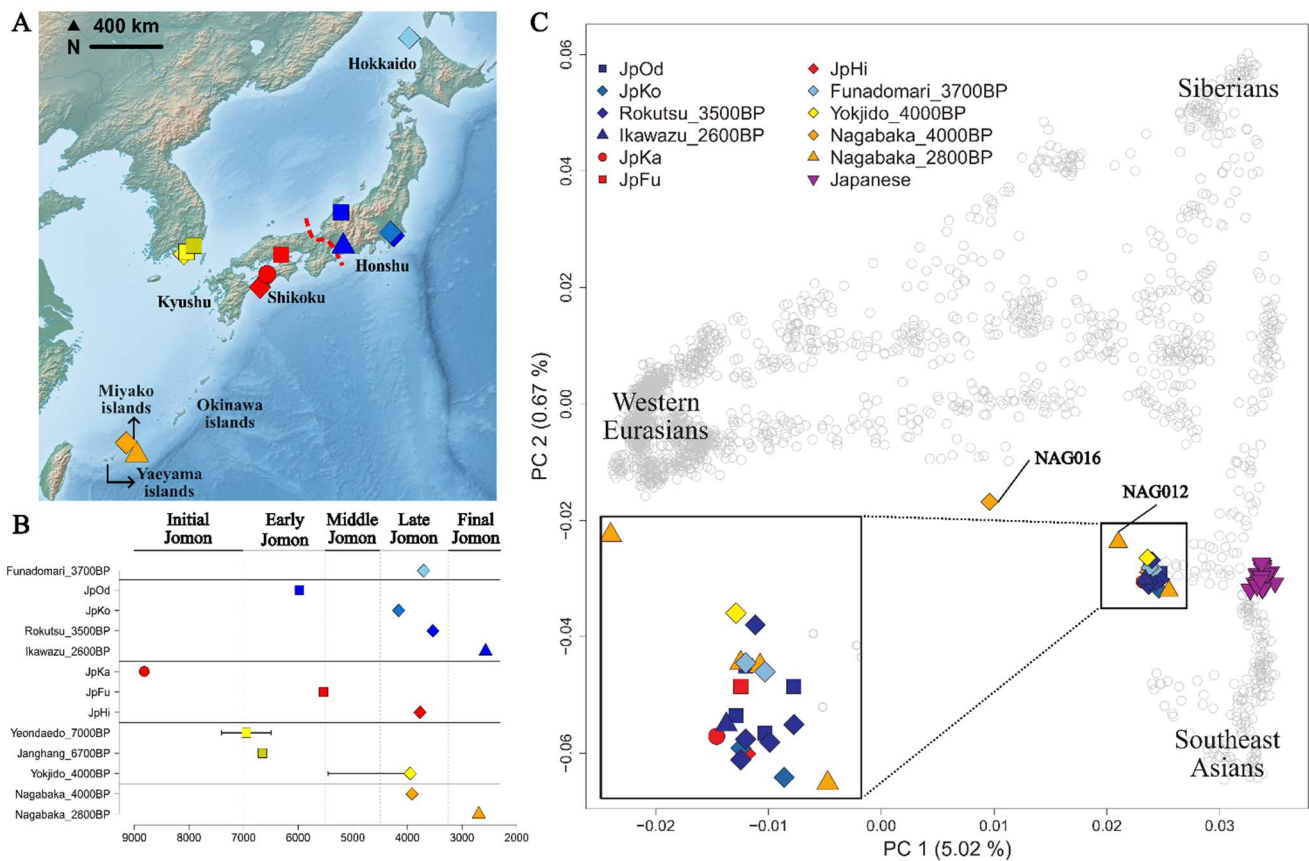
archaeological site and date information (Figure 1, Table 1 and Table S1). Among the individuals used, we flagged two individuals for low quality: the Yokjido individual (TYJ001) was potentially contaminated to a small degree (6% contamination based on its mitochondrial capture data) and the oldest Nagabaka individual (NAG016; Nagabaka\_4000BP) was heavily contaminated and of low coverage (27,652 out of 1,233,013 SNPs in the 1240K panel were covered). Because the unknown contaminants are a priori unlikely to be of the Jomon origin, which no longer exists among the present-day individuals, we included them in a subset of the analyses where contamination would not affect the tests in a qualitative manner. We also used four additional prehistoric individuals from the southern coast of Korea who were reported to have a Jomon genetic affinity: two from the Janghang Neolithic cemetery site in Busan city ("Janghang\_6700BP") and the other two from the Yeondae-do shell midden site in Tongyeong city ("Yeondaedo\_7000BP") [20].

We performed principal components analysis (PCA) to make a visual summary of the genetic profile of the Jomon-related individuals in comparison to present-day Eurasian populations (Figure 1C). Consistent with previous studies reporting a homogeneous genetic profile across the Jomon-related individuals [19], the Jomon-related individuals form a tight and distinct cluster separated from other populations. Two individuals deviating from the cluster are from Nagabaka (NAG012 and NAG016): both with low coverage and one with heavy contamination (NAG016).

To investigate a fine-scaled genetic stratification within the Jomon-related individuals, we performed PCA exclusively with Jomon, Yokjido, and Nagabaka individuals. In this analysis we observe a separation of Nagabaka and Yokjido individuals from the other Jomon individuals (Figure S4A). When we apply PCA only to the Jomon individuals in the mainland Japan, excluding Nagabaka and Yokjido, we observe a separation between Jomons from western Japan, eastern Japan (Chubu and Kanto), and Hokkaido (Figure S4B).

Considering the low coverage nature of most Jomon-related individuals, we measured the level of genetic diversity within each Jomon-related group by calculating pairwise genotype mismatch rate (PMR) between individuals (Figure S3 and Table S3). PMR values between individuals from different Jomon groups (mean = 0.191) are overall similar and much lower than those from present-day East Asians (mean = 0.241), such as Han Chinese and Japanese, suggesting overall reduced genetic diversity within the Jomon metapopulation. Interestingly, Nagabaka\_2800BP individuals show even more reduced PMR (mean = 0.154), implying a strong population bottleneck specific to Nagabaka. The distribution of runs of homozygosity (ROH) segments provides a

similar pattern (Figure S5). That is, the Jomon-related individuals overall show an accumulation of ROH segments, a signature of reduced genetic diversity, and Nagabaka individuals tend to have more ROH segments than most other Jomon individuals.



**Figure 1** Ancient Jomon-related groups used in this study. (A) Geographical location of the sites of each Jomon-related group used in this study. The red dotted line in Honshu marks the boundary between western and eastern Japan. Site names are listed in (B). (B) The average estimated dates of each Jomon-related group are represented as color-filled shapes. For groups not directly radiocarbon dated, the reported lower and upper bounds based on archaeological contexts are represented as the horizontal bars. The base map was obtained from the Natural Earth public domain map data set ([https://www.naturalearthdata.com/http://www.naturalearthdata.com/download/10m/raster/HYP\\_LR\\_SR\\_OB\\_DR.zip](https://www.naturalearthdata.com/http://www.naturalearthdata.com/download/10m/raster/HYP_LR_SR_OB_DR.zip)) and modified using R v4.2.0. (C) Jomon-related individuals (color-filled shapes other than present-day Japanese) were projected onto the top two PCs calculated with 2,077 present-day Eurasians (gray circles). Among present-day Eurasians, we highlighted present-day mainland Japanese with purple-filled downward triangles. A zoom-in plot of the Jomon cluster is shown in the bottom-left. Population labels and the geographic locations of present-day Eurasian individuals are presented in Figures S1-S2 and Table S2.

**Table 1** List of Jomon-related individuals used in this study. This list includes meta information of 27 Jomon-related individuals used in this study. Date information represent the 2-sigma range of the calibrated dates for directly radiocarbon-dated individuals and the context-based estimate for the others. More detailed metadata of the 27 Jomon-related individuals is provided in Table S1.

ID	Group	Date (in BP)	Locality	Molecular Sex	1240K SNP coverage	Ref.
JpFu1	JpFu	5478–5590	Funagura shell-midden, Kurashiki, Honshu, Japan	F	727,906	[19]
JpHi01	JpHi	3685–3850	Hirajo shell-midden, Ailnan, Shikoku, Japan	F	482,623	[19]
JpKa6904	JpKa	8646–8991	Kamikuroiwa rock shelter, Kamiukena District, Shikoku, Japan	F	1,195,740	[19]
JpKo13	JpKo	3847–3978	Kosaku shell-midden, Funabashi, Honshu, Japan	F	954,090	[19]
JpKo2	JpKo	4294–4514	Kosaku shell-midden, Funabashi, Honshu, Japan	F	1,055,386	[19]
JpOd181	JpOd	5751–5917	Odake shell midden, Toyama, Honshu, Japan	M	1,002,446	[19]
JpOd274	JpOd	6119–6289	Odake shell midden, Toyama, Honshu, Japan	M	924,161	[19]
JpOd282	JpOd	5737–5902	Odake shell midden, Toyama, Honshu, Japan	M	706,962	[19]
JpOd6	JpOd	5934–6179	Odake shell midden, Toyama, Honshu, Japan	F	686,632	[19]
FUN23	Funadomari_3700BP	3550–3960	Funadomari shell mound, Hokkaido, Japan	F	1,198,565	[18]
FUN5	Funadomari_3700BP	3500–3800	Funadomari shell mound, Hokkaido, Japan	M	1,080,627	[18]
IK002	Ikawazu_2600BP	2720–2418	Ikawazu shell mound, Aichi, Central Honshu, Japan	F	875,674	[17]
NAG012	Nagabaka_2800BP	N/A	Paimmi-nu-Nagabaka, Okinawa, Japan	M	23,329	[20]
NAG016	Nagabaka_4000BP	3976–3856	Paimmi-nu-Nagabaka, Okinawa, Japan	F	27,689	[20]
NAG019	Nagabaka_2800BP	2746–2510	Paimmi-nu-Nagabaka, Okinawa, Japan	F	648,493	[20]
NAG037	Nagabaka_2800BP	N/A	Paimmi-nu-Nagabaka, Okinawa, Japan	M	14,628	[20]
NAG038	Nagabaka_2800BP	2771–2744	Paimmi-nu-Nagabaka, Okinawa, Japan	F	509,055	[20]
TYJ001	Yokjido_4000BP	ca. 3950	Yokjido shell midden, Tongyeong, Korea	F	180,722	[20]
TYD006	Yeondaedo_7000BP	ca. 6950	Yeondaedo shell midden, Tongyeong, Korea	M	40,677	[20]
TYD007	Yeondaedo_7000BP	ca. 6950	Yeondaedo shell midden, Tongyeong, Korea	M	79,697	[20]
GDI002	Janghang_6700BP	6639–6841	Janghang Neolithic cemetery site, Busan, Korea	F	118,299	[20]
GDI008	Janghang_6700BP	6651–6495	Janghang Neolithic cemetery site, Busan, Korea	M	92,626	[20]
I13882	Rokutsu_3500BP	3045–3005	Rokutsu Shell Mound, Japan	F	613,276	[21]
I13883	Rokutsu_3500BP	2970–2570	Rokutsu Shell Mound, Japan	M	488,319	[21]
I13884	Rokutsu_3500BP	3945–3895	Rokutsu Shell Mound, Japan	F	724,205	[21]
I13885	Rokutsu_3500BP	3035–2995	Rokutsu Shell Mound, Japan	F	156,169	[21]
I13886	Rokutsu_3500BP	3685–3645	Rokutsu Shell Mound, Japan	M	801,582	[21]



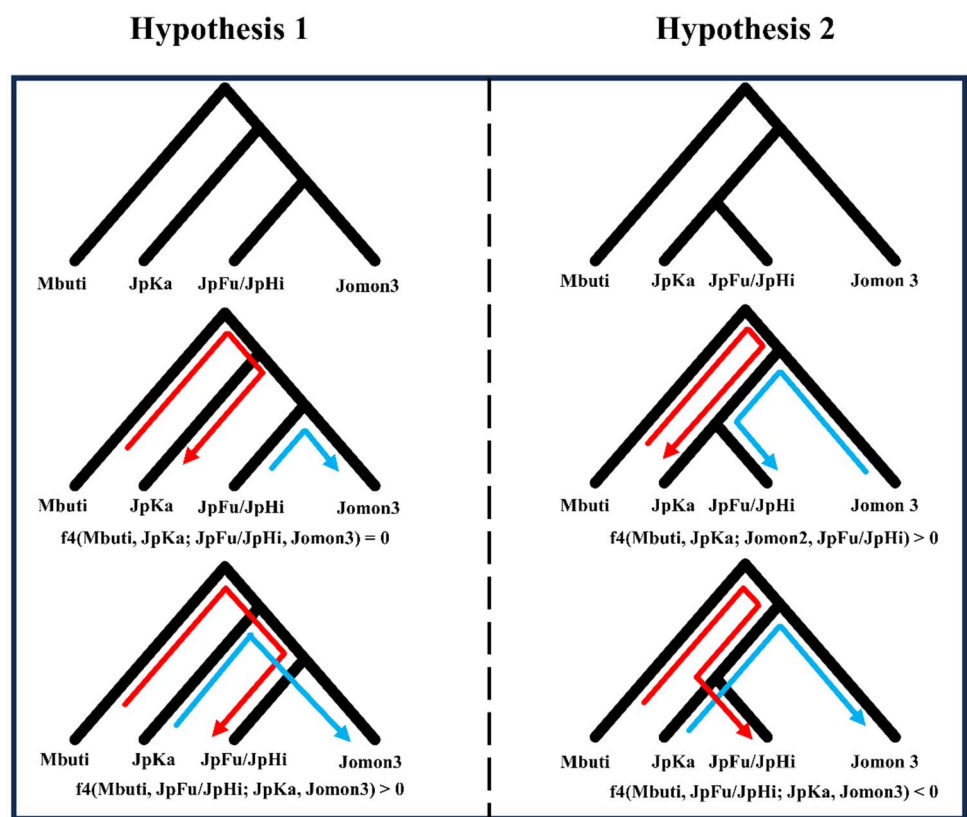
### 3.2 The Initial Jomon individual as a common outgroup to all later Jomon individuals

To investigate the population structure among the Jomon-related groups, we first measured the genetic affinity between each pair of the Jomon-related groups using the outgroup- $f_3$  statistic in the form of  $f_3(\text{Mbuti}; \text{Jomon 1}, \text{Jomon 2})$  (Figures S6–S7 and Table S4). We used Mbuti, a Central African rainforest hunter-gatherer population, as an outgroup and applied the analysis to 9 out of 11 Jomon-related groups, excluding Nagabaka\_4000BP and Yokjido\_4000BP due to contamination. When included, they showed consistently lower outgroup- $f_3$  values than other pairs (Figure S6A). We find that the Initial Jomon individual from Shikoku (JpKa; dated to *ca.* 9,000 BP) shows a relatively low genetic affinity with other Jomons (Figure S6B). Among all pairs, the pair of an Early Jomon individual from western Honshu (JpFu, dated to *ca.* 5,600 BP) and a Late Jomon individual from Shikoku (JpHi, dated to *ca.* 3,800 BP) shows the highest value (Figure S7 and Table S4).

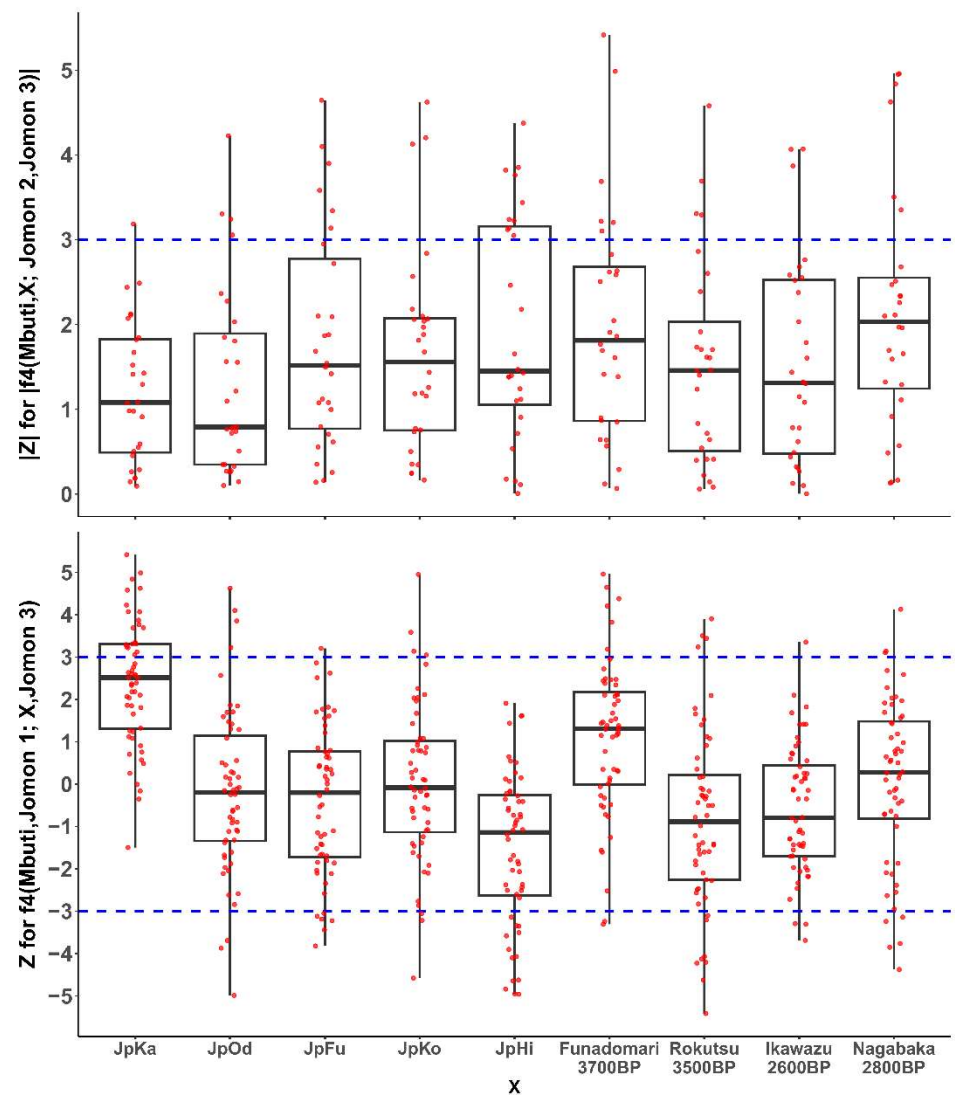
Inspired by the outgroup- $f_3$  results and the presence of the Initial Jomon individual, we explicitly compared two competing hypotheses regarding the population structure of the Jomons: (1) the oldest Jomon individual JpKa forms a common outgroup to all of the later Jomon individuals, and (2) the Jomon population in western Japan (JpKa, JpFu, JpHi) shows a population continuity over a 5,000-year-period (Figure 2). To distinguish between the two hypotheses, we calculated  $f_4$  statistics in the form of  $f_4(\text{Mbuti}, \text{Jomon 1}; \text{Jomon 2}, \text{Jomon 3})$  for all triplets of the Jomon-related groups (Figure 3, Figures S8–S9 and Table S5). Under the former hypothesis,  $f_4(\text{Mbuti}, \text{JpKa}; \text{Jomon 2}, \text{Jomon 3})$  is expected to be zero for all (Jomon 2, Jomon 3) pairs because JpKa is a common outgroup to all later Jomon groups. In contrast, under the latter hypothesis, JpKa is supposed to be genetically closer to later Western Jomon groups (JpFu/JpHi) than to the other Jomons, thus we predict  $f_4(\text{Mbuti}, \text{JpKa}; \text{Jomon 2}, \text{Jomon 3})$  to be significantly positive when Jomon 3 is later Jomon populations from western Japan (*i.e.*, JpFu and JpHi). Likewise,  $f_4(\text{Mbuti}, \text{JpFu/JpHi}; \text{JpKa}, \text{Jomon 3})$  will be positive under the former hypothesis while it will be negative under the latter.

For the statistic  $f_4(\text{Mbuti}, \text{JpKa}; \text{Jomon 2}, \text{Jomon 3})$ , only 1 out of the 28 Jomon group pairs has  $|Z| > 3$  value:  $f_4(\text{Mbuti}, \text{JpKa}; \text{Funadomari}_3700\text{BP}, \text{JpFu}) = 3.187$  s.e.m. (Figure 3A, Figure S8 and Table S5). The other eight Jomon groups have 3 to 10 pairs with  $|Z| > 3$  values when they are placed in the second population, making them less likely to be a common outgroup to the other Jomons (Figure 3A, Figure S8 and Table S5). Furthermore,  $f_4(\text{Mbuti}, \text{Jomon 1}; \text{JpKa}, \text{Jomon 3})$  are significantly positive in many (Jomon 1, Jomon 3) pairs and in general tend to be positive in its value, preferring the former hypothesis over the latter (Figure 3B, Figure S8 and Table S5).

The second statistic,  $f_4(\text{Mbuti}, \text{JpFu/JpHi}; \text{JpKa}, \text{Jomon 3})$  are mostly  $|Z| < 3$ , matching the prediction by neither hypothesis (Table S5). Comparing other Jomon groups' affinity to JpKa and JpFu/JpHi by  $f_4(\text{Mbuti}, \text{Jomon 1}; \text{JpKa}, \text{JpFu/JpHi})$ , the results are not statistically significant but mostly positive. We speculate that the Early Jomon JpFu may have a partial genetic link with JpKa, the earlier individual from a nearby region, while formally testing this admixture hypothesis may need more ancient genomes to enhance statistical power. Therefore, the oldest Jomon individual, JpKa, is likely to represent a common outgroup to the available Jomon groups, including those from western Japan.



**Figure 2** Two competing hypotheses regarding population structure of the Jomon. We suggest two competing hypotheses with  $f_4$  statistics the expectation of which can distinguish between the two. (Left side) Hypothesis 1 assumes that the oldest Jomon from western Japan, JpKa, is a common outgroup to later Jomons including those from the nearby region (JpFu/JpHi). (Right side) Hypothesis 2 assumes a genetic continuity in western Japan, suggesting that the older JpKa and later JpFu/JpHi form a clade against those from eastern Japan. Red and skyblue arrows represent drift paths from population 1 to 2 (red) and population 3 to 4 (skyblue) in  $f_4(\text{population 1}, \text{population 2}; \text{population 3}, \text{population 4})$ , respectively.



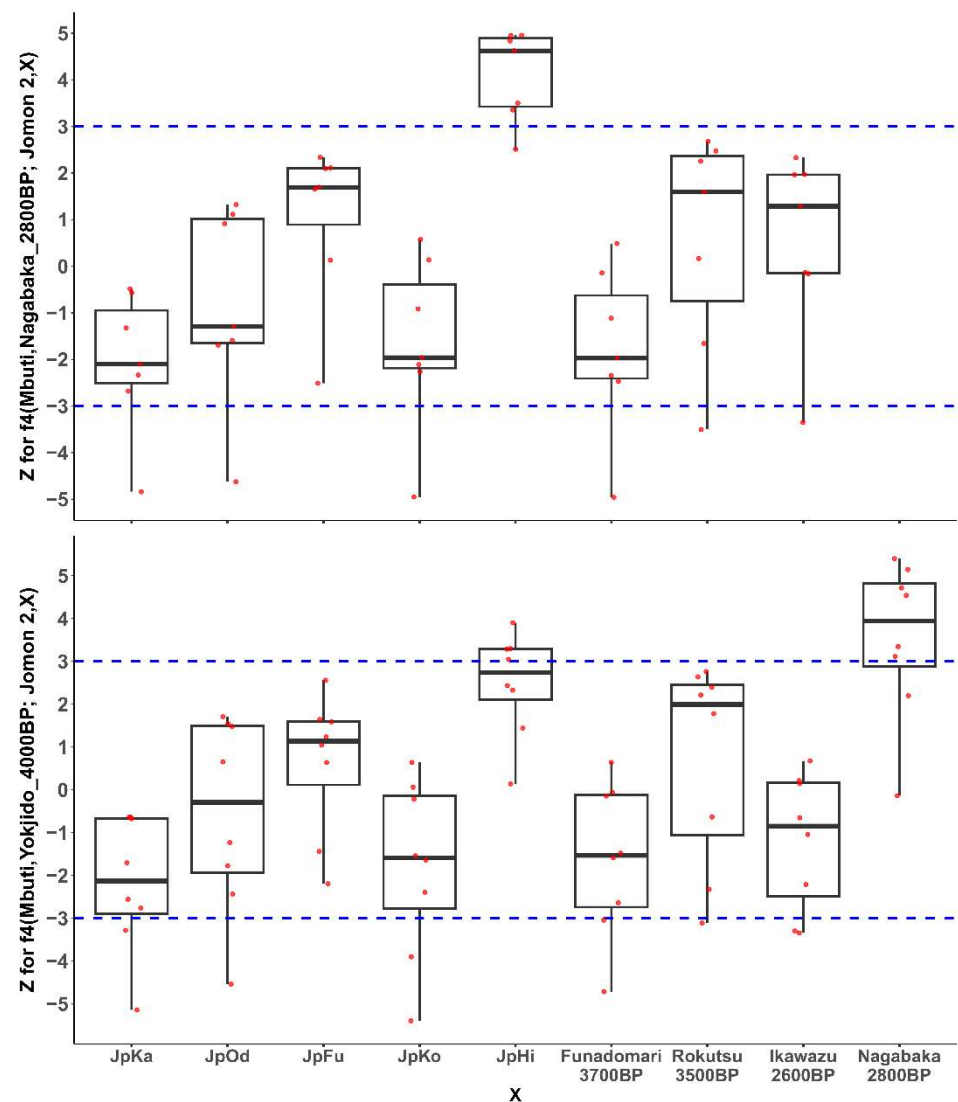
**Figure 3** Cladality test for all pairs of Jomon individuals. We calculated  $f_4$  statistics between the Jomon groups to identify the most distantly related one among them (*i.e.*, a common outgroup). (A) We present absolute Z-scores of the  $f_4$  statistics in the form of  $f_4(\text{Mbuti}, X; \text{Jomon 2}, \text{Jomon 3})$  using a box-whisker plot. Z-scores are calculated by a 5cM block jackknife resampling approach. This statistic is expected to be zero when  $X$  represents the common outgroup. (B) We present Z-scores of the  $f_4$  statistics in the form of  $f_4(\text{Mbuti}, \text{Jomon 1}; X, \text{Jomon 3})$ . Positive values indicate an excess shared genetic drift between (Jomon 1, Jomon 3) pairs against  $X$ .

Finally, we applied the same analysis to the second oldest Jomon group from the Early Jomon Odake shell-midden site from north-central Honshu (JpOd; dated to *ca.* 6,000 BP). We find no Jomon pairs that are asymmetrically related to JpOd by observing  $f_4(\text{Mbuti}, \text{JpOd}; \text{Jomon 2}, \text{Jomon 3})$  within 3 s.e.m. in all Jomon pairs but those including JpKa:  $f_4(\text{Mbuti}, \text{JpOd}; \text{JpKa}, \text{Jomon 3}) > 3$  s.e.m. for all later Jomon groups from eastern Japan (including Chubu, Kanto, and Hokkaido) (Table S5).

### 3.3 The genetic affinity of the Late Jomon in western Japan and Jomon-related individuals

We investigated possible origins of individuals from the Nagabaka ("Nagabaka\_2800BP") and the Yokjido shell midden sites ("Yokjido\_4000BP"), who exhibited a Jomon-like genetic profile, although these sites and regions are not directly associated with the Jomon archaeological culture. We found that JpHi, the Late Jomon from Shikoku, is the closest Jomon group with Nagabaka\_2800BP:  $f_4(\text{Mbuti}, \text{Nagabaka\_2800BP}; \text{other Jomon}, \text{JpHi})$  are mostly significantly positive ( $Z = 2.5$  to  $4.9$ ) (Figure 4A and Table S5). The older Early Jomon individual from western Honshu, JpFu, is second most closely related to Nagabaka\_2800BP although the difference is not statistically significant:  $f_4(\text{Mbuti}, \text{Nagabaka\_2800BP}; \text{other Jomon}, \text{JpFu}) = 0.1$  to  $2.3$  s.e.m. except for JpHi ( $Z = -2.5$ ) (Table S5). The Jomon-related population would have been already in Nagabaka by *ca.* 4,000 BP, considering a clear Jomon affinity of the older Nagabaka individual (Nagabaka\_4000BP; directly dated to *ca.* 4,000 BP) [20]. Taken together, the Late Jomon population from western Japan, related to JpFu/JpHi, was likely a source of the Jomon-related population in southern Ryukyu.

Likewise, we find that JpHi and Nagabaka\_2800BP are the closest Jomon-related group with Yokjido\_4000BP:  $f_4(\text{Mbuti}, \text{Yokjido\_4000BP}; \text{Jomon}, \text{JpHi}/\text{Nagabaka\_2800BP}) = 2.3$  to  $5.4$  s.e.m. and  $f_4(\text{Mbuti}, \text{Yokjido\_4000BP}; \text{Nagabaka\_2800BP}, \text{JpHi}) = 0.1$  s.e.m. (Figure 4B and Table S6). A previous study reported the Jomon ancestry contribution in prehistoric groups along the southern coast of Korea: Yeondaedo\_7000BP and Janghang\_6700BP [20]. Repeating the same analysis, we find that JpHi seems to be the closest Jomon-related group with them:  $f_4(\text{Mbuti}, \text{Yeondaedo\_7000BP}; \text{other Jomon}, \text{JpHi}) = 0.0$  to  $1.6$  s.e.m. and  $f_4(\text{Mbuti}, \text{Janghang\_6700BP}; \text{other Jomon}, \text{JpHi}) = 1.2$  to  $2.7$  s.e.m., but none of the tests are statistically significant (*i.e.*,  $Z < 3$ ) due to small sample size and low coverage (Table S6). To summarize, we suggest that the dispersal of the Jomon-related populations into southern Korea and the Ryukyu islands, clearly observed by *ca.* 4,000 and 2,800 BP in the two regions, respectively, is likely to have originated from western Japan, in agreement with the geographic proximity of these regions. While it is possible that the Jomon ancestry found in the earlier individuals in these regions (*ca.* 6,500–7,000 BP in southern Korea (Janghang\_6700BP and Yeondaedo\_7000BP) and *ca.* 4,000 BP in Miyako) may have been derived from the same source, we caution that the currently available genome data lack a resolution to distinguish between different Jomon sources. Future ancient genome sampling over these regions, as well as across the Japanese archipelago, will help us narrow down the time window and true sources of the Jomon ancestry in these regions.



**Figure 4** The genetic affinity of Nagabaka\_2800BP and Yokjido\_4000BP with the Jomon groups. (A) We present the  $f_4$  statistics in the form of  $f_4(\text{Mbuti}, \text{Nagabaka\_2800BP}; \text{Jomon } 2, X)$  to find the Jomon groups most closely related to Nagabaka\_2800BP. Z-scores of  $f_4$  statistics are calculated by a 5cM block jackknife resampling approach and presented by box-whisker plots. (B) We present the  $f_4$  statistics in the form of  $(\text{Mbuti}, \text{Yokjido\_4000BP}; \text{Jomon } 2, X)$  to find the Jomon groups most closely related to Yokjido\_4000BP. A positive value obtained from this calculation indicates high genetic affinity between X and the targets (Nagabaka\_2800BP and Yokjido\_4000BP) against other Jomon groups.

#### 4. Discussion

The origins and history of the Jomon people, who had occupied the Japanese archipelago for more than 14,000 years, have long been investigated by archaeologists and geneticists. Recent advances in archaeogenomics have finally made a major breakthrough by decoding

dozens of ancient Jomon genomes [17–21]. Although these studies clarified a distinct genetic origin of the Jomons and their overall homogeneous genetic profiles, they focused less on reconstructing the genetic diversity and relationship among the Jomons. Here we investigate the Jomon population structure over time in a comprehensive manner based on a compilation of the Jomon genomes so far available.

We find that the Initial Jomon individual from Shikoku, JpKa, forms an outgroup common to later Jomon groups in both western and eastern Japan, while having a residual affinity with later groups in the nearby regions in western Japan. The only pair of Jomon groups that breaks symmetry, JpFu and Funadomari, may be due to this residual affinity between JpKa and JpFu. Alternatively, this may be due to Funadomari-specific genetic connection, *i.e.*, a link around the Sea of Okhotsk, suggested by the observation that Asiatic Eskimos and Ulchi from the Sakhalin Island, among the present-day worldwide populations, are closer to Funadomari than to JpKa, by the  $f_4$  statistic of the form  $f_4(\text{Mbuti, worldwide; Funadomari, JpKa})$  (Table S7). A previous study reported a similar connection between the Ainu from Hokkaido and the populations around the Sea of Okhotsk, although this signal may be due to a more recent genetic exchange between them [12]. The next oldest Jomon group, the Early Jomon JpOd, in contrast shows a clear genetic affinity with all later Jomons from eastern Japan. A parsimonious scenario is that the eastern Jomon population expanded into the west and partially replaced the local western population at some point within a broad time range of *ca.* 9,000 and 5,500 BP (*i.e.*, between JpKa and JpFu). We caution that due to sparse sampling of the Jomon genomes over space and time the representativeness of our findings may not be guaranteed.

While the Jomons have been frequently assumed to be strongly isolated from the populations outside the Japanese archipelago, recent archaeological studies highlight prolonged cultural contacts with continental populations prior to their major contact with the Yayoi people in the late first millennium BCE [41–43]. These studies reported the appearance of material cultural elements, such as domesticated plants (e.g., azuki and soybeans) and bronze objects, from the continent to the Jomon-period Japan. Interestingly, the recent archaeogenomic studies reported a Jomon-like genetic profile in ancient individuals outside the Jomon archaeological context, including the Miyako island in the southern Ryukyu and the Yokjido site in the southern coast of Korea [20]. The Jomon-like individuals in both sites harbor the strongest genetic affinity with the Late Jomon individual from western Japan (JpHi; dated to *ca.* 3,800 BP). In both regions, the earliest appearance of the Jomon ancestry is far older than the time of JpHi while older individuals there are of low quality and thus unable to pinpoint the affinity to

specific Jomon groups: *ca.* 4,000 BP in Miyako (Nagabaka\_4000BP) and *ca.* 6,500–7,000 BP in southern Korea (Janghang\_6700BP and Yeondaedo\_7000BP). Therefore, the spatial and temporal origins of the Jomon populations who contributed to these early populations remain obscure. Further sampling of the Jomon genomes, especially the Early/Middle Jomons from Kyushu, the westernmost major island in Japan, will provide a pivotal piece of information to reconstruct the outbound genetic connection of the Jomons with the Eurasian continent.

## Supplementary Materials

The following supplementary materials can be downloaded at: [HPGG2303040008SupplementaryMaterials.zip](#).

1. Figure S1. Present-day Eurasian populations used in principal component analysis.
2. Figure S2. Geographic location of present-day Eurasian populations used in principal component analysis.
3. Figure S3. Pairwise genotype mismatch rate within and between the Jomon-related groups.
4. Figure S4. PCA results of the Jomon-related individuals.
5. Figure S5. Small effective population size of the Jomons shown by runs of homozygosity segments.
6. Figure S6. Heatmap of outgroup-f3 statistics of the Jomon-related groups.
7. Figure S7. Outgroup-f3 statistics of Jomon-related groups.
8. Figure S8. Genetic symmetry test between Jomon-related groups.
9. Figure S9. Genetic affinity test of Jomon-related groups.
10. Table S1. Meta information of Jomon-related individuals used in this study.
11. Table S2. List of present-day populations and non-Jomon ancient population used in this study.
12. Table S3. Pairwise mismatch rate between Jomon Individuals.
13. Table S4. The genetic affinity between Jomon groups.
14. Table S5. F4 statistic for all triplets of the Jomon-related groups.
15. Table S6. F4 statistics for comparing the Jomon group pairs with regard to their genetic affinity to the Jomon-related groups outside the Jomon archaeological contexts.
16. Table S7. The relative genetic affinity between JpKa and other Jomon-related groups to present-day world-wide populations.

## Ethics Statement

Not applicable.

## Consent for Publication

Not applicable.

## Availability of Data and Materials

The genotype data for the 1240K panel have been deposited in the Edmond Data Repository of the Max Planck Society [<https://edmond.mpg.de/dataset.xhtml?persistentId=doi:10.17617/3.CXKGCX>]. All analyses performed in this study are based on publicly available programs. Program names, versions, and non-default options are described in detail in the Methods section. All scripts used for the analyses presented in this study are publicly available via the Github repository ([https://github.com/CWJeongLab/HPGG\\_Jomon](https://github.com/CWJeongLab/HPGG_Jomon)).

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## Competing Interests

The authors have declared that no competing interests exist.

## Author Contributions

Conceptualization: CJ; Methodology: GJ, HG, HM, CJ; Investigation: GJ, HG; Visualization: GJ, HG, HM; Supervision: CJ; Writing—original draft: GJ, HG; Writing—review & editing: GJ, HG, HM, CJ.

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