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Demic Diffusion of the Yayoi People in the Japanese Archipelago

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The present study examines the 3-dimensional data of human crania from the Yayoi period (800 BC to AD 250) of the Japanese archipelago by geometric morphometrics to investigate demic diffusion patterns. This is the first study on the Yayoi crania using their 3D data and geometric morphometrics with a much larger number of skeletal remains outside of the Kyushu regions than previous studies. The comparative results between the Jōmon and Yayoi samples show that the Yayoi people not only in the eastern parts but also in the western parts of the archipelago are significantly different from the final Jōmon people and the Yayoi people were not strongly affected by the Jōmon people. A relatively gradual geological cline is also found among the Yayoi population, suggesting that the immigrants from the continental East Asia moved from the western parts to the eastern parts of the archipelago though the causes of the morphological changes are unclear.

Keywords
Yayoi, human skeletal remains, 3D data, geometric morphometrics

Introduction

Agriculture has been regarded as one of the most significant innovations in human evolutionary history, because it caused drastic social and biological changes. Since the origins and processes of its adoption are diverse, comparative studies across space and time have been conducted (e.g., Bellwood, 2005; Kennett & Winterhalder, 2006; Lee & DeVore, 1968; Rindos, 1984). Demic versus cultural diffusion have been an axis of the debate: Archaeologists and anthropologists have intensively argued on which of the migration of agriculturists or the adoption by hunter-gatherers played a more important role in the spread of agriculture (e.g., Patin et al., 2014; Skoglund et al., 2012). Since it is not dichotomous, the relative importance of demic versus cultural diffusion has been argued.

In the Japanese archipelago, the Yayoi period (800 BC to AD 250) has been defined as the phase of the onset of agriculture in Japan. Many have assumed that migrants from the continental East Asia arrived at the northern Kyushu region (e.g., Nakahashi, 2015) and the Yayoi cultural package was formed, which included cultural elements imported from the continental East Asia, ones derived from the preceding Jōmon culture, and newly innovated items (e.g., Kaneda et al., 2022; Morioka, 2018; Noshita et al., 2022a, 2022b; Shitara, 2019); and then the package spread across the Kyushu, Honshu, and Shikoku islands, replacing or interbreeding with the indigenous Jōmon inhabitants. This spread has been also assumed to trigger or set the foundation of drastic social changes, including increasing population, higher frequency of intergroup conflicts, more rigid social hierarchies than previous periods, and etc. (e.g., Nakagawa et al., 2021; Nakao et al., 2016; Nakazono, 2004).

Despite its long history of investigation, the relative importance of demic versus cultural diffusion was still unclear due to several reasons. First, although analyses of ancient DNA have provided information transforming previous understandings of the past society in Europe, because of soil condition and resource scarcity, investigations on ancient DNA have progressed only gradually compared to Europe, i.e., the region and time spans are not sufficiently covered by ancient DNA analyses in Japan. Thus, analyses of skeletal remains are still meaningful as a proxy of genetic relationships but the above issue can also hold for studies of skeletal remains: Previous studies tended to focus on the northern Kyushu region, which has been assumed to be the origin of the Yayoi cultural package and thus be "typical", and skeletal remains in this regions tend to be well preserved at least partly due to burial customs than those in other regions (e.g., Matsushita & Naito, 1989; Nakahashi, 2015; Nakahashi & Nagai, 1989; Nakazono, 2004; see Naito, 1981, as an exception). Second, skeletal remains have been often dichotomized into "Jōmon" or "Yayoi" types, which could be troublesome to discuss interbreeding.

In the present study, we examine the diffusion patterns of the Yayoi people based on patterns in morphological variation of skeletal remains from the Jōmon and Yayoi populations. We collected three-dimensional data of human skeletal remains from the Kyushu to the Kanto regions (Figure 1). We also employ geometric morphometrics to quantify their spatiotemporal variation. As far as we know, this is the first study on the Yayoi people using 3D data and geometric morphometrics. Our results indicate that the Jōmon and the Yayoi people can be morphologically distinguished and suggest the possibility

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of their less frequent interbreeding. Moreover, we found a regional cline in a morphological variation in the Yayoi population, suggesting the movements of migrants from the west to the east without interbreeding.

Methods

Data set

Our dataset is composed of three-dimensional models of 101 well-preserved skulls from 31 sites of the Yayoi period and 45 from 2 sites of the final Jōmon period for comparison (see Table1, Figure 1, and supplementary data S1 for details). Although we could not get permission to measure skeletal remains of the Yayoi period in the Kyushu and Sanin regions owned by a few institutions, our dataset included a much larger number of skeletal remains outside of the Kyushu regions than previous studies (e.g., Naito, 1981). Furthermore, our dataset still included representative Yayoi sites such as Doigahama site, Kanenokuma site, and Kuma-Nishioda site (Chikushino city board of education, 1993; Fukuoka city board of education, 1985; Shimonoseki city board of education & Doigahama Anthropological Museum, 2014).

Laser scanning (using three models of laser scanner, Creafrom HandySCAN BLACK, Creafrom HandySCAN BLACK Ellite, and Einscan Pro HD) and SfM/MVS techniques (using Agisoft Metashape 1.6.4 for reconstruction of 3D models from 2D photos) were used to construct three-dimensional models (see Kaneda et al., 2022; Nakagawa, Kaneda, et al., 2022, for more details of SfM/MVS). It is noteworthy that we confirmed no significant difference in three-dimensional models constructed by different ways (Kaneda et al., 2022; Nakagawa, Kaneda, et al., 2022; Nakao et al., 2022).

Data processing

Because the original three-dimensional models were composed of too many meshes (from one to six million meshes) and were unsuitable for some software for the following analyses, we reduced the mesh numbers by the "Simplification: Quadric Edge Collapse Decimation" filter in Meshlab (Cignoni et al., 2008) to almost three-hundred thousand meshes. Previous research also confirmed that this procedure does not significantly influence the morphological features of three-dimensional models (Noshita et al., 2022a, 2022b).

Data analysis

We quantified morphological variation based on landmark-based geometric morphometrics. We obtained the three-dimensional coordinates of 31 landmarks (see also Nakagawa, Yoshida, & Nakao, 2022, for the locations) based on traditional biometrics (e.g., Baba, 1981). Selected landmarks are summarized in Figure 2 and Table 2. If some parts of crania are lacked and we needed to complement the focal landmark, we inverted remained parts along the median line through the nasion, prosthion, and bregma (i.e., central line of the crania) (e.g., Fantini et al., 2008; Nakagawa, Yoshida, & Nakao, 2022) or used estimate.missing function based on the thin-plate-spline method in the geomorph package 4.0.4 (Adams et al., 2022). Landmark coordinates are normalized by the Procrustes superimposition method (Gower, 1975). We carried out the principal component analysis to summarize the morphological variation.

All analyses were conducted by Blender (version 3.4.1; Blender Online Community, 2018), R (version 4.2.1; R Core Team, 2020) with geomorph 4.0.4 (Adams et al., 2022) and ggplot2 3.4.0 packages (Wickham, 2016), and Rstudio (2022.07.0+548; Rstudio Team, 2020).

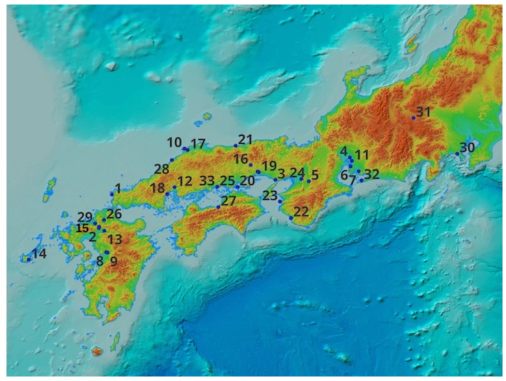

Figure 1. Site locations where human skeletal remains in the present research were excavated. 1. Doigahama, 2. Kuma-Nishioda, 3. Shinpou, 4. Asahi, 5. Osadera, 6. Houkaiji, 7. Shinmido, 8. Annomae, 9. Nagamine, 10. Inome, 11. Atsuta, 12. Bishamondai, 13. Daifukumura, 14. Ohama, 15. Yamaemura, 16. Yokosakakyuryo, 17. Aoki, 18. Takahata, 19. Myojinyama, 20. Shirasagiyama, 21. Aoyakamijichi, 22. Shinjo, 23. Chinoshima, 24. Kitoragawa, 25. Yuzugahama, 26. Tateiwa, 27. Yokochiyama, 28. Nimasakanada, 29. Kanenokuma, 30. Hasekoji, 31. Getsumeisawa, 32. Ikawazu, 33. Tsukumo. The map is based on the color altitude map published by Geospatial Information Authority of Japan with information of the sea area from the Hydrographic and Oceanographic Department, Japan Coast Guard, and modified by HN using QGIS (3.20.3).

Table 1. The number of the samples. The areas are arranged from the eastern to western regions. The M_Kyushu (Middle Kyushu) region includes sites No. 8 and 9, N_Kyushu (Northern Kyushu) No. 2, 13, 14, 15, 26, and 29, Sanyo No. 12, 16, 18, 19, 20, 25, and 33, Sanin No. 1, 10, 17, 21, and 28, Shikoku No. 27, Kinki No. 3, 5, 22, 23, and 24, Tokai No. 4, 6, 7, 11, and 32, Chubu No. 31, and Kanto No. 30 in Figure 1.

	Jōmon	Early	Middle	Late	Unknown	Total
M_Kyushu			4			4
N_Kyushu			33	1		34
Sanyo	27			4	1	32
Sanin		3	4	20	3	30
Shikoku			1	1		2
Kinki		2	1	5		8
Tokai	18	1	6	5		30
Chubu		1				1
Kanto			4	1		5
Total	45	7	53	37	4	146

Table 2. Selected landmarks. All landmarks are defined in Caple & Stephan (2016).

No.	Selected metrical points	No.	Selected metrical points
1	Nasion	17	left Zygomaxillare
2	Nasospinale	18	Lambda
3	Prosthion	19	Opisthokranion
4	right Maxillofrontale	20	right Asterion
5	right Frontomalare orbitale	21	right Entomion
6	right Ektokonchion	22	left Asterion
7	right Orbitale	23	left Entomion
8	right Frontotemporale	24	Orale
9	right Jugale	25	Staphylion
10	right Zygomaxillare	26	Basion
11	left Maxillofrontale	27	Bregma
12	left Frontomalare orbitale	28	right Krotaphion
13	left Ektokonchion	29	right Sphenion
14	left Orbitale	30	left Krotaphion
15	left Frontotemporale	31	left Sphenion
16	left Jugale		

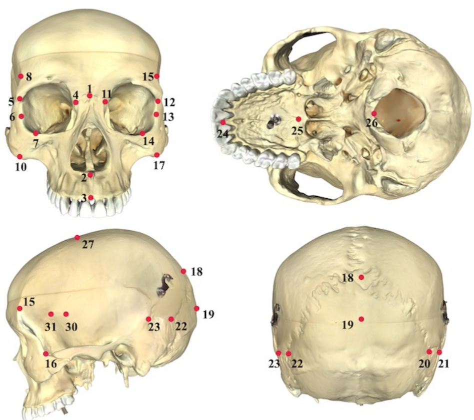

Figure 2. The locations of the landmarks. The screenshot of 3D human crania is from SH-7 model by KYOTO KAGAKU.

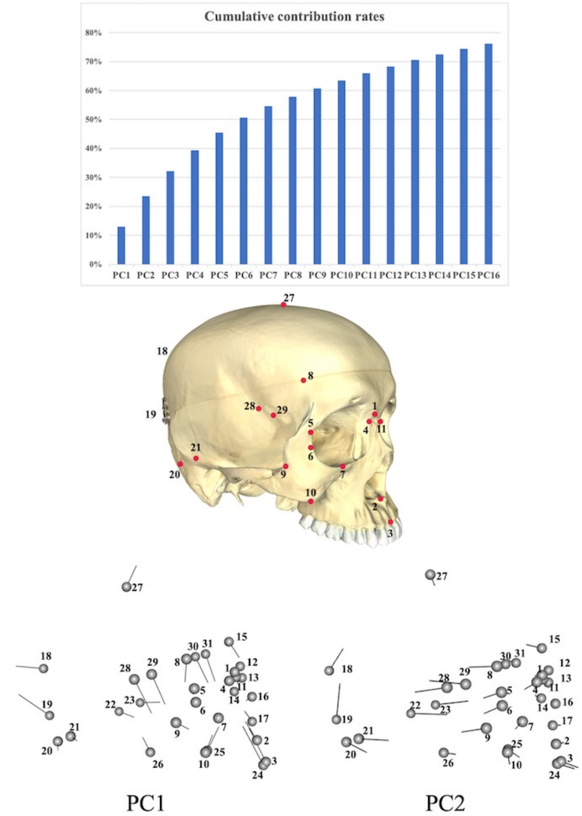

Figure 3. The results of PCA for the Jōmon and Yayoi crania. The cumulative contribution rates and the 3D locations of landmarks the PC1 and PC2 grab, where the right side is the cranial front. The directions and lengths of the bars indicate the direction and degree of landmark movements according to change of each PC score. The screenshot of 3D human crania is from SH-7 model by KYOTO KAGAKU.

Results

The results of the principal component analysis for comparison between the Jōmon and Yayoi periods indicate that the cumulative contribution rates are over 75% before PC17. The PC1 mainly captures the face height and anterior-posterior length. When the scores are smaller, the face is higher and the anterior-posterior length is shorter, i.e., the Yayoi people tended to have higher faces and shorter anterior-posterior length. The PC2 refers to the anterior-posterior length and the position of the teeth (Figure 3). The PC1 clearly grabs the difference between the Jōmon and Yayoi periods. The PC2 shows a relatively gradual geological cline from the northern Kyushu area, where the immigrants from the continental East Asia reached first (Figure 4). We also examined the correlation between the PC2 and the geological distance from the Northern Kyushu (i.e., the Kanenokuma site) based on the longitude of each site, which supports the geological cline (r = .410, p < .001). The results from analyzing the Yayoi crania without the Jōmon crania are also consistent with the cline (see the PC1 and PC2 in the supplementary material S2 and supplementary data S3). Variations between sexes are not significant. The difference between the Jōmon and the Yayoi people in the PC1, and gradual geological clines in the PC1 to PC2 are also found in both sexes (see supplementary figure S4).

Discussion

The results of the comparison are consistent with and confirm previous research arguing that the Jōmon and Yayoi people are different or distinguished populations and that the clearest difference is observed in their face height and anterior-posterior length shown by the PC1 (e.g., Matsushita & Naito, 1989; Naito, 1981; Nakahashi, 2015; Nakahashi & Nagai, 1989).

However, our results suggest that the eastern Yayoi samples in the present study were not strongly affected by the Jōmon people. The PC1 indicates that the scores of the Jōmon population tend to be higher and if the Jōmon

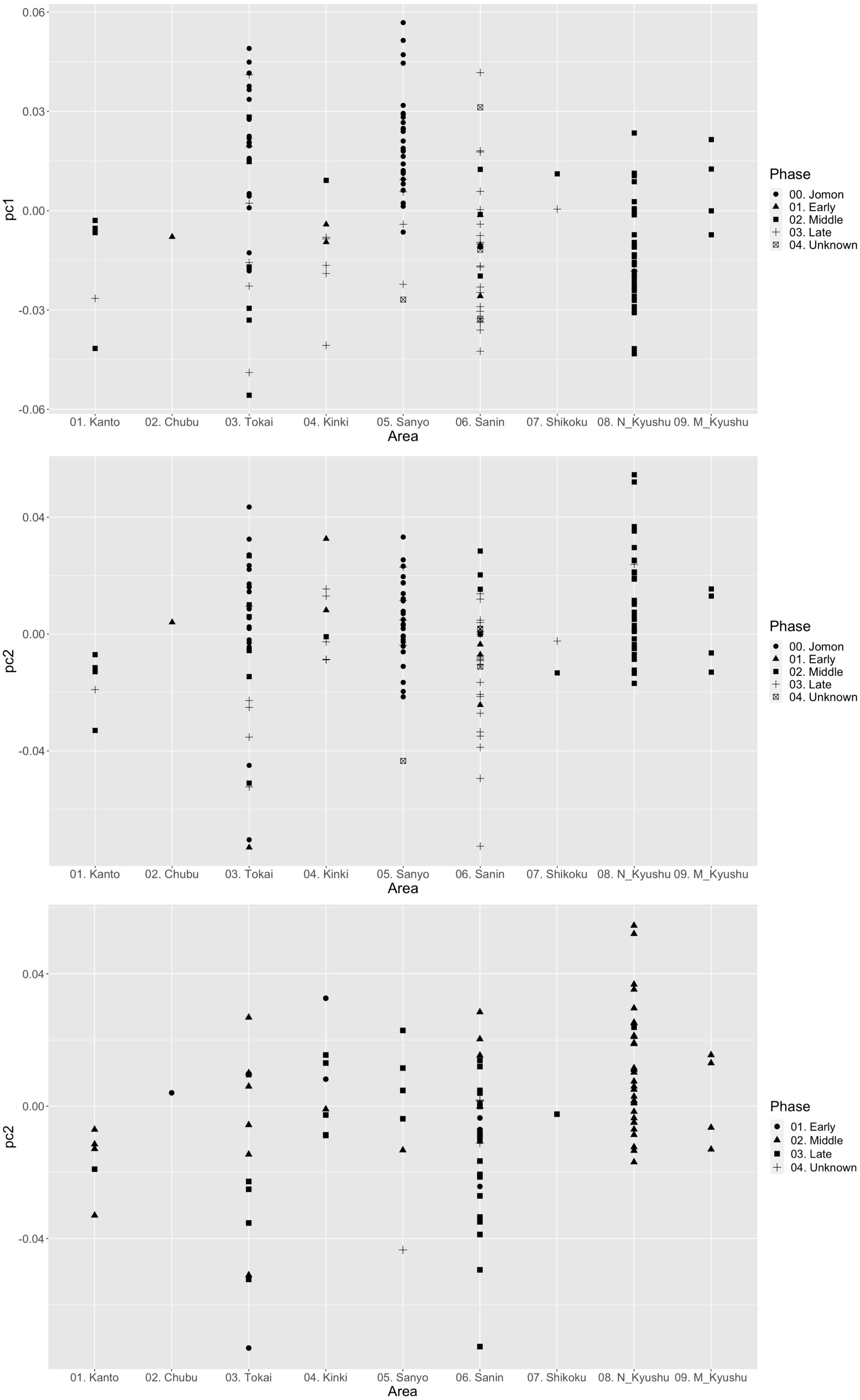

Figure 4. The scatter plots of the PC1 and PC2 from the Jōmon and Yayoi or only Yayoi samples.

and Yayoi people interbred, the scores of the eastern Yayoi population should be higher though they are not. The present results are not consistent with the previous studies, suggesting that the Jōmon and Yayoi population interbred based on human skeletal remains both with the Jōmon and the Yayoi characteristics (e.g., Hasekōji shūhen iseki hakkutsu chōsadan, 2002; Kobe city board of education, 2003; Matsumura, 2003). DNA analyses of skeletal remains from the Aoyakamijichi site recently argue that the Jōmon and Yayoi people interbred at the site though its degree was not so significant (Kanzawa et al., 2021). The present results possibly support the results though the morphological distances of the Aoyakamijichi people from the Jōmon people suggested by the PC1 do not correspond to the DNA distances from the people of the above research. This discrepancy might be due to a generally admitted fact that the relationships between morphology and genes are not completely straightforward, i.e., interbreeding of the Jōmon and Yayoi people were not possibly reflected to their morphological differences. Recent works suggest that the degree of the interbreeding might depend on the population size (e.g., Watanabe & Ohashi, 2023), which should be taken into account in the future work.

The PC2 showing a relatively gradual geological cline from the northern Kyushu region suggests that if the first immigrants reached the northern Kyushu region, the immigrants moved from the northern Kyushu region to the other regions of the archipelago. It should be noted, however, that the causes of the morphological clines are unclear. The PC1 suggests the possibility that morphological variations of the eastern Yayoi people might not be caused by interbreeding with the Jōmon people. Much archaeological research suggests that inter-regional differences and intra-regional cohesions were higher in the later Yayoi periods (e.g., Masaoka & Matsumoto, 1992; Terasawa & Morioka, 1989), and which possibly influences the geological cline.

Temporal and spatial variations are also found. Skeletal remains from the Aoyakamijichi site and Shinmido shell midden of the late Yayoi period tends to have opposite principal component scores against the sites from the northern Kyushu region. On the other hand, the scores of Chinoshima and Shinjo site of the late Yayoi period are similar to the ones from the northern Kyushu area (see Figure 3).

Evolutionary implications of our findings should be discussed. First, if the Yayoi and the Jōmon people did not frequently interbreed as the present research suggests, it is plausible that the spread of agriculture did not depend solely on cultural diffusion because some of the immigrant population should start to engage in agriculture by themselves at least.

Relatedly, the present results suggest the immigrants might tend to segregate though the segregation did not imply they always came into conflicts. Some studies argue that higher rates of injuries are found on human skeletal remains from western sites of the Yayoi period (especially in the northern Kyushu region) and that population increase (and the lack of land by rice farming) is one of the direct causes (Nakagawa et al., 2021). Although both the indigenous people and the immigrants plausibly faced novel adaptive problems caused by their contact, the problems possibly did not lead to conflicts. This might be due to the fact that their subsistence and living areas were largely different (i.e., hunting and gathering or rice farming).

Second, the inferred diffusion pattern of the Yayoi people is also consistent with cultural diffusions of archaeological remains such as Ongagawa pottery of the early Yayoi period. It has been commonly claimed that the pottery spread with the first immigrants and the techniques of rice farming to the eastern parts of the archipelago in the early Yayoi period because their shapes were relatively uniform though regional differences were larger in the more distant regions from the northern Kyushu region (e.g., Kaneda et al., 2022; Morioka, 2018; Noshita et al., 2022b).

Some limitations of the present study should be discussed. First, as argued in the Introduction, we could not access Yayoi samples from the Kyushu and Sanin regions owned by a few institutions, which makes our samples from these regions seemingly limited. Actually, some previous studies have pointed out that regional differences among the northern, eastern-northern, and southern Kyushu regions are found (e.g., Matsushita & Naito, 1989; Naito, 1981), which could not be discussed in the present research. However, it is plausible that this does not significantly influence the results. The main aim of the present research is to examine the diffusion pattern from the northern Kyushu regions. Our samples still include ones from some representative sites from the above areas, and it is generally argued that samples from the areas are not significantly variable.

Second, the present study did not divide the Yayoi sample into more detailed subperiods of the Yayoi period, i.e., early, middle, and late periods, and the areas and subperiods of samples are rather biased. As argued above, for instance, we could not ignore the temporal or regional differences shown by site of the late periods in the present study and some previous studies (e.g., Matsushita & Naito, 1989). Thus, we admit that the present results refer only to the overall demic patterns in the whole Yayoi period with a relatively lower resolution. It should be noted that since conditions of human skeletal remains in the eastern parts of the Yayoi period are much worse than the western parts, finer results need future excavations with much more samples.

Third, other parts of human skeletal remains than crania and other kinds of archaeological remains should be integratedly examined and compared for investigating their adaptive transitions. Even though the immigrants and the indigenous people did not frequently interbreed but also not engage in conflicts, it remains unclear how they adapted to their novel meeting. For instance, how did the indigenous people change their subsistent strategy? And how adaptive or non-adaptive changes were they (e.g., Kennett & Winterhalder, 2006)? More various aspects on the diffusion of the Yayoi period should be explored in the future works.

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Author contribution

All designed the research. HN, TN, and TK gathered the 3D data. HN and TK analyzed the data and HN wrote the original draft. All edited it and approved the final manuscript.

Ethical statement

Data gathering and using the data were properly permitted by each institution (see the supplementary data S1 for the details of the institution). The details and the numbering of the permission depend on the institution.

Supplementary material

Electric supplementary materials are available online.

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