

## Article

# Macro-Scale Population Patterns in the Kofun Period of the Japanese Archipelago: Quantitative Analysis of a Larger Sample of Three-Dimensional Data from Ancient Human Crania

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**Abstract:** The present study collected a larger set of three-dimensional data on human crania from the Kofun period (as well as from previous periods, i.e., the Jomon and Yayoi periods) in the Japanese archipelago (AD 250 to around 700) than previous studies. Three-dimensional geometric morphometrics were employed to investigate human migration patterns in finer-grained phases. These results are consistent with those of previous studies, although some new patterns were discovered. These patterns were interpreted in terms of demic diffusion, archaeological findings, and historical evidence. In particular, the present results suggest the presence of a gradual geological cline throughout the Kofun period, although the middle period did not display such a cline. This discrepancy might reflect social changes in the middle Kofun period, such as the construction of keyhole-shaped mounds in the peripheral regions. The present study implies that a broader investigation with a larger sample of human crania is essential to elucidating macro-level cultural evolutionary processes.

**Keywords:** human skeletal remains; Japanese archaeology; Kofun; 3D data; geometric morphometrics

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## 1. Introduction

Humans are incredibly adaptable and versatile. Various theories have emphasized human plasticity in behavior, cognition, and learning abilities [1–3]. Morphologies can also respond to diverse environments and can be modified during ontogeny, resulting in individual differences despite having the same genetic background. Despite these considerations, it has been argued that physical traits provide insight into biological trajectories to a certain extent [4–8]. Furthermore, morphometric research offers unique advantages compared to DNA studies: it is easier to obtain larger and less biased samples, especially in the context of Japanese prehistory. Therefore, anthropologists continue to investigate human morphological traits to glean clues regarding human evolutionary pathways [4–12].

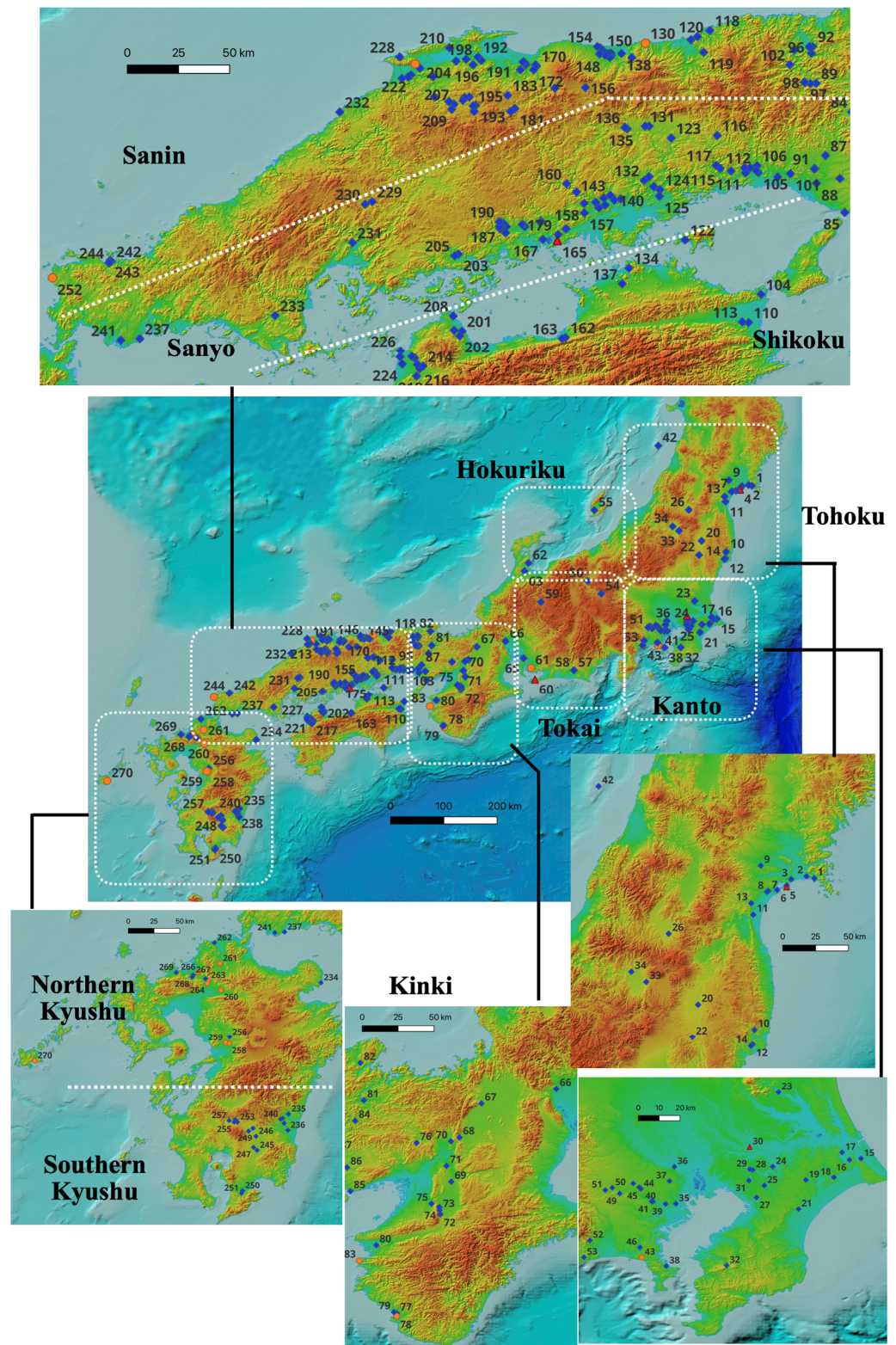
The present research relies on a significantly larger sample of three-dimensional (3D) data from ancient human crania in the Kofun period of the Japanese archipelago to infer human macro-scale population patterns than previous relevant research. While the collection of 3D data is becoming increasingly popular in various disciplines, smaller samples have often been employed in biological anthropology owing to technological

challenges (i.e., time, effort, and costs associated with obtaining precise 3D data reconstruction) [5,7]. Three-dimensional models offer richer information than traditional 2D data, although adequate information for estimating macro-scale patterns may not be obtained from restricted samples. Furthermore, 3D models are gaining traction in many disciplines, including biology, archaeology, and anthropology, while quantitative analyses remain relatively rare, primarily because of limited sample sizes.

The Kofun period, the focus of this research, represents a state formation or early state period that followed the Yayoi period (800 BC–AD 250) [13,14]. Archaeological and anthropological evidence suggests that during the Yayoi period, agriculture spread across the Japanese archipelago, social hierarchies became clearer than in the Jomon period (13,000 BC–800 BC), and warfare began [15–17]. In the subsequent Kofun period, social hierarchies were further strengthened, and a central political organization was established, particularly around the Kinki region (Figure 1), resulting in increased stability within Japan [13,14]. In the early phase (mid AD 250–375), larger Kofuns, typically the zenpou-kouen fun or keyhole-shaped mounds, were mainly constructed around the Kinki region. Subsequently, in the middle phase (375–500), larger Kofuns were also built in peripheral regions, including the Sanyo, Kyushu, Kanto, and Tohoku regions. In the late phase (500–600) and the final phase (after 600 to around 700), a few large keyhole-shaped mounds were observed. Instead, clustered circle or square mounds, as well as tunnel tombs, were constructed in many regions. Given their sizes and the presence of richer grave goods, many agree that these larger mounds served as burials for individuals of power during that period [13,14,18]. This Kofun period is of significant importance in unraveling the processes through which states and civilizations were established in the ancient Japanese archipelago.

Previous research compared traditionally measured biodistances from the Kofun period from different regions of the Japanese archipelago to infer regional populational interactions. Possible explanations for the several geographical disparities discovered were examined. For instance, it has been claimed that a geographical cline in the biodistances between Northern Kyushu and eastern areas during the Kofun era may be explained by the migration of people from the Korean peninsula, who then had an impact on people in the Japanese archipelago [19–25].

However, some concerns have persisted. First, earlier studies did not examine finer or more precise time periods, such as early, middle, late, and final. We should investigate cranial differences in finer sub-periods since the Kofun period spanned over 400 years [25]. In this study, the Kofun period was divided into three sub-periods: early, middle, and late (including final). Second, additional archaeological evidence must be coupled with anthropological data to fully understand the underlying cultural evolutionary processes. Although previous studies did not mention spatiotemporal changes in archaeological remains such as pottery or burial patterns and historical records, because such evidence is also critical for inferring and understanding demic and relevant cultural diffusion, synthetic perspectives are required. Third, as previously indicated, when 3D models are employed, the sample sizes are often small. The current study interprets substantially larger samples of anthropological data by referring to archaeological information to estimate the cultural macro-scale evolutionary processes in the Japanese archipelago during the Kofun period.



**Figure 1.** Sites investigated in the present research: Red triangles represent Jomon sites, orange circles represent Yayoi sites, and blue rhombi represent Kofun sites. See the below table for the site name and phase. The map is based on the color altitude map published by the 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).

## 2. Materials and Methods

We collected 3D data on human crania from the Kofun period, spanning the Tohoku to Southern Kyushu regions (Figure 1 and Table 1). The total number of samples was 693, including individuals over fifteen years old because it is more difficult to estimate sexes under fifteen-year-old individuals [26,27]: 264 females, 421 males, and 8 of unknown sex (Table 2). This dataset also incorporates samples from the previous Jomon period (14,000 BC to 800 BC) and the Yayoi period. The inclusion of samples from the Jomon and Yayoi periods allowed for the investigation of continuous or discontinuous changes from these earlier periods (see Table 1 and Supplementary Table S1 for more detailed information). Notably, samples from the Northern Kyushu region are relatively limited because certain institutions do not grant permission to examine crania. However, the samples collected in this study were sufficient to achieve the intended objectives. It is important to note that the samples from the Kofun period were generally excavated from various types of kofuns (with the exception of samples from the Nashikibata site in the Tohoku region), suggesting that they likely held relatively higher social ranks.

**Table 1.** Summary of archaeological sites used in this study.

ID	Site	Phase	Area	ID	Site	Phase	Area
1	Nashikibata	Kofun	01. Tohoku	136	Ashidaguchi	Kofun	06. Sanyo
2	Goshozan	Kofun	01. Tohoku	137	Yamadayama	Kofun	08. Shikoku
3	Yamoto	Kofun	01. Tohoku	138	Monden	Kofun	07. Sanin
4	Enohama	Kofun	01. Tohoku	139	Iimoriyama	Kofun	06. Sanyo
5	Satohama	Jomon	01. Tohoku	140	Sakotadozan	Kofun	06. Sanyo
6	Shimizu	Kofun	01. Tohoku	141	Natsudani	Kofun	07. Sanin
7	Ichikawabashi	Kofun	01. Tohoku	142	Yonesato	Kofun	07. Sanin
8	Sanno	Kofun	01. Tohoku	143	Minamisaka	Kofun	06. Sanyo
9	Yamahara	Kofun	01. Tohoku	144	Nakamine	Kofun	07. Sanin
10	Kosaruda	Kofun	01. Tohoku	145	Sawaberi	Kofun	07. Sanin
11	Niki	Kofun	01. Tohoku	146	Ohazama	Kofun	07. Sanin
12	Chiyozuru	Kofun	01. Tohoku	147	Ezaki	Kofun	06. Sanyo
13	Kumanodo	Kofun	01. Tohoku	148	Ikisu	Kofun	07. Sanin
14	Ryugasaki	Kofun	01. Tohoku	149	Kume	Kofun	06. Sanyo
15	Bari	Kofun	02. Kanto	150	Seto	Kofun	07. Sanin
16	Atamadaikita	Kofun	02. Kanto	151	Yura	Kofun	07. Sanin
17	Joyama	Kofun	02. Kanto	152	Damichihigashi	Kofun	07. Sanin
18	Kijinodai	Kofun	02. Kanto	153	Tonoyama	Kofun	06. Sanyo
19	Yamada	Kofun	02. Kanto	154	Tsumanami	Kofun	07. Sanin
20	Shojiki	Kofun	01. Tohoku	155	Sademon	Kofun	06. Sanyo
21	Shinjuku	Kofun	02. Kanto	156	Ienoue	Kofun	06. Sanyo
22	Fukaado	Kofun	01. Tohoku	157	Mabi	Kofun	06. Sanyo
23	Ukabubo	Kofun	02. Kanto	158	Kariya	Kofun	06. Sanyo
24	Tattadai	Kofun	02. Kanto	159	Wakamizuyama	Kofun	06. Sanyo
25	Monoi	Kofun	02. Kanto	160	Akabane	Kofun	06. Sanyo
26	Tozukayama	Kofun	01. Tohoku	161	Ishii	Kofun	06. Sanyo
27	Kusakari	Kofun	02. Kanto	162	Kyogaoka	Kofun	08. Shikoku
28	Kanoshibayama	Kofun	02. Kanto	163	Yokochiyama	Yayoi	08. Shikoku
29	Hiradodai	Kofun	02. Kanto	164	Motomura	Kofun	06. Sanyo
30	Nakazuma	Jomon	02. Kanto	165	Tsukumo	Jomon	06. Sanyo
31	Sekibadai	Kofun	02. Kanto	166	Kitadanihina	Kofun	07. Sanin
32	Ichijuku	Kofun	02. Kanto	167	Mobirahachiman	Kofun	06. Sanyo

33	Komasakanitta	Kofun	01. Tohoku	168	Kitsunedani	Kofun	06. Sanyo
34	Haizuka	Kofun	01. Tohoku	169	Sekitoyama	Kofun	06. Sanyo
35	Sannnoyokoana	Kofun	02. Kanto	170	Sekishufu	Kofun	07. Sanin
36	Akabanedai	Kofun	02. Kanto	171	Kusaka	Kofun	07. Sanin
37	Higashinakano	Kofun	02. Kanto	172	Koshikiyama	Kofun	07. Sanin
38	Takayama	Kofun	02. Kanto	173	Unknown	Kofun	07. Sanin
39	Dorinoko	Kofun	02. Kanto	174	Miyahata	Kofun	07. Sanin
40	Enpukuji	Kofun	02. Kanto	175	Kameyama	Kofun	06. Sanyo
41	Shimosakunobe	Kofun	02. Kanto	176	Higashimunakata	Kofun	07. Sanin
42	Tekiana	Kofun	01. Tohoku	177	Fukikoshi	Kofun	06. Sanyo
43	Hasebekoji	Yayoi	02. Kanto	178	Ozakoyama	Kofun	07. Sanin
44	Hanezawadai	Kofun	02. Kanto	179	Ishizuchiyama	Kofun	07. Sanin
45	Osawa	Kofun	02. Kanto	180	Kasugayama	Kofun	07. Sanin
46	Takigakubo	Kofun	02. Kanto	181	Uchinokurayama	Kofun	07. Sanin
47	Deyama	Kofun	02. Kanto	182	Maruyama	Kofun	07. Sanin
48	Maehara	Kofun	02. Kanto	183	Inga	Kofun	07. Sanin
49	Nakawada	Kofun	02. Kanto	184	Kamejuyama	Kofun	06. Sanyo
50	Sakanishi	Kofun	02. Kanto	185	Aruji	Kofun	06. Sanyo
51	Yamane_owada	Kofun	02. Kanto	186	Yamanokami	Kofun	06. Sanyo
52	Shimoozaki	Kofun	02. Kanto	187	Shiroyama	Kofun	06. Sanyo
53	Azumamura	Kofun	02. Kanto	188	Terayama	Kofun	06. Sanyo
54	Karamatsu	Kofun	04. Tokai	189	Chihara	Kofun	06. Sanyo
55	Keramaki	Kofun	03. Hokuriku	190	Otateyama	Kofun	06. Sanyo
56	Yotsuya	Kofun	04. Tokai	191	Shimadaike	Kofun	07. Sanin
57	Tennogaya	Kofun	04. Tokai	192	Matoba	Kofun	07. Sanin
58	Uto	Kofun	04. Tokai	193	Koikeoku	Kofun	07. Sanin
59	Hinokiyama	Kofun	04. Tokai	194	Takinotanijiri	Kofun	07. Sanin
60	Ikawazu	Jomon	04. Tokai	195	Miyanotawa	Kofun	07. Sanin
61	Shinmido	Yayoi	04. Tokai	196	Iwayaguchi	Kofun	07. Sanin
62	Wakikata	Kofun	03. Hokuriku	197	Kamibunnakayama	Kofun	07. Sanin
63	Zugawajogahira	Kofun	03. Hokuriku	198	Fukurojiri	Kofun	07. Sanin
64	Kodo	Kofun	03. Hokuriku	199	Genzobo	Kofun	07. Sanin
65	Otakamachi	Kofun	04. Tokai	200	Kofuke	Kofun	07. Sanin
66	Hanaokayama	Kofun	04. Tokai	201	Ninotani	Kofun	08. Shikoku
67	Uchioroshi	Kofun	05. Kinki	202	Noda	Kofun	08. Shikoku
68	Usayama	Kofun	05. Kinki	203	Kaimochiyama	Kofun	06. Sanyo
69	Maezuka	Kofun	05. Kinki	204	Iwaya	Kofun	07. Sanin
70	Higashiyamashogunzuka	Kofun	05. Kinki	205	Mitachi	Kofun	06. Sanyo
71	Horikiri	Kofun	05. Kinki	206	Nishimineue	Kofun	08. Shikoku
72	Taishoike	Kofun	05. Kinki	207	Nitachugakko	Kofun	07. Sanin
73	Teraguchi	Kofun	05. Kinki	208	Ainotani	Kofun	08. Shikoku
74	Chayama	Kofun	05. Kinki	209	Kawakohara	Kofun	07. Sanin
75	Kannonzuka	Kofun	05. Kinki	210	Fudenoo	Kofun	07. Sanin
76	Houki	Kofun	05. Kinki	211	Bikunibara	Kofun	07. Sanin
77	Isoma	Kofun	05. Kinki	212	Koujiroshimosako	Kofun	07. Sanin
78	Shinjo	Yayoi	05. Kinki	213	Sawahira	Kofun	07. Sanin
79	Tachido	Kofun	05. Kinki	214	Taninouchi	Kofun	08. Shikoku
80	Ibemaeyama	Kofun	05. Kinki	215	Hirano	Kofun	07. Sanin
81	Inabayama	Kofun	05. Kinki	216	Tanchiyama	Kofun	08. Shikoku

82	Hidarisaka	Kofun	05. Kinki	217	Hatadera	Kofun	08. Shikoku
83	Chinoshima	Yayoi	05. Kinki	218	Dondabara	Kofun	08. Shikoku
84	Takiyama	Kofun	06. Sanyo	219	Aoki	Yayoi	07. Sanin
85	Maikohama	Kofun	06. Sanyo	220	Setokazetoge	Kofun	08. Shikoku
86	Yoroki	Kofun	06. Sanyo	221	Yoshifuji	Kofun	08. Shikoku
87	Toitsume	Kofun	06. Sanyo	222	Egedani	Kofun	07. Sanin
88	Saijo	Kofun	06. Sanyo	223	Koshiinoue	Kofun	07. Sanin
89	Kakitsubo	Kofun	06. Sanyo	224	Tsudayama	Kofun	08. Shikoku
90	Horiyama	Kofun	06. Sanyo	225	Asagara	Kofun	07. Sanin
91	Shuhenjiyama	Kofun	06. Sanyo	226	Wakesakanami	Kofun	08. Shikoku
92	Kayaga	Kofun	07. Sanin	227	Omaruyama	Kofun	08. Shikoku
93	Hanayama	Kofun	07. Sanin	228	Inome	Kofun	07. Sanin
94	Tsuboi	Kofun	07. Sanin	229	Ujigamishoda	Kofun	06. Sanyo
95	Tsutsue	Kofun	07. Sanin	230	Jogadani	Kofun	06. Sanyo
96	Tadachi	Kofun	07. Sanin	231	Bishamondai	Yayoi	06. Sanyo
97	Umeda	Kofun	07. Sanin	232	Nimasakanada	Kofun	07. Sanin
98	Mukaiyama	Kofun	07. Sanin	233	Ikadayama	Kofun	06. Sanyo
99	Muraiyama	Kofun	07. Sanin	234	Akimachi	Kofun	09. N_Kyushu
100	Haneyama	Kofun	07. Sanin	235	Sakamotonoue	Kofun	10. S_Kyushu
101	Komaruyama	Kofun	07. Sanin	236	Atoe	Kofun	10. S_Kyushu
102	Nishiinoue	Kofun	07. Sanin	237	Osuga	Kofun	06. Sanyo
103	Himeji	Kofun	06. Sanyo	238	Rokunohara	Kofun	10. S_Kyushu
104	Takeshimaontakejinja	Kofun	08. Shikoku	239	Joshinbaru	Kofun	10. S_Kyushu
105	Toboyama	Kofun	06. Sanyo	240	Motochibaru	Kofun	10. S_Kyushu
106	Tenkojiyama	Kofun	06. Sanyo	241	Ozaki	Kofun	06. Sanyo
107	Myojinyama	Kofun	06. Sanyo	242	Sainoki	Kofun	07. Sanin
108	Shirasagiyama	Kofun	06. Sanyo	243	Sukumozuka	Kofun	07. Sanin
109	TasunoTaiikukan	Kofun	06. Sanyo	244	Morigasuwa	Kofun	07. Sanin
110	Egeyama	Kofun	08. Shikoku	245	Shimokawahigashimakinobaru	Kofun	10. S_Kyushu
111	Tossaka	Kofun	06. Sanyo	246	Dera	Kofun	10. S_Kyushu
112	Shinguhigashiyama	Kofun	06. Sanyo	247	Kashino	Kofun	10. S_Kyushu
113	Sekkuyama	Kofun	08. Shikoku	248	Ohagi	Kofun	10. S_Kyushu
114	Shimodanishiyama	Kofun	06. Sanyo	249	Asahidai	Kofun	10. S_Kyushu
115	Nishinoyama	Kofun	06. Sanyo	250	Kitaushiroda	Kofun	10. S_Kyushu
116	Yokosakakyuryo	Kofun	06. Sanyo	251	Nakao	Kofun	10. S_Kyushu
117	Maruo	Kofun	06. Sanyo	252	Doigahama	Yayoi	07. Sanin
118	Uratomi	Kofun	07. Sanin	253	Ebino	Kofun	10. S_Kyushu
119	Itodani	Kofun	07. Sanin	254	Hirohata	Kofun	10. S_Kyushu
120	Midoriyama	Kofun	07. Sanin	255	Hisamizako	Kofun	10. S_Kyushu
121	Kaichidani	Kofun	07. Sanin	256	Toyookamiyamoto	Kofun	09. N_Kyushu
122	Takatsubo	Kofun	08. Shikoku	257	Shimauchi	Kofun	10. S_Kyushu
123	Ochiyama	Kofun	06. Sanyo	258	Nagamine	Yayoi	09. N_Kyushu
124	Katayama	Kofun	06. Sanyo	259	Annomae	Yayoi	09. N_Kyushu
125	Kitayama	Kofun	06. Sanyo	260	Daifukumura	Yayoi	09. N_Kyushu
126	Nakajima	Kofun	06. Sanyo	261	Tateiwa	Yayoi	09. N_Kyushu
127	Numa	Kofun	06. Sanyo	262	Minaminomae	Kofun	09. N_Kyushu
128	Nishikarube	Kofun	06. Sanyo	263	Yamaemura	Yayoi	09. N_Kyushu
129	Tagajinja	Kofun	06. Sanyo	264	Kuma-Nishioda	Yayoi	09. N_Kyushu
130	Aoyakamijichi	Yayoi	07. Sanin	265	Yunoki	Kofun	09. N_Kyushu

131	Gedoyamaminami	Kofun	06. Sanyo	266	Kanenokuma	Yayoi	09. N_Kyushu
132	Sasai	Kofun	06. Sanyo	267	Unaijaku	Kofun	09. N_Kyushu
133	Bessho	Kofun	07. Sanin	268	Katanawa	Kofun	09. N_Kyushu
134	Matsuyama	Kofun	08. Shikoku	269	Senri-okubo	Kofun	09. N_Kyushu
135	Kumesannari	Kofun	06. Sanyo	270	Ohama	Yayoi	09. N_Kyushu

**Table 2.** The number of the samples.

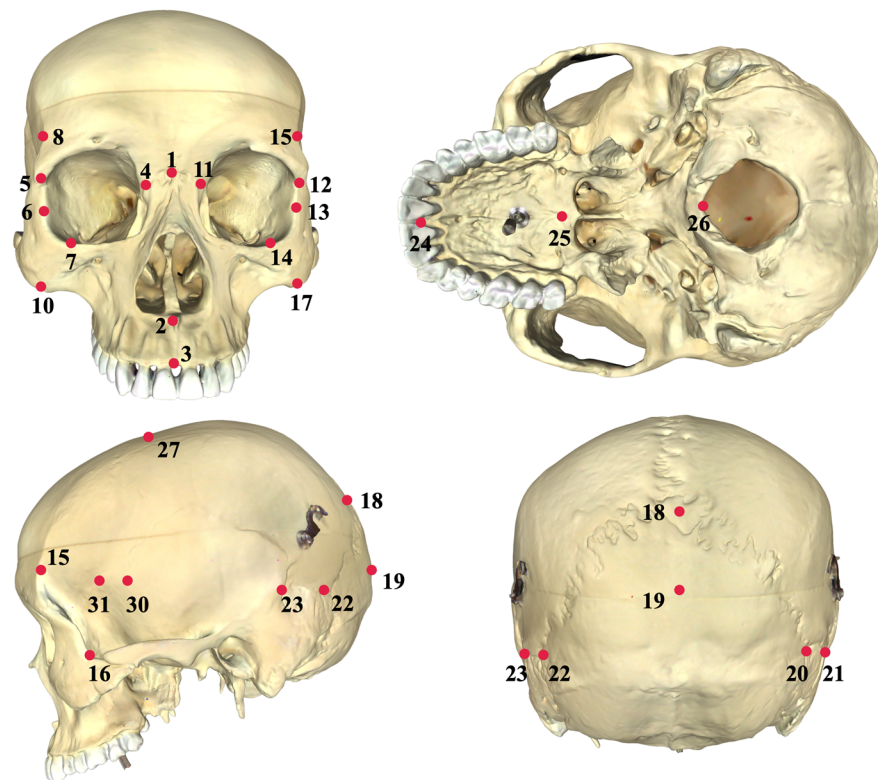
Phase/Sample Sizes	Female	Male	Unknown	Total
Jomon	33	49		82
Yayoi	25	55	1	81
Early Kofun	26	33	1	60
Middle Kofun	59	91	2	152
Late Kofun	120	186	4	310
Unknown Kofun	1	7		8
Total	264	421	8	693

Three types of laser scanners (i.e., AMETEK Creaform HandySCAN BLACK, HandySCAN BLACK™ | Elite (PA, USA), and Shining 3D Einscan Pro HD (Zhejiang, China)) and SfM/MVS, based on two-dimensional photos, were used to collect 3D data. Previous research has confirmed that 3D models reconstructed using these methods do not exhibit significant differences and maintain fidelity to the original crania [28–30]. Given that the original 3D models consist of numerous meshes, making subsequent analyses challenging, we reduced the number of meshes to 1% to 10% of the original using Meshlab [31]. The reduction rates were determined based on the original mesh sizes, which varied depending on the method used. Additionally, it has been demonstrated that the reduced models generated using Meshlab remain highly similar to the original ones [32].

Landmark-based geometric morphometrics (GM) and principal component analysis (PCA) were used to examine the reduced 3D models. For the analysis, we used R (version 4.2.1) and R studio (2022.07.0 + 548) as well as the geomorph package (version 4.0.4) in R [33–35]. Representative and/or less confusing thirty-one points were selected as landmarks from the traditional craniometric points [36], and were located on the 3D models (see Figure 2 and Table 3 for the selected landmarks). The geometric configurations of the landmarks were analyzed using GM and PCA.

**Table 3.** The selected Landmarks. 9, 28, and 29 are not depicted in Figure 2.

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



**Figure 2.** Landmark locations. The 3D model is based on the SH-7 model by KYOTO KAGAKU. The numbers correspond to those in Table 3.

PCA was used to examine the geometric arrangement of the identified landmarks. We attempted to compensate for missing parts in the 3D models by inverting the reserved parts along the median line via the nasion, prosthion, and bregma, following previous relevant research [29,37,38]. If missing pieces could not be rebuilt using the methods described above, we used the geomorph package's estimate.missing function, based on the thin-plate-spline method [33].

Sexes and ages of samples are mainly based on published excavation reports. When no information was given, we determined them by examining the pelvis and crania (including post-cranial features and sizes of the zygomatic arch and mastoid process) for sexes [39], the facies symphysialis [40], and the cranial suture for ages [41,42] because they are standard ways of estimating the sexes and ages of the Japanese human skeletal remains [27].

We analyzed the 3D data in two main steps. In Study 1, 3D data encompassing the Jomon to Kofun periods were included to investigate diachronic morphological changes during the prehistoric and ancient periods in Japan. In Study 2, we specifically examined the 3D data using the Yayoi and Kofun periods (see Supplementary Table S2 for the details), narrowing our focus to the spatiotemporal morphological changes observed during the Kofun period.

### 3. Results

#### 3.1. Study 1

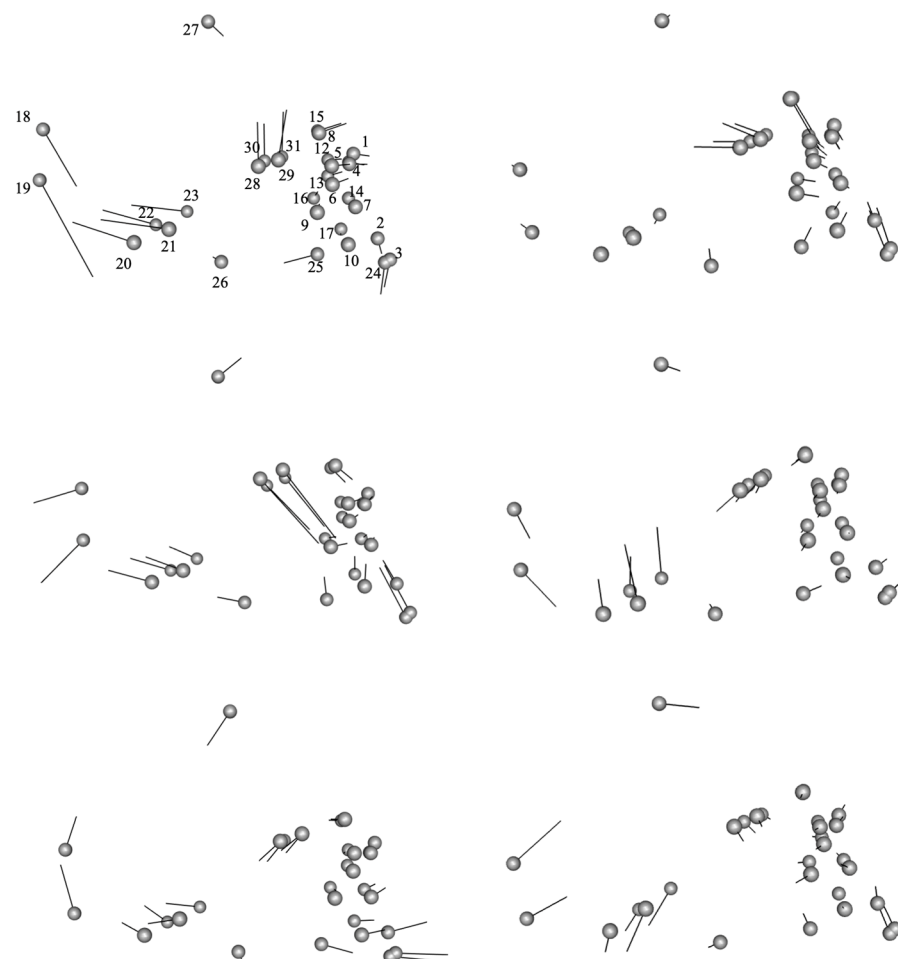
The results of the PCA showed that the cumulative contribution rates exceeded 75% by the Principal Component (PC) 20 (Table 4). To conserve space, we focused on PCs 1–6 that accounted for >5% each. PC1 was primarily related to vertical facial and occipital height, temporal length, and width. PC2 encompasses facial oblique height and width, occipital height, and length. PC3 primarily correlates with the anterior–posterior position of the teeth and occipital height, while PC4 is related to facial oblique height. PC5 was



mainly related to occipital height, while PC6 was linked to facial width and occipital length (Figure 3). Notably, individuals in the Jomon period tended to have wider and lower faces and longer occipital and temporal regions.

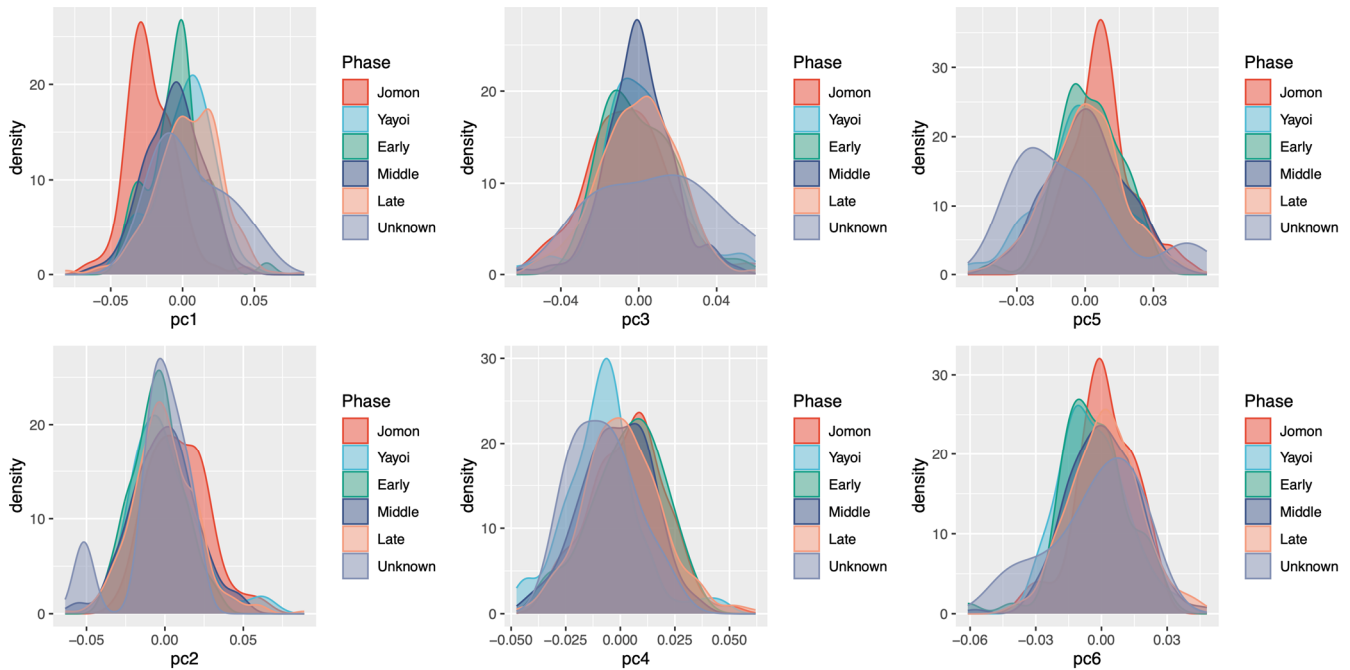
**Table 4.** Contribution rates of the PCA results in each Study.

<i>Study 1</i>	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Contribution rate	11%	9%	8%	6%	6%	5%	3%	3%	3%	2%
Cumulative contribution rate	11%	19%	27%	34%	40%	45%	48%	51%	54%	57%
PCs	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19	PC20
Contribution rate	2%	2%	2%	2%	2%	2%	2%	2%	2%	1%
Cumulative contribution rate	59%	62%	64%	66%	68%	70%	71%	73%	74%	76%
<i>Study 2</i>	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Contribution rate	10%	9%	8%	6%	6%	5%	4%	3%	3%	3%
Cumulative contribution rate	10%	19%	27%	33%	39%	44%	48%	51%	55%	57%
PCs	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19	
Contribution rate	2%	2%	2%	2%	2%	2%	2%	2%	1%	
Cumulative contribution rate	59%	62%	64%	66%	68%	70%	72%	73%	75%	



**Figure 3.** Configurational changes in landmarks captured by each PC in Study 1. From top to bottom: PC1 to PC3 in the left column, and PC 4 to PC6 in the right columns. Each screenshot captures the right side of the crania. The numbers in PC1 correspond to the ones in Table 3. The bars from the points indicate the degree of change according to each PC.

Temporal variations were clearly observed between the Jomon people and the Yayoi or Kofun people in PC1 (Figure 4). Noteworthy, no significant differences between the sexes were observed (Supplementary Figure S1).



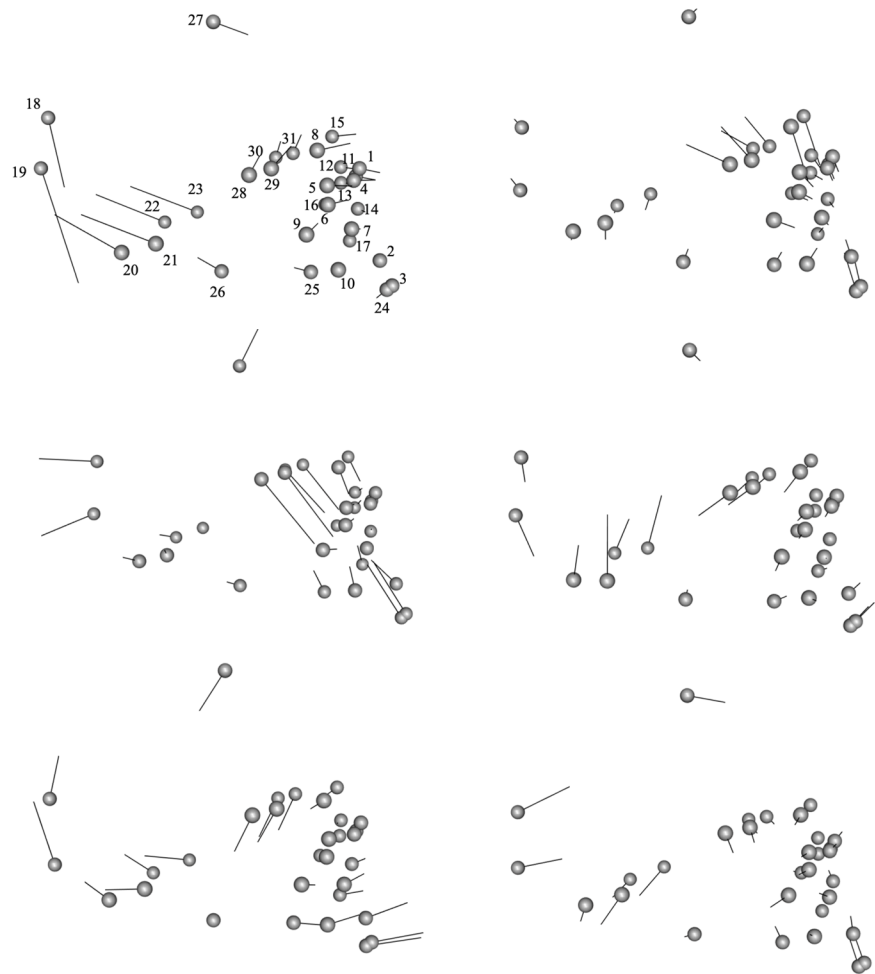
**Figure 4.** The kernel density estimates of PC Scores (temporal variations) in Study 1.

### 3.2. Study 2

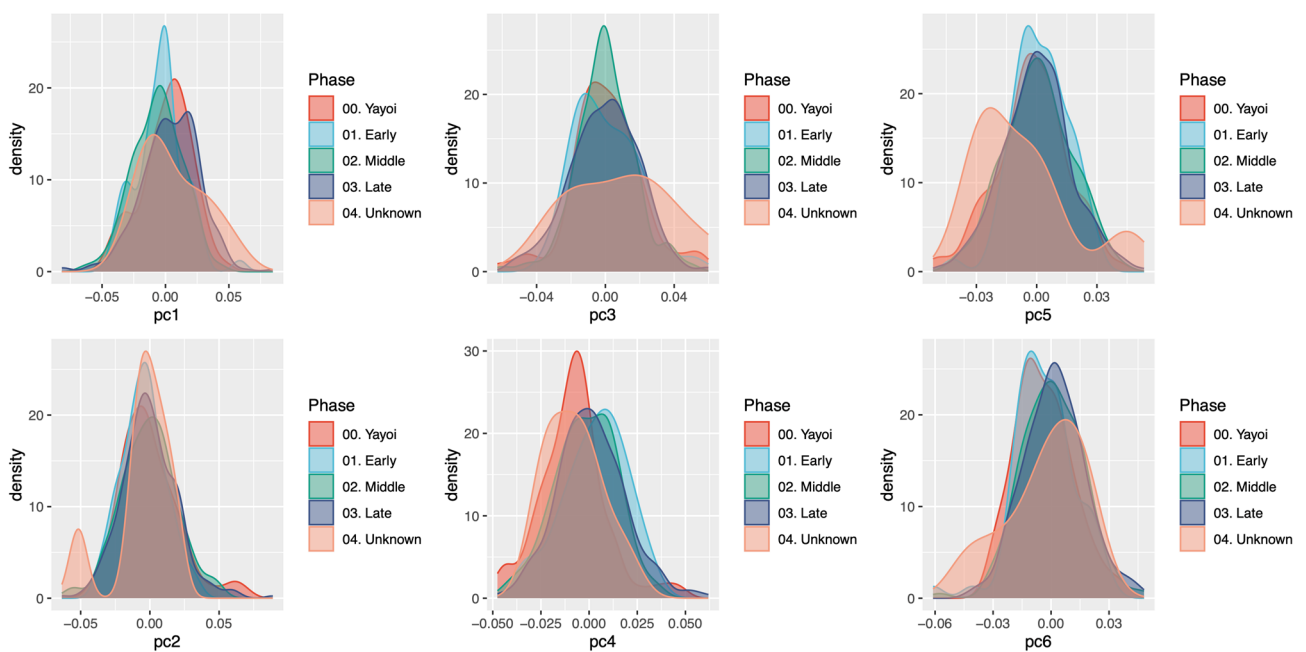
The PCA results revealed that the cumulative contribution rates exceeded 75% by PC 19 (Table 4). For the sake of space, more than 5% of the PCs were also focused on here. PC1 primarily encompasses the occipital width and length and the height of the lambda and opisthokranion. PC2 refers to the facial height and occipital length. The anterior–posterior length is also reflected in PC3, and as PC3 is larger, the foretooth is more anteriorly positioned. PC4 captures facial length and height. When PC5 was larger, the post-cranial parts were lower, and the foretooth was more anteriorly positioned. Finally, PC6 captures the facial width and occipital overall size (Figure 5).

Temporal differences are unclear, although an exception could be PC4, where samples from the Yayoi period are relatively different from those from the Kofun period. Note that we did not find any significant variations among the samples among Kofun subperiods (Figure 6).

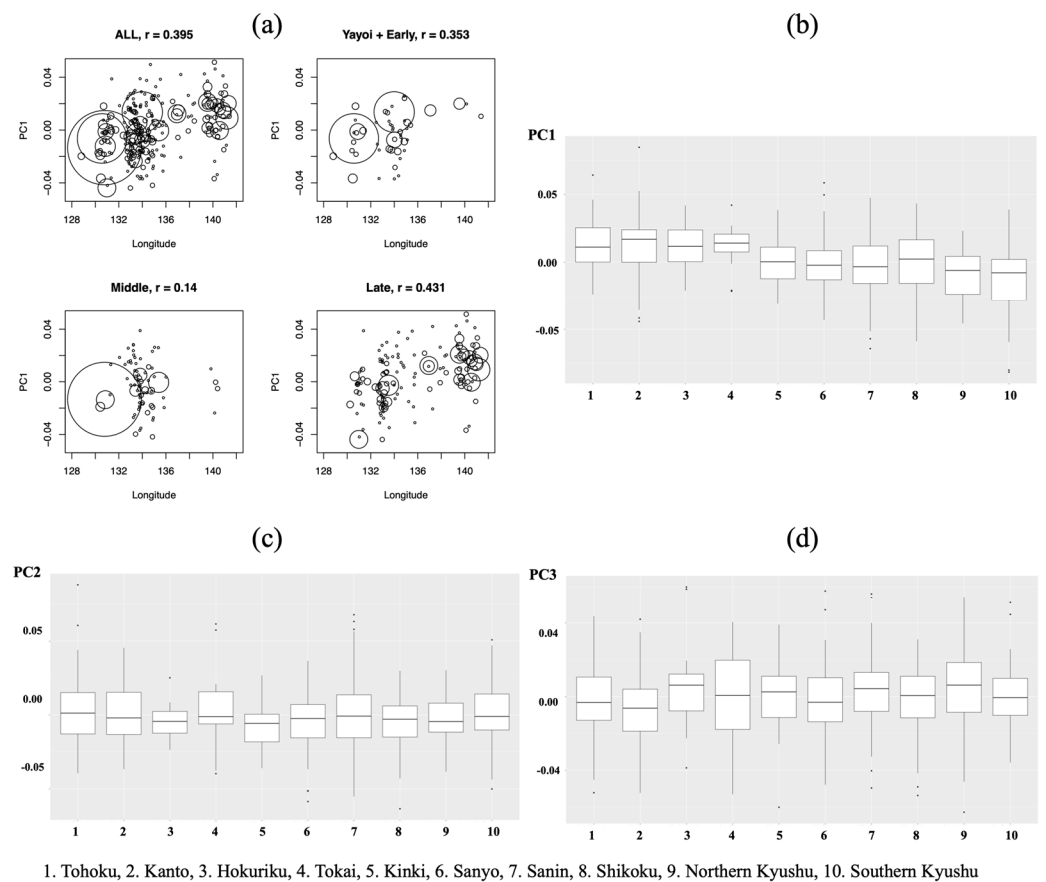
Figure 7 shows the relatively clear spatial variations in PC1 (Figure 7). When all the data from the Yayoi and Kofun periods are plotted, a gradual geographical cline is found in PC1. The cline was found in both sexes (Supplementary Figure S1). The early and late Kofun periods also showed a geographical cline in the PC1, and sexual variations were not found (Supplementary Figure S1), although it is noteworthy that samples in the eastern regions are temporally biased.



**Figure 5.** Configurational changes in landmarks captured by each PC in Study 2. From top to bottom: PC1 to PC3 in the left column, and PC 4 to PC6 in the right columns. The numbers in PC1 correspond to the ones in Table 3.



**Figure 6.** The kernel density estimates of PC Scores (temporal variations) in Study 2.



**Figure 7.** (a) The mean PC1 scores for each site plotted against longitude in the whole, early (including the Yayoi), middle, and late Kofun periods and boxplots of (b) PC1, (c) PC2, and (d) PC3 scores in each region. The size of a circle is proportional to the number of samples at the focal site. The correlation coefficients are calculated between PC1 scores attributed to individuals, not the average scores attributed to sites, and longitude.

#### 4. Discussion

Using 3D data and landmark-based geometric morphometrics, the present study quantified spatio-temporal variation in the morphology of skulls in the Kofun periods with those in the Jomon and Yayoi periods as a reference for comparison. Our study is consistent with previous studies in various aspects. First, the most prominent trend between the eastern and western parts of the Japanese archipelago during the Kofun period was observed in PC1 (Figure 7). PC1 scores were higher in the eastern part (indicating longer occipital length and higher positions of lambda and opisthokranion) than in the western part. This aligns with the traditional claim that individuals in the western regions are more strongly influenced by those who migrated from the Korean peninsula, resulting in a shorter anterior–posterior length [25]. Our results are consistent with this previous observation. Similarly, although samples from the Northern Kyushu region during the Kofun period are limited, their overall distribution patterns fall between those observed in Southern Kyushu and those in more eastern areas [19].

Second, during the middle and late subperiods, the Southern Kyushu region displayed the most negative scores in PC1, indicating the shortest anterior-posterior length. This aligns with the findings of several studies (e.g., [43]). Additionally, many archaeological studies argue that during the middle and late periods, the Southern Kyushu region had relatively unique cultures, as evidenced by unique pottery styles (Narikawa-type pottery) and burial customs (i.e., underground tunnel tombs [44,45]). These distinctive cultural elements are plausibly reflected in or associated with observed patterns in morphological variation.

Third, a previous study suggested that the eastern and western parts of the Sanin region are relatively closer to the Sanyo and Northern Kyushu regions, respectively [22]. The PC1 scores from the late Kofun period support this previous claim, although the pattern was not as clear in other periods (Supplementary Figure S2).

New patterns were also found with evolutionary or archaeologically meaningful implications. First, the results of Study 1 (especially PC1) suggest that the Jomon people were rather different from the Yayoi and Kofun people in the facial height and the anterior–posterior length (Figure 4), which is consistent with the results of Study 2 indicating that temporal differences are not significant among the Yayoi and Kofun periods (Figure 6), with a potential exception of PC4 relevant to face shape. There has been a debate about the ancestry of the Yayoi and Kofun people. A major issue is the relative importance of interbreeding between the Yayoi people and immigrants from continental East Asia. A naïve interpretation of our results is that continuity between the Yayoi and Kofun people existed, although it is still unclear how skull morphology can be influenced by genetic components. However, the ancestry of the Yayoi people is also important in the interpretation. It has been discussed to what extent interbreeding between the Jomon people and immigrants from continental East Asia played a role in the formation of the Yayoi people. A relevant study suggested that the Jomon people and people from continental East Asia might not regularly interbreed [38]. If so, it can be hard to distinguish the contribution of the Yayoi people or immigrants from continental East Asia to the Kofun people. Although the mechanism is still unclear, the large overlap in morphological variation between the Yayoi and Kofun people could be an important step in further research.

Second, we subdivided the entire Kofun period into three sub-periods (i.e., early, including the Yayoi for ensuring adequate samples, middle, and late). The results indicate that similar geological clines were present in the overall, early (including the Yayoi), and late Kofun periods. We examined the correlation between the PC1 and the longitude of each site, which supports the geological cline (early:  $r = 0.3534$ ,  $p < 0.01$ , middle:  $r = 0.1404$ ,  $p = 0.08$ , late:  $r = 0.4309$ ,  $p < 0.01$ ). A comparable geological cline was highlighted in a previous study on the Kofun period [19]. The present study substantiates this finding with 3D models with larger sample sizes than those in previous studies. Notably, the cline was not evident in the middle of the Kofun period. Although this could be due to the few samples in the eastern regions, another interpretation might be possible. The middle period witnessed relatively profound social changes within the Kofun period: although larger keyhole-shaped mounds were constructed mainly in the Kinki region during the early period, they were also built in other regions such as the Sanyo, Tohoku, Kyushu, and Kanto regions in the middle period, when power was relatively decentralized and people likely moved or migrated more extensively [13,46]. These social changes are in line with the outcomes of the present study, suggesting that demic diffusion was broader and more intricate during the middle period.

Third, PC1 and PC2, in particular, exhibited highly similar patterns in the Tokai, Kanto, and Tohoku regions during the late Kofun period. Furthermore, the latter two regions showed significant similarity in PC3 (Figure 7). This similarity strongly suggests that human migrations or interactions were notably more frequent, especially during the late period. This pattern aligns with extensive archaeological research, which argues that specific populations continuously immigrated from the Tokai and Kanto regions to Tohoku based on pottery distribution patterns. Historical writings also support this, suggesting that immigration during the late period was part of national policy [47–49].

Fourth, previous studies have claimed that significant intergroup conflicts did not occur during the Kofun period based on, for example, a smaller number of injured skeletal remains compared with the preceding Yayoi period [13,18]. Our results showed no clear geographical variation in PCs except for PC1 in the Kofun period. This is more plausible to be interpreted as a result of large-scale interaction, including trade and migration, than large-scale warfare or conflicts.

Some limitations and issues need to be acknowledged. First, as previously mentioned, the individuals buried during the Kofun period generally held higher social ranks. Even if the present study could accurately reflect migration patterns in the Kofun period, these patterns might be limited to individuals with higher social standing. It is important to note, however, that the present results align closely with relevant archaeological arguments based on material culture, including pottery inferred to be used by commoners [47–49].

Relatedly, the present study included larger samples than previous studies, although the samples might be spatially and/or temporally biased, especially in the Early Kofun period. Using PCA, in general, groups with small sample sizes tend to be evaluated as variations of groups with large sample sizes. Well-preserved skeletal remains, however, are rarely excavated. Developments both in analytical methods and archaeological understanding of spatiotemporal variation in burial systems are required.

Second, although the present study divided the Kofun period into three subperiods, archaeological remains may offer much finer temporal resolutions, potentially rendering the temporal divisions in the present study insufficient. This temporal challenge can be addressed through radiocarbon dating, necessitating further research.

Third, although physical traits are expected to reflect or be related to their genetic background to some extent, as highlighted in the Introduction, genetic data can provide a precise population history of the Jomon, Yayoi, and Kofun people. However, due to the challenging conditions of studying human skeletal remains in the Japanese archipelago, including acidic soil conditions, it takes time to analyze genomic data at a level of spatial and temporal resolution similar to the present study. Again, it should be noted that our results are consistent with previous genetic studies, suggesting a relatively minor genetic contribution of the Jomon people to the Yayoi people. A recent notable example is the Aoyakamijichi site of the late Yayoi period in Tottori prefecture [38,50].

## 5. Conclusions

The present research employed a considerably large sample of human crania from prehistoric and ancient periods, namely, the Jomon, Yayoi, and Kofun periods, in the Japanese archipelago. The goal was to investigate and interpret physical and demographic patterns, with particular focus on the Kofun period. While the current findings and previous research are in broad agreement, some critical patterns were newly identified and interpreted using various data sources. Although physical patterns should be thoroughly examined in conjunction with other relevant data, the present research shows that a larger sample of 3D data could offer finer results than traditional 2D biodistances and still substantially contribute to understanding human evolutionary pathways.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/humans4020008/s1>. Table S1: Metadata and data analyzed in Study 1; Table S2: Metadata and data analyzed in Study 2; Figure S1: Sexual differences of Study 1 and Study 2; Figure S2: Regional differences in Study 2.

**Author Contributions:** All designed the research. H.N., T.N., K.T. and A.K. gathered the 3D data. H.N. and K.T. analyzed the data, and H.N. wrote the original draft. All authors have read and agreed to the published version of the manuscript.

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**Institutional Review Board Statement:** Ethical approval was not required for the present study according to the local legislation and institutional requirements (i.e., Japanese laws regulating archaeological human remains in Japan). Owners of all samples are described in Supplementary File Table S1.

**Informed Consent Statement:** Informed consent was not required for the present study because this study examined human skeletal remains. The human skeletal remains examined in the study have been checked by local boards, and they do not have verifiable living descendants.

**Data Availability Statement:** The data presented in this study are available on request from the corresponding author due to ethical reasons on human skeletal remains.

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**Conflicts of Interest:** The authors declare no conflicts of interest associated with this manuscript.

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