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Analyzing historic human-suid relationships through dental microwear texture and geometric morphometric analyses of archaeological suid teeth in the Ryukyu Islands

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ABSTRACT

We investigated human-suid interactions to understand how suids could coexist with humans in the Ryukyu Islands, Japan, for centuries despite the limited carrying capacity of each island and their overlapping nutritional needs with humans. We carried out dental microwear texture analysis (DMTA) and geometric morphometric (GMM) analysis on suid remains excavated from different localities on the Ryukyu Islands to determine their feeding patterns. The DMTA results suggested that humans approximately 7000 to 4400 BP probably reared/kept some suids before slaughter. Their "wild" molar shape suggested that they lived in proximity to the wild ecosystem and were probably not part of the domestic stock. Our results showed that suids belonged to a reared population that was captured by hunting for delayed consumption. The emerging picture is that suids were fed leftovers or other by-products of human activities. Thus, we conclude that suids and humans created an interdependent relationship instead of becoming competitors, which enabled them to coexist on the islands.

The DMTA results suggested that the pig husbandry system of the islands varied during the 17th–19th centuries. In the central region of the islands, pigs were fed a much softer diet than natural resources in a floored stall, whereas in the southern region, pigs were allowed to range freely around human settlements. The GMM analysis of the outline shape of the teeth of suids from this period showed that they were morphologically similar to the modern native domestic breed found on the Ryukyu Islands, regardless of geographical setting of each archaeological site. These results suggest that some suids were transported overseas.

1. Introduction

The Ryukyu Islands are located in the southwestern part of the Japanese archipelago. Suids (i.e., wild boar and domestic pigs) first appeared on these islands during the latter part of the Late Pleistocene (ca. 30000 BP), and so were human beings; suids were sparsely represented in faunal assemblages on the islands until the Holocene (Fujita, 2014; Kawamura et al., 2016). Although the origin of the early Pleistocene suids is unclear, modern boar inhabiting the islands show a genetic affinity to boar in Vietnam (Ishiguro et al., 2008).

The subsistence economy on the islands significantly changed around the 12th – 15th century AD, and this change appears to be associated with the beginning of agriculture. It is widely accepted that animal husbandry in the Ryukyu Islands started with the introduction of domestic animals from the East or Southeast Asian communities. Suid remains in archaeological sites before this period have been regarded as remains of wild game procured through hunting, whereas those found after the period have been classified as domestic individuals (e.g., Kaneko, 2003; Takamiya et al., 2016). However, a debate has emerged over the interaction between humans and suids before livestock management practices were introduced in the Ryukyu Islands. Matsui et al. (2005) reported that assemblage of Gushibaru Shellmidden (approximately 4800–1700 BP) contained notably large individuals. They assumed that the individuals as pigs imported from Japanese Mainland. Furthermore, Minagawa et al. (2005) concluded that some of the *Sus* remains found in the Ryukyu Islands may have been imported to the islands from agricultural areas overseas after being raised by humans, because of a substantially low value of $\delta^{13}C$ and high value of $\delta^{15}N$

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observed in the assemblage of Gushibaru site and Nogini Shellmidden B-site (7000–4400 uncal. BP). Takahashi et al. (2012) also detected a high similarity in mt DNA sequence among individuals of Noguni Shellmidden B-site and modern Sus inhabiting East- and Southeast-Asa. They deduced that some of the archaeological *Sus* in the Ryukyu Islands were imported from those areas as a domestic breed.

Although a decrease in body size is the most significant and traditionally accepted change associated with domestication (Rowley-Conwy et al., 2012), size reduction as a domestication syndrome, and therefore, as a marker for early domestication is currently debated. Lord et al. (2019) argued that adaptations to human-modified environments are more essential in animal domestication rather than selective breeding. Furthermore, Harbers et al. (2020) reported that the calcaneus shape of boar will be an effective marker for detecting the changes in behaviors associated with captive rearing. Additionally, it is difficult to use the archaeological remains from the Ryukyu Islands to establish whether body-size reduction occurred during the husbandry process or whether it was an adaptation to the limited carrying capacity of the islands (Foster, 1964). Therefore, here, we focused on two questions 1) whether humans kept the pigs alive before slaughter, and 2) whether suids were traded as merchandise among the islands.

To address the first question, we focused on a dietary reconstructive approach, that is, we determined whether suids relied on artificial resources rather than natural resources. Dental microwear is a micro-level scar left on the tooth enamel surface during mastication. Especially, dental microwear texture analysis (DMTA) has been applied to quantify three-dimensional coordinates of the surface textures through “roughness” parameters (e.g., Ungar et al., 2003; Schulz et al., 2010). Microwear is especially efficient for assessing the diet of suids at the time of slaughter or hunting, because it reflects the diet and foraging behavior of the animal in the few days before death (Teaford and Oyen, 1989a, 1989b), and this helps predict the likely feeding habits of these ancient suids (Ward and Mainland, 1999). Contrary to this finding, Yamada et al. (2018b) reported that the tooth surface textures do not always significantly differ between specimens from modern pigs and those of boar, although the former show rougher surfaces. Therefore, considering the omnivorous diet of suids, the DMTA results are not suitable for a dichotomous distinction between pigs and boars. Instead, the DMTA is useful for detecting whether human beings slaughtered the animals immediately or kept them captive and fed them for some time because the tooth surface textures reflect the physical characteristics of the diet consumed several weeks before slaughter (Grine, 1986).

To investigate whether and how suids were traded among the islands, the phylogenetic relationships between archaeological remains should be clarified. Previous studies involving geometric morphometric (GMM) analysis have suggested that tooth outline shapes of suids can be another indicator of their genetic background (Evin et al., 2015; Yamada et al., 2018a). In other herbivores, phylogenetic affinity, determined based on the mtDNA sequence, coincided well with tooth shape similarity of dental enamel folding (Cuchhi et al., 2017, 2019). Therefore, comparison of morphological similarities between assemblages excavated from geographically distant areas on the islands would enable to evaluate the probability of suid migration to and from overseas. This comparison would also inform the discussion as to whether native domestic breeds were established on each island after the introduction of breeding techniques in the 15th century or before.

Even to date, the pig husbandry system shows a high diversity correlated with multiple factors, such as climate, vegetation, and community culture, making it difficult to trace relationships between humans and pigs by using a single methodology (Price and Hongo, 2019). Cucchi et al. (2016) and Balasse et al. (2019) reported that morphologically distinctive individuals also showed distinctive isotopic ratio values, which suggesting they were fed by humans. Here, we performed the DMTA to investigate the transition of the husbandry system on the Ryukyu Islands and used the GMM analysis to reveal whether the suids had been traded among the Ryukyu Islands.

2. Materials and methods

The Ryukyu Islands are divided into three groups known as the northern, central, and southern Ryukyus by two deep straits, the Tokara and Kerama Gaps. Here, we analyzed 10 archaeological sites from the central (i.e., Okinawa and Ie Islands) and southern Ryukyus (i.e., Miyako, Ishigaki, Iriomote, and Hateruma Islands, see also Fig. 1, Table 1).

2.1. *Central Ryukyus*

The Ara Shellmidden has been estimated approximately 2000 BP (Okinawa Board of Education, 1983), whereas the Gushibaru Shellmidden has been estimated approximately 4800–1700 BP (Okinawa Board of Education, 1997). Both sites are located in the Ie Island, 6 km north of Okinawa Island. The Noguni Shellmidden B site, on the west coast of Okinawa Island, was excavated from 1980 to 1981. The site yielded at least 611 suid mandible remains. The layer bearing the highest number of suids was carbon (^{14}C) dated at 6000 uncal. BP (Kishimoto, 1984). Of these, 17.5% of specimens did not exhibit a full eruption of canines. The body size was estimated to be approximately 10% smaller than that of the modern wild boar currently inhabiting the Ryukyu Islands (Kawashima and Muraoka, 1984).

To study pig husbandry system in the 17th–19th century AD, remains from the Futenma Old Settlement, excavated from 2008 to 2014, and the Wakuta Old Kiln sites, excavated from 1986 to 1987, were analyzed. Pigs were the most abundant species excavated in both sites. Most remains were from animals under 2 years of age, based on the state of eruption of the lower teeth (Kaneko, 1993). Their bones were often broken with cut marks on their surfaces, indicating that they were leftovers from human consumption.

2.2. *Southern ryukyus*

The Pinza-Abu cave site located on Miyako Island, excavated from 1982 to 1984, yielded a large number of mammal fossils (Hasegawa, 1985). Two charcoal samples have been ^{14}C-dated at 25800 and 26800 uncal. BP (Hamada, 1985). Although the suid remains were limited to only a few molars, all of them were larger than those found in the modern wild boar currently inhabiting the Ryukyu Islands (Kawashima et al., 1985; Hayashi, 1985). The Shimotabaru Shellmidden site, located on the Hateruma Island, was ^{14}C-dated at 3500–3700 uncal. BP (Kin, 1986a). The site was excavated from 1983 to 1984 and yielded at least 283 individuals. These included specimens from individuals in the age groups of 0.5–1.5 years (32.4%) and 1.5–2.5 years (52.7%) (Kaneko, 1986).

To study pig husbandry system in the 17th–19th AD, in southern Ryukyus, three sites located on the Miyako Island were investigated; the Uruka-Mutuzuma site, excavated in 1986 (10 fragmental remains of the skull and mandible), the Miyaguni-Motojima site, excavated from 2007 to 2012 (40 fragmental remains of the skull, mandible, and teeth), and the Shinan site, excavated from 2003 to 2003 (751 fragmental remains including 70 teeth). Approximately two-thirds of all domestic mammal specimens excavated from the Shinan site were suid remains (based on the number of identified specimens). Tooth eruption in these specimens suggested that, in most cases, they were slaughtered between 1.5 and 2.5 years of age (Kaneko, 2003). Due to the limited number of samples, the three assemblages were compiled as one group for the GMM analysis.

The Uruka-Mutuzuma site was excavated by Gusukube-Cho Board of Education, whereas the others were excavated by Okinawa Prefectural Board of Education. All specimens in are stored in Okinawa Archaeological Center.

2.3. *Modern comparative specimens (Table 1b)*

For the DMTA, we processed the data of the modern wild and stall-

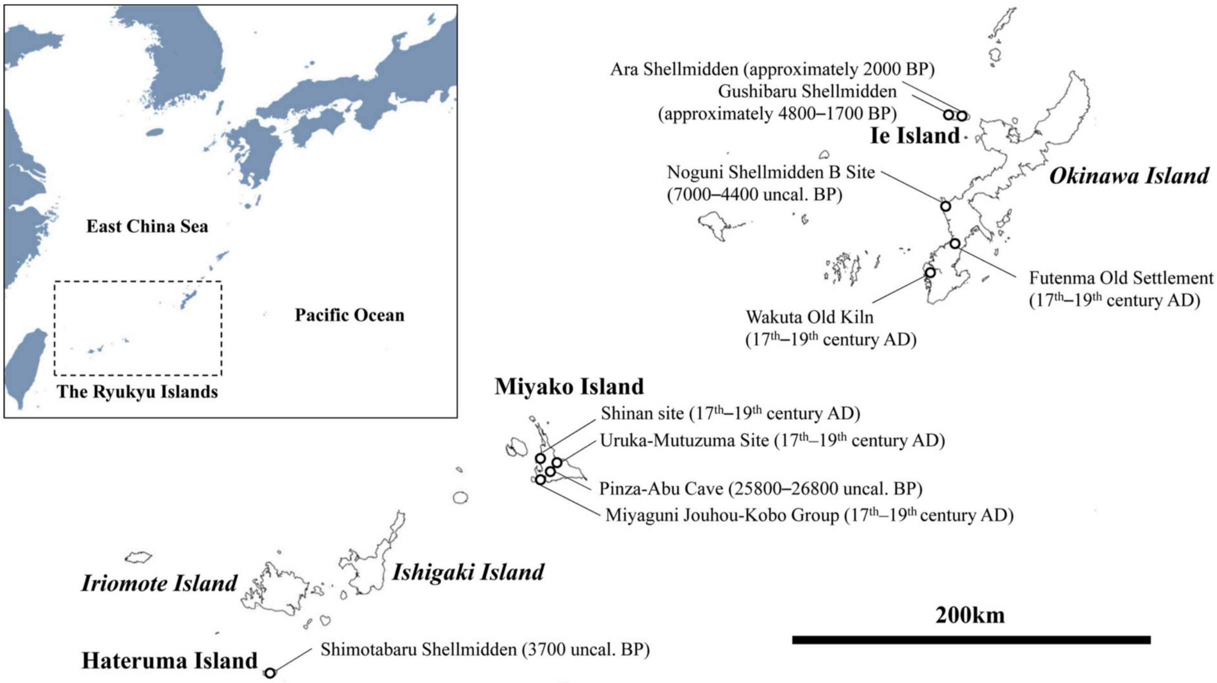

Fig. 1. Geographical and chronological setting of archaeological remains. The island where modern wild boar are distributed is shown in italic typeface.

Table 1
Number of specimens for each analysis.

(a) archaeological remains										
Site	Age	DMTA						GMM		Institution
		M1	M2	M3	M1	M2	M3	dp4	M3	
Futenma Old Settlement	17th–19th century AD	2	3	0	0	0	0	0	0	OPAC
Wakuta Old Kiln	17th–19th century AD	25	7	0	0	0	0	30	0	
Noguni Shellmidden B site	7000–4400 uncal. BP	1	16	16	0	0	0	12	34	
Ara Shellmidden	apploximately 2000 BP	2	10	3	0	0	0	5	9	
Gushibaru Shellmidden	apploximately 4800–1700 BP	4	22	6	0	0	0	29	11	
Shinan Site	17th–19th century AD	6	2	0	0	0	0	4	0	
Miyaguni-Motojima	17th–19th century AD	0	0	0	0	0	0	3	0	
Uruka-Mutuzuma	17th–19th century AD	0	0	0	0	0	0	2	0	
Pinza-Abu Cave	25800–26800 uncal. BP	0	1	2	2	1	1	0	3	
Shimotabaru Shellmidden	3700 uncal. BP	6	10	0	0	0	0	9	4	

(b) modern comparatives						
Locality	Status	GMM		DMTA		Institution
		dp4	m3	m1	m2	
Okinawa Island	wild boar	41	25	0	0	UMUT
Iriomote Island		26	7	6	3	NMNS
Ishigaki Island		27	0	17	6	OPM
Okinawa Island	native pig	5	0	0	0	YPM
Japanese mainland	stall-fed boar	0	0	8	3	DCIFC

M_1: lower first molar, M_2: lower second molar, M_3: lower third molar, M^1: upper first molar, M^2: upper second molar, M^3: upper third molar, dp_4: lower fourth deciduous premolar, OPAC: Okinawa Prefectural Archaeological Center. UMUT: The University Museum, The University of Tokyo, NMNS: National Museum of Nature and Science, Tokyo, OPM: Okinawa Prefectural Museum and Art, YPM: Yamanashi Prefectural Museum, DCIFC: Date City Institute of Funkawan Culture.

fed populations provided by Yamada et al. (2018b). The Ryukyu wild boar, *Sus scrofa riukiuanus*, consume roots, rhizomes, fruits, and nuts throughout the year on Iriomote Island (Ishigaki et al., 2007). However, the stall-fed boar, *S. s. leucomystax*, mainly feed on corn in concrete-floored stalls. The body weights of *S. s. riukiuanus* and *S. s. leucomystax* ranged from 40 to 50 and 50–150 kg, respectively (Abe, 2008). We also used the DMTA to examine a wild population that is hunted in Ishigaki Island.

For the GMM analysis, we used the tooth outline data of modern Ryukyu wild boar hunted in Okinawa, Ishigaki, and Iriomote Islands, presented by Yamada et al. (2018a), along with those of five Okinawa native pig specimens, the Nakijin-Agu pig (Nakijin Agu Farm, Japan). Although the origins of the Agu breed has not been fully understood, it is generally believed that the ancestors of these pigs were introduced to the islands from the Asia in the latter half of the 15th century when the Ryukyu Dynasty began to trade with China. However, they were nearly extinct by the early 20th century. The modern-day Agu pigs have been bred by backcrossing a few surviving individuals. A recent molecular study supports the hypothesis that the ancestors of the Agu pig were introduced from the Asia (Touma et al., 2019).

2.4. Dental microwear texture analysis

Following the data-collection process of Yamada et al. (2018b), the lingual side of the occlusal enamel facets of the lower molars was replicated using high-resolution silicone (Affinis light body, Coltene, Switzerland), and scanned using a confocal laser microscope (VK-9700; Keyence, Japan) with a 100 × objective lens. As an exception, the counterpart surfaces of the upper molars were included for specimens from the Pinza-Abu cave assemblage to increase the number of specimens. The surface data were mirrored in the x- and z-axes, leveled to remove the inclination of the mold, using Mountains Map 7 software (Digital Surf, France). The large-scale curvatures of the mold surface and the non-measured points (slopes angled over 10% of the total variation) were digitally removed. We also deleted the upper and lower spikes as noise peaks (threshold = 0.10% and 99.9%, respectively), and replaced them by the mean of the neighboring points.

After these preparations, the International Organization for Standardization (ISO) 25178 surface roughness parameters were calculated. This study evaluated one of the height parameters, "Sq," which indicates the root mean square height (i.e., the standard deviation of the height distribution) from the averaged plane. The parameter was tested among groups using a pairwise comparison test. The combination of a soft diet and a low amount of soil and dust contamination during foraging leads to a high frequency of tooth-to-tooth contact wear. This creates rough textures on the tooth enamel surface (Schulz et al., 2013). The rough surfaces show a high elevated texture, which results in a high value of the Sq parameter, indicating the standard deviation of height distribution (Schulz et al., 2013). The Sq value of suids fed soft diets would be high, whereas those consuming natural resources by rooting would show low values (Yamada et al., 2018b).

2.5. Geometric morphometric analysis

Following the procedure by Yamada et al. (2018a), modified after Evin et al., (2013), the occlusal views of the lower deciduous fourth premolar and third molar were photographed using a Reflex Camera (Nikon D7100, Sigma 50 mm F/2.8 Micro). The first and second landmarks are the constricted points at the mesio-buccal and mesio-lingual sides, respectively. Whereas, the third and fourth landmarks are the points at the dist-lingual and dist-buccal sides, respectively (Fig. 2). Semi-landmarks were set on the outline between the landmarks, which were the most abundant around the dental socket using tpsDig2 ver. 2.17 software (Rohlf, 2013). The landmark coordinates of each tooth were then digitally superimposed using the generalized Procrustes analysis (GPA) (Perez et al., 2006; Zelditch et al., 2012). We used tpsRelw ver. 1.54 (Rohlf, 2014) for performing sliding semi-landmark, whereas Morpho J ver. 1.06 (Klingenberg 2011) was used for performing the GPA.

The difference in the centroid size between groups was tested using the analysis of variance (ANOVA) with a pairwise comparison test and visualized using a box plot. Pearson's product-moment correlation between the centroid size and common allometric component (CAC; Mitteroecker et al., 2004) was also tested. The shape differences were tested using Procrustes ANOVA and visualized using a between-group principal component analysis (bg PCA). To avoid spurious results induced by the high dimensionality of the shape parameters compared with the number of observation (Mitteroecker and Bookstein, 2011), we performed a PCA and used only the PC scores explaining 99% of the total variance as variables in a bg PCA. All the statistical analyses were performed using R. ver. 4.0.3. (R Core Team, 2020). Procrustes ANOVA and pairwise comparison were performed using the R package "geomorph" (Adams and Otárola-Castillo, 2013). The ANOVA was performed using the package "stats" (R Core Team, 2020), and bg PCA was performed using the package "Morpho" (Schlager, 2017).

3. Results

3.1. Dental microwear texture analysis

3.1.1. Central Ryukyus

Among the ancient suids, the median values of the DMTA parameters in central Ryukyus were higher than those in southern Ryukyus. Especially, the Noguni B assemblages, located on the Okinawa Island, showed significantly higher DMTA values than those obtained from the southern Ryukyus specimens (Table 2a, Fig. 3a). High values indicate high elevated, rough textures. However, the values of the Noguni B assemblage parameters ranged within those obtained from modern boar inhabiting southern Ryukyus (Fig. 3c).

In contrast, the tooth surfaces of suids from both Wakuta Old Kiln and Futenma Old Settlement sites were characterized by rough, random textures (Fig. 3b). The high values of the roughness parameters for suids in these sites suggest a considerable amount of "soft" food in their diet.

3.1.2. Southern ryukyus

The Sq values of suids in the two prehistoric sites, the Pinza-Abu cave and the Shimotabaru Shellmidden, were significantly lower than those obtained from modern wild boar that inhabit southern Ryukyus (Table 2a). Whereas, the Sq values of suids during the 17th–19th century AD (i.e., the Shinan site), as observed in the suids of prehistoric times, were significantly lower than those obtained from archaeological suid specimens of central Ryukyus, modern stall-fed boar, and wild boar inhabiting southern Ryukyus (Table 2b).

3.2. Geometric morphometric analysis

3.2.1. Central Ryukyus

The GMM analysis results indicate that the outline shapes of the lower deciduous fourth premolars obtained from three sites before the introduction of domesticated animals on central Ryukyus were similar to those of modern boar inhabiting the Okinawa Island (Fig. 4a, Table 3a). The lower third molar analyses also indicated the similarity between archaeological and modern specimens from the same region (Fig. 4b,

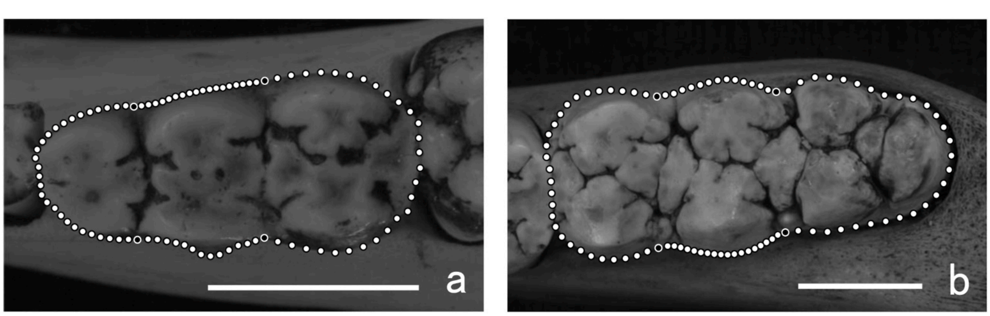

Fig. 2. Landmark setting on the left lower fourth deciduous premolar (a) and third molar (b) of *Sus scrofa* in the occlusal view. Black circle with white outline: landmark, white circle: semi-landmark. Scale bar = 1 cm.

Table 2
Pairwise comparison of surface roughness parameters (Sq: ISO25178) between archaeological assemblages and modern comparatives.

(a) the archaeological suids before the introduction of domesticated animals.

	Ara Shellmidden	Gushibaru Shellmidden	Noguni Shellmidden B Site	Pinza-Abu Cave	boars in Iriomote Island	boars in Ishigaki Island	stall-fed boar
Gushibaru Shellmidden	1.00	–	–	–	–	–	–
Noguni Shellmidden B Site	**0.03**	0.07	–	–	1.00	1.00	–
Pinza-Abu Cave	1.00	1.00	**0.04**	–	0.16	**0.02**	–
Shimotabaru Shellmidden	1.00	0.24	**< 0.01**	1.00	**0.03**	**< 0.01**	**0.01**
boars in Iriomote Island	0.13	0.46	–	–	–	–	–
boars in Ishigaki Island	**0.01**	**0.03**	–	–	1.00	–	–
stall-fed boar	**0.03**	**0.04**	0.29	0.11	0.73	0.30	–

(b) the archaeological suids during the 17th–19th century AD.

	Futenma Old Settlement	Shinan	boars in Iriomote Island	boars in Ishigaki Island	stall-fed boar
Shinan	0.34	–	0.07	**0.01**	–
Wakuta Old Kiln	1.00	**0.02**	1.00	1.00	0.45
boars in Iriomote Island	1.00	–	–	–	–
boars in Ishigaki Island	1.00	–	1.00	–	–
stall-fed boar	1.00	**0.03**	0.64	0.30	–

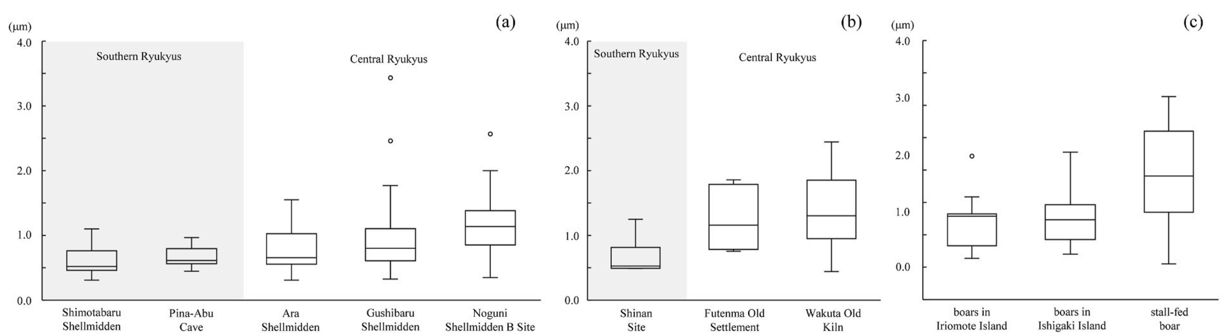

Fig. 3. Boxplots of surface roughness parameters (ISO 25178–2, Sq). The box encloses the 25th and 75th percentiles, with the horizontal line representing the median. Outliers (open circles) are beyond 1.5 times the interquartile range. (a) Archaeological suids before the introduction of domesticated animals, (b) archaeological suids during the 17th–19th century AD, (c) modern comparative specimens.

Table 3b).

The tooth outline shape of suids from central Ryukyus during the 17th–19th century AD, the Wakuta Old Kiln site, was different from the modern wild boar inhabiting southern Ryukyus and from most of the boar inhabiting central Ryukyus along the PC1 and PC2 axes, respectively (Fig. 4c, Table 3c). Instead, the archaeological suid remains showed morphological similarities to the modern Okinawa native domestic pigs.

3.2.2. *Southern ryukyus*

The tooth outline shapes of the archaeological suid remains before the introduction of domesticated animals were distinct from those of the other assemblages (Table 3a, b). Although the archaeological suid remains from Hateruma Island (i.e., the Shimotabaru site) were plotted in the range of the modern boar that inhabit the Ishigaki Islands, located 40 km northwest of the Hateruma Island (Figs. 1 and 4a), there were significant differences in mean shape between them. All three specimens from the Pinza-Abu cave site showed positive values along the PC1 axis, and they were distinctive from the modern and archaeological suid remains from southern Ryukyus (Fig. 4b).

The GMM analysis could be applied to three assemblages from the Miyako Island during the 17th–19th century AD. The tooth outline shapes of most of the specimens closely resembled those of the modern native pigs established on the Okinawa Island (Table 3c). Of the archaeological specimens, only one was plotted with the wild boar inhabiting southern Ryukyus (Fig. 4c).

3.2.3. *Centroid size variation among the groups*

Several significant differences were detected among the groups (Fig. 5, Table 4). Although the correlation between the centroid size and CAC was significant (<0.05) in each dataset, coefficient of correlation between the centroid size and CAC was low; 0.41, 0.37, and 0.47 for the datasets shown in Fig. 6 (a), (b), and (c), respectively.

4. Discussion

4.1. *Defining the ecological niche of suids before the introduction of domesticated animals*

The high values of Sq in the Noguni B assemblages indicate that they had specific foraging ecology characterized by low frequencies of rooting or consuming a less fibrous diet. Additionally, their bodies are distinctly smaller than those of modern wild boar in central Ryukyus (Kawashima and Muraoka, 1984), and contemporary archaeological suid remains found in central Ryukyus (Takahashi et al., 2012). Therefore, it is difficult to attribute the dwarfing of the Noguni B assemblage to the "island effect". However, as shown by the GMM results, the tooth outline shapes of the Noguni B assemblage specimens were not different from those found in the modern and archaeological suid remains on the Okinawa Island. Moreover, the assemblage contains both juveniles with deciduous premolars and mature individuals with fully worn third molars, suggesting that suids in the site were not systematically slaughtered at specific ages.

Zeder (2012) proposed the "prey pathway" as one of the processes of

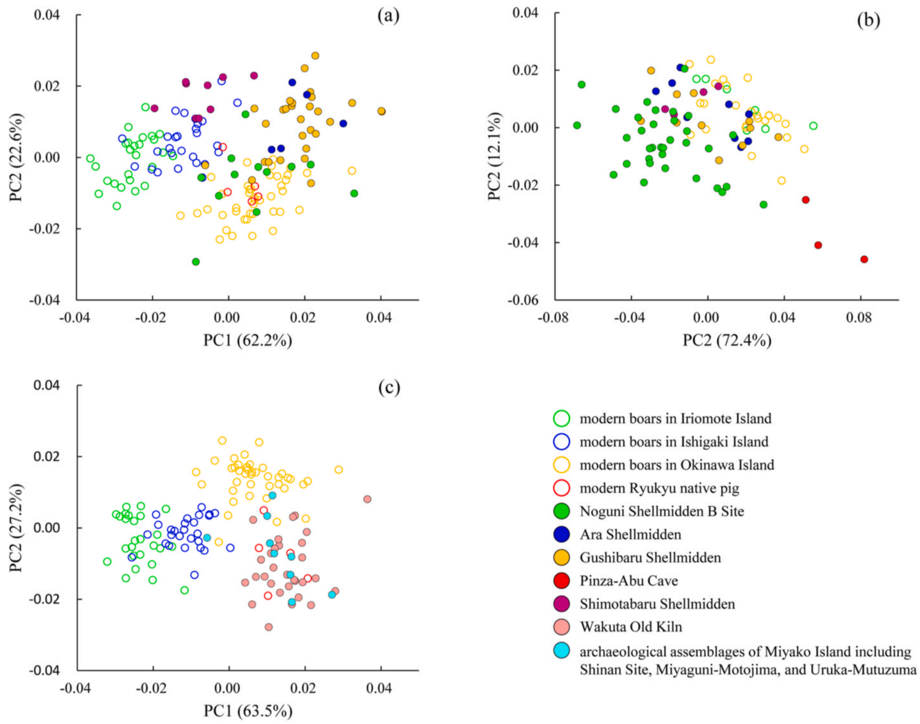

Fig. 4. Between-group principal component plot for the tooth outline shapes of archaeological assemblages and modern comparative specimens. (a) Lower fourth deciduous premolar of the archaeological suids before the introduction of domesticated animals, (b) lower third molar of the archaeological suids before the introduction of domesticated animals, (c) lower fourth deciduous premolars of the archaeological suids during the 17th −19th century AD.

animal domestication. The pathway began as a change in hunting strategies from immediate slaughter to keeping the catch alive, probably to increase prey availability. Temporary management strategies developed into actual herd management and, eventually, the controlled breeding of managed animals. In fact, the Noguni Shellmidden site yield few hunting instruments, such as arrowheads (Okinawa Prefectural Board of Education, 1984). Therefore, humans in these periods probably captured suids using traps, such as pitfalls. If humans brought suids back to the settlement alive, they could then decide whether to slaughter them immediately or to confine them for a few months for delayed consumption as supposed in the prey pathway. Significantly high Sq values of the Noguni B assemblage suggest that the feeding behavior in this site was different from that in the other assemblages. The scenario that they were primarily prey animals but were temporarily managed instead of being slaughtered immediately is consistent with these results. Dwarfing of the body size while retaining the characteristics of the tooth shape of wild suids in the Noguni B assemblage imply that they were in the initial stage of the prey pathway. However, even after thousands of years, the teeth outline shape of suids in the Okinawa Islands was not distinctive from that of modern wild boar (Fig. 4, Table 3). The results suggest that among the Ryukyu Islands, the interaction between humans and suids had been that of a hunter and prey, respectively. Although delayed consumption had been popular in some settlements, their custom did not result in the development of the domestication process as supposed by the prey pathway.

Zeder (2012) also proposed another process, the “commensal pathway.” This pathway focuses on animals that come into initial contact with humans when feeding on refuse or preying on other animals attracted to human settlements. At some point in their association with humans and human habitats, these animals developed closer social or economic bonds with their human hosts than other commensals inhabiting this niche. These bonds eventually brought them into a domestic partnership with humans, and it is quite possible that suids were scavenging leftovers or waste around human settlements. However, before applying the scenario to the Noguni B assemblage, it is necessary to discover why other suids before the introduction of domesticated animals showed significantly lower Sq values.

Minagawa et al. (2005) revealed that the stable nitrogen isotope ratio ($\delta^{15}N$) value of the Gushibaru Shellmidden assemblage was distinctly higher than that of typical modern herbivores and even higher than that of the Noguni B assemblages. They proposed that suids from the Gushibaru Shellmidden had been imported from agricultural areas overseas, such as northern China or the Korean Peninsula. However, in our study, the Sq values of the Gushibaru Shellmidden assemblage were significantly lower than those of the modern stall-fed boar (Table 2a). Another possibility is that the frequent consumption of marine resources (e.g., seaweed), which contain a high level of $\delta^{15}N$ (Deniro and Epstein, 1981), affected the stable isotope ratios in the archaeological suid remains found in the Ryukyu Islands. Although Minagawa et al. (2005) have highlighted the effect of marine organism consumption, they considered mainly fish and mollusk. The effect of seaweed consumption should also be addressed in future studies.

The GMM analysis results produced another enigma regarding the dispersal process of suids in southern Ryukyus. Although the tooth shape of the Shimotabaru assemblage in the Hateruma Island and that of modern wild boar inhabiting the Ishigaki Island overlapped (Fig. 4a and b), significant differences were detected between them. The former site yielded specimens from almost 300 suid individuals, and it was the second-largest find among the archaeological assemblages of the Ryukyu Islands. Most of these individuals were over 1.5 years old at the time of slaughter. The Hateruma Island has another site, the Ohdomarihama Shellmidden site, dated 1350–1770 uncal. BP (Kin, 1986b). The site yielded specimens from at least 98 suid individuals, which occupied 87.6% of the vertebrate remains in this site (Shimabukuro, 1986), suggesting that suids have been one of the principal food resources for human beings on the Hateruma Island for 2000 years. Contrarily, no modern wild suid inhabit the Hateruma Island. Although the terrestrial vegetation of the island at this period is unknown, the introduction of suids from the neighboring Iriomote Island, approximately 25 km north of the Hateruma Island, would have been more sustainable than hunting

Table 3
Results of Procrustes ANOVA and pairwise comparison of mean outline shapes among the archaeological suids and modern comparative specimens.

(a) lower fourth deciduous premolar of the archaeological suids before the introduction of domesticated animals.

	Df	SS	MS	Rsq	F	Z	Pr(>F)
group	5	0.045964	0.0091928	0.3594	14.811	10.992	**0.0001**
Residuals	132	0.081927	0.0006207	0.6406			
Total	137	0.127891					

	Ara Shellmidden	Gushibaru Shellmidden	boars in Iriomote Island	boars in Ishigaki Island	modern Ryukyu native pig	Noguni Shellmiddern B Site	boars in Okinawa Island
Gushibaru Shellmidden	0.05	–	–	–	–	–	–
boars in Iriomote Island	**0.01**	**0.01**	–	–	–	–	–
boars in Ishigaki Island	**0.01**	**0.01**	**0.01**	–	–	–	–
modern Ryukyu native pig	**0.01**	**0.01**	**0.01**	**0.01**	–	–	–
Noguni Shellmiddern B Site	**0.01**	**0.01**	**0.01**	**0.01**	0.06	–	–
boars in Okinawa Island	**0.01**	**0.01**	**0.01**	**0.01**	**0.01**	0.07	–
Shimotabaru Shellmidden	**0.01**	**0.01**	**0.01**	**0.03**	**0.01**	**0.01**	**0.01**

(b) lower third molar of the archaeological suids before the introduction of domesticated animals.

	Df	SS	MS	Rsq	F	Z	Pr(>F)
group	7	0.056695	0.0080993	0.39828	13.805	11.369	**0.0001**
Residuals	146	0.085655	0.0005867	0.60172			
Total	153	0.14235					

	Ara Shellmidden	Gushibaru Shellmidden	boars in Iriomote Island	Noguni Shellmiddern B Site	boars in Okinawa Island	Pinza-Abu Cave
Gushibaru Shellmidden	0.86	–	–	–	–	–
boars in Iriomote Island	0.09	0.09	–	–	–	–
Noguni Shellmiddern B Site	**0.01**	**0.01**	**0.01**	–	–	–
boars in Okinawa Island	0.26	0.08	0.06	**0.01**	–	–
Pinza-Abu Cave	**0.01**	**0.01**	**0.02**	**0.01**	**0.01**	–
Shimotabaru Shellmidden	0.23	0.29	0.11	0.08	**0.01**	**0.01**

(c) lower fourth deciduous premolars of the archaeological suids during the 17th–19th century AD.

	Df	SS	MS	Rsq	F	Z	Pr(>F)
group	6	0.056737	0.0094562	0.3513	7.7622	6.1407	**0.0001**
Residuals	86	0.104767	0.0012182	0.6487			
Total	92	0.161504					

	boars in Iriomote Island	boars in Ishigaki Island	Assemblage of Miyako Island[a]	modern Ryukyu native pig	boars in Okinawa Island
boars Ishigaki Island	**0.01**	–	–	–	–
Assemblage of Miyako Island[a]	**0.01**	**0.01**	–	–	–
modern Ryukyu native pig	**0.01**	**0.01**	0.56	–	–
boars in Okinawa Island	**0.01**	**0.01**	**0.01**	**0.01**	–
Wakuta Old Kiln	**0.01**	**0.01**	0.42	0.77	**0.01**

[a] Archaeological specimens from Shinan, Miyaguni Jouhou-Kobo Group, abd Uruka-Mutuzuma Sites.

and slaughtering native individuals. However, the GMM analysis results in this study did not support this idea. The tooth outlines of modern wild boar from the Iriomote Island were morphologically distinct from those of the specimens found in the Shimotabaru site (Table 3a, b). Therefore, to determine the dispersal process of suids in the Ryukyu Islands, additional datasets including populations in near the islands (e.g., China, Southeast Asia) are required. Additionally, if these animals were transported alive, low values of Sq parameters suggest that they were not fed. The age of the individuals also suggests that suid husbandry was not common in the Hateruma Island communities until the introduction of domesticated animals.

4.2. *Husbandry system for suids during the 17th–19th century AD*

Significantly high ISO values of suid remains in the archaeological sites of central Ryukyus suggest that their diet consisted mainly of foods that were considerably softer than natural resources such as nuts and roots. Besides the deliberate provisioning of leftovers, pigs could also benefit from these resources around the settlements, adopting the role of refuse disposers, as reported in northern Ryukyus in the 19th century

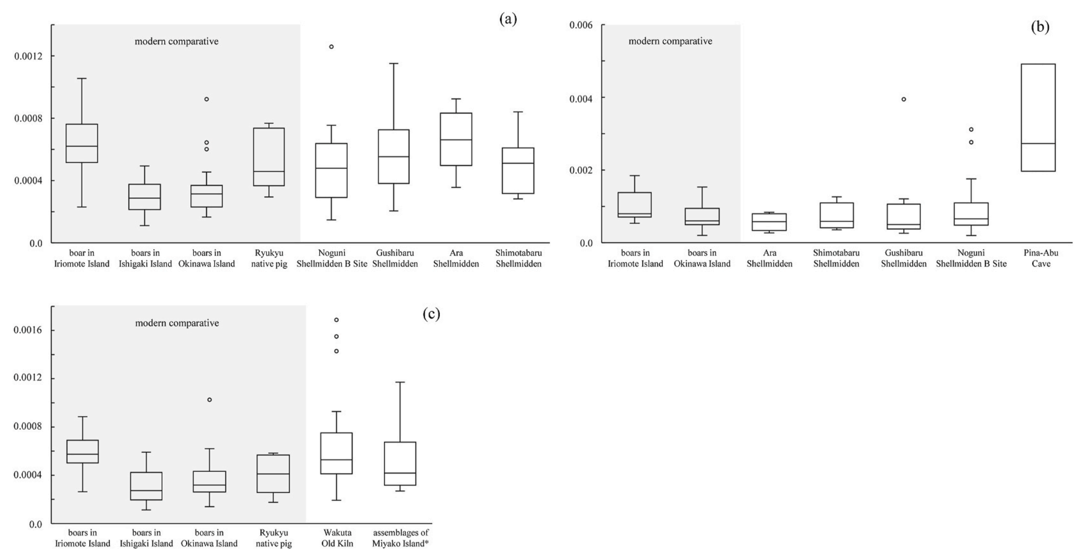

Fig. 5. Box plots of the centroid sizes of the teeth outline shapes of archaeological assemblages and modern comparative specimens. (a) Lower fourth deciduous premolar of the archaeological suids before the introduction of domesticated animals, (b) lower third molar of the archaeological suids before the introduction of domesticated animals, (c) lower fourth deciduous premolars of the archaeological suids during the 17th–19th century AD. * Archaeological specimens from Shinan, Miyaguni Jouhou-Kobo Group, and Uruka-Mutuzuma Sites.

Table 4
Pairwise comparisons of log centroid size among the assemblages.

(a) lower fourth deciduous premolar of the archaeological suids before the introduction of domesticated animals.

	Ara Shellmidden	Gushibaru Shellmidden	boars in Iriomote Island	boars in Ishigaki Island	modern Ryukyu native pig	Noguni Shellmiddern B Site	boars in Okinawa Island
Gushibaru Shellmidden	1.00	–	–	–	–	–	–
boars in Iriomote Island	1.00	1.00	–	–	–	–	–
boars in Ishigaki Island	0.04	0.00	0.00	–	–	–	–
modern Ryukyu native pig	1.00	1.00	1.00	0.29	–	–	–
Noguni Shellmiddern B Site	1.00	1.00	0.99	0.12	1.00	–	–
boars in Okinawa Island	0.08	0.00	0.00	1.00	0.23	0.26	–
Shimotabaru Shellmidden	1.00	1.00	0.99	0.04	1.00	1.00	0.12

(b) lower third molar of the archaeological suids before the introduction of domesticated animals.

	Ara Shellmidden	Gushibaru Shellmidden	boars in Iriomote Island	Noguni Shellmiddern B Site	boars in Okinawa Island	Pinza-Abu Cave
Gushibaru Shellmidden	1.00	–	–	–	–	–
boars in Iriomote Island	1.00	1.00	–	–	–	–
Noguni Shellmiddern B Site	1.00	1.00	1.00	–	–	–
boars in Okinawa Island	1.00	1.00	1.00	1.00	–	–
Pinza-Abu Cave	0.31	0.50	0.41	0.19	0.13	–
Shimotabaru Shellmidden	1.00	1.00	1.00	1.00	1.00	0.83

(c) lower fourth deciduous premolars of the archaeological suids during the 17th–19th century AD.

	boars in Iriomote Island	boars in Ishigaki Island	Assemblage of Miyako Island[a]	modern Ryukyu native pig	boars in Okinawa Island
boars Ishigaki Island	0.00	–	–	–	–
Assemblage of Miyako Island[a]	1.00	0.07	–	–	–
modern Ryukyu native pig	0.42	1.00	1.00	–	–
boars in Okinawa Island	0.00	0.75	0.32	1.00	–
Wakuta Old Kiln	1.00	0.00	1.00	1.00	0.00

[a] Archaeological specimens from Shinan, Miyaguni Jouhou-Kobo Group, and Uruka-Mutuzuma Sites.

(Nagoshi, 1984). In fact, the consumption of human feces by pigs was a common practice in the Ryukyu Islands until the early 20th century (Hagihara, 2009), although the consequence of such practices on the consumers' dental microwear is unclear. The relatively high variation in the Sq among individuals from the Wakuta assemblage was similar to the results obtained for the modern stall-fed boar (Yamada et al., 2018b). Modern stall-fed management with artificial hay and keeping the pigs from rooting enhances tooth-to-tooth contact wear, which

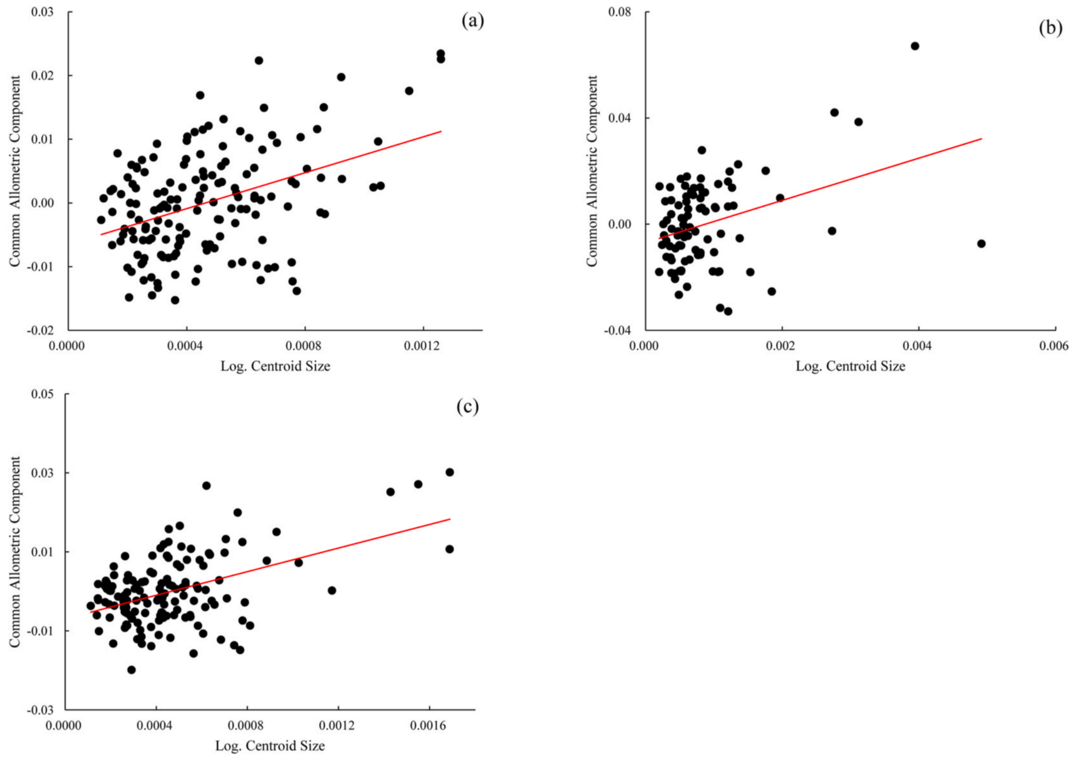

Fig. 6. Regression between the tooth outline centroid size and its common allometric component of archaeological assemblages and modern comparative specimens. (a) Lower fourth deciduous premolar of the archaeological suids before the introduction of domesticated animals, (b) lower third molar of the archaeological suids before the introduction of domesticated animals, (c) lower fourth deciduous premolars of the archaeological suids during the 17th–19th century AD.

probably causes a rough and random surface texture. The DMTA results of the Wakuta assemblage specimens suggest that the husbandry systems in the site were characterized by a soft foraging diet in a floored stall.

The oldest literature record of pig husbandry in the Ryukyu Islands, written around the 15th century, mentioned that people in central Ryukyus had already husbanded pigs, whereas people in southern Ryukyus had not (Hagihara, 2009). Our DMTA results also revealed that suid remains in the archaeological sites of southern Ryukyus exhibited significantly flat tooth surfaces compared with those from Wakuta, located in Central Ryukyus ($p < 0.05$). This suggests that the foraging conditions of the former were similar to those of wild individuals, rather than stall-fed animals. However, the results of the GMM analysis showed that their deciduous premolars were morphologically distinct from those of the modern boar on these islands. Instead, the tooth shapes of southern Ryukyus assemblage specimens overlapped with the archaeological suid remains in central Ryukyus' sites and modern native pig (Fig. 4c). Considering that the GMM analysis results corresponded with the phylogenetic affinities among the modern groups (e.g., Evin et al., 2015; Yamada et al., 2018a), the idea that domestic breeds were introduced and dispersed in the Ryukyu Islands during the 17th–19th century AD can reasonably explain the morphological similarity between the assemblages. The Ryukyu Dynasty actively traded with the surrounding communities in China and Southeast Asia (Okamoto, 2008; Sakamaki, 1964). The domestic suids were likely to be a merchandise item in the trade. Considering the humid subtropical climate, the transportation of pigs was probably more favorable while they were still alive rather than in the form of meat, and this is also suggested by the fact that the body parts that are not rich in meat, such as mandibles, were also included in the assemblage. The tooth outline similarities observed between the Miyako and Okinawa Island assemblages during various periods may be the result of artificial transportation. This raises the question whether the people in the Miyako Island just consume pigs or raise them. Morphological similarities between the suids of the Miyako Island and both archaeological and modern suids of central Ryukyus indicate that the pig husbandry system on the Miyako Island did not establish an original domestic lineage. Low values of Sq parameters of the suids suggest that a pig husbandry system relying on forage or human waste, as in central Ryukyus, was not popular in the southern Ryukyus community. Instead, after the introduction of domestic breed, people in southern Ryukyus kept pigs by feeding wild plants in paddock or by allowing them to free range around the settlement. These foraged pigs were distinct from scavenging wild boar as the tooth outline shape of the formers had similarities with that of modern native pigs and wild boar in Central Ryukyus. However, their husbandry systems would not have led to the establishment of a new breed on each island.

5. Conclusion

This study demonstrated the combination of ecological and morphological approaches can be used to assess the relationship between human and animal interactions before the phenotypic change associated with breeding occurred. Our results suggest that the notable dietary flexibility of suids is the key that enabled wild suids to thrive with humans, despite hunting pressures and the islands' ecological limitations. As omnivores, suids can fully exploit different niches within the anthropic ecosystem. Instead of competing with humans over dietary resources, wild suids probably approached human settlements to scavenge human leftovers and waste, as is seen even now. Humans also captured suids alive and, instead of immediate slaughtering, and fed them. Contrarrily, the DMTA results suggested that breeding custom had not developed until the introduction of domestics. Therefore, among the Ryukyu Islands, although delayed consumption of suids had been popular in some settlements, their custom had not resulted in the development of the domestication process as supposed by the prey pathway. Before the introduction of livestock management practice, suids probably inhabited areas close to human settlements. In contrast, domestic suids during the 17th–19th century AD were clearly under more intensive management and fed with leftovers or by-products of human activities. During this period, the morphology of pig remains was standardized, suggesting that the trade of pigs among the islands was initiated, whereas their husbandry system depended on local custom.

For further studies, the determination of the husbandry system for suids in each settlement (i.e., house hold or extensive herding) is necessary. It is also necessary to conduct archaeobotanical studies to evaluate the effect of vegetation difference among the islands based on the DMTA results before applying the approach. The GMM analysis results suggested that some of the domestic suids were probably transported from the Okinawa Island during the 17th–19th century AD. Whether the suids during this period are the direct ancestors of the modern native domestic breed must be determined in future studies.

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Declarations of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2021.105419.

References

Abe, H. (Ed.), 2008. A Guide to the Mammals of Japan, second ed. Tokai University Press., Kanagawa, pp. 108–109.

Adams, D.C., Otárola-Castillo, E., 2013. geomorph: an R package for the collection and analysis of geometric morphometric shape data. Methods Ecol. Evol. 4, 393–399. https://doi:10.1111/2041-210X.12035.

Balasse, M., Cucchi, T., Evin, A., 2019. Wild game or farm animal? Tracking human-pig relationships in ancient times through stable isotope analysis. In: Stépanoff, C., Vigne, J.-D. (Eds.), Hybrid Communities. Biosocial Approaches to Domestication and Other Trans-species Relationships. Routledge Studies in Anthropology. Routledge, London, pp. 81–96. https://doi.org/10.4324/9781315179988-12.

Cucchi, T., Dai, L., Balasse, M., Zhao, C., Gao, J., Hu, Y., Yuan, J., Vigne, J.-D., 2016. Social complexification and pig (*Sus scrofa*) husbandry in ancient China: a combined geometric morphometric and isotopic approach. PloS One 11, e0158523. https://doi.org/10.1371/journal.pone.0158523.

Cucchi, T., Mohaseb, A., Peigné, S., Debue, K., Orlando, L., Mashkour, M., 2017. Detecting taxonomic and phylogenetic signals in equid cheek teeth: towards new palaeontological and archaeological proxies. R. Soc. Open. Sci. 4 https://doi.org/10.1098/rsos.160997.

Cucchi, T., Stopp, B., Schafberg, R., Lesur, J., Hassanin, A., Schibler, J., 2019. Taxonomic and phylogenetic signals in bovini cheek teeth: towards new biosystematic markers to explore the history of wild and domestic cattle. J. Archaeol. Sci. 109, 104993. https://doi.org/10.1016/j.jas.2019.104993.

Deniro, M.J., Epstein, S., 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochem. Cosmochim. Acta 45, 341–351. https://doi.org/10.1016/0016-7037(81)90244-1.

Evin, A., Cucchi, T., Cardini, A., Strand Vidarsdottir, U., Larson, G., Dobney, K., 2013. The long and winding road: identifying pig domestication through molar size and shape. J. Archaeol. Sci. 40, 7735–7743. https://doi.org/10.1016/j.jas.2012.08.005.

Evin, A., Dobney, K., Schafberg, R., Owen, J., Vidarsdottir, U., Larson, G., Cucchi, T., 2015. Phenotype and animal domestication: a study of dental variation between domestic, wild, captive, hybrid and insular *Sus scrofa*. BMC Evol. Biol. 15, 6. https://doi.org/10.1186/s12862-014-0269-x.

Foster, J.B., 1964. Evolution of mammals on islands. Nature 202, 234–235. https://doi.org/10.1038/202234a0.

Fujita, M., 2014. Interaction between animals and human in Pleistocene Ryukyu islands. In: Takamiya, H., Niizato, T. (Eds.), Collection of Papers on Empirical Studies Dealing Environmental and Cultural Change during Prehistoric and Protohistoric Times in the Ryukyu Islands. Rokuichi Shobo., Tokyo, pp. 29–40.

Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. J. Hum. Evol. 15, 783–822. https://doi.org/10.1016/S0047-2484(86)80010-0.

Hagihara, S., 2009. Folklore history of meat eating. In: Furuie, S., Oguma, S., Hagihara, S. (Eds.), Folklore of Japan. 12. Life of Southern Islands. Yoshikawa-Kobunkan., Tokyo, pp. 196–278.

Hamada, T., Okinawa Prefectural Board of Education, 1985. ^{14}C age of charcoal from pinza-abu cave deposits, Miyako island, Okinawa, Japan. In: Pinza-Abu: Reports on Excavation of the Pinza-Abu Cave. Okinawa Prefectural Board of Education, Naha, p. 180.

Harbers, H., Neaux, D., Ortiz, K., Blanc, B., Laurens, F., Baly, I., Callou, C., Schafberg, R., Haruda, A., Lecompte, F., Casabianca, F., Studer, J., Renaud, S., Cornette, R., Locatelli, Y., Vigne, J.-D., Herrel, A., Cucchi, T., 2020. The mark of captivity: plastic responses in the ankle bone of a wild ungulate (*Sus scrofa*). R. Soc. Open. Sci. 7, 192039. https://doi.org/10.1098/rsos.192039.

Hasegawa, Y., Okinawa Prefectural Board of Education, 1985. Conclusion. In: Pinza-Abu: Reports on Excavation of the Pinza-Abu Cave. Okinawa Prefectural Board of Education., Naha, Japan, pp. 181–184.

Hayashi, Y., Okinawa Prefectural Board of Education, 1985. Larger wild boar from pinza-abu cave, Miyako island, Okinawa, Japan. In: Pinza-Abu: Reports on Excavation of the Pinza-Abu Cave. Okinawa Prefectural Board of Education., Naha, pp. 75–78.

Ishigaki, C., Shinzato, T., Aramoto, M., Wu, L., 2007. Feed plant, dressing and utilization of carcass of Ryukyuan wild boar in Iriomote Island. In: The Science Bulletin of the Faculty of Agriculture, vol. 54. University of the Ryukyus, pp. 23–27.

Ishiguro, N., Sasaki, M., Iwasa, M., Shigehara, N., Hongo, H., Anezaki, T., Long, V.T., Hao, P.X., Trach, H.X., Nam, N.H., Thanh, V.N., 2008. Morphological and genetic analysis of Vietnamese *Sus scrofa* bones for evidence of pig domestication. Anim. Sci. J. 79, 655–664. https://doi.org/10.1111/j.1740-0929.2008.00577.x.

Kaneko, M., Okinawa Prefectural Board of Education, 1986. Vertebrate remains. In: Report on the Excavation Research of the Shimotabaru Site. Okinawa Prefectural Board of Education., Naha, pp. 113–126.

Kaneko, M., Okinawa Prefectural Board of Education, 1993. Vertebrate remains. In: 1993. Report on the Excavation Research of the Wakuta Old Kiln. Okinawa Prefectural Board of Education., Naha, pp. 176–191.

Kaneko, M., Okinawa Prefectural Board of Education, 2003. Vertebrate remains. In: Report on the Excavation Research of the Shinan Site. Okinawa Prefectural Board of Education., Naha, pp. 101–115.

Kawamura, A., Chang, C.H., Kawamura, Y., 2016. Middle Pleistocene to Holocene mammal faunas of the Ryukyu Islands and Taiwan: an updated review incorporating results of recent research. Quat. Int. 397, 117–135. https://doi.org/10.1016/j.quaint.2015.06.044.

Kawashima, Y., Muraoka, M., Okinawa Prefectural Board of Education, 1984. Mammal bones from B site of the Noguni shellmidden group. In: Noguni: Report on the Excavation Research of Site B of the Noguni Shellmidden Group. Okinawa Prefectural Board of Education., Naha, pp. 181–199.

Kawashima, Y., Ishimine, D., Oyama, S., Okinawa Prefectural Board of Education, 1985. Comparison of modern Ryukyu wild boar and boar from pinza-abu cave, Miyako island, Okinawa, Japan. In: Pinza-Abu: Reports on Excavation of the Pinza-Abu Cave. Okinawa Prefectural Board of Education, Naha, pp. 79–82.

Kin, M., Okinawa Prefectural Board of Education, 1986a. Conclusion. In: Report on the Excavation Research of the Shimotabaru Site. Okinawa Prefectural Board of Education., Naha, pp. 127–128.

Kin, M., Okinawa Prefectural Board of Education, 1986b. Conclusion. In: Report on the Excavation Research of the Ohdomarihama Site. Okinawa Prefectural Board of Education., Naha, pp. 155–156.

Kishimoto, Y., Okinawa Prefectural Board of Education, 1984. ^{14}C age of charcoal and shell from Site B of the Noguni shellmidden group. In: Noguni: Report on the Excavation Research of Site B of the Noguni Shellmidden Group. Okinawa Prefectural Board of Education., p. 200

Klingenberg, C.P., 2011. MorphoJ: an integrated software package for geometric morphometrics. Available at: http://www.flywings.org.uk/MorphoJ_page.htm. (Accessed 22 October 2017).

Lord, K.A., Larson, G., Coppinger, R.P., Karlsson, E.K., 2019. The history of farm foxes undermines the animal domestication syndrome. Trends Ecol. Evol. 5, 125–136. https://doi.org/10.1016/j.tree.2019.10.011.

Matsui, A., Ishiguro, N., Hongo, H., Minagawa, M., 2005. Wild pig? Or domesticated boar? An archaeological view on the domestication of *Sus scrofa* in Japan. In: Vigne, J.-D., Peters, J., Helmer, D. (Eds.), The First Steps of Animal Domestication: New Archaeological Approaches, Proceedings of the 9th ICAZ Conference. Oxbow Books., Oxford, Durham, pp. 148–159.

Minagawa, M., Matsui, A., Ishiguro, N., 2005. Patterns of prehistoric boar *Sus scrofa* domestication, and inter-islands pig trading across the East China Sea, as determined by carbon and nitrogen isotope analysis. Chem. Geol. 218, 91–102. https://doi.org/10.1016/j.chemgeo.2005.01.019.

Mitteroecker, P., Gunz, P., Bernhard, M., Schaefer, K., Bookstein, F.L., 2004. Comparison of cranial ontogenetic trajectories among great apes and humans. J. Hum. Evol. 46, 679–698. https://doi:10.1016/j.jhevol.2004.03.006.

Mitteroecker, P., Bookstein, F., 2011. Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. Evol. Biol. 38, 100–114.

Nagoshi, S., 1984. Folklore Reports of Amami-Oshima Islands at the End of the Edo Period. Heibonshya, Tokyo.
Okamoto, H., 2008. Foreign policy and maritime trade in the early Ming period focusing on the Ryukyu Kingdom. Acta Asiatica 95, 35–55.
Okinawa Board of Education, 1983. In: Report on the Excavation Research of the Ara Shellmidden on Ie Island. Okinawa Prefectural Board of Education., Naha, p. 119.
Okinawa Prefectural Board of Education, 1984. In: Noguni: Report on the Excavation Research of Site B of the Noguni Shellmidden Group. Okinawa Prefectural Board of Education., Naha, p. 200.
Okinawa Board of Education, 1997. In: Report on the Excavation Research of the Gushibaru Shellmidden. Group. Okinawa Prefectural Board of Education., Naha, p. 223pp.
Perez, S.I., Bernal, V., Gonzalez, P.N., 2006. Differences between sliding semi- landmark methods in geometric morphometrics, with an application to human craniofacial and dental variation. J. Anat. 208, 769–784. https://doi.org/10.1111/j.1469-7580.2006.00576.x.
Price, M., Hongo, H., 2019. The archaeology of pig domestication in Eurasia. J. Archaeol. Res. https://doi.org/10.1007/s10814-019-09142-9.
R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/. Accessed 22 February.
Rohlf, F.J., 2013. tpsDig2, Digitize Landmarks and Outlines. State University of New York at Stony Brook. Available at: http://life.bio.sunysb.edu/morph/. (Accessed 22 October 2017).
Rohlf, F.J., 2014. tpsRelw, Relative Warps Analysis, Version 1.54. Stony Brook, NY: State University of New York at Stony Brook. Available at: http://life.bio.sunysb.edu/morph/. (Accessed 22 October 2017).
Rowley-Conwy, P., Albarella, U., Dobney, K., 2012. Distinguishing wild boar from domestic pigs in prehistory: a review of approaches and recent results. J. World Prehist. 25, 1–44. https://doi.org/10.1007/s10963-012-9055-0.
Sakamaki, S., 1964. Ryukyu and Southeast Asia. J. Asian Stud. 23, 383–389. https://doi.org/10.2307/2050757.
Schlager, S., 2017. Chapter 9 - Morpho and Rvcg –shape analysis in R: R-packages for geometric morphometrics, shape analysis and surface manipulations. In: Zheng, G., Li, S., Székely, G.((Eds.), Statistical Shape and Deformation Analysis. New York Academic Press., NY, pp. 217–256.
Schulz, E., Calandra, I., Kaiser, T.M., 2010. Applying tribology to teeth of hoofed mammals. Scanning 32, 162–182. https://doi.org/10.1002/sca.20181 PMID: 20949615.
Schulz, E., Piotrowski, V., Clauss, M., Mau, M., Merceron, G., Kaiser, T.M., 2013. Dietary abrasiveness is associated with variability of microwear and dental surface texture in rabbits. PloS One 8, e56167. https://doi.org/10.1371/journal.pone.0056167.
Shimabukuro, H., Okinawa Prefectural Board of Education, 1986. Vertebrate remains. In: Report on the Excavation Research of the Ohdomarihama Site. Okinawa Prefectural Board of Education., Naha, pp. 148–154.
Takahashi, R., Ishiguro, N., Matsui, A., Anezaki, T., Hongo, H., 2012. Morphological and molecular phylogenetic characteristics of dwarf *Sus* specimens from the Noguni shell middens in the Ryukyu Islands. Anthropol. Sci. 120, 39–50. https://doi.org/10.1537/ase.100929.
Takamiya, H., Hudson, M.J., Yonenobu, H., Kurozumi, T., Toizumi, T., 2016. An extraordinary case in human history: prehistoric hunter-gatherer adaptation to the islands of the Central Ryukyus (Amami and Okinawa archipelagos), Japan. Holocene 26, 408–422. https://doi.org/10.1177/0959683615609752.
Teaford, M.F., Oyen, O.J., 1989a. Differences in the rate of molar wear between monkeys raised on different diets. J. Dent. Res. 68, 1513–1518. https://doi.org/10.1177/00220345890680110901.
Teaford, M.F., Oyen, O.J., 1989b. In vivo and in vitro turnover in dental microwear. Am. J. Phys. Anthropol. 80, 447–460. https://doi.org/10.1002/ajpa.1330800405.
Touma, S., Shimabukuro, H., Arakawa, A., Oikawa, T., 2019. Maternal lineage of Okinawa indigenous Agu pig inferred from mitochondrial DNA control region. Asian-Australas. J. Anim. Sci. 32, 501–507. https://doi.org/10.5713/ajas.18.0378.
Ungar, P.S., Brown, C.A., Bergstrom, T.S., Walker, A.C., 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. Scanning 25, 185–193. https://doi.org/10.1002/sca.4950250405.
Ward, J., Mainland, I.L., 1999. Microwear in modern rooting and stall-fed pigs: the potential of dental microwear analysis for exploring pig diet and management in the past. Environ. Archaeol. 4, 25–32. https://doi.org/10.1179/env.1999.4.1.25.
Yamada, E., Anezaki, T., Hongo, H., 2018a. Tooth outline shape analysis of the Ryukyu wild boar (*Sus scrofa riukiuanus*) and the Japanese wild boar (*S. s. leucomystax*) by geometric morphometrics. Mamm. Stud. 43, 99–107. https://doi.org/10.3106/ms2017-0080.
Yamada, E., Kubo, M.O., Kubo, T., Kohno, N., 2018b. Three dimensional tooth surface texture analysis on stall-fed and wild boars (*Sus scrofa*). PloS One 13, e0204719. https://doi.org/10.1371/journal.pone.0204719.
Zeder, M.A., 2012. Pathways to animal domestication. In: Gepts, P., Famula, T.R., Bettinger, R.L., et al. (Eds.), Biodiversity in Agriculture: Domestication, Evolution, and Sustainability. Cambridge University Press., Cambridge, pp. 227–259.
Zelditch, M., Swiderski, D.L., Sheets, H.D., Fink, W.L., 2012. Geometric Morphometrics for Biologists: A Primer, second ed. Elsevier Academic Press., Amsterdam, p. 488.