An Osteometrical Study of the Cranium and Mandible of Ryukyu Wild Pig in Iriomote Island

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ABSTRACT. We measured crania and mandibles of Ryukyu wild pigs from Iriomote Island. Sex and age were determined by observation of lower teeth. From the present data, the growth pattern was established for some items. For several parts of the cranium and mandible, the relative growth coefficient was compared. The results obtained here are summarized as follows: (1) Although sexual dimorphism was already shown in the younger group, a significant difference in profile length and length from the angle was not seen in the adult group. (2) As the animal grew, the proportion of length to width became larger in the skull. (3) The visceral cranium grew more rapidly in length than the cerebral cranium. On the other hand, growth of the cerebral cranium contributed to width in cranial development. (4) The body of the mandible was shown to grow more rapidly in length than the ramus of the mandible. (5) The growth pattern of some items was related to that of their associated muscles. These basic data are expected to be compared with data from other populations of the same subspecies and Japanese wild pig. The comparisons will contribute to the establishment of origin and phylogeny of this animal.—KEY WORDS: cranium, mandible, osteometry, *Sus scrofa*, wild pig.

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Two subspecies of wild pigs are found in Japan: Japanese wild pig (*Sus scrofa leucomystax*) and Ryukyu wild pig (*Sus scrofa riukiuanus*). The latter subspecies is distributed only in Nansei Islands, in the southernmost part of Japan. There have been a few reports of osteometrical studies in this species. Imaizumi [9] dealt with cranial osteology of wild pigs including the Ryukyu wild pigs for taxonomical research, while some researchers used osteometrical data on Ryukyu wild pigs from the view of archaeology [8, 19, 20]. Although these investigations certainly demonstrated that Ryukyu wild pig is much smaller in body size than the Japanese subspecies, age determination of the specimens has not yet been performed in detail. In addition, as the sample size is not large for any age, the growth pattern of the animal remains unclear. Taking notice of not only body size but also nonmetric characteristics, Imaizumi [9] regarded Ryukyu wild pig as an independent species. In a previous report [7] that examined mandibles obtained from Amami-Oshima Island by means of multivariate analysis, we distinguished Ryukyu wild pig from the Japanese subspecies in both size and shape vectors. Kurosawa *et al.* concluded that Ryukyu wild pig from Amami-Oshima Island is distinguishable from Japanese wild pig in genetic data [13, 14]. However, it was also reported that Ryukyu wild pig from Iriomote Island was not genetically separated at the species level from Japanese wild pig [14, 15]. It is impossible to resolve the problems of phylogenic relationships among wild pigs without osteometrical data on growth patterns. In this study, therefore, we examined osteometrically the crania and mandibles of Ryukyu wild pigs from Iriomote Island. To discuss the growth pattern exactly, the determination of sex and age was performed on all specimens. The method of allometry was adopted to confirm the difference in the growth among some parts of the cranium and mandible.

MATERIALS AND METHODS

We used 25 pairs of crania and mandibles, and 10 mandibles of Ryukyu wild pigs from Iriomote Island, most of which have been obtained before 1973, and used in the study of Imaizumi [9] and stored in the National Science Museum, Japan. The crania were measured for 13 items, while the mandibles were evaluated by 14 measurements. Most measurements were performed according to the methods of Driesch [2], while some other items were evaluated as described by Duerst [3] and Abe [1] (Tables 4, 5). Measurements were carried out with a vernier caliper to the nearest 1 mm. Some samples were partially broken; therefore, the number of specimens measured did not agree with the total number of specimens for a few items.

Although the method for determining age was essentially based on a previous report [6], histology of annual layers in cement or dentin was not used as a criterion here. In this study, we classified the specimens into 5 age groups (Age groups I, II, III, IV and V) according to the eruption and attrition pattern of lower teeth (Table 1).

Sex was determined by the length of canine in Age group III, IV and V. As the length of canine revealed two perfectly separate ranges at each age, we regarded the group with a larger canine as male and the group with a smaller one as female according to the previous study [6]. The size of the canine root by X-ray photographs is useful for the determination of sex of young specimens [6] such as Age group I where the permanent canine had not yet erupted. In the present study, sex determination by the length of canine was impossible for Age group II because

Table 1. Age groups of Ryukyu wild pig estimated from the eruption and attrition of lower tooth[a)]

Age group	I	C	P	M
I	123	1	1234	I
I	12III	1	1234	I
II	12III	I	12III IV	I II
II	12III	I	I II III IV	I II
II	I II III	I	I II III IV	I II
III[b)]	I II III	I	I II III IV	I II III
IV[b)]	I II III	I	I II III IV	I II III
V[b)]	I II III	I	I II III IV	I II III

a) Arabic numerals indicate temporary teeth, whereas roman numerals show permanent teeth.
b) The status of eruption and attrition of third molar was examined to distinguish the Age group III, IV and V [6].

Table 2. The range of size of canine (mm)

Length of canine		
Age group	Male	Female
I[a)]	6–10	7
II[a)]	13–19	10–15
III	33–35	17–18
IV	38–39	18–23
V	34–37	17–20

Length of canine alveolus		
Age group	Male	Female
I	5–6	2–3
II	5–8	6
III	11–12	7–9
IV	12–16	8–11
V	14–15	8

a) X-ray examination was performed in Age group I and II to determine the sex.

Table 3. Age and sex composition of specimens

Age group	Male	Female
I	5(0)[a)]	4(0)
II	8(1)	2(1)
III	2(1)	2(1)
IV	3(2)	3(1)
V	3(1)	3(2)

a) Numbers of mandible without cranium are indicated in parenthesis.

they could not be separated into two groups. Therefore, X-ray photographs were also used for Age group II. Similar to the previous study [6], two groups of obviously different canine root sizes were discerned by X-ray photographs, and we considered the group with larger canine roots as male and the group with smaller ones as female.

For some measurements, the statistical significance of differences between males and females was determined by Student's *t*-test. After demonstrating sexual dimorphism, we discussed the growth pattern of some items. In particular, allometrical techniques were applied to several measurements. In the crania, the values of profile length were located in the X-coordinates, while those of another 12 items were plotted in the Y-coordinates. After the values were converted to logarithms, the relative growth coefficients were computed in the regression equation $\log Y = A \log X + B$. In the mandibles, the length from the angle was plotted in the X-axis, and then analyzed for allometrical changes.

RESULTS

The range of length of the canine and the length of canine alveolus in males and females for each age group are presented in Table 2. The age and sex of the specimens are shown in Table 3, while the mean value and standard error of measurements in the crania and mandibles are given in Tables 4 and 5.

Figures 1 and 2 show the growth pattern of the profile length and the length from the angle, respectively. Growth was obviously rapid from Age group I to II, especially in the female. Slow growth was observed through Age group IV. Even in Age group I, a significant difference between males and females was clearly found in both measurements.

Table 6 shows the results of allometrical analysis. The relative growth coefficients are shown for some items. At first, the relative growth coefficients in males resembled those in females except for the greatest breadth across the nasals. In measurements of length, the relative growth coefficient of facial length was obviously larger than that of median frontal length. Growth of the items of width such as the zygomatic breadth, greatest frontal breadth, and greatest breadth across the nasals was slower than that of most measurements of length. The zygomatic breadth and greatest frontal breadth developed more rapidly than the greatest breadth across the nasals, which hardly grew in males.

In the mandible, the maximum alveolus length and the length of symphysis showed a positive allometrical correlation in both males and females (Table 6). All measurements of the width showed a negative allometrical correlation in the mandible. The items of height had relative growth coefficients almost equivalent to 1 except for the height of the mandible at M_1 in males.

DISCUSSION

A few investigators have attempted to determine the age of wild pig specimens [6, 16, 18]. Matschke [16]

Table 4. The mean value (mm) and standard error of measurements of crania on each Age group[a)]

		Age group														
		I			II			III			IV			V		
	SEX	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.
Profile length	M	5	197.2	7.3	7	238.4	5.9	1	248.0		1	263.0		2	263.0	2.0
	F	4	165.8	6.7	1	220.0		1	243.0		2	262.5	4.5	1	258.0	
Facial length	M	5	92.0	4.1	7	111.1	3.2	1	122.0		1	132.0		2	130.0	0
	F	4	73.0	4.3	1	104.0		1	120.0		2	124.5	5.5	1	128.0	
Median frontal length	M	5	107.6	2.6	7	126.9	3.7	1	127.0		1	131.0		2	135.0	3.0
	F	4	94.0	2.3	1	117.0		1	126.0		2	138.0	0	1	133.0	
Greatest length of the nasals	M	5	82.6	3.9	7	101.9	2.6	1	112.0		1	122.0		2	120.0	1.0
	F	3	64.7	6.2	1	96.0		0			2	116.5	4.5	1	121.0	
Median palatal length	M	5	112.8	4.7	7	138.3	3.5	1	149.0		1	158.0		2	159.5	0.5
	F	4	92.8	4.5	1	127.0		1	141.0		2	157.0	3.0	1	153.0	
Lateral length of the premaxilla	M	5	67.4	2.8	7	84.3	2.6	1	90.0		1	96.0		2	91.5	2.5
	F	4	53.8	3.9	1	77.0		1	87.0		2	91.0	1.0	1	94.0	
Greatest inner length of the orbit	M	5	27.6	1.2	7	29.9	0.5	1	33.0		1	32.0		2	34.5	0.5
	F	4	25.8	0.5	1	30.0		1	31.0		2	34.0	1.0	1	34.0	
Zygomatic breadth	M	5	85.4	2.7	7	97.7	2.5	1	101.0		1	112.0		1	111.0	
	F	4	74.5	1.5	1	91.0		0			2	113.5	4.5	1	108.0	
Greatest frontal breadth	M	5	61.4	1.9	7	67.6	1.5	1	67.0		0			2	75.0	1.0
	F	4	54.3	1.1	1	64.0		1	68.0		2	75.0	2.0	1	73.0	
Least breadth between the orbits	M	5	44.8	1.7	7	50.7	0.9	1	49.0		1	55.0		2	55.0	2.0
	F	4	40.0	1.2	1	47.0		1	51.0		2	55.5	0.5	1	56.0	
Greatest breadth across the nasals	M	5	22.2	1.1	7	22.7	0.4	1	20.0		1	21.0		2	23.0	1.0
	F	4	19.0	0.9	1	22.0		1	24.0		2	22.5	0.5	1	23.0	
Facial breadth between the infraorbital foramina	M	5	29.0	1.0	7	32.0	0.6	1	31.0		1	35.0		2	35.5	0.5
	F	4	26.5	1.0	1	30.0		1	32.0		2	29.5	4.5	1	33.0	
Greatest neurocranium breadth	M	5	57.4	1.0	7	60.0	0.5	1	59.0		1	63.0		2	61.5	1.5
	F	4	53.8	0.5	1	58.0		1	59.0		2	61.0	0	1	63.0	

a) The measurements were based on Driesch [2].

proposed classifying the specimens into age groups, based on the eruption of teeth using known-age wild pigs. In addition to Matschke's method, examination of molar attrition was carried out in two other reports. Relative age can be determined by these methods. Therefore, we fundamentally used the above-mentioned methods for age classification in this study.

In a previous study, examination of annual layers in cement or dentin was adopted to determine the age of Japanese wild pigs [6]. Nishimura [18] applied the same method to Ryukyu wild pigs and pointed out that annual layer data are partially available for Ryukyu wild pigs. However, we suggest that absolute age is difficult to estimate from histological data, since the animals are distributed in a region that is devoid of obvious seasonal change. Therefore, histological study of teeth was not undertaken in this study.

The values of the length of canine and/or the length of canine alveolus were considered effective for sex determination for Age groups II to V in Japanese wild pigs [6]. In Ryukyu wild pig, however, the range of the length of canine could not be separated into two groups in Age group II. Therefore, the specimens of Age group II should be also examined using X-ray photographs as was done for Age group I. The length of canine alveolus, whose distribution was not separable into two groups for most Age groups, seems not to be reliable as an index of sex distinction, unlike that in Japanese wild pigs.

The absolute growth pattern of profile length resembled that of the length from the angle (Figs. 1, 2). These two items were found to highly correlate with body weight and/or head and body length in Japanese wild pigs [1]. Therefore, Figs. 1 and 2 reveal the fundamental growth pattern of this animal. The present study indicated that sexual dimorphism of profile length also occurs in the younger group of Ryukyu wild pigs, similar to that of Japanese wild pigs [1]. However, a significant difference between males and females was not noticed in the older age groups in either the profile length or the length from the angle. This does not agree with the results of external measurements in Japanese and Belovezhskaya populations that demonstrate sexual dimorphism in the older age groups [10, 12]. Since the sample size of the older group was small in this study, especially in the cranial measurements, subsequent examinations of sexual dimorphism in the older age groups will be needed.

A few reports [7, 8, 19, 20] point out that Ryukyu wild pig is obviously smaller in body size than Japanese one. In comparison with the data concerning Japanese wild pig [1, 11], Tables 4 and 5 show that the mean values of many

Table 5. The mean value (mm) and standard error of measurements of mandible on each Age group[a)]

		Age group														
		I			II			III			IV			V		
	SEX	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.	N	MEAN	S.E.
Length from the angle	M	5	134.0	5.3	8	160.0	3.1	2	172.5	1.5	3	189.0	3.1	3	192.7	7.2
	F	4	111.5	5.0	2	143.0	5.0	2	167.5	5.5	3	181.3	1.5	3	176.7	2.6
Length from the condyle	M	5	144.6	5.8	7	172.3	3.8	2	184.0	2.0	3	207.3	4.6	3	208.3	8.8
	F	4	120.3	4.2	2	156.5	6.5	2	180.0	6.0	3	193.3	2.2	3	191.3	2.4
Aboral height of the vertical ramus	M	5	61.0	2.1	7	73.9	1.5	2	77.0	4.0	3	89.3	3.2	3	86.3	1.9
	F	4	49.5	1.2	2	67.0	3.0	2	81.0	1.0	3	82.6	0.9	3	80.3	0.3
Oral height of the vertical ramus	M	4	68.3	2.1	7	80.4	1.4	2	82.5	2.5	3	92.0	3.2	3	89.3	0.8
	F	4	53.5	1.7	2	72.0	2.0	2	82.5	1.5	3	87.0	1.0	3	83.7	1.9
Middle height of the vertical ramus	M	5	56.6	1.7	8	68.4	1.2	2	70.0	3.0	3	80.3	3.8	3	78.0	1.5
	F	4	46.0	1.4	2	64.0	1.0	2	74.0	1.0	3	76.0	1.0	3	73.7	0.7
Height of the mandible[b)] at M_1	M	5	22.8	0.9	8	27.5	1.1	2	30.0	1.0	3	35.0	1.5	3	34.3	2.4
	F	4	19.3	0.8	2	25.0	1.0	2	28.5	0.5	3	31.3	0.3	3	32.0	0.7
Length of symphysis[c)]	M	5	37.4	1.6	8	42.8	1.3	2	48.0	1.0	3	58.0	2.5	3	59.7	5.7
	F	4	28.3	2.5	2	37.0	2.0	2	41.5	3.5	3	52.7	2.6	3	48.7	2.2
Length between[d)] Condylion mediale and Coronion	M	4	15.8	0.9	7	20.3	2.5	2	18.5	0.5	3	21.0	1.0	3	18.7	0.9
	F	4	14.3	1.0	2	17.5	3.5	2	19.0	0.0	3	18.7	0.3	3	19.7	1.3
Maximum alveolus[e)] length	M	5	81.0	1.8	8	101.1	2.1	2	124.5	1.5	3	133.0	3.2	3	135.3	5.5
	F	4	71.5	2.7	2	87.5	7.5	2	119.5	3.5	3	130.3	1.8	3	127.0	2.1
Breadth of two halves between the condyle processes	M	5	69.8	2.6	8	82.1	2.0	2	85.0	3.0	2	101.0	4.0	3	95.5	5.5
	F	4	59.3	1.8	2	76.5	0.5	2	84.0	4.0	3	89.0	1.0	3	89.3	0.9
Breadth of two halves between the most lateral points of the two angles	M	5	75.2	2.3	7	84.7	1.8	2	86.5	0.5	3	98.3	3.3	3	95.3	3.0
	F	3	65.7	1.8	2	76.5	0.5	1	86.0		3	92.7	0.3	3	89.3	1.7
Breadth of two halves between the coronoid processes	M	2	61.0	0	4	65.3	0.5	2	67.5	0.5	3	73.3	1.2	3	73.3	2.0
	F	4	51.8	1.4	1	59.0		1	69.0		3	70.7	0.7	3	71.0	0.6
Breadth of the mandible[f)] across the outer borders of M_1	M	5	38.8	0.5	8	41.6	0.8	2	44.5	1.5	3	45.7	2.4	3	49.0	1.2
	F	4	37.0	1.1	2	41.0	1.0	2	45.0	1.0	3	45.0	1.2	3	47.0	0.6
Thickness of ramus at M_1[g)]	M	5	15.0	0	8	16.5	0.3	2	17.0	0	3	19.7	0.9	3	19.3	0.9
	F	4	13.3	0.5	2	15.5	1.5	2	17.0	0	3	17.0	0.6	3	16.3	0.9

a) The measurements without footnote were based on Driesch [2].
b) Synonym of Höhe des Unterkiefers in der Mitte von M_1 [3].
c) Synonym of Länge der Symphyse [3].
d) Synonym of Condylocoronoidlänge [3].
e) The measurement was based on Abe [1].
f) Synonym of Breite des Unterkiefers auf der Höhe des M_1 [3].
g) Synonym of Breite je einer Mandibel auf der Höhe des M_1 [3].

parts of Ryukyu wild pig are certainly smaller in most Age groups.

In the crania, the facial length grew more rapidly than the median frontal length, indicating that growth of visceral cranium is more rapid than that of cerebral cranium in measurements of length. The items of breadth grew more slowly than those of length. That is, as the animal grows, the proportion of length to width seems to become gradually larger in the cranium.

In contrast to the items of length, the growth of the visceral cranium is slower in width than that of cerebral cranium. In short, the growth of the visceral cranium may contribute to the length, whereas that of the cerebral cranium may share the width in development of the cranium.

Positive allometrical correlation for the maximum alveolus length and the length of symphysis denotes that length of the body of mandible mainly contributes to the length from the angle in the mandible growth, whereas the development of the ramus of mandible is relatively insignificant. This finding is consistent with the fact that eruption of cheek teeth occurs in the newly-appeared body of mandible. As suggested from the relative growth coefficient of items in the mandible, the proportion of length to width seems to become larger in the developing mandible as well as in the cranium.

The relative growth coefficient of the breadth of the two halves between the most lateral points of the angles was larger than that of the breadth of the two halves between the coronoid processes in the mandible, whereas that of

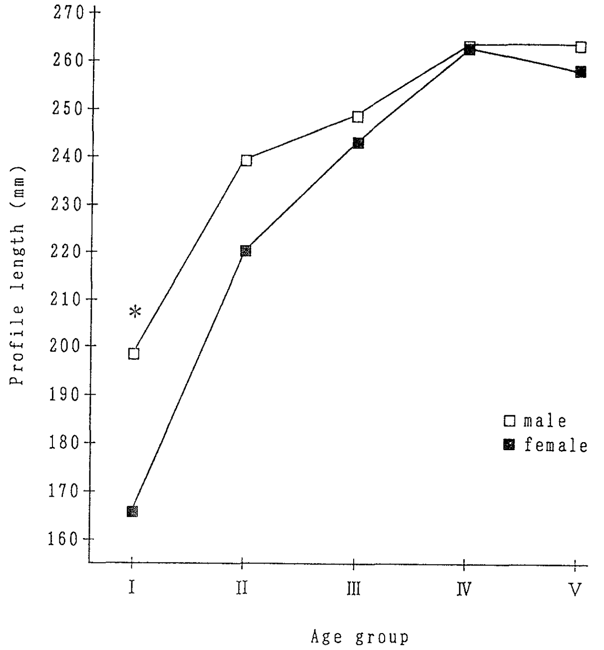

Fig. 1. The growth pattern of profile length. Points dotted represent the mean value. Significant difference between male and female: * $P<0.05$.

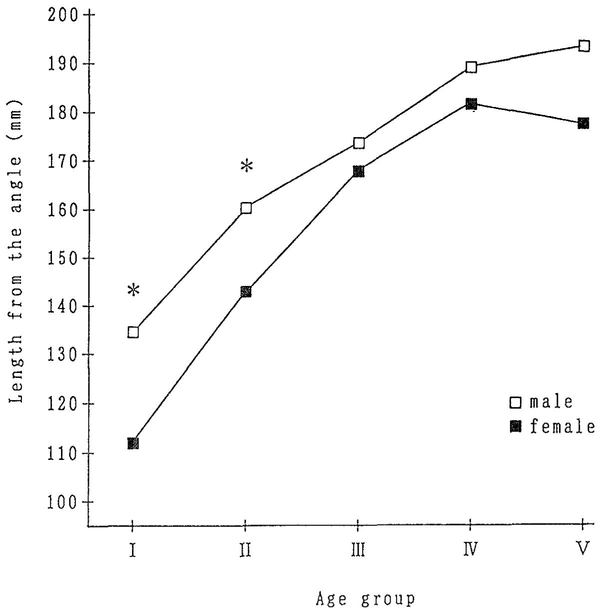

Fig. 2. The growth pattern of length from the angle. Points dotted represent the mean value. Significant difference between male and female: * $P<0.05$.

the zygomatic breadth was larger than that of the greatest neurocranium breadth in the cranium (Table 6). Since the masseter muscle originates in the zygomatic arch and converges on the Gonion laterale, while the temporal muscle originates in the lateral surface of cranium and inserts in the coronoid process [4], it can be said that measurements corresponding to the masseter muscle grow rapidly, although those pertaining to the temporal muscle

Table 6. Relative growth coefficient in some items
1. CRANIUM

	SEX	A[a)]	B[b)]
Profile length		1	0
Facial length	M	1.12	−1.42
	F	1.23	−1.99
Median frontal length	M	0.80	0.48
	F	0.80	0.47
Zygomatic breadth	M	0.83	0.04
	F	0.85	−0.04
Greatest frontal breadth	M	0.63	0.78
	F	0.66	0.60
Greatest breadth across the nasals	M	0.18	2.10
	F	0.46	0.61
Greatest neurocranium breadth	M	0.27	2.61
	F	0.29	2.48

2. MANDIBLE

	SEX	A[a)]	B[b)]
Length from the angle		1	0
Aboral height of the vertical ramus	M	0.98	−0.67
	F	1.04	−0.98
Middle height of the vertical ramus	M	0.90	−0.38
	F	1.01	−0.91
Height of the mandible at M_1	M	1.22	−2.85
	F	1.00	−1.77
Length of symphysis	M	1.28	−2.68
	F	1.24	−2.53
Maximum alveolus length	M	1.33	−2.12
	F	1.25	−1.61
Breadth of the two halves between the most lateral points of the two angles	M	0.88	−0.09
	F	0.81	0.28
Breadth of the two halves between the coronoid processes	M	0.60	1.12
	F	0.65	0.87
Breadth of the mandible across the outer borders of M_1	M	0.56	0.92
	F	0.46	1.46

*$\log Y = A \log X + B$: regression equation.
a) Relative growth coefficient, A.
b) B.

develop slowly. The relationship between the growth of measurements and that of muscles should be examined in more detail from the viewpoint of functional anatomy.

Imaizumi [9] considered Ryukyu wild pig as an independent species from Japanese wild pig. In multivariate analysis dealing with mandibles obtained from Amami-Oshima Island, we distinguished Ryukyu wild pig from Japanese subspecies in both size and shape vectors [7]. Kurosawa *et al.*, dealing with genetic studies on blood groups and polymorphisms of serum protein, concluded that Ryukyu wild pig from Amami-Oshima Island was distinguishable from the Japanese subspecies [13, 14]. However, the genetic data indicated that Ryukyu wild pig from Iriomote Island is not separable at the species level from Japanese wild pig [14, 15]. It has been suggested that this animal was introduced to Nansei Islands by ancient people [8, 17, 20]. However, fossil records appear to indicate that the animal migrated to the islands in Würm epoch when a land bridge connected the continent and Nansei Islands [5]. These conflicting problems on the taxonomy, phylogeny and paleontology will be solved by evaluating osteometry of the modern wild pig. Our osteometrical data, including the basic growth pattern, the occurrence of sexual dimorphism, and the relative growth coefficient of some measurements, can be effectively used to examine the origin and the history of this animal. In the future, a detailed comparison of the two kinds of wild pigs in Japan will be necessary to confirm them. In addition, a comparative osteometrical study is also needed among populations living on Nansei Islands.

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