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Morphological discrimination of the Ryukyu spiny rat (genus *Tokudaia*) between the islands of Okinawa and Amami Oshima, in the Ryukyu Islands, southern Japan

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Abstract. Thirty-eight museum specimens of the Ryukyu spiny rat, belonging to the genus *Tokudaia* Kuroda, 1943 (Rodentia, Muridae), from the islands of Amami Oshima and Okinawa, in the Ryukyu Islands (=the Nansei Islands), southern Japan, were examined and measured. Each specimen was classified into one of five age groups (I–V) determined by the wear of the three upper molars. The spiny rat of Okinawa has on average within age groups III and IV a statistically longer and wider skull and a longer molar row than that of Amami Oshima. However, neither the posterior nor the central parts of the skull length and width differ between the two islands. Against the same size of head and body length (H&BL) or incisor - the third upper molar length (I-M3), the spiny rat of Okinawa has longer I-M3 or narrower zygomatic arches than the spiny rat of Amami Oshima. The Okinawan spiny rat has a wider first upper molar (wM1 $\geqq$ 1.9 mm), whereas that of Amami Oshima is wM1 $\leqq$ 1.8 mm. The Okinawan spiny rat has the palatine foramen of the skull situated more posteriorly than that of Amami Oshima. These findings indicate conclusively that the spiny rat populations on the two islands of Amami Oshima and Okinawa have distinctly different morphological characteristics, in addition to having different karyotypes, and as such they should be regarded as distinct species. The spiny rat of Amami Oshima should be named as *Tokudaia osimensis* (Abe, 1933) while that of Okinawa should be known as *Tokudaia muenninki* (Johnson, 1946).

Key words: *Tokudaia osimensis*, *Tokudaia muenninki*, Okinawa, Amami Oshima.

The Ryukyu spiny rat (genus *Tokudaia* Kuroda, 1943) belongs to a genus that is endemic to Japan and that is distributed only on the islands of Amami Oshima, Tokuno Shima and Okinawa, in the Ryukyu Islands of southern Japan. The spiny rat is now regarded as endangered in Japan because of its extremely low population density; some attention has been paid to it from the perspective of biological conservation (Murakami and Kaneko 1997). Recent studies have demonstrated that chromosome features of the spiny rat differ among the three islands (Honda et al. 1977, 1978; Tsuchiya 1981; Tsuchiya et al. 1989). Furthermore, genetic studies of serum protein and DNA reveal differences between the populations occurring on the islands of Amami Oshima and Tokuno Shima (Tsuchiya et al. 1989; Suzuki et al.

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1999).

No recent morphological studies, however, have been carried out comparing the Ryukyu spiny rats of the three islands. Musser and Carleton (1993) and Musser and Koopman (1994) mistook Tsuchiya (1981) and Tsuchiya et al. (1989) and considered that three species had been distinguished using morphological and chromosomal features. As a consequence of that mistake, Musser and Carleton (1993) recognised two distinct species, *Tokudaia osimensis* from Amami Oshima and *T. muenninki* from Okinawa, and regarded Tokuno Shima population as a distinct species that had not been named. In contrast, Corbet and Hill (1992) and Kaneko (1994) recognized just one species of Ryukyu spiny rat *T. osimensis*, because full documentation of chromosomal and morphological differences is necessary for the recognition of a distinct species (Corbet and Hill 1994).

The purpose of this study was to examine the morphological differences between the spiny rats of Amami Oshima and Okinawa, and to revise their taxonomic status dependent on those results. It was not possible to examine the spiny rat of Tokuno Shima, because it is protected as a Japanese National Natural Monument, and no museum specimens have been preserved.

Materials and methods

The external and cranial measurements of thirty-eight museum specimens of the Ryukyu spiny rat were recorded. All of the specimens are deposited in the following institutions or my private collection: the National Museum of Natural History, Washington, D.C. (USNM); the National Science Museum, Tokyo, Japan (NSMT); the Zoological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan; the University of the Ryukyus, Okinawa, Japan; the Okinawa Prefecture Museum (OPM); Kaneko's private collection (K). Twenty specimens including the holotype of *Tokudamys osimensis muenninki* Johnson, 1946 (USNM 278757) were collected from the island of Okinawa, and 18 specimens were from the island of Amami Oshima.

External measurements of the lengths of head and body (H&BL), tail (TL), hind foot including nail length (HFL cu), and ear (EL) were obtained from labels attached to museum specimens. The length of the hind foot, not including nail length (HFL), was measured with 0.1 mm accuracy using a divider by the author, from skins or specimens preserved in alcohol. Paired structures were measured on the left side. The following 17 skull measurements were taken to the nearest 0.1 mm using a dial caliper by the author (the minimum accuracy=0.05 mm): condylobasal length (CBL)=distance between the occipital condyle and the anterior point of premaxillae; the greatest length of the skull (TSL)=the distance from the tip of the nasals to the posterior margin of the occiput; molar length (ML)=distance from the anterior edge of the alveolus of the first upper molar to the posterior edge of the third upper molar; incisor to the third upper molar length (I-M3)=distance between the most anterior point of the incisor and the most posterior edge of the third upper molar; condyle to zygomatic length (C-Z)=distance between the occipital condyle and the anterior-superior edge of the premaxillae; condyle to the first upper molar length (C-M1)=distance between the occipital condyle and the anterior edge of the first upper molar; length of diastema (Dias)=distance from the posterior edge of the upper incisive alveolus to the anterior edge of the alveolar space of the upper molar row; length of incisive foramen (IFL)=maximum length of the palatine slit; length of nasal (NL)=maximum length of the nasal bone; interorbital width (IOW)=least diameter of the frontal bones between the orbits; zygomatic width (ZW)= maximum spread of the zygomatic arches; first molar width (wM1)=maximum width of the first upper molar; molar width (MW)=maximum distance between the lateral border of the first upper molar on both sides; condyle to bullae length (C-B)=distance between the occi-

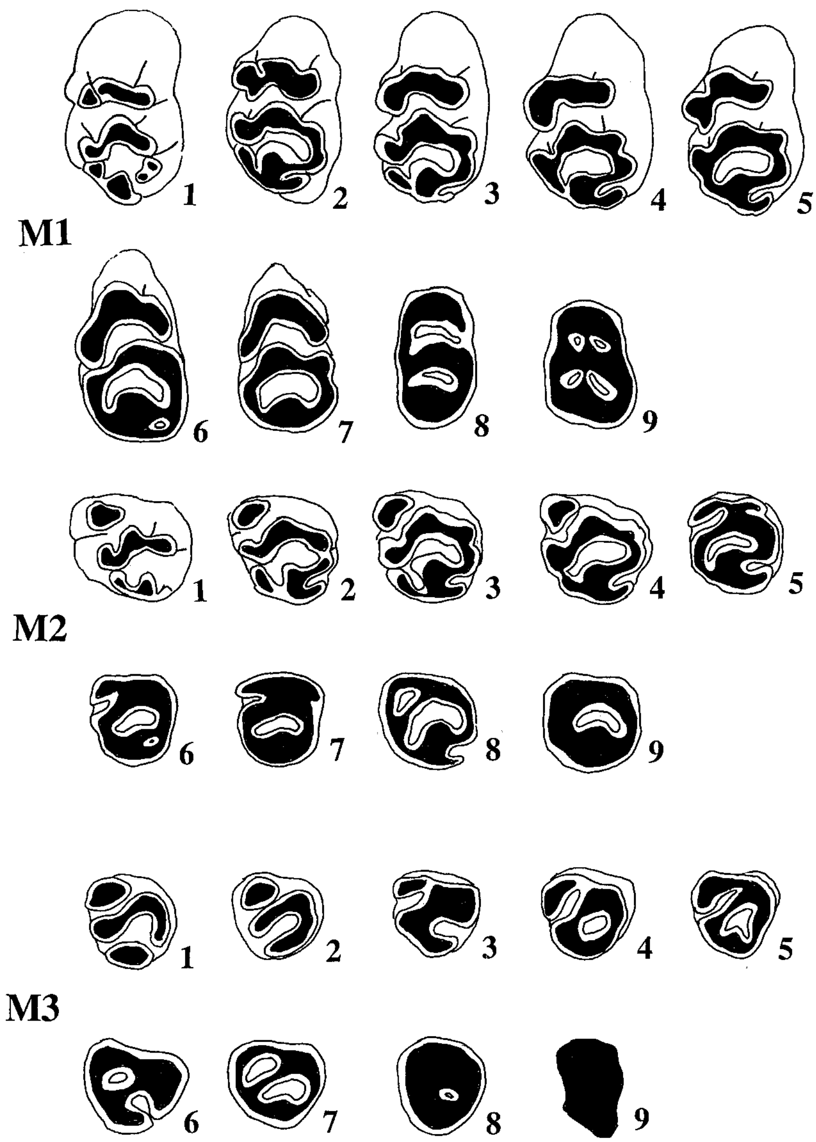

Fig. 1. Age criteria (1–9) of tooth wear on the first (M1), second (M2), and third (M3) upper molars of the Ryukyu spiny rat. The total score (reached by adding the number of each molar) is grouped into one of the following five categories (age groups I, II, III, IV, or V). Age group I=3–6; age group II=7–12; age group III=13–18; age group IV=19–24; and age group V=25–27.

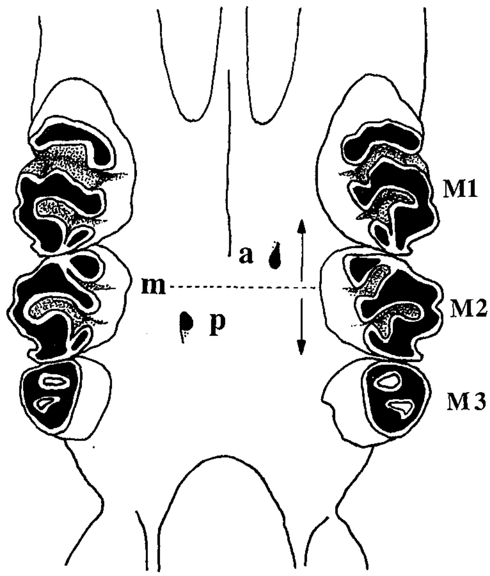

Fig. 2. The position of the palatine foramen (a, m, and p) between the upper molar row (M1, M2, and M3) on both sides. The position "m" lies on the posterior end of the anterostyle of the second molar on both sides.

pital condyle and the anterior point of the tympanic bullae; condyle to the third upper molar length (C-M3)=the length is given by subtracting ML from C-M1; length of tympanic bulla (BL)=maximum length of the tympanic bulla; width of tympanic bulla (BW)=maximum width of the tympanic bulla.

Enamel patterns on the upper three molars were used to determine relative age groups. First, close-up photographs of the upper molar rows were taken of museum specimens using an accessory close-up lens (1.75 × magnification) attached to an Olympus camera. Second, enamel patterns on the occlusal surface of the molars were drawn using a Nikon SMZ-10 stereo microscope at 6.6 × magnification. Third, one of the age criteria (1–9) as shown in Fig. 1 was assigned to each molar of each specimen according to drawings of the enamel patterns. Finally, each specimen was grouped into one of the five age groups, I (3–6), II (7–12), III (13–18), IV (19–24), and V (25–27), based on total scores by adding the number of each upper molar.

The position of the palatine foramen of the skull was classified as follows (Fig. 2): a= the foramen lies anteriorly from the posterior end of the anterostyle (t1) named by Miller (1912) on the second upper molar; m=the foramen lies just at the posterior end of the anterostyle on the same molar; p=the foramen lies posteriorly from the posterior end of the anterostyle on the same molar.

Two regression lines of Y measurements on X ones were tested statistically on the differences in slope and in position using the analysis of covariance (Snedecor 1956).

Results

The average, standard deviations and ranges of the external and cranial dimensions of spiny rats from the islands of Okinawa and Amami Oshima were compared in relation to their assignment to five age groups (Tables 1–4). Measurements of specimens belonging to age groups I and V could not be compared statistically between the two islands because of the small sample size. The number of measurements showing a statistical difference between the two islands increases from age group II to IV. Most of the measurements of the Okinawan spiny rat are statistically greater than those of the Amami spiny rat (in age groups III and IV; $P<0.05$, Student's t-test). In age groups III and IV, there were statistically significant differences between the two island populations between the averages of H&BL and HFL, but not between TL and EL. In age groups III and IV, statistically significant differences were found between the averages of most of the cranial measurements except for C-B, BL, IOW, and MW, which are either posterior parts of the skull length (C-B and BL) or central parts of the skull width (IOW and MW). No significant differences were found in the averages of ML among age groups I–IV in the Okinawan spiny rat ($F=1.09$, $df/df=3/14$, $P>0.05$) or among age groups II–IV in the Amami spiny rat ($F=2.60$, $df/df=2/13$, $P>0.05$). The linear regression of ML on age was not significant, indicating that ML is constant throughout age groups II, III and IV.

The relationship between H&BL and TL shows that the tail ratio is about 60–100% in the Okinawan and Amami spiny rats (Fig. 3). The Okinawan spiny rat has a slightly smaller tail ratio (average$\pm SD=74.1\pm8.01$%, $n=15$) than the Amami spiny rat (average$\pm SD=80.1\pm10.54$%, $n=17$), but the averages of the two island populations was statistically insignificant (Mann-Whitney U-test, $Us=170.5$, $0.1<P<0.2$).

Statistically significant relationships between CBL and I-M3 can be found in both the Okinawan spiny rat ($r=0.965$, $df=16$, $P<0.001$) and the Amami spiny rat ($r=0.954$, $df=12$, $P<0.001$; Fig. 4). The two regression lines are statistically different in their position (analysis of covariance; $F=32.649$, $df/df=1/29$, $P<0.005$). The skull of the Okinawan spiny rat has a slightly longer I-M3 than does the Amami spiny rat for the same sized CBL. The Okinawan spiny rat has a skull with a CBL of more than 36 mm and an I-M3 of more than 20 mm, proportions not found in the Amami spiny rat. From hereon we use I-M3 as a standard skull measurement, because within the pooled samples from the two islands the posterior parts of some skulls were broken thus more measurements were available for I-M3 than for CBL.

Statistically significant relationships between H&BL and I-M3 were found in both Okinawan ($r=0.772$, $df=16$, $P<0.001$) and Amami spiny rats ($r=0.679$, $df=14$, $0.001<P<0.01$; Fig. 5). The two regression lines of I-M3 on H&BL for the two taxa are statistically different in position (analysis of covariance; $F=34.965$, $df/df=1/31$, $P<0.005$). It follows that the Okinawan spiny rat has a slightly longer I-M3 than the Amami spiny rat for the same size of H&BL.

Three significant relationships between I-M3 and cranial measurements demonstrate the main differentiation of the skulls between the two island rat taxa. Statistically significant relationships between I-M3 and C-M3 were found in both the Okinawan ($r=0.905$, $df=16$, $P<0.001$) and the Amami spiny rats ($r=0.825$, $df=12$, $P<0.001$; Fig. 6). The two regression lines of C-M3 on I-M3 for the two taxa are statistically different in position (analysis of covariance; $F=64.986$, $df/df=1/29$, $P<0.005$). Thus, the Okinawan spiny rat has a shorter C-M3 than the Amami spiny rat for the same size of I-M3. This indicates that the anterior parts of the skull (I-M3) increase more in the Okinawan spiny rat than in the Amami spiny

Table 1. External and cranial measurements (mm) of the Okinawan spiny rat, identified as *Tokudaia muenninki*.

Age group	Items	H&BL	TL	HFL	EL	CBL	TSL	ML	I-M3	C-Z	C-M1	Dias
I	Average	116.75	95.40	31.35	20.40	31.20	35.00	6.00	17.80	22.50	19.35	8.75
	SD	6.718	1.980	0.495	0.849	1.273	0.990	0.141	0.424	1.414	0.636	0.212
	Max.	121.5	96.8	31.7	21.0	32.1	35.7	6.1	18.1	23.5	19.8	8.9
	Min.	112.0	94.0	31.0	19.8	30.3	34.3	5.9	17.5	21.5	18.9	8.6
	n	2	2	2	2	2	2	2	2	2	2	2
II	Average	137.50	105.67	32.10	19.97	35.05	38.85	6.08	19.56*	24.90	21.95*	10.18
	SD	18.592	9.713	2.048	3.573	1.609	2.199	0.263	1.128	0.942	0.705	0.675
	Max.	154.0	114.0	34.4	24.0	36.9	41.3	6.3	20.6	25.8	22.7	10.9
	Min.	119.0	95.0	29.8	17.2	33.0	36.3	5.7	17.9	23.6	21.0	9.6
	n	4	3	4	3	4	4	4	5	4	4	4
III	Average	144.01*	107.04	32.68*	21.93	35.85*	40.14*	6.11*	19.93*	25.40*	22.13*	10.60*
	SD	12.026	9.524	0.684	1.564	1.049	0.993	0.203	0.529	0.983	0.789	0.436
	Max.	158.0	119.0	34.0	23.5	37.3	41.4	6.4	20.6	27.4	23.2	11.3
	Min.	126.0	92.0	31.8	19.6	34.2	39.0	5.8	19.3	24.4	20.8	10.1
	n	8	7	8	6	8	7	9	9	8	8	9
IV	Average	161.67*	114.67	33.50*	23.17	37.13*	41.65*	6.33*	20.60*	27.07*	23.03*	11.00*
	SD	3.786	15.144	1.323	0.764	0.757	0.636	0.306	0.625	0.551	0.231	0.265
	Max.	166.0	132.0	35.0	24.0	38.0	42.1	6.6	21.3	27.6	23.3	11.3
	Min.	159.0	104.0	32.5	22.5	36.6	41.2	6.0	20.1	26.5	22.9	10.8
	n	3	3	3	3	3	2	3	3	3	3	3
V	*n*=1	175	50+	32	25	38.2	41.7	6.1	20.9	27.0	23.8	11.4

* The average is statistically significantly different (Student's *t*-test) between the same two measurements of animals in the same age group from the two islands.

Table 2. Cranial measurements (mm) of the Okinawan spiny rat, identified as *Tokudaia muenninki*.

Age group	Items	IFL	NL	IOW	ZW	wM1	MW	C-B	C-M3	BL	BW
I	Average	6.75	14.30	6.95	15.40	2.00	7.10	8.40	13.40	6.30	5.35
	SD	0.636	0.283	0.071	0.283	0.000	0.283	0.141	0.849	0.424	0.071
	Max.	7.2	14.5	7.0	15.6	2.0	7.3	8.5	14.0	6.6	5.4
	Min.	6.3	14.1	6.9	15.2	2.0	6.9	8.3	12.8	6.0	5.3
	n	2	2	2	2	2	2	2	2	2	2
II	Average	7.80*	16.16*	7.24	17.25	2.0	7.65*	9.73	15.48	7.15	5.68*
	SD	0.418	0.764	0.365	1.240	0.163	0.420	0.492	0.960	0.507	0.150
	Max.	8.3	17.2	7.8	18.9	2.3	8.2	10.3	16.3	7.6	5.8
	Min.	7.4	15.3	6.9	15.9	1.9	7.2	9.1	14.1	6.5	5.5
	n	5	5	5	4	4	4	4	4	4	4
III	Average	7.97*	17.14*	7.37	17.30*	2.0*	7.70*	9.79	15.94*	6.89	5.66*
	SD	0.296	0.646	0.346	0.823	0.100	0.387	0.372	0.605	0.295	0.250
	Max.	8.5	18.2	7.8	18.7	2.2	8.3	10.3	16.7	7.4	6.0
	Min.	7.5	16.2	6.7	15.9	1.9	7.2	9.3	14.8	6.6	5.3
	n	9	8	9	8	9	9	8	8	8	8
IV	Average	8.27*	17.30*	7.87*	18.63*	2.0*	7.97	9.77	16.53*	7.40	5.73*
	SD	0.208	0.520	0.321	0.379	0.000	0.252	0.416	0.153	0.700	0.252
	Max.	8.5	17.6	8.1	18.9	2.0	8.2	10.1	16.7	8.2	6.0
	Min.	8.1	16.7	7.5	18.2	2.0	7.7	9.3	16.4	6.9	5.5
	n	3	3	3	3	3	3	3	3	3	3
V	*n*=1	7.8	18.4	7.5	19.5	2	7.8	10.1	17.3	7.1	6.1

* The average is statistically significantly different (Student's *t*-test) between the same two measurements of animals in the same age group from the two islands.

Table 3. External and cranial measurements (mm) of the spiny rat identified as *Tokudaia osimensis* on Amami Oshima.

Age group	Items	H&BL	TL	HFL	EL	CBL	TSL	ML	I-M3	C-Z	C-M1	Dias
I	$n=1$	89	61	24.5				5.0				
II	Average	121.13	99.13	30.85	25.75	32.53	36.30	5.42	17.16*	23.37	20.50*	9.30
	SD	14.505	10.617	1.310	4.272	0.493	0.656	0.837	1.161	0.569	0.436	0.696
	Max.	138.5	107.0	32.4	32.0	33.1	37.0	5.5	17.9	24.0	21.0	9.9
	Min.	103.0	83.5	29.2	23.0	32.2	35.7	5.3	15.1	22.9	20.2	8.1
	n	4	4	4	4	3	3	5	5	3	3	5
III	Average	130.25*	101.92	29.97*	22.50	32.67*	36.60*	5.33*	17.62*	23.63*	20.55*	9.57*
	SD	6.130	12.192	1.088	0.837	1.472	1.420	0.197	0.605	0.973	1.045	0.427
	Max.	140.0	114.0	31.7	23.0	35.4	39.2	5.6	18.7	25.4	22.4	10.3
	Min.	123.0	84.0	28.8	21.0	31.2	35.0	5.0	16.9	22.9	19.4	9.1
	n	6	6	6	6	6	6	6	6	6	6	6
IV	Average	139.82*	112.94	30.62*	20.16	33.55*	37.03*	5.56*	18.32*	24.23*	21.08*	10.10*
	SD	7.783	9.603	0.614	2.060	0.443	0.222	0.182	0.303	0.350	0.250	0.255
	Max.	149.0	125.0	31.5	23.0	33.9	37.2	5.8	18.6	24.6	21.4	10.5
	Min.	129.0	100.0	30.0	18.1	32.9	36.7	5.4	18.0	23.8	20.8	9.8
	n	5	5	5	5	4	4	5	5	4	4	5
V	$n=1$	160	135	34	21.5	35.6	38.6	5.6	19.3	25.3	21.9	11.1

* The average is statistically significantly different (Student's *t*-test) between the same two measurements of animals in the same age group from the two islands.

Table 4. Cranial measurements (mm) of the spiny rat identified as *Tokudaia osimensis* on Amami Oshima.

Age group	Items	IFL	NL	IOW	ZW	wM1	MW	C-B	C-M3	BL	BW
I	$n=1$	5.3				1.5					
II	Average	6.60*	14.63*	6.56	16.25	1.70	6.82*	9.50	14.93	7.05	5.15*
	SD	0.721	0.275	0.586	0.173	0.701	0.327	0.265	0.404	0.265	0.058
	Max.	7.5	14.9	7.2	16.5	1.8	7.1	9.8	15.4	7.4	5.2
	Min.	5.5	14.3	5.6	16.1	1.6	6.3	9.3	14.7	6.8	5.1
	n	5	4	5	4	5	5	3	3	4	4
III	Average	6.87*	14.92*	7.15	16.42*	1.73*	6.98*	9.45	15.05*	7.08	5.33*
	SD	0.579	0.479	0.251	0.595	0.082	0.232	0.602	0.878	0.382	0.288
	Max.	7.6	15.8	7.4	17.3	1.8	7.2	10.4	16.7	7.7	5.7
	Min.	6.2	14.5	6.8	15.6	1.6	6.6	8.8	14.3	6.6	4.9
	n	6	6	6	6	6	6	6	6	6	6
IV	Average	7.22*	14.94*	7.34*	17.03*	1.76*	7.34	10.08	15.30*	7.18	5.30*
	SD	0.192	0.688	0.152	0.737	0.055	0.397	0.377	0.365	0.192	0.200
	Max.	7.5	15.7	7.6	18.1	1.8	7.8	10.4	15.7	7.4	5.5
	Min.	7.0	14.0	7.2	16.5	1.7	6.8	9.5	14.9	6.9	5.1
	n	5	5	5	4	5	5	5	4	5	5
V	$n=1$	7.6	15.2	7.4		1.7	7.8	10.1	16.2	7.2	5.4

* The average is statistically significantly different (Student's *t*-test) between the same two measurements of animals in the same age group from the two islands.

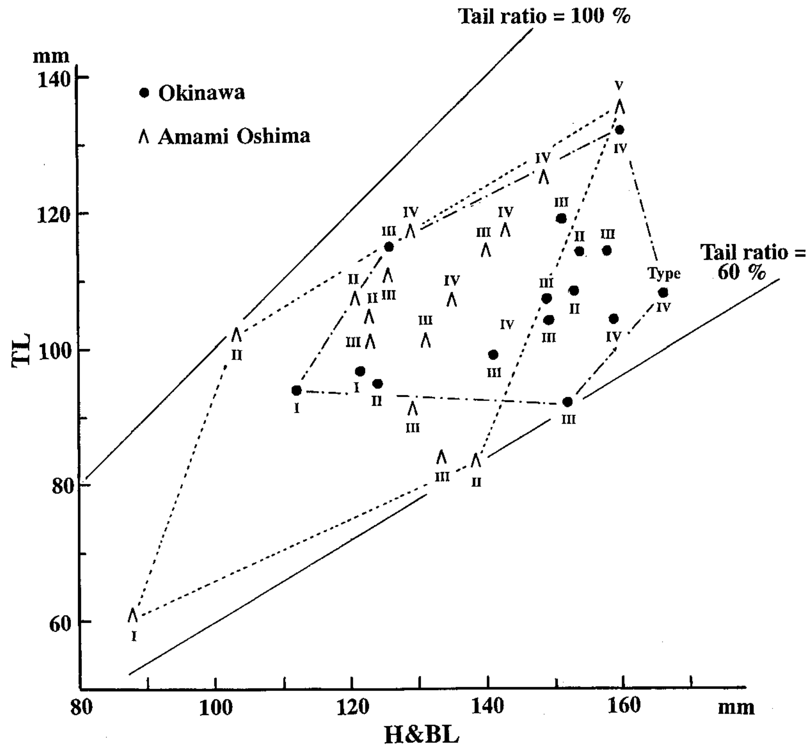

Fig. 3. The relationship between H&BL and TL. Age groups are shown as I–V. "Type" indicates the holotype of *Tokudamys osimensis muenninki* (USNM 278757).

rat in comparison with the posterior parts of the skull (C-M3).

Statistically significant relationships between I-M3 and Dias were found in both the Okinawan ($r=0.916$, $df=17$, $P<0.001$) and the Amami spiny rats ($r=0.950$, $df=15$, $P<0.001$; Fig. 7). The two regression lines of Dias on I-M3 for the two island taxa differ statistically in their position (analysis of covariance; $F=25.338$, $df/df=1/33$, $P<0.005$). The Okinawan spiny rat has a shorter Dias than the Amami spiny rat for the same size of I-M3. Conversely, for the same size of Dias, the Okinawan spiny rat has a longer I-M3 (about 1 mm) than the Amami spiny rat. As mentioned above, ML is constant throughout the various age groups of both taxa and the averages of ML are greater in the Okinawan form (about 0.6–0.8 mm) than in the Amami Oshima form for the same age (see Tables 1 and 3). It follows that the longer anterior parts of the skull (I-M3) in the Okinawan spiny rat are mainly attributed to ML, because I-M3 is composed of Dias and ML with a short transversal depth of the incisor.

Statistically significant relationships between I-M3 and ZW were found in both the Okinawan ($r=0.851$, $df=17$, $P<0.001$) and the Amami spiny rats ($r=0.780$, $df=13$, $0.001<P<0.01$; Fig. 8). The two regression lines of ZW on I-M3 for the two taxa are statistically different in position (analysis of covariance; $F=11.305$, $df/df=1/29$, $P<0.005$). Thus, the Okinawan spiny rat has narrower zygomatic arches than the Amami spiny rat for the same size of I-M3.

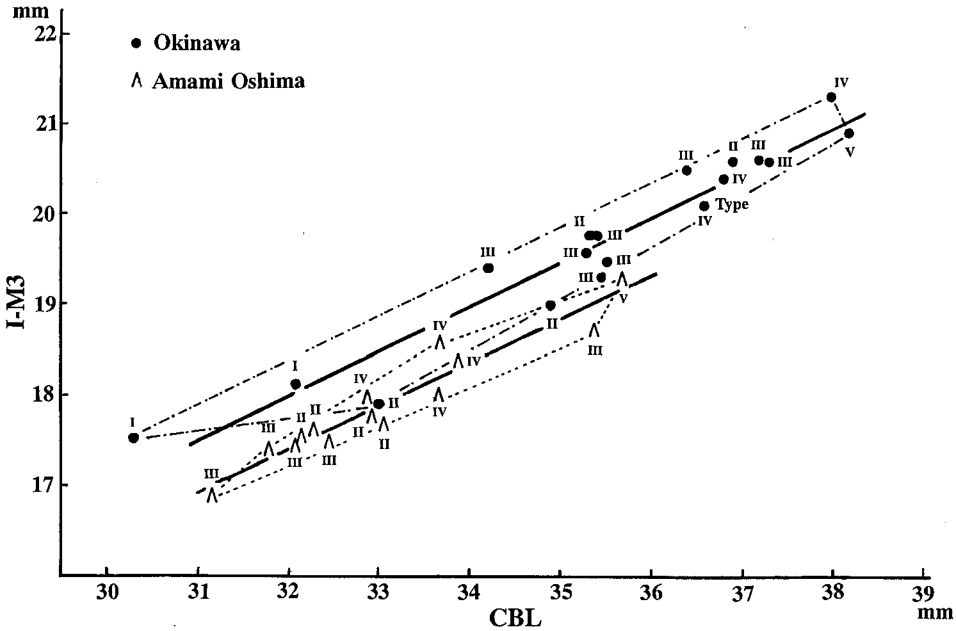

Fig. 4. The relationship between CBL and I-M3. Age groups are shown as I–V. "Type" indicates the holotype of *Tokudamys osimensis muenninki* (USNM 278757). Regression lines are I-M3=0.497 (CBL)+2.085 for Okinawan specimens, and I-M3=0.480 (CBL)+2.040 for Amami Oshima specimens.

According to the relationship between ML and wM1 (Fig. 9), the Okinawan spiny rat has a longer molar row (ML≧5.7 mm) and the Amami spiny rat is ML≦5.8 mm, although the range of ML overlaps from 5.7 to 5.8 mm in the two taxa. The overlapping range of the Okinawan spiny rat occurs in slightly younger age groups (II and III) than that of Amami Oshima (age group IV). The Okinawan spiny rat is wM1≧1.9 mm, whereas that of Amami Oshima is wM1≦1.8 mm. Thus, we can discriminate between the two taxa on the basis of the size of wM1.

The position of the palatine foramen also differs between the two island populations (Table 5). In the Okinawan spiny rat the position is posterior on both sides (p/p), or a posterior and middle position on one side (p/m), whereas in the Amami spiny rat the position is either anterior on both sides (a/a) or the middle position on both sides (m/m). Thus, the palatine foramen lies more posteriorly in the Okinawan spiny rat than in the Amami spiny rat.

The measurements of the holotype, *Tokudamys osimensis muenninki* (USNM 278757), are as follows: H&BL=166 mm; TL=108 mm; HFL (cu)=35 mm; HFL=32.5 mm; EL=24 mm; CBL=36.6 mm; TSL=41.2 mm; ML=6.0 mm; I-M3=20.1 mm; C-Z=26.5 mm; C-M1=22.9 mm; Dias=10.8 mm; IFL=8.5 mm; NL=17.6 mm; IOW=8.0; ZW=18.9; wM1=2.0 mm; MW=8.2 mm; C-B=10.1; C-M3=16.5 mm; BL=6.9 mm; and BW=5.5 mm. The specimen has prominent mammae indicating that it was adult, and belongs to age group IV (7 on M1, 8 on M2, and 7 on M3).

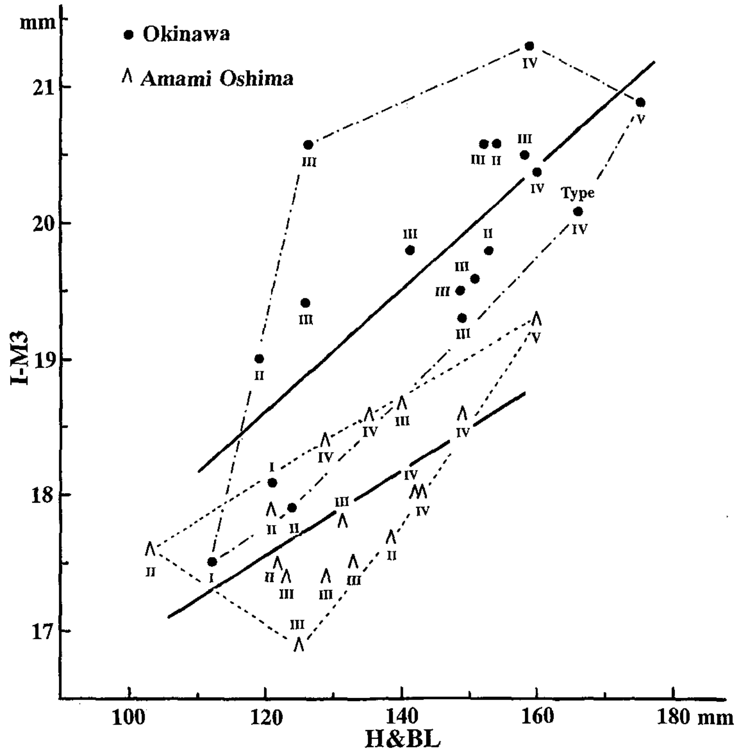

Fig. 5. The relationship between H&BL and I-M3. Age groups are shown as I–V. "Type" indicates the holotype of *Tokudamys osimensis muenninki* (USNM 278757). Regression lines are I-M3=0.045(H&BL)+13.248 for Okinawan specimens, and I-M3=0.032 (H&BL)+13.738 for Amami Oshima specimens.

Discussion

The Ryukyu spiny rat was first described by Abe (1933) as a new subspecies, *Rattus jerdoni osimensis*, based on four specimens collected from the island of Amami Oshima. Four syntypes were described, but they are presumed to have been deposited in Hiroshima University where they were destroyed in the Second World War. Tokuda (1941) revised the classification of the taxon assigning it to a new genus as *Acanthomys osimensis*, which has quite different characters from *Rattus*. However, because the genus *Acanthomys* was preoccupied by *Acanthomys* Lesson, 1842, Kuroda (1943) proposed the creation of a completely new genus, *Tokudaia*, and also reported the occurrence of the species on the island of Okinawa. Unaware of the new generic name created by Kuroda (1943), Johnson (1946) assigned the Okinawan form as a new subspecies of another new genus *Tokudamys osimensis muenninki*. Johnson (1946) remarked that *Tokudamys osimensis muenninki* has larger head and body and skull lengths, and a shorter tail (average=73% in tail ratio) than *T. o. osimensis* from Amami Oshima (average=87% in tail ratio). Because *Tokudamys* was antedated by *Tokudaia*, the Ryukyu spiny rat has been accepted as *Tokudaia osimensis osimensis* on Amami Oshima and *T. o. muenninki* on Okinawa (Ellerman and Morrison-Scott 1951; Kuroda 1957, 1965; Imaizumi 1960; Corbet and Hill 1992).

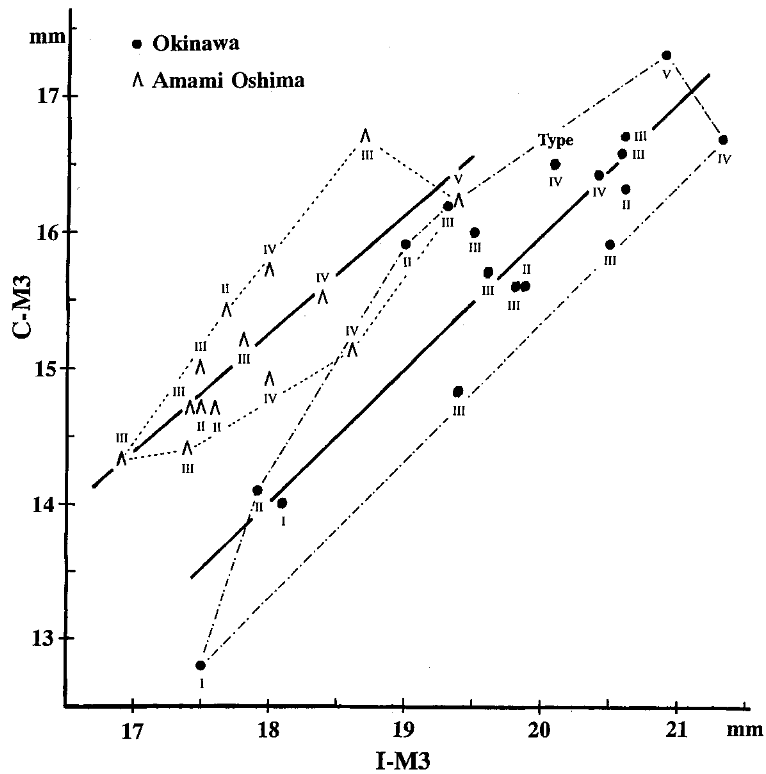

Fig. 6. The relationship between I-M3 and C-M3. Age groups are shown as I–V. "Type" indicates the holotype of *Tokudamys osimensis muenninki* (USNM 278757). Regression lines are C-M3=0.969 (I-M3)−3.368 for Okinawan specimens, and C-M3=0.873 (I-M3)−0.469 for Amami Oshima specimens.

According to Honda et al. (1977, 1978), Tsuchiya (1981) and Tsuchiya et al. (1989), karyological features in the autosomes and sex chromosomes vary among the spiny rat populations of Amami Oshima, Tokuno Shima, and Okinawa. The diploid numbers of both females and males are 25 on Amami Oshima, 45 on Tokuno Shima, and 44 on Okinawa. The Y-chromosome has disappeared in the populations of Amami Oshima and Tokuno Shima (Honda et al. 1977, 1978). Furthermore, Tsuchiya et al. (1989) and Suzuki et al. (1999) showed that serum protein, mitochondrial DNA, and nuclear ribosomal DNA differ between the populations of Amami Oshima and Tokuno Shima. Based on their results, Tsuchiya (1981), and Tsuchiya et al. (1989) suggested that the spiny rats of Okinawa, Amami Oshima and Tokuno Shima should be considered as three distinct species, while Suzuki et al. (1999) suggested that the spiny rats of Amami Oshima and Tokuno Shima are not conspecific.

Musser and Carleton (1993) and Musser and Koopman (1994) misinterpreted Tsuchiya (1981) and Tsuchiya et al. (1989) as having distinguished three species on the basis of both morphological and chromosomal features. Consequently, Musser and Carleton (1993) considered there to be two distinct named species, *Tokudaia osimensis* from Amami Oshima, and *Tokudaia muenninki* from Okinawa, as well as a distinct, but unnamed, species on Tokuno Shima, and they were followed by Nowak (1999).

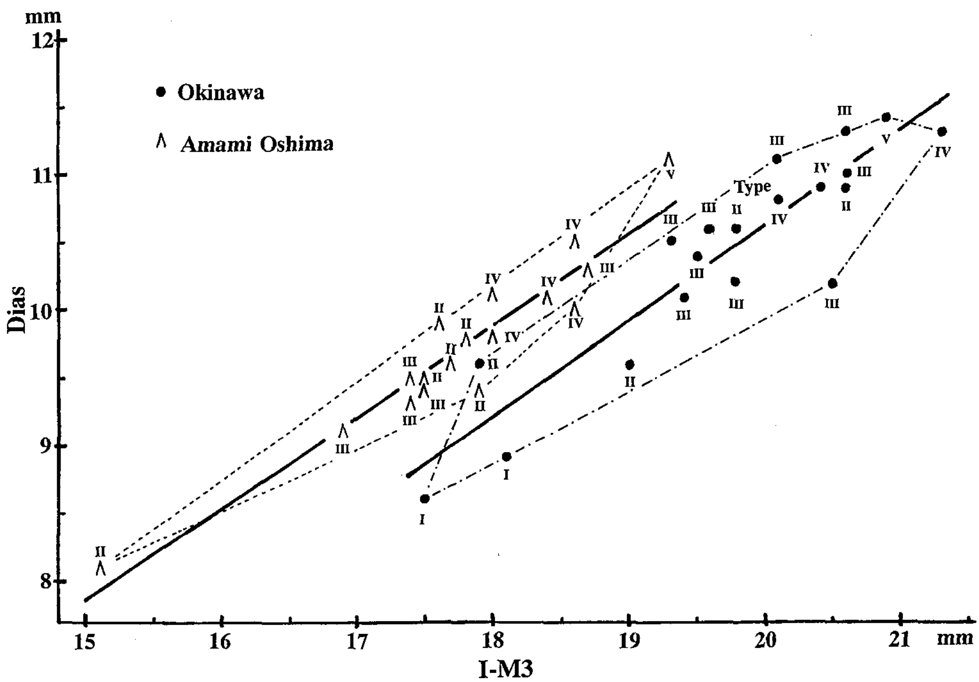

Fig. 7. The relationship between I-M3 and Dias. Age groups are shown as I–V. "Type" indicates the holotype of *Tokudamys osimensis muenninki* (USNM 278757). Regression lines are Dias=0.696 (I-M3)−3.326 for Okinawan specimens, and Dias=0.674 (I-M3)−2.254 for Amami Oshima specimens.

Corbet and Hill (1992) and Kaneko (1994), however, recognized just one species, the Ryukyu spiny rat *Tokudaia osimensis*, because full documentation of the differences correlating chromosomal and morphological data were not available (Corbet and Hill 1994).

The present results indicate that the Ryukyu spiny rat does in fact show morphologically differentiated growth patterns between the islands of Okinawa and Amami Oshima. Absolute growth of same age individuals was differentiated as follows. The Okinawan spiny rat has, externally, a longer head and body and hind foot than the Amami spiny rat; the Okinawan spiny rat has a longer skull, longer anterior parts, a longer molar row, wider zygomatic arches and wider tympanic bullae than the Amami spiny rat. Differentiation between the Okinawan and the Amami spiny rats was possible in the relationships either between I-M3 and H&BL, between I-M3 and CBL, between I-M3 and C-M3, between I-M3 and Dias, between I-M3 and ZW, or between ML and wM1. These findings indicate that the Okinawan spiny rat has longer anterior parts of the skull, contributed by longer ML, and narrower zygomatic arches, than does the Amami spiny rat for the same size of I-M3. Furthermore, the position of the palatine foramen also differed between the two island populations; the Okinawan spiny rat has a more posterior foramen than does the Amami spiny rat. Because the two taxa can also be differentiated on the basis of their chromosomal features (Honda et al. 1977, 1978; Tsuchiya 1981; Tsuchiya et al. 1989), I recognize that the two rat taxa of the Okinawa and Amami Oshima, are two distinct species. I designate the Amami spiny rat as *Tokudaia osimensis* (Abe, 1933) and the Okinawan spiny rat as

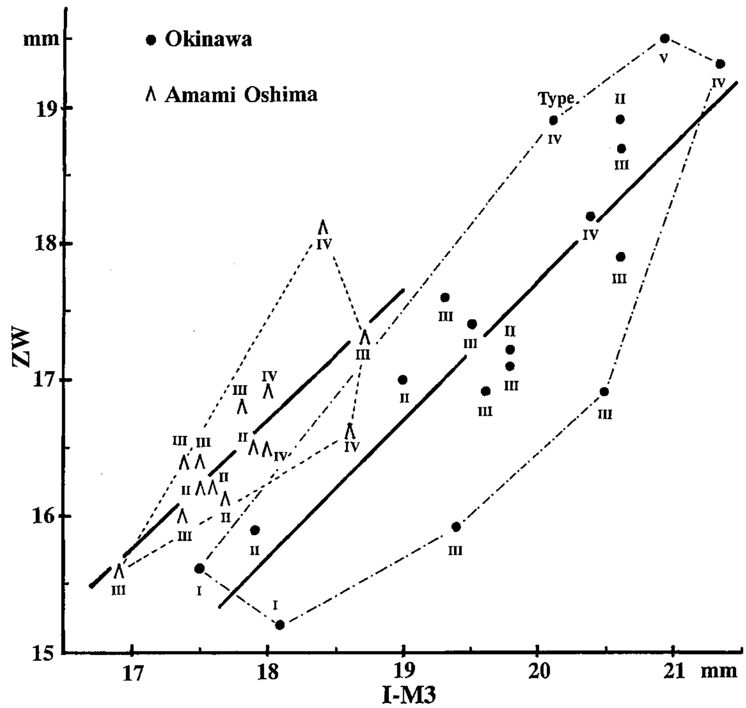

Fig. 8. The relationship between I-M3 and ZW. Age groups are shown as I–V. "Type" indicates the holotype of *Tokudamys osimensis muenninki* (USNM 278757). Regression lines are ZW=1.008 (I-M3)−2.447 for Okinawan specimens, and ZW=0.952 (I-M3)−0.420 for Amami Oshima specimens.

Tokudaia muenninki (Johnson, 1946).

In this study, the Okinawan spiny rat had a longer upper molar row (ML≧5.7 mm), while the Amami spiny rat was ML≦5.8 mm, although the range of 5.7–5.8 mm overlapped

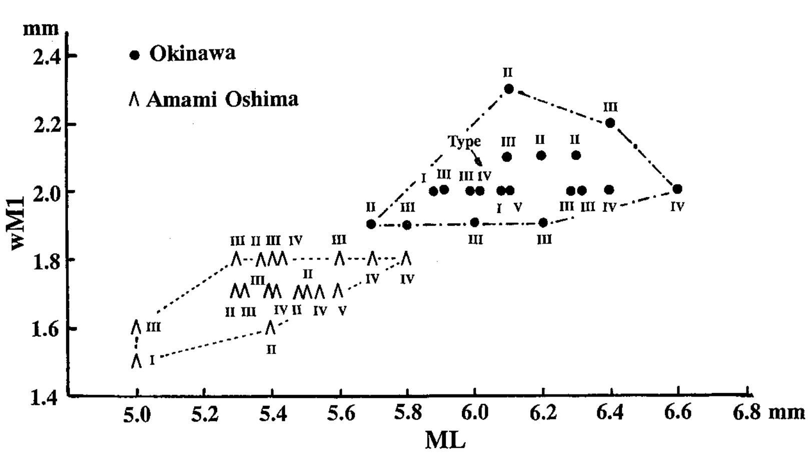

Fig. 9. The relationship between ML and wM1. Age groups are shown as I-V. "Type" indicates the holotype of *Tokudamys osimensis muenninki* (USNM 278757).

Table 5. The position of the palatine foramen in the Okinawan (Ok) and Amami (Am) spiny rats in relation to five age groups.

Position*	Age group				
	I	II	III	IV	V
a/a	Am=2	Am=4	Am=9	Am=2	
m/m				Am=1	Am=1
p/m		Ok=1	Ok=1	Ok=2	
p/p		Ok=4	Ok=3	Ok=4**	Ok=1

* a=anterior, p=posterior, m=middle (see Fig. 2).

** The holotype of *Tokudamys osimensis muenninki* (USNM 278757) is included.

between the two taxa. The specimens reported by Abe (1934) and Kuroda (1943) had ML measurements of 5.3 mm, 5.3 mm, and 5.5 mm (three specimens from Amami Oshima), and 6.6 mm (one specimen from Okinawa). Thus, those early ML measurements provide further confirmation of the present findings that there are clear differences between the two island populations. Neither Abe (1934) nor Kuroda (1943), however, gave other skull or tooth measurements comparable with those made during this study.

According to photographs and figures published by Abe (1934), Tokuda (1941) and Abe (2000), the position of the palatine foramen of the skull in the Amami spiny rat differs as follows. Two specimens were shown with the palatine foramen in anterior positions on both sides or an anterior and middle position on one side (Abe 1934), and one specimen with an anterior palatine foramen on both sides (Tokuda 1941; Abe 2000). Thus, these illustrations also serve to support the present results confirming a difference in the position of the palatine foramen between the two island populations.

With regards to fossil specimens collected from Minatogawa on Okinawa dated to the late Pleistocene, and identified as *T. osimensis* by Kowalski and Hasegawa (1976) and Kawamura (1989), their measurements (ML and wM1) actually suggest the following identification. Three specimens (Kawamura 1989) are *T. muenninki* based on ML=6.66 mm and wM1=1.97 mm (KUJC 100553), ML=6.34 mm and wM1=1.88 mm (KUJC 100557), and ML=6.02 mm and wM1=1.86 mm (KUJC 100558). Two specimens (Kowalski and Hasegawa 1976) are *T. osimensis*, because based on ML=5.0 mm (NSMT-M 10360), and ML=5.2 mm (NSMT-M 10361). One of the specimens with an ML of 5.8 mm (NSMT-M 10362) reported by Kowalski and Hasegawa (1976) is within the range of overlap between the two species (Fig. 9), however, it is possible to identify the specimen as *T. muenninki* of age group III, based on their illustration. Thus, these fossil remains indicate that both *T. osimensis* and *T. muenninki* lived on the island of Okinawa in the late Pleistocene. Re-examination of the fossil specimens is necessary, however, to reconfirm their measurements.

Classification

The historical usage of the sub-specific/specific names *osimensis* and *muenninki* in relation to the associated taxa, their distribution, type locality, and type specimens can be summarized as follows:

Tokudaia osimensis (Abe, 1933)

Distribution: the island of Amami Oshima, the Ryukyu Islands, southern Japan.

Type locality: Mt. Kiyago-kan, Sumiyo Village, Amami Oshima.

Syntypes: four specimens without registration, and presumably destroyed in Hiroshima in 1945.

Rattus jerdoni osimensis; Abe 1933, p. 942; Abe 1934, p. 107; Kuroda 1938, p. 67; Kuroda 1940, p. 137.

Rattus fulvescens osimensis; Ellerman 1941, p. 193.

Acanthomys osimensis; Tokuda 1941, p. 95.

Tokudaia osimensis; Kuroda 1943, p. 61; Ellerman and Morrison-Scott 1951, p. 558; Kuroda 1957, p. 14; Imaizumi 1960, p. 152; Kuroda 1965, p. 684; Walker 1968, p. 873; Corbet and Hill 1980, p. 168; Honacki, Kinman and Koeppl 1982, p. 557; Nowak, 1983, p. 695; Corbet and Hill 1986, p. 190; Sokolov, 1988, p. 189; Corbet and Hill 1991, p. 178; Nowak 1991, p. 803; Tang 1992, p. 217; Corbet and Hill 1992, p. 391; Musser and Carleton 1993, p. 670; Kaneko 1994, pp. 104, 169, 178 and 180; Nowak 1999, p. 1501; Abe 2000, pp. 94 and 232.

Tokudamys osimensis osimensis; Johnson 1946, p. 169.

Tokudaia muenninki (Johnson, 1946)

Distribution: the north of the island of Okinawa, the Ryukyu Islands, southern Japan.

Type locality: Hentona, western coast of northern Okinawa, the Ryukyu Islands.

Holotype: USNM 278757

Tokudaia osimensis; Kuroda 1943, p. 61; Walker 1968, p. 873; Corbet and Hill 1980, p. 168; Nowak 1983, p. 695; Corbet and Hill 1986, p. 190; Corbet and Hill 1991, p. 178; Nowak 1991, p. 803; Tang 1992, p. 217; Kaneko 1994, pp. 104, 169, 178 and 180; Abe 2000, pp. 94 and 232.

Tokudamys osimensis muenninki; Johnson 1946, p. 169.

Tokudaia osimensis muenninki; Ellerman and Morrison-Scott 1951, p. 558; Kuroda 1957, p. 14; Imaizumi 1960, p. 152; Kuroda 1965, p. 684; Misonne 1969, p. 219 and pl. III; Corbet and Hill 1992, p. 391.

Tokudaia muenninki; Musser and Carleton 1993, p. 670; Nowak 1999, p. 1501.

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Appendix

Specimens Examined

Okinawa

USNM 278752, USNM 278754–56, USNM 278757 (the holotype of *Tokudamys osimensis muenninki* Johnson, 1946), USNM 278758–63; OPM 32935–37; NSMT-M 08422, NSMT-M 14377; three specimens preserved in the Zoological Laboratory, Faculty of Agriculture, Kyushu University (without registration); one specimen preserved in the University of the Ryukyus (without registration).

Amami Oshima

NSMT-M 07661, NSMT-M 07695–96, NSMT-M 07699, NSMT-M 07705, NSMT-M 07710–12, NSMT-M 07714–16, NSMT-M 09192, NSMT-M 09237, NSMT-M 11632, NSMT-M 28668–70; K0699 (Kaneko's private collection).