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Skull and tooth morphology of Finnish and Japanese raccoon dogs

Kaarina Kauhala, Suvi Viranta, Mayumi Kishimoto, Eero Helle & Iwao Obara

Kauhala, K. & Helle, E., Finnish Game and Fisheries Research Institute, P.O. Box 6, FIN-00721 Helsinki, Finland
Viranta, S., Department of Geology, P.O. Box 11, FIN-00014 University of Helsinki, Finland.
Kishimoto, M., Wildlife Management Office, 5-8 Fuda Tama-ku, Kawasaki 214, Japan
Obara, I., Department of Education, National Science Museum, Tokyo, Ueno Park, Taito-Ku, Tokyo 110, Japan

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The skull and tooth morphometrics of Finnish and Japanese raccoon dogs (*Nyctereutes procyonoides ussuriensis* and *N. p. viverrinus*, respectively) were examined and compared. The skulls of Finnish raccoon dogs were larger overall than those of Japanese raccoon dogs (tanukis) and were also larger relative to occipital condyle breadth, i.e. body size. Almost all measurements differed among samples in relation to skull size, indicating differences in skull shape. Mandible width and jaw height were the best measurements for discriminating among populations; the mandible is both absolutely and relatively more robust and the jaws more powerful among Finnish than among Japanese raccoon dogs. Japanese raccoon dogs have a relatively longer rostrum and longer tooth rows than Finnish raccoon dogs. Although the absolute measurements of most teeth of Finnish raccoon dogs were larger than those of Japanese raccoon dogs, the relative measurements of molars in particular were larger in Japan than in Finland, indicating a larger grinding surface among Japanese raccoon dogs. We suggest that *viverrinus* has adapted to a milder climate and less carnivorous diet than *ussuriensis*. The Japanese raccoon dog is smaller and, due to its less carnivorous diet, its head has become decreased in size and the jaws less powerful; however, since its diet consists largely of invertebrates and coarse plant material, its molars have increased relative to skull size.

1. Introduction

The raccoon dog (*Nyctereutes procyonoides*) originates from eastern Asia. At present, six subspecies are known in various parts of Asia: *N. p. procyonoides* in many parts of China and northern Vietnam, *N. p. ussuriensis* originally in southeastern parts of Russia and eastern China, *N. p. orestes* in Yunnan Province of China, *N. p. viverrinus* in Japan (except Hokkaido), *N. p. albus* in Hokkaido, and *N. p. koreensis* in Korea (Ellerman & Morrison-Scott 1951). Russians introduced *N. p. ussuriensis* to European Russia during the first half of this century (Lavrov 1971). From these introductions raccoon dogs have spread to other European countries, including Finland (Nowak 1984, Helle & Kauhala 1991). Finnish raccoon dogs, thus, belong to the subspecies *ussuriensis*.

Raccoon dogs have probably occurred in Japan for about 18 000 years, and the Japanese population has been isolated from the mainland population for about 12 000 years since the Sea of Japan opened (Ward *et al*. 1987). Due to a different environment and long isolation, evolutionary change may have occurred in the Japanese population.

Some differences exist among populations: Finnish raccoon dogs (*N. p. ussuriensis*) have 54 chromosomes as does *N. p. procyonoides*, but Japanese raccoon dogs (*N. p. viverrinus*) have only 38 chromosomes (Mäkinen *et al*. 1986, Ward *et al*. 1987). There are 10 homologous autosomes and the remaining chromosome arms are homologous because the chromosome number has decreased in Japan via Robertsonian translocations (Mäkinen *et al*. 1986, Ward *et al*. 1987), which often occurs when new species evolve (Mayr 1976). This suggests that *viverrinus* is a more recent form than *procyonoides* or *ussuriensis*. Finnish raccoon dogs are also larger, able to accumulate larger fat reserves during autumn, dormant during winter, and have thicker fur than Japanese raccoon dogs or tanukis (Korhonen *et al*. 1990). The Japanese raccoon dogs may live in groups, at least in some areas (Ikeda *et al*. 1979, Ward & Wurster-Hill 1989), whereas Finnish raccoon dogs appear to be strictly monogamous (Kauhala *et al*. 1993a). The subspecies *viverrinus* and *ussuriensis* are, thus, rather different and probably should be classified as distinct species. The aim of the present study was to compare the skull and tooth morphometrics of Finnish and Japanese raccoon dogs to obtain more information on the species status of *viverrinus*.

2. Material and methods

Raccoon dog skulls were collected from hunters in southern Finland during 1986–1992 (n = 65). The skulls of Japanese raccoon dogs were collected between 1974 and 1992 from several regions in Honshu, the main island of Japan (n = 104), and were kept in the National Science Museum, Tokyo, and in Tochigi Prefectural Museum. Age was determined from the incremental lines in the tooth cementum (Morris 1972); we used longitudinal sections of canines (Kauhala & Helle 1990), and all specimens < 1 year of age were excluded to be sure that the skull is fully grown. The skulls were cleaned and 22 measurements taken to the nearest 0.1 mm (Fig. 1). Jaw thickness (JT) was measured as transversal width of the lower jaw beneath m1. Measurement error was estimated by measuring 5 skulls for 5 times and calculating mean measurement error (CV %).

Differences between the Finnish and Japanese samples and between sexes within each sample were analyzed using the t-test (two-tailed), discriminant analysis, and principal component analysis (Ranta *et al*. 1989). The significance level was 0.05, and it was tested using the sequential Bonferroni technique according to Rice (1989). We first examined the differences in the absolute measurements between the samples, using log transformated measurements in the discriminant and principal component analyses (on correlation matrix). We then examined the differences between samples in relative measurements: ln(a/size) or ln$a$ – ln(size), and ln(a/OCB) or ln$a$ – ln(OCB) (occipital condyle breadth), where a refers to each measurement, and 'size' to (CL) – (RL) (condylobasal length and rostrum length, respectively), i.e. a measurement for skull size that is independent of RL. By dividing the measurements with the size of the skull we obtained information on the differences in skull shape, and by dividing the measurements with OCB we obtained information on the size of the measurements in relation to body weight (*see* Martin 1980).

We also compared some other relative measurements to determine possible differences in relative lengths of tooth rows between Finnish and Japanese raccoon dogs. These measurements included: ln(UT) – ln(CL), ln(RL) – ln(CL), and ln(LT) – ln(ML), where UT = length of upper tooth row, LT = length of lower tooth row, and ML = mandible length.

We measured all teeth, except canines, of the 2 samples; canines were omitted because they had been removed from most skulls for age determination. For the incisors and premolars only total lengths were measured, while total lengths and widths were measured for the molars. For the lower carnassial (m1), the length of the trigonid, consisting of the 3 anteriormost cusps (para-, proto- and metaconid), was also measured.

Means and standard deviations were calculated for each sex in both groups, and both differences between Finnish and Japanese samples and between the sexes were studied using the t-test. Ratio diagrams were used to visualize the results (*see* Simpson, 1941). Discriminant and principal component analyses similar to those run for the cranial measurements were applied to the dental measurements.

3. Results

3.1. Absolute measurements

The skulls of Finnish raccoon dogs were larger than those of Japanese raccoon dogs. All meas-

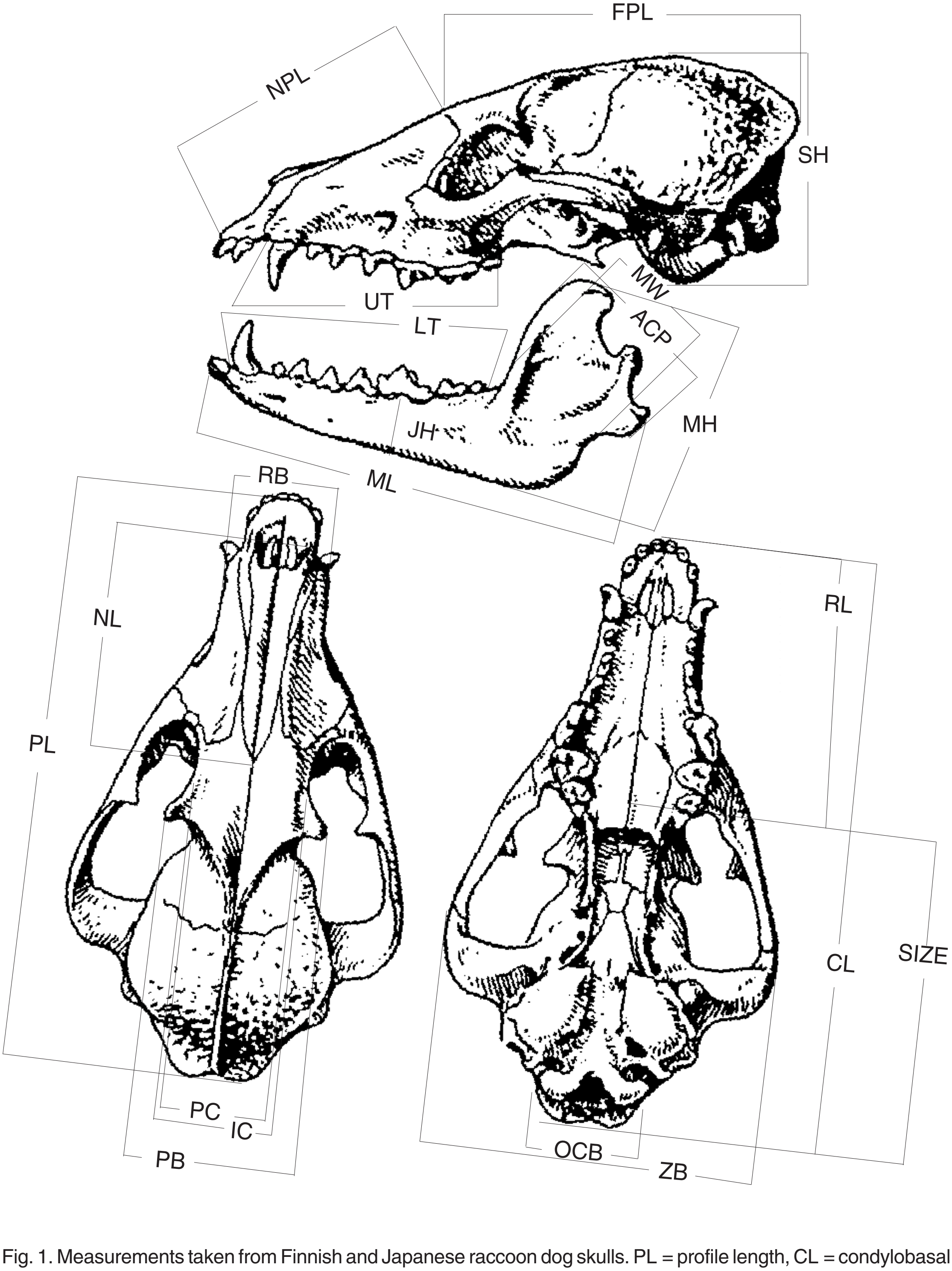

Fig. 1. Measurements taken from Finnish and Japanese raccoon dog skulls. PL = profile length, CL = condylobasal length, Size = (CL) – (RL), ZB = zygomatic breadth, RB = rostrum breadth, IC = interorbital constriction, PB = postorbital breadth, PC = postorbital constriction, SH = skull height, FPL = frontal + parietal length, NPL = nasal + premaxillary length, UT = length of upper tooth row, NL = nasal length, RL = rostrum length, OCB = occipital condyle breadth, ML = mandible length, MH = mandible height, LT = length of lower tooth row, ACP = from angular process to coronoid process, MW = mandible width, and JH = jaw height.

urements, except postorbital breadth (PB) and postorbital constriction (PC), of Finnish raccoon dogs were larger than those of tanukis (Table 1). PB did not differ between populations, and PC was larger in Japan than in Finland. All measurements overlapped, however, to some extent (Fig. 2). According to discriminant analysis, mandible width (MW) and jaw height (JH) were the best measurements for identifying the origin of the skulls, and 100% of the skulls could be correctly classified using these criteria (Fig. 3A). According to principal component analysis, the skulls could also be correctly identified as belonging to Finnish or Japanese populations (Fig. 3B). The first 2 principal components explained 77% of the total variance. The most important measurements affecting the 1st component were profile length (PL), CL and ML, and those affecting the 2nd component were interorbital constriction (IC), PB, and PC.

The relative measurement ln(RL) – ln(CL) was greater in Japan (t = – 10.2, df = 98, $p < 0.001$), as was ln(UT) – ln(CL) (t = – 12.5, df = 96, $p < 0.001$) and ln(LT) – ln(ML) (t = – 9.3, df = 151, $p < 0.001$), indicating that tooth rows were relatively longer in Japan than in Finland. The mandible is more curved in Japanese raccoon dogs than among Finnish raccoon dogs (Fig. 4).

Most teeth of Finnish raccoon dogs were also larger in their absolute measurements than those of Japanese raccoon dogs; only the postcarnassial lower dentition differed from this pattern (especially m2; Fig. 5, Table 2). The 2 posterior lower molars (m2 and m3) were longer in Japanese males and m2 also in Japanese females than in the Finnish sample; the width of m2 was similar to that of the Finnish sample. According to discriminant analysis, the lengths of the lower premolars p1 and p2 were the best dental measurements for identifying the origin of the lower dentition (Eigenvalue = 3.56, Wilks' lambda = 0.220, F = 4.82, df = 14, p = 0.001), and P1 was the best dental measurement to identify the origin of the upper dentition (Eigenvalue = 2.48, Wilks' lambda = 0.287, F = 5.91, df = 13, $p < 0.001$).

3.2. Measurements relative to occipital condyle breadth (OCB)

Most measurements relative to OCB were smaller in Japanese raccoon dogs, which indicates that the skull of tanukis is smaller in relation to body size (Table 3). Only PB and PC were larger among Japanese than among Finnish raccoon dogs. UT, LT, IC and RL relative to OCB did not differ among populations, indicating that although the skull was relatively smaller in Japan, the tooth rows were not shorter in relation to body weight.

Premolars and m1 were larger relative to OCB in Finland, but m2 and M2 were relatively larger in Japan; M1 and m3 did not differ in size relative to OCB among populations (Table 4). According to discriminant analysis, the lengths of p1 and P1 appeared to be the best indicators for the origin of the dentitions (lower dentition: Eigenvalue = 2.71, Wilks' lambda = 0.270, F = 3.94, df = 11, p = 0.007; upper dentition: Eigenvalue = 3.24, Wilks' lambda = 0.236, F = 13.6, df = 10, $p < 0.001$).

3.3. Measurements relative to skull size

All cranial measurements relative to skull size, except rostrum breadth (RB), differed among populations, indicating differences in skull shape (Table 5). Mandible height (MH), mandible width (MW), jaw height (JH) and ACP (from angular process to coronoid process; *see* Fig. 1) were relatively larger in Finland, which suggests that the mandible is more robust in Finland than in Japan. All other measurements were relatively larger in Japan than in Finland; most of these measurements were connected with the length of tooth rows, again indicating the relatively longer tooth rows of the Japanese raccoon dog.

Discriminant analysis again resulted in 100% correct classification of skulls (Fig. 6A); the best measurements for identification proved to be JH and MW. The skulls could also be well classified on the basis of principal component analysis (Fig. 6B). The first 2 principal components explained 69% of the total variance. The most important measurements affecting the 1st component were PL, RL, and CL, and those affecting the 2nd component were ACP, MH and MW.

Dental measurements relative to skull size differed less between the 2 samples than the absolute measurements; however, the molars especially were relatively larger in Japan than in Finland (Table 6), indicating a larger grinding surface among Japanese raccoon dogs. According to

Table 1. The absolute skull measurements of Finnish (Fin) and Japanese (Jap) raccoon dogs (*n*, mean, SD) and the results of *t*-tests (*t*, df, *p*). Size = condylobasal length – rostrum length, PL = profile length, CL = condylobasal length, ZB = zygomatic breadth, RB = rostrum breadth, IC = interorbital constriction, PB = postorbital breadth, PC = postorbital constriction, SH = skull height, FPL = frontal + parietal length, NPL = nasal + premaxillary length, UT = upper tooth row, NL = nasal length, RL = rostrum length, OCB = occipital condyle breadth, ML = mandible length, MH = mandible height, LT = lower tooth row, ACP = angular process – coronoid process, MW = mandible width, JH = jaw height and JT = jaw thickness. *p*-values were corrected using sequential Bonferroni correction (Rice 1989). Mean measurement error (CV %) is also given.

Measurement		*n*	mean (mm)	SD	*t*	df	*p*	CV (%)
Size	Fin	63	63.96	2.83	20.9	107	< 0.001	
	Jap	104	55.26	2.18				
PL	Fin	62	124.1	3.80	16.7	124	< 0.001	0.14
	Jap	103	114.1	3.64				
CL	Fin	63	122.0	3.55	22.1	129	< 0.001	0.16
	Jap	104	109.5	3.47				
ZB	Fin	65	70.9	2.47	18.7	138	< 0.001	0.2
	Jap	103	63.6	2.52				
RB	Fin	55	22.8	0.87	20.4	106	< 0.001	0.52
	Jap	103	19.9	0.83				
IC	Fin	65	23.9	1.33	7.9	124	< 0.001	0.44
	Jap	103	22.3	1.18				
PB	Fin	57	33.8	2.67	– 0.6	102	NS	0.26
	Jap	96	34.1	2.25				
PC	Fin	65	19.8	1.36	– 6.9	139	< 0.001	0.56
	Jap	100	21.3	1.40				
SH	Fin	64	46.5	1.55	15.8	125	< 0.001	1.26
	Jap	97	42.7	1.40				
FPL	Fin	65	69.6	2.79	12.9	131	< 0.001	0.56
	Jap	102	64.0	2.65				
NPL	Fin	63	57.8	3.18	9.2	115	< 0.001	0.68
	Jap	103	53.4	2.71				
UT	Fin	65	45.6	1.61	8.0	141	< 0.001	0.56
	Jap	102	43.6	1.69				
NL	Fin	62	45.5	2.89	6.4	120	< 0.001	0.28
	Jap	102	42.6	2.64				
RL	Fin	65	58.0	1.98	12.1	131	< 0.001	0.26
	Jap	104	54.3	1.89				
OCB	Fin	65	23.9	0.88	6.9	142	< 0.001	0.60
	Jap	104	22.9	0.93				
ML	Fin	65	92.0	3.12	17.2	143	< 0.001	0.14
	Jap	99	83.2	3.33				
MH	Fin	65	51.3	2.32	24.4	133	< 0.001	0.24
	Jap	102	42.4	2.25				
LT	Fin	59	53.3	1.62	10.9	140	< 0.001	0.46
	Jap	101	50.2	1.96				
ACP	Fin	65	39.9	2.10	20.1	116	< 0.001	0.40
	Jap	103	33.7	1.71				
MW	Fin	64	22.7	1.17	25.7	126	< 0.001	0.38
	Jap	103	18.1	1.08				
JH	Fin	54	14.7	0.68	22.4	116	< 0.001	1.2
	Jap	67	11.8	0.73				
JT	Fin	54	6.9	0.48	6.8	106	< 0.001	2.0
	Jap	67	6.4	0.42				

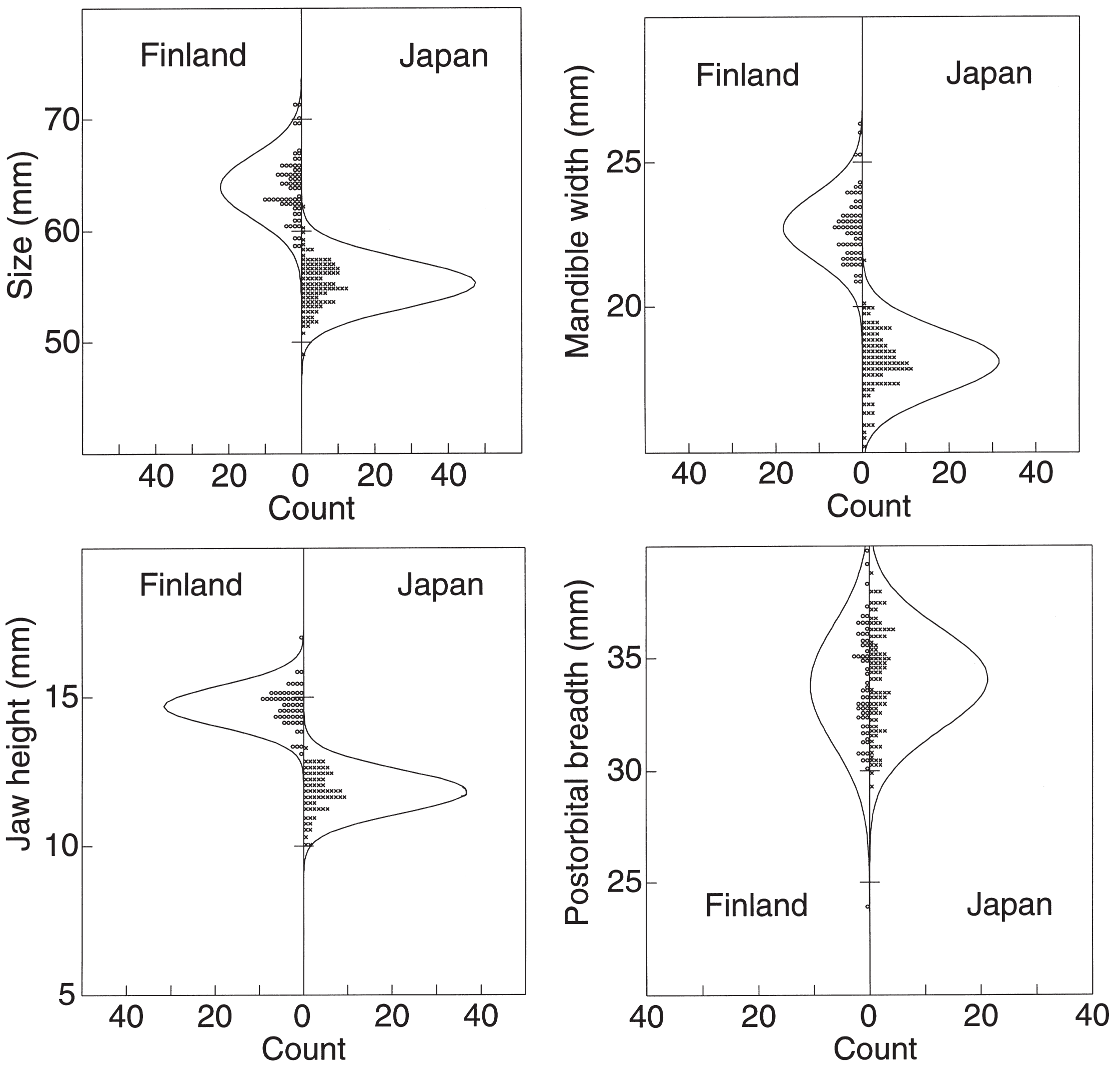

Fig. 2. Examples of skull measurements of Finnish and Japanese raccoon dogs. Mandible width and jaw height were the best measurements for identifying the origin of skulls, and skull size (CL – RL) also differed between populations, but postorbital breadth overlapped largely among populations.

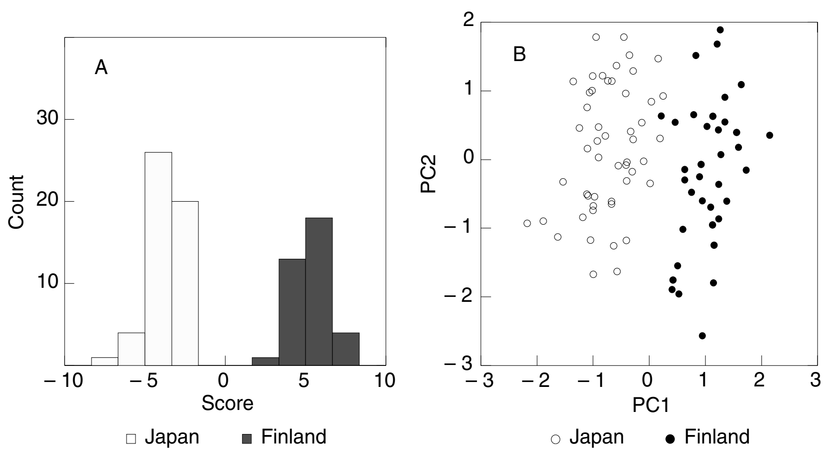

Fig. 3. The results of discriminant (A) and principal component (B) analyses, based on skull measurements of Finnish and Japanese raccoon dogs. Eigenvalue for discriminant analysis = 19.6, Wilks' lambda = 0.049, F = 60.7, df = 21, p < 0.001.

Fig. 4. Photographs of skulls of Finnish and Japanese raccoon dogs. The smaller is Japanese and the larger is Finnish. Both are 1-year-old females.

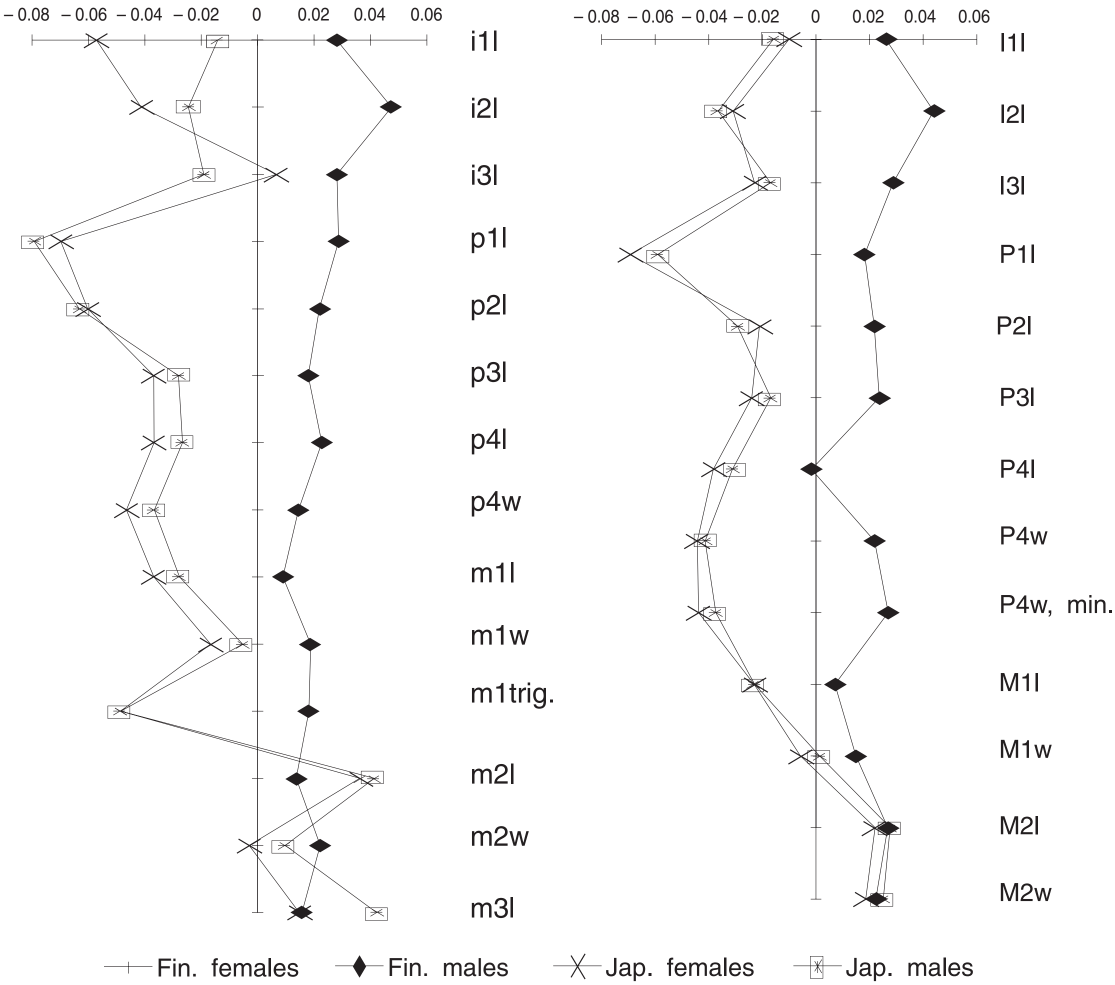

Fig. 5. Ratio diagrams comparing the lower (left panel) and upper (right panel) dentition of Japanese and Finnish raccoon dogs (Finnish females as zero line).

Table 2. Dental measurements of Finnish (Fin) and Japanese (Jap) raccoon dogs (*n*, mean, SD) and results of the *t*-tests (*t*, df, *p*). Upper teeth indicated with upper cases, maximum lengths (l) for all the teeth and widths (w) for carnassials and postcarnassials are provided; *p*-values were corrected using sequential Bonferroni correction (Rice 1989). Mean measurement error (CV %) is also given.

Measurement		*n*	mean	SD	*t*	df	*p*	CV %
i1l	Fin	42	2.00	0.37	2.06	63	NS	10.0
	Jap	23	1.80	0.37				
i2l	Fin	42	2.68	0.48	2.87	65	< 0.005	2.9
	Jap	25	2.36	0.36				
i3l	Fin	41	3.28	0.46	1.19	64	NS	8.4
	Jap	25	3.09	0.46				
p1l	Fin	58	3.30	0.33	6.66	77	< 0.001	5.0
	Jap	21	2.70	0.46				
p2l	Fin	57	5.69	0.46	7.44	96	< 0.001	2.9
	Jap	41	4.82	0.71				
p3l	Fin	58	6.20	0.45	6.69	98	< 0.001	2.6
	Jap	42	5.64	0.36				
p4l	Fin	59	7.31	0.56	6.99	112	< 0.001	1.5
	Jap	55	6.64	0.45				
p4w	Fin	58	3.71	0.26	6.49	88	< 0.001	2.3
	Jap	32	3.34	0.26				
m1l	Fin	60	12.62	0.51	10.26	127	< 0.001	1.2
	Jap	69	11.61	0.59				
m1w	Fin	60	5.18	0.26	4.87	127	< 0.001	2.2
	Jap	69	4.95	0.27				
m1trig.	Fin	57	7.57	0.65	9.37	124	< 0.001	1.8
	Jap	69	6.64	0.47				
m2l	Fin	60	6.28	0.46	– 5.75	126	< 0.001	3.1
	Jap	68	6.77	0.49				
m2w	Fin	59	4.35	0.32	1.24	125	NS	4.5
	Jap	68	4.28	0.30				
m3	Fin	42	2.93	0.53	– 0.91	56	NS	7.3
	Jap	16	3.06	0.43				
I1l	Fin	33	2.75	0.34	2.07	60	NS	2.2
	Jap	29	2.60	0.24				
I2l	Fin	33	3.41	0.41	4.22	61	< 0.001	2.0
	Jap	30	3.03	0.29				
I3l	Fin	33	3.93	0.46	2.52	61	NS	2.0
	Jap	30	3.66	0.38				
P1l	Fin	54	3.71	0.32	7.96	77	< 0.001	0.8
	Jap	25	3.15	0.21				
P2l	Fin	59	5.64	0.46	4.50	85	< 0.001	1.9
	Jap	28	5.19	0.40				
P3l	Fin	59	5.64	0.46	4.67	97	< 0.001	0.8
	Jap	40	6.19	0.38				
P4l	Fin	58	10.43	0.61	7.70	121	< 0.001	1.2
	Jap	65	9.66	0.51				
P4w	Fin	58	5.62	0.41	9.01	121	< 0.001	1.9
	Jap	65	4.98	0.38				
P4 (min)	Fin	58	4.80	0.35	10.22	120	< 0.001	1.1
	Jap	64	4.25	0.24				
M1l	Fin	60	8.71	0.45	6.30	123	< 0.001	1.9
	Jap	65	8.19	0.46				
M1w	Fin	60	9.25	0.52	2.13	123	NS	1.4
	Jap	65	9.06	0.47				
M2l	Fin	60	5.19	0.46	– 1.75	123	NS	2.3
	Jap	65	5.34	0.50				
M2w	Fin	60	5.97	0.59	1.83	123	NS	1.2
	Jap	65	6.13	0.39				

discriminant analysis the length of m2 was the most helpful for discriminating among populations (lower dentition: Eigenvalue = 2.23, Wilks' lambda = 0.310, $F = 7.14$, df = 10, $p < 0.001$; upper dentition: Eigenvalue = 2.63, Wilks' lambda = 0.275, $F = 11.1$, df = 10, $p < 0.001$).

3.4. Sexual dimorphism

3.4.1. Skull measurements

Only zygomatic breadth (ZB) differed between sexes in Finland and ZB, nasal + premaxillary

Table 3. The relative skull measurements against occipital condyle breadth [ln(measurement) – ln(condyle breadth)] of Finnish (Fin) and Japanese (Jap) raccoon dogs (*n*, mean, SD) and the results of *t*-tests (*t*, df, *p*). Size = condylobasal length – rostrum length, PL = profile length, CL = condylobasal length, ZB = zygomatic breadth, RB = rostrum breadth, IC = interorbital constriction, PB = postorbital breadth, PC = postorbital constriction, SH = skull height, FPL = frontal + parietal length, NPL = nasal + premaxillary length, UT = upper tooth row, NL = nasal length, RL = rostrum length, ML = mandible length, MH = mandible height, LT = lower tooth row, ACP = angular process – coronoid process, MW = mandible width, JH = jaw height and JT = jaw thickness; *p*-values were corrected using sequential Bonferroni correction (Rice 1989).

Measurement		*n*	mean	SD	*t*	df	*p*
Size	Fin	63	0.98	0.052	13.1	112	< 0.001
	Jap	104	0.88	0.043			
PL	Fin	62	1.64	0.053	4.4	119	< 0.001
	Jap	103	1.61	0.048			
CL	Fin	64	1.63	0.058	7.7	120	< 0.001
	Jap	104	1.56	0.051			
ZB	Fin	65	1.09	0.056	8.1	124	< 0.001
	Jap	103	1.02	0.049			
RB	Fin	55	– 0.05	0.057	8.8	112	< 0.001
	Jap	103	– 0.14	0.058			
IC	Fin	65	0.00	0.064	2.8	141	NS
	Jap	103	– 0.03	0.067			
PB	Fin	57	0.35	0.095	– 3.1	94	< 0.002
	Jap	96	0.40	0.071			
PC	Fin	65	– 0.19	0.081	– 9.3	139	< 0.001
	Jap	100	– 0.07	0.083			
SH	Fin	64	0.66	0.058	3.8	131	< 0.001
	Jap	97	0.63	0.055			
FPL	Fin	65	1.07	0.061	3.9	132	< 0.001
	Jap	102	1.03	0.058			
NPL	Fin	63	0.89	0.065	4.7	133	< 0.001
	Jap	103	0.84	0.066			
UT	Fin	65	0.65	0.056	1.1	138	NS
	Jap	102	0.64	0.057			
NL	Fin	62	0.65	0.072	3.0	124	< 0.003
	Jap	102	0.61	0.068			
RL	Fin	65	0.88	0.057	2.1	126	NS
	Jap	104	0.86	0.052			
ML	Fin	65	1.35	0.059	6.7	133	< 0.001
	Jap	99	1.29	0.057			
MH	Fin	65	0.76	0.060	15.9	139	< 0.001
	Jap	102	0.61	0.062			
LT	Fin	59	0.80	0.056	1.94	120	NS
	Jap	102	0.78	0.055			
ACP	Fin	65	0.52	0.073	12.4	115	< 0.001
	Jap	103	0.39	0.058			
MW	Fin	64	– 0.05	0.067	17.5	133	< 0.001
	Jap	103	– 0.24	0.066			
JH	Fin	54	– 0.48	0.063	15.6	117	< 0.001
	Jap	67	– 0.67	0.069			
JT	Fin	54	– 1.24	0.090	3.3	110	< 0.001
	Jap	67	– 1.29	0.084			

length (NPL), nasal length (NL), ML and MH in Japan (Table 7). When dimorphism existed, the measurements of males were always larger than those of females.

Discriminant analysis could correctly classify 69% of the Japanese, but only 31% of the Finnish skulls; thus, all measurements overlapped between the sexes, especially in Finland, but slight sexual dimorphism was present in Japan (Japan: Eigenvalue = 1.38, Wilks' lambda = 0.42, F = 1.91, df = 21, p = 0.054; Finland: Eigenvalue = 0.73, Wilks' lambda = 0.58, F = 0.48, df = 21, p = 0.936).

According to principal component analysis, sexual dimorphism is very slight among raccoon dogs (Fig. 7). However, the difference in PC1 scores

Table 4. Dental measurements relative to occipital condyle breadth; p-values were corrected using sequential Bonferroni correction (Rice 1989).

Measurement		*n*	mean	SD	*t*	df	*p*
p1l	Fin	37	– 0.86	0.047	5.17	56	< 0.001
	Jap	21	– 0.93	0.065			
p2l	Fin	36	– 0.62	0.036	4.68	75	< 0.001
	Jap	41	– 0.69	0.076			
p3l	Fin	37	– 0.51	0.036	4.01	77	< 0.001
	Jap	42	– 0.61	0.026			
p4l	Fin	38	– 0.51	0.042	3.84	91	< 0.001
	Jap	55	– 0.54	0.030			
p4w	Fin	37	– 0.81	0.029	3.47	67	< 0.001
	Jap	32	– 0.84	0.033			
m1l	Fin	39	– 0.28	0.025	4.09	106	< 0.001
	Jap	69	– 0.30	0.025			
m1w	Fin	39	– 0.63	0.216	1.48	107	< 0.001
	Jap	69	– 0.67	0.026			
m1trig.	Fin	37	– 0.50	0.039	5.16	104	< 0.001
	Jap	69	– 0.54	0.033			
m2l	Fin	39	– 0.58	0.031	– 7.15	105	< 0.001
	Jap	68	– 0.53	0.032			
m2w	Fin	38	– 0.74	0.034	– 1.35	104	NS
	Jap	68	– 0.73	0.031			
m3	Fin	26	– 0.91	0.086	– 1.26	40	NS
	Jap	16	– 0.88	0.060			
P1l	Fin	35	– 0.81	0.040	6.02	57	< 0.001
	Jap	24	– 0.87	0.033			
P2l	Fin	39	– 0.62	0.041	2.67	63	< 0.010
	Jap	26	– 0.65	0.035			
P3l	Fin	39	– 0.55	0.039	3.06	74	< 0.003
	Jap	27	– 0.57	0.027			
P4l	Fin	37	– 0.36	0.028	2.61	98	< 0.011
	Jap	63	– 0.38	0.025			
P4w	Fin	37	– 0.63	0.034	5.62	98	< 0.001
	Jap	63	– 0.67	0.035			
P4w (min)	Fin	37	– 0.70	0.033	6.20	97	< 0.001
	Jap	62	– 0.73	0.025			
M1l	Fin	39	– 0.44	0.026	1.55	100	NS
	Jap	63	– 0.45	0.027			
M1w	Fin	39	– 0.41	0.030	– 1.50	100	NS
	Jap	63	– 0.40	0.025			
M2l	Fin	39	– 0.66	0.042	– 3.14	100	< 0.002
	Jap	63	– 0.64	0.039			
M2W	Fin	39	– 0.61	0.055	– 3.86	100	< 0.001
	Jap	63	– 0.57	0.031			

between sexes was significant both in Finland and in Japan (Finland: $t = -2.7$, df = 34, $p = 0.011$, Japan: $t = -2.9$, df = 47, $p = 0.006$). When we analysed the PC1 scores with a two-way ANOVA, using population and sex as factors, we found a major difference between populations, a minor difference between sexes and no difference in the degree of sexual dimorphism between populations

Table 5. The relative skull measurements against skull size [ln(measurement) – ln(size)] of Finnish (Fin) and Japanese (Jap) raccoon dogs (*n*, mean, SD) and the results of *t*-tests (*t*, df, *p*). PL = profile length, CL = condylobasal length, ZB = zygomatic breadth, RB = rostrum breadth, IC = interorbital constriction, PB = postorbital breadth, PC = postorbital constriction, SH = skull height, FPL = frontal + parietal length, NPL = nasal + premaxillary length, UT = upper tooth row, NL = nasal length, RL = rostrum length, OCB = occipital condyle breadth, ML = mandible length, MH = mandible height, LT = lower tooth row, ACP = angular process – coronoid process, MW = mandible width, JH = jaw height and JT = jaw thickness; *p*-values were corrected using sequential Bonferroni correction (Rice 1989).

Measurement		*n*	mean	SD	*t*	df	*p*
PL	Fin	61	0.66	0.028	– 14.4	114	< 0.001
	Jap	103	0.73	0.025			
CL	Fin	63	0.65	0.025	– 10.3	108	< 0.001
	Jap	104	0.68	0.020			
ZB	Fin	63	0.10	0.040	– 6.2	112	< 0.001
	Jap	103	0.14	0.033			
RB	Fin	53	– 1.03	0.043	– 1.6	107	NS
	Jap	103	– 1.02	0.043			
IC	Fin	63	– 0.99	0.055	– 9.1	122	< 0.001
	Jap	103	– 0.91	0.050			
PB	Fin	56	– 0.64	0.075	– 13.1	101	< 0.001
	Jap	96	– 0.49	0.064			
PC	Fin	63	– 1.18	0.077	– 18.1	131	< 0.001
	Jap	100	– 0.95	0.076			
SH	Fin	62	– 0.32	0.043	– 8.9	120	< 0.001
	Jap	97	– 0.26	0.038			
FPL	Fin	63	0.09	0.039	– 9.9	128	< 0.001
	Jap	102	0.15	0.038			
NPL	Fin	62	– 0.10	0.051	– 8.1	122	< 0.001
	Jap	103	– 0.04	0.048			
UT	Fin	63	– 0.34	0.037	– 16.3	133	< 0.001
	Jap	102	– 0.24	0.038			
NL	Fin	61	– 0.34	0.061	– 8.3	124	< 0.001
	Jap	102	– 0.26	0.059			
RL	Fin	62	– 0.09	0.047	– 10.7	110	< 0.001
	Jap	104	– 0.02	0.039			
OCB	Fin	63	– 0.98	0.052	– 13.3	111	< 0.001
	Jap	104	– 0.88	0.043			
ML	Fin	62	0.37	0.026	– 9.7	132	< 0.001
	Jap	99	0.41	0.027			
MH	Fin	63	– 0.22	0.040	7.1	136	< 0.001
	Jap	102	– 0.27	0.042			
LT	Fin	58	– 0.18	0.036	– 13.7	131	< 0.001
	Jap	102	– 0.10	0.040			
ACP	Fin	63	– 0.47	0.040	3.7	138	< 0.001
	Jap	103	– 0.50	0.043			
MW	Fin	62	– 1.03	0.043	10.7	153	< 0.001
	Jap	103	– 1.12	0.056			
JH	Fin	54	– 1.47	0.054	7.3	115	< 0.001
	Jap	67	– 1.55	0.055			
JT	Fin	54	– 2.23	0.063	– 4.8	117	< 0.001
	Jap	67	– 2.17	0.069			

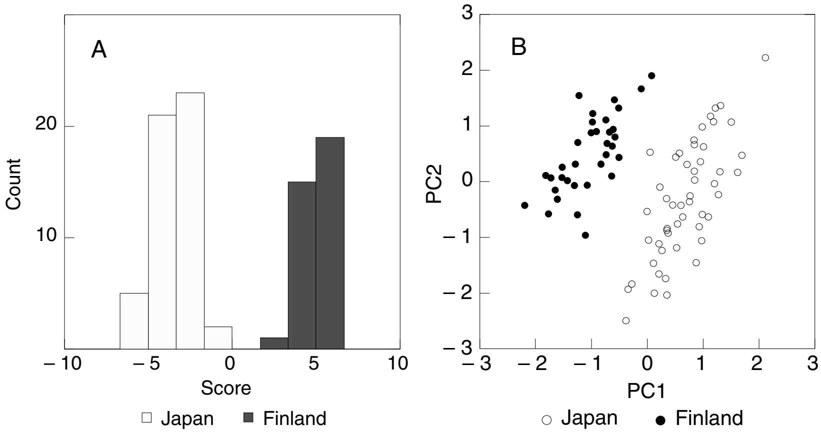

Fig. 6. Results of discriminant (A) and principal component (B) analyses, based on relative skull measurements [ln(measurement) – ln(skull size)] of Finnish and Japanese raccoon dogs. Eigenvalue for discriminant analysis = 16.9, Wilks' lambda = 0.056, $F = 51.5$, df = 21, $p < 0.001$.

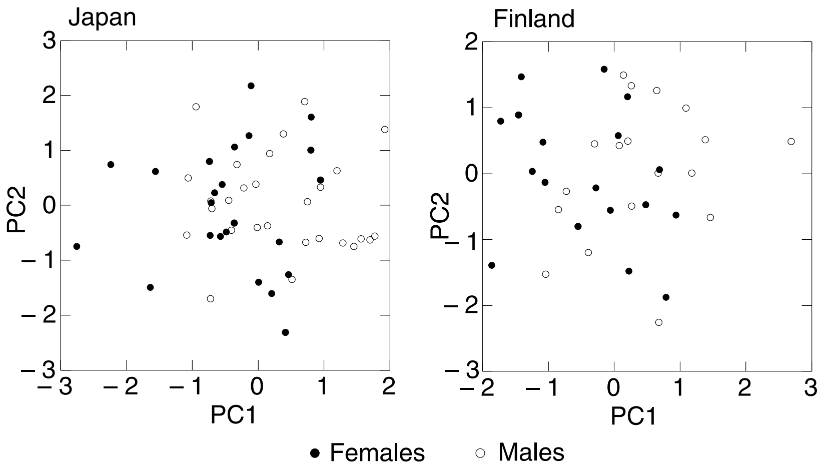

Fig. 7. Sexual dimorphism in Finnish and Japanese raccoon dog skulls based on principal component analysis.

(sex: $F = 14.6$, $p < 0.001$, area: $F = 345.9$, $p < 0.001$, sex × area: $F = 0.008$, NS). Male: female ratio was 1.01 for skull size both in Finland and in Japan, and male: female ratio was 1.00 for OCP both in Finland and Japan, indicating no sexual dimorphism in skull or body size.

3.4.2. Tooth measurements

In Japan, no dimorphism existed, whereas 2/27 dental measurements were dimorphic in Finland (Table 8). When we analysed the PC1 scores with a two-way ANOVA, we found a major difference between populations, no difference between sexes and no difference in the degree of sexual dimorphism between populations (sex: $F = 2.2$, NS, area: $F = 33.3$, $p < 0.001$, sex × area: $F = 0.06$, NS).

4. Discussion

Finnish raccoon dogs are larger and have larger skulls than Japanese raccoon dogs; 20/22 absolute measurements were larger in Finland than in Japan. Ward and Wurster-Hill (1990) reported that the mean CL of *viverrinus* was 108.7 mm for males and 108.1 mm for females, which is somewhat less than that reported here (mean 109.5 mm). According to Ward and Wurster-Hill (1990), the mean CL for *procyonoides* males is 112.2 mm and for females 108.0 mm, and the mean CL for *orestes* males is 106.0 mm and for females 108.5 mm. According to Stroganov (1969), *ussuriensis* is somewhat larger, with a mean CL of 122.0 mm for males and 116.6 mm for females. All other subspecies are thus probably smaller than *ussuriensis,* which has adapted to colder areas than the others. Adaptation to cold climate and monogamy may also explain the lack of sexual dimorphism in size; natural selection may have favored large females due to advantages in thermoregulation. Since *ussuriensis* is apparently strictly monogamous, natural selection has probably not favored larger males; in fact, larger size in males would be disadvantageous, because large animals need more food than smaller animals. Consequently, the optimum size for males might be the same as for females.

The skulls of Finnish raccoon dogs are also larger relative to body weight; 15/21 measurements were larger in Finland than in Japan, rela-

Table 6. Dental measurements relative to size; *p*-values were corrected using sequential Bonferroni correction (Rice 1989).

Measurement		*n*	mean	SD	*t*	df	*p*
p1l	Fin	37	– 1.29	0.044	1.42	56	NS
	Jap	21	– 1.31	0.064			
p2l	Fin	37	– 1.07	0.125	– 0.26	76	NS
	Jap	41	– 1.06	0.082			
p3l	Fin	37	– 1.01	0.033	– 3.39	77	< 0.001
	Jap	42	– 0.99	0.028			
p4l	Fin	38	– 0.94	0.040	– 2.79	91	NS
	Jap	55	– 0.92	0.030			
p4w	Fin	36	– 1.24	0.033	0.44	67	NS
	Jap	32	– 0.84	0.033			
m1l	Fin	39	– 0.71	0.023	– 5.45	106	< 0.001
	Jap	69	– 0.68	0.027			
m1w	Fin	39	– 1.09	0.023	– 8.37	106	< 0.001
	Jap	69	– 1.05	0.028			
m1trig.	Fin	37	– 0.93	0.041	– 1.27	104	NS
	Jap	69	– 0.92	0.034			
m2l	Fin	39	– 1.10	0.031	– 4.78	106	< 0.001
	Jap	69	– 0.93	0.105			
m2w	Fin	36	– 1.17	0.037	– 3.21	103	< 0.002
	Jap	69	– 1.12	0.083			
m3	Fin	27	– 1.35	0.121	– 2.63	40	NS
	Jap	15	– 1.27	0.063			
P1l	Fin	35	– 1.24	0.042	0.45	57	NS
	Jap	24	– 1.24	0.037			
P2l	Fin	39	– 1.05	0.045	– 2.80	63	NS
	Jap	26	– 1.03	0.036			
P3l	Fin	39	– 0.98	0.037	– 3.73	75	< 0.001
	Jap	38	– 0.95	0.024			
P4l	Fin	37	– 0.79	0.028	– 5.83	98	< 0.001
	Jap	63	– 0.76	0.026			
P4w	Fin	37	– 1.05	0.034	– 1.62	97	NS
	Jap	62	– 1.48	0.037			
P4 (min)	Fin	37	– 1.13	0.034	– 0.90	98	NS
	Jap	62	– 1.11	0.028			
M1l	Fin	39	– 0.87	0.025	– 6.99	100	< 0.001
	Jap	63	– 0.83	0.029			
M1w	Fin	39	– 0.84	0.028	– 10.33	100	< 0.001
	Jap	63	– 0.79	0.026			
M2l	Fin	39	– 1.09	0.040	– 8.89	100	< 0.001
	Jap	63	– 1.02	0.041			
M2w	Fin	39	– 1.04	0.050	– 9.93	100	< 0.001
	Jap	63	– 0.96	0.032			

tive to OCB. OCB has been shown to correlate well with body weight (Martin 1980). The relatively smaller head of Japanese raccoon dogs may be related to their less carnivorous diet (Fig. 8).

Differences were also apparent, however, in the skull shape between Finnish and Japanese raccoon dogs; 20/21 of the measurements relative to the skull size differed among populations. The mandibles of the Finnish raccoon dogs were more robust than those of the Japanese raccoon dogs, again indicating differences in diet. UT and LT and RL were, however, relatively longer in Japan than in Finland, an indication of the very large molars of Japanese raccoon dogs.

PC was larger in Japan, both in absolute and relative scale, than in Finland. The anterior fibers of the temporalis muscle are attached to the skull in the postorbital area in carnivores (Ewer 1985). When the postorbital area is concave (curved inside) and consequently PC is small, the anterior part of the temporalis muscle is large. This means an increase in the force of the fully opened jaw (Wiig 1982); thus, the small PC in Finnish raccoon dogs correlates with the robust mandible and more powerful jaws. The sagittal (interparietal) crest is also much more pronounced in Finnish than in Japanese raccoon dogs (Fig. 4).

The absolute sizes of most teeth were larger in Finnish than in Japanese raccoon dogs. The teeth of Japanese raccoon dogs were, however, larger relative to skull size, indicating that the teeth probably decrease in size more slowly than does the rest of the skull. This has resulted in the more curved mandible in Japanese raccoon dogs; if the

Table 7. Sexual dimorphism in absolute skull measurements of Finnish and Japanese raccoon dogs. Size = condylobasal length – rostrum length, PL = profile length, CL = condylobasal length, ZB = zygomatic breadth, RB = rostrum breadth, IC = interorbital constriction, PB = postorbital breadth, PC = postorbital constriction, SH = skull height, FPL = frontal + parietal length, NPL = nasal + premaxillary length, UT = upper tooth row, NL = nasal length, RL = rostrum length, OCB = condyle breadth, ML = mandible length, MH = mandible height, LT = lower tooth row, ACP = angular process – coronoid process, MW = mandible width, JH = jaw height and JT = jaw thickness; *p*-values were corrected using sequential Bonferroni correction (Rice 1989).

Measurement	Finland	Japan
Size	–	–
PL	–	–
CL	–	–
ZB	+	+
RB	–	–
IC	–	–
PB	–	–
PC	–	–
SH	–	–
FPL	–	–
NPL	–	+
UT	–	–
NL	–	+
RL	–	–
OCB	–	–
ML	–	+
MH	–	+
LT	–	–
ACP	–	–
MW	–	–
JH	–	–
JT	–	–

Table 8. Sexual dimorphism in dental measurements of Finnish and Japanese raccoon dogs; *p*-values were corrected using sequential Bonferroni correction (Rice 1989).

Measurement	Finland	Japan
i1l	–	–
i2l	–	–
i3l	–	–
p1l	–	–
p2l	–	–
p3l	–	–
p4l	–	–
p4w	–	–
m1l	–	–
m1w	+	–
m1trig.	–	–
m2l	–	–
m2w	–	–
m3	–	–
I1l	–	–
I2l	–	–
I3l	–	–
P1l	–	–
P2l	–	–
P3l	–	–
P4l	–	–
P4w	–	–
P4 min w	+	–
M1l	–	–
M1w	–	–
M2l	–	–
M2w	–	–

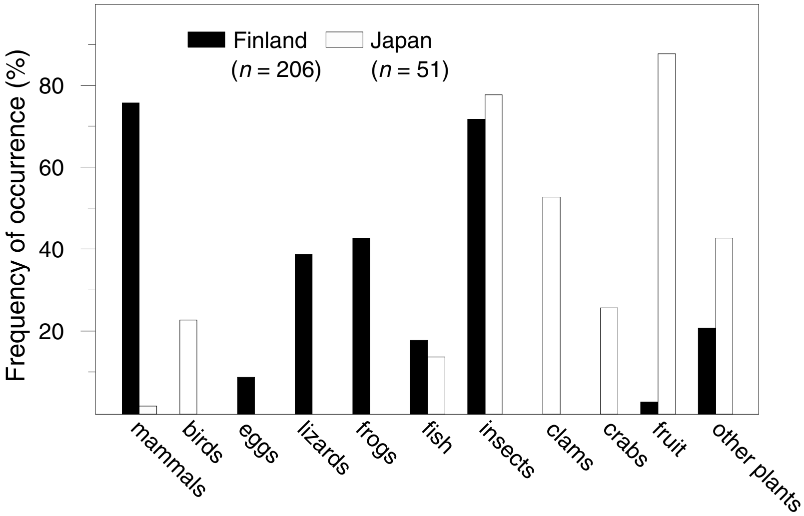

Fig. 8. Frequency of occurrence of various food items in raccoon dog faeces during early summer in Finland and Japan. Data for Finland are from Kauhala *et al.* (1993b), and data for Japan are from Ikeda (1985).

mandible were not curved, not enough space would be available for the relatively larger teeth. An interesting analogy exists between this and the evolution of the domestic dog (*Canis familiaris*): when domestic dogs evolved from wolves (*C. lupus*) the skulls also decreased in size, but the teeth decreased at a slower rate resulting in a more curved mandible in the dog compared with the wolf (Clutton-Brock 1995).

The molars of Japanese raccoon dogs are especially large compared with those of Finnish raccoon dogs, and particularly the m2. The molars are needed for grinding the chitinous exoskeletons of insects and other invertebrates and coarse plant material which are consumed more by Japanese than by Finnish raccoon dogs (Ikeda 1985, Kauhala *et al*. 1993b, Sasaki & Kawabata 1994, Fig. 8).

In conclusion, the differences in skull size and shape and tooth size most probably result from differences in the diet; in Finland about 76% of raccoon dog scats contained remains of mammals (Kauhala *et al*. 1993b), whereas Japanese raccoon dogs rarely eat mammals (Ikeda 1985), i.e. the Finnish raccoon dogs are more carnivorous than Japanese raccoon dogs. Japanese raccoon dogs have adapted to a milder climate, are smaller, and have less powerful jaws but larger molars for grinding insects and fruits than Finnish raccoon dogs.

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