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GEOGRAPHIC VARIATION IN THE SKULL OF THE RINGED SEAL, *PUSA HISPIDA*

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A sample of 244 ringed seal (*Pusa hispida*) skulls from 7 localities was examined morphometrically to describe the pattern of geographic variation and to assess subspecies-level taxonomy. Analyses of covariance revealed significant differences among specimens from Lake Saimaa, Lake Ladoga, and other areas. Saimaa seals are robust and short in the skull portion related to feeding, whereas Ladoga seals have narrower skulls and smaller bulla. On scatter plots of canonical discriminant scores obtained using size-free scores, Ladoga and Saimaa specimens were almost separated, but other specimens overlapped and could not be distinguished. Saimaa seals were the most distant, followed by Ladoga seals in the unweighted pair-group method using arithmetic average clustering and neighbor-joining phenograms. These results showed that although ringed seals from Lake Ladoga and Saimaa were considerably differentiated, specimens from other localities were not distinguishable from each other, suggesting similar selection pressure or extensive gene flow especially in the Arctic basin. Further recognition of subspecies for the Arctic seals was not supported.

Key words: geographic variation, *Pusa hispida*, ringed seals, skull morphometry, subspecies

Ringed seals, *Pusa hispida*, are small seals adapted to life on ice. They have a circumpolar distribution, which is the largest range among the northern pinnipeds (Fig. 1), and are the most numerous seals in the northern hemisphere (Frost and Lowry 1981). They are considered to be the closest relative to the Baikal (*P. sibirica*) and Caspian (*P. caspica*) seals (Frost and Lowry 1981). In the traditional taxonomy these seals were included in genus *Phoca* (Frost and Lowry 1981; Wozencraft 1993). However, recent molecular studies reveal that genus *Phoca* (sensu lato) includes species from 2 distinct clades (tribes Phocinii and Cystophorini) and 3 clades in Phocinii—*Phoca* (sensu stricto), *Pusa*, and *Halichoerus*, which are closely related to one another (Árnason et al. 1995; Carr and Perry 1997; Mouchaty et al. 1995; Perry et al. 1995). On the basis of these results, Carr and Perry (1997) and Rice (1998) concluded that genus *Pusa* should be retained, if we preserve the widely recognized *Halichoerus*.

Many subspecies have been described in the ringed seal, including *P. hispida hispida*, coast of Greenland and Labrador; *P. h. beaufortiana*, Beaufort Sea; *P. h. birulai*, northern coast of Siberia; *P. h. botnica*, Baltic Sea; *P. h. krascheninikovi*, Bering Sea; *P. h. ladogensis*, Lake Ladoga; *P. h. ochotensis*, Okhotsk Sea; *P. h. pomororum*, White Sea and the southern and eastern coasts of Barents Sea; *P. h. saimensis*, Lake Saimaa; and *P. h. soperi*, west coast of Baffin Island.

Although some subspecies descriptions include a comparison of skull morphology, they are based on a small number of spec-

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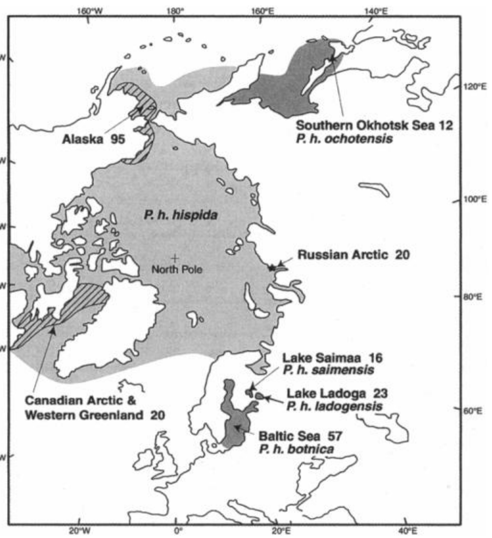

FIG. 1.—Polar view showing geographic ranges of *P. hispida* subspecies, and localities and numbers of the specimens used in the present study. Localities of Alaskan and Canadian Arctic specimens are indicated by the hatched area, and Dikson, where Russian Arctic sample was obtained, is indicated by a star.

imens, and intersubspecific differences are not clearly addressed (Andersen 1943; Naumov and Smirnov 1936; Nordquist 1899; Smirnov 1929). On the basis of geographic separation of the range, King (1964) and Scheffer (1958) reduced the number of subspecies to 6, lumping Arctic subspecies under *P. h. hispida*. Further morphological comparisons of skulls were carried out but represented limited geographic sampling. Fedoseev and Nazarenko (1970) found no morphological differences between skulls from the Barents and Bering seas, and Youngman (1975) reported no significant differences between skulls from the Beaufort Sea and the eastern Canadian Arctic. On the other hand, comparisons among specimens from Lake Saimaa and Lake Ladoga, and those from the Baltic and White seas revealed considerable differentiation (Hyvärinen and Nieminen 1990; Müller-Wille 1969). Five subspecies, including the Bering Sea *P. h. krascheninikovi* to *P. h. hispida*, are generally recognized now (Frost and Lowry 1981; Rice 1998; Fig. 1). However, the overall geographic variation in *P. h. hispida* and across other subspecies has not been studied. We examined skulls of ringed seals from several localities throughout their range to describe the geographic variation and assess the validity of subspecies-level taxonomy.

MATERIALS AND METHODS

We examined 244 skulls (Appendix I), including skulls collected at Dikson, Russia, in the Japanese–Russian joint research expedition program for ringed seals in 1995 and now deposited in the National Science Museum, Tokyo, Japan.

We divided the specimens into 7 geographic samples: Alaskan coast, eastern area of Canadian Arctic, Baltic Sea, Lake Saimaa, Lake Ladoga, Russian Arctic, and Okhotsk Sea (Fig. 1). We did not separate Alaskan specimens into those from the Arctic and from the Bering Sea because their localities were continuous, and Fedoseev and Nazarenko (1970) reported no differences between the Bering and the Arctic seals. Canadian Arctic sample included specimens from Baffin Island through the Labrador coast and also 1 from western Greenland and 1 stranded on the Massachusetts coast.

We made 30 measurements on each specimen with calipers to the nearest 0.1 mm, following Burns et al. (1984; Appendix II; Fig. 2). All specimens were measured by 1 person (M. Amano) to avoid interobserver errors.

Sample size and size range varied among localities. For example, Alaskan samples included a wide range of specimens from small to large, but Okhotsk samples were seriously biased toward smaller seals (Fig. 3). Further, the size of seals varies with ice conditions (e.g., seals that breed on fast ice, or ice attached to land, tend to be larger than those that breed on pack ice—McLaren 1958).

Therefore, we used statistical methods that reduce the effect of size. First, we applied an analysis of covariance (ANCOVA) with the common slope model, assuming that slopes for all samples are the same, using condylobasal length as a covariate and post hoc pairwise comparisons with the Tukey method (Zar 1996). We disregarded the differences in slope because slopes of regression lines should be affected by the biased range of the covariate variable. Second,

TABLE 1.—Summary of descriptive statistics on cranial measurements for geographic samples of *P. hispida*. Measurements (in mm) are shown as adjusted means of log-transformed values based on ANCOVAs. For measurement numbers and abbreviations, see Fig. 2 and Appendix II.

Measure-ments	Alaska			Baltic			Canada		
	n	$\bar{X}$	*SD*	*n*	$\bar{X}$	*SD*	*n*	$\bar{X}$	*SD*
2. PL	94	1.823	0.017	57	1.821	0.017	19	1.815	0.022
3. LUTR	95	1.711	0.014	56	1.706	0.014	19	1.712	0.011
4. GWM	95	1.989	0.013	57	1.999	0.016	19	2.001	0.020
5. GWC	95	1.921	0.015	57	1.924	0.015	19	1.929	0.016
6. ZW	94	1.980	0.014	57	1.983	0.018	19	1.976	0.014
8. LM	79	1.996	0.009	55	1.992	0.010	14	1.993	0.009
9. HMC	82	1.595	0.027	55	1.603	0.026	16	1.588	0.027
10. LLTR	78	1.635	0.018	55	1.626	0.015	14	1.634	0.016
12. LNAS	91	1.541	0.045	56	1.554	0.040	19	1.525	0.038
13. LMFN	92	1.352	0.042	56	1.356	0.038	19	1.341	0.045
14. WNAS	93	0.769	0.072	57	0.787	0.075	19	0.774	0.076
15. WEN	94	1.315	0.024	57	1.325	0.027	18	1.322	0.027
17. IOW	94	0.738	0.076	57	0.835	0.068	19	0.804	0.074
18. LPM	91	0.776	0.040	53	0.795	0.043	19	0.808	0.044
19. WPL	95	1.510	0.023	56	1.524	0.027	19	1.529	0.021
20. WPH	92	1.397	0.029	56	1.397	0.027	19	1.408	0.030
21. WB	93	1.436	0.027	55	1.448	0.021	19	1.463	0.027
22. LB	92	1.538	0.022	57	1.529	0.022	19	1.553	0.018
23. WCD	93	1.722	0.020	57	1.731	0.018	19	1.734	0.021
24. WFM	92	1.465	0.034	57	1.474	0.031	19	1.467	0.042
25. HFM	89	1.357	0.047	55	1.354	0.042	19	1.364	0.043
26. LSN	93	1.340	0.032	57	1.281	0.044	19	1.324	0.041
27. DMP	94	1.257	0.062	56	1.268	0.073	19	1.238	0.064
28. LJ	93	1.640	0.020	57	1.631	0.026	18	1.625	0.037
29. HJ	94	0.877	0.079	57	0.886	0.057	18	0.866	0.047
30. WB2	94	1.545	0.020	57	1.544	0.016	19	1.561	0.022

multiple-group principal components analysis using log-transformed data was carried out to discriminate the size and size-free axes (Thorpe 1983). Then, we ran canonical discriminant function analyses based on these size-free scores to distinguish specimens from each locality. To increase the sample size, we excluded 11 characters (12, LNAS; 13, LMFN; 14, WNAS; 15, WEN; 17, IOW; 18, LPM; 25, HFM; 26, LSN; 27, DMP; 28, LJ; and 29, HJ—Fig. 2; Appendix II) from the analyses. SAS was used for statistical analyses (SAS Institute Inc. 1989). Finally, we constructed the unweighted pair-group method using arithmetic average clustering (UPGMA) and neighbor-joining phenograms with Mahalanobis distances based on the size-free scores of multiple-group principle components analysis to illustrate the overall patterns of skull shape among localities using PHYLIP version 3.5 (Felsenstein 1993).

Relatively few specimens were not identified by sex, and sex ratio was biased in some samples (Appendix I). Before the analyses, we examined sexual dimorphism with univariate and multivariate analyses of covariance (MANCOVAs) using the Alaskan and Baltic Sea samples, which have larger sample sizes. We found no effect of sex in the MANCOVAs (Wilks' lambda = 0.37 and 0.28 for Alaskan and Baltic samples, respectively; $P > 0.05$), but ANCOVAs revealed strong sexual differences in 3 characters (7, height of cranium; 11, height of mandible behind last molar; 16, width of snout at canines—Fig. 2; $P < 0.01$) for Alaskan specimens, so we omitted these characters. Thus, we combined specimens of both sexes in the analyses that include all samples. Although the analyses found weak differences ($P = 0.03$) in the width of external nares (15) for Baltic and the greatest width at mastoids (4) for Alaskan specimens, we included these measurements in subsequent analyses. Sexual differences in size and robust-

TABLE 1.—Extended.

Ladoga			Okhotsk			Russia			Saimaa		
n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD
23	1.819	0.019	11	1.830	0.019	15	1.826	0.021	16	1.812	0.016
22	1.717	0.012	12	1.727	0.014	20	1.713	0.009	16	1.691	0.015
23	1.976	0.015	12	1.986	0.010	19	1.991	0.016	16	1.990	0.012
23	1.901	0.014	12	1.912	0.016	19	1.920	0.011	16	1.919	0.014
23	1.966	0.019	12	1.972	0.023	19	1.976	0.018	16	1.995	0.013
23	2.000	0.007	12	1.996	0.009	20	1.997	0.009	14	2.009	0.010
23	1.581	0.026	12	1.598	0.031	19	1.601	0.023	14	1.634	0.029
23	1.640	0.015	12	1.649	0.011	20	1.636	0.013	13	1.618	0.017
23	1.527	0.041	10	1.527	0.042	20	1.558	0.048	15	1.549	0.042
23	1.352	0.042	11	1.375	0.024	20	1.371	0.041	16	1.361	0.038
23	0.698	0.067	11	0.742	0.089	20	0.781	0.085	16	0.736	0.079
22	1.321	0.022	11	1.321	0.035	18	1.314	0.031	16	1.300	0.023
23	0.717	0.068	11	0.743	0.095	20	0.763	0.062	16	0.784	0.087
21	0.776	0.042	5	0.753	0.039	20	0.794	0.037	16	0.751	0.031
22	1.491	0.028	12	1.548	0.026	18	1.543	0.023	16	1.518	0.020
23	1.373	0.029	12	1.397	0.026	13	1.407	0.033	16	1.411	0.037
23	1.433	0.026	12	1.432	0.033	19	1.435	0.024	16	1.439	0.021
23	1.516	0.023	12	1.535	0.022	18	1.543	0.016	16	1.542	0.017
23	1.710	0.017	12	1.719	0.024	20	1.724	0.018	16	1.705	0.016
23	1.446	0.031	12	1.453	0.033	20	1.471	0.034	16	1.431	0.028
22	1.348	0.035	11	1.349	0.023	18	1.364	0.040	16	1.351	0.031
23	1.338	0.038	11	1.299	0.069	19	1.306	0.022	16	1.303	0.033
23	1.223	0.057	11	1.247	0.124	15	1.273	0.069	15	1.253	0.074
22	1.617	0.022	10	1.630	0.022	19	1.631	0.026	14	1.675	0.015
22	0.839	0.081	10	0.893	0.112	20	0.855	0.076	14	0.887	0.035
23	1.525	0.020	12	1.543	0.020	19	1.543	0.018	16	1.543	0.014

ness are reported to vary geographically (McLaren 1993), and different sex ratios could affect the results. Therefore, we also carried out ANCOVAs and canonical discriminant analysis using only male samples, although no Lake Saimaa specimens were used, and only a few Canadian (5) and Okhotsk (3) specimens were included. Female specimens were too few to analyze separately (Appendix I).

RESULTS

Results of the ANCOVAs showed considerable differences among Saimaa seals, Ladoga seals, and others (Tables 1–3). Seals from Lake Saimaa are larger in mandible measurements, zygomatic width, and jugal length but smaller in length of toothrow and length of premolar (Table 2). This indicates that the Saimaa seals are wide and short, or robust, in the skull portion related to feeding. On the other hand, seals from Lake Ladoga are smaller in width of skull and in length and width of tympanic bulla (Table 2). Narrower skulls of Ladoga seals were also shown in the results for male specimens (Table 3). Patterns of differences were the same when analysis included both sexes and when analysis was done only on males (Tables 2 and 3).

Figure 4 shows the scatter plots between 1st and 2nd and between 1st and 3rd canonical discriminant scores, using 26 measurements from all specimens without missing values. The Ladoga and Saimaa specimens were differentiated from the others, but other specimens overlapped and could not be distinguished. Canonical discriminant function analysis following multiple-group principal components analysis using

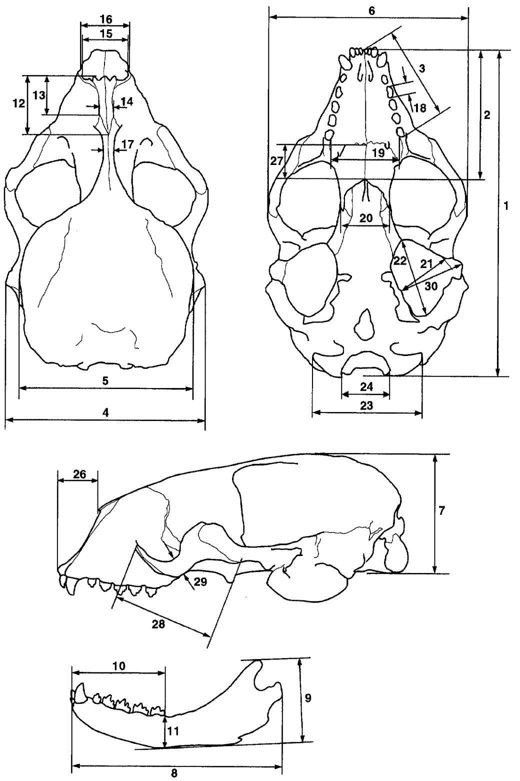

FIG. 2.—Skull measurements of *P. hispida*. Numbers refer to characters listed in Appendix II.

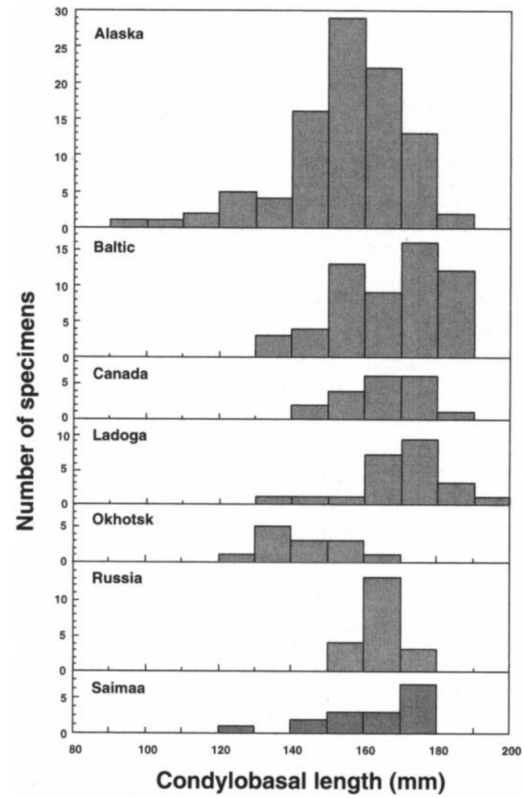

FIG. 3.—Frequency distribution of the condylobasal lengths of *P. hispida* specimens from different localities.

male specimens only was similar, but a tendency to separate Alaskan and Baltic specimens was more obvious (Fig. 5).

In the UPGMA phenogram, Saimaa seals, followed by Ladoga seals, were the most distant from the others (Fig. 6a). Branch lengths among other samples were short and less than half of those of the Saimaa and Ladoga samples. A similar relationship was observed in the neighbor-joining phenogram (Fig. 6b). Again, the Saimaa and Ladoga samples were situated far from the others. The branching pattern among other samples differed from that of the UPGMA tree, indicating little morphological differentiation among them.

DISCUSSION

Ringed seals from Lake Ladoga and Saimaa showed considerable morphological differentiation from seals at other localities. Similarly, Hyvärinen and Nieminen (1990) examined the differentiation of skull morphology of Baltic, Lake Saimaa, and Lake Ladoga ringed seals and found significant differences. Lake Saimaa seals have higher tympanic bullae and shorter toothrows, Ladoga seals have smaller braincases, and Baltic seals have wider occipital condyles and foramina magna. Conspicuous differentiation among the 3 populations supports the idea that Ladoga and Saimaa seals were isolated about 8,000–9,000 years ago, and gene flow between the lakes and the Baltic Sea has been substantially limited (Hyvärinen and Nieminen 1990; Müller-Wille 1969).

Patterns of morphological differentiation differed between Ladoga and Saimaa seals,

TABLE 2.—Comparisons of cranial measurements among geographic samples of *P. hispida* by ANCOVAs with Tukey's multiple comparison method using specimens of both sexes; significant differences ($P < 0.05$) are shown. For measurement numbers and abbreviations, see Fig. 2 and Appendix II.

Measurement	Differences among samples
3. LUTR	Okhotsk > Alaska, Baltic, Canada, Saimaa; Ladoga > Baltic, Saimaa; Alaska, Baltic, Russia > Saimaa
4. GWM	Alaska, Baltic, Canada, Russia, Saimaa > Ladoga; Baltic, Canada > Alaska
5. GWC	Alaska, Baltic, Canada, Russia, Saimaa > Ladoga; Canada > Okhotsk
6. ZW	Saimaa > Alaska, Canada, Okhotsk, Ladoga, Russia; Alaska > Ladoga
8. LM	Saimaa > Alaska, Baltic, Canada, Ladoga, Okhotsk, Russia; Ladoga > Baltic
9. HMC	Saimaa > Alaska, Baltic, Canada, Ladoga, Okhotsk, Russia; Baltic > Ladoga
10. LLTR	Alaska, Okhotsk, Ladoga, Russia > Saimaa; Alaska, Okhotsk, Ladoga > Baltic
14. WNAS	Alaska, Baltic, Canada, Russia > Ladoga
15. WEN	Baltic > Saimaa
17. IOW	Baltic > Alaska, Okhotsk, Ladoga, Saimaa; Canada > Alaska, Ladoga
18. LPM	Baltic, Canada, Russia > Saimaa; Canada > Alaska
19. WPL	Alaska, Baltic, Canada, Okhotsk, Russia, Saimaa > Ladoga; Baltic, Canada, Okhotsk, Russia > Alaska; Okhotsk > Alaska, Baltic, Ladoga, Saimaa
20. WPH	Alaska, Baltic, Canada, Russia, Saimaa > Ladoga
21. WB	Canada > Alaska, Okhotsk, Ladoga, Russia
22. LB	Canada, Russia, Saimaa > Ladoga; Canada > Baltic
23. WCD	Alaska, Baltic, Canada, Russia > Saimaa; Baltic, Canada > Ladoga
24. WFM	Alaska, Baltic, Canada, Russia > Saimaa; Baltic > Ladoga
26. LSN	Alaska > Baltic, Okhotsk, Russia, Saimaa; Canada > Baltic
28. LJ	Saimaa > Alaska, Baltic, Canada, Okhotsk, Ladoga, Russia; Alaska > Ladoga
30. WB2	Alaska, Baltic, Canada, Russia > Ladoga; Canada > Alaska, Baltic, Ladoga

TABLE 3.—Comparisons of cranial measurements among geographic samples of *P. hispida* by ANCOVAs with Tukey's multiple comparison method using male specimens; significant differences ($P < 0.05$) are shown. Saimaa samples are not included. For measurement numbers and abbreviations, see Fig. 2 and Appendix II.

Measurement	Differences among samples
3. LUTR	Ladoga > Baltic
4. GWM	Baltic, Canada > Alaska, Ladoga; Canada > Russia
5. GWC	Alaska, Baltic, Canada, Russia > Ladoga
6. ZW	Alaska, Baltic > Ladoga
8. LM	Ladoga > Baltic
14. WNAS	Alaska, Baltic > Ladoga
16. WSN	Baltic > Alaska
17. IOW	Baltic > Alaska, Ladoga, Russia
18. LPM	Baltic, Canada, Ladoga > Alaska; Ladoga > Baltic, Russia
19. WPL	Baltic, Canada, Okhotsk, Russia > Ladoga, Baltic, Russia > Alaska
20. WPH	Baltic, Canada, Russia > Ladoga
26. LSN	Alaska, Ladoga > Baltic, Okhotsk, Russia
28. LJ	Alaska > Ladoga
29. HJ	Okhotsk > Ladoga
30. WB2	Canada > Alaska, Baltic, Ladoga

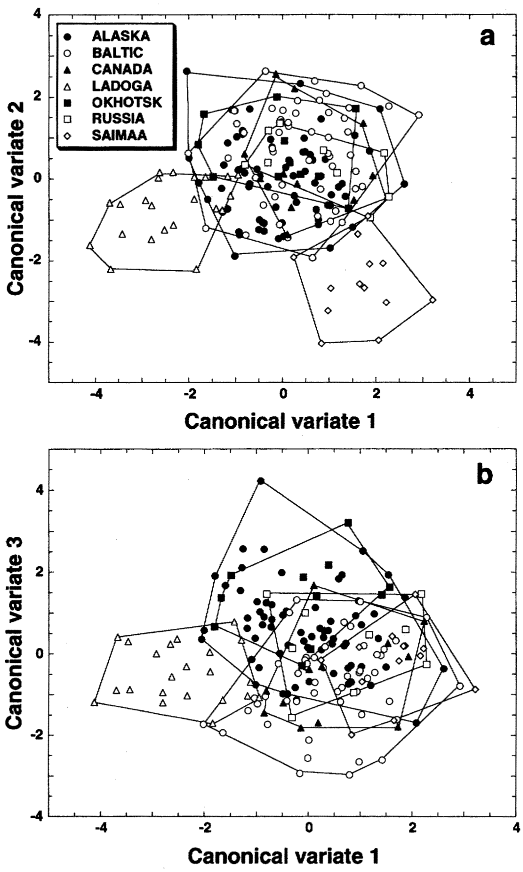

FIG. 4.—Scatter plots of a) the 1st versus 2nd and b) the 1st versus 3rd canonical discriminant variates based on the size-free multiple-group principal component scores for all specimens.

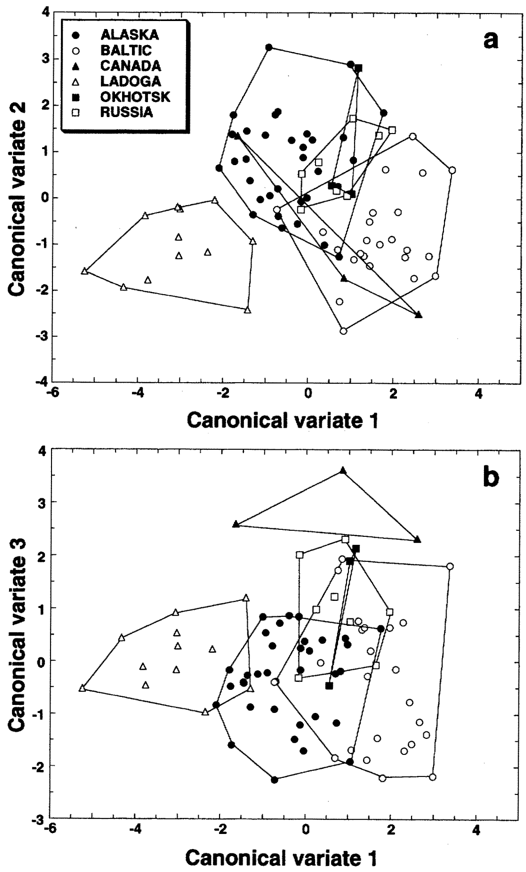

FIG. 5.—Scatter plots of a) the 1st versus 2nd and b) the 1st versus 3rd canonical discriminant variates based on the size-free multiple-group principal component scores for male specimens.

suggesting distinctive selection pressures. Environmental differences between the 2 lakes were discussed by Müller-Wille (1969) and Hyvärinen and Nieminen (1990), and the latter argued that dependence on hearing ability in the turbid Lake Saimaa caused relatively large bulla in the Saimaa seals. However, we found that bullar length and width in Saimaa seals were not relatively larger than in Arctic samples.

Ringed seals are known to feed on planktonic crustaceans and fish (Chapskii 1996; Lowry et al. 1978, 1980; McLaren 1958; Söderberg 1975). However, the dominant prey of the Saimaa ringed seals are small schooling fishes, and crustaceans are not important in the diet (Kunnasranta et al. 1999). This difference in feeding habit may be related to morphological differences in feeding apparatus between Saimaa seals and others. On the other hand, it is not easy to explain the narrower cranium and smaller bulla of the Ladoga seal based on habitat differences. Isolation in small lakes and bottleneck effects were also suggested for the Saimaa ringed seals that have experienced serious population depletion (Hyvärinen and Nieminen 1990), and such events may impact the rapid fixation of morphological variants.

Our results revealed little differentiation among Arctic ringed seals. Russian Arctic specimens were collected near Dikson, which is located near the border of the

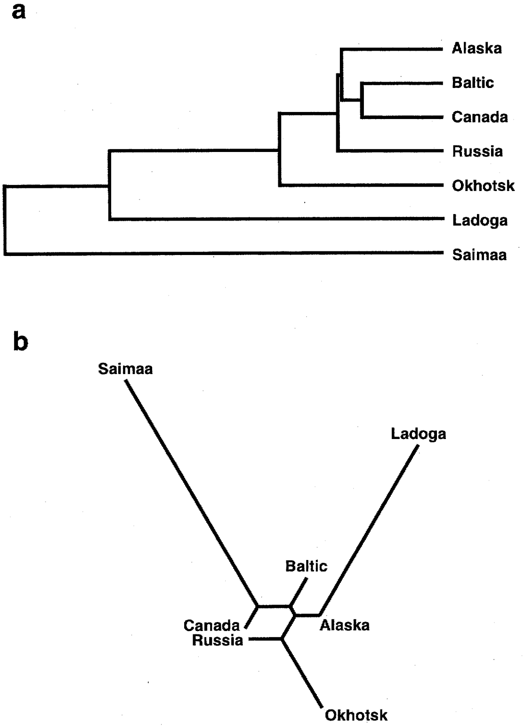

FIG. 6.—a) UPGMA and b) neighbor-joining phenograms based on the Mahalanobis distances obtained from the size-free multiple-group principal component scores for all specimens.

range between *P. h. pomororum* and *P. h. birulai* (Ognev 1962; Smirnov 1929). ANCOVAs did not support the diagnostic features reported for these subspecies: longer and higher braincase, and shorter and wider rostrum for *P. h. pomororum*; lower braincase, large molar, wider snout for *P. h. birulai* (Ognev 1962; Smirnov 1929). The fact that no meaningful differences were observed between skulls from the Barents and Bering seas (Fedoseev and Nazarenko 1970) also questions the validity of *P. h. pomororum*. Furthermore, continuous distribution along the Russian Arctic coast would seem unlikely to permit strong differentiation of seals from the White and Barents seas and the Siberian coast. Lack of differentiation among North American samples corroborates the results of Youngman (1975). We, therefore, conclude that division of subspecies in the Arctic is untenable.

Subspecies recognition of *P. h. ochotensis* was not supported. For the Okhotsk specimens, our sample size was small, and most of the specimens seemed to be juveniles. Reported length of adult skulls is about 150–170 mm, although this subspecies was characterized by its smaller size (Naumov and Smirnov 1936; Ognev 1962). Moreover, we should note that some of the characteristics that Naumov and Smirnov (1936) pointed out, such as attenuate rostrum with wider base and longer toothrow are consistent with our results. Reevaluation of the results with a larger sample size of adults is needed.

The Baltic sample was not fully discriminated in the canonical discriminant analyses, but the Baltic ringed seal has a completely isolated distribution and was originally discriminated by its distinct dark pelage (Bobrinskii 1944; Ognev 1962). We believe the subspecific name for this population should be retained. This population has been declining because of overexploitation (Kokko et al. 1999) and, recently, reproductive inhibition thought to be caused by the toxic effects of pollutants (Helle et al. 1976a, 1976b; Olsson et al. 1994).

In conclusion, we consider it reasonable to recognize 5 subspecies in *P. hispida*: *P. h. hispida*, *P. h. botnica*, *P. h. ladogensis*, *P. h. ochotensis*, and *P. h. saimensis*.

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APPENDIX I

Specimens examined.—The 244 specimens of *P. hispida* examined are listed here by museum abbreviations and specimen identification numbers. Abbreviations for museums are as follows: MCZ, Museum of Comparative Zoology; MZH, Zoological Museum, University of Helsinki; NSMT, National Science Museum, Tokyo; SMNH, Swedish Museum of Natural History; UAM, University of Alaska Museum. Sex is indicated after the number: F, female; M, male; U, unknown.

ALASKA: MCZ 37621U; UAM 2088M, 5008F, 5009M, 7110U, 7112M, 7183M, 11565M, 11566M, 11567U, 11568M, 11569M, 11570M, 11575F, 11576M, 11577M, 11578F, 11579M, 11580M, 11581F, 11587M, 11588M, 11892M, 11895M, 11896M, 11897F, 11898M, 11899M, 15658M, 15659F, 15671F, 15692M, 15698M, 16599M, 16600F, 16601M, 16602U, 16603M, 19055M, 19056M, 19057F, 19058F, 19059F, 19060F, 19061M, 19064F, 19066F, 19068F, 19069U, 19070U, 19071M, 19072M, 19074M, 19075M, 19077M, 19078U, 19081M, 19082M, 19083M, 19084F, 19085F, 19086M, 19088M, 19089F, 19090M, 19091M, 19092M, 19093M, 19094M, 19095F, 19096F, 19097M, 19098F, 19100F, 19102F, 19104M, 19105F, 19106M, 19110M, 19111M, 19112M, 19115M, 19118F, 28914F, 28915F, 28916F, 28917F, 28918F, 28920U, 28921F, 28923F, 28926M, 33994F, 33995F, 36249U.

BALTIC SEA: SMNH 825045M, 825056U, 825063M, 835018M, 835167M, 835172M, 835181M, 845065F, 845115F, 845167F, 855071M, 855087M, 855111F, 855123F, 855131F, 875072M, 875154F, 875304F, 875314M, 875350M, 885069M, 885071F, 885108F, 885113F, 885180M, 885181F, 885191F, 885222F, 885229M, 885230F, 885239F, 885245M, 895072F, 895126M, 895168F, 905079U, 905103M, 905104F, 915044F, 915102M, 915103F, 915108M, 915110M, 915113F, 915135M, 925062F, 925083M, 925107M, 925120F, 925147F, 925148F, 935020M, 935184U, 935188F, 945073M, 945098M, 945179M.

CANADIAN ARCTIC: MCZ 7743U, 7745U, 7746U, 7747U, 8512U, 21809U, 29804U, 47066U, 47447U, 60957F; MZH 67F, 107M, 193F, 198F, 250M, 254F; UAM 11584M, 11585F, 11586M, 11590M.

LAKE LADOGA: MZH 1225M, 1256M, 1258M, 1268M, 1271F, 1276F, 2100M, 2111M, 2124M, 2128M, 2131M, 2155M, 2203M, 2204F, 2205F, 2210F, 2211F, 2214M, 2215F, 2216F, 2221M, 2226F, 3695U.

LAKE SAIMAA: MZH 31.506U, 1154U, 2293U, 2295U, 5689U, 5692U, 5693U, 5694F, 5699F, 5704U, 6291U, 6296F, 6461U, 6462U, 6463U, 6464U.

OKHOTSK SEA: NSMT 1881U, 4823F, 12954U, 13745U, 28991F, 28993M, 29022F, 29030M, 29032F, 29034M, 29060U, 29062F, 29638U.

RUSSIAN ARCTIC: NSMT 30062M, 30067F, 30073M, 30074F, 30078M, 30079F, 30082F, 30083M, 30085M, 30089M, 30090M, 30091M, 30092M, 30093M, 30094M, 30096M, 30099M, 30100M, 30102M, 30104M.

APPENDIX II

Measurements made on skulls of *P. hispida* (as shown in Fig. 2): 1, condylobasal length (CBL); 2, palatal length (PL); 3, length of upper toothrow—from tip of rostrum to hindmost point of last molar (LUTR); 4, greatest width at mastoids (GWM); 5, greatest width of cranium (GWC); 6, greatest zygomatic width (ZW); 7, height of cranium (HC); 8, length of mandible—from tip of mandible to most distant point on condyle (LM); 9, height of mandible at coronoid process (HMC); 10, length of lower toothrow—from tip of mandible to hindmost point of last molar (LLTR); 11, height of mandible behind last molar (HM); 12, length of nasals (LNAS); 13, distance from point where left maxillofrontal suture contacts nasal to anterior end of left nasal (LMFN); 14, width of nasals across the points where maxillofrontal sutures contact nasals (WNAS); 15, maximal width of external nares (WEN); 16, width of snout at canines (WSN); 17, least interorbital width (IOW); 18, greatest anterior–posterior length of 2nd upper premolar (LPM); 19, width of palate behind last molars (WPL); 20, least width of palate at pterygoid hamuli (WPH); 21, width of bullar notch anterior to auditory process–middle of carotid foramen (WB); 22, greatest length of bulla (LB); 23, greatest width at condyles (WCD); 24, greatest width of foramen magnum (WFM); 25, greatest height of foramen magnum (HFM); 26, length of snout from anterior edge of nasals (LSN); 27, distance from posterior end of intermaxillary suture to medial edge of palate (DMP); 28, greatest length of jugal (LJ); 29, minimal height of jugal (HJ); 30, width of bulla from tip of auditory process to anterior margin of carotid foramen (WB2).