

VARIATIONS IN THE SKULL OF THE BEARDED SEAL

T. H. MANNING



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ERIGNATHUS BARBATUS (ERXLEBEN)**

by

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Abstract

Fourteen measurements taken on 260 skulls are described and analysed using variance, covariance, reduced major axes, and discriminant functions. No sexual variation is found. Changes in relative growth with age are demonstrated and discussed. Skulls from the Atlantic adult population are shown to be significantly larger than those from the Pacific in most dimensions. An important exception, nasal breadth, is significantly smaller. Differences in the regression coefficients between the Atlantic and Pacific populations are probably not significant, but some differences in position of the regression lines are highly significant. The results are compared with those of some previous authors and the boundaries between the populations considered. The recognition of *E. b. nauticus* for the Pacific population is justified.

VARIATIONS IN THE SKULL OF THE BEARDED SEAL, *ERIGNATHUS BARBATUS* (ERXLEBEN)

by

T. H. MANNING

Introduction

The main purpose of this study was to clarify the taxonomic status of *Erignathus barbatus nauticus* (Pallas). In the process skull measurements of males and females, and of adults and subadults were compared to estimate differences and to study the effects of differential growth. Scheffer (1958) accepted the division of *E. barbatus* into an Atlantic and Pacific race largely as a matter of convenience. Of those who have compared skulls from the two regions, Allen (1902) and Anderson (1930, 1946) found no differences, but Osgood (1904) and Ognev (1935) both commented on the shorter and broader nasals of the Pacific form, *E. b. nauticus*, as well as giving differences indicating a heavier rostrum and a generally more brachycephalic appearance. Both authors seem to have relied more on general appearance than on detailed measurements, though Ognev (1935) gave these for eleven specimens of each race. I, on the other hand, have not been able to examine good series from the Atlantic and Pacific simultaneously and therefore have relied entirely on measurements.

Materials and Methods

Fourteen measurements were taken on each of 260 skulls. These skulls were divided into two main groups, referred to as the Atlantic and Pacific series. The Atlantic series of 134 skulls consisted of 33 from Hudson Bay, Hudson Strait and Ungava Bay, 24 from Labrador and Newfoundland, 3 from east Baffin Island, 8 from Barrow Strait and Lancaster Sound, 46 from Greenland, 18 from Svalbard and 2 from Norway. The Pacific series of 118 skulls included 1 from Herschel Island, 1 from eastern Siberia and 2 from Japan. The remaining 114 were from Alaska, mainly Point Barrow and the coast to the south-west. The breakdown by sex and age was as follows: Atlantic series. Adults: 18 ♂♂, 16 ♀♀, 56 sex unknown. Subadults: 3 ♂♂, 5 ♀♀, 34 sex unknown. Foeti: 2 ♂♂. Pacific series. Adults: 27 ♂♂, 24 ♀♀, 15 sex unknown. Subadults: 17 ♂♂, 23 ♀♀, 12 sex unknown. Six specimens (5 adults + 1 foetus) taken in the central and western Canadian Arctic between Pelly Bay and Amundson Gulf were considered likely to be intermediate and were therefore excluded from both series. Also excluded were two specimens from the Russian Arctic.

The measurements taken were as follows (see also Figs. 1-3):

CBL. Condylbasal length. From the left condyle to the tip of the premaxillae.

ZB. Zygomatic breadth. Taken across the zygomata midway between the posterior extremity of the jugals and the glenoid fossae, using narrow points of the calipers.

MB. Mastoid breadth. Maximum breadth across the mastoid processes.

BB. Braincase breadth. Greatest breadth between the ridges formed at the junction of the parietals and the squamosals.

LIB. Least interorbital breadth. Least breadth obtainable with narrow points of calipers.

NL. Nasal length. From the posterior extremity to the anterior extremity of the left nasal.

NB. Nasal breadth. Taken across both nasals at the posterior tip of the premaxillae.

CB. Condyle breadth. The greatest external breadth.

PB. Palatal breadth. The greatest breadth between the palatal borders of the maxillae.

RB. Rostral breadth. The greatest breadth between the outer border of the maxillae anterior to the posterior border of the canines.

MTL. Maxillary tooththrow length. Measured at the alveoli.

BH. Braincase height. With the bar of the calipers touching the supraoccipital and held perpendicular to the long axis of the skull, one jaw was extended along the basioccipital between the condyles, the other along the central line of the parietals and, when it was present, in the groove between them.

PML. Premaxilla-maxilla length. From the tip of the premaxilla to the posterior border of the zygomatic process of the maxilla. The anterior bar of the calipers was placed on the left premaxilla to give the greatest measurement, and the posterior bar on the maxilla to give the least measurement, using the narrow points of the calipers.

PL. Palatal length. Taken on the midline from the posterior border of the palatines to the anterior border of the premaxillae, using the wide points of the calipers.

CPL. Condylopalatal length. Obtained by subtracting PML from CBL. All measurements were taken on the left side when undamaged. The narrow points of the calipers measured 1 mm, the wide points 3.5 mm.

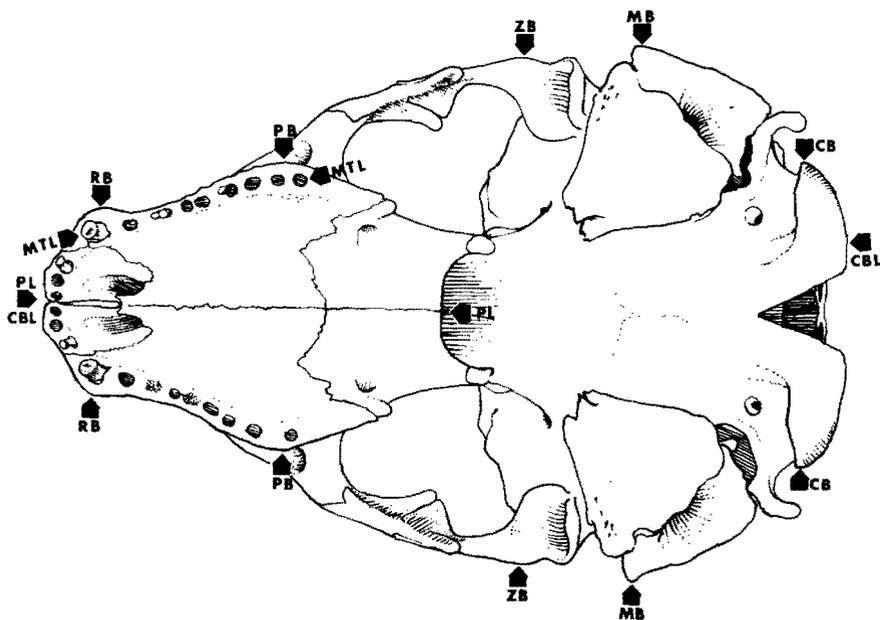


Fig. 1. Measurements of bearded seal skulls. See text, pages 2 and 3, for definitions.

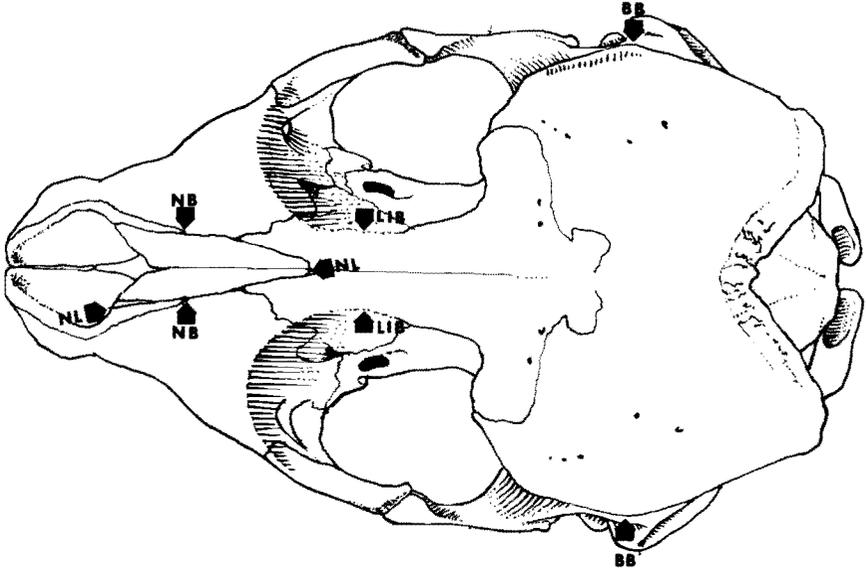


Fig. 2. Measurements of bearded seal skulls. See text, pages 2 and 3, for definitions.

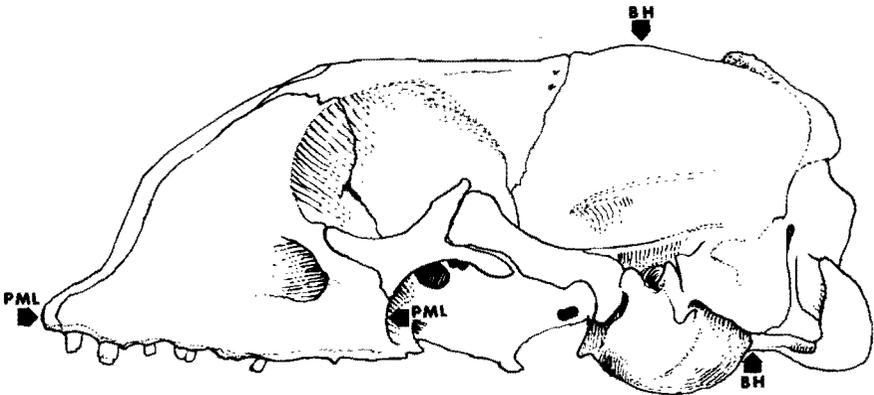


Fig. 3. Measurements of bearded seal skulls. See text, pages 2 and 3, for definitions.

Analysis of variance was used to test differences between sexes and between populations, covariance analysis to test differences between sexes, ages, and populations, and discriminant functions to test differences between populations. The independent variate was condylobasal length, representing total skull size. Since, like the dependent variates, it was subject to sampling and other errors, and since the correlation coefficients were rather low, the regressions considerably underestimate the true functional relationship. Reduced major axes are therefore given as an alternative in Table 3. They have also been used in Figs. 4-6 and in the discussion of changes in relative growth, for which regressions are particularly inappropriate. Standard errors for the reduced major axes and for means adjusted by these axes were calculated by the formulae given by Kermack and Haldane (1950), but according to Simpson, et al (1960) there are no accurate tests for differences in their slope or position. In this instance, Bartlett's best fit lines seemed to offer little advantage over regressions, as the independent variates could not be grouped without overlap, and sampling errors clearly affected the grouping. Perhaps because of this, the best fit lines were found to lie near and on either side, rather than always above, the regressions. A similar inconsistency was noted by McIntosh (1955).

Results

Sexual Differences

Using the skulls of adults, as defined below, two way analysis of variance between males and females and between Atlantic and Pacific samples showed no significant sexual difference for any measurement, and only in the cases of least interorbital breadth ($F=3.12$, d.f. 1:76) and of maxillary toothrow length ($F=3.43$, d.f. 1:76) was significance approached. Two way covariance analysis with condylobasal length as the independent variate also showed no significant interactions or differences in slope of the regression lines, but the least interorbital breadth regression line for males was significantly above that for females ($F=5.27$, d.f. 1:75). However, in view of the number of comparisons made, it is reasonable to ascribe this difference to sampling error and to assume that any differences which may exist between the sexes are small and not detectable with the material available. It was further assumed that sexual differences which could not be detected in the adults would not be found in the young. The sexes were therefore combined in all further tests. Potelov (1968) also found no sexual dimorphism in bearded seal skulls.

Age Criteria and Relative Growth

The skulls were divided into two age groups depending on the condition of the basisphenoid-basioccipital suture. All those in which this suture was fused were considered adult, though some growth even in length occurs after fusion. The overlap in condylobasal length between the smallest adult and the largest subadult was 16 mm in the Atlantic and 13 mm in the Pacific series. Allowing for the difference in numbers between the adult and subadult series, the mid-points in the overlap in the parent populations were estimated to be 215 mm for the Atlantic and 212 mm for the Pacific. These lengths are therefore estimates of the average lengths at which the basisphenoid and basioccipital bones fuse. It follows that the increase in condylobasal length which occurs after fusion is equal to the difference between the mean length at which fusion occurs and the mean condylobasal length finally attained. The latter will be higher than the 226.3 mm and 222.8 mm given in Table 1 for the adult Atlantic and Pacific series respectively, since these series evidently contain some growing individuals. From 12 to 15 mm would therefore be a reasonable estimate of the average increase in condylobasal length after fusion. A more critical definition of adults would have been preferred, but no satisfactory criterion was found. Tooth wear was not used, since the teeth are evidently undergoing phylogenetic degeneration and considerable variation within a single age group appeared probable. Certainly the teeth of some specimens with fused basisphenoid-basioccipital sutures showed less wear than some in which that suture was unfused.

Using Potelov's graph (1968) of condylobasal length plotted against age, and allowing for the smaller mean condylobasal length of his series, the age at which the basisphenoid-basioccipital suture fuses appears to be about five years. About one third of the Atlantic series and nearly half the Pacific series are below this age. The difference is not quite significant $\chi^2=3.5$.

The regression coefficients of the adults differ significantly from those of the subadults when zygomatic breadth, mastoid breadth and maxillary toothrow length are used as the dependent variates (Table 3). However, with the first two, the regressions (b) are higher in the subadults than in the adults, whereas the reverse is true for the reduced major axes (B). Since $b = B \times r$ this effect is clearly the result of the higher subadult correlations. Since specimens taken over the whole of the subadult range will normally have higher correlations than adults, comparison of the regressions of adults and subadults has, therefore, little meaning unless the range of the former is limited so that $Sx^2_1 \approx Sx^2_2$. A comparison of the variance ratios in the last column of Table 2 with the difference between the adjusted subadult

TABLE 1. STATISTICS FOR UNADJUSTED MEASUREMENTS (SEXES COMBINED). A = Atlantic, P = Pacific. SD is the pooled within population standard deviation for all adults. CV_1 is the coefficient of variation derived from this and the unweighted mean of the means for the two populations. CV_2 and CV_3 are the coefficients of variation for the species as a whole derived from the mean of all adults and all sub-adults respectively and from the corresponding standard deviations. F is the variance ration for testing the significance of the differences between the sample means of the adults in the two populations. The asterisks indicate significant differences between the adult samples at the 5, 1, 0.5 and 0.1 percent levels.

	Numbers		Means \pm SE		F	SD	CV_1	CV_2	CV_3
	A	P	A	P					
CBL	80	63	226.31 \pm .81	222.84 \pm .92	8.02**	7.28	3.24	3.30 \pm .20	6.57 \pm .49
ZB	80	63	132.39 \pm .55	130.33 \pm .62	6.08*	4.95	3.76	3.81 \pm .23	6.63 \pm .49
MB	83	64	137.86 \pm .48	135.30 \pm .55	12.38****	4.37	3.20	3.31 \pm .19	6.73 \pm .50
BB	82	64	115.21 \pm .47	115.38 \pm .53	0.06	4.21	3.65	3.64 \pm .21	4.32 \pm .32
LIB	84	65	25.25 \pm .31	26.54 \pm .35	7.71**	2.83	10.94	11.18 \pm .65	10.45 \pm .77
NL	79	64	57.33 \pm .47	52.73 \pm .53	42.17****	4.22	7.66	8.63 \pm .51	9.22 \pm .70
NB	82	64	18.59 \pm .24	19.96 \pm .27	14.46****	2.18	11.29	11.80 \pm .65	10.83 \pm .83
CB	82	64	71.64 \pm .32	69.23 \pm .36	26.90****	2.85	4.05	4.36 \pm .25	6.20 \pm .47
PB	83	66	73.36 \pm .38	70.59 \pm .42	23.77****	3.45	4.79	5.11 \pm .30	7.03 \pm .53
RB	82	65	46.16 \pm .31	44.85 \pm .35	7.80**	2.83	6.22	6.33 \pm .37	9.29 \pm .69
MTL	82	66	64.63 \pm .33	62.34 \pm .37	21.62****	2.98	4.69	4.98 \pm .29	6.20 \pm .46
BH	80	65	85.89 \pm .33	84.29 \pm .37	10.18***	2.99	3.52	3.61 \pm .21	4.51 \pm .36
PML	84	66	97.94 \pm .44	96.27 \pm .49	6.38*	4.01	4.13	4.19 \pm .24	6.74 \pm .50
PL	76	66	110.18 \pm .55	107.48 \pm .59	11.27***	4.78	4.39	4.53 \pm .27	8.36 \pm .62

TABLE 2. VARIANCE RATIOS (F) RESULTING FROM TWO-WAY COVARIANCE ANALYSES BETWEEN THE ATLANTIC AND PACIFIC SERIES AND THE ADULT AND SUBADULT SERIES. Condylbasal length representing total skull size is the independent variant. All the regressions (4 parallel lines) are significant at the 0.1 percent level. In the other columns, asterisks indicate significance at the 5, 1, 0.5, and 0.1 percent levels. There are 3 d.f. for the greater mean square for slope, 1 d.f. for the other ratios. Significant differences in slope are not here differentiated between population and age. (see text).

	Number	Regression	Slope		Interaction		Position	
			Pop. and Age	Pop. and Age	Pop.	Age		
ZB	233	365.23	1.94	0.35	0.06	20.44****		
MB	239	284.43	3.95**	0.93	2.38	4.33*		
BB	238	61.18	0.62	0.02	2.63	0.51		
LIB	241	45.83	0.75	0.13	23.75****	0.01		
NL	231	121.81	3.74*	8.00***	32.59****	1.17		
NB	233	12.16	1.50	1.35	43.86****	5.00*		
CB	234	76.95	0.48	5.90*	44.55****	3.45		
PB	238	205.05	1.09	6.89**	7.04**	3.32		
RB	238	203.95	0.81	0.00	2.31	9.93****		
MLT	237	213.02	2.48	0.05	25.81****	4.57*		
BH	233	59.05	0.60	0.27	9.44****	0.32		
PML	241	878.88	1.04	0.06	0.10	6.91**		
PL	232	645.00	0.69	0.01	4.38*	19.20****		

TABLE 3. REGRESSIONS, CORRELATIONS AND REDUCED MAJOR AXES. These are the means for the Atlantic and Pacific series, calculated from their pooled sums of squares and products. Significant differences between the regressions of adults and subadults at the 5 and 1 percent levels are shown by asterisks. Standard errors for the regressions are the same as those for the reduced major axes.

	Regression			Correlation			Reduced Major Axis		
	Ad.	sad.	A. and S.	Ad.	Sad	A. and Sad.	Adults	Subadult	Ad. and Sad.
ZB	.417*	.534*	.586	.614	.895	.930	.680 ± .0448	.597 ± .0280	.630 ± .0153
MB	.338*	.450*	.449	.558	.857	.900	.605 ± .0414	.525 ± .0282	.499 ± .0412
BB	.209	.281	.236	.361	.744	.740	.579 ± .0447	.378 ± .0263	.319 ± .0140
LIB	.130	.100	.113	.332	.527	.621	.392 ± .0302	.190 ± .0169	.182 ± .0092
NL	.317	.231	.274	.547	.722	.801	.580 ± .0406	.320 ± .0236	.341 ± .0135
NB	.066	.038	.072	.220	.294	.529	.301 ± .0241	.130 ± .0135	.136 ± .0076
CB	.164	.150	.133	.419	.563	.652	.392 ± .0295	.266 ± .0234	.204 ± .0102
PB	.262	.284	.299	.542	.824	.872	.484 ± .0333	.344 ± .0204	.343 ± .0110
RB	.196	.228	.256	.496	.852	.886	.395 ± .0283	.267 ± .0147	.289 ± .0087
MTL	.269**	.186**	.241	.650	.773	.876	.413 ± .0258	.240 ± .0162	.275 ± .0087
BH	.165	.136	.139	.403	.502	.644	.410 ± .0312	.271 ± .0250	.216 ± .0109
PML	.460	.408	.458	.827	.942	.962	.556 ± .0254	.433 ± .0154	.476 ± .0113
PL	.503	.534	.598	.766	.919	.955	.657 ± .0355	.581 ± .0242	.626 ± .0156
CPL	.497	.466	.402	.761	.897	.913	.653 ± .0355	.520 ± .0242	.441 ± .0129

TABLE 4. *Y* INTERCEPTS AND ADJUSTED MEANS. The first column gives *Y* intercepts and their standard errors for the reduced major axes (Table 3) of the subadults. The second column shows subadult means adjusted along these axes to a condylobasal length of 130 mm, the mean for the three foetal skulls (139.00 mm for rostral breadth which could be measured on only two skulls). Following the standard error is the difference adjusted mean minus foetal mean. In the third column, the subadult means are adjusted to the adult condylobasal length with the difference, adjusted mean minus adult mean. The means used are the unweighted means of the means of the Atlantic and Pacific series.

	<i>Y</i> intercepts	Adjusted to Foetus		Adjusted to Adult	
ZB	— 3.5 ± 5.45	74.0 ± 1.84	—6.7	130.6 ± 0.91	—0.9
MB	+20.4 ± 5.48	88.4 ± 1.84	+1.6	138.4 ± 0.93	+1.7
BB	+35.1 ± 5.12	84.2 ± 1.72	+1.9	120.0 ± 0.87	+4.7
LIB	—14.3 ± 3.29	10.4 ± 1.11	—9.4	28.3 ± 0.57	+2.5
NL	—15.9 ± 4.60	25.7 ± 1.55	—7.3	56.0 ± 0.78	+0.8
NB	— 8.4 ± 2.63	8.5 ± 0.90	—3.5	20.9 ± 0.46	+1.7
CB	+14.9 ± 4.56	51.9 ± 1.33	+1.5	74.7 ± 0.79	+4.1
PB	— 4.2 ± 3.98	40.5 ± 1.37	—5.1	73.0 ± 0.67	+0.9
RB	—14.6 ± 2.86	20.1 ± 0.96	—7.8	45.4 ± 0.48	—0.2
MTL	+ 9.1 ± 3.15	40.5 ± 1.06	—0.4	63.1 ± 0.53	—0.5
BH	+28.2 ± 4.87	63.5 ± 1.65	—3.5	89.1 ± 0.84	+4.0
PML	— 1.3 ± 3.00	55.1 ± 1.01	0.0	96.1 ± 0.50	—1.2
PL	—23.0 ± 4.71	52.5 ± 1.59	—7.2	107.4 ± 0.78	—1.5
CPL	+ 3.4 ± 4.71	71.0 ± 1.59	+0.8	120.0 ± 0.78	+4.5

TABLE 5. JOINT NONOVERLAP AND SIGNIFICANCE OF DIFFERENCE BETWEEN POPULATIONS. The first column gives the percent joint nonoverlap and significance of difference for the unadjusted measurements of adults. The next three columns give the joint nonoverlap and significance of difference for measurements adjusted to a common condylobasal length by the regressions of Table 3. The last three columns give the joint nonoverlap for measurements adjusted by the reduced major axes of Table 3. Asterisks against the unadjusted and regression adjusted measurements show the significance of difference at the 5, 1, 0.5 and 0.1 percent levels. Plus signs indicate that the mean of the Pacific series is largest, minus signs that the mean of the Atlantic series is largest.

	Unadjusted		Regression		Reduced Major Axis		
	Adult	Adult	Subadult	Adult and Subadult	Adult	Subadult	Adult and Subadult
CBL	-59**						
ZB	-58*	-53	+54	+51	+51	+56	+52
MB	-61****	-57*	+51	-53	-52	+55	-51
BB	+50	+55	+58	+55*	+59	+62	+59
LIB	+59**	+63****	+63***	+63****	+66	+68	+66
NL	-70****	-68****	-59*	-65****	-61	-53	-61
NB	+62****	+65****	+75****	+68****	+68	+77	+71
CB	-66****	-63****	-74****	-69****	-56	-66	-63
PB	-65****	-62****	+52	-56*	-55	+56	-53
RB	-59**	-55	-52	-53	+51	+51	-50
MTL	-66****	-61****	-68****	-62****	-56	-62	-59
BH	-60***	-57*	-60*	-58***	-50	-52	-53
FML	-58*	+50	-53	+50	+53	-50	+51
PL	-61***	-56	-54	-53	-52	-52	-52

means and the adult means in Table 4 shows that the significance of difference in position of the regression lines can also be misleading when, as in this case, there is a big difference between \bar{x}_1 and \bar{x}_2 . The manner in which this comes about can be clearly seen if the regressions of Table 3 are plotted on the graphs (Figs. 4-6).

From Table 3 it appears probable that most of the reduced major axes of adults and subadults differ significantly. Also, the adult values are, in all cases, higher than those of the subadults, and whereas the reduced major axes of the subadults frequently pass through or near the adult centroid, the reverse does not occur (Figs. 4-6). Since the reduced major axes are ratios of the standard deviations, with that of condylobasal length the common denominator, the higher adult values evidently result from a relatively greater decrease in the standard deviation of condylobasal length when passing from subadult to adult. Indeed, for some measurements, there is little difference between the standard deviation of the subadults and adults, and in two, least interorbital breadth and nasal breadth, the subadults, at least in the present samples, are less variable than the adults (Table 1). In most mammals, growth in skull length usually ceases earlier than growth in breadth, but it seems probable that the relatively small standard error for condylobasal length in adults results less from an early reduction in growth in this dimension than from less variability in it after all growth has ceased. The reduced major axes values for the subadults are those of mass growth and result from two factors: 1) size differences such as would occur in a series of the same physiological age and 2) true growth as represented by the mean of the individual growth curves. It is possible, therefore, that if a sufficient series of equal aged specimens could be analysed, their reduced major axes would be similar to those of the adults.

The curves of relative mass growth for mastoid breadth, braincase breadth, condyle breadth and braincase height, all measurements of the braincase, evidently take the same general form; their reduced major axes have large positive Y intercepts and the foetal measurements lie close to these axes (Table 4, Figs. 4-6). In the later stages of growth, between the subadult and adult centroids, curvature is evident as braincase growth decreases more rapidly than growth in length of the skull as a whole. Condylopalatal length, which is also a measurement of the posterior part of the skull, and maxillary toothrow length, both have this form, but it is less well marked. The reverse curve, in which the subadult reduced major axis lies below the ratio of the adult means and has a large negative Y intercept, is best illustrated by palatal length, rostral breadth and nasal length, all measurements of the anterior portion of the skull. However, the foetal

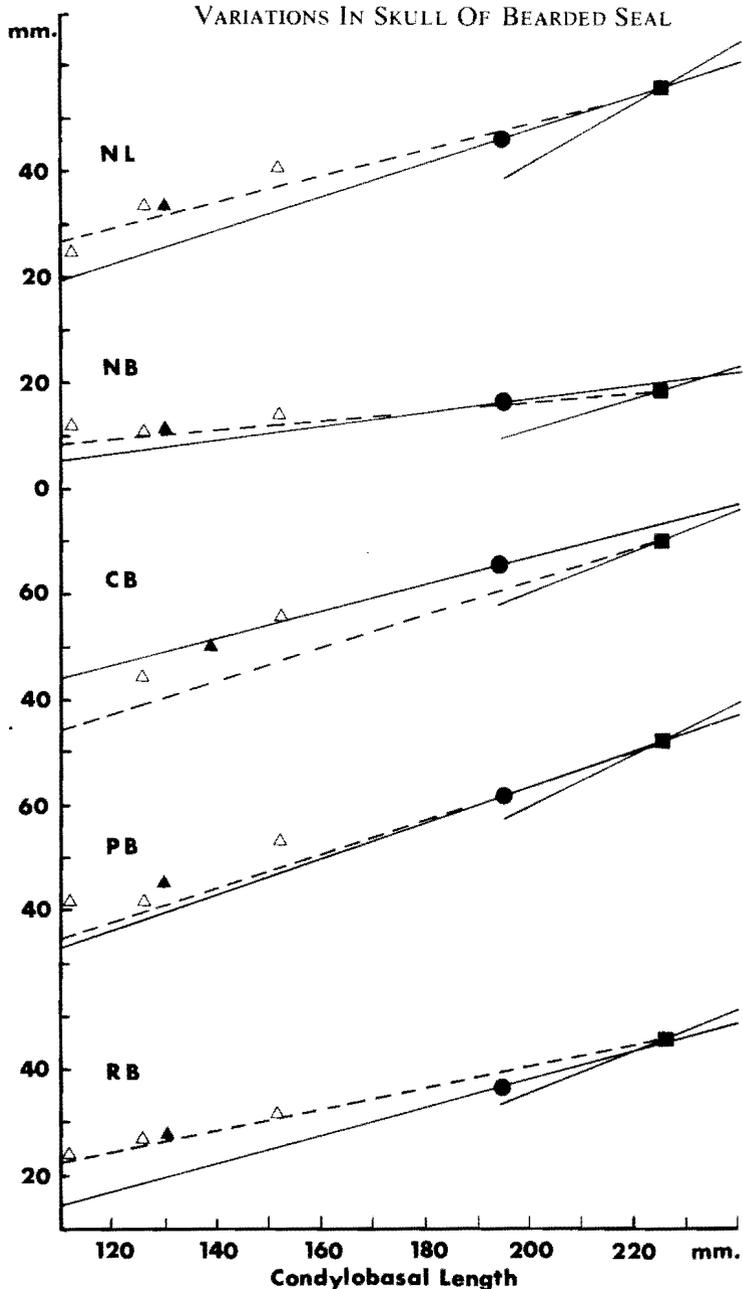


Fig. 4. Reduced major axes and ratios. Short lines = reduced major axes of adults. Long lines = reduced major axes of subadults. Broken lines = ratios of adults. See text, pages 2 and 3, for definitions.

■ = adult centroid, ● = subadult centroid, ▲ = foetal centroid, △ = individual foetus.

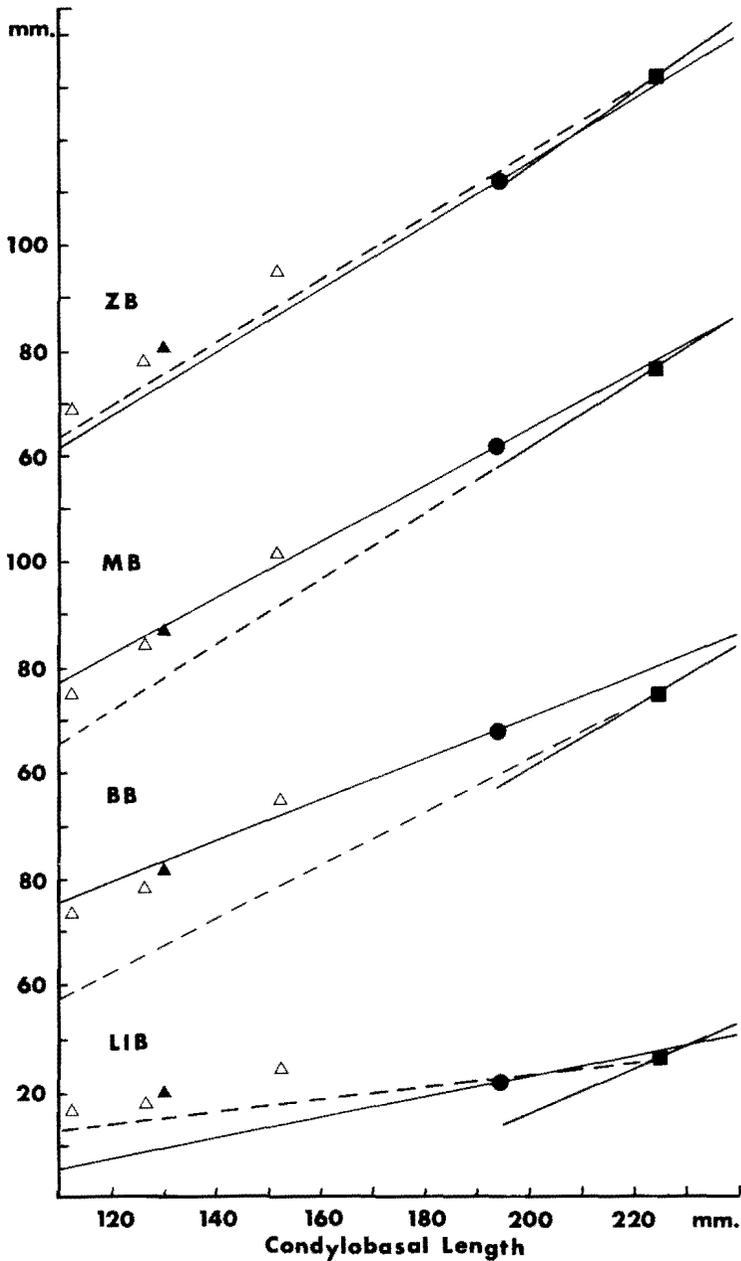


Fig. 5. Reduced major axes and ratios. Short lines = reduced major axes of adults. Long lines = reduced major axes of subadults. Broken lines = ratios of adults. See text, pages 2 and 3, for definitions.

■ = adult centroid, ● = subadult centroid, ▲ = foetal centroid,
 △ = individual foetus.

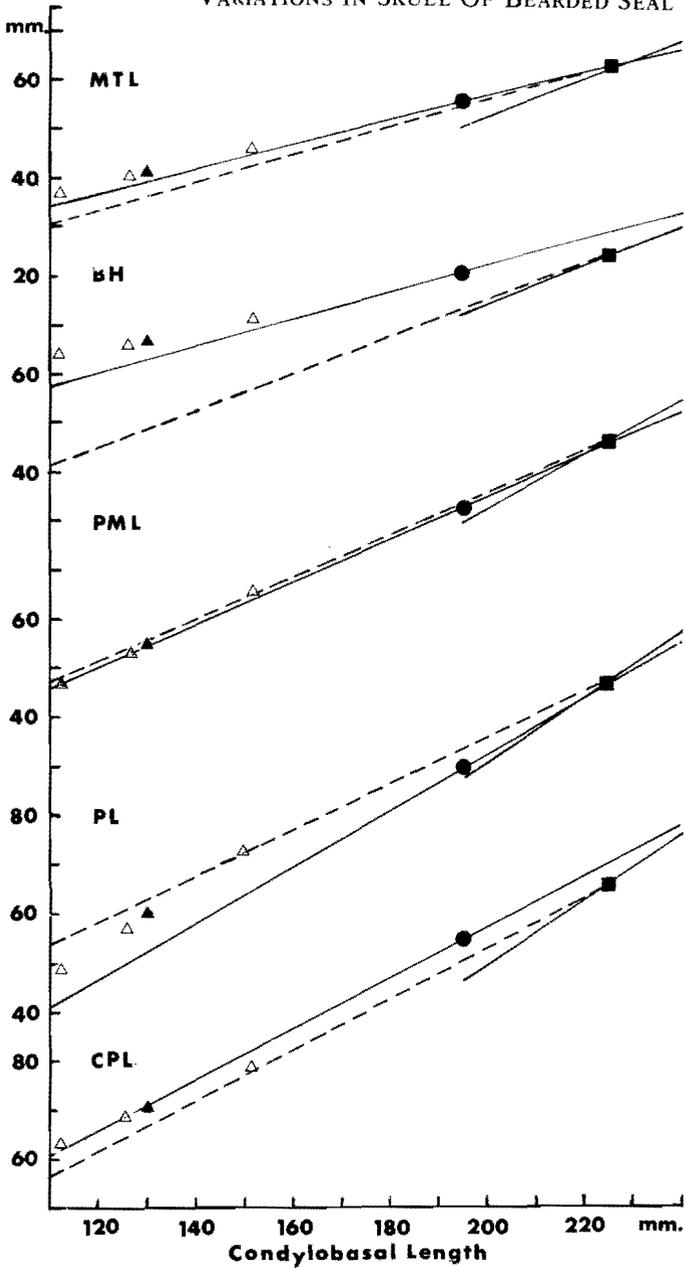


Fig. 6. Reduced major axes and ratios. Short lines = reduced major axes of adults. Long lines = reduced major axes of subadults. Broken lines = ratios of adults. See text, pages 2 and 3, for definitions.

■ = adult centroid, ● = subadult centroid, ▲ = foetal centroid, △ = individual foetus.

measurements suggest that at that early stage, the ratios of these measurements with condylobasal length are similar to those of the adults. If these foetal measurements are representative of the foetal population, there must, therefore, be a decrease in the relative growth of the parts they measure during early post-natal life, followed by increased growth in the older subadults. Logarithmic treatment would tend to straighten the first group of curves but exaggerate the second, as well as obscuring the underlying causes of the curvature. The reduced major axes of the other measurements lie close to the lines which represent the ratios of the adult means and which pass from the origin to the adult centroid. Their relative growth rates are therefore probably fairly constant at all stages of growth, though in the case of least interorbital breadth the centroid for the foetal sample lies well above the projection of the subadult reduced major axis. The meaning of this is not clear, but the correlation between least interorbital breadth and condylobasal length is low (Table 3) and in some mammals, the polar bear for instance (Manning 1971), least interorbital breadth remains constant at all post-natal ages. Possibly, therefore, the subadult reduced major axis for this measurement is influenced more by variation in final adult size than in change of size with age. In the bearded seal the zygoma are weak and their breadth, which averages less than that across the mastoids, probably does not continue to increase into old age, as it does in many of the Fissipedia. This may be the reason for the similarity of the ratio of the adult means, and the subadult and adult reduced major axes.

It can readily be seen from the graphs (Figs. 4-6) that if the projection of a reduced major axis does not pass through the origin, subsamples taken from different points along it will have different ratios. In the case of mastoid breadth, where the Y intercept is positive, the ratios will increase with decreasing size. In the case of palatal length, where the intercept is negative, they will decrease with decreasing size. Only if the reduced major axis passes through the origin will the ratios remain constant. Ratio changes during growth do not therefore necessarily mean a change in relative growth rate at some particular point. This accounts for some of the differences between my estimates of where changes in relative growth rates occur and those estimates made by Potelov (1968), who depended on ratios alone.

Geographical Differences

The means of the Atlantic and Pacific series and the significance of their differences are given in Table 1, their joint nonoverlaps in Table 5. The differences are significant in 13 of the 14 measurements, and of these 13, all except two, nasal breadth and least interorbital breadth, are greater

in the Atlantic series. In the preceding section it was pointed out that there was a higher, though not significantly higher ($0.1 > P > .05$), proportion of specimens with open basisphenoid-basioccipital sutures in the Pacific series. If this is not a sampling error, but due to some factor such as higher hunting pressure in the west, the smaller mean measurements in the adult Pacific series might, at least in part, be caused by a higher proportion of not quite fully grown skulls in that series. To test this hypothesis, both series were divided into three equal parts according to their condylobasal lengths and the two groups with the greatest lengths compared. The difference, 3.75 mm, is slightly greater than that between the means of the full adult series given in Table 1. It appears reasonable, therefore, to take this and the other size differences at their face value.

Covariance analyses for comparison of the Atlantic and Pacific series are more reliable than those for comparison of adults and subadults, since both the correlations and the means of the independent variable are similar. This reliability is illustrated by the similarity of the percent joint non-overlaps after adjustment by regressions and by reduced major axes (Table 5). Of the two significant differences in regression coefficients (Table 2), one, mastoid breadth, is partly due to a difference between populations in the subadult series. When the subadults are analysed separately, there are also two other significant differences, zygomatic breadth and maxillary tooththrow length. There are, however, no significant differences between populations in the adult series and as the differences in subadults could be caused by differences in average age of the samples, they are probably best disregarded. This leaves eight measurements which show significant differences in position of the Atlantic and Pacific regression lines (Table 2). In three measurements there is significant interaction between population and age. In nasal length and palatal breadth, this is caused by a much greater difference in the adults ($P < .001$) than in the young ($P < .05$ and $P < .05$ respectively) (Table 5). In condyle breadth, population differences are significant ($P < .001$) for both age groups, but age differences are significant only in the Atlantic series.

The joint nonoverlaps between the adjusted means of the Atlantic and Pacific series are given in Table 5. This table clearly shows the broad, short nasals of the Pacific population referred to by Osgood (1904) and Ognev (1935). Also, the relatively short maxillary tooththrow length is consistent with Osgood's statement that there is less space between the last two upper molars in *E. b. nauticus*. The broader rostrum relatively more inflated in the region of the maxillae above the line of infraorbital foramen, referred to by Ognev and in rather different words by Osgood might be a reflection of the wider least interorbital breadth and wider nasals of the

Pacific series. However, my measurements appear to contradict Osgood when he says that the braincase and palate are wider. I have no measurements to test Ognev's statement that the rostrum is more elevated or the osseous tubercle on the maxilla more marked, but this appears to be the region in which the Pacific skulls are enlarged.

In an attempt to obtain a more complete separation of the two adult populations, discriminant functions were used with 2, 3, 4 and 5 variables. The first two, nasal length and nasal breadth, gave a joint nonoverlap of 75%. The addition of condyle breadth increased it to 76%, of palatal breadth to 77% and finally of maxillary toothrow length to 78.5%. The functions are: $100X = 0.2042x_1 - 0.2905x_2$; $100X = 0.1757x_1 - 0.2943x_2 + 0.1507x_3$; $100X = 0.1529x_1 - 0.3068x_2 + 0.1278x_3 + 0.1126x_4$; $100X = 0.1451x_1 - 0.3075x_2 + 0.1179x_3 + 0.0785x_4 + 0.1138x_5$.

The joint nonoverlaps are not large by some subspecific standards, but the differences are numerous and in many cases highly significant. Also, as Table 5 shows, they are not dependent on a common size difference. I therefore do not hesitate to recommend the continued recognition of the two subspecies, *E. b. barbatus* and *E. b. nauticus*. Their type localities are south Greenland (Ognev 1935) and Penjina Bay, Sea of Okhotsk (Scheffer 1958). Both localities appear to be central to the east-west distribution of their respective races. Topotypes may, therefore, be expected to show the differences here described in more exaggerated form than do the present series, which are drawn from wide-spread populations.

With five variables the difference between the Atlantic and Pacific discriminant values is 0.0191 and the mid-point 0.2324. The mean for five adult specimens from the central and western Canadian arctic is 0.2289, an intermediate figure, but, as might be expected, rather closer to the mean of the Pacific series. Clearly, more specimens are needed from the central and western Canadian arctic to determine the exact boundary between the races. In the palaeartic, Scheffer (1958) gave the range of *E. b. nauticus* as westward to the Laptev Sea, and Ognev (1935) included a specimen from west Taymyr in that race. His most easterly specimens of *E. b. barbatus* were from Novaya Zemlya. Potelov (1968, Table 1) gave the condylo-basal length of 27 males and 33 females over ten years old from the White, Barentz and Kara seas as 221.23 and 220.47 mm respectively. These measurements are actually smaller than the mean of my Pacific series, even after 1 mm has been subtracted to compensate for the slight diagonal component in my measurements. Five of Potelov's other measurements appear to correspond exactly to mine. In his Table 2, he gave indices of these with condylo-basal length as the denominator. Since for two of the measurements, mastoid breadth and rostral breadth, there is little differ-

ence between the adjusted means of the Atlantic and Pacific series (Table 5), they need not be considered. The weighted means of the combined male and female indices of the other three measurements, least interorbital breadth, nasal length and condyle breadth, for Potelov's specimens over four years old are 11.23, 24.92 and 31.86. The corresponding indices of my Atlantic series are 11.21, 25.44 and 31.80, and of the Pacific series 11.96, 23.77 and 31.21. Apparently Potelov's series was drawn from a population with skulls similar in shape to those of my Atlantic series, but of rather smaller size. The mean discriminant for 18 adult specimens from east Greenland, Svalbard and Norway, which were included with the Atlantic series in all the preceding calculations, is 0.2372. This, as expected, is closer to the mean of the Atlantic series than the Pacific.

Summary of Conclusions

The single significant difference between males and females was considered to result from sampling error.

Fusion of the basisphenoid-basioccipital suture is the best criterion for separation of subadults and adults, although there is an average increase of 12 to 15 mm in condylobasal length after fusion.

Covariance and regression analyses do not give a true picture of changes in skull shape with growth and are unsatisfactory for the comparison of shape of adult and subadult skulls. Reduced major axes are more useful and in the present case show that measurements associated with the braincase tend to reach a maximum at an earlier age than does condylobasal length. Some measurements of the anterior part of the skull appear to grow relatively slowly in early post-natal life and more rapidly in late subadult life.

Skulls in the Pacific adult series average smaller than those in the Atlantic series in nearly all dimensions (mostly $P < .001$), but nasal breadth ($P < .001$) and least interorbital breadth ($P < .005$) are significantly greater. There are significant differences (mostly $P < .001$) in the position of the regression lines of seven measurements in the adults and six measurements in the subadults. The greatest joint nonoverlaps are 70% for an unadjusted measurement, 75% for a measurement adjusted by regression, 77% for a measurement adjusted by reduced major axes. A discriminant function using five measurements gives a joint nonoverlap of 78.5%. These differences are considered adequate for recognition of the Pacific form *E. b. nauticus*. One boundary of the two races is probably somewhere in the central Canadian arctic, the other in the central palaeartic.

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