by T. H. Manning

Geographical variation in the polar bear Ursus maritimus Phipps

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Cover drawing by Brenda Carter

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Acknowledgements Perspective

In Canada the polar bear is not only a spectacular animal which will become an increasing attraction to tourists but an important part of the Eskimo's economy and way of life. The survival of this animal under conditions of modern arctic penetration and exploitation has been of international concern for several years. Since 1965 scientists from all countries with arctic territories, Canada, Denmark, Norway, the United States, and the U.S.S.R., have agreed to work together and to pool their knowledge to ensure that those responsible for conservation and control receive the best advice available. While at the present time, a complete ban on hunting would be both impracticable and unfair, it is necessary to develop regulations that will permit a maximum yield while ensuring that the population is maintained near its optimum in all areas.

One difficulty facing conservationists has been a lack of knowledge of polar bear movements. If, as some zoologists believed, there was a circumpolar movement governed mainly by the direction of ice drift, over-hunting in one area or even in one country would mean a general reduction in the total bear population but would not immediately result in local extermination. On the other hand, if there was little movement and particularly if some populations were genetically isolated owing to restricted denning and mating areas, local extermination particularly on the periphery of the range could easily occur. Details of the life history and movements of the polar bear will eventually be worked out from tagged animals, but over the whole polar range of the species this is bound to be a long and expensive project.

This study shows that there are regional differences in the size of adult bears. From this it may be supposed that there is no large-scale circumpolar movement and that some populations may be partially isolated with ancestral breeding and denning areas to which most individuals return. Moreover, the population (Alaska south) which shows the greatest differences is that in which the largest and finest bears occur. It is also the population which has suffered most from over-hunting, and it may already be too late to preserve its original characteristics in full.

Абстракт

Рассматриваются критерии, применявшиеся ранее для определения пород Ursus maritimus. и устанавливается, что они не имеют никакой диагностической ценности. Проводятся измерения 628 черепов. Эти черепа распределяются по полу, возрасту (три группы) и географическому местонахождению (Шпицберген, восточная Гренландия, Канада — западная Гренландия, северная Аляска и южная Аляска). СССР представлен лишь несколькими черепами с Новой Земли и из восточной Сибири. Демонстрируется прогрессия увеличивающихся размеров черепов от восточной Гренландии к западу до Берингова пролива. Выводятся заключения о наличии подобной же прогрессии на восток поперек палеарктики. Исходя из расстояния между затылочными мыщелоками (condylobasal length), можно определить в окончательном населении 93 процента самцов и 83 процента самок. Разница приобретает значение на уровне одного процента. Ковариантный анализ и многоэтапная проверка по системе Дункана указывают на наличие географически определенных особенностей в форме черепов, но эти разницы невелики и совпадения, если таковые вообще встречаются, носят лишь косвенный характер. Типичным местонахождением Ursus maritimus является Шпицберген около нижнего конца прогрессии размеров. Обсуждается возможное возникновение населения южной Аляски на противоположном конце. Имеются основания считать его обособленным на уровне подвида, но до окончания исследований не вносится предложений о закреплении за ним особого названия. Признается вымершим вид U. m. tyrannus и существующей породой вокруг северного полюса — U. m. maritimus. Обычные статистические данные для анализа вариации и ковариации приводятся в виде таблиц. Коэффициент регрессии населения показывает лишь одно существенное отклонение; по полу отклонений нет, но по возрасту их девять. Эти последние главным образом обусловлены различиями по времени, когда прекращается рост в длину и ширину. Коэффициенты вариации сравниваются с коэффициентами у Rangifer tarandus, Canis lupus и Clethrionomys rutilus.

Abstract

Criteria previously used to distinguish races of *Ursus maritimus* were examined and found to be of no diagnostic value. Seventeen measurements were taken on 628 skulls. The skulls were segregated by sex, age (three groups), and geography (Spitzbergen, east Greenland, Canada – west Greenland, Alaska north, and Alaska south). The U.S.S.R. was represented by only a few skulls from Novaya Zemlya and east Siberia. A cline of increasing skull size from east Greenland westward to Bering Strait is demonstrated. A similar cline eastward across the palaearctic is inferred. Based on condylobasal length 93 per cent of males and 83 per cent of females in the end populations are separable. The difference is significant at the one per cent level. Covariance analysis and Duncan's multiple range tests suggest geographical differences in skull shape, but these differences are small and consistent, if at all, only in an involved manner. The type locality of *U. maritimus* is Spitzbergen, near the small end of the size cline. The possible origin of the Alaska south population at the opposite end is discussed. Present evidence indicates it could be considered subspecifically distinct, but is left unnamed pending further investigation. The fossil form *U. m. tyrannus* is recognized and the extant circumpolar race therefore stands as *U. m. maritimus*. The usual statistics associated with variance and covariance analysis are tabulated. There is only one significant difference among regression coefficients of the populations and none between sexes, but there are nine in the age groups. These are mainly caused by differences between the time at which growth in length and in breadth ceases. The coefficients of variation are compared with those of *Rangifer tarandus*, *Canis lupus*, and *Clethrionomys rutilus*.

Résumé

L'auteur étudie les critères utilisés jusqu'ici pour différencier les races d'*Ursus maritimus* et constate qu'ils sont sans valeur diagnostique. Dix-sept mensurations ont été faites sur 628 crânes. Ces derniers sont répartis selon le sexe, l'âge (en trois groupes) et la situation géographique (Spitzberg, est du Groenland et Canada, d'une part, et ouest du Groenland, nord de l'Alaska et sud de l'Alaska, d'autre part). La Russie n'est représentée que par quelques crânes provenant de la Nouvelle-Zemble et de l'est de la Sibérie. Les mensurations révèlent qu'il existe un cline aux dimensions crâniennes croissantes, de l'est du Groenland au détroit de Béring. L'existence d'un cline similaire est présumée vers la longueur des concyles occipitaux. Environ 93 p. 100 des mâles et 83 p. 100 des femelles peuvent être distingués dans les populations extrêmes. La différence est significative au niveau de un p. 100. L'analyse de covariance et les tests des choix multiples de Duncan ont révélé des différences de forme crânienne selon la situation géographique, mais ces divergences sont minimes et vaguement consistantes, tout au plus. La localité typique de l'habitat d'*Ursus maritimus* est le Spitzberg, près de la zone où les dimensions crâniennes sont les plus faibles. L'auteur traite de l'origine probable de la population du sud de l'Alaska à l'autre extrémité du cline. Les données acquises permettent de croire que ce pourrait être une sous-espèce distincte, mais on ne l'a pas nommée en attendant une étude plus poussée. La forme fossile d'*U. tyrannus* est reconnue et la race circumpolaire existante est *U. maritimus*. Les statistiques de l'analyse de variance et de covariance sont mises en tableaux. On ne signale qu'une différence significative parmi les coefficients de régression des populations et aucune entre les sexes; toutefois, il en existe neuf dans les groupes d'âge. Ces différences résultent ordinairement de la durée de la croissance en longueur et en largeur. Les coefficients de variation sont comparés avec ceux de *Rangifer tarandus*, de *Canis lupus* et de *Clethrionomys rutilus*.

List of tables

Introduction

Before 1908 the polar bear was thought to be a single monotypic circumpolar species. In that year Knotterus-Meyer (1908) published a confused description of four new species and one new race. He also used the name *Ursus marinus* Pallas, previously considered a synonym of *U. maritimus* Phipps, for the bears of the Ob and Yenisey area even though he lacked material from the coasts of arctic Russia and Siberia. Thus in all he recognized seven forms: two from Spitzbergen, two from Greenland, one from the Labrador coast, one from Ungava Bay, and one from the central palaearctic. He divided these forms into two main groups, "short heads" and "long heads". In the "short heads", cranial length was not more than 3 cm greater than facial length; in the "long heads" it was 3 cm to 6.3 cm greater. Knotterus-Meyer thought the "short heads" occupied the coasts of inland seas and channels such as those of the Canadian archipelago and west Greenland, whereas the "long heads" lived along the oceanic shores like those of east Greenland and Spitzbergen. My measurements of cranial length minus facial length (Table 2), which may not correspond exactly to those of Knotterus-Meyer but which when compared with each other should give a similar result, suggest that the bears of east Greenland have a comparatively short cranium and long face.* This is directly contradictory to Knotterus-Meyer's observations. The other criteria he gives for the separation of his species are mostly subjective and difficult to follow. Certainly he had no clear idea of the extent of age, sex, and individual variations (cf. Birula, 1932:110).

Succeeding authors reduced Knotterus-Meyer's species to subspecies which they accepted or rejected without critical study until Birula (1932) attempted a revision. Whereas Knotterus-Meyer's material was derived entirely from Spitzbergen and the eastern nearctic, Birula had only two specimens from Greenland, the rest being from Spitzbergen and the palaearctic. Following Miller (1912), Birula correctly assigned Phipps' name *maritimus* to the Spitzbergen population, placing Knotterus-Meyer's names *spitzbergensis* and *jenaensis* in synonymy. To the population of west Greenland he gave a new name, *groenlandicus*. He also recognized as distinct the Russian and Siberian population under the name *marinus*. Owing to lack of specimens he reached no decision on the status of *eogroenlandicus* and *labradorensis*, though he says that Knotterus-Meyer's measurements provide no cause to suspect important differences between these populations and those of Novaya Zemlya and Siberia.

Birula (1932:110) appears to have used three main characters to differentiate the west Greenland population from topotypical *maritimus*, but since he had only one specimen that definitely came from west Greenland he was forced to rely on Knotterus-Meyer's measurements. The first of Birula's three characters was the cranial index (zygomatic breadth/total skull length). The means for his figures (p. 107-8) are west Greenland, four males .53 mm, two females .56 mm; Spitzbergen, three males .63 mm, five females .56 mm. Even the difference between the males is not significant and my covariance analysis (Table 5) of adult males contradicts these figures and suggests that zygomatic breadth is relatively greater in the Canada – west Greenland population than in that of Spitzbergen. Moreover, since the zygoma continue to increase in width long after growth in length has ceased, a few really old specimens in a small series would affect the results. Birula's second character was the difference between the length of the cranium and face which I have discussed above. Later, Birula (1932:128) appeared to consider this character invalid and does not mention it in his summary (p. 111). Birula's third character, the size of the depression along the frontal suture, is difficult to measure and is, as he says (p. 106), dependent on age. The measurements he gives show no significant differences. For

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*As might be expected, the difference between cranial length and facial length increases with skull size like other measurements (Table 3).

separation of *maritimus* and *marinus*, Birula (p. 128) relied on the cranial index. However, the means for his figures (p. 126) are Siberia, two males .58 mm, five females .57 mm; Spitzbergen, four* males .61 mm, five females .56 mm, and the difference is therefore clearly not significant.

It may be concluded on these grounds that neither Knotterus-Meyer nor Birula has produced any justification for sub-specific differentiation in *U. maritimus*.

When the present study was begun, its main object was to see if there were geographical differences of a subspecific order in *U. maritimus*. For this purpose 17 measurements were taken on 487 skulls in museums in Britain, Canada, Denmark, Norway, Sweden, and the United States between 1959 and 1961. It was not practicable at that time to visit the U.S.S.R., and as there were very few skulls from arctic Russia in western museums I expected to make use of the measurements published by Birula (1932). In taking my measurements I therefore followed his descriptions as far as possible. In 1966 two new major collections became available. One consisted of 87 skulls from Alaska, the other of 77 skulls from Spitzbergen. The measurements from these two series, together with those of a few skulls in the Bergen and Tromsø museums, and a few recent additions in the Copenhagen museum, were therefore incorporated with the previous data. By 1966 all countries with polar bear populations were taking an interest in the biology and the conservation of the species and the emphasis of this study was turned to detecting differences, possibly well below the subspecific level, which might indicate the existence of partially discrete populations.

New collections are now rapidly accumulating from several areas so that it should soon be possible to check with new material the statistical conclusions reached here. It is also hoped that it may be possi-

ble to measure collections in the U.S.S.R. or that someone there will make a companion study of the palaearctic region. For these reasons I have not included Birula's measurements and the present study must be looked upon as the first part of a continuing project. The tabulated statistics are therefore given in greater detail than might otherwise be necessary.

The specimens grouped by place, age, and sex are listed in Table 1. Locations named in the text are illustrated on the map (Fig. 1).

The area covered was divided into five major geographical regions: Spitzbergen, east Greenland, Canada – west Greenland, Alaska north, and Alaska south. The boundaries of these regions, which vary greatly in size, were determined partly by the availability of specimens, partly by natural barriers or partial breaks in the distributions of the species, and partly by apparent phenotypic differences between the populations.

Spitzbergen forms a natural unit, though bears from there are presumably in regular contact with those from east Greenland and Franz Josef Land. Franz Josef Land is the nearer, and three specimens from it have been included with the Spitzbergen series. If more specimens had been available, this region would have been treated separately.

East Greenland appears to be another natural unit. There is no connection between the east Greenland ice and that of the Labrador coast (Vibe, 1967). However, a few of the bears that may drift with the ice around Cape Farewell perhaps make contact with those from Davis Strait, although, as Vibe says, most are probably killed by the Eskimos along the southwest coast of Greenland. Possibly the nine specimens from this part of the west coast should have been included in the east Greenland population or omitted entirely. There are no specimens from the north coast of Greenland, and while this could be attributed to lack of hunters and collectors, it also seems likely that bears are scarce in that region.

Canada – west Greenland is by far the largest of the five regions considered. There are more specimens from it than from any of the other regions, and originally I attempted to divide it into four parts. This division was finally abandoned because, with the exception of a good series from Barrow Strait, the collecting localities are widely scattered and, without more knowledge of population centres and distribution,

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*Birula gives measurements for four Spitzbergen specimens in this comparison but for only three in that on p. 107-8 referred to above.

Figure 1. Map of polar bear range.

it is not practicable to group the specimens satisfactorily. When more material is available it will be possible to concentrate on certain areas and omit specimens from intermediate regions.

Polar bears are thought to be scarce in the Mackenzie Delta area and although there may be considerable movement across the Beaufort Sea ice, lack of specimens from the coast between Cape Bathurst and Point Barrow makes the Alaskan boundary a convenient dividing line. The separation of Alaska north from Alaska south along a line stretching northwest from Point Lay was suggested to me by Mr. Jack Lentfer, as the largest bears were reported south of that line. It is a surprising boundary, but apparently is justified by the results. Five specimens from eastern Siberia (Kolyuchin Island 2, Kamchatka Peninsula 1, Komandor Island 2) have been included with the Alaska south series.

The specimens were originally divided into four age classes (Manning, 1964). In the youngest class three groups of sutures were open:

1) that between the basisphenoid and the basioccipital;
2) those between the maxillae and the premaxillae; and
3) those surrounding the nasals.

This class is believed to include males up to about 4 years and females up to about 3½ years. In the second youngest class the basisphenoid-basioccipital suture is closed. In the third the sutures between the maxillae and the premaxillae are also closed. These two classes are grouped as subadults. Their combined age span probably covers about 1 year and 9 months. Adult males, in which all three groups of sutures are closed, are therefore not less than about 5¾ years old and adult females not less than about 5¼.

Many specimens have no sex data on the labels. Fortunately these can be sexed with reasonable accuracy by skull characters. The resultant error is estimated to be about three per cent in the adults and 10 per cent in the young. Since even in the sexed mate-

rial there appears to be an error of about three per cent (cf. Kurtén, 1955:40), I have included unsexed adults and subadults, which are almost as easy to sex as the adults, but have discarded all unsexed young. A very few specimens have been discarded because of apparent errors in labelling, but only if there was some external evidence, such as an apparent male marked female and an apparent female marked male taken at about the same time.
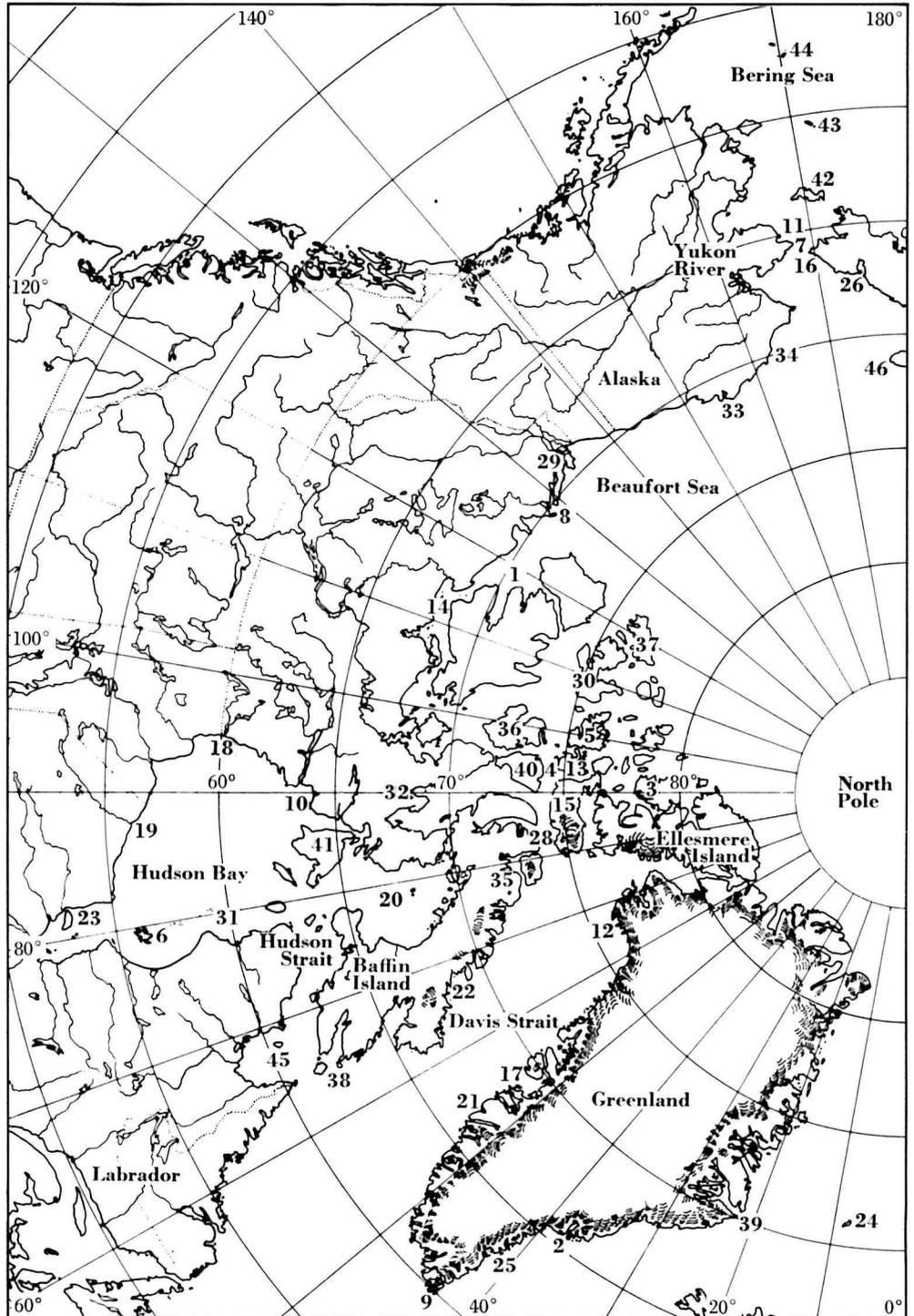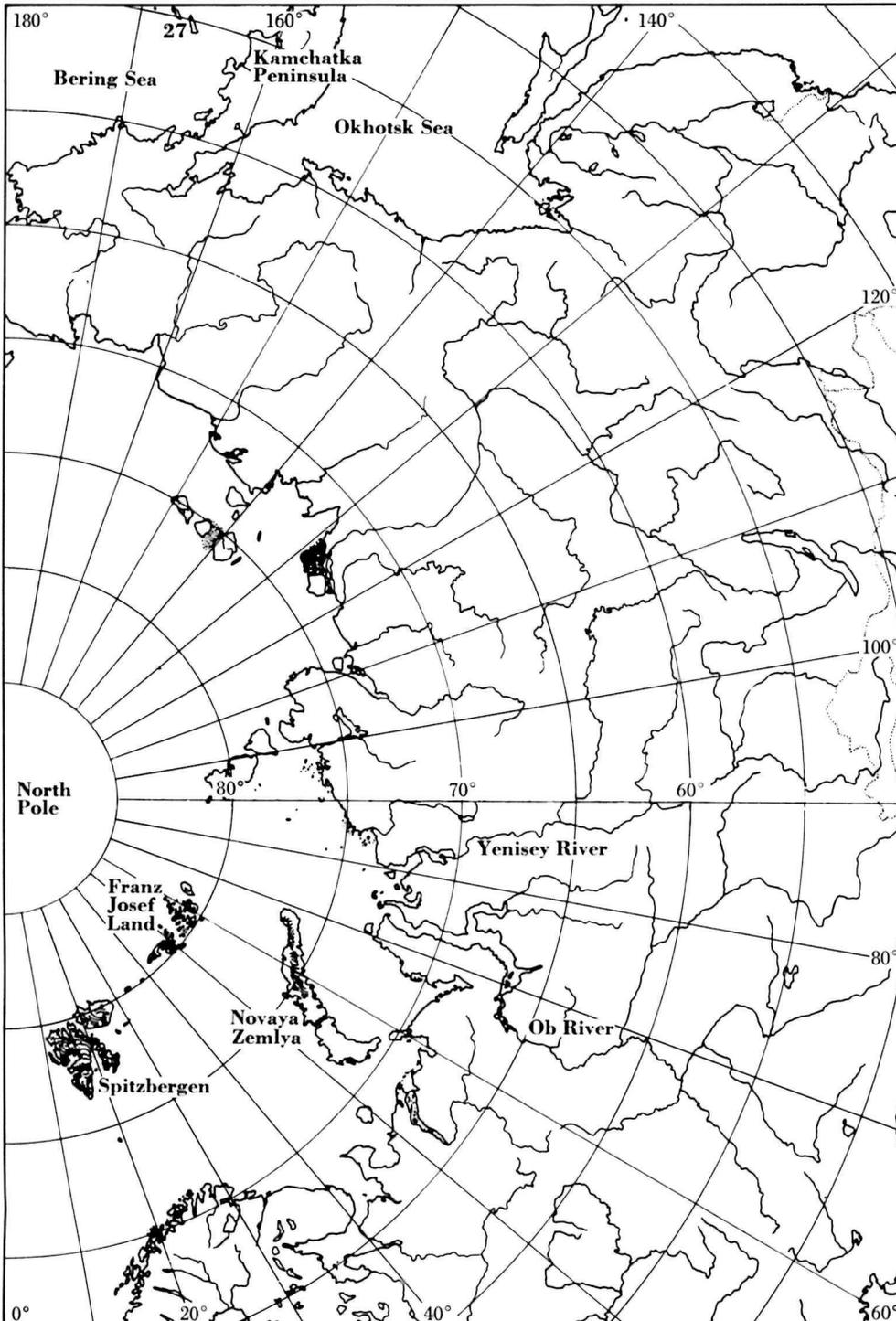
1	Amundsen Gulf	44	St. Paul Island
2	Angmagssalik	45	Ungava Bay
3	Axel Heiberg Island	46	Wrangel Island
4	Barrow Strait		
5	Bathurst Island		
6	Belcher Islands		
7	Bering Strait		
8	Cape Bathurst		
9	Cape Farewell		
10	Cape Fullerton		
11	Cape Prince of Wales		
12	Cape York		
13	Cornwallis Island		
14	Coronation Gulf		
15	Devon Island		
16	East Cape		
17	Egedesminde		
18	Eskimo Point		
19	Fort Severn		
20	Foxe Basin		
21	Holsteinborg		
22	Home Bay		
23	James Bay		
24	Jan Mayen Island		
25	Kangerdlugssuaq		
26	Kolyuchin Island		
27	Komandor Island		
28	Lancaster Sound		
29	Mackenzie Delta		
30	Melville Island		
31	Ottawa Islands		
32	Pelly Bay		
33	Point Barrow		
34	Point Lay		
35	Pond Inlet		
36	Prince of Wales Island		
37	Prince Patrick Island		
38	Resolution Island		
39	Scoresby Sound		
40	Somerset Island		
41	Southampton Island		
42	St. Lawrence Island		
43	St. Matthew Island		

Table 1
Number and origin of specimens by age and sex

	Adults				Subadults				Young			Total
	♂♂	♂♂?	♀♀	♀♀?	♂♂	♂♂?	♀♀	♀♀?	♂♂	♀♀	Sex?	
Spitzbergen population												
Spitzbergen	17	6	15	6	11	3	10	1	24	10	9	
Franz Joseph Land		1		1						1	2	
Total	**17**	**7**	**15**	**7**	**11**	**3**	**10**	**1**	**24**	**11**	**11**	**117**
East Greenland population												
East Greenland[a]		1				1	2				3	
Northeast Greenland[b]	14	7	9	6	3	1		5	7	6	14	
Southeast Greenland[c]	1	6		2				2		1	3	
Jan Mayen Island											1	
Total	**15**	**14**	**9**	**8**	**3**	**2**	**2**	**7**	**7**	**7**	**21**	**95**
Canada – west Greenland population												
West Greenland[d]						1			2			
Southwest Greenland[e]	1	2				1	2			1	2	
Central west Greenland[f]		2		2		2			1		8	
Northwest Greenland and east Ellesmere Island	2	7	1	4		3		4		1	9	
West Ellesmere, Axel Heiberg, and north Devon Islands				1	2		1	1	3	1	1	
Melville and Prince Patrick Islands					1				1			
Barrow Strait and Lancaster Sound[g]	21	3	10	2	2	1	2		11	19	5	
South and central east Baffin Island[h]				1							8	
Ungava Bay and Hudson Strait		4	1	2		2					2	
Labrador Coast		3	1				1				2	
East Hudson Bay[i]		3		1	1	1	2	1		2	1	
Northwest Hudson Bay[j]		6				1				1	3	
Southwest Hudson Bay[k]	1	2	1	1				1			2	
James Bay	3				2	2	2		2	1	2	
Foxe Basin	1	1				1		1				
Pelly Bay			2					1	1			
Coronation Gulf				1							1	
Amundsen Gulf	2		2	2	3		3		5	7	4	
Mackenzie Delta		1										
Total	**31**	**34**	**18**	**17**	**11**	**15**	**13**	**9**	**26**	**33**	**50**	**257**
Alaska north population												
North coast east of Point Barrow				2							1	
Point Barrow vicinity	6	9	2	5	4	2	1	1	21	8	13	
Point Barrow southwest to and including Point Lay	1	2	1	3				1	2		11	
Total	**7**	**11**	**3**	**10**	**4**	**2**	**1**	**2**	**23**	**8**	**25**	**96**
Alaska south population												
North of Bering Strait[l]	6		7	1	6	1	1		18	5	4	
South of Bering Strait[m]	1	2				1		1	2		7	
Total	**7**	**2**	**7**	**1**	**6**	**2**	**1**	**1**	**20**	**5**	**11**	**63**
Grand total	**77**	**68**	**52**	**43**	**35**	**24**	**27**	**20**	**100**	**64**	**118**	**628**

Description of measurements

Note to Table 1:

Specimens listed under ♂ ♂ ? and ♀ ♀ ? had no original sex data. The places listed should be considered in a broad sense to include the surrounding land or sea.

[a] East Greenland = specimens not further identified.

[b] Northeast Greenland, from latitude 79° to and including Scoresby Sound.

[c] Southeast Greenland = Kangerdlugssuaq and Angmagssalik.

[d] West Greenland = specimens not further identified.

[e] Southwest Greenland = Holsteinborg and southward.

[f] Central west Greenland = Cape York to Egedesminde.

[g] Barrow Strait and Lancaster Sound include the south part of Bathurst Island, Cornwallis Island, the south part of Devon Island, the north part of Prince of Wales Island, the north part of Somerset Island, and Pond Inlet.

[h] South and central east Baffin Island = from Home Bay to Resolution Island.

[i] East Hudson Bay includes the Ottawa and Belcher Islands.

[j] Northwest Hudson Bay = the south coast of Southampton Island and Cape Fullerton.

[k] Southwest Hudson Bay = Eskimo Point to Fort Severn.

[l] Includes specimens from East Cape and from Cape Prince of Wales, as well as a single specimen from Kolyuchin Island.

[m] Includes specimens from Yukon River, St. Lawrence Island, St. Matthew Island, St. Paul Island, and Kamchatka Peninsula.

All measurements were taken with bar calipers on the left side unless that side had been damaged. They were checked once and any serious discrepancies were rechecked. Measurements 1, 2, 3, 4, 5, 6, 7, and 17 were taken to the nearest millimeter, the remainder to .1 mm. Measurements with an asterisk are believed to be the same as or very similar to those used by Birula (1932).

1. CBL = Condylobasal length.* From the anterior extremity of the left premaxilla (not teeth) to the posterior extremity of the left condyle.

2. MPL = Molar–premaxilla length. One jaw of the calipers was placed across the posterior border of both M2's, either at the widest point of the cingula or the alveoli, whichever gave the greater measurement. The other jaw was placed across the anterior extremity of the premaxillae, thus giving the distance along the central line of the skull. If the caliper jaws are not long enough, the bar of a spare pair or some other piece of metal may be placed across the back of the teeth and the measurement taken from this.

3. MB = Mastoid breadth.* Greatest breadth across the mastoid processes.

4. ZB = Zygomatic breadth.* Greatest breadth across the zygoma. Where the squamosal and jugal had parted, it was assumed that the squamosal gave the correct breadth.

5. SB = Supraorbital breadth.* Maximum breadth across the supraorbital processes.

6. CL = Cranial length.* From the inion to the mid-point between the supraorbital processes. A line can be drawn on the skull joining the extremities of the processes. The inion is here defined as the most posterior point on the skull at or near the junction of the lambdoidal and sagittal crests. Occasionally there is a second protuberance well below this which would give a greater measurement. This is ignored if it is clearly below the roughened and pitted triangle which lies in the centre line below the lambdoidal crest.

7. FL = Facial length.* From the mid-point between the supraorbital processes to the extremity of the premaxillae.

8. MSH = Maxilla–supraorbital height. Distance between the highest part of the lower border of the left maxilla posterior to M2 and a point on the dorsal surface of the frontal immediately above this. This point is approximately on a line joining the extremities of the supraorbital processes and immediately posterior to the angle formed by the left supraorbital process and the inner border of the orbit.

9. LCB = Least cranial breadth.* The least width of the cranium posterior to the supraorbital processes.

10. IB = Interorbital breadth.* Minimum width between the orbits measured across the frontals.

11. BC = Breadth at canines.* Greatest breadth of the rostum at or above the canines. This is normally 5 to 10 mm above the alveoli of the canines, but in very young animals with permanent canines only partially grown, it is distinctly higher up.

12. PB = Palatal breadth. Distance between the outer borders of the alveoli of the posterior root of M1.

13. LP4–M2 = Length P4 to M2. Distance between the anterior extremity of the cingulum of P4 and the posterior border of the cingulum of M2.

14. LM2 = Crown length of M2.* From the posterior border of the cingulum to the anterior border at a point in line with the two outer cusps.

15. LM1 = Crown length of M1.* From the posterior border of the cingulum near the mid-line or, if it gave a greater length, genal to the mid-line but never lingual to it, to the anterior border in line with the two outer cusps.

16. CH = Coronoid height. With the bar of the calipers at right angles to the long axis of the mandible, one jaw was placed on the top of the coronoid process, the other at the bottom of the angle.

17. CPL = Condylopalatal length. From the left condyle to the posterior border of the palate, either at the centre or on the side, whichever gave the greater measurement. The palatal notch which occurs in some young skulls was not included.

Figure 2. Measurements of polar bear skulls.
Drawn by Brenda Carter. The initials given for
each measurement are those used in the text and
the tables.
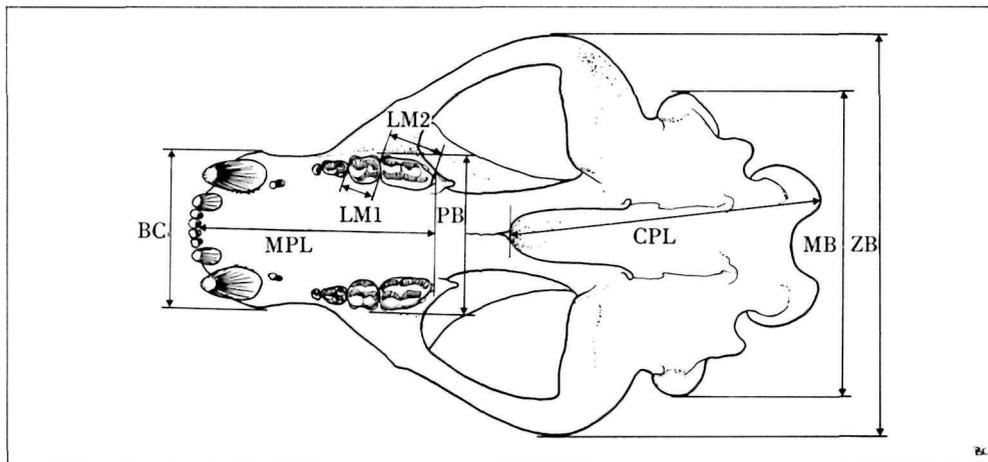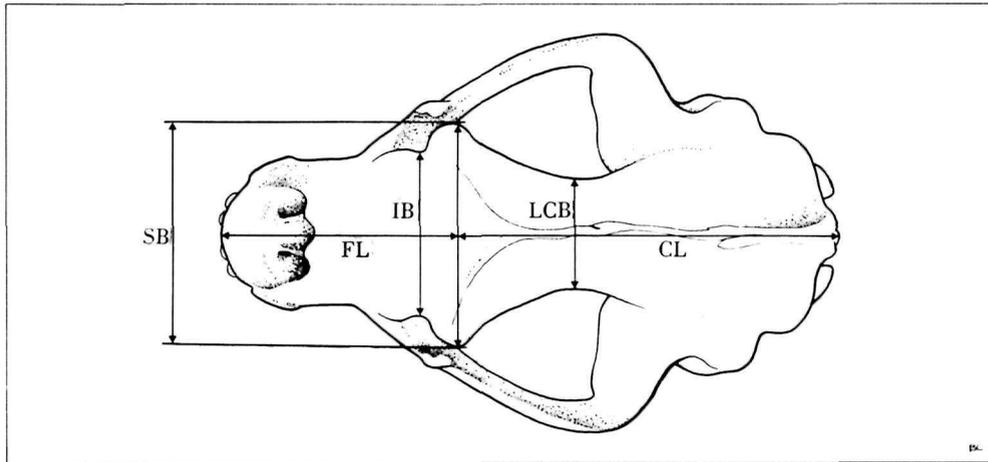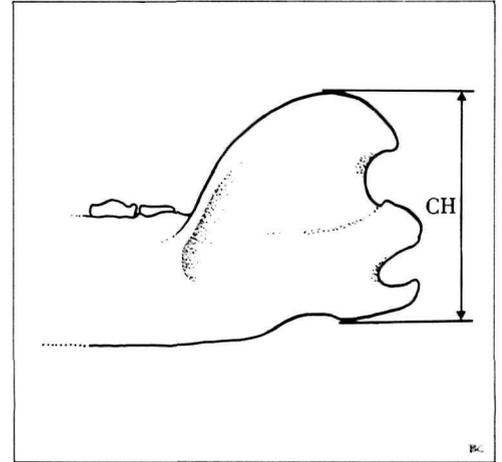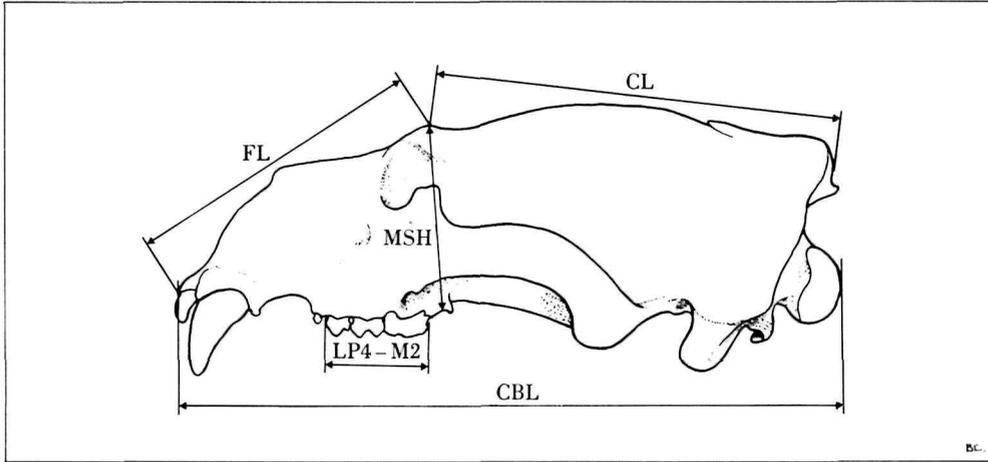
Table 2

Statistics of absolute measurements

Measurements	N	F	Variances	Spitzbergen	East Greenland	Canada – west Greenland	Alaska north	Alaska south	CV ± SE
Adult males									
CBL	137	18.91****	164.2	376.2 ± 2.73	369.3 ± 2.56	384.0 ± 1.60	392.0 ± 3.11	407.2 ± 4.27	3.34 ± 0.20
MPL	136	9.31****	26.84	149.1 ± 1.13	147.8 ± 1.04	152.8 ± 0.65	154.2 ± 1.26	155.4 ± 1.73	3.41 ± 0.21
MB	124	9.30****	65.92	173.0 ± 1.82	170.7 ± 1.73	180.0 ± 1.08	181.2 ± 2.03	184.7 ± 2.71	4.56 ± 0.29
ZB	128	16.6 ****	120.8	233.4 ± 2.46	228.0 ± 2.29	244.7 ± 1.42	244.7 ± 2.67	256.5 ± 3.89	4.56 ± 0.28
SB	133	12.14****	54.16	130.2 ± 1.57	124.8 ± 1.47	133.6 ± 0.95	133.7 ± 1.78	142.9 ± 2.45	5.56 ± 0.34
CL	134	10.90****	118.6	223.8 ± 2.44	217.7 ± 2.18	228.3 ± 1.37	232.6 ± 2.64	242.4 ± 3.63	4.79 ± 0.29
FL	137	9.76****	63.36	190.4 ± 1.70	191.0 ± 1.59	194.3 ± 0.99	199.4 ± 1.93	206.9 ± 2.65	4.08 ± 0.24
MSH	135	21.77****	21.28	103.9 ± 0.98	100.1 ± 0.92	106.2 ± 0.59	108.1 ± 1.12	115.6 ± 1.54	4.36 ± 0.26
LCB	128	2.75*	15.10	70.3 ± 0.85	68.6 ± 0.78	71.3 ± 0.51	71.4 ± 0.97	72.3 ± 1.37	5.48 ± 0.34
IB	136	11.84****	34.00	95.8 ± 1.24	92.9 ± 1.17	99.1 ± 0.73	99.4 ± 1.41	107.1 ± 1.94	5.95 ± 0.36
BC	126	15.77****	18.16	97.2 ± 0.91	94.3 ± 0.85	99.7 ± 0.56	102.0 ± 1.10	106.1 ± 1.61	4.31 ± 0.27
PB	134	19.15****	13.77	87.3 ± 0.81	84.1 ± 0.76	89.5 ± 0.47	92.6 ± 0.91	93.5 ± 1.24	4.17 ± 0.25
LP4–M2	133	4.51***	6.06	62.0 ± 0.52	61.3 ± 0.49	63.5 ± 0.31	63.4 ± 0.60	62.8 ± 0.93	3.91 ± 0.23
LM2	134	2.62*	3.24	27.5 ± 0.39	27.0 ± 0.36	28.3 ± 0.23	27.9 ± 0.44	27.5 ± 0.60	6.46 ± 0.39
LM1	134	9.32****	0.441	20.1 ± 0.14	19.7 ± 0.13	20.3 ± 0.08	20.8 ± 0.16	20.6 ± 0.23	3.26 ± 0.19
CH	117	5.47****	18.81	108.0 ± 0.97	107.2 ± 0.97	111.0 ± 0.58	112.4 ± 1.08	112.4 ± 1.77	3.93 ± 0.25
CPL	132	13.06****	54.25	185.9 ± 1.61	183.5 ± 1.54	189.2 ± 0.94	194.5 ± 1.79	201.6 ± 2.46	3.89 ± 0.24
CL–FL	132	3.58**	83.08	32.20 ± 2.04	26.31 ± 1.79	33.51 ± 1.17	33.24 ± 2.21	36.75 ± 3.22	28.44 ± 1.75
Young, subadult, and adult males combined									
LP4–M2	290	5.39****	6.59	61.8 ± 0.33	61.5 ± 0.42	63.2 ± 0.24	62.2 ± 0.38	62.9 ± 0.44	4.09 ± 0.16
LM2	294	4.65***	3.24	27.5 ± 0.23	27.2 ± 0.30	28.3 ± 0.17	27.3 ± 0.26	27.8 ± 0.30	6.48 ± 0.26
LM1	294	8.55****	0.477	20.0 ± 0.09	19.7 ± 0.11	20.3 ± 0.06	20.4 ± 0.10	20.5 ± 0.11	3.31 ± 0.13
LCB	279	3.96**	11.73	70.2 ± 0.46	68.9 ± 0.56	70.8 ± 0.33	71.0 ± 0.52	71.8 ± 0.57	4.85 ± 0.21
Adult females									
CBL	89	9.66****	85.83	330.4 ± 2.07	325.8 ± 2.32	335.4 ± 1.61	336.5 ± 2.57	343.7 ± 3.50	2.78 ± 0.21
MPL	89	3.72**	16.33	133.2 ± 0.90	133.2 ± 1.01	136.2 ± 0.70	136.6 ± 1.12	137.7 ± 1.53	2.94 ± 0.22
MB	77	3.84**	25.93	143.0 ± 1.24	141.8 ± 1.31	145.5 ± 1.00	143.5 ± 1.47	150.0 ± 1.92	3.53 ± 0.28
ZB	85	1.90	60.75	196.5 ± 1.79	193.1 ± 2.08	198.4 ± 1.38	197.8 ± 2.16	202.1 ± 2.95	3.95 ± 0.30
SB	85	2.56*	28.66	104.8 ± 1.23	104.5 ± 1.38	105.9 ± 0.95	105.0 ± 1.54	111.2 ± 2.02	5.06 ± 0.39
CL	87	5.57****	44.99	191.0 ± 1.50	187.0 ± 1.73	191.6 ± 1.19	192.2 ± 1.86	201.4 ± 3.54	3.50 ± 0.26
FL	89	2.41	30.99	168.5 ± 1.24	169.5 ± 1.39	171.0 ± 0.97	170.0 ± 1.54	175.7 ± 2.10	3.27 ± 0.24
MSH	89	3.67**	11.50	85.6 ± 0.76	85.5 ± 0.85	86.5 ± 0.59	87.1 ± 0.94	90.8 ± 1.28	3.92 ± 0.29
LCB	88	1.52	11.68	65.8 ± 0.76	67.1 ± 0.85	66.0 ± 0.60	65.6 ± 0.95	68.9 ± 1.29	5.15 ± 0.39
IB	88	2.53*	19.36	79.8 ± 1.01	79.9 ± 1.10	80.9 ± 0.77	80.8 ± 1.22	85.6 ± 1.66	5.44 ± 0.41
BC	88	1.35	13.02	81.4 ± 0.83	80.9 ± 0.90	82.4 ± 0.63	82.7 ± 1.00	84.3 ± 1.36	4.39 ± 0.33
PB	89	1.77	10.58	77.8 ± 0.73	77.3 ± 0.81	78.5 ± 0.57	79.5 ± 0.90	80.5 ± 1.23	4.15 ± 0.31
LP4–M2	86	2.80*	4.95	55.6 ± 0.51	56.1 ± 0.56	57.2 ± 0.39	56.4 ± 0.64	57.1 ± 0.91	3.40 ± 0.26
LM2	89	2.33	3.00	23.9 ± 0.39	24.7 ± 0.43	25.3 ± 0.30	24.4 ± 0.48	25.1 ± 0.65	7.01 ± 0.52
LM1	89	3.10*	0.380	18.6 ± 0.14	18.3 ± 0.15	18.7 ± 0.11	19.0 ± 0.17	18.9 ± 0.23	3.30 ± 0.25
CH	85	4.28***	8.33	90.1 ± 0.65	88.6 ± 0.75	91.5 ± 0.51	92.2 ± 0.87	92.5 ± 1.09	3.18 ± 0.24
CPL	87	6.56****	23.83	163.3 ± 1.09	161.6 ± 1.26	165.0 ± 0.86	166.5 ± 1.35	172.3 ± 1.85	2.96 ± 0.22
CL–FL	87	3.48*	37.57	22.55 ± 1.37	16.80 ± 1.58	20.52 ± 1.07	23.00 ± 1.77	25.71 ± 2.32	29.05 ± 2.20
Young, subadult, and adult females combined									
LP4–M2	194	9.43****	5.66	55.3 ± 0.38	55.2 ± 0.42	57.5 ± 0.25	57.2 ± 0.51	57.4 ± 0.66	4.20 ± 0.21
LM2	199	9.02****	4.15	23.8 ± 0.32	23.7 ± 0.36	25.7 ± 0.22	24.5 ± 0.42	24.9 ± 0.54	8.23 ± 0.41
LM1	199	13.67****	0.369	18.5 ± 0.09	18.2 ± 0.11	18.8 ± 0.06	19.2 ± 0.12	19.2 ± 0.16	3.25 ± 0.16
LCB	183	1.25	10.95	66.5 ± 0.60	66.9 ± 0.58	67.0 ± 0.36	65.9 ± 0.68	68.3 ± 0.96	4.95 ± 0.26

Statistical methods and results

For the comparison of most of the absolute as opposed to relative measurements, only the skulls of adult specimens (all three sutures closed) were used. The exceptions were the three tooth measurements and the least cranial breadth. For these measurements specimens of all ages were pooled and the resulting statistics are given at the bottom of Table 2 for comparison with those of the adults. It is certainly legitimate to combine the three age groups for the statistics of M1 and M2 since once the teeth are erupted there is no further growth in crown length, and wear at the cingulum is very slight. It also appears legitimate to treat the length P4–M2 in this way as the three teeth involved are in contact at all ages and do not appear to alter their angle of contact appreciably. Justification for combining the cranial breadths of the three age groups was based on the figures themselves. In the Canada – west Greenland samples, for instance, the means for young, subadult, and adult males are 70.0, 70.3, and 71.3 mm, and for females 67.9, 67.2, and 66.0 mm. Thus in the males there is an apparent increase with age and in the females an apparent decrease. It may be assumed that these are chance differences and that least cranial breadth is almost independent of age.

The variances given in Table 2 and used for calculating the standard errors of the means are the pooled within-population variances. Bartlett's test (Snedicor, 1950: 251) was used to check the homogeneity of these variances before pooling. Out of the 17 measurements there were four significant differences in the males and one in the females; all were near the five per cent level. The four measurements which showed significant differences in the males were condylobasal length, interorbital breadth, length of M1, and condylopalatal length: the single measurement in the females was palatal breadth. The four differences among males were evidently caused by a high variance in the small sample from Alaska south and this in turn may be attributed to one unusually small and possibly incorrectly sexed

specimen and to two large specimens which may date from a time when the bears in the Alaska south region were larger than at present. The females in the Alaska south series are mostly recent specimens and are all from north of Bering Strait. They do not show the high variance of the males of this population and the cause of the single significant difference between population variances is not evident. Considering the four measurements in which specimens of all ages are used, there is again a significant difference for the length of M1 in the males, but here it seems to be caused by a difference among the means for adults, subadults, and young in the Alaska north series. This difference, which is significant at the one per cent level, may be caused by some wrongly sexed specimens among the subadults and young. Under the above circumstances it seemed justifiable to disregard the population differences and use the pooled variances for estimating the coefficients of difference and the significance of the differences of the means.

It is plain from Tables 2 and 3 that there is a cline of increasing general skull size from east Greenland, where the skulls average smallest, to Alaska south where they average largest. The means for most measurements of the Spitzbergen sample are slightly larger than those of the east Greenland sample and although the differences are significant for none of the measurements on the females and for only a few on the males, it seems reasonable to suppose that this is the start of another cline of increasing size going eastwards across the palaearctic towards Alaska. In the nearctic the greatest differences among the five populations occur between east Greenland and Canada – west Greenland, and between Alaska north and Alaska south. Between Alaska north and Alaska south there is probably a step or at least a steepening of the cline. However, since the largest specimens are from south of Bering Strait at the extremity of the species' range, the cline probably continues through the Alaska south population. From east Greenland to

west Greenland and across Canada to Alaska north the cline may be smoother. Although the differences, as shown by the coefficients of difference, between the Alaska north and the Alaska south populations are of a magnitude similar to those between the east Greenland and the Canada – west Greenland populations, they are based on fewer specimens and, as indicated by the levels of significance in Table 3, are more likely to be affected by sampling errors.

Condylobasal length is usually the most reliable measurement of over-all skull size. Between the two extreme populations, east Greenland and Alaska south, it gives a joint non-overlap (Mayr et al., 1953) of 93 per cent in males and 83 per cent in females. For adjacent populations starting with Spitzbergen and east Greenland the joint non-overlaps are 61, 75, 62, and 72 per cent for males and 60, 70, 52, and 65 per cent for females. The highest joint non-overlap in the males, 95 per cent between the extreme populations, is given by mandibular–supraorbital height and in the females by cranial length and condylopalatal length, both giving a separation of 86 per cent. There are likewise a number of measurements (Table 3) which in the present samples would give a higher joint non-overlap between adjacent populations than is given by condylobasal length. However, as these measurements must be selected empirically their apparent efficiency needs to be treated with extreme caution. It is, however, apparent from Table 6 that the skulls of adults from populations with the larger means for condylobasal length are on the average relatively wider and higher, so that measurements in these dimensions may be expected to give better separation than those of length.

Tooth measurements are of particular interest because they are constant at all ages and because the correlation between them and condylobasal length is low. They may therefore to some extent be looked upon as independent criteria. The teeth of Canada – west Greenland bears average distinctly larger than those of east Greenland, but

Table 3
Coefficients of difference and the significances of difference between means of absolute measurements

Measurement	Males					Females					
	Spitzbergen: east Greenland	East Greenland: Canada – west Greenland	Canada – west Greenland: Alaska north	Alaska north: Alaska south	East Greenland: Alaska south	Spitzbergen: east Greenland	East Greenland: Canada – west Greenland	Canada – west Greenland Alaska north	Alaska north: Alaska south	East Greenland: Alaska south	Males: females
CBL	0.27	0.57***	0.31*	0.59**	1.48***	0.25	0.52**	0.06	0.39	0.97***	2.20***
MPL	0.12	0.48***	0.14	0.12	0.73***	0.00	0.37*	0.05	0.14	0.56*	1.80***
MB	0.14	0.57***	0.07	0.22	0.86***	0.12	0.36*	−0.20	0.64**	0.80***	2.61***
ZB	0.24	0.76***	0.00	0.54*	1.30***	0.22	0.34*	−0.04	0.28	0.58*	2.46***
SB	0.37*	0.60***	0.01	0.62**	1.23***	0.03	0.13	−0.08	0.58*	0.62**	2.18***
CL	0.28	0.49***	0.20	0.45*	1.13***	0.30	0.34*	0.04	0.69*	1.07***	2.09***
FL	−0.04	0.21	0.32*	0.47*	1.00***	−0.09	0.13	−0.09	0.51*	0.56*	1.72***
MSH	0.41**	0.66***	0.20	0.81***	1.68***	0.01	0.15	0.09	0.55*	0.78**	2.46***
LCB	0.22	0.35**	0.01	0.12	0.48*	−0.19	−0.16	−0.06	0.48	0.26	0.73***
IB	0.25	0.53***	0.02	0.66**	1.22***	−0.01	0.11	−0.01	0.55*	0.65**	1.78***
BC	0.34*	0.63***	0.27	0.48*	1.38***	0.07	0.21	0.04	0.22	0.47*	2.20***
PB	0.43**	0.73***	0.41**	0.12	1.27***	0.08	0.18	0.15	0.15	0.49*	1.58***
LP4 – M2	0.14	0.45***	−0.02	−0.12	0.30	−0.11	0.25	−0.18	0.16	0.22	1.34***
LM2	0.14	0.36**	−0.11	−0.11	0.14	−0.23	0.17	−0.26	0.20	0.12	0.85***
LM1	0.30*	0.45***	0.38**	−0.15	0.68***	0.24	0.32*	0.24	−0.08	0.49*	1.25***
CH	0.09	0.44**	0.16	0.00	0.60*	0.26	0.50**	0.12	0.05	0.68**	2.70***
CPL	0.16	0.39**	0.36**	0.48*	1.23***	0.17	0.35*	0.15	0.59*	1.10***	1.98***
CL – FL	0.32*	0.39***	−0.01	0.19	0.57**	0.47**	0.30	0.20	0.22	0.73**	0.85***
LP4 – M2	0.06	0.33***	−0.19*	0.14	0.27*	0.02	0.48***	−0.06	0.04	0.46**	1.15***
LM2	0.08	0.30**	−0.28**	0.14	0.17	0.02	0.49***	−0.29*	0.10	0.29	0.68***
LM1	0.22*	0.44***	0.07	0.07	0.59***	0.25*	0.49***	0.33**	0.00	0.82***	1.17***
LCB	0.19	0.28**	0.29	0.12	0.42***	−0.06	0.02	−0.17	0.36*	0.21	0.56***

Note:
Only the adjacent populations and the two populations east Greenland and Alaska south, which are at opposite ends of the size cline, are compared. For this reason the significance of difference has been estimated by t rather than Duncan's multiple range test. One, two, and three asterisks indicate significance at the 5, 1, and .1 per cent levels respectively. The figures give the coefficient of difference calculated from the formula $\frac{\bar{x}_1 - \bar{x}_2}{2\sqrt{V}}$ where V is the pooled variance given in Table 1. Minus signs are used when the greater mean is from the population which according to most of the measurements (including condylobasal length) contained the smaller individuals. The final column gives the coefficient of difference and the significance of difference for the comparison of male and female samples from the Canada – west Greenland population.

from Canada through Alaska north to Alaska south the cline of increasing size noted in the other skull measurements becomes relatively less steep for length M1 and even appears to reverse for the lengths M2 and P4–M2. Of course these last two measurements are not independent and the shortness of length P4–M2 in Alaska specimens is probably due chiefly to the M2 component. M2 is very variable both in size and shape (CV: males 6.5, females 8.2), and as Kurtén (1964:17) suggests it is probably in the process of evolutionary degeneration.

The teeth in high arctic populations of some other species are relatively large. and the smallness of some of the teeth in the Alaska south population may be a reflection of either its present or its past environment (see Taxonomy section). A difference in tooth size relative to skull size could also result from a change in skull size, and presumably over-all body size, which has as yet not been matched by a change in tooth

size. A comparison of 13 male and 10 female skulls from Hudson Bay with 37 male and 33 female skulls from Barrow Strait shows no evidence of smaller teeth in those from the southern area, perhaps because of the relatively short period since the retreat of the ice from these regions.

The marked increase (Tables 2 and 3) in the significance of the difference among populations for the length P4–M2 and the length M2 in the females when the young and subadults are included results from the

Table 4
Comparison of coefficients of variation

Species	Condylobasal length		Zygomatic breadth		Mastoid breadth	
	Males	Females	Males	Females	Males	Females
Ursus maritimus	(137) 3.34 ± .20	(89) 2.78 ± .21	(128) 4.56 ± .28	(85) 3.95 ± .30	(124) 4.56 ± .29	(77) 3.53 ± .28
Rangifer tarandus	(47) 3.54 ± .36	(33) 2.92 ± .36	(34) 3.75 ± .45	(25) 3.76 ± .53	(33) 5.18 ± .64	(26) 3.84 ± .53
Canis lupus	(27) 2.64 ± .36	(8) 2.0 ± .51	(27) 3.67 ± .50	(10) 3.0 ± .67	(27) 3.87 ± .53	(11) 3.8 ± .77
Clethrionomys rutilus	(71) 1.91 ± .16		(95) 2.84 ± .21			

Note:
The figures in parenthesis are the number of specimens. All animals were classed as adults in the original publications, but some *R. tarandus* may not have quite attained full growth. In *C. rutilus* the sexes are pooled.

smaller teeth in the east Greenland samples of these two age groups. The difference among the three age groups from east Greenland is significant at the one per cent level for length M2 and very near that level for length P4–M2. Kurtén (1955:43) noted a similar difference between young and adult cave bears and suggested that it might result from selection pressure and thus indicate an evolutionary trend. It seems possible, however, that tooth size may be affected by nutrition or similar non-genetic factors. If these factors also affect the life span of the individual, the tooth size of young bears would average less than that of old bears though this would be without evolutionary significance. In the present instance, since the difference is not upheld by the males and does not occur in the other populations, it is probably the result of sampling errors. The difference is, in part, caused by three young specimens with very small M2's. Two of these specimens were taken on the same day and are possibly siblings. In the males there is a significant difference at the one per cent level among the age groups for the length of M1, but this may be caused by errors in sexing the subadults and young.

The coefficient of difference between males and females in the Canada – west Greenland population is given in the last column of Table 3. Since the degree of sexual dimorphism varies in polar bears, being disproportionately large in those populations in which the mean size of individuals is large (Manning, MS), no attempt has been made to obtain the mean sexual difference for the pooled populations. Females also differ from males in being less individually variable, as can be seen from the smaller within-population variances and coefficients of variation. Individual variation is, however, not sufficiently low in the females to counteract the small between-population differences, and the coefficients of difference as well as the significance of the differences between the female population means are in most instances considerably less than those of the males.

Large individual variation in skull measurements is often attributed to bears. Comparisons of some coefficients of variation with those of three other species are therefore given in Table 4. The figures for *Clethrionomys rutilus* and *Rangifer tarandus* are derived from those given by Manning (1956, Tables 5 and 7; 1960, Tables 3, 16, and 18) and were obtained, like those for *U. maritimus*, from the within-population variance (Table 2) and the actual mean of all specimens irrespective of their area of origin. It must be remembered, therefore, that these coefficients are not strictly comparable with the coefficients of variation for a species as a whole, as the latter would combine both individual and geographical variation. For instance, the coefficient of variation for polar bear condylobasal length with geographical variation included would be 4.15 ± .25 instead of 3.34 ± .20 with geographical variation excluded. The figures for *Canis lupus* were taken from Manning and Macpherson (1958, Table 30). Three separate populations were combined there, but the geographical differences are small.

It appears that there is little difference between the coefficients of variation for *U. maritimus* and *R. tarandus*, though those for the latter might have been slightly lower if adults had been more rigorously defined. *C. lupus* may be a little less variable and *C. rutilus* distinctly less variable. However, there seems to be no reason to consider *U. maritimus* exceptional. Previous ideas of its variability were no doubt fostered by failure to recognize and exclude immature specimens. Differences in skull shape between young and adults certainly appear large, as is indicated by comparison of the age groups in the last column of Table 5. A similar comparison for other species would be interesting.

Most of the differences shown by the means of the 17 measurements used (Tables 2 and 3) result from variation in total skull size and this variation in size overrides and masks any differences there may be in shape. As a result, the measurements are not independent and with the possible exception of tooth measurements, equally satisfactory results could be obtained from condylobasal length alone. In an attempt to eliminate size as a factor and in order that skulls of subadult and young bears could also be used, a series of covariance analyses were carried out using condylobasal length as the independent variable (Table 5).

Table 5

Means of skull measurements adjusted to a standard condylobasal length

Measurement		Spitzbergen	East Greenland	Canada	Alaska north	Alaska south		
				Males				
MPL	Adult	(21) 150.5 ± 0.73	(25) 151.2 ± 0.71	(64) 151.6 ± 0.43	(17) 150.4 ± 0.85	(9) 146.9 ± 1.27		150.1
	Subadult	(13) 150.3 ± 0.94	(5) 151.5 ± 1.58	(26) 150.5 ± 0.64	(6) 150.0 ± 1.33	(8) 150.5 ± 1.31		150.6
	Young	(19) 137.0 ± 0.66	(7) 136.7 ± 1.08	(26) 137.8 ± 0.56	(21) 136.4 ± 0.63	(20) 136.9 ± 0.71	13.3	150.3
MB	Adult*	(20) 175.3 ± 1.43	(22) 174.6 ± 1.40	(57) 178.8 ± 0.84	(16) 175.9 ± 1.68	(9) 173.3 ± 2.44		175.6
	Subadult	(12) 171.6 ± 2.16	(5) 174.1 ± 3.60	(19) 172.3 ± 1.68	(6) 169.4 ± 2.98	(7) 170.2 ± 3.17		173.7
	Young**	(20) 138.7 ± 1.07	(6) 138.7 ± 1.95	(26) 136.0 ± 0.92	(18) 134.1 ± 1.11	(18) 138.9 ± 1.22	21.4	158.7
ZB	Adult*	(20) 237.2 ± 1.76	(23) 234.4 ± 1.71	(60) 242.6 ± 1.01	(17) 236.9 ± 2.00	(8) 241.2 ± 3.06		238.5
	Subadult*	(12) 226.5 ± 2.45	(4) 232.5 ± 4.48	(26) 226.7 ± 1.62	(6) 220.0 ± 3.36	(7) 214.9 ± 3.87		224.1
	Young	(20) 179.2 ± 1.39	(6) 181.0 ± 2.53	(26) 179.2 ± 1.20	(17) 174.8 ± 1.49	(19) 175.6 ± 1.56	28.6	206.6
SB	Adult	(22) 131.6 ± 1.22	(25) 129.0 ± 1.21	(60) 132.5 ± 0.74	(17) 129.1 ± 1.46	(9) 132.5 ± 2.19		130.9
	Subadult	(13) 127.4 ± 1.48	(5) 129.4 ± 2.48	(26) 125.8 ± 1.01	(6) 123.6 ± 2.10	(8) 120.2 ± 2.05		125.2
	Young	(19) 100.1 ± 1.23	(7) 101.8 ± 2.00	(25) 98.9 ± 1.05	(21) 96.7 ± 1.16	(20) 98.4 ± 1.31	16.3	115.5
CL	Adult	(20) 226.1 ± 1.67	(25) 224.3 ± 1.58	(63) 225.8 ± 0.96	(17) 225.2 ± 1.90	(9) 225.6 ± 2.84		225.4
	Subadult	(13) 221.1 ± 1.97	(5) 219.0 ± 3.32	(26) 224.6 ± 1.35	(6) 222.2 ± 2.80	(7) 224.0 ± 2.83		222.2
	Young*	(20) 189.1 ± 1.24	(7) 186.4 ± 2.08	(26) 186.4 ± 1.07	(21) 184.0 ± 1.20	(20) 189.5 ± 1.36	30.4	217.6
FL	Adult	(22) 192.2 ± 1.11	(25) 196.0 ± 1.11	(64) 192.5 ± 0.66	(17) 193.7 ± 1.33	(9) 194.0 ± 1.98		193.7
	Subadult	(13) 195.2 ± 1.84	(5) 195.0 ± 3.09	(26) 194.0 ± 1.26	(6) 190.3 ± 2.79	(8) 194.4 ± 2.67		193.8
	Young	(20) 171.4 ± 0.94	(7) 174.4 ± 1.57	(26) 171.4 ± 0.81	(21) 171.6 ± 0.91	(20) 172.4 ± 1.03	23.4	195.6
MSH	Adult**	(22) 104.9 ± 0.69	(25) 103.0 ± 0.68	(62) 105.3 ± 0.41	(17) 105.0 ± 0.82	(9) 108.4 ± 1.23		105.3
	Subadult	(13) 104.0 ± 0.97	(5) 104.0 ± 1.63	(26) 102.1 ± 0.66	(6) 103.7 ± 1.37	(8) 102.8 ± 1.34		103.3
	Young*	(19) 83.8 ± 0.63	(7) 86.4 ± 1.04	(25) 84.7 ± 0.55	(21) 83.0 ± 0.60	(20) 85.4 ± 0.69	12.5	97.2
LCB	Adult	(21) 71.9 ± 0.82	(25) 71.9 ± 0.79	(58) 70.0 ± 0.50	(16) 67.8 ± 0.98	(8) 64.5 ± 1.47		69.2
	Subadult	(13) 71.6 ± 0.80	(5) 70.9 ± 1.34	(25) 70.5 ± 0.55	(6) 70.0 ± 1.13	(8) 70.3 ± 1.11		70.7
	Young	(20) 69.9 ± 0.64	(7) 69.7 ± 1.07	(26) 70.2 ± 0.55	(21) 70.6 ± 0.62	(20) 70.3 ± 0.70	1.9	72.0
IB	Adult	(22) 96.9 ± 0.94	(25) 96.1 ± 0.94	(63) 97.8 ± 0.57	(17) 95.8 ± 1.13	(9) 98.9 ± 1.68		97.1
	Subadult*	(13) 95.2 ± 1.09	(5) 97.8 ± 1.83	(26) 93.7 ± 0.74	(6) 92.2 ± 1.54	(8) 89.3 ± 1.51		93.6
	Young	(20) 74.9 ± 1.10	(7) 77.9 ± 1.85	(26) 74.6 ± 0.96	(21) 73.6 ± 1.07	(20) 74.7 ± 1.21	12.5	87.6
BC	Adult*	(22) 98.1 ± 0.66	(25) 96.8 ± 0.66	(57) 99.2 ± 0.41	(15) 99.2 ± 0.84	(7) 100.6 ± 1.27		98.8
	Subadult	(13) 95.0 ± 0.77	(5) 96.6 ± 1.29	(24) 92.4 ± 0.55	(6) 92.2 ± 1.09	(8) 92.4 ± 1.07		93.7
	Young	(20) 80.4 ± 0.62	(7) 81.4 ± 1.05	(25) 80.9 ± 0.55	(21) 80.9 ± 0.61	(20) 81.9 ± 0.69	9.1	90.2
PB	Adult**	(21) 88.0 ± 0.68	(24) 85.8 ± 0.67	(63) 88.9 ± 0.39	(17) 90.6 ± 0.79	(9) 89.1 ± 1.17		88.5
	Subadult	(13) 86.9 ± 0.74	(5) 88.6 ± 1.25	(26) 86.5 ± 0.51	(6) 87.6 ± 1.06	(8) 86.4 ± 1.03		87.2
	Young	(20) 78.4 ± 0.55	(7) 78.7 ± 0.93	(26) 79.5 ± 0.48	(21) 79.5 ± 0.54	(20) 80.9 ± 0.61	6.1	85.5
LP4 – M2	Adult	(22) 62.3 ± 0.49	(25) 62.1 ± 0.49	(62) 63.2 ± 0.29	(7) 62.5 ± 0.59	(7) 61.2 ± 0.93		62.3
LM2	Adult*	(21) 27.7 ± 0.38	(25) 27.6 ± 0.36	(62) 28.2 ± 0.22	(17) 27.4 ± 0.44	(9) 26.2 ± 0.65		27.4
LM1	Adult*	(22) 20.2 ± 0.13	(25) 19.9 ± 0.13	(62) 20.3 ± 0.08	(17) 20.6 ± 0.16	(8) 20.1 ± 0.24		20.2
CH	Adult	(20) 108.8 ± 0.87	(20) 109.1 ± 0.93	(55) 110.6 ± 0.52	(16) 110.2 ± 1.04	(6) 109.4 ± 1.66		109.6
	Subadult	(13) 108.1 ± 1.09	(5) 111.0 ± 1.84	(21) 108.7 ± 0.84	(6) 107.4 ± 1.54	(6) 106.6 ± 1.69		108.3
	Young*	(20) 88.6 ± 0.75	(7) 90.5 ± 1.25	(24) 89.6 ± 0.67	(20) 86.3 ± 0.74	(19) 87.2 ± 0.85	15.3	103.7
CPL	Adult	(21) 188.0 ± 0.68	(23) 188.7 ± 0.68	(62) 186.9 ± 0.40	(17) 188.2 ± 0.79	(9) 187.4 ± 1.18		187.8
	Subadult	(12) 187.9 ± 1.20	(5) 190.2 ± 1.94	(26) 188.2 ± 0.79	(6) 188.4 ± 1.64	(8) 186.6 ± 1.60		188.3
	Young*	(20) 162.9 ± 0.65	(7) 164.7 ± 1.09	(25) 161.3 ± 0.57	(20) 163.4 ± 0.65	(20) 163.2 ± 0.72	25.6	188.7

Table 5

Means of skull measurements adjusted to a standard condylobasal length (continued)

Measurement		Females						
		Spitzbergen	East Greenland	Canada	Alaska north	Alaska south		
MPL	Adult	(20) 133.1 ± 0.60	(16) 134.6 ± 0.69	(33) 134.4 ± 0.50	(13) 134.5 ± 0.78	(7) 133.2 ± 1.11	16.3	150.3
	Subadult	(6) 134.2 ± 1.04	(9) 133.4 ± 0.85	(23) 132.6 ± 0.53	(3) 134.2 ± 1.55		17.2	150.8
	Young	(7) 123.4 ± 0.78	(7) 124.6 ± 0.86	(32) 125.7 ± 0.37	(8) 125.0 ± 0.74	(5) 124.5 ± 0.99	22.1	146.7
MB	Adult	(17) 142.7 ± 0.99	(15) 143.1 ± 1.08	(26) 143.8 ± 0.85	(12) 140.7 ± 1.26	(7) 145.3 ± 1.72	17.2	160.3
	Subadult*	(6) 138.6 ± 1.73	(9) 140.2 ± 1.41	(23) 142.9 ± 0.88	(3) 135.3 ± 2.58		21.1	160.3
	Young	(6) 126.5 ± 1.70	(7) 123.5 ± 1.76	(29) 122.6 ± 0.79	(8) 121.1 ± 1.48	(5) 121.8 ± 2.01	31.7	154.8
ZB	Adult**	(19) 196.2 ± 1.33	(14) 194.7 ± 1.56	(32) 195.6 ± 1.11	(13) 194.1 ± 1.67	(7) 194.2 ± 2.40	29.0	224.0
	Subadult	(5) 185.6 ± 2.78	(9) 187.5 ± 2.05	(21) 190.5 ± 1.33	(3) 184.2 ± 3.75		26.0	213.0
	Young	(6) 164.4 ± 2.27	(7) 163.3 ± 2.33	(29) 164.0 ± 1.04	(8) 161.0 ± 1.98	(5) 162.1 ± 2.67	44.4	207.4
SB	Adult	(19) 104.8 ± 0.92	(15) 105.9 ± 1.04	(32) 103.8 ± 0.75	(12) 102.8 ± 1.18	(7) 105.6 ± 1.66	20.3	124.9
	Subadult	(6) 101.8 ± 1.78	(9) 102.4 ± 1.45	(22) 102.4 ± 0.92	(3) 96.2 ± 2.66		19.1	119.8
	Young*	(6) 91.6 ± 1.50	(7) 90.9 ± 1.54	(32) 89.7 ± 0.65	(8) 84.7 ± 1.31	(5) 87.7 ± 1.76	26.3	115.2
CL	Adult	(20) 190.8 ± 1.09	(15) 188.7 ± 1.27	(32) 189.0 ± 0.91	(13) 188.8 ± 1.40	(7) 194.3 ± 2.01	25.9	216.2
	Subadult	(5) 192.6 ± 2.39	(9) 188.3 ± 1.80	(23) 189.8 ± 1.12	(3) 187.4 ± 3.28		38.3	227.8
	Young	(6) 170.1 ± 2.39	(7) 166.7 ± 2.45	(31) 166.8 ± 1.06	(8) 167.8 ± 2.08	(5) 174.7 ± 2.80	44.4	213.6
FL	Adult	(20) 168.3 ± 0.86	(16) 171.4 ± 0.98	(33) 168.9 ± 0.71	(13) 167.1 ± 1.11	(7) 169.6 ± 1.59	22.3	191.4
	Subadult	(5) 168.4 ± 1.87	(9) 170.2 ± 1.41	(23) 168.6 ± 0.88	(3) 170.3 ± 2.56		22.2	191.6
	Young*	(7) 155.0 ± 1.02	(7) 157.6 ± 1.13	(32) 154.5 ± 0.48	(8) 157.0 ± 0.96	(5) 154.1 ± 1.30	36.1	191.7
MSH	Adult	(20) 85.5 ± 0.54	(16) 86.6 ± 0.62	(33) 85.2 ± 0.45	(13) 85.4 ± 0.70	(7) 87.2 ± 1.00	13.1	99.1
	Subadult	(6) 83.8 ± 1.17	(9) 84.1 ± 0.95	(23) 85.4 ± 0.60	(3) 83.4 ± 1.74		14.4	98.6
	Young	(7) 76.5 ± 0.91	(7) 78.1 ± 1.02	(31) 76.7 ± 0.43	(8) 75.4 ± 0.86	(5) 76.2 ± 1.17	19.3	95.9
LCB	Adult	(20) 65.8 ± 0.75	(16) 67.5 ± 0.85	(32) 65.5 ± 0.63	(13) 65.0 ± 0.96	(7) 67.7 ± 1.38	4.4	70.7
	Subadult	(4) 67.9 ± 1.45	(9) 67.9 ± 0.97	(21) 66.9 ± 0.63	(3) 66.5 ± 1.78		6.2	73.5
	Young*	(6) 69.1 ± 1.14	(7) 68.0 ± 1.17	(32) 68.3 ± 0.50	(8) 64.7 ± 0.99	(5) 65.4 ± 1.34	4.4	71.5
IB	Adult	(19) 79.7 ± 0.74	(16) 81.3 ± 0.83	(33) 79.3 ± 0.60	(13) 78.7 ± 0.93	(7) 81.1 ± 1.34	16.5	96.5
	Subadult	(6) 76.9 ± 1.58	(9) 79.1 ± 1.29	(22) 78.1 ± 0.82	(3) 73.5 ± 2.36		12.7	89.6
	Young*	(7) 70.5 ± 1.17	(7) 69.8 ± 1.30	(32) 68.2 ± 0.55	(8) 65.4 ± 1.10	(5) 68.9 ± 1.48	20.4	89.0
BC	Adult	(19) 81.4 ± 0.67	(16) 81.9 ± 0.74	(33) 81.2 ± 0.54	(13) 81.2 ± 0.84	(7) 81.1 ± 1.20	11.8	93.2
	Subadult	(6) 77.7 ± 1.03	(9) 76.8 ± 0.84	(23) 70.3 ± 0.53	(3) 78.6 ± 1.54		10.0	85.8
	Young	(7) 73.6 ± 0.88	(7) 71.2 ± 0.98	(31) 72.8 ± 0.42	(8) 72.5 ± 0.83	(5) 72.1 ± 1.12	14.8	87.2
PB	Adult	(20) 77.7 ± 0.60	(16) 78.1 ± 0.68	(33) 77.5 ± 0.49	(13) 78.2 ± 0.77	(7) 77.7 ± 1.10	10.4	88.2
	Subadult	(6) 75.7 ± 0.87	(9) 75.0 ± 0.71	(23) 77.0 ± 0.45	(3) 76.5 ± 1.30		7.2	83.2
	Young	(7) 74.0 ± 0.84	(7) 72.4 ± 0.93	(32) 73.8 ± 0.40	(8) 72.4 ± 0.79	(5) 74.6 ± 1.07	9.3	82.7
LP4–M2	Adult	(19) 55.6 ± 0.50	(16) 56.3 ± 0.56	(33) 57.0 ± 0.40	(12) 56.1 ± 0.66	(6) 56.5 ± 0.96	2.3	58.6
LM2	Adult	(20) 23.9 ± 0.39	(16) 24.8 ± 0.44	(33) 25.2 ± 0.32	(13) 24.2 ± 0.50	(7) 24.8 ± 0.71	1.1	25.7
LM1	Adult	(20) 18.6 ± 0.14	(16) 18.3 ± 0.16	(33) 18.7 ± 0.11	(13) 19.0 ± 0.18	(7) 18.8 ± 0.25	0.3	19.0
CH	Adult	(20) 90.0 ± 0.51	(15) 89.5 ± 0.61	(32) 90.5 ± 0.43	(11) 91.2 ± 0.71	(7) 89.8 ± 0.95	9.6	99.8
	Subadult	(6) 89.8 ± 1.43	(8) 89.2 ± 1.27	(20) 91.1 ± 0.76	(3) 90.8 ± 2.17		8.0	98.2
	Young**	(7) 80.3 ± 1.09	(7) 79.2 ± 1.21	(30) 81.6 ± 0.53	(8) 77.5 ± 1.03	(5) 77.9 ± 1.38	23.7	103.0
CPL	Adult	(20) 163.2 ± 0.55	(15) 163.3 ± 0.64	(32) 162.8 ± 0.46	(13) 163.5 ± 0.71	(7) 165.9 ± 1.01	23.2	186.9
	Subadult	(6) 161.1 ± 0.88	(9) 162.4 ± 0.72	(23) 161.8 ± 0.45	(3) 160.8 ± 1.31		24.4	185.9
	Young	(7) 148.4 ± 0.97	(7) 147.1 ± 1.07	(32) 146.5 ± 0.46	(8) 146.7 ± 0.91	(5) 148.2 ± 1.23	41.6	189.0

Note:

The figures in parentheses are the number of specimens. The means for adult and subadult males are adjusted to a standard condylobasal length of 380 mm, those of young males and adult and subadult females to a standard length of 330 mm, and those of young females to one of 300 mm. The regressions used are those given in Table 9. The figures in the penultimate column show the amount that must be added to bring the adjusted means on the same line to a standard condylobasal length of 380 mm. The last column gives the unweighted means of the five (four in one case) population means adjusted to a condylobasal length of 380 mm in all cases. One and two asterisks denote significant differences among the adjusted means on the corresponding line at the 5 per cent and 1 per cent levels respectively.

Table 6
Summary of significant differences in position of the regression lines

Measurement	Sex	Spitzbergen: east Greenland			Spitzbergen: Canada–west Greenland			Spitzbergen: Alaska north			Spitzbergen: Alaska south			East Greenland: Canada–west Greenland			East Greenland: Alaska north			East Greenland: Alaska south			Canada–west Greenland: Alaska north			Canada–west Greenland: Alaska south			Alaska north: Alaska south		
		A	S	Y	A	S	Y	A	S	Y	A	S	Y	A	S	Y	A	S	Y	A	S	Y	A	S	Y	A	S	Y	A	S	Y
MPL	♂ ♂																																
	♀ ♀																																
MB	♂ ♂							−**						+*																+*			
	♀ ♀					+*																			−*								
ZB	♂ ♂				+*								−*	+**			−*			−*			−*				−*						
	♀ ♀																																
SB	♂ ♂																																
	♀ ♀									−*									−*							−*							
CL	♂ ♂									−*																				+*			
	♀ ♀																																
FL	♂ ♂																																
	♀ ♀																		−*						+*								
MSH	♂ ♂									+*				+**						−*	+*		−*	+*					+*			+*	
	♀ ♀																																
LCB	♂ ♂																																
	♀ ♀									−*															−*								
IB	♂ ♂										−*						−*			−*						−*							
	♀ ♀									−*								−*															
BC	♂ ♂													+*			+*			+*													
	♀ ♀																																
PB	♂ ♂										+*			+**			+**			+*			+*										
	♀ ♀																																
LP4-M2	♂ ♂																																
	♀ ♀																																
LM2	♂ ♂																									−*							
	♀ ♀																																
LM1	♂ ♂													+*			+*																
	♀ ♀																																
CH	♂ ♂									−*										−*						−*			−*				
	♀ ♀																									−**			−*				
CPL	♂ ♂																			−*						+*			+*				
	♀ ♀																																

Note:
A = adult; S = subadult; Y = young.
A plus is used when the dependent variate is relatively greater in the population with the larger independent variate (condylobasal length), a minus when it is relatively smaller. One and two asterisks denote a significant difference at the 5 per cent and 1 per cent levels respectively.

In only one case (facial length of young females $P < .01$) was there a significant difference among the regression coefficient of the five population samples. This single difference may be ascribed to chance and has therefore been ignored in preparing Tables 5 to 10. A comparison of the within-population variances of Table 2 with the variances from regression in Table 7 shows that the introduction of regression has, in most measurements, reduced the variances of the adults by about half. Tooth measurements and least cranial breadth are only slightly correlated with condylobasal length (Table 8), and the variances are therefore only slightly reduced by regression.

As usual in comparisons of geographical populations of a single species, more differences in position than in slope of the regression lines are significant. In the males there are 11 significant position differences at the five per cent level and three at the one per cent level. In the females there are five at the five per cent level and one at the one per cent level. The measurements and age groups in which these differences occur are indicated by asterisks in Table 5.

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Duncan's multiple range test (Duncan, 1951) was used to distinguish which of the five populations were responsible for the differences. The results of these tests are assembled in Table 6. There are no significant differences between the east Greenland and the Spitzbergen samples. This reinforces the conclusion reached from the absolute measurements that these two populations are very similar. There are also only four significant differences between the Alaska north and the Alaska south samples. However this probably results partly from the small number of specimens in the samples, particularly in that from Alaska south. Certainly the large number of specimens in the Canada – west Greenland sample will have increased the likelihood of significant differences between this sample and those compared with it.

Apart from the negative evidence supporting the similarity of the Spitzbergen and east Greenland populations, the differences between the adjusted means are disappointingly random. They give no indication of clines in skull shape, nor is there any evidence that the skulls of any one population are consistently broader or narrower than those of any other. Moreover, the differences in the adults are not supported by corresponding differences in the subadults and young. A careful inspection of Table 6 does, however, suggest a pattern. Thus 11 out of 12 significant differences in the breadth measurements of the skulls of adults indicate that these skulls average relatively broader in those populations which have the larger mean condylobasal length, whereas of the 22 significant differences in the subadults and young, all but three indicate relatively narrower skulls in the populations with the larger mean condylobasal length. There are no significant differences for coronoid height in the adults or subadults, but four significant differences in the young suggest that this measurement also is relatively small in populations containing large individuals. Maxilla–supraorbital height follows the breadth measurements in seven out of eight significant differences.

Table 7
Variances from regression

Measurement	Males			Females		
	Adult	Subadult	Young	Adult	Subadult	Young
MPL	11.08	10.60	8.08	7.29	6.19	4.20
MB	39.33	22.59	22.09	16.79	17.17	17.08
ZB	59.85	67.12	37.40	33.53	35.91	30.47
SB	32.14	26.13	27.72	15.92	18.09	13.33
CL	55.34	46.49	29.85	23.63	27.74	33.67
FL	27.02	40.40	17.00	14.82	16.97	7.24
MSH	10.23	11.21	7.49	5.93	7.82	5.71
LCB	13.80	7.60	7.93	11.19	8.09	7.66
IB	19.40	14.17	23.73	10.51	14.28	9.47
BC	9.48	7.05	7.55	8.52	6.09	5.40
PB	9.46	6.64	6.02	7.15	4.35	4.88
LP4–M2	5.226			4.839		
LM2	2.908			2.995		
LM1	0.375			0.382		
CH	14.80	14.14	10.83	5.30	11.36	8.19
CPL	9.48	15.94	8.17	6.04	4.39	6.49

Note:
These are the mean squares or variances from the parallel line regressions of the five population samples.

Table 8
Coefficients of correlation

Measurement	Males			Females			Adult males	Adult females
	Adult	Subadult	Young	Adult	Subadult	Young		
MPL	.768**	.819**	.958**	.748**	.815**	.970**	.976**	.921*
MB	.639**	.743**	.959**	.601**	.720**	.942**	.896*	.840
ZB	.713**	.839**	.961**	.674**	.666**	.952**	.932*	.953*
SB	.641**	.813**	.914**	.672**	.674**	.936**	.944*	.833
CL	.733**	.830**	.971**	.694**	.830**	.943**	.996**	.911*
FL	.759**	.746**	.972**	.726**	.741**	.980**	.951*	.796
MSH	.723**	.823**	.952**	.646**	.723**	.941**	.988**	.878*
LCB	.306**	.291*	.445**	.232*	.411*	.508**	.901*	.185
IB	.658**	.828**	.880**	.681**	.565**	.925**	.974**	.833
BC	.694**	.845**	.920**	.594**	.635**	.921**	.990**	.990**
PB	.564**	.764**	.875**	.577**	.575**	.841**	.950*	.962**
LP4–M2	.380**			.187			.749	.510
LM2	.331**			.111			.431	.388
LM1	.395**			.078			.905*	.893*
CH	.469**	.806**	.954**	.610**	.388*	.952**	.941*	.931*
CPL	.909**	.903**	.988**	.866**	.919**	.986**	.990**	.965**

Note:
One and two asterisks denote significance of correlation at the 5 per cent and 1 per cent levels respectively. The first six columns are the mean within-population coefficients of correlation between condylobasal length and the measurement indicated at the left. The last two columns are the coefficients of correlation of the five population means.

Table 9

Weighted mean regression coefficients

Measurement	Adult	Subadult	Young	All ages
Male				
MPL	(136) .310 ± .023	(58) .290 ± .028	(93) .265 ± .009	.274 ± .008
MB	(124) .417 ± .046	(49) .528 ± .072	(88) .427 ± .014	.433 ± .016
ZB	(128) .650 ± .058	(55) .778 ± .072	(88) .572 ± .018	$P < .01$
SB	(133) .383 ± .041	(58) .450 ± .045	(92) .326 ± .016	$P < .05$
CL	(134) .618 ± .051	(57) .634 ± .060	(94) .608 ± .016	.612 ± .017
FL	(137) .472 ± .035	(58) .448 ± .055	(94) .468 ± .012	.467 ± .010
MSH	(135) .264 ± .022	(58) .305 ± .029	(92) .250 ± .009	.257 ± .008
LCB	(128) .094 ± .026	(57) .052 ± .024	(94) .039 ± .008	.047 ± .008
IB	(136) .300 ± .030	(58) .350 ± .033	(94) .249 ± .014	$P < .05$
BC	(126) .232 ± .022	(56) .265 ± .024	(93) .182 ± .008	$P < .005$
PB	(134) .162 ± .021	(58) .192 ± .022	(94) .122 ± .007	$P < .05$
LP4–M2	(133) .076 ± .016			
LM2	(134) .047 ± .012			
LM1	(134) .021 ± .004			
CH	(117) .168 ± .030	(51) .310 ± .034	(90) .306 ± .011	$P < .001$
CPL	(132) .520 ± .021	(57) .524 ± .035	(92) .512 ± .009	.514 ± .008
Female				
MPL	(89) .326 ± .032	(41) .344 ± .041	(59) .276 ± .041	.287 ± .010
MB	(77) .343 ± .054	(41) .422 ± .068	(55) .396 ± .020	.392 ± .018
ZB	(85) .580 ± .071	(38) .520 ± .101	(55) .565 ± .026	.564 ± .024
SB	(85) .406 ± .050	(40) .383 ± .071	(58) .329 ± .017	.341 ± .017
CL	(87) .517 ± .060	(40) .765 ± .087	(57) .553 ± .027	$P < .05$
FL	(89) .446 ± .046	(40) .443 ± .068	(59) .451 ± .013	.450 ± .015
MSH	(89) .262 ± .029	(41) .288 ± .046	(58) .241 ± .012	.247 ± .011
LCB	(88) .088 ± .041	(37) .123 ± .048	(58) .055 ± .013	.063 ± .013
IB	(88) .329 ± .039	(40) .255 ± .063	(59) .255 ± .014	.264 ± .014
BC	(88) .235 ± .035	(41) .199 ± .040	(58) .185 ± .011	.192 ± .011
PB	(89) .207 ± .032	(41) .144 ± .034	(59) .117 ± .010	$P < .05$
LP4–M2	(86) .045 ± .027			
LM2	(89) .021 ± .021			
LM1	(89) .005 ± .007			
CH	(85) .195 ± .028	(37) .161 ± .068	(57) .296 ± .013	$P < .005$
CPL	(87) .463 ± .030	(41) .481 ± .034	(59) .521 ± .012	.511 ± .010
Male and female				
MPL				.278 ± .006
MB				.422 ± .012
ZB	.631 ± .044	.723 ± .055	.570 ± .014	
SB	.389 ± .031	.435 ± .034	.327 ± .011	
CL	.594 ± .038	.663 ± .045	.593 ± .013	
FL				.462 ± .010
MSH				.255 ± .006
LCB				.052 ± .007
IB	.307 ± .023	.329 ± .027	.251 ± .010	
BC	.233 ± .018	.250 ± .019	.183 ± .005	
PB	.173 ± .017	.181 ± .017	.121 ± .005	
LP4–M2	.068 ± .013			
LM2	.041 ± .010			
LM1	.017 ± .003			
CH	.176 ± .029	.285 ± .028	.303 ± .008	
CPL				.513 ± .006

Note:
The figures in parentheses are the number of specimens. The first three columns give the regression coefficients (5 parallel lines) obtained by summation of the sums of squares and products of the five populations. Where there are no significant differences between the regression coefficients of the three age groups, their weighted mean (15 parallel lines) is given in the last column. Where there is a significant difference this is also shown in the last column. There are no significant differences between the regression coefficients of males and those of females either for those measurements where the age groups had to be treated separately or in those where they could be combined, and the weighted means for the combined sexes are given in the last section of the table.

Table 10

Coefficients of variation

Measurement	Males			Females		
	Adult	Subadult	Young	Adult	Subadult	Young
MPL	2.19 ± .13	2.17 ± .20	2.05 ± .15	1.99 ± .15	1.87 ± .20	1.66 ± .15
MB	3.53 ± .22	4.25 ± .43	3.40 ± .26	2.94 ± .23	2.93 ± .32	3.43 ± .33
ZB	3.21 ± .20	3.67 ± .35	3.40 ± .26	2.93 ± .23	3.17 ± .36	3.44 ± .33
SB	4.29 ± .26	4.10 ± .38	2.63 ± .19	3.77 ± .29	4.17 ± .47	4.16 ± .39
CL	3.27 ± .20	3.08 ± .29	2.87 ± .21	2.54 ± .19	2.76 ± .31	3.51 ± .33
FL	2.67 ± .16	3.28 ± .30	2.37 ± .17	2.26 ± .17	2.43 ± .27	1.76 ± .16
MSH	3.03 ± .18	3.27 ± .30	3.18 ± .23	2.81 ± .21	3.29 ± .36	3.15 ± .29
LCB	5.26 ± .33	3.91 ± .37	4.00 ± .29	5.04 ± .38	4.23 ± .49	4.11 ± .38
IB	4.50 ± .27	4.05 ± .38	6.40 ± .47	4.01 ± .30	4.85 ± .54	4.57 ± .42
BC	3.11 ± .20	2.83 ± .27	3.34 ± .24	3.56 ± .27	3.15 ± .35	3.23 ± .30
PB	3.46 ± .21	2.98 ± .28	3.06 ± .22	3.41 ± .26	2.73 ± .30	3.02 ± .28
LP4–M2	3.64 ± .22			3.36 ± .26		
LM2	6.12 ± .37			7.00 ± .52		
LM1	3.03 ± .18			3.31 ± .25		
CH	3.49 ± .23	3.51 ± .35	3.65 ± .27	2.53 ± .19	3.73 ± .43	3.62 ± .34
CPL	1.63 ± .10	2.13 ± .20	1.73 ± .13	1.49 ± .11	1.29 ± .14	1.76 ± .16

Note:
These are the coefficients of variation after eliminating the over-all size factor in so far as this can be measured by condylobasal length. The figures were obtained by dividing the standard error from regression x 100 by the mean of the specimens pooled from all five populations.

Thus it appears that relative to other populations the young and subadults in populations with a large mean condylobasal length have narrow skulls, whereas the adults in these populations have wide skulls. Conversely, in populations with a small mean condylobasal length the young and subadults have wide skulls and the adults have narrow skulls. Actually, the true significance of the figures is difficult to evaluate since the breadth measurements are likely to be at least as well correlated with each other as they are with condylobasal length (Table 8). Also, the same independent variate, condylobasal length, has been used throughout. If there is in fact a change in shape of the skull of one population relative to another during growth it is clearly necessary to keep the age groups separate even for covariance analysis. In polar bears this is also necessary because of the differences between the regression coefficients of the three age groups (Table 9). The significant differences (six in the males and three in the females) occur mostly in the breadth and height measurements. In males the mean regression coefficients of all breadth and height measurements are adult .297, subadult .358, young .275. Evidently, at about four years of age longitudinal growth decreases more rapidly than growth in breadth and height. Actually some breadth measurements, notably zygomatic breadth, continue to increase well into old age and long after growth in length has ceased. Since, however, we are here dealing with mass rather than individual growth, the effect is masked by variations in adult size. The mean breadth and height coefficients for females are adult .294, subadult .277, young .271. From this it appears that growth in length and breadth ends at about the same time in females, and when the female regressions are projected to a standard condylobasal length of 380 mm it can be seen (Table 5, last column) that subadult and adult females have relatively narrower and lower skulls than males. Kurtén (1964:18–20), using specimens of both sexes and all ages combined, noted an increase in skull width relative to length above a certain size. There can be little doubt, however, that the change is dependent on age and sex rather than on size and to understand the reason for the change, specimens of different age and sex must be separated when possible.

Since the divisions between the age groups do not necessarily coincide with the changes in the slope of the regression lines, it is possible that some of the differences in the adjusted population means may be caused by variations in the average age of the specimens in corresponding age groups of different populations. When new series become available it will be interesting to see if the differences among the populations still conform to the present pattern.

The coefficients of variation given in Table 10 estimate the variation in shape after removal of the size factor by regression on condylobasal length. The coefficients for adults may be compared with those for total variation in Table 2. Table 10 indicates that shape, like total size, is

less variable in females than in males. If the skulls classed as young had all been of the same age, their shape would probably have been distinctly less variable than that of adults, but as their ages varied, change of shape with age has undoubtedly affected the coefficients of variation and there is little difference between the three age groups.

It has been shown above that none of the described forms of recent *U. maritimus* can be distinguished by the characters used by previous authors. Tables 2 and 3, however, demonstrate that there is a cline of increasing skull size from the east Greenland population across the nearctic to the Alaska south population. This cline, which is more obvious in the males, is probably under genetic control, since there is no evidence that it is affected by the various ecological conditions encountered between east Greenland and Alaska south. Also, in spite of the difference in climate there appears to be no marked size difference between the bears in the northern part of the Canada – west Greenland region and those to the south in southern Hudson Bay. To maintain the genetic difference evinced by the cline the populations must of course be reasonably stable and non-migratory, and Pedersen's theory (1956) of a circumpolar movement becomes untenable.

Other differences between the four populations into which the nearctic area was divided have been discussed above and are shown in Tables 5 and 6. Though statistically significant, the degree of separation afforded by these differences is small and they need not be considered here except to note that, since in adults those populations which contain the larger individuals appear to have relatively wider and higher skulls, these measurements may be expected to and in some of the present samples do give a slightly greater degree of separation than does condylobasal length. I think, however, it is wiser to use condylobasal length alone as an estimate of total skull size rather than to make an empirical selection from the other measurements. The joint non-overlap for these other measurements can be obtained from Table 3 if desired.

The type locality of *U. maritimus* is Spitzbergen (Phipps, 1774:185). The average size of bears in that population is slightly larger than in the east Greenland population, but on the available evidence no one would hesitate to combine these two populations into a single race. The

joint non-overlap in condylobasal length between the east Greenland and the Alaska south samples is 93 per cent for males and 83 per cent for females. All the adult females and most of the adult males in the Alaska south series are from north of Bering Strait where some intergradation must be expected. The few specimens from south of Bering Strait are large, and it is reasonable to suppose that if a good series were obtained from there the joint non-overlap between it and that of the east Greenland population would be greater. It must be noted, however, that the largest of the skulls from south of Bering Strait, that from St. Paul Island, dates from 1875 or earlier. The second largest, one from St. Lawrence Island, also dates from about that period (H. B. Collins, *in litt.*). The much reduced modern population may therefore have been affected by migration from the north.

At the present time there is no obvious geographical barrier separating the Alaska south population and the Alaska north population. Sufficient genetic isolation for the observed differences to evolve may have been provided by segregated denning and breeding areas, particularly at a time when bears were more numerous south of Bering Strait and when perhaps their range extended considerably farther south down the Siberian coast. Ice conditions in the Okhotsk Sea resemble those of southern Hudson Bay (United States Navy, 1946), and two specimens in the U.S. National Museum from the Komandor Islands and one in the British Museum from the Kamchatka Peninsula are evidence of the southern extent of the polar bear's range in that region.

It is also possible that during the Wisconsin glaciation a population of polar bears was isolated south of the Bering Strait land bridge which at its maximum development was over 500 miles wide (Hopkins, 1967: 462). If so, these bears would have lived under very different ecological conditions to those north of the bridge and some morphological change would be expected during the seven thousand odd years that the

bridge was wide enough to be an effective barrier. With the disappearance of the land bridge, gene flow would have resulted in regression of the distinguishing characters of this hypothetical population which presumably was numerically small. On the other hand, genes from the southern population may have been swamped north of Point Lay by the larger and perhaps more mobile population of the Arctic Ocean, though admittedly the gene for small tooth size seems to have spread through the Alaska north population. I think the possibility that the Alaska south population is descended from a semi-isolated group of bears, coupled with the observed morphological differences and the fact that the Alaska south population occupies the extremity of a cline, justifies subspecific separation. However, since there is no name available and a good possibility of additional specimens being obtained, it is best to postpone a decision.

The joint non-overlap for the condylobasal length of the Canada – west Greenland and the Alaska north population is only 62 per cent for males and 52 per cent for females (Table 3). They therefore form a single unit morphologically midway between the east Greenland and the Alaska south populations. The mean condylobasal length of the pooled samples from the Canada – west Greenland and Alaska north populations is 385.7 mm for males and 335.7 mm for females. Using the original within-population variance (Table 2), the joint non-overlap between the combined Canada – west Greenland and Alaska north samples and the east Greenland samples is 74 per cent for males and 70 per cent for females. Between the combined Canada – west Greenland and Alaska north samples and the Alaska south samples it is 80 per cent for males and 67 per cent for females. These figures are below those normally required for subspecific differentiation.

However, should the Alaska south population eventually be named it would be convenient to have a name for the population which occupies the large area between east Greenland and northern Alaska. There are several names available. Of these *U. m. labradorensis* Knotterus-Meyer has priority. It is probable, however, that much of the palaearctic population would, on the criteria of size alone, be referable to the same race which would then go under the name of *U. m. marinus* Pallas. Whether the similarity between the central nearctic and the central palaearctic bears is due to to a common origin and gene interchange through contact north of the Alaska south population or merely to the fact that both occupy an intermediate position on independent but similar clines remains to be determined.

The type of *U. m. tyrannus* Kurtén is an ulna of Late Pleistocene age from Kew Bridge, London, England. Kurtén (1964) makes a good case for referring this specimen to *U. maritimus* and by reason of its large size is clearly justified in considering it racially distinct from extant populations. I now have measurements for eight skulls with matching ulnae. Though this small series is obviously inadequate for predictions outside the sample range it is worth noting for a rough comparison that the reduced main axis gives a condylobasal length of 447 mm corresponding to the Kew Bridge ulna length of 485 mm. The largest skull I have seen is USNM 83594 with a condylobasal length of 436 mm. This skull was obtained (picked up ?) about 1875 on St. Paul Island, Alaska. The second largest, also an old skull, is from St. Lawrence Island, Alaska, and is 12 mm smaller. Since the Kew Bridge ulna appears to be the only specimen of *U. maritimus* definitely of Pleistocene age (Kurtén, 1964), it is too early to speculate whether *U. m. tyrannus* may have been an isolated population or whether the average size of bears in the whole circumpolar region was at that time much larger than at present. In the latter case the Alaska south population could be a relict of these large bears.

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