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Former occurrences of geese (Genera *Anser* and *Branta*) in ancient West Greenland: morphological and biometric approaches

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Abstract. Goose remains from 16 prehistoric localities ranging from the beginning of the Saqqaq period, c. 2400 B.C., to Colonial times, c. 1850 A.D. were examined in order to elucidate the prehistoric distribution of goose populations in Central West Greenland. The site of Nipisat I, Sisimiut/Holsteinsborg District, dated to c. 2000-500 B.C., provided nearly 1800 goose remains which were compared to extant Greenland goose species of the genera *Branta* and *Anser*. The Nipsat I geese were significantly smaller than the White-fronted Geese *Anser albifrons flavirostris* and could be assigned to the genus *Branta* based on the unpneumatised furcula. The presence of juvenile goose bones and 63 percent of the femora containing medullary bone demonstrated that the Nipisat I geese bred or at least staged in close proximity to the coast. The following scenario is suggested: a *Branta* species, presumably a smaller subspecies of Canada Goose *Branta canadensis*, may have co-existed with White-fronted Geese, documented in the interior of the Nuuk/Godthåb District since at least c. 1000-1400 A.D. and the interior of the Sisimiut/Holsteinsborg District since at least c. 1200-1300 A.D. The Brent Goose *Branta bernicla hrota*, was established as a member of the Greenland avifauna 4000-4500 years ago and possibly earlier.

Key words: West Greenland, subfossil goose bones, *Anser*, *Branta*, morphology, biometrics, medullary bone, ancient goose populations.

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I. INTRODUCTION

Several authors have drawn attention to the difficulties in identifying postcranial goose bones to species (e.g., BACHER 1967; ALLISON 1985), and even on the generic level only very few diagnostic morphological features seem to distinguish *Anser* from *Branta*.

From 16 prehistoric localities in low arctic Greenland (Fig. 1) goose remains have been retrieved that could not be identified to species by morphological criteria. At most sites e.g. localities 8-10, 12-14 and 16 (Fig. 1) goose bones were comparable in size to bones of Greenland White-fronted Goose *Anser albifrons flavirostris* DALGETY & SCOTT, 1948 (GOTFREDSEN 1999), a

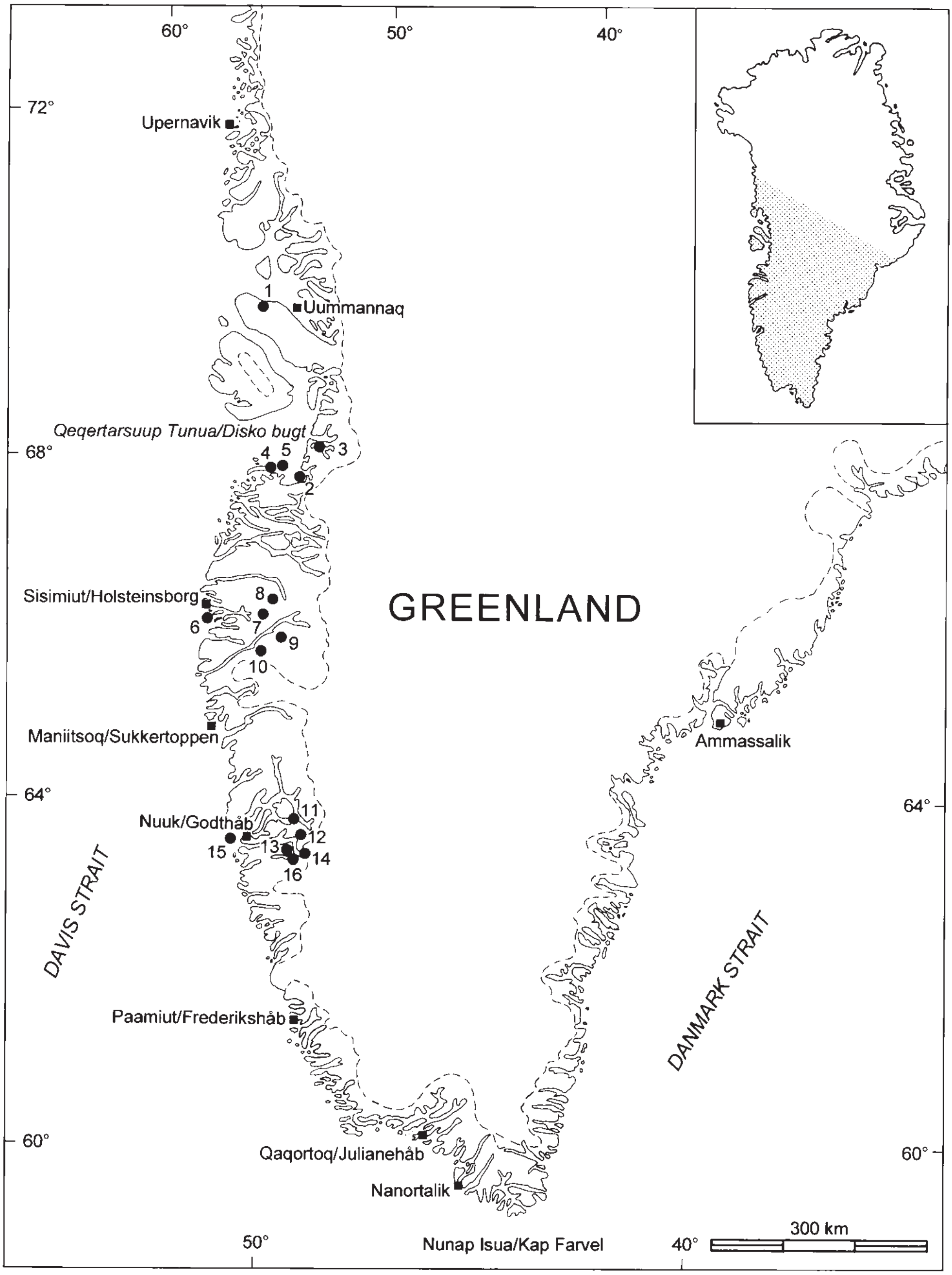

Fig. 1. Localities with goose remains in low arctic Greenland. Numbers refer to locality numbers listed in Table I. ■ indicates major towns. Stippled line on the map demarcates the inland ice and large ice caps.

present-day breeding bird on the west coast of Greenland (Salomonsen 1967; Fox et al. 1999). However, the goose bones from the coastal locality Nipisat I (Fig. 1) were smaller than the bones of White-fronted Geese. Whereas most localities yielded only a few bones, Nipisat I produced a very large find of 1745 well-preserved goose bones (Table I). This provided an opportunity to combine biometric and morphological studies in an attempt to address whether one or several species occurred in the Nipisat I sample and to try to identify the species in question.

Table I

Archaeological localities of low arctic Greenland with goose remains. The localities are either dated archaeologically or by ^{14}C. Datings shown with an arrow (e.g., 2030→520 BC) indicate that bones occur throughout the time interval. Datings shown with a hyphen (e.g., 1000-1400 AD) indicate that bones date somewhere within the time interval. NISP designates the number of goose bones at the sites. ZMK refers to collections at the Zoological Museum, Copenhagen. All localities are shown in Fig. 1

Locality No & Name	Position	Dating	Culture	NISP	Reference	Catalogue reference
1 Ikorfat	70°46'N 53°07'W	–	Saqqaq	1	–	ZMK 121/1958
2 Qeqertasussuk	68°35'N 51°04'W	2400→1400 BC	Saqqaq	1	Grønnow & Meldgaard (1988); Grønnow (1994)	ZMK 70/1983
3 Qajaa	69°07'N 50° 42'W	1900→900 BC	Saqqaq	2	Meldgaard (1983,1991); Møhl (1986)	ZMK 350/1983
4 Niivertussannguaq	68°38'N 52° 19'W	2180-1320 BC	Saqqaq	3	Olsen (1998); Andreasen (1998)	ZMK 50/1995
5 Ikkarlussuup Timaa	68°44'N 52° 09'W	–	Dorset	1	Jensen et al. (1995); T. Andreasen (unpubl.)	ZMK 47/1995
6 Nipisat I	66°49'N 53°30 'W	2030→520 BC	Saqqaq	1745	Møbjerg (1998); Gotfredsen (1997,1998)	ZMK 136/1989
7 Malmquist Site	66° 49'N 51°31'W	c. 450 BC	Dorset	7	Kramer (1996)	ZMK 152/1977
8 Aasivissuit	67°06'N 51°10'W	1200→1850 AD	Thule	151	Grønnow et al. (1983)	ZMK 135/1978
9 Ivnajuatoq	66°31'N 51°20'W	–	Thule	5	M. Meldgaard (unpubl.)	ZMK 71/1983
10 690 m. Pladsen	66°34'N 52°00'W	–	Thule	1	M. Meldgaard (unpubl.)	ZMK 93/1981
11 Itinnera	64°23'N 50°24'W	c. 1500 BC	Saqqaq	1	Møhl (1972); J. Møhl (unpubl.)	ZMK 114/1966
12 V 51 Sandnes	64°15'N 50°12'W	1025→1325 AD	Norse	5	McGovern et al. (1996)	ZMK 75/19981
13 V 54 Nipaatsoq	64°06'N 50°07'W	1000-1400 AD	Norse	10	McGovern (1979), Møhl (1982)	ZMK 137/1977
14 GUS	64°05'N 50°04'W	–	Norse	31	Arneborg et al. (1998); G. Nyegaard & I. B. Enghoff (unpubl.)	ZMK 3/1991
15 Itissaalik	64°07'N 52°06'W	1700-1800 AD	Thule	1	Gulløv (1983, 1997)	ZMK 143/1972
16 Tasersuaq	64°04'N 50°05'W	–	Thule	3	Kapel (1993); G. Nyegaard (unpubl.)	ZMK 26/1991

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II. MATERIALS AND METHODS

Morphology

According to BACHER (1967: 36, fig. 51), *Branta* exhibits a bilateral compression of the spina sterni externa of the sternum in 80% of all individuals, while in *Anser* it is usually pointed ('Bei Anser ist sie meist spitzkegelig'). The furcula is generally identifiable to genus ('Zum anderen ist die Furcula der beiden Gattungen gewöhnlich zu unterscheiden'), since in *Branta* it is unpneumatised while in *Anser* it is pneumatised (BACHER 1967). BACHER (1967) also suggested the use of size and proportions when determining the species of postcranial goose skeletons. A morphological comparison between recent Greenland goose species and the subfossil sample from Nipisat I, incorporated all limb bones, the coracoid, scapula, furcula and sternum, adults and subadults, of the following species: White-fronted Goose *Anser albifrons* (SCOPOLI, 1769) (26 ♂♂, 21 ♀♀, 2 unsexed), Pink-footed Goose *Anser brachyrynchus* BAILLON, 1833 (24 ♂♂, 17 ♀♀, 2 unsexed), Greater Snow Goose *Anser caerulescens atlanticus* (KENNARD, 1927) (1 ♂, 1 ♀), Lesser Snow Goose *Anser caerulescens caerulescens* (LINNAEUS, 1758)(1 ♀), Canada Goose *Branta canadensis* (LINNAEUS, 1758) (3 ♂♂, 4 ♀♀, 1 unsexed), Barnacle Goose *Branta leucopsis* (BECHSTEIN, 1803) (17 ♂♂, 11 ♀♀) and Brent Goose *Branta bernicla* (LINNAEUS, 1758) (25 ♂♂, 10 ♀♀).

Biometrics

The biometric analysis included the coracoid, humerus, and femur because of their high frequency in the Nipisat I bone assemblage and because they represent the trunk, wings, and legs. Humerus length and wing length are strongly correlated (ERICSON 1987: 20, 51), the latter normally within genera considered a good measure of the general size of birds (SELANDER & JOHNSTON 1967; ERICSON 1987). For the recent goose species only skeletons of known sex and osteologically mature bones with completely fused epiphyses were measured. Seven measurements were taken on the humerus: Greatest length (GL), proximal breadth (Bp) (in the present paper Bp^1), smallest breadth of the corpus (SC), and distal breadth (Bd) followed the definition of von den DRIESCH (1976). Bp, however, is very difficult to measure and therefore the proximal breadth (in the present paper Bp^2) as defined by FICK (1974:21) including the crista lateralis, was measured too (Fig. 2). Depth of the proximal end Dp and depth of distal end Dd are according to MÜNZEL (1987: 169, 170) (Fig. 2). On the femur, seven measurements were taken: GL, medial length (Lm), Bp, Dp, SC, and Dd are according to von den DRIESCH (1976) while the definition of distal breadth Bd followed MÜNZEL (1987:171) (Fig. 3). All measurements of the coracoid: GL, Lm, basal breadth (Bb) and breadth of the facies articularis basalis (BF) are according to von den DRIESCH (1976). All measurements were measured to the nearest 0.01 mm using a Mitutoyo Digimatic Caliper.

In total 63% of the subfossil femora contained medullary bone, and therefore derived from adult breeding females. Geese pair for life (OGILVIE 1978; OWEN 1980; MADSEN 1989) and adult breeding birds arrive at the breeding grounds in pairs and stay together during the breeding period (OWEN 1980). The sex ratio is expected to be 1:1 in the goose population, although some populations may have a surplus of male non-breeders (OWEN et al.1978). It is assumed that nearly all the goose bones at Nipisat I are from adult breeding birds of both sexes. The apparent preponderance of femora with medullary bone may be explained taphonomically. Bones filled with granular calcium tissue are expected to have a better preservation potential than hollow bones. The preservation potential of the

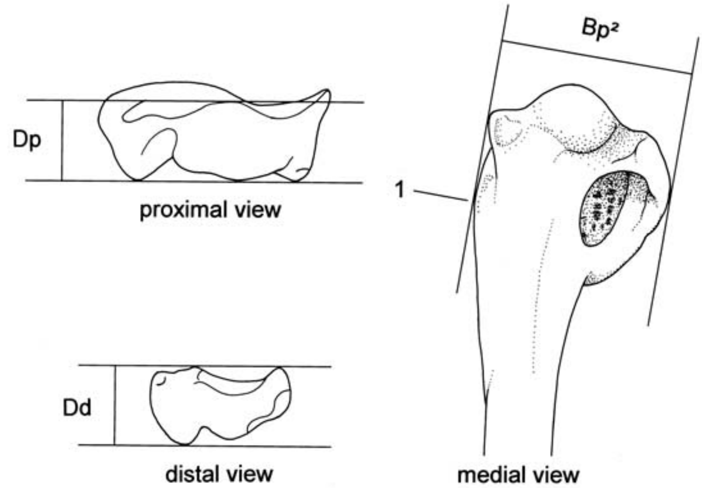

Fig. 2. Definitions of measurement for humerus. Bp^2– breadth of the proximal end including the crista lateralis indicated with 1, according to the definition of FICK (1974). Dp – depth of the proximal end and Dd - depth of the distal end are according to definitions of MÜNZEL (1987).

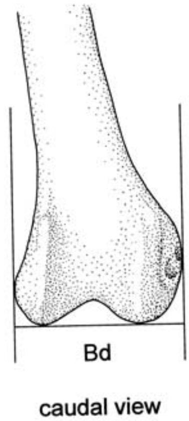

Fig. 3. Definition of the measurement Bd – breadth of the distal end of femur. The measurement is taken from the caudal side and the condylus medialis and lateralis are in one plane and the slide calliper is perpendicular to this plane according to MÜNZEL (1987).

humerus and coracoid, which contained no medullary bone, is expected to be equal in both sexes. Therefore it is assumed that the sex ratio for coracoid and humerus is 1:1.

In a previous analysis measurements of Pink-footed Goose and Brent Goose were compared with the dimensions of the Nipisat I goose bones. The Nipisat I geese were significantly larger then male Brent Geese ($p<0.01$) and significantly smaller than female Pink-footed Geese ($p<0.01$) when means of greatest length of the humerus and femur were tested in a student's t-test (GOTFREDSEN unpublished poster 1992). All three subspecies of the polytypic Brent Goose are of similar size (CRAMP & SIMMONS 1977). The smallest humeri of the Nipisat I sample had larger foramina pneumatica than humeri of Brent Geese. Therefore these two goose species were excluded from the present biometric analysis. The Greater Snow Goose was excluded due to its considerably larger size. In the present analysis, the prehistoric goose remains were compared to the extant species of geese in Greenland: White-fronted Goose and Barnacle Goose, kept at the Zoological Museum, University of Copenhagen. Barnacle Goose is a monotypic species with no geographical variation (MADGE & BURN 1988: 146; HOYO et al. 1992: 584). The specimens included in this survey are therefore considered representative of the population, although the measured Barnacle Geese are mainly from the European population. The measured White-fronted Geese comprise specimens of the Greenland White-fronted Goose ssp. *A. a. flavirostris* (5 males & 4 females) which is slightly larger than the nominate race (MADGE & BURN 1988: 138). Data on *Anser albifrons albifrons* (SCOPOLI, 1769) and *A. albifrons flavirostris* were pooled to maximise the sample, although two variables GL and Lm of the femur differed.

Statistics

All groups were analysed using descriptive statistics.

One-way analysis of variance (ANOVA model I) tests for significant difference between the means of the various groups (SOKAL & ROHLF 1995). This test assumes normally distributed observations, which was tested in a Kolmogorov-Smirnov One-Sample Test for Normality.

Tukey HSD Test for Unequal N tests which groups are significantly different from each other (SOKAL & ROHLF 1995).

Several main statistical assumptions are required:

1) Random sampling from the parent population (SOKAL & ROHLF 1995: 393), which is considered fulfilled for both recent and subfossil samples.

2) Independence of different observations (SOKAL & ROHLF 1995: 393). According to MORALES (1993), birds very seldom appear as whole skeletons in anthropogenic sites. The Nipisat I goose remains were deposited over a very long time period and many taphonomic factors may have influenced the bone assemblage removing and destroying bones. To maximise sample size, both right and left bone elements were included in the analysis.

3) An analysis of variance requires that the variances are equal for all samples (SOKAL & ROHLF 1995: 397). Bartlett's test for homogeneity of variances and Hartley's F_{max} –test tested homogeneity of variance.

Sexual dimorphism

There is some sexual dimorphism within goose bones (BACHER 1967) therefore the modern geese were tested for differences in variance between sexes. Female subfossil femora could be recognised and was therefore tested separately against the recent samples of female femora.

Temporal control

Due to a complex stratigraphy, the culture layers could not be separated into chronologically separable strata (MØBJERG 1998: 110; T. MØBJERG pers. comm. 1999), and therefore the Nipisat I goose bones were pooled. The ^{14}C datings of the site indicate that the goose remains were deposited gradually over 1000-1500 years. Pooling of bones covering this considerable time span representing many goose generations may cause some problems, and may potentially represent several subspecies or species (PIMENTAL 1958). This issue will be discussed below.

All tests are tested at a significance level of 5%.

III. RESULTS

Morphology

Only the sternum, furcula, and femur showed traits useful for separating the modern representatives of the genus *Branta* from *Anser*. The shape of the spina sterni externa was difficult to assess due to intraspecific variation. Three states were observed: i) pointed, ii) slightly bilaterally compressed, and iii) fully bilaterally compressed. All three states were observed in both genera (Table II). How-

Table II

Spina sterni externa of the sternum. Shape and degree of bilateral compression in six goose species of *Anser* and *Branta*. (See text for explanation)

Species	Total No.	Pointed		Degree of bilateral compression		Total % bilaterally compressed
		No.	%	Slight	Full	
Anser albifrons	49	40	(82)	5	4	(18)
A. brachyrynchus	42	34	(81)	6	2	(19)
A. caerulescens	3	2	(67)	1	0	(33)
Branta canadensis	8	0	(0)	2	6	(100)
B. leucopsis	28	5	(18)	5	18	(82)
B. bernicla	35	0	(0)	5	30	(100)

ever, *Anser* had the highest frequency of specimens with a clearly pointed spina sterni externa, e.g., 82% in White-fronted Goose, and 81% in Pink-footed Goose compared to 18% in Barnacle Goose, and none in Brent Goose. The variation in shape of the spina sterni externa seemed not to be correlated with age or sex. Because the spina sterni externa is often broken off in subfossil samples only four specimens could be assessed in the Nipisat I sample of which three were fully bilaterally compressed and one was pointed.

Pneumatisation of the furcula exhibited three stages: i) fully pneumatised, ii) slightly pneumatised, and iii) not pneumatised (Fig. 4A-C). In *A. albifrons* this feature seemingly was independent of sex and age since both males and females and subadults showed all three stages. In all pneumatised specimens, the position of the pneumatic foramina was found in an area between the tuberositas scapularis and tuberositas coracoidei, as described by WOOLFENDEN (1961:65) (Fig. 4A-B). The furcula was pneumatised in 90% of all *A. albifrons*, 86% of all *A. brachyrynchus*, and 100% of all *A. caerulescens* (Table III). In *Anser* the furcula pneumatisation exhibited a substantial variation, with

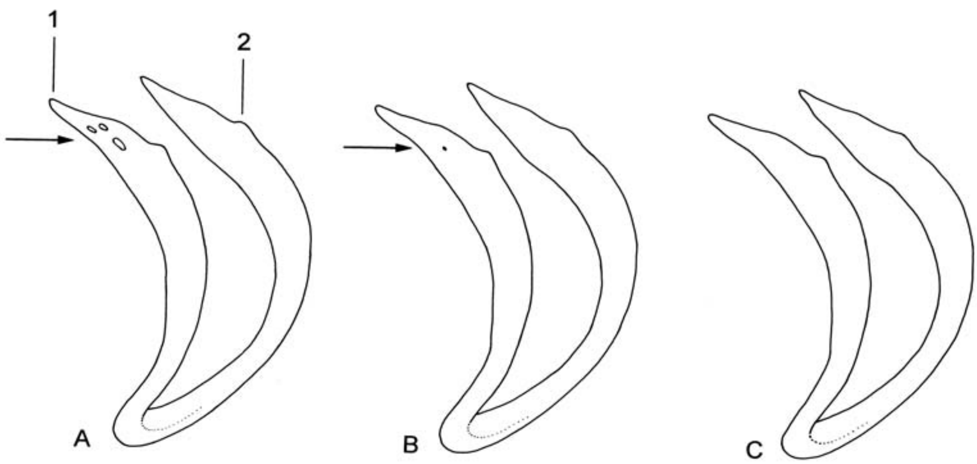

Fig. 4. Pneumatisation of furcula of *Anser* and *Branta*. A – Fully pneumatised furcula with foramina pneumatica indicated by an arrow; B – Slightly pneumatised furcula with small, barely visible foramina pneumatica indicated by an arrow; C – Furcula without foramina pneumatica. 1 – indicates the tuberositas scapularis and 2 – the tuberositas coracoideus.

Table III

Degree of pneumatisation of the furcula in six goose species of *Anser* and *Branta*. (See text and Fig. 4 for explanation)

Species	Total No.	Degree of pneumatisation		Total % pneumatised	Not pneumatised	
		Full	Slight		No.	%
Anser albifrons	48	34	9	(90)	5	(10)
A. brachyrynchus	43	28	9	(86)	6	(14)
A. caerulescens	3	2	1	(100)	0	(0)
Branta canadensis	8	0	0	(0)	8	(100)
B. leucopsis	28	0	0	(0)	28	(100)
B. bernicla	34	0	0	(0)	34	(100)

for instance 9 specimens (19%) of *A. albifrons* showing very little or insignificant pneumatisation (Fig. 4B). All the examined furcula of *Branta* were not pneumatised (Table III). Out of four complete furcula and 20 left branches from the Nipisat I sample one specimen had an inconspicuous foramen pneumaticum (Fig. 4B) while 23 lacked pneumatic foramina.

The shape of proximal trochanter major of the femur was difficult to assess because of a high variation both in *Anser* and *Branta* (Table IV). Nontheless, in most *Anser* specimens the proximal extension of the trochanter major was situated in the middle, and a curved posterior rim was found (WOOLFENDEN 1961:68). In *Branta* at least two-thirds of the specimens had the most proximal extension of the trochanter major situated anteriorly and possessed a straight posterior rim. Of the Nipisat I sample 84% of a total of 32 femora exhibited an anterior position and 84% had a straight posterior rim.

Table IV

Trochanter major of the femur. Position of most proximal extension (pE) and shape of posterior rim (Pr) in six goose species of *Anser* and *Branta*. (See text for explanation)

	Total No.	pE midlength		pE anterior		Pr curved		Pr straight	
		No.	(%)	No.	(%)	No.	(%)	No.	(%)
Anser albifrons	31	29	(94)	2	(6)	29	(94)	2	(6)
A. brachyrynchus	42	34	(81)	8	(19)	39	(93)	3	(7)
A. caerulescens	3	1	(33)	2	(67)	3	(100)	0	(0)
Branta canadensis	8	0	(0)	8	(100)	0	(0)	8	(100)
B. leucopsis	24	8	(33)	16	(67)	5	(21)	19	(79)
B. bernicla	34	5	(15)	29	(85)	10	(29)	24	(71)

Biometrics

All groups were normally distributed. For all variables, tests for homogeneity of variance showed that the groups did not have equal variances. However, ANOVA tests are robust towards data with heterogeneity of variance (SOKAL & ROHLF 1995: 401, 407).

For descriptive statistics see Appendix 1, Tables IA-G, IIA-H, and IIIA-G.

The variances of the subfossil geese did not differ from the variances in modern geese populations, (e.g., humerus (Appendix 1, Tables IC, F & G). The variances in female femora were even lower in the Nipisat I geese than in modern female geese (Appendix 1, Tables IIB, E and H), which probably is due to the small sample size of modern geese. The range in GL humerus in *A. albifrons*, *B. leucopsis*, and the Nipisat I geese is 17.5 mm, 13.7 and 19.4 respectively (Appendix 1, Tables IC, F and G). The range of the Nipisat I geese is only slightly (2 mm) larger than that of *A. albifrons* and can easily be explained by the larger sample size from Nipisat I, which indicate that only one goose species is represented in the ancient goose sample at Nipisat I.

In all variables the Nipisat I geese were significantly smaller than the *A. albifrons* ♂♂ and the pooled group of *A. albifrons* (Appendix 2, Tables IA-G, IIA-G, IIIA and D, VA-G, VIA-G, and VIIA-D). Except for Lm and Bb in the coracoid (Appendix 2, Tables IIIB and C), this group also differed from *A. albifrons* ♀♀. All variables showed significant difference between femora of female Nipisat I geese and those of female *A. albifrons* (Appendix 2, Tables IVA-G).

The Nipisat I geese were found to be significantly smaller than *B. leucopsis* ♂♂ in the majority of variables, except e.g., GL of the humerus (Appendix 2, Tables IA-G, IIA-G, and IIIA-D). Compared to *B. leucopsis* ♀♀, the Nipisat I geese (all) showed significant differences only in one variable in femur (Appendix 2, Table IID). For the pooled samples there were also significant differences in the majority of variables, except in GL of the humerus between *B. leucopsis* (all) and the Nipisat I geese (all) (Appendix 2, Tables VA-G, VIA-G, and VIIA-D). The female Nipisat I geese proved to be different from female *B. leucopsis* in two variables of the femur only (Appendix 2, Tables IVD and G).

Considerable overlaps between males and females, and between the recent species and the subfossil geese were detected and were most pronounced in the coracoid (Fig. 5). The Nipisat I sample

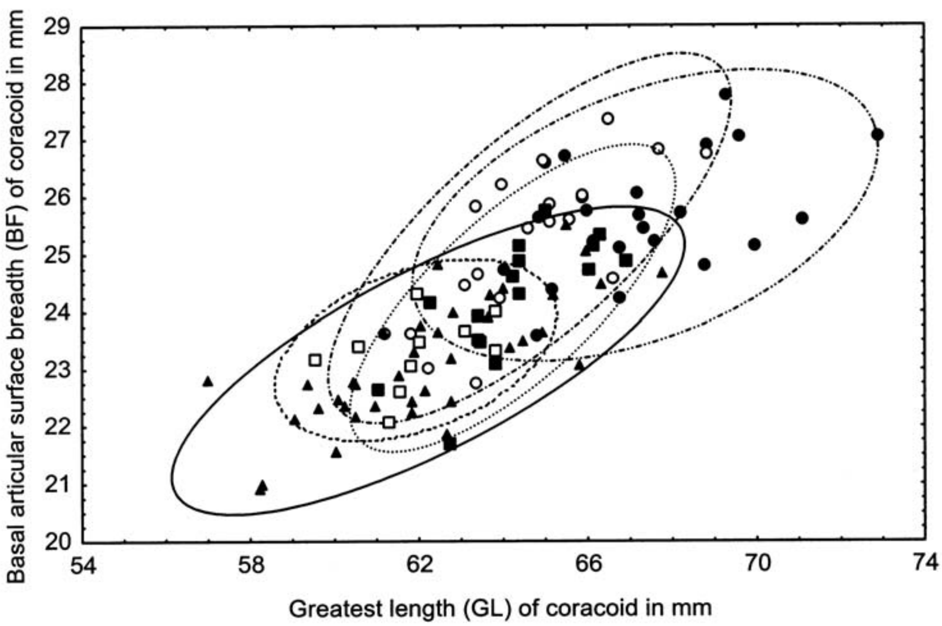

Fig. 5. Scatter-plot of five groups of geese for coracoid BF and GL.● = *Anser albifrons* ♂♂,❍ = *Anser albifrons* ♀♀, ■ = *Branta leucopsis* ♂♂, □ = *Branta leucopsis* ♀♀, and ▲ = Nipisat I geese. 95% confidence intervals are shown with stippled lines for recent geese and solid line for the Nipisat I geese.

exhibited no difference in humerus (GL) from any group (e.g., ♂♂, ♀♀, and both sexes pooled) of the Barnacle Goose. However, measurements of depth of, e.g., proximal femur of female Nipisat I geese were different from and smaller than those of the female Barnacle Geese (Fig. 6). Thus the geese at Nipisat I seem to have been of a size comparable to the Barnacle Goose, although probably even a little smaller and more delicately built.

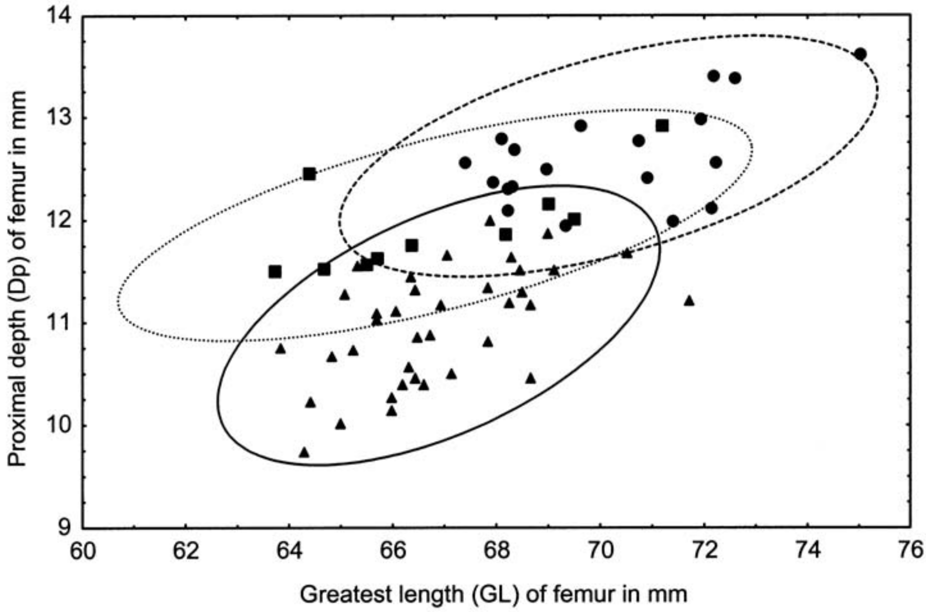

Fig. 6. Scatter-plot of three groups of female geese for femur Dp and GL.● = *Anser albifrons* ♀♀, ■ = *Branta leucopsis* ♀♀, and ▲ = Nipisat I ♀♀ geese. 95% confidence intervals are shown with stippled lines for recent geese and solid line for the Nipisat I geese.

IV. DISCUSSION

Morphology

In the present study features described for the humerus, coracoid, and tibiotarsus to separate *Branta* and *Anser* (WOOLFENDEN 1961: 104-105) could not be verified, most likely because that investigation was based on only 6 specimens of *Anser* and 18 of *Branta*. The above-mentioned features are completely blurred by intraspecific variation when more specimens are included. The shape of the trochanter major proved to be of some potential; although variation within species is considerable. The extent to which the spina sterni externa was pointed in *Anser* confirmed the results of BACHER (1967). Only the occurrence and position of pneumatic foramina in the furcula seem to have taxonomic significance when separating *Branta* from *Anser* (BACHER 1967: 36; WOOLFENDEN 1961: 65). None of the four features discussed in the present paper are absolute, and can therefore only be used for large samples of subfossil goose bones. However, the lack of pneumatised furcula, except for one slightly pneumatised specimen in the Nipisat I sample strongly suggests that the Nipisat I geese should be assigned to *Branta*.

The geese at Nipisat I

ERICSON (1987: 95) found the humerus of Scandinavian Eider *Somateria mollissima* (LINNAEUS, 1758) to be on average 2% longer in the Viking Age (c. 1200 years ago), and the length of the ulna in Brünnich's Guillemot *Uria lomvia* (LINNAEUS, 1758) in northern Scandinavia has decreased c. 2.5% over a period of 4200-3500 years (data from HUFTHAMMER 1982: 35). The difference in mean value of GL humerus between the Nipisat I geese and the modern White-fronted Geese is 9.2 mm or 6.6%, which would be an unlikely large size increase in 2500-4000 years. Evolutionary forces may, however, act differentially in various groups of birds. Recent studies of Lesser Snow Goose in La Pérouse Bay, Hudson Bay, showed that mean adult body weight and size changed significantly over decades (COOKE et al. 1995). However, the results of both the metric and the morphological analysis of the present study demonstrated that the Nipisat I geese were comparable in size to Barnacle Geese and belonged to the genus *Branta*.

In all 95% of the Nipisat I goose remains derived from adult birds while 5% were from juveniles comprising both newly hatched goslings and nearly fledglings, and more than half of the femora contained medullary bone. Goose species breeding in the Arctic have developed different strategies to acquire enough nutrient reserves for reproduction. Most species build up stores on the wintering grounds before spring migration starts, but have to feed at one or more spring staging areas before reaching the breeding grounds (see, e.g., EBBINGE & SPAANS 1995), as in the case of White-fronted Goose (FOX et al. 1983; FOX & STROUD 1988). Some species may in addition feed on the breeding grounds prior to incubation (CHOINÈRE & GAUTHIER 1995), while some may rely on feeding on the breeding grounds (e.g., RAVELING 1978). The calcium reserves are in most species acquired on the breeding grounds, e.g., Cackling Canada Goose *Branta canadensis minima* RIDGWAY, 1885, deposited medullary bone during the last 6-7 days of rapid ovarian development, after arrival on the breeding grounds (RAVELING et al. 1978; KRAPU & REINECKE 1992).

Medullary bone builds up in a period of 1-2 weeks before egg laying, is present throughout the egg-laying period, and gradually is resorbed after the last egg has been laid (SIMKISS 1961; TAYLOR 1970). The femora of the Nipisat I geese contained medullary bone in various degrees, as some were completely filled with calcium tissue (Fig. 7C) and some contained very little (GOTFREDSEN 1999). This implies that i) the birds were killed early in the staging period until the females had built up the calcium reserve, or ii) they were hunted when the calcium build-up was completed and were well into the egg-laying period, or both (Fig. 8). The admittedly scarce occurrence of juvenile bones in the midden suggests that hunting took place not only during staging but also during the breeding period. Both juvenile bones and bones with medullary bone occurred throughout the midden layers.

Fig. 7. Goose femora from the Saqqaq site Nipisat I (Table I, no 6). A – Intact femur; B – Longitudinally sectioned hollow femur; C – Longitudinally sectioned femur completely filled up with medullary bone. (Photograph by Geert BROVAD).

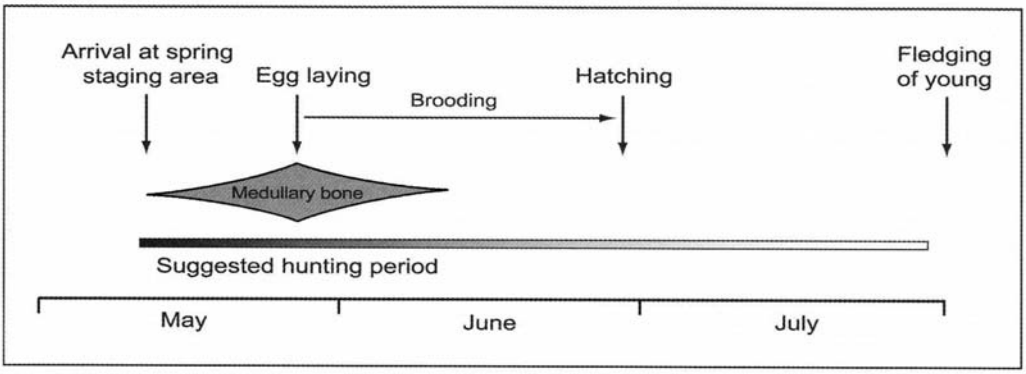

Fig. 8. Presumed primary hunting period at the Saqqaq site Nipisat I (Table I, no 6). Schematic representation of medullary bone formation in goose bone seen in relation to arrival at staging areas and timing of egg-laying. The exact timing of arrival would depend of the climatic situation and the goose species in question.

The Nipisat I geese therefore may have consisted primarily of spring staging and breeding birds presumably breeding close to the outer coast in the Sisimiut/Holsteinsborg District. The Inuit traditionally travelled far on hunting expeditions and may have brought the geese to the site from a far greater distance and the geese may have staged further inland. However, the goose bones comprised 14% of the total number of bird bones at Nipisat I (GOTFREDSEN 1998), which would not suggest occasional hunting inland. Today primary staging areas of White-fronted Geese in West Greenland are located at the bottom of the fjords and in the interior, which are the areas first free of snow (GLAHDER 1999). Since the inhabitants of Nipisat I first hunted geese c. 4000 years ago the relative sea level had fallen about 20 m (FUNDER 1989) and land/sea configuration has changed. Furthermore, it has been suggested that there was a more pronounced seasonality 2500 years ago, with a larger June insolation (P. MAYEWSKI pers. comm. 1999; O'BRIEN et al.1995). Snow-free patches early in the season with suitable food for the breeding populations of geese may have been situated closer to the coast in prehistoric Greenland.

Goose species presently occurring at the West Greenland coast

White-fronted Goose – From historical time until recently the only widespread breeding goose species in low arctic West Greenland primarily from the northern Nuuk/Godthåb District to the Upernavik District (64-73 N) was the White-fronted Goose (e.g., HOLBØLL 1843: 433; BERTELSEN 1932: 19; SALOMONSEN 1967: 98; FOX et al. 1999: 130). It breeds dispersed in the interior close to marshes and plains, preferably on the mainland (e.g., OGILVIE 1978; FOX & STROUD 1988), and probably has occurred and bred in the interior of Sisimiut/Holsteinsborg District since at least c.1200-1400 A.D. (at localities 8-10) (Fig.1) and in the interior of Nuuk/Godthåb District since at least c. 1000-1400 A.D. (at localities 12-14 and 16) (Fig. 1) (GOTFREDSEN 1999).

Brent Goose – The only migrating species in West Greenland, which occurs during spring and especially autumn from the Qeqertarsuup Tunua/Disko Bugt northwards to Upernavik District. The Light-bellied Brent Goose *Branta bernicla hrota* (Müller, 1776), now breeding in high arctic Canada (MERNE et al.1999: 298), was earlier in the 20th century considered a breeding bird in the extreme North and Northeast Greenland (SALOMONSEN 1950; 1967:117). Today part of the Svalbard population breeds in the eastern part of North Greenland (BOERTMANN & GLAHDER 1999). The Brent Goose breeds in colonies preferably in low tundra with lakes on the mainland or small island off the coast (HJORT et al. 1987; SALOMONSEN 1967; OGILVIE 1978). Only one prehistoric record of this species was recorded in the low arctic Greenland at Ikorfat, locality 1 (Fig. 1), however, Brent Goose remains from sites in North Greenland demonstrate that Brent Geese probably belonged to the Greenland avifauna for at least 4000-4500 years (GOTFREDSEN 1999).

Canada Goose – Occasionally, one of the smaller subspecies of Canada Goose e.g., Richardson's Canada Goose, *Branta canadensis hutchinsii* (RICHRADSON, 1832), a high arctic breeder, is seen on the coast of West Greenland and it has been reported breeding on the Nussuaq Peninsula (SALOMONSEN 1967: 126; BENNIKE 1990) and as far south as Qeqertarsuaq/Disko Island (R. M. KRISTENSEN pers. comm. 1999). JOHNSGAARD (1978) even considered it to breed regularly in the Ilulissat/Jacobshavn District (69 N). In 1863 a *B. canadensis* (subspecies not stated) bred on the Qeqertarsuaq/Disko Island and a skin was sent to the Zoological Museum in Copenhagen (REINHARDT 1865). Another yet larger subspecies, *Branta canadensis parvipes* (CASSIN, 1852), a low arctic breeder, was observed in small flocks in the southern part of Qeqertarsuup Tunua/Disko Bugt and the interior of the Sisimiut/Holsteinsborg District in the 1960s. These observations were, however, doubted by SALOMONSEN (1967: 126). Since the 1970s a yet larger subspecies, *Branta canadensis interior* TODD, 1938, another low arctic breeder, only slightly smaller than nominate race (MADGE & BURN 1988: 147), has been recorded as a breeding bird from the Nuuk/Godthåb District up to the Qeqertarsuup Tunua/Disko Bugt area (BOERTMANN 1994: 16). In recent years the Canada Goose has expanded its breeding range and numbers in West Greenland (BOERTMANN 1994: 16; FOX et al. 1996; GLAHDER et al. 1996) and in 1998 it was recorded breeding in the Avanersuaq municipality, North Greenland (BOERTMANN & MOSBECH 1999). In some areas, e.g., Disko Island, Canada Geese even outnumber the White-fronted Geese (BENNIKE 1990). The ancient goose remains from Nipisat I may derive from a smaller subspecies of Canada Geese. Considering the large variability and intergrading between Canada Goose populations and/or subspecies (see OGILVIE 1978; OWEN 1980), it is difficult to point out which subspecies it may have been, especially when we are faced with the problems of changes in size through time. However, taking into account its present breeding distribution (Fig. 9) and its size the Richardson's Canada Goose would be a likely candidate. Wing measurements of this subspecies are 349-412 mm (means: ♂♂: 391 mm, ♀♀: 371 mm) (PALMER 1976) and for the slightly larger Barnacle Goose 376-429 mm (means: ♂♂: 410, ♀♀ 392 mm) (MADGE & BURN 1988).

Snow Goose – The Greater Snow Goose is considered a high arctic breeder, however, it is known to breed in small numbers as far south as Qeqertarsuup Tunua/Disko Bugt (BOERTMANN 1994: 15; BOERTMANN & GLAHDER 1999). It is a colonial breeder nesting by lakes and coastal lagoons primarily on the mainland (e.g., OGILVIE 1978; BOERTMANN 1994). The Greater Snow Goose occurs along the West Greenland coast as a summer vagrant (BOERTMANN 1994). The Lesser Snow Goose, however, is considered a rare visitor to West Greenland from breeding grounds in arctic Alaska and Canada and winter grounds in USA (SALOMONSEN 1967: 112; BOERTMANN 1994: 16). Compared to the very few measurements obtained from the literature (MÜNZEL 1987) and one skeleton from the Zoological Museum, Copenhagen, it seems that the ancient goose bones from Nipisat I are within the size range of the Lesser Snow Goose. However, the Snow Geese belonging to *Anser* are probably not represented among the Nipisat I geese.

Pink-footed Goose – The Pink-footed Goose breeds on the northeast coast of Greenland (BOERTMANN 1994: 15). The species is a rare vagrant with only one record from the southwest coast (BOERTMANN 1994: 15). Based on morphological and biometric evidence, there is very little chance that this species is represented among the goose remains from Nipisat I.

Barnacle Goose – Barnacle Geese have been sighted a few times along the west coast of Greenland (BOERTMANN 1994: 16) and stragglers are seen on the Canadian east coast (GODFREY 1986). It has been suggested that Barnacle Geese spread eastwards from an original North American centre quite recently, i.e., after the last glaciation (OGILVIE 1978: 32). The species normally breeds among rocky crags or on steep cliffs in high arctic regions (MADGE & BURN 1988: 148, OGILVIE 1978: 119). However, recently Barnacle Geese from the Nowaya Zemlya population have established breeding colonies in the temperate Baltic area (GANTER et al. 1999). One might speculate that the species may have had wider breeding ranges in former times (D. BOERTMANN pers. comm. 1999). Flyways and winter grounds of Barnacle Geese (Fig. 9) would not suggest that the Nipisat I goose remains derived from Barnacle Geese, however it cannot be totally ruled out.

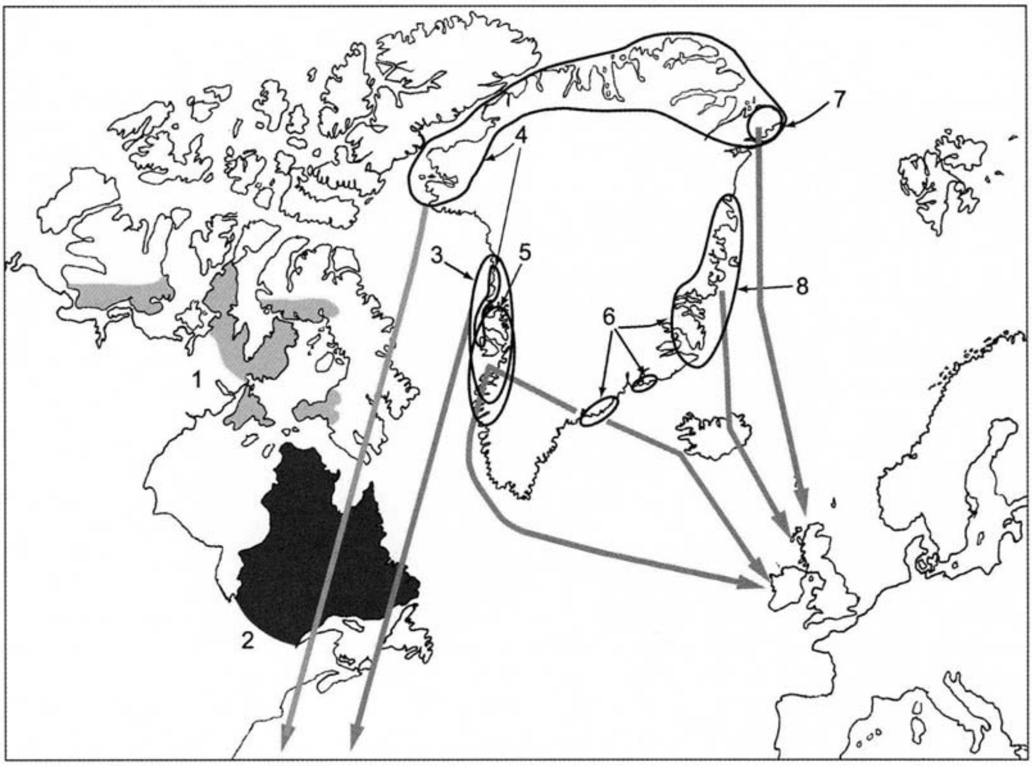

Fig. 9. Present breeding distribution and migration routes to winter quarters of six extant Greenland goose species and two subspecies of Canada Goose with an eastern Canadian distribution. 1 – Richardson's Goose; 2 – Interior Canada Goose; 3 – Canada Goose; 4 – Snow Goose; 5 – White-fronted Goose; 6 – Pink-footed Goose; 7 – Brent Goose; 8 – Barnacle Goose. (Information compiled from MADGE & BURN 1988; BOERTMANN 1994; PALMER 1976).

Changes in breeding ranges in recent and ancient times

During the 20th century the Greenland goose population has changed dramatically in size and breeding distribution. Examples are the decrease in breeding range of the Light-bellied Brent Goose in North Greenland since the 1950's (MERNE et al. 1999), and the increase in the breeding ranges of Greater Snow Goose in the High Arctic (REED et al. 1990) and Canada Goose in low arctic West Greenland (FOX et al. 1996; BOERTMANN & GLAHDER 1999). Seen from that perspective goose populations may have colonised and disappeared from the west coast of Greenland several times. The reasons for these fluctuations may be many; however, a primary factor is probably the climate and in more recent years man. The effects of agricultural development have had an immense impact on goose population during the present century (in combination with hunting regulations), because the geese have benefited from the easy access to cereal grains and grasses (KRAPU & REINICKE 1992; MADSEN et al. 1999). The reduced mortality due to protection and better foraging abilities at the wintering grounds has increased the abundance of the majority of goose species, which has to some extent influenced breeding ranges.

Breeding ranges can change within decades. This is seen today in West Greenland with the expansion of breeding Canada Geese. The reasons for this recent expansion of Canada Geese are still not fully understood as it appears that the population of interior Canada Geese has actually decreased in numbers in the past years (BOERTMANN & GLAHDER 1999). New breeding grounds can be reached by chance and if the breeding requirements are fulfilled, the geese will return. In recent times a breeding colony of Lesser Snow Geese was founded around 1963 at La Pérouse Bay, southern Hudson Bay because the breeding birds were prevented from reaching their more northerly breeding grounds by adverse weather condition (COOKE et al. 1995). Recent goose studies have provided insights into the effects of events on mortality and showed that apparently robust populations of geese may be susceptible to stochastic events which cause numbers to fall below thresholds defining unfavourable conservation status (FOX & MADSEN 1999).

In this respect it is therefore noteworthy that geese, probably a smaller subspecies of Canada Goose, staged and bred not far from the outer coast in the Sisimiut/Holsteinsborg District for a period of 1000-1500 years. This may indeed indicate fairly stable conditions for prolonged periods. It might be speculated that the Canada Geese were always members of the Greenland avifauna, but in fluctuating numbers, and that different subspecies of the species may have colonized or recolonized West Greenland. The other possibility is that the Barnacle Geese were more widespread in former times. The White-fronted Goose too was established as a breeding bird at least c. 1000 A.D. and possibly much earlier (GOTFREDSEN 1999). From the scarce subfossil evidence from sites of older date (besides Nipisat I) it is still not known whether the White-fronted Goose and a medium sized *Branta* coexisted in Central West Greenland for some time. In order to solve this question more prehistoric goose remains from settlements in West Greenland should be retrieved and studied possibly combined with studies on ancient DNA.

V. CONCLUSIONS

The distribution of breeding geese c. 2500-4000 years ago at the Central West Greenland may well have differed from the present-day situation. In the Sisimiut/Holsteinsborg District, geese of a smaller size than today's White-fronted Goose and of a comparable size to Barnacle Goose staged in spring or early summer and bred presumably in close proximity to the coast for more than a millennium (c. 2000-500 B.C.) or for shorter periods of time during that time span. This goose species, which belonged to the genus *Branta*, was presumably a subspecies of Canada Goose coming from eastern arctic Canada. The possibility, however, that the Barnacle Goose were more wide spread in ancient Greenland cannot be totally ruled out.

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Appendix 1

Descriptive statistics

Table I. Discriptive statistics of humerus for seven groups. Measurements are in mm

IA: Humerus of *Anser albifrons* ♂♂						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	24	150.61	142.62	156.98	13.14	3.62
Bp^1	24	34.00	32.35	36.09	0.93	0.97
Bp^2	24	31.14	29.74	32.76	0.69	0.83
Dp	24	12.03	11.13	13.90	0.33	0.57
SC	24	9.92	9.04	10.79	0.26	0.51
Bd	24	22.05	21.40	23.21	0.27	0.52
Dd	24	12.99	12.44	13.87	0.15	0.39
IB: Humerus of *Anser albifrons* ♀♀						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	18	144.57	139.51	153.19	13.35	3.65
Bp^1	17	32.90	31.55	34.33	0.55	0.74
Bp^2	18	30.30	29.12	31.91	0.61	0.78
Dp	16	11.81	10.90	12.63	0.23	0.48
SC	18	9.95	9.22	10.57	0.12	0.35
Bd	18	21.43	20.41	22.43	0.29	0.54
Dd	18	12.63	11.91	13.42	0.13	0.36
IC: Humerus of pooled sample of *Anser albifrons*						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	42	148.02	139.51	156.98	22.04	4.70
Bp^1	41	33.52	31.55	36.09	1.03	1.02
Bp^2	42	30.78	29.12	32.76	0.82	0.91
Dp	40	11.94	10.90	13.90	0.29	0.54

SC	42	9.93	9.04	10.79	0.20	0.45
Bd	42	21.78	20.41	23.21	0.37	0.61
Dd	42	12.83	11.91	13.87	0.17	0.41
ID: Humerus of *Branta leucopsis* ♂♂						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	17	140.60	134.64	144.48	9.32	3.05
Bp^1	17	31.85	29.98	33.62	0.99	0.99
Bp^2	17	29.18	27.42	31.03	0.77	0.88
Dp	17	11.69	10.74	12.83	0.39	0.63
SC	17	9.44	8.87	10.70	0.18	0.43
Bd	17	20.98	20.07	21.78	0.22	0.47
Dd	17	12.24	11.18	12.92	0.15	0.39
IE: Humerus of *Branta leucopsis* ♀♀						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	10	135.80	130.78	139.48	7.92	2.81
Bp^1	10	30.75	29.41	32.31	0.73	0.85
Bp^2	10	28.11	26.94	29.56	0.52	0.72
Dp	10	11.14	10.64	11.91	0.20	0.44
SC	10	9.11	8.73	9.83	0.15	0.38
Bd	10	20.35	19.33	21.43	0.39	0.62
Dd	10	11.89	11.27	12.61	0.20	0.45
IF: Humerus of pooled sample of *Branta leucopsis*						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	27	138.82	130.78	144.48	14.07	3.75
Bp^1	27	31.44	29.41	33.62	1.16	1.08
Bp^2	27	28.78	26.94	31.03	0.93	0.96
Dp	27	11.49	10.64	12.83	0.39	0.62
SC	27	9.32	8.73	10.70	0.19	0.44
Bd	27	20.75	19.33	21.78	0.36	0.60
Dd	27	12.11	11.18	12.92	0.19	0.44
IG: Humerus of pooled sample of geese from Nipisat I						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	53	138.82	129.46	148.82	20.82	4.56
Bp^1	55	29.99	27.12	32.65	1.63	1.27
Bp^2	40	27.80	25.68	29.95	1.16	1.08
Dp	40	10.85	9.33	12.70	0.42	0.65
SC	82	9.14	7.93	10.74	0.19	0.44
Bd	73	19.95	18.59	22.47	0.64	0.80
Dd	63	11.78	10.75	13.60	0.40	0.63

Table II. Discriptive statistics of femur for eight groups. Measurements are in mm

IIA: Femur of *Anser albifrons* ♂♂						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	25	72.39	68.37	76.37	3.25	1.80
Lm	25	69.14	65.48	72.99	3.27	1.81
Bp	25	16.54	15.13	18.09	0.55	0.74
Dp	25	12.80	11.92	13.51	0.20	0.45
SC	25	7.18	6.50	7.84	0.07	0.26
Bd	25	17.80	16.52	19.98	0.59	0.77
Dd	25	13.72	12.71	14.67	0.36	0.60

IIB: Femur of *Anser albifrons* ♀♀

Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	19	70.17	67.37	75.02	4.50	2.12
Lm	19	67.10	64.20	71.40	4.26	2.06
Bp	19	16.26	14.92	17.85	0.57	0.75
Dp	19	12.62	11.95	13.62	0.23	0.48
SC	19	7.39	6.96	8.04	0.11	0.33
Bd	18	12.37	16.33	18.88	0.40	0.63
Dd	18	13.24	12.09	14.21	0.24	0.49

IIC: Femur of pooled sample of *Anser albifrons*

Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	42	71.49	67.37	76.37	4.94	2.22
Lm	42	68.32	64.20	72.99	4.68	2.16
Bp	42	16.41	14.92	18.09	0.58	0.76
Dp	42	12.74	11.95	13.62	0.21	0.46
SC	42	7.29	6.68	8.04	0.08	0.29
Bd	41	17.65	16.33	19.98	0.54	0.73
Dd	39	13.53	12.09	14.67	0.36	0.60

IID: Femur of *Branta leucopsis* ♂♂

Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	16	68.59	66.03	70.72	2.06	1.44
Lm	15	64.52	62.67	66.94	1.60	1.26
Bp	16	15.75	13.47	17.95	1.23	1.11
Dp	16	12.00	11.05	12.98	0.32	0.57
SC	16	7.04	6.77	7.45	0.04	0.20
Bd	16	17.07	15.86	17.92	0.31	0.55
Dd	16	12.82	11.54	13.78	0.42	0.65

IIE: Femur of *Branta leucopsis* ♀♀

Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	10	66.81	63.70	71.18	6.24	2.50
Lm	10	63.06	60.00	67.31	6.99	2.64
Bp	10	15.39	14.22	16.24	0.46	0.68
Dp	10	11.95	11.51	12.92	0.21	0.46
SC	10	6.75	6.41	6.93	0.03	0.16
Bd	10	16.32	15.73	16.77	0.14	0.38
Dd	10	12.45	11.79	13.34	0.43	0.66

IIF: Femur of pooled sample of *Branta leucopsis*

Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	26	67.90	63.70	71.18	4.26	2.06
Lm	25	63.93	60.00	67.31	4.09	2.02
Bp	26	15.61	13.47	17.95	0.94	0.97
Dp	26	11.98	11.05	12.98	0.27	0.52
SC	26	6.92	6.41	7.45	0.05	0.23
Bd	26	16.78	15.73	17.92	0.37	0.61
Dd	26	12.68	11.54	13.78	0.44	0.66

IIG: Femur of pooled sample of geese from Nipisat I

Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	51	66.66	61.85	71.71	3.24	1.80
Lm	54	63.09	59.54	67.05	2.70	1.64
Bp	69	15.12	13.58	16.74	0.60	0.78

Dp	56	10.94	9.73	12.00	0.27	0.52
SC	171	6.73	5.96	7.50	0.10	0.32
Bd	51	15.79	14.65	17.44	0.44	0.66
Dd	50	11.86	10.70	13.14	0.27	0.52
IIH: Femur of female geese from Nipisat I						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	39	66.57	63.85	71.71	2.71	1.64
Lm	42	62.98	59.54	67.05	2.78	1.67
Bp	51	15.02	13.58	16.72	0.51	0.72
Dp	41	10.89	9.73	12.00	0.28	0.53
SC	108	6.69	5.97	7.47	0.10	0.31
Bd	42	15.71	14.65	17.44	0.39	0.62
Dd	42	11.77	10.70	12.76	0.22	0.47

Table III. Discriptive statistics of coracoid for seven groups. Measurements are in mm

IIIA: Coracoid of *Anser albifrons* ♂♂						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	22	67.38	63.99	72.87	5.09	2.26
Lm	22	57.27	53.78	62.36	4.57	2.14
Bb	19	27.54	26.29	29.56	0.73	0.86
BF	22	25.68	23.59	27.78	1.07	1.03
IIIB: Coracoid of *Anser albifrons* ♀♀						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	20	64.63	61.19	68.78	3.81	1.95
Lm	20	55.25	52.82	58.95	3.11	1.76
Bb	20	26.75	24.44	29.03	1.62	1.27
BF	20	25.27	22.79	27.37	1.73	1.31
IIIC: Coracoid of pooled sample of *Anser albifrons*						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	42	66.07	61.19	72.87	6.30	2.51
Lm	42	56.31	52.82	62.36	4.82	2.20
Bb	42	27.14	24.44	29.56	1.32	1.15
BF	42	25.48	22.79	27.78	1.39	1.18
IIID: Coracoid of *Branta leucopsis* ♂♂						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	16	64.22	61.00	66.88	2.49	1.58
Lm	16	54.80	52.33	57.27	1.70	1.30
Bb	16	26.07	24.09	27.55	0.88	0.94
BF	16	24.23	21.70	25.77	1.19	1.09
IIIE: Coracoid of *Branta leucopsis* ♀♀						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	10	61.93	59.50	63.81	1.87	1.37
Lm	10	53.06	50.51	55.92	2.10	1.45
Bb	10	25.30	24.01	26.03	0.35	0.60
BF	10	23.33	22.10	24.34	0.42	0.65
IIIF: Coracoid of pooled sample of *Branta leucopsis*						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	26	63.34	59.50	66.88	3.47	1.86

Lm	26	54.13	50.51	57.27	2.52	1.59
Bb	26	25.77	24.01	27.55	0.80	0.89
BF	26	23.88	21.70	25.77	1.06	1.03
IIIG: Coracoid of pooled sample of geese from Nipisat I.						
Variable	Valid N	Mean	Minimum	Maximum	Variance	S.D.
GL	41	62.19	57.00	67.75	6.78	2.60
Lm	48	53.93	49.19	59.32	5.39	2.32
Bb	8	25.42	22.51	27.43	2.43	1.56
BF	45	23.09	20.68	25.52	1.32	1.15

Appendix 2

The results of Tukey's HSD test for differences among groups.

Table I. The results of Tukey's HSD test for differences in humerus for five groups.
+ significant ($p<0.05$), o non significant values.

IA: GL in humerus					
Groups	*A. albifrons* ♂♂	*A. albifrons* ♀♀	*B. leucopsis* ♂♂	*B. leucopsis* ♀♀	Nipisat all
A. albifrons ♂♂		+	+	+	+
A. albifrons ♀♀	+		+	+	+
B. leucopsis ♂♂	+	+		O	O
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	O	O	
IB: Bp^1 in humerus					
A. albifrons ♂♂		+	+	+	+
A. albifrons ♀♀	+		+	+	+
B. leucopsis ♂♂	+	+		O	+
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	+	O	
IC: Bp^2 in humerus					
A. albifrons ♂♂		+	+	+	+
A. albifrons ♀♀	+		+	+	+
B. leucopsis ♂♂	+	+		O	+
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	+	O	
ID: Dp in humerus					
A. albifrons ♂♂		O	O	+	+
A. albifrons ♀♀	O		O	O	+
B. leucopsis ♂♂	O	O		O	+
B. leucopsis ♀♀	+	O	O		O
Nipisat all	+	+	+	O	
IE: SC in humerus					
A. albifrons ♂♂		O	+	+	+
A. albifrons ♀♀	O		+	+	+
B. leucopsis ♂♂	+	+		O	O
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	O	O	
IF: Bd in humerus					
A. albifrons ♂♂		+	+	+	+
A. albifrons ♀♀	+		O	+	+

B. leucopsis ♂♂	+	O		O	+
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	+	O	
IG: Dd in humerus					
A. albifrons ♂♂		O	+	+	+
A. albifrons ♀♀	O		O	+	+
B. leucopsis ♂♂	+	O		O	O
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	O	O	

Table II. The results of Tukey's HSD test for differences in femur for five groups. + significant ($p<0.05$), o non significant values

IIA: GL in femur					
Groups	*A. albifrons* ♂♂	*A. albifrons* ♀♀	B. leucopsis ♂♂	*B. leucopsis* ♀♀	Nipisat all
A. albifrons ♂♂		+	+	+	+
A. albifrons ♀♀	+		O	+	+
B. leucopsis ♂♂	+	O		O	+
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	+	O	
IIB: Lm in femur					
A. albifrons ♂♂		+	+	+	+
A. albifrons ♀♀	+		+	+	+
B. leucopsis ♂♂	+	+		O	O
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	O	O	
IIC: Bp in femur					
A. albifrons ♂♂		O	O	+	+
A. albifrons ♀♀	O		O	O	+
B. leucopsis ♂♂	O	O		O	O
B. leucopsis ♀♀	+	O	O		O
Nipisat all	+	+	O	O	
IID: Dp in femur					
A. albifrons ♂♂		O	+	+	+
A. albifrons ♀♀	O		O	+	+
B. leucopsis ♂♂	+	O		O	+
B. leucopsis ♀♀	+	+	O		+
Nipisat all	+	+	+	+	
IIE: SC in femur					
A. albifrons ♂♂		O	O	+	+
A. albifrons ♀♀	O		+	+	+
B. leucopsis ♂♂	O	+		O	+
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	+	O	
IIF: Bd in femur					
A. albifrons ♂♂		O	+	+	+
A. albifrons ♀♀	O		O	+	+
B. leucopsis ♂♂	+	O		O	+
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	+	O	

IIG: Dd in femur					
A. albifrons ♂♂		+	+	+	+
A. albifrons ♀♀	+		O	+	+
B. leucopsis ♂♂	+	O	O	O	+
B. leucopsis ♀♀	+	+			O
Nipisat all	+	+	+	O	

Table III. The results of Tukey's HSD test for differences in coracoid for five groups. + significant ($p<0.05$), o non significant values

IIIA: GL in coracoid					
Groups	*A. albifrons* ♂♂	A. *albifrons* ♀♀	*B. leucopsis* ♂♂	*B. leucopsis* ♀♀	Nipisat all
A. albifrons ♂♂		+	+	+	+
A. albifrons ♀♀	+		O	O	O
B. leucopsis ♂♂	+	O		O	O
B. leucopsis ♀♀	+	O	O		O
Nipisat all	+	+	O	O	
IIIB: Lm in coracoid					
A. albifrons ♂♂		+	+	+	+
A. albifrons ♀♀	+		O	O	O
B. leucopsis ♂♂	+	O		O	O
B. leucopsis ♀♀	+	O	O		O
Nipisat all	+	O	O	O	
IIIC: Bb in coracoid					
A. albifrons ♂♂		O	+	+	+
A. albifrons ♀♀	O		O	+	O
B. leucopsis ♂♂	+	O		O	O
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	O	O	O	
IIID: BF in coracoid					
A. albifrons ♂♂		O	+	+	+
A. albifrons ♀♀	O		O	+	+
B. leucopsis ♂♂	+	O		O	+
B. leucopsis ♀♀	+	+	O		O
Nipisat all	+	+	+	O	

Table IV. The results of Tukey's HSD test for differences in femur for three female groups. + significant ($p<0.05$), o non significant values

IVA: GL in femur			
Groups	*A. albifrons* ♀♀	*B. leucopsis* ♀♀	Nipisat ♀♀
A. albifrons ♀♀		+	+
B. leucopsis ♀♀	+		O
Nipisat ♀♀	+	O	
IVB: Lm in femur			
A. albifrons ♀♀		+	+
B. leucopsis ♀♀	+		O
Nipisat ♀♀	+	O	
IVC: Bp in femur			
A. albifrons ♀♀		+	+
B. leucopsis ♀♀	+		O
Nipisat ♀♀	+	O	

IVD: Dp in femur			
A. albifrons ♀♀		+	+
B. leucopsis ♀♀	+		+
Nipisat ♀♀	+	+	
IVE: SC in femur			
A. albifrons ♀♀		+	+
B. leucopsis ♀♀	+		O
Nipisat ♀♀	+	O	
IVF: Bd in femur			
A. albifrons ♀♀		+	+
B. leucopsis ♀♀	+		O
Nipisat ♀♀	+	O	
IVG: Dd in femur			
A. albifrons ♀♀		+	+
B. leucopsis ♀♀	+		+
Nipisat ♀♀	+	+	

Table V. The results of Tukey's HSD test for differences in humerus for two recent and one sub-fossil pooled group. + significant ($p<0.05$), o non significant values

VA: GL in humerus			
Groups	*A. albifrons* all	*B. leucopsis* all	Nipisat all
A. albifrons all		+	+
B. leucopsis all	+		O
Nipisat all	+	O	
VB: Bp^1 in humerus			
A. albifrons all		+	+
B. leucopsis all	+		+
Nipisat all	+	+	
VC: Bp^2 in humerus			
A. albifrons all		+	+
B. leucopsis all	+		+
Nipisat all	+	+	
VD: Dp in humerus			
A. albifrons all		+	+
B. leucopsis all	+		+
Nipisat all	+	+	
VE: SC in humerus			
A. albifrons all		+	+
B. leucopsis all	+		O
Nipisat all	+	O	
VF: Bd in humerus			
A. albifrons all		+	+
B. leucopsis all	+		+
Nipisat all	+	+	
VG: Dd in humerus			
A. albifrons all		+	+
B. leucopsis all	+		O
Nipisat all	+	O	

Table VI. The results of Tukey's HSD test for differences in femur for two recent and one subfossil pooled group. + significant (p<0.05) o non significant values

VIA: GL in femur			
Groups	*A. albifrons* all	*B. leucopsis* all	Nipisat all
A. albifrons all		+	+
B. leucopsis all	+		O
Nipisat all	+	O	
VIB: Lm in femur			
A. albifrons all		+	+
B. leucopsis all	+		O
Nipisat all	+	O	
VIC: Bp in femur			
A. albifrons all		+	+
B. leucopsis all	+		O
Nipisat all	+	O	
VID: Dp in femur			
A. albifrons all		+	+
B. leucopsis all	+		+
Nipisat all	+	+	
VIE: SC in femur			
A. albifrons all		+	+
B. leucopsis all	+		+
Nipisat all	+	+	
VIF: Bd in femur			
A. albifrons all		+	+
B. leucopsis all	+		+
Nipisat all	+	+	
VIG: Dd in femur			
A. albifrons all		+	+
B. leucopsis all	+		+
Nipisat all	+	+	

Table VII. The results of Tukey's HSD test for differences in coracoid for two recent and one subfossil pooled group. + significant (p<0.05) o non significant values

VIIA: GL in coracoid			
Groups	*A. albifrons* all	*B. leucopsis* all	Nipisat all
A. albifrons all		+	+
B. leucopsis all	+		O
Nipisat all	+	O	
VIIB: Lm in coracoid			
A. albifrons all		+	+
B. leucopsis all	+		O
Nipisat all	+	O	
VIIC: Bb in coracoid			
A. albifrons all		+	+
B. leucopsis all	+		+
Nipisat all	O	O	
VIID: BF in coracoid			
A. albifrons all		+	+
B. leucopsis all	+		+
Nipisat all	+	+	