Defining populations of the Beluga (*Delphinapterus leucas*) using morphometry and ultrastructure of teeth

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ABSTRACT

The population structure of beluga whales (*Delphinapterus leucas*) in the waters of Greenland and the Canadian Arctic has not yet been convincingly established. In this study, an attempt was made to use tooth morphometrics and ultrastructural characteristics to determine whether there was a significant difference between belugas taken in North and Southwest Greenland (Upernavik and Sissimiut municipalities, resp.). Also, a small dataset containing belugas from the Northern coast of Alaska was compared to the Greenland datasets.
Morphometric data indicate that there is indeed a significant difference between belugas in North and South Greenland, as well as between those datasets and the one from Alaska. This might indicate that Greenlandic waters serve as wintering quarters for two different beluga populations, rather than one.
The ultrastructural characteristics as a whole did not yield significant results but this is probably due to lack of focus in the studying process; it is expected that more detailed research will show the value of these characteristics.

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INTRODUCTION

Beluga whales

When venturing up into the Arctic, at the right place and right time, one might very well come across groups of nearly pure white whales, either close to shore or surrounded by pack-ice. If one sticks a hydrophone under water and listens, one will hear an enormous variety of whistles, clicks and gurgles, clearly emitted by these animals. These are beluga whales.

Belugas or White Whales (*Delphinapterus leucas*) are highly social members of the Toothed Whales, or Odontoceti. The species is included in the family Monodontidae together with its close relative, the Narwhal (*Monodon monoceros*) which it closely resembles in general anatomy and lifestyle. Some authors also include the tropical Irrawaddy Dolphin (*Orcaella brevirostris*) in this family, but recent studies using molecular data have cast doubt on this assumption (Lint *et al.*,1992; Martin, 1996).

As toothed whales go, they can be considered somewhat larger than average. Females weigh in at ± 0.4 – 1 tonnes and typically reach 3 – 3.5 metres in length. The males tend to grow larger, up to 4 – 4.5 metres; they might weigh as much as 1 – 1.5 tonnes when fully grown. Their most striking characteristic is their obvious lack of pigmentation, for these animals are almost purely yellowish-white. As newborns, they are still a dark grey, but their skin soon starts to fade to light gray and then to a cream-like white. Apart from that, their thick layer of blubber and their distinct heads (due to a marked discontinuity between head and body, or a "neck") gives them a chubby, slightly obese appearance (fig.1.1). All in all, the only other Arctic species with which this whale could possibly be confused is the Narwhal, and even then only under compromised sighting conditions.

Fig.1.1. General appearance of the beluga (*Delphinapterus leucas*)
(from Darling *et al.*,., 1995)

Distribution

These whales are usually limited to the Arctic and sub-Arctic (Fig.1.2). There has been some disagreement among authors precisely how to classify the distribution of this species: it occurs either circumpolar or amphiboreally along most coasts in this region as well as in open water, the only requirement being leads or holes in the sea ice to breathe. Populations occur along the coasts of Greenland, throughout Canada and Alaska, in the waters around Kamtchatka and the Chukchi Sea, and westward in the Laptev, Kara, Barents and White seas, as well as along the northern Norwegian coast and Spitsbergen. Due to near-permanent ice cover, belugas are not found in the western parts of the East Siberian Sea between the New Siberian islands (roughly 130°E) and the Kolyma delta (roughly 160°E). At the southern end of their range, belugas are normally limited to water temperatures below 15°C (Gurevich, 1980). However, 'wandering' animals have been known to stray far south of their usual range, ending up along the coasts of, among others, Holland and Japan. The southernmost record of a wild beluga comes from Atlantic City, New Jersey (39°22'N) (Anthony, 1928; from Gurevich, 1980).

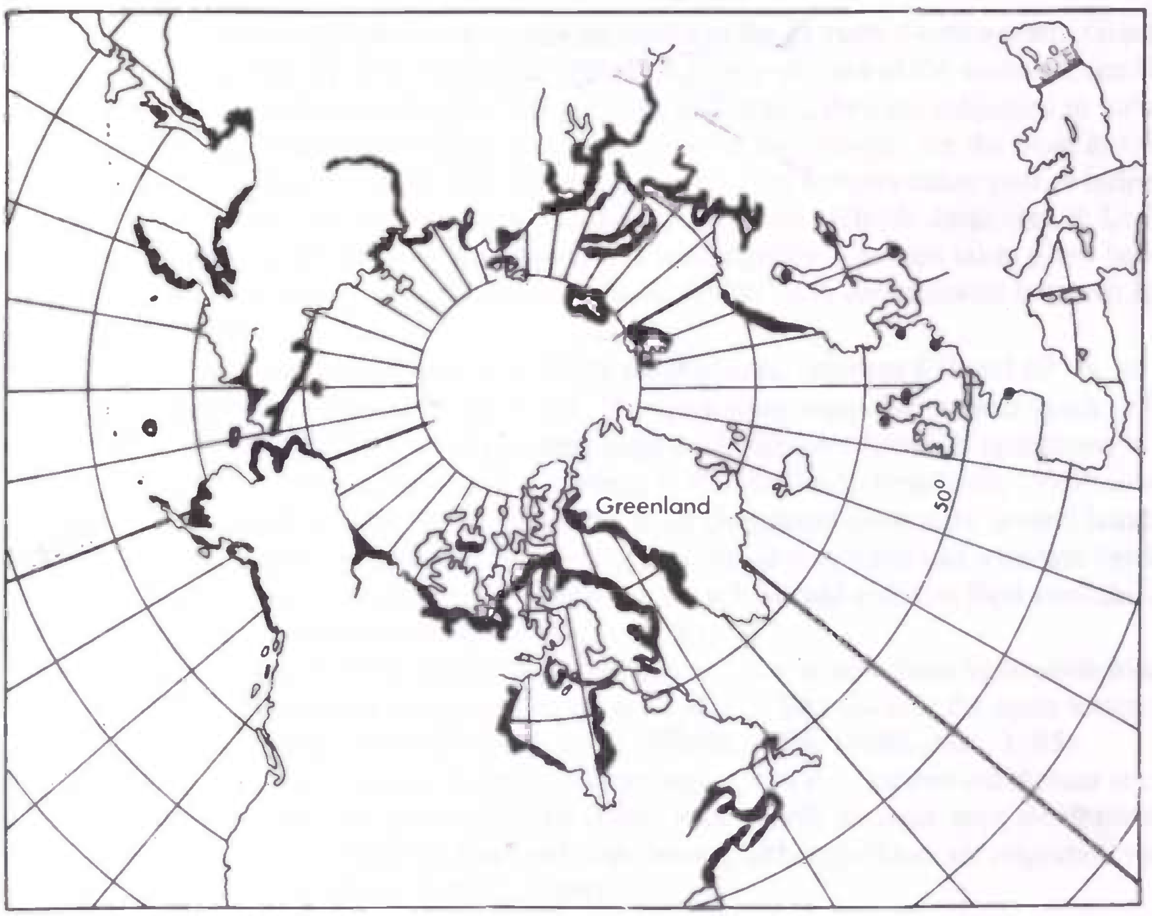


Fig.1.2. Distribution pattern of the beluga (modified after Gurevich, 1980)

Due to the large fluctuations in ice cover in Arctic seas, many beluga populations are migratory, often travelling great distances over a year. By contrast, some populations (such as the animals of the St.Lawrence estuary) are sedentary. For many migratory populations, the exact migration routes and wintering areas are still unknown; this is largely due to the inaccesibility of these areas during winter for detailed scientific study.
The overall population structure of belugas has also been the subject of controversy. In particular, it has long been unclear whether different populations are separated from another to such a degree to warrant the description of new subspecies; these have often been described on the basis of body length. Adjacent populations may vary greatly in size, as seen in, for example, belugas from different locations in Siberia (Klumov, 1937; from Gurevich, 1980; Stewart, 1994). In general, it appears that whales inhabiting waters under oceanic influence attain the largest body sizes, while those whales living in estuarine conditions stay the smallest. Additionally, the level of variability at a genetic level between different populations has been proven to be quite high, implying limited mixing between such populations (O'Corry-Crowe & Lowry, 1997). In short, many populations are, at present, only tentatively identified. This is an unfortunate state of affairs for management purposes.

Belugas in Greenland

The Beluga stock which is of main interest here summers in the extreme Northwestern Greenland (Avanersuaq municipality; fig.1.3), with a probable link to populations in the eastern Canadian High Arctic. As the whales migrate southward ahead of the pack ice in autumn, they are subjected to quite intense hunting pressure by the Inuit communities along the coast; in fact belugas are the most heavily exploited whale species in Greenland waters (Heide-Jørgensen, 1991). The hunters either pursue individual animals by kayak at sea (Sissimiut) or drive entire pods ashore (Upernavik) (Heide-Jørgensen & Lockyer, in press; J.Jensen, pers.comm.). In the north (e.g. in Upernavik municipality) the hunt takes place between September to December, while in the south (e.g. in Sissimiut municipality) it is concentrated between January to May (Berthelsen *et al.*,1989).
Nowadays, most whales winter just south of the Disko Bay area, between 67° and 69° N, in Sissimiut and Maniitsoq municipalities. As recent as the 1920s, Beluga whales were also present south of 66° N, ranging down to Nuuk district and at that time supporting large-scale drivenet fisheries operations in that area. From 18^{th} and 19^{th} century literature, as reviewed by Winge (1902; in Heide-Jørgensen, 1994), it is clear that belugas commonly ranged down to 60° N along the West Greenland coast only several hundred years ago. Even though changing seawater temperatures during this period may have had a certain detrimental effect, it can safely be assumed that increased hunting pressure from Inuit and reduced food availability due to overfishing by Western agencies contributed to this decline.
The spring migration of most West Greenlandic belugas appears to take them back north along the coast up above the Disko Bay area, where they presumably cross Baffin Bay towards the open waters around Thule and the Lancaster Sound area (Heide-Jørgensen & Teilmann, 1994; Smith *et al.*, 1985).
On the East Greenland coast, belugas are rare, presumably due to the extreme conditions encountered in this area, as well as a general lack of suitable habitat (Dietz *et al.*,1994). Belugas seen along the eastern coast probably represent stragglers from the Svalbard populations, although the exact migration route of the latter population is still unknown (Gjertz & Wiig, 1994).

In general, the current status of the "Baffin Bay stock" (considered to comprise all belugas along the West Greenland coast and those in the Canadian High Arctic) is considered 'vulnerable': the large catches being made annually along the Greenland coast very probably exceed the net recruitment rate (Heide-Jørgensen & Reeves, 1996; Heide-Jørgensen & Lockyer, in press).

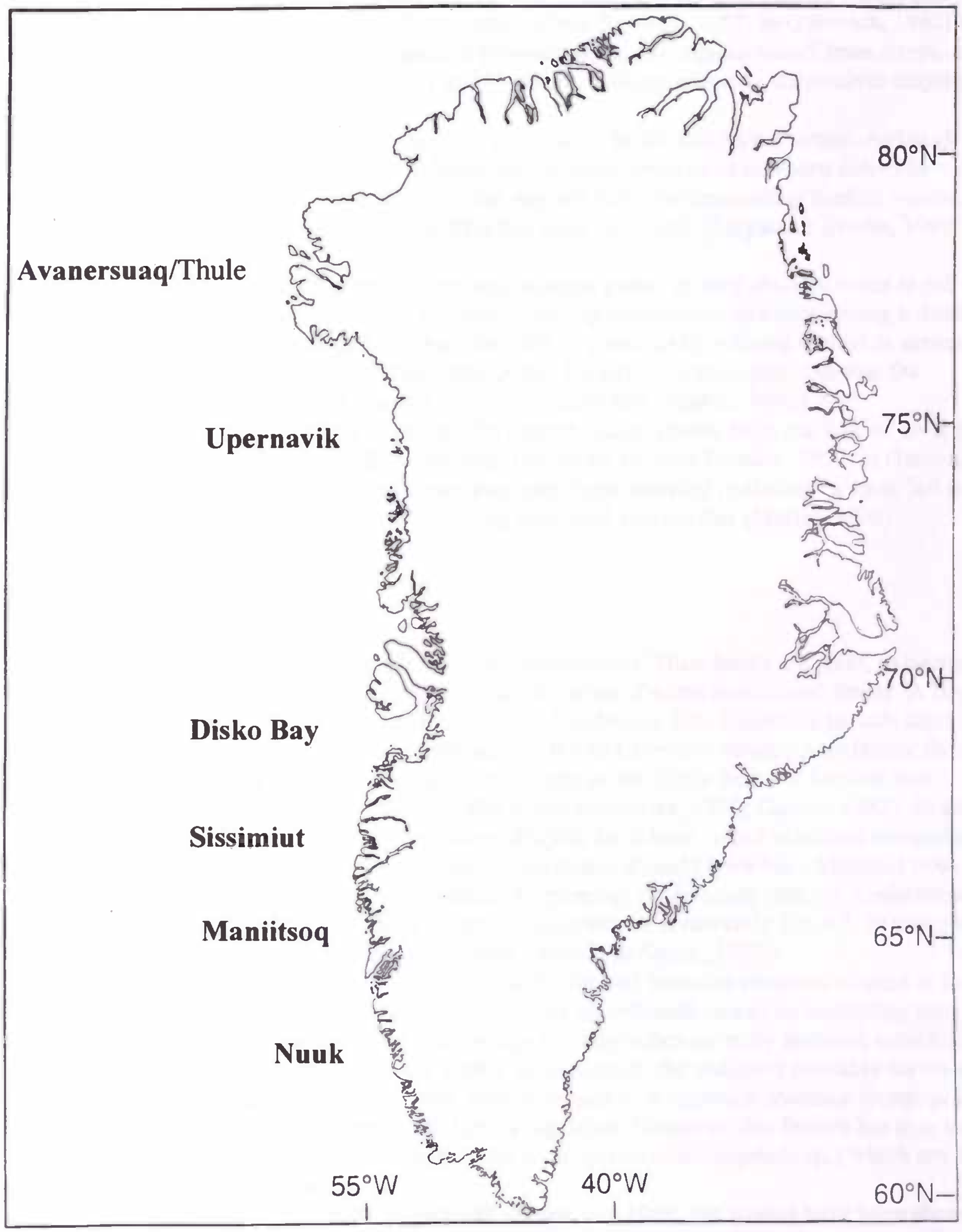


Fig.1.3. An overview of Greenland, showing locatities (muncipalities) mentioned in the text.

In their summering areas, belugas will often come as far inland as the retreating ice cover permits them (Smith & Martin, 1994). Large groups of whales aggregate in summer in shallow coastal waters and bays. There are presumably several reasons for this. Some authors (e.g. Tomilin, 1957; in Gurevich, 1980) have speculated that the high concentrations of plankton in these areas, due to organic runoff from rivers, attract species such as Arctic Cod (*Arctogadus glacialis*) and Capelin (*Mallotus villosus*), themselves major prey items for belugas.
A different incentive for the whales to congregate here might have to do with reproduction. Although few beluga births have been witnessed, many of the whales seen in these areas have newborn calves in attendance. It is thought that the river water is somewhat warmer than the surrounding marine waters, and that this would give neonates an advantage in their first few days after birth (Sergant & Brodie, 1969; Martin, 1996).
In recent years, the theory that, at least in some locations, belugas gather in very shallow water to rub off molting skin has gained wider support. Belugas are unique among odontocetes in experiencing a distinct annual molt of their outer skin (Martin, 1996), which they try to speed up by rubbing their skin across coarse sediment. Presumably this is facilitated by fresh water. Finally, it is quite probable that the aggregation in these locations also serves a social purpose of some sort (Martin, 1996).
Beluga whales are often seen far upstream in rivers. The current record comes from the Argun' river in Siberia, where a beluga was spotted about 2000 km from the Arctic Ocean (Tomilin, 1957, in Gurevich, 1980). Their habit of frequenting coastal areas sometimes gets them stranded in shallow waters, left behind by the tide. If they are not harrassed during low tide, they may well survive this (Martin, 1996)

Diet

Beluga whales appear to be rather catholic in their dietary preferences. Their beaks are short, in contrast to the elongated beaks of pelagic piscivorous delphinids: an indication of a less specialised feeder. A large fraction of their diet consists of various species of benthic and midwater fish. Examples include sand lance (*Ammodytes americanus*) and capelin (*Mallotus villosus*) for the St.Lawrence estuary population; flatfish, cod (*Gadus morhua*) and herring (*Clupea harengus*) for belugas in the White Sea; and keta salmon (*Oncorhynchus keta*) for the population around Sakhalin Island (Gurevich, 1980; Gaskin, 1982). In addition to this, various benthic invertebrates, as well as remains of squid, have been found in beluga stomachs (Heide-Jørgensen & Teilmann, 1994). Although some of this material could have been liberated from fish stomachs, it seems that these prey items are an important supplement for foraging belugas. Unfortunately, knowledge of the benthic ecosystem in the High Arctic offshore waters is currently limited, so that most of our knowledge is derived from beluga stomach dissections (Martin & Smith, 1992).
Additional evidence for a benthic foraging technique could be derived from the presence of sand in the stomach. This is usually presented as evidence for the handling of sediment-coated or burrowing prey (Gurevich, 1980). Partially as a consequence of this, beluga teeth are often severely abraded, sometimes worn down to the gumline in old animals (Martin, 1996). Additionally, the sediment probably serves as a gizzard, as also seen in many birds; stones and sand, moved around by a muscular stomach lining, grind the food into small fragments which are then ready for further digestion. However, this feature has also been observed in Harbour Porpoises (*Phocoena phocoena*) and Pilot whales (*Globicephala* sp.) which are not primarily benthic foragers (Slijper, 1962).
Acquisition of this prey can take place both inshore and in open sea. Here, the whales have been shown to routinely reach depths of 350 m, presumably foraging on the sea bed (Martin,1992). However, studies with belugas wearing satellite-linked dive recorders in offshore conditions have shown that the whales are capable of reaching depths of at least 872 m (Heide-Jørgensen *et al.*,1998; Martin, 1992).

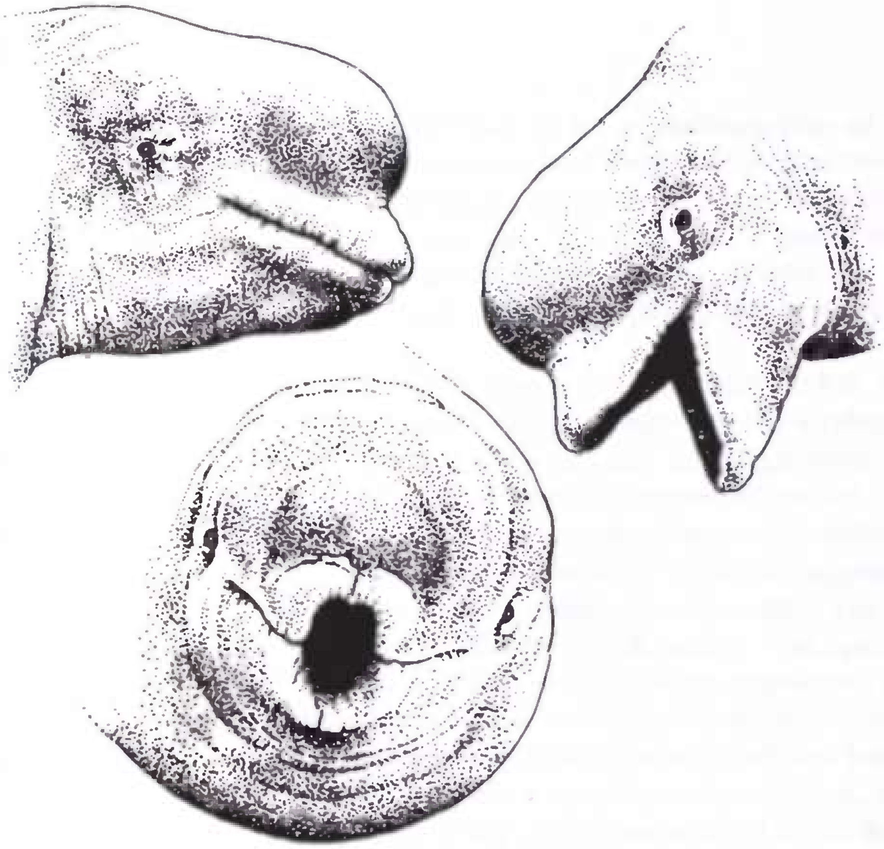


Fig.1.4. Examples of different facial expressions in belugas (from Macdonald [ed.], 1984).

Belugas are unusual among whales in possessing flexible labial musculature (Martin, 1996), thus being capable of changing the shape of their lips (fig.1.4). This feature, particularly apparent in oceanaria, permits them to show a number of different facial expressions. It also enables them to squirt jets of water from their mouth with surprising accuracy, and it is generally assumed that this adaptation (shared only with the Irrawaddy dolphin) serves to uncover burrowing prey items from the sea bed .

Human influences

Belugas have constituted a major part of the diet of many indigenous Arctic peoples for at least several 100 years (but see Savelle (1994) for a critical review). Western whalers started taking substantial numbers of Beluga from the second half of the 19th century onward, because of the depletion of local Bowhead stocks, and also because they were considered a nuisance and competition with fishermen. In addition, large industrial projects connected with mining and prospecting for gas or oil in the Arctic have put a high pressure on most, if not all, populations, not in the least due to soaring pollution levels. It is obvious that this species requires close monitoring in order to keep populations from decreasing. Migratory stocks are the most vulnerable, because they are usually subject to a large number of threats over the course of their journeys.

It is in this regard that it has become highly important to find out exactly how the different Beluga populations are faring, so they can be managed accordingly. Unfortunately, as indicated earlier, knowledge of population structure in Beluga is somewhat patchy; in some cases it is even unclear how many populations there are (Gurevich, 1980).

Beluga teeth

For conservation purposes, it is necessary to get an understanding of how populations are built up; that is, what the age-classes are. Cetaceans have always been considered notoriously difficult in this respect because, until comparatively recently, no method existed to accurately calculate a whale's age. As early as the 19th century, zoologists had noted that when Odontocete teeth were cut transversally, a pattern of light and dark (or, in thin sections for microscopical imaging, opaque and translucent) lines could be seen. Such a pattern was later also shown to exist in the earplugs and baleen strips of Mysticetes (see Gaskin, 1982, for a historical overview).
Since whales are homodont (i.e. teeth keep growing throughout life, and "milk teeth" are absent), it was not a big step to assume that these incremental lines were somehow related to life history events, and could therefore give a reliable indication of a whale's age. Although some uncertainty still remains, it has been generally agreed that, in the great majority of whale species studied, one set of light and dark layers gets laid down each year. Such a set of lines is nowadays commonly called a Growth Layer Group, or GLG (Perrin & Myrick, 1980). A considerable amount of evidence suggests, however, that belugas are unique among Odontocetes in that two GLG's are being laid down each year.
The exact process that causes GLGs to form is still unclear. The opaque and translucent bands seen under a microscope correspond to regions of the tooth which are, respectively, rich and poor in calcium. This would seem to be directly influenced by the levels of calcium ions in the bloodstream during the deposition of the layer, and thus directly to the animal's overall physical condition. Important events in an animal's life, such as birth, sexual maturity, food depletion, pregnancy and parturition, all have a direct influence on the Ca-content of the blood, and thus might in principle be detected in the deposition pattern in the teeth. In one such case, involving teeth of a Dusky dolphin (*Lagenorhynchus obscurus*) from Peru, it was even possible to find evidence of the 1982 – 1983 El Nino event, which led to a decline in prey stocks and, presumably, was the cause of decreased Ca-deposition or active resorption (Manzanilla, 1988).
As mentioned before, in the case of the Beluga, it has long been a subject of controversy as to how many GLGs are actually deposited annually (Goren *et al.*, 1987; Brodie *et al.*, 1990; Heide-Jørgensen *et al.*, 1994). Opinions have by now converged on the formation of 2 GLG's per annum; this research was greatly facilitated by the use of teeth from two captive whales of (approximately) known age (Lockyer, pers.comm.).

Beluga teeth are made up of dentine, surrounded by cementum, which is built up (as are bone and enamel) by odontoblasts out of hydroxyapatite crystals. Each such crystal is composed of several thousand unit cells, built up of $3Ca_3(PO_4)_2 \cdot Ca(OH)_2$ (Bhaskar, 1976). In cross-section, the GLGs stand out clearly; the overall impression is that of a series of cones stacked on top of one another. No enamel cap is present, which is unusual for odontocetes (although the general buildup of the tooth resembles that of the sperm whale; Lockyer, pers.comm.).
The odontoblasts are situated in the pulp cavity, from where they secrete the dentine. From each cell emanates a tubule, through which the cells stay in contact with the outermost layer of dentine. The cementoblasts are situated around the root of the tooth on the outside (Bhaskar, 1976).

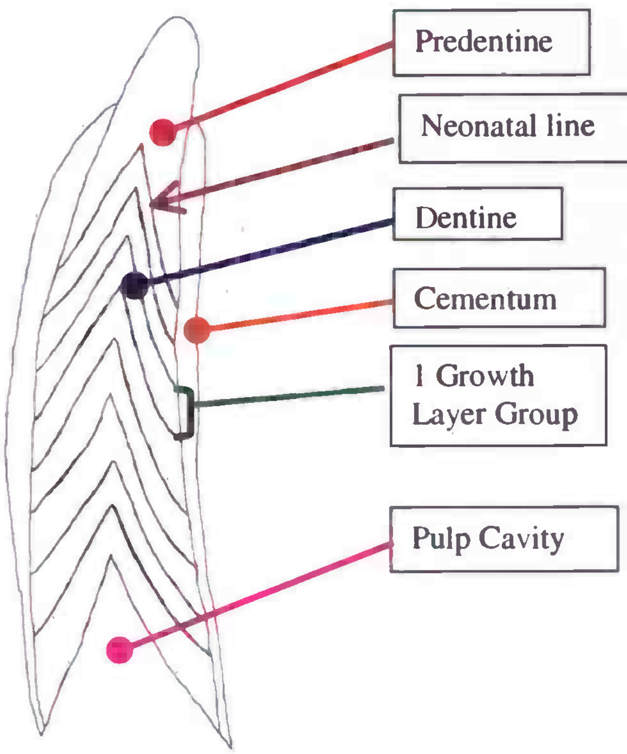


Fig.1.5. A generalised overview of a beluga tooth section (adapted from Brodie *et al.*, 1990). The animal possesses 8 GLGs + 1 Neonatal line, so it would be ± 4 years old.

The tip of the tooth is initially covered with prenatal dentine or predentine, which – in cross-section - is bordered at the bottom by a distict linear feature: the neonatal line (fig.1.5). This indicates the animal's birth, and serves as a reference to calibrate the GLGs. In older animals (possessing about 20 GLGs; Heide-Jørgensen *et al.*, 1994) the prenatal dentine has worn down to below the neonatal line, thus obscuring the earliest GLGs; this can result in an underestimation of the animal's age. The amount of wear that teeth have been subject to is not only correlated with the age of the animal, but also with the position of the teeth in the jaw, as well as the abrasiveness of the ingested material. In general, the teeth in the middle of the mandible are not only the largest, but also the least worn (Heide-Jørgensen *et al.*, 1994). The pulp cavity of the teeth gradually becomes shallow with age, but does not occlude as, for example, in members of the genus *Stenella* (Sergeant,1973); this means that additional GLGs continue to be laid down. In old animals (possessing > 30 GLGs) this can result in very closely packed dentinal lines, which can be quite difficult to read accurately.

The cementum also shows GLG banding, but this can be complicated to read. Unlike most small cetaceans, the cementum surrounding the dentine can become quite thick.
GLGs are most easily counted in the dentine, while counting the cementum can often be difficult due to the closeness of the lines. Counting the cementum can still provide a valuable addition/calibration of the dentine counts, however.
Apart from GLGs, other, more anomalous characteristics, previously described in other species, also occur in beluga teeth, for example pulp stones (concentric inclusions of errant material in the dentine of odontoblastic origin), marker lines (distinct layers in the tooth, different from the boundary layers in the GLGs), or dentinal resorption (disturbance of laminated dentinal tissue); for a comprehensive overview, see Lockyer (1993; 1995).
Research by Lockyer on teeth of Harbour Porpoises (Lockyer, 1995) indicated that it was, in fact, possible to distinguish between subpopulations on the basis of anomaly incidence in tooth morphology. Such a tool has obvious potential in species management.

One of the reasons for this study was the conviction by several workers in the field (notably J.Jensen) that animals from different locations could be readily identified by the general appearance of their teeth. Therefore, this study attempted to discern whether teeth from previously recognised Beluga subpopulations do, in fact, exhibit distinct morphological characteristics which can be used to define these subpopulations. I did this by studying beluga teeth from 2 different locations along the West Greenland coast (specifically, from Upernavik and Sissimiut municipalities), as well as material from the Northern coast of Alaska. Part of the material was sectioned but otherwise left untreated, while the remainder of the tooth was cut into thin sections, decalcified and stained. The untreated sections were studied using polarised light to enhance contrast, while the stained sections were studied in normal transmitted light.

MATERIALS & METHODS

Selection of specimens

The teeth which were used in this study were part of a large collection of Beluga tooth specimens, consisting of the untreated teeth from the two mandibles of each animal, which had been taken by native Inuit hunters during the whales' annual migration down the West Greenland coast in the early 1990's (this material had previously been used by Heide-Jørgensen *et al.,* (1994) in their age analysis). A considerable fraction of this material had been collected by the hunters themselves, who did not necessarily share (among others) Heide-Jørgensen *et al.,*'s interest in obtaining the entire jaw. Many specimens, therefore, only consisted of the teeth from the front half of the mandible (No. 1 – 5, counted from the front).

From each such specimen, at least one tooth had previously been cut on a Buehler Isomet precision saw, to acquire a thin (150 – 200 μ) section for imaging under a polarized light microscope (these particular teeth were stored in a mixture of water and glycerol at room temperature, while the remaining teeth of each specimen were stored in a deep freezer at –20 - –25°C. Additional (haplotype) information was available for a relatively small subsample (n = 60); this group served as the basis for my analysis, to which other animals were later added.

Age analysis on beluga is often hampered by the fact that their teeth are often severely eroded, up to the point when the neonatal line (indicating the animal's birth) has completely worn away. From that point on, only the animal's *minimal* age can be established by reading the dentinal GLGs. In general, the teeth near the front of the jaw are worn down most, while those near the back are usually worn least. However, the latter are often rather small and therefore difficult to read. For this reason, it was attempted to secure teeth from a middle position (4 – 7) for each specimen. Unfortunately, the breakdown of the Isomet 1000 precision saw made it impossible to achieve this.

From the rather large collection, it was decided to take a smaller subsample and subject this to more detailed analysis. The entire collection was first divided up into 6 different age categories: 0-<4, 4-<8, 8-<12, 12-<16, 16-<20, and 20-<24. Insufficient animals of higher age were present in the dataset to justify the formation of an older age group. Subsequently, each of these age groups was composed of 8 animals. In the ideal case, these animals were all captured in the same season, but due to the imperfection of the dataset, several adjustments to this ideal had to be made. For instance, several age groups of both populations had to be "filled up" by admitting animals which had been caught several years before. This might constitute a flaw in the data. On the other hand, where more than 8 animals were present (as was the case in the younger age groups), a subset was arbitrarily sampled using a random number generator. In three cases (the Upernavik age groups "16-<20" and "20-<24", as well as the Sissimiut age group "20-<24") the desired number of 8 constituents of the subsample was not reached, due to unavailability of specimens. The disappearance of the neonatal line in older animals (usually over 10 years old), which made it impossible to estimate their exact age, introduced another error in the data; for these animals, only minimum age could be inferred. Yet another bias presented itself when teeth from two previously selected specimens from the highest age categories (Upernavik 5 and 6) turned out to be too large; the sections would not physically fit onto the slides. For this reason, these specimens had to be discarded from the subsample, although there was no replacement available. This reduced both age groups to 7 specimens. All in all, for most analyses each area subset consisted of 46 animals.

In addition, the complete tooth sets of 4 animals were prepared, to test for possible differences in layer deposition, special characteristics, etc. in teeth at different positions in the jaw.

Finally, a dataset acquired by Lockyer on beluga teeth from Alaska (and checked for the same parameters) was also included. This dataset consisted of 24 animals of unknown sex. Analysis of these teeth generally focused on parametric data, which were used to compare them with both Greenlandic groups.

Methods

To test different treatment methods, teeth were prepared in the following way. Using thermoplastic cement (Buehler ltd.), untreated teeth were fastened to a home-made 4 cm-long wooden block, which fit in the chuck of a Buehler Isomet™ 1000 precision saw. If possible, teeth were positioned with their lingual side facing the blade; this usually produced cleaner cuts.

Thin sections (150 – 200 μ) were made using a 4" cutting blade, at 300 – 450 rpm. Teeth were cut through the crown and root so that the section was close to the midline, exposing as much of the internal structure and the pulp cavity as possible. These sections were subsequently studied under polarized light, using a Leica MZ-12 microscope. Particularly fine examples of internal structures were imaged using a video camera, and prepared for presentation.
The remaining halves of the untreated teeth were removed from their encasings, subsequently placed in perforated plastic histological containers (perforated plastic bags, in the case of large teeth) and labeled. To reinforce their internal structure, the teeth were placed overnight in a 4% formalin solution; this measure was introduced after several specimens produced extremely fragmentary sections.
After this treatment, the teeth were placed in RDO (a commercially available decalcification agent) for a restricted period of time, depending on the volume of the specimen; normally, this treatment did not exceed 24 hrs. After this period, decalcification effectivity was tested by gently attempting to flex the tooth laterally. Only in the case of very large teeth, frequently encountered in old animals, was the immersion period extended to approx. two days. On some occasions, the teeth were stored in a mixture of tapwater and alcohol to conserve them, so that cutting could take place the following day.

The decalcified tooth halves were subsequently mounted on the cutting stage of the MSE freezing microtome, using a commercially available mounting medium (Bright Cryo-M-bed Embedding Compound). This was allowed to freeze over, applying a cryospray (Bright No. 22) to speed up the process.
In general, tooth halves were mounted with the strongest curved side facing the blade. This served to facilitate the cutting process, although its effect in small teeth may have been limited.
Teeth which were mounted so were subsequently cut in 50 μ increments, until a clear-through cut of the entire tooth had been achieved. The knife settings were then adjusted to 25 μ, although this proved to be unworkable in some very fragile teeth (i.e. only delivered partial sections). An attempt was made to acquire a minimum of six relatively clear and legible cuts, but this was sometimes impossible to achieve.
The knife used in the freezing microtome was replaced and sent away for resharpening after approx. 50 teeth had been cut. Since several replacements were available, this did not seriously hamper proceedings.

Unfortunately, in the case of the largest teeth (often belonging to the oldest specimens) the freezing capacity of the microtome was inadequate to ensure complete, thoroughly frozen specimens. As such, sections obtained from these teeth were very fragile and seldomly complete. It was experiences such as these that prompted the decision to include a formalin treatment in the entire procedure.

Once enough thin sections had been prepared, the microtome was temporarily shut off. The sections were placed in new histological containers, wrapped in pieces of fine nylon mesh (to prevent loss of samples), and placed in Ehrlich's haematoxylin for staining. The time needed for staining depended on the degree of "ripening" the stain had undergone; on several occasions, teeth had to be incubated for 2 – 3 days to produce the desired effect. After this treatment, the teeth were placed in water (of alkaline pH), to "blue" and enhance the contrast in the specimens.
The stained sections were then brought upon 4 % gelatin-coated microscope slides (76 x 40 mm) and briefly allowed to dry. When the sections had dried sufficiently (this was left to the discretion of the observer), they were mounted permanently using DPX mounting medium and glass cover slips (40 x 50 mm). These sections required several days to harden off completely.

Stained sections were imaged with a Meiji Techno Binocular microscope, under 15 x magnification. A standardized form was used to record data (for a complete overview, see Appendix 1).

In the original experimental setup, it had been proposed to let the dataset consist entirely of new specimens. Unfortunately, the untimely breakdown of the Isomet™ precision saw forced us to rethink this plan and come up with a different approach. In the new setup, untreated sections (for microscopy under polarizing light) would be taken from those teeth already sectioned by Heide-Jørgensen *et al.*,(1994). Most of the remaining material of these teeth was still available, so one remaining half of each tooth was subsequently decalcified, sectioned and stained. A small number of teeth which were deemed absolutely necessary for further analysis and could not be cut at our facility were taken to the United States (Southeast Fisheries Science Center, NMFS, 101 Pivers Island Road, Beaufort, North Carolina 28516-9722, USA) to be prepared in close collaboration with Dr. A. Hohn.

Parametric Data

From all the selected specimens from the Upernavik, Sissimiut and Alaska areas, three measurements were taken to establish the general proportions of the tooth (also fig.2.1):

- ✧ Maximum Width of Cementum, taken at the *widest* part of *one side* of the cementum, at a right angle to an imaginary line running through the middle of the dentine, from tooth tip to center of pulp cavity.

- ✧ Maximum Width of Dentine, taken at the *widest* part of the dentine, between the first cemental GLG on either side, at a right angle to an imaginary line running through the middle of the dentine, from tooth tip to center of pulp cavity.

- ✧ Maximum Length of Dentine, taken from the tip of the tooth to the dentine at the tip of the *opposite* edge of the pulp cavity. In young animals, predentine was also measured.

These three values were used to calculate the following ratios:

- ✧ Maximum Width of Cementum vs. Maximum Width of Dentine, essentially a way of scaling growth of cementum against growth of dentine.

- ✧ Maximum Width of Dentine vs. Maximum Length of Dentine, which served as a general quantifier for tooth size.

In general, the measurements were taken from untreated sections, because these represented the best approximation to the midline of each specimen. The measurements were generally taken using an in-built micrometer in the binocular's eyepiece. For the Maximum Length of Dentine-measurement, a 5 cm calibration unit was used in unison with the aforementioned micrometer.

Non-parametric Data

By far the largest amount of data gathered in these experiments was non-parametric in nature (also fig. 2.2). Characteristics which were recorded in this way included the following:

<u>Dentinal GLGs</u>: The number of GLGs in the dentine was counted 2 –3 times, to arrive at an "average" count. Also, the <u>Boundary Layer</u> defining each GLG was checked for clarity, colour and possible replication (also fig.2.3, 2.4). If present, the neonatal line (NL) was recorded, as was the extent of wear at the tip.

<u>Cemental GLGs</u>: The number of GLGs in the cementum was counted 2 – 3 times, just as the dentine.

<u>Marker lines</u>: The dentine was searched for the presence and position of Marker Lines. These are distinct lines in the GLG which are not related to the boundary layer, but nevertheless show distinct staining affinity. These lines can be either light or dark.

In the cementum, comparable layers are named Darkly Staining Layers (DSL); their general presence was also noted.

Accessory lines: The dentine was searched for the presence and relative abundance of Accessory lines in the area beneath each Boundary Layer. Such lines run parallell to, but are much less prominent than, the Boundary Layers; they often occur in great numbers.

Tooth shape, size and clarity: The clarity of the entire tooth was noted, as well as the shape of the entire tooth and that of the tip. This gives information on the speed of erosion.

Pulp stones: These concretions form when odontoblasts get loosened from their basal tissue and become enclosed in the dentine. These cells keep on secreting dentine of their own, eventually leading to concentric nodules in the dentine. These objects can appear in animals of all ages, but are usually found in older animals. Pulp stones do not occur in cemental tissue (Bhaskar, 1976; also fig.2.3, 2.4).

Pathologies: The dentine was scanned for two different types of pathologies:

1) dentinal resorption, in which dentinal tissue has been resorbed and repaired, resulting in disruption of the GLG pattern (Lockyer, 1995).

2) mineralisation interference, in which GLG deposition has been disrupted, resulting in irregular wavy GLG patterns; in most cases, the lines themselves are uninterrupted (Lockyer, 1995)

An example of the difference between untreated and stained sections can be seen in fig.2.3. Fig.2.4 shows a second example of a stained section, in which several characteristics mentioned above stand out quite clearly.

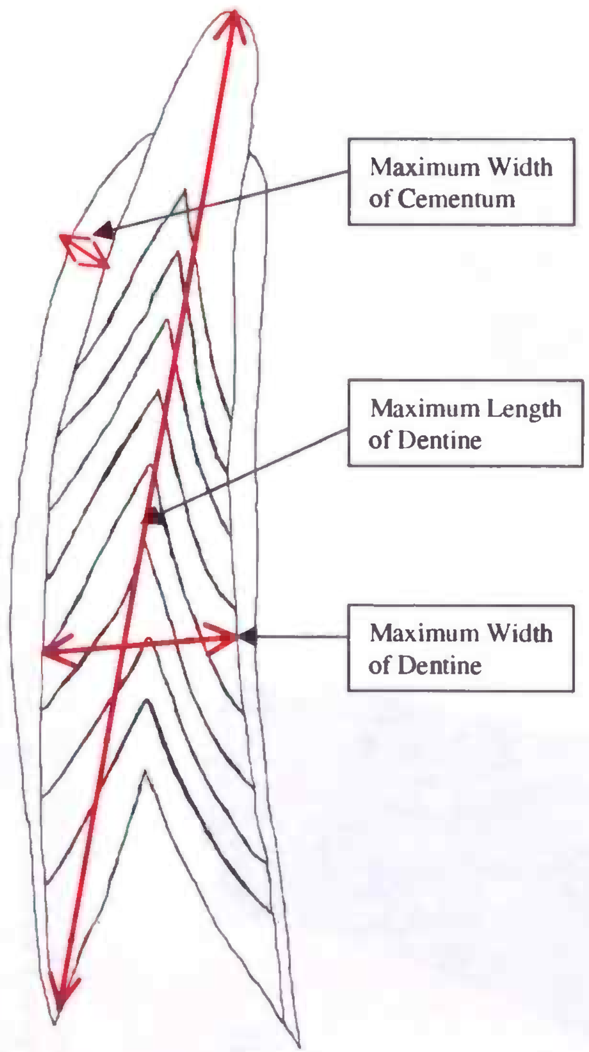


Fig.2.1. A schematic overview of the measurements taken from every tooth (mm).

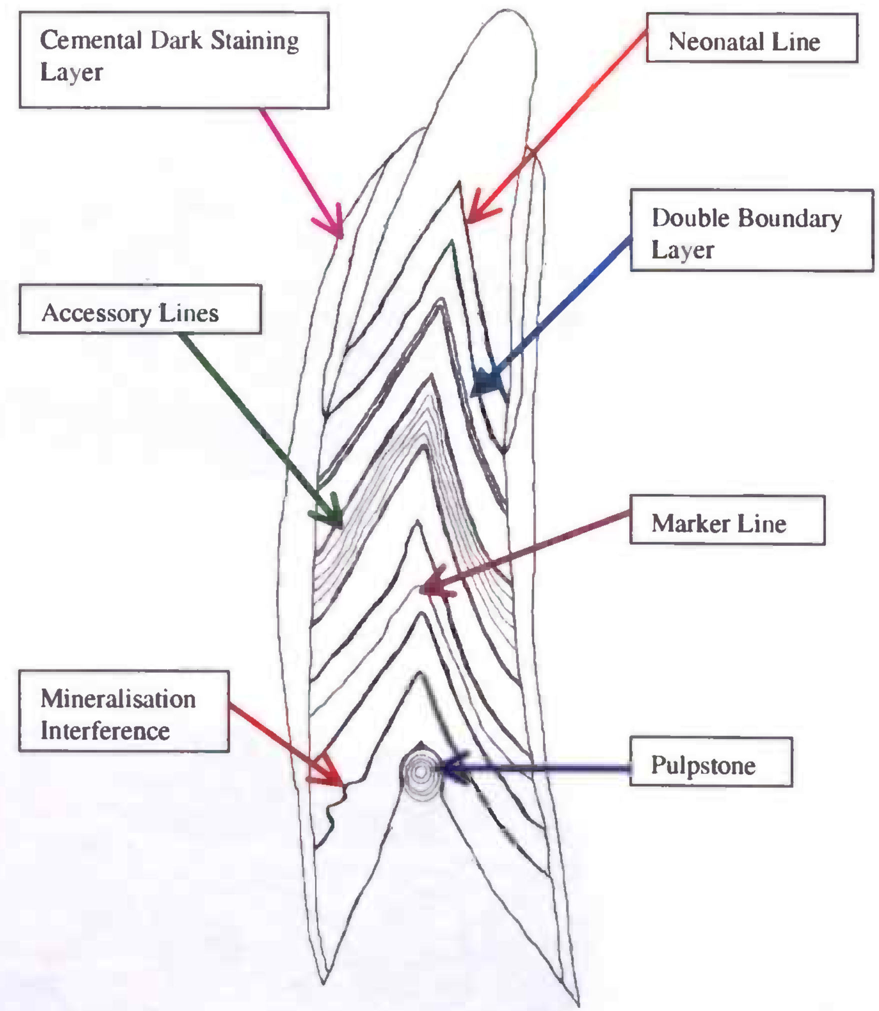


Fig.2.2. A schematic overview of different types of anomalies encountered in beluga teeth.

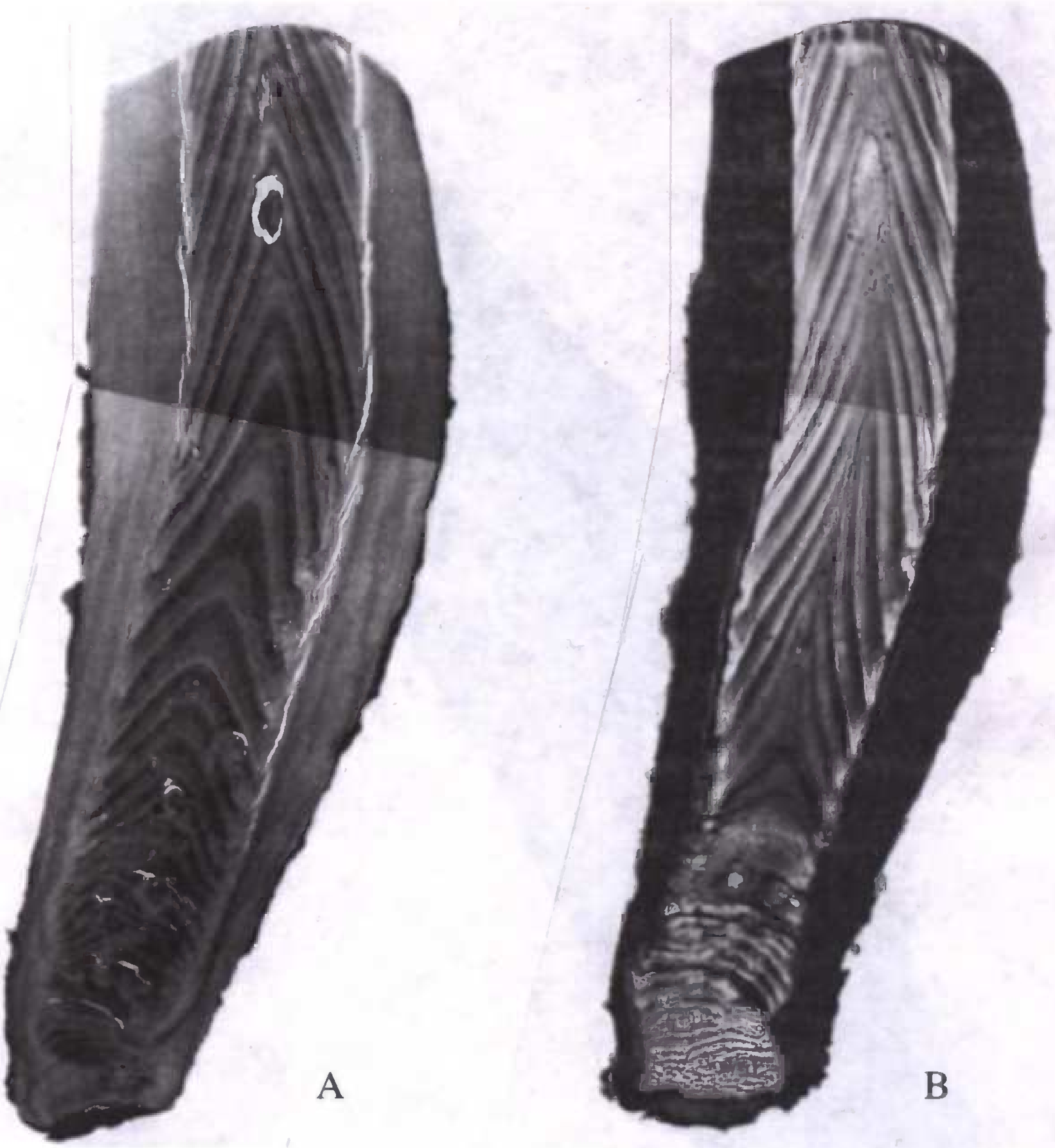


Fig. 2.3. Stained (A) and untreated (B) sections of Sissimiut-2331 (H5). Tooth size ≐ approx. 3 cm from root to tip. There are clear differences in readability between the two sections; many details do not show up in the untreated section. Note the twists in the dentinal column near the pulp cavity; these are more pronounced in (A) than in (B), because the latter section was taken closer to the midline (note also the difference in shape of corresponding GLGs in the dentine). The single pulpstone near the tip is apparent in both sections. Picture courtesy Dr.Aleta Hohn.

Fig.2.4. Stained section of Sissimiut-2337 (V6). Tooth size = approx. 3 cm in this picture. Of note are the distinct dentinal GLGs near the tip, with many Double (Light) Boundary Layers. Several large clusters of Pulpstones are also present. Picture courtesy Dr.Aleta Hohn.

Recording procedures

The characteristics described above were recorded in the following way:

Dentinal GLGs – a count of the GLGs in the dentine was conducted, as thoroughly as the material permitted, preferrably from untreated sections.

Cemental GLGs – a count of the GLGs in the cementum was conducted, as thoroughly as the material permitted, preferrably from untreated sections.

Clarity of GLGs – The Clarity Index of each specimen was recorded on a three-level scale:
1 (poor)
2 (moderate)
3 (clear)
Intermediate classification (1-2 and 2-3) was also possible and depended on the reader. This analysis was performed using stained sections

GLG type – The type of GLG bundary layer was recorded (Light, Dark or Mixed (Light and Dark)) using stained sections.

Boundary layer – The presence of Single, Double and Triple boundary layers was recorded using stained sections. In addition, the colour of boundary layers was recorded for the whole tooth (Light, Dark and Mixed (Light and Dark)).

Accessory lines – The presence of accessory lines was recorded on a four-level scale:
0 (not visible)
1 (few)
2 (several)
3 (many throughout)

Tooth shape – A general description was given of both the general tooth shape and the shape of the tip in cross-section.
Tooth shape categories were established by observing the curvature of the tooth with respect to the pulp cavity. In essence, a straight line was drawn alongside the cementum surrounding the pulp cavity; if the tip of the tooth curved, but did not cross this line, the specimen was labeled "Slightly Curved". If the tip did cross this line, it was labeled "Strongly Curved". Where no significant curvature was obserevd, the specimen was labeled "Cylindrical".
The presence/absence of the neonatal line, as well as the relative amount of wear, was noted. If the predentine had not yet worn away to expose the 1st GLG, the specimen was noted as "unworn". All this was done on untreated sections.

Pulpstones – The occurence of pulpstones was rated on a four-level scale:
– (none present)
+ (few/discrete)
++ (several/diffuse)
+++ (many throughout)

Also, a statement was made on the appearance of the pulp stones:
C (clusters)
S (single)
R ("root" or occuring in the pulp cavity)
Both stained and untreated sections were used for this analysis.

Cemental characteristics – The presence/absence of Dark Staining Layers in the cementum was recorded, using stained sections.

Marker lines – the presence and colour (dark vs. light) of marker lines, as well as their approximate position in the tooth, were recorded, using stained sections.

Mineralisation interference – The presence/absence of any mineralisation interference was recorded (+/-) using stained sections, although untreated sections were used to double-check.

Dentinal resorption – The presence/absence of dentinal resorption was recorded (+/-) using stained sections, although untreated sections were used to double-check.

Statistical analysis

The data gathered in the fashion decribed above were subjected to several forms of statistical analysis. For parametric data, trendline analysis at age was usually the first method used. Additional information was obtained using Z- or t-tests, when necessary. Sometimes a. Analysis of Variance was also performed.
By far the most important test for goodness of fit using non-parametric data was the Chi-square test.
All tests, together with the accompanying statistical background, were derived from Zar (1984) and Fowler & Cohen (1992).

RESULTS

Readability of the material

Most of the material used to make stained sections originated from teeth which had already been cut (to obtain an untreated section) with the precision saw. This naturally meant that a large part of the tooth's midsection had been either cut away or destroyed in the process. Unfortunately, many of the older teeth tended to consist of a comparatively thin cone or cylinder of dentine, surrounded by a thick layer of cementum. The thin sections from the freezing microtome were thus often taken from less desireable areas surrounding the midsection. This meant that such sections sometimes did not contain the entire succession of GLGs, which rather limited their use. In such cases, the untreated sections provided most of the useful information.

Readibility could also be hampered by errors made during the staining process of the thin sections. One such frequently encountered error was *overstaining*, in which case the sections had been left in the haematoxylin for too long. This resulted in extremely dark specimens, which were often quite difficult to read.
Other specimens were found to be stained in a strong reddish hue, rather than the desired purple – blue one. This was due to a too short an incubation time in water, after haematoxylin staining. These specimens were often lacking in general contrast.

A recurring problem when reading GLGs in beluga is that the teeth tend to erode rather rapidly, destroying the neonatal line at a relatively young age (Heide-Jørgensen *et al.*, 1994). Apart from the obvious fact that this makes it impossible to know the animal's exact age, it also made it difficult to decide whether Boundary Layers are, in fact, dark or lightly coloured at their apical edge. In some cases, where both parts of the GLG were approximately equal in thickness, this could be very frustrating indeed.

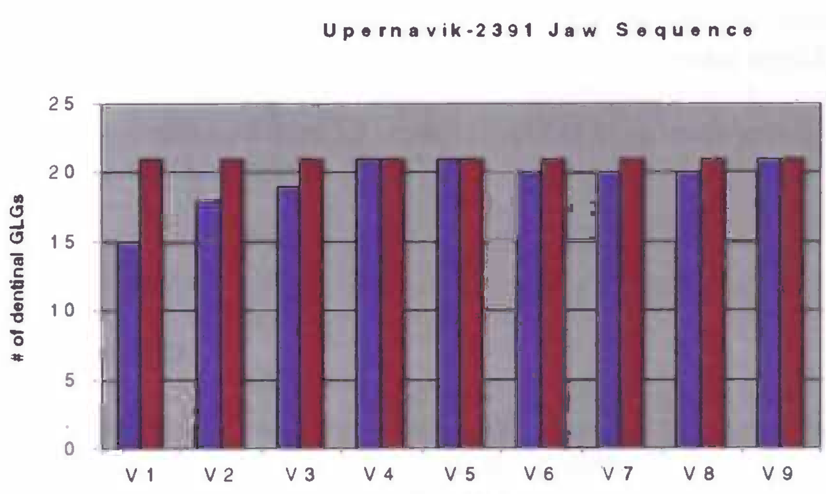


Fig. 3.1.The difference between Observed and Expected dentinal GLGs in teeth from different positions.

When different teeth from the same specimen were analysed for their GLG count, the front teeth were generally the most eroded (fig.3.1, Appendix 1). In the case shown here (Upernavik-2391), the first tooth differed by as much as 6 GLGs (or 28.6 %) from teeth further backwards.
In this analysis, one of four intended jaw sequences (Upernavik-2389) produced nearly unreadable tooth sections, and was discarded. In the case of jaw sequence Sissimiut-2421, sections from the two most posterior teeth (positions 7 and 8) were also unintelligible; these two sections were left out of further analysis.

Biases

A number of biases was encountered in the database:

1) AGE AS SELECTION CRITERION. In general, there were more animals available from younger age groups. On the one hand, this meant that some animals in these groups had to be discarded; on the other hand, it proved to be difficult to find sufficient animals from the oldest age groups.

2) SEX. In the animals collected at Sissimiut, there was a strongly skewed sex-ratio deviating from unity (this was not the case in the Upernavik sample).

3) POSITION OF TEETH. In the Upernavik sample, there was a clear bias towards teeth being positioned near the apical end of the jaw. Since these teeth tend to erode faster than teeth further back, they are less useful for age determination. This bias is most probably due to a sampling artifact. The Sissimiut sample, on the other hand, consisted mostly of teeth from middle positions (3-6) in the jaw.

4) SIZE OF TEETH RELATIVE TO POSITION IN JAW. As seen in the jaw sequence experiments (Appendix 1), teeth from both anterior and posterior positions (1 – 2 , and 7 – 8) in the jaw tend to be generally smaller in general proportions than teeth from around halfway in the jaw (positions 4 to 6). As will be seen below, several significant differences occur between these parameters in the Sissimiut and the Upernavik dataset. It can be confidently expected that these differences would stand out even more prominently if unworn teeth from all animals could have been used.

Parametric data

General remarks

In all statistical tests used, the level of significance was taken to be $p = 0.05$. That is, a result was taken to be statistically significant at $p < 0.05$.

All measurement analyses started with producing scatterplots, showing the general distribution of the parameter in question against age. It soon became apparent that animals of ages 0-2 were relatively useless when looking at these data, since such teeth tended to exert unreasonable weight on the trendline of the entire dataset, there being very little difference between them. For this reason, the age group "0-2 yr" was excluded from further analysis.

Maximum Width of Cementum

Teeth from Upernavik and Sissimiut (age >2, sexes combined) showed a significant difference in Maximum Width of Cementum (M.W.Cem.) when plotted as scatterplots (fig.3.2). Cemental width of Sissimiut specimens was significantly thinner than that of Upernavik (t = 2.89, d.f.= 72). Both trendlines were significant for their dataset.
When further analysis was performed to see whether there was a possible relation to sex, an interesting pattern emerged . When the Upernavik males and females were tested against each other, there was no significant difference between them (both in trendline analysis and a T-test, Appendix 2). Likewise, when Upernavik females were tested (with trendline analysis) against Sissimiut females for differences in their M.W.Cem., the former had no significantly thicker M.W.Cem. than the latter. However, when Upernavik *males* were tested (with trendline analysis) against the Sissimiut females, the difference was significant (2.8 and 1.9 mm, resp.; t = 2.83, d.f.= 47): the M.W.Cem. of the Sissimiut females was much thinner than that of Upernavik males.

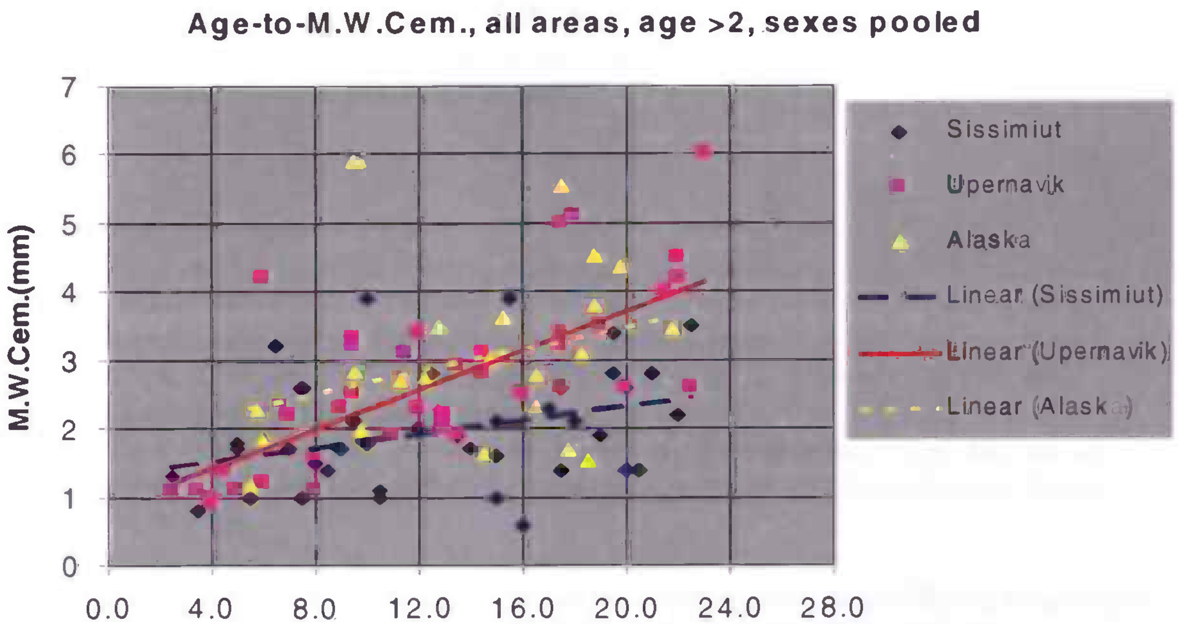


Fig. 3.2. Difference between Max.Width of Cementum in Upernavik, Sissimiut and Alaska databases.

When the data from the Alaskan animals were included in the comparison, the scatter in the Alaskan dataset proved too high for significant trendline analysis. When Analysis of Variance was performed, it indicated a significant difference between the three datasets (F = 7.226661, d.f.= 120). This was graphically represented by fig. 3.3, in which there is a clear difference in variance between the Sissimiut sample on the one hand, and the Alaska + Upernavik samples on the other hand. So, Alaskan animals are comparable to those in N-Greenland (Upernavik), as far as their M.W.Cem. is concerned.

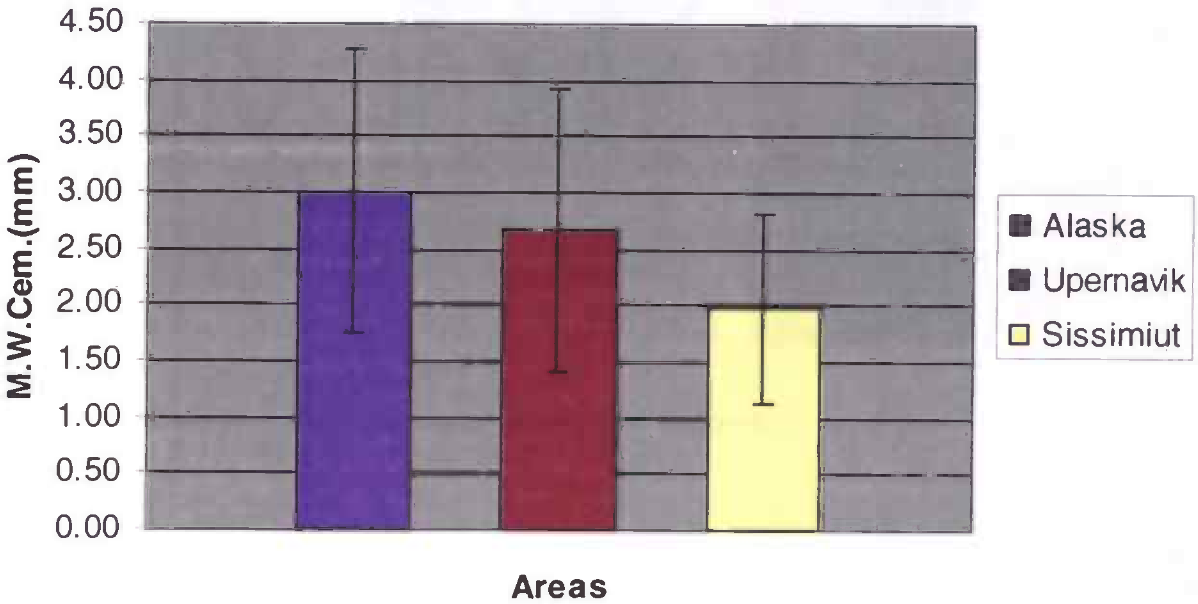


Fig.3.3. Result of analysis of Variance of M.W.Cem.-values between Upernavik, Sissimiut and Alaska datasets

Maximum Width of Dentine

Trendlines of Maximum Width of Dentine (M.W.Den.) derived from scatterplots (data in Appendix 1) were not significant for their datasets (sexes pooled, age >2). Nor was there a significant difference between the two areas (4.8 and 5.0 mm, respectively): in fact, the M.W.Den. was completely independent from variation with age.
When tested for variation of M.W.Den. by sex, no significant differences were discovered. Likewise, there was no significant difference between Upernavik and Sissimiut females in their average M.W.Den.

Regression analysis showed that the Alaska dataset was not significantly different from either the Upernavik or the Sissimiut dataset in its M.W.Den. Essentially, all three datasets exhibited too much scatter for any significant regression line to appear. Further analysis using Analysis of Variance supported the conclusion that there was no significant difference in variance between the three populations.

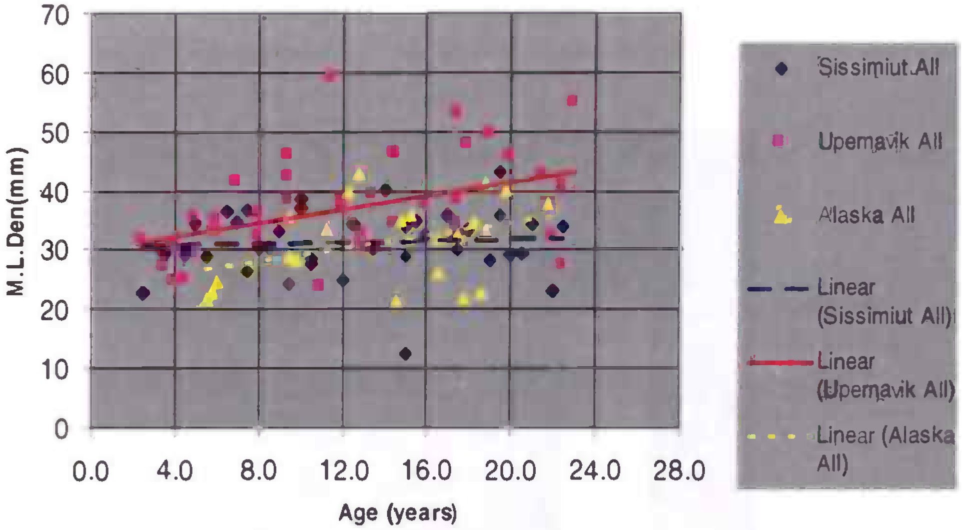


Fig.3.4. Difference between Max.Length of Dentine in Upernavik, Sissimiut and Alaska databases (ages >2, sexes pooled).

Maximum Length of Dentine

When the Maximum Length of Dentine (M.L.Den.) of Upernavik and Sissimiut animals (sexes pooled, age >2) was compared using trendline analysis, the Sissimiut dataset turned out to possess too much scatter for any useful analysis (fig.3.4).
When the same data were compared using a T-test for comparison of means, the two populations turned out to be significantly different (Appendix 3). Upernavik specimens possessed a significantly higher average M.L.Den. than Sissimiut ones (37.3 and 31.4 mm, respectively; T = 3.72747, d.f.= 76).
When tested for variation of M.L.Den. by sex (trendline analyis and T-test), Upernavik males and females turned out to be significantly different for their M.L.Den. (t = 2.75342, d.f.= 37). In particular, males had a significanty higher average M.L.Den. (40.5 mm) than females (34.0 mm). No significant difference was found in average M.L.Den. between Upernavik and Sissimiut females (T-test).

When the Alaska dataset was included in the analysis (trendline analysis, Analysis of Variance; fig. 3.5, Appendix 3), its M.L.Den. was shown to be not significantly different from that of the Sissimiut dataset. The M.L.Den. of both sets differed significantly from Upernavik (31.4 mm and 31.4 mm versus 37.3 mm, respectively; F = 8.420842, d.f.= 2, 99). In general, the animals from North Greenland (Upernavik) possess longer teeth than animals from either Southwest Greenland (Sissimiut) or Alaska.

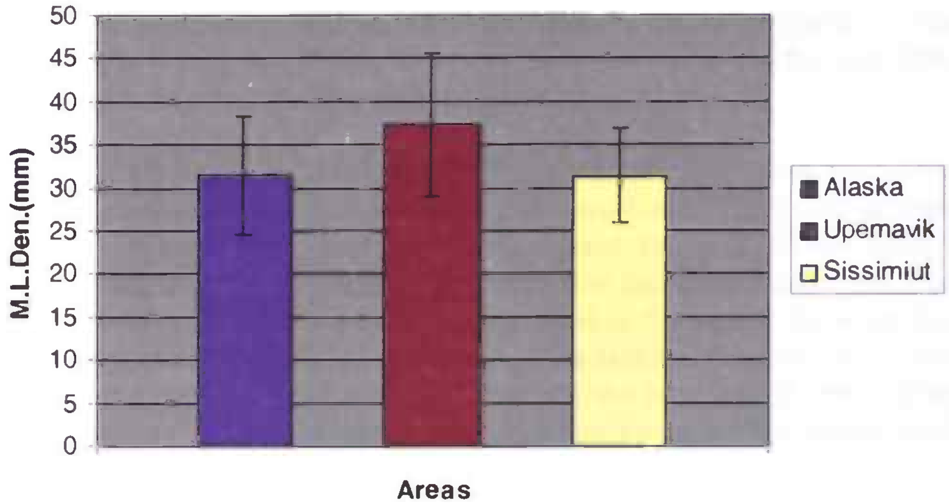


Fig. 3.5. Results of analysis of Variance for Max.Length of Dentine in Upernavik, Sissimiut and Alaska datasets

Ratios: 1) Max.Width of Cementum / Max.Width of Dentine

This ratio, hereafter called Ratio-1 for convenience, was proven to be significantly different between animals from Upernavik and Sissimiut (sexes pooled, age>2). Specifically, Ratio-1(Upernavik) was 0.56, while Ratio-1(Sissimiut) was 0.42. In both trendline analysis and Z-tests, the difference between the two datasets was significant (Appendix 4).

There was no significant difference between Upernavik males and females with respect to distribution of Ratio-1. Neither was there a significant difference between females from Upernavik and Sissimiut (results from both T-test and trendline analysis).

The average Ratio-1 of the Alaska dataset did not differ significantly from that of the Upernavik dataset. Unfortunately, scatter was too great for regression analysis to be performed on the Alaskan specimens. Also, the variance of the three datasets differed substantially, so a direct Analysis of Variance was not allowed either. The problem lay in the data distribution of the three datasets: only the Alaskan specimens were distributed according to a normal distribution. Only after a logarithmic transformation of the data could an Analysis of Variance be performed (Appendix 4). The result was that the Alaskan dataset did not differ significantly from the Upernavik dataset, but both differed significantly from the Sissimiut dataset (Tukey test, Appendix 4).

2) Max.Width of Dentine / Max.Length of Dentine

The trendline describing the relationship of this ratio (hereafter to be called Ratio-2, out of convenience) to age in the Sissimiut sample (sexes pooled, age>2) was not significant; the "Upernavik" trendline of Age-to-Ratio-2 was significant. Trendline analysis of these two datasets revealed no significant differences between them; however, when a Z-test for the comparison of the means of these two datasets was applied, the result was significant (Z-score = 1.97547; Appendix 5).

There was no significant difference between females from Upernavik and Sissimiut in Ratio-2. Neither was there a significant difference between males and females from Upernavik (both in T-tests and in trendline analysis).

When the two Greenlandic datasets were compared to the Alaskan specimens for Ratio-2 in regression analysis, no significant differences were found. There was no significant relationship between Ratio-2 and age in the Alaska dataset. When an Analysis of Variance was performed on the three datasets, the result was that there was a significant difference between the three. A subsequent Tukey test failed to distinguish between the datasets, however (Appendix 5). This is a reflection of the fact that Analysis of Variance testing is more powerful than the Tukey test, and thus delivers less Type II errors. (Zar, 1984: pp. 190). A larger sample size might possibly amend this problem, but this should not be considered a viable option.

Non-parametric data

General remarks

By far the largest fraction of non-parametric characteristics included in this study was in some way connected with affinity for stain. Indeed, it often proved to be quite difficult to recognise a given character, previously identified in a stained section, in untreated material from the same specimen. Therefore, all data presented here are derived from stained sections, unless specifically stated otherwise.

In all statistical tests used, the level of significance was taken to be $p = 0.05$. So, results were taken to be statistically significant at $p < 0.05$.

GLG Counts

Even though age determination was not the primary focus of this study, all specimens were checked 2-3 times for their GLG count (and, consequentially, their age) in both dentine and cementum. Counts were done on untreated sections under polarised light, to increase clarity, although in some cases additional use had to be made of stained sections to improve readability. Most of these specimens (the entire Upernavik and Sissimiut dataset) had been counted before (Heide-Jørgensen *et al.*, 1994) by experienced readers. My own results were compared to these (Appendix 1). Generally there was only a slight difference between the two values.

In both Greenlandic populations, 84.8 % of all counts differed with 0 – 1 dentinal GLG from previous measurements by Heide-Jørgensen *et al.* This was considered to be insignificant. In the case of counts in the cementum, there is a clear difference between the two Greenlandic populations. Cemental GLG counts deviated from previous counts far more in the Sissimiut dataset, than in the dataset from Upernavik. In the former, 34.8 % of all counts differed by 0 – 1 GLG from previous measurements, whereas in the latter, the result was 54.3 %. No cemental GLGs were counted for the Alaska dataset; since this was the first time these were read for GLGs, no comparison could be made.

The greatest errors occurred when reading old teeth, which had a large number of finely spaced GLGs, particularly in the cementum. In a very few cases (Sissimiut-2426 and Upernavik-1840), the difference between my own observations and previous counts was so large that the animals would have to be classified in an older age group to account for it (in other words, I counted more GLGs in untreated sections (with stained sections as backup)). After some deliberation, it was decided to use the results of the more experienced readers (i.e. Heide-Jørgensen *et al.*, 1994) in this study.

Tooth Shape

Apart from taking measurements, information on the tooth shape was recorded in a number of ways. General shape of both tooth tip and entire tooth were recorded, as was the relative degree of wear, from untreated sections (since these usually approached the midline closest). All statistical tests were chi-square tests. The data gathered on the Alaskan specimens did not include tooth shape, and did not permit a comparison with the Greenland datasets.

There was a distinct change in shape of the tooth tip with age, Generally, in young individuals, the teeth are bluntly pointed. As the animals get older, the tooth tip becomes more and more rounded, eventually becoming completely flattened in some specimens. There was no difference between Upernavik males and females, or between Upernavik and Sissimiut females.

A clear sign of the degree to which wear has set in is to check the state of the neonatal line. In this study, Wear was defined as the neonatal line being either exposed or not visible (i.e. disappeared). The graph in fig. 3.6 shows this clearly: in all the youngest animals of both Greenlandic datasets, the neonatal line is still fully visible. Wear sets in around age 5, and by the age of 10, the neonatal line has been lost in most animals. There was no significant difference between Upernavik males and females, or between Upernavik and Sissimiut females.

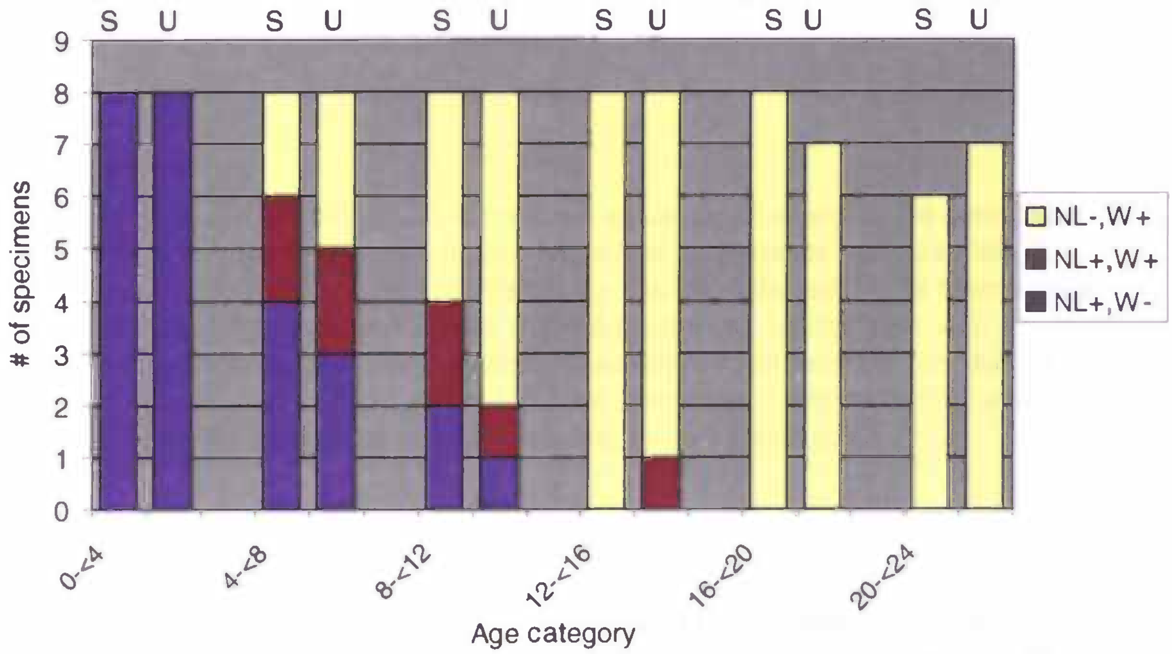


Fig.3. 6. The onset of wear in teeth from Sissimiut (S) and Upernavik (U). Sexes, positions pooled.
NL = Neonatal Line, W = Wear.

The overall shape of the teeth was not related to either location or age category in any statistically significant manner. Nor was there any relationship to sex. There did appear to be a significant relationship between overall toothshape and tooth position in the Upernavik dataset (Appendix 6): Cylindrical teeth tended to be positioned further back than either Strongly Curved, or Slightly Curved teeth. There was also a significantly larger number of Strongly Curved teeth in position 1-2 (Chi-square value = 13.428, d.f= 6, $p<0.05$).

Pulpstones

No significant difference was recorded in pulpstone density between the two Greenland datasets (ages, sexes pooled). When Upernavik males and females were compared, no significant differences were present; nor were there any such differences between females from Upernavik and Sissimiut.
As expected, the abundance of pulpstones increased with age: whereas only 4 animals younger than 4 in the entire dataset (16.7 %) contained any pulpstones, all animals from age 11 and onward possessed at least a few pulpstones. In several cases the pulpstones occurred throughout the dentine, obscuring other characteristics such as GLGs.

In the Alaska dataset, pulpstones were present in all animals at least from age 9.5 onward. This is rather late when compared to the two Greenland samples, but is probably an artifact due to small sample size (24 specimens). No significant differences in pulpstone abundance were detected when comparing all three datasets (chi-square analysis).

The categories used in determining the distribution of pulpstones in the tooth (Single, Clustered, Root) proved somewhat unsatisfactory in this case; sample sizes were generally too small to say anything meaningful about trends in distribution within datasets. There was no significant difference between the Upernavik, Sissimiut and Alaska datasets concerning pulpstone distribution.

Pathologies

Dentinal resorption (defined in Lockyer, 1995) was not encountered in any of the specimens examined. Mineralisation interference did, in fact, occur, but its presence was rare. Only 7 cases of mineralisation interference were recorded in the Sissimiut dataset, while there were 8 cases in the dataset from Upernavik and 2 cases in the dataset from Alaska. This was considered too small a sample size for any meaningful analysis, apart from the fact that all these cases occurred in animals of age 8 and older. Two specimens (Upernavik 1865 and 2506) were excluded on the grounds of being too unclear to read accurately.

Staining Characteristics: Boundary Layers

Two specimens (Upernavik 1865 and 2506) were excluded on the grounds of being too unclear to read accurately, and three more specimens (Sissimiut 2440 and Upernavik 2184 and 2203) because they were neonates who did not yet show their first boundary layer and were thus useless for this particular analysis.
Four different tooth types were recognised, each showing a specific pattern of boundary layer: "Single"; "Single + Double"; "Double"; "Single + Double + Triple". When looking at the general distribution of the boundary layer type (i.e. the number of boundary layers per GLG) among the two Greenland subsamples (all ages, sexes pooled), there was no significant difference. All four recognised tooth types were present in the same frequencies in both areas. "Double" and "Single + Double + Triple" were by far the rarest categories, numbering only one and four specimens each.

When general distribution of the boundary layer type was tested in both areas against age groups, no significant relationships were found in Upernavik. However, there were several significant relationships ($p<0.05$) in the Sissimiut dataset (Chi-square = 25.05, d.f.=15, see also Appendix 7):

- "Single"-teeth are overrepresented in Age Group 1-<4
- "Single + Double"-teeth are overrepresented in Age Group 4-<8
- "Single + Double + Triple"-teeth are overrepresented in Age Group 12-<16

When sexes were separated, there was no significant difference between Upernavik males and females, or between Upernavik and Sissimiut females. For this particular analysis, yet another specimen (Upernavik 2581) was sacrificed because its sex was unknown.

The second analysis concerned itself with the colour of the respective boundary layers. Three different categories were recognised: "Light", "Dark", and "Mixed". From chi-square analysis, it was clear that distributions among the datasets were not homogeneous: "Dark" was much rarer than either of the two other types in both datasets. Between the two datasets, there was no significant difference in distribution (chi-square, all ages, sexes pooled).

When sexes were separated, there was no significant difference in distribution of boundary layer colour between Upernavik males and females, or between Upernavik and Sissimiut females. For this particular analysis, one specimen (Upernavik 2581) was again sacrificed because its sex was unknown.

Unfortunately, it turned out that the Alaskan data had not been gathered using the exact same categories as the Greenland data. As such it proved impossible to do a meaningful comparison between the different datasets.

Staining Characteristics: Dark Staining Layers (DSLs) in the cementum

Commencing the analysis of DSL counts, it was found that there was no significant difference between presence/absence numbers in both Greenland datasets (chi-square; ages, sexes pooled).
However, when sexes were considered independently in Upernavik, there were significantly more males with DSLs present than would be expected (Appendix 8). Upernavik females did not show such a difference. When the two sexes were then compared, they did not differ significantly. Neither was there a significant difference in DSL presence between females from Upernavik and Sissimiut.

With regard to a possible age effect, all age classes in each dataset were tested against each other for DSL presence/absence. No such effect was discovered in either of the datasets. Finally, there was no significant relationship between presence/absence of DSLs and tooth position in either of the datasets.

When both Greenland datasets were compared to the Alaska dataset (by means of Chi-square-analysis), there was a significant difference between both Greenland groups on the one hand, and the Alaska group on the other hand (Chi-square = 6.961342, d.f.=2, $p<0.05$). There were far less DSLs present in the Alaska dataset than expected (Appendix 8).

Staining Characteristics: Tooth Clarity

Within each area, the Clarity Index distribution did not differ significantly: all classes were present in generally the same frequencies. When age classes were concerned (sexes pooled), there turned out to be a significant difference between the classes in the Upernavik dataset (Appendix 9): animals in the oldest age group (20-<24 years old) possessed significantly more teeth which were the most difficult to read (a C.I. of 1). The largest (significant) fraction of "clearly readable" teeth (C.I. = 3) was found in age group 8-<12, and the next clearest type ("moderate to clear", C.I.=2-3) turned out to be significantly more present in age group 4-<8. No such obvious difference was present in the Sissimiut dataset.
No significant differences could be found when Upernavik males and females (ages pooled) were compared for Clarity Index distribution. No differences were observed between Sissimiut and Upernavik females (ages pooled).

The Alaska dataset showed a significant result: there were far less "moderate to clear" and "clear" teeth (C.I. of 2-3 and 3) present than would have been expected (Appendix 9).

However, when the three datasets were tested against each other for differences (chi-square; ages, sexes pooled), no significant difference was found between them.

Staining Characteristics: Accessory Lines

Four specimens were excluded from analysis: Upernavik 2203 and 2223 (neonates which did not yet have their first full GLG) and Upernavik 1865 and 2506 (generally impossible to read accurately). No difference was found in the general distribution of accessory lines among the two Greenland datasets. When Accessory line presence was tested against age groups for both datasets, no significant relation was discovered.
No significant difference was found between Upernavik and Sissimiut datasets (sexes, ages pooled) for accessory line frequence distribution. Neither was there a difference between Upernavik males and females, or between Upernavik and Sissimiut females.

Unfortunately, comparable data for the Alaskan data had not been gathered.

Staining Characteristics: Marker Lines

Four specimens were excluded from analysis: Upernavik 2203 and 2184 (neonates which did not yet have their first full GLG) and Upernavik 1865 and 2506 (generally impossible to read accurately).
The *number* of Marker lines (both Dark and Light) present in both Greenland datasets was not evenly distributed. The great majority of specimens showed between 0 and 2 Dark and Light marker lines in the entire tooth (69.6 % and 76.2 % had between 0 and 2 Dark lines; 93.4 % and 95.2 % had between 0 and 2 Light lines; Sissimiut and Upernavik, respectively). So, the presence of Marker lines (of either colour) was rare.

An analysis was done to see whether the presence of Dark marker lines exerted any influence on the presence of Light marker lines. For both Greenland datasets, chi-square analysis was carried out comparing frequencies of both Marker line colours. No significant result was found in either case.

Analysing the *position* of the marker lines proved impractical; this depended on an accurate age determination of the specimen in question which, for reasons outlined previously, was not feasible.

Unfortunately, comparable data for the Alaskan data had not been gathered.

DISCUSSION

General Remarks

At the onset of this project, there was a general feeling that the usage of non-parametric characteristics would show new and unsuspected differentiation within and between the two Greenland datasets. This, unfortunately, did not prove to be the case. The great majority of characteristics were either strongly linked with Age (for example the abundance of Pulpstones) and showed no difference between sexes and/or areas, or they appeared to be essentially random (as in the occurrence of Accessory Lines). This does not mean that, in the latter case, the *cause* of such characteristics occurring is governed by random events, but rather that these characteristics are formed in response to individual life history events, rather than events working across areas and/or populations. As such, the database would have to be greatly expanded to discover any significant results; an option not directly feasible, given the effect on beluga population levels.

The parametric results, on the other hand, proved to be far more significant and useful than initially expected. These results have lent extra weight to the claim that there is, in fact, a clearly visible difference in proportions between Upernavik and Sissimiut teeth (North vs. Southwest Greenland). The comparison of these two groups with a distinct outgroup (the Alaska dataset) put these differences in a wider perspective.

Factors influencing tooth growth and development

The size which a given beluga tooth will reach depends on several factors. First, of course, there is a genetic component, determining i.e. the general size of the jaw, thus setting limits beyond which the animal cannot grow. The size of the jaw naturally determines the size of any number of tooth sockets, and thus teeth (which is itself under genetic control), it can contain.
Furthermore, as has been shown conclusively in the jaw-sequence experiment, not all teeth in the jaw are of equal sizes. Teeth in the middle of the jaw tend to be proportioned somewhat larger than teeth at either the anterior or the posterior end. This difference can also be assumed to be governed by genetic processes.
When a beluga is born, its teeth have just barely erupted. Since the neonate depends on milk from the mother for at least six months (Martin, 1996), the teeth are of limited use at this point in its life.
As soon as it starts to ingest solid food, the teeth are subject to wear. Initially this is not very impressive: teeth from two-year olds tend to be shaped exactly as teeth from neonates, except for being slightly larger. However, as the animal gets older, the wear becomes more and more pronounced. Sometimes, two teeth in mandible and maxilla scrape against each other when handling prey, thus giving rise to irregular erosion patterns (this also commonly occurs in other species of cetaceans, including Pilot whales and Killer Whales (Lockyer, pers.comm.)). As has been stated before, the teeth which experience the greatest stress are probably the ones positioned at the anterior end of the jaw, if only because they are usually used for handling of prey.

Finally, since beluga teeth grow continuously through life (but not with a continuous rate, i.e. amount of dentine deposited per year) the size difference between teeth in the same jaw but under slightly different "erosion regimes" is likely to become more pronounced with increasing age.

Biases

Sex-distribution

A recurring problem in the analysis of possible sex-related characteristics was the fact, that so very few animals in the Sissimiut dataset were males (7 out of 46, or only 15.2 % of total). This made it difficult to say anything meaningful about the difference between the two populations, when such an effect was discovered in the Upernavik dataset (as was the case with Max.Length of Dentine). Unfortunately, the sexes of animals in the Alaska dataset were not available either. It can only be surmised that the chances of finding a comparable effect in the Sissimiut and Alaska datasets are quite high, if only sample sizes are large enough and specimens are selected with a sex ratio close to unity in mind.

Position

The unfortunate breakdown of the Isomet precision saw forced me to change the focus of the project. Instead of selecting and preparing new material from the entire database, I would make use of previously prepared teeth (i.e. which had been cut on the same machine some time before).
This had the advantage that the dataset was read for GLGs at least once already; these counts were used to compare my own counts against.
On the other hand, this forced me to use teeth from less desirable positions in the jaw. In particular the Upernavik dataset consisted of a significant amount of teeth from the first and second position (45.7 %). By their very nature, teeth at these positions are liable to wear; any measurements will therefore be influenced by the absence of a larger than average amount of tooth material. Comparisons which were made for e.g. Max. Length of Dentine between the Upernavik and Sissimiut datasets (and which were significant), are therefore likely to be even more strongly significant, when teeth from comparable positions are used.
Likewise, the disappearance of several GLGs due to erosion poses serious problems for age determination. As soon as the neonatal line disappears (at around age 10, or after 20 GLGs), it becomes impossible to accurately determine the exact age of an animal. This means that all age determination from that age onward is more or less suspect. This problem will get even worse if teeth from unfavourable positions are used (see above). In other words, teeth from animals which are determined by GLG counts may be seriously underestimating the animal's true age. This is a particular problem with benthic feeders such as belugas, who routinely ingest coarse sediment, as well as hard-shelled or –scaled prey items.

Sampling method

The teeth samples used in this and previous analyses had been collected during the annual hunt by several Inuit communities, over the course of several years (at least from 1989 up to 1995). Primary agents in this process were the hunters, who were willing to let researchers sample the catch for (among others) teeth. It proved too time-consuming to procure the entire mandible from each specimen, so many specimens (most of them in Upernavik municpality) were collected by cutting off the lower jaw with a chainsaw (Heide-Jørgensen *et al.*, 1994). This, unfortunately, greatly increased the fraction of teeth from the front positions in the entire dataset. As explained above, these teeth are the most unreliable when it comes to GLG count, Max.Length of Dentine-measurements, etc. So the sampling was largely done by people who had no immediate interest in the quality of the samples; this is reflected in the datasets.

Another problem concerning possible sampling error is that catch methods differ greatly in Upernavik and Sissimiut District. In Northwest Greenland (Upernavik), belugas are caught by driving entire pods ashore as they migrate along the coast. Catches here tend to show a distinct overrepresentation of young animals (91 % of all animals are under 10 years old). This led to the point where animals from other areas within the Upernavik District had to be included to maintain approximately equal sample sizes. The sex ratio was close to unity.
In contrast, the catching method in Southwest Greenland (Sissimiut) involves pursuit of individual belugas by boat or kayak. Catches made in this area show a much wider spread among age classes (only 56.6 % of all animals are under 10 years old). In that respect, the Sissimiut sample gives a much better approximation of beluga age classes. However, as discussed above, the sex ratio in this sample is decidedly skewed towards females.
The main problem in this case was that it might not be particularly informative to undertake comparative studies of two samples which have been gathered in such different ways. The possibility for sampling error was quite high.

Observer difference

One final problem was represented by the fact, that not all observations were done by the same observer (myself). Instead, the data on the Alaska specimens were obtained by Lockyer & Hohn (pers.comm.). Although characteristics had been discussed thoroughly, the possibility of a distinct observational bias cannot be excluded at this point. This was apparent when records of several non-parametric characteristics turned out to be incomparable between the different datasets due to a different method of data gathering.

Parametric results:

Measurements and Ratios

The case of the Maximum Width of the Cementum was an example of a characteristic, which delivered far more useful information than initially expected. At the onset of the project, this characteristic was only included to give information about the general proportions of the tooth in question (using the M.W.Cem.-to-M.W.Den.-Ratio, or Ratio-1). However, there turned out to be a significant difference between the Upernavik and Sissimiut datasets: the cementum of

Upernavik animals was much thicker than that of Sissimiut animals. This was primarily due to the males from Upermavik; the effect therefore appears to be sex-related. However, there was no significant difference between Upernavik females and either Upernavik males or Sissimiut females. Upernavik females thus appear to be intermediate between the wide teeth of Upernavik males and the narrow teeth of Sisismiut females.
Also, the Alaskan dataset possessed cementum of a thickness comparable to that of the Upernavik sample, and thus thicker than that of the Sissimiut sample.
Since cementum is secreted by the tissue surrounding the entire tooth, rather than the pulp cavity, it is restrained in thickness only by the size of the tooth socket in the jaw. Its primary function is to provide anchorage for collagen fibers that secure the tooth to alveolar bone (Bhaskar, 1976). At this point, no information on the average tooth socket size of belugas from the respective areas is available, but it can be expected that animals from North Greenland and Alaska will probably possess wider sockets than animals from Southwest Greenland.

When looking at the Maximum width of the Dentine, no such striking differences were found. In fact, there was no significant difference *at all* between either the two Greenland samples or the Alaska sample. This means that this characteristic is either genetically fixed (there is an upper limit wider than which no tooth can be) or that any external factors governing dentinal width are likely to be very localised, affecting only individuals, rather than entire populations.

For Maximum Length of the Dentine, the difference between the two Greenland samples was again significant: teeth from Upernavik animals were generally much longer than teeth from Sissimiut animals. For the greatest part, this difference could be accounted for by the males in the Upernavik sample, who tended to possess significantly longer teeth than females from the same sample. The Alaskan animals were comparable to the Sissimiut specimens in this regard.

All in all, the following picture emerges:

- The WIDEST teeth (due to cemental width) are found among Alaskan and North Greenland animals.
- The NARROWEST teeth (due to cemental width) are found among Southwest Greenland animals.
- The LONGEST teeth are found among North Greenland animals. This is possibly a general sex-related characteristic.
- The SHORTEST teeth are found among Southwest Greenland and Alaskan animals.

This translates in:

- The LARGEST teeth, *in overall proportions*, are found among males in North Greenland. These possess not only the longest dentine (which is a good indication of overall tooth length) but also the widest cementum.
- The SMALLEST teeth, *in overall proportions*, are found among animals in Southwest Greenland. These possess not only the shortest dentine (which is a good indication of overall tooth length) but also the narrowest cementum.

A comprehensive overview is given in fig.4.1.

Although these size differences are partially explained by the fact that males are generally larger than females (particularly when looking at M.L.Den. in the Upernavik sample), the fact remains that teeth from Southwest Greenland are significantly smaller in overall proportions than teeth from North Greenland. This validates the "hunch" by J.Jensen and others who, based on their own observations, had earlier predicted that such a difference would be found. Strangely, there is more difference in overall tooth proportions between animals from North Greenland and Southwest Greenland (separated by a mere 1,000 kms) than between animals from either of these two populations and animals from Alaska – which is at least 3,000 km away from Greenland.

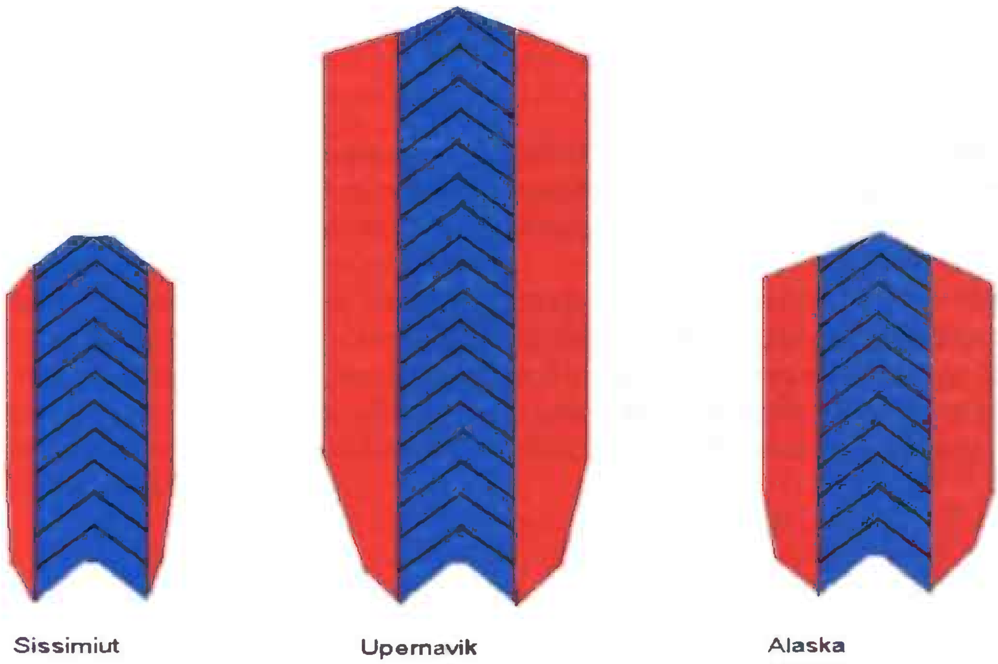


Fig.4.1. A schematic overview of untreated sections from the Sissimiut, Upernavik and Alaska datasets. Alaskan and Upernavik teeth are wider than Sissimut teeth due to thicker cement, but Upernavik teeth are also longer.

Setting aside differences between the two Greenlandic stocks and Alaska for the moment, the results from this investigation clearly do not show support for the theory that all Belugas, found along the West and Northwest Greenland coasts, are part of one population derived from the Canadian High Arctic.
The fact that there are also differences between both Greenland datasets and the Alaska dataset in tooth proportions indicates, that the usage of these measurements gives significant, internally coherent results when used to compare between different populations or areas. As such it shows promise as a new tool to analyse population structure in this and other species.

GLG counts

Generally, the counts of dentinal GLGs in samples from Greenland did not differ strongly from those done earlier on the same material by Heide-Jørgensen *et al.*, (1994). However, in the case of the cemental GLGs, there was a significant difference between the two Greenland datasets. The cemental GLGs in the Sissimiut sample were much more difficult to count accurately than were those in the Upernavik sample.
This is most probably due to the difference in cemental thickness between the two datasets: since the cementum among specimens from North Greenland is thicker, its GLGs are correspondingly easier to read.

Non-parametric results

Initially, there were high expectations of the so-called "non-parametric characteristics"; it was assumed that, since they were (probably) controlled by both genetic and environmental factors, they would be useable tools to separate populations.

Unfortunately, this proved not to be the case. Very few significant results were obtained from analyses using these data. In some cases (discussed in more detail below) the distribution of a character was essentially random, not clearly linked to factors as Area of Origin, or Sex. In other cases, it became clear that the all-important factor influencing the distribution was Age: the character was simply more abundant among older animals. In cases such as these, the character itself was of limited use.

Tooth Shape

As expected (belugas being homodont), there was no extreme difference in tooth shapes from different positions. The differences which were detected (the difference between Cylindrical, Slightly Curved and Strongly Curved) were related to curvature of the tooth. This itself depends largely on the amount of wear a tooth is exposed to: it was assumed that wear or abrasion could cause or increase the curvature of a tooth.
In the Upernavik dataset, a significant result was found in that the teeth in posterior positions (7 and 8) tended to be shaped Cylindrically, whereas Strongly Curved teeth were found mostly near the anterior end of the jaw. Unfortunately, the Sissimiut dataset did not show this pattern. Also, the sample size in the Upernavik dataset was rather small. Therefore, more research on this subject must be done to verify whether there is, in fact, a significant corellation between General Tooth Shape and Position in the jaw.

The same line of reasoning applies to the shape of the tooth tip. The general trend seems to be that all teeth start out being pointed, the point being composed of predentine. As the animal ages, the tooth tips gradually become more and more rounded, and even become completely flat in older specimens. This is a clear sign of the extent of wear that beluga teeth must endure.

Pulpstones

The case of the pulpstones is a prime example of a characteristic that did not bring the desired results, e.g. resolution power. Although the analysis was begun under the impression that specimens from Upernavik possessed more pulpstones than specimens from Sissimiut, this could not be proven by statistical analysis. The only result, as expected, was an increase of pulpstone density at higher age.

No signifiacnt difference was found between pulpstone distribution among the different datasets. All in all, the presence and abundance of pulpstones did not yield any useful information. However,

it did signify the need for a better understanding of the underlying causes of pulpstone formation and development.

Essentially, pulpstones are formed when odontoblasts are detached from the surrounding tissue and become embedded in the surrounding dentinal mass, while still secreting dentine of their own. At present, it is unclear what precisely causes such cells to detach. The characteristic is also common in other cetaceans, from e.g. Harbour Porpoise (Lockyer, 1995) to Pilot Whales (Lockyer, 1993) to Sperm Whales (Boschma, 1938).

The latter author, discussing the occurrence of pulpstones in Sperm Whale teeth, already states that "it is possible that the formation of [pulpstones] in the teeth of Sperm Whales is favoured by a change in external circumstances, e.g., differences in temperature or food." If this is indeed the case, one would expect pulpstones to be more abundant among migratory species of cetaceans, when compared to sedentary species. Indeed, it might also be possible to show differences between populations of the same species which are either migratory or sedentary. The beluga could serve as a prime subject in this, with both populations which perform extensive migrations (e.g. the Mackenzie Delta population) and sedentary ones (e.g. the populations at Cook Inlet and the St.Lawrence estuary).

Pathologies

The fact that no cases of dentinal resorption were discovered among a combined dataset of this size (116 specimens from Upernavik, Sissimiut and Alaska) gives a clear indication that the characteristic is rare, and that its occurence is most probably not linked to any given population. Such a result differs strongly from data obtained by Lockyer (1993, 1995, 1999) for Pilot Whales and Harbour Porpoise, respectively. The trait is comparatively rare in Harbour Porpoise, but common among Pilot Whales; in these species, there is a difference between incidence of dentinal resorption between different populations. Also, at least among Pilot Whales, the characteristic appears to be sex-related, occurring far more frequently among older males.

Mineralisation interference occurred only rarely throughout the datasets of all areas under consideration here. The only sensible remark that could be made on the occurrence of this character was that it only occurred in animals above age 8. Again, this is a clear difference with both Harbour Porpoise and Pilot Whale (Lockyer, 1995; 1993). In both species, the character was widespread and could be used to discern among populations.

The use of Boundary Layers (B.L.s) as a tool to distinguish between populations proved unsatisfactory, since few significant differences could be discovered in either Number-of-Lines or Colour-of-Lines distribution between populations. Concerning Number-of-Lines, the occurrence of double or triple lines as Boundary Layers appeared to be just significant in Sissimiut (a Chi-square test statistic of 25.05, where the table value $X_{0.05, 15} = 25.00$). Since no such relationship could be discovered in the Upernavik dataset, and since the difference with the test statistic is so small, I would like to treat this result with caution.
Also, the category "Double" was based on just one, fairly young specimen; in hindsight, it seemed reasonable to expect that this animal might very well have formed at least one Single B.L., had it lived long enough.

In the analysis of "Colour-of-Lines", the only categories were Light, Dark, and Mixed. Dark was obviously the rarest in both Greenland datasets, whereas Light and Mixed were approximately equally abundant. Comparatively early in the analysis, it became clear that "Mixed" was turning into a "wastebin" category, and that future attempts should be made to make a further distinction. For example, a specimen possessing 1 Light and 9 Dark B.L., and a specimen possessing 1 Dark and 9 Light B.L., would both be categorised as Mixed, although they are clearly different. So, some distinction should be made between *degrees* of "mixedness".

Also, the ratio of Dark and Light B.L. in a specimen designated as Mixed was not always constant; rather, the area towards the pulp cavity seemed to contain more Light B.L. when compared with the rest of the tooth, at least in older animals. However, this might be influenced by the increasingly narrow and constricted layering of the GLGs themselves, making recognition difficult.
A final problem concerning the different categories was that erosion of teeth could make a decisive difference in characterisation. A specimen whose Dark B.L. *had already been worn away* would only show Light B.L. and be classified accordingly, and wrongly. The only possible solution to this problem is the use of teeth which have experienced the least amount of wear, from the middle of the jaw.
At present, it is not yet clear what factor, or factors, cause Boundary Layers to differ in either colour or number. Stainability may reflect the degree of mineralisation of the tooth structure, and thus be indirectly related to nutrition (Lockyer, pers.comm.).

Dark Staining Layers

Ther was no significant difference in DSL distribution between the two Greenland datasets. However, both differed substantially from the Alaska dataset, which had far less DSLs present than would be expected. This has nothing to do with thickness of cementum, as it has been previously established that the Alaskan dataset has more or less the same average M.W.Cem. as the Upernavik dataset, which contains significantly more DSLs. Some other factor must therefore be responsible.
One such factor might be observer bias: not all specimens were studied by the same person, so some difference in registration could have occurred inadvertently.

Tooth Clarity Index (C.I.)

Several significant results were obtained in the analysis of this characteristic. First of all, there was a significant relationship between distribution of "clarity classes" and Age categories in the Upernavik dataset. However, since the sample sizes in each category were so small (not exceeding 4 animals per age category-to-C.I.), these results are probably due to sampling error; especially because such a result was not obtained from the Sissimiut dataset.
In the Alaska dataset, the distribution of C.I. differed significantly from expected values; teeth seemed to be far less clear than either Greenland dataset. However, this did not bear out in statistical analysis. One possible cause of this might be observer bias (as explained above). Otherwise, the deposition of the dentine could have been influenced by some unknown, but local, environmental or genetic factor, making the contrast in the dentine that much less distinct. The limited size of the Alaskan dataset currently prevents a decisive conclusion.

Marker Lines

The Marker Lines analysis of the Greenland datasets did not yield significant results, apart from the fact that Marker Lines of either colour were shown to be relatively rare occurrences. This might mean that the presence of one colour of Marker line does not influence the presence of the other colour of Marker line; on the other hand, it might also mean that teeth which do not possess Dark Marker lines are also less likely to possess Light Marker lines; i.e. the liability to produce marker lines could be linked.
However, the occurence of Marker Lines might also be linked to environmental stresses such as food availability, and the effect this has on nutrition. It could therefore be expected that the frequency of Marker Lines might be higher among animals that experience a variety of environmental circumstances (geographic areas) in a year. So, the characteristic would be useful, albeit indirectly, for population structure analysis.

The greatest obstacles were encountered when trying to analyse the position of Marker Lines within the dentine. The underlying assumption was that marker lines at the same positions in different individuals would give an indication of some environmental effect which had affected all these individuals. However, this assumption hinges critically on the ability to accurately assess the animal's age. As we have seen, this becomes nearly impossible when the neonatal line has disappeared. In other words: no analysis of Marker Line position among different specimens can be done if there is uncertainty about their ages. Further research will have to be done on this characteristic to improve its usefulness.

Accessory Lines

No significant differences in Accessory Line density were observed between the two Greenland datasets. This probably indicates that the causes of Accessory Line deposition do not limit their influence to distinct populations, but rather that all belugas exhibit this characteristic to a certain extent.
The process which causes accessory lines to form is not yet completely understood. Studies by Myrick *et al.*,. (1984) on captive Hawaiian spinner dolphins (*Stenella longirostris*) indicate that, in this species at least, incremental lines within each GLG are laid down in correspondence with lunar monthly cycles. This hypothesis has not yet been tested in belugas. Since it has by now been convincingly established that two GLGs are deposited annually in this species, it would be interesting to see whether the number of Accessory Lines within each GLG closely agrees with the expected number; that is, 6 to 7 (since, roughly speaking, there are 13 lunar months in each calendar year). Such a result would be suggestive of an important role played by lunar cycles in the formation of this characteristic.

One or two populations?

The results discussed above seem to indicate that there is less contact between belugas in North and Southwest Greenland than previously assumed. The original assumption, or "zero hypothesis" (all belugas found along the Western Greenlandic coasts are members of the same wintering population, which summers in Northwest Greenland and the Canadian High Arctic) has therefore become suspect. Rather, the animals found in Southwest Greenland may well constitute a (semi-)distinct population in their own right.

Projects using satellite telemetry to determine the movements of belugas in the Canadian High Arctic (e.g. Martin *et al.,* 1993; Richard *et al.,* 1998; Smith & Martin, 1994) have provided clues, but as yet no firm evidence, that animals from this stock may winter along the coast of North Greenland (fig.4.2). This was primarily due to transmitter failure before tagged animals reached Greenlandic waters. Alternatively, the animals could have wintered in the North Water between Devon and Ellesmere Island and Greenland (Finley & Renaud, 1980; Richard *et al.,* 1998).

One of the conclusions reached by using satellite telemetry has been the surprising discovery that belugas routinely dive down to depths of several 100 m, presumably to forage on the seabed (Heide-Jørgensen *et al.,* 1998; Martin *et al.,* 1998; Richard *et al.,* 1997). During winter, this can take up to 80 % of their time (Heide-Jørgensen *et al.,* 1998). This discovery has important implications, because it means that, on average, only a fifth of all belugas present in a given area will be present at 0 to 5 m depth, below which they cannot be detected by aerial survey (Richard *et al.,* 1994).
It is therefore likely that the fraction of the Canadian High Arctic population wintering in polynyas in the North Water is several times higher than previously assumed. Still, results gathered by several authors (e.g. Martin *et al.,* 1993; Richard *et al.,* 1998; Smith & Martin, 1994) seem to suggest that belugas seen in winter along the North Greenland coast constitute a significant fraction of the Canadian High Arctic stock; the rest of this stock is presumed to winter in the North Water.

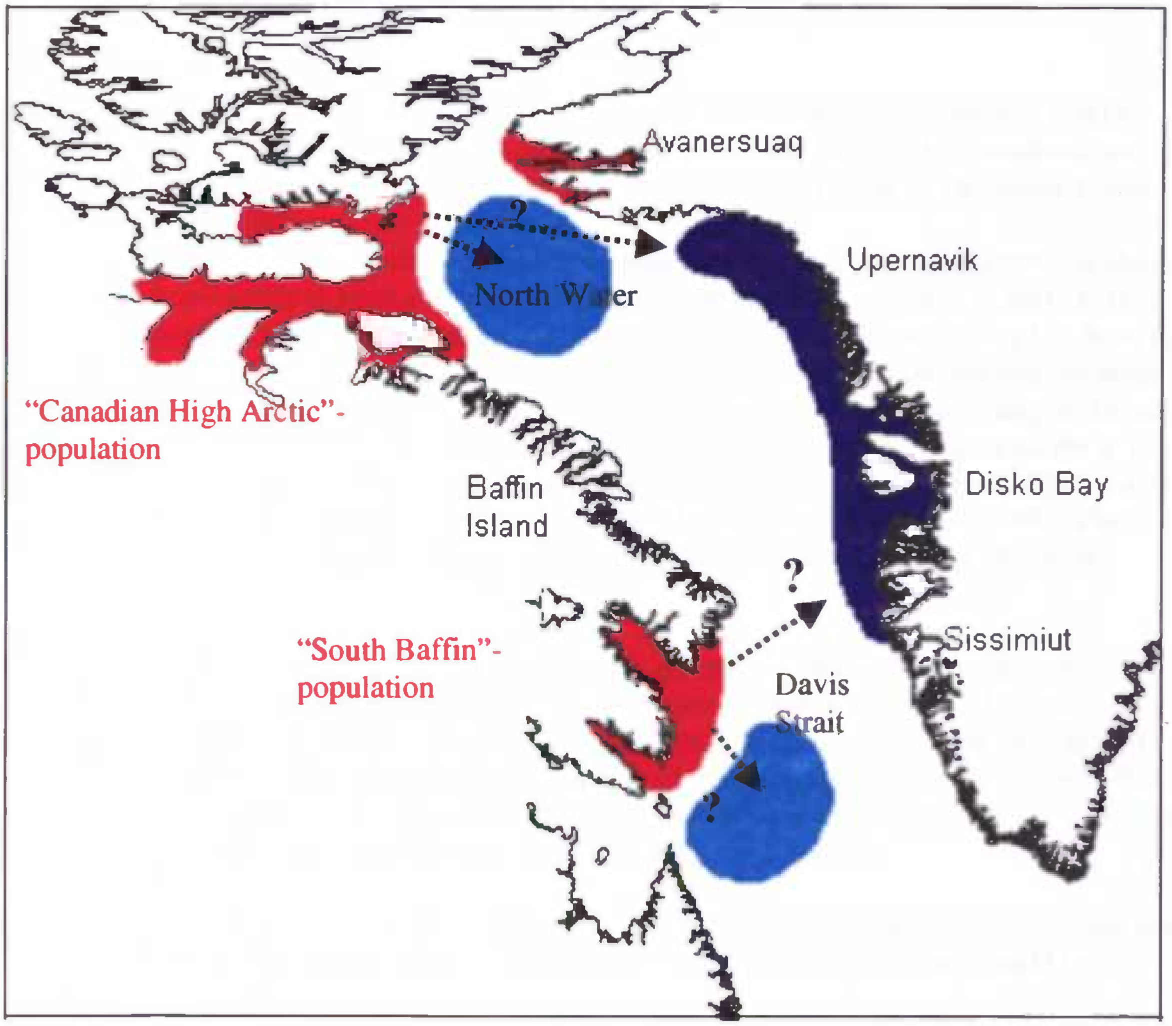


Fig.4.2. An overview of probable beluga distribution around Baffin Bay/Davis Strait. Primary summering areas (red) include the Canadian High Arctic and Southern Baffin Island, including Cumberland Sound (mentioned in text). The western coast of Greenland is the major coastal wintering area (dark blue) while the North Water in northern Baffin Bay and the mouth of Hudson Strait serve as offshore wintering areas (light blue). Fall migration routes are indicated.

The final remaining question must then be: if the belugas found in Southwest Greenland do not come from North Greenland, where then do they come from? The most logical option is directly from Canada (fig.4.2). Indeed, this possibility was already raised by Degerbøl & Nielsen (1930), who stated that several whales caught in Southwest Greenland contained in their flesh Canadian bullets, pointing towards a western, rather than a northern origin.
The closest recognised population is the one found summering in the southeast of Baffin Island, most noticeably in Cumberland Sound. However, this stock has witnessed serious decline in recent years (Brodie *et al.*, 1981) and may not be large enough to support an annual mean take of close to 100 animals (average take of Sissimiut municipality between 1971 – 1987; Heide-Jørgensen, 1994).
Sergeant and Brodie (1969) claimed that there was a significant difference in general body proportions between the populations in Cumberland Sound and "Sukkertoppen, West Greenland" , or Sissimiut municipality. In this particular paper, Sissimiut measurements from Degerbøl & Nielsen were used. However, these measurements are somewhat suspect, and a recent analysis by Doidge (1990) has shown the size differences between these groups to be far less pronounced than previously reported.
The wintering grounds for the Cumberland Sound population are as yet unknown. Possible wintering areas include southward towards the mouth of Hudson Bay and the offshore area of Davis Strait (Brodie *et al.*, 1981). There have also been several reports of sightings of belugas

in Spring in the middle of extensive pack-ice in Davis Strait (Mitchell & Reeves, 1981). Interestingly, water depths between southern Baffin Island and Southwest Greenland are relatively shallow, in the order of 500 to 700 m; comparable to depths in the North Water Berthelsen *et al.*, 1989).

In the light of the recent discoveries concerning beluga diving capabilities mentioned above, it might be possible for at least a fraction of the southern Baffin population to cross Davis Strait to winter in Southwest Greenland. Furthermore, it might not be necessary for them to forage extensively during migration if they had "fattened up" on their summering grounds. The assumption therefore is that adverse conditions do not permit belugas to stay in the area around Baffin Island, and that Southwest Greenland serves as a wintering ground for at least a fraction of the population. There are large areas of relatively shallow waters (0-200 m) up to nearly 100 km from the coast known as the Halibut Banks (Berthelsen *et al.*,1989) which support, among others, a large commercial shrimp fishery. This might be an attractive wintering area for belugas.

Little work has been done on assessing swimming speeds of belugas. Some data have been published on belugas at their summer grounds by Smith & Martin (1993) and on migrating belugas by Richard *et al.*,(1997). There is some variation in these results, but they indicate that traveling belugas in ice conditions are capable of reaching speeds around 6 km/h. This would make it possible for them to cross Davis Strait (which is only ~500 kms wide between Southern Baffin Island and Southwest Greenland) within a few days.

An interesting point in this case is the decidedly skewed sex-ratio found among animals from Sissimiut municipality. The number of females present is much higher than would be expected.

Also, the few males present in the Sissimiut dataset were all relatively young animals, between 1.5 and 10 years old. This might indicate that Southwest Greenland predominantly serves as a wintering area for females, and that mature males, which are capable of deeper diving (Martin, 1996; Richard *et al.*,1997) might spend the winter in the offshore waters of Davis Strait.

Taking all this into account, one would expect the beluga population along the Northwest Greenland coast (Upernavik municipality) to originate in the Canadian High Arctic, whereas belugas in Southwest Greenland would primarily be females, originating in the area around southern Baffin Island. Presumably there is also an area in between the two wintering grounds where the two populations meet, e.g. the area around Disko Bay, which incidentally has been recognised as an important site for wintering belugas (Heide-Jørgensen *et al.*,1993).

However, more research is evidently needed to study migratory routes and capabilities of the known populations. This could be achieved by a more extensive tagging program using satellite telemetry, in both the summer grounds in the Canadian High Arctic, Northwest Greenland (Thule District) and Southeast Baffin Island, as well as on the winter hunting grounds at different locations along the western coast of Greenland. In addition, genetic research could yield valuable insights.

Another issue which this study was unable to resolve was the presence of belugas along the Northeastern coast of Baffin Island, between Cape Dyer (to the north of Cumberland Sound) and Eclipse Sound (to the south of Lancaster Sound). No reference at all could be found to belugas being present in this area. This might mean that there simply are no belugas present, but could also mean that the area is not frequented by hunters and/or beluga researchers. In the light of a possible connection between Canadian and Greenlandic populations, it might certainly be worthwhile to shed more light on this issue.

Tissue samples had originally been collected together with the teeth (by Heide-Jørgensen *et al.*,(1994); Lockyer, pers.comm.), but the derived haplotype data were only available from ca. 50 % of both the Upernavik and Sissimiut specimens at the time this study was undertaken. This was deemed too small a sample and so these data were not analysed any further. In the near future, as more haplotype data on these specimens become available, such an analysis should certainly be performed.

CONCLUSIONS

The results from this investigation show that there are several consistent differences in tooth morphology between belugas caught in North and Southwest Greenland. This is suggestive of some degree of isolation between the two areas. Further research is needed to confirm this hypothesis, preferrably on a genetic level.
If the two areas do, in fact, constitute two sub-populations, this has important implications for management purposes in both Greenland and Canada. There has been widespread concern that the annual take of close to 1,000 animals along the entire West Greenland coast is far above carrying capacity for any beluga population; indeed, no other small cetacean in Greenland is subject to such intense hunting pressures (Heide-Jørgensen, 1991). Management will become more complicated if the animals wintering along the Greenland coast are actually derived from two small, rather than one large, population. This is particularly so because, in recent years, an increasing fraction of catches has gone unreported (Heide-Jørgensen, 1991), while the total catch has increased due to the availability of e.g. fast dinghies with outboard engines.

In addition, the use of non-parametric techniques as the ones used in this investigation needs to be reviewed for belugas. In several cases, more precise measurements are possible using altered search categories. In other cases, the characteristic provided no significant results and could probably be discarded in future analysis.
It is of great importance that several of the non-parametric characteristics be defined more precisely for their use in belugas than is currently the case. These preliminary trials, using pre-defined characteristics found useful in other species, demonstrate that beluga teeth are very different in many details of morphology to species such as pilot whale and harbour porpoise, not least the GLG incremental rate.

BIBLIOGRAPHY

Berthelsen, C., I.H.Mortensen, E.Mortensen [ed.] (1989). Kalaallit Nunaat / Grønland Atlas. P.J.Schmidt A/S, Vojens, DK. 130 pp.

Bhaskar, S.N. [ed.] (1976). Orban's histology and embryology. The C.V.Mosby Company, St.Louis, U.S.A., 8th Edition. 470 pp.

Boschma, H. (1938). On the teeth and some other particulars of the sperm whale (*Physeter macrocephalus* L.). Reprint of *Temminckia* 3; E.J.Brill Publishers, Leiden, NL. 278 pp.

Braham, H.W. (1984). Review of Reproduction in the White Whale, *Delphinapterus leucas*, Narwhal, *Monodon monoceros*, and Irrawaddy Dolphin, *Orcaella brevirostris*, with Comments on Stock Assessment. *Report of the International Whaling Commission* (Special Issue 6): pp 81 - 89

Brodie, P.F., J.L.Parsons, D.E.Sergeant (1981). Present status of the White Whale (*Delphinapterus leucas*) in Cumberland Sound, Baffin Island. *Report of the International Whaling Commission* 31: pp 579 - 582

Brodie, P.F. (1982). The Beluga (*Delphinapterus leucas*); Growth at Age based on a captive specimen and a discussion of factors affecting natural mortality estimates. *Report of the International Whaling Commission* 32: pp 445 - 447

Brodie, P.F., J.R.Geraci, D.J.St.Aubin (1990). Dynamics of Tooth Growth in Beluga Whales, *Delphinapterus leucas*, and Effectiveness of Tetracycline as a Marker for Age Determination. *In* T.G.Smith, D.J.Aubin, and J.R.Geraci [ed.] Advances in research on the Beluga whale, *Delphinapterus leucas*. *Canadian Bulletin of Fisheries and Aquatic Sciences* 224: pp 141 - 148

Dietz, R., M.P.Heide-Jørgensen, E.W.Born, C.M.Glahder (1994). Occurence of Narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in East Greenland. *Meddelelser om Grønland, Bioscience* 39: pp 69 - 86

Darling, J.D., C.Nicklin, K.S.Norris, H.Whitehead, B.Wursig (1995). Whales, dolphins and porpoises. National Geographic Society, Washington, U.S.A. 232 pp.

Degerbøl, M. & N.L.Nielsen (1930). Biologiske iagttagelser over og maalinger af hvidhvalen (*Delphinapterus leucas* (Pall.)) og dens fostre (English summary included). *Meddelelser om Grønland* 77: pp 117 - 144

Doidge, D.W. (1990). Age-length and length-weight comparisons in the beluga, *Delphinapterus leucas*. *In* T.G.Smith, D.J.Aubin, and J.R.Geraci [ed.] Advances in research on the Beluga whale, *Delphinapterus leucas*. *Canadian Bulletin of Fisheries and Aquatic Sciences* 224: pp 59 - 68

Finley, K.J. & W.E.Renaud (1980). Marine mammals inhabiting the Baffin Bay North Water in winter. *Arctic* 33(4): pp 724 - 738

Fowler, J. & L.Cohen (1990). Practical Statistics for Field Biology. John Wiley & Sons, Chichester, UK., 1st Edition. 227 pp.

Gaskin, D.E. (1982). The Ecology of Whales and Dolphins. Heinemann Educational Books, Inc., London, U.K. 459 pp.

Gjertz, J. & Ø.Wiig (1994). Distribution and catch of white whales (*Delphinapterus leucas*) at Svalbard. *Meddelelser om Grønland, Bioscience* 39: pp 93 - 97

Goren, A.D., P.F.Brodie, S.Spotte, G.C.Ray, H.W.Kaufman, A.J.Gwinnett, J.J.Sciubba, J.D.Buck (1987). Growth layer groups (GLGs) in the teeth of an adult belukha whale (*Delphinapterus leucas*) of known age: Evidence for two annual layers. *Marine Mammal Science*, 3(1): pp 14 - 21

Gurevich, V.S. (1980). Worldwide Distribution and Migration Patterns of the White Whale (Beluga), *Delphinapterus leucas* (literature review). *Report of the International Whaling Commission* 30: pp 465 - 480

Heide-Jørgensen, M.P. (1991). Small cetaceans in Greenland: Hunting and biology. *North Atlantic Studies* 2 (1-2): pp 55 - 58

Heide-Jørgensen, M.P., H.Lassen, J.Teilmann, R.A.Davis (1993). An index of the relative abundance of wintering belugas, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, off West Greenland. *Canadian Journal of Fisheries and Aquatic Sciences*, 50 (11): pp 2323 - 2335

Heide-Jørgensen, M.P. (1994). Distribution, exploitation and population status of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in West Greenland. *Meddelelser om Grønland, Bioscience* 39: pp 135 - 149

Heide-Jørgensen, M.P., J.Jensen, A.H.Larsen, J.Teilmann, B.Neurohr (1994). Age estimation of white whales (*Delphinapterus leucas*) from Greenland. *Meddelelser om Grønland, Bioscience* 39: pp 187 - 193

Heide-Jørgensen, M.P. & J.Teilmann (1994). Growth, reproduction, age structure and feeding habits of white whales (*Delphinapterus leucas*) in West Greenland waters. *Meddelelser om Grønland, Bioscience* 39: pp 195 - 212

Heide-Jørgensen, M.P. & R.R.Reeves (1996). Evidence of a decline in beluga, *Delphinapterus leucas*, abundance off West Greenland. *ICES Journal of Marine Sciences*, 53: pp 61 - 72

Heide-Jørgensen, P.R.Richard, A.Rosing-Asvid (1998). Dive patterns of Belugas (*Delphinapterus leucas*) in waters near Eastern Devon Island. *Arctic*, 51 (1): pp 17 - 26

Heide-Jørgensen, M.P. & C.Lockyer (revised 9/11/1998). Age and sex distributions in the catches of belugas, *Delphinapterus leucas*, in West Greenland and in western Russia. Submitted/in press, *Journal of Wildlife Biology*, 26 pp.

Hohn, A.A., M.D.Scott, R.S.Wells, J.C.Sweeney, A.B.Irvine (1989). Growth Layers in teeth from known-age, free-ranging bottlenose dolphins. *Marine Mammal Science*, 5 (4): pp 315 - 342

Kapel, F.O. (1977). Catch of Belugas, Narwhals and Harvour Porpoises in Greenland, 1954-75, by year, month and region. *Report of the International Whaling Commission* 27: pp 507 – 520

Lint, D.W., J.W.Clayton, W.R.Lillie, L.Postma (1990). Evolution and systematics of the Beluga Whale, *Delphinapterus leucas*, and other Odontocetes: a Molecular Approach. *In* T.G.Smith, D.J.Aubin, and J.R.Geraci [ed.] Advances in research on the Beluga whale, *Delphinapterus leucas*. *Canadian Bulletin of Fisheries and Aquatic Sciences* 224: pp 7-22

Lockyer, C. (1993). A Report on Patterns of Deposition of Dentine and Cement in Teeth of Pilot Whales, genus *Globicephala*. *Report of the International Whaling Commission* (Special Issue 14): pp 137 - 161

Lockyer, C. (1995). A Review of Factors involved in Zonation in Odontocete Teeth, and an Investigation of the Likely Impact of Environmental Factors and Major Life Events on Harbour Porpoise Tooth Structure. *Report of the International Whaling Commission* (Special Issue 16): pp 511 - 529

Lockyer, C. (1999). Application of a new method of investigating population structure of Harbour Porpoise, *Phocoena phocoena*, with special reference to the North and Baltic seas. ICES WGMMHA working paper 18/99: 38 pp

Macdonald, D.[ed.]. (1984). The Encyclopedia of Mammals : 1. Equinox (Oxford) Ltd., Oxford, U.K. 447 pp.

Manzanilla, S.R. (1988). The 1982-1983 El Nino event recorded in dentinal growth layers in teeth of Peruvian dusky dolphins (*Lagenorhynchus obscurus*). *Canadian Journal of Zoology*, 67: pp 2120-2125

Martin, A. & T.G.Smith (1992). Deep diving in wild, free-ranging Beluga whales, *Delphinapterus leucas*. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: pp 462-466

Martin, A.R., T.G.Smith, O.P.Cox (1993). Studying the behaviour and movements of high Arctic belugas with satellite telemetry. *Symposium of the Zoological Scoiety of London*, 66: pp 195 - 210

Martin, A. (1996). Beluga whales. Colin Baxter Photography Ltd., Moray, UK. 72 pp.

Martin, A.R., T.G.Smith, O.P.Cox (1998). Dive form and function in belugas *Delphinapterus leucas* of the eastern Canadian High Arctic. *Polar Biology*, 20: pp 218 - 228

Mitchell, E. & R.R.Reeves (1981). Catch history and cumulative catch estimates of initial population size of cetaceans in the Eastern Canadian Arctic. *Report of the International Whaling Commission* 31: pp 645 - 682

Myrick Jr., A.C., E.W.Shallenberger, I.Kang, D.B.MacKay (1984). Calibration of dental layers in seven captive Hawaiian Spinner dolphins, *Stenella longirostris*, based on tetracycline labeling. *Fishery Bulletin*, 82 (1): pp 207 - 225

Myrick Jr., A.C. & L.H.Cornell (1988). Calibrating dental layers in captive bottlenose dolphins, *Tursiops truncatus*, from serial tetracycline labels and tooth extractions. *Selected Papers on Bottlenose Dolphins*, Leatherwood & Reeves [ed.], Academic Press, San Diego, U.S.A.

G.M.O'Corry-Crowe & L.F.Lowry (1997). Genetic ecology and management concerns for the beluga whale (*Delphinapterus leucas*). *Molecular genetics of marine mammals*, A.E Dizon, S.J.Chivers and W.F.Perrin [ed.] Special Publication 3: pp 249 – 274 by the Society for Marine Mammalogy

Ognetov, G.N. & V.A.Potelov (1982). Peculiarities of white whale distribution and populations dynamics in the White Sea. *Report of the International Whaling Commission* 32: pp 415 - 418

Perrin, W.F. & A.C.Myrick, Jr. [ed.] (1980). Report of the workshop "Growth of Odontocetes and Sirenians: Problems in Age Determination". *Report of the International Whaling Commission* (Special Issue 3): pp 1 - 50

Richard, P., P.Weaver, L.Dueck, D.Barber (1994). Distribution and numbers of Canadian High Arctic Narwhals (*Monodon monoceros*) in August 1984. *Meddelelser om Grønland, Bioscience* 39: pp 41 - 50

Richard, P.R., A.R.Martin, J.R.Orr (1997). Study of summer and fall movements and dive behaviour of Beaufort sea belugas, using satellite telemetry: 1992-1995. *Environmental Studies Research Funds* No. 134, Calgary, CA. 36 pp.

Richard, P.R., M.P.Heide-Jørgensen, D.St.Aubin (1998). Fall movements of belugas (*Delphinapterus leucas*) with satellite-linked transmitters in Lancaster Sound, Jones Sound, and Northern Baffin Bay. *Arctic* 51 (1): pp 5 - 16

Savelle, J.M. (1994). Prehistoric evidence of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in the eastern Canadian Arctic. *Meddelelser om Grønland, Bioscience* 39: pp 101 - 117

Sergeant, D.E. & P.F.Brodie (1969). Body size in white whales, *Delphinapterus leucas*. *Journal of Fisheries Research Board of Canada*, 26: pp 2561 – 2580

Sergeant, D.E. & P.F.Brodie (1975). Identity, abundance, and present status of populations of white whales, *Delphinapterus leucas*, in North America. *Journal of Fisheries Research Board of Canada*, 32: pp 1047 – 1054

Slijper, E.J. (1962). Whales. Hutchinson & Co. (Publishers) Ltd., London, U.K., 475 pp.

Smith, T.G., M.O.Hammill, D.J.Burrage, G.A.Sleno (1985). Distribution and abundance of belugas, *Delphinapterus leucas*, and Narwhals, *Monodon monoceros*, in the Canadian High Arctic. *Canadian Journal of Fisheries and Aquatic Sciences*, 42: pp 676 – 684

Stewart, R.E.A. (1994). Size-at-age relationships as discriminators of white whale (*Delphinapterus leucas*) stocks in the eastern Canadian Arctic. *Meddelelser om Grønland, Bioscience* 39: pp 217 - 225

Zar, J.H. (1984). Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, New Jersey, U.S.A., 2nd Edition. 718 pp.

Appendix 1: All data used in statistical analyses in this study

IDNO	DISTR	POS	SEX	AGE	YEAR	M.W.Cem.	M.W.Den.	Ratio1	M.W.Den	M.L.Den	Ratio2	Den-GLGs	DGLG-Exp	Cem-GLGs	CGLG-Exp	PS amoun	PS loc.	ML dark	ML light	M-Int	Dent-R	DSL	GLG-type	Bnd-L	Acc.L.	NL	Wear(tip)	shpTip	shpTth	GLG-Clar
2440	Sissimiut	H2	1	0.5	94	0.4	2.5	0.16	2.5	13	0.1923	1		1		-		-	-	-	-	-	Too young	Too young	•	•	-	pointed	sl.cr	2
2436	Sissimiut	H3	1	1.0	94	0.7	3.6	0.1944	3.6	18.8	0.1915	2		2		•	c	-	-	-	-	-	L	S,D(1)	•	•	-	pointed	sl.cr	2-3
2448	Sissimiut	H2	1	1.0	94	0.6	3.2	0.1875	3.2	17.6	0.1818	2		2		-		D(2)	-	-	-	-	L	S	••	•	-	pointed	sl.cr	2-3
2444	Sissimiut	V4	2	1.5	94	0.9	4	0.2250	4	21.7	0.1843	3		3		•	s	-	-	-	-	DSL	Mixed?	S	•••	•	-	pointed	sl.cr.	2-3
2439	Sissimiut	V4	2	2.0	94	1.2	5.3	0.2264	5.3	28.6	0.1853	4		4		-		D(2,3,4)	L(2,3)	-	-	DSL	L	S,D(2)	•••	•	-	pointed	sl.cr.	1-2
2447	Sissimiut	H5	1	2.0	94	0.8	4.7	0.1702	4.7	12.9	0.3643	4		4		-		D(3)	-	-	-	-	Mixed (Mo	S	••	•	-	pointed	sl.cr.	2-3
2428	Sissimiut	H2	1	2.5	94	1.3	4.1	0.3171	4.1	22.8	0.1798	5		5		-		-	-	-	-	DSL	L	S	••	•	-	pointed	sl.cr	2
2446	Sissimiut	V5	2	3.5	94	0.8	4.7	0.1702	4.7	29.4	0.1599	7		8	7	•	s	D(4,5,6,7)	-	-	-	DSL	L	S,D(1)	•••	•	-	rounded	cyl	2
2457	Sissimiut	H4	2	4.5	94	1.5	5.3	0.2830	5.3	29.3	0.1809	9		9		•	s	D(2,5,7)	L(4)	-	-	DSL	Mixed	S,D(3)	•••	•	-	rounded	sl.cr.	2
2358	Sissimiut	V2	2	5.0	94	1.7	6	0.2833	6	34.6	0.1734	10		10		-		D(1,4,6,8,1	-	-	-	DSL	Mixed	S,D(2)	•••	•	•	flat	sl.cr.	2
2450	Sissimiut	V2	1	5.0	94	1.8	5.3	0.3396	5.3	34.5	0.1536	10		10		••	s	D(5,7,8,9)	-	-	-	DSL	Mixed	S,D(2)	•••	•	•	rounded	sl.cr.	2-3
2456	Sissimiut	V6	1	5.5	94	1	4.3	0.2326	4.3	28.8	0.1493	11		10.		•	s	D(3,7)	-	-	-	DSL	L	S,D(2)	••	•	-	rounded	sl.cr	2-3
2455	Sissimiut	H3	2	6.5	94	3.2	4.9	0.6531	4.9	36.6	0.1339	13		13		•	c	D(1,3,11)	-	-	-	DSL	Mixed	S,D(3)	•••	•	-	rounded	cyl.	1-2
1758	Sissimiut	H6	1	7.0	94	1.7	6.6	0.2576	6.6	34.6	0.1906	14		12	14	-		D(2,3)	-	-	-	DSL	Mixed	S,D(2)	••	-	•	rounded	sl.cr	1-2
2429	Sissimiut	V3	1	7.5	94	2.6	5	0.5200	5	36.7	0.1362	14		13	14	•	c	D(3,10)	L(4)	-	-	DSL	L	S,D(4)	•••	-	•	rounded	sl.cr	2
2427	Sissimiut	V8	1	7.5	94	1	5	0.2000	5	26.4	0.1894	14	15	7	14	•	s	-	-	-	-	-	D	S,D(4)	•	•	-	rounded	sl.cr	1
2425	Sissimiut	H4	1	8.0	94	1.5	4.7	0.3191	4.7	30.5	0.1541	16		13	16	••	c,s	D(9,13,14)	-	-	-	-	L	S,D(12)	•	.	•	rounded	sl.cr.	2-3
2449	Sissimiut	H5	1	8.5	94	1.4	5.4	0.2593	5.4	30.3	0.1782	17		15	17	••	c,r	D(3)	L(7)	-	-	DSL	Mixed	S,D(4)	•	-	•	rounded	sl.cr.	3
2434	Sissimiut	H6	1	9.0	94	1.7	6	0.2833	6	33.1	0.1813	18		12	18	•	c	D(3,8,9,13	-	-	-	-	Mixed	S,D(11)	••	•	•	rounded	cyl.	2
2431	Sissimiut	V6	1	9.5	94	2.1	4.3	0.4884	4.3	24.3	0.1770	19		15	19	•	s	-	L(3)	-	-	-	Mixed	S,D(4)	•••	•	-	rounded	sl.cr.	2
2423	Sissimiut	V1	1	10.0	94	1.8	3.2	0.5625	3.2	37	0.0865	16	20	15	20	•••	c	-	L(13,14)	•	-	-	L	S,D(4)	••	-	•	flat	sl.cr.	1-2
2441	Sissimiut	H3	2	10.0	94	3.9	4.1	0.9512	4.1	38.8	0.1067	20		19	20	-		D(5)	-	-	-	-	L	S,D(4)	••	-	•	flat	sl.cr.	2
2421	Sissimiut	V6	1	10.5	94	1.1	3.9	0.2821	3.9	27.6	0.1413	21		18	21	•	r	-	L(1)	-	-	-	Mixed	S	•	•	.	rounded	cyl.	2
2430	Sissimiut	V4	1	10.5	94	1	3.3	0.3030	3.3	26.5	0.1156	21		7	21	-		-	-	-	-	-	Mixed	S	••	•	•	rounded	sl.cr.	3
2414	Sissimiut	H7	1	12.0	94	2	4.3	0.4651	4.3	25	0.1720	24		21	24	•	s	-	-	-	-	-	Mixed	S,D(1)	••	-	•	rounded	sl.cr.	1-2
2453	Sissimiut	H5	1	12.5	94	2.6	5.7	0.4912	5.7	34.4	0.1657	25		23	25	•••	c,s	D(3,4,5)	-	-	-	-	L	S,D(6),T(3	••	-	•	rounded	cyl.	2-3
2581	Sissimiut	V7	0	13.5	93	1.9	5.1	0.3725	5.1	30.3	0.1683	27		19	27	•	s	D(3)	L(10,12,15	•	-	DSL	D	S	•••	-	•	rounded	cyl	3
2438	Sissimiut	H2	1	14.0	94	1.7	5.1	0.3333	5.1	40.2	0.1269	25	28	19	28	•••	c,r	D(8,17,19)	-	•	-	DSL	L	S,D(2)	•	-	•	flat	sl.cr.	1
2420	Sissimiut	V6	1	15.0	94	1	4.9	0.2041	4.9	28.9	0.1696	30		23	30	•	s	D(5,13,15)	-	-	-	-	L	S,D(3)	•	-	•	rounded	cyl.	1-2
2422	Sissimiut	V2	1	16.0	94	2.1	5.1	0.4118	5.1	34.1	0.1496	29	30	26	30	••	r,s	D(15,19)	-	•	-	-	Mixed	S,D(4)	••	-	•	flat	sl.cr.	2
2432	[redacted]ut	H1	1	16.0	94	1.6	3.6	0.4444	3.6	12.4	0.2903	28	30	28	30	•	s	-	-	-	-	DSL	Mixed	S	•••	-	•	flat	sl.cr.	2
2424	Sissimiut	V5	1	16.5	94	3.9	7.7	0.5065	7.7	34.9	0.2206	31		28	31	•••	c	D(2)	-	-	-	-	Mixed	S,D(2)	•	-	•	flat	irr.	1-2
2337	Sissimiut	V6	1	16.0	94	0.6	5.8	0.1034	5.8	32.6	0.1779	38	32	20	32	•••	c,r	D(3,4,5,12	L(7,8,9,10)	•	-	DSL	L	S,D(12)	•••	-	•	rounded	sl.cr.	3
2350	Sissimiut	V6	1	17.0	94	2.3	5.2	0.4423	5.2	35.9	0.1448	34		31	34	•	c	D(3,22,25)	L(24,26)	-	-	-	L	S,D(9)	••	-	•	rounded	sl.cr.	3
2345	Sissimiut	H6	1	17.5	94	2.6	4.6	0.5652	4.6	32.9	0.1398	32	35	28	35	••	c,r	D(4,8,10,1	-	•	-	-	L	S,D(2)	••	-	•	rounded	sl.cr.	1
2445	Sissimiut	H6	1	17.5	94	1.4	4.8	0.2917	4.8	30.1	0.1595	35		24	35	••	c,s	D(18,28)	L(32)	-	-	DSL	Mixed	S,D(5)	•	-	•	rounded	sl.cr.	1-2
2339	Sissimiut	H6	1	18.0	94	2.1	4	0.5250	4	33.6	0.1190	35	36	28	36	•	s	D(33,34)	-	-	-	DSL	D	S	••	-	•	rounded	sl.cr.	1-2
2352	Sissimiut	V8	1	19.0	94	1.9	4.2	0.4524	4.2	28.3	0.1484	38		18	38	•	s	D(10)	L(4,5)	-	-	-	L	S,D(4)	•	-	•	rounded	sl.cr.	1
2354	Sissimiut	V3	1	19.5	94	3.4	5.4	0.6296	5.4	43.3	0.1247	39		34	39	••	c,r	D(32,33)	L(10,31,38	-	-	DSL	L	S	•••	-	•	rounded	sl.cr.	2-3
2358	Sissimiut	H2	1	19.5	94	2.8	4.4	0.6364	4.4	35.9	0.1226	39		33	39	••	c,s	D(32)	L(13)	-	-	-	L	S,D(8)	•	-	•	flat	sl.cr.	1-2
2331	Sissimiut	H5	1	20.0	94	2.6	4.4	0.5909	4.4	29.1	0.1512	40		38	40?	•	c	-	-	-	-	DSL	Mixed	S,D(4)	•	-	•	flat	cyl.	3
2418	Sissimiut	H6	1	20.0	94	1.4	4.2	0.3333	4.2	29.2	0.1438	40		40	25	•	s	-	-	-	-	-	L	S,D(5)	••	-	•	rounded	sl.cr.	1
2452	Sissimiut	V8	1	20.5	94	1.4	3.3	0.4242	3.3	29.5	0.1119	44	45	20	45	•	s	D(25,32)	L(30)	-	-	DSL	L	S	•••	-	•	rounded	cyl.	1-2
2433	Sissimiut	V4	1	21.0	94	2.8	4.8	0.5833	4.8	34.4	0.1395	44	42	42		•	s	-	L(8)	-	-	DSL	L	S,D(7)	•	-	•	rounded	cyl.	1
2426	Sissimiut	V3	1	22.0	94	2.2	3.8	0.6111	3.6	23.2	0.1552	51	44	12	44	•••	s	-	-	-	-	-	L	D	•	-	•	flat	cyl.	2
2327	Sissimiut	V4	1	22.5	94	3.5	3.8	0.9211	3.8	34	0.1118	44	45	41	45	••	c,s	-	-	•	-	DSL	L	D	•••	-	•	rounded	sl.cr.	3

Abbreviations:

IDNO=	Identification Number	Den-GLGs=	# of Dentinal GLGs	M-Int.=	Mineralisation Interference	NL=	Neonatal Line
DISTR=	District, area of sampling	Den-GLGs-Exp.=	# of Dentinal GLGs previously counted	Dent-R.=	Dentinal Resorption	Wear(Tip)=	Wear of tip of tooth
M.W.Cem.=	Maximum Width of Cementum	Cem-GLGs=	# of Cemental GLGs	DSL=	Dark Staining Layers	shpTip=	Shape of Toothtip
M.W.Den.=	Maximum Width of Dentine	Cem-GLGs-Exp.=	# of Cemental GLGs previously counted	GLG-Type=	Type of GLG present	shpTth=	Shape of Tooth
M.L.Den.=	Maximum Length of Dentine	PS amount=	# of Pulpstones	Bnd-L.=	Presence, colour of Boundary Layers	GLG-Clar.=	Clarity of GLFGs
Ratio1=	M.W.Cem./M.W.Den.	PS loc.=	Location of Pulpstones	Acc.L.=	Accessory Lines		
Ratio2=	M.W.Den./M.L.Den.						

IDNO	DISTR	POS	SEX	AGE	YEAR	M.W.Cem	M.W.Den.	Ratio1	M.W.Den.	M.L.Den	Ratio2	Den-GLGs	DGLG-Exp	Cem-GLGs	CGLG-Exp	PS amoun	PS loc.	ML dark	ML light	M-Int	Dent-R	DSL	GLG-type	Bnd-L	Acc L	NL	Wear(tip)	shpTip	shpTth	GLG-Clar
2203	Upernavik	V2		1	0.0	92	0.2	2	0.1	2	10.7	0.186916	0		0		-		too young	too young	-	-	-	too young	too young	too young	+	-	pointed	st.cr.	2
2184	Upernavik	V2		1	0.5	93	0.4	3	0.133333	3	14.1	0.212766	1		1		-		too young	too young	-	-	DSL	too young	too young	+	+	-	pointed	st.cr.	2
2223	Upernavik	V1		2	1.0	93	0.6	2.9	0.206897	2.9	14.4	0.201389	2		2		-		-	-	-	-	-	D	S	-	+	-	pointed	st.cr.	2
2190	Upernavik	H4		1	1.5	93	0.9	4.2	0.214286	4.2	24.8	0.169355	3		3		-		D(2)	-	-	-	-	L	D	+++	+	-	pointed	st.cr.	1-2
1727	Upernavik	H4		1	2.0	92	0.9	4.2	0.214286	4.2	22.4	0.1875	4		4		-		D(3)	L(2)	-	-	DSL	Mixed	S	+	+	-	pointed	st.cr.	1-2
2194	Upernavik	V2		2	2.0	93	0.6	3.1	0.193548	3.1	28.9	0.107266	4		3	4	-		D(2,3)	-	-	-	-	Mixed	S,D(2)	++	+	-	pointed	st.cr.	2-3
1715	Upernavik	H3		2	2.5	92	1.1	5.2	0.211538	5.2	31.6	0.164557	5		5		-		D(3)	-	-	-	DSL	Mixed	S,D(1)	++	+	-	pointed	st.cr.	1-2
2187	Upernavik	V4		2	3.5	93	1.1	5	0.22	5	27.2	0.183824	7		7		+	s	-	-	-	-	-	L	S	++	+	-	pointed	st.cr.	2
2192	Upernavik	V5		1	4.0	93	0.9	4.6	0.195652	4.6	24.7	0.186235	7	8	6	8	+	s	D(1)	L(4)	-	-	-	L	S,D(2)	++	+	-	pointed	cyl.	2-3
2198	Upernavik	H6		2	4.0	93	1	4.6	0.217391	4.6	30.7	0.149837	8		8		-		D(8)	-	-	-	DSL	Mixed	S	++	+	-	pointed	st.cr.	2-3
1730	Upernavik	V4		1	4.5	92	1.4	5.1	0.27451	5.1	25	0.204	9		8	9	-		-	-	-	-	DSL	L	S	+	+	-	pointed	cyl.	2
2185	Upernavik	V5		2	5.0	93	1.1	5.6	0.196429	5.6	35.4	0.158192	11	10	10		+	s	-	L(4,5)	-	-	DSL	Mixed	S,D(3)	+++	+	+	pointed	st.cr.	2-3
2201	Upernavik	V3		2	5.0	93	1.1	4.7	0.234043	4.7	29.3	0.16041	10		10		+	s	D(6,7,8)	-	-	-	DSL	L	S	++	+	+	pointed	st.cr.	2
1720	Upernavik	V2		2	6.0	92	4.2	5.4	0.777778	5.4	35	0.154286	12		10	12	++	c	D(1,3,4,6,7)	L(7)	-	-	-	L	S	+++	-	+	rounded	st.cr	3
1728	Upernavik	V6		1	6.0	92	1.2	5.1	0.235294	5.1	32.8	0.155488	13	12	12		+	s	D(5,10)	-	-	-	-	Mixed	S,D(3),T(2)	+++	-	+	rounded	st.cr.	2
1737	Upernavik	V2		2	7.0	92	2.2	5.5	0.4	5.5	41.4	0.13285	14		14		+	c	-	L(4,7)	-	-	DSL	Mixed	S,D(5)	++	-	+	flat	st.cr.	2
1702	Upernavik	H2		1	8.0	92	1.1	5.8	0.189655	5.8	32.2	0.180124	16		16		+	s	D(3)	-	+	-	DSL	Mixed	S	++	+	+	rounded	st.cr.	1-2
1742	Upernavik	H3		1	8.0	92	1.6	6	0.266667	6	36.2	0.165746	16		15	16	+	s	-	-	+	-	DSL	Mixed	S,D(8)	+++	-	+	rounded	st.cr.	2
2200	Upernavik	H1		1	9.0	93	2.3	4.7	0.489362	4.7	28.1	0.16726	16		17	18	-		D(9)	L(6,10,12,14	+	-	DSL	Mixed	S,D(5)	++	+	-	rounded	st.cr.	1-2
1721	Upernavik	H1		2	9.5	92	3.3	5.3	0.622642	5.3	42.2	0.125592	19		19		+	c	D(8,13)	-	-	-	DSL	L	S,D(4)	+++	-	+	rounded	st.cr.	3
1744	Upernavik	H2		2	9.5	92	2.5	5.1	0.490196	5.1	38.3	0.133159	19		16	19	+	c,r	D(12)	L(3,6)	-	-	DSL	Mixed	S,D(3)	+++	-	+	rounded	st.cr.	3
1749	Upernavik	V2		2	9.5	92	3.2	4.9	0.653061	4.9	46.1	0.106291	19		17	19	++	c,s	D(3,13)	L(5)	-	-	DSL	Mixed	S,D(2)	+	-	+	flat	st.cr.	1-2
2229	Upernavik	V2		1	11.0	93	1.9	4.8	0.395833	4.8	23.6	0.20339	22		18	22	+++	s	-	-	+	-	-	L	S,D(6)	++	-	+	flat	st.cr.	3
1733	Upernavik	V5		2	11.5	92	3.1	8.2	0.378049	8.2	59	0.138983	23		23		++	c	D(5,8,13)	-	-	-	DSL	L	S,D(2)	+++	-	+	flat	cyl.	1-2
2189	Upernavik	V2		1	12.0	93	2.3	4.7	0.489362	4.7	37.7	0.124668	24		22	24	+	r	D(4,7,10)	-	-	-	-	Mixed	S,D(5)	++	-	+	rounded	st.cr.	1
2224	Upernavik	H4		1	12.0	93	3.4	5.8	0.586207	5.8	38.5	0.150649	30	24	25	24	+++	c,r,s	-	-	-	-	-	D	S	++	-	+	flat	st.cr.	1-2
1747	Upernavik	H3		1	13.0	92	2.2	4.1	0.536585	4.1	31	0.132258	27	26	23	26	+	s	D(5,7,10,14,	-	-	-	-	L	S,D(11)	+	-	+	flat	st.cr.	2
1959	Upernavik	H3		1	13.0	93	2	5	0.4	5	32.8	0.152439	27	26	23	26	++	c,s	-	-	+	-	DSL	L	S,D(12),T(3	++	-	+	rounded	st.cr.	3
1853	Upernavik	V7		2	13.5	93	2.9	4.5	0.644444	4.5	39.2	0.114796	27		25	27	++	c,r	D(8,10,21)	L(24)	-	-	DSL	L	S,D(1)	+	-	+	flat	cyl.	1-2
2202	Upernavik	H4		1	13.5	93	1.9	5.4	0.351852	5.4	39.6	0.136364	26	27	22	27	++	c,r	D(5)	-	+	-	-	Mixed	S	+	+	+	rounded	st.cr.	1
1700	Upernavik	H6		2	14.5	92	2.8	4.5	0.622222	4.5	46.3	0.097192	28	29	23	29	++	c,s	-	-	-	-	DSL	Mixed	S,D(2)	+++	-	+	rounded	cyl.	2
1865	Upernavik	H3		1	14.5	93	3.1	4	0.775	4	34.3	0.116618	29		29		+++	s	??????	??????	??????	??????	??????	??????	??????	??????	-	+	rounded	st.cr.	3
1897	Upernavik	H4		1	16.0	93	2.5	6.5	0.384615	6.5	37.8	0.171958	34	32	33	32	+++	c,s	D(10,23,31,:	L(4,28,30)	+	-	DSL	L	S,D(8)	+	-	+	rounded	st.cr	2-3
1840	Upernavik	H4		1	17.5	93	2.6	5.2	0.5	5.2	38.4	0.135417	42	35	32	35	++	s	-	-	-	-	DSL	Mixed	S,D(3)	+	-	+	rounded	st.cr.	1-2
1953	Upernavik	V2		1	17.5	93	3.2	4.5	0.711111	4.5	34.4	0.130814	35	35	37	35	+++	c,r,s	-	-	+	-	-	Mixed	S,D(5)	+	-	+	rounded	st.cr.	1-2
2173	Upernavik	V2		2	17.5	93	5	4.6	1.086957	4.6	53.1	0.086629	35		27	35	+++	c,r	D(24,27,28)	-	-	-	DSL	L	S,D(5)	+	-	+	rounded	st.cr.	1-2
2208	Upernavik	H5		1	17.5	93	3.4	5.2	0.653846	5.2	32.7	0.159021	37	35	33	35	+	s	D(4,31)	-	-	-	-	L	S	+	-	+	rounded	cyl.	1
1998	Upernavik	H1		2	18.0	93	5.1	3	1.7	3	47.9	0.06263	35	36	35	36	+	s	D(2,3)	-	-	-	DSL	Mixed	S,D(8)	++	-	+	rounded	st.cr.	2-3
1701	Upernavik	V3		2	18.0	92	3.5	7	0.5	7	49.6	0.141129	38		38		+++	c,r,s	D(22,31)	-	-	-	DSL	Mixed	S	++	-	+	rounded	st.cr.	1
1883	Upernavik	V4		1	20.0	93	2.6	5.4	0.481481	5.4	45.8	0.117904	40		33	40	++	c,s	-	L(8,16)	-	-	DSL	Mixed	S	++	-	+	pointed	st.cr.	2
202	Upernavik	H1		1	21.5	90	4	3.6	1.111111	3.6	42.5	0.084706	43		34	43	+	c,s	-	-	-	-	-	L	S,D(8)	+	-	+	flat	st.cr.	1
1902	Upernavik	H1		2	22.0	93	4.2	3.9	1.076923	3.9	36.6	0.106557	42	44	39	44	+	c	D(31)	-	-	-	DSL	Mixed	S,D(4)	+	-	+	rounded	st.cr	1
2183	Upernavik	H1		1	22.0	93	4.5	3.9	1.153846	3.9	32.2	0.121118	44		42	44	+	s	-	-	-	-	DSL	Mixed	S,D(2)	+	-	+	flat	st.cr	1
2172	Upernavik	V2		1	22.5	93	2.6	5.1	0.509804	5.1	27.3	0.186813	45		39	45	+++	c,s	D(4,8,14)	-	-	-	DSL	L	S,D(3)	++	-	+	rounded	st.cr.	2-3
2388	Upernavik	V6		1	22.5	93	2.6	3.8	0.684211	3.8	40.7	0.093366	45		35	45	+	s	D(5,14,25,2	-	-	-	DSL	Mixed	S,D(2)	+	-	+	rounded	st.cr.	1-2
2508	Upernavik	V2		0	23.0	94	6	5.5	1.090909	5.5	54.7	0.100548	46		43	46	++	c	??????	??????	??????	??????	??????	??????	??????	???????	-	+	flat	st.cr.	1

Abbreviations:

IDNO=	Identification Number	Den-GLGs=	# of Dentinal GLGs	M-Int.=	Mineralisation Interference	NL=	Neonatal Line
DISTR=	District, area of sampling	Den-GLGs-Exp.=	# of Dentinal GLGs previously counted	Dent-R.=	Dentinal Resorption	Wear(Tip)=	Wear of tip of tooth
M.W.Cem.=	Maximum Width of Cementum	Cem-GLGs=	# of Cemental GLGs	DSL=	Dark Staining Layers	shpTip=	Shape of Toothtip
M.W.Den.=	Maximum Width of Dentine	Cem-GLGs-Exp.=	# of Cemental GLGs previously counted	GLG-Type=	Type of GLG present	shpTth=	Shape of Tooth
M.L.Den.=	Maximum Length of Dentine	PS amount=	# of Pulpstones	Bnd-L.=	Presence, colour of Boundary Layers	GLG-Clar.=	Clarity of GLFGs
Ratio1=	M.W.Cem./M.W.Den.	PS loc.=	Location of Pulpstones	Acc.L.=	Accessory Lines		
Ratio2=	M.W.Den./M.L.Den						

IDNO	DISTR	POS	SEX	AGE	YEAR	M.W.Cem	M.W.Den	Ratio1	M.W.Den.	M.L.Den	Ratio2	Den-GLGs	DGLG-Exp	Cem-GLGs	CGLG-Exp	PS amoun	PS loc.	ML dark	ML light	M-Int	Dent-R	DSL	GLG-type	Bnd-L	Acc.L.	NL	Wear(tip)	shpTip	shpTth	GLG-Clar
LDL-8-92	Alaska			1	92	0.171	2.85	0.06	2.85	15.22	0.187254	1.5	?	?	?	-	none	?	?	-	-	-	D	?	?	•	?	?	?	1
LDL-7-92	Alaska			1	92	0.5415	3.61	0.15	3.61	18.92	0.190803	2.5	?	?	?	-	none	?	?	-	-	-	D	?	?	•	?	?	?	1
LDL-20-92	Alaska			5.5	92	1.1825	4.73	0.25	4.73	21.54	0.219591	11	?	?	?	-	none	?	?	-	-	-	D	?	?	-	?	?	?	1-2
LDL-4-92	Alaska			8	92	2.27	4.54	0.5	4.54	22.87	0.198513	11.5	?	?	?	-	none	?	?	-	-	-	D	?	?	•	?	?	?	1-2
LDL-5-92	Alaska			6.0	92	1.855	5.3	0.35	5.3	24.76	0.214055	12	?	?	?	-	none	?	?	-	-	-	D	?	?	•	?	?	?	1
LDL-10-92	Alaska			9.5	92	5.91	5.91	1	5.91	35.76	0.165268	19	?	?	?	•••	c	?	?	•	-	-	D	?	?	-	?	?	?	1
LDL-14-92	Alaska			9.5	92	2.8405	4.37	0.65	4.37	28.99	0.150742	19	?	?	?	•	c,s	?	?	-	-	-	D	?	?	-	?	?	?	1
LDL-6-92	Alaska			10	92	1.98	3.96	0.5	3.96	28.19	0.140475	19.5	?	?	?	•	c,r	?	?	-	-	DSL	D	?	?	-	?	?	?	2
LDL-16-92	Alaska			11	92	2.7	5.4	0.5	5.4	33.4	0.161677	22.5	?	?	?	•••	c,r	?	?	-	-	DSL	D	?	?	-	?	?	?	1-2
LDL-24-92	Alaska			12	92	2.743	4.22	0.65	4.22	40.01	0.105474	24.5	?	?	?	•	c	?	?	-	-	DSL	D	?	?	-	?	?	?	1-2
LDL-2-92	Alaska			13	92	3.471	5.34	0.65	5.34	43.03	0.124099	25.5	?	?	?	•	s	?	?	-	-	DSL	Mixed	?	?	-	?	?	?	2
LDL-3-92	Alaska			14.5	92	1.632	5.44	0.3	5.44	21.2	0.256604	29	?	?	?	••	c,s	?	?	-	-	DSL	D	?	?	-	?	?	?	1-2
LDL-1-92	Alaska			15	92	3.025	6.05	0.5	6.05	34.91	0.173303	29.5	?	?	?	•••	c,r,s	?	?	-	-	-	Mixed	?	?	-	?	?	?	1-2
LDL-12-92	Alaska			15	92	3.594	5.99	0.6	5.99	35.6	0.167318	30.5	?	?	?	•••	c	?	?	-	-	-	D	?	?	-	?	?	?	1-2
LDL-21-92	Alaska			16.5	92	2.772	6.16	0.45	6.16	31.97	0.192681	33	?	?	?	••	c	?	?	-	-	-	D	?	?	-	?	?	?	1
LDL-22-92	Alaska			16.5	92	2.312	5.78	0.4	5.78	26.03	0.222051	33	?	?	?	•••	c,r	?	?	•	-	DSL	Mixed	?	?	-	?	?	?	2
LDL-17-92	Alaska			17.5	92	5.522	5.02	1.1	5.02	32.69	0.153564	35	?	?	?	•	c,r	?	?	-	-	-	Mixed	?	?	-	?	?	?	1-2
LDL-23-92	Alaska			18	92	1.694	4.84	0.35	4.84	22.01	0.2199	35.5	?	?	?	•	c	?	?	-	-	DSL	D	?	?	-	?	?	?	1
LDL-19-92	Alaska			18	92	3.1005	4.77	0.65	4.77	34.56	0.138021	36.5	?	?	?	••	c,r	?	?	-	-	-	D	?	?	-	?	?	?	1-2
LDL-9-92	Alaska			18.5	92	1.526	4.36	0.35	4.36	22.96	0.189895	37	?	?	?	•	s	?	?	-	-	DSL	D	?	?	-	?	?	?	1
LDL-15-92	Alaska			19	92	4.509	5.01	0.9	5.01	41.12	0.121839	37.5	?	?	?	•	c,r	?	?	-	-	-	Mixed	?	?	-	?	?	?	2
LDL-18-92	Alaska			19	92	3.806	3.46	1.1	3.46	33.06	0.104658	37.5	?	?	?	•	s	?	?	-	-	-	D	?	?	-	?	?	?	1-2
LDL-11-92	Alaska			20	92	4.344	5.43	0.8	5.43	40.1	0.135411	39.5	?	?	?	•••	c,r	?	?	-	-	-	Mixed	?	?	-	?	?	?	2
LDL-13-92	Alaska			22	92	3.451	4.93	0.7	4.93	37.63	0.131012	43.5	?	?	?	•	s	?	?	-	-	-	D	?	?	-	?	?	?	1-2

Tooth Sequences

IDNO	DISTR	POS	SEX	AGE	YEAR	M.W.Cem	M.W.Den	Ratio1	M.W.Den.	M.L.Den	Ratio2	Den-GLGs	DGLG-Exp	Cem-GLGs	CGLG-Exp	PS amoun	PS loc.	ML dark	ML light	M-Int	Dent-R	DSL	GLG-type	Bnd-L	Acc.L.	NL	Wear(tip)	shpTip	shpTth	GLG-Clar
2391	Upernavik	V1	1	10.5	93	1.8	3.3	0.545455	3.3	25.1	0.131474	15	21	14	21	•	s	-	-	-	-	-	L	S,D(5)	•	-	•	flat	st.cr.	1-2
		V2	1	10.5	93	2.3	3.5	0.657143	3.5	23.4	0.149573	18	21	15	21	•	s	-	L(16,18)	-	-	-	Mixed	S,D(4)	•	-	•	rounded	st.cr.	1-2
		V3	1	10.5	93	2.1	4.6	0.456522	4.6	46.7	0.098501	19	21	19	21	•	s	D(12,19)	L(16,18)	?	-	-	Mixed	S	••	-	•	rounded	st.cr.	1-2
		V4	1	10.5	93	2.3	4.5	0.511111	4.5	35.7	0.12605	21	21	15	21	•	s	-	-	-	-	-	Mixed?	S	•	-	•	flat	st.cr.	1
		V5	1	10.5	93	2.2	4.6	0.478261	4.6	39	0.117949	21	21	19	21	•	s	D(12,16,20,	L(21)	•	-	-	Mixed	S,D(2)	•	•	•	rounded	cyl.	2
		V6	1	10.5	93	2.1	4.5	0.466667	4.5	36.3	0.123967	20	21	20	21	•	s	D(16,19,20)	-	-	-	DSL	Mixed	S,D(1)	••	•	•	rounded	cyl.	1-2
		V7	1	10.5	93	1.8	3.3	0.545455	3.3	29.6	0.111486	20	21	20	21	•	s	D(16,18)	L(20)	-	-	-	Mixed	S,D(1)	••	•	-	rounded	st.cr.	2
		V8	1	10.5	93	1.6	3.7	0.432432	3.7	24.9	0.148594	20	21	19	21	•	s	D(14,15)	-	-	-	-	Mixed	S	•	•	•	irregular	cyl.	2
		V9	1	10.5	93	0.8	3.3	0.242424	3.3	25.9	0.127413	21	21	13	21	•	s	D(20)	-	-	-	-	Mixed	S	•	•	-	rounded	st.cr.	2
2421	Sisimiut	H1	1	10.5	94	1.9	3.9	0.487179	3.9	18.6	0.209677	17	21	16	21	•	s	D(4,5,8,9,15	-	•	-	-	L	S,D(1)	•	-	•	flat	st.cr.	2
		H2	1	10.5	94	2.2	4.7	0.468085	4.7	24.4	0.192623	19	21	17	21	•	s	D(15,16)	L(10)	•	-	-	L	S,D(4)	••	-	•	flat	st.cr.	2
		H3	1	10.5	94	2.4	4.5	0.533333	4.5	25.4	0.177165	19	21	18	21	•	s	-	-	?	-	-	L	S,D(5)	••	-	•	irregular	st.cr	2
		H4	1	10.5	94	2.4	4	0.6	4	26.2	0.152672	19	21	17	21	•	s	D(16)	L(12)	-	-	-	Mixed?	S,D(1)	•	-	•	flat	st.cr.	1
		H5	1	10.5	94	2.4	4.7	0.510638	4.7	25.9	0.181467	21	21	15	21	•	s	D(17,19)	-	-	-	-	Mixed	S,D(6)	••	-	•	rounded	cyl.	1-2
		H6	1	10.5	94	2.2	4.2	0.52381	4.2	25.2	0.166667	21	21	19	21	•	s	D(9,15)	L(13)	-	-	-	Mixed	S,D(4)	••	•	•	irregular	cyl	1-2
		H7	1	10.5	94	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????
		H8	1	10.5	94	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????	??????
2430	Sisimiut	H1	1	10.5	94	2.1	3.5	0.6	3.5	24.1	0.145228	19	21	?	21	•	c	?		-	-	-	Mixed?	S	•	-	•	flat	cyl.	1
		H2	1	10.5	94	1.7	4.5	0.377778	4.5	31.4	0.143312	20	21	18	21	•	c	D(8,15)	L(17)	-	-	-	Mixed?	S	••	-	•	rounded	st.cr.	2-3
		H3	1	10.5	94	1.4	4.5	0.311111	4.5	27.6	0.163043	23	21	13	21	•	c, r	D(8,15)	-	-	-	DSL	Mixed	S,D(2)	••	-	•	flat	st.cr.	2
		H4	1	10.5	94	1.6	3.1	0.516129	3.1	26.1	0.118774	22	21	10	21	•	s	D(13,21)	L(19)	-	-	-	Mixed	S,D(5)	•	•	•	rounded	st.cr.	1-2
		H5	1	10.5	94	0.7	4.3	0.162791	4.3	28.1	0.153025	22	21	9	21	•	-	D(6,10)	L(14)	-	-	-	L	S,D(5)	•	•	-	rounded	st.cr.	2

Abbreviations:

IDNO=	Identification Number	Den-GLGs=	# of Dentinal GLGs	M-Int.=	Mineralisation Interference	NL=	Neonatal Line
DISTR=	District, area of sampling	Den-GLGs-Exp =	# of Dentinal GLGs previously counted	Dent-R.=	Dentinal Resorption	Wear(Tip)=	Wear of tip of tooth
M.W.Cem.=	Maximum Width of Cementum	Cem-GLGs=	# of Cemental GLGs	DSL=	Dark Staining Layers	shpTip=	Shape of Toothtip
M.W.Den.=	Maximum Width of Dentine	Cem-GLGs-Exp.=	# of Cemental GLGs previously counted	GLG-Type=	Type of GLG present	shpTth=	Shape of Tooth
M.L.Den.=	Maximum Length of Dentine	PS amount=	# of Pulpstones	Bnd-L.=	Presence, colour of Boundary Layers	GLG-Clar.=	Clarity of GLFGs
Ratio1=	M.W.Cem./M.W.Den.	PS loc.=	Location of Pulpstones	Acc.L.=	Accessory Lines		
Ratio2=	M.W.Den./M.L.Den.						

Appendix 2: Tests concerning Maximum width of Cementum. Only tests which yielded significant results are included

Trendline Analysis — For difference in M.W.Cem. Between Upernavik Males and Sissimiut Females

Upernavik Males

x(av)=	10.44118	SP=	106.3882
y(av)=	2.788235	SP^2=	11318.46
sum(X)	177.5		
sum(Y)	47.4	SS(Y)=	30.29765
sum(XY)	601.3		
n	17	SS(X)=	586.9412
sum(X^2)	2440.25		
sum(Y^2)	162.46		
b(UM)=	0.1813		

RESVAR 0.734256

SE(b(UM)) 0.035369

t= 5.125913
df= 15
Consult appendix 2: SIGNIFICANT

In other words, the trendline is significant

Sissimiut Females

x(av)=	13.82353	SP=	64.01471
y(av)=	1.944118	SP^2=	4097.883
sum(X)	470		
sum(Y)	66.1	SS(Y)=	20.34382
sum(XY)	977.75		
n	34	SS(X)=	1019.941
sum(X^2)	7517		
sum(Y^2)	148.85		
b(SF)=	0.0628		

RESVAR 0.510189

SE(b(SF)): 0.022365

t= 2.807899
df= 32
Consult appendix 2: SIGNIFICANT

In other words, the trendline is significant

Compare trendlines UM and SF

b(UM)=	0.1813	b(SF)-b(UM	0.1185
SE(b(UM))	0.035369	SE(bSF-bU	0.041847
b(SF)=	0.0628	t=	2.831719
SE(b(SF)):	0.022365	df=	47

STRONGLY SIGNIFICANT

So, a significant difference between Upernavik males and Sissimiut females

ANOVA — For comparison of M.W.Cem. of the three datasets

	Alaska	Upernavik	Sissimiut	Overall
n=	22	40	40	102
AVx=	3.01	2.6675	1.9775	
stdevX=	1.253415	1.25031	0.836196	
VARx=	1.571048	1.563276	0.699224	
SUMx=	66.24	106.7	79.1000	252.04
(SUMx)^2	4387.671	11384.89	6256.81	
SUMx^2=	232.43	345.59	183.69	761.71

	SS	df	s^2	F
Between	17.69868	2	8.84934	7.226661
Within	121.2295	99	1.224541	
Total	138.9282			

Fmax-test: 2.246845 < Table value

Proceed with ANOVA

Correction Term:
CT= 622.7834

SS(total)
SSt= 138.93

SS(between)
SS(betw.)= 17.69868

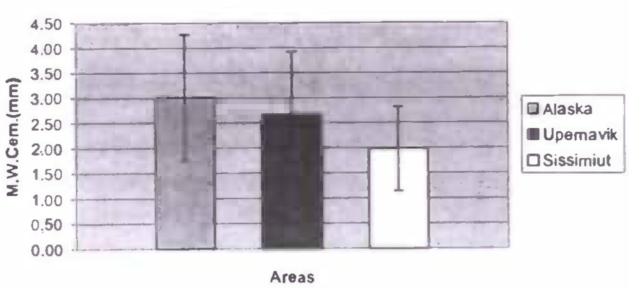
SS(within)
SS(with.)= 121.23
df(SSt)= 101
df(SSbetw) 2
df(SSwith): 99

s^2(betw) 8.84934
s^2(with) 1.224541

F= 7.226661 > table value (l.o.s.=0,05, 2, 120= 3.0718)

In other words, H0 is rejected;
There is a significant difference in variance between the three populations

Average M.W.Cem., overall; sexes pooled, age >2



Appendix 3: Tests concerning Maximum Length of Dentine. Only tests which yielded significant results are included

T-TEST For analysis of differences in M.L.Den. between Sissimiut and Upernavik

	Sissimiut	Upernavik
n	40	40
x	31.4	37.3
s	5.495266	8.342268
s^2	30.19795	69.59343
x-x	-6	
n+/n*	0.05	
n-1)s^2	1177.72	
n-1)s^2	2714.144	
	3891.864	
n+n-2	78	
	2.494784	
	1.579489	
t-test=	-3.727472	

t(crit) at df =76: l.o.s.(df=60, l.o.s.=0.05,2-tl) = 2.000
SIGNIFICANT
In other words, there is a significant difference between the two areas

T-TEST For analysis of differences in M.L.Den. between Upernavik Males and Females

	Females	Males
n	22	17
x	33.99545	40.52353
s	5.90258	8.884152
s^2	34.84045	78.92816
x-x	-6.528075	
n+/n*	0.104278	
n-1)s^2	731.6495	
n-1)s^2	1262.851	
	1994.5	
n+n-2	37	
	5.621152	
	2.370897	
t-test=	-2.75342	

t(crit) at df =37: l.o.s.(df=40, l.o.s.=0.05,2-tl) = 2.021
SIGNIFICANT
In other words, there is a significant difference between the two sexes

ANOVA: For comparison of M.L.Den. of the three datasets

	Alaska	Upernavik	Sissimiut	Overall
n=	22	40	40	102
AVx=	31.48136	37.2875	31.40	33.38962
stdevX=	6.935449	8.342268	5.495266	
VARx=	48.10045	69.59343	30.19795	
SUMx=	692.59	1491.5	1256	3440.09
(SUMx)^2	479680.9	2224572	1577536	
SUMx^2=	22813.8	58328.5	40616.1	121758.4

F(max)Tes 2.304575 < Table-Value
But probably not allowed because of high variance!!!
ANOVA:
Correction Term:

	CT=	116021.8
SS(total)		
	SSt=	5736.6
SS(between)		
	SS(betw.)=	834.6269
SS(within)		
	SS(with.)=	4901.973
	df(SSt)=	101
	df(SSbetw)	2
	df(SSwith)	99
	s^2(betw)	417.3135
	s^2(with)	49.51488

F= 8.428042 exceeds table value
In other words, H0 is rejected;
There is a significant difference in variance between the three populations

Which population differs significantly from which?
Tukey Test:

rank	1	2	3
x(av)	31.4	31.48136	37.2875
n	40	22	40

Comparison:	Difference	SE	q	q(0.05, 120, 3)	Conclusion
A vs. U	-5.806136	1.32071	-4.396224	3.356	Av. M.L.Den. is not equal in Alaska and Upernavik
A vs. S	0.08	1.32071	0.061606	3.356	Av. M.L.Den. is equal in Alaska and Sissimiut
S vs. U	-5.89	1.112597	-5.291674	3.356	Av. M.L.Den. is not equal in Sissimiut and Upernavik

Appendix 4: Tests conceming Ratio-1. Only tests which yielded significant results are included

Z-test:	For comparison of Ratio-1 between Upemavik and Sissimiut
x-x	0.140045
s^2/n1	0.002756
s^2/n2	0.000898
sqrt	0.060454
1/sqrt	2.31654
SIGNIFICANT	So, the two datasets are different

ANOVA For comparison of Ratio-1 of the three datasets

	Alaska	Upemavik	Sissimiut	Overall
n=	22	40	40	102
AVx=	0.602273	0.562465	0.42242	
stdevX=	0.249989	0.332043	0.189571	
VARx=	0.062495	0.110252	0.035937	
SUMx=	13.25	22.49859	16.89678	52.64537
(SUMx)^2	175.5625	506.1864	285.5012	
SUMx^2=	9.2925	16.9545	8.539084	34.78608

Fmx-test 3.067909 > Table value

Variances not homogeneous!
ANOVA not allowed!

ANOVA after logarithmic data transformation

	Alaska	Upemavik	Sissimiut	Overall
n=	22	40	40	102
AVx=	-0.25575	-0.31804	-0.41884	
stdevX=	0.181228	0.247291	0.189571	
VARx=	0.032844	0.061153	0.042526	
SUMx=	-5.62656	-12.7214	-16.7538	-35.1018
(SUMx)^2	31.65819	161.8347	280.6892	
SUMx^2=	2.128723	6.430821	8.675742	17.23529

Fmx-test 1.861938 < Table value

ANOVA:		
Correction Term:		
	CT=	12.07975
SS(total)		
	SSt=	5.155538
SS(between)		
	SS(betw.)=	0.422359
SS(within)		
	SS(with.)=	4.733179
	df(SSt)=	101
	df(SSbetw	2
	df(SSwith):	99
	s^2(betw)	0.211179
	s^2(with)	0.04781

	SS	df	s^2	F
Between	0.422359	2	0.211179	4.417066
Within	4.733179	99	0.04781	
Total	5.155538	101		

F= 4.417066 > table value
In other words, H0 is rejected;
There is a significant difference in variance between the three populations

Tukey Test

Comparison	Difference	SE	q	q(0.05, 99, 3)	Conclusion
A vs. U	0.062283	0.041039	1.517646	3.356	A not significantly different from U
A vs. S	0.163092	0.041039	3.974053	3.356	A significantly different from S
S. vs. U	-0.10081	0.034572	-2.91588	3.356	S not significantly different from U

Appendix 5: Tests concerning Ratio-2. Only tests which yielded significant results are included

Z-test:	For comparison of Ratio-2 between Upernavik and Sissimiut
x-x	-0.01512
s^2/n1	2.78E-05
s^2/n2	3.08E-05
sqrt	0.007655
1/sqrt	-1.97547
SIGNIFICANT	So, the two datasets are different

ANOVA For comparison of Ratio-2 of the three datasets

	Alaska	Upernavik	Sissimiut	Overall
n=	22	40	40	102
AVx=	0.167552	0.13988	0.155002	
stdevX=	0.041925	0.332043	0.189571	
VARx=	0.001776	0.001112	0.001232	
SUMx=	3.686153	5.59521	6.200067	15.48143
(SUMx)^2	13.58772	31.30638	38.44083	
SUMx^2=	0.654536	0.826031	1.009053	2.489621

	SS	df	s^2	F
Between	0.011552	2	0.005776	4.45643
Within	0.128317	99	0.001296	
Total	0.139869	101		

Fmx-test 1.596686 < Table value

ANOVA:

Correction Term:

	CT=	2.349752
SS(total)		
	SSt=	0.139869
SS(between)		
	SS(betw.)=	0.011552
SS(within)		
	SS(with.)=	0.128317
	df(SSt)=	101
	df(SSbetw)	2
	df(SSwith)	99
	s^2(betw)	0.005776
	s^2(with)	0.001296

F= 4.45643 > table value

In other words, H0 is rejected;

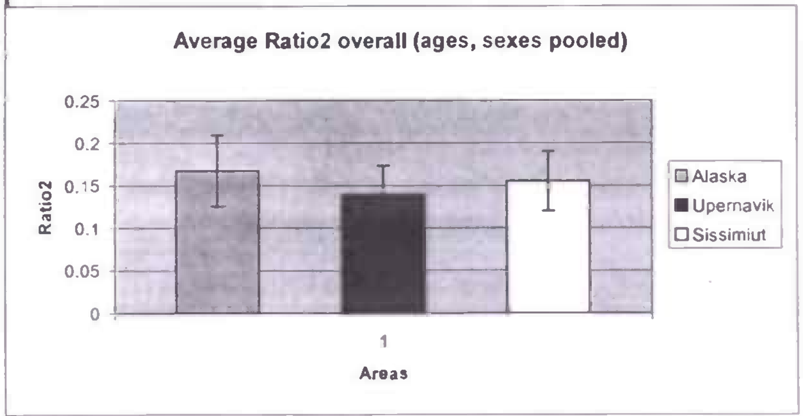
There is a significant difference in variance between the three populations

Tukey test for inequal sample sizes

	xb-xa	SE	Q	Q (0.05, 99, 3)
A-U	0.027672	0.020173	1.371735	3.356
A-S	0.012551	0.020173	0.622152	3.356
S-U	0.015121	0.016994	0.889794	3.356

NOT SIGNIFICANT

Sample sizes apparently not large enough



Appendix 6: Tests concerning toothshape. Only tests which yielded significant results are included

Chi-square test comparing toothshape to position within Upernavik dataset

Upernavik type to position (ages, sexes pooled)

		sl.cr.	st.cr.	cyl.	Total
Position	1-2	8	12	1	21
	Expected	9.586957	8.673913	2.73913	
	(O-E)^2/E	0.262693	1.275417	1.10421	
	3-4	10	5	1	16
	Expected	7.304348	6.608696	2.086957	
	(O-E)^2/E	0.994824	0.39159	0.566123	
	5-6	3	2	3	8
	Expected	3.652174	3.304348	1.043478	
	(O-E)^2/E	0.11646	0.514874	3.668478	
	7-8	0	0	1	5
	Expected	2.282609	2.065217	0.652174	
	(O-E)^2/E	2.282609	2.065217	0.185507	
	Total	21	19	6	46

Chi-square 13.428
df= 6
SIGNIFICANT

* significantly more StrongCurved teeth in 1-2 than expected
* significantly less Cylindrical teeth in 1-2 than expected
* significantly less Cylindrical teeth in 3-4 than expected
* significantly less SlightCurved teeth in 7-8 than expected

Appendix 7: Tests concerning Boundary Layers. Only tests which yielded significant results are included

Chi-square test comparing Boundary Layer Colour to Age category within Sissimiut dataset

1-<4	Single	Single+Dou	Double	Single+Double+Triple	
O:	4	3	0	0	
E:	1.711111	4.822222	0.311111	0.155556	
(O-E)^2/E	3.06176	0.688582	0.311111	0.155556	4.217009
4-<8	**Single**	**Single+Dou**	**Double**	**Single+Double+Triple**	
O:	0	8	0	0	
E:	1.955556	5.511111	0.355556	0.177778	
(O-E)^2/E	1.955556	1.124014	0.355556	0.177778	3.612903
8-<12	**Single**	**Single+Dou**	**Double**	**Single+Double+Triple**	
O:	2	6	0	0	
E:	1.955556	5.511111	0.355556	0.177778	
(O-E)^2/E	0.00101	0.043369	0.355556	0.177778	0.577713
12-<16	**Single**	**Single+Dou**	**Double**	**Single+Double+Triple**	
O:	2	5	0	1	
E:	1.955556	5.511111	0.355556	0.177778	
(O-E)^2/E	0.00101	0.047401	0.355556	3.802778	4.206745
16-<20	**Single**	**Single+Dou**	**Double**	**Single+Double+Triple**	
O:	2	6	0	0	
E:	1.955556	5.511111	0.355556	0.177778	
(O-E)^2/E	0.00101	0.043369	0.355556	0.177778	0.577713
20-<24	**Single**	**Single+Dou**	**Double**	**Single+Double+Triple**	
O:	1	3	2	0	
E:	1.466667	4.133333	0.266667	0.133333	
(O-E)^2/E	0.148485	0.310753	11.26667	0.133333	11.85924
			Test statistic=		25.05
				d.f.=	15

Critical level = 25.00 at (l.o.sign.= 0.05)
A SIGNIFICANT ASSOCIATION

SINGLE=OVERREPRESENTED IN 0-<4
SINGLE&DOUBLE=OVERREPRESENTED IN 4-<8
SINGLE&DOUBLE&TRIPLE=OVERREPRESENTED IN 12-<16
DOUBLE&DOUBLE=OVERREPRESENTED IN 20-<24

Appendix 8: Tests concerning Dark Staining Layers in Cementum. Only tests which yielded significant results are included

Chi-square test comparing Dark Staining Layer presence to Area

	present	absent	Total
Sissimiut	29	17	46
Expected	26.22807	19.77193	
(O-E)^2/E	0.292953	0.388611	
Upernavik	28	16	44
Expected	25.08772	18.91228	
(O-E)^2/E	0.338069	0.448459	
Alaska	8	16	24
Expected	13.68421	10.31579	
(O-E)^2/E	2.361134	3.132116	
Total	65	49	114

Chi-square 6.961342
df=2
SIGNIFICANT
So, significantly less DSLs in Alaska dataset

Chi-square test testing Dark Staining Layer presence in Upernavik males:
(with Yates' correction)

H0: frequencies in males do not differ from unity
H1: frequencies in males differ from unity

	present	absent	Total
O	15	4	19
E	9.5	9.5	
O-E	5.5	5.5	
(|O-E|-½)^:	25	25	
/E	2.631579	2.631579	

Chi-square 5.263158
df= 1
SIGNIFICANT
So, more DSLs are present than would be expected

Appendix 9: Tests concerning Tooth Clarity Index. Only tests which yielded significant results are included

Chi-square test comparing C.I. to Age Category in Upernavik dataset

clarity of GLGs

AgeCat.	1	2	3	4	5	Total
0-<4	0	3	4	1	0	8
E	1.391304	2.26087	2.086957	1.217391	1.043478	
(O-E)^2/E	1.391304	0.241639	1.753623	0.03882	1.043478	
4-<8	0	0	4	3	1	8
E	1.391304	2.26087	2.086957	1.217391	1.043478	
(O-E)^2/E	1.391304	2.26087	1.753623	2.610248	0.001812	
8-<12	0	4	1	0	3	8
E	1.391304	2.26087	2.086957	1.217391	1.043478	
(O-E)^2/E	1.391304	1.337793	0.566123	1.217391	3.668478	
12-<16	2	2	2	0	2	8
E	1.391304	2.26087	2.086957	1.217391	1.043478	
(O-E)^2/E	0.266304	0.0301	0.003623	1.217391	0.876812	
16-<20	2	3	0	2	0	7
E	1.217391	1.978261	1.826087	1.065217	0.913043	
(O-E)^2/E	0.503106	0.527711	1.826087	0.820319	0.913043	
20-<24	4	1	1	1	0	7
E	1.217391	1.978261	1.826087	1.065217	0.913043	
(O-E)^2/E	6.360248	0.483755	0.373706	0.003993	0.913043	
Total	8	13	12	7	6	46

Chi-square 35.78706
df= 20
SIGNIFICANT (at l.o.s.=0.05)
In other words, the GLG-clarity-distribution differs significantly
from an even distribution within Upernavik

Chi-square test comparing C.I. to Age Category in Alaska dataset.
Clarity of GLG's

AgeCat.	1	2	3	4	5	Total
0-<4	2	0	0	0	0	2
E	0.666667	0.916667	0.416667	0	0	
(O-E)^2/E	2.666667	0.916667	0.416667	#DIV/0!	#DIV/0!	
4-<8	1	2	0	0	0	3
E	1	1.375	0.625	0	0	
(O-E)^2/E	0	0.284091	0.625	#DIV/0!	#DIV/0!	
8-<12	2	1	1	0	0	4
E	1	1.833333	0.833333	0	0	
(O-E)^2/E	0.333333	0.378788	0.033333	#DIV/0!	#DIV/0!	
12-<16	0	4	1	0	0	5
E	2	2.291667	1.041667	0	0	
(O-E)^2/E	1.666667	1.273485	0.001667	#DIV/0!	#DIV/0!	
16-<20	3	3	2	0	0	8
E	2.666667	3.666667	1.666667	0	0	
(O-E)^2/E	0.041667	0.121212	0.066667	#DIV/0!	#DIV/0!	
20-<24	0	1	1	0	0	2
E	0.666667	0.916667	0.416667	0	0	
(O-E)^2/E	0.666667	0.007576	0.816667	#DIV/0!	#DIV/0!	
Total	8	11	5	0	0	24

Chi-square #DIV/0!
df= 20
SIGNIFICANT (at l.o.s.=0.05)
In other words, the GLG-clarity-distribution differs significantly
from an even distribution within Alaska