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**LA THÈSE A ÉTÉ
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A PRELIMINARY STUDY OF THE REPRODUCTIVE ANATOMY OF THE
FEMALE MUSKOX (OVIBOS MOSCHATUS).

by
Janice Rowell

A Thesis
presented to the University of Ottawa
in partial fulfillment of the
requirements for the degree
of Master of Science
in the
Department of Biology

Ottawa, Ontario, 1980
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ABSTRACT

Various aspects of the reproductive anatomy of 23 wild female muskoxen were documented and compared with similar structures in cattle, sheep and goats. In general, the reproductive tract of the non-pregnant muskox resembled that of sheep and goats, although species as well as individual variations were found in the gross anatomy of the cervix.

The placenta and the arrangement of fetal membranes during late pregnancy were typical of Artiodactyla, being considered morphologically closer to those of sheep and goats than cattle. Endometrial hyperplastic cysts were found in all eight pregnant tracts but were not considered pathological.

Endometrial pigmentation, found in all parous non-pregnant tracts was believed to be hematogenous as opposed to melanoblastic in origin.

The information on the ovaries was incomplete though these data support the assumption that the muskox is seasonally polyestrous and monovular. Follicular development and early corpus luteum formation appeared similar to these processes in domestic animals. Conversely, the ovaries of eight tracts collected during late pregnancy showed no morphological evidence of the corpus luteum, a condition not found among the domestic species. Histologically the corpus luteum of late pregnancy appeared to be highly regressed and non-functional. One pregnant specimen had

two corpora lutea and it has been suggested that one of these may represent an accessory corpus luteum.

A unique aspect of the muskox uterus was a prominent muscular band, found on the antimesometrial border, which was associated with parity. It has been suggested that a large lymphatic pathway developed in this region during pregnancy though the function of the pathway is not clear.

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INTRODUCTION

The muskox (Ovibos moschatus) is a species indigenous to arctic North America and Greenland. A remarkable feature of this species is its ability not only to survive but to reproduce in such a harsh environment. Despite the inherent difficulties of studying these animals, our understanding of their ability to survive is slowly growing. Our knowledge of muskox reproductive anatomy and physiology, however, remains rudimentary.

Current information on muskox reproduction has been gained from behavioural observations and assessments of calf crop. What is lacking is a foundation of anatomical information required to properly understand the reproductive mechanisms used by this species.

There are diverse reasons for acquiring information on muskox reproduction. The more obvious and perhaps the more urgent reasons are related to the survival of the species. The population of muskoxen in Canada is estimated at approximately 19,000 (Gray, 1977). In 1960 they were declared a species in danger of becoming extinct (Holloway, 1970) and are currently protected by the government. Since then their numbers have slowly increased but these animals are a traditional source of food for the Inuit (Gray, 1977) and, through management, limited hunting by selected communities is permitted. This management of the animals is complicated through

pressure exerted by oil and mineral exploration and the threat that these industries pose to the habitat of the species.

As well as the desire to maintain a natural wild population, the success of Alaska's domestication project (Wilkinson, 1971a) has generated a growing interest in the agricultural potential of the muskox. Any such use would certainly require more information on their reproduction.

Finally, there are reasons for studying reproduction in muskoxen that go beyond those directly applicable to the management and harvest of the species. Our present day knowledge of reproduction has arisen from the study of only a handful of the world's species and this lack of information on numerous taxonomic groups is an obvious deficiency in our understanding of reproduction. The genus Ovibos is in the family Bovidae which also includes domestic cattle, sheep and goats. Although domestic ungulates have received close scientific scrutiny, information on muskox reproductive biology should enhance our understanding of reproduction in the whole group and offer insight into the reproductive process of a wild ungulate subjected to a different and often extreme set of selective pressures.

It is the aim of this study to describe, in as much detail as the available material has allowed, the anatomy of the female reproductive tract. In establishing base-

3

line information, observations of all morphological structures have been recorded. Due to the limited availability of specimens and the restraints on collection, much complementary information on functional aspects of reproduction was not available. Interpretations of morphological structures have been made in the light of the available literature on muskoxen or where this was not possible, through comparisons with taxonomically related species, specifically cattle, sheep and goats. The information obtained has been discussed in the context of providing: 1) a broad morphological foundation which will allow future research to focus attention on particular areas, and, 2) more information on the taxonomic relationships between the muskox and related ungulates.

LITERATURE REVIEW

2.1 REPRODUCTIVE BIOLOGY OF THE MUSKOX

There exist in the literature several references to muskox reproductive biology. However, the information is scattered and what is available was collected under a wide range of conditions from various wild, introduced, and captive populations. With the exception of Gray (1973, 1977 and unpublished data) few studies have concentrated on a natural population in one area over a number of years.

The earliest information, related by whalers and explorers (Hone, 1934), offered few scientific insights

and need not be further considered here. More current information arises from studies on the behaviour of wild and captive herds or indirectly through assessments of population levels and composition.

The muskox is a seasonal breeder, breeding in the late summer or early fall (Tener, 1965; Gray, 1973; Smith, 1976) In this study I have distinguished between the rutting and the breeding seasons. The term rutting season is used to refer to the entire season where the male engages in sexually related behaviour. This includes agonistic encounters with other males to protect a harem as well as sexual behaviour towards the female. The term breeding season refers to the time when the cows are receptive to the courting bull and courtship activity frequently terminates with copulation. Although copulation has rarely been observed in the wild (Gray, 1973; Smith, 1976) the approximate time of occurrence can be estimated from calving dates. The breeding season is shorter than, and most probably confined within, the rutting season (Tener, 1965; Gray, 1973; Smith, 1976).

Among wild muskoxen, the rut is estimated to begin in early to mid July and to continue through to September. (Harrington, 1961; Pederson, 1962) or early October (Tener, 1965; Gray, 1973; Smith, 1976; Hubert, 1977), although the first signs of rutting have been noted as early as June (Tener, 1965) or even May. (Gray, unpublished). Most authors agree that August and the first part of September are the months of most intense courtship

with breeding occurring at this time. In small captive herds in Vermont and at the Alberta Game Farm the rutting season did not begin until mid-August, a delay of approximately one month (Teal, 1959; Oeming, 1965). Problems in defining the limits of the rutting and breeding seasons arise from the lack of an established criterion for assessing the beginning of the rut and the lack of observations later than October to establish the end of the rut.

The beginning of the rutting season is marked by the behaviour of the bull (Tener, 1965; Gray, 1973; Gray and Rowell, 1976; Smith, 1976). Estrous behaviour in cows is much more difficult to detect as it is quite subtle and has only been described in the wild by Smith (1976). The most substantial information on estrus has come from captive herds. Wilkinson (1973) who did not observe any estrous behaviour among the captive animals in Alaska, estimated cycle length from temporal spacing of births. He suggested that 'a complete cycle may last 5-7 days with the interval between each cycle lasting up to 14 days'. For the Alaska herd, he estimated that approximately 4 cycles occurred in a breeding season. Bourque (personal communication) who worked with the captive herd at Fort Chimo, Quebec, observed estrus to occur every 21 days and to last for a maximum of 12 hours. He noted that during heat, the cow produced a profuse mucous secretion. This presumably matted the dense

hair in the anogenital region to facilitate copulation.

In reference to estrous behaviour, he describes the cow as being 'very desirous of the bull' accepting the male every 30 minutes (Bourque, cited in Gray, 1973).

Estrous synchrony within a harem has been suggested by Smith (1976), though Wilkinson (1973) disagrees. The wide spread in calving dates suggest that a finely tuned synchrony does not exist.

Available estimates of gestation length, 249-252 days (Alendal, 1971a) and 242 ± 5 days (Wilkinson, 1973), are in close agreement.

The calving season occurs from mid-April through to June with peak calving concentrated in mid-May (Tener, 1965; Wilkinson, 1973; Gray, 1973; Gray and Rowell, 1976; Smith, 1976; Hubert, 1977). Cows generally give birth to one calf and twinning, though it has occurred, is considered rare (Pederson, 1962; Tener, 1965; Wilkinson, 1971b).

Difficulties during pregnancy and parturition have been reported twice in the wild (Jennov, 1933; Norment, 1980). Among the captive animals at Alaska, three abortions have been reported, as well as 13 calves that were lost at birth (Wilkinson, 1973).

Estimates of age at sexual maturity vary. Tener (1965) estimated 4 years for cows and 6 years for bulls in wild populations. However, among introduced and captive herds, cows have bred at 15-16 months (Oeming,

1965; Alendal, 1971a; Wilkinson, 1973). In general it is considered that cows breed first at the age of 39 or 51 months, depending on the forage quality of their habitat (Tener, 1965; Spencer and Lensink, 1970; Wilkinson, 1973; Alendal, 1974; Hubert, 1977). Among the captive animals in Alaska, Wilkinson (1973) cited a minimum breeding weight of 400 pounds.

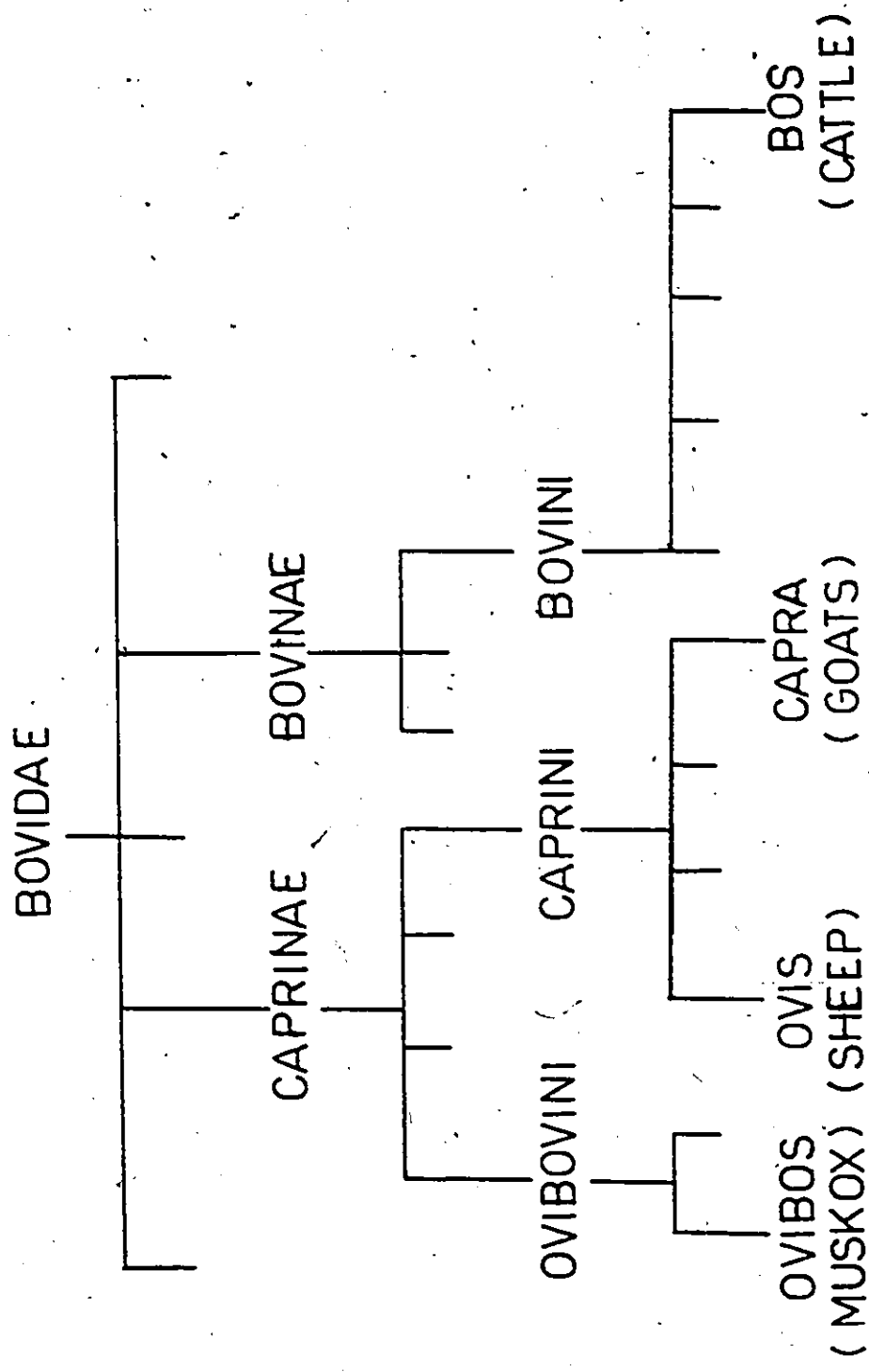
Breeding success is difficult to judge and is generally determined by calf production. Cows are believed to calve every other year (Tener, 1965; Wilkinson, 1971a; Gray, 1973; Hubert, 1977) although exceptions to this were noted on Nunivak Island (Smith, 1976) and in captivity (Oeming, 1965; Wilkinson, 1973). Estimates of calf production vary from location to location and from year to year within a location (Vibe, 1958; Pederson, 1962; Gray, 1973; Gray and Rowell, 1976; Ferns, 1977). The overall annual calf production is generally considered to be low (Tener, 1965; Freeman, 1971) with years of high production balanced by years of low production. Tener (1954, in Harington, 1961) estimated the calf to cow ratio at about one in four. Calf survival has been related to predation pressure as in areas such as Nunivak Island where there is no predation calf survival is high (Wilkinson, 1973). Climatic variables resulting in drastic reductions of winter forage have been cited as the major cause of the lowered breeding success (Vibe, 1958; Tener, 1965; Gray, 1973; Ferns, 1977; Hubert, 1977).

The only account in the literature of the reproductive anatomy of female muskoxen is a brief description of the location of the uterus in a six month old calf (Sack and Ballantyne, 1965). There are apparently no reported studies of reproductive histology and physiology.

In the absence of extensive physiological data on muskoxen, an understanding of the animals' responses to variables such as climate and lowered nutrient levels must come indirectly through comparisons between muskoxen and related ungulates. The taxonomic classification of muskoxen is based largely on morphological and behavioural characteristics. Comparative studies include the work of Moody (1958) who worked on muskox blood proteins, that of Chisholm and Hopkins (1957) who studied fatty acids in muskoxen and Sloan et. al. (1961) who compared whey protein patterns in muskox-milk with related species.

Since Zimmerman (1780) first classified the muskox in the genus Bos, there has been considerable debate as to the relationship of the muskox to cattle, sheep, goats and bison. deBlainville (1816) placed muskoxen in a separate genus, Ovibos, to indicate the animals' relationship both to cattle and to sheep. Allen (1913) accepted the new genus but found strong similarities between muskox and bison skulls, body form, dentition and coat. The presently accepted classification for the muskox is in the family Bovidae, subfamily Caprinae, tribe Ovibovini, genus Ovibos (Simpson, 1945; Fig. 1).

Figure 1. Taxonomic relationship between muskoxen and the domestic species (Simpson, 1945).



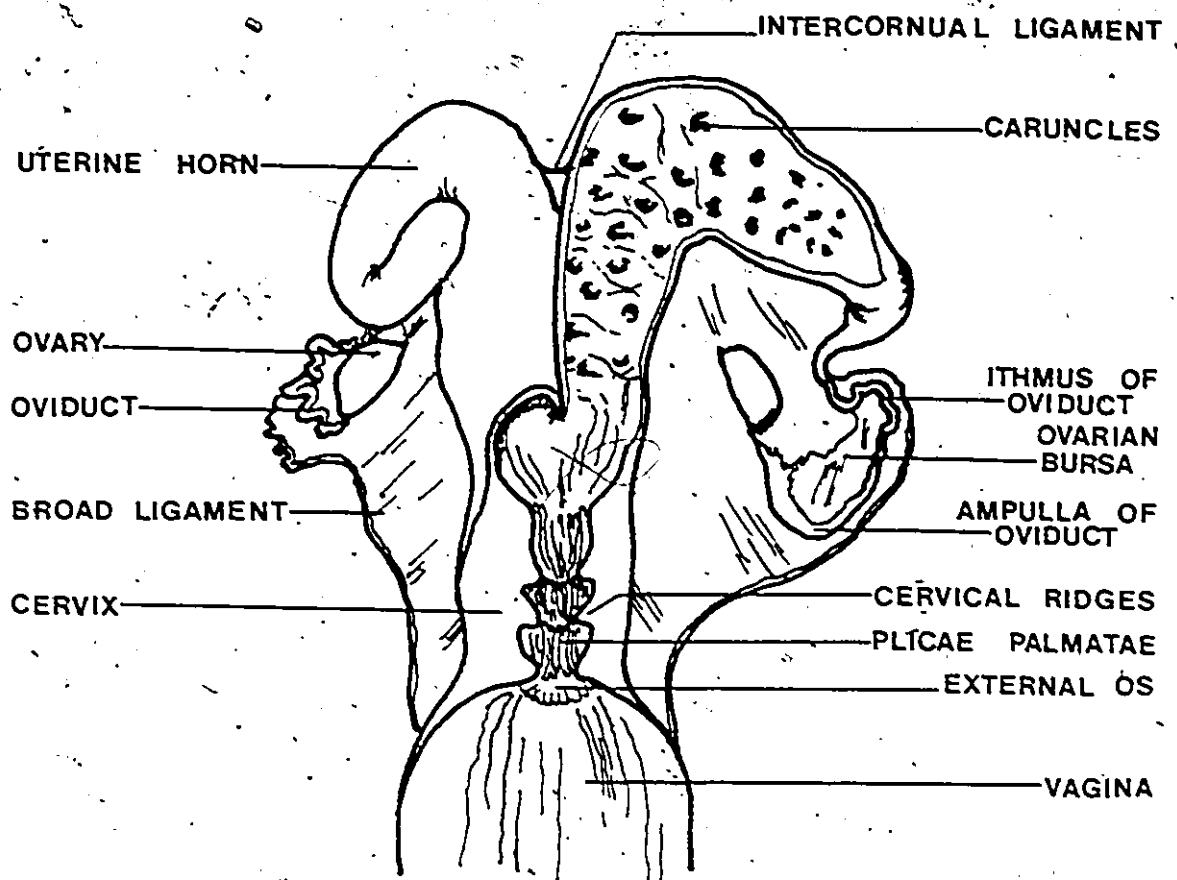
The takin, Budorcas taxicolor, is considered the nearest living relative of the muskox. The original difficulty in determining the taxonomic position of the muskox illustrates the complexity of assessing relationships between species. Muskoxen have characteristics similar to those of sheep and goats, others that resemble those of cattle and bison and some that are different from both groups. However, it is useful to compare them to cattle, sheep and goats because of their common characteristics and the large amount of information that is available for the domestic species.

2.2 REPRODUCTIVE BIOLOGY OF OTHER ARTIODACTYLA

The classification of the muskox as a member of the Artiodactyla, and a ruminant, makes certain suggestions or predictions about broad aspects of the species' reproductive morphology.

Fig. 2 is a schematic representation of a ruminant uterus. Though the features depicted are ones commonly associated with most ruminants, a great deal of variety exists with respect to the prominence, number and size of each of the structures. Until recently a mammalian order has been associated with one type of uterus: duplex, bicornuate, or simplex. Among the Artiodactyla the uterus was thought to be invariably bicornuate. However, as the number of species that have been studied increases, exceptions have been found; both the sable antelope and

Figure 2. Schematic diagram of the uterus of the domestic ruminants. The vagina, cervix and right uterine horn have been opened and the right oviduct uncoiled to show it's relationship with the ovarian bursa. In this diagram the uterus has been transected just caudal to the external os of the cervix.



the blue wildebeest have a duplex uterus (Mossman, 1976.) The bicornuate uterus has been found in a number of unrelated orders suggesting that this uterine form arose independently along various evolutionary lines. It may have arisen independently more than once within the Artiodactyla. Mossman's (1976) classification of the bicornuate uterus is subdivided into the long bicornuate uterus; usually associated with litter bearing species, and the medium and short bicornuate uteri, associated with species that produce one or two large, relatively precocious young but these categories are also general and subject to exceptions within the Artiodactyla. For example, the pronghorn, which has a long bicornuate uterus, produces only two precocious young (O'Gara, 1969); Finnish Landrace sheep, a breed having a medium bicornuate uterus, normally bear an average 3.4 young (Bradford et. al., 1971).

Asymmetry in both the size of uterine cornua and in ovarian activity occurs among the Artiodactyla. In 5 genera of ruminants the right cornu is almost always significantly larger even though both ovaries are equally active (Wimsatt, 1975). This difference in size is evident even in immature and non-parous animals. Domestic cattle ovulate more commonly from the right than the left ovary (Rajakoski, 1960). Ovarian dominance has also been reported in the waterbuck which ovulates predominantly from the left ovary (Spinage, 1969). Asymmetry

in either uterine cornua or in ovarian performance can carry with it the possibility of a reduction in productivity. The alpaca is a species that appears to ovulate equally from both ovaries though only the left cornu successfully supports gestation. Even though blastocyst migration towards the fertile cornu increases productivity, embryonic loss is estimated at 40-50% (Fernandez-Baca, et al., 1970ab). The bactrian camel is also characterized by very low fertility, although in this species anatomical abnormalities were cited as the main cause (Novoa, 1970).

Among the ruminants the cotyledonary placenta is of the epitheliochorial type (using Steven's (1975) modification of Grosser's (1909) classification). The number and size of the cotyledons vary between species and between breeds within a species (Amoroso, 1956, Steven, 1975), and Amoroso subdivided the species on the basis of cotyledonary number. Polycotyledonary animals have the greatest number of cotyledons (e.g. goats and giraffes range from 160-180 cotyledons) while the oligocotyledonary species, represented by many members of the Cervidae, have only 5-8 cotyledons. Sheep and cattle occupy an intermediate position.

There is, as well, a wide diversity in the shape of the cotyledon, well illustrated by Amoroso (1956) who does not ascribe any particular physiological importance to the wide variation in size, form and structure of

the ruminant cotyledon. Steven (1975), though in general agreement with Amoroso, points out that the shape of the cotyledon does appear to affect the shape of the fetal villi which in turn, may affect the patterns of fetal and maternal circulation.

Cotyledonary placentae are associated with superficial "implantation", or attachment of fetal membranes. The vascular elements between the fetal and maternal components are established through a highly vascular and very extensive allantois. The allantois does not completely surround the amnion but narrows as it passes to one side of the sac. The umbilical cord lies completely within the amnion, the vessels branching in either direction to vascularize the allantois. In some ruminants, such as some members of the Cervidae, the amnion does not become vascularized at all (Hamilton, et al., 1960) while in sheep and cattle vascularization of the amnion does occur to a limited extent (Steven, 1975).

Small plaques or pustules found on the amnion overlying the umbilicus have been reported for a variety of ungulates (Amoroso, 1956; Hamilton et al. 1960; Steven, 1975). These pustules contain glycogen in considerable amounts though their functional significance has not been established (Steven, 1975).

Histological descriptions of placentation in the ruminants are too numerous to cover here so the reader is referred to the excellent reviews by Amoroso (1956) and

Steven (1975). Additionally, Wimsatt (1950) gives a classic description of the sheep placenta, documenting a placental hematoma found in this species. More recent studies on the histology and the ultrastructure of the bovine placentome have been presented by King et. al. (1979, 1980).

The cervix of ruminants can generally be classified into different groups by structure. Ruminants are characterized by a distinct external os, mucosal folds lining the cervix and firm, thick musculature (Kanagawa and Hafez, 1968). The folds of the mucosa form secondary and tertiary folds that give a false impression of glandular tissue. Of the three domestic species, the goat is the only one said to have tubular glands in the cervix (Eckstein and Zuckerman, 1956; Hafez, 1968), but Mattner (1966) and Morton and Glover (1974) did not confirm this finding. Morton and Glover (1974) attribute this discrepancy to breed differences in goats or possibly to exposure to phytoestrogens, in that they found sheep treated with phytoestrogens developed coiled, tubular-looking glands in the cervix.

The epithelium of the ruminant cervix is columnar and contains goblet cells and occasional ciliated columnar cells (Dellman and Brown, 1976). This epithelium is secretory and responsible for the production of cervical mucus. The cervical mucus plays a central role in directing sperm migration. The mucus acts to orient

sperm and direct it toward the cervical wall and crypts which function as a sperm reservoir thus preventing premature migration of the sperm into the uterus (Mattner, 1966). Morton and Glover (1974) found that sperm could survive for longer periods of time in the cervix than in the uterus, Fallopian tubes or vagina.

At estrus, or under a strong estrogen influence, Heydon and Adams (1979) found that the cervical mucus became more watery and increased in 'stringiness'. This allows the mucus to direct the course of the sperm. These researchers found differences in stain reaction between the luminal cervical epithelium and the epithelium in the deeper crypts. The cells at the base of the crypts produced a sialomucin and responded more strongly to estrogen than did the luminal cells which produced a sulfomucin. According to Heydon and Adams (1979) the greater quantities of mucus at the base of the crypts result in more sperm being guided to these areas.

Despite the functional similarity of the cervix in various ruminants there is a good deal of morphological variation in the shape of the cervical lumen, the number and arrangement of the annular ridges and the complexity of the plicae palmatae. Fooden (1967) compared the anatomy of the male penis and the female vagina and cervix and put forth the hypothesis of the 'lock-and-key' specialization of genitalia to prevent disadvantageous hybridization.

A comprehensive review of the oviduct has been written by Hunter (1977) and the utero-tubal junction has been described by Anderson (1928). The oviduct is another structure that responds to estrogen stimulation. The secretory epithelium of the oviduct changes cyclically, ranging from low to tall columnar cells with the transient appearance of cilia (Trautman and Fiebiger, 1957; Dellman and Brown, 1976). The oviduct is usually divided into two functional portions, the ampulla and the isthmus. The ampulla is responsible for collection and initial transport of the ova following ovulation; the isthmus is characterized by peristaltic contractions and cilia that cause movement towards the isthmo-ampullary junction. This is believed to facilitate sperm transport and hence fertilization. In most species fertilization occurs in the oviduct and the zygote is held at the isthmo-ampullary junction for a variable length of time (Hunter, 1977).

The ovaries are one of the most dynamic components of the female reproductive tract, serving both as a source of ova and as an endocrine organ. Because of this, the morphological features of the ovary, which are constantly changing cyclically as well as seasonally, reflect the reproductive status of an animal. There are numerous comparative reviews of the ovary (Jones, 1978; Zuckerman and Weir, 1977; Mossman and Duke, 1973) as well as classical studies on single species such as

sheep (Grant, 1936) and the goat (Harrison, 1948).

The ovary can be divided into two major areas, the medulla and the cortex. Among ruminants the cortex commonly surrounds the medulla except in the region of the hilus. The medulla is composed of fibrous connective tissue that contains the blood and lymph vessels. The cortex on the other hand, is highly cellular in nature contains the follicles, corpora lutea, and the atretic scars of both.

The non-follicular components of the ovaries are primarily the surface epithelium, medullary cords, and the rete ovarii. The surface or germinal epithelium is cuboidal and becomes stretched cuboidal in older, parous animals. The function of the surface epithelium is not clearly understood: though it is no longer considered to contribute new germ cells to the ovarian population, it is believed to contribute to folliculogenesis (Peters, 1978; Harrison and Weir, 1977). The medullary cords are remnants or vestiges of embryonic components that have found their way into the medulla and many of these are blind tubules (Peters, 1978). The rete ovarii probably occur in the ovaries of most mammals but research on the specific origins and functions of this organ are lacking in most species. It is also an embryonic remnant of the tubular connection from the mesonephros and the gonad (Duke, 1978) and until recently was considered a non-functional, vestigial organ (Duke, 1978).

However, Byskov (1978) has suggested that the rete interacts with cortical elements to initiate meiosis.

Follicular development has been reviewed by many authors. Generally the primordial follicles are found in the peripheral cortex and in ruminants they are evenly distributed in this area. (Dellman and Brown, 1976). Polyovular follicles have been described in a variety of species (Peters, 1978). Although previously recorded as abnormalities, it is now suggested that they may be a normal stage in the early process of folliculogenesis (Peters, 1978) as they are most frequently found in embryonic and immature ovaries (Harrison and Weir, 1977). Polynuclear ova have also been described (Peters, 1978; Harrison, 1948) though recent evidence indicates that these are degenerating oocytes in which the fragmented nucleus gives the appearance of several nuclear bodies (Peters, 1978).

As the follicle increases in size, it migrates deeper into the cortical stroma. Follicular growth has been divided into two phases. In the first phase, the oocyte grows rapidly until it is almost adult size while the follicle grows slowly. In the second phase, the oocyte grows slowly while the follicle increases dramatically in size (Harrison and Weir, 1977). While the ultimate size of the oocyte is not related to body size, the size of the mature follicle is (Parkes, 1931). The number of follicles that ovulate is, again, not related

to body size but does appear to be a species characteristic, there being a tendency within a species to ovulate the same number of follicles at each estrus.

By the time a follicle has reached maximum development it has migrated to the outer regions of the ovary and, in many species, protrudes noticeably on the surface. Ovulation is the process whereby the ovum, surrounded by the cumulus oophorus, is released into the peritoneal cavity and is subsequently swept up by the infundibulum. The remaining components of the follicle collapse into the antral cavity and luteinize. During luteinization the granulosa cells, vascularized by vessels of the theca, enlarge and differentiate into luteal cells which secrete progesterone. The large luteal cells cease mitotic division within a short period after luteinization. The thecal cells undergo change and some are believed to contribute to the luteal population. Subsequent increase in luteal size results from the hypertrophy of the large luteal cells themselves.

Several types of corpora lutea have been described. A true corpus luteum develops from the follicular elements remaining in the ovary after ovulation. A corpus hemorrhagicum develops when hemorrhage occurs from thecal vessels shortly after ovulation resulting in a corpus luteum with a central blood clot. Accessory corpora lutea result from the luteinization of unruptured follicles. A corpus atreticum results when the

thecal cells luteinize in a follicle after the granulosa has degenerated.

The new active luteal cells contain abundant phospholipids, smooth and agranular endoplasmic reticulum and large mitochondria bearing tubular cristae. The final size of the mature corpus luteum has been related to follicle size (Brambell, 1956). As the luteal cells regress they begin to accumulate cholesterol signifying a reduction in steroid synthesis. Regression in corpora lutea has been described as being similar whether it is of a corpus luteum of the cycle, pseudopregnancy, pregnancy or lactation (Brambell, 1956). However, studies by Bjersing (1978) suggest that cyclic regression differs from regression after hysterectomies in ewes.

The scar remaining after regression is termed the corpus albicans. Harrison and Weir (1977) state that corpora albicantia may persist for varying and unknown lengths of time in the fissipeds, pinnipeds, and certain cervids and proboscids but do not mention persistence in the Bovinae or Caprinae.

Very few of the follicles that begin developing will ovulate; the great majority of them will undergo atresia. The histological appearance of atresia varies between species and phase of follicular growth (Jones, 1978). Atresia in most preantral follicles is found in the oocyte itself (Weir and Rowlands, 1977). Atretic changes in vesicular follicles show a greater variety.

The two main forms of atresia in vesicular follicles have been termed oblitative and cystic. In oblitative atresia, the granulosa and thecal cell layers hypertrophy and begin to fold inward to occupy the antrum, followed by atrophy. In cystic atresia, both the granulosa and the theca layers may atrophy or only the granulosa layer will atrophy and the theca will either luteinize, fibrose or hyalinize. In cattle, cystic follicles that do not regress may interfere with estrous cycles and fertility (Dellman and Brown, 1976). In mammals the ratio of healthy to atretic follicles remains constant throughout the reproductive period. In sheep about 68% of ovarian follicles are atretic (Brand and deJong, 1973). Because of the high proportion of atretic follicles and the constant occurrence of atresia, a physiological role for the large atretic follicles has been investigated. Hay and Moor (1978) found that cultured atretic sheep follicles produced much less estrogen than cultured non-atretic follicles on the first day of culture. By the third day, the atretic follicles secreted large amounts of progesterone. The potential for steroid secretion has led to the belief that atresia represents a functional change

rather than a degenerative process (Weir and Rowlands, 1977).

Hormones (including the gonadotrophins and steroids) and their degree of interaction are vital to reproduction and it is perhaps in this area of endocrinology that species differences are most striking. The nature of the hormones affecting reproduction and complexities of their interactions have been reviewed by many authors. The textbooks of Austin and Short (1972) give a comprehensive comparative description while that of Cole and Cupps (1977) reviews the hormonal basis of reproduction among domestic animals. In the simplest terms, FSH is responsible for follicular growth and development. Tonic secretion of LH, which promotes steroid synthesis by all cell types in the ovary, increases the estrogen secretion of the developing follicle. The increasing quantities of circulating estrogens have a positive feed-back effect on the hypothalamus which results in a large preovulatory surge of LH. Following ovulation, the resulting corpus luteum produces progesterone which in turn increases vascularization, enhances glandular activity and reduces excitability of the myometrium. These actions prepare the uterus to

receive the zygote. If fertilization is not successful the corpus luteum regresses and a new cycle begins.

Alternatively if fertilization is successful, the corpus luteum persists and maintains the progestational environment necessary for pregnancy (Baird, 1972). The lifespan of the corpus luteum of pregnancy varies between species.

Sheep can maintain a pregnancy without a corpus luteum after 50-60-days while goats require a corpus luteum for the full duration of the pregnancy (Heap, 1972). In sheep, the progesterone necessary for pregnancy maintenance after 50-60 days is of placental origin. The placenta has recently been recognized as a major endocrine gland during pregnancy producing protein hormones such as placental lactogen as well as steroid hormones (Heap, 1972):

Placental lactogen is a protein hormone that exhibits growth promoting and lactogenic activities equivalent to those of human growth hormone (hGH) though it does not cross-react immunologically with anti-hGH (Chan et. al., 1976). The source of placental lactogen is believed to be the giant binucleate cells in the trophoblast (Flint et. al., 1979). Placental lactogen has been found in cattle, sheep and goats though it has not, as yet,

been found in the horse (Forsyth et. al., 1975).

The endocrinology of pregnancy involving maternal recognition of the embryo's presence, the changing requirements of the developing embryo and parturition encompass a diverse range of hormonal interactions that are not yet fully understood (Steven, 1975; Sauer, 1979; Thorburn and Challis, 1979).

Any initial study of reproduction in an unknown ruminant must take account of the fact that the Artiodactyla exhibit considerable species variation in a variety of reproductive phenomena. These include ovulation rates, spontaneous versus induced ovulation length of luteal phases and delayed implantation. The number of ova that will ovulate during any cycle is a species characteristic that is not necessarily related to the number of offspring. The pronghorn for example, gives birth to two offspring but ovulates between 3-7 ova (O'Gara, 1969).

Ovulation is spontaneous in most domesticated ruminants but the Camelidae are induced ovulators (Novoa, 1970). In these animals, a neural stimulus induced by copulation is required to release the pre-

ovulatory LH surge. These species are characterized by long periods of estrus, 21-36 days in the alpaca (San-Martin et. al., 1968).

The timing of ovulation relative to estrus is another species characteristic. In sheep, ovulation generally occurs 24-27 hours after the onset of estrus (estrus usually lasts for 30 hours in this species) while cattle have a 12 to 22 hour estrus with ovulation occurring approximately 10 hours after the end of estrus (in Asdell, 1946).

The life of the corpus luteum of the cycle varies considerably between species, ultimately determining cycle length. Regression of the corpus luteum occurs on the 14th or 15th day in sheep, resulting in a cycle length between 16.5-17.5 days while in cattle marked corpus luteum regression is not evident until 19 days after ovulation resulting in a cycle length of 20 days (in Asdell, 1946).

Accessory corpora lutea formed from luteinized follicles occur in some species and this may also vary within a species. Kelly and Challies (1978) found 59.8% of pregnant red deer had accessory corpora lutea while the

remaining animals maintained pregnancy with one corpus luteum.

Delayed implantation in the order Artiodactyla, has only been found in the roe deer and even in this species it may only occur in some of the animals (Aitken et. al., 1974).

The effect of lactation on reproductive performance in ruminants is another area that is poorly understood. Prolactin has been associated with lactation and lactational anestrus. However some species, both domestic (cow) and wild (kob), will ovulate post partum with little interference from lactation (Asdell, 1946). Cyclicity can be induced in anestrus ewes by the administration of PMSG (Pregnant Mare's Serum Gonadotrophin) followed by LH (McNeilly and Land, 1979) though fertility is reduced. Experimentally inducing estrus during lactation has been shown to further reduce fertility by impairing the process of implantation (Rhind et. al., 1980a). A comparative review of the endocrinology of mammary growth and lactation has been written by Forsyth and Hayden (1977).

The complexity of the endogenous hormonal balance governing reproduction is further complicated by external

factors which may act to enhance or inhibit hormonal levels. Photoperiod has long been regarded as the most important stimulus regulating the breeding season in mammals (Turek and Campbell, 1979). An hypothesis for feedback control of seasonal breeding in the ewe is based on the changing sensitivity of the hypothalamic-hypophyseal complex to the negative feedback action of ovarian estradiol-17 (Legan and Karsh, 1979; Karsh et al., 1979, 1980). The change in sensitivity is brought about by photoperiodic stimuli, most likely acting independently of the estradiol (Karsh et al. 1980). This hypothesis has only been tested in the Suffolk ewe. Turek and Campbell (1979) point out the many deficiencies in our knowledge of the effects of photoperiod as well as the inconsistencies. Most temperate region ungulates respond to photoperiod. Sheep, with the exception of the fine woolled, tropical breeds, are considered to be short day breeders (Asdell, 1946). Soay sheep exhibit a sensitivity to photoperiod similar to that predicted for the wild ancestor of modern sheep, which is presumed to have evolved in a cold, temperate climate (Lincoln and Davidson, 1977). It is particularly interesting to note that Icelandic

Sheep breed from mid-December through January with peak breeding occurring 4-7 weeks after the shortest day. In these sheep there is ample evidence of sporadic out-of-season estrous activity resulting in lambing during any month of the year (Dyrmondsson, 1979). In contrast, goats in Norway breed primarily in July to September (Lyngset, 1968b).

As well as photoperiod other external cues such as temperature and the presence of the opposite sex are known to stimulate breeding (Turek and Campbell, 1979). Lincoln et. al., (1972) suggests that odour from hinds as well as past sexual experience may act as additional proximate cues for the onset of rut in red deer stags. The presence of a male has also been correlated with the initiation of estrous cycle activity in goats (Ott et. al., 1980).

MATERIALS AND METHODS

3.1. GENERAL APPROACH

In attempting to clarify aspects of muskox reproductive biology it is first important to establish the anatomy of the reproductive tract. Comparison of the muskox reproductive tract with those of a better known species allows limited interpretation and some prediction of function. However, as the foregoing review points out there can be a wide variety of reproductive patterns among ruminants in spite of close morphological similarity. The approach to this study must, therefore, be broad in scope and allow for a correspondingly wide range of possibilities in the interpretation of structure.

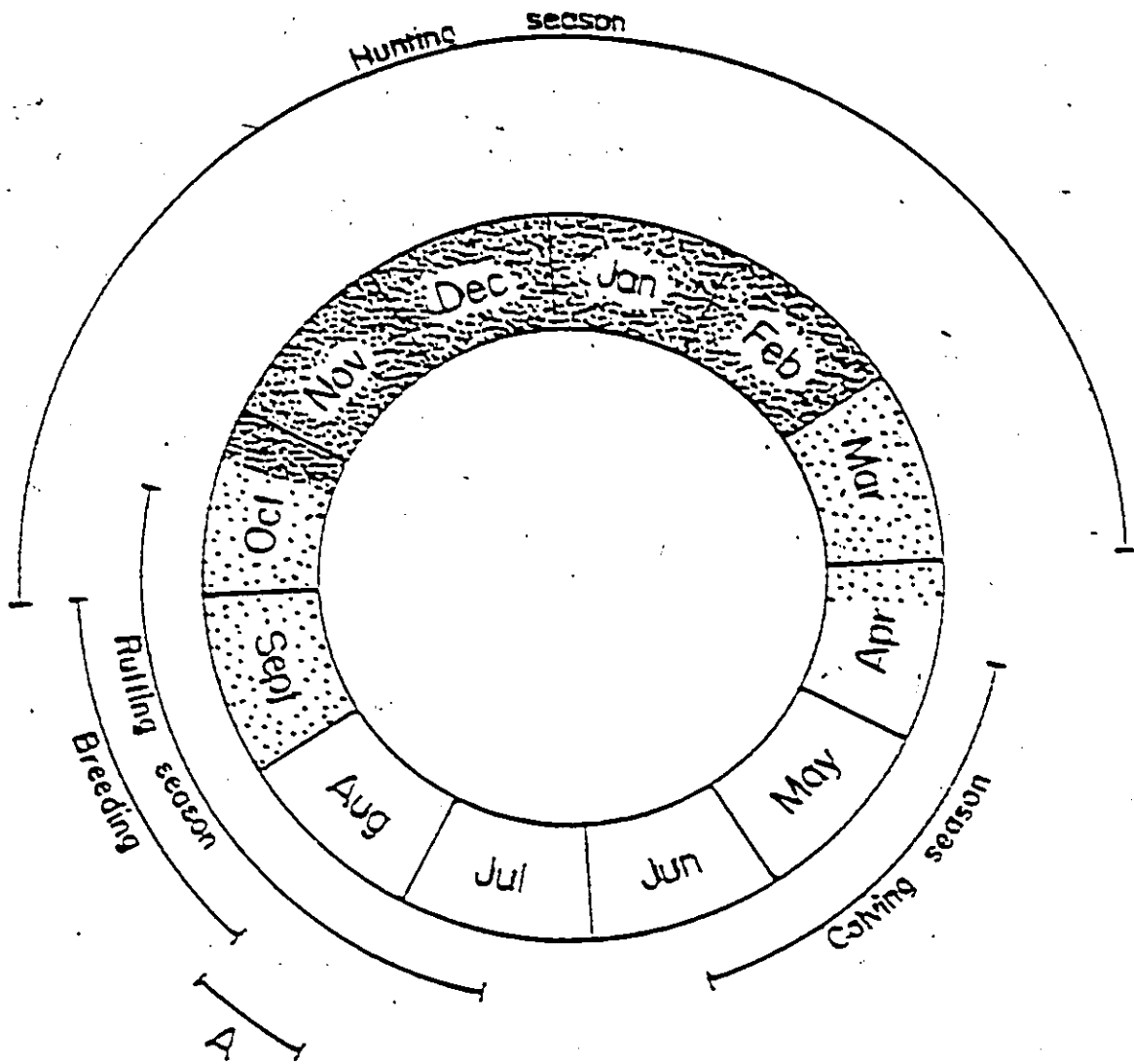
3.2 COLLECTION AND FIELD OBSERVATIONS

a) Time of Collection

The muskox is a protected species and only limited hunting by native hunters is permitted. This hunting is controlled by community quotas and is permitted only during a set hunting period. These restrictions immediately limited possible collections to the period of October 1 to March 31, encompassing the late breeding season and most of the gestation period (Fig. 3).

Grise Fiord was one of two communities that had a high quota (25 animals) and the hunters from this community agreed to assist in the collection. There were however,

Figure 3. A schematic representation of the reproductive seasons of the muskox. The heavy stippling on the inner circle represents the dark season; the light stippling, the transition between light and dark and an absence of stippling, the season of 24 hour sunlight. The bars along the outside represent rutting, breeding and calving seasons as well as the annual hunting season; 'A' indicates the time of the August hunt.



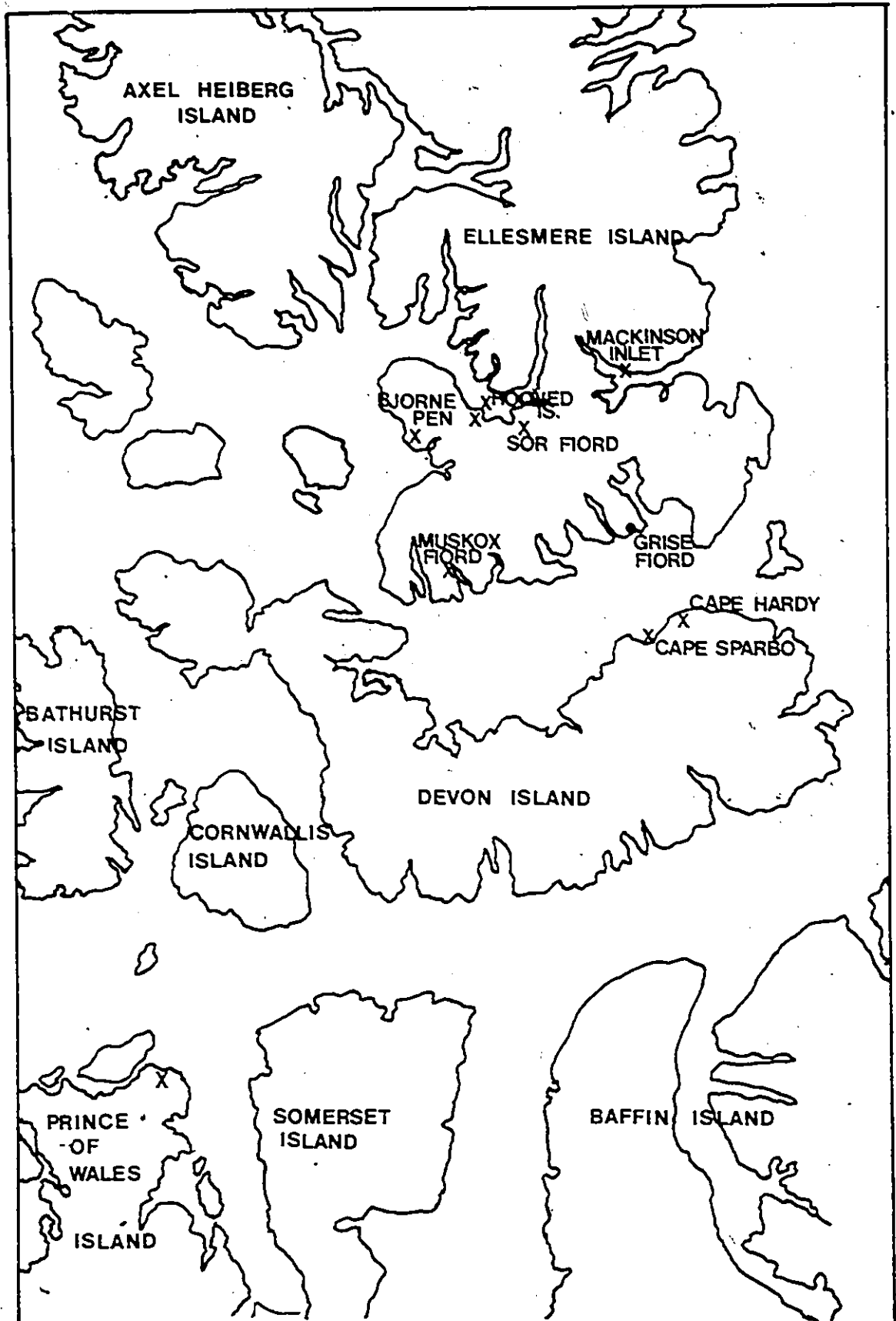
some unforeseen difficulties in collecting from Grise Fiord. Hunting was done by snow machine over vast areas of rocky terrain and sea ice, muskoxen being found anywhere from 40-150 miles away. Unpredictable weather conditions in October often made overland or sea ice travel impossible. Twenty-four hour darkness descends at the end of October and remains until mid-February. As hunting is very rarely carried out in the dark it was generally confined to the end of February and throughout March. These additional restrictions, combined with the uncertainty of hunting success, usually resulted in fewer than 25 animals being collected during any season with approximately half of these being female.

To overcome some of the above restrictions, a hunt was arranged (by special permission from the Northwest Territories Government) in August. Hunting in August, which involved the use of a helicopter (Bell 206 jet ranger), made it possible to collect animals immediately before the breeding season. The August collection of material was made easier by the above 0°C temperatures. Fig. 4 depicts the hunting locations and Appendix I lists the animals collected in each area.

b) Collection Procedures

Collections of the reproductive tracts were accomplished by one of two methods. In the early stages of the project the Hunter's and Trapper's Association

Figure 4. Map of the islands of the eastern high arctic showing areas where muskoxen were collected. Each hunting location is marked by an X. The X on Prince of Wales Island is only an estimate. The four animals shot here were collected by hunters from Resolute Bay (Cornwallis Island) and were not accompanied by detailed information. All the other hunting was done by hunters from Grise Fiord. Scale: 2.5 cm = 100 km.



for each community holding muskox hunting rights was approached through the local game officer and the hunters were asked to return reproductive tracts from the animals they shot to the game officer. Only the communities of Grise Fiord and Resolute Bay responded. The frozen specimens received were, unfortunately, not accompanied by any background information. Further, the hunters consistently removed the fetus from pregnant tracts. A total of 11 tracts were obtained in this manner, 5 non-pregnant and 6 pregnant.

The second approach to collecting was to accompany the hunters and collect the reproductive tracts personally. This enabled the accumulation of additional relevant information.

The method of travel, as mentioned, was overland by skidoo and sled. The distance travelled varied, but as much as 200 miles could be covered before returning to the community with the excursions lasting up to 8 days. A trip of this scale necessitated carrying overnight supplies and additional gasoline, all of which reduced the amount of collecting equipment that could be taken. On long trips particularly when travelling, the preservative could not be kept warm.

When a herd of muskoxen was spotted each hunter shot one animal. As many as 7 animals were collected at one time, separated by as much as one mile. After the hunters had shot the muskoxen the animal's jugular vein

was cut and blood samples were collected directly into open vacutainers. The tubes were stoppered and worn on a belt underneath the parka to prevent freezing and consequent hemolysis. After separation (usually overnight) the serum was poured into smaller vials and frozen.

Following blood collection, the hunters immediately began skinning their animals. In the cold conditions a skinned carcass cooled and began to freeze within an hour so that only a minimum of time could be spent on any one animal. In some cases a choice had to be made as to which animals would be sampled fresh. Tracts from the remaining animals shot at the same time had to be left and collected frozen.

The udders of all cows were checked to see if milk could be expressed and the fat in the mesentery and around the heart and kidneys was assessed visually as 'excellent', 'good', or 'poor'. Marrow from the femur was checked and categorized by colour; white indicating a healthy animal and pink or red jelly indicative of an undernourished or starved animal.

The tracts were briefly checked in situ for any obviously unusual features before they were excised. Removal was done by cutting caudal to the external os of the cervix and then through the suspending ligaments close to the body wall to include as great a length of the blood vessels as possible. Specimens 77 - 18 and 77 - 19 were shot near a small hunting cabin. These

tracts were excised as described and flushed for ova before collections for histology were made.

From non-pregnant females, tissue specimens for fixation were taken from one side of the tract. The specimens taken were: a small piece of uterine horn (cut just above the external bifurcation), a section of Fallopian tube, a piece of cervix, a piece of vagina, and the ovary (bisected longitudinally). They were collected and preserved in labelled 5 dram vials containing A.F.A. (acetic acid, 10%; commercial formalin, 10%; ethyl alcohol, 30%; and distilled water, 50% by volume), as this fixative can withstand extremely low temperatures without freezing. The preservative was warmed before the tissue was added by immersing it in heated water on a Coleman stove or, when this was not possible, by inserting the vials into the freshly opened abdomen of the animals.

In the case of pregnant animals, the tract was again examined in situ for morphological features and to determine the side of pregnancy. Samples of allantoic and amniotic fluid were aspirated into 20 or 30 ml disposable plastic syringes and frozen. Both ovaries were sectioned longitudinally and visually examined for the presence of a corpus luteum. They were then labelled as to side and preserved as described above. The uterus was removed, opened, and samples of placental tissue were preserved before releasing the fetal fluids and exposing the fetus. Samples of fetal tracheal fluid were aspirated into 2 ml disposable syringes and frozen. Attempts to collect

fetal blood were unsuccessful. The fetal reproductive tract, adrenals, kidney and a preorbital gland were collected and preserved. The uterus, fetal membranes and fetus were frozen for transportation back to Grise Fiord and Ottawa.

Whenever possible the teeth from the lower jaw were collected in order to age the animal by tooth section. There was a reluctance on the part of some hunters to skin the head to remove the jaw as they felt that this reduced the market value of the hide. In these instances teeth were not collected.

c) Outcome of Collections

Many problems were encountered in the above collecting procedures. The greatest obstacle was the cold. In March the temperatures commonly fell to -40° or -50° C. This severely affected the kind and amount of equipment that could be used, as well as the quality of the collection. Equipment such as cameras could only be used for brief periods and even then with difficulty. Despite the precautions taken during blood sampling, much of the blood hemolysed.

The cold temperatures also affected the preservation of the tissue samples. Though the fixative did not freeze, its penetration of the tissue was slow and the deeper tissue layers froze before fixation was complete.

The cold also reduced manual dexterity, particularly

after the hands were wet, and necessitated the wearing of bulky clothing at all times.

The August trip alleviated many of the problems arising from sub-zero temperatures. Travel by helicopter did, however, add other restrictions. With two people to collect and three hunters, the amount of supplies that could be carried in the helicopter was greatly reduced. This trip suffered the most from an insufficient supply of preservative. It did, however, prove the most successful of all the collecting trips. As a result of the improved collecting conditions, extensive photography and in situ examination of the ligamentous attachments of three cows were made possible.

Table 1 summarizes the number of tracts collected either frozen or preserved, the number of animals from which blood was collected, teeth were sectioned and latex castings were done.

3.3 LABORATORY EXAMINATION AND ANALYSES

a) Reproductive Anatomy

(i) Morphological Studies

Non-pregnant tracts (11 of 23) were thawed in warm saline. While still partially frozen, a small piece of uterine horn was removed from three of the tracts (78-19, 78-31, 78-33) and these were immediately refrozen to act as control tissue for hormonal extractions from pregnant specimens (see appendix II). When completely

Table 1. Collected specimens classified as to the reproductive condition of the female muskoxen from which they were taken and the studies in which they were used.

REPRODUCTIVE CONDITION	TRACTS COLLECTED			SERUM COLLECTED	LATEX CASTS	TEETH SECTIONED
	TOTAL NUMBER	FROZEN	FIXED ¹			
Parous, non-pregnant	10	3	7 (5P;2G)	5	5	3
Pregnant	8	6	2 (2P;0G)	2	0	6
Non-parous	5	3	2 (1P;1G)	2	2	3
TOTALS	23	12	11 (8P;3G)	9	7	12

1 - Fixed material is categorized as poor (P) or good (G).

thawed, the weight of the tract and measurements of the ovaries, uterine horns and cervix were recorded and the tracts were photographed. Specimens 76-6, 76-8, 76-9 were flushed for the presence of ova before dissection. Drawings accompanied written descriptions of any unusual features.

Eight pregnant uteri (77-12, 77-13, 78-27, 78-32, 78-37, 78-38, 78-39, 78-40) were similarly described and photographed. Ovaries, when present, were removed, measured, and sectioned four times transversely for visual examination. They were then frozen for cryostat sectioning as described below. If the fetus had been previously removed by the hunters, the uterus was opened by cutting along the antimesometrial border for the full length of both horns. The side of pregnancy was confirmed by locating remnants of the umbilical cord and amnion. The fetal membranes were separated from the maternal caruncles and pieces of maternal caruncle and fetal cotyledon were collected separately and refrozen to be sent out for hormonal analyses (see appendix II). The cervix, removed by transecting the uterine body cranial to the internal os, was fixed in 10% buffered formalin. After fixation, the cervix was dissected along a frontal or sagittal plane for description of the cervical lumen. Pieces of endometrial tissue from the antimesometrial border were fixed in buffered formalin along with small cysts and nodules found attached to the placentomes. The uterus and fetal membranes were weighed

and photographed separately. The two tracts received with a fetus intact (77-12, 77-13) were similarly weighed, described and photographed. Each uterus was carefully opened along the antimesometrial border and the fetal membranes were separated from the uterus after recording their relationship to the fetus. Before photographing, analine ~~blue~~ dye was injected into the allantoic cavity to distinguish it from the amniotic. The fetus was removed, sexed, weighed and refrozen.

(ii) Histological Studies

Fixed tissues were embedded in paraffin wax using routine procedures (Lillie, 1965) except that dehydration times were lengthened by 1-1 1/2 hours and toluene was substituted for xylene as a clearing agent. Wax embedded tissues were sectioned at 8-10 μ . Serial sections were made of all ovaries (except 76-6, 76-8, 76-9) sectioning at 10 μ , and mounting every 10th section. With the exception of representative samples from each of the tissues, all staining was done routinely with Gill's Hematoxylin and Eosin (Fisher Scientific). The other sections were stained with Masson's Trichrome (Putt, 1972). These tissues were left in Bouin's fluid for 24 hours between dehydration and staining because the mordant improved the quality of the stain reaction. Special staining techniques for the identification of lipofuscins: Mallory's Reaction, Gemlin's Reaction, Long Ziehl-Neelsen

Test, were from Lillie (1965). Tests for fluorescence were made at the Animal Diseases Research Institute.

Tissues to be sectioned on the cryostat were placed, frozen, into cryostat embedding medium (Tissue-Tek II, OTC compound, Tek Products, Miles Laboratory Inc.) and refrozen. They were then sectioned at 10 μ and fixed for 2 minutes in 10% buffered formalin and rinsed before being stained with hematoxylin and eosin or Masson's Trichrome.

Tissue samples from three tracts received frozen from the October collecting (76-6, 76-8, 76-9) as well as additional samples from frozen pregnant uteri were thawed first and then fixed in 10% buffered formalin. These tissues were processed for wax embedding as described above.

The slides were examined under either a Reichert Zetopan research microscope or a Zeiss Compound light microscope. Cellular components were identified and recorded. To facilitate descriptions of follicular development in the ovaries, follicles were classed in major developmental categories. These categories were taken from Mossman and Duke (1973) and are as follows:

PRIMORDIAL - oocytes having a simple squamous epithelium around their periphery.

PRIMARY - when the epithelial cells enlarge to form a simple low columnar epithelium, the primordial follicle is considered a primary follicle.

SECONDARY - the simple columnar cells multiply to form a stratified cuboidal follicular epithelium or

granulosa.

VESICULAR - transformation from secondary to Graafian follicles occurs with the progressive formation of large intracellular fluid-filled spaces. These spaces enlarge to form the antrum.

Some follicles which had a recognizable theca interna but lacked an antrum were classified as secondary. Follicles were traced through the serial sections and counted only when the ova were identified or, in the absence of the ovum, at the largest point of the follicle.

In many cases the deeper layers of the muskox tissues were damaged by freezing either before or during fixation. To act as a control, comparable tissue from 7 sheep and 11 goats were frozen at -30° to -70° C, thawed, fixed in buffered formalin and processed as described for the muskox. Additional samples from the same species were fixed fresh and processed with the other tissues.

Corpora lutea from prefrozen ovaries of goat and sheep were used as a guideline for identifying the corpora lutea found in the muskox ovaries. Though most of the comparative interpretations came from the literature, direct comparisons with domestic species were used when additional information or clarification was required.

b) Vasculature of the reproductive tract

Latex injection of the vascular system of 6 non-pregnant tracts was carried out according to the methods

of Del Campo et. al. (1974). The tracts were placed on a dry surface at room temperature and were swabbed with warm saline to prevent drying. The ovarian, uterine and vaginal branch of the uterine arteries on the side of the uterus that had not been cut for histology were cannulated using polyethylene tubing filled with saline. The free end of the tube was attached to an 18 or 21 gauge needle fitted to a 5 or 10 ml disposable syringe filled with saline and the arterial system was flushed with warm saline. The uterine branch of the ovarian vein and the vaginal vein on the same side were cannulated and flushed with warm saline in a similar manner. Major areas of leakage were clamped off with hemostats. After the organs were flushed the syringes were removed and were replaced by similar syringes containing latex (red for the arterial system and blue for the venous). The latex (Ward's Natural Science Establishment Inc. Rochester, N.Y.) was first filtered twice through 4 layers of gauze and diluted with distilled water (1 vol. water to 4 vols. red latex; 1 vol. water to 3 vols. blue latex). This dilution reduced viscosity and thus the amount of injection pressure required when casting. Dilutions were chosen after trying various combinations on sheep uteri that had been found and thawed.

Injection of the latex was done slowly with an even pressure and one cannulated vessel in each system (vaginal artery and the uterine branch of the ovarian vein) was

left open to allow the saline to escape. These were then clamped to increase the injection pressure. Areas of latex leakage were clamped off. Injections were stopped when any distortions of the vessels were noted or if a vessel ruptured. Retrograde injection through the utero-ovarian vein was unsuccessfully attempted because of the pressure of the venous valves. Venous injection was therefore primarily through the vaginal vein. The general direction of flow of the latex and approximate areas injected were recorded on diagrams. Following latex injection of the tracts the cannulae were removed, the vessels were tied off and the tract was trimmed, pinned to a piece of cardboard and fixed in A.F.A. After complete fixation the tracts were washed in 50% alcohol and dehydrated through a graded series of alcohols. They were cleared, stored and photographed in benzyl benzoate (Table 2). Photography of the latex specimens followed the methods of Del Campo et. al. (1974).

c) Age Determinations

(i) Adults

Teeth were sectioned following the general outline given by Thomas (1977). The first incisors from all jaws collected were decalcified in formic acid (10% formic acid, 5% formalin and 85% distilled water) for two weeks, neutralized in distilled water for 12 hours and sectioned at 15 on the cryostat. Several sections from

Table 2. Sequential procedure for preparation of cleared latex injected specimens.

Procedure #	Solvent	Time (h)	Remarks
Fixation	A.F.A.	48	Specimen was fastened to a cardboard in desired shape.
	<u>ethanol and peroxide</u>		Each solution was replaced at 12 h intervals
	50%	24	
	60%	24	
	70%	24	hydrogen peroxide (1-1.5 ml/l) aids the bleaching
Removal of alcohol and clearing	80%	24	
	<u>ethanol</u>		
	87%	24	
	90%	24	
	95%	24	
Clearing	100%	24	
	1,1 benzene, 100%	12	
	ethanol		
	benzene		
	benzyl benzoate		
		3	May cause bulging of latex Specimens preserved permanently and photographed in this solvent

* each bath contained 1.5 l of solvent

each tooth were stained in varying concentrations (.01, .02, .05) of toluidine blue for variable lengths of time (1 sec, 2 sec, 5 sec, 2 hr and overnight). The cementum lines were counted from those sections that were most clearly stained. This was not consistent for any single concentration of stain or time interval but tended to vary with individual teeth.

(ii) FETUS

Each of four fetuses was thawed, weighed and measurements of its crown-rump length and of a hindfoot were taken. Their external features were described following the table of developmental characteristics given by Evans and Sack (1973). After being photographed, the fetuses were refrozen.

To estimate the age of the fetuses, the cube root was taken of 28 birthweights extracted from the literature (Oeming, 1965; Tener, 1965; Alendal, 1971; Spencer and Lensink, 1970; Wilkinson, 1973). The cube root was then plotted against gestation length which was assumed to be 250 days. The growth rate, a , can then be derived from the formula $W^{1/3} = a(t-t_0)$ where $W^{1/3}$ = cube root of weight; t = full gestation length; $t_0 = 0.2 \times$ full gestation length (an arbitrary estimate that incurs an error of approximately 10%; Huggett and Widdas, 1951). Using the derived fetal growth rate and the formula, the approximate stage of gestation could be estimated for the fetuses of known weight.

RESULTS

4.1 REPRODUCTIVE ANATOMY

a) Suspensory Ligaments

Field observations on the three females collected in August (78-41, 78-42, 78-44) showed that the broad ligament was the major suspending ligament. This structure, a prominent peritoneal fold, was attached medially to the body of the uterus; laterally it merged with the parietal pelvic peritoneum and extended cranially beyond the pelvic brim. The suspensory ligament, a membranous fold of the broad ligament, contained the ovarian vessels. The round ligament was well developed and was easily distinguished as a band of muscular tissue located in a membranous fold on the ventral surface of the broad ligament and can be seen in Plate 1 which depicts the in situ position of the non-pregnant uterus.

b) The Non-pregnant Uterus

(i) Morphology

The reproductive tracts of 10 female muskoxen (76-1, 76-6, 76-8, 77-18, 77-19, 78-26, 78-31, 78-33, 78-41, 78-44), collected during the three different sampling times were assessed as parous non-pregnant females and were similar in their anatomical characteristics. Weights and dimensions of the tracts, transected just caudal to the external os of the cervix, are shown in Table 3. The body of the uterus measured 0.5 to 2.0 cm from the internal os to the septa and the horns were

PLATE 1

THE REPRODUCTIVE TRACT in situ

Figure 1. The in situ position of the uterus from a mature, parous muskox (78-44) collected in August. The animal has been placed on its back and the abdomen opened such that the uterus is viewed from the ventral aspect. The scale (inches on top; metric below) has been placed at the cranial end. Uterine horn, Ut; ovary, O; Fallopian tube, F; bladder, B.

Figure 2. The same uterus, depicted in Fig. 1 above, has been raised to show the dorsal surface and the suspending ligaments. Suspensory ligament, a; broad ligament, b; round ligament, c.



Table 3. Weights, dimensions and caruncular counts on the reproductive tracts of mature and immature non-pregnant muskoxen.

Reproductive Status	Weight of Uterus (g)	Length of Horn (cm)		Caruncular count ¹	Length of Cervix (cm)
		Left	Right		
Mature					
76-1 +	*	28	26	(78)(95) 173	7.5
76-6	*	35	39	(85)(83) 168	9.0
76-8	*	34	33	*	7.5
77-18	102.3	19	*	*	*
77-19	101.0	*	15	*	*
78-26	178.7	*	21	*	*
78-31	112.6	18	*	*	*
78-33	94.9	17	*	*	7.2
78-41	*	*	*	*	9.0
78-44	*	*	*	*	
Immature					
76-9	*	17	*	*	3.5
77-11	48.4	13	10	*	3.8
78-24	50.4	14	15	(69)(74) 143	3.1
78-28	*	*	*	*	*
78-42	*	12	14	140	5.0

1.1 (Left horn)(Right horn) Total

* - not determined

+ - labelling code is found in appendix 1

approximately equal in length and averaged 26 cm from the bifurcation to the utero-tubal junction. They were coiled 1 - 1 1/2 times and the coiled arterioles were visible on the external surface as prominent transverse striations. A single intercornual ligament was found (Plate 2, Fig. 1).

A muscular band of tissue approximately 5 mm deep ran along the antimesometrial border of the uterus (Plate 3, Fig. 1) and in two specimens appeared continuous with the intercornual ligament (Plate 3, Fig. 2). In the other 8 specimens this continuity was not evident (Plate 3, Fig. 3). The muscular band ran from the bifurcation of the uterus along the horn and disappeared a short distance before the utero-tubal junction.

The endometrium contained numerous caruncles which were roughly arranged in four longitudinal rows extending from the body into the two uterine horns. The caruncles varied between 4 x 3 mm to 8 x 4 mm in length and fusion of two, or occasionally more, was common. The caruncles near the cervix and those near the utero-tubal junction were generally smaller in size. With the exception of the smaller ones at the ovarian end of the horn, all caruncles contained a dark pigment in the central depression. No similar pigment was seen in the intercaruncular area (Plate 4, Fig. 1). The number of caruncles per horn (in pregnant and non-pregnant uteri) ranged from 49 to 102 with an average number of 81.

PLATE 2

THE EXCISED UTERUS

Figure 1. A uterus from a mature, parous muskox (76-1) seen from the dorasal surface. The horns have been uncoiled to show their length and the tapering towards the utero-tubal junction. A single intercornual ligament was found between the uterine horns. The forceps (upper portion of photograph) are displaying the muscular band.

Figure 2. A uterus from a non-parous female muskox (78-24). This immature tract is substantially smaller in size and lacks a muscular band. The white areas on the uterine horns are the result of freezer burn.



PLATE 3

THE MUSCULAR BAND IN THE PAROUS NON-PREGNANT UTERUS

Figure 1. The appearance of the muscular band (M) on the mature, non-pregnant tract of a muskox (78-26). The forceps are pinching the muscular band which runs along the antimesometrial border of both uterine horns.

Figure 2. In this specimen, a parous, non-pregnant muskox (78-26), the muscular band (M) appears continuous with the intercornual ligament (IC).

Figure 3. In most specimens the muscular band (M) did not appear continuous with the intercornual ligament (IC) but could be seen on the dorsal surface of the Ut. horn in front of the intercornual ligament. At the level of external fusion of the uterine horns the muscular band melded with the uterine musculature and was no longer evident morphologically. (From specimen 78-31, a parous non-pregnant muskox).

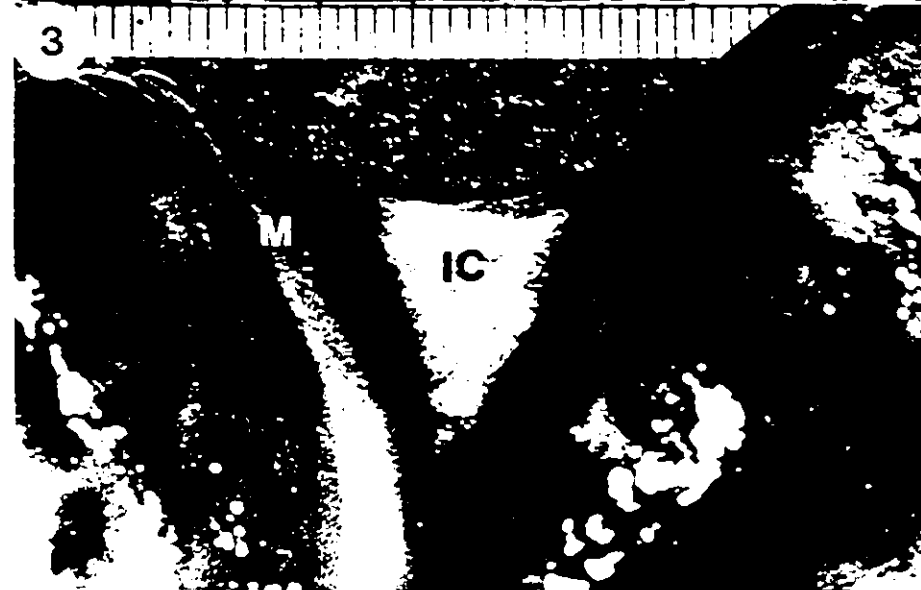
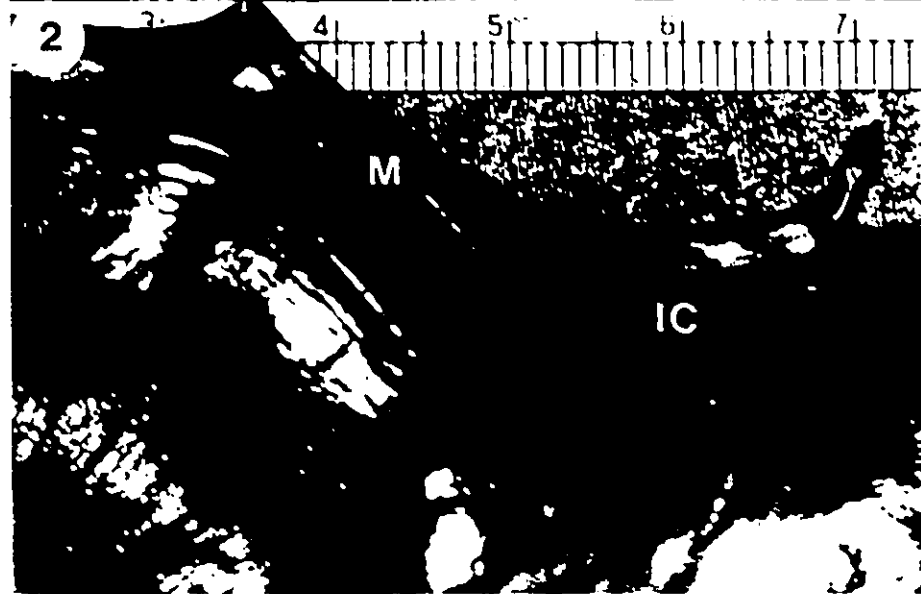
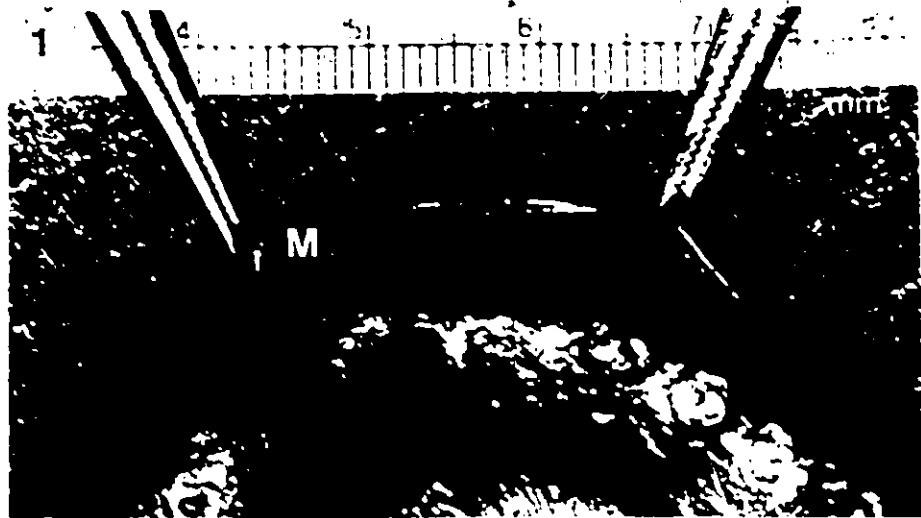
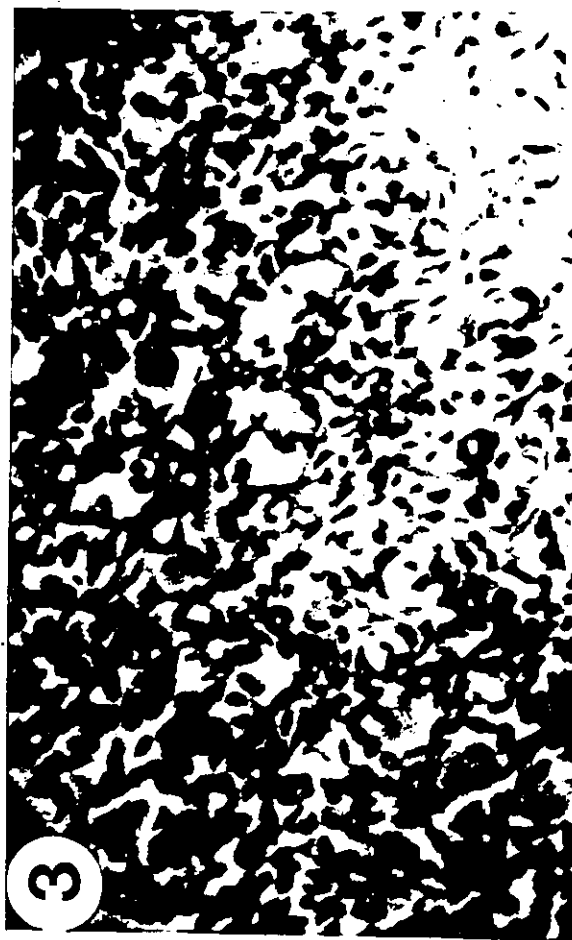


PLATE 4

PIGMENTATION IN THE UTERUS AND PLACENTA

- Figure 1. The opened uterine horn of a parous, non-pregnant muskox (78-26) to show the dark pigmentation on the caruncles.
- Figure 2. The opened uterus of an immature muskox (78-42) to show the lack of pigmentation in the uterus.
- Figure 3. Lipofuscins in the endometrial stroma of a parous non-pregnant muskox. H & E (X500).
- Figure 4. Cross section through a placentome from a pregnant muskox showing the pigment accumulation in the fetal trophoblast. The pigmented epithelium is in contact with pools of extravasated blood. H & E (X250).



The uteri of 5 animals (76-9, 77-11, 78-28, 78-42, 78-24) collected from the three hunting seasons were judged to be from non-parous females. Because teeth were collected from three of these animals, they could be aged. Of these, the eldest was four years old, Table 8. These tracts, though similar to the mature non-pregnant tracts in many respects were smaller, 48-50 gms in the two tracts that were weighed, (Plate 2, Fig. 2) and had an average horn length of 14 cm (Table 3). The convoluted arterioles, while present, did not make the pattern of striations that was so prominent in the parous animals. All five tracts lacked the prominent muscular band along the antimesometrial border although fine striations were visible under close examination. The caruncular count was similar to that of the parous animals (Table 3) but the caruncles lacked any pigmentation (Plate 4, Fig. 2).

(ii) Histology

Because of the difficulties cited in the materials and methods section the histological preparations were generally of a poor quality. All specimens collected in March and October suffered from freezing damage but the extent of the damage was variable and there were portions of each tissue that could be used. The best histological results were from two parous (78-41, 78-44) and one non-parous (78-42) animals collected in August.

The uterus was lined with stratified low columnar

epithelium (Plate 5, Fig. 1) and was highly glandular in nature. The endometrial glands were simple, branched tubular glands lined by a columnar epithelium (Plate 5, Fig. 2). The extent to which the glands coiled tended to increase towards their base near the muscularis (Plate 5, Fig. 3). Conversely the caruncles were non glandular (Plate 5, Fig. 4) and were composed of a highly cellular connective tissue which contained stromal cells, plasmocytes, macrophages and numerous large pigmented cells which were largely concentrated beneath the epithelium of the caruncle. These pigments gave negative results for iron using Mallory's Reaction and for bilirubin using Gemlin's Reaction. They did, however, react positively to the Long Ziehl-Neelson Test for acid fast lipofuscins and under fluorescent microscopy gave a positive reaction, fluorescing an orange-yellow to brown colour, characteristic of lipofuscins (Lillie, 1965) (Plate 4, Fig. 3).

The muscularis consisted of an inner thick band of circular smooth muscle fibres with a thinner band of longitudinal smooth muscle fibres outside, towards the serosa (Plate 6, Fig. 1). The outer, longitudinal muscle layer was not as well defined and also contained some bundles of circular muscle tissue. It was more densely cellular than the circular layer. The boundary between the two layers was not always distinct (Plate 6, Fig. 2). In general the layers were separated by a vascular layer, the stratum vasculare, containing the arteries, veins and

PLATE 5

UTERINE HISTOLOGY IN THE NON-PREGNANT TRACT

- Figure 1. The uterine epithelium from a mature anestrous muskox (77-19) showing the stratified columnar epithelium (arrow). (X500)
- Figure 2. Cross section of an endometrial gland lined by high columnar cells from a parous, non-pregnant muskox (78-44) collected in August. (X500)
- Figure 3. Cross section of the uterine stroma in a non-parous muskox (78-42) collected in August. The endometrial glands increased their coiling near the muscular layer. Muscularis, M; endometrial stroma, S; uterine glands, arrow. (X3.5)
- Figure 4. Cross section of a caruncle from a mature, non-pregnant muskox (78-41) collected in August, showing the aglandular nature of the caruncle (arrow). (X12)



PLATE 6

UTERINE HISTOLOGY IN THE NON-PREGNANT TRACT

- Figure 1. Cross section of the uterine horn of a mature, non-pregnant muskox (78-41). The blood vessels (arrow) are embedded in the circular muscle layer. The longitudinal muscle layer is reduced to a thin strip under the blood vessels. Endometrial stroma, a; circular muscle layer, b; longitudinal muscle layer and serosa, c. (X3.5)
- Figure 2. Close up of the blood vessels seen in Fig. 1 above to show the greatly thickened vascular walls. The division between the circular and longitudinal muscle layers is obscured in this specimen. (X250)
- Figure 3. Cross section of the uterine horn of a non-parous muskox (78-42) collected in August. The vascular elements were substantially reduced and appeared as small collections of capillary-like vessels in this specimen. Endometrial stroma, a; circular muscle layer, b; longitudinal muscle layer and serosa, c. (X3.5)



lymphatics.

In some samples the larger blood vessels were found embedded in the circular muscle layer and these vessels were characterized by extremely thick walls, large lumens and appeared to be surrounded by a network of lymphatics (Plate 6, Fig. 2). Further, in these specimens a thin layer of circular muscle could be seen between the vessels and the longitudinal layer. In such cases the division between the circular and the longitudinal fibres was obscured. In two specimens, the circular muscle fibres could be seen extending through the longitudinal layer and forming a thin strip, 2-3 cell layers thick, immediately under the stratified squamous epithelium of the serosa.

The prominent muscular band seen on the antimesometrial border consisted primarily of the serosa and longitudinal smooth muscle fibres. Histologically the tissue in this area did not differ from other regions of the uterine horn and appeared to be a fold of the outer muscle layer (Plate 7, Fig. 1). In the central portion was a network of large spaces joined by thin strands of connective tissue containing small capillaries. Some of these spaces appeared to have an endothelial lining and resembled large lymphatics but they did not contain any substance recognisable as lymph nor any sign that they contained lymphocytes (Plate 7, Figs. 2 and 3).

The network of connective tissue and lymphatic-like

PLATE 7

THE HISTOLOGY OF THE MUSCULAR BAND IN THE NON-PREGNANT UTERUS

Figure 1. A cross section of the uterine horn of a mature, non-pregnant muskox (78-44). The section was taken from the antimesometrial border. The muscular band (MB) forms a prominent fold in the tissue containing capillaries (arrow) and elements of the stratum vasculare. (X31)

Figure 2. Higher magnification of the muscular band, from the specimen, depicted in Fig. 1 above, to show the vascular elements enclosed by muscular tissue. (X75)

Figure 3. The tip of the muscular band from the same specimen in Figs. 1 and 2 showing the lymphatic-like elements penetrating throughout the muscular tissue (open arrows). (X125)

1



vessels was continuous with the stratum vasculare of the uterine muscularis on both sides of the muscle band so that the muscular band appeared to be a fold of the outer muscular layer which enclosed elements of the vascular layer.

Histologically the 5 non-parous tracts were similar to those of the mature, non-pregnant animals except that they lacked the large, thick walled vessels (the vascular elements were present but very much reduced in size) and there was a complete absence of lipofuscins in the caruncular stroma (Plate 6, Fig. 3).

c) The Pregnant Uterus

(i) Estimation of Stage of Gestation

Eight pregnant animals were collected over a period of two years. All of these animals were taken either at the end of February or in March, a time of year normally associated with the last trimester of pregnancy.

A more definitive measure of the stage of pregnancy could only be obtained by estimating fetal age. Of the eight tracts collected, only four contained a fetus, all of which were male. Fetal weights, crown-rump measurements and hindfoot measurements are listed in Table 4. Subjective observations are found in Table 5 and photographs in Plate 8. It is not possible to apply any of the criteria of Evans and Sack (1973) directly to the muskox in the absence of fetuses of a known age. However, their

Table 4. Dimensions of four muskox fetuses and their estimated ages.

Muskox Fetus Number	Date of Kill	Weight (kg)	Crown- rump (cm)	Ear (mm)	Hindfoot (cm)	C-l(S) ² (cm)	Estimated Age (da.)
12	3/3/77	5.18	44.2	4.8	16.5	54.4	207
13	3/3/77	5.02	43.5	4.6	17.0	54.5	205
27	10/3/78	6.00	46.4	5.5	19.5	58.6	215
32	20/3/78	7.49	48.5	6.0	21.5	63.0	229

1 - day/month/year

2 - crown-rump, spinal measurements

Table 5. Fetal development and stage of gestation - Subjective assessments of morphological features from Evans and Sack (1973).

Feature	Muskox Fetus Number			Approximate Time of appearance in	
	12	13	27	32	Cattle (gestation 280 da.) Sheep (gestation 147 da.)
Hooves dew claws and hooves hard	no	no	hooves hard, dew claws not as hard	hooves hard, dew claws not as hard	150 da.
Hair tactile hairs appear on face	present	present	present	present	76 da. 75-90 da.
eyelashes and fine hair on chin	no eye- lashes	no eye- lashes	eyelashes present	eyelashes present	150 da.
colour mark- ings appear	just beginning	just beginning	markings evident	markings evident	150 da. 104 da.
hair cover- ing complete	soft fetal hair	soft fetal hair	coarse, long hair	thicker and longer hair than others	230 da. 116 da.
wobly hair begins to grow	none	none	(see above)	(see above)	120 da.
Eyelids separated	inner can- thus begin- ning to open	inner can- thus begin- ning to open	partially open	completely open	196 da. 119-126 da.

PLATE 8

FIVE MUSKOX FETUSES OF LATE PREGNANCY

The fetuses, collected in March, are arranged according to size and weight; from the right, 78-32, 78-27, 78-12, 78-13, Mu-1. Mu-1 is a female specimen donated by the National Museum and, although the lightest in weight, it is more advanced in coat colour and development than specimens 78-12, and 78-13.



data are of some value in comparing the development of the muskox fetus to those of the domestic species. There is some consistency in the sequence of appearance of histological characteristics such as colour and coat development and the opening of the inner canthus of the eye. Plate 9, Figs. 1-4 shows the coat differences encountered in the fetuses. Based on the formula of Huggett and Widdas (1951) the slope for fetal growth acceleration was found to be 0.11 cm/da. Estimates of fetal ages derived from this slope are found in Table 5.

(ii) Morphology

The side of pregnancy in the eight animals was equally divided between the right and left with the corpus luteum of pregnancy when found, always located in the ovary ipsilateral to the pregnant horn.

In late pregnancy the uterus was located ventrally in the abdominal cavity and ranged in weight (without fetus or fetal membranes) from 2.3 to 2.9 kg (Table 6). Both horns were enlarged though the pregnant horn was noticeably larger. Nevertheless, the horns still described a single coil. The arterioles, which appeared as transverse striations on the non-pregnant tract, were no longer tightly coiled but almost completely straightened out. The ovaries were found close to the uterine body on the dorsolateral aspect and on the dorsal surface, the distended body of the uterus folded over the cervix,

PLATE 9

COMPARISON OF FETAL DEVELOPMENT

- Figure 1. Head and shoulder region of a male muskox (78-13). Although it cannot be seen in this picture the inner canthus of the eye was only beginning to separate and no eyelashes were present. Estimated age is 205 days.
- Figure 2. Head and shoulder region of a male muskox fetus (78-32). The coat is dense with coarse long hair. Though not visible here the eyes were completely open and eyelashes were present. Estimated age is 229 days.
- Figure 3. Hind legs of fetus 78-13, depicted above in Fig. 1, showing the fine fetal hair and relative lack of colour markings.
- Figure 4. Hind legs of 78-32 depicted above in Fig. 1 showing the advanced coat development and colour markings. The white hair on the legs is stiffer and shorter than the body hair.

1

13



2

32



3

13



4

32



Table 6. Measurements taken from the reproductive tracts of eight pregnant muskox.

Specimen Number	Weight of Uterus (kg)	Weight of Fetal Membranes (kg)	Caruncular Count ¹	Length of Cervix (cm)
77-12	2.9	1.3	(58)(73) 131	10
77-13	2.8	1.3	(86)(95) 181	11
78-27	2.9	1.1	(95)(68) 163	13
78-32	2.5	1.3	(87)(80) 167	15
78-37	2.7	1.6	* * 60	10
78-38	2.5	1.4	(49)(100) 149	15
78-39	2.5	1.6	(87)(102) 189	13.5
78-40	2.3	1.3	155 ²	16

- 1 - (Left horn)(Right horn) Total
 * - high degree of caruncular fusion
 2 - total count taken only

(Plate 10, Fig. 1).

The muscular band of tissue on the antimesometrial border was not immediately visible, particularly in uteri still containing a fetus and fetal fluid but under close examination, this band could be found on the non-pregnant horn (Plate 11, Fig. 1). Removal of the fetus and fluids relaxed the uterus sufficiently to allow recognition of the muscular band which was found to be approximately 3 cm in depth and ended abruptly a short distance from the utero-tubal junction (Plate 11, Figs. 2 and 3). The muscular band appeared to be avascular and lacked the prominent arterioles of the uterine horn. In the fully distended uterus this tissue apparently formed a flat strip 5-6 cm wide along the antimesometrial border and was only loosely connected to the underlying muscularis.

Dissection of the uterus revealed a placenta that extended into both horns and involved all caruncles except for a few of the small or more distal ones. The septa dividing the uterine horns had become quite enlarged and had placentomes on both sides while the antimesometrial border was relatively free of placentomes, (Plate 12, Figs. 1 and 2). The placentomes were ellipsoid, saucer-shaped structures with a rim or lip around the edge and varied in size. The largest ones were pedunculate and measured 8-9 cm in length and were generally located in the central portion of the pregnant horn near the site of attachment of the umbilical cord (Plate 12, Fig. 3). The

PLATE 10

THE PREGNANT UTERUS

Figure 1. The excised pregnant muskox uterus (77-13), dorsal view. The enlarged left horn contains the fetus. The ovary is visible close to the uterine body (small arrow). Dark stripes running across the uterine horn are the coiled arterioles which have been straightened out by the stretching of the uterus (large arrow).

Figure 2. The fetus and fetal membranes, from the specimen in Fig. 1 above after removal of the uterus. The amnion has been opened to expose the fetus. The allantochorion contains the greater number of cotyledons.



PLATE 11

THE MUSCULAR BAND DURING PREGNANCY

Figure 1. The right uterine horn of a pregnant muskox (77-13) showing the muscular band on the horn opposite the side of pregnancy. This is before the removal of the fetus and fluids.

Figure 2. After removal of the fetus and fluids the muscular band (M) could be identified as an avascular area along the antimesometrial border. The coiled arterioles (arrow), are straightened out due to pregnancy, and can be seen up to the band but not in it (from the same specimen depicted in Plate 10 and Fig. 1 above).

Figure 3. The muscular band ended abruptly (arrow) a short distance from the utero-tubal junction (from the same specimen depicted in Plate 10 and Figs. 1 and 2 above).

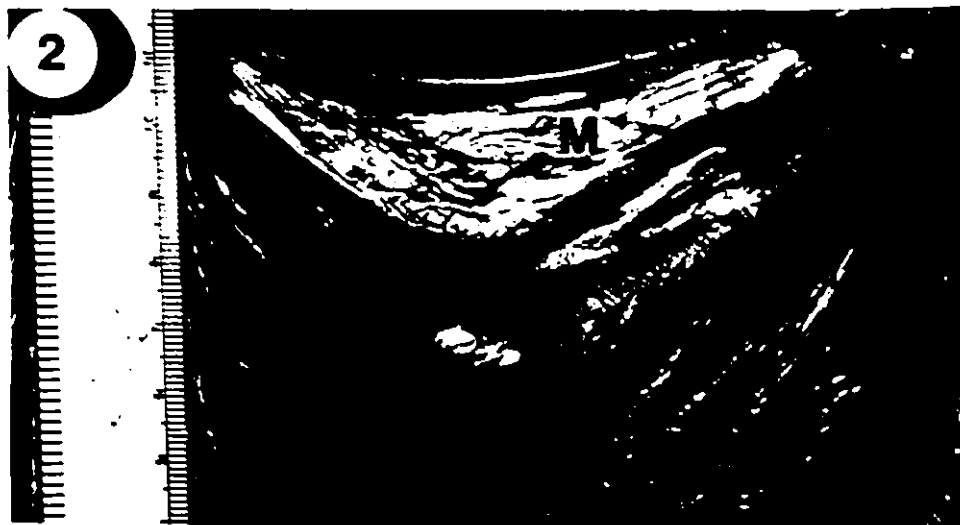
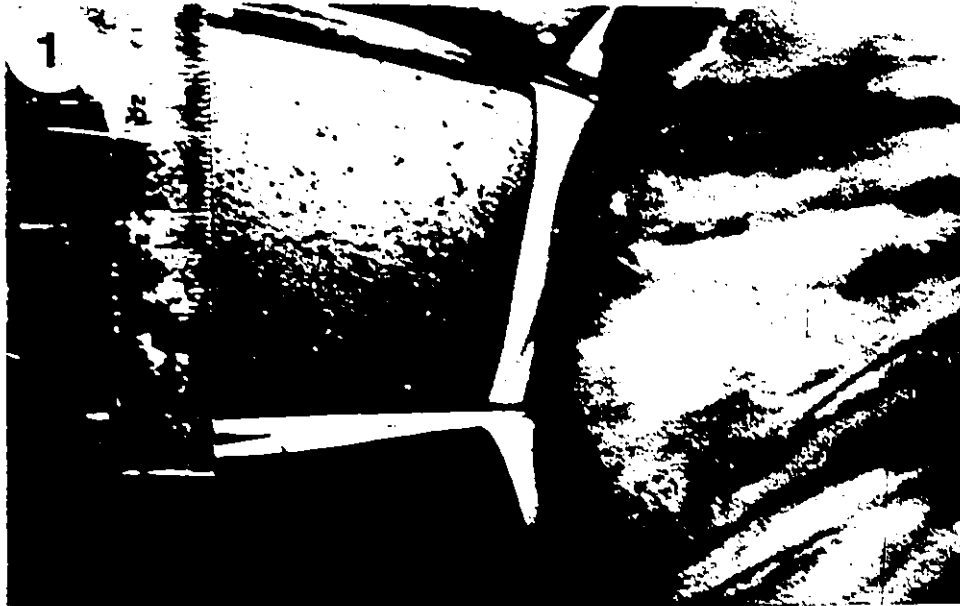


PLATE 12

THE PREGNANT UTERUS

Figure 1. The uterus from a pregnant muskox collected in March after dissection and removal of fetal tissues. The uterus was opened by cutting along the antimesometrial border. The forceps (upper left and lower middle) mark the position of the septum.

Figure 2. The septum from the same uterus depicted in Fig. 1 above showing large well developed caruncles.

Figure 3. The characteristic ellipsoid shape of a single caruncle from the uterus in Fig. 1 and 2 above showing a slight lip or rim around the edge. Two small hyperplastic cysts can be seen on the edge (arrows).

1



2



3



caruncles were arranged approximately in rows although fusion of the caruncles and the distortion of the uterus made this arrangement less evident than in non-pregnant tracts. Of the caruncles in each tract an estimated 5 - 10% contained nodules on the mucosal surface which were reddish-brown in colour and highly irregular in shape. Rarely, small pockets of similar tissue were found in the intercaruncular areas (Plate 13, Fig. 1).

Small yellow-white cysts were found in all the pregnant uteri and although most of these cysts were on the maternal endometrium associated with a caruncle a few were located in the intercaruncular area as well. Their shape ranged from spheroidal to long and slender, some protruded noticeably, and others formed low amorphous masses. The largest cyst measured 13 x 15 mm (Plate 13, Fig. 1).

The amnion and the allantois separated as a unit from the maternal tissue and without fetal fluids they ranged in weight from 1.1 to 1.6 kg (Table 6). The membranes consisted of an extensive chorio-allantois and an amnion which surrounded the fetus (Plate 10, Fig. 2 and Plate 14, Fig. 1 and 4). The allantois did not surround the amnion but passed over it on one side. The allantoic stalk originated from the urachus at the distal end of the umbilicus and curved up one side of the amnion to branch into the two sections or arms of the allantois, one arm going into each horn of the uterus. The arrangement formed a 'T' shape pattern at the umbilicus (Plate 14, Fig. 1

PLATE 13.

THE PLACENTA

- Figure 1. The endometrial surface of a maternal caruncle showing a hyperplastic cyst (a). The nodules (b) appeared as areas of extra placental tissue. These were found almost exclusively in association with the maternal caruncles. Specimen was taken from a pregnant muskox collected in March.
- Figure 2. Cross section of a hyperplastic cyst such as seen in Fig. 1 above. Although the tissue had been previously frozen the cells could be identified as squamous epithelial cells. (X12)
- Figure 3. Cross section of a placentome showing fetal villi (a) interdigitating with maternal tissue (b). The specimen was taken from a pregnant muskox collected in March (78-27). The uterus was collected with the fetus and membranes. (X500)
- Figure 4. Close up of the same tissue as seen in Fig. 3 above showing the large binucleate cells in the trophoblast epithelium (arrow). (X500)

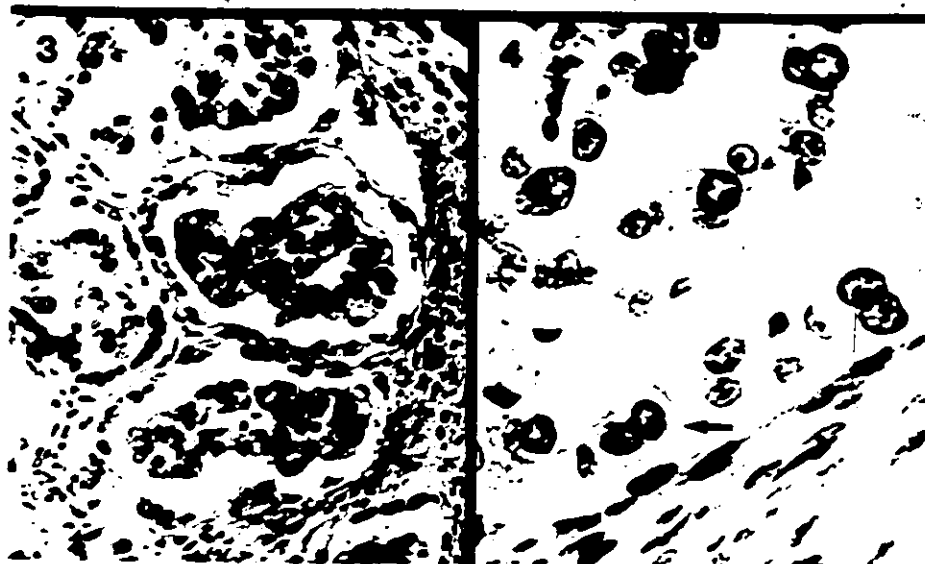
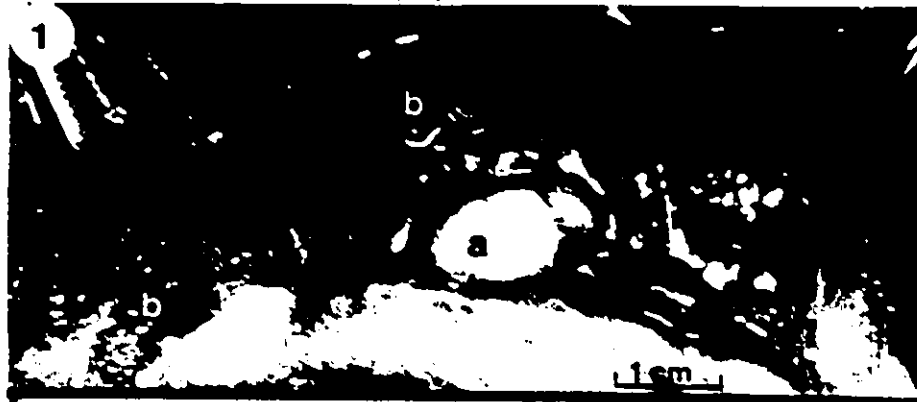


PLATE 14

FETAL MEMBRANES

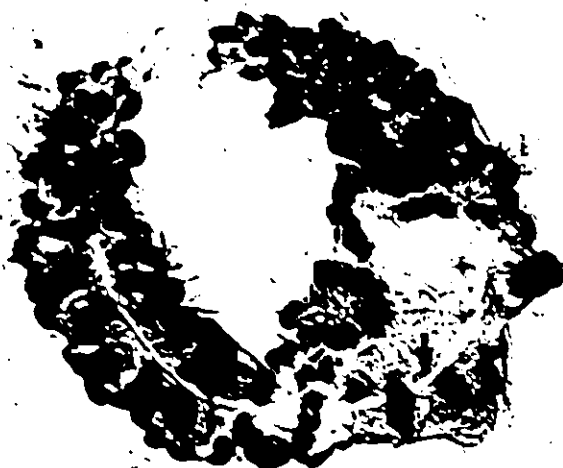
Figure 1. Fetal membranes after separation from the uterus of a pregnant muskox collected in March. The enlarged portion (a) is the amnion. The major vessels can be seen extending in both directions from this area (arrow).

Figure 2. Necrotic tip at the extremity of the allanto-chorion from the same specimen depicted in Fig. 1.

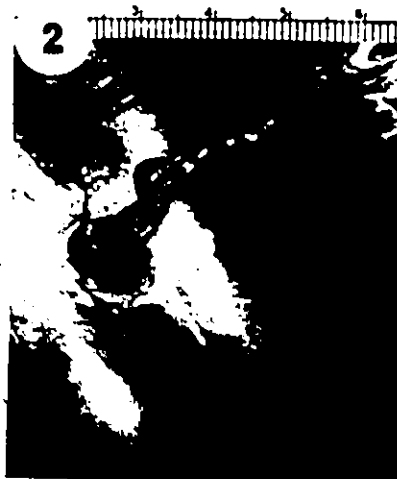
Figure 3. Small white plaques found in the region of the umbilicus in the 8 pregnant muskox tracts collected.

Figure 4. The arrangement of the muskox fetal membranes. The amnion has been opened and the fetus extracted without cutting the umbilicus. The allantois (A) can be seen crossing over the remnants of the amnion (a) to join the umbilicus (arrow). The forceps were used to seal leaks. In this specimen the muskox is still frozen and a piece of frozen fetal fluid is attached to the ventral portion of the animal. The fetus was taken from a pregnant muskox uterus (77-12) collected in March.

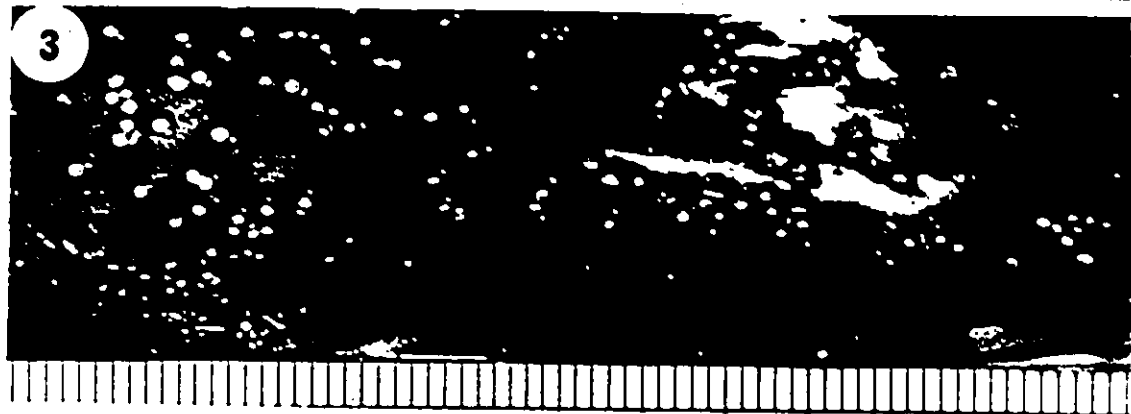
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3



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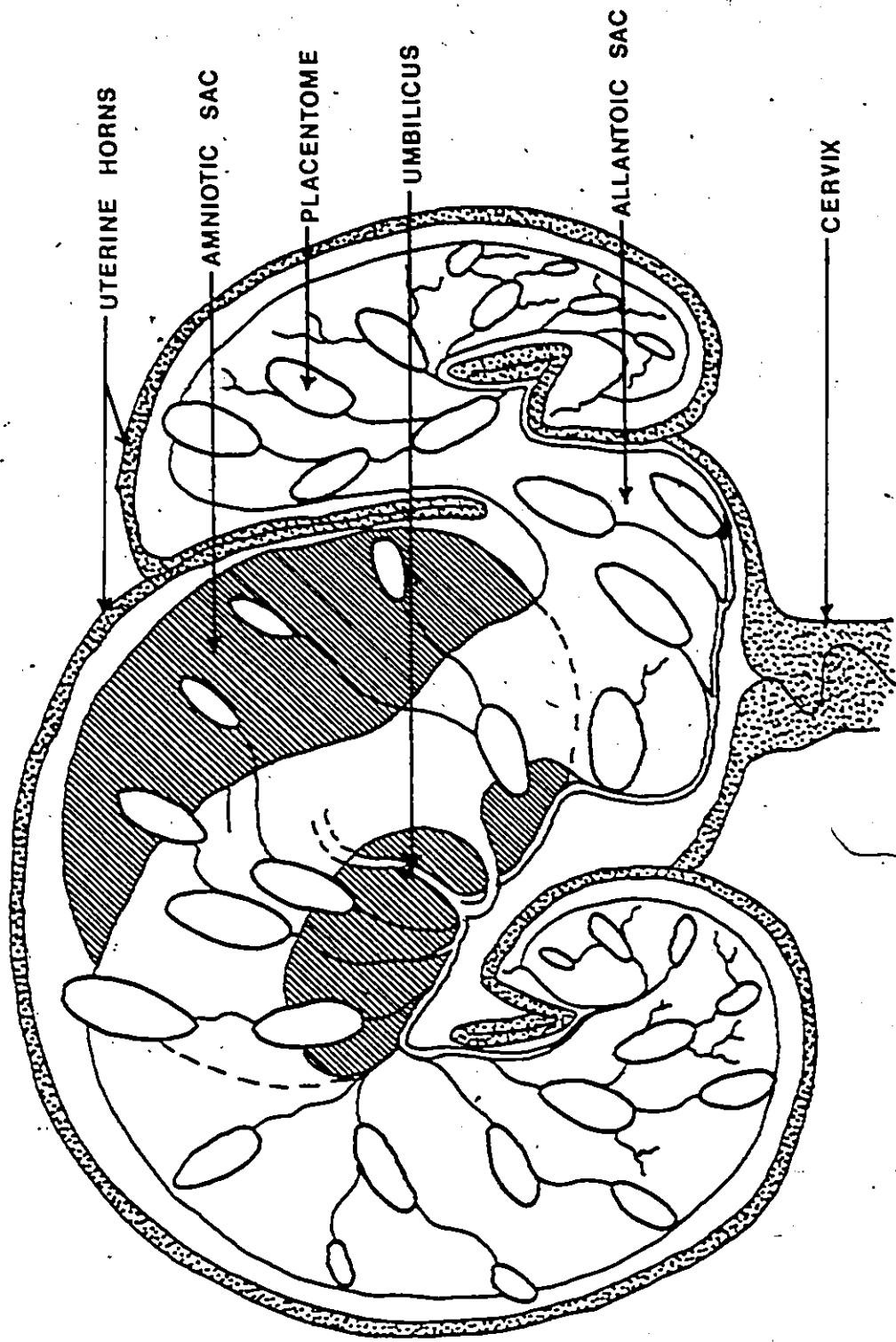
and 4). The allantois was considerably narrower in the region of the amnion and a necrotic tip was found at both ends (Plate 14, Fig. 2).

As seen in cross-section the umbilicus contained two arteries at opposite poles, two veins to the inside of the arteries, and a relatively large urachus in the middle. A large vein and artery ran the length of the allantois in both directions with smaller vessels going to the cotyledons. On the fetal membranes, over the area of the umbilicus, clusters of white spherical bodies approximately 1 mm in diameter were evident (Plate 14, Fig. 3). The arrangement of the fetal membranes is shown diagrammatically in Fig. 5.

(ii) Histology

Because most of the central portion had been destroyed by freezing, the histological preparations of the placentomes were poor. However, enough tissue was properly preserved to give an indication of the fetal/maternal attachment. The long branching villi of the fetal trophoblast were lodged deep in the maternal crypts and were surrounded by projections of maternal tissue. Fetal capillaries were found in close apposition with the trophoblast epithelium which contained large binucleate cells (Plate 13, Figs. 3 and 4). Near the surface, at the base of the fetal villi, pools of extravasated blood were found and were presumably of maternal origin. Some erosion of

Figure 5. A schematic diagram of the fetal membranes during late pregnancy in the muskox. The allantoic sac can be seen extending into both horns of the uterus. The allantois narrows as it crosses the amnion and forms a 'T' shape at the umbilicus. In order to clarify the relationship of the membranes, the fetus has not been drawn in this diagram.



Arrangement of the fetal membranes in the muskox uterus

maternal tissue was evident in this region but the tissue preservation was too poor to determine its extent. The epithelium of the trophoblast, in the region of the extravasated blood, was filled with an orange-brown pigmented substance (Plate 4, Fig. 4).

The nodules on the placentomes, though difficult to section, appeared to be areas of additional placentation. The yellow cysts appeared, histologically, to be endometrial hyperplastic cysts. Carotenization of the epithelial cells within the cyst gave the structure a yellow colour (Plate 13, Fig. 2).

The muscle band from the pregnant tracts revealed a band of longitudinal smooth muscle fibres under the serosa and overlying a fine mesh or network of very large vessels which consisted of a thin layer of cells presumed to be endothelial in nature. These vessels were filled or partially filled with a densely packed substance that was strongly basophilic. This substance was always found within the confines of a vessel. There was some evidence of valves within these vessels (Plate 15, Figs. 1 and 2). On the basis of the existing data the vessels were diagnosed as lymphatics and the substance within the vessels was believed to be derived from ruptured lymphocytes.

d) The Uterine Cervix

(i) Morphology

The cervix was a firm, thick-walled structure

PLATE 15

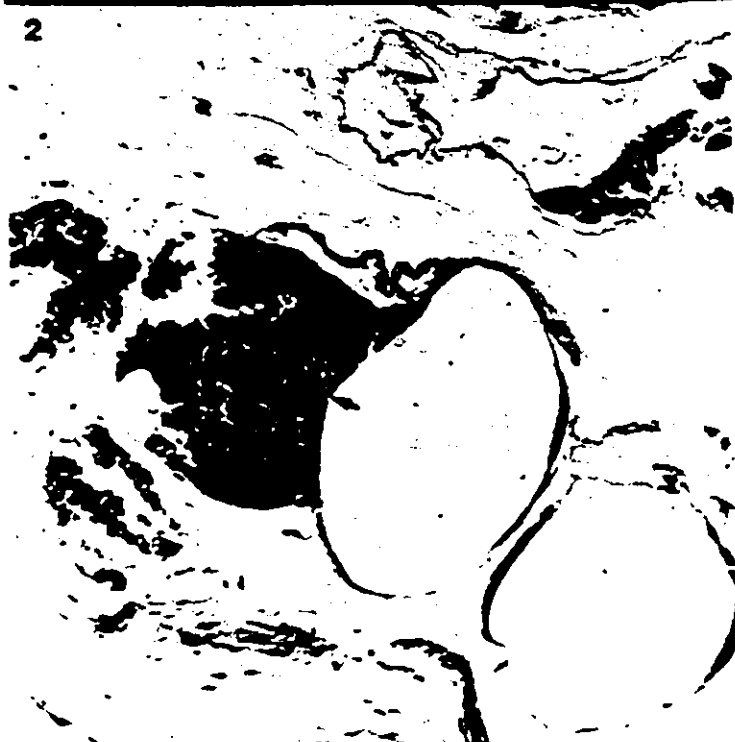
HISTOLOGY OF THE MUSCULAR BAND DURING PREGNANCY

Figure 1. These sections were taken from frozen tissue from the antimesometrial border of a pregnant muskox uterus. Although the tissue has been damaged the section does show a layer of muscular tissue (A) and a layer of vascular elements surrounded by diffuse connective tissue elements (B). (X31).

Figure 2. The vascular elements from the section depicted in Fig. 1 above had a thin wall and contained a substance that was strongly basophilic. The well defined boundary (arrow) suggests the possible existence of valves. (X125)



2



that averaged 8 cm from the internal to the external os in a mature non-pregnant animal, 13 cm in the pregnant animal and 4 cm in the non-parous animal (Tables 3 and 6). When sectioned along a frontal plane the cervical lumen appeared as a prominent 'S' shape. When sectioned dorsally, four ridges or annular rings, 1.5 to 2 cm apart, were evident (Plate 15, Figs. 1 and 2). The cervical mucosa was elaborately folded forming a very complex 'plicae palmatae' (Hafez, 1973). The mucosal folds were directed towards the uterine end and produced many branched gland-like furrows (Plate 16, Fig. 3).

The external os of the cervix was prominent and exhibited some individual variation. In 20 of the 23 specimens there was a definite projection resembling an epiglottis that protruded either from the dorsal or ventral border and covered the entrance to the cervix. In the cows collected in August this structure was swollen and protruded noticeably (Plate 17, Figs. 2 and 3). The floor of the vagina near the external os was folded into small ridges that became more accentuated as the cervical opening was approached.

The specimens were dissected caudal to the external os of the cervix. This procedure resulted in variable amounts of vaginal tissue being attached to the tract. However, in 14 specimens a small fold in the vaginal wall was found and in the pregnant specimens and the older, parous animals this fold was found close to, and partially

PLATE 16

CERVICAL LUMEN

Figure 1. The excised cervix of a pregnant muskox (78-39) that has been fixed in buffered formalin and sectioned along a frontal plane. A black thread (right side) traces the 'S' shaped lumen which is completely plugged with a thick mucus. The internal os is at the top of the photograph and the external os towards the bottom.

Figure 2. The cervix from a mature, non-pregnant muskox (76-1) opened dorsally. (external os, Ex0)

Figure 3. The plica palmata of the cervix from a mature, non-pregnant muskox (78-26). The ridges formed by the thick musculature can be seen on either side.



PLATE 17

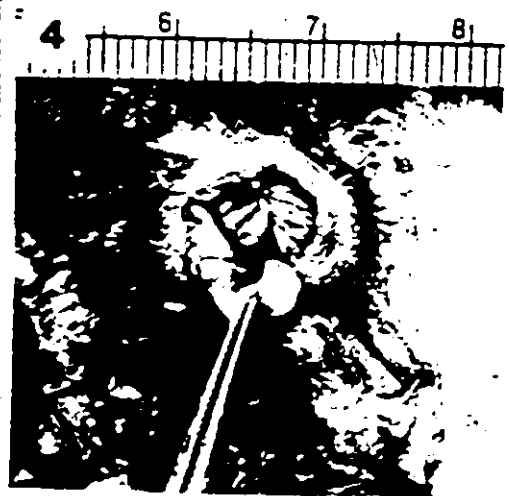
THE EXTERNAL AND INTERNAL OS CERVIX

Figure 1. The external os of the cervix from a mature, non-pregnant muskox collected in March. The forceps are lifting a small fold in the vaginal tissue which partially surrounds the opening to the cervix. In this specimen the flap was found on the dorsal wall.

Figure 2. The same specimen depicted in Fig. 1 above showing the epiglottis-like structure at the cervical opening. There was a great deal of individual variation in the shape and position of this structure ranging from pendulous to almost vestigial. The specimen depicted here was considered intermediate.

Figure 3. The external os collected from a muskox approaching the breeding season (78-41). The external os is swollen and protrudes noticeably into the vaginal lumen. Photograph taken in the field.

Figure 4. The internal os from a mature, non-pregnant muskox.



surrounding, the external os (Plate 17, Fig. 1). In the non-parous tracts it was located 2 - 5 cm away.

The internal os was less defined and more consistent in appearance and can be described as a small annular ring and mucosal folding that formed a rosette pattern (Plate 17, Fig. 4).

In late pregnancy the cervix was longer (Table 6) and plugged with a thick, viscous mucus for its entire length.

(ii) Histology

The cervical mucosa was lined by a high columnar non-ciliated secretory epithelium. Within the cells numerous small vacuoles were seen near the luminal surface and the nuclei were located basally. Large cells containing a prominent central nucleus were also found among the columnar cells of the epithelium (Plate 18, Fig. 1). The mucosa was elaborately folded with secondary and tertiary folds, but there was no evidence of coiled tubular glands (Plate 18, Fig. 2). The thick cervical musculature was high in collagenic fibres and its arrangement was not as uniform as those of the uterus although they did appear to form a band of loosely arranged circular muscle fibres. The inner muscle bundles formed the annular ridges.

PLATE 18

HISTOLOGY OF THE CERVIX

Figure 1. The epithelium lining the cervix from a parous, non-pregnant muskox (78-44) collected just prior to the breeding season showing the secretory columnar cells with clear vesicles near the apical portion (arrows). A large hollow cell with a prominent central nucleus is also shown. These cells were found dispersed among the columnar cells.. (X500)

Figure 2. A cross section of a portion of the cervix from a parous, non-pregnant muskox to show the secondary (a) and tertiary (b) folds. No coiled tubular glands were found. (X43)



e) The Oviduct

(i) Morphology

The oviduct was a thin walled tube that was only moderately coiled with the isthmus being more tightly coiled than the ampulla. The isthmus comprised the narrow portion of the tube near the uterine horn while the ampulla increased in diameter from the isthmus towards the fimbria (Plate 19, Fig. 1). The fimbria attached at one end to the mesovarium at the caudal edge of the ovarian hylus while the other pole of the fimbria became continuous with the ovarian bursa forming a roomy, widely opened pocket (Plate 19, Fig. 1).

On dissection the utero-tubal junction was marked by a slight muscular ridge in two of the 15 specimens (78-18, 78-26; Plate 19, Fig. 2), but this ridge was poorly marked in the others. In the five tracts that were flushed (one of them 78-18) fluid was found to pass easily between the uterine horn and the oviduct.

(ii) Histology

Histologically the oviduct was composed of a mucosa, muscularis and serosa. The mucosa formed large primary and secondary folds with the folding being most elaborate near the ostium abdominale. In this portion of the tube the muscle wall was greatly reduced, being composed mainly of a band of circular smooth muscle fibres and vascular elements (Plate 19, Fig. 3). The muscularis

PLATE 19

THE OVIDUCT

Figure 1. The oviduct from a parous, non-pregnant muskox (78-33) showing the increasing diameter towards the fimbria (F). The isthmus portion (i) is more highly coiled than the ampulla (A). The cranial portion of the fimbria is attached to the ovarian bursa (Ovb) which normally covers the outer half of the ovary.

Figure 2. The tip of the uterine horn (H) and the isthmus of the oviduct (O) have been opened dorsally to show the slight muscular ridge (pointer). This ridge was only found in two specimens. The specimen depicted here (78-18) was flushed before dissection and fluid was found to pass easily between the uterine horn to the oviduct.

Figure 3. Cross section of the ampulla portion of the oviduct from a parous, non-pregnant muskox (78-41) showing the elaborate mucosal folding and thin muscular wall. (X31)

Figure 4. Cross section of the isthmus portion of the oviduct from the same specimen in Fig. 3 above.

(cont'd)

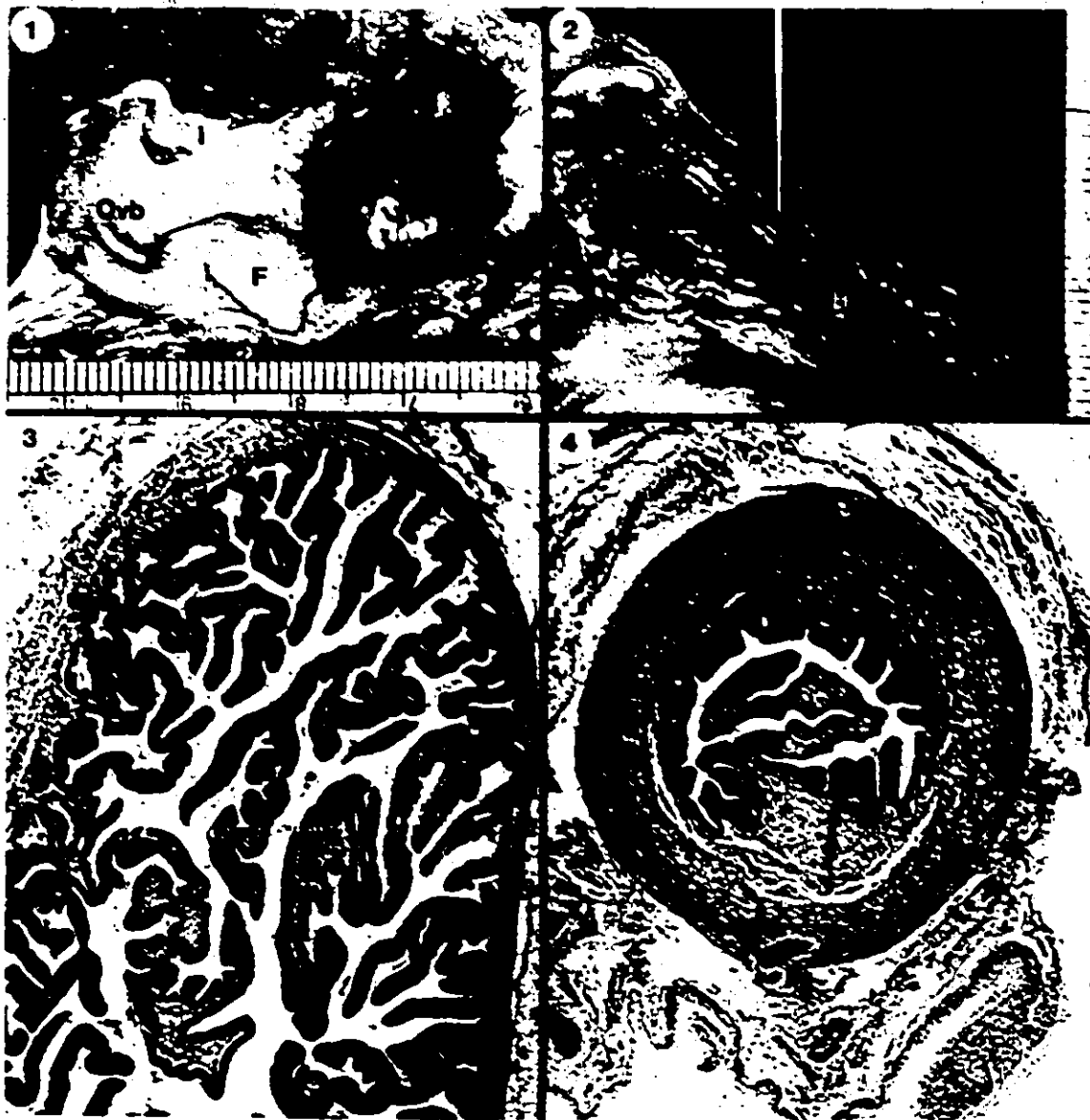


Plate 19 (cont'd)

The muscular wall is much thicker with more clearly defined circular and longitudinal muscle layers. The mucosal folding is greatly reduced. (X31)

thickened towards the isthmus and uterine horn and became continuous with the circular muscle layer of the uterus. In the isthmic portion of the fallopian tube the mucosal folding was greatly reduced (Plate 19, Fig. 4).

The epithelium of the mucosa was generally high columnar. Cilia predominated in the fimbria and lower portions of the ampulla. In some specimens, the epithelium appeared pseudostratified. In the August specimens, the epithelium of the isthmus was high columnar with some ciliated cells. The number of isthmic ciliated cells was not as great as in the ampulla. In the March specimens the epithelium of the isthmus appeared to be of a non-ciliated low columnar type.

f) The Ovaries During Anestrus

The ovaries from a total of 23 muskoxen were collected in March, August and October. These collecting times can be loosely categorized by the reproductive status of the females during each collection period. Thus March represents either the anestrus season or late gestation (depending on whether or not the animal was pregnant); August represents the period immediately preceding the breeding season; and October represents the late breeding season or early pregnancy.

Of the animals collected in March, seven were non-pregnant: three were judged to be non-parous and four were parous. Of the four parous animals, three were

lactating at the time of collection. Because the gross features of ovaries from the parous and the non-parous females were similar they will be dealt with together.

(i) Morphology

The ovaries of the non-pregnant, anestrus animals were almond shaped structures attached along one edge to the dorsal surface of the broad ligament at approximately the level of the external bifurcation of the uterine horns. They averaged 20.3 mm in length by 14.4 mm in width by 8.3 mm in depth (Table 7).

The ovaries were covered by the ovarian bursa on the lateral side only and were thus exposed to the peritoneal cavity. Numerous small antral follicles were visible as translucent points on the ovarian surface but these follicles did not protrude significantly from the normal outline of the surface of the ovary. There was no indication of large Graafian follicle development nor of corpora lutea. The ovarian surface contained no obvious stigmata or scars.

(ii) Histology

The histology of these specimens was poor due to a combination of inadequate fixation and freezing but despite these drawbacks many of the tissue elements were recognizable.

In the immature animals the epithelial covering varied

Table 7. Dimensions taken from the ovaries of mature (non-pregnant), immature and pregnant muskoxen.

Reproductive Status	Ovarian Dimensions (mm)					
	Left			Right		
	1 L	2 W	3 D	L	W	D
Mature						
76-1	18	12	4	18	12	4
76-6	25	14	5	29	17	9
76-8	23	15	8	25	22	12
77-18	20	15	9	*	*	*
77-19	18	12	7	*	*	*
78-26	*	*	*	19	12	8
78-31	15	13	9	*	*	*
78-33	*	*	*	19	11	7
78-41	25	16	11	28	18	12
78-44	20	17	8	20	20	16
Immature						
76-9	20	12	8	20	14	11
77-11	14	10	7	13	9	6.5
78-24	16	12	7	17	13	6
78-28	*	*	*	*	*	*
78-42	21	17	9	24	18	8
Pregnant						
77-12	30	13	5'	*	*	*
77-13	*	*	*	*	*	*
78-24	*	*	*	*	*	*
78-32	*	*	*	*	*	*
78-37	31	15	5'	24	19	6
78-38	26	11	6	33	9	4'
78-39	28	12	5'	23	14	7
78-40	21	11	4	33	11	6'

1 - Length

2 - Width

3 - Depth

* - not determined

' - ovary adjacent to the pregnant horn

from a distinctly cuboidal cell type to epithelial cells that were flattened and contained elongated nuclei. In the mature animals, the epithelial layer was stretched so that it made identification of distinct cells very difficult. In these animals, the germinal epithelium was largely reduced to a thin darkly staining layer except for portions near the hilus that retained their cuboidal shape (Plate 20, Fig. 1). Indentations of the epithelium into the cortical stroma were not seen. Occasionally small pits were seen on the surface of the immature ovaries but there was no evidence of their continuation into the cortex.

The tunica albuginea underlying the germinal epithelium varied in thickness and was high in collagenous fibres.

There was no discrete boundary between the cortical stroma and the medulla. The cortical layer was relatively thin and covered the medulla except at the hilus. In general the medulla occupied the larger portion of the ovary and, in some areas, extended almost to the tunica. The major constituents of the medulla were blood vessels and lymphatics which entered the ovary through the cranial end of the hilus. The blood vessels were highly coiled, had very thick walls and large lumens and were enmeshed in a dense connective tissue framework.

The cortex was highly cellular and contained most of the developing germ cells. Capillaries and lymphatics

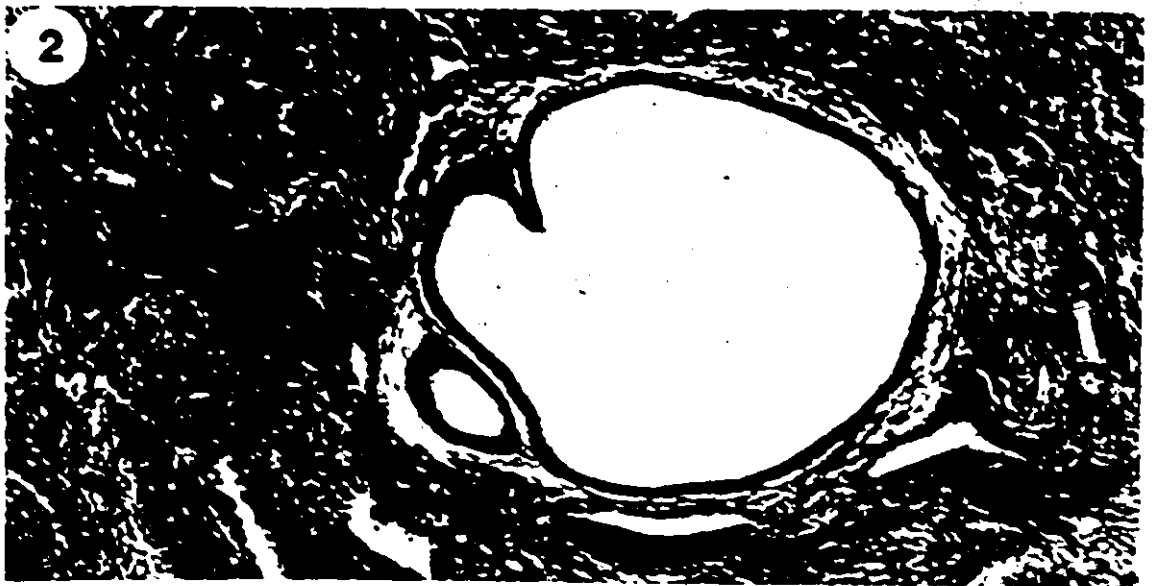
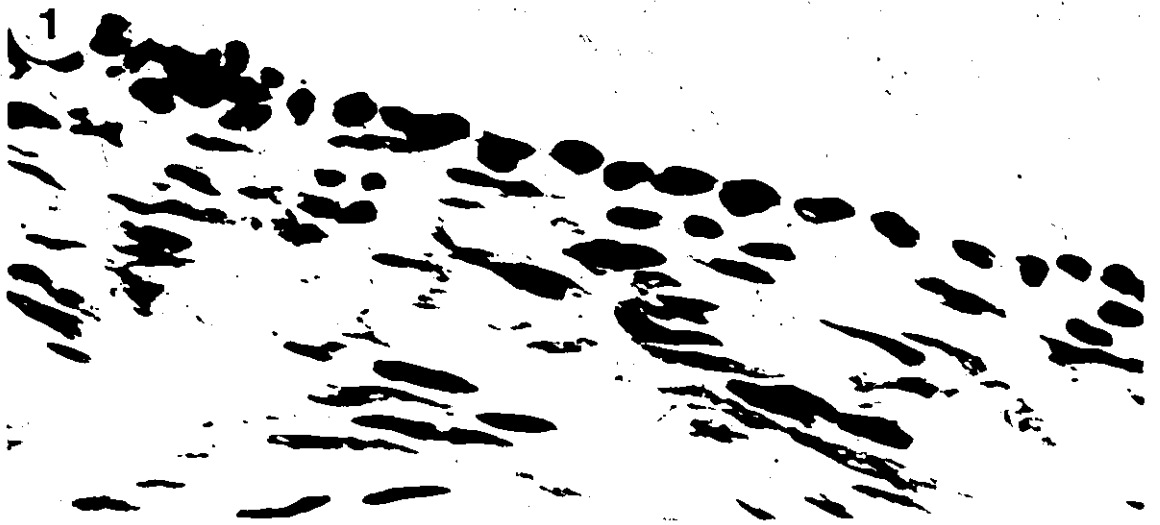
PLATE 20

NON-FOLLICULAR COMPONENTS OF THE OVARY

Figure 1. The cuboidal epithelium near the hilus of the ovary from a parous, non-pregnant muskox collected during anestrus with a portion of the fibrous tunica albuginea underneath. (X500)

Figure 2. Cross section of an irregularly shaped tubule lined by a columnar epithelium. These tubules were found near the hilus of the ovary and were identified as tubules of the rete ovarii. This section was from the hilus portion of the ovary from a mature, non-pregnant muskox collected during anestrus. (X75)

Figure 3. Cross section of a small tubule bearing a columnar epithelium found in the cortical stroma. These most probably represent part of a small tubule of the rete ovarii. Section is from the same muskox ovary depicted in Fig. 1 above. (X500)



ran throughout the cortex. Tubules lined with a columnar epithelium were found in the stroma (Plate 20, Fig. 2).

Near the hilus and closely associated with the medulla were collections of coiled tubules with irregularly shaped lumens. The tubules were lined by a simple columnar epithelium and were identified as tubules of the rete ovarii. Although these tubules were positively identified in the hilar portion only, small tubules with a columnar epithelium were occasionally found in the cortical stroma (Plate 20, Fig. 3) and were presumed to be part of the rete complex.

Primordial follicles consisting of an oocyte surrounded by a layer of epithelial cells, were found in the cortical stroma underlying the tunica albuginea. Primary follicles were generally found in the same region (Plate 21, Figs. 1 and 2). These follicles had an added investment of cuboidal epithelial cells that were more columnar in appearance (Plate 21, Figs. 2 and 4) and in many cases, a zona pellucida surrounded the oocyte. Polynuclear oocytes were not seen. Polyovular follicles were not obvious though some primordial follicles were found in close contact with no visible epithelial cells separating the oocytes (Plate 21, Fig. 3).

An estimated 80-90% of the secondary follicles were found deeper in the cortex closer to the medulla than to the tunica (Plate 22, Figs. 1 and 2). Follicles, classed here as secondary, included those follicles that had developed a granulosa bound by a basement membrane

PLATE 21

FOLLICULAR DEVELOPMENT

Figure 1. A collection of oocytes (arrow) found under the tunica albuginea. These cells lack an epithelial investment. The section is from the ovary of a parous, non-pregnant muskox collected just prior to the breeding season. (X500)

Figure 2. Primordial (a) and primary (b) follicles found close together under the tunica albuginea. Section is from the ovary of a parous non-pregnant muskox collected during anestrus. (X500).

Figure 3. A cluster of primordial follicles in close apposition with no apparent epithelial cell investment between them. The section is from the ovary of a parous, non-pregnant muskox collected during anestrus. (X500)

Figure 4. Primary follicle surrounded by cuboidal cells. From the same ovary depicted in Fig. 1 above (X500)

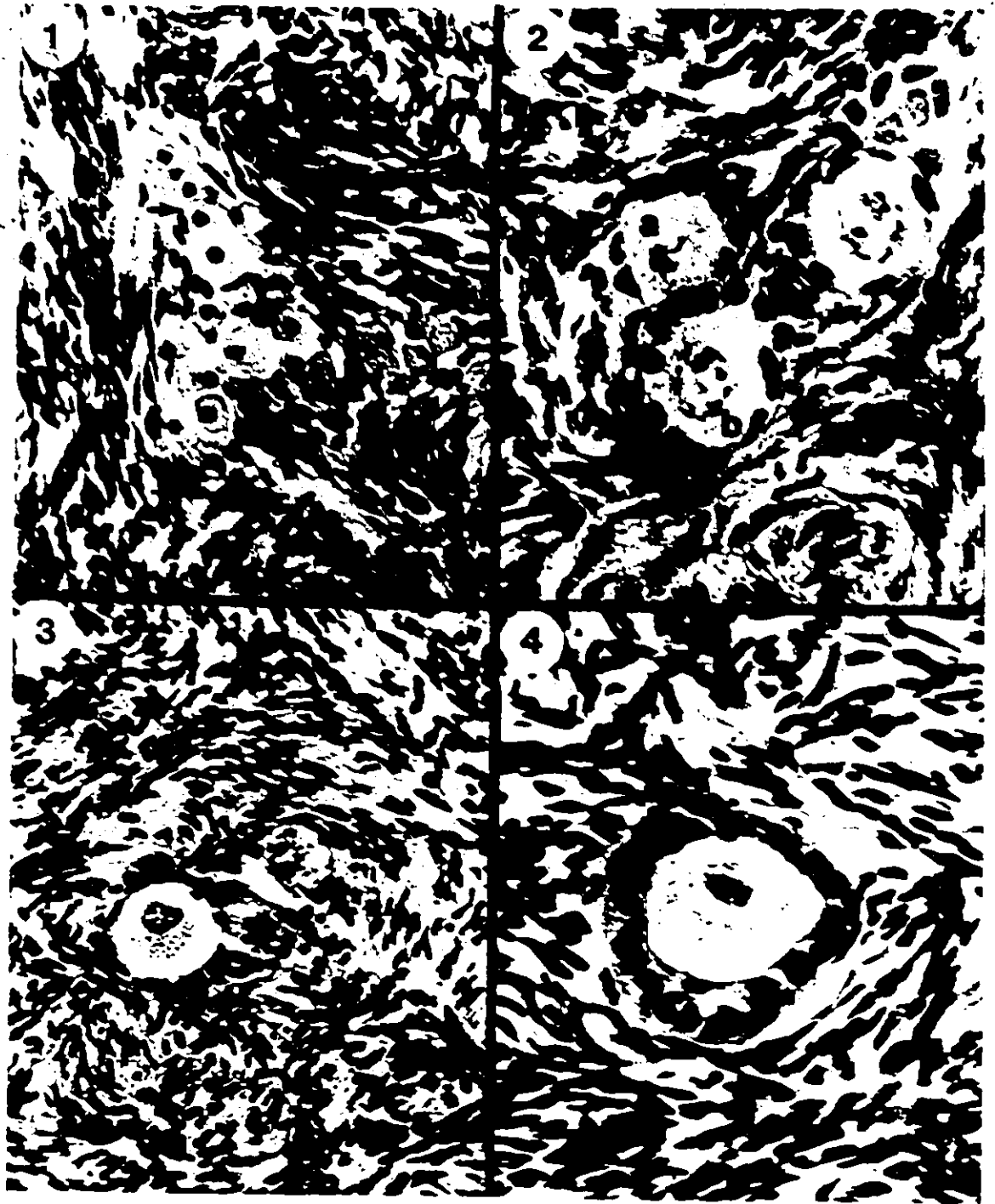


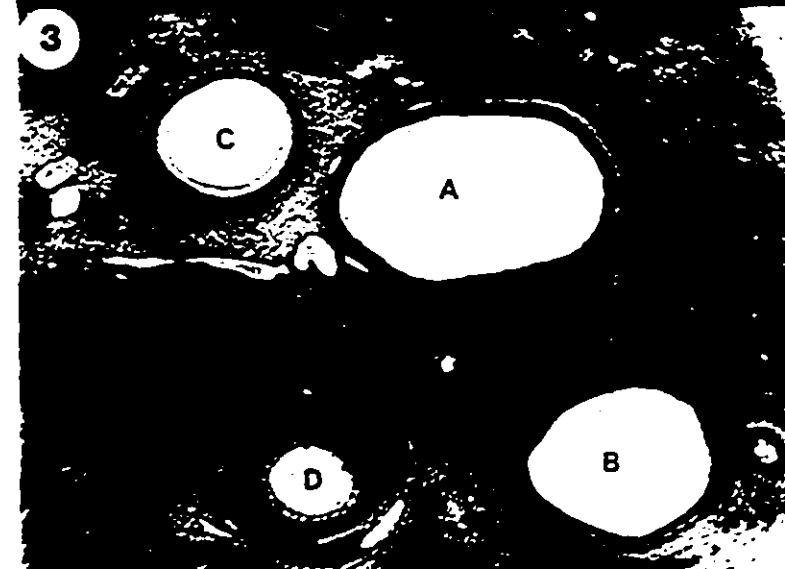
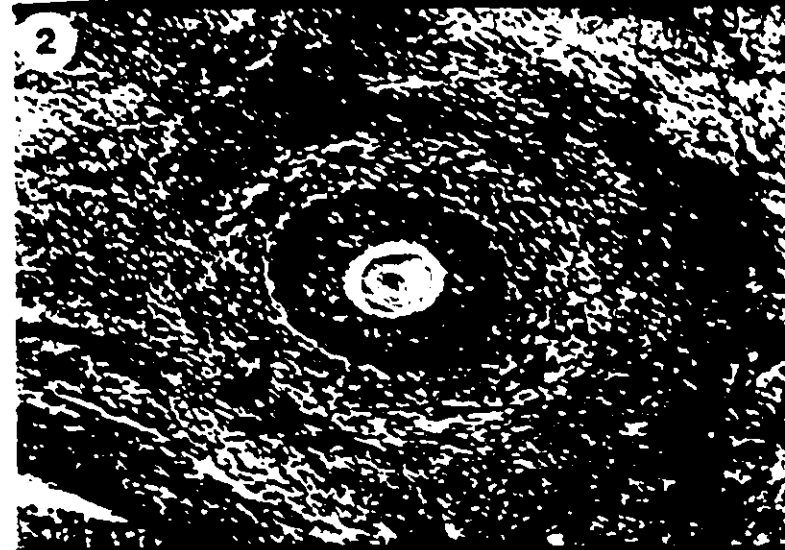
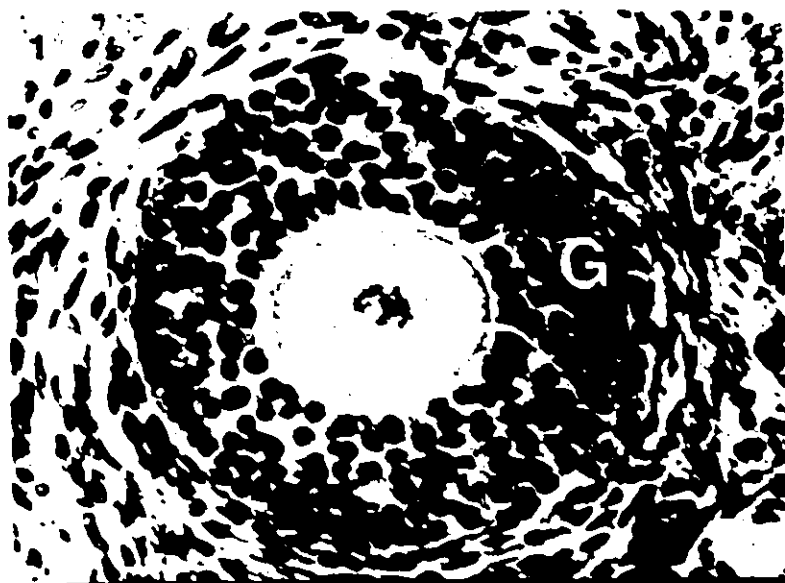
PLATE 22

FOLLICULAR DEVELOPMENT

Figure 1. Secondary follicle showing the granulosa (G) bounded by a basement membrane (arrow). From the ovary of a parous, non-pregnant muskox collected during anestrus. (X500)

Figure 2. Secondary follicle showing a distinct theca interna (T) composed of spindle shaped cells. From a parous, non-pregnant muskox collected during anestrus. (X500)

Figure 3. Vesicular follicles in the ovary of a parous, anestrous muskox. Follicles A and B were healthy while C and D were undergoing atresia. A secondary follicle just developing an antrum can be seen to the right of B. (X12)



(Plate 22, Fig. 1) as well as those that had also developed a distinct theca interna (Plate 22, Fig. 2). In the muskox the theca interna is easily distinguished before the development of the antrum. In two instances secondary follicles which were found near the surface displayed a slightly uneven form of development. This condition was only found in the smaller secondary follicles. The thin theca interna surrounding these follicles appeared to proliferate in the area closest to the tunica giving the follicle a triangular appearance. Vesicular follicles were found throughout the ovary, though most were located deep in the cortex, partially in the medulla. These Graafian follicles contained an oocyte bounded by a zona pellucida and surrounded by a cumulus oophorus. The antrum was lined by granulosa cells (Plate 22, Fig. 3). The granulosa cells lining the antrum were polyhedral in shape while those adjacent to the outside basement membrane displayed a columnar appearance. Outside the basement membrane was a highly vascularized theca interna. The cells of the theca interna were elongated to polyhedral with spheroidal nuclei. The theca externa was composed of spindle-shaped cells and was loosely defined and often discontinuous. The granulosa of the antral follicles contained numerous, prominent, spheroidal structures containing a substance that stained identically to follicular fluid. These appeared to be bound by a thin membrane with the surrounding cumulus cells radially arranged and

slightly columnar in appearance (Plate 23, Fig. 1).

These structures were identified as 'Call-Exner' bodies and were found in antral follicles of varying size and stage of development. They occurred in many, but not all, antral follicles in both mature and immature animals (Plate 23, Figs. 2 and 3).

In the anestrous animals the follicles, though numerous, never exceeded 2 mm in diameter.

Follicular atresia occurred at all stages of follicle development. The atretic process in primary and secondary follicles was not easily recognized in the early stages. In the final stages of small follicle degeneration the oocyte was collapsed, the zona pellucida had a hyaline appearance and the granulosa, in the case of secondary follicles, had pycnotic nuclei and was heavily invaded by stromal connective tissue. The resulting connective tissue scars were small and often contained a central lumen with remnants of the zona pellucida (Plate 24, Fig. 1).

Atresia of the antral or vesicular follicles was represented by a variety of forms, presumably indicative of various stages in the process. It was not possible to reconstruct the process on the limited number of specimens available but the major forms diagnostic of atresia can be identified.

Atresia in many follicles followed the descriptions of this process in cattle, sheep and goats, (Jones, 1978; Weir and Rowlands, 1977; Dellman and Brown, 1976). The

PLATE 23

'CALL-EXNER' BODIES

Figure 1. Close up of a Call-Exner body in the granulosa of a vesicular follicle. A thin membrane lines the central cavity with the columnar appearing granulosa cells arranged radially around the outside. From the ovary of a parous, non-pregnant muskox collected during anestrus. (X500)

Figure 2. Vesicular follicle from the same specimen in Fig. 1 above showing numerous prominent Call-Exner bodies (arrows). (X43)

Figure 3. Call-Exner bodies in an atretic follicle. Though the granulosa layer is thinning the Call-Exner bodies remain prominent. Occasionally they were found floating 'intact' within the antrum of degenerating follicles. From a parous, non-pregnant muskox collected during anestrus. (X125)

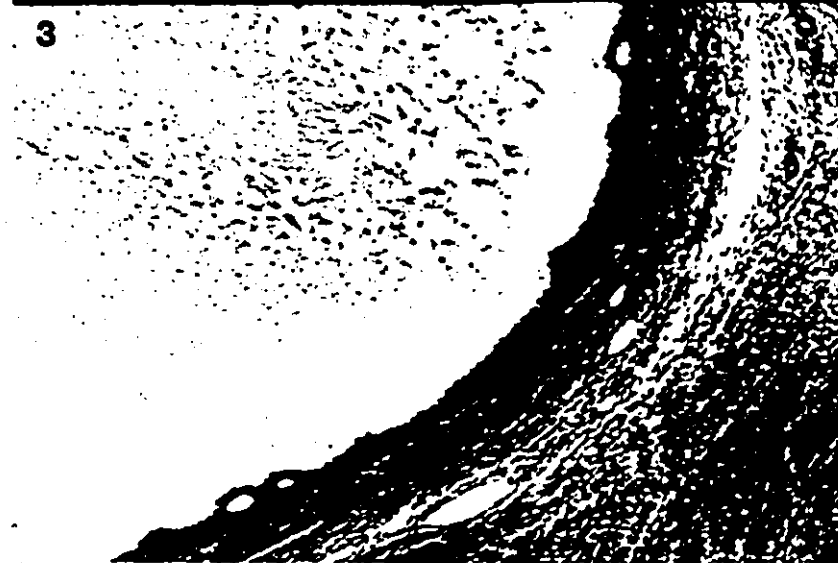


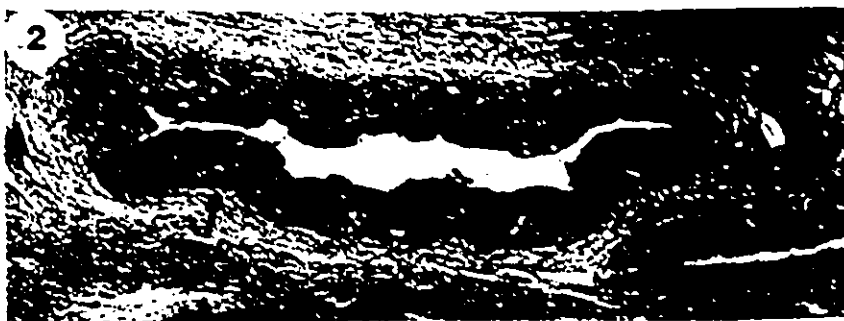
PLATE 24

FOLLICULAR ATRESIA

Figure 1. Scar remaining from the degeneration of a small early vesicular or secondary follicle. Hyalinized remnants of the ovum and zona (arrow) remain in the cavity. From the ovary of a parous non-pregnant muskox collected during anestrus. (X125)

Figure 2. Collapsed vesicular follicle undergoing atresia. The theca interna (arrow) has hypertrophied and grown into the folded areas. From the ovary of a parous non-pregnant muskox collected during anestrus. (X43)

Figure 3. Advanced stage of atresia in a vesicular follicle. The antral fluid (a) was achromatic and contained pycnotic nuclei (arrow). The granulosa has been invaded by cells of the theca interna. From the ovary of a parous, non-pregnant muskox collected during anestrus. (X125)



follicular granulosa in the muskox follicle showed definitive signs of atresia such as pycnotic nuclei with granulosa cells found floating free in the antrum. In some of these follicles the oocyte and the cumulus oophorus appeared to retain their integrity though dissolution of the cumulus was a common observation particularly where it attached to the granulosa. The theca interna in these cases appeared unaffected. Some of the follicles believed to be atretic were found in a collapsed state. These structures showed extensive thecal hypertrophy and, in some cases, hypertrophy of the basal layers of the granulosa. In many cases it appeared as though the granulosa had collapsed and the theca had grown in or thickened in the folded areas (Plate 24, Fig. 2). Oocytes were rarely found in collapsed follicles and where they did occur they were found floating free and appeared to be degenerating.

In more advanced stages of atresia thecal overgrowth was found to be very prominent. At this stage the swollen thecal cells were commonly seen to invade the granulosa. The follicular fluid was generally achromatic and filled with debris and follicle collapse was common. Strands of stromal connective tissue were beginning to invade the theca (Plate 24, Fig. 3).

The cortical stroma and, to some extent, the medulla contained a large number of discrete areas of collagenic connective tissue identified as scars. Scars of atretic

Graafian follicles were the most common. These structures stained routinely with hematoxylin and eosin and were positive for collagen with Masson's Trichrome. The strands of collagen radiated from an eccentric lumen which sometimes contained remnants of the zona pellucida.

Scars of corpora lutea were less visible in routinely stained sections. These scars consisted of dense collections of collagenic connective tissue of irregular shape. An outer connective tissue capsule was rarely evident. Associated with these structures were very thick walled vessels many of which were achromatic and appeared sclerotic while others contained blood cells. Some of the scars contained pigment cells similar in appearance to lipofuscins. These scars rarely had any apparent connection with the surface epithelium and varied widely in size and shape, being distorted by developing follicles. Few specimens were adequately fixed for fine cellular analysis and it was difficult to separate small cell lacunae from artifact. In the absence of definitive information on the corpora lutea, and because of the small sample size, a classification of the origin of the scar tissue was not attempted.

g) The Ovaries Immediately Preceding the Breeding Season

Three females were taken on August 12 and 13, 1978. Two were parous females (78-41 and 78-44) while the third was non-parous (78-42). In the ovaries of these

animals there were no fresh corpora lutea nor was there any sign of recent ovulation on the surface epithelium. However, specimens 78-41 and 78-44 each had one large follicle in one ovary measuring 12 mm and 17 mm respectively and these follicles were large enough to cause visible protrusions on the ovarian surface (Plate 25, Fig. 1). In both cases the contralateral ovary contained no follicle larger than 3mm. Specimen 78-42 had one medium-sized follicle in each ovary measuring 7 mm and 9 mm in diameter (Plate 25, Fig. 2). The large follicles were tentatively classed as preovulatory follicles because of their size and the time of the collection relative to their breeding season. The ovaries of these three animals were similar in all other respects to the descriptions given for the anestrous animals.

h) The Ovaries During the Breeding Season

(i) Morphology

The two females taken in 1977 (Nos. 77-18 and 77-19) were both lactating and their ovaries appeared inactive. Antral follicles were visible in gross section but none of these exceeded 2 mm in diameter. There was no evidence of a corpus luteum or of a recent ovulation in either ovary.

The three tracts collected in 1976 (76-6, 76-8 and 76-9) were, as mentioned, received in a frozen condition. It could not be established whether or not these animals

PLATE 25

THE OVARIES BEFORE THE BREEDING SEASON

Figure 1. The bisected ovaries of a mature, non-pregnant muskox (78-44) collected in August and photographed in the field. The cavity (A) is the site of a large 17mm follicle.

Figure 2. The ovaries of an immature muskox (78-42) collected in August and photographed in the field. The dark areas (arrows) are large developing follicles. In the right ovary the follicle can be seen to protrude noticeably.

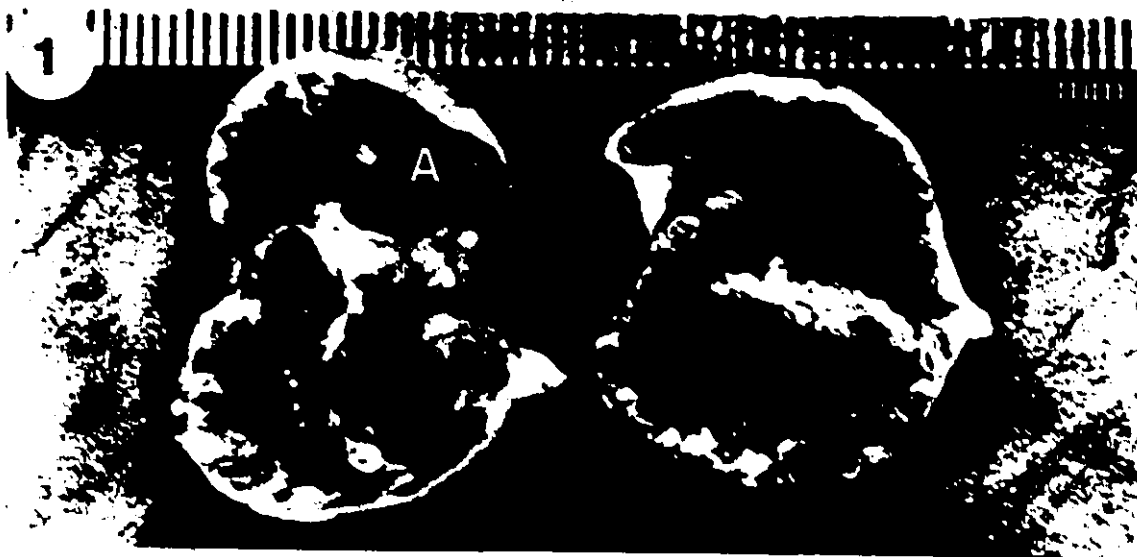


PLATE 26

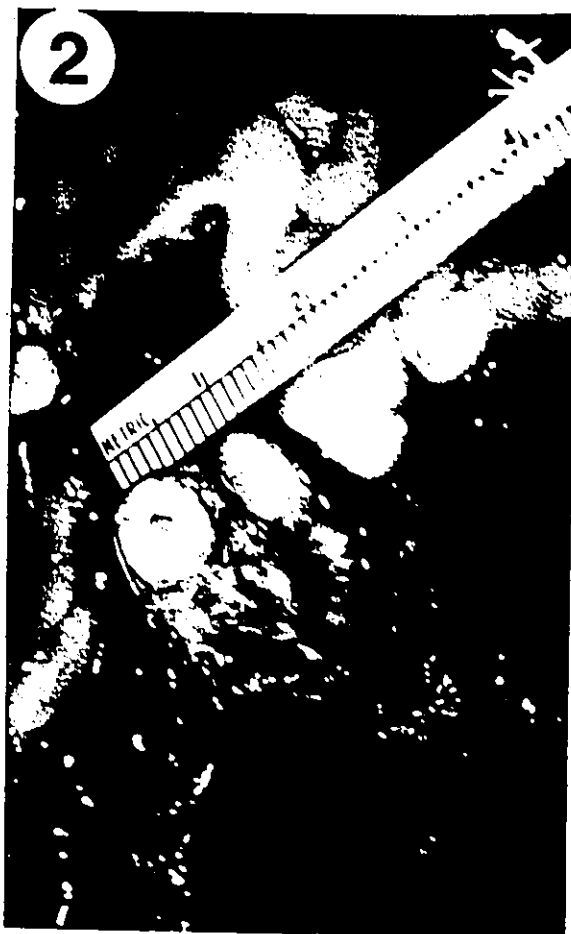
THE OVARIES DURING THE BREEDING SEASON

Figure 1. The right ovary of a non-parous muskox (76-9) showing a protrusion from a corpus luteum.

Figure 2. The same ovary bisected to reveal a corpus luteum with a small central cavity.

Figure 3. The right ovary of a parous muskox (76-8) with a protruding corpus luteum and stigma. The needle is in an apparent rupture point just behind the corpus luteum.

Figure 4. The left ovary of the parous muskox (76-8) with a rupture point on the surface (the needle is inserted in the rupture).



were pregnant because the uterine flushes, which did not reveal any embryos, were considered inadequate.

The ovaries of all three animals contained easily recognized corpora lutea that shared many morphological characteristics with those of sheep and goats. Muskox 76-8 had a corpus luteum in the right ovary with a stigma still evident on the surface. This ovary also contained a second, regressed, luteal structure evident on bisection. The corpus luteum of the right ovary noticeably distorted the shape of this ovary and the stigma formed a rosette pattern. Recent rupture points were found on the surface of both ovaries from this specimen (Plate 26, Figs. 3 and 4). Because the rupture points did not connect with any structure resembling a corpus hemorrhagicum within the ovary it seems likely that they resulted from mechanically ruptured follicles.

The left ovary of specimen 76-6 was slightly distorted on one side and had what appeared to be a reddish brown corpus luteum with an obvious stigma (Plate 27, Fig. 1). On bisection a corpus luteum measuring 14 mm in diameter was identified and described as a solid mass without a central cavity. In addition there was a smaller luteal body in the same ovary (Plate 27, Fig. 2). The right ovary of 76-6 had a marked depression on the ovarian surface which was identified as the stigma of a recent ovulation (Plate 27, Fig. 3). On bisection a hemorrhagic mass was found in the ovarian stroma that connected with the stigma and confirmed the diagnosis of recent ovulation (Plate

PLATE 27

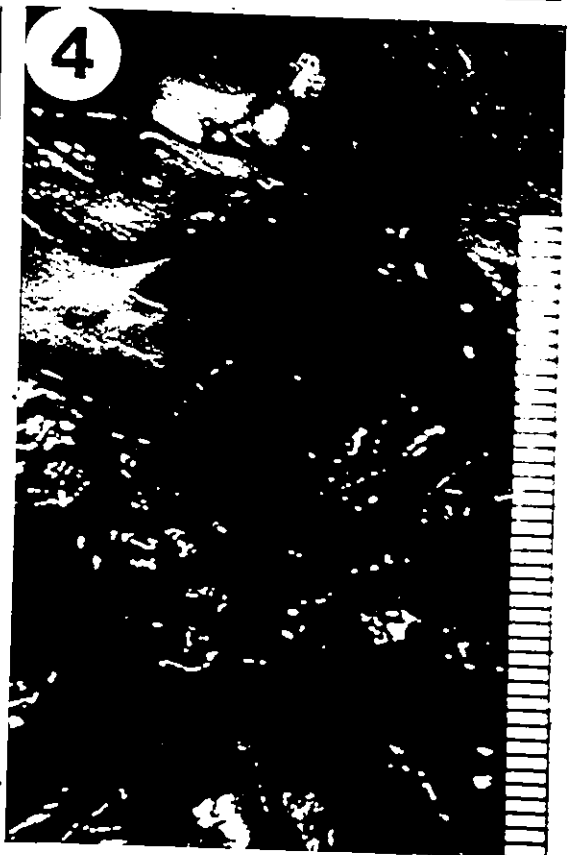
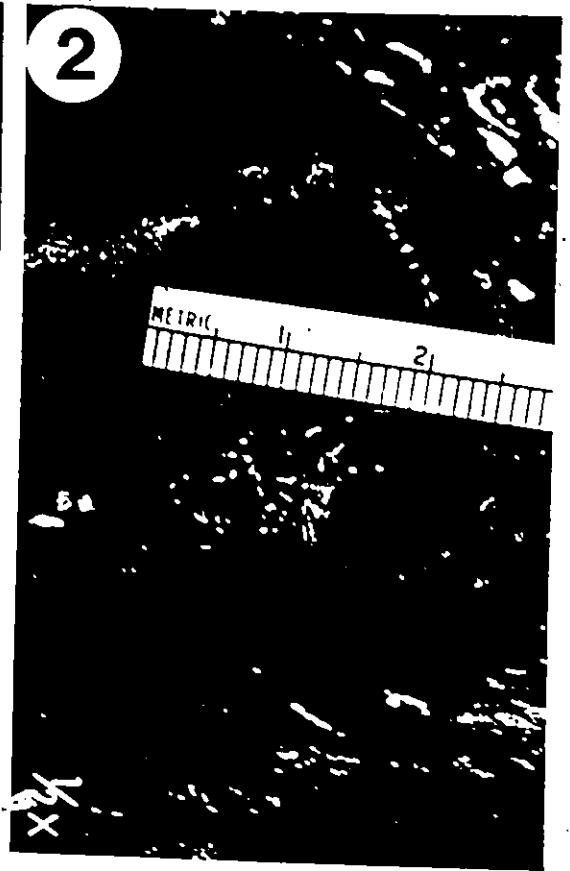
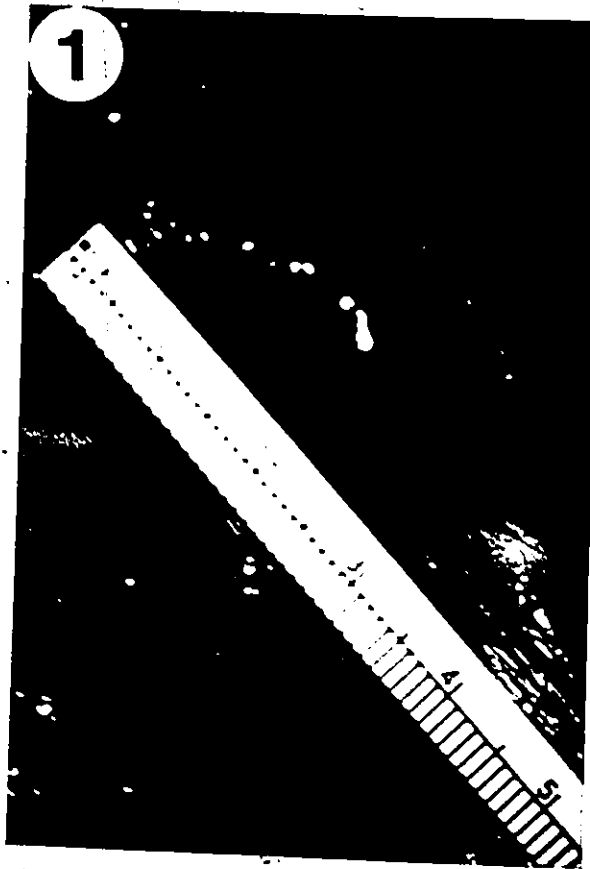
THE OVARIES DURING THE BREEDING SEASON

Figure 1. The left ovary of a parous muskox (76-6). The dark discoloured area to the right is a corpus luteum. To the left of the ovary is a small cyst.

Figure 2. The same ovary as in Fig. 1 above but bisected to reveal a large corpus luteum and a smaller one to the left of this.

Figure 3. The right ovary of the same muskox (76-6) showing a small rupture point on the surface.

Figure 4. The same ovary as in Fig. 3 above bisected to reveal a corpus hemorrhagicum.



27, Fig. 4). Specimen 76-9 had a large protruding corpus luteum 7.5 mm in diameter on the right ovary. On bisection the corpus luteum had a small central cavity.

(ii) Histology

The corpus luteum of the muskoxen appeared as a solid spherical mass surrounded by a connective tissue capsule. There appeared to be two cell types, large lightly staining cells which were the predominating type and a smaller darker staining cell. Interspersed throughout the corpus luteum were strands of connective tissue containing vascular elements. Larger blood vessels were found primarily around the periphery. In corpora lutea that were judged to be older the luteal structure was smaller and more compact. Cellular definition was lost, nuclei were fewer, appeared elongated, and the outer connective tissue capsule was less well defined (Plate 28, Figs. 1-3 and Plate 29, Figs. 1-3).

The large corpus luteum of 76-8, when compared to goat and sheep controls, appeared to be regressing. In specimen 76-6 the larger corpus luteum was judged to be a more recent structure and possibly just beginning to regress. The second luteal body which was very compact and losing outer definition, was identified as a more highly regressed corpus luteum.

In no case did an animal appear to have two corpora lutea at the same stage of development or regression.

PLATE 28

HISTOLOGY OF THE CORPORA LUTEA

Figure 1. Overview of the ovary from a parous, non-pregnant muskox (76-6) collected during the late breeding season showing two corpora lutea. (X5)

Figure 2. Close up of the smaller corpus luteum (A) in Fig. 1 above showing the reduced number of nuclei and cellular compaction. (X75)

Figure 3. Close up of the larger corpus luteum (B) in Fig. 1 above showing a greater number of nuclei and degree of cellular definition. (X75)

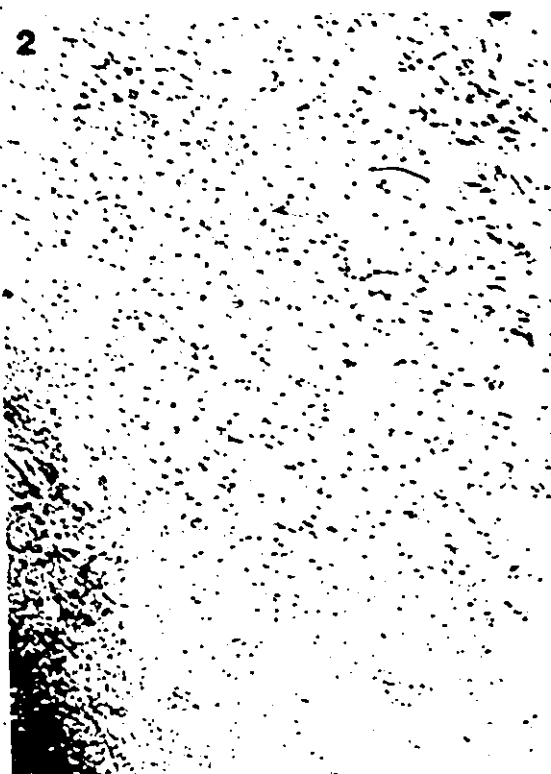


PLATE 29

HISTOLOGY OF THE CORPORA LUTEA

Figure 1. A portion of the corpus luteum from a non-parous, non-pregnant muskox (76-9) collected during the breeding season. (X12)

Figure 2. Close up of the same corpus luteum depicted in Fig. 1 above to show the degree of cellular compaction and the preponderance of nuclei. (X75)

Figure 3. A small corpus luteum in the right ovary of a parous, non-pregnant muskox (76-8) collected during the breeding season. The loss of an outer capsule, cellular compaction and reduction in the number of nuclei suggest that the corpus luteum is regressing. (X12)

Figure 4. Luteal-like structure found in the ovary of a lactating, anestrous cow (78-26) collected in March. The structure appears similar to the regressing corpus luteum of the cycle though it contained substantially more connective tissue and ovarian lipofuscins. (X43)



An apparently regressing corpus luteum was found in the right ovary of a lactating cow (78-26) collected in March. It was a spherical structure with numerous pigmented cells and thin strands of connective tissue. Because of extensive tissue damage, there was no accurate means of aging this structure though the abundant connective tissue and the ovarian pigments suggested a more advanced stage of regression than seen in the corpus luteum of animals during the breeding season (Plate 29, Fig. 4).

i) The Ovaries During Pregnancy

(i) Morphology

The ovaries of six pregnant specimens were received frozen and two fresh specimens (78-27 and 78-32) were preserved in A.F.A. but because of the difficulty in keeping the preservative warm fixation was less than ideal. The ovaries from all eight pregnant tracts were elongated, laterally flattened structures situated near the uterine body on the dorso-lateral surface. They averaged 28 mm in length, 13 mm in width and 5 mm in thickness (Table 7). There were no obvious morphological differences or features between the ovaries adjacent to the pregnant horn and those of the non-pregnant horn (Plate 30, Figs. 1-3).

In seven of the eight pairs of ovaries, gross sectioning along a longitudinal plane allowed identification of the cortex, medulla and small antral follicles but no structures resembling corpora lutea were visible.

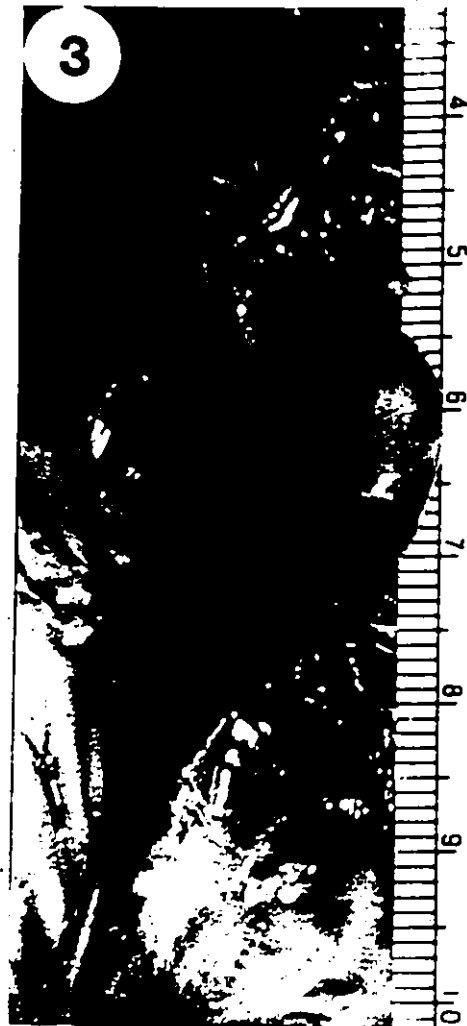
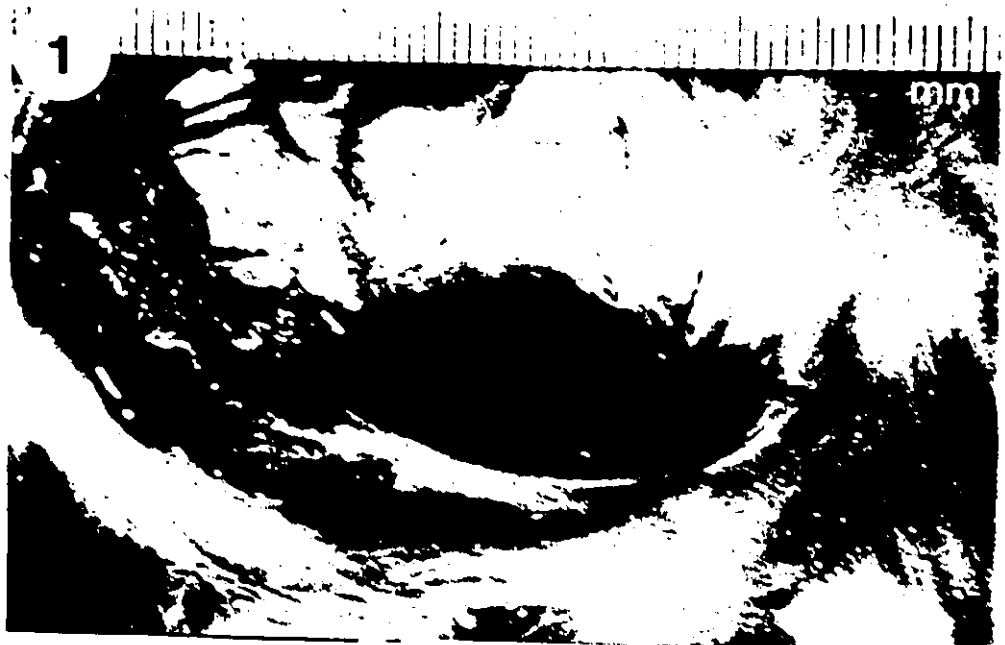
PLATE 30

THE OVARIES OF PREGNANCY

Figure 1. The ovary (arrow) on the side of pregnancy in a pregnant muskox (77-12) collected in late February.

Figure 2. The left ovary from a pregnant muskox (78-39) collected in March. The pregnancy was on the left side.

Figure 3. The right ovary from the same muskox depicted in Fig. 2 above. In this specimen the slightly greater length of the left ovary (Fig. 2) can be attributed to the greater degree of muscle stretching that occurred in the pregnant horn. The left ovary was smaller in width and depth than the right ovary.



(ii) Histology

Histological sectioning of the pairs of ovaries revealed, with one exception, only one regressed luteal structure per pair and, as mentioned earlier, this was consistently found in the ovary ipsilateral to the pregnant horn. These regressed corpora lutea stained heavily for connective tissue with Masson's Trichrome and contained numerous ovarian pigments similar to the lipofuscins identified in the endometrium. The corpora lutea were distorted in shape and showed only limited evidence of a connective tissue capsule (Plate 31, Figs. 1-2). In all other respects these ovaries resembled the ovaries of the anestrous animal. Numerous small follicles were present but none exceeded 2 mm in diameter.

In the single ovary which showed more than one luteal structure (from a muskox from Prince of Wales Island, 78-38) there was an easily recognizable luteal body that appeared as a pale white area in gross section. Histologically this structure had the solid appearance of a regressing corpus luteum of the cycle (Plate 32, Fig. 2). It was an oval-shaped structure containing a small central cavity filled with connective tissue. A portion of the structure was slightly distorted by the presence of a developing follicle. A second structure was found in the same ovary that resembled the corpus luteum of the other seven animals: a large diffuse area filled with connective tissue and numerous ovarian lipofuscins (Plate 32,

PLATE 31

HISTOLOGY OF THE CORPUS LUTEUM OF PREGNANCY

Figure 1. Highly regressed luteal-like structure (CL) found in the ovary from the pregnant side of muskox (78-27). This structure was not identified macroscopically. It stained heavily for connective tissue with Masson's Trichrome and contained numerous pigmented structures. (X43)

Figure 2. The corpus luteum from muskox (78-32). The structure is invaded by strands of connective tissue (arrow) and also contained numerous pigmented structures. (X75)

1



2

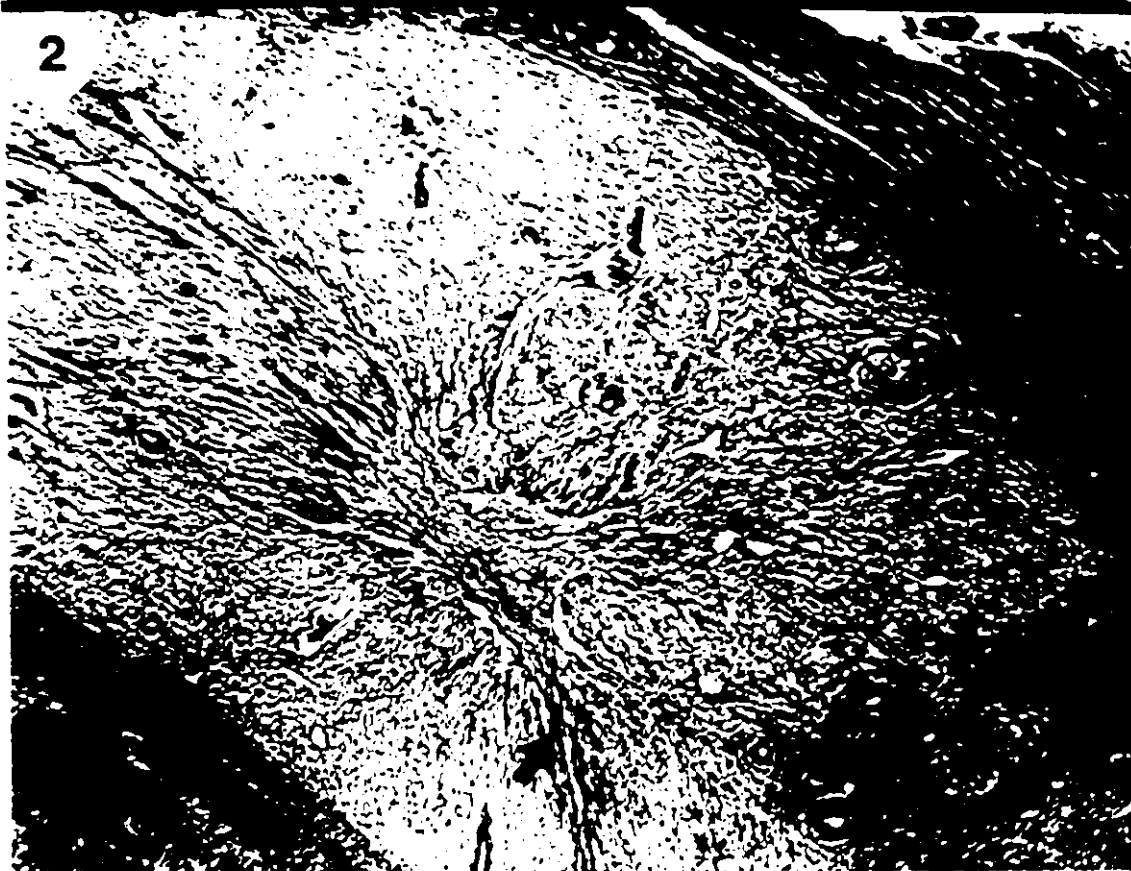


PLATE 32

HISTOLOGY OF THE CORPUS LUTEUM OF PREGNANCY

Figure 1. A cross section of the ovary of a pregnant muskox (78-38) collected in March. Above the medulla is a large area of luteal-like tissue (A) similar in character to the corpus luteum of pregnancy found in the other 7 animals. In the lower right corner is a small portion of another corpus luteum (B) that was identified in macroscopic section. (X12)

Figure 2. The corpus luteum (B) that was identified macroscopically in Fig. 1 above. This structure resembles the older corpus luteum of the cycle. (X43)

1



2

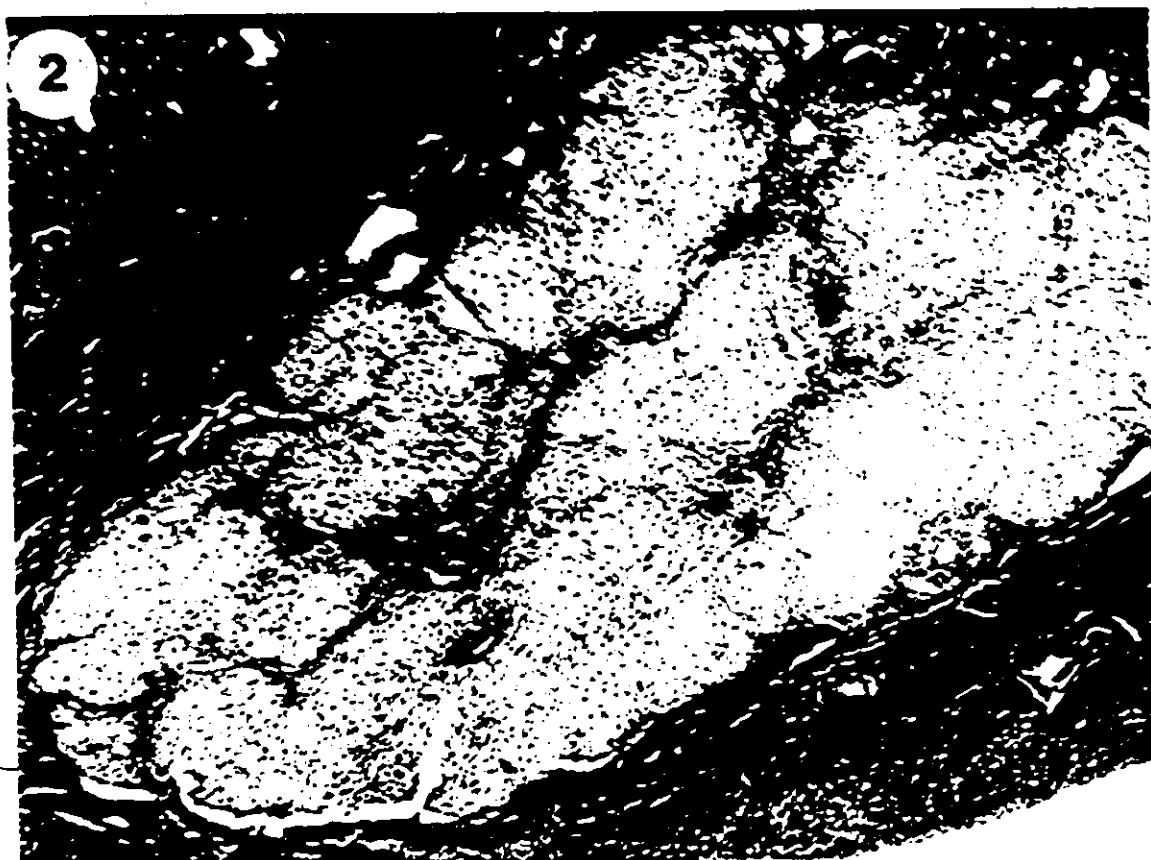


Fig. 1). Thick-walled blood vessels appeared to join it to the medullary tissue.

j) Vasculature of the Reproductive Tract

The latex injection technique used here was developed for use in fresh material that was collected especially for latex casting (Ginther, 1976). The musk-ox tracts were all frozen and most of the six tracts used for this purpose had been excised with very short vessels and attached ligaments. Leakage from the cut edges of the tissues proved to be a major drawback to complete injection. Cannulation of some of the smaller arteries, particularly the coiled ovarian artery, proved difficult, resulting in only three of the six specimens having completely injected ovarian arteries. The small vessels of the immature tract ruptured easily during the latex injection.

(i) Arterial

The major arterial supply to the uterus came from the uterine artery and the uterine branch of the vaginal artery. Both these vessels arise together from the internal iliac. The uterine artery travelled through the broad ligament on the ventral ~~surface~~ of the specimens. It appeared to be carried by the round ~~ligament~~ up to the level of the ovary. Just below the level of the ovary, the uterine artery divided into two branches with

PLATE 33

THE VASCULATURE OF THE UTERUS

- Figure 1. A dorsal view of the vasculature in the right horn of a parous, non-pregnant muskox. In this specimen the ovary has been removed and the ovarian vein remains uninjected. The uterine branch of the ovarian artery (UBOA) can be seen following the uterine branch of the uterovaginal vein (UBOV). This artery bypasses the ovary on the ventral surface and continues on to supply the tip of the uterine horn (UH). A dense network of arteries and veins can be seen along the mesometrial edge (ME) of the uterine horn. (X1 1/2). O. indicates position of ovary; UBVV, uterine branch of vaginal vein; UBVA uterine branch of vaginal artery.
- Figure 2. The ventral view of the vasculature in the right horn of a parous, non-pregnant muskox. The uterine artery (UA) with its extensive dichotomous branching is clearly visible. (X1 1/2)
- Figure 3. The ovarian vasculature (dorsal) from an immature, non-pregnant muskox. The ovarian artery (OA) is highly coiled and in close apposition



Plate 33 (cont'd)

to the uterine branch of the uteroovarian vein (UBOV). A single ovarian artery can be seen entering the cranial portion of the ovarian hilus. The ovarian pedicle is similar in the immature and parous animal. (X2) O, ovary; UBUV, uterine branch of uterine vein.

Figure 4. The ventral surface of the left horn from an immature muskox. In this specimen the uterine artery (UA) displays dichotomous branching though the size and degree of coiling is noticeably reduced in both the uterine artery and the coiled arterioles (CA) (compare with Fig. 2). In this specimen the arteries were extremely fragile and had a tendency to rupture under injection pressure (the red ball (R) on mesometrial border as a result of such a rupture). (X2)

each of these dividing into two branches again. This dichotomous branching continued down to the level of the coiled arterioles. In this manner the uterine artery supplied the central and largest portion of the adjacent horn. The small arterial vessels in the body and cervical area were supplied by the ~~uterine~~ branch of the vaginal artery.

The ovarian artery was substantially smaller than the uterine artery in diameter and was found in close apposition to the ~~utero~~-ovarian vein. (Plate 33, Fig. 3). This artery followed an extremely tortuous path, wrapped around the uterine vein and entered the ovary through the cranial end of the ovarian hilus (Plate 33, Fig. 3). In these specimens only one vessel was found to enter the hilus of the ovary. A small uterine branch of the ovarian artery followed the utero-ovarian vein. This vessel was much smaller in diameter than the ovarian artery and was not coiled. It followed, for a distance, the uterine branch of the ovarian vein, eventually by-passing the ovary on the ventral surface to supply the tip of the horn. (Plate 33, Fig. 1).

With this one exception, the ovarian arterial supply was essentially separate from the supply to the uterus.

(ii) Venous

The major uterine venous drainage was via the uterine branch of the utero-ovarian vein and the uterine

branch of the vaginal vein (Plate 33, Fig. 1). The veins were substantially larger in diameter than the arteries, had very thin walls and strong valves. The valves effectively impaired retrograde injection of fluid through the utero-ovarian vein. Injection of fluid through the vaginal vein moved cranially without obvious resistance and emptied through the uterine branch of the ovarian vein. Fluid also drained from the horn tips, ventrally past the ovary, and, occasionally, filled the ovarian veins (Plate 33, Fig. 3). The ovarian veins were very hard to inject properly. Unlike the ovarian artery, the ovarian vein was not coiled though it commonly branched two or more times as it approached the hilus (Plate 33, Fig. 3). The drainage was not confined to a specific region of the hilus. Because the tracts were dissected, a true assessment of the direction of venous flow was extremely difficult to make. It is possible that venous drainage travels cranially and empties through the uterine branch of the utero-ovarian vein, however, it seems more likely that the uterine branch of the vaginal vein, like the sheep's, does not have valves and would therefore present no resistance to the latex injection (Trautman and Fiebiger, 1952).

The degree of branching and coiling of the veins was far more complex than the arterial system and bilateral anastomoses seemed to be extensive.

The veins and arteries formed a dense interwoven

network at the mesometrial edge of the uterine horn (Plate 33, Fig. 1). Arteries were often found encircled by very fine branches arising from a larger vein.

In immature specimens the arrangement was similar though the vessels themselves were substantially smaller; this being particularly noticeable in the venous system (Plate 33, Figs. 3 and 4). The branching of the uterine artery appeared greatly reduced (Plate 33, Fig. 4).

The coiled arterioles were extremely fine and the degree of coiling was not as extensive as in the mature tracts (Plate 33, Fig. 4). The coiling of the ovarian artery was identical to that seen in the mature condition. The vessels of these specimens were very fragile and ruptured easily under injection pressure.

The most noticeable differences found in the pregnant animals were the increased size of the major vessels and the straightening of the coiled arterioles. Latex injections were not done on the pregnant tracts so an assessment of vascular changes resulting from pregnancy was not made.

(iii) The Muscular Band

Latex did not penetrate the muscular band on the antimesometrial border of the uterus whether injected through the arterial or the venous system. However, preliminary flushing of the tract with saline caused the muscular band to fill with fluid and become turgid.

4.2 AGE ESTIMATIONS FOR MATURE ANIMALS

The age estimates were based solely on a count of the annulations in the cementum of the first incisors and are found in Table 8. Among the six pregnant specimens, the eldest was 16 years and the youngest was 5 years suggesting that this cow was bred at 4 years of age. The ages of three parous cows ranged from 7-10 years and the three non-parous cows from 3-4 years. There was no apparent relationship between the size of the reproductive tract and the age of the cow.

Table 8. Age estimates based on numbers of rest lines (cementum annulations) counted in the first incisors of muskox teeth. (Teeth could not be collected for all specimens).

SPECIMEN	PARITY	ANNULATIONS	AGE ESTIMATE (yrs)
77-12	pregnant	11-16	12-15
77-13	pregnant	7-9	8-10
78-27	pregnant	5-7	6-8
78-37	pregnant	4-5	5-6
78-38	pregnant	14-15	15-16
78-40	pregnant	4-5	5-6
78-26	parous	6	7
78-33	parous	5-7	6-8
78-44	parous	8-9	10-11
77-11	non parous	2	3
78-24	non parous	2	3
78-42	non parous	3	4

DISCUSSION

5.1 THE REPRODUCTIVE TRACT

a) Suspensory Ligaments

The suspensory ligaments of the muskox uterus were similar to those of the domestic species¹. Common to all these animals is the muscular broad ligament. The cranial portion of this ligament forms the mesovarium, the ligament that holds the ovaries in position, and the mesosalpinx, the extensive ligament that forms the roomy ovarian bursa which communicates with the peritoneal cavity (Bassett, 1965). The smooth muscle fibres found in the suspending ligaments are used to either elevate the uterus towards the rectum or to let it sink ventrally (Nickel et al. 1973).

The round ligament, arising from the ventral surface of the broad ligament, is considered by Sisson (1940) to be fairly well developed in ruminants. In the muskox, this ligament was more pronounced than in cattle, sheep or goats and was characterized by a prominent band of smooth muscle tissue along the cranial edge. The position of the round ligament in the muskox, its high degree of development, caudal flank attachment and the prominent bands of smooth muscle tissue suggest that this ligament functions as a strong additional support for the uterus.

¹ Domestic species is used here to refer to cattle, sheep and goats.

b) The Non-pregnant Uterus

The basic morphological features of the non-pregnant uterus of muskoxen paralleled those of cattle, sheep and goats (Eckstein and Zuckerman, 1956; Hafez, 1968; Asdell, 1946) and conformed to the ruminant pattern. All display the type of uterus classified by Mossman (1976) as medium-length bicornuate. The characteristic features of this type of uterus are two cornua externally fused for a large portion of their length. Internally a median septum separates the two cornua but stops short of the internal os of the cervix, leaving a small undivided portion. This constitutes the true corpus of the uterus (Eckstein and Zuckerman, 1956). The cornua of the muskox were symmetrical as are those of domestic species (Edwards, 1965; Lyngset, 1968a). The general morphological features of the non-pregnant tracts are similar between all four species. However, this does no more than reflect a common reproductive pattern found among a large number of ruminants. On a more subtle level, though, there are distinctions between the species. Sheep and goats are more closely allied and differ from cattle in having ovaries of a more uniform, bean-shaped appearance with less vividly coloured corpora lutea. Further, the horns of the uterus are more highly coiled and taper towards the utero-tubal junction and have a single intercornual ligament (Eckstein and Zuckerman, 1956). These three characteristics are all features found in the muskox uterus and on the basis of

uterine morphology suggest a slightly stronger relationship between the muskox and the sheep and goats than between muskoxen and cattle.

The number of caruncles on the endometrium of the muskox uterus averaged 162, ranging between 131-189. On this basis the muskox could be classified with the goats as polycotyledonary (Amoroso, 1956). In sheep, the total number of cotyledons varies between 88-96 and in cattle between 70-142 (Amoroso, 1956). The physiological significance of such a classification, if any exists, is not at all clear. Although the number of cotyledons ultimately determines placental size, the ability of individual cotyledons to increase their size as partial compensation for reduced numbers obscures any direct relationship (Alexander 1964a, 1964b).

Pigmentation in the muskox uterus was consistently localized in the caruncular areas and these pigmented structures were histologically identified as lipofuscins. Steven (1975) describes lipofuscins in the sheep placenta as iron-free pigment granules derived from the envelopes of ingested red cells. Dellman and Brown (1976) describe lipofuscin granules as containing lipid droplets, pigment and some hydrolytic enzymes. These granules are found in a variety of cell types and because they tend to increase in numbers with age of the animal, they are referred to as the 'wear and tear' pigment. Lipofuscins are considered one of the end products of lysosomal activity (Dellman

and Brown, 1976) and have been found in the endometrium of a number of domestic ungulates.

Endometrial pigmentation is reported as being common only in the sheep (Dellman and Brown, 1976) though Lyngset (1968a) found partial to complete pigmentation of the uterine mucosa of the goat in 5-10% of the specimens he examined. Pigmentation is usually found confined to the caruncles, though in sheep and goats it does occur in the intercaruncular areas as well. This pigment has been associated with melanin granules (Dellman and Brown, 1976; Eckstein and Zuckerman, 1956) and is found in nulliparous as well as multiparous ewes. In contrast, the pigmentation found in the muskox uterus was absent in the five tracts judged to be non-parous. These five nulliparous tracts also lacked lipofuscins in the endometrial stroma. Taken together, these observations seem to suggest that the pigmentation of the muskox uterus is related to an accumulation of lipofuscins resulting from pregnancy. The fact that identical lipofuscins were present in control tissues from non-pigmented sheep and goat uteri may point to different functional origins and hence different properties of the pigment granules in the different species.

The nulliparous uteri were identified by their consistently small size, lack of vascular development, absence of caruncular pigmentation and absence of a muscular band. The ages of three of the animals were consistent with the deduction that they were nulliparous.

c) The Pregnant Uterus

(i) Estimation of the stage of gestation

Of eight pregnant tracts, all collected in late winter (end of February and throughout March) only four contained a fetus. The only means available to estimate the stage of gestation was through aging the fetus. The formula proposed by Huggett and Widdas (1951) carries with it an estimated factor that results in approximately a 10% error as determined by the above authors. The use of birthweights only to establish the curve must also be viewed as an additional source of error. These factors are discussed by Huggett and Widdas (1951) who conclude that the errors incurred do not reduce the formula's acceptability, particularly for comparative purposes.

The resulting slope for the muskox (0.11 cm/da) falls below the estimated range for most mammals (0.12 to 0.15 cm/da) set by Huggett and Widdas (1951). The muskox fetal growth curve falls in the upper range of those species known to have delayed implantation. It is, however, highly probable that the small sample size, coupled with inherent sources of error, are responsible for the relatively low slope found here.

The estimated ages for the four fetuses places the time at which they would have been born from early to the end of April. The earliest recorded sighting of a muskox calf is April 16 (Gray and Rowell, 1976) and it is not unreasonable to expect some births to occur a week earlier.



(ii) Anatomy

The similarities between the non-pregnant tracts of the muskox and the domestic species point to similarities that can be expected to occur during pregnancy. For example, the caruncles lining the uterus determine that the type of placenta must be cotyledonary or multiplex and adeciduate.

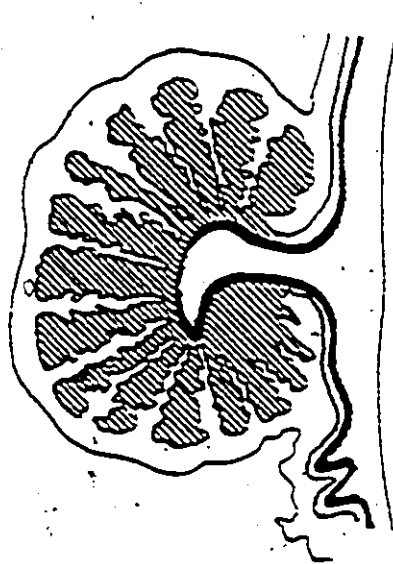
The placentome of the muskox in late pregnancy differs in shape from those of any of the domestic species though it can be considered closer to those of sheep and goats (i.e. with a broad base attachment and a concave surface) than to the placentome of cattle which is more convex (Fig. 6).

In seven of the eight pregnant tracts the number of caruncles ranged between 131-189. Alexander (1964a) found a positive correlation between birthweight of sheep fetuses and the number of intact cotyledons. However, carunclectomy did not appear to affect fertility and only interfered with pregnancy when more than 60 caruncles were removed. A reduction in caruncle number was partially compensated for by an increase in the weight of individual caruncles. The final weight of the fetus may, however, be limited by the number of caruncles (Alexander, 1964b). It is interesting to note that specimen 78-37 had only 60 caruncles. As she was pregnant at the time of collection in late March it can be assumed that the reduction in caruncles by almost half did not seriously affect her pregnancy. Unfortunately the fetus was not collected with the uterus.

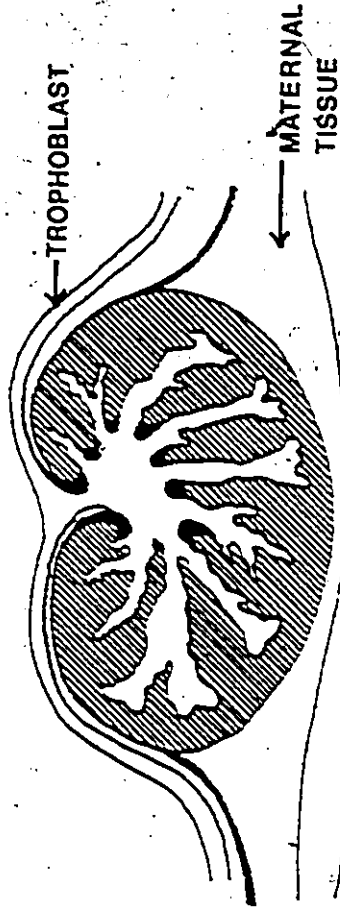
The preservation of the placentome for histology was

Figure 6. A schematic representation of the gross morphology of the placentome of late pregnancy in cattle, sheep, goats and muskoxen. The domestic species have been taken from Amoroso (1956).

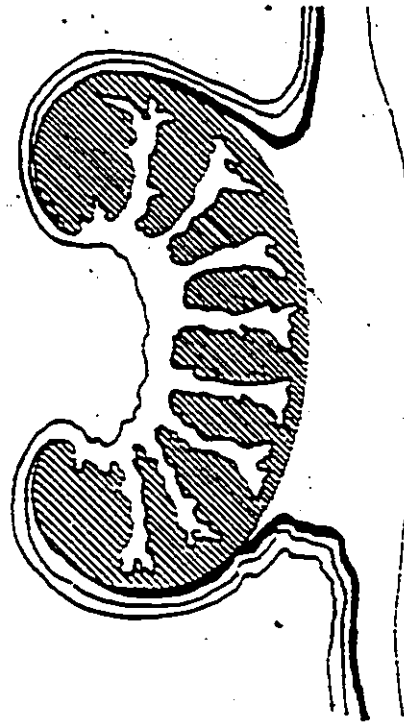
THE GROSS FORM OF THE PLACENTOME



COW



SHEEP



GOAT



MUSKOX

poor, but sections that could be used suggest a fetomaternal arrangement similar to descriptions given for the domestic species of fetal villi interdigitating with maternal septa (Steven, 1975; Wimsatt, 1950). There was a well-developed chorionic epithelium on the trophoblast in which giant binucleate cells were identified. These cells have been identified in a large number of ruminant placentae.

The cotyledonary placenta in ruminants is usually defined histologically as epitheliochorial (using Steven's (1975) modification of Grosser's (1909) classification). Although the histology of the muskox placentome did not allow detailed identification, it is reasonable to predict, given the other similarities, that this histological classification would apply to the muskox placentae.

The extravasated blood found near the base of the fetal villi may indicate the existence of a hemaphagous organ described in sheep by Wimsatt (1950) and Steven (1975) and in goats by Harrison and D'Silva (1956). Ungulate placentae in general lack a hemaphagous organ although the trophoblast will often ingest relatively small amounts of red blood cells. In sheep, however, significant amounts of blood do accumulate in the central depression of the caruncle. The maternal erythrocytes are ingested by adjacent trophoblast cells which subsequently accumulate intracytoplasmic deposits of non-ferruginous hematogenous pigment (Wimsatt, 1950). The strong pigmentation in the muskox trophoblast epithelium in the region of the blood

pools as well as the macroscopic appearance of thick sections of the placentomes suggest that a similar situation may be occurring though the full extent of this process cannot be assessed.

Uterine glands in the intercaruncular region or corresponding areolae on the chorion were not noticed morphologically in the pregnant specimens. Wimsatt (1950) who described the development of the uterine glands in sheep, points out that they are much harder to see near term. The chorion of the sheep had little tendency to adhere to the endometrium near term and Wimsatt suggests that fetal movements may prevent continuous apposition of the specific chorionic areas over the uterine glands. The intercaruncular chorion of the muskox showed no tendency at all to adhere to the endometrium and the lack of morphological evidence of the uterine glands may result from a situation similar to that in sheep, though it must be remembered that these observations were made on frozen and thawed material.

In a cotyledonary placenta, an extensive highly vascular allantoic membrane is a characteristic feature. Like the domestic species, the muskox fetal membranes consist of an amnion surrounding the fetus and an extensive allantois. As in other ruminants, the allantoic sac does not surround the amnion but crosses over it on one side forming a 'T' shape where it joins the umbilicus. This arrangement of fetal membranes is identical to that seen

in the three domestic species. In all four species the umbilical cord lies exclusively within the amnion. The umbilical vessels as they leave the amnion, branch in either direction to vascularize the two arms of the allantois.

In many species it has been assumed that the chorion is vascularized only in the regions where it comes in contact with the allantois (Steven, 1975). However, the muskox as well as cattle and sheep have a number of placentomes on the amnio-chorion. In the domestic species these placentomes are vascularized by branches of the umbilical arteries which traverse the mesoderm between the two membranes (Steven, 1975).

The necrotic tips found at both ends of the muskox allantois are also found in cattle and sheep and are believed to result from a restricted blood supply to these areas (Amoroso, 1956). The condition in cattle is not as marked as it is in sheep and this led Hammond (1927) to speculate that the more adequate blood supply to the extremities of the chorionic sac facilitated the free-martin condition in cattle. Mellor (1969) has advanced a theory for sheep involving the annular suture that forms when two chorions meet and fuse. It is the nature of the suture and its immunological properties and not the vasculature, that determines the degree of vascular anastomosis which gives rise to the free-martin condition. Twinning is considered rare in muskox. The only reported case involved

stillborn twins both of which were female, (Wilkinson, 1971b). A report was not made on the nature of the membranes or their possible degree of fusion so the behaviour of the chorion under conditions of twinning cannot be assessed in the muskox.

The small plaques found on the muskox amnion in the region of the umbilical cord have also been described in a variety of ruminants (Steven, 1975) though no explanation for their presence has been advanced.

The small, yellow, cyst-like structures identified histologically as epithelial hyperplastic cysts, were found in all the pregnant tracts. Because they occurred in all pregnant tracts in relatively low numbers, the condition was not considered pathological. These cysts fit the description given by Jubb and Kennedy (1970) of endometrial cysts, a condition which, in some ewes, is presumed to develop during the process of uterine involution. The cysts are said to arise from the blockage of ducts of the glandular tissue adjacent to the caruncular stalk.

The small areas of placental tissue found on the under-surface of the caruncles and very occasionally in the intercaruncular area appeared microscopically to be areas of additional placental attachment. The additional areas of placentation in the muskox, although similar to morphological descriptions of adventitial placentation, did not appear to represent a pathological condition. These areas were small and almost completely localized to the immediate

region of the placentome. Adventitial placentation has been described as a pathological condition in the domestic ruminants and related to inadequate placentome development (Jubb and Kennedy, 1970).

Hamilton et. al. (1960) describe the formation of small accessory placentomes in members of the Cervidae but do not consider that these are new placentomes. They suggest that these result from the existence of small regions of caruncular tissue found outside the main caruncles.

To briefly summarize, the morphological aspects of late pregnancy in the muskox are typical of the ruminant pattern. The shape of the placentome and the possible existence of a hematoma are features more closely related to sheep and goats than to cattle. The histological description of the fetal maternal relationship cannot be described here though it is probably in the broad classification of epitheliochorial. The common occurrence of the endometrial cysts as well as the extraplacental tissue in the muskoxen examined do suggest that a detailed study of placentation in this species would be of comparative interest and might prove valuable in indicating the etiology of these structures in the domestic species.

d) The Muscular Band

The 5mm deep muscular band running from the bifurcation for two-thirds the length of each horn and

stopping a short distance from the utero-tubal junction was an especially prominent and interesting feature of the non-pregnant tracts. The band had no attachments with any ligaments or any part of the body wall thus precluding the possibility that its role is that of a supporting ligament. Although the band was absent in the non-parous condition, close examination revealed fine striations on the serosa of the cornua along the antimesometrial border. Histologically this band was a continuation of the uterine serosa, longitudinal smooth muscle layer and the stratum vasculare. In the non-pregnant tract, the muscular band appeared to be a pinching of the outer muscle layer trapping elements of the vascular layer in between. The only histological feature that appeared slightly exaggerated was the large number of 'spaces' in the stratum vasculare, many apparently lined by endothelial cells.

Because this band is associated with parity, it seems likely that its function is connected with pregnancy. However, brief in situ examination of two pregnant tracts did not reveal any obvious sign of this tissue. On closer examination of the excised tracts the band could be found on the non-pregnant horn. After removal of the fetus and fluids, the band was also found on the pregnant horn and measured approximately 3 cm in depth. The inability to find the band on the fully distended uterus can be explained by the fact that during pregnancy the muscular band becomes a flat strip of tissue approximately 6 cm wide over

the antimesometrial surface. It lacks any of the coiled arterioles as these are found embedded at the base of the circular muscle layer. Of particular note was the fact that this strip of tissue was only loosely connected to the underlying circular muscle layer. In attempting to recover a small piece for fixation, the muscle strip continually separated from the underlying tissue, being attached by a fine, almost hairlike, mesh of fibres. Histological examination was very limited as the tissue had been previously frozen. However, sectioning did reveal a large number of apparently vascular elements filled with a strongly basophilic substance. These vessels consistently had very thin walls and showed some evidence of having valves. The basophilic substance was always contained within these vessels which appeared to be either veins or lymphatics. To interpret the vessels as veins one has to assume that the vessel walls had been denuded by freezing damage and the debris was then seen filling the vessels. There are, however, reasons why this seems unlikely. All the vessels had extremely thin walls. If this is the result of freezing damage the uniformity seems peculiar as there was no gradation in the thickness of the vessel walls. Further, the strong basophilic substance within the vessels suggests that the debris is primarily ruptured nuclear elements where as the cells from the lining of a vessel could be expected to contain more cytoplasm. On no occasion did these vessels fill with

latex when the venous system was injected. Given the size of the vessels it seems extremely unlikely that, if they were veins, they would always remain uninjected by latex. Until adequately fixed specimens from the pregnant tract can be examined, the vessels have been tentatively identified as lymphatics and the basophilic substance in their lumens as ruptured lymphocytes.

The muscular band in the non-pregnant tract can then be viewed as exactly what it appears to be: a pinching of the outer tissue layers. This pinching presumably occurs during involution and results from the loose connection of the outer tissue layers to the inner muscular layer in this region. The band appears essentially non-functional in the absence of pregnancy, but during pregnancy, the distention of the uterus stretches the band until it becomes a flat strip overlying the antimesometrial border. Development of the large lymphatics during the first pregnancy could ultimately be responsible for the permanent separation of the two tissue layers (Fig. 7).

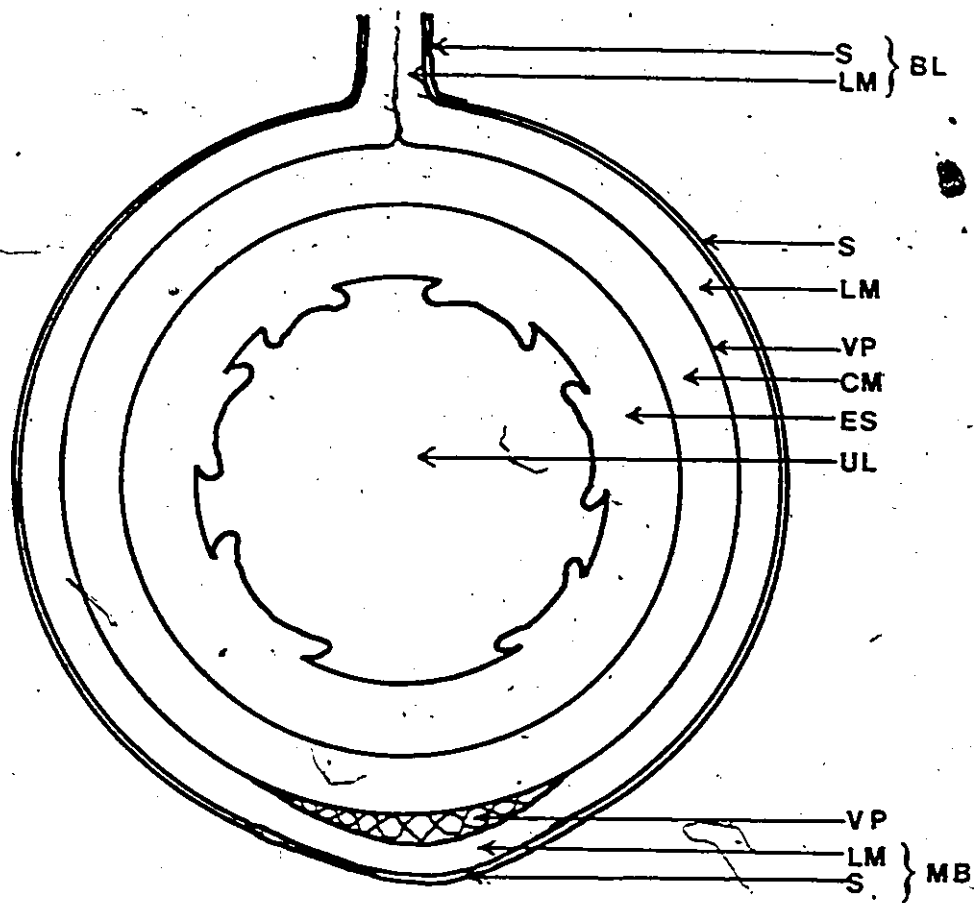
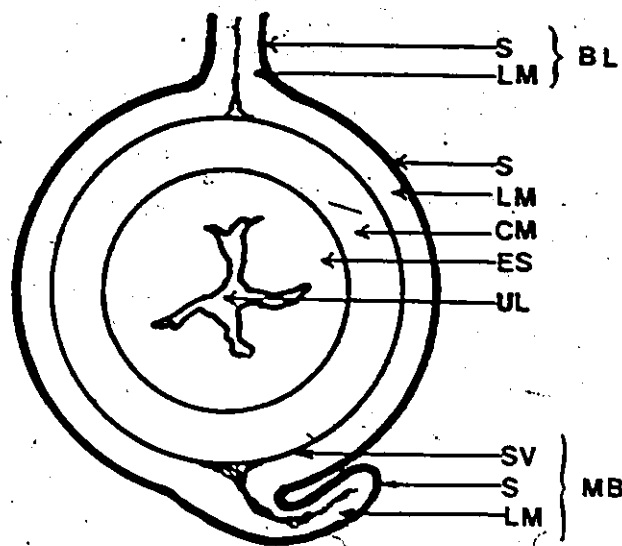
If the above morphological interpretation is correct, the functional element of the tissue becomes the well developed lymphatic pathway extending along most of the length of the horns. It should be stressed that the muscular band stops abruptly at a point approximately one third of the distance from the utero-tubal junction to the intercornual ligament. It is possible that the lymphatic vessels continue on in the stratum vasculare and come

Figure 7. A schematic representation of the muscular band in the mature non-pregnant condition (A) and during pregnancy (B) in the muskox.

A. A cross section of uterine horn from a mature non-pregnant muskox. The muscular band is depicted as a fold of tissue on the anti-mesometrial border and is composed of the longitudinal muscle layer and ~~serosa~~. Elements of the stratum vasculare (a thin layer of vascular components that separates the circular and longitudinal muscle layers) become trapped within this fold of tissue.

B. A cross section of the uterine horn during pregnancy. The muscular band is depicted as a strip of tissue that is only loosely connected to the inner circular smooth muscle layer. It is suggested that the development of a lymphatic pathway in this region during pregnancy separates the two muscle layers.

S-serosa; LM-longitudinal smooth muscle band;
BL-broad ~~ligament~~; CM-circular smooth muscle
layer; ES-endometrial stroma; UL-uterine lumen;
MB-muscular band; VP-vascular pathway.



into communication with the ovary. This would represent a unique situation as Meckly and Ginther (1969) could not find any lymphatic communication between the ovary and the uterus in sheep, though Kotwica (1980) has recently speculated about such a pathway in pigs. One could speculate that these lymphatics perform a drainage function whereby tissue fluids would passively drain down to the lower point of the uterus where they could be collected by the vessels. The role of lymphatics and lymph is poorly understood in ungulate reproduction. The possibility of an involvement of lymph, immunological or otherwise, in mechanisms associated with the establishment and maintenance of pregnancy or with the uterine control of luteolysis in the estrous cycle, cannot be overlooked.

There is no analagous structure in sheep, goats or cattle. Histologically the antimesometrial border of the non-pregnant animal is similar to the muskox except that it lacks the prominent fold of tissue with its concentration of large lymphatic vessels. Specimens from pregnant domestic animals were not available for sectioning. Because of the histological and morphological similarities between these species and the muskox it is reasonable to speculate that the condition found in the muskox could represent an exaggeration of a similar condition in the domestic species. To my knowledge no one has examined the uterine lymphatic pathways during late pregnancy in any of the domestic species and so such a study would be of considerable

interest.

e) The Uterine Cervix

The cervix of the muskox conformed to the ruminant pattern in basic morphology having a thick muscular wall, complex plicae palmatae and annular ridges. The mucosa was elaborately folded with secondary and tertiary folds and like cattle and sheep there were no coiled tubular glands as reported in goats (Hafez, 1973). More recent work suggests that this may be specific to only some breeds of goat (Morton and Glover, 1974). The epithelium was simple columnar and did not appear ciliated suggesting that it is secretory. The presence of numerous clear vesicles in the apical portion of the cells supports this contention. The epithelium contained large spherical cells with a prominent central nucleus as opposed to the basal nucleus associated with goblet and mucus secreting cells. Goblet cells have been identified in the cervical epithelium of the domestic species (Dellman and Brown, 1976) and Trautman and Fiebiger (1952) have described large hollow cells that penetrate into the underlying stroma. The cells in the muskox cervical epithelium do not appear to connect to the stroma. In the absence of critical staining procedures, these cells can only tentatively be identified as specialized cells that are possibly mucus secreting.

The cervix of the muskox most probably functions, in the manner described for domestic species, as a reservoir

for spermatozoa (Mattner, 1966; Hafez, 1973; Morton and Glover, 1974). Morphological variations do exist between the three domestic species as well as in the muskox. The external os of the muskox cervix was very prominent and in all but two specimens there was an epiglottis-like structure. The wall of the vagina was thrown into a fold that partially covered the external os. The function of this fold is not clear though one could speculate that it acts as a pocket to trap or hold the seminal fluid near the cervix. Morton and Glover (1974) have demonstrated that in ruminants characterised by vaginal insemination, survival of spermatozoa in the vagina is very low. The success of the insemination depends, in part on the numbers of spermatozoa that will gain entrance to the cervix. A fold in the vaginal wall could prevent too rapid a removal of seminal fluid from the vagina.

The cervical canal in muskoxen is very convoluted. Along a sagittal section the cervix appears to form a prominent 'S' shape while the dorsal section revealed four annular ridges. The canal appears to be an exaggeration of the spiral form described in cattle.

During pregnancy the cervix was enlarged in length and width and was plugged along its entire length with a thick, viscous mucus, a condition that has been described for a number of species. Hafez (1973) has suggested that during late pregnancy the muscles of the uterine myometrium cause the stromal muscles of the cervix, which are spirally

arranged, to unwind, much like the opening of an iris diaphragm.

The species differences seen in the cervix do not necessarily affect the functional capacity of this structure (Hafez, 1973). In connection with Fooden's (1967) 'lock-and-key' hypothesis, it is interesting to note that the penis of the bull muskox resembles that of cattle and lacks the urethral process of the caprids (my own unpublished observations).

e) The Oviduct

The oviduct of the muskox presented no unique features. The histological differences occurring between the ampulla and the isthmus portion are identical to the regions of the oviduct described for many species.

The cow and sheep differ from most eutherian mammals in lacking some specialized structure, sphincter muscle or villi, to reduce fluid passage from the uterus into the oviduct (Andersen, 1928). Only two of the muskox tracts exhibited any morphological evidence of a muscle sphincter at the utero-tubal junction. In these specimens (78-18; 78-26) a slightly thickened muscular ridge was evident. Specimen 78-18 was one of two tracts flushed for ova. Neither of the flushed tracts presented any apparent resistance to the fluid passage between the uterus and oviduct. The muscular ridge found in the two mentioned specimens may represent individual exaggeration of the

muscles in the utero-tubal region.

f) Vasculature

The arteries of the muskox uterus were characterized by thick walls and extensive dichotomous branching. The veins, though they had much thinner walls, had substantially larger lumens than the arteries and contained strong valves that made retrograde injection of the venous system difficult. This situation is similar in sheep and cattle. Venous injections were successfully made through the uterine branch of the vaginal vein. Trautman and Feibiger (1952) state that the veins in the cervical regions of domestic ruminants lack valves. This would account for the relative ease of venous injection via this route.

The thick walled convoluted arteries of the parous tracts contrasted markedly with those from the non-parous tracts which were very fine vessels that appeared less tortuous. Trautman and Feibiger (1952) and Dellman and Brown (1976) have described a similar phenomenon in parous, domestic animals. The walls of the vessels from parous animals have thickened intimae with a marked increase in elastic tissue.

During pregnancy, the major vessels had increased in diameter and the coiled arterioles of the non-pregnant uterus were, in late pregnancy, completely straightened due to the extensive stretching of the uterus.

The arrangement of the vascular elements is identical

to that of sheep, goats and cattle. Of particular interest in this pattern is the separate arterial supply to the uterus, (the uterine artery) and to the ovary (the ovarian artery) coupled with a common venous drainage, the utero-ovarian vein. The intimate apposition of the ovarian artery along a portion of the utero-ovarian vein has given rise to a hypothesis of unilateral local transfer of information from the uterus to the ovary (see Ginther, 1976). This theory suggests that the uterine luteolysins, probably prostaglandin $F_{2\alpha}$, and possibly luteotrophic (embryonic) factors are transferred from the uterine vein to the ipsilateral ovarian artery by a process of passive diffusion (Ginther, 1976; Walsh et. al., 1979). Though some authors have failed to demonstrate this pathway (Coudert and Phillips, 1974) there is a large body of evidence supporting the theory (DelCampo and Ginther, 1974; Lee and O'Shea, 1974; Mapletoft and Ginther, 1975; Land et. al., 1976; Walsh et. al., 1979). Given the similarities in the vascular arrangement of the muskox uterus to that of sheep, it is reasonable to propose a similar mechanism between the ovary and the uterus in the muskox.

5.2 THE OVARIES

a) Anatomy

The external shape position and relative size of the muskox ovaries are very similar to those of sheep and goats. In this feature they differ from the more irregular

shape of the cow ovary, particularly in multiparous cows. Edwards (1965) recorded a slightly greater dimension in the right ovary of cattle which he related to the more frequent occurrence of corpora lutea and mature follicles in this ovary. Greater activity of the right ovary in cattle has also been reported by others (Hammond, 1927; Wright, 1950; Rajakoski, 1960). A similar preponderance of right ovarian activity has been reported in both sheep and goats (Casida et. al., 1966; Lyngset, 1968c). The measurements of the 23 muskox ovaries in this study did not suggest greater activity for one ovary than for the other, but a much larger sample size would be required to confirm or refute this.

The major histological components described in the muskox ovaries are comparable with, and, in many cases, are typical of the ruminant ovary.

The single layered cuboidal epithelium surrounding the ovary is common to many mammals. The stretched appearance of these cells has been described in the domestic animals (Trautman and Fiebiger, 1952). No invaginations or sub-surface crypts were found in the germinal epithelium of the muskox ovary. The role of the epithelial crypts and their relationship to cyclical activity has not been clearly established for any species (Harrison and Weir, 1977; Duke, 1978).

The tunica albuginea underlying the epithelium contained many collagen fibres and was of varying thickness. Harrison

(1948) has suggested that the thick tunica of the goat ovary was responsible for maintaining the smooth surface integrity of the ovary. In the muskox, only fresh corpora lutea and large follicles protruded to any noticeable extent and it could be speculated that the tunica functions in a similar manner here.

The cortex of the muskox ovary comprises a relatively thin layer that completely surrounds the medulla except at the hilus. There was no discrete boundary between these two regions of the ovary and this condition is similar to that seen in domestic species. The cortex, which was highly cellular in nature, contained follicles at varying stages of development and atresia as well as scars of old atretic follicles and corpora lutea. There were no cell types descriptive of interstitial tissue. Artiodactyla are characterized by their lack of discrete areas of interstitial tissue (Mossman and Duke, 1973).

The large irregular tubules found in the hilus, as well as the smaller ones found less frequently in the cortex, have been identified as tubules of the rete ovarii. The rete ovarii is a remnant of the tubular connection from the mesonephros and the gonad (Duke, 1978). The rete tubules have been intimately connected with the process of folliculogenesis in a variety of species. The cells of the rete have been identified as the source of the follicular envelope (Peters, 1978).

In describing the follicular development in the

muskox ovary the general classification outlined by Mossman and Duke (1973) was used here as these categories can be applied to follicular development in a wide variety of mammals. In the muskox ovary the stages of follicular development closely parallel those of other ruminants, suggesting that the histological development of the follicle does not deviate significantly from sheep or, in fact, ruminants in general. Polynuclear oocytes were not identified in the muskox and there was only limited evidence to suggest the existence of polyovular follicles although these follicles have been recorded in a wide variety of species (Peters, 1978). Their specific development and significance is not clear though they have been found most frequently in embryonic and immature ovaries.

The development of a thecal cone in secondary follicles was described by Harrison (1948) in the goat. There was very limited evidence from this study for a similar phenomenon in the muskox. Harrison, (1948) related this development to an uneven vascular supply to the theca, as this condition was always observed in follicles that had not, as yet, sufficiently developed their own capillary network. There were only two follicles that showed any sign of thecal cone development in the present study, both being found just under the tunica. The majority of the developing follicles had already migrated to the deeper cortical layers before and during the establishment of the thecal investment.

The antral follicles were histologically identical to

the Graafian follicles of the sheep and goat. Call-Exner bodies were a prominent feature of the granulosa of the muskox follicles. Call-Exner bodies have been identified in both sheep and goats, and are believed to arise from either the liquefaction of a central granulosa cell or through the combined secretory action of the granulosa cells (Brambell, 1956; Motta and Nesci, 1969). The liquid formed within the Call-Exner bodies is identical, histochemically, to the follicular fluid (Mossman and Duke, 1973).

The number and pattern of distribution of the Call-Exner bodies in the muskox follicle was not characteristic of any phase or stage of follicular development. They appeared, instead, to occur in a random fashion in both healthy and atretic follicles. There is, at present, no explanation for the large number of prominent, well-developed Call-Exner bodies found in the muskox follicles. Mossman and Duke (1973) attribute no functional significance to these structures.

The early formation of the corpus luteum could not be examined in detail. The only specimens available were from tissues that had been frozen. The macroscopic appearance of the muskox corpus luteum paralleled that in sheep and goats and was similar to Grant's (1936) and Harrison's (1948) description from these species. Of the corpora lutea examined, only one resembled the corpus hemorrhagicum commonly found in cattle though only occasionally found in sheep and goats. A central cavity, when it appears in the corpus luteum of sheep or goats, rarely persists for any

length of time. In cattle, on the other hand, this may persist for the functional life of the corpus luteum. In the muskox specimen the corpus hemorrhagicum was considered to be newly formed. All the other corpora lutea appeared as a compact mass of luteal tissue. The histological sections, when compared with comparable tissue from the domestic animals, presented a similar picture. The muskox corpora lutea appear to have two cell populations, a large luteal cell predominating with smaller cells interspersed.

The assessment of luteal age could not be based on histological observations of cellular degeneration. The use of cellular compaction, reduction in the number and size of nuclei, and distortion of shape are not as reliable an indicator of luteal age as observations of cellular degeneration. However, these criteria appeared acceptable when compared with information on corpora lutea regression in goats and sheep (Cole and Miller, 1935; Grant, 1936; Harrison, 1948).

Because serial sections were not done on the three pairs of ovaries collected during the breeding season, the corpora lutea could not be classified as corpora lutea resulting from an ovulation, accessory corpora lutea or secondary corpora lutea. To distinguish corpora lutea in terms of their origin, one requires more detailed information than was available here.

Follicular populations were not counted in the muskox ovary and no comparison between healthy and atretic

follicles could be made. However on a qualitative level, the number of atretic follicles was considered proportionately high, particularly in the ovary of late pregnancy, a condition similar to that reported in sheep.

The atretic follicles identified in the muskox ovary are comparable to descriptions of atresia in the domestic species. The prominent form of atresia among the vesicular follicles could be designated as obliterative (Dellman and Brown, 1976). There was evidence to suggest cystic atresia was occurring in some of the Graafian follicles but there was no indication that the theca luteinized to any significant extent. Instead it appeared that after thecal hypertrophy the cells gradually atrophied but the possibility of a transient stage of thecal lutenization is acknowledged.

b) Ovarian Morphology and the Reproductive Cycle

The ovaries of the non-pregnant muskoxen collected in March showed little or no ovarian activity. Although follicular growth was evident no follicle exceeded 2mm in diameter and the ovaries from parous and non-parous animals were similar in this respect. None of the cows had levels of estrogen exceeding 0.1 ng/ml or progesterone exceeding 0.5 ng/ml (Appendix II). These hormonal levels, coupled with the appearance of the ovaries, appear to be indicative of the anestrus condition. The testosterone levels for the bulls, collected at the same time from the same herds, were found to range from 0.2-1.2 ng/ml. (Appendix II). These

values; when compared to two values obtained in the early breeding season (13.1 and 14.5 ng/ml), were considered low enough to suggest relative testicular inactivity.

The condition of the muskox ovaries was identical to descriptions given for anestrus sheep and goats. Follicular development up to a limited size, usually under 5 mm, can occur in the absence of hormonal stimulation. This feature is found in both mature and prepuberal ruminants (Bjersing, 1978).

The only exception to the above anestrus condition was found in a lactating, non-pregnant cow (78-26). The right ovary of this cow possessed a structure that appeared to be a regressing corpus luteum which was more characteristic in size and shape of the regressing corpus luteum of the cycle than the corpus luteum of late pregnancy. It is not known whether this corpus luteum remained from an aborted or reabsorbed pregnancy or whether it arose from a late ovulation. Ovulation during anestrus has been reported in sheep (Land, 1978). Wilkinson (1973) cites two cases of muskoxen at Fairbanks, Alaska, that gave birth late in the season, suggesting that the cows had conceived in January. Alendal (1971b) cites a similar case in Norway. In both these instances the authors reported on animals that have been reintroduced to more southerly habitats substantially lush than in the high arctic range and cited these factors as possibly being responsible for the late cycling. However, this late cycling was recorded only because the cow also

became pregnant. The difference between their animals and those of the high arctic may reside as much in the seasonality of the bull as that of the female. Lincoln et. al. (1972) has suggested that sheer physical exhaustion on the part of a stag may set limits on the breeding season of the red deer. It is not known how long female muskoxen that fail to conceive will continue to cycle.

A collection of specimens was conducted in mid-August because of the numerous reports of mating behaviour occurring in mid to late August (Tener, 1965; Gray, 1973; Smith, 1976). The ovaries of three cows taken at this time did not contain any recent corpora lutea or fresh ovulation sites, suggesting that they had not begun to cycle. Levels of progesterone (less than 18 pg/ml) were consistent with the above observations. The two mature cows each had one large follicle per pair of ovaries, measuring 12 mm (78-41) and 17.5 mm (78-44) and these follicles were substantially larger than any others in the ovaries. The final size of the mature follicle is generally related to body size and is relatively constant for a species. While there is no baseline information available on the size of the preovulatory follicle in muskoxen, cattle preovulatory follicles range between 15-20 mm and those of sheep are approximately 10 mm (Dellman and Brown, 1976). It is therefore not unreasonable to expect the size of the pre-ovulatory follicle of the muskox to fall between this range. If this is the case, a follicle of 17.5 mm could be designated as pre-ovulatory.

In sheep, preovulatory enlargement is still not evident as late as 4 hours after the onset of estrus. The follicular volume does not begin increasing until shortly before 36 hours after the onset of estrus. In cattle, the final preovulatory growth phase occurs 3-4 days before ovulation (Greenwald, 1978). Estradiol secretion rate in sheep increases two days before estrus with a peak reached 24 hours before estrus (Greenwald, 1978). In cattle, peripheral levels of estrogen begin to increase three days (peaking four hours) before estrus (Greenwald, 1978). The peripheral levels of estrogen measured in the muskox cows were 45 pg/ml (78-41) and 50 pg/ml (78-44). These levels were close to and in both cases, lower than circulating estrogen levels in the anestrous muskox suggesting that a preovulatory increase in estrogen had not occurred. This contrasts with the morphological evidence of follicle size and appears to indicate that the final preovulatory growth surge in the muskox follicles had not yet begun (assuming that an increase in estrogen is associated with the final preovulatory growth of the muskox follicle). However, it should be stressed that the specific values for hormonal levels quoted here cannot be considered representative of general hormonal levels for this species. Not only is the sample size very small but only one sample was taken (following the animals death). Given the wide daily fluctuations in hormonal levels in domestic species and the complicating variables of stress and post mortum collection the values

found in this study may not provide a true picture of the hormonal status of the individual animals.

Very low systemic concentrations of estrogen (15 pg/ml) will induce sexual receptivity in sheep and goats but only after the hypothalamus has been exposed to progesterone. (Robertson, 1977). Ewes slaughtered just after the onset of their first estrus have corpora lutea in their ovaries, indicating that, though it is their first estrus, it is not their first ovulation. Whether progesterone priming is necessary for estrous behaviour in muskoxen cannot be determined on the existing data. Wilkinson (1973) suggests that most cows in the captive herd at Alaska were impregnated in the second or third cycle. It remains a distinct possibility that a silent ovulation is a prerequisite to estrus in this species. If such is the case, successful breeding could not have been expected before September in the two cows collected in August.

The third cow collected in this season had two medium-sized follicles measuring 8 and 9 mm. There are no steroid levels for this animal but the evidence suggests that the preovulatory growth of an individual follicle had not yet begun. The fact that there was only a single large follicle in the ovaries of each of the previous two cows, coupled with the fact that corpora lutea of pregnancy were also single (discussed later) suggests that muskoxen are monovular.

Of the five animals collected in the late breeding

5

season, two were definitely known to be lactating and their ovaries showed no activity. The ovaries resembled those of the anestrus condition. Because the physical condition, based on qualitative fat assessment, was considered good, lactational anestrus was most probably the cause of their lack of ovarian activity. Lactational anestrus is a well recognized phenomenon in sheep, however the resulting lowered fertility is believed to arise from embryonic death and implantation failure and not from a lack of ovarian activity (Rhind et. al., 1980a).

The remaining three cows collected late in the breeding season, two parous and one non-parous, presented a situation that can only be speculated on. The ovaries of the two mature cows (76-6; 76-8) taken on October 30, 1976, contained two easily recognizable corpora lutea per pair of ovaries and, in 76-8, a recent rupture indicating a fresh ovulation. It could not, however, be established whether or not these animals had conceived. If they were pregnant, the embryos must have been at a pre-attachment stage and broken down to an unrecognizable form by the freezing and thawing. The corpora lutea in the ovaries of these animals were judged qualitatively as being at varying stages of regression suggesting that they were not the same age. This implies that these two cows were still cycling at the end of October, having had at least two infertile cycles prior to collection. Infertile cycles among most wild ungulates studied to date are considered anomalous (Sadleir, 1969; Thomas, 1970).

It is possible that these two cows represent an extreme case of infertile cycling that should not be extrapolated to the majority of the animals. Even if the cows were bred successfully at the end of October, the resulting calves would not be born before the end of June whereas the majority of muskox calves are believed to be born in early May.

The estimated ages of the corpora lutea support the idea that only one follicle ruptures at each estrus though it does not preclude the possibility that some of the luteal structures represented accessory corpora lutea. In the absence of serial sections for these three cows, the latter possibility could not be excluded. However the overall regressed appearance of the small corpora lutea would point to their having a cyclical origin. A further possibility, at least for 76-6; is that the larger more active corpus luteum in a pair of ovaries may have been the corpus luteum of pregnancy, while the fresh ovulation occurred after conception. This condition has been reported in both red deer (Kelly and Challies, 1978) and in elk (Morrison, 1960). Though this is a possibility in muskoxen, it is considered unlikely in the absence of any evidence of a conceptus. The possibility that continued cycling resulted from the absence of a breeding bull cannot be excluded, though it does seem improbable. During the breeding season the number of solitary bulls and small bachelor herds increases and these males are commonly found in the proximity of the harems (Gray, 1973). The splitting and mixing of herds is

high (Gray, 1979) thus the probability of encountering a breeding bull is further increased. A mature apparently breeding bull was collected from the same herd as the two cycling cows but this does not prove that he had been present throughout the entire breeding season, nor that he was fertile.

Clearly these alternative explanations cannot be decided between from the present ovarian morphology. Whichever is correct, it remains unknown whether it is representative of the species or reflects local conditions. Only a more closely conducted study of the ovaries during the breeding season and early pregnancy will answer these questions.

The third cow in this collection (76-9) had one large, apparently active corpus luteum with reduced follicular activity in the rest of the ovary. It is probable that this animal was pregnant. A portion of the right horn ipsilateral to the corpus luteum had been accidentally removed during dissection by the Inuit hunters and they reported that she was pregnant. The condition of her ovaries supports such an interpretation. However there was no evidence in the uterus of a conceptus or indications of early implantation.

The most striking feature found in the ovaries of the eight pregnant animals collected in spring was the highly regressed appearance of the corpus luteum. In seven of the eight pairs of ovaries only one structure resembling a corpus luteum was evident. This, again, lends support for

the suggestion that the species is, in the wild, mon-ovular. Each regressed corpus luteum was found in the ovary adjacent to the pregnant horn, equally on the right and left sides, indicating that asymmetry of ovarian function is not likely and also that blastocyst migration does not commonly occur. Blastocyst migration in single sheep pregnancies is not common, though in the case of twins it does occur (Mossman, 1976).

The right ovary of one pregnant muskox (78-38) contained two corpora lutea at apparently different stages of regression. The larger of the ~~two~~ was histologically identical to the corpora lutea of the other seven animals. The second corpus luteum was recognized in macroscopic section and appeared similar to Grant's (1936) description of the regressing corpus luteum of pregnancy in preparturient sheep. Histologically, though, the compact mass did not appear as regressed as the larger corpus luteum. It may have been an accessory or a secondary corpus luteum. As previously mentioned accessory corpora lutea have been reported to occur in 59.8% of red deer (Kelly and Challies, 1978). Why they are found in some, but not all, pregnant deer (and, possibly muskoxen) is not known.

Though the corpora lutea of sheep are not essential beyond day 50-60 of gestation, they are still macroscopically visible as "apparently" functional until three weeks prior to parturition (Cole and Miller, 1935; Grant, 1936). The final stage of regression sets in immediately post

partum (Grant, 1936). The corpus luteum of late pregnancy in muskoxen was not visible in macroscopic section and, histologically, did not appear at all functional. Regression of the muskox corpus luteum of pregnancy must, therefore, be occurring at a faster rate or at a comparatively earlier stage of pregnancy than happens in sheep. Of the three domestic species, sheep are the only ones that can consistently maintain pregnancy during the last trimester in the absence of a corpus luteum (Moor et. al., 1969). Goats require a functional corpus luteum throughout the entire period of gestation (Linzell and Heap, 1968). Cattle usually require a corpus luteum throughout gestation, though ovariectomy between days 200-240 does not always result in abortion (Hafez, 1968).

Systemic levels of progesterone, measured in two cows, averaged 2.1 ng/ml. So, presumably as in other animals, this progesterone was of feto-placental origin. Linzell and Heap (1968) suggest that, in sheep, placental secretion is five times greater than ovarian secretion in the last half of pregnancy.

Follicular development in the ovaries of the pregnant animals was similar to that in ovaries during anestrus, with no follicle measuring more than 2 mm in diameter. Estrogen levels in the pregnant muskox however, were found to be 42.5 pg/ml (78-27) and 54.5 pg/ml (78-32). These levels of estrogen, relatively high when compared to anestrus muskoxen, must therefore also be presumed to originate

from the placenta. Rising estrogen levels are a well known feature of late pregnancy in all the domestic ruminants.

There were other indications of a major endocrine role for the placenta, at least in the last trimester of pregnancy.

Muskox placental extracts demonstrated the presence of placental lactogen (Appendix II). In pregnant sheep and goats, prolactin levels are low until shortly before parturition. Total lactogenic activity is therefore largely accounted for by placental lactogen (Forsyth and Haydon, 1977). Though levels of placental lactogen among the domestic species show considerable individual variations, there is a general pattern of an increase in the hormone from mid-pregnancy on (Forsyth and Haydon, 1977). The measurements of placental lactogen in the muskox showed a wide range in values. This may have been due, in part, to variable contamination of fetal cotyledon with maternal caruncle as well as to fluctuations in the secretion of the hormone.

The muskox ovaries were not subjected to detailed ovarian analysis involving identification of scar tissue to interpret ovulation, ovulation incidence and past pregnancies. Analysis of this nature has been conducted on black-tailed deer (Golley, 1957; Thomas, 1970) and white-tailed deer (Cheatum and Morton, 1942) but proved unsuccessful when applied to elk (Morrison, 1960). Ovarian analysis relies on the fact that only the corpora lutea of pregnancy

becomes highly pigmented, allowing the resulting albicans to be distinguished from scars of cyclical corpora lutea; the development and regression of luteal structures must follow a predictable pattern and the ovulation rate and fertility must be reasonably constant to lend accuracy to the interpretation of ovarian structures.

In elk, few if any of these criteria could be filled. The regressing corpora lutea of a cycle became pigmented, the size and shape of scars varied greatly, post conception ovulation occurred and there was a possibility that some follicles luteinized (Morrison, 1960).

Studies such as Morrison's in the elk point out the potential danger of extrapolating from one species to another. Ovarian analyses cannot be undertaken on the muskox without a greater understanding of the functional role of luteal development and regression and a better understanding of the ovulation incidence. The highly regressed corpus luteum of pregnancy, the possibility of accessory corpora lutea forming in some but not all individuals, the possibility of repeated cycling during the breeding season, as well as the occurrence of cycling late in the season suggest that the ovarian events in the muskox are not following a predictable pattern upon which assumptions can be based.

5.3 AGE ESTIMATIONS

The ages of muskoxen, determined here by tooth section

of the first incisor, are estimates only. The age range found in the pregnant animals was, however, of interest. The eldest cow was an estimated 15-16 years old at the time of collection; extreme wear on her teeth supported this estimate. The greatest known age of a muskox cow is 23 and muskoxen are believed to live 25 years or more (Tener, 1965). The 16 year old cow in this collection suggests that successful breeding extends late into the animal's life, corroborating Wilkinson's (1973) suggestion that cows may still breed successfully beyond 20 years.

The youngest pregnant animals were 5-6 years of age by tooth section suggesting that they were bred at 52 months (4 1/3 years). It should be mentioned, however, that in specimen (78-40), the fourth molar was just erupting and her first and second permanent molars were still covered by the remains of the deciduous molars, suggesting an age of 3-4 years (Tener, 1965) and a breeding age of 2 1/2 or 3 1/2 years. As mentioned in the introduction breeding at 30 months of age is not uncommon among captive and reintroduced populations though it has not been recorded in the wild. This may be due in part to the difficulty involved in assessing age by horn development and coat condition. It seems reasonable to suggest that under favourable conditions wild cows can also breed at 2 1/2 to 3 1/2 years.

The non-parous animals were aged at three and four years by tooth section although specimen 78-42 a non-parous cow had deciduous caps remaining on her permanent teeth

that exhibited a much higher degree of wear than those of the pregnant cow aged at 5. Tener (1965) points out that rate of tooth wear probably varies with locality, food habits and hardness of the particular plant species. Whether these factors affect tooth eruption is not clear.

5.4 GENERAL DISCUSSION AND SUMMARY

The sample size available for this study was not large enough within any single season to derive firm conclusions on the reproductive process in muskoxen. Because sampling from wild populations is logistically difficult and captive herds are scarce and rarely used for experimental manipulations, it becomes important to find parallels with well-studied species. Morphological similarities allow limited interpretations of function as well as predictions on reproductive performance. However, while this aids our understanding of muskox reproduction it cannot be assumed that the reproductive process in the muskox is identical to that of the domestic species. It is perhaps the differences, more than the similarities, existing between these species that can contribute most to our understanding of ungulate reproduction in general.

A summary of the major findings in this study of muskox reproductive anatomy is as follows:

- 1) The gross morphology of the uterus, its suspending ligaments, the ovaries and the oviduct are very similar to sheep and goats.

2) The cervix is typical of Artiodactyla. Though there is a species and individual variation, the morphology of the cervix more closely resembles the cervix of cattle than of sheep and goats (the penis of the male is similar in gross morphology to that of cattle as well).. Insemination is most probably vaginal with the cervix functioning as a reservoir for spermatozoa as it does in the domestic ungulates.

3) Pigmentation in the uterus appears to be related to parity and seems to be associated with the accumulation of lipofuscins in the endometrial stroma.

4) A prominent muscular band along the antimesometrial surface of the uterus appears to be associated with parity, arising from the formation of vascular elements (possibly lymphatics) during the first pregnancy. The function of this well developed vascular pathway is, as yet, not clear.

5) The placenta (placentomes and the associated arrangement of fetal membranes) is typical of most of the ungulates with the maternal portion of the placentome being more like those of sheep and goats than of cattle. The evidence suggesting the formation of a hemophagus organ in the placentome of the muskox is similar to the condition described in sheep and goats.

The hyperplastic cysts and additional areas of placental attachment were not considered pathological because of the relatively low numbers found in any one individual and their ubiquity. Hyperplastic cysts have been described

occasionally in sheep and additional areas of placentation in some cervids.

6) Pregnancies were evenly distributed between the right and left horns and there was no evidence to suggest asymmetry of ovarian or uterine function.

7) The vasculature of the reproductive tract is very similar to that seen in the domestic species. The theory of a unilateral local effect of the uterus on the adjacent ovary, proposed for cattle, sheep and goats, could, therefore, also apply to the muskox.

8) The information on the ovaries is still incomplete. The histological appearance of ovarian structures is typical of ruminants, suggesting that follicular development and early corpus luteum formation are similar to descriptions of this process in domestic species. However, interpretations of ovarian events are not clear. Muskoxen appear to be seasonally polyestrous and monovular. The size of the pre-ovulatory follicle could not be determined. A follicle of 17.5 mm diameter was not associated with elevated estrogen levels, though it is possible that this follicle was close to ovulation.

During the breeding season two lactating cows showed no obvious morphological evidence for ovarian activity suggesting that lactational anestrus occurs. Three cows exhibited evidence of repeated cycling as late as October for unexplained reasons.

9) Among the 15 cows collected in March, some were

pregnant, some lactating and not pregnant and others immature. One cow had evidence of a regressing corpus luteum suggesting an ovulation in late December or January. The corpora lutea in the pregnant animals were all highly regressed and not visible in gross section. In 7 of the 8 cases there was only one corpus luteum which was always found in the ovary on the side of the pregnancy. In one case there were two corpora lutea, apparently of different ages. One of them may have been an accessory corpus luteum or have originated from a post-conception ovulation. The regressing corpora lutea were all associated with a large quantity of pigments similar to the lipofuscins of the endometrium.

The results listed above point to a number of areas that warrant more study.

The many anatomical similarities between the muskox reproductive tract and that of sheep suggest that the muscular band in the muskox may not be unique but rather an exaggeration of the condition that may exist unnoticed among domestic species. Clarification of the histological components of the antimesometrial border during pregnancy in the muskox as well as fluid sampling from these vessels would aid in an understanding of their function. It would also be of particular interest to inject these vessels in a pregnant tract with dye or latex to determine the extent of the vascular pathway. Parallel studies in sheep and goats may reveal a reduced though similar structure.

Placentation, as well as the associated cysts and extra-placental areas, warrant further investigation and documentation. A study of placentation could involve a more thorough analysis of the hormonal levels in the placenta, particularly as the corpus luteum in late pregnancy is so regressed.

A detailed assessment of ovarian activity is necessary before any conclusions on the breeding pattern of this species can be determined. Such an analysis requires a much larger sample size, particularly during the breeding season and into the first half of gestation. To complete a collection of this nature, it would be essential to recover embryos or blastocysts both to diagnose pregnancy and to document early embryonic development. Without such a documentation phenomena such as delayed implantation cannot be excluded as a reproductive feature of muskoxen.

The suggestion in this study of infertile cycling in the fall specimens warrants a more detailed study to determine the frequency of this phenomenon as well as the cause of the underlying infertility. The specimens collected here may represent an isolated situation or be indicative of a more widespread condition. The infertility may be related to body condition and reproductive status (i.e. lactation) or arise from a behavioural situation whereby a fertile bull was not available at the time of estrus. Either condition would have serious herd-management implications.

Complementary anatomical and hormonal studies of

reproduction in male muskoxen are also required. The observation that rutting behaviour may precede breeding by 1 to 1 1/2 months may be related to the time required for the full development of spermatogenic cycle which is considered a biological constant that varies between species (Ortavant, et. al., 1977). This process is estimated to take 30 days in rams first entering the breeding season.

Intensity of male courtship activity, and its accompanying energy demands, may work as powerful limiting factors to the breeding season.

Age at puberty is generally related to body condition and specific weight. It has been demonstrated that muskoxen in captivity breed earlier than their wild counterparts. Among wild muskoxen, cows are not believed to breed before they are four years old. The ages determined in this study by tooth section do not contradict these assumptions though the pattern of tooth eruption and wear do. The sample size here is too small to resolve whether or not cows breed before they are four years of age.

This study has established a baseline of anatomical information and in so doing has pointed to a number of areas that deserve more rigorous study. It has also demonstrated the similarities existing between the reproductive tracts of muskoxen and sheep, indicating that sheep can be used as a valid model for comparative interpretations. Answers to some of the questions raised in this study

should be easier to obtain now that they are defined and should considerably enhance our understanding of muskox reproductive physiology. Such understanding will, in turn, provide wildlife managers with information for a more sophisticated approach to protecting and harvesting the species and allow a more realistic approach to the logistics involved in the possible agricultural use of the animals. In addition, the comparative aspects of information that can be obtained uniquely from the muskox will contribute one of the most valuable features to be gained from studies of this fascinating species.

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APPENDICES

APPENDIX I. Index of Muskox Specimens

All the specimens collected in conjunction with this study are listed below. The underlined specimen numbers refer to those females that were used in the thesis. Most of the male tracts were incomplete and not included here though they have been retained for future study.

The labelling code documents the year and sequence of collection.

All hunting locations are marked on the map found in text Fig. 3.

Appendix I, Table 1. List of muskox specimens with their sex, date and place of kill as well as the hunter who collected the animal.

Specimen Number	Sex	Date	Place	Hunter
76-1	F	Mar/76	Ellesmere Is. (Sor Fiord)	Killiktee
76-2	M	Mar/76	Ellesmere Is. (Sor Fiord)	Okookoo
*76-3	F	Jun 10/74	Bathurst Is.	Killiktee
*76-4	M	May 15/71	Bathurst Is.	
76-5	M	Mar/76	Ellesmere Is. (Sor Fiord)	
76-6	F	Oct. 25/76	Ellesmere Is. (Sor Fiord)	Imoshee
76-7	M	Oct. 25/76	Ellesmere Is. (Sor Fiord)	Pijamini
76-8	F	Oct. 25/76	Ellesmere Is. (Sor Fiord)	Akpaleakpik
76-9	F	Oct. 25/76	Ellesmere Is. (Sor Fiord)	Akeagok
77-10	M	Mar. 3/77	Ellesmere Is. (Sor Fiord)	Tookilkee
77-11	F	Mar. 3/77	Devon Is. (Cape Hardy)	Jopee
77-12	F	Mar. 3/77	Devon Is. (Cape Sparbo)	Judah
77-13	F	Mar. 3/77	Devon Is. (Cape Sparbo)	Markusie
77-14	F	Feb. 29/77	Devon Is. (Cape Sparbo)	Akeagok
77-15	M	Feb. 29/77	Devon Is. (Cape Sparbo)	Akeagok
77-16	M	Feb. 29/77	Devon Is. (Cape Sparbo)	Issac

Appendix I, Table 1, (cont'd)

77-17	M	Mar. 19/77	Ellesmere Is. (Hooved Is.)	Silasee
77-18	F	Oct. 30/77	Ellesmere Is. (Sor Fiord)	Pijamini
77-19	F	Oct. 30/77	Ellesmere Is. (Sor Fiord)	Looty
77-20	M	Oct. 30/77	Ellesmere Is. (Sor Fiord)	Akeagok
77-21	M	Oct. 30/77	Ellesmere Is. (Sor Fiord)	Imoshee
78-22	M	Mar. 10/78	Devon Is. (Cape Hardy)	Jimmy
78-23	M	Mar. 10/78	Devon Is. (Cape Hardy)	Tookilkee
78-24	F	Mar. 10/78	Devon Is. (Cape Hardy)	Sam Willy
78-25	F	Mar. 10/78	Devon Is. (Cape Hardy)	Elijah
78-26	F	Mar. 10/78	Devon Is. (Cape Hardy)	Jopee
78-27	F	Mar. 10/78	Devon Is. (Cape Hardy)	Paulasee
78-28	F	Mar. 10/78	Devon Is. (Cape Hardy)	Tookilkee
78-29	M	Mar. 15/78	Ellesmere Is. (Muskox fiord)	Akeagok
78-30	M	Mar. 15/78	Ellesmere Is. (Muskox Fiord)	Kavavow
78-31	F	Mar. 20/78	Ellesmere Is. (Mackinson Inlet)	Kiguktak
78-32	F	Mar. 20/78	Ellesmere Is. (Mackinson Inlet)	Pijamini

Appendix I, Table 1 (cont'd)

<u>78-33</u>	F	Mar. 20/78	Ellesmere Is. (Mackinson Inlet)	Simonee
<u>78-34</u>	M	Mar. 20/78	Ellesmere Is. (Mackinson Inlet)	Kiguktak
<u>78-35</u>	M	Mar. 20/78	Ellesmere Is. (Mackinson Inlet)	Simonee
<u>78-36</u>	M	Mar. 20/78	Ellesmere Is. (Mackinson Inlet)	Simonee
<u>78-37</u>	F	Mar. 28/78	Prince of Wales Is.	Idlout
<u>78-38</u>	F	Mar. 28/78	Prince of Wales Is.	S. Idlout
<u>78-39</u>	F	Mar. 28/78	Prince of Wales Is.	P. Manik
<u>78-40</u>	F	Mar. 28/78	Prince of Wales Is.	Sudlovinick
<u>78-41</u>	F	Aug. 12/78	Ellesmere Is. (Bjorne Peninsula)	Pijamini
<u>78-42</u>	F	Aug. 12/78	Ellesmere Is. (Bjorne Peninsula)	Kisudluk
<u>78-43</u>	M	Aug. 12/78	Ellesmere Is. (Bjorne Peninsula)	Kisudluk
<u>78-44</u>	F	Aug. 13/78	Ellesmere Is. (Bjorne Peninsula)	Pijamini
<u>78-45</u>	M	Aug. 13/78	Ellesmere Is. (Bjorne Peninsula)	Kisudluk

* Specimens donated by the National Museum of Natural Science, Ethnology Division

APPENDIX II a Determinations of Steroid Hormones.

The serum collected from both male and female muskoxen was assayed by radioimmunoassay for progesterone, estrogen and testosterone. Progesterone determinations were done at the Animal Diseases Research Institute, Ottawa following the procedures of Abraham et. al. (1971) with modifications outlined by Betteridge et. al. (1977). Serum samples were also sent to the lab of Dr. Raeside, University of Guelph, for determination of progesterone, estrogen or testosterone levels by radioimmunoassay. The results of these assays are listed in Tables 1 and 2.

Progesterone levels did not exceed 0.5 ng/ml except in samples from the two pregnant cows. In these animals (78-27 and 78-32) progesterone was found to be between 1.2 and 3.1 ng/ml.

Estrogen levels were all low even from three cows collected in August. The highest levels were found in the same two pregnant cows mentioned above.

Testosterone was low in all the bulls with the exception of two mature bulls (78-43 and 78-45) collected in August. They had testosterone levels of 13.1 ng/ml and 14.5 ng/ml respectively.

b. Determination of Placental Lactogen.

Tissue samples of fetal cotyledon from 7 pregnant tracts were assayed for placental lactogen by a radioreceptor assay. These determinations were done by Dr. Isabel

Appendix II. Table 1. Progesterone levels in muskox serum.

CONDITION	MUSKOX NUMBER	SEASON	PROGESTERONE (ng/ml, unless otherwise listed)	
			OTTAWA	GUELPH
MATURE COW non-pregnant non-lactating	78 - 25	anestrus	<18 pg	0.35
	78 - 41	proestrus	<18 pg	0.33
	78 - 44	proestrus	<18 pg	0.42
MATURE COWS non-pregnant lactating	78 - 26	anestrus	<18 pg	0.40
	78 - 31	anestrus	<18 pg	0.43
	78 - 33	anestrus	<18 pg	0.48
MATURE COWS pregnant	78 - 27	----	3.09	1.40
	78 - 32	----	2.69	1.17
JUVENILE COWS	78 - 24	anestrus	<18 pg	0.45
	78 - 28	anestrus	<18 pg	0.37
	78 - 42	proestrus	<18 pg	0.45

Appendix II. Table 2. Estrogen and testosterone levels in muskox serum.
CONCENTRATION (ng/ml)

CONDITION	MUSKOX NUMBER	SEASON	ESTROGEN	TESTOSTERONE
MATURE COWS	78 - 25	anestrus	0.080	
non-pregnant	78 - 41	proestrus	0.045	
non-lactating	78 - 44	proestrus	0.050	
MATURE COWS	78 - 26	anestrus	0.060	
non-pregnant	78 - 31	anestrus	0.070	
lactating	78 - 33	anestrus	0.105	
MATURE COWS	78 - 27	----	0.425	
pregnant	78 - 32	----	0.545	
JUVENILE COWS	78 - 24	anestrus	0.080	
	78 - 28	anestrus	0.055	
	78 - 42	proestrus	0.095	
MATURE BULLS	78 - 22	anestrus		0.480
	78 - 23	anestrus		0.220
	78 - 30	anestrus		1.212
	78 - 43	proestrus		13.125
	78 - 45	proestrus		14.500
JUVENILE BULLS	78 - 34	anestrus		0.325

Forsyth at the University of Reading, Shinfield, U.K.

Samples of non-pregnant uterus from three muskoxen were used as controls.

Lactogenic activity is listed in Table 3. Placental lactogen was found in all 7 pregnant samples assayed.

Appendix II, Table 3. Placental lactogen from placental tissue extractions.

SPECIMEN	TISSUE	TOTAL LACTOGENIC ACTIVITY		
		$\mu\text{g/ml}$ extract	$\mu\text{g/mg}$ protein	$\mu\text{g/g}$ wet wt.
78-12	Fetal cotyledon	4.13	0.569	20.8
78-13	Fetal cotyledon	1.44	0.269	7.2
78-27	Fetal cotyledon	2.40	0.314	12.0
78-32	Fetal cotyledon	20.2	2.26	101.4
78-37	Fetal cotyledon	14.1	1.79	70.1
78-39	Fetal cotyledon	8.56	0.881	42.7
78-40	Fetal cotyledon	2.27	0.377	11.5
CONTROLS				
77-19	Uterine horn	0.075	0.008	0.37
78-31	Uterine horn	.01	.001	.05
78-33	Uterine horn	0.020	0.003	0.10