FALKLAND ISLANDS DEPENDENCIES SURVEY

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THE ELEPHANT SEAL

(*Mirounga leonina* Linn.)

III. THE PHYSIOLOGY OF REPRODUCTION

By

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National Institute of Oceanography
and formerly Falkland Islands
Dependencies Scientific Bureau

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CONTENTS

I. INTRODUCTION

THE reproductive organs and the processes of reproduction in the Pinnipedia have until recently received relatively little attention, and then mainly from an anatomical point of view. Harrison, Matthews and Roberts (1952) gave a summary of the more important papers. Despite its economic importance the elephant seal has received even less attention than many of the other seals. There are several general accounts of its life history and reproductive behaviour but there has been no account of the anatomical and histological changes which take place during the life of the individual and during the annual cycle.

In earlier papers in this series, various aspects of the biology of the elephant seal in the Falkland Islands Dependencies have been described. An account has been given of the methods of collection, the amount and quality of material, and fixatives employed (Laws 1953d). The histological material considered in this paper comprises specimens from eighty-eight male and eighty-four female elephant seals. Most of it was Bouin-fixed and was stored for one to three years in 80 per cent alcohol before being subjected to laboratory examination. It was then treated by standard methods, was embedded, cut at 8 μ and stained with Heidenhain's iron haematoxylin, using eosin as a counter-stain. Duplicate slides of about half the female material were stained by Heidenhain's Azan method. The Zenker-fixed, post-osmicated *corpus luteum* material was cut and mounted without additional staining. The laboratory work was carried out by the author at the Department of Zoology, Cambridge, and the slides of histological preparations are deposited with the Falkland Islands Dependencies Scientific Bureau, London.

The elucidation of the sexual cycle of this species has been greatly advanced by the method of age determination which is based on the examination of growth rings in the canine teeth (Laws, 1952 and 1953b) and by the resulting knowledge of the growth rates of the two sexes throughout life (Laws, 1953d). There can be few published studies of the reproductive cycle of wild populations, and certainly none dealing with a phocid, where the ages of individual animals are known with some degree of precision. Reproductive behaviour has been described in a separate paper (Laws, 1956) and frequent reference will be made to it. The reproduction of the elephant seal was the subject of a thesis submitted to the University of Cambridge for the degree of Doctor of Philosophy (Laws, 1953c).

The physiology of reproduction in the elephant seal has many facets and the task of presentation is a difficult one. In order to avoid confusion, the sexes are considered separately and the cylical variations in the activity of the various organs, during ontogeny and annually, are described. An attempt has then been made to correlate the results so obtained, both with the other organs and with overt behaviour.

II. THE MALE REPRODUCTIVE CYCLE

A. ANATOMY OF THE REPRODUCTIVE ORGANS

HARRISON, Matthews and Roberts (1952) have described the gross anatomy of the male reproductive organs in the grey seal (*Halichoerus grypus*) and harbour seal (*Phoca vitulina*); those of the elephant seal do not differ from them markedly, and the relative size and position of the various organs varies little with age.

The testes are abdominal, as in all the *Phocidae*, lying lateral and ventral to the pelvis and covered by muscle. Each is compressed dorso-ventrally and lies in an inguinal pouch, connected with the abdominal cavity by a patent inguinal canal. The size of the testes varies considerably with age, being about 6 cm. by 2 cm. in the new-born and up to 21 cm. by 10 cm. in a breeding bull aged nine years. There is possibly an enlargement of the late foetal testes as has been noted in *Halichoerus* (Amoroso, Harrison, Matthews and Rowlands, 1951).

The epididymis lies along the lateral part of the testis and is continuous at its posterior end with the *vas deferens* which runs forwards through the inguinal canal and crosses ventral to the ureter. The root of the penis is attached by the two crura to the pubic arch and the *corpora cavernosa* extend forwards ventral to the pubic symphysis, enclosed within a fibrous sheath in the blubber superficial to the abdominal muscles. The *os penis* occupies the anterior part of the sheath and is the ossified anterior part of the *corpus cavernosum penis*; the urethra occupies a ventral groove in the bone. The glans is firmly attached to the distal end

and the urethra opens at the tip of a pointed process about 2 to 3 cm. long in the adult. The penis is retracted within a tube which opens in the mid-ventral line about two thirds of the distance from anus to umbilicus. In the newly born the invagination is shallow and the penis is not protrusible, only the tip being free. By the end of the first year, however, the invagination has increased to about 10 cm. in depth and in the adult the erected penis may project over 30 cm. outside the body.

B. Sexual Maturity

The age at which sexual maturity is attained in the male may be defined as the age at which viable sperm are first produced. Histological examination of testis and epididymis material from all age groups, covering the whole year, is therefore the only sure means of establishing it. Changes in the size and form of the genitalia may, however, be expected to occur at sexual maturity.

1. *Gross Age Changes in the Genitalia*

a. *Os Penis or Baculum*

The *bacula* of sixty-five elephant seals representative of all year groups were collected. The *baculum* of M72, aged thirty-one months, shows the basic form, which by deposition and resorption of bone may be considerably altered in older animals (Figure 1). The length is 169 mm. and it is more or less straight. At a distance of 41 mm. from the bulbous proximal end are two prominent ventral processes which are the points of attachment of the ischio-cavernosus muscles; the bone reaches its greatest depth at this point. The ventral surface is grooved forwards from these processes to accommodate the urethra and there is a well-marked dorsal keel.

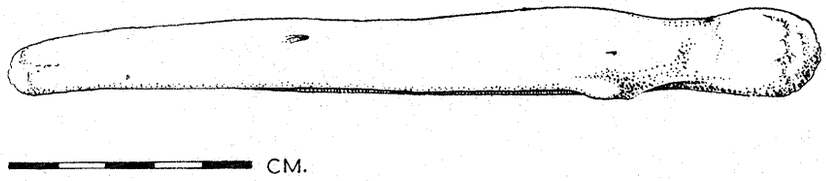

FIGURE 1. *Os penis* of male M72, aged 31 months, viewed from left side.

Individual variations occur. In young animals the *os penis* is usually curved dorsally in the centre, but with age there is a progressive change towards a straighter and more uniform appearance. The ventral processes disappear and the ventral groove becomes shallower, until at six to seven years the ventral surface is flat for four-fifths of its length. At the same time the dorsal keel becomes sharper, especially at the proximal end where it may have a very irregular profile. This is especially marked in M119, aged seven years, with an *os penis* 332 mm. long. Two other variations were noted: first, absence of a dorsal keel and persistence of one ventral process at a variable distance along the bone; and, second, curvature dorsally, to right or left, or a spiral twist in the direction of the long axis. For example, in the *bacula* of M84 aged seven years, and M121 aged nine years, of lengths 310 mm. and 331 mm. respectively, there is no dorsal keel and one of the ventral processes persists. In each case the process is very prominent and is on the right side, but in the former it is only 65 mm. from the proximal end of the bone, whereas in the latter it is situated 183 mm. from the proximal end. The *bacula* of both M84 and M121 have a marked dorsal curvature. The change in the shape of the *baculum* is neither so constant nor so well marked as to be of use as an indication of sexual maturity or age.

Murie (1936) reported a comparatively large proportion of broken *bacula* in his walrus material, but Fay (1953) found only two out of 110 broken, and both were from new-born walrus calves. None of the sixty-five elephant seal *bacula* in the present material showed any sign of breakage but one specimen from Marion Island, made available to me by Mr. R. W. Rand, has a large swelling suggesting a healed fracture. Scheffer (1950) does not mention any fractured specimens among his sample of fur seal *bacula*.

In assessing the growth of the *os penis* during life, only length and volume have been considered. Lengths were measured with calipers, and volumes by displacement of water. Density was determined immediately

after preparation by means of a proportional method, but no balance was available for determining the actual weights nor have they been calculated from volume and density. Owing to the different treatment and histories of the *bacula* after preparation, weights taken up to three years later were not considered sufficiently reliable.

In Figure 2 the average length of the *bacula* of different age groups has been plotted and a curve showing the increase in length drawn. There is a sudden increase in the rate of growth in the fourth to fifth years which suggests that sexual maturity is probably attained at four years of age. This may be correlated with the increased body length in the elephant seal at this age (Laws, 1953, Figure 21). The rate of increase in volume of this bone (Figure 2) shows no such discontinuity and the specific gravity determinations of forty-nine *bacula* do not show any marked changes associated with maturity. Although there are conspicuous individual variations the average density increases with age from 1.15 gms. per cc. at birth to

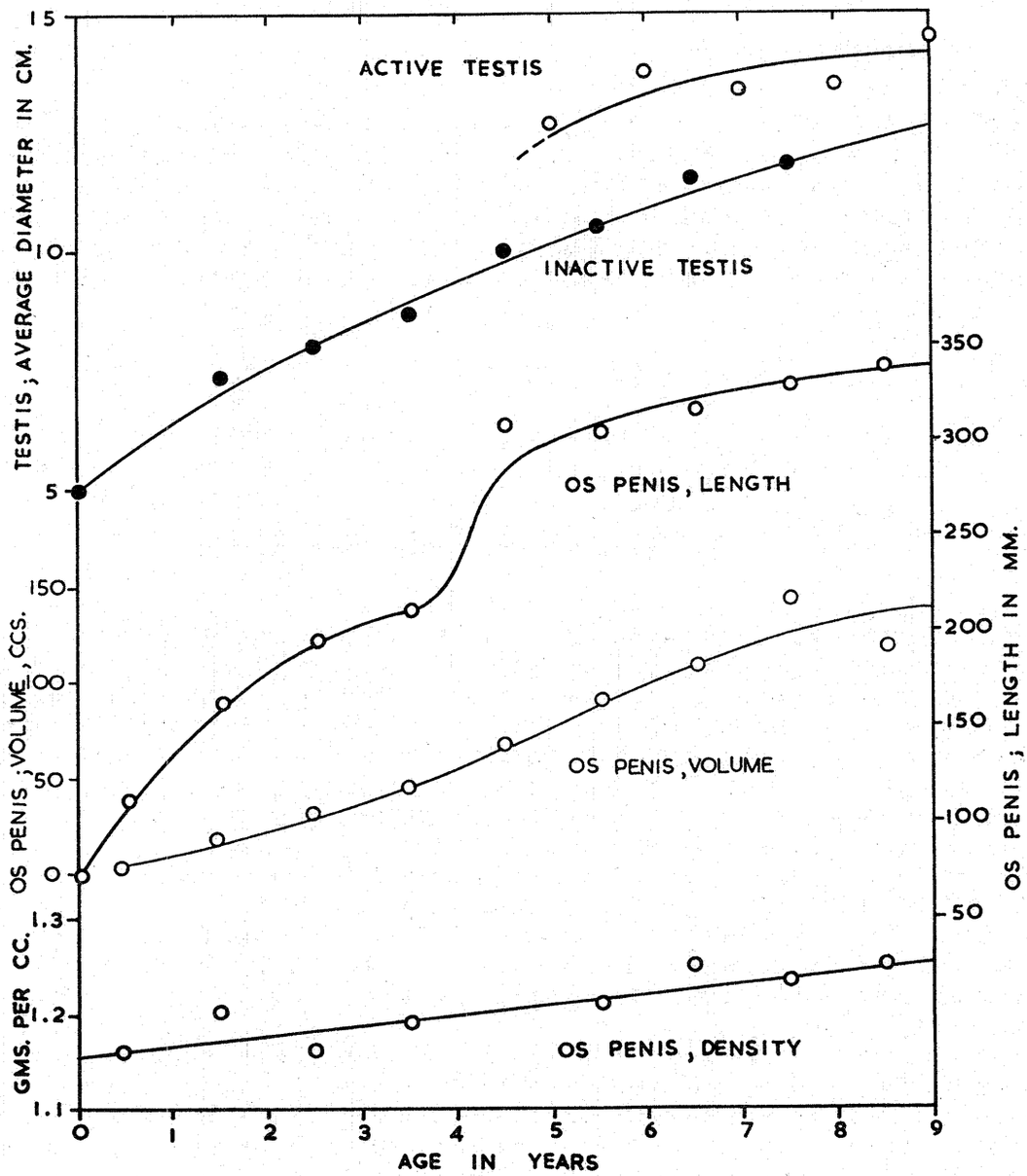

FIGURE 2. Average diameters of the testes of 60 elephant seals, average length of the *os penis* of 65 elephant seals, average *os penis* volume of 51, and average *os penis* density of 49 elephant seals. The curves are drawn through the average values by years.

1.25 gms. per cc. at ten years. The highest specific gravity measured was 1.31 gms. per cc. for the *baculum* of M119, aged seven years.

Consequently, although weights have not been determined, the curves for increase in density and volume of the *baculum* show that the rate of increase in weight will be similar.

Havinga (1933) states that the *baculum* of *Phoca vitulina* grows more rapidly towards the end of the third year, and Fisher (1952) believes there is some evidence that a similar situation exists in the Pacific harbour seal. Scheffer and Slipp (1944), however, found no evidence of this acceleration. Hamilton (1939a, p. 257) also states that rapid enlargement of the *os penis* occurs in the three-year-old leopard seal (*Hydrurga leptonyx*). Rand (1949), Scheffer (1950), and Fay (1954) found a relation between *baculum* size and body length in several pinnipeds but no evidence for accelerated growth prior to sexual maturity. It may well be that it is only in the more precocious phocidae that such rapid growth of the *baculum* is necessary.

b. *Testes*

Measurements of the length and breadth of sixty testes were made. The first series of measurements showed that there was no constant difference in size between the two organs and the later measurements were taken at random from either, depending on accessibility. The mean average diameter, $\frac{1}{2}$ (length + breadth), has been calculated for the different year groups and is set out in Figure 2; the material taken at the time of the breeding season (September to November) has been plotted separately from the non-breeding measurements. This figure shows that the inactive testis increases steadily in size with increasing age from birth to nine years. There is, unfortunately, no data for animals above nine years of age, but animals of nine to eleven years of age are probably in their prime as breeders. After sexual maturity is attained, the average diameter of the testis is about 20 per cent greater in the breeding season than in the non-breeding season, which represents a very considerable increase in volume. Scheffer (1950) was unable to demonstrate a seasonal variation in the size of the testis of the northern fur seal (*Callorhinus ursinus*). From this data it is apparent that sexual maturity, as shown by the enlargement of the testis in the breeding season, occurs before the age of five years, which is in agreement with the conclusion reached by consideration of the lengths of the *bacula*. Unfortunately no measurements are available for the beginning of the fifth year, when sexual maturity is thought to be attained.

2. *Histology*

a. *Testis Development*

The earliest testis material examined is from M73.10, a foetus of length 41 cm., and M78.9, of length 49 cm. (Table I). Their estimated age relative to parturition is about minus four months. Figure 3a and Plate Ia show the appearance of the testis of M78.9. The tubules have an average diameter of 72 μ, are devoid of a lumen and are separated by well-developed interstitial tissue. The basement membrane is very thin (0.7 μ) and there is a peripheral ring of small cells with well-defined oval nuclei about 6 μ in diameter and one or two conspicuous dark-staining nucleoli. These correspond to the "generative cells" described by Allen (1904). Centrally they form a cytoplasmic syncytium, in which lie a few larger cells (c.30 μ diameter) with lightly-staining cytoplasm and a spherical nucleus 12–20 μ in diameter, pale, with a fine chromatin network and large deeply-staining nucleolus; a number of these cells exhibit mitotic figures. They are the primordial germ cells.

The testis of H5 (Figure 3b), aged two weeks, has tubules only 52 μ in diameter; the peripheral cells are smaller and crowded and no primordial germ cells are visible. There are no other very young specimens for comparison, but it would appear that M73.10 and M78.9 show an enlargement of the testis owing to development of the interstitial tissue similar to that which has been noted in the late foetal and neonatal testes of *Halichoerus grypus* (Amoroso, Harrison, Matthews and Rowlands, 1951). The appearance of the testis from a 49 cm. elephant seal foetus, M78.9 (Plate Ia), is very similar to that of the 48 cm. foetus of *Phoca vitulina* described and figured by Harrison, Matthews and Roberts (1952, Plate I, Figure 3). In *Mirounga*, however, this enlargement apparently occurs at an earlier stage of development and by birth has ceased to be noticeable. Several pups examined between birth and five days showed no marked enlargement of the testes.*

* Bonner (*Nature*, **176,** p. 982, 1955) gives testis weights from four elephant seals collected, from full-term to 2–3 weeks of age, but they are inconclusive. The prostate and adrenals, however, decline sharply in weight.

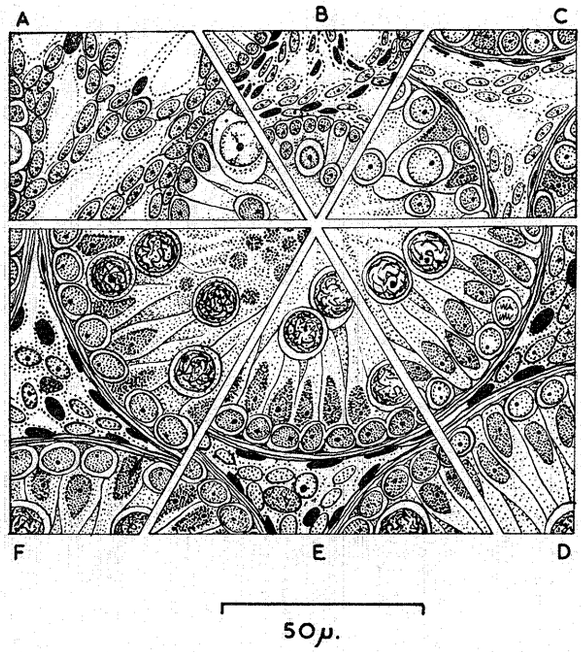

FIGURE 3. The appearance of the immature testis at various ages. A—M78.9, foetus 4 months pre-partum; B—H5, pup aged 2 weeks; C—H306, aged 5½ months; D—H358, aged 14 months; E—H335, aged 25 months; F—H327, aged 37 months.

In H306, aged five and a half months, the individual tubules are closely apposed; the average tubule is 85 μ in diameter, with a basement membrane about 1.25 μ thick. The spermatogonia and Sertoli cells have differentiated. The former are about 7–10 μ in diameter with granular cytoplasm, spherical nuclei 6 μ in diameter and a conspicuous nucleolus. The Sertoli nuclei are darker-stained, often triangular in shape with an indefinite border. Some of the spermatogonia have enlarged and moved to a more central position (Figure 3c). The interstitial tissue is greatly reduced, and the majority of the cells have pale-staining nuclei.

In H358, aged fourteen months (Figure 3d), the testis is beginning to assume a more adult appearance. The spermatogonia are relatively few in number and have a slightly lighter-staining nucleus than the Sertoli cells. They are 6–9 μ in diameter and many show mitotic figures. The Sertoli cells have indistinct boundaries and ovoid nuclei about 5 by 7 μ in diameter. The central syncytium is very homogeneous but there are irregular breaks in some tubules. Scattered in the syncytium are the spermatocytes; these are spherical cells, 15 μ in diameter, with light-staining cytoplasm and a well-defined resting nucleus of 10 μ diameter.

Several specimens illustrate the third year and a definite cycle of activity is apparent. At twenty-five months (H335, Figure 3e) there are several generations of spermatocytes, and many show irregular outline and vacuolisation of the cytoplasm. Of rare occurrence are some large lightly-stained spermatocytes, which have a pale oval nucleus (12 μ) with a fine chromatin network and conspicuous nucleolus. The nuclei of the other spermatogonia are oval, 7 μ long, and the Sertoli nuclei are slightly larger. At twenty-six months (H356) there are more large spermatogonia. In H377, twenty-eight months old, the majority of the tubules have mitotic spermatogonia and the Sertoli cells form a syncytium; some tubules have a few spermatocytes enlarging, moving centrally and degenerating. H311 (thirty months), H134 and M72 (thirty-one months) present a similar appearance.

In the fourth year, spermatid formation occurs for the first time. In H327 (thirty-seven months) many of the spermatocytes are enlarged and spaces in the epithelium containing nuclear fragments indicate their fate. In most tubules there are large numbers of degenerating spermatids (Figure 3f). H330, H331 and H343 (thirty-eight months) and H312 (thirty-nine months) have a majority of tubules similar to Figure 3f, but some resemble H377. In H343 there are a few "giant cells" (see p. 13) arising from the fusion of spermatocytes. The lumen when patent is irregular. In all the fourth year testes the tubules are closely apposed and the interstitial cells are few in number and small in volume, light- and dark-nucleated cells being present in approximately equal numbers.

H332, aged forty-nine months, and H340, aged fifty months, show the typical facies of the post-oestrus adult (p. 12) with degenerating spermatids and spermatozoa.

We may conclude, therefore, that the male elephant seal first produces sperm during the fourth year of life, probably at an age of forty-seven months.

The testes from seven males, nine years of age and older, have been examined histologically (Table II). Five of these were taken in the breeding season between September 8th and November 11th (age 107 to 132 months), and the tubules of the testis exhibit normal spermatogenesis comparable with the conditions in younger mature animals. The other two, taken on March 13th and April 2nd, show the typical anoestrus appearance with "giant cell" formation (see p. 13). It is therefore probable that the male elephant seal is potent up to an age of at least eleven years. Kenyon, Scheffer, and Chapman (1954, p. 49) quote evidence for a similar condition in the northern fur seal (*Callorhinus ursinus*).

Bulls do not usually play an active part in the breeding rookeries until they are six years old, when as subordinate bulls they may intercept cows entering or leaving the harems. At South Georgia, however, younger bulls do play a prominent part in the breeding rookeries, but this situation is probably a result of sealing operations. It has been suggested (Laws, 1953c, 1956) that the virgin females mate for the first time at sea, in which case young sexually mature bulls probably have an important rôle in their impregnation. It has been shown that the bulls of this group begin to haul out on land in the second half of November so that they are in the area at the right time, and the histological appearance of the testes of H332 (November 10th) and H340 (December 20th) also supports this hypothesis. If it is valid, then there is no delay between the attainment of sexual maturity and what may be called "breeding maturity", although some years must pass before sexually mature males are strong enough to maintain a harem.

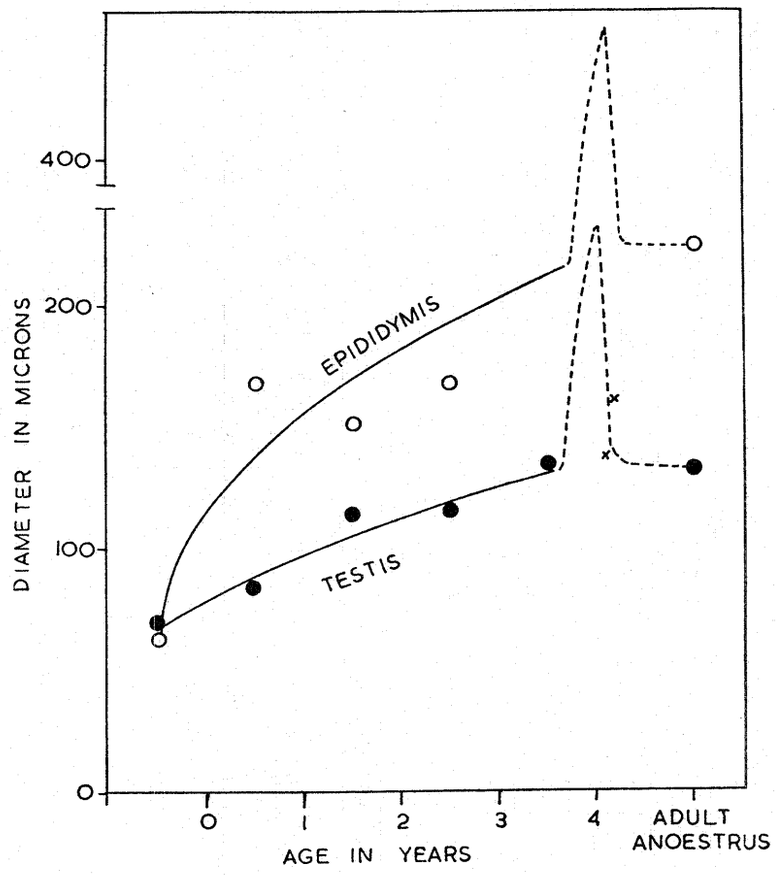

FIGURE 4. Growth of seminiferous tubules and epididymis in immature and newly mature males. The probable increase during the first breeding season is indicated, and records from two newly mature individuals are shown by crosses.

Station No.	Date	Age (months)	Average diameter in μ	
			Testis tubules	Epididymis
M73.10	10.v.51	—4½	70	55
M78.9	28.v.51	—4	72	70
H5		½	52	—
H370	8.i.50	1	60	192
H369	8.i.50	2	84	192
H296	23.ii.49	4	106	168
H306	7.iv.49	5½	85	115
H334	17.xii.49	14	117	142
H358	4.i.50	14	117	—
H287	16.ii.49	16	118	168
H295	23.ii.49	16	98	136
H378	16.ii.50	16	120	—
H309	13.iv.49	18	109	154
H335	17.xii.49	25	117	—
H356	4.i.50	26	110	—
H359	5.i.50	26	126	226
H360	5.i.50	26	110	204
H361	5.i.50	26	122	160
H377	15.ii.50	28	115	155
H311	25.iv.49	30	107	140
H134	25.v.48	31	117	147
M72	4.v.51	31	112	141
H327	6.xii.49	37	137	—
H331	16.xii.49	38	135	—
H330	16.xii.49	38	136	—
H343	20.xii.49	38	135	—
H357	4.i.50	39	131	—
H312	26.iv.49	42	131	—

TABLE I. Measurements of seminiferous tubules and epididymides of immature elephant seals. (Average of 10 tubules.)

Male No.	Date	Age in months	Testis Tubules			Epididymis		
			Diam. in μ	Height of epithelium in μ	Type in order	Diam. in μ	Height of epithelium in μ	Sperm present or absent
H353	2.i.50	74	166	50	E, F	202	50	0
H354	2.i.50	98	186	70	A, B, C	310	62	+
H355	3.i.50	86	186	70	C, D, A; G.C.	320	45	0
H302	12.iii.49	101	132	45	E, G; G.C.	—	—	—
H304	13.iii.49	125	141	52	E, F, G; G.C.	—	—	—
M52	2.iv.51	125	156	50	E, F, D; G.C.	243	53	0
M53	3.iv.51	53	141	45	E, D; G.C.	297	55	0
M57	5.iv.51	53	132	40	E, F.	166	23	0
M59	5.iv.51	89	146	43	E, F; G.C.	280	38	0
M60	5.iv.51	89	134	43	D, E.	316	50	0
M62	6.iv.51	77	134	50	E, G.	214	43	0
M63	6.iv.51	—	166	50	E, D, C.	270	63	0
M64	6.iv.51	65	117	50	E, G.	146	30	0
M77	23.v.51	79	132	38	E, F, D; G.C.	216	43	0
M84	31.viii.51	83	226	65	A, C, B.	330	63	+
M86	7.ix.51	83	234	60	A.	354	65	0
M88	8.ix.51	59	210	58	A, C, B.	363	63	+
M89	8.ix.51	83	224	75	A, C, B.	455	68	+
M90	8.ix.51	107	207	60	A, B, C.	341	45	+
M91	8.ix.51	83	212	63	A, B, C.	455	68	+
M92	8.ix.51	95	212	55	A, B, C.	363	55	+
M93	8.ix.51	107	219	63	A, B, C.	389	65	+
M94	8.ix.51	83	207	58	A, C, B.	340	45	+
M95	8.ix.51	59	218	55	A, C, B.	—	—	+
M97	8.ix.51	83	222	63	A, C, B.	—	—	+
M98	8.ix.51	71	222	65	A, C, B.	—	—	+
M99	8.ix.51	—	214	55	A, C, B.	—	—	+
M100	8.ix.51	59	226	60	A, B, C.	—	—	+
M101	8.ix.51	83	224	58	A, C, B.	—	—	+
M102	8.ix.51	107	212	60	A, C, B.	—	—	+
M104	10.ix.51	95	219	53	A, C, B.	—	—	+
M106	10.ix.51	71	210	63	A, C, B.	—	—	+
M110	10.ix.51	71	234	58	C, A, B.	—	—	+
M117	10.ix.51	83	226	60	A, C, B.	—	—	+
M151	11.xi.51	85	207	63	C, A, B.	424	78	+
M156	12.xi.51	85	207	60	A, B, C.	443	65	+
M160	15.xi.51	121	219	68	A, B, C.	375	63	+
M163	15.xi.51	61	195	60	A, C, B.	380	68	+
H322	16.xi.49	132	219	68	A, C, B.	—	—	—
H325	4.xii.49	61	156	58	E, F; G.C.	270	50	0
H326	6.xii.49	73	156	58	C, A, E.	279	52	0
H337	19.xii.49	86	144	50	C, D, E, F; G.C.	393	50	0
H344	20.xii.49	—	152	45	E, F.	299	75	0
H340	20.xii.49	50	161	43	D, E, F.	310	70	0
H332	20.xii.49	49	137	47	D, E, F.	—	—	—
H350	30.xii.49	62	186	53	E, F, C, A.	250	55	0

TABLE II. Results of examinations of testes and epididymides of 46 elephant seals over 4 years old. Measurements are averages of 10 tubules; for types of seminiferous tubules refer to Figure 5. G.C.=Giant cells.

b. *Epididymis Development*

Although, as is well known, the diameter of the epididymis increases along its length, the effects of this progressive change have been minimised by taking histological samples from the same part of the epididymis. The diameters of the epididymides of seventeen immature animals (average of ten random loops) are set out in Table I.

Two of these are from foetuses. There are only seven tubules in cross-section in M73.10, and they are 55 μ in diameter with an epithelium 16 μ high, whereas M78.9, which is barely two weeks older, has eighteen convolutions in the section. The lining of the latter is simple columnar epithelium, 21 μ high, with pale oval nuclei; the lumen is small and irregular and the external diameter of the tubule is 70 μ.

Aged five and a half months, H306 has many loops of the epididymis in cross-section, 115 μ in diameter with epithelium 29 μ high. The nuclei of the columnar epithelium are arranged in two layers.

Older adolescent males show a tendency towards an annual cycle of activity. Thus, H359, taken in January aged twenty-six months, has an epididymis 226 μ in external diameter, with columnar epithelium 53 μ high. There is a basal layer of polygonal cells with round moderately-stained nuclei, and a superficial layer of ciliated columnar cells with basal darker-stained nuclei; the lumen is empty. In H311, taken in April aged thirty months, the tubule is 140 μ in diameter and the epithelium height, 38 μ. There are several layers of irregularly crowded nuclei and the cilia are less well developed. Lying free in the irregular lumen are epithelial cells, and many are in process of desquamating. M72, taken in May, has more large desquamated cells and debris in the lumen.

C. The Annual Cycle of the Testis in the Mature Male

Several authors have described the histology of seal testes at different times of the year. Bertram (1940) gave evidence showing that in the Weddell Seal there is a period of about a month in which the males are potent and he also noted a similar cycle in the crabeater seal. These observations have recently been confirmed by Harrison, Matthews and Roberts (1952) on a larger sample of three species of Antarctic seals. Kenyon, Scheffer and Chapman (1954) give the result of a recent histological examination of testes from northern fur seals (*C. ursinus*) of known age, and earlier papers by Oliver (1913) and Starks (1928) give descriptions of the process of spermatogenesis in this species.

1. *Phases of Tubule Activity*

In the course of the histological examination of forty-six adult testes, seven distinct phases of tubule activity have been observed: they are illustrated in Figure 5, and described below. In Table II the types of tubules found in individual specimens are set out in the order of their occurrence.

Phase A. Figure 5a has been drawn from sections of the testis of M91. The tubules, 210 μ in diameter with an epithelium 75 μ high, are closely packed. The basement membrane is relatively thick (c. 4 μ), and the spermatogonia are 10–12 μ in diameter, with lightly-staining granular cytoplasm, a darker oval nucleus (7 μ) and one or two conspicuous deeply-stained nucleoli. Occasionally, there are in the tubules spermatogonia undergoing division. In some there are larger spermatogonia with oval nuclei about 20–22 μ in diameter, having a single large nucleolus 5 μ across. These cells bear a great resemblance to the "winter spermatogonia" described below except that their nuclei are darker-staining. The chromatin of the nuclei of some of these spermatogonia condenses as they migrate inwards, having the appearance of a typical spermatocyte. Some then divide but in the majority the volume increases and the cytoplasm assumes a watery appearance. Vacuolisation follows nuclear fragmentation and chromotolysis, until the cell is represented merely by a clear space within the epithelium, surrounding a disorganised mass of cellular debris. By the time that near-ripe spermatozoa are present in the lumen, dissolution is complete.

The Sertoli cells are hypertrophied, having an indistinct cell boundary and an irregular nucleus with a single, eccentric darkly-staining nucleolus. The nucleus, which may be up to 17 μ long, although more commonly 10 μ, is either located next to the basement membrane or lies central to the spermatogonia. To their central ends are attached maturing spermatids, with tails projecting into the lumen. Cell inclusions, some of which are rod-like, are numerous in the cytoplasm. Between the Sertoli cells there are irregular

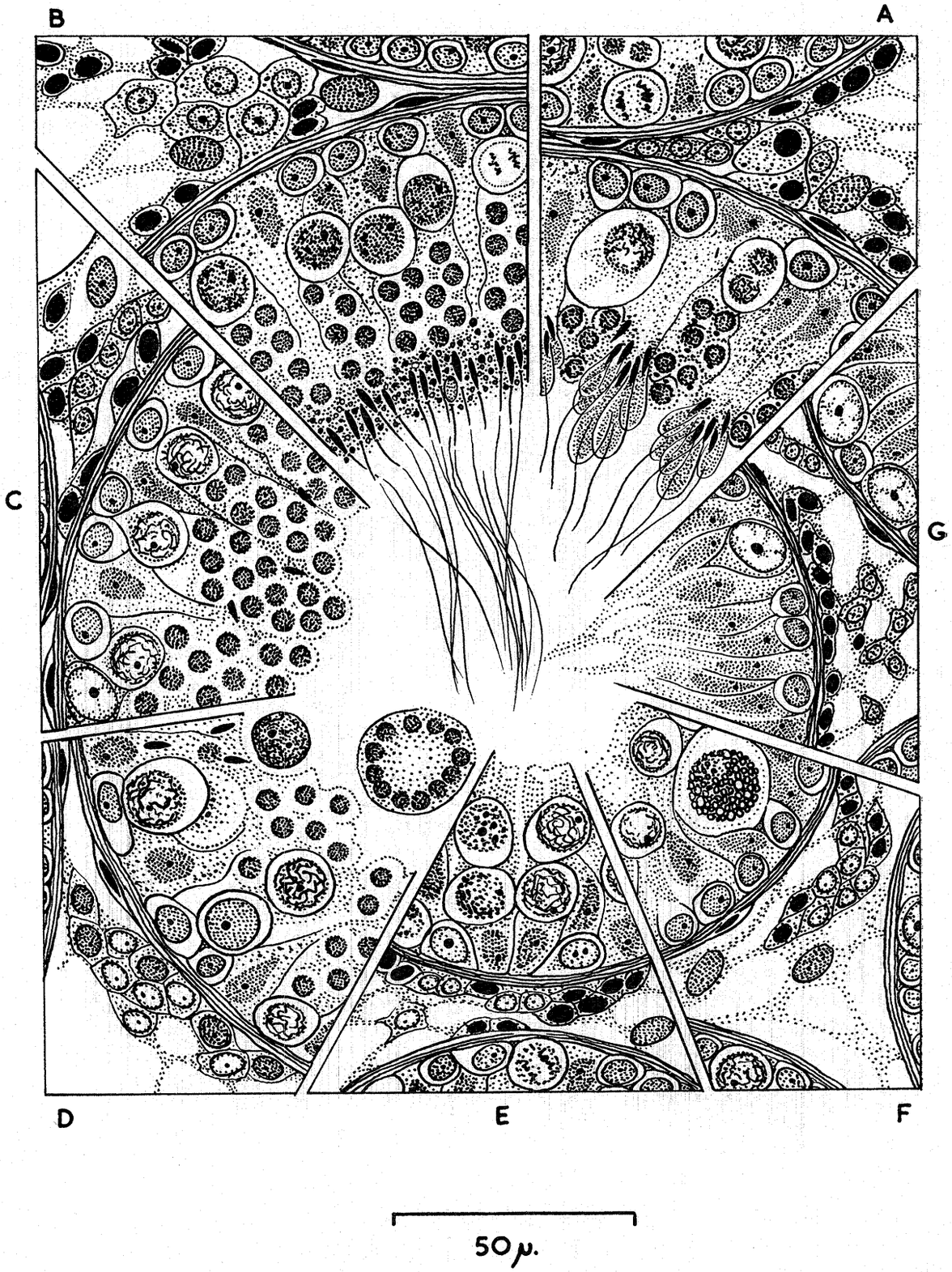

FIGURE 5. The annual cycle of activity in the mature testis. A—M91, aged 83 months; Sept. 8th; B—M160, aged 121 months, Nov. 15th; C—H355, aged 86 months, Jan 3rd; D—H350, aged 62 months, Dec. 30th; E—M62, aged 77 months, April 6th; F—M77, aged 79 months, May 23rd; G—H302, aged 101 months, March 3rd.

columns of spermatids and spermatocytes. Mitotic figures are absent. Individual Leydig cells are large and of irregular and indistinct shape. There are two types (Plate Ib), characterised by light- and dark-staining nuclei.

Phase B. The tubules of M160 average 217 μ in diameter with an epithelium 67 μ high. The spermatogonia are similar to those described above, but there are few spaces in the epithelium marking the location of degenerating cells. "Winter spermatogonia" are uncommon but some spermatogonia have large dark nuclei of granular appearance. Spermatocytes are present in greater numbers than in *Phase A* and the Sertoli cells present a similar appearance except at their distal ends, where the nearly ripe spermatozoa line the lumen, their heads in darkly-staining cellular debris and their tails free in the lumen. Separated by the elongated Sertoli cells are columns of spermatids, each of which is about 12 μ in diameter.

The sperm are typically mammalian (Plate Ic). The over-all length is about 42 μ, of which the head comprises 6 μ and the neck and connecting piece 10 μ. The head is flattened in one plane and is about 4.5 μ broad; when seen sideways (the usual arrangement in a cross-section of the tubule) it is about 1 μ thick. The interstitial tissue is similar to *Phase A* but there is a higher proportion of cells with light-staining nuclei.

Phase C. In H355 the spermatogonia nuclei are darker-staining and about 6 μ in diameter. A more or less continuous layer of spermatocytes is present and the columnar arrangement of the groups of spermatids is lost when they come together by shrinkage of the Sertoli cells. The Sertoli cells do not have obvious cell inclusions and their nuclei are indistinct. Spermatids and fragmenting sperms are found in the lumen of some tubes, and disintegrating sperm in the epithelium. The size of the interstitial cells has decreased.

Phase D. The tubules are not so closely packed together as in *Phase C* and there are large intertubular spaces. There is a decline in the size of the interstitial cells and both types stain less deeply. Most of the spermatids have become detached and pass into the lumen where they are often found as large discrete cells ("giant cells") with many nuclei, which have been formed by fusion of spermatids (Figure 5d, Plate Id). The basement membrane of the tubule is about 3 μ thick. The spermatogonial nuclei are 5–7 μ in diameter with one or two distinct nucleoli, but the cell boundary is indistinct. Frequently the spermatogonia are enlarged with watery cytoplasm and a shrunken nucleus; they move away from the basement membrane, fragment and pass into the lumen as cellular debris. A few large spermatogonia are present, having large pale-staining nuclei and a large dark nucleolus (Plate Ic). They resemble the cells first described by Van Beneden and later called "winter spermatogonia" by Courrier (1927).

It is difficult to distinguish the degenerating spermatogonia from the spermatocytes except by their position in the epithelium; the spermatocyte nuclei tend to have distinct outlines and are very granular. The Sertoli cells are small with indistinct nuclei. Bordering the lumen there may be spermatids and a few degenerating sperms.

Phase E. In M62 the basement membrane is about 2 μ thick and the tubules are loosely packed; the size of the interstitial cells is still diminishing. The number of spermatogonia relative to Sertoli cells is reduced and the irregular Sertoli nuclei, 10–12 μ long, lie either close to the base or central to the spermatogonia. The spermatogonia nuclei, 9 μ in diameter, are lightly-stained, spherical and have a prominent nucleolus; some have a well-defined nuclear boundary and fine chromatin network; others have an indistinct dark-staining mass of chromatin with undifferentiated nucleolus. The former resemble and probably develop into "winter spermatogonia" which are present in small numbers. Spermatocytes and migrating spermatogonia have watery cytoplasm, condensed nuclear material and, usually, a very dark-staining nucleolus. The border of the lumen is a cytoplasmic syncytium of the Sertoli cells.

Phase F. This next stage, illustrated by M 77, is superficially similar. The majority of the spermatogonial nuclei are darker and smaller (5–7 μ) but there is an increase in the number of "winter spermatogonia" with egg-shaped nuclei from 7–12 μ in diameter. All spermatocytes have watery cytoplasm with nuclei in various stages of fragmentation; some of the spermatogonia are similarly affected. Only the Sertoli cells show no signs of degeneration; their nuclei are smaller, darker, with a distinct nucleolus and tend to an ovoid shape. The degeneration of the spermatogonia often results in several Sertoli cells occurring in a regular series,

without interspersed spermatogonia and reminiscent of columnar epithelium. In the majority of tubules the nuclei of the spermatogonia and Sertoli cells present a regular two-layered appearance.

Phase G. In this stage, by elimination of the degenerating elements, a simplified arrangement obtains approximating to the immature tubule; this is the true anoestrus condition. In H302, the majority of the tubules have no lumen and a thin basement membrane. The spermatogonia are small and ill-defined, with nuclei about 7 μ in diameter and one or two distinct, darkly-stained nucleoli; some exhibit mitotic figures. The numbers of spermatogonia have increased, and the diameter of the tubules has diminished so they form a continuous layer at the periphery of the tubule. Among them are "winter spermatogonia" (Plate Ie) which are present in greater numbers at this stage than in any other. The Sertoli cells, radially arranged, form a vacuolated cytoplasmic syncytium which entirely fills the lumen. Their very indistinct nuclei are situated in a layer central to the spermatogonia.

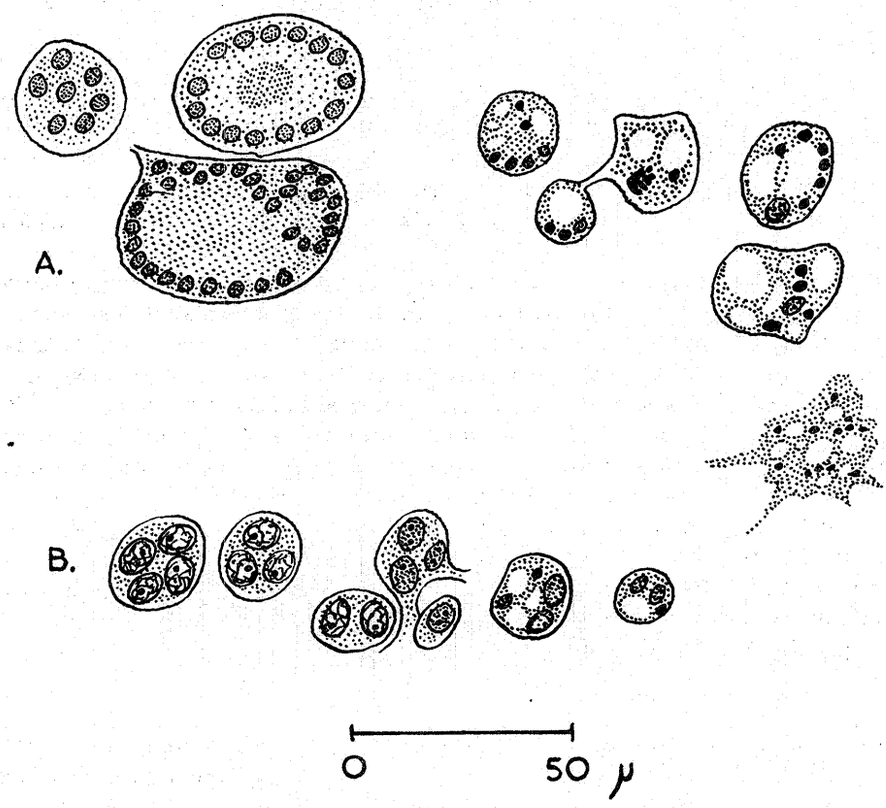

FIGURE 6. Giant cells from seminiferous tubules. A. From spermatids; B. From spermatocytes.

2. *Giant Cell Formation*

The discrete multinucleate masses of protoplasm known as "giant cells" (Moore, 1924) or teratocytes (Courrier, 1927), generally arise through the coalition of contiguous cells of the epithelium. They are a feature of *Phase D* and are present in various stages of degeneration later; they first form in December and may be recognised until April and May. All stages in the formation of giant cells, from the union of two cells to large homogeneous masses containing as many as thirty-two well-stained nuclei, have been observed (Figure 6 and Plate Id). The first cells which form giant cells are the spermatids, which become detached from the epithelium when spermatogenesis ceases, but later spermatocytes also may fuse to form giant cells with, as a rule, two to four large, lightly-stained nuclei. In some specimens, cells similar to those produced

by fusion of spermatocytes are located deep in the epithelium. It is known that in other mammals Sertoli cells occasionally phagocytose degenerating spermatids and spermatozoa (Maximov and Bloom, 1943) and in elephant seal H304 this has been observed. It seems, therefore, that in the elephant seal giant cells may arise in three ways.

By January, the giant cells formed by fusion or phagocytosis of the spermatids are degenerating and degeneration of the spermatocyte giant cells follows. The nuclei condense and extensive vacuoles appear in the cytoplasm. By fragmentation, a mass of unorganised cellular debris is left which may pass into the epididymis but is usually resorbed in the seminiferous tubules (Figure 6).

Giant cell formation is a relatively frequent phenomenon in testis degeneration, whether natural or artificially induced. It has been observed in seasonal degeneration of the testis of various mammals. The figures of the giant cells of *Erinaceus* (Courrier, 1927) and of *Talpa* (Tandler and Gross, 1911) bear a close resemblance to the spermatid type of giant cell in the elephant seal testis. The figure of tubules in the testis of *Rhinolophus* (Courrier, 1927, from an unpublished drawing of Van Beneden), shows giant cells similar to those arising in the elephant seal by fusion of spermatocytes. Moore (1924) describes and figures artificially-induced giant cell formation in testis degeneration resulting from artificial abdominal retention of Guinea pig testes, and Fukui (1923) describes similar cells produced as a result of heat degeneration.

The causative factors in the elephant seal are obscure. The influence of the long period of fasting leading to Vitamin E deficiency, and the high solar radiation temperatures may be important. Hamilton (1939b, p. 143) mentions and figures "teratocytes" in the testis of the southern sea-lion, *Otaria byronia*, occurring in the winter.

3. *Cyclical Variations in the Diameter of the Seminiferous Tubules*

Measurements of the average diameter of testis tubules (average of ten random cross-sections) are listed in Table II and plotted in Figure 7; they show the existence of a cycle of activity. The seminiferous tubules reach an average diameter of over 220 μ during the breeding season (August to November) and then shrink to less than 140 μ during the winter, approximating to the immature tubules (Table I). The enlargement of the entire testis during the breeding season (p. 5) is mainly brought about in this way. Although there is an increase in the size of the individual Leydig cells at this time, the total volume of interstitial tissue remains relatively small; it is compressed into the angular spaces between the seminiferous tubules.

D. The Annual Cycle of the Epididymis in the Adult

There are great variations in the diameter of the adult epididymis during the year (Table II, Figure 7), and sperm are present during the breeding season, but the changes are merely an extension of those observed in adolescent males.

It is now apparent that the cyclical variation in the diameter of the adult epididymis is out of phase with that of the seminiferous tubules, its maximum diameter occurring slightly later, as might be expected. This is demonstrated most strikingly by the earliest specimen M84 (August 31st); it has testes in full breeding condition, the seminiferous tubules being 226 μ in diameter (the third largest measured), while the epididymis diameter of 330 μ is the smallest measured in the breeding season. The average diameter of nine epididymides collected in August and September is 376 μ, while from four specimens collected in November it is 405μ . The corresponding values of the seminiferous tubules are 218 μ and 209 μ. The epididymis probably reaches a diameter of about 450 μ in the breeding season and declines to about 220 μ in anoestrus.

Selected specimens illustrate the varying appearance of the epithelium. M84, from August, has epithelium 63 μ high. There is a basal layer of polygonal cells with lightly-stained nuclei, and a superficial layer of tall ciliated columnar cells, with pale-staining elongated nuclei, containing a conspicuous nucleolus. The lumen contains large numbers of sperm and is lined by long cilia which usually adhere to form a brush border. In M88, from September, the epithelium is of similar height but the nuclei are irregularly arranged and the nuclei of the superficial layer are darker and frequently have two nucleoli (Plate If). They are mainly basal in position, but a few are apical and more darkly-stained. Other specimens taken at this time show compression of the epithelial cells; some are more darkly-staining, and may be thrown into ridges. Although

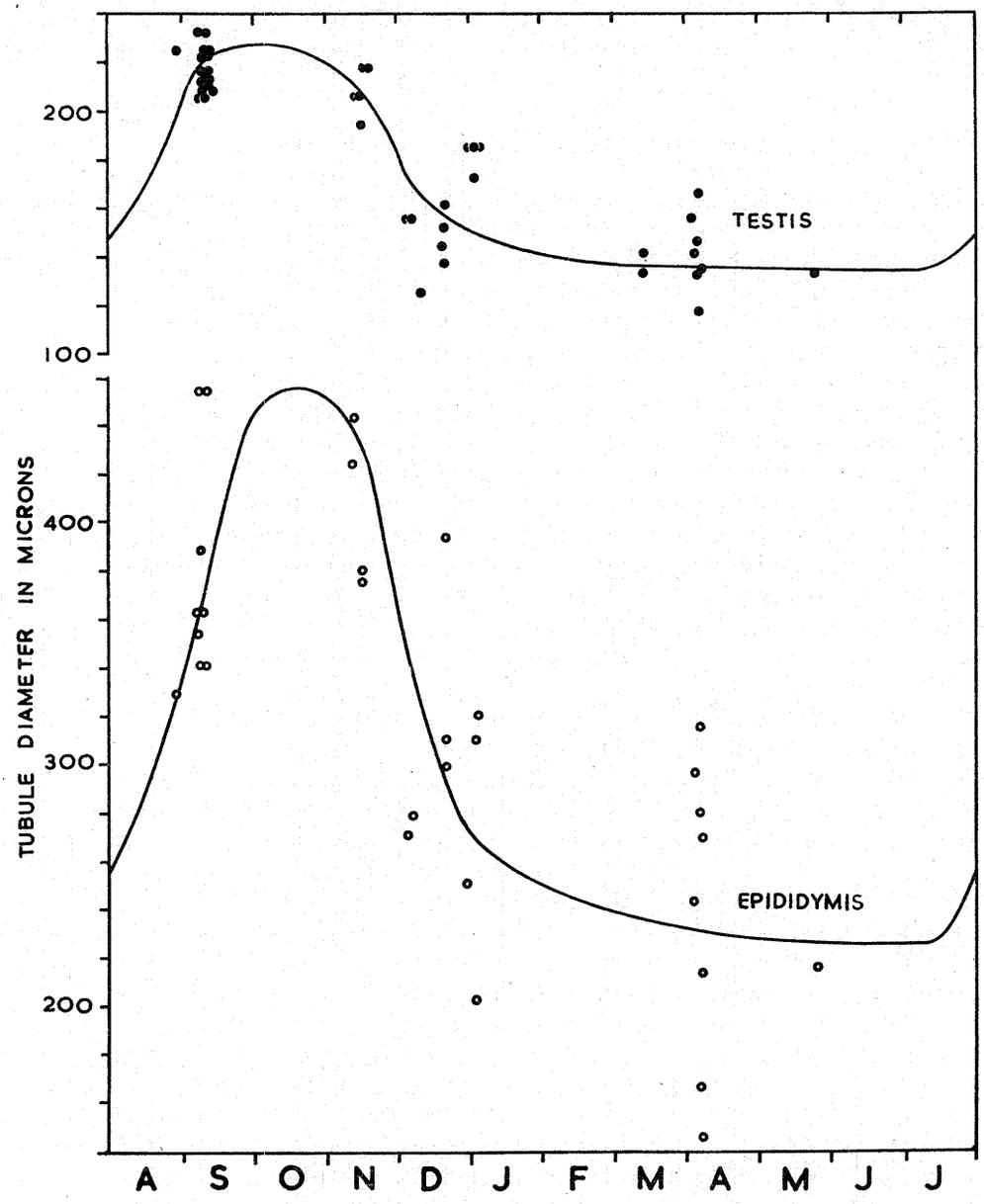

FIGURE 7. Average diameters of the seminiferous tubules and epididymides of mature male elephant seals (over 4 years old) plotted by months.

few mitoses are seen, it is likely, in view of the number of cells containing two nucleoli, that this is a phase of proliferation, bringing about the enlargement of the epididymis lumen in order to accommodate the spermatozoa being produced.

After the breeding season there is much individual variation in the appearance of the epithelium. Generally, however, by March or April the epithelium is low, with several layers of irregularly arranged polygonal cells (M57), although in places it may retain traces of the superficial columnar cells, much shortened (M64, Plate Ig). The cilia are reduced in numbers and in length. By the end of April and in May the epididymides contain cellular debris and have an irregular lumen with many desquamating cells (M62 to M77).

It is suggested that this is the typical anoestrus appearance and that the epididymis is subject to the same hormonal stimuli as the seminiferous tubules and, during rut, to mechanical distension by the products of spermatogenesis.

E. Correlations and Duration of Rut

The elephant seal testis material has been examined and classified according to the order of occurrence of the phases described above, and the results are presented in Table II. It has already been shown (p. 5) that the average diameter of the testis increases by about 20 per cent in the breeding season. A similar hypertrophy has been shown to occur at this time in certain other mammals (Allanson, 1932, 1934; Brambell, 1935), and Harrison, Matthews and Roberts (1952, Table II) give measurements which suggest that the testes of Antarctic seals possibly enlarge during the breeding season.

The duration of the various phases in a continuous cycle of tubule activity is variable. At the height of the breeding season tubule sections in *Phases A* and *C* are predominant, because near-ripe sperm (*Phase B*) are only attached for a short time before they assume a free existence in the lumen and pass into the epididymis, but in September and November (and, by inference, October) *Phases A–C* are present in the seminiferous tubules. Owing to the inaccessibility of the elephant seal during the winter, when it leads a pelagic existence, the earliest material available is from M84 (August 31st). Spermatogenesis is taking place and the epididymis is packed with sperm. The complete absence of sperm in the epididymis of M86, taken on September 7th, and the absence of phases of spermatogenesis later than *A*, indicate that the process is just beginning. As a result of their experiments Asdell and Salisbury (1941) conclude that, in the rabbit, approximately one week is needed for the establishment of each successive layer in the seminiferous tubules and two weeks for the spermatids to grow their tails.

It is therefore reasonable to assume that, on average, spermatogenesis begins no earlier than the middle of August, and is at its height by mid-September.

It is believed that as the sperm travel through the epididymis, some essential maturation process occurs which takes about three weeks (Asdell, 1946, p. 32). On account of this the first successful matings would be expected to take place at the end of the first week in October. From consideration of the date of first births (September 19th), the pairing season would be expected to begin nineteen days later, on October 8th. At South Georgia the first successful (prolonged) matings were observed on this date.

In material taken before mid-November, the testis tubules exhibit *Phases A–C* of spermatogenesis and the epididymis contains sperm. There is no December material available from South Georgia, but at the South Orkneys stages of degeneration have appeared by December 4th and giant cells are present in some numbers. Thus *Phases A–F* are represented by December and January testes, but only in H354 (January 2nd) are there any tubules in *Phase B*. In this animal there was only a small amount of sperm in the epididymis, probably insufficient for fertile mating, and many of the spermatozoa appear to be degenerate. McLean and Rowlands (1942) showed that spermatozoa secrete hyaluronidase which removes the cumulus from tubal ova and permits fertilisation. A high concentration of sperm is necessary for this and consequently animals may cease to be functionally fecund before spermatozoa disappear from the epididymis.

The factors controlling or inhibiting sperm production in mammals are imperfectly known. In mammals which have a continuous production of sperm and no anoestrus period, experimental induction of testis degeneration leads to the sudden cessation of spermatid maturation, and to their loosening and degeneration in the lumen. Thus it is possible for a tubule to pass from *Phase A* to *Phase E* directly, and it seems likely that in the elephant seal spermatogenesis ceases suddenly at the end of November. In December and January *Phase D* is probably the average condition. No material from February is available but in March and April *Phase E* is the commonest, with some tubules in *Phases D*, *F* and *G*. There is a gap of four months between the April material and the September material, apart from M77 (May 23rd), and it seems likely that during this period the majority of the seminiferous tubules regress to *Phase G*.

The paucity of interstitial tissue in the testis of the elephant seal has made it difficult to describe the annual cycle of the Leydig cells in any detail. Sufficient has been noted to suggest that in their cycle they resemble those mammals which show an increased activity of these cells during the rut. In the elephant seal the changes take the form of an enlargement of the individual cells from an area of about 30 sq. μ in anoestrus to 110 sq. μ in the breeding season, and there is no evidence of proliferation of the interstitial tissue. Allanson (1932) has found a similar cycle of the interstitial cells in ferrets, and Hill (1939) reports

hypertrophy of the individual cells in the weasel from 80–90 sq. μ in November, up to 250 sq. μ in the breeding season (March to July). Deanesley (1935) has also noted a similar condition in the stoat, although the cyclic variations are not so marked.

F. Discussion

It has now been established that in the male southern elephant seal sexual maturity is attained at an age of about four years, although the development of the proboscis (a secondary sexual character) is not completed until much later, and the male is not usually sufficiently powerful to acquire and maintain a harem before the age of seven years. The latter part of the period between the attainment of sexual maturity and the maintenance of a harem is spent as a subordinate male on land, individuals hauling out progressively earlier each year. Histological examination of the reproductive organs affords no grounds for supposing that sexual activity declines with age, at least up to eleven years, when the bull elephant seal is probably in his prime, both physically and sexually. However, owing to commercial sealing activities few animals at South Georgia attain this age and in a sample of 100 killed commercially none surpassed it (Laws, 1953a), although it is thought that in a natural state the maximum longevity is about twenty years (Laws, 1953d). It is therefore possible that in an untouched population the potency of the male declines at ages in excess of fourteen or fifteen years, but it is much more likely that animals die before losing their potency. It has been shown that large old bulls can retain dominance by vocalisation and threat postures without exchanging blows with rivals (Laws, 1953c, 1956), and therefore with great economy of effort.

The bull elephant seal hauls out at the end of August at South Georgia, and rather later in higher latitudes, and remains on shore or on the fast ice (in late seasons at the South Orkney Islands) for up to nine weeks. During the whole of this time he goes without food, living on the thick but diminishing layer of blubber. Males in their prime hold and defend from the depredations of other males, harems varying in size from a few cows to over a hundred. In the commercially exploited rookeries studied at South Georgia (mainly in sealing divisions I and II; Laws 1953a) the average size of the harems was forty-five, and in the reserve at Dartmouth Point the ratio was 25:1. It is instructive to compare these figures with similar data for the northern fur seal, *Callorhinus ursinus*, in which the sexual dimorphism is much more pronounced and the harem system more highly developed. Bartholomew and Hoel (1953) found the ratio of breeding females to harem-maintaining males studied, to be 39:1, although owing to the absence of cows at sea the average harem size *at any one time* is sixteen cows. Kenyon, Scheffer and Chapman (1954, p. 51) conclude that the size of the average harem is between forty and fifty cows. The large size of the present-day elephant seal harems is the more remarkable when it is realised that, unlike the fur seal, the cow elephant seal remains on shore throughout the lactation period and departs only when the pup is weaned. She is therefore in the harem for a period averaging about a month before departing, as opposed to nine days before the first departure to sea of the female fur seal (Bartholomew and Hoel, 1953). These authors also found that the duration of the first trip to sea was five days and of subsequent trips eight days, and that two days or less were spent on shore between trips to sea. The average size at any one time of the northern fur seal harems in the Pribilof Islands is thus half that of the elephant seal harens at South Georgia, and it has been suggested (Laws, 1956) that this difference is the result of sealing operations at South Georgia.

In view of the long period of fasting and struggle to which the bull elephant seal is subjected, it might seem from a teleological point of view to be rather wasteful for it to reach full spermatogenesis almost a month before the majority of females come on heat. Presumably this is to be explained as a result of polygamy and the need to acquire a harem in the early stages of rookery organisation. The male hormones, building up aggressive behaviour which is of advantage in sexual fighting, then result in the beginning of spermatogenesis.

The season of male breeding potency ends during the last week in November (Laws 1953c, 1956), probably as a result of a combination of factors of which the eight weeks fast is the most obvious. However, there is some evidence that the younger males or subordinate bulls remain in breeding condition some weeks longer, possibly because they do not fast so rigorously.

Throughout the remaining nine months of the year the bull elephant seals testes remain in an inactive condition, characterised by the small size of the tubules, the absence of stages in spermatogenesis later than spermatocytes, and by the presence of "winter spermatogonia".

Station No.	Date	Ovarian Dimensions in mm.				Ovarian volume in ccs.		Ovary with active corpus luteum
		Right	Average	Left	Average	R.	L.	
M9	17.iii.51	21 ×	—	33 × 16	24.5	—	—	L
M11	19.iii.51	30 × 19	24.5	21 × 10	15.5	—	—	R
M12	19.iii.51	29 × 6	17.5	31 × 6	18.5	—	—	O
M14	19.iii.51	31 × 8	19.5	27 × 10	18.5	—	—	O
M16	19.iii.51	42 × 29	35.5	28 × 12	20.0	—	—	R
M17	21.iii.51	26 × 14	20.0	37 × 20	28.5	—	—	L
M18	21.iii.51	32 × 14	23.0	36 × 18	27.0	—	—	L
M19	29.iii.51	33 × 12	22.5	34 × 15	24.5	4	4	O
M32	10.iv.51	38 × 20	29.0	29 × 14	21.5	12	8	R
M66	24.iv.51	27 × 12	19.5	30 × 12	21.0	3	2	O
M67	25.iv.51	33 × 19	26.0	32 × 13	22.5	10	4	O
M68	28.iv.51	31 × 23	27.0	41 × 22	31.5	7	13	L
M69	1.v.51	32 × 17	24.5	30 × 17	23.5	6	7	O
M70	1.v.51	33 × 18	25.5	36 × 15	25.5	8	8	L
M73	10.v.51	31 × 10	20.5	47 × 22	34.5	4	12	L
M74	12.v.51	34 × 20	27.0	30 × 15	22.5	6	5	O
M75	16.v.51	36 × 11	23.5	23 × 12	17.5	6	6	R
M76	16.v.51	37 × 13	25.0	47 × 19	33.0	10	22	L
M78	28.v.51	36 × 10	23.0	35 × 27	31.0	6	—	L
M79	28.v.51	36 × 13	24.5	33 × 12	22.5	6	6	O
M80	10.viii.51	28 × 9	18.5	27 × 17	22.0	5	5	O
M81	10.viii.51	24 × 12	18.0	33 × 11	22.0	6	5	O
M83	21.viii.51	42 × 17	29.5	43 × 9	26.0	20	10	R
M123	29.ix.51	31 × 13	22.0	30 × 7	18.5	—	—	R
M124	30.ix.51	38 × 13	25.5	—	—	—	—	R
M126	2.x.51	35 × 11	23.0	32 × 16	24.0	9	7	R
M128	4.x.51	43 × 8	25.5	38 × 7	22.5	—	—	R
M133	5.x.51	31 × 13	22.0	30 × 7	18.5	—	—	R
M134	6.x.51	34 × 11	22.5	32 × 13	22.5	—	—	L
M138	9.x.51	36 × 8	22.0	31 × 19	25.0	—	—	R
M139	9.x.51	25 × 11	18.0	—	—	—	—	R
M143	12.x.51	30 × 13	21.5	29 × 15	22.0	—	—	R
M144	12.x.51	35 × 11	23.0	—	—	—	—	R
M146	12.x.51	33 × 15	24.0	32 × 14	23.0	—	—	R

TABLE III. Dimensions of the ovaries of thirty-four elephant seals. Volumes measured by displacement of water in graduated cylinder. (O=no *corpus luteum*.)

III. THE FEMALE REPRODUCTIVE CYCLE

A. GENERAL

1. *Anatomy of the Reproductive Organs*

ALTHOUGH Harrison, Matthews and Roberts (1952) have described in detail the gross anatomy of the genitalia of several phocids, they did not examine any elephant seal material and it is convenient to give a brief account here. Some of the changes associated with age have also been determined since the age of all specimens is known.

Figure 8 is derived from a dissection of the reproductive organs of a two-day-old female. It illustrates the condition of the genitalia of the virgin female, which differ only slightly from the organs of the adult, non-pregnant animal.

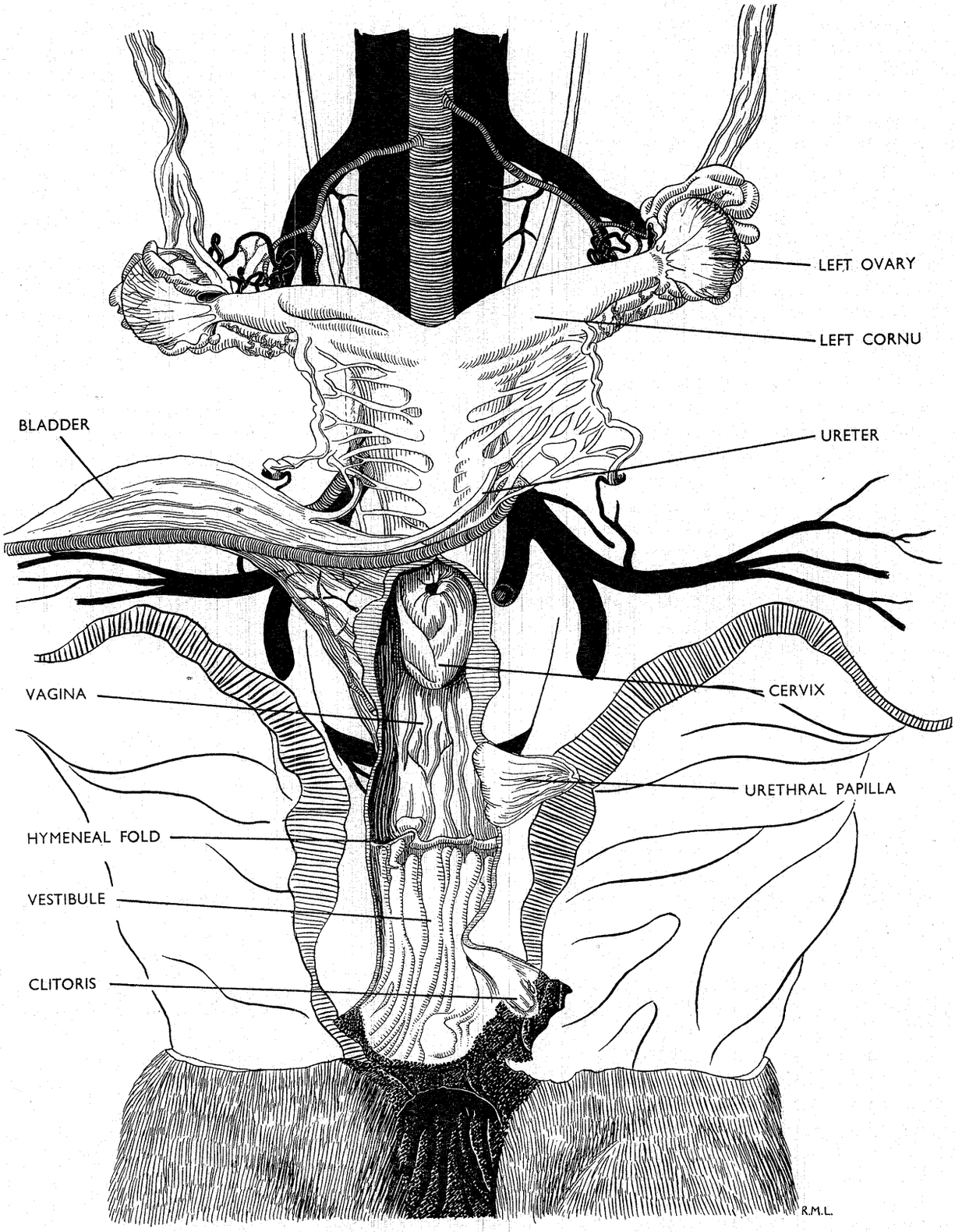

FIGURE 8. Dissection of the reproductive organs of a two-day-old female elephant seal.

The ovaries lie close to the dorso-lateral wall of the abdomen. They are greyish-pink in colour and present either a smooth or a wrinkled appearance according to the stage in the sexual cycle. The smooth surface may be pitted with a few luteal stigmata. The size of the ovaries remains more or less unchanged with age, but the volume varies greatly during pregnancy (Table III and Figure 10). The average diameter of ovaries with *corpora lutea* of pregnancy is 28.2 mm. and their volume 12.7 ccs.; the average diameter of ovaries without *corpora lutea* of pregnancy is 21.7 mm. and their volume 6 ccs. The ovary is attached by a strong round ligament to the broad ligament near the lateral end of the uterine cornu, and a thinner suspensory ligament runs antero-dorsally, almost to the diaphragm. The ovary is enclosed within a thin-walled bursa which opens dorso-medially into the peritoneal cavity (the opening invariably being about 1 cm. in diameter) with a fimbriated border which was never observed to occlude the hole, as Hamilton (1939b) reports for *Otaria byronia* at ovulation.

In the adult, there are often one or more vesicles (*appendices vesiculosae*), reaching a size of up to 1 cm. in diameter; these usually arise from the fimbriated border, but occasionally do so from the bursa itself. The fallopian tube opens from the *bursa ovarii* and is thrown into several convolutions traversing the border of the ovary to effect a junction with the uterine cornu on the dorsal side. The lumen of the tube is discrete where it enters the cornu in a low papilla. In M12 (five months old) the tube was 14.2 cm. long when straightened, and in M144 (three years old) it was 18 cm. in length.

The uterus is bicornuate but the septa is incomplete, the lumen of the two horns joining to form a short common uterus, and the cervix projects about 3 cm., with the external *os uterus* opening ventrally into the vagina. The vagina extends from the cervix to the vestibule where it terminates in a conspicuous hymeneal fold which, in the adult, is 1 cm. broad with projections up to 2 cm., marking the terminations of the four main ridges into which the mucus membrane of the vagina is thrown. In the two-day-old female figured, the hymen is perforated by a single opening.

The bladder lies ventrally to the vagina and the large urethral papilla opens into the vestibule just below the hymeneal fold. The mucosa of the vestibule has shallow longitudinal folds and shows a marked line of transition to the dark pigmented ectoderm. The clitoris, which varies considerably in size according to age and sexual condition, is located ventrally. It occupies a shallow groove lined with unpigmented epithelium projecting beyond the general frontier between pigmented and unpigmented epithelium.

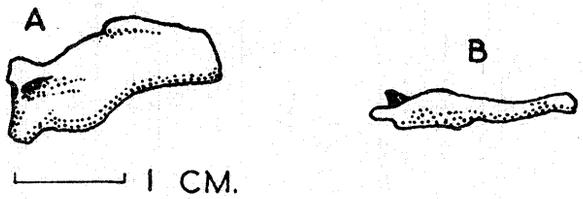

FIGURE 9. Os clitoridis of female M148, aged 84 months. A. Dorsal view; B. Viewed from left side. Anterior end is to the left.

A homologue of the *os penis* was found in the largest female killed (M148, length 138 in., age eighty-four months). The bone was 19 mm. long, irregular and flattened dorso-ventrally (Figure 9). In some other females a cartilage was found in the same position. Clitoris bones from *Callorhinus ursinus* and *Phoca vitulina* have been described by Scheffer (1949), from *Zalophus californianus* by Sierts (1950), and from the walrus (*Odobenus rosmarus divergens*) by Fay (1953). Mansfield (in press) has recently reported the common occurrence of an *os clitoridis* in the Weddell seal (*Leptonychotes weddelli*).

Changes in the proportions of the sexual organs occur with age and reproductive activity. They are indicated graphically in Figure 10. As mentioned above, the size of the ovaries changes little with age, but increases greatly in the ovary controlling pregnancy. The uterine cornua show an increase in length from about 4 in. to 7.5 in. in the first two years of life; they then average 7.5 in. but with wide variations, owing mainly to distension during pregnancy. The length of the common uterus which increases from about 2 in. at birth to 3.5 in. on the attainment of sexual maturity, likewise shows considerable variations during pregnancy. The vagina increases in length at a uniform rate throughout life, from about 4 in. at birth to 11 in. or

more when fifteen years old. The length of the vestibule, in contrast, remains at about 5 in., and possibly decreases slightly with age.

One old cow (M13) exhibits regression of the genitalia which are no larger than those of an immature female five months old.

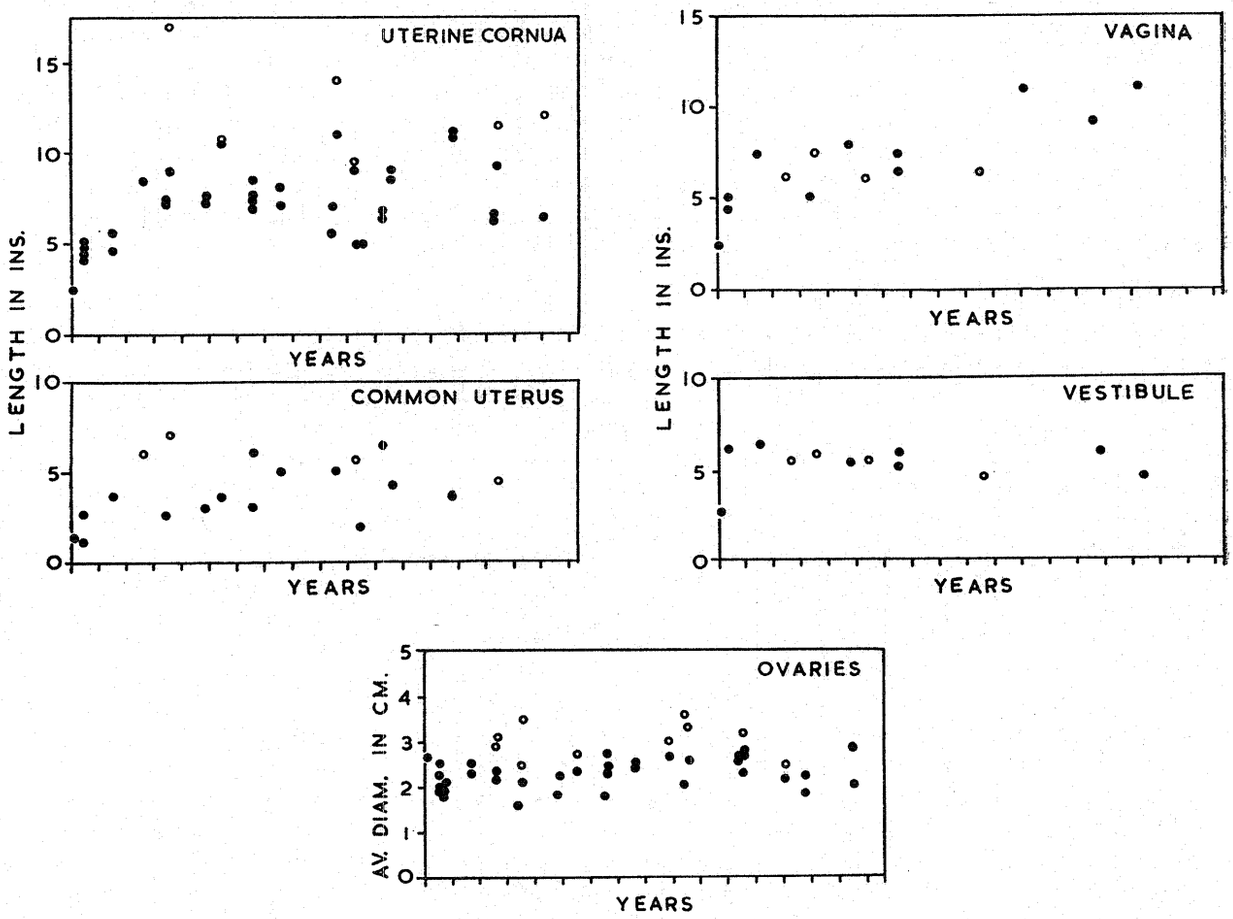

FIGURE 10. Age variations in the size of the female reproductive organs. Individual measurements are plotted against age, and specimens associated with a foetus are drawn as white circles.

2. *Sexual Maturity*

By examination of the ovaries it has been established that the female normally becomes pregnant for the first time in the third year (nineteen specimens). One female (M130) is known to have produced a pup at two years of age, which means that she was impregnated when only one year old, and two are thought to have pupped for the first time at four years of age, but with few exceptions sexual maturity is attained in the female at an age of about two years. It has been established (Laws, 1953c, 1956) that very few second-year cows haul out on land, and it would appear that most of this class remain at sea from an age of about seven months until they come ashore to moult at twenty-six to twenty-seven months, mating for the first time when twenty-four months old.

3. *Bilateral Alternation in Function of the Reproductive Organs*

There appears to be a definite tendency for the right ovary to ovulate first, for in fourteen out of nineteen pregnant cows in their first pregnancy the *corpus luteum* was in the right ovary. Examination of the ovaries

of twenty-six marked females, kept under observation and accurately dated in the ovarian cycle (Figure 13h. and Table V), show that it is invariably the follicles in the ovary which was without a *corpus luteum* during the recent pregnancy, that enlarge and ovulate after parturition. In other words, there is an alternation in the function of the ovaries from year to year. As no cases of migration of the embryo to the opposite cornu were observed, it follows that the uterine horns also alternate in function. The old *corpus luteum*, properly *corpus albicans*, persists for over a year after the termination of the pregnancy in which it was functional (p. 37). It has been possible to expand the data on the bilateral activity of the ovaries by taking the *corpora albicantia* into account. The ages being known from tooth rings, the proportion of *corpora lutea* in right and left ovaries in a particular age group has been inferred from the location of *corpora albicantia* in the following age group as well as from records of the *corpora lutea*. The distribution of *corpora lutea* (directly observed and inferred from *corpora albicantia*) between the right and left ovaries of different age groups is set out in Table IV. It illustrates the alternation of the ovaries controlling pregnancy during the first four years of sexual maturity and confirms that the right ovary usually ovulates first. Afterwards, individual variations and "missed pregnancies" obscure the alternating pattern.

4. "*Missed Pregnancies*"

Taking the presence of a typical *corpus luteum* as a criterion of pregnancy, the number of non-pregnant mature female elephant seals in the material, under twelve years of age, is eight and they are spread over a number of years. Six of these either failed to conceive or to implant, and the other two lost the foetus after implantation. While realising that such a small number is inadequate for supporting any definite conclusions it is yet instructive to compare the cyclical function of the ovaries with the number of non-pregnant seals. Assuming sexual maturity to be attained at the end of the second year, there is only one non-pregnant seal out of thirty-two in the first four years of sexual maturity. In the seventh and eighth years, which would correspond to the fifth and sixth pregnancy if none were missed, there are four missed or interrupted pregnancies and one interrupted pregnancy out of thirteen animals between seventy-two and ninety-six months old. One female in the eleventh year of age had a necrotic foetus in the uterus and, dismissing M13 in which the ovaries are senile, the next "missed pregnancies" occur in the twelfth year when there are two out of twelve in this group. It is suggested that, subject to individual variations, the ovarian function alternates regularly until the fifth or sixth pregnancy, when "missed pregnancies" first become frequent, owing to the cow pupping too late in the season to ensure impregnation or failure of the blastocyst to implant. Necrotic embryos are recorded from the presumed fifth and eleventh pregnancies.

There is some doubt as to whether the proportion of "missed pregnancies" in the sample corresponds to their frequency in the population. Clearly, the production of a large, rapidly growing foetus means that proportionately more time must be spent feeding by the pregnant cows, whereas the non-pregnant cows are not subject to these demands and may possibly remain ashore longer. If this be so, "missed pregnancies" will be over-represented in the sample. On the other hand, there may be other factors influencing cows of the two classes, for it has been shown (Laws, 1956) that the two-year-old females spend most of their time at sea and probably mate aquatically at the same time as the older cows which have missed a pregnancy. Also, it is possible that a proportion of the females assumed to be pregnant with a free blastocyst, may in fact be non-pregnant.

5. *Average Number of Pregnancies*

Elsewhere (Laws, 1953d), it has been stated that the average expectation of life of the female elephant seal after the first pregnancy is of the order of seven years. If each cow misses on average one pregnancy, she would therefore bear seven pups during her lifetime. If this is correct then approximately one-eighth, or 12.5 per cent of the mature cows, will fail to bear pups each year.* From the significant material collected, six out of forty-three cows were certainly non-pregnant, a proportion of 13.9 per cent which, allowing for the smallness and possible bias of the sample collected, seems to be in agreement with the theoretical figure.

Only one senile female elephant seal has been collected (M13, aged 125 months); it shows marked regression of all genitalia which are no larger than in a typical yearling. The histological appearance of the reproductive tract is also indicative of senility. However, as it is the only senile individual in the material, it is reasonable to assume that most cows continue to produce pups until they die.

* Probably rather less, owing to the operation of mortality.

Year of age	No. of "missed pregnancies"	Number of ovaries with:						% of C.L. to each ovary	
		C.L.				Corpora albicantia			
		Observed		Inferred					
		R.	L.	R.	L.	R.	L.	R.	L.
3rd	0	14	5	0	1	0	0	70	30
4th	0	2	4	0	2	0	1	25	75
5th	1	2	0	3	0	0	2	100	0
6th	0	1	3	1	1	3	0	34	66
7th	1+1*	4	1	0	2	1	1	57	43
8th	2	2	0	0	2	0	2	50	50
9th	0	3	0	3	2	0	2	75	25
10th	0	2	3	1	1	3	2	43	57
11th	1*	1	1	4	5	1	1	45	55
12th	2	5	5	0	0	4	5	50	50
Total	8	36	22						

TABLE IV. Frequency distribution by age groups of: "missed pregnancies", number of ovaries (right or left) with *corpora lutea* observed (and inferred from *corpora albicantia* of following year). The percentage of the total *corpora lutea* on either side in each age group is indicated.
* Aborted or necrotic foetus.

6. *The Annual Cycle*

Harrison, Matthews and Roberts (1952) have described the gross anatomy of the young female reproductive organs in several other species of seal. For the most part their account could apply equally well to the elephant seal material which has been examined.

There appears to be little or no late foetal or neonatal activity of the reproductive organs, such as has been described in *Halichoerus*, but no special investigation was made. The foetus of M83 (killed on August 21st, 1951) length 86 cm., is the largest female foetus examined and the ovaries were not noticeably enlarged, nor is any special development of the insterstitial cells apparent. The 125 cm. foetus of M126, killed just after haul-out, and therefore about eight days pre-partum, also showed no sign of marked enlargement of the reproductive organs. Likewise, field dissections of suckling elephant seal pups showed no obvious neonatal enlargement. It has been shown above (p. 5) that the testes of the male elephant seal pups 40–50 cm. in length show great development of the interstitial tissue, and it is likely that if similar activity occurs in the ovary then it is at a similar early stage in development and is unrepresented in the present material.*

There is strong circumstantial evidence which suggests that the virgin female elephant seals are impregnated for the first time at sea, probably early in the breeding season, by the younger males. Owing to their inaccessibility during this period, it is not possible to describe the early part of the first pregnancy. The account which follows is, therefore, essentially an account of the annual reproductive cycle of the mature cow which has already undergone one or more successful pregnancies. It differs considerably from that of the primiparous female, because it is complicated by the need for recovery from the previous pregnancy, parturition and suckling. The alternating function of the two sides of the reproductive tract is consequently most important.

a. *Chronology of Events in the Female*

The reproductive behaviour of the female elephant seal has been described (Laws, 1956) but it will be convenient to give a brief résumé before dealing with the physiology of the female cycle.

* However, three specimens reported by Bonner (*Nature*, **176**, p. 982, 1955) show a decline in weight for one ovary from 6 gm. at full-term to 3 gm. at 29 days.

After a gestation period of under twelve months, the parous females haul out on land (or fast ice) and give birth to their single pup about five to eight days later. They then suckle the pup for a period averaging twenty-three days before departing to sea. During the whole of this time they do not feed, but use up the reserves of fat laid down during the winter, while the pup grows from one hundred pounds in weight to over four hundred pounds. The cows experience a post-partum heat, towards the end of lactation, which begins from thirteen to twenty-four days after parturition (averaging eighteen days) and probably lasts for several days. In the next section it will be shown that the embryo does not immediately develop further than the blastocyst stage, but remains free in the lumen of the uterus until after the summer moult some four months later, when it implants and develops in the normal way. This phenomenon of delayed implantation is common to most of the pinniped species which have been studied.

It has been shown that both sexes are on land only for a limited part of the year, and, as it is not possible to collect material except on land (unlike the northern fur seal which is occasionally hunted pelagically; Wilke, 1951), coverage of certain parts of the cycle, in particular the post-lactation period, is incomplete. Adequate reasons have already been given for treating the South Georgia and South Orkney Islands material together (see Laws, 1956, Figure 8, for comparison of breeding seasons).

It is generally stated that pinnipeds are monoestrus. Oestrus follows soon after parturition in most species and pupping is confined to a short, well-defined period. As a result of the seal population concentrating from the open ocean to the pupping localities, both sexes are present in great numbers within a relatively small area. Consequently, females coming on heat rarely escape impregnation while the males are in rut, and pregnancy supervenes. The male elephant seal has a definite anoestrum extending over several months (see above), but the female probably has a polyoestrus cycle throughout the year if for any reason she fails to become pregnant or loses the embryo. Thus, M69 had a 10.3 mm. follicle in the left ovary on May 1st and had ovulated recently, but the only other females with follicles of a similar size were more than eleven days post-partum and about to enter oestrus. Four other non-pregnant females had possibly ovulated outside the breeding season. As already mentioned, 13.9 per cent of the specimens collected were non-pregnant, so that in 80–90 per cent of the mature female population each year the polyoestrus cycle is suppressed and a monoestrus condition is the rule. Hamilton (1939b) has suggested that the southern sea-lion (*Otaria byronia*) is polyoestrus and that both sexes may be sexually active throughout the year, although the majority of females become pregnant shortly after pupping.

b. *Delayed Implantation of the Blastocyst*

In most mammals the ovum is fertilised in the fallopian tube, undergoes cleavage and within a few days enters the uterus and implants in the uterine mucosa. In the second season at Signy Island (1949), however, it became apparent that in the elephant seal there was a delay of several months between mating and implantation of the blastocyst (Laws, 1949, 1953, 1953d).

Owing to the practical difficulties of field work in the Antarctic, the free-blastocyst period is represented by only one specimen in which the blastocyst was observed. The assumption has been made in this paper, that females are pregnant and in the free vesicle stage if an apparently normal *corpus luteum* is associated with the absence of a visible embryo on examination of the uterus. The histological appearance of the material in the series is sufficiently consistent to justify this assumption, although there may be some abortions during this period (see Rand, 1952). It is possible, however, that degenerative changes would not

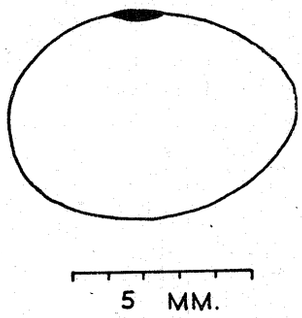

FIGURE 11. Unimplanted blastocyst from right uterine cornu of female H379.

appear until after the normal time of implantation. In females which had necrotic embryos, the *corpus luteum* was much smaller than usual and showed extensive and quite distinctive fatty degeneration of the luteal cells.

Although a careful field examination of the uterine cornua was invariably made, no free ova or small blastocysts were recovered. The earliest embryo collected was an egg-shaped, transparent blastocyst, 8 mm. in longest diameter, which was taken undamaged from the right uterine horn of H379 on February 18th, 1950. The blastocyst filled the lumen and had a pear-shaped embryonic shield 1 mm. long (Figure 11). There were no signs of an attachment site, and the nidus which Harrison, Matthews and Roberts (1952) have described and figured for a 1 mm. blastocyst of *Lobodon carcinophagus* is probably a fixation artefact. Sections of this 8 mm. blastocyst show a thick, protective *zona pellucida* and migrating trophoblast cells. Attachment sites were found in eight cows killed at Signy Island in late February and early March, and four larger embryos (1–5 mm.) attaching to the uterine mucosa, with reddish zone of attachment about 2–3 cm. across, were collected at South Georgia on March 19th and March 21st (M11, M15, M16, M17). Mansfield examined a female (H1040) at Signy Island on February 23rd with a similar swelling in the uterus about the size of a small hen's egg. Three small embryos (M6, M9, M18), under 4 cm. c.r., which were collected at South Georgia on March 17th and 21st must have attached several weeks earlier, probably at the end of February (see Figure 12). This material suggests that attachment of the blastocyst occurs, on average, at the beginning of March although there is considerable individual variation.

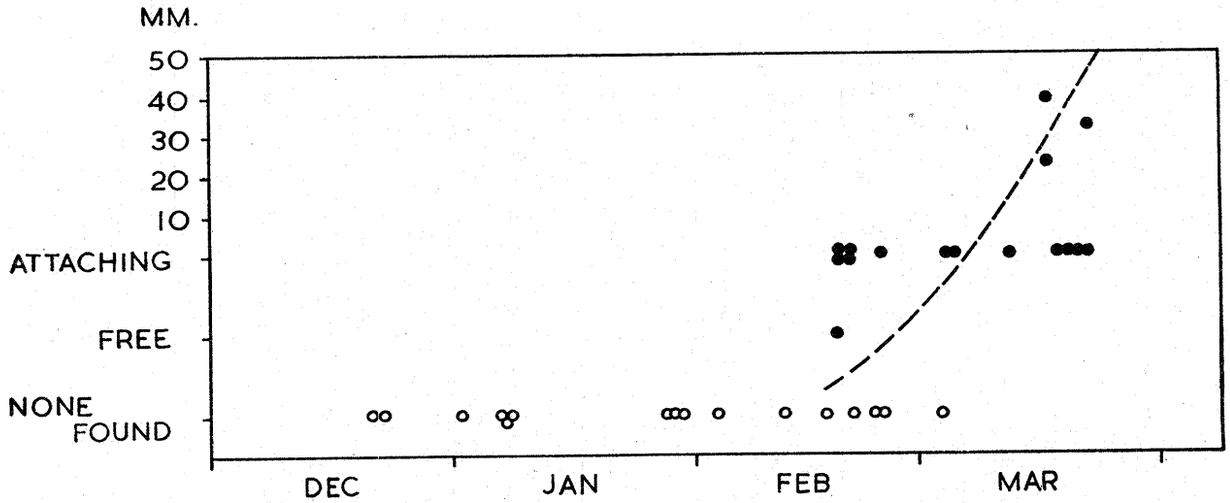

FIGURE 12. Records of small embryos, attaching blastocysts, free and presumed free blastocysts, to show time of implantation.

Gibbney (1953) at Heard Island was able to confirm the existence of free blastocysts. He found no embryos in females examined in the field during December 1952, and January and early February 1953, though he figures a 0.3 mm. blastocyst in the sectioned uterus of a female seal killed in mid-December, and suggested that it was probably attached. In view of the 8 mm. free blastocyst described above, this seems unlikely. Five females collected in late February and the first days of March at Heard Island had small swellings in the uterus. One of these was sectioned and a 1.5 mm. embryo found.

Since the average date at which the cows are impregnated and pregnancy begins is about November 8th at South Georgia, it follows that attachment of the blastocyst is delayed for about four months and development is suspended or reduced during this period. The 0.3 mm. blastocyst suggests that the free blastocysts are present in the uterus during this period. At some time between the beginning of February and mid-March it swells to fill the lumen of the uterine cornu, loses the *zona pellucida*, and attaches.

Hamlett (1935) and Hansson (1947) have reviewed the occurrence of delayed implantation in many different mammals. In the pinnipedia it is probably of common occurrence but of varying length. Of the *Otariidae* it is known in the northern fur seal (*C. ursinus*) (Enders, Pearson and Pearson, 1946; Pearson and Enders, 1951) and the Cape fur seal (*A. Pusillus*) (Rand, 1952). From a re-examination of Hamilton's (1934, 1939b) published data in the light of present knowledge, it appears that there is a period of delayed implantation in *Otaria byronia* of about three months.*

* See Hamilton (1939b), p.154.

When the foetal lengths in Hamilton's (1939b) Table X are plotted against the dates, a foetal growth curve is obtained which suggests that implantation occurs, on average, at the end of April. As regards the breeding season, Hamilton (1934, p. 299) says "It cannot be definitely stated when the breeding season begins or ends; it is at its height in the first half of January, but some pups are born in December and pairing goes on until near the end of January. The break up of the harems is gradual and its effects are visible early in February. . . . The season may be taken as being approximately December to February. . . ." From this it is reasonable to conclude that, on average, impregnation occurs in mid-January and implantation at the end of April. The period of delay in implantation will then be about three months. It appears that delayed implantation does not occur in the walrus (Collins, 1940, Fay, 1952).

In the *Phocidae*, delayed implantation is known to occur in the harp seal (*P. groenlandica*), the hooded seal (*C. cristatus*) (Bertram, 1940), the harbour seal (*P. vitulina*) (Fisher, 1954), the bearded seal (*E. barbatus*) (Chapsky and Kovolev, 1938), the crabeater seal (*L. carcinophagus*) (Harrison, Matthews and Roberts, 1952), and probably occurs in the Weddell seal (*L. weddelli*) and grey seal (*H. grypus*), but not in the leopard seal (*H. leptonyx*).

A discussion of the probable causative factors and the mechanism controlling the period of delay is presented later (p. 58).

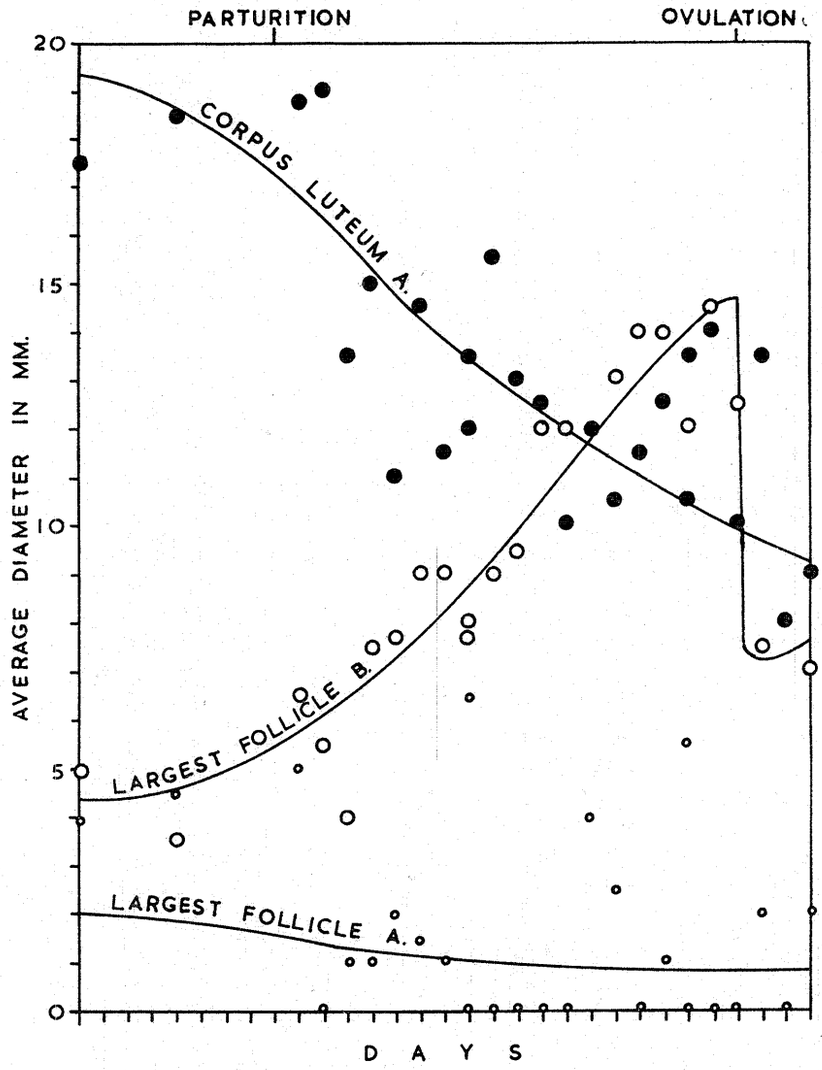

FIGURE 13. The oestrus cycle in the ovaries of 26 marked female elephant seals of known age relative to parturition. Average diameters of the regressing *corpus luteum* (*Corpus luteum A*), the largest follicle in the same ovary (A) and in the other ovary (B), are set out against the known age in days relative to parturition.

c. *Growth of the Embryo after Implantation*

Owing to the absence of pregnant cow elephant seals during the winter months, the number of embryos collected is small. Excluding those near-term foetuses which were examined, only ten embryos and foetuses are available. Details of the embryonic material are set out in Table X and illustrated in Figure 14 in which a curve showing the approximate rate of growth in length is shown. Of the eight foetuses over 10 cm. long, the two which had probably implanted latest are M76 (aged nine years) and M68 (aged eleven years).

The placenta is of zonary type and the width of the smallest measured was 4 cm. and its thickness 8 mm. It was associated with a 32 mm. embryo. At full term the placenta may be more than 25 cm. in width and 3.8 cm. thick.

The female elephant seal usually gives birth to a single pup weighing about 100 pounds and measuring about 50 in. from nose to tail; twins are rare. The sex ratio at birth is 54.9 per cent male, 45.1 per cent female (Laws, 1956).

B. The Ovarian Cycle

1. *Introduction*

Hamilton (1939b) has described the gross structure, and cyclical and age changes of the ovaries of the Falkland sea-lion (*O. byronia*). He concludes that the *corpora lutea* disappear fairly rapidly after parturition. In another otariid, the northern fur seal (*C. ursinus*), Enders, Pearson and Pearson (1946) and Pearson and Enders (1951) have described the gross anatomy of the ovaries and show that the *corpus luteum* disappears about nine months after ovulation has taken place in the opposite ovary. Follicular growth in the ovary with the *corpus luteum* is greatly suppressed from the middle of pregnancy until several months after parturition the following year. Fay (1952) has examined a number of ovaries of the Pacific walrus (*O. rosmarus divergens*) and observes that the *corpus luteum* is visible, in external observation of the ovary, for perhaps a month after birth, and for an undetermined period in sections. He believes that in this species ovulation does not occur annually. In *Erignathus barbatus*, pregnancies may be in alternate years (Sleptsov, 1943) but in all other seals, so far as is known, the rhythm is annual.

Bertram (1940) describes the gross structure of the ovaries and the annual cycle of the Weddell seal (*Leptonychotes weddelli*). He concludes that the ovaries alternate in function and that the *corpus luteum* persists for a long time, perhaps for the life of the animal. He suggests that since there is one ovulation per year, the number of old *corpora* may be used in estimating the age of the female. The material for the crabeater seal (*Lobodon carcinophagus*) is too small for valid conclusions. Recent work by Mansfield (in press), who has attempted to correlate the numbers of *corpora albicantia* with tooth rings, suggests that the *corpora albicantia* do not persist indefinitely. Hamilton (1939a) discusses the ovarian cycle of the leopard seal (*H. leptonyx*) and concludes that in this species the presence of several *corpora albicantia* suggests that there are several ovulations each breeding season. The conclusions of these authors are mainly derived from macroscopic examination of the ovaries.

Subsurface crypts, oogenesis and the *corpus luteum* in the ovaries of several species, are described in a series of papers (Matthews and Harrison, 1949; Harrison, 1950; Harrison and Matthews, 1950).

Harrison, Matthews and Roberts (1952) give a detailed account of the structure of the ovaries in several pinniped species, and an account of the secretory cycle of the *corpus luteum*. Mansfield (in press) has described the gross and microscopic appearance of the ovaries of the Weddell seal (*L. weddelli*). His material comprised a number of marked females in the South Orkneys, the majority of which are accurately dated relative to parturition.

In the present study of the southern elephant seal, the material comprises eighty-three pairs of ovaries collected by the author. The ages of these seals are known from the growth zones in the teeth and twenty-six of these pairs of ovaries are from marked seals accurately dated relative to parturition. In a preliminary examination, the volumes of a number of ovaries were determined by displacement of water in a graduated cylinder and their measurements taken. Then, before embedding and sectioning for microscopical examination, they were sliced parallel to the long axis into sections approximately 2 mm. thick, in order to examine their gross structure. Drawings of all the sections were then made and the average diameter, $\frac{1}{2}$ (length + breadth), of the *corpus luteum*, *corpus albicans*, and largest follicle were recorded, small calipers being used. The calipers were then set at 3 mm. and at 6 mm. and follicles were classified according to the length of

Station No.	Age post-partum in days	Actual age in months	Ovary with recently active corpus luteum	Ovary with recent Corpus Luteum					Other Ovary				
				Follicles				Size of corpus luteum	Follicles				Size of corpus luteum
				No. atretic	No. 3–6 mm.	No. over 6 mm.	Size of largest		No. atretic	No. 3–6 mm.	No. over 6 mm.	Size of largest	
M126	— 8	36	R	7	1	0	4.0	17.5	2	7	0	5.0	—
M133	— 4	36	R	6	3	0	4.5	18.5	19	2	0	3.5	—
M124	+ 1	36	R	0	2	0	5.0	18.7	5	8	1	6.5	—
M123	+ 2	36	L	0	0	0	—	19.0	—	14	0	5.5	—
M128	+ 3	96	R	—	0	0	1.0	13.5	3	3	0	4.0	6.0
M134	+ 4	48	L	0	0	0	1.0	15.0	12	1	2	7.5	—
M129	+ 5	36	R	—	0	0	2.0	11.0	0	13	2	7.7	—
M132	+ 6	36	R	0	0	0	1.5	14.5	8	10	5	9.0	—
M125	+ 7	72	L	0	0	0	1.0	11.5	0	8	3	9.0	2.5
M130	+ 8	24	L	5	2	2	6.5	13.5	11	5	1	8.0	—
M148	+ 8	84	L	0	0	0	—	12.0	12	6	4	7.7	3.0
M127	+ 9	144	L	1	0	0	—	15.5	3	3	2	9.0	—
M135	+10	36	R	1	0	0	—	13.0	9	3	2	9.5	—
H320	+11	205	R	4	0	0	—	12.5	29	2	1	12.0	4.0
M141	+12	36	R	0	0	0	—	10.0	5	2	3	12.0	—
M137	+13	36	R	0	1	0	4.0	12.0	—	0	2	—	—
M140	+14	108	R	3	0	0	2.5	10.5	15	7	3	13.0	—
M142	+15	84	R	0	0	0	—	11.5	19	2	3	14.0	—
M136	+16	36	L	5	0	0	1.0	12.5	19	0	3	14.0	—
M143	+17	36	R	0	0	0	—	13.5	18	1	3	—	—
M147	+17	36	R	0	2	0	5.5	10.5	0	1	2	12.0	—
M138	+18	36	R	11	0	0	—	14.0	10	2	3	14.5	—
M139	+19	72	R	0	0	0	—	10.0	5	1	1	12.5	—
M146	+20	36	L	7	0	0	2.0	13.5	30	0	1	—	7.5*
M145	+21	84	R	0	0	0	—	8.0	11	0	—	—	—
M144	+22	48	R	12	0	0	2.0	9.0	6	2	1	6.0	7.0*

TABLE V. Follicle counts and measurements and *corpus luteum* measurements from 26 pairs of ovaries from marked female elephant seals of known age relative to parturition. (*=developing *corpus luteum*.)

Station No.	Date	Age months	Ovary with active corpus luteum	Ovary Controlling Pregnancy					Other Ovary				
				Follicles				Size of corpus luteum	Follicles				Size of corpus luteum
				No. atretic	No. 3–6 mm.	No. over 6 mm.	Size of largest		No. atretic	No. 3–6 mm.	No. over 6 mm.	Size of largest	
H341	20.xii.49	26	R	19	10	7	7.0	19.0	23	6	5	7.5	—
H346	21.xii.49	38	L	14	13	2	6.0	15.5	25	11	2	5.5	—
H352	1.i.50	111	L	10	6	3	6.0	18.5	18	8	5	5.0	14.0
H362	6.i.50	27	L	14	8	0	4.5	18.0	24	11	0	6.0	—
H363	6.i.50	123	L	7	9	4	6.0	15.5	0	0	0	—	6.0
H368	7.i.50	183	L	18	3	3	5.0	20.0	6	6	2	6.0	4.0
H285	27.i.49	75	R	13	14	3	5.5	17.0	3	7	0	5.0	—
H372	27.i.50	123		8	7	3	7.5	13.5	2	4	1	6.0	7.5
H373	28.i.50	135	R	14	10	2	8.5	15.0	0	0	0	—	7.0
H374	3.ii.50	172	R	15	12	3	7.5	19.0	2	0	0	2.5	7.5
H375	11.ii.50	64	L	19	8	0	4.5	17.0	3	0	0	—	5.0
H288	16.ii.49	52	R	11	8	4	6.5	18.0	6	7	2	—	4.5
H289	19.ii.49	136	L	22	17	0	4.0	18.0	16	15	5	—	6.0
H290	19.ii.49	136	L	13	10	5	7.0	21.5	9	5	2	7.0	6.0
H291	19.ii.49	112	L	6	14	2	8.5	20.5	0	0	0	—	7.0
H292	19.ii.49	76	R	18	4	3	5.5	16.0	1	1	3	7.0	5.5
H293	19.ii.49	88	R	23	18	1	5.5	20.0	1	2	2	6.0	7.5
H379	18.ii.50	52	R	21	17	1	6.0	17.5	12	4	0	5.0	3.5
H297	4.iii.49	137	L	22	13	2	7.0	15.0	9	7	1	6.0	3.0
H299	4.iii.49	137	R	5	2	1	7.0	16.0	12	2	2	6.5	4.0
H300	4.iii.49	100	R	10	5	5	8.0	18.5	3	9	1	5.5	3.5
H301	11.iii.49	137	R	11	19	2	6.0	19.5	—	5	1	5.5	6.0
M6	17.iii.51	113	R	13	8	0	5.0	13.0	8	2	0	3.0	6.0
M9	17.iii.51	137	L	10	3	2	7.5	19.5	5	2	0	4.5	6.7
M11	19.iii.51	41	R	2	4	1	6.0	20.0	2	3	2	6.7	5.5
M15	19.iii.51	41	L	7	12	0	5.5	16.0	7	12	0	5.5	—
M16	19.iii.51	113	R	24	17	1	6.2	23.5	0	3	0	4.5	8.5
M17	21.iii.51	185	L	8	7	0	5.5	19.0	0	6	2	7.0	6.5
M18	21.iii.51	65	L	12	12	4	6.5	18.5	0	2	1	6.5	8.0
H307	7.iv.49	29	L	15	5	3	6.5	17.0	19	5	3	6.5	—
M32	10.iv.51	29	R	16	16	4	7.5	19.5	16	16	0	5.5	—
M68	28.iv.51	138	L	15	10	5	8.5	20.5	14	14	0	4.5	5.5
M73	10.v.51	43	L	7	4	0	4.0	23.0	8	8	0	5.7	—
M76	16.v.51	115	L	33	3	0	3.7	23.5	7	2	0	3.0	6.0
M78	28.v.51	31	L	14	8	1	6.0	21.5	24	9	0	4.5	—
M83	21.viii.51	106	R	7	0	0	2.0	22.0	13	3	0	4.0	5.0

TABLE VI. Follicle counts and measurements, and *corpus luteum* measurements from 36 pairs of ovaries from pregnant elephant seals.

their longest diameter. (Thus an ovary may have several follicles in the size group over 6 mm., when the "average diameter" of the largest follicle is only 5.5 mm.) Any more detailed examination was impracticable. Macroscopically "atretic follicles" (represented by scar tissue, or with dense, opaque contents) were also counted. These findings are summarised in Tables III to VIII.

Station No.	Date	Age in months	Right Ovary				Left Ovary			
			Follicles				Follicles			
			No. atretic	No. 3–6 mm.	No. over 6 mm.	Size of largest	No. atretic	No. 3–6 mm.	No. over 6 mm.	Size of largest
M5	17.iii.51	5	4	0	0	2.3	2	1	0	3.0
M12	19.iii.51	5	0	1	0	3.0	0	2	0	3.5
M14	19.iii.51	5	2	11	0	5.5	1	9	0	4.3
M19	29.iii.51	5	31	0	0	3.0	13	1	0	3.3
M66	24.iv.51	7	—	10	0	4.0	—	7	0	4.5
M79	28.v.51	19	0	0	0	2.3	—	1	0	3.0

TABLE VII. Follicle counts and measurements from 6 pairs of ovaries from immature elephant seals.

2. *The Cycle of Normal Pregnancy*

a. *Post-partum Oestrus*

Table V sets out the size and number of follicles and *corpora lutea* in the ovaries of twenty-six parturient and post-partum females, and the probable rate of growth of the follicle destined to ovulate is illustrated by Figure 13. Figure 14 shows the position of the immediately post-partum period in relation to the annual ovarian cycle.

The development of the follicles in non-pregnant females agrees with the description given by Hansson (1947) for the mink (*Mustela vison*) and although detailed studies were not made, the nine stages of follicular development described by this author are fully represented in the elephant seal material. The mean diameter of the primary oocyte is 25 μ; growth is rapid until the ovum is about 90 μ in diameter and the follicle 150 μ, when antrum formation leads to increased growth of the follicle, while the rate of growth of the ovum slows down. In a follicle measuring 1.3 mm. in diameter the ovum was 141 μ in diameter, and, while the follicle undergoes enlargement to about 15 mm., the ovum does not show any further growth. The granulosa is occasionally folded and supporting ridges, such as those described by Harrison, Matthews and Roberts (1952), are present. The fusion of these folds to give a solid mass of granulosa cells enclosing fluid-filled spaces, which these authors described, has occasionally been seen in the elephant seal material.

In cows approaching parturition, the *corpus luteum* of pregnancy has already begun to regress (M126, M123). The size is reduced and there is a small central cavity which, after parturition, fills with white scar tissue (Fig. 15d). Although there is considerable individual variation, this ovary usually has no follicles over 3 mm. in diameter until after ovulation, and the average size of the largest follicle declines from 2 mm. at parturition to 1 mm. at ovulation.

Prior to parturition, the largest follicle in the other ovary, which is destined to liberate a single ovum and so initiate the next pregnancy, averages 4 mm. in diameter. There is no true anoestrum, for immediately after parturition this ovary shows considerable activity as the inhibiting effect of the *corpus luteum* wanes and the follicles enlarge, one increasing in diameter at a rate of about 0.5 mm. per day, to a maximum of about 15 mm. at ovulation. At parturition there are, on average, only four follicles over 3 mm. in diameter and none over 6 mm.; five days later there are ten over 3 mm. and four over 6 mm. Then, as the follicle which is destined to ovulate enlarges, it monopolises space and inhibits the growth of the other follicles, so that at ovulation (nineteen days post-partum) there is only one large follicle and usually one follicle 3–6 mm. in diameter (Table V and Figure 16). Figures 15a and 15h show the appearance of typical sections of the ovaries of parturient and oestrus females.

Station No.	Date	Age in months	Right Ovary					Left Ovary					Notes
			Follicles				Size of corpus luteum	Follicles				Size of corpus luteum	
			No. atretic	No. 3–6 mm.	No. over 6 mm.	Size of largest		No. atretic	No. 3–6 mm.	No. over 6 mm.	Size of largest		
M80	10.viii.51	58	0	1	0	3.3	6.0	2	5	0	4.5	4.5	Recent ovulation
M74	12.v.51	79	14	10	3	8.0	—	12	7	0	5.5	10.5	? necrotic foetus
M75	16.v.51	79	7	3	0	3.0	12.5	9	6	0	5.0	—	Necrotic foetus
H286	16.ii.49	88	19	10	2	6.5	14.0	5	0	0	2.5	6.0	
M69	1.v.51	91	0	0	0	—	9.5	1	1	1	10.3	—	? about to ovulate
M13	19.iii.51	125	0	0	0	—	—	0	0	0	—	—	Senile condition
M67	25.iv.51	139	30	24	2	6.0	—	31	6	0	4.5	12.0	Necrotic foetus
M70	1.v.51	139	4	13	1	6.5	6.5	13	16	3	7.3	6.7	Recent ovulation
M81	10.viii.51	166	0	1	0	3.0	7.5	4	5	1	6.5	4.0	Recent ovulation

TABLE VIII. Follicle counts and measurements and *corpus luteum* measurements from 9 pairs of ovaries from non-pregnant elephant seals.

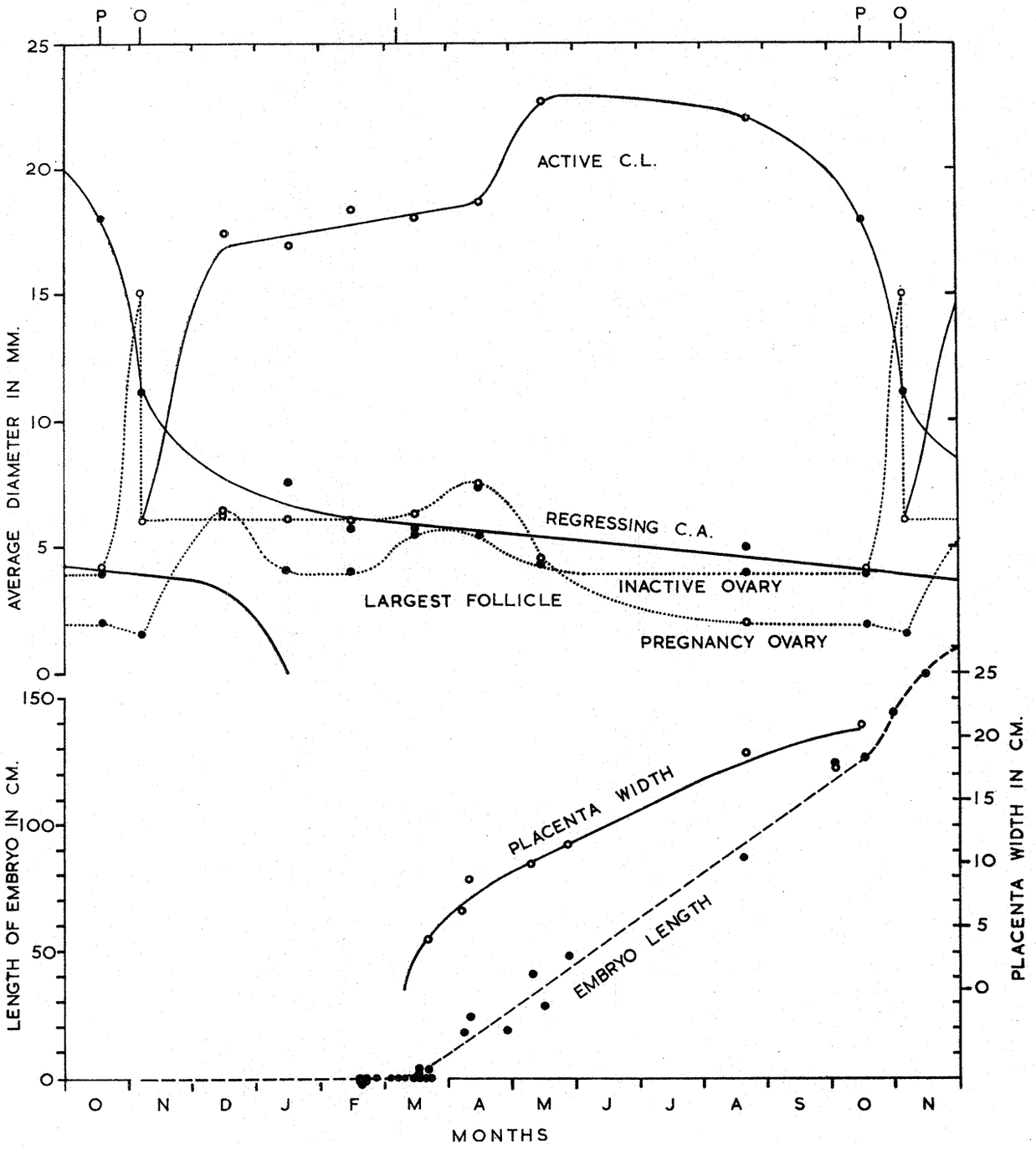

FIGURE 14. Above: the average diameters of the active *corpus luteum*, regressing *corpus albicans*, and largest follicle in each ovary throughout the year. The values of the post-partum period are from 26 marked cows; the remainder are presented as monthly averages, and smoothed curves have been drawn. Below: the average curves of increase in size of the placenta and embryo drawn from individual measurements, except for the post-natal growth of the pup which is averaged from a large series of measurements.
The dates of parturition (P), ovulation (O) and implantation of the blastocyst (I), are indicated.

b. *Ovulation*

The time-relations of ovulation and acceptance of the bull by the cow are not very clear. Nor is it known whether ovulation is spontaneous or dependent on the stimulus of coitus. The observed presence of ovulating cows in May, is strong presumptive evidence for spontaneous ovulation (p. 43). It has been established that the cows accept the bull for the first time, on average, eighteen days after parturition (Laws, 1956) and it was suggested that oestrus normally lasts until the pup is weaned (i.e. for about five days). From the examination of the ovaries (Figure 13), it appears that ovulation occurs round about the nineteenth day, so that impregnation and ovulation are approximately contemporaneous. Normally, where several follicles of approximately equal size are present, the rupture of the ripest follicle would inhibit the rupture of the others (Hammond, 1952). For the elephant seal, in which there is only one large follicle, it would take several days for the second largest follicle to mature and the formation of a new *corpus luteum* prevents this. In the event of a bull not being available at ovulation it is possible that, in cows pupping early in the season, a second follicle would mature within several weeks depending on the duration of dioestrum, so that a successful mating could perhaps occur at the second ovulation. The chances of this occurring are small, but it may explain the condition of those few ovaries with more than one *corpus albicans*. The behaviour of female Y/X which lost her pup in a storm in 1948 and remained in the breeding area for forty-two days (Laws, 1956), is perhaps significant.

c. *The Free-Blastocyst Period (November to March)*

The Ovary Controlling Pregnancy

Follicles. At the time of ovulation in November there are, on average, only two follicles over 3 mm. in diameter; one of these ovulates, and the maximum follicle size then remains constant at just over 6 mm. until March. The average number of follicles over 6 mm. in diameter rises to 4.5 in December and then declines progressively until March, when there are only 1.5. The average number of follicles 3–6 mm. in diameter shows a similar rise in December, decreases to eight in January and rises to twelve in February, thereafter falling to 9.5 in March (Figure 16). The numbers of "atretic" follicles, which are generally of small size, show similar fluctuations (Figure 17). Large numbers of primary follicles are present until January but fewer in February. After January all the larger follicles, and most of the smaller ones are atretic (Table XI).

In other words, there is great follicular activity just after ovulation. It is suggested that, in December, an average of sixteen primary follicles grow to a size greater than 3 mm. and about four of these reach 6 mm. They do not ripen but enter atresia. A few more primary follicles enlarge in January and February to the 3 mm. level (about four, since this is the increment on the January average) and no more enlarged follicles are produced in March (possibly because of the paucity of primary follicles in February). The follicles which do reach the maximum size undergo a type of cystic atresia. They generally start to become atretic when the granulosa is differentiated into a basal columnar layer overlain by several irregular layers of polygonal granulosa cells. A *corona radiata* has formed round the ovum and the stalk of the *discus proligerus* is vacuolated. The vascular layer of the theca is greatly developed and there is usually luteinisation of the *theca interna* cells. The further development of a healthy follicle of this size to one ready to ovulate, consists chiefly in pre-ovulationary expansion by the increased volume of *liquor folliculi*. Such maturation does not follow and cystic atresia begins. The first signs are an increase in the amount of connective tissue in the theca, and the breaking off from the granulosa of characteristic cells with eccentric nuclei, which are found throughout the liquor. The staining properties of the fluid change at the same time from a homogeneous to a very granular appearance. The connective tissue sheath becomes more extensive and invests the remainder of the granulosa; the ridges of the mature follicle disappear. Further atresia may then take the form of a very gradual shrinkage; follicles in cystic atresia appear to persist for some months. In the smaller follicles atresia begins either with great proliferation of the granulosa to fill the antrum, or granular degeneration of the granulosa, followed by fibroblast invasion of the follicle. In both cases, connective tissue is laid down and the remains of the follicle persist for some time as scar tissue. The larger of these are the "atretic" follicles detailed in Tables V and VI and Figure 17; the variation in their numbers is related to the variations in the numbers of other follicles.

In certain ovaries, the primary follicles undergo swelling and vacuolation of the cytoplasm of the ovum, so that a large clear space remains in the stroma. The distribution of these follicles is shown in Table XI

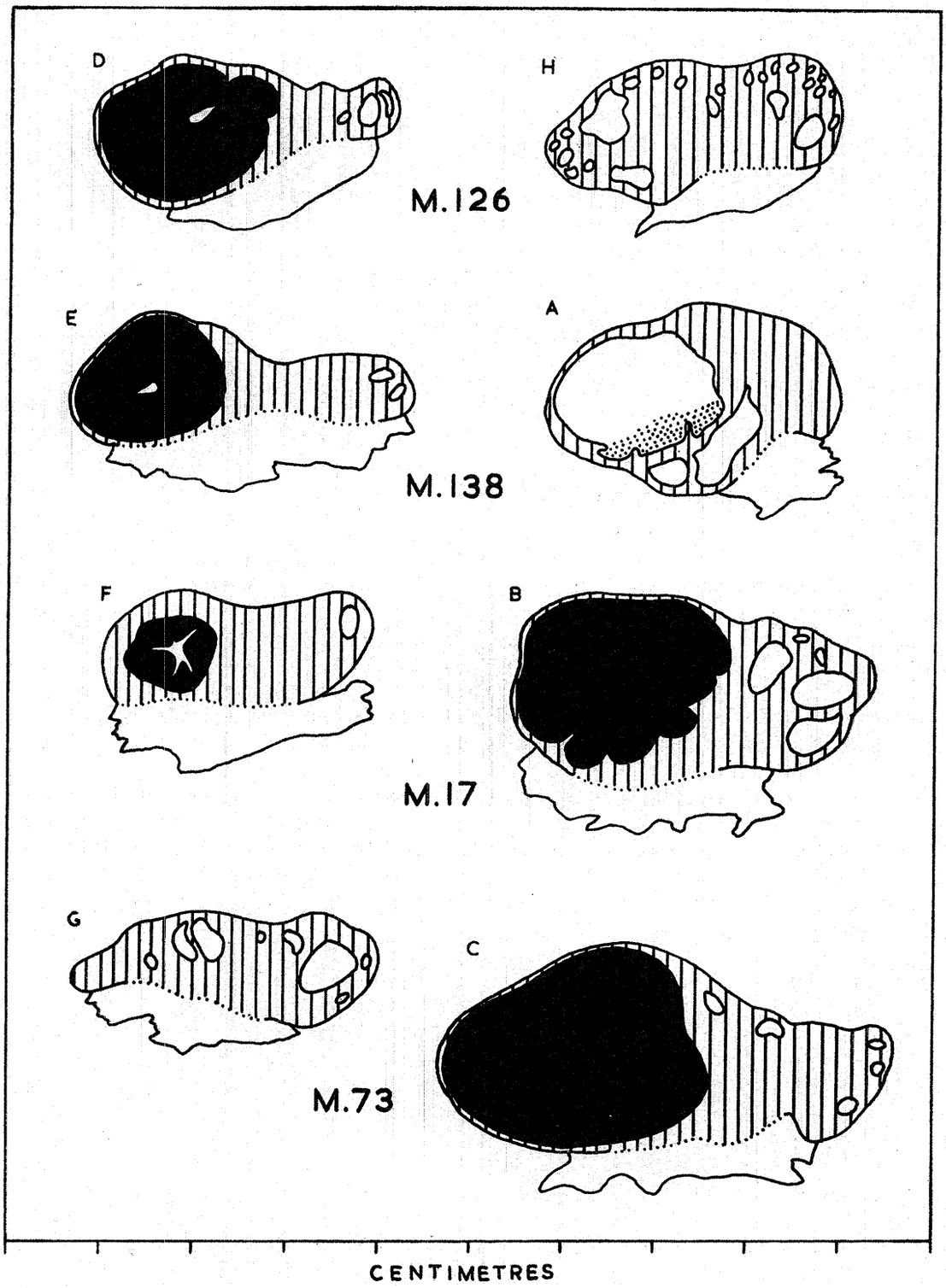

FIGURE 15. Scale drawings of representative sections of the ovaries of 4 female elephant seals to illustrate the annual cycle of the *corpus luteum* and follicles. M126, Oct. 2nd, about 8 days before parturition; M138, Oct. 9th, with an 18 days old pup; M17, March 21st, blastocyst implanting; M73, May 21st, *corpus luteum* at maximum size. *Corpus luteum* or *corpus albicans*, black; follicles white. Figures A–H represent stages in a typical two-year cycle of one ovary. M126 and M73, being primiparous, do not have a *corpus albicans*.

(as "A"); they appear to be present mainly at the time of implantation of the blastocyst. They have also been observed at the time of ovulation and just after.

Thus, during the free-blastocyst stage of the reproductive cycle, there is an initial outburst of follicular activity in December followed by decreased activity when no follicles reach a size much above 3 mm. before becoming atretic. The larger follicles probably persist, in cystic atresia, with theca lutein cells (Marshall, 1922), throughout January and February.

The Corpus Luteum. After ovulation, the collapsed follicle undergoes a transformation into the *corpus luteum* which controls at least part of pregnancy. As the cows leave their pups when they are weaned and go to sea to recuperate from the physiological strain of pupping and lactation, there is no material available which represents the early growth of the *corpus luteum*. However, it may be assumed by analogy with other mammals, that its initial rate of growth is rapid and that it soon attains a considerable size. By mid-December it is about 17.3 mm. in average diameter and slowly increases to about 18.0 mm. in March, when implantation occurs (Figure 14).

The histological appearance of the material examined has been summarised in Table XIII. The account which follows is based upon these specimens; most of the individual variations probably result from the specimens taken at a similar date being at different stages in the cycle, owing to differences in the dates of conception.

In the *corpora lutea* from December (Plate IIc) the luteal cells are large (25–30 μ in diameter), polygonal or oval in shape and with an eccentric nucleus (10 μ in diameter). Some cells are bi-nucleate. The cytoplasm is generally slightly darker-staining around the nucleus. Most of the cells are vacuolated and four types of vacuoles have been observed. The cell may be partly or wholly foamy in appearance, owing to the presence of many very small vacuoles. There may be a few small vacuoles, or three to four large ones; occasionally there is a single large vacuole, 60–80 μ in diameter, usually associated with a degenerate nucleus. The cells are closely packed and the interstitial spaces are therefore small. There are usually large numbers of migrating endothelial cells and a capillary network is developing, but mainly confined at this stage to the periphery of the gland. There is very little connective tissue, except in association with the septa which

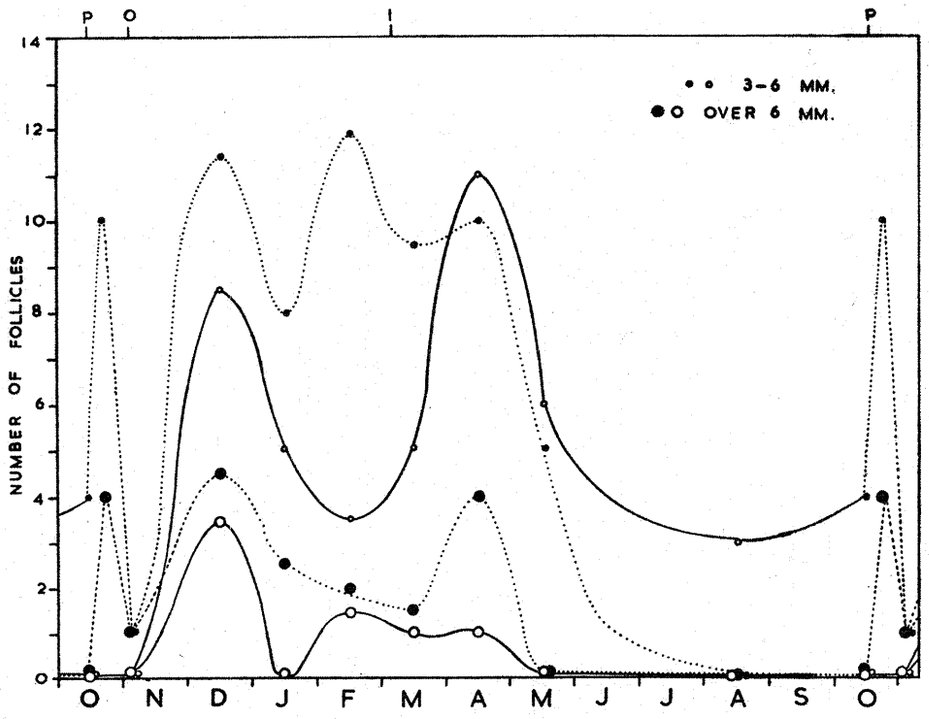

FIGURE 16. The average number of follicles of different sizes in the ovaries examined, set out by months. Black circles are ovary of pregnancy, white circles the other ovary. P=parturition, O=ovulation, I=implantation of the blastocyst.

partly divide the gland into lobes. These septa appear to be the same structures which are present in some of the follicles (Figure 15a) and they carry larger blood vessels than the body of the gland. The *theca interna* is represented by a few cells with elongate oval nuclei and small vacuoles.

The January *corpora lutea* are similar in appearance to those from December but the cells tend to be slightly smaller (*c.* 27 μ) and have fewer vacuoles. There are thick-walled blood vessels at the periphery and slightly more connective tissue.

From February until implantation in early March, the cells are larger, averaging 30 μ in diameter (27–50 μ), rounded or polygonal, with vesicular nuclei 10–13 μ in diameter. Some are bi-nucleate. There are more cell deaths during the early part of this period. In some cells the nuclei disintegrate before vacuoles form, but usually there is peripheral vacuolation of the cytoplasm, darkening of the perinuclear crescent, and condensation of the nuclear material to many small dark-walled vacuoles, which stain orange by Heidenhain's Azan method. Most of the cells are without vacuoles, but when present they are similar to those seen in December material; in addition, there are some cells like the "mulberry" cells described by Corner (1945). The main characteristic of the healthy luteal cells from mid-February (Plate IId) is the presence of a crescentic area around the nucleus, staining darkly with haematoxylin and as a number of small red granules with Heidenhain's Azan stain. From February 19th onwards the darkly-stained crescent is absent and a number of lighter-stained areas with darker centres, which exhibit birefringence, are seen at the periphery of the cell and in the intercellular spaces. These are thought to represent the recrudescence of secretory activity, associated with the presence of an enlarging blastocyst in the uterus. There is no great increase in the amount of connective tissue, but in H374 there is a connective tissue core to the gland. The vascularisation is either unchanged or shows more small capillaries spreading inwards from the periphery and tending to divide the luteal tissue into groups of from six to twenty cells in places. The *theca interna* cells, when they are present, are located as sparse groups of cells at the base of the connective tissue trabeculae. They have little cytoplasm and measure 10–12 μ in diameter.

Immediately before implantation, the cells are more rounded and measure 27–35 μ in diameter. Secretory activity is greater, and the interstitial spaces are larger and filled with what are thought to be secretory

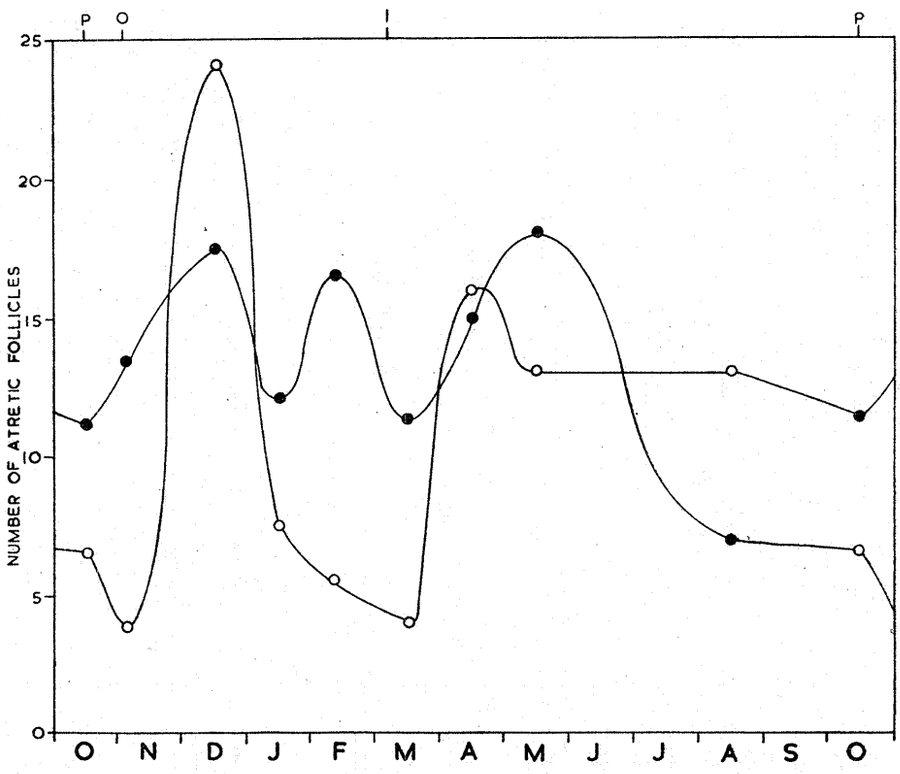

FIGURE 17. Numbers of "atretic" follicles. Black circles are ovary of pregnancy, white circles the other ovary.

products. There is an increase in the numbers and extent of the capillaries so that the luteal cells become divided into groups of from six to fifteen cells.

The Zenker-fixed, post-osmicated material gives a better impression of the extent of vacuolation of the luteal cells. The vacuoles appear to represent the coalition of larger numbers of small lipoid globules, staining black with osmic acid. They are almost entirely confined to the cytoplasm of the luteal cells and are not seen in the intercellular spaces.

The "Inactive" Ovary. In the ovary containing the regressing *corpus luteum* (now *corpus albicans*) of the previous pregnancy, the average diameter of the largest follicle increases from about 2 mm. at ovulation to about 6 mm. in December, when there are, on average, twelve over 3 mm. maximum diameter and 3.5 over 6 mm. The average diameter of the largest follicle falls to 4 mm. in January and February but increases to 5.5 mm. in March. Likewise, the numbers of follicles decline from December to March when the numbers of follicles over 3 mm. in maximum diameter show a slight increase. The numbers of "atretic" follicles show a corresponding increase to twenty-four in December, then decrease to four in March (see Figure 17).

Thus, this ovary also shows a burst of follicular activity after ovulation but, possibly in correlation with the small numbers of primary follicles present in January and February (Table XI), the numbers of 3–6 mm. follicles continue to decline in February when there is slight increase in the numbers in the other ovary. In December, the size of the largest follicle increases to equal that of the largest follicle in the other ovary, declines in January and February to 4 mm., and increases in March to almost equal the largest in the ovary controlling pregnancy (Figure 14). It is possible that the December size maximum is misleading (being based on only two specimens, one of them primiparous) but the graph of the numbers of follicles appears to be confirmatory (Figure 16). The histological appearance of these follicles is the same as in the other ovary.

The average diameter of the regressing *corpus luteum* (*corpus albicans*) decreases from 11.0 mm. at ovulation to 5.5 mm. in March, and then decreases less rapidly until the following breeding season when it may be completely resorbed. The central fluid-filled cavity, present at parturition, has become a white, stellate scar by March (Figure 15f). Changes in the histological structure of the gland are in the direction of increasing fibroblast activity and the laying down of connective tissue, associated with sclerotic blood vessels. By March no traces of the original luteal cells remain.

Date	Ovary controlling pregnancy		Other ovary		No of. specimens
	Corpus luteum	Largest follicle	Corpus luteum	Largest follicle	
Oct. 18th*	—	4.0	18.0	2.0	26
Nov. 11th†	—	15.0	11.0	1.5	
December	17.3	6.5	—	6.5	2
January	16.8	6.1	7.5	4.1	7
February	18.3	6.1	5.7	4.0	10
March	18.0	6.3	5.7	5.5	11
April	18.7	7.5	7.5	5.5	3
May	22.7	4.5	—	4.4	3
Aug. 28th	22.0	2.0	5.0	4.0	1
October			3.9	—	3

TABLE IX. Average size of largest follicle and *corpus luteum* in each ovary, in mm. Figures represent average of two diameters at right angles.
*, parturition and †, ovulation, averages from Figure 32.

Station No.	Date	Length (mm.)	Placenta width (cm.)	Sex
H379	18.ii.49	B	—	—
H289	19.ii.49	A_1	—	—
H290	19.ii.49	A_1	—	—
H292	19.ii.49	A_1	—	—
H293	19.ii.49	A_1	—	—
H1040	23.ii.49	A_1	—	—
H297	4.iii.49	A_1	—	—
H300	4.iii.49	A_1	—	—
H301	4.iii.49	A_1	—	—
M15	19.iii.51	A_2	—	—
M16	19.iii.51	A_2	—	—
M11	19.iii.51	A_2	—	—
M17	21.iii.51	A_2	—	—
M9	17.iii.51	23	—	—
M18	21.iii.51	32	4.0	—
M6	17.iii.51	39	—	—
H307	7.iv.48	186	6.3	male
M68	28.iv.51	192	—	male
M32	10.iv.51	248	8.8	—
M76	16.v.51	282	—	male
M73	10.v.51	410	10.0	male
M78	28.v.51	490	11.5	male
M83	21.viii.51	863	18.8	female
M126	2.x.51	1250	17.5	female

TABLE X. Embryos and placentae of the elephant seal.
(B=blastocyst, A_1=attaching, A_2=implanted).

Station No.	Date	Ovary of Pregnancy						Other Ovary					
		State of follicles			Primary follicles		Crypts	State of follicles			Primary follicles		Crypts
		Over 6 mm.	3–6 mm.	Under 3 mm.	Numbers	State		Over 6 mm.	3–6 mm.	Under 3 mm.	Numbers	State	
H341	Dec. 20	H	H	H	+++	H	O						
H346	Dec. 21	H	H	H	+++	H	O						
H363	Jan. 6	A	AH	AH	+++	H	O	O	AH	AH	+	H	O
H285	Jan. 27	A	AH	H	+++	H	O						
H372	Jan. 27							O	AH	AH	+	H	O
H374	Feb. 3	A	A	AH	O	—	O	O	O	AH	O	—	O
H375	Feb. 11	O	A	AH	+	H	O	O	O	AH	+++	H	O
H286	Feb. 16	A	AH	AH	+++	H	O	A	AH	AH	+	H	O
H288	Feb. 16	A	AH	AH	++	A	O	A	A	AH	+	A	O
H379	Feb. 18	A	A	AH	+	H	O	O	A	AH	+	H	O
H289*	Feb. 19	A	A	A	+	H	O						
H290*	Feb. 19							A	A	AH	+	H	O
H291	Feb. 19							O	O	AH	+	A	O
H292*	Feb. 19	A	A	AH	+	H	O	A	A	AH	+	H	O
H293*	Feb. 19	A	A	AH	+	A	O						
H297*	Mar. 4	A	AH	AH	+	A	+++						
H299	Mar. 4	A	AH	AH	O	—	O	A	A	AH	+++	H	++++
H300*	Mar. 4	A	A	AH	O	—	O	A	A	AH	++++	H	O
H301*	Mar. 4	A	A	AH	++	H	O	A	A	AH	+++	H	O
M11*	Mar. 19	A	AH	AH	+	HA	O	A	A	AH	++	H	++
M15*	Mar. 19	O	AH	AH	++++	HA	++	O	AH	H	++++	HA	++
M16*	Mar. 19	A	AH	AH	+	H	O	O	AH	H	+	H	O
M17*	Mar. 21	O	A	AH	O	—	+	A	AH	AH	++	AH	+
M9*	Mar. 17	A	AH	AH	O	—	O	O	AH	AH	++	H	++
M18*	Mar. 21	A	A	A	++	H	++	A	A	A	+	H	O
M6*	Mar. 17	O	A	A	+	H	+	O	A	A	+	H	+
H307*	Apr. 7	A	A	A	+	H	O	O	A	A	+	H	O
M68*	Apr. 28	A	A	A	+	A	O	O	A	A	++	H	O
M32*	Apr. 10	A	A	A	+	H	+	O	A	A	++	H	O
M76*	May 16	O	A	A	+++	H	++++	O	A	A	++	H	++++
M73*	May 10	O	A	A	+	H	++	O	A	A	++++	H	O
M78*	May 28	A	A	A	+	H	++++	O	A	A	++++	H	O
M83*	Aug. 21	O	O	A	+	A	++	O	A	A	+	A	++

TABLE XI. The results of the histological examination of the ovaries of 33 pregnant female elephant seals. The condition of the majority of the follicles is indicated (A=atretic; H=healthy), also the relative numbers of primary follicles and sub-surface crypts. (*=implanting or implanted embryo).

Station No.	Date	Ovary with largest C.L.						Other Ovary					
		State of follicles			Primary follicles		Crypts	State of follicles			Primary follicles		Crypts
		Over 6 mm.	3–6 mm.	Under 3 mm.	Numbers	State		Over 6 mm.	3–6 mm.	Under 3 mm.	Numbers	State	
M13	Mar. 19	O	O	O	O	—	+	O	O	O	O	—	++++
M67	Apr. 25	A	A	A	O	—	++	A	A	A	O	—	+
M69	May 1							HA	HA	H	++	H	O
M70	May 1	A	A	AH	+	H	++++	HA	HA	H	++	H	++
M74	May 12							HA	HA	H	+	H	+
M75	May 16	A	A	AH	O	—	+	A	A	H	+	H	++++
M80	Aug. 10	A	A	AH	++	H	+	AH	HA	HA	++	H	O
M81	Aug. 10	A	AH	AH	+	H	O	HA	HA	HA	+	H	O

TABLE XII. The results of the histological examination of the ovaries of 8 non-pregnant adult female elephant seals. Explanation as for Table XI.

Station No.	Date	Luteal Cells						Interstitial Tissue					Theca interna	Embryo
		Size (μ)	Shape	Nucleus	Vacuoles	Secretion	Staining (Haemotoxylin)	Spaces	Endothelial cells	Capillaries	Peripheral B.V.s	Connective tissue		
H341	Dec. 20	25–30	Polygonal	10 μ, eccentric	+++++	—	Darker perinuclear	Small	Many	++	++	+	Few cells vacuolated	Free
H346	Dec. 21	20–30	Oval	10 μ ,,	++++	—	,, occasional	,,	Few	+	+	+	,,	,,
H362	Jan. 6	25–30	Polygonal or oval	—	++	—	,,	,,	,,	+	+	+	,,	,,
H285	Jan. 27	23–27	,,	—	+++	—	—	—	—	—	—	—	—	,,
H374	Feb. 3	*c.* 25	,,	—	++++	—	Occasional darker crescent	,,	Many	++	++	++ Core	—	,,
H375	Feb. 11	,,	,,	—	++++	—	,,	,,	,,	++	++	++	Not seen	,,
H286	Feb. 16	27–50	,,	10–13 μ, more binuclear	+	—	,,	More (cell deaths)	Many	+++	++	+	Not seen	,,
H288	Feb. 16	—	,,	Some degen.	+	—	,,	Large	Fewer	++	++	—	Not seen	,,
H379	Feb. 18	28–30	,,	Some binuclear	++	—	,,	,,	,,	++	++	++	Sparse cells 10–12 μ	,,
H289	Feb. 19	—	Indistinct boundaries	Some degen.	+	+	Dark area more pronounced	,,	—	++	+	++	,,	Attaching
H290	Feb. 19	—	Polygonal or rounded	More degen.	+	+	,,	,, +secretion	—	+	++	+	,,	,,
H291	Feb. 19	*c.* 30	,,	8–12 μ, more binuclear, many degen.	+	+	,,	Small	—	+	+	+	Sparse at base of trabeculae	Free
H292	Feb. 19	,,	,,	,,	+	+	—	,,	—	++	++	+	,,	Attaching
H293	Feb. 19	,,	,,	,,	+	+	—	,,	—	++	++	+	,,	,,
H297	Mar. 4	,,	,,	,,	+	+	—	,,	—	++	++	+++ Core	,,	,,
H299	Mar. 4	*c.* 27	More rounded	,,	++	—	More uniform	Larger	—	++++	++	++	Indistinct from I.T.	Free
H300	Mar. 4	30–35	,, outline more distinct	,,	+	+	Occasional dark area	,,	—	++	++	++	,,	Attaching
H301	Mar. 4	,,	—	Fewer degen.	+	+++	Clear periphery	,,	—	+++	++	+++	,,	,,
M11	Mar. 19	*c.* 25	Irregular border crinkled	*c.* 8 μ, vesicular	+	++++	,,	,,	—	++++	++	+++	Aggregated 15 μ, nuclei 6–8 μ	Attached
M15	Mar. 19	,,	,,	,,	+	++	,,	,,	—	+++	++	++	,,	,,
M16	Mar. 19	*c.* 30	Usually rounded	,,	+	+++	,,	,,	—	+++	++++	+++ Core	Indistinct from I.T.	,,
M17	Mar. 21	*c.* 27	Irregular crinkled border	,,	—	+	,,	,,	—	++++	+++	+++	,,	,,
M9	Mar. 17	*c.* 28	,,	,,	—	+	Uniform	,,	—	+++++	+++	+++	,,	23 mm.
M18	Mar. 21	*c.* 23	,,	,,	+	+	,,	,,	—	+++	+++	+++	,,	32 mm.
M6	Mar. 17	,,	,, shrunken	,,	+	++++	Clear periphery	,,	—	++++	+++	+++	,,	39 mm.
H307	Apr. 7	25–27	Polygonal, expanded and healthy	10 μ ,,	+	++++	,,	,,	—	++++	+++	+++++	,,	186 mm.
M68	Apr. 28	*c.* 28	Similar to M11 but less shrunken	,,	—	+++	,,	,,	—	++++	+++	+++	,,	192 mm.
M32	Apr. 4	,,	,,	,,	—	++++	,,	,,	—	++	++	++	,,	248 mm.
M76	May 16	,,	,,	,,	—	+++	,, small dark granules	,,	—	++++	++	++++ Core	,,	282 mm.
M73	May 10	28–30	,,	10 μ, some degen.	—	+++	,,	V. large	—	+++++	+++	+++++	Sparse cells 15 μ, nuclei 7 μ	410 mm.
M78	May 28	,,	,,	,,	++++	—	,,	,,	—	++++	+++	++++	Indistinct from I.T.	490 mm.
Periphery		*c.* 20	Shrunken	Many pyknotic	+++++	—	Dark	,,	—	++	—	++++++	—	
M83	Aug. 21	*c.* 30	Rounded polygonal	8–10 μ, vesicular	++	++	Boundaries darker staining	Small	—	+++++	+++	++++	—	863 mm.
Periphery		*c.* 20	Shrunken	Pyknotic	+++	—	,,	V. large	—	+	—	+++++	—	

TABLE XIII. Summary of the histological appearance of the *corpora lutea* of pregnancy of 32 elephant seals.

[*To face p. 40*

d. *Implantation*

The Ovary Controlling Pregnancy. At the time of implantation when the blastocyst is enlarging to fill the lumen of the uterus, distending it and attaching, there is no significant change in either the size or the numbers of follicles in the ovary controlling pregnancy.

There are, however, progressive changes in the histology of the *corpus luteum.* It is then, like that of M17 (Figure 15b), irregular in shape and with a lobulated appearance. The luteal cells are smaller (25–27 μ) with an 8 μ nucleus, and of irregular polygonal shape with a crinkled border (Plate IIe and f). There is great secretory activity. The periphery is a mass of irregular non-staining areas which exhibit birefringence and are separated by cytoplasmic strands. The clear areas extend inwards towards the nucleus, and the remainder of the cytoplasm is unevenly granular. Some cells have small very darkly-staining granules. Occasional cells have one or two medium-sized vacuoles, and some have groups of small vacuoles within a single cytoplasmic sac. Occasionally, the whole cell is enlarged vacuolated and degenerate. There is a great increase in the numbers of the larger thick-walled blood-vessels at the periphery and in the trabeculae. The capillaries have increased so that they now cut off blocks of from six to eight cells at the periphery of the gland, and twenty to thirty at the centre. The amount of connective tissue is increasing and H297 and M16 have a connective tissue core. The former has a fluid-filled central vesicle measuring 3 by 4 mm. in diameter, with collagen strands running through it. The *corpora lutea* at this stage are represented by two specimens of Zenker-fixed, post-osmicated material (M11 and M15). They confirm the lipoid distribution suggested by the presence of vacuoles. The lipoid globules are smaller and less abundant than in earlier specimens. The *theca interna* is not always in evidence, but in M11 its cells are aggregated in the vicinity of the connective tissue septa at the periphery and have the appearance of small copies of inactive luteal cells, about 15 μ in diameter, with nuclei 6–8 μ in diameter.

The "Inactive" Ovary. The only change observed in this ovary at the time of implantation is a slight increase in the size of the largest follicle from an average diameter of 4.0 mm. in Feburary to 5.5 mm. in March. There is still, on average, only one follicle over 6 mm. in maximum diameter and the number of small follicles (3–6 mm. maximum diameter) increases by 1.5. There also appears to be a much greater number of primary follicles in specimens collected at this time (Table XI).

e. *The Post-Implantation Period*

The Ovary Controlling Pregnancy

Follicles. Owing to the pelagic habit of the species in winter there are, unfortunately, only six relevant specimens from April and May and one in August to illustrate this period, so that the conclusions reached are only tentative.

The placenta increases rapidly in size during the first month after implantation so that by early April it is about 7 cm. broad and about 1.5 cm. thick (Figure 14). At this time, the average diameter of the largest follicle has increased from 6 mm. (at implantation) to 7.5 mm. and usually shows luteinisation of the *theca interna* cells. The average number of follicles over 6 mm. in maximum diameter has increased from 1.5 to 4, and there has been a similar increase in the number of small follicles which become atretic. By May, the stimulus responsible for this increase has ended and there are no follicles over 6 mm. in maximum diameter; the average size of the largest has decreased to 4.5 mm. and all are in cystic atresia. Similarly, the average numbers of follicles 3–6 mm. in greatest diameter, has decreased from eleven in April to six in May. This rapid decline in both size and number of follicles is probably maintained, for the single August specimen has no follicles over 3 mm. in maximum diameter and the average diameter of the largest is only 2.0 mm. Ovaries of seals near term present a similar picture.

Corpus Luteum. Bearing in mind the paucity of material, the size of the *corpus luteum* appears to increase regularly until April when it measures 18.7 mm. in average diameter. Then in May, two months after the average date of implantation, there is a sudden increase in size to a diameter of 22.7 mm. There is little reason to doubt this figure because the variation in the three specimens representing this month is only 2 mm. The size of the only *corpus luteum* from August is 22.0 mm. so it seems that it remains constant or declines slightly during these four months (Figure 14).

The histology of the *corpus luteum* associated with embryos between 2 and 3 cm. long (M9, M18, M6) is similar to that associated with implanting embryos. The cells are slightly more shrunken (*c.* 23 μ) with a

uniformly granular cytoplasm and rather less secretory activity of the cells, although the large intercellular spaces are filled with secretory products. There are occasional cells with vacuoles taking up most of their area. The vascularisation is more complete but still not as abundant as one would expect by comparison with other carnivores.

H307, taken on April 7th, had a 186 mm. embryo. The luteal cells are polygonal and not shrunken, but only 26 μ in diameter and with 10 μ nuclei. The average diameter of the entire gland is only 17 mm. (less than the December average) so that it may not be typical. M68, taken on April 28th, had a 192 mm. embryo and the average diameter of the *corpus luteum* was 20.5 mm. The luteal cells were slightly less shrunken than those of *corpora lutea* associated with embryos under 3 mm. long. There are large intercellular spaces in these specimens but no increase in vascularisation and the secretory activity is similar to that of the March specimens (Plate IIg). There is an increase in the amount of connective tissue. No *theca interna* cells were distinguishable from interstitial tissue at the periphery.

The May specimens are similar in appearance, except that in M73 and M76 many of the luteal cells have a dark-staining crescent to one side of the nucleus which is composed of small granules staining very darkly with haematoxylin, and grey by the Azan method. A few *theca interna* cells were distinguished at the periphery of the *corpus luteum* of M73. They were about 15 μ in diameter with nuclei 6 μ across. This was the only specimen, between mid-March and the end of pregnancy, in which *theca interna* cells were distinguishable. The vascular network is increasing so that the luteal tissue is divided into groups of six to eight cells.

By the end of May, M78, bearing a 49 cm. foetus, presents a similar histological picture at the periphery of the *corpus luteum*, but in the centre the cells are shrunken (about 20 μ in diameter), many with pyknotic nuclei, and considerable amounts of connective tissue are being laid down. The vascular supply at the centre of the gland is greatly reduced. The intercellular spaces of the luteal tissue of M73 and M78 are very large, and it seems that the large size of the gland at this time must be due to the fluid content, since the size of the individual cells either remains constant or diminishes. In M73 and M78 the cells are heavily vacuolated, more so than any specimens taken after H375 on February 11th.

In M83, taken on August 21st and bearing an 86 cm. foetus, the appearance of the peripheral and central luteal cells is also dissimilar. The peripheral cells are large (30 μ), polygonal and closely packed. They have moderately-stained vesicular nuclei, 8–10 μ in diameter. There are few vacuoles and little secretory activity. The luteal cells have a darkly-stained border which does not seem to be an artefact. In the central part of the gland the cells are shrunken (*c.* 20 μ), degenerate, with pyknotic nuclei, and are heavily vacuolated. The intercellular spaces are very large and there have been many cell deaths. Consequently, the central tissue consists of a number of necrotic cells in a connective tissue network, with fluid-filled spaces. These changes appear to result in the *corpus luteum* having a fluid-filled central cavity at full-term (Figure 15d).

Zenker-fixed, post-osmicated material throws further light on the cytology of the *corpus luteum* associated with implanted embryos. Rossman (1942) has made a detailed study of the presence of lipoids in the *corpus luteum* of the rhesus monkey, and shows that the regressing *corpus luteum* accumulates a substance which he calls luteolipin. It is characterised by positive staining with Sudan III, in spite of its insolubility in lipin and hydrocarbon solvents, and positive staining by Bauer's method. A similar substance has been demonstrated in elephant seal *corpora lutea* from May by staining with Sudan III, and the histological picture of osmicated elephant seal material is identical with his figures for the retrogressing *Macaca rhesus corpus luteum* (Plate II, Figures 9 and 10).

In the *corpus luteum* of elephant seal M18 (embryo 32 mm.) there are very few black-stained lipoid globules, usually one per cell, but occasional cells contain many very small globules. In M6 (embryo 39 mm.) there are slightly more lipoid globules but when present they are usually in the intercellular spaces. Many cells have a lightly-stained nucleus, surrounded by very small, dark granules. The large intercellular spaces contain fine, granular material, unstained by osmic acid. In the osmicated luteal cells of M68 (embryo 192 mm.) there are many more black lipoid globules, and fatty degeneration of occasional luteal cells appears to be taking place. The centres of the cells have many small lipoid granules but the perpihery is clear. M32, with a 248 mm. foetus, shows a smaller amount of lipoid material.

By May, there are many large lipoid globules in the cells and in the intercellular spaces. The dark-staining area, which has been described from M73 (foetus 41 cm.), is represented in this material by many small lipoid globules giving the cells a characteristic appearance, with a black ring surrounding the nucleus. Staining of Bouin-fixed, paraffin-embedded material with Sudan III, suggests that some of the small lipin

droplets are a chromolipin. In M78, which has the larger foetus, there is slightly less osmic-stained material. There are some cells with many medium-sized vacuoles outlined by small lipoid globules. The *corpus luteum* of M83 (foetus 86 cm.) presents such an appearance after osmication.

At parturition, the *corpus luteum* has already begun to regress and the average diameter is then about 18.0 mm. The luteal cells are still recognisable; their appearance in M128, three days post-partum, is shown in Plate IIh. The cells become progressively more shrunken and phagocytosis begins (Plate IIh), so that just after the initiation of the following pregnancy it measures, on average, only 11.0 mm. The central part of the *corpus luteum* is then hard connective tissue, which is laid down between the heavily vacuolated shrunken luteal cells. Phagocytosis reduces the luteal tissue and over several months hyaline degeneration of the connective tissue produces a *corpus albicans*.

The "Inactive" Ovary. The follicles in this ovary show changes in April which are similar to but smaller than those in the active ovary. The size of the largest follicle is 5.5 mm. and the numbers of follicles, 3–6 mm. in diameter, increases.

In May, there is a decline in both size and numbers of follicles, and it appears that throughout the remainder of pregnancy the maximum follicle size is 4 mm., which is twice as large as the largest follicle in the ovary containing the *corpus luteum*. The number of 3–6 mm. follicles in the August specimen (M83) is three, whereas there are none in the opposite ovary; at parturition there are, on average, 5.5 follicles over 3 mm. in diameter, whereas the other ovary has none over 3 mm. The post-partum changes have been described.

3. *Non-pregnant Mature Females*

Material from nine non-pregnant mature females was collected and the results of examination of the ovaries are summarised in Tables VIII and XII. As already noted, one (M13) was senile, two had necrotic foetuses in the uterus, and the remainder were in various stages of dioestrum. The dioestrus cycle appears to be similar to the early stages of normal pregnancy, as shown by December material. The two females which had necrotic foetuses in the uterus (M67 and M75) had *corpora lutea* 12.0 and 12.5 mm. in diameter. The average diameter of normal *corpora lutea* at this time of year is about 20.0 mm. One of the remaining six, M74, had grey-brown granular material in the left uterine cornu and the *corpus luteum* measured 10.5 cm. This may also have been a case of intra-uterine mortality.

The ovaries of the other non-pregnant females all showed unmistakable signs of recent ovulations. Thus M69 (May 1st) had one recently ruptured follicle and haemorrhages into some of the other follicles; the largest was 10.3 mm. in diameter. M70 (May 1st) had many follicles up to 7.3 mm. and two *corpora lutea* of 6.5 mm. and 6.7 mm., the latter evidently recently formed. In H286 (February 16th) a recently ruptured follicle and a recent *corpus luteum* are present, and M80 and M81 (August 10th) both show signs of recent ovulations.

These *corpora lutea* may represent interrupted pregnancies, regression following failure to implant at the usual time, or they may be cyclic *corpora lutea*. Their regression is different from the normal regression of the late pregnancy *corpus luteum* which has been described. The cells appear to shrink rapidly, and fatty degeneration is more complete. Post-osmicated material is consequently very black and shows uniform fatty degeneration, individual cells containing many lipoid droplets of all sizes. There is evidence of extensive connective tissue invasion or hyaline degeneration.

4. *Sub-surface Crypts*

The occurrence of sub-surface crypts in the germinal epithelium of pinnipeds and other mammals has recently been reported (Harrison and Matthews, 1950; Harrison, Matthews and Roberts, 1952). Similar formations have been found in the ovaries of the elephant seal, and there appears to be a seasonal variation in their numbers and extent. They have been noted in the ovaries of adolescent females, normally pregnant females and females in dioestrous. They are also present in the ovaries of a senile female (M13), which otherwise exhibits extreme regression of the reproductive organs. During pregnancy, the crypts are first observed in the ovaries of seals in which the blastocyst is about to implant and reach their maximum development towards the end of pregnancy (Table XI). They are also present (though in markedly fewer numbers) in the ovaries of parturient and post-partum females, and are not present in ovaries collected from December to February, that is, in the free-blastocyst period.

It appears, then, that in the elephant seal crypts develop when the embryo is about to implant, increase in numbers and depth during the latter part of pregnancy and disappear shortly after parturition. Harrison, Matthews and Roberts (1952) report maximum crypt development in the species they studied, "during the few weeks after parturition and at the time of ovulation or just after".

The writer agrees with these authors that, in the adult seal, the germinal epithelium is not a source of germ cells; he has observed precociously developing oocytes, not only during the breeding season but occasionally throughout the year (they are listed in Table XI as abnormal primary follicles), and he subscribes to their conclusion that the crypts do not merely serve to bring the source of granulosa cells closer to the oocytes. There is nothing to conflict with their suggestion that the crypts indicate, in a vestigial form, the pattern of a primitive gonad. In this connection, their development in the supposedly senile female, M13, is perhaps significant.

5. Discussion

Harrison, Matthews and Roberts (1952) say that there is "some follicular growth in both ovaries of seals which are ovulating for the first time". It has been established that, in the elephant seal, the ovaries alternately release a single ovum annually, and that in females mating for the first time the right ovary usually releases the ovum (p. 21) although follicles probably develop in both ovaries.

Enders, Pearson and Pearson (1946) found that in their material from post-partum *Callorhinus ursinus* the ovary destined to ovulate has large numbers of follicles, but the opposite ovary has no follicles over 3 mm. After ovulation, follicular development in both ovaries is suppressed. They state that the *corpus luteum* of pregnancy suppresses follicular development in that ovary from a few weeks after parturition until several months after parturition the following year. The opposite ovary shows increasing follicular development towards the end of pregnancy. Harrison, Matthews and Roberts (1952) were able to confirm this in their material, which included *C. ursinus*, and Antarctic and European phocids. They believe that there is little evidence for follicular growth during delayed implantation but that two periods of follicular stimulation occur after implantation of the blastocyst. The first of these occurs from a week after implantation up to the 50 mm. embryo stage, and the second, some time before the foetus is 48 cm., in *Phoca vitulina*, continuing during the remainder of gestation, through parturition and until ovulation.

In the elephant seal (for which more representative material is available) the picture of follicular activity is more complicated and differs from their account of the cycle in the species they studied. Suppression of follicular development has been shown to occur during the later stages of gestation, so that the average size of the largest follicle in the ovary with a recent *corpus luteum* is only 2 mm., and in the other ovary 4 mm. Follicular development is suppressed in the former ovary until after ovulation. In the ovary destined to liberate an ovum there is a steady growth in the size of the largest follicle from 4 mm. just before parturition, to about 15 mm. at ovulation nineteen days after parturition (Figures 13 and 14). During the early part of this period, the average number of follicles over 3 mm. increases from four to fourteen, but as the follicle destined to ovulate increases in size, they become atretic and at ovulation there are only two follicles over 3 mm., one of which ovulates. This suggests that the suppression of follicular development is possibly caused by mechanical pressure, but it is more likely to be related to the nutritive level of the female, because she fasts for twenty-eight days during the breeding season and draws upon her reserves when suckling the pup. Furthermore, the size of the largest follicle in the other ovary declines from 2mm. at the beginning of this fast to 1 mm. at ovulation. In this ovary the former *corpus luteum* is retrogressing and the mechanical pressure is therefore decreasing.

In the northern fur seal (*C. ursinus*) there is never more than one follicle of ovulating size. Enders, Pearson and Pearson (1946) state that at the approach of ovulation there may be as many as three follicles over 8 mm. in diameter; the largest they measured was 12.5 mm., probably close to ovulation.

It has been shown that in the elephant seal there is, after ovulation, a period of follicular development when the follicles in both ovaries increase in size and numbers. During the remainder of the free-blastocyst stage the follicles do not reach a greater size than about 6 mm. before becoming atretic, but persist in a state of cystic atresia for some time, often showing luteinisation of the *theca interna* cells. There is a progressive decline in the numbers and size of follicles until implantation occurs. Then, after implantation, there is an increase in the total number of follicles in each ovary and individual follicles reach a greater size before becoming atretic. This corresponds to the first period of follicular activity noted by Harrison, Matthews and Roberts (1952) in other species. When the embryo is about 3–4 cm. long, there is a very

marked decrease in their size and numbers which is probably maintained throughout the remainder of gestation. There is no evidence for a recrudescence of follicular activity in the elephant seal when the embryo is about 48 cm. long, and at this time the follicles are still decreasing in size and numbers. Follicular activity remains at a very low level in the ovary containing the *corpus luteum*, until after ovulation, and in the other ovary at a relatively low level until parturition.

It is suggested that the increased follicular development in both ovaries in November or December, is related to the improved nutritive state of the females. Immediately beforehand, they have been hauled-out on land and undergoing a rigorous fast. The follicular development in March and April, especially the activity of the *theca interna*, is probably related to trophoblastic activity (Harrison, 1948a).

It is generally accepted that, as a rule, ovulation does not occur during pregnancy, but there are a few exceptions. It is well known that in the mare the *corpus luteum* of pregnancy regresses after about thirty days; it is replaced by a set of accessory *corpora lutea* by luteinisation of all follicles with antra, the larger ones of which ovulate (Asdell, 1946; Amoroso, Hancock and Rowlands, 1948). Recently Perry (1953) claims that ovulation occurs during pregnancy in the African elephant (*Loxodonta africana*). Hansson (1947) has shown that during the period of delayed implantation in the mink (*Mustela vison*) oestrus, mating and ovulation can occur. Cycles of follicular development occur in the rat during pregnancy (Long and Evans (1922), Nelson (1929), Swezy and Evans (1930)), and Swezy (1933) has shown that the number of follicles ripening in association with oestrous cycles during pregnancy, is greater than the number ripening in normal oestrus. *Corpus luteum* cysts sometimes form, the granulosa degenerating and the *theca interna* luteinising. Pearson (1949) describes the formation of additional *corpora lutea* during pregnancy in the rodent *Lagidium peruanum*.

In *Elephantulus* (Van der Horst and Gillman, 1945) the follicular activity is not rhythmical, as in the rat, but three distinct phases are apparent. In early pregnancy small cystic follicles are abundant and undergo atresia. When the embryo is from 10 to 20 mm. long, large cystic follicles are formed instead and then disappear while small cystic follicles reappear. The phases of follicular activity in *Elephantulus* thus provide a parallel with the type of follicular activity in the ovaries of the elephant seal, although in the former the theca cells do not become luteinised. Moreover, in the elephant seal as in *Elephantulus*, large cystic follicles develop at the time when the *corpus luteum* resumes its activity (see below).

Harrison, Matthews and Roberts (1952) have stated that in the Antarctic seals examined by them, the *corpus luteum* reaches a diameter of 20–26 mm. just after implantation, and is thus nearly twice the diameter of the mature follicle (13 mm.). In many other mammals the mature follicle is approximately seven-eights of the size of the mature *corpus luteum* (Corner, 1921; Harrison, 1948b). It is perhaps significant that in the elephant seal during the period of delay in implantation, the *corpus luteum* is about 18 mm. in diameter, which is approximately one-fifth larger than the mature follicle, whereas after implantation it increases to 22 mm., or nearly half as large again as the mature follicle.

The histological changes in the *corpus luteum* during pregnancy do not appear to be markedly different from those described in seals by Harrison, Matthews and Roberts (1952), or in some other mammals showing delayed implantation (Wright, 1942; Hamlett, 1932, 1935). In the elephant seal, the cells contain heavy deposits of lipoid material (represented by vacuoles in Bouin-fixed paraffin-embedded material and staining black in Zenker-fixed post-osmicated material), during the period of delay. Then, at the time of implantation, the fat globules disappear and an active secretory phase supervenes which persists until after the *corpus luteum* reaches it maximum size, when lipoid material again appears in the luteal cells. This material apparently consists of discrete droplets of chromolipin, associated with larger droplets of fat. Progressive degenerative changes continue throughout the remainder of gestation and increase greatly just before parturition. The suppression of follicular development, which occurs after April, appears to be related to the increase in the average size of the *corpus luteum* from 18.7 mm. in April to 22.7 mm. in May.

In the mink (*Mustela vison*) the *corpus luteum* presents an entirely different appearance during the free-blastocyst phase (Hansson, 1947, Figure 52). On histological grounds, it looks as though the cells of the mink *corpus luteum* do not reach maturity until just before implantation, whereas in the elephant seal they develop further initially and then show retrogressive changes (vacuolation) until an active secretory phase supervenes immediately before implantation.

In the African elephant, Perry (1953) believes that the vacuoles in the *corpus luteum* during early pregnancy represent an active phase during which substances are slowly released from the vacuoles. In the pregnancy *corpora lutea* of *Elephantulus* a single large fat vacuole appears and disappears in turn in every

cell (Van der Horst and Gillman, 1946) while the embryo grows from 20 to 30 mm. These authors suggest that, during this phase, there is a drop in the output of luteal secretion and that it is a period of readjustment. There follows a period of active growth when the volume of the *corpora lutea* is doubled and this is followed by degeneration. A similar rapid enlargement of the *corpora lutea* occurs in the rat and mouse in the middle of pregnancy (Long and Evans, 1922; Deanesley, 1930). In some mustelids, the *corpora lutea* associated with free blastocysts are small and inconspicuous (Wright, 1942; Hamlett, 1935). In the cat, Dawson and Kosters (1944) have demonstrated three phases of luteal activity, the period of readjustment occurring early in pregnancy during the fifteenth to seventeenth days. From the cases quoted above, it is apparent that the varied activity of the elephant seal ovary during pregnancy is not without precedent.

Little further light has been thrown on the factors responsible for the maintenance of the *corpus luteum* in a relatively inactive state during the period of delayed implantation. The appearance of the uterine mucosa and of the vagina (described in later sections) suggests stimulation by oestrogens. No progestational changes are observed in the uterine mucosa during the greater part of the free-blastocyst stage, and the extensive vacuolation of the luteal cells probably reflects a reduction or complete cessation of secretory activity, so that little or no progesterone is produced. Harrison, Matthews and Roberts have suggested that oestrogens are produced by the *theca interna* cells of the *corpus luteum* during this period. In the elephant seal material, the more marked changes in the uterine mucosa during delayed implantation are apparently related to oestrogen secretion by the *theca interna* of the follicles in December which, together with the persistent *theca interna* of the *corpus luteum*, is probably responsible for the maintenance of the *corpus luteum*, as these authors suggest. Dubreuil and Rivière (1946) state that in the human *corpus luteum* (*corpus gestationis*) the cells of the *theca interna* may be very conspicuous during pregnancy, and they emphasise the dual nature of the secretion of the *corpus luteum*.

C. The Cyclical Variations in the Uterine Mucosa During Pregnancy

1. *Introduction*

The appearance of the uterus and its mucosa in various immature seals, has been described in some detail by Harrison, Matthews and Roberts (1952), and their account applies more or less equally to the elephant seal. They have also described the appearance of the uterine tube. The precocious development and activity of the uterus and its glands in the late foetal and newborn common and grey seals described by them, has not been observed in the elephant seal, but the material available was sparse.

Owing to the pelagic habit of the two-year-old female elephant seal, there is no material illustrating the appearance of the uterus just prior to the initiation of the first pregnancy. The following account is, therefore, a general description of the cyclical changes in the uterine mucosa of females which have undergone at least one previous pregnancy. It differs from the primiparous cycle in that parturition and suckling are imposed upon the early stages, although recovery is extremely rapid. From each female killed, segments were taken from the middle of both uterine cornua and fixed in Bouin's picro-formal for subsequent histological examination. In view of the large amount of material which has been examined it is not possible to describe it all in detail. It has accordingly been summarised in Tables XIV and XV, but specimens typical of certain stages in the cycle are described below in more detail.

The alternation in function of the ovaries and uterine cornua, from year to year, has already been established. The two horns of the uterus, the one for convenience called "active" and the other "sterile", are therefore dealt with separately.

2. *The Annual Cycle of the Uterine Cornu in which the Embryo Implants*

a. *At Parturition*

During the later stages of pregnancy the sterile cornu (which will usually be the active cornu in the following cycle) shows proliferative changes. Female M83 (August 21st) had an 86 cm. foetus in the right cornu of the uterus. The mucosa of the left horn is about 2.0 mm. thick and has many large fairly straight glands, basally up to 125 μ in external diameter. They have cubical or low columnar epithelium (10–12 μ) actively secreting with vacuoles up to 5 μ, and secretory globules about 0.5 to 1.0 μ in size, darkly-stained by haematoxylin, which are not seen in earlier specimens; the nuclei are dark-staining. Some of the glands

Station No.	Date	Surface Epithelium				Glands				Gland Epithelium				Stroma		
		Height (μ)	Type	Cilia	Secretion	Numbers	Coiled or straight	Length mm.	Ext. diameter (μ)	Height (μ)	Type	Cilia	Secretion	Sub-epithelial	Deeper	Vascularisation
M126	Parturition —8 days	14	Low columnar	O	Basal vacs	Many ++++	Coiled & distended	2.6	75–150	12	Cubical	O	++++	Moderate numbers of leucocytes	Thin oedematous	+++
M124	+1	14	,,	O	,, Mucus	++++	,,	—	60–120	10–12	,,	O	++++	,,	,,	+++
M123	+2	14	,, pseudo-stratified in parts	O	,,	++++	Straighter	—	50–75	10–12	,,	O	+++++	,,	,,	+++
M128	+3	20–25	Col., rounded ends	O	O	+++	,,	1.8	50–60 (neck 30)	8–10	,,	O	+++++	,,	,,	+++++
M134	+4	25–30	,,	O	Basal ++++	+++	,,	—	—	—	,, , or low Columnar	O	+++++	To lumen ,,	Less oedema	++++
M129	+5	—	—	O	—	—	—	0.9	—	—	—	O	—	—	—	—
M132	+6	12	Cubical, some leucocytes	O	Basal +	++	Straight	1.0	40–50	—	,,	O	++	Few leucocytes	S. compactum, oedema	+++
M125	+7	10–13	Cub., or low col.	O	O	Few	,,	—	30–40	—	Columnar, nucleus apical or central	O	++	,,	Slight oedema	+++++
M130	+8	18	Col., pseudo-strat., rod cells	O	O	Few	,,	0.5	40–50	—	,,	O	+	Many leucocytes	,,	+++
M148	+8	15	Col., pseudo-strat.	O	O	,,	,,	2–2.8	50–75	—	,, or cubical	O	+	,,	,,	+++++
M127	+9	— 25	Cub. or low col. pseudo-strat.	O	+	,,	Slightly tortuous	*c.* 1.5	*c.* 50	—	,,	O	+	Few leucocytes	,,	+++
M135	+10	25–35	Col., pseudo-strat., some leucocytes	O	O	,,	Straight	*c.* 1.0	40–50	12	,,	O	+	,,	S. compactum	++
H320	+11	28	,,	O	—	,,	,,	2.0	35–50	—	,,	O	++	,,	—	+
M141	+12	30	,,	O	—	,,	,,	—	—	—	,,	O	++	,,	S. compactum, oedema	+
M140	+14	24	,,	O	O	,,	,,	1.8	40–50	13	,,	O	+++	,,	No oedema	++++
M142	+15	Similar to M140; darker staining sub-epithelial; brown pigment from laking of red blood cells.														
M136	+16	30	Col., basal nuclei, and pear-shaped, apical nuclei + cilia	++	+ Apical	Few	Straight	1.0	40–50	—	Col., basal nuclei	+	++++	,,	,,	+
M143	+17	30	,,	++	,,	,,	,,	—	40–60	15	Col., central nuclei	+	++++	Some lymphocytes	Moderate oedema	+++
M147	+17	—	,,	++	,,	,,	,,	—	—	—	,,	—	++	,,	,,	+++
M138	+18	15	Columnar	O	+ Basal	+	Tortuous	—	Up to 110	8	Col. or cub.	O	++++	,,	,,	+++
M139	+19	30	As M136, some lymph invasion	+++	O	Many ++++	,,	1.0	50–75	—	,,	O	+++	More lymphocytes	,,	+++++
M146	+20	—	,,	++++	+	++++	,,	—	—	—	Columnar	++	+	,,	No oedema	++++
M145	+21	—	,,	+	+	+++++	,,	—	60–75	—	,,	+	++	Many lymphocytes	Some oedema	++++
M144	+22	—	More lymphocytes	+	—	+++++	,,	—	—	—	,,	O	++++	,,	,,	++++
H341	Dec. 20	36	Col., pseudo-strat., rod cells	++	+++	++++	,,	0.5–1.0	70	24–30	Col., central nuclei	O	+	,,	Dense, no oedema	+++
H346	Dec. 21	36	,,	++	+++	++++	,,	0.5–0.7	70	24–30	,, basal orange pigment	O	+	,,	Slight oedema	++
H352	Jan. 1	12–36	,,	+	++	+++	Very tortuous	—	75–102	24–30	Col., basal nuclei	O	+	,,	,,	++
H362	Jan. 6	50	,,	O	O	+++	Straight	1.0	72–82	24	,,	O	+	,,	Dense	++
H363	Jan. 6	—	Discontinuous	O	O	+	,,	—	—	—	,,	O	O	,,	Thin	++
H368	Jan. 7	10–30	,,	+?	O	+	,,	—	—	—	,,	O	O	,,	,,	++
H285	Jan. 27	*c.* 20	Col., discontinuous	O	O	+	,,	1.0	—	20	Col., central nuclei	O	O	,,	Oedema	++++
H372	Jan. 27	—	,, rod cells	O	O	+	,,	—	30–75	—	Col. basal nuclei	O	O	,,	,,	—
H373	Jan. 28	—	,,	O	O	Very few	,,	—	30–75	—	,,	O	O	,,	,,	—
H374	Feb. 3	—	Sloughed in places	O	O	,,	,,	0.8	30–50	—	,,	O	O	,,	,,	++++
H375	Feb. 11	25–30	Col., badly fixed	—	—	+	,,	0.6–1.3	40–60	—	,,	O	O	,,	More dense	—
H286	Feb. 16	10–24	Col., crowded, rod cells	O	O	+++	Tortuous	—	*c.* 75	20	,,	O	O	,,	,,	+++++
H288	Feb. 16	24	Col., pseudo-strat.	O	+	+	,,	0.5	40–50	15–20	,,	O	O	,,	,,	++
H289*	Feb. 19	20	,, sloughing in parts	O	+	+	Straight	0.7	50	15–20	,,	O	O	,,	,,	+++
H290*	Feb. 19	Bad fixation; similar to H289														
H291	Feb. 19	,,														
H292*	Feb. 19	30	Col., pseudo-strat., rod cells	O	+	+	Straight	1.0	50–85	24	,,	O	+	,,	,,	++++
H293*	Feb. 19	20–30	,,	O	+	++	Slight coiling	0.5–1.5	—	—	,,	O	+	Few lymphocytes	Oedema	++++
H297*	Mar. 4	20	,,	O	++	++	,,	0.7–1.9	50–75	20–25	Col., central nuclei	O	—	Many lymphocytes	,,	++++
H299	Mar. 4	35	Col., crowded, few rod cells	—	—	+++	Very tortuous	2.0	40–60 85	25 15	,,	O	++	,,	,,	++
H300*	Mar. 4	Similar to H299, but epithelium lower, more pseudo-strat.														
H301*	Mar. 11	10 25	Sloughed areas low col., intact, col.	—	—	+	Tortuous	0.5–0.7	—	—	,,	O	++	,,	,,	++
M18†	Mar. 21	25	Col. or pseudo-strat. some rod cells	O	+	++	,,		50		,,	O	++	,,	,,	++
M6†	Mar. 17	15–20	Col. with frayed border or strat. polygonal	O	O	++	Straight	0.4	30–40 50	15–20 10	Low cubical	O	O	Few lymphocytes	,,	+

TABLE XIV. Summary of the histological appearance of the uterine cornu in which the embryo is to implant. The material comprises 24 females dated relative to parturition, and 24 females collected between December and March (implantation).

*=attaching blastocyst present; †=attached embryo, 3–4 cm., c.r.

[*To face p. 46*

have cystic enlargements, with lower epithelium and largely pyknotic nuclei. The surface epithelium is smooth, 15 μ high, with moderately-stained uncrowded nuclei and coarsely granular basophil cytoplasm showing few signs of secretory activity. The stroma is thinly cellular, slightly oedematous and moderately well vascularised. There are scattered sub-epithelial concentrations of leucocytes.

In M126, estimated to be eight days pre-partum, the foetus was in the right cornu. The mucosa of the left horn is 2.5 mm. high, with many coiled and distended glands. Near the surface they are 75 μ in diameter, and up to 150 μ at the base. The gland epithelium is 12 μ high, cuboidal, with clear cytoplasm showing secretory activity and containing some vacuoles. The lumen of the gland contains secretory products. The surface epithelium is 14 μ high, of low columnar type, usually with a central moderately-stained nucleus, clear basal zone and apical mucified part. Owing to the open necks of the glands, the epithelium presents a folded and "serrated" appearance. The stroma is similar to that of M83 and the lumen contains mucus and some polymorphonuclear lymphocytes.

Within a few days after parturition there are changes in the appearance of the mucosa. In M128, taken three days after parturition, the right cornu is recovering from the previous pregnancy. The surface epithelium of the left cornu is thrown into many small folds and the stroma is thinly cellular and oedematous, well vascularised, with large numbers of lymphocytes and leucocytes in sub-epithelial aggregations (Plate IIIa). There are numbers of glands which are only slightly tortuous, with a neck part about 0.3 mm. long and a total length up to 1.8 mm. The neck is 30 μ in external diameter and the remainder 50–60 μ in diameter. The gland epithelium is 8–10 μ high, cubical, with many vacuoles and secretory products. Usually the nucleus is central or apical and the vacuoles take up most of the cytoplasm. The secretion is in the form of small neutrophil or basophil droplets. The columnar surface epithelium is 20–25 μ high with rounded ends to the cells and a pale-staining, oval, central nucleus, 8 μ in diameter. There are many mitotic figures. The cytoplasm is lightly-staining, somewhat granular and contains no secretory products.

In M132, taken six days after parturition, the mucosa is only about 1.5 mm. thick, the glands are fewer, almost straight, and only 40–50 μ in diameter and 1.0 mm. in length. The deeper parts of the glands have columnar epithelium, and exhibit some secretory activity, but more superficially it is cubical with fewer secreting cells; the secretion in the lumen is neutrophil or basophil. The surface epithelium is 12 μ high, smooth, cuboidal, the nuclei sometimes arranged parallel with the surface; there are a few vacuoles. The stroma is slightly oedematous, and there is a stratum compactum which is seven cells thick in places. There are no sub-epithelial leucocytes but some are passing through the epithelium into the lumen. The appearance is one of inactivity, in great contrast to that of M126 and M128.

b. *Ovulation*

For several days the mucosa presents an appearance similar to that of M132, with the glands straight and relatively inactive. The surface epithelium proliferates, increases in height and, by crowding of the cells, assumes a pseudo-stratified appearance.

As ovulation approaches, the mucosa has smooth or slightly serrated surface epithelium which is about 30 μ in height. There are two types of cells; one narrow, columnar, with a well-stained nucleus, and the other pear-shaped with a round lightly-stained apical nucleus. The latter bear cilia about 4 μ long. Usually neither exhibit secretory activity but there may be small basal vacuoles (Plate IIIb). There are many tortuous glands up to 1 mm. long and 50–75 μ in external diameter. The epithelial cells tend to be columnar with moderately-stained basal nuclei and apical vacuoles (Plate IIIc). Some have a clear basal zone and central nucleus, and there are ciliated cells which usually have an apical nucleus (Plate IIId). The stroma is slightly oedematous, with extensive sub-epithelial vascularisation; laking and disintegration of the red corpuscles has occurred and some of the lymphocytes and epithelial cells contain brown debris from this source. There are sub-epithelial aggregations of lymphocytes, but few leucocytes, and none of these cells are seen in the lumen.

The scattered ciliated cells are found in the surface and gland epithelium of specimens from sixteen days post-partum onwards.

c. *The Free-Blastocyst Period (November to March)*

Specimens from December and early January present a rather different appearance from those taken near ovulation. For example, H341, H346 and H352 differ from oestrus females mainly in having a more deeply serrated border to the mucosa (because the necks of the glands are open), less secretion in the gland

epithelium and fewer ciliated cells. The cells of the surface epithelium show variable staining properties (Plate III e and g) and the nuclei are displaced apically by what are probably glycogen deposits. The presence of glycogen has not been demonstrated in the elephant seal by histochemical methods, but is assumed to be present by analogy and comparison with the figures given by Dawson and Kosters (1944). The glands are shorter (about 0.6 mm.) but of similar diameter (70 μ). Large concentrations of lymphocytes are passing through the surface epithelium to the lumen and in some parts appear to form a definite layer near the surface of the epithelium. The stroma is more dense with a stratum compactum and many small sub-epithelial capillaries.

During January and February, the uterine mucosa assumes a very inactive appearance; H374, taken on February 3rd, is typical of the period. The mucosa is 2.7 mm. in thickness and the necks of the very few glands present do not open, so that the surface epithelium is smooth. It is mainly composed of tall, crowded, columnar cells, but there are a few darkly-stained "rod" cells which are thought to be the result of this crowding. The glands are straight, up to 1.8 mm. long, much narrower than in the December specimens (30–50 μ) and lined by columnar epithelium with basal, variably-stained nuclei. There is no trace of secretory activity either in the glands or surface epithelium. The stroma is slightly oedematous, with a narrow stratum compactum and large numbers of lymphocytes passing through the epithelium.

d. *Implantation*

As the time of attachment of the blastocyst approaches, the uterine mucosa rapidly assumes a more active appearance. In H299, the blastocyst had not begun to attach but the mucosa is 2.5 mm. thick with folds up to 5.5 mm. high. There are moderate numbers of glands (not so abundant as in December) up to 2 mm. long, very tortuous basally, 40–60 μ in diameter, and patent throughout so that the surface is fringed or serrated. Their epithelium is columnar, 25 μ high, showing basal secretory activity and mitotic figures; some are 85 μ in diameter with a lower epithelium (15 μ). The surface epithelium is 35 μ high, columnar, with apical moderately-stained oval nuclei and clear secretory vacuoles in the basal cytoplasm. The cells are crowded but not pseudo-stratified, and there are a few rod cells. There are local aggregations of lymphocytes and in parts they invade the epithelium. The stroma surrounding the glands is dense, the remainder thin and oedematous.

Before implantation, the blastocyst swells to fill the lumen, loses the zona pellucida, and the trophoblast attaches at a number of points, digesting the uterine epithelial cells (Plate IIIf). The trophoblast proliferates, the uterine glands enlarge further, although at first only superficially, and the typical pinniped labyrinthine structure develops (Plate III h and IVa). The histology of the placenta will not be described here.

The para-placental zone of the mucosa of a specimen with a 39 mm. embryo (M6) is similar to the mucosa of H299 described above. It is about 2.0 mm. thick, with a serrated border (Plate IIIi), and surface epithelium 25 μ high, composed of columnar or pseudo-stratified cells with apical nuclei. There are basal secretory products. The glands are sparse, about 50 μ in diameter, with epithelium 15 μ high showing some secretory activity.

3. *The Annual Cycle of the "Sterile" Cornu*

a. *After Parturition*

Immediately after parturition, only the basal part of the uterine mucosa remains in the placental zone. Both there and in the para-placental region the mucosa is very oedematous and engorged with blood. The size of the cornu diminishes rapidly as involution progresses.

In M128, three days post-partum, the cornu which bore the foetus was almost equal in size to the other cornu and regeneration of the mucosa in the placental area has already begun. The epithelium is 20–25 μ high with large columnar cells containing apical, very pale-staining, vesicular nuclei, 8–10 μ in diameter, often showing mitotic figures (Plate IVb, and cf. Plate IIIa). The cytoplasm is granular and darker-stained than the nucleus; there is some evidence of basal secretory activity. Crypts, representing the basal parts of the large uterine glands associated with the placenta, extend 0.8 mm. deep in parts. The new glands form below these and are 30–50 μ in diameter, with cubical epithelium 8 μ high. Secretory activity is evidenced by the many large vacuoles. There are large numbers of polymorphonuclear leucocytes in the oedematous, very thinly-cellular stroma, but none in the lumen of the uterus. The sub-epithelial network of capillaries is very prominent.

Station No.	Date	Surface Epithelium				Glands				Gland Epithelium				Stroma		
		Height (μ)	Type	Cilia	Secretion	Numbers	Coiled or straight	Length mm.	Ext. diameter (μ)	Height (μ)	Type	Cilia	Secretion	Sub-epithelial	Deeper	Vascularisation
	Post-partum															
M124	+1 day	Very oedematous; bases of glands with almost continuous covering of epithelium														
M123	+2	,,	,,	,,	,,	,,	,,									
M128	+3	20–25	Cubical, large	O	++++	Few	Straight	0.8	30–50	8	Columnar	O	++++	Very many leucocytes	Thin, oedematous	+++++
M134	+4	—	,, desquamating	O	++++	,,	,,	—	40–50	—	,,	O	++++	,,	,,	+++++
M129	+5	—	,,	O	++++	,,	,,	0.5	—	—	—	O	+++++	,, invade lumen	,,	++++
M125	+7	—	Columnar	O	+++	,,	,,	—		—	—	O	++++	,, ,,	,,	+++
M130	+8	—	Cub. or Col., central nuclei	O	++	,,	,,	—	50–60	—	—	O	++++	Few leucocytes	,,	+
M148	+8	25	Col., pseudo-strat.	O	O	,,	,,	—	50–75	18	Col., basal nuclei	O	+++	,,	,,	+++
M127	+9	—	Cubical	O	+++	,,	,,	—	—	—	—	O	++++	Many leucocytes	,,	++++
M135	+10	20	Col., pseudo-strat.	++	++	,,	,,	0.4–0.6	30–40	—	,,	O	+++	Few leucocytes	,,	++
H320	+11	35	,,	O	++	,,	,,	1.7	—	—	,,	O	++	No leucocytes	,,	++
M141	+12	20–25	,,	O	+	++	,,	—	50–60 (neck 35)	—	,,	O	++	Many leucocytes	,,	+
M137	+13	—	,, lymphocytes	O	+	Few	,,	0.9	40–50	—	,,	O	+	Few lymphocytes	,,	+
M142	+15	25	,, ,,	O	O	,,	,,	0.7	*c.* 50	20	,,	O	+	,,	,, sclerotic b.v.'s	+
M136	+16	30	Col., basal nuclei, pear-shaped	++	++	++	,,	1.0	40–50	—	,,	O	+	,,	Oedematous	++
M147	+17	—	,, lymphocytes	++	++	++	,,	—	—	—	,,	O	++	,,	,,	+++
M138	+18	—	,, rod cells	+++	+	+++	Tortuous	—	—	—	,,	++	++	,,	,,	+++
M139	+19	—	,,	+++	O	+++	,,	—	40–60	—	,, central nuclei	O	++	,,	,,	+++
M145	+21	30	Col., clear basal, rod cells	++	++	++	Straight	2.3	60–85	—	,, ,,	+	++	,,	,,	++++
M144	+22		,, lymphocytes	++++	++	++	,,	—	—	—	,, ,,	O	+	,,	,,	++
H341	Dec. 20	—	Col., pseudo-strat., rod cells	+++	+++	+++	Tortuous	—	—	—	,, ,,	O	+	Many lymphocytes	,,	++ sclerotic
H346	Dec. 21	—	,,	++	+++	+++	,,	—	—	—	,, ,,	O	+	,,	,,	++ ,,
H352	Jan. 1	—	,,	++	++	+++	,,	1.0	—	—	,, ,,	O	+	,,	,,	++ ,,
H362	Jan. 6	40–50	,,	+++	+	+++	,,	—	Some 138	12	Col. or cub.	O	+	,,	Compact	++
H363	Jan. 6	—	,,	O	+	Few	Straighter	—	—	—	Columnar	O	+	,,	Thin	++
H368	Jan. 27	10–30	,,	O	+	,,	Straight	0.3–1.0	—	10–30	,,	O	+	,,	—	+
H374	Feb. 3	—	,,	O	O	,,	,,	—	40	—	,,	O	—	,,	,,	++++
H375	Feb. 11	25–30	,,	O	O	,,	Less straight	0.5–0.8	40–60	—	,,	O	O	,,	Denser	+++
H288	Feb. 16	—	,,	O	O	,,	Straight	0.2–0.3	—	—	,,	O	+	,,	Thin	+ sclerotic
H289*	Feb. 19	10	Col., not strat.	O	O	,,	,,	—	*c.* 50	—	,,	O	—	,,	Denser	++ ,,
H290*	Feb. 19	—	Col., pseudo-strat	O	O	,,	,,	—	—	—	,,	O	+	,,	Thin	+ ,,
H292*	Feb. 19	30	,, rod cells	O	+	,,	,,	1.0	—	—	,, basal nuclei	O	+	,,	Denser	+++ ,,
H293*	Feb. 19	20–30	,,	O	+	,,	,,	—	—	—	,, ,,	O	—	,,	,,	+++ ,,
H379*	Feb. 18	15–20	,, + apical nuclei	O	+++	+++	Very tortuous	—	50–60 Some 75	20–25	,, central nuclei	O	++	,,	,,	++
H297*	Mar. 4	20	,,	+	++	+++	,,	0.7	50–75	20–25	,, ,,	O	+	,,	Oedema	+++
H300*	Mar. 4	*c.* 20	,,	O	++	+++	,,	—	—	—	,, ,,	O	+	,,	,,	++
H301*	Mar. 11	*c.* 25	,,	O	++++	++++	Tortuous	—	—	—	,, basal nuclei	O	+++	,,	,,	++++
M11†	Mar. 19	15–20	,,	O	++++	+++	,,	0.4	30–50	20–25	,, ,,	O	+++	Few lymphocytes	Denser	+++
M15†	Mar. 19	12–15	Col., or cub.; no rod cells	O	+++	+++	Straighter	1.0	60–80 Some 100	—	,, ,,	O	+++	,,	Thin, oedematous	++++
M17†	Mar. 21	—	Col., pseudo-strat.; apical n., rod cells	O	+++	+++	,,	—	—	—	,, ,,	O	++	,,	,,	++
M9†	Mar. 17	15–30	,,	+	+	Few	,,	0.6–1.5	50–65 Some 100	20 10	,, ,, Cubical	O	+	,,	,,	+
M6†	Mar. 17	20	,,	O	+	,,	,,	—	40–50	—	Columnar, central nuclei	O	O	,,	,,	++
H307	Apr. 7	25	,,	O	+++	,,	,,	—	60–75	—	,, ,,	O	++	No lymphocytes	Denser	++
M68†	Apr. 28	—	,,	O	++	,,	,,	—	40–50 Some 60	—	,, ,, Cubical	O	++	,,	Oedema	++
M32†	Apr. 10	25	,,	O	++	,,	Straight	—	*c.* 75	—	Columnar	O	++	Few lymphocytes	,,	++
M76†	May 16	18	,,	O	+	++	,,	—	50–75 Some 110	15 7–8	,, Cubical	O	++++	,,	,,	++
M78†	May 28	*c.* 20	,,	O	+	+++	,,	—	—	—	,,	O	++++	,,	,,	++
M83†	Aug. 21	15	Cubical	O	O	++++	,,	—	Up to 125	10–12	,,	O	++++	,,	,,	+++
Parturient																
M126	— 8 days	14	Low col.	O	+++	++++	Coiled & distended	2.6	75–150	12	,,	O	++++	More leucocytes	,,	+++

TABLE XV. Summary of the histological appearance of the sterile uterine cornu, from parturition through 12 months to the next birth. The material comprises 21 females dated relative to parturition and 28 females collected between December and August.
*=attaching blastocyst in other cornu; †=attached embryo in other cornu.

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In M134, four days post-partum, the endometrium presents a similar appearance but the surface epithelium is less compact and there is some desquamation. The apical nuclei are well-stained, and the cytoplasm has a basal clear zone and many small vacuoles and eosinophil inclusions. The few glands are 40–50 μ in external diameter and have many secretory vacuoles and neutrophil droplets.

The mucosa of female M129, five days post-partum, is similar but there are enormous aggregations of lymphocytes which pass through the epithelium to the lumen in large numbers.

Eight days after parturition, M130 has epithelial cells either similar to those shown in Plate IVb, or crowded, elongated columnar cells with or without basal vacuoles.

The glands are still very few in number, about 50–60 μ in external diameter, with vacuolated epithelial cells, some containing eosinophil secretion. There is a stratum compactum extending about 50 μ deep to the epithelium, and there are few phagocytes.

In the right cornu of M135, ten days post-partum, the appearance of the mucosa is almost the same as that of the other cornu. The surface epithelium has narrow, pseudostratified, columnar cells, about 20 μ high. The cytoplasm is darker than the nucleus and granular; some of the cells are ciliated. The glands are few in number, straight, about 0.4 to 0.6 mm. long, and 30–40 μ in external diameter. The epithelium shows mitotic figures and there are apical vacuoles in the cells. The stroma has a compact zone, 40 μ thick.

The right cornu of H320, taken eleven days after parturition, is similar but has surface epithelium 35 μ high with a clear basal zone. The glands are straight and up to 1.7 mm. long. The stratum compactum is about 100 μ thick and there are large numbers of phagocytes present.

b. *Ovulation*

The appearance of the endometrium varies little in individuals approaching ovulation. The surface epithelium is from 25 to 30 μ high usually with apical nuclei, some ciliated cells, and some have basal vacuoles. The glands increase slightly in number and are about 1.0 mm. long, fairly straight, and 40–50 μ in external diameter. Their epithelium is about 20 μ high with apical vacuoles in the cytoplasm of the individual cells. Increasing amounts of yellow-brown pigment are present in the epithelial and sub-epithelial cells, resulting from the breakdown of red blood corpuscles. The epithelium continues to be invaded by phagocytes.

In M138, eighteen days post-partum, the endometrium is 1.5 mm. thick, with folds to 5 mm., and there are more ciliated cells in the surface epithelium. Owing to compression, cells similar to the "rod" cells, "stiftchenzellen" or "intercalar" cells which have been described in other mammals (Corner, 1921; Dawson and Kosters, 1944), make their appearance. They are narrow, with dark-stained cytoplasm and nuclei, and are most numerous between the necks of the glands when these are close together. Glandular development is greater than in earlier specimens and the epithelial cells have basally placed nuclei with apical vacuoles; a clear basal zone (not vacuolated) begins to make an appearance in the cytoplasm. One day later, the mucosa of M139 is similar, but the clear basal zone in the cells lining the glands is more pronounced; the mucosa of M146 (twenty days post-partum) is also similar.

The endometria of M145 and M144, twenty-one and twenty-two days post-partum respectively, show some degenerative changes. The surface epithelium is 30 μ high, the ciliated cells are losing their cilia, and the nuclei shrink and stain more darkly. In the other type of epithelial cell, the nucleus elongates, becomes lighter-staining with the development of a clear basal zone, and assumes a central position. There is great variability in the staining properties of individual cells. The glands are up to 2.3 mm. long, fairly straight, and 60–85 μ in external diameter. There is usually a clear basal zone in the epithelial cells which also have apical vacuoles. The nuclei are small, rounded, and very darkly-staining. A few ciliated cells persist.

c. *The Free-Blastocyst Period (November to March)*

The mucosa of the "sterile" cornu of H341, taken on December 20th, is similar to the opposite cornu, but shows more "fringing" of the lumen, owing to the open necks of the glands, and a greater concentration of dark-staining cells beneath the epithelium. The cells of the surface epithelium are more crowded than in the other cornu and there are more ciliated cells. The basal cytoplasm of the cells is clear and the nuclei are central or apical. The sterile cornua of H346, H352 and H362, from December and early January are all similar. In the following weeks, the glands decline in numbers and in length and become much straighter. The secretory activity of both glandular and surface epethelium declines and cilia are absent. However, ciliated cells are present in the surface epithelium of H297, taken on March 4th.

Material collected in February shows a similar picture, but there is no serration or fringing of the epithelium which is usually smooth and continuous, unbroken by the open necks of glands.

d. *Implantation*

Just before implantation of the blastocyst in the opposite uterine cornu, serration of the surface epithelium of the sterile cornu develops and the mucosa assumes an appearance of great activity. The glands increase in number and become very tortuous. They are 40–60 μ in diameter, patent throughout, with the nuclei confined to the basal third of the epithelial cells. The pseudo-stratified surface epithelium (25–30 μ high) shows apical displacement of the nuclei correlated with the development of clear basal areas. Scattered rod cells are present. In H379, from mid-February, a blastocyst was about to enlarge and implant, but retained the zona pellucida. The mucosa of the sterile horn is 0.6–1.5 mm. thick. It has many tortuous glands, though not as many as the December specimens, and the lumen is serrated or fringed owing to the open necks of the glands. The surface epithelium is 15–20 μ high with apical dark-staining oval nuclei; the cytoplasm has a clear basal zone. A few darker rod cells are present. The glands are 50–60 μ in external diameter in parts 75 μ wide and cyst-like. Their epithelium is 20–25 μ high, with dark-staining central nuclei in the columnar cells and some have vacuoles in the cytoplasm; secretory products are present in the lumen of the glands. Many leucocytes are present and invade the epithelium.

The endometrium of other specimens from the second half of February and early March is similar, but in some it retains a less active appearance. It seems clear that just before the time when the blastocyst implants in the other cornu, the mucosa in the sterile horn also shows considerably increased activity. A blastocyst had just attached in the left cornu of M15 and the mucosa of the right cornu shows similar activity to that of H379. The glands are up to 1.0 mm. long, well supplied with capillaries, and patent throughout so that the lumen is fringed. They are usually fairly straight, but some are intricately coiled and occasionally reach 100 μ in diameter. The epithelial cells have dark- and light-stained nuclei in approximately equal numbers and they are crowded, central or basal in position, and with supranuclear secretory vacuoles. The surface epithelium is 12–15 μ high, cubical or columnar, with moderate- or dark-stained nuclei and basal secretory activity. No rod cells are present. M11, M16 and M17 present a similar appearance.

e. *Post-Implantation*

The right uterine cornu of M18, which had a 32 mm. embryo in the left cornu, shows decreased activity and there is only slight fringing of the lumen (Plate IVc). Female M9 had a smaller embryo (23 mm. c.r.) but the sterile cornu shows even less activity of the mucosa (Plate IVd) and the surface epithelium has both ciliated and non-ciliated cells (Plate IVe). There is very little secretory activity.

In the following weeks the activity declines further and the relatively inactive appearance persists until the embryo is about 18 cm. in length, when there appears to be a recrudescence of secretory activity. H307 had a 186 mm. embryo in the left cornu and the field notes record "much mucus in the right cornu"; histological examination showed that the apical part of the columnar cells of the surface epithelium (about 5 μ) was heavily mucified and was breaking away into the lumen leaving a ragged border to the epithelium. M73 had a 410 mm. foetus in the left uterine cornu and the mucosa of the right cornu had a serrated surface (Plate IVf). The glands are up to 1.5 mm. long, lined with cubical or columnar epithelium with centrally located nuclei and well-defined basal vacuoles. The surface epithelium is 25 μ high, columnar with pale-staining central or apical nuclei. The cytoplasm is clearer basally, but elsewhere has small basophil granules. Apically there is a ragged border, as if apocrine secretion had recently occurred, as in H307.

The mucosa of comparable specimens presents a similar appearance. M78 with a 49 cm. foetus, shows greater vacuolation of the gland epithelium than any other specimens examined. The glands are about 50 μ in external diameter with the epithelium 15 μ high. Occasionally they are cyst-like and up to 110 μ in diameter, lined by cubical epithelium 7–8 μ high, with pyknotic nuclei. The surface epithelium is like that of M73 but only 18 μ high. The stroma of these specimens (H307, M73, M76 and M78) has a sub-epithelial zone staining black with haematoxylin (Plate IVf) and bright orange by the Azan method, but this may well be a fixation artefact.

The appearance of M83, approaching parturition, has already been described (p. 46). It shows great secretory activity in the gland epithelium but very little in the surface epithelium.

4. *The Uterine Mucosa of Non-pregnant Mature Females*

In the apparently senile female examined (M13) the uterine cornua are remarkable for the small lumen, smooth cuboidal surface epithelium, very simple, straight and narrow glands, and extensive subepithelial vascularisation (Plate IVj).

The histology of the uterine mucosa of the other non-pregnant mature females has also been examined. In general, the appearance is one of inactivity, with very smooth cuboidal surface epithelium, short, fairly straight narrow glands and little or no secretory activity.

5. *Discussion*

The cyclical variations in the appearance of the mucosa of the uterine horns during pregnancy in the elephant seal, have been described. The changes in the appearance of the common uterus appear to be similar but less marked. Harrison, Matthews and Roberts (1952) have described three phases of activity in the uterus of Weddell and crabeater seals during early pregnancy, but they were, as they remark, "handicapped by insufficient material, lack of field notes, and the great difficulty of establishing the point in its reproductive life at which an animal was killed".

In the parous female elephant seal during late pregnancy and through parturition, both horns of the uterus show proliferative changes: increased size and distension of the uterine glands and active secretion.

The low, cuboidal, surface epithelium in late pregnancy is smooth and the glands large and straight and their epithelium secreting; the stroma is thinly cellular and oedematous. Just before parturition, the glands are large, much coiled, and showing great secretory activity. The opening of the necks gives the lumen a serrated appearance. The cells of the surface epithelium at this time are low columnar with centrally placed nuclei. Shortly after parturition the glands have become less tortuous, but the columnar surface epithelial cells have continued to grow and are now 20–25 μ tall. In other words, the glandular development and regression precedes that of the surface epithelium.

Six days after parturition the mucosa presents an inactive appearance. The surface epithelium is smooth and cuboidal, the glands fewer, smaller, and more or less straight. There are few secretory products. The pre-partum activity of the uterus of the elephant seal may be compared with the activity of the genitalia of the late foetal and neonatal seals, described by Harrison, Matthews and Roberts (1952). It suggests that such late foetal and neonatal activity may also occur in the elephant seal although it has not been noted. Since, in the elephant seal, there is no evidence of increased follicular activity in the ovaries at the end of pregnancy (p. 41), the source of oestrogens producing these changes is probably the placenta.

Harrison, Matthews and Roberts (1952) suggest that in the species they studied there are no marked changes in the mucosa of uterus or vagina at the time of receiving the male, but in the elephant seal during pro-oestrus, the uterine mucosa shows proliferative changes. These correspond to the follicular phase which Dawson and Kosters (1944) described in the cat. The surface epithelium changes from low cuboidal to pseudo-stratified with two types of cell, one with basal or central nucleus and the other ciliated with apical nucleus. The glands increase in extent and become very tortuous but the surface remains smooth since the necks of the glands do not open widely.

The presence of ciliated cells in the uterine glands and surface epithelium of seals has not previously been recorded, nor do they appear to be present in other carnivores (Asdell, 1946; Hansson, 1947; Dawson and Kosters, 1944; Evans and Cole, 1931). In the pig, ciliated cells are found in the glands but do not fluctuate in numbers during the cycle (Corner, 1921; Snyder and Corner, 1922). In the rabbit, there is a ciliated zone of the surface epithelium but there is no cyclical variation in their numbers (Parker, 1931). In several marsupials, the glandular epithelium is ciliated during heat (Asdell, 1946).

The glandular development probably continues after ovulation (though specimens are lacking), for the later specimens from December to January present a much more active appearance than during oestrus. The surface epithelium is thrown into narrow folds and there is some fringing indicating the presence of progesterone. The surface epithelium is 36 μ high, not pseudo-stratified but composed of tall columnar cells which have the nuclei displaced apically by what appear, by analogy with other carnivores, to be basal glycogen deposits. The glands are wide and very tortuous, the epithelium consisting of tall columnar cells with slight secretory activity. This phase in the elephant seal appears to correspond to what Dawson and Kosters (1944) term the luteal phase in the cat's cycle. Hansson (1947) states that in the mink (*Mustela vison*), which also exhibits delayed implantation, there is no tendency to increase glycogen deposits after

ovulation and no apical displacement of the nuclei until implantation. Throughout the remainder of the free-blastocyst stage in the elephant seal cycle, the surface epithelium is smooth, and the cells crowded, with central nuclei. The glands are few, straight and narrow, showing no secretory activity.

At the time of implantation, the changes are similar to those which occur in the mink. The cells of the surface epithelium are 35 μ high with apical nuclei and basal vacuoles (probably representing glycogen deposits). The lumen is fringed and the glands are fairly numerous, but fewer than in the post-oestrus phase, quite tortuous and 40–60 μ in diameter, the necks open. Their epithelial cells are tall columnar with basal secretory vacuoles. The cystic dilations of the uterine glands noticed in late pregnancy have made their appearance.

The numbers and activity of the glands in the para-placental zone of the active cornu fall off shortly after implantation and the mucosa loses the fringed appearance.

The changes in the histology of the uterine mucosa can be related to the cycles of follicular activity already described (p. 44) and to the appearance of the *corpus luteum* (p. 45). There is no reason to suppose that the follicular phase of the endometrium differs, to any great extent, from that in other carnivores. The appearance in the initial free-blastocyst phase is probably the result of the rise in the level of circulating oestrogens (preceded by a limited progesterone secretion) associated with the burst of follicular activity at this time.

During the latter part of the free-blastocyst stage, the decline in follicular activity and the inactive appearance of the *corpus luteum* are reflected in the structure of the endometrium. Progestational changes do not occur until just before implantation, and they are undoubtedly caused by progesterone acting on an oestrogen-primed mucosa. The paucity of glands compared with December specimens suggests that there are smaller quantities of circulating oestrogens, a conclusion which is supported by the ovarian cycle.

The endometrial cycle in the sterile cornu is characterised by rapid post-partum recovery. Otherwise the changes are similar, but slightly less marked than those in the active cornu. There is slight evidence for a recrudescence of activity when the embryo is about 18 cm. long. This, again, can be related to a burst of follicular activity, the oestrogens produced apparently causing mucification of the epithelium.

D. The Annual Cycle of the Vaginal Mucosa

From each female killed, a specimen of the vaginal wall was taken from about half-way between the hymeneal fold and the *cervix uteri*, and fixed for subsequent histological examination.

1. *The Cycle of Normal Pregnancy*

a. *Post-partum Oestrus*

At the time of parturition and just after, the vaginal epithelium is thrown into several large folds, each of which is subdivided by a number of branching clefts (Plate Va). The height of the epithelium is about 50 μ on the surface and up to 100 μ or more in the clefts. Three layers are distinguishable. Typically, there is a basal layer of columnar or polyhedral cells with basal, dark-staining, oval nuclei and clear basal cytoplasm. The cells are often crowded and there are some cell deaths. Occasional mitotic figures are also present. There is an irregular intermediate layer of pale-staining polyhedral cells which, when present, is not always distinct from the basal layer. Superficially, there is a layer of tall columnar mucified cells which have basal oval nuclei, more lightly-stained than those in the deeper layers, basophil cytoplasm and an apical mucified zone. In parts there is only a single layer of columnar mucified cells with central nuclei. The lumen contains mucus, cell debris and desquamated cells. There are many lymphocytes and a few polymorphonuclear leucocytes in sub-epithelial aggregations. The stroma is evenly cellular and slightly oedematous, and is moderately well vascularised. Usually there are many large polymorphonuclear leucocytes in the intermediate and superficial layers of the epithelium, each surrounded by a clear space which suggests that they are digesting the epithelium. Often there are large cysts in the deep clefts, containing leucocytes and mucus. A mucus flow is visible from the vulva of cow elephant seals about to give birth to their pups.

In M129, five days post-partum, the components of the epithelium are generally more crowded and there

is greater folding of the epithelium. Typically, it is 100–125 μ high in the clefts and there are few traces of an intermediate layer. The superficial layer consists of very elongated, thin, mucified cells about 50 μ high, with a basal pale- or moderately-stained nucleus which often contains two nucleoli (Plate Vb). There are more sub-epithelial leucocytes and lymphocytes which are actively invading the epithelium.

About one week after parturition the epithelium begins to assume a different appearance. The changes occur first on the surface of the folds and later in the clefts. Usually the superficial layer shrinks and the chromatin of the nucleus condenses, so that there appears to be a dark-staining band lining the lumen of the vagina (Plate Vc and d). The basal layer proliferates but is often obscured by the invasion of leucocytes and lymphocytes which increases at this time; usually two or three layers of nuclei can be seen. The intermediate layers increase and become the most prominent. Their cells are light-staining, large, polyhedral, and have large pale-staining nuclei of variable size, and one or two nucleoli. The lymphocytes and leucocytes tend to be concentrated in the basal layers and also just below the superficial layer, which they apparently digest (Plate Vd), causing it to desquamate so that the epithelium becomes transitional in structure. The lumen of the vagina contains much cellular debris (mainly dark-staining chromatin), mucus and phagocytes. There are fewer leucocytes and lymphocytes in the sub-epithelial zone, the latter predominating.

Stratification and cornification of the cells of what was formerly the intermediate layer follows and papillae, previously absent, make their appearance. Often the superficial layer is not detached but persists as a layer of degenerate, low cubical cells, with little cytoplasm and very dark-staining nuclear material situated basally. In the clefts, these cells consist of an almost circular sac of mucus with the nucleus represented by a line of very dark-staining chromatin at the base.

The appearance of the lining epithelium of the vagina of M141, taken twelve days after parturition, is illustrated in Plate Ve. Apart from the discontinuous superficial layer representing the remains of the columnar mucified cells, the epithelium (thirteen cells thick) presents a stratified appearance with the more superficial cells cornified.

All specimens taken in oestrus have this typical mammalian, stratified, cornified appearance, and there are leucocytes or lymphocytes in the epithelium but none in the lumen of the vagina. The papillae increase in height and often have a central cleft. The appearance of the stroma does not change.

b. *The Free-Blastocyst Period* (*November to March*)

During the period when the blastocyst is free in the uterus the appearance of the vaginal epithelium is variable (Table XVI), but it is not difficult to follow the cycle of activity. Usually the epithelium of the surface of the folds undergoes changes before the epithelium deep in the clefts.

Female H341, taken on December 20th, was primiparous. The folds of the vaginal epithelium are 4 mm. across, with clefts 2 mm. deep, and numerous papillae projecting into the sub-epithelial tissues; some are 0.3 mm. long with a lumen extending part of the way. The epithelium has three layers and is not cornified. There is a basal zone (two or three layers of cells) in the clefts of columnar epithelium, with large moderately-stained vesicular nuclei some of which are being phagocytosed by leucocytes. The intermediated layer is a single thickness of large polyhedral cells with light-staining, vesicular nuclei. Superficially, there is usually a single layer of low columnar cells with basal nuclei and apical mucus (like Plate Vc). Owing to the invasion of the epithelium by many polymorphonuclear leucocytes, which phagocytose the cells of the intermediate layer, the surface layer is often breaking away. The sub-epithelial tissue is dense and contains few leucocytes. H346 and H362 are similar; H352, taken on January 1st, is also similar but has compound papillae 0.6 mm. deep, with transitional epithelium 75 μ high. There is no distinct superficial layer and the epithelial cells are progressively lighter-staining towards the lumen, suggesting cornification. There are great numbers of lymphocytes in the epithelium, each surrounded by a clear zone, and many lymphocytes are closely packed in a sub-epithelial zone some 400 μ deep.

Throughout the period of the delay in implantation of the blastocyst, the superficial low columnar mucified cells are present in parts of the epithelium. Elsewhere, the epithelium is transitional like that shown in Plate Vf which is a section of the vagina lepithelium of female H300 (blastocyst just attaching) taken on March 4th. The basal layers are obscured by lymphocytes and, superficially, there are usually two layers of very large polyhedral cells with large, oval, pale-staining, vesicular nuclei which are occasionally distorted.

Station No.	Date	Epithelium						Lumen	Lymph or leucocytes	Stroma	Vascular-isation
		Folds or clefts	Papillae	Height	Layers		Superficial				
					Basal	Intermediate					
M133	Partum —4 days	++++ branched	O	40	Col., basal nuclei	1 layer polyhedral	Tall, col., mucified	Debris, mucus	+++++	Oedema	++
M124	+1	++ folds	O	50–75	,,	2–3 layers ,,	,,	,,	++++	,,	++
M123	+2	++++ branched	O	*c.* 80 (125)	,,	Undifferentiated	,,	,,	++++	,,	+++
M128	+3	,,	O	—	,,	1 layer polyhedral	,,	,,	++++	,,	+++
M129	+5	Similar to M123									
M132	+6	++++ branched	O	60–100	,, pseudo-strat.	Polyhedral proliferation, large	Degeneration of mucified cells	,,	++++	,,	+++
M125	+7	Small folds glands	O	—	,,	,,	As M133 in clefts As M132 on folds	,,	++++	,,	+++
M130	+8	,,	O	50 (150)	,,	,,	Remains of mucified or cornified squamous	,,	++	,,	+++
M148	+8	,,	O	—	,,	,,	,,	,,	+	,,	+++
M127	+9	Shallow	O	—	,,	,,	,,	,,	++++	,,	++++
M135	+10	,,	O	25	O	O	Tall, col., mucified	Little debris	++	,,	+++
M141	+12	,,	++ 1 mm.	60 (100)	Stratified		Cornified (usually), remains of mucified	,,	++	,,	+
M137	+13	,,	++ 1.6 mm.	60 (175)	,,	Vacuolated	No mucified cells	O	++	Denser	+++
M140	+14	Compound glands	O	—	Pseudo-strat.	Large polyhedral	Col., mucified	Debris, mucus	++	Oedema	+++
M142	+15	Simple folds	+	—	Stratified on folds		,, in clefts	,,	++	,,	+++
M136	+16	Few	+++	—	Stratified		Not cornified	O	+	,,	+++
M143	+17	,,	+++	—	,,		Few mucified cells	O	+	,,	+++
M147	+17	Deep folds	+	—	,,		,,	Debris	Few	,,	—
M138	+18	,,	+	—	,,		,,	,,	,,	,,	—
M139	+19	,,	+	—	,,		Cornified, no mucus	,,	,,	,,	++++
M146	+20	,,	+	—	,,		,,	O	O	,,	++++
M145	+21	,,	+	—	,,		,,	O	O	,,	++++
M144	+22	,,	+	—	,,		,,	O	O	,,	++++

Station No.	Date	Epithelium						Lumen	Lymph or leucocytes	Stroma	Vascular-isation
		Folds or clefts	Papillae	Height	Layers		Superficial				
					Basal	Intermediate					
H341	Dec. 20	Deep folds	+++ 0.3 mm.	30 (50)	1 layer col., basal nuclei	1 layer, large polyhedral	Col., mucified or degenerate	Debris and leucocytes	+++++	Dense	+
H346	Dec. 21	,,	+++	40	1–2 layers	Several layers	,, desquamating	,,	+++++	,,	+
H362	Jan. 1	Compound glands	+++	50 (75)	,,	,,	O	,,	+++++++	,,	++
H363	Jan. 6	,,	+++	20 (60)	,,	,,	O	,,	++++++	,,	++
H368	Jan. 7	Few clefts	++++	55 (75)	,,	Undifferentiated	Absent (usually) or cub., mucified	Debris	++++	,,	+++
H373	Jan. 21	,, +++++	++++	—	,,	Large polyhedral, cornified	,,	—	++++	,,	+++
H374	Feb. 3	++	++++	—	,,	,, not cornified	Usually present, mucified	—	++++	,,	+++
H375	Feb. 11	++++	++++	—	,,	,,	,,	—	Few	,,	+
H379*	Feb. 18	—	—	45	,,	,,	Absent or mucified	—	++++	,,	++
H292*	Feb. 19	++++ branching	++++	30 (50)	,,	,,	Absent or degenerating mucified	—	Few	,,	++
H300*	Mar. 4	++++	++++	30–40 (60)	,,	,, or absent	Absent (usually) or low columnar	,,	+	,,	+++
M11†	Mar. 19	++++ glands	—	—	,,	Desquamating	Absent (usually) or occasionally mucified	Debris and leucocytes	Few	,,	+++
M15†	Mar. 19	Few	—	50	,,	,,	,,	,,	,,	,,	—
M17†	Mar. 21	++++ glands	—	—	,,	,,	Mucified in glands	,,	++++	Thin	++++
M6†	Mar. 17	++++ glands	—	20–45	,,	,,	Mucified or absent	,,	+++	—	—
M32†	Apr. 10	Few	Few	50 (70)	,,	Several layers small cells	Col., mucified ++++ (30 μ)	Mucus	++	,,	+
M73†	May 10	,,	O	—	,,	,,	,,	,,	Few	,,	+
M76†	May 16	,,	Few	50–60 (75)	2–3 layers	Large polyhedral	Squamous	O	O	,,	+
M83†	Aug. 21	+++++ glands	O	15–38	,,	Several layers of small cells	Absent or col. mucified	O	++	Oedema	+

TABLE XVI. Summary of the histological appearance of the vaginal mucosa from parturition onwards. The material comprises 23 females dated relative to parturition, and 19 collected between December and August.

*=attaching blastocyst in the uterus; †=attached embryo in the uterus.

Height of epithelium; unbracketed—on surface of folds, bracketed—in clefts.

c. *Implantation*

In M11, which has an attaching blastocyst in the uterus, the general appearance of the vaginal epithelium is like Plate Vg. Both the superficial and intermediate layers are usually absent and the lumen contains a large amount of cellular debris, the large nuclei of the former intermediate layer being especially prominent, together with many leucocytes and lymphocytes. In the basal layers which remain there are many cell deaths, initially indicated by darkly-stained nuclei, and large numbers of lymphocytes are invading the epithelium. The variation in the staining properties of the epithelial cells is remarkable. Occasionally there is an intermediate layer of very pale-staining polyhedral cells (like those shown in Plate Vf) and more rarely a few superficial cells of degenerate, columnar, mucified appearance. In M15 and M17, the picture is similar but there are more mucus cells, especially in the deep clefts.

d. *The Post-Implantation Period*

There was a 39 mm. embryo in the uterus of M6 (March 17th) and the appearance of the vagina shows some differences from those previously described. The most obvious change is the increase in the number of superficial cells of regular columnar appearance, heavily mucified, and with a rounded free border. The lymph invasion is variable; it is largely confined to the basal and intermediate layers, but in parts completely obscures the epithelium.

In female M32, which carried a 248 mm. embryo, the surface epithelium is 50 μ high, and that in the clefts 60–70 μ. The basal layer is a single row of columnar cells. The intermediate zone usually consists of several layers of small polyhedral cells with a darkly-staining nucleus, and, superficially, a layer of columnar cells about 30 μ high, with a basal, well-stained, nucleus and the entire cytoplasm mucified. These cells are taller in the clefts, and on the folds the basal and intermediate layers are so obscured by the lymphocytes and leucocytes that there appears to be only a single-layered epithelium, as in Plate Vh.

The vaginal epithelium of M73 and M78 taken in May, is like that of M32, but in M76 which was taken on May 16th, the vaginal epithelium has a superficial, squamous layer. The basal zone is two or three cells thick, and a proportion of them are very darkly-stained and appear to be pushed through the superficial layers to the lumen where they disintegrate. The intermediate zone consists of several layers of very large polyhedral cells with abundant cytoplasm and some dark granular inclusions; the nuclei are large and vesicular. In parts where the superficial layer is absent, the large polyhedral cells give an irregular border to the epithelium (like Plate Vf). In places, there are isolated cells resembling the columnar, mucified cells seen earlier in pregnancy, but they are confined to the bottom of the clefts. More usually the epithelium has a superficial squamous layer, with pale nuclei and cornified cytoplasm. The epithelium is 50–60 μ on the surface of the folds, and 75 μ at the bottom of the clefts. There are no leucocytes and few lymphocytes.

The vaginal epithelium of M83, taken on August 21st, which had a foetus estimated to be about one month from full term, has lower epithelium which is only 15–38 μ high on the surface of the folds. It is thrown into many small folds and branched, gland-like clefts (like Plate Va). The cells are similar to those of M32, having a superficial layer of columnar, mucified cells with very darkly-staining basal nuclei (Plate Vh). There are moderate numbers of lymphocytes, which are digesting the intermediate layer in places so that the superficial layer breaks away. As usual, these changes are more prominent on the surface of the folds than in the clefts.

2. *The Vaginal Epithelium in Non-pregnant Mature Females*

All non-pregnant mature females examined (except M13, which was senile) have vaginal epithelium similar to that found during the free-blastocyst stage of the normal pregnancy cycle, with a superficial layer of columnar, mucified cells in various stages of activity.

Even the vaginal epithelium of M69, which had recently ovulated and was thought to be about to ovulate again (since the left ovary contained a follicle 10.3 mm. in diameter), was of this type.

In the senile female, M13, the epithelium is low; usually there are two layers, 15 μ high, but in parts there is only one. The basal layer is of the usual columnar type. The more superficial layers are paler-staining and often arranged parallel with the surface (Plate Vi). There are few phagocytes. Cords of cells (of the basal layer type) ramify in the stroma to a depth of 0.6 mm. There are a few mucus-filled cysts along their length, and in places there are deep narrow clefts up to 1 mm. long. The stroma is thinly cellular, with much connective tissue, and many small capillaries near the surface.

3. *Discussion*

The changes in the vagina of several fissiped carnivores have been described (Marshall, 1933; Hamilton and Gould, 1940; Evans and Cole, 1931; and Foster and Hisaw, 1935). In general, there is proliferation of stratified epithelium during pro-oestrus, reaching maximum thickness and cornification during oestrus. Desquamation occurs at the end of oestrus and stratified, high columnar cells are present during pregnancy and pseudopregnancy. High or low columnar cells are typical of the anoestrus epithelium. Leucocytic invasion of the lumen occurs before and after heat, but not in the pro-oestrus or oestrus.

In the material which they examined, Harrison, Matthews and Roberts (1952) found no traces of epithelial thickening or cornification when they expected it, but it now seems that the absence of such a phase may be the result of insufficient material having been examined. Copulation has never, so far as is known, been observed in the Antarctic seals (*Lobodoninae*) and the time of oestrus has not yet been certainly established (Bertram, 1940); in these species it does not follow after parturition as rapidly as in the elephant seal, and it is suggested that it is not fully represented in any material which has been collected. Yet these authors state that the absence of noticeable oestrus behaviour may be correlated with the relatively slight changes observed by them in the reproductive tract of Antarctic seals.

It has been shown that the elephant seal vagina undergoes an oestrus cycle similar to that of the fissiped carnivores, but differs from it in having a superficial mucified layer at certain other times. In the elephant seal distinct changes of behaviour have been observed when females were on heat (Laws, 1956), although they are not as marked as in fissipeds. The thickening and cornification of the vaginal epithelium during oestrus, and the changes in the uterine mucosa at the same time, are those produced by the action of oestrogens. The heavy mucification of the superficial layer of the vaginal epithelium at parturition, has not been described by Harrison, Matthews and Roberts (1952) in other species of seals. However, the occurrence of lesser mucification of the superficial layer of the vaginal epithelium of the elephant seal, in December and April, parallels their description of the vaginal mucosa during the period of delay in the implantation of the blastocyst, and later in pregnancy. This type of mucification is possibly the result of progesterone acting on an oestrogen-primed mucosa, and is common in rodents, during pseudo-pregnancy and pregnancy, and in the cow and some species of deer during the latter part of pregnancy.

Since the ovaries of parturient female elephant seals do not show much follicular or secretory activity, while both the uterine and vaginal mucosa exhibits increased activity which declines rapidly after parturition, it is reasonable to assume that the hormones responsible are produced by the placenta towards the end of pregnancy. Harrison, Matthews and Roberts (1952) have remarked that it is probable that the seal's placenta produces a chorionic gonadotropin which is responsible for the enlargement and activity shown by the reproductive organs of foetal and neonatal grey and common seals. It is not certainly known whether the reproductive tract of the foetal and neonatal elephant seal shows such hypertrophy and activity, and the changes observed in the uterine cornua suggest the action of small amounts of oestrogen only (p. 46). It is suggested that this hormone is produced in a free form by the placenta in late pregnancy and results in very heavy mucification of the superficial layer of the vaginal mucosa which declines just after parturition.

The desquamation and extensive leucocytic invasion of the vagina observed at implantation, is similar to the changes normally occurring at this time in carnivores not showing delayed implantation. It is brought about by the action of progesterone.

IV. CONCLUSIONS

As a rule, the male elephant seal becomes sexually mature at about four years of age and the average female when two years old; at this time the virgin females and the young, sexually mature males probably mate aquatically.

It seems likely, by comparison with older females, that the primiparous females haul out on land about forty-nine weeks after their impregnation, and give birth to their single pups eight days later. They are re-impregnated from eighteen to twenty-three days after parturition, their pups being weaned after a further few days. During the breeding season they fast for about twenty-eight to thirty-one days.

The bulls do not normally participate in the terrestrial breeding behaviour until they are at least five to seven years old. Their testes are in active spermatogenesis when they begin to haul out in early September, at least a month before the first parous cows come on heat, and individuals remain ashore during their rut for over eight weeks without feeding. Then, towards the end of November, they cease to produce sperm and lose interest in the cows.

It is believed that after the birth of the first pup the individual females give birth to their pup about a week later each year (Laws, 1956). After a number of years, the cow pups so late in the season that the chances of males still being present in breeding condition are slight. In that season the cow fails to be impregnated and probably undergoes a number of dioestrus cycles, succeeded by a period of anoestrum. Then, in the following spring, males are again present in breeding condition and she mates aquatically, probably at the same time as the virgin cows since neither group are seen on land. The following pregnancies are again retarded by about a week in successive years, and the average mature female dies in her twelfth year after producing seven pups.

Conversely, the males appear to haul out earlier each year after attaining sexual maturity, so that they spend progressively more time on land and take an increasingly active part in terrestrial breeding.

The breeding behaviour and the social structure of the rookeries have been described in an earlier paper (Laws, 1956). It was there suggested that terrestrial mating is the common condition in the elephant seal and the polygynous otariids, because of the time relations of oestrus and lactation which means that the cow remains in the vicinity of her pup during oestrus. If oestrus did not occur until after the weaning of the pup, there would appear to be no evolutionary or genetic advantage in the maintenance of the harem structure. The usual condition among the other *Phocidae* is for oestrus to occur after weaning of the pup, and mating is aquatic.

It appears that in all the pinniped species for which accurate information is available, the duration of that part of pregnancy which extends from implantation to parturition is about seven to eight and a half months (Laws, 1956; Sleptsov, 1943). As a group, they have a very well-defined annual pupping season. This might be maintained either by having an interval of several months between parturition and mating, by delaying implantation for several months, or by a combination of these two mechanisms. Examples of each of these types of annual cycle are found in the *Phocidae*. The elephant seal has a post-partum heat only nineteen days after parturition and a long free-blastocyst phase lasting several months. In the Weddell seal, oestrus occurs about two months after parturition; in the crabeater seal, three months; and in the leopard seal, about four months after parturition. The length of the free-blastocyst phase is inversely related to the length of the interval from parturition to oestrus. On the basis of physical characters the genus *Mirounga* is generally believed to be the most specialised of the *Phocidae* (Flower, 1881). This implies that post-partum heat during lactation and a long free-blastocyst period, which are features of the elephant seal cycle, possibly represent the end of an evolutionary series.

Concerning the processes of selection which have resulted in this mechanism for fixing the time of the breeding season, we are reduced to speculation. We have seen that the male elephant seals are apparently in breeding condition several weeks before the majority of the females come on heat. This is, no doubt, to be explained as a result of sexual selection, for those males which are in breeding condition before the females come on heat will father most pups. Aggressive behaviour and the acquisition of harems are governed by male hormones which initiate and control the production of sperm, and in the elephant seal this precocity has been hastened by the development of the harem system.

In other species in which oestrus occurs in the females some months after parturition, there might also be competition amongst the males. Those males which come into rut early would be most successful in reproducing themselves, and it is possible that this would favour the advancement of oestrus among the females. Once delayed implantation was established in the group, the extension of the period of delay might be expected to follow. Some confirmation of this is afforded by the fact that the degree of gregariousness of phocids appears to be related to the length of the free-blastocyst period; the elephant seal is the most highly gregarious phocid and so far as we know has the longest delay in implantation. The leopard seal, which is one of the most solitary seals, has little or no delay between mating and implantation. The Weddell seal is intermediate in both respects. In an aquatic mammal like the seal, the females of which haul out on land for a short time to bear their pups, it is reasonable that a mechanism which advances the mating season should develop. Breeding then occurs when the animals are still concentrated in a relatively small area instead of widely dispersed over vast areas of open ocean. It is an explanation which would not apply to a

	Late pregnancy	Parturition	Pro-oestrus	Oestrus	Post-ovulation	Free-blastocyst period		Implantation	Development of embryo	
						I	II		I	II
FOLLICLES	Small		Grow in one ovary	One reaches 15 mm.—ovulates	Not known	Many grow and become cystic	Cystic atresia	Cystic atresia	Many grow and become cystic	Small in cystic atresia
CORPUS LUTEUM					Not known	Cells vacuolated theca interna present	Vacuoles disappear	Secretory droplets precede implantation	Reaches maximum size	Vacuoles reappear
ENDOMETRIUM	Great coiling of glands and secretory activity		Glands become straight; no secretion; surface smooth	Glands much coiled slight serration of surface. Nuclei of surface epithelium apical	Not known	Glands very much coiled; surface serrated or fringed. Nuclei of surface epithelium apical	Glands become straight surface smooth	Glands tortuous, secreting		
	Surface smooth	Surface serrated						Surface fringed or serrated		Surface smooth
VAGINAL MUCOSA	Cells columnar, mucified, crowded. Some leucocyte invasion		Transitional degeneration of mucified cells	Stratified, squamous cornified; no leucocyte invasion	Desquamation?	Single superficial layer of low columnar mucus cells	Transitional	Desquamation and leucocyte invasion	Single superficial layer of mucus cells	Stratified squamous
Hormones Diagnosed	OESTROGEN from placenta		F.S.H. but little OESTROGEN	OESTROGEN from follicles	? PROGESTERONE F.S.H.	OESTROGEN and PROGESTERONE	PROGESTERONE increasing	PROGESTERONE	F.S.H. PROGESTERONE OESTROGEN (from follicles)	PROGESTERONE diminishes OESTROGEN (from placenta)

TABLE XVII. Summary of main events in the reproductive tract during the annual cycle of the adult female elephant seal.

terrestrial mammal and, by implication, the phenomenon of delayed implantation may have arisen in different ways in various groups.

We have been considering the phenomenon in the Pinnipedia, taking the time of birth as the fixed point in the annual cycle. Fries (1880), dealing with a terrestrial mammal, took the time of mating as the fixed point in the cycle and concluded that the free-blastocyst stage is a mechanism ensuring that the young is born at a certain optimum season, which allows it to attain nutritional independence before the following winter.

A consideration of the diversity of animals in which delayed implantation is a feature of the annual cycle, supports the hypothesis that the phenomen has developed independently in a number of groups. The occurrence of delayed implantation is known in the armadillo (*Dasyphus novemcinctus*), the roe deer (*C. capreolus*), the badgers (*M. meles* and *T. americana*), the marten (*M. americana*), the weasels (*M. frenata* and *M. cicognam*), the stoat (*M. mustela*), the bear (*Euarctos americanus*), many rodents and several marsupials (Hamlett, 1935; Wright, 1942a; Sharman, 1954; Deanesley, 1943; Hansson, 1947).

There is also some evidence that the hormonal factors responsible for delayed implantation vary from one group to another.

Hansson (1947) has studied, in great detail, the phenomenon of delayed implantation in the mink (*Mustela vison*). In this animal during the free-blastocyst stage, the reproductive tract shows a more or less pronounced oestrus condition, the female exhibits oestrus behaviour and may permit mating and also ovulate. The *corpus luteum* has a very inactive appearance and Hansson believed that delayed implantation is due to oestrogen incretion continuing after ovulation. Experimentally he found that during the free-blastocyst stage the administration of progesterone, or progesterone and oestrogen, did not affect the condition of the animal. However, if ovariectomy preceded the administration of progesterone, the oestrus condition ceased and normal progestational changes occurred. From this, he concluded that the ovaries secrete oestrogen which suppresses the effect of progesterone. He attributed delayed implantation to the delayed release of luteotrophine (the hormone which controls the *corpus luteum* secretion) from the anterior pituitary, while the circulating oestrogens prolong the life of the *corpus luteum*.

In the elephant seal the cycle is probably similar, except that progesterone is probably produced in small amounts during the first part of the free-blastocyst period.

In Table XVII, the histological changes in the ovaries and reproductive tract are summarised, and an attempt is made to diagnose the endocrine factors responsible for these changes. It is concluded that progesterone is not produced towards the end of pregnancy, since in the sterile cornu and para-placental region of the gravid cornu the surface of the endometrium is smooth and there is no fringing. The coiling of the uterine glands and the extensive mucification of the vagina is probably associated with the production, by the placenta, of oestrogens which sensitise the uterus to oxytocin (Marshall and Moir, 1952). The ovary probably produces little or no oestrogen at this time.

The sudden cessation of oestrogen production by the placenta at parturition, is reflected in the reduced activity and coiling of the endometrial glands which become straight and simple shortly after parturition. Similar changes are apparent in the vagina, the epithelium becoming transitional with a superficial layer of degenerate mucified cells.

With the reduction of oestrogen secretion, the anterior pituitary probably commences to secrete follicle-stimulating hormone (F.S.H.) and the follicles in one ovary rapidly increase in size. The production of oestrogens by these follicles probably regulates the production of F.S.H. so that only one follicle ovulates. The presence of circulating oestrogens is shown by the cornification of the vaginal mucosa, which is usual in carnivores at this time, and by coiling of the uterine glands; slight folding of the surface epithelium due to crowding results in a serrated border to the lumen.

In the absence of material from the post-ovulation period we have little evidence of the further developments. From the histology of the reproductive tract in later specimens, however, it appears that the *corpus luteum* develops in the usual mammalian fashion and secretes progesterone which results in further coiling of the uterine glands, opening their necks, and so leads to some fringing of the lumen and secretion. Moreover, the nuclei of the columnar cells of the surface epithelium are displaced apically. In the cat, the nuclei are displaced apically by deposits of glycogen which reach their maximum seven days after ovulation (Dawson and Kosters, 1944). Desquamation of the vaginal epithelium also occurs. It would appear, then, that the progestational changes necessary for implantation do take place, but for some reason the blastocyst does not implant. In the mink, however, Hansson (1947) concludes that the delay in implantation is due to

the absence of the progestational changes in the uterus. The nuclei of the surface epithelium are basal in position until implantation.

During the first part of the free-blastocyst stage in the elephant seal there is a wave of follicular development. The follicles do not reach maturity, but luteinisation of the *theca interna* occurs and they pass into cystic atresia. It has been shown that progesterone prevents pre-ovulationary differentiation and causes cystic atresia (Gillman, 1941; Van der Horst and Gillman, 1945, 1946). Oestrogens are probably produced by the cells of the *theca interna* of follicles and *corpus luteum*, causing mucification of the vaginal epithelium.

At some time during the first month of the free-blastocyst period, the *corpus luteum* probably ceases to secrete progesterone and vacuolar degeneration begins. It is possible that the vacuoles represent reservoirs of progesterone, which is slowly released (Perry, 1953). The synergistic action of oestrogens and progesterone is generally accepted, and it is postulated that during the period of delayed implantation there is a gradual waning of the oestrogenic stimulus. This is reflected in the histology of the reproductive tract: the uterine glands become straight and the lumen smooth; mucification of the vaginal mucosa ceases and it becomes transitional in appearance. Concurrently, readjustment of the *corpus luteum* leads to the disappearance of the vacuoles from the luteal cells, and the hormone balance gradually shifts in favour of progesterone. The refractile granules, seen in the luteal cells just before implantation, are probably progesterone or its precursor. Associated with this is the desquamation of the vaginal epithelium and the invasion of the lumen by leucocytes, which is usual in mammals at the time of implantation. The slight coiling of the uterine glands (appreciably less than in the post-ovulation period) suggests that oestrogen is present in minimum quantities, and that the fringing of the lumen and the glandular secretion represent the progestational changes. At this time the blastocyst enlarges and implants.

Shortly after implantation there is another wave of follicular activity, resulting in the production of numbers of cystic follicles which slowly degenerate. The oestrogens which they apparently release cause mucification of the vaginal epithelium, increased coiling of the uterine glands, and are perhaps responsible for the increased growth of the *corpus luteum* which follows this wave of follicular development.

It seems probable that the oestrogens from the ovaries suppress the production of F.S.H., and that the placenta then secretes oestrogen in gradually increasing amounts until the end of pregnancy. Progesterone is undoubtedly secreted by the *corpus luteum* during the post-implantation period and secretion probably gradually wanes as the oestrogenic activity of the placenta increases.

This interpretation of the factors responsible for the histological changes observed in the elephant seal material examined is necessarily speculative, but if it is correct then oestrogens are responsible for prolonging the life of the *corpus luteum* during the free-blastocyst period, as in the mink. The factors which prevent implantation initially remain unknown, but it seems that the endometrium shows normal progestational changes. It may be that the occurrence of ovulation during lactation, in the elephant seal, affects the implantation of the blastocyst in some way. It is well known that when ovulation takes place in lactating mice, implantation is retarded for a period of time proportional to the size of the litter (Hamlett, 1935), and Asdell (1946, p. 18) believes that the life of the *corpus luteum* is related to the prolactin level in the anterior pituitary. The nature of the stimulus responsible for the resumption of secretory activity in the *corpus luteum* prior to implantation is unknown, but Hansson (1947) believes that in the mink it is due to the delayed release of luteotrophin. This invites the question "What promotes the release of luteotrophin?".

It has already been pointed out that implantation bears a close relationship to the moult of the elephant seal (Laws, 1956), and it is perhaps significant that mating occurs after the moult in *E. barbatus*, *P. vitulina*, and *P. hispida* (Sleptsov, 1943). In no case is implantation known to have occurred in the elephant seal before the moult, but always just after it has ended. Although this may be coincidental, it seems likely that a change in the endocrine factors in the anterior pituitary is involved, causing a further shift in the balance between the amounts of circulating oestrogens and progesterone. Thus, recent work reviewed by Burrows (1945), Cameron (1945) and Speert (1948) suggests that oestrogens exert a general inhibitory action on the growth of epidermis and hair. On the other hand, Shaffner (1954) has recently demonstrated that progesterone stimulates the growth of feather papillae. At the time of the moult, which involves rapid growth of hair and epidermis, the level of circulating oestrogens might be expected to be low. This implies that the mechanism controlling delayed implantation may vary in different groups of mammals, but since it has already been shown that there are differences in this respect between the mink and elephant seal, it is not improbable.

V. SUMMARY

1. This paper is based on specimens from the reproductive organs of eighty-eight male and eighty-four female elephant seals, the ages of which were determined from growth rings in the teeth.

2. The male reproductive organs are briefly described.

3. From a consideration of the *os penis*, size of the testes, and histological development of the testis and epididymis, it is concluded that the male elephant seal attains sexual maturity at an average age of about forty-seven months. For the first few years of maturity the males do not take part in the terrestrial matings but probably mate aquatically with non-parous females. In the material examined, there is no sign of a decline in male potency up to at least eleven years of age.

4. The annual cycle of activity of the seminiferous tubules in the male has been established, and the histology described. The tubules attain a diameter of 220 μ during the breeding season (August to November) and shrink to less than 140 μ during the winter. The enlargement of the entire testis during the breeding season is brought about in this way, and the volume of interstitial tissue does not alter greatly although variations in the size and cytology of the interstitial cells have been observed.

All stages of spermatogenesis are seen in testes collected prior to mid-November, and nearly all of the males have entered anoestrus by December. The production of multi-nucleate giant cells accompanies the beginning of anoestrus and is interpreted as being a type of rapid degeneration of the germinal epithelium.

5. The epididymis also undergoes enlargement during the breeding season, reaching its maximum diameter of about 450 μ later than the seminiferus tubules. It shrinks to about 220 μ in anoestrus. The accompanying variations in the histology have been described.

6. The anatomy of the female reproductive organs is described and the occasional occurrence of an *os clitoridis* reported.

7. From ovarian evidence, sexual maturity is usually attained at about twenty-four months in the female, but one female is known to have become mature at twelve months and two matured at three years.

8. In the majority of females the right ovary ovulates first and the ovaries alternate in function in successive pregnancies. This is necessitated by the rapid onset of post-partum heat.

9. From the proportion of non-pregnant animals in the material it is inferred that, with individual variations, the ovaries alternate in function until the fifth or sixth pregnancy, when "missed pregnancies" first become frequent, partly owing to the retardation of pupping. Each cow reaching maturity produces an average of seven pups during her lifetime.

10. There is some evidence that if a female is not successfully fertilised during the breeding season a number of dioestrus cycles ensue, probably followed by an anoestrous period. In almost 90 per cent of the population of mature females, the first ovulation results in pregnancy and the polyoestrous condition is suppressed.

11. Implantation of the blastocyst is delayed for about four months, from November until March. For most of this period the blastocyst remains small, but one egg-shaped, transparent, unattached blastocyst measuring 8 mm. in longest diameter was collected in February.

12. The growth in length of the embryo from implantation to parturition is shown.

13. The variations in the histology of the reproductive tract throughout the annual cycle are described, and conclusions are drawn as to the endocrine factors responsible.

14. Follicular development in the non-pregnant female conforms to the usual mammalian pattern. The mean diameter of the ovum in the primary follicle is 25 μ; growth is rapid until the ovum is about 90 μ in diameter and the follicle 150 μ, when antrum formation and secretion of *liquor folliculi* results in increased growth of the follicle, while the ovum grows more slowly up to about 140 μ.

At the end of pregnancy, neither ovary has any follicles over 4 mm. in diameter, but immediately after parturition, the follicles in the ovary without the regressing *corpus luteum* enlarge rapidly. At ovulation, about nineteen days later, only one follicle ovulates having reached the size of 15.0 mm. In the latter part of proestrum, the development of other follicles is suppressed. The follicles in the ovary containing the regressing *corpus luteum* continue to regress until after ovulation. Then both ovaries exhibit a burst of follicular activity, evidenced by an increase in the number and size of follicles, and the numbers of small atretic follicles. The follicles do not undergo pre-ovulationary differentiation but become cystic and gradually regress during the free-blastocyst period. After implantation, when the embryo is about 15–20 mm. long, there is a second similar phase of follicular activity, and for the remainder of pregnancy the follicles are small and atretic. It is possible that a third phase of follicular activity occurs, but there is no material from June and July available to verify this.

15. The *corpus luteum* appears to develop in the usual mammalian fashion so that it measures about 17.3 mm. in December. Growth during the free-blastocyst period is slow, and at implantation in March it is about 18.0 mm. in diameter. Two months after implantation, when the embryo measures about 30 mm., the *corpus luteum* again increases rapidly from an average diameter of 18.7 mm. to 22.7 mm. This is preceded, and perhaps caused, by the burst of follicular activity. The luteal cells during the period of delay are at first heavily vacuolated, then the vacuoles disappear and refractile secretory droplets develop in the cytoplasm just prior to implantation. At implantation, the secretion fills the intercellular spaces, and the vascularisation is more extensive. After implantation, the cells gradually shrink and connective tissue is laid down. The intercellular spaces increase and it appears that the enlargement of the gland observed in May is brought about by accumulation of fluid. These changes are most marked in the centre, and result in the *corpus luteum* having a fluid-filled central cavity near term. Retrogression is accompanied by the accumulation of luteolipin in the luteal cells.

The *theca interna* cells persist as small clusters at the periphery of the *corpus luteum*, at least until implantation.

At parturition, the *corpus luteum* is about 18.0 mm. in diameter and the luteal cells are still recognisable. They become progressively more shrunken, so that just after the initiation of the next pregnancy it measures about 11.0 mm. and has a hard connective tissue core. Phagocytosis and hyaline degeneration produce a *corpus albicans* which usually persists until the following breeding season.

16. Towards the end of pregnancy changes occur in the endometrium; the glands proliferate, become very tortuous, and exhibit secretory activity. Following parturition, this appearance of activity diminishes, the glands becoming smaller and almost straight and the surface epithelium low cuboidal. Then further proliferation occurs, and during oestrus the endometrium has many greatly coiled glands and a pseudo-stratified surface epithelium with two types of cell, one of which bears cilia. Ciliated cells are also found in the glands. In the post-ovulation material there are fewer ciliated cells and the necks of the glands open widely, giving the border of the lumen a serrated or fringed appearance. During the free-blastocyst period the mucosa reverts to the inactive condition, progestational changes occurring just before implantation.

17. The vaginal mucosa of females approaching parturition is characterised by hypertrophy and mucification of the superficial layer. This is succeeded, after parturition, by desquamation of the mucus cells and by stratification and cornification of the superficial layer during oestrus. After ovulation desquamation of the cornified layers occurs, and during the first part of the free-blastocyst period a superficial layer of mucified columnar cells is present. The epithelium later becomes transitional and desquamation occurs at implantation. After implantation mucification of the epithelium again occurs, and is followed by stratification and slight cornification.

18. An attempt is made to elucidate the endocrine factors responsible for these histological changes. It appears that during the free-blastocyst period both oestrogen and progesterone are secreted. The endocrine balance gradually moves in favour of progesterone, possibly being influenced by the moult process which precedes implantation.

In a brief discussion of the phenomenon of delayed implantation in the Pinnipeds, a hypothesis is advanced which explains that, by means of delaying implantation of the blastocyst, mating can occur when the animals are more concentrated geographically, thus ensuring greater reproductive efficiency.

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VII. REFERENCES

ALLANSON, M. 1932. The reproductive process of certain mammals. III. The reproductive cycle of the male ferret. *Proc. roy. Soc.*, B, **110**, 295.

————. 1934. Seasonal variation in the reproductive organs of the male hedgehog. *Phil. Trans.*, B. **223**, 277–303.

ALLEN, B. M. 1904. The embryonic development of the ovary and testis of the mammals. *Amer. J. Anat.*, **3**, 89.

AMOROSO, E. C., J. L. HANCOCK & I. W. ROWLANDS. 1948. Ovarian activity in the pregnant mare. *Nature, Lond.*, **161**, 355–6.

————, R. J. HARRISON, L. H. MATTHEWS & I. W. ROWLANDS. 1951. Reproductive organs of near term and new-born seals. *Nature, Lond.*, **168**, 771.

ASDELL, S. A. 1946. *Patterns of Mammalian Reproduction.* Comstock, Ithaca, X+437 pp.

———— & G. W. SALISBURY. 1941. The rate at which spermatogenesis occurs in the rabbit. *Anat. Rec.*, **80**, 145.

BARTHOLOMEW, G. A., Jr., & P. G. HOEL. 1953. Reproductive behaviour of the Alaska fur seal *Callorhinus ursinus*. *J. Mammal*, **34**, 4, 417–36.

BERTRAM, G. C. L. 1940. The biology of the Weddell and crabeater seals; with a study of the comparative behaviour of the Pinnipedia. *Brit. Grahamld. Exped.*, 1934–37, *Sci. Rep.*, **1**, 1–139.

BRAMBELL, F. W. R. 1935. Reproduction in the common shrew (Sorex araneus Linnaeus) *Phil. Trans.*, B, **225**, 1–62.

BURROWS, H. 1945. *Biological Actions of Sex Hormones.* Cambridge.

CAMERON, A. T. 1945. *Recent Advances in Endocrinology.* London.

CHAPSKY, K. & K. KOVOLEV. 1938. Game mammals of the Barents' and Kara Seas. *Trans. arct. Inst., Leningr.*, **123**, 1–70.

COLLINS, G. 1940. Habits of the Pacific walrus (*Odobenus divergens*). *J. Mammal.*, **21**, 138–44.

CORNER, G. W. 1921. Cyclic changes in the ovaries and uterus of the sow and their relations to the mechanism of implantation. *Contr. Embryol. Carneg. Instn.*, **9**, 85.

————. 1945. Development organisation and breakdown of the corpus luteum in the rhesus monkey. *Contr. Embryol. Carneg. Instn.*, **31**, 117.

COURRIER, R. 1927. Étude sur le determinisme des charactères sexuels secondaires chez quelques mammifères. *Arch. Biol., Liège*, **37**, 175–329.

DAWSON, A. B. 1941. The development and morphology of the corpus luteum of the cat. *Anat. Rec.*, **79**, 155–77.

———— & B. A. KOSTERS. 1944. Pre-implantation changes in the uterine mucosa of the cat. *Amer. J. Anat.*, **75**, 1–38.

DEANESLEY, R., 1930a. The corpora lutea of the mouse with special reference to fat accumulation during its oestrous cycle. *Proc. roy. Soc.*, B, **106**, 578–95.

————. 1930b. The development and vascularisation of the corpus luteum in the mouse and rabbit. *Proc. roy. Soc.*, B, **107**, 60–76.

————. 1934. The reproductive processes of certain mammals. Part VI. The reproductive cycle of the female hedgehog. *Phil. Trans.*, B, **223**, 239.

————. 1935. The reproductive processes of certain mammals. IX. The Stoat. *Phil. Trans.*, B, **225**, 459–92.

————. 1943. Delayed implantation in the stoat (Mustela mustela). *Nature, Lond.*, **151**, 365–6.

DUBREUIL, G. & M. RIVIÈRE. 1946. Morphologie et histologie des corps progestatifs et gestatifs de l'ovaire féminin. *Gynécologie*, **43**, 65, 97 and 130.

ENDERS, R. K., O. P. PEARSON & A. K. PEARSON. 1946. On certain aspects of reproduction in the fur seal. *Anat. Rec.*, **94**, 213–26.

EVANS, H. M. & H. H. COLE. 1931. An introduction to the study of the oestrus cycle in the dog. *Mem. Univ. Calif.*, **9**, 65.

FAY, F. H. 1952. The Pacific walrus. A progress report of field investigations conducted during 1952. MS. Arctic Inst.

————. 1953. The Pacific walrus. A progress report of laboratory work on the specimens collected in the 1952 field season. MS. Arctic Inst.

————. 1954. The Pacific walrus. A progress report of field and laboratory work in 1954. MS. Arctic Inst.

FISHER, H. D. 1952. The status of the harbor seal in British Columbia. *Bull. Fish. Res. Bd. Canada., No.* 93.

————. 1954. Delayed implantation in the harbour seal, *Phoca vitulina* L. *Nature, Lond.*, **173,** 879–80.

FLOWER, W. H. 1881. On the elephant seal, *Macrorhinus leoninus* Linn. *Proc. zool. Soc., Lond.*, **1881,** 145–62.

FOSTER, M. A. & F. L. HISAW. 1935. Experimental ovulation and resulting pseudopregnancy in anoestrus cats. *Anat. Rec.*, **62,** 75.

FRIES, S. 1880. Über die fortpflanzung von Meles taxus. *Zool. Anz.*, **3,** 486.

FUKUI, N. 1923. On a hitherto unknown action of heat ray on the testicles. *Japan med. World*, **3.**

GIBBNEY, L. 1953. Delayed implantation in the elephant seal. *Nature, Lond.*, **172,** 590.

GILLMAN, J. 1941. A quantitative study of the inhibition of the ovary and of the turgescent perineum of the normal baboon produced by a single injection of estradiol benzoate. *Endocrinology*, **29,** 633–8.

HAMILTON, J. E. 1934. The southern sea lion, *Otaria byronia* (De Blainville). "*Discovery*" *Rep.*, **8,** 269–318.

————. 1939a. The leopard seal, *Hydrurga leptonyx* (De Blainville). "*Discovery*" *Rep.*, **18,** 239–64.

————. 1939b. A second report on the southern sea lion, *Otaria byronia* (De Blainville). "*Discovery*" *Rep.*, **19,** 121–64.

HAMILTON, W. J. & J. H. GOULD. 1940. The normal oestrus cycle of the ferret. The correlation of the vaginal smear and the histology of the genital tract, with some notes on the distribution of glycogen, the incidence of growth, and the reaction to intravitam staining by trypan blue. *Trans. roy. Soc. Edin.*, **60,** 87.

HAMILTON, W. J. & R. J. HARRISON, 1951. Cyclical changes in the uterine mucosa and vagina of the goat. *J. Anat., Lond.*, **85,** 316–24.

HAMLETT, G. W. D. 1932a. Observations on the embryology of the badger. *Anat. Rec.*, **53,** 283.

————. 1932b. The reproductive cycle of the armadillo. *Z. wiss. Zool.*, **141,** 143.

————. 1935. Delayed implantation and discontinuous development in mammals. *Quart. Rev. Biol.*, **10,** 432–7.

HAMMOND, J. 1927. *The Physiology of Reproduction in the Cow.* Cambridge.

————. 1941. Fertility in mammals and birds. *Biol. Rev.*, **16,** 165.

————. 1952. Fertility. In: *Marshall's Physiology of Reproduction* Vol. II. Ed. A. S. Parkes. London.

HANSSON, A. 1947. The physiology of reproduction in mink (*Mustela vison, Schreb.*) with special reference to delayed implantation. *Acta zool. Stockh.*, **28,** 1–136.

HARRISON, R. J. 1948a. The changes occurring in the ovary of the goat during the oestrus cycle and in early pregnancy. *J. Anat., Lond.*, **82,** 21–48.

————. 1948b. On the development and fate of the corpus luteum in the vertebrate series. *Biol. Rev.* **23,** 296–331.

————. 1950. Observations on the seal ovary. *J. Anat., Lond.*, **84,** 400.

———— & L. H. MATTHEWS. 1950. Sub-surface crypts in the cortex of the mammalian ovary. *Proc. zool. Soc. Lond.*, **120,** 699.

————, ———— & J. M. ROBERTS. 1952. Reproduction in some pinnipedia. *Trans. zool. Soc., Lond.*, **27,** 437–531.

HAVINGA, B. 1933. Der Seehund (*Phoca vitulina* Linn.) in den Hollandischen gewassern. *Tijdsher ned. dierk. Ver.*, **III,** 79–111.

HILL, M. 1939. The reproductive cycle of the male weasel (*Mustela nivalis*). *Proc. zool. Soc. Lond.*, **109,** B, 481–512.

HISAW, F. L. 1947. The development of the Graafian follicle and ovulation. *Physiol. Rev.*, **27,** 95.

KENYON, K. W., V. B. SCHEFFER & D. G. CHAPMAN. 1954. A population study of the Alaska fur seal herd. *U.S. Fish and Wildlife Service, Spec. Sci. Rep. Wildlife* No. 12, 1–77.

LAWS, R. M. (Unpublished). F.I.D.S. Base H Biological Report. Dec. 1948–Nov. 1949. MS. F.I.D.S. Sci. Bureau, unpublished report No. 71/50.

————. 1952. A new method of age determination for mammals. *Nature, Lond.*, **169,** 972.

————. 1953. The life history of the elephant seal. *The Challenger Soc., 3, no. V, Abstr. of papers* 1952, *p. 18.*

————. 1953a. The elephant seal industry at South Georgia. *Polar Rec.*, **6,** No. 46, 746–54.

————. 1953b. A new method of age determination for mammals with special reference to the elephant seal *Mirounga leonina* Linn. *Falkland Islands Dependencies Survey Sci. Rep.*, No. 2, 11 pp.

————. (1953c, unpublished). Reproduction of the southern elephant seal *Mirounga leonina* Linn. Ph.D.Thesis, Univ. Cambridge, xviii + 191 pp.

————. 1953d. The elephant seal (*Mirounga leonina* Linn.) I. Growth and Age. *Falkland Islands Dependencies Survey Sci. Rep.* No. 8, 1–62, 5 pls., 28 figs.

————. 1956. The elephant seal (*Mirounga leonina* Linn.) II. General and reproductive behaviour. *Falkland Islands Dependencies Survey Sci. Rep.*, No. 13, 1–88, 7 pls., 30 figs.

LONG, J. A. & H. M. EVANS. 1922. The oestrus cycle in the rat and its associated phenomena. *Mem. Univ. Calif.*, **6,** 1–148.

MCLEAN, D. & I. W. ROWLANDS. 1942. Rôle of hyaluronidase in fertilisation. *Nature, Lond.*, **150,** 627.

MANSFIELD, A. W. (In press). The breeding behaviour and reproductive cycle of the Weddell seal (*Leptonychotes weddelli* Lesson). *Falklands Islands Dependencies Survey Sci. Rep.*

MARSHALL, F. H. A. 1922. *The Physiology of Reproduction.* London.

————. 1933. Cyclical changes in the vagina and vulva of the ferret. *Quart. J. exp. Physiol.*, **22,** 131.

———— & J. C. MOIR. 1952. Parturition. Ch. 19 in: *Marshall's Physiology of Reproduction*, **2** (Ed. A. S. Parkes), 496–524.

MATTHEWS, L. H. & R. J. HARRISON. 1949. Subsurface crypts, oogenis and the corpus luteum in the ovaries of seals. *Nature, Lond.*, **164,** 587–8.

MAXIMOV, A. A. & W. BLOOM. 1943. *Textbook of Histology*. London.

MOORE, C. R. 1924a. Testicular reactions in experimental cryptorchids. *Amer. J. Anat.*, **34,** 269–316.

————. 1924b. The function of the scrotum. *Amer. J. Anat.*, **34,** 337–58.

MURIE, O. J. 1936. Notes on the mammals of St. Lawrence Island, Alaska. *Appendix* 3. *In: Archeological excavations at Kukulik, St. Lawrence Island, Alaska, by Otto Wm. Geist and Froelich G. Rainey*. **2,** *Misc. Publ. Univ. of Alaska. Washington.*

NELSON, W. O. 1929. Oestrus during pregnancy. *Science*, **70,** 543.

OLIVER, J. R. 1913. The spermatogenesis of the Pribilof fur seal (*Callorhinus ursinus* Jordan and Clarke). *Amer. J. Anat.*, **14,** 473–99.

PARKER, G. H. 1931. The passage of sperms and eggs through the oviducts of terrestrial vaetebrates. *Phil. Trans.*, B, **219,** 381–419.

PARKES, A. S. 1931. The reproductive processes of certain mammals. II. The size of the Graafian follicle at ovulation. *Proc. roy. Soc.*, B, **109,** 185.

PEARSON, O. P. 1949. Reproduction of a South American rodent, the mountain viscacha. *Amer. J. Anat.*, **84,** 143–73.

PEARSON, A. K. & R. K. ENDERS. 1951. Further observations on the reproduction of the Alaskan fur seal. *Anat. Rec.*, **111,** 695–711.

PERRY, J. S. 1953. The reproduction of the African elephant, *Loxodonta africana. Phil. Trans.*, B, **237,** 93–149.

RAND, R. W. 1949. Studies on the Cape fur seal. (*Arctocephalus pusillus*, Schreber). 3. Age-grouping in the male. *Union of South Africa, Govt. Guano Is. Admin. Progress Report*, 23 pp.

————. 1952. Fur Seals. Research and Management. *Invest. Rep. Div. Fish. S. Afr.* No. 15, 1–6. The Govt. Printer, Pretoria, S.A.

ROSSMAN, I. 1942. On the lipin and pigment in the corpus luteum of the rhesus monkey. *Contr. Embryol. Carneg. Instn.*, **30,** 99–109.

SCHEFFER, V. B. 1949. The clitoris bone in two pinnipeds. *J. Mammal.*, **30,** 269–70.

————. 1950. Growth of testes and baculum in the fur seal, *Callorhinus ursinus. J. Mammal.*, **31,** 384–94.

———— & J. W. SLIPP. 1944. The harbor seal in Washington State. *Amer. Midl. Nat.*, **32,** 373–416.

SHAFFNER, C. S. 1954. Feather papilla stimulation by progesterone. *Science*, **120,** 345.

SHARMAN, G. B. 1954. Reproduction in marsupials. *Nature, Lond.*, 173, 302–3.

SIERTS, W. 1950. Os clitoridis von *Zalophus californianus* Less. und *Sciurus vulg. fuscoater* altum. *Neue Ergebn. und Probleme der Zoologie, Leipzig*, 938–9.

SLEPTSOV, M. M. 1943. (On the biology of reproduction of the pinnipedia of the Far East.) (*Russian w. Engl. Summ.*) *Zool. Zh.* **22,** 109–28.

SNYDER, F. F. & G. W. CORNER. 1922. Observations on the distribution and function of the uterine ciliated epithelium in the pig, with reference to certain clinical hypotheses. *Amer. J. Obstet. Gynec.*, **3,** 358–66.

SPEERT, H. 1948. Local action of sex hormones. *Physiol. Rev.*, **28,** 23–50.

STARKS, D. J. 1928. The spermatogenesis of the Pribilof fur seal (*Callorhinus alascanus* Jordon & Clarke). *Amer. J. Anat.*, **40,** 471–99.

STOCKARD, C. R. 1928. Cellular changes in the fluid of the mammalian vagina. *Special Cytology*, **2,** sect. 33. (*Ed. E. V. Cowdry*) *New York.*

SWEZY, O. 1933. *Ovogenesis and its Relation to the Hypophysis*. Science Press, Philadelphia.

———— & H. M. EVANS. 1930. Ovarian changes in the rat. *Science*, **71,** 46.

TANDLER, J. & S. GROSS. 1911. Über den saisondimorphismus des Maulwurfhodens. *Arch. EntwMech.Org.*, **33,** 297–302.

VAN DER HORST, C. J. & J. GILLMAN. 1945. The behaviour of the Graafian follicle of *Elephantulus* during pregnancy, with special reference to the hormonal regulation of ovarian activity. *S. Afr. J. med. Sci.*, **10,** *Biol. Suppl.*, 1–14.

————, ————. 1946. The corpus luteum of *Elephantulus* during pregnancy—its form and function. *S. Afr. J. med. Sci.* **11,** *Biol. Suppl.*, 87.

WILKE, F. 1951. Pelagic fur seal research off Japan in 1950. *Preliminary study Natural Sources Section, General Headquarters, Supreme Commander for Allied Powers, Tokyo*, No. 67, 35 pp.

WRIGHT, P. L. 1942a. Delayed implantation in the long-tailed weasel (*Mustela frenata*), short-tailed weasel (*M. cicognam*) and marten (*Martes americana*). *Anat. Rec.*, **83,** 341–53.

————. 1942b. A correlation between the spring moult and spring changes in the sexual cycle of the weasel. *J. exp. Zool.*, **91,** 103–10.

————. 1947. Sexual cycle of the male long-tailed weasel (*Mustela frenata*). *J. Mammal.*, **28,** 243–52.

ZANDER, J. 1954. Progesterone in human blood and tissues. *Nature, Lond.*, **174,** 406–7.

ZUCKERMAN, S. & A. S. PARKES. 1932. The menstrual cycle of the primates. V. The cycle of the baboon. *Proc. zool. Soc. Lond.*, 1932, 138.

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PLATE I

(Lines represent 50 μ)

a. Section of the testis of a 49 cm. foetus (M78.9).

b. Section of the testis of M90, aged 107 months, September 8th, in phase A.

c. Section of the testis of M117, aged eighty-three months, September 10th, in phase B.

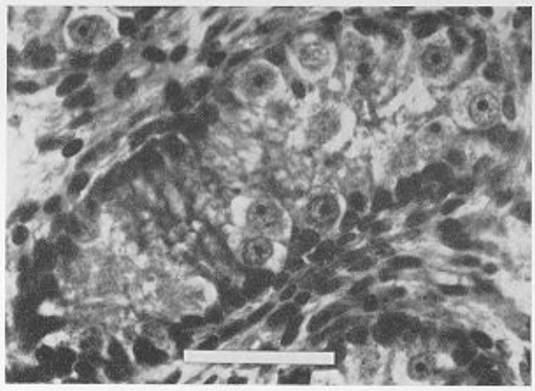
d. Section of the testis of H337, aged eighty-six months, December 19th, showing giant cells.

e. Section of the testis of M53, aged fifty-three months, April 3rd, showing winter spermatogonia.

f. Section of the epididymis of M88, aged fifty-nine months, September 8th, showing brush border.

g. Section of the epididymis of M64, aged sixty-five months, April 6th; desquamation beginning.

h. Section of ovary of H294, aged four months, showing developing follicles.



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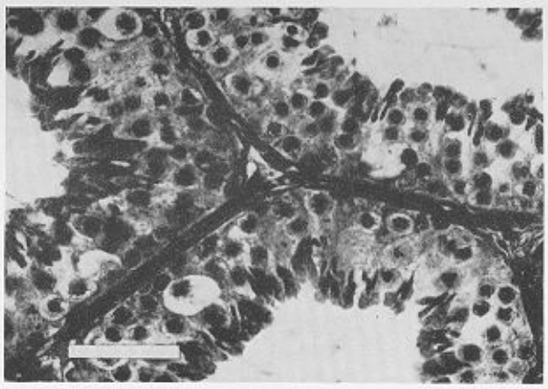

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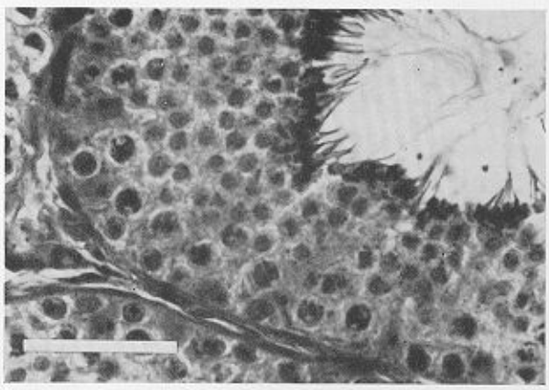

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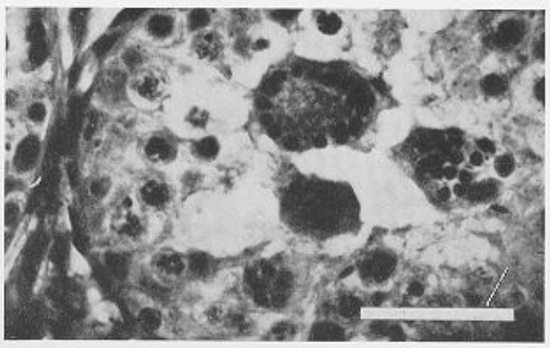

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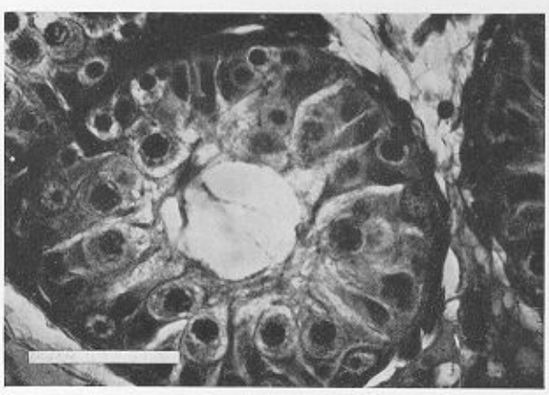

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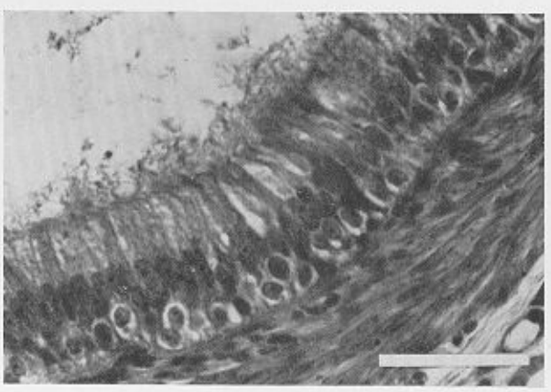

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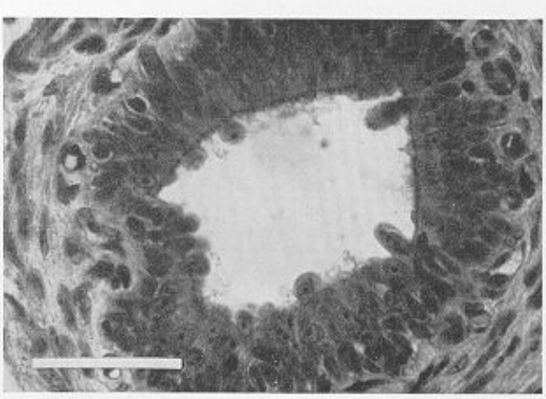

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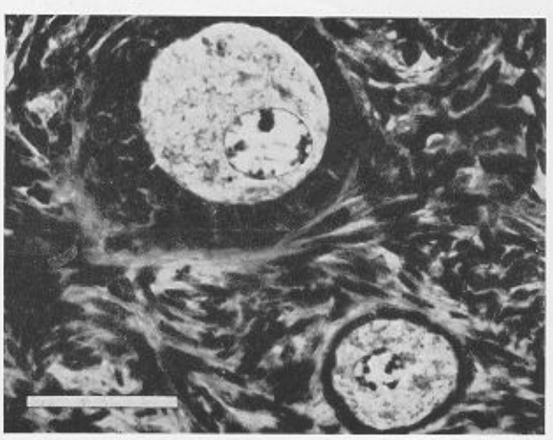

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PLATE II

(*Lines represent* 50 μ)

a. Section of ovary of H294, aged four months; follicle showing stage of incipient antrum formation.

b. Section of ovary of H294, aged four months; follicle with large antrum and ovum surrounded by *discus proligerus*.

c. Section of *corpus luteum* of H341, aged twenty-six months, December 20th, showing vacuolation of luteal cells.

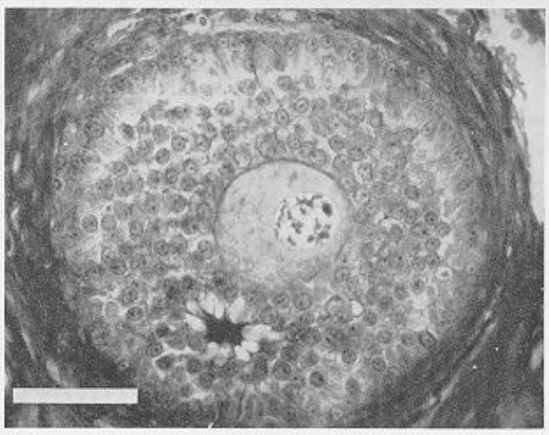
d. Section of *corpus luteum* of H286, aged eighty-eight months, February 16th.

e. Section of *corpus luteum* of M16, aged 113 months, March 19th; note refractile granules.

f. Section of *corpus luteum* of M17, aged 185 months, March 21st.

g. Section of *corpus luteum* of M32, aged twenty-nine months, April 10th, foetus 248 mm.

h. Section of *corpus luteum* of M128, aged ninety-six months, three days post-partum.



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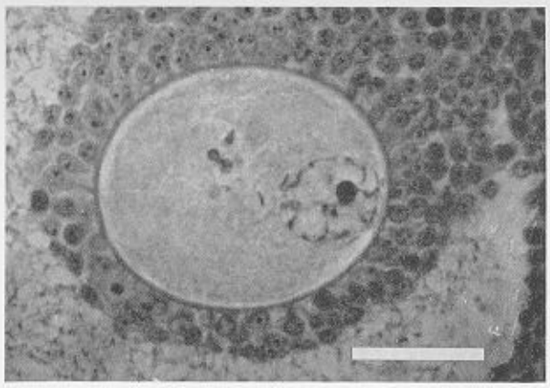

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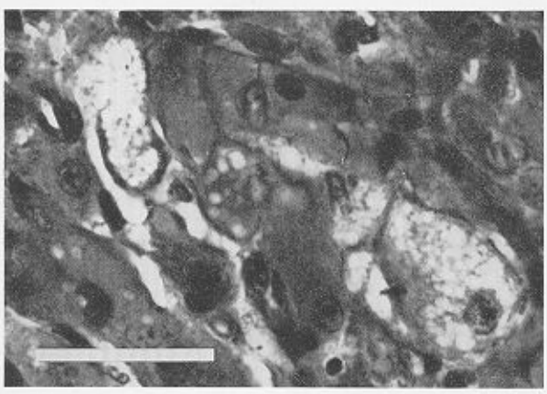

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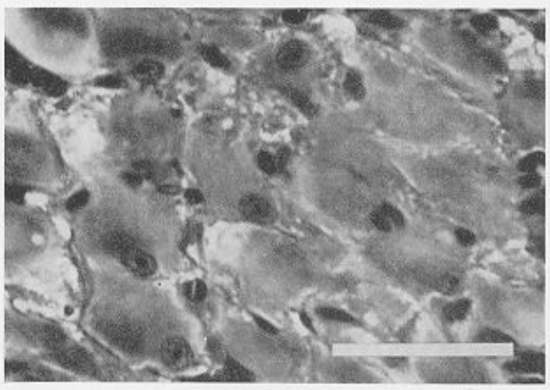

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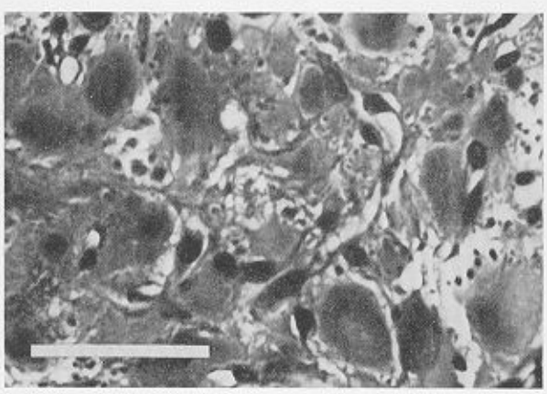

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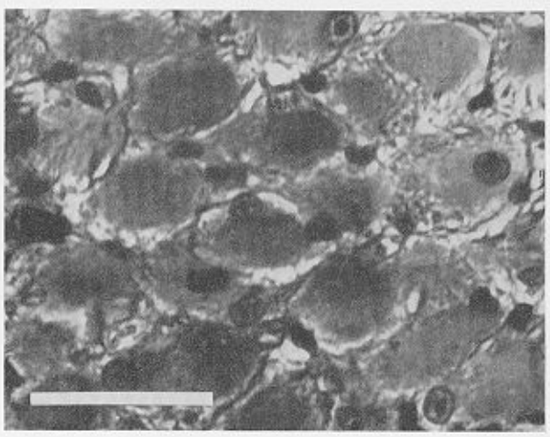

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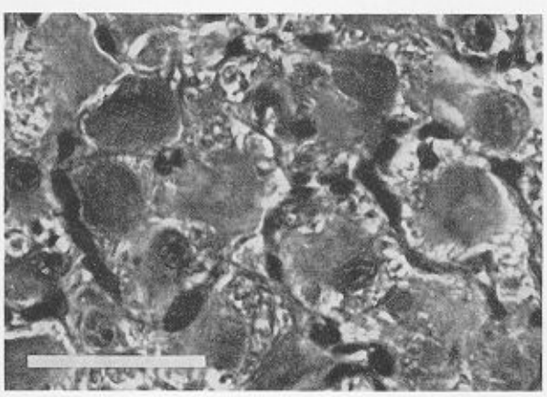

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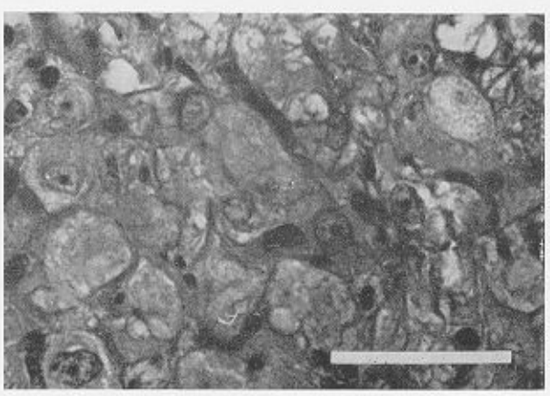

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PLATE III

a. Section of left (recently sterile) uterine horn of M128, aged ninety-six months, three days post-partum. Line represents 100 μ.

b. Section of right (recently sterile) uterine horn of M136, aged thirty-six months, sixteen days post-partum. Note basal vacuoles in epithelium. Line represents 50 μ.

c. Section of left (recently sterile) uterine horn of M140, aged 108 months, fourteen days post-partum. Note apical vacuoles in glands. Line represents 50 μ.

d. Section of gland in right (recently sterile) uterine horn of M136, aged thirty-six months, sixteen days post-partum. Note cilia. Line represents 50 μ.

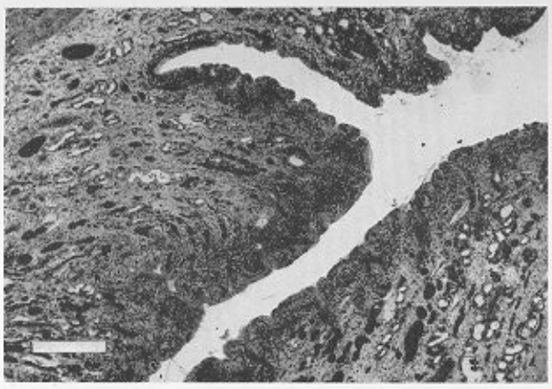
e. Section of right (active) uterine horn of H341, aged twenty-six months, December 20th. Line represents 500 μ.

f. Section of left (active) uterine horn of M15, aged forty-one months, March 19th; implanting trophoblast. Line represents 50 μ.

g. Section of right (active) uterine horn of H341, aged twenty-six months, December 20th; showing probable basal glycogen deposits and apical displacement of nuclei. Line represents 50 μ.

h. Section of left (active) uterine horn of M15, aged forty-one months, March 19th. Note implanting blastocyst. Line represents 500 μ.

i. Section of para-placental zone of right (active) uterine horn of M6, aged 113 months, March 17th, with 39 mm. embryo. Line represents 500 μ.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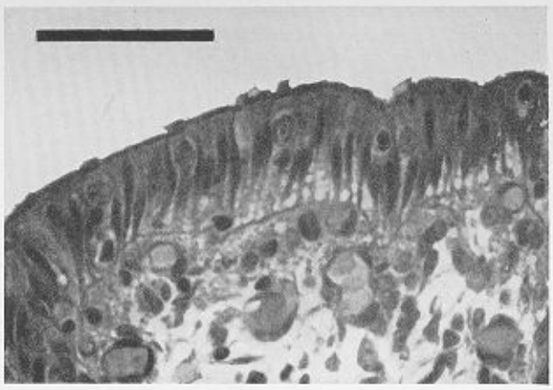
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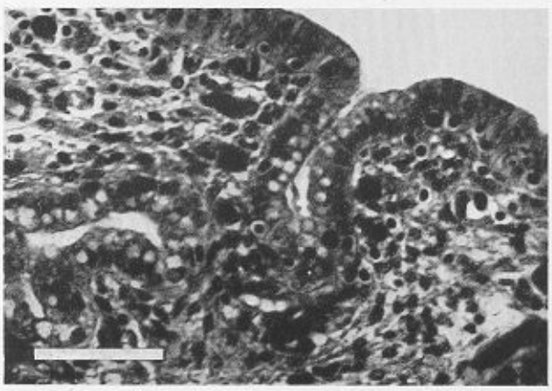
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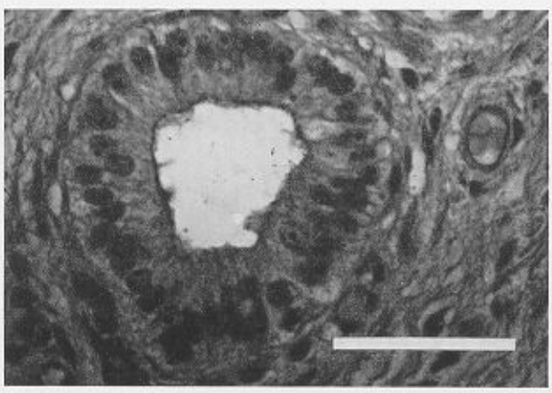
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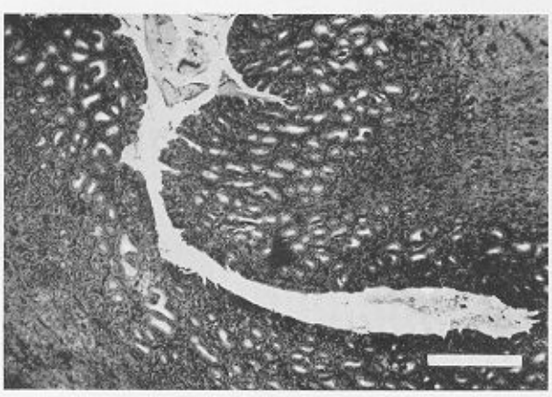
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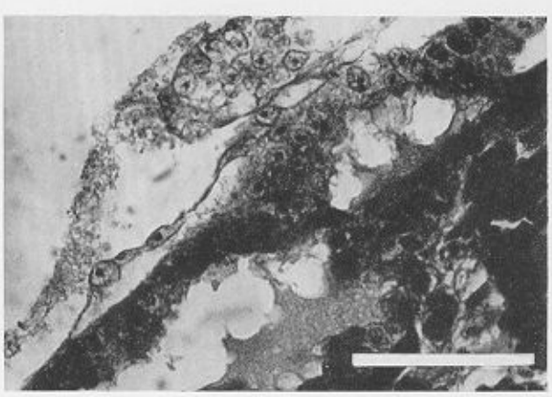
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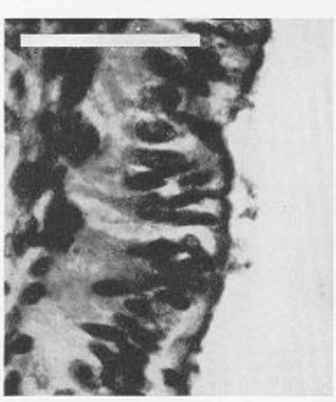
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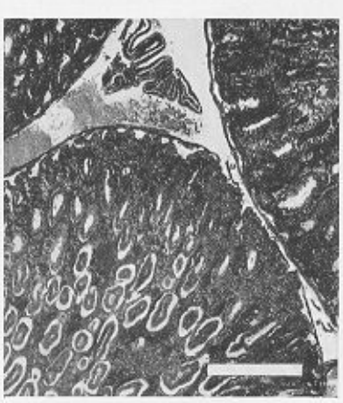
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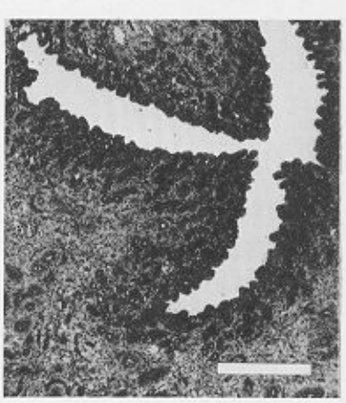
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PLATE IV

a. Section of developing placenta of M18, aged sixty-five months, March 21st. Line represents 500 μ.

b. Section of right (recently active) uterine horn of M128, aged ninety-six months, three days post-partum. Line represents 50 μ.

c. Section of right (sterile) uterine horn of M18, aged sixty-five months, March 21st, with 32 mm. embryo in left horn. Line represents 500 μ.

d. Section of right (sterile) uterine horn of M9, aged 137 months, March 17th, with 23 mm. embryo in left horn. Line represents 500 μ.

e. Section of right (sterile) uterine horn of M9, aged 137 months, March 17th. Line represents 50 μ.

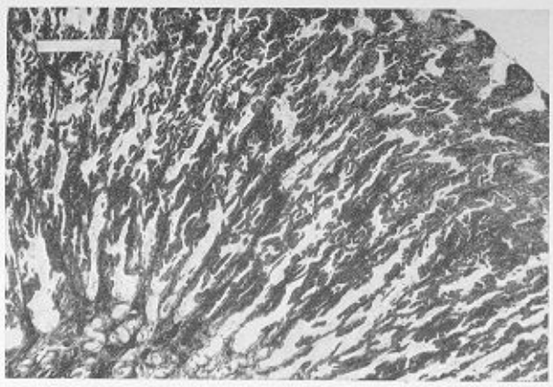
f. Section of right (sterile) uterine horn of M73, aged forty-three months, May 10th, with 41 cm. foetus in left horn. Line represents 500 μ.

g. Section of left uterine horn of M67, aged 139 months, April 25th; note thick walled arteries. Line represents 500 μ.

h. Section of *corpus luteum* of M67, aged 139 months, April 25th. Line represents 500 μ.

i. Section of *corpus luteum* of M73, aged forty-three months, May 10th, with 41 cm. embryo. Line represents 500 μ.

j. Section of left uterine horn of M13, aged 125 months, March 19th. Line represents 500 μ.



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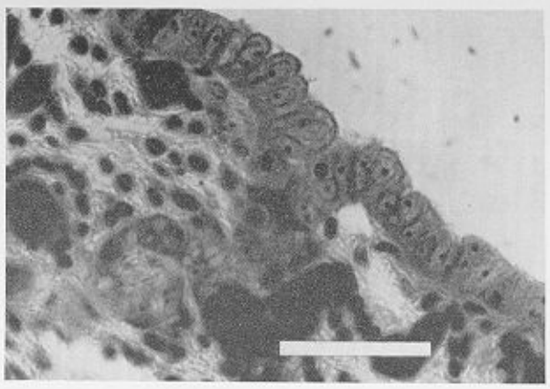

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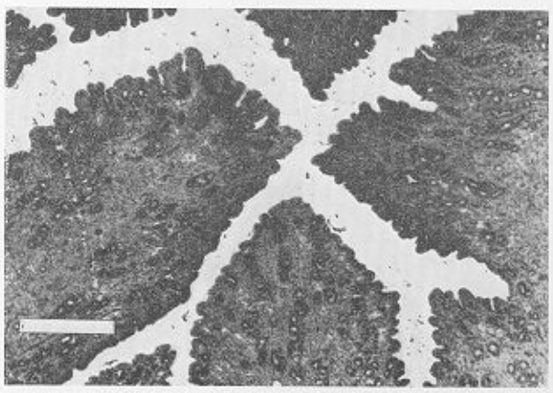

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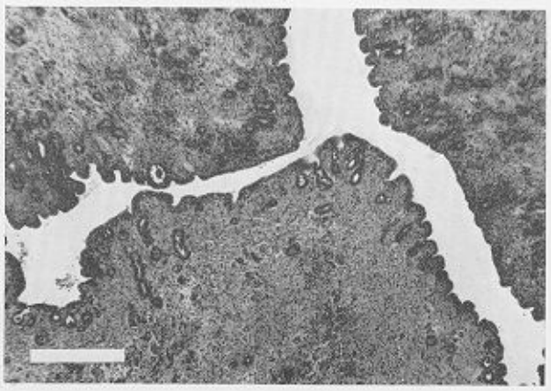

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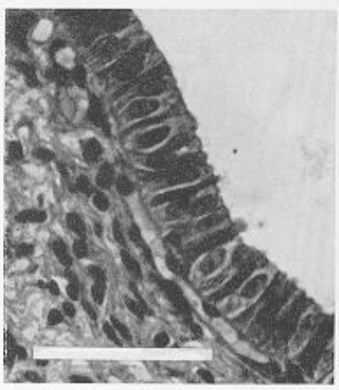

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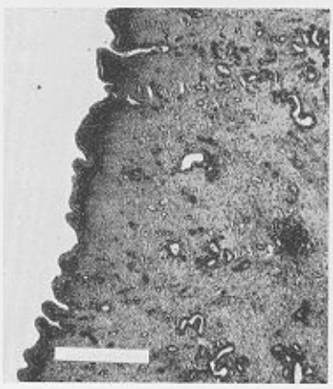

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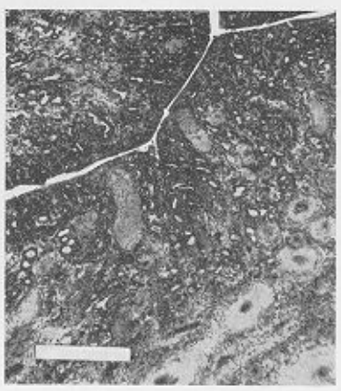

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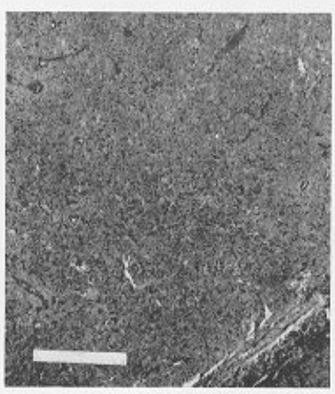

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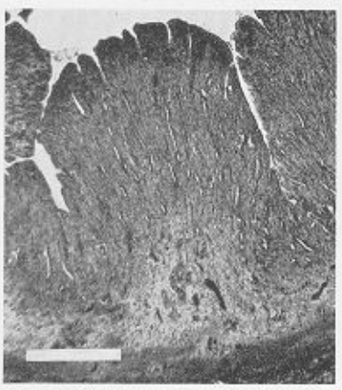


j

PLATE V

a. Section of the vagina of M128, aged ninety-six months, three days post-partum. Line represents 500 μ.

b. Section of vaginal epithelium of M129, aged thirty-six months, five days post-partum. Note superficial mucified cells. Line represents 50 μ.

c. Section of vaginal epithelium of M132, aged thirty-six months, six days post-partum. Note degenerating mucified cells and proliferation of intermediate layers. Line represents 50 μ.

d. Another section of the vaginal epithelium of M132. Line represents 50 μ.

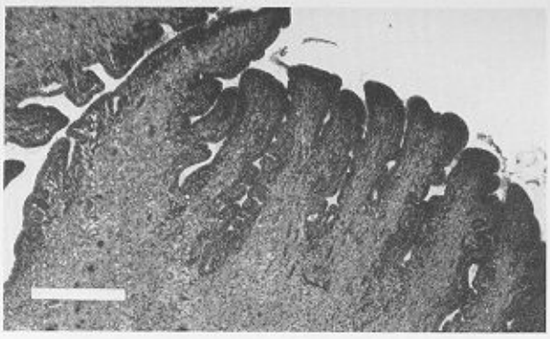
e. Section of vaginal epithelium of M141, aged thirty-six months, twelve days post-partum. Cornification advanced. Line represents 50 μ.

f. Section of vaginal epithelium of H300, aged 100 months, March 4th. Blastocyst implanting. Line represents 50 μ.

g. Section of vaginal epithelium of M11, aged forty-one months, March 19th. Blastocyst implanting. Line represents 50 μ.

h. Section of vaginal epithelium of M32, aged twenty-nine months, April 10th, with 248 mm. foetus. Note superficial mucified cells. Line represents 50 μ.

i. Section of vaginal epithelium of M13, aged 125 months, March 19th. Line represents 50 μ.



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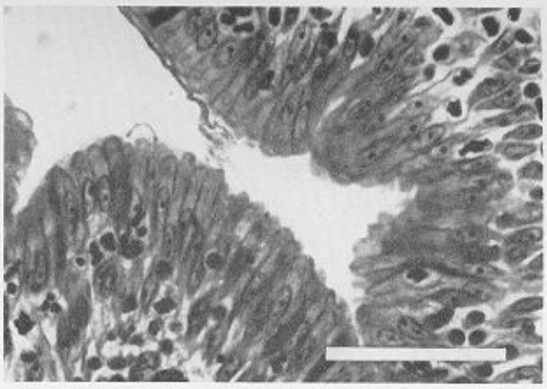

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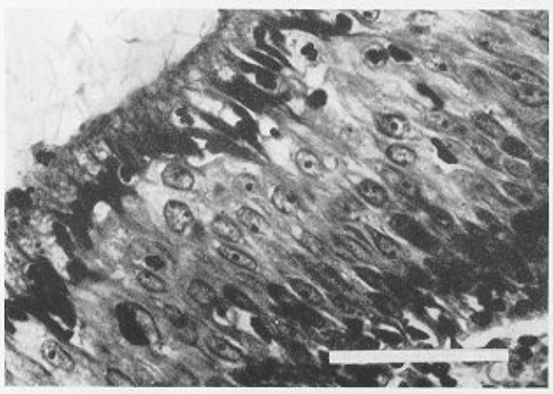

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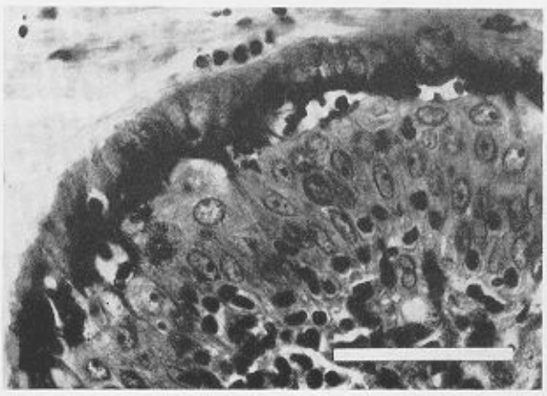

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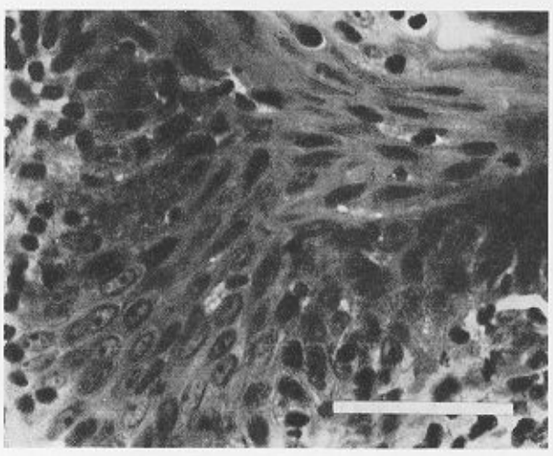

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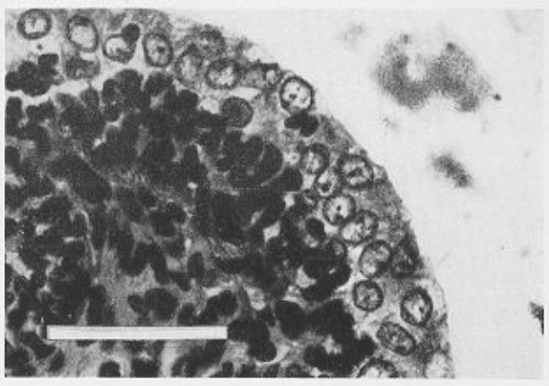

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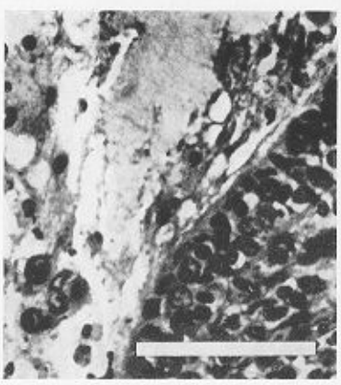

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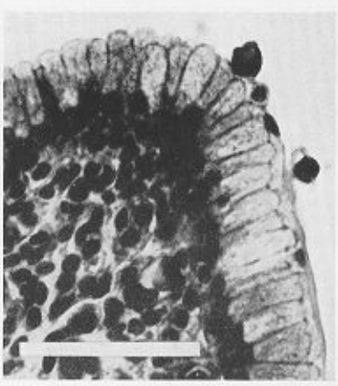

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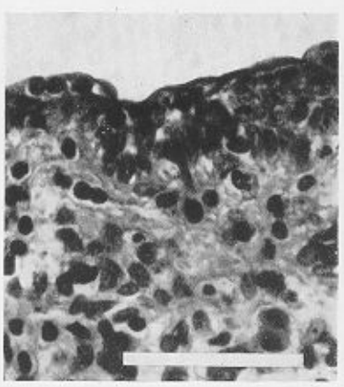

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