ON THE STRUCTURE AND DEVELOPMENT OF THE BURSA OVARICA and INFUNDIBULUM TUBAE in ELEPHANTULUS MYURUS JAMESONI: with special reference to the OVARIAL BURSA in MAMMALS, and to its FUNCTION.

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A DISSERTATION PRESENTED FOR
THE DEGREE OF MASTER OF SCIENCE
in the WITWATERSRAND UNIVERSITY.

1950.

Theses.

A C K N O W L E D G E M E N T.

The material examined for this thesis, is part of a collection of serial sections of Elephantulus myurus jamesoni, collected by Prof. C. J. van der Horst for his studies on this animal.

I have to thank Prof. van der Horst for the use of his material, and also for his untiring help and advice during my years under him.

I N D E X.

CHAPTER I.

The Bursa Ovarica in Mammals.

It is well known that in many invertebrates, even in some lower vertebrates, as in e.g. a large number of bony fishes, the ovary is tubular and continues directly into the duct apparatus of the female genitals. However, in many lower vertebrates, e.g. amphibians, there is no continuity, and no protection of the ovary in the coelomic cavity. In a large number of mammals we find an ovarial pocket developed, and it would seem that this structure would safeguard the passage of the eggs from the ovary to the oviduct at ovulation, as the mammalian ovum is relatively small and not many may be produced during ovulation.

Even if the bursa ovarica possesses some significance on this account in certain varieties of mammals, its more or less complete development has no direct relation to the procreative faculty of the animal group in question.

As early as the beginning of the last century a capsule or bladder was described which in several groups of mammals surrounded the ovary more or less completely. In mustela foina there is a complete sac round the ovary. In bats there is a similar bursa only here there is an opening into the abdominal cavity, but this opening is so small that the bursa could almost be looked upon as being entirely closed. Zuckerkandl gave a detailed account of the ovarial bursa in certain groups of mammals in his "Zur Vergleichenden Anatomie der Ovarial Taschen".

There is a strong variation in the structure of the bursa ovarica in mammals. Animals such as the dog, hedgehog, squirrel and bat have only a small opening through which the

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ovary protrudes into the peritoneal cavity. Ungulates and rabbits have a wide communication between the periovarial cavity and the coelomic cavity, and it is in these animals that there is a periodic opening and closing of the bursa ovarica.

Zuckerkandl and others have pointed out that the bursa ovarica is, in the main, histologically in complete accordance with the structure of the abdominal cavity, to which it is connected both anatomically and genetically.

By definition, a bursa ovarica is a peritoneal pocket developed as a result of the folding and twisting of the oviduct about the ovary. The supporting membranes of the oviduct, namely, the dorsal and ventral mesosalpinx, become stretched between the loops and so produce a pocket termed the bursa ovarica. Such a structure, which often encloses the ovary completely, is to be found in most mammals. Its presence is probably due to the fact that the relatively small ova, only a few of which are ovulated at a time, may become lost in the comparatively large body cavity were this structure lacking.

In the mouse Agduhr found an ovarian bursa completely enclosing the ovary from the abdominal cavity, and he traced the development of this bursa in the embryo. He found that in the mouse and in the white rat the main function of the bursa ovarica and tuba uterina was to convey the eggs after ovulation from the ovary to the uterine tube, and through the latter down to the uterus for fertilization. But he stressed that the importance of the bursa should not be over-rated as far as its role in egg transport is concerned. (Refer to Chapter VII).

Sobotta has shown that in the rabbit and also in the guinea-pig, the bursa ovarica is rather small and the ovary protrudes from it into the body cavity. This ovary is thus exposed to the peritoneal fluids. However, at the time of ovulation the bursa ovarica closes completely. In the rabbit this closure of the bursa is brought about by the action of the ventral mesosalpinx, which has well developed muscular fibres.

Zuckerkandl has also shown that a bursa ovarica in anoestrous may be anything from a shallow widely open pocket barely covering one side of the ovary (as is found in the rabbit), to a completely closed structure (as is found in the mouse). In the open type of bursa, e.g. rabbit and guinea-pig, there is the periodic opening and closing of the pocket in oestrous and anoestrous. Just before ovulation the bursa is drawn over the ovary, and except for a narrow slit the periovarian capsule encloses the periovarial cavity from the peritoneal cavity. This greatly enhances the chances of the discharged ova reaching the tubal egg chamber for fertilization. There are bundles of smooth muscle fibres running in the dorsal and ventral mesosalpinx from the uterus, and these, when they are stimulated are responsible for this action. Sobotta also thought it most probable that all those animals described by Zuckerkandl (1897) as having an open or poorly developed bursa ovarica might have such a closure of the bursa before ovulation.

Zuckerkandl also described an extensively developed infundibulum tubae replacing the bursa ovarica in Halmaturus Lessoni and Halmaturus Giganteus. In these animals however, the greatly enlarged infundibulum has not been drawn over the ovary and does not cover it.

In Suncus there is a closed bursa ovarica formed almost exclusively by the dorsal mesosalpinx. ~~Also in~~

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Also in Erinaceus Frontalis the bursa is a peritoneal structure formed by the dorsal and ventral mesosalpinx. In neither of these Insectivores is there any abnormal enlargement of the infundibulum tubae.

In Elephantulus there is a definite bursa ovarica formed by the dorsal and ventral mesosalpinx and the ligamentum ovarii and the mesovarium (van der Horst), but the ovary does not lie in it. The bursa is closed at all times except for a narrow slit in its postero-ventral surface. Here the greatly enlarged infundibulum tubae forms the periovarian capsule. In Macroscelides proboscideus and also in Petrodomus Tetradactylus, as described by Zuckerkandl, the greatly expanded infundibulum tubae covers the ovary entirely as in Elephantulus. These mammals shall be discussed later on in this work.

De Lange studied the ovarian bursa of Galeopitheous, Tupaja, and Chrysochloris. In Galeopithecus he found an ovary exposed in the body cavity, and it had an open type of bursa. The periodic opening and closing of this bursa is brought about by the particularly well developed erectile tissue in the ventral mesosalpinx. By the contraction of these oblique muscle fibres the bursa is drawn over the ovary at the time of ovulation. By their relaxation, and by the contraction of the muscle fibres in the dorsal mesosalpinx, the bursa is opened again when ovulation is over. In Galeopithecus there is also a particularly well developed system of venous blood cavities in the ovarian mesenteries. Dr. de Lange thought it unlikely that in this animal the blood cavities around the ovary were only developed to serve a nutritive function. They form a spongy sinus system, and there are also strongly developed Lymph cavities.

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The arterial system is not well developed and the arteries are fewer in distribution and smaller in size than the veins. De Lange compares the blood system here to that of the corpus cavernosum of the penis and is of the opinion that the blood becomes damned up in these cavities when the muscles, in which they are developed, contract. This might aid in the closure of the bursa ovarica.

In Tupaja there is also an ovarian bursa which is in open communication with the peritoneal cavity. The opening and closing of this pouch is much as in Galeopithecus, only here there is no excessive development of the blood and lymphatic vessels. The contraction and relaxation of the muscle fibres brings about this periodic development of the bursa. By the contraction of the oblique fibres in the ventral mesosalpinx the bursa is drawn over the ovary at the time of ovulation.

It is of interest here to briefly describe the condition of the ovary of Homo. Here the ovaries are attached by a thick membranous mesovarium to the broad ligament which supports the uterus. The ovaries are also attached to the side of the uterus by a broad ligament. Another suspensory ligament carrying blood vessels and nerves extends upwards from the ovary along the wall of the pelvis. The ovary is covered by a layer of columas epithelium, which is regarded as a modification of the peritoneum.

The coelomic opening of the ostium tubae in Homo is funnel-shaped. This funnel-shaped infundibulum tubae partially surrounds the ovary. The margin of the infundibulum is drawn out into numerous prolonged portions known as the fimbriae which surround the ovary and by a ciliary action convey the ova to the uterine tube.

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We therefore see that there are numerous structural differences in the bursa ovarica of the ovary of mammals, but that in all specimens there is some attemrt to protect the ovary and ova in the body cavity.

CHAPTER II.

The Bursa Ovarica of the Centetidae.

Another type of periovarial pouch has been described more recently by Landau in the Centetidae. He studied the ovary and its bursa in Hemicentetes, and it is of interest to discuss his findings.

In Hemicentetes the bursa is a widened and enlarged pouch of the infundibulum of the ostium tubae. This pouch is so developed as to spread out over the ovary towards the hilus ovarii. It does not however, completely enclose the ovarium and there is a wide communication between the periovarial and peritoneal cavities.

Morphologically Landau did not clearly understand what part the blood vessels and the lymphatic vessels in the hilus ovarii play in the opening and closing of the infundibulum tubae when this is drawn over the ovary to completely envelop it before ovulation. De Lange had found a very strongly developed system of blood and lymphatic vessels in Galeopithecus, and even though the vessels are not exceptionally well developed in the Centetidae, Landau thought that they might play some part in the opening and closing of the bursa.

In Hemicentetes there are smooth muscle fibres present in the wall of the ovarial pouch. These muscles are not particularly well developed, but could aid the action of the retractor muscle in closing the infundibulum before ovulation. It would seem, however, that the retractor muscle (from the peripheral part of the uterus to the ovary), is the most important apparatus for this closure.

In Hemicentetes it seems more probable (according to Landau) that the muscular action of the retractor apparatus is aided not so much by extra blood pressure, but by the large amounts of periovarial fluid which is found round the ovary just before ovulation.

The periovarial pouch, apart from the previously mentioned bursal ostium, at the region of the hilus, has a number of smaller holes in its wall. These perforations are found in the thinner areas of the wall, and at the bases of the folds in the wall. These folds are completely flattened out when the infundibulum tubae is drawn over the ovary, before ovulation. This, and their fine structure make it possible that they have arisen secondarily and accidentally as perforations.

Landau however, thought that these perforations served a function in the closure of the ovarian pouch. He promulgated the theory that there is an interchange of fluids through these perforations, and that they are specially adapted perforations for such an exchange. By the alternate contraction and relaxation of the wall of the pouch, by the retractor muscle, Landau maintained that the fluid was forced inwards and outwards in such a manner as to aid in the process of the closure of the periovarian sac before ovulation.

This stresses the question as to where the fluid in the ovarial pouch originates. It is usually and with justice, accepted that the fluid is identical with coelomic fluid, (only bacteriologically purer), and as such it is a Transudate of the blood. Landau however, states that in Hemicentetes the bursal wall shows both ciliary and secretory elements, as is the case in the ostium tubae and especially in the ampullary part of the tube. The secretory function of these wall cells is increased before ovulation.

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This is understandable, but it is difficult to believe that the peritoneal fluid should play any part, as one of the functions of the ovarian capsule is to protect it from the more or less harmful peritoneal fluid. One must believe that the perforations arose accidentally as a result of the wearing away of the bases of the folds of the pouch.

We can, therefore, conclude that in Hemicentetes, the infundibulum tubae is drawn over the ovary, but not completely so and that this complete envelopment is brought about by the action of the retractor muscle of the ovary, by the action of the muscle fibres in the wall of the pouch itself and aided by pressure caused by the periovarial fluid just before ovulation.

In Elephantulus and in the Macroscelidae in general - as previously mentioned - the ovary is quite enclosed by the expanded infundibulum tubae and that this envelopment is complete at all times except for a very narrow slit in the region of the mesovarium. The infundibulum is thrown into a number of folds in the region round the mesovarium, but no perforations are to be found. These folds allow for an increase in area as the ovary increases in size after ovulation and also protect the slit-like opening of the pouch before ovulation. The periovarial fluid plays no secondary role in Elephantulus.

CHAPTER III.

The Bursa Ovarica of the Chrysochloridae.

Dr. Daniel de Lange made a special study of the ovarian bursa of the Chrysochloridae. In Chrysochloris he found that the infundibulum tubae of the ostium tubae is also extensively developed. No matter what stage in the oestrous or anoestrous cycle this infundibulum is completely drawn over the ovary. His Figure 9 shows the infundibulum tubae drawn over the ovary as an ovarian capsule, much as is found in Elephantulus. The infundibulum was drawn over the ovary by contraction of the oblique muscle fibres of the ventral mesosalpinx, so that the ovary is completely enveloped by it.

Three golden moles which I personally studied, namely Amblysomus Hottentotus, Eremitalpa Grantii and Chrysotricha Obtusirostris have a similar capsule formed by the greatly developed infundibulum tubae, as is found in Elephantulus. This capsule surrounded the ovary during oestrous and anoestrous.

It can therefore be accepted as a general feature of the chrysochloridae that the further development of the infundibulum tubae transforms it into an ovarian pouch for the protection of the ovary.

It therefore seems unlikely that Dr. de Lange's Figure 7 was a drawing of a golden mole, as it is so completely different from the others. With all the other members of this family showing such a close resemblance in the structure of the infundibulum tubae, one has to suspect that Dr. de Lange received a wrongly labelled animal. Further specimens were sent to him but unfortunately he died before being able to rectify his article.

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I shall refer to De Lange's Figure 8 in greater detail in Chapter VI, as it shows a similar abnormality as witnessed in Elephantulus.

We thus see that the Chrysochloridae have an even better developed infundibulum tubae than the Centetidae, as in the Golden moles the ovary is always surrounded by a completely closed pouch.

CHAPTER IV.

The Structure of the Bursa Ovaria, the Infundibulum Tubae and the Ovarian Membrane in the Adult Female of Elephantulus.

In Elephantulus, another member of the Insectivores with a permanent ovarian capsule formed entirely by the infundibulum tubae, we find the following arrangement of the ovary, its surrounding pouch and its membranes.. They have been described in great detail by Dr. C.J. van der Horst.

The anterior part of the uterus in Elephantulus is connected by the mesometrium to the dorsal wall of the body cavity. At the top of the uterus, the mesometrium starts to split into a medial and a lateral part, the former is the ligamentum ovarii proprium, and the latter the mesosalpinx. These two ligaments have at first a common attachment to the dorsal coelomic wall, but more anteriorly they separate completely from one another and the mesosalpinx is attached more laterally and the ligamentum ovarii more medially to the coelomic wall. In Elephantulus the ventral mesosalpinx is well developed caudal to the ovary and it comes to an end at the posterior region of the ovarium. The dorsal mesosalpinx can be followed along the whole length, but lateral to the ovary. The ligamentum ovarii proprium can be followed in an anterior direction and it continues in the region of the hilus ovarii with the mesovarium. In front of the ovary it becomes the ligamentum suspensorium ovarii and this again fuses with the anterior extension of the dorsal mesosalpinx. The fused ligament then extends further in an anterior direction up to the dorsal lateral corner of the abdominal cavity, lateral to the posterior end

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of the kidney.

In Elephantulus, there is, therefore, a definite bursa ovarica formed by the dorsal and ventral memosalpinx and the ligamentum ovarii and the mesovarium. The same structure has been described by Zuckerkandl (1897), Gerhardt (1904), Sobotta (1916) and de Lange (1922) for various other mammals. The reason for the development of this ovarian pouch is that the mammalian eggs are relatively small and would be lost in the extensive abdominal cavity.

In Elephantulus, however, the ovary never lies in this bursa ovarica. In one specimen which had ovulated and had the infundibulum at the anterior end of the ovary as in the very young female, the ovary remained naked and did not lie in the bursa. The bursa ovarica remains closed at all times except for a narrow slit, no matter what the stage in the cycle is.

Although the ovary is not lying in this bursa, it is nevertheless quite enclosed and not lying freely exposed in the abdominal cavity. In Elephar[illegible] as in Hemicentetes (Landau 1938), the infundibulum tub[illegible] greatly expanded compared with that of other mammals. This expanded infundibulum surrounds the ovary completely. According to Sobotta, the infundibulum of the Monotremes, Marsupials and the Cetaceae is also very large and encloses the ovary completely. In Elephantulus, the infundibulum encloses the ovary like a sac, the opening of which is folded up and lightened around the mesovarium. The ovary just fits into this sac, there being only a narrow space left between the surface of the ovary and the infundibulum. But near its margin, where it embraces the mesovarium, the infundibular

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wall is thrown into many irregular folds. It seems certain that this arrangement allows for the greater enlargement of the ovary either when the massive corpora lutea form after ovulation or when large cysts develop in the ovary.

In Elephantulus, the uterine lip of the infundibulum is very well developed, and extends beyond the ovary. This uterine lip is for the greater part outside the bursa ovarica, as in the rabbit (Sobotta). However, as the ventral mesosalpinx does not partake in the formation of the sac round the ovary, the eggs would never come into contact with the uterine lip. Therefore, the uterine lip in Elephantulus does not function as in the rabbit where it prevents the eggs from escaping through the slit-like opening of the bursa into the abdominal cavity.

In front of the uterine lip, the margin of the infundibulum is fused to the mesovarium, but this fusion is only along ~~the along~~ the medial side of the mesovarium. The lateral part of the margin although often narrowly pressed against the mesovarium remains free. Thus the medic-anterior margin of the infundibulum in Elephantulus most probably corresponds to the ovarian lip of the infundibulum of the rabbit and other mammals.

The ostium tubae is found at the caudo-lateral side of the ovary. This is also very unusual, as in most other mammals the tube loops round the ovary drawing the mesosalpinx with it, thus forming the greater part of the bursa ovarica. The ostium tubae in such cases is situated at the side of the ovary away from the uterus as in the human female . In Elephantulus there is no such loop of the tube, and the ostium tubae is found at the uterine pole of the ovary

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from which place the infundibulum stretches out and covers the whole ovary.

Around the ostium tubae, the inner wall of the sac covered by the mucosa is drawn out into irregular outgrowths - the fimbriae ovaricae. The mucosal cells are here cylindrical and ciliated. But over the greater part of the ovarial sac, the inner wall is quite smooth and the epithelium is considerably thinner than in the fimbriated region. In the folded part of the sac around the mesovarium the mucosa consists again of cylindrical ciliated cells.

CHAPTER V.

The development of the Bursa Ovarica and Infundibulum Tubae in Elephantulus.

In regard to the actual development of the ovarical bursa we have but scanty and very incomplete statements in the literature on this subject. There are however two different views on the development of the bursa ovarica in mammals. According to one view it is developed from the same embryonic tissue as the ovary, but Zuckerkandl more rightly declares that the bursa is a secondary formation, arising after the ovary is formed, by the developments of rudiments round about the embryonic ovary.

In the mouse which has a complete bursa ovarica enclosing the ovary, Agduhr found that this bursa developed in the embryo solely from mesotubarium inferius together with certain parts of the mesonephros. The mesotubarium superius plays no essential part in the development of the bursa. This ovarian bursa of the mouse is formed by the dorsal and ventral mesosalpinx, and so it is probable that the bursa ovarica in Elephantulus, though it does not surround the ovary, has a similar embryonic origin.

In Elephantulus, as in all other mammals, the excretory system appears earlier than the urinary system in embryological development. The gonads develop intimately associated with the primitive nephric system in the very young embryo.

First to appear is the most primitive pronephros. This develops far cephallically in the body. Soon the pronephros degenerates and more caudal to it the mesonephros has appeared. This also degenerates and caudal to it develops the metanephros or permanent kidney.

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While the mesonephros is still the dominant organ of excretion the gonads appear as a thickened ridge on the ventro-mesial surface. This ridge thickens, but early in their development the gonads show no indications as to whether they are to develop into ovaries or testes. (Refer to Figure II). Along with the neuter gonads develop two systems of ducts - the Müllerian duct and the Wolffian duct.

(The ducts developing caudally to the degenerating pronephric are the mesonephric ducts. These ducts receive the mesonephric tubules and they are termed the Wolffian ducts. At a considerably later stage in the development the metanephric ducts develop from the caudal end of the mesonephros. These ducts remain to establish the metanephros or permanent kidney).

The Müllerian duct first appears close beside and parallel to the mesonephric or Wolffian duct, (Figure II). At first it only extends a short distance caudad, but as it develops, it does so in a caudal direction. It is the primordial structure from which the oviducts, uterus and vagina arise in the female. It is considered that phylogenetically the Müllerian ducts arose directly from the mesonephric ducts; however, ortogenetically they seem to arise side by side from the same parent tissue.

If the embryo is to develop into a male or female there is a completely different development in the duct system of the mesonephros. If the individual is to develop into a female the Müllerian duct system develops so as to give rise to the oviducts, uterus and vagina. The Wolffian duct remains rudimentary, If the individual develops into

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a male the systems are reversed and the Mullerian duct remains rudimentary.

In the young embryo (Figure II and Figure A) one sees the Müllerian duct extending a short distance caudad. Anteriorly it opens into a caudally directed structure known as the ostium tubae. This more or less funnel-shaped opening developing at the cephalic end of the Müllerian duct differs in its detailed configuration and in its relationship to the ovary in different mammals. The genital gland is posterior to the ostium tubae and medial to the elongate mesonephros. This gland is attached at its anterior wall to the dorsal body wall. The metanephros or permanent kidney is found at the posterio-lateral margin of the mesonephros, and its metanephric duct or ureter opens into the cloaca along with the mesonephric duct.

The Müllerian ducts are paired along their entire length when they first appear, but in all mammals the fusion of the Müllerian ducts occurs at their caudal ends. In Elephantulus, as in most Insectivores and Prosimians the fusion is carried only a short distance caudally, resulting in a bicornuate uterus as described by van der Horst.

In a slightly more advanced embryo the sex is determinable. The ovary has assumed a triangular shape (Figure III) and lies at the posterio-lateral margin of the kidney. It retains this position throughout life, Along its anterior and lateral surface runs the oviduct. The ovary is attached by the mesovarium to the body wall. From this mesovarium there extends in a caudal direction the ligamentum proprium ovarii. This attaches the ovary posteriorly to the genital

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cord.

At this stage the dorsal mesosalpinx is represented by a thickened ridge which includes anteriorly bits of mesonephric tubules as well as the anterior end of the Wolffian duct. The mesonephric tubules and ducts may remain recognizable to a variable extent in the mesovarium of different mammals. Usually these remain embedded in the mesovarium as a cluster of blind tubules and traces of a duct and these vestiges are called epoöphoron.

The ventral mesosalpinx is quite clearly represented in Figure III. The bursa ovarica as formed by the dorsal and ventral mesosalpinx and in an embryo at this stage of development, it is a shallow depression. We thus see that the bursa ovarica has a peritoneal derivation.

At the cranial end of the oviduct is the caudally directed ostium tubae and this region has become distinctly swollen, thus marking the beginnings of the enlarged infundibulum tubae of the adult. The lips of the infundibulum have also grown out and we see the uterine lip attached to the free edge of the ventral mesosalpinx. It extends for at least half the length of the ovary.

Just before birth (Figure IV, Embryo neonatus) the embryo has the ovary situated in the same position as in the previous stage. Thus we see that the descensus of the ovaries is slight compared with that of the ovaries of other mammals. (The urino-genital system had arisen in the dorsal body wall covered by the mesothelial lining of the coelom. Although the ovaries move through far less distance in Elephantulus myurus than they do in other mammals their change in position can be noted. As they increase

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in size both the gonads and their ducts sag farther into the body cavity and eventually take up a position at the posterior end and lateral to the kidney. In doing so they pull with them the peritoneal folds around them. These folds remain attached to the dorsal and lateral body walls and become reinforced by fibrous tissue to form the ligaments suspending the ovary).

In the embryo as in Figure IV, a distinct dorsal and ventral mesosalpinx suspend the oviduct. This oviduct terminates in such an embryo at the anterio-lateral margin of the ovary in a greatly enlarged infundibulum tubae. This infundibulum shows a growth in a cranial direction. There is a very well developed uterine lip present and a much shorter ovarian lip which becomes attached to the mesovarium. The infundibulum tubae in such a specimen is a deep hood-like structure in front of the ovary. Posteriorly this infundibulum is in wide communication with the peritoneal cavity. Thus, during embryonic life there is a wide communication between the periovarial cavity and the peritoneal cavity.

In a young animal after birth whose ovary bears follicles surrounded by a single layer of granulosar cells, one sees a large and extensive infundibulum at the anterior end of the ovary. The ovary still remains quite bare in the body cavity although the infundibulum is quite large and extensive enough to cover it (Fig V).

Owing to the cranial enlargement of the infundibulum the supporting membranes have also become drawn in a cranial direction. The anterior end of the mesovarium and the dorsal mesosalpinx are here located far more cephalically than before. In such a specimen the ovary is partly protected by the lips of the infundibulum which have grown down around it.

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In the next stage we find a young animal which has not yet ovulated, but whose ovary has at least one or two follicles having a double layer of granulosar cells the ovary is completely covered by the infundibulum. This is seen in Figure VIX which has the ovary encapsuled by the infundibulum tubae. Thus it appears that the infundibulum becomes drawn over the ovary at a stage well before ovulation and when the division of the follicular cells has begun. This envelopment of the ovary is very sudden and it is not clear quite how this muscular action is activated.

The envelopment of the ovary is a permanent one and was found in all mature specimens that were examined. Only two abnormalities in the development of the infundibulum tubae as a periovarial capsule, were found out of the vast number of specimens studied.

This ovarian capsule formed by the infundibulum of the ostium tubae retains its position during the oestrous cycle and during anoestrous and so no muscular action will alter the position of this capsule in Elephantulus.

The oviduct now opens into the periovarial capsule at the postero-lateral corner of the ovarium and this was the case in all the specimens examined except for the one abnormality referred to in Chapter VI.

Thus we see that in Elephantulus the ovarian mesenteries and ligaments have a purely suspensory function and have no extra development of muscle fibres as is found in certain other mammals.

It would seem that this envelopment of the ovary by the infundibulum is brought about because of the incomplete development of the true bursa ovarica. When the ovary

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had developed to a stage, well before ovulation, and the muscles activating the infundibulum had received their stimulus, they caused the envelopment of the ovary. This action is brought about by the smooth muscle fibres present in the ligamentum ovarii suspensorium and in the ligamentum ovarii proprium relaxing. At the same time the fibres in the ventral mesosalpinx contract and as these fibres radiate out in the periovarial sac they must pull this sac round the ovary. This is all brought about by one muscular action.

When the envelopment of the ovary is complete the infundibulum forms a sac enclosing the ovary rather tightly. It nevertheless allows for an easy passage for the eggs from the surface of the ovary to the tubal egg chamber. The sac-like periovarian capsule is complete except for a constricted opening around the mesovarium. Here the membrane is much folded and the ovarian lip is fixed to the mesovarium lip for a short distance. The plicated edge of the infundibulum in the region of the mesovarium only protrudes inwards into the periovarian cavity and no folds protrude outwards into the peritoneal cavity. The purpose of these folds is to allow for an increase in the size of the ovarian pouch after ovulation,when the corpora lutea form.

The uterine lip of the infundibulum tubae is very well developed and grows down past the ovary to fuse with the free surface of the ventral mesosalpinx. It does not however have any protective function as the infundibulum itself surrounds the ovary.

CHAPTER VI.

Anomalies in the Development of the Bursa Ovarica and Infundibulum Tubae in Elephantulus.

Out of the vast collection of serial sections I examined I found only two abnormalities in the development of the infundibulum tubae as a periovarian capsule in Elephantulus myurus.

The first abnormality was found in an adult female which had ovulated. The ovary contained numerous ripe follicles, many of them showing formation of fluid. The development of the ovary itself was quite normal. In this specimen the infundibulum tubae was of normal formation and size, morphologically its development being complete. However, the infundibulum was lying at the anterior end of the ovary and had not been drawn over the ovary. The lips of the infundibulum had grown down around the ovary in a normal manner. (Refer to Figure I).

We have to presume that in such a specimen, the muscular action for drawing the infundibulum over the ovary had not taken place. All other development was normal and only the final envelopment of the ovary had failed, leaving the ovary posteriorly exposed in the peritoneal cavity.

The ovulation of this female was quite normal and the ova had found their way down the ostium tubae. There had been a recent abortion of a 25 mm. embryo from this specimen. From such a specimen one can only concluded that the importance of the infundibulum as a periovarian capsule is not as great as is always believed.

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It is of interest to note here that Figure VIII in De Lange's "Oven den bouw van het ovarium zakje ....." dealing with the infundibulum tubae of Chrysochloris, is an abnormality. Dr. de Lange does not refer to it as such, but from my studies it seems to compare with the above-mentioned abnormality as found in Elephantulus. The infundibulum tubae in this Chrysochloris had not been drawn over the ovary. As in Elephantulus the abnormality was a muscular one, for had the normal muscular action taken place, the infundibulum was large and extensive enough to have covered the ovary.

The second abnormality I found in Elephantulus was much more striking than the first. Here the ovary had also developed normally. The ovary was that of a younger animal which had ovulated. The follicles were in the multi-layered stage of development. (This ovary was also an excellent example of one which produces many ova in a single follicle. There were as many as three ova in a single follicle). There were also many early corpora lutea in this ovary, indicating a recent ovulation.

In this specimen the oviduct passed the ovary at its lateral side as a narrow tube and ended approximately 1.5 cm. in front of the ovary (Refer to Figure G) in a very small funnel-shaped opening in the abdominal cavity. This oviduct actually passed through the mesovarium. The ostium tubae had completely retained its embryonic position, size and form. (FIG. VII).

As a result of this embryonic ostium no extensive infundibulum tubae had been developed and so the ovary was completely bare in the abdominal cavity. (Refer to Figure H).

/Although

Although the development of the ostium tubae and oviduct had been arrested in their early embryonic development, their embryonic form had in no way impaired their normal function. There were the full complement of ova in the tube - this in Elephantulus myurus may amount to about 60 eggs and these had reached an end at the ostium tubae. Even a small detached corpus luteum was found lying in the tube. The ova and corpus luteum must have found their way over the considerable distance between ovary and ostium, through the abdominal cavity to the very small and immature ostium tubae.

A very late blastula or early blastocyst was found lying free in the egg chamber. It has been recorded that an egg has passed from one uterine horn to the other and as the other horn and oviduct of this specimen were quite normal one might surmise that in this case an egg had passed from the normal horn and settled in the abnormal. This possibility is excluded in this case as there were a number of ova both in the abnormal tube and in the upper end of the uterus.

From this second abnormality we can draw three important conclusions : -

i) That the development of the ovary and of its tubes are quite independent of each other. That is, that the Mullerian duct and the genital gland in the embryo have no effect on each other as far as development is concerned. Also that the two ovaries develop quite independently of each other as the one was quite normal in this specimen.

ii) That the ova even though they are relatively small in the large abdominal cavity , had found their way to the ostium tubae.

iii) That the ciliary influence of this small, embryonic ostium tubae was strong enough to influence the passage of the ova in the peritoneal cavity, over a comparatively great distance.

CHAPTER VII.

The Functional Role of the Bursa Ovarica.

From the fact that ovulation had taken place and that the absence of an ovarian capsule did not unduly affect the course of the eggs, as was seen in the previous chapter, we can better work out and understand the function of the bursa ovarica in mammals.

The functions of the bursa ovarica and fallopian tubes may be said to consist chiefly in the conveyance of the egg, after ovulation, from the ovary down to the uterus. But one should not overrate the importance of this role to such an extent that it has been supposed that animals lacking this organ must therefore possess less generative power. Here, as we find in other parts of the organism, the compensatory faculties of the different organs are very great. It is clear that the smooth muscle tissue found in the ligament apparatus of the ovary plays a predominating part in the functions referred to.

Agduhr came to the conclusion from his observations that the bursa ovarica and perhaps the oviduct as well, may under certain conditions perform another function, viz. to serve as a depository for sperms. This, however, conflicts with the results of Sobotta and others who have investigated the fate of the sperms within the genital organs of the female, and always found them to be disintegrating after a lapse of time.

It is more likely that the bursa ovarica has the task of hindering the migration of spermatozoa into the abdominal

/cavity

cavity and this function may be better ascribed to animals having a permanently closed bursa, i.e. the bat.

In Elephantulus, as in other animals with a periovarian capsule complete at the time of ovulation, it had been thought that a suction caused by the active expansion and contraction of the ovarian tube would have brought about this transportation. But a simple tube cannot expand and suck by its own effort. Also, any such a suction would press the periovarial capsule against the wall of the ovary and thus block any passage for the egg. Therefore suction would not have the desired effect.

In Elephantulus there is the complete capsule around the ovary. At each ovulation about sixty eggs are set free from each ovary. The infundibulas pouch encloses the ovary rather tightly although leaving enough room for an easy passage for the eggs. The plicated portion of the infundibulum around the opening allows for the expansion of the capsule when the sixty odd corpora lutea are formed after ovulation. These corpora lutea greatly increase the size of the ovary, but this increase is only brought about over a period, as not all the ova are discharged at once. Therefore the folds can be slowly stretched out so as to allow for the envelopment of the greatly enlarged ovary.

The entrance from the capsule to the oviduct is located near the posterior end of the periovarial sac and gives access to the ampullary part of the Fallopian tube. It is thought that the ova are transported from their place of liberation on the surface of the ovary and into the ampullary part of the tube by a ciliary action and not by a suction brought about by the Fallopian tube (van der Horst).

/These

These cilia are abundantly present round the opening of the periovarial sac, on the fimbriae ovaricae and on the first section of the ampullary part of the Fallopian tube.The only possible function cilia could have in this area is the function of aiding the transport of the ova.

It therefore seems that the greatly developed infundibulum tubae in Elephantulus, or the true bursa ovarica of other mammals, has the functions of partly protecting the ovary from the peritoneal fluids and also of preventing the discharge, at random, of ova into the body cavity. In the case where the infundibulum tubae had not encapsuled the ovary the ova still managed to find their way to the ostium tubae, but were it normal it would greatly enhance their chances of reaching the tubal egg chamber. In its absence the ciliary action of the ostium tubae alone enabled the ova to reach their destination in the one abnormal specimen examined.

In the second abnormal specimen examined one must also conclude that the ova reached the ostium tubae by a ciliary action. The action in this case would only be a very feeble one as the ostium tubae is so immature. Yet it was sufficient to attract the eggs and to transport them over the large distance between the ovary and the ostium tubae.

In Elephantulus, as in other mammals, there is a remote chance that the ova could escape through the slit-like opening of the infundibulum tubae (or bursa ovarica) round the mesovarium. Such an occurrence is known to occasionally occur and should such an ovum be fertilized an extra-uterine pregnancy would result.

/Sobotta

Sobotta found that in certain animals the wall of the bursa ovarica is subject to periodical distension connected with the presence of a serous fluid in the periovarial cavity. Such a fluid greatly increases in quantity before ovulation. One would imagine that if such were the case, the presence of additional fluid would make the action of the cilia even more effective in this region. They would create a current in the direction of the ostium tubae.

The periovarial sac has evolved in mammals in various forms and stages of perfection. The function of this often complicated structure is obvious. It facilitates the transport of the eggs into the Fallopian tube and it prevents them from escaping in the abdominal cavity.

Nevertheless the one abnormal specimen examined shows that such a structure is not absolutely necessary and that no harm is done when the Fallopian tube retains its embryonic form and position in the abdominal cavity.

It does seem remarkable that such an organ as varied and complicated as the periovarial capsule, can be dispensed with, without impeding the functional capacity of the animal.

SUMMARY.

Elephantulus myurus jamesoni has a fully developed bursa ovarica formed by the mesosalpinx, the mesovarium and the ligamentum ovarii proprium and the ligamentum suspensorium ovarii. The ovary however never lies in this bursa.

We find the ovary is lying in a pouch formed by the enormously enlarged infundibulum tubae and that this is the case in all adult females independent of the stage of the oestrous cycle. The only communication between the periovarial and peritoneal cavity is a slit-like opening round the mesovarium. This opening is protected by the folds of the infundibulum tubae and so there is very little chance of the ova escaping into the peritoneal cavity.

The infundibulum starts developing early in the embryonic life as a swollen opening of the ostium tubae. The growth of the infundibulum proceeds cranially from the anterior end of the ovary. It forms an extensive cap over the anterior part of the ovarium. This becomes drawn over the ovary just prior to the first ovulation, the action is very rapid and the result is permanent. At no time during adult life is there any change in the position of the infundibulum tubae. The periovarial cavity is therefor completely enclosed from the peritoneal cavity, except for a narrow slit-like opening in the region of the mesovarium.

One presumes that the functional role of the greatly enlarged infundibulum tubae is to serve as periovarian pouch protecting the ovary from the fluids of the

peritoneal cavity and also preventing the ova from escaping into the coelomic cavity.

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