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The Passage of Sperms and of Eggs through the Oviducts in Terrestrial Vertebrates

G. H. Parker

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VII. *The Passage of Sperms and of Eggs through the Oviducts in Terrestrial Vertebrates.*

By G. H. Parker (*Zoological Laboratory, Harvard University*).

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1. *Introduction.*

The two elementary effectors, cilia and muscles, are found throughout almost the whole range of the animal kingdom. In such simple organisms as sea-anemones these two effectors are about equally developed and are usually mutually concerned in many of the common activities of these animals, such as the production of the respiratory currents, the appropriation of food, and the like. Vertebrates, on the other hand, with their growth in bulk have in large measure discarded cilia and have developed muscles as the almost exclusive means of response. Nevertheless, in parts of their bodies such as the reproductive system, both kinds of effectors, cilia and muscles, are mutually active and co-operate in carrying out certain functions of this important system. No one can observe the active oviduct of a vertebrate without being impressed by its striking resemblance to the responding cœlenterate body. Peristalsis, antiperistalsis, and other co-ordinated muscular movements combined with ciliary activity, are the elements on which both the organs of cœlenterates and the oviducts of vertebrates appear to rely for successful operation. The oviducts possess the remarkable property of conducting the reproductive elements in two opposite directions; sperms are conveyed by them from the exterior to the neighbourhood of the ovary and ova, or embryos are transported in the reverse direction. These two processes of inward and outward conduction are not unlike the swallowing of food by the gullet of the sea-anemone and the discharge of excrement by the same organ. Are the operations of the vertebrate oviduct performed in the same way as those of the gullet of the cœlenterate or not? In other words, do the oviducts exhibit muscular movements associated with normal or reversed ciliary beat to accomplish the appropriate transfer of the vertebrate genital products, or are these responses in vertebrates based on entirely different principles? These and other related problems are discussed in the following pages.

The material upon which the present studies were based consisted of specimens of the eastern painted tortoise, of the domesticated pigeon, and of the rabbit. I am under

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obligations to Professor W. E. CASTLE, of the Bussey Institution, and to Mr. A. J. WATERMAN, of the Harvard Zoological Laboratory, for much help in procuring satisfactory rabbits and in the handling of the animals. The expenses of the investigation were met in large part by a grant from the Committee for Research in Problems of Sex of the National Research Council. To this Committee and to Professor CASTLE and Mr. WATERMAN I wish to express my sincere thanks for their generous assistance. I am also indebted to Miss M. F. WOLFE for much help in the experimentation and in the preparation of the manuscript for publication.

2. *Oviducts of Turtles and of Pigeons.*

A. *Structural.*—The sauropsid oviduct has been the object of investigation for over a century. The most recent extended account of this organ is by GIERSBERG (1923), whose monograph contains a very full bibliography. In consequence of economic importance, much of the previous work has been done on the oviducts in fowls, but those in other birds as well as in many reptiles have also been studied. The work presented in this section was carried out on the ducts of the eastern painted tortoise, *Chrysemys picta* (SCHNEIDER), and of the common pigeon, *Columba livia* GMEL.

In the mature female of *Chrysemys picta*, each oviduct (fig. 1) is a much convoluted tube in which, as in other tortoises, five regions may be distinguished (GIERSBERG, 1923). Beginning next the ovary these regions are the infundibulum, the albumen-secreting portion, the intermediate portion, the uterus, and the vagina (fig. 2). In the quiescent oviduct the infundibulum hangs freely in the body cavity often at some distance from the ovary. It is followed by the much convoluted albumen-secreting portion, which is collapsed and flattened and resembles a band of thick tape. This portion is a little less than a centimetre wide and when loosely unfolded it may measure ten centimetres in length. It will, however, easily stretch to over twice this length. It is separated from the uterus by a slight constriction, the intermediate portion. This is a centimetre or less in extent and corresponds in position to the isthmus of the bird's duct. The intermediate portion is followed by the uterus, a relatively thick-walled firm, tubular organ some four centimetres long and twelve millimetres or more wide. In cross section the uterus is approximately circular as contrasted with the flattened outline of the albumen-secreting part. The last region in the duct is the vagina, a firm, muscular segment not very sharply marked off from the uterus. The vagina connects the uterus with the cloaca into which it opens by its own special aperture.

During the period of sexual activity the oviducts of *Chrysemys* may more than double their length, as has been observed by GIERSBERG (1923, p. 19) in other tortoises. This increase is noticeable in both the albumen-secreting portion and in the uterus. In June each uterine tube contains commonly two, three, or rarely more eggs in process of receiving their shelly covering. This condition agrees with the observations of the elder AGASSIZ (1857, p. 490) that *Chrysemys picta* lays in all from five to seven eggs.

Cunningham (1922, p. 57) states that in *C. cinerea* the average number of eggs is seven, with a range of four to fourteen. In *C. picta* the eggs are laid, according to Agassiz (1857, p. 497), between June 11 and 25, or, according to Rogers (1917, p. 74), even as late as July 4. Individuals opened during June are commonly found to have in them either ovarian eggs or uterine eggs. Although I have examined many specimens at this time of year I have never seen one in which eggs were in the albumen-secreting portion of the duct. Since the eggs necessarily pass through this portion they presumably do so rather rapidly. They must remain in the uterus a much longer time awaiting the formation of the shell and the final act of laying. The production of albumen and shell and the subsequent storage of the completed eggs are the processes that necessitate the increase in the length of the active as contrasted with the quiescent oviduct.

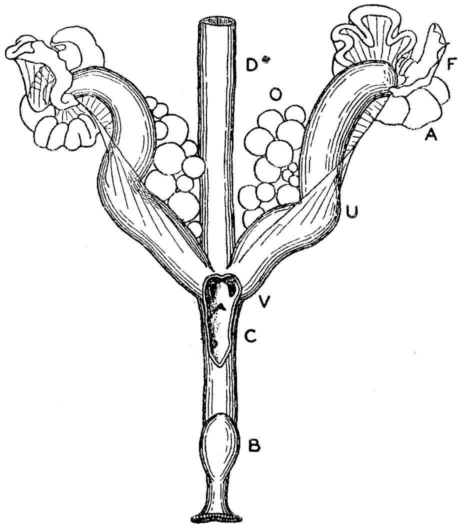

Fig. 1.—Diagram of the reproductive organs of a female tortoise (*Chrysemys picta*).

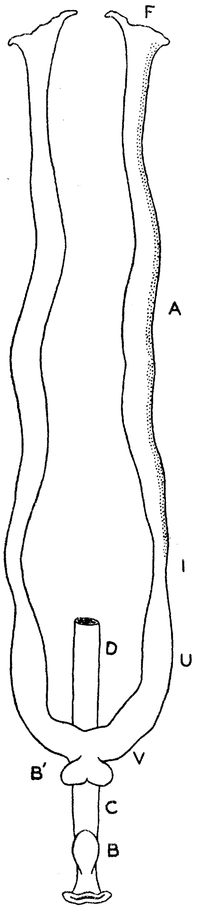

Fig. 2.—The same, dissected and spread out. The dotted area corresponds to the pro-ovarian ciliary tract.

A, albumen-secreting portion of oviduct; B, urinary bladder; B′, respiratory bladders; C, cloaca; D, digestion tube; F, infundibulum; I, intermediate portion of oviduct; O, ovary; U, uterus V, vagina.

In *Chrysemys* the inner surface of the quiescent duct is characteristically different for the five regions. The surface of the infundibulum is slightly wrinkled, more or less transversely, a structural condition that gives way gradually to the moderate longitudinal corrugations of the albumen-secreting portion. These corrugations, some twenty in number, run through the whole length of this region and become very attenuated and fine as they pass into the intermediate portion. Eventually they are replaced by the coarse longitudinal folds of the uterus. The uterine folds, unlike those in the preceding sections, are commonly transversely twisted. They straighten out and almost disappear as they pass over into the short vagina. The inner surface of the active oviduct exhibits much the same conditions as that of the quiescent one, except that in the active state the uterus, in consequence of its elongation and distention with eggs, loses most of its folds. The whole length of the duct is ciliated in *Chrysemys*, as in other turtles (GIERSBERG, 1923). The ciliated cells are commonly in small groups more or less separated from each other by gland cells, but in most instances this separation is so slight that the ciliation may be described as practically continuous.

In the single oviduct of the pigeon the five regions described for the tube in the tortoise are easily recognisable. They have long been identified in the fowl and in other birds (SURFACE, 1912; PEARL and CURTIS, 1912; KAUPP, 1918; GIERSBERG, 1923; BUCKNER *et al.*, 1925). The resting tube in the pigeon possesses a well-developed infundibulum, about half a centimetre in depth, that leads to an albumen-secreting portion some five and a half centimetres long (figs. 3 and 4). This is followed by a short isthmus, a few millimetres in length and a thick muscular uterus about a centimetre long. The uterus connects with a short vagina. I have found the total length of the resting duct to be about eight centimetres; according to KRAUSE (1922, p. 306) it may be as short as 4·5 to 5 centimetres. Its interior is marked with numerous longitudinal corrugations that become more pronounced and even convoluted in the uterus. According to HARPER (1904) the active duct may reach a length of 12 to 15 inches, four or five times as long as the resting organ. This proportional increase agrees well with that shown in the tabulations given for other birds by GIERSBERG (1923, pp. 3 and 6), and takes place notwithstanding the fact that the eggs of birds are not stored in the oviducts as in the case of the tortoise, but are laid almost as soon as the shell is formed. In the pigeon (HARPER, 1904, p. 352), the fowl (PATTERSON, 1910, p. 107; CREW, 1926, p. 230), and probably in most other birds, only one egg at a time ordinarily passes through the oviduct. Thus the uterus of the bird is principally concerned with the production of the shelly covering of the egg and has little to do with storage, one of its important functions in tortoises and in other reptiles. The oviduct in the pigeon, is ciliated from end to end, like that in other birds (SURFACE, 1912; KAUPP, 1918; KRAUSE, 1922; GIERSBERG, 1923; BRADLEY, 1928).

B. *Functional.*—It is not unusual to find a male and female *Chrysemys picta* in copulation during the autumn. However, after such activities, the oviducts of these turtles, according to CUNNINGHAM (1922, p. 60), contain no sperms, a condition that confirms Agassiz's opinion (1857, pp. 289 and 491) that these autumn unions do not result in the fertilisation of eggs. The effective pairing season for this tortoise is the late spring. In a female opened by me early in June, the surfaces of the ovaries were covered with fluid rich in active sperms. At that time no ovarian eggs had been freed, but the sperms had reached a position where, presumably, fertilisation would normally have been accomplished.

In the pigeon and the hen, the eggs appear to be fertilised as they leave the ovary (Harper, 1904, p. 356; Crew, 1926, p. 230). They are then actively taken up by the infundibulum (Coste, 1847; Harper, 1904, p. 355; Patterson, 1910, p. 107), which is applied for this purpose to the ripe follicle shortly after the preceding egg has been laid. In the hen the sperms may reach the ovary about 24 hours after copulation (Crew, 1926, p. 237). Here they remain viable for as long as twenty days (Crew, 1926, p. 237). Their power to fertilise may occasionally reach this limit also (Curtis, 1930),

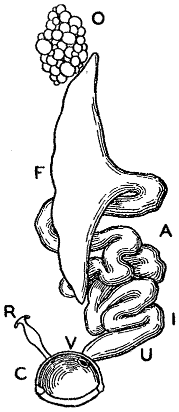

Fig. 3.—Diagram of the reproductive organs of a female pigeon.

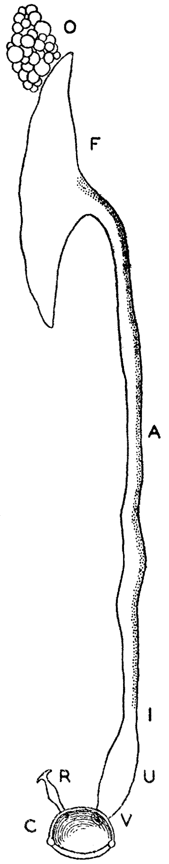

Fig. 4.—The same, dissected and spread out. The dotted area corresponds to the pro-ovarian ciliary tract.

A, albumen-secreting portion of oviduct; C, cloaca; F, infundibulum; I, isthmus; O, ovary; R, rudimentary right oviduct; U, uterus; V, vagina.

though ordinarily it covers not more than half this period (Crew, 1926, p. 231) and even less in the pigeon (Riddle and Behre, 1921, p. 248). In the hen and the pigeon the egg makes the complete passage of the oviducts and is laid in an hour or so less than a day (Harper, 1904, p. 351; Patterson, 1910, p. 107; Crew, 1926, p. 230). This downward passage is accomplished chiefly by oviducal muscular movements which, however, may be supplemented by ciliary action (Cushny, 1902; Harper, 1904, p. 355).

Thus the downward passage of the eggs of reptiles and of birds is easily accounted for, but the upward movement of the sperms, against the ciliary current, is not so clearly understood. That this upward transfer takes place there is, of course, not the least doubt, for active sperms have been found abundantly about the ovaries of both birds and reptiles. In general it has been assumed that the sperms attain this position by swimming against the ciliary current, much as fishes swim up-stream. That this type of rheotaxis is the means of ascent for the sperms was accepted as highly probable by Verworn (1895), and was believed to have been experimentally proved for the hen by Adolphi (1906, *a*, p. 143).

If the oviduct of a painted tortoise is thoroughly irrigated with Ringer's solution and a section of it is cut out, split lengthwise and so folded that a longitudinal band of cilia on its inner face can be inspected under the microscope, a strong ciliary current beating toward what was the external opening of the duct will usually be clearly seen. If now a large number of active tortoise sperms are introduced into the fluid next the cilia, it will be noted, first, that the sperms swim irregularly in all directions, and next that quite aside from their own motion, they are swept headlong in the direction of the ciliary current. So vigorous is this current that the swimming of the sperms themselves, never very persistent or long-continued, plays almost no part in their ultimate distribution. In no single instance in many such preparations were they seen to head-up and swim persistently against the current. In other words, rheotaxis was not exhibited by these sperms. Yet rheotaxis has been repeatedly ascribed to such elements. Lott, as early as 1872, stated that the sperms in the dog swam against the current, and Roth (1893, 1904) and particularly Adolphi (1905, 1906) made similar statements for the sperms of many animals. The method of demonstration used by these investigators was somewhat different from that just described. Adolphi showed that if a slow current is produced in a thin layer of fluid contained between a cover-slip and a glass slide and rich in active sperms, these elements will orient to the current and swim against it. It is easy to confirm this observation with sperms from the tortoise. Thus, when a gentle current is produced in such a preparation, the majority of the sperms swing round till their heads point against the current and many of them swim up-stream. In such a preparation almost all the sperms touch the glass with their heads, which are slightly adhesive. By adjusting the strength of the current appropriately the sperm can be made to swing with its head as a centre till it comes to rest with its tail pointing down-stream. If now it loosens its hold and swims, its course, for a short time at least, will be up-stream. This method of orientation and the resultant directed locomotion may be repeatedly induced. It is precisely like that seen in fishes ascending a stream the banks of which are near enough to be touched or seen frequently. It is a true rheotaxis.

In the tortoise's oviduct, however, the conditions are unlike those on the glass slide. The great majority of sperms in the duct are not in contact with its walls, but are suspended in a relatively voluminous mass of fluid that has a motion of its own. In this fluid the sperms are swept along and, though they swim of themselves, the direction of their swimming has no relation to that of the general current. They are to be compared to fish, not in a stream with banks on either side, but in an extended oceanic current which sweeps them onward without, however, directing their individual courses. Under such conditions rheotaxis plays no part in the resulting movements. As the majority of sperms are in such a general current, and as this current is relatively strong, it is not surprising to find these elements, whose own proper swimming is relatively insignificant, swept along with the general current toward its own goal. The only sperms that, in my opinion, could exhibit rheotaxis such as that seen in the glass-slide preparations are those temporarily in touch with the walls of the oviduct. These may in some measure be thus directed up-stream, but they so quickly lose contact with the wall and fall back into the general current that in preparations of the oviduct wall of the kind described they are negligible in number. From these observations I conclude, contrary to the commonly accepted opinion, that in accounting for the transfer of the sperms in the oviduct of the tortoise, rheotaxis is an insignificant element; the vast majority of sperms are simply swept along by the general ciliary current.

If rheotaxis is a negligible factor in the ascent of sperms through the oviducts of the tortoise, how then is this process accomplished? It has been repeatedly shown that in the gullet of the sea-anemone the ciliary beat in the presence of food juices reverses and that the ciliary current thus produced is changed in direction from outward to inward (PARKER and MARKS, 1928). Could not such a reversal take place in the oviducts whereby the usual outward current would be converted temporarily into an inward one by some constituent of the spermatic fluid? To test this possibility, extracts were made from the testis, epididymis, vas deferens, and cloacal wall of the tortoise and applied singly and in combination to the oviduct. These tests, however, failed completely to induce reversal. As they were carried out with considerable fullness, I concluded from the evidence thus obtained that ciliary reversal is not concerned with the ascent of the sperms in the ducts of tortoises.

Rheotaxis and ciliary reversal having been shown to be ineffectual in the tortoise, I undertook a close inspection of the ciliation of the oviducts in this animal. A section of the duct about a centimetre long was excised, opened and placed under the microscope so that it could be rolled on its longitudinal axis in such a way as to allow an inspection of the ciliary beat step by step across the whole of its interior. To my surprise the inner face of the oviduct exhibited two ciliary systems. The general surface of the duct was covered with cilia that beat toward the exterior, as has been commonly maintained for this structure as a whole. In preliminary papers on this subject (PARKER, 1928, *a*, 1928, *b*), I designated these cilia from the direction in which they beat as abovarian cilia. In addition to these, however, I found on one side of the duct a straight narrow band of cilia, two to three millimetres wide, in which the direction of the stroke was the reverse of that of the abovarian cilia ; that is, it was toward the ovary. These were designated pro-ovarian cilia, and their presence in the tortoise has recently been confirmed by LUCAS (1930). As subsequent investigation showed me, this band extends from the infundibulum to the intermediate part of the oviduct, but not into the uterus, as I at first supposed. It extends along that edge of the flattened duct which is attached to the mesosalpinx and is marked externally by blood-vessels and by more or less pigment.

The band of pro-ovarian cilia, which is the novelty in this connection, is most convincingly demonstrated by the method already described. If a transverse segment of the oviduct from the midst of the albumen-secreting portion is split longitudinally, folded lengthwise upon itself so that its inner surface is outermost and its ciliated edge inspected, the direction of the ciliary beat can be easily observed. If the region selected is near, but not too near, the pro-ovarian cilia, the abovarian current can be clearly seen. A slight rolling of the preparation in an appropriate direction is all that is necessary to pass from abovarian to pro-ovarian cilia. The two sets are immediately adjacent and the direction of their stroke is their chief difference. In histological preparations of the duct made so as to include both sets of cilia, I have not been able to distinguish one set structurally from the other. Nor is it easy to demonstrate the two sets by means of carmine and other such materials. Both kinds of cilia are usually covered with a fairly heavy coating of mucus, and carmine and other such light substances when discharged on the ciliated surfaces usually rest immobile on the mucus. If, however, by means of a delicate brush the mucus is carefully removed and a finely divided material of some weight, such as powdered anthracite coal, is discharged on the membrane, such particles of coal as fall on the pro-ovarian band can be seen under the microscope to move in one direction and such as fall on the abovarian field in the other. As already stated, when fluid containing sperms is discharged over appropriately folded pieces of the duct, the sperms are swept along either in the pro-ovarian or in the abovarian current.

Extended observations on the oviduct of the pigeon have led to results almost identical with those obtained from the duct of the tortoise. In the pigeon's oviduct a pro-ovarian ciliary band of about one-fourth the width of the total duct can be demonstrated from the infundibulum to the uterus (PARKER, 1930, *a*). The remainder of this upper part of the oviduct and the whole of the lower part, the uterus and the vagina, are covered with abovarian cilia. Active sperms in the pigeon, as in the tortoise, are swept by these two ciliary systems in appropriate directions.

From what has been demonstrated in the ciliation of the oviducts of the tortoise and of the pigeon it seems reasonable to conclude that in these two animals sperms are normally transported toward the ovary from the isthmus to the infundibulum by means of the band of pro-ovarian cilia. How the sperms reach the lower end of this band; that is, how they pass through the vagina and uterus, is still to be discussed. In the painted tortoise the distance under consideration may be as much as ten centimetres or even more and in the pigeon about eight centimetres. I have no direct observations to show how the sperms of these animals traverse the stretches under consideration. This may be accomplished by their own locomotion. Sperms, even though undirected, would finally attain the region of the isthmus through indiscriminate swimming, after which the pro-ovarian current would carry them to the infundibulum. But there are other features of oviducal activity that may be concerned in this transfer. It is well known that in the hen, double eggs, so-called, may occur; thus eggs that have received a shelly coating may be subsequently covered with albumen and again covered with a second shell. It is also known that bits of barnyard refuse, such as feathers and the like, may be contained occasionally inside the egg-shell of the hen. It has been experimentally shown that if the lower end of the hen's oviduct is ligated, eggs even with a shell fully formed may be discharged into the body-cavity of the bird (Pearl and Curtis, 1914). Most authors have rightly assumed that these facts are not to be understood except on the assumption that the oviduct of the hen can reverse its action and can pass bodies upward as well as downward through its extent (Parker, 1906; Curtis, 1916). It is, therefore, possible that at the time of copulation the relatively voluminous spermatic discharge may be carried by reversed muscular action up the oviduct of the hen to the not very distant isthmus; from this point onward the pro-ovarian ciliary tract would accomplish the remainder of the transportation. In favour of this initial muscular transfer I have, however, no direct observations beyond the fact that at the conclusion of the ordinary pairing of the cock and the hen the cloaca of the latter can be seen to undergo an excessive outward and inward movement suggestive of vigorous muscular activity of the attached inner parts. Possibly such reversed oviducal movements excited by copulation play an important part, if appropriately timed, in the formation of double eggs; for such eggs after having gone down the duct temporarily, must move up again before they pass finally down the duct to be laid.

From the foregoing discussion the following general conclusions, based chiefly on the oviducal conditions in birds, but believed to apply equally well to the oviducts in reptiles, may be drawn. The spermatic fluid received in the cloacal region of sauropsids is probably transported over the lower part of their oviducts (vagina and uterus) by muscular action, antiperistaltic in nature, after which the sperms, rather as scattered individuals than as a single mass, ascend the remainder of the duct (isthmus to infundibulum) along the pro-ovarian ciliary tract. In these operations reversal of ciliary action plays no part, and undirected as well as directed types of sperm locomotion (rheotaxis) are at best very subordinate factors. The significant elements in this transfer are the reversed muscular movement of the lower part of the oviduct and the pro-ovarian ciliary current of the upper part. The downward passage of the sauropsid egg through the oviduct is generally admitted to be due almost entirely to muscular action supplemented possibly to some slight degree by the action of the abovarian cilia.

3. *Oviducts of Rabbits.*

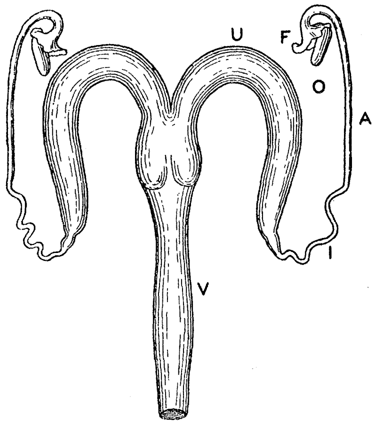

Fig. 5.—Diagram of the reproductive organs of a female rabbit. A, ampulla of uterine tube; F, infundibulum; I, isthmus of uterine tube; O, ovary; V, vagina.

A. *Introductory.*—The mammalian oviduct, to use that term in its widest sense, is well known to consist of three parts: the vagina, the uterus, and the uterine or Fallopian tube (fig. 5). In the rabbit the vagina is a relatively thin-walled, single, median tube some seven to eight centimetres in length and, in the collapsed condition, about two centimetres wide. A study of the living epithelium of the freshly prepared vagina confirms Krause's statement (1921, p. 158) that this membrane near the exterior is a pavement epithelium, near the interior a single layer of mucous cells, and that it is nowhere ciliated. Following the vagina are two thick-walled uteri, each of which in the resting state has a length of about seven to eight centimetres and a diameter of approximately eight millimetres. The uteri, which have been well described by Chipman (1902), open independently into the vagina and together afford a good example of the so-called bipartite type of organ. Each uterus communicates with the vagina by a constricted portion, the cervix (Hammond and Marshall, 1925; Walton, 1930), which is about a centimetre and a half in length. The cervix opens into the vagina through a low, corrugated papilla which projects a short distance into the vaginal cavity. In a freshly killed rabbit this opening, the external mouth of the uterus, is easily probed in either direction. In fresh organs not previously manipulated, coloured fluid under slight pressure can be made to flow through this opening, either upward or downward, though the passage downward is accomplished with somewhat greater ease than that in the reverse direction.

The uterus at its end opposite the vagina diminishes rapidly in calibre and passes rather abruptly into the uterine tube. The opening leading from the uterus into the tube is hidden among the membranous folds at the upper end of the uterine cavity. This opening in the rabbit, as in the sow (Andersen, 1928), is sometimes provided with an incomplete papilla projecting into the uterus. Andersen was unable to inject coloured fluid from the uterus of the rabbit into the tube, but I found this relatively easy to accomplish, as in fact Andersen herself did in the sheep and the sow. Injection in the opposite direction through this passage in the rabbit was also easily performed. Whether the freedom of this passage varies with the physiological state of the animal, as suggested by the work of Lee (1925, *a*; 1925, *b*), remains to be ascertained.

The body of the rabbit's uterus is lined with a mucous epithelium mostly devoid of cilia (Krause, 1921, p. 157). But over the region of the cervix, that is for about one centimetre and a half inward from the vaginal mouth of the uterus, the epithelium is richly ciliated and the current produced by these cilia is from the uterus to the vagina. A moderate ciliation is also to be observed about the tubo-uterine aperture ; the direction of the beat in this field is likewise toward the vagina (Hoehne, 1908, 1911). In one rabbit I observed an irregular band of cilia extending from the tubo-uterine aperture downward through much of the body of the uterus. The current on this band was outward. Such cilia may already have been seen in the rabbit by Wyder (1886). I am disposed to regard them as abnormal in position, for in the many rabbits examined by me I have seen nothing to lead me to believe that the epithelium lining the body of the uterus is regularly provided with even such cilia as these. Further, my observations agree with those of Snyder and Corner (1922) on the pig, that such ciliation as there is in the rabbit uterus does not change with alterations in the physiological condition of the adult animal.

The uterine tube in the rabbit extends from the top of the uterus almost to the ovary. It is eight to ten centimetres long and from a millimetre and a half to three millimetres wide. Its lower portion, the so-called isthmus, is somewhat convoluted and relatively narrow. Its upper part, the ampulla, is wider, less tortuous, and describes an extended loop in its passage toward the ovary near which it terminates in an open infundibulum. Internally the uterine tube is partly divided by the tubal folds which with numerous subsidiary projections extend from the wall of the tube into its cavity. These folds are more fully developed in the ampulla than in the isthmus. The whole interior of the tube including its folds is covered with an epithelium, partly ciliate and partly glandular. As will be shown later, in discussing the movement of the sperms and the ova, the direction of the ciliary beat in the uterine tube is outward, that is, toward the uterus.

The reproduction of the rabbit has been so fully investigated, especially by members of the Cambridge school of embryology, from Heape and Assheton to Marshall and Hammond, that what might be called physiological constants have been established for the movements of sperms and of eggs in this animal. Thus it is generally stated, as a result of Heape's work (1905), that sperms reach the ovarian end of the rabbit's uterus about two hours after copulation. They arrive in the region of the infundibulum two hours later, or four hours after they have been deposited in the vagina by the male. Ten hours after copulation the egg follicles in the ovary rupture and the eggs are liberated to pass to the tube and thence to the uterus. According to these reckonings sperms would be on hand in the region of the infundibulum some six hours before the eggs arrive there. Rabbit sperms are known to retain their fertilising power in the upper female ducts for at least thirty hours, and the eggs to survive without fertilisation for from two to four hours (Hammond and Asdell, 1926). The egg is fertilised in the uterine tube, through which it passes in about three to four days (Bischoff, 1842, *a* ; Lewis and Gregory, 1929, *a*, 1929, *b* ; Pincus, 1930), after which it enters the uterus.

Some seven days after coitus it becomes fixed on the uterine wall (ASSHETON, 1894) and about thirty days after pairing the young are born.

The statements of times given in the preceding paragraph are open to a certain amount of qualification. HEAPE's declaration (1905, p. 262) that sperms require four hours to reach the region of the infundibulum in the rabbit, implies a slower rate of migration than would be inferred from HENSEN's observation (1876, p. 231; 1881, p. 113) that rabbit sperms reached the ovary in two and three-quarter hours. In my own tests on rabbits I have twice found active sperms close to the infundibulum three hours after copulation. I am, therefore, inclined to believe that HEAPE's estimate of four hours is somewhat long. In small mammals, such as the rat, sperms reach the ovarian end of the uterus, according to HARTMAN and BALL (1930), in less than two minutes after ejaculation. This very short period lends credence to LEUCKART's statement (1853, p. 919) that he and BISCHOFF found guinea-pig sperms in the middle of the tube of this animal a quarter of an hour after copulation.

Notwithstanding the fact that rabbit sperms may live thirty-eight days in the male ducts (HAMMOND and ASDELL, 1926) and from seven to nine days in an environment essentially external (IWANOW, 1926; WOLF, 1921), their ability to fertilise, as already stated, lasts after their entrance into the female tracts at most some thirty hours. Their life in the exterior, even up to forty-nine hours and under conditions of transportation, has been shown by WALTON (1926) not to prevent their power to fertilise, though YAMANE and KATO (1928) set some twenty-four hours as the extreme for such capacity. HAMMOND (1930), however, has shown that rabbit sperm at 10° C. may retain the power to fertilise for as much as ninety-six hours. In spite of these variations in the time limits for rabbit sperms, these results agree fairly well with those for most other mammals as noted by YOCHEM (1929).

The liberation of the egg of the rabbit, ordinarily put at about ten hours after coitus, is subject to variation. Thus WALTON and HAMMOND (1928, p. 192) have shown that when the actual time of ovulation is followed closely, the period between coitus and discharge of the egg may vary from nine and three-quarters to thirteen and a half hours. Notwithstanding the various fluctuations in the times for the several phases in rabbit reproduction, they are so regulated that abundant overlap is given, whereby the successful union of egg and sperm is insured.

B. *Ascent of sperms.*—During copulation sperms are deposited by the male rabbit at the upper end of the vagina in close proximity to the external mouths of the uteri. The passage of these sperms from their region of deposit into the uterus has been attributed to their own unaided locomotion by a number of workers, among whom are HOEHNE (1911, p. 822), MARSHALL (1922, p. 174), and WALTON (1930, p. 3). HENSON (1876, p. 231; 1881, p. 109), HEAPE (1898) and others, however, have ascribed this transfer to the muscular activities of the containing female organs, an opinion long ago expressed by BECK (1874) for the reproductive activities of man, and more recently, advocated by FELDMAN (1920, pp. 26 and 35), who adds confirmatory statements based on observations on the horse. Several of these workers have attributed muscular suction to the uterus, a view accepted by PLACZEK (1926, p. 116) for man.

The experimental evidence on this question so far as the rabbit is concerned comes chiefly from the work of WALTON (1930, *b*). This investigator injected coloured fluid into the vagina of the female rabbit and, after allowing her to pair with the male, found none of this fluid in the cervix. From this result he concluded that fluids do not penetrate the cervix of the rabbit in consequence of coitus and that sperms arrive in that part through their own motility. At about the same time and without knowledge of WALTON'S results, I published (PARKER, 1930, *b*) a brief account of my own experiments on rabbits. In this account I noted that if the female rabbit is killed and examined as quickly as possible (three or four minutes) after coitus, living sperms will be found in the lower part of the uterus. As the period just mentioned was too short a time for the sperms to swim from the vagina to the point in the uterus where they were found, I concluded that the muscular activity of the containing parts must have been responsible for the transfer.

My method of procedure was to allow a male rabbit to copulate with a female and, immediately at the conclusion of the operation, to kill the female by breaking her neck. Then I opened her abdomen and with clean, sharp scissors severed the uterus near the upper boundary of the cervix. The time was taken by a stop-watch from the instant the male fell off the female till the moment when the uterus was cut. In my early tests this period was from three to four minutes, but as I acquired greater skill I reduced it to as short a time as 53 seconds. In one set of five rabbits the range in time was between one minute fifty seconds and three minutes, and in all these cases sperms were present in the uterus just above the cervix, though such elements were not present midway the length of the uterus. In a similar observation made by HENSEN (1876, p. 230) in which, however, the time was not very closely recorded, it was found that the sperms could be identified in the rabbit cervix five minutes after coitus. In another group of my cases, three in all, with intervals at 53, 55, and 80 seconds, no sperms whatever were found in the severed upper part of the uterus, though in each instance an abundance of active sperms was observed in the vagina. Finally, in a third group made up of four cases in which the intervals ranged from three minutes to over an hour, again no sperms were found in the severed part of the tube, though these elements were abundantly present in the vagina.

In discussing these several cases, the one in which sperms were found in the uterus after the briefest period is of most importance. This one, as already stated, had an interval of one minute and fifty seconds, or a total of 110 seconds, between the end of copulation and the severance of the duct. The highest point at which sperms were found in this animal was thirteen millimetres above the external mouth of the uterus. LLOYD-JONES and HAYS (1918, p. 480) have stated that the sperms of the rabbit swim 0·05 millimetres per second, a rate that coincides almost exactly with my own observations and is very close to similar measurements in the sperms of other mammals as given by ADOLPHI (1905, 1906, *a*, 1906, *b*). Assuming that in the rabbit under consideration the sperms swam directly up the canal of the cervix at the rate given and that they were not otherwise assisted in their migration, it would have required them a little over four minutes to reach the uppermost point at which they occurred, a distance that they actually travelled in one minute and fifty seconds. This computation, however, is based upon the assumption that the sperms swam directly up the tube. But their method of locomotion is not of this kind; they swim indiscriminately in all directions and therefore they would move up such a tube more slowly than at the rate given. LLOYD-JONES and HAYS (1918), who have worked on this question, assume that the rate of forward locomotion of sperms should be reduced to one half in estimating what might be called their rate of diffusion. Accepting this revision, it would appear that in the instance under consideration the sperms, if they advanced purely by their own locomotion, would reach the thirteen millimetre point only after a little over eight minutes instead of four, a still greater divergence from the observed time of one minute and fifty seconds. In the slowest of the five examples under consideration in which the sperms reached a level of fifteen millimetres, the time to traverse this distance calculated as in the preceding instance is ten minutes, a period much longer than that actually consumed, namely, three minutes. It is results of this kind that, in my opinion, throw grave doubt on WALTON's contention that rabbit sperms pass from the vagina to the uterus by their own locomotion, unassisted by other means.

In discussing this question personally with Dr. WALTON, he pointed out to me that my method of dealing with the rabbit called for sudden and rather violent death, often associated with vigorous muscular movements, and that these movements might well force sperms from the vagina into the uterus. Since this aspect of the problem was brought to my attention, I have watched carefully the way in which the rabbits succumb, and in one instance at least I observed a female that died quietly without exhibiting any special movements whatever. Care in handling this animal was exercised, that she might not be subjected to undue pressure. Nevertheless, she showed on examination an abundance of sperms in the uterus. Not only has this condition been seen, but in seven of the twelve instances recorded, it will be recalled that sperms were absent from the uterus though present in the vagina. These seven animals died with as much muscular movement as any others, and since in them the sperms remained in the vagina, I conclude that the muscular activities associated with the sudden death of the rabbits had no influence in forcing the sperms from the vagina into the uterus. I am, therefore, convinced that from this standpoint, my method of procedure is not open to objection.

Thanks to Dr. WALTON, I had an opportunity of witnessing a demonstration of his method in which the retention of coloured fluid in the vagina of the rabbit subsequently paired with a male was shown beyond doubt. Although this result was very clearly demonstrated, I am not prepared to admit that it is conclusive evidence that fluid may not be transferred from vagina to uterus in normal copulation. In my opinion it is quite possible that the injection of the coloured fluid into the vagina before copulation puts the female in such a state that she fails to exhibit the normal response, and that in consequence of this failure the fluid remains in the vagina. In such experiments I am at a loss to understand the advantage of using an artificial mixture when the test may be made just as well with the natural spermatic fluid, whose presence can be detected by the microscope as certainly as the artificially coloured fluid can be seen by the unaided eye. I am inclined to regard the use of an artificial mixture as an objectionable feature in the procedure, and I suspect that this very defect may be the occasion of Dr. Walton's experimental results rather than that they represent the normal response of the parts concerned. Assuming the correctness of this interpretation and bearing in mind the time relations of the transfer of sperms as already stated, I conclude that muscular activity plays an important part in the transmission of these elements from the rabbit's vagina to its uterus.

With this conclusion in mind, it may be well to review the three sets of cases of insemination already noted in the preceding paragraphs. Heape (1898) described in some detail those muscular movements in the rabbit which he believed to be concerned with the transfer of sperms from the vagina to the uterus. The following excerpt from his paper (1898, p. 206) is a brief statement of his opinion: "It is not clear how the spermatozoa naturally find their way from the vagina to the uterus; but, from certain experiments which I have made on rabbits, I am inclined to think that the greater part of it is drawn in by a sucking action of the uterus. The os, which is placed above the ventral wall of the vagina, appears to dip down into the midst of the spermatozoa as they lie on the floor of the vagina and in conjunction with peristaltic contraction of the uterus, to be withdrawn again, and this action appears to be repeated more than once at intervals. . . . This sucking action of the uterus in the rabbit above mentioned, was induced by stimulating the erectile tissue of the vulva." As Walton (1930) states, no details of the experimental method used by Heape are given in his paper, but it is quite evident from the description quoted that in some way not made clear to the reader, Heape was enabled to observe the movements of the parts in the sexual activity of the female. It is these movements that, according to him, are primarily concerned with the transfer of the sperms from the vagina to the uterus.

Of the three sets of cases referred to in the previous paragraphs the first showed sperms in the uterus from one minute fifty seconds to three minutes after coitus. In my opinion, copulation in each of these instances was associated in the female with a normal muscular response whereby the spermatic fluid was transferred from the vagina to the uterus. In the third set, in which no sperms were found in the uterus, I assume that no effective response had occurred. In the second set, in which the interval was from fifty-three to eighty seconds and in which no sperms were found in the uterus, I believe either that no response was induced or that if one was started it was checked so early by some element in the death of the animal that it failed to become an effective means of transferring the sperms.

When these three sets of cases are considered from the standpoint of the time of year at which they occurred, an important relation is discoverable. The first set, all of which were successful uterine inseminations, date from the spring; the second and third set, failures in uterine inseminations, were from the autumn and early winter. As is well known (HAMMOND and MARSHALL, 1925, p. 196) the height of the breeding season for rabbits is May; the autumn and winter together constitute a period of quiescence in this respect, an anœstrum. I therefore believe that the cases herein recorded may be regarded as reflecting such seasonal differences. In my opinion, uterine insemination is usually dependent upon a vigorous, female, muscular response which may be excited with ease in the spring and with difficulty, or not at all, in the autumn and winter. This hypothesis receives a certain amount of support from the following observations on four female rabbits inseminated in the autumn. Two of these animals were killed immediately after copulation and examined for sperms in their uteri. No sperms were found there, though many were present in the vaginæ. The remaining two were allowed the usual period for the production of young, but failed to bring forth offspring. In my opinion, the infertility of these females was due to the inability of the sperms of themselves to pass above the vagina, a step that at another time of year might have been accomplished as a result of vigorous muscular response.

At first sight it might seem that a fair test of the efficiency of muscular action in the transfer of sperms would be found in artificial insemination. If muscular action is necessary to carry sperms from the vagina to the uterus, then artificial insemination in which there would be no such response ought to be followed always by a sterile outcome. But the sexual organisation of the rabbit is such that this test is not so applicable as it at first appears to be. It is well known on the basis of many investigations that the rabbit is peculiar in that it does not discharge its eggs as most mammals do, at intervals related to the physiological rhythm of the female, but as a consequence of coitus and the resulting muscular response. This response is without doubt the muscular activity associated with the female sexual orgasm, and I agree with HAMMOND and MARSHALL (1925, p. 70) when they assert that ovulation in the rabbit is probably dependent upon this orgasm. The liberation of the rabbit's egg, as already stated, occurs about ten hours after copulation. From the experimental work of FRIEDMAN (1929, *a*, 1929, *b*) and of SCHNEIDER (1930) it appears quite certain that this discharge is a humoral response, and not a nervous one, as was assumed by some of the older workers (MARSHALL, 1922, pp. 134, 561). The liberation of the egg appears to be dependent upon the presence of a hormone whose production is induced by the female orgasm. Since artificial insemination may be performed without exciting this response, the resulting infertility may arise from failure in the liberation of eggs quite as much as from the absence of sperms. Investigators have met this dilemma by following artificial insemination by copulation with a vasectomised male, whereby a non-inseminating orgasm could be excited, with the consequent liberation of eggs, or the omission of this step when no eggs were desired (YAMANE and EGASHIRA, 1924, 1925; HAMMOND and ASDELL, 1926). The results of such tests have been a large percentage of fertility from artificial inseminations followed by a spermless copulation and a small percentage when copulation was omitted. That there should have been any fertility at all on the omission of copulation is difficult to explain. The way in which an egg would be liberated under such circumstances has not been made clear. Probably, as HAMMOND and MARSHALL (1925, p. 71) maintain, eggs are never discharged except as a result of an orgasm, and in instances like those just mentioned where they were believed to have been spontaneously ejected (WEIL, 1873; IVANOV, 1900), an unintentional orgasm probably had been excited. It is well known that such a response may be induced by other means than copulation; thus the manipulation of the rabbit's vulva, or even the simple jumping of one female rabbit by another (HAMMOND and MARSHALL, 1925, p. 70) may be followed by ovulation and pseudo-pregnancy. It must be clear from this discussion that artificial insemination is not a simple method for the discovery of the means by which rabbit sperms progress from the vagina to the uterus. It can be used only with great circumspection.

In my own experimental tests I attempted to inseminate female rabbits artificially and without exciting an orgasm. HEAPE (1905) believed this step a possible one. Two females during the breeding season were very lightly etherised, so as to reduce their excitability, and a considerable volume of spermatic fluid from the vaginæ of other females recently in coitus was injected into the corresponding cavities of the desensitized individuals. Each etherised animal recovered from the anæsthetic in a few minutes. One was killed five minutes after insemination and the other one an hour after that operation. In both cases no sperms were found in the uteri though these elements were abundant in the vaginæ. The etherisation of the females was so slight that I am convinced that the drug had no influence on the motility of the sperms, and the fact that no sperms were found in the uteri leads me to conclude that the transfer of these elements from vagina to uterus is ordinarily accomplished by other means than unassisted sperm activity.

In dealing with this problem, it must be kept in mind that in mammals that ovulate at regular intervals, particularly in man, there is much evidence to show that sperms may pass from the vagina to the uterus without the intervention of an orgasm (MARSHALL, 1922, p. 174; PLACZEK, 1926, p. 117). Although this evidence is of necessity not always all that could be desired, it is nevertheless often so circumstantial that it would be hazardous to deny its importance. Experimental results from the rabbit point in the same direction. HAMMOND and ASDELL (1926, p. 172) report several instances of artificial insemination made after sterile coitus and followed by fertile outcome, a result very difficult to explain except on the assumption that the sperms entered the uterus purely by their own locomotion. YAMANE and KATO (1928, p. 462), in their account of artificial insemination in this animal, state that it was their practice to inject the spermatic fluid into the uterus. In one instance, however, the injection was made into the vagina only. Nevertheless, this insemination resulted in fertility. Whether the act of injection excited or failed to excite an orgasm is not stated. Probably the determination could not have been made. This instance, therefore, is not so clear as are those reported by Hammond and Asdell, which afford very strong evidence that in the rabbit sperms may at times pass from the vagina to the uterus as a result of their unaided locomotion. In my opinion, the usual successful insemination of the rabbit is one in which the transfer of sperms from the vagina to the uterus is accomplished by a vigorous muscular response of the parts concerned, that is, by the female orgasm. This transfer, however, as just stated, may be brought about under certain circumstances by the locomotor activity of the sperms themselves (Walton, 1930).

What enters the cervix and lower portion of the uterus of the rabbit as a result of successful copulation is a volume of spermatic fluid rather than individual sperms. At least the sperms are so abundant in that region as to produce this impression. I have never seen, however, any evidence in the rabbit of a special secretion, like the so-called Kristellerscher Schleimstrang (Placzek, 1926, pp. 99 and 107) of man, by which sperms may be entangled and carried en masse into the uterus. What is transferred in the rabbit seems to be a considerable volume of spermatic fluid, which may well be moved by suction. Such an operation, however, could scarcely be expected to transport individual sperms, for they are too small.

Having reached the uterus the sperms, according to Heape (1905), pass up this tube to its ovarian end in about two hours. My own observations lead me to conclude that this passage may be accomplished normally in less time, approximately in an hour and a half. How they progress up this tube is a matter of uncertainty. Leuckart (1853, p. 919) believed that they were transported by antiperistalsis, an opinion shared by Rouget (1858), Martin (1895), Lim and Chao (1927) and others. Marshall (1922, p. 174) has advanced the opinion that either they swim against a ciliary current or progress by their own unaided efforts. As the mucous epithelium of the body of the rabbit's uterus is almost without cilia, there is no reason to suppose that a directive current is present in this organ (Lim and Chao, 1927, p. 196), and consequently it is very unlikely that Marshall's first suggestion finds application. That the uterus of the rabbit is capable of both antiperistalsis and peristalsis has been shown by the older (Kehrer, 1907) as well as by the more recent workers (Wijsenbeek, 1922; Wijsenbeek and Grevenstuk, 1922). Moreover, according to the observation of Reynolds (1930, p. 425), the muscular activities of the uterus are much increased by coitus. But that any of these movements are concerned with the transfer of sperms seems to me extremely doubtful. As previously mentioned, the sperms, after they have reached the body of the uterus, are no longer a collected mass. At this stage they progress as individuals and the fluid in which they move is so inconsiderable that a muscular wave in the wall of the containing organ could scarcely act upon them. It seems therefore doubtful if peristalsis or antiperistalsis plays any significant part in their progression. In my opinion the sperms rise through the uterus by their own locomotor powers. This opinion is based on the following experimental evidence.

If active sperms are injected into the distal end of a uterus in a freshly killed rabbit and the animal set aside, in two hours' time they will be found at the proximal end of that organ. If a similar injection is made at the proximal end of the uterus active sperms will be found in about the same time at the distal end. During such tests the uteri were kept under inspection and no peristaltic or antiperistaltic movements were observed. The length of tube traversed by the sperms was about seven centimetres, a distance that would be covered by the straight-away swimming of a rabbit sperm in a little less than twenty-five minutes. The fact that it required about two hours to cover this distance is consistent with the observation that sperms do not swim straight ahead, but with great irregularity, and that what has been called in this paper their rate of diffusion may reasonably be expected to be much less than their rate of individual locomotion. In consequence of these results I agree with MARSHALL (1922, p. 174) in his second assumption, that sperms ascend the uterus of the rabbit as individuals by their own locomotion and not by other means. This conclusion is consistent with the observations of LIM and CHAO (1926, 1927), who by a surgical operation reversed a segment of the rabbit uterus without, however, inhibiting pregnancy. I therefore believe that so far as the ascent of the sperms is concerned, the uterus of the rabbit is a non-polarized tube. It serves merely as a channel through which in an hour or two the sperms may make their way by their own locomotion to the entrance into the uterine tube.

The walls of the uterus in close proximity to the opening of the uterine tube are moderately ciliated and the current produced by these cilia, as already stated, is downward, that is, in the direction of the vagina. How the sperms enter the tube from the uterus is not known. For reasons already given, I doubt if they are aided in this transfer by the muscular movements of the adjacent parts. Nor do I believe that they swim against the ciliary current. In my opinion they are advanced by a system of currents and counter-currents, that will be discussed in connection with the uterine tube itself and that probably has its beginning at this point.

The uterine tube in the rabbit resembles in many respects a miniature oviduct from the tortoise. It is provided with an elaborate system of longitudinal folds (fig. 7) more extensively developed, however, than the longitudinal corrugations in the sauropsids. Like the oviducts in the tortoise, the tubes in the rabbit are completely ciliated. Observations on many of these tubes at various stages of sexual activity and quiescence confirmed the statements by SNYDER and CORNER (1922), by SNYDER (1923, 1924) and by NOVAK and EVERETT (1928) to the effect that the cilia at all times maintain a relatively uniform condition and give no evidence of transformation into gland cells as claimed by MOREAUX (1913). As this is the most completely ciliated portion of the mammalian duct it is here, if anywhere, that the two ciliary systems found in the sauropsids, the pro-ovarian and the abovarian (PARKER, 1928, *a*, 1928, *b*), might be looked for.

In consequence of this possibility, much care was spent in study of the rabbit's uterine tubes. In all, nine pairs of these organs were examined. Each was irrigated freely with RINGER's solution, cut transversely into four pieces, approximate quarters, and split lengthwise often into several strips. When a section of tube is thus split and laid open, the folds attached to its inner face flatten out like the leaves of an opened book. Consequently many of the smaller folds and much of the surface of many of the larger folds are covered by adjacent parts and their ciliation is thus hidden from view. Nevertheless, by manipulating such preparations, most surfaces can be exposed and the ciliary beat observed. In all such preparations, with three exceptions, the beat was vigorously toward the uterus, that is, abovarian. In three instances single folds were found in which the beat on the margin of the fold was clearly pro-ovarian. These folds were very close to the cut edge of the preparation, and on readjusting the tissues slightly the part carrying these apparently pro-ovarian cilia disappeared. It is my belief, though in this I cannot be positive, that these apparently exceptional cilia were on folds partly cut loose from the walls of the tube and consequently free to turn either up or down. If by accident such a fold became turned in a direction the reverse of normal, its cilia would beat in opposition to those of the rest of the preparation. Slight manipulation might readjust such a fold so that it would fall back into normal position, in which case it would seem to disappear. This, in my opinion, was the actual state of affairs, rather than that I was dealing with real pro-ovarian cilia, interesting as it would have been to have found them.

A second method of attack on this problem was by injection. If a small amount of India ink ground up in RINGER's solution is injected by means of a fine hypodermic needle into the uterine tube of the rabbit and allowed to remain there an hour or so, the dark injection will be seen to make its way gradually both up and down the tube. If the tube contained both abovarian and pro-ovarian cilia, the ink particles should be carried down the tube in the region of one system and up in that of the other. When such injected preparations were fixed histologically without subjecting them to undue pressure and cut into transverse sections, a study of these sections showed no such localisation of the ink as would justify the conclusion that there were two systems of cilia present in the tube. Each end of the cloud of ink particles presented much the same appearance and nowhere showed a special tendency to follow particular tracts. Therefore, I believe that the uterine tubes of the rabbit are provided with only one system of cilia, the abovarian, and that the conventional statement of the textbooks to the effect that the tubal cilia in rabbits beat toward the exterior is entirely correct and calls for no alteration.

Although the passage of sperms upward through the uterine tubes has been suggested by a few investigators (LEUCKART, 1853, p. 919; HENSEN, 1876, p. 232; ROTH, 1904, p. 336) as possibly due to an antiperistalsis of the tube itself, the vast majority of workers (LOTT, 1872; HENSEN, 1876, 1881; KRAFT, 1890; ROTH, 1893, 1904; VERWORN, 1895; ADOLPHI, 1905, 1906, *a*, 1906, *b*; GODLEWSKI, 1910–1914, 1926; HOEHNE, 1911, 1920; FELDMAN, 1920; STENDEL, 1926) have scarcely considered this suggestion but have declared in favour of the opinion that sperms are rheotactic and ascend the tube by swimming against its ciliary current. In attempting to ascertain how the sperms ascend the tube in the rabbit, I carried out tests somewhat in line with those already tried on the ducts in the tortoise and in the pigeon.

If a piece of freshly opened uterine tube is appropriately placed in an abundance of RINGER's solution and observed under the microscope, a strong abovarian ciliary current can be easily seen. Blood corpuscles and bits of organic detritus are driven onward at a rapid rate. If, now, such a preparation is flooded with RINGER's solution containing an ample supply of active rabbit sperms, these sperms, like the particles of detritus, are also swept along by the ciliary current, the rate of which is such that the locomotor activities of the sperms are of little avail against the general rush. The individual sperms in the rabbit, as in the tortoise and the pigeon, when thus suspended in the general current, swim in any direction and show no evidence of rheotaxis. The current is most rapid next the cilia and diminishes as one recedes from them. The gradient of change of rate must be considerable, and yet it has no observable orienting effect upon the sperms which, as already stated, swim indiscriminately with the current, against it, or across it. The sperms appear to be no more directed by the general current than a blindfolded swimmer would be by any general current in which he might be immersed. The fate of the sperms in contact with the ciliated surfaces is peculiar and will be discussed later, but those in the body of the stream are quite undirected by it and give no evidence of rheotaxis. This statement is made in full recognition of the fact that it is in opposition to the opinion of the great majority of workers, who have based their views, however, not on observations on sperms moving in a considerable depth of fluid next oviducal cilia, but on these elements next glass, in very shallow fluid artificially moved. Under such circumstances, as I have already pointed out, a rheotaxis can be easily demonstrated, but such conditions can scarcely be said to reproduce those of the uterine tubes. When the state in the oviduct is more nearly imitated, as in the present experiments, the evidence for rheotaxis disappears. I therefore conclude that in the rabbit, as in the tortoise and in the pigeon, rheotaxis plays no real part in the ascent of the sperms.

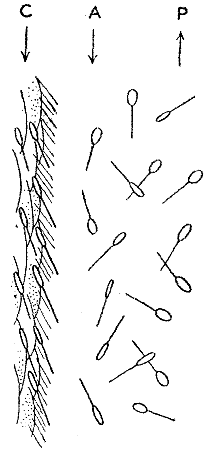

FIG. 6. — Freehand sketch of the edge of a fold from the uterine tube of a rabbit showing the distribution of living sperms on the fold and in the adjacent fluid. A, abovarian ciliary current; C, ciliated epithelium on uterine fold; P, pro-ovarian counter-current.

Antiperistalsis has been suggested by a number of the older investigators (BISCHOFF, 1842, *b*; LUDWIG, 1861; FUNKE, 1863–1866) as a means of transporting sperms upward through the uterine tubes. The movements of these tubes have been very fully studied by recent workers who, with very few exceptions, ascribe to them an undulatory motion, neither peristaltic nor antiperistaltic, but like the segmentation of the intestines (VON MIKULICZ-RADECKI, 1926, p. 324). This movement is believed to result in a mixing of the contents of the tube rather than in progression. Kok (1925, *a*, 1925, *b*), however, has declared in favour of a true peristalsis in the tubes of the rabbit and has also asserted that antiperistalsis may be seen, though he looked upon this process as abnormal.

It is by no means easy to observe in the rabbit the movements of the living tube. This organ is small and often much embedded in fat, so that observation without considerable preparatory cutting is commonly impossible. Of the many active tubes that I have watched closely, immediately after coitus and later, I have never seen one that showed unquestionable antiperistalsis. Undulatory movements are commonly present, and waves can be seen passing down the tubes to such a degree as to warrant the assumption of peristalsis (Westman, 1926, *a*, 1926, *b*), but movements that progress toward the ovary have never been observed by me. I am, therefore, convinced that antiperistalsis, if present at all, is rare and must be at best a wholly unimportant factor in the transportation of sperms in the rabbit.

Nor is it at all likely that progress by diffusion, such as occurs in the uterus and is dependent on the irregular swimming of the sperms, takes place in the tube. For the tube, unlike the uterus, is richly ciliated and its abovarian current is much too strong to allow the locomotion of the sperms themselves to become effective. If rheotaxis, antiperistalsis, and spermatic diffusion are not means of transfer, how, then, do the sperms pass up the tube ? This passage is accomplished, in my opinion (Parker, 1930, *b*) through the abovarian cilia, whose action induces in the intact tube a system of currents and counter-currents, heretofore unsuspected, and by means of which the sperms may be carried step by step toward the ovary. The presence of these currents and their method of action can be demonstrated both by injections and by direct observation.

If a tube embedded in its surrounding fat, and with its uterine and ovarian connections intact, is floated in Ringer's solution at body temperature, the movements of its fluid contents can be studied by injection. By means of a hypodermic needle a very small amount of India ink can be discharged into the cavity of the tube about midway its length, and the progress of the ink along the tube can be watched through its translucent walls. Great care must be taken not to exert undue pressure on the walls, for by this means the ink can be made to flow quickly and easily in either direction. If, however, all external pressure is avoided and the tube, locally alive, is allowed to remain suspended in the warm Ringer's solution, the ink will be found in about an hour to have flowed out at the infundibulum on the one hand, and on the other to have reached a point well toward the opening into the uterus. In another hour or so it will have passed into the cavity of the uterus. Thus the particles of ink make their way in the course of time both up and down the tube on whose walls the cilia beat continuously downward. Tests of this kind were made a number of times and with uniform outcome.

In attempting to explain the passage of the ink through the tube it might be assumed that the ink particles simply diffused through the lumen. But as the distance covered in an hour was four or five centimetres it is clear that the rate of the ink is much too high for diffusion. The condition in the interior of the tube was therefore investigated. If a rabbit tube in a fresh state is laid open in some depths of RINGER's solution under a microscope, the ciliary currents in the spaces between its folds can be seen to take diverse courses. In any given space the currents immediately next the ciliated faces run in an abovarian direction. Spaces of this kind, however, are definitely limited. At short distances up and down the tube such spaces are shut off by the temporary approximation of their surrounding folds, thus establishing for the time being closed compartments. At the lower end of such a compartment the abovarian ciliary currents would be blocked, were it not that the fluid is free to return up the centre of the compartment almost to its top, where it can reverse again and pass down the ciliated walls. Thus a circulation of fluid is established in each temporary compartment, abovarian in direction on the sides next the cilia and pro-ovarian in the central region, with transfers from one to the other at each end of the compartment (fig. 8). A cross section of such a compart-

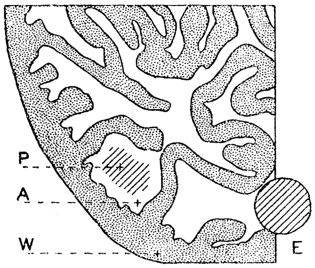

FIG. 7.—Diagram of a quadrant of a transverse section from the uterine tube of a rabbit.

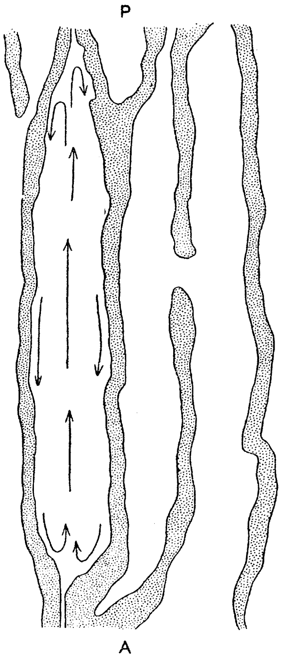

FIG. 8.—Diagram of a longitudinal section from the uterine tube of a rabbit. Three compartments are shown, in one of which the circulation is indicated by arrows; abovarian currents next the ciliated walls and pro-ovarian currents in the axis of the compartment.

A, abovarian ciliary current on the periphery of a compartment; E, outline of egg drawn to the same scale as the tube; P, pro-ovarian counter-current in the middle of a compartment; W, wall of the uterine tube.

ment (fig. 7) would show the abovarian current next the wall and the pro-ovarian one near the middle. The two currents would be separated by a certain amount of dead water. Sperms introduced into such a compartment would be carried quickly its whole length and thus become diffused throughout its interior.

The temporary compartment just described is the type of space that, many times multiplied, makes up the cavity of the uterine tube. At any one moment hundreds of such compartments must exist in the tube. They are, however, extremely temporary, for the undulatory or segmental motion of the tube opens and closes them continually. Thus they are subjected to endless change, slowly dissolving and reforming with the movements of the tube and never twice in exactly the same place. As a result of these continuous adjustments the fluid contents of one compartment establish relations with those of others, and pass now upward, now downward, thereby carrying the suspended particles by this somewhat haphazard process eventually to one or other end of the tube. In this way the movement of ink particles from the mid-length of the tube to its uterine and its ovarian mouths is believed to take place. India ink injected into either end of the tube finds its way in a similar manner along the whole length of the tube. When an injection is made at the uterine end some of the ink escapes into the uterus, but much of it can be seen to progress slowly along the tube toward the ovary. It is in this way that the sperms are believed to make their way from the uterine aperture of the tube to its infundibulum. Thus the temporary tubal compartments with their fluid circulation induced by abovarian cilia are believed to be the means of transporting sperms even in a pro-ovarian direction.

The simple inversion of such a system of temporary compartments with its currents and counter-currents should not apparently interfere seriously with its operation. Nevertheless this inversion, as carried out surgically by Kuo and Lim (1928) on the rabbit and the pig, resulted in infertility. Infertility thus induced may, however, be due quite as much to the inability of the eggs to descend as of the sperms to ascend the tube. Although simple section and reanastomosis of the tube without reversal did not prevent pregnancy, showing that the experimental surgery in the case had been very successful (Kuo and Lim, 1928), it is still possible that when reversal was performed the tubal folds may have become so involved as to have rendered the compartment system inoperative. In such an event the transportation of the sperms may have been seriously interfered with, a condition which of itself may have caused infertility, for if the sperms are detained far down the tube the unfertilised egg may die before it reaches them. Inversion of the tube, then, may have more serious consequences for the compartment system than at first sight would seem likely.

The compartment system depends for its successful working on a reasonably complete ciliary lining in the tube as a whole. Such a lining is present in the rabbit and in most other mammals, but in some forms it is said to be at least partly deficient. It was long ago pointed out by Hoehne (1911) that in the development of the mammalian uterine tube the ciliation appears first at the infundibulum and proceeds thence to the ampulla and later to the isthmus. When development is incomplete the deficiency, as would be expected, is at the lower end of the tube. In some mammals, such as the rat and the mouse (Gage, 1904; Schaffer, 1908; Fischel, 1914), though the ampulla is ciliated the isthmus is normally never so. This condition might seem to present a serious objection to the compartment hypothesis as proposed, but it must be remembered that in all mammals the compartment system is limited in extent. In the rabbit the system reaches to the uterus. Up to that level the sperms are believed to make their way by their own locomotor powers. In the rat and in the mouse this means of progress is probably continued up to the ampulla, after which the ascent is made through the compartments. The absence of cilia from the lower part of the tube of the rat and the mouse is, then, no real objection to the compartment hypothesis.

In all my experiments on the uterine tubes where injections of India ink were used, I was impressed with the quickness with which the ink flowed through the tubes in either direction as a result of the slightest local pressure. The walls of the tube are non-resistant and a limited pressure even very small in amount will drive such fluids with great freedom along the tube. Pressures of this kind under entirely natural conditions must often influence the tubes. The normal movements in the abdominal cavity of the living rabbit, such as intestinal peristalsis, must impinge frequently on the uterine tubes, and it is easy to see how under such circumstances the fluid contents of the tubes, possibly carrying sperms, would be driven one way or the other as these accidental pressures make themselves felt. Such a pressure, if applied appropriately, might well drive the fluid contents of the tube almost instantly over a large part of its length and thus, depending upon the direction, immensely facilitate or retard the ascent of any contained bodies. But whatever may be claimed for such pressures or other like factors, the evidence at hand convinces me that the ascent of the sperms through the tubes of the rabbit is chiefly due to the counter-currents combined with the action of the temporary system of compartments already described.

When a preparation of the tubal folds in Ringer's solution containing many active sperms is studied, the distribution of these cells is found to be peculiar. In the beginning they are to be seen swimming indiscriminately in the general ciliary current. As they come from time to time in contact with the epithelium of the folds they adhere by their heads to this layer and, swinging about like a weathervane, orient with their tails pointing in the direction of the flow of current (fig. 6). They are, therefore, headed approximately up-stream and were they to swim they might well be regarded as rheotactic. Although I have watched such preparations for long periods at a time, I have never seen a sperm once attached loosen itself and swim away. Once adherent to the wall of the tube, they always remain so, though they exhibit even in the attached condition what appear to be swimming movements. This phenomenon agrees in several respects with the thigmotaxis of sperms described many years ago by Dewitz (1886) for the roach and observed subsequently in the sperm cells of other animals by Massart (1889), von Dungern (1902), Buller (1902) and others. It is apparently dependent upon the possession of an adhesive head and a special form of body, conditions that in a measure remove it from the realm of a real organic response.

A very similar condition was long ago observed by Löw (1902), who, however, regarded it as a case of chemotaxis such as has been described in plant spermatozoids by Pfeffer (1884) and in the sperms of other organisms by Massart (1889), Verworn (1895) and later workers. I have never seen anything in the responses of rabbit sperms, however, to lead me to believe that they were chemotactic toward the tubal walls. So far as I could observe, they merely collided with these walls and stuck to them. I am inclined to agree with Buller (1902) that in sperm reactions chemotaxis is not such an important factor as some workers have been led to believe. Although the chemical environment may exert almost no directive influence on the sperms of such animals as the rabbit, the importance of this environment for the life of such cells, as Kugota (1929) has shown, is unquestionable.

In the rabbit the sperms, according to my observations, do not become attached in any considerable numbers to the uterine wall. This is contrary to the statement made by Löw (1902), who claimed that these elements were attracted to this wall as well as to that of the tube. In my preparations very few sperms, if any, were attached to the uterine epithelium, whereas that of the tube was literally covered with them. On this epithelium they seemed to adhere to the exposed surfaces of the gland cells rather than to those of the ciliated cells, though on this point I cannot be perfectly certain. I attribute this difference to the mere physical peculiarities of the walls of these two parts rather than to what might excite in the sperms any form of chemotaxis.

An examination of the tubes from a rabbit in the late stages of a successful insemination showed some sperms attached to the tubal walls and others free in the fluids of the tubal compartments. I, therefore, conclude that the attachment of sperms to the tubal walls is not a product of laboratory experimentation, but is a normal process in the reproduction of this animal. Whether fertilisation is accomplished in the rabbit by the free sperms or by the attached ones or by both, I am unable to say, but in the discussion that follows on the migration of the rabbit's egg it will be shown that this body in its downward passage through the tube wipes the tubal surfaces over which it passes in such a way that it might pick up from them any sperm that would lie in its path. It is conceivable that insemination as a preparatory step to fertilisation may mean the coating of the tubal surfaces with a sufficiency of sperms to ensure engagement with the descending egg. Such sperm cells having once attained their positions on the tubal epithelium would be reasonably secure from dislodgment by pressure and other like adjustments that might involve serious changes in the distribution of the free sperms.

My inspection of a considerable number of rabbit ducts after successful insemination led to the conviction, entertained by most workers in this field, that the sperms diminish steadily and rapidly in numbers as the ducts are ascended. Hammond and Marshall (1925, p. 103) state that at about the time the eggs are ready to enter the tubes in the rabbit the vagina was seen to contain numerous sperms, the cervix a plentiful supply, the lower uterus few, the upper uterus fewer, and the tube very few. What happens to the sperms in their ascent whereby they become diminished in number is difficult to say. At the outset the muscular activity in the region of the cervix leaves a large proportion behind, as can be seen by the residue in the vagina. In the lower uterus many penetrate the walls and are there absorbed, if we are to credit the account of Kohlbrugge (1912). In the body of the uterus the diffusion-like method of progress would again tend to thin the numbers in ascent. Finally, in the compartments of the tube a further spreading would occur, so that, as the table published by Hammond and Marshall shows (1925, p. 103), it is often impossible to identify any sperms at all in this part of the reproductive apparatus. Such a reduction, however, must not be carried too far, for, as Walton (1927) has shown, when the inseminating mixture in the rabbit is diluted so as to contain between 3,000 and 4,000 sperms per cubic centimetre, sterility intervenes. Thus, at all steps in the ascent of the sperms, the several processes whereby this progress is accomplished call for a steady reduction in the number of sperms, a state of affairs entirely confirmed by what is seen in the ducts on direct inspection.

The ascent of the sperms through the reproductive tracts of the rabbit is by no means a simple process and involves an array of factors more numerous than many of the older workers suspected. The operation appears to be initiated in the region of the cervix by rhythmic muscular movements, which probably extend upward over the uterus and may even reach the uterine tube, though there is no reason to assume that the movements of these parts, possibly antiperistaltic in character, contribute in any important way to the progress of the sperms. The second important factor in this operation is the locomotor activities of the sperms themselves. They swim indiscriminately in all directions and thus bring about a kind of diffusion which leads necessarily to a rate of progress less than that of the rate of swimming of the individual sperms. It is entirely possible that this means of ascent may in some measure replace that due to muscular action, should for any reason the muscles fail. A third factor is seen in the abovarian cilia of the tubes. These cilia, in association with the tubal folds and musculature, establish a system of elongated temporary compartments whose counter-currents transport the sperms to the region of the infundibulum. Rheotaxis appears to play no significant part in this process. Finally, the irregular pressure of adjacent organs in action, such as the intestine and the like, must exert considerable influence on the motion of the fluid contents, especially in the tubes. These pressures, however, may be effective as often in a downward as in an upward direction. Though these several factors may be described separately, their separation is distinctly artificial. The activities of the tracts are without question ordinarily due to a combination of them, and in all cases they certainly overlap to such a degree that what often seems to be a comparatively simple operation is in truth relatively complex. The ascent of the sperms through the reproductive tracts, as thus outlined, depends in large part upon the action of the tracts themselves, and even the active swimming of the sperms has been shown to result in a rather mechanical type of progression that lacks the selective element associated with the assumed rheotaxis of older accounts. That this is a serious loss in the general scheme of ascent I do not believe. It is a pure assumption that the most vigorous sperm individually is best for reproduction. The selection which is thus assumed may have no significance whatever in determining the nature of the final outcome. In my opinion this aspect of the process may be abandoned without serious loss.

C. *Descent of eggs.*—The eggs of the rabbit, liberated from the ovarian follicles about ten hours after coitus, are not vigorously ejected from their containing structures, as was surmised by LEUCKART (1853, pp. 756, 868), but are slowly squeezed out on the surface of the ovary, an operation directly observed by WESTMAN (1926, *a*, 1926, *b*) through a KATSCH-BORCHERS' window. The importance of muscular action in approximating the infundibulum to the ovary, and of an erection of the surrounding parts to facilitate the entrance of the eggs into the uterine tube, has been emphasised by numerous writers (KIWISCH, 1851; ROUGET, 1858; LODE, 1894; GERHARDT, 1905; WESTMAN, 1929). Since the mammalian egg possesses of itself no locomotor capacity, its movements are due entirely to the transporting powers of the surrounding organs. LODE (1894) showed that ascaris eggs placed in the abdominal cavity of the rabbit were subsequently found in the animal's uterine tubes and even in the uterus itself. According to PINNER (1880) and to WESTMAN (1926, *a*), ink and other like suspensions discharged in the neighbourhood of the infundibulum pass into the tube. Whether these transfers are due to the cilia of the infundibular region, all of which beat toward the tube, or to suction produced by the peristalsis of the tube cannot be definitely stated. WESTMAN (1929) has shown that in the monkey and rabbit during sexual quiescence peristaltic movements of the tubes are relatively feeble. During sexual activity the fimbriæ are applied closely to the ovary and peristalsis is much more vigorous. A day or so later it subsides to even less than what it is in the quiescent phase. These observations favour the opinion that peristalsis is of importance in the transport of the eggs from the surface of the ovary to the beginning of the tube, but they do not show that this process may not be supplemented by the infundibular cilia. As PINCUS has demonstrated (1930), eleven hours after coitus or about one hour after ovulation the eggs in the rabbit accumulate in a mass at the upper end of the uterine tube from which they begin the descent of the tube. They are fertilised in from an hour and a half to three hours after ovulation. In about three to four days they pass through the tube and enter the uterus. Their rate of passage down the tube is probably like that of the eggs of the pig, as investigated by ANDERSEN (1927), rapid in the ampulla and slow in the isthmus.

The means by which the egg passes through the tube has been the subject of most heated controversy. Many investigators, including a number of earlier ones (MÜLLER, 1835–1837; PINNER, 1880; LODE, 1894; VON EBNER, 1902; HOEHNE, 1908, 1911; GROSSER, 1914, 1915; CHILD, 1922; BANDLER, 1924; KUO and LIM, 1928), have regarded the tubal cilia as the exclusive means of transportation for the eggs. Others have looked upon tubal peristalsis as the only method of moving these bodies (CALDANI, 1786; LUDWIG, 1858–1861; ROUGET, 1858; HENSEN, 1881; SOBOTTA, 1895, 1914, 1915, 1916, 1922; SECKINGER, 1923; SECKINGER and CORNER, 1923; PUTNIN, 1924; VON MIKULICZ-RADECKI, 1926; KOK, 1927, *b*). Still a third group has expressed the opinion that the movement of the eggs is accomplished by a combination of cilia and muscle (BISCHOFF, 1842, *b*; GEGENBAUR, 1892; EDEN, 1915; GROSSER, 1918; CORNER, 1923; ANDERSEN, 1927). Which of these opinions is correct it is difficult to state.

It has been shown already in discussing the migration of sperms that the uterine tube of the rabbit is completely ciliated and that all cilia beat toward the uterus. It is also well established that the walls of the tube are provided with muscles and are actively mobile (GUTHMANN, 1922; SECKINGER, 1923, 1924; SECKINGER and CORNER. 1923; SECKINGER and SNYDER, 1924, 1926), showing especially segmentation (KOK, 1925, *a*, 1925, *b*; VON MIKULICZ-RADECKI, 1926) and, notwithstanding the declaration of VON MIKULICZ-RADECKI to the contrary, abundant peristalsis and occasional anti-peristalsis (KOK, 1925, *a*, 1925, *b*, 1926; WESTMAN, 1926, *a*, 1926, *b*). KOK (1927, *a*) has recently shown good reason to assume a reflex innervation in the tubes. The fact that in some mammals, such as the mouse and the rat, the tubes are partly devoid of cilia makes it highly probable, as already pointed out by SOBOTTA (1914), that peristalsis at least is one effective factor in moving the eggs. But proof of this kind affords no ground on which to deny the participation of cilia in the process.

It has been claimed by a number of workers (KEHRER, 1863; HEIL, 1893; HOFMEIER, 1893; VON MIKULICZ-RADECKI, 1926) that the ciliary beat of the tube is not sufficiently strong to move the eggs of the rabbit. It is true that material such as grains of carmine and the like, if placed on the ciliated surface of an opened uterine tube, will often remain motionless where they were placed, even though the subjacent cilia are in full activity. The mammalian egg and other such objects might be expected to fare in a similar manner. This is not because these bodies are too heavy, but because they are too light. They rest on the thin layer of mucus that commonly covers the cilia, and that is often in one way or another anchored to fixed parts of the tubal epithelium. Consequently the mucus with the attached particles shows no motion. If the added particles had sufficient weight they would either press the mucus firmly against the cilia or actually break through the mucus and come thus to rest on the cilia themselves, in either case attaining a position in which the cilia could work upon them effectively as motivators. This condition may be seen when on a ciliated layer a few lead filings are spread in place of the carmine particles. The lead will often be a means of demonstrating motion where the carmine fails. Mammalian eggs have a specific gravity only a little above that of water and consequently when, as in the tests thus far reported, they are allowed merely to rest in fluid on the ciliated surface, they do not press firmly enough against the cilia to enable these bodies to act upon them effectively. Could the egg be pressed with some vigour against the cilia, these elements would then be able to move it.

The structure of the uterine tube in mammals is precisely such as to meet these requirements. The cavity of the tube is not simple, but is split up by the tubal folds into the series of longitudinal canals or compartments, as I have elsewhere termed them, that run varying distances up and down the tube and that in consequence of the tubal movements are undergoing continual change. When these compartments are measured they are found to be almost always a little too small for the free passage of the egg. The minimum diameter of the rabbit egg is about 0·12 millimetres (Painter, 1928; Hartman, 1929; Castle and Gregory, 1929). This may be considerably increased by the presence of follicular cells as the egg enters the tube, or by the addition of albumen as it passes through that structure. If, however, a circle of the minimum size of the egg is drawn to scale on a camera outline of a transverse section of the tube (fig. 7), it will be evident at once that the egg cannot pass through the tube without pressing the tubal folds slightly away from one another, a process that will bring the surface of the egg into such intimate contact with the cilia of the tube as to place these bodies in a most advantageous position for communicating motion to the egg. In fact, the tube possesses a structure which in form and proportions is most admirably adapted to the propulsion of the egg by cilia.

It is a common experience of those who have worked much with cilia, that when these effectors are being tested at about the limit of their capacity, a small amount of extraneous motion, like a slight vibration, will enable them to continue to transport an object which otherwise might come to a standstill. Such slight movements disengage the moving object from momentary hindrances and thus facilitate its transportation. It is quite probable that the segmental movements of the tube are of importance in this respect in helping the egg onward and thus aid to dislodge it from time to time at places in the tube where it might otherwise be stranded temporarily. No one would deny that the peristalsis of the tube must be a factor of the greatest importance in the propulsion of the egg, but in my opinion the tubal cilia play a part in this operation quite as significant as the muscles. I, therefore, side with those who assume that the tubal muscles and the cilia combine in transporting the egg through the uterine tube.

The passage of the developing egg from the tube into the uterus occurs about three to four days after ovulation. Excepting in close proximity to the tubo-uterine aperture and to the cervix the uterine epithelium is almost entirely without cilia. Muscular movement of the uterine walls (Keye, 1923) appears to be the only means left for the transfer of the eggs, but the exact method by which these bodies distribute themselves through the uterus is not known. It seems highly improbable, in consequence of the close agreement between the number of eggs liberated and the number of young born, that the distribution of the eggs through the uterus can be haphazard, with death as a means of elimination where the young are too closely placed. Nor is there reason to believe that unequal growth of the uterine wall adjusts overcrowding. The problem of the uterine localization of mammalian embryos is in this respect quite obscure. The eggs, though without powers of locomotion in themselves, certainly exhibit unusual migratory capacity. External migration, that is, the passage of an egg from one ovary across the abdominal cavity and down the tube of the opposite side, seems to be clearly established for man (SFAMENI, 1927), though there appears to be no evidence for it in such mammals as the pig (CORNER, 1921) and the rabbit (PARKES, 1924). Internal migration, that is, the passage of the egg from the uterine horn of one side through the body of the uterus to the other horn, is supported by many observations, experimental and otherwise, especially on the pig (HAMMOND, 1914 ; CORNER, 1921 ; WARWICK, 1926 ; KELLY, 1928). It is to be noticed in this type of migration that apparently both peristalsis and antiperistalsis are involved, for the eggs first pass down one horn of the uterus and then up the other. However, it may be maintained, since there are no direct observations on this point, that peristalsis and antiperistalsis in reality play no part here, and in truth no one knows what the nature of the operation is.

Notwithstanding the observations of LEOPOLD (1880) to the contrary, it is improbable that either external or internal migration takes place in the rabbit. The occurrence of internal migration is highly improbable, for the rabbit uterus is strictly bipartite and it is extremely unlikely that an egg from the uterus of one side could pass into the cavity of the vagina, cross this space, and enter the uterus of the other side. External migration in the rabbit is not so unlikely, but PARKES' careful experimental tests (1924), all of which were followed with negative results, led him to conclude that this type of translocation was very rare in the rabbit, if in fact it occurred at all. He is probably correct in attributing LEOPOLD'S declaration of positive results to some oversight in experimental procedure, such as the regeneration of an ovary supposed to have been completely removed. But, notwithstanding the fact that the eggs of rabbits are more restricted in their range of movements than those of most other mammals, they nevertheless do distribute themselves through some seven to eight centimetres of uterine tube on their own side, by means that, so far as can be seen, must be purely muscular. After the rabbit embryos have reached full term they are born through being expelled from the uterus by what is essentially a vigorous peristalsis which, as observed by LUDWIG and LENZ (1923) through a KATSCH-BORCHERS' abdominal window, takes place first in one uterus and then in the other. Thus the downward passage of egg and embryo in the rabbit is much simpler than the upward passage of its sperms. In the region of the uterine tube the movement of the egg is accomplished through the combined action of cilia and of muscles, and in that of the uterus and the vagina through muscles alone.

4. *Discussion.*

If the preceding account is correct, the activities of the female generative ducts in the higher vertebrates involve both muscles and cilia to almost equal extents. In this respect these ducts resemble the bodies of sea-anemones and other such cœlenterates in which these two effectors constitute the chief responding elements. Moreover, enough of the mechanism for the nervous control of the vertebrate reproductive tube is contained within its substance (Kok, 1927, *a*) to justify a belief in a certain degree of neuro-muscular independence for it, another point in which it resembles not only the body but parts of the body of a cœlenterate (Parker, 1919). These resemblances are probably more than superficial and point to a constitutional likeness in organisation that, if not inherited, is at least inherent in such systems.

The female generative ducts in the tortoise, the pigeon, and the rabbit are provided with a continuous musculature. The activity of this musculature near the external ends of the ducts appears to be the normal first step in the transfer by the female of the spermatic fluid from the region of deposition by the male to a point higher in the ducts. It involves ordinarily only the lower parts of these structures and is the muscular component of the female sexual orgasm. It may spread, however, presumably as waves of antiperistalsis, up the ducts even to their ovarian ends. This, at least, is the conclusion that I draw from the fact that at copulation rat sperms pass from the vagina of this animal to the apex of its uterine horn in less than two minutes (Hartman and Ball, 1930) and that fully formed eggs in the hen may be discharged through the infundibulum into the bird's abdominal cavity (Pearl and Curtis, 1914).

These ducts also exhibit typical peristalsis, in that waves course over them from their deep ends next the ovaries outward to the exterior. Such waves are the obvious means of moving large eggs like those of the tortoise and of the pigeon through the length of the ducts. In the pigeon the egg traverses approximately thirty-five centimetres of tube in a little less than twenty-four hours. In the pigeon, and especially in the tortoise, the peristaltic activity of the duct is broken into two rather distinct periods. The first is marked by the action of the upper portion of the duct, during which the egg proper passes through the albumen-secreting region and receives its coat of egg-white. Then follows shell-formation and, especially in the tortoise, storage; after which the second period of peristalsis intervenes, resulting in the final act of egg-laying. In the rabbit the two periods are widely separated. The first includes the peristalsis of the uterine tube and is of importance in transferring the eggs in the course of three or four days from the ovary to the uterus, a process in which the tubal cilia are also involved. After the distribution of the eggs in the uterus (an operation that must be muscular in nature) each egg becomes attached to the uterine wall and grows in the course of some twenty-seven days into a full-term embryo, whereupon the second period of peristalsis intervenes and the young rabbit is expelled from the uterus at birth. Thus in the rabbit a long interval of quiescence separates the two periods of peristaltic action.

The cilia of the ducts in the tortoise, the pigeon and the rabbit give no evidence whatever of reversal of stroke in response to substances dissolved, for instance, in the spermatic fluid. In this lack of reactiveness to their chemical environment these cilia are quite unlike those on the lips of certain sea-anemones, where meat juices induce a temporary reversal. It was natural to look for this reversal in the vertebrate ducts, for it has recently been demonstrated by TWITTY (1928) in the integument of larval amphibians. Nevertheless, it appears not to be a part of duct activity. The ciliation of the ducts in the tortoise and the pigeon is complete; the direction of the stroke is abovarian throughout, except that in the albumen-secreting portion, as already stated, a narrow pro-ovarian tract occurs. This tract is believed to be the means of conducting the sperms to the neighbourhood of the ovary. In the ducts of the rabbit, the cilia, instead of being continuous, form two distinct areas, a lower one in the region of the uterine cervix and an upper one in that of the uterine tube including the aperture to the uterus. In both these areas the direction of the stroke is abovarian. The area about the cervix is probably protective, in that it prevents foreign material from entering the uterus. The upper area, particularly in the region of the uterine tube itself, has the double function of conducting sperms upward and eggs downward. From what has already been stated, it is not only clear how this double action may be carried out, but it is also evident that the two phases of it, one pertaining to the sperm and the other to the egg, may proceed at one and the same time without interference. The downward passage of an egg may take place without in the least disturbing the upward passage of the sperm even in the same compartment. This rather remarkable state of affairs can be summarised in what may be called the rule of action for the mammalian uterine tube: small bodies, such as particles of ink or individual sperms, are carried by the currents in the compartments of the tube either upward or downward; large bodies, such as eggs, are conducted through the same spaces by peristalsis and direct ciliary action always downward.

So far as sperms are concerned, the significant points in this relatively novel view of the action of the tubes are, first, the abandonment of rheotaxis as an important element in explaining the advance of the sperms, and, secondly, the substitution for this type of response of an activity of the tube itself, whereby small particles, with or without locomotor powers, are conducted in gradually diminishing numbers either way along the tube, and eventually on the part of some to the ovary.

Thus it is possible to bring in line with the conduction of sperms the transport of small, non-motile cells to such a region as that of the ovary. Any minute particle, whether it has locomotor power or not, may be carried by the currents and countercurrents of the compartments either up or down the tube. Such particles may in time spread from uterus to ovary or the reverse. In this way germs of disease may be carried from one end of the tube to the other, and cells or other bits of tissue may be conveyed with equal freedom throughout the structures under consideration. This hypothesis makes clear the means by which in man living epithelial cells liberated from the surface of the menstruating uterus may pass upward to the ovary, there to give rise to such pathological growths as the so-called chocolate or hæmorrhagic cysts. In this respect the hypothesis just advanced affords support to SAMPSON's theory of the origin of these abnormalities (SAMPSON, 1921, 1922; JACOBSON, 1922; GRAVES, 1923), for it assumes a type of transportation equally effective for particles with or without their own means of locomotion.

5. *Summary.*

1. In the tortoise and the pigeon the spermatic fluid deposited by the male in the cloaca of the female is probably transferred by the muscular action (antiperistalsis) of the parts immediately concerned to the isthmus. From the isthmus to the ovary the sperms are carried by the current of the pro-ovarian ciliary band, whose stroke is toward the ovary and the reverse of that of the other cilia (abovarian) in the oviducts of these two animals.

2. Sperms from the tortoise and from the pigeon do not swim against the ciliary currents of their oviducts, but are swept onward in these currents. Sperm rheotaxis in these animals is a laboratory artefact.

3. In the rabbit the spermatic fluid deposited by the male in the vagina of the female is normally transferred by the muscular action of this region to the uterus through its cervix. This action is the muscular component of the female sexual orgasm. This process under special conditions may be replaced by the locomotor activities of the sperms themselves.

4. The sperms pass from the lower end of the rabbit's uterus to the upper end of that organ by their own locomotor powers.

5. The sperms are not carried normally through the uterine tube by antiperistalsis nor do they swim against the ciliary currents (abovarian) of these tubes. Sperm rheotaxis in the rabbit, as in the turtle and the pigeon, is a laboratory artefact.

6. The cavity of the uterine tube in the rabbit is broken up by its folds and muscles into a system of temporary longitudinal compartments on the walls of which there are ciliary currents (abovarian) and in the centres of which there are counter-currents (pro-ovarian). These compartments are temporary in that under the muscular activity of the tube they are forming, disappearing, and reforming continually. Thus they give opportunity for frequent exchange of contents.

7. In consequence of the currents and counter-currents in the system of tubal compartments, sperms and other small particles are transported in a somewhat accidental way up or down the tubes. Sperms that enter the lower end of the tube from the uterus may eventually be discharged at the upper end next the ovary.

8. In the tortoise and the pigeon the large eggs pass down the oviducts under peristalsis, which occurs in two periods: first, the passage downward through the albumen-secreting region of the duct; and, second, the outward passage in egg-laying.

9. In the rabbit the eggs pass down the uterine tubes as a combined result of peristalsis and ciliary action. The eggs are of such a size as to press against the sides of a compartment and thus make fully available the effectiveness of the ciliary stroke.

10. After a lengthy quiescent development in the uterus, the young rabbit is born as a result of a second period of peristaltic activity.

11. The rule of action for the compartment system in the uterine tube of the rabbit and probably of other mammals is that small particles, sperms and the like, are carried both up and down the tubes, while large particles, eggs and the like, are carried always down the tubes.

12. The possibility of transporting small non-motile particles up (as well as down) the tubes supports SAMPSON's contention that hæmorrhagic or chocolate cysts are growths from uterine epithelial cells freed in the course of menstruation and carried by the compartment system to the ovary.

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