THE REPRODUCTIVE ORGANS OF CETACEA.

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THE Cetacea have become modified for aquatic life, and it has been an interesting task for the morphologist to trace the changes which have been brought about by a more and more complete adaptation to the habitat. The reproductive organs are peculiarly interesting in this respect, for all the events connected with reproduction take place in aquatic and pelagic conditions.

The general disposition of the organs and their general morphology are already known from the investigations made by Weber, Guerin, Rapp, Van Beneden, Hunter, Owen, Cleland, and recently by Hepburn; but the modifications they present in relation to function do not appear to have been clearly stated, and I find it necessary, therefore, to give a re-statement of the facts of structure with reference to some of the common Delphinidæ.

About 1889–1890 I had the opportunity of examining male fœtuses of various toothed whales in the laboratory of Professor D'Arcy W. Thompson, Dundee, and it was the intention to publish the results in the series of researches which were at that period issued from his department. But financial difficulties intervened and the series came to an end. I have the permission of Professor Thompson to incorporate in this paper the figures which were made so long ago.

This year, 1917, the fishermen at Cullercoats have captured many porpoises in the salmon drift-nets, and the investigation of some of these gave the opportunity of re-examining the structural modifications. Although this species is the one which has been most frequently examined, it will be convenient to describe as fully as is necessary the organs in both sexes.

The sexes are easily distinguished. In the female the anal and vulval openings are close together, and may indeed occupy the same recess. On each side of the vulva is the slit-like opening in which is lodged the teat of the mammary gland. In the male the similar opening of the preputial pouch is centrally situated, and the anal opening is far removed from it posteriorly. In front of the latter is a small aperture in which the reduced teats of the mammary gland are situated.

Phocæna communis. Female. (Figs. 1 and 2.)

The females examined, four in number, measured 4 ft. 3 ins. to 4 ft. 5 ins. in length, and the anterior end of the vulval opening was situated about 2 ft. 5 ins. to 2 ft. 7 ins. from the anterior end. The vulva varied from 3 to 4½ ins. in length. The anal opening is usually separated from the vulval opening by a ridge, but, as has already been stated above, it may actually be enclosed in the vulval aperture.

In all respects, except at the uterine end of the vagina, the organs have a simple structure. The elongated, only slightly wrinkled ovaries are situated on the dorsal proximal aspect of the Fallopian tube. The Fallopian tube is much coiled, and ends in a uterus which, meeting its fellow, descends without fusion to open just above the os in a small part of the uterus common to both tubes. The cervix descends into the vagina as a short cylindrical structure. It is beset externally with numerous deep, longitudinal folds which are continued into the canal leading from its free flattened vaginal surface to the uterus.

The vagina is much modified in the region next to the uterus; the ventral wall is continuous with, or occupies practically the same plane as, the uterus, but the dorsal wall is distended into a cavity which forms a prominent swelling. Associated with this expansion are certain folds of the vaginal walls, which clearly subserve an important function. The transverse folds of the mucous membrane of the upper part of the vagina are highly developed, and in addition two immense folds, almost encircling the vagina, convert the upper part of the tube into a recess which may be called the spermathecal recess (fig. 1). The upper fold springs from the ventral wall, thus serving to occlude the cervix and the os. The other is a similar transverse outgrowth of the dorsal wall, which carries the opening from the vagina into the spermathecal recess to the ventral side. The folds which define this chamber are clearly liable to be moved backwards and forwards, but it is important to note that in their normal disposition they form a passage from the vagina proper to the spermathecal recess of the vagina, which begins as a narrow opening on the ventral side and is continued between the two folds as a passage which opens into the recess dorsally.

Immediately below the folds the vagina is a spacious cavity, wrinkled internally by transverse and longitudinal shallow grooves, and it has a smooth and velvety surface. The transverse grooves are more prominent in the upper region of the vagina, and the longitudinal in the lower, a few of these latter extending into the vulva. The aperture between the vagina and vulva is a very small one. The sphincter vaginæ muscle is well

developed, encircling the tube in this region, and under usual conditions practically closes the passage.

The external opening extends from the anus, or immediately in front of the anus, forwards as a long slit leading into a flattened, roomy cavity, rapidly narrowing to the opening into the vagina. The lateral walls are more or less grooved, and the anterior angle is occupied by the clitoris. The latter forms a prominent ridge, and ends near the vaginal opening in a distinct glans-like projection. Anteriorly it divides into two arms or crura, which, however, have nothing to do with the corpora cavernosa. Each corpus arises from the pelvic bone in the same region as that of the male, and, descending on the internal side of the erector muscle, the two fuse as

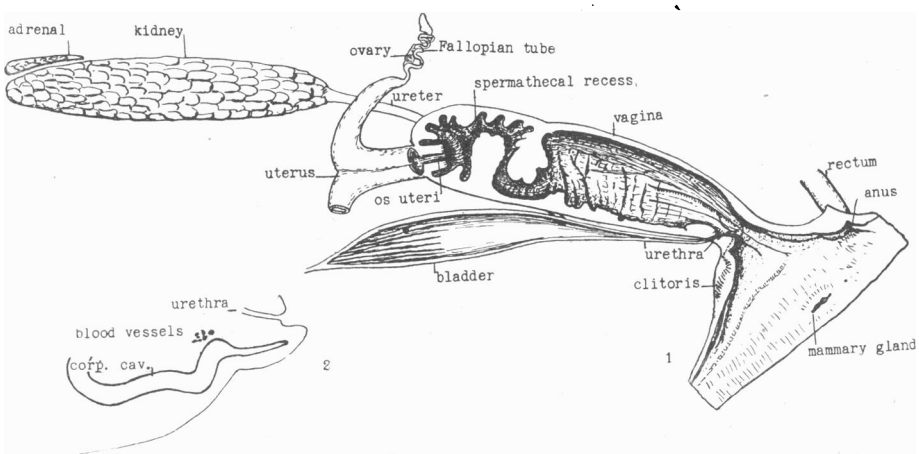

FIG. 1.—1, Longitudinal sectional view of reproductive organs of female porpoise (half natural size); 2, sectional drawing of clitoris to show disposition of corpus cavernosum (natural size).

the muscles do above the clitoris. The single corpus cavernosum, resulting from the fusion, enters the clitoris near the middle of the body of that organ and is bent backwards towards the glans. It presents another distinct curve in front of the glans, which it enters, after narrowing considerably, and occupies its ventral free region. The corpus in the clitoris is surrounded by a thin sheath and by erectile and fibrous tissues. The disposition of these structures will be found to be important when the structure of the penis is considered. The glans, it will be noted, is not a true glans, as it is traversed by the corpus cavernosum; but its position and appearance serve to indicate that it is the glans invaded and reinforced by the corpus cavernosum. The clitoris is surrounded by a preputial fold which, beginning above the glans in the urethral prominence, extends on each side to the anterior end of the clitoris, where the two folds approxi-

mate but do not fuse. The folds are especially prominent anteriorly. The disposition of the preputial fold is interesting, since it homologises the external part of the clitoris with the free part of the penis which occupies the preputial pouch of the male. Immediately beyond the clitoris is the opening of the urethra, defined as a medium, short, longitudinal opening between two transverse grooves. It occupies the anterior part of a median prominence just internal to the glans clitoris, and which marks also the beginning of the preputial fold.

As has already been remarked, on each side of the external opening there is a slit which lodges the cylindrical teat of the mammary glands, on the free end of which there is one opening.

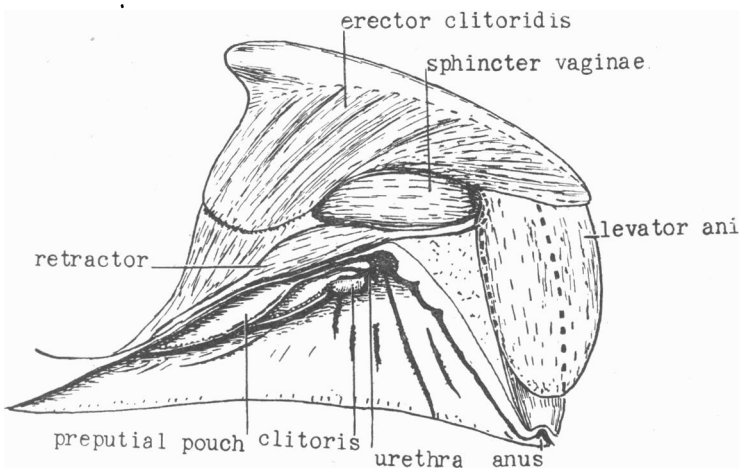

FIG. 2.—Pelvic and associated muscles of female porpoise. (Natural size.)

The muscles of this region are interesting (fig. 2). The pelvic bone is smaller in the female than in the male, but associated with it are the usual muscles and others connected with the external opening. The erector clitoridis springs practically from the whole outward border of the bone. The two muscles practically surround the corpora cavernosa at their origin, the mesial side next the vagina only being uncovered, and the muscles fuse as the corpora do, just above the clitoris, both muscles thus being concentrated in the sheath of the corpus and the neighbouring region of the clitoris. The levator ani arises from the internal border of the pelvic bone and is inserted into the lateral walls of the lower part of the rectum. The sphincter vaginæ is well developed. It encircles, and is connected to, the lower part of the vagina, and it also embraces the urethra. The lower half only is seen in fig. 2, the upper half being covered by the

erector muscle. Below it comes into close association with the clitoris. The retractor clitoridis arises from the rectum, and is associated at its origin likewise with the sphincter; and passing forwards in a tunnel between the erector, the levator ani, and the sphincter, as a long tendon, it expands into a muscle above the clitoris and is inserted at the base of the preputial pouch.

The female organs are thus, apart from the spermathecal folds of the upper part of the vagina, simple and typical. As will be seen, their condition, and especially the presence of the spermathecal recess, helps us to understand the remarkable modifications in the male. The narrow entrance to the vagina may be said to be an adaptation to occluding the cavity of the vagina from the sea, and the spermathecal recess to preventing the semen leaving the vagina on the withdrawal of the penis. The spermathe-

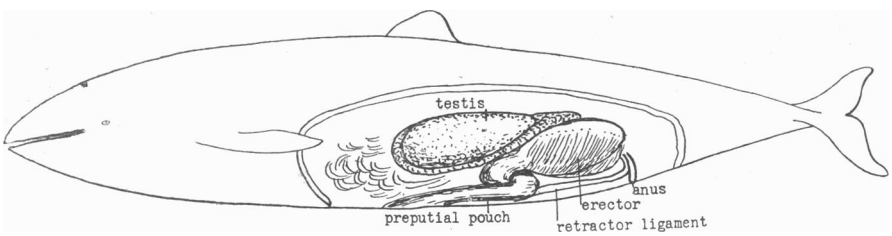

FIG. 3.—Diagram to show disposition and relative size of mature male organs of porpoise measuring 4 ft. 5 ins.

cal recess is a remarkable modification, since it has taken place in spite of the equal periodical difficulties connected with the birth of the young. The deep folds of the upper part of the vagina permit of considerable distension, and are evidently modifications connected with birth.

Phocæna communis. Male. (Figs. 3–7.)

In the male the testes undergo an enormous development in the summer, as will be apparent from fig. 3, which indicates the relative disposition of the organs in a mature male measuring 4 ft. 5 ins. They also increase greatly in weight; one testis in this male weighed 500 grams, in another 600 grams, and in still another 700 grams. On the other hand, in a male measuring 4 ft. the testis was only 2½ ins. long and the weight 1–2 grams. Associated with the huge testis the epididymis is highly developed. The duct becomes much folded posteriorly to the testis, and the folds are still retained as the vas deferens passes to the space between the bladder and the ureter. The two vasa deferentia approach one another behind the bladder and pass downwards side by side to open separately

on the eminence of the floor of the urethra, called the verumontanum. Between the openings, and slightly posterior to them, the verumontanum presents another, or a pair of openings which lead into a blind tube lying between and behind the terminal ends of the vasa deferentia. The opening is crescent-shaped, and may be single or paired, but in each case the cavity is a single one occupied by a slight ridge projecting from the floor. From its position this tube, with its single or double opening, answers to the uterus masculinus or sinus pocularis. In the porpoise the sinus has usually two apertures on the verumontanum. The vasa deferentia and the epididymes are highly developed and are capable of containing a large quantity of sperms. It is to be noted that seminal vesicles are absent.

In this region of the urethra the numerous ducts of the prostate glands open along parallel lines in the depression on each side of the verumontanum, below the level of the openings of the vasa deferentia. They thus lie near the angle where the first sharp bend of the urethra takes place. The verumontanum begins at the base of the bladder as a narrow ridge expanding to receive the ducts above mentioned opposite the prostate glands, and it narrows again in the region occupied by the ducts of the prostate gland. Cowper's glands are absent.

The urogenital duct beyond the prostatic region is surrounded by penial structures, the disposition of which is highly interesting. The duct itself is enclosed by a corpus spongiosum, which, beginning in a bulb, extends to the tip of the penis. The corpora cavernosa arise from the pelvic bones, and in passing between those bones unite almost immediately to form a single corpus cavernosum, which extends likewise to nearly the end of the penis. The corpus cavernosum consists of a vascular part surrounded by a tough fibrous sheath, and the disposition of each of these in the various regions will be plain from an inspection of fig. 6. The sheath expands postero-medially near its origin into a process, rectangular in section. The process invades the accelerator muscle; the two processes approach one another below the prostate gland and almost meet behind it. In this region the processes are connected by a thin fascia. It will be seen from fig. 4 that at the anterior end the corpus cavernosum is suddenly reduced to a rounded shape together with its sheath, and is thrown into a distinct fold, being bent downwards and to the right side before running forwards to the end of the penis; the meaning of this will be discussed presently. The anterior end of the penis is enclosed in a preputial pouch, the skin of which, both that of the pouch and that covering the penis, is remarkably thin. That of the pouch is thrown into longitudinal folds allowing of lateral distension. The opening is like that of the vulva, but it is situated practically in the middle of the body, and the pouch is also con-

stricted to a narrow opening at about the same depth as that of the vulva. The free part of the penis occupying the pouch is, because of the bend in the corpus cavernosum mentioned above, sharply resolved into two regions—a proximal, continuous with and having the same structure as the main body of the penis, and a distal, which is long, narrow, and almost round in section. The urethra opens by a longitudinal slit on the ventral aspect of this latter part of the penis near the tip (figs. 4 and 6).

The whole structure, from the prostatic part of the urethra to the free part of the penis in the resting condition, is thrown into (1) the fold mentioned above at the origin; (2) the double fold shown in fig. 3, involving

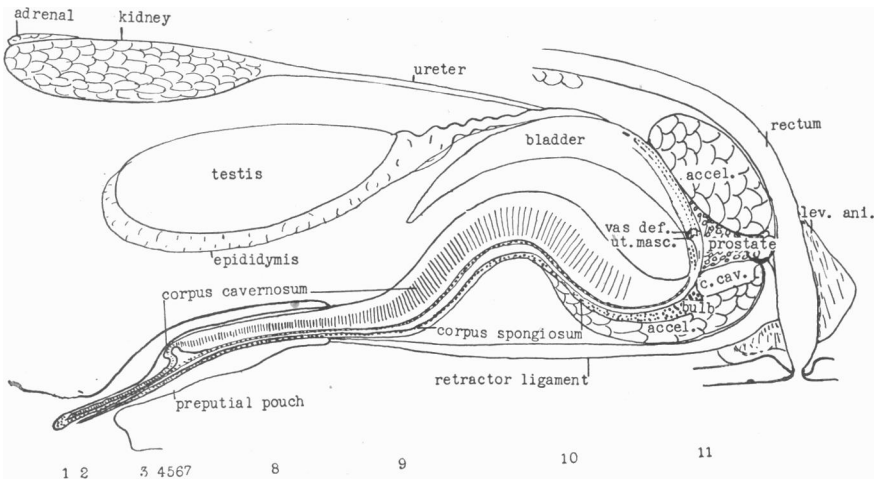

FIG. 4.—Longitudinal sectional view of reproductive organs of male porpoise. (Half natural size.) *c.cav.*, on the right, points to the tendon-like process of the sheath of the corpus cavernosum which invades the accelerator muscle.

nearly the whole of the proximal part of the penis behind the preputial pouch. The corpus cavernosum of the clitoris presents similar folds; compare figs. 1 and 4.

The penis is highly developed, and the muscles associated with it are strong and massive. The erector penis muscle arises from the whole length of the large pelvic bone, and is inserted into the sheath of the corpus cavernosum as far forwards as near to the beginning of the second fold mentioned above. The two muscles enclose the corpora cavernosa at their origin, and each corpus is also attached to the pelvic bones by a strong ligament extending to near the anterior extremity of the bone. The accelerator urinæ muscle is especially strongly developed around the bulb and the prostate; the fibres are concentrated in the process of the sheath

of the corpus cavernosum mentioned above. The processes and the fascia connecting them serve to separate the prostate gland above from the bulb

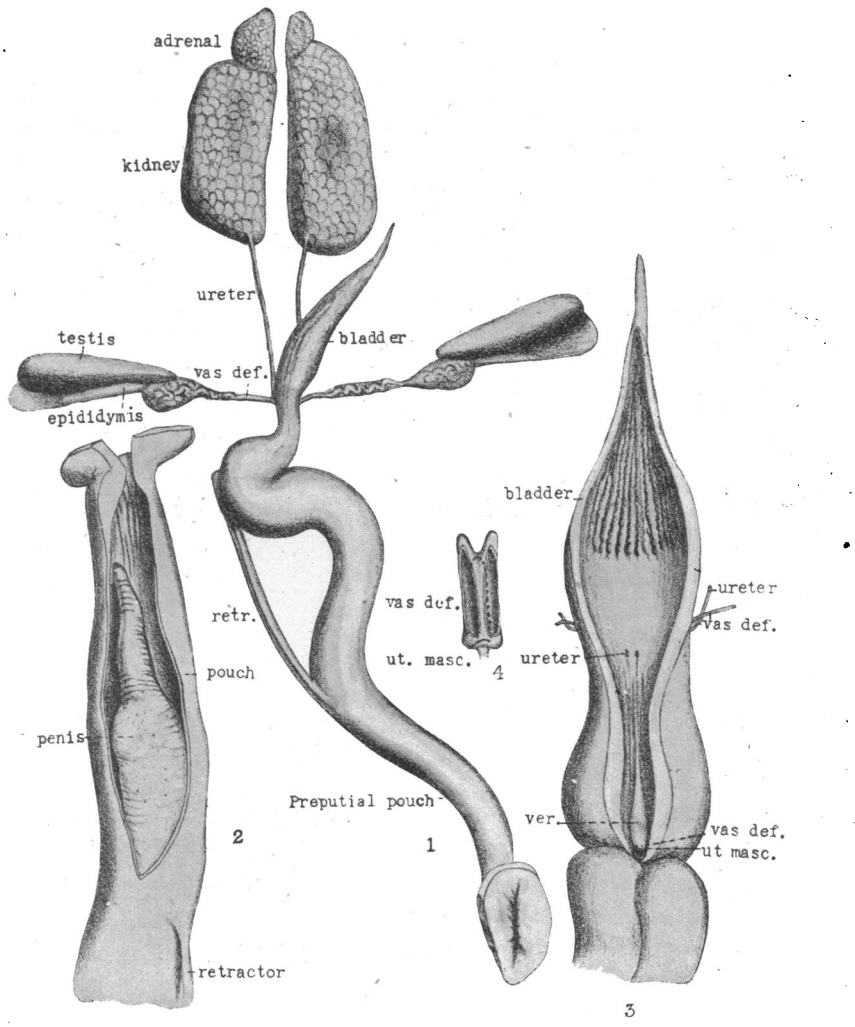

FIG. 5.—General dissection of the reproductive organs of male porpoise. 1, The general relationship of the organs in the adult, but immature, state; 2, the preputial pouch and penis; 3, the bladder and verumontanum region of the urethra; 4, dissection of verumontanum.

below. A strong, double, elastic retractor ligament extends from the rectum, and the transverse process of the sheath of the corpus cavernosum, forwards

below the accelerator muscle to be inserted into the base of the preputial pouch.

This is the general structure with reference to the penis in the retracted

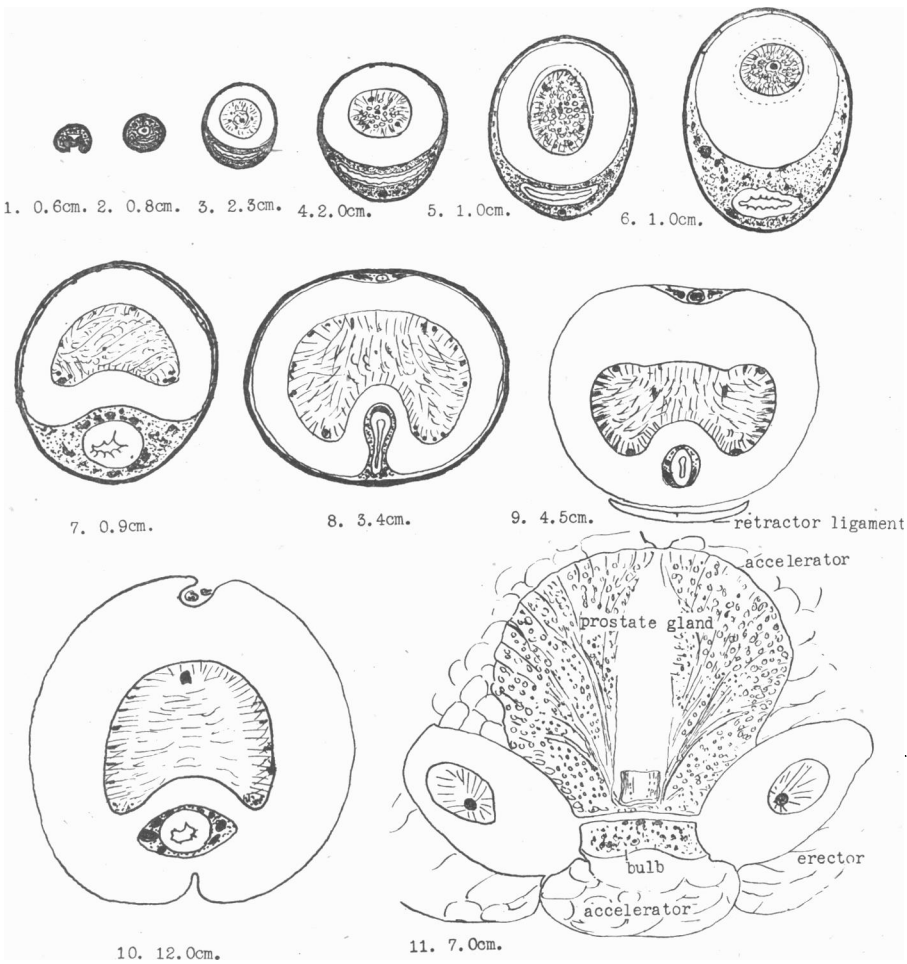

FIG. 6.—Transverse sections of penis of porpoise. The numbers below fig. 4 indicate the levels of the successive sections. The sheath of the corpus cavernosum is unshaded.

condition, when it is withdrawn within the preputial pouch. In a state of erection the penis may be protruded to a length which brings the tip as far forwards as opposite the pectoral fin, even the pectoral girdle. As will be seen from fig. 3, its direction during erection is forwards and only at a

small angle outwards; and as will be seen further from fig. 7, the erection brings about a remarkable change in the disposition of the proximal and distal parts of the preputial portion of the penis. They become still more sharply defined, the proximal part being stiff and hard, like the main part of the penis posteriorly, while the distal, terminal part remains pliable, especially where the two parts are joined together. In attaining this condition a corkscrew-like movement is given to this terminal part of the penis.

It has already been noted that the vagina is relatively short. In the female figured it measured, from the opening of the vagina to the second fold, 7·5 cm., and in another female about 9 cm. The latter is just about the length of the distal end of the erected penis. It is evident, therefore, that this is the only part of the penis which enters the vagina.

The pairing of these creatures must be a difficult proceeding, and the

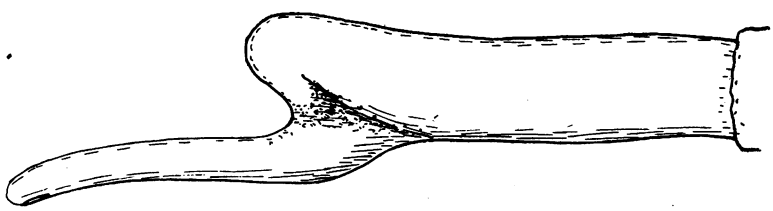

FIG. 7.—The preputial part of the penis when erected.

above structural modifications are meant to make it effective. They apparently range themselves in ventral apposition in such a manner as to bring the respective openings together. The head of the female will therefore be in advance of that of the male. The latter may be able to assist matters with his pectoral fins, and the female by flexing the caudal fin so as to form a groove for the body of the male. When erection takes place, the first part of the penis to emerge is the narrow, free end, which will therefore enter the vulva, and the rotation which is being communicated to it will enable it to gain access to the vagina; the blunt end of the proximal part of the penis will abut against the front wall of the vulva, adapting itself to the clitoris. The direction of the free end of the penis is such that it will pass the first fold of the vagina and bend upwards the second. The outlet of the penis is on the ventral side near the tip, and consequently the discharge is projected into the spermathecal recess. The bulb is compressed as well as the prostate by the accelerator muscle, and it is evident, therefore, that the terminal part of the penis is subject to a slight expansion during ejaculation. It is evident, also, that as a result of the erection the female is carried forwards and some little distance away

from the male, and at this period the bodies of the two may be subject to some degree of rotation. This is met by the joint in the penis at the base of the copulatory part, allowing for a wide range of movement. From this it may be gathered that discharge follows immediately, for any movement will likely result in separation. When the discharge has taken place and erection ceased, the retractor ligament withdraws the penis once more into the preputial pouch. In all the males examined a discharge, rich in spermatozoa, could be obtained by simply pressing the penis, and sometimes even without. Living sperms were obtained in this way a day after death. The immature males similarly yielded a discharge, but the ejaculate did not contain sperms. In both cases the ejaculate contained other cells, as prismatic cells from the vasa deferentia and lymphocytes. The immature males are apparently capable of conjugation, for they have been captured in the same part of the net as the females.

The fact that the urogenital duct is filled with the spermatic fluid in the mature male, and with a discharge in the immature male, points to a recent copulation. But this simple and obvious conclusion does not meet the conditions. A male was brought in injured but alive, and remained in the floor pool for a couple of days before it died. In this case also the urogenital duct was fully occupied by sperms. It cannot be said, then, that copulation had taken place sufficiently recently to account for this, for urination must have occurred in the meantime, and that this was so was indicated by the small quantity of urine in the bladder.

We may take it that in the act of micturition the bladder is emptied, and it is the function of the accelerator urinæ muscle to clear the urine from the urogenital duct of the penis. The difference between this act and that of discharge during copulation is that the pulsations of the accelerator eject the contents of the urogenital duct, which is filled immediately by the simultaneous peristaltic contractions of the vasa deferentia. In the case of urination there is no supply to draw upon; in the other there is a supply. We can thus account for the penial part of the duct being filled with sperms after copulation, but it is evident that the duct will be cleared of sperms at the next urination.

We can only account, then, for the presence of sperms in the urogenital duct in the above cases by a choice between two explanations. The first is that the pressure of sperms into the duct is steadily maintained by the contraction of the vasa deferentia apart from copulation; the second is that erection and discharge has taken place as a result of drowning.

The first explanation is not satisfactory, for in the resting condition the penis is not at all likely to be thus so completely occupied by the spermatic fluid injected. It is not likely, either, that the duct will be in this

way filled and emptied at every act of urination. It is also necessary to take note of the fact that in no case had the females associated with the males been in copulation, for the vagina and the spermathecal recess were free of sperms. Yet in the case of two of the females a discharge was freely issuing from the narrow opening of the vagina, bathing the clitoris. In all the females the spermathecal recess was occupied by a thick, viscid uterine discharge, although the latter may have had no connexion with the immediate act of copulation. The absence of sperms in these added evidence of significant value pointing to the second explanation, and that both sexes are affected.

There cannot be any doubt, however, that pairing takes place in the summer, although, so far, we have not obtained a female which shows that it had actually taken place. This may be due to the female immediately after the event quitting the inshore waters.

The penis, then, is greatly modified in the porpoise, the copulatory part being differentiated from the rest, from which it is separated by a joint allowing of a wide range of movement. In the state of erection it is still pliable, and it may therefore be said to be adapted to obtaining easy access to the vagina, to changes of position of the bodies of both the male and the female, and also to yielding to pressure if access to the vagina has not been obtained.

It is probable, therefore, that the preputial pouch has a vaginal importance, and, in the case of successful copulation, the copulatory part of the penis is, because of the continuity to begin with between the preputial pouch and the vagina, prevented from coming into contact with the water, as the rest of the free part of the penis must do during erection.

The prevalence of porpoises near the shore during the summer months when drift-net fishing is taking place, and their absence at other seasons, have led to the conclusion that their advent is due to their feeding on salmon. In the case of all those that were examined it is interesting to point out that food was only obtained in the stomach of two, a female and an immature male, and in each case it was gadoid, probably young whiting, much digested.

There is no doubt that at this season, July and August, the porpoises are pairing, and their appearance near the shore at this period may be described, therefore, as a migration for that purpose. It is also fairly clear that in the region where the salmon-fishing takes place males are more commonly captured than females. It seems warrantable to conclude that the males frequent the inshore waters and the females enter the region when they come into season, departing after pairing has taken place. Mr W. J. M. Menzies of the Scottish Fishery Board has informed me that

four porpoises caught in the salmon nets on the shores of the Moray Firth and which he examined, were all males. Porpoises are common both in the Atlantic and Pacific, and no doubt in both regions an inshore migration takes place for the birth of the young and for pairing.

Lagenorhynchus albirostris. An abnormal male.

This white-beaked dolphin, which measured 5 ft. 2 ins., was caught in the salmon nets on the north side of the mouth of the Tyne, and was landed at Cullercoats on August 24, 1911. The urogenital organs were removed and preserved by Mr Storrow. They were labelled "male," and they prove on examination to be essentially male, but they are so abnormal in position and structure as to warrant a somewhat detailed description.

In the first place, the preputial pouch, instead of being central in position, is far back, close to the anus, thus in the position of the vulva. The free part of the penis is very short, only $3\frac{1}{2}$ ins. long, but has the gradually tapering shape and the structure of the species. The pouch is proportionally short; its wall is furrowed, but is more like the vagina in structure. It is constricted externally into a narrow neck, and the anterior angle of the external opening is occupied by two ridges which almost suggest a clitoris in appearance. The position of the mammary glands could not be ascertained, as the posterior part of the pouch had been removed, but it is more than probable that they were paired and situated on either side of the preputial pouch. In association with the short pouch and the near proximity of the rectum, the retractor ligament only measured about $1\frac{3}{4}$ in. It was inserted at the base of the preputial pouch. The proximal part of the penis between the preputial pouch and the prostatic region is also strikingly short, although it presents the usual folds of the normal condition. It is flexed ventrally from the region of the prostatic ducts, and is then directed dorsally to the left side and again to the right before it enters the pouch. This is the normal disposition, but the whole structure is dwarfed. The urogenital duct is that of the male, and ends in a horizontal slit terminally; and this is also the normal condition.

A small prostate is present, and the ducts open as usual below the openings of the verumontanum. The expanded portion of the verumontanum presents the paired openings of the vasa deferentia, and below them the Λ-shaped opening of the uterus masculinus.

But what makes the specimen particularly interesting is the presence of small testes, each with an epididymis and a coiled Wolffian duct, together with a Müllerian duct. The Müllerian ducts meet and fuse, but they are altogether unconnected with the uterus masculinus, which latter has the normal disposition (fig. 9). It is difficult to imagine the circumstance which

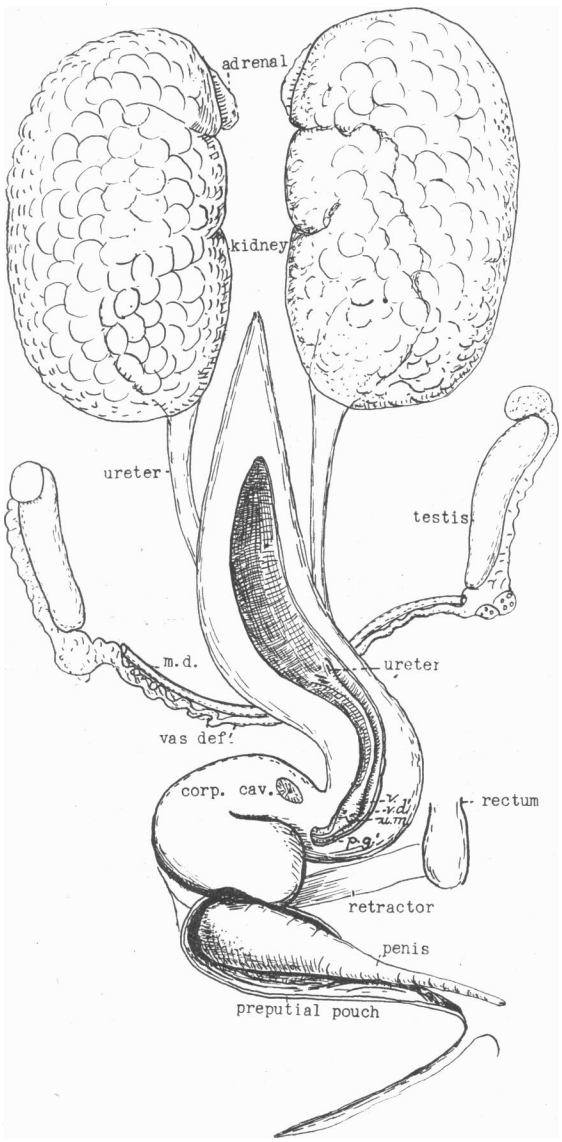

FIG. 8.—The general disposition of the organs of an abnormal male *Lagenorhynchus albirostris*, in ventral view. (Half natural size.)

v., verumontanum; *v.d.*, opening of vas deferens; *u.m.*, uterus masculinus; *p.g.*, opening of prostate gland; *m.d.*, Müllerian duct.

has led to a disappearance of the oviduct in the interval separating the uterus masculinus from the Müllerian duct, and this feature raises, therefore, some degree of doubt as to the identity of the sinus pocularis with the Müllerian duct.

The bladder and the kidneys and ureters are in striking contrast (as will be seen from fig. 8) with the rest of the structures as regards size.

Sections were made of the testis at different levels. They were found

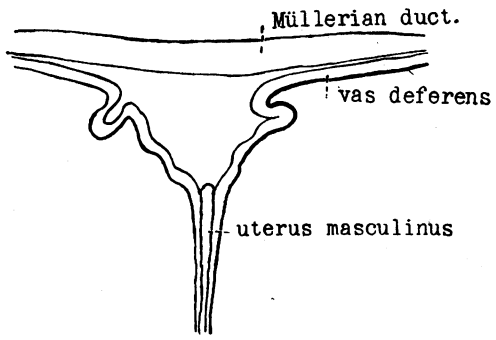

FIG. 9.—The relationship of the Müllerian and Wolffian ducts in the abnormal Lagenorhynchus.

to present numerous tubules of the usual character, but no ova were to be seen.

Lagenorhynchus albirostris. The normal male organs.

Fortunately, I have drawings of the normal male organs of a fœtus of *Lagenorhynchus albirostris*, which are produced here in fig. 10, and which will be described briefly with especial reference to the abnormal specimen an account of the organs of which has just been given. These were made long ago, as has been stated, in the Zoological Department of the University College, Dundee.

The disposition of the organs in the body is already well known,[1] and it is almost exactly the same as in the porpoise. The penis, it will be observed, is situated forwards from the anus, and in front of the latter are the small paired openings of the mammary glands. Internally, the organs except in their general relationship, are very like those which have just been described in the abnormal specimen. The testes are elongated, the epididymes are large, each projecting beyond the testis in a caput epididymis (the latter is somewhat exaggerated in the abnormal specimen). The

[1] Hunter, *Structure and Œconomy of Whales.* Cleland, *Journ. Anat. and Phys.*, vol. xviii. p. 334.

vasa deferentia pass as usual from the epididymes to open separately in the verumontanum. The uterus masculinus has a Λ-shaped aperture immediately below the openings of the vasa deferentia, and the shape of the

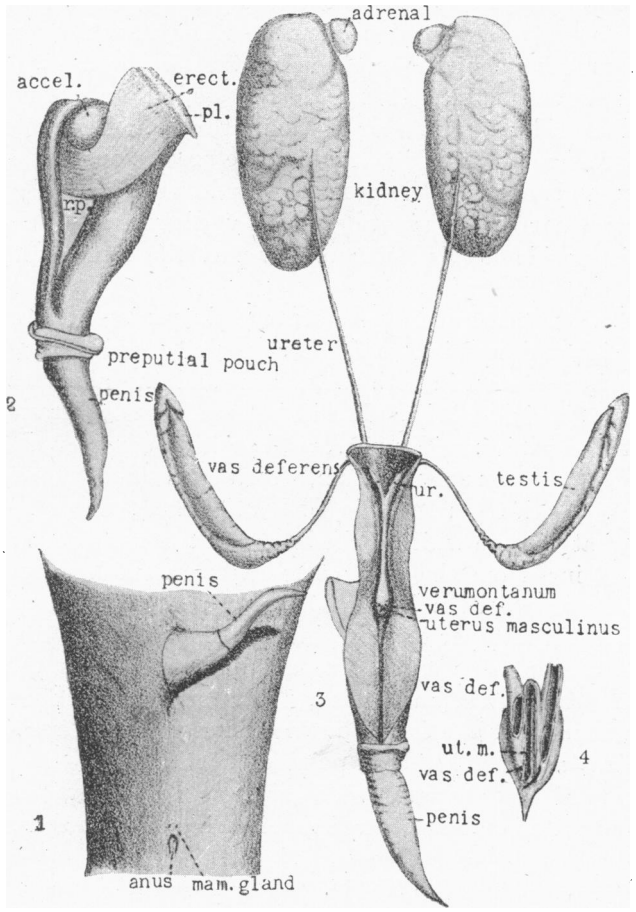

FIG. 10.—The normal male organs of a fœtal *Lagenorhynchus albirostris*. 1, The disposition of the penis, mammary glands, and anus; 2, the penial muscles; 3, the organs from the ventral aspect; 4, dissection of verumontanum.

opening is also that of the lumen of the structure, for a crest projects into the cavity from the floor throughout its length. The crest becomes gradually reduced towards the blind end of the single sinus.

Cleland (*loc. cit.*) stated that in the white-beaked dolphin "there are four openings into the floor of the first part of the urethra. The two

upper are the openings of the vasa deferentia; and immediately beyond these are two larger openings distinct one from the other, and both leading up into a single sinus pocularis." Such a variation, it has been noted above, is also found in the porpoise, the cavity in both cases being a single one, but the opening single or double. The ridge, it will be noted, on the floor is more prominent in Lagenorhynchus than in Phocæna.

The verumontanum, in both the normal and the abnormal specimens, is a longitudinal ridge on the floor of the urethra. It begins near the base of the bladder as a double ridge on which the ureters open, fuses to a single ridge, and expands opposite the prostate gland to receive the openings just mentioned, and narrows again to gradually disappear in the urogenital duct. On either side of this latter narrow part the numerous openings of the prostate glands occur in rows.

The general structure and musculature of the penis are the same as those of the porpoise, and require no further special description. The urethra opens, as has been stated, in both the normal and the abnormal specimens, terminally by a horizontal slit. It will be seen from the drawings that the free part of the penis rapidly narrows, but it is occupied throughout its length by a single corpus cavernosum, which ends some little distance from its extremity. With regard to this, Cleland (*loc. cit.*) made the significant observation that "in the white-beaked dolphin the combined corpora cavernosa, about 2 ins. from the free extremity, are suddenly compressed as if by removal of more than half their substance on the ventral side, and then expand again to taper to the point." This is so like the formation of the penis of the porpoise as to give the impression that the function is essentially the same. Cleland added, "It is such an arrangement as will allow the slender end to be folded down on meeting with resistance in the erect condition"; but, as has been pointed out, the jointed end of the penis of the porpoise is the only part which gains access to the vagina, and it may be that this is the case also with reference to Lagenorhynchus.

Notes on the Male Organs of other Species of Delphinidæ.

A few notes may be added here with reference to one or two other species which were dissected in Dundee. In a fœtal beluga, *Delphinapterus* (*Beluga*) *leucas*, about 12 ins. long, the penis was found to be rounded and tapering as in Lagenorhynchus. The verumontanum presented three openings, the vasa deferentia and the uterus masculinus. The latter is interesting, as distally it is stretched out into a flattened cavity (fig. 11). A fœtal narwhal (*Monodon monoceros*) was dissected, and the general disposition of the organs is shown in fig. 12, and from these it will be noted that the penis has a similar shape to those already described.

From the drawings in my possession the conditions in the dolphin (*Delphinus delphis*) appear to be fundamentally different. The penis is

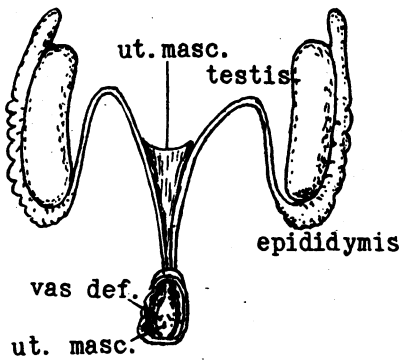

FIG. 11.—The vasa deferentia and uterus masculinus of a fœtal beluga (*Delphinapterus leucas*).

evidently short and only slightly tapering (fig. 13). There is some evidence in the drawing of a change in the corpus cavernosum near the extremity similar to that described in the other species, but it would be necessary to

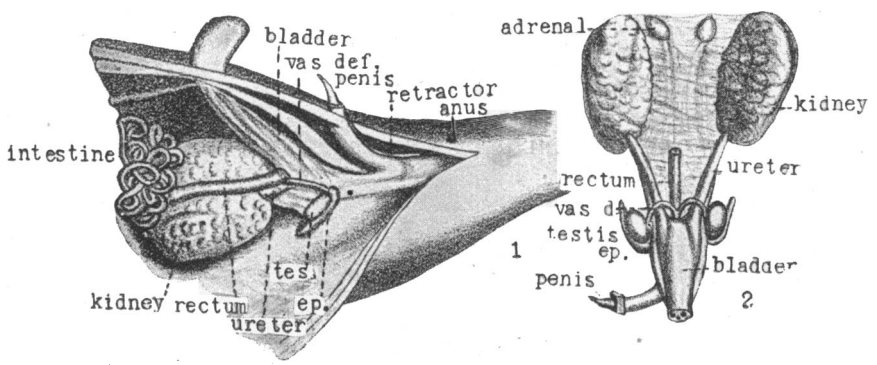

FIG. 12.—1, A general dissection of a fœtal narwhal (*Monodon monoceros*) to show disposition of male organs; 2, the reproductive organs in ventral view. It will be noted that the bladder has been reflected backwards.

examine the species afresh to establish the point. The pouch is evidently proportionally short. There appear to be only two openings on the verumontanum, those of the two vasa deferentia The two openings are approximated into a crescent-shaped aperture leading into the separate vasa

deferentia, a narrow septum separating the terminal portions of the ducts, in which no trace of a uterus masculinus was found (fig. 14).

The penis of *Kogia breviceps* was described by Benham,[1] and it is evident that in it the corpus cavernosum suffers a reduction in size anteriorly,

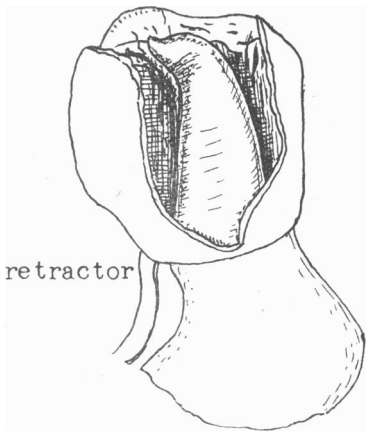

FIG. 13.—Penis and preputial pouch of dolphin (*Delphinus delphis*).

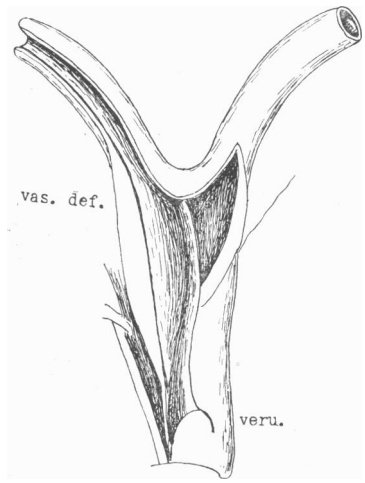

FIG. 14.—The verumontanum of the dolphin.

becoming circular in section. This modification of the preputial part of the penis appears therefore to be general in whales.

GENERAL CONSIDERATION.

A. *Morphological.*

The reproductive organs of the Cetacea, so far as may be gathered from a consideration of the foregoing species, are of a generalised mammalian type, with special modifications connected with the pelagic life of the group. It is in connexion with the muscles relating to these organs that the pelvic bone has been preserved, and it is worth noting that it is smaller in the female than in the male.

It would be interesting to know to what extent the spermathecal recess is developed in the females of other species.

The separation of the penis of the porpoise into a special copulatory jointed to a non-copulatory part is a remarkable modification, and has been led up to, doubtless, by the penis becoming narrow anteriorly, as is the case

[1] 1901, *Proc. Zool. Soc.* (ii.), p. 123.

in so many toothed whales. There is no true glans, but it appears to be the fact, from a consideration of the structure of the clitoris, that the glans has been secondarily invaded by the corpus cavernosum.

In other respects the organs do not arouse a great deal of interest. The absence of Cowper's glands is certainly worthy of remark, for they are so constantly present in mammalia. They are absent also in Arctoid Carnivora. The absence of seminal vesicles is not of such moment, for it is a feature which is not uncommon in primitive types, as monotremes, marsupials, the sloth, and in seals and other Carnivora. It is not necessary, in the case of a group so modified as the Cetacea, to make a point as to the abdominal position of the testes.

The uterus masculinus is generally present as a single tube lying between the terminal ends of the vasa deferentia. The opening of this single sinus pocularis is usually one in the fœtal stage, but may be, and usually is, double in the adult. The condition of the sinus in association with independent Müllerian ducts in an abnormal male Lagenorhynchus is noteworthy. A sinus pocularis does not appear to be represented in primitive mammals, and its presence here in a reduced condition is thus of interest. But the question of its homology will have to be reconsidered.

The preputial pouch must be considered also as a primitive feature, and in relation to the condition of life of the Cetacea its presence is plain. From the fact that the penis is everted in some of the (and especially in the younger) fœtuses, it may be held to be secondary in origin. Associated with the pouch is a retractor ligament which in some cases appears to be more or less muscular in composition. In the porpoise it is a strong double elastic ligament extending from the rectum to the preputial pouch.

Both the pouch and the retractor muscle are represented in the female. The muscle is especially interesting, for it originates in a tendon, expands above the clitoris into a muscle, and narrows again to be inserted into the prepuce. The presence of a retractor may also be said to be a primitive feature.

The erector penis and the accelerator muscles are strongly developed in the male. The erector clitoridis, though small in comparison with the corresponding muscle of the male, is well developed, and the sphincter vaginæ (accelerator) is also a prominent muscle encircling the opening of the vagina. It comes into association with the erector and also with the levator ani. Sebaceous glands occur in the preputial pouch in both sexes, and their secretion in the case of the male is always evident.

B. *Physiological.*

It is more than probable that the act of micturition necessitates the protrusion of the anterior end of the penis from the preputial pouch. If this be the case, it means that the penis is erected to some degree. The bladder is strong and muscular, and no doubt can be completely emptied by the contraction of its muscular wall, and it is evident that this is followed by the long urethral duct being emptied by the action of the accelerator muscle.

In the case of the female there appears to be little doubt that urination is accompanied by an erection of the clitoris. As will be seen from figs. 1 and 2, the urethral duct, in the resting condition, points towards the posterior wall of the entrance into the vagina. The corpus cavernosum of the clitoris, as will be seen from fig. 1, is so constructed and disposed as to make it apparent that during erection the main part of it will be straightened, and this will have the effect of bending forwards and downwards the glans, thus bringing the opening of the urethra to a ventral position and directed outwards. At the same time the distension of the whole structure will result in the clitoris and the urethral opening being carried downwards. In this case it is not necessary to consider that any muscular effort is required except that of the bladder, but the terminal end of the urethra is enclosed in the sphincter vaginæ.

It has been suggested that the males frequent the inshore waters during the pairing season, and that the females enter the region as they come into season. Whether this be the case or not, it is evident that the migration is due to a periodical development of the gonads. During the summer porpoises are very common inshore, and they may frequently be seen swimming in pairs. Mennell and Perkins[1] refer to their "grotesque gambols on the surface of the water, especially during the herring season."

As has been stated, we have not yet come across a female which has been in copulation. But the attempt has been made to indicate how the act is accomplished in pelagic conditions, and what is said about the porpoise will apply in the main to the other Cetacea.[2] It is not necessary to repeat that description here, but a few words may be added as to the physiological changes which are more or less specialised in the porpoise and other Cetacea.

The vulva is prepared for the reception of the penis by the descent of the erected clitoris, the glans being rotated forwards. This puts the

[1] *Trans. Tyneside Field Club*, vol. vi., 1863–64.

[2] A summary of the scanty knowledge we possess is given on p. 219 of Millar's *Mammalia of Great Britain and Ireland*, vol. iii.

retractor clitoridis on the stretch, and this muscle may be said to join synchronously in the pulsations of the erector muscle.

The erection of the penis similarly brings about an elongation of the retractor ligament. It is apparently a gradual process, for complete erection appears to be postponed until copulation. When the penis is protruded the free end of the copulatory part enters the vulva and is directed into the vaginal opening distending the sphincter muscle. The whole of the copulatory part of the penis gains access to the vagina; the main body of the penis, culminating as it does in a prominent knob, only reaches the vulva where it abuts against the clitoris.

It has been noted above that in the case of two of the females a discharge was seen to be issuing from the narrow opening of the vagina. The exact nature of the glands which give rise to this has not yet been determined. It is probable that in association therewith the sphincter muscle of the vagina is thrown into a pulsation. If this takes place, as is more than likely, on the withdrawal of the penis, water may thus be introduced into the vagina, but the folds which guard the spermathecal recess will obviate any danger of the ejaculate being lost.

The levator ani in both cases may be said to help by keeping the parts taut.

The presumption that erection and discharge may take place as a result of drowning raises interesting physiological questions as to the factors. It cannot be said to be the result of direct stimulation of either of the centres. It seems to be due to want of oxygen or perhaps more probably to the effects of the general fatigue produced by struggling. An examination of other cases of the kind, in relation to this, may point to the cause.

Notes on Literature.

The peculiar disposition of the corpus cavernosum in the porpoise does not appear to have been described by any of the many authors who have examined the male organs of this species. The fact that there is no true glans has generally been noted. Beauregard and Boulart,[1] and also Daudt[2] have found, as I have found, that the preputial pouch is a secondary formation; but it is not necessary because of that to call the pouch pseudo-preputial as Daudt proposes.

The musculature in the case of the Greenland whale has been described by Struthers,[3] and in the case of the Grampus by Turner.[4]

[1] *Journ. d. l'Anatomie et de la Physiologie*, 18 ann., 1882.
[2] *Jenaische Zeitsch.*, Bd. xxxii., 1898.
[3] *Journ. Anat. and Phys.*, vol. xv., 1881.
[4] *Ibid.*, vol. xxvi., 1892.

Daudt failed to see the preputial pouch in the female porpoise, but indicated its presence in other toothed whales, Beluga and Hyperoodon, and he observed it, as others have done, in Balænoptera. He appears, however, in some cases, to have confused the body of the clitoris with the preputium.

Daudt has described the two folds which form the spermathecal recess in the porpoise, but without indicating their significance, and his figure does not clearly indicate their disposition. Watson and Young[1] found eight such folds in Beluga, and Daudt said there were ten, the cervix being the first of the series. With reference to this genus I can now say that the penis is pointed, the free portion being spindle-shaped. Sections of the penis of a fœtal Beluga measuring 17·5 cm. show that, as in Lagenorynchus, the corpus cavernosum suddenly becomes reduced in size and rounded in section. This reduced part of the corpus cavernosum springs from the dorsal region of the body, and extends near to the extremity. The penis, as in the porpoise and as in Lagenorynchus, is therefore resolved into a proximal fixed part and a distal flexible part. This is associated in the case of the Beluga female with a succession of structures which resemble the cervix in structure, and probably in function. With their development the cervix has disappeared as such, and is probably represented by the small fold at the uterine end of the vagina which marks the first of the series. Daudt found that in Hyperoodon there were four to five such folds, and in Balænoptera there were about ten. There seems to be some degree of variation in Balænoptera with regard to the number and the disposition of the folds, for in the species described by Beauregard and Boulart the number is less than that described by Daudt, and the lower folds appear to undergo some degree of anastomosis.

The Female Organs of the Greenland Whale (Balæna mysticetus).

Since the foregoing was written I have examined the female organs of a fœtus, measuring 41 cm., of the Greenland whale. This specimen was presented to the Natural History Society of Newcastle in 1835 by T. R. Batsom, and is preserved in the Hancock Museum.

So far as I know, the organs have not been described with reference to this species, and they present some features of interest. The vulva is quite small, measuring only 5 mm. in diameter, and is rounded in shape. The anal opening is situated about 5 mm. posteriorly, and the minute openings of the mammary glands are placed on either side but somewhat

[1] *Trans. Roy. Soc. Edinburgh*, vol. xxix., 1879.

anterior to the vulva. The vulva was found to be occupied by a clitoris, which is elongated and coiled. It is thus so far like the penis in shape as to indicate that the penis is long and tapering, as it is in so many of the Cetacea.[1] The clitoris springs from the base of a shallow preputial pouch and it is evident, therefore, that it represents, as in the porpoise, the free preputial part of the penis. The preputial pouch completely surrounds the clitoris, and is continued by folds with the eminence on which the urethra opens. Beyond the vulva there is a long, roomy vagina. Near the vulva the wall of the vagina is thrown into longitudinal folds, and these can be traced, especially on the dorsal side, along rather more than

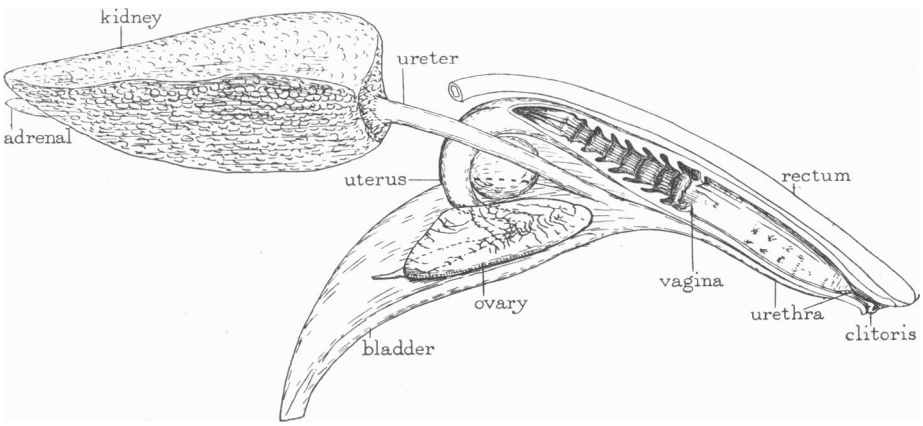

FIG. 15.—The urino-genital organs of a female fœtus of the Greenland whale, measuring 41 cm. (×2.)

half its length. Otherwise the lower part of the vagina has a smooth wall in which pit-like depressions occur at intervals. The upper part of the vagina is occupied by a series of transverse folds similar to those which have been described in the species mentioned above. There are seven complete rings, a trace of an eighth at the upper end of the series, and at the lower end two incomplete folds on the right and left sides. They are traversed by longitudinal folds, which are especially well marked at the upper end and are almost absent from the incomplete folds at the lower end.

As in the other cases in which such folds have been found, the condition is accompanied by the absence of the cervix. If it be the fact, as the structure certainly indicates, that the cervix has disappeared, we have in these cases the development of a series of folds which have replaced the

[1] Struthers, *Journ. Anat. and Phys.*, vol. xv., 1881.

cervix in function. The vagina has thus been peculiarly modified in a large number of the Cetacea, in a manner which appears to be without parallel in other Mammalia, and is even strikingly different from the conditions in the porpoise.

In the light of the foregoing description it may be suggested that they have a double function. The penis will have to pass through a number of the folds at least, and it is probable, therefore, that they have been developed for the purpose of promoting the discharge. It will be noted that the folds are directed downwards and they are highly muscular. It is possible, therefore, that the folds are expanded and contracted, and depressed and raised, and such movements would have the effect of sending the spermatic fluid upwards, to and towards the uterus. Even in the case of the porpoise it is quite possible that the two folds are thrown into similar movements.

The uterus a short distance above the folds divides into the two horns, which are bent ventrally and backwards. The Fallopian tube presents a few folds, and, like the large funnel into which it opens, is directed forwards. The ovary is large, and it is beset with numerous furrows as it is in Balænoptera. The broad ligament is occupied on each side by a round fat body, such as was found by Beauregard and Boulart in Balænoptera.