XII. *On the Mode of breeding of the Oviviviparous Shark, and on the Aeration of the fœtal Blood in different Classes of Animals.* *By* Everard Home, *Esq. F. R. S.*

Read June 7, 1810.

THAT some of the shark tribe do not lay their eggs, but hatch them within the body, and that others lay them in the same manner as the skate, has long been known; but nothing seems to have been accurately made out upon either of these subjects, I am therefore induced to lay before the Society the following observations.

In my examination of the squalus maximus, an account of which is published, I found that it closely resembled in its internal structure, the squalus acanthius of LINNÆUS, a fish common on the Sussex coast, which made me pay particular attention to the anatomy of all the parts of this species of dog-fish.

In December, which is the breeding season of this particular species of dog-fish, I procured specimens of the male, and of the female, in all the different stages of impregnation; from the dissection of these is drawn up the following account of the organs of generation.

The male organs were found in two very different states; in one, the testicles were small, and the penis scarcely discernible; in the other, the testicles were larger, the epididymus and vas deferens turgid with semen, and the penis put on the appearance of a projecting infundibular canal, capable of con-

veying the semen into the oviduct of the female, resembling in its form, the penis of the squalus maximus, only upon an infinitely smaller scale.

The pendulous bodies close to the oval fins of the male, which have been mistaken for penises, by many physiologists, and by others more rightly considered as claspers, to lay hold of the female, bear a close resemblance in their form to those of the squalus maximus, which have been described in my account of that fish, under the name holders, and from every part of their mechanism, there can be no doubt that they perform that office. In the breeding season, they become more fleshy than at other times, the muscles at that time being enlarged.

The insertion of the penis into the female, is not unlike that of the common fowl, but the penis is fitted to inject the semen further into the oviduct than can be done by the grooved penis of the cock.

When the holders are spread out, so as to embrace the female, even after the fishes are dead, the penis is brought forward by that means, so as readily to enter the external orifice of the oviducts, to which it is guided by the prominence of the clitoris. The holders are represented in this expanded state in the annexed drawing.

The mode in which the semen enters the penis is so unlike what is met with in other animals, that it deserves to be particularly explained.

The vasa deferentia are convoluted in their course, but become straight and much enlarged at the lower part, and instead of going on to the penis, terminate by two wide orifices on the posterior surface of what may be called the

urinary bladder, which is of an oval shape, and partially divided into two by a septum, on each side of which the ureters enter it. From this cavity, the penis is continued like the neck of a Florence flask, and the semen, before it can arrive at the penis, fills the bladder, and is propelled by the action of the muscular coats of that cavity, by which means the semen acquires velocity, and the penis is rendered turgid during the whole time that such force is applied to the liquid passing through it.

This bladder at other times is a reservoir for the urine, which must be considered a secondary office in a fish constantly living in water.

The situation and appearance of the testicles are seen in the annexed drawing, which makes a description of them unnecessary.

The female organs, before they undergo the necessary changes to form the eggs, and prepare them to receive the influence of the male, are very little developed; the ovaria are not larger than the testicles of the male before the breeding season, and resemble them both in their appearance and situation; the oviducts are so small as with great difficulty to be traced, and the clitoris is just large enough to be distinguished. When the eggs are formed, all these parts develope themselves.

The ovaria became exceedingly vascular, and the yolks become conspicuous in all the stages of their increase, from the size of a pea to that of a walnut, and when arrived at that size, they pass into the oviduct.

The number of yolks which are ready at any one time to pass into the oviduct, varies exceedingly in different fishes,

and even in the two ovaria of the same fish. I have seen five of the full size in one ovarium, and only two in the other; in another fish there were three in each, and so on to a great variety.

The oviducts enlarge, and become exceedingly extended. In a fish 27 inches long, each oviduct was 26 inches in length; its internal surface was formed into three distinct cavities, separated from one another by contractions in the coats of the canal. The first of these begins from the orifice that receives the yolk, and is pyramidal in its form; it is ten inches in length, and gradually diminishes in its capacity, the coats being extremely elastic, which throws the internal membrane into folds in a longitudinal direction, taking a very serpentine course. At the termination of this portion, the contraction is formed by the interposition of a substance of a fibrous structure, and light grey colour, between the external coat and internal membrane, forming a circular band, which is divided into three equal parts by two circular parallel lines on the internal membrane. This band is half an inch broad, and its internal surface has a glandular appearance. The second cavity is only six inches long, its internal membrane is very vascular, and thrown into plicæ in a longitudinal direction, longer, thicker, and less numerous than those of the first portion; they are smeared over with mucus. This cavity is separated from the third, by a transverse fold of the internal membrane in a contracted state.

The third portion is ten inches long, and forms the cavity in which the eggs are retained, till the young fishes are formed, and capable of taking care of themselves. The eggs, however, are not loose in the oviduct, as in birds, but a certain number,

corresponding to the number of yolks that are in a state to leave the ovarium at the same time, are inclosed in a membranous bag, piled one upon the other. This bag, at its upper end, is grasped by the contraction which separates the middle and lower portion of the oviducts; the other extremity, which is in the form of a blunted cone, is loose and moveable in the surrounding cavity; the eggs are inveloped in a transparent jelly, which occupies every part of the bag, beyond that in which the eggs are contained.

The clitoris becomes so much enlarged as to project externally; its base swells out into the form of a heart, as it is painted upon cards, only that it is much more pointed; the posterior surface adheres closely to the parts behind it, for one half of its length, the other half is loose, and on its upper surface there is a groove passing on each side, towards the orifices of the two oviducts. The nymphæ are formed by a fold of the termination of the rectum, and project laterally; they are very vascular, and compose the external orifice of the vestibulum, beyond which are the contracted openings of the oviducts. After impregnation has taken place, the pendulous portion of the clitoris becomes flaccid and narrow.

When the young dog-fish is completely formed, the yolk remains attached to the belly by a long chord, consisting of blood vessels, and the fish swims about in the surrounding jelly with this attached to it. If the bag is torn, and the fish is taken out and put into water, it swims about, but if the vessels going to the yolk are wounded, the fish immediately dies.

What number of the shark tribe have this particular mode of hatching their eggs is not at present known, but there is

reason to believe, that it is very general, since the eggs or the empty shells belonging to this tribe of fishes, are rarely met with.

The squalus maximus, I have no doubt, is of this kind; and from the following memorandum of my late friend Dr. PATRICK RUSSELL, given to me by Sir JOSEPH BANKS, the large shark met with between the Tropics, breeds in the same way.

"A shark caught on the 14th of November, 1781, in lat. 7° N. measured 8 feet 7 inches, the tail included. The head and body of a dark bluish colour, the breast and belly of a silver white. Upon opening the belly, the two oviducts were distended with young ones contained within an inner cavity, swimming in a white gelatinous liquid, thicker than the liquor amnios of quadrupeds.

"The right oviduct contained 21 young ones, the left 20; of these 25 were males, and 16 females; they were all nearly of the same length, between 9 and 10 inches, and each of them had the yolk attached to its belly, by a chord of considerable length.

"In the lat. 5° N. another female shark was caught 7 feet long; it had only 8 young ones, 4 on each side."

Of the oviparous shark I could obtain no information, but what is contained in BOHADSCH, in whose works there is an engraving of the egg, and of the shark to which it belonged, caught in the Mediterranean. So little has this subject been attended to by naturalists, that no mention is made that I know of, in any author, of such eggs being met with upon the coast of Great Britain; I was, however, so fortunate as to find a shark's egg on the sea beach at Worthing in Sussex, in Sept. 1809, and in the course of that month, procured several

of them containing young sharks in all the different stages of their growth. The egg which is represented in the annexed drawing, is exactly similar to the engraving in BOHADSCH: when minutely examined, there is on each side of the egg a small slit, for the admission of salt water within the shell.

In the latter end of October, a young dog-fish was sent me 13 inches long, which exactly resembled the embryo in the egg, and proves to be the squalus canicula of LINNÆUS; it had been feeding on the worms met with in the sand banks, some of which were found in its stomach.

The oviviparous and oviparous dog-fishes, differ materially in the form of their stomachs. In the first, the pyloric portion is short and wide, in the other, long and narrow like an intestine. As there are larger sharks with both these kinds of stomach, it is reasonable to believe they have also the same difference in their mode of breeding.

The gelatinous liquid which surrounds the ova of the dog-fish, was found to differ exceedingly in its properties from other animal jellies, for when the membranous bag containing it, was immersed in proof spirit, for the purpose of preserving the ova in their natural situation, the jelly, instead of coagulating, as was expected, expanded so much as to burst the bag. So striking a peculiarity led to a further consideration of it, and a suggestion naturally arose in my mind, that there might be a similarity between it and the jelly, with which the ova of the frog are surrounded. I therefore requested my friend Mr. W. BRANDE, to examine the chemical properties of both these substances, and shall subjoin his account of them.

That the jelly in the oviviparous dog-fish, is formed in the

middle portion of the oviduct, there can be no doubt; but the exact part in which the jelly of the frog is formed, has not been ascertained, which led me to make the following observations respecting it.

In some frogs that were kept in a damp cellar through the winter, no visible change took place in the ovaria or oviducts, although frequently examined, by immersing parts of them in water at different temperatures, till the 10th of February; at that time a portion of the oviduct, when immersed in water at 80°, swelled out so as to double its size, and when the water was at 120° expanded very rapidly. On the 25th of February the oviducts were seen to enlarge, and on slitting them open, the internal surface was smeared over with a ropy fluid. A portion of oviduct two or three inches long, in water heated to 120°, swelled out into a mass of transparent jelly which filled a half pint tumbler, and all traces of the coats of the oviduct were lost.

Upon shewing this jelly to Sir JOSEPH BANKS, he said that it very much resembled what he had seen when a boy, in the country during the winter months, upon the ground, and on the boughs of trees, called star-shot jelly, from being supposed to be formed by falling stars; and that it would be worth while to compare them together, and determine whether the common opinion mentioned by PENNANT, which Sir JOSEPH BANKS had always believed, was correct. The jelly is said to be brought into this state, by the frog having been swallowed by a bird, and the warmth and moisture of the stomach, making the jelly in the oviducts expand so much, that the bird is obliged to reject it by vomiting. Sir JOSEPH BANKS procured some star-shot jelly from Lincolnshire, and Mr. W. BRANDE

found that it was in all its chemical properties, the same with that formed in the oviduct of the frog, and when saturated with water, resembled the jelly in the oviduct of the dog-fish.

The consideration of the properties of this jelly, with which the ova of the oviviviparous dog-fish and of the frog, are surrounded, and the purposes it is intended to answer, led me to take a view of the various modes by which the fœtal blood is aerated in the different classes of animals. The provisions of nature for this very important purpose, form a beautiful series.

The ova of many fish, as the salmon and trout, are laid in the sand and gravel, and the fœtal blood of the embryo is aerated by means of the surrounding water; these fishes, therefore, are found to spawn as near as possible to the sources of springs, where the water, coming from the earth, is in a state of high aeration. The ova of other fish, which spawn in waters less impregnated with air, are deposited on the leaves of water plants and weeds, that give out oxygen, by means of which, the embryo has its blood aerated. The tench and the pike are of these kinds.

The ova of the perch are surrounded by a jelly as that in the frog, which imbibes water, probably for aerating the fœtal blood.

These observations were suggested to me, by my friend Professor DAVY, who has made it a part of his amusements to attend to the habits of fishes.

The ova of the oviparous shark, skate, and all that tribe, although too strong in their coats to be penetrated by the sea water, have natural apertures for its admission and escape,

there being two on each side of the egg, so that there is a current of sea water constantly supplying the egg with air.

In the ovivivipárous sharks the ova have no hard covering, being contained within the body of the fish, they are surrounded by the same jelly as in the frog, and the sea water is applied to the membrane in which they are inclosed, the opening of the oviduct admitting it for that purpose.

In the bird, the eggs being surrounded by atmospherical air, are supplied with it through the porous texture of the shell, which readily transmits it to the membranes of the embryo.

In all these tribes, the mode, in which the air is applied to the fœtal blood is as follows. Besides the common circulation of the blood from the heart of the embryo, to the different parts of its frame, there is a lesser circulation from the arteries to the membranes, which inclose the embryo, and which are in contact with the aerated water, or air, in which the egg is deposited; in this circulation, the blood attracts the air through the membrane, and conveys it into the system. In birds, the young are fed and taken care of by the parents, after the eggs are hatched, and in them this fœtal circulation is immediately stopped, on the embryo breaking the shell, and the yolk is drawn up into the belly as a supply of nourishment, till the stomach has acquired the powers of digestion.

In the ovivivipárous sharks, the young ones swim about in the jelly, which surrounds the ova, with the yolk attached to the belly by a long vascular chord, till fitted to swim in the sea, and all this time the blood is aerated from these membranes. After the young leaves the bag in which the eggs are contained, the yolk is taken into the belly, as in the bird.

In the opossum tribe, and all the pouched animals in New South Wales, there is a peculiarity in the form of the female organs of generation, which has not been understood; this is a communication between the uterus and vagina during the formation of the embryo, by means of one or two lateral canals. These I described in my account of the female organs of generation of the Kanguroo, and was led to believe, from the coagulated state of the parts, which had been a year preserved in spirit, that the openings into the vagina were closed; but this mistake was afterwards corrected in my account of the Wombat, in which I stated from Mr. BELL, who examined the uterus with the embryo in it, "On opening the vagina, it was found to terminate at the common neck of the uteri; on each side of which, were the openings of the lateral canals, and in the middle between them, the meatus urinarius, with a slender fleshy pedicle on each side of it. Behind the meatus urinarius, were two orifices leading to the uteri, but they were filled with a thick gelatinous substance, which rendered them completely impervious." These lateral canals enlarge very much, as the embryo begins to form; at one end they open freely into the uterus, and at the other into the vagina; they are distended with jelly, and are employed to keep up a communication with the external air, for the purpose of aerating the fœtal blood; their appearance in the kanguroo is seen in the annexed drawing.

As the embryo in all the animals of this tribe is contained in a soft egg, which, from the description of Mr. BELL, the only person who has attentively examined it, has no connection with the internal membrane of the uterus, some apparatus like the lateral canals became necessary for the aeration of

the fœtal blood. The embryo in these animals, therefore, forms the intermediate link between the ova that are deposited in the oviduct, and hatched there, and the fœtus formed in the uterus; it resembles the first, in the mode by which the fœtal blood is aerated, and the second, in the situation in which it is deposited, and in the mode of its being supplied with nourishment after birth.

In quadrupeds in general, and the human species, the fœtal blood is aerated in a very different manner, from that which has been described; for although the fœtal circulation sends a portion of its blood to the whole of the membranes in which the embryo is inclosed, as in oviparous animals, the influence of the external air is excluded, from the coats of the uterus, to which these membranes every where adhere. The fœtal blood is however close enough to that in the vessels of the uterus, to have the air in the maternal blood communicated to it.

There are three different structures of the membranes of the fœtus for this purpose; one of these is the whole of the fœtal membrane next the uterus, being extremely vascular, as in the horse and ass; the second, is having only particular portions of it loaded with blood vessels, as in the deer; the third, is having only one large mass, into which the fœtal blood vessels pass to a certain depth, beyond which is a cellular structure, filled with blood from the arteries of the uterus, and taken up by the uterine veins, so that in this instance, there is a greater mass of blood belonging to the mother, nearly in contact with the fœtal blood, than in other animals.

From the series of facts which has been detailed, it appears, that oxygen is essentially necessary for the action of the

vivifying principle in all classes of animals; and that it is not simply applied to the blood, but mixed with that fluid while circulating in the arteries, since, if this were not the case, there would be no means of aerating the fœtal blood in the higher orders of animals.

Experiments on the Jelly formed in the Oviduct of the Frog, and Oviviviparous Shark, by Mr. W. Brande, *F. R. S.*

The substance contained in the oviduct of the frog, is of a whitish colour, nearly opaque and extremely viscid. It does not mix with water, but at common temperatures expands slowly in that fluid to about twelve times its original bulk.

At a temperature of 100°, this expansion is much more considerable, and the substance puts on the appearance of an attenuated and nearly transparent jelly, but none of it is dissolved.

The expansion seems to depend on the absorption of water by the gelatinous substance, the proportion of water taken up being very great. A piece of the unexpanded substance of the size of a large pea, requires rather less than three ounces of water for its complete expansion, and a mass of jelly equal in bulk to three ounces is formed.

This substance dried at a temperature of 212°, becomes brittle, but when it is put in this state, into moderately warm water, it again expands, becoming nearly as bulky as before.

Digested in alcohol it becomes brittle and opaque, and contracts to about one half of its original bulk. If in this contracted and perfectly brittle state, it be put into warm water, it again expands as before. But when once expanded, it is neither hardened nor coagulated by alcohol.

It is soluble in nitric, sulphuric, and muriatic acids.

Nitric acid, diluted with its weight of water, when poured upon the substance recently removed from the oviduct, changes its colour to a deep yellow, and rapidly dissolves it on the application of a moderate heat. This solution is of a pale yellow colour. The caustic fixed alkalies render it slightly turbid when not added in excess; in this case the mixture becomes perfectly transparent.

Muriatic acid at a boiling temperature, dissolves the recent substance very rapidly, forming a solution of a deep blue colour,* in which no precipitation is produced by the alkalies.

Concentrated sulphuric acid dissolves the substance from the oviduct slowly, and forms a pale brown solution. If heat be applied, the colour approaches to black.

No change is produced by the alkalies in these sulphuric solutions.

The substance is very rapidly dissolved by a boiling solution of caustic potash. The compound is imperfectly saponaceous, its transparency is not disturbed by the addition of sulphuric or of muriatic acid; but nitric acid added in a small excess, renders it slightly turbid.

None of the solutions which have been described, afford any precipitation on the addition of tannin, neither does water, in which the substance has been boiled, yield even the smallest traces of gelatine.

* The blue colour of this solution, is instantly destroyed by the addition of an alkali: it seems to arise from the formation of a very minute portion of prussiate of iron. Mr. HATCHETT has observed, that some of the varieties of albumen afford a blue solution, when long digested in muriatic acid: this is probably from the same cause. Phil. Trans. 1800.

No coagulation is produced in this substance, by VOLTAIC electricity, from 30 double plates of four inches.

These experiments shew, that the substance from the oviduct of the frog, is of a peculiar nature: its characteristic property being the remarkable power of expansion, by the absorption of water.

It is distinguished from gelatine by its insolubility in water, and by affording no precipitate with solutions containing tannin: from albumen, by not coagulating on the application of acid, or electricity, and by forming compounds with the alkalies, which are not saponaceous. In some of its other properties, it would appear, as far as regards its chemical habitudes, to be a substance, intermediate between albumen and gelatine.

The gelatinous substance from the egg of the dog-fish, has the properties of that from the oviduct of the frog in its expanded state, and is consequently analogous to what has been termed star-shot jelly.

EXPLANATION OF THE PLATES.

PLATE IX.

An internal view of the belly of the oviviviparous dog-fish, squalus acanthias, of LINNÆUS: to show the organs of generation in their natural situation, when in a state fit for impregnating the female.

a The heart.

b b The liver.—The left lobe is cut away to expose the parts behind.

c The æsophagus.

d The cardiac portion of the stomach.

e The pyloric portion.

f The small cavity between the pylorus and duodenum.

g The duodenum.

h h The valvular intestine.

i i An appendix to the intestine with which it communicates.

k k The testicle.

l l The vas deferens, the lower portion of which is straight, and distended with semen.

m The cavity which is the reservoir of semen, and urinary bladder.

n The kidney.

o The penis.

p p Two external openings leading into the cavity of the abdomen.

q q The two holders in their collapsed state.

PLATE X.

The holders in their extended state, as they appear when the male is clasping the female. In this state of the parts, the

penis is brought forward, and projects externally. On each side of it is seen the opening which leads into the cavity of the abdomen.

The parts are of the natural size.

Plate XI.

An internal view of the abdomen of the female squalus acanthias of Linnæus, to show the organs of generation in the maiden state.

a The heart.

b b The liver.

c c The stomach.

d The spleen.

e e The valvular intestine.

f The appendix.

g g The ovaria.

h h The openings of the oviducts, by which they receive the ova from the ovaria.

i i The course of the oviduct.

k k The oviduct on the opposite side.

l The clitoris.

m m The kidnies.

Plate XII.

Shows the oviduct of the squalus acanthias, with the ova in it, and the young fish after it has left the mother; also the ovum of the squalus canicula or oviparous dog-fish, and the young.

Fig. 1. The oviduct taken out of the body.

a The orifice which receives the ova, beyond which the oviduct is slit open.

b b The first portion of the oviduct.

c c The second portion.

d d The third portion, containing the ova inclosed in the capsule; they are three in number; beyond them the capsule comes to a point, and these processes are filled with a transparent jelly.

Fig. 2. The young squalus acanthias.

Fig. 3. The ovum of the squalus canicula, containing the young fish, with the yolk attached to it; and shewing the slits by which the salt water gets to the membranes of the young: the bristle enters one aperture, and comes through the other.

Fig. 4. The young squalus canicula.

PLATE XIII.

The uterus and lateral canals of the kanguroo, in the impregnated state.

a a The vagina.

b b The openings of the lateral canals into it.

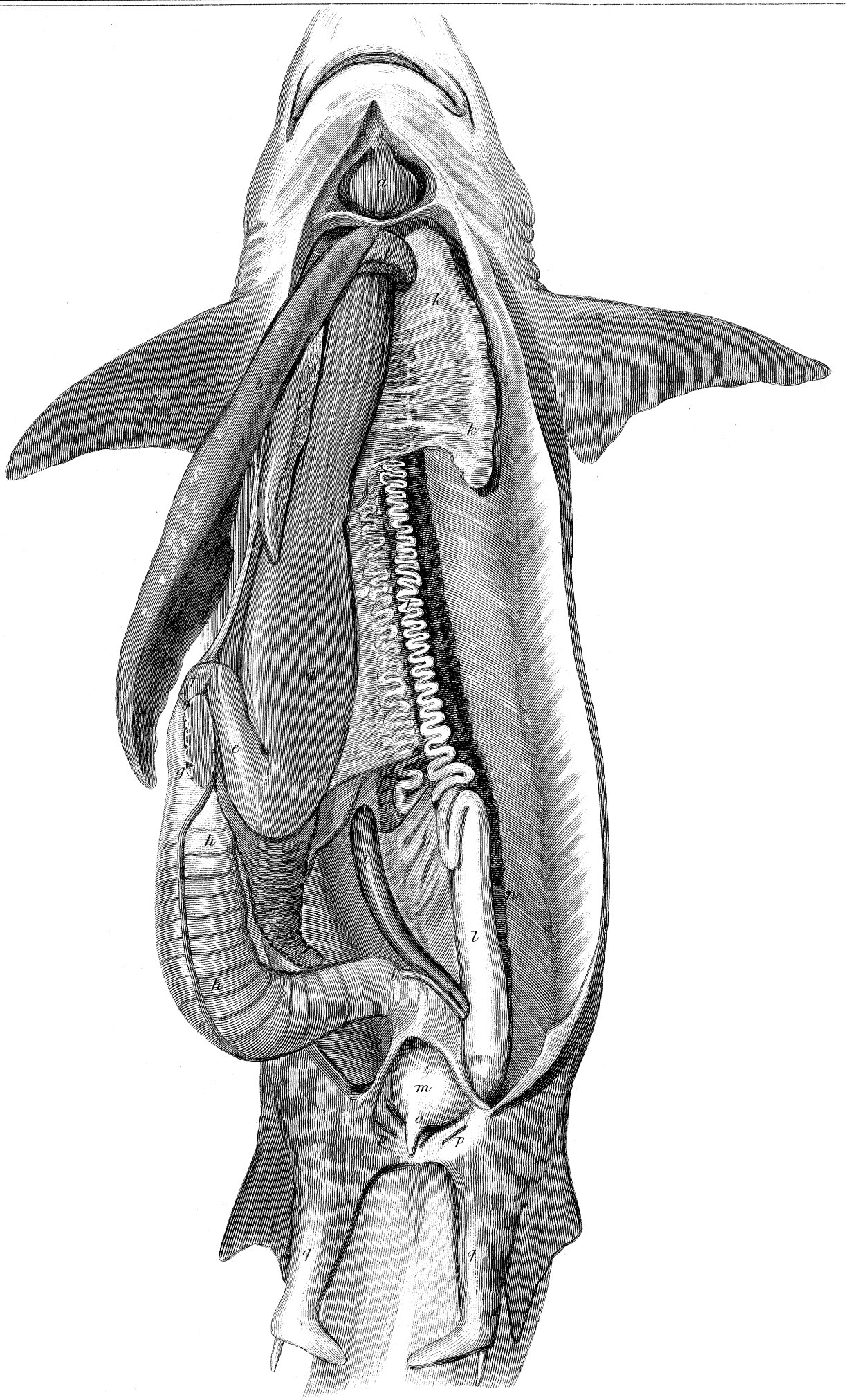
c c c c The two lateral canals, one laid open.

d d The two sides of the uterus.

e e The openings of the fallopian tubes.

f The imperfect septum of the uterus.

g The ovarium slit open to shew the corpus luteum.



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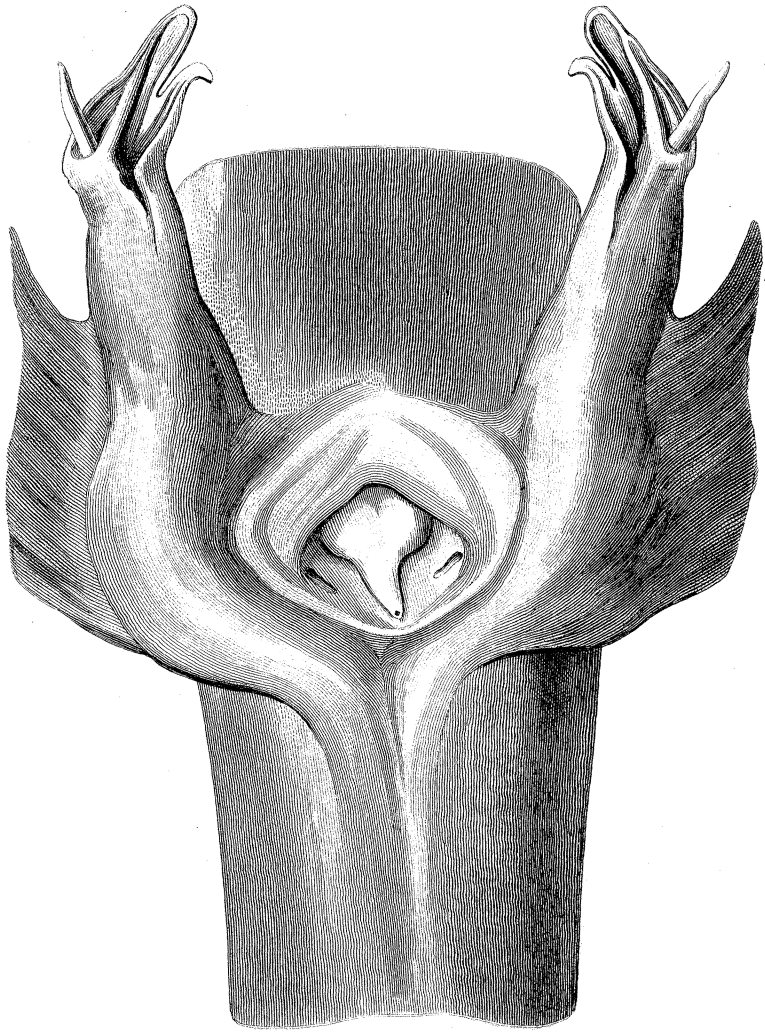

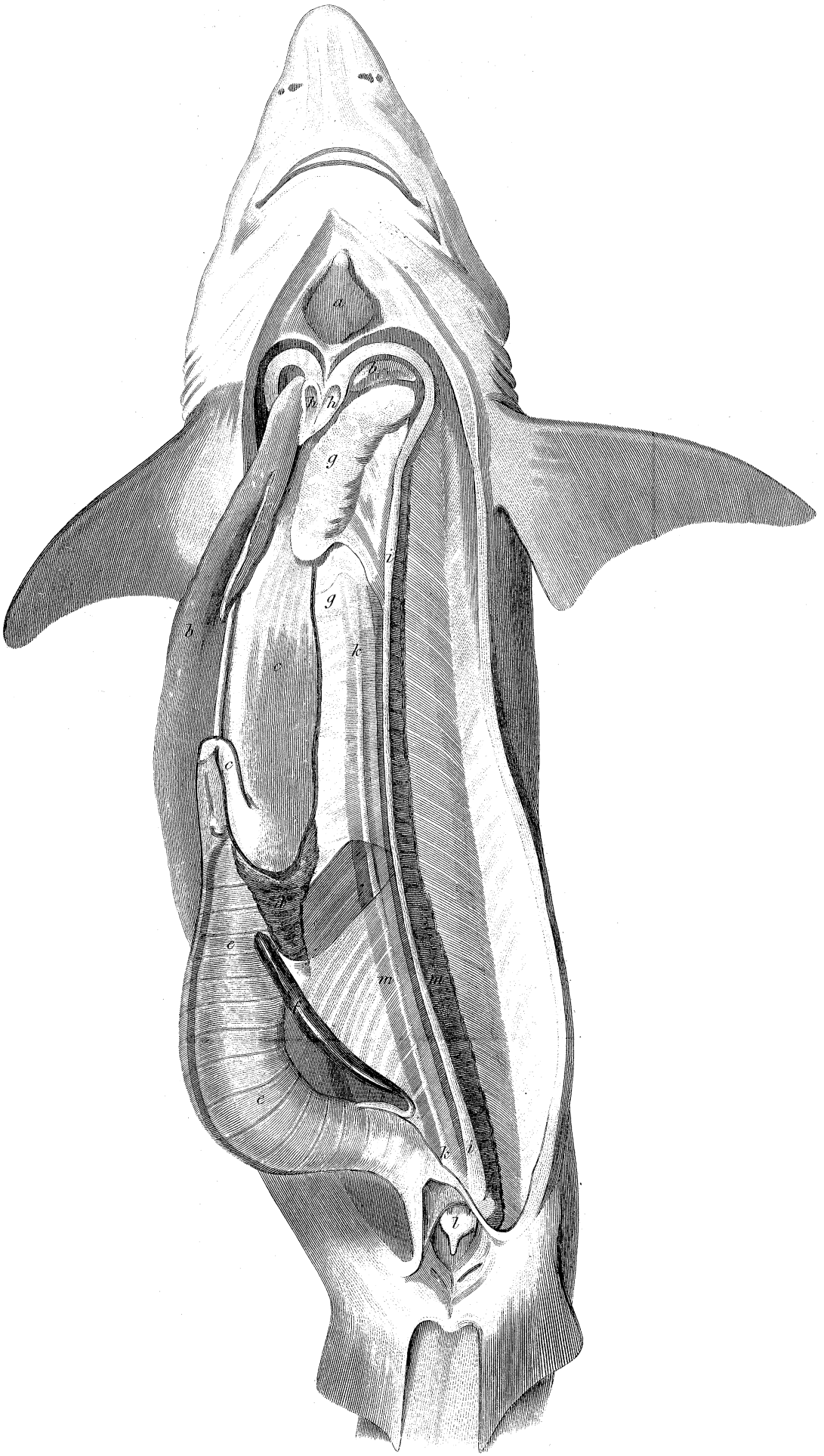

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Fig. 1.

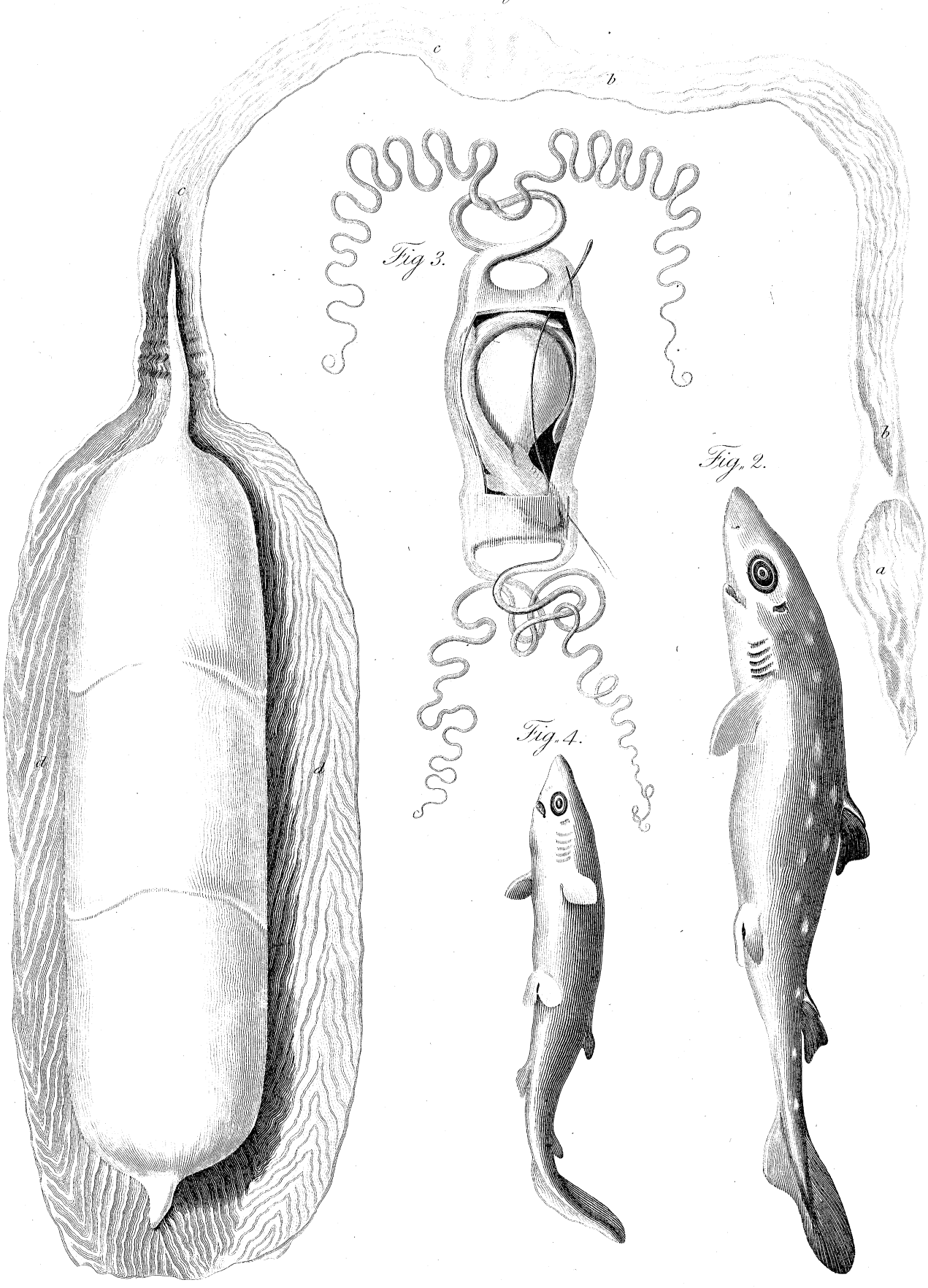

Fig 3.

Fig. 2.

Fig. 4.

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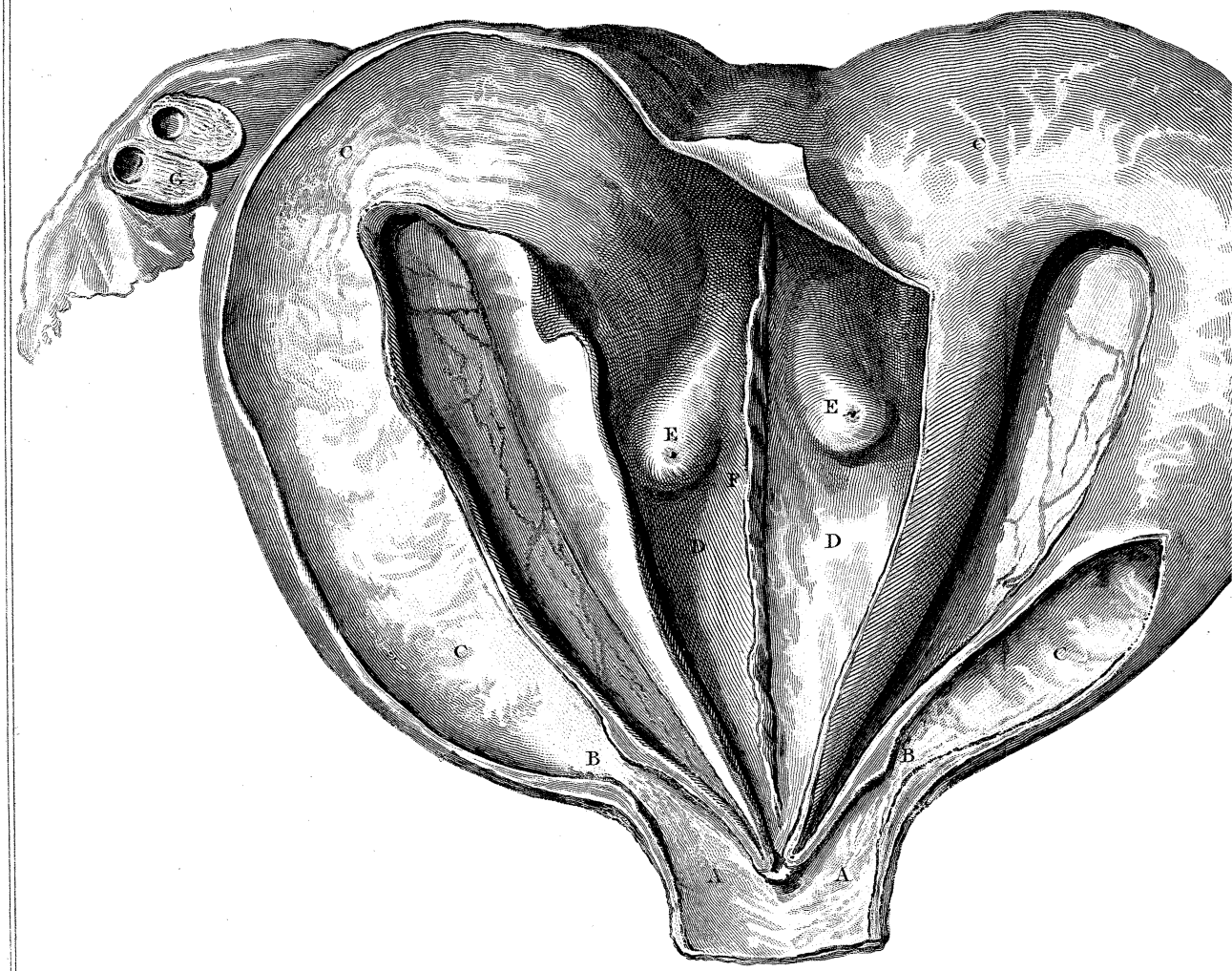
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