

STAGES IN THE DEVELOPMENT OF THE PICKED OR SPINY DOGFISH, *SQUALUS ACANTHIAS* LINN.

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INTRODUCTION

In a previous paper, von Bonde (1945), I described various features of the external development of the oviparous Banded Dogfish, *Haploblepharus edwardsii*. The present species, which attains a length of 915 mm., belongs to the group whose development is classified as ovoviviparous. This species (Plate I, Fig. 1) is very common in the Cape and Natal waters of South Africa and its distribution ranges along the Atlantic coasts of Africa, Europe, and North America and to the Mediterranean.

An egg-case containing three developing embryos (Plate II) was laid by a female in one of the tanks of the Sea Point Aquarium.

FEMALE REPRODUCTIVE ORGANS

The only secondary external sexual characters in the female are the pair of cloacal papillae situated one on either side of the median line immediately posterior to the cloacal aperture. The female contains a paired ovary situated in the usual position towards the anterior end of the coelom. These ovaries (Plate I, Fig. 2, r.ov., l.ov.) change in shape and size according to whether the female is gravid or not, although the cycle of the ovarian growth of the ova is such that ripe ova are again in evidence immediately after the young are born. The paired oviducts are not so highly differentiated in structure and function in their anterior half as those of *Haploblepharus edwardsii*, since the ovum or ova is usually enclosed in a very thin transparent chitinous capsule which is not as highly specialized as the egg capsules or mermaid's purses of the oviparous species. The posterior half of each oviduct, as will appear later, is much more highly developed and specialized in conformity with the ovoviviparity of this species. The oviducts meet in the middle line at the anterior end of the coelom and open into the body cavity by a single orifice. By making a transverse incision immediately posterior to the edge of the pectoral girdle and carrying this incision laterally and then anteriorly and lifting the ventral muscular wall, the confluence of the oviducts is exposed. This common opening of the oviducts is attached by a mesentery in the middle line to the surface of the ventral wall of the coelom (Plate I, Fig. 4, f.t.o. and m.). This common opening is wide and funnel-shaped and lies right over the antero-ventral part of the ovaries so that immediately after a ripe ovum escapes from the ovary it is taken up by the lips of the funnel and passed backward along the fallopian tube (Plate I, Fig. 4, f.t.).

Each oviduct may be divided into five distinct portions as follows:

(1) The fallopian tube (Plate I, Figs. 2 and 4, f.t.) is extremely narrow, thin-walled and comparatively short. This portion is followed by (2) the albumen gland (a.g.) which in this species is very small, thick-walled and muscular, the internal surface being richly supplied with glands secreting the albumen which covers the ovum. The albumen gland is followed by (3) the nidamental gland (n.g.) which is a long thin tube of about the same diameter as the fallopian tube. Here the transparent chitinous egg capsule is secreted. The nidamental gland opens posteriorly into (4) a very wide saccular uterus (u.) in which the development of the embryo takes place. The uterus in turn narrows into (5) a short vagina (v.) which opens into the cloaca. In immature females the vaginal orifices are separated from the cloaca by a membrane or hymen which during copulation is pierced by means of the special claws of the claspers (see below). It is interesting to note that in those Elasmobranchs in which the shape of the claspers of the male is flat, the vaginal orifices are slit-shaped, while in those forms in which the claspers are provided with hooks, the lining of the vagina is thickened (Daniel, 1934).

The uterus, which was described in detail by Widakowich (1907a), is more or less typical of those species displaying viviparity or ovoviviparity. In *S. acanthias* each uterus is a greatly enlarged sac with well defined boundaries. The mucous membrane of each uterus varies greatly in conformity with the development of the ovaries. Thus, when the ovaries are large and contain ripe ova ready for fertilization, the mucous membrane of the uterus is more or less smooth. In gravid females, on the other hand, this mucous membrane is thrown into longitudinal rows of flaps known as papillae or villi, each of which is a leaf-like structure with very thin walls (Plate III, Fig. 10, p.). The border of each papilla is thickened by a blood vessel. The blood supply to the uterus is exceedingly profuse (Daniel, op. cit.). The arterial supply consists in part of the anterior and in part of the posterior oviducal arteries which break up into branches to the rows of papillae. Each terminal artery runs along the free borders of the papillae to supply each single papilla with blood. The blood from each papilla is drained by central veins into a main uterine vein. The two systems are connected by a capillary net around the surface of the papilla.

Ercolani (1879) described the viviparous Selachians according to the various aspects of the relationships between the developing eggs and the inner wall of the uterus, and, according to the degree of these relationships, he differentiated four classes:

1. Naked contact between the homogeneously smooth mucous membrane of the uterus and the surface of the egg (*Plagiostomi acotyledonale*). *Squatina angelus* and *Heptanchus cinereus* are cited by him as examples.

2. Complicated contact between both surfaces, the complication being due to the presence of numerous folds in the secreting mucous membrane of the mother which causes an appreciable increase of the inner surface (*Plagiostomi acotyledonale*). *Squalus acanthias* and *Scymnus lichia* are cited as examples.

3. The complicated contact is differentiated by a more or less significant new structure of papillae on the folds of the secreting mucous membrane of the uterus by means of which its inner surface and activity are extraordinarily enlarged (*Alcuni selachii*). *Torpedo* and *Pteroplatea micrura* are cited as examples. (Note: According to the development of the papillae in the uterus it appears as though *S. acanthias* should be placed in this group rather than in Group 2.)

4. The relationship is no longer due to contact but to an intimate union between a part of the absorbing upper surface of the egg with a part of the secreting surface of the uterus. Both surfaces form folds which interlace and at the same time fuse with each other. Thus a type of rudimentary placenta is formed which is comparable with the mammalian placenta (*Plagiostomi cotyledonale*). *Carcharias glaucus* and *Mustelus laevis* are cited as examples.

In *S. acanthias* the papillae of the mucous membrane arise from a cutaneous development of the convoluted marginal arteries. The papillae are twisted around their longitudinal axes. The changing form of the papillae is due partly to a purely mechanical and partly to a reflex action. There appears to be no relationship between the gestation period and the length of the papillae. The uterus is supplied with blood from two capillary systems, viz., (a) the organotropic and (b) the embryonotropic. The latter forms a capillary network which covers the papillae and also the remaining part of the inner wall of the uterus. The capillary network receives its blood from the marginal arteries and releases it into the basal veins. These do not possess any separate musculature but are embedded in the muscular fasciculi of the uterus which open towards the papillae.

Widakowich (1907b) described the closing device ("Verschlussvorrichtung") situated between the portion I have designated as the nidamental gland and the dome of the uterus (Plate I, Fig. 2A, 2B, c.d.). The gravid uterus (Plate I, Fig. 2, u.) has a cylindrical shape with conical ends pointing anteriorly and posteriorly. The uterine arteries are strong walled (Plate I, Fig. 2A, a.) and run laterally along the nidamental glands. The uterine vein (ve.) runs in close proximity to the artery. The closing device is necessary since the uteri, as soon as the embryos reach a definite age and their enveloping membranes rupture, are filled with a large quantity of nutrient yolk, which, but for this closing device, would be forced along the whole length of the oviducts during any contraction of the uterus, or external pressure from the distension of the alimentary channel, or the movements of the embryos in the uteri should the yolk sac be ruptured. During the time of rut and fertilization there is a strong hyperaemia of the whole genital tract; hence the genital tract is well supplied with blood vessels. The function of the papillae above referred to will be dealt with later.

MALE REPRODUCTIVE ORGANS

The morphology of the male reproductive system follows the general plan of all Elasmobranchs. The testes are paired and occupy the anterior half of the

PLATE I

FIGURE 1. Left lateral view of *Squalus acanthias*.

FIGURE 2. Dissection of a gravid female showing the reproductive organs.

FIGURE 2A. Closing device (c.d.) in oviduct (after Widakowich).

FIGURE 2B. Internal surface of the dome at the anterior end of the uterus showing the closing device. The dome has been invaginated to bring the closing device into prominence, hence it appears nipple-shaped.

FIGURE 3. Egg capsule containing single ovum in early stages of development.

FIGURE 4. Portion of the anterior ends of fallopian tubes (f.t.) showing their confluence and coelomic orifice (f.t.o.).

FIGURE 5. Clasper of male.

FIGURE 6. Claw (cl.) and spur (sp.) of clasper greatly enlarged.

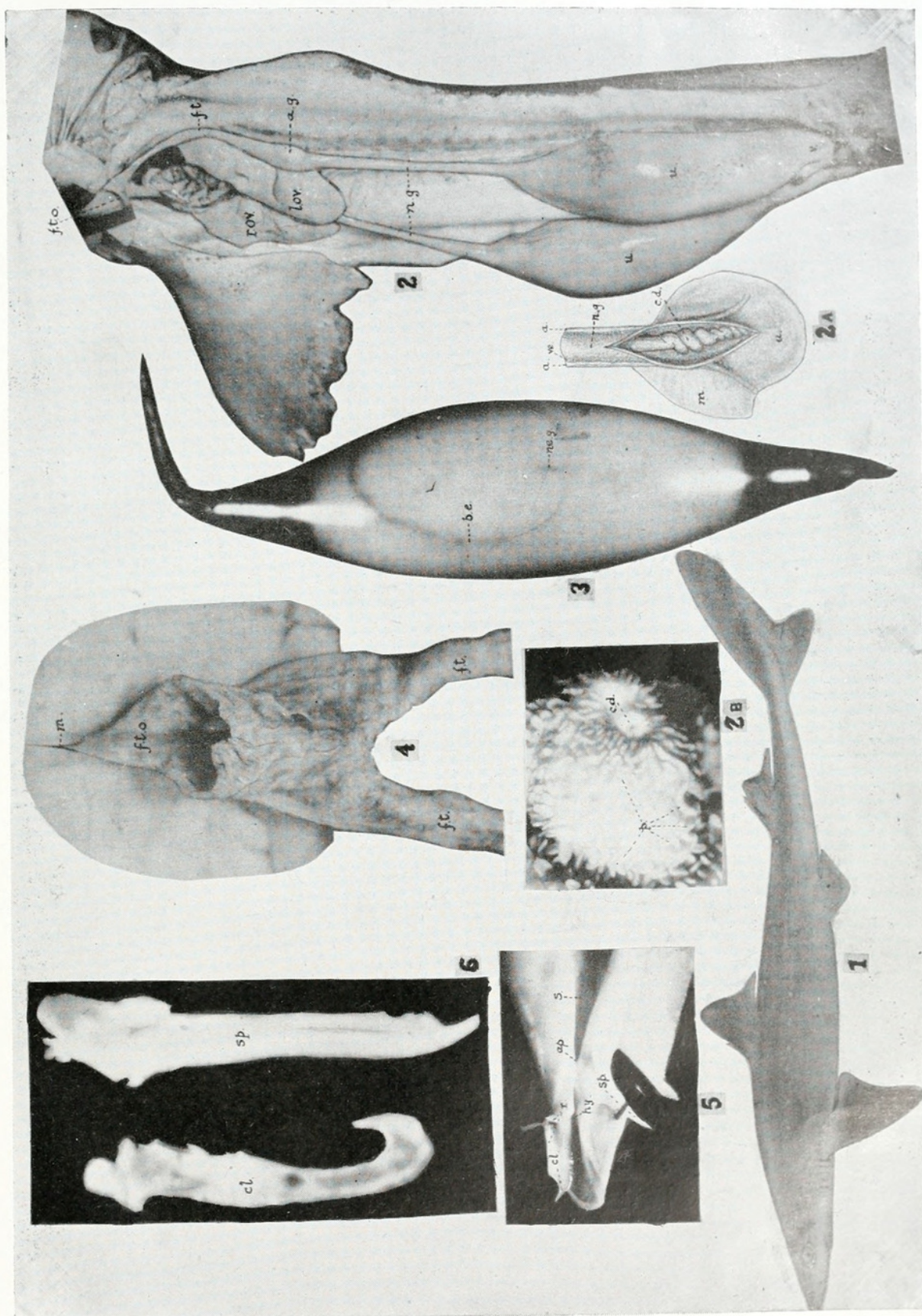


PLATE I

coelom. From the anterior end of each testis the vasa efferentia lead to the epididymus which is much coiled. The epididymus eventually widens out into the vas deferens which expands and joins its fellow in the middle line posteriorly, opening into the cloaca by a single pore.

The external secondary sexual characters of this species present certain distinctive features. As in all Elasmobranchs the basal element (basipterygium) of each pelvic fin is prolonged as a stout, backwardly-directed rod, sharply demarcated from the remainder of the fin, forming an intromittent organ, called the clasper or myxopterygium. A transverse section of the proximal half of the clasper shows it to be almost completely round, the internal cartilaginous skeleton forming a tube filled with a thick muscular substance through the center of which passes a duct. In the distal end the skeleton only occupies the ventral part of the clasper, being continued right to the tip. The latero-dorsal wings of this part of the clasper are formed of thickened skin, the outer wing being folded over the curved inner wing to form a canal which is continuous with the above-mentioned duct in the proximal half. This duct opens through the hypopyle into an open channel which is continued to the tip of the clasper (see Plate I, Fig. 5, hy.). On the outer surface near the hypopyle, a strong spiny spur (sp.) arises. On the inner ventral surface a claw (cl.), which extends to the tip of the clasper, is situated. This claw is much curved and, like the spur, is movable. Its function is probably to rupture the hymen. By pressing the distal end of the clasper, the spur is erected, and forms an important organ of attachment, penetrating and even lacerating the tissues of the female (Leigh-Sharpe, 1920). The spur in its retracted position lies alongside the claw in the same groove. The rhipidion (r.) in the normal intromittent position of the clasper covers the dorsal part of the groove and also the claw and the spur. The siphon (s.) is comparatively small and is situated immediately beneath the skin of the pelvic fin. The apopyle (ap.) lies some distance from the cloaca and relatively near to the hypopyle.

DEVELOPMENT

It was not possible to study the complete development of the present species along the lines described in my previous paper (op. cit.) and it is, therefore, necessary to refer to the description of embryos of various lengths taken from gravid females. The gravid uteri shown in Plate I, Fig. 2, u. each contained a single egg capsule with a single ovum (Fig 3.), one being infertile.

A brief description of the primary phases in Selachian development is as follows: At the time of fertilization the ovum is usually in the shape of a large spherical mass, similar to the yolk of an avian ovum, but its shape may become roughly cylindrical as in the present case, the shape being determined by that of the enclosing egg capsule. The greater part of the egg is formed of peculiar oval spherules of food-yolk held together by a protoplasmic network (Balfour, 1881). The yolk is completely covered by the albumen which is thick and glairy and transparent except at the polar extremities. The protoplasm is concentrated in a small lens-shaped area, the germinal disc or "orange spot," and is situated much nearer to the broader end of the egg. Yolk spherules are also present in this disc, but are much smaller and of a different character. Segmentation is meroblastic or discoidal as in all telolecithal eggs, being confined to the germinal disc.

The blastoderm is thus formed and at the close of segmentation the blastoderm forms a lens-shaped disc thicker at one end than the other, the thicker end being known as the embryonic end where the future embryo develops. The three germinal layers become established and shortly after this the rudimentary embryo consists of an oblong plate which extends inwards from the periphery of the blastoderm. This plate is the medullary plate and along its axial line a shallow groove, the neural groove, is formed. The embryo now progressively increases in length and a certain number of mesoblastic somites become formed. The increase in length of the body takes place normally by growth in the region between the last mesoblastic somites and the end of the tail. The anterior part of the body is not completely folded off from the blastoderm and the neural groove becomes converted into the neural canal. As soon as the embryo has become folded off from the yolk both in front and behind, the separate parts of it are easily recognizable. The embryo is attached to the yolk by a distinct stalk, which gradually narrows and elongates and is known as the umbilical cord. The blastoderm continues to grow in all directions and by circumscrescence it provides a protective vascular covering of the yolk mass, but these extra embryonic structures will eventually be resorbed. The protective covering is developed from the ectoderm, whilst the vascular covering arises from the mesoderm. Before completely covering the yolk mass, however, at a certain stage a yolk blastopore, which is that portion of the surface of the yolk mass not yet covered by the blastoderm, is formed. The yolk blastopore is related to gastrulation since circumscrescence is an important factor in gastrulation and it assists in laying down the definitive endoderm. On the ventral surface of the head of the embryo the stomodaeum is formed, which eventually gives rise to the mouth, while some little distance from the posterior end of the embryo the proctodaeum will eventually give rise to the anus. At a somewhat later stage the gill clefts are formed, being at first six pairs in number, but soon the anterior pair becomes separated from the rest to give rise to spiracles. The first rudiment of the heart becomes visible during the 38 somite stage and has a cavity situated between the mesoderm and the endoderm. All the visceral clefts, including the spiracles, show long filiform external gills which project out for some distance from the sides of the head. These external gills lie against the front wall of the spiracle and the front walls of the visceral clefts. It appears as though they are specially developed to facilitate respiration during the earlier stages of development, either intra-uterine or intracapsular. They disappear some time before the close of the embryonic stage. The young Selachian has all the external characters of the adult when hatched, and can immediately swim about and fend for itself, but before hatching, the yolk has been completely absorbed by the developing embryo and the yolk sac and umbilical cord decrease in size until eventually they are only shown in the form of an umbilicus which persists for about 14 days after birth. The vitelline circulation becomes developed at a stage before the closure of the yolk blastopore. During the circumscrescence of the blastoderm its edge has remained thickened and this feature persists until the whole of the yolk is covered. In this thickened edge a circular vein arises which brings the blood back from the yolk sac to the embryo. The first stage in the development of the vitelline circulation is the formation of a single artery which emerges from the umbilical cord and proceeds cephalad along the blastoderm under cover of the head of the embryo. This arterial trunk divides to form two arcuate branches that turn laterad and then posterad towards the posterior margin

of the blastoderm. These arterial branches eventually meet posteriorly and give off numerous small secondary branches, some of which connect with small veins emptying into a venous ring close to the margin of the blastoderm. The main trunk of the vitelline vein drains the venous ring and runs straight to the umbilical cord (Smith, 1942). When the yolk blastopore has completely closed, the venous ring disappears and the area formerly occupied by the yolk blastopore is traversed by a continuation of the main trunk of the vitelline vein. This trunk receives numerous small veins usually joining it at right angles. Since the venous trunks are only developed behind the embryo, it is only the posterior part of the arterial ring which gives off branches. At a still later stage the arterial ring embraces the whole yolk, but later vanishes in its turn, as did the venous ring before it. There is then present a single arterial trunk and a single venous trunk. The arterial trunk is a branch of the dorsal aorta, and the venous trunk enters the heart together with the splanchnic vein. The venous trunk enters the body on the right side and the arterial leaves on the left of the umbilical cord.

The yolk sac persists during the whole of the embryonic life and in the majority of Elasmobranch embryos there arises within the body walls an outgrowth from the umbilical canal into which a large amount of the yolk passes. This outgrowth forms an internal yolk sac. In viviparous species a remarkable peculiarity arises in that the vascular surface of the yolk sac becomes raised into a number of folds which fit into corresponding depressions in the vascular walls of the uterus. The yolk sac becomes in this way firmly attached to the walls of the uterus and the two together constitute a kind of placenta (Balfour, op. cit.).

We may now proceed to a description of the various embryos obtained from gravid females:

1. The earliest stage found is that shown in Plate I, Figure 3. The large ellipsoidal yolk mass, having an axial length of 58 mm., is shown enclosed in the transparent egg capsule which had an overall length of 100 mm. The oval shaped blastoderm, measuring 29 mm. along its longer axis, lies on the posterior half of the yolk and at the rounded anterior end it shows the formation of the neural groove (neg.). The thickened edge of the blastoderm (b.e.) is well shown. The egg capsule is composed of an extremely thin membrane which is wholly transparent except at the polar regions where the capsule tapers to a sharply pointed end posteriorly and a blunter pointed end anteriorly. These ends are designated anterior and posterior in relation to the position of the embryo and not in regard to the position the capsule takes in the gravid uterus. The figure shows the capsule in the position in which it lies in the uterus, the blunter anterior end being directed posteriorly in relation to the female. The yolk has a thin covering of glairy albumen over the whole surface, but towards the poles the albumen is much thicker and becomes more or less opaque and is loosely attached to the capsule. Encapsulated eggs, which were removed from the uteri, were placed in a large pneumatic trough with running sea water. After a few days the capsules invariably ruptured around the equator and albumen was only found in the pointed polar ends. Compared with the egg cases of oviparous species, the egg capsules of *S. acanthias* contained very little albumen.

2. Plate II shows an egg capsule containing developing triplets (em. 1, 2, 3). These embryos were about 40 mm. in length, the total length of the capsule being

180 mm. The yolk was rounded in conformity with the shape of the enveloping capsule. All attempts to keep these embryos alive after the extrusion of the capsule failed. Embryo 2 ruptured its yolk sac and died, the remaining two embryos also succumbing in rapid succession.

3. The next stage is shown in Plate III, Figures 7A and B. These embryos were taken from a gravid female which had a single egg capsule in each uterus, each capsule containing a set of twins. Immediately after the female was opened, the capsules were removed from the uteri and placed in running sea water in a pneumatic trough. It was not possible to determine their age at this stage. After three days, one capsule ruptured and the embryos freed themselves from their enveloping membrane and lived for about twelve days. The twins in the other capsule died after five days and it is interesting to note that then they were smaller than their counterparts, although at the time of removal from the uteri, all the embryos were of equal size, viz., 45 mm. in length. The longitudinal diameter of the yolk sac at this time was 80 mm. The live embryos, a week later, had attained a length of 65 mm. The longitudinal diameter of the yolk sac was now 70 mm., thus showing

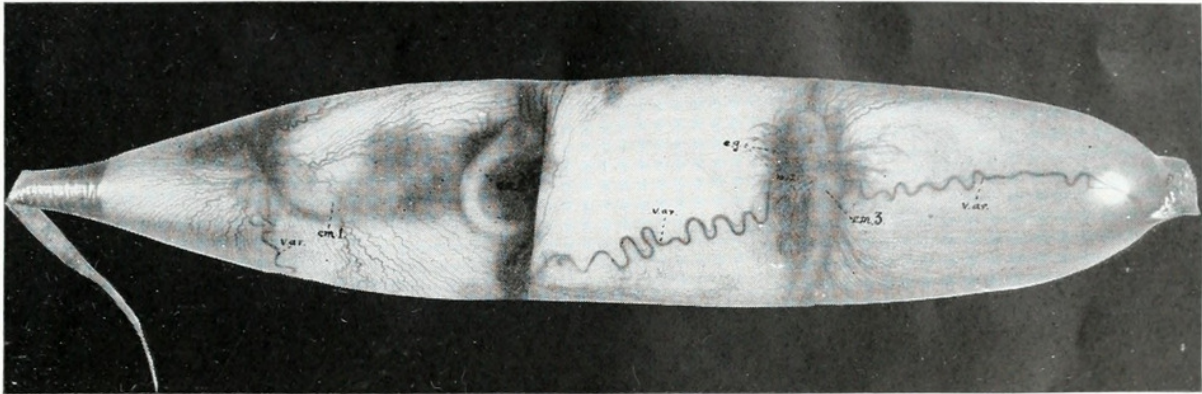


PLATE II

Egg capsule containing three developing embryos.

a corresponding decrease as the embryo grows. The umbilical cord (u.c.) was relatively long and hollow, forming a tubular connection between the yolk sac and the intestine of the embryo. By a gentle pressure on the yolk sac it was possible to force particles of yolk along the umbilical cord into the embryo's intestine. Its walls were very thin and laterally in them ran the vitelline vein (v.v.) and artery. The internal anatomy was well developed at this stage, the alimentary canal being completely formed with a spiral valve developed in the valvular intestine. The liver was developed and the heart had assumed the typical Selachian form. The external gills (Figs. 8 and 9, e.g., sp.g.) had reached their maximum development. After twelve days the other pair died and the external gills were then beginning to shrivel up.

4. A more advanced embryo is shown in Plate IV, Figure 12. Here the external gill filaments had disappeared. The yolk sac was now relatively small and the umbilical cord short and thick. The embryo had assumed the typical adult form except for the yolk sac.

5. The most advanced stages of development found in a gravid female occurred

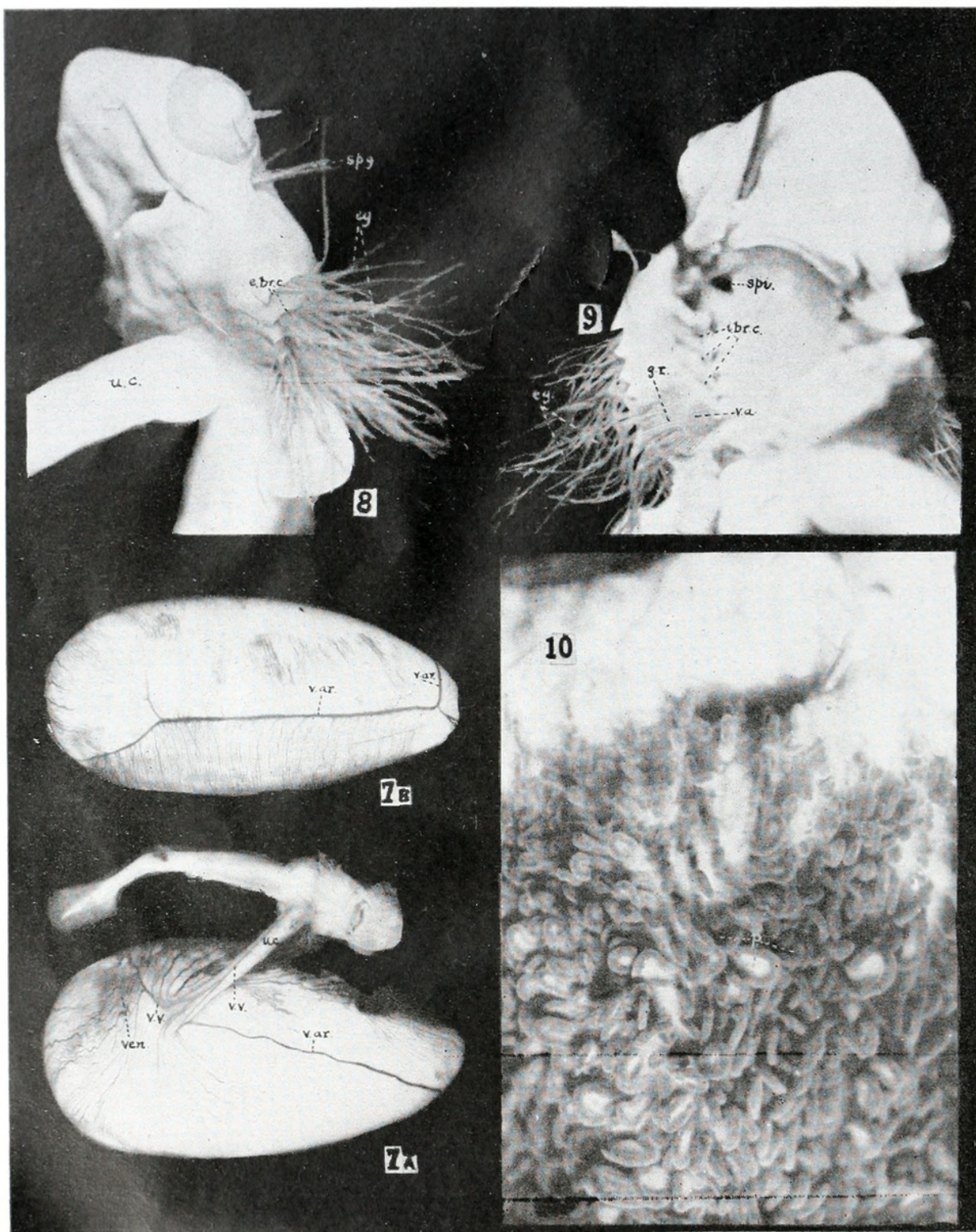


PLATE III

FIGURE 7A. A 70 mm. embryo showing the vitelline circulation and the attachment to yolk by the umbilical cord (u.c.).

FIGURE 7B. The hemisphere opposite to the one to which this embryo is attached.

FIGURE 8. Cephalic end of the same embryo showing the external gill filaments (e.g.) and the spiracular gill filaments (sp.g.).

FIGURE 9. Dissection of the buccal cavity of the same embryo showing the external gill filaments attached to the visceral arches (v.a.). The internal branchial clefts (i.br.c.) are also shown.

FIGURE 10. A portion of the internal surface of the uterus, much enlarged, showing the papillae (p.).

in a female 800 mm. in length. Here the six embryos were at the point of birth. They were 220 mm. in length and differed from the one shown in Plate IV, Figure 12 principally in the fact that the yolk had been completely resorbed and the re-

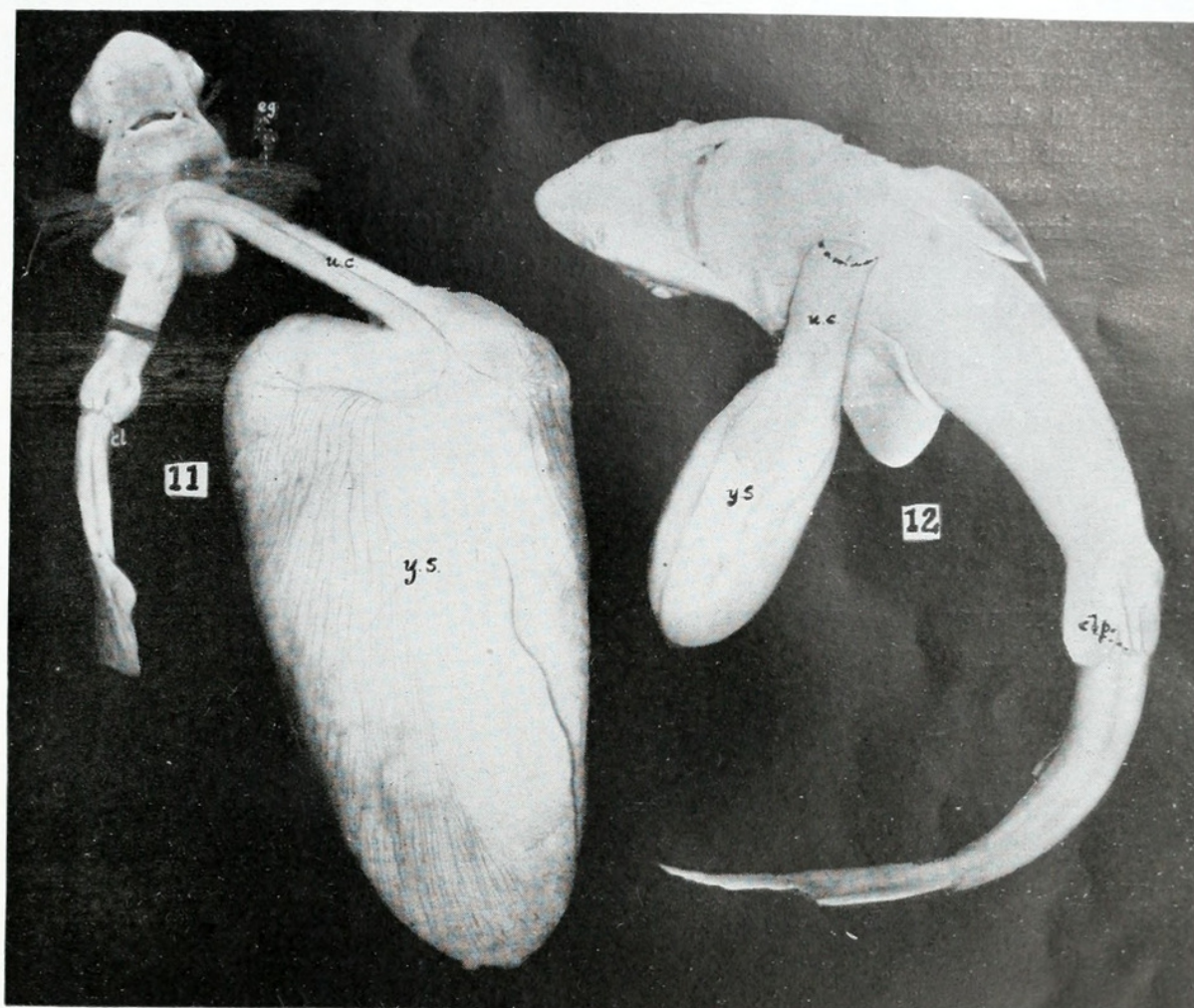


PLATE IV

FIGURE 11. Entire embryo of 100 mm. attached to the yolk sac.

FIGURE 12. More advanced embryo 140 mm. in length. The dotted line at the proximal end of the umbilical cord (u.c.) shows the relative size of the yolk sac in a 220 mm. embryo.

ABBREVIATIONS

a. uterine artery, a.g. albumen gland, ap. apophyle, b.e. edge of blastoderm, c.d. closing device, cl. claw, clp. clasper, e.br.c. external branchial cleft, e.g. external gill filaments, em. 1, 2, 3. developing embryos, f.t. fallopian tube, f.t.o. coelomic orifice of same, g.r. gill rakers, hy. hypopyle, i.br.c. internal branchial cleft, l.ov. left ovary, m. mesentery, n.g. nidamental gland, ne.g. neural groove, ov. ovary, p. papillae, r. rhipidion, r.ov. right ovary, s. siphon, sp. spur, sp.g. spiracular gill filaments, spi. spiracle, u. uterus, u.c. umbilical cord, v. vagina, v.a. visceral arch, v.ar. vitelline artery, v.v. vitelline veins, ve. uterine vein, ven. venules, y.s. yolk sac.

maining yolk sac only 5 mm. in length. The embryos had the same coloration as the adults. It was not possible to determine the age of these embryos so that up to the present the gestation period is unknown.

EXTERNAL GILLS

Gudger (1940, pp. 626, 627) writing about external gill filaments in shark embryos states—"The embryos of all nonplacental viviparous sharks and rays known to me have long external gills. The eggs of these Elasmobranchs have thin diaphanous shells, through which uterine fluids readily penetrate. These fluids are milk-like secretions of the uterine mucosa and serve as food for the growing embryos, which absorb this food through their long filamentous gills. It has been indicated that the relatively thick shells of *Chlamydoselachus* are burst by the growing embryo, are cast off into the uterus, and are then or later thrown out into the sea. Two investigators (Hawkes, 1907 and Smith, 1937) have found highly vascularized areas in the wall of the right uterus (cf. my Plate III, Fig. 10). These observations suggest that these areas might have served to secrete foodstuffs into the uterus. Then the long gestation period and the enormous size of the relatively late embryos still attached to large yolk sacs seem to indicate that these embryos grow not at the expense of the yolk alone. All these things lead to the inevitable question—'Do the external gills of the embryos of *Chlamydoselachus* serve to absorb food from a uterine secretion?' . . . It seems quite sure that in any case these external gills of the non-extruded juvenile sharks serve as respiratory organs."

Further, Gudger (op. cit., pp. 559-562) in dealing with the matter of intra-uterine gestation and respiration states (p. 561) "on the whole it seems quite probable that the young of both sharks (*Ginglymostoma* and *Chlamydoselachus*) may receive some oxygen by diffusion from the uterine wall into the fluids surrounding the embryo. Furthermore, from my knowledge of uterine gestation in other sharks and rays, I am strongly of the opinion that the uterine wall in both (sharks) secretes liquid food materials to nourish the young after they are freed from the egg capsules. . . . The long external gills of embryos of rays and of other sharks, when bathed in the uterine fluid, may take in not only oxygen but mineral salts and possibly other food substances as well. The rich plexus of vitelline capillaries will also be bathed in the fluid of the uterine cavity and they may absorb some food and oxygen from it. If this takes place in *Chlamydoselachus*, it must go on for a long time, until and even after the yolk is resorbed, and this yolk must be used up before the fish is born, else the free oceanic life of this little shark would be very brief."

There are many points of similarity between the present species and that described by Gudger. *Squalus acanthias* is ovoviviparous and at a certain stage of incubation the egg capsule bursts and the embryo is free to lie in the uterus. I have dissected gravid females in which parts of the capsule were found in the uterus. Plate IV, Figure 11, shows an embryo which lay completely free in the uterus with the remains of the capsule lying near the vagina, evidently ready to be extruded. The fact that it has been possible for me to keep some embryos of this species alive in sea water for some time after their removal from the uterus seems to indicate that the external gills must have a function purely respiratory. It is of interest to note that in all dissections of the uteri of gravid females the embryos lay with their heads pointed towards the cloaca and this leads me to infer that the relatively wide vaginal openings into the cloaca permit of sea water entering the uteri for the respiratory functions of the growing embryo. (Compare the provision of respiratory slits in the mermaid's purses of oviparous sharks through which water can enter to provide

respiration by means of the external gills—von Bonde, op. cit.) The external gill filaments are doubtless precocious growths of normal gills and they are eventually lost during later development. Compare Figures 11 and 12 which portray embryos of greatly varying stages of development. In the latter figure the external gill filaments have completely disappeared and the functional gills are typically adult in structure. The occurrence of external gill filaments protruding from the spiracular cleft is conclusive evidence that the spiracular cleft in sharks was primarily a gill cleft with a respiratory function.

Widakowich (1907a) states that the external gills are lost as soon as the egg capular membrane disappears. This is contrary to my observations on embryos kept alive artificially in sea water, and also on those which had burst the egg capsule and were lying free in the uterus, but he does corroborate the view that these transitory gills do not serve the purpose of taking up nutrient material.

There is an alternative possibility in connection with the respiration of the embryo during the time that it has the external gill filaments. In no case has it been possible to observe any connection between the mucous lining of the uterus and the yolk sac even faintly resembling a placenta. This occurrence of a placental development in *S. acanthias* is much featured by Widakowich (op. cit.), but it seems more probable that the papillae of the uterus, which are richly supplied with blood vessels, can, by a process of osmosis, aerate the blood of the developing embryo through the capillary system in the external gill filaments. As mentioned before, Ercolani (op. cit.) grouped this species under his second group of uterine developments and he mentioned the fact that these papillae are in close contact with the vitelline membrane of the yolk. I am convinced, however, that at no stage during the intra-uterine development of the embryo does the mother play any part in the nourishment of the embryo by means of the external gill filaments, the yolk sac alone functioning in this capacity. This contention is, moreover, strengthened by the fact that the yolk sacs in all gravid females dissected by me never showed any convolutions into which the vascular papilla of the uterus could fit. There is of course a possibility that here also there may be an osmotic transference of blood from the surface vascular papillae to the vitelline circulation, but I cannot see that such a function is necessary to the developing embryo. I, therefore, lean to the view that the sole function of these vascular papillae is to provide aeration through the external gill filaments, this function being in addition to that previously described where such aeration takes place by means of the sea water entering the uterus.

THE VITELLINE CIRCULATION

The earliest stages of the yolk sac circulation are shown in Plates II and III, Figures 7A and 7B. The vitelline blood vessels finally spread out over the whole yolk sac. Their function is to carry the nutrient yolk to the developing embryo. The early stages of the circulation were briefly described above. In all young embryos of *S. acanthias* a vitelline artery arises from the dorsal aorta and runs along the left side of the umbilical cord and thence forward from the yolk stalk (u.c.) over the surface of the yolk sac (v.ar.). In earlier embryos, this artery is sinuous (Plate II, v.ar.) but later it becomes straightened out. Its usual course runs from the umbilical cord to the anterior sharper apex of the yolk sac but there

are variations where it runs obliquely across the yolk sac to the sides. In every case, however, it curves over the yolk sac and branches into two, one arm being short whilst the other passes straight back along the ventral surface of the yolk sac (Fig. 7B, v.ar.) and then forks into two branches. On this ventral surface the vitelline artery gives off numerous side branches at right angles to itself whilst no branches are seen arising on the dorsal surface of the yolk. Posteriorly, on the dorsal surface there is a single main vitelline vein (Fig. 7A, v.v.) which drains a dendritic group of venules (ven.). This main vitelline vein runs along the right side of the umbilical cord and enters the heart with the splanchnic vein. In its course along the umbilical cord the main vitelline vein is joined by smaller veins near the yolk sac.

SUMMARY

1. *Squalus acanthias* is an ovoviviparous dogfish with a wide range of distribution.
2. The male and female reproductive systems, especially the internal structure and the closing device of the uterus, are described.
3. Oviparous development takes place in a thin transparent egg capsule, different from the usual Selachian egg capsules, up to a certain stage, when the capsule ruptures and then the development becomes viviparous.
4. Embryos at different stages of development are described. Some capsules contained single embryos, others twins and still another triplets.
5. The functions of the 'external gills are dealt with, it being concluded that their function is primarily respiratory.
6. The vitelline circulation is described.

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