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in Trygon Bleekeri.

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THE ANNALS
AND
MAGAZINE OF NATURAL HISTORY.

[SIXTH SERIES.]

No. 54. JUNE 1892.

LXII.—*Natural History Notes from H.M. Indian Marine Survey Steamer 'Investigator,' Commander Richard Frazer Hoskyn, R.N.*, commanding.*—Series II., No. 3. *On Utero-gestation in Trygon Bleekeri.* By A. ALCOCK, M.B., Surgeon I.M.S., Surgeon-Naturalist to the Survey.

[Plate XIX.]

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§ 1. *Introduction.*

ONE of the most interesting of the discoveries made by the 'Investigator' in recent years is that there are certain Elas-

* This paper was far advanced before the lamented death of Captain Hoskyn, and so I leave it associated with his name, whose breadth of mind, whose high intellectual reach, and whose generous concessions to the interests of science are an irreparable loss to naval exploration.

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mobranch fishes in which the female develops during pregnancy a vast system of uterine glands that secrete a nutrient fluid, or uterine milk, for the nurture of the developing embryo.

In this paper there will be given a detailed account of the phenomenon as lately reinvestigated in the species—*Trygon Bleekeri*, Blyth—in which it was first noticed by us.

As is well known, reproduction among the Elasmobranchii is effected by the internal impregnation of the female.

In some, as in the familiar instance of the ray, the female after impregnation lays eggs, which are enveloped in a tough leathery capsule secreted by the oviduct.

In others, as familiarly exemplified by many sharks, the egg undergoes its changes and the embryo completes its development in the terminal part of the oviduct, which is now enlarged and elaborated to form a true uterus for the reception and retention of the embryo. In this case, as has long been known, a true placenta is formed, differing from the Mammalian placenta in the particulars which follow from the one main general fact that it is the yolk-sac, instead of an allantois, that furnishes the foetal part of the structure.

There is yet a second method of viviparity known to occur among the Elasmobranchs, and to some particulars of it this paper is devoted. In this method while, on the one hand, the egg is retained and the embryo nourished within an oviductal enlargement or uterus, on the other hand no sort of vascular connexion is formed between the parent and the foetus. Here the expenditure of tissue comes altogether from the maternal side, the whole of the egg being devoted to the foetus and none of it being set aside to form vascular absorbent structures.

In passing, one cannot but remark upon the interesting fact that in the primitive Elasmobranch group we find in co-existence all the methods of reproduction that occur in the higher Vertebrate phyla, namely (1) oviparity, with large-yolked eggs enclosed in a more or less rigid shell, (2) viviparity, with the formation of a placenta, and (3) aplacental viviparity.

So far as we are at present aware the method of uterogestation now under consideration reaches its perfection in the Batoidei; and of the six families into which this suborder is divided it has been observed in three, namely the Torpedinidæ, the Trygonidæ, and the Myliobatidæ.

In *Torpedo*, as Professor Wood-Mason and I have elsewhere recalled, it was investigated in furthest detail by Dr. John Davy, who, in pregnant females, noticed (1) foetuses lying naked in the uterus and unattached to it by any form of

placenta, (2) a glairy milky or bloody fluid, which he supposed to be in some way absorbed by the foetus, and (3) the gradual increase in weight of the foetus as gestation proceeded. Davy left unsettled the questions (1) of the immediate origin of the milky fluid, (2) of its immediate destination, and (3) of the direct manner of increase in size of the embryo.

It has been reserved for the 'Investigator,' thanks to the profusion of the Batoid fishes in the warm estuaries of the Coromandel coast, to extend and amplify the observations of Davy, and to draw a more finished and exact picture of the aplacental viviparity of this interesting group. The material collected by the 'Investigator' confirms the older observations as to (1) the absence of any structural connexion between foetus and mother, (2) the presence of a creamy albuminous fluid in the gravid uterus, and (3) the increase of the foetus in size and weight as pregnancy advances; while it adds to our knowledge the following necessary facts:—(4) the presence of special secretory glands in the mucous membrane of the gravid uterus, (5) the existence of arrangements for conducting the uterine secretion into the pharynx of the foetus, and (6) the presence of the unchanged or little changed secretion in the alimentary canal of the foetus.

As references to original papers are appended, it is not necessary here to do more than mention that the above observations have been made, and in every instance verified at least once, in *Trygon Bleekeri*, Blyth, *Trygon walga*, M. & H., *Pteroplatea micrura* (Bl. Schn.), and *Myliobatis Nieuhofti* (Bl. Schn.). In the first-named species, which was the first to come under my notice, the observations were made under particularly unfavourable circumstances, and I therefore seek an opportunity, in describing a second pregnant female of this species recently captured by the 'Investigator,' to make some corrections and numerous additions to my original report.

§ 2. *The Pregnant Female and the Gravid Uterus of Trygon Bleekeri.*

A female of *Trygon Bleekeri*, Blyth, measuring in extreme length, from tip of snout to tip of tail, 9 feet 7 inches, in length of disk 3 feet, and in greatest breadth of disk only an inch and a half less, was caught in Cocanada Bay (at one of the mouths of the river Godávári) on the 12th January last. The abdomen was distended, being strongly convex instead of flat.

On opening the abdomen the internal organs of generation,

consisting of a large ovary and oviduct, are found on the left side only. In my original paper ('Journal of the Asiatic Society of Bengal,' vol. lix. pt. ii. p. 53), describing a large female of this species taken in one of the estuaries of the river Mahánadi in December 1888, I stated that the right oviduct alone was present. I was writing from rough notes taken when the specimen, which was hopelessly large for preservation, was hastily dissected by the dim light of a ship's lantern in one of the scuppers of the ship; and I think it very probable that I may have mistaken my bearings, for these reasons—first, that owing to the position of the large spiral gut on the right side we have an obvious physical preference for the development of the left oviduct, and secondly, that in all the pregnant rays that I have since dissected, where only one oviduct is present it is always the left.

The terminal portion of the (left) oviduct formed a large oval fleshy tumour or uterus, the end of which projected into the cloaca like an "*os uteri*" into a vagina. On opening this a single male foetus was found to fill its cavity, the foetus lying naked, tightly folded, and unattached in any way to the parent. It had the following dimensions:—Extreme length, from tip of snout to tip of tail, 3 feet, length of body-disk 8 inches, and breadth of body-disk 8 inches. On removing it attention is next attracted to the sticky, greasy, creamy material which is smeared over the inner surface of the uterine wall, and when this is removed the uterine mucous membrane is exposed. The mucous membrane has a shaggy appearance, owing to the presence of a dense crowd of long filamentous villi; it is of a vivid scarlet colour, owing to its vascularity, and has an odour much like that of raw beef.

On dividing the uterus all down one side and turning it inside out under water the villi are beautifully seen. They clothe the whole organ so thickly—like the bristles of a broom or like a thick coarse fur—that the surface from which they spring is entirely concealed. In a square of a quarter of an inch (after contraction in spirit) there are about 210 villi, and as the internal superficial dimension of the uterus (after contraction in spirit) is about 20 square inches, the total number of villi must be about 67,200.

Beneath (1) the villi, which constitute the mucous membrane, the wall of the uterus in transverse section shows, from within outwards, (2) a submucous stratum in which is a very distinct *muscularis mucosæ* of both longitudinally and circularly disposed fibres—the former greatly predominant—

running into the bases of the villi; the contraction of the circular fibres, the bundles of which curve into the bases of the individual villi, would chiefly shorten the villi, while the contraction of the longitudinal fibres would chiefly compress the villi together, both actions serving equally to squeeze out the milk from the glands, which, as we shall presently see, make up so large a part of the villi: outside the sub-mucosa is (3) a thick layer of muscular fibres in an encircling band, (4) an equally thick layer of longitudinally-arranged muscular fibres, and (5) a loose fibrous coat in which many large blood-vessels run.

§ 3. *The Secretory Uterine Villi, or Trophonemata.*

For these Professor Wood-Mason and I have elsewhere used the term trophonemata (or "nursing filaments"), to denote their milk-secreting function, since the word "villus," in its associations with human physiology, has now come to connote the very opposite function of absorption. They vary in length, in the specimen under description, from half an inch to an inch and a quarter, the usual length being about three quarters of an inch; in breadth they range from about $\frac{1}{50}$ inch near the base to $\frac{1}{20}$ inch near the tip; and in thickness they are about $\frac{1}{10}$ inch through the centre, and about $\frac{1}{25}$ of an inch through either margin.

They are thus quite flat throughout, and are distinctly spatulate at their free end. They usually arise separately and are unbranched; but often two or three, and sometimes as many as twenty, are found to branch from a single stout peduncular base. Running longitudinally up the centre of each, in strong relief, is a cylindrical swelling which, as will presently be seen, is the single central vein.

When a trophonema is stained (in carmine) and examined under a low power what first arrest attention are the blood-vessels. Running along the edge on each side is seen (1) an arteriole which at the tip, without any subdivision, becomes simply confluent, so that the lateral marginal framework of the trophonema is a long narrow arterial loop.

In the concavity of this loop, coursing down the middle of the trophonema, is (2) a large vein, half as broad again as either of the arterioles; it is only at the tip of the trophonema that the vein shows any subdivision into affluents.

The arterial loop and the vein come clearly into view on deep focusing; a superficial focus displays (3) a dense polygonal meshwork of capillaries over the whole surface of the trophonema.

By careful focusing we find that the entire capillary network and the edge of the trophonema in which the arterial loop runs are covered by a layer of pavement epithelium. With very little teasing in glycerine the arterial loop can be cleanly stripped from the rest of the trophonema, except at the very tip.

This, then, is what is seen on simple examination of a magnified trophonema—a pair of lateral arterial pillars meeting to form a long narrow arch, a central venous column standing in the middle of the archway, and a superficial lattice-wall of capillaries enclosing the whole. From this point of view a trophonema is simply a long compressed cone of blood-vessels.

It must be particularly mentioned that the dimensions above given apply only to the specimen under description. In the Mahánadi specimen the trophonemata were shorter and very much finer and more delicate. And it may be broadly stated that in all the species of Batoids hitherto examined in this connexion on board the 'Investigator' the trophonemata vary in size with every individual.

In a transverse section of a trophonema we see (1) the sections of the artery standing out on each side like a pair of ears, (2) the large vein occupying the centre, and, arranged almost in a ring round the vein, close together (and perpendicular to (3) the sections of the superficial capillaries), (4) a number of glandular follicles which have next to be described. We also see (5) sections of capillaries round the arteries and between the glands.

§ 4. *The Glands of the Uterine Villi, or Trophonemata.*

As above implied, the glands occupy only the middle part of a section—about the middle two thirds of a transverse section made anywhere through the basal half of a trophonema; there are none at the edge of the trophonema where the arterial loop runs. They are somewhat club-shaped and lie close together, being separated from one another, those of the same side by capillary channels, and those of the opposite faces of the trophonema by the central vein and by the deep capillaries, as well as by a small amount of connective tissue. They lie in pocket-like depressions, and show (in section) the following structure:—(1) a broadish vestibule, lined by short columnar epithelium, and (2) an usually double bulbous base (the gland proper), each bulb consisting of a compact wedge of large broad-based tapering cells arranged like the coats of an onion in vertical section.

In any transverse section of a trophonema we find the vestibules of some of the glands opening widely to the surface between transverse sections of two superficial capillaries, others issuing by narrowed openings between two more or less obliquely cut capillaries, while others again end blindly, being covered by a superficial capillary in longitudinal section, which itself lies beneath a layer of pavement epithelium.

It may now be stated that the examination of numerous sections made in various planes shows that the glands are faintly compound, and that they consist of a collecting well or vestibule, into the bottom of which the short lumina of the true secreting bulbs open on all sides.

A very delicate basement membrane delimits the glands in their bulbous portion.

The epithelium, as above noticed, is of two kinds: in the bulbs it consists of large, long, broad-based tapering cells, in which a single nucleus lies close to the basement membrane; in the vestibule or well we find short columnar or almost cubical cells in which the single nucleus is more central.

The nucleus stains deeply with carmine, the rest of the cell, which is faintly granular, taking the stain very lightly.

In some of the vestibules lightly stained coagula are noticed.

There are other unimportant histological details; but the main facts which sections exhibit are that a trophonema consists essentially of a dense vascular network, encasing in its meshes simple glands with bulbous loculi, protected by a layer of pavement epithelium which is fenestrated over the openings of the glands. The amount of connective tissue, except at the very base of the trophonema, is insignificant, and the trophonemata are practically built of blood-vessels and secreting epithelium.

It is not easy to make an exact estimate of the number of glands borne on a single trophonema, and the following calculation can only be regarded as a probable approximation. Taking the area of the orifice of a vestibule at an average of $\cdot 001$ square millimetre, and, since in any one plane at least two glands open into every vestibule, assuming that the space between the vestibules occupied by superficial capillaries is given up to an equivalent of vestibular orifices, and calculating the glandular surface of an average trophonema at 22.8 square millimetres, we should get in each trophonema 22,800 glands.

§ 5. *The Nature of the Secretion.*

The amount of secretion available for examination was so small—only about a fluid drachm, including débris of trophonemata—that no satisfactory results have been obtained.

The capture was at a distance from the ship, and to guard against putrefaction the secretion was removed and bottled and covered with strong (rectified) spirit. By the action of the spirit it was at once coagulated.

When fresh it looked like custard, or, rather, like thin pus; it was viscid, had a sticky greasy feel, and a heavy sweetish meaty smell. Prolonged heat at 212° Fahr. leaves a translucent horny cake (albumin). Fresh Fehling's solution gave no reaction (no sugar), but the quantity tested was so small that the inference must be quite uncertain. A greasy white film (probably fat) was left wherever the secretion touched the bottle.

A portion of the clot macerated in water, stained in carmine, and examined in glycerine, shows an abundance of formed elements. Besides epithelium, which may perhaps be adventitious, there are to be seen crowds of round granular cells of a uniform diameter of about $\frac{1}{2000}$ of an inch. Of these some, though quite transparent, possess no nucleus at all, fewer others have two or more nuclei, while the great majority have a single small excentric nucleus. There are also to be observed free nuclei.

In the Mahánadi specimen the secretion, which was abundant glairy and turbid, was tested only for albumin, and coagulated in lumps when heated.

The secretion thus seems to vary; and it may be mentioned that in *Pteroplatæa micrura*—a viviparous fish allied to the Trygons, and one which carries its young in the same way—the secretion changes with the advance of gestation.

As to the nature of the secretion, then, all that can at present be predicated is that it is very rich in albumin and that it contains a remarkably large proportion of corpuscles and nuclei.

§ 6. *The Fœtus of Trygon Bleekeri.*

On removing the fœtus we are first attracted by the large size of the spiracles, which are full of the creamy uterine secretion.

It may perhaps be of advantage to recall the fact that the spiracles are the first pair of branchial clefts, which, in many

Elasmobranch fishes, remain as direct channels between the pharynx and the external medium.

There is also noticed a small external yolk-sac about as big as a raisin, with a thread-like stalk which perforates the body-wall, and, expanding, is attached to the anterior end of the spiral gut on the ventral aspect.

The yolk-sac is empty and is evidently dwindling; in the more advanced foetus of the Mahanadi specimen it had altogether disappeared.

On opening the abdomen of the foetus the greatly distended spiral gut is seen lying to the right*, and the left lobe of the liver to the left*. The stomach is small and empty and is pushed up beneath the pectoral arch.

The small short duodenum, which is guarded at the pylorus by a stout valve-like fold, is, like the anterior part of the spiral gut, full of coagulated lumps of the uterine secretion. The posterior three-fourths of the spiral gut is stuffed with viscid, grumous, bile-stained matter.

The rectum is sharply constricted off from the spiral gut and looks like a solid cord; dorsal to it lies the rectal gland in a fold of mesentery common to it and the testes, to which last it is intimately adherent.

The liver is of large size and perfectly colourless; the spleen is also large.

The left testis is several times larger than the right, perhaps because the pressure of the distended spiral gut has hindered the growth of the latter.

The external gill-slits are closed; their anterior edges are finely pectinated.

On laying open the capacious pharynx the wide internal orifice of the spiracle is displayed. It lies in the same plane with the branchial clefts proper, and symmetrically with them, so that its homodynamy with them is of diagrammatic plainness, and it differs from them chiefly in being widely open, while they are closed by the close approximation of the branchial bars.

It only remains further to remark, concerning the foetus, that while its generic and subgeneric characters are quite distinct, it has not yet acquired its full specific characters. Except for a large centro-dorsal boss surrounded by a few small tubercles its skin is quite smooth; its tail-spine is well developed, but entirely sheathed in skin. Its colour is much like that of the adult, but lighter, being uniform brown dorsally and olive-grey below except along the abdomen.

* *I. e.* of the foetus.

[The colours of the mother are dark brown dorsally and olive-brown ventrally, except on the thorax and abdomen, which are blotched with white.]

§ 7. *Recapitulation and Conclusion.*

To recapitulate: in *Trygon Bleekeri*, as twice observed in the pregnant state, we find a single uterus containing a single naked foetus unattached structurally to the mother; we find the uterine mucous membrane to be produced into long villi which consist almost exclusively of blood-vessels and glands; and we find the viscid, turbid or milky, and richly albuminous secretion of the latter free in the uterine cavity. In the present case the secretion is observed unchanged in the spiracles, and in coagula filling the "duodenum" and the anterior part of the spiral gut, of the foetus.

Elsewhere Professor Wood-Mason and I have shown that in the nearly related *Pteroplatea micrura* the uterine villi (trophonemata) actually pass into the spiracles of the foetus; and I have quite recently observed this same disposition of the trophonemata in *Trygon walga*.

The specimen from which these particulars have been recorded was too large for preservation; its skin has been sent to the Indian Museum.

Besides the classical text-books and the classical memoir of Johannes Müller, "Ueber den glatten Hai des Aristoteles" (Abhand. Ak. Wiss. Berl. 1840), the following papers refer specially to the subjects of the uterine villi and aplacental viviparity of the Batoidei:—John Davy, "Observations on the Torpedo," Phil. Trans. 1834; Trois, "On the Uterine Villi of *Myliobatis noctula* [and *Centrina Salviani*]," Atti del Instituto Veneto, vol. ii.; Haswell, P. L. S., N. S. Wales, vol. iii. 1889, on *Urolophus*; Alcock, "Observations on the Gestation of some Sharks and Rays," Administration Report of the Marine Survey of India for the Official Year 1888-89, and Journ. As. Soc. Beng. vol. lix. part ii. (*Trygon Bleekeri* and *Myliobatis Nieuhofii*); Wood-Mason and Alcock, "On the Uterine Villiform Papillæ of *Pteroplatea micrura*," Proc. Roy. Soc. vol. xlix., and "Further Observations on the Gestation of Indian Rays," Proc. Roy. Soc. vol. l. (*Trygon walga*, *Pteroplatea micrura*, and *Myliobatis Nieuhofii*).

EXPLANATION OF PLATE XIX.

Fig. 1. The distal half of a trophonema, $\times 10$, showing *m*, the non-glandular margin in which runs *a*, the artery; and *g*, the glandular centre with *v*, the central vein.

Fig. 2. The tip of a trophonema, $\times 42$, showing *c*, the superficial capillary plexus; the other letters as before.

Fig. 3. Transverse section of a trophonema in its basal half, $\times 188$; *m*, *a*, *v* as before; *c*, the superficial capillaries of the glandular centre, and *c'*, the superficial capillaries of the non-glandular margin, in section; *g*, a gland in vertical, and *g'*, one in obliquely transverse section.

P.S.—Since the above was written I have been fortunate enough to obtain two female specimens of *Trygon Bleekeri*; in both the left oviduct alone is developed.

LXIII.—Description of a new Species of Antedon from Mauritius. By F. JEFFREY BELL, M.A.

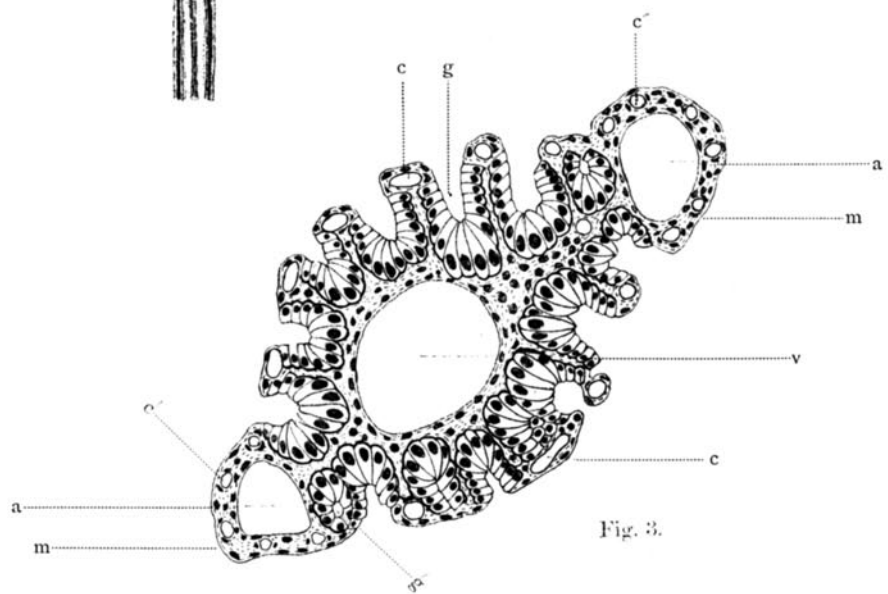
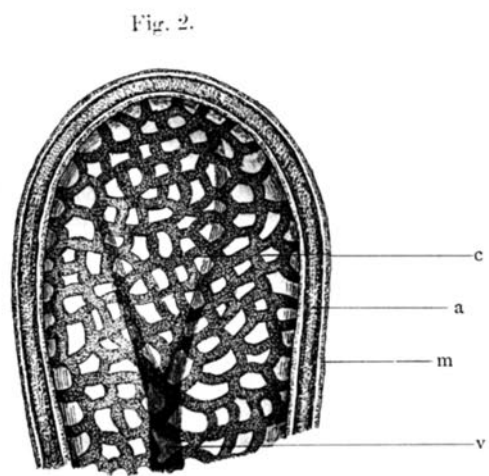
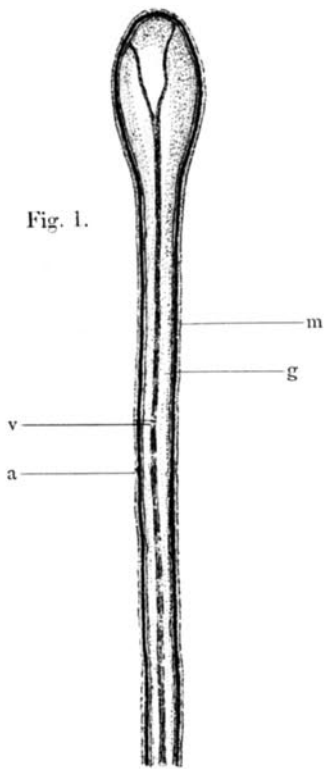
[Plate XVIII.]

THE Trustees of the British Museum have lately acquired some specimens of an *Antedon* from Mauritius which not only appears to be “new,” but to present some very interesting relations to a group of already known species.

The group which the late Dr. P. H. Carpenter called (Chall. Rep. Comat. p. 227) the *palmata*-group consisted of bidistichate species with an unplated disk and a first pinnule smaller than its successors.

Of these some have a pinnule on the third brachial, and of those with two or more postradial axillaries some have the rays free laterally. Of these, three species—*A. tuberculata*, *A. spicata*, and *A. indica*—have the second pinnule stiff and styliform, of twelve to eighteen much elongated joints. With them the Mauritian species is to be placed, but it is to be distinguished from them by the following characters:—

- (1) The marginal projections at the sides of the rays are continued on to the most proximal brachial joints.
- (2) The second pinnule, though “stiff and styliform,” is not extraordinarily so, and the joints, though no more than twenty, are not abnormally long.
- (3) The disk is as small as in *A. indica*, and the centro-dorsal occupies the whole of its aboral surface.



TRYGON BLEEKERI.