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“..... per litora spargite muscum,
Naiades, et circum vitreos considite fontes:
Pollice virgineo teneros hic carpite flores:
Floribus et pictum, divæ, replete canistrum.
At vos, o Nymphæ Craterides, ite sub undas;
Ite, recurvato variata corallia trunco
Vellite muscosis e rupibus, et mihi conchas
Ferte, Deæ pelagi, et pingui conchylia succo.”
N. Parthenii Giannettasii Ecl. 1.

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I.—*Natural History Notes from H.M. Indian Marine Survey Steamer ‘Investigator,’ Lieut. Gordon S. Gunn, R.N., commanding.*—Series II., No. 4. *Some Observations on the Embryonic History of Pteroplatea micrura.* By A. ALCOCK, M.B., Surgeon-Naturalist to the Survey.

[Plate IV.]

1. Introduction.

PROFESSOR WOOD-MASON and I have shown that in *Pteroplatea micrura* the ovum is retained within the uterus, and, further, that the uterine mucous membrane is furnished with nursing-filaments, or trophonemata, which secrete a “milk” that supplies the embryo with nutriment during the later stages of its development and up to the day of its birth.

Though we had examined a good many pregnant females, we had not up to the time that our researches were published met with any that exhibited the earlier stages of embryonic development. But in February last, while the ‘Investigator’ was surveying the Godáviri Delta, I was fortunate enough to capture a female of *Pteroplatea micrura* (Bl. Schn.) in an early stage of pregnancy—double in the right uterus and triple in the left; and in this paper I propose to give, first, a

short account of three matters of interest in connexion with this specimen, namely: (1) the form of the young embryo itself, (2) the structure and relations of the gill-filaments, which in this stage make up a large part of the bulk of the embryo, and (3) the structure of the maternal nursing-filaments, or trophonemata, which at this stage appear to be only preparing for their special secretory function—and, lastly, to offer some suggestions (1) as to the bearing of the facts of the individual history of these embryos upon the problem of the ancestral history of the genus, and (2) as to a possible interpretation through these embryos of the phenomenon of aplacental viviparity among the Elasmobranch fishes.

2. *The Early Embryo of Pteroplatæa micrura.*

The embryo* now to be described is about 29 millim. long; it has a remarkable generalized shark-like form (fig. 1), its snout, its gill-openings, and its tail having a Selachoid and not at all a Batoid appearance.

The *snout* is produced far beyond the mouth and is bluntly conical.

The *gill-openings*, from whatever aspect seen, are remarkable. From the dorsal view the branchial region forms on each side an inflated chamber in which the broad branchial bars are plainly visible; anteriorly the first slit forms the wide-open spiracle, but the other slits, five in number, are closed, and are conspicuous only because of the large blood-vessels which run in them. From the side view six nearly equidistant clefts are seen, the first being the spiracle and the other five being still closed but very plainly visible on account of their vascularity. It is only ventrally that the gill-slits, here very short and comparatively inconspicuous, are open to give issue to a cloud of delicate filaments, many of which when straightened out are nearly twice the length of the embryo itself, and the sum of which forms at least one third of the whole volume of the embryo.

The *trunk* is cylindrical and Selachoid and ends in a thick cylindrical shark-like tail, which bears terminally a long ventral and a shorter but deeper dorsal tail-fold.

The *pectoral fins* are large, their base being coextensive with the length of the trunk; each is prolonged forward, parallel with but quite separate from the branchial region, and in the same plane with the head, into a tapering bar, which, however subsequently curled, starts with an inward

* One embryo, typical of all, has been selected for this description.

twist. If the head were more depressed, and if at the same time the prolongation of the pectoral fins were broader and more truncated, the result would be a by no means fanciful resemblance to *Rhina*.

The *ventral fins* are small and lie well free from the hinder limit of the pectorals.

The embryo is still attached by a broad cord, about 12 millim. long, springing from the belly between the front border of the pectoral fins, to a large yolk-sac, which appears to consist entirely of a diffuent yolk hardly more stable than oil, enclosed in a membrane of extreme tenuity. The gill-filaments are in intimate relation with this yolk, closely and completely enveloping it on all sides. The cord of attachment is so delicate, yet so broad withal, that I have not succeeded in cutting complete transverse sections; but this much is quite certain, both from examination of partial transverse sections and from examination of portions of a stained cord mounted flat as transparent objects in glycerine, that it consists of a solid mass of close-packed large-nucleated cells, and is longitudinally traversed by numerous lacuniform channels of very irregular outline and of unequal size, and that these channels contain NOT BLOOD-CELLS, BUT SMALL SPHERULES OF YOLK ONLY. In short, nothing of the nature of a distinctly defined artery or vein, or indeed of any vessel containing blood-cells, is to be made out; and this must be looked upon as a fact of the highest significance, not merely when we come to seek an explanation of the use of the gill-filaments in this species, but when we come to consider the much wider question of embryonic nutrition among the aplacentally viviparous Elasmobranchs in general.

3. *The Gill-filaments of the Early Embryo of Pteroplatea micrura.*

These issue ventrally from all the gill-slits except the spiracle, and closely embrace the yolk-sac; if they have any additional attachment to the uterine wall it must be of the feeblest nature. Their total volume in the fresh state was not less than one third that of the entire embryo.

They vary in length, most of them being considerably longer than the embryo itself; their breadth is about 0.5 millim. and their thickness is quite inappreciable by the unaided eye.

A filament stained with carmine, mounted flat in glycerine, and examined as a transparent object under a low power (fig. 2) has a uniformly granular appearance—due to the

close crowding of the very large nuclei of epithelial cells that closely invest its surface—and shows a longitudinal light band occupying a little more than its median third, flanked by a dark band occupying on each side a little less than its marginal third; and when the end of the filament is brought into view the lateral dark bands are found to directly inosculate round its tip. The dark marginal band is in fact a broad capillary filled with blood-clot, disposed in a long narrow loop.

Under a higher power the surface of the filament is seen to be uninterruptedly covered with polygonal epithelial cells in the closest possible contact with one another. These cells are remarkable in consisting of little but a large vesicular nucleus lying within a thin and difficultly visible capsule of cell-protoplasm; the nuclei have a diameter varying from 7·5 to 10 micromillimetres, and are often polygonal by mutual compression.

A transverse section of a filament looks like a pair of *pince-nez* (fig. 3), each lens of the *pince-nez* being formed of a cross-section of a simple capillary tube, with a wall one cell thick, enclosed in a frame formed by a single row of large nucleated epithelial cells, and the bridge of the *pince-nez* being formed of two rows of these cells with a layer of flat nuclei, continued across from the capillary wall on each side, between them.

To recapitulate and restate: a gill-filament is nothing more than a long narrow loop of a capillary of wide bore with a wall one cell thick, enclosed in a folded sheet, also only one cell thick, of small epithelial cells which consist of little but a great nucleus.

As to the function of the gill-filaments: their vascularity and the nature of their epithelium clearly indicate great activity. They do not seem to have any attachment to the uterine wall, but, on the other hand, the manner in which they enfold the yolk-sac leads to the belief that they assist in absorbing the nutrient yolk. And the irregular indefinite nature of the channels of the stalk of the yolk-sac, which channels, moreover, seem to carry only yolk-particles and not blood, seems to give strong support to this view.

4. *The Uterine Trophonemata of Pteroplatea micrura in the Earlier Stages of Pregnancy.*

The structure of the nursing-filaments when in active function for the benefit of the foetus has already been described and figured by Professor Wood-Mason and myself (*vide* 'Proceedings of the Royal Society,' vol. xlix. pp. 359–367),

and all that is now necessary is to draw attention to the slight but significant differences which are observed in this earlier stage while the embryo has still an ample fund of yolk to draw upon—differences which enable us to picture the mode of development of the milk-secreting elements.

In the specimen under notice the nursing-filaments mainly differ to the naked eye from those originally described in being altogether smaller and in being uniformly distributed like a coarse thick fur over the entire surface of the uterine mucous membrane, instead of being restricted to certain definite areas.

Their average length is 11 millim. and their average width about 1.25 millim. at the base and about 0.75 millim. near the tip, and they are flat with a tendency to curl.

When a trophonema is stained with carmine and examined in glycerine as a flat transparent object, under a low magnifying power, the blood-vessels first attract attention. Running in the margin, from base to apex on each side, is seen a small artery which at the tip of the filament flows each into its fellow, either in a single loop or, after a single acute-angled bifurcation, in a double loop, as shown in fig. 4. All along its course this marginal arterial loop sends off from its concavity numerous small branches, which form a dense superficial capillary plexus with its long narrow meshes transverse to the long axis of the trophonema; and deeply beneath this plexus, running up the middle of the trophonema in its basal half only, is a spiral vein of some size. Higher magnification shows that the surface of the trophonema is uniformly covered with pavement epithelium, which dips down, but does not become discontinuous, in the slightly excavated intercapillary meshes.

A transverse section of a trophonema (fig. 5) shows at either extreme the artery and near the middle the wider but not very much wider vein cut straight across, the superficial capillaries cut through in various planes, and at the circumference of the section an unbroken ring of pavement epithelium presenting slight depressions in many places between the cut capillaries. Beneath the epithelium, stretching from artery to artery but not round the arteries, on both faces of the narrow section, is a long close line of pocket- or bulb-shaped nests of cells, which in some cases are quite solid, in other cases are hollowed out in the centre, and in yet other cases form true acini "pointing," to use a surgical metaphor, towards the superficial intercapillary depressions of the surface epithelium above alluded to.

It is unnecessary to go further into histological detail, since

enough has been said to enable us to understand the meaning of these appearances.

In transverse sections of a trophonema taken from a long-gravid uterus in which the foetus, having used up all the yolk, is now demanding other nourishment, there is, as has been shown in the paper already quoted, little to be seen but two opposed rows of bulb-shaped milk-secreting glands with funnel-shaped mouths, separated by a vascular space. These glands take the place of the more or less solid nests of cells seen in the above-described sections of trophonemata from a gravescent uterus. And in comparing this less mature with that more mature stage we come to the conclusion that in *Pteroplatea micrura*, as Professor Wood-Mason and myself have already shown to be the case in *Trygon walga*, the secreting glands of the nursing-filaments, like the alveoli of the milk-glands in Mammals, begin as solid nests of epithelium, which, with the onset of active secretion, gradually become hollow chambers by the breaking down and exfoliation of their core.

5. Considerations as to the Descent of the *Pteroplatean Alliance.*

I hope before long to give a more complete account of the embryonic history of *Pteroplatea micrura*, from which perhaps it may be more permissible than it can be from the meagre facts just recorded to attempt to retrace the pedigree of the Trygons. But on account of the recent revival of interest in the phylogeny of the Batoidei it will, I trust, be considered pardonable to touch a few points, from all of which we can, without straining, bring these embryos into the field of vision.

It is impossible to see these little embryos without in the first place being struck by their shark-like form; and when next attention is fixed upon the gill-openings—their conspicuous dorsad extension and their relation to the prolonged pectoral fins—one is immediately reminded of *Rhina*. Indeed all that is needed is to straighten out and flatten the pectoral fins and to depress the head in order to get a strong resemblance to that interesting intermediate form. Or, if we leave the pectoral prolongations untwisted and imagine them in this condition fused with the head, we get a remarkable likeness to *Ceratoptera* and *Dicerobatis*.

The descent of the Trygonidæ from a shark-like ancestor is of course, from what is well known of *Raja* and *Torpedo*, only what would be expected; but I do not know whether or not the suggestion that the line of descent passes (1) through

a *Rhina*-like form, and (2) through a Myliobatoid form, is equally familiar. At any rate it is a suggestion that arises quite naturally from an external view of the pectoral fins and gill-slits of these embryos of *Pteroplatea micrura*.

Professor G. B. Howes, in his most interesting paper "On the Pectoral Fin-Skeleton of the Living Batoid Fishes" &c. (P. Z. S. 1890, pp. 675-688), incidentally suggests an alliance between *Rhina* and the Ceratopterine Myliobatoids; and Herr Otto Jaekel (SB. Ges. nat. Fr. Berlin, March 1890), in a paper of great interest, for the knowledge of which I am indebted to Professor Howes, has drawn attention to the importance of the disposition of the gill-slits in relation to the pectoral fins for the purposes of a natural (phylogenetic) classification of the entire order, and has laid stress upon the Batoid affinities of *Rhina*.

6. *Considerations as to the Origin of Aplacental Viviparity among the Elasmobranchs.*

If it is premature to jump from these embryos back to their supposed ancestral relatives, it is equally premature to attempt from them alone to interpret the meaning of the aplacental viviparity of the Batoid fishes as a whole. The subject, however, is so very tempting that one cannot refrain from recording certain suggestions that naturally arise out of an examination of the yolk-sacs and umbilical cords of these embryos of *Pteroplatea*.

The methods of reproduction among Elasmobranchs are three, namely (1) oviparity, (2) viviparity with the formation of a placenta, and (3) viviparity without the formation of a placenta.

We know how the second naturally arises directly out of the first; the large egg is retained in the terminal portion of the oviduct, and in the process of development, from early common arrangements by which "nutriment from the yolk-sac is brought to the embryo partly through the umbilical canal and so into the intestine, and partly by means of blood-vessels in the mesoblast of the yolk-sac" * and so into the general circulation, we come at last in these viviparous forms to later special arrangements by which, when the yolk is finished, nutriment from the maternal blood-vessels in the uterine mucous membrane is brought to the embryo by means of the greatly developed foetal blood-vessels of a yolk-sac which has now, after the disappearance of the yolk and the

* Balfour, 'Comparative Embryology,' 2nd edition, vol. ii. p. 64.

obliteration of the communication between the umbilical canal and the intestine, become a placenta.

Now from the non-vascular condition of the yolk-sac and umbilical canal in the embryos under consideration we may venture to surmise the possibly equally direct origin of aplacental viviparity from simple oviparity.

Here again the large egg remains in the terminal portion of the oviduct, and in the process of development external gills which had originally "very possibly become specially developed to facilitate respiration within the egg" * become otherwise specialized to absorb nutriment from a yolk-sac which has only the single communication with the embryo through the umbilical canal and intestine. When the yolk is all finished the nutriment which is secreted from the maternal glands naturally follows, in the absence of any absorptive blood-vessels in the empty yolk-sac, the already established route through the branchial clefts, one of which (the spiracle), being unobstructed by gill-filaments, becomes at last the exclusive channel of supply.

I should like, in concluding this paper, to express my obligations to Professor Howes for his extreme kindness in sending out to me on loan, at great risk owing to distance, his own copies of Herr Jaekel's and others' papers on the subject of the affinities of the Batoids—an act of kindness and consideration which a ship's naturalist, cut off for months from all but a few standard classics, can hardly over-appreciate.

EXPLANATION OF PLATE IV.

- Fig. 1.* Embryo of *Pteroplatea micrura*, from dorso-lateral aspect; nat. size, but with only a few of the gill-filaments represented, for the sake of clearness. *s*, spiracle.
- Fig. 2.* End of a gill-filament, showing the marginal capillary filled in places with blood-clot. $\times 42$.
- Fig. 3.* Transverse section of a gill-filament, showing the marginal capillary in section and the single fold of epithelium. $\times 188$. For the sake of clearness the blood-clot is represented in one limb of the capillary only, and the spaces between the nuclei of the surface epithelium are a little exaggerated.
- Fig. 4.* End of a trophonema, or nursing-filament, seen as a transparent object in glycerine, showing the marginal artery and the superficial capillary plexus. $\times 42$. The median vein is not seen so near the end.
- Fig. 5.* Obliquely transverse section through a nursing-filament, showing the glands still in the form of solid bulbs lying beneath a still unbroken surface of epithelium. $\times 110$. *a*, *a*, arteries; *v*, vein; *c*, *c*, superficial capillaries.

* Balfour, *op. et tom. cit.* p. 62.



Alcock, A. 1892. "I.—Natural history notes from H.M. Indian marine survey steamer 'Investigator,' Lieut. Gordon S. Gunn, R.N., commanding.—Series II., No. 4. Some observations on the embryonic history of *Pteroplatæa micrura*." *The Annals and magazine of natural history; zoology, botany, and geology* 10, 1–8. <https://doi.org/10.1080/00222939208677367>.

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