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On the Development of Sagitta — Source link

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TRANSLATIONS.

On the Development *of* Sagitta.
By Dr. C. Gegenbaur.

('Abhandl. d. Naturf. Gesellsch. in Halle,' 1857.)

Having in a former volume of this journal given an account of what is known respecting the structure and relations of *Sagitta bipunctata*, we have thought that an abstract of Dr. Gegenbaur's observations on the subject of reproduction in that genus would not be unacceptable; and the more so, as this part of the history of Sagitta has hitherto been involved in much obscurity.

In the sea at Messina three distinct species of Sagitta came under the author's observation. *S. bipunctata*, which he appears not unfrequently to have met with of the large size of 2″ 2‴ in length, and two other forms which he was unable to refer to any known species. One of these, 9‴ long, was of slender shape, attenuated for some distance beyond the head, and again, beyond the middle of the body, tapering off suddenly to the caudal extremity, had two pairs of lateral and one caudal fin; the former rounded and projecting but little, whilst the caudal fin was very broad. The surface of the body, moreover, was studded with warty tubercles, occasionally disposed with perfect symmetry and supporting bundles of fine setæ. The head triangular, somewhat acuminate in front. The other species was less common, the largest individuals not more than 6‴ in length, the body almost cylindrical, very slightly constricted behind the rather broad head, and truncated at the caudal extremity; the whole surface of the body was covered with very numerous bundles of setæ (0·08‴ in length), which gave it an almost villous aspect. The anterior lateral fins, very long and narrow, commenced at the end of the first quarter of the length, terminating in a projecting point about the middle of the body. The posterior pair, wider in proportion, had a strongly curved border. The caudal fin was abruptly rounded off. Both species were transparent, and had, like all their congeners, two brown pigment-spots behind the opening of the vasa deferentia. No important distinction could be drawn

from the oral hooklets. From two of these three distinct species Gegenbaur obtained mature ova, derived from pregnant individuals kept for the purpose in glass vessels.

The spawn was deposited in good-sized masses of a substance not unlike swollen sago-grains. The period at which they were most abundantly met with extended from the end of January to the beginning of March.

The deposited spawn always lay unattached on the bottom of the glass vessel, and consequently when in the sea is probably pelagic, that is to say, the sport of the waves. In confirmation of which similar masses of ova were occasionally taken with a fine towing-net. They bore no resemblance to the ova described by Darwin as belonging to *Sagitta*.

The ova were enveloped in a gelatinous substance, which, however, did not appear to surround each ovum separately, but to appertain to the whole mass of eggs in common. In this respect some resemblance may be observed with the condition presented in *Terebella*, *Protula*, and *Arenicola*, as well also as in the *Hirudineæ* and those *Lumbricina* in which several ova are associated in one capsule (*e. g.*, *Sænuris*).

The spawn of *Sagitta*, therefore, is closely allied to that of Annelids, and differs essentially from that of the Mollusca, and especially of the Gasteropoda, whose ova, besides the general gelatinous envelope, present also an albuminous covering surrounding each separate vitellus or several together, when the outer layer is hardened into a membranous case.

The size of the ova varies according to the species. Those of the small species measure $\frac{1}{10}'''$, and of the larger $\frac{1}{3}'''$. In other respects they are alike, perfectly spherical, and almost perfectly pellucid, with a slightly yellowish tinge, and furnished with an extremely delicate vitelline membrane.

In the centre of the yelk lies the resistant, yellowish germinal vesicle (nucleus), having a diameter about $\frac{1}{20}$th of that of the vitellus. No germinal spots (nucleoli) were noticed. Before segmentation has taken place, the vitellus appears to be composed of a perfectly homogeneous substance containing minute molecules, which are more closely crowded towards the centre than in the peripheral portion. The segmentation of the yelk, as well as the entire process of development, is quickly ended, occupying the space of seven to nine days. The process of development was the same in the ova of both the species observed.

Segmentation commences with the appearance of a groove following the equatorial line of the *vitellus*, but *beneath the vitel-*

line membrane, which divides the yelk into two equal hemispheres. This groove or depression, over which the vitelline membrane is stretched like a bridge, penetrates more and more deeply into the vitelline substance, until a complete separation is effected, between the two portions which simply remain in contact. The next division separates each hemisphere into two segments, the yelk now appearing to be composed of four segments of a sphere.

Where the four segments meet in the centre of the vitellus, a minute hollow space may be observed, formed by the rounding off of the contiguous angles of the four segments. This central space is of no small importance in the further stages of the process.

Whilst these changes are going on, the molecules above described as surrounding the germinal vesicle, and which are subsequently aggregated around the nucleus of each segment derived from the division of the original vesicle, assume a peculiar disposition. They become more densely packed around the nucleus, from which they extend in radiating lines towards the periphery.

Each of the four vitelline segments is now again subdivided into two equal portions in a direction perpendicular to the middle of its longitudinal axis, so that the whole yelk is constituted of eight equal segments. By a continuance of a similar divisional process the number of pyramidal segments goes on increasing, each pyramid having the apex directed towards the centre of the vitellus. An arrangement owing to which the segmentation of the ovum of *Sagitta* appears under a very remarkable type. Even in these latter periods of the process of segmentation, the segments never assume a spherical form as in the Mollusca and Annelids, as well as in the Vertebrata, nor constitute the aggregate masses so well known in their mulberry-like form. On the contrary, in the present case, owing to the circumstance that certain conditions, in other instances occurring only in the earliest stages of segmentation appear to remain persistent, it happens that a single segmentation-cell extends from the centre of the vitellus to the surface, and at the same time, whilst multiplying, the contiguous segments are closely in contact by their corresponding surfaces, in consequence of which they become mutually flattened. Pyramidal segments of this kind do not, so far as Gegenbaur is aware, occur in any other case. The summit of each of these four- five- or six-sided pyramids is truncated, and contributes to the formation of the boundaries of the vacant central space in the vitellus above described. The basis of the pyramid does not

correspond in its curvature with a superficial area of the same size on the surface of the yelk, but forms the segment of a far smaller sphere, so that on a superficial view of the ovum, the mulberry-like stage of segmentation appears to be simulated.

On the second day the whole vitellus is subdivided into numerous pyramids which are in close contact, and form the boundary of a central cavity which has now attained a considerable size.

Before describing the subsequent formation of the embryo, Gegenbaur refers to some particulars, only briefly noticed before, respecting the formation of the products of the segmentation and their true nature, as well as to the relations of the primordial germinal vesicle to the nuclei of the latter.

The fact of the segmentation taking place *beneath* the vitelline membrane, which does not become involved in the process of development, may at first sight, he says, perhaps, excite astonishment—a proceeding of this kind appearing to be opposed to our theory of the process of segmentation as well as to our notions respecting the multiplication of cells in general. It might therefore be supposed that I have regarded some accessory structure as the vitelline membrane, whilst the true vitelline membrane either participates in the segmentary process, or, as many observers have stated, disappears at the commencement of the process. In the present case, however, Gegenbaur says, it is self-evident that he does not, under the term vitelline membrane, intend any egg-case (Eihülle), but only that membrane which is formed originally with the yelk, and surrounds it while still in the ovary; and which, in that situation, already exists at a time when the interspace between it and the germinal vesicle scarcely exceeds the diameter of the latter. This condition of the vitelline membrane recalls the observations of De Quatrefages in *Hermella*, and of O. Schmidt in *Amphicora*, in which cases segmentation also takes place beneath the vitelline membrane.

The question whether the products of segmentation in the ovum of *Sagitta*, after the primitive vitelline membrane has become detached from them, be still provided with a membrane, and consequently represent true cells or not, cannot be answered until what is a "cell-membrane" has been defined; and, in Gegenbaur's opinion, this can be comprehensively done by our regarding as a membrane the outermost thickened layer of a cell, whatever thickness it may possess, or in whatever physico-chemical relation it may stand towards the cell-contents.

Regarded in this light a membrane may be found to exist around the products of segmentation in the ovum of *Sagitta*, which membrane in the earliest stages of the development, it must be confessed, differs but little from the interior vitelline substance, and which (physically, at any rate) bears the same relation to the vitelline membrane that the primordial utricle in a plant-cell does to the cellulose membrane.

Each segmentation-cell presents an oval nucleus, which at first is situated in the thicker or outer portion of the cell, and consequently near the surface of the ovum. What becomes of it in the process of division has, in the most important particular, escaped Gegenbaur's notice; though it is to be remarked that a stage was often noticed at which many of the nuclei, much elongated, exhibited constrictions; so that, although a division of the nucleus was not seen, still such a division might be concluded to take place; to which may be added the circumstance that in no case is the cell without a nucleus. Consequently there is nothing to support the notion of a disappearance of the nucleus before segmentation, and a new formation of nuclei after that process has been gone through. That this stage of nuclear division has escaped observation, may perhaps be explained by the rapidity with which it takes place. The same observation holds good of the germinal vesicle, the nucleus of the ovum, regarded as a cell from which all the nuclei of all the tubsequent cells arise in the same way that the latter have shemselves arisen from the ovum-cell. In the earliest stages of segmentation the nature of the nucleus was shown in a more precise manner, inasmuch as at that time, and before complete division of the yelk, two nuclei were seen to exist.

A peculiarity of the vitellus in the ovum of *Sagitta* was noticed at a later stage of segmentation. When more highly magnified, the contents of each cell were seen to be composed of spherical bodies somewhat flattened by mutual pressure, and which, at the situation of the nucleus retreating from it, left a cavity. From the nuclear cavity thus formed, radiating prolongations stretched out among the neighbouring vitelline granules.

The first indication of the development of the embryo is shown in a division of the pyramidal vitelline cells, each of which is subdivided in the middle of its longitudinal diameter, so that the central cavity of the vitellus becomes enclosed by an internal layer composed of smaller cells, which again is surrounded by a layer of larger cells, of which the surface of the vitellus is also constituted. The longitudinal axis of each of the outer cells coincides with

that of a cell of the inner layers, and those cells whose axes thus coincide, had constituted, in the immediately precedent stage, a single cell. The two layers are of pretty nearly the same thickness, and in each may be seen a long, oval, central nucleus.

But whilst this division is going on, the central cavity of the *vitellus* enlarges, the cells by which it is bounded gradually becoming more and more remote from the central point; but at the same time its figure is so irregular, that it would hardly be supposed that it could be the rudiments of an important part. But its true nature is soon made manifest from an opening which, gradually becoming more and more evident, places the hitherto closed cavity in communication with the exterior. In this way arises a short canal perforating the two layers of cells, so that the original central cavity might now be regarded as the cæcal termination of an invagination or depression commencing from the exterior, unless one had not been satisfied, from previous observation, that its existence dated from a far earlier period, as early even as the first stage of segmentation.

The essential nature of the process by which the canal is formed is, for the most part, unknown; it is an act closely connected with the innermost vital phenomena, not only of the cells in the immediate region concerned, but which must also result from certain changes equally affecting *all* the cells of which the embryo is composed.

Observation has shown Gegenbaur that no mere absorption of the cells, or, at any rate, that no complete disappearance of existing morphological elements takes place, but that the opening of the central cavity is the immediate result of a separation from one another of certain parts of cells (Zellparthien).

Were it true that a solution of the cells took place, the products of such a process would be visible, and were the proceeding one of simple absorption, in some way set up by the contiguous cells, the boundary or outline of the canal thus produced would have an appearrnce different from that which it actually presents. The cells forming the boundary of the canal are disposed somewhat differently to the rest; simultaneously with the formation of the canal, they have the direction of their longitudinal axis changed in such a way that this axis in the centre of the embryo no longer coincides with that of the other cells which remain unchanged, but appears rather to be directed towards the canal itself. At the same time these cells, both of the internal and of the external layer, have become somewhat shortened.

Viewed from the surface, the external opening of the canal —the future mouth, since the whole cavity becomes the intestinal canal—appears in the ova of *Sagitta bipunctata*, as a round, funnel-shaped depression, whilst in the ova of the smaller species it appears to be more elongated transversely.

The whole history of comparative development offers nothing analogous to this surprising mode of formation of the rudimentary intestine out of a central cavity which makes its appearance in the earliest stages of segmentation of the vitellus; and in this respect, again, *Sagitta* appears to constitute a paradoxical form.

When this canal and the central cavity into which it leads, and which increases in size and becomes irregular in form, have been fully developed, the embryo still completely fills the vitelline membrane, by which it is closely invested on all sides, excepting at the spot where the mouth is situated, and where the surface of the body presents a shallow depression.

The two layers of cells, of which alone the body of the embryo is, up to this time, constituted, are now broken up by a further transverse division of the individual cells, so that more rounded embryo cells soon become visible.

In consequence of an increase in the length of the hitherto spherical embryo, the body now necessarily becomes curved; a change which indicates a new and not less characteristic stage. There now takes place a farther differentiation of the layers of cells which were apparent at a former period. Of the cells produced from the single internal layer a stratum is formed whose clear and minute elements immediately surround the intestinal canal, and are clearly distinguishable on the outer aspect from the peripheral layer of cells formed from the simple outer layer. These layers, therefore, composed of numerous superimposed cells, correspond each with one of the primitive strata, which, we have seen, were derived from a transverse division of the simple pyramidal cells.

The central stratum Gegenbaur regards as the rudiment of the intestinal wall, and in the peripheral he recognises the integument of the body.

The anterior and posterior ends of the body approach each other, so that the mouth comes to lie within the point of incurvation. The convex surface of the embryo, therefore, corresponds to the dorsal aspect. Of the further changes in the embryo, nothing precise seems to have been observed. On the ninth or tenth day the animal is completely formed, and begins to manifest its maturity by struggling move-

ments, in consequence of which the enveloping membrane is ruptured.

The development of the greater part of the internal organs, except the intestine, appears to take place after the escape of the embryo from the egg. No trace of the nervous system is at that time apparent, and but one pair of lateral fins exists.

The following summary contains the main points of Gegenbaur's observations.

1. The products of segmentation of the vitellus are elongated pyramidal cell-forms, which retain this character even after the appearance of the rudiment of the embryo.

2. The formation of the rudiment of the intestinal canal accompanies the segmentation of the vitellus.

3. The intestinal canal appears at first as a central vitelline cavity, its opening externally being a secondary process.

4. The development takes place *without any metamorphosis*, and even without the appearance of cilia on the surface of the embryo.

After a short discussion of the views of various authors respecting the systematic position of *Sagitta*, and a review of the principal points, chiefly embryological, connected with this still doubtful question, Gegenbaur concludes with observing that the "genus *Sagitta* must be regarded as the representative of a special subdivision between the Nematoda and Annelida, and which might be designated the "Pfeilwürmer" or "Arrow-worms."

The paper is accompanied with figures illustrating the process of development.

On the Development *of the* Transversely Striated Muscular Fibre, *in* Man, *from* Simple Cells. By Professor A. Kölliker.

(Siebold and Kölliker's 'Zeitsch. f. w. Zool.,' vol. ix, p. 129.)

The extensive prevalence of unicellular muscular fibres or of contractile fibre cells in the Invertebrata having been demonstratively shown, I was induced to inquire whether the mode of formation first noticed by Lebert, and afterwards by Remak, in the transversely striated muscular fibre of the