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STUDIES IN AUSTRALIAN ATHECATE HYDROIDS.

No. IV. Development of the Gonophores and Formation of the Egg in *Myriothela harrisoni*, Briggs.*

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(Figures 1-3.)

INTRODUCTION.

The following account of the development of the gonophores and the formation of the egg in *Myriothela harrisoni* is based on a single female and several male specimens collected on the undersides of rocks below low-water mark at Bulli, forty miles south of Sydney. Although *M. harrisoni* is a diœcious form, it bears a distinct resemblance in its gross morphology to *M. cocksi*, which occurs under similar conditions on the coasts of Great Britain and western Europe. Both species have a chitinous investment by perisarc covering the hydrorhiza and forming a firm basis of attachment to the surface of the sub-stratum. This likeness is further emphasized by a study of the development of the gonophores and the formation of the egg, which follows through a series of stages very similar in their general details to those I have already described for *M. australis*.

Unfortunately, corresponding stages in *M. austro-georgiæ* are not available for comparison, since Jäderholm figures only a fairly advanced male and female gonophore. In his drawings on plate iii, figure 1 shows a female gonophore before the fusion of the plasmodial areas to form the definitive ovum, while figure 2 depicts a male gonophore in which the sub-umbrellar cavity appears to be filled with densely-packed secondary spermatocytes. Although Thomson's figures[1] illustrating his "Note on the Gonostyles of two Antarctic Siphonophora" refer to *M. austro-georgiæ*, they are too diagrammatic and lacking in detail to be of any value for comparative work.

The paper concludes with a brief discussion on the geographical distribution of the members of the genus *Myriothela*. Previous to the discovery of *M. australis* and *M. harrisoni*, the representatives of the genus had hitherto been recorded only from the circumpolar seas of the Northern and Southern Hemispheres, but the range of *Myriothela* must now be extended to include the warm coastal waters of eastern Australia in the neighbourhood of Lat. 34° South.

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* For Numbers I, II and III see RECORDS OF THE AUSTRALIAN MUSEUM, Vol. xvi, No. 7, 1928, p. 305; Vol. xvii, No. 5, 1929, p. 244; Vol. xviii, No. 1, 1930, p. 5.

[1] Thomson.—Proc. Roy. Phys. Soc. Edinb., xvi, 1904-1906, pp. 19-22.

Development of the Gonophores in Myriothela harrisoni.

The fully-developed blastostyle consists of an irregularly lobed base with a narrow, cylindrical, distal portion continued into a single terminal tentacle, generally resembling those of the tentacle-bearing region of the hydranth, but flatter distally and of larger size. The blastostyle has no mouth, but contains an extensive gastric cavity communicating with the general body-cavity of the hydranth.

In *M. harrisoni* all the gonophores on a blastostyle are of the same sex, and throughout any one individual the sex of the gonophores is uniform. The mature gonophores are sub-spherical in shape, somewhat flattened distally, and are either sessile or very shortly pedunculate. They exhibit no definite arrangement on the blastostyle, except that the mature ones are borne distally and appear terminal in position, having grown so large as to push the single tentacle to one side.

The lobes at the base of the blastostyle represent developing gonophores.

In the male, the blastostyle bears two or three ripe gonophores, up to 450 μ in diameter, and three or four in process of development. The only female individual was cut into sections before the diœcious habit was discovered and entire blastostyles are not available for comparison. A reconstruction from the sections shows a mature female gonophore occupying a terminal position at the distal extremity of the blastostyle. On the proximal side of this is a smaller gonophore whose sub-umbrellar cavity is filled with closely-packed oogonia and a few primary oocytes. A second blastostyle carries two young gonophores in which the oogonia are clearly discernible. The ripe female gonophore has a diameter almost twice that of the male. Both male and female gonophores have an apical opening representing a velar aperture similar in appearance and structure to the opening which I have already described in the gonophores of *M. australis*.

Development of the Male Gonophores.

The first stage in the formation of the male gonophore is due directly to the evagination of the endoderm cells of the blastostyle. This penetrates deeply into the ectoderm, and the interstitial cell at the apex of the evagination divides to form a rounded mass of cells which becomes cut off from the rest of the endoderm by the formation of a thin though definite, non-cellular layer. The ectoderm surrounding this mass of cells remains stratified and heavily charged with nematocysts except over the outer surface of the evagination where the ectoderm is reduced to a single layer of epithelial cells (Fig. 1). The pressure exerted by this penetration causes the ectoderm to bulge outwards so that even at this early stage in the development of the gonophore the ectoderm appears slightly raised above the general surface of the blastostyle.

The *Glockenkern*, thus established, increases in size and a split occurs in the cell-mass where a small eccentrically-placed cavity is formed. As this enlarges, the cells in the roof of the cavity become arranged in a single layer, while those on the floor form a cushion in which the cells are arranged in several layers. This cavity or chamber is at first spherical in shape and constitutes the *Anlage* of the sub-umbrellar cavity. Very soon, however, it becomes flattened and appears semicircular in section with its floor composed of a mass of cells which quickly become differentiated from those occupying the two lateral wings.

At this stage, owing to the rapid growth of the gonophore, the ectoderm is forced outwards and forms a distinct projection on the surface of the blastostyle.

The gonophore, thus coming to project completely on the exterior, is covered by ectoderm which is reduced to a single layer of columnar cells over its summit and sides, but which remains as a stratified layer rich in nematocysts around its base.

The gastric endoderm now begins to proliferate rapidly, forming numerous villi that project into the gastric cavity and reduce considerably the extent of its lumen. As this cavity continues to enlarge the endoderm cells become heavily

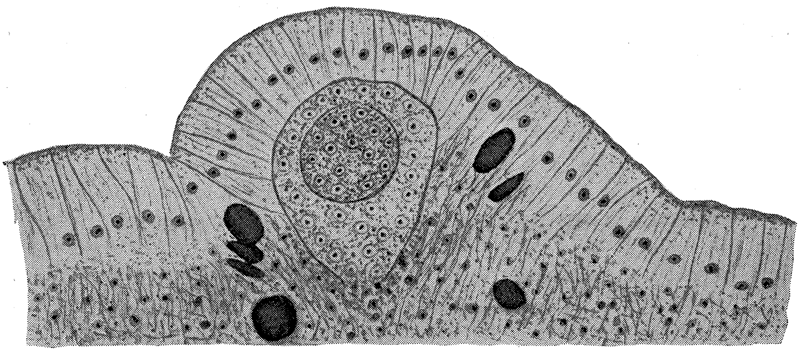

Figure 1.
Myriothela harrisoni, Briggs. Very young male gonophore.

charged with nutritive spheres which form a very important nutritive material for the development of the gonophore. The outgrowth of the gastric endoderm gives rise to the manubrium. This forces back the cells on the floor of the sub-umbrellar cavity, thus reducing the cavity to a narrow cleft of crescentic form with its horns prolonged laterally over the sides of the manubrium.

Owing to the internal pressure produced by the outgrowth of the spadix, the endoderm-lamellæ occupying the roof of the sub-umbrellar cavity commence to separate in the axis of the gonophore. At this point the endoderm-lamellæ eventually become widely separated leaving a distinct gap across which stretches a very narrow band of mesoglœa. In *M. cocksi*, Benoit has described a similar separation of the endoderm-lamellæ, but the gap forms a funnel which becomes filled with a mass of non-cellular substance. In *M. harrisoni*, at this stage, the gap remains open for a time while the endoderm cells surrounding it proliferate and arrange themselves in two layers. It is at this point in *M. cocksi* that the cells of the endoderm-lamellæ become excavated to form the circular canal, but in *M. harrisoni*, as well as in *M. australis*, the cells remain solid, forming a compact mass, and the circular canal fails to develop.

At the same time the cells occupying the two lateral wings of the sub-umbrellar cavity form an epithelium which becomes closely applied to the endoderm-lamellæ except in the axis of the gonophore. Here the cells of the sub-umbrellar epithelium enter the gap between the endoderm-lamellæ and come into close contact with the columnar cells of the ectoderm. Throughout the whole of its extent the sub-umbrellar epithelium is separated from the other cell layers by a very thin layer of supporting lamella.

The outgrowth of the manubrium also affects the cells on the floor of the sub-umbrellar cavity, causing them to form a crescent-shaped mass over the surface of the spadix. From the cells of this layer are derived the male reproductive elements. An examination of the gonophore at this stage discloses that it has assumed a sub-spherical form, 180 μ in diameter, and developed a very short peduncle by which it retains its connection with the blastostyle. At the distal pole of the gonophore the ectoderm has become raised into a small circular patch composed of deep columnar cells lying directly above the gap between the endoderm-lamellæ. The ectoderm at the flattened distal extremity of the gonophore is armed with scattered nematocysts of the cylindrical variety corresponding to Benoit's "nématocystes fonctionnels," which in *M. cocksi* disappear before this stage in the development is reached.

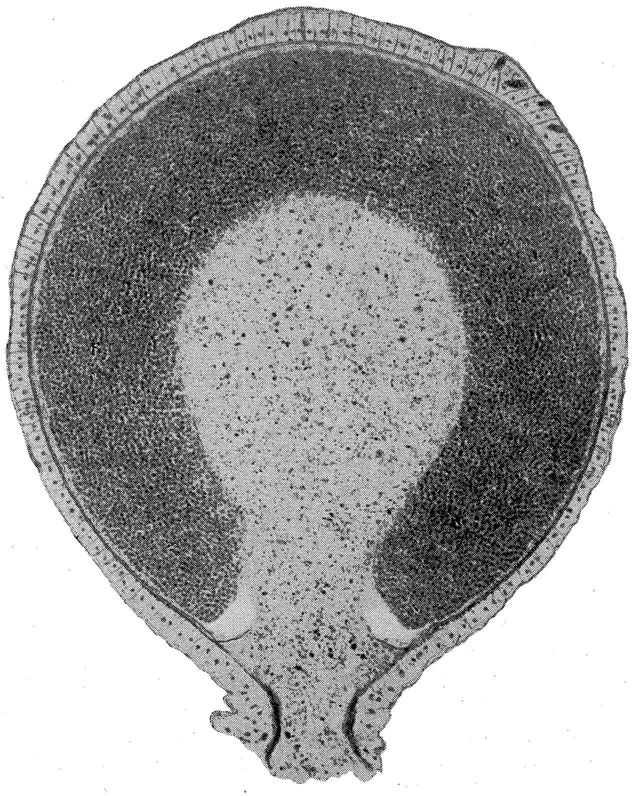

Figure 2.
Myriothela harrisoni, Briggs. Male gonophore with secondary spermatocytes completely filling the sub-umbrellar cavity.

The first stage in spermatogenesis begins in the mass of cells covering the spadix and is accompanied by a rapid multiplication of their nuclei. Then the cytoplasm breaks up and comes to surround each nucleus, forming the spermatogonia in the central part of the mass. These cells are not very unlike those of the gastric endoderm except that their nuclei are slightly larger, and the nucleoplasm appears lighter in colour and less granular. In these respects they agree with the condition observed by Benoit among the spermatogonia in the central part of the germinal mass, although in *M. cocksi* these cells contained large quantities of nutritive material.

The layer of spermatogonia increases in extent, and by rapid division the spermatogonia give rise to the primary spermatocytes. From these are derived the secondary spermatocytes which completely fill the sub-umbrellar cavity (Fig. 2). They form an extremely compact mass of very small cells measuring only 2 μ in diameter. When viewed in vertical section this mass of secondary spermatocytes has a characteristic horse-shoe shaped form which fits closely over the surface of the spadix. The gonophore (Fig. 2) has now acquired a diameter of 375 μ and is completely covered by ectoderm in which the cells are reduced to a single layer throughout its whole extent. At the distal pole, the raised patch of ectoderm lying directly above the gap between the endoderm-lamellæ becomes invaginated at the centre to form a small pit-like depression which breaks through into the sub-umbrellar cavity. The velar aperture thus established is lined by a deep columnar epithelium whose cells are derived from the ectoderm. In Part I, I have already figured on Plate III, fig. 5, a vertical section through the distal pole of the male gonophore. This shows clearly the condition of the apical opening representing the velar aperture as it occurs at this stage in the development of the gonophore.

The mature male gonophore reaches a diameter of 450 μ and is occupied by an extremely large number of spermatozoa. These completely fill the sub-umbrellar cavity which has increased in size owing to the partial expulsion of the spadix into the gastric cavity of the blastostyle. The spermatozoa have small, intensely chromatic, spherical heads and long lightly-staining tails. They are arranged in bundles with the tails in parallel rows turned in different directions.

In the definitive gonophore, the sub-umbrellar epithelium increases considerably in thickness and the musculo-epithelial cells are produced into short muscle processes which lie close against the inner surface of the supporting lamella. If my interpretation of the function of the velar aperture be the correct one, then these muscle processes by their contraction would aid materially in the discharge of the spermatozoa through this opening at the distal pole of the gonophore.

In the absence of such an opening in the gonophores of *M. cocksi*, the spermatozoa leave the sub-umbrellar cavity of the gonophore and passing down the gastric cavity in the peduncle enter the gastric cavity in the peduncle of the female gonophore and so reach the mature ovum which, at this stage, has not yet been expelled. This passage of the spermatozoa is made possible by the fact that in *M. cocksi* the male and female gonophores are borne on the same blastostyle.

Although my most advanced stages among the male gonophores of *M. harrisoni* are undoubtedly sexually mature, I have never detected spermatozoa in the peduncle of the gonophore or in the gastric cavity of the blastostyle.

Development of the Female Gonophores.

The description of the development of the female gonophores in *M. harrisoni* is based on rather scanty material derived from the only female specimen in the collection. Three stages are represented, the youngest consisting of a small gonophore, 160 μ in diameter, in which the oogonia are clearly discernible. The second stage is slightly more advanced and its sub-umbrellar cavity is filled with closely-packed oogonia and a few primary oocytes. The third stage contains a number of plasmodial areas with well-defined outlines separated from one another by thin non-cellular partitions which extend from the spadix to the epithelium of the sub-umbrellar cavity.

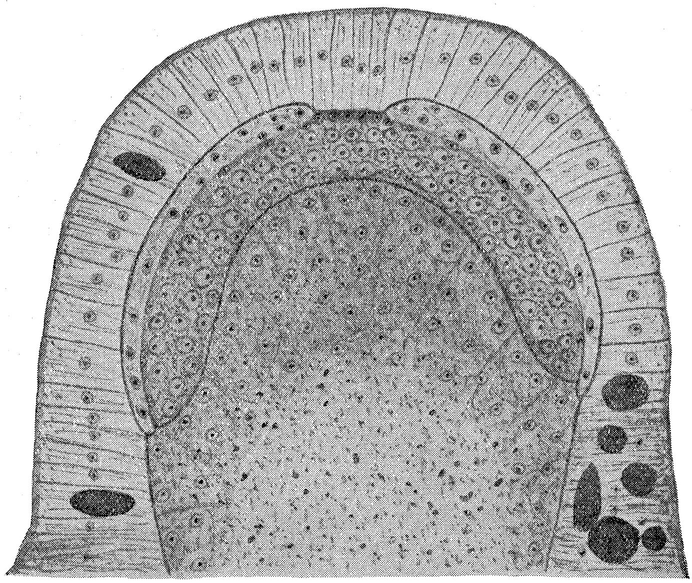

Figure 3.
Myriothela harrisoni, Briggs. Female gonophore, Stage I.

Stage I:

In this stage the gonophore is represented by a sessile, sub-spherical body, 160 μ in diameter, in which the ectoderm is reduced to a single layer of columnar cells (Fig. 3). The oogonia completely fill the entire space between the sub-umbrellar epithelium. When viewed in vertical section, the oogonia are seen to be arranged in a crescent-shaped mass with the horns prolonged for a considerable distance over the lateral regions of the manubrium. The gastric endoderm presents a very characteristic appearance due to the development of the villi which completely fill the gastric cavity. The cells are crowded with nutritive spheres probably of a lipoid nature, forming a very important nutritive substance for the development of the gonophore.

Stage II:

The gonophore has now reached a diameter of 300 μ, and is connected with the blastostyle by an extremely short peduncle. The oogonia fill the sub-umbrellar cavity and retain the appearance of a crescent-shaped mass when viewed in vertical section. At the distal extremity of the spadix, some of the oogonia have increased in size to give rise to the primary oocytes which press closely against the other cells and assume a polygonal form. Each primary oocyte consists of a large cell, 24 μ in diameter, with a large eccentrically-placed nucleus of 9 μ

diameter. The nucleolus is 3 μ in diameter, and is formed of dense chromatin. Around the nucleolus is a clear zone beyond which is a fine network of threads carrying numerous chromatin granules.

Stage III:

In this stage there are present in the gonophore some six or seven large plasmodial areas completely separated from one another by thin, non-cellular partitions which extend from the spadix to the epithelium of the sub-umbrellar cavity. By means of these partitions, the sub-umbrellar cavity is divided into a number of chambers each enclosing a plasmodial mass with its very characteristic nucleus which is discernible as an oval, lightly-staining body enclosed by a slightly-wrinkled nuclear membrane. The nucleus has a diameter of 39 μ and occupies an eccentric position just beneath the outer surface of the plasmodial area.

Scattered through the cytoplasm are the Pseudozellen representing the slightly degenerate nuclei of the primary oocytes which were the last to fuse with the plasmodial areas. The cytoplasm is charged with yolk which is of two kinds. There are small, simple yolk spheres and compound yolk spheres which form the largest elements in the plasmodial areas.

Geographical Distribution of Myriothela.

The discovery of two new species of *Myriothela* in the Southern Hemisphere is extremely interesting since the range of the genus must now be extended from the Antarctic circumpolar seas to include the more temperate waters of the coast of New South Wales. Both *M. australis* and *M. harrisoni* occur in the neighbourhood of Lat. 34° South, and their presence in this part of the Pacific Ocean is by no means a fortuitous one since the two species appear to be well-established and exhibit a number of outstanding characters which differentiate them from the other representatives of the genus.

In his discussion on the geographical distribution of the northern species, *M. phrygia*, Broch remarks that "the genus *Myriothela* is recorded from the northern seas and from the Antarctic Ocean. The spread and rare occurrence of the individuals prevents us from deciding whether the genus is in fact bipolar, as the finds hitherto recorded seem to indicate." Although *M. phrygia* is essentially a deep-sea form, occurring mainly in the icy waters of the high Arctic regions, nevertheless there is a record by the "Michael Sars" Expedition that this species was found in the warm Atlantic waters to the south of the Wyville Thomson Ridge which separates the marine faunas in the deep water on either side of this natural barrier. Broch suggests that there is a possibility that the animal had been carried there by the Arctic currents from northern regions. In that event the currents conveyed the animal at an early period of life to the new locality where it was able to subsist and develop further.

The distribution of *M. cocksi* has been confused to a certain extent with that of *M. phrygia*, but the former species is known definitely to occur as a shallow-water form on the coasts of Great Britain and western Europe.

The propriety of referring all four species described by Bonnevie to the genus *Myriothela* is open to some doubt; for the sake of completeness I include them as representatives of the genus in the Northern Hemisphere.

Jäderholm's *M. austro-georgiæ* has a circumpolar distribution in the Southern Hemisphere, occurring at South Georgia, South Orkneys, Booth-Wandel Island, and Kerguelen Island. Hickson and Gravely have recorded the occurrence of *Myriothela* (?) from McMurdo Bay, Antarctica, but the brief description and figure are not sufficient to establish the generic status of their specimen.

The Australian species of *Myriothela* were discovered as a result of shore collecting. The specimens of *M. australis* occurred on the lobes of the thallus of a seaweed at Maroubra Bay, near Sydney, New South Wales, while *M. harrisoni* was gathered on the undersides of rocks below low-water mark at Bulli, forty miles south of Sydney.

The discontinuous distribution of the genus *Myriothela* in the Southern Hemisphere is more apparent than real, since a hitherto undescribed species of *Myriothela* collected by the Australasian Antarctic Expedition at Macquarie Island in Lat. 55° South represents a link in the chain of distribution which begins in Antarctic and Sub-Antarctic seas and extends to the warm coastal waters of eastern Australia.

The occurrence of *Myriothela* in Lat. 34° South, suggests at once the possibility that the specimens are stragglers which have reached the shores of Australia in the currents from the south in much the same manner as *M. phrygia* has been carried into the warm waters of the Atlantic. The Australian species, however, possess such well-marked characters and appear to be so well-established that they support rather the theory of a universal cold sea in earlier geologic times with the subsequent elimination of certain types from the intervening areas as they became warm.

SUMMARY.

1. The development of the male and female gonophores in *M. harrisoni*, Briggs, is described and figured.
2. All the gonophores on a blastostyle are of the same sex, and throughout any one individual the sex of the gonophores is uniform.
3. The mature gonophores are sub-spherical in form, somewhat flattened distally, and are either sessile or very shortly pedunculate.
4. The male gonophore appears as an endodermal evagination which penetrates deeply into the ectoderm. The interstitial cell at the apex of the evagination divides to form a rounded mass of cells which becomes cut off from the rest of the endoderm by a thin, non-cellular layer.
5. A split occurs in the cell-mass where a small eccentrically-placed cavity is formed. This constitutes the *Anlage* of the sub-umbrellar cavity.
6. Spermatogenesis begins in the mass of cells covering the spadix, and spermatogonia, primary spermatocytes, secondary spermatocytes and spermatozoa can be recognized.
7. In the development of the female gonophore, oogonia and primary oocytes are formed.
8. The primary oocytes fuse into cytoplasmic masses which later combine into plasmodial areas each with a definitive nucleus.
9. The plasmodial areas have well-defined outlines separated from one another by thin non-cellular partitions, which extend from the spadix to the sub-umbrellar epithelium.
10. The Pseudozellen represent the degenerate nuclei of the primary oocytes which were the last to fuse with the plasmodial areas.

11. There are two main types of yolk in the egg: (*a*) small, simple yolk spheres, and (*b*) compound yolk spheres which form the largest elements in the egg.
12. The geographical distribution of *Myriothela* supports the theory of a universal cold sea in earlier geologic times, with the subsequent elimination of certain types from the intervening areas as they became warm.

Conclusions.

1. The Australian species of *Myriothela*, *M. australis* and *M. harrisoni* are diœcious but the development of the gonophores and the formation of the egg follow through a series of stages very similar in their general details to those described for the northern form, *Myriothela cocksi* (Vigurs).

2. The gonophore arises from the blastostyle and its first appearance always begins as an evagination of the endoderm. When the *Glockenkern* is established a split occurs in the cell-mass where a small cavity is formed. This enlarges into a chamber which constitutes the *Anlage* of the sub-umbrellar cavity. The outgrowth of the gastric endoderm gives rise to the manubrium. This forces back the cells on the floor of the sub-umbrellar cavity and the endoderm-lamellæ separate in the axis of the gonophore. From the cells on the floor of the sub-umbrellar cavity are derived the reproductive elements. The definitive gonophore always bears an opening, the velar aperture, at its distal pole.

3. The first stage in spermatogenesis begins in the mass of cells covering the spadix and is accompanied by the rapid multiplication of their nuclei. Then the cytoplasm breaks up and comes to surround each nucleus, forming the spermatogonia in the central part of the mass. By division, the spermatogonia give rise to the primary spermatocytes. From these are derived the secondary spermatocytes which in turn form the spermatozoa with small, intensely chromatic, spherical heads and long, lightly-staining tails.

4. In the female gonophore the cells of the germinal mass are arranged in several layers; those in the outer layer form the external epithelium of the future spadix, while the others represent the mother-cells of the future reproductive elements and form the oogonia. These multiply and increase in size to give rise to the primary oocytes which press closely against one another and assume a polygonal form.

5. The first appearance of egg-formation occurs among the primary oocytes situated in the lower layers of the cell-mass. Here two primary oocytes come into close contact and their cytoplasm fuses to form a small cytoplasmic mass. The sub-umbrellar cavity gradually fills with these cytoplasmic masses which increase in size by accretion of either new primary oocytes, or of previously-formed cytoplasmic masses. The final absorption of all the primary oocytes into these cytoplasmic masses is followed by the fusion of the masses themselves, forming a number of large plasmodial areas completely separated by non-cellular partitions. The definitive egg is produced by the withdrawal of the partitions and the subsequent fusion of the plasmodial areas.

6. The Pseudozellen represent the slightly degenerate nuclei of the primary oocytes which were the last to fuse with the cytoplasmic masses. The cytoplasm of the mature ovum becomes charged with yolk which constitutes the deutoplasm of the egg. There are two main types of yolk: (*a*) small, simple yolk spheres which vary greatly in size, and (*b*) compound yolk spheres which form the largest elements in the egg. There is never any observable connection between the Pseudozellen and the formation of the yolk spheres.