MORPHOLOGY AND HISTOLOGY OF THE REPRODUCTIVE SYSTEM OF SAGITTA PLANCTONIS STEINHAUS, 1896 (CHAETOGNATHA)

by

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ABSTRACT

The morphology and histology of the reproductive organs of Sagitta planctonis forma planctonis and of S. planctonis forma zetesios are described. No difference in number of oocytes was observed. The existence of a temporary oviduct is questionable. It may be possible that the so-called accessory fertilization cells are not actually participating in fertilization, but they may have a resorptive or secretory function.

I. INTRODUCTION

Taxonomic relations and differences between the two taxa Sagitta planctonis forma planctonis Steinhaus, 1896 and S. planctonis forma zetesios Fowler, 1905 were evaluated recently (Pierrot-Bults, 1975), but since microanatomical research on the reproductive organs in this species could not be found in literature, a study was carried out to describe the reproductive organs in these taxa. Differences in the general morphology of the sexual organs of the two formae of Sagitta planctonis have been described. Alvarino (1969), for example, found a difference between planctonis and zetesios in the number of rows of ova, viz. three rows in planctonis and four to five rows in zetesios.

The reproductive organs in other chaetognaths have been described, amongst others in Sagitta bipunctata Quoy & Gaimard, 1827 (cf. Hertwig, 1880; Grassi, 1883; Stevens, 1903, 1905, 1910; Ghirardelli, 1968), S. setosa Müller, 1847 (recorded as S. bipunctata; cf. Burfield, 1927), S. elegans Verrill, 1873 (cf. Stevens, 1905, 1910), Spadella cephaloptera Busch, 1851 (cf. Ghirardelli, 1953a), Petrosagitta draco (Krohn, 1853) (cf. Ghirardelli, 1953b), Sagitta lyra Krohn, 1853 and S. hexaperta d'Orbigny, 1843 (cf. Ghirardelli, 1961, 1968).

Like all other chaetognaths, S. planctonis forma planctonis and S. planctonis forma zetesios are protandric hermaphrodites. In the present paper the female reproductive organs are described first (§ IV), the male reproductive organs are described in a later section (§ V).

II. MATERIAL AND METHODS

For the present study 12 specimens were selected from the collections of:

Zoological Museum Copenhagen (Dana Expedition):
st.a. 3978VII 30°S 13°E 13-2-1930 5 specimens.
United States National Museum (Ocean Acre Program1):)
sta. 12-7C 32°N 64°W 28-8-1971 3 specimens;
sta. 12-27C 32°N 64°W 3-9-1971 1 specimen;
sta. 14-10C 32°N 64°W 7-6-1972 1 specimen.
Zoological Museum Amsterdam (Tridens cruise):
sta. 7 39°N 21°W 1-6-1972 2 specimens.

All specimens were fixated and preserved in formalin 4%, except for the specimens from the Tridens cruise, which were treated with Bouin. The specimens were embedded in paraffin and cross-sectional 5 μm thick. Staining was carried out after Crossmon (cf. Romeis, 1948) for 11 specimens and with haematoxylin-eosin for one of the Tridens cruise specimens. The staining methods were adapted after Romeis (1948).

III. ABBREVIATIONS USED IN THE FIGURES

<table>
<thead>
<tr>
<th>Abbreviation</th>
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<tr>
<td>bm</td>
<td>basement membrane</td>
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<td>ep</td>
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<td>ge</td>
<td>germinal epithelium</td>
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<td>gl</td>
<td>glandular epithelium</td>
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<td>go</td>
<td>genital opening</td>
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<td>genital papilla</td>
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<td>in</td>
<td>intestine</td>
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<td>mu</td>
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<td>oc</td>
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<td>oviduct</td>
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<td>ov</td>
<td>ovary</td>
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<td>sc</td>
<td>suspension cell</td>
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<td>sperm</td>
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<td>sv</td>
<td>seminal vesicle</td>
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<td>sy</td>
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<td>te</td>
<td>testis</td>
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1) supported by funds from the U.S. Navy.
IV. THE FEMALE REPRODUCTIVE ORGAN

Hertwig (1880) and Grassi (1883) were the first authors to give a detailed description of the ovaries in chaetognaths. According to these authors the two cylindrical ovaries run laterally, parallel with the intestine. The dimensions of the ovaries vary with maturity and with the species. The part of the ovary facing the intestine contains the ova. The part of the ovary facing the body wall is according to Hertwig (1880) an oviduct, also serving as a seminal receptaculum. Grassi (1883) calls this duct the ovispermaduct. The wall of the oviduct forms in cross section a crescent in Sagitta bipunctata and S. setosa (Hertwig, 1880, pl. XII fig. 13; Grassi, 1883, pl. XI fig. 7; Stevens, 1903, pl. XX figs. 1-2; Stevens, 1905, pl. XVI fig. 1; Stevens, 1910, fig. 22; Burfield, 1927, pl. VI fig. 40; Ghirardelli, 1968, fig. 9B).

According to Stevens (1903, 1905, 1910) the duct is not an ovispermaduct but merely a sperm duct serving as a receptaculum seminis, blind at its anterior end with a posterior opening. The wall of the sperm duct has indistinct cell walls and large deep-staining nuclei. An epithelial cell layer of crescent shape in cross section surrounds this syncytium and forms the wall of the oviduct (figs. 1-2). The oviduct is temporary, only seen in the period of egg delivery. The eggs are connected to the sperm duct by the suspension cells (called by Stevens “accessory fertilization cells”). Sperm passes through these cells to fertilize the ova and fertilized ova push their way through the epithelial wall of the oviduct. The posterior opening of the oviduct is closed normally. Burfield (1927) and Ghirardelli (1968) supported Stevens’ theory about a temporary oviduct and the role of the “accessory fertilization cells”.

The size of the oviduct is variable, it can be long as in Sagitta bipunctata (cf. Ghirardelli, 1968, fig. 29) or very short as in Spadella cephaloptera (cf. Ghirardelli, 1968, fig. 33). In transverse sections of Sagitta hexaptera (cf. Grassi, 1883, pl. XI fig. 5), of S. setosa (Burfield, 1927, pl. XII fig. 93) and of S. enfleta Grassi, 1883 (Ghirardelli, 1968, fig. 9A) the epithelial wall of the oviduct has not a crescent shape.

Though differences in ovary structure do exist between certain species, no difference could be found between the two infraspecific taxa of Sagitta planctonis. Externally no morphological difference in the ovaries of S. planctonis forma planctonis and S. planctonis forma zetesios was observed. Two specimens from the Dana Expedition are shown in fig. 3. In cross sections differences in ovary structure between the two taxa were not found either (fig. 4). The following general description, applicable for both taxa, is largely based on the freshly preserved specimens from the Triton cruise, yielding better results due to fixation in Bouin.

In cross sections of S. planctonis (fig. 5) no crescent-shaped supporting structure formed by the epithelial wall of the oviduct was observed.
This epithelial wall consists of a columnar or cuboidal epithelium with large nuclei and a thin basement membrane lining the median side of the duct. The outer side is lined with strongly squamous epithelium, which is sometimes hardly discernible. The nuclei of the epithelium cells are large and in Crossmon stain intensive red, showing strands and granules. The cytoplasm looks reticulated by green-staining strands.

The syncytium is lining the inner side of the epithelial wall. In the present species the syncytium is very thin and loose in comparison to that found in S. bipunctata and S. setosa and has a mucoid aspect. Very often it is no longer attached to the epithelial wall, probably due to artefacts. A few nuclei scattered through the syncytium are deeply and homogeneously staining with eosin, without strands and granules, contrary to the nuclei of the epithelial wall. The syncytium does not seem to form a wall, since it is too loose and in some places even lacking. Enclosed by the epithelial wall is the oviduct, also serving as a seminal receptaculum.

The posterior end and opening of the oviduct is lined with a layer of apparently semi-stratified or simple columnar epithelium showing glandular function (fig. 6). The nuclei stain more darkly red and are more granulous than those of the oviduct-wall epithelium, anterior of the opening. Blue staining secretion granulae can be observed. On
the outside of the body wall these glandular cells form the genital papilla (fig. 7).

The secretory product may act to attract the spermatozoa towards the opening of the oviduct and/or to wrap the ova in a gelatinous secretion mass before they are leaving the oviduct. The eggs of *S. hispida* Conant, 1895 (cf. Conant, 1896), *Pterosagitta draco* (cf. Ghirardelli, 1953b) and *Spadella cephaloptera* (cf. Ghirardelli, 1953a) are reported to be surrounded by such a gelatinous layer, but no record in the literature on the eggs of *Sagitta planctonis* could be traced.

The tissue in the genital opening forms a kind of closing plug and does not assume the aspect of a sphincter (fig. 7).

The germinal epithelium is situated medial in the epithelial cell layer of the oviduct. The germinal cells are not separated from the lumen of the oviduct by normal epithelium (fig. 5B).

The smallest oocytes are found closest to the germinal cells, showing very large intensively staining granules in the nucleus, and staining more deeply red both in karyo- and cytoplasm. The larger oocytes are situated more laterad and more

Fig. 5. Cross section through the trunk of *S. planctonis*: A, a young specimen (stage II); B, the ovary enlarged; C, a mature specimen (stage IV); D, an ovary enlarged. For abbreviations see § III.
The development of the ova is not well known. According to Hertwig (1878) and Boveri (1890) the general oogenesis results in one ovum from one oogonium. The oogonium forms a primary oocyte, which has a diploid chromosome number. After a period of growth, when the primary oocyte has reached about the size of the mature ovum, the meiotic division or first maturation division takes place, showing the first polar spindle, forming one big daughter cell, the haploid secondary oocyte. The other daughter cell is the small abortive first polar body. The secondary oocyte divides again forming the ovum and the second daughter cell, the second polar body, which degenerates as well. Boveri (1890) found eggs of *S. bipunctata* showing the first polar spindle and containing a spermatozoan during spawning.

The moment of fertilization is species-specific; in some animals fertilization occurs already before the first meiotic division, in other groups fertilization takes place when the ovum is fullgrown and the second polar body removed (Austin, 1965). In chaetognaths the exact moment of fertilization is not yet known.

The suspension cells in the ovaries were first described by Grassi (1883) as a peduncle formed by a modified germinal cell. Stevens (1903, 1905, 1910) regarded them as "accessory fertilization cells". This author described them as two cells with a fertilization canal for the passage of sperm. In the broad portion of the canal there is a large spindle-shaped body, possibly to attract the sperm. The epithelial cells surrounding the outer suspension cell are reported to show degeneration.

In *S. planctonis* the suspension cells are seen both in immature and mature ovaries. In immature ovaries, without sperm in the oviduct, these cells have nearly the same aspect as the epithelial cells (fig. 8). The nuclei of the epithelial cells stain very darkly and homogeneously red and the nuclei of the suspension cells stain slightly less dark but also homogeneously red.

In more mature ovaries the structure of the suspension cells is very different from the normal epithelial wall cells (fig. 9). Usually the suspension cells form pairs. The upper cell is flat and is embedded in the egg, sometimes hardly showing more than a mere flat nucleus. The other cell is in connection with the lumen of the duct or the syncytium and forms part of the epithelial wall. This cell is mostly larger than the surrounding epithelial cells and often elongated, hence Grassi (1883) named it a peduncle. The nucleus is granulous and has the same general aspect as the nuclei of

Fig. 6. Epithelium in the posterior part of the trunk of *S. planctonis* near the genital opening. For abbreviations see § III.

Fig. 7. Cross section through the posterior part of the trunk of *S. planctonis* showing the genital opening. For abbreviations see § III.

towards the intestine (figs. 5B & D, 7) and show less intensive staining karyo- and cytoplasm and fewer granules in the nuclei. The cytoplasm shows the reticulation characteristic of older oocytes (fig. 9).
the epithelial cells though often more pale. The structure of the cytoplasm is peculiar. Strands of hyaline plasma alternate with non-staining areas which are stated to be vacuoles (Ghirardelli, 1968). The basement membrane is not continuous, neither beneath the epithelial cells, nor beneath the suspension cells. It shows numerous openings, allowing secretion or absorption. Ghirardelli (1968) remarks that the contents of the suspension cells seem to flow into the lumen of the duct, perhaps with the function to attract the sperm.

Fig. 9 shows three oocytes with suspension cells. The smallest oocyte is about 2.5 times larger than the oocyte shown in fig. 8. Oocytes of all size classes may thus be connected to suspension cells. In fig. 9 they all seem to be functional. Ghirardelli (1968) observed the contents flowing out. Often a homogeneously red staining substance in the cell is to be seen, simultaneously with this expulsion, which intergrades with the cell substance. The suspension cells could have the function to absorb substances from the mucoid syncytium. In vertebrates syncytia are described for the uterus (uterine mucous membrane) and by some authors for the testes (Sertolian syncytium) serving as a feeding substance (Maximow & Bloom, 1957).

The theory of Bordas (1920; see Ghirardelli, 1968), according to which the crescent cells have a trophic function for the oocytes, is not supported by Ghirardelli (1968) because transition of nuclei from epithelial wall cells to germinal cells has never been observed.

In old ovaries, when apparently the largest eggs are already produced, the germinal epithelium is not found anymore. The epithelial wall of the oviduct is in some places broken and lost, leaving only the lateral sides of this epithelial wall intact (fig. 10). Eggs could have passed through these
openings. The syncytium is very thin and probably does not act as a wall at all. It is of mucoid nature and could serve as a feeding substance. In very old ovaries with only a few immature oocytes left, the median epithelium of the oviduct seems to degenerate. The cytoplasm vacuolates and the nuclei seem to be pycnotic. Only the lateral parts of the epithelium show normal nuclei.

The theory of Stevens (1903, 1905, 1910) about a temporary oviduct, since then accepted by subsequent authors (Burfield, 1927; Ghirardelli, 1968), seems a little farfetched. When the egg is passing through the epithelial wall it pushes aside the syncytium and the sperm. Seen in cross section, syncytium and sperm are then situated near the lateral body wall because the egg enters the oviduct from the median side. There is neither reason to believe that there is a real difference between oviduct and seminal receptaculum, nor is it impossible for the spermatozoa to reach the eggs when they are in the oviduct. Stevens (1903, 1905, 1910) believed the fertilization to occur by means of the “accessory fertilization cells”. The syncytium seems not to act as a barrier for the spermatozoa at that time. It is not clear why the syncytium should be called a wall, separating sperm and egg, when the egg is passing through the oviduct.

In S. planctonis the presence of a temporary oviduct does not seem very probable. The syncytium is hardly present in mature ovaries and its structure is very loose. In cross sections of old ovaries with the epithelial wall of the oviduct broken down, sperm has penetrated inside the ovary. Apparently the syncytium did not prevent the sperm from moving inside the ovary (fig. 11). The epithelial wall of the oviduct may break in different places along the length of the ovary. The sperm was never seen penetrating further up or down in the ovary, only just beyond the opening in the epithelial wall.

Close to the genital opening, outside the ovaries one observes an area bordered by a layer of small columnar or cuboidal epithelium with very dark-staining homogeneous nuclei and a clear basement membrane. This epithelium lines the dorsal side of the ovary on the outside, the lateral body wall and the median side of the dorsal muscle band (figs. 6 & 12). The surface of this epithelium is not very smooth but it was not possible to ascertain if any cilia were present.

Ghirardelli (1968) observed the ovaries of Spadella to be wrapped in a thin membrane of flat cells, with strongly stainable nuclei. In S. planco-
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Fig. 13. *S. planctonis* forma *planctonis* with thin and short ovaries (Zoological Museum Amsterdam coll. no. Vch 370-5). For abbreviations see § III.

Fig. 14. Cross section of *S. planctonis* (the same specimen as in fig. 13), showing: A, an immature ovary and loose mature eggs; B, enlargement of the area indicated in A of a different slide. For abbreviations see § III.

with a few spermatozoa. It is generally believed that, after spawning is finished, the specimens die. In this specimen there seems to have been regeneration of the ovaries. This phenomenon could not be traced in the literature, it may be an exception not normally occurring in chaetognaths.

V. THE MALE REPRODUCTIVE ORGAN

The chaetognath male reproductive organ has been adequately described by Burfield (1927). It consists of testes and vasa deferentia situated in the tail cavity, and seminal vesicles laterally on the outside of the tail. Like the ovaries (fig. 10A) they are paired symmetrically along the median septum. This septum consists of a membrane covered on both sides by a simple cubical epithelium. This epithelium is, according to Burfield (1927), probably ciliated. In *Sagitta planctonis* ciliation could not be observed (fig. 15).

Also the mouth and duct of the vas deferens is reported to be ciliated in chaetognaths (Ghirardelli, 1968) but this was not clear in *S. planctonis* (fig. 17). The vas deferens is formed from the lateral epithelium of the tail cavity. Folding of this

Fig. 15. Cross section through the tail cavity of *S. planctonis*. For abbreviations see § III.
The seminal vesicles of *S. planctonis* are of the simple type. They consist of a layer of epidermis, lined with small cells which seem to produce a mucous-like substance (figs. 15, 18). In comparison with the glandular cells seen in the seminal vesicles of *S. setosa* and *S. serratodentata* they are very inconspicuous. There is no indication of an

layer into two lips and closing more posteriorly results in the formation of the canal situated dorsally. The canal opens posteriorly at the level of the anterior part of the seminal vesicles. Just before this opening the vas deferens turns more ventrally (fig. 16). The germinal cells of the testes are situated close to the septum dividing trunk and tail coelom. Groups of spermatogonia are developing from this germinal layer into the tail cavity where they are ripening into spermatocytes, spermatids and finally spermatozoa, gradually filling the whole tail cavity.

The seminal vesicles of the different species are described in detail by Tokioka (1939). This author distinguished four groups: the *enflata*-type, very simple seminal vesicles like those in *S. enflata* and *S. lyra*; the *bedoti*-type, not yet differentiated in knob and trunk like those in *S. minima* Grassi, 1881; the *robusta*-type, more complex vesicles with a knob and a trunk like those in *S. setosa* and *S. bipunctata*; and the *serratodentata*-type, most complexly built vesicles like those in *S. serratodentata* Krohn, 1853.

Fig. 16. Cross sections of the vas deferens near the seminal vesicle in *S. planctonis*, showing: A, vas deferens situated dorsally and anterior of seminal vesicle; B, vas deferens more ventrally on level of seminal vesicle; C, vas deferens opening into seminal vesicle. For abbreviations see § III.

Fig. 17. Anterior opening of the vas deferens in *S. planctonis* seen in cross section. For abbreviations see § III.

Fig. 18. Seminal vesicle of *S. planctonis* in cross section. For abbreviations see § III.
initial place to burst. Remnants of the vesicles are just two strands of outer epidermis (fig. 19).

When the seminal vesicles are not filled they are hardly discernible (fig. 15). They are seldom found full of sperm, one specimen with one vesicle filled was found among 550 specimens of *S. planctonis* (fig. 3B). Probably the time between filling and bursting is very short. Most mature individuals show the remnants of a vesicle (fig. 19), either with a tail cavity still full of sperm or an empty tail cavity. This proves that the seminal vesicles have to regenerate before the remaining sperm can be delivered.

VI. SEXUAL STAGES

Examining *Sagitta planctonis* histologically, five sexual stages can be distinguished:

— Individuals in stage I of development show in one cross section very small ovaries, with oogonia and one or two oocytes in development. On the lateral side a cluster of small cells with very dark staining nuclei is present. The germinal epithelium and the oogonia are difficult to distinguish from the cells which are going to form the epithelial wall of the oviduct. Neither the oviduct, nor the syncytium is to be seen. In these specimens the testes consist of a small lump of spermatogonia on the anterolateral side of the tail cavity.

On the outside the reproductive organs are hard to observe. Often, staining with methylene blue is necessary to reveal them. The ovaries are very thin and reach to about the anterior end of the posterior fin. The testis is seen as a boomerang-shaped structure along the septum which divides trunk and tail cavity and the lateral body wall.

— Individuals in stage II of development show in cross section still thin ovaries with few oocytes. On the lateral side the oviduct can be distinguished, and the syncytium starts to develop. The testis tissue in this stage starts to fill the entire tail cavity with lumps of spermatogonia and spermatocytes originating from the primordium. Seminal vesicles start to develop.

Seen in the intact specimen, the ovaries are still very thin but growing in length reaching to about halfway the anterior fins. The tail cavity is filled, though not entirely, with testes, but seminal vesicles are not yet seen from the outside.

— In individuals in stage III of development the ovaries show in cross section a considerable increase in width. Oogonia and small and large oocytes are found. The epithelial wall of the oviduct and the syncytium are fully developed. Sperm can be present in the seminal receptaculum. The primordium of testis tissue is not seen anymore in this stage. The whole tail cavity is filled with spermatocytes and spermatozoa and seminal vesicles are seen, either still empty or filled with sperm or ruptured. The refilling of the seminal vesicles is obvious from our slides.

In the intact animal the ovaries have grown considerably in width. They reach about halfway the anterior fins. The tail is full and seminal vesicles or remnants of seminal vesicles are seen. In this stage sperm is transferred, either to the seminal receptaculum of the same individual (self-fertilization) or to those of another individual (cross-fertilization) (Ghirardelli, 1968; Dallot, 1968).

— In stage IV of development, cross sections of the ovaries show them fully developed. They are so wide that the intestine is compressed laterally and the whole trunk cavity is filled. The oviduct, now taking also the function of a seminal receptaculum is full of sperm and most of the oocytes are very large though still small oocytes and oogonia are seen. In some places the epithelial wall of the oviduct is degenerated, probably due to the passage of ova into its lumen. The testis is inactive. Mostly the tail cavity is empty or nearly empty, showing only remnants of testis tissue but without reproductive cells.

From the outside the ovaries look long and wide. They reach to the level of the ventral ganglion or even beyond it to the neck region. The tail
is empty or nearly empty with remnants of seminal vesicles.

— In stage V of development the ovaries show disordered structure, without reproductive cells other than small oocytes. The aspect of the male organs is the same as in stage IV.

The morphology of the ovaries also points to inactivity as they lost their original shape, they are curved and shorter than in stage IV.

In determining developmental stages in chaetognaths the fact must be borne in mind that this is strictly arbitrary. The individuals are growing their entire life and not jumping from one definite sexual stage into another. The growth rate and oogenesis may vary largely with environmental conditions probably mostly influenced by temperature (Sameoto, 1971). When in these hermaphro-
dite animals the male and the female activities are fulfilled more simultaneously, the stages II and III are no longer separable. This occurs when the spe-
cies in general shows a less protandric cycle or when the male cycle is incidentally shortened due to telescoping (cf. Van der Spoel, 1971).

Without sectioning, only 3 sexual stages can be distinguished for species with a largely coinciding male and female cycle (slightly protandric) such as S. serratodentata and S. setosa and 4 sexual stages for species with a more protandric cycle such as S. planctonis (cf. Pierrot-Bults, 1975). The spent specimens are in these cases included in the mature specimens.

VII. DISCUSSION

The reproductive organs of S. planctonis seem to be of a simple type in comparison to those of S. bipunctata. The structure of the epithelial wall of the oviduct is simple and not of a specific (crest-
ten) shape. The syncytium is very loose and thin and in older ovaries hardly present. The number of oocytes is highly variable. In one cross section the highest number found was 12 (fig. 4B), the lowest number was 6. The number of oocytes de-
deps on the state of development and on the fact whether spawning did occur already or not.

In specimens with typical planctonis characters 6 to 10 oocytes were seen in cross sections. In specimens with typical setesios characters 6 to 12 oocytes were seen in cross sections. So a differ-
ence in the ovaries, more specifically in number of oocytes, is not expected to be of taxonomic value. In the male organs a difference in structure is neither found nor could this be expected as these organs are very primitively built.

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