Histological examination of the chaetognathan morphological structure in the region of a supposed trunk-tail septum

A.P. Kassatkina & M.V. Stolyarova

Kassatkina, A.P. & Stolyarova, M.V. 2008. Histological examination of the chaetognathan morphological structure in the region of a supposed trunk-tail septum. *Zoosystematica Rossica*, **17**(2): 61-70.

A histological examination was conducted based on sections done in series in transverse and longitudinal directions of *Aidanosagitta macilenta* (Sagittidae, Chaetognatha) in a region which includes the anterior parts of the testes and the posterior part of the ovaries. We found that, in mature individuals (the 4th stage of maturation), the anterior parts of the testes are located in front of the posterior part of the ovaries. The anterior parts of the testes have a ventral position adjoining the ventral muscular bands. The ovaries are located more dorsally than the testes at the level of lateral fields. A transverse trunk-tail septum between testes and ovaries was not revealed. These data support an idea that a structure which was earlier treated as a tail-trunk septum is actually the anterior edges of the testes. Both longitudinal coelomic cavities continue into the tail region without any transverse septa. The paired tail cavities as can be seen from their composition and functions represent the testes consisting of a peripheral compact portion with undifferentiated germ cells and a space where the maturation of cells occurs. The tail is distinguished anatomically as a post-anal portion of the body but it is not a true segment as it is not separated from a trunk part of the body by the trunk-tail septum. The body of Chaetognatha consists of two true parts (segments). A mesenterial septum divides the body longitudinally-symmetrically from a trunk-head septum down only to the caudal end of the gut. In the tail region there is a medial septum formed by the medial walls of testes. Gonads in both females and males do not have any duct connecting them with a gut cavity. The ovaries and the testes are covered by a coelomic lining and a duct between the ovaries and the testes is absent.

A.P. Kassatkina, V.I. Il'ichev Pacific Oceanological Institute, Far Eastern Branch, Russian Academy of Sciences, 43, Baltiyskaya St., Vladivostok, 690041, Russia. E-mail: apkas@mail.ru

M.V. Stolyarova, Saint-Petersburg State Pediatric Medical Academy, 2, Litovskaja St., St Petersburg, 194100, Russia. E-mail: mezozoy@mail.ru.

Introduction

The first mention of such septum in sagitta relates to the beginning of the 19th century (Darwin, 1844). It is good visible in living specimens as more or less clear border between trunk and tail regions situating behind the anus and separating ovaries and testes. From dorsal or ventral side it looks like two arcs bended forward to the head (Fig. 1).

On its definition trunk-tail division represents transverse complete septum (Ivanov, 1937; Kühl, 1938; Beklemishev, 1944; Hyman, 1959; Beauchamp, 1960) and is regarded as a structure (independent organ) dividing the body cavity into trunk and tail coeloms (Doncaster, 1902; Dogel, 1975; Shinn, 1997) that is used for determination of phylogenetic position of chaetognaths. As a result of Kovalevskiy's studies of Sagittae ontogenesis (Kowalevsky, 1871) it was revealed that young, just hatched individuals possess only one septum – a trunk-head one, while the second one – trunk-tail septum – is absent. The subsequent numerous embryological studies (Bütschli, 1873; Hertwig, 1880; Doncaster, 1902; Büchner, 1910; Stevens, 1910; Kotori, 1979, and many others) have confirmed Kowalevsky's results. On the data of Doncaster (1902) the formation of trunk-tail septum starts at 3-4th day after the hatching. Considerably more late appearance of the trunk-tail septum in ontogenesis prooves it is a secondary structure and does not allow to consider it as a true metameric division in difference to the trunk-head septum (Davidov, 1914; Beklemishev, 1952; Hyman, 1959). According to imagination of some authors this is only the coelomic division since it divides the coelomic cavity but does not separate trunk and tail muscles (Hyman, 1959; Shinn, 1997). Therefore the definitive coelom of chaetognaths consists of three spaces: head

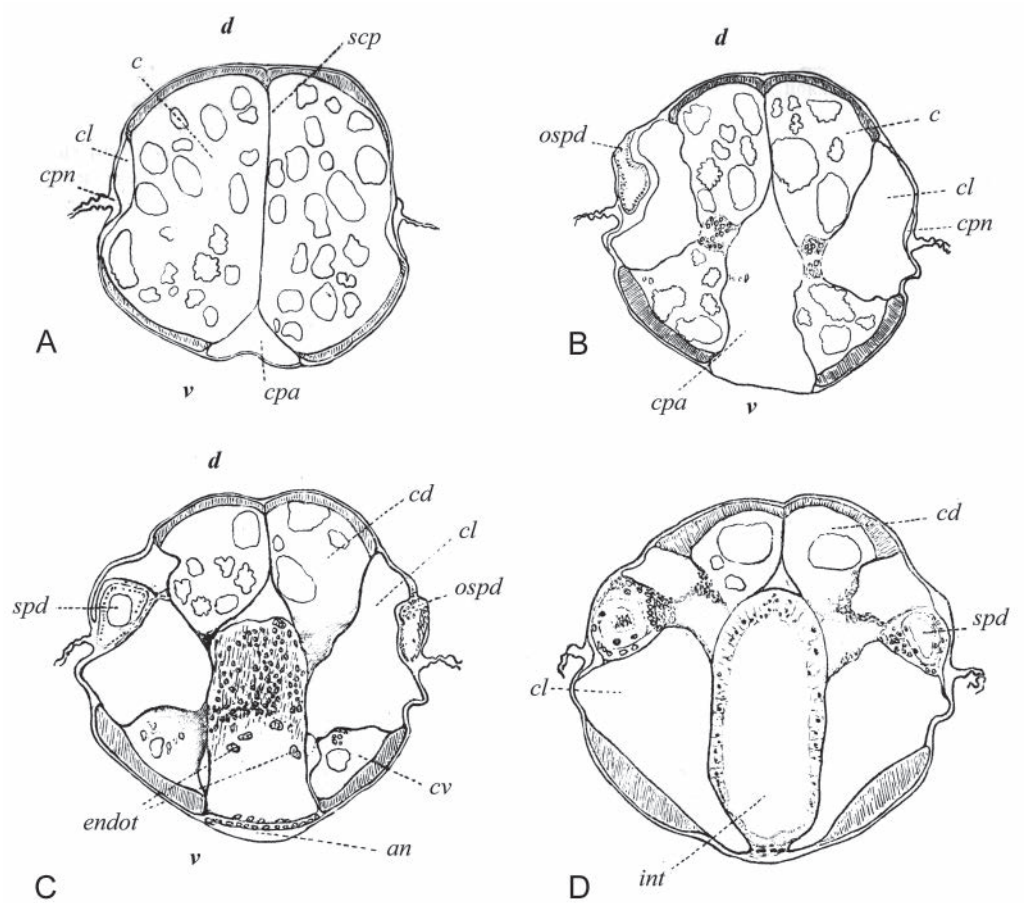

Fig. 1. Transverse sections of *Sagitta bipunctata* (from Elpat'evskiy, 1913). **A**, section of the tail region directly behind the "transverse septum"; **B**, section directly behind the anus and before the section A; **C**, section through the posterior wall of the gut; **D**, section through the posterior gut; *an*, anus; *c*, cavities in which developing germinal products are present; *cd*, dorsal portion of the cavity "c"; *cv*, a ventral portion of the cavity "c"; *cl*, a lateral cavity between the cavity "c" and the wall of the body; *cpa*, the postanal cavity; *cpn*, the cavity at the base of the fins; d, dorsal side; *endot*, endothelial lining; *int*, intestin; *ospd*, opening of the seminal duct of the ovary; *sep*, the dorso-ventral septum; *spd*, the seminal duct of the ovary; *v*, ventral side.

cavity and paired trunk-tail cavities that are head and trunk-tail coeloms (Hyman, 1959) and Chaetognatha are two-segmented animals (Davidov, 1914; Beklemishev, 1952). Despite this in literature there is a steady idea of the presence in chaetognaths the head, trunk and tail coeloms as indipendent parts of body cavity. According to Ivanova-Kazas (1977) the coelom in Sagitta's hatching is subdivided only into two segments but definitive cavities are represented by three paires of coelomic sacs and their relation to the hatchings cavities remains unclear. In new report on the anatomy of chaetognaths (Shinn, 1997) the proofs are considered at the ultrustructural level that the hatchings coelom of chaetognaths does not disappear but only becomes narrower and then widens again that is definitive coelom corresponds the hatchings one. Also on Schinn's mind already at the earliest stages exists the trunk-tail septum represented by some cells surrounding primary germ cells and connecting them to the gut and the wall of the body (scheme 97 – Shinn, 1997). This conclusion can not be regardered as correct since the lumen of the coelomic cavity is yet absent at this stage.

Despite of extensive researches, a question on the existence of a transverse trunk-tail septum remains problematic. Histological descriptions of trunk-tail septum are absent. Doncaster (1902) having studied histological sections of sagitta from the stage of embryo to adult animal brings the horizontal and cross sections. It is impossible to define on horizontal sections if the complete transverse septum dividing coelom exists. Doncaster places only 5 drawings of cross sections of individuals at different degree of maturation (Doncaster, 1902: Figs 32, 33, 38, 39,

41) that are odd, do not compose the series, do not include testes and can not give the whole picture of gonads location.

The attempt of finding out the trunk-tail septum composition at the histological level was done by Elpat'evskiy (1913). Studing a series of cross sections of *Sagitta bipunctata* in direction from the tail region to the gut Elpat'evskiy did not reveal a structure as a whole that might be considered as transverse septum. On cross sections through the tail region (Fig. 2A, B) he observed paired cavities containing male germ cells and the walls of these cavities do not everywhere contact to the body wall. Elpat'evskiy comes to conclusion that the cavity of the tail region is a space of testis as inside it the male germ cells undergo development. On the sections through the caudal end of a gut continuations of these cavities, as well as a gut and posterior portions of ovaries are seen (Fig. 2C, D). Elpat'evskiy notes the endothelium that covers the surface of gonads and goes over the surface of a gut bordering the strands which connect the gonads with a gut (Fig. 1D). These broad strands he called the "sleeves" or "canals". As a result of examination of adult individuals sections Elpat'evskiy asserted that posterior septum as an uniform independent formation in this region is absent, and there is "rather complex formation composed of endothelial borders of various cavities of a body," however, in a figure of general view he showed a transverse septum (Fig. 1: *dis*; after Elpat'evskiy, 1913, 1914). Also the figure shows the "canals" ("sleeves") going from a gut to the female gonads and to the back end of a body. Referring to this figure, Filatova (1951) assumed, that a cavity of intestine through a special duct (Fig. 1: *d.oi*) is interconnecting with a cavity of the female gonad and through it the lymphatic liquid is flowing into the female gonad cavity while washing the oocytes by a special nutritious liquid.

At the early stages of maturation the medial ends of the cavities existing around the rudiments of the ovaries look as a tube connecting both ovaries. By Elpat'evskiy (1910, 1914) observations of *Flaccisagitta inflata* development, further on, this tubular structure similar to the gut diverticulums, gradually removes the ovaries and the testes from a gut to the lateral sides of an animal. We observed a similar picture on alive young individuals of *Aidanosagitta macilenta* Kassatkina, 1971, and with some variations for the species spat of *Leptosagitta collariata* Kassatkina, 1973. However, further destiny of the structures which are located between a gut and germ cells, remained problematic for the lack of histological studying of this part.

From the observations on living specimens and first histological studies the passage at once had happened to the ultrustructural organization of chaetognathans. As a result a complete picture was not composed and a trunk-tail septum was not convincingly shown. Shinn (1997) brings the detailed information on the structure of tissues at the ultramicroscopic level not concerning a problem of composition of organs and their arrangement.

In the most of reports is postulated the existence of transverse complete trunk-tail septum and as a consequence – the presence of separate tail coelom. At this the important level is absent – histological analysis of composition of a trunk-tail septum region.

So longe as a notion of posterior (trunk-tail) division is used to state the presence of a tail coelom and a tail segment it is necessary to have exact data of its structure. The aim of this paper is to study the location of the ovaries relatively to the testes; whether their coats are the material forming the septum. At obduction of adult individuals of *Parasagitta liturata* Kassatkina, 1973, at the 4th stage of maturation we did not manage to find out a transverse septum between the ovaries and testes, and with the purpose of its search we undertook the histological studying of the caudal part of ovaries and the forepart of testes, i.e. that part of an animal body where the truncal-caudal septum should be located.

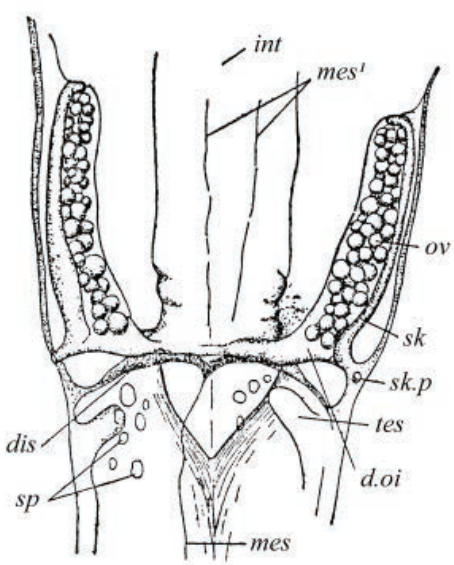

Fig. 2. A region of the posterior transverse septum in *Sagitta inflate* (from Filatova, 1951, after Elpat'evskiy, 1913); *dis*, transverese septum of the tail region; *d.oi*, canal connecting a gut to the ovary; *int*, intestin; *mes*, longitudinal mesenterial septum; *mes*^{1}, longitudinal mesenterial septum of the trunk region; *ov*, ovary; *sk*, seminal duct of the ovary; *sk.p*, opening of the seminal duct; *sp*, male germinal products; *tes*, testes.

Material and method

The material was selected from plankton samples, taken totally from a bottom up to a surface with the help of Juday net in the Peter-the-Great Bay. Species of *Leptosagitta collariata* Kassatkina, 1973, *Aidanosagitta macilenta* Kassatkina, 1971, and *Parasagitta liturata* Kassatkina, 1973, of the 1st-4th stages of maturity were investigated. Both living individuals and those fixed in 10% formaldehyde with using MBC-10 binocular observation were investigated. The object for histological studying was choosen a dominant species of the Peter – the-Great Bay *A. macilenta* at the 0-4th stage of maturity. For histological purposes the material was fixed in 10% formaldehyde or in Bowen mixture and wax-embedded. Also the fixation by 1% glutaraldehyde with postfixation by 2% ozmium tetroxide and following embedding in araldit were used. Histological sections of 5-7 microns thick were stained by a standard technique of Mayer hematoxylin, by Boemer hematoxylin and eosin, and according to Nissl method. Also were used araldit sections of 1 micron thick stained with toluidin blue.

Results

Longitudinal and cross sections of the body of *A. macilenta* made in the region of the supposed trunk-tail septum were examined. Figures 3 A and 3B represent longitudinal araldite sections of *A. macilenta* (0 stage of maturity) in frontal and sagittal planes; Figs 4-6 represent the cross histological sections of *A. macilenta* (4th stage of maturity) which are consistently taking place through the foreparts of testes and posterior parts of ovaries (note that the section in Fig. 4A is located closer to the head, and the section in Fig. 5A-B shows a caudal part of the ovaries at the level of the rectal orifice, and the section in Fig. 6A passes through a cover of the ovaries behind the rectal orifice, and the section in Fig. 6B behind the rectal orifice and ovaries).

Hatchlings. At the 0 stage of maturity paired cavities of tail region look on longitudinal sections as epithelial sacs which contact to each other on midline forming a medial septum (Fig. 3A). Their anterior rounded surface is faced to the gut and touches to it composing an appearance of two semi-circles. Between them and a gut there is a small triangular space where a medial septum is absent. Each ethithelial sac on its lateral side contains compact germ cells mass over which surface in some sites germ cells come forward and on its anterior rather widened end the outflow of small groups of germ cells into the cavity occurs. The compact cell mass continues at considerable distance tapering to the posterior end of the body. It has a clear border which looks as a very thin membrane not containing nuclei. Many authors founding on the idea of trunk-tail septum separating trunk and tail coeloms consider the lateral mass of germ cells as a testis and the cavity enclosing to it as a tail coelom. Elpat'evskiy (1913) regards this formation as a gland properly and enclosing cavity as a cavity of testis since the maturating germ elements circulate inside it. After Elpat'evskiy the testis consists of gland properly and a cavity in which the maturating germ elements are weighing and moving and of excretory duct with a spermatic vesicle. We consider the point of view of Elpat'evskiy as more based. It is logical to regard the lateral mass of germ cells as a compact portion of testis (gland properly) and a space bordering upon it as a cavity of testis necessary to maturation of germ cells during the process of circulation. The most of cells in compact portion of testis look as a mass of low differentiated cells. The cells leaving the anterior edge have rather big size and more big nuclei. Perhaps there is here a gradient of distribution of germ cells on the degree of differentiation from posterior to anterior border. It may be supposed that compact portion of testis represents itself a mass of spermatogonia where there mitotic division occurs. At the anterior edge occurs a separation of groups of cells (sinsytially connecting to each other) which apparently entered meiosis and passed prophase of 1-st meiotic division. Thin bordering envelope apparently plays a role of a barrier separating maturating germ cells from spermatogonia. On data of Shinn (1997) it is formed by cytoplasmic processes of cells of lateral fields. Parallel to it comes also very thin plate having taken in literature a name "lateral mesentery". On the slides flattened nuclei of cells are seen in it. Lateral mesentery is similar to very thin envelope (second one) bordering a space close by compact portion and giving a possibility of outflow of germ products only at the anterior edge. The general epithelial envelope surrounds both portions of testis (Fig. 3A) and contacts on a short distance to coat of a gut and in one of points touches coat of ovary. These sections clearly indicate that a single structure which is situated on a place of supposed trunk-tail septum and has a cross arrangement is anterior borders of testes. They are convoluted in a form of arcs in direction to a gut that completely coincide with pictures observed on living or fixed individuals.

Right and left halfs of tail cavity each has own "division" (anterior wall) which are frequently bended in direction to a gut but may differ from each other by their shape, do not pass one into another, turn on midline along the axis of the body and laterally along the muscular wall that is in tail region there are two cavities borded by an epithelium. Trunk-tail "septum" observed on

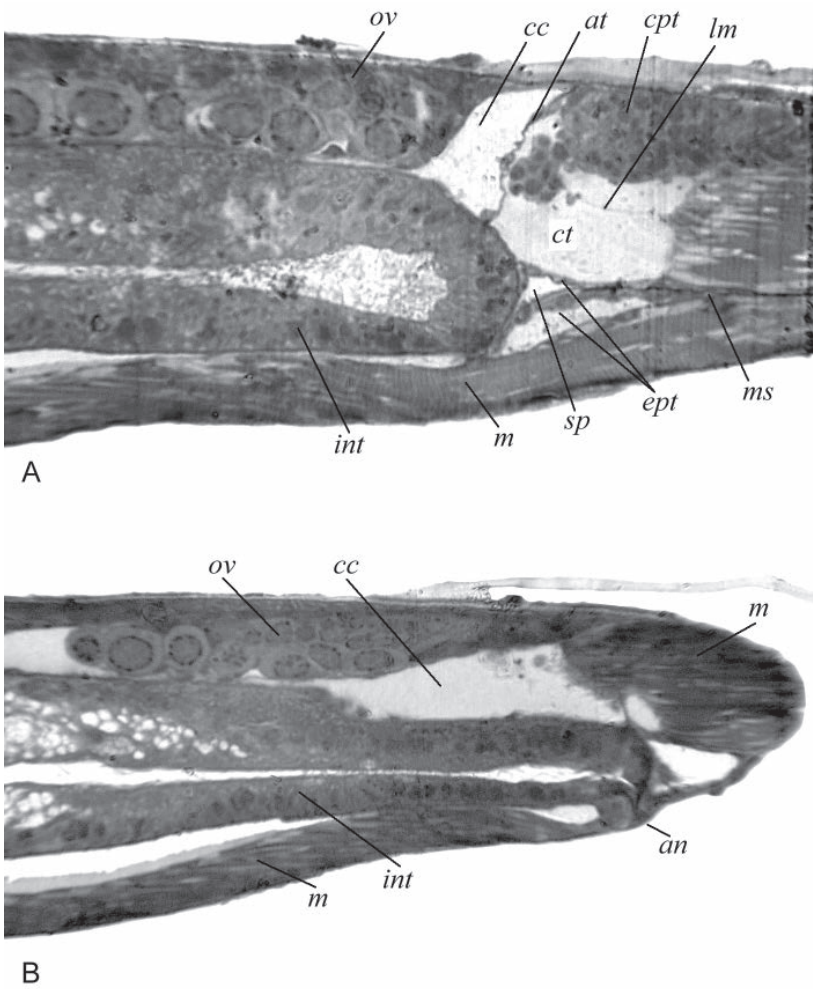

Fig. 3. Longitudinal sections of *Aidanosagitta macilenta* (0 stage of maturation): **A**, frontal plane; **B**, sagittal plane; *an*, anus; *at*, anterior border of the testis; *cc*, coelomic cavity; *cpt*, compact portion of the testis; *ct*, cavity of the testis; *ept*, epithelial covering of the testis; *int*, intestin; *lm*, lateral mesentery; *m*, muscles; *ms*, medium septum; *ov*, ovary; *sp*, space.

alive and fixed specimens is attaching to each other (but not fusing) anterior edges of the epithelial sacs. These epithelial sacs contain developing and circulating inside their cavity male germ cells and represent theirselves testes. Testis functions as an unit organ surrounded by general coat comparable with coats of gut and ovaries. Thus trunk-tail division (septum) is absent, on its place are situated the anterior borders of testes which contact to each other and produce the illusion of septum. This impression is intensified by that the edges of testes also contact to gut. And there are small distances where borders of testes come in contact with coat of ovaries. Sagittal sections also show that behind ovaries and gut after anus there is no transverse septum (Fig. 3B). Ovaries in their turn contact laterally to gut (Fig. 3B). That is in Chaethognata there is a complex of organs consisting of gut, ovaries and testes which are fixed with the help of medial mesentery and by attaching to each other and to the walls of a body.

Epithelium of anterior portion of testes is arranged in a form of arcs and forms convex surface that may touch the surface of caudal end of a gut (Fig. 3A). In this region epithelial cells are big, their nuclei are good seen. They corresponds to “podocytes” of Shinn (1997). In midline the epithelium of the right and left testes come in contact forming a medial septum. Here epithelium consists of flat cells with dark nuclei and corresponds ciliated cells and coelotelium after Shinn. Laterally epithelium is not distinguished. Perhaps here it closely contacts with low cells located in a region of lateral fieldes.

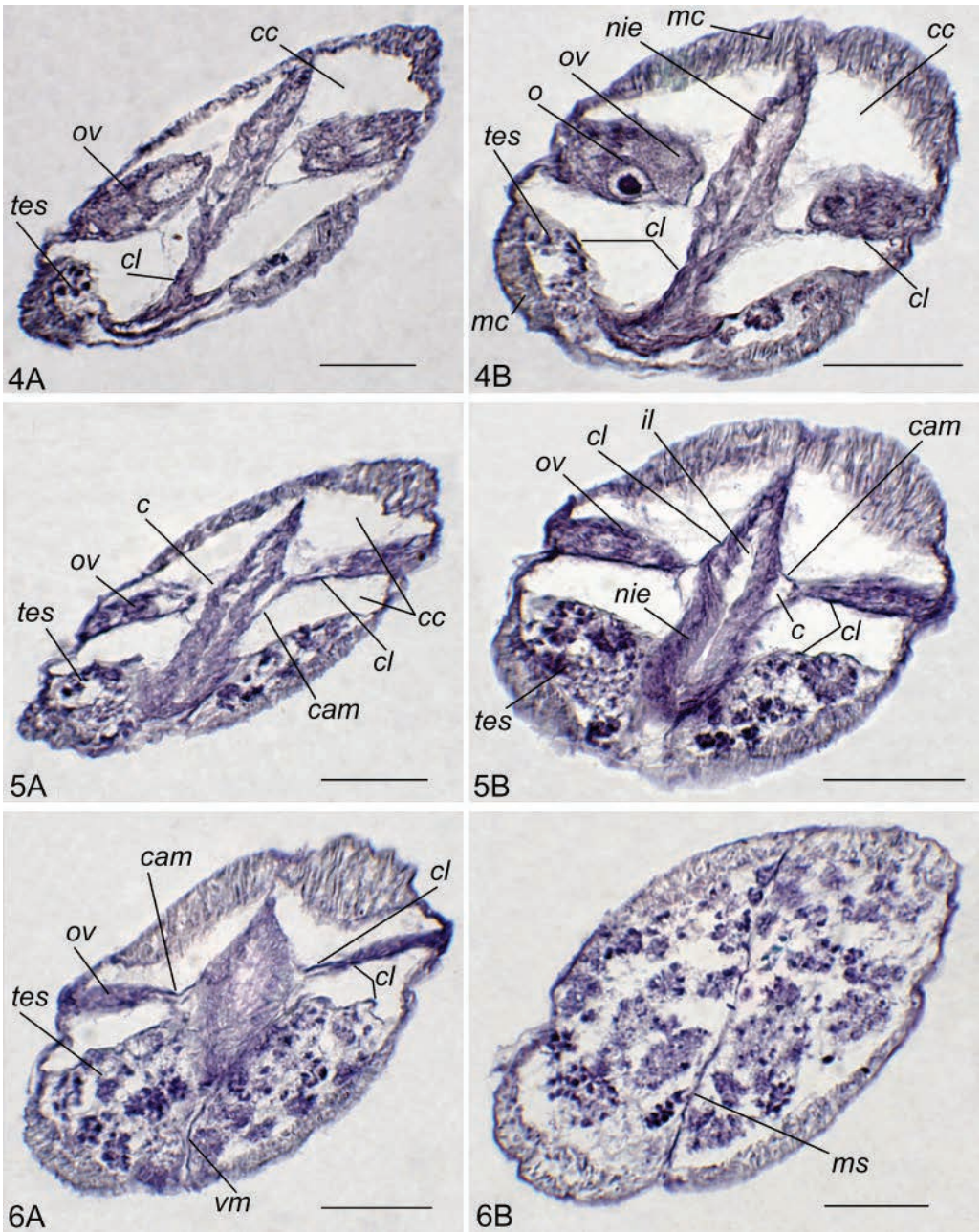

Fig. 4. Transverse sections of *Aidanosagitta macilenta* (4th stage of maturation) through the anterior portions of the testes and the posterior portions of the ovaries before the anus: A – section through a top of testis; B – section is more caudal than previous one; *cc*, coelomic cavity; *cl*, coelomic lining; *nie*, nuclei of intestinal epithelium cells; *mc*, muscle cords; *o*, oocyte; *ov*, ovary; *tes*, testis. Scale bar: 0.05 mm.

Fig. 5. Transverse sections of *Aidanosagitta macilenta* (4th stage of maturation) in the region of the anus: **A**, anterior section; **B**, posterior section; *cam*, cords of amorphous material; *c*, cavity between the intestine and the ovaries; *il*, intestinal lumen (other abbreviations as in Fig. 4). Scale bar: 0.05 mm.

Fig. 6. Transverse sections of *Aidanosagitta macilenta* (4th stage of maturation) behind the anus. **A**, section at the level of posterior end of ovaries and blind portion of gut behind anus; **B**, section behind the blind portion of gut; *vm*, ventral mesentery (other abbreviations as in Figs 3-5). Scale bar: 0.05 mm.

Such idea of male gonad composition is confirmed by the presence of general coat of this organ. Also it explains "unintelligible" convolution of "trunk-tail septum" since this is not true division but contacting walls of right and left testes. The presence of localized zone of low differentiated cells situation and of space into which maturating germ elements pass are also typical to testes. Thus paired cavities that are situated behind a gut after so-named "trunk-tail septum" are not tail coelom but are the cavities of organs – testes.

Adults. Under visual observation of individuals at 4th stage of maturity so-named "posterior septum" is revealed not behind anus but before it that has leaded to supposition of its complex configuration. At this stage the testes grow forward and penetrate a region of a trunk. Naimly therefore on the same cross section of mature individuals (4th stage) in a region of "trunk-tail septum" the ovaries and the testes are present simultaneously.

Structure of the gut, ovaries and testes is well seen on cross sections of *A. macilenta* (4th stage of maturity) (Figs 4-6). They are situated in general coelomic cavity but not in different cavities as it is supposed in traditional literature. On photos we present six serial sections in direction from the head caudad. It is seen that the volume of testes increases while the volume of ovaries decreases, and that, behind the ovaries and the end of the gut, the testes fill in the internal space of the tail region.

Histological structure of a gut. In the wall of the gut there are distinct lightly stained nuclei of the lengthened shape referred to the gut epithelium cells. Nuclei of these cells are at a small angle to the surface in a central part or closer to the basal part of cells, forming one line (Fig. 4B, 5B: *nie*). The external surface of the gut is covered by a single-layered squamous coelomic epithelium (Fig. 5B: *cl*). Cell nuclei of this epithelium are applanate, intensively stained; their structure is not distinguished. Nuclei of cells of coelomic epithelium are at significant distance from each other. In the area of gonad location the gut is compressed on both sides and has a narrow lumen. At a level of antral parts of testes the gut ventally passes to a narrowing which then forms a horizontal widening having a small cavity. These sites are also covered by coelomic epithelium (fig. 4 A, B: *cl*). Lateral edges of the widening adjoin testes. In the next areas the ventral widening is absent. More caudally the gut decreases in size, and then disappears, and then its place is occupied by medial septum (fig. 6 B: *ms*). Supporting structures for a gut are dorsal and ventral mesentery on which surface the nuclei of coelomic epithelium cells are observed (Fig. 6A: *vm*). On sections it was impossible to define "sleeves" (Elpat'evskiy, 1913) coming from a gut to testes though on slides it is seen that coats of these organs contact to each other.

Histological structure of testes. Testes are more caudal with regard to the ovaries. Their anterior parts are in front of the posterior parts of the ovaries, and the caudal parts reach the end of a body. The anterior parts of testes have a ventral position, while adjoining the ventral muscular bands (Figs 4-6). Also they contact the gut wall, and in a tail region where the gut ends, they are located on both sides of the medial septum (Fig. 6B). At the 4th stage of maturation the cavity of the testes becomes filled of maturing germ cells. In the testes there are small cells with darkly stained nuclei which frequently occur by groups in a form of rosette, and presenting themselves, obviously, different stages of spermatozoa development. Between the cells groups there are small light spaces being parts of testes cavity. It is not still clear if in the walls of this cavity of *A.macilenta* there are cilia which, in Kühl's opinion (Kühl, 1938), create circulation and move spermatocytes inside the cavity. Most likely, the circulation is achieved in some species for the account of almost continuous movement of chaetognaths muscles. On the surface side, testes are bounded by squamous coelomic epithelium (Figs 4B, 5B, 6A: *cl*). On cross sections the compact lateral portion of testis is not distinguished perhaps in connection with that it is weakly separated from a cavity or probably along the maturation all the cells from the compact portion are spent on spermatozoa development and pass into a cavity of testes.

Histological structure of the ovaries. Ovaries are situated forward to anus, locating on each side from the gut at a level of lateral fields. In the ovaries at the given stage of development there are large oocytes with very large nuclei and nucleoli (Fig. 4 A, B: *o*). Spaces between oocytes are not observed but after ovules passing outside (at 3rd-4th stage of maturity) a cavity inside the organ is revealed. Ovaries are bounded by squamous cells of coelomic epithelium (Figs 4B, 5A-B, 6A: *cl*). The supporting structures fixing the ovaries position are lateral lateral fields which they adjoin, and the gut wall to which the ovaries are connected with the help of very thin bands of amorphous substance (Figs 5A-B, 6A: *cam*), covered with squamous cells of coelomic epithelium (Figs 5B, 6A: *cl*). In a space bounded by the gut wall, the ovaries wall and connecting bands, there is a small cavity (Figs 5A-B: *c*). Apparently naimly these "canals" Elpat'evskiy calls "sleeves" cosidering them as lymphatic space connected with the ovaries and providing a function of delivery of nutrients to oocytes. Noted by him endothelium (coelomic epithelium) passing from the surface of the ovaries over the surface of the gut and thus bounding the "canals" is seen also on our

preparations. Now there are no sufficient data to decide if these spaces are lymphatic that is belong to pecular vascular system but their nutritional function is not excepted. The terminal parts of ovaries are connected with a gut by strands covered by epithelium and bordering narrow tubular spaces directed towards each other and coming in cross direction (Fig. 6 A: asc) and perhaps corresponding "connecting tubules" observed on living material.

Coelomic lining. On cross-sections of different species of chaetognaths it is visible, that the coelomic cavity is distinctly bounded. Cells covering it, apparently, are very much thinned as the preparations show only their applanate darkly stained nuclei (Fig. 4 A, B; 5 A, B; 6 a: *cl*). These cells limiting a space, probably, can be considered as coelomic epithelium which is also called coelothelium, endothelium, peritoneal epithelium. Whether coelomic epithelium is independent tissue or it is a modified layer of muscular (myoepithelial) cells remains unclear. It is known (Welsch, Storch, 1983; Stolarova, Kassatkina, 1990), that in cytoplasm of epithelial cells, adjacent to an external surface of the gut, there are myofilament bundles. In some species to this layer adjoins a layer of coelothelium which covers also the surface of muscle bands, mesenteries and gonads (Berezinskaja, Malakhov, 1993). In *Ferosagitta hispida* coelothelium is described as consisting of small and flat cells lying at considerable distances from each other and covering the surface of all the inner organs (Shinn, 1997). But it is not clear enough a structure of that part of the coelomic covering of *A. macilenta*, that lies on a surface of muscular bands, gonads, and mesenteries.

Discussion

Doncaster' paper (Doncaster, 1902) which is referred to all the following researches unconditionally receiving his point of view does not contain however proper analysis of composition of trunk-tail septum on the basis of sections series. In connection with this it was unknown if this organ really exists or it is only optical border arising as a result of combination of gonads coats at view from dorsal or ventral side. Sections series of *A. macilenta* (0 and 4 stages of maturation) having done in a region of supposed trunk-tail septum in three mutually perpendicular planes (transverse, sagittal and frontal) show that trunk-tail septum does not exist and tail cavities are bounded by epithelium and on their structure and fulfilling functions are the testes. Testis – mail gonad – consists of compact portion containing mass of spermatogonia and bounded by very thin membrane and of maturing spermatocytes loosely curculating in cavity adjoining the compact mass of testis. Cavity and compact mass together are surrounded by epithelium that consists of a single layer of cells. They compose the organ – testis. Inside cavity there is a thin division – lateral mesentery. On the place of trunk-tail septum are situated the anterior edges of testes. The conclusion about absence of trunk-tail septum explains the data of Elpat'evskiy (1913) that cavities containing male sex elements not everywhere adjoin body walls and each other (Fig. A, B). The cavities observed belong to testes that are located in tail but their anterior portions spread into trunk region (Fig. C, D). The spaces between testes and body wall belong to trunk coelom which is continuing into tail region. Also the space behind intestine and between anterior parts of testes (Fig. 3A) is a portion of coelom. Thus coelomic cavity surrounds intestine and then penetrates tail region where is observed as small spaces between testes and body wall. Such cavity corresponds the name "trunk-tail coelom". Inside this general cavity lay intestine and gonads covered by coelomic epithelium. Position of these organs is fixed with mesenteries (for intestine), adjoining body wall (for gonads) and touching of gonads coats to intestine coat in some points. The absence of septum and presence of unified coelomic cavity may have functional significance for equilibrium of pressure in coelomic fluid and also for unimpedimental providing of nutrition of developing sex cells both in ovaries and in testes.

At the 0 stage of maturation anterior edges of testes are behind intestine and ovaries, at 4 stage their anterior edges grow forward and will be located before posterior portions of ovaries. Naimly therefore in developing chaetognaths a "septum" is observed behind anus and in mature individuals it is observed before anus that is occurs its "transposition" forward to the head end.

The presence on cross section simultaneously the ovaries and the testes means that transverse septum between them is absent. The attempt to explain this arrangement of gonads by complicated space configuration of septum contradicts its definition "transverse". Neither transverse nor complicated in shape septum does not devide coelom on the boundary between trunk and tail. The anterior edges of testes do not compose a transverse septum as they do not completely adjoin to each other and to the coats of gut and ovaries (Fig. 3 A). Spaces between testes and body wall were noted by Elpat'evskiy (1913) in *Sagitta bipunctata* (Fig. 2 A-D). Simultaneous presence of the ovaries and the testes on cross sections are seen on the drawings of cross sections of *Sagitta bipunctata* (Elpat'evskiy, 1913) (Fig. 2 C, D) and on cross sections of *Ferosagitta hispida* (Shinn, 1997, Fig. 59 A, B) and apparently such

arrangement of gonads is typical to all Chaetognatha. Elpat'evskiy indicates cavities of testes containing maturating sex elements but Shinn gives them definition "tail coelom" (Shinn, 1997, Fig. 59 B) and on the same transverse section indicates trunk coelom how it is not paradoxical. If these cavities are assumed to represent tail coelom it is evident they do not correspond this definition while these cavities penetrate trunk portion of a body and trunk coelom continues into tail region, that is these spaces are present simultaneously in trunk and in tail locating one above another and this contradicts the idea of trunk and tail coeloms separated by transverse septum. Despite evidently artificial considerations Shinn on one of these sections marks as posterior septum the testis ventral wall which in this cross section is cut across and consequently has longitudinal horizontal arrangement and by no means can not correspond posterior septum. About ECM (extracellular matrix) location Shinn reports very indefinitely saying it is observed at the level of lateral fields.

On the base of results received and embryological data it is possible to imagine the way of gonads formation and their arrangement in a following sequence. At the stage of larvae appear mesodermal strands moving from the intestine to the body wall – in connection with migration of primary germ (sex) cells in this direction. At this early stage on horisontal section or at view from above the boundary between female and male primary germ cells looks as trunk-tail septum. This process may be considered as a beginning of the formation of gonads rudiments. This time appear the tail cavities which in further development become a portion of testes.

At 0 stage exists certain organization of tail cavities. They have epithelial coat, lateral mesentery, contain compact mass of germ cells which are released in a form of cell groups at its anterior end. The circulating germ cells begin to fill in these cavities. The testis is forming as an organ where occur both proliferation of low differentiated cells (compact portion of testis) and maturation of spermarocytes (cavity of testis). Anterior wall of testes reaches to posterior end of a gut. At this stage the tail region grows rapidly (Ivanov, 1937).

At the 4th stage the cavity of testes is filled by maturating germ cells. The growth of testes takes place – their anterior parts penetrate the trunk region and are located before anus and posterior parts of ovaries. It is shown by cross sections of different species of chaetognaths: Elpat'evskiy (1913), Shinn (1977), present report. The testes occupy not the whole space of the tail region (Fig. 2 A-D).

Studing of histological sections of *A. macilenta* shows that intestine and gonads are not communicating formations, they lie in coelomic cavity and are lined by coelomic epithelium. The gut has no diverticulums to the ovaries or testes; the communication between the gut and gonads occurs only by way of testes adjoining the gut wall, and by connection of the ovaries with the gut by thin apparently supporting bands (Fig. 5 A B: asc). An assumption about the liaison channel existing between the gut lumen and the cavity of ovaries and testes, through which there is a nutrients transport from the gut directly to gonads (Elpat'evskiy, 1914; Filatova, 1951), appeared baseless, – such lumen does not exist. Hence, the point of view about supply of special nutritious liquid to oocytes directly from the gut is erroneous. Oocytes nutrition can be carried out from coelomic liquid which, washing walls of the gut and gonads, is capable to carry out the transport and trophic functions, while transferring nutrients from the intestinal epithelium through thin coelomic epithelium to surrounding organs. Direct communication through the channel between the ovaries and testes is also absent. The "sleeves" marked by Elpat'evskiy, similar to "tubules" connecting ovaries probably correspond to the bands, going from the gut to gonads.

As a result of the carried out study it was not revealed a transverse trunk-tail septum. As a trunk-tail septum, apparently, it was accepted testes edges and bands between gonads and intestine. The body cavity behind the trunk-head septum is single; there is no other transverse septum.

Ovaries and testes are separated from each other by coats consisting of cellular coelomic lining, they are in a single cavity of the body. The testes since the 2nd stage of maturity fill in tail region behind anus, almost completely replacing the coelom. Baseless are assumptions, that the products of testes (in particular, spermatocytes at various stages of maturation) circulate in the coelomic cavity; this assumption is found in many manuals and determinants (Kühl, 1938; Hyman, 1959; Beauchamp, 1960, Kassatkina, 1982,). Photos of sections show that the cavity of testes is separated from a coelomic cavity by special cellular lining. And coelomic cavity is almost reduced and represented only by small spaces located between testes and body wall not occupied by testes. The determination "tail coelom" may be used only in meaning "tail portion of coelom".

Conclusions

1. Ovaries and testes consist of compact mass of cells and cavity which are together bounded by coelomic epithelium. The cavity of testis has internal incomplete longitudinal septum – lateral mesentery.

2. Ovaries and testes are not communicated with each other and with a cavity of intestine. Any channels of such connection between them are absent.

3. At the 0 stage of maturation anterior edges of testes reach caudal part of intestine, their coat touches at short distances the gut coat and coats of ovaries and their cavity contains few developing germ cells. At the 4th stage of maturity anterior edges of testes grow into the trunk region and are located before posterior portions of ovaries, this time the testes cavity is filled by maturating germ elements.

4. A trunk- tail septum as a single structure or a one consisting of merging walls of internal organs is not revealed. The anterior edges of testes are situated at its supposed place.

5. Medial mesentery surrounds intestine but does not continue behind it. At small distance from gut begins medial septum of tail region formed by medial walls of testes.

6. Chaetognatha body as a whole consists of two genuine parts (segments). Coelomic cavity is uniform, as both longitudinal body cavities have not cross-section septa and behind the intestine they fuse together and continue into tail region. Tail is anatomically distinguished as postanal portion of the body but it is not a third segment because it is not separated from a trunk part of the body by a transverse trunk-tail septum.

Acknowledgement

This study was supported by a grant of the Russian Foundation for Basic Research, FEB RAS-RFBR 06-04-96034-P_vostok_a, and grants of the Far East Brach of the Russian Academy of Sciences, 06-I-II18-080 and 06-III-A-07-253.

References

Beauchamp, P. 1960. Chaetognatha. *In*: Grassé, M. P.-P. (Ed.) *Traité de Zoologie.* **5**(2): 1500-1520. Masson et C ie éditeurs, Paris.

Beklemishev, V.N. 1964. Basis of the invertebrate comparative anatomy. V.1: 445 p. *Moscow. "Nauka"*. (In Russian).

Berezinskaya, T.L. & Malakhov, V.V. 1993. Ultrastructure of the trunk and caudal coeloms in *Serratosagitta pseudoserratodentata* (Chaetognatha). *Zoologicheskiy Zhurnal*, **72**: 36-47. (In Russian with English summary).

Büchner, P. 1910. Die Schicksale des Keimplasmas der Sagitten in Reifung. Befruchtung, Keimbahn, Ovogenese und Spermatogenese. *Anat. Anz. Iena*, **1**(17-22): 233-288.

Bütschli, O. 1873. Zur Entwicklung der Sagitta. *Z. wiss. Zool.*, **23**: 409-413.

Darwin, C. 1844. Observations on the structure and propagation of the genus *Sagitta*. *Ann. Nat. Hist.*, **13**(1): 360.

Davidov, K.N. 1914. *Kurs embriologii bespozvonochnykh* [Embryology of invertenrates]. Sotrudnik", Saint-Petersburg – Kiev. 502 p. (In Russian).

Dogel, V.A. 1975. *Zoologiya bespozvonochnykh.* [Zoology of invertebrates]. Vysshaya shkola, Moscow. 559 p. (In Russian).

Doncaster, L. 1902. On the development of Sagitta with notes on the anatomy of the adult. *Quart. J. Microsc. Sci.*, **46**: 1-267.

Elpat'evskiy, V.S. [Elpatiewsky, W.S.] 1910. Die Entwiklungsgeschichte der Genitalprodukte bei Sagitta. I. Die Entwiklung der Eier. *Biologicheskiy Zhurnal*, **1**(4): 1-10.

Elpat'evskiy, V.S. 1913. Origin of the ovum and embryological development of *Sagitta.* Part 1: Origin of the ovum. *Izvestiya Obschestva Lubiteley Estestvoznanya, Antropology, Etnography*, **126**(1): 1-69. (In Russian).

Elpatiewsky, V.S. 1914. Origin of the ovum and embryological development of *Sagitta.* Part 2: Embryological development. *Izvestye Obschestva Lubiteley Estestvoznanya, Antropology, Etnography*, **126**(2): 1-48. (In Russian).

Filatova, Z.A. 1951. Class Chaetognatha. *In*: Zenkevich, L.A. (Ed.) *Rukovodstvo po zoology*, **3**(2): 592-608. Sovetskaya nauka, Moscow. (In Russian).

Hertwig, G.O. 1880. Die Chaetognathen, ihre Anatomie, Systematik und Entwicklungsgeschichte. Vol. 7. Jena. 330 p.

Hyman, L.H. 1959. Phylum Chaetognatha. *In*: *The Invertebrates*, **5**: 1-71. McGraw-Hill, New York.

Ivanov, P.P. 1937. *Obshchayai i sravnitel'naya embryologiya* [General and comparative embryology]. Biomedgiz, Moscow-Leningrad. 809 p. (In Russian).

Ivanova-Kazas, O.M. 1977. *Sravnitel'naya embriologiya bespozvonochnykh zhivotnykh: trokhofornyye, shchupal'tsevyye, shchetinkochelyustnyye, pogonofory* [Comparative embryology of invertebrates: Trochozoa, Tentaculata, Chaetognatha, Pogonophora]. Nauka, Moscow. 312 p. (In Russian).

Kassatkina, A.P. 1982. *Shchetinkochelyustnyye morye SSSR I sopredel'nykh vod* [Chaetognaths of the seas of USSR and adjacent waters]. Nauka, Leningrad. 136 p. (In Russian).

Kotori, M. 1979. The biology of Chaetognatha in the Bering Sea and the northwestern North Pacific Ocean, with emphasis on *Sagitta elegans* Verrill (review). *Bulletin of Plankton Society of Japan*, **26**: 25-39.

Kowalevsky, A.O. 1871. Embriologische Studien an Wurmen und Artropoden. Entwicklungsgeschichte der Sagitta. *Mémoires de l'Academie Imperiale des Sciences de St. Petersbourg*, **16**(7[12]): 1-70.

Kühl, W. 1938. Chaetognatha. *In*: *Bronns Klassen und Ordnungen des Tierreiches*, **4**(4[2]). Akad. Verl.-Ges., Leipzig. 226 p.

Shinn, G.L. 1997. Chaetognatha. *In*: Harrison, F.W. & Ruppert, E.E. (Eds.) *Microscopic Anatomy of Invertebrates*, **15**: 103-220. Wiley-Liss, New York.

Stevens, N. 1910. Further studies on reproduction in Sagitta. *Journal of Morphology*, **21**: 279-319.

Stolyarova, M.V. & Kassatkina, A.P. The fine structure of the intestinal epithelium in a primitive member of Sagittidae (Chaetognatha). *Tsytologiya [Cell and Tissue Biology]*, **32**(7): 671-676. (In Russian).

Welsch, U & Storch, V. 1983. Enzyme histochemical and electron microscopical observations on the digestive tract of *Sagitta elegans*. *Zoologische Jahrbücher. Abteilung fur Anatomie und Ontogenie der Tiere*, **109**: 23-33.

Received 10 May 2008, accepted 15 December 2008