Reproductive Biology of Invertebrates. Volume I:
Oogenesis, Oviposition, and Oosorption
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# 25. CHAETOGNATHA

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## I. INTRODUCTION

The Chaetognatha are a group of enterocoelous, slender, transparent to translucent bilaterally symmetrical animals (Alvariño, 1963, 1965, 1967, 1969, for bibliography). The phylum includes only six genera, *Spadella* (benthic), and the pelagic *Eukrohnia*, *Krohnitta*, *Pterosagitta*, *Heterokrohnia*, and *Sagitta*. The benthic genus, *Spadella* comprises 12, *Eukrohnia* 5, *Krohnitta* 3, *Pterosagitta* 1 and *Heterokrohnia* 3 species; the genus *Sagitta* (with more than 40 species) includes most of the known species of Chaetognatha. The genus *Sagitta* appears to be the most successful and most highly evolved of the group; species of this genus inhabit the greatest variety of oceanic environments and bathymetric levels. The adult Chaetognatha of various species range in length from < 3 mm to > 100 mm. The body is divided into three morphologically well-differentiated regions, head, trunk, and tail, by transverse septa, and there is no communication across the trunk and tail septum (Fig. 1).

The Chaetognatha are hermaphroditic, but the female and male gonads are separated spatially in the body, and further, their maturity is separated temporally. The ovaries are in the trunk, together with the digestive tract, and the testes are in the tail, together with the seminal vesicles.

The reproduction of Chaetognatha has been discussed by several authors, mainly Grassi (1883), Ghirardelli (1968), Reeve (1970), and others. However, misconceptions in the description and interpretation of some aspects of the reproductive process persist in the literature. There is need for an anatomical study, and for relevant physiological interpretations based on morphology as well as behaviour. This review on the biology of reproduction is based on the anatomy of the reproductive organs and their function. The chaetognaths are difficult to maintain in the laboratory; experimental information is therefore scanty. The results should be considered within certain limitations: the behaviour of the animals in the laboratory would not accurately represent their normal life in the oceans. There is need for experimentation and more observations to understand their physiology and responses to changes in the environment, life cycle, and feeding conditions.

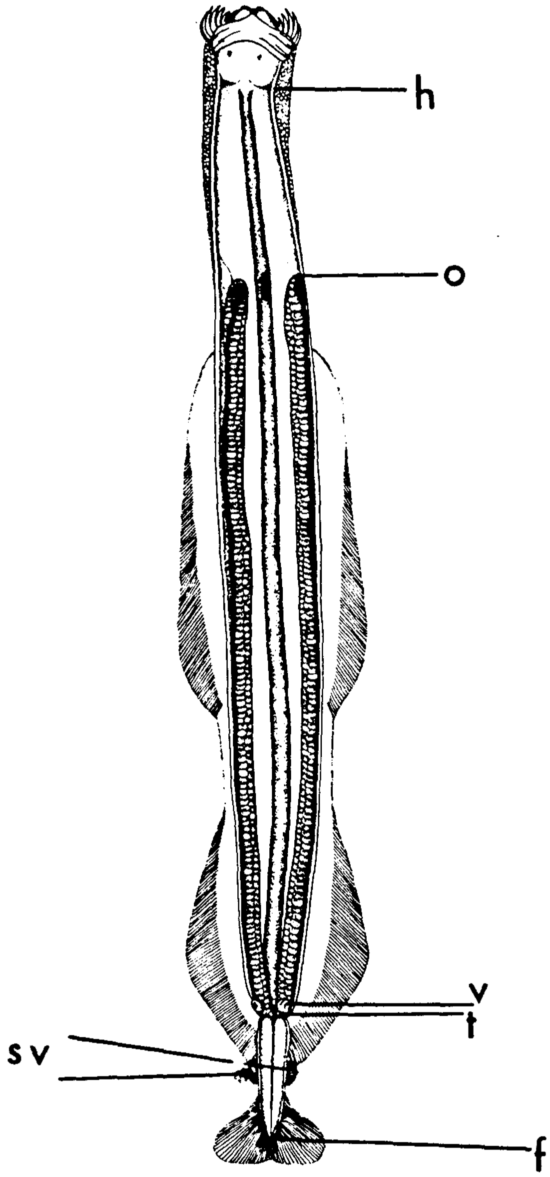

Fig. 1. *Sagitta scrippsae* (dorsal view) showing the disposition of female gonads in the trunk, and of the testes and seminal vesicles in the tail. Trunk, from h to t; ovaries, o to v; tail, t to f; sv, seminal vesicles

## II. FEMALE REPRODUCTIVE SYSTEM

The first description of the morphology of the female reproductive apparatus in chaetognaths was given by Grassi (1883). Earlier observations by Butschli (1873), Hertwig (1880), and Grassi (1881) are only short notes. The female reproductive system (Fig. 1) is located totally in the trunk cavity and is separated from the male reproductive system by the transverse septum. The ovaries are elongated tubes, round in cross-section, lying at the posterior part of the trunk. They are attached to the body wall by a thin mesentery continuous with the lining of the trunk cavity in the region of the lateral line (Burfield, 1927; Alvariño, 1963, 1967); another fibrous ligament connects the posterior end of the ovary to the transverse septum near the anus. I have observed that the final extension of the fibrous mesentery reaches slightly further than the maximum extent of the full mature ovary.

Each ovary has, on its side facing the body wall, a seminal receptacle, which is in the form of a tube or thin canal running along the whole length of the ovary, and opening at its lowest end into the vaginal region. The sperm are stored in this receptacle after copulation. There is no direct communication between the ovary proper (zone occupied by the ova) and the seminal receptacle. Krohn (1853), and Leuckart and Pagenstecher (1858) had described the receptacle as a sperm pouch (*samentasche*). Keferstein (1862) considered it an oviduct, Wilms (1844) an excretory duct, and Huxley (1852), a ciliated canal. Grassi (1881) indicated that the 'spermduct' lumen varied in size with the quantity of spermatozoa contained, and that the walls were formed by single layer of cells. Stevens (1910) and Elpatiewsky (1913) described two layers of cells, the inner one a syncytium.

The seminal receptacle when full, forms an ampulla at the upper closed end. The masses of spermatozoa within the seminal receptacle are in a state of continuous movement, depending on the amount of spermatozoa stored therein. The seminal receptacle turns posteriorly at right angles into the vaginal cavity; the latter opens out through the external genital papilla. The walls of the vagina have two epithelial layers, an inner one formed of tall cylindrical cells with large vesicular nuclei and an outer one formed of thin, flat cells with elongated nuclei. The genital papilla is formed of glandular cells arranged in small cupula. Several elongated and fusiform elements make a sphincter that serves to close the orifice of the seminal receptacle. Both the ovary and seminal receptacle are covered by a thin endothelium.

The ovary, when mature, is full of linear rows of oocytes, attached to the lining of the ovary. All oocytes in the ovary are usually at the same stage of development, but not in *Sagitta bipunctata*. In animals full of ripe ova, the intestine may be displaced to one side by the bulky ovaries. The degree of maximum forward extension of the ovaries in the trunk cavity varies considerably with species. For instance, the ovary of *S. hispida* may extend up to the region of the ventral ganglion, and in *S. ferox* and *S. septata*, to the neck, while the mature ovaries of *S. enflata* occupy only a small portion of the total trunk length.

The penetration of the spermatozoa into the ova does not occur, as stated by several authors, while the ova are still in the ovary. The ova in the ovary of chaetognaths are not embryonated eggs, but only mature ova. If the ova were to be fertilized while still within the ovary, the development of the zygote would immediately follow, but this does not occur. I have observed and determined that the ova in the ovary are not zygotes. Therefore, it appears that fertilization of the ova takes place at the time of extrusion of the ova into the vaginal cavity, when the sperm are also released into that cavity from the seminal receptacle.

### A. The Ovaries

The ovaries are two tubes situated right and left and opening to the vaginal cavity, and to the outside by the genital papillae, the latter located dorsal to the insertion of the lateral fins. Genital papillae and fins have respectively a dorsal and ventral position related to the lateral line of the body of the chaetognaths. In this manner, the opening is ventrally protected by the fins. The length the ovaries attain in fully mature individuals, varies with species, a characteristic used in diagnosing the species. The ovaries of various species of Chaetognatha have been described by Alvariño (1963, 1967, 1969), and only a summary is given here. The extension and length of the ovaries are related to other anatomical structures of the animal, such as anterior and posterior ends of the anterior or posterior fins, the ventral ganglion, and the neck region. Data on ovary characteristics for most species of chaetognaths are presented in Table. 1. Ovaries in *Eukrohnia bathypelagica* fill the body cavity and extend up to one-third the distance from ventral ganglion to tail septum, and appear to accumulate fatty tissue. The ovaries of immature specimens are coiled in an unusual way, but the coiling disappears progressively with maturity. In *E. fowleri*, ovaries are short and thick, and the seminal receptacle is large. In *E. hamata*, ovaries extend halfway between the caudal septum and neck; in *E. minuta*, ovaries are short (Silas and Srinivasan, 1969) and straight. Pieces of brood sacs were observed hanging from oviducts of most species in the genus *Eukrohnia* (Alvariño, 1967, 1968). In *Krohnitta mutabbii* and *K. pacifica*, ovaries extend to a level close to the region of the ventral ganglion, and in some cases, might extend up to near the neck region, while in *K. subtilis*, ovaries are short, reaching only the anterior end of the paired fins. The ovaries of *Pterosagitta draco* are long, wide tubes which extend up to the anterior septum in the neck, completely filling the trunk cavity in fully mature specimens.

In species of the *Sagitta* group 'maxima' (*S. gazellae*, *S. lyra*, *S. maxima*, *S. scrippsae*), and in *S. hexaptera*, the ovaries reach up to the region of the

Table 1
Chaetognatha: length of ovaries and arrangement and size of ova

| Species | Length of ovary | % of total length | Arrangement of ova | Size of ova (mm) | Average no. of ova per ovary |
|---|---|---|---|---|---|
| *Eukrohnia bathyantarctica* | 2.7 | 8.9 | 2 lines | 0.2 | 20 |
| *Eukrohnia bathypelagica* | 8.5 | 35 | 2 lines, occasionally 3 | 0.33 | ~42 |
| *Eukrohnia fowleri* | 4.8 | 12 | 2 lines | 1.5 | 6–8 |
| *Eukrohnia hamata* | 7.7 | 18 | 4 lines, ending at top in 1 ovum | 0.08 | 130 |
| *Eukrohnia minuta* | 1 | < 10 | 1 line | 0.11 | 11 |
| *Krohnitta mutabbii* | 2–2.6 | 35 | 1 line | 0.15 | ~20 |
| *Krohnitta pacifica* | 3.5 | 56 | 1 line | 0.1 | 18–20 |
| *Krohnitta subtilis* | 1.4–1.9 | 12 | 2 lines | 0.2 | 12 |
| *Pterosagitta draco* | 3.6 | 50 | 2 lines | 0.2 | 45 |
| *Sagitta gazellae* | 52 | 63 | 8 lines | 0.6 | 800 |
| *Sagitta lyra* | 17 | 46 | 4 lines | 0.2 | > 200 |
| *Sagitta scrippsae* | 40 | 67 | 4 lines | 0.5 | > 300 |
| *Sagitta maxima* | 53 | 59 | 5 lines, ending in 1 at the top | 0.3 | > 400 |
| *Sagitta hexaptera* | 27 | 54 | 3 lines | 0.5 | ~ 250 |
| *Sagitta enflata* | First cycle 0.6 | 11 | 3 lines | 0.16 | 12 |
|  | Last cycle 6 | 24 | 3 lines | 0.2 | > 100 |
| *Sagitta pulchra* | 13 | 57 | 2 lines, occasionally 3 | 0.1 | ~ 200 |
| *Sagitta bierii* | 4.6–5.6 | 33 | 2 lines | 0.13 | 50 |
| *Sagitta pacifica* | 6–7 | 53 | 1 line | 0.08 | ~50 |
| *Sagitta pseudoserratodentata* | 3–4 | 43 | 1 line | 0.1 | 20 |
| *Sagitta serratodentata* | 5 | 48 | 1 line, occas. extra line | 0.09 | ~40 |
| *Sagitta tasmanica* | 9–11 | 59 | 2 lines | 1.4 | ~160 |
| *Sagitta bombayensis* | 4–5 | 30 | 1 line | 0.1 | 30 |
| *Sagitta bruuni* | 6 | 44 | 2 lines | 0.12 | 60 |
| *Sagitta crassa* | 2.6–2.8 | 19 | 1 line | 0.13 | 18 |
| *Sagitta euneritica* | 3.9–5.8 | 39 | 3 lines | 0.1 | ~120 |
| *Sagitta euxina* | 6 | 27 | 2–3 lines | 0.2 | 70–80 |
| *Sagitta friderici* | 2 | 15 | 2 lines | 1.3 | 50 |
| *Sagitta peruviana* | 7 | 59 | 2 lines | 0.1 | 130 |
| *Sagitta popovicii* | 1.7 | 30 | 1 line | 1.6 | 9–10 |
| *Sagitta setosa* | 1.5 | 10.8 | 2 lines | 0.25 | 36 |
| *Satitta tenuis* | 1.8 | 23 | 2 lines | 0.05 | 80 |
| *Sagitta bipunctata* | 5–6 | 36 | 2 irregular lines | 0.1 | 70 |
| *Sagitta macrocephala* | 7–8 | 37 | 4 lines, ending in 1 at the top | 0.17 | 150 |
| *Sagitta helenae* | 6.5–7 | 50 | 2 lines | 0.1 | 120 |
| *Sagitta marri* | 14 | 52 | 2 lines | 0.2 | 70 |
| *Sagitta planctonis* | 18 | 51 | 4–6 lines | 0.2 | > 400 |
| *Sagitta zetesios* | 25 | 60 | 3 lines | 0.2 | > 300 |
| *Sagitta bedoti* | 6.5 | 45 | 3 lines | 0.8 | 150 |
| *Sagitta nagae* | 9–11 | 38 | 2 or 3 lines | 0.16 | 150 |
| *Sagitta elegans* | 6.8–13.6 | 34 | 2 lines | 0.30 | 90 |
| *Sagitta minima* | 1.1 | 11 | 1 line | 0.2 | ~4 |
| *Sagitta decipiens* | 6 | 41 | 1 line | 0.14 | 20 |
| *Sagitta ferox* | 10–12 | 67 | 3 lines | 0.1 | > 200 |

Table 2 (*cont.*)

| Species | Length of ovary | % of total length | Arrangement of ova | Size of ova (mm) | Average no. of ova per ovary |
|---|---|---|---|---|---|
| *Sagitta hispida* | 4–5 | 41 | 2 lines | 0.1 | 80 |
| *Sagitta robusta* | 6–8 | 66 | 1 line | 0.1 | > 60 |
| *Sagitta tokiokai* | 10–14 | 67 | 4 lines | 0.3 | < 300 |
| *Sagitta neglecta* | 4 | 51 | 1 line | 0.15 | 30 |
| *Sagitta regularis* | 2.4 | 41 | 1 line | 0.2 | 12 |
| *Sagitta bedfordii* | 1–1.2 | 32 | 1 line | 0.2 | 4–5 |
| *Sagitta johorensis* | 1.2 | 28 | 1 line | 0.1 | 9–10 |
| *Sagitta oceania* | 3 | 47 | 1 line | 0.2 | 10 |
| *Sagitta septata* | 3.5 | 59 | 1 line | 0.1 | 30 |

ventral ganglion, except in *S. lyra*, in which they extend only three-quarters the length from the posterior septum to the ventral ganglion. In *S. enflata*, fully mature ovaries reach either two-thirds the extent of posterior fins on the trunk, or to the anterior end of posterior fins, or up to anterior fins, depending upon whether the specimens are in the first, second, or last maturity cycle. It was suggested, that this polymorphism could be genetically controlled. However, the presence of a few gigantic ova, and the fact that the conjunctive mesenteric cord attaching the ovaries to the body wall reached up to the level of the anterior fins (maximum extent of the ovary in the largest individuals) appear to indicate that these organisms undergo a continuous process of growth and ovarian maturation (Alvariño, 1963, 1967) at all locations inhabited by the species. In Fig. 2A, is shown an ovary with newly developing oocytes together with three abnormally large ova. The latter are probably remnants of the previous maturity cycle, which continued to receive a nutrient supply with the new ones. The *S. pulchra* ovaries reach, in fully mature individuals, the level of the ventral ganglion.

In species of the 'serratodentata' group (*S. bierii*, *S. pacifica*, *S. pseudoserratodentata*, *S. serratodentata*, and *S. tasmanica*), ovaries reach up to or about the level of midlength of anterior fins. In most neritic species (*S. bruuni*, *S. bombayensis*, *S. crassa*, *S. euneritica*, *S. euxina*, *S. friderici*, *S. peruviana*, *S. popovicii*, *S. setosa*, and *S. tenuis*), the ovaries reach various levels of the anterior fins; in *S. bruuni*, they extend up to the level of the anterior quarter of the anterior fins. The conjunctive mesenteric filament (clearly visible in this species) extends to the level of the anterior end of the ventral ganglion, which indicates the possibility that the ovaries may reach a level close to that region. In the 'bipunctata' group, *S. bipunctata* ovaries are long, reaching the anterior third of the anterior fins, and in *S. helenae* and *S. macrocephala*, ovaries reach the level of the ventral ganglion. In the group 'planctonis', the *S. marri* ovaries extend to a region close to the ventral ganglion, while those of *S. planctonis* and *S. zetesios* extend to the neighbourhood of the neck.

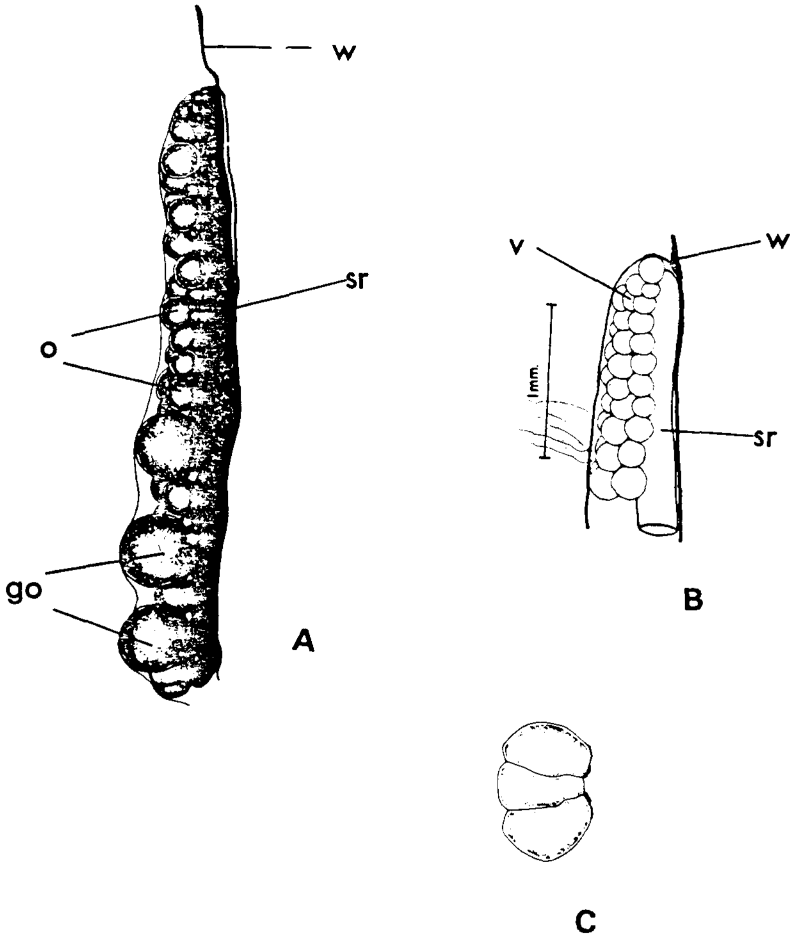

Fig. 2. (A) Dorsoventral view of ovary and ova of *S. enflata*, in second cycle of maturity. Giant ova remain from previous maturity cycle. (B) Dorsoventral view of ovary and ova of *S. macrocephala*; (C) upper view of disposition of ova in ovary of *S. tokiokai*. go, Giant ova; o, developing ova; sr, seminal receptacle filled with sperm in (A), empty in (B); v, ova; w, conjunctive or mesenteric cord attaching ovary to the body wall

In the 'bedoti' group, the ovaries of *S. bedoti* reach the region of the ventral ganglion, and in *S. nagae* to the anterior end of the anterior fins. In the group 'elegans', they extend to the anterior half of the anterior fins (*S. decipiens* and *S. elegans*); in *S. minima*, they are short, reaching the anterior middle part of the posterior fins. In species of the group 'hispida', the ovaries of *S. ferox*, *S. robusta*, and *S. tokiokai* extend to the neck region, and those of *S. hispida* to the region of the ventral ganglion. In the 'neglecta' group (*S. neglecta* and *S. regularis*), the ovaries extend to the region of the ventral ganglion. Finally, in the group 'oceania', the ovaries reach the level of the ventral ganglion in

*S. bedfordii*, *S. johorensis*, and *S. oceania*, but in *S. septata*, they extend to the neck.

## III. ORIGIN OF FEMALE GERM CELLS

The germ cells of chaetognaths, discovered by Butschli (1873), can be distinguished early in development. He described in the gastrula of *Sagitta*, pluricellular formation at the bottom of the archenteron and identified it as the primordium of the germinal line. Hertwig (1880), however, stated that this 'anlage' was formed at first by two cells. Apparently, segregation of the germinal line is still more precocious, being present in unsegmented newly laid eggs. The discrepancy found by various authors is probably due to differences in fixation and the time at which the germ cell determinant has been observed.

In chaetognaths, Elpatiewsky (1913) was the first to describe the structure of the germ cell determinant; Buchner (1910), Ghirardelli (1953a,b), Stevens

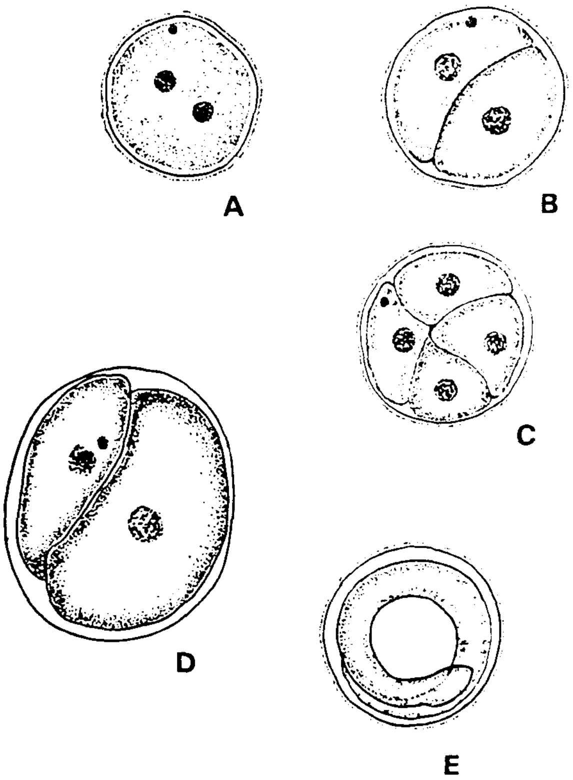

Fig. 3. Development of the egg. (A, B) The germinal cell can be observed as a dot at the top; in (C) it is at the top left; (D) indicates the two blastomeres and the identification of the germinal blastomere; (E) doubly coiled embryo in the egg of a chaetognath

Fig. 4. Representation of micrograph of germ cell determinant of *Spadella cephaloptera*

(1910), and Vasiljev (1924) also studied this formation. The germ cell determinant can be usually seen near the periphery of the egg, often surrounded by large yolk globules, in a well-defined boundary, although no membrane is present to isolate it from the cytoplasm. The germ cell determinant appears as an irregularly shaped, more or less branched filamentar mass, with large grains and plaques all tangled together. The constituents do not seem to be homogeneous, but form loops of various forms and variable opacity, due to the different nature of the formations. Grains and small plaques tend to settle around the nucleus of the germ cell.

The germ cell divides into two unequal portions (Stevens, 1910; Elpatiewsky, 1913) which divide further during or after gastrulation, forming four cells. The spermatogonia are derived from the cell receiving less quantity of the determinant, while oogonia originate from the largest cell. On hatching, two primitive cells situated in front of the caudal septum give rise to the female line (ovary, ova, and receptaculum seminis), and the other two situated behind the septum give rise to the male germ line (testis, sperm, and seminal vesicles). The primitive germ cell in the gastrula and larva of *Sagitta* is easily recognizable *in vivo* by its large size and typical voluminous nucleus. In *Spadella cephaloptera*, by destroying the blastomere containing the germ cell determinant with a fine needle, it was possible to demonstrate that the other blastomere may provide a gastrula devoid of germ cells (Ghirardelli, 1954) (see Figs. 3 and 4).

## IV. ARRANGEMENT OF OVA IN THE OVARY

The ova are arranged in the ovaries in linear rows. The number of rows of ova per ovary is a specific characteristic and ranges from 1 to 8 per ovary (Figs. 5–18). In species of *Spadella*, benthic in habits, ova are few, but large and arranged in one row along the ovary. The number of ova per ovary ranges from 3 or 4 in small tropical species and in *Spadella*, to more than 800 in *S. gazellae*, an Antarctic species. In tropical species with short life span and a continuous reproductive cycle, and in species which protect the eggs by laying them in pouches (*Eukrohnia*), or in clutches in sheltered locations (*Spadella*), the ova are fewer and larger than in species of cold and temperate waters

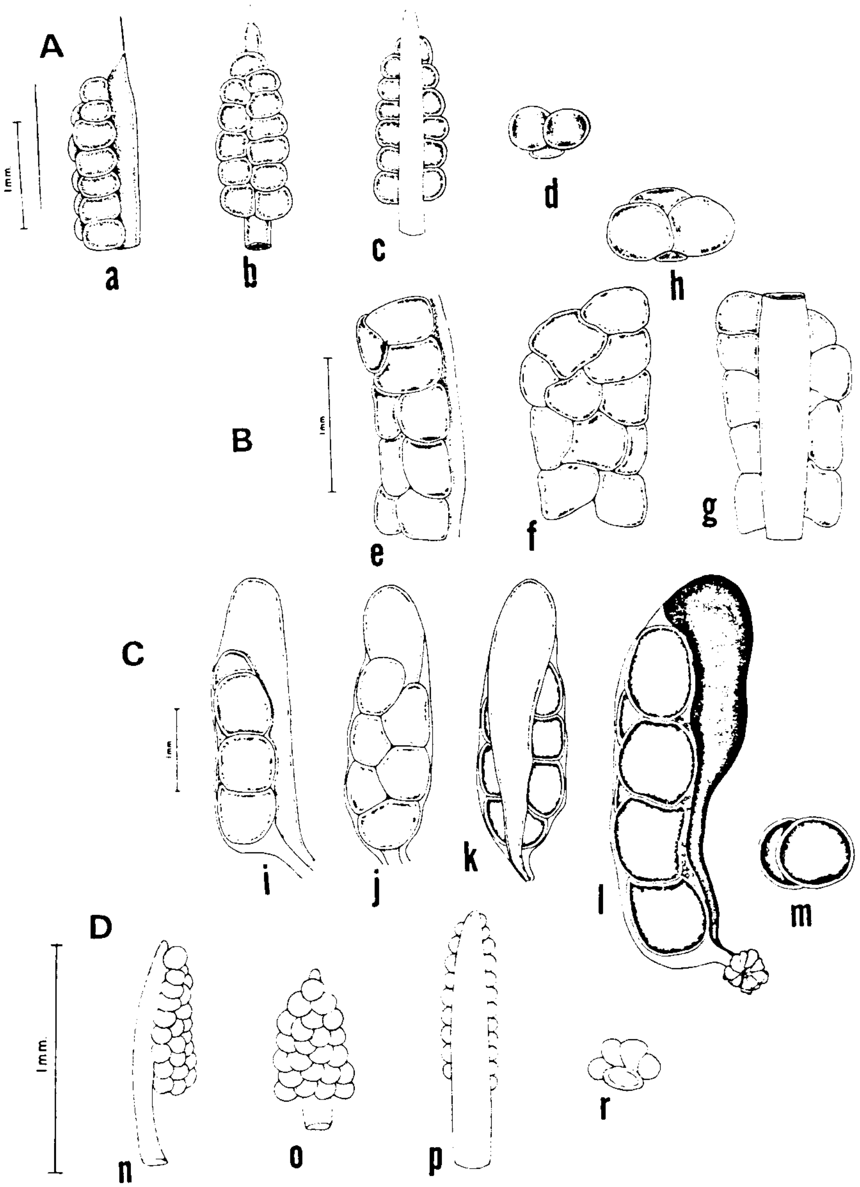

Fig. 5. Disposition of the ova in the ovary of (A) *Eukrohnia bathyantarctica*, and (B) *E. bathypelagica*; (C) *E. fowleri*; (D) *E. hamata*. a, e, i (stage 3), and n, dorsoventral view; b, f, j, and o, latero-internal view; c, g, k, and p, latero-external view; d, h, m, and r, upper view; l, dorso-ventral view of stage 4. Note the well-developed seminal receptacle in all the four species. (From Alvariño, 1967, 1969.)

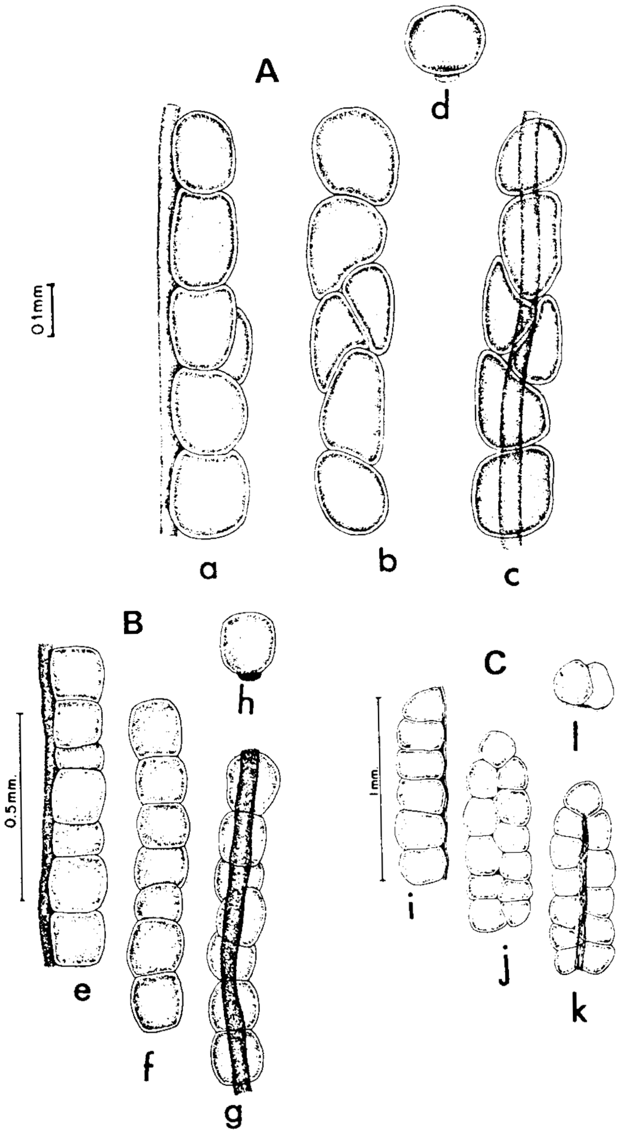

Fig. 6. Disposition of the ova in the ovaries of (A) *Krohnitta mutabbii*, (B) *K. pacifica*, and (C) *K. subtilis*. a, e, and i, Dorsoventral view; b, f, and j, latero-internal view; c, g, and k, latero-external view; d, h and l, upper view. (From Alvariño, 1963, 1967, 1969.)

laying the eggs freely in the sea. The size of the ova is reflected on the size of the embryo and the larva; larger larvae are stronger than small-sized ones, but in warm waters, development of small larvae is fast, due to increase in metabolic rate.

In Table 1 are included most of the pelagic species of chaetognaths, and

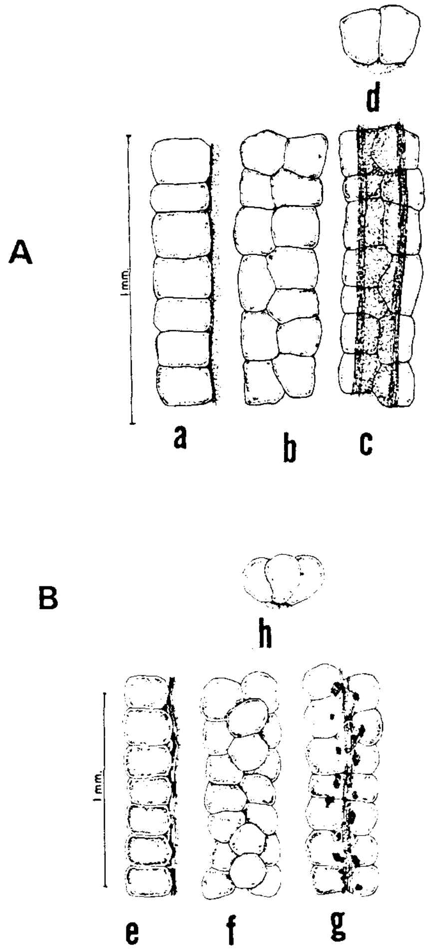

Fig. 7. Disposition of the ova in the ovaries of (A) *Pterosagitta draco*, and (B) *Sagitta pulchra*. a, e, Dorsoventral view; b, f, latero-internal view; c, g, latero-external view; d, h, upper view. (From Alvariño, 1967, 1969.)

information on the length of the ovaries, the percentual length the ovaries occupy in terms of the total length of the animal, arrangement of ova in the ovaries, size of the ova, and average number of ova per ovary. The strategic role of ova and ovaries in the ecology of the species and in the abundance of chaetognath populations is discussed elsewhere (Alvariño, Volume VI).

The relationship between ovary length and size of the ova (see Table 1) indicates the number of gametes which will be potentially transformed into eggs and produce a new generation. The average length of ripe ovaries (Russell, 1932) of adult *S. elegans* of different sizes and the ratio of their ovary length to total body length show that in small adults the length of the ovary is less in

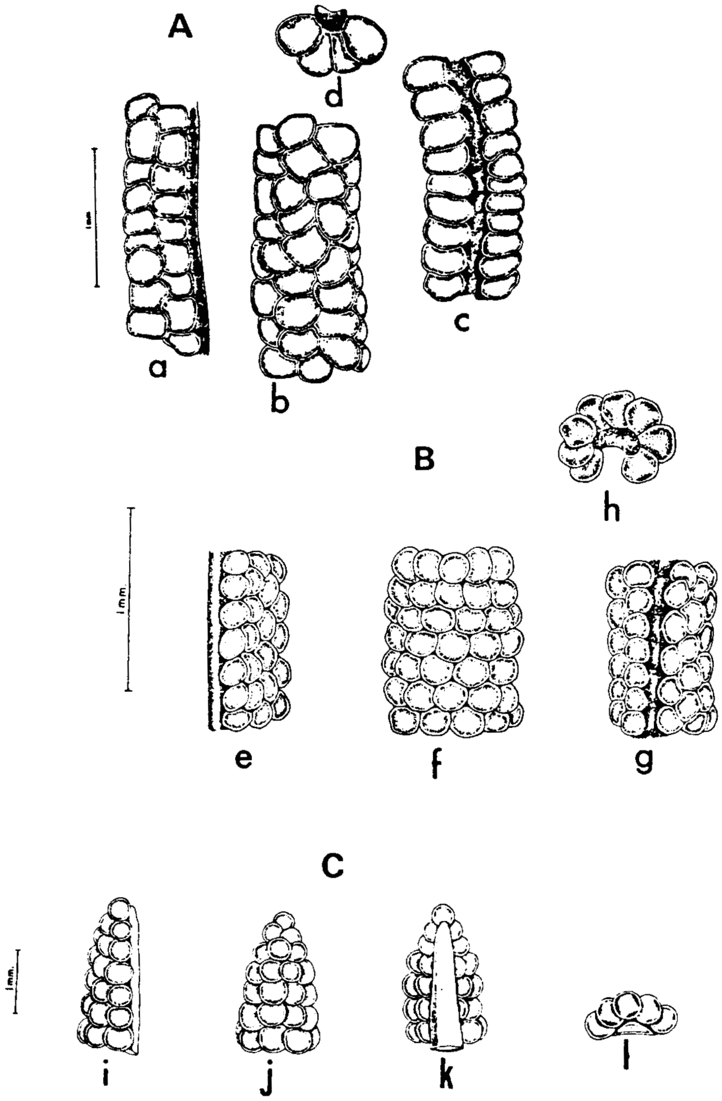

Fig. 8. Disposition of the ova in the ovaries of (A) *Sagitta lyra*, (B) *S. gazellae* and (C) *S. maxima*. a, e, and i, Dorsoventral view; b, f, and j, latero-internal view; c, g, and k, latero-external view; d, h, and l, upper view. (From Alvariño, 1967, 1969.)

proportion to the total length of the body than in large adults. There is no evidence of any marked decrease in diameter of ripe ova at different times of the year. Therefore, the number of eggs produced per individual must be greatest during the early months of the year, when the adults reach their largest size; in later summer, eggs are few due to the small size of the breeding individuals.

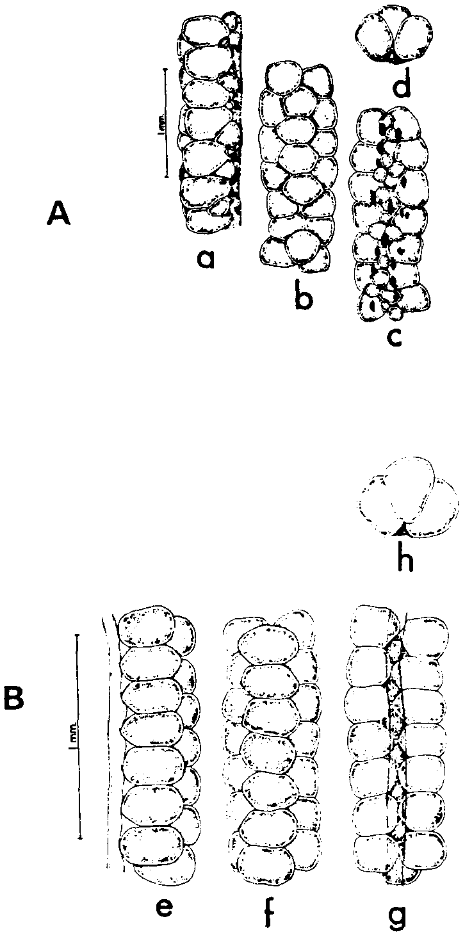

Fig. 9. Disposition of the ova in the ovaries of (A) *Sagitta hexaptera* and (B) *S. enflata*. a, e, Dorsoventral view; b, f, latero-internal view; c, g, latero-external view; d, h, upper view. (From Alvariño, 1963, 1967, 1969.)

## V. OOGENESIS

The oogonium gives rise to 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, meiotic division or first maturation division takes place, resulting in a large daughter cell and a small abortive first polar body. The secondary oocyte divides again, forming the ovum and a secondary daughter cell or second polar body which degenerates. In this way, the chromosome number is reduced to haploid.

Oogenesis has been described for *S. elegans* (Stevens, 1910), *S. bipunctata* (probably *S. friderici* or *S. elegans*) (Stevens, 1905, 1910; Bordas, 1920, see

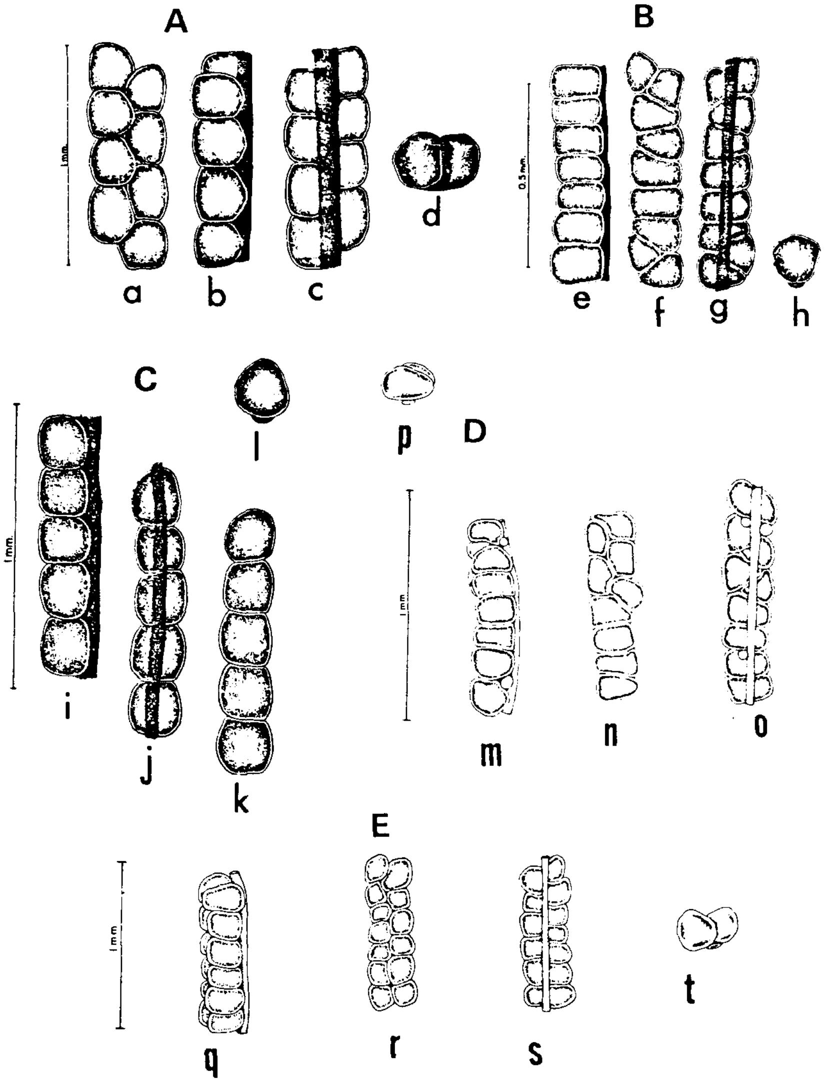

Fig. 10. Disposition of the ova in the ovaries of (A) *Sagitta bierii*, (B) *S. pacifica*, (C) *S. pseudoserratodentata*, (D) *S. serratodentata*, and (E) *S. tasmanica*. a, e, i, m and q, Dorsoventral view; b, f, j, n and r, latero-internal view; c, g, k, o and s, latero-external view; d, h, l, p and t, upper view. (From Alvariño, 1963, 1967, 1969.)

also 1912), *S. bipunctata* (Burfield, 1927), *Spadella cephaloptera* (Vasiljev, 1924; John, 1933) and *Pterosagitta draco* (Ghirardelli, 1968). Oocytes of all size classes may be connected to suspension cells, which serve to absorb substances from the mucoid syncytium, a thin layer with mucoid structure and serving as feeding substance for developing oocytes. Maturation and growth of

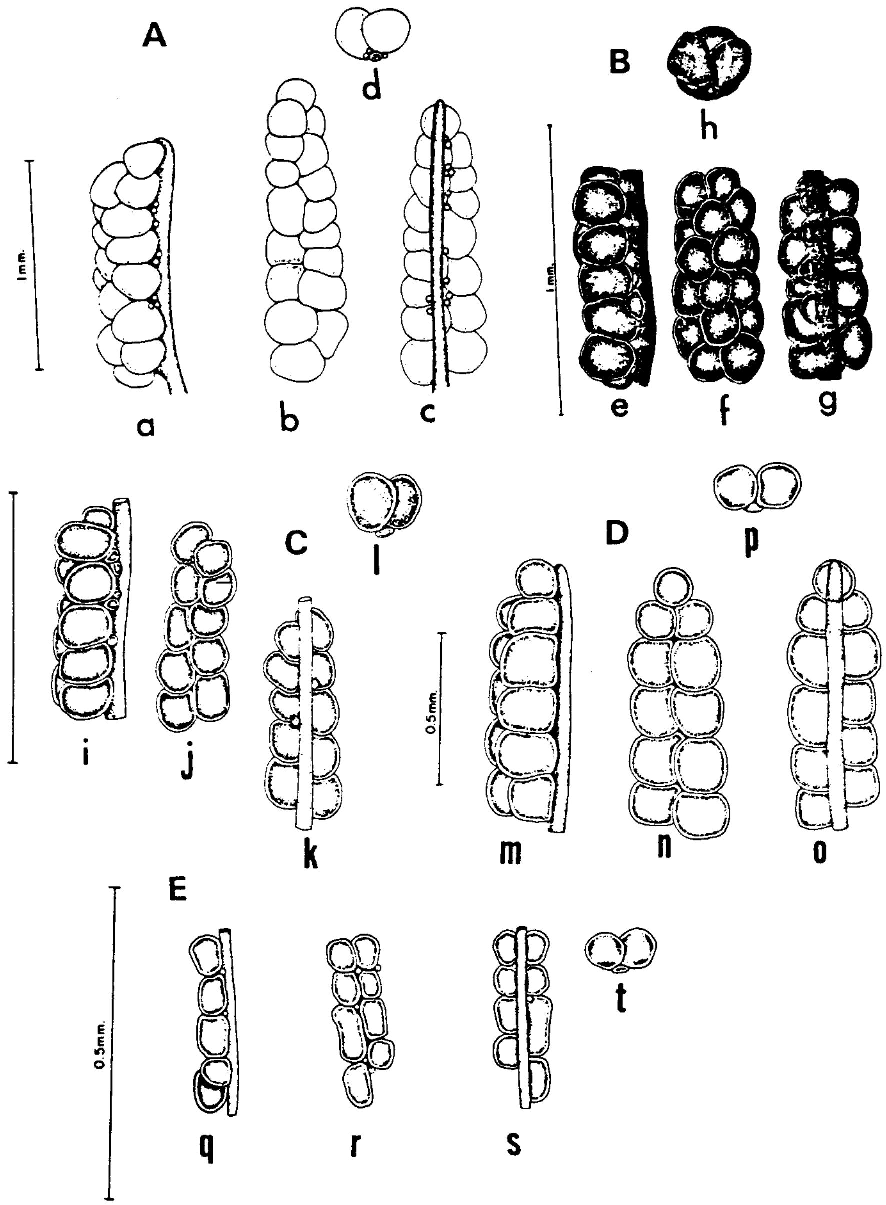

Fig. 11. Disposition of the ova in the ovaries of (A) *Sagitta bruuni*, (B) *S. euneritica*, (C) *S. friderici*, (D) *S. setosa*, and (E) *S. tenuis*. a, e, i, m, and q, Dorsoventral view; b, f, j, n, and r, latero-internal view; c, g, k, o, and s, latero-external view; d, h, l, p, and t, upper view. (From Alvariño, 1963, 1967, 1969.)

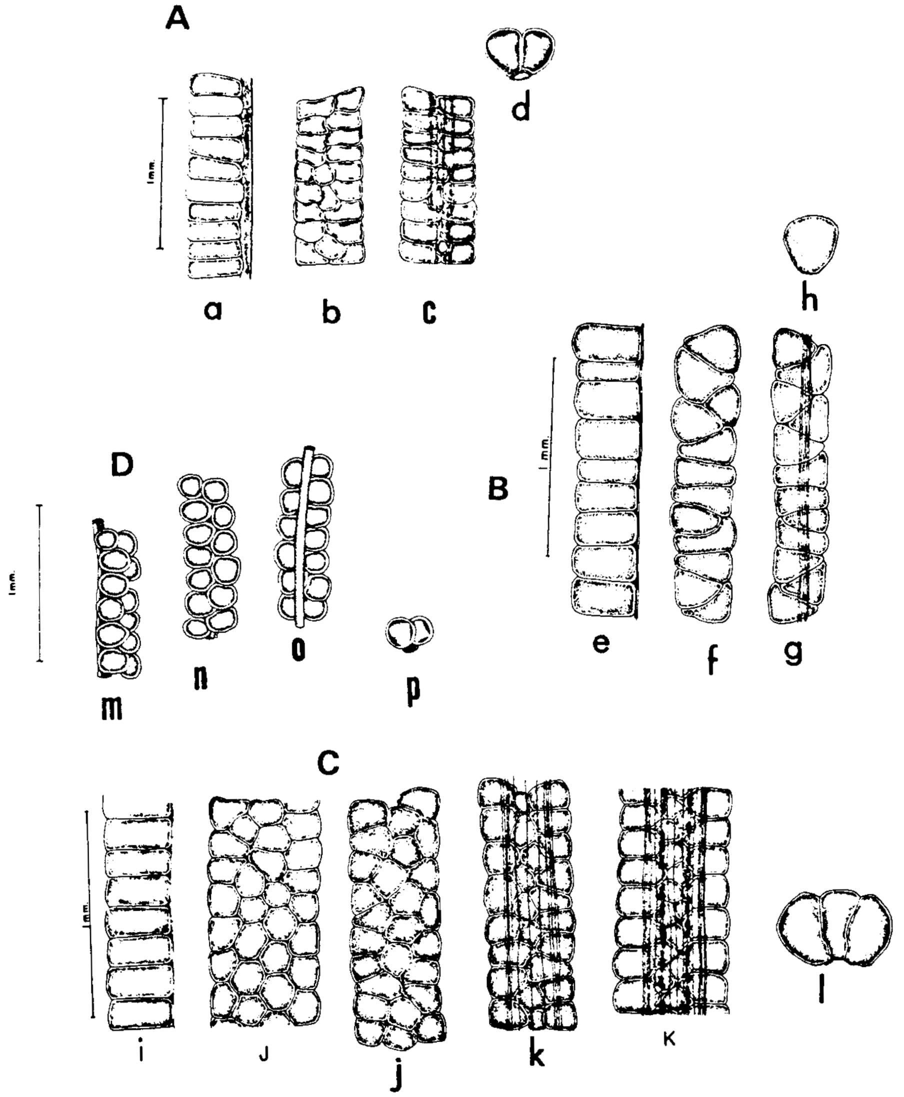

Fig. 12. Disposition of the ova in the ovaries of (A) *Sagitta ferox*, (B) *S. robusta*, (C) *S. tokiokai*, and (D) *S. hispida*. a, e, i, and m, Dorsoventral view; b, f, j, and n, latero-internal view; c, g, k, and o, latero-external view; d, h, l, and p, upper view. (From Alvariño, 1967, 1969.)

oocytes have been described by Stevens (1905) and Bordas (1920) who indicated that the ovaries might include oocytes of various sizes. These authors studied the so-called nuclear net, a series of grains and small plaques appearing in the oocytes during their first period of growth (about 10–15 $\mu$m in diameter), with nucleus at a late pachytene stage. These structures appear to be, according

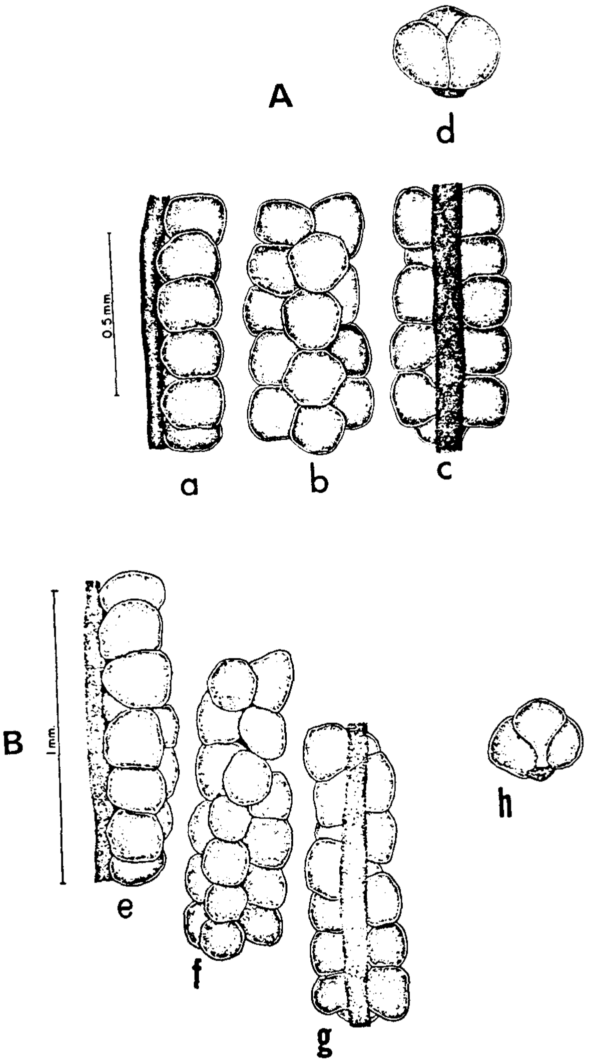

Fig. 13. Disposition of the ova in the ovaries of (A) *Sagitta bedoti* and (B) *S. nagae*. a, e, Dorsoventral view; b, f, latero-internal view; c, g, latero-external view; d, h, upper view. (From Alvariño, 1967.)

to Ghirardelli (1968), abundantly supplied with RNA, some polysaccharides, and proteins. No nucleolus was observed in the ova of *S. cephaloptera* (Ghirardelli, 1961; Ghirardelli and Brandi, 1961), which indicates that the functions of the nucleolus are probably assumed by the small plaques of the so-called nuclear net. Granulation begins to appear inside the nuclear membrane, giving at times the impression of these formations entering into direct contact with the cytoplasm. Their number increases during the second

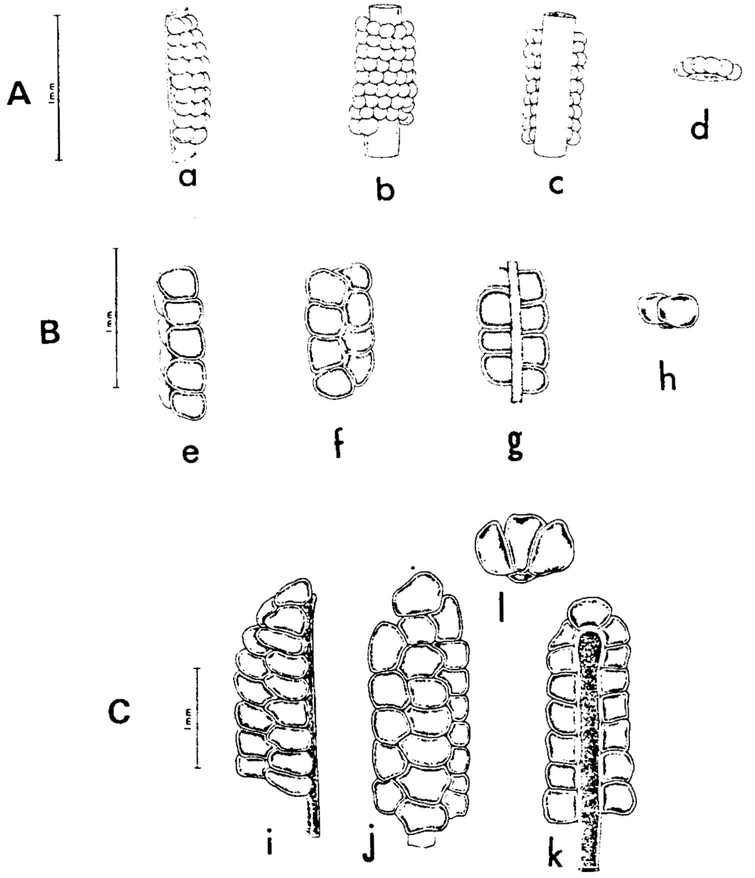

Fig. 14. Disposition of the ova in the ovaries of (A) *Sagitta planctonis*, (B) *S. marri*, and (C) *S. zetesios*. a, e and i, Dorsoventral view; b, f and j, latero-internal view; c, g and k, latero-external view; d, h, and l, upper view

period of growth (oocytes > 30 $\mu$m in diameter) when synthesis of the specific yolk protein is most active.

A relation has been observed (Ghirardelli, 1961) between the quantity of RNA present in plaques of the nuclear net and in the cytoplasm. During the first period of growth, i.e. when the nucleus is in the synaptic stage, there is an increase in RNA content of the cytoplasm; RNA is often distributed in concentric rings around the nucleus. During vitellogenesis, both cytoplasm and small plaques of nuclear net have less RNA. The greatest concentration of RNA generally occurs in small oocytes located near the seminal receptacle. This may support the hypothesis of Bordas (1920) that the seminal receptacle may have trophic functions, producing substances which may affect the development of oocytes.

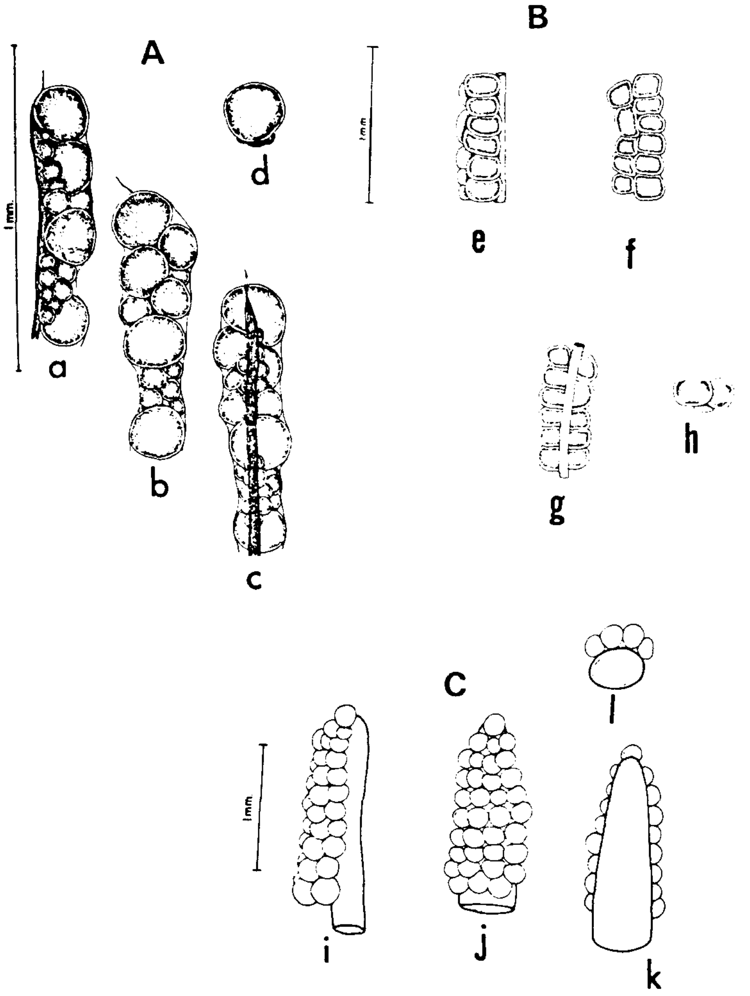

Fig. 15. Disposition of the ova in the ovaries of (A) *Sagitta bipunctata*, (B) *S. helenae*, and (C) *S. macrocephala*. a, e, and i, Dorsoventral view; b, f, and j, latero-internal view; c, g, and k, latero-external view; d, h, and l, upper view

## VI. GONAD INDEX

The most widely used and simple quantitative method for estimating reproductive activity is the gonad index, which is basic in handling large numbers of individuals (Giese and Pearse, 1974). It is calculated in various ways, but is usually the ratio of the gonad wet weight or volume to wet weight or volume respectively of the whole animal. This method may be adequate for some animals, but cannot be used for chaetognaths.

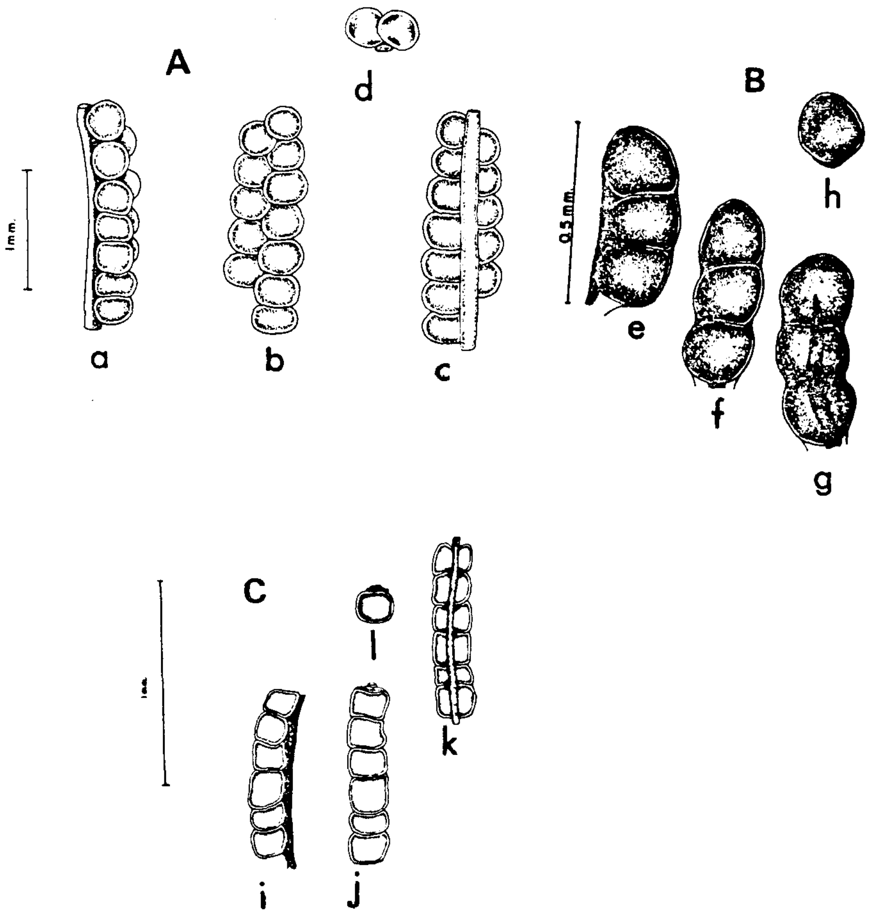

Fig. 16. Disposition of the ova in the ovaries of (A) *Sagitta elegans*, (B) *S. minima*, and (C) *S. decipiens*. a, e, and i, Dorsoventral view; b, f, and j, latero-internal view; c, g, and k, latero-external view; d, h, and l, upper view. (From Alvariño, 1963, 1967, 1969.)

Chaetognaths are transparent to translucent animals, and the gonad index can be estimated by measuring the length of the ovaries in relation to the length of the animal and the size and number of ova per animal. The male gonad index is easily measured by the development of the seminal vesicles, but this does not seem to have a definitive correlation to reproduction. On the other hand, the female gonad index has a direct significance in the population, inasmuch as the relative reproductive condition of animals of variable size can be measured and changes in gonads at different times detected. Combined with histology, the gonad index is valuable in assessing reproductive changes in chaetognath populations.

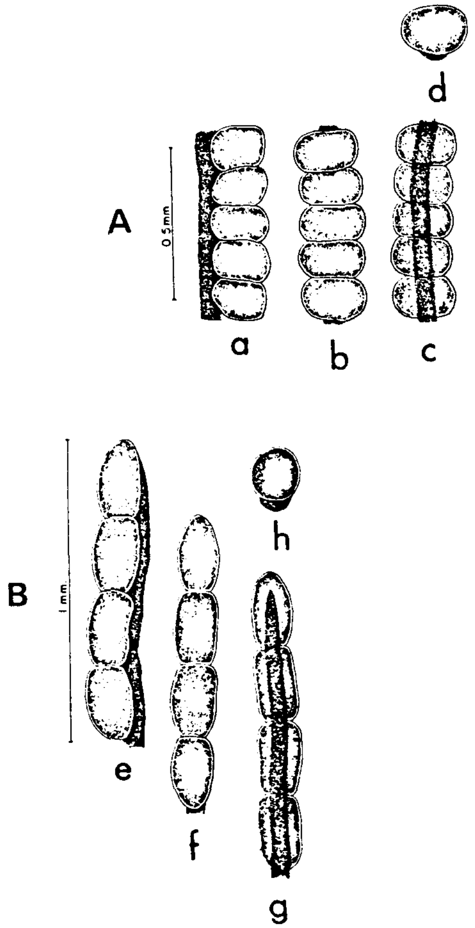

Fig. 17. Disposition of the ova in the ovaries of (A) *Sagitta neglecta* and (B) *S. regularis*. a, e, Dorsoventral view; b, f, latero-internal view; c, g, latero-external view; d, h, upper view. (From Alvariño, 1963, 1967, 1969.)

## VII. THE EGG

Chaetognath eggs are transparent and contain abundant yolk, the most transparent being those of *Sagitta enflata*. The eggs of *Spadella* have an elastic shell that can be removed, but the vitelline membrane is delicate. Electron microscope studies by Ghirardelli (1968) show that the eggshell is comprised of two well-defined layers, an external fibrillar layer 0.1 $\mu$m across, and an internal granular layer which is thicker. The vitelline membrane which is elastic has three layers closely connected with the cytoplasm (Ghirardelli, 1963). The structure of the membrane may perhaps explain the difficulty in separating the two blastomeres experimentally.

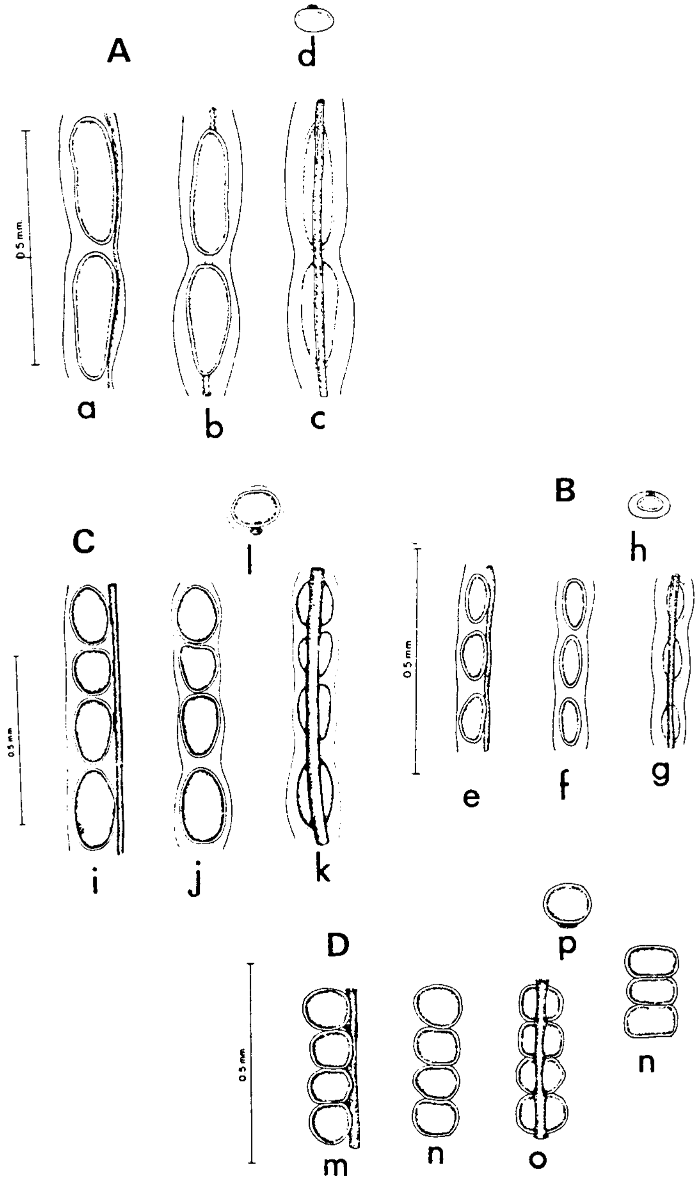

Fig. 18. Disposition of the ova and part of ovary of (A) *Sagitta bedfordii*, (B) *S. johorensis*, (C) *S. oceania*, and (D) *S. septata*. a, e, i, and m, Dorsoventral view; b, f, j, and n, latero-internal view; c, g, k, and o, latero-external view; d, h, l, and p, upper view. (From Alvariño, 1967.)

The eggs of *Sagitta crassa* and *S. bipunctata* are enclosed by a firm transparent shell and have a large vitelline space. The eggs of *S. enflata*, *S. elegans*, *S. ferox*, *S. hispida*, and *S. minima* are likewise surrounded by a firm membrane, but a perivitelline space is absent.

Egg size is in part phenotypically determined, and is in part under genetic control. Large eggs generally produce large larvae. Planktonic organisms from cold waters produce large larvae and juveniles, which are best adapted to search for food (Barnes and Barnes, 1968). The fertilized ova of *S. nagae* measure 0.16–0.20 mm at deposition, and 0.18–0.28 mm in diameter when fixed more than 10 hours later (Nagasawa and Marumo, 1978). The eggs of *P. draco* measured 0.36–0.40 mm (Sanzo, 1937), and those of *S. elegans* from the Gulf of Maine (Sherman and Schaner, 1968), Bay of Fundy and Gulf of St. Lawrence (Huntsman and Reid, 1921), 0.33 mm and from Bedford Basin 0.31 to 0.34 mm (Zo, 1973). The *S. setosa* eggs from the Black Sea ranged from 0.333 to 0.379 mm, and those of *S. euxina* were 0.30 mm in diameter (Elian, 1960). The *S. bipunctata* eggs are 0.20 mm, and those of *S. crassa* 0.35 mm (Murakami, 1959). Studies by Alvariño (1968) show that eggs of species belonging to the more advanced genus are probably the best equipped for survival.

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