SOME OBSERVATIONS ON *PELAGOSPHAERA* LARVAE

(Sipunculoidea)

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INTRODUCTION

In the material of the "Galathea" Expedition there are some specimens of the pelagical sipunculid larvae, the type of which was originally described by MINGAZZINI (1905) under the name of *Pelagosphaera aloysii*. The Committee and Prof. K. G. WINGSTRAND have been so kind as to place four specimens at the disposal of the present writer. The technical work has been supported by grants from the Swedish Natural Science Research Council.

The larvae were collected epipelagically off Natal (Feb. 17, 1951): St. 200, Lat. 29°39'S, Long. 37°01'E. Depth to bottom: 5020 m.

MINGAZZINI's description of *Pelagosphaera aloysii*, which he erroneously considered an adult sipunculid, was soon followed by others. SENNA (1906) described some similar larvae which were collected during the same plankton expedition, the circumnavigation of the globe by the Italian ship "Liguria". In his detailed description, which was also based on sectioned material, SENNA corrected the erroneous assumption that these pelagical sipunculids are adults. Independently of SENNA's paper SPENGEL (1907) showed that *Pelagosphaera* must be a pelagical larva, probably belonging to the genus *Sipunculus*. He had no new material but compared MINGAZZINI's description and figures with the larva of *Sipunculus nudus*, which was well known to him and described in papers by MÜLLER (1850), KROHN (1851), KEFERSTEIN & EHLERS (1861) and HATSCHEK (1884).

HEATH (1910) observed two specimens, which were described both in living condition and after fixation also to some extent regarding their histological structures. DAWYDOFF (1930) made some interesting observations on living specimens which differed in several details from those described in previous papers.

After DAWYDOFF *Pelagosphaera* larvae have been recorded by STEPHEN (1941) and FISHER (1947). In *table 1* is given a survey of the different reports dealing with *Pelagosphaera* larvae. It is obvious that the larvae are neither restricted to the surface layers nor to the deeper layers. They have been collected both near the coast and in the open sea and are widely distributed in the oceans of the world. All the larvae are described to be spherical or somewhat elongated. The size varies between 0.5 and 6 mm. The more elongated larvae of *Sipunculus nudus* measure only about 0.3 mm. As will be seen in the following, the descriptions in the papers mentioned above indicate that all these recorded larvae do not belong to a single species. In fact there is no reason to presume all of them to belong to the genus *Sipunculus*.

Table 1.

Described by	Year of publ.	Locality	Depth	Size mm	Number of larvae
MINGAZZINI, P.	1905	Between New Zealand and New Caledonia	0-500 m	6	1
SENNA, A.	1906	In Indonesian and Ceylonese waters	50-400 m	1.8-3.2	3
HEATH, H.	1910	Monterey bay, Calif.	surface	2.5-3.2	2
DAWYDOFF, C. N.	1930	Off the coast of Annam	surface	0.5-1.5	> 30
STEPHEN, A. C.	1941	Off southeast Africa	300-1200 m	5	1
FISHER, W. K.	1947	Between Bermuda and the coast of Florida.	0-150	3-6	many
ÅKESSON, B.	1961	Off Natal	0-5020 m	8-10	4

MORPHOLOGY

Only four specimens are available for the present study. They all have the introvert withdrawn. They are spherical or slightly ellipsoidal with the main axis from the mouth of the withdrawn introvert to the end of the ventral nerve cord. During the preservation the body wall has been deformed in some regions, (Pl. I, Fig. 1) but this is easily repaired if some of the preservation fluid is injected into the body cavity. The larvae have a remarkable size varying from 9.8 by 7.8 mm. to 10.5 by 8.2 mm. Even when stored in 70 % alcohol they are nearly transparent. They are all in the same stage of development.

The body wall is covered by an iridescent cuticula secreted from the underlaying epidermal layer and of about equal thickness, 5 μ. Numerous small pores belonging to the epidermal organs are irregularly scattered over the surface. These pores are extremely narrow and not elevated over the surface on papillae as in most sipunculids. The body wall musculature is thin, as could be expected in such a transparent pelagical larva. It consists of the outer circular and inner longitudinal layers. The connective tissue, dermis, which is normally found between the circular muscle layer and the epidermis, is practically absent. The longitudinal muscle layer is divided into 36 separate bundles, but this division is very insignificant. In sections the layer has the form of a continuous stratum.

There are three pairs of main retractors, two dorsal pairs and a ventral one. One of the two dorsal pairs extends from about the equatorial plane to the dorso-lateral part of the cephalic region. The other dorsal retractor pair extends from about 1.4 mm more anterior on the body wall at the same distance from the median plane and inserts laterally in the cephalic region. The ventral retractor pair extends from the equatorial plane of the body wall to the ventral part of the cephalic region. In addition to the retractor muscles there are also a number of delicate muscular strands extending from the body wall to the cephalic region and also to the intestine. The most conspicuous of these strands is a ventral pair which may possibly be interpreted as a second pair of ventral retractor muscles.

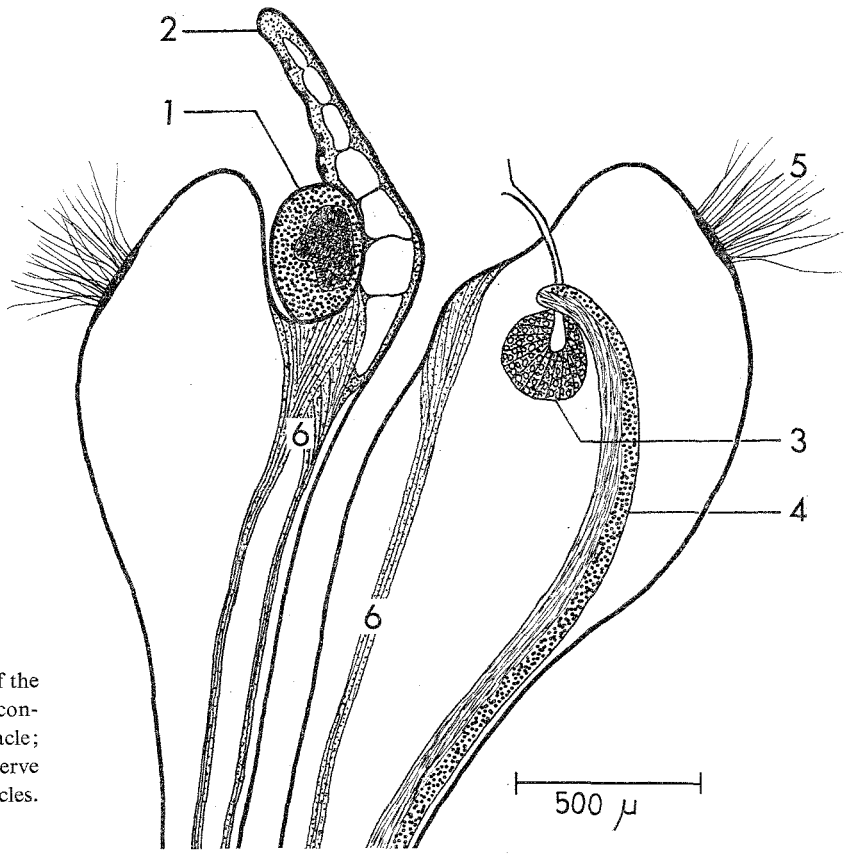
The most interesting part of these larvae is the inverted cephalic region with its appendages. All the specimens examined have the introvert withdrawn, but it is relatively easy to imagine the position of the structures in an extended condition. Such a reconstruction of an extended head of a *Pelagosphaera* larva is seen drawn in Text-figure 1. The mouth has the form of a wide funnel, which narrows to form the oesophagus. The ciliated epithelium of the dorsal part of the mouth continues in the epithelium of a single, conspicuous tentacular fold. This fold is divided into two parts by a median furrow. The brain is situated at the base of the aboral side of the tentacular fold.

In sagittal sections the brain seems to be somewhat compressed in a dorso-ventral direction, but possibly this is only a result of the inverted condition. The dorsal surface of the brain forms a continuation of the surrounding epidermal layer.

The circumoesophageal connectives fuse and form the ventral nerve cord, which is free from the body wall in the anterior part and attached by long lateral nerves. It is followed by two insignificant paraneural muscles. The nerve cord ends in the region of a terminal organ. Ventral to the oesophagus, connected with the anterior end of the nerve cord, there is a glandular organ, which consists of two hemispherical lobes whose cavities fuse into a common duct. The duct is attached to the nerve cord and the connectives. In the distal part it is also attached to the ventral wall of the oral disc. The most distal part of the duct projects into the funnel-like cavity of the mouth. In this part it is covered by the ciliated columnar epithelium cells of the oral disc. The mouth of the duct is somewhat distended and divided into two lateral laps.

The tentacular fold contains cavities belonging to the polian systen. The cavities form a system of intercommunicating channels separated by strands of connective tissue. This tentacular system communicates with a subcerebral chamber and a vessel along the dorsal part of the oesophagus. There is, however, no trace of the circular vessel round the beginning of the oesophagus, which is found in most sipunculids.

The digestive tract forms a simple loop. It is much shorter than in other sipunculid larvae and has no tendency to form a coil. The first part, the oesophagus, is relatively narrow. It is followed by a sac-like evagination, the stomach according to HEATH's terminology. This part narrows to form the intestine, which is followed by the very short proctodaeal rectum. This opens in the body wall somewhat anterior to the attachment of the shortest dorsal retractor pair.



Text-fig. 1. A scheme of the head of the *Pelagosphaera* larva in an extended condition. 1, cerebral ganglion; 2, tentacle; 3, glandular organ; 4, ventral nerve cord; 5, metatroch; 6, retractor muscles.

The two nephridia have a lateral or slightly ventro-lateral position at the level of the anus. The size is about 0.9 by 0.5 mm. The nephrostome and the nephridiopore are close together separated only by a membrane which reaches about four-fifths of the distance to the free end of the nephridium.

In the coelomic fluid are found red corpuscles, amoebocytes and giant multinucleated bodies. The first two types are also found in the polian system.

COMPARISONS

As most of the older reports deal only with the morphology in broad outline, it may be convenient now to make a comparison between them and the description given above.

From the *table 1* is seen that the animals from the "Galathea" expedition are larger than any of the others. However, the larval characters of the "Galathea" animals are beyond doubt. There are no traces of gonads.

It is obvious that all larvae described in this and previous papers are sipunculid larvae. Nothing else is suggested except by HEATH, who points out certain similarities with the Echiurid larvae, especially those of *Echiurus pallasii*. However, this mistake depends on the fact that he is not clear about the morphology of the larvae under normal condition, i.e., when the introvert is extended. What HEATH considers as the mouth is nothing but the opening on the boundary between the trunk and the invaginated introvert. What is described as a conspicuous dorsal sac of the pharynx is the part of the head dorsal to the tentacular fold. Also SENNA mentions the dorsal sac. According to HEATH all six retractors are attached to this region. This condition has not been seen by others, and it is impossible to evaluate this statement. Also with respect to the ciliation these larvae differ from those described in other papers, i.e., when any ciliation is mentioned at all. Only from the dorsal diverticulum are cilia mentioned and no cilia are found ventral to the mouth. The larvae of SENNA and DAWYDOFF have a metatroch like the "Galathea" larvae. In the other papers nothing is said about ciliation.

For the taxonomic account of the sipunculids the

number and arrangement of the retractor muscles have a great significance. In the larvae described by MINGAZZINI, SENNA and HEATH the retractor number is 6, but FISHER mentions 4 retractors and 8 delicate strands. FISHER's statement agrees fairly well with the condition in the larvae of *Sipunculus nudus* (HATSCHEK 1883). These larvae have 4 retractors and, at least during the first pelagic stage, another 4 accessory retractors, which disappear in the beginning of the metamorphosis. These accessory retractors are very delicate structures as compared with the persistent ones.

Another thing of taxonomic value is the arrangement of the muscle layers of the body wall. Judging from the descriptions and especially from the pictures all the larvae have the longitudinal muscle layer separated into bundles, although the separation is indistinct in some of them. The "Galathea" larvae have 36 bundles like the larva described by STEPHEN. Those described by FISHER all have 56 bundles except one which has a brown and opaque body wall and not over 15 muscle bundles. This single specimen is suggested to belong to a different species. For comparison it ought to be mentioned that the *Sipunculus nudus* larvae like the adult animals have 32 longitudinal muscle bundles (HATSCHEK 1.c.).

With respect to the body wall DAWYDOFF's observations are very interesting. Instead of the insignificant papillae, irregularly scattered over the surface, which are reported from the other larvae, these have prominent papillae arranged in longitudinal rows on the trunk. In connection with the metamorphosis the epidermal organs, which open on the papillae, secrete an envelope in the shelter of which the metamorphosis occurs.

DAWYDOFF states that his larvae have protonephridia in addition to metanephridia of the normal sipunculid type. However, as the present writer has tried to show in an earlier paper (ÅKESSON 1958, pp. 68-69) he has probably mistaken the ventral glandular organ for the protonephridia.

As can be seen from the foregoing, it is most probable that the larvae described in this and previous papers represent a number of different species. Larvae in the same stage of development with 15, 36 and 56 longitudinal muscle bundles cannot belong to the same species. When also the number of retractor muscles and the arrangement of the epidermal papillae are considered, it is obvious that they represent at least 4, perhaps 5 different species. The possible relations between the larvae and the hitherto known adult sipunculids will be discussed after the description of the histological structures.

HISTOLOGY

The Body Wall

The morphology of the body wall has been dealt with above. With respect to the histology the epidermal organs are of the most interest. They are of two types which closely resemble two of the three types found in the genus *Sipunculus*. (METALNIKOFF 1900; ÅKESSON 1.c.). The most conspicuous type is the bicellular glandular organ. This consists of two bulb-shaped cells pressed together. In the distal part of each cell there is a small receptacle. The two receptacles open with a common, very narrow duct through the cuticula. Each gland cell has two nuclei, one in the distal part and one in the proximal part. The whole organ is approximately spherical with a diameter of 25-40 μ.

The other epidermal organ type is much smaller, an elongated mass of sensory cells with a size of 10 by 20 μ. This organ type is always connected with the bicellular glandular one. They have a position close to the delicate connective sheath which surrounds the first organ type and open on the surface only 7-8 μ from the glandular duct.

The Cerebral Ganglion

The cerebral ganglion shows an internal structure very similar to that of the ganglion of *Sipunculus nudus*. In order to understand the special conditions in the *Pelagosphaera* ganglion, it is necessary, however, to give a short survey of the relations between the cerebral ganglion and the surrounding tissues in sipunculids.

In most sipunculids the cerebral ganglion is elongated along the transversal axis. In the early trochophora the apical plate is terminal. Later it is moved to a more dorsal position. A comparative study of the later development (ÅKESSON 1958, fig. 77) indicates that this includes turnings around the transversal axis. All sipunculid species retain the epithelial position of the cerebral ganglion. In the adults of all species except *Onchnesoma steenstrupi* it is the anterior margin of the ganglion which retains the connection with the surrounding ectoderm. This part of the ganglion forms a special organ, the cerebral organ. The function of the organ is not known. In larval stages it has a strong secre-

tory activity. It is nonciliated and in the adults always covered by a thick cuticula.

In *Pelagosphaera* the turning of the cerebral ganglion has only reached a stage corresponding to that of a *Sipunculus nudus* larva in the first beginning of the metamorphosis. The free, epithelial part has a dorsal position and forms the whole flattened dorsal surface of the ganglion. Perhaps it is not quite correct to describe the position of the ganglion so in detail when all the larvae studied have the introvert withdrawn, but as a matter of fact the movements of the introvert in sipunculids will not change the relative position of the cerebral ganglion.

The oesophageal connectives enter the cerebral ganglion ventrally at some distance from the lateral margin. Within the ganglion they continue in the central neuropile mass. They are also connected with a posterior ventral commisure and with a posterior dorsal commisure. These two posterior commissures are homologous with the posterior dorsal commissure and the anterior dorsal commissure respectively in the brain of *Sipunculus nudus* (ÅKESSON l.c., pp. 122 ff.).

In close connection with the oesophageal roots two pairs of nerves are given off. The strongest one is given off from the most lateral part of the ganglion. It innervates the body wall in the head region. The other nerve pair innervates the ventral side of the tentacular fold. From this pair is also given off nerve branches to the dorsal and lateral parts of the oral disc. Together with other small branches from the connectives they form the origin of the intestinal plexus. From the dorso-lateral part of the ganglion another pair of strong tentacular nerves is given off without any connection with the connectives.

Three types of ganglion cells can be observed in the cerebral ganglion. The first type, which includes the majority of the cells, is very small, poor in cytoplasm and obviously unipolar. The diameter of the rounded nucleus is 5 μ. There is a certain concentration of this type in the lateral part of the ganglion, corresponding to the position of the globuli in the genus *Sipunculus*. However, the aggregated cells are impossible to distinguish from other small ganglion cells.

The other type is richer in cytoplasm and has a length of 15-18 μ. The slightly elongated nucleus has a length of 7-8 μ. This type is most frequent along the anterior margin of the ganglion.

In the posteroventral part of the ganglion we can find the third type, giant cells with a length of 30-35 μ and a large nucleus, 12-14 μ, rich in chromatin.

All these three cell types correspond to cell types found in the cerebral ganglion of members belonging to the genus *Sipunculus*. In fact, all structures in the brain of *Pelagosphaera* are to be compared with structures in the brain of this genus.

In the most lateral part of the cerebral ganglion two rudimentary ocular tubes can be found. They are insignificant infoldings covered by a thickened cuticula. The cells round the infoldings are somewhat pigmented. It is only from the comparative study of other sipunculids that it is possible to localize these eye rudiments.

Within the ganglion without any connection with the surrounding brain capsule another pair of photoreceptory organs is found. It consists of two cup-shaped pigmented aggregations of cells which have the concavity in a lateral direction. Obviously it is the inverse larval eyes corresponding to those pictured by GEROULD (1907, fig. 90) from *Golfingia vulgare* and by HATSCHEK (figs. 69-73) from *Sipunculus nudus*. Also SENNA pictures two types of eyes in his *Pelagosphaera* larvae.

The Tentacle

The tentacle forms a conspicuous transversal fold between the brain and the mouth (Pl. II, fig. 2). At the base the fold has a breadth of 1.1 mm, which is more than the breadth of the cerebral ganglion. The ciliated epithelium on the oral side consists of slender cylindrical cells with a length of about 30 μ. The strong basement membrane of this epithelium layer is covered on the other side with the flat epithelium cells of the tentacular cavities.

The aboral side of the tentacular fold is covered with a peculiar epithelium layer. On the surface it has secreted a cuticula. Cilia are lacking. The nuclei of the cells are situated near the surface together with most of the cytoplasm. From the proximal part of the cells slender fibrous strands transverse the wall to the basement membrance under the tentacular cavities. Together with connective fibers these strands form a meshwork which is filled with large acidophilic cells. This part seems to give the stability to the tentacular fold and probably it also forms a shelter for the exposed cerebral ganglion.

On the aboral side and especially on the lateral margins of the tentacular fold a special type of sensory organs is to be found. The organs have been described by the present writer under the name of "tentacular eyes" (ÅKESSON 1958 pp. 139 ff.). They have been found on three members of the

genus *Sipunculus: S. nudus, S. angasi,* and *S. norvegicus*. They are not known from other sipunculid genera. In the *Pelagosphaera* larvae the organs do not give the same impression of photoreceptory organs as in the *Sipunculus* species owing to the fact that the pigmentation is lacking. A single organ has the form of a deep cylindrical depression, which is lined with ciliated cells (Pl. II, fig. 3). The cells of the surrounding surface are also ciliated. There is an increased number of cells around the proximal part of the depression. Some of these cells are supporting cells, but judging from the structure of the organ of the *Sipunculus* species, some are sensory cells. In these species there is also a strong pigmentation in both the epithelium cells and in the sensory cells. However, the principal structure is exactly the same in the *Pelagosphaera* larvae.

The Glandular Organ

The glandular organ which opens on the ventral median part of the oral disc is a typical larval organ, which has been described among others by HATSCHEK from the *Sipunculus nudus* larvae. In the *Pelagosphaera* larvae the organ is a large structure, the gland and the duct measure together about 1 mm (Text-fig. 1). The main part of the two hemispherical lobes of the proper gland consists of slender secretory cells with a length of about 110 μ. The surface of the gland is covered with a delicate sheet of connective tissue. The secretion shows in azan a basophilic staining reaction. The nuclei of the glandular cells are somewhat ellipsoidal, 8 by 5 μ. In the four specimens available for the histological study each glandular lobe is separated into two halves, the gland cells of which are in different phases of secretory activity.

The gland cells reach to a central cavity with a diameter of about 100 μ. As can be seen in fig. 6 (Pl. IV) the glandular cells only form the lining of two quadrants in a transversal section. The walls in the other two quadrants are ciliated. A closer study of the ciliated areas shows that each quadrant consists of a single arched cell. A number of such large ciliated cells forms two distinct areas in the median plane of the organ. They continue in the proximal part of the duct. In the rest of the duct the wall consists of a large number of ciliated cells. The most distal part of the duct projects over the surface of the oral disc and forms a narrow funnel, which is divided into two lobes by a median furrow.

HATSCHEK's opinion that the glandular organ arises as a stomodaeal evagination is supported by the fact that the ciliated cells are lined with a delicate cuticula.

In respect to the histological structures there is no close connection between the glandular organ and the central nervous system. The gland is situated dorsal to the most anterior part of the ventral nerve cord. It projects free into the coelom and is attached to the fork of the oesophageal connectives only by means of the duct. The duct passes between the connectives and the oesophagus wall, and the surrounding sheet of connective tissue is partly common with that of the connectives and the anterior part of the ventral nerve cord. No nerves have been observed passing from the connectives or nerve cord to the glandular organ.

In his papers about the development of the sipunculids GEROULD (1903 and 1907) has pointed out the similarities between the glandular organ and a similar organ in the heteropod *Firoloides* (FOL 1876). Both structures are stomodaeal evaginations which are more or less reduced in adult condition, but except for these similarities it seems difficult to get anything out of this comparison. Within the sipunculid group, however, there is another organ which deserves to be mentioned in this connection. In the genera *Aspidosiphon, Siphonosoma* and *Phascolosoma* (previously *Phymosoma* or *Physcosoma)* the most anterior part of the ventral cord is in close contact with a tubular organ which seems to be an epidermal invagination. (SPENGEL 1912, pp. 268 ff.; ÅKESSON 1958, pp. 107 ff.). The tube opens on the surface in the ventral median line immediately posterior to the cervical collar. In some species, for instance in *Phascolosoma granulatum,* the innermost part of the tube penetrates the connective tissue sheet of the nerve cord and forms within this an enlarged cavity. The cavity is filled with a solid body, which is probably derived from the cuticula of the tube. According to SPENGEL the organ must be interpreted as a statocyst. But in some species, for instance in *Siphonosoma cumanense* and *Aspidosiphon clavatus,* the organ has a somewhat different structure and cannot function as a statocyst.

When comparing the glandular organ of the *Sipunculus* and *Pelagosphaera* larvae with "the ventral sensory organ" in the genera mentioned above we will find striking similarities. Both organs have an ectodermal origin and have resulted from invaginations in the ventral median plane. Both are closely connected with the anterior end of the ventral nerve cord. As a matter of fact there is nothing speaking

against an assumption that the organs are homologous. Unfortunately nothing is known about the development of the genera *Phascolosoma, Aspidosiphon* and *Siphonosoma*. These three genera form a distinct group among the sipunculids not only owing to the presence of the ventral sensory organ but also in having the same types of epidermal organs and the same arrangement of the lateral nerves of the ventral nerve cord. (ÅKESSON l.c., pp. 227ff). The different position of the external opening of the duct will not form any insuperable difficulty to explain. Among the sipunculids there are several examples of similar displacements. The retractor muscles can be attached with their posterior part in the first third of the trunk, in the second third or sometimes in the most posterior part of the trunk. The anus is usually situated between the first and second third of the trunk, but in the genus *Onchnesoma* the anus has a position just posterior to the head.

The Metatroch

It is quite obvious that a larva with the spherical form and the size of the *Pelagosphaera* must have some kind of floating apparatus for the pelagical mode of life. The body proper is covered with a cuticula, but around the "head" we find a prominent circlet of ciliated cells, a metatroch. As all the four animals studied have the introvert withdrawn, the metatroch is found in the cavity in which we also find the cerebral ganglion, the tentacle, the mouth and the duct of the glandular organ.

The cilia of the metatroch cells are extremely long, 170 μ. For comparison it ought to be mentioned that the cilia of the oral disc and the tentacle have a length of only 10 μ.

The metatroch cells form an about 85 μ broad continuous girdle around the head. They are slender cylindrical cells with a length of about 35 μ. Some of the cells seem to have begun to degenerate and have lost their nuclei.

In the margin of the metatroch girdle, both the anterior and posterior margin, there is a zone from which the ciliated cells probably are regenerated. The cells in this zone have big rounded nuclei with a diameter of 10-12 μ. The cells of the zone have no cilia. They show the same staining reaction as the metatroch cells. The boundary between the metatroch and the surrounding cells is not at all as sharp as in other sipunculids (GEROULD 1907, ÅKESSON 1958).

It may be questioned whether the metatroch has not a second function in addition to acting as a floating organ. In the first part of the intestine of two of the animals is found a dense mass of long metatroch cilia mixed with small organisms, which could not be identified. It is not quite improbable that the cilia are sticky and that small planktonic organisms adhere to them and afterwards are swallowed together with the cilia.

The Ventral Nerve Cord

The ventral nerve cord is of the ordinary sipunculid type, i.e., it is completely unpaired and without any trace of metamerism. In the introvert region and in the anterior part of the trunk region the nerve cord is accompanied by two paraneural muscles. These parts of the nerve cord are attached to the body wall by means of long lateral nerves. More posteriorly the cord is more closely attached to the body wall. The lateral nerves are surrounded by a strong connective sheath in which also muscle fibers are seen.

In most sipunculids the ventral half of the nerve cord is occupied by the nerve cells, the dorsal half by the neuropile. In the *Pelagosphaera* larvae, however, the nerve cells also occupy the lateral parts of the cord (Pl. III fig. 4).

Two types of cells can be distinguished. One of them, which is very poor in cytoplasm and has slightly elongated nuclei, has a lateral position. The other type is situated in the median plane completely separating the members of the first type into two lateral parts. These cells have more cytoplasm and rounded nuclei (Pl. III, figs. 4 and 5). However, the position of the two cell types gives no evidence of any paired origin of the nerve cord. From the study of the regeneration ability of sipunculids (SCHLEIP 1934, 1935; WEGENER 1938) it is known that the ventral nerve cord contains a strand of regeneration cells which often has a median position. The present writer has seen the same regeneration cells in several sipunculid species, especially markedly in *Onchnesoma steenstrupi* (ÅKESSON l.c. fig. 71). It is possible that the regeneration strand in all sipunculids is nothing but a strand of neuroblasts, which in larvae and juvenile animals successively forms new neurons and in an injured animal differentiates into the ectodermal part of the regenerate.

The Terminal Organ

The posterior end of the ventral nerve cord is closely connected to a strange organ, the terminal organ,

DISCUSSION

The *Pelagosphaera* larvae are the largest reported sipunculid larvae. In fact the specimens from the "Galathea" expedition have a volume several times that of adult sipunculids of many species, for instance *Golfingia minuta* and the members of the genus *Onchnesoma*. However, the larval characters are indisputable. First of all the absence of recognizable reproductive organs ought to be mentioned, but also the striking similarities with the well known larvae of *Sipunculus nudus* and the presence of typical larval organs – metatroch, inverse eyes and the glandular organ, all justifying the conclusion that the specimens studied are in larval stages.

Of the about 250 hitherto described sipunculid species the developmental history is known from only half a dozen. Four of these belong to the genus *Golfingia,* which is considered the most primitive among the genera. The development of *Phascolion strombi* is very similar to that of the *Golfingia* species. All these five species have a very short, lecitotropic pelagic stage or no pelagic stage at all *(Golfingia minuta)*. Different from these species *Sipunculus nudus* has a planktotropic stage of about one month. *S. nudus* differs also in many other details from the primitive type found in the other species (HATSCHEK 1884, GEROULD 1903). However, nothing is known about the development of any members of the other genera, e.g., *Dendrostomum, Phascolosoma, Siphonosoma, Aspidosiphon* and *Xenosiphon*. Under such conditions it is quite impossible to refer the *Pelagosphaera* larvae to any single species, not even to any of the genera. From the descriptions in this and older papers it is evident that the *Pelagosphaera* larvae belong to a number of different species. The striking similarities between the *Pelagosphaera* larvae and the larvae of *Sipunculus nudus* were already pointed out by SENNA (1906) and SPENGEL (1907). Also the histological structures of the *Pelagosphaera* larvae support an assumption that the animals are closely related. The epidermal organs are of the *Sipunculus type* (ÅKESSON 1958 pp. 227 ff.) as also the terminal organ and the tentacular eyes. However, the single tentacle dorsal to the oral disc and possibly also the glandular organ connect the larvae to the genera *Phascolosoma* and *Aspidosiphon*. Possibly the terminal organ is a primitive structure. It is found in adult condition only in the members of the genera *Sipunculus* and *Xenosiphon* disregarding the report of CUENOT (1902) that *Siphonosoma arcassonense* is provided with four glandular appendages around the terminal end. A similar glandular terminal organ is found in the larvae of *Golfingia elongata* from Roscoff (ÅKESSON 1961). Here the secretion of the organ adheres the larvae to *Zostera* roots and other objects in the intertidal zone.

With respect to the histology of the cerebral ganglion the *Pelagosphaera* larvae agree in most details with the genus *Sipunculus*. The central neuropile and the commissures have just the same relative position, the differences depend upon the turning around the transversal axis in the later developmental stages of members of the genus *Sipunculus*.

It is a well known fact that the metamorphosis can be postponed in many marine invertebrates if the suitable conditions do not exist (THORSON 1952). The considerable size of the *Pelagosphaera* larvae is perhaps reason for placing them in this category but the enormously developed metatroch which is specialized as a floating apparatus and for the collecting of food and is not seen in the planktotropic larvae of *Sipunculus nudus,* speaks in favour of an assumption that the *Pelagosphaera* larvae have normally a very long planktotropic pelagical stage. Nothing is known about the metamorphosis except the scanty observations in DAWYDOFF's paper.

To summarize, it is obvious that the *Pelagosphaera* larvae studied here belong to a species whose development is of the *Sipunculus* type. The most probable genera to which the species should be referred are *Sipunculus* or *Xenosiphon*.

SUMMARY

1. The material consists of four larvae which were collected by the "Galathea" Expedition. Similar sipunculid larvae have been described by other authors, the first time they were supposed to be adult, pelagical sipunculids.

2. The morphology of the larvae is described. They are slightly ellipsoidal when the introvert is withdrawn. The length is more than 10 mm. The body wall is thin and almost transparent. The longitudinal muscle layer is separated into 36 bundles. Two dorsal and one ventral pair of retractor muscles are attached on the large cephalic region. A single

tentacle forms the dorsal boundary of the funnel-like mouth. The duct of a large glandular organ opens in the ventral wall. A metatroch with large cilia surrounds the cephalic region. The intestine forms a simple loop between the mouth and the anus. The terminal end of the ventral nerve cord is connected with a terminal organ.

3. The morphology is compared with the morphology of other recorded *Pelagosphaera* larvae. It is concluded that the *Pelagosphaera* larvae must belong to at least 4, probably 5 different species.

4. The histology of the different regions is described. In many details the *Pelagosphaera* larva agrees with the structures found in adult or larval stages of *Sipunculus nudus*.

5. A hypothesis is put forward that the glandular organ which opens in the ventral median plane of the oral disc and the ventral sensory organ of the genera *Siphonosoma, Phascolosoma* and *Aspidosiphon* are homologous.

6. The metatroch cilia have a double function, forming both a floating apparatus and a food-collecting apparatus.

7. The taxonomic position of the *Pelagosphaera* larvae is discussed.

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