The Epistome of *Phoronis psammophila* (Phoronida)

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With 5 Figures

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Abstract

The Epistome of *Phoronis psammophila* contains a coelomic cavity the extension of which is broader than the lip itself. It follows the lophophoral arms over their whole length. — The boundaries of this Epistome-coelom can communicate in some cases at its sides with the Mesocoel across small slits between the branches of the lophophoral bloodvessels. — The two basic branches (T-shaped) of the median bloodvessel lies free in the Epistome-coelom. The nervous-ganglion is situated medially in the epidermous epithelium on the upper side of the epistomal lip. — The formation of this coelom by regeneration is studied and described.

Introduction

The phylogenetic systematic situation on the basis of Coelomata was discussed again in the last years. Especially the works of Ulrich (1951), Remane (1949) and Jägersten (1955) gave impulses for new investigations. They refer to earlier studies by Masterman (1898) on Phoronida; he tried to establish correlations between Pterobranchia, Enteropneusta, Echinodermata and Phoronida — just becoming known at that time — stressing the regionation of these animals: He found in all cases a regionation of the body in three regions — corresponding with the coelom — which he termed “archimeric segmentation”. He was also convinced, that one could trace this mode of regionation back to the conditions prevailing in Coelenterates: (1) The bilateralsymmetric construction of the body to a radial-symmetric building plan of a medusa, (2) the 3 pairs of coelomic compartments to gastric pouches radial-symmetrically arranged (Fig. 1). For Masterman these Coelomata with a three-regionated body comprised the basis of Coelomata; he termed them Archicoelomata.

This term did not prevail at that time, but the “archimeric segmentation” of the body in the sense of Masterman plays an important role in the phylogenetic-systematic considerations of notable contemporaries. They saw in this type of body regionation more than an accidental arrangement of body parts. While they introduced different terms, following nomenclatory-rules, the correct term remains “Archicoelomata”.

Masterman’s ideas were revived, re-interpreted and extended by Ulrich (1951), Remane (1949) and Jägersten (1955) to a theory of phylogenetic processes on the basis of Coelomata and the derivation of Coelomata from “Coelenterata” as well.

The phylogenetic union of Archicoelomata exists primarily between (1) the Phoronida as a basal group of Tentaculata and (2) the Pterobranchia as the original group of Hemichordata (compare Siewing 1967, 1973 b, 1974). Therefore, it seems justified to subject the Phoronida to a particularly detailed analysis in
respect to their body-regionation; and a study should base on the investigation of as many and different Phoronidan species as possible, in order to obtain well founded results.

Fig. 1. The derivation of Archicodoma construction from a medusa-like ancestor following Masterman's opinion (after Masterman)

The diaphragm marks the limit of the Epistome-coelom below and the orally on the oral side (Siewing 1973, 1974). This paper presents a species of a medium size: Phoronis psammophila. As will be shown, there exists notable deviations from previous investigations, these do not affect, however, their principle value. Special attention is drawn to the boundary between coelomic cavity of Epistome and the boundaries of the Mesosoma.

**Results**

The Epistome of Phoronis psammophila forms an epidermal upper lip over the mouth-opening in the interior of which are parts of mesoderm (muscles, connective tissue, coelom-epithelium), (Fig. 2 d–f). This lip extends along the basis
Fig. 2. Photographs of a series of sagittal sections beginning laterally (a) and ending in the median plane (f).

**Abbreviations:**
- d = diaphragma
- Ec = Epistome-coelum
- Ep = Epistome
- cs = coelomic septum
- g = ganglion
- i = intestine
- lov = lophophoral-bloodvessel
- lv = lateral vessel
- M = Metacoel
- m = Mesocoel
- mv = median-bloodvessel
- ne = Nephridium
- oes = oesophagus
- wbc = wound-healing cells
of the inner tentacular row laterally and anally. Its function, hitherto unknown, was analysed by Pauss (1974) in *Phoronis ijimai*; it extends (1) to the static support of Lophophore, as well as (2) to the food intake. Similar connections may exist in *Ph. psammophila*, if one considers the structure of the epistome itself, or that of its coelomic cavity and of the muscle fibres in its interior.

The Epistome-coelom is considerably more expanded than the lip itself; basically it extends to the diaphragma and to the oesophagus, anally up into the lips of the lophophore (Fig. 2 c–f). The boundaries of this coelom could be defined with certainty: (1) On the outside it is limited by the epidermal layer and on the upper side by a sheet, which is termed by de SELYS-LONGCHAMPS (1907) “cloison lophophorale”. In fact, it seems that, in the regeneration process, this sheet develops by laying together on the anlage of the post-buccal-tentacles over regenerating lateral-mesentery (Fig. 4) and not — as thought de SELYS-LONGCHAMPS (1907) by “... soudure entre l’épiderme de la face postéro-supérieure de l’epistome et l’épiderme de la face orale des tentacules internes”.

![Figure 3. Somewhat oblique sagittal sections in the epistomial region demonstrating the slits between Epistome-coelom (Ec) and Mesocoel (m)](image)

(2) The diaphragm marks the limit below and the oesophagus orally the limits of the Epistome-coelom (Fig. 4). If one begins in the median plane, this coelom is bordered laterally against the Mesocoel only by the left respectively the right lateral-bloodvessel (Fig. 2 a, b; 5 a), and if one proceeds then laterally, it is limited furthermore by the two lateral branches of the median bloodvessel which is running in the Lophophores and which lay previously in the interior of the Epistome-coelom (Fig. 2 e–f; mv). And finally a coelomic sheet forms a latero-anal and a latero-oral limit.

Therefore in *Ph. psammophila* the Epistome-coelom is limited on the lateral and oral side by the Mesocoel up to the Diaphragma (Fig. 2 a, b) and in the median line by the Metaeocel (Fig. 2 c–f).

In the course of regeneration the epistomal cavity develops by a successive replacement (1) of the Lateralmesenteries which form the coelomic separating sheet in the anlage of the Lophophore (Emc 1972); (2) by the development of the Diaphragma; (3) by the development of the Lophophoral-bloodvessels (Fig. 4).

Beside this one observes in the upperlip that there remains last cells of the wound-closing following the regeneration (Fig. 4) (Emc 1973).
The Epistome-coelom is developed before the upper lip is finally differentiated, which grows rapidly in the next time in a longitudinal direction (Fig. 4). Connected with the proceeding regeneration of the post buccal tentacles the laying together of the latter with the coelomic sheet can be observed. Laterally this
separating sheet disappears in the proceeding development between the Lophophoral-bloodvessels (Fig. 4); only in the latero-anal and the latero-oral basic region of the Epistome-coelom it remains visible.

Fig. 5. Cross-sections in the epistomial and mesosomal region: a) slits between Epistome-coelom (EC) and Mesosoma-Coelom (m); b), c) Epistome-coelom (Ec) in Ph. iijimai completely closed against the tentacular-coelom

Fig. 6. Sagittal section in the median plan of Ph. iijimai (a) and Ph. muelleri (b) for comparison

Discussion

The analysis of the structure of Epistome and its coelomic cavity in Ph. psammophila shows that this region is an independent body part, which agrees in this independence with the other species investigated up to the present day: Ph. iijimai and Ph. muelleri. Moreover, we have shown in the expansion and the positional relation special similarities to Ph. iijimai. The Epistome-coelom runs as a tube-like
canal along the arms of the Lophophores and recalls in the manner approximately the U-shaped Lophophores. Therefore some time ago I expressed the opinion that this part of Epistome-coelom may support the Lophophores; like Ph. iijimai also in this species a system of muscle fibres is present, which may enable an extensive and manifold mobility of the Lophophores on the basis of the “hydro-skeleton” of the Epistome-coelom.

The comparative investigation has now shown that the expansion of the Epistome-coelom correlates directly with the size of the Lophophores: In Ph. muelleri it is extremely small and restricted to the basis of epistomous fold (Siewing 1974, Fig. 6 a, b; 5 a—c); in Ph. psammophila it could be shown above a considerable extension along the Lophophores (Fig. 2 c); in Ph. iijimai finally the Epistome-coelom is extended in the direction to the anus in such an extensive way, that the two legs of the coelom (like the Lophophores approach the median plane, so that the coelom is sectioned twice in parasagittal sections).

As the largeness of the Lophophores as a feeding organ is correlated with the body largeness, the Epistome-coelom may show a different extension according to the body-volume. Possibly up to the present day the difference in information about the Epistome-coelom of Phoronida — which therefore seemed to be uncertain — may be based on this correlation.

Also here the informations concerning the connections between Epistome-coelom and Mesosoma-coelom find an elucidation too: It could be shown, that there can be observed in this species, in several specimens, small split like passages between the vasa afferentia respectively v. efferentia, which separate normally the Epistome-coelom and the Mesosoma-coelom in the distal areal of the Lophophores (Siewing 1973 a, Paaro 1974). It seems to be thinkable, that there exists the passage or any other opening, which has missed Siewing (1973 a) to explain an ingenious operating of the hydroskeleton in the Epistome. Perhaps this split may be enlarged respectively closed by a different volume of the two bloodvessels — corresponding to the functional requirement.

Concerning the morphologic judgement — which means the questions of homology — of the Epistome-coelom this finding is irrelevant: The homology of the said coelom within the Prosoma-coelom in the remaining Archicoelomata. Then concerning the nature as an independant coelom it is not decisive that it is hermetically closed, but that it is a question of a comparable homologous unit. This is certain here. Therefore, it is certified once more that the Phoronida are archimerous animals and in this sense members of the Archicoelomata.

Summary

1. The epistome of Phoronis psammophila contains a coelomic cavity whose extensions is broader than the lip itself. It follows the Lophophore-arms over their whole length.
2. The boundaries of this Epistome-coelom could be defined with certainty.
3. The Epistome-coelom can be communicate in some cases at its sides with the Mesocoel between the branches of the Lophophoral bloodvessels.
4. The two basic branches (T-shaped) of the median bloodvessel lies free in the Epistome-coelom. The nervous ganglion lies medial in the epidermous epithelium on the upper side of the epistomal lip.
5. The formation of this coelom by regeneration has been studies and described.
Zusammenfassung

1. Das Epistom von Phoronis psammophila enthält ein Coelom, dessen Ausdehnung größer ist als die Lippe selbst. Es folgt den Lophophorarmen auf deren gesamter Länge. 
2. Die Abgrenzungen dieses Epistom-coeloms können mit Sicherheit definiert werden. 
5. Die Bildung dieses Coeloms durch Regeneration wird studiert und beschrieben.

Literatur

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