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PHORONIDEA FROM BRAZIL

by

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1. INTRODUCTION

In the history of systematic zoology, Mayr *et al.* (1953, p. 5) distinguish three periods prior to the "New Systematic". The systematic of the Phoronidea is still in the second period of the above division, as, in this group, the specimens of which are not easy to be found, the taxonomical progress has been slow. That is my explanation for the difficulties that the detailed study has brought about in the specific determination. Little is known about the geographical and ecological variation (du Bois-Reymond Marcus 1949, p. 158) as also about the variation within the populations, so that the concepts of the "New Systematics" (Huxley 1940) are for the moment only precariously applicable to the group. The small number of species (about 15) notwithstanding the considerable number of works on the matter, have not yet been surely defined. The specific characters are not yet fixed and the classification must necessarily be made by comparing the descriptions. However, the absence of certain details in the descriptions and the great variability of most of the characters make it difficult to take an accurate decision. It is probable that species intimately related with one another constitute minor systematic units. It must be determined what degree of dissimilarity still allows to place two individuals within one and the same species. As regards the larvae the difficulties are still greater. The many insufficiently described ones have induced authors who have only studied some morphological structures, as Menon and Masterman, or their occurrence, as Hedgpeth, to neglect the classification.

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The complete development from the egg has not yet been obtained. All the sequences of development and metamorphosis had, as starting point, successive stages obtained from plankton. The relation of most of the larvae to adults is uncertain, based only on the identity of the occurrence.

The family Phoronidae is generally regarded as containing only one genus: *Phoronis*. Within this genus there are different groups, that perhaps could be considered as new genera. Besides, groups of very related "species" with characters that intergrade perfectly can be discerned. The determination of the species depends much on the judgment of the specialist. Therefore, I do not know if the combinations of the conditions of the various characters within these groups really represent species or if they are due to their variability. Probably the closely related species are of more recent evolution and therefore their taxonomic differences are still small. The studies of the populations and the exact determination of the life-history will solve these problems.

2. THE MATERIAL

The adults were obtained in the upper littoral of Santos (Ilha Porchat) and Cananéia (about 200 km southwest of Santos), State of São Paulo. The larvae were obtained from plankton samples, belonging to the collections of the Oceanographic Institute, according to Table 1.

3. METHODS

Adults and larvae, excluding those obtained from plankton samples, were fixed in Bouin, Pampel, Formaldehyd 4%, Lang, nearly always after anaesthesia with $MgCl_2$ (Pantin 1948, p. 6) or cristals of $MgSO_4$, always with the best results. The Bouin fixative, however, did not give good results for the fixation of the larvae, since even when the fixation is rapid, the picric acid impregnates so much that later coloring, either "in toto" or histological, becomes difficult. Histological sections from 3 to 8 microns were stained with hematoxylin-eosin, Mallory and Calleja. Very small larvae were stained "in toto" with carmine before embedding. Descalcifications were carried out, or in the fixative itself (Pampel) or with HCl 1%. The larvae were reared in small individual aquaria (stender dish, 50 mm in diameter, 25 mm in height), with stabilized sea water ventilated twice a day by means of a common injection syringe. Only exceptionally was the water changed.

4. SYSTEMATICAL PART

I. *Phoronis hippocrepia* Wright 1856

a) Phoronis

(Figs. 1-33)

The abundante material of this species consisted of pseudocolonies, boring in empty oyster-shells, and some solitary individuals, found on the bivalve *Martesia striata* (L.) or under encrusting bryozoans and polychaete tubes. The winding dwelling burrows situated inside the shell have an external opening, more or less oval, of 0.7 and 0.8 mm diameters. The yellowish chitinous tubes (Hyman 1958, p. 107) can projects outwards about 2 mm (Fig. 1), sometimes naked, sometimes covered by a layer of detritus with some sand grains. In the non-boring specimens the sand grains may extend over the whole tube. Maximum length of the tube 14 mm. The different layers of which it is formed are homogenous, acidophilous, and there are in some cases eosinophilous granules, very similar to those encountered in the epithelial cells of the ampulla and of the base of the lophophore. The maximum length of the fixed animals was 16 mm, the length of the lophophore about 2 mm, that of the body about 10 mm and of the ampulla about 4 mm. Generally only the lophophore appears above the surface; however in conditions not yet determined, the animals come out of the tube for up to 8 mm. The width of the lophophore, from end to end of the tentacles, was 4 mm; the tentacles varied between 0.04 and 0.06 in width; the width of the body, at the base of the lophophore was 0.5 mm, at the muscular region from 0.2 to 0.5 mm, and the ampulla was from 0.4 to 0.7 mm wide. I counted at the most 120 tentacles; individuals with 75 tentacles may already be found carrying embryos in the tentacular crown. Newly collected animals are transparent and of a pink or flesh color; after some time in the aquarium they become white. In the lophophoral concavity of expanded animals, the lophophoral organs appear clearly as two milk-white protuberances, and behind them are the ridges of the nephridial canals. Embryos can be seen in various stages of development (Fig. 2). The body has marked annular striae, especially noticeable after the fixation that may also produce constrictions and enlargements. The ampulla is homogeneous, narrow at its beginning and then increases in thickness; no circular groove was noticed. Its surface is smooth. The external tentacles show a ciliated epithelium only laterally and on the face turned towards the buccal cavity, while the internal tentacles have their whole

TABLE 1

Catalogue number	Locality		Date	Time	Depth (m)		Haul Duration (min)	Temperature (°C at 0 m)	Salinity (‰ at 0 m)	Tide	Net(*)
					Local	Haul					
K 30	SANTOS	Santos Bay	27/ 7/50	—	—	—	—	—	—	—	—
—	SANTOS	Alcatrazes Is.	8/10/54	—	—	?10	—	—	—	—	—
—	Paraná-Paranaguá (inlet waters)		5/ 9/52	—	—	—	—	—	—	—	—
II 48	CANANÉIA	Bom Abrigo Is.	9/10/54	0810	17	12-15	5	24.90	—	falling	C
IV 199	CANANÉIA	Mar de Cananéia (inlet waters)	3/ 7/55	0845	11	9-11	2	19.40	24.98	rising	A
IV 207	CANANÉIA	Mar de Cananéia (inlet waters)	16/ 7/55	1125	15	14	2	18.50	—	rising	A
IV 252	CANANÉIA	Mar de Cananéia (inlet waters)	14/10/55	1552	14	13	2	21.40	31.11	falling	B
IV 254	CANANÉIA	Mar de Cananéia (inlet waters)	21/10/55	1558	14	sup.	2	22.30	24.70	rising	B
IV 255	CANANÉIA	Mar de Cananéia (inlet waters)	29/10/55	1057	14	sup.	2	22.30	24.85	rising	B
IV 256	CANANÉIA	Mar de Cananéia (inlet waters)	29/10/55	1101	14	13	2	22.70	26.98	rising	B
M 70-72	CANANÉIA	Prainha (inlet waters)	27/10/55	1645-1710	12	6	5	—	—	falling	Clarke-Bumpus
—	CANANÉIA	Bar	1/ 2/56	1000	—	—	—	—	—	—	—

N 36		Near Flamengo Beach		—	—	—	—	—	—	falling	—
N 45-47		—	3/ 7/55	1700-1730	—	1	—	23.00	—	falling	—
N 46		—		2330	—	1	—	22.50	—	rising	—
N 34		Flamengo Bay	26/ 7/55	0900	12	2	15	22.50	—	falling	B
N 51		—	7/ 8/55	1100	—	1	15	20.00	34.72	rising	A
N 53		—	21/ 8/55	1000	15	sup.	—	23.80	33.30	high	Apstein
N 54		—		2200	—	6-8	—	23.20	33.62	rising	Apstein
N 60-61		—	10/ 9/55	1800	19	?sup.	10	24.50	32.65	rising	C
N 64		—	11/12/55	2200	9	sup.	—	27.00	—	rising	C
N 68		Southern approach to Flamengo Bay		0815	9	sup.	—	27.00	—	rising	C
N 69		Flamengo Bay		—	9	sup.	—	—	—	rising	C
N 71		Flamengo Bay	17/12/55	0730	—	sup.	—	25.00	—	falling	B
N 81		—	9/ 6/56	2215	9	sup.	5	—	—	rising	B
N 82		Off South Islet	20/10/56	1155	18	sup.	—	21.60	—	rising	C
—		Saco da Ribeira	8/11/56	1000	—	sup.	—	26.00	—	high	—

U B A T U B A

(*) A — Plankton net 1.00 m in length and 0.25 m mouth diameter, Swiss silk gause 18 xx.
B — Idem, Swiss silk gause 6 xx.
C — Pelagic net, 2.90 m in length and one meter square opening, Swiss silk gause 22 GG and 36 GG.
K — Kitahara quantitative plankton net, 1.10 m in length and 0.24 m mouth diameter, Japanese silk gause n.º 13.

TABLE 1 (*Continuation*)

Catalogue number	Station number	Cruise	Position		Date	Time	Haul	Haul duration (min)	Depth (m)		Temperature (°C)	Salinity (‰)	Net(*)
			Latitude	Longitude					Local	Haul			
M 44	10	"IGARATY"	24°06.0'S	45°43.0'W	28/ 6/54	1330	Horizontal	—	—	0-3	21.85	34.20	Standard
M 54						1630	Horizontal	—	—	0-3	21.85	34.20	Standard
M 66	2	"UNGAVA"	23°04.0'S	44°30.0'W	13/ 7/55	0755	—	15	36	c.30	—	—	—
M 67	3		23°04.0'S	44°14.0'W	13/ 7/55	1030	Vertical	5	52	40-0	—	—	—
M 68						1100	—	15	52	40	—	—	—
M 69						1100	Horizontal	15	52	2	—	—	—
M 74	2	"PRESIDENTE VARGAS"	24°44.0'S	45°59.0'W	25/ 9/55	1605	Horizontal	—	70	sup.	20.70	33.23	Standard
M 77	4		25°45.5'S	46°36.9'W	26/ 9/55	0150	Vertical	—	125	0 10 20 30 50 54	20.55 20.35 20.94 21.05 17.53 —	33.64 33.57 34.84 35.88 35.77 —	Standard
M 79	5		26°19.7'S	46°58.5'W		0615	—	—	130	—	—	—	Standard
M 151-152	75	"SOLIMÕES"	28°00.0'S	48°22.0'W	5/11/56	1800	Vertical	20	58	0 10 20 ?30	20.40 19.61 18.91 16.04	35.16 35.21 35.22 35.48	Standard
M 178	106		26°09.9'S	47°48.0'W	15/11/56	1100	Vertical	20	58	0 10 20 ?30	22.71 21.90 21.86 20.94	34.59 34.81 35.45 35.74	Standard
M 179	107		26°25.0'S	47°35.0'W		1305	Horizontal	20	66	sup.	23.07	35.57	Standard

M 208	58	"TOKO MARU"	32°41.5'S	51.29.0'W	25/ 1/57	1215	Vertical	—	50	0 3 10 25 40	23.60 23.44 23.42 22.75 —	— 32.80 32.84 32.84 —	—
M 251	115		02°00.0'S	44°02.0'W	6/ 4/57	1400-1425	Vertical	—	28	0 2 10 16	27.90 27.93 27.93 —	— 36.13 36.13 —	—
M 253	119		03°00.0'S	45°30.0'W	8/ 4/57	0415-0440	Vertical	—	38	0 2 10 31	26.70 26.74 26.63 26.63	— 12.61 35.49 35.96	K
M 258	129		00°33.0'N	46°00.0'W	10/ 4/57	0415-0445	Vertical	—	52	0 2 5 10 27 40	27.90 27.73 27.46 27.47 27.27 —	— 28.65 28.98 34.79 35.80 —	K
M 259-260	130		00°50.0'N	45°42.5'W	10/ 4/57	1735-1930	Vertical	—	630	0 2 45 67 77	27.50 27.49 27.53 26.22 —	— 34.84 35.91 36.16 —	K
M 268	137		01°22.2'N	46°53.2'W	20/ 4/57	0525-0555	Vertical	—	54	0 2 5 10 15	27.40 27.35 27.37 27.38 —	32.41 32.41 32.44 —	K

(*) A — Plankton net 1.00 m in length and 0.25 m mouth diameter, Swiss silk gause 18 xx.
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surface ciliated. The length of the cilia averages 7 to 10 microns. The epithelium cells of the tentacles are columnar, with small, elongated nuclei (Fig. 18, *a*). The epithelium on the sides is thinner. On the exterior side of the external tentacles gland cells may occur (Fig. 18, *e*), with contents stained red by Mallory. I observed such cells also on the side of the internal tentacles that faces the oral cavity. "Corps en massue" and granules of yellow pigment are rare in the tentacle cells. The basal membrane is well developed and attains even 1 micron in thickness; stained with Mallory it shows an orange and blue coloration. Muscle fibres lie outside the basal membrane.

The cuticule is 1 micron thick at the base of the lophophore and 0.7 microns in the muscular region; it is absent in the ampulla. The epidermis consists of lining, gland and supporting cells (Cori 1939, p. 77). The first are columnar with elongated nuclei, situated in the lower third of the cell. Vesicular gland cells have basal nuclei and vesicular-shaped secretion, 4 microns in diameter, or eosinophilous granules. Since they are specially numerous in the epithelium of the ampulla (Fig. 20, *h*) they probably secrete the chitinous tube. Club-shaped gland cells with granular or homogeneous contents, basophilous, are also present. I did not succeed to detect the very thin supporting cells in the epithelium of the ampulla. "Corps en massue" are not only present in the anterior part of the body, but also in the muscular part and in the ampulla. Here they are club-shaped (Fig. 10, *x*), and there nail-shaped (Fig. 17, *f*). They have in average 22 microns in length by 3 to 4 microns in width, the nail-shaped ones protruding about 3 microns. Their proximal part is usually tapering. Deeply-stained with Erhlich's hematoxilin, they are light blue with the exterior part orange-coloured in preparations stained with Mallory. I consider these setiform proeminences as secretion products.

Lophophoral organs (Fig. 3) are present in all individuals, even in those with embryos in incubation, as observed by Silén (1952, f. 55). They were not seen in non-boring specimens with 40 to 50 tentacles. They are, on the whole, similar to the simple lophophoral organs (Selys-Longchamps 1907, p. 57). The protuberant part of the organ, located near the median line (Fig. 3, *c*), is lined, as already described, with cuboidal epithelium, with long cilia, about 12 microns long. I consider the internal cavity, blind in its superior part, as lophophoral canal. In the epithelium, lining the anterior part of the lophophoral canal, I identified the same types of cells as those referred by Cori (1890, p. 553) and Selys-Longchamps (loc. cit.). The various studied individuals showed, however, different aspects of the cells considered as

glandular by Cori (t. 26, f. 16, 17, II) and probably sensorial by Selys-Longchamps (t. 5, f. 5). In the little developed organ these cells look like sensory cells. The large and round nucleus, slightly chromatic, is placed in the inferior wider part of the cell. Otherwise, the nuclei are in the central part of the cells, lying just below the row of nuclei of the common epithelial cells. The cytoplasm appears finely granular, eosinophilous. In the well developed organ I found vesicular cells, with peripheral nuclei and contents either finely granular, eosinophilous, or homogeneous, stained blue with Mallory. These cells gather in the part of the organ that unites with the last inner tentacles, situated near the median line. Silén (1952, p. 17 and f. 19) considers the median projecting part of the lophophoral organ as exclusively sensory since he found there only sensorial cells. All leads to believe that the above mentioned gland cells proceed from such nervous cells that may have both potencies, sensory and glandular (cf. also McIntosh 1881). They probably represent neuro-secretory elements and the change in the position of the nucleus occurs in connexion with the elaboration of the secretion (Scharrer 1941a, f. 5). The part of the organ, which in the present species is constituted by the thickened lateral epithelium lining the inner row of tentacles (Figs. 3,4, *a*), is of variable extension. Certainly it coincides with the brooding pouch of *P. psammophila* (Selys-Longchamps 1907, p. 60) and the lophophoral gland or glandular ridge of *P. australis* (Torrey 1901, p. 288). It is mainly composed of tubular gland cells with fine granular contents (Fig. 16, *l*). The epithelial cells are here very thin, but widen near the surface. In a case of developed lophophoral organs I found in this thickened lateral part vesicular cells (Fig. 16, *j*), as they are described for the protuberant part. The lophophoral organs bear a certain structural resemblance to the retro-cerebral glands of the Chaetognatha (Kuhl 1938, pp. 98 ff.) and to the cerebral organ of the Nemertini, especially the Tubulanidae (Böhmig 1928-33, p. 100). The function of the retro-cerebral organs is still problematic (Kuhl 1923) ; a neurosecretory activity was presumed for the cerebral organ (Scharrer 1941b). The function of the lophophoral organs cannot be settled. Without denying the possibility of their neurosecretory activity, I consider them until further proof as glandular (Cori 1890; Benham 1890). Their secretion probably serves as an envelope for eggs and embryos (Gilchrist 1919, p. 494). In individuals with embryos in the tentacular crown, the epithelium of the tentacles to which the embryos cling (Fig. 3, *b*), exhibits a thickening with granular eosinophilous cell contents. On each side of the bottom of the brood-pouch I found a small pit (Fig. 4, *f*).

Longitudinal muscles bundles, 26 to 30 in number (Figs. 7, 8), are distributed as follows: $\frac{8\text{-}11 \mid 9\text{-}13}{3\text{-}\ 5 \mid 3\text{-}\ 6}$. The arrangement is more constant in the boring specimens, whose most frequent formula is: $\frac{11 \mid 10}{4 \mid\ 4}$. The arrangement of the fibres within the bundles shows considerable variation, due not only to fixation but also to the physiological condition of the animal. Individuals that have remained in the aquarium for some time have lower muscle bundles and the body cavity full of muscular fragments, what suggests self-digestion. Marginal fibres (Silén 1952, p. 109), inconspicuous or apparent, 3 to 5 in number, on each side of the bundle (Fig. 21 A, D, *p*), have approximately the same height along the whole length of the muscular region. The different height of the central fibres gives different aspects to the bundle (Fig. 21, A-F). They are fusiform and alternate within the bundle, so that, in cross-sections (Fig. 21, A) they show Cori's type of concentric arrangement (cf., 1939, p. 88, f. 80). The centro-lateral fibres are sometimes more developed giving a penniform aspect to the bundle; at other times the centro-median fibres are more developed. In the distal region, the bundle may show a certain doubleness. In some individuals each component of the bundle can separate itself, thus producing the variations in number. In the proximal part of developed specimens a syncytial connective tissue appears between the bundles (Fig. 21 B, *q*), projecting towards the body cavity (see also Fig. 7). These are swellings of the peritoneum, where the radial fibres are inserted, many of them crossing the body-cavity. I found caecal vessel branches inside some bundles (Fig. 21 C, *m*).

The nervous sub-epithelial plexus agrees with the description of Silén (1954b) for *P. hippocrepia*. I noticed concentrations of neurones, not only in the ganglion (praeoral field), but also in the nerve ring. Unipolar motor neurones are present, with their fibres crossing the interstices of the basal membrane. There are two giant fibres emerging from the ganglion and individualizing approximately at the level of the nephridial canals where the right one has a diameter of 4.2 microns and the left one of 0.7 microns. The diameters of both fibres are very variable; the left fibre diameters vary between 3.6 and 10.0 microns and right ones between 4.3 and 7.0 microns. This variation suggests a winding of the fibre, as was observed by Cori (1937, f. 85; 1939, f. 96) in living specimens. In cross-section the fibres look like a tube, hollow or filled with an homogeneous mass; I even sometimes noticed granules (perhaps the punctated tissue of Pixel 1912, p. 265). Once I found a nucleus inside the fibre (Fig. 19, *v*). I

was not able to discern the enveloping sheet of the fibre, but the crescent-shaped nucleus (Fig. 19, *i*), visible around the fibre certainly belongs to it. Bifurcation of the right fibre (Fig. 19, *s*) and peripheral ramifications are present; the course of the latter could not be followed.

The whole alimentary canal is ciliated. The crescent-shaped epistome overlays the mouth. This is coated with columnar epithelium. The funnel-shaped oesophagus has a thick wall formed by tall and thin columnar cells; their elongated nuclei very rich in chromatin are densely packed. An infundibuliform valve (du Bois-Reymond Marcus, 1949, p. 160, t. 3, f. 8) is absent. Along the whole length of the metasoma the proventriculus exhibits a slightly differentiated median ciliated band. It consists of a columnar epithelium. Stomach as usual; only one individual showed a fold of the gastric epithelium protruding into the lumen forming various irregular papillae. In the stomach there is a distinct ciliated band. Although Andrews (1890) describes it as not composed of gland cells, I found a tubular gland with eosinophilous granules on each side (Fig. 24, *d*). Initial part of the intestine with thick wall. The lining cells are columnar, ciliated, with nuclei in the middle part and glandular with globular proximal part, when filled with eosinophilous granular secretion (Fig. 25 A, *e*) ; round nuclei lie in the lower third of the cells and a narrow duct penetrates between the common cells. Therefore Silén (1952, p. 119) at first thought that this epithelium was stratified, later on he came to the conclusion (p. 120) that it is pseudostratified. The pseudostratification disappears in fasting individuals (Fig. 25 B) ; the epithelium becomes thinner with cuboidal cells of regular height and rather central nuclei. Rare nuclei are found a little lower; certainly they belong to the above mentioned gland cells. In some individuals I found blood corpuscles in the lower part of the gastric epithelium (cf. Silén, op. cit., f. 43), proving that they pass from the peri-gastric sinus to the stomach wall. I also observed blood corpuscles in the lumen of the stomach of some individuals (Cori 1890, p. 526), mostly in those that had remained for some time in aquaria.

The circulatory system corresponds to the schema given by Selys-Longchamps (1907, p. 21) and Cori (1939, p. 107). The ring-like lophophoral vessel (Figs. 11, 13, *m*) is formed by two independent arches, one superior afferent and another efferent, inferior, more external, as observed by Ikeda (1901, p. 584) and Brooks & Cowles (1905, p. 105). In fixed, contracted animals both arches are juxtaposed; propably therefore Cori (1890, p. 543) considered such a vessel as single. The afferent and efferent blood vessels are of variable form and caliber in their whole lenght, ac-

cording to their state of repletion. Caecal vessels occur along the whole extension of the efferent blood vessel, attaining even the right anal cavity, although they do not anastomose with the afferent blood vessel as referred by Dyster (1858, p. 253). The blood sinus (Fig. 9, *r, z*) agrees with the description of Selys-Longchamps (loc. cit.). Only the afferent blood vessel merges more quickly into the peri-gastric sinus than the afferent one. Blood lacunae in the ampulla communicate with the sinus (Fig. 10, *w*). I observed blood extravasations in the body cavity of some animals (Cori 1890, p. 541), and blood corpuscles in the intestine of specimens in bad physical conditions. The blood corpuscles vary in diameter from 6.4 to 9.6 microns, the ratio of the corpuscle to its nucleus is 4:1. I also found in the vessels agglomerations of gold-yellow pigment, 7 microns in size, more frequent however in the blood sinus.

The diaphragm contains masses of supporting substance. Especially in young individuals this thickening may fill the whole anal space. The supporting substance (Figs. 5, 6, *k*) proceeding from the basal membrane has some fusiform cells scattered in its homogeneous mass; it stains orange and blue with Mallory, as cartilaginous tissue. The diaphragm therefore agrees in general outline with the descriptions of Benham (1890, p. 137) and Masterman (1896, p. 62). In the lophophore cavity of some individuals I found numerous sexual cells (Figs. 3-5, *d*), including ovocytes and even some vitelline spherules in the tentacle cavity. This leads to the supposition that openings are present in the diaphragm either naturally or at least artificially, as a result of a sudden fixation (see Fig. 5). The lateral mesenteries are interrupted at level of nephrostome. They present openings (Gilchrist 1907, p. 159) through which pass the caecal vessels and generative products (Fig. 8, *n*). Coelomic liquid was only observed in animals in bad condition, as a basophilous coagulum. Besides the fusiform corpuscles, I discerned yellow granules in the body cavity and sexual cells, vitelline spherules and formations similar to sporozoon cysts. Fusiform corpuscles were rarely seen within the cells of the fat body (Fig. 8, *x*). Their presence depends, undoubtedly, not only on the time when the animal was collected but also on its physiological condition. They were absent during the reproduction period, although the fat body was very developed. They were rare after that period, then they were only found in the body cavity. A greater quantity of these corpuscles was discovered in an animal fixed in November after a month in aquarium. The dimensions of such corpuscles are very variable; the values of some of them in microns are: 14 by 3; 21 by 4.2; 16.8 by 2.8; 30 by 10. Their structure is homogeneous, without striation. All of the different hypotheses proposed as to the meaning of the

fusiform corpuscles contain doubtful elements. It is quite true that they are very similar to muscle fibres (Selys-Longchamps 1907, p. 113) and it is not improbable that they are muscle fragments in degeneration. Besides, animals fasting for a long time had the body cavity full of fragments, identified as muscular. I would therefore be prone to accept the muscular origin of the fusiform corpuscles, if it were not for the aspect they present in *P. ovalis*, where they are similar to blood corpuscles. The explanation of Cori (1890) must therefore not be disregarded. A globular formation 15 microns in diameter, with thickened wall, rare nuclei, having inside an annular formation, full of eosinophilous granules was found in the body cavity of an individual. I also observed colourless spheroidal bodies (Fig. 26) with eosinophilous granules in the central part. Both structures are probably related and represent a cyst.

Paired fat bodies (Figs. 9, 10, *v*) are developed not only on the efferent vessel, but also on the caecal vessels emanating from the latter. Although Silén (1952, p. 119) considers the organ as unpaired, I agree with Selys-Longchamps (1907, p. 108) that it is paired, the right body being formed, as Cori stated (1939, p. 117), by the walls of the caecal vessels entering the corresponding oral chamber. Selys-Longchamps (loc. cit.) considered *P. hippocrepia* as belonging to the group of species in which the fat body only develops on the caecal vessels of the ampulla. In the present material I also found the fat body developed in the muscular region, suggesting that the difference only refers to a growth stage. The fat body cells average 10 microns in size; they are pyramid-shaped; the small nucleus is situated near the base. Besides muscular fragments I found in the fat body globular corpuscles with yellow pigment, 8 to 12 microns in diameter. Vitelline spherules are abundant, especially during the development of the reproductive organs.

The nephridia show a certain structural variation. All studied specimens showed essentially a bent nephridial canal protruding as a ridge into the lophophoral concavity and opening with a small pore above and laterally to the anus. The proximal branch of the nephridial canal is inconspicuous in most individuals and placed horizontally (Fig. 15, *h*); it only represents the connection of the ascending branch with the nephrostome. Only one specimen, the most developed one, presented a short descending vertical canal (Fig. 5, *h*). The single nephrostome (Figs. 5, 12, 14, *g*) agrees with the one referred for *P. psammophila, P. mülleri* and *P. gracilis*. Due to the lack of lateral mesenteries at the height of the nephrostome and to the interruption of the lateral wall of the latter, the oral and anal chambers communicate (Figs. 12, 13,

15, *p*). The nephrostome walls of one individual showed folds (Cori 1890, p. 536, t. 27, f. 9), produced by fixation. The lower wall of the left nephrostome may be prolonged downwards shortly (Fig. 6) ; the one of the right nephrostome (Figs. 6, 7, *p*; 13, *q*) is always prolonged longitudinally to a relatively enormous length. It is short only in very young animals. I did not see in the renal epithelium the brown concretions mentioned by Cori (1939, p. 115). In one individual I found blood corpuscles inside the nephrostome (Fig. 12) but this does not indicate any relation with the circulatory system.

The gonads (Fig. 27) develop in the left oral chamber on the efferent vessel walls as well as on the walls of some caecal vessels. The testis (*f*) lies on the anal, the ovary (*h*) on the oral side of the vessel. The reproductive cells arise from proliferating peritoneal cells, as referred by Ikeda (1903, p. 142). Groups of sexual cells are first met on the anterior wall of the lateral vessel (Fig. 9, *y*), anlage of testis. Later they can be seen not only on the posterior wall of this vessel but also on the wall of the peri-gastric sinus. After the reproductive period I did not find any trace of gonads but only well developed fat body, differing from *P. viridis* (Rattenbury 1953, p. 187). It was difficult to follow the sequence of the spermatogenesis, not only owing to the small size of the elements, but also because the different stages are not in a regular sequence. Generally the younger sexual cells are found near the efferent vessel (Fig. 32, *a*) while the spermatozoa (*e*) appear on the periphery. Spermatogonia and spermatocytes form cohesive groups and it was difficult to discern the outlines of the cells. The spermatogonia are rather rounded or polygonal cells, about 8 microns in size, with large spherical nuclei of about 4 microns. In the resting stage the nuclear chromatin appears homogeneous but not deeply stained. I did not observe the division of spermatogonia in mature testis, which leads to believe that division and maturation are not simultaneous. The primary spermatocytes (Fig. 33 A) are very similar to the spermatogonia, differing only in size; they reach 4 to 6 microns in diameter with 2.6 to 4 microns nuclei. The cell membrane is not conspicuous and the cytoplasm is slightly stained. The secondary spermatocytes (Fig. 33 C) less than 3 microns in size consist almost exclusively of the nucleus; the latter, deeply chromatic, averages 2 microns. The second division of maturation was rarely observed. The youngest spermatid I saw (Fig. 33 D) had an oval shape and a round nucleus. I could not analyse the spermiogenesis completely. Some phases, arranged in an order that may correspond to the ontogenetic sequence, are shown in Fig. 35 D-M. In the spermatid nucleus the chromatin,

initially uniformly distributed, settles gradually on the periphery until it forms a ring that grows thicker as more chromatin becomes evident (D). The spermatid reaches then 5 microns in diameter. I observed the migration of the nucleus towards one of the cell poles (E) and the formation of vacuoles inside the nucleus. Then the chromatin settles at the superior pole. Mitochondria were not distinct and centrosoma was noticed only once. The axial thread of the tail is either originally very thin or is formed later, after the disappearance of the cytoplasm around the head of the spermatozoon. Fig. 33 F show the outline of the definitive spermatozoon, still with remnants of the spermatid cytoplasm. The nuclear vacuole, that gradually becomes smaller and disappears after the elimination of the cytoplasm (G), can still be noticed. In the testis, the spermatozoa have a long straight head (Fig. 33 I). When completely formed (Fig. 33 J-K), they consists of a vesicular head, about 2 microns long by 1.2 microns thick, that has a basophilous thickening at its superior end, perhaps a penetration organ. The middle piece, heavily basophilous on the edges, has a light central zone; it is 2 to 2.6 microns long. The tapering tail reaches about 10 microns. The whole spermatozoon is about 12 to 15 microns long. The spermatozoa of nonboring specimens were bigger, about 20 microns, with a head about 2.6 microns and a middle piece 4.2 microns long. I observed spermatids developing together in the same cytoplasmic mass (Fig. 33 L-M) ; this suggests that, as in the Miriapoda (Tuzet, Bessière & Manier 1957), the maturation division concerns only the nuclei of the spermatocytes, while the protoplasm remains undivided. Such spermatids appear often in the body cavity. Fusiform formations (Fig. 33 N) about 7 microns long by 0.9 microns thick, with pale or granular contents were rare in the testis; they might represent nutritive cells. I have rarely noticed in the testis a free, rather club-shaped formation (Fig. 33 P) about 9 microns long that might be a phase of spermiogenesis. It looks like phase *i* of Ikeda (1903, f. 6).

The oögonia are polygonal cells varying from 6 to 8 microns in size with a round, chromophilous central nucleus of about 3 to 4 microns. The cellular outlines of the oögonia are very indistinct, and the cytoplasm is slightly stained. They are disposed along the wall of the caecal vessels. Between the oögonia some flat cells of peritoneal nature penetrate. Some phases of the mitosis are drawn in Fig. 28 A-D. The ovocytes grow inside the fat body cells which become very big and degenerate in a advanced stage. In a mature ovary the fat body disappears and there remain only vestiges of the cellular membranes (Fig. 31). The primary ovocyte (Fig. 29) begins usually spherical; as it grows,

it takes an ovoid shape. The small and central germinal vesicle increases in size and takes a more excentric position (G-K). The initially basophilous cytoplasm looses its basophilia gradually and then becomes acidophilous. In the germinal vesicle a lightly stained nucleolus becomes evident on whose edge a basophilous crescent appears. The nucleolus divides and one of its products breaks down. The nucleolus is about 6.5 microns in size. In a developed ovocyte 71×55 microns), on the edge of the germinal vesicle, I noticed the comma-shaped body (Fig. 29, J, *c*) reported by Ikeda (1903, p. 108). The linin network becomes evident in the germinal vesicle of 48 by 37 microns ovocytes; in this case the germinal vesicle itself is 30 by 19 microns. At this time the cytoplasm is slightly basophilous. The mature ovocytes leave the ovary easily as now the fat body cells are practically desintegrated. They fall into the body cavity, and through the holes of the lateral mesentery they enter the anal chamber. Exceptionally some remain in the oral chamber. In the body cavity the ovocytes have an acidophilous cytoplasm; their nuclear membrane as well as the nucleoli have disappeared; the spindle of the first meiotic division is present, perpendicular to the surface of the ovocyte; it is about 20×8 microns in size chromosomes in metaphase arrangement (Figs. 29 L-M; 30). The external membrane is very thin; it stains blue with Mallory. Ovocytes of 80×46 and of 100×53 microns were found in the body cavity. The chromosomes are about 2 microns in size. I was able to make out seven to eight pairs of bivalent chromosomes of which two pairs are dot-shaped; two pairs V-shaped; and two pairs rod-shaped. I could not determine the shape of two pairs forming a figure that may represent an inversion. One of the dot-shaped pairs always showed polar movement. Vitelline spherules (Fig. 31, *s*), vary from 6.5 to 15 microns in size; some of them with granular contents probably represent abortive ovocytes. They do not disappear as the sexual cells develop, as Ikeda stated (op. cit., p. 44).

In the present species, at least the boring specimens are simultaneous hermaphrodites. The few examined non-boring individuals generally showed either exclusively male cells and a great number of vitelline spherules in the body cavity or ovocytes and rare spermatozoa. I found spermatozoa not only within the ovary amidst the ovocytes (Fig. 31, *z*), but also many in the body cavity, as mentioned above. At least in a certain number of ovocytes, the penetration of the spermatozooan is precocious, taking place in the body cavity and, in some cases, in the ovary itself. This fact agrees with the observations for *P. viridis* (Rattenbury 1953), for which internal fertilization is the rule. Meanwhile the presence of spermatozoa in the nephridia (Fig. 6, *r*) does not

exclude penetration of foreign sperm and, consequently, cross-fertilization. For Kowalevsky (1867, *fide* Leuckart 1867) self-fertilization is the rule in simultaneous hermaphrodite species. I never observed the elimination of polar bodies in the body cavity and I think I may corroborate the observations that it takes place in the tentacular crown (Ikeda 1903; Silén 1952, p. 157). Newly shed living eggs are of a spherical form, approximately 84 microns in size and about 98 microns in the two-blastomere phase. I did not obtain a further development of the eggs outside the tentacular crown, and I did not see the cleavage stages in sectioned animals. It is known from the literature (Kowalesvsky, op. cit.; Foettinger 1882; Brooks & Cowles 1905; Rattenbury 1954) that the cleavage shows traces of the spiral type. At the beginning of gastrulation, the embryo has a size of about 60 microns (Fig. 37). The blastocoelic cavity is reduced due to the increase in size of the cells of the vegetative pole. The gastrula is oval (Fig. 34 A), about 90 microns in its greater diameter. The blastopore is large, round, about 20 microns in size.

b) Actinotrocha

(Figs. 34-55)

Stage devoid of tentacles, although already outlined (Fig. 34 B, C) — Total length varying from 89 to 125 microns; hood about 40 microns long and 70 microns wide; maximum width of body, about 65 microns; anal papilla little developed, about 10 microns long, the ratio of total length (t.l.) to anal papilla (a.p.) is 8.9 to 12.0:1. On the middorsal part of the hood a thickening of the epithelium is already distinct, with some round pale-colored nuclei belonging to sensory cells. Such a thickening represents the anlage of the ganglion. The whole hood dorsal epithelium except that of the ganglion region, is composed of columnar cells with elongated nuclei. The body epithelium is composed of cuboidal cells with large, round nuclei taking up nearly the hole height of the cell. In the region of the post-oral ciliated ring the epithelium consists of columnar cells with elongated and deeply chromatic nuclei. The digestive tube consists of an oval mouth, transverse to the main axis of the body, a short oesophagus, a bulky stomach, and a blind intestine. The oesophagus is narrower than the stomach. The digestive tube is lined by columnar epithelium with large nuclei; in some cases the stomach cells are full of eosinophilous granules. In the gastric cavity I also found some vitelline spherules. In the intestine the epithelium is cuboidal (Fig. 42, *g*). A ventral groove is present, in which the cells are higher than

the adjacent ones and have densely packed nuclei. The body cavity contains many mesenchymal cells, of which only the 5 microns large nuclei are distinct. Some of them already lie against the stomach wall, originating the future splanchnopleure (Fig. 43). The posterior pit (Fig. 42, *h*) is little developed.

Stage with one pair of tentacles (Fig. 34 D) — Total length: 126 to 166 microns; the hood is about 50 microns long and 50 to 100 microns wide; maximum width of the body about 57 microns; anal papilla 20 to 38 microns in length, ratio values of t.l.:a.p. are 6.4 to 4.3:1. The hood epithelium (Fig. 38, *a*) and the ganglion are the same as the preceding stage. But the latter shows an intense proliferation of cells, not regularly disposed as in the remainder of the epithelium. There are no gland cells and no peri-anal ciliated ring. The buccal vestibule (Fig. 40, *c*) is lined with tall and large columnar cells, without contents. The epithelium of the tentacles (Fig. 41, *f*) consists of very thin columnar cells with elongated, deeply-stained nuclei. The anus is opened. The metasoma is represented by a thickening of the ventral region, with an intense proliferation of cells. The terminal nephridia are formed by a long canal (Fig. 38, *d*) extending to the median region of the stomach. There are no blood corpuscles. Mesenchymal cells are present in the body cavity (Fig. 41, *d*).

Stage with four tentacles (Fig. 34, E, G) — Total length: 158 to 328 microns; average length of hood 128 microns, width 158 microns; maximum width of body averages 100 microns; ventral tentacles generally longer, about 53 microns long and 30 microns wide; anal papilla varying from 50 to 120 microns, the ration t.l.:a.p. from 3.0 to 2.7:1. Peri-anal ciliated ring about 100 microns in diameter and 20 microns thick. In this stage the larvae may exceptionally be found swimming. The metasoma (ventral pouch) is represented by a short invagination. The cells lining it are columnar with small, nearly basal nuclei. The somatopleure shows only the large, round nuclei of its so squamous cells. There are rare mucous gland cells in the dorsal epithelium of the hood. The developed ganglion shows several pale colored vesicular nuclei belonging to sensory cells whose outlines were not distinct. The trunk coelom is almost completely formed. The nephridia, no longer terminal extend even downwards into the anal papilla. Mesenchymal cells, as described for the preceding stages, numerous in the trunk cavity and concentrated near the buccal opening (Fig. 39, *d*). Here they represent the primordia of blood corpuscles, as stated by Caldwell (1882, p. 377). The ventral groove extends to near the opening of the metasoma. The oral vestibule (Fig. 39, *c*) is lined with alveolar epithelium. Light brownish

pigment is concentrated in a strip on each side of the margin of the bood; a spot of pigment is present in the distal end of each tentacles.

Stage with six tentacles (Fig. 34 F, H) — The larva may attain as much as 430 microns in length; hood length up to 130 microns, and maximum width 200 microns; maximum width of body 100 microns; the anal papilla varying from 120 to 200 microns, the ratio t.l.:a.p. is 2.7 to 2.0:1. Individuals in this stage of development may show an incomplete differentiation of the tentacles, the ventral pair being well developed and the other two pairs represented by a swelling of the post-oral ciliated ring. Through fixation the tentacles may contract considerably, taking a mammiloid appearance. Maximum length of tentacle 37 microns, and 13 microns thick. Peri-anal ciliated ring 150 microns in diameter and about 20 microns thick. Body on the whole whitish, with some scattered pigment dots. Pigment concentrations as in the previous stage; some pigment granules are also grouped in the peri-anal ciliated ring. The metasoma is developed as a wide sac (Fig. 34, F, *m*). Some mucous gland cells are to be found in the epithelium covering the hood. There are many mesenchymal cells in the body cavity. The renal canal runs along the lateral wall of the body and over the septum. This canal consists of cuboidal cells with basal round nuclei; it opens laterally to the opening of the metasoma. The trunk coelom is completely formed. Ventral mesentery present. Peri-anal ciliated ring consists of very thin cells with small nuclei and long cilia. The primordium of the lophophoral coelom of the adult is represented by a ventral mass of mesenchymal cells. A nerve is distinct in the ventral side of the body. In the metasoma epithelium there are some pigment granules. Anlage of blood-corpuscle mass present.

Stage with eight tentacles (Figs. 34 J, K; 35; 36 A, B) — In this stage the larva may exceptionally still be within the tentacular crown of the parent, becoming free only just before complete maturation. Pigment and coloration as in the previous stage. Total length about 500 microns; hood 200 microns long and approximately as wide; maximum width of body, about 250 microns. In most of the fixed larvae the peri-anal ciliated ring is withdrawn inwards (Figs. 34 J; 36); it is up to 200 microns in diameter and 50 microns thick. Anal papilla well developed, the ratio t.l.:a.p. is 2.0 to 1.6:1. In the hood (Fig. 45, *p*) and the lower part of the body (Figs. 45, 50, *p*) there are many vesicular mucous gland cells with small nuclei at the base. These cells are rare in the body. The whole epithelium of the body is ciliated, with longer cilia in the prae-oral and peri-anal rings. Here they

are about 40 microns long. The ganglion (Fig. 44, *l*) consists of ganglion cells and nervous substance deeply placed, prolonged into two nervous tracts that extend forwards. In more advanced larvae I observed an accumulation of gland cells in front of the ganglion some of them sole-shaped, so that I think they belong to the sensory organ. Hood cavity with some mesenchymal cells, some fusiform in shape, perhaps connective-muscular elements. The tentacle number may sometimes attain 10, the last dorsal pair represented by a small protuberance of the epithelium only. Tentacles (Fig. 49) with trunk coelom diverticulum, sometimes only represented by mesenchymal cells; inside the tentacles some blood corpuscles were also noticed. Metasoma opens a little to the left. In the more advanced larvae it forms a series of folds (Fig. 34 K, *m*) surrounding the digestive tube, almost filling the whole body cavity (Fig. 51, *k*). In the metasoma epithelium "corps en massue" (Fig. 44, *s*) are already found and also rare pigment granules. The circular layer of the musculature covering the metasoma (Fig. 51, *q*) appears first, then the longitudinal one, differentiated into bundles (Fig. 44, *q*). The pigment is distributed as in the preceding stage. In fixed specimens the hood always appears pulled down over the body, its lower edge together with the fore part of the body delimits the wide vestibular cavity. The digestive tube is similar to that of the preceding stages. The stomach is voluminous (Fig. 44, *e*) ; in the fixation its fore part may be produced into one or two small diverticula; their epithelium is not different from that of the stomach. The part between the stomach and the intestine is very conspicuous; it consists of columnar epithelium with elongated and deep stained nuclei. Rectum small (Fig. 52, *g*). A large blood sinus situated in the ventral part of the oesophagus (Figs. 44, 45, *j*). Rare blood corpuscles on both sides of the ventral region lie above the insertion of the tentacles (Fig. 46, *n*). In a fully developed stage the blood sinus extends laterally forward and downward. A dorsal vessel (Figs. 46, 47, 51, *r*) is present. It seems that there is also a ventral vessel (Fig. 51, *y*). The blood corpuscles, 5 to 8 microns in diameter, do not show very regular outlines. The nuclei are generally round but also horseshoe-shaped (Fig. 48). Nephridia without peculiarities, similar to those of the preceding stage (Fig. 47, *z*). Very small, hardly distinct solenocytes. One pair of ventral muscles in the trunk (Fig. 52, *x*). The lophophoral coelom (Fig. 46, *v*) develops ventro-dorsally as in *Actinotrocha sabatieri* (Selys-Longchamps 1907, p. 134).

Metamorphosis stages (Figs. 53-55) — A detailed description of metamorphosis cannot be given since it was obtained only in few larvae. Besides the present species does not constitute a

favourable material. The metamorphosis stages described in the literature were obtained from mature larvae collected from plankton. Even so, according to the data of Selys-Longchamps (1903, p. 39, 47) metamorphosis only took place in very few of the collected specimens. The living metamorphosing larva is opaque, only the red of the blood corpuscle mass being distinct. The metamorphosis of the present species was obtained even without a special substratum. As to this detail the present species, according to the observations of Silén (1954, p. 234), is of rather irregular behaviour. Thorson (1946, p. 154) also obtained the metamorphosis of *A. branchiata* without the presence of a specific substratum. Usually the larva settles on the right side, at the bottom of the recipient; in one case under a piece of shell, the ventral side turned towards the shell. The evagination of the metasoma seemed to be difficult for the larvae, differing from the observations of Menon (1902, p. 474) and Veillet (1941, p. 5) who stated that the metasoma is fully evaginated in 1 minute. The expulsion of the metasoma starts with violent contractions of the trunk. As soon as a bit of metasoma is eliminated it also contracts. The contractions are followed by resting periods. The metasoma evaginates slowly. Most part of the tentacle is cast off, and sometimes the tentacle fragments fall into the mouth. The complete metamorphosis up to the point when the individual presented remainder of an anal papilla, took about two hours. Meek (1917, p. 37) indicates a quarter of an hour for the whole process of metamorphosis.

Larva at the beginning of the evagination of the metasoma (Fig. 53 A) — It is about 520 microns long. The hood has become relatively small in relation to the body. Eight, rarely 10, larval tentacles; no definitive tentacles. These originate later from the larval ones. I observed in sections that the dorsal epithelium of the hood already shows signs of desintegration. There is a distinct accumulation of gland cells in front of the ganglion, probably belonging to the sensory organ. Blood system as in the mature larva; meanwhile it was possible to discern a blood vessel going forwards, leaning against the dorsal wall of the oesophagus (prolongation of dorsal vessel?); it runs beyond the buccal opening and disappears on the level of the vestibulum. Longitudinal muscles of metasoma already differentiated into bundles (Fig. 54, *b*). Basal membrane was observed (*c*); the epithelium cells of the evaginated metasoma show round nuclei, placed near the proximal part (*a*).

Larva with totally evaginated metasoma and without hood (Fig. 53 B) — The larva reaches more than 300 microns in

length; its maximum width on the level of the metasoma is 170 microns. The anal papilla is voluminous; it is reabsorbed little by little (Fig. 53 C). In the larva of Fig. B the peri-anal ciliated ring is present but withdrawn and I do not know if due to fixation or to natural transformation into the rectum. In the newly metamorphosed young I found the afferent and efferent blood vessels developed, both leaning against the stomach wall (Fig. 55, *f, g*). My metamorphosed individuals seemed to be normal, whereas the specimens of Roule (1900, f. 79-89) appear to me to proceed from an anomalous metamorphosis, known in the literature (Selys-Longchamps 1903, p. 40). In these specimens there are no traces of muscles, and the coelom is full of cells.

OCCURRENCE — Eulittoral of the State of São Paulo: Santos (Ilha Porchat) and Cananéia (Ilha do Cardoso), in the first locality, in empty oyster-shells, in the second isolated specimens; Ubatuba (about 135 km E of Santos), only larvae-samples n.° 64 and 68.

FURTHER DISTRIBUTION — Coast of Great-Britain; English Channel; West coast of Sweden; Mediterranean; Japan? (Uchida & Iwata 1955).

DISCUSSION — The present material agrees with *Phoronis hippocrepia*, except for the nephridia, in which it differs fundamentally. In this character it is more similar to *P. psammophila*. In all specimens I studied there was one single nephrostome; the interruption of its lateral wall, forerunner of the double funnel, represents either a variation of the *P. hippocrepia*-type or only a growth stage. The variation of the nephrostome in other species, for example *P. mülleri* (Silén 1952, p. 123), shows that its systematic importance must not be exaggerated. *Phoronis hippocrepia* and *P. psammophila* are very closely related "species", so closely that Cori studying both in detail (1890), considered them at first as distinct, then (1932, 1937) as synonymous, and, finally, again distinguished them (1939). After a carefull analysis of the various descriptions of these two "species" and bearing in mind the great variability of most of the anatomic characters, I ascertained that the only real difference between the adults is their sexuality: *hippocrepia* being simultaneous hermaphrodite, and *psammophila* unisexual or proterandric hermaphrodite. *Phoronis sabatieri*, also similar to the two above mentioned species, is considered either a distinct species (Selys-Longchamps 1907) or, perhaps identical with *psammophila* (Cori 1939). It has also been identified with *hippocrepia*. *Phoronis ijimai, P. capensis, P. gracilis* and *P. architecta* are also very similar to the above mentioned

species. I consider *P. ijimai* as different from *hippocrepia*, since it exhibits only three pairs of chromosomes (Ikeda 1903). I am disposed to unite *capensis* with *hippocrepia*, as the divergence mentioned by Gilchrist (1907) seems only to represent a particular growth stage (cf. Masterman 1896, p. 62) *Phoronis gracilis* considered as a distinct species by Selys-Longchamps (1903), who discovered and studied it in detail, was brought together with *hippocrepia* by Silén (1952) since the typical specimens were only juveneles of *hippocrepia*. *Phoronis architecta*, closely related to *psammophila* could also be approached to *hippocrepia*, but it differs from both in the aspect of the nephridial canal (Brooks & Cowles 1905, f. 67-75). *Actinotrocha hippocrepia* described by Silén (1954a) differs from my description, which agrees much more with that of *A. pallida* (ibid.). The fact that such larvae, externally very similar, have been described from specimens collected simultaneously in the plankton, suggests a possible confusion. The comparison of the developmental sequence of both larvas (Forneris 1957), based on data of Selys-Longchamps (1903; 1907) and Silén (1954a) with the present results (Table 2), shows a greater conformity of *A. pallida* with the Brazilian actinotrocha. *Actinotrocha sabatieri* is another larva closely related to *hippocrepia;* it differs from it in the masses of blood corpuscles, perhaps three in number, one ventral on the level of the root of the tentacles and perhaps two lateral ones, placed farther forward. The latter are perhaps nephridia, as, according to Schepotieff (1906), the observations of Roule (1900) are erroneous and based on poorly preserved material. *Actinotrocha ikedai, A. wilsoni* A and *A. hatscheki* respectively related with *P. ijimai, P. architecta* and *P. psammophila* differ from one another as well as from *A. hippocrepia* and *A. sabatieri*, the larva of *P. sabatieri*. My report seems to point out that dissimilar larvae give origin to adults very closely alike. This may due to the fact that larvae are more susceptible to mutations that affect their anatomic features. In this case the differences between the adults must be considered as having a specific value, while the absolute specific characters are the larval ones. It is also possible that the same species produces larval forms, phenotypically different (Giard 1892), according to the environment and the habitat. In this case different larvae of identical adults will be synonyms. Only the knowledge of the species life-history will solve this problem (Trewavas 1931, p. 48). My opinion can be stated as follows: Provisionally I consider the species occurring in Santos and Cananéia as *Phoronis hippocrepia*, notwithstanding the small divergences in the adults and a certain difference in the larvae. It is possible that the material from Cananéia represents a form of *hippocrepia*, different from that of Santos. I consider *P. capensis* as a doubt-

TABLE 2 — *Actinotrocha hippocrepia* — Differential characters of the successive developmental stages.

Number of larval tentacles	0	2	4	6	8
Size (micron)	125-89	166-128	328-158	430-220	500-250
Values for t.l.:a.p.	1.2-8.9	6.4-4.3	3.0-2.7	2.7-2.0	2.0-1.6
Metasoma	absent	primordium present	present as a short invagination	present as a large sac	fully developed forming a series of circumvolutions
Peri-anal ciliated ring	absent	id.	present	fully developed	id.
Mass of blood-corpuscles	absent	id.	primordium present	id.	one large, on the ventral side of the oesophagus; globules cluster in each side of the body, situated near the insertion of the tentacles
Muscles	absent	id.	id.	id.	one pair in the trunk
Ganglion	primordium	id.	developed	id.	id.
Dorsal vessel	absent	id.	id.	id.	developed
Stomach diverticle	absent	id.	id.	id. or a single present	if present, non-vacuolated
Lophophoral coelom	absent	id.	id.	primordium	developed
Glands in the epithelium	absent	id.	some glands in the hood	id.	id. and also in the lower part of the body
Nephridia	primordium present	terminal nephridia	nephridia not terminal, open under the anus	nephridia open laterally to the metasoma opening	id.
Metasoma muscles	—	—	only the nuclei of the somatopleure are visible	id.	longitudinal muscle bundles differentiated

full species, very probably a synonym of *hippocrepia*. For the moment I maintain as species *psammophila* and *sabatieri*, which will be considered as definitive, if *A. hastscheki* proves to be the larva of the first and if the characters of *A. sabatieri* are confirmed. *Phoronis ijimai* and *P. architecta* are valid for the moment. If the future reveals that all these species are valid, there will be no doubt that they form an "Artenkreis" since they must have descended from a common stem.

c) Biological notes.

The boring *Phoronis* are collected together with pebbles found on the ebb tide mark. Empty old oyster-shells are attached to such pebbles; in these shells perforated in a high degree, the phoronids take shelter. They live in burrows, not only in the shell itself, but also between it and the substratum. The non-boring specimens are found adhering to the fauna covering the rocks, also on the ebb tide mark. The animals thrive well in crystallization dishes, 20 cm in diameter by 10 cm in depth, in stalilized sea water, ventilated twice a day by means of a common injection syringe. In the aquarium I placed, besides the pebbles, some foliaceous green algae, probably *Ulva*. The maximum survival period was one year (specimen of Cananéia). After that time, the specimen first lost the lophophore, then withdrew within the tube and did not come out any more. The descalcification of the shell fragment revealed its disappearance. The species stands the putrefaction of all the bigger accompanying animals. Even when the pseudo-colonies seem dead, the chitinous tubes still contain individuals, generally without lophophore, ready to regenerate. This fact, contrary to the observations of Cerfontaine (1902, p. 262), occurred not only in the summer, but was also frequent after reproduction. When environmental conditions are unfavourable, many individuals remain in the tubes, but one or two always appear at the surface. I did not observe annual renewal of the aggregations, after reproduction (Ikeda 1901, p. 581). The specimens bear about three hours of desiccation. The density of the population is much lower than that of *P. ovalis* (du Bois-Reymond Marcus 1949): 17 individuals were counted in 7.5 cm^2. The chitinous tubes sometimes coalesce, but remain individualized. I did not observed any vegetative propagation. Only one individual occurred, similar to the one drawn by Selys-Longchamps (1907, t. 8, f. 11), but it may have been a young animal. Many newly collected animals exhibited a regenerating lophophore. In the aquarium the autotomy was not simultaneous in all animals. When

the lophophore is going to be cast off, the tentacles lose their rigidity and the lophophore folds. A constriction appears at about 0.5 mm below the base of the lophophore. More or less 45 minutes later the lophophore falls off (26.5°C temperature). Together with the lophophore embryos are eliminated and the anal papilla, nephridia, ganglion, circular nerve and end part of the intestine are lost. The body heals quickly, the end becoming round. The isolated lophophore moves for a while at the bottom of the dish; then the tentacles fall to pieces and degeneration begins. The regeneration of a new functionating lophophore takes place in *Phoronis hippocrepia* in 48 hours (Dyster 1858, p. 251) and in *P. vancouverensis* in 4 days (Rattenbury Marsden 1957, p. 314, table 1) whereas in the latter species a complete regeneration lasts about 16 days (ibid.).

In normal conditions, and especially in strong incident light, the tentacles remain well rigid with active cilia. In some cases they bend over the brood-pouch, sometimes they interlace, may be to protect the embryos. The animals are practically motionless; the tentacles scarcelly make small inward, and sometimes, outward bending movements. These movements undoubtely depend on proper stimuli. Thus, when a strange particle sticks to the inner face of the tentacle, its distal end turns outwards thus cleaning the tentacle. The tentacles around the oral cavity frequently bend towards it to further the entrance of alimentary particles. If one squeezes the base of the lophophore, all external tentacles turn outwards in the direction of the stimulus. The lophophore and the anterior part of the body may also execute oscillatory movements, as well as bend totally downwards; some animal stretch very far out of the tube. These movements may have the purpose to explore the surroundings for food. Newly collected animals are very sensitive. The least movement of the water provokes the retreat of the organism into the tube (Van Beneden 1858, p. 14, 20); they reappear only after a long time and slowly. They gradually get accustomed and do not react quickly any more, unless they are exposed to a strong stimulus. Taken out of the water they retreat into the tube and when put back into the water they are slow in coming out again; the same happens when they are strongly irritated. Removed from the chitinous tube, they only secrete a transparent substance, not showing movements of the ampulla, as the species living in sand or in slime. In these the ampulla has a burrowing function (Selys-Longchamps 1907, p. 36). The wall of the ampulla adheres to the chitinous tube, when in the secreting phase, so that the animal is damaged when one attempts to remove it.

Water currents in the lophophore coincide completely with the descriptions of Gilchrist (1907, p. 161) concerning *P. capensis*. The blood circulation is not regular. The blood does not ascend simultaneously in all tentacles and the pulsations are variable. At a temperature of 24°C I counted 10 pulsations per minute, what agrees with the observations made in other species (McIntosh 1888, p. 18; Cori 1930). At a temperature of 26°C I counted 12 pulsations per minute.

In nature the animals live in the zone where rocks are beaten by the surf therefore in a zone of agitated waters. In the quiet water of aquaria, the eliminated faeces may remain in the concavity of the lophophore and even envelop the embryos. The faeces are fusiform, reddish in the newly collected animals; after a stay in the aquarium they are grey. In the first case they may have fed on larvae of Ectoprocta, for example, of the red *Watersipora cucullata*, noticed near the habitat of *Phoronis*. I rarely observed the dejection with the lophophore completely turned downwards. The food is mainly composed by diatoms, among which *Coscinodiscus* sp. and *Cyclotella meneghiniana;* in the aquarium they feeded protozoans and detritus.

The present species is evidently not necessarily boring. It possesses a destroying activity, since individuals from Cananéia found on mollusc shells were nestled into a groove of the shape of their body. The association with *Polydora ciliata* (Polychaeta) undoubtedly favours the boring habitat of *Phoronis hippocrepia*. In Cananéia, where I did not find the mentioned annelid, the species was not discovered in burrows. In the case of the Polychaeta the perforation is chiefly mechanic (Hempel 1957, pp. 117, ff.) ; in the case of the *Phoronis*, incapable of mechanical perforation and devoided of acid secretion (Gilchrist 1907, p. 161), the destruction of the lime must be connected to respiratory processes (Marcus 1938, p. 278). *Polydora ciliata* occurs also in living shells; the phoronids, with one exception only (Silén, 1956, p. 96), were always observed in dead shells. In these perforation is easier, as the periostracum is often damaged; the same occurs in the crevices and cavities of the shells, the places chosen by the larva for metamorphosis (Silén 1954a). According to Hempel (loc. cit.), the calcite of the shell is chiefly destroyed mechanically. As the oyster shell is a shell of pure calcite, the chemical attack is minute. Therefore I believe that an initial colonizing by the polychaetes favours a later occupation by phoronids. Some larvae certainly avail themselves of previously bored cavities. I observed newly metamorphosed animals in burrows too large for having been bored by *Phoronis* itself. *Polydora* lines its burrow with a tube that always projects outward and is covered with debris,

what is not the rule in *Phoronis*. I found the species only in the flat valve of the oyster. The preference of this valve by epibiontes is known from the literature (Korringa 1951, p. 37). As *Phoronis* lives in the tidal zone, a zone of intense struggle for life (Pearse 1950, p. 22), it is quite natural that it looks for shelter in a more secure and permanent habitat. In the present species the occurrence in aggregations seems merely fortuitous, certainly due to favourable environment. However, gregariousness (see Knight-Jones 1951, p. 32) is not excluded.

My observations of individuals in the reproductive period and with embryos in the tentacular crown extend from July to March. Specimens from Santos were collected from July to December; those of Cananéia were mainly obtained in January and February. During all these months I found embryos in the lophophore. The animals collected at the end of February had embryos until the beginning of March. The animals first gathered (August 1953) did not show any signs of reproduction, and during the next six months, when they were fixed, no reproduction took place. Never did I obtain the beginning of reproduction in the aquarium. The animals collected in reproductive stage normally continued the process in the aquarium. In none of the plankton samples obtained from Santos or Cananéia I was able to find larvae of the present species, perhaps because the mesh of the net used was not fine enough to retain so small larvae. Two of them however were obtained in Ubatuba in December, showing that at that time, at least, reproduction takes place there. On the whole reproduction period of the present species lasts at least 8 months, and the possibility of 10 months, the longest observed for the group, in *P. architecta* (Brooks & Cowles 1905, p. 176) appears not impossible. The number of embryos contained in the brood pouch is variable. The maximum observed was 12, viz. 7 on the left, and 5 on the right side. Newly shed eggs remain on the bottom of the brood-pouch and the larvae follow each other more or less chronologically, the more advanced stages are the uppermost. In an animal well expanded out of the tube I counted 23 eggs ready to be freed, aligned in the body cavity. Individual reproduction lasts more than 15 days. This period was observed in a specimen already with embryos, which during that time went to spawning in the aquarium. The eggs rise slowly, helped by the contractions of the afferent vessel. Contrary to the observations of Silén (1954a, p. 219), daylight does not inhibit the elimination of the eggs in the present species. The egg takes about four days to develop into a young larva. It is very difficult to know the exact time, as the observed animals, newly collected, retreated into their tubes at the least agitation of the water. The

marked animals remained for days in their tubes so that the duration of the development had partly to be calculated by interpolation. Until the stage of two tentacles and, exceptionally, until the stage with eight tentacles the larva lives in the lophophoral concavity. The removing of younger embryos lying at the bottom is difficult, not only owing to their small size but also because the adult interlaces its tentacles or retreats into the tube. The larvae attach themselves by means of the hood, in an inverted position. The ciliated peri-anal ring of the most advanced larvae appears above and its cilia are very active. From time to time the hood executes somes movements or to let water in or to free the larva, attached to the epithelium of the brood-pouch or to younger stages by mucous secretion. I observed larvae of specimens from Cananéia freeing themselves with six tentacles. The free swimming period lasts 9 to 12 days, at temperatures varying between 16.5 and 22.8°C. The larva swims quickly, rises to the surface, then dives to the bottom of the dish; this movement is frequently repeated. The larva is very contractile; doubles itself up. It moves the hood very little. The hood remains close to the body; only rarely the larva lifts it and projects it a little forward. The tentacles, not very long, move little. The mature larva moves along the substratum as if looking for a suitable place to metamorphose. Whether there is a shell or not, all the metamorphoses I saw were realized out of it or at the most under it. The complete metamorphosis, unto the individual with a remainder of anal papilla, takes about two hours; the metasoma grows by 300 microns in about one hour and 40 minutes, while the body is shortened by about 100 microns. The greatest part of the larval tentacles degenerated.

Summing up, we have:

Reproductive period: July to March.

Duration of individual reproduction: more than 15 days.

Egg to young larva: about four days.

Free-swimming period: 9 to 12 days.

Metamorphosis: two hours.

The species is evidently eurythermic; it suffered in the aquarium temperatures ranging from 16 to 27°C and, exceptionally, from 14 to 30°C. The salinity changed from 30.63 to 37.38 °/₀₀.

As accompanying fauna occur in Santos: Foraminifera (many *Textularia* and *Rotalia;* also *Miliolida*) ; Ciliata: *Folliculinopsis andrewsi* and others tentatively classified as *Cothurnia* and *Lacrimaria;* Polycladida; Nemertini, once a *Tubulanus rhabdotus* Cor-

rêa; Archiannelida (*Dinophilus*); Polychaeta: *Polydora* (*Leucodora*) *ciliata* Johnston, *Exogone* sp., *Syllis variegata* Grube, *Aldouinea* sp., *Halosydnella brasiliensis; Phoronis ovalis* Wright; Entoprocta: *Pedicellina nannoda* Marcus (rare); Ectoprocta: *Thalamoporella evelinae* Marcus and *Watersipora cucullata* (Busk.). In Cananéia I found near the phoronids, algae; Polycladida; Pantopoda: *Anoplodactylus carvalhoi* Marcus, *Anoplodactylus strictus* Marcus and *Ammothella appendiculata* (Dohrn); Nudibranchia: *Spurilla neapolitana braziliana* MacFarland (February 1956); Lamellibranchia: *Martesia striata* (L.); Ascidiacea.

II. *Phoronis ovalis* Wright 1856

(Figs. 56-63)

Phoronis ovalis Wright 1856, p. 167; Harmer 1917, p. 123; Cori 1932, p. 126; 1937, p. 130; 1939, p. 162; Brattström 1948, p. 5; du Bois-Reymond Marcus 1949, p. 157; Silén 1952, p. 135; Lönöy 1953, p. 7.

In the same biotope as *P. hippocrepia* I found *P. ovalis*, already described from that same locality (du Bois-Reymond Marcus 1949). The present material consisted of colonies boring in empty oyster-shells. The burrows have an oval-shaped external orifice of 0.27 and 0.10 mm diameters. Some individuals are completely transparent, others are pigmented. The brownish pigment was observed either only at the distal portion of the tentacles or over the whole body. The latter was frequently the case in regenerating individuals or in those that were going to cast off their lophophore. Cuticular processes (du Bois-Reymond Marcus, op. cit., p. 159 and f. 10, t) were only seen in few individuals, hence they are not constant formations. They were absent in all individuals of one colony.

Tentacles up to 26 in number. Their external part with conspicuous cuticle, the remainder with long cilia. "Corps en massue" up to 8.2 microns in size, plentiful in the tentacles of some individuals and rare in the body epithelium.

Median, single lophophoral organ (Figs. 62, *l*; 63, *b*) represented by a thickening of the anterior epithelium of the bottom of the lophophoral concavity. Its structure is similar to that of the lophophoral organs of *P. hippocrepia*. Vesicular cells with peripheral nuclei are mostly accumulated in the central part; in the depth there is mass of nervous fibres. It is true that some of these vesicular cells have the appearance of neurons (*vide* right side of Fig. 63) with their single axon going towards the nerve layer.

Muscle bundles: 27 to 34 in number (Fig. 59, *f*) distributed 14 to 21 on the left and 13 to 18 on the right side. Marginal muscle fibres, three to four in number, on each side of the bundle (Fig. 61). In none of my specimens I found the paired thickening of the ganglion with connecting commissure and I believe it is caused by fixation (cf. Silén 1954b, p. 5). Giant fibres, about 2.5 microns in diameter, located near the prolonged lower wall of the nephrostome (Fig. 61, *k*). They were however not found in all individuals and therefore their presence cannot yet be considered as specifically constant.

Small nephridia, with a short nephridial sub-epithelial canal and small nephrostome (Figs. 56, 57, 62, *a, g*). In some individuals the lower wall of the nephrostome is prolonged downwards, longitudinally to two thirds of the length of the muscular region of the body (Fig. 58, *h*). This prolongation of the lower wall of the nephrostome which is not constant, led du Bois-Reymond Marcus (op. cit., p. 122) to consider the nephrostome as long.

The stomach epithelium showed the appearance of syncytium (Lönöy 1953, f. 12) only in animals in poor physiological conditions.

Caecal vessels present in the inferior third of the length of the lateral vessel; they fuse in the ampulla, forming lacunae. The accessory vessel opens into the peri-gastric sinus, running, farther on, through the whole muscular region, closely adhering to the descending branch of the digestive tube (Fig. 59, *c*). Blood corpuscles 7 and 9 microns in diameter and their nucleus 2 to 2.5 microns.

Body cavity with some fusiform, eosinophilous corpuscles 10×5 microns and 20×6 microns in size. They are abundant in individuals during the regenerative process. I found roundish corpuscles 6 microns in average with golden-yellow granules in the body cavity and also in the vessels.

Fat body present in both chambers of the body cavity. Paired ovaries, the left more bulky than the right one (Fig. 60, *p*), occupied the whole body cavity in November. The ovocytes with almost simultaneous development exhibit vitelline nuclei, one or two in number, strongly basophilous and crescent- or bar-shaped (Fig. 60, *s*) as in the ovocytes of *P. mülleri* (Selys-Longchamps 1907, p. 118 and t. 7, f. 5). Vitelline nuclei are frequent in ovocytes of Ectoprocta where they consist of ribonucleins (Chrétien 1957, p. 30, f. 2, 3, R). Two nucleoli are present; they fuse in the large ovocytes. None of the sectioned specimens had testis. In the developed ovary of one individual I noticed one single spermatozoon, similar in structure to the one described for *P. hip-*

pocrepia. Total length about 10 microns, the head being 1.4 microns in length and the small middle piece 1 micron. There are doubts as to whether *P. ovalis* is dioecious or a proterandric hermaphrodite. With Harmer (1917, p. 129) I admit it to be unisexual. Besides the budding individuals (du Bois-Reymond Marcus 1949, t. 3) I found the same types of individuals in the regenerative process and in transverse fission represented by Harmer (op. cit.). Individuals with invaginated body wall were rare. I seldom observed the loss of the lophophore although conditions in the aquarium were not the best. Moreover, the species is much less resistant than *P. hippocrepia;* when fasting for a long time, they reabsorb themselves. While descalcifying a colony I thought to be dead, I found in the chitinous tubes remains of strongly pigmented tissue. I did not see regeneration from tentacular crowns (Silén 1955, p. 160). In March 1955 I observed pigmented globular formations about 150 to 250 microns in size within small chitinous tubes with annular thickenings; I attempted to rear them, but without success. Through the work of Silén (1954a) I identified these formations as larvae of *P. ovalis*. The stage represented on p. 244, f. 21C of Silén's work occurred in my material within the chitinous tube and not swimming.

OCCURRENCE — Santos (Ilha Porchat), in empty oyster-shells, on the ebb tide mark.

FURTHER DISTRIBUTION — East coast of Great-Britain, Heligoland?, Öresund, west coast of Sweden; Brazil; New Zealand (Silén 1956, p. 94).

DISCUSSION — Of all the characters described for the first specimens of the species from Brazil and not known from *P. ovalis* material of other provenances, the nephridium (Silén 1952, p. 122) and the cuticular processes of the chitinous tube are doubtful still after the studies of Lönöy (1953). Both are inconstant features in the Brazilian material and therefore of little systematic value. The long lower wall of the nephrostome prolonged downwards present in the more developed Brazilian specimens has not yet been observed in the North Sea specimens. This structure is very variable in other species and undoubtedly due to growth. I therefore agree with the conclusions of Lönöy (op. cit.), that the Brazilian material is con-specific with the European one. The diagnosis of the species given by Silén (op. cit., p. 135) may be completed as follow: Chitinous tube: smooth or with cuticular processes. Length: up to 13 mm. Tentacles: maximum 27. Lophophoral organ: a single median. Giant fibres: two, about 2.5 microns in diameter, but not always conspicuous. Longitudinal

muscles: 26 to 39 bundles, diversified into marginal and central fibres. Accessory vessel: in the whole extension of the metasoma, merging into the peri-gastric sinus. Blood-corpuscles: 5 to 9 microns in diameter. Nephridia: with a single, small nephrostome, whose lower wall may be short or long. Unisexual?. Ovary paired. Assexual propagation: transverse fission and budding. Larva: not actinotrocha.

III. Actinotrochae

a) *Actinotrocha bella* (new technical name)

(Figs. 64-89)

Stage with 18 larval tentacles (Fig. 64 A) — Total length 0.55 mm; hood 0.19 mm long and 0.30 mm wide; maximum width of body 0.19 mm; peri-anal ciliated ring 0.21 mm in diameter and 0.046 mm thick; tentacles 0.25 mm long and 0.026 mm wide. Relatively large hood placed in horizontal position; body already well developed as well as the peri-anal ciliated ring. Ventral tentacles shorter than the body. Pigment absent. Hood epithelium composed of cuboidal cells with large nuclei occupying almost the whole height of the cell. Ventral epithelium of the body composed of narrow columnar cells with elongated, very thin and deeply-stained nuclei. At the insertion level of the tentacles the whole lining epithelium is homogeneous, composed of columnar cells with elongated nuclei (Figs. 66, 67, *q*). In the posterior region of the body it becomes flat. Gland cells absent. Some mesenchymal, fusiform cells present in the hood cavity; some of them attached to the body walls. Wide buccal vestibule lined with epithelium not differing from that lining the hood. Buccal aperture and oesophagus covered by columnar epithelium whose thin cells have elongated, densely arranged nuclei. The wall of the bulky stomach (Figs. 66, 67, *i*) forms folds. It is composed of cells similar to those of the diverticulum. This is single, composed of cuboidal cells with large round, heavily chromatic nuclei situated at the base of the cells. Close to the ventral-lateral wall of the stomach I noticed a cell proliferation (Fig. 67, *n*), perhaps the primordium of blood cells. Two digestive areas (Figs. 66, 67, *m*) at different levels. Metasoma present as a short invagination. One pair of dorsal muscles inserted near the root of the last dorsal pair of tentacles (Fig. 67, *k*). Nephridia simple (*j*). Trunk coelom developed (*l*). First blood cells noticed.

Stage with 22 tentacles (Fig. 64 B) — Total length up to the extremity of the ventral tentacles 0.55 mm; up to the peri-anal

ciliated ring 0.48 mm; hood 0.18 mm long and 0.22 mm wide; maximum width of body 0.20 mm; peri-anal ciliated ring 0.12 mm in diameter and 0.04 mm thick. Hood of medium size; ventral tentacles longer than the body which presents itself contracted. Granules of yellow pigment present in the hood on the outer side of the tentacles and in the peri-anal ciliated ring. Epithelium covering the lower part of the body composed of squamous cells with narrow, elongated, transversely disposed nuclei (Fig. 68, *q*). Subepidermic muscular layer (*r*) is underlaid by the very thin somatopleure, whose elongated nuclei are here and there hardly distinguished. At the level of hood root the dorsal covring epithelium becomes thicker. The ventral body epithelium from the fore end to the aperture of the metasoma is constituted of columnar, ciliated cells (Fig. 65, *g*), representing the remainder of the ventral thickening. The little invaginated metasoma (Fig. 70, *v*) consists of epithelial cells lined with the somatopleure, the large round nuclei of which are noticed. Peri-anal ciliated ring (Fig. 69, *y*) composed of numerous thin cells. A single diverticulum (Fig. 65, *e*) present. Oesophagus valve provided with strong annular muscles. Stomach constituted of columnar cells with round nuclei situated mainly in the middle or in the proximal third of the cells. Intestine making a loop; the region between stomach and intestine (Fig. 68, *p*) is formed by an epithelium of columnar thin cells with elongated heavily chromatic nuclei. End part of intestine (Fig. 69, *p*) composed of cuboidal cells with round nuclei and rare vesicular gland cells with basal nucleus. Hood septum present. Roundish amoebocytes in the body cavity, average 5 microns in diameter and their nucleus 2 microns. Other amoebocytes with round or horseshoe-shaped nucleus are attached to the stomach wall. Ventral mesentery developed (Figs. 68, 69, *s*).

Stage with 24 tentacles (Fig. 71 A) — Hood not lying on the body, which is somewhat bulky. Total length 0.70 mm; hood 0.40 mm wide; maximum width of the body about 0.30 mm at the insertion level of the ventral tentacles; long, filiform tentacles, the ventral ones, 0.20 mm long extend nearly as far as the peri-anal ciliated ring; they are 0.02 mm thick. Peri-anal ciliated ring 0.20 mm in diameter and 0.03 mm thick. Hood epithelium very thin with squamous cells and round nuclei; however, in the medio-ventral part of the hood the epithelium is quite thick composed of thin cells with deeply-staining nuclei. In the hood cavity rare mesenchymal cells with round nuclei. No sensory organ; ganglion only conspicuous in section. Body epithelium composed of squamous cells with elongated nuclei placed transversely. Metasoma (Fig. 71 A, *a*) represented by a small tube that partially surrounds the right side of the stomach; opens to the left a little

lower than the root of the ventral tentacles. Digestive tube as in the preceding stage; a single diverticulum with rare vesicular gland cells (Fig. 74, *p*) and globular basophilous formations (*k*) with round nuclei. Stomach so bulky that it enters the root of the tentacles; there exists a zone of intense proliferation of cells as in the stage with 20 tentacles. Mass of blood corpuscles only represented by a few rare globules. Nephridia (Figs. 72, 73, *m*) open laterally, a little above the aperture of the metasoma. The canal is formed by cells of small height with nuclei in the proximal side. Many cells are apposed to the canal on the outside. Round solenocytes are 2 microns in size. One pair of retractors in the hood; they merge on the level of the last pair of dorsal tentacles. The developing ventral pair of muscles of the trunk is inserted near the external opening of the nephridia. Ventral mesentery on the last part of the intestine. Hollow tentacles (Fig. 72, *g*) with rare pale nuclei of mesenchymal cells in the cavity. They are covered by a ciliated columnar epithelium with elongated, chromatic nuclei either basal or median, on the lateral and anterior face. The epithelium is flat on the posterior face.

Stage with 38 tentacles (Figs. 71 B, B_1) — Larva with bulky body; hood of medium size. Peri-anal ciliated ring developed and undulated. Long and filiform tentacles. Caecal vessels present on the left side. Metasoma well developed. An elliptical sensory organ present. On the sides of the mouth two brownish prominences (Fig. 71 B, *c*) and in the region a little above the insertion of the ventral tentacles, an oval brownish formation (*d*), placed with its longer axis perpendicular to the length of the larva. In sections these structures proved to be masses of blood corpuscles which will be described below. Total length 1.10 mm; hood 0.60 mm long; the latter is as broad as long; maximum width of the body 0.50 mm; peri-anal ciliated ring 0.35 mm in diameter and 0.10 mm thick. Ventral tentacles about 0.50 mm long and 0.04 mm thick. Dorsal epithelium of the hood (Fig. 82) consists of rare gland cells with acidophilous droplets; rather tall columnar cells with oval nuclei placed in the central part or in the upper third; club-shaped gland cells (Fig. 82, *a*) with basophilous granular contents; oval glandular cells with marginal, infero-lateral nuclei without contents. Ventro-median epithelium (Fig. 75, *s*) constituted of columnar, ciliated cells with elongated and central nuclei. Ventro-lateral epithelium (*v*) with cuboidal cells of pale cytoplasm and small nuclei. Body epithelium is low, with small, elongated nuclei (Figs. 77-80). In the posterior part of the body the epithelium is either flat (Fig. 85, *i*) or thin with the proximal part of the cell reticular and small round nuclei situated in the upper third (Figs. 84, 86, *e*). The subepithelial muscle layer 2 to 3 microns thick (Figs. 84, 85, *f*) is slightly stained

by eosine. I found some eosinophilus gland cells in the ventral epithelium at the insertion level of the tentacles. The epithelium covering the peri-anal ciliated ring is composed of low columnar cells (Fig. 86, *e*) with small and round nuclei situated either in the upper or in the inferior part. Vesicular cells, obviously glands, are also present. The ciliated ring is formed of very thin cells (Fig. 81, *y*) with long cilia; their nuclei are small and elongated, situated at different levels, even in the upper part. The lateral and anterior epithelium of the tentacles is composed of columnar ciliated cells with elongated nuclei placed perpendicularly to the surface. Fibrillar nervous substance seems present in the anterior face of the tentacle. Sensory organ (Fig. 83, *c*) consists of an accumulation of gland cells with basophilous droplets; sole-shaped (*d*) and club-shaped cells (*a*) are frequent. In the depth of the organ there is a 6 microns nerve (*b*) extending forward (Fig. 82, *b*). The ganglion (Fig. 76, *a*) is situated in a slight pit of the epithelium; it is covered with common epithelial cells, intermingled with round slightly chromatic nuclei belonging to cells of which I could not detect the outlines. They might be nuclei of sensory cells. Nervous substance present in the deep part of the organ; its central part continues forward in the nerve reaching the sensory organ. In the nervous substance I discovered scarce ganglionar unipolar cells; their body is 5 microns in size and the round nucleus 3 microns. I observed some nervous tracts in the hood without being able to follow their course. Nervous substance is also present in the external edge of the hood (Fig. 75, *u*). Nerves 5 microns in diameter were also identified within the nervous substance of the epithelium enveloping the peri-anal ciliated ring. Digestive tube as in the former stages. Stomach (Figs. 78, 79, *j*) placed dorsally in relation to the metasoma possesses an epithelium formed of columnar cells with round nuclei situated at different levels from the upper third to the lower one; also columnar cells with elongated and narrow, deeply-staining nuclei and gland cells with contents represented by eosinophilous drops about 3 microns in size (Fig. 87, *p*). Dorsal ciliated band (*h*) present, composed of thin cells with chromatic nuclei; along this band eosinophilous gland cells of the above described type are noticed. In the ventral epithelium of the stomach, opposite to the band, there is also a zone of cells which look like those of the band. In the proximal part of the stomach gland cells are rare. The single diverticulum (Fig. 77, *e*) is formed of high columnar cells with round, small nuclei situated at different levels, seldom in the base but also in the distal end. The cytoplasm of these cells is spongy-like. Rare gland cells with eosinophilous drops are also present in the diverticulum. Rectum (Fig. 80, *z*) covered by low columnar ciliated epithelium with round nuclei

situated in the central part or in the proximal third. I found diatoms, mostly *Coscinodiscus*, in the stomach cavity and also enclosed in the cells of its wall. Ventral mesentery (Fig. 80, *x*) present over a short extension. Hood cavity crossed by rare fusiform cells with cytoplasm slightly stained. In the trunk coelom I found star-shaped cells (coelomocytes) with small, round, peripheral nucleus and slightly eosinophilous cytoplasm (Fig. 80, *v*), and also oval cells with round rather central nuclei. I also found such cells attached to the subepithelial layer (Fig. 85, *g*). Metasoma initially sinistrorse later turns towards the right forming a series of folds and reaching the inferior part of the trunk (Fig. 71 B, *a*). Its epithelium is formed of columnar cells with basal nuclei and of gland cells with granular eosinophilous contents. Granules of this type are also found in the cavity. Club-shaped basophilous gland cells filled with small granules are plentiful in the median part and rare in the lower metasoma. Gland cells with eosinophilous drops, 1 micron in size, are rare in the metasoma epithelium. Longitudinal muscles of the metasoma already differentiated into bundles. One pair of retractors in the hood; they extend from the ganglion to the last pair of dorsal tentacles (Figs. 76, 77, *b*). I could follow two pairs of ventro-lateral muscles (Fig. 77, *g*) from the ventral wall below the buccal opening to a little below the insertion of the ventral tentacles. These muscles lie in the praeseptal cavity (Fig. 88, *q*), and possibly they represent the elevator of the metasoma and nephridia (cf. Cori 1939, f. 42). One ventral pair of muscles in the trunk, is inserted just in front of the peri-anal ciliated ring. Curved nephridial canal placed obliquely (Fig. 78, *k*) with the concavity turned upwards, opens laterally into a tiny pore, beneath the insertion of the ventral tentacles. Rare solenocytes with pale colored nuclei. Lophophore coelom of adult incompletely developed. Definitive tentacles absent and owing to the maturity of the larva I believe that they develop from the larval ones. Circulatory system well developed. Bulky superior blood arch (Figs. 76, 77, *d*) surrounds ventrally the eosophagus and the unpaired diverticulum, projecting forward in a latero-dorsal position until it reaches the level of the buccal opening. The two branches of the blood arch are connected by a thin vessel situated between the eosophagus and the diverticulum (Fig. 77). The blood arch extends downwards adhering to the lateral walls of the stomach, turns around each nephridium and ends near the lateral wall of the body at the level of the tentacles roots (Fig. 78, *h*). This arch is lined by thin epithelium and attached to the body wall by means of connective fibres (Fig. 77). Blood corpuscles are about 8 microns in size and with 2 microns nuclei. Dorsal vessel (Fig. 87, *n*) developed, adhering to the dorsal wall of the stomach.

From it numerous caecal vessels (*l*) emanate filling the trunk coelom; some even attain the ventral side. They are absent on the right side. They seem to have the same origin as the dorsal vessel, viz., folds of the peritoneum. Structurally they consist of a cluster of small deeply chromatic nuclei delimiting a cavity (Fig. 89, *l*). The outlines of the cells were not distinct.

OCCURRENCE — Stations n.° 115, 119, 129, 130 and 137 of the cruise of "Toko Maru", all along the northeast Brazilian coast, at the height of the city São Luís, State of Maranhão.

DISCUSSION — The above described larval stages were all considered as belonging to the same species owing to structural similarities, mainly, regarding the subepithelial muscle layer, the digestive tube, and the nephridia. The assumption that these stages represent the development of one and the same species can only be proved by rearing these larvae. The most advanced stage, the only one that enables a sure classification, does not agree with any of the already described larvae. To distinguish the present larva from those known through literature, I enumerate them, giving their disjunctive characteres, mainly the external ones.

A. ashworthi — Length: 0.65 mm, with 20 larval tentacles and anlage of definitive ones; three blood corpuscle masses, arranged as in *A. sabatieri*.

A. branchiata — Length: 2.00 mm, with 30 to 32 larval tentacles and 26 to 28 definitive ones arranged in two symmetrical groups, independent from the larval ones; paired diverticulum, vacuolated; two ventral masses of blood corpuscles connected with nephridia; pigment contained in amoebocytes.

A. gegenbauri — Length: 2.50 mm, with 24 larval tentacles; metasoma absent; three masses of blood corpuscles.

A. hatscheki — Length: 0.62 mm, with 16 larval and 10 definitive tentacles; two stomach diverticula; no sensory organ.

A. henseni — Length: 0.30 mm, with about 13 larval tentacles; no metasoma. As this is a very young larva, there is some chance that it belongs to the developmental sequence of *A. bella*, owing to its occurrence in northern Brazilian waters.

A. hippocrepia — Length: 0.70 mm, with up to 10 tentacles; a ventral mass of blood corpuscles on level of eosophagus and some globules grouped laterally above the roots of tentacles; pigment present.

A. ikedai A — Length: 1.00 to 1.50 mm, with 16 tentacles; sensory organ absent; two pairs of blood corpuscle masses, one at the level of the diverticulum, the other in front of the septum, on both sides of the stomach; dorsal vessel only exceptionally formed.

A. ikedai B — Length: 2.00 to 2.50 mm, with about 28 larval tentacles; two ventral blood masses at the level of the roots of tentacles; (very similar to *A. branchiata*).

A. ikedai C — Length: 1.50 mm, with up to 24 tentacles; sensory organ absent; two blood masses sidewards of eosophagus; circular muscles of body wall form a thick layer (as in *A. bella*); one pair of bottle-shaped glandules, on each side of the ganglion.

A. ikedai D — Length: 4.00 to 5.00 mm, with 40 to 48 larval tentacles; definitive tentacles represented by a thickening of the wall of the larval ones; sensory organ absent.

A. metschnikoffi — Length: 0.60 mm, with 16 to 18 larval tentacles, anlage of definitive tentacles present; three blood corpuscle masses, two near the diverticulum and one ventral in front of the root of the ventral tentacles.

A. pallida — Length: up to 0.60 mm, with 10 to 12 larval tentacles; a single ventral mass of blood corpuscles, in the fore part of the stomach.

A. sabatieri — Length: 1.00 to 1.50 mm, with 12 larval tentacles; 10 definitive tentacles; ? three masses of blood corpuscles, two near the diverticulum and one in the insertion region of the ventral tentacles; pigment present.

A. wilsoni A — Length: 1.02 mm, with 18 larval tentacles; definitive tentacles as thickening of the inferior wall of the root of the larval ones; two masses of blood corpuscles; sensory organ absent; pigment present.

A. wilsoni B — Length: 1.22 mm, with up to 26 larval tentacles; definitive tentacles in two groups, independent of the larval ones; four masses of blood corpuscles, two dorso-lateral and two ventro-lateral.

Insufficiently characterized are: *A. brownei, A. dubia, A. gardineri, A. goodrichi, A. haswelli* A and B, *A. menoni* A, B, C and X, *A. ornata, A. seylisi, A. shearei, A. spauldingi, A. schepotieffi* A and B, and the actinotrochae described by Masterman and

Steuer. I did not find any relationship between the young stages of *A. bella* and others, previously studied but, mostly, incompletely described.

b) *Actinotrocha chata* (new technical name)

(Figs. 90-91)

Stage with 10 tentacles (Fig. 90) — Hood of medium size: body voluminous in the prae-tentacular region; anal papilla not very developed; peri-anal ciliated ring present. Total length (t.l.) 530 microns; maximum width 200 microns; ventral tentacles about 184 microns long; peri-anal ciliated ring 117 microns in diameter, and 28 microns thick; anal papilla (a.p.) 211 microns long; the ratio of t.l. to p.a. is 2.5:1. Metasoma represented by a thickening of the ventral wall of the body; its epithelium shows some gland cells (Fig. 91, *x*). The somatopleure (*s*) consists of cells with distinct large nuclei. The ventral mesentery connects the metasoma to the stomach wall (*v*). The hood epithelium is constituted by cuboidal cells. The ganglion is represented by a thickening of the dorsal epithelium of the hood. Diverticulum as well as blood masses absent. Some vesicular cells present in the epithelium of the peri-anal ciliated ring. Nephridium consists of a small canal opening at the level of the metosoma plate. Digestive tube as in the young stages of *A. wilsoni* B, described below.

OCCURRENCE — Ubatuba, one specimen in plankton sample n.° 82.

DISCUSSION — I have no reference of 16-tentacle larvae with primordium of metasoma previously described. Since the structure of this larva is similar to that of the young *A. wilsoni* B of the same sample, the possibility of the present larva being a young *A. wilsoni* B with delayed development of the metasoma cannot be excluded.

c) *Actinotrocha wilsoni* B (technical name)

(Figs. 92-118)

Stage with eight to 10 tentacles (Fig. 92 A, B) — Total length: 257 to 447 microns; hood 95 to 180 microns long and about 152 microns wide; width of body from 85 to 136 microns; ventral tentacles 123 to 142 microns long and 20 microns thick; anal papilla 47 to 136 microns long, the ratio of t.l. to a.p. is 5.4

to 3.2:1. Small hood, sometimes pulled down over the body, sometimes in vertical position; the post-buccal region is the most developed. Anal papilla small with rudimentary peri-anal ciliated ring, only noticed in sections. Ventral tentacles long, exceeding the body. Body epithelium squamous (Figs. 97, 98), in most of its extension; ventro-median epithelium of hood (Fig. 95, *b*) formed of columnar cells with elongated, deeply-stained nuclei; laterally the epithelium is constituted of cuboidal cells with round, basal nuclei and some vesicular gland cells with lateral nuclei. Very thin fibres, perhaps connective-muscular elements, cross the hood cavity (Fig. 96). Ganglion (Fig. 92 A) in total view, roundish or kidney-shaped. Structurally it consists of an epithelial thickening (Fig. 95, *a*) with numerous nuclei and nervous substance deeply placed, where I could discern two nerves. The digestive tube is constituted of a quite small round mouth; a short oesophagus; a stomach (Fig. 97, *e*), initially wide, suddenly narrowing downwards (Fig. 98, *e*), and a globous terminal intestine. The oesophagus ends in a valvular formation. The stomach, at its proximal end, consists of cuboidal cells, with large, round nuclei; dorsally the epithelium is columnar with a few gland cells. Only one digestive area was present. Metasoma absent. Fusiform mesenchymal cells present in the body cavity. The ventral thickening (Figs. 95, 96, *b*) extends from the buccal region to in front of the insertion of the tentacles. Nephridium (Fig. 98, *i*) formed of a long canal of narrow caliber. It is situated in the body cavity, supported by thin fibres; it ends internally with rare solenocytes and opens a little above the anus.

Stage with 12 larval tentacles — The larva differs little from the preceding stage. Total length 396 to 476 microns; hood 136 to 176 microns long. Body up to 117 microns wide. Ciliated ring 57 microns in diameter and 16 microns thick. Ventral tentacles up to 224 microns long and 15 microns thick. Ratio of t.l. to a.p. from 3.5 to 3.2:1. A stomach diverticulum present; its epithelium does not differ from that of the stomach and contains a few cells with pale vacuoles. Stomach with outline of two digestive areas, where the epithelium is thicker. Metasoma represented by a slight thickening of the epithelium. Free mesenchymal cells from a layer in the wall of the body and of the digestive tube (Figs. 101, 104, *f*), delimiting the trunk coelom. The latter is of lacunar origin; not only elements supplied by the digestive tube (Selys-Longchamps 1907, p. 132) but also, certainly, elements from the wall of the nephridium (Cowles 1904, p. 174) contribute to its lining. Nephridium (Fig. 99, *i*) in its initial part remains in the body cavity; it opens at the level of the peri-anal ciliated ring. The nephridial canal is composed of cuboidal cells with

large central round nuclei (Fig. 104, *i*). Mesenchymal cells (Fig. 100, *g*) with large round nuclei are distinct in the body cavity.

Stage with 16 to 18 larval tentacles (Figs. 92 C, 93 A) — Total length up to 650 microns; hood up to 228 microns long and about 350 microns wide; maximum width of body about 200 microns; ventral tentacles up to 285 microns long and 22 microns thick; peri-anal ciliated ring up to 150 microns in diameter, and 40 microns thick. Ratio of t.l. to a.p. from 3.6 to 2.5:1. In the specimen of Fig. 92 C the anal papilla is quite contracted. The metasoma is represented by a short invagination (Fig. 107, *k*). On the whole the body epithelium is squamous with hardly distinct nuclei. The columnar epithelium with elongated and deeply stained nuclei is only present in the remainder of the ventral thickening and at the level of the insertion of ventral tentacles. In the ganglion some pale nuclei, probably belonging to sensory cells are noticed; nervous substance in depth were noticed. The buccal opening is lined with columnar, very thin cells, with elongated nuclei situated in the central part. Stomach with varying epithelium according to the digestive phase. The nuclei of its cells may lie in the upper and vacuoles in the inferior part; these vacuoles may present contents, which are stained orange with Mallory. There are two digestive areas with enclosed alimentary particles (Fig. 108, *n*). The fore-part of the stomach may protrude into two diverticula, but this is not the rule. The rectum also has cells with vacuoles. Ventral mesentery (Fig. 107, *m*) present. Metasoma (*k*) formed of columnar, ciliated cells with basal nuclei; there are also rare cells with granular cytoplasm. Its lining consists of cells that have quite conspicuous large nuclei. Simple nephridial canals (Fig. 108, *i*) open laterally to the opening of the metasoma. Solenocytes are 4 microns in size. Lateral aggregations of mesenchymal cells with large roundish nuclei (Fig. 108, *g*) show the primordia of the ventral masses of blood corpuscles.

Stage with 20 larval tentacles (Fig. 92 D, E) — Total length up to 760 microns; hood up to 250 microns long, and exceptionally 450 microns wide. The ventral tentacles are very long and may exceed the length of the body when it is quite contracted (Fig 92 D); they reach up to 300 microns and are 20 microns thick. Peri-anal ciliated ring is about 200 microns in diameter and 300 microns thick. Ratio of t.l. to a.p. on an average 2.9 to 2.3:1, may also be 4.0:1. Metasoma represented by a developed tube. The ventral pair of blood corpuscle masses is apparent (Fig. 106, *x*). The body may be voluminous when expanded; it may also be curved backwards. I observed in the hood a dorsal 5 microns

nerve and one pair of dorsal muscles, which extends from the ganglion to the insertion level of the dorsal tentacles. It represents the retractor of the hood. In the hood cavity of one individual I noticed the presence of gregarines (Figs. 102 A; B, *s*). Stomach diverticulum single or paired. The cells of its wall may contain vacuoles and their nuclei are placed in the proximal part. A diverticulum of the trunk coelom penetrates into the tentacles (Fig. 114). Nephridial canal (Fig. 106, *i*) curved; solenocytes are distinct. Dorsal vessel little developed. In the digestive tube I found, besides spicules and diatoms an egg in segmentation.

Advanced larva (Figs. 92 F-G; 93 B; 94) — The larva has up to 26 larval tentacles and a maximum of 20 definitive ones arranged in two series, on each side under the larval tentacles (Fig. 92 G; 93 B). Maximum total length was 1.45 mm; maximum breadth of body 0.50 mm; peri-anal ciliated ring up to 0.30 mm in diameter and about 0.09 mm thick; ventral tentacles up to 0.45 mm long; ratio of t.l. to a.p. up to 1.8:1. Definitive tentacles appear in larvae with 22 larval tentacles. There is a certain variation in the number and time of their appearance, as was already observed by Steuer (1933) in *A. branchiata*. Exceptionally a larva with 20 tentacles had them. They are situated at the root of the larval ones but are independent from them. I found granules of light brown pigment in the hood epithelium on the inferior face of the larval tentacles and in the peri-anal ciliated ring. The pigment is diffusedly scattered and not contained in amoebocytes. The larva may be slender (Fig. 93 B) or, on the contrary, quite stout (Fig. 92 G). Usually the contraction provokes the appearance of the diverticula; in the stout larva represented in Fig. 93 G, even a part of the metasoma penetrated into the fore part of the body. The hood either stands in a vertical position or covers the buccal opening. The two living larvae I observed were transparent with orange pigment. The body epithelium is so thin that a complete analysis was not possible; that of the hood is very low, except in the dorsal part, where it is thickened, formed of tall columnar and some gland cells. In the ventro-median portion, above the buccal opening (Figs. 109; 112, *w*), the cells are also columnar. The digestive tube is also very long, forming a loop in the end part. Bulky stomach, consists of low columnar cells; in the animal fixed in fully relaxed condition the stomach epithelium becomes very thin, as a result of a considerable enlargement of the cavity. However, in other specimens the stomach epithelium appears very high (Fig. 113) and with some gland cells containing eosinophilous drops (*v*). Stomach diverticulum paired (Fig. 110, *c*) or absent, seldom vacuolated (Fig. 109, *c*); sometimes, due to fixation, only one is distinct. Two ventro-lateral digestive areas

(Fig. 115, *z*) are present. Terminal intestine formed of cuboidal cells. The anus is lined with narrow columnar cells with elongated nuclei. Ganglion (Figs. 109, 110, *a*) located in a small invagination of the epithelium. Sensory organ (Figs. 112, 118), roundish or oval, protrudes in front of the ganglion, but may be found in a hollow. Its gland cells with basophilous granules, are very thin and elongated (Fig. 118, *p*). A developed nerve is found in the depth (*n*). Some connective-muscular elements occur in the hood cavity. Prae-oral septum hardly recognizable (Fig. 112, *q*). Dorsal retractors of the hood were noticed (Fig. 115, *m*). A pair of muscles is also present in the trunk. Four blood corpuscle masses, two dorso-lateral (Fig. 115, *j*) and two ventro-lateral (*h*) to the stomach. By fixation the pair or dorsal masses may reach the level of the oesophagus (Fig. 110, *j*). This pair is present in larvae with 22 larval tentacles. Blood corpuscles are 6 to 7 microns in diameter with 2 microns nuclei. Dorsal and latero-dorsal vessel present (Fig. 105, *z*, *y*; 115, *x*). The dorsal vessel extends downwards to the transition zone between the stomach and the rectum. Nephridia are connected with the ventral pair of blood corpuscle masses (Fig. 117, *i*). The curved nephridial canal (Fig. 111, *i*) is situated above the septum. Its superior part is provided with a few solenocytes (*u*), denoting an involution. Metasoma well developed, forms a series of folds, some of them short, others extending as far as the peri-anal ciliated region. In the larvae represented in Figs. 92 F and G, 93 B, the variation in metasoma arrangement in advanced stages can be seen. The opening is usually situated to the right, at a short distance of the insertion of ventral tentacles. The metasoma is connected to the ventral wall of the body, as well as to the stomach through a mesentery. Its epithelium is formed of columnar cells with their nuclei in the lower third and of numerous vesicular cells. Longitudinal muscles only differentiated into bundles in quite old larvae (Fig. 116, *l*). The metasoma region that will be the ampulla does not show any muscles in its lining. It was possible to discern a 4 microns nerve in the metasoma epithelium. I observed in the hood, ventro-laterally, a limited subepithelial space, where some blood corpuscles were present (Fig. 112, *s*). In the maximal developmental stage, a few caecal vessels are noticed at the level of the stomach. The atrial pit (Fig. 103, *v*), in one single specimen, certainly represents a formation due to fixation. The contents of the alimentary canal is constituted of diatoms, *Noctiluca*, some sponge spicles and once a veliger. Several larvae in plankton are found mutilated; the loss of part of the tentacles is frequent. The metamorphosis of the larvae also took place in the plankton; the evaginated metasoma, however, was irregular. The mature larva swims near the bottom of the recipient in rather

wide circles, resting sometimes in an inverted position with the hood downwards; it is, however, often found in a vertical position. The tentacles also move away from the body when swimming. The red of the ventral blood corpuscles masses are apparent in the transparent body; later on they conjoin. The larval tentacles fall off (Fig. 94) and only the definitive ones remain. One of the larvae in the anaesthetic ($MgSO_4$), began the metamorphosis. It is known from literature that metamorphosis can be induced by certain chemical agents (Lynch 1952, p. 369) but in this case it might also be a mere coincidence (pp. 379, ff.). About 15 minutes after the beginning of the metamorphosis (27°C) hystolysis starts in the hood. A section of the metasoma revealed 48 longitudinal muscles bundles. The body of this metamorphosing larva averaged 697 microns; the ratio of t.l. to a.p. was 1.7:1.

OCCURRENCE — Coastal waters from Ubatuba towards the south until near Lagoa Mangueira (State of Rio Grande do Sul); inlet waters of Cananéia and Paranaguá. The southermost occurrence (34°41.5'S) was in waters proceeding from Mar del Plata (Dr. I. Emílsson's personal communication).

SEASONAL OCCURRENCE — The seasonal occurrence at different localities was not very regular perhaps depending on the quantity of phytoplankton. Occurred July to February. In Cananéia, where periodical collections were made, it occurred during the months of July, October (maximum), February. The occurrence in Ubatuba was irregular, but also more plentiful in October. It supports temperatures ranging from 18.5 to about 27.0°C and salinities from 24.70 to about 35.00 °/₀₀; it is clearly euryhaline. The quantity of larvae per sample is shown in Table 3. The larvae of samples n.° 151-152 were in bad condition which may indicate that the environment was not favourable.

FURTHER DISTRIBUTION — North West Atlantic: Chesapeake Bay and Beaufort Harbour (North Carolina).

DISCUSSION — The four blood corpuscles masses, two ventro-lateral and two dorso-lateral are the characteristic of *A. wilsoni* B. The present developed larvae agree in all their main features with *A. wilsoni* B and there was perfect conformity as regards the sequence of their development (Wilson 1881, p. 205; Brooks & Cowles 1905, p. 85). *Actinotrocha branchiata* (Selys-Longchamps 1903) very similar to the present larva differs from it in size, in the number of larval and definitive tentacles and in the presence of only two masses of blood corpuscles. Other larvae showing four blood corpuscle masses are *A. ikedai* A, which in

TABLE 3

Catalogue number	Young larva up to 16 tentacles	Well developed larvae	Metamorphosing larvae	Total
K 30	—	15	—	15
M 44	1	—	—	1
M 54	—	2	—	2
n/n. Alcatrazes	2	11	4	17
n/n. Paranaguá	2	—	—	2
II 48	—	2	—	2
IV 199	—	1	—	1
207	—	1	—	1
252	3	1	—	4
254	—	4	—	4
255	1	1	—	2
256	7	7	—	14
M 70-72	3	24	—	27
n/n. Bar	—	2	—	2
M 66	1	—	—	1
67	—	3	—	3
68	1	3	—	4
69	2	10	—	12
N 34	1	—	—	1
45-47	—	3	—	3
46	—	1	—	1
36	1	1	—	2
51	—	1	—	1
53	1	—	—	1
54	—	3	—	3
60-61	—	9	—	9
69	—	1	—	1
71	—	1	—	1
81	1	1	—	2
82	15	4	—	19
n/n. Saco da Ribeira	—	1	—	1
M 74	—	1	—	1
77	—	1	—	1
79	—	1	—	1
151-152	11	60	6	77
177	1	1	1	3
178	—	3	—	3
208	1	—	—	1

its maximum development has only 16 tentacles, and *A. menoni* X, insufficiently described. *Actinotrocha ikedai* B is also, in its general appearance, very similar to *A. wilsoni* B. However, it seems to me that *A. ikedai* B is the same as *A. branchiata*. The larvae with eight to 10 tentacles (Figs. 92 A, B; 93 A) are very similar in their external appearance to *A. hatscheki* (Selys-Longchamps 1907, t. 11, f. 11-13) not sufficiently characterized. I consider the advanced larvae as surely identical with *A. wilsoni* B. The young stages I described from the plankton were related to the above mentioned larva, as it seemed to me that besides structural resemblances, they represent stages of the same sequence of development. To corroborate that they effectively belong to *A. wilsoni* B, it will be necessary to resort to rearing. Table 4 gives a summary of the main characters that differentiate the various developmental stages of the present larva.

5. SUMMARY

1. The demarcation of the species of Phoronidea is difficult because of the great variability of the characters which does not enable the fixing of good differential characters yet. The studies of populations and of life-histories must be undertaken to allow an accurate systematic definition. Within the family Phoronidae, generally considered as composed of only one genus, *Phoronis*, groups of very divergent species can be distinguished, which must perhaps be considered as genera or at least sub-genera. Owing to the intergradation of the specific characters within such groups, it is not possible to know if they really represent species of form minor specific units.

I. *Phoronis hippocrepia* Wright 1856 — from Santos, Cananéia and Ubatuba; in the first locality boring in oyster shells; in the second non-boring specimens; and in the third only larvae.

a) Phoronis (Figs. 1-33) — The single nephrostome is the main characteristic of the specimens; through the interruption of the lateral mesentery at the level of the nephrostome the communication between the anal and oral cavities is assured. Longitudinal muscle bundles 26-30 in number, arranged according to the formula: $\frac{8\text{-}11 \mid 9\text{-}13}{3\text{-}5 \mid 3\text{-}6}$; marginal fibres, three to five in number, on each side of the bundle. Giant fibres of variable diameter: 4.7 to 7.0 microns, the right one, and 3.6 to 10.0 microns, the left. Blood corpuscles from 6.4 to 9.6 microns in diameter. Lophophoral organs also present in specimens with embryos in the tentacular

TABLE 4 — *Actinotrocha wilsoni* B — Differential characters of the successive developmental stages.

No. of larval tentacles	8-10	12	16-18	20	22-24	26	0
Size (micron)	257-447	396-476	400-650	500-760	640-920	825-1450	700-1520
No. of definitive tentacles	0	0	0	0-some	12-14	19-20	20
Values for t.l.:a.p.	5.4-3.2	3.5-3.2	3.6-2.5	3.7-2.3	2.7-1.9	2.5-1.8	1.7-1.4
Mass of blood-corpuscles	absent	id.	primordium of the ventral pair	ventral pair present	primordium of the dorsal pair	two pairs present	conjunction of the pairs
Sensorial organ	absent	id.	id.		sometimes present	present	present
Metasoma	absent	epithelial thickening	little tube	developed tube	well developed tube	fully developed	id. or evaginated
Nephridia	not terminal	id.	open laterally to the meta-soma opening	the curved canal opens lateral to the metasoma opening	id.	id.	solenocytes in regression
Dorsal vessel	absent	id.	id.	id.	present	developed and with caecal vessels	id.

crown. Simultaneous hermaphrodite, at least the specimens from Santos. Eggs: 100 microns. Spermatozoa: 20 microns, with vesicular head. Seven to eight pairs of chromosomes.

b) Actinotrocha (Figs. 34-55)— Primordium of metasoma appears in the larva with one pair of tentacles; peri-anal ciliated ring is present in the larva with four tentacles in which the anlage of the blood-corpuscle mass appears. Ganglion already developed in this larva. Metasoma of the four-tentacle larva forms a small invagination. Nephridia are not terminal any more. Rare glands present in the hood epithelium. In the larva with six tentacles the metasoma forms an ample sac; the primordium of the lophophore coelom appears. Stomach diverticulum absent or single without vacuolization. Nephridia open laterally to the metasoma aperture. In the advanced larva (eight to 10 tentacles) the metasoma forms a series of folds; its longitudinal muscles are differentiated into bundles; a large ventral mass of blood corpuscles is present ventral to the eosophagus and a few corpuscles are grouped on each side at the insertion level of the ventral tentacles. Lophophore coelom well developed; dorsal vessel present; a pair of ventral muscles in the trunk. On the dorsal surface of the hood there is an accumulation of gland cells perhaps the sensory organ. During metamorphosis the evaginated metasoma shows longitudinal muscle bundles. Larval tentacles degenerate. Afferent and efferent vessels are already formed.

c) The following observations were made: Maximum survival in aquarium: one year; observed breeding season: July to March; duration of individual reproduction: over 15 days; development: egg to young larva — four days; pelagic perid — 9 to 12 days; metamorphosis — two hours. Irregular blood circulation, with about 10 pulsations per minute (temperature of 24°C). Food: mostly diatoms, also protozoans and detritus. Not necessarily a boring species. The occurrence in aggregations seems accidental. Maximum of 12 embryos in the brood-pouch. The larvae become free with four tentacles and, exceptionally, in aquarium, shortly before metamorphosis. Swim in more or less large circles, diving often; shortly before metamorphosis, swim on the bottom. Metamorphosis was obtained even without special substratum. Eurythermic species (temperatures from 16 to 27°C) endures salinities from 30.63 to 37.38 °/₀₀.

II. *Phoronis ovalis* Wright 1856 (Figs. 56-63) — from Santos, in oyster shells. A single median lophophoral organ (Figs. 62, *l*; 63, *b*) ; three to four marginal fibres along each side of the longitudinal muscle bundle; two giant fibres 2.5 microns in dia-

meter (Fig. 61, *k*), not always noticed. Lower lip of the nephridial funnel short or long, prolonged downwards. Larva observed in March.

III. a) *Actinotrocha bella* (new technical name) — from plankton collected off the northeast coast of Brazil.

Stage with 18 to 22 tentacles (Fig. 64 A, B) — Metasoma present as a small tube; no mass of blood corpuscles, sensory organ and dorsal vessel. Peri-anal ciliated ring developed. A pair of retractors in the hood; a single diverticulum, vacuolated; nephridia placed above the septum, open laterally the aperture of the metasoma.

Stage with 24 tentacles (Fig. 71 A) — Definitive tentacles absent. Stomach diverticulum single. Metasoma represented by a small invagination. Nephridium constituted by a large nephridial canal. Subepithelial muscle layer present. No mass of blood corpuscles and sensory organ. Narrow body cavity.

Stage with 38 tentacles (Fig. 71, B, B_1) — Definitive tentacles absent. A large blood sinus (Fig. 76, *d*) ventral to the oesophagus, extending laterally to the mouth; on the lower side it stretches out along the ventral part of the diverticulum (Fig. 77, *d*) ending near the nephridial canal (Fig. 78, *h*). Sensory organ (Fig. 83, *c*) consists of accumulations of basophilous gland cells and a nerve deeply placed. Dorsal vessel (Fig. 79, *p*) and caecal vessels (*l*) developed. Metasoma with longitudinal muscles differentiated into bundles (Fig. 79, *n*). A pair of dorsal retractors in the hood (Figs. 76, 77, *b*). Two pairs of ventral muscles in the trunk. Peri-anal ciliated ring developed and undulated (Fig. 81). These advanced larvae were related to the young larvae mentioned above by similarities of structure. Only their rearing will enable to confirm they belong to the same ontogenetic sequence.

b) *Actinotrocha chata* n. t. n. (Fig. 90) — This young larva with 16 tentacles was found in plankton from Ubatuba. The metasoma presents itself in the stage of an epithelial thickening; no mass of blood corpuscles and sensory organ; ganglion present. It is probable that this larva represents a young *A. wilsoni* B with delayed development.

c) *Actinotrocha wilsoni* B — Larva distributed in the coastal waters of Ubatuba (100 km to the NE of Santos) towards the South down to lat. 28°00'S, off Lagoa Mangueira (State of Rio Grande do Sul); it is also found in the inlet waters of Cananéia and Paranaguá. Occurs July to February, maximum in October.

Euryhaline; it was found at temperatures from 18.5 about 27.0°C. Larva with eight to 10 tentacles has no metasoma, no diverticulum, no mass of blood corpuscles; terminal nephridia open above the anus. In the 12-tentacle stage the metasoma appears as a thickening. In the stage with 16 to 18 tentacles the ventral pair of blood corpuscle masses appears. Nephridia then open laterally to the metasoma orifice. Metasoma represented by a small tube. The dorsal pair of blood corpuscle masses appears in the larva with 22 tentacles. Usually the definitive tentacles appear in the 22-tentacle larva. They reach a maximum of 26, the maximum of definitive ones being 20. In the mature larva the sensory organ is present (Fig. 118). Stomach diverticulum may be absent, paired or single, rarely vacuolated. Longitudinal muscles of the metasoma are differentiated into bundles. Anomalous metamorphosis may occur in the plankton. Larval tentacles are cast off shortly before metamorphosis. The pairs of blood corpuscle masses conjoin during metamorphosis. The evaginated metasoma showed 48 longitudinal muscle bundles and one nerve. The developed larva is transparent, with orange pigment; it swims on the bottom of the recipient in large circles, resting sometimes in an inverted position; the tentacles are a swimming aid, standing aloof from the body. The developed larvae are identical with *Actinotrocha wilsoni* B, whose young stages are not known. The present young stages described from plankton, were related to *A. wilsoni* B, but only their rearing will confirm that they represent the ontogenetic stages of this larva.

6. RESUMO

Phoronis hippocrepia Wright de Santos, Cananéia e Ubatuba, vive no eulitoral, na zona de máxima vasante, perfurando conchas de ostra ou sôbre fauna que recobre rochas. Hermafrodita simultânea, com fecundação precoce interna. A eliminação dos corpúsculos polares dá-se na câmara incubadora. Larvas aí se desenvolvem até o estádio de 4 tentáculos, excepcionalmente até o de 8 tentáculos. As seguintes observações foram feitas: máximo de sobrevivência em aquário: 1 ano; época de reprodução: julho a março; duração da reprodução individual: mais de 15 dias; desenvolvimento: do ôvo à larva jovem — 4 dias; em natação livre — 9 a 12 dias; metamorfose — 2 horas. Máximo de 12 embriões na câmara incubadora. O adulto, quase imóvel, é muito sensível quando recém-coletado; perde parte da sensibilidade quando no aquário. Circulação sanguínea irregular, com cêrca de 10 pulsações por minuto. Alimentação: principalmente diatomáceas; também protozoários. Espécie não necessàriamente cavadora. A ocorrência em agregados parece acidental. Larva nada em círculos, subindo à superfície e mergulhando em seguida; perto da metamorfose, nada no fundo. Espécie euritérmica (temperaturas de 16 a 27°C), suporta salinidades de 30,63 a 37,38 ‰.

Phoronis ovalis Wright observada em Santos no mesmo biótopo de *P. hippocrepia*. Às descrições anteriores acrescenta-se: órgão lofoforal mediano,

impar; fibras gigantes pares, 2,5 micra de diâmetro, nem sempre conspícuas; fibras marginais e centrais presentes em cada feixe muscular longitudinal; nefróstoma pequeno com sua parede inferior curta ou prolongada para baixo. A larva aberrante foi reconhecida dentro de pequenos tubos chitinosos, em março.

Actinotrocha bella (nome técnico novo) do plancton coletado ao largo da cidade de São Luís (E. do Maranhão) mostra, no máximo estádio obtido, 30 tentáculos larvais; os tentáculos definitivos são ausentes. Grande seio sanguíneo anterior. Divertículo impar do estômago. Metasoma desenvolvido, com musculatura longitudinal diferenciada em feixes. Órgão sensorial presente, constituído por uma acumulação de células glandulares basófilas. Retratores no capuz e no tronco. Vaso dorsal e lateral bem como capilares desenvolvidos. Camada muscular subepitelial presente.

Actinotrocha chata (nome técnico novo) do plancton de Ubatuba, refere-se a uma larva jovem com 16 tentáculos, que pode representar uma *A. wilsoni* B com desenvolvimento retardado.

Actinotrocha wilsoni B (nome técnico) das águas costeiras de Ubatuba para o sul até 34°41,5'S (altura da Lagoa Mangueira), e águas interiores de Cananéia e Paranaguá. No máximo estádio de desenvolvimento possui 26 tentáculos larvais e até 20 definitivos; êstes dispõem-se em duas séries, uma de cada lado, sob os larvais. A larva é caracterizada pelas quatro massas de glóbulos sanguíneos que se fundem na metamorfose. Próximo da metamorfose os tentáculos larvais degeneram, permanecendo apenas os definitivos. O capuz começa a desintegrar-se 15 minutos após o início da evaginação do metasoma. Metamorfose no plancton ocorre, mas de modo anormal. Larva encontrada de julho a fevereiro com máximo em outubro. O adulto desconhecido, possui 48 feixes musculares longitudinais e uma única fibra gigante.

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8. REFERENCES

ANDREWS, E. A.

1890. On a new American species of the remarkable animal *Phoronis*. Ann. Mag. Nat. Hist., ser. 6, 5, p. 445-449.

BENHAM, W. B.

1890. The anatomy of *Phoronis australis*. Quart. J. Microsc. Sci. n. ser., v. 30(2) p. 125-158, pl. 10-13.

BENEDEN, P. J. van

1858. Notice sur un annélide céphalobranche sans soies, désigné sous le nom de Crepina. Ann. Sci. Nat. (4), Zool. 10, p. 11-23.

BÖHMIG, L.

1923-33. Nemertini. Handbuch der Zoologie. Kükenthal & Krumbach, v. 2, part 1, p. 1-110.

BRATTSTRÖM, H.

1943. *Phoronis ovalis* Wright, eine für die skandinavische Fauna neue Phoronide aus dem Öresund. Lunds Univ. Aarsskr. n.F. Avd. 2, v. 39, n.° 2 (Kungl. Fys. Sällsk. Handl. n.F., v. 54, n.° 2), p. 1-17.

BROOKS, W. K. & COWLES, R. P.

1905. *Phoronis architecta*, its life history, anatomy and breeding habits. Mem. Nat. Acad. Sci. Washingt., v. 10 (4) p. 71-147, t. 1-17.

CALDWELL, W. H.

1882. Preliminary note on the structure, development and affinities of *Phoronis*. Proc. R. Soc. London, v. 34, p. 371-383, 2 diagr.

CERFONTAINE, P.

1902. Recherches expérimentales sur la régéneration et l'hétéromorphose chez *Asteroides calycularis* et *Pennaria cavolinii*. Arch. Biol., v. 19, p. 245-262.

CHRÉTIEN, M.

1957. Histologie et développement de l'ovaire chez *Alcyonidium gelatinosum* (L.) (Bryozoaire cténostome). Bull. Lab. Mar. Dinard fasc. 43, p. 25-51.

CORI, C. J.

1890. Untersuchungen über die Anatomie und Histologie der Gattung *Phoronis*. Zeitschr. wiss. Zool., v. 51 (1891), fasc. 2-3 (1890), p. 480-568, pl. 22-28.

1930. Phoronidea. Fr. Dahls: Die Tierwelt Deutschlands. Part 17, p. 14-24.

1932. Phoronidea. G. Grimpe, Tierwelt der Nord- und Ost-See, v. 7c, p. 101-132.

1937. Phoronidea. Handbuch der Zoologie. Kükenthal & Krumbach, v. 3 (2), p. 67-138.

1939. Phoronidea. Bronns Klassen des Tierreichs, v. 4 (1), p. 1-183.

COWLES, R. P.

1904. Origin and fate of the body cavities and the nephridia of the *Actinotrocha*. Johns Hopkins Univ. Circ. (2), n.° 2, p. 168-177.

du Bois-Reymond Marcus, E.

1949. *Phoronis ovalis* from Brazil. Bol. Fac. Fil. Ci. Letr. S. Paulo, Zool., v. 14, p. 157-171, figs. 1-17.

Dyster, F. D.

1858. Notes on *Phoronis hippocrepia*. Trans. Linn. Soc. London, v. 22, p. 251-256, pl. 44.

Foettinger, A.

1882. Note sur la formation du mésoderme dans la larve du *Phoronis hippocrepia*. Arch. Biol., v. 4, p. 679-686, pl. 31.

Forneris, L.

1956. Actinotrochae. Cons. Perm. Intern. Expl. Mer, Fiches d'Ident. Zooplankton, Sheet 69.

Giard, A.

1892. Nouvelles remarques sur la Poecilogonie. Compt. Rend. Ac. Sci. Paris, v. 114, p. 1549-1552.

Gilchrist, J. D. F.

1907. New forms of Hemichordata from South Africa. 1. *Phoronopsis albomaculata* g. et sp. n. 2. *Phoronis capensis* sp. n. Marine Investig. South Africa, v. 5 (1908) (Trans. S. Africa Phil. Soc., v. 17 — 1907), p. 151-171, pl. 16-17.

1919. Reproduction by transverse fission in *Phoronopsis*. Quart. J. Microsc. Sci. n. ser., v. 63, p. 493-507, pl. 29.

Harmer, S. F.

1917. On *Phoronis ovalis* Strethill Wright. Quart. J. Microsc. Sci. n. ser., v. 62, p. 115-148, pl. 7-9.

Hedgpeth, J. W.

1954. Phoronida. Gulf of Mexico, its origin, waters and marine life. Fishery Bull. Fish. & Wildlife Service, v. 55, Bull. 89, p. 367.

Hempel, C.

1957. Über den Röhrenbau und die Nahrungsaufnahme einiger Spioniden (Polychaeta sedentaria) der deutschen Küsten. Helgoländer Wiss. Meeresunters., v. 6(1), p. 100-135.

Huxley, J.

1940. The New Systematics. vii+583 p. Oxford University Press. London.

Hyman, L. H.

1958. The occurrence of chitin in the lophophorate phyla. Biol. Bull., v. 114(1), p. 106-112.

Ikeda, I.

1901. Observations on the development, structure and metamorphosis of *Actinotrocha*. J. Coll. Sci. Imp. Univ. Tokyo, Japan, v. 13, p. 507-592, pl. 25-30.

1903. On the development of the sexual organs and their products in *Phoronis*. Annot. Zool. Jap. Tokyo, v. 4, p. 141-153.

KNIGHT-JONES, E. W.

1951. Aspects of the setting behaviour of larvae of *Ostrea edulis* on Essex oyster beds. Rapp. Proc. Verb., v. 128, p. 30-34.

KORRINGA, P.

1951. The shell of *Ostrea edulis* as a habitat. Arch. Neerl. Zool., v. 10, p. 32-152, pl. 4-14.

KOWALEVSKY, A.

1867. Über die Anatomie und Entwicklung von *Phoronis*. (In Russian, translated by R. Leuckart — 1867 — Arch. f. Naturgesch., v. 33 (2), p. 163-304).

KUHL, W.

1923. Das Retrocerebralorgan der Chaetognathen. Frankf. Senck., 4, 16 p., 5 pl.

1938. Chaetognatha. Bronns Klassen des Tierreichs, v. 4, p. 1-226.

LÖNÖY, N.

1953. A comparative anatomical study on *Phoronis ovalis* Wright from Norwegian, Swedish and Brazilian waters. Univ. Bergen Aarbok 1953, Naturv. ser. n.º 2, p. 1-23, figs. 1-29.

LYNCH, W. F.

1952. Factors influencing metamorphosis of Bugula larvae. Biol. Bull., v. 103 (3), p. 369-383.

MARCUS, E.

1938. Bryozoarios perfuradores de conchas. Arq. Inst. Biol., v. 9, p. 273-296.

MASTERMAN, A. T.

1896. Preliminary note on the structure and affinities of *Phoronis*. Proc. R. Soc. Edinburgh, v. 21, p. 59-71.

MAYR, E., LINSLEY, E. G. & USINGER, R. L.

1953. Principles and methods of systematic Zoology. 328 p. McGraw-Hill, New York.

McINTOSH, W. C.

1881. Notes on Phoronis dredged by H.M.S. Challenger. Proc. R. Soc. Edinburgh, vol. 11, p. 211-217.

1888. Report on *Phoronis buskii* n. sp., dredged during the voyage of H.M.S. Challenger, 1873-76. Zool., part 75, p. 1-27, pl. 1-3.

MEEK, A.

1917. On the Phoronidea. Rep. Dove Mar. Lab. n. ser., v. 6, p. 33-48.

MENON, K. R.

1902. Notes on *Actinotrocha*. Quart. J. Microsc. Sci. n. ser., v. 45, p. 473-484, pl. 26.

PANTIN, C. F. A.

1948. Notes on microscopical technique for zoologists. viii+79 p. Cambridge Univ. Press.

PEARSE, A. S.

1950. The emigrations of animals from the sea. xii+210 p. The Sheerwood Press, Publ. Dryden, New York.

PIXEL, H. L. M.

1912. Two new species of the Phoronidea from Vancouver Island. Quart. J. Microsc. Sci. n. ser., v. 58 (1913) (230) (1912), p. 257-284.

RATTENBURY, J. C.

1953. Reproduction in *Phoronopsis viridis*. The annual cycle in the gonads, maturation and fertilization of the ovum. Biol. Bull., v. 104 (2), p. 182-196.

1954. The embryology of *Phoronopsis viridis*. J. Morph., v. 95 (2), p. 289-349, 40 figs.

RATTENBURY MARSDEN, J.

1957. Regeneration in *Phoronis vancouverensis*. J. Morph., v. 101 (2), p. 307-324.

ROULE, L.

1900. Étude sur le développement embryonnaire des Phoronidiens. Ann. Sci. Nat. Zoologie (8) v. 11, p. 51-249, pl. 2-16.

SCHARRER, B.

1941a. Neurosecretion. II. Neurosecretory cells in the central nervous system of cockroaches. J. Comp. Neur., v. 74 (1), p. 93-108.

1941b. Idem. III. The cerebral organ of the nemerteans. J. Comp. Neur., v. 74 (1), p. 109-130.

SCHEPOTIEFF, A.

1906. Ueber einige Actinotrochen der norwegischen Fjorde. Zeitschr. wiss. Zool., v. 84, p. 79-94, pl. 5-6.

SELYS-LONGCHAMPS, M. de

1903. Ueber *Phoronis* und *Actinotrocha* bei Helgoland. Wissensch. Meeresunters. n.F. v. 6, Abt. Helgoland, p. 1-55, pl. 1-2.

1907. Phoronidea. Fauna u. Flora des Golfes v. Neapel, M. 30, x+280 p., 12 pl. Berlin (R. Friedländer & Sohn).

SILÉN, L.

1952. Researches on Phoronidea of the Gullmar Fiord area (West coast of Sweden). Ark. Zool., ser. 2, v. 4, p. 95-140.

1954a. Developmental biology of Phoronidea of the Gullmar Fiord area (West coast of Swden). Acta Zool., v. 35, p. 215-257.

1954b. On the nervous system of *Phoronis*. Ark. f. Zool. ser. 2, v. 6, p. 1-40.

1955. Autotomized tentacle crowns as propagative bodies in *Phoronis*. Acta Zool., v. 36, p. 159-165.

1956. On shell-burrowing Bryozoa and Phoronis from New Zealand. Trans. Roy. Soc. New Zealand, v. 84 (1), p. 93-96.

STEUER, A.

1933. Zur Fauna des Canal di Leme bei Rovigno. 3. Ueber die Phoronidea und Ihre Larven. Thalassia, v. v. (1), p. 27-37.

THORSON, G.

1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Öresund). Medd. Komm. Danm. Fisk. Havunders. ser. Plankton, v. 4 (1), p. 1-523.

TORREY, H. B.

1901. On *Phoronis pacifica* sp. n. Biol. Bull., v. 2, p. 283-288.

TREWAVAS, E.

1931. Enteropneusta. Great Barrier Reef Exped. 1928-29. Sci. Rep., v. 4 (2), p. 39-67.

TUZET, D., BRESSIÈRE, C. & MANIER, J. F.

1957. La spermatogénèse des Polydesmes: *Plagiodesmus oatypus* Chamberlin et *Polydesmus complanatus* Linné. Bull. Inst. Roy. Sc. Nat. Belgique, v. 33 (18), p. 1-11.

UCHIDA, T. & IWATA, F.

1955. The fauna of Akkeshi Bay. XXII. Phoronidea. Publ. Akkeshi Mar. Biol. Stat., n.° 5, p. 1-3, 1 pl.

VEILLET, A.

1941. Description et mécanisme de la métamorphose de la larve Actinotroque de *Phoronis sabatieri* Roule. Bull. Inst. Océan. (Monaco), v. 38 (810), p. 1-10.

WILSON, E. B.

1881. The origin and significance of the metamorphosis of *Actinotrocha*. Quart. J. Microsc. Sci., v. 12, p. 202-218, p. 14-15.

PLATE 1

Phoronis hippocrepia Wright

Fig. 1 — View of lophophore emerged from tube.

Fig. 2 — Above view of lophophore; larvae inside brood-pouch.

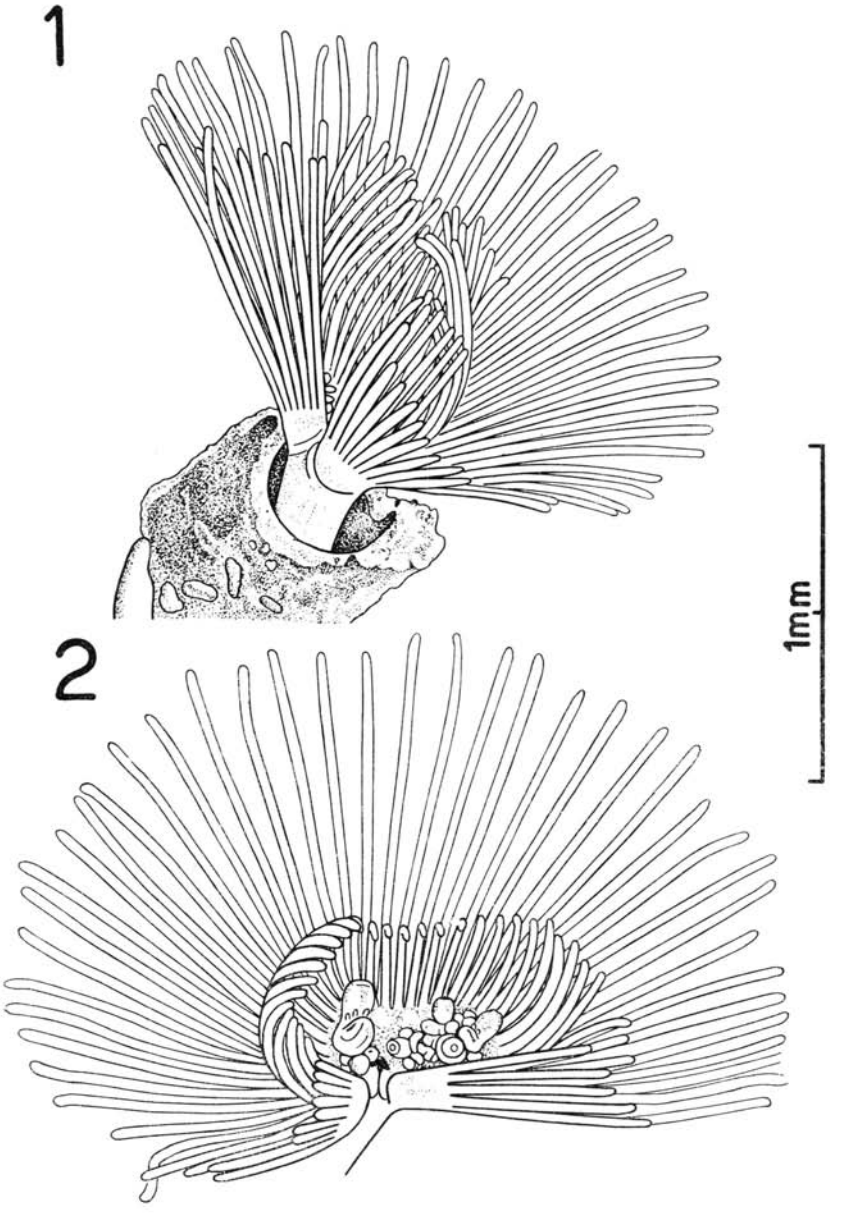
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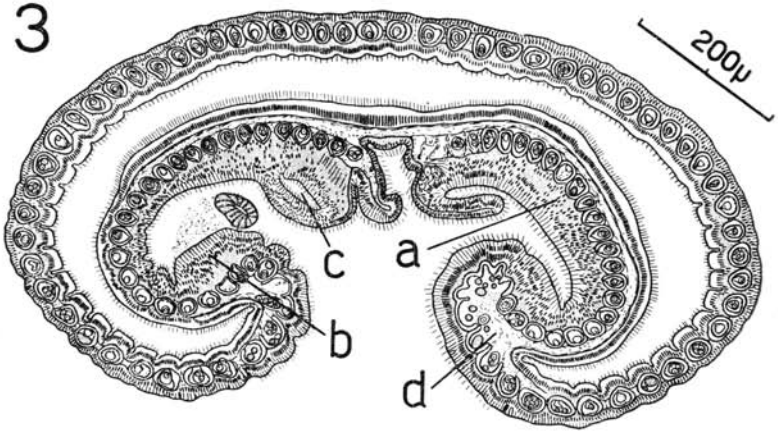
PLATE 2

Phoronis hippocrepia Wright

Fig. 3 — Transverse section through base of lophophore; left side, on level of median part of lophophoral organ; right side, on base of same.

Fig. 4 — Section of body on level of nephridiopore.

a — lateral thickening of lophophoral organ; *b* — attachment of embryos; *c* — protuberant portion of lophophoral organ; *d* — lophophore coelom; *e* — ascending nephridial canal; *f* — pit.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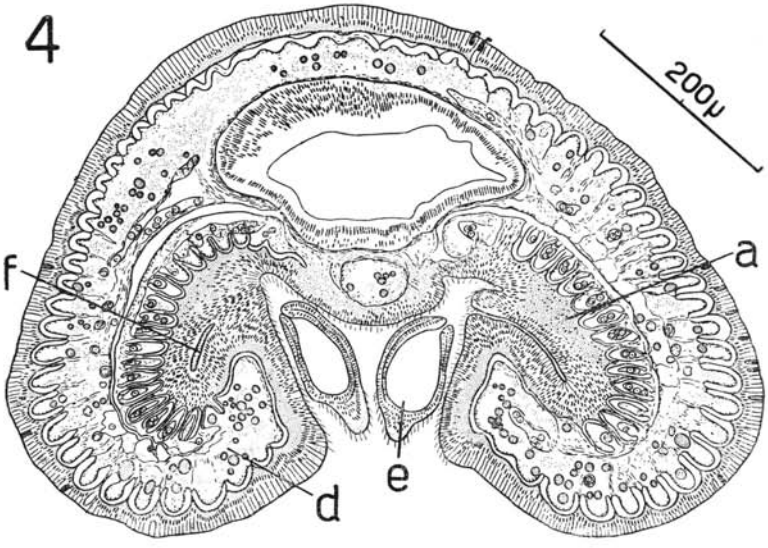
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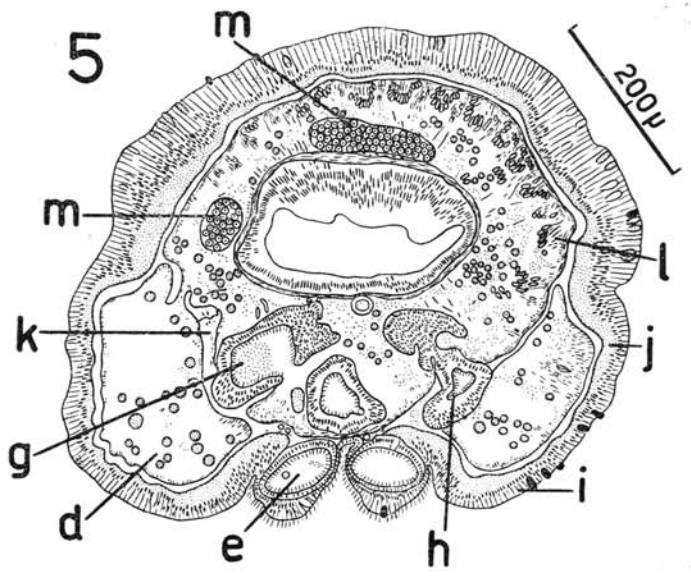
PLATE 3

Phoronis hippocrepia Wright

Fig. 5 — Transverse section of body on level of nephrostome.

Fig. 6 — Idem, on level of prolonged lower wall of nephrostome.

d — lophophore coelom; *e* — ascending nephridial canal; *g* — nephrostome; *h* — descending nephridial canal; *i* — epithelium; *j* — nervous system; *k* — basal membrane; *l* — longitudinal muscle bundle; *m* — efferent blood vessel; *n* — left lateral mesentery; *p* — prolonged lower wall of nephrostome; *q* — afferent blood vessel; *r* — spermatozoon; *s* — giant fibre; *u* — caecal vessel; *v* — fat body; *x* — fusiform corpuscle.


5
m
m
k
g
d
e
h
i
j
l
200μ

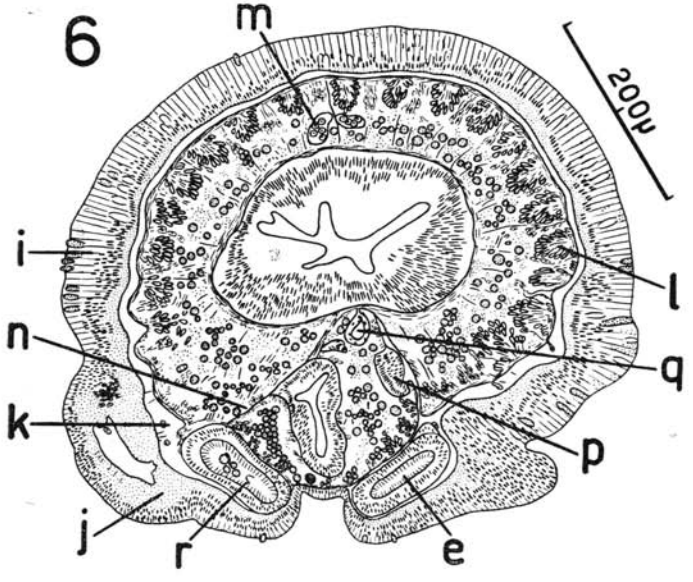

6
m
i
n
k
j
r
e
p
q
l
200μ

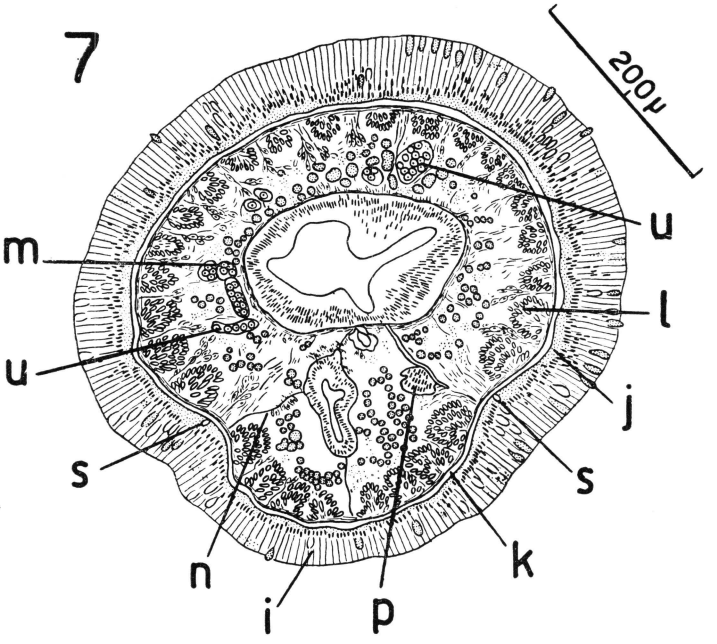
PLATE 4

Phoronis hippocrepia Wright

Fig. 7 — Transverse section of body a little below fig. 6.

Fig. 8 — Idem, of muscular part of body.

(For lettering see Plate 3)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k
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p

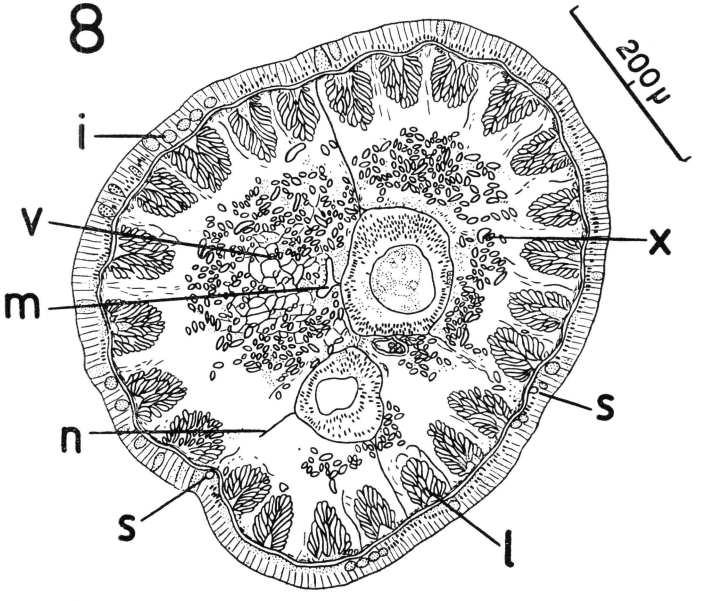

8
200μ
i
v
x
m
s
n
s
l

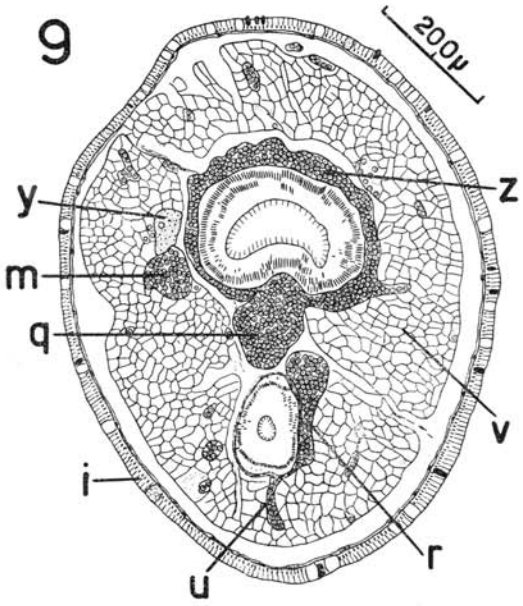
PLATE 5

Phoronis hippocrepia Wright

Fig. 9 — Transverse section of uppermost part of ampulla on level of blood sinus.

Fig. 10 — Idem, on level of curvature of digestive tube.

i — epithelium; *m* — efferent blood vessel; *q* — afferent blood vessel; *r* — peri-intestinal sinus; *u* — caecal vessel; *v* — fat body *x* — "corps en massue"; *y* — primordium of gonad; *w* — blood lacunae; *z* — peri-gastric sinus.


9
200μ
y
z
m
q
v
i
r
u

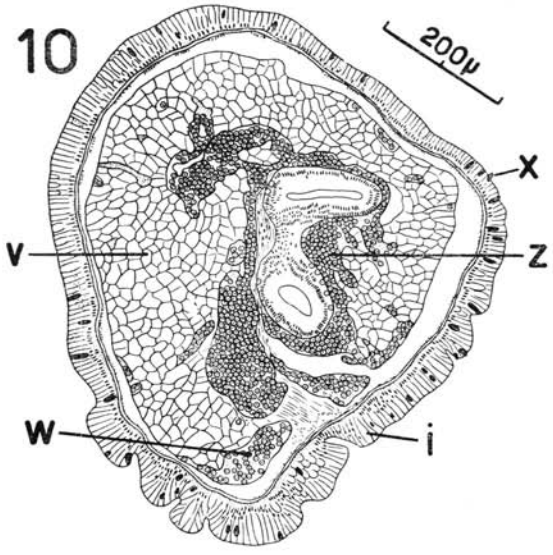

10
200μ
x
v
z
w
i

PLATE 6

Phoronis hippocrepia Wright

Fig. 11
Fig. 12 } Series of frontal sections through oral region of body.
Fig. 13

Fig. 14
Fig. 15 } Sagittal sections through oral region of body.

a — lateral thickening of lophophoral organ; *b* — median part of same; *e* — nephridial canal; *f* — epistome; *g* — nephrostome; *h* — descending nephridial canal; *k* — basal membrane; *m* — lophophoral ring vessel; *n* — lateral mesentery; *p* — opening on lateral wall of nephrostome; *q* — prolonged inferior edge of nephrostome; *s* — ovum; *u* — tentacular vessel.

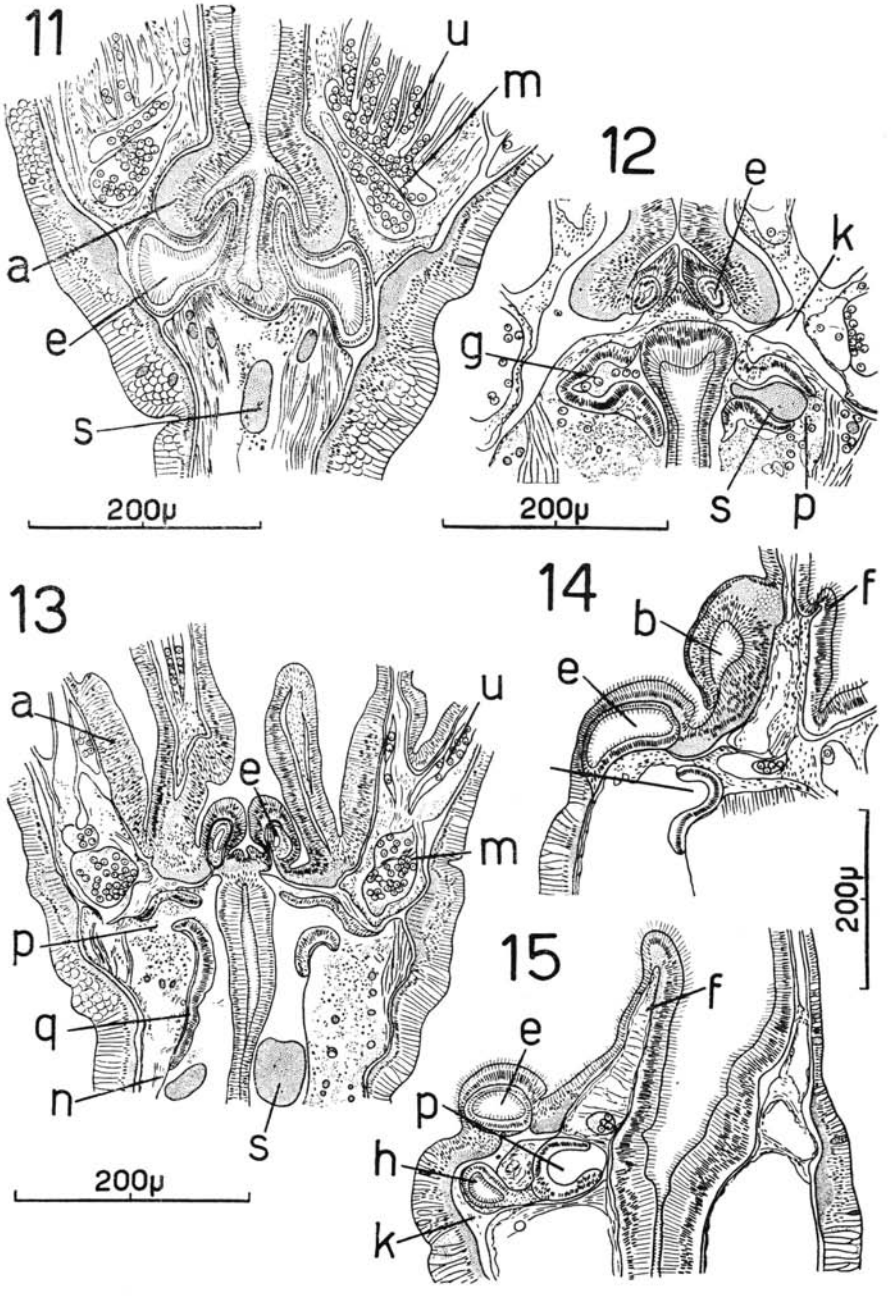

11
u
m
a
e
s
200µ
12
e
k
g
s
p
200µ
13
a
u
e
m
p
q
n
s
200µ
14
b
f
e
200µ
15
f
e
p
h
k

PLATE 7

Phoronis hippocrepia Wright

Fig. 16 — Longitudinal section of lateral part of lophophoral organ.

Fig. 17 — Portion of longitudinal section of epidermis of fore body.

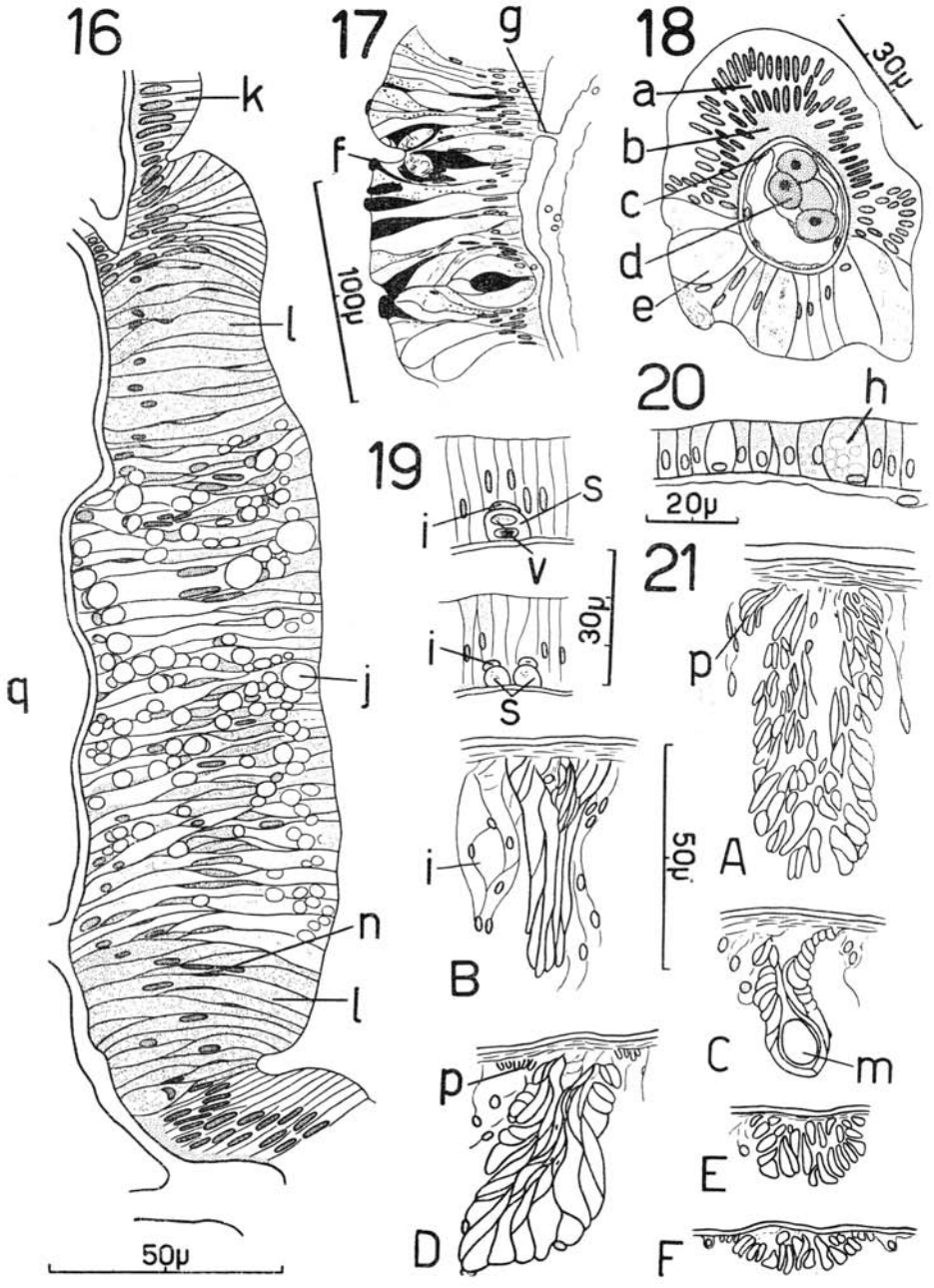
Fig. 18 — Tentacle in transverse section.

Fig. 19 — Section through epidermis showing giant fibre.

Fig. 20 — Section of epithelium of ampulla.

Fig. 21 — Different aspects of longitudinal muscle bundle in transverse section. A-D: through metasoma; E-F: near ampulla.

a — epithelium of inner face of tentacle; *b* — nervous substance; *c* — muscle fibres; *d* — tentacular caecal vessel; *e* — gland cell; *f* — "corps en massue"; *g* — interstice of basal membrane; *h* — eosinophilous gland cell; *i* — nucleus; *j* — secretion vesicle; *k* — tentacle; *l* — tubular gland cell; *m* — blood vessel; *n* — nucleus of supporting cell; *p* — marginal muscle fibre; *q* — peritoneum; *s* — giant fibre; *v* — nucleus inside giant fibre.


16
k
l
q
j
n
l
50µ
17
g
f
100µ
18
30µ
a
b
c
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e
20
h
20µ
19
s
i
v
i
30µ
s
21
p
i
50µ
A
B
C
m
p
D
E
F

PLATE 8

Phoronis hippocrepia Wright

Fig. 22 — Portion of epithelial papila of stomach wall, in transverse section.

Fig. 23 — Portion of stomach wall, showing blood corpuscles.

Fig. 24 — Epithelium of ciliated band, in transverse section.

Fig. 25 — Intestine in transverse section. A-B: different digestive phases.

Fig. 26 — Two coelomic corpuscles.

Fig. 27 — Transverse section of gonads.

Fig. 28 — A-E: oögonia; B-C: prophase; D: metaphase; E: primary ovocyte.

Fig. 29 — A-M: growth stages of primary ovocytes, showing changes undergone by germinal vesicle; L-M: metaphase of first maturation division.

Fig. 30 — Spindle of first maturation division, with chromosomes arranged in metaphase.

Fig. 31 — Section of a portion of mature ovary.

a — eosinophilous gland cell; *b* — blood corpuscle; *c* — coma-shaped body; *d* — gland cell with fine granular eosinophilous content; *e* — vesicular gland cell; *f* — testis; *g* — efferent blood vessel; *h* — ovary; *i* — caecal vessel; *j* — oögonia; *l* — fat body; *m* — primary ovocyte; *s* — vitelline spherule; *z* — spermatozoon.

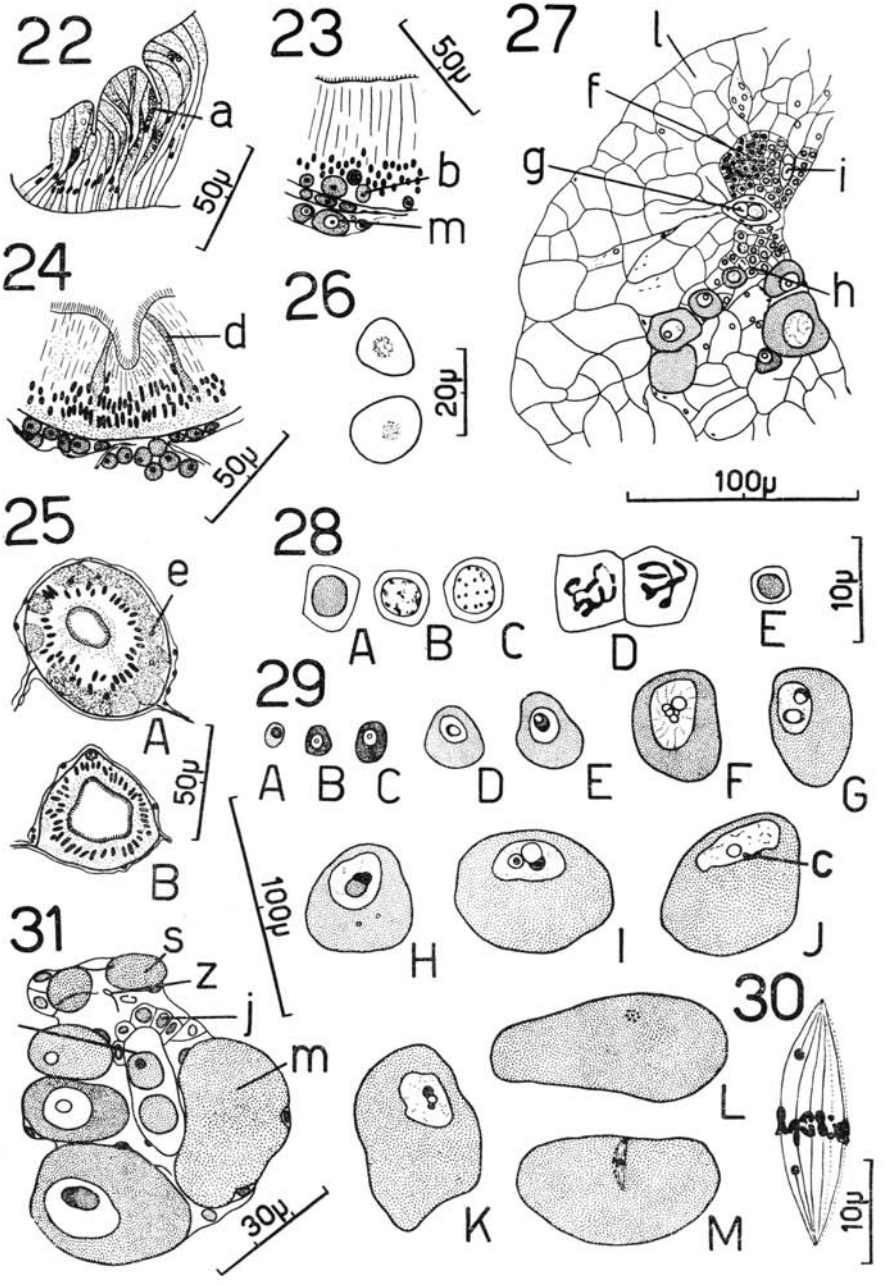

22
a
50µ
23
50µ
b
m
27
l
f
g
i
h
100µ
24
d
50µ
26
20µ
25
e
A
B
50µ
28
A B C D E
10µ
29
A B C D E F G
100µ
H I J
c
31
s
z
j
m
30µ
K L M
30
10µ

PLATE 9

Phoronis hippocrepia Wright

Fig. 32 — Section through testis.

Fig. 33 — Spermatogenesis. A: primary spermatocytes; B: prophase; C: secondary spermatocyte; D: spermatids; E-J: spermiogenesis; K: spermatozoa; L-M: spermatids developing together; N: fusiform bodies; P: club-shaped formation.

Fig. 34 — Successive stages of development: A — gastrula; B — larva devoid of tentacles, right side view; C — larva with primordium of first pair of tentacles, left side view; D — two-tentacle larva, ventral view; E — four-tentacle larva, left side view; F — six-tentacle larva, ventral view; G — larva with primordium of third pair of tentacles, left side view; H — six-tentacle larva, contracted, dorsal view; I — six-tentacle larva, left side view.

a — primary spermatocyte; *b* — division of maturation; *c* — secondary spermatocyte; *d* — spermatid; *e* — spermatozoa; *i* — caecal vessel; *j* — fat body; *m* — metasoma.

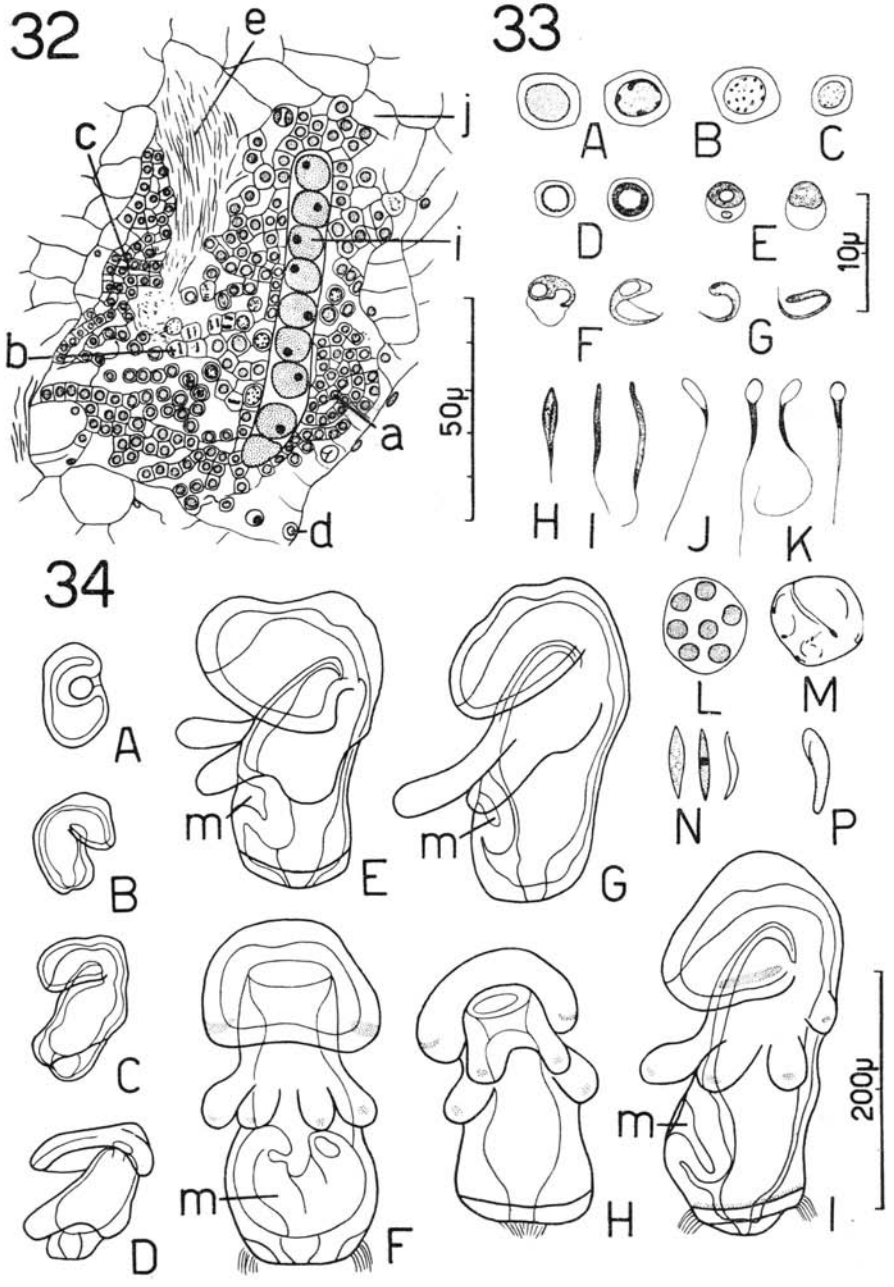

32
e
j
c
i
b
a
d
50µ
33
A
B
C
D
E
10µ
F
G
H
I
J
K
34
A
B
C
D
m
E
F
m
G
m
H
L
M
N
P
m
I
200µ

PLATE 10

Phoronis hippocrepia Wright

Actinotrocha

Fig. 34 — J — larva with eight tentacles, ventral view; K — advanced larva, ventral view.

Fig. 35 — Free-swimming larva, left side. Cananéia.

Fig. 36 — Larvae from plankton: A — ventral view; B — right side view. Ubatuba.

Fig. 37 — Section of embryo at beginning of gastrulation.

Fig. 38 — Section through larva with two tentacles.

a — hood; *c* — stomach; *d* — nephridial canal; *e* — tentacle; *m* — metasoma; *u* — blood corpuscle mass.

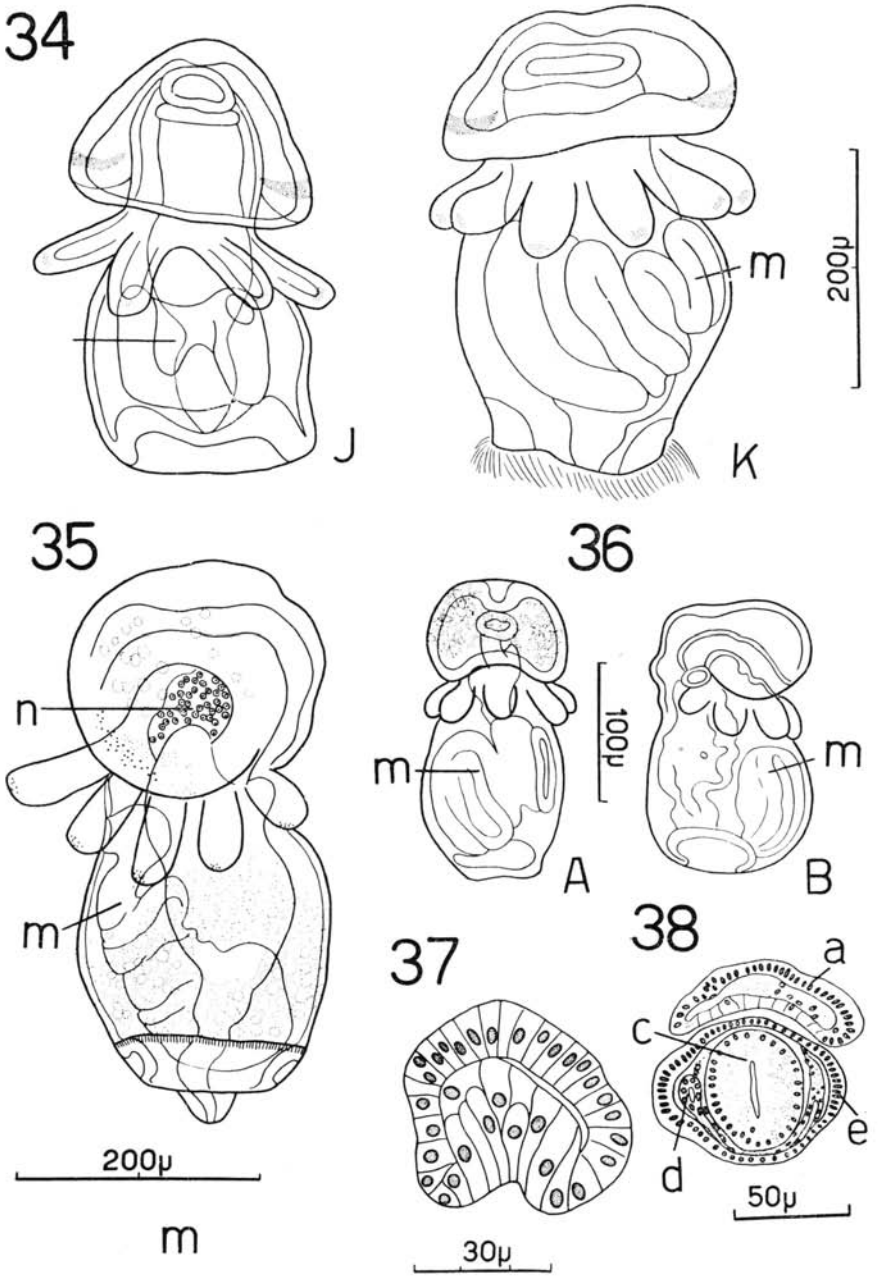

34
J
m
200µ
K
35
n
m
200µ
m
36
m
100µ
A
m
B
37
30µ
38
a
c
e
d
50µ

PLATE 11

Phoronis hippocrepia Wright

Actinotrocha

Fig. 39 — Transverse section of larva with outline of second pair of tentacles, on level of base of hood.

Fig. 40 — Idem, of hood of two-tentacle larva.

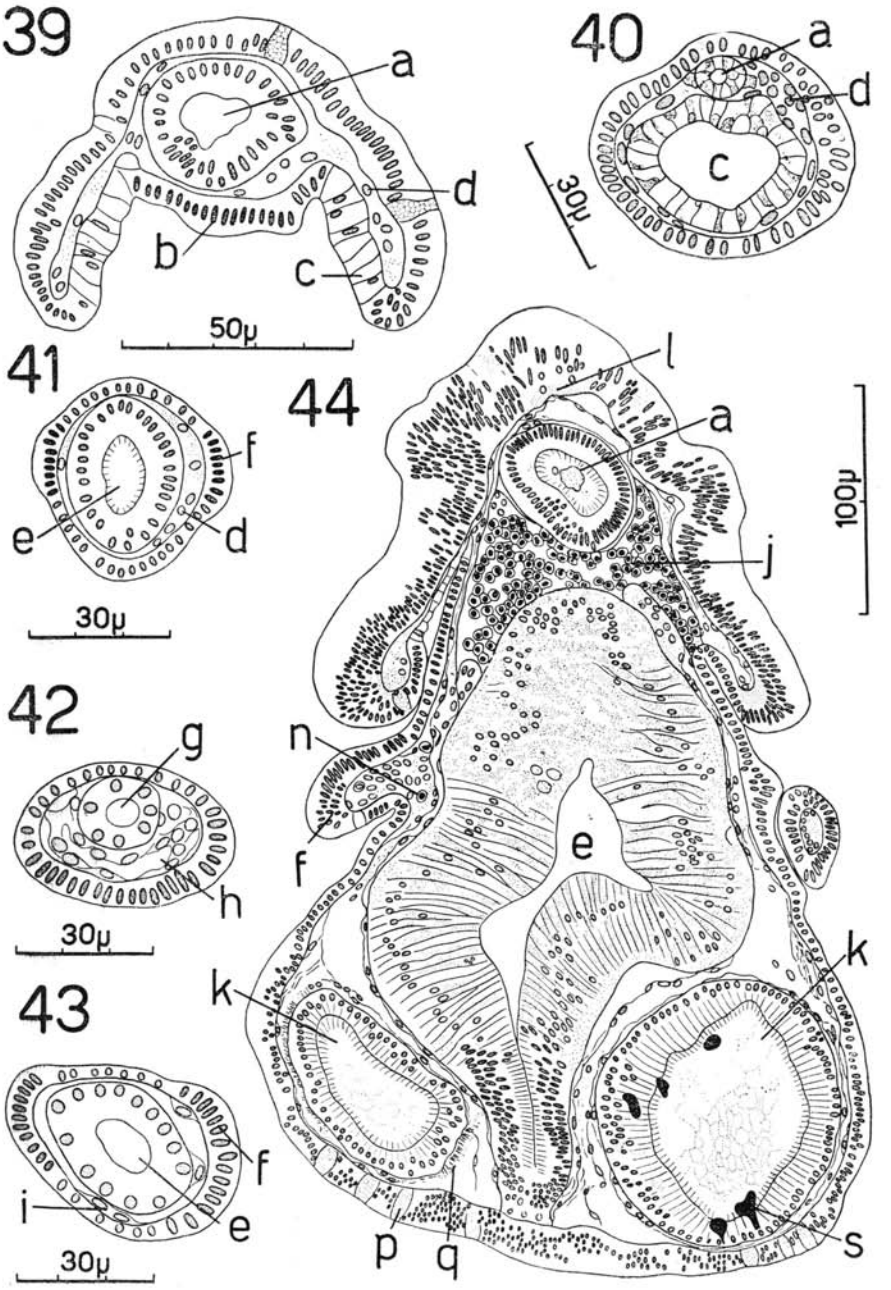
Fig. 41 — Idem, of body of same larva.

Fig. 42 — Idem, of lower body of larva with outline of first pair of tentacles.

Fig. 43 — Idem, of the medium part of body.

Fig. 44 — Frontal section of eight-tentacle larva.

a — oesophagus; *b* — ventral thickening; *c* — buccal vestibule; *d* — nucleus of mesenchymal cell; *e* — stomach; *f* — tentacle; *g* — rectum; *h* — anlage of nephridium; *i* — mesenchymal cells disposing in layer; *j* — ventral blood corpuscle mass; *k* — metasoma; *l* — ganglion; *n* — lateral blood corpuscle mass; *p* — mucous gland cell; *q* — muscles; *r* — dorsal vessel; *s* — "corps en massue"; *v* — adult lophophoral coelom; *x* — ventral retractor; *y* — ventral vessel?; *z* — nephridial canal.


39
a
b
c
d
50µ
40
a
c
d
30µ
41
e
f
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30µ
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g
h
30µ
43
i
e
f
30µ
44
l
a
j
100µ
n
f
e
k
k
p
q
k
s

PLATE 12

Phoronis hippocrepia Wright

Advanced actinotrocha

Fig. 45 — Transverse section on level of ventral blood corpuscle mass.

Fig. 46 — Somewhat oblique section of fore body.

Fig. 47 — Transverse section of body a little above the roots of tentacles.

Fig. 48 — Blood corpuscles.

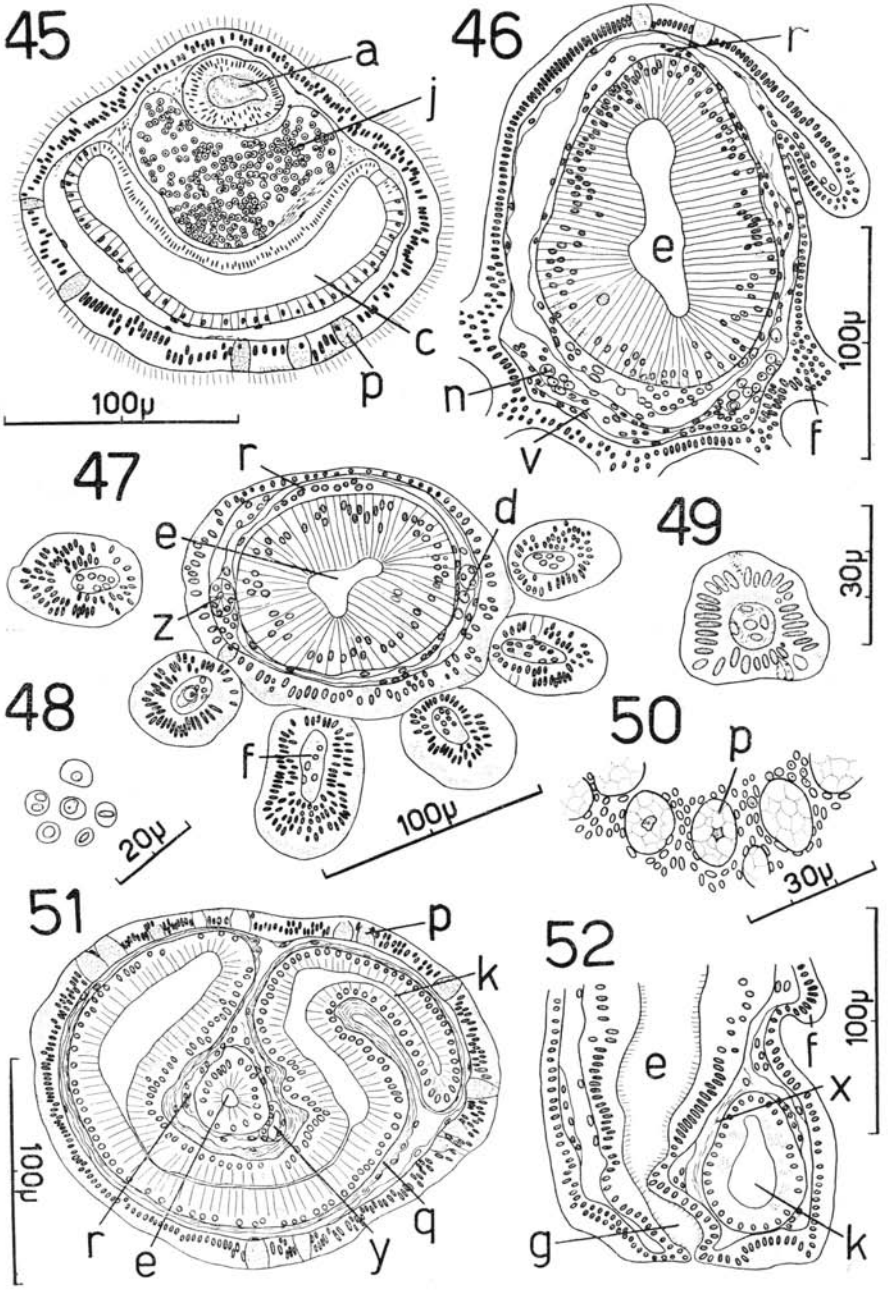
Fig. 49 — Larval tentacle, transverse section.

Fig. 50 — Superficial section of body epithelium on level of peri-anal ciliated ring.

Fig. 51 — Transverse section of inferior part of body.

Fig. 52 — Sagittal section of the inferior part of body.

(For lettering see Plate 11)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a
j
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100µ
46
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e
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v
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100µ
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r
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d
z
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100µ
49
30µ
48
20µ
50
p
30µ
51
p
k
r
e
y
q
100µ
52
e
f
x
g
k
100µ

PLATE 13

Phoronis hippocrepia Wright

Metamorphosing stages

Fig. 53 — A — larva at beginning of metamorphosis; B — individual with metasoma fully everted and without hood; C — young newly metamorphosed with remainder of anal papilla.

Fig. 54 — Transverse section of metasoma of individual at beginning of metamorphosis.

Fig. 55 — Transverse section of newly metamorphosed specimen.

a — epithelium; *b* — longitudinal muscle bundle; *c* — basal membrane; *d* — stomach; *e* — intestine; *f* — efferent blood vessel; *g* — afferent blood vessel; *m* — metasoma.

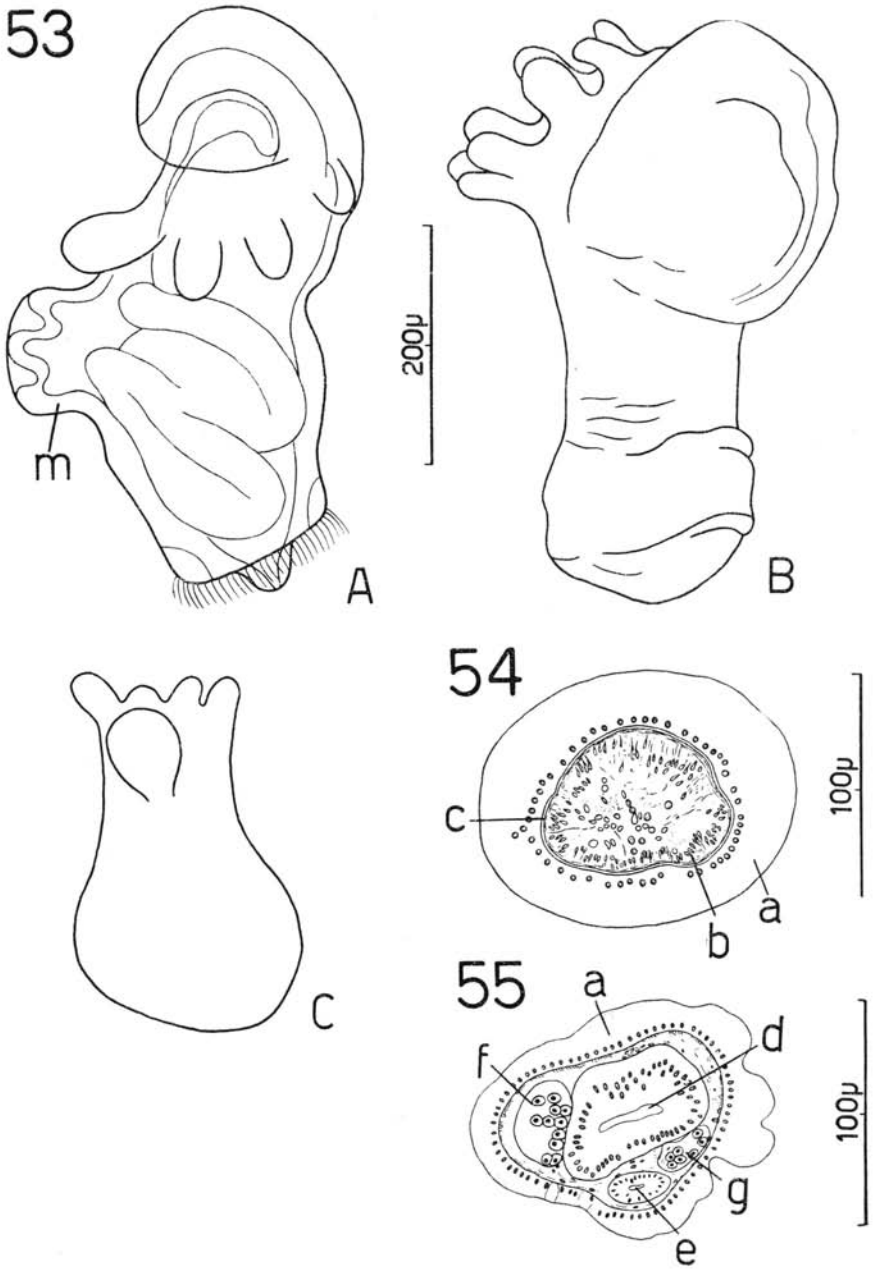

53
m
A
200µ
B
C
54
c
b
a
100µ
55
a
d
f
g
e
100µ

PLATE 14

Phoronis ovalis Wright

Figs. 56-58 — Nearly consecutive transverse sections of oral region of body. Fig. 57 shows nephrostome and Fig. 58 prolonged inferior edge of same.

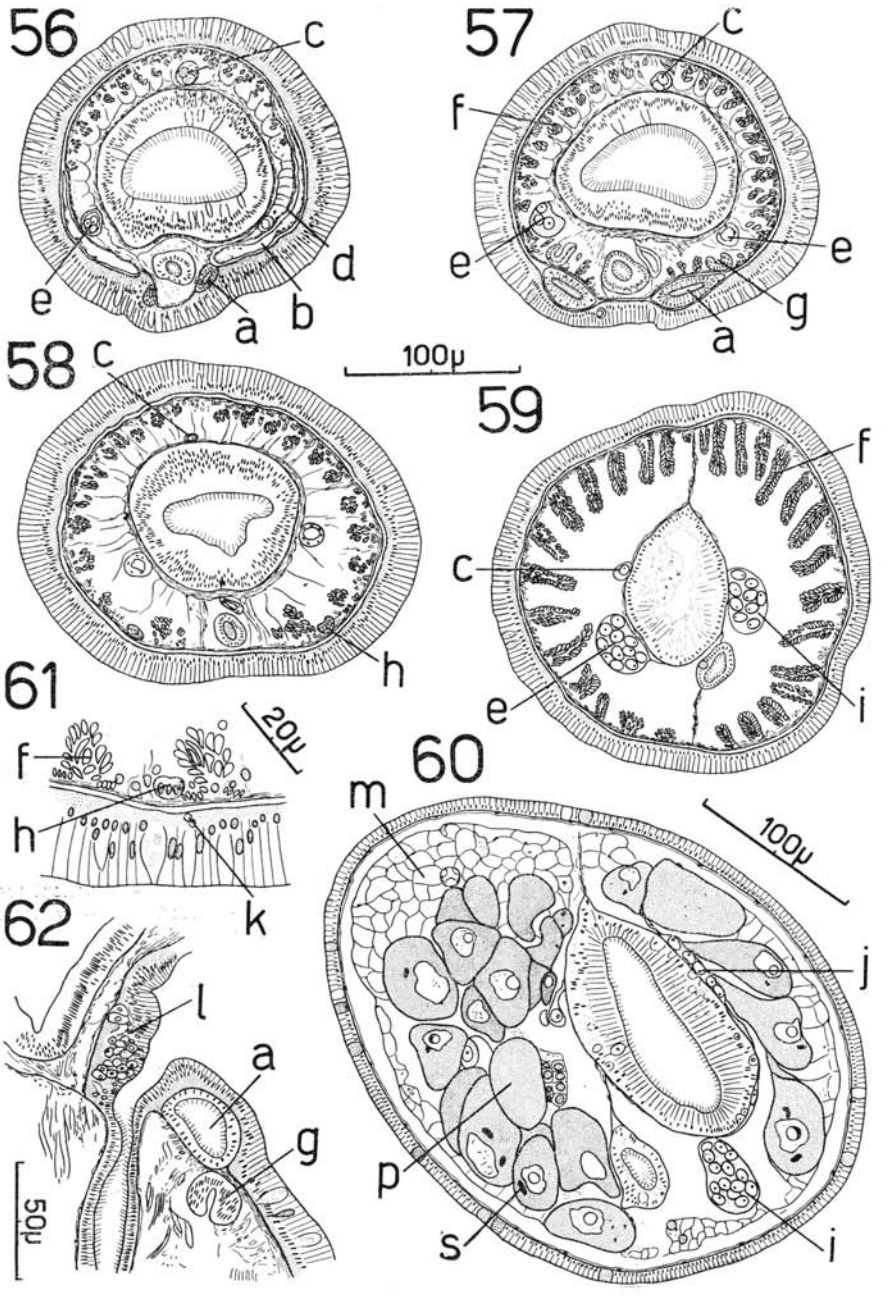
Fig. 59 — Section through muscular region of body.

Fig. 60 — Transverse section of ampulla.

Fig. 61 — Transverse section of epithelium on level of prolonged edge of nephrostome.

Fig. 62 — Portion of saggital section of oral region of body.

a — nephridial canal; *b* — lophophore coelom; *c* — accessory vessel; *d* — diaphragm; *e* — efferent vessel; *f* — longitudinal muscle bundle; *g* — nephrostome; *h* — prolonged edge of nephrostome; *i* — afferent vessel; *j* — peri-gastric sinus; *k* — giant fibre; *l* — lophophoral organ; *m* — fat body; *p* — ovary; *s* — vitelline nucleus.


56
c
e
a
b
d
57
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f
e
e
g
a
100μ
58
c
h
59
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c
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i
61
20μ
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h
k
60
m
100μ
j
p
s
i
62
l
a
g
50μ

PLATE 15

Phoronis ovalis Wright

Fig. 63 — Portion of transverse section through oral region of body, showing the lophophoral organ.

Actinotrocha bella, n. t. n.

Fig. 64 — A — 18-tentacle larva, left side view; B — 22-tentacle larva, contracted, right side view.

Fig. 65 — Transverse section of 64 B larva on level of base of hood.

Fig. 66 — Transverse section of fore body of 64 A larva.

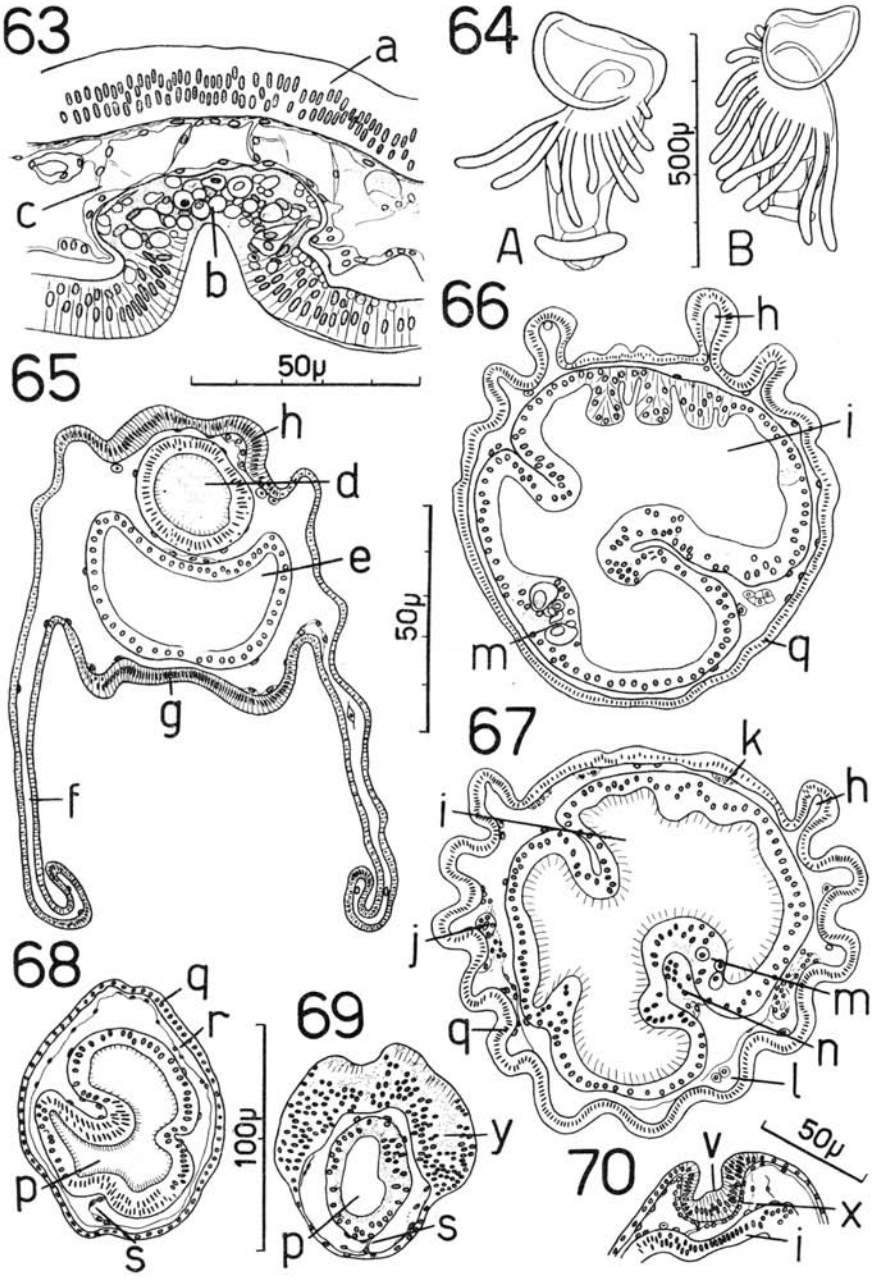
Fig. 67 — Idem, on level of roots of ventral tentacles.

Fig. 68 — Transverse section of lower part of body of 64 B larva.

Fig. 69 — Oblique section of same larva on level of peri-anal ciliated ring.

Fig. 70 — Section of metasoma of same larva.

a — oesophagus epithelium; *b* — lophophoral organ; *c* — lophophore coelom; *d* — oesophagus; *e* — diverticulum; *f* — hood; *g* — ventral thickening; *h* — tentacle; *i* — stomach; *j* — nephridial canal; *k* — dorsal muscle; *l* — coelom; *m* — digestive area; *n* — proliferation of cells; *p* — intestine; *q* — epithelium; *r* — subepithelial muscle layer; *s* — ventral mesentery; *v* — metasoma; *x* — somatopleure; *y* — peri-anal ciliated ring.


63
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c
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50μ
64
500μ
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65
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66
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q
67
k
h
i
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q
n
l
68
q
r
100μ
p
s
69
y
p
s
70
v
50μ
x
i

PLATE 16

Actinotrocha bella, n. t. n.

Fig. 71 — A — 24-tentacle larva, ventral view; B-B_1 — 38-tentacle larva, ventral and left side view.

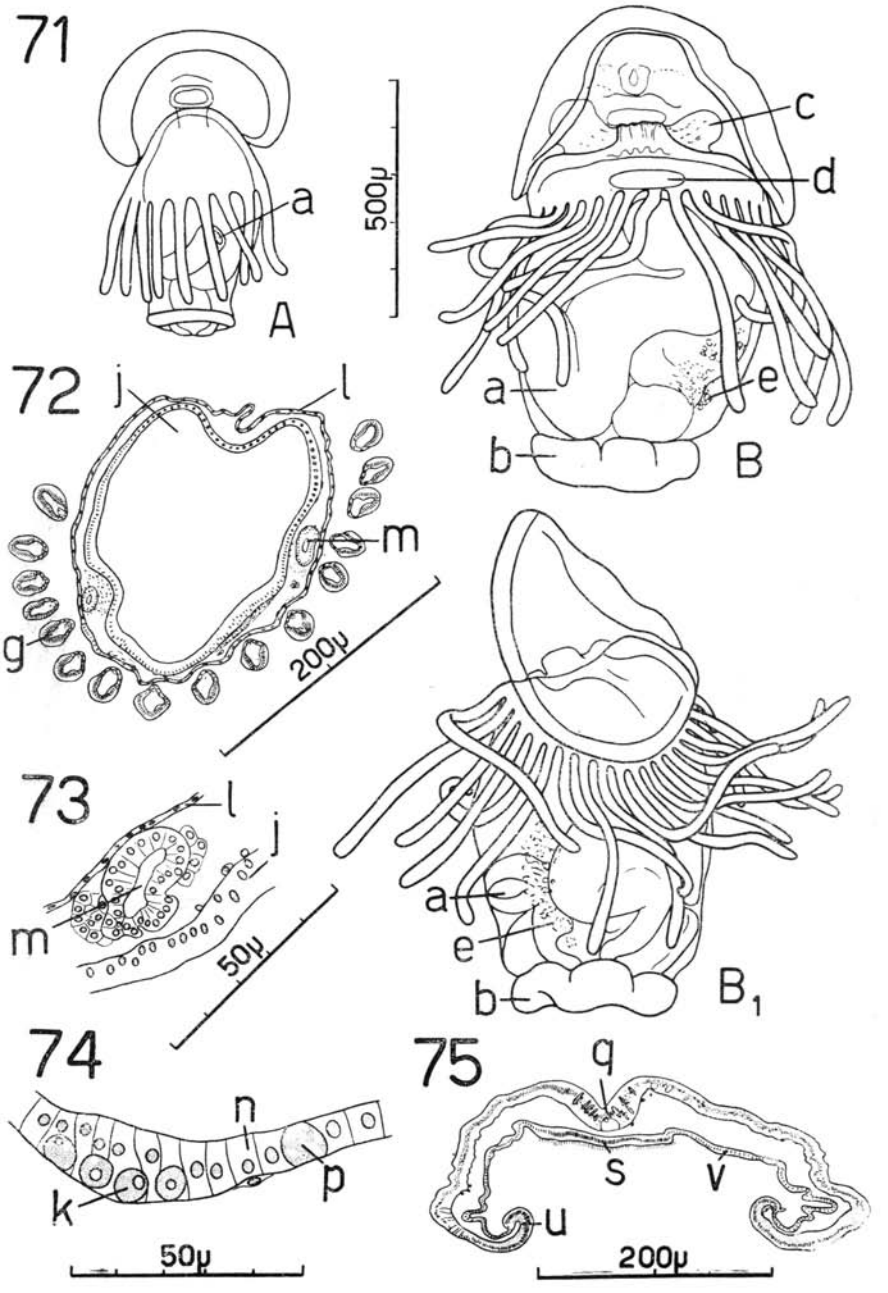
Fig. 72 — Transverse section of body of 71 A larva.

Fig. 73 — Portion of nephridial canal of the same larva.

Fig. 74 — Portion of epithelium of diverticulum in transverse section.

Fig. 75 — Transverse section of hood of 71 B larva.

a — metasoma; *b* — peri-anal ciliated ring; *c* — anterior mass of blood corpuscles; *d* — ventral mass of blood corpuscles; *e* — caecal vessels; *g* — tentacle; *j* — stomach; *k* — globular bodies; *l* — epithelium; *m* — nephridial canal; *n* — epithelium of diverticulum; *p* — gland cell; *q* — sensory organ; *s* — ventro-median epithelium of buccal vestible; *u* — nervous substance; *v* — ventro-lateral epithelium.


71
a
A
500µ
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72
j
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73
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50µ
a
e
b
B1
74
n
k
p
50µ
75
q
s
v
u
200µ

PLATE 17

Actinotrocha bella, n. t. n.

Fig. 76 — Transverse section of 71 B larva on level of base of hood.

Fig. 77 — Idem, on level of diverticulum.

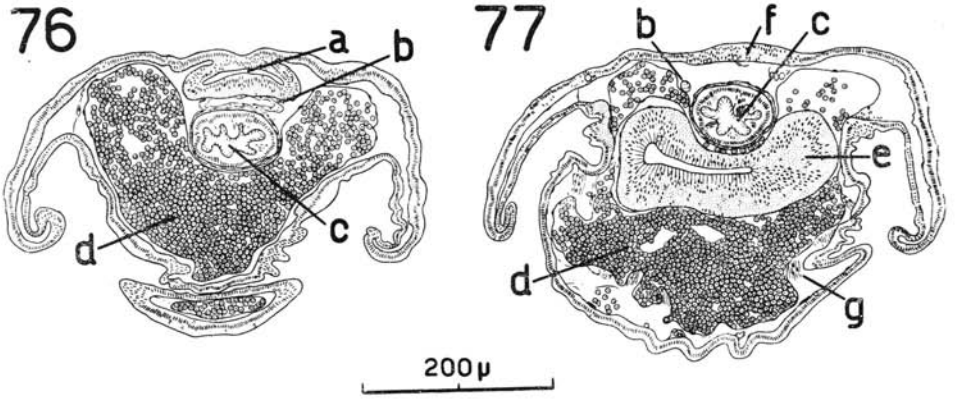
Fig. 78 — Idem, a little above the metasoma opening.

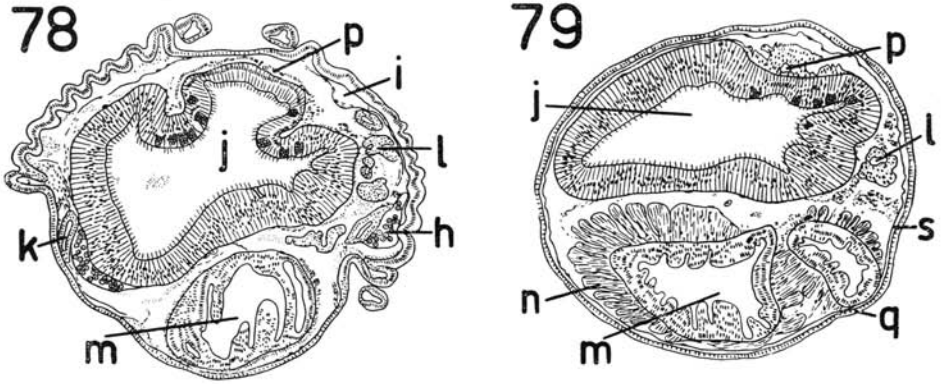
Fig. 79 — Idem, on level of median part of body.

Fig. 80 — Idem, on level of lower part of body.

Fig. 81 — Idem, of peri-anal ciliated ring.

a — ganglion; *b* — dorsal retractor; *c* — eosophagus; *d* — blood sinus; *e* — diverticulum; *f* — inferior portion of ganglion; *g* — ventral muscle; *h* — inferior blood corpuscle mass; *i* — prae-septal cavity; *j* — stomach; *k* — nephridial canal; *l* — caecal vessel; *m* — metasoma; *n* — longitudinal muscle bundle; *p* — dorsal vessel; *q* — epithelium; *s* — subepithelial muscle layer; *v* — star-shaped cell; *x* — ventral mesentery; *y* — peri-anal ciliated ring epithelium; *w* — nervous substance; *z* — rectum.


76
a
b
c
d
77
b
f
c
e
d
g
200 µ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p
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j
l
k
h
m
79
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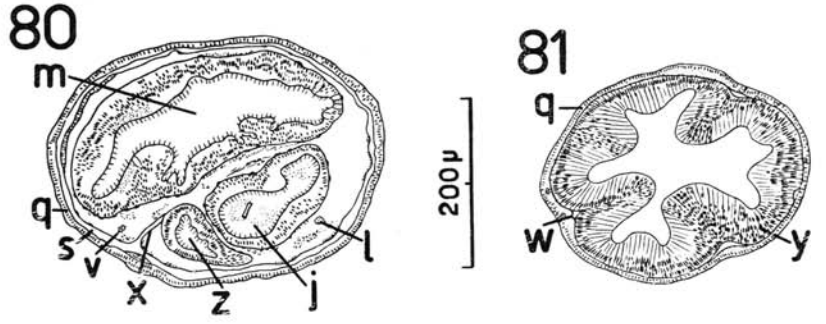
j
l
s
n
q
m


80
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q
s
v
x
z
j
l
200 µ
81
q
w
y

PLATE 18

Actinotrocha bella, n. t. n.

Fig. 82 — Section of dorsal epithelium of hood.

Fig. 83 — Transverse section of sensory organ.

Fig. 84 — Section of epithelium of median region of body.

Fig. 85 — Section of epithelium of lower body.

Fig. 86 — Section of epithelium of region of peri-anal ciliated ring.

Fig. 87 — Transverse section of dorsal wall of stomach.

Fig. 88 — Portion of section of root of one ventral tentacle.

Fig. 89 — Caecal vessels in transverse section.

Actinotrocha chata, n. t. n.

Fig. 90 — Total left side view.

Fig. 91 — Transverse section of the metasomic plate.

a — basophilous gland cell; *b* — nerve; *c* — sensory organ; *d* — sole-shaped gland cell; *e* — epithelium; *f* — subepithelial muscle layer; *g* — star-shaped cell; *h* — ciliated band of stomach; *i* — squamous epithelium; *j* — stomach epithelium; *k* — blood corpuscle mass; *l* — caecal vessel; *m* — tentacle; *n* — dorsal vessel; *p* — eosinophilous gland cell; *q* — elevator of metasoma and nephridium; *s* — somatopleure; *u* — trunk coelom; *v* — mesentery; *x* — metasoma.

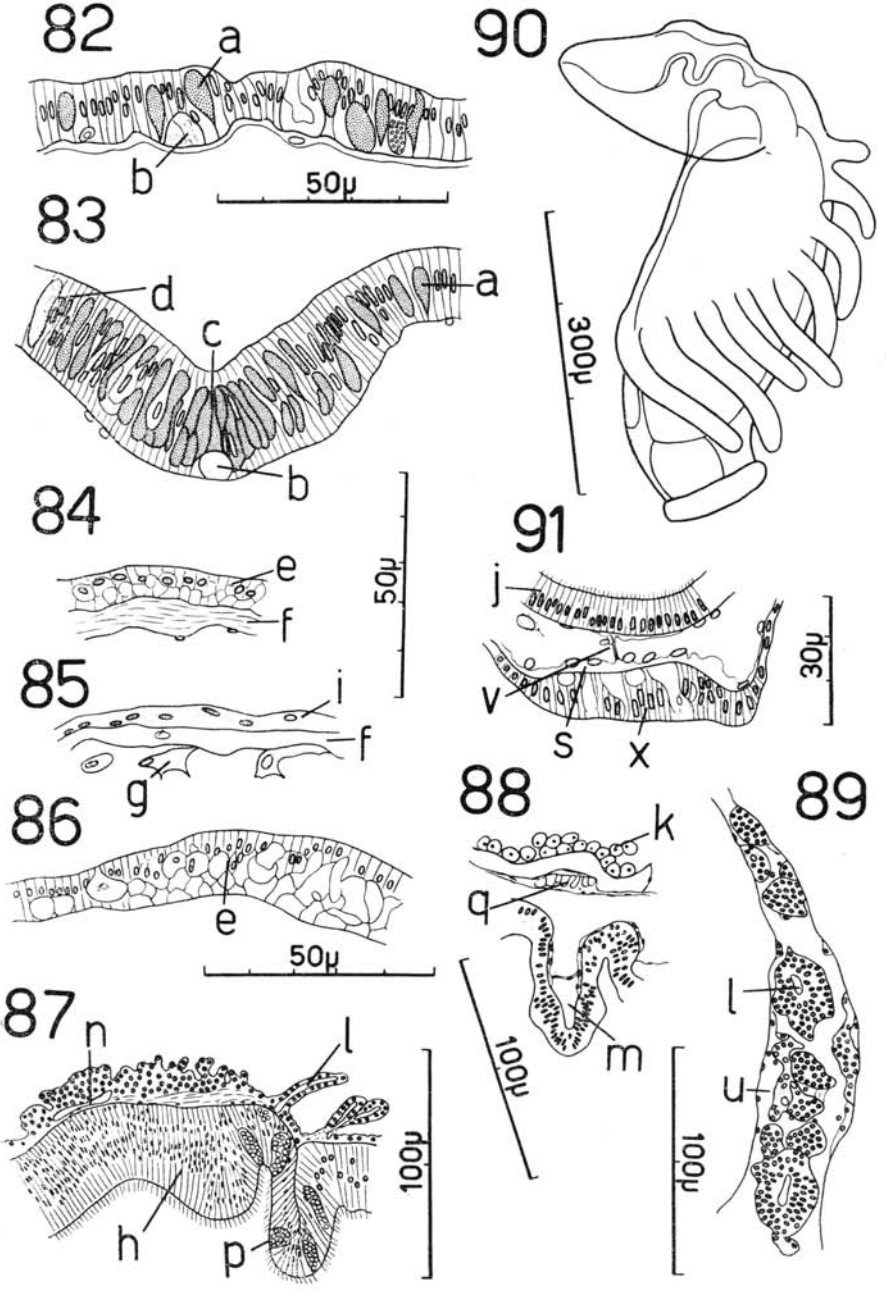
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PLATE 19

Actinotrocha wilsoni B

Fig. 92 — A — Eight-tentacle larva, ventral view; B — 10-tentacle larva, right side view; C — 18-tentacle larva, left side view; D — 20-tentacle larva, contracted, ventral view; E — voluminous larva with 20 tentacles, ventral view; F — 22-tentacle larva, ventral view; G — fully developed voluminous larva with 26 larval tentacles and 20 definitive ones, ventral view. Ubatuba.

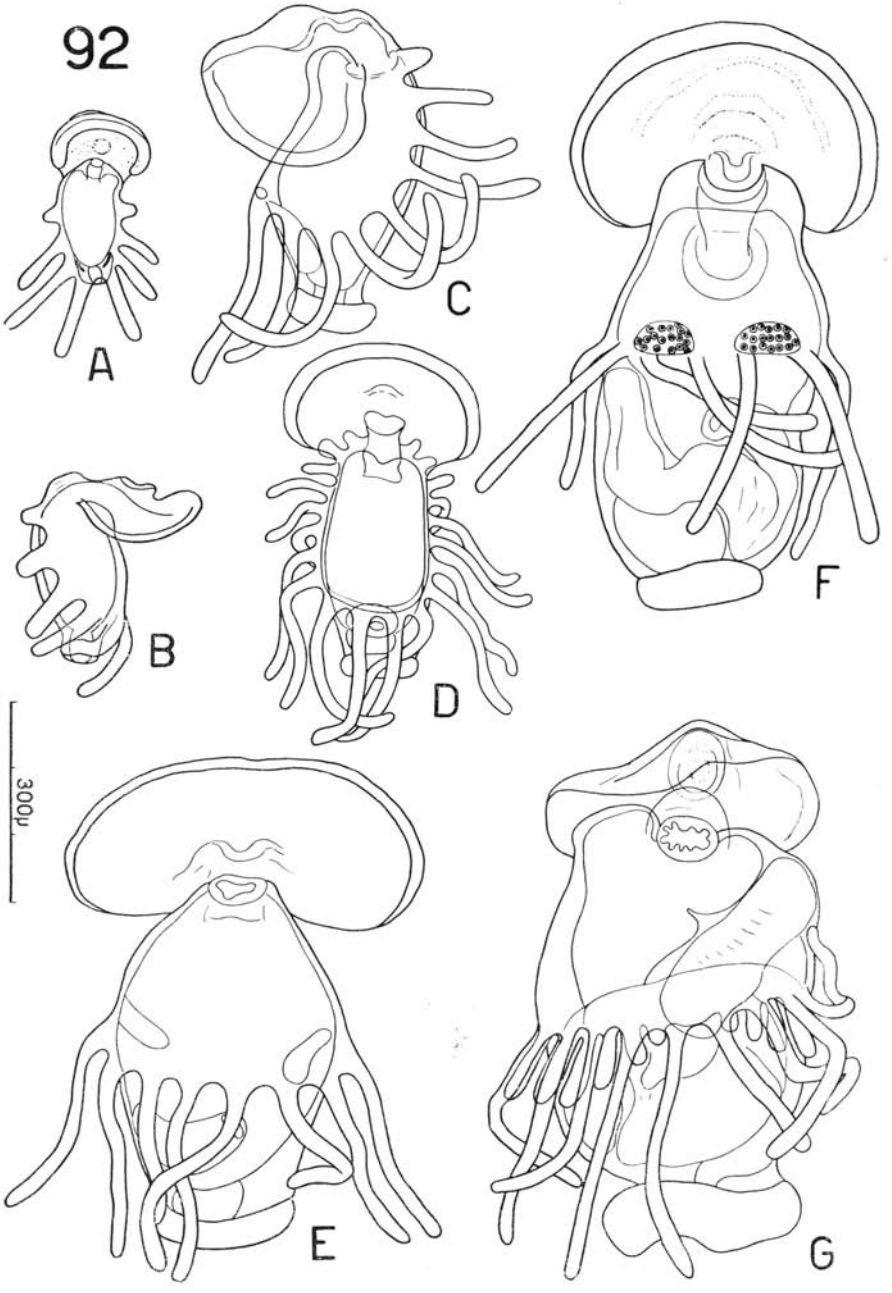
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PLATE 20

Actinotrocha wilsoni B

Fig. 93 — A — 16-tentacle larva, ventral view; B — fully developed slender larva with 26 larval tentacles and about 20 definitive ones. Alcatrazes.

Fig. 94 — Metamorphosing larva; only definitive tentacles present; right side view. Cananéia.

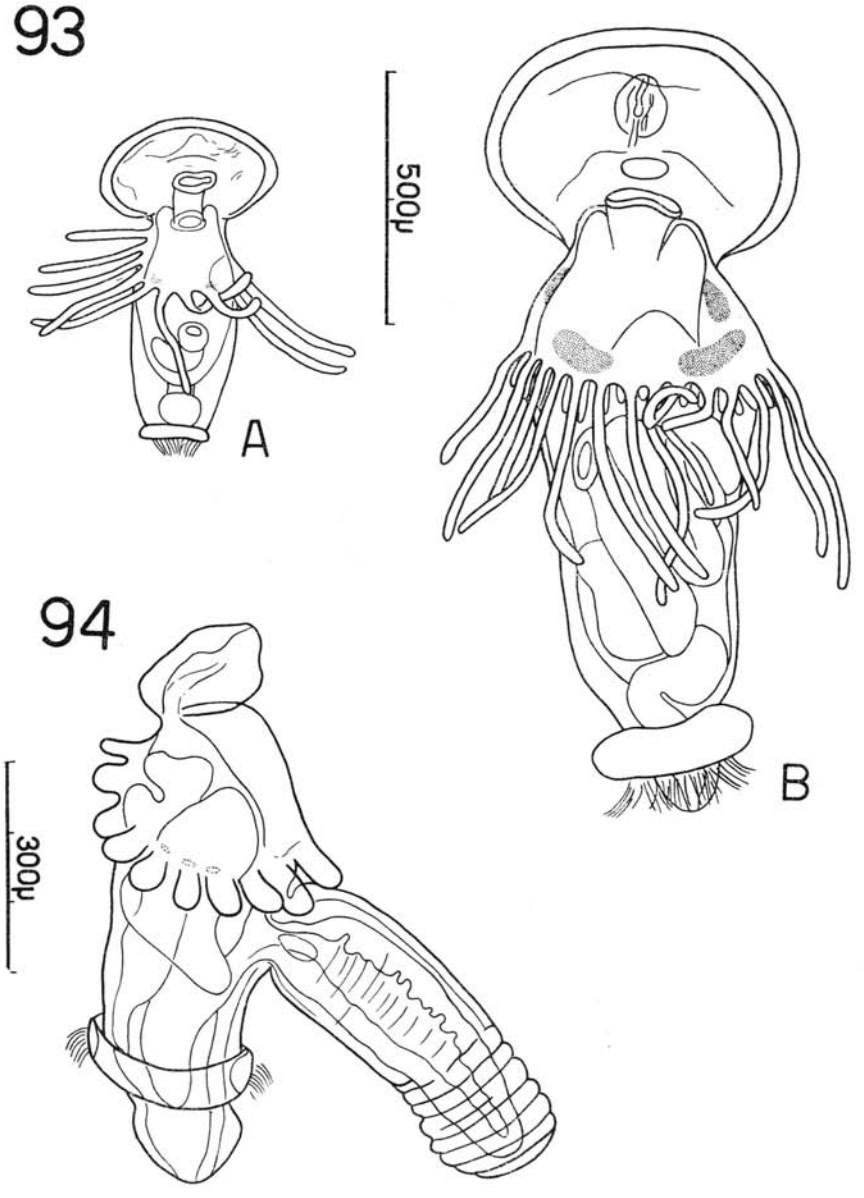
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PLATE 21

Actinotrocha wilsoni B

Fig. 95 — Transverse section of hood of eight-tentacle larva on level of ganglion.

Fig. 96 — Idem, on level of base of hood.

Fig. 97 — Idem, on level of fore region of body.

Fig. 98 — Idem, on level of roots of ventral tentacles.

Fig. 99 — Same of 12-tentacle larva.

Fig. 100 — Transverse section of lower part of body of same larva.

Fig. 101 — Idem, on level of peri-anal ciliated ring.

Fig. 102 — A — gregarines; B — transverse section of hood of 20-tentacle larva.

Fig. 103 — Ventro-lateral epithelium of body a little below buccal opening.

Fig. 104 — Nephridium of 12-tentacle larva in transverse section.

Fig. 105 — Dorsal and lateral vessels in transverse section.

Fig. 106 — Portion of transverse section of 20-tentacle larva on level of insertion of ventral tentacles.

Fig. 107 — Transverse section of body of 16-tentacle larva.

Fig. 108 — Portion of transverse section of body on level of insertion of ventral tentacles of same larva.

a — ganglion; *b* — epithelium; *c* — oesophagus; *d* — tentacle; *e* — stomach; *f* — mesenchymal cells disposing in layer; *g* — mesenchymal cell of body cavity; *i* — nephridial canal; *k* — metasoma; *l* — somatopleure; *m* — mesentery; *n* — digestive area; *p* — buccal vestibule; *q* — diverticulum; *s* — gregarine; *v* — atrial pit; *x* — mass of blood corpuscles; *y* — lateral vessel; *w* — peri-anal ciliated ring; *z* — dorsal vessel.

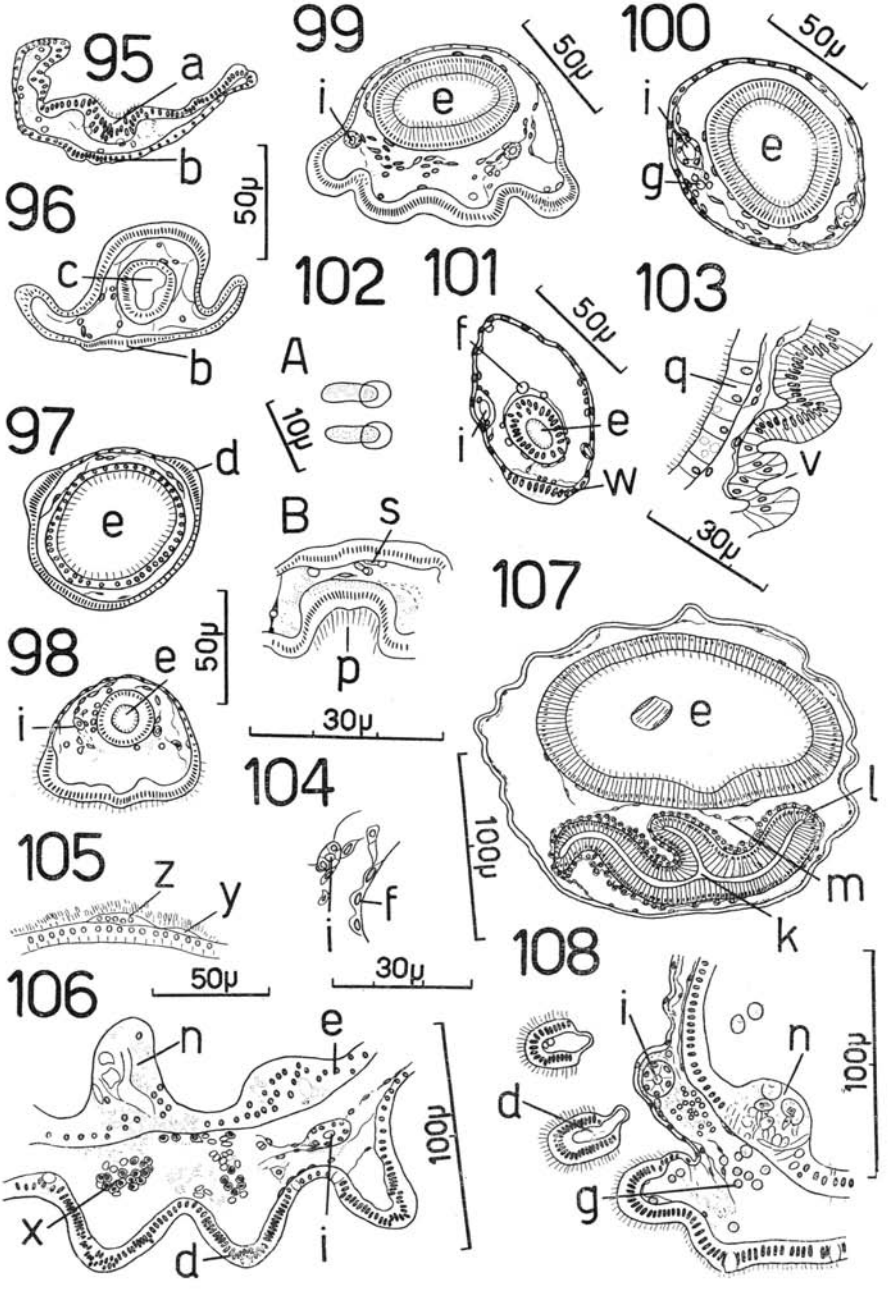
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PLATE 22

Actinotrocha wilsoni B

Fig. 109 — Transverse section of hood of advanced larva.

Fig. 110 — Frontal section of superior part of body.

Fig. 111 — Nephridium in transverse section.

Fig. 112 — Median section of hood.

Fig. 113 — Epithelium of stomach in transverse section.

Fig. 114 — Larval tentacle in transverse section.

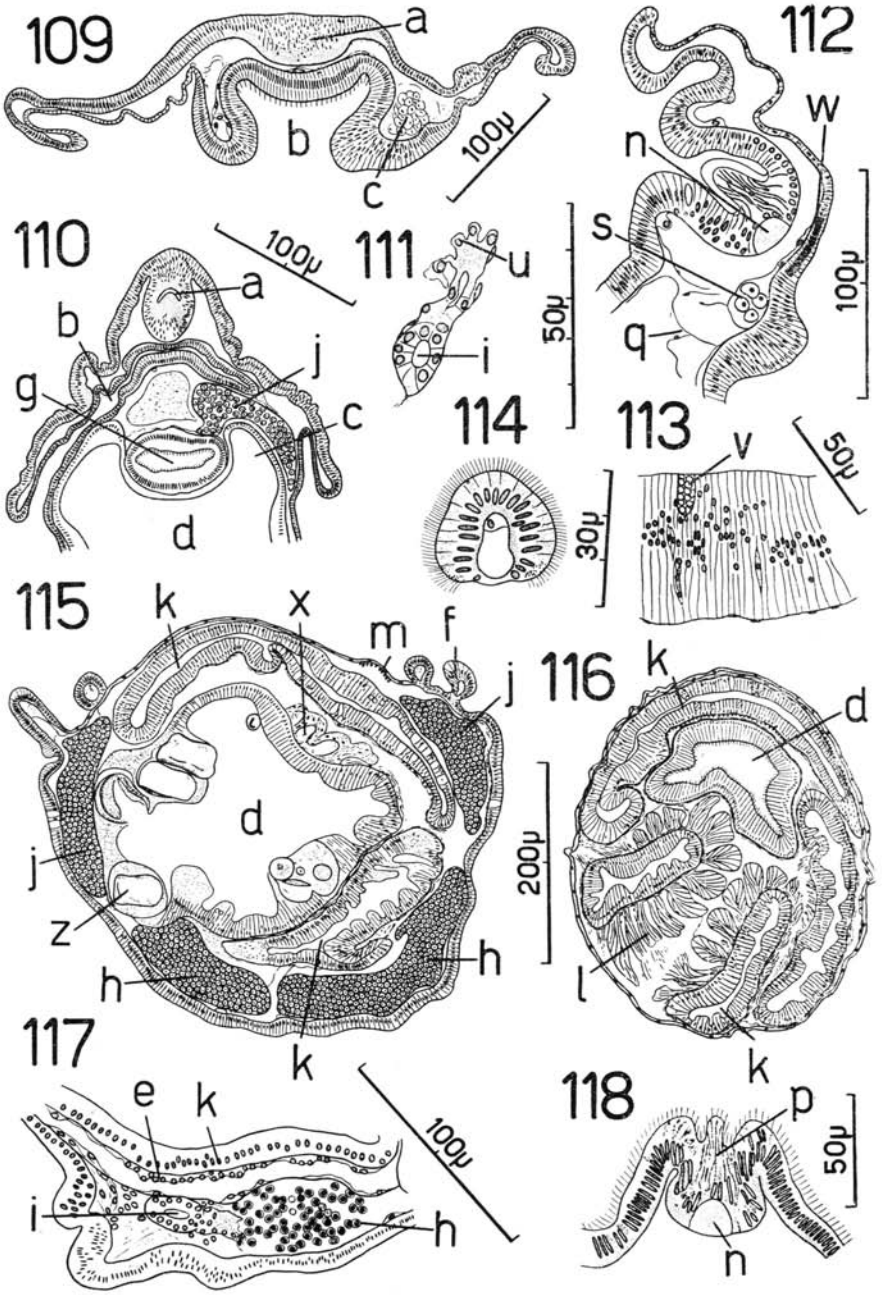
Fig. 115 — Transverse section of fore part of body.

Fig. 116 — Idem, of lower part of body.

Fig. 117 — Portion of transverse section of body, showing ventral mass of blood corpuscles.

Fig. 118 — Sensory organ in transverse section.

a — ganglion; *b* — buccal vestibule; *c* — diverticulum; *d* — stomach; *e* — somatopleure; *f* — tentacle; *g* — oesophagus; *h* — ventral mass of blood corpuscles; *i* — nephridial canal; *j* — dorsal mass of blood corpuscles; *k* — metasoma; *l* — longitudinal muscle bundle; *m* — dorsal retractor; *n* — nerve; *p* — basophilous gland cell; *q* — septum; *s* — ventral vessel of hood; *u* — solenocytes; *v* — eosinophilous gland cell; *x* — dorsal vessel; *w* — ventral thickened epithelium; *z* — digestive area.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