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## I — INTRODUCTION

Several papers have been published on the Enteropneusta of Brazil (J. W. Spengel, 1893; F. Müller, 1898; P. Sawaya, 1950; L. Forneris & P. Sawaya, 1953; T. Björnberg, 1952, 1953, 1953 a, 1955). Few observations though, have been made on their developmental history and none on the relationship of the larvae to the adults found and their general distribution on the coast of Brazil.

Although many of the larvae collected off the coast of Brazil have been described (Björnberg, 1953, 1955), hitherto little attention has been paid to the great variability of their specific characteristics. The reinvestigation of numerous carefully fixed larvae showed that tornariae *mourei* and *lilianae*, previously described from fixed material (Björnberg, 1953 a) are conspecific and belong to *Balanoglossus clavigerus* D. Chiaje. As the use of the name tornaria *stiasnyi* might lead to the supposition that this is the larva of *Glandiceps stiasnyi* (Rao, 1953), its name has been changed to *nordestina* in this paper.

*Tornaria dubia* (Spengel, 1893, p. 378) was collected off the coasts of Paraná, of Santa Catarina, of Baía and of Sergipe (States of Brazil) and exists also in the Mediterranean Sea. Spengel only gave a brief account of its anatomy (Spengel, 1893, p. 378). It therefore calls for more detailed studies. Stages of metamorphosis of these larvae were not obtained in Brazil, but were received from Algiers (Mediterranean Sea). Their study in the present work permits a more complete account of the development of the larva.

Larvae previously described as tornaria *weldoni* (Stiasny, 1921), tornaria *cairnsiensis* (Trewawas, 1931) and tornaria *setoensis* (Stiasny, 1929) were taken off Florianopolis and from 19°21,0' S to 05°44,3' N off the coast of Brazil. Tornariae *mor-*

*gani* and *chierchiai I* were also collected off Rio Grande do Sul, Santos and from 22°39,0' S to 05°44,3' N off the coast of Brazil. The variation and morphology of these larvae will be examined comparatively and the implications, resulting from this, established with reference to their external as well as their internal anatomy.

This paper is therefore an account of the taxonomy and distribution of the Enteropneusta found on the shores of Paraná, of São Paulo and in the waters from 34°49,0' S to 05°44,3' N off Brazil, from 1952 to 1958.

The collection of the samples was made by the staff working at the Instituto Oceanográfico's Laboratory in Cananéia and during several cruises along the Brazilian coast by ships belonging to this Institute, to the Brazilian Navy and to the Japanese Government (see the Addenda). A large part of the field work and processing of the data was done by the physical oceanographic staff of the Instituto Oceanográfico; another part by the research staff of the Brazilian Navy under the direction of Com. P. C. Moreira da Silva; and the "Toko-Maru" data, by the Japanese research staff of this vessel under the direction of Prof. H. Nakamura. The writer feels indebted to all these and to the officers and men of the vessels used in the various cruises.

In the sampling of the larvae the author had the kind help of Dr. M. Vannucci, Dr. L. Forneris, Mrs. Morigushi, Mrs. Casari and Mr. Lupi. Mrs. Casari also helped in the preparation of some of the slides used for this paper and Mr. Lupi helped in the typing and organization of the list of the Addenda. To all these the author wishes to express the greatest thanks.

Copepods were determined thanks to the help of Prof. J. Paiva Carvalho; Prof. Müller-Melchers and Mr. C. Teixeira classified the diatoms; and Dr. Vannucci, the medusa.

To those who have aided in the collection of adult enteropneusts, the author is greatly indebted.

## II — MATERIAL AND METHODS

The adults were collected on the beaches of the States of Paraná and São Paulo (Brazil). The rearing of the adults as

well as the artificial fertilization was tried in São Paulo and in Curitiba (Paraná, Brazil), but with no success.

Forty five adults were narcotized with a Mg Cl<sub>2</sub> solution in sea water. Fixatives used for the adults were formalin (10% solution in sea water), Bouin, Susa, 70° alcohol or Pampel.

The larvae were collected off the Brazilian coast from 34°49,0' S to 05°44,3' N. Plankton hauls were taken regularly at various stations, the positions of which are shown on Map 1. The positions of the stations of the various expeditions which also collected plankton are registered on the station lists. Few quantitative hauls were made from the ships "Emilia" and "Almirante Saldanha". Nearly all collections were made by oblique hauls from fixed depths up to the surface (See the Addenda).

Immediately after being captured, the larvae kept alive for rearing purposes, were placed in finger bowls in a 220 cc volume of sea water. The water was changed at least twice a day. The temperature was maintained more or less constant at 26° C by putting a wet cloth around the finger bowls. In this way it was possible to rear the larvae from the "Krohn" stage up to metamorphosis. Rearing experiments were tried at Cananéia during January and February for three succeeding years.

No anaesthesia was used for the larvae. The drawings of the living material were made without the use of narcotization media for the animals. The use of very dilute solutions of lactic acid as a narcotic (Morgan 1894, p. 6) was tried without success. Of the 3.205 larvae obtained, 84 were sectioned for histological and anatomical studies. Mallory's triple stain, haemalum or haematoxylin and eosin were used for staining the larvae and the adult sections. Fixed in Bouin and Pampel the external features of the larvae were better kept than fixed simply with formalin at 4%.

### III — THE LARVAE

#### 1 — VARIABILITY OF THE SIZE AND SHAPE

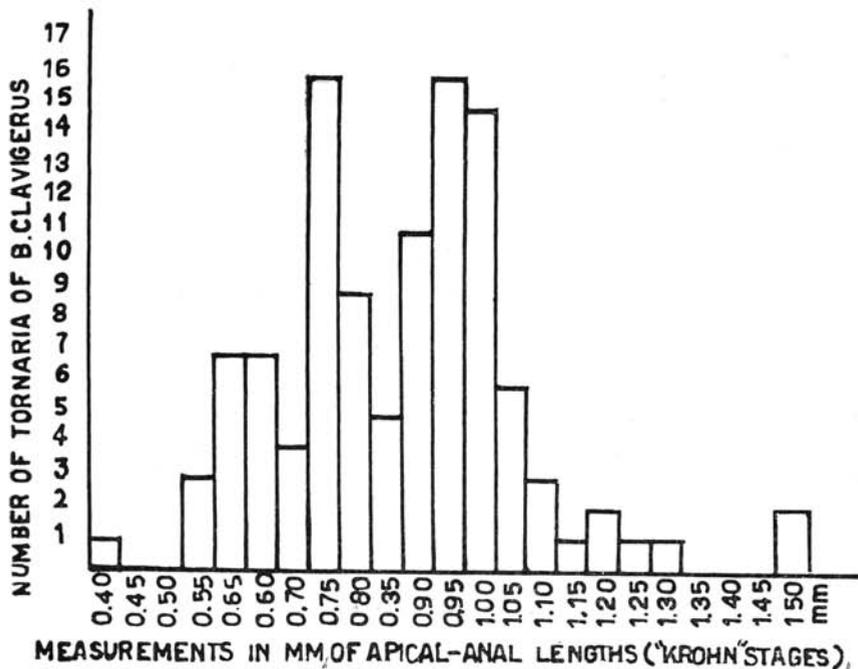
a) SIZE — The size of the "Krohn" stage as well as of the other stages of development of the tornaria of *B. clavigerus* varies considerably as is shown in the Table 1 and in the Histogram 1.

TABLE 1  
 APICAL-ANAL LENGTHS IN MM OF TORNARIAE OF *B. CLAVIGERUS* WHEN ALIVE AND WHEN  
 FIXED IN SEVERAL STAGES OF DEVELOPMENT  
 (The numbers in brackets refer to the number of animals measured).

STAGES OF DEVELOPMENT													
Müller		Heider		Young — Metschnikoff — Advanced				Krohn		Spengel			
		Alive	Fixed	Alive	Fixed	Alive	Fixed	Alive	Fixed	Alive	Fixed		
0,25	—	0,29	0,24	0,35 (2)	0,29	0,63	0,40 (2)	1,00	0,43	1,1	0,83		
0,28	—	0,33	0,26 (2)	0,36	0,30 (3)	—	0,42	1,15	0,56	1,3	0,86		
—	—	0,34	0,27	0,40	0,31	—	0,45	1,20	0,63 (3)	—	—		
—	—	0,35	—	0,42	0,32	—	0,46 (2)	1,25	0,72	—	—		
—	—	0,40	—	—	0,33 (3)	—	0,47 (2)	1,29	0,75 (7)	—	—		
—	—	—	—	—	0,35	—	0,48	1,35	0,77 (3)	—	—		
—	—	—	—	—	—	—	0,49 (2)	1,50	0,83 (3)	—	—		
—	—	—	—	—	—	—	0,50 (3)	1,60	0,86 (2)	—	—		
—	—	—	—	—	—	—	0,51 (2)	—	0,90 (4)	—	—		
—	—	—	—	—	—	—	0,53	—	0,95 (5)	—	—		
—	—	—	—	—	—	—	—	—	1,00 (6)	—	—		
—	—	—	—	—	—	—	—	—	1,13	—	—		
—	—	—	—	—	—	—	—	—	1,22	—	—		

The histogram was obtained by the frequency distribution of the apical-anal lengths of a hundred larvae of *tornaria mourei* type, measured after fixation in the "Krohn" stage.

HISTOGRAM 1



HEIGHT FREQUENCY OF TORNARIAE OF *B. CLAVIGERUS* IN THE "KROHN" STAGE

They show two frequency maximums, one at 0,75 and another at 0,95 mm. A number of these larvae examined when alive in the same stage, varied in length from 1,00 mm to 1,50 mm and are thus slightly smaller than the European *tornaria* of *B. clavigerus*, which are often 2 mm or a little more in length (Stiasny 1914, p. 259; Burdon-Jones 1957, p. 4).

Table 2 shows the apical-anal measurements of the "Krohn" stage of *tornaria nordestina*. Comparing these sizes with those of *tornaria mourei* at the same stage of development we find that *tornaria nordestina* is generally larger.

TABLE 2

APICAL-ANAL LENGTH IN MM OF *TORNARIA NORDESTINA* (FIXED)

"Metschnikoff" stage	Locality	"Krohn" stage	Locality
0,60	Cananéia (Canal Norte)	1,10	Cananéia (B. Abrigo Is.)
0,66	" " "	1,17	Cananéia (Argolão)
0,71	" " "	1,20	Ubatuba
0,80	" " "	1,25	Cananéia (Argolão)
0,80	Cananéia (B. Abrigo Is.)	1,30	Cananéia (B. Abrigo Is.)
0,88	Cananéia (Canal Norte)	1,45	Cananéia (Canal Norte)
1,20	Santos	1,45	Florianópolis
—	—	1,54	"
—	—	1,57	Santos
—	—	1,75	Ubatuba
—	—	2,90	Recife

Fifty *tornariae chierchiae I* or *morgani*, measured in the "Krohn" stage of development, after fixation in a solution of 4% formalin, varied from 2,2 mm to 6 mm in apical-anal length. Though not trustworthy, because of the small number of measured animals, a bimodal distribution is also indicated. The most frequent size of the "Krohn", stage is 4 mm. In the "Spengel" stage the apical-anal length is from 4,4 mm to 9 mm, thus generally larger than in the "Krohn" stage. Larvae collected in the shelf waters off Brazil are 4,4 mm to 5,0 mm long, when in the "Spengel" stage. Some of those collected from the Brazil Current (several miles off the coast) are very long (8 to 9 mm).

Size, number of tentacles and shape of the lateral lobe and saddle were mentioned by Stiasny (1929, p. 75) to differentiate *tornaria weldoni* from *tornaria setoensis*. Several larvae are found in the same plankton sample (M<sub>537</sub>) which answer the description of these two larvae, but a lot of intermediate forms are found as well, all in the same stage of development. This suggests that these larvae really belong to only one species, with very variable characters. The shape of this larva will be mentioned again later. As for the size, Stiasny (1929, p. 74; 1921, p. 223) and Trewawas (1931, p. 55) measured 3,0 mm to 2,5 mm length for *tornaria setoensis* and 2,5 mm for *tornaria weldoni*. The Brazilian larvae measure 1,3 to 2,0 mm apical-anal length

(12 young "Krohn" stages with one sausage shaped pair of coeloma); 1,5 to 3,4 mm apical-anal length (9 well developed "Krohn" stages with two pairs of sausage shaped coeloma); 3,0 to 2,5 mm length (5 old "Krohn" stages, with, at least one rectangular shaped pair of coeloma and another, either sausage or rectangular shaped). The measurements show wide overlapping from the original lengths mentioned in the literature. The "Spengel" stage varies from 2,5 mm to 1,0 mm (in 7 animals). The "Metschnikoff" stage varies from 1,1 mm to 2,5 mm in 4 animals.

*Tornaria dubia* is always found at a great distance off the coast and measures 3,3 to 0,8 mm in length in the "Spengel" stage and 1,15 to 0,85 mm in the "Krohn" stage.

The plankton collected near to the beaches at certain times of the year (from September one year to April the following year) contains numerous tornariae in all stages of development up to and including early metamorphosis. The "Krohn" and "Spengel" stages of the larvae are usually of the smaller size in these samples. When plankton is collected at a greater distance off the coast tornariae are usually in the "Krohn", "Spengel" or "Agassiz" stages of development and are large in comparison with those captured near the coast. Large larvae captured at a greater distance from the coast seem to result from an ability of the species to prolong its larval existence, when unable to find a proper settling medium. It is probably a phenomenon of delayed metamorphosis (Wilson 1958, p. 88).

The largest forms of tornariae occur in waters of high salinity (more than 35.00 ‰) or in samples which are taken from layers of high salinity among others. The waters of high salinity and high temperature belong to the Brazil Current, a branch of the South Equatorial Current, which runs along the Brazilian coast in a N-S direction. This may answer for the fact that *tornaria dubia*, from the Mediterranean, *tornaria morgani* and *tornaria weldoni* all from the northern hemisphere, are also found in the south of Brazil. It may also explain why the two larvae which show the largest size in the plankton, apparently belong to the two adult forms of *Ptychoderidae* which have the largest distribution (*Ptychodera flava* and *Balanoglossus carnosus* or *B. gigas*).

b) SHAPE — According to Stiasny and Stiasny-Wijnhoff (1931, p. 53-52) the following characteristics are of specific importance: the shape of the tornaria, the number of secondary saddles and lobes, the form of the dorsal and lateral primary and secondary saddles, the width of the oral area, the height and depth of the buccal aperture, the position of the first coelomopore and the form of the digestive tube.

The shape of the tornaria is conditioned by the stage of development of the larva. Its variability in different larvae in the same stage of development is also conditioned by the quantity of jelly-like substance, which fills the blastocoel. Thus the shape of tornaria *dubia* varies very little because it has a more viscous and voluminous blastocoelic fluid which gives the tornaria more rigidity. The other tornariae which have been examined show a very variable shape in the living (compare Figs. 1, 2, Pl. 1) as well as in the fixed animals (compare Figs. 3-6, Pl. 1 and Figs. 11-13, Pl. 3). The blastocoelic fluid of these animals is less viscous and voluminous. Fixatives also have an influence on the shape of the larvae. Drawings of tornaria *mourei* in the "Krohn" stage of development fixed in 4% formalin sometimes show the apical plate pointed, the anal area contracted or distended and the ventral belt in a horizontal position. In Pampel (Fig. 4, Pl. 1) the ventral belt is kept in a vertical position as in living specimens. Figures 1-6 (Pl. 1) show the variability of width of the oral area and of the position of the mouth opening in living and in fixed specimens. Variability of the inferior lateral lobes of tornaria *chierchiae* I (Fig. 7, Pl. 2), of tornaria *nordestina* and of tornaria *weldoni* (Fig. 9, Pl. 2) have also been recorded. In these larvae this character is largely due to the length of time in which the animals have been kept in the fixative and the nature of the fixative. Tornariae *nordestina* recently fixed in Bouin and kept in 70° alcohol, show no lateral lobe (Fig. 11, Pl. 3). Other larvae fixed in 4% formalin or in Bouin and stored a long time in alcohol, show a large lateral lobe (Fig. 13, Pl. 3). The inferior dorsal lobe may also vary in shape and in depth and is also larger in animals stored for a long time after fixation. The variability of the inferior dorsal lobes of 27 tornariae *chierchiae* I in the "Krohn" stage of development may be observed in Figure 8 (Pl. 2). The

lobe is considered between the first tentacle of the lateral lobe and the first tentacle of the post-oral field. Animals examined soon after being captured, do not show either deep lateral lobes or deep inferior dorsal lobes. Spengel (1893, p. 379) examined tornariae of the *chierchii* I and of the *morgani* type from the Atlantic and the Pacific Oceans and considered them as belonging to the same species of animal. Stiasny and Stiasny-Wijnhoff (1931, p. 111) examined the figures published by Spengel and considered them as belonging to different species. Although Pacific larvae of this type were not available for comparison with the Atlantic specimens, one is inclined, in view of the great variability of their characters to consider the larvae as belonging to the same species. The number of tentacles on the lateral lobe, varies from 7 to 10, with a greater frequency of 9, in larvae from 3 to 4,4 mm length in the "Krohn" stage of development.

Table 3 shows the variability in the number of tentacles and of size of the tornaria *weldoni* found in Brazilian waters.

TABLE 3

VARIABILITY OF THE NUMBER OF TENTACLES ON THE VENTRAL, UPPER LATERAL AND DORSAL LOBES OF TORNARIA WELDONI IN THE "KROHN" STAGE

Size of the larva	NUMBER OF TENTACLES ON THE			COELOMA	
	Ventral Lobe	Lateral Upper Lobe	Dorsal Upper Lobe	Trunk	Collar
1,3 mm	7-5	3-3	6-5	very small	absent
1,3 mm	8-6	3-2	4-6	small	very small
1,5 mm	10-10	6-9	9-8	small and very thin	absent
1,7 mm	12-8	7-7	6-8	sausage shaped	sausage shaped
1,8 mm	9-6	3-2	6-6	large rectangular	sausage shaped
1,9 mm	10-10	7-7	8-9	sausage shaped	small
2,0 mm	10-9	8-9	9-9	sausage shaped	small
2,0 mm	6-55	2-2	6-5	large rectangular	sausage shaped
2,5 mm	12-9	6-7	9-10	large rectangular	sausage shaped
2,5 mm	15-12	7-7	11-11	large rectangular	sausage shaped
2,2 mm	13-10	6-8	10-12	large rectangular	large rectangular
3,5 mm	11-9	7-6	9-9	sausage shaped	small

The *weldoni* and the *setoensis* tornariae probably also belong to the same species because of the identity of the lateral lobes, the shape of the primary, secondary and dorsal lobes, the ventral saddle as well as of the aspect of the proboscis coelom (Figs.

14-17, Pl. 3). The number of tentacles on the primary saddle cannot be considered as a specific characteristic because it varies generally in all animals with tentacles. When the living tornaria *mourei* is compared with the tornaria of *B. clavigerus*, no difference can be detected either. Even the anal ring (which had been hitherto overlooked — Björnberg 1953a, p. 83) exists. Brazilian larvae are smaller than the European ones, but size can be a function of food and temperature.

## 2 — FEATURES OF THE LARVAL STAGES AND BIOLOGICAL NOTES

a) THE "MÜLLER" STAGE — *External Morphology* — Tornariae *chierchiae* I, *nordestina* and *mourei* or of *B. clavigerus* (0,25 mm) are very much alike at this stage. The epithelium shows four different regions. The region of the ciliated bands is made up of small, basophil cells, with several layers of nuclei. The prae- and post-oral areas, surrounded by the ciliated bands, show one layered, basophil cells with one layer of nuclei. The oral area has very thin epithelial cells. The apical plate shows nervous cells (which are small pluristratified, densely stained by staining liquids), long, large and also very small cells and pigmented cells, which make up the eye spots. The eye spots, just as Spengel described (1893, p. 390-395), are already conspicuous.

*Internal morphology* — The wall of the oesophagus, of the intestine and the anus is constituted by large, flat cells, with large basophil nuclei and sometimes goblet cells. All are ciliated. The oesophagus is surrounded by fine muscular fibers. The stomach wall shows larger, flat and less basophil cells. The anus walls are strongly ciliated. All the tornariae, even the very youngest examined have a thin proboscis coelom communicating with the exterior by a pore. The coelomic epithelium is made of loose, large, rounded cells with big nuclei. A muscular band runs from the coelomic wall to the apical plate. The coelomic pore and the coelomoduct walls are formed of the same kind of cells which constitute the external epithelium of the areas

surrounded by the ciliated bands. The same has been observed for the tornaria of *B. clavigerus* (Stiasny 1913, p. 60-62).

*Behaviour* — The swimming movement of the tornaria *mourei* at this stage is in a spiral course as shown by Ritter and Davis (1904, p. 189) for tornaria *ritteri* and by Burdon-Jones (1952, p. 567) for *Saccoglossus horsti*. The telotroch is not visible yet at this stage.

b) THE "HEIDER" STAGE (Figs. 18-20, Pl. 4) — *External morphology* — Tornaria *nordestina* and tornaria *mourei* show a telotroch with large, high ciliated cells. The cilia increase in length as the larva gets nearer to the "Krohn" stage of development.

*Internal morphology* — The internal morphology of tornaria *mourei* and of the larva of *B. clavigerus* is the same in this stage. Fixed tornariae *chierchiae I* can be distinguished from the above mentioned larvae at this stage of development by the extreme length and the paper-like flatness of the protocoel (Figs. 21-22, Pl. 4).

*Environmental conditions* — Young stages of tornaria *mourei* (Fig. 18, Pl. 4) and of tornaria *nordestina* can be found very near to the beaches (a few meters away only in Ubatuba). These tornariae were nearly always collected during the flood of the tide which is known to bring in water of higher salinity. The very young tornariae *chierchiae I* (Fig. 20, Pl. 4) were collected on the continental shelf or on its slope, off the mouths of the Amazon and Tocantins rivers, sometimes at a distance of several miles off the coast. Tornaria *mourei* and tornaria *nordestina* have not been found off the shelf waters. Shelf waters off Brazil are usually made up of mixed waters of high temperature and salinities between 35.00 ‰ and 36.00 ‰. Coastal waters are also of mixed origin and have high temperatures and low salinities (35.00 ‰ or less). The wide continental shelf off the mouths of the Amazon and Tocantins rivers is under the influence of the South Equatorial Current, from which the Brazil Current is a branch. It is a water mass of high temperature and high salinity (36.00 ‰ or more). Tornaria *chierchiae I*, *weldoni* and *dubia* are found in these waters or in the mixed shelf waters.

c) THE "METSCHNIKOFF" STAGE — *External morphology*

The ciliated circumoral band forms saddles and lobes. *Tornaria nordestina* has little swellings of the epithelium along the ciliated bands (Fig. 12, Pl. 3), which the other larvae do not show. The cells outside the ciliated bands have flattened out and are not so numerous relatively to the area (Fig. 23, Pl. 5) as in the "Müller" stage. Therefore the transparency of the external epithelium of the larva increases in larvae in this stage of development. This fact is only observed in fixed animals. The ciliated ventral band shows the beginning of the formation of the lateral lobe. The same features can be observed in the European *B. clavigerus* and in *tornaria mourei* in the "Metschnikoff" stage of development. The ciliated bands (CB) when coloured with eosin show rose coloured fibrillae (MF) which might be of muscular nature in *tornaria chierchiae I* (Fig. 24, Pl. 5).

*Internal morphology* — A double wall of large, strongly ciliated cells, with very little affinity for the staining materials, is formed between the last portion of the gut and the stomach. The center of this diaphragm-like partition is pierced by the pyloric opening. The cells which form the walls of the anus opening are small, cubical and of ectodermal nature. In *tornaria nordestina* the final gut differs from the funnel shaped one of *tornaria mourei*, because it assumes the form of a long, inflated cone. The gut of *tornaria chierchiae I* has a very narrow lumen in comparison with *tornaria mourei*, *nordestina* and *dubia*. The cells which form the walls of the oesophagus and the ciliated band of the stomach show large secretion globules at their basis. The oral funnel is very long because the mouth is situated at a very high level. The nuclei of the gut cells, as well as of the cells of the oral area, are much smaller in *tornaria chierchiae I* than in the other *tornariae*.

The proboscis coelom is larger in this stage, but there is no sign of the mesocoel or the metacoel in the young "Metschnikoff" stage of the *tornariae* here studied. In *tornaria mourei* the same origin of the coeloma is observed as in *B. clavigerus* (Stiasny 1913, p. 68; 1914, p. 271). In the living animal they are not visible. The trunk coeloma and the collar coeloma of *tornaria nordestina* seem to originate from two evaginations of the wall of the middle gut at different levels (Fig. 25, Pl. 5) for the

same aspects were found as those pictured by Morgan (1891, p. 413-414). More living and fixed tornariae *nordestina* must be studied to solve this problem. The tornaria *dubia* shows a protocoel in the "Metschnikoff" stage which is different from that of tornaria *chierchiae* I, although in both the lumen is very narrow. At the end of it there is a very short coelomoduct, made of cells of the epidermal type, which communicates with the exterior by the coelomopore (Fig. 27, Pl. 6). Tornaria *weldoni* in the "Metschnikoff" stage has a short coelomoduct on the protocoel also, but it is longer than in tornaria *nordestina*. The protocoel is very long (Fig. 15, Pl. 3). The trunk coeloma are already present. The collar coeloma seem to arise from a flat mass of larger cells situated outside the last third of the stomach. Both coeloma in tornaria *weldoni* are situated nearer to the oesophagus than in the other tornariae.

The cardiac vesicle in tornaria *mourei* originates at the same time as the collar and trunk coeloma (Fig. 26, Pl. 5). It also appears through multiplication of ectodermal cells as described by Stiasny (1914, p. 266) and thus, the non homology of the proboscis coelom and the cardiac vesicle, is again demonstrated to be true. After formation, the cardiac vesicle moves away from the epithelium into a hollow formed dorsally and posteriorly to the proboscis coelom (Fig. 29, Pl. 6). In *B. clavigerus* this does not happen until the beginning of the "Krohn" stage, (Stiasny 1914, p. 259). Otherwise, the "Metschnikoff" stage of tornaria *mourei* and of *B. clavigerus* are identical.

*Environmental conditions* — Tornariae *mourei* and *nordestina* in this stage are found in coastal waters and in shelf waters. Tornariae *weldoni*, *chierchiae* I and *dubia* are separated from samples of shelf waters and of waters belonging to the South Equatorial or to the Brazil Currents.

d) THE "KROHN" STAGE — *External morphology* — This is characterized by the presence of secondary saddles or tentacles on the ciliated bands. The epithelium found on the tentacles and secondary saddles shows many pluristratified nuclei, strongly basophil (Fig. 40, Pl. 10-FC.). The nuclei are polymorphic (PN) in the area between the ciliated bands on the tentacles of tornaria *chierchiae* I (Fig. 24, Pl. 5), in the "Krohn" stage. In

the oral area there are frequently cells with two nuclei. In this larva the prae- and post-oral fields are covered by an epithelium with many glandular cells and with muscular fibrils. *Tornaria nordestina* is more transparent than others when it has been fixed, because the external epithelium of the oral field is thinner and larger than in *tornaria mourei* or in the *tornaria* of *B. clavigerus*. The position of the future nervous dorsal cord is already visible in the form of a dorsal thickening of the epidermis (Fig. 32, Pl. 7-CN). In *tornaria dubia* it is already marked out on the dorsal side of the post-oral belt (Fig. 28, Pl. 6-CN).

*Internal morphology* — In the "Krohn" stage of *tornaria nordestina* the ventral boundary between the stomach and the oesophagus (which appears clearly in *B. clavigerus* and in *tornaria mourei* — Fig. 33, Pl. 7) is not noticeable (Fig. 34, Pl. 7). In *tornaria nordestina* the dorsal epithelium is thinner and the ventral epithelium thicker in the oesophagus. The ventral ciliated band continues well into the stomach and is longer than in *B. clavigerus* or in *tornaria mourei*. The stomach walls of *tornaria nordestina* are also thinner than those of *tornaria mourei* (compare Fig. 34 and 33, Pl. 7). The final gut is much larger than in *B. clavigerus* or in *tornaria mourei* and is cone shaped instead of funnel shaped (Fig. 12, Pl. 3). The stomach wall cells are also more frequently protruding into the lumen of this organ, either with pseudopodia or the whole cell. *Tornaria dubia*, when cross-sectioned at this stage, already shows a polygonal outline (Fig. 37, Pl. 7) and the oesophageal wall is made of cells which do not contain secretory globules and which are pseudostratified. The mouth of *tornaria weldoni* and of *setoensis* is situated in a higher position than in the other *tornariae* in this stage (Fig. 17, Pl. 3).

The protoeol at this stage has already enveloped the migrated cardiac vesicle with two leg-like projections, the future right and left coelomic pouches of the proboscis of the adult. The left communicates, by a coelomoduct with the proboscis pore. These may be observed in all the larvae studied. In *tornaria nordestina* the "muscularization" of the protoeol wall is less pronounced than in *tornaria mourei* or in *B. clavigerus* at this stage (Fig. 38, Pl. 8). The protoeol in *tornaria dubia* has two horn-like lateral projections to which fibers (Fig. 37, Pl. 8-FF)

are attached, which originate at the telotroch (Fig. 36, Pl. 8-TE). In tornaria *chierchii* I the ventral projections of the proto-coel wall are long and thin ("lateral diverticula", Morgan, 1891).

The collar and trunk coeloma are already differentiated (Fig. 33, Pl. 7). In tornaria *nordestina* they are sausage-shaped, well separated one from the other (Fig. 10, Pl. 2-CEL). In tornaria *weldoni* they have the same form initially as in tornaria *nordestina*, but soon they acquire a rectangular shape and move away from the stomach wall and up, as is shown in Figure 17 (Pl. 3). If we compare tornaria *mourei* with those of *B. clavigerus* from Naples as described by Spengel (1893, figs. 5-10, pl. 22) we find them identical. The *B. clavigerus* larvae from Trieste, described by Stiasny (1914, p. 271) do not always show the collar coelom in the "Krohn" stage.

*Behaviour* — The living tornaria *mourei* in the "Krohn" stage shows slower forward and backward movements than the younger animals. These larvae are photopositive when placed in an aquarium at this stage of development. Ritter & Davis (1904, p. 196) have shown that light has a very slight or no influence at all on tornaria *ritteri*. More experiments are necessary to prove that tornaria *mourei* does not move towards the lighted side of the aquarium because the diatomeae on which it feeds thrive there. In the sea tornariae of this stage were usually collected from 20 cm or more depth (less illuminated), not from quite superficial hauls.

Movements of contraction of the mouth were observed in tornaria *mourei*. The taking in of the food is accomplished by the lowering of the floor of the oesophagus as indicated by the arrows in Figure 30 (Pl. 6).

In the "Krohn" stage the cardiac vesicle suffers contraction waves from the wall not enveloped by the proto-coel, to the opposite end as indicated by arrows in Figure 29 (Pl. 6). Contractions were observed every 16 seconds. The apical aplate also moves frequently by contraction of the muscular band, which connects it with the proto-coel walls.

e) THE "SPENGL" STAGE — *External morphology* — The tornaria becomes less transparent, because its epithelium thickens and gets more secretory. The larva diminishes in length

and there is an involution of the secondary saddles and lobes of the ciliated band in tornaria *mourei* (Fig. 39, Pl. 8) and in *B. clavigerus* larvae. When alive, those larvae show pigment spots on the ciliated bands. In tornaria *dubia*, *weldoni* and *chierchiae I* there is also an involution of the secondary saddles and lobes and a loss of transparency, but many of these larvae captured in this stage were much larger than those typically in the "Krohn" stage. In tornaria *nordestina* it is difficult to distinguish this from the "Krohn" stage, because in this larva the circum-oral ciliated band does not form secondary lobes and tentacles, or secondary saddles. This tornaria also seems to go on growing in size after the "Krohn" stage. Up to now a characteristic "Krohn" stage of development, like the one established by Stiasny and Stiasny-Wijnhoff (1931, p. 44), has not been found in the plankton for this tornaria. It is therefore necessary to correct what is written in Björnberg (1953a, p. 101) about figures 9, 10, 11 and 12 which are young "Krohn" stages of development or "Metschnikoff" stages and not "Spengel" stages. Stiasny himself (1925, p. 435) observed a similar case when he described a larva without secondary lobes and saddles on the ciliated band in the "Krohn" stage. Morgan did so too (1891, p. 414) from a New England tornaria.

*Internal morphology* — In tornaria *mourei* and in tornaria *chierchiae I* in this stage, exactly as described for *B. clavigerus* (Stiasny 1914, p. 282 & 283), the anal area protrudes more than in the preceding stage and numerous secretory cells can be observed in the external epithelium. The same morphology is observed in this stage for tornaria *mourei* and for *B. clavigerus*. In the "Spengel" stage tornaria *dubia* (Fig. 35, Pl. 8-LW) has secretion in the form of globules only on the lateral walls of the stomach where the cells are also taller than in the ventral and dorsal regions, where they are flat. The walls of the pharynx in other tornariae thicken and dilate so as to give rise in the following stages to the branchial pouches (Fig. 38, Pl. 8-BRP). The gastric cells of tornaria *mourei* protrude into the lumen of the stomach and their nuclei are more basophil than in the cells of the walls of the final gut and of the pylorus. In tornaria *nordestina* the branchial pouches are already formed in this stage (Fig. 41, Pl. 9), much earlier, than in *B. clavigerus*.

The coeloma grow very large in the "Spengel" stage. The apical wall of the protocoel (Fig. 38, Pl. 8) loses its transparency, because of the increase in muscular fibers in all directions. The splanchnopleura is histologically differentiated from the somatopleura, which is very muscular in the meso- and metacoel. At the height of the trunk coelom in *tornaria nordestina* the gastric epithelium is made of cubic cells instead of cylindrical cells as in the remaining wall of the stomach (Fig. 42, Pl. 10). This may favour the hypothesis that the mesocoel originates from a cellular delamination of the gastric wall in *tornaria nordestina*. In *tornaria weldoni* the proboscis coelom is horse-shoe shaped when seen laterally in a fixed *tornaria* and it shows a characteristic ring of muscular fibers (Fig. 31, Pl. 6) and a very short coelomoduct. The proboscis coelom in *tornaria dubia* is larger than in *B. clavigerus* and there is no sign of evagination in the wall of the pharynx so as to form the branchial pouches.

*Environmental conditions* — *Tornariae* in this stage and in the preceding one are also found at a great distance from the coast. *Tornariae chierchiae I*, *dubia* and *weldoni* in this stage were collected from waters of the Brazil or of the South Equatorial Currents.

f) THE "AGASSIZ" STAGE — *Morphology* — The larva is now nearly opaque because the external epithelium has thickened considerably and is much differentiated (Fig. 46, Pl. 11). There are only indications in *tornaria mourei* of the former circum-oral ciliated bands in the form of pigment cells (Fig. 47, Pl. 11-PI). Externally this larva shows a conspicuous yellow band, near to the constriction which separates the proboscis from the trunk. The apical plate is provided with eyes. These are deeply situated in the epithelium. This is already pseudostratified (Fig. 44, Pl. 10-EP), as may be observed by the number of strata of nuclei. A simple epithelium of small transparent cells forms the dorsal and anal field. The telotroch is still composed of very tall cells in one strata, with very long cilia (Fig. 43, Pl. 10-TE). In the region of the ciliated bands numerous smaller nuclei, with great affinity for colouring material and placed very closely together, may still be observed. The oral field diminishes in extension and disappears at the beginning of the metamorphosis. Spengel

(1893, p. 388 and 389) observed the same phenomenon in the European larvae of *B. clavigerus*. During the transition from "Spengel" to the "Agassiz" stage a double protuberance of the pharynx gives rise to the first pair of branchial pouches (Fig. 38, Pl. 8-BRP). In *tornaria nordestina* in the "Agassiz" stage the beginning of the formation of 4 pairs of branchial pouches can be seen (Fig. 41, Pl. 9).

The stomach epithelium is very thickened. The cell nuclei, have finished their migration towards the basal part of the cells (Fig. 44, Pl. 10-EPI). There is secretion in the form of small globules in the distal parts of some cells. In the basal part of all the cells there is a differentiation of the cytoplasm, which gives rise to secretory granules during the metamorphosis.

Comparing the sections of the proboscis coelom and cardiac vesicle with those of Stiasny (1914), one comes to the conclusion that the development of the proboscis organs of *tornaria mourei* is the same as those of *B. clavigerus* in Europe. The same is true of the formation of the proboscis diverticulum which appears as an evagination of the pharynx wall (Fig. 45, Pl. 10-DIV).

The trunk and collar muscles originate from the somatopleura of the meta- and mesocoel (Fig. 44, Pl. 10-OM). The thin splanchnopleura adheres to the surfaces of the final gut. The *tornaria nordestina* in this stage reveals a tardy development of the collar and trunk coeloma, which are still very small if compared with the coeloma of the other larvae in this stage (Fig. 48, Pl. 11).

*Behaviour* — At this stage the animal still swims about actively, but, it passes a long time at the bottom of the aquarium with the mouth turned downwards. It is perhaps at this stage that the change in the diet of the animals takes place. From living algae or plankton (a copepod was also found inside the stomach of a larva), it begins eating dead "débris" from the bottom. Some animals accumulate sand round their mouth region at this stage.

g) THE METAMORPHOSIS — *External morphology* — In the following stage of development (Fig. 49, Pl. 11) the *mourei* larva diminishes in size and changes its external form. It loses the *tornaria* features and becomes barrel-shaped with two constrict-

tions (Fig. 50, Pl. 11). The proboscis acquires the form which it will have in the adult and the boundary between the collar and the trunk appears (Fig. 50, Pl. 11). Metamorphosis is rather quick, when compared with the slow development of the tornaria. In 24 hours the tornaria passes from the "Agassiz" stage to the stage of initial metamorphosis. In 72 hours time it passes from the stage of one pair of branchial pouches to the stage of three pairs of branchial pouches. Branchial slits can not be observed in the living larvae. Figures 49 to 53 (Pl. 11) represent the living animal in the initial stages of metamorphosis. The first animal (Fig. 49, Pl. 11) has the branchial pouches only outlined, but, the neural groove, which results from the dorsal, median, longitudinal invagination is very conspicuous. In the following stage (Fig. 50, Pl. 11) the separation between the collar and the trunk appear. The first pair of branchial pouches, originally kidney shaped, subsequently assume the form of a horse-shoe (Fig. 50, Pl. 11). The dorsal nervous cord (Fig. 54, Pl. 12) is formed by the fusion of the lips of the neural groove (Fig. 55, Pl. 12). In the following stage there are already two pairs of branchial pouches, which may be seen under the collar (Fig. 51, Pl. 11). There are cilia only on the telotroch. The larva during metamorphosis loses its transparency and turns yellow in its posterior portion and whitish-light-ocre in its anterior region.

*Internal morphology* — The walls of the median hind gut thicken exceedingly and are folded in a very complicated manner. In transverse sections these organs show cells containing a lot of mucus and granular secretions, all on the side of the cell turned towards the lumen of the digestive tube (Fig. 43, Pl. 10). This partly explains the loss in transparency of the larva. The pharynx evaginations are very much accentuated. They give rise to the branchial pouches (Fig. 58, Pl. 12-BRP). Consequently there is a differentiation of the epithelium of the pharynx into epithelium of the branchial pouches and glandular epithelium. The first is an epithelium of flat cubic cells; the second covers the digestive part of the pharynx. When the branchial pouch becomes U-shaped (Fig. 45, Pl. 10) its epithelium becomes very transparent on the outer side of the pouch. At the same time there is an invagination of the epidermis from the outer side towards the pouch formed in the inner side. These formations,

when they fuse with each other, give rise to the collar pore (Fig. 59, Pl. 13-PBR). The first branchial pore opens into the collar pore. The most advanced larva obtained has three pairs of functional branchial pouches, and one rudimentary pair (Fig. 56, Pl. 12). In the first pair a noticeable thickening is observable, from which the branchial skeleton develops (Fig. 58, Pl. 12-SK).

Anteriorly the pharynx gives rise to the proboscis diverticulum (or stomochord) which is easily observed in the animal in advanced metamorphosis (Fig. 60, Pl. 13). In the adult the diverticulum is turned towards the dorsal side of the proboscis. It may be the pressure of the strong anterior proboscis muscles, which does not permit the development of the diverticulum forwards, whereas the pressure of the ground ventrally would turn it dorsally. Spengel (1893, p. 442) explains the formation of the ventral proboscis vessel suggesting that the proboscis diverticulum, on growing forwards, carries with it part of the coelomic wall and thus, doubles it up. The blood runs inside the doubled up wall, which is usually called the ventral septum of the proboscis. The continuation of the ventral vessel in the collar and the dorsal vessel of the same appear through the growth of the two lateral collar coeloma. Thus the coelomic walls almost touch each other dorsally and ventrally and the blood runs in the space left between them.

The glomerular vessels appear on the wall of the proboscis vesicle, originated from the cells of the coelomic wall (Fig. 60, Pl. 13). It seems that the cells situated on the anterior surface of the proboscis diverticulum also take part in the formation of these central organs (Fig. 60, Pl. 13). In advanced stages of metamorphosis there is a thickening of the basal membrane of connective tissue under the proboscis diverticulum. It is the beginning of the future skeleton (Fig. 60, Pl. 13-SK). The same has been observed by Spengel in the development of *B. clavigerus*.

Two metamorphosis stages of *tornaria dubia* were sent to me from Algiers. Comparing them with the corresponding stages of *tornaria mourei*, the following characteristics were noted: 1) large secretory cells in the external epithelium (Fig. 61, Pl. 13); 2) the nuclei of the cells are larger; 3) the coelomic walls of the proboscis, collar and trunk are less muscular; 4) the eye spots are no more visible at the beginning of the meta-

morphosis; 5) the branchial pouches are less developed; 6) there are numerous glandular cells on the wall of the digestive tube, with much mucus and many secretion granules (Fig. 62, Pl. 13-EPI).

*Behaviour* — Finally (Fig. 53, Pl. 11) the collar is well separated from the trunk and probably branchial slits already exist. The animal at this time of its development already burrows in the sand at the bottom of the aquarium. It behaves like a little worm, crawling on its ventral surface. The larva up to then showed active swimming movements and buried itself in the mud only temporarily. Now it remains buried in one place with just the proboscis protruding above the sand. This behaviour is typical of *Saccoglossus horsti* (Burdon-Jones 1952, p. 577). It lives on dead algae and "débris", which fall to the bottom of the aquarium. An interval of time in which the tornaria did not ingest food (as proposed by Ritter and Davis 1904, p. 181) was not observed.

*Environmental conditions* — All the planktonic larval stages of *B. clavigerus* and the initial stages of metamorphosis may occur in one haul, as was observed by Morgan for the New England tornaria (1891, p. 408). Here also numerous small crustaceans (copepods chiefly) are present in the catches where a lot of tornariae are captured. The associated fauna consisted of about 76% of copepods of which *Paracalanus aculeatus* Giesbrecht, *P. parvus* (Claus), *Acartia lilljeborghii* Giesbrecht, *Eucalanus subcrassus* Giesbrecht, *Centropages furcatus* Kröyer, *Oithona* sp., *Ctenocalanus vanus* Giesbrecht, *Temora stylifera* (Dana), *Corycaeus giesbrechti* F. Dahl, *C. gracilis* Dana, *Microsetella* sp. and *Oncaea* sp. were the most common. Other crustacea present were *Penilia avirostris* Dana and *Lucifer* sp. which amounted to about 8% of the total catch. There were also Copelata (3% approximately of the total number of Metazoa); larvae of Polychaeta, Chaetognatha (*Sagitta enflata* Grassi and *S. bipunctata* Quoy & Gaim.), *Doliolum denticulatum* Quoy & Gaim., *Thalia democratica* Forskal, *Liriope tetraphylla* (Cham. & Eysen.), Siphonophora (Fam. Diphyidae Eschsch.), eggs and fish larvae, *Ceratium tripos* (Müller), *C. massilense* (Gourret), *C. fusus* (Ehr.) and numerous diatoms (chiefly *Cos-*

*cinodiscus* Ehr., *Rhizosolenia* Ehr., and *Actinocyclus* Ehr.). The tornariae appeared in a percentage of 0.4% more or less in the samples where they were very frequent. Table 4 gives a few ratios of the number of tornaria per settling volume of plankton per litre of sea water sampled.

TABLE 4  
RATIOS OF TORNARIAE, PER VOLUME OF PLANKTON, PER QUANTITY OF SEA WATER

Sample Number	Number of tornariae	Settling volume of tornariae	Settling volume of plankton	Number of litres of sea water sampled
M-421	12	0.2 cc /	10 cc /	12,000
M-450	6	0.3 cc /	15 cc /	42,000
M-519	7	0.8 cc /	22 cc /	18,000
M-522	15	0.5 cc /	15 cc /	40,000
M-524	6	0.1 cc /	40 cc /	50,000
M-531	7	0.7 cc /	27 cc /	50,000
M-537	51	0.9 cc /	25 cc /	36,000
M-538	11	0.3 cc /	23 cc /	40,000
E-2	261	0.1 cc /	6 cc /	7,948

### 3 — DISTRIBUTION OF THE TORNARIAE, THEIR CORRELATION WITH THE ADULT DISTRIBUTION AND PROBABLE IDENTITY

a) TORNARIAE *mourei* AND *liliana*e — Maps number 1 and 3 give the occurrence of *B. clavigerus* (adult) and of tornariae *mourei* and *liliana*e. Apart from minor details, the development of tornaria *liliana*e and of tornaria *mourei* agree almost absolutely with the development and the various stages of the tornaria of *B. clavigerus*. The little details in which they differ in relation to the European tornariae are possibly caused by ecological differences between the Brazilian and the Mediterranean waters. The animals which develop in higher temperatures are generally smaller and get to the adult stage more rapidly. The differences noted between tornaria *mourei* and *liliana*e (Björnberg 1953a, p. 91) were fixation artefacts. Both are

tornariae of *B. clavigerus*. Similarly tornaria *tergestina* (Stiasny 1927, p. 37-45), which differs from the larva of *B. clavigerus* merely in the size and the degree of inflated stomach, is also an ecophenotype. The positions of the samples from which the larvae were obtained are indicated in the addenda list.

Nearly all the larvae used in this study were collected in the vicinity of a beach (see Map 1), Cambriú, off Cananéia (State of São Paulo). The samples of plankton collected off this beach, or nearby, from October to the end of March, frequently contain a great quantity of larvae in all stages of development. *B. paranaensis* is the only enteropneust found on Cambriú beach. On nearby beaches of the Cananéia region (Map 1), the same species is found. No other enteropneust occurs on those beaches and no other larvae in the neighbouring waters, so it appears that *B. paranaensis* and *B. clavigerus* are conspecific. The same larva also occurs off Santos, Ubatuba, Santa Catarina and Paraná, all places from which adults have been described under several names (*B. nonatoi*, *B. catharinensis*, *B. paranaicola*).

b) TORNARIAE *chierchiae* I — Map 2 gives the distribution of the tornariae *chierchiae* I, *morgani* and *grenacheri* and of *P. flava* and *P. bahamensis*. The addenda list gives the occurrence of the Brazilian larvae.

Tornariae *chierchiae* I and *grenacheri* are found in the Pacific, Indian and Atlantic Oceans and in the Red Sea. Tornaria *morgani* is recorded off Indonesia, Japan, West Indies, Cabo Verde, Cabo S. Roque, between Georgetown and Pará (Stiasny 1934, p. 20). Intermediate forms between those of tornaria *morgani* and *chierchiae* I or *grenacheri* have been found off Fernando de Noronha Is. and off the Brazilian coast (from 30° 25,0' to 05° 44,3' N).

Their characters are intermediate between those of larvae considered as tornariae of *Ptychodera flava* and those of larvae considered as tornariae of *Ptychodera bahamensis*. Spengel (1893, p. 379) was the first to examine the tornariae of this type (tornariae *grenacheri*, *morgani* and *chierchiae* I) from the Atlantic and the Pacific, and considered them as identical. Stiasny & Stiasny-Wijnhoff (1931, p. 111) considered tornaria

*morgani* (the larva of *P. bahamensis*) as being different from *tornaria chierchiae I* (the larva considered as belonging to *P. flava*). It seems though that Stiasny & Stiasny-Wijnhoff only studied fixed animals and the drawings of Spengel and of Morgan. The Saba (Leeward Is.) *tornariae* drawn by Stiasny (1921, fig. 7-12), were badly preserved (Stiasny & Stiasny-Wijnhoff 1931, p. 141). Among the Pacific larvae some occur which are similar to those which live in the Atlantic, as for instance, *tornaria morgani* (Stiasny 1929, p. 86), *tornaria susakiensis* (Tokio-ka 1937, p. 342), *tornaria sp. valde affinis morgani* (Stiasny 1935, p. 1032), *tornaria snelliusi* (Stiasny 1935, p. 1029).

*Tornaria susakiensis* looks exactly like a drawing of *tornaria morgani*, generally found in the Atlantic. *Tornaria snelliusi* is also very much like *tornaria chierchiae I*. The only difference between them is the absence of the dorsal inferior lobe in *tornaria snelliusi*. But this character, to which Stiasny gives so much importance, is very variable as is easily proved by the drawing made of several dorsal lobes of *tornaria chierchiae I* (Fig. 7, Pl. 2). The form of the lobe varies with the type of fixative used, the moment of fixation, the duration of the fixation. *P. flava* and *P. bahamensis* are anatomically indistinguishable, except for two characters, viz. size smaller in *P. flava*) and thickness of the limiting membrane in the collar coelomoducts (thicker in *P. bahamensis*). This and the known variability of *P. flava* coupled with the remarkable similarity of the larvae greatly enhances the probability that *P. flava* and *P. bahamensis* are conspecific.

c) *TORNARIA weldoni* — Map 4 shows the distribution of *tornaria weldoni* and similar *tornariae* (*cairnsiensis*, *setoensis*, *ritteri* and *krohni*) and of the adults (*B. carnosus*, *B. biminiensis*, *B. jamaicensis* and *B. gigas*).

A larva called *weldoni* occurs in the Atlantic in the places where *B. gigas*, *B. biminiensis* and *B. jamaicensis* live (Florianoópolis and West Indies). This larva does not belong to the adults of other species which occur in these regions and whose larvae are known. By exclusion, they may only belong to the species *B. gigas*. There are also larvae called *cairnsiensis* and *setoensis* in the Pacific, off Australia and off Japan, where *B. carnosus* occurs. Both larvae are very similar to *weldoni*. They

differ only by the shape of the lateral lobe and by the distance between the coeloma of the trunk and of the collar. These are next to one another in *cairnsiensis* and separated from each other in *weldoni* during the "Krohn" stage. The *weldoni* tornaria was found also in Australia (Trewawas 1931, p. 61). Ritter & Davis described tornariae with the external aspect of *cairnsiensis* and *weldoni*, which they consider as belonging to only one species. They are the *ritteri* tornariae. As they were studied alive (Ritter & Davis 1904, p. 171), the descriptions given merit higher consideration than those of other authors who studied fixed material, the shape of which may have altered considerably during storage.

Tornaria *weldoni* has 6 to 4 secondary saddles in the "Krohn" stage (Stiasny & Stiasny-Wijnhoff 1931, p. 138), tornaria *setoensis* has 8 to 10 tentacles (Stiasny 1939, p. 75), or 5 to 12 tentacles (Trewawas 1931, p. 55) and tornaria *cairnsiensis* 4 to 8 tentacles (Trewawas 1931, p. 57). Intermediate forms and larger specimens than these, with more tentacles are found off the Brazilian coast (see table 3). Because of the great variability of the larval characters (shape, number of tentacles, size) it is more prudent to consider the tornariae *cairnsiensis*, *weldoni*, *setoensis* and *ritteri* (all very similar to each other) as belonging to one species, until their biological cycles have been determined. Tornaria *krohni* (Stiasny & Stiasny-Wijnhoff 1931, p. 65) from the Mediterranean also seems to be an ecophenotype of this species.

Spengel (1893, p. 126) described a species of *Balanoglossus* (*B. apertus*) from Rio de Janeiro, which has not been found again. Tornaria *weldoni* probably does not belong to it, for this species has not been found in the West Indies, in whose waters the tornaria *weldoni* is very frequent.

The tornariae *weldoni*, *cairnsiensis*, *setoensis* and *ritteri* probably belong to *B. gigas*.

d) *TORNARIA dubia* occurs in the Mediterranean and South Atlantic (off Santa Catarina, off Paraná, off Espírito Santo and Trindade Is., off Alagoas and off Piauí). The positions of the occurrences of the larva can be found in the addenda lists Map 5. This larva probably belongs to the species *Glandiceps*

*talaboti*. Thus the existence of this species should be expected on our continental shelf.

e) *TORNARIA nordestina* — Map 6 gives the distribution of this larva. The similarity between this larva and *tornaria hubbardi* has been recorded (Björnberg 1953a, p. 87-88 and 92-93). Stiasny & Stiasny-Wijnhoff (1931, p. 190-191) suggested that it belonged to the genus *Schizocardium*. This possibility is not excluded.

The larger quantity of specimens, better fixed (in Bouin and Pampel) permitted a better study of these larvae, since their external shape was not so very altered by their long storage in formalin at 4%. These larvae then showed a great resemblance to the *tornariae* described by Morgan (1891) from the northern Atlantic coast of the United States and to those described by Stiasny (1925) from Heligoland. The early development of the branchial pouches, the origin and the aspect of the coeloma approximate these larvae to the one described by Morgan (1891, fig. 6, pl. 24). It is not identical to this larva though, because it has a lateral lobe. This is very large and not deep. There are also characteristic swellings of the epithelium near the ciliated bands and the anus, which were not observed in the northern *tornaria* by Morgan. As the lateral lobe is very shallow in the recently fixed larvae, it is possible that it does not exist at all in the living specimens, which were not observed. The same may be said of the swellings of the epithelium, which are not always visible in the fixed material. The *tornaria* of Heligoland has very deep lateral lobes and a size more like that of the Brazilian larvae. The coeloma are of a different aspect, according to the description of the same by Stiasny & Stiasny-Wijnhoff (1931, p. 158, 159). The branchial pouches in the Heligoland larva only appear just before metamorphosis.

*Glossobalanus crozieri* occurs in the Bermudas and in São Sebastião. The *tornaria* of New England could be the larva of this animal, and in this case there is a probability that *tornaria nordestina* also belongs to this species. Spengel (1893, p. 90) recorded *Glossobalanus minutus* from Rio de Janeiro, but hitherto it has not been found again. It might also be the adult

of the tornaria discussed here, but this is not very probable because tornaria *nordestina* has not been found in other places where *G. minutus* is also found.

#### IV — THE ADULTS

##### 1 — ANATOMICAL VARIATIONS IN THE VARIOUS ADULTS AND THEIR SYSTEMATIC IMPLICATIONS

a) GENERAL REMARKS — *Balanoglossus paranaicola*, *B. paranaensis* (Björnberg, 1952), *B. eufrosinoi*, *B. nonatoi*, and *B. catharinensis* (Sawaya & Forneris, 1953) all very much like *B. clavigerus*, were found in the São Paulo, Paraná and Santa Catarina beaches. The small anatomical differences between these animals and *B. clavigerus* are the general thickness of the circular muscle sheath in the proboscis, the size of the muscular dorso-ventral plate, the aspect and lumen of the proboscis diverticulum, the position of the protocoel pore, the number of vessels in the glomerulus, the presence of blood in the cardiac vesicle, the extension of the cardiac vesicle, the form of the skeletons and the quantity of skeletal material, the length of the dorsal mesentery, the number of nervous dorsal roots in the collar, the size and presence of the blind caeca on the branchial pouches, the number of synapticula, the difference in aspect of the gonads.

b) EXTERNAL FEATURES — The variation in size of the adults of the European *B. clavigerus* is well known. Thus, *B. robinii*, described as a giant species, was considered by Spengel (1893, p. 137) as conspecific with *B. clavigerus*. In Brazil, *B. paranaicola* is also a very large animal when compared to *B. paranaensis* and to *B. eufrosinoi*. It occurs on the Ilha do Mél and in Ubatuba (see map 3). Its colours are also more vivid than those of the animals of other localities. The size of the animals from the same beach also varies. As the caudal and hepatic regions are frequently lost, only the lengths of the proboscis, the collar and the branchio-genital regions of the living animals were added and compared. The sizes obtained were:

from 7,2 to 19 cm in the Santos animals; from 6,4 to 25,4 cm in the Ilha do Mél animals; from 4,7 to 9,7 cm in the Caiobá animals. The hepatic region is approximately two thirds of the added lengths of the proboscis, the collar and the branchio-genital regions. The caudal region is twice as long as the hepatic region. The total length of an animal from the Ilha do Mél may be as long as 70 cm when alive. An animal from Caiobá in the same conditions, does not grow to 15 cm in length.

The width of the genital wings is also variable. The Ilha do Mél animals have genital wings with almost double the width of those from Caiobá and from Santos.

The measurements obtained by Spengel (1893, p. 138-139) from the European animals (*B. clavigerus* and *B. robinii*) and those obtained by Sawaya and Forneris (1953, p. 8, 9, 18, 19) from the Brazilian animals (*B. eufrosinoi*, *B. nonatoii* and *B. catharinensis*), do not differ from the measurements just mentioned (see table 5). The great distension capacity of these animals is also known.

TABLE 5

LENGTH OF THE SEVERAL PARTS OF *B. CLAVIGERUS*, AS MEASURED BY SPENDEL, SAWAYA & FORNERIS AND BJÖRNBERG (in CM)

Region	European animals (Spengel)	Brazilian animals (Sawaya & Forneris)	Brazilian animals (Björnberg)
Proboscis	alive	0,5 — 1,4	0,3— 1,5
	fixed	0,60—0,70	0,2— 0,7
Collar	alive	0,5 — 1,1	0,5— 1,0
	fixed	0,45—0,85	0,5— 0,7
Branchial	alive	4,0 — 4,5	1,0— 7,0
	fixed	2,0 —3,00	0,8— 5,5
Genital	alive	10,00	2,0—15,5
	fixed	5,0 —6,0 or more	4,00—12,20
Hepatic	alive	6,5 — 9,1	1,5—11,3
	fixed	up to 7,00	8,0 — 8,4
Caudal	alive	6,0	3,0—15,5
	fixed	—	10,0 2,0— 4,0 incomplete

The measurements of *Balanoglossus gigas* from São Sebastião, those presented by Maser for *B. carnosus* (1913, p. 390) and those of Spengel (1893, p. 160) for *B. gigas* do not differ either.

c) ANATOMICAL VARIATIONS OF *Balanoglossus clavigerus* DELLE CHIAJE — *Proboscis* — The epidermis of the proboscis is the same in the various animals collected here (*B. nonatoi*, *B. paranaensis*, *B. paranaicola*, *B. catharinensis*, *B. eufrosinoi*) and in *B. clavigerus* from Europe.

The muscular sheath is thicker than the nervous sub-epithelial layer (in the most anterior part of the proboscis) or it is a fifth of the thickness of the same (in the region of the proboscis neck) in the 21 Brazilian specimens examined from the Paraná and São Paulo beaches.

The width of the circular muscular layer in cross-sections depends not only on the fixatives used but also on the state of contraction of the animal, at the moment of fixation. In the European animals the circular muscles show a thickening near the proboscis neck (Spengel 1893, figs. 5 and 9 *rmb*), which originates a sphincter. This has not been found in any of the Brazilian animals. The longitudinal muscular sheath may be more developed in animals like those from Ilha do Méil, which live in more compact sand and less developed in those from Caiobá. The dorso-ventral muscular plate is less developed ventrally or not observable in all the Brazilian animals hitherto described. Dorsally, it is more developed, as in the European animals (Spengel 1893, p. 142). It occurs from the anterior region to the central organs of the proboscis (before the diverticulum of the same up to its median region or its inferior third).

The proboscis diverticulum is more or less straight in the larva (Fig. 59, Pl. 13) and in the adult its tip is strongly curved dorsally. The lumen may be continuous (Fig. 64, Pl. 14), regularly interrupted or only partially interrupted in animals from the same locality (Fig. 63, Pl. 14-LDIV). In the young Brazilian and in the European animals it shows a continuous lumen (Spengel 1893, p. 143). At the basis of the proboscis the lu-

men dilates, forming two ventro-lateral pouches, posteriorly separated by the skeleton of the proboscis.

The proboscis coelom, dorsally subdivided by the cardiac vesicle into two lateral pouches, is ventrally divided by a septum which is initially incomplete. The ventral vessel is situated in this septum. The ventral septum finishes where the coelomatic ventral pouch begins, the same as in the European *B. clavigerus*. The two coelomatic dorso-lateral ramifications of the protocoeel reach the neck of the proboscis and there the left coelomatic pouch communicates with the exterior by a median or left pore. The right coelomatic pouch does not open on the exterior.

The proboscis skeleton varies in the greater or smaller quantity of chondroid tissue and therefore in compactness. The skeleton of the animals from Caiobá and Ilha do MéI, have numerous cavities full of pigment (melanin?) (Fig. 65-CSK, Pl. 14) in the older animals. In the younger ones there is nothing of the kind. The keel may be more or less rounded, the superior plate may be larger or smaller and the skeleton wings or lateral expansions may be present or not, according to more or less skeletal tissue present (Fig. 65, Pl. 14). One skeleton only, of the many examined, was quite different from the others, perhaps resulting from a regeneration, or from abnormal development. The extent of the malformation can be observed if the Figure 66 (Pl. 14-SK) from a cross-section of the collar of the abnormal animal is compared with a cross-section of the same region taken from a normal animal (Fig. 67, Pl. 14).

*Collar* — The oblique muscles are different in the dorsal and on the ventral side, the five epithelial regions, the longitudinal muscles, the annular blood vessel are characteristics which present no divergence in the several European or in the Brazilian animals mentioned at the beginning of this chapter. The variable characters of the collar in the same animals are the length of the dorsal mesentery, always shorter than the ventral (it begins after the third nervous root, in the European animals, and in the Brazilian it may also appear after the second nervous root); the longitudinal length of the perihæmal cavities (which do not reach the proboscis pore), the presence or absence of the medullar posterior canal and of the neuropore, as well as the presence or absence of the anterior epidermic pouch and neuro-

pore, belonging to the medulla of the collar. The number of nervous dorsal roots from the medulla may also vary from one to two or to four (Fig. 68, Pl. 15).

*Trunk* — The branchial pouches are numerous. They may or may not show blind branchial caeca in the Brazilian animals (Fig. 69-BS, Pl. 15). These caeca are small in the Brazilian animals and very large in the European ones. The synaptacula may also vary in number from 13 to 30 in the same skeletal basket. They are more numerous in the median region than at the beginning or at the end of the branchial basket. The post-branchial canal (Fig. 71, Pl. 15) appears in the older animals and may or not present a blind caecum (Fig. 70, Pl. 15).

All these observations correct what was wrongly ascribed to *B. paranaensis* in other papers (Björnberg 1953, p. 144-145 and 151).

The different forms assumed by the ventral pharynx vary according to the fixative used.

The gonads are exactly as those described by Spengel (1893, p. 153, 154) for *B. clavigerus*. The variation shown by the gonads in Brazilian animals are usually the result of differences in age. The lateral septa, the dorsal and ventral mesenteries show but little variations in their extension and size. No secondary pores were observed. No differences were observed between the hepatic and caudal regions of the Brazilian and of the European animals.

In conclusion, *B. paranaensis*, *B. paranaicola*, *B. catharinensis*, *B. eufrosinoi* and *B. nonatoi* are conspecific with *B. clavigerus*.

d) SPECIFIC VARIATIONS OF *Balanoglossus gigas* SPENGLER — During a study of the function of the hepatic pouches of *Balanoglossus gigas* (Björnberg, 1951), the great variability of this species was noted.

*Proboscis* — The cross-sections of the proboscis show a great similarity to those made by Maser on *B. carnosus* (Maser, 1913). The glomerulus is very large, enveloping the cardiac

vesicle completely (Fig. 73, Pl. 16-GL), the splanchnotheca is very thin, the cardiac vesicle (*H*), is very large (Fig. 72, Pl. 16). The proboscis diverticulum has two ventral pouches and two dorsal pouches (Figs. 74-76, Pl. 16-DC, VC), which are generally fused. The skeleton is relatively strong (Fig. 77, Pl. 16). It is nearly identical with that of *B. carnosus* and that of *B. biminiensis*, described by Willey (1899, p. 289), also with that of *B. gigas*, described by Spengel (1893, p. 159) if it is taken into consideration that this author cross-sectioned the animal in a slightly oblique direction when compared to Willey's or to Maser's sections (Fig. 81, Pl. 17). The ventral coelomatic pouch in the examined animals is also enveloped by skeletal tissue at the posterior region (Fig. 78, Pl. 17-VCC). From the anterior region of the skeleton two horns protrude (Fig. 75, Pl. 16-SK), similar to those observed in animals described as *B. carnosus*, *B. biminiensis* and *B. jamaicensis*. In *B. biminiensis* by Van der Horst (1929, p. 190) the skeleton shows a different aspect from that described by Willey (1899, p. 290). It is thus, a species the chief character of which seems to be the variation in the form of the skeleton. The terminal vesicle of the dorsal coelomic pore of the proboscis has a blind pouch, subdivided into two, a smaller one on the right and one on the left (Fig. 76, Pl. 16-BP). One of the specimens examined had one pore as in *B. carnosus*; the other, had two as in *B. jamaicensis*. Both characters are found in *B. biminiensis*.

*Collar* — There is an anterior vestibular cavity (an epidermic pouch) anterior to the medulla of the collar. There are two very thick and long nervous roots.

*Trunk* — The number of synaptacula is from 18 to 30 (Fig. 80, Pl. 17-SY) the same as in *B. gigas*, *B. carnosus* and *B. biminiensis*. The branchial pouches are provided with long blind sacs (Fig. 80, Pl. 17-BS), characteristic of the other above mentioned species. The caudal region also presents a pygochord. The genital region (Fig. 79, Pl. 17) and the hepatic regions are exactly like those described in *B. gigas* and *B. carnosus*. No anatomical differences were noted which might permit a separation of these animals into four species.

e) NOTES ON *Glossobalanus crozieri* V. d. Horst — From the three species studied this was the one which showed the least divergence from the original description by v. d. Horst in 1924 (Horst 1939, p. 696). The longitudinal pleats in the ventral dilation of the collar pore were not observed.

## 2 — CLASSIFICATION OF GENERA AND SPECIES

Owing to the anatomical variation of the adults and of their larvae and considering the similarity of the specific characters just studied it seems advisable to classify the genera and the species found in Brazil as follows:

Fam. *PTYCHODERIDAE* Spengel, 1893

Genus *BALANOGLOSSUS* Delle Chiaje, 1829

a) *BALANOGLOSSUS CLAVIGERUS* Delle Chiaje, 1829

*Ptychodera clavigera* Spengel 1893,

*Balanoglossus clavigerus* v. d. Horst 1939.

*B. paranaensis* Björnberg 1952.

*B. paranaicola* Björnberg 1952.

*B. eufrosinoi* Sawaya & Forneris 1953.

*B. nonatoi* Sawaya & Forneris 1953.

*B. catharinensis* Sawaya & Forneris 1953.

DIAGNOSIS — To Spengel's (1893, p. 137) and to Van der Horst's (1939, p. 704) diagnosis the following may be added:

*Mode of life* — The worm builds tubular galleries of 0,5 cm in diameter by digging in the fine sand of the beaches reached by the waves from the open sea. The gallery which has the shape of an U letter goes up to 20 or 30 cm in depth approximately, with lateral ramifications.

*Size and external aspect* — Variable. The limits of variation are registered on Table 5. The genital wings may show 2 to 6 mm in width.

*Internal anatomy* — Variable thickness of the circular muscular layer. The proboscis diverticulum is more or less curved, and its lumen may be continuous or not. The splanchnotheca has a variable width. The glomerulus also varies in size and its glomerulus vessels are more or less ramified and in larger or smaller number. The cardiac vesicle varies in width and the proboscis skeleton may contain more or less skeletal substance (Fig. 63, Pl. 14). In the collar there are one to four nervous roots. The neuroporus, the anterior epidermic pouch and the posterior canal of the medulla may be present or not. In the genital region there may or there may not be a postbranchial canal according to the age of the animal. The dorsal glomerulus is only observed in young animals.

*Larva* — *Tornariae mülleri* (Spengel), *krohni* (Spengel), *tergestina* (Stiasny), *mourei* and *liliana* (Björnberg). The development as described by Stiasny (1913, 1914) and by Spengel (1893). The larva, alive or fixed, shows variation of the external form, specially in the "Krohn" stage, in which it may vary from 0,40 to 1,50 mm, when fixed, and from 1,00 to more than 2,00 mm, when alive. The form of the digestive tube may vary also (cylindrical or spherical) and finally the time at which the coeloma appear (end of the "Metschnikoff" stage or beginning of the "Krohn" stage).

DISCUSSION — The great variability of the species, as has been established in the preceding chapter, is coincident with the large distribution of the same on the Brazilian coast, from the Rio Grande do Sul up to the Amazon. The only character not observed in the Brazilian specimens and found in the European ones is the muscular sphincter at the basis of the proboscis, but it was verified that the thickness of the proboscis musculature varies also. Therefore it does not seem right to consider the Brazilian animals as a subspecies or a species different from *B. clavigerus* in Europe, until all the animals of the Brazilian beaches and those of the European ones are properly studied. In consequence *B. paranaensis*, *B. paranaicola*, *B. eufrosinoi*, *B. natoi*, *B. catharinensis* and *B. clavigerus* are considered conspecific.

The adults spawn at the end of August, so the larvae appear in the plankton in our waters during September, or at the earliest

in August. After the end of April, the following year, they are rare in the plankton samples. The species may live in places near the mouths of rivers (Amazon, Paranaguá Bay, Santos and São Luiz beaches, etc.) or in places with great daily variations of salinity. In these there are a lot of diatoms in the plankton. Adults which may suffer great variations of salinity give their larvae very favourable conditions of nutrition.

OCCURRENCE — Adults — Rio de Janeiro, coast of São Paulo, Paraná and Santa Catarina. Larvae — In Brazilian waters from 32° 16,2' S, off Lagoa dos Patos (Rio Grande do Sul) up to 0° 50,0' N, off the mouth of the Amazon river. It has not yet been found in the region between Rio de Janeiro and Rio Grande do Norte (see Map 3).

REMAINING DISTRIBUTION — Mediterranean and coast of Brittany.

b) *BALANOGLOSSUS GIGAS* (Spengel) 1893

*Ptychodera gigas* Spengel 1893.

*Balanoglossus carnosus* Willey 1899; Maser 1913; Tre-wawas 1931; Horst 1939.

*Balanoglossus biminiensis* Willey 1899; Horst 1939.

*Balanoglossus jamaicensis* Willey 1899; Horst 1939.

*Balanoglossus gigas* Horst 1939.

DIAGNOSIS — *Mode of life* — They dig galleries in the sand of the beaches, where the sand is muddy and full of bits of shells, near the mangrove or in coral sand. Their tubular galleries measure 1 cm in diameter, they are more tortuous than those made by *B. clavigerus* and different too, for they are always full of mucus. The galleries are 30 cm deep, more or less.

*Length of the animal* — up to 2,5 m.

*External anatomy* — Proboscis nearly totally or at least partially enveloped by the collar. Collar very long with an annular groove between the first and the second of the third part of it, and a stronger yellow margin at the end of the collar. The genital wings envelop the branchial and geni-

tal regions completely. They are larger in the middle of the genital region, and come to an end before the hepatic region. The branchial and hepatic regions are exactly as they have been described by Willey and V. d. Horst for *B. carnosus*.

*Colour* — The immature animals and males are yellow and orange coloured. The females are yellow and grey to lilac coloured on the genital wings. According to Willey they may still show brown and alternating red bands, when they live in coralline regions (West Indies).

*Internal anatomy* — The circular muscles do not form a sphincter at the basis of the proboscis. The longitudinal muscles are more or less strong and show strands radially. The muscular dorso-ventral plate is well developed. The ventral septum does not reach the end of the ventral coelomatic cavities. The ventral coelomatic pouch generally protrudes into the skeleton (Fig. 78, Pl. 17), but it may also not do so. Only the coelomatic pouch on the left is in communication with the ectodermic vesicle of the coelomopore. This may be incompletely divided into two equal or unequal pouches and both may communicate with the exterior by means of one or two pores. In this case there are two ectodermal pouches, each communicating with its own pore. The proboscis diverticulum may have four blind pouches: two dorsal and two ventral, or one only lumen, by fusion of the pouches. All intermediate stages with two partially fused pouches, and three fused pouches may be found. The dorsal glomerulus is very large. The skeleton is strong or weak, formed by three parts: the superior plate, the main mass, the keel and the crura or arms of the skeleton. The plate may be more or less skeletal, and may present two anterior horns. These may be more or less ramified and penetrate more or less into the proboscis diverticulum. The crura extend backwards a very short way and then curve in a right angle towards the ventral side of the collar. The collar shows a dorsal mesentery more or less developed, a dorsal nervous cord containing no central canal but many little cavities and from one to three dorsal nervous roots. These are very thick. The coelomopore of the collar has one dorsal fold.

*Trunk* — The branchial region has branchial pouches with enormous blind caeca; synapticulla of the branchial skeleton from 18 to 50 in number; and gonads, which do not begin right after the collar. The margin of the genital pleurae show no gonads, the secondary genital pores are lateral to the sublateral line. There are two ciliated grooves in the caudal and in the hepatic regions. There is a pycchord.

*Larva* — Probably tornariae *weldoni*, *cairnsiensis* or *setoensis*.

DISCUSSION — Several facts point to the probability that *B. gigas*, *B. carnosus*, *B. biminiensis*, *B. jamaicensis* really belong to one species only, although so widely distributed. They do not even show a morphological distinctiveness, which is considered as “only a general not an infallible guide in delimitting a species” (Cain 1954, p. 97). The occurrence of many varieties has already been observed to be a common fact in two species of the family Ptychoderidae: *P. flava* (Horst, 1932; Pampapathi Rao, 1952) and *B. clavigerus*. There are two populations “geographically definable” (Cain 1954, p. 69-70): the Atlantic (*B. gigas*, *B. biminiensis* and *B. jamaicensis*) and the Pacific (*B. carnosus*, and perhaps *B. numeensis*). They are “taxonomically distinct” (Cain, loc. cit.) and therefore can be assigned to the rank of sub-species (Cain, loc. cit.). The term semi-species suggested by Mayr (Cain 1954, p. 70) is perhaps the best employed in this case; but to prove whether they are species, genetically isolated, or whether they are still sub-species is practically impossible, owing to the great difficulty in collecting and rearing these animals.

*B. carnosus*, *B. biminiensis*, *B. jamaicensis* and *B. gigas* are considered as conspecific because of the great similarity of their anatomical features. The larvae which are related geographically to the adults mentioned, also seem to be of one species only. *B. numeensis* (Maser, 1913) from New Caledonia might be another sub-species or species very closely related to *B. gigas carnosus*. *B. studiosorum* (V. d. Horst 1940, p. 335) of Inyack Is. (Portuguese East Africa) is closely related to *B. numeensis*; but from the related forms it is the one which shows the greatest morphological divergence from *B. gigas*. It is possible that *B.*

*gigas carnosus*, *B. numeensis* and *B. studiosorum* constitute a polytypic species (Cain 1954, p. 72) which might be united into one super-species, dispersed throughout the Indo-Pacific and Indian Oceans. There were apparently not enough barriers to produce the isolation necessary for the formation of new species in the West Atlantic.

It would be more prudent to consider two subspecies of the species *B. gigas*: the Atlantic and the Pacific subspecies, with the following diagnosis:

a') *BALANOGLOSSUS GIGAS GIGAS*

DIAGNOSIS — Very large, sometimes up to 2,5 m. Frequently two pores of the coeloma of the proboscis. Large wing-like expansions and protuberant keel on the skeleton. More variability of the skeleton. Proboscis diverticulum with variable form of a more or less square outline in cross-section or even with the outline of an eight. Two dorsal and two ventral pouches at the basis of the diverticulum, which may be fused or not. Larva: tornaria *weldoni* or *setoensis* more frequently.

OCCURRENCE — São Sebastião.

DISTRIBUTION — Brazil (Florianópolis and São Sebastião), Bahamas, Bermudas, Curaçao, Tobago, Jamaica.

b') *BALANOGLOSSUS GIGAS CARNOSUS*

DIAGNOSIS — Smaller length (up to one meter). Generally the coelomoduct of the proboscis finished by a vesicular pouch divided incompletely and with only one pore. Wing-like expansions and keel of the skeleton more or less pointed. Proboscis diverticulum with more or less square outline, in a cross-section. Larva: tornaria *cairnsiensis* probably.

DISTRIBUTION — Japan (Misaki), Maledives, Australia (Low Islands), New Caledonia, Kei Is., Amboina, New Britain, Indochina (Map 4).

Genus *GLOSSOBALANUS* Spengel 1901

c) *GLOSSOBALANUS CROZIERI* Van der Horst 1924

LENGTH — 2,5 cm.

DISCUSSION — The characters which the Brazilian and the Bermudian animals have in common are the presence of a skeleton with a very large keel and very long crura, hardly curved at all (Figs. 83-87, Pl. 18-SK), the situation and aspect of the proboscis pore (Figs. 85-84, Pl. 18-PP), the presense of 4 dorsal nervous roots the first of which being very thick (Fig. 88, Pl. 19-RND), 8 synapticula in the branchial skeleton (Fig. 89, Pl. 19-SY), the left ciliated groove in the abdominal region of the digestive tube. The only anatomical divergences observed in this animal when compared to the specimen of Bermudas, are the larger glomerulus, which also extends itself over the proboscis diverticulum (Fig. 82, Pl. 18-GL), and the fact that there are no large ventral longitudinal folds in the collar pore (Fig. 90, Pl. 19-PC). The characters mentioned above and the size of the animal, which was mature classify it in this species.

LARVA — ?

OCCURRENCE — São Sebastião \* (under the stones exposed during very low tide).

REMAINING DISTRIBUTION — Bermudas.

## V — SUMÁRIO

Vários trabalhos foram publicados sôbre os enteropneustos do Brasil (J. W. Spengel, 1893; F. Müller, 1898; P. Sawaya, 1950; L. Forneris & P. Sawaya, 1953; T. Björnberg, 1952, 1953, 1953a e 1955). Poucas observações haviam sido feitas quanto ao desenvolvimento dos mesmos e quanto à relação das larvas com os adultos e sua distribuição geral na costa do Brasil. Os adultos foram coletados nas praias do Paraná e de São Paulo (Brasil) e as larvas, ao largo da costa brasileira desde 34° 49,0' S até 05° 44,3' N, desde o ano de 1952 até o ano de 1958. Nos *adenda* estão indicados os pontos onde se fizeram coletas, quase

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(\*) The author is indebted to Prof. L. R. Tommasi for the specimen here described.

tôdas superficiais. Criamos algumas das larvas capturadas. Outras, das 3.205 larvas obtidas para êste estudo, fixadas em Bouin e Pampel conservaram melhor os caratêres externos que as fixadas simplesmente em formol.

Tornária *mourei* apareceu em grandes números no plancton coletado ao largo de Cananéia e seu desenvolvimento foi observado. Coincidiu inteiramente com o descrito por Stiasny (1913, 1914) para as larvas européias de *Balanoglossus clavigerus*. A metamorfose da larva também confirmou o que Spengel (1893) havia verificado para *B. clavigerus* em Nápoles. Durante êstes estudos, notou-se uma grande variação de forma e de outros caratêres da larva e dos adultos desta espécie. Verificou-se a variação e a gradação entre sí de caratêres considerados anteriormente como específicos dos *Balanoglossus*: *B. clavigerus*, *B. paranaensis*, *B. paranaicola*, *B. eufrosinoi*, *B. catharinensis*, *B. nonatoi* em animais pertencentes à mesma população e localidade. Por êsse motivo, foram considerados sinônimos de *B. clavigerus*. A única diferença entre o espécime europeu e os brasileiros é a presença de um esfíncter na base da proboscis, caráter que não pareceu suficiente para considerar os animais brasileiros como subespécie, pois constatou-se nitidamente a variabilidade da grossura da musculatura circular da proboscis. Verificou-se também que os aspectos diferentes de tornárias *mourei* e *liliana* eram artefactos de fixação da tornária de *B. clavigerus*. Tornária *tergestina* (Stiasny, 1927) poderia quando muito ser considerada um ecofênótipo da tornária de *B. clavigerus*.

Ocorreram em águas brasileiras as tornárias *weldoni*, *cairnsiensis* e *setoensis* e outras larvas de tamanho maior e intermediário entre as precedentes. Observou-se, ainda, a presença de indivíduos com número de tentáculos intermediário. Em todos os exemplares mencionados chamou atenção a forma característica da protocela com o celomoduto curto, assim como a forma e o afastamento dos celomas em relação ao estômago. Geograficamente pareceu que tornária *weldoni* e demais larvas parecidas já mencionadas, são relacionadas com *Balanoglossus gigas*, *B. biniensis* e *B. jamaicensis* (das Índias Ocidentais e das Bahamas) e com *B. carnosus* (do Pacífico). Tanto *B. gigas* como sua larva provável apresentam uma variação de caratêres somente ultrapassada pela variabilidade de *B. clavigerus*. Isso parece

indicar que *B. biminiensis*, *B. jamaicensis*, *B. carnosus* e *B. gigas* sejam sinônimos. Só o estudo do ciclo completo destes animais resolverá esse problema. Neste trabalho atribuímos duas subespécies a *B. gigas*: 1) *B. gigas gigas*, de tamanho maior, atlântica e 2) *B. gigas carnosus*, de tamanho menor, pacífica. Lembrando a variação de caracteres de tornária *weldoni*, parece possível concluir que tornária *ritteri* é apenas uma variação da mesma, e que tornária *krohni* do Mediterrâneo é um ecofenótipo provavelmente.

Foi constatada a variabilidade dos caracteres considerados específicos das tornárias *morgani*, *chierchiae I*, e *grenacheri* em amostras de águas brasileiras do sul até o norte; nas mesmas amostras verificou-se a presença de tornárias com caracteres intermediários entre elas. Isto levou à suposição de que estas larvas, assim como tornárias *susakiensis* (Tokioaka, 1937) e *snelliusi* (Stiasny, 1935), sejam na realidade pertencentes à mesma espécie, provavelmente *Ptychodera flava*.

Tornárias *dubia* idênticas às do Mediterrâneo, ocorreram ao largo do Uruguai e do Brasil (Estados de Sta. Catarina, Paraná, Espírito Santo, Alagoas, Maranhão). Estas larvas, relacionadas por Stiasny ao *Glandiceps talaboti*, ainda não encontrado ao largo do Brasil, mostram muito pequena variação de forma. Isto pode ser devido ao fato destas tornárias possuírem o líquido blastocélio mais volumoso e viscoso. Foi possível verificar que as bôlsas branquiais nestes animais só aparecem muito tarde, durante a metamorfose. As bôlsas celomáticas são relativamente menos musculares que as de outras larvas no mesmo estágio de desenvolvimento.

O nome de uma das larvas, que ocorre desde o Rio Grande do Sul até Ubatuba, foi aqui mudado para *nordestina*, a fim de não permitir a confusão desta larva (inicialmente denominada *stiasnyi*) com a tornária de *Glandiceps stiasnyi* (Pampapathi Rao, 1953). O desenvolvimento e a origem dos celomas assim como a ausência de lóbos e de linguetas secundárias no estágio "Krohn" em tornária *nordestina* aproximam-na anatômicamente da tornária de New England descrita por Morgan. Esta, provavelmente, pertence a *Glossobalanus* e não a *Schizocardium*, como havia sido proposto em outro trabalho. *Glossobalanus minutus* assinalado anteriormente por Spengel (1893) no Rio de Janeiro,

nunca mais foi encontrado, mas, registou-se neste trabalho a coleta recente de *Glossobalanus crozieri* em São Sebastião. A larva de New England poderia pertencer a essa espécie, descrita originalmente das Bermudas.

Verificou-se que a tornária de *B. clavigerus* alimenta-se de diatomáceas (uma vez foi encontrado um copépodo em seu estômago). Quando colocada em aquário, move-se para o lado iluminado. Foram medidos seus batimentos cardíacos. As larvas jovens são encontradas muito próximas das praias ou em água rasa e os estágios mais velhos de desenvolvimento, somente a uma certa distância da costa e em profundidades maiores. As maiores tornárias capturadas foram encontradas à distância de várias milhas da costa.

O fenômeno de metamorfose retardada explicaria o aparecimento de larvas grandes de *B. clavigerus*, de tornárias *chierchiae I* e *weldoni* em estágios “Krohn”, “Spengel” e “Agassiz” de desenvolvimento em amostras coletadas longe da costa. Este fenômeno é importante para a dispersão da espécie e sua sobrevivência.

As águas superficiais (até 200 m de profundidade) das costas brasileiras podem ser classificadas em 3 tipos principais: águas costeiras de salinidade muito variável, mais baixa que 34 ‰, e de temperatura alta em geral; águas misturadas de plataforma, de salinidade aproximadamente de 35 ‰ e de temperatura alta; e finalmente, águas da corrente do Brasil ou da corrente Sul-Equatorial, de salinidade acima de 36 ‰ e de temperatura alta. Nestas últimas são encontradas as larvas maiores em estágios “Krohn”, “Spengel” e “Agassiz” do tipo *chierchiae I*, *dubia* e *weldoni*. As tornárias do *B. clavigerus*, *chierchiae I* e *nordestina* foram encontradas nos três tipos de águas — as jovens próximas da costa. Tornárias *dubia* e *weldoni* ocorreram em geral em águas de salinidade mais alta. Nas amostras onde apareceram tornárias de *B. clavigerus* em grande quantidade, determinou-se a fauna e a flora planctônicas acompanhantes. Quando possível, foi ainda relacionado o número e volume de tornárias com o volume de plancton por litro de água amostrada (Tabela 4).

## VI — ADDENDUM

### (LIST OF THE STATIONS WHERE THE SAMPLES WERE COLLECTED)

The temperature and salinities of the water mentioned in the lists were usually those of the surface, and those taken at the greatest depth from which the haul was made. These data therefore refer to the maximum and minimum which the larva may actually suffer. Where only one salinity and one temperature are indicated they refer to the surface temperature and surface salinity of the sea water. Off Cananéia the salinity was not always mentioned and the ebb and flow of the tide was mentioned instead. During the ebb the water was almost brackish and during the flow of the tide it showed up to 35 ‰ of salinity.

In brackets, after the position of each station, comes the name of the nearest town or geographical landmark and the name of the ship from which the plankton was collected. As each expedition used different numbers for its stations, the sample number by which it is kept in the Instituto Oceanográfico's Plankton Museum (Catalogue number) has also been mentioned in the lists so as to permit a rapid reference.

The following papers should be consulted for further physical and chemical data and other details about the cruises: Emilsson (1956); Vannucci (1957); Brasil (AGI) — 1957-1959; Japan (Nat. Dep. Fisheries) — 1958.

Details about the plankton nets used and mentioned in the lists may be also found in Sverdrup et al. (1954, p. 377-379).

# STATION LIST

Station	Catalogue Number	Position	Date	Time (h)	Temperature of Water (°C)	Salinity ‰	Depth of Haul	Local Depth	Larvae Number	Type of Net
—	—	Canancía	28/ 9/52	—	—	—	—	—	8 <i>nordestina</i> 1 <i>B. clavigerus</i>	—
2 ex	—	I. do Bom Abrigo	7/ 5/53	0900	—	flow	8-5 m	—	2 <i>nordestina</i>	Zooplankton
2 ex	II-2	I. do Bom Abrigo	24/ 1/53	0948	27.00	flow	10 m	16 m	1 <i>B. clavigerus</i>	?
2 ex	II-18	I. do Bom Abrigo	27/ 1/54	0720	26.00	ebb	—	—	20 <i>B. clavigerus</i>	Pelagic
2 ex	II-19	I. do Bom Abrigo	7/ 1/54	0715	26.00	ebb	bottom	17 m	1 <i>nordestina</i>	?
2 ex	II-22	I. do Bom Abrigo	16/ 3/54	0910	27.00	flow	16-14 m	17 m	1 <i>nordestina</i>	Pelagic
2 ex	II-48	I. do Bom Abrigo	9/10/54	0810	24.9	ebb	15-12 m	17 m	5 <i>nordestina</i> 107 <i>B. clavigerus</i>	Pelagic
2 ex	II-58	I. do Bom Abrigo	23/ 4/55	0822	24.4	flow	16-14 m	17 m	11 <i>nordestina</i>	Zooplankton
2 ex	II-94	I. do Bom Abrigo	17/ 1/56	0640	27.00	34.35	surface	12 m	2 <i>nordestina</i> 140 <i>B. clavigerus</i>	Zooplankton
2 ex	II-95	I. do Bom Abrigo	17/ 1/56	0651	26.00	34.78	11 m bottom	12 m	2 <i>nordestina</i> 300 <i>B. clavigerus</i>	Phytoplankton
—	—	Santos	8/11/54	1200	—	—	surface	—	1 <i>nordestina</i>	Phytoplankton
—	—	Santos	1/12/54	morning	—	—	surface	—	2 <i>nordestina</i>	Phytoplankton
—	—	Santos	7/10/54	—	—	—	surface	—	5 <i>nordestina</i>	Phytoplankton
—	—	Alcatrazes	30/11/54	—	—	—	surface	10 m	1 <i>nordestina</i>	Phytoplankton
2	IV-249	Argolão	7/10/55	1631	20.40	29.13	13 m bottom	14 m	5 <i>nordestina</i>	Zooplankton

# STATION LIST

Station	Catalogue Number	Position	Date	Time (h)	Temperature of Water (°C)	Salinity ‰	Depth of Haul	Local Depth	Larvae Number	Type of Net
2	IV-252	Argolão	14/10/55	1552	21.4	31.11	13 m bottom	14 m	4 <i>nordestina</i> 2 <i>B. clavigerus</i>	Zooplankton
2	IV-255	Argolão	29/10/55	1057	22.3	24.85	surface	—	1 <i>nordestina</i>	Zooplankton
2	IV-256	Argolão	29/10/55	1101	22.7	26.98	13 m bottom	14 m	11 <i>B. clavigerus</i> 12 <i>nordestina</i>	Zooplankton
3 ex	XI-23	Canal Norte	27/10/54	0730	23.00	cbb	8 m	10 m	1 <i>B. clavigerus</i>	?
3 ex	XI-25	Canal Norte	23/12/54	0930	24.9	flow	11-9 m	11 m	36 <i>B. clavigerus</i>	Zooplankton
3 ex	XI-27	Canal Norte	8/ 1/55	0920	26.8	flow	10-9 m	11 m	4 <i>B. clavigerus</i>	Pelagic
3 ex	XI-30	Canal Norte	12/ 1/55	0818 0920	27.1 21.8	ebb —	surface 10-9 m	11 m 11 m	1 <i>B. clavigerus</i> 1 <i>nordestina</i>	?
3 ex	XI-36	Canal Norte	2/ 2/55	0825	28.5	flow	surface	11 m	60 <i>B. clavigerus</i>	?
3 ex	XI-39	Canal Norte	11/ 2/55	0835	28.5	flow	11-9 m	11 m	115 <i>B. clavigerus</i> 4 <i>nordestina</i>	?
3 ex	XI-40	Canal Norte	11/ 2/55	0825	28.8	flow	surface	—	1 <i>nordestina</i> 11 <i>B. clavigerus</i>	?
3 ex	XI-41	Canal Norte	24/ 2/55	1440	28.00	flow	5 m bottom	7 m	1 <i>B. clavigerus</i>	?
3 ex	XI-51	Canal Norte	7/ 2/57	0845	27.5	30.84	surface	10 m	1 <i>nordestina</i>	Zooplankton
—	N-37	Ubatuba	3/ 7/55	—	—	—	—	—	2 <i>nordestina</i>	?
—	—	Ubatuba	7/ 9/55	—	—	—	bottom to surface	—	20 <i>B. clavigerus</i>	?

# STATION LIST

Station	Catalogue Number	Position	Date	Time (h)	Temperature of Water (°C)	Salinity ‰	Depth of Haul	Local Depth	Larvae Number	Type of Net
—	N-68	Ubatuba	11/12/55	0815	27.00	flow	surface	9 m	1 <i>nordestina</i>	?
—	N-82	Ubatuba	20/10/56	1155	21.6	flow	—	9 m	437 <i>nordestina</i>	?
1	M-1	Fernando de Noronha (4 km off the coast)	20/ 1/54	0930	27.00	36.07	surface	100 m	1 <i>chierchiae I</i>	—
1	M-2	Fernando de Noronha (4 km off the coast)	20/ 1/54	1000	27.00	36.07	surface	100 m	1 <i>chierchiae I</i>	—
2	M-4	Fernando de Noronha (4 km off the coast)	21/ 1/54	1200	—	—	30 m	150 m	1 <i>chierchiae I</i>	—
8	M-14	Fernando de Noronha (4 km off the coast)	27/ 1/54	1000	29.00	—	surface	300 m	1 <i>chierchiae I</i>	—
9	M-16	Fernando de Noronha (4 km off the coast)	27/ 1/54	1200	29.00	—	surface	—	1 <i>chierchiae I</i>	—
—	M-21	20°40'S - 35°10'W (Jaseur Bank) "Baependi" & "Vega"	16/ 6/50	—	—	—	—	—	1 <i>weldoni</i>	—
—	M-24	20°30'S - 29°22'W (Trindade Is.) "Baependi" & "Vega"	18/ 6/50	—	—	—	up to 25 m	—	3 <i>weldoni</i>	—
1	M-27	I. da Trindade	9/ 6/50	—	—	—	10 m	—	2 <i>chierchiae I</i>	—
4	M-68	23°04'S - 44°14'W "Ungava"	13/ 7/55	1100	—	ebb	40 m bottom	52 m	2 <i>B. clavigerus</i>	?

# STATION LIST

Station	Catalogue Number	Position	Date	Time (h)	Temperature of Water (°C)	Salinity ‰	Depth of Haul	Local Depth	Larvae Number	Type of Net
5	M-69	23°04'S - 44°14'W "Ungava"	13/ 7/55	1100	—	ebb	2 m surface	52 m	1 <i>B. clavigerus</i>	?
2	M-74	24°44'S - 45°59'W "Presidente Vargas"	25/ 9/55	1605	20.70 20.19	33.23 33.60	70 m wire out	—	1 <i>B. clavigerus</i>	Standard
72	M-148	27°13'S - 47°08'W "Solimões"	3/11/56	0640	20.71 21.00	35.87 36.05	50 m wire out	213 m	3 <i>nordestina</i> 3 <i>weldoni</i> 1 <i>dubia</i>	Standard
73	M-149	27°18'S - 47°31'W "Solimões"	3/11/56	1100	21.20 21.10	36.67 35.54	50 m wire out	135 m	1 <i>dubia</i> 3 <i>weldoni</i> 2 <i>nordestina</i>	Standard
76	M-153	28°24'S - 48°30'2 W (Florianópolis) "Solimões"	5/11/56	2100	19.37 16.48	35.64 35.40	50 m wire out	62 m	4 <i>dubia</i>	Standard
77	M-154	28°24'S - 48°30'2 W (Florianópolis) "Solimões"	5/11/56	2300	20.61 20.84	35.52 35.65	25 m wire out	80 m	3 <i>dubia</i>	Standard
82	M-159	30°25'S - 48°03'W "Solimões"	6/11/56	1320	20.60 20.34	35.43 36.80	50 m wire out	615 m	3 <i>chierchiae I</i>	Standard
106	M-178	26°09'S - 47°48'W "Solimões"	15/11/56	1100	21.90 22.71	34.59 34.81	50 m wire out	58 m	2 <i>B. clavigerus</i>	Standard
107	M-180	26°25'S - 47°35'W "Solimões"	15/11/56	1305	23.07	35.57	50 m	66 m	3 <i>B. clavigerus</i> 2 <i>dubia</i>	Standard

# STATION LIST

Station	Catalogue Number	Position	Date	Time (h)	Temperature of Water (°C)	Salinity ‰	Depth of Haul	Local Depth	Larvae Number	Type of Net
108	M-181	25°58.0'S-47°12.0'W "Solimões" (off Guaratuba)	15/11/56	1720	22.42 21.90	35.85 35.86	50 m wire out	73 m	1 <i>dubia</i> 3 <i>B. clavigerus</i> 2 <i>nordestina</i>	Standard
110	M-183	25°01.8'S-46°24.0'W "Solimões"	16/11/56	0015	22.00	35.56	25 m wire out	63 m	3 <i>nordestina</i> 5 <i>B. clavigerus</i>	Standard
111	M-184	24°39.0'S-46°03.0'W "Solimões"	20/ 3/57	0300	22.03	35.44	25 m wire out	57 m	3 <i>nordestina</i>	Standard
47	M-201	30°57.5'S-50°06.5'W "Toko-Maru"	21/ 1/57	1500	20.02 24.2	33.711 35.769	42 m	100 m	2 <i>B. clavigerus</i>	Kitabara
48	M-202	30°53.5'S-50°19.5'W "Toko-Maru"	21/ 1/57	1855	19.09 23.44	34.018 35.913	41 m	49 m	2 <i>B. clavigerus</i>	Kitabara
55	M-207	32°16.2'S-51°57.3'W "Toko-Maru"	24/ 1/57	0715	22.6 23.84	32.015 32.919	16 m	20 m	1 <i>B. clavigerus</i>	Kitabara
71	M-216	34°49.0'S-52°10.0'W "Toko-Maru" (Limit Brazil-Uruguay)	29/ 1/57	1045 1135	24.1 22.89	33.314 35.345	50 m	260 m	1 <i>dubia</i>	Kitabara
99	M-243	09°29.5'S-33°35.7'W "Toko-Maru" (off Maceió)	16/ 3/57	0510 0725	27.7 24.62	36.762 36.780	50 m to 0 m	100 m	1 <i>weldoni</i> 1 <i>chierchii I</i>	Kitabara
105	M-246	07°28.5'S-34°17.0'W "Toko-Maru"	20/ 3/57	0515 0645	27.89 28.00	36.744	50 m	100 m	1 <i>chierchii I</i> 1 <i>nordestina</i>	Kitabara
107	M-247	01°30.0'S-34°16.0'W "Toko-Maru"	28/ 3/57	0525 0730	24.77 27.57	35.823 36.076	50 m	100 m	2 <i>chierchii I</i>	Kitabara

## STATION LIST

Station	Catalogue Number	Position	Date	Time (h)	Temperature of Water (°C)	Salinity ‰	Depth of Haul	Local Depth	Larvae Number	Type of Net
115	M-251	02°00,0'N-44°02,0'W "Toko-Maru"	6/ 4/57	1400 1425	27.9 27.93	36.130	20 m	20 m	1 <i>B. clavigerus</i>	Kitahara
117	M-252	00°44,0'N-45°45,0'W "Toko-Maru"	8/ 4/57	0105 0135	27.00 28.06	9.290 35.354	20 m	20 m	2 <i>B. clavigerus</i> 2 <i>chierchiae I</i>	Kitahara
119	M-253	00°30,0'N-45°30,0'W "Toko-Maru"	8/ 4/57	0415	26.7 26.74	12.611 35.498	20 m	40 m	1 <i>B. clavigerus</i>	Kitahara
121	M-254	00°02,0'N-44°56,0'W "Toko-Maru"	8/ 4/57	0940 1015	27.5 27.45	35.805 35.823	20 m	50 m	4 <i>chierchiae I</i>	Kitahara
123	M-255	00°36,5'N-44°23,0'W "Toko-Maru"	8/ 4/57	1830 2015	27.12 27.46	35.985 36.094	50 m	150 m	9 <i>chierchiae I</i>	Kitahara
125	M-256	00°23,0'N-46°55,0'W "Toko-Maru"	10/ 4/57	0305 0345	26.9 27.81	6.582 30.444	bottom	20 m	1 <i>chierchiae I</i>	Kitahara
129	M-258	00°33,0'N-46°00,0'W "Toko-Maru"	10/ 4/57	1415 1445	27.9 27.73	28.657 35.805	20 m	50 m	1 <i>chierchiae I</i> 75 <i>B. clavigerus</i>	Kitahara
130	M-259	00°50,0'N-45°42,5'W "Toko-Maru"	10/ 4/57	1735 1930	26.22 27.53	34.848 36.166	50 m	150 m	3 <i>B. clavigerus</i>	Kitahara
130	M-260	approx. 00°50,0'N - 45°00,0'W "Toko-Maru"	10/ 4/57	1735 1930	26.22 27.53	34.848 36.166	50 m	150 m	40 <i>chierchiae I</i>	Kitahara
137	M-268	01°22,2'N-46°53,2'W "Toko-Maru"	20/ 4/57	0525 0555	27.35 27.44	32.412 35.805	20 m	20 m	3 <i>chierchiae I</i>	Kitahara
141	M-272	01°31,0'N-48°00,0'W "Toko-Maru"	21/ 4/57	0745 0810	26.7 27.34	12.412 35.444	20 m	50 m	6 <i>chierchiae I</i>	Kitahara

# STATION LIST

Station	Catalogue Number	Position	Date	Time (h)	Temperature of Water (°C)	Salinity ‰	Depth of Haul	Local Depth	Larvae Number	Type of Net
159	M-292	04°51.5'N-50°07.0'W "Toko-Maru"	24/ 4/57	1205 1330	26.82 27.85	28.008 35.823	50 m	150 m	15 <i>chierchiae</i> I	Kitahara
161	M-294	04°31.0'N-50°35.2'W "Toko-Maru"	24/ 4/57	1735 1803	27.9 27.26	22.033 36.094	20 m	50 m	2 <i>chierchiae</i> I	Kitahara
256	M-363	26°00.0'S-44°15.0'W "Alm. Saldanha"	14/10/57	1700	—	—	surface	1.000 m	1 <i>chierchiae</i> I	Standard
304	M-421	00°05.0'N-45°07.0'W "Alm. Saldanha"	18/11/58	1045	26.84 26.79	36.35 36.31	0-48 m	56 m	11 <i>chierchiae</i> I	Hensen
309	M-431	02°57.5'N-48°12.0'W "Alm. Saldanha"	26/11/58	1035	27.10 23.23	36.40 36.26	0-91 m	101 m	2 <i>chierchiae</i> I 8 <i>weldoni</i>	Hensen
315	M-442	05°44.3'N-51°01.0'W "Alm. Saldanha"	28/11/58	0930	27.88 26.92	35.75 36.24	0-29 m surface	663 m	10 <i>chierchiae</i> I 2 <i>weldoni</i>	Hensen
315	M-443	05°44.3'N-51°01.0'W "Alm. Saldanha"	28/11/58	0930	27.88 26.68	35.75 36.18	0-92 m	663 m	2 <i>chierchiae</i> I 2 <i>weldoni</i>	Hensen
316	M-444	05°30.5'N-50°28.0'W "Alm. Saldanha"	28/11/58	1900	27.33 27.06	36.17 36.17	0-39 m	2.745 m	1 <i>chierchiae</i> I	Hensen
319	M-450	04°57.0'N-46°55.5'W "Alm. Saldanha"	30/11/58	0700	27.39 27.37	36.15 36.15	0-25 m	3.292 m	6 <i>chierchiae</i> I	Hensen
327	M-467	00°44.0'N-45°26.0'W "Alm. Saldanha"	12/12/58	1830	27.33 19.24	36.27 36.17	0-100 m	736 m	5 <i>chierchiae</i> I	Hensen
328	M-469	01°10.0'N-46°08.0'W "Alm. Saldanha"	13/12/58	0700	27.11 24.15	36.17 36.31	0-85 m	700 m	11 <i>weldoni</i> 1 <i>chierchiae</i> I	Hensen

# STATION LIST

Station	Catalogue Number	Position	Date	Time (h)	Temperature of Water (°C)	Salinity ‰	Depth of Haul	Local Depth	Larvae Number	Type of Net
338	M-488	00°25,0'N-44°11,0'W "Alm. Saldanha"	18/12/58	1800	27.27 27.01	36.17 36.22	0-91 m	1,000 m	1 <i>chierchiae</i> I	Hensen
338	M-489	00°25,0'N-44°11,0'W "Alm. Saldanha"	18/12/58	1800	27.27 27.01	36.17 36.22	0-91 m	1,000 m	3 <i>chierchiae</i> I	Hensen
339	M-490	00°27,0'S-43°16,0'W "Alm. Saldanha"	19/12/58	1430	27.20 26.99	36.15 36.22	0-73 m	1,600 m	1 <i>chierchiae</i> I	Hensen
340	M-492	01°10,0'S-41°55,0'W "Alm. Saldanha"	20/12/58	0830	27.09 25.55	36.22 36.92	0-91 m	120 m	1 RS	Hensen
341	M-494	01°31,0'S-41°24,0'W "Alm. Saldanha"	20/12/58	1800	27.06 27.08	36.15 36.33	0-25 m surface	1,521 m	2 <i>weldoni</i>	Hensen
341	M-495	01°31,0'S-41°24,0'W "Alm. Saldanha"	20/12/58	1800	27.06 25.54	36.15 36.82	0-91 m	1,521 m	1 <i>weldoni</i>	Hensen
344	M-501	03°39,5'S-37°39,0'W "Alm. Saldanha"	27/12/58	0830	26.66 24.88	36.27 37.01	0-102 m	1,378 m	1 <i>B. clavigerus</i> 2 RS	Hensen
345	M-502	03°49,5'S-36°51,0'W "Alm. Saldanha"	27/12/58	1830	26.74 26.70	36.15 36.24	0-25 m	2,185 m	1 <i>chierchiae</i> I 2 RS	Hensen
345	M-503	03°49,5'S-36°51,0'W "Alm. Saldanha"	27/12/58	1830	26.74 26.70	36.15 36.24	0-72 m	2,185 m	2 <i>B. clavigerus</i>	Hensen
346	M-504	03°53,0'S-36°00,5'W "Alm. Saldanha"	28/12/58	0600	26.56 26.60	36.24 36.18	0-20 m surface	225- 180 m	1 <i>weldoni</i>	Hensen
350	M-509	03°47,0'S-33°23,0'W "Alm. Saldanha"	29/12/58	1800	26.70 26.55	36.20 36.15	0-22 m horiz.	1,080 m	2 BP	Hensen

# STATION LIST

Station	Catalogue Number	Position	Date	Time (h)	Temperature of Water (°C)	Salinity ‰	Depth of Haul	Local Depth	Larvae Number	Type of Net
350	M-510	03°47,0'S - 33°23,0'W "Alm. Saldanha"	29/12/58	1800	26.70 21.44	36.20 32.26	0-122 m vertical	1,080 m	2 <i>chierchiae</i> I	Hensen
353	M-514 515	04°58,5'S - 33°01,0'W "Alm. Saldanha"	30/12/58	1800	26.75 23.22	36.44 35.97	0-100 m	4,320 m	1 <i>chierchiae</i> I	Hensen
355	M-519	07°41,0'S - 34°25,0'W "Alm. Saldanha"	31/12/58	2000	27.30 27.17	36.55 36.55	0-91 m	1,500- 1,200 m	7 <i>chierchiae</i> I 7 <i>weldoni</i>	Hensen
P 2	M-520	22°39,0'S - 41°12,0'W "Alm. Saldanha"	6/11/58	1915	23.80 surface	?	0-58 m	63 m	1 <i>chierchiae</i> I	Hensen
P 4	M-522	21°25,0'S - 38°46,0'W "Alm. Saldanha"	7/11/58	1940	26.30 surface	?	0-104	1,260? m	15 <i>chierchiae</i> I	Hensen
P 7	M-524	21°21,0'S - 38°31,0'W "Alm. Saldanha"	8/11/58	1915	24.70 surface	?	?	300 m	5 <i>chierchiae</i> I	Hensen
P 8	M-525	19°21,0'S - 37°42,0'W "Alm. Saldanha"	9/11/58	0700	25.30 surface	?	0-131 m	300 m?	3 <i>chierchiae</i> I 2 <i>weldoni</i> 6 <i>dubia</i>	Hensen
P 9	M-526	18°16,0'S - 37°43,0'W "Alm. Saldanha"	9/11/58	1700	25.30	?	?	122 m?	11 <i>weldoni</i>	Hensen
P 11	M-528	10°45,0'S - 35°09,0'W "Alm. Saldanha"	12/11/58	1915	26.30	?	0-130 m	more than 1,000 m	9 <i>chierchiae</i> I 4 <i>dubia</i>	Hensen
P 12	M-529	09°40,0'S - 34°26,0'W "Alm. Saldanha"	13/11/58	0700	26.50 surface	?	surface	more than 2,000 m	3 <i>chierchiae</i> I 8 <i>weldoni</i>	Hensen
P 13	M-530	08°08,0'S - 34°13,0'W "Alm. Saldanha"	13/11/58	1915	26.60 surface	?	0-122 m	1,260 m	1 <i>chierchiae</i> I 4 <i>weldoni</i>	Hensen

# STATION LIST

Station	Catalogue Number	Position	Date	Time (h)	Temperature of Water (°C)	Salinity ‰	Depth of Haul	Local Depth	Larvae Number	Type of Net
P 14	M-531	06°27,0'S - 34°12,0'W "Alm. Saldanha"	14/11/58	0750	26.30 surface	?	0-131 m	more than 1,000 m	7 <i>chierchiae</i> I	Hensen
P 16	M-533	03°42,0'S - 35°16,0'W "Alm. Saldanha"	15/11/58	0740	26.20 surface	?	0-140 m	2,880 m	4 <i>chierchiae</i> I 1 <i>B. clavigerus</i>	Hensen
P 17	M-534	02°43,0'S - 36°20,0'W "Alm. Saldanha"	15/11/58	1920	26.50 surface	?	0-120 m	3,420 m	3 <i>chierchiae</i> I	Hensen
P 19	M-536	01°41,0'S - 32°50,0'W "Alm. Saldanha"	16/11/58	1930	?	?	?	3,420 m	5 <i>weldoni</i>	Hensen
P 20	M-537	01°08,0'S - 41°32,0'W "Alm. Saldanha"	17/11/58	0740	26.90 surface	?	0-118 m	3,210 m	1 <i>dubia</i> 51 <i>weldoni</i> 1 <i>chierchiae</i> I	Hensen
P 21	M-538	00°49,0'S - 42°59,0'W "Alm. Saldanha"	17/11/58	1920	26.90 surface	?	0-100 m	2,880 m	5 <i>dubia</i> 3 <i>weldoni</i>	Hensen
4	E-1	25°07,9'S - 47°48,4'W "Emilia"	10/1/58	1350	19.46 27.51	34.47 35.44	18.0 m	19 m	450 <i>B. clavigerus</i>	Hensen
4	E-2	25°07,9'S - 47°48,4'W "Emilia"	10/1/58	1400 1415	19.46 27.44	34.47 35.44	18 m	19 m	260 <i>B. clavigerus</i>	Clarke-Bumpus

**LEGEND:**

R S — regressive stage

B P — badly preserved specimen.

## VII — REFERENCES

BJÖRNBERG, T. K. S.

1951. On the structure and hepatic functions of *Balanoglossus gigas*. Paper presented at the III Annual Meeting of the "Sociedade Brasileira para o Progresso da Ciência".
1952. Nota prévia sôbre a ocorrência de dois *Balanoglossus* nas costas do Paraná. *Dusenía* vol. 3 (5), p. 367-372.
1953. On a *Balanoglossus* from the coast of Paraná, Brazil. *Dusenía* vol. 4 (2), p. 127-160, 12 pls.
- 1953a. Três novas tornárias (Enteropneusta) das costas sul do Brasil. *Ból. Inst. Ocean.* t. 4 (1/2), p. 81-102, 2 ests.
1955. Sôbre quatro tornárias do Atlântico e do Mediterrâneo. *Bol. Inst. Ocean.* t. 6 (1/2), p. 197-212.

BRASIL. MINISTÉRIO DA MARINHA.

- 1957-1959. Diretoria de Hidrografia e Navegação. Ano Geofísico Internacional. Public. DG-06-V-VIII.

BURDON-JONES, C.

1952. Development and biology of the larva of *Saccoglossus horsti* (Enteropneusta). *Phil. Trans. R. Soc. London ser. B*, n.º 639, vol. 236, p. 553-590.
1957. Hemichordata — Enteropneusta. Fiches d'identif. du zooplankton, Zooplankton Sheet n.º 70, 6p. Conseil Intern. pour l'Exploration de la Mer.

CAIN, A. J.

1954. Animal species and their evolution. London, Hutchinson's Univ. Libr., 190 p.

EMÍLSSON, I.

1956. Relatório e resultados físico-químicos de três cruzeiros oceanográficos em 1956. *Contrib. Avulsas do Inst. Ocean., Ocean. Física*, n.º 1, 70 p.

HORST, J. C. VAN D.

- 1929-1930. Observations on some Enteropneusta. "Papers fr. Dr. Mortensen's Pacific Expedition 51". *Vidensk. Med. Dansk. Naturh. Foren.* Bd. 87, p. 135-200.
1932. Die Enteropneusta-gattung *Ptychodera*. *Zool. Anz.* Bd. 99, p. 98-100.
1939. Taxonomie. Systematische Beschreibung der Enteropneusten Arten. Hemichordata. Klassen u. Ordn. des Thierreichs von H. G. Bronn, Bd. 4, Abt. 4, Teile 5/6, p. 308-408, 655-725.
1940. Enteropneusta from Inyack Island, Delagoa Bay. *Ann. S. African Mus.* vol. 32, part 5, p. 293-380.

JAPAN. NATIONAL DEPARTMENT OF FISHERIES.

1958. Relatório das pesquisas de campo da pesca das Américas Central e do Sul pelo "Toko-Marú", 1956-1957. Dep. Nacional de Pesca. (in Japanese).

MASER, O.

1913. Über *Balanoglossus carnosus* (Willey u. eine ihn nahestehende, neue Art von Neucaledonien. Zool. Jahrb. Anat. Bd. 33, p. 362-430, Taf. 25-29.

MORGAN, T. H.

1891. The growth and metamorphosis of tornaria. J. Morph. vol. 5, p. 407-459.  
1894. The development of *Balanoglossus*. J. Morph. vol. 9 (1), p. 1-86, 6 pl.

MÜLLER, F.

1898. Observações sôbre a fauna marinha da costa de Sta. Catharina. Rev. Mus. Paulista vol. 3, p. 31-40.

PAMPAPATHI RAO, K.

1952. Significance of variation in *Ptychodera flava*. Evolution vol. 6 (3), p. 342-343.  
1953. The development of *Glandiceps* (Enteropneusta; Spengelidae). J. Morph. vol. 93 (1), p. 1-18.

RITTER, W. E. & DAVIS, B. H.

1904. Studies on the ecology, morphology and speciology of the young of some Enteropneusta of Western North America. Univ. Calif. Public. Zool. vol. 1 (5), p. 171-210, pls. 17-20.

SAWAYA, P.

1950. Reencontro de *Balanoglossus gigas* Fr. Müller no litoral brasileiro. Bol. Inst. Paul. Ocean. vol. 1 (1), p. 135-138.

SAWAYA, P. & FORNERIS, L.

1953. Enteropneustos brasileiros. Univ. S. Paulo. Bol. Fac. Fil. Cienc. Letras 165, Zool. 18, p. 5-50, 8 ests.

SPENDEL, J. W.

1893. Die Enteropneusten des Golfes von Neapel. "Fauna u. Flora des Golfes von Neapel". Mon. 18, XII + 758 p.

STIASNY, G.

1913. Studien über die Entwicklung des *Balanoglossus clavigerus* Delle Chiaje. I. Die Entwicklung der Tornaria. Zeitschr. f. Wiss. Zool. Bd. 110, p. 36-75, Taf. 4-6.  
1914. Studien über die Entwicklung des *Balanoglossus clavigerus* Delle Chiaje. II. Darstellung der weiteren Entwicklung bis zur Metamorphose. Mitt. Zool. St. Neapel Bd. 22, p. 255-290, Taf. 6-9.

STIASNY, G.

1921. Über Westindische Tornarien, nebst einer übersicht über die bisher bekannten tentakulaten Tornarien. Versl. van. de Gew. Verg. Natuurk. d. Wis. Afd. Deel 29, p. 219-253.
1925. Die Tornaria von Helgoland. Zeitschr. Wiss. Zool. Bd. 125, p. 435-447.
1927. Eine neue Tornaria aus der Adria. Zool. Med. 's Rijks Mus. Nat. Hist. Deel 10, p. 37-45.
1929. Die Tornarien von Japan. Zool. Jahrb. Abt. System. Bd. 56, p. 67-92.
1934. Über einige exotische Tornarien. Verh. Konink. Akad. Wetens. Amsterdam. Afd. Natuurk. Deel 34 (2), p. 1-27.
1935. Die Tornarien der Snellius Expedition. Proc. Sect. of Sciences. Konink. Akad. Wetensch. Amsterdam, vol. 38 (6-10), p. 1026-1036.

STIASNY, G. & STIASNY-WIJNHOFF, G.

1931. Die Tornarien. Erg. Fortsch. d. Zool. Bd. 7, p. 38-208, 84 figs., 7 taf., 7 maps.

SVERDRUP, H. V., JOHNSON, M. V. & FLEMING, R. H.

1954. The Oceans. New York, Prentice-Hall Inc., X + 1087 p.

TOKIOKA, T.

1937. *Tornaria susakiensis* n. sp., a new tentaculated tornaria larva. Annot. Zool. Jap. vol. 16, p. 341-344.

TREWAWAS, E.

1931. Enteropneusta. Great Barrier Reef Exped. 1928-29, vol. 4 (2) British Mus. (N. H.), p. 39-67, 18 fig.

VANNUCCI, M.

1957. On Brazilian Hydromedusae and their distribution in relation to different water masses. Bol. Inst. Ocean. vol. 8 (1/2), p. 23-110.

WILLEY, A.

1899. Enteropneusta from the South Pacific, with notes on the West Indian species. Zool. Res. part 3, p. 223-334, pl. 26-32.

WILSON, D. P.

1958. Some problems in larval ecology related to the localized distribution of bottom animals. in "Perspectives in Marine Biology" ed. by A. A. Buzzati-Traverso. Berkely & Los Angeles, Univ. Press, XVI + 621 p.

## VIII — EXPLANATION OF PLATES

*Abbreviations used:*

BRP	— Branchial pouch	LW	— Lateral wall of stomach
BP	— Blind pouch	MA	— Maser's cross-section
BS	— Branchial blind sac	MED	— Collar medulla.
BSK	— Branchial skeleton	MF	— Muscular fibers?
CB	— Ciliated band	NG	— Neural groove
CD	— Coelomduct	OM	— Origin of muscular fibers
CEL	— Coeloma	P	— Branchial pore
CEL 2	— Collar coeloma	PBR	— Pore of the branchial pouch
CEL 3	— Trunk coeloma	PC	— Collar pore
CN	— Nervous cord	PG	— Genital pore
CSK	— Skeleton cavity	PH	— Pharynx
DC	— Dorsal pouches of the diverticulum	PI	— Pigment cells
DIV	— Proboscis diverticulum	PN	— Polymorphous nucleus
E	— Eye	PP	— Protoceol pore
EP	— External epithelium	PBRC	— Postbranchial cavity
EPI	— Internal epithelium	SK	— Skeleton
ESM	— Muscular fibers of the oesophagus	SP	— Spengel's cross-section
FC	— Ciliated band	SPL	— Splanchotheca
FF	— Muscular fibers	ST	— Stomach
GL	— Glomerulus	SY	— Synapticula
GO	— Gonad	T	— Willey's cross-section
H	— Protoceol	TE	— Telotroch
INT	— Intestine	VC	— Ventral cavity of diverticulum
LDIV	— Lumen of diverticulum	VCC	— Ventral coelomatic cavity

PLATE I

- Fig. 1 — Living specimen of tornaria of *B. clavigerus* (1,25 mm long). Lateral view.  
Fig. 2 — Living specimen of *B. clavigerus* tornaria (1,4 mm). Lateral view.  
Fig. 3 — Larva of *B. clavigerus* fixed in Bouin (0,8 mm long).  
Fig. 4 — Larva of *B. clavigerus* fixed in Pampel. Lateral view.  
Fig. 5 — Larva of *B. clavigerus* fixed in 4% formalin. Lateral view.  
Fig. 6 — Larva of *B. clavigerus* fixed in 4% formalin. Captured at a great distance from the coast. Large form.

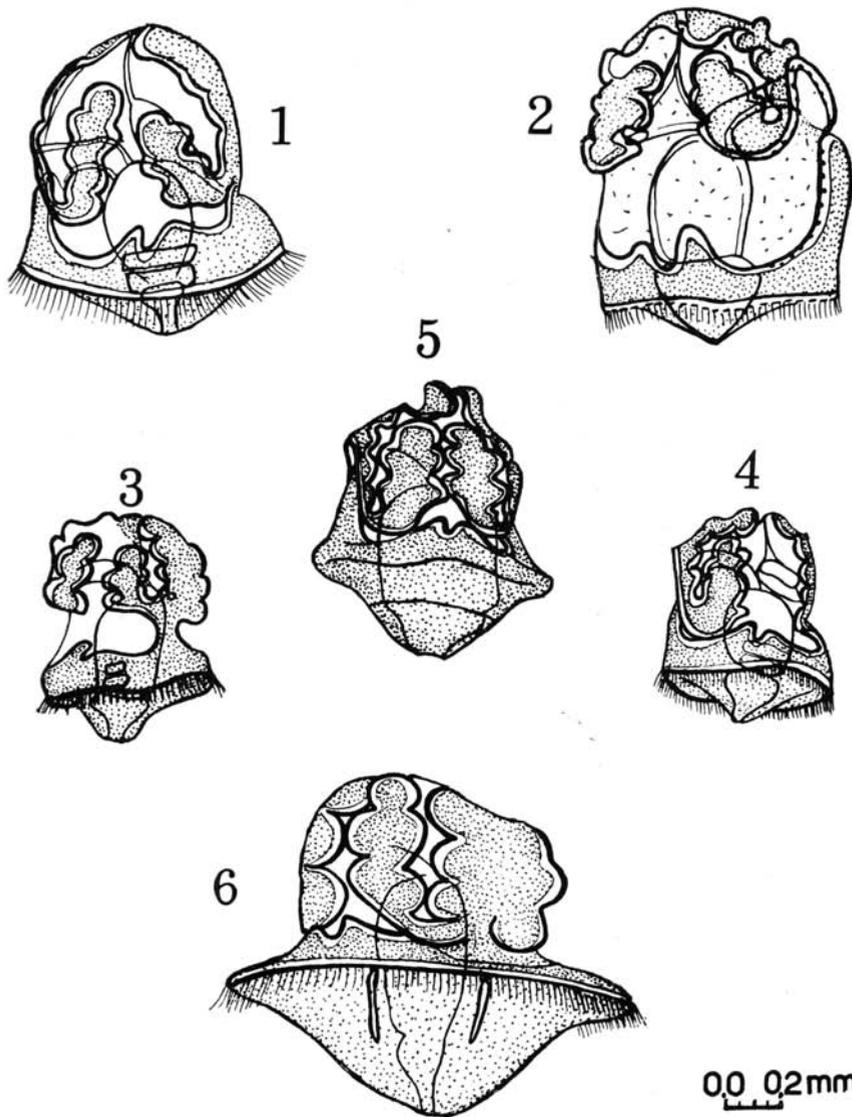
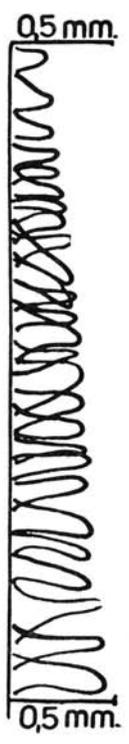
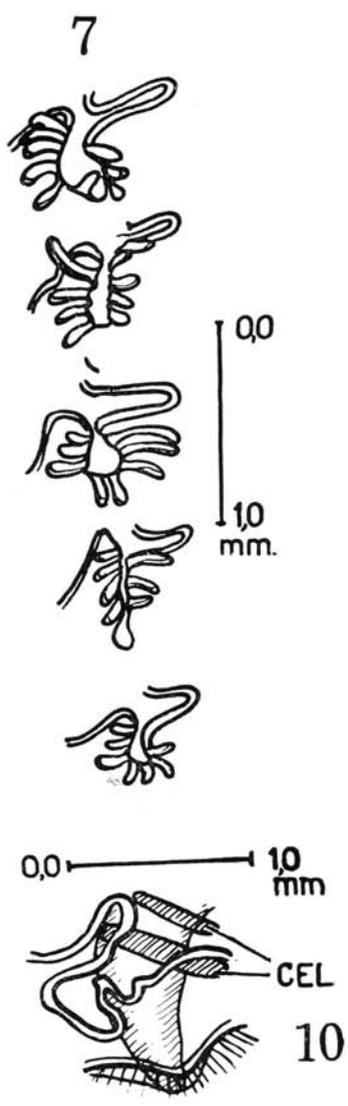


PLATE II

- Fig. 7 — The lateral and inferior dorsal lobes and the tentacles of the lateral lobe of several tornariae *chierchiae* I from 2,20 mm to 3,75 mm long.
- Fig. 8 — Inferior dorsal lobes of 28 tornariae *chierchiae* I in the "Krohn" stage (all fixed at the same time in 4% formalin).
- Fig. 9 — Lateral lobe of 6 tornariae *weldoni*.
- Fig. 10 — The coeloma of a giant larva, captured at a great distance from the coast (*tornaria nordestina*).



8



PLATE III

- Fig. 11 — *Tornaria nordestina* fixed in Bouin and observed immediatly afterwards ("Spengel" or "Agassiz" stage).
- Fig. 12 — *Tornaria nordestina* recently fixed in Bouin ("Krohn" stage).
- Fig. 13 — *Tornaria nordestina* fixed in 4% formalin ("Krohn" stage).
- Fig. 14 — Latero-ventral view of *tornaria weldoni*. "Krohn" stage.
- Fig. 15 — Dorsal view of *tornaria weldoni*. "Krohn" stage.
- Fig. 16 — Lateral view of *tornaria weldoni* in "Krohn" or "Spengel" stage.
- Fig. 17 — *Tornaria weldoni*. Lateral view of an old "Krohn" stage.

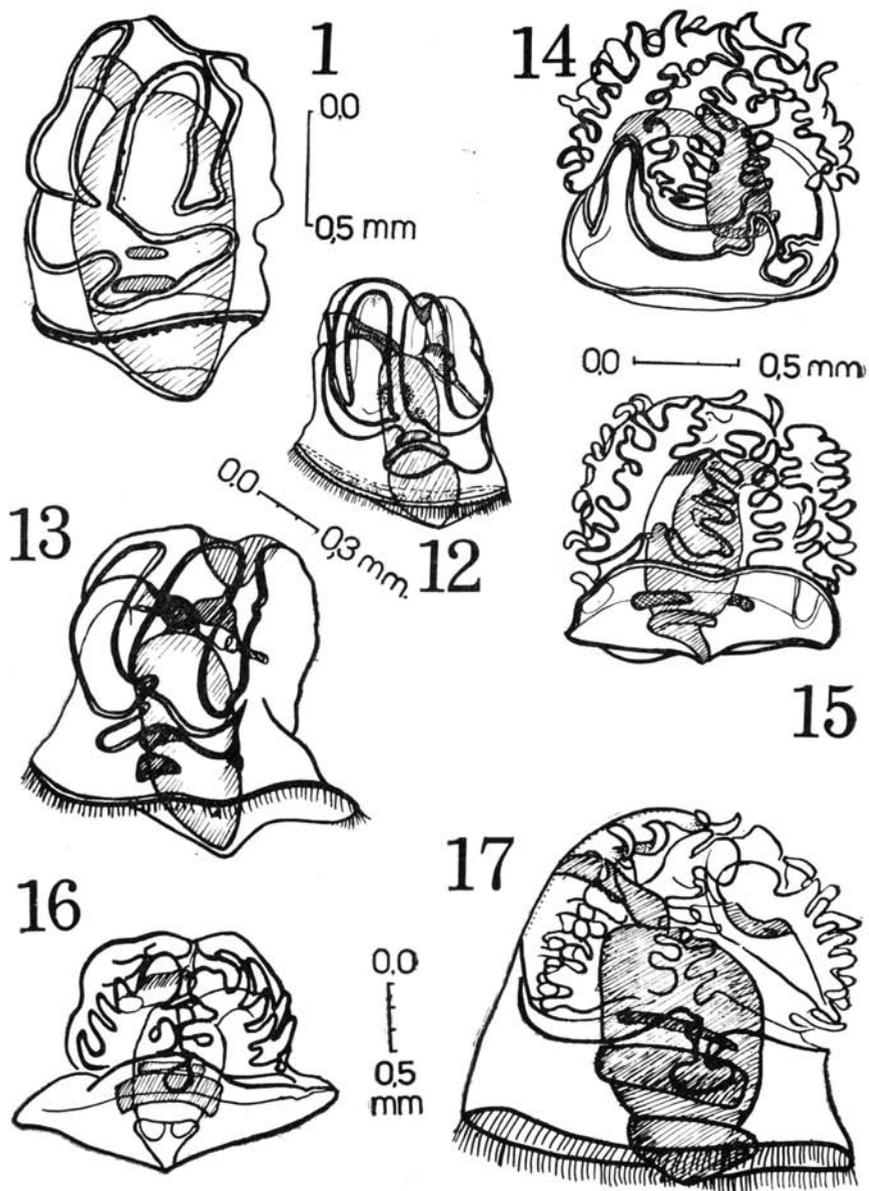


PLATE IV

- Fig. 18 — Living specimen of *B. clavigerus* ("Müller" stage). Ventral view. (0,25 mm).
- Fig. 19. — Reconstruction of *B. clavigerus clavigerus* "Heider" stage from several sections parallel to the horizontal plane.
- Fig. 20 — *Tornaria chierchiae I* in "Müller" stage. Fixed material. (0,13 mm).
- Fig. 21 — *Tornaria chierchiae I* in "Heider" stage. Fixed material. (0,20 mm).
- Fig. 22 — *Tornaria chierchiae I* in young "Metschnikoff" stage. Dorsal view.

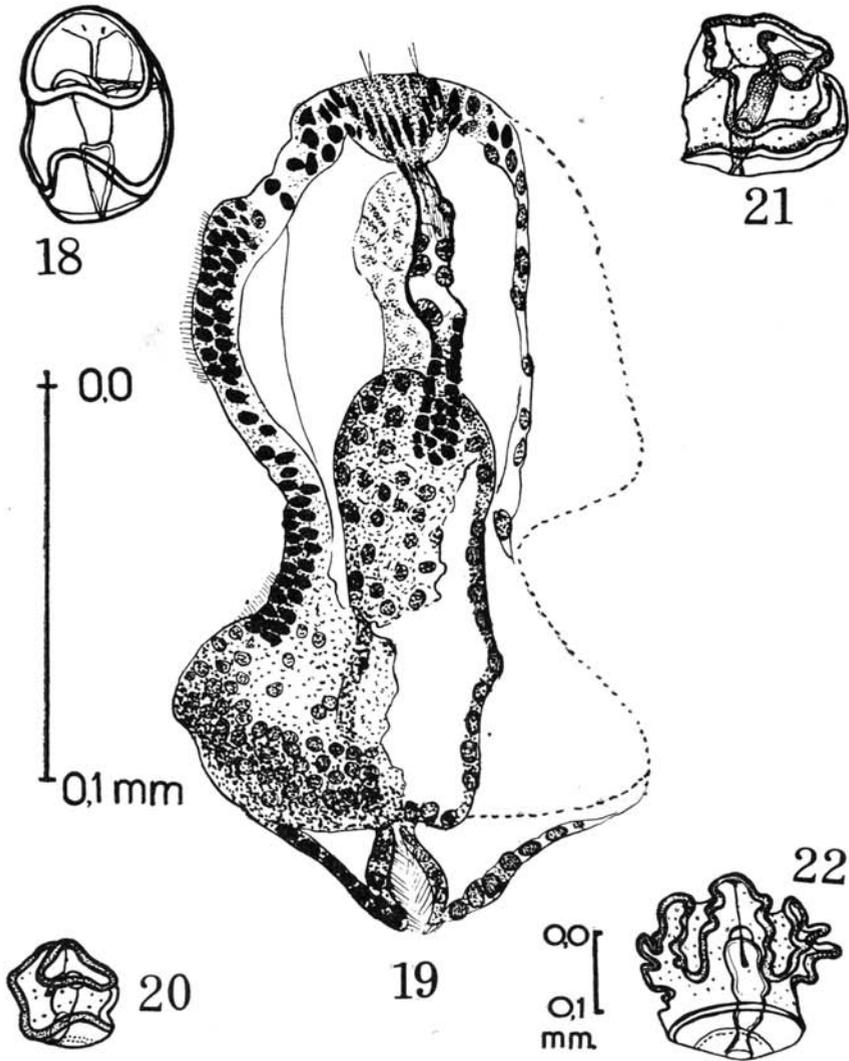


PLATE V

- Fig. 23 — Longitudinal section through young "Metschnikoff" stage (0,25 mm long) of *B. clavigerus*.
- Fig. 24 — *Tornaria chierchiae* I. Epithelium of tentacle. Surface view.
- Fig. 25 — Horizontal section of *tornaria nordestina* in very advanced "Metschnikoff" stage: detail showing origin of the coeloma.
- Fig. 26 — *B. clavigerus*. Detail of the cardiac vesicle in advanced "Metschnikoff" stage, in a sagittal section.

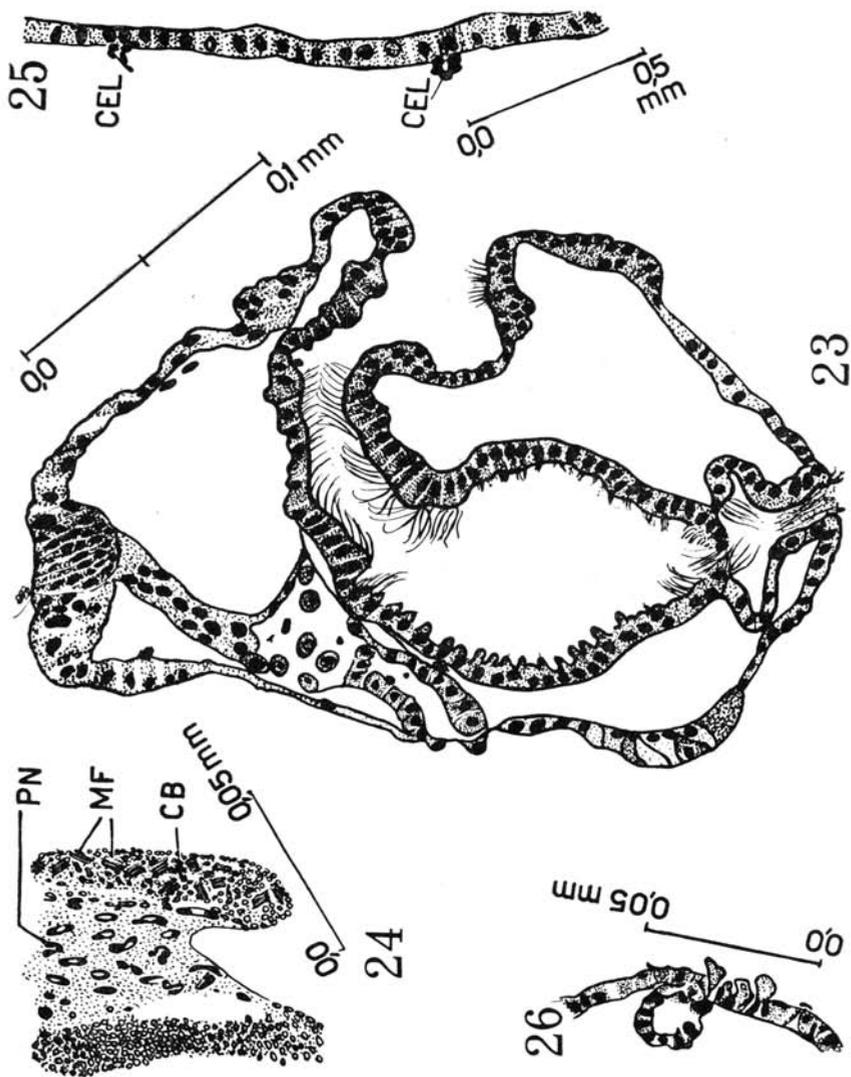
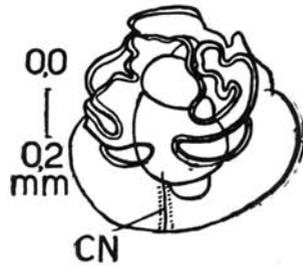
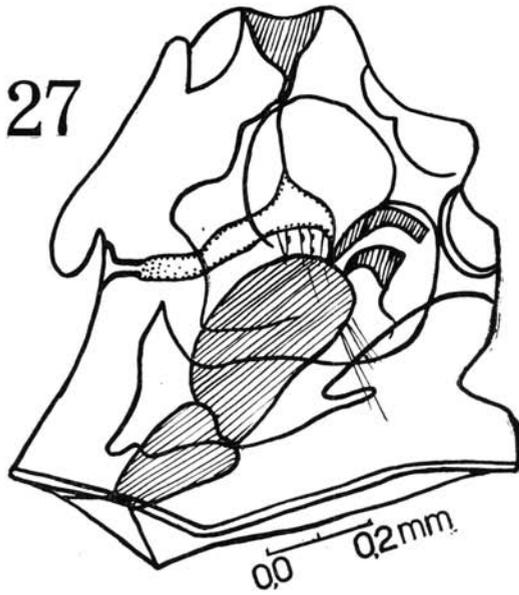


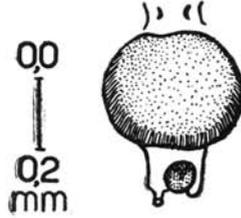
PLATE VI

- Fig. 27 — Lateral view of tornaria *dubia* fixed in 4% formalin. (Internal anatomy).
- Fig. 28 — Fixed "Krohn" to "Spengel" stage of tornaria *dubia* (1.0 mm long). Dorso-apical view.
- Fig. 29 — *B. clavigerus*. Dorsal view of living proboscis coelom and cardiac vesicle, with indications of movements of the same.
- Fig. 30 — *B. clavigerus* tornaria. Lateral view, showing internal anatomy, with indications of movements of the oesophagus.
- Fig. 31 — Tornaria *weldoni* in "Krohn" stage. Schematic view of eyes, proboscis coelom and cardiac vesicle.

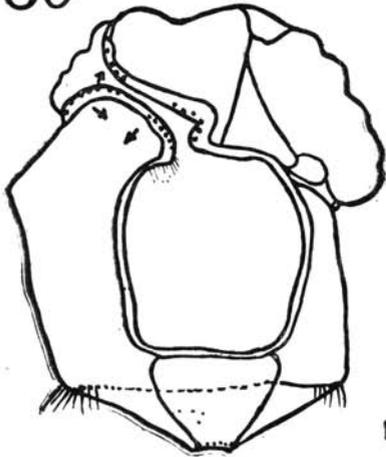


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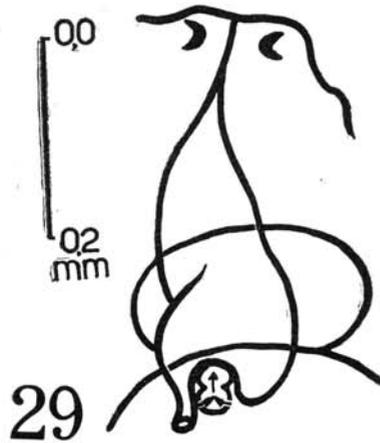
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30



0.0  
0.2 mm



29

PLATE VII

Fig. 32 — Detail of cross-section of advanced "Korhn" stage of *B. clavigerus*, showing dorsal nervous cord.

Fig. 33 — Sagittal section of tornaria in "Krohn" stage of *B. clavigerus*.

Fig. 34 — The same of tornaria *nordestina*

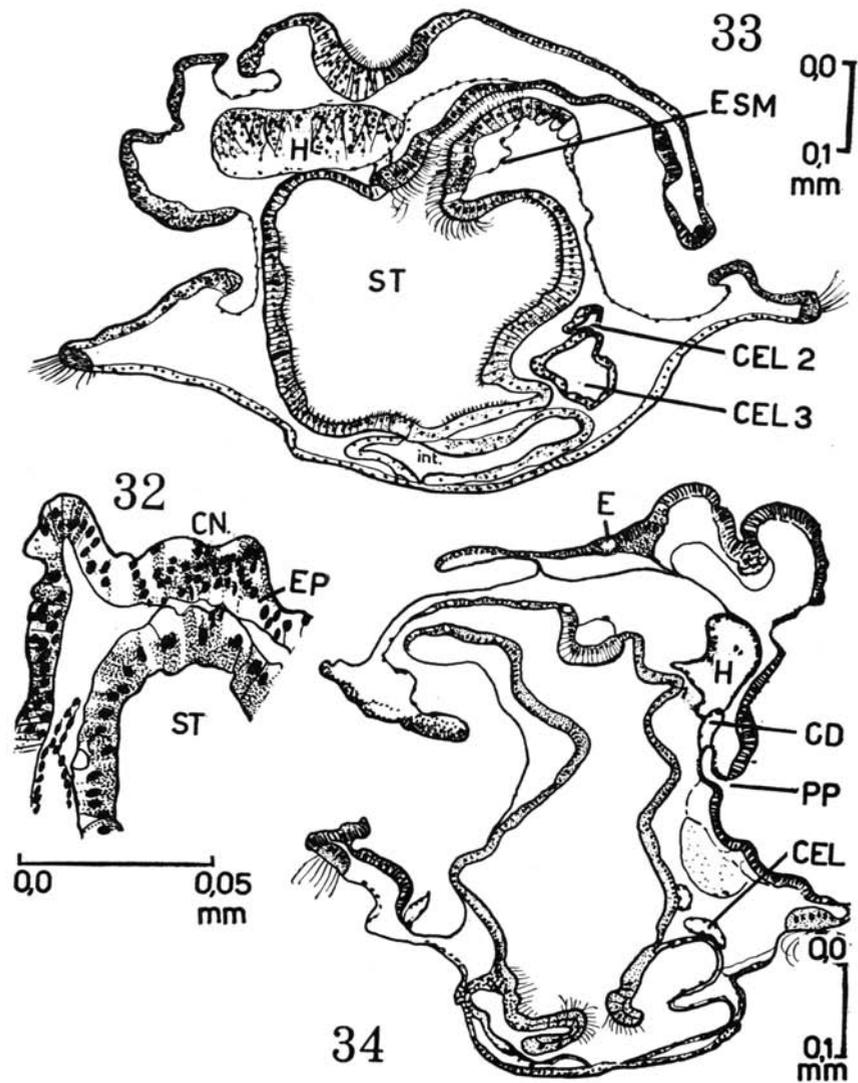


PLATE VIII

- Fig. 35 — Detail of cross-section of the stomach of tornaria *dubia* (1,05 mm long).  
Fig. 36 — Cross-section of the same tornaria through the telotroch.  
Fig. 37 — Cross-section of the same tornaria through the stomach.  
Fig. 38 — Cross-section through the tornaria of *B. clavigerus* in the "Spengel" to "Agassiz" stage.  
Fig. 39 — Dorsal view of "Krohn" to "Spengel" stage of development of *B. clavigerus* from the living.

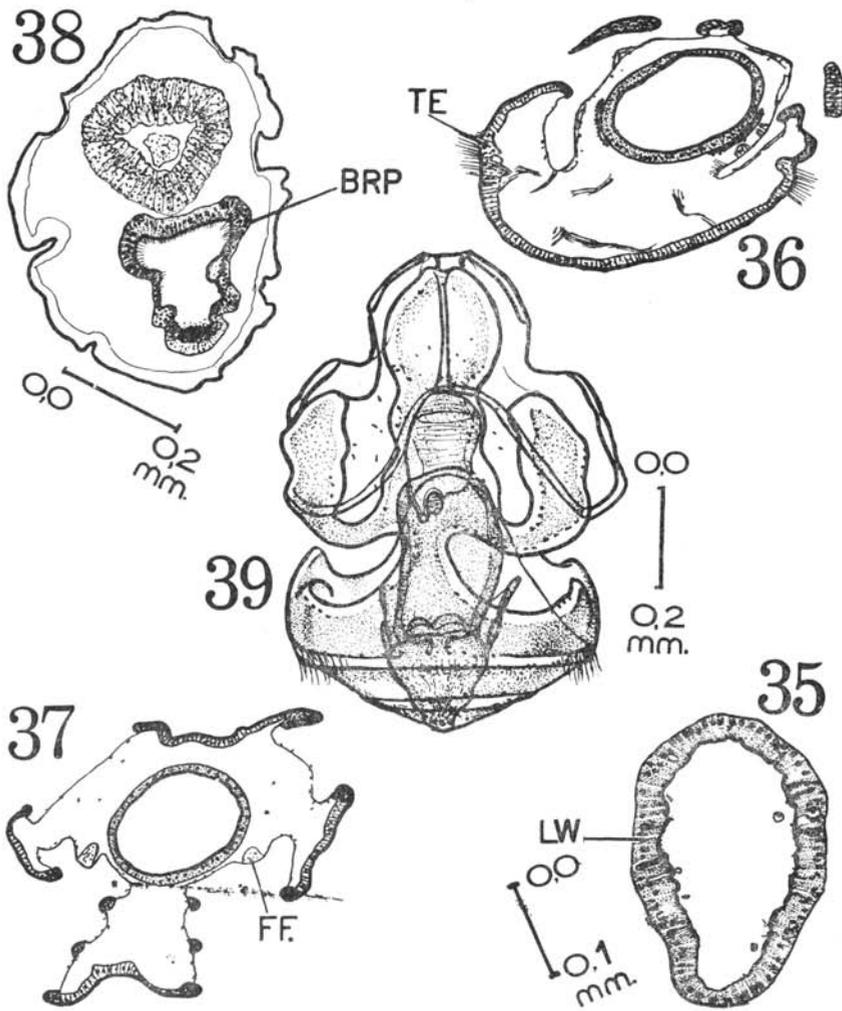


PLATE IX

Fig. 40 — Detail of cross-section of "Krohn" stage of *B. clavigerus*.

Fig. 41 — Cross-section of tornaria *nordestina* in the "Agassiz" stage.

Fig. 42 — Epithelium of stomach and coeloma of a "Spengel" stage of tornaria *nordestina*.

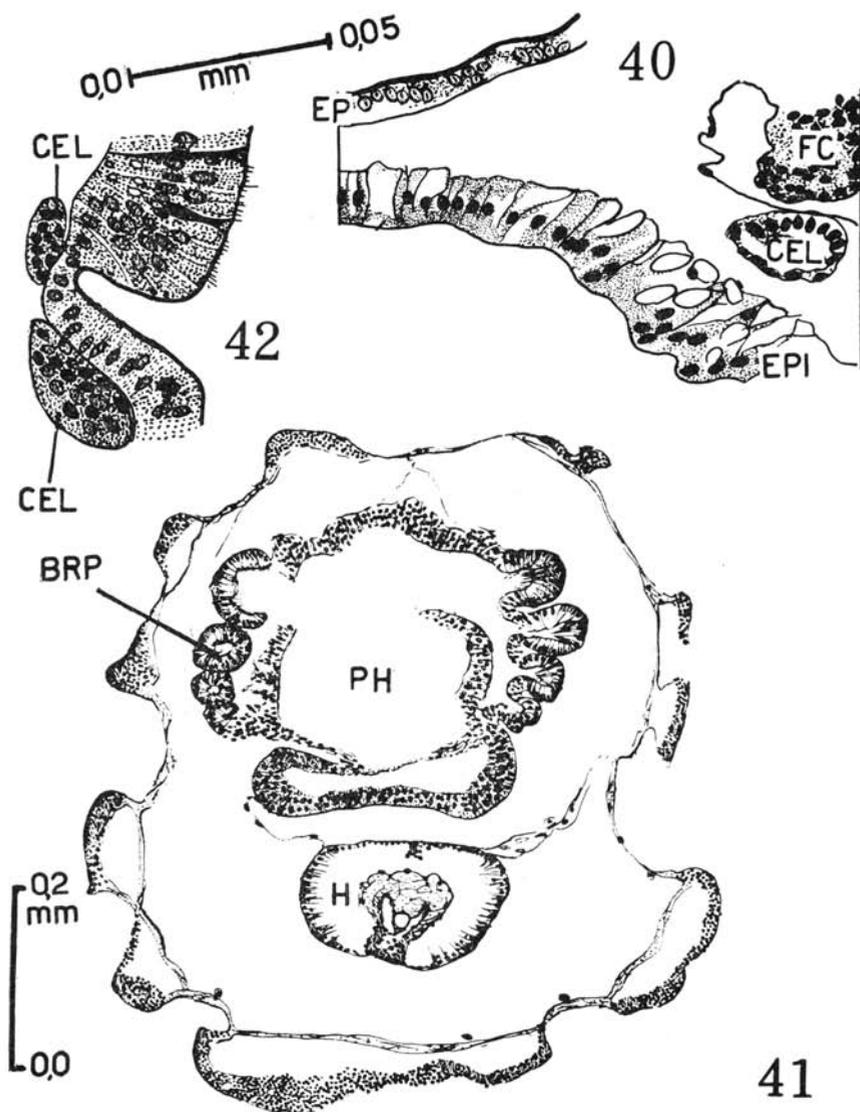
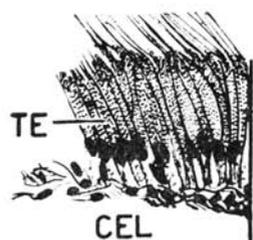


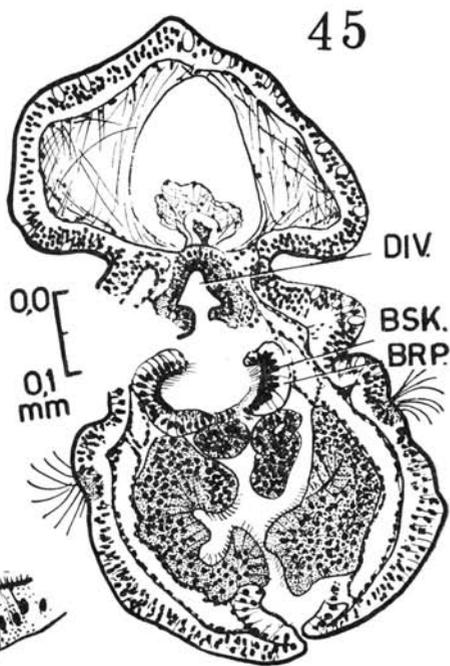
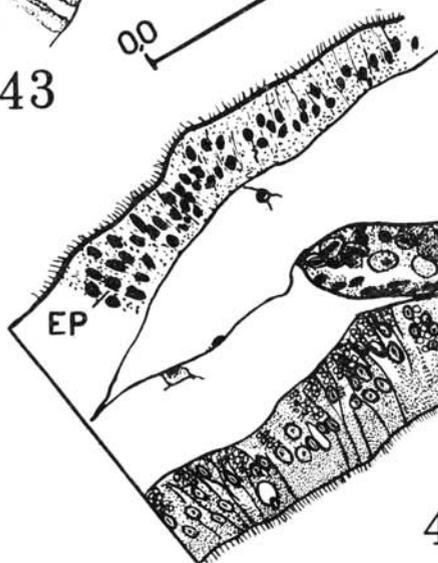
PLATE X

- Fig. 43 — Cross-section through larva in metamorphosis of *B. clavigerus*. Detail.  
Fig. 44 — Detail of sagittal section of larva in "Agassiz" stage of *B. clavigerus*.  
Fig. 45 — Horizontal section of larva in metamorphosis (0,73 mm long) of *B. clavigerus*.



43

0.05 mm



OM

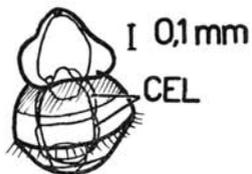
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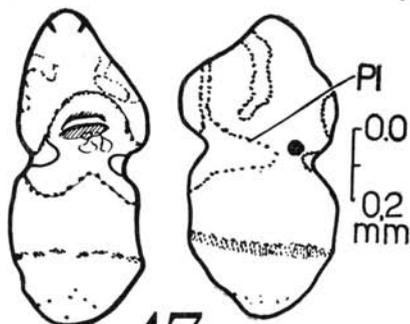
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PLATE XI

- Fig. 46 — Dorsal view of advanced "Agassiz" stage of development of *B. clavigerus*.  
Fig. 47 — "Agassiz" stage fixed in Bouin. Ventral and dorsal views.  
Fig. 48 — Coeloma of larva in "Spengel" stage of a 3,3 mm long tornaria *dubia*.  
Fig. 49 — Initial metamorphosis of *B. clavigerus*. From the living.  
Fig. 50 — The same after the preceding stage. Origin of branchial pouches.  
Fig. 51 — Larva in metamorphosis, one day after the stage figured in Fig. 49.  
Fig. 52 — The same, with three pairs of branchial pouches.  
Fig. 53 — The same, with four pairs of branchial pouches.



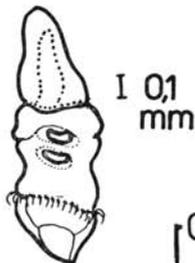
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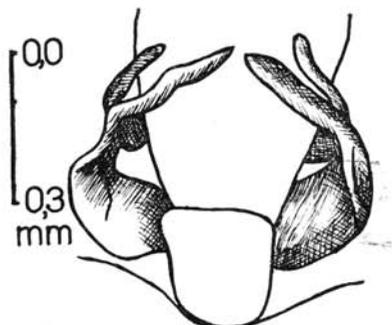
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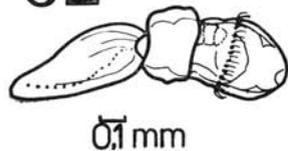


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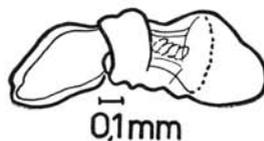


PLATE XII

- Fig. 54 — The nervous medulla of the collar in the larva of *B. clavigerus*. Cross-section.
- Fig. 55 — The neural groove in the larva of *B. clavigerus* in metamorphosis. Cross-section.
- Fig. 56 — Lateral view of larva of *B. clavigerus* with four pairs of branchial pouches after coloration with borax-carmines and clearing in clover oil.
- Fig. 57 — Sagittal section through larva in metamorphosis.
- Fig. 58 — Detail of Fig. 57, as indicated in the square.

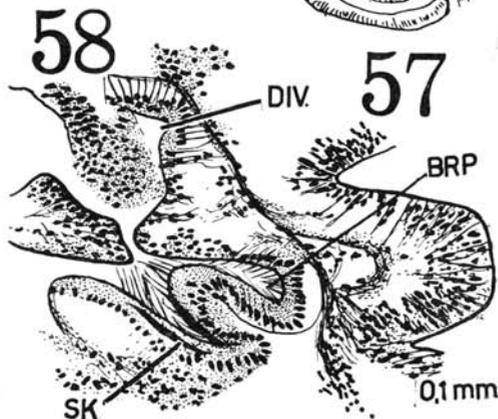
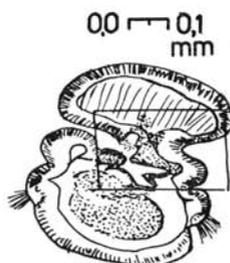
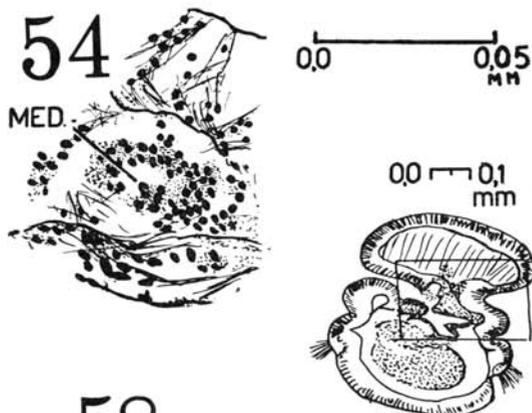
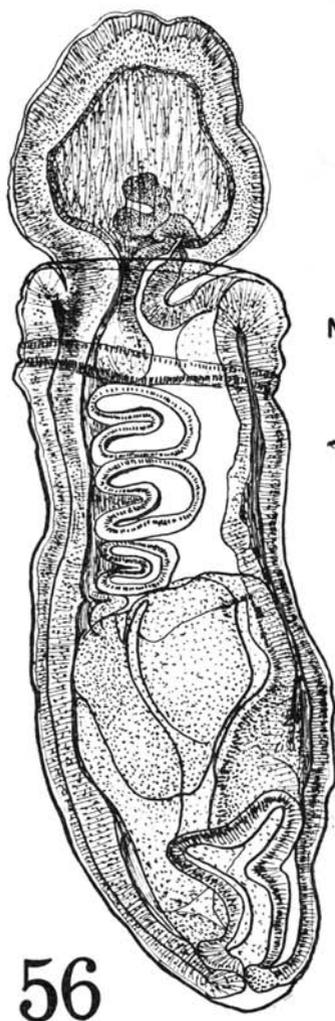


PLATE XIII

- Fig. 59 — Cross-section of larva of *B. clavigerus* (0,76 mm long) at the level of the branchial pore. Metamorphosis.
- Fig. 60 — Sagittal section of the proboscis of the larva figured in Fig. 56, Pl. 12.
- Fig. 61 — External epithelium of larva in metamorphosis, obtained by rearing of tornaria *dubia*.
- Fig. 62 — Detail of cross-section through tornaria *dubia* in metamorphosis, showing ectoderm, mesoderm and endoderm.

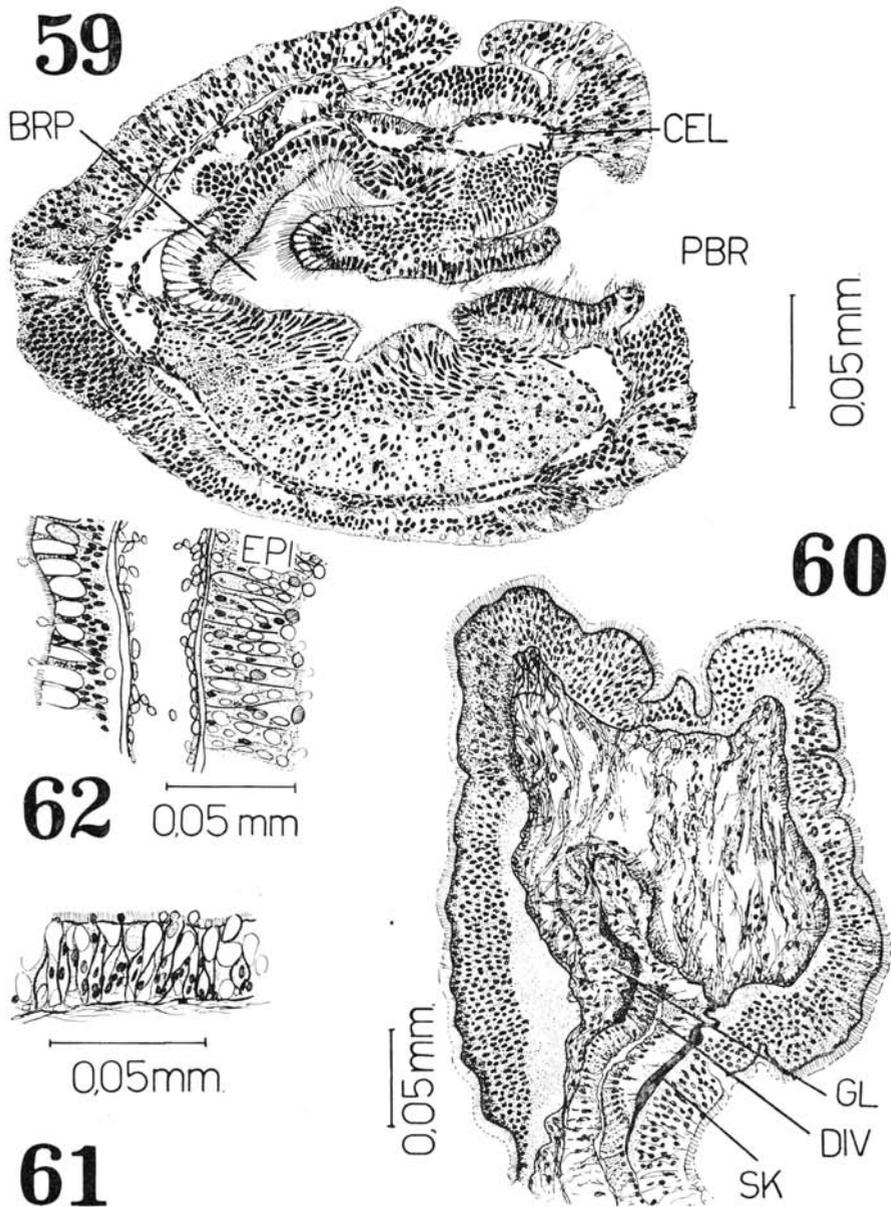


PLATE XIV

- Fig. 63 — Detail of sagittal section of proboscis of *B. clavigerus*, showing skeleton, diverticulum, etc. (Schematically).
- Fig. 64 — Detail of horizontal section of the same (proboscis diverticulum).
- Fig. 65 — Ventral view of skeleton of *B. clavigerus* obtained by maceration in potash at 1%.
- Fig. 66 — Cross-section of the collar of *B. clavigerus*, showing abnormal growth of the skeleton.
- Fig. 67 — The same, showing normal growth of the skeleton.

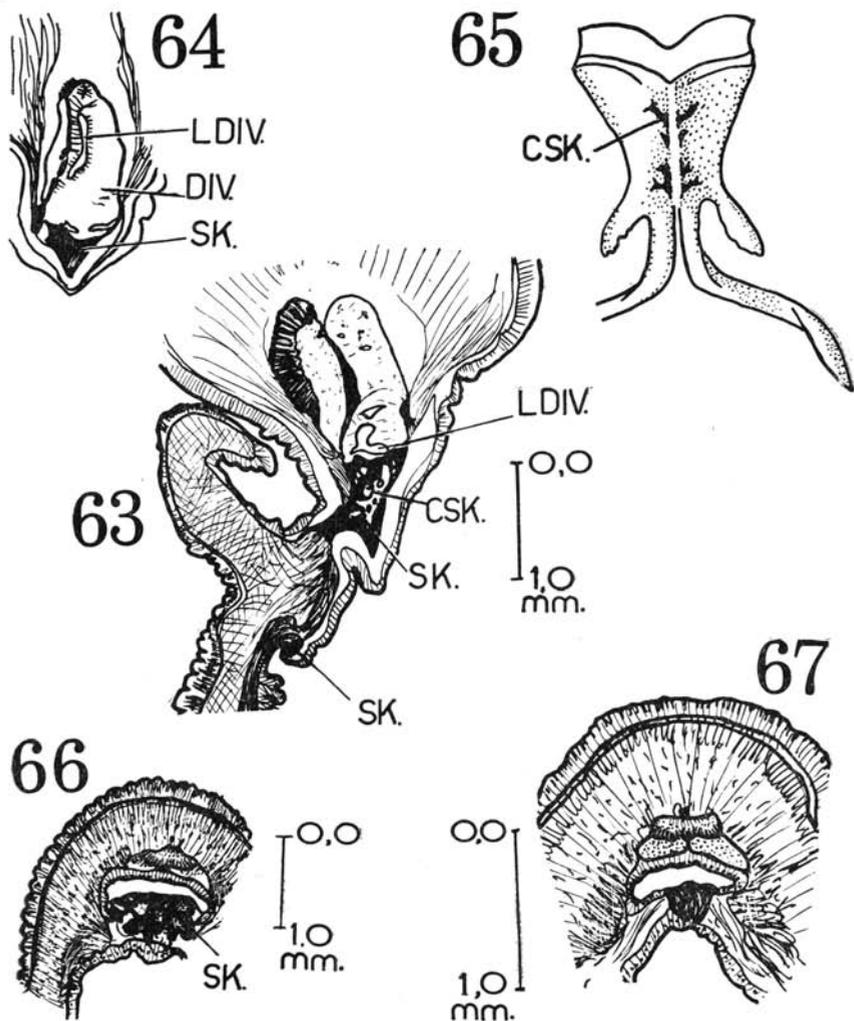


PLATE XV

- Fig. 68 — Detail of cross-section through collar region, showing dorsal medulla and nervous roots of *B. clavigerus*.
- Fig. 69 — Detail of cross-section through branchial region (*B. clavigerus*).
- Fig. 70 — Detail of sagittal section through transitional region between the branchial and the genital regions, showing postbranchial canal with blind pouch (*B. clavigerus*).
- Fig. 71 — The same without blind pouch (*B. clavigerus*).

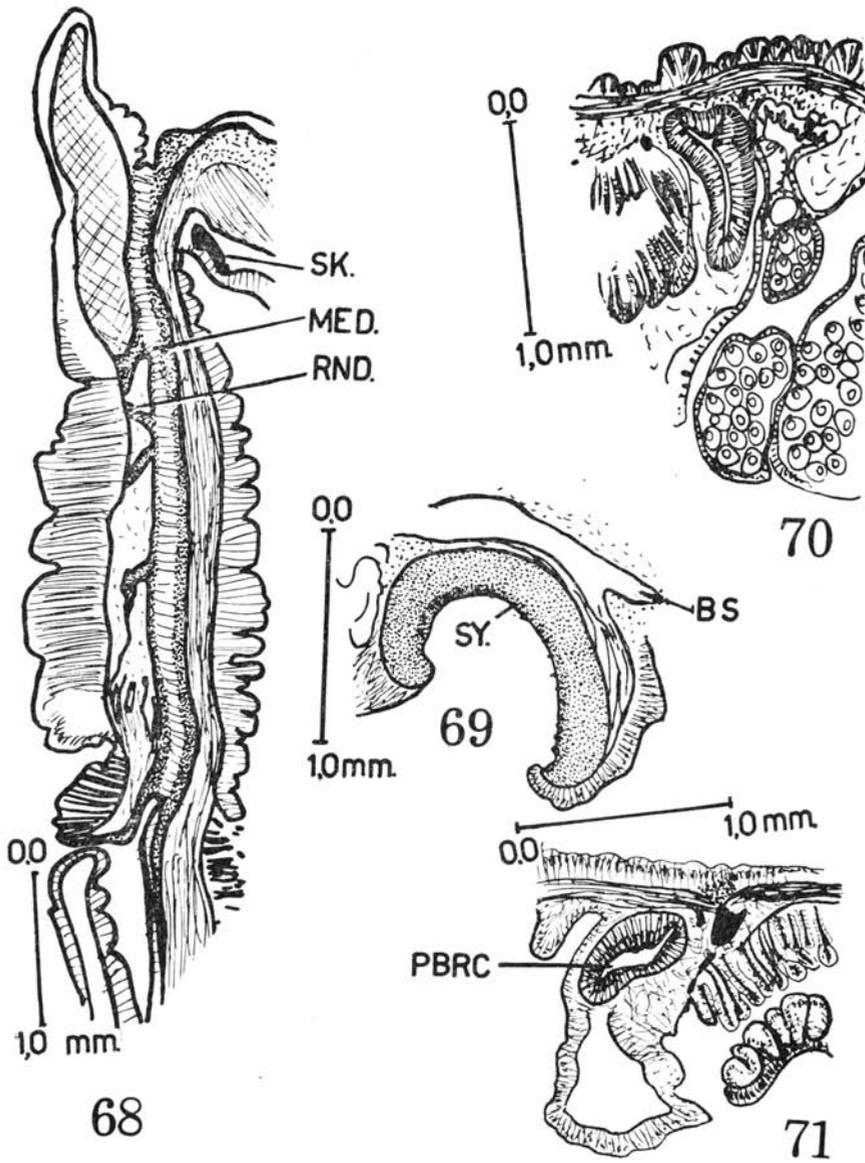


PLATE XVI

- Fig. 72 — *Balanoglossus gigas* (100 cm long). Cross-section of proboscis.
- Fig. 73 — The same anterior to the preceding section.
- Fig. 74 — Cross-section through the proboscis-neck in the same animal.
- Fig. 75-76 - Serial sections of proboscis neck and anterior collar region below the section of figure 74.
- Fig. 77 — The skeleton of *B. gigas* obtained by maceration in a solution of soda at 1%. Ventral view. The ramifications of the plate have not been represented in the drawing.

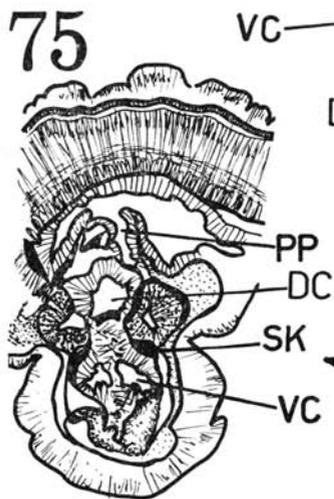
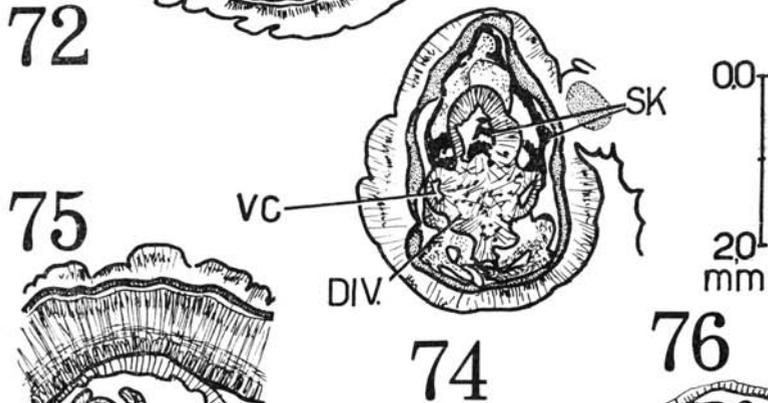
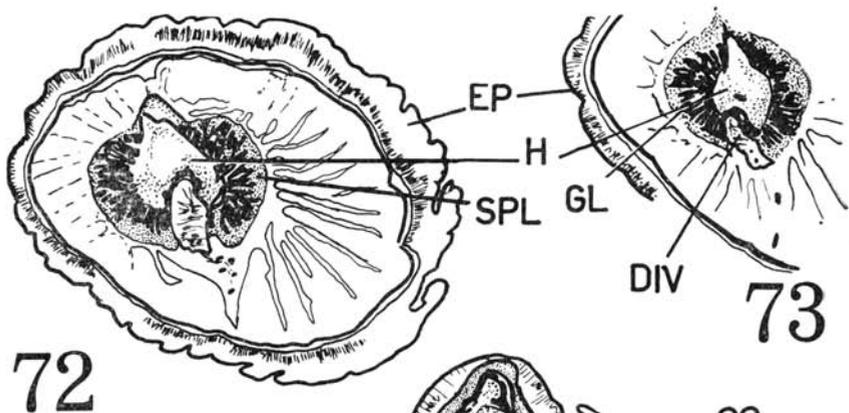


PLATE XVII

- Fig. 78 — Detail of cross-section through the wings of the proboscis skeleton at the height of the collar of *B. gigas*.
- Fig. 79 — Cross-section through the genital region of *B. gigas*.
- Fig. 80 — Branchial region of the same in cross-section.
- Fig. 81 — Schematic representation of longitudinal section of *B. gigas* with the directions of Spengel's (SP), Maser's (MA), and Willey's or the author's sections (T).

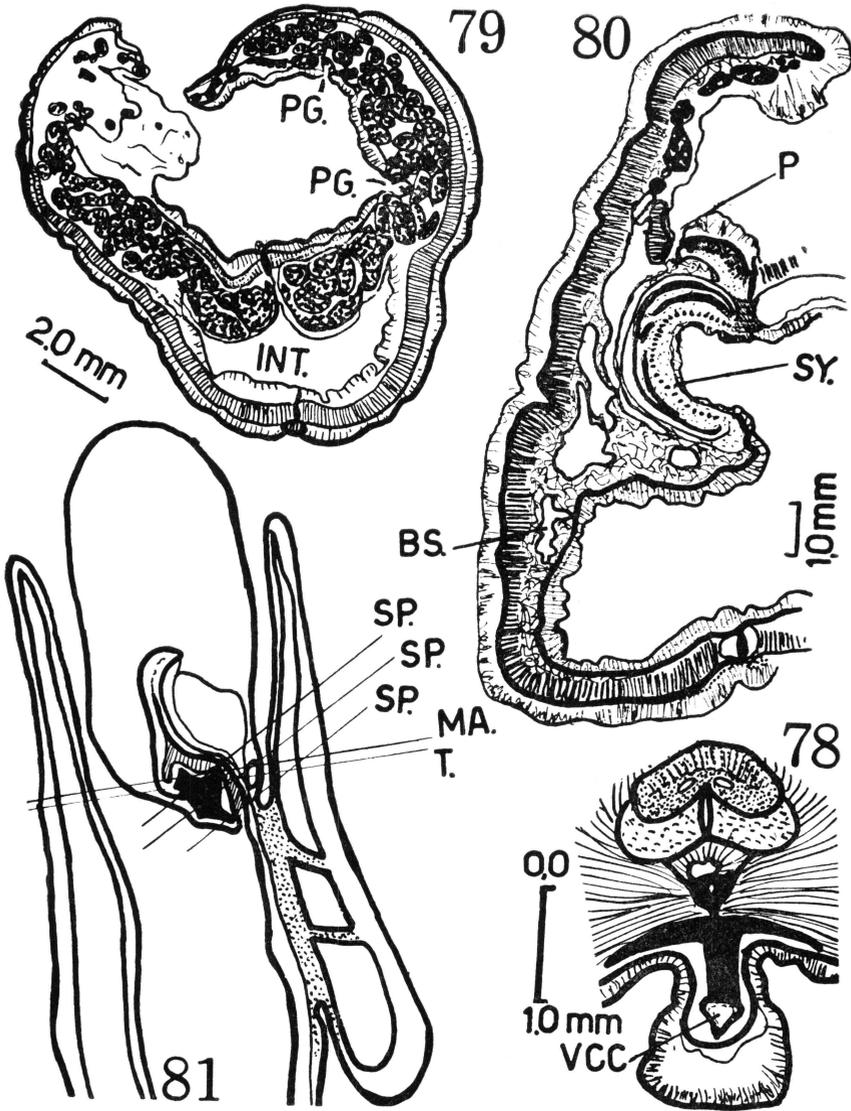


PLATE XVIII

Fig. 82 — Cross-section through the central proboscis organs of *Glossobalanus crozieri*.

Fig. 83-85 - Serial sections through the proboscis neck at the height of the proboscis pore.

Fig. 86-87 - Serial cross-sections through the keel of the skeleton of the proboscis.

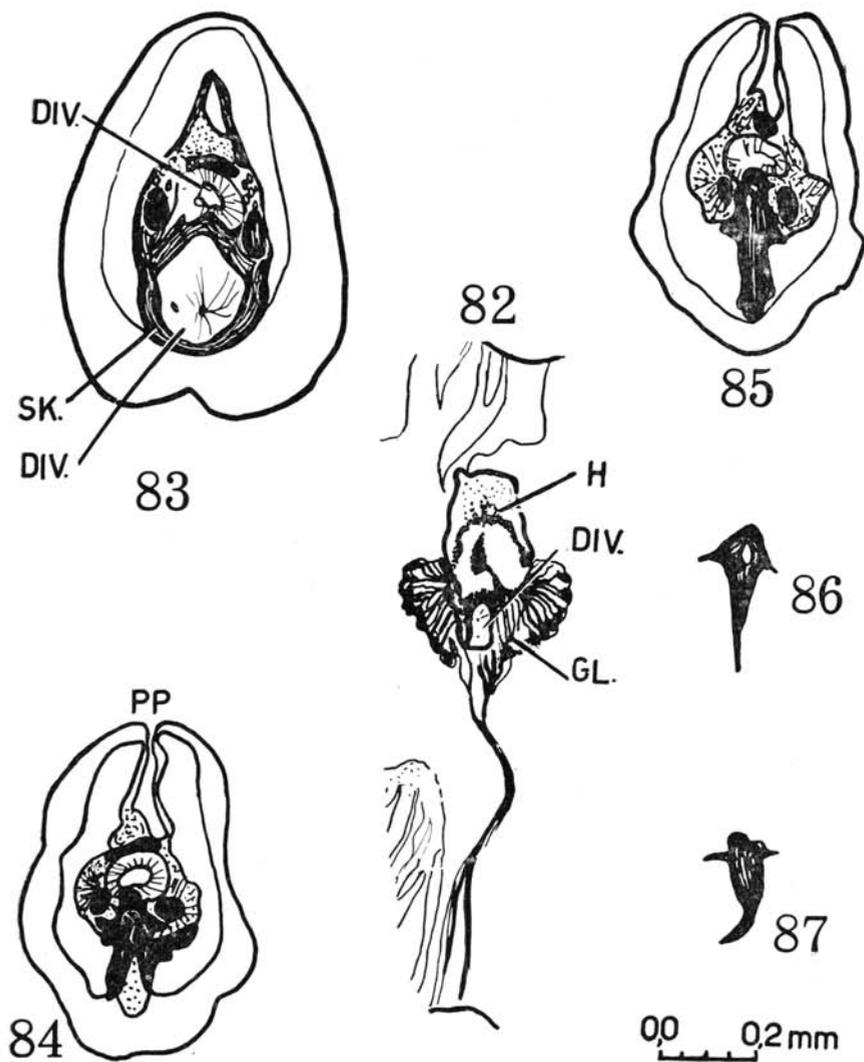


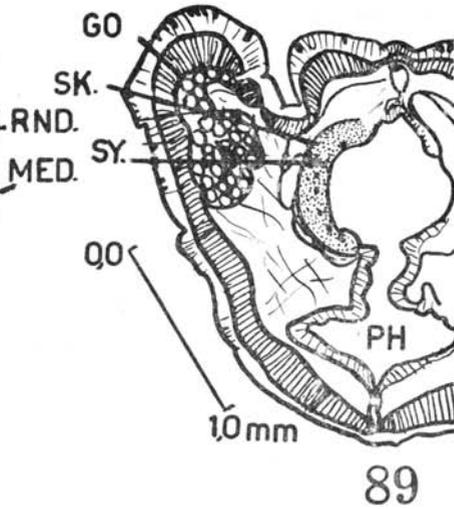
PLATE XIX

Fig. 88 — Detail of cross-section through the first nervous root of the medulla of *Glossobalanus crozieri*.

Fig. 89 — Cross-section through the branchial region of *G. crozieri*.

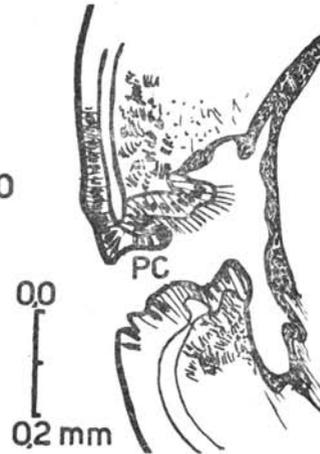
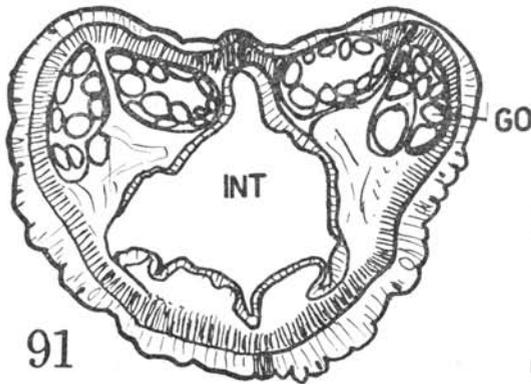
Fig. 90 — Cross-section through the collar-pore of *G. crozieri*.

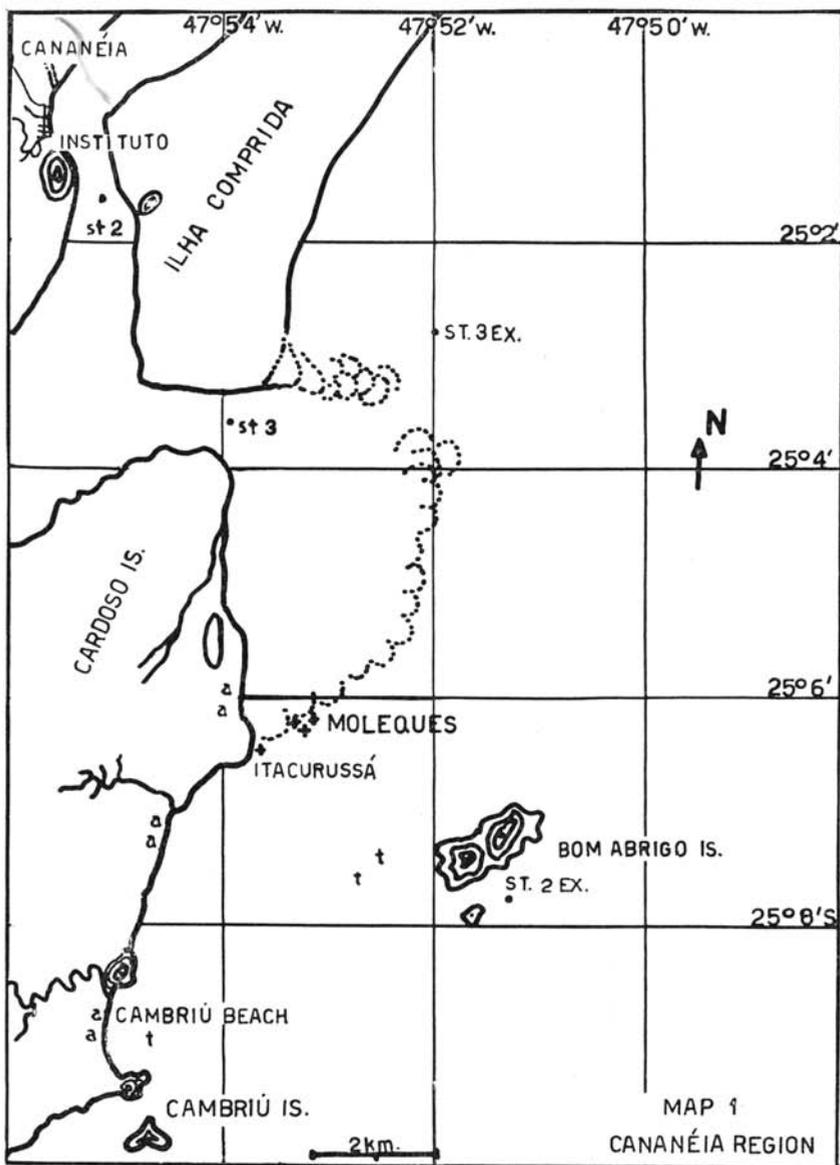
Fig. 91 — Cross-section through the genital region of *G. crozieri*.



00 — 1,0 mm

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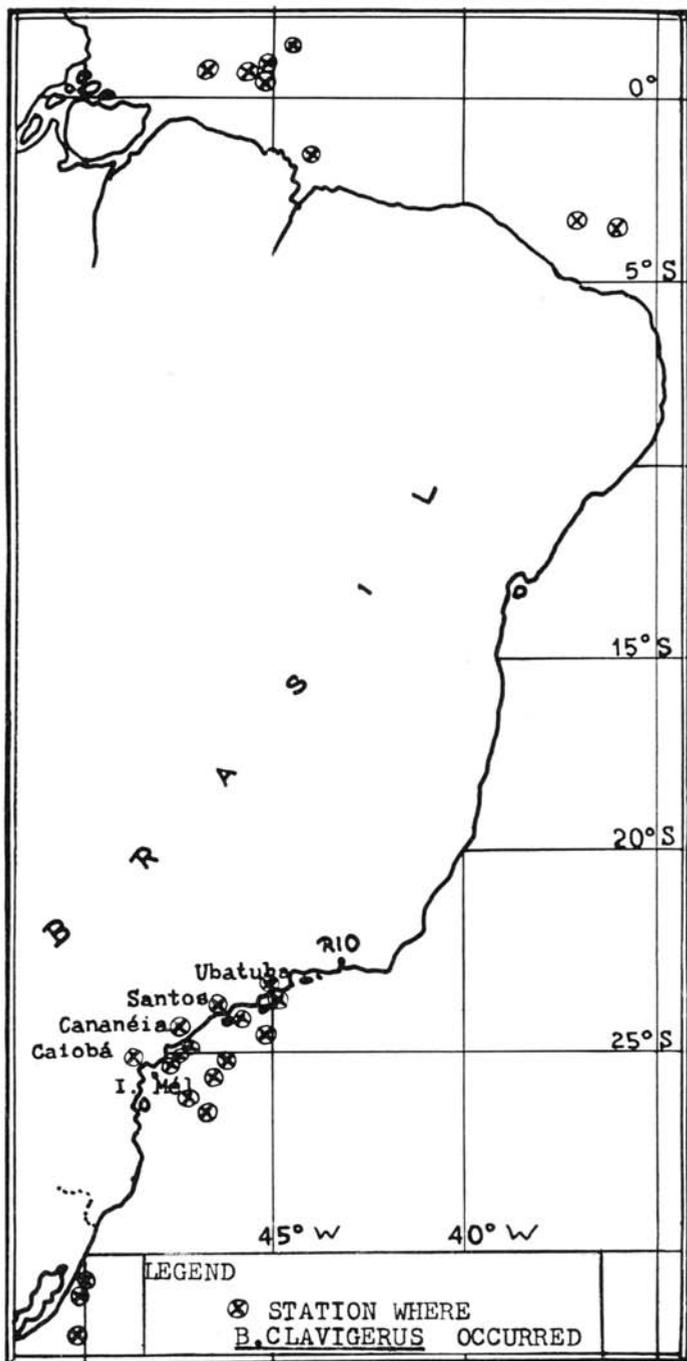




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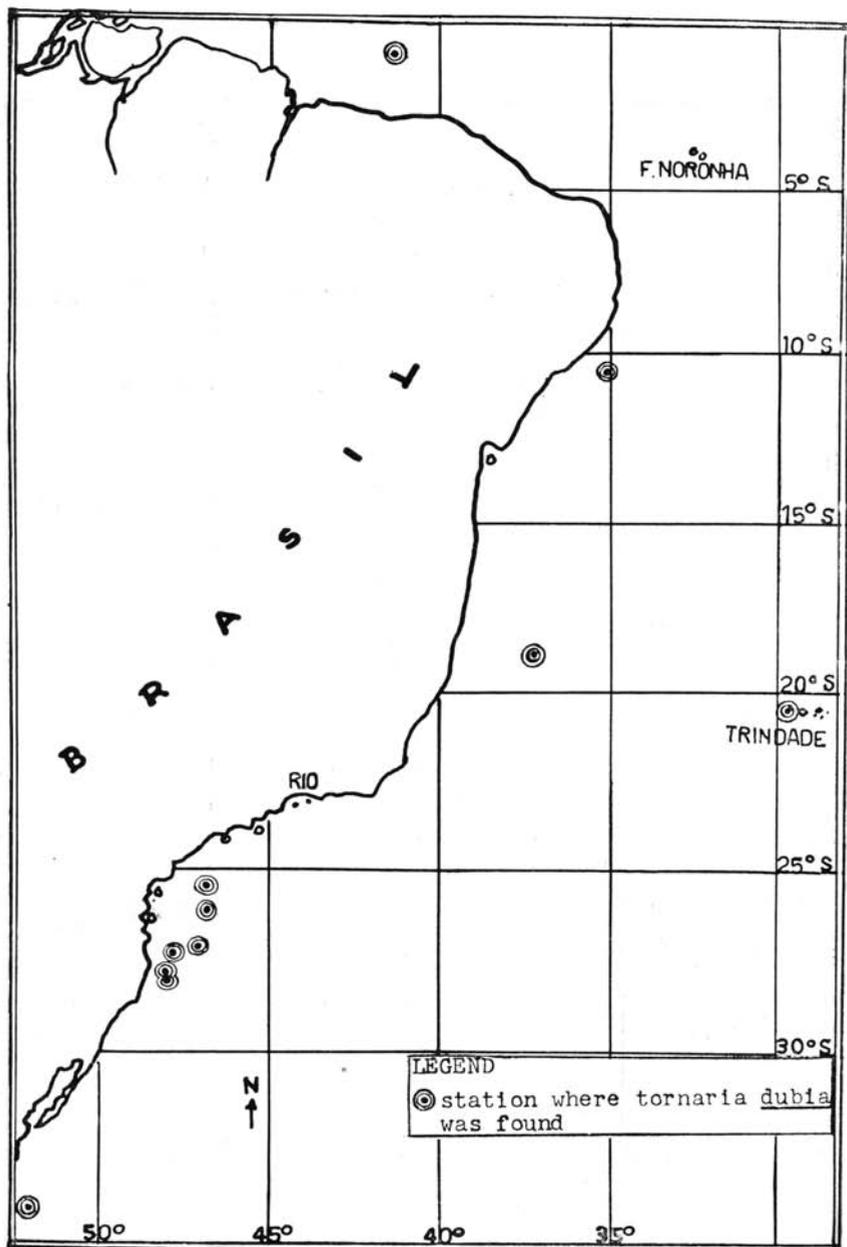
MAP 1 — CANANÉIA REGION

- st = Fixed stations
- ST = Fixed stations off the sand banks
- a = Places where adults were found
- t = Other places where larvae were collected

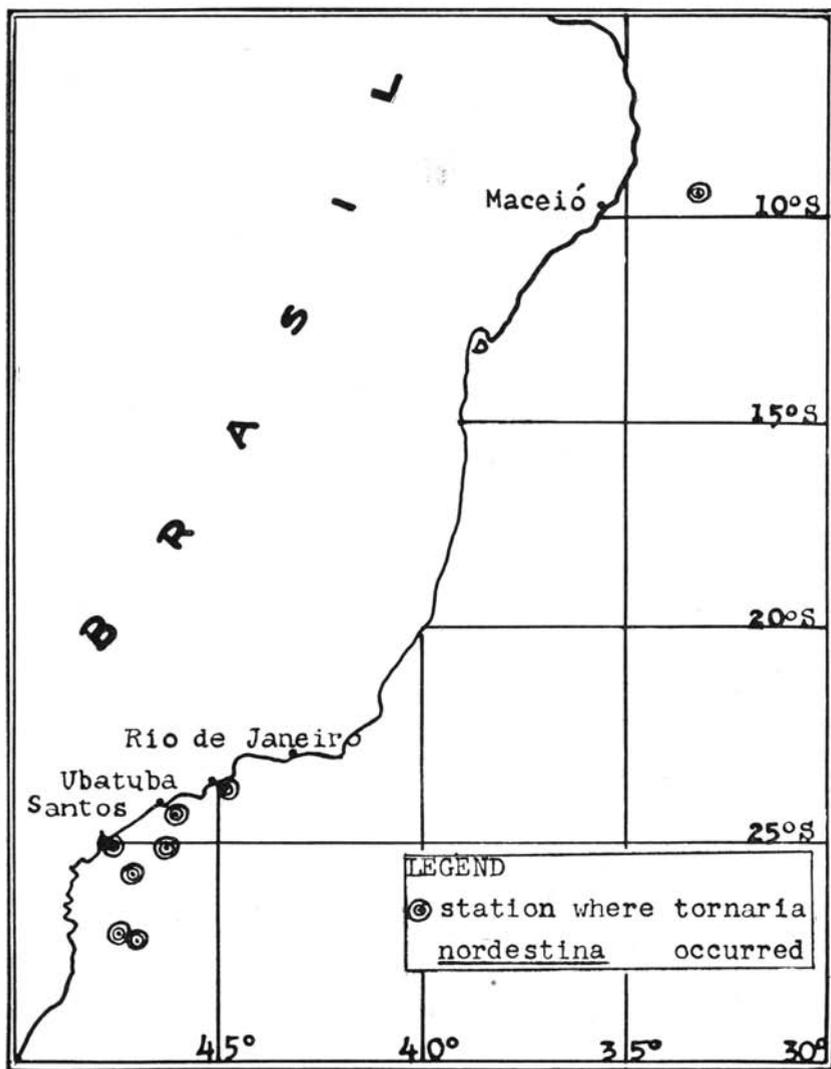


MAP 3 — OCCURRENCE OF *B. CLAVIGERUS*





MAP 5 — OCCURRENCE OF *TORNARIA DUBIA*.



MAP 6 — OCCURRENCE OF *TORNARIA NORDESTINA*.