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## CHAPTER 1

# Introduction to the Morphology, Phylogenesis, and Systematics of Lower Deuterostomia

### Jean E. A. Godeaux

## I. Phylum Hemichordata Bateson, 1885 (Van der Horst, 1932) (Stomochordata, Dawydoff, 1948).

### A. INTRODUCTION

The Hemichordata are exclusively marine coelomates which occur from the tidal area to rather great depths (e.g., *Glandiceps abyssicola*). They are either free-living, and then reaching a large size (*Balanoglossus gigas;* 1.5 meters), or sessile, colonial, or aggregated and then microscopic (*Rhabdopleura* sp., $<1$ mm) organisms. They are particle feeders, trapping their food by the way of their mucous secretions and ciliary activity.

The Hemichordata are Deuterostomia; the cleavage of the egg is radial and the coelomes appear by typical enterocoely. The larva is generally swimming and undergoes a progressive metamorphosis. The body of the adult is soft and has a perfect bilateral symmetry. It is divided into three segments, or metameres—the protosoma, mesosoma and metasoma—separated by more or less deep transverse grooves (Fig. 1). The phylum is divided into two classes (Willey, 1899), the members of which, in spite of quite dissimilar appearances, have the same embryological pattern and fundamentally identical anatomical structures.

1. Enteropneusta (Fig. 1), or acorn-worms, (e.g., *Balanoglossus* sp., *Ptychodera* sp.) are naked, free-living, wormlike animals, either creeping under stones or burrowing into sand. The body is devoid of any sense organ or appendage. Sexes are separated; regeneration, but probably not asexual reproduction, is possible.

2. Pterobranchia are aggregated or colonial, either tube-dwelling (*Cephalodiscus* sp., *Rhabdopleura* sp.) or naked (*Atubaria* sp.) animals. They are both sexual and blastogenetic organisms; sterile individuals have been observed in *Atubaria*. The body, globular, devoid of any visible sense organ, is provided with a kind of lophophore of tentaculated arms on the second segment, giving a superficially bryozoan habitus. Because of the extensive growth of the ventral side at the time of the settling and metamorphosis of the larva, the digestive tract is U-shaped and the anus and gonopores dorsally open, close to the aper-

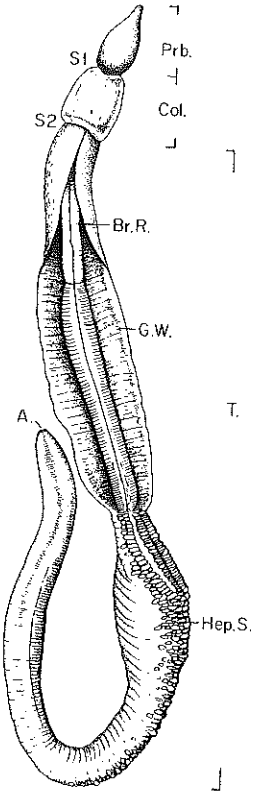

FIG. 1. *Balanoglossus clavigerus.* A = anus; Br.R. = branchial region of the trunk; Col. = collar (mesosoma); G.W. = genital wings; Hep.S. = hepatic sacculations; Prb. = proboscis (protosoma); s1, s2 = grooves between the three main parts of the body; T = trunk (metasoma). (From Spengel, after Dawydoff, 1948.)

ture of the protective tube, the coenecium or tubarium. We convergently find a plan common to all the sessile coelomates—Kamptozoa, Bryozoa, Phoronida, Crinoidea and Tunicata (Ascidiacea). In *Cephalodiscus,* the unconnected zooids live side by side in the tubes of the coenecium; in *Rhabdopleura,* the individuals are bound together by the black stolon giving off a branch to every zooid.

The Hemichordata are ancient animals as several ordovician prints have been described as tubes of fossil Rhabdopleuridae (Kozłowski, 1970). Considerable investigations have been done on the hemichords and several treatises have been devoted to them (Spengel, 1893; Delage and Hérouard, 1898; Bergensen and Broch, 1932; Van der Horst, 1932, 1939; Dawydoff, 1928, 1948; Hyman, 1959; Barrington, 1965), especially because of Batesons' attempts (1884, 1885, 1886) to include these organisms among the lower chordates.

*Remark*

The graptolites, marine and colonial fossil organisms, known from the palaeozoic era and classically associated to Cnidaria, represent a third extinct class, Graptolithina, believed at one time to be related to Pterobranchia (Kozłowski, 1947, 1948). The relationship was disproved, however, by Bohlin, (1953) and Hyman, (1959). Their skeletal formations contain scleroproteins but no trace of chitin (Foucart and Jeuniaux, 1965).

### B. GENERAL FEATURES

The Hemichordata are triplobastic organisms provided with five coelomic cavities (as obvious also in some echinoderm larvae) lined by a flat epithelium—an odd and rather reduced protocoele in the protosoma, a pair of mesocoeles in the mesosoma and a pair of metacoeles in the metasoma. The pore of the protocoele, in some case duplicate, early opens into the future nuchal groove. Those of the mesocoeles open at the limit between the meso and metasoma. The metacoeles are closed.

The protosoma of the Enteropneusta (Fig. 2) is a strongly muscular and vascularized tool (proboscis) used in burrowing. In Pterobranchia (Fig. 3), the protosoma develops as a stalked, discoidal, and glandular shield which secretes the tubular coenecium (an outer skeleton devoid of chitin and poor in proteins, Foucart *et al.*, 1965).

The mouth opens ventrally between the two first segments. It is just a simple hole without lips or teeth, but protected in the Pterobranchia by the oral lamellae directing the food to the gut.

The mesosoma, or collar, of the Enteropneusta is short and devoid of appendage. Its musculature is well developed. The most interesting anatomical fact is a middorsal nervous depression, which in some higher species (Ptychoderidae) transforms into an intraepidermic tube opened at both ends by a kind of neuropore. Instead of this structure, the Pterobranchia possess an intraepidermic ganglionic mass furnishing nerves to the arms of the lophophore.

The metasoma or trunk of *Balanoglossus* is very long and slender. It shows numerous branchial slits, contains the straight digestive tract and gonads (without any connections with the metacoeles). Several successive sections can be defined by pseudometameric structures—foremost the numerous branchial slits, then the gonads and the hindmost swellings of the body wall due to the "hepatic" lobules differentiated

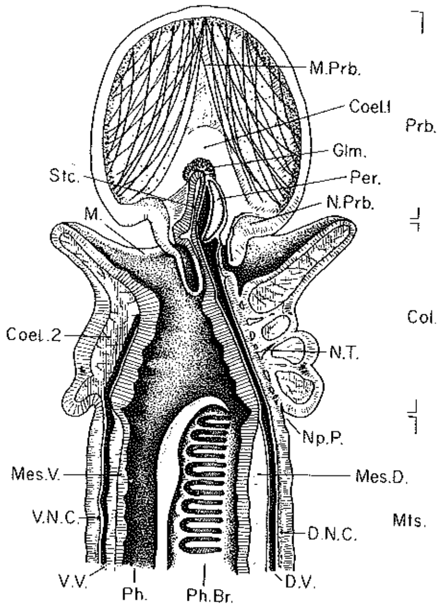

FIG. 2. Sagittal hemisection in the fore end of a *Balanoglossus*. Coel. 1 = protocoele; Coel. 2 = mesocoele; Col. = collar (mesosoma); D.N.C. = dorsal nervous cord; D.V. = dorsal blood vessel; Glm. = glomerulus; M. = mouth; Mes.D., Mes.V. = dorsal and ventral mesenteries; M.Prb. = musculature of the proboscis; Mts. = metasoma; Np.P. = posterior neuropore; N.Prb. = nerve ring of the proboscis; N.T. = nervous tube; Per. = pericardium; Ph. = pharynx; Ph.Br. = branchial region of the pharynx; Prb. = proboscis (protosoma); Stc. stomochord; V.N.C. = ventral nervous cord; V.V. = ventral blood vessel. (From Spengel, after Dawydoff, 1948.)

into the gut. The multiple gonads have their own tiny pores. The anus is terminal.

In Pterobranchia, the metasoma is protected by the skeleton; it also contains the main viscera—digestive apparatus and gonads. The musculature is weak. A single pair of lateral branchial pores is present in *Cephalodiscus,* but is lacking in *Rhabdopleura.* The simplicity of the branchial system may be related to the presence of a protective coenecium and of a lophophore and to the strong reduction of the size of the animals. On the ventral face protudes the long muscular stalk, involved in the budding. The metasoma shows no sign of segmentation.

## C. ONTOGENESIS

With respect to the mass of yolk, the development of the egg of the enteropneusts is either condensed or indirect. Condensed develop-

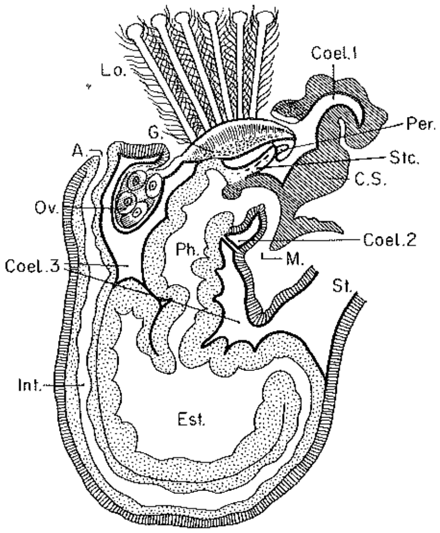

FIG. 3. Sagittal section in *Cephalodiscus dodecalophus;* general organization of the zooid. A. = anus; Coel. 1 = protocoele; Coel. 2 = mesocoele; Coel. 3 = metacoele; C.S. = cephalic shield; Est. = stomach; G. = ganglion; Int. = intestine; Lo. = lophophore; M. = mouth; Ov. = ovary; Per. = pericardium; Ph. = pharynx; St. = stolon; Stc. = stomochord. (From Harmer, after Dawydoff, 1948.)

ment gives an oval, completely ciliated, and swimming larva (this swimming stage may be lacking), which quickly undergoes a progressive metamorphosis. The indirect development is like that of an echinoderm, giving a planktonic ciliated larva, the tornaria. At first this larva was considered the larva of a starfish (Joh. Müller, 1849) but was later identified by Metschnikoff (1870). The metamorphic changes are more pronounced in this case (Fig. 4).

The cleavage is holoblastic, equal or subequal, and of the radial type; it gives a ciliated blastula transforming into a gastrula by invagination of the vegetal hemisphere. The blastopore is posterior, never moves toward the ventral side (cf. echinoderm larva), and, by its permanent position, corresponds to the anus of both the larva and adult. The mouth is always a ventral neoformation. Any calcareous inner skeleton is missing. The five coelomic cavities appear independently or not, but always by enterocoely. The Hemichordata are, then, true Deuterostomia.

The tornaria is globular, with a well developed blastocoele (Fig. 4a). The digestive tract is a single endoblastic tube with an intermediary large gastric pouch. Above this, the flattened anterior coelomic cavity, the future proboscis coelom, is triangular and bound to the apical ner-

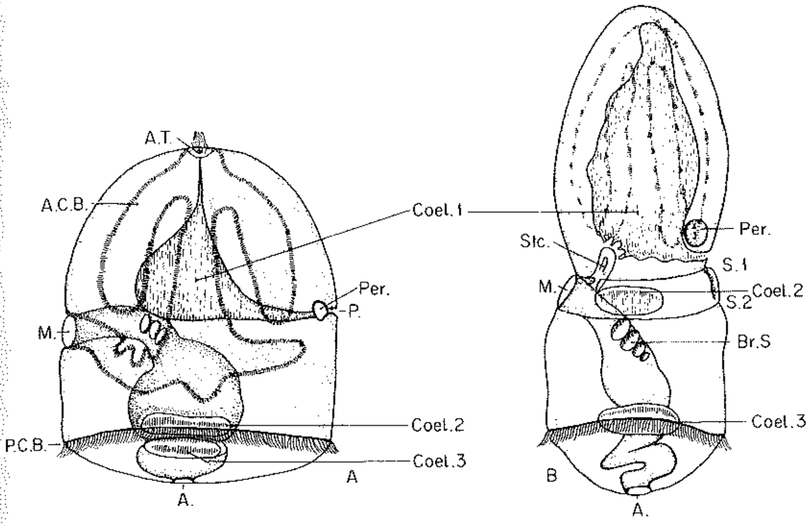

FIG. 4. Tornaria—two stages of metamorphosis (A) old tornaria, (B) young worm. A. = anus; A.C.B. = anterior ciliary band; A.T. = apical thickening; Br.S. = branchial slits; Coel. 1 = protocoele; Coel. 2 = mesocoele; Coel. 3 = metacoele; M. = mouth; P = pore of the protocoele; P.C.B. = posterior ciliary band; Per. = pericardium; S. 1, S. 2 = grooves between the three parts of the body; Stc. = stomochord. (After Dawydoff, 1948.)

vous thickening by a muscular string (generally contractured by fixatives); the cavity opens dorsally. Later, not far from the pore, will appear the contractile heart vesicle, which may be of coelomic origin. The mesocoeles and metacoeles are poorly developed in the larva and swell later on during metamorphosis.

The epidermis develops two locomotor ciliary bands. The upper one around the mouth becomes more and more complicated and very sinuous. The lower one remains a single ring of tall ciliated cells around the anal area.

The larva changes into adult by elongation of the body (Fig. 4b), settling on the bottom and disappearance of the now useless cilia. Two transverse constrictions separate the three segments of the future adult, and, thanks to their allometric growth, the collar and especially the trunk become the main parts of the body (see Burdon-Jones, 1952, 1956a).

The development of the Pterobranchia is direct. The larva is ciliated and swims before settling. Moreover, the Pterobranchia are capable of asexual reproduction; buds (*Cephalodiscus*) develop as extroflections of the ectomesoblastic wall of the stalk and the newly formed zooids remain associated as in a true colony (*Rhabdopleura*) or as a group of neighbour individuals (*Cephalodiscus*).

The affinities between Enteropneusta and Pterobranchia could be clarified if the former are considered as neotenic larvae of the latter (Burdon-Jones, 1952; Vandel, 1961).

## D. STRUCTURE AND HISTOLOGY OF THE MAIN SYSTEMS AND ORGANS

### 1. *Enteropneusta*

The ectoderm is pseudostratified and composed of several kinds of high ciliated and secretory cells. It is in close contact with the underlying nervous plexus covering the whole body (Knight-Jones, 1952). The nervous fiber layer lies above the conspicuous basement membrane separating the neuroectoderm from the mesodermic musculature. Study of the fine structure was done by Nørrevang, (1965a,b) and Dilly *et al.*, (1970). In the trunk, the nervous plexus concentrates into two longitudinal strands, one midventral, the other middorsal, joined by a prebranchial ring. The middorsal strand runs forward to the proboscis forming a nervous ring around its base; in the collar, the same strand is transformed by invagination into the neurocord with a lumen often reduced to a series of small lacunae. Only the floor of this cord is of a nervous nature very similar to the nervous plexus; it does not receive or give off any trunks, but contains giant nerve cells and axons (Bullock, 1946). This neurocord has been held as homologous to the spinal cord of the chordates, despite quite a different type of organization.

There are two muscular layers of mesoblastic origin. The outer is circular and always very thin; the inner is longitudinal. The latter is very important in the proboscis, reducing the coelom to a small cavity. Burrowing results from the peristaltic activity of these muscles. In the collar, the longitudinal strands are also well developed, playing an important role in the locomotion processes. In the trunk, the circular musculature is feeble or wanting, and only the longitudinal layer is important, especially on the ventral side (Fig. 5). In these two last segments, the muscles wrap the coelomic cavities partitioned by the dorsal and ventral mesenteries, supporting the dorsal and ventral longitudinal blood vessels and the digestive tract.

In higher species, the metacoeles send into the mesosoma the peripharyngeal and perihaemal diverticula, beside the pharynx and the dorsal blood vessel, respectively.

The digestive tract runs straight from the mouth to the anus. The buccal cavity dorsally gives off a more or less long cecum (Fig. 2) with vacuolized walls, extending into the protosoma. This preoral cecum

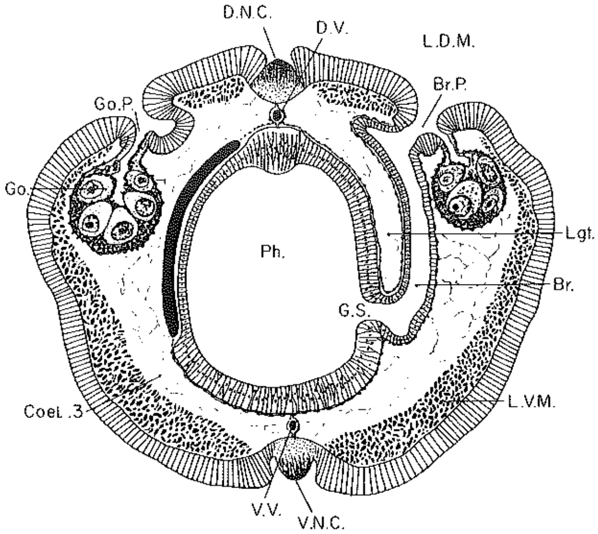

FIG. 5. Transverse section in the branchiogenital region of the trunk of *Saccoglossus* sp. Br. = branchiae; Br.P. = branchial pore; Coel. 3 = metacoele; D.N.C. = dorsal nervous cord; D.V. = dorsal blood vessel; Go. = gonad; Go.P. = pore of the gonad; G.S. = gill slits; L.D.M., L.V.M. = longitudinal dorsal and ventral musculature; Ph. = pharynx; V.N.C. = ventral nervous cord; V.V. = ventral blood vessel. (After Dawydoff, 1948.)

is the so-called "hemichord" (Bateson, 1885), or more correctly, stomochord (Dawydoff, 1948), considered the most characteristic organ of the Hemichordata (Stomochordata). Below the buccal diverticulum lies a tabular thickening of the basement membrane (scleroproteins), the proboscis skeleton, with two posterior horns (the crurae) strengthening the sides of the buccal opening.

In the anterior part of the metasoma, the walls of the gut are pierced by numerous (10–200 pairs) gill slits. Each primary slit is eventually divided into two secondary slits by a septum; they are supported by skeletal rods (which in fact are but local thickenings of the basement membrane like the proboscis skeleton). This branchial apparatus recalls the system of the *Amphioxus*. But as the slits open dorsally and as nothing suggests either the peribranchial cavity or the endostylar groove of the later animal, the gills of Enteropneusta and Cephalochorda are analogous, not homologous, organs.

Posterior to the branchial section and the esophagus is the intestine with dorsal paired sacculations, the "hepatic" lobes. In the intestine, digestion and absorption take place.

The blood system is composed of the two main longitudinal vessels connected by several meshworks of small vessels and lacunae spread over the gut, gonads, branchial system and muscles. In the protosoma, above the hemichord, the dorsal vessel swells into a central sinus, overlayed by the pulsating heart vesicle acting as a propeller of the blood into the glomerulus, a specialized part of the coelomic epithelium, the real function of which is still unknown. The colorless blood runs forward in the dorsal vessel and backward in the ventral one.

No excretion apparatus, like nephridia, are known; as the protocoele opens exteriorly, the glomerulus is supposed to be of an excretory nature, although there is no experimental support for this hypothesis.

The numerous gonads lay between the body wall and the metacoeles, even penetrating into the lateral aliform processes in the Ptychoderidae. The minute gonopores open dorsally.

### 2. *Pterobranchia*

The general plan of organization is only slightly modified from that of Enteropneusta. The striking differences are the development of the nervous thickening below the lophophore, the weakness of the musculature, and the reduction (*Cephalodiscus, Atubaria*) or the absence (*Rhabdopleura*) of the branchial system. The buccal cecum is very short and does not penetrate into the dorsal shield. A heart vesicle is present in the protosoma, surrounding the blood sinus. The gonad (simple or duplicate) is dorsally located between the stomach and the hindgut. Both metacoeles extend into the ventral stalk and give the coelomic cavities of the blastozooids.

## E. AFFINITIES

The affinities with the echinoderms (Ubaghs, 1969) are incontestable; the parallelism between both developments and the similarity of the larval organisms are striking—the same type of cleavage, retention of the blastopore as the anus, and especially the five enterocoelous coelomic cavities, the first one opening early to the outside by a dorsal pore. The main differences are the lack of any skeletogenous mesenchyme and of a necrotic metamorphosis in Hemichordata. Moreover, their larval symmetry remains unaltered in the adult organism.

The Hemichordata, and more precisely the Enteropneusta, also look very close to the Pogonophora. The body is trisegmented and contains five coelomic pouches. But important differences in the internal anatomical features prohibit the inclusion of Hemichordata and Pogonophora in a single phylum. As already stated, the resemblances between Pterobranchia and different sessile organisms, even belonging to the deuterostomian group (Crinoidea, Ascidiacea), are pure convergence.

On the other hand, the presence of the gut diverticulum (alias hemichord), of a dorsal nervous tube, the pharyngotremy, the apparently metameric distribution of the gills and gonads in the trunk have repeatedly incited eminent zoologists to relate the Chordata to the Hemichordata or even to the Echinodermata (Bateson, 1884, 1885, 1886; Delage and Hérouard, 1898; Willey, 1899; Gislén, 1930; Jefferies, 1967). This hypothesis is still a matter of controversy, for the characters invoked generally seem to be more the result of convergence phenomena than proof of real affinities. Otherwise, in the ontogenetic processes of the Hemichordata, nothing evokes the neurula stage specific of the Chordata phylum.

## F. SYSTEMATICS

Two classes, Enteropneusta and Pterobranchia, have been recognized. (Bergensen and Broch, 1932; Van der Horst, 1932; Dawydoff, 1948; Hyman, 1959).

*First Class*—Enteropneusta are distributed among four families, the characteristic features of which are the complexity of the branchial apparatus, the size and the shape of the stomochordal diverticulum, the length and the shape of the crurae, and the presence or the absence of the peripharyngeal and perihaemal diverticula.

*First Family*—Protobalanidae, with a single species. Pieces of the branchial skeleton free, coeloms with a permanent embryonic condition, glomerulus little developed, no metacoelic diverticula. This family is sometimes included in the next one (Burdon-Jones, 1956b). *Protobalanus* (*Protoglossus*) *koehleri.*

*Second Family*—Harrimaniidae. Branchial synapticula wanting, perihemal diverticula wanting, hepatic sacculations not visible from outside, gonads simple. *Harrimania kupfferi; Saccoglossus* (*Dolichoglossus*)*kowalevskii.*

*Third Family*—Spengelidae. Stomochord long, divided into three segments, (the median swollen, the hindmost wormlike), crurae long, hepatic lobulations and lateral aliform processes wanting. *Glandiceps talaboti* (larva = *Tornaria dubia*); *Glandiceps abyssicola* (from a depth of 4500 meters); *Schizocardium braziliense.*

*Fourth Family*—Ptychoderidae, with the largest and most differentiated species. Crurae short, perihaemal and peripharyngeal diverticula present, metacoeles segmented by transverse septa, lateral genital wings, hepatic lobulations prominent, division of the pharyngeal cavity into a dorsal branchial and a ventral digestive parts. *Balanoglossus clavigerus; Ptychodera flava.*

*Second Class*—Pterobranchia include two families and a few genera.

*First Family*—Cephalodiscidae. (a) Genus *Cephalodiscus,* with four subgenera according to the structure of the coenecium. *Cephalodiscus* (*Orthoecus*) *densus. Cephalodiscus* (*Demiothecia*) *dodecalophus.* (b) Genus

*Atubaria.* Coenecium wanting, structure recalling that of Cephalodiscus. A single species, *A. heterolopha.*

*Second Family*—Rhabdopleuridae = genus *Rhabdopleura.* Coenecium as a network of creeping tubes with free erect chambers housing the zooids. *Rhabdopleura normani, R. compacta.*

### *Remark*

*Planctosphaera pelagica* (Spengel, 1932; Van der Horst, 1936; Damas and Stiasny, 1961) is a spherical larva of a very large size. Its structure is not fundamentally different from the structure of a tornaria and *P. pelagica* seems no more than the larva of a still unknown and maybe abyssal hemichordate.

## C. ECOLOGY AND GEOGRAPHIC DISTRIBUTION

Enteropneusta are largely widespread, especially in tropical, subtropical, and temperate waters. They are lacking in the Antarctic area but at least one species is living in the Arctic Ocean and is circumpolar. Many species are only known by one or a few specimens. Some species are endemic, others widely distributed (for more details, see Hyman, 1959). *Balanoglossus clavigerus* lives on the southern and western coasts of Europe; *Harrimania kupfferi* is characteristic of the North and Baltic Seas; *Ptychodera flava* is known from the eastern coasts of Africa to Galapagos Islands; *Saccoglossus kowalevskii* is met from Massachusetts to Carolina and on European coasts.

Pterobranchia easily escape the observers. Genus *Cephalodiscus* is especially known from the Southern Hemisphere, e.g., *Cephalodiscus dodecalophus,* first discovered in the Strait of Magellan. *Atubaria heterolopha* was found for the first time in a dredging along the Japanese coast. Genus *Rhabdopleura* is known from the Northern Hemisphere, e.g., *Rhabdopleura normani* or *R. compacta* dredged along the European coasts. (See Stebbing, 1970.)

## REFERENCES

Barrington, E. J. W. (1965). "The Biology of Hemichordata and Protochordata." Oliver & Boyd, Edinburgh.

Bateson, W. (1884). *Quart. J. Microsc. Sci.* **24**, 208.

Bateson, W. (1885). *Quart. J. Microsc. Sci.* **25**, Suppl., 81.

Bateson, W. (1886). *Quart. J. Microscr. Sci.* **26**, 511 and 535.

Bergensen, B., and Broch, H. (1932). *In* "Handbuch der Zoologie" (W. G. Kükenthal and T. Krumbach, eds.), Vol. 3, Part 2, No. 2, Book 8, p. 1. de Gruyter, Berlin.

Bohlin, B. (1953). *Bull. Geol. Inst. Univ. Uppsala* **34**, 107.

Bullock, T. H. (1946). *Quart. J. Microsc. Sci.* **86**, 55.

Burdon-Jones, C. (1952). *Phil. Trans. Roy. Soc. London, Ser. B* **236**, 553.

Burdon-Jones, C. (1956a). *In* "Handbuch der Zoologie" (W. G. Kükenthal and T. Krumbach, eds.), Vol. 3, Part 2, No. 2, Book 9, p. 57. de Gruyter, Berlin.

Burdon-Jones, C. (1956b). *Proc. Zool. Soc. London* **127**, 35.

Damas, D., and Stiasny, G. (1961). *Acad. Roy. Belg., Cl. Sci., Mem., Collect. 4* [2] **15**, 1.

Dawydoff, C. (1928). "Traité d'Embryologie comparée des Invertébrés," Masson, Paris.

Dawydoff, C. (1948). *In* "Traité de Zoologie" (P. P. Grassé, ed.), Vol. 11, p. 367. Masson, Paris.

Delage, Y., and Hérouard, E. (1898). *In* "Traité de Zoologie concrète," Vol. 8, p. 3. Schleicher Fr., Paris.

Dilly, P. N., Welsch, U., and Storch, V. (1970). *Z. Zellforsch. Mikrosk. Anat.* **103**, 129.

Foucart, M. F., and Jeuniaux, C. (1965). *Ann. Soc. Roy. Zool. Belg.* **95**, 39.

Foucart, M. F., Bricteux-Grégoire, S., and Jeuniaux, C. (1965). *Sarsia* **20**, 35.

Gislén, T. (1930). *Zool. Bidr. Uppsala* **12**, 199.

Hyman, L. (1959). "The Invertebrates. Smaller Coelomate Groups," Vol. 5, p. 72. McGraw-Hill, New York.

Jefferies, R. P. S. (1967). *Symp. Zool. Soc. London* **20**, 163.

Knight-Jones, E. W. (1952). *Phil. Trans. Roy. Soc. London, Ser. B* **236**, 315.

Kozłowski, R. (1947). *Biol. Rev. Cambridge Phil. Soc.* **22**, 93.

Kozłowski, R. (1948). *Palaeontol. Pol.* **3**, 1.

Kozłowski, R. (1970). *Acta Palaeontol. Pol.* **15**, 3.

Metschnikoff, E. (1870). *Z. Wiss. Zool.* **20**, 131.

Müller, J. (1849). *Abh. Koenigl. Akad. Wiss. (Berlin)* p. 230, Koenigl. Akad. ed., Berlin.

Nørrevang, A. (1965a). *Vidensk. Medd. Dan. Naturh. Foren.* **128**, 325.

Nørrevang, A. (1965b). *Ann. N.Y. Acad. Sci.* **118**, 1052.

Spengel, J. W. (1893). *Fauna Flora Neapel* **18**, 1.

Spengel, J. W. (1932). *Rep. Sci. Res. "Michael Sars" North Atl. Deep-Sea Exp. 1910.* Vol. **5** (Bergen).

Stebbing, A. R. D. (1970). *J. Mar. Biol. Ass. U.K.* **50**, 209.

Ubaghs, G. (1969). *In* "Chemical Zoology" (M. Florkin and B. J. Scheer, eds.), Vol. 3, p. 3. Academic Press, New York.

Vandel, A. (1961). *Annee Biol.* **37**, 5.

Van der Horst, C. J. (1932). *In* "Handbuch der Zoologie" (W. G. Kükenthal and T. Krumbach, eds.), Vol. 3, Part 2, No. 2, Book 8, p. 33; Book 9, p. 1. de Gruyter, Berlin.

Van der Horst, C. J. (1936). *Quart. J. Microsc. Sci.* **78**, 605.

Van der Horst, C. J. (1939). *Bronn's Klassen* **4**, Part 4, Book 2, No. 2, p. 1.

Willey, A. (1899). *Quart. J. Microsc. Sci.* **42**, 223.

## II. Phylum Pogonophora Beklemishev 1944
## (Brachiata, Ivanov 1955a,b)

### A. INTRODUCTION

Pogonophora are solitary, benthonic, and tube-dwelling organisms inhabiting the seas from a few meter depths to the abyss. They were hardly known before 1950, and their characterization as a new phylum is therefore rather recent.

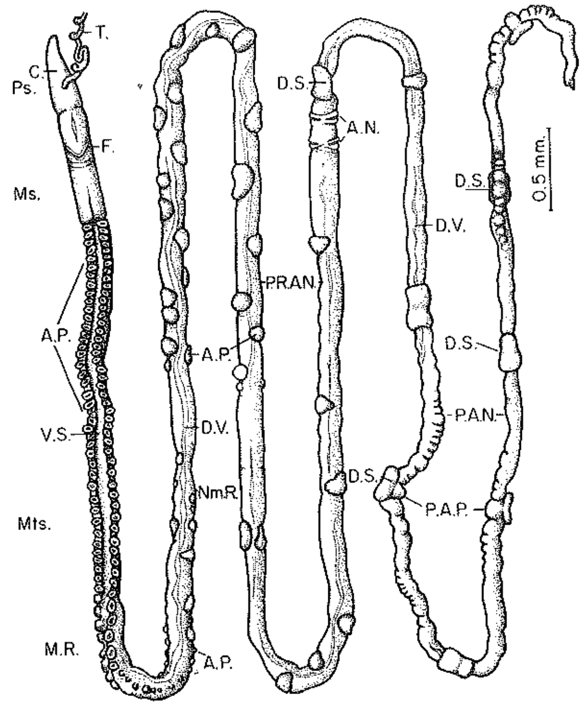

FIG. 6. *Siboglinum caulleryi,* general view of a female animal (the tentacle and the hind part of the body are omitted). A.N. = annuli (girdles); A.P. = adhesive papillae; C. = cephalic lobe; D.S. = dorsal shields; D.V. = dorsal blood vessel seen by transparency; F. = frenulum; M.R. = metameric part of the preannular region of the metasoma; Ms. = mesosoma; Mts. = metasoma; Nm.R. = nonmetameric part of the preannular region; P.A.N. = postannular region of the metasoma; P.A.P. = postannular papillae; P.R.A.N. = preannular region of the metasoma; Ps. = protosoma; T. = base of the tentacle; V.S. = ventral sulcus. (After Ivanov, 1963.)

Pogonophora are oviparous, with separated sexes, and probably unable to bud; regeneration is possible. The long and slender wormlike body has perfect bilateral symmetry and, mainly because of its trisegmental organization (Fig. 6), evokes the Enteropneusta as previously stressed by Caullery (1914a,b, 1948) when he described the first species, *Siboglinum weberi.* Nevertheless the pogonophores can be distinguished from the enteropneusts by several peculiar anatomical features, among which the lack of any digestive tract is notable. Digestion is assumed to be performed by the tentacular apparatus adorning the first segment (Ivanov, 1955b, 1960, 1963; Jägersten, 1957; Nørrevang, 1965; Gupta and Little, 1966, 1970).

The phylum is quite homogeneous; a simple class and two orders (Athecanephria and Thecanephria) are generally accepted. More than fifteen genera have been recognized and about one hundred species described up to now. The pogonophores are probably very ancient organisms, but owing to the softness of their tissues, no fossil print was ever found; however, attempts to relate *Hyolithellus micans* of the Cambrian epoch to the phylum have been made (Poulsen, 1963; Carlisle, 1964).

During the two last decades, the pogonophores have been subjected to intensive investigations, results of which are presented and discussed in several monographs and publications (Caullery, 1948; Ivanov, 1957a,b, 1959, 1960, 1963; Dajoz, 1958; Hyman, 1959; Southward and Southward, 1963; Southward, 1963; Cutler, 1965a; Johansson, 1968; Kirsteuer, 1969; Nørrevang, 1965, 1970a,b; Webb, 1964c, 1965, 1969a,b), where the readers should refer for more details. New species are regularly discovered and our knowledge of these curious animals is still progressing.

## B. GENERAL FEATURES

The three unequal parts of the body—the protosoma, mesosoma and metasoma—are limited by transverse grooves, and correspond, according to Ivanov's conceptions, to the five coelomic sacs appearing during embryogenesis. This opinion is still a matter of controversy (see Webb, 1969a; Nørrevang, 1970b).

The protosoma is very short and bears dorsally a conical cephalic lobe, sometimes delimited posteriorly by a narrow groove, and ventrally a more or less great number of long and contractile mucous and ciliated tentacles or arms. There is a simple one in *Siboglinum*, a few in *Oligobrachia* and *Heptabrachia*, and as many as 223 in *Spirobrachia grandis*. The tentacles are richly vascularized and enclose a tubular part of the protocoele. The disposition of the tentacles is highly variable and is of great value in systematics. The tentacular crown is horseshoelike, with one or many rows of arms in *Oligobrachia dogieli* or *Polybrachia barbata*. It forms an almost complete ring in *Lamellisabella zachsi*, and it spirals on a corkscrewlike helical extension of the protosoma in *Spirobrachia grandis* (Ivanov, 1960, 1963). The two pores of the unpaired protocoele open lateroventrally at the end of the protosoma. The coelomoducts carry on excretory functions thanks to close connections with the blood system (Fig. 7).

The mesosoma, short and cylindrical, is more or less sharply distinct from the preceding segment and devoid of coelomic pores and appendages. The most evident feature is a pair of pigmented cuticular crests, the frenulum (Fig. 6), running obliquely on the lateral faces.

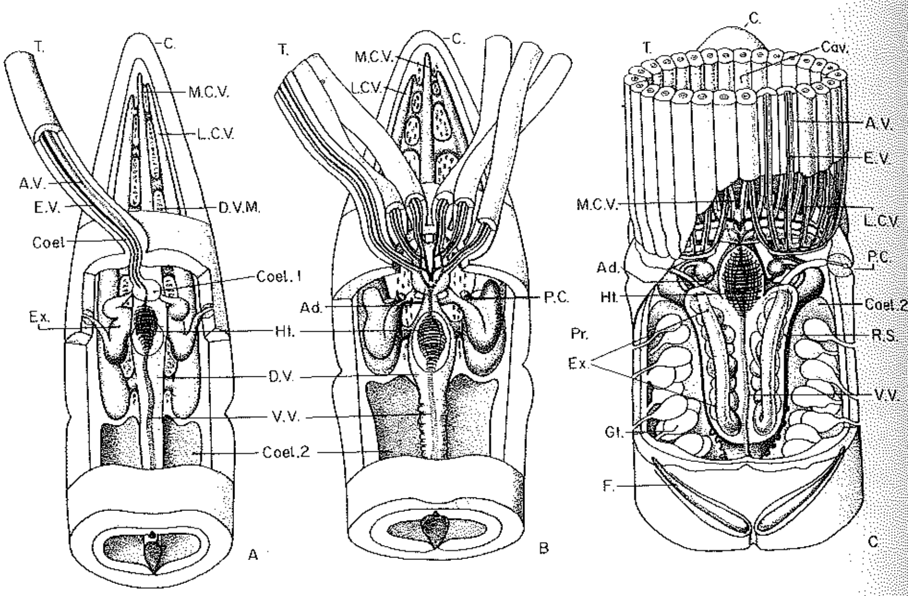

FIG. 7. Stereograms of the structure of the front end of the body of various Pogonophora in ventral view: (A) *Siboglinum caulleryi,* (B) *Oligobrachia dogieli,* (C) *Lamellisabella zachsi.* Ad. = anastomosing canal of the coelomoducts; A.V. = afferent vessel of the tentacle; C. = tip of the cephalic lobe; Cav. = intertentacular cavity; Coel. = coelomic canal of the tentacle; Coel. 1, Coel. 2 = protocoele and mesocoele; D.V. = dorsal vessel; D.V.M. = dorsoventral muscles; E.V. = efferent vessel of the tentacle; Ex. = excretory portion of the coelomoduct; F. = frenulum; Gt. = globular glands; Ht. = heart; L.C.V., M.C.V. = lateral and median cephalic vessels; P.C. = pore of the coelomoduct; Pr. = pericardial sac; R.S. = renal sac; T. = tentacles; T.C. = tentacular crown; V.V. = ventral vessel. (After Ivanov, 1963.)

The frenulum a very constant structure, may be used by the animal to attach itself to the inner surface of its tube. Frenulum is lacking to *Lamellibrachia barhami* (Webb, 1969b).

The metasoma or trunk is very long and evidently divided from the mesosoma. Various structures are visible (Fig. 6). The median region bears two to five muscular dorsolateral girdles (annuli) with small cuticular and denticulated plates. The preannular region shows from the forepart: (1) a pair of coelomic pores, the gonopores, opening ventrally in the male, laterally in the female; (2) a dorsal ciliary band; (3) a ventral sulcus with a row of numerous adhesive papillae, with a pseudometameric arrangement, bordering each side; and (4) behind the sulcus, some thickened papillae scattered on the ventral face. In the postannular region are visible pseudometameric papillae either dorsal and glandular (Athecanephria) or ventral and adhesive (Thecanephria). All these papillae probably help creeping of the animal in its tube. The apparent metamerism of the papillae is the result of a secondary phenomenon, for it is more evident in the higher genera (e.g., *Lamellisabella*), but otherwise never observed at the level of the inner structures. Webb (1964b) wrote of a true metamerism occurring in *Sclerolinum brattstromi* (see also Ivanov, 1965).

The lack of any digestive tract, and therefore of both mouth and anus, hinders an indisputable definition of the ventral face. Following Johansson (1937) and Ivanov's (1960, 1963) conceptions, it is admitted that the cephalic lobe of the protosoma and the ciliary band of the mesosoma lie on the dorsal side and consequently that the tentacular apparatus of the protosoma and the preannular adhesive protuberances of the metasoma are on the ventral side.

### C. ONTOGENESIS

The development of the pogonophores remains imperfectly known. Our information results from the compilation of fragmentary observations of several authors on different species (Ivanov, 1957a, 1960, 1963, 1970; Webb, 1964a, 1965; Nørrevang, 1970a). So far, only sexual reproduction has been reported. The very yolky, round or elongated eggs are laid by the female into the upper part of the tube where development proceeds. The abundance of the vitellus disturbs the pattern of cleavage which is neither radial nor spiral. The cleavage is unequal, with oblique segmentation planes, and quickly becomes asynchronous. The first larva is a compact morula. Gastrulation occurs by delamination of large yolky cells which give a kind of endoblastic rudiment without any trace of archenteron; the blastopore never appears. Between the ectodermal outer layer and the gut rudiment are a few small cells of mesenchymatous nature. The coelom (Fig. 8) arises by enterocoely. An anterior unpaired sac, the future protocoele, and a lateral pair soon dividing by pinching into two pairs—the mesocoeles and the metacoeles of the adult (cf. *Saccoglossus pusillus*, an enteropneust whose eggs are rich in yolk, Ivanov, 1963).

On the other hand, Nørrevang (1970a), on serial sections of well preserved embryos, observed the coelomic pouches forming in a way similar to that described in the annelids, questioning again the position of the pogonophores among the Deuterostomia and concluding in favor of a prostomian relationship.

There is no metamorphosis. The larva undergoes a progressive growth (Fig. 8); the three segments of the adult organism, corresponding to

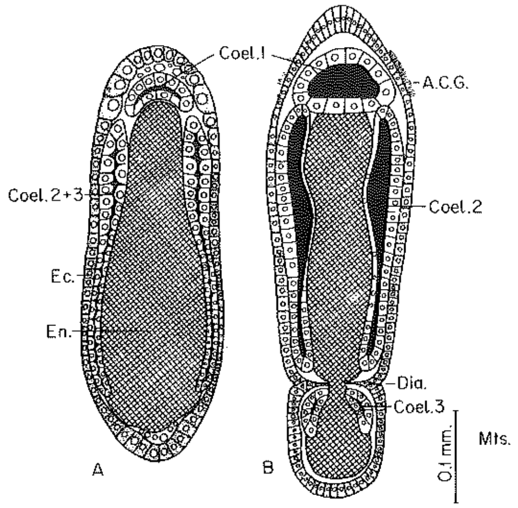

FIG. 8. Diagrams of *Siboglinum caulleryi* illustrating (A) the detachment of the coelomic sacs, and (B) the first stage of the segmentation of the body. A.C.G. = anterior ciliary girdle; Coel. 1, Coel. 2, and Coel. 3 = first, second, and third coelomic sacs; Dia. = diaphragm; Ec. = ectoderm; En. = endoderm. (After Ivanov, 1963.)

the larval coelomic cavities (Ivanov, 1960, 1963, contested by Webb, 1969a), become delimited by transverse grooves. The coelomic cavities are separated each from the other by septa and surround a long endoblastic rudiment which extends into the three differentiating segments, but without any trace of an enteric lumen or buccal or anal openings. The first tentacle soon appears on the supposed ventral side of the protosoma; two ciliated ectodermal girdles—one on the protosoma, the second on the metasoma—and a longitudinal ciliary field on the mesosoma represent the locomotor larval apparatus (Fig. 7) (perhaps remnants of a former free-swimming stage). Ectodermal bristles are also present on the mesosoma and metasoma of the late embryos. In the younger embryos, the metasoma is short but quickly grows in length and size at the end of the larval period.

Many problems remain unsolved owing to the deficiencies in our knowledge of the embryonic development. Definition of the real orientation of the animal, the fate of the endoblastic layer, and the type of development of the coelomic pouches are questions always without satisfactory answers. Much work is still to be done, and successful rearing of embryos from the egg would help us to clear up the problem of the close affinities of the pogonophores.

### D. STRUCTURE AND HISTOLOGY OF THE MAIN SYSTEMS AND ORGANS

Monostratified and well furnished with unicellular and multicellular glands, the ectoderm secretes the chitin–protein tube (Foucart *et al.*, 1965) and the polysaccharidic cuticle covering the whole surface of the body and of which the adhesive and toothed plates and the crests of the frenulum are but local thickenings. The inner wall of the tentacle (where the cuticle remains especially thin) bears a fringe of unicellular absorptive pinnules bordered with rows of ciliary cells (Fig. 9). Intracellular capillaries running through the whole length of the pinnules secure both oxygenation of the blood and distribution of the dissolved food substances absorbed by numerous microvilli (Nørrevang, 1965; Gupta and Little, 1970).

Below the ectoderm lies the nervous plexus with groups of neurons intermingling with bundles of fibers. Like the Hemichordata, the Pogonophora are epithelioneural organisms. The nervous plexus condenses in a middorsal tract (Fig. 10) with an anterior ganglionic mass, the brain, giving off a dorsoventral ring from which arise the tentacular nerves. The nervous system is separated from the circular and longitudinal smooth muscle layers by a basal membrane. The longitudinal muscular layer is well developed and is lined within by a thin peritoneal epithelium. The inside of the three segments is occupied by the coelomic pouches. The odd protocoele is saclike and extends to the tip of the tentacles; the mesocoeles are closed, a feature characteristic of the phylum, and without any apparent special function. The metacoeles are invaded by the gonads, which develop inside the dorsal mesentery (Fig. 11).

The vascular system is closed. Hemoglobin is present in the blood (Manwell *et al.*, 1966). Two main dorsal and ventral longitudinal vessels lie in the mesenteries (Fig. 10 and 11). They are connected together by an anterior ring and a few posterior commissural vessels. The dorsal vessel gives off lateral branches to the gonads. In the mesosoma, at the base of the tentacular crown, the ventral vessel is differentiated into a contractile ampulla, the heart (Fig. 7), overlaid in the Athecanephria by the so-called pericardial vesicle, of unclear origin and lacking in the Thecanephria. The heart pushes the blood forward into the capillaries of the tentacles; thence the blood runs backward in the dorsal vessel. In the protosoma of the Athecanephria (e.g., *Siboglinum, Oligobrachia*), above the heart, the dorsal vessel divides into three parallel branches; the two lateral ones are in close connection with the excretory section of the protocoelomoducts. In the Thecanephria (e.g., *Lamellisabella, Polybrachia, Spirobrachia*), the ventral wall of the dorsal vessel

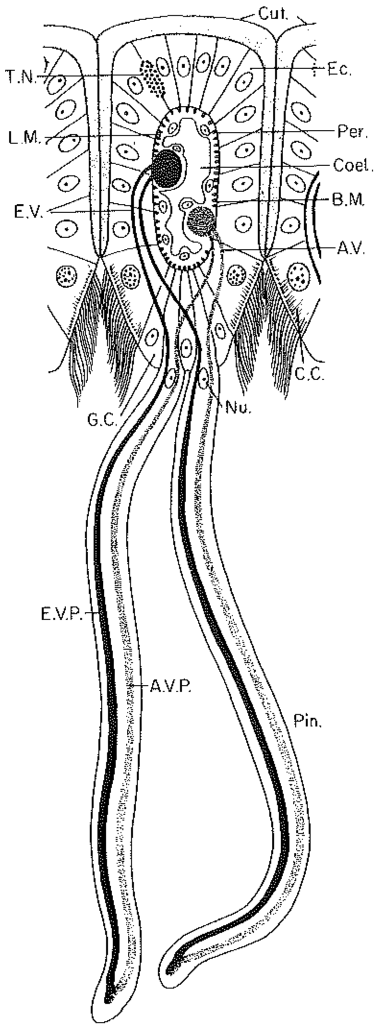

FIG. 9. Transverse section of a tentacle of *Lamellisabella zachsi*, diagram reconstructed from several sections. A.V. = afferent blood vessel (stippled); A.V.P. = afferent blood vessel of the pinnule; B.M. = basement membrane; C.C. = ciliated cell; Coel. = coelomic canal; Cut. = cuticle; Ec. = ectoderm; E.V. = efferent blood vessel (black), E.V.P. = efferent blood vessel of the pinnule; G.C. = gland cell; L.M. = longitudinal muscles; Nu. = nucleus of the pinnule; Per. = peritoneum; Pin. = pinnule; T.N. = tentacular nerve. (After Ivanov, 1963.)

grows out around each excretory duct as a renal sac. In this order, the coelomoducts are very long and coiled, protruding into the mesocoeles. Excretion processes result from direct discharge of the excreta from the blood into the ducts of the protocoele.

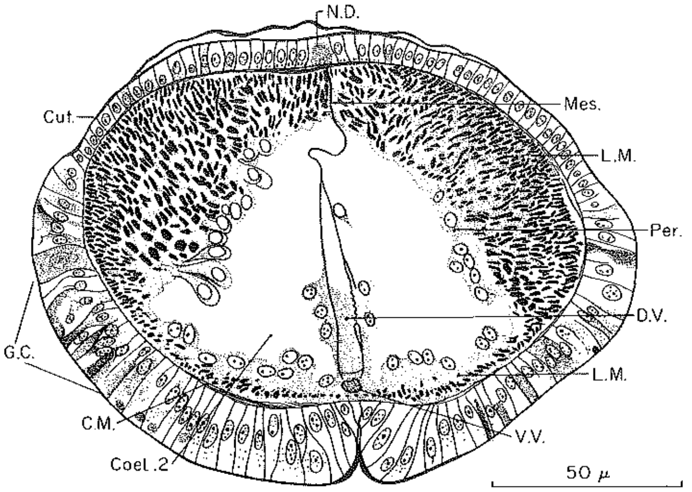

FIG. 10. Transverse section in the mesosomal region of *Siboglinum caulleryi.* C.M. = circular musculature; Coel. 2 = mesocoele; Cut. = cuticle; D.V. = dorsal blood vessel; G.C. = ectodermal gland cells; L.M. = longitudinal musculature; Mes. = mesentery; N.D. = dorsal nerve trunk; Per. = peritoneum; V.V. = ventral blood vessel. (After Ivanov, 1963.)

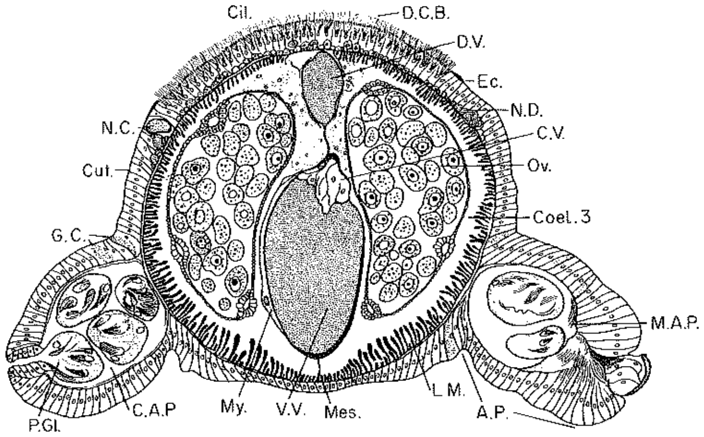

FIG. 11. Transverse section in the metameric region of the metasoma of a female *Polybrachia annulata.* A.P. = adhesive papillae; C.A.P. = coelom of the papilla; Cil. = cilia; Coel. 3 = metacoele; Cut. = cuticle; Cut.P. = cuticular plaque; C.V. = corpus cardiacum; D.C.B. = dorsal ciliated band; D.V. = dorsal blood vessel; Ec. = ectoderm; G.C. = ectodermal gland cell; L.M. = longitudinal musculature; Mes. = mesentery; M.A.P. = muscular layer of papilla; My. = myocyte; N.C. = nervous cord; N.D. = dorsal nervous plate; Ov. = ovary; Per. = peritoneum; P.Gl. = pyriform gland; V.V. = ventral blood vessel. (After Ivanov, 1963.)

## E. AFFINITIES

The systematic relationship of the pogonophores remains controversial, for our present knowledge, as already stated, is still very incomplete; this has been discussed in several papers (Ivanov, 1959, 1960, 1963, 1970). According to Ivanov (1960, 1963), the coelomic cavities develop by enterocoely, proving the pogonophores are true Deuterostomia. Unfortunately, the embryology is very aberrant, and recently Nørrevang (1970a,b) concluded that coelom formation more precisely recalls what is shown by the annelids.

The number and disposition of the coelomic cavities and the trisegmental division of the body support the views of closer affinities of the Pogonophora with the Hemichordata, especially the Enteropneusta, and throughout with the Echinodermata. The total disappearance of the digestive tract and therefore the absence of any structure like gill slits or stomochord, the development of a tentacular apparatus taking over the digestive processes, the fate of the coelomic cavities (protocoelomoducts assuming an excretory function, metacoelomoducts acting as gonoducts), and the presence of a thick cuticle and of a protective tube, all features highly characteristic of the pogonophore organization militate against the inclusion of Pogonophora among Hemichordata. Moreover the lack of vegetal micromeres and of any mesenchymatous skeleton (as well as the maintenance of the primitive bilateral symmetry) distinguishes the Pogonophora from the Echinodermata. In such present conditions, Pogonophora may be regarded as a distinct phylum in the lower Deuterostomia. But if further investigations support Nørrevang's interpretation, (1970a,b), the position of the pogonophores would be completely reviewed as Protostomia.

## F. SYSTEMATICS

A first key of determination has been presented by Ivanov in 1963, but since that time a revision of the previous scheme has been suggested by Webb (1969b). Following Ivanov's conceptions (1963), the phylum includes a single class, Pogonophora, with two orders—Athecanephria and Thecanephria.

*First Order*—Athecanephria with two families, Oligobrachiidae and Siboglinidae. Distinct protosoma and mesosoma, tentacles never very numerous (1–12) and always free, metasoma with metameric glandular areas and dorsal shields, globulous protocoele with separated rather short excretory ducts in close contact with the lateral cephalic blood vessels, a ventral pericardial vesicle in the mesosoma, spindle-shaped spermatophores.

*First Family*—Oligobrachiidae, the most primitive family with three genera. *Oligobrachia, Birsteinia, Nereilinum.*

*Second Family*—Siboglinidae, with two genera, *Siboglinum* (more than 40 species identified) and *Siboglinoides.* The first species, described by Caullery (1914a,b), is *Siboglinum weberi.*

*Second Order*—Thecanephria, with three families: Polybrachiidae, Lamellisabellidae, and Spirobrachiidae. Protosoma and mesosoma less distinct; tentacles free or more or less fused; metasoma with metameric transverse rows of adhesive cuticular plates, but without dorsal shields and glandular areas; horseshoe-shaped, sometimes asymmetrical, protocoele; long and coiled excretory protocoelomoducts enclosed in renal sacs; no pericardium.

*First Family*—Polybrachiidae, with several genera. The tentacles (2–70) are always free and disposed on one or several horseshoe-shaped rows. *Heptabrachia subtilis* is an abyssal species collected in the Japan Trench below 9700 meters.

*Second Family*—Lamellisabellidae, with a single genus and 4 species. The tentacles are fused in a cylinder projecting from below the cephalic lobe. *Lamellisabella zachsi* (Ushakov, 1933) recalls a sabellid worm.

*Third Family*—Spirobrachiidae, with a single genus and 2 species. The numerous tentacles are fused and carried on by a spiral outgrowth of the protosoma; the structure looks like the spire of a spirograph. *Spirobrachia grandis* with a 6-whirled pseudolophophore and more than 200 tentacles.

For Webb (1969b), according as the frenulum is present (the most frequent case) or not, it is possible to distinguish two classes—the Frenulata, corresponding to Ivanov's single class, and the Afrenulata with a single order and an unique species, *Lamellibrachia barhami* (gen. nov. sp. nov.). The tentacular crown is compound of two symmetrical series of fused arms; the excretory ducts, without any relation with the protocoele, are located on both sides of the heart and open exteriorly by a single ventral aperture close to the base of the tentacular apparatus. Moreover, the mesosoma bears two aliform processes overlapping ventrally and characterizing the order Vestimentifera.

## G. Ecology and Geographic Distribution

Although some pogonophores have been collected at moderate depths, most of them live in the abysses. A few species, e.g., *Siboglinum caulleryi, Oligobrachia dogieli,* are eurybathic. The pogonophores mainly inhabit soft bottoms (mud, sand, or ooze), but sometimes they inhabit decaying wood (*Sclerolinum brattstomi,* Webb, 1964b). They are probably suspension feeders on the small particles dropping from the surface to the bottom of the oceans.

Species are very diversified, and at least at some places, the individuals are an abundant and a characteristic element of the benthic community. For instance, from the Kurile-Kamchatka Trench, some two thousand specimens, belonging to two species of pogonophores (among a total a little more than five thousand animals) were collected in a single dredging.

The pogonophores, discovered in the Malay Archipelago by the Siboga Expedition (Caullery, 1914a,b) were subjected to intensive investigations (Ivanov, 1949, 1951, 1952, 1955b, 1956a,b, 1957b, 1960, 1963, 1971) after the Russian oceanographic cruises in the North Pacific Ocean, giving an apparent greater frequency in this area. Since about 1960, numerous species of pogonophores have been recorded from the coasts of western Europe and Africa (Webb, 1965; Southward and Southward, 1967), of America, (Cutler, 1965b; Ivanov, 1971), of New Zealand, and eventually in the Antarctic region. Phylum Pogonophora has, then, a world distribution and probably any increase of investigation in the Southern Hemisphere would result a rise of the number of known families, genera, and species.

## REFERENCES

Carlisle, D. B. (1964). *Biochem. J.* **90**, I.C.

Caullery, M. (1914a). *C. R. Acad. Sci.* **158**, 2014.

Caullery, M. (1914b). *Bull. Soc. Zool. Fr.* 39, 350.

Caullery, M. (1948). *In* "Traité de Zoologie" (P. P. Grassé, ed.), Vol. 11, p. 494. Masson, Paris.

Cutler, E. B. (1965a). *Ann. Mag. Natur. Hist.* 8, 145.

Cutler, E. B. (1965b). *Pac. Sci.* **19**, 422.

Dajoz, R. (1958). *Annee Biol.* **34**, 225.

Foucart, M. F., Bricteux-Grégoire, S., and Jeuniaux, C. (1965). *Sarsia* **20**, 35.

Gupta, B. L., and Little, C. (1966). *J. Mar. Biol. Ass. U.K.* **46**, 351.

Gupta, B. L., and Little, C. (1969). *J. Mar. Biol Ass. U.K.* **49**, 717.

Gupta, B. L., and Little, C. (1970). *Tissue Cell* **2**, 637.

Hyman, L. H. (1959). "The Invertebrates. Smaller Coelomate Groups," Vol. 5, p. 208. McGraw-Hill, New York.

Ivanov, A. V. (1949). *Zool. Zh.* **28**, 79.

Ivanov, A. V. (1951). *Dokl. Akad. Nauk SSSR* **76**, 739.

Ivanov, A. V. (1952). *Zool. Zh.* **31**, 372.

Ivanov, A. V. (1955a). *Dokl. Akad. Nauk SSSR* **100**, 175, 381, and 595.

Ivanov, A. V. (1955b). *Syst. Zool.* **4**, 171.

Ivanov, A. V. (1956a). *Zool. Zh.* **35**, 1863.

Ivanov, A. V. (1956b). *Syst. Zool.* **5**, 165.

Ivanov, A. V. (1957a). *Zool. Zh.* **36**, 1127.

Ivanov, A. V. (1957b). *Zool. Jahrb., Abt. Syst. Oekol., Geogr. Tiere* **85**, 431.

Ivanov, A. V. (1959). *Proc. Int. Congr. Zool., 15th, 1958* pp. 345 and 629.

Ivanov, A. V. (1960). *In* "Traité de Zoologie" (P.-P. Grassé, ed.), Vol. 5, p. 1521. Masson, Paris.

Ivanov, A. V. (1963). "Pogonophora." Academic Press, London.

Ivanov, A. V. (1965). *Cah. Biol. Mar.* **6**, 311.

Ivanov, A. V. (1970). *Z. Zool. Syst. Evolutionsforsch.* **8**, 109.

Ivanov, A. V. (1971). *J. Zool.* **164**, 271.

Jägersten, C. (1957). *Zool. Bidr. Uppsala* **32**, 67.
Johansson, K. E. (1937). *Zool. Anz.* **117**, 23.
Johansson, K. E. (1968). *In* "Handbuch der Zoologie" (W. G. Kükenthal and T. Krumbach, eds.), Vol. 3, Part 2, No. 18, Book 6, p. 1. de Gruyter, Berlin.
Kirsteuer, E. (1969). *Fortschr. Zool.* **20**, 129.
Manwell, C., Southward, E. C., and Southward, A. J. (1966). *J. Mar. Biol. Ass. U.K.* **46**, 115.
Nørrevang, A. (1965). *Sarsia* **21**, 37.
Nørrevang, A. (1970a). *Sarsia* **42**, 7.
Nørrevang, A. (1970b). *Z. Zool. Syst. Evolutionsforsch.* **8**, 161.
Poulsen, V. (1963). *Biol. Medd.* **23**, 1.
Southward, A. J., and Southward, E. C. (1963). *J. Mar. Biol. Ass. U.K.* **43**, 57.
Southward, E. C. (1963). *Oceanogr. Mar. Biol. Annu. Rev.* **1**, 405.
Southward, E. C., and Southward, A. J. (1967). *Symp. Zool. Soc. London* **19**, 145.
Ushakov, P. V. (1933). *Zool. Anz.* **104**, 205.
Webb, M. (1964a). *Sarsia* **15**, 49 and 57.
Webb, M. (1964b). *Sarsia* **16**, 47.
Webb, M. (1964c). *Sarsia* **16**, 59.
Webb, M. (1965). *Sarsia* **20**, 21.
Webb, M. (1969a). *Sarsia* **38**, 9.
Webb, M. (1969b). *Bull. Mar. Sci.* **19**, 18.

## III. Phylum Chaetognatha Leuckart 1854

### A. INTRODUCTION

The Chaetognatha are transparent, free-living, marine, generally planktonic, sometimes benthonic, carnivorous, and protandric hermaphrodite coelomates (Fig. 12). Their slender body has a perfect bilateral symmetry. The length of these animals ranges from a few millimeters to about 10 cm. The most common genus is *Sagitta* (arrow-worm). Fossil prints are known from the middle Cambrian (Walcott, 1911).

The morphology and the systematics of the chaetognaths have been considered in many articles, reviews, and treatises (Hertwig, 1880; Lameere, 1931; Trégouboff and Rose, 1957; Hyman, 1959; de Beauchamps, 1960; Tokioka, 1965a,b; Ghirardelli, 1952, 1968; Alvariño, 1969; Kirsteuer, 1969; Dallot, 1970). From the ecological point of view, these animals are of a special interest (e.g., Russel, 1935, 1939; J. Furnestin, 1938; M. L. Furnestin, 1957, 1966; Alvariño, 1965, 1969).

### B. GENERAL FEATURES AND INTERNAL ANATOMY

The whole body is covered with a thin cuticle; its main parts are (1) the head, round, bearing the ventral mouth, the rows of teeth and the grasping spines (chetae), the dorsal eyes, the ventral vestibular organs and, in *Spadella cephaloptera* (a benthonic species) a pair of lateral tentacles; the head is protected by the hood and (2) the trunk,

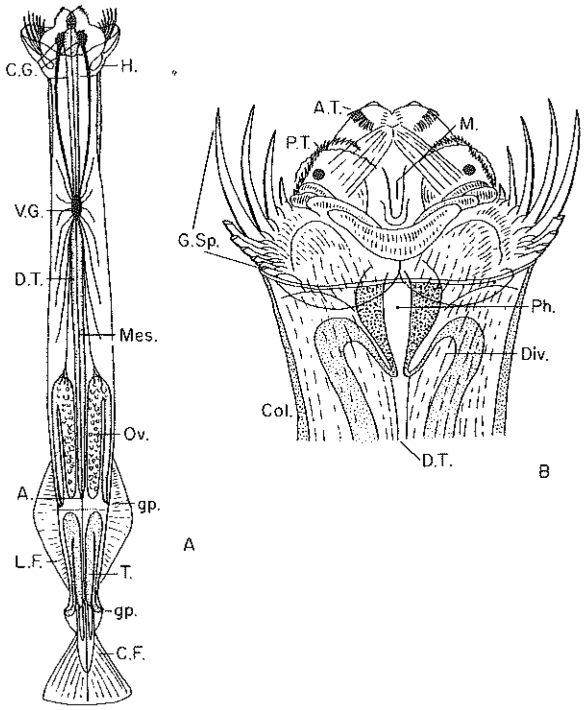

FIG. 12. Chaetognatha. (A) general anatomy, (B) ventral view of the head of *Sagitta*. A. = anus; A.T. = anterior teeth; C.G. = cerebral ganglion; C.F. = caudal fin; Col. = collarette; Div. = intestinal diverticula; D.T. = digestive tract; gp. = genital pores; G.Sp. = grasping spines; H. = hood; L.F. = lateral fin; M. = mouth; Mes. = mesentery; Ov. = ovary, Ph. = pharynx; P.T. = posterior teeth; T. = testicle; V.G. = ventral ganglion. (After Trégouboff and Rose, 1957.)

long and straight, separated from the head by the neck region and provided with lateral and terminal, horizontal, cuticular extensions—the lateral fins and the tail-fin; these fins are the only appendages; the anus is ventral, opening in front of the tail fin. The internal anatomy is very simple. The circulatory and excretory apparatus are completely lacking. Other systems are often reduced.

Below the cuticle is the ectoderm, generally flat and monostratified, with rather scarce glandular areas. It is lined interiorly by a basement membrane.

The musculature is striated, well developed, and complicated in the head region in relation to the seizing spines and the mouth. But only a longitudinal musculature is present in the trunk, distributed between two dorsal and two ventral bands. This musculature is not separated from the inner cavities by a peritoneal membrane, and it is not clear if these cavities correspond or not to the enterocoelous coelomic pouches developing during embryogenesis and temporarily disappearing in the larva. The cavities are reduced in the head; in the trunk is a dorsoventral mesentery (supporting the gut), and the two cavities are secondarily partitioned by a transverse caudal septum. These mesenteries are continuing the epidermic basement membrane. The ovaries lie in the anterior pair of compartments, and the testes in the posterior pair. Both sexual organs are U-shaped; the inner tube is the gland, the outer one is the gonoduct, opening laterally. The testes are provided with seminal vesicles and oviducts with seminal receptacles which collect the spermatophores (Ghirardelli, 1959; Ghirardelli and Arnaud, 1966). According to the species self or cross-fertilization may occur.

The digestive system is a tube without glands, running straight from the mouth to the anus. Behind the mouth is the esophagus, a muscular and glandular organ (Dallot, 1970).

The nervous system consists of several ganglia connected by commissural nerves. In the head is the cerebral ganglion furnishing the different parts of the region—musculature, eyes, mouth, vestibular organs. The cerebral ganglion is bound to the ventral ganglion of the trunk by two "peripharyngeal" commissures. Numerous nerves are radiating from the ventral ganglion, forming a plexus on the basement membrane (Trégouboff and Rose, 1957; Hyman, 1959; Ghirardelli, 1968; Kirsteuer, 1969).

### C. ONTOGENESIS

The embryology of the chaetognaths is only known in a few species. The egg is moderately loaded with minute granules of vitellus. The cleavage is holoblastic, giving a blastula of which a gastrula quickly arises by emboly. The blastopore is posterior and is the future anus (Hertwig, 1880; Ghirardelli, 1968).

Very soon, two primordial germ cells appear in the archenteric wall, enlarge, and detach. The archenteron is eventually divided into three cavities by two longitudinal folds progressing from its anterior wall to the posterior one. The median cavity is a tube, the future intestine, open behind by the blastopore. The mouth and the stomodaeum will appear later on the ventral face as neoformations. The two lateral cavities, despite the originality of their mode of formation, are enterocoeles. In a second step, a transverse septum divides each cavity into a smaller anterior head coelom and a larger posterior trunk coelom.

The chaetognaths are therefore true Deuterostomia, but may be neotenic larvae (Vandel, 1961). In any case, only two segments are present. The larva escapes from its envelopes as a young worm, a 1 mm long and already recognizable chaetognath. There is no metamorphosis in the proper sense, the larval structure progressively perfecting to the adult one. The coelomic cavities are now solid but will become hollow again at the end of the growth.

### D. Affinities and Systematics

The affinities are not known. In the adult structure, a lot of general characters—e.g., the cuticle, the lack of a ciliary ectoderm, the muscular strands, the gut straight and without digestive glands, and the kind of coelom—recall the nematodes, probably by convergence (see Ghirardelli, 1968, for discussion of the problem).

The systematics, especially of the young, is difficult, considering the number, shape, and size of the lateral fins and of the tail; the number of teeth and seizing spines; the position and/or the structure of the eyes, ventral ganglion, and ovaries, etc. More than forty species have been described.

One species is benthonic and coastal—*Spadella cephaloptera.* The other species are pelagic, epipelagic, mesopelagic, or even bathypelagic. Distributions both horizontal and vertical have been considered many times (Russel, 1935, 1939; J. Furnestin, 1938; Fraser, 1952, 1958; Ghirardelli, 1952; M. L. Furnestin, 1957; David, 1958; Bieri, 1959; Alvariño, 1962, 1964, 1965, 1967, 1969; Bainbridge, 1963; Sund and Cummings, 1966).

A few species are cosmopolitan—e.g., *Eukrohnia hamata, Sagitta maxima*—some inhabit the three main Oceans—e.g., *Pterosagitta draco* (a bathypelagic species), *Sagitta enflata, Sagitta lyra. Sagitta setosa* is found in coastal and somewhat diluted waters (North Sea with residual populations in Mediterranean and Adriatic Seas). *Sagitta elegans* lives in the North Atlantic Ocean; *Sagitta gazellae, Eukrohnia bathyantarctica,* etc., are antarctic species. *Sagitta robusta* and *Sagitta pacifica* have been recorded from the Indian–Pacific areas (Alvariño, 1969).

### E. Ecology

The chaetognaths are important members of the plankton for several reasons. In some oceans, they constitute a large part of the total amount of the planktonic animals and, from this point of view, play an important role as food for the fishes. In other regions, they are of increasing interest as hydrological indicators, since the varous species are associated with a particular type of environment, giving valuable information on the water qualities and therefore on the local fishing possibilities (Russel, 1935, 1939; J. Furnestin, 1938; Fraser, 1952; M. L. Furnestin, 1966; Bieri, 1959; Bainbridge, 1963). On the west European coasts, *Sagitta elegans* is related to the herring and *Sagitta tasmanica* to the whiting (see M. L. Furnestin, 1966).

REFERENCES

Alvariño, A. (1962). *Bull. Scrips Inst. Oceanogr.* 8, 1.
Alvariño, A. (1964). *Pac. Sci.* 18, 64.
Alvariño, A. (1965). *Oceanogr. Mar. Biol., Annu. Rev.* 3, 115.
Alvariño, A. (1967). *Pac. Sci.* **21**, 274.
Alvariño, A. (1969). *Trab. Inst. Espan. Oceanogr.* **37**, 1.
Bainbridge, V. (1963). *Bull. Mar. Ecol.* **6**, 40.
Bieri, R. (1959). *Limnol. Oceanogr.* **4**, 1.
Dallot, S. (1970). *Bull. Mus. Hist. Natur., Paris* [2] **42**, 549.
David, P. M. (1958). *'Discovery' Rep.* **29**, 201.
de Beauchamps, P. (1960). *In* "Traité de Zoologie" (P.-P. Grassé, ed.), Vol. 5, p. 1500. Masson, Paris.
Fraser, J. H. (1952). *Scot. Home Dep., Mar. Res.* **2.**
Fraser, J. H. (1958). *Cons. Int. Explor. Mer, Zooplankton* Sheet 1 (1st rev.).
Furnestin, J. (1938). *Rev. Trav. Off. Peches Mar.* **11**, 425.
Furnestin, M. L. (1957). *Rev. Trav. Inst. Sci. Tech. Peches Mar.* **21.**
Furnestin, M. L. (1966). *In* "Eléments de Planctonologie appliquée," pp. 7 and 51. Inst. Sci. Tech. Pêches Mar., Paris.
Ghirardelli, E. (1952). *Pubbl. Sta. Zool. Napoli* **23**, 296
Ghirardelli, E. (1959). *Rend. Accad. Naz. 40* [*Quaranta*] [10] **4.**
Ghirardelli, E. (1968). *Advan. Mar. Biol.* **6**, 271.
Ghirardelli, E., and Arnaud, J. (1966). *Arch. Zool. Ital.* **51**, 309.
Hertwig, O. (1880). *Jena. Z. Naturwiss.* **14**, 196.
Hyman, L. H. (1959). *In* "The Invertebrates. Smaller Coelomate Groups," Vol. 5, p. 1. McGraw-Hill, New York.
Kirsteuer, E. (1969). *Fortschr. Zool.* **20**, 129.
Lameere, A. (1931). *In* "Précis de Zoologie," Vol. 2, p. 341. Doin, Paris.
Russel, F. S. (1935). *J. Mar. Biol. Ass. U.K.* **20**, 309.
Russel, F. S. (1939). *J. Cons. Perm. Int. Explor. Mer.* **14**, 171.
Sund, P. N., and Cummings, K. C. (1966). *Bull. Inst. Fr. Afr. Noire* **28A**, 1322.
Tokioka, T. (1965a). *Publ. Seto Mar. Biol. Lab.* **12**, 335.
Tokioka, T. (1965b). *Publ. Seto Mar. Biol. Lab.* **13**, 231.
Trégouboff, G., and Rose, M. (1957). "Manuel de Planctonologie méditerranéenne," 2 vols. CNRS, Paris.
Vandel, A. (1961). *Annee Biol.* 37, 5.
Walcott, C. (1911). *Smithson. Misc. Collect.* **57**, 109.

## IV. Phylum Cephalochorda Ray Lankester 1877 (Leptocardii J. Müller 1841; Acrania Haeckel 1866)

### A. INTRODUCTION

Cephalochorda, e.g., *Branchiostoma lanceolatum* (Pallas) and *Br. belcheri* Gray, are marine, benthic, and microphagous animals. As adults, they live buried in coarse sand, projecting only the anterior tip of the body, the rostrum, which bears the mouth. They are caught from the tidal area to depths of many tens of meters and are widespread, for they are only absent in the cooler and polar waters. Larvae are planktonic during a more or less long period of their life and after metamorphosis drop to the sea bottom.

The phylum includes a single class with two main genera, *Branchiostoma* (the lancelet) and *Asymmetron,* and a score of species. The pelagic larval life is longer and, as stressed by the generic name, the asymmetry of the body is pronounced in the latter genus. No fossil is known with certainty; the enigmatic *Jamoytius kerwoodi,* held by White (1946) as close to the origin of the Cephalochorda, could be an Agnatha (Ritchie, 1960).

To the zoologists of the last century, mainly as a consequence of Kowalevsky's impressive discoveries (1867, 1877), the lancelet appeared as bridging the gap between Invertebrata and Vertebrata. This hypothesis strongly stimulated investigations, and a considerable number of publications appeared devoted to the descriptive embryology (Lankester, 1875, 1898; Hatschek, 1882, 1892; Wilson, 1892, 1893; Mac Bride, 1898, 1909; Cerfontaine, 1906), to the anatomy and to the structure of the main systems (Legros, 1902; Goodrich, 1933, 1934; Franz, 1927, 1933; Joseph, 1928; Weichert, 1958), and to the experimental embryology (Conklin, 1932, 1933; Tung *et al.,* 1958, 1960, 1962). Different phylogenetic schemes have been proposed (Willey, 1894; Franz, 1927; Garstang, 1928; Gislén, 1930; Gregory, 1936, 1946, 1951; Brien and Dalcq, 1948; Drach, 1948; de Beer, 1954; Berrill, 1955; Whitear, 1957; Bone, 1960a; Gutmann, 1969). Results are summarized in several reviews and treatises (Willey, 1894; Franz, 1927; Pietschmann, 1929; Brachet, 1935; Dalcq, 1935, 1941; Lameere, 1941; Brien and Dalcq, 1948; Drach, 1948; Berrill, 1955; Waddington, 1956). During the last decades, histological investigations with the electron microscope have been carried on and many classic opinions must now be reformed (for references, see Godeaux, 1963, 1967).

### B. General Features

*Branchiostoma lanceolatum,* the best known species (only 5 or 6 cm in length) is a naked, depigmented, and spindlelike animal, with an elongate, laterally compressed body and a lanceolate tail fin (Fig. 13). Few anatomical details are visible from outside. There is no true head, no sense organs, and no paired appendages. An impaired fin, but a simple skinfold, is running from the mouth to the atriopore, along the middorsal line of the whole body and on the midventral line of the tail. The gaping mouth lies on the left side, a little behind the rostrum; jaws and teeths are wanting, and a meshwork of solid buccal cirri selects

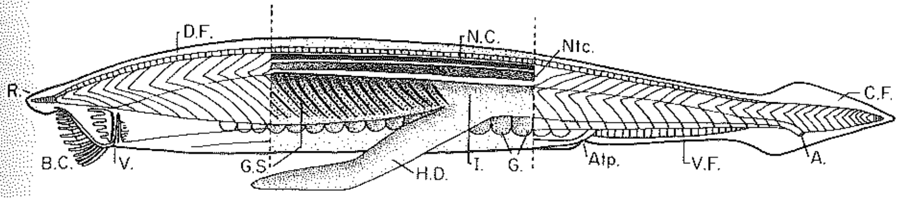

FIG. 13. *Branchiostoma lanceolatum,* lateral view. A. = anus; Atp. = atriopore; B.C. = buccal cirri; C.F. = caudal fin; D.F. = dorsal fin; G. = gonads; G.S. = gill slits; H.D. = hepatic diverticulum; I. = intestine, N.C. = nervous cord; Ntc. = notochord; R. = rostrum; V. = velum; V.F. = ventral fin. (After Drach, 1948, modified.)

the food particles carried by the inflow of water. The trunk is long compared with the tail. Below the anterior part of the trunk, two parallel longitudinal folds, the metapleural folds (Fig. 14), are visible, ending at a peculiar outlet, characteristic of the cephalochordates, the atriopore, through which the water flows out from the internal gills. At the limit between trunk and tail is the anus, located in the ventral fin.

The internal general anatomy strikingly proves the close relationships of the Cephalochorda with the Vertebrata. In the sagittal plane are superposed: (1) a dorsal tubular nervous system, (2) a solid rodlike skeletal axis, the notochord, extending here from the rostrum to the tail fin, (3) a ventral straight digestive tract, held by a dorsal mesentery into an abdominal cavity and bearing pharyngeal clefts. Between the chordal axis and the skin are stretched metameric zigzaging membranes (myocommata or myosepta) to which the segmented and longitudinal striped muscles firmly attach. (Figs. 13–14).

But the lancelet anatomy also shows significant peculiarities in every system, supporting the conclusion that the cephalochordates constitute a separate phylum with its own evolutive line. The ectoderm is a single layer of cylindrical mucous cells covered by a thin mucous layer and overlaying a network of anhyst collagen fibers (Olsson, 1961). The nervous system lacks a brain, spinal ganglia, and mixed myelinized nerves (Peters, 1963; Eakin and Westfall, 1962). At the fore end of the neural cord is a thin-walled cerebral bladder with a black dot in front (ocellus?) and a neurosecreting infundibulum (Olsson, 1962).

The cellular organization of the spinal cord has been intensively studied by Bone (1959, 1960b), who described many kinds of neurons and the tracks of the fibers, proving this organ more primitive than any found in the vertebrates. Numerous black spots (Hesse's eyes) are scattered along the ependymar canal; each eye is a two-cell structure; a receptor cell is associated to a melanocyte (Eakin and Westfall, 1962). The notochord is only a pile of discoid cells surrounded by two col-

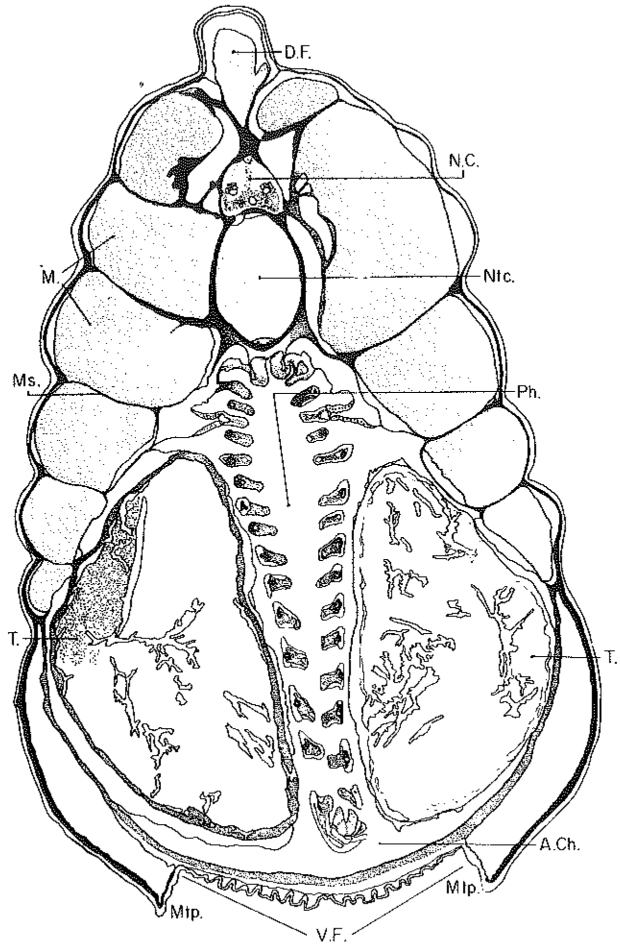

FIG. 14. *Branchiostoma lanceolatum*, transverse section in the anterior part of the pharyngeal region. A.Ch. = atrial (peribranchial) chamber; D.F. = dorsal fin; M. = muscles; Mtp. = metapleural folds; Ms. = myosepta; N.C. = nervous cord; Ntc. = notochord; Ph. = pharynx with gill slits, T. = testicles; V.F. = ventral folds.

lagenous sheaths supporting the fibrous neural arch and the myocommata (Eakin and Westfall, 1962). Connections between spinal cord and notochord have been examined by Flood (1970). The skeleton is wanting, but locally the connective tissue becomes denser, forming the axis of the buccal cirri, the subendostylar plates, and the bars and trabecula of the branchial septa. The musculature is made of large mononucleated platelike cells occupying the whole section of the myotome and of narrow lateral fibers (Peachey, 1961; Flood, 1968). The large fibers exhibit the microscopic pattern of the striated vertebrate muscle (Peachey, 1961). The digestive tract is provided with a weak musculature and its contents move mainly by ciliary activity. Beyond the mouth is a stomodaeal cavity separated from the pharynx by the velum, a filter with twelve tentacles. The branchial slits, ciliated and numerous (up to 180 pairs), open into the internal U-shaped peribranchial chamber (atrium) issuing at the atriopore. This cavity arises from a downgrowth of the ventral ectoderm progressing between the pharyngeal and the body walls, at the expense of the coelomic cavity. The midventral line of the pharynx is occupied by a ciliary and glandular groove, the endostyle (Olsson, 1963), of particular importance in the physiology of the Lancelet. Mucous secretions trap the food particles penetrating the pharynx, and ciliary activity carries them to the gut. The endostyle, like the thyroid gland, fixes iodine (Thomas, 1956; Barrington, 1958; Covelli *et al.*, 1960; Tong *et al.*, 1962). The branchial system is probably more involved in the capture of the food than in gaseous exchanges. The only glandular organ associated with the gut is the hepatic cecum, lying along the right side of the pharynx. Enterochromaffine cells are present in the gut walls (Gerzeli, 1961).

Above the gill slits are the segmented nephridia (up to 90 pairs) provided with particular solenocytes applied against vascular plexus related to aortic arches and pouring into the paired dorsal aortas (Fig. 15). Each nephridium excretes its products through the dorsal coelomic remnant into the peribranchial chamber; these organs are quite different from the segmentary tubules of the vertebrates, in structure as well as in location (Brandenburg and Kümmel, 1961). The genital system (sexes are separated) consists of some 26 metameric pairs of lateroventral gonads, without connection with the dorsal mesentery and without gonoducts, protruding when ripe into the atrium. The gametes fall into this cavity and are expelled through the atriopore with the outflow from the gills. Again, the gonads are exceptional for their unusually high number and their aberrant location.

Among all systems, the vascular one appears the less divergent from that of a fish, with the same fundamental arrangement of the main vessels. The aortic arches are of course more numerous and the "cephalic" part is reduced. A hepatic portal vein supplying the hepatic cecum has been identified. A true heart is wanting; a ventral thin-walled and one-chambered sinus (*Leptocardii*) is visible behind the pharynx at the beginning of the subbranchial artery supplying the gills. There is no pericardial cavity. The main vessels are pulsating. The blood is colorless without globules, but contains proteins (for references, see Godeaux, 1963, 1967).

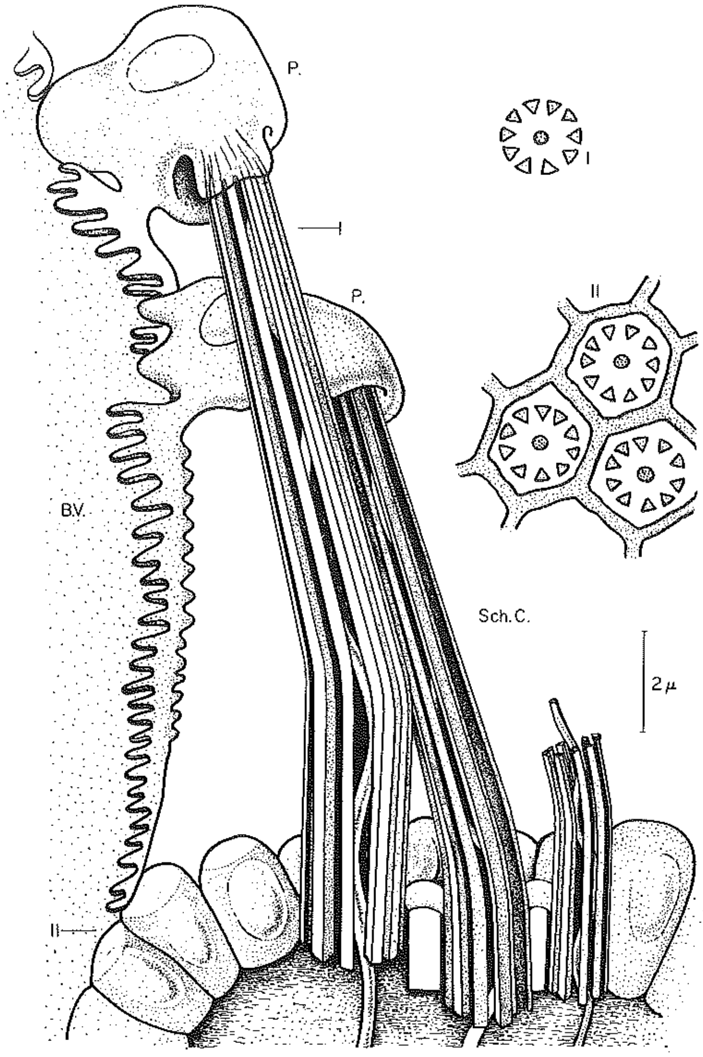

FIG. 15. *Branchiostoma lanceolatum*, diagrammatic representation of the excretory cells (cyrtopodocytes). B.V. = blood vessel; P. = podocyte; Sch.C. = subchordal coelom; I–II = cross-sections of the excretory duct. (After Brandenburg and Kümmel, 1961.)

## C. ONTOGENESIS

The egg is oligolecithal and of the regulation type; the cleavage is complete, equal, and radial. The pattern of the potential germ layer materials is similar to that described in Urochorda and Vertebrata

(Conklin 1932, 1933; Drach, 1948; Tung *et al.*, 1962a; Waddington, 1956). The sagittal plane of the embryo and adult is generally the first cleavage plane (Tung *et al.*, 1958). Segmentation gives a blastula (some 1000 cells), which, by emboly, transforms into a diblastic gastrula. The outer layer will give the ectoderm and the nervous system and the inner layer, lining the archenteron, the chord, the coelomic pouches (by enterocoely), and the gut. A polarity of the germ is soon evident; the blastopore is posterior and topographically corresponds to the anus of the adult.

The middorsal epiblast flattens into a neural plate soon covered by a languet growing from the lower blastoporal lip over the blastopore. The neural plate transforms into a tube open in front to the exterior by the neuropore and behind in the archenteron by the neurenteric tube. The evolution from neutral epiblast to specialized neuroblast is induced, as in the amphibians, for instance, by the dorsal lip of the blastopore (see Tung *et al.*, 1962b). The roof of the archenteron is the anlage of the skeletal axis. On both sides of this notochord and from the anterior part of the embryo progressively develop the paired coelomic pouches. The lower part of the archenteron after closure is the future digestive tract.

The embryo is the *neurula*, highly characteristic of the chordates; nothing evokes it in the lower Deuterostomia (e.g. in Hemichordata). The development of the amphioxus is at the beginning a simplified model of the vertebrate embryogenesis, but later on progressively diverges. At the stage of two pairs of coelomic pouches, the embryo escapes its envelopes and actively swims by means of the cilia covering its ectoderm (an invertebrate character); the cilia disappear as soon as the somatic musculature is differentiated.

The two first pairs of coelomic pouches recognizable in the embryo are numbers 2 and 3. The first pair individualizes rather late (after the fourteenth pair) and gives the Hatschek's diverticula. The right one is the future coelomic cavity of the rostrum, the left one opens to the exterior and becomes the ciliary praeoral pit of the larva, the future rotatory (wheel) organ occupying the roof of the stomodaeal cavity in the adult. The posterior coelomic saccules appear by schizocoely.

The early evolution of the coelom is identical to what is known from any vertebrate embryo. The outer epithelium, applied against ectoderm, transforms into somatopleura (dermis); the inner wall gives in front of the digestive tract the splanchnopleura and dorsal mesentery and, at the level of the chordal and neural anlagen, the sclerotome and myotomes. The myoblasts invade the upper part of the saccules and form the longitudinal striped musculature. In the lower half of the pouches, as the myocommata disappear, the cavities confuse in an abdominal cavity. Secondarily, the chordal axis passes the spinal cord and gives its shape to the rostrum; a main character of the phylum has now appeared.

The embryo becomes a larva at the end of a series of complex processes, the significance of which is still a mystery. A strong asymmetry develops, involving most of the organs. On the left side is the mouth, on the lateroventral wall of the gut appear the endostylar anlage, and on the right side, an enigmatic tube, the club-shaped gland (perhaps a former intestine) and a single series of primary branchial slits, topographically right, but morphologically left. A second series will open in the older larva above the first one. The mouth is in front of the first four or five slits. The asymmetry of the body is also obvious at the level of the nerve roots and the myocommata.

## D. METAMORPHOSIS

At least in *Branchiostoma lanceolatum,* the asymmetry is greatly reduced by the metamorphosis. During this process, several organs are modified, both anatomically and histologically, but it is impossible to give here more than a short account of the main modifications.

As a consequence of an overlapping of the larval mouth by ectodermal outgrowths giving the definitive buccal aperture and the cirri, the lips of the primitive mouth, pushed in the back of the newly formed stomodaeal cavity, become the velum between this vestibule and the pharynx. (Fig. 16).

Nothing of great interest can be detected in the integument (ectoderm always monostratified and derm anhyst), the striated muscles, and the notochord. The structure of the neural chord becomes more complicated with a great number of specialized neurons (Bone, 1960). The asymmetry remains conspicuous at the level of the nerve roots and myosepta. Below the pharynx, the two metapleural folds, less visible in the larva, develop and the peribranchial cavity appears; the gill slits are now internal and become symmetrical by gliding of the first series from the right to the left side; moreover, each slit is divided into two secondary slits by a narrow tongue growing down from the dorsal to the ventral edge (Fig. 16). The ventral wall of the pharynx is now occupied by the endostylar groove, and along the right side, the hepatic cecum sets in place. Less is known about the nephridia; they are probably of mesoblastic origin. The double series of gonads develops along the lateroventral parts of the trunk. Each gonad belongs, in fact, to the next

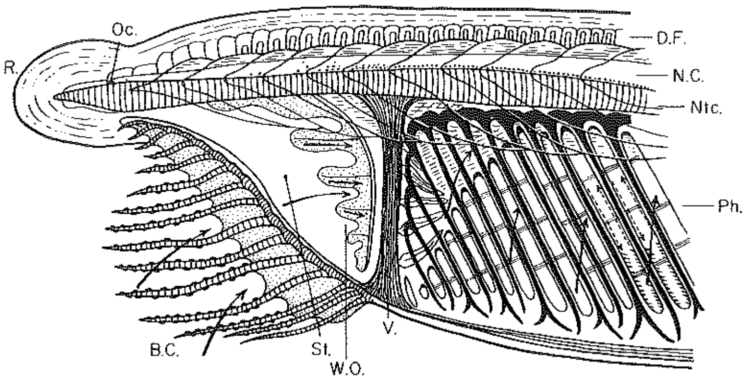

FIG. 16. *Branchiostoma lanceolatum,* hemisection of the anterior part of the body. B.C. = buccal cirri; D.F. = dorsal fin; N.C. = nervous cord; Ntc. = notochord; Oc. = ocellus; Ph. = pharynx with the gill clefts (skeletal rods in black); R. = rostrum; St. = stomodaeum; V. = velum; W.O. = wheel organ. (From Franz, after Drach, 1948.)

metamere; this is a simple example of the extraordinary complexity of cephalochordate embryology.

In *Asymmetron,* the pelagic life is longer and the metamorphosis delayed. *A. pelagicus* and *A. valdiviae* show a single row of primary branchial slits, and the rudiments of the right series of gonads give a neotenic appearance. The asymmetry is kept pronounced in the adult, for it has a single row of gonads.

### E. AFFINITIES

There is no doubt that the cephalochordates are closely related to the vertebrates, as they have in common the same map of germ layers, the neurula stage, and the same general structural plan. The question arises as to whether the lancelet is a kind of archetype, a degenerated or secondarily simplified vertebrate, or simply the representative of a collateral stem of the chordates.

As stated above, the similarities between amphioxus and vertebrates are of a very general type. Moreover, they are more striking in a younger specimen than in an adult. Amphioxus distinguishes itself by several peculiarities among which are the monostratified ectoderm, the permanent notochord, the lack of any skeleton, the structure of the pharyngeal region with its numerous gill clefts and the surrounding atrium, the structure and the position of the nephridia, the location and the high number of the gonads, etc. Endocrine glands, so important in vertebrate physiology, are practically wanting; if some endostylar cells are able to combine iodine, metamorphosis (like in lampreys) is neither initiated by thyroxine nor inhibited by thiouracil (Wickstead, 1967).

Amphioxus has no true head, no true brain, and no sense organs (Fig. 16); the medullar part of the nerve cord is proportionately more developed in relation with the trend to the sedentariness. One cannot find any remnant of secondarily degenerated vertebrate typical structures (eyes, paired appendages) like the rudimentary eyes in the blind cave fishes. Most probably, amphioxus is not a degenerated animal; it must be rather considered as the representative, specialized to a microphagous and sedentary way of life, of a small collateral branch separated early from the main trunk of the chordates and having developed anatomical particularities.

The relationships with the invertebrates are less obvious. In common with Echinodermata and Stomochordata are only the type of cleavage of the eggs, the position of the blastopore, and the enterocoelous mode of formation of the coelomic pouches (Deuterostomia). Moreover, the anatomical characters (stomochord, neural chord, gill slits), usually invoked in favor of phylogenetic relationships with the Enteropneusta, could be the result of convergence phenomena. The comparison formerly attempted by Gislén (1930) between amphioxus and some palaeozoic carpoid Echinodermata, only known by the prints of their shells, is less convincing (for discussion, see Willey, 1894; Garstang, 1928; Gregory, 1951; Drach, 1948; Berrill, 1955; Whitear, 1957; Bone, 1960; Gutmann, 1969).

## F. SYSTEMATICS

The phylum of the Cephalochorda comprises a single order, Amphioxi, with a single family, Branchiostomatidae, distributed between two genera, *Branchiostoma* and *Asymmetron.*

### 1. *Branchiostoma*

The genus *Branchiostoma* (amphioxus *sensu stricto*) includes numerous species, sometimes sympatric, inhabiting the shores of the tropical and temperate seas. The taxonomic characters are the shape of the body, of the rostrum, and of the caudal fin; the number of dorsal and preanal fins chambers; the position of the anus; and the mean number (myotome frequency) of the myotomes and their distribution along the body (preatrioporal, postatrioporal, and postanal sectors). The asymmetry is relatively less pronounced. *Branchiostoma lanceolatum* (Pallas) was first described by Pallas (1774) as a nudibranch mollusk, *Limax lanceolatus; Branchiostoma belcheri.*

The systematics as well the phylogeny and the geographical distribution of the *Branchiostoma* species have been discussed in recent papers (African species—Webb, 1955, 1956a,b,d, 1957; Massé, 1964. American species—Boschung and Gunter, 1962, 1966. Asian species—Webb, 1956a,c; Azariah, 1965. Australian species—Whitley, 1932; Kelly, 1966. European species—Webb, 1956d).

### 2. *Asymmetron*

The genus *Asymmetron* groups several species, the representatives of which are remarkable by the persistance of the larval asymmetry. At the time of the metamorphosis (length = 9 mm), the branchial basket gains the second series of gill slits and the right gonads are already recognizable; the left series never appears.

The systematics is based on the shape of the rostrum and of the tail (urostyle), the myotome number, the number of the gill slits and of the gonads, and the position of the fins. This genus is relatively less known, e.g., *Asymmetron* (*Epigonichthys*) *lucayanum,* both swimming and burrowing (Andrews, 1893; Massé, 1964), *Asymmetron cultellus* (Massé, 1964; Wickstead, 1964). The description of the species, together with their ecology, is done in a few papers (Whitley, 1932; Bone, 1957; Massé, 1964; Wickstead, 1964).

To the *Asymmetron* sp. are related four forms, formerly placed in the genus *Amphioxides* as members of the family Amphioxididae (Goldschmidt, 1905). *Amphioxides pelagicus* Günther, having up to 27 primary slits and large gonad rudiments, is the giant larva of some yet undetermined Asymmetron, perhaps *A. lucayanum* (Bone, 1957; Wickstead, 1964). Owing to their neotenic appearance, the amphioxides support the view that the Chordata arose by paedomorphosis of some protochordate larva (Berrill, 1955; Bone, 1957).

## G. ECOLOGY AND GEOGRAPHIC DISTRIBUTION

The amphioxus lives in marine waters but appears to be tolerant to a rather broad range of salinity and temperature variations. Most probably, in each species, numerous geographic races could be recognized.

The common lancelet, *Branchiostoma lanceolatum* (Pallas), has been recorded from the west and southern European coasts (from Bodö, Norway, 67° N, to Naples), on the northern and east African coasts (Webb, 1957), and occurs on the east Indian coast (Azariah, 1965). In the European area, four populations are recognized by Webb (1956d). Experiments (Courtney and Webb, 1964) prove that *B. lanceolatum* is active between 3° and 27°C. *Branchiostoma caribaeum* Sundevall, of the gulf of Mexico, lives in dilute seawater, between 15.4 and 33.1‰

salinities (Boschung and Gunter, 1966). The behavior and breeding seasons of the amphioxus and the sand in which they live buried have been analyzed by Azariah (1965).

The *Asymmetron* sp. seem more sensitive to low temperature, for they are only found in the circumtropical areas of the three oceans. The prolonged pelagic life favors the dissemination of the species. *A. lucayanum* has been recorded from the Bahamas, Philippine and Maldive Islands, the African coasts, and the Red Sea.

The cephalochordate larvae are able to swallow diatom chains as well as calanid copepods (Wickstead and Bone, 1959; Webb, 1969). The larvae (*B. belcheri*) undergo a daily vertical migration; they are caught mainly on the bottom where they feed during daylight, but they migrate to the upper layers after sunset, escaping the nocturnal bottom-feeding predators (Wickstead and Bone, 1959).

## REFERENCES

(For the literature prior to 1930, see references in Berrill, Brien, Dalcq, Drach, Franz, Gislén, and Pietschmann).

Azariah, J. (1965). *J. Mar. Biol. Ass. India* **7**, 348.
Barrington, E. J. W. (1958). *In* "Comparative Endocrinology" (A. Gorbman, ed.), p. 250. Wiley, New York.
Berrill, N. J. (1955). "The Origin of the Vertebrates." p. 168. Oxford Univ. Press, London and New York.
Bone, Q. (1957). *Nature (London)* **180**, 1462.
Bone, Q. (1959). *Quart. J. Microsc. Sci.* **100**, 509.
Bone, Q. (1960a). *J. Linn. Soc. London, Zool.* **44**, 252.
Bone, Q. (1960b). *J. Comp. Neur.* **115**, 27.
Boschung, H. T., and Gunter, G. (1962). *Tulane Stud. Zool.* **9**, 245.
Boschung, H. T., and Gunter, G. (1966). *Copeia* **3**, 485.
Brachet, A. (1935). "Traité d'Embryologie des Vertébrés." Masson, Paris.
Brandenburg, J., and Kümmel, G. (1961). *J. Ultrastruct. Res.* **5**, 437.
Brien, P., and Dalcq, A. (1948). *In* "Traité de Zoologie" (P.-P. Grassé, ed.), Vol. 11, p. 535. Masson, Paris.
Conklin, E. G. (1932). *J. Morphol.* **45**, 69.
Conklin, E. G. (1933). *J. Exp. Zool.* **64**, 303.
Courtney, W. A. M., and Webb, J. E. (1964). *Helgolaender Wiss. Meeresunters.* **10**, 301.
Covelli, I., Salvatore, G., Sena, L., and Roche, J. (1960). *C. R. Soc. Biol.* **154**, 1165.
Dalcq, A. (1935). "L'Organisation de l'Oeuf chez les Chordés. Etude d'Embryologie causale." p. 21 and 39. Gauthier-Villars, Paris.
Dalcq, A. (1941). "L'Oeuf et son Dynamisme organisateur." p. 383. Albin Michel, Paris.
de Beer, G. (1954). "Embryos and Ancestors." Oxford Univ. Press, London and New York.
Drach, P. (1948). *In* "Traité de Zoologie" (P.-P. Grassé, ed.), Vol. 11, pp. 545 and 931. Masson, Paris.

Eakin, R. M., and Westfall, J. A. (1962). *J. Cell. Biol.* **12**, 646.
Flood, P. R. (1968). *Z. Zellforsch. Mikrosk. Anat.* **84**, 389.
Flood, P. R. (1970). *Z. Zellforsch. Mikrosk. Anat.* **103**, 115.
Franz, V. (1927). *Ergeb. Anat. Entwicklungsgesch.* **27**, 464.
Franz, V. (1933). *In* "Handbuch der vergleichenden Anatomie der Wirbeltiere" (L. Bolk *et al.*, eds.), Vol. 6, p. 451. Urban & Schwarzenberg, Munich.
Garstang, W. (1928). *Quart. J. Microsc. Sci.* **72**, 51.
Gerzeli, G. (1961). *Nature (London)* **189**, 237.
Gislén, T. (1930). *Zool. Bidr. Uppsala* **12**, 199.
Godeaux, J. (1963). *Fortschr. Zool.* **16**, 341.
Godeaux, J. (1967). *Fortschr. Zool.* **18**, 350.
Goodrich, E. S. (1933). *Quart. J. Microsc. Sci.* **75**, 723.
Goodrich, E. S. (1934). *Quart. J. Microsc. Sci.* **76**, 499 and 655.
Gregory, W. K. (1936). *Biol. Rev. Cambridge Phil. Soc.* **11**, 311.
Gregory, W. K. (1946). *Quart. Rev. Biol.* **21**, 348.
Gregory, W. K. (1951). "Evolution Emerging," 2 vols. Macmillan, New York.
Gutmann, W. F. (1969). *Zool. Anz.* **182**, 1.
Kelly, O. E. S. (1966). *Univ. Queensl. Pap., Dep. Zool.* **2**, 259.
Lameere, A. (1941). *In* "Précis de Zoologie," Vol. 6, p. 1. Doin, Paris.
Massé, M. (1964). *Rec. Trav. St. Mar. Endoume* **35**, 269.
Olsson, R. (1961). *Z. Zellforsch. Mikrosk. Anat.* **54**, 90.
Olsson, R. (1962). *Ark. Zool.* [2] **15**, 347.
Olsson, R. (1963). *Acta Zool. (Stockholm)* **44**, 299.
Peachey, L. D. (1961). *J. Biophys. Biochem. Cytol.* **10**, 159.
Peters, A. (1963). *J. Comp. Neurol.* **12**, 287.
Pietschmann, V. (1929). *In* "Handbuch der Zoologie" (W. G. Kükenthal and T. Krumbach, eds.), Vol. 6, Part 1, No. 1, Book 1, p. 2. de Gruyter, Berlin.
Ritchie, A. (1960). *Nature (London)* **188**, 647.
Thomas, I. M. (1956). *J. Mar. Biol. Ass. U. K.* **35**, 203.
Tong, W., Kerkof, P., and Chaikoff, I. L. (1962). *Biochim. Biophys. Acta* **56**, 326.
Tung, T. C., Wu, S. C., and Tung, Y. F. Y. (1958). *Sci. Sinica* **7**, 1280.
Tung, T. C., Wu, S. C., and Tung, Y. F. Y. (1960). *Sci. Sinica* **9**, 119.
Tung, T. C., Wu, S. C., and Tung, Y. F. Y. (1962a). *Sci. Sinica* **11**, 629.
Tung, T. C., Wu, S. C., and Tung, Y. F. Y. (1962b). *Sci. Sinica* **11**, 805.
Waddington, G. H. (1956). "Principles of Embryology." Allen & Unwin, London.
Webb, J. E. (1955). *Proc. Zool. Soc. London* **125**, 421.
Webb, J. E. (1956a). *Sci. Rep. Murray Exped.* **10**, 121.
Webb, J. E. (1956b). *Atlantide Rep.* **4**, 167.
Webb, J. E. (1956c). *Proc. Zool. Soc. London* **127**, 119.
Webb, J. E. (1956d), *Proc. Zool. Soc. London* **127**, 125.
Webb, J. E. (1957). *Ann. S. Afr. Mus.* **43**, 249.
Webb, J. E. (1969). *Mar. Biol.* **3**, 58.
Weichert, C. K. (1958). "Anatomy of the Chordates." McGraw-Hill, New York.
White, E. I. (1946). *Geol. Mag.* **88**, 89.
Whitear, M. (1957). *Ann. Mag. Natur. Hist.* [12] **10**, 338.
Whitley, G. P. (1932). *Aust. Zool.* **7**, 256.
Wickstead, J. H. (1964). *J. Linn. Soc. London, Zool.* **45**, 191 and 201.
Wickstead, J. H. (1967). *J. Mar. Biol. Ass. U.K.* **47**, 49.
Wickstead, J. H., and Bone, Q. (1959). *Nature (London)* **184**, 1849.

## V. Phylum Tunicata Lamarck 1816
## (Urochorda Herdman 1910).

### A. INTRODUCTION

The Tunicata are marine, benthonic, or pelagic animals, collected at every latitude, from sea level to the great depths. These organisms are solitary, social, or colonial, generally hermaphrodite. Budding occurs in the social (e.g., *Clavelina lepadiformis*) or colonial (*Morchellium argus, Perophora viridis, Botryllus schlosseri*) tunicates. Except in some families, where metagenesis prevails (Salpidae—*Salpa cylindrica*), the animal is capable of both types of reproduction. All are filter feeders except a few strongly modified species which are macrophagous.

At first sight (Fig. 17), the systematic position of the tunicates is far from evident. The body is protected by the tunic (test), a saclike

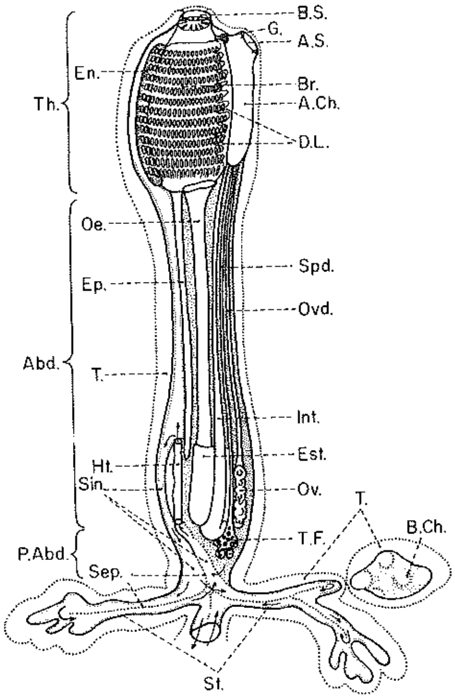

FIG. 17. *Clavelina lepadiformis,* general anatomy of the zooid. Abd. = abdomen; A.Ch. = atrial chamber; A.S. = atrial siphon; B.Ch. = bud chamber; Br. = branchial wall; B.S. = buccal siphon; D.L. = dorsal languets; En. = endostyle; Ep. = epicardia; Est. = stomach; G. = nervous ganglion; Ht. = heart; In. = intestine; Oe. = esophagus; Ov. = ovary; Ovd. = oviduct; P.Abd. = post abdomen; Sep. = septa; Sin. = blood sinus; Spd. = spermduct; St. = vascular stolons; T. = tunic; T.F. = testicular follicles; Th. = thorax, (After Brien, 1948.)

outer cover, characteristic of the phylum (Lamarck, 1816), secreted by the ectoderm (mantle) and classically considered to be made of cellulose (tunicine). It bears two siphons, the inhalant buccal siphon and the exhalant cloacal siphon, very close in the sessile tunicates (Ascidiacea). The presence of these two siphons, the microphagous mode of nutrition, and the sessile condition of most species led the zoologists of the last century to the conclusion that tunicates were mollusks (*mollusques acéphales sans coquille,* Cuvier, 1817; de Blainville, 1824) until Kowalevsky (1867, 1871) demonstrated they are genuine Chordata. The larva or tadpole, when emerging from the egg, displays the stratification of the main axial systems characteristic of the chordates. The larva (in fact a transient notfeeding embryo), after a short swimming free life, undergoes an astonishing metamorphosis, losing all the chordate features. A full, both anatomical and physiological, divorce happens between the larval and adult organizations. Any attempt at a homologization between the organs of the adult tunicates and of the vertebrates therefore becomes problematic.

The tunicates are Deuterostomia. The cleavage of the egg is radial, but no coelomic cavity develops, and as the larva does not feed, the anus does not open. No sign of metamerism is obvious. Nevertheless their deuterostomian quality is out of doubt thanks to the similarities between the developmental patterns of the tunicates, cephalochordates and vertebrates. The phylum is distributed among three classes:

### 1. *Ascidiacea*

Ascidiacea (sea squirts) are sessile, living attached to stones or seaweeds, sometimes buried into the sand. They are often capable of asexual reproduction, producing large colonies with numerous individuals (blastozooids). The connections between the blastozooids are more or less strong, according to the grade of evolution of the species. The solitary ascidians are not budding and reach a greater size than the colonial ones.

The class comprises 4 orders and about 25 families. The orders are (1) Aplousobranchia, with a simple branchial wall; (2) Phlebobranchiata, with a network of blood vessels against the inner wall of the pharynx; (3) Stolidobranchiata, with branchial walls folded and enforced by longitudinal bars; and (4) Aspiraculata devoid of any branchial apparatus and deep sea-living animals.

### 2. *Thaliacea*

Thaliacea are holoplanktonic animals, generally recorded from the temperate and tropical seas; only a few species are known from cold

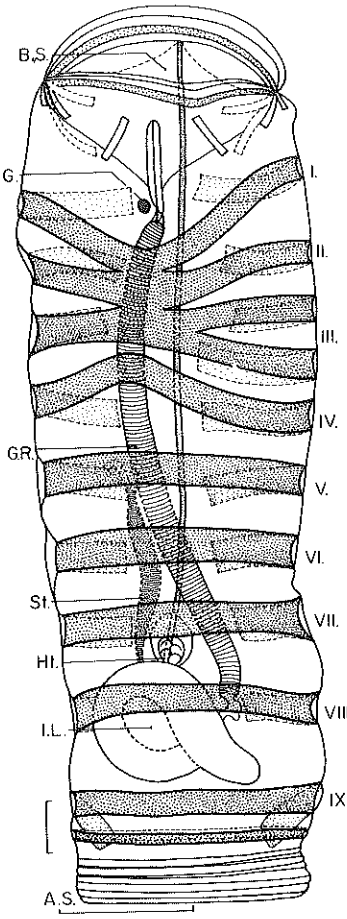

FIG. 18. *Salpa cylindrica,* oozooid, dorsal view (tunic is missing) (scale: 1 mm). A.S. = atrial siphon; B.S. = buccal siphon; G. = ganglion; G.R. = gill ridge; Ht. = heart; I.L. = intestinal loop; I–IX = body muscles; St. = stolon.

waters. This class is probably polyphyletic. All species are budding and often metagenetic. The siphons are located at both ends of the main axis of the body, the consequence of a backward migration of the atrial aperture. The branchiae are often simple and abdomen always reduced (Fig. 18). There are only three families—Doliolidae, Pyrosomidae, and Salpidae.

### 3. *Appendicularia*

Appendicularia (Copelata or Larvacea, Fig. 19) are minute holoplanktonic animals, found even in cold waters. They have a neotenic appear-

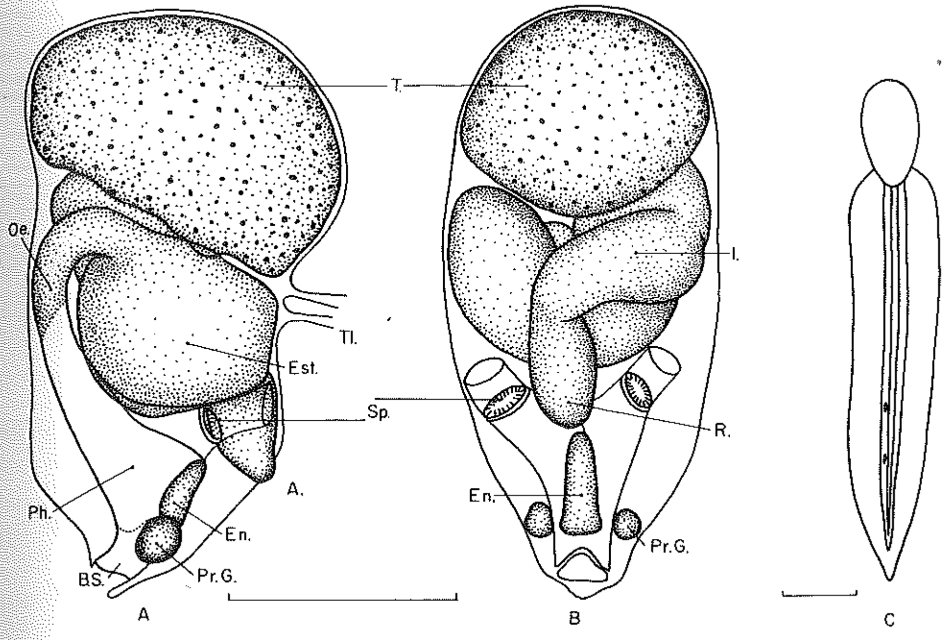

FIG. 19. *Oikopleura dioica.* (A) lateral view, (B) ventral view, (C) general aspect (scale: 250 μ). A. = anus; B.S. = buccal siphon; En. = endostyle; Est. = stomach; I. = intestine; Oe. = esophagus; Ph. = pharynx; Pr.G. = prebuccal glands; R. = rectum; Sp. = spiracula; T. = testis; Tl. = tail. (After Fenaux, 1967.)

ance and look quite similar to the ascidian tadpole. Their anatomy reveals, besides the permanent larval organs, a mixture of general and specialized adult structures. Three families are recognized—Oikopleuridae, Fritillariidae, and Kowalevskaiidae.

Despite the different modes of life and the anatomical alterations, the general plane of the tunicate structure remains obvious in the three classes. Owing to the softness of the body, no fossil has been identified with certainty. *Oesia disjuncta,* from the middle Cambrian, described as a worm (Walcott, 1911) should be a gigantic Appendicularia. On the other hand, spicules similar to those of the *Didemnidae* (Ascidiacea) have been recorded from the Pliocene (Durand, 1948).

During the two last centuries (literature in Hopkinson, 1913) and especially after Kowalevsky (1867, 1871), the tunicates have been submitted to intensive investigations. It is impossible to give more than a short and very incomplete account of the results. Most of them have been summarized in numerous reviews and treatises dealing with descriptive and experimental embryology, blastogenesis, morphology, systematics, and phylogeny:

Ascidiacea—Kowalevsky (1867, 1871), Herdman (1882, 1886, 1888), Chabry (1887), Lahille (1890), Conklin (1905, 1911, 1931), Dawydoff (1928), Harant and Vernières (1933), Dalcq (1935, 1938, 1941, 1959), Huus (1937), Pérès (1943, 1948), Van Name (1945), Brien (1948, 1958, 1970, 1971), Berrill (1950, 1955), Waddington (1956), Barrington (1958, 1963), Reverberi (1961), Labrousse (1963), Godeaux (1963, 1964a,b), Millar (1966a,b).

Thaliacea—Uljanin (1884), Neumann (1906, 1913, 1934), Ihle (1912, 1935, 1937), Metcalf (1918), Metcalf and Hopkins (1919), Dawydoff (1928), Harant and Vernières (1938), Thompson (1948), Ivanova-Kazas (1956, 1960, 1962), Trégouboff and Rose (1957), Godeaux (1957, 1963, 1969), Fenaux (1968), Godeaux and Goffinet (1968), Braconnot (1970, 1971).

Appendicularia—Delsman (1910, 1912), Ihle (1913), Dawydoff 1928), Lohmann (1933), Harant and Vernières (1938), Thompson (1948), Trégouboff and Rose (1957), Fenaux (1963, 1967).

During the last decade, electron microscope and scanning microscope have been intensively used.

## B. GENERAL FEATURES

A primitive simple Ascidia, *Clavelina lepadiformis,* common on rocky shores, can be chosen as an example (Fig. 17). The body, 2–3 cm long and covered by a yellowish hyaline tunic, is divided into three regions—the thorax, the abdomen, and the postabdomen.

The thorax bears the two siphons; the buccal one is ventral, the cloacal is dorsal. Inside of the thorax is the pharyngeal cavity, the sides of which are pierced by numerous rows of ciliated branchial slits (stigmata). The midventral line is occupied by an endostylar groove, rather similar to the same organ in amphioxus. Along the dorsal edge are the dorsal languets. The pharynx is surrounded by the lateral peribranchial chambers and the dorsal atrium extending to the cloacal siphon. Between the two siphons is the neural complex consisting of a dorsal ganglion, a ventral "gland," and a vibratile tube which opens into the prebranchial part of the pharynx.

The abdomen contains the twisted digestive tube composed of the esophagus, the stomach pouch, and the intestine. The only gland is the pyloric gland. The abdominal cavity (which is a hemocoel not a coelom) is divided by two fused and flattened blind pharyngeal outgrowths, the epicardia, playing the role of a mesentery and dividing the abdomen into a dorsal part with the gut and the gonads and a ventral region with the heart.

The postabdomen in *Clavelina lepadiformis* is a network of roots and stolons anchoring the animal on the stone; these stolons play an important role in the asexual propagation of this ascidian (Fig. 17). In some colonial ascidians closely related to the Clavelinidae, the Polyclinidae (e.g., *Morchellium* sp., *Polyclinum* sp.), the postabdomen is a conical sac and contains the epicardia, the gonads and the heart.

In the Ascidiacea, it is possible to stress several steps on the evolutionary line. First, the postabdomen disappears (in *Aplidium* sp. among the Polyclinidae). Afterward the abdomen is also reduced (*Ciona intestinalis*) and eventually vanishes as a distinct region, the gut, heart, and gonads being pushed on the side of the pharynx (*Ascidia* sp., *Perophora* sp.). With the abdomen disappear the epicardia. The gonads, enclosed within the loop of the gut in the Aplousobranchia and Phlebobranchiata (Enterogona), migrate into the pleurae between the mantle and the atrial epithelium in the Stolidobranchiata (Pleurogona).

In the Thaliacea, the postabdomen is always wanting; the digestive loop, the heart, and, when they are present, the gonads and/or the stolon are concentrated in a postpharyngeal abdomen. In active swimmers like the Doliolidae and the Salpidae (Fig. 18), the branchial basket is simple; the animals propel through the water by contracting their annular body muscles. The Pyrosomidae, able to build up tremendous colonies (up to 3 or 4 meters), drift passively; their musculature is feeble, practically limited to the siphonal sphincters; the lateral branchial basket, large and complicated, evokes that of a phlebobranch Ascidia.

In the Appendicularia (Fig. 19), the appearance is that of a tadpole—a complete tail, with a neural cord, a notochord, and two bands of striped muscles (and perhaps remnants of the digestive tract), is retained. But the buccal siphon, the ganglionic mass with a statocyst, the endostyle, and the heart are of an ascidian type. The U-shaped digestive tube, the two ventral branchial apertures (spiracula) at the hind end of the pharynx, and the gigantic polyploid ectodermal cells (oikoplasts) secreting a complex house (which is more an efficient food-trapping tool than a protective cover) are peculiar to the appendicularians. There is no atrium or cloacal siphon. The tail is twisted and lies on the ventral side; it plays as well as an organ securing the mobility of the animal as a propeller for the stream of water flowing through the cavities of the house.

## C. ONTOGENESIS

The embryological development has been considered in a tremendous number of papers. The solitary Ascidiacea have moderately yolky eggs. The map of the presumptive areas is identical to the Amphioxus and Vertebrata (Amphibia) maps. But except prior to the fecundation, the regulation power of the egg is nill (mosaic egg); after separation, each of the two first blastomeres only gives an half embryo (Conklin, 1931; Dalcq, 1935, 1941; Waddington, 1956; Reverberi, 1961; Labrousse, 1963). The cleavage is holoblastic, radial, equal, or subequal; it leads to a morula which very quickly gastrulates by emboly at the stade of about 76 cells. The blastopore is posterior. Soon the gastrula is replaced by the neurula. On the back of the embryo, a middorsal stripe of ectoblast separates and forms the neural groove which closes into a neural tube open in front to the exterior by the neuropore and behind in the archenteron by the neurenteric canal. Below the neuroblast is the inductive chordoblast along which is the mesoblast. There is no enterocoely. The ventral part of the former archenteron closes, swells at the fore end and tapers to the hind end.

The body of the tadpole divides into a globulous cephalenteron and a slender tail. (Fig. 20). A few structures are differentiated. The

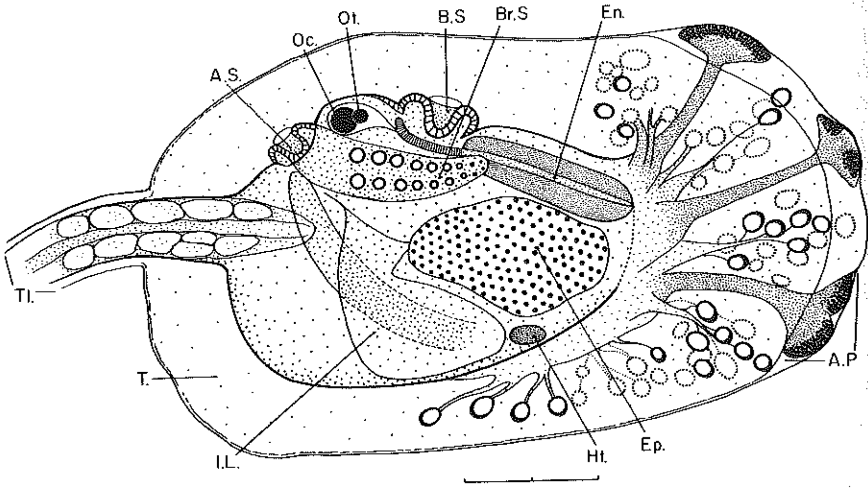

FIG. 20. *Amaroucium* sp., tadpole, view from the right side (scale: 100 μ). A.P. = adhesive papillae; A.S. = atrial siphon; B.S. = buccal siphon; Br.S. = branchial septum with two rows of stigmata; En. = endostyle; Ep. = epicardia with yolk globules; Ht. = heart; I.L. = intestinal loop; Oc. = ocellus; Ot. = otolith; T. = tunic; Tl. = tail.

cephalenteron bears three anterior adhesive papillae. The neural tube is swollen in a cerebral vesicle with two sense organs, a dorsal ocellus and a ventral otolith. The digestive vesicle is closed. At the limit between the cephalenteron and the tail lies a ring of embryonic mesoblast where the pericardic cavity will appear later on. The tail contains a dorsal undifferentiated nervous cord, a median single row of 40 notochordal cells flanked by 2 bands of striped muscles and a ventral transitory endoblastic string, proving the tail is preblastoporal and no more than the specialized hind part of the trunk. The tail is locomotory.

After a short time, the tadpole becomes negatively phototropic and attaches to a substrate by means of its adhesive papillae. After the onset of the metamorphosis, the tail is digested as a pseudovitellus, and the adult structures develop from the undifferentiated tissues of the cephalenteron. In tunicates, the metamorphosis is necrotic.

In the Thaliacea, a few eggs ripen. In Doliolidae, the development results in a tadpole (Godeaux, 1957; Braconnot, 1970). In Pyrosomidae, the egg is enormous and its cleavage meroblastic; the embryo remains very simple, degenerating soon after production of the primary blastozooids (Neumann, 1913; Godeaux, 1957; Ivanova-Kazas, 1956, 1960, 1962). In Salpidae, the animal is viviparous and yolk is absent; the embryo develops bound to the mother by a kind of placenta (Brien, 1928, 1948).

Little is known about the embryology of the Appendicularia. The early development of the egg (Delsman, 1910, 1912) follows the same scheme as the egg of an oviparous ascidia, but gastrulation already occurs at the 30-cell stage, and the main organs (nervous system, notochord, musculature) are composed of a very small number of cells; e.g., there are only 20 notochordal cells as opposed to about 40 cells in an ascidian tadpole.

### D. METAMORPHOSIS AND ORGANOGENESIS

As soon as the larva is fixed by its adhesive papillae to a substrate in the solitary species (or even before the release of the larva in the case of the incubating colonial species), the metamorphosis sets in and the internal structures of the cephalenteron undergo a 180° rotation so that the buccal siphon is now situated at the top of the young animal, opposite to the attachment base.

The different systems of the definitive animal quickly differentiate, and after a few days, the young animal is actively filtering the water. The buccal siphon is an ectodermal invagination covered by the tunic and opening into the pharynx soon after settling of the larva. From the endodermal pouch arise the ample pharynx with the midventral endostyle, the epicardia (in the lower species) and the intestinal loop. On both sides of the pharynx, the ectoderm invaginates into the hemocoel and forms two peribranchial cavities; as the metamorphosis proceeds, these two orifices fuse middorsally in the atrial siphon, an ectodermal depression also lined by the tunic. Although of ectodermal origin, the peribranchial chamber in Ascidiacea cannot be homologized to the atrium of the amphioxus. The gill slits (stigmata) pierce the lateral pharyngeal and the inner atrial monolayered walls applied one against the other, and the mesenchyme interposed in between these walls. The manner of formation of the stigmata is of great interest for the understanding of the phylogeny of the Tunicata; the stigmata derive from primary independant perforations, the protostigmata (for details, see Brien, 1948). From the larval nervous vesicle, which loses the larval sense organs, arises the adult system. The dorsal wall proliferates the cerebral ganglion, the ventral one folds into the neural "gland," and in front the tube becomes ciliated and opens into the pharynx by the dorsal tubercle. Behind, the larval tube degenerates into a thin aneural dorsal cord. The spaces between the mantle, the atrium, and the digestive system are a hemocoel filled with a loose connective tissue in the lacunae of which the blood flows. Two main vessels, the dorsal and the subendostylar sinus, above and below the pharyngeal cavity, are connected by a network of smaller lacunae running throughout the body. In some species, blood lacunae penetrate the tunic (e.g., *Phallusia mammillata, Botryllus schlosseri*) or partake in the budding processes (e.g., *Clavelina lepadiformis, Perophora viridis*). The heart is quite special. The pericardial bladder develops inside a ventral mesoblastic nodule and is probably homologous to a coelomic pouch. The inner wall deeply invaginates and the lips of the groove grow closer together. The resulting tube, open at both ends in the hemocoel lacunae, is the heart, enclosed in a thin membrane, the pericardium. The cardiac contractions are peristaltic waves passing from one end to the other, with a periodic reversal of the direction of the beats. The various blood cells—such as the cardiopericard, the muscles, and the gonads—originate in the mesoblastic crescent lying in the larva between the cephalenteron and the tail. The ascidians are strongly contractile (up to 50% of the rest length) thanks to these muscles (e.g., *Ciona intestinalis*), even when the tunic is leathery (e.g., *Halocynthia papillosa*). There is no well defined excretion organ, except accumulation kidneys like the renal sac of the Molgulidae, which contains brownish concretions. Direct excretion could also take place at the level of the branchiae. A few species are dioecious (e.g., *Oikopleura dioica*, Fig. 19) but self fertilization is difficult and with a high degree of abnormality (Sabbadin, 1971); there is either protandry, or protogyny. The location of the gonads is variable and valuable for the Stolidobranchiata systematics (Van Name, 1945; Berrill, 1950).

In Thaliacea, a real metamorphosis only takes place in the Doliolidae, which have a larval stage. The sequence of events is exactly that described in an ascidian tadpole. The adult oozooid develops in the trunk as a barrel-shaped animal which swims with the help of nine muscular rings. After a few days, most of the viscera undergo a complete degeneration and the oozooid becomes a nurse. Buds actively produced by the ventral stolon migrate along the sides of the nurse up to the dorsal spur (located above the atrial siphon and sometimes longer than the animal itself) where development proceeds (Neumann, 1906; Godeaux, 1957; Braconnot, 1971). In Pyrosomidae, no trace of a larva can be found; the very simple oozooid just develops in order to build up the stolon (Neumann, 1913; Ivanova-Kazas, 1956, 1960, 1962; Godeaux, 1957). In Salpidae, in relation with the viviparity, the development (very peculiar on account of the interference of the kalymmocytes) is truly direct (Brien, 1948).

### E. Asexual Reproduction

Among the chordates, the tunicates are the only organisms capable of asexual reproduction (blastogenesis). From the budding result colonies with numerous individuals (hundreds to thousands, e.g., *Pyrosoma spinosum*) embedded in a common matrix. The colonial status is polyphyletic, as proved by the organization of the colonies and the composition of the buds. In lower species (Aplousobranchia, Pyrosomidae), the animals lie near one another, but in higher species (Perophoridae, Botryllidae, Polystyelinae), the individuals are bound by a common vascular system.

In Ascidiacea, the bud is theoretically composed of two monolayered vesicles with some mesenchyme in between. The outer bladder is always of ectodermal origin and never gives more than the ectoderm and the tunic of the new blastozooid. On the contrary, the inner vesicle has a variable origin according to the order or even the family. It derives from the endodermal epicardia (most of the Aplousobranchia and the Diazonidae), from the hemocoel mesoderm (Clavelinidae and Perophoridae), or from the atrial ectoderm (Botryllidae and Polystyelinae). From this vesicle arise the main organs of the new organism (blastozooid)—the whole digestive system, the peribranchial cavities with atrium and cloacal siphon, the heart, and often the nervous system. When parts of the mother's gut are associated with the epicardial vesicle (Aplidinae, Didemnidae, Diazonidae), they give the intestinal loop of the blastozooid. In this case, the potentialities of the epicardia are restricted (see Brien, 1948, 1958).

Two conclusions may be forwarded: (1) the inner vesicle, whatever its origin, furnishes the main organs of the blastozooid; the potentialities of the differentiated tissues are conditioned by their location in the bud, and (2) the blastozooids cannot be distinguished from the maternal oozooid.

In the class of the Thaliacea, the composition of the buds varies in the different families. In the simplest case, found in the Pyrosomidae, the blastogenesis is a strobilization since only the nervous complex is neoformed. As the tissues of the budding areas in the successive zooids remain undifferentiated, the secondary stolons must be considered as cuttings of the stolon of the oozooid (Godeaux, 1957). In Salpidae, the very complex stolon appears precociously in the embryo. It lengthens and repeatedly constricts off groups of blastozooids, where two rows of individuals lie side by side. In these metagenetic animals, both forms, having very different appearances, (Fig. 18), were once considered different species (Thompson, 1948; Berrill, 1950; Trégouboff and Rose, 1957; Godeaux and Goffinet, 1968). In Doliolidae, the fate of the different components of the stolon is yet not fully understood (Neumann, 1906; Godeaux, 1957) and much remains to be worked out in that field. The Doliolidae are probably the only coelomate animals exhibiting such a degree of polymorphism (Braconnot, 1970, 1971). The oozooid passes through three transient forms—tadpole, fully organized oozooid, and simplified nurse. From the buds successively arise three different kinds of blastozooids—the spoonlike and simplified trophozooids, the barrel-shaped (with 8 ring muscles only) phorozooids (sterile), and gonozooids (hermaphrodite). As Braconnot (1971) demonstrated, gonozooids and phorozooids are quite similar, the only difference being the presence or the absence of the gonads.

In the Appendicularia, budding is wanting.

Tunicata are also remarkable for their high regeneration power. The neural complex is very easily and quickly replaced in *Ciona intestinalis* (Pérès, 1943). In *Clavelina lepadiformis*, a new thorax is regenerated with the help of the epicardia, etc. (Brien, 1948, 1970, 1971). Winter buds are known in many species.

### F. Histology of the Main Organs

The tunic is highly characteristic of the phylum. After Löwy and Kölliker (1846), it is generally admitted that this cover is made of some kind of cellulose (Berthelot's tunicin, 1872; see Godeaux, 1964a). As a matter of fact, the tunic is variable in hardness as well as in appearance in the different orders. It is soft or even fluid in the aplousobranchs, the salps and pyrosoms, and in lower phlebobranchs; more or less cartilaginous in higher phlebobranchs and some salps; fibrous, hard, and even thorny in the solitary stolidobranchs. In most Didemnidae and some Polycitoridae (*Cystodites* sp.), calcareous spicules are scattered throughout the tunic (Monniot, 1970). Recent investigations (Smith, 1970; Smith and Dehnel, 1970, 1971) have proved that the tunic, besides a large amount of water (up to 95%), also contains proteins and acidic mucopolysaccharides and that the ternary component (cellulose?) only represents a part of the dry weight. The tunic is protected by a cuticle. The matrix of the test, elaborated by the ectoderm, is often invaded by hemocoel cells, providing additional material (Pérès, 1948).

The monolayered ectoderm is loosely connected to the tunic, except at the level of the siphons and of the stolons. Below the ectoderm, the hemocoel exhibits an extraordinary diversity of cells, both immobile and mobile (Pérès, 1943). Among them, the hemoblasts (lymphocytes) keep juvenile and are capable of various differentiations, playing an important role in the regeneration processes (nervous complex, Pérès, 1943) or in blastogenesis (e.g., *Clavelina lepadiformis* and *Perophora listeri*, see Brien, 1948, 1958, 1970, 1971; *P. viridis*, Freeman, 1964). Some blood cells contain pigment conditioning the color of the animal (e.g., *Clavelina lepadiformis*). The pigmentation is genetically controlled in *Botryllus schlosseri* (Sabbadin and Graziani, 1967). Except in Molgulidae, only diffuse excretion organs are found in the ascidians. The excretion products (uric acid, Sabbadin and Tontodonati, 1967) crystallize inside the vacuole of blood cells (nephrocytes) concentrating in the loose mesenchyme embedding the organs (Azéma, 1937).

The musculature is well developed in tunicates. Its structure is not well known, but the electron microscope shows something similar to the hexagonal pattern of the striated fiber. The heart muscle is striped. The cerebral ganglion is a rounded organ with an outer layer of neurons surrounding an inner mass of axons from which emerge the nerve roots. The function of the neural gland is still questioned; it probably has nothing in common with the hypophysis, but influences the reproduction processes (Huus, 1937; Sengel and Georges, 1966; Georges, 1971) and is capable of phagocytosis (Pérès, 1943; Godeaux, 1964b; Ivanova-Kazas, 1966). The ciliary duct and pit act as way in (in colonial tunicates) or way out (in solitary tunicates).

The digestive system can be divided into two main parts—the pharynx where the food is trapped and the intestinal loop where digestion and resorption are performed. The inward flow of water carrying food and oxygen is secured by the cilia covering the gill slits. The particles are limed by the mucous secreted by the endostyle and spread over the inner wall of the pharynx. The food pellets are led to the esophagous by the cilia along the dorsal languets. The structure of the endostyle has been submitted to many investigations in the two last decades. The organ binds radioactive iodine into thyroid hormones (Barrington, 1963; Salvatore *et al.*, 1960; Roche *et al.*, 1962), and the electron microscope reveals that the endostyle is more than a mucous-secreting organ (literature in Godeaux, 1971). In the gut, the ciliary cells are intermingled with glandular and mucous areas. Enterochromaffin cells are present (Gerzeli, 1963). The structure and functions of the system have been recently reviewed by Fenaux (1968) and Thomas (1970). To the gut is annexed the pyloric gland, the nature of which is not clearly understood. This organ seems to be both excretory and digestive (Fouque, 1953).

### G. AFFINITIES

For the reasons (with the sole exception of the enterocoely) afforded for the Cephalochorda, the Tunicata are true Chordata but are early specialized to a mode of life characterized by sedentariness and by microphagy. The pelagic tunicates are secondarily free-swimming animals. If direct relationships with the mollusks are definitely excluded, the parallelism between the evolutionary lines of the Urochorda and the Pelecypoda must be stressed. At the beginning is a small larva reduced to a minimum from which arose successful series with a progressive complexity of the branchial systems and even an extreme stem with simplified or missing branchiae and carnivorous habits (Septibranchia and Aspiraculata).

There has been great interest in the tunicates, mainly in the Anglo-saxon literature, about their possible relationships. Several hypothesis, all speculative owing to the lack of fossil documents, have been forwarded. For some authors (Willey, 1894; Franz, 1927; Gregory, 1946, 1951), the tunicates are simply chordates which underwent an extensive degeneration when adopting sessile habits and from which arose original lineages. The tadpole is only the trace of a remote free-living ancestor. In this case, the tunicates form a lateral branch, more away from the main stem of the chordates than the amphioxus.

For other authors, the planktonic larvae must be held as secondary interpolations in the life cycle of the sedentary adults, favoring the propagation of the species, a more or less acute metamorphosis occuring at the time of the settling. For Garstang (1928), the sedentary ancestor could have been a kind of pterobranch. He suggested that the secondarily appearing propagating larvae give on one hand the ascidian stock and on the other hand, by neoteny, the chordate stock. The sequence would be: Echinodermata—Hemichordata—Protochordata—Vertebrata. Garstang's hypothesis (1928) was exhaustively discussed by Berrill (1955), who proposed a somewhat different conception. In his view, tadpoles are an invention of the sessile ascidians, and then tadpoles, because of a prolonged pelagic life and increasing swimming power, become, by a neotenic process the ancestors of the chordates. (For discussion, see also de Beer, 1954; Whitear, 1957; Bone, 1960; Millar, 1966b.)

## H. SYSTEMATICS

The phylum Tunicata is composed of three classes—Ascidiacea, Thaliacea, and Appendicularia.

### *1. Ascidiacea*

The class Ascidiacea is diversely divided according to the author (Lahille, 1890; Harant and Vernières, 1933; Van Name, 1945; Harant, 1948; Berrill, 1950; Millar, 1966a). For convenience, four orders will be recognized. The systematic characters are the mode of subdivision of the body, the presence or the absence of the epicardia, the structure of the branchial basket, the location of the gonads within the gut loop (Enterogona) or in the pleurae (Pleurogona), and the type of budding.

*First Order*—Aplousobranchia. Budding, colonial or social ascidians, often incubating eggs and larvae, enterogonid, branchial septum simple without folds and internal blood vessels, postabdomen present in some species, epicardia always present and partaking in the budding in most of the species. Four families. Social species: *Clavelina lepadiformis.* Colonial species: *Amaroucium constellatum; Aplidium pallidum, Distaplia magnilarva, Didemnum maculosum.*

*Second Order*—Phlebobranchiata. Solitary or colonial ascidians, postabdomen always wanting, abdomen with epicardia in the lower species, missing in the higher species and then viscera on the left (right) side of the pharynx, enterogonid, branchial septum with internal longitudinal vessels but secondarily missing, no branchial folds. Numerous families. Budding species: *Diazona violacea, Perophora viridis.* Solitary species: *Ciona intestinalis, Ascidiella aspersa, Phallusia mammillata, Corella parallelogramma.*

*Third Order*—Stolidobranchiata. Solitary and large or colonial, budding and small ascidians, branchial septum with longitudinal internal vessels and folds (sometimes secondarily missing), no abdomen, hepatic gland and renal sac in some species, gonads scattered on one or both sides of the trunk (Pleurogona), neural gland above the ganglion, atrial budding. In the solitary species, the tunic is leathery. Four families. Solitary species: *Microcosmus sulcatus, Halocynthia aurantium, H. papillosa, Styela (Cynthia) partita, Polycarpa mamillaris, Molgula manhattensis.* Colonial species: *Metandrocarpa taylori, Botryllus schlosseri.*

*Fourth Order*—Aspiraculata. Solitary, small, deep-sea living, macrophagous ascidians with branchial system absent. Two genera: *Hexacrobylus indicus, Gasterascidia sandersi* (Monniot and Monniot, 1968).

### 2. *Thaliacea*

The class Thaliacea comprises three families and a few genera and species. Budding, solitary or colonial, often metagenetic, pelagic animals, siphons at the opposite ends of the barrel-shaped zooid, abdomen reduced, branchial septum with a single protostigmate divided or not into stigmata (Neumann, 1934; Brien, 1948; Tokioka, 1937; Thompson, 1948; Ivanova-Kazas, 1956, 1960, 1962; Godeaux, 1951, 1969; Godeaux and Goffinet, 1968; Braconnot, 1970, 1971). *Doliolum mülleri, D. denticulatum, Thalia democratica, Salpa cylindrica, Pyrosoma atlanticum, P. spinosum.*

### 3. *Appendicularia* (*Larvacea*)

The class Appendicularia (Larvacea) is divided into three families. Appendicularia are planktonic, often minute organisms, hermaphrodite and not budding, living in a house secreted by the ectoderm and periodically replaced, with no branchiae, no atrium, no cloacal siphon but two spiracula. Heart and endostyle sometimes missing. Mixture of larval and adult characters (Lohmann, 1933; Fenaux, 1967). *Oikopleura dioica, Megalocercus abyssorum* (length >30 mm), *Fritillaria pellucida, Kowalevskaia tenuis.*

## I. ECOLOGY AND GEOGRAPHIC DISTRIBUTION

The tunicates, especially the ascidians and appendicularians, are widespread in cold as well as in warm waters. The Thaliacea are mainly confined to warmer waters; like Chaetognatha, they are hydrological indicators, e.g., *Salpa fusiformis* in the North Atlantic Ocean (Fraser, 1949; Hunt, 1968).

Most of the tunicates are of a little economic value; a single species (*Microcosmus sulcatus*) is edible. But owing to their abundance, at least in some regions, the appendicularians are an important source of food for young fish. Tunicates are active filter-feeding organisms, swallowing bacteria and clarifying waters. As the gut transit is quick, fecal pellets can be used as food by the detritus feeders (Paoletti, 1970). Some species are able to live in highly polluted harbor waters (e.g., *Ciona intestinalis, Botryllus schlosseri*) or in dilute coastal waters (*Oikopleura dioica*).

## REFERENCES

(For the references prior to 1930, see reviews by Berrill, Brien, Dalcq, Huus, Ihle, Lohmann, and Neumann).

Azéma, M. (1937). *Ann. Inst. Oceanogr.* (*Paris*) **17**, 1.

Barrington, E. J. W. (1958). *In* "Comparative Endocrinology" (A. Gorbman, ed.), p. 250. Wiley, New York.

Barrington, E. J. W. (1963). "An Introduction to General and Comparative Endocrinology." Oxford Univ. Press, London and New York.

Berrill, N. J. (1950). *In* "The Tunicata" (The Ray Society, ed.), Vol. 133, p. 1. Adlard & Son, Dorking.

Berrill, N. J. (1955). "The Origin of Vertebrates." p. 14. Oxford Univ. Press, London and New York.

Bone, Q. (1960). *J. Linn. Soc. London, Zool.* **44**, 252.

Braconnot, J. C. (1970). *Arch. Zool. Exp. Gen.* **111**, 629.

Braconnot, J. C. (1971). *Arch. Zool. Exp. Gen.* **112**, 5.

Brien, P. (1948). *In* "Traité de Zoologie" (P.-P. Grassé, ed.), Vol. 11, p. 553. Masson, Paris.

Brien, P. (1958). *Annee Biol.* **34**, 241 and 273.

Brien, P. (1970). *Arch. Biol.* **81**, 441 and 633.

Brien, P. (1971). *Mem. Acad. Roy. Belg., Cl. Sci.* **39**, 92.

Conklin, E. G. (1931). *J. Exp. Zool.* **61**, 1.

Dalcq, A. (1935). "L'Organisation de l'Oeuf chez les Chordés. Etude d'Embryologie causale." p. 371. Gauthier-Villars, Paris.

Dalcq, A. (1938). *Arch. Biol.* **49**, 397.

Dalcq, A. (1941). "L'Oeuf et son Dynamisme organisateur." p. 383. Albin Michel, Paris.

Dalcq, A. (1959). *Arch. Biol.* **71**, 93.

de Beer, G. (1954). "Embryos and Ancestors." p. 60. Oxford Univ. Press, London and New York.

Durand, S. (1948). *C.R. Acad. Sci. Paris,* **227**, 683.

Fenaux, R. (1963). *Vie et Milieu,* Suppl. 16, p. 1.

Fenaux, R. (1967). *In* "Faune de l'Europe," Vol. **2**, p. 1. Masson, Paris.

Fenaux, R. (1968). *Annee Biol.* [4] **7**, 345.

Fouque, G. (1953). *Ann. Inst. Oceanogr.* (*Paris*) **28**, 189.

Fraser, J. H. (1949). *Scot. Home Dep., Fish. Div., Sci. Invest.* **1**, 1–44.

Freeman, G. (1964). *J .Exp. Zool.* **156**, 157.

Garstang, W. (1928). *Quart. J. Microsc. Sci.* **72**, 51.

Georges, D. (1971). *In* "4th European Marine Biology Symposium" (D. J. Crisp, ed.) p. 561. Cambridge Univ. Press.

Gerzeli, G. (1963). *Pubbl. Sta. Zool. Napoli* **33**, 117.

Godeaux, J. (1957). *Ann. Soc. Roy. Zool. Belg.* **88**, 1.

Godeaux, J. (1963). *Fortschr. Zool.* **16**, 341.

Godeaux, J. (1964a). *Stud. Gen.* **17**, 176.

Godeaux, J. (1964b). *Publ. Univ. Off. Congo Elisabethville* **7**, 51.

Godeaux, J. (1969). *Ann. Soc. Roy. Zool. Belg.* **99**, 69 and 153.

Godeaux, J. (1971). *C. R. Acad. Sci., Ser. D* **272**, 592.

Godeaux, J., and Goffinet, G. (1968). *Ann. Soc. Roy. Zool. Belg.* **98**, 49.

Gregory, W. K. (1946). *Quart. Rev. Biol.* **21**, 348.

Gregory, W. K. (1951). "Evolution Emerging," 2 vols. Macmillan, New York.

Harant, H. (1948). *In* "Traité de Zoologie" (P.-P. Grassé, ed.), Vol. 11, p. 895. Masson, Paris.

Harant, H., and Vernières, P. (1933). *Faune Fr.* 27.

Harant, H., and Vernières, P. (1938). *Faune Fr.* 33.

Hopkinson, I. (1913). "A Bibliography of the Tunicata, 1469–1910" (The Ray Society, ed.), p. 1. Dulan, London.

Hunt, H. G. (1968). *Bull. Mar. Ecol.* **6,** 225.

Huus, J. (1937). *In* "Handbuch der Zoologie" (W. G. Kükenthal and T. Krumbach eds.), Vol. 5, Part 2, No. 6, Book 35, p. 545. de Gruyter, Berlin.

Ihle, J. E. W. (1935). *In* "Handbuch der Zoologie" (W. G. Kükenthal and T. Krumbach eds.), Vol. 5, Part 2, No. 5, Book, 26, p. 401. de Gruyter, Berlin.

Ihle, J. E. W. (1957). *"Bronn's Klassen"*. Vol. 3. Suppl. 2, Book 2, 4, p. 241.

Ivanova-Kazas, A. M. (1956). *Zool. Zh.* **35,** 1193 (English summary).

Ivanova-Kazas, A. M. (1960). *Dokl. Akad. Nauk SSSR* **136,** 494.

Ivanova-Kazas, A. M. (1962). *Cah. Biol. Mar.* **3,** 191.

Ivanova-Kazas, O. M. (1966). *Arch. Anat. Histol. Embryol. Moscou.* **51,** 48. (English summary).

Labrousse, M. (1963). *Annee Biol.* [4] **2,** 469.

Lohmann, H. (1933). "Handbuch der Zoologie" (W. G. Kükenthal and T. Krumbach eds.), Vol. 5, Part 2, Book 1, p. 15. de Gruyter, Berlin.

Millar, R. H. (1966). "Marine Invertebrates of Scandinavia." Vol. 1. Universitetetsforlaget (Oslo).

Millar, R. H. (1966b). *In* "Some Contemporary Studies in Marine Science" (H. Barnes, ed.), p. 519. Allen & Unwin, London.

Monniot, C., and Monniot, F. (1968). *Bull. Inst. Oceanogr.* **67,** 48.

Monniot, F. (1970). *Arch. Zool. Exp. Gen.* **111,** 303.

Neumann, G. (1934). *In* "Handbuch der Zoologie" (W. G. Kükenthal and T. Krumbach, eds.), Vol. 5, Part 2, No. 3, Book 13, p. 203. de Gruyter, Berlin.

Paoletti, A. (1970). *Rev. Int. Oceanogr. Med.* **18,** 33.

Pérès, J. M. (1934). *Ann. Inst. Oceanogr. (Paris)* **21,** 229.

Pérès, J. M. (1948). *Ann. Inst. Oceanogr. (Paris)* **23,** 345.

Reverberi, G. (1961). *Advan. Morphog.* **1,** 55.

Roche, J., Salvatore, G., and Rametta, G. (1962). *Biochim. Biophys. Acta* **63,** 154.

Sabbadin, A. (1971). *Develop. Biol.* **24,** 379.

Sabbadin, A., and Graziani, G. (1967). *Riv. Biol.* **60,** 559.

Sabbadin, A., and Tontodonati, A. (1967). *Monit. Zool. Ital.* [N.S.] **1,** 185.

Salvatore, G., Vecchio, G., and Macchia, V. (1960). *C.R. Soc. Biol.* **154,** 1380.

Sengel, P., and Georges, D. (1966). *C.R. Acad. Sci., Ser. D* **263,** 1876.

Smith, M. (1970). *Biol. Bull.* **138,** 354 and 379.

Smith, M., and Dehnel, P. (1970). *Comp. Biochem. Physiol.* **35,** 17.

Smith, M., and Dehnel, P. (1971). *Comp. Biochem. Physiol.* **40B,** 615.

Thomas, N. W. (1970). *J. Mar. Biol. Ass. U.K.* **50,** 429 and 737.

Thompson, H. (1948). "Pelagic Tunicates of Australia." CSIR, Australia, Melbourne.

Tokioka, T. (1937). *Annot. Zool. Jap.* **16,** 219.

Trégouboff, G., and Rose, M. (1957). "Manuel de Planctonologie méditerranéenne," 2 vols. CNRS, Paris.

Van Name, W. G. (1945). *Bull. Amer. Mus. Natur. Hist.* **84,** 1.

Waddington, G. H. (1956). "Principles of Embryology." Allen & Unwin, London.

Whitear, M. (1957). *Ann. Mag. Natur. Hist.* [12] **10,** 338.