POGONOPHORA

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by

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AUTHOR'S PREFACE TO THE ENGLISH EDITION

The first edition of this book was published in 1960 as one of a series "Fauna of the U.S.S.R." produced by the Zoological Institute of the Academy of Sciences of the U.S.S.R. I there summarized and analysed all that was then known about Pogonophora, not confining my attention merely to the species found in the seas bordering the Soviet Union. Until quite recently the Pogonophora were still a great zoological curiosity and only a few zoologists had any chance of studying them. It is with great gratification that I see that the number of those now studying these animals is increasing rapidly. As Dr. D. B. Carlisle has rightly said, Pogonophora are numbered amongst the rather common animals of the oceans. They are found indeed in nearly all seas. About 80 species have been described (71 in the present publication) and, indeed, in all likelihood the number will soon reach three figures.

The material for my studies was collected by many Soviet oceanographical expeditions, but particularly by those sent out by the Institute of Oceanology of the Acadamy of Sciences of the U.S.S.R. on board R.V. *Vityaz'*. I studied the morphology and embryology of Pogonophora within the walls of my *alma mater*, Leningrad University, and their systematics at the Zoological Institute of the Academy of Sciences. I am greatly indebted to all these establishments. In 1961 I was highly gratified to receive the Lenin Prize for my work on the Pogonophora.

I hope that the English edition of my book will be favourably received, that it might help zoologists in studying Pogonophora and interest biologists, both research workers and teachers. This edition would not have seen the light of day were it not for the great labour expended by Dr. D. B. Carlisle, who not only translated it but also brought it up to date and added many valuable and interesting notes. I ask Dr. Carlisle to accept my deep gratitude and I am also sincerely grateful to Dr. Eve C. Southward for her substantial additions. I also thank Academic Press and all those who, in one way or another, helped the publication of the book.

20 May 1963 A. V. IVANOV

FROM THE AUTHOR'S PREFACE TO THE RUSSIAN EDITION

The Pogonophora form a group of invertebrates of high systematic rank in whose structure some of the essential features of the primitive Deuterostomata have been preserved. An understanding of their organization will bring us nearer to the construction of an overall scheme of systematic classification of the animal kingdom and help elucidate the phylogeny of the Deuterostomata. The secondary or false metamerism which is just beginning to develop in pogonophores helps us to understand the metameric structure of the Enteropneusta and the origin of the segmental structure in the Acraniata and Vertebrata. And the Pogonophora are interesting from the physiological point of view, as Metazoa which lack a gut and feed exclusively by means of tentacles.

Forty-five years have passed since the first report of a pogonophore (Caullery, 1914). Even eight years ago [i.e. early 1952] only three species were known, their organization remained almost unknown and their systematic position was obscure. Since then, however, there has been a considerable increase in pogonophoran material, chiefly owing to the various cruises of R.V. *Vityaz*' sent out by the Institute of Oceanology of the Academy of Sciences of the U.S.S.R.

The lively interest shown by wide circles of zoologists and the lack of publications giving any details of the morphology and systematics of Pogonophora have stimulated me to undertake the composition of this work. In the first part I have, to the extent permitted by our present state of knowledge, summarized the morphology, embryology, ecology, classification and other general questions. An abridged version of this part has already appeared in French (Ivanov, 1960a). In the systematic part of the work I have given descriptions and diagnoses of all the forms known at present. Some features of species which have been described earlier are given more accurately and in greater detail. In particular, my earlier reports on the morphology of the girdles, toothed platelets and tubes (Ivanov, 1952, 1957a) have been checked upon new material, corrected and supplemented.

Many questions on the morphology, physiology, embryology, ecology, systematics and geographical distribution of the Pogonophora are still far from clear or have not even been touched upon, and we are far from drawing up any reasonably complete list of species. The growing scale of deep-sea exploration and the discovery of pogonophores in many different parts of the world, including the shores of Western Europe, justify the hope that many more investigators will join in research on these creatures.

January 1960

TRANSLATOR'S PREFACE

During the 1920's, when R.R.S. *Discovery II* was working in the Antarctic and Subantarctic, one of the commonest disappointments in collecting from the sea-bed was to bring up the dredge from abyssal depths after ten or twelve hours work only to find the net clogged with masses of fibres. Often enough the dredge-bag was so filled with this disgusting mass of 'gubbins' as to preclude the possibility of having taken any material of significant biological interest, and the whole haul would be jettisoned overboard, after the briefest of rough sortings. This happened so often that the biologists on board coined the term "Gubbinidae" as a familial name for this annoying material. Looking back on his period on board R.R.S. *Discovery*, Professor Sir Alister C. Hardy, F.R.S., tells me that the Gubbinidae were obviously Pogonophora and many tons of pogonophores must have been shovelled overboard by some of the leading marine biologists of the day. The poignant part of this tale is that the *Discovery* Investigations had a strict rule that no biological material collected should be thrown away on board ship; it should all be preserved and brought back to England. The rule existed just to prevent this very happening—the discarding of material of supreme biological interest merely because it went unrecognized. Quite obviously the biologists of the day did not even realize that the Gubbinidae were biological entities. It is possible that enough of the Gubbinidae are still to be found amongst the preserved collections of R.R.S. *Discovery* to afford the basis for a study of the Pogonophora of the Antarctic and it may be worthwhile for someone to search through the collections.

It is quite obvious from this tale that Pogonophora form the dominant element of the fauna over quite large stretches of the sea-bed and that their existence remained unrecognized long after they had first forced themselves upon the attention of marine biologists. The earliest reports of Pogonophora date from the period when the *Discovery* scientists were shovelling the Gubbinidae overboard, but we have had to wait until the collections of the last decade made by the Soviet R.V. *Vityaz'* had been analysed by Professor A. V. Ivanov before we could appreciate the importance of the group. Professor Ivanov's monograph is the first comprehensive treatment of the phylum.

In preparing this English edition I have made an attempt to bring it up to date. In the three years which have passed since the original Russian edition the accelerating pace of deep-sea research has extended our knowledge of the Pogonophora. New species have come to light, more is known of the geographical distribution of the group, the animals have been observed alive and more is known of their biology. Inclusion of this new material has produced a book which is half as long again as the original.

The greater part of the new material was provided by Professor Ivanov, who besides sending me descriptions of new species for inclusion in this edition also provided a copiously annotated copy for the purpose of the translation. Besides this the greatest contribution has been made by Dr. Eve C. Southward, working at the Plymouth Laboratory of the Marine Biological Association of the United Kingdom. She has provided the description of one new species and has sent me extensive notes on her observations on both living and dead material. In addition, I have drawn upon her recently published work and in particular upon the results of her re-examination of the original material collected in the East Indies by R.V. *Siboga*, material upon which was based the first description of a pogonophore. Amongst other authorities whose work has contributed towards this edition I would single out Dr. Olga Hartman, who has lent a set of original drawings for reproduction here and has allowed me to print a modified description of *Siboglinum veleronis* Hartman.

Though the basis of the translation has been the annotated copy, which thus differs in many minor ways from the published version of the Russian original, the author and I have nevertheless felt it desirable to indicate in some way the additional material, wherever feasible, by enclosing it in square brackets, whatever its source. The illustrations have retained their original numbers and additional figures have been interpolated with a prefixed letter (for example, the new figure A133 will be found after Fig. 133). New tables have been inserted with the same convention, but where pre-existing tables have been enlarged I have given no indication. Except where an acknowledgement is given in the legend, additional figures have been drawn by Professor Ivanov.

I have transliterated proper nouns from the Russian according to the proposals put forward by the Royal Society, though at a late stage in proof-correcting I have noticed some inconsistencies which were not worth altering. This adherence to the Royal Society system has had the unfortunate result that it is not immediately obvious, for example, that *Diplobrachia belajevi* has been named after Dr. G. M. Belyaev. Geographical names have not been transliterated (it is difficult to identify Trezhuri Island with Treasury Island, at least in print). Localities have instead been named according to the appropriate British Admiralty chart of the area. Where the name given in the "Times" Atlas differs greatly from that on the charts or where the charts do not name a feature (this applies chiefly to the deep-sea trenches) the Atlas name is given additionally or instead. The precise locality of a few species is given in geographical coordinates. More usually the latitude and longitude of a neighbouring named locality are given to the nearest degree, in order that the reader may the more easily find it on the chart.

When this edition was in page proof I received the descriptions of yet more new species of pogonophores from Professor Ivanov. These arrived too late for inclusion and their publication has been arranged in the *Journal of the Linnaean Society*, together with revised keys. The description of another European species of *Siboglinum* by Dr. Southward should appear in the *Journal of the Marine Biological Association of the U.K.* at about the time of publication of this monograph.

In preparing this translation I have eschewed any attempt at a literal translation, preferring more often to catch the sense. In the present tense a Russian sentence, particularly if it is purely descriptive, may be complete without a finite verb. Rather than supply the implied part of the verb "to be" I have often chosen to translate a noun by a verb. Common Russian idiom has usually been replaced by an English equivalent, but I have endeavoured to retain idiom and turns of phrase which seem more personal to the author. I have also tried to echo the balance in his choice between latinate and vernacular expressions ("posterior" and "hind", "gut" and "alimentary canal", for example). In creating an English terminology for Pogonophora I have been guided by Dr. Eve C. Southward and we have agreed on a standard set of terms.

I should like to thank numerous publishers for permission to reproduce text and illustrations: Messrs. Masson & Cie, who first published many of Professor Ivanov's original figures. Messrs E. J. Brill (publishers of the *Siboga Reports*), the Trustees of the South African Museum, the Council of the Marine Biological Association of the United Kingdom, and the Editorial Boards and Publishers of the *Canadian Journal of Zoology*, of *Pacific Science*, and of *Cahiers de Biologie Marine*. Amongst individuals who have afforded material or intangible help I would particularly like to thank Dr. F. S. Russell, F.R.S., Dr. A. J. Southward (whose rude remarks I have sometimes ignored, no doubt to my cost), Dr. L. H. N. Cooper, Mr. J. E. Moorhouse (who has prepared the systematic index), and my wife.

May 1963 D. B. C.

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PART I

General Account

CHAPTER 1

Introduction

Phylum POGONOPHORA BEKLEMISHEV, 1944

(Synonyms: Phylum Pogonofora Ulrich, 1950; Phylum Brachiata Ivanov, 1955)

The deuterostomic nature of the Pogonophora is amply indicated by their general body plan and the enterocoelic mode of formation of the coelom. The major body-axis of the pogonophora, as in the Enteropneusta, is homologous with the axis of symmetry of protaxial animals. This is apparent from the correspondence of the antero-posterior polarity of the body with that of the egg. The archetypal 3-segmented plan has been preserved in the adult structure of the Pogonophora and in this respect they are like the Hemichordata and sharply distinguished from the remaining deuterostomate phyla in which the primitive 3-segmental organization has undergone very complicated transformations during the process of evolution (e.g. in the Echinodermata and the Chordata).

The chief peculiarities of the phylum Pogonophora, distinguishing them from other Deuterostomia, are as follows:

1. The development of tentacles on the first segment of the body;
2. The possession of coelomoducts in the first and third segments;
3. The primitive close connexion of the gonad with the coelom;
4. The development of a distinct heart on the ventral blood-vessel;
5. The complete suppression of a gut in the adult structure;
6. The strong cuticularization of the integument;
7. The profound secondary modification of embryonic development.

In the phylum Pogonophora there is only one class, the class Pogonophora.

Historical survey

The honour of the discovery of the first pogonophore belongs to the eminent French zoologist Maurice Caullery, who, in 1914, described material collected by the Netherlands *Siboga* Expedition in the seas of the Malayan Archipelago. He lumped the whole of this material together under the name *Siboglinum weberi* [the expedition was led by M. Weber] when some thirty years later, in 1944, he published a monograph on *S. weberi* in which he described the organization of this animal (Fig. 1*A*). [The material has been further examined by Dr. Eve Southward (1961) who has found that it consists of some sixteen species belonging to at least four genera and two families.] Thus because of the mixture of species, which Caullery did not detect, and because of the bad state of preservation of some of the material, it was not possible for him to elucidate the entire structural plan of *Siboglinum*, and, until 1951 the position of this genus in the animal kingdom was not determined. In a classification published in 1948, however, Caullery placed *Siboglinum* after the classes Enteropneusta and Pterobranchia as an addendum to the phylum Stomochorda (= Hemichordata), on the supposition that its organization was similar to that of this phylum.

The second representative of the class—*Lamellisabella zachsi*—was found by P. V. Ushakov in 1932 in the Sea of Okhotsk. The characteristic appearance (Fig. 1*B*) of this tubicolous animal, recalling that of the sedentary polychaetes, led Ushakov astray and he ascribed *Lamellisabella* to the family Sabellidae, merely putting it in a separate subfamily (Ushakov, 1933). A few years later, however, Johansson (1937, 1939) studied two incomplete specimens of *L. zachsi* in sectioned material and concluded that this animal had nothing in common with the Annelida, nor indeed with any other phyla, and created for it a new class, which he called Pogonophora [Gr. πώγων—beard, φέρω—bearer]. Johansson described many features of the organization and noted the 3-segmental nature of the body. Most of his conjectures turned out to be in general correct, though his interpretation of the segmentation of the coelomic cavities is no longer accepted.

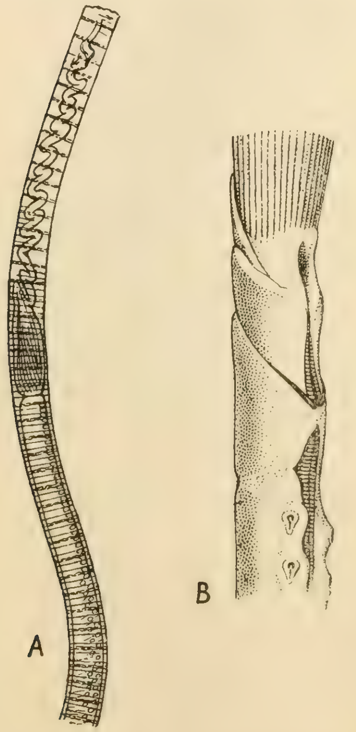

Fig. 1. The earliest illustrations of Pogonophora.
A – *Siboglinum weberi* in its tube. (After Caullery, 1914.)
B – The front end of the body of *Lamellisabella zachsi* viewed from the side and somewhat ventrally. (After Ushakov, 1933).

The publication of the work of Caullery and Johansson aroused lively interest among zoologists and the question of the systematic position of the Pogonophora was a subject of animated debate. In 1938 Reisinger ascribed *Lamellisabella* to the Vermes Oligomera (in the sense of Bütschli, 1910, and Krumbach, 1937), considering that the Pogonophora took their place alongside the Phoronidea and the Enteropneusta. [It was not yet realized that *Siboglinum* was related to *Lamellisabella*.] Then Beklemishev (1944) pointed out that the major features of the organization of *Lamellisabella* suggested that the Pogonophora should be placed with the Hemichordata, and a comparison of *Lamellisabella* with the Enteropneusta and with the Pterobranchia forced him to consider the Pogonophora as an independent primitive phylum of the Deuterostomia. Later, when the organization of *Lamellisabella* became better known, several of Beklemishev's arguments fell down, but nevertheless the position of the Pogonophora in the classificatory scheme was abundantly confirmed. The idea that *Siboglinum* was related to the Hemichordata was advanced independently by Dawydoff (1948), on the basis of a detailed analysis of this genus from the data of Caullery. Ulrich (1950), however, after a detailed discussion of the data of Johansson on *Lamellisabella*, placed the Pogonophora as a distinct phylum of the Archicoelomata, on a par with the phyla Chaetognatha, Tentaculata, Enteropneusta (= Hemichordata) and Echinodermata. Further grounds for the ascription of the Pogonophora to the Deuterostomia were, however, adduced by Ivanov (1955), who placed the class in a new phylum (which he named the Brachiata), when the architectural plan of the Pogonophora became clearer.

It is interesting that for rather a long time no one attempted to compare the structure of *Siboglinum* with that of *Lamellisabella*, though it was manifest that both of them belonged to the same systematic group (Ivanov, 1951).

In 1949 Ivanov described a third species of pogonophore—*Lamellisabella* (or *Polybrachia*) *gorbunovi*—this time from the Arctic Ocean. Then the number of known species quickly began to grow, thanks mainly to the expeditions of R.V. *Vityaz'* (1949–1958) to the western parts of the Pacific Ocean. From the collections of R.V. *Vityaz'* were described first five species and four genera and then an additional twelve species and two genera (Ivanov, 1952, 1957a). The Danish deep-sea expedition of circumnavigation on R.V. *Galathea* produced yet another new genus—*Galathealinum*—from the Celebes Sea (Kirkegaard, 1956a). Jägersten (1956) described *Siboglinum ekmani* from the Skagerrak. Numerous new forms (two new genera, nineteen species) have been described very recently from Soviet expeditions to various seas. Southward and Southward (1958, 1959) have described two new species of *Siboglinum*, a new species of *Oligobrachia* and one of *Diplobrachia* taken in the Atlantic Ocean near the shores of Western Europe. [E. C. Southward (1961–1962) has described eight new species and one new genus from South Africa, Canada and Malaya (this last on the basis of a re-examination of the *Siboga* material). Ivanov (1961a) has described two new genera and three new species, Hartman (1961) a new species from American waters and numerous authors have added to the known distribution of previously known or nondescript species (Brattström, 1959; Brattström and Fouchald, 1961; Hartman and Barnard, 1960; Kirkegaard, 1961a; Menzies *et al.*, 1959; Moskalev, 1961; Parker, 1962), and this English edition adds eleven new species to the list.]

This abundance of new material has allowed, during the last decade, far more detailed investigations into the organization of the Pogonophora than was possible before 1950. Their feeding mechanisms have largely been elucidated, their embryological development and geographical distribution have been studied, a workable system of classification has been erected and firm foundations have been laid on which to judge of their systematic position in the animal kingdom (Ivanov, 1952, 1955a, b, c, 1956a, b, 1957a, c). Jägersten (1956) has made interesting observations on the histology of *Siboglinum* and in 1958 Brunet and Carlisle carried out a chemical analysis of the tubes of various Pogonophora and showed that they consisted largely of chitin. Recent papers of Ivanov (1958a, b, 1959a) have been devoted to the structure of the genital and nervous systems and to the phylogeny of the class. Finally, Ivanov (1960a) has published a review of the organization of the Pogonophora. In this summary the results of his investigations into the different organ systems (integument, glands, and circulatory, excretory and coelomic systems) were collected together for the first time.

CHAPTER 2

External Morphology and the General Body Plan

The general body plan of Pogonophora

The complete absence of a gut in the Pogonophora in the adult condition, though it appears so surprising, is already well established and has been verified in many forms (Caullery, 1944; Ivanov, 1952, 1955a, 1960a; Jägersten, 1956). Until very recently the question of how pogonophores feed seemed altogether mysterious. Not surprisingly, therefore, Caullery (1944) assumed that the specimens at his disposal must represent torn-off zooids from polymorphic colonies and that it was by chance that no gastrozooids had been collected. This hypothesis, advanced by Caullery in a very guarded manner, seemed to fit the facts, and even as recently as 1956 Jägersten subjected it to serious discussion, not arriving, however, at any definite conclusion.

The investigation, however, of more and diverse material clearly rules out any idea of a colonial nature in the Pogonophora. In a series of complete specimens (two species of *Lamellisabella*, *Oligobrachia dogieli*, *Heptabrachia beringensis* and several species of *Siboglinum*) the hind end of the body has been described (Ivanov, 1952, 1957a), which completely eliminates any possibility of interpreting individual pogonophores as zooids from a colony. The problem of their feeding has also been decided; as shown by an analysis of the structure, the Pogonophora are capable only of external digestion, carried out by means of the tentacular apparatus (Ivanov, 1955b). This immediately removes all grounds for the colonial hypothesis.

The other major problem of the architectonics of pogonophores is the question of the orientation of the body. Since the embryological development has been inadequately studied, and the mouth and gut are absent in the adult, it is difficult to decide which is the ventral and which the dorsal side of the body. In the present work, as in my earlier papers and in accordance with the opinion first advanced by Johansson (1939), the dorsal side of the body is taken to be that on which lie the cephalic lobe, containing the brain, and the tract of ciliated epithelium (p. 18), and along which runs the median nerve tract. The ventral side is accordingly taken to be that to which the tentacles are attached and along which are disposed the metameric adhesive papillae of the trunk (p. 45).

Jägersten (1956), however, following Caullery (1944) and Dawydoff (1948), takes the opposite view of the orientation of the body. In his opinion, the ciliated band on the trunk represents the remnant of the primitive organ of locomotion, which was developed on the ventral side in crawling ancestors. Furthermore, Jägersten assumes that the tentacles were already developed in these creeping ancestors of the Pogonophora on the side away from the substratum, i.e. on the dorsal side.

These arguments possess, however, the character of unproven speculative supposition, and strong objections may be raised against each of them. Indeed, there is no evidence whatever that the ciliated band ever served a propulsive function or that it was ever part of a ventral locomotory organ. Rather there can be no doubt that it represents the remnant of a general ciliated epithelium. A crawling type of ancestral form is thus clear supposition. On the contrary, the development of tentacles was, in all likelihood, bound up with a sedentary way of life.

It is perhaps more reasonable to consider that since the Pogonophora, in common with the lower Deuterostomia, display a trisegmental structure (p. 11), their median nerve cord, always well developed for the whole length of all three segments of the body, must be dorsal.

External anatomy

The vermiform and, for the most part, threadlike body of the Pogonophora has the characteristic shape of a sedentary animal, bearing on the anterior end a crown of tentacles like that of sedentary polychaetes, phoronids, bryozoans or Pterobranchia. The superficial resemblance to sedentary polychaetes is often enhanced by the presence on the trunk of more or less metameric paired adhesive papillae with cuticular plaques, creating the impression of polymeric segmentation looking like that of annelids.

Size and colouration

The length of the body varies between wide limits. Amongst the smallest species we may take as typical *Siboglinum pellucidum* and *S. minutum*, in which the body is no more than 5·5 cm long and only 0·1 mm (100μ) broad, [while *S. veleronis* is only 0·065 mm (65μ) across.] Amongst the largest species are *Lamellisabella zachsi* (Fig. 2) and *Spirobrachia grandis*. The length of the latter species, including the tentacular crown, probably exceeds 25 cm, while the trunk may reach 2·5 mm in diameter. The more slender *Zenkevitchiana longissima*, however, with a breadth of no more than 0·8 mm, may reach 36 cm long, [while *Galathealinum brachiosum*, of which we do not

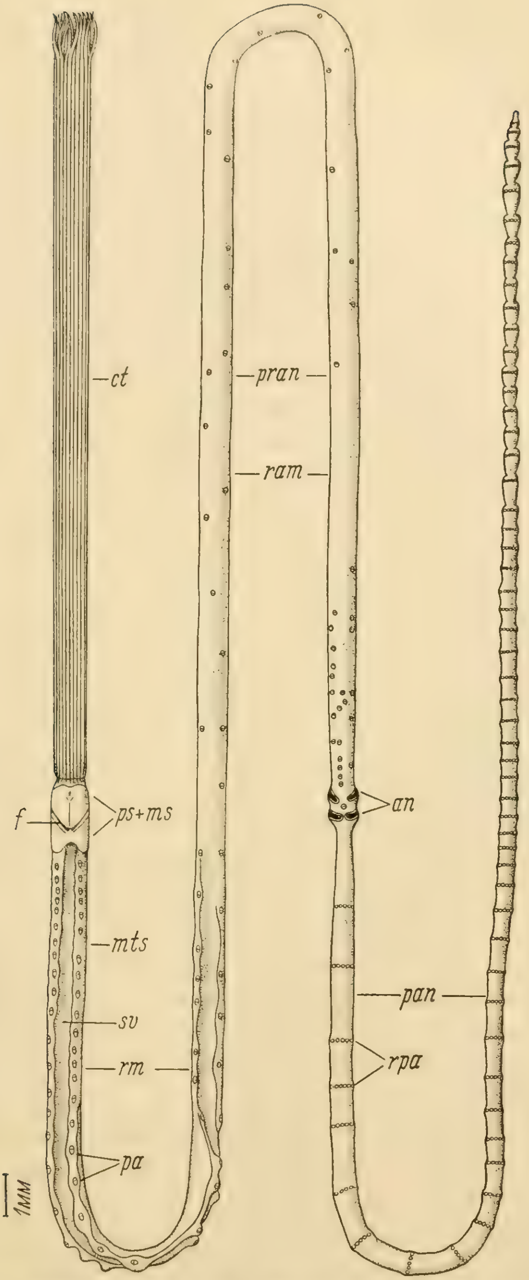

Fig. 2. *Lambellisabella zachsi*, viewed from the ventral side.
an – girdles (annuli); *ct* – tentacles; *f* – bridle (frenulum); *mts* – metasoma; *pa* – papillae; *pan* – post annular region of metasoma; *pran* – preannular region of metasoma; *ps + ms* – the forepart of the body, formed from the fusion of the protosoma and mesosoma; *ram* – the nonmetameric region of the metasoma; *rm* – the metameric region of the metasoma; *rpa* – transverse rows of adhesive papillae; *sv* – ventral sulcus of the metameric region of the metasoma. (After Ivanov, 1952).

possess a complete specimen, is probably larger than either, attaining a diameter of 1·5 mm and a length of some 30–45 cm.]

The bodily proportions are extraordinary. One of the features of the Pogonophora which strikes one at first glance is the unusual elongation of the body (Fig. 2). The length is always at least 100 times the breadth. Thus in *Siboglinum caulleryi* the length to breadth ratio may be 600:1, in *S. minutum* 550:1, in *Oligobrachia dogieli* 400:1 and in *Heptabrachia subtilis* 200:1. One of the species which is least elongated—*Spirobrachia beklemischevi*—has a body which is at least 100 times as long as broad.

The small and medium-sized forms are semi-transparent, almost colourless or whitish. The circulatory vessels may be seen through the body wall filled with red blood, which gives the tentacles a rosy-pink or red hue. In the males the whitish mass of the genital system may usually be seen in the anterior part of the trunk and in the postannular region, while in the females the yellowish yolky eggs may be seen in the front part of the preannular region. The large *Spirobrachia grandis* is distinguished by the brick-red colour of the body. [The glandular patches of epidermis on the mesosoma of *Siboglinum inerme* and some other species of this genus are whitish in the living animal and the cephalic lobe is brownish.]

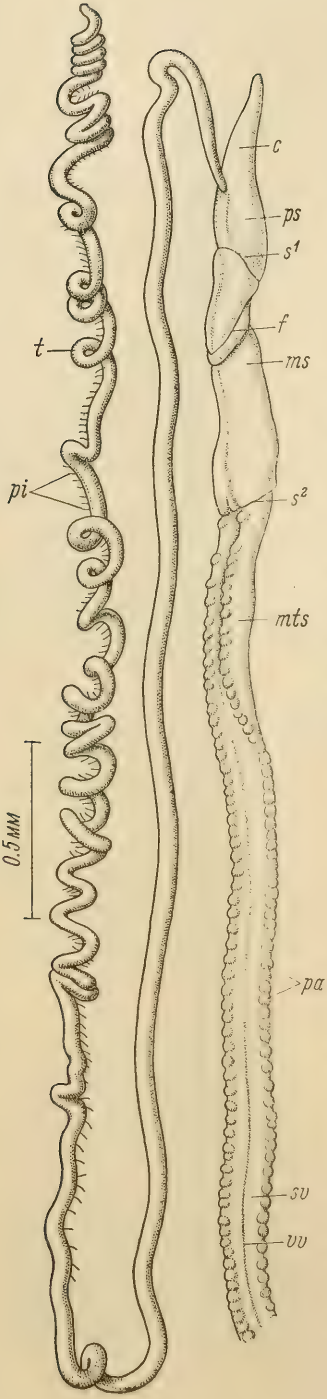

Fig. 3. The front part of the body of *Siboglinum caulleryi*, viewed from the left side and somewhat ventrally.
c – cephalic lobe; *f* – bridle (frenulum); *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle; *vv* – ventral blood vessel seen by transparency. (After Ivanov, 1957a.)

The divisions of the body

The body of the Pogonophora consists of three segments greatly differing in their length—the protosoma, mesosoma and metasoma (Figs. 2–5, 7, 8, 15, 16, 20), which correspond to the proboscis (or cephalic shield or preoral lobe), the collar and the trunk respectively of the Hemichordata (Ivanov, 1952, 1955a). The protosoma is furnished with a protuberant antero-dorsal cephalic lobe (Figs. 3, 5, 8, 15) and with long tentacles. The mesosoma and metasoma lack appendages. External distinctions between the segments are by no means present in all the Pogonophora. In the more advanced forms the protosoma fuses with the mesosoma to form a combined fore-part of the body. [The term fore-part of the body will be used to refer to protosoma + mesosoma.] Between the mesosoma and metasoma, on the other hand, the boundary is always very clearly defined.

Apart from this true (or primary) segmentation there is a secondary division of the body into regions. Thus the metasoma in all Pogonophora is divided into two sharply distinguished regions (Figs. 2, 8, 16). In some forms, moreover, the protosoma, and in others the mesosoma, may be secondarily divided by one or more annular grooves.

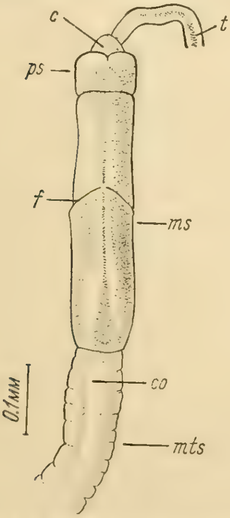

Fig. 4. Front part of the body of *Siboglinum minutum* from the dorsal side.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle (frenulum); *ms* – mesosoma; *mts* – metasoma; *ps* – protosoma; *t* – tentacle.

The protosoma is the first and shortest segment of the body. Usually it is much shorter than the mesosoma and rarely is it noticeably longer than broad. For the most part it is more or less cylindrical, but in *S. minutum* it makes a pair of lateral swellings (Fig. 4).

In the majority of Pogonophora (all the Athecanephria, *Heptabrachia*, *Polybrachia* etc) the protosoma is divided from the mesosoma by an annular groove, complete or interrupted dorsally or ventrally (Figs. 3, 4, 8, 15). Sometimes this groove makes a sharp bend on the dorsal side, arching backwards (*Oligobrachia*, Fig. 15; *Siboglinum caulleryi*, Fig. 3) or forwards (*Heptabrachia subtilis*). In *Zenkevitchiana*, *Lamellisabella* and *Spirobrachia* the protosoma is not externally distinguishable (Figs. 2, 5, 16), but is fused with the mesosoma to form part of an integral fore-part of the body (Ivanov, 1957a).

The cephalic lobe only rarely looks like a simple prolongation of the protosoma, narrowing to the tip (*Siboglinum weberi*; *S. caulleryi*, Fig. 3; *S. pellucidum*, Fig. 20). Usually it is rather sharply differentiated, and in some forms (*S. fedotovi*, Fig. 6; *S. plumosum* and other species of this genus; and also in *Polybrachia* and *Galathealinum*) it is delimited from the protosoma by a pretentacular groove. The cephalic lobe is usually conical or triangular and not infrequently dorso-ventrally flattened.

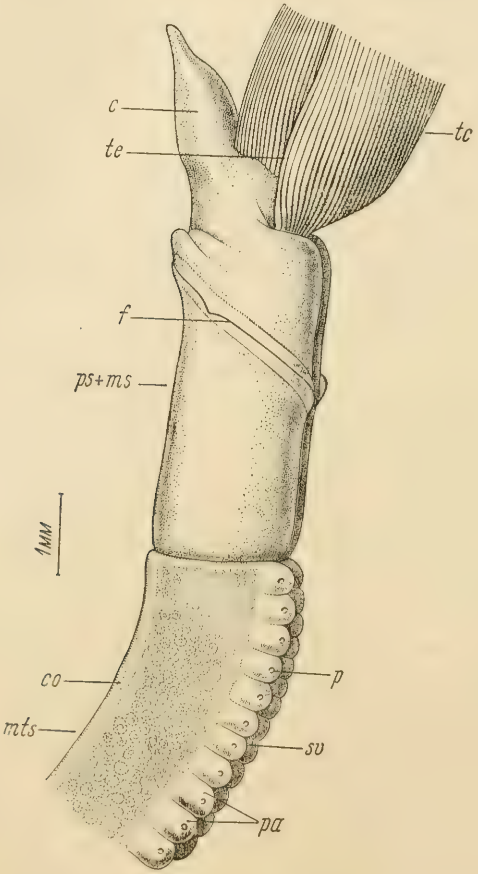

Fig. 5. Front end of the body of a female *Spirobrachia grandis* from the right side.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – keel of the bridle; *mts* – metasoma; *p* – adhesive plaques; *pa* – adhesive papillae; *ps* + *ms* – the fore-part of the body formed by fusion of the protosoma and the mesosoma; *sv* – ventral sulcus between the rows of adhesive papillae; *tc* – tentacular crown; *te* – outermost tentacle.

The tentacles, anatomically part of the protosoma, are always remarkable for their considerable length (Figs. 2, 7, 16). In number they vary from one to 200 or more. In view of the complexity of their structure and of their great physiological importance they will receive separate treatment (pp. 25 to 79).

It should be noted that the Spirobrachiidae are distinguished from all other Pogonophora by the development of a lophophore—a peculiar unpaired outgrowth of the protosoma bearing the major part of the tentacles (p. 27).

The mesosoma, or second segment of the body, is cylindrical or slightly flattened dorso-ventrally. Not infrequently its dorsal and ventral surfaces are marked by median furrows. A most characteristic and invariable feature of the mesosoma is the bridle or frenulum, represented by a pair of brown or black (rarely paler) cuticular keels or crests developed in the fore-part of the segment (Figs. 2–8, 15, 16). Beginning in the mid-ventral line the keels run obliquely forward on to the lateral surfaces of the body, then on to the dorsal side, gradually tapering as they do so. Usually they lie on more or less elevated epidermal ridges. In certain species the thickened ventral ends of the keels of the bridle do not come into contact, though they lie close together (*Siboglinum plumosum*, *S. robustum*, *S. taeniaphorum*, *Polybrachia barbata*, *Lamellisabella zachsi*, etc), in others they touch (*Polybrachia annulata*, *Lamellisabella johanssoni* etc), and finally, in a third group, they fuse together (*Oligobrachia* and many species of *Siboglinum*). The dorsal ends of the keels of the bridle are usually separated from one another, but in *Heptabrachia subtilis*, *Spirobrachia grandis*, *Siboglinum frenigerum*, *S. vinculatum* and *S. buccelliferum* they coalesce.

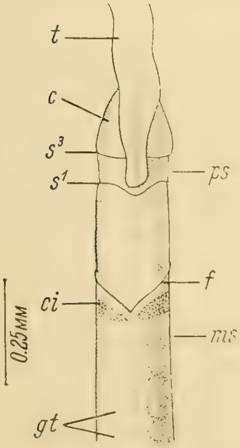

Fig. 6. Front end of the body of *Siboglinum fedotovi* from the ventral side.
c – cephalic lobe; *ci* – glandular girdle; *f* – bridle; *gt* – globular gland seen by transparency; *ms* – mesosoma; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^3 – pretentacular groove separating the cephalic lobe from the protosoma; *t* – tentacle.

It is difficult to determine the functional significance of the bridle. I doubt whether it serves to support the fore-part of the body against the edge of the tube when the animal is extended. The filmy, soft and very delicate walls of the fore-part of the tube in the majority of Pogonophora (p. 120) render such an interpretation doubtful. It is more likely that the bridle permits the animal to cling on to the inner surface of the tube as it moves up and down, or serves for temporary anchoring of the front end of the body deep inside the tube. In the larger species the bridle, as a rule, is better developed; it is especially powerfully developed in *Lamellisabella johanssoni*.

The region of the mesosoma situated in front of the bridle sometimes appears ringed, in consequence of one (in *Heptabrachia gracilis*), or two or three (in *H. beringensis* and *Polybrachia*—Fig. 7) secondary annular grooves (Ivanov, 1952, 1957a). A pair of auricular lobes are developed in this region in *Galathealinum*, enveloping the sides of the body (Kirkegaard, 1956a).

Behind the bridle in some species of *Siboglinum* [and *Nereilinum*] there is an epidermal glandular girdle or belt interrupted dorsally and sometimes ventrally (*Siboglinum weberi*, *S. cinctutum*, *S. fedotovi*—Fig. 6, *S. plumosum*, etc). In *S. taeniaphorum* and *S. atlanticum* this girdle is prolonged into a pair of cutaneous glandular ribbon-like tracts, extending along the ventral side of the mesosoma almost to its hind end (Fig. 128*B*). Sometimes numerous rounded sacculate glands may be seen through the body wall in the mesosomal region (*S. pellucidum*, Fig. 119*A*; *Nereilinum murmanicum*, Fig. A95*C*; *Siboglinoïdes dibrachia*, Fig. Y133*A*; *Lamellisabella zachsi*, etc).

The metasoma or trunk is distinguished by its unusual length and makes up the greater part of the body. It is always divided from the mesosoma by a sharp annular groove, straight or somewhat oblique, or more or less indented on the dorsal or ventral side. In *Lamellisabella* it is clearly marked only on the dorsal side.

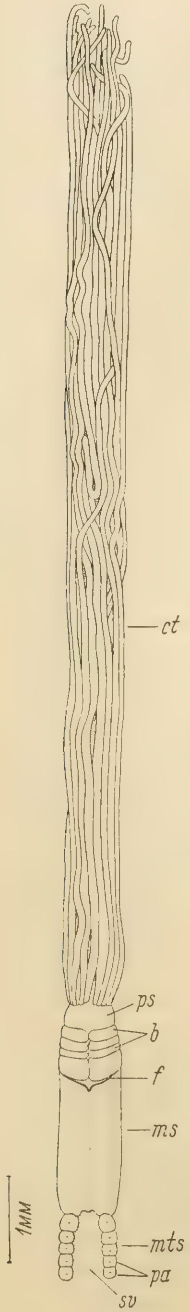

Fig. 7. Front part of the body of a female *Polybrachia annulata* from the ventral side.
b – secondary annuli of the mesosoma; *ct* – tentacular crown; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *ps* – protosoma; *sv* – ventral sulcus. (After Ivanov, 1960a.)

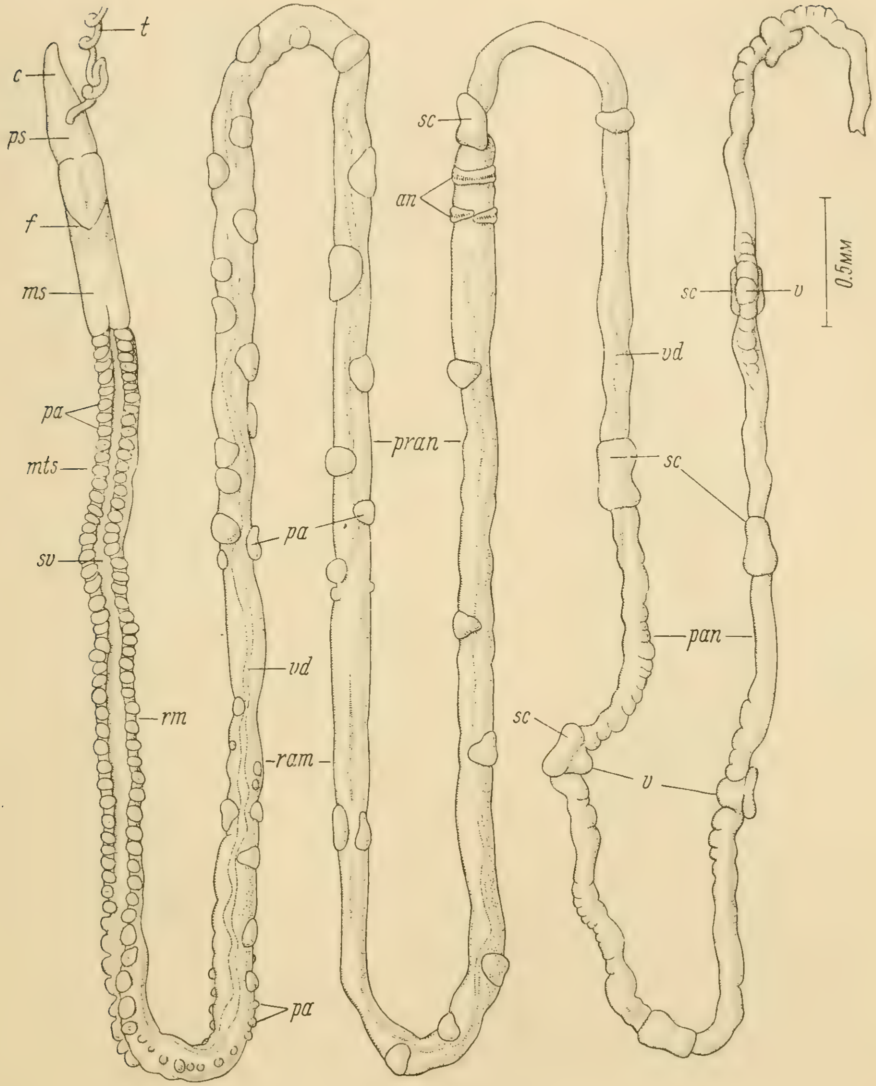

Fig. 8. A female *Siboglinum caulleryi.* The tentacle and hind part of the body are omitted. *an* – girdles; *c* – cephalic lobe; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pan* – postannular region of the metasoma; *pran* – preannular region of the metasoma; *ps* – protosoma; *ram* – nonmetameric part of the preannular region of the metasoma; *rm* – metameric part of the preannular region of the metasoma; *sc* – dorsal shields; *sv* – ventral sulcus; *t* – tentacle; *v* – postannular papillae; *vd* – dorsal blood vessel seen by transparency.

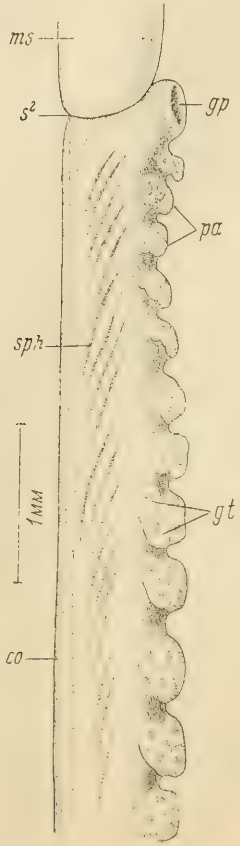

Fig. 9. Front part of the metasoma of *Zenkevitchiana longissima* from the right side.
co – dorsal ciliated band; *gp* – male genital aperture on the genital papilla; *gt* – pyriform glands; *ms* – hind part of the mesosoma; *pa* – adhesive papillae; s^2 – groove between the mesosoma and the metsaoma; *sph* – spermatophores seen by transparency. (After Ivanov, 1957a.)

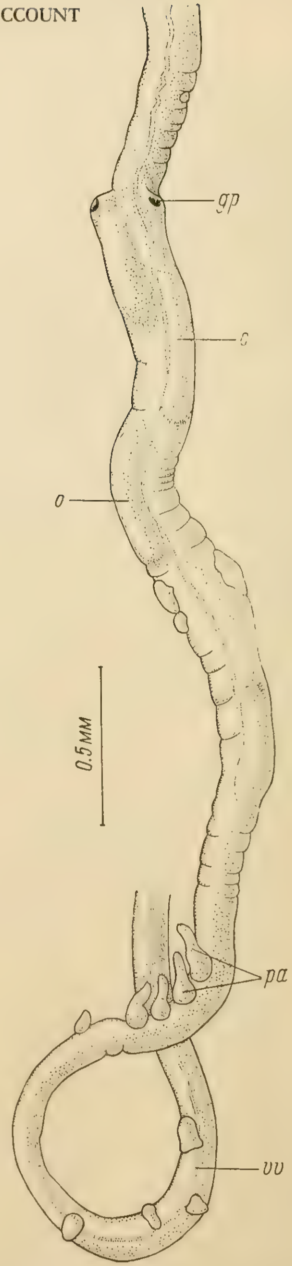

Fig. 10. Part of the metasoma of a female *Siboglinum caulleryi* in the region of the genital openings and the zone of thickened papillae. Seen from the ventral and partly from the left side.
gp – genital opening; *o* – egg seen by transparency through the body wall, lying in the oviduct; *pa* – papillae of the thickened zone; *vv* – ventral blood vessel seen by transparency. (After Ivanov, 1960a.)

The metasoma changes considerably from one end to the other. Two main regions can be distinguished—in front the preannular region reaches to the peculiar girdles [or annuli], behind which is situated the postannular region (Figs. 2, 8, 16) (Ivanov, 1952).

The preannular region is furnished in its anterior part with a rather wide longitudinal ventral sulcus which gradually opens out backwards (Figs. 2, 3, 8, 16, etc). The sulcus is bounded at the sides by lateral ridges, each bearing a single row of adhesive papillae which are round, oval or conical protuberances furnished with small cuticular plaques (Figs. 5, 16). In the primitive *Oligobrachia dogieli*, however, [and in *Nereilinum murmanicum*] adhesive papillae are absent from this region (Fig. 15), and in *Siboglinum*, *Siboglinoïdes* and *Zenkevitchiana* they lack plaques (Figs. 3, 8, 9). By means of these papillae and their plaques the animal, in all probability, clings to the inner surface of the tube as it moves up and down inside it (Johansson, 1939; Ivanov, 1952). Thus the papillae play the same role as the parapodia of the tubicolous polychaetes and deserve the appellation of locomotory, adhesive or attachment organs.

On the front part of the metasoma, in all pogonophores except *Oligobrachia* [and *Nereilinum*], the arrangement of the adhesive papillae is distinguished (though somewhat imperfectly) by a definite metamerism, which it is impossible to consider as other than secondary (Ivanov, 1952, 1957a). Farther back, however, the metamerism for the most part breaks down and shortly thereafter the adhesive organs are found in scattered disorder, though in the majority of species they are usually restricted to the ventral side. In almost all the Pogonophora the greater part of the preannular region of the trunk is characterized by just such a higgledy-piggledy scattering of the adhesive organs. Thus the anterior metameric part of the metasoma is followed by a posterior non-metameric part (Figs. 2, 8, 16). Amongst the haphazard adhesive organs of the non-metameric part one may single out, however, a group of particularly large papillae, lying ventrally a little in front of the girdles. These papillae, usually conical and furnished with cuticular plaques (except in a few species of *Siboglinum* which lack them also from other parts of the body), are arranged in a single dense mid-ventral row (e.g. in *Siboglinum caulleryi*, Fig. 10; and *Heptabrachia gracilis*) or without any definite order (in *Siboglinum vinculatum*, *Heptabrachia subtilis*, *H. abyssicola*, *Polybrachia annulata*—Fig. 11, etc). They constitute the "zone of thickened papillae". The number of these papillae varies from three (*Siboglinum taeniaphorum*), or five (*S. caulleryi*) to several dozen (*Polybrachia annulata*, etc). In *Spirobrachia* there is no zone of thickened papillae.

The preannular region of the trunk is distinguished also by the possession of a broad dorsal ciliated band of integument (Caullery, 1944; Johansson, 1939), which begins at the front end of the metasoma and stretches usually to the end of the metameric part (Figs. 4, 5, 9, 15). In *Polybrachia annulata* there is another similar dorsal ciliated band in the zone of thickened papillae.

Two or three girdles [or rarely four or five] of toothed platelets lie in the middle section of the trunk. Most frequently there are two girdles placed close together one behind the other on muscular ridges. They are usually interrupted ventrally (Figs. 2, 12, 16), and in many species either or both girdles are broken also on the dorsal side. Between the girdles, or in front or behind them as well, are usually several well-developed mid-ventral papillae, furnished almost always with adhesive plaques. In *Siboglinum pinnulatum* and *S. bogorovi* there is a considerable gap between the two girdles. A whole series of species of *Siboglinum* is characterized by the possession of three girdles, of which the first two lie close together and the third is situated quite a long way behind them (e.g. *S. robustum*, *S. buccelliferum etc*). [*Siboglinoïdes dibrachia* is unusual in possessing four or five girdles disposed in two groups with a considerable space between the two.] In some species of *Siboglinum* the number of girdles is subject to individual variation. Each girdle (or annulus) consists of two or several rows of very small (never more than 30μ long) oval chitinous* platelets Figs. 12, 13), [sometimes called uncini by some authors by analogy with the uncini of polychaetes]. Their surface is covered with tiny teeth (Caullery, 1944). Each platelet shows

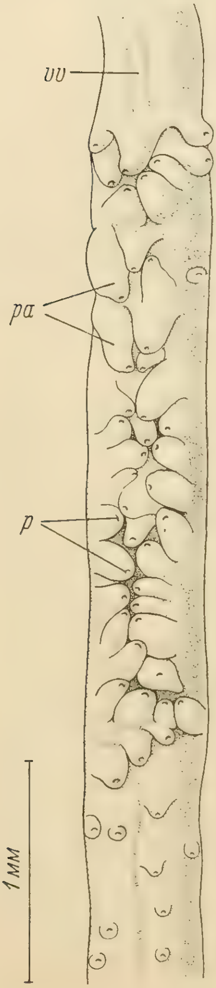

Fig. 11. Part of the metasoma of a female *Polybrachia annulata* in the region of the thickened papillae. From the ventral side.
p – adhesive plaques; *pa* – papillae of the thickened zone; *vv* – ventral blood vessel seen by transparency.

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* Chitin is unproven—D.B.C.

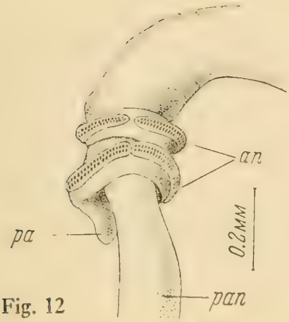

Fig. 12

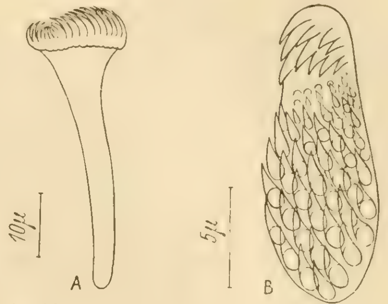

Fig. 13

Fig. 12. The girdles of *Siboglinum caulleryi* in a distended condition.
an – girdles; *pa* – median papilla behind the girdles; *pan* – the beginning of the postannular region of the metasoma.

Fig. 13. Toothed bristles of *Polybrachia annulata*.
A – a bristle from the side; *B* – toothed platelet of bristle.

externally only its head of cutaneous bristles or teeth (Fig. 13, see also Fig. 31). The teeth, arranged in rows on the surface, form two groups—an anterior group, which usually consists of comparatively few small and weakly developed thorns or teeth, regularly pointing backwards, and a posterior group, consisting of numerous longer teeth, pointing forwards. In different species of *Siboglinum* all degrees of reduction of the anterior teeth may be observed. Thus in *S. buccelliferum* and *S. pinnulatum* the two groups are almost equally developed, in the majority of species the anterior group is more or less rudimentary, and in *S. minutum* and *S. vinculatum* it has completely disappeared. The girdles, without any doubt, serve to fix the middle part of the body firmly in the tube, when, as must happen, the animal is disturbed and instantly withdraws the front end of the body and the tentacles into the tube by contraction of the longitudinal musculature.

Behind the girdles there is usually a noticeable narrowing or waist, after which the postannular section of the trunk begins. This latter is very long and more or less cylindrical, tapering towards the hind end and rather different in the two orders. In the

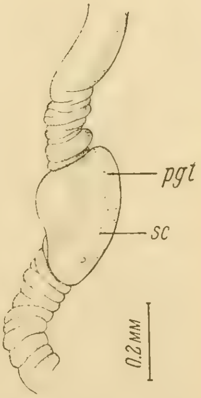

Fig. 14. Dorsal shield of the postannular region of the metasoma of *Siboglinum caulleryi*. Seen from the side.
pgt – pore of pyriform gland; *sc* – dorsal shield. (After Ivanov, 1960a.)

Athecanephria comparatively large metameric dorsal glandular shields are found along its whole length (Figs. 8, 14); only in the primitive *Oligobrachia* are they relatively feebly developed (Ivanov, 1957a). In the Thecanephria the post-annular region is furnished with more or less regular ventral transverse metameric rows of small adhesive papillae with rod-like cuticular plaques (Ivanov, 1952), while dorsal shields are absent (Figs. 2, 16).

The single pair of genital apertures lies on the metasoma. In the male they are round or slit-like and located on protuberant genital papillae, lying ventrally at the boundary between the mesosoma and the metasoma in front of the first pair of metameric adhesive papillae (Figs. 9, 15). In the female the lateral genital apertures are situated in the middle of the metasoma a little in front of the zone of thickened papillae (Fig. 10).

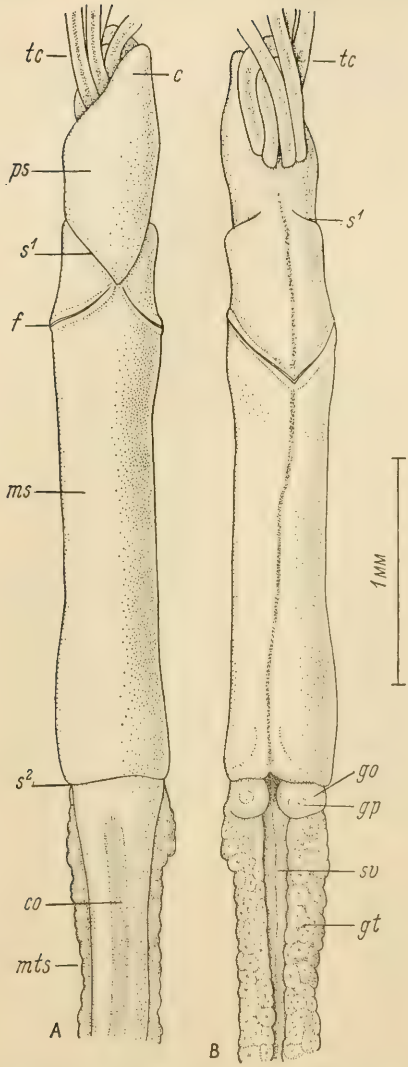

Fig. 15. Front part of the body of a male *Oligobrachia dogieli*, *A* – in dorsal, and *B* – in ventral view.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *go* – genital papilla; *gp* – genital aperture; *gt* – pyriform glands, disposed higgledy-piggledy in two latero-ventral rows; *ms* – mesosoma; *mts* – metasoma; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *tc* – tentacular crown. (After Ivanov, 1957a.)

The secondary metamerism of the metasoma

From the facts cited above about the external morphology of the different genera and species we may draw several inferences about the origin and development of the metameric adhesive papillae in pogonophores.* We may note

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* By metamerism, following Beklemishev, I mean any regular repetition along the axis of the body of parts similar to one another.

first of all that in the most primitive known pogonophore, *Oligobrachia dogieli* (Fig. 15), there is no metameric arrangement of the adhesive papillae (Ivanov, 1957a, 1959f). This fact alone is sufficient to show that the metameric papillae of Pogonophora are a secondary acquisition. It also strongly contraverts the recent conclusion of Hartman (1954) that the metameric papillae of Pogonophora may be considered as a manifestation of true segmentation and that the adhesive papillae with their cuticular plaques are homologous with the parapodia of Polychaeta. In the rest of the Athecanephria [with the exception of the almost equally primitive *Nereilinum murmanicum*] we already find a rather large number of metameric papillae—e.g. 50–55 pairs in *Birsteinia vitjasi*, 50–75 pairs in *Siboglinum caulleryi* (Fig. 8). In *Birsteinia* and *Siboglinum*, however, representing independent lines of development (p. 141), the metameric arrangement of the papillae has been independently acquired (Ivanov, 1957a). In the Thecanephria we see the same picture of gradual metamerization of the papillae. Thus in *Heptabrachia gracilis* there are always *c.* 17–18, in *H. abyssicola* 14–20 and in *H. beringensis* 24–26 pairs of metameric papillae. In representatives of other genera the metamerism affects more and more papillae, as may be seen in Table 1, until finally in *Spirobrachia* the transformation involves the majority of these organs in the anterior section of the trunk (Fig. 16).

TABLE 1

		Number of pairs of metameric papillae	Approximate number of nonmetameric papillae	Ratio of lengths of the metameric to the nonmetameric parts of the trunk
Athecanephria	*Oligobrachia dogieli*	0	Very many	—
	Birsteinia vitjasi	50–55	Many	?
	Siboglinum caulleryi	50–75	Many	1 : 5
Thecanephria	*Heptabrachia gracilis*	17–18	Very many	?
	Heptabrachia abyssicola	14–20	Very many	1 : 10
	Polybrachia annulata	22–28	250–360	1 : 10
	Zenkevitchiana longissima	38*	Many	?
	Spirobrachia beklemischevi	160–180	15–50	5 : 1
	Spirobrachia grandis	220*	?	?

* Counted in a single specimen only.

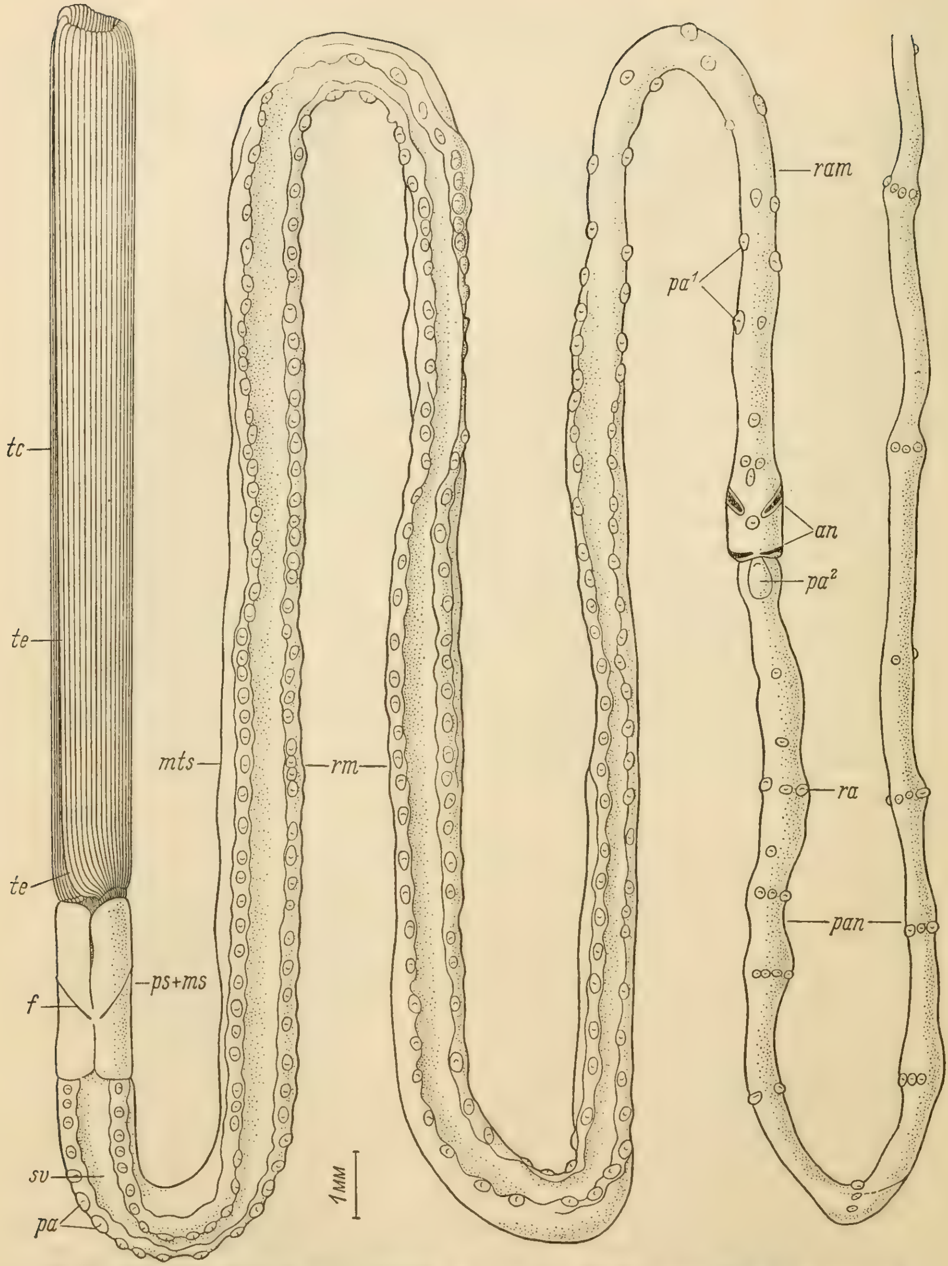


Fig. 16. *Spirobrachia beklemischevi* – a female in ventral view. The hind part of the body is omitted. *an* – girdles; *f* – bridle; *mts* – metasoma; *pa* – metameric papillae; *pa*^{1} – non-metameric papillae; *pa*^{2} – median papilla, lying behind the girdles; *pan* – postannular region of the metasoma; *ps* + *ms* – the fore-part of the body formed by fusion of the protosoma with the mesosoma; *ram* – non-metameric part of the preannular region of the metasoma; *ra* – ventral transverse row of papillae; *rm* – metameric part of the preannular region *sv* – ventral sulcus; *tc* – tentacular crown; *te* – outermost tentacle. (After Ivanov, 1957a.)

We may note that in all species the number of metameric papillae is not fixed but is, on the contrary, subject to very great individual variation. It is interesting also that as the number of pairs of metameric papillae increases their metamerism does not become more regular and perfect. In this respect the lower forms are not distinguished from the more advanced, and in the one as in the other, numerous irregularities and considerable individual idiosyncrasy are displayed in the arrangement of the metameric papillae. To speak of a paired arrangement of the papillae is to use a merely relative term.

This imperfect metamerism is sufficiently characteristic of and peculiar to the Pogonophora to stand out in comparison with the segmentation of the polymeric Annelida, for instance the Polychaeta. The metamerism of the latter, as is well known, is distinguished by its great regularity and steadiness. It could not be otherwise, for it is an inevitable expression of the very method of development of the segments during ontogeny. The post-larval segments, originating one behind the other in the sub-terminal zone of growth of the metatrochophore form identical sets of organs (P. P. Ivanov, 1928, 1937, 1944). It is natural, therefore, that the metamerism of the post-larval section of the body of the Annelida is one of the most highly developed and perfect, and in comparison the metamerism we encounter in the Pogonophora appears to be of a different nature.

It long ago became apparent that a metameric disposition of the organs of an animal may be the result of totally different processes. Thus Meĭer (Meyer) (1890) and Lang (1903) admitted the possibility of the division of the whole body of the animal by metamerism in those cases when a metameric arrangement of the organs presented some physiological advantage (e.g. in connexion with locomotion). On the other hand, according to Hatschek (1878), the metamerism of the annelids arose merely as a result of the ability of the hypothetical ancestor (the "trochozoon") to form, on the hind end of the body, small uniform parts, which could develop either as separate individuals or as segments of a common organism. Quite recently the question of the pathways by which metamerism could develop was examined in detail by Beklemishev (1952), who investigated at length the manifestations of metamerism throughout the animal kingdom. Beklemishev distinguished the following three modes of origin of metamerism:

1. Metamerism regulating an originally disorderly disposition of similar parts or organs. Metamerism arising in this way will not become perfect and regular or firmly stabilized, and is characteristically incomplete. Not infrequently a certain lack of agreement is apparent between the metamerism of different organs.

2. Metamerism formed by the differentiation of parts or organs along an originally uniform whole.

3. The combination of originally independent similar parts or organs into one metameric whole. In this case the metamerism usually arises as a result of the incomplete cross-division of the animal into a series of metamerically disposed sections of the body or zooid.

As emphasized by Beklemishev, the third type of metamerism is significantly different from the first two in its initial stages. The metamerism develops not in a whole organism originally lacking it, but by means of the association of non-metameric units of a lower order. In the Annelida these units are clearly post-larval segments, forming by division in the zone of growth of the metatrochophore or of the embryo. The metamerism of the Annelida is thus of the third type.

But from the foregoing it should be obvious that the adhesive papillae in Pogonophora indicate metamerism of the first kind, i.e. a superimposed regulating metamerism. It is equally clear that the metamerism of pogonophores cannot possibly be considered a result of the combination of originally separate parts of the body. Thus, by its very nature, it has nothing in common with the perfect metamerism or segmentation of the annelids. Nor can we admit the possibility of the second type of metamerism in Pogonophora, for it is inconceivable that the adhesive papillae arose by chopping up an originally continuous band into short lengths.

Another interesting feature is the diminution in the number of papillae in the non-metameric part of the trunk as their number in the metamerically organized part increases. To use the terminology of Dogel' (1936, 1954), they become oligomeric. To some extent this happens because a larger and larger proportion of them become involved in the metameric region, which in this way increases in length at the expense of the non-metameric part—a sort of creeping metamerization (Table 1). But this is not the whole explanation, for the proportional reduction in the random papillae is greater than the proportional increase in the metameric.

Though an accurate count of the non-metameric papillae is difficult because of their great variability in number in different individuals, a rough estimate can be made. In all the species with a comparatively small number of paired metameric papillae the non-metameric papillae are very numerous (e.g. *Heptabrachia*, *Polybrachia annulata*). In this respect *Heptabrachia subtilis* is of particular interest, for it has hundreds of adhesive plaques scattered on the dorsal as well as on the ventral side of the greater part of the trunk. But in *Spirobrachia beklemischevi* the comparatively short non-metameric part bears never more than 50 papillae and in some individuals far fewer (Fig. 16).

It is also of interest that the cuticular plaques on the anterior metameric papillae are more highly differentiated than on the papillae farther back; this is especially striking in the higher more specialized species. Thus in *Lamellisabella* they are distinguished by their complex shape, and function as a rather efficient catch mechanism, while the plaques on the scattered papillae of the middle part of the trunk are still very primitive (Fig. 34). In the higher species, moreover, special pulvilli or cushions are developed on the metameric papillae which bear the cuticular plaques. These are found in *Birsteinia* among the Athecanephria and *Lamellisabella* and *Spirobrachia* among the Thecanephria. In this way the localization and differentiation of a multiplicity of organs proceed parallel with the superposition of order.

Everything mentioned above tends to show that the development of secondary metamerism (or pseudometamerism) in the Pogonophora has come about by the imposition of order upon an originally disorderly array of a great many similar organs. Evidently in the process of evolution the metamerization of the papillae of the preannular region of the trunk began at the anterior end. Then it spread backwards, engrossing an ever-increasing number of these organs. In the first stage of evolution all the adhesive papillae, to all appearances, are completely higgledy-piggledy (Ivanov, 1957a, 1959f).

The tentacles

The tentacles of the Pogonophora should perhaps rather be called arms or brachia, since they are extensions of the body enclosing a coelomic canal. They are attached at the front end of the protosoma, ventral to the base of the cephalic lobe, and in all species, except in the unitentaculate *Siboglinum*, they form a tentacular crown.

The number of tentacles fluctuates between wide limits: *Siboglinum* (Fig. 3) has only one tentacle; [*Siboglinoïdes*, *Sclerolinum* and *Nereilinum*, two;] *Diplobrachia*, two to four; *Oligobrachia* (Fig. 15), six to nine; *Heptabrachia*, five to thirteen; *Cyclobrachia*, nine; *Birsteinia*, 12; *Zenkevitchiana*, 14; *Polybrachia* (Fig. 7) four to 70 or more in different species; *Lamellisabella zachsi* (Fig. 2), 28 to 31; *Galathealinum bruuni*, more than 105; *Spirobrachia grandis* as many as 223; [and *Galathealinum brachiosum*, 268].

The most primitive species possess few tentacles [6–8]: e.g. *Oligobrachia* and *Heptabrachia*. The single tentacle of *Siboglinum* appears to be the result of secondary oligomerization, as is clear from the peculiarities of its innervation (Ivanov, 1956b, 1958b). In pogonophores each tentacle is innervated by a single nerve, the left tentacles receiving nerves from the left side and the right from the right side of the brain. In *Siboglinum* the nerve of the single tentacle arises asymmetrically on the right side of the brain (Fig. 36). This suggests that, in this genus, only a single right tentacle remains of the whole tentacular apparatus.

[Other genera in both orders of Pogonophora also show signs of a reduction in the number of tentacles, though no other genus has been found in which there is only a single tentacle. But in two genera of the Thecanephria and in two of the Athecanephria we find species with only a pair of tentacles. In the latter order *Nereilinum* and *Siboglinoïdes*, belonging to the Oligobrachiidae and Siboglinidae respectively, occupy an intermediate position between *Oligobrachia* and *Siboglinum.* The right tentacle of the pair in these two genera corresponds to the single tentacle of *Siboglinum* and to the tentacle which appears first in the ontogeny of *Oligobrachia*; the left pair is homologous with the second tentacle of *Oligobrachia*, i.e. with the left anterior tentacle. Amongst the Thecanephria *Diplobrachia* and *Sclerolinum* each possess only two tentacles and we may presume that they are homologous with the anterior pair of tentacles of the Oligobrachiidae. Ivanov (1961a) is of the opinion that in *Diplobrachia* they represent all that remains of a complete tentacular crown found in its ancestors, and it is of course necessary to add that not all species of this genus possess only two tentacles, despite the name. It seems not improbable that future investigation may reveal the existence of species of the Thecanephria in which the process of oligomerization of the tentacles has been carried to extremes as it has in the unitentaculate Athecanephrian *Siboglinum*, and we must beware of automatically ascribing any form with but a single tentacle to this genus—D.B.C.]

[Thus in several parallel lines of evolution of the Pogonophora a reduction of tentacles has occurred.] On the other hand, in a series of genera (*Polybrachia*, *Lamellisabella* and *Spirobrachia*) we see a picture of successive multiplication of tentacles accompanied by increasing complexity of organization (Ivanov, 1952)—a typical example of the polymerization of organs in the sense of Dogel' (1954).

In forms with a few or a moderate number of tentacles, such as *Oligobrachia*, most species of *Heptabrachia* and *Birsteinia*, the area of their attachment to the body is horseshoe-shaped, with the ends of the horseshoe turning in on the ventral side (Fig. 17*A*, *B*), and the whole crown is bilaterally symmetrical. In some forms, however, the ventral ends approach in the mid-line to form a complete circle of tentacles, e.g. in *Cyclobrachia*, *Heptabrachia beringensis*, *Zenkevitchiana* and *Lamellisabella* (Fig. 17*E*).

In the polytentaculate *Polybrachia* and *Galathealinum* the primitive horseshoe is retained, but the tentacles are disposed not in one but in two or even three rows, e.g. in *Polybrachia annulata* (Fig. 17*C*). This feature is even more strongly marked in *P. barbata* (Fig. 17*D*) and in *Galathealinum bruuni* in which the tentacles are many rows deep in the horseshoe base of the crown.

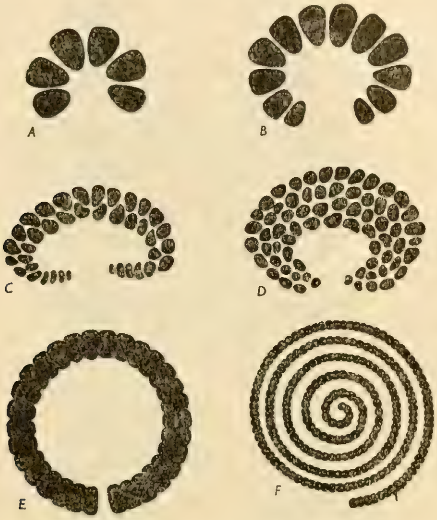


Fig. 17. Diagram of arrangements of the bases of the tentacles in various species of Pogonophora. *A – Oligobrachia dogieli*; *B – Birsteinia vitjasi*; *C – Polybrachia annulata*; *D – P. barbata*; *E – Lamellisabella zachsi*; *F – Spirobrachia grandis*. (After Ivanov, 1960a.)

A quite different phylogenetic path of multiplication of the tentacles has taken place in *Spirobrachia*. Here the tentacles remain in a single row in the crown but the right-hand end of the horseshoe is greatly extended and twisted into a dextral centripetal spiral (Fig. 17*F*). In this way the uniserial arrangement of tentacles is preserved while at the same time allowing for a great increase in their number as they form an asymmetrical spiral crown. But even this proved inadequate and the necessity for yet more tentacles has been satisfied by the development of a new structure, a corkscrew-like helical extension of the protosoma, the lophophore, lying within the base of the crown and bearing the greater part of the tentacles (Fig. 18). In this way the right half of the crown has become hypertrophied in *Spirobrachia* (Ivanov, 1952, 1957a).

Though useful as a specific distinction, the number of tentacles is by no means invariable within a given species. Thus in adult, sexually mature individuals of *Polybrachia annulata* the number varies between 26 and 39, and in *Spirobrachia beklemischevi* from 39 to 72. Detailed investigation has shown that in adult *Lamellisabella zachsi* the number of tentacles gradually increases by the growth of a very few new tentacles, whose formation is concentrated at the ventral ends of the horseshoe of the crown. In *Spirobrachia* a particularly active zone of formation of new tentacles is located at

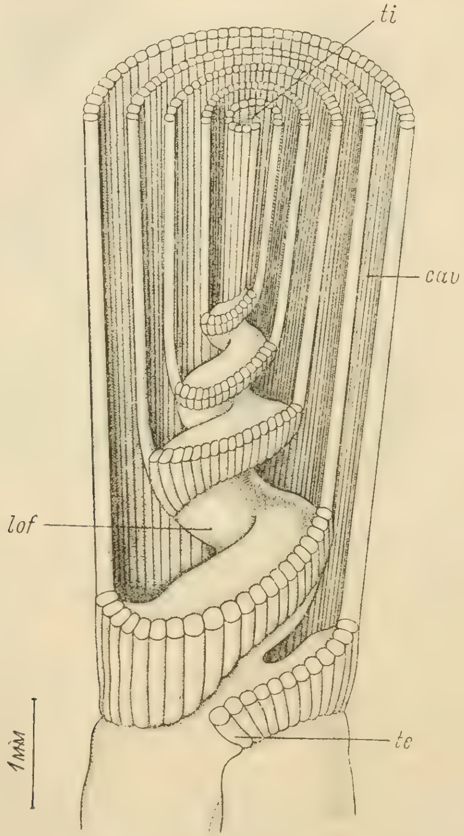


Fig. 18. Tentacular crown of *Spirobrachia grandis*. Viewed from the ventral side; ventral tentacles cut away.
cav – intertentacular cavity; *lof* – lophophore; *te* – outermost tentacle; *ti* – innermost tentacle. (After Ivanov, 1960a.)

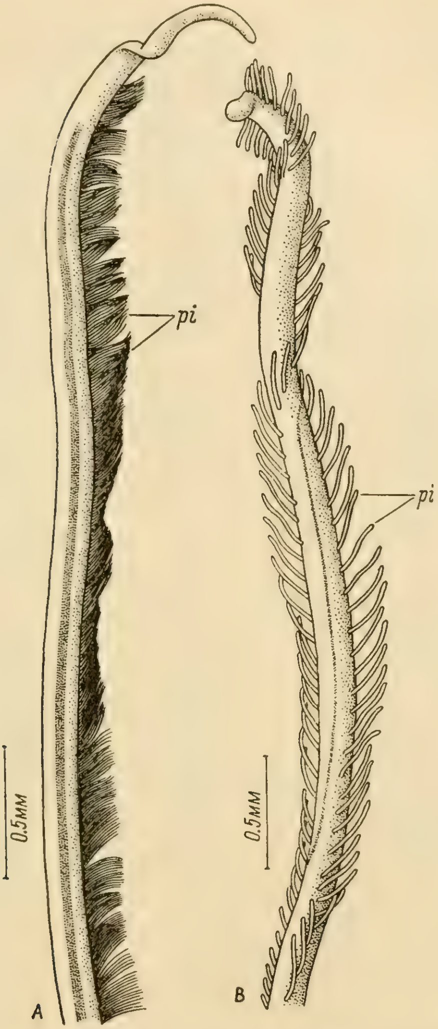


Fig. 19. The distal ends of tentacles of *A – Lamellisabella zachsi*; and *B – Siboglinum plumosum*. (After Ivanov, 1960a.)

the tip of the lophophore, in other words at the right end of the corkscrew of tentacles. These data, obtained from the study of adults, are fully consonant with what is known of the ontogenetic development of the tentacles (Ivanov, 1957b).

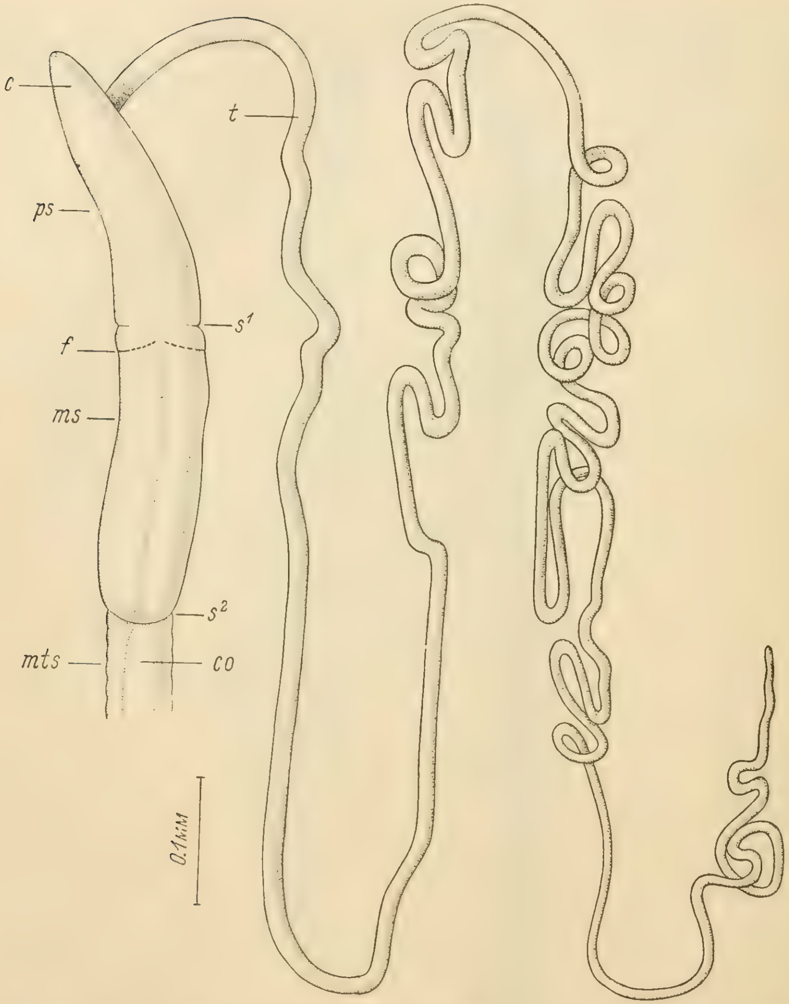


Fig. 20. *Siboglinum pellucidum.* The fore-part of the body in dorsal view. Pinnules are absent. *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *ms* – mesoma; *mts* – metasoma; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *t* – tentacle. (After Ivanov, 1957a.)

The two highest families of pogonophores—the Lamellisabellidae and the Spirobrachiidae—are distinguished by the firm longitudinal adhesion of the tentacles, of which only the distal ends remain free and detached. Each tentacle is stuck to the next by a substance which covers the cuticle. In

Lamellisabella, which has a ring of tentacles (Fig. 17*E*), this results in the formation of a long hollow tentacular cylinder (Figs. 2, 58), while in *Spirobrachia* a tentacular plate is formed which is twisted into a spiral, not unlike a rolled up newspaper (Figs. 18, 59).

Each tentacle, except on its basal part, bears numerous very fine delicate filiform pinnules, almost meriting the name of "villi". They are rarely more than 750μ long and are found on the inner surface of the tentacles so that they always jut out inside the crown into the intertentacular cavity. They are arranged in one or, more often, in several dense longitudinal rows, alternating with each other in adjacent rows. Thus in one group of species of *Siboglinum* (e.g. *S. caulleryi* and *S. cinctutum*) the pinnules of the tentacle form only one row, in which, however, may be seen the rather faint traces of a biserial arrangement (Fig. 3). Other species of this genus (*S. plumosum*, *S. ekmani* etc) are characterized by two rows of pinnules (Fig. 19*B*), a condition found also in *Oligobrachia* and *Birsteinia*. In *Lamellisabella zachsi* the pinnules form three rows and in *Spirobrachia grandis* four rows. It should be remarked that in a whole series of species of *Siboglinum* the tentacle lacks pinnules. Thus according to the observation of Southward and Southward (1958b) there are no pinnules in living specimens of *S. inerme*. I have observed no pinnules in *S. pellucidum* (Fig. 20), *S. bogorovi*, *S. hyperboreum*, *S. variabile*, *S. tenue*, *S. meridiale*, *S. norvegicum* and *S. minutum*.

The tentacular crown is very long in all Pogonophora. In *Polybrachia annulata*, for instance (Fig. 7), the crown reaches 16 mm while the front end of the body is only *c.* 0·5 mm across. The single tentacle of *Siboglinum* (Figs. 3, 20) is relatively even longer and able to twist up into a tight corkscrew (Fig. 56) (Caullery, 1944).

CHAPTER 3

The Integument and Associated Structures

A characteristic feature of the integument is the great development of the cuticle, which covers the whole surface of the body. Even on those few regions where a ciliated epithelium is developed, such as the dorsal ciliated band of the metasoma and parts of the tentacles (pp. 33 and 79), there is still a delicate cuticle.

The epidermis

The detailed structure of the epidermis varies, of course, both in different species and in the different parts of the body in one and the same individual. Almost always, however, the epidermis consists of epidermal cells, gland cells and nervous elements, ganglionic and sensory cells, and more or less delicate layers of nerve fibres. The epidermis lies on a basement membrane against which abuts the circular muscle layer.

The height of the epidermis and its richness in glandular and nervous elements vary considerably in the different parts of the body. Some species, chiefly the larger ones, are distinguished by the inordinate overall thickness of the epidermis. The thickest epidermis is found on the cephalic lobe in the protosomal region (Figs. 37, 38, 43), in the mesosoma (Figs. 29, 30, 39), and also on the metameric region of the trunk (Figs. 33, 68) and in the post-annular region (Figs. 22, 46). In the middle part of the trunk—that is, in the males in the region of the strongly developed glandular region of the sperm-ducts, and in the females in the hind region of the ovary where it is crowded with large oocytes—the epidermis is usually grossly distended and attenuated (Fig. 45), sometimes to the extent that it is a mere membrane (Figs. 61, 63, 69).

The epidermis consists of cylindrical, more or less narrow cells, whose nuclei are frequently all situated at the same level. The epidermal cells are penetrated by numerous tonofibrillae which join the cuticle to the basement membrane (Figs. 29, 38) (Jägersten, 1956; Ivanov, 1960a).

Unicellular glands are particularly abundant on the front end of the body and in general they are more weakly developed in the middle and hind parts of the trunk. They are large goblet or tubular gland cells, more or less distended with secretion (Figs. 21, 27, 67). Amongst them may be distinguished mucus glands, tubiparous glands [i.e. secreting the substances of which the tube is formed] and albumen glands (Ivanov, 1960a). Only the tubiparous glands are found along the whole length of the body. Spindle-shaped secretory bodies with longitudinal striations are found in the unicellular tubiparous glands of the mesosoma (Jägersten, 1956). These cells also contain granular masses of secreta which give a positive reaction for polysaccharides (Fig. 21) (Ivanov, 1960a). Only in a few spots does the epidermis assume a continuous glandular nature. Thus a strong concentration of glands is found in the tall epithelium at the tip of the cephalic lobe. In many species of *Siboglinum* the epidermis behind the bridle is remarkable for its richness in unicellular glands with granules of a seemingly proteinaceous or albuminous secretion; here they may form a glandular girdle, usually incomplete (Fig. 6), or longitudinal glandular ribbons along the mesosoma (in *S. taeniaphorum* and *S. atlanticum*). In the nonmetameric region of the trunk aggregations of gland cells are frequently encountered forming thickened areas of integument. Finally, there are the very characteristic dorsal glandular shields of the Athecanephria, arranged metamerically in the postannular region of the trunk (Figs. 8, 14). Each shield consists of very large gland cells whose secretion takes the form of rather large rounded granules (Fig. 22).

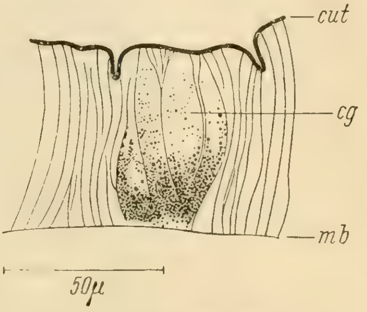


Fig. 21. Single-celled glands in the epithelium of *Lamellisabella zachsi*, stained for polysaccharides. *cg* – group of unicellular glands with granular secretion; *cut* – intensely stained cuticle; *mb* – basement membrane. (After Ivanov, 1960a.)

The layer of nerve fibres lying between the basal ends of the epidermal and gland cells and the underlying basement membrane can scarcely be regarded as an essential constituent of the epidermis *per se*, yet it is invariably found there (Figs. 27, 29, 38). In definite places, which seem to be the central parts of the nervous system or its main paths of conduction, the nerve layer reaches a particularly strong degree of development (Ivanov, 1956b).

The cells of the epithelial dorsal ciliated band (Fig. 23) are furnished with dense and comparatively short cilia. In spite of this the epithelium of the tract is covered, in the majority of species, with an extremely thin but distinct cuticle under which lie the rows of basal granules of the cilia. In each cell the cone of root-threads of the cilia, with the apex towards the nucleus, may readily be seen. There are no gland cells in this region, but the nervous elements are well developed, possessing both a layer of nerve fibres and of ganglionic cells. In *S. caulleryi* the ciliated band appears to have lost its cilia (Fig. 33).

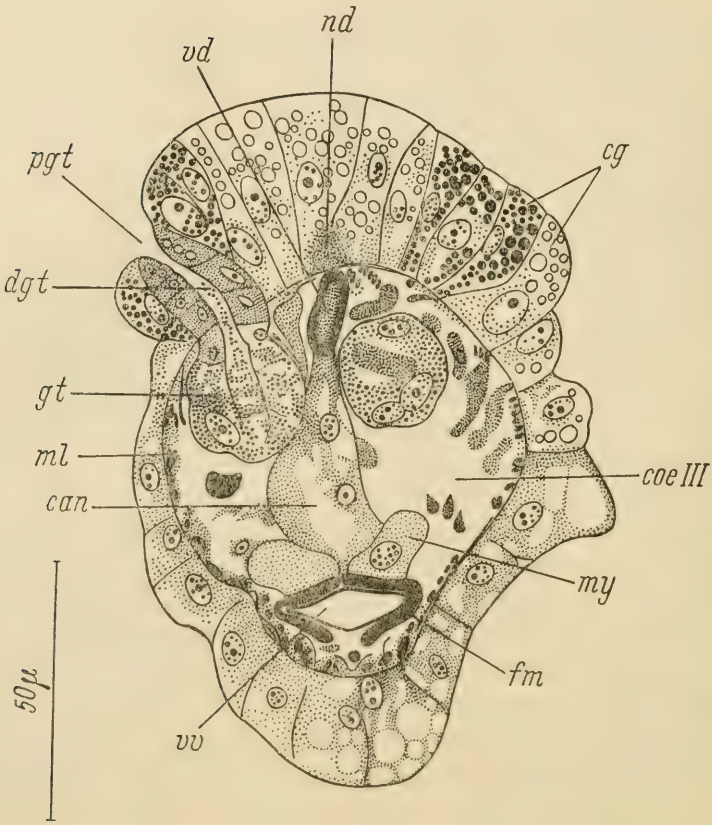


Fig. 22. Transverse section through the postannular region of the metasoma of a female *Siboglinum caulleryi.*
can – median coelomic canal; *cg* – gland cells of the dorsal shield; *coe* III– coelom of the metasoma; *dgt* – duct of pyriform gland; *gt* – pyriform gland; *fm* – muscle fibres of the ventral vessel; *ml* – layer of longitudinal muscle; *my* – muscle cell of the ventral vessel; *nd* – dorsal nerve strand; *pgt* – pore of pyriform gland; *vd* – dorsal blood vessel; *vv* – ventral vessel. (After Ivanov, 1960a.)

The cuticle and its derivatives

The cuticle

The cuticle consists of a transparent colourless substance which often stains differentially. It appears to be formed as a result of the secretory activity of epidermal cells, in whose distal parts small granules and droplets of secretion are often visible, staining in the same way as the cuticle and merging into it (Fig. 37). Sometimes the cuticle consists of two layers—a thinner stainable inner layer and an outer layer. The thickness of the cuticle

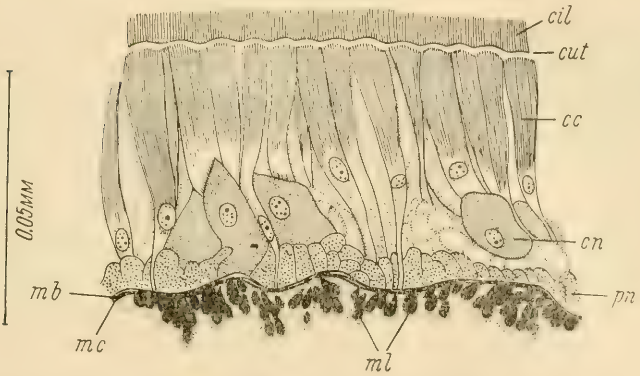


Fig. 23. Epithelium of the dorsal ciliated band of *Lamellisabella zachsi*.
cc – ciliated cell; *cil* – cilia; *cn* – ganglionic cell; *cut* – cuticle; *mb* – basement membrane; *mc* – layer of circular muscle; *ml* – layer of longitudinal muscle; *pn* – nerve fibres. (After Ivanov, 1958b.)

varies considerably from one part of the body to another; as a rule it is more strongly developed at the front end of the body and on the ventral side. In the larger species (*Spirobrachia grandis* and *Lamellisabella*) it reaches its greatest development in the zone of attachment of the tentacles and on the tentacles themselves, joining them together rather firmly. But without doubt the cuticle possesses great elasticity and extensibility, as testified by the powerful subcutaneous musculature and by the longitudinal muscle fibres of the tentacle. The substance of the cuticle gives a positive periodic-Schiff reaction, i.e. it contains polysaccharide (Figs. 21, 28).

Amongst the undoubted derivatives of the cuticle we may enumerate the keels of the bridle and the plaques of the adhesive papillae.

The keels of the bridle

The keels of the bridle (cf. p. 13) appear as simple thickenings of the cuticle projecting more or less above the surface of the body and possessing their own yellowish, brown or black pigmentation (Fig. 29). In a few larger species they are considerably thickened: in *Lamellisabella johanssoni* the height of the keels reaches 140μ. In such a species the keels possess a more or less lamellar structure with parallel layers of cuticular substance arranged along the keel perpendicular to the body surface. In the tiny *Siboglinum minutum* the keels are very delicate, each seeming no more than a thin cuticular thread broken up into small rodlets (Fig. 24). In *Diplobrachia* irregular cuticular corpuscles are attached

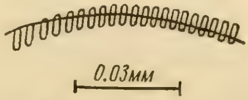


Fig. 24. Keel of the bridle of *Siboglinum minutum*, greatly enlarged. (After Ivanov, 1957a.)

along the hind edge of the crests of the keels (Fig. 149*E*). Finally, in *Siboglinum tenue* and *S. hyperboreum* the bridle is represented by a rather broad cuticular tract along which runs a single fine dark thread-like thickening (Fig. 120*D*). [See also pp. 361 and 436.]

The adhesive plaques

The adhesive plaques are localized thickenings of the cuticle lying on the surface of the adhesive papillae in many species. For the most part they are round, oval or horseshoe-shaped on the papillae of the front part of the trunk and secreted by many cells of the epidermis (Fig. 25), while on the non-metameric and postannular parts of the trunk (Fig. 34*C*) the smaller rod-like plaques are each produced by a single large cell (Fig. 35). The former type often have the appearance of transversely oval scales with a thickened front edge (e.g. in most Thecanephria, Fig. 34*D*, and in *Birsteinia*), but in *Lamellisabella* (Fig. 34*A*, *B*) they have a complex shape and seem to be rather well adapted as catch mechanisms (p. 47).

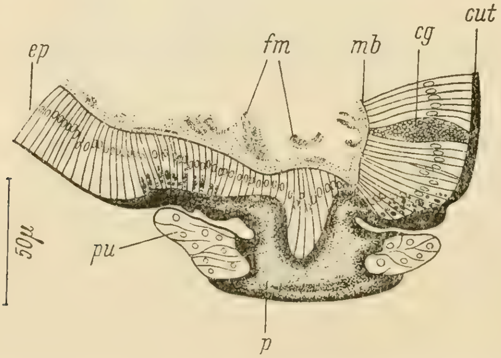


Fig. 25. Section through an adhesive plaque of the metameric region of the metasoma of *Lamellisabella zachsi*.
cg – gland cell; *cut* – cuticle; *ep* – epithelium; *fm* – muscle fibre; *mb* – basement membrane; *p* – plaque; *pu* – pulvillus. (After Ivanov, 1960a.)

The toothed bristles of the girdles

Amongst the epidermal formations may also be included the toothed platelets of the girdles so characteristic of the Pogonophora and recalling, as pointed out by Caullery (1914), the uncini of sedentary polychaetes. [Indeed the term "uncini" is applied to these platelets by such authors as Hartman (1961)]. The location of the toothed platelets has been described above (p. 18), and, as already stated, each platelet is the head, as it were expanded and appearing to lie on the surface of the body, of a long bristle. This broadened terminal plate-like head is attached to a long narrow stalk, penetrating deeply into the thick epidermis of the girdle (Jägersten, 1956). In the majority of species the greater part of the sharp teeth on the surface of the head of the bristle point forwards (Figs. 13, 26*B*), indicating that the function of the toothed platelets is to anchor the trunk firmly to the walls of the tube at the moment of rapid withdrawal of the animal. The head of the bristle, i.e. the platelet, consists of a solid yellowish transparent substance without noticeable structure, and, as may be seen after several staining methods, rather sharply delimited from the stalk. The colourless stalk, displaying thin longitudinal striations, lies directly between epidermal cells. Its external surface is formed of a very thin layer, which stains in the same way as the cuticle of the epidermis. To the inner end of the stalk is attached a conical cell transpierced by fine tonofibrillae which bind it to the basement membrane of the epidermis. There is neither a particular socket for the bristle nor a special musculature connected to the stalk (Fig. 26). Jägersten (1956), however, in describing the toothed platelets of *Siboglinum ekmani*, wrote that the stalk plunged into a special cavity of the epidermis and was furnished at its inner end with muscle fibres.

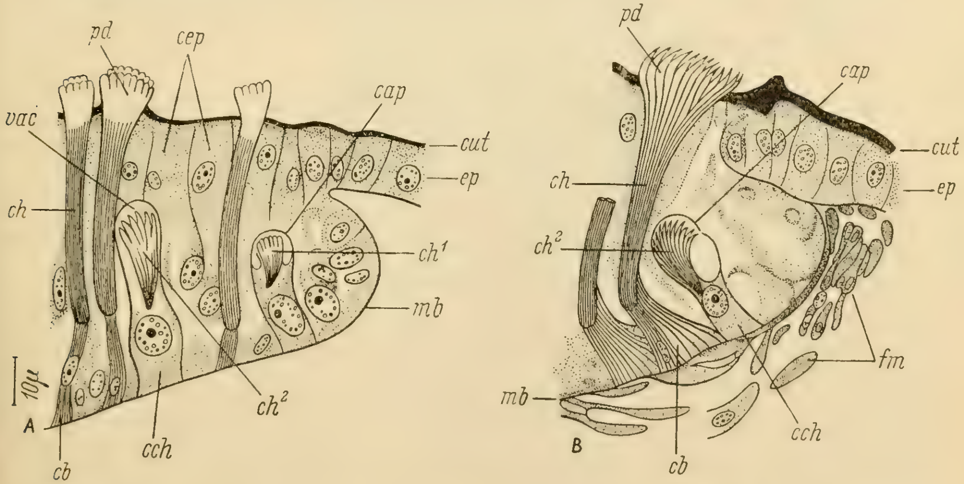


Fig. 26. Epithelium of the girdles and the toothed bristles of *Lamellisabella zachsi*. *A* – in transverse section; *B* – in longitudinal section.
cap – cap over a developing toothed bristle; *cb* – basal cell of a bristle; *cch* – cell which forms a bristle; *cep* – epidermal cell; *ch* – stem of bristle; *ch*¹, *ch*² – young developing bristles; *cut* – cuticle; *ep* – epidermis; *fm* – muscle fibres; *mb* – basement membrane; *pd* – toothed platelet head type of bristle; *vac* – vacuole around a young bristle. (After Ivanov, 1960a.)

The number of toothed bristles apparently gradually increases throughout life thanks to the appearance of new ones deep in the epidermis along the front edge of the girdles. Each bristle is formed inside a single cell. First, next to the nucleus appears a round inclusion, which then grows bigger, gradually taking on the shape of the toothed head. The inner end of such a young head is pointed and there is no stalk. The head lies within a large vacuole. The enveloping cell grows larger and soon afterwards forms a tight mantle protecting the sharp teeth of the head. Then, in the same way, the cell forms the stalk too, so that the bristle gradually grows. Finally the head penetrates the cuticle and emerges as a toothed platelet on the external surface of the girdle (Ivanov, 1960a).

The cell which forms the bristle remains at its base in the capacity of basal attachment cell and tonofibrillae appear within it. Later this cell may degenerate to a greater or lesser degree leaving behind the bundle of tonofibrillae which may look somewhat like muscle fibres (Fig. 26).

The basement membrane

The basement membrane is always well developed. This thin structureless supporting membrane, underlying the epidermis, in appropriate places unites with other limiting membranes, attaching organs and tissues to the epithelium above; instances may be found in the fascia of the mesentery of the mesosoma and metasoma.

The multicellular epidermal glands

Apart from the single-celled glands mentioned above, all pogonophores have multicellular glands of cutaneous origin entering into the composition of the epidermis and sticking down into the coelom. Like the scattered gland cells they certainly secrete tube material. [For this reason Ivanov refers to them as tubiparous or tube-forming glands. The usual rule for the English nomenclature of anatomical features demands, however, that an organ should not be named for its known (or supposed) function, but from its appearance, topography or anatomy. In this edition, therefore, these glands are termed globular or pyriform glands according to their shape, or collectively as flask-shaped glands: the distinction may or may not be valid—D.B.C.]. Two categories may be distinguished: the globular glands lying in the coelom of the mesosoma and metasoma, and the pyriform glands located in the coleomic cavity of the adhesive papillae. There is no fundamental distinction to be drawn between them (Ivanov, 1960a).

These large flask-shaped glands with longer or shorter multicellular ducts open on to the surface of the body (Fig. 27). The walls of the gland are formed of large cells with basal nuclei. Their secretion has an extraordinary nature, consisting of two components—a granular material and large oblong laminar bodies like those which are often encountered in the solitary gland cells of the epidermis. On the outside the gland is clad with a thin layer of muscle fibres and a peritoneal epithelium. The duct of the gland is formed by a layer of small cells, secreting a thicker or thinner cuticle which lines its lumen. The external aperture of the gland is often well marked in animals examined *in toto*.

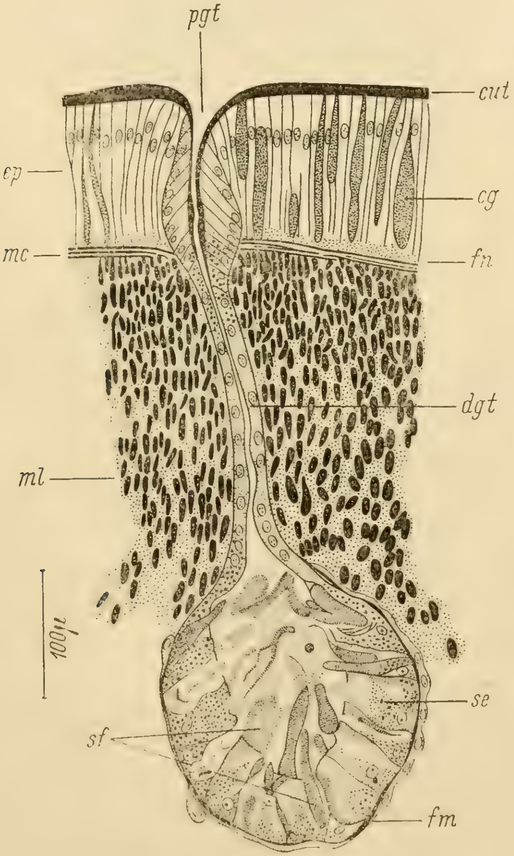


Fig. 27. Pyriform gland of *Spirobrachia grandis* from the metameric region of the metasoma. *cg* – gland cell; *cut* – cuticle; *dgt* – duct of the gland; *ep* – epidermis; *fm* – muscle fibres of the gland; *fn* – nerve layer of the epidermis; *mc* – layer of circular muscles; *ml* – layer of longitudinal muscles; *pgt* – pore of the gland; *se* – granular secretion; *sf* – lamellar secretion. (After Ivanov, 1960a.)

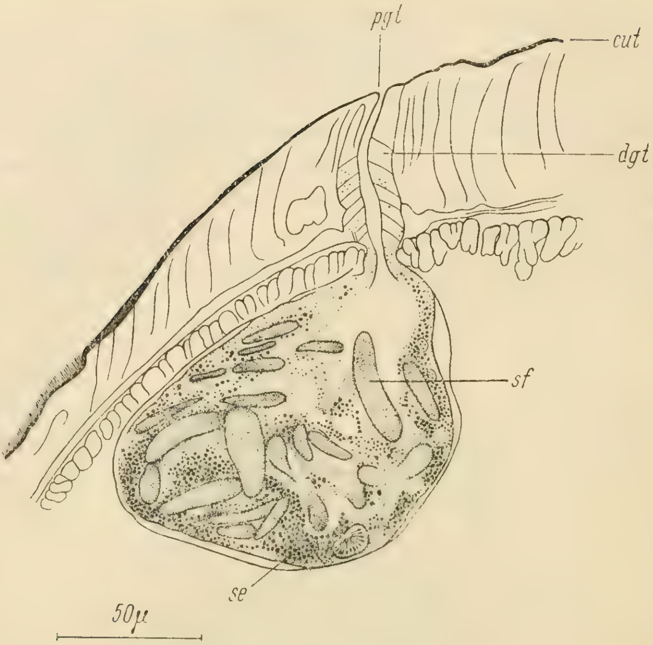


Fig. 28. Pyriform gland of *Lamellisabella zachsi* from the metasomal region, after staining for polysaccharides.
cut – cuticle; *dgt* – duct of the gland; *pgt* – pore of the gland; *se* – granular secretion; *sf* – lamellar secretion. (After Ivanov, 1960a.)

The granular secretion of the flask-shaped glands gives a positive reaction for polysaccharides in the periodic acid-Schiff test (Fig. 28), i.e. it displays the same chemical nature as the substance of the tube (p. 122). Polysaccharide is unevenly distributed in the laminar bodies, forming a thin envelope over the surface of each of these bodies and penetrating into its interior as fine veins which tunnel through the otherwise homogeneous substance (Ivanov 1960a).

A large number of flask-shaped glands is concentrated in the coelomic sacs of the mesosoma (see Pl. III, facing p. 92), but in *Siboglinum caulleryi* they are not numerous in this region but confined chiefly to the hind part of this segment. In the Thecanephria the main mass of glands lies in the coelom of the metasoma. In the front part of the trunk they are particularly numerous, while in the nonmetameric part of the metasoma they are encountered more rarely, since they are apparently ousted by the strongly developed genital organs. In front of the girdles their number increases once more and finally there are many in the postannular region.

There are few flask-shaped glands in the coelom of the trunk in Athecanephria, except in the postannular region, where, in *S. caulleryi* for example, the glands are situated in metameric groups of six in the region of each dorsal glandular shield, onto whose surface they open (Figs. 14, 22).

The anterior metameric papillae, moreover, house glands whose ducts open onto the ventral or external surface of the papilla. In *Spirobrachia*, *Lamellisabella* and *Siboglinum caulleryi* each papilla houses only one gland (Fig. 33), but in other species there may be several glands in each papilla (Figs. 9, 68).

CHAPTER 4

Musculature and Papillae

Musculature

The Pogonophora possess a true dermal muscle sac, consisting of smooth muscle fibres. The circular muscle layer lies immediately under the basement membrane of the epidermis and under this again lies the more strongly developed longitudinal layer of the musculature. The dermal muscle sac is most weakly developed in the postannular section of the trunk.

The circular muscle layer is very thin but it is present in all Pogonophora over the whole of the body. It is most strongly developed over a small region immediately behind the girdles, where its contraction often produces the impression of a waist at this point, especially in preserved animals. The circular muscle fibres seem to be very long thin spindle-shaped cells (Figs. 27,29).

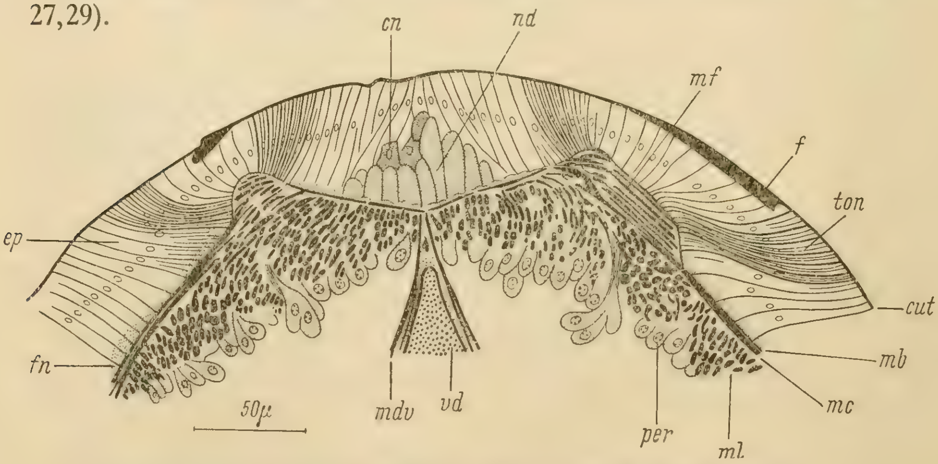


Fig. 29. Part of a transverse section of *Polybrachia annulata* at the level of the bridles. *cn* – ganglionic cell; *cut* – cuticle; *ep* – epidermis; *f* – keel of the bridle; *fn* – nerve layer of epidermis; *mb* – basement membrane; *mc* – layer of circular muscle; *mdv* – dorso-ventral muscle fibres; *mf* – musculature of the bridle; *ml* – longitudinal muscle layer; *nd* – dorsal nerve trunk; *per* – peritoneum; *ton* – groups of epidermal cells especially rich in tonofibrillae; *vd* – dorsal blood vessel. (After Ivanov, 1960a.)

The musculature of the bridle is a specialized part of the circular layer of muscle which forms a thick cushion under the keels (Fig. 29). When this musculature contracts, the pleating of the cuticle which results causes a ridge of epidermis to protrude, on which are situated the cuticular keels. In this way the keels may be forced against the walls of the tube and hold the forepart of the body fast (Ivanov, 1958b).

The longitudinal musculature forms a continuous layer, attaining, in large species, a considerable thickness. Only in a few parts of the body does it become thinner, such as mid-ventrally and mid-dorsally, along the lines of attachment of the mesentery (p. 64). It is usually developed to roughly the same extent along the whole length of the body, except for a slight thickening in front and a gradual dwindling in the postannular region of the trunk. In *Siboglinum weberi*, however, the major part of the longitudinal muscle fibres is concentrated on the dorsal side; in the middle part of the mesosoma they are divided into two dorso-lateral tracts, which a little farther back turn onto the sides of the body where they become more powerful; finally, in the hind part of the mesosoma the fibrous tracts become uniformly dispersed all round the body (Caullery, 1944). The same is true of the muscle tracts in

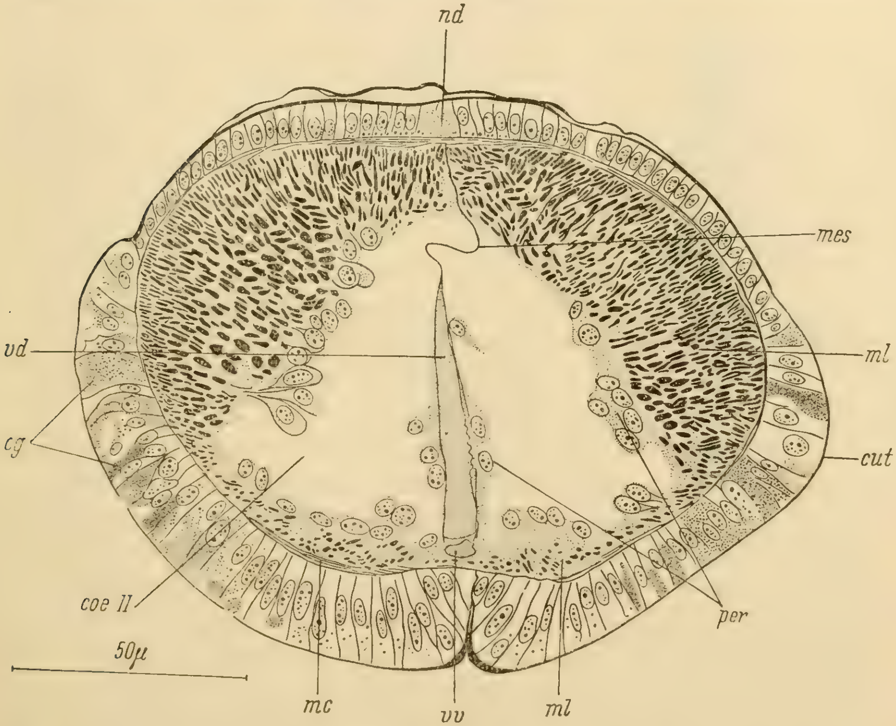


Fig. 30. Transverse section of *Siboglinum caulleryi* in the mesosomal region.
cg – gland cells of the epidermis; *coe* II – coelom of the mesosoma; *cut* – cuticle; *mc* – circular musculature; *mes* – mesentery; *ml* – longitudinal musculature; *nd* – dorsal nerve trunk; *per* – peritoneum; *vd* – dorsal blood vessel; *vv* – ventral blood vessel. (After Ivanov, 1960a.)

S. caulleryi (Fig. 30) and *S. minutum*, and in all likelihood, in all species of this genus. In *Lamellisabella* and *Spirobrachia* the longitudinal muscle layer forms a pair of considerable thickenings on the ventral side of the body in the front part of the metasoma.

The longitudinal musculature consists of very long ribbon-like fibres, arranged, in transverse section, perpendicular to the circular muscle layer. Not infrequently the fibres form only a single layer (Fig. 33), but in the larger species (*Polybrachia*, *Lamellisabella*, *Spirobrachia*) they are arranged in many layers (Figs. 27, 29, 39, 45, and 52). On the side of the muscle layer which is towards the body cavity is a continuous layer of cells with round nuclei. Some of these cells appear to be the myocytes, so that the muscle cells are of the nematode type, each consisting of a cytoplasmic body containing the nucleus, jutting out into the coelom with the contractile portion of the cell applied to the body wall (Johansson, 1939). It is clear that the muscle fibres of the cephalic lobe in *Oligobrachia dogieli* are also of this nematodal type (Fig. 43), but in the middle region of the trunk in *Lamellisabella* the longitudinal muscle cells possess nuclei which lie inside the ribbon-like fibres themselves or else are closely applied to the broad face of the fibres (Fig. 26*B*). Thus, in this part of the body at least, there is no continuous cell-layer delimiting the longitudinal muscle layer from the coelom, but on the contrary the coelom may be considered devoid of peritoneal elements.

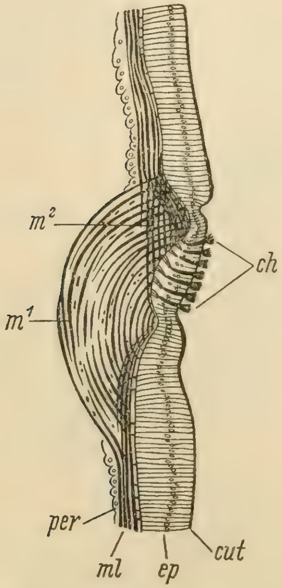


Fig. 31. Musculature of the girdle of toothed bristles of *Lamellisabella zachsi* in longitudinal section. *ch* – toothed bristles; *cut* – cuticle; *ep* – epidermis; m^1 – muscle fibres causing the girdle to protrude; m^2 – muscle fibres pulling in the girdle; *ml* – longitudinal muscle layer; *per* – peritoneum. (After Ivanov, 1960a.)

At the level of each girdle of toothed bristles a special muscular ridge is developed at the expense of the longitudinal layer of the dermal muscle sac (Fig. 31). Its contraction thrusts the region of the girdle outwards so permitting the toothed heads of the bristles to hook onto the walls of the tube (Fig. 12). Some of the fibres of this muscular ridge join the basement membrane of the girdle to a small portion of the cutaneous epithelium which lies a little in front of it. It is interesting that each fibre is attached to the basement membrane of the girdle at a point where the conus of tonofibrillae of the basal cell of a toothed bristle is attached. As may readily be conceived, the contraction of these fibres must result in retraction of the girdle and thus facilitate the disengagement of the toothed platelets from the walls of the tube (Ivanov, 1960a).

A proportion of the fibres of the longitudinal muscle layer turn inwards at the boundary between the mesosoma and the metasoma to enter into the structure of the transverse muscular diaphragm, which separates the cavities of these segments. The diaphragm consists of radial and dorso-ventral fibres. Some of the latter cross over between the dorsal and ventral blood vessels in a sort of chiasma (Fig. 32).

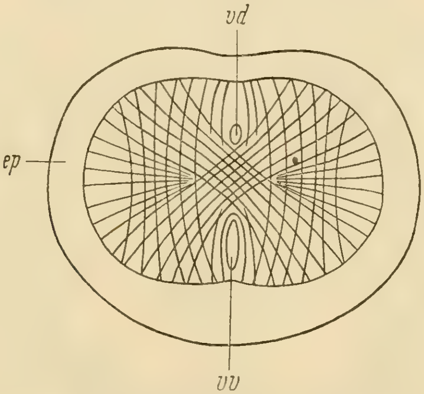


Fig. 32. Diagram of the arrangement of muscle fibres in the diaphragm of *Siboglinum caulleryi*. *ep* – epidermis; *vd* – dorsal blood vessel; *vv* – ventral vessel. (After Ivanov, 1960a.)

The adhesive papillae

The papillae, whose disposition has already been described (Chapter 2), are characteristic organs of the trunk. These outgrowths of the body may contain a portion of the coelom or may be completely filled by muscle. Several types of papillae may be distinguished, though intermediate forms may be encountered.

The papillae in the fore-part of the trunk in all Pogonophora, including *Siboglinum*, possess their own proper part of the coelom, separated off from the general body cavity by a basement membrane and by the layer of cutaneous musculature. In *Polybrachia*, *Lamellisabella* and *Spirobrachia* the coelom of the papillae is voluminous and contains a liquid clearly different from the coelomic fluid of the trunk (Fig. 68). In the papillae of *Siboglinum* the coelom is often almost imperceptible, since it is usually wholly filled by a large multicellular pyriform gland (Fig. 33). The epidermis of these papillae in many Athecanephria contains large gland cells, with big vacuoles of transparent secretion, concentrated at the base of the papillae on the medial side (Fig. 33). The basement membrane of the papillae is joined to that of the trunk. Beneath it lie muscle fibres running in various directions, including around the papillae; a few muscle fibres cross the coelomic cavity of the papilla covered in a sheath of peritoneal epithelium (Fig. 68).

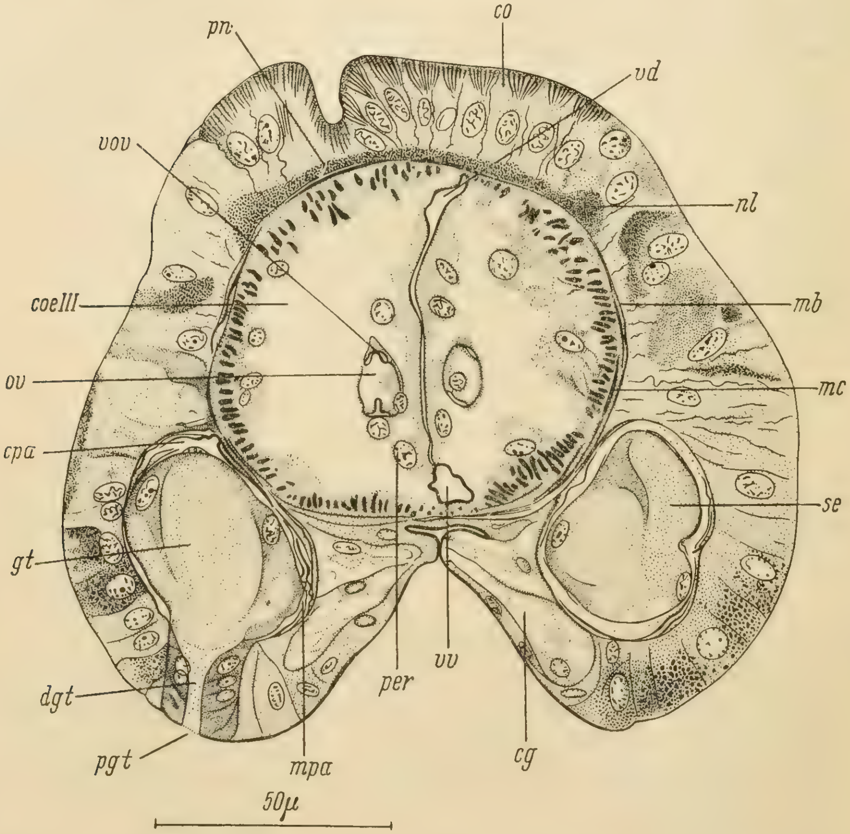


Fig. 33. Transverse section of *Siboglinum caulleryi* in the metameric region of the metasoma. *cg* – ventral gland cells; *co* – dorsal ciliated band (cilia not drawn); *coe* III – coelom of the metasoma; *cpa* – coelom of adhesive papilla; *dgt* – duct of pyriform gland; *gt* – pyriform gland; *mb* – basement membrane; *mc* – circular muscle fibres; *mpa* – muscle fibres of papilla; *nl* – lateral thickening of dorsal nerve layer; *ov* – oocyte; *per* – peritoneum; *pgt* – pore of pyriform gland; *pn* – dorsal nerve layer; *se* – secretion in cell of pyriform gland; *vd* – dorsal blood vessel; *vov* – ovarian blood vessel; *vv* – ventral vessel. (After Ivanov, 1960a.)

In the Thecanephria (except *Zenkevitchiana*) and in *Birsteinia*, amongst the Athecanephria, the metameric papillae are each furnished with a cuticular plaque which is always secreted by a group of many epidermal cells. The plaque is situated at the very tip of the papilla, but in *Birsteinia*, *Lamellisabella* and *Spirobrachia* they lie on special oval or heart-shaped pulvilli (Fig. 34*A*). In the majority of species the plaques look like transversely oval (or, in *Heptabrachia abyssicola*, round) scales, each with a thickened brown or black front rim. Their dimensions in different species may vary between 15μ and 110μ (Fig. 34*D*) (Ivanov, 1952, 1957a).

In *Lamellisabella* the plaque may take on a rather peculiar shape. As in other Pogonophora, it is scale-like and semi-transparent, and tapers towards the back and side edges. Its outline is circular. The front rim of the plaque is

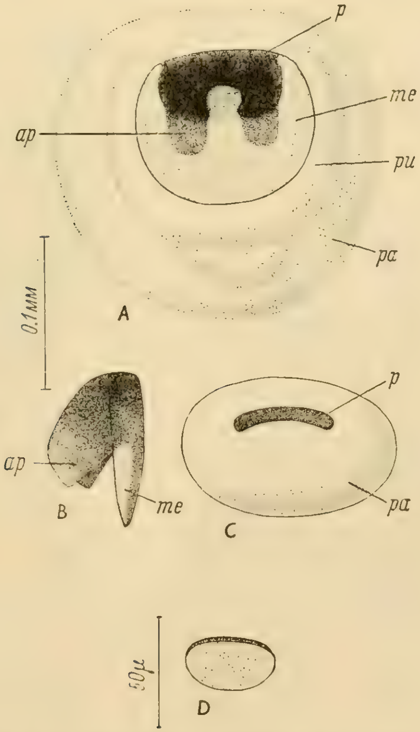


Fig. 34. *A* – adhesive papilla of *Lamellisabella johanssoni* from the metameric region of the metasoma; *B* – adhesive plaque of the same species in side view; *C* – papilla of the same species from the non-metameric region of the metasoma; *D* – adhesive plaque of *Zenkevitchiana longissima* from the middle region of the metasoma.
ap – apodeme of plaque; *me* – membrane of plaque; *p* – plaque; *pa* – papilla; *pu* – pulvillus. (After Ivanov, 1957a.)

formed of two massive roots fused at the base—stout parallel brown or black fangs, which appear to be apodematous outgrowths deeply penetrating into the thickness of the pulvillus and into the epidermis of the papilla. These roots run out from the plaque at an angle of *c.* 45°, their ends directed obliquely backwards into the papilla (Fig. 34*B*). On external examination of the whole structure (from the ventral side of the animal) these roots and their common base may be seen by transparency, lying below the surface of the plaque in a sort of horse-shoe whose ends curve backwards (Fig. 34*A*). The sides and hind edge of the plaque are free and may catch lightly onto the internal surface of the tube. Thus the apodemes of the plaques of *Lamellisabella* are nothing more than a specialized form of the hoop-shaped thickenings of the front rim of the plaques of other Pogonophora (Ivanov, 1957a).

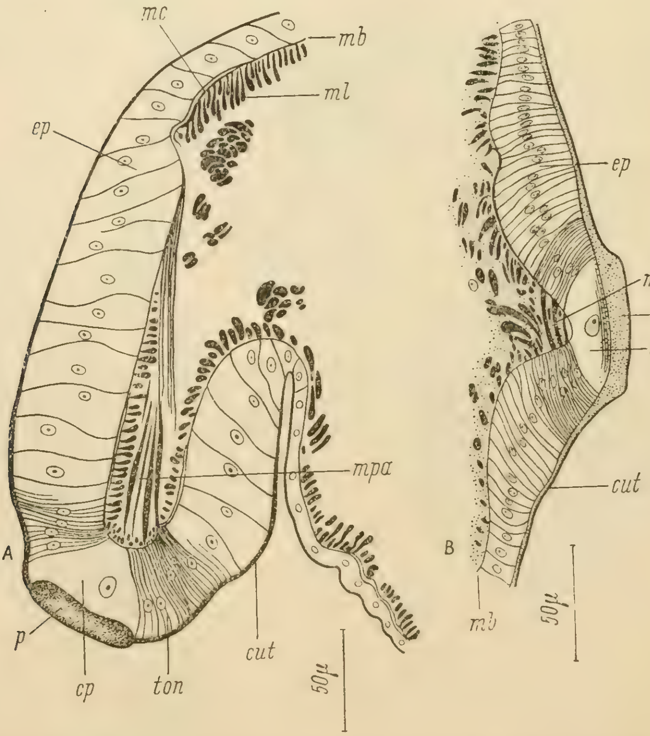


Fig. 35. Structure of the adhesive papillae in the middle and hind parts of the trunk. *A* – section through a papilla of *Polybrachia annulata* from the thickened zone; *B* – section of a papilla of *Lamellisabella zachsi* from the postannular region of the metasoma.
cp – cell which secretes the cuticular plaque; *cut* – cuticle; *ep* – epidermis; *mb* – basement membrane; *mc* – circular muscle fibre; *ml* – longitudinal muscle fibre; *mpa* – muscle fibre of papilla; *p* – cuticular plaque; *ton* – tonofibrillae in epidermal cells. (After Ivanov, 1960a.)

The scattered papillae of the nonmetameric part of the metasoma are distinguished by their feebler development. Often they possess a more or less extensive coelomic cavity, but this communicates broadly with the coelom of the trunk. The large conical papillae in the zone of thickening have an especially well developed musculature in two parts—a circular musculature derived from the longitudinal layer of the cutaneous muscle sac, and longitudinal muscle fibres which play the role of retractors and are distinct from the longitudinal muscle layer of the trunk (Fig. 35*A*). Plaques, if they are developed on these papillae, are each secreted by one single large cell, or occasionally by a very few such cells. It is interesting that the epidermal cells surrounding the latter are exceptionally rich in tonofibrillae, which form a strong bond between the edge of the plaque and the basement membrane (Ivanov, 1959b). The plaque itself may be similar to that on the metameric papillae or sharply distinguished from them by its hoop-like or rod-like shape.

Finally, the metameric papillae of the postannular region, found only in the Thecanephria, are notable for their inconsiderable size and weak development. The small cavity of these papillae is filled up with longitudinal and circular muscle fibres (Fig. 35*B*). The plaques here are transverse rods, somewhat bent forwards (Ivanov, 1952).

CHAPTER 5

Nervous System and Sense Organs

Nervous System

It has already been stated that the nervous system of pogonophores is wholly contained within the thickness of the cutaneous epithelium. In this respect it compares with the nervous system of the Hemichordata and the Phoronidea [and the Priapuloidea], and with the ectonervous system of starfish and sea lilies. Histologically, the nervous system of Pogonophora strongly recalls that of Enteropneusta (Ivanov, 1958b).

The nerve layer is indistinctly divided from the rest of the epidermis, so that it is rather difficult to delimit the region of the central nervous system. To all appearances, there is often a continuous nerve net, with local thickenings which are more or less rich in ganglionic cells (Figs. 23, 38).

A voluminous nerve mass which may be termed the brain lies in the greatly thickened epidermis of the dorsal side of the protosoma. Anteriorly it extends far in front of the level of attachment of the tentacles, leaving clear only the glandular epidermis of the anterior half of the cephalic lobe, while posteriorly it reaches the hind end of the protosoma. At the level of attachment of the tentacles the brain expands in lateral projections, reaching right round onto the ventral side of the body where they meet, thus forming a complete nerve ring. The nerves of the tentacles arise from the lateral parts of this ring. The longitudinal unpaired dorsal nerve tract begins immediately behind the brain and extends to the hind end of the body (Fig. 36).

The antero-dorsal part of the brain is distinguished by its considerable thickness and consists of two indistinctly divided layers—a basal fibrous layer and an overlying layer of multipolar and unipolar nerve cells. The latter lie scattered between the epidermal cells in small cavities (which may, however, be artefacts), and are distinguished by their large nuclei and homogeneous cytoplasm which not infrequently contains Nissl bodies. There are also spindle-shaped bipolar sensory cells with elongated oval nuclei. The fibrous layer of the brain consists of thick longitudinal and transverse bundles of nerve fibres. The basal parts of epidermal cells extend between the groups of nerve cells and the bundles of fibres. There are no gland cells in the region of the brain (Fig. 37). Amongst the fibre bundles the most powerful are the dorsal transverse commissure, situated behind the cephalic lobe, and a pair of dorsal longitudinal bundles lying opposite the two cephalic dorso-ventral muscles (Fig. 38) (Ivanov, 1958b).

The latero-ventral parts of the cerebral nerve ring consist for the most part of transverse nerve fibres; nerve cells are comparatively few here. The posterior part of the brain, situated behind the nerve ring, looks like no more than the very beginning of the dorsal nerve tract. It has a fibrous nature and

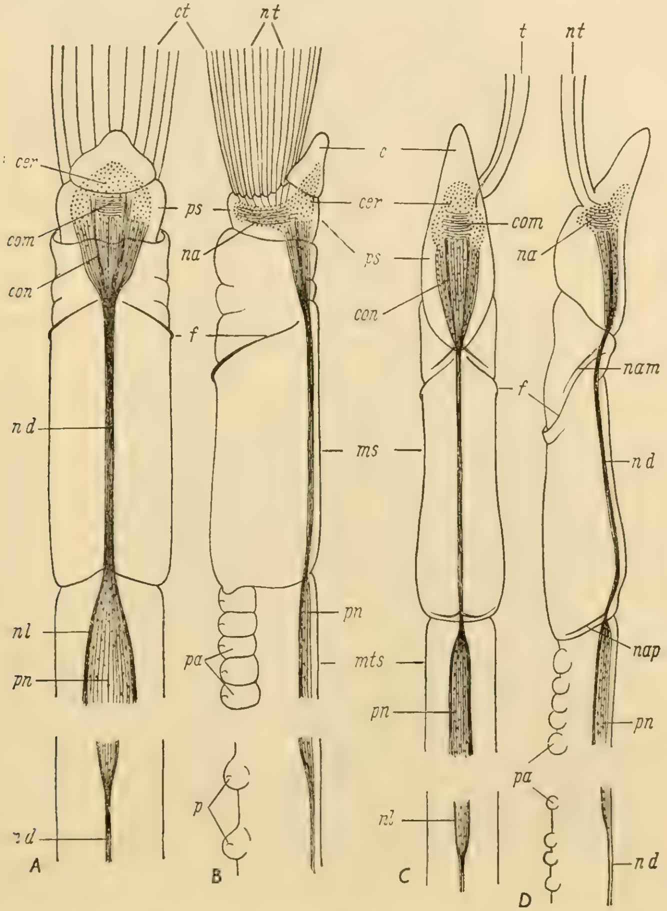


Fig. 36. Diagrams of the nervous system of *Polybrachia annulata*, *A* – in dorsal view, and, *B* – from the left side, and of *Siboglinum caulleryi*, *C* – in dorsal view, and *D* – from the left side.
c – cephalic lobe; *cer* – cerebral ganglion (brain); *com* – transverse commissure; *con* – longitudinal fibre bundle; *ct* – tentacular crown; *f* – bridle; *ms* mesosoma; *mts* – metasoma; *na* – nerve ring of protosoma; *nam* – nerve ring of mesosoma; *nap* – nerve ring at boundary between mesosoma and metasoma; *nd* – dorsal nerve trunk; *nl* – thickened edge of dorsal nerve plate; *nt* – tentacular nerve; *p* – cuticular plaques; *pa* – papillae; *pn* – dorsal nerve plate; *ps* – protosoma; *t* – tentacle. (After Ivanov, 1958b)

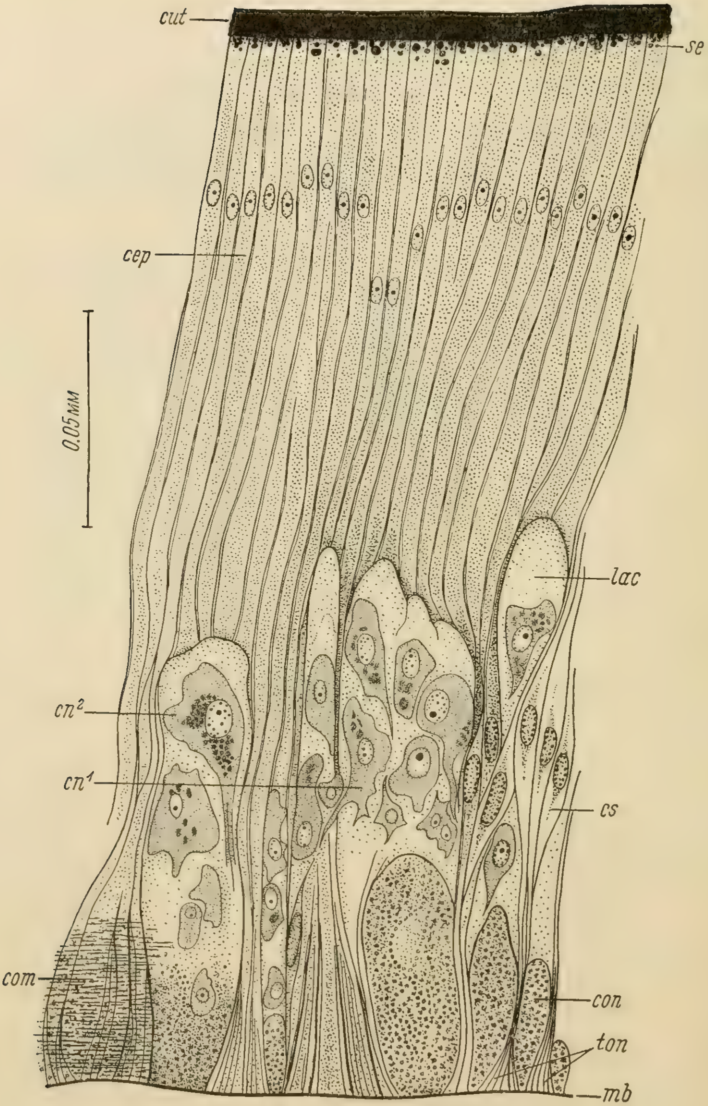


Fig. 37. Epidermis of *Spirobrachia grandis* in the brain region, in transverse section.
cep – epidermal cell; *cn*¹ – multipolar nerve cell; *cn*² – unipolar nerve cell; *com* – transverse commissure; *con* – longitudinal bundle of nerve fibres; *cs* – sensory cell; *cut* – cuticle; *lac* – lacuna; *mb* – basement membrane; *se* – secretory droplet of cuticular substance; *ton* – tonofibrillae. (After Ivanov, 1958b.)

is very poor in nerve cells. It is comparatively thin. Two stouter bundles often run amongst the numerous longitudinal fibres in this region, and seem to represent the longitudinal bundles running along the line of the dorso-ventral muscles of the protosoma. These bundles are much more prominent in the Athecanephria, in connexion with the stronger development of these muscles (Fig. 52).

The dorsal nerve tract consists of densely crowded bundles of longitudinal nerve fibres. It is narrow in the region of the mesosoma, but in the front part of the metasoma it expands to form the thin nerve plate of the dorsal ciliated band (Figs. 33, 36, 68). This consists of small fibre bundles which are more or less separated from each other by the basal ends of the ciliated epidermal cells. Large nerve cell bodies are attached to the distal sides of these bundles.

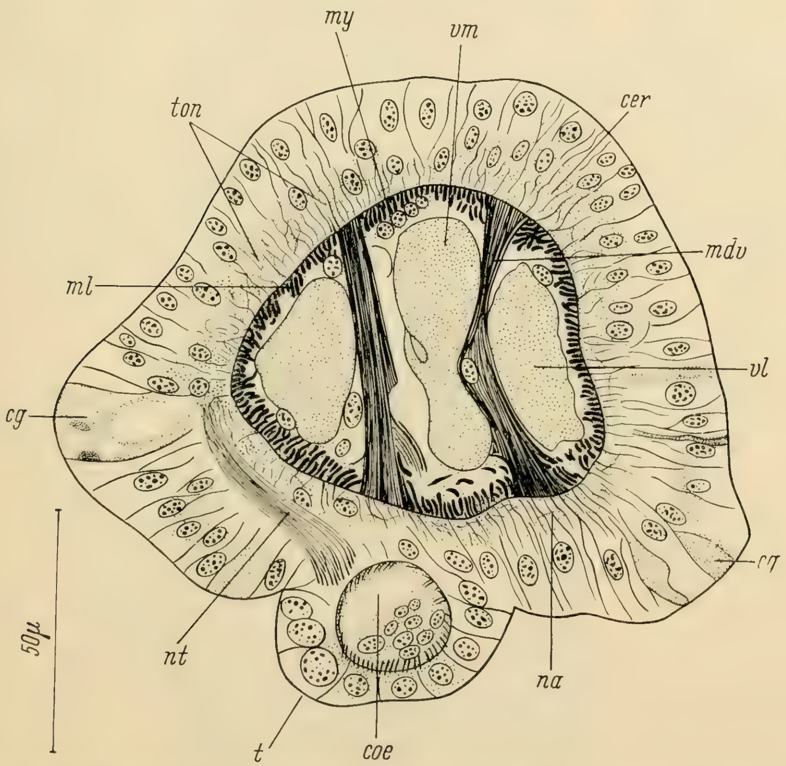


Fig. 38. Transverse section of *Siboglinum caulleryi* at the level of the attachment of the tentacle. *cer* – brain; *cg* – gland cell; *coe* – coelomic canal of tentacle; *mdv* – dorso-ventral strand of muscle fibres; *ml* – longitudinal muscle fibres; *my* – cell body (myocyte) of longitudinal muscle fibre; *na* – nerve ring of protosoma; *nt* – tentacular nerve; *t* – base of tentacle; *ton* – tonofibrillae; *vl* – lateral cephalic blood vessel; *vm* – median cephalic blood vessel. (After Ivanov, 1958b.)

The sides of the nerve plate, extending a little beyond the edges of the ciliated band, are formed by thicker bundles of nerve fibres (Figs. 33, 68). Behind the ciliated band the nerve tract becomes narrower once more and it is made up of fewer fibre bundles (Ivanov, 1958b).

The dorsal nerve trunk of *Spirobrachia* in the region of the mesosoma is worthy of consideration (Ivanov, 1958b). The mid-dorsal part of the epidermis is here invaginated to form a narrow median groove at the bottom of which lies the nerve trunk (Fig. 39). The groove is particularly strongly developed in the front part of the mesosoma and gradually flattens out towards its hind end (Fig. 171*B*). It is perhaps worth remarking that the sinking-in of a dorsal nerve trunk by the formation of a nerve groove, which is then followed by its separation from the overlying epidermis as a nerve tube, is a process extremely characteristic of the Enteropneusta and the Chordata. An analagous and equally characteristic process occurs in the formation of the epineural canals of the Echinodermata, which contain the trunks of the ectoneural system in their epithelial walls.

The dorsal nerve trunk of *Lamellisabella*, *Polybrachia* and *Spirobrachia* possesses giant nerve fibres or neurocords (Ivanov, 1958b). They are found along the whole length of the preannular region of the trunk (Fig. 40) and extend also into the mesosoma (Fig. 39). The ganglion cells to which they

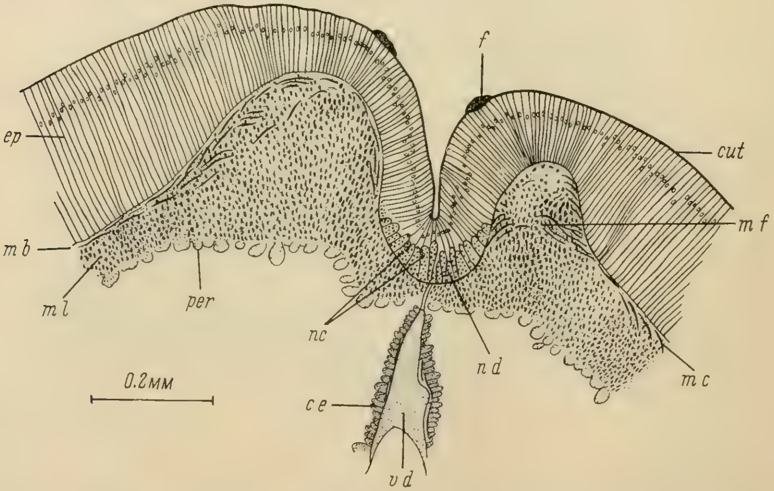


Fig. 39. Dorsal nerve furrow of *Spirobrachia grandis*: transverse section in the mesosomal region. *ce* – chlorogogenic cells; *cut* – cuticle; *ep* – epidermis; *f* – keel of bridle; *mb* – basement membrane; *mc* – circular musculature; *mf* – muscle fibres of the ridge of the bridle; *ml* – longitudinal musculature; *nc* – neurocords (giant nerve fibres); *nd* – dorsal nerve trunk; *per* – peritoneum; *vd* – dorsal blood vessel. (After Ivanov, 1958b.)

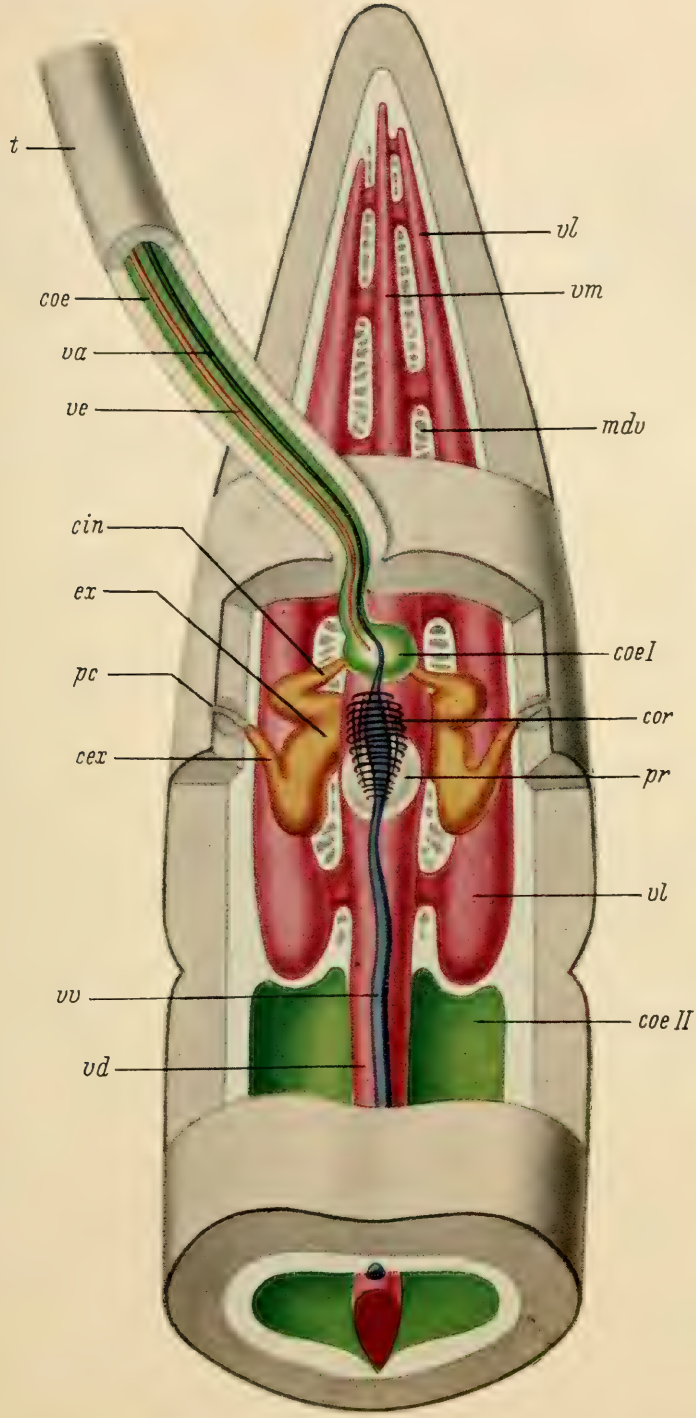


Plate I. Stereogram of the structure of the front end of the body of *Siboglinum caulleryi*, in ventral view.

cex – distal canal of coelomoduct; *cin* – proximal canal of coelomoduct; *coe* – coelomic canal of tentacle; *coe I* – protocoele; *coe II* – mesocoele; *cor* – heart; *ex* – excretory portion of coelomoduct; *mdv* – dorso-ventral muscles; *pc* – external pore of coelomoduct; *pr* – pericardial sac; *t* – tentacle; *va* – afferent vessel of tentacle; *vd* – dorsal vessel; *ve* – efferent vessel of tentacle; *vl* – lateral cephalic vessel; *vm* – median cephalic vessel; *vv* – ventral vessel. (After Ivanov, 1960a.)

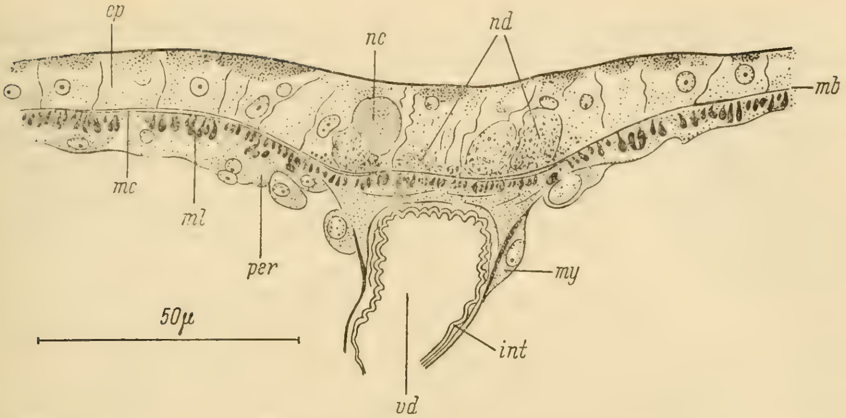


Fig. 40. Dorsal nerve trunk of *Polybrachia annulata* in the middle of the metasoma, in transverse section.
ep – epidermis; *int* – intima of dorsal blood vessel; *mb* – basement membrane; *mc* – circular muscle fibre; *ml* – longitudinal muscle fibre; *my* – muscle cell-body (myocyte); *nc* – neurocord (giant nerve fibre); *nd* – dorsal nerve trunk; *per* – peritoneum; *vd* – dorsal blood vessel. (After Ivanov, 1958b.)

belong, however, seem to lie in the region of the brain and it is not unlikely that they are the large unipolar cells mentioned above.

Since the giant nerve fibres of other invertebrates (nemertines, annelids, Phoronidea, Enteropneusta, [Crustacea and cephalopods]) are axons of motor nerve cells, it is not improbable that the development of the neurocords in pogonophores is connected with the necessity for instantaneous contraction of the longitudinal musculature at the moment of "panic withdrawal" into the protection of the tube (Ivanov, 1952). Such rapid contraction must occur only in those parts of the body in front of the girdles of toothed bristles, with which the animal fixes itself firmly to the walls of the tube, i.e. in the preannular region of the body. Correspondingly the neurocords do not extend behind the girdles.

The ganglion cells in the dorsal nerve trunk are few, but at the level of the girdles they increase in number. In a few forms (e.g. *Lamellisabella zachsi*) this ganglionic concentration is clearly connected with the innervation of the special musculature of the girdles (p. 44) (Ivanov, 1958b). In the postannular region the narrow dorsal nerve trunk may be traced to the hind end of the body (Fig. 22).

Over the rest of the body the nerve-net of the epidermis consists of a slender and in places interrupted layer of nerve fibres. At the level of the bridle, however, and at the border between the mesosoma and the metasoma the net is developed somewhat more strongly, and in some species (e.g. in *Siboglinum caulleryi*, *Lamellisabella zachsi* and *Spirobrachia grandis*) more or less complete nerve rings may be developed in these places (Fig. 36*C*, *D*). In the last two of these species both the anterior and posterior nerve rings contain ganglion cells as well. Jägersten (1956) also found the posterior nerve ring in *Siboglinum ekmani* and correctly emphasized that its presence in Pogonophora is an important feature which they share in common with Enteropneusta.

Each tentacle is innervated by one nerve (Figs. 36, 55, 57–59) running along its outer side in the thickness of the epidermis (Johansson, 1939; Ivanov, 1958b). There are no nerve cell bodies in the tentacles.

It has not proved feasible to investigate the innervation of the internal organs of pogonophores. It is possible that this is carried out by the nerve fibres of the cutaneous nerve layer penetrating through the basement membrane of the epidermis, just as is found in *Phoronis* (Silén, 1954). Nervous elements have not been found in the coelomic cavities in Pogonophora (Ivanov, 1958b).

The central nervous system of Pogonophora, like that of Hemichordata and Chordata, is thus fundamentally a longitudinal dorsal nerve trunk. Pogonophora differ from Enteropneusta, however, in the absence of any ventral trunk in the metasomal region. The latter is always well developed in Enteropneusta and in the metasoma has a greater physiological significance than the dorsal nerve trunk (Bullock, 1940). We may agree with Jägersten (1956) that the nerve ring encircling the body at the border of the mesosoma and metasoma corresponds to the prebranchial transverse commissure of Enteropneusta, which connects the dorsal and ventral nerve trunks. Furthermore, the cerebral ring of Pogonophora (the brain together with its ventral commissure) seems to correspond to the anterior nerve ring developed at the base of the proboscis in many Enteropneusta (Knight-Jones, 1952). Finally, in the Pogonophora, as in the Enteropneusta, the nervous system retains its epithelial site. As regards the histological features of the dermal nerve plexus, which have not been studied in any detail in Pogonophora, we may for the present note only the general outline of the similarity with Enteropneusta.

Amongst the essential differences between the nervous systems of the two groups under comparison we may note in Pogonophora the absence of a ventral nerve trunk, the absence of any nerve tube and the development of a brain in the protosomal region. As is well-known, the dorsal nerve trunk of Enteropneusta forms, in the region of the collar, a nerve tube detached from the integument (Spengel, 1877; Shimkevich, 1889; Dawydoff, 1948). In

Pogonophora there is no nerve tube, but it is worth noting that in *Spirobrachia* spp. the nerve trunk of the mesosoma lies at the bottom of a deep furrow or median invagination of the epidermis, which may be considered, in all likelihood, as the beginnings of a protected unexposed sub-epidermal nervous system, to wit as the first stage in the formation of a nerve tube.

Physiological experiments performed upon *Balanoglossus* and *Saccoglossus* provided evidence (Bullock, 1940) that the nerve tube of the collar, which was formerly thought to play the role of the central co-ordinating organ or brain (Dawydoff, 1948), had no great spontaneous activity and thus appeared to be a conducting tract on a par with other sections of the nervous system. It has also been stated (Knight-Jones, 1952) that there is a considerable predominance of longitudinal fibres in the nerve tube, similar to those of other longitudinal nervous pathways.

A rather complex system of longitudinal and transverse nerve fibre bundles, including the preoral ring, has been described in the proboscis of *Saccoglossus* (Knight-Jones, 1952). Koshtoyants (1957) considers that in this region not only are stimuli conducted but that it also serves a "neuro-reflector" function, and that "nervous impulses concerned with the integration of the motor activity of the animal as a whole" arise here. Nevertheless there is no anatomical expression whatsoever in the proboscis of Enteropneusta of any ganglionic cluster which might be considered as a central part of the nervous apparatus. From the data of Bullock (1945) and Knight-Jones (1952) the nerve cells of Enteropneusta appear to have a more or less diffuse distribution throughout the integumentary epithelium.

On the other hand, the mass of the dorsal cluster of ganglionic cells in the protosoma of Pogonophora seems to be a true, though very primitive, central section of the nervous system, deserving to be called the brain. Though its fine structure remains unknown it is clear that it possesses the proper architectonics, if only because of the arrangement of the main fibre bundles within it. In this respect the nervous system of Pogonophora is considerably more advanced than that of Enteropneusta. Another indication of its higher differentiation is the comparatively feeble development of the general epidermal nerve net.

A last anatomical distinction between the two groups lies in the degree of development of their giant nerve fibres. In Enteropneusta they are confined to the collar, where they run along embedded in the walls of the nerve tube (Spengel, 1884, 1893) and seem to be the axons of large unipolar nerve cells situated in the same part of the nervous system (Bullock, 1944, 1945; Knight-Jones, 1952). In Pogonophora the neurocords or giant nerve fibres run rather a long way back from the edge of the mesosoma and occupy all that region of the body which lies in front of the girdles of the trunk.

Thus the nervous system of Pogonophora, while displaying to some extent a common architectonic line with that of Enteropneusta, at the same time shows a whole series of significant divergencies.

Sense organs

Besides the solitary sense cells of the cephalic lobe possibly only the dorsal ciliated band of the metasoma may be regarded as a sense organ. Dawydoff (1948), however, conjectured that the bridle of *Siboglinum weberi* (which, in agreement with the original description of Caullery, he considered to be an oblique groove) might be fringed by narrow cells homologous with the sensory organs of the proboscis of *Saccoglossus cambrensis* (Brambell and Cole, 1939). From description given above (pp. 13 and 35), it is clear that neither in its structure nor by the location of the cuticular keels is it possible to compare the bridle with the proboscidial sensory organ of Enteropneusta or to ascribe to it a sensory function.

The dorsal ciliated organ of the trunk, with its well-developed basal nerve layer furnished with ganglionic cells is, in all probability, a chemo-receptor. According to Jägersten (1956) this is the rudiment of a special organ of locomotion which was developed in the ancestors of Pogonophora. The strong development of the ganglionic elements, however, imparts to the ciliated band the character of a functional rather than of a rudimentary organ.

CHAPTER 6

The Coelom and its Derivatives—the Excretory System

The extensive body cavity of Pogonophora, in which lie the internal organs —the circulatory system, the coelomoducts, the genital organs and the multicellular pyriform glands—is a true coelom. This is not only apparent from the morphology of the adult animal but is confirmed by the embryological development (Ivanov, 1957b). The descriptions given earlier make it sufficiently clear that pogonophores are segmented trimeric animals. The coelomic cavities correspond with the segments. Each segment possesses its proper secondary body cavity—an unpaired coelom in the protosoma and paired coelomic sacs in the mesosoma and metasoma. Thus the Pogonophora possess the same set of coelomic sacs as the Hemichordata and as the tornaria and dipleurula larvae.

The paired coeloms of the mesosoma and the metasoma come into contact in the sagittal plane, forming a mesentery (Figs. 30, 45, 68). As in Hemichordata and Annelida the dermal musculature is formed from the sheet of tissue external to the coelom—the somatopleura. All the coelomic cavities are lined by a peritoneal epithelium, which also clothes the surface of the internal organs.

The protocoele

In comparison with the body cavities of the other two segments, the invariably unpaired coelomic sac of the protosoma—the first coelom or protocoele—is very small. It occupies a small part of the protosoma near the base of the tentacular apparatus. The tentacular coelomic canals originate from it and the afferent and efferent blood vessels of the tentacles run across its cavity. The inner ends of the first pair of coelomoducts open into the first coelom. In all the Athecanephria the coelom of the protosoma is a simple sac, but in the Thecanephria it takes the shape of a horse-shoe whose ends curl down onto the ventral side (Ivanov, 1955a, 1955c). The walls of the protocoele are formed of a very delicate peritoneal epithelium.

The first coelom is especially small in *Siboglinum* where it is displaced somewhat to the right side, presumably in connexion with the single tentacle which is developed on the right side of the body in this genus (p. 25, 51); even in the adult the tentacle remains attached just a little to the right of the mid-ventral line (Pl. I, facing p. 54), and the coelomic canal leading to the tentacle pierces right through the right proximal dorso-ventral muscle bundle.

The coelom of the protosoma is considerably larger in *Oligobrachia.* The tentacular canals spring from the frontal and latero-ventral surfaces from points arranged in a horse-shoe, in accordance with the shape of the base of the tentacular crown. The internal apertures of the coelomoducts open at the postero-lateral corners of the protocoele (Pl. II, facing p. 68).

The horseshoe-shaped protocoele of the Thecanephria is arranged parallel to the bases of the tentacles, so that it reflects the shape of the tentacular crown. Thus in *Lamellisabella*, with its tentacular crown forming almost a complete circle, the ventral ends of the coelomic horse-shoe almost meet (Pl. III, facing p. 92). In *Spirobrachia* the right wing of the crown is hypertrophied and a considerable fraction of the tentacles are situated on a large corkscrew-shaped lophophore; the right half of the coelomic horse-shoe is correspondingly elongated inside this outgrowth of the protosoma, following its shape and reaching right to the tip (Fig. 41).

It is possible that the pericardial sac of the Athecanephria is a derivative of the protocoele, but since the nature of the pericardium is not at all clear we may more usefully discuss it in the chapter on the circulatory system (p. 75) with which it seems to be functionally connected.

At this point we may conveniently consider the various interpretations of the coelom of the protosoma which have been put forward by earlier authors (Johansson, 1939; Jägersten, 1956). My own interpretation, based on a study of a number of genera of Pogonophora does not agree with either of them (Ivanov, 1955a, 1955b).

On the basis of his study of *Lamellisabella zachsi* Johansson suggested that the horseshoe-shaped cavity at the base of the tentacles (he called it the tentacular coelom) communicated with the paired coelomic sacs of the mesosoma. If this were so then the same condition would exist in the Pogonophora as in the Pterobranchia, in which the tentacles belong to the second or collar segment. My investigations on abundant and varied material emphatically repudiate this interpretation.

Then behind the first coelom Johansson found an unpaired cavity which, he supposed, communicated with the first coelomoducts and lay medially between the front ends of the coelomic sacs of the mesosoma. This thin-walled sac, however, is present in only a proportion of the Pogonophora and is characteristic, though Johansson could not know it, of the Thecanephria alone (Ivanov, 1955c). Histologically its walls clearly show that it is a deep invagination of the ventral wall of the dorsal blood vessel surrounding the excretory portions of the coelomoducts, and it cannot be considered as an independent coelomic cavity.

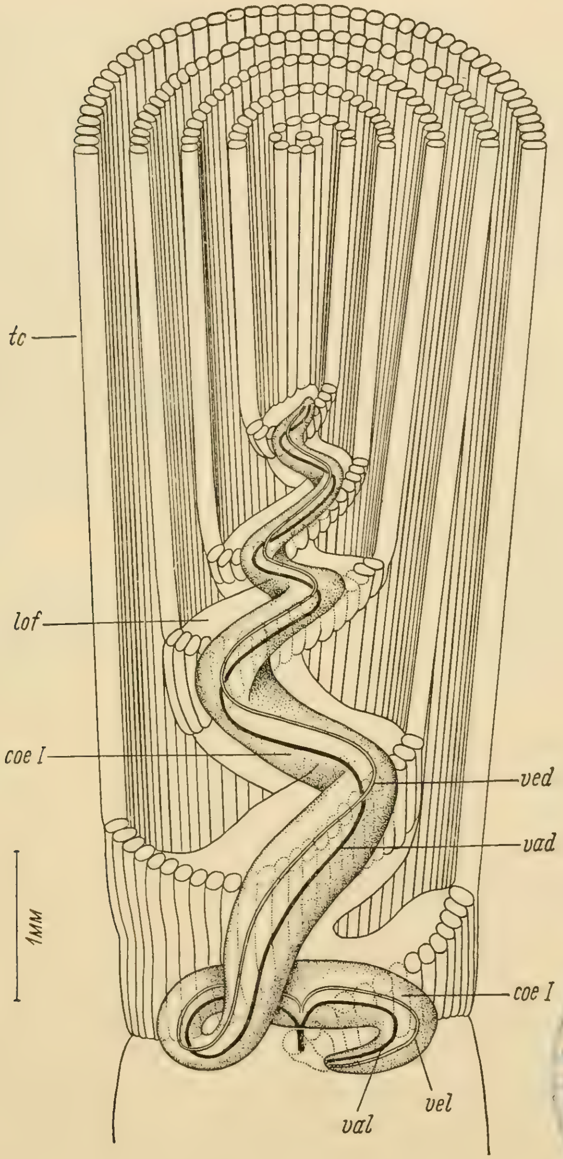
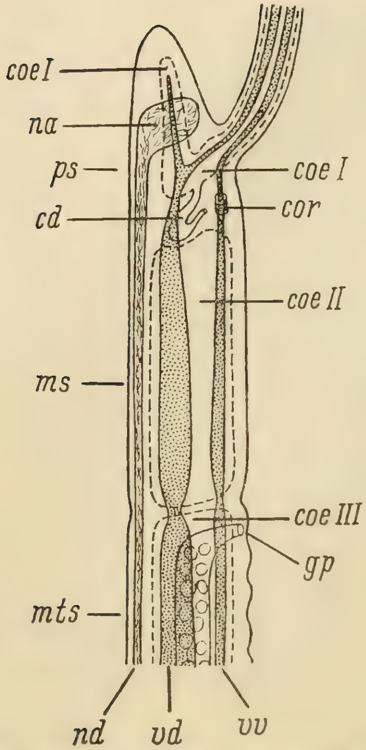


Fig. 41. Diagram of the arrangement of the protocoele of *Spirobrachia grandis*, in ventral view. *coe I* – protocoele; *lof* – lophophore; *tc* – tentacular crown, with the ventral tentacles cut away; *vad* – right afferent vessel of the tentacular crown; *val* – left afferent vessel of the tentacular crown; *ved* – right efferent vessel of the crown; *vel* – left efferent vessel of the crown. (After Ivanov, 1960a.)



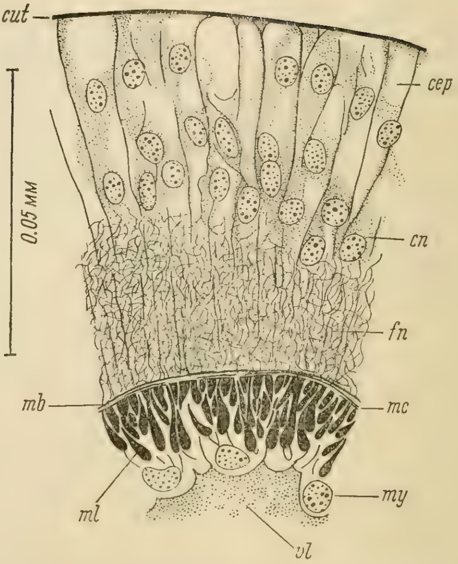


Fig. 43. Transverse section of the body wall of *Oligobrachia dogieli* in the region of the protosoma. *cep* – epidermal cell; *cn* – nerve cell; *cut* – cuticle; *fn* – layer of nerve fibres; *mb* – basement membrane; *mc* – circular muscle fibres; *ml* – longitudinal muscle fibres; *my* – muscle cell-body (myocyte); *vl* – lateral cephalic vessel. (After Ivanov, 1958b.)

Fig. 42. Diagram of the structure of the front end of the pogonophoran body according to Jägersten.
cd – nephridium; *coe I* – first coelom; *coe II* – second coelom; *coe III* – third coelom; *cor* – heart; *gp* – genital aperture; *ms* – mesosoma; *mts* – metasoma; *na* – cervical nerve ring; *nd* – nerve trunk; *ps* – protosoma; *vd* – dorsal blood vessel (called ventral by Jägersten); *vv* – ventral vessel (called dorsal by Jägersten). (After Jägersten, 1956.)

Jägersten considered the cavity at the base of the tentacle in *Siboglinum ekmani* to be merely the central part of the protocoele, thinking that three blind coelomic pockets run forward from it into the cephalic lobe to house the three cephalic blood vessels (Fig. 42). My own studies of the protosoma, however, in *S. caulleryi*, *Oligobrachia dogieli* and a whole series of the Thecanephria, do not corroborate this view. The cavity which gives rise to the coelomic canals has clearly defined limits and never extends into the cephalic lobe. The cells between the cephalic blood vessels and the body wall, which might at first glance be regarded as peritoneal elements, are apparently myocytes of the longitudinal musculature of the dermal muscle sac (Fig. 43). Jägersten is, however, right to the extent that derivatives of the wall of the protocoele are present in the cephalic lobe.

The protocoele is much more extensive at the end of embryological development than in the adult animal (Ivanov, 1957b). Its front wall later fragments on the formation of the musculature, however, and amongst its derivatives are found the interesting dorso-ventral muscle bundles first described by Caullery (1914) in *Siboglinum weberi* and later by Jägersten (1956) in *S. ekmani.* They have now been observed in all Pogonophora. These muscles, which are most strongly developed in the Thecanephria, are arranged at short irregular intervals in two longitudinal rows between the median and lateral blood vessels (Pls. I, II). They join the ventral to the dorsal body wall, with their ends inserted into the basement membrane of the epidermis (Figs. 38, 52). Each bundle consists of rather thick smooth muscle fibres with peripheral nuclei. To judge from the strong development of these muscles they perform some important function. Their contraction must flatten the cephalic lobe dorso-ventrally and so force blood out of the extensive cephalic vessels. It may readily be supposed that their periodical contraction may in large measure assist the flow of blood through these vessels. This can scarcely be their only function, however, and it is possible that by contracting rhythmically they push the blood from the cephalic vessels into the dorsal vessel, thus effectively assisting the work of the heart in propelling the blood along the ventral vessel (pp. 73, 74).

The mesocoele

The extensive coelomic sacs of the mesosoma—the mesocoeles—are separated from the protocoele by a considerable space which is occupied by a connective tissue and more or less widely spaced muscle fibres running in different directions. The heart, part of the main blood vessels and the whole or part (in the Thecanephria) of the protocoelomoducts also lie between the coelomic cavities of the protosoma and the mesosoma. No clear dissepiments or muscular diaphragm can be discerned here (see Pls. I, II, III).

The front ends of the mesocoeles reach the level of the heart and in the Athecanephria are contiguous with the hind ends of the lateral cephalic vessels (see Pls. I, II). The mesocoeles are separated from each other by a delicate mesentery containing dorso-ventral muscle fibres and supporting the dorsal and ventral blood vessels. In the Thecanephria the front ends of the coeloms are secondarily pushed apart into a lateral position by the considerable broadening of the dorsal blood vessels in this region and the intrusion of the coelomoducts of the protosoma between them (see Pl. III, facing p. 92).

There are no mesosomal coelomoducts in any known pogonophore.

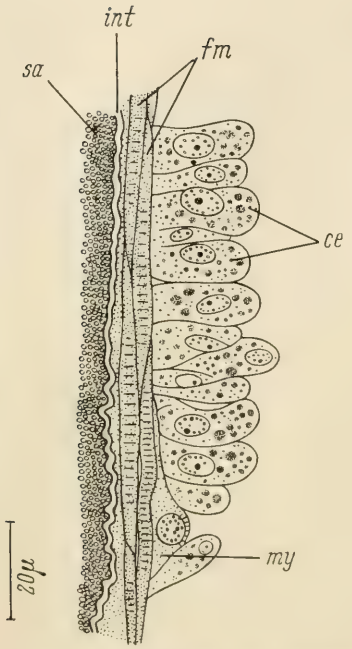


Fig. 44. The wall of the dorsal vessel of *Spirobrachia grandis* in transverse section. *ce* – peritonal cell, containing excretory inclusions; *fm* – contractile fibres of myocytes; *int* – intima of the vessel; *my* – muscle cell-body (myocyte) and nucleus; *sa* – blood. (After Ivanov, 1960a.)

The walls of the mesocoele form a peritoneal epithelium which is particularly apparent on the surface of the dorsal blood vessel and its blind lateral outgrowths. The peritoneal cells here are tall and large, and as a rule are filled with numerous excretory granules so that they may be regarded as chloragogenous cells (Fig. 44). The internal surface of the longitudinal musculature is lined by a more or less broken layer of round cells which are attached by a narrow constriction or at the base (Fig. 30). A thin layer of peritoneal cells covers the surface of the multicellular flask-shaped glands which lie in the coelom of the mesosoma.

The mesocoele is divided from the colelomic sacs of the metasoma by a well-developed transverse muscular diaphragm (Johansson, 1937; Ivanov, 1955a).

The metacoele

The coelomic sacs of the trunk—the metacoeles—extend the whole length of the third segment. As with the coeloms of the mesosoma they are divided from each other by a more or less muscular mesentery, but a little in front of the girdles the mesentery disappears between the dorsal and ventral blood vessels for a considerable length so that the right and left coelomic sacs are in communication with one another. At the level of the girdles a special median cavity begins, formed from the walls of the coelom (Figs. 22, 46).

The walls of the metacoele are clad with a peritoneum which in the forepart of the trunk is generally similar to that of the mesosoma. The splanchnopleura has a particularly tall and distinctive epithelium. On the surface of the dorsal vessel and the numerous small lateral branch vessels, and to some extent also on the ventral vessel and dorsal to it on the mesentery, the peritoneum is formed of tall narrow cells stuffed with excretory granules (Figs. 61, 68, 69, (Ivanov, 1958a, 1960a).

In *Polybrachia annulata* and *Lamellisabella zachsi* the somatopleura is highly modified in the middle part of the trunk from the level of the zone of thickened papillae to the beginning of the postannular region. It is grossly thickened here, forming a very characteristic spongy tissue, not unlike a parenchyma filling the whole body cavity (Fig. 45). In the peripheral zone this tissue has numerous round or star-shaped cells with oval nuclei, joining into an irregular network by means of their own cytoplasmic processes. The cells which lie contiguous to the longitudinal musculature are bound up with them into long bundles. Vacuoles devoid of nuclei are developed between the cells. The central part of the body cavity is occupied by similar masses. What function is performed by this highly distinctive tissue is unknown. It cannot be doubted, however, that it is not an artefact but represents a modification of the peritoneum (Ivanov, 1960a).

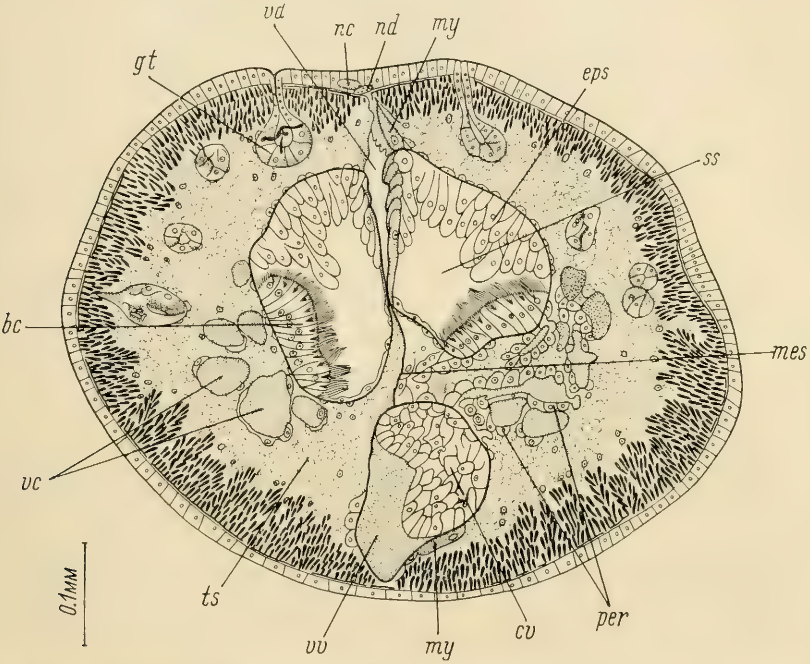


Fig. 45. Transverse section of a male *Lamellisabella zachsi* somewhat in front of the girdles of the metasoma.
bc – ciliated band of sperm sac; *cv* – corpus cardiacum; *eps* – epithelium of sperm sac; *gt* – pyriform gland; *mes* – mesentery; *my* – muscle cell-bodies (myocytes) of the vessels; *nc* – neurocord (giant nerve fibre); *nd* – dorsal nerve trunk; *per* – peritoneum; *ss* – sperm sac; *ts* – spongy coelomic tissue; *vc* – commissural blood vessel; *vd* – dorsal vessel; *vv* – ventral vessel. (After Ivanov, 1958a.)

Another very characteristic modification of the peritoneal epithelium is the pleating of the splanchnopleura which may be observed in the same species and is probably to be found in other pogonophores also. The lateral blood vessels become particularly numerous by the time the level of the zone of thickened papillae is reached. They are supported by folds of the basement membrane which run out as sheetlets joining it to the mesentery or to the ventral blood vessel. These pleats are covered on both sides by a continuous layer of hyaline peritoneal cells (Figs. 45, 69). The pleats anastomose with one another in many places to produce irregular closed cavities lined with peritoneum. One such enclosed pocket is regularly present a little in front of the girdles situated between the dorsal and ventral blood vessels at the point where the mesentery disappears, and it extends backwards to the hind end of the body. The walls of this structure, which in view of its constancy I have called the median coelomic sac, are formed of a delicate epithelium in whose cells small round intensely staining granules may be observed. The outline and diameter of this sac are very variable, changing in accordance with shape and development of the surrounding peritoneal folds (Figs. 22, 46). To judge from the fact that the median sac is also present in *Siboglinum caulleryi*, it may be present in all pogonophores (Ivanov, 1960a).

The median coelomic sac widens out in the front part of the postannular region and the splanchnopleural folds take on the appearance of massive lappets and expand so much that they almost fill the entire body cavity. The large cells which form these lappets are arranged in many layers and shaped irregularly (Fig. 46). They are vacuolated and usually contain seemingly excretory granules, yellowish or muddy brown in colour. The cells of the somatopleura in this region also take on the same nature and in the latero-ventral part of the trunk form a rather thick layer several cells deep (Fig. 46).

In the hind end of the trunk the folds of the splanchnopleura diminish considerably in size but the cells retain their peculiarities.

The metasoma has a pair of strongly developed coelomoducts, which will be described and discussed in connexion with the nature and functioning of the genital system (p. 90).

The excretory system

The excretory function is carried out by the coelomoducts of the protosoma and, in the mesosoma and metasoma, by the cells of the splanchnopleura which seem to act as a kidney of accummulation; that is to say they act as nephrocytes storing the excreta in an insoluble form.

The single pair of protosomal coelomoducts are always well developed in

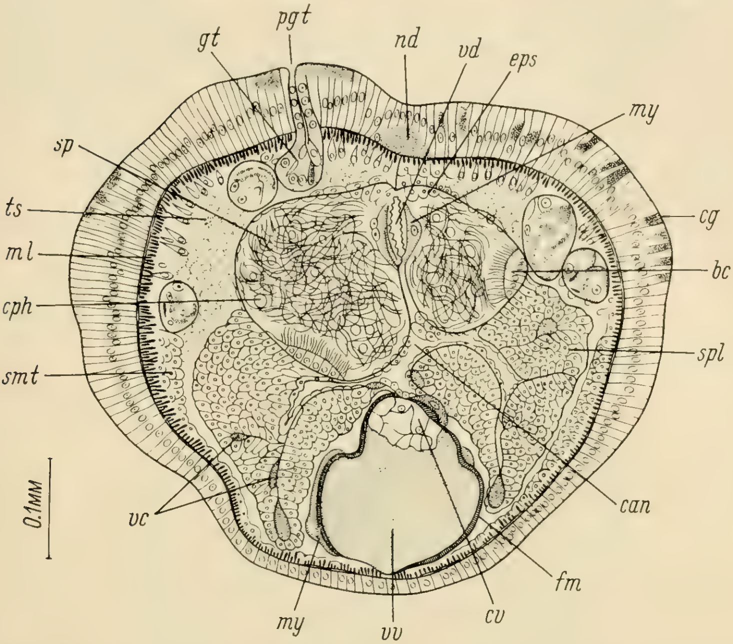


Fig. 46. Transverse section of a male *Lamellisabella zachsi* in the postannular region of the metasoma. *bc* – ciliated band of the sperm sac; *can* – median coelomic canal; *cg* – gland cell of epidermis; *cph* – sperm mother cell, lacking spermatozoa; *cv* – corpus cardiacum; *eps* – epithelium of sperm sac; *fm* – muscle fibre; *gt* – pyriform gland; *ml* – longitudinal muscle layer; *my* – myocyte; *nd* – dorsal nerve trunk; *pgt* – pore of pyriform gland; *smt* – somatopleura; *sp* – spermatozoa in the sperm sac; *spl* – splanchnopleura; *ts* – spongy coelomic tissue; *vc* – commissural vessels; *vd* – dorsal vessel; *vv* – ventral vessel. (After Ivanov, 1960a.)

all Pogonophora (Ivanov, 1955a, 1955b). They are, however, only discovered with difficulty in the smaller species of *Siboglinum* and then only in well-fixed material. This must be the reason why they were described in neither *S. weberi* nor *S. ekmani* (Caullery, 1944; Jägersten, 1956).

The coelomoducts are epithelial ciliated canals putting the protocoele into communication with the external medium and hence appertaining to the protosoma. They are thus evidently homologous with the proboscis pores of the Hemichordata.

Each coelomoduct consists of three parts: first a proximal canal, communicating with the coelom, then an excretory section, shaped like a backwardly pointing U-bend, and finally a distal discharge canal. This last terminates in a thicker epidermal ampulla opening to the exterior by an external pore. The proximal canals are attached to the coelomic sac apposite to one another and run above the dorsal blood vessel (Pls. I, II, III).

There are important differences in the topography of the excretory system and in the degree of development of the coelomoducts between the Athecanephria and the Thecanephria. In the Thecanephria the coelomoducts are comparatively short, lying wholly within the protosoma, and their excretory sections are closely apposed to the lateral cephalic vessels. They are far bigger in the Thecanephria, extending back beyond the hind margin of the protosoma; their excretory portions are almost median and enclosed within a sac-like outgrowth of the ventral wall of the dorsal blood vessel (Ivanov, 1955a).

As a typical athecanephrian we may select *Oligobrachia dogieli* for description. In this species the U-shaped excretory portion of the coleomoduct is very broad and lies on the ventral surface of the lateral cephalic vessel. The discharge branch is short and the external pore is located on the ventral side of the body behind the tentacles (Pl. II, facing p. 68).

The coelomoducts of *Siboglinum caulleryi* have essentially the same structure. The excretory function, however, is carried out not only by the U-shaped part of the organ but by a considerable part of the proximal canal also and by the anastomosing duct which joins the proximal canals of opposite sides. The coelomoducts closely invest the median cephalic vessel on the dorsal and lateral sides, and then turn outwards to abut upon the lateral cephalic vessels. Running from the protocoele the proximal canals gradually broaden then turn up onto the dorsal side where they communicate with one another by means of a wide sac-like anastomosis. Then the ducts become narrow again and closely invest the median cephalic vessel. The U-shaped part of each coelomoduct lies on the lateral cephalic vessel. Its distal section gradually runs into the discharge canal. The ampulla is situated on the ventral side of the body (Pl. I, facing p. 54).

The coelomoducts of the Thecanaphria, as stated above, are very much larger and their excretory portions are strongly developed. The internal ends of the coelomoducts are much elongated, making numerous bends and loops (Fig. 47), and the surface of the excretory epithelium is thus considerably expanded. The proximal canals, opening from the protocoele, form characteristic expansions at the point of the junction with the anastomosing transverse duct. The ampullae of the distal canals open on the dorso-lateral surface of the protosoma at the very base of the tentacular crown. The sole exception to this pattern, to all appearances, is *Lamellisabella zachsi* in which the coelomoducts do not communicate at all with the coelom (see Pl. III, facing p. 92).

The histological structure of the coelomoducts is the same in all species. No ciliated tract runs directly from the coelom into the proximal canals, but

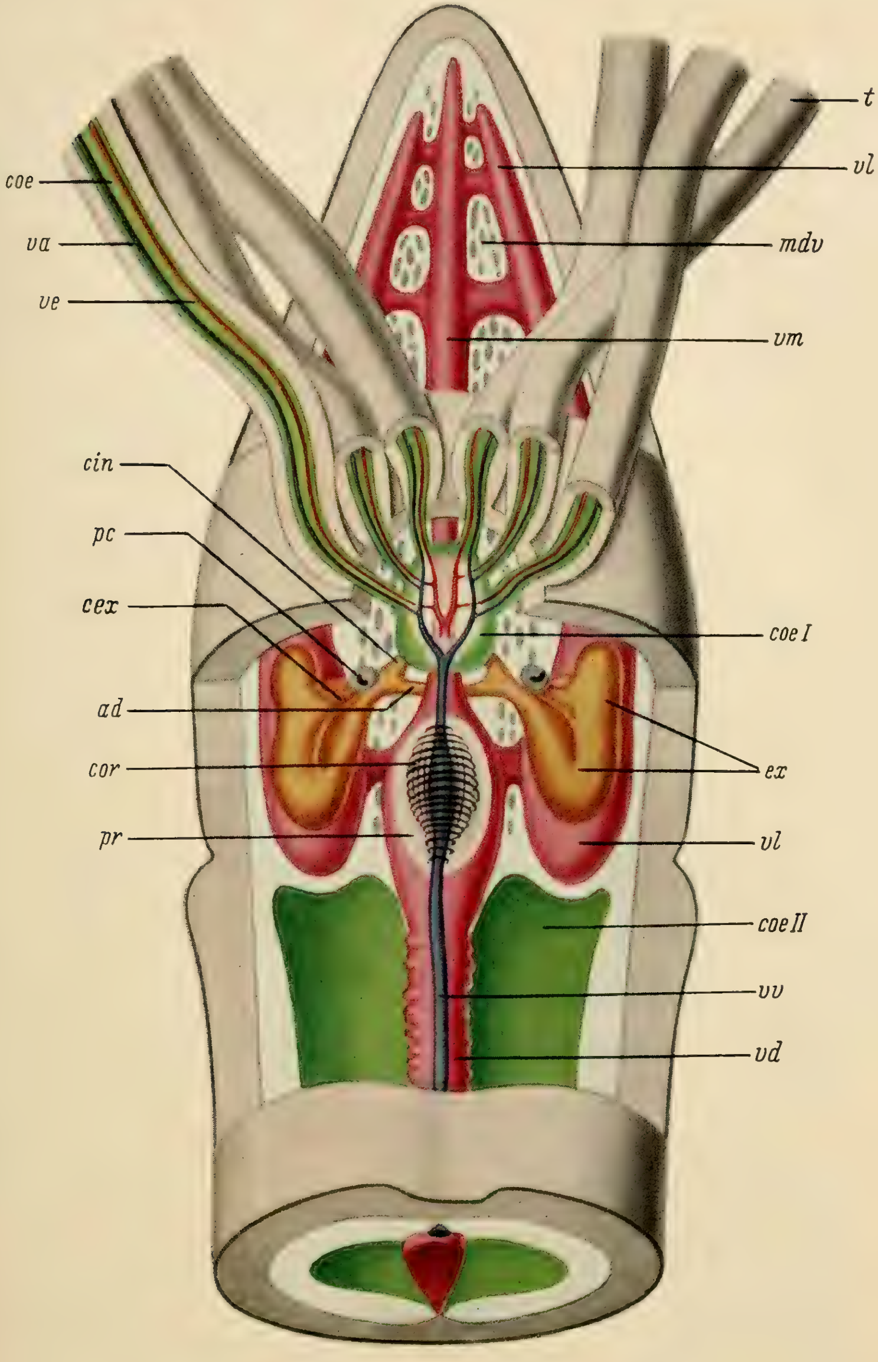


Plate II. Stereogram of the structure of the front end of the body of *Oligobrachia dogieli*, in ventral view.

ad – anastomosing canal of the coelomoducts; *cex* – distal canal of coelomoduct; *cin* – proximal canal of coelomoduct; *coe* – coelomic canal of tentacle; *coe I* – protocoele; *coe II* – mesocoele; *cor* – heart; *ex* – excretory portion of coelomoduct; *mdv* – dorso-ventral muscles; *pc* – external pore of coelomoduct; *pr* – pericardial sac; *t* – tentacle; *va* – afferent vessel of tentacle; *vd* – dorsal vessel; *ve* – efferent vessel of tentacle; *vl* – lateral cephalic vessel; *vm* – median cephalic vessel; *vv* – ventral vessel. (After Ivanov, 1960a.)

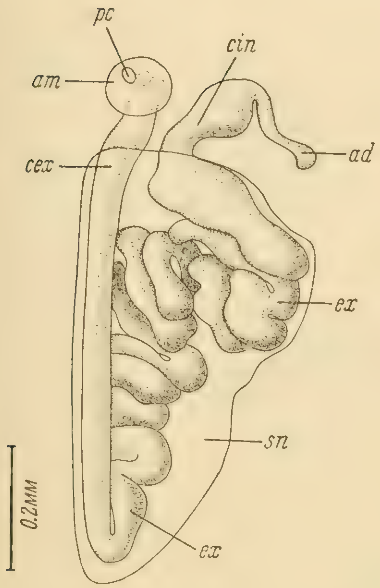


Fig. 47. Left coelomoduct of the protosoma of *Lamellisabella zachsi*, seen from the left side: a graphic reconstruction from sections.
ad – anastomosing canal of coelomoducts; *am* – ampulla; *cex* – distal canal of coelomoduct; *cin* – proximal canal of coelomoduct; *ex* – excretory portion of coelomoduct; *pc* – external pore of coelomoduct; *sn* – "renal sac" – an invagination of the ventral wall of the dorsal vessel in which lie the excretory portions of the coelomoducts.

the walls of these canals consist of cubical ciliated cells. The excretory section is formed of rounded nephrocytes, furnished with bundles of long cilia and stuffed with brown excretory granules, which are not infrequently encountered in the lumen of the organ also (Fig. 48*A*, *B*). The excretory duct consists of low ciliated cells. Finally the ampullae lie wholly within the thickness of the epidermis and to some extent look like mere invaginations, but in *Spirobrachia* and *Lamellisabella* they consist of two parts—a proximal expansion, formed of ciliated cells, and a distal external part with a dilated lumen, clad with a thin layer of cuticle instead of cilia (Fig. 48*C*).

Concentrations of granules in the cells of the coleomoducts reveal by their brown colour that they are excretory inclusions. They increase greatly in number towards the distal end of the organ, particularly in the larger Thecanephria, and in the regions in close contact with the blood vessels they account for the intensely staining nature of the coelomoducts. Excretory matter probably passes into them from the blood, and to all appearances this is their chief function. The coelomoducts may also serve to regulate the amount of body fluid in the protocoele and hence the amount in the coelomic canals of the tentacles also.

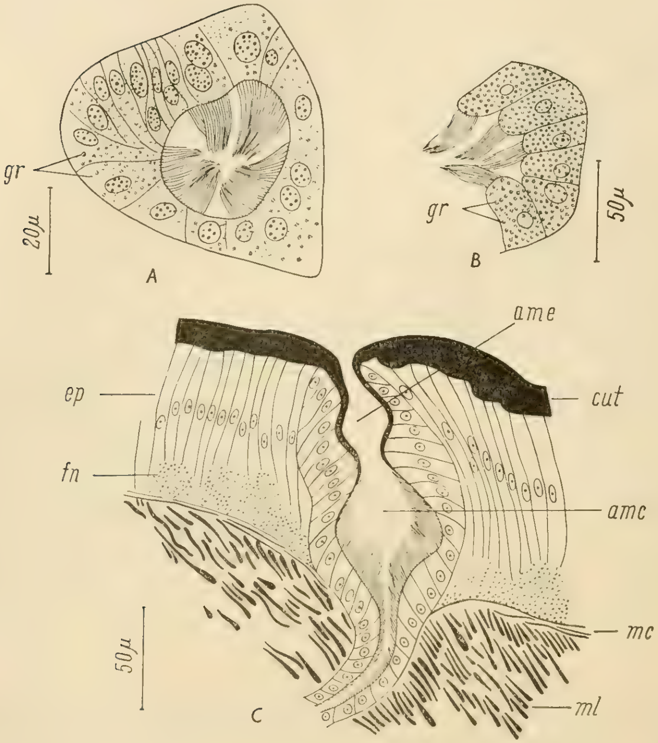


Fig. 48. Pogonophoran coelomoducts. *A* – transverse section of the excretory part of the coelomoduct of *Oligobrachia dogieli*; *B* – the same of *Lamellisabella zachsi*; *C* – ampulla of the coelomoduct of *Lamellisabella zachsi.*

amc – ciliated portion of ampulla; *ame* – outer part of ampulla; *cut* – cuticle; *ep* – epidermis; *fn* – nerve layer of epidermis; *gr* – excretory granules; *mc* – circular muscle layer; *ml* – longitudinal muscle layer. (After Ivanov, 1960a.)

CHAPTER 7

The Blood-Vascular System

The Pogonophora possess a strongly developed closed blood-vascular system. Two blood vessels, a dorsal and a ventral (Caullery, 1914, 1944; Johansson, 1939), running the whole length of the body are connected anteriorly by the vascular system of the tentacular apparatus and posteriorly by lateral transverse commissural vessels. In the fore-part of the body both longitudinal vessels lie in the mesenteries. Part of the ventral vessel in the mesosomal region is differentiated to form a heart (Ivanov, 1955a). A peculiar organ inside the ventral vessel has been called the "corpus cardiacum".

The blood vessels

The dorsal vessel reaches its greatest calibre near the protocoelomoducts. In the Thecanephria it is particularly broad here and envelops the excretory portions of the coelomoducts from below, forming around them the long "renal sacs" in which they are bathed by blood on all sides. The dorsal vessel is considerably narrower in front of the level of the heart, and narrow vessels open into it from the ventral side, carrying blood from the tentacular apparatus.

Three parallel branches extend from the dorsal vessel into the cephalic lobe where they terminate blindly. One of them—the median cephalic vessel—is a direct continuation of the dorsal vessel; the other two—the lateral cephalic vessels—branch off at the level of the heart (Fig. 52, Pls. I, II). The cephalic vessels are joined to one another by an asymmetrical plexus of transverse anastomosing vessels. The posterior ends of the lateral vessels project backwards in the Athecanephria as a pair of sac-like expansions. Longitudinally grouped bundles of dorso-ventral muscle fibres run in spaces between the cephalic vessels and their transverse anastomoses (Pls. I, II).

The dorsal vessel is much flattened from side to side in the region of the mesosoma and takes up almost the whole space between the dorsal body wall and the ventral vessel (Fig. 30). Its side walls are usually covered with numerous caeca (Pls. II, III), and the ventral wall is thrown into a few parallel longitudinal folds. The intima of the vessel is here covered on the outside by a layer of cells, apparently a continuation of the peritoneal epithelium (Fig. 49). Passing through the diaphragm the dorsal vessel becomes much narrower (Fig. 32), but in the metasoma it becomes once more

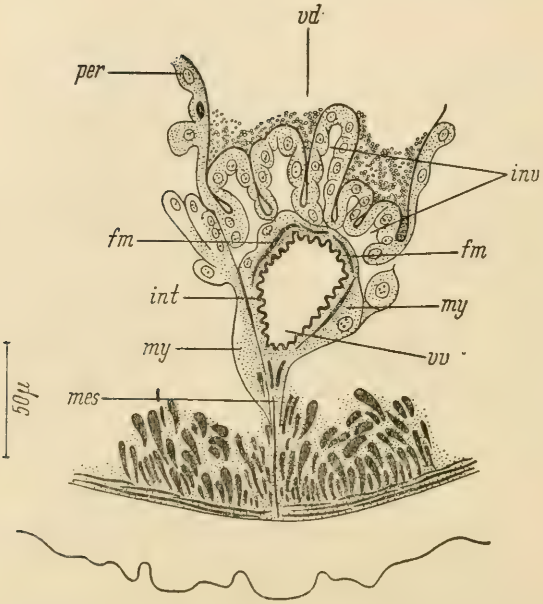


Fig. 49. Groove-like invaginations of the ventral wall of the dorsal vessel in ***Polybrachia annulata***, in transverse section.
fm – muscle fibre; *int* – intima of the vessel; *inv* – invaginations of the dorsal vessel; *mes* – mesentery; *my* – myocytes; *per* – peritoneum; *vd* – dorsal vessel; *vv* – ventral vessel. (After Ivanov, 1960a.)

considerably taller in the sagittal plane, though still flattened from side to side (Figs. 33, 45, 64, 67).

In the female, paired longitudinal lateral vessels branch off from the dorsal vessel immediately behind the diaphragm to run in the walls of the ovary (Johansson, 1939). They are very long and extend without branching to the hind end of the ovary. Their number varies, according to the size of the animal, from two to five pairs [*Siboglinum*: two pairs (Fig. 33); *Polybrachia* (Fig. 68) and *Lamellisabella zachsi*: three pairs; *Spirobrachia grandis*: five pairs]. In the male the dorsal vessel gives off numerous, not especially long, irregular lateral branches in the front part of the trunk, running along the internal walls of the spermducts (Fig. 64).

In the posterior part of the trunk, beginning at the level of the zone of thickened papillae, the dorsal vessel becomes considerably smaller in diameter and comes to lie in the dorsal body wall. The number of lateral branches running from it increases and some of them are quite large. They are suspended from folds of peritoneum and extend backwards for a considerable distance, frequently branching irregularly (Fig. 45). In the posterior half of the trunk, beginning a little in front of the first girdle, the lateral branches communicate with the ventral vessel.

Throughout its length the ventral vessel keeps nearly the same diameter and only at the very front end, in the protosoma, is it greatly distended to form the muscular heart. In front of the heart it becomes slender, turns towards the dorsal side and enters the protocoele. Here it forks into two symmetrical branches—the vessels of the tentacular crown, from which start the afferent vessels of the tentacles (Pls. II, III).

Two vessels—afferent and efferent—run in the coelomic canals of each tentacle, communicating with each other by means of the capillaries of the pinnules (p. 80, Figs. 53–55). The efferent vessels from the tentacles open into the pair of efferent vessels in the protocoele, which in turn pour the blood into the dorsal blood vessel (Pls. II, III).

The walls of the blood vessels consist of a structureless membrane, which, as a rule, is connected with the system of membranes bounding the peritoneum or forming the basement membranes of the epidermis. This intima is noticeably thicker in the dorsal and ventral vessels. There is no endothelium (Figs. 22, 45, 49). Large often isolated cells may, it is true, frequently be encountered on the internal surface of the vessels, but these, however, appear to be temporarily attached cellular elements of the blood. Both main vessels are clad in a layer of circular muscle which has an unusual structure. Its myocytes are of the nematode type, with a cytoplasmic part, containing the nucleus, projecting into the body cavity, and a comparatively narrow spindle-shaped contractile fibre possessing true transverse striations. Such muscle fibres are to be found all along both the longitudinal vessels (Figs. 44, 46). The striated musculature is particularly well developed on the ventral vessel and in particular on its posterior half, where the large cytoplasmic perikarya of the myocytes cover the vessel in a complete layer (Figs. 22, 46, 50).

The heart

In appearance the heart is simply a thickened portion of the ventral blood vessel, with a particularly powerfully developed mantle of muscle fibres. Its size is directly correlated with the degree of development of the tentacular apparatus. Where most tentacles enter into the structure of the crown the heart is biggest. In the unitentaculate *Siboglinum* it is poorly developed (Pl. I); in *Polybrachia*, *Lamellisabella* (Pl. III) and *Spirobrachia* it reaches a considerable size.

The lumen of the heart is bounded by a comparatively stout membrane

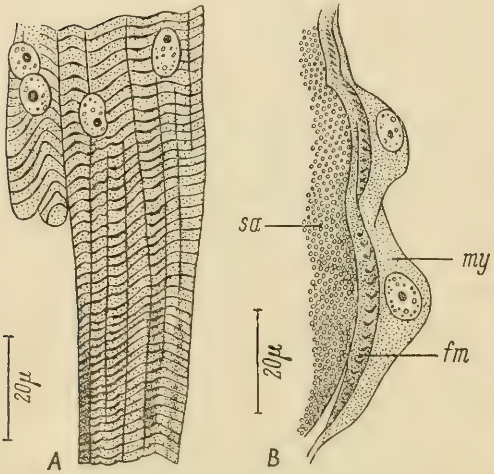


Fig. 50. Striated muscle fibres from the wall of the ventral blood vessel of *Lamellisabella zachsi*. *A* – tangential section; *B* – transverse section.
fm – contractile fibre; *my* – myocyte; *sa* – blood in the ventral vessel. (After Ivanov, 1960a.)

which appears to be a continuation of the intima of the ventral vessel. When the heart is contracted the intima forms numerous longitudinal folds. A rather spongy connective tissue layer is developed around it, consisting of irregular and often stellate cells. Outside this again we see the first signs of the muscular mantle, consisting of a few circular layers interspersed with streaks of diagonal (or possibly spiral) muscle fibres. In different layers these run in opposite senses, forming right-hand and left-hand spirals around the heart (Fig. 51). Finally, on the outside are the longitudinal fibres. So far as we know the muscle fibres of the heart are smooth, unstriated fibres [unlike those of the blood vessels]. The heart is not sharply delimited on the outside from the surrounding connective tissue.

When the heart is full of blood its cavity is grossly distended and the intima loses its folds and, indeed, becomes highly stretched. The whole structure of the heart and its location at the base of the tentacular crown suggest that it is a contractile organ whose function it is to drive the blood through the system of tentacular vessels. [Observations upon living *Siboglinum* spp., in which the red blood may be seen to circulate and the heart to contract rhythmically, tend to confirm this suggestion—D.B.C.]

The pericardium

In the Athecanephria a small epithelial sac lies close to the heart on the dorsal side. It is completely closed, and half moon-shaped in transverse

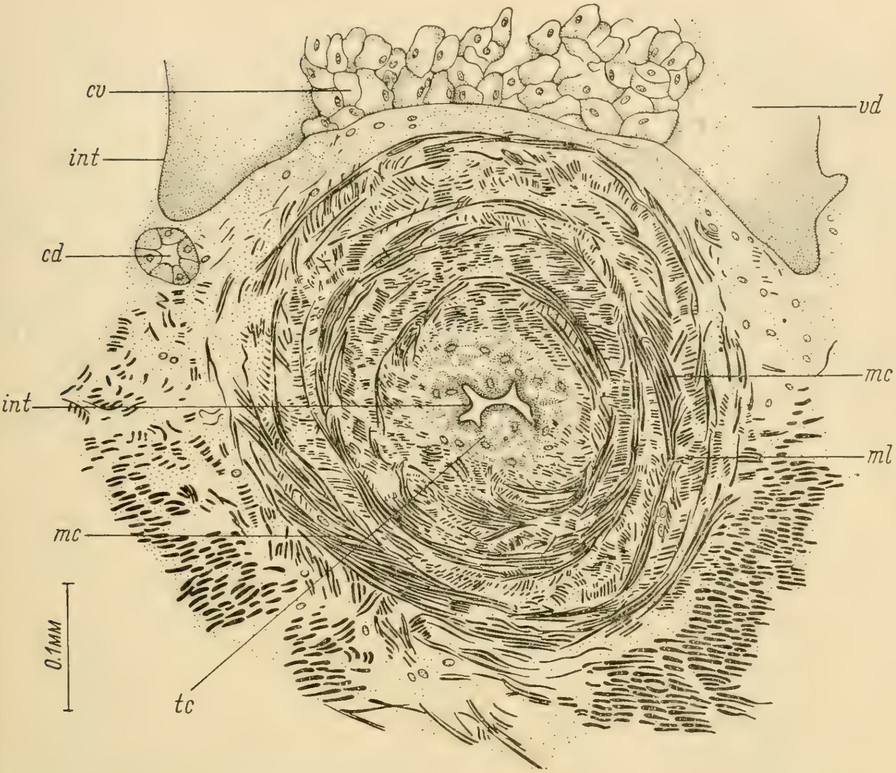


Fig. 51. Transverse section of the heart of *Spirobrachia grandis*.
cd – coelomoduct; *cv* – corpus cardiacum in the dorsal vessel; *int* – intima of the vessel; *mc* – circular muscle fibres; *ml* – longitudinal muscle fibres; *tc* – connective tissue; *vd* – dorsal blood vessel. (After Ivanov, 1960a.)

section (Fig. 52). It was discovered in *Oligobrachia*, *Birsteinia* and *Siboglinum* and named the pericardium (Ivanov, 1955a). The nature of this organ remains uncertain. It is not known how far it may be homologized with the cardio-pericardial sac of the Hemichordata. There is no evidence as yet about the ontogenetical origin of this sac, but we cannot exclude the possibility that it develops during organogenesis by separation of part of the protocoele. The functional significance of the pericardium, on the other hand, is fairly clear. It plays the role of a pouch or cushion making the expansion of the heart easier, and so, as regards its physiology, it is sharply distinguished from the cardio-pericardium of the Enteropneusta.

The Thecanephria lack a pericardium, and it is possible that its role is taken over by the renal sacs, which lie above the hind part of the heart.

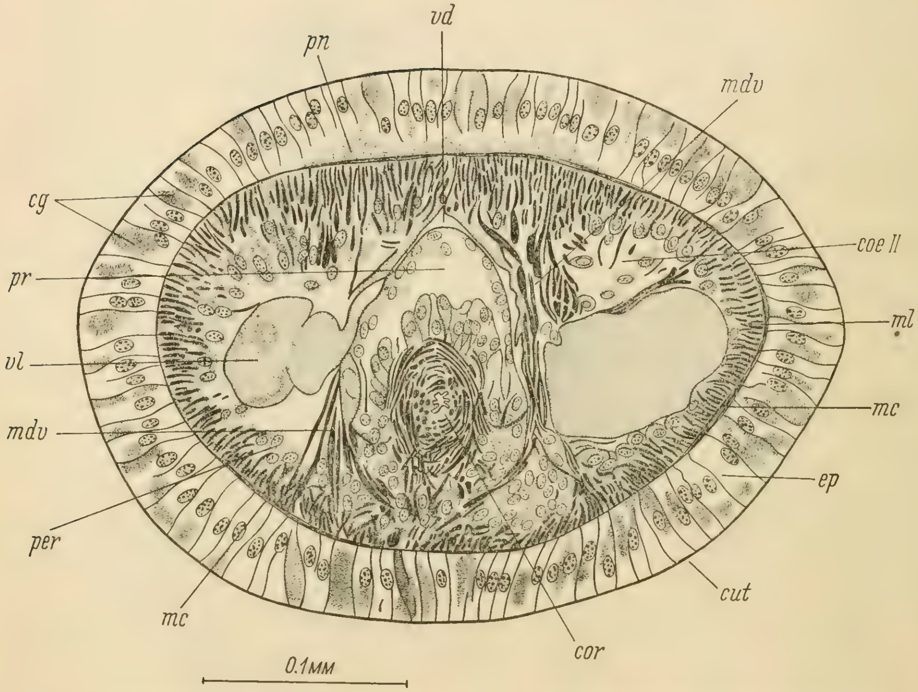


Fig. 52. Transverse section of *Oligobrachia dogieli* at the level of the heart and of the pericardium. *cg* – gland cell of epidermis; *coe II* – coelom of mesosoma; *cor* – heart; *cut* – cuticle; *ep* – epidermis; *mc* – circular muscle layer; *mdv* – dorso-ventral bundle of muscle fibres; *ml* – longitudinal muscle layer; *per* – peritoneum; *pn* – dorsal nerve plate – the origin of the dorsal nerve trunk; *pr* – pericardial sac; *vd* – dorsal blood vessel; *vl* – hind part of the lateral cephalic vessel. (After Ivanov, 1960a.)

The corpus cardiacum

With the exception of *Siboglinum*, in all the Pogonophora which have been investigated there is a very odd cellular formation within the ventral vessel. This was described by Johansson (1939) as mesenchymatous tissue, but it would be better named the corpus cardiacum (Ivanov, 1956b, 1960a).

This long uninterrupted tract, consisting of large clearly vacuolated cells, is attached to the dorsal wall of the ventral vessel. It is never present in the mesosoma. It is separated from the lumen of the vessel by a structureless bounding membrane which merges into the intima of the vessel, although the latter is considerably thicker. The cells of the corpus cardiacum are piled together in disorder. They are shaped like irregular polygons and are usually pressed close together (Figs. 45, 46, 61, 63, 64, 68, 69). The cytoplasm is densely supplied with small granules of glycogen. Thus at least one of the functions of a corpus cardiacum—the accummulation of food reserves—is performed by this organ. An haematopoietic function seems to be excluded since its cells have never been observed to divide to form the cellular elements of the blood. It is possible that the main functional significance of the corpus cardiacum lies in its role as a sort of valve, allowing the blood to pass in only one direction. Chink-like spaces filled with blood are frequently visible here and there between its cells. These lacunae probably communicate through narrow apertures in the limiting membrane both with the lumen of the vessel itself and also with the lateral vessels which carry blood from the dorsal vessel. One can well imagine that when the ventral vessel is wide and relaxed the blood runs freely into it from the lateral vessels through these chink-like gaps in the corpus cardiacum. But when the ventral vessel contracts the cells of the corpus cardiacum are compressed by the blood pressure, the lacunae between them are clenched tight shut and the blood cannot run back into the lateral vessels. This hypothesis remains unproven for the moment until the supposed links between these lacunae in the corpus cardiacum and the lumina of the vessels have been successfully demonstrated. It is possible, finally, that when waves of contraction run along the walls of the ventral vessel they tightly compress the corpus cardiacum which, without doubt, greatly aids the complete evacuation of the blood from the contracted region, forcing it forward into the next section of the vessel which is momentarily broad and relaxed.

Johansson (1939) looked upon the cellular tissue in the ventral vessel as the rudiments of a gut. No factual evidence, however, has been presented to support this idea.

A structure analagous to the corpus cardiacum is developed in the dorsal vessel of the Thecanephria. It is situated in the very front part of the vessel where it is attached to the dorsal wall. In *Lamellisabella* and *Spirobrachia* it is developed to such an extent that it blocks a considerable part of the lumen of the vessel in front of the renal sac (Fig. 51).

The blood

While working aboard R.V. *Vityaz'* I have repeatedly observed that in all Pogonophora the blood of the living animal is red.

[This is because the blood contains haemoglobin, Southward and Southward, 1963.]

The blood plasma contains masses of very small unnucleated bodies [in fixed and stained material]. It is doubtful from their appearance whether one may legitimately interpret them as cellular elements and in sections they sometimes give the impression of large-grained coagulations (Fig. 49). Free lymphocytes may often be encountered in the blood—rather small round or oval cells with obvious nuclei. The lymphocytes often settle on the walls of the vessels and sometimes they may be seen here in such numbers that one may mistake them for elements of an endothelium.

Circulation of the blood

Although direct observation on the circulation of the blood is lacking, a series of morphological features of the blood-vascular system make it possible to arrive at reasonable conclusions about the direction of flow of the blood.

As will later become apparent there is no alimentary canal in pogonophores, its function being taken over by the tentacles. These organs also carry out the respiratory function. In consequence the blood running out of the tentacles must be more saturated both with foodstuffs and with oxygen than is the blood which flows into them. The organs most in continuous need of food substances and oxygen—the brain, and the ovary in the female—are supplied by branches from the dorsal vessel, so that it is reasonable to suppose that the blood in this vessel comes direct from the tentacles. Then the heart, developed on the ventral vessel at the base of the tentacular crown, is the only possible propulsive organ, pumping the blood through the whole system of tentacular vessels. Clearly a muscular heart is necessary to overcome the very great resistance of the fine capilliaries of the pinnules of the tentacular apparatus (p. 80), a resistance which could not be overcome by the unaided pulsation of the ventral vessel. Thus we may reasonably conjecture that the blood moves forward in the ventral vessel, through the heart into the tentacles and thence backwards from the head in the dorsal vessel (Ivanov, 1955a, 1960a).

As we have seen (p. 63) contraction of the dorso-ventral musculature of the protosoma probably in some measure assists, if not the circulation then at least the renewal of the blood in the cephalic vessels.

[The beating of the heart has been observed in living *Siboglinum*. Ivanov's conjectures are confirmed, for the blood may be seen to pass from the heart into the tentacles and thence back into the dorsal vessel—D.B.C.]

CHAPTER 8

The Tentacular Apparatus and External Digestion

Both Caullery (1914, 1944) and Johansson (1939) remarked on the absence of any gut in Pogonophora, and in later years this astonishing fact was confirmed in species after species (Ivanov, 1952, 1955a, 1956b, 1960a; Jägersten, 1956). Mouth and anus are likewise missing and do not appear even during embryonic development (Ivanov, 1957b).

Pogonophora must, however, require a large and steady supply of food. This is apparent from their high basic productivity, as evinced by the great accummulation of yolk and fat in the large eggs, by the intensive secretory activity of the numerous multicellular glands which pour out the materials for the very long and often thick-walled tube, and by the formation of new tentacles which often continues even in the sexually mature animal. [The possession of a closed circulation and pigmented blood also implies a high metabolic rate.]

The key to the problem of how these sedentary inhabitants of the sea bed feed, though wholly lacking the usual digestive system, is given by an analysis of their tentacular apparatus.

The structure of the tentacles

Except for a few species of *Siboglinum*, which lack pinnules, the structure of the individual tentacles is very uniform throughout the Pogonophora. The greatest known modifications of the tentacles are found in *Lamellisabella zachsi* and *Spirobrachia grandis* (Ivanov, 1955b, 1960a).

The wall of the tentacle consists of a hollow cylinder whose outer layer is formed of more or less tall epidermal cells. Under the basement membrane of these cells lies a single layer of very fine muscle fibres, then comes the peritoneal endothelium lining the coelomic canal. The afferent and efferent blood vessels run in the coelom (Figs. 53, 55). The surface of the tentacle is covered by a cuticle which is thicker on those sides which are on the outside of the crown. The tentacular nerve runs up the outer side of the tentacle in the thicker epidermis there, always, however, lying a little to one side, asymmetrically (Fig. 55). On the side which faces into the crown the surface of the tentacle bears a row of pinnules like a fringe (p. 31). The pinnules are flanked on each side by a single row of gland cells and then by a single row of large ciliated cells outside these, before the cuticle begins (Fig. 55).

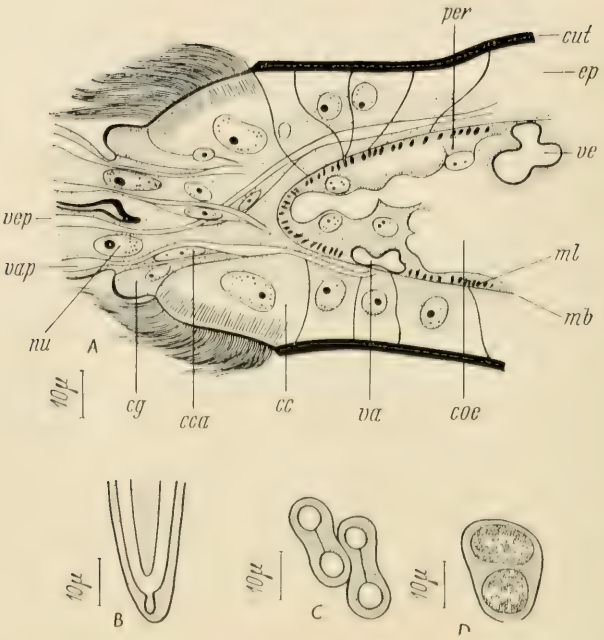


Fig. 53. Part of a transverse section of a tentacle of *Lamellisabella zachsi* (*A*), and sections of tentacular pinnules of the same species: *B* – longitudinal section of the distal end of a pinnule; *C* – transverse section of two adjacent pinnules; and *D* – transverse section of a pinnule with the capillaries full of blood.

cc – ciliated cell; *cca* – cell adjacent to capillary; *cg* – gland cell; *coe* – coelomic canal; *cut* – cuticle; *ep* – epidermis; *mb* – basement membrane; *ml* – longitudinal muscle fibre; *nu* – nucleus of pinnule; *per* – peritoneum; *va* – afferent vessel of tentacle; *vap* – afferent capillary of pinnule; *ve* – efferent vessel of tentacle; *vep* – efferent capillary of pinnule. (After Ivanov, 1960a.)

Each pinnule represents a single cylindrical epidermal cell, projecting far beyond the surrounding epidermis, but with the nucleus near the base within the thickness of the epidermis proper. Its surface is covered by the finest imaginable cuticle. The homogeneous cytoplasm of the pinnule is pierced by two long thin parallel canals, which, however strange it may seem at first glance, are nothing less than intracellular blood vessels and are often found filled with the characteristic small blood granules (Fig. 53*D*). These capillaries run the whole length of the cell to join near the tip of the pinnule (Fig. 55). They possess their own walls formed of a very thin structureless intima. A thin membrane of the same substance links the walls of the two capillaries and forms a sort of longitudinal ribbon up the centre of the pinnule (Fig. 53*C*). Quite obviously one of these capillaries must be the afferent and the other the efferent vessel of the pinnule.

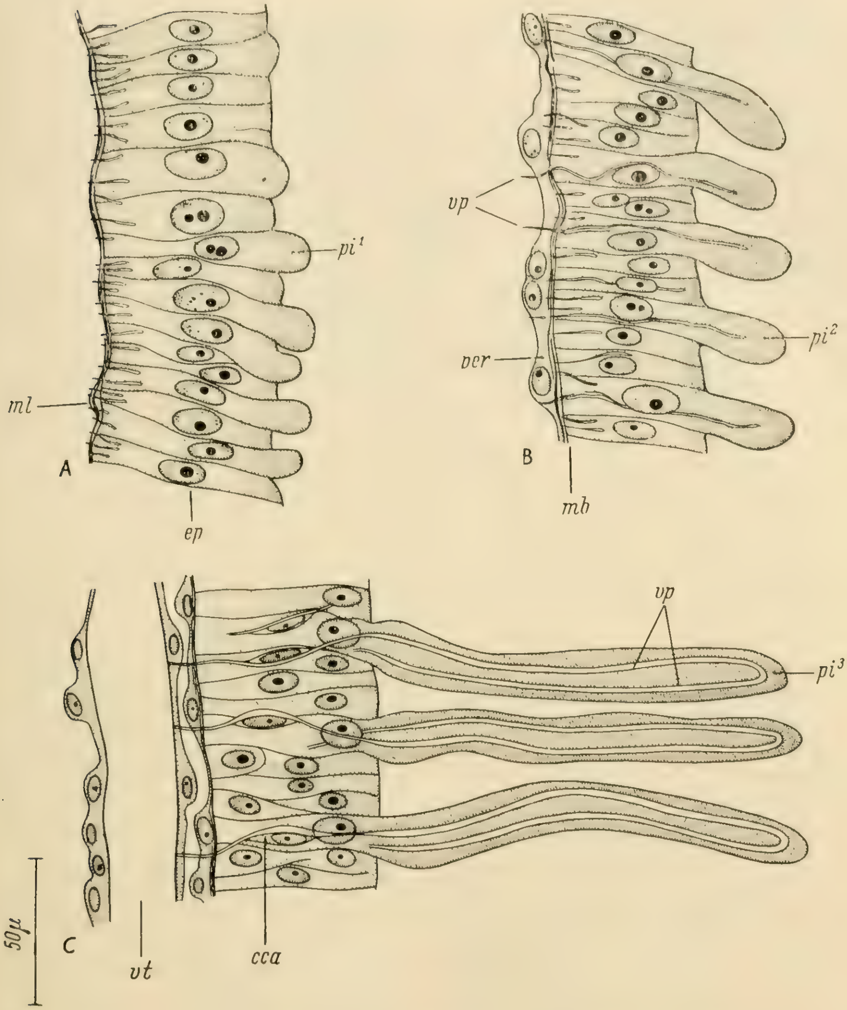


Fig. 54. Development of pinnules of *Lamellisabella zachsi*. Three successive stages (*A*, *B* and *C*) in longitudinal sections.
cca – cell adjacent to capillary; *ep* – epidermis of tentacle; *mb* – basement membrane; *ml* – longitudinal muscle fibre; *per* – peritoneum; pi^1, pi^2, pi^3 – successive stages of growth of the pinnules; *vp* – capillaries of pinnules; *vt* – vessel of tentacle. (After Ivanov, 1960a.)

Where they leave the base of the pinnule the capillaries turn in opposite directions to run between the cells of the epidermis and communicate with the corresponding tentacular vessels. Since the pinnules are usually arranged in dense serried ranks, the intracellular parts of the capillaries present a characteristic pattern in transverse sections (Figs. 53–55).

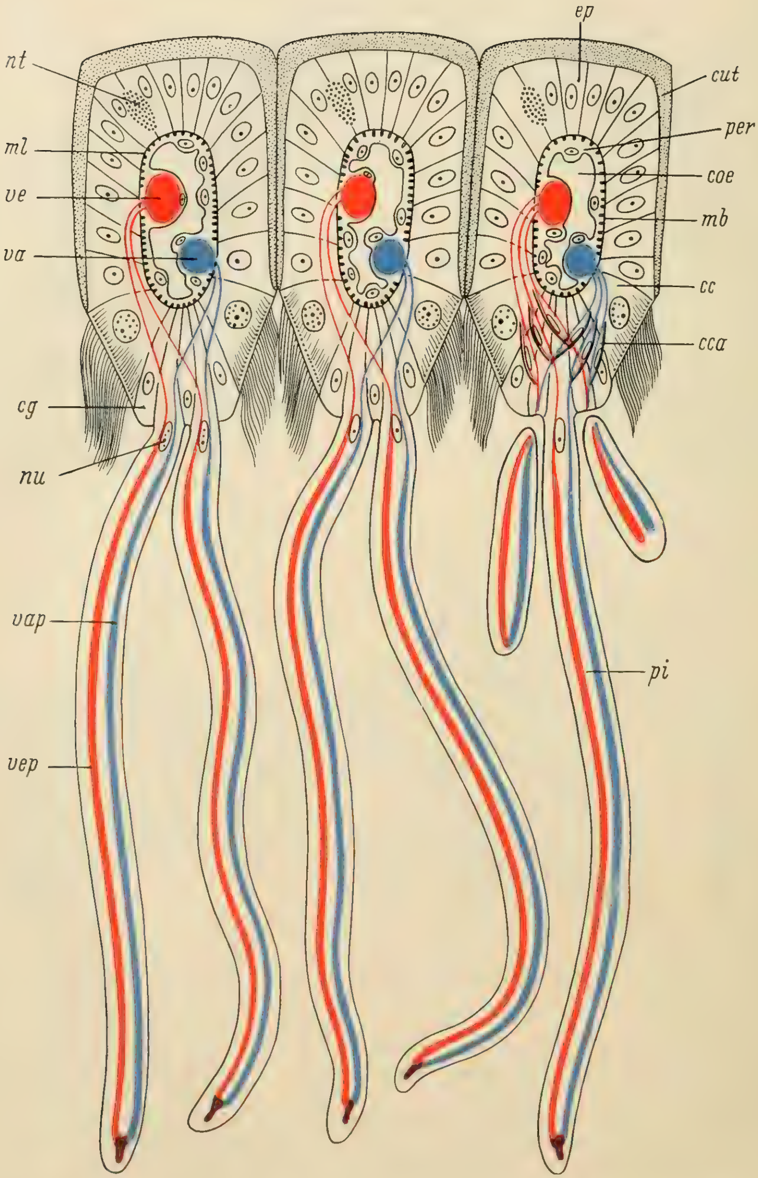


Fig. 55. Transverse section of three adjacent tentacles of *Lamellisabella zachsi*. Diagram reconstructed from several sections.
cc – ciliated cell; *cca* – cell alongside capillary; *cg* – gland cell; *coe* – coelomic canal; *cut* – cuticle; *ep* – epidermis; *mb* – basement membrane; *ml* – longitudinal muscle fibre; *nt* – tentacular nerve; *nu* – nucleus of pinnule; *per* – peritoneum; *pi* – pinnule; *va* – afferent vessel of tentacle; *vap* – afferent vessel of pinnule; *ve* – efferent vessel of tentacle; *vep* – efferent capillary of pinnule. (After Ivanov, 1955b.)

Thus in each capillary two parts may be distinguished—the long intracellular part inside the pinnule and the short intercellular section linking it to the corresponding tentacular vessel. It is interesting to observe that a single spindle-shaped cell with an elongated nucleus (Fig. 53, *cca*) is always found lying against the wall of the intercellular section.

The vessels of the tentacle itself are usually of different diameters because of the unequal content of blood. They lie asymmetrically on opposite sides of the tentacle, the afferent vessel nearer to the pinnular internal side of the tentacle and the efferent opposite, nearer to the epidermal nerve (Fig. 53). The thin intima of the vessels is closely bound to the basement membrane of the epidermis (Fig. 53).

In its histological structure the whole system of blood vessels of the tentacles presents a series of paradoxical features. Not only is the presence of intracellular vessels surprising but so also is the way in which they form a single unified system with vessels of a more normal type. For a complete understanding of these singular features it is necessary to study the ontogenetic development of the tentacles and pinnules.

It is clear from what has been written above that the pinnules represent specialized epidermal cells. Their origin, growth and differentiation are not limited to one period in postembryonic development but continue throughout the whole life history of the animal. On each tentacle there is a narrow zone where new pinnules are forming, lying between the short basal part (which always lacks pinnules) and the remaining part, which is furnished with fully formed pinnules. The earliest stages in pinnule formation can be studied in the proximal part of this zone. Distally they become progressively more differentiated until they are fully formed pinnules. A few successive stages in pinnule development are illustrated in Fig. 54.

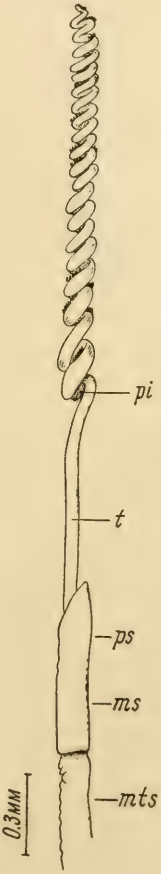


Fig. 56. Front part of the body of *Siboglinum timorense*. *ms* – mesosoma; *mts* – metasoma; *pi* – pinnule; *ps* – protosoma; *t* – tentacle. (After Caullery, 1944, with modifications.)

The function of the tentacular apparatus

The tentacles undoubtedly perform some function which is very important in the life of the animal. The structure of the tentacular crown varies enormously in different forms (p. 25), whilst all the remaining organization of the body is distinguished by its comparatively great constancy. The tentacular apparatus appears to be the key organ system in the evolution of pogonophores and gives, therefore, a whole series of important systematic pointers for the separation of families and genera.

In spite of all the variation in numbers of tentacles and in the morphology of the crown (p. 27), the tentacular apparatus presents a fundamental unity. Thus in all forms except *Siboglinum*, the tentacles lie parallel to one another enclosing [if there are enough of them] an intertentacular cavity. Even in the unitentaculate *Siboglinum* [and in the bitentaculate genera] an intertentacular cavity of a sort may be present, for in life, and often in fixed material too, when the tentacle is retracted into the tube it is wound into a tight corkscrew (Fig. 56). [In the bitentaculate genera the two tentacles are often found twined round each other in a multiple helix].

The form of the intertentacular cavity may vary. Thus in *Polybrachia* for the greater part of their length the tentacles lie parallel in concentric circles between which lie concentric cavities (Fig. 57). In *Lamellisabella* and *Spirobrachia*, which possess a more regular tentacular apparatus, the tentacles are

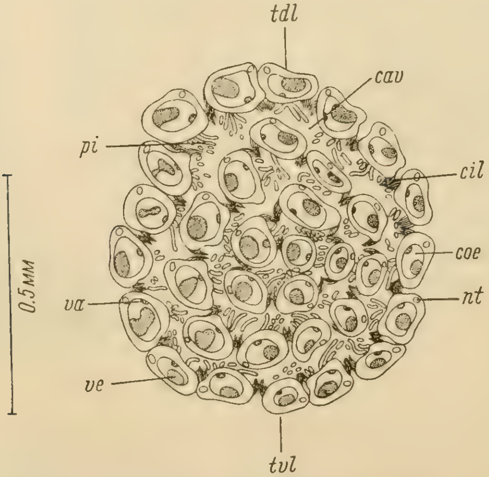


Fig. 57. Transverse section of tentacular crown of *Polybrachia annulata*.
cav – intertentacular cavity; *cil* – ciliated band; *coe* – coelomic canal of tentacle; *nt* – tentacular nerve; *pi* – pinnule; *tdl* – left dorsal tentacle; *tvl* – left ventral tentacle; *va* – afferent vessel; *ve* – efferent vessel. (After Ivanov, 1959b.)

joined together for most of their length thus forming a permanent intertentacular cavity. In the former genus it occupies the whole space inside the long cylindrical crown (Fig. 58), while in the latter it makes a sort of spiral cavity like the jam in a swiss roll (Fig. 59). An extraordinarily constant feature which must be stressed is that in all species the pinnules project into the intertentacular cavity where they form a densely interwoven tangle.

Where adjacent tentacles touch one another rows of ciliated cells are found (in the majority of species), and where the tentacles are fused into a tentacular plate (in *Lamellisabella* and *Spirobrachia*) these cells form longitudinal ciliated furrows (Figs. 57, 58, 59).

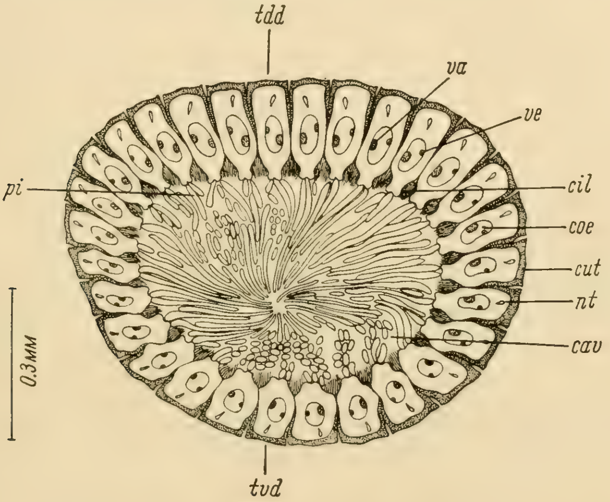


Fig. 58. Transverse section of tentacular crown of *Lamellisabella zachsi*.
cav – intertentacular cavity; *cil* – ciliated band; *coe* – coelomic canal; *cut* – cuticle; *nt* – tentacular nerve; *pi* – pinnule; *tdd* – right dorsal tentacle; *tvd* – right ventral tentacle; *va* – afferent vessel; *ve* – efferent vessel. (After Ivanov, 1955b.)

Respiration is undoubtedly one of the functions of the tentacular apparatus. In no other aquatic animal, indeed, do we see either such a finely divided respiratory organ or one with such a perfect blood system. To all appearances neither the pinnules themselves nor their intracellular vessels is indispensable for gaseous exchange, which may also be accomplished without their aid. It is manifest that the whole apparatus of the tentacles carries out yet another important function besides respiration.

We are thus led to the conclusion that the tentacular apparatus serves in addition for food collecting and digestion, and for absorption of the products of digestion (Ivanov, 1955b).

Being sedentary animals pogonophores can possess only a passive type of feeding adapted to filtration or collecting plankton and detritus. The ciliated bands along the sides of the tentacles suck water from the tip of the crown of tentacles down into the intertentacular cavity and thence out between the bases of the ventral tentacles, where there is always an aperture of some kind even in those species where the tentacles are joined together. It is possible that the microscopic organisms and particles of detritus floating in the water are trapped in the dense network of pinnules which, in this way, play the role of filter.

The possibility of phagocytic digestion by cells of the tentacles may be excluded because of the strong development of the cuticle. The characteristic picture of intracellular digestion, usually so easily demonstrable in sections, has been seen in neither the tentacles nor the pinnules. There thus remains only the absorption of dissolved food substances.

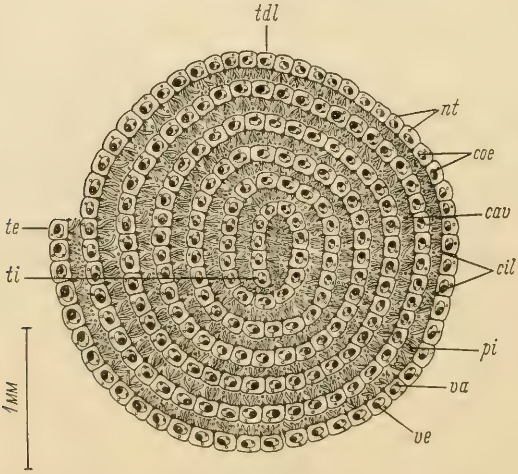


Fig. 59. Transverse section through tentacular crown of *Spirobrachia grandis*. *cav* – intertentacular cavity; *cil* – ciliated band; *coe* – coelomic canal of tentacle; *nt* – tentacular nerve; *pi* – pinnule; *tdl* – left dorsal tentacle; *te* – outermost marginal tentacle; *ti* – innermost marginal tentacle; *va* – afferent vessel; *ve* – efferent vessel. (After Ivanov, 1960a.)

Digestive enzymes probably act in the intertentacular cavity, secreted by the epidermis of the tentacles or perhaps by special gland cells which may sometimes be seen at the base of the pinnules. Digestion of the food possibly takes place in this same cavity. The dissolved food substances are then absorbed by the pinnules which play the role of a sort intestinal layer of villi and take these materials into the blood in their intracellular capillaries.

Thence they pass into the vessels of the tentacle and to the dorsal vessel to be distributed around the whole body.* Perhaps the filtration of water by the tentacular apparatus and the digestion of food do not proceed simultaneously; that is to say, first a supply of food is amassed and then the animal digests it with the tentacular crown withdrawn into the tube. This hypothesis, based for the moment only on the results of morphological studies, stands in need of experimental confirmation. It offers an explanation, however, for such enigmatic features as the complete absence of any gut despite clear evidence of a continual abundant intake of food, the peculiar structure of the tentacular apparatus, and the characteristic development of the blood system [which is exceptionally complex for so small an animal].

Thus the Pogonophora represent a unique and complete exception among free-living non-parasitic animals in lacking a gut and possessing external digestion.

In 1957 Jägersten pointed out the possibility of another solution to the problem of their feeding mechanism. In his opinion one cannot exclude the possibility that the tentacles absorb dissolved amino acids, which, perhaps, form in the surface layers of the mud by bacterial action. The acceptance of this hypothesis, however, leaves a whole series of peculiarities of the tentacular apparatus unexplained, and in particular the facts that the pinnules are always so located that they are turned towards the inside of the tentacular crown (or, in other words, they lie within the intertentacular cavity) and that an intertentacular cavity is formed by the fusion of one tentacle to the next in the highest forms. Moreover the presence of free amino acids in sea water in a quantity sufficient for the nutrition of animals by means of absorption is extremely doubtful.

[It is perhaps worth pointing out that Ivanov's and Jägersten's hypotheses are mutually exclusive, i.e. we cannot assume that pogonophores might supplement a solid diet by the absorption of dissolved food substances. For Jägersten's hypothesis demands that food be absorbed while the tentacular crown is extended, while Ivanov's demands a cycle of activity in which absorption takes place in the retracted crown, the expanded crown serving only for collecting food. It cannot be doubted that the basic metabolism of Pogonophora is high and that they must have a high rate of food capture. If Ivanov's hypothesis is correct, therefore, the ciliary current down through the intertentacular cavity must have a high velocity. Under such conditions secretion of digestive enzymes into the cavity would be useless, particularly

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* N. G. Khlopin has remarked that the Pogonophora may be designated "Brachiotropha" (Gr. *βρᾱχῑων*—arm, *τροφός*—feeding).

at the low temperature at which pogonophores live, for they would be swept away before they could operate. It becomes necessary, therefore, to postulate that digestion and absorption of the trapped food take place at a different time and under conditions when the tentacles are enfolded to surround an almost closed cavity through which little or no water is flowing. Now on Jägersten's hypothesis absorption must take place when the tentacles are open to the water and the cilia are maintaining a strong current. The two hypotheses cannot then be complementary and Ockham's razor would demand the abandonment of Jägersten's hypothesis, at least for the time being.

There remains Ivanov's hypothesis. This clearly accounts for all the anatomical peculiarities of the multitentaculate forms, but what of the unitentaculate *Siboglinum*, or, indeed, of the bitentaculate genera? Not enough is known of the latter, but it is worth spending a little time examining the former.

An intertentacular cavity is formed in *Siboglinum* by the tight helical coiling of the single tentacle, leaving a cavity down the centre. We can imagine such a coiled tentacle protruding from the mouth of the tube with a ciliary current maintained through it, swirling round amongst the pinnules where these are present, for the cilia (where present) certainly beat along the tentacle and hence must maintain a spiral water current. But the muscular action needed to maintain the coil of the tentacle unsupported by the tube is difficult to envisage. Many of the smaller species of *Siboglinum*, moreover, lack pinnules to trap food particles in the way assumed by Ivanov. It is perhaps important in this context that it is only in species of this one genus that pinnules are known to be absent. Should we not then look to another, possibly supplementary, mode of feeding in *Siboglinum*?

Kirkegaard (1961) has attempted to observe feeding in living *S. ekmani* maintained at low temperatures in the laboratory. He found that they were sensitive to light and remained withdrawn in the tube when he attempted visual observations. But like many nocturnal marine animals they are insensitive to red light and although observations of such a fine object as the tentacle of *S. ekmani* is difficult in dim red light it is nevertheless possible. Under such conditions, in healthy animals the tentacle may be seen protruding from the tube, not coiled as Ivanov's hypothesis would demand but extended and questing over the surface of the surrounding substratum like the arm of a blind man groping for food. On at least two occasions an animal has been seen to pick up a particle, perhaps a rhizopod or perhaps a particle of detritus, coil the tentacle around it and retreat into the tube.

When a living *Siboglinum* is examined under the microscope it is not uncommon to see parts of the tentacle coiled into a tight helix much smaller than the diameter of the tube, while another portion is bloated with red blood and occupies the whole width of the tube. I would suggest that such a region represents a part of the tentacle where digestion of a trapped food particle is taking place, digestion, that is, of a food particle picked up by a prehensile tentacle, though in all fairness it should be added that Dr. A. J. Southward believes that the swollen parts represent damaged portions of the tentacle.—D.B.C.]

CHAPTER 9

The Reproductive System

All the information we have so far amassed about the organization of the Pogonophora suggests that they possess only sexual means of reproduction. The supposed presence of external budding in *Siboglinum* (Caullery, 1944) and the more recent supposition of internal budding (Jägersten, 1956) have received no confirmation. The "internal buds" reported by Jägersten in *S. ekmani* appear to be artifacts resulting from one part of the trunk contracting on fixation and becoming enveloped by another part rolling around it.

The Pogonophora have separate sexes but there is no pronounced external sexual dimorphism. The sexes are distinguished externally only by the position of the genital aperture (p. 20).

The most characteristic features of the reproductive system of the Pogonophora are as follows:

1. They possess a single pair of gonads lying in the metasomal segment—in the hind half of the trunk in the male and in the front half in the female.
2. The single pair of metasomal coelomoducts are transformed into gonoducts (Ivanov, 1955a).

The male reproductive system

The male reproductive organs have been studied in *Polybrachia*, *Lamellisabella* and, in part, in *Siboglinum* (Ivanov, 1958a). They consist of a pair of seminiferous sacs or testes and a pair of tubular spermducts.

The testes or sperm sacs

The testes stretch from the level of the zone of thickened papillae to the hind end of the body. They consist of rather broad canals immediately adjoining the dorsal part of the mesentery, which in places forms, with the dorsal vessel, a vertical partition between them (Fig. 60). The testes are separated from the ventral vessel by a considerable distance, but anteriorly they are so large that they extend the whole distance between the dorsal and the ventral body walls.

The walls of these sacs consist of a ciliated epithelium which appears to be a continuation of the splanchnopleura that covers the mesentery and the dorsal vessel. Correspondingly the basement membrane too of the wall of the

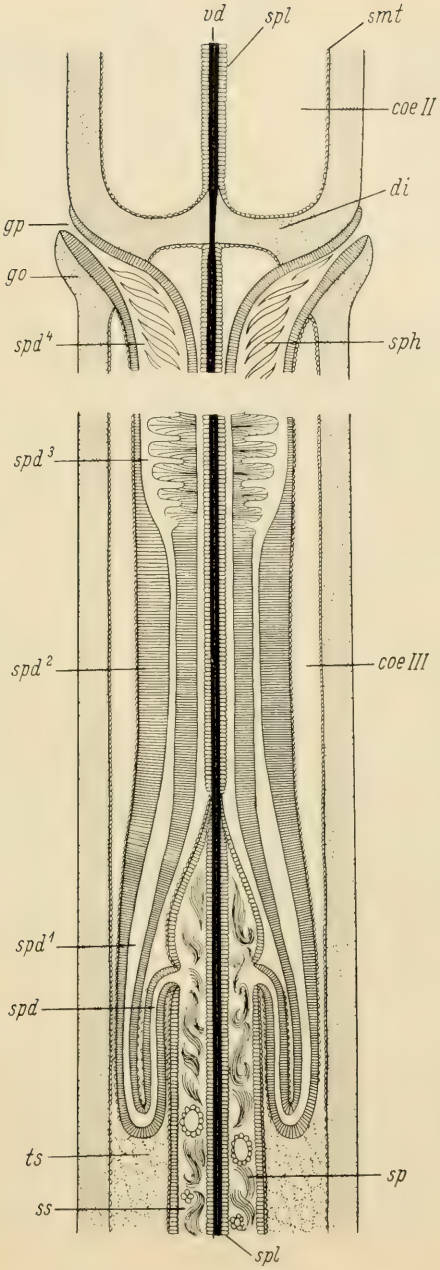

Fig. 60. Diagram of the male reproductive system of *Lamellisabella*.
coe II – mesocoele; *coe III* – metacoele; *di* – muscular diaphragm; *go* – genital papilla; *gp* – genital aperture; *smt* – somatopleura; *sp* – sperm; *spd* – spermduct; spd^1, spd^2, spd^3, spd^4 – parts of the sperm duct with distinctive histological structure; *sph* – spermatophore; *spl* – splanchnopleura; *ss* – sperm sac; *ts* – spongy coelomic tissue; *vd* – dorsal blood vessel. (After Ivanov, 1958a.)

sac is continuous with the membrane of the mesentery and with the intima of the blood vessel. Ventrally the partition between the sacs preserves the full nature of a mesentery, with peritoneal cells amongst which may be seen a number of groups of excretory cells and of cytoplasmic cell bodies of the myocytes of the dorsal vessel. Externally the sacs are clothed with a very thin layer of circular muscle fibres and peritoneal cells (Fig. 61).

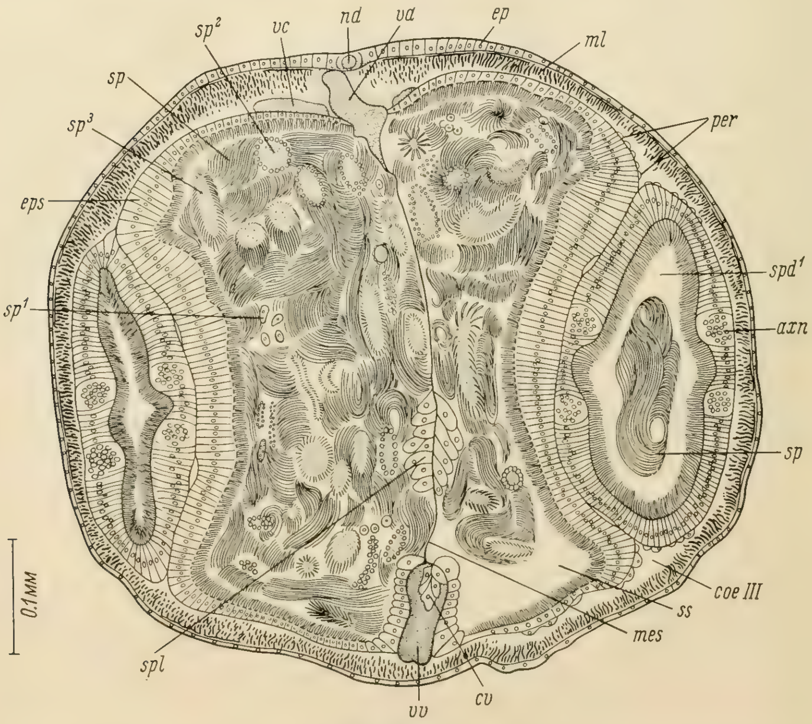

Fig. 61. Transverse section of a male *Lamellisabella zachsi* at the level of the front end of the sperm sacs.
axn – longitudinal ridge, rich in nuclei, in wall of spermduct; *coe III* – metacoele; *cv* – corpus cardiacum; *ep* – epidermis; *eps* – ciliated epithelium of sperm sac; *mes* – mesentery; *ml* – longitudinal muscle layer; *nd* – dorsal nerve trunk; *per* – peritoneum; *sp* – sperm; sp^1, sp^2, sp^3 – successive stages in spermatogenesis; spd^1 – spermduct; *spl* – excretory cell of the splanchnopleura; *ss* – sperm sac; *vc* – commissural vessel; *vd* – dorsal vessel; *vv* – ventral vessel. (After Ivanov, 1958a.)

The ciliated epithelium, however, is well developed only in the anterior part of the testis, where it is formed of cylindrical cells. A little farther back in each sac only narrow longitudinal ciliated ribbons remain, located on the latero-ventral walls; the rest of the epithelium has lost its cilia and comes to

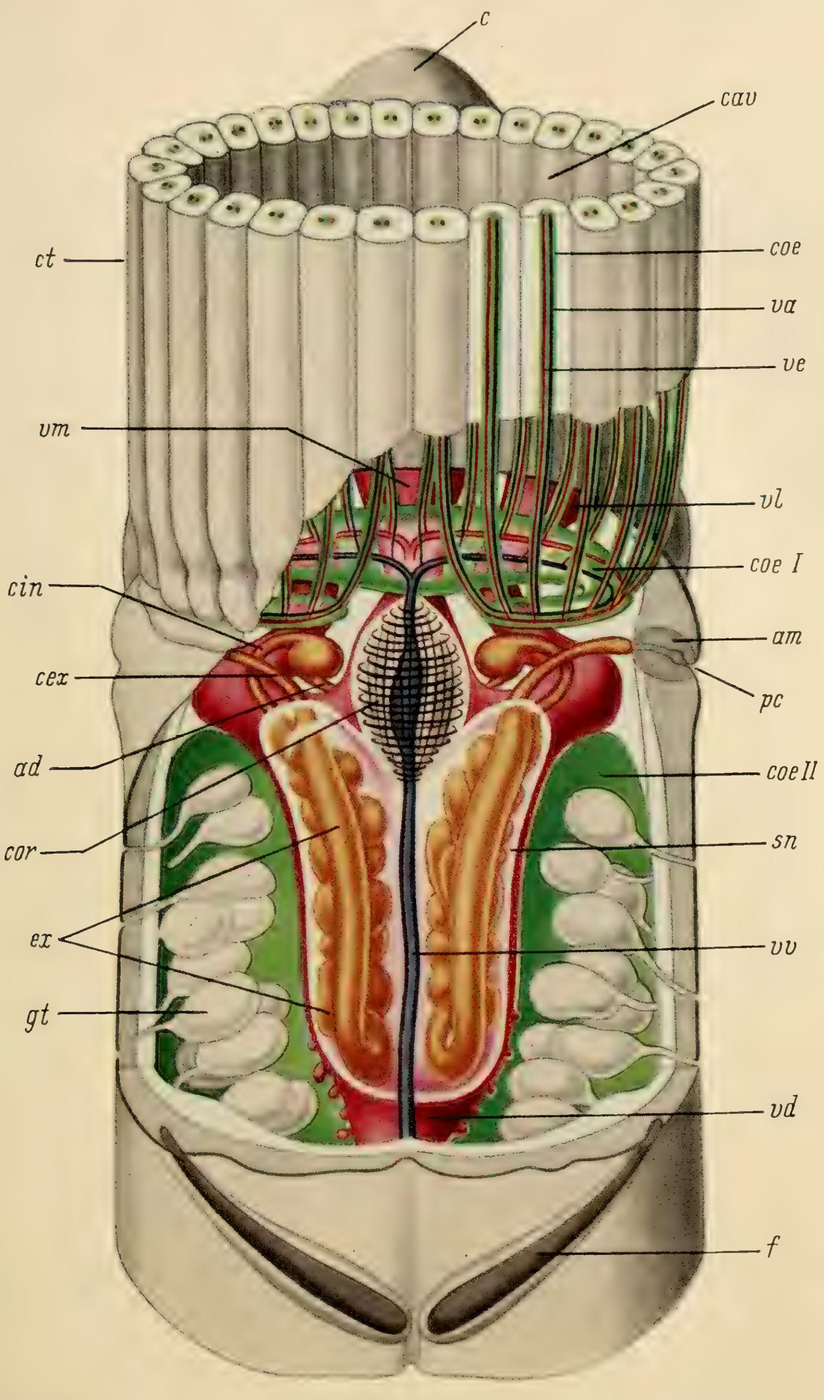

Plate III. Stereogram of the structure of the front end of the body of *Lamellisabella zachsi*, in ventral view.

ad – anastomosing canal of the coelomoducts; *am* – ampulla of coelomoduct; *c* – tip of cephalic lobe; *cav* – intertentacular cavity; *cex* – distal canal of coelomoduct; *cin* – proximal canal of coelomoduct; *coe* – coelomic canal of tentacle; *coe I* – protocoele; *coe II* – mesocoele; *cor* – heart; *ct* – tentacular crown; *ex* – excretory portion of coelomoduct; *f* – keel of bridle; *gt* – globular gland; *pc* – external pore of coelomoduct; *sn* – "renal sac" – an invagination of the ventral wall of the dorsal vessel in which lie the excretory portions of the coelomoducts; *va* – afferent vessel of tentacle; *vd* – dorsal vessel; *ve* – efferent vessel of tentacle; *vl* – lateral cephalic vessel; *vm* – median cephalic vessel; *vv* – ventral vessel. (After Ivanov, 1960a.)

consist of a rather spongy layer of large transparent cells (Fig. 45). Finally, in the postannular region of the sperm sac this layer is hardly developed at all and often only the ciliated bands remain. These consist of large well-differentiated cells with long cilia (Fig. 46).

The lumen of the sperm sac contains a fluid filled with floating masses of male germ cells. The latter are found in all stages of spermatogenesis from spermatogonia to ripe sperm and form characteristic morulae or packets consisting of cells all at the same stage of development (Fig. 62). Amongst them one sometimes comes across comparatively large rounded cells which appear to be gonocytes. One of the succeeding stages is represented by conjoined groups of four cells (Fig. 62*A*). Their further multiplication produces characteristic multicellular spermatospheres or morulae. Part of the protoplasm of the cells is extruded into the centre of the morula in one common

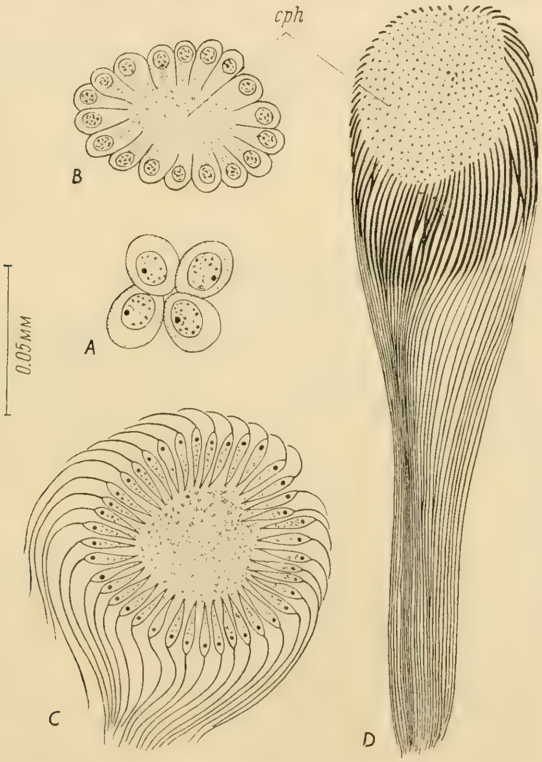

Fig. 62. Successive stages in spermatogenesis of *Lamellisabella zachsi*. *A* – 4-cell stage; *B* – spermatocyte morula; *C* – spermatid mass; *D* – mass of sperm.
cph – cytophore. (After Ivanov, 1958a.)

enucleate mass—the cytophore; the cells come to lie on the surface of this cytophore into which their cytoplasm seems to merge (Fig. 62*B*). At the spermatid stage the germ cells are still joined into morulae or spermatospheres (Fig. 62*C*). A short time after the sperm are formed they become detached from the cytophore. The ripe sperm are filiform and consist of thread-like deeply staining heads and long tails (Fig. 62*D*).

Sometimes early stages of spermatogenesis appear to predominate in the anterior part of the sperm sacs, though usually all stages are mixed together and may be encountered at all levels. It remains quite unknown whether compact groups of gonocytes forming some sort of germinal epithelium are to be found in some place on the walls of the anterior part of the sacs.

Thus it is clear that these organs are true sperm sacs. In a general way they recall the sperm sacs of oligochaetes and leeches and, as in these annelids, they represent specialized portions of the coelom; their walls appear to be a variety of coelomic epithelium. The general nature of the fluid filling the cavity, with the characteristic spermatospheres or morulae, also recalls the contents of the sperm sacs in oligochaetes and leeches.

The ciliated bands on the walls of the sperm sacs apparently serve to circulate the fluid containing the germ cells, and the cilia covering the sides of the anterior part of the sperm sac presumably serve also to propel the clumps of ripe sperm into the spermducts. The presence of a common boundary between the sperm sacs and the dorsal blood vessel ensures a richly sufficient supply of nutriment for the developing germ cells.

The spermducts

The front end of the sperm sac communicates with the corresponding spermduct which first runs backwards to form a loop before turning forwards alongside the mesentery to the border between the mesosoma and the metasoma where it turns down onto the ventral side to open to the exterior through the genital papilla of that side (Figs. 9, 15, 60). The spermducts are thick-walled epithelial tubes, furnished externally with a thin layer of muscle fibres and peritoneal epithelium, and attached to the ventral body wall by a delicate mesentery (Fig. 64). The histological structure of the walls varies considerably in the different regions. Thus in *Lamellisabella zachsi*, near the point of attachment to the sperm sac the epithelium of the spermduct consists of tall ciliated cells which are remarkable for details of the structure of the ciliary roots. The root-threads run from the basal granules of the cilia and form, as a rule, a characteristic cone, gathered together into a rather stout bundle which extends to the basal end of the cell where it diverges once more into separate threads. These then run out into a tangled complex of fine filaments. The impression is thus created of a continuous net-like layer at the base of the epithelium uniting the root-threads of separate cells. A little farther forward the ciliated epithelium changes on the inside wall of each spermduct to form a deep longitudinal furrow along whose base large gland cells are exposed. Opposite this furrow, on the other wall of the spermduct, there is a low longitudinal keel. A little farther forward again the furrow broadens out into a longitudinal depression bounded at the sides by ridges and similar ridges form on the opposite wall of the spermduct. The ridges are peculiar structures: a rather dense tract of small cells without clear cell boundaries lies within each ridge as a sort of syncytium, so that in transverse section these tracts look like compact heaps of nuclei (Fig. 61).

The middle part of the spermduct is distinguished by the very thick walls and correspondingly narrow lumen (Fig. 60). The ciliary band remains, but

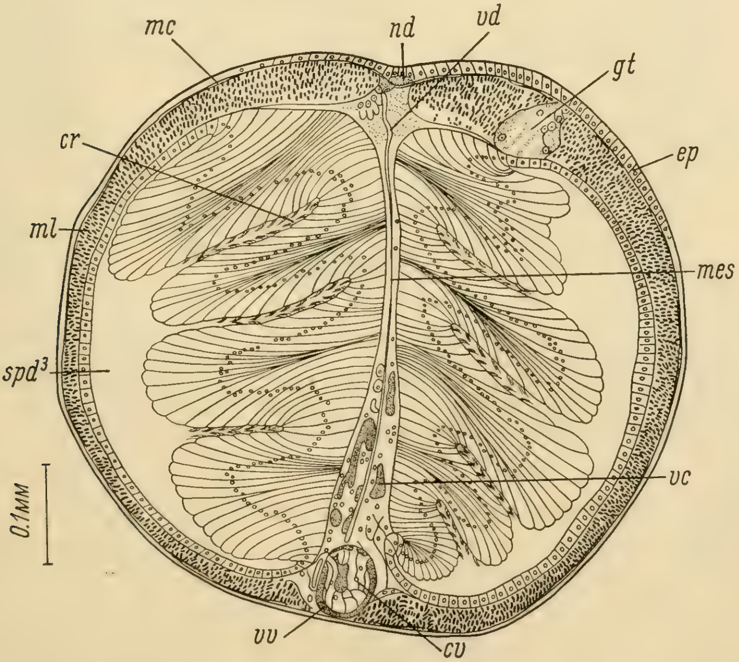

Fig. 63. Transverse section of a male *Lamellisabella zachsi* a little behind the metameric part of the metasoma.

cr – crypt in spermduct wall; *cv* – corpus cardiacum; *ep* – epidermis; *gt* – pyriform gland; *mc* – circular muscle layer; *mes* – mesentery; *ml* – longitudinal muscle layer; *nd* – dorsal nerve trunk; *spd*³ – spermduct; *vc* – commissural vessel; *vd* – dorsal vessel; *vv* – ventral vessel. (After Ivanov, 1958a.)

the cells are full of secretion. Still farther forward the lateral part of the wall of the spermduct thins out again and loses its cilia, then the inner wall turns inwards, becomes thicker again and glandular crypts develop on whose sides little bunches of cilia may be seen (Fig. 63). Finally, the long anterior or distal part of the spermduct, lying in the metameric region of the metasoma, is lined with very tall ciliated cells (Fig. 64).

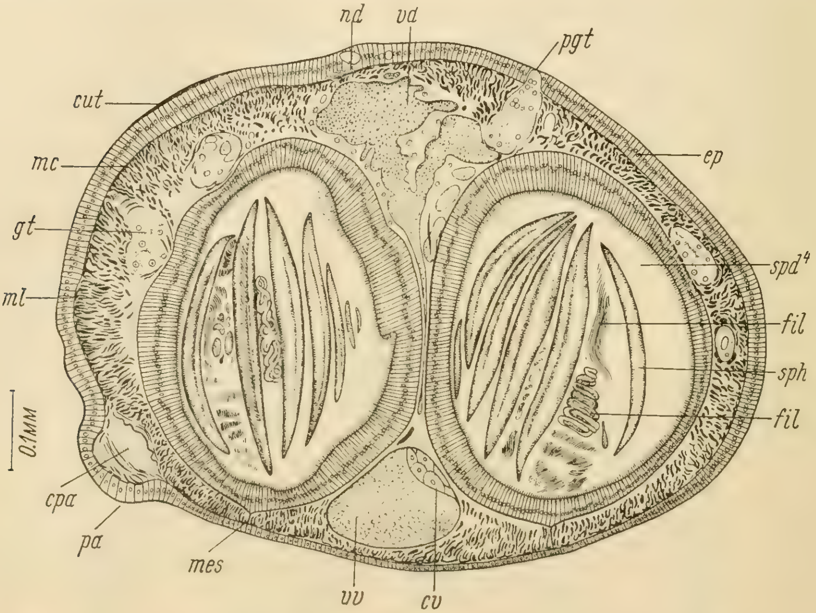

Fig. 64. Transverse section of a male *Lamellisabella zachsi* in the metameric region of the metasoma. *cpa* – coelom of adhesive papilla; *cut* – cuticle; *cv* – corpus cardiacum; *ep* – epidermis; *fil* –filaments of spermatophores; *gt* – pyriform gland; *mc* – circular muscle fibre; *mes* – mesentery of spermduct; *ml* – longitudinal muscle fibre; *nd* – dorsal nerve trunk; *pa* – papilla; *pgt* – pore of pyriform gland; *spd*^{4} – spermduct; *sph* – spermatophore; *vd* – dorsal blood vessel; *vv* – ventral vessel. (After Ivanov, 1958a.)

The spermatophores are formed in the proximal parts of the spermduct. The envelope of the spermatophore is undoubtedly produced by the secretory activity of the gland cells of the epithelium. The fully moulded spermatophores lie in the distal part of the spermduct (Fig. 64), arranged in a single row in each spermduct parallel to each other and all pointing the same way—outwards and forwards (Fig. 60). Alongside each spermatophore lies its attached filament.

The lumen of the spermduct represents a ciliated canal by means of which a part of the coelom communicates with the exterior. It may thus fairly be accounted a coelomoduct.

The spermatophores

The spermatophores represent thin-walled elongated packets containing the sperm. In the Athecanephria they are spindle- or cigar-shaped (Fig. 65*A*) and in the Thecanephria they are leaf-shaped (Fig. 65*B*) (Ivanov, 1957a). Their size varies in rough accord with the size of the animal. Thus in *Siboglinum minutum* the spermatophores are no more than 120μ long, while in *Spirobrachia grandis* they reach 2·5 mm. The shape and size of the spermatophores make good specific distinctions (Ivanov, 1952, 1957a).

A long thin filament is attached to one end of the envelope of the spermatophore and folded up into a tight skein which lies on the surface of the spermatophore (Fig. 65). It seems possible that the filament unwinds when the spermatophore is released into the water and serves as a flotation device, or it may become entangled in the tube of the female. The walls of the spermatophore contain much polysaccharide.

[It seems to me unlikely that either of the suggestions put forward by Ivanov for the function of the filament of the spermatophore represents the

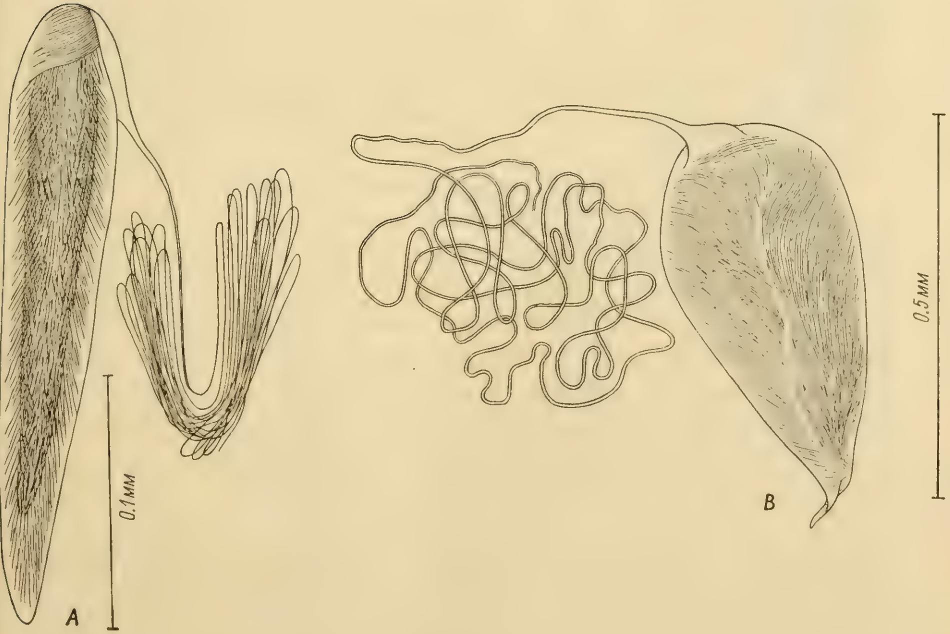

Fig. 65. Spermatophores. *A* – *Siboglinum fedotovi*; *B* – *Lamellisabella johanssoni.* (After Ivanov, 1957a.)

facts. We know that fertilization of the egg takes place within the tube of the female (p. 103); it is not an external fertilization. Now both Ivanov's suggestions take it for granted that the spermatophores are released into the water to be carried willy-nilly by the currents until they chance to meet a female. But this is almost unknown in marine animals. Fertilization by means of water-borne sperm is common enough, but not when the sperm are organized into spermatophores. Water-borne fertilization entails a great wastage of sperm and seems only possible if the sperm are released singly into the water, to drift about like grass pollen in the air. The organization of the sperm into spermatophores in other marine animals can be taken as an indication that the sperm is actively transferred in some way, usually by some form of copulation. The spermatophores of Pogonophora are exceptionally large—usually longer than the animal is wide—and correspondingly few in number. It is all the more likely, therefore, that they are actively transferred to the female rather than discharged into the water to drift in the plankton. We know that pogonophores often, or indeed usually, occur in dense stands: Hartman (1961) has recorded over 100 in 0.5 m^2 and Southward (1958) suggests that they may be dominant elements in the fauna in places off the English coast. I would suggest, therefore, that the spermatophores are transferred to the female by an adjacent male by some manipulation of the tentacles, perhaps in a way recalling the copulation of barnacles, and that the filament plays some part in this active transfer—D.B.C.]

The female reproductive system

The female reproductive system has been studied in *Polybrachia*, *Lamellisabella*, *Spirobrachia* and *Siboglinum* (Ivanov, 1958a).

The pair of long ovaries lie in the coelom in the first half of the metasoma and their front ends are attached to the mesentery immediately behind the muscular diaphragm, while the hind ends reach to the level of the zone of thickened papillae. At this same level the oviducts begin. They are not attached in any way to the ovaries. The internal or proximal end of the oviduct lies a little in front of the external genital aperture (Fig. 66).

The ovaries

In small immature females the gonocytes appear immediately behind the diaphragm on the lateral surfaces of the dorsal vessel under the peritoneum which they push outwards to bulge into the coelom (Fig. 67). These gonadal primordia then begin to grow fast, plunging farther and farther into the body cavity on each side of the mesentery until they have finally become transformed into a pair of long sausage-like outgrowths stretching far back from their point of attachment near the diaphragm. Simultaneously, the peritoneal cells on their surface multiply at the same rate and so come to form the ovarian walls. Longitudinal blood vessels run inside these walls from the region of attachment of the ovaries and supply the growing germ cells with food substances and oxygen (Figs. 33, 68).

The peritoneal epithelium which covers the surface of the ovary consists mainly of small flat cells. Under them lies a thin basement membrane continuous with the intima of the ovarian blood vessels. The inner surface of the membrane lacks cellular elements, but the blood vessels are covered on all sides with tall cells, sometimes arranged in more than one layer (Fig. 68).

I have already remarked that the number of blood vessels in each ovary varies in different species, in accordance with the size of the animal, from two to five. In *Siboglinum* and *Oligobrachia* one vessel runs along the dorsal side and one along the ventral side of the ovary (Fig. 33). In *Polybrachia annulata* and *Lamellisabella zachsi* a third latero-ventral

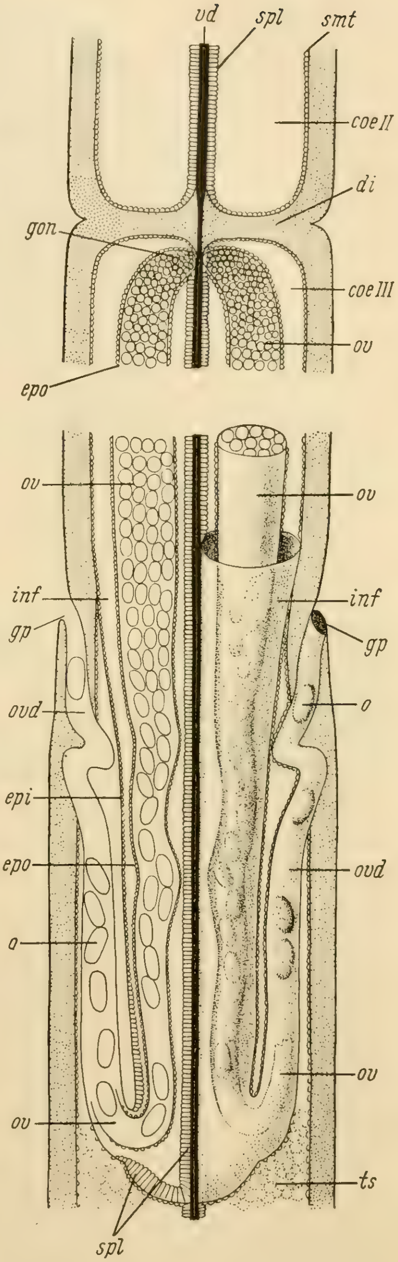

Fig. 66. Diagram of the female reproductive system of Pogonophora. On the right side of the figure the funnel and the oviduct are shown stereographically. *coe II* – mesocoele; *coe III* – metacoele; *di* – muscular diaphragm; *epi* – wall of funnel of coelomoduct; *epo* – peritoneal wall of ovary; *gon* – ocgonia; *gp* – genital aperture; *inf* – funnel of coelomoduct; *o* – egg; *ov* – ovary; *ovd* – oviduct; *smt* – somatopleura; *spl* – splanchnopleura; *ts* – spongy coelomic tissue; *vd* – dorsal blood vessel. (After Ivanov, 1958a.)

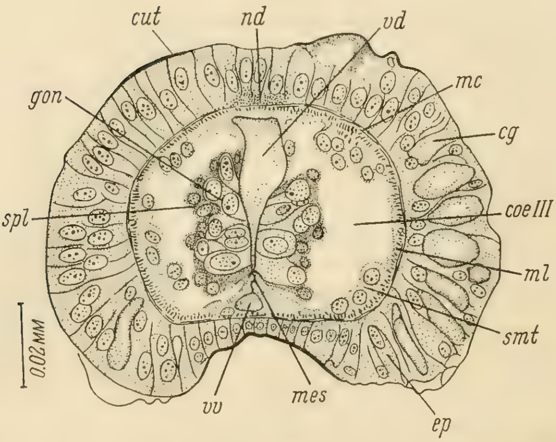

Fig. 67. Transverse section of a young female *Siboglinum caulleryi* a little behind the muscular diaphragm.
cg – gland cell of epidermis; *coe III* – coelom of metasoma; *cut* – cuticle; *ep* – epidermis; *gon* – oogonia; *mc* – circular muscle fibre; *mes* – mesentery; *ml* – longitudinal muscle fibre; *nd* – dorsal nerve trunk; *smt* – somatopleura; *spl* – splanchnopleura; *vd* – dorsal blood vessel; *vv* – ventral vessel. (After Ivanov, 1958a.)

vessel is added to these two (Fig. 68). In *Spirobrachia grandis*, finally, there are additional vessels in the lateral and medial walls, so that each ovary in this species has five vessels.

The cavity of the ovary is usually filled with tightly packed germ cells (Fig. 66) and only in the hind part do the large oocytes come to lie more or less free. The smallest oocytes are found in a particularly compact anterior region of the gonad. As we move backwards along the ovary we find that the germ cells increase in size and their cytoplasm becomes enriched with yellowish granules and droplets of yolk and oil. The largest oocytes and ripe eggs are found in the hindmost part of the gonad (Fig. 66).

Pogonophora appear to lack follicle cells.

The hind end of the ovary lies within the broad funnel of the proximal end of the oviduct or even penetrates right into the oviduct proper. In the mature female the wall of the ovary splits at this point and the ripe eggs tumble out into the lumen of the genital duct (Fig. 66).

The oviduct

As we have seen, there is no direct connexion between the ovaries and their ducts. The latter represent a pair of epithelial U-shaped coelomoducts. The internal broader limb of each of these tubes opens out into a funnel and may

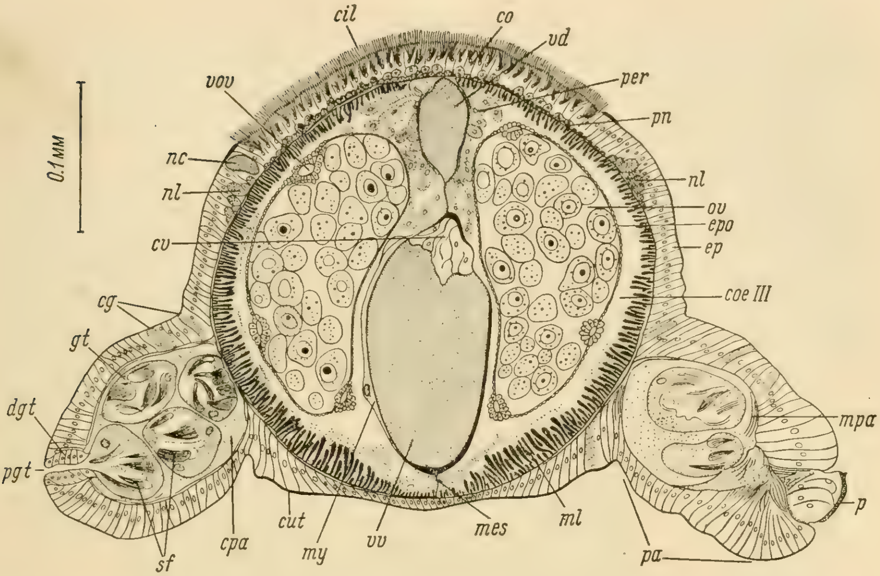

Fig. 68. Transverse section of a female *Polybrachia annulata* in the metameric region of the metasoma.
cg – gland cell of epidermis; *cil* – cilia; *co* – dorsal ciliated band; *coe III* – metacoele; *cpa* – coelom of adhesive papilla; *cv* – corpus cardiacum; *cut* – cuticle; *dgt* – duct of pyriform gland; *ep* – epidermis; *epo* – epithelial wall of ovary; *gt* – pyriform gland; *mes* – mesentery; *ml* – longitudinal muscle layer; *mpa* – muscle layer of papilla; *my* – myocyte; *nc* – neurocord (giant nerve fibre); *nl* – thickened marginal region of dorsal nerve plate; *ov* – ovary; *p* – cuticular plaque; *pa* – papilla; *per* – peritoneum; *pgt* – pore of pyriform gland; *pn* – dorsal nerve plate; *sf* – lamellar secretion of pyriform gland; *vd* – dorsal blood vessel; *vov* – ovarian vessels; *vv* – ventral vessel. (After Ivanov, 1958a.)

perhaps best be called the ovifunnel or ovarian funnel; the external narrower limb forms the oviduct proper. The funnels fuse with the two sides of the mesentery, which thus comes to form their common median wall, with the dorsal vessel pushing between them from above. The anterior lip of each funnel fuses with the body wall and the hind end is continuous with the oviduct, which runs forward from the hind end of the funnel (after making a U-bend) between the body wall and the funnel itself. Then it penetrates into the longitudinal muscle layer of the dermis and runs for a short distance embedded in this layer before it finally opens through the latero-ventral genital pore. This is all shown diagrammatically in Fig. 66.

The walls of the funnel consist of a low unciliated epithelium, which becomes considerably thicker towards the hind end of the organ, especially towards the point of union with the oviduct, and takes on a glandular nature.

The epithelium lies on a delicate basement membrane, and sparse muscle fibres are scattered on the outside of the funnel. Where the funnel takes up the whole width of the coelom its external surface, contiguous with the body wall, lacks peritoneal epithelium, but where it becomes narrower and ceases to occupy the whole cavity it is covered externally with a peritoneum. The mesentery preserves its characteristic cellular elements in the region of the funnels and rows of excretory cells are especially well developed here together with folds of splanchnopleura containing small lateral blood vessels (Fig. 69).

The walls of the oviducts are very thin but rather rich in circular muscle fibres. They consist of a very low epithelium which grows taller only near the external genital aperture (Fig. 69).

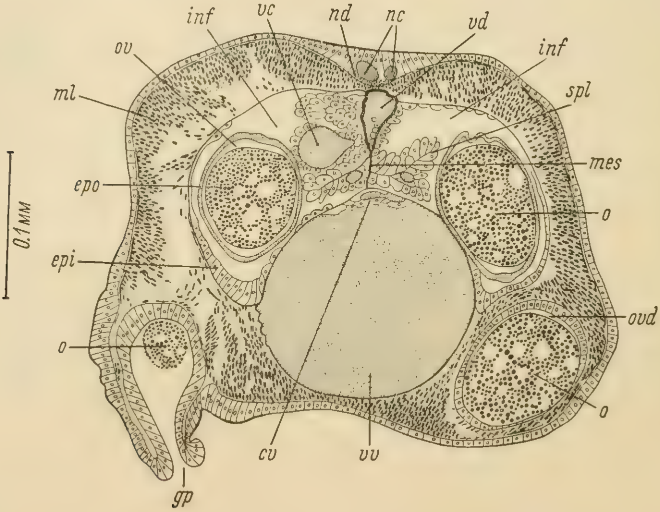

Fig. 69. Transverse section of a female *Polybrachia annulata* at the level of the genital apertures. *cv* – corpus cardiacum; *epi* – epithelium of funnel; *epo* – peritoneal wall of ovary; *gp* – genital aperture; *inf* – lumen of funnel of coelomoduct; *mes* – mesentery; *ml* – longitudinal musculature; *nc* – neurocord (giant nerve fibre); *nd* – dorsal nerve trunk; *o* – eggs; *ov* – ovary; *ovd* – oviduct; *spl* – splanchnopleura; *vc* – commissural blood vessel; *vd* – dorsal vessel; *vv* – ventral vessel. (After Ivanov, 1958a.)

CHAPTER 10

Embryological Development

At the time of writing only two publications have presented original observations on the embryology of Pogonophora. In 1957 I wrote an account of the embryological stages of *Siboglinum caulleryi* with a few observations on *Oligobrachia dogieli* (Ivanov, 1957b). Almost simultaneously the work of Jägersten appeared, in which he gave an account of the late embryo of a species of *Siboglinum*. Embryos of another species were also found in 1957 by E. C. Southward and A. J. Southward, who managed to observe them alive for a short time. Unfortunately the results of these observations remain unpublished. This chapter therefore is based largely upon my own observations, many of which must perforce be of a preliminary nature and will probably be corrected and extended in the future.

The clutch of eggs

A female pogonophore lays her eggs in the anterior part of her own tube, in whose protection they remain throughout embryological development. Clutches of eggs have been studied in four species of *Siboglinum*, including *S. caulleryi* and *S. inerme*, and in *Oligobrachia dogieli* and *Lamellisabella zachsi*, i.e. in representatives of both orders. In *Siboglinum caulleryi* a clutch consists of 10–30 eggs lying in a single row one behind the other in the tube in front of the animal which has laid them (Fig. 70). Sometimes the tentacle of the female may be seen twisting between the eggs. In *Oligobrachia dogieli* a clutch of 42 eggs was once observed, also disposed in a single row, and a second clutch consisted of 45 embryos.

The eggs lie in the tube one behind the other and are not stuck together by any form of cement. In those species in which the eggs are elongated (*Siboglinum*) they are all orientated in the same way in the tube—front

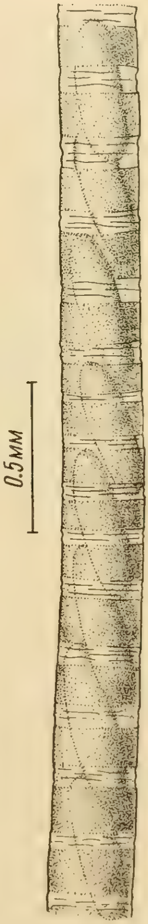

Fig. 70. Eggs of *Siboglinum caulleryi*, lying in the tube. (After Ivanov, 1957b.)

end up. So far as may be judged from *Siboglinum caulleryi* and *Oligobrachia dogieli* the eggs of a single clutch develop synchronously, from which we may conclude that they are all laid at once, not as a succession.

We do not know how long the eggs take to develop. It is obvious, however, that the female must remain within the tube for the whole period until hatching, and it is doubtful, to say the least, whether she can feed during this time. [It is perhaps worth pointing out that the total reproductive capacity of one female, as judged by the number of oocytes in the ovary, is far greater than a single clutch of eggs, so that we cannot seriously advance the hypothesis that the female reproduces once and then dies, as happens in many marine animals.]

The egg

The majority of Pogonophora (except *Siboglinum*) possess round or broadly elliptical eggs (Fig. 71*A*). The egg is always very rich in yolk and after fertilization has a delicate soft fertilization membrane.

The egg of *Siboglinum* is much elongated, reaching 650μ in length, round at the ends and very slightly curved. One end of the egg is clearer,

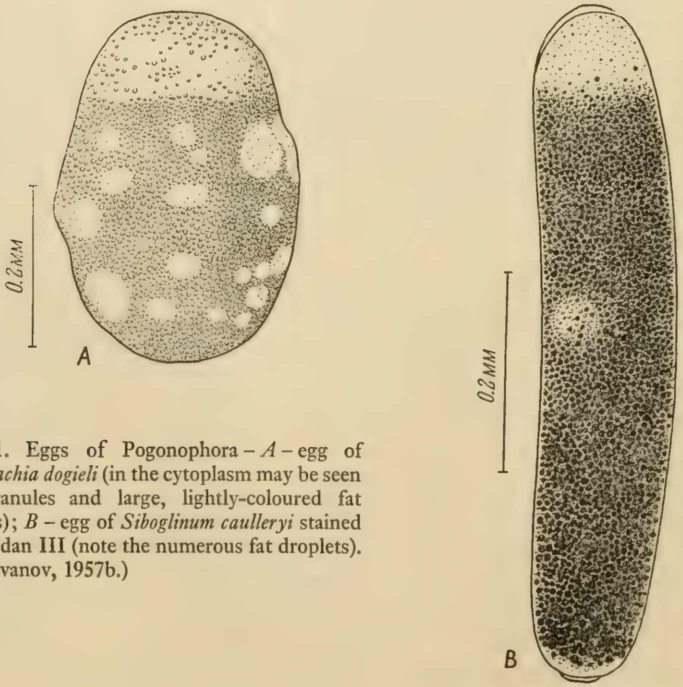

Fig. 71. Eggs of Pogonophora – *A* – egg of *Oligobrachia dogieli* (in the cytoplasm may be seen yolk granules and large, lightly-coloured fat droplets); *B* – egg of *Siboglinum caulleryi* stained with Sudan III (note the numerous fat droplets). (After Ivanov, 1957b.)

homogeneous and semi-transparent; the opposite end stains heavily and appears granular because of the mass of cellular inclusions. The cytoplasm is filled with yolk granules and oil droplets, whose number and size drop off sharply towards the homogeneous end of the egg (Fig. 71*B*).

Study of the later stages of development shows that the homogeneous clear end of the egg becomes the anterior end of the animal. It has not been established whether the convex or the concave side of the egg forms the dorsal side of the animal. Since the egg, in addition to its anterio-posterior polarity shows a distinction between a concave and a convex surface, it possesses a definite bilateral symmetry, which is reinforced by the displacement of the nucleus and its immediate perikaryon, poor in inclusions, to the concave side (Fig. 71*B*).

The egg is deposited into the tube before fertilization. The nucleus immediately migrates to the anterior end into the region which is free of cytoplasmic inclusion and there apparently undergoes reduction division. Fertilization then takes place in the tube, while the nucleus of the ovum is at the anterior end. The fertilization membrane is then formed and the fertilized nucleus returns to its former position in the middle of the egg. Because of this return it was not at first realized that the polar bodies are actually formed near the anterior pole, despite their being found there.

There are thus two indications—the position of the polar bodies and the distribution of food reserves—to show that the animal-vegetative axis of the egg coincides with its antero-posterior axis. The main body axis of the adult pogonophore thus corresponds to that of a protaxonic animal.

Cleavage and gastrulation

The egg undergoes total unequal cleavage. As the first sign of impending cleavage it becomes noticeably shorter. The first plane of cleavage runs obliquely across the egg and divides it into two equal-sized blastomeres (Fig. 72). At the second division both blastomeres divide simultaneously, each into two unequal cells. Of the four cells resulting, the two larger lie at the anterior and posterior ends of the egg and the two smaller amidships, side

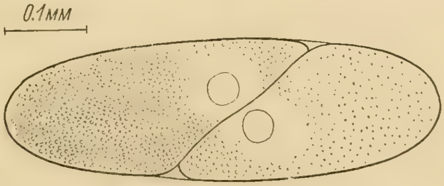

Fig. 72. Cleavage of the egg of *Siboglinum caulleryi*: 2-cell stage. (After Ivanov, 1957b.)

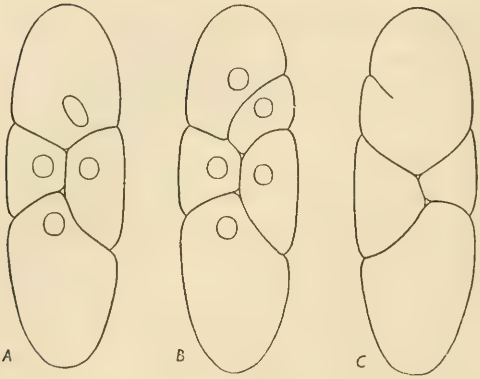

Fig. 73. Cleavage in *Siboglinum caulleryi*: *A* – 4-cell stage, from the flattened side of the embryo; *B* – stage of five blastomeres, from the flattened side of the embryo; *C* – the same from the convex side. (After Ivanov, 1957b.)

by side (Fig. 73*A*). The nuclei remain on the concave side of the egg at the time of the first two divisions and now take up a position at the surface of the egg.

Cleavage now ceases to be synchronous. The big anterior blastomere divides first into a large anterior and a smaller lateral cell, resulting in a 5-cell stage (Fig. 73*B*, *C*). The further progress of cleavage remains unknown.

By the next known stage cleavage has already produced 80–85 blastomeres. Differences in cell size are particularly noticeable. Very large cells are situated at the hind end of the embryo and on the concave side, where their arrangement shows a regular bilateral symmetry. On the concave surface of the embryo, moreover, a pair of very large eye-catching cells lie near the anterior end. On the convex side the size of the blastomeres increases gradually from small at the anterior pole to large at the posterior end of the embryo (Fig. 74).

In a further stage, consisting of 130–140 blastomeres, the same general arrangements of the cells is retained. On the convex side of the embryo, however, the transition between small and large blastomeres is more abrupt, taking on the nature of a boundary (Fig. 75*A*). On the concave

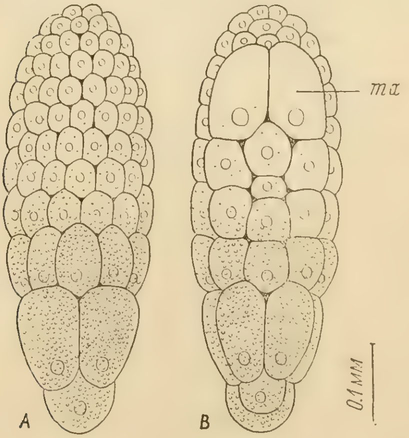

Fig. 74. Embryo of *Siboglinum caulleryi* at the 80–85 cell stage: *A* – from the flattened side of the embryo; *B* – from the convex side. *ma* – anterior pair of large blastomeres. (After Ivanov, 1957b.)

side the regular arrangement is somewhat disturbed and the difference in size between the anterior and posterior cells is less sharp. In the centre of this surface two median cells can often be distinguished, lying one in front of the other. They stain more deeply than the surrounding elements, apparently because of the nature of the yolk granules that they contain (Fig. 75*B*). It is of interest that the pair of large anterior cells of the concave side of the embryo remain unchanged at this stage and their division has apparently ceased while the remainder go on cleaving (Fig. 75*B*).

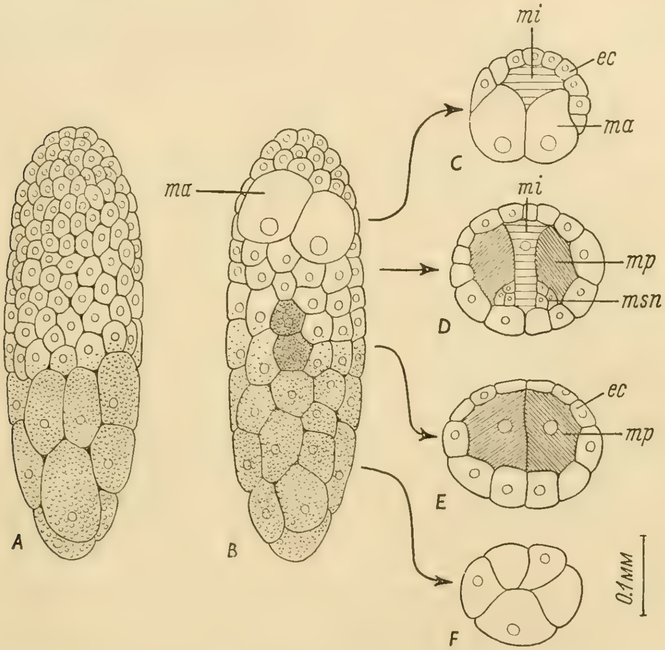

Fig. 75. Gastrula of *Siboglinum caulleryi* at the 130–140-cell stage: *A* – from the flattened side of the embryo; *B* – from the convex side; *C*, *D*, *E*, *F* – transverse sections at the levels indicated. *ec* – ectoderm; *ma* – large half-buried cell, lying near to the anterior pole; *mi* – anterior, median, internal cell; *mp* – pair of posterior internal cells; *msn* – mesenchyme cells. (After Ivanov, 1957b.)

In embryos of this age other cells besides those lying on the surface can be distinguished. Large blastomeres lie wholly within the embryo occupying an interstitial position. They resemble the pair of large cells which lie half-submerged near the anterior pole on the concave side of the embryo (Fig. 75*B*). Three massive cells amongst the internal elements catch the eye at once, in sections; they occupy a large part of the anterior end of the embryo. One of them lies in front near the convex side. This large median elongated cell is a little flattened from side to side (Fig. 75*C*, *D*). Its hind end is wedged in between the anterior ends of the hind pair of internal cells, which are very large and meet in the sagittal plain farther back (Figs. 75*D*, *E*). In addition to these three large cells there are also two groups of very small polygonal cells inside the embryo, lying symmetrically on either side in the anterior part underneath the external layer of cells on the concave side, between the half-submerged cells and the pair of internal macromeres (Fig. 75*D*).

Thus amongst the distinct groups of blastomeres developed by this stage we may already distinguish a mosaic of organ primordia. The small cells of the external layer represent ectoderm and the three large internal cells the beginning of an archenteron whose formation is not yet complete at this stage. The small internal cells, to judge from their position between the ectoderm and the rudimentary archenteron, are mesodermal in nature and probably mesenchymal elements. Their isolation would argue in favour of this supposition. The fate of the anterior pair of half-submerged macromeres remains unknown. It is interesting to note that the hind part of the embryo still lacks any differentiation into presumptive areas (Fig. 75*F*). The large blastomeres, rich in yolk, which form this part of the embryo, possibly become cells of the archenteron or they may enter into the formation of the coelom.

It is clear from this discussion that we may regard this stage as representing in essence a gastrula, despite the lack of a blastocoele and of an epithelial presumptive archenteron. Nor is any blastopore formed and nothing remains to show its primitive position.

The early stages of *Siboglinum* thus show no trace of a radial or spiral type of cleavage, but instead cleavage very soon produces a bilateral symmetry. This form of cleavage in all cases known to us is a secondarily modified process and presumably this is true of the cleavage of Pogonophora also. The peculiar nature of cleavage in *Siboglinum* is evidently associated with the elongated shape of the egg and the abundance of yolk and oil droplets in the cytoplasm, and it is possible that in species with nearly spherical eggs cleavage may follow a more primitive pattern. To all appearances the first two cleavage planes in *Siboglinum* are considerably deflected from their presumed primitive median position. The reason for this appears to be that cleavage in a very elongated egg is so affected by the surfeit of food reserves that it is forced out of the longitudinal plane into a diagonal position.

The peculiar character of cleavage in *Siboglinum* appears also in its inequality. Amongst the blastomeres definite groups are sharply distinguished by their dimensions, position, special yolk content, natural colouration and staining reactions in sectioned material. In other words, there is a point of sharp differentiation of the blastomeres giving the cleavage a determinate character. On that account one cannot separate early development into distinct periods of cleavage, gastrulation and early organogenesis.

As for gastrulation, all that can be stated with any certainty is that it does not take place by either immigration or invagination. The peculiar internal cells, which later give rise to the archenteron and coelom, apparently arise by means of cleavage within a compact morula or sterroblastula. It may be that there is some degree of overgrowth of the larger cells by the smaller at this point, i.e. of epiboly.

Formation of the coelom

Soon the embryo increases a little in size and its front end becomes somewhat broader. Formation of the ectoderm is now completed. Near the anterior end a rather prominent girdle is distinctly visible consisting of two transverse rows of larger ectodermal cells (Fig. 76*A*). A similar but narrower

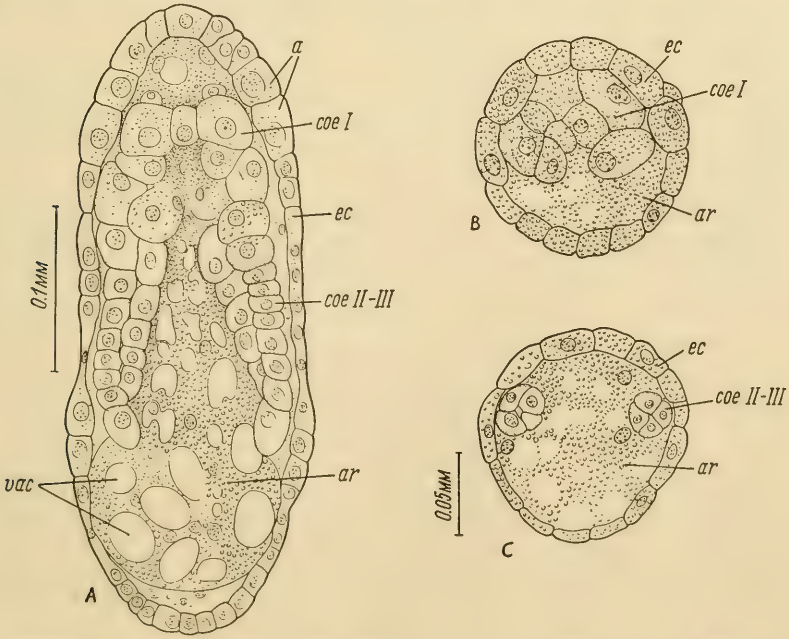

Fig. 76. Formation of the coelom in *Siboglinum caulleryi* – *A* – embryo from the flattened side; *B* and *C* – transverse sections at the anterior end and through the centre of the embryo respectively. *a* – cells of the anterior ectodermal girdle; *ar* – archenteron; *coe I* – primordium of anterior coelom; *coe II-III* – lateral pouches – common primordia of the second and third coelomic cavities; *ec* – ectoderm; *vac* – vacuoles representing the site of fat droplets. (After Ivanov, 1957b.)

girdle of a single row of large cells is found near the posterior end. The ultimate fate of these girdles has not been traced, but it is probable that they later develop into the ciliated bands (pp. 112, 116).

Almost the whole of the internal space of the embryo is occupied by a dense mass of large cells of the archenteron, which are very rich in yolk and oil. There is no sign that these cells are anywhere organized into any kind of epithelium. At the front end of the archenteron active cell division has produced the rudiments of the first coelom in the form of a large unpaired pocket. It consists of large round cells, rich in yolk, and, at first sight, loosely epithelial in arrangement (Fig. 76*A*). The pair of narrow lateral pouches, which are the common rudiments of the second and third coeloms, appear at about the same time (Fig. 76*A*). These grow from the lateral surfaces of the archenteron on its anterior third, and it is possible that their origin is associated from the first with that of the anterior coelom. At the posterior end the tube-like lateral pockets are blind. The narrow lumen of each pouch can be seen in transverse sections to lie between four or five cells (Fig. 76*C*). The base of the pouch can be seen to merge imperceptibly on the medial side into the cell mass of the archenteron, while on the lateral side it runs into the walls of the first coelom. It is apparent that the initial formation of the lateral pockets proceeds as a result of increasingly local multiplication of cells of the archenteron or of the latero-posterior parts of the first coelomic pouch. The lateral pouches then grow vigorously backwards.

The complete separation of the coelomic pouches from the central cell mass next takes place. The latter may now be regarded as a purely endodermal gut primordium, though it must be emphasized once more that it shows no trace of an enteric cavity. The pair of lateral coelomic sacs reach at this stage almost to the hind end of the embryo (Fig. 77*A*).

Finally a deep annular wasp-waist appears in the hind part of the embryo dividing off a small posterior region of the body which represents the trunk segment or metasoma (Fig. 77*B*). The endoderm in this hind segment, which is proper to the metasoma, remains connected by a narrow stalk to the rest of this tissue, but the hind ends of the coelomic sacs are pinched off and their cavities become the third coelomic cavities or metacoeles (Fig. 77*B*). At the same time a broad ciliated ring or girdle, furnished very densely with short cilia, is differentiated near the front end of the embryo.

The coelom of Pogonophora thus arises by enterocoely, as is general in Deuterostomia. The anterior part of the archenteron forms an unpaired pouch—the first coelom—and a pair of lateral pouches originate in conjunction with this to give rise ultimately to the second and third coelomic cavities.

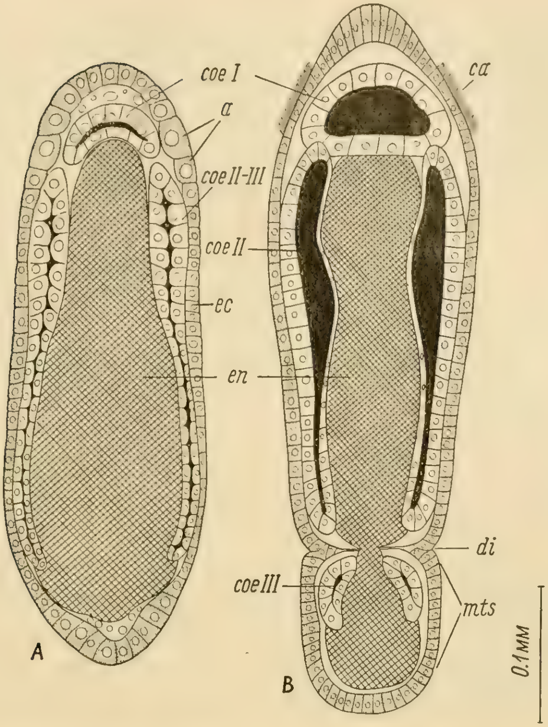

Fig. 77. Diagrams of *Siboglinum caulleryi* illustrating: *A* – the detachment of the coelomic sacs, and, *B* – the first stage of segmentation.
a – cells of the anterior ectodermal girdle; *ca* – anterior ciliary girdle; *coe I*, *coe II* and *coe III* – first, second and third coelomic sacs; *di* – diaphragm; *ec* – ectoderm; *en* – endoderm; *mts* – metasoma. (After Ivanov, 1957b.)

The anterior and lateral coelomic pouches then become separated and the latter become pinched across to form the second and third coelomic sacs. The coelomic pouches are thus formed in a similar way to that found in *Saccoglossus pusillus* (Enteropneusta), whose egg is also rich in yolk (Fig. 78) (Davis, 1908).

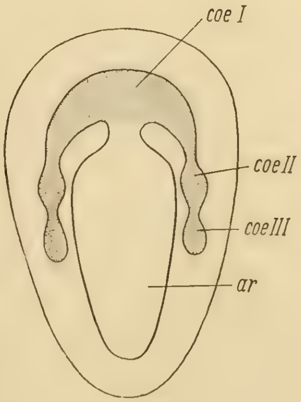

Fig. 78. Formation of the coelomic sacs in *Saccoglossus* pusillus (Enteropneusta.)
ar – archenteron; *coe I* – protocoele; *coe II* – mesocoele; *coe III* – metacoele. (After Davis, 1908, from Korschelt.)

Later stages of development

The next known stage of development has been recorded from *Oligobrachia dogieli.* Segmentation of the body has already proceeded to completion and tentacle rudiments are present, so that it is at last possible to distinguish dorsal and ventral sides. The body of the embryo is already much elongated and almost cylindrical, and plainly divided into three segments (Fig. 79). The protosoma is by no means small; its front end is conical and drawn out to form the cephalic lobe. It is divided from the mesosoma behind by an annular groove. The much thickened epidermal epithelium on the tip of the cephalic lobe consists of tall cells, but elsewhere on the protosoma it is more or less thin. A considerable part of it is densely covered with the short cilia of the anterior ciliated band.

The tentacles are found on the ventral side of the protosoma, just in front of its posterior edge. A small tongue-like outgrowth situated a little to the right of the mid-ventral line is the rudiment of the first tentacle (Fig. 79.) Quite soon a small wart-like thickening of the ectoderm may be observed to its left. This represents the rudiment of the next tentacle to be formed—the first left tentacle— thus completing the first pair.

The mesosoma has already undergone considerable growth in length and now makes up a large part of the larva. There is no sign yet of the bridle. Almost the whole dorsal surface of the front half of the mesosoma is covered with short cilia.

The metasoma is very small and more or less egg-shaped. It is only about 1½ times as long as it is broad. It is divided from the mesosoma by a sharply nipped-in waist. A narrow ciliated band is developed on the surface of the metasoma with a few bristles lying in front of it. The latter form a bundle on each side of the body, consisting of two or three rather thick short bristles which stick out. The ends of the bristles are slightly swollen and rounded, and they point sideways and somewhat forwards (Fig. 79). They consist of a clear transparent substance and reach a length of 48μ.

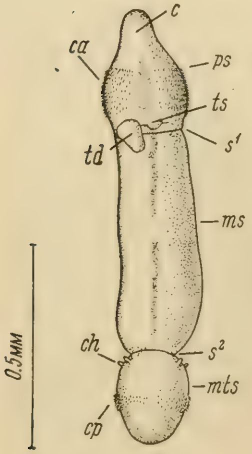

Fig. 79. A segmented embryo of *Oligobrachia dogieli*, at the stage of the first appearance of tentacles, seen from the ventral side.

ms – mesosoma; *mts* – metasoma; *ps* – protosoma; s^1 – groove between protosoma and mesosoma; s^2 – groove between the mesosoma and the metasoma; *td* – first tentacle; *ts* – bud of second tentacle. (After Ivanov, 1957b.)

The internal structure of this embryo of *Oligobrachia* has been insufficiently studied because of the bad state of preservation of the material. Considerable histological differentiation is present in the body wall—there is a thin cuticle, single gland cells may be observed in the epidermis and sparse longitudinal and circular muscle fibres of the dermal muscle sac may be discerned under the epithelium. The transverse diaphragm between the mesosoma and the metasoma is already well pronounced, but its muscle fibres are as yet but feebly developed.

But as before a large part of the internal space is occupied by the cell mass of the endoderm, not only in the mesosoma and metasoma, but in the protosoma too, where it begins well forward of the tentacle rudiments. In this archenteric primordium the cells are largely higgledy-piggledy. Only in the protosoma and in the front part of the mesosoma is there some sort of definite arrangement, with large pyramidal cells whose summits meet in the centre (Fig. 80*A*), in such a way that a very narrow space is left between them, perhaps representing the lumen of the enteron. There is no trace of mouth or anus.

The coelomic sacs look like nothing more than double membranes squeezed between the body wall and the gut primordium. The anterior coelom remains unpaired but takes up an asymmetrical position towards the right side of the body (Fig. 80*A*). A coelomic canal runs from it into the rudiment of the first tentacle.

Blood vessels are already present—at least the dorsal and ventral vessels (Fig. 80*B*). Their walls consist of a thin structureless membrane and their lumina are filled with the small enucleate bodies so characteristic of the blood of these animals.

Turning now to the bristles of the metasoma, we may observe that each is formed inside a separate multicellular thin-walled sac, so that there are two or three sacs lying in a row in each bundle of bristles. The sacs are situated between the epidermis and the gut rudiment, piercing right through the internal and external walls of the coelom. Each sac consists of three to five cells with round nuclei but with no clear cell walls. The single bristle lies in the middle of this syncytium, resting with its broader end in the epidermis which bulges outwards to accommodate it but is not at first pierced by it. The sac has no connexion with the epidermis. All its constituent cells are identical and bear the same relationship to the bristle (Fig. 81*A*). It is natural, therefore, to infer that all of them take part in forming the bristle. In any case, we have here no such special formative cell located at the base of the bristle such as we find in the parapodia of Polychaeta.

A little later the bristles pierce through the epidermis one by one and stick out above the body surface. The bristle sac then fuses with the epidermis and spreads out (Fig. 81*B*). There are no muscle fibres associated with the bristle.

The last known stage of development (Fig. 82) has been studied in a few embryos from a single batch in *Siboglinum caulleryi*. Externally these embryos already resemble the adult but are sharply distinguished by the

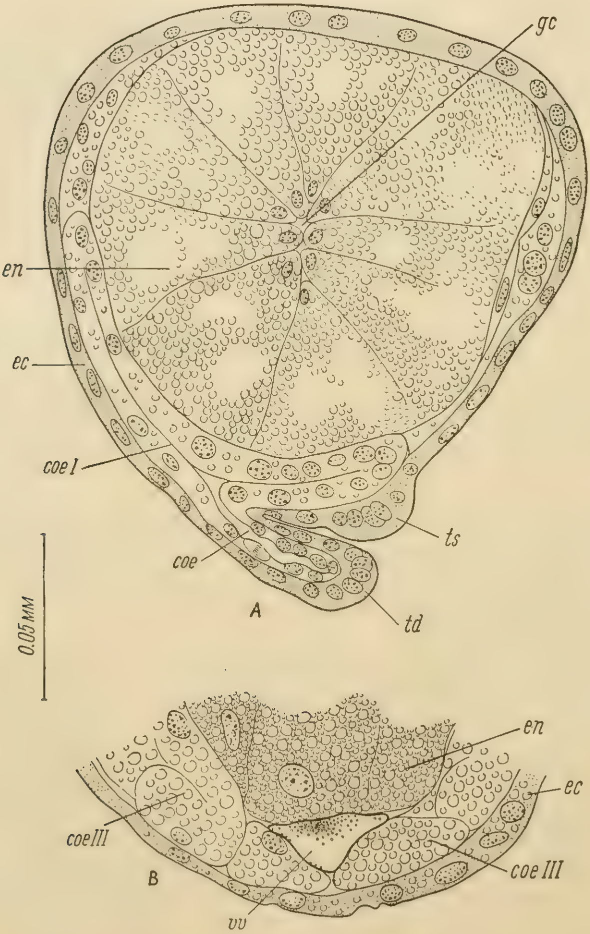

Fig. 80. Transverse sections through a late embryo of *Oligobrachia dogieli*: *A* – section at the level of the tentacular buds; *B* – section through the metasoma.
coe – coelmoic canal of tentacle; *coe I* – protocoele; *coe III* – metacoele; *ec* – ectoderm; *en* – endoderm; *gc* – gastrocoele; *td* – first tentacle; *ts* – bud of second tentacle; *vv* – ventral blood vessel. (After Ivanov, 1957b.)

metasoma which still remains very short and completely lacks any trace of the definitive organs, retaining its embryonic character.

The body by now is 1.9 mm long. The protosoma already possesses almost the same proportions as in the adult and it is furnished with a rather long tentacle which is attached somewhat to right of the mid-ventral line. There

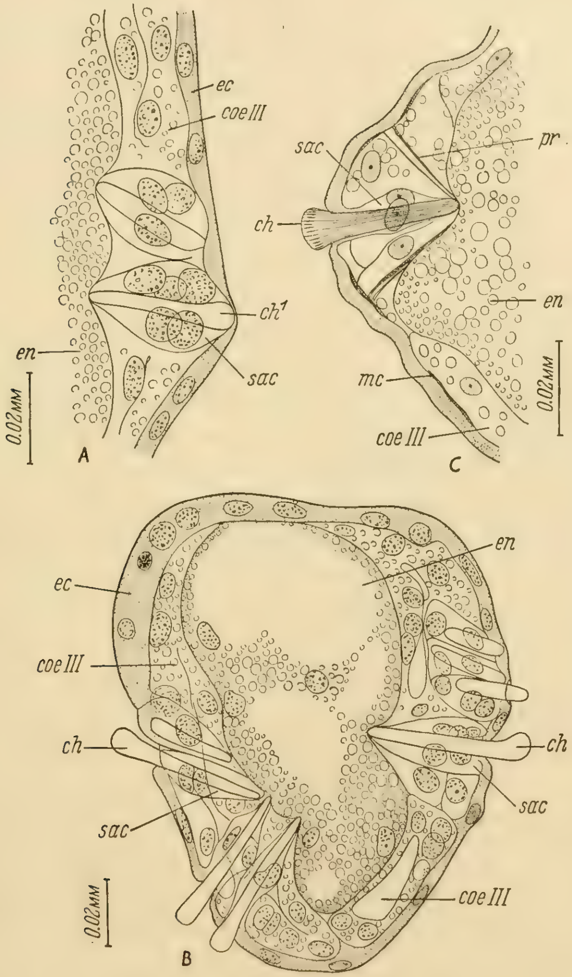

Fig. 81. Transverse sections through the metasoma of late embryos: *A* – Bristle sacs and young bristles in *Oligobrachia dogieli*; *B* – section through the metasoma of the same species, with well-formed bristles (lower magnification); *C* – bristle sac of *Siboglinum caulleryi*.
ch – bristles; *ch*¹ – young bristle which has not yet pierced through the ectoderm; *coe III* – coelom of metasoma; *ec* – ectoderm; *en* – endoderm; *mc* – circular muscle fibre; *pr* – muscle fibre – bristle protractor; *sac* – bristle sac. (After Ivanov, 1957b.)

is no trace of any other tentacle rudiment. A broad coelomic canal runs inside the tentacle lined with peritoneum, but there is no blood vessel as yet, nor any trace of pinnules. Little doubt thus remains that the single tentacle of the adult *Siboglinum* is formed on the right side of the body and that it is homologous with the first-formed tentacle on the right in *Oligobrachia*. There is still a broad ciliated belt in front of the tentacle.

The mesosoma is very long. There is still no bridle but a girdle of thickened epithelium, glandular in nature, is developed in the anterior part of the segment. The short metasoma is cut off from the mesosoma by a wasp-waist and an internal diaphragm. The posterior half of the metasoma is much thicker than the rest and bears a narrow ciliated band which is more strongly developed on the dorsal side. Eight bristles, grouped into two dorsal and two ventral pairs, lie in front of this belt (Fig. 82).

The gut rudiment, which lacks any perceptible lumen, takes up a considerable part of the body. There is neither oral nor anal aperture. The histological structure of the bristle sacs is similar to that of the embryo of *Oligobrachia*, but the internal ends of the bristles have fine muscle fibres attached, acting as protractor muscles and inserted in the body wall (Fig. 81*C*).

Thus during the course of embryological development in the Pogonophora, the posterior segment—the metasoma—is the first to be divided off and only after this has taken place are the protosoma and mesosoma separated. The metasoma nevertheless lags behind the anterior two segments in growth and retains an embryonic structure. Its growth in size and length and its differentiation must take place when the young animal, released from the maternal tube, is already leading an independent existence and is perhaps preparing its own tube. The late differentiation of the metasoma is manifested in particular in the tardy appearance of the posterior ciliated girdle. It is known that in

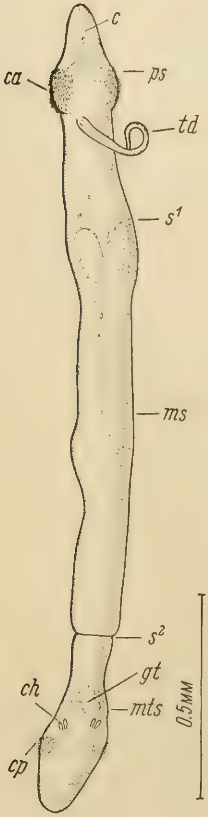

Fig. 82. Late embryo of *Siboglinum caulleryi*, seen from the ventral side. *c* – cephalic lobe; *ca* – anterior ciliary girdle; *ch* – bundle of provisional bristles; *cp* – posterior ciliary girdle; *gt* – pyriform glands seen by transparency; *ms* – mesosoma; *mts* – metasoma; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *td* – right anterior (and only) tentacle. (After Ivanov, 1957b.)

Enteropneusta, both at the tornaria stage and during the early stages of metamorphosis, the region of the metasoma is very tiny and for a time remains much smaller than the proboscis and collar, but then it rapidly increases in length. The grooves between the segments usually arise simultaneously, but in *Saccoglossus pusillus* (which is very like *Siboglinum* in the amount of yolk in the egg, in the way coelomic cavities are formed and in the lack of a pelagic larval stage) the metasoma is divided off first (Davis, 1908).

The ciliated girdles appear to be provisional formations. In adult pogonophores there is no trace of them, though it is not clear whether there is any developmental connexion between the posterior ciliated girdle and the dorsal ciliated band on the trunk of the adult. Two hypotheses may be advanced to account for the possible functional significance of the ciliated structures: the cilia might facilitate exit from the maternal tube or assist in respiration by drawing a current of water over the developing embryo. The first hypothesis is less likely since the whole ciliary system, with its very short cilia, seems hardly strong enough to propel the animal to the outside. [The late embryo of *Siboglinum inerme*, removed from the maternal tube, has been seen to swim by means of the ciliated girdles (see Pl. IV *D*)—D.B.C.]

The two girdles, together with the dorsal ciliated area of the mesosoma, apparently represent remnants of the larval locomotor system preserved from the time when ancestors of the Pogonophora possessed a free-swimming larval stage. In particular, the metasomal girdle is probably homologous with the posterior ciliated ring of the tornaria, which first appears in this larva after all the other cilia have been formed.

Amongst the provisional "larval" organs one must also include the bristle sacs and their bristles. To all appearances the bristles serve to support the body against the internal wall of the tube when the young animal is creeping forth and moving along by means of contractions of the dermal musculature.

A very interesting point is the way in which the tentacles arise one after the other, not simultaneously,

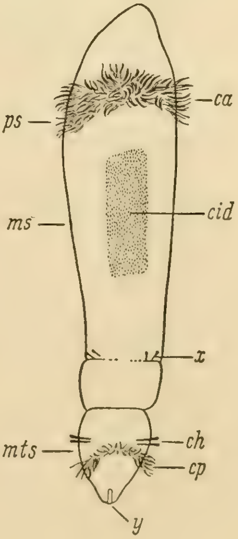

Fig. 83. Late embryo of *Siboglinum* sp., seen from the dorsal side. *ca* – anterior ciliary girdle; *ch* – provisional bristles of metasoma; *cid* – ciliated field of mesosoma; *cp* – posterior ciliary girdle; *ms* – mesosoma; *mts* – metasoma; *ps* – protosomal region; *x* – provisional bristles of mesosoma; *y* – terminal invagination of integument. (After Jägersten, 1957; orientation of body and interpretation of segmentation changed.)

in *Oligobrachia dogieli*, which has six to eight or even nine tentacles in the adult. As we have already seen (p. 27) new tentacles continue to be formed even in the sexually mature state and their formation is concentrated at the ends of the horse-shoe base of the tentacular crown. It is likely, therefore, that the same thing occurs in ontogeny. Evidently the process of successive formation and growth of tentacles, first begun in the embryo, continues throughout life and possibly ceases only in old age. The right anterior tentacle is the first to be formed, then its pair on the left side. After that they probably appear right and left alternately, thus maintaining the symmetry of the crown.

The question of the nature of the single unpaired tentacle of *Siboglinum* arises in this connexion. We have already seen that it is homologous with first tentacle of *Oligobrachia*. It is possible to speculate that it is the primitive condition in Pogonophora to produce only the one tentacle and that all the rest are a secondary development. Viewed in this light *Siboglinum* would be the most primitive genus and the origin of a single tentacle during ontogeny might be looked upon as recapitulation. But this supposition runs counter to the observation that the tentacle of *Siboglinum* is innervated from the right side of the brain (p. 26 and Fig. 38) and this same nerve runs asymmetrically up the right side of the tentacle. It is difficult to imagine that such asymmetry is primitive in an animal which in all other respects shows a strong bilateral symmetry. It is easier to postulate a secondary reduction of the number of tentacles. In *Siboglinum*, then, only the right anterior tentacle remains out of the whole tentacular crown. It is apparent that the reduction of the rest of the tentacles was accomplished by a failure of the later stages of development of the crown, i.e. in the terminology of A. N. Severtsov (1939), through "negative anaboly". Thus the presence of only a single tentacle in *Siboglinum* is the result of secondary reduction of the greater part of the crown, and at the same time represents an embryonic feature carried on into adult life.

The archenteron is probably formed by delamination within a compact mass of cells, from which the coelomic primordia are later divided off. An epithelial gut rudiment begins to form after a great delay but a blastopore and a secondary mouth are completely lacking. All these features clearly show the pronounced secondary changes in the embryonic processes and are undoubtedly associated with the absence of a gut in the adult.

Nothing is yet known about the ultimate fate of the gut rudiment, a question of the greatest importance. To judge from the organization of the adult, in which no trace of gut remains, the gut primordium serves only as the main food reserve of yolk and oil, and soon after the young animal takes up an independent existence it is probably entirely resorbed. Its cells seem to represent nothing more than a stock of yolk-filled endoderm.

Jägersten (1957) described late embryos of *Siboglinum* sp. from the Skagerrak. The embryos, found in the maternal tube (three specimens), were very similar to the most advanced embryos described from *Oligobrachia dogieli*, possessing a separated metasoma with tufts of comparatively large bristles, anterior and posterior ciliated bands and the dorsal ciliated patch on the mesosoma, but still lacking any tentacular rudiment. Besides the large bristles of the metasoma Jägersten also noticed very small lateral bristles in the mesosomal region and behind the posterior metasomal ciliated band (Fig. 83). Such bristles have not been found in the embryos of *Siboglinum caulleryi* and *Oligobrachia dogieli*.

Without sufficient foundation Jägersten regarded the posterior divided portion as conjoined protosoma and mesosoma. He thus misorientated the body of the embryo, regarding as the front end that which is in fact the posterior end. If a tentacle rudiment had been present he would of course have avoided this mistake. He also decided that the ciliated patch in the middle of the body was ventral—a decision linked with his concept of the determination of the dorsal and ventral surfaces of the body of the adult (p. 8). And finally, Jägersten described a small indentation at the tip of the metasoma [the front end of the embryo in his view] and interpreted it as the rudiment of a stomodaeum. Its location at the hind end of the body, not joined to the endodermal mass in any way, excludes the possibility of any such construction.

Possible changes of organization during the postembryonic period

The fully formed young animal probably makes its way out of the maternal tube without any assistance from the mother and immediately begins to make its own little tube. There must be sufficient food reserves still stored in the cells of the endoderm to enable it to form the tentacular apparatus and so to begin feeding.

The structure of the young animal soon after emergence from the maternal tube is unknown. One can readily imagine, however, the changes in organization which are happening at this age. The mesosomal bridle is being differentiated, the metasoma is growing rapidly in length, all the definitive organs are formed, including the dorsal ciliated band, the adhesive papilla and the girdles of toothed platelets. At the same time many internal organs make their first appearance—the multicellular flask-shaped glands, the nervous system, many of the blood vessels, the heart, coelomoducts and reproductive system.

CHAPTER 11

The Tube

The tube of Pogonophora is never branched. It is almost cylindrical, though usually tapering very slowly indeed from the front end backwards. [An exception is *Siboglinum atlanticum* which is wider than anteriorly (Southward and Southward, 1958 — D.B.C.]. Its length is several times the length of the animal, varying from 15–20 cm in the smaller species of *Siboglinum* to 150 cm in *Zenkevitchiana longissima*. The diameter varies from 0.1 mm in *Siboglinum minutum* and *S. tenue* to 2.8 mm in *Spirobrachia grandis*.

The structure and general nature of the tube are essentially similar in all Pogonophora. The tubes of *Siboglinum*, *Oligobrachia*, *Diplobrachia* and some other genera are pliable and comparatively soft, *Zenkevitchiana* has a parchment-like, whitish elastic tube and *Polybrachia*, *Lamellisabella* and *Spirobrachia grandis* have very rigid thick-walled brown or black tubes. Details of the structure of the tube often serve well for specific diagnosis.

The tube may be uniform along its whole length or consist of very close dense rings alternating with clear elastic interspaces (Figs. 84*A*, 85). The rings may be equal and regular (*Siboglinum caulleryi*, *Oligobrachi dogieli*

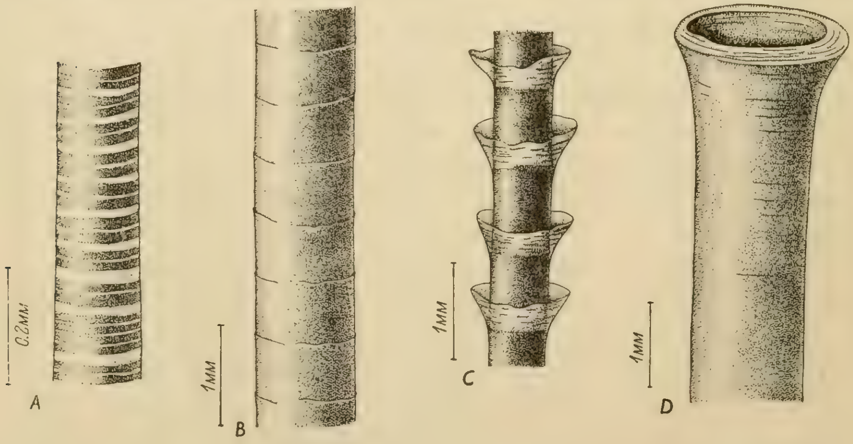

Fig. 84. Tubes of various Pogonophora: *A* – *Siboglinum fedotovi*; *B* – *Lamellisabella johanssoni*; *C* – *Polybrachia annulata*; *D* – *Spirobrachia beklemischevi*. (After Ivanov, 1957a.)

and many others), they may have irregular edges (*Siboglinum minutum* for example), or sometimes they may be quite irregular in outline (*Heptabrachia subtilis*). The tubes of a few species of *Siboglinum* are distinguished by each ring splitting to form a doublet (e.g. *S. fedotovi*, Fig. 84*A*) or neighbouring rings may anastomose or fuse (*S. ekmani* and *S. plumosum*, for example). In some forms irregular rings are found only in the hind part of the tube (*Polybrachia annulata*) or they may be discovered only after stripping off an external fibrous layer (*Birsteinia*, *Lamellisabella zachsi*).

Transverse or annular lines or narrow striations repeated at rather long but regular intervals, may sometimes be noticed on the surface of the tube as well as the rings (*Siboglinum ekmani*, according to Jägersten, 1956; *S. fedotvi*, *Diplobrachia japonica* and others). They are also found on tubes which lack rings (perhaps more frequently indeed) and are said to divide the tube into segments. Segmented unringed tubes are found in *Zenkevitchiana*, *Polybrachia*, *Lamellisabella johanssoni* (Fig. 84*B*) and the posterior part of the tube of *Spirobrachia beklemischevi*. The front edge of each segment of the tube of many Polybrachiidae is furnished with a membranous funnel-like frill (Fig. 48*C*).

In the majority of Pogonophora the long anterior part of the tube is different from the rest. The walls are thin and soft, they are usually transparent and too flimsy to support their own weight (Fig. 85). It is possible that when the animal has retreated into the depths of the tube the walls of this region collapse and by closing

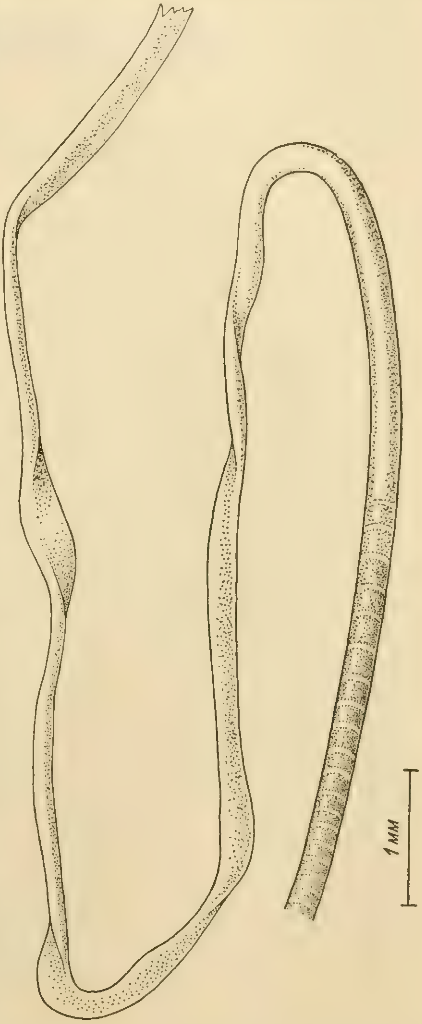

Fig. 85. Tube of *Siboglinum caulleryi*. The front part of the tube lacks rings, and is flimsy and transparent, with walls which collapse easily. (After Ivanov, 1957a.)

the top of the tube serve a protective function. In *Lamellisabella* and *Spirobrachia*, on the other hand, the thick-walled rigid anterior part of the tube ends in a broad funnel (Fig 84*D*).

The wall of the tube is always laminated (Fig. 86). The surface layer is often much the thickest. In *Birsteinia* and *Heptabrachia subtilis* a considerable part of the tube is covered with a special external fibrous or felt-like layer (Ivanov, 1957a). The walls of the tube in many species of *Siboglinum* and in *Diplobrachia japonica* frequently contain thicker or thinner yellowish or brownish annular fibres. The tube grows in thickness from the internal surface, thanks to the production of new layers. Such thickening of the walls is undoubtedly accompanied by considerable increase in length.

Fig. 86. Longitudinal section of the wall of the tube of *Siboglinum ekmani*. The lamellar structure of the tube is conspicuous (After Jägersten, 1956.)

Chemical investigations of the tubes of pogonophores have given interesting results. The biochemist N. V. Fishenko, at the Institute of Cytology of the Academy of Sciences of the U.S.S.R., found that the material of the tubes appeared to be polysaccharide, yielding a reducing sugar upon acid hydrolysis. The chemical nature of this polysaccharide was clarified by Brunet & Carlisle (1958), who reached the conclusion that the tubes of three species of *Siboglinum* and *Zenkevitchiana longissima* contained chitin. [The tubes gave a clear chitosan reaction and acid hydrolysis yielded glucosamine and several amino acids, but no glucose or any other monosaccharide; enzymic hydrolysis yielded N-acetylglucosamine. Fishenko's "reducing sugar" must be glucosamine. The tube, then, must consist of chitin and protein. No sulphur-containing amino acids were found, so the protein can only be hardened by tanning, not by sulphur cross-links; that is to say it is a schlerotin, not a keratin. This is confirmed by the aroma given off by burning —the tube of *Zenkevitchiana* smells like the wings of a locust when burnt, not like burning hair. Rudall (1962) has confirmed the presence of chitin in pogonophore tubes by X-ray diffraction studies. It is perhaps worth mentioning that the organic remains of graptolites have yielded glucosamine upon acid hydrolysis and N-acetylglucosamine upon enzymic hydrolysis —D.B.C.].

CHAPTER 12

Ecology

The contemporary Pogonophora are apparently no mere fragments of a formerly rich group which has become almost extinct. Until recently this might have seemed a reasonable point of view, but oceanographic expeditions are discovering new species of Pogonophora each year, from the Pacific Ocean [and elsewhere] and the group seems to be a flourishing one consisting preeminently of abyssal forms. They are enormously abundant in places. In certain well investigated spots in the northwest Pacific Ocean trawling brings up masses of inhabited and empty pogonophoran tubes, which may clog the trawl bag and dangle from the frame and bridles. [Hartman (1961), in a quantitative haul off the Californian coast found a density of *Siboglinum veleronis* of 200/m^2]. If we can judge from the abundance of inhabited and empty pogonophoran tubes mixed with mud they play an important role in the benthos of many parts of the abyss. The majority of Pogonophora are inhabitants of abyssal or hadal depths, of which they are especially characteristic, but many species may be encountered also in comparatively shallow places. Out of the 44 known species*, 25 (58 per cent) have been found at depths greater than 3000 m. Of these only 9 species dwell also at shallower horizons and 16 species (37 per cent of the total described species) have not been found at depths less than 3000 m. A few forms, however, dwell in the bathyal or even sublittoral zones. Such species, among others, are characteristic of the Sea of Okhotsk. It is interesting to note that some of these shallow water forms are encountered also in abyssal depths. Sixteen species of pogonophores are known from depths less than 1000 m, 11 of which are not encountered below the 1000 m line, but a few species (e.g. *Oligobrachia dogieli* and *Siboglinum caulleryi*) possess a wide vertical distribution, going down to depths of more than 2000 m. *S. caulleryi* in particular invites comment, for it is able to live in shallow water in the Sea of Okhotsk (even as shallow as 22 m), but it has also been found in the Kuril-Kamchatka Trench at a depth of 8164 m. [I believe this is the greatest known bathymetric range of any species of marine organism—D.B.C.]

Ten of the known pogonophoran species are encountered in the greatest depths of the sea, dwelling below the 5000 m line, and eight of them are

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* This was written in 1959.

adapted exclusively to these hadal depths. *Heptabrachia abyssicola*, *H. subtilis*, *Cyclobrachia auriculata*, *Diplobrachia japonica*, *Zenkevitchiana longissima*, *Lamellisabella johanssoni* and *Spirobrachia beklemischevi* are typical hadal species. The greatest depth at which pogonophores have been found is 9735 m.

Besides the species of Pogonophora which have been described, we have available abundant material collected in recent years by the Soviet expedition of R.V. *Vityaz*' and R.V. *Ob*', including another thirty or so species, largely of the genus *Siboglinum*. It is not practicable to describe these species because of the fragmentary nature of the material, but we can obtain a general picture of their vertical distribution, as follows: 17 of these nondescript species inhabit depths greater than 3000 m. Eight of these were taken in depths between 5000 and 9000 m. Eleven species were found at depths less than 3000 m. All these animals were taken on a muddy bottom.

Pogonophora lead a sedentary tubicolous life and other animals may settle on the stiff very long tubes of such species as *Lamellisabella zachsi* and *Polybrachia annulata*. Foraminfera, siliceous sponges, hydroids, alcyonarians, small actinians (Hormathiidae), serpulids, bryozoans, ascidians and even stalked sea lilies have been found attached in this way, and the chitin-like cup-shaped scyphistoma colonies of *Stephanoscyphus* are especially common [the scyphistoma stage of *Nausithoe* - Coelenterata Scyphozoa Coronatae]. The characteristic localization of these epibionts indicates that a considerable part of the pogonophoran tube projects freely above the surface of the seabed, arranged more or less vertically, while the remaining basal part is apparently deeply submerged in the sediment. The soft flimsy tubes of species of *Siboglinum* and the elastic white tubes of the hadal *Zenkevitchiana* have no epibionts and are apparently almost wholly submerged in the sediment. [Marks on the tube of *Siboglinum* spp. have been interpreted by Southward and Southward (1958b) as marking the level of the surface of the mud, and it is possible that the anterior ends of these tubes lie more or less flat on the surface of the sediment—D.B.C.]

Pogonophores probably form dense stands. This follows from their lack of a pelagic larva. [It is also confirmed from the quantitative haul of Hartman (1961) and the work of A. J. Southward (1958)].

Pogonophora are frequently numerous and very characteristic organisms of benthic biocoenoses. Thus in the northwest part of the Sea of Okhotsk the coastal shallow-water stretches of muddy bottom (depth 90–200 m) are densely occupied by *Siboglinum caulleryi*. In the Bering Sea between depths of 1400 and 5000 m *Polybrachia annulata* frequently appears to predominate sharply in numbers over the other forms in the complex biocoenosis, of which almost all the sedentary representatives (Coelenterata, Porifera, Ascidiacea and Bryozoa) dwell on the tubes of the pogonophores. Amongst the carnivorous species of this biocoenosis the anomuran decapod crustacean *Munidopsis* apparently feeds on *Polybrachia* (M. Sokolova, unpublished).

Since they are sedentary filter-feeders pogonophores probably depend to a considerable degree on the amount of food particles suspended in the water and on the bacterial flora developed in it. They are therefore most numerous in those places where there is a more or less continuous local concentration of organic matter near the bottom depending on a swift steady bottom current and on the conformation of the sea bed (Sokolova, 1956). This is also quite clear from the fact that in land-locked seas and in deep trenches the pogonophoran fauna is far more diverse than in the open reaches of the ocean far from continental land-masses. [It may also be useful to speculate that the conditions which Pogonophora need to meet their food requirements may be met in two other ways also. Firstly, an area of convergence of two surface currents may lead to a steady down-flow of surface water relatively rich in plankton: some of the pogonophores found in the subantarctic far from land appear to be situated in regions of the Subantarctic Convergence (see Fig. 87). Secondly, cascading of water down canyons in the continental slope may also provide abundant food: the Pogonophora collected off the mouth of the English Channel were found in just such places—D.B.C.]

It is doubtful whether pogonophores ever leave their tubes, so that they cannot adapt to free life in the open. Inside the tube, however, they are probably active and swift-moving, now poking the front end of the body, with the tentacular apparatus, out of the tube, now drawing it back in again. In this respect they recall the sedentary tubicolous polychaetes. The long tube is always considerably longer than the animal itself and does not impede its mobility. The numerous adhesive papillae, with their associated cuticular plaques, serve to support it against the inner wall of the tube. The strong development of the longitudinal dermal musculature and the greater length of the animal when fixed inside the tube than when fixed out of it indicate its tremendous ability to extend and contract. Thrusting out the front end of the body from the tube is possibly accomplished by great extension of the trunk, whose hind part remains firmly attached to the walls of the tube by means of the toothed platelets of the girdles. When irritated or when danger threatens from outside the animal apparently disappears in a flash into the depths of the tube in consequence of the simple contraction of the longitudinal musculature and the steadfast adhesion of the girdles to the tube walls, an action which can surely be called an "evasive reaction". These conclusions are confirmed by the histological findings also: they possess giant nerve fibres apparently serving for the rapid propagation of impulses to the longitudinal musculature which shortens part of the trunk (Ivanov, 1958b).

There is apparently no necessity for the animal to poke out the whole tentacular apparatus for collecting food particles in the intertentacular cavity (through which runs the stream of filtered water). It may be sufficient if only the distal end of the crown is pushed out. How *Siboglinum* collects its food is not clear. Amongst several possibilities one may suggest that *Siboglinum* gathers food particles from the surface of the mud, searching the surrounding area of the sediment with the single tentacle. And then the tentacle perhaps twists up into a corkscrew around a small quantity of food particles and then withdraws into the tube where digestion takes place. [This has been seen to happen—D.B.C.]. It may be that all Pogonophora periodically withdraw into the tube for digestion of the food gathered by the tentacular apparatus. It cannot be doubted, however, that the female, having laid the eggs in the anterior part of her own tube, is forced to stay in the bottom of the tube all the time that the embryos are developing.

These ideas are purely speculative for the moment and need examination on the living animal.

[Kirkegaard (1961) has attempted to observe *Siboglinum ekmani* in the living state. They live well in the laboratory if kept cool, but he never saw them emerge from the tube and suggested that they were light-shy. This has been confirmed and it is necessary to use dim red light to observe the behaviour of the animal, which will only poke its front end out of the tube in the absence of the rest of the spectrum. No specific light-receptors have been demonstrated and the whole animal may well be equally sensitive to light—D.B.C.]

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Fig. 87. Map of the geographical distribution of Pogonophora. Distribution of most recent species is illustrated in Fig. YZ133, p. 332.

CHAPTER 13

Geographical Distribution*

Many species of Pogonophora are found in "The Eastern Sea" [i.e. the seas bordering the eastern extremity of the Soviet Union] and in the adjacent parts of the northern Pacific Ocean. This is more a result of the detailed investigations which the deep-sea benthos of these parts of the ocean have received rather than any evidence that they are particularly abundant here. The very wide distribution of the Pogonophora is amply demonstrated by their recent discovery in all parts of the world (see Fig. 87 for records up to 1960).

As a result of the cruises of R.V. *Vityaz'* in the western parts of the Pacific Ocean, it has become apparent that in and around the Kuril-Kamchatka Trench, the Japan Trench and the Bougainville Trench pogonophores are characteristic and constant members of the bottom fauna (Fig. 87), while over vast areas of the oceanic floor they are very few and far between (Ivanov, 1957a). In the Atlantic Ocean all finds of pogonophores have been found on the continental slope rather than the ocean floor.

In the Sea of Japan, to all appearances, there is only one species—*Oligobrachia dogieli*. As is generally known there is no true abyssal fauna in this basin, probably because of the shallow straits which impede the entrance of oceanic abyssal animals. In this connexion it is of importance to notice that *O. dogieli* is one of the few eurybathic pogonophores. In the neighbouring Sea of Okhotsk it inhabits depths of 119–572 m, and, in particular, it is found near the Strait of Sōya Kaikyō (= La Pérouse Strait, between Sakhalin Island and Hokkaido).

The Bering Sea and the Sea of Okhotsk each possess a rich pogonophoran fauna, with an interesting and quite different facies in the two seas. The same may be said of the Kuril-Kamchatka and Japan Trenches and of the other deeps.

In the Bering Sea eleven species of Pogonophora have been found, of which seven are not found elsewhere. In general the pogonophoran fauna of this sea is very rich and diversified, and in a few places, at depths of 3000–4000 m one may encounter a whole complex of Pogonophora consisting of

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* Much of this chapter has been rewritten, partly by the author and partly by the translator—D.B.C.

three to six species inhabiting the one spot. Such an association almost always includes *Polybrachia annulata*, *Heptabrachia gracilis*, *Siboglinum fedotovi* and *S. pellucidum*, and often also *Birsteinia vitjasi*, *Spirobrachia grandis* and *Lamellisabella zachsi.*

Two distinct ecological groups of species are found in the Sea of Okhotsk. One group, confined to shallow and moderate depths, is characteristic of the northern basin and includes *Oligobrachia dogieli*, *Siboglinum caulleryi* and *S. plumosum.* The other group of species, characteristic of the southern abyssal region of the Sea of Okhotsk, comprises *Lamellisabella zachsi* and *Polybrachia annulata.* It is of interest that there are no endemic species (except perhaps for *Siboglinum plumosum*) in this sea. It may be that the pogonophoran fauna of the Sea of Okhotsk arose fairly recently by penetration of species from the Kuril-Kamchatka Trench and the Bering Sea into this basin.

Near the east coast of Japan are found *Siboglinum japonicum* and *S. cinctutum.* Another variety of this species, *S. c.* var. *subtile*, has been described from the Malay Archipelago.

The benthos of the East China Sea still remains almost unknown, but here too new species of Pogonophora have been discovered. Unfortunately little can be written about them because of the fragmentary nature of the material.

Undoubtedly the seas richest in Pogonophora are those of the Malay Archipelago. In the Flores, Banda, Savu, Ceram, Timor and Arafura Seas the complex of species first named *Siboglinum weberi* was found—the first known material of the class and long known to science (Caullery, 1914). The Danish *Galathea* Expedition took *Galathealinum bruuni* (Kirkegaard, 1956a) in the Celebes Sea; it is probably a characteristic abyssal form of this basin. To the north of the coast of Morotai Island, in the Moluccas, *Siboglinum pinnulatum* and *S. taeniaphorum* are found at 500 m depth (Ivanov, 1960b). *Siboglinum weberi* sensu stricto is known from the Bali, Ceram, Flores, Java, Arafura and Timor Seas. Nine species are known from a single station in the Java Sea and seven from a station in the Flores Sea.Althogether R.V. *Siboga* took 16 species from the seas of the Malay Archipelago, only one of which (*Siboglinum cinctutum*) is known from elsewhere and that as a separate variety. *Siboglinoïdes dibrachia* has also been taken in the Timor Sea and south of Java. Thus, 20 species in all are recorded from these waters, belonging to at least six genera, and all but two are seemingly endemic (Southward, 1961).

The Coral Sea, to all appearances, also has a diverse pogonophoran fauna. At any rate, a few trial dredgings and trawlings made by R.V. *Vityaz'* in the northern parts of this sea yielded a whole series of new species. Here

Siboglinum microcephalum, *S. buccelliferum*, *S. robustum* and *S. frenigerum* were found together with yet another species of *Siboglinum*, still undescribed.

The pogonophoran faunae of the Yellow Sea and of the South China Sea remain completely unknown. In the Philippine Sea, i.e. in the extensive area of waters lying to the east of the Philippines, Taiwan (Formosa) and Okinawa, R.V. *Vityaz*' made several trial dredgings in different places and nowhere found Pogonophora. Since the Philippine Sea is not one of the typical coastal waters it is very probable that the pogonophoran fauna is here very scanty. In this respect apparently the Philippine Sea is like the open reaches of the Pacific Ocean.

Several species of *Siboglinum* (*S. vinculatum*, *S. variablile*, *S. bogorovi* and *S. tenue*) are found off all the coasts of the North Island of New Zealand. An unknown species of the same genus (to judge by the broken fragments of tubes) was also taken considerably to the south of New Zealand. There have recently been new finds off New Zealand, not yet published.

The bottom fauna of the deep water trenches of the western parts of the Pacific Ocean is currently the subject of intensive research. Most of the characteristic ultra-abyssal or hadal species of Pogonophora were taken on cruises of R.V. *Vityaz*' in the Kuril-Kamchatka Trench, the Japan Trench and the Bougainville Trench. In the Kuril-Kamchatka Trench more than ten species have been found, of which seven have been described. Four species have not been found elsewhere, amongst which *Zenkevitchiana longissima* and *Spirobrachia beklemishevi* are particularly worthy of mention. The Japan Trench has been studied far less thoroughly, but it is worth noting that three species encountered—*Lamellisabella johanssoni*, *Diplobrachia japonica* and *Heptabrachia subtilis*—appear to be endemic. Finally, in the Bougainville Trench were found *Cyclobrachia auriculata*, representing a new genus, and fragments of tubes of two nondescript species of *Siboglinum*.

Successful trawlings made by R.V. *Galathea* and R.V. *Vityaz*' in the Philippine, Mariana, Tonga and Kermadec Trenches yielded no Pogonophora whatever. In all likelihood, however, Pogonophora will be found in the Philippine Trench, since they are a characteristic element of the bottom fauna of nearby continental depths. In the trenches far from continental land-masses, on the contrary (Mariana, Tonga and Kermadec Trenches), it is rather unlikely that any Pogonophora will be found.

Only a handful of species have been described from the eastern Pacific Ocean. The first to be recorded were *Krampolinum galatheae* and *Lamellisabella ivanovi*, both from the Gulf of Panama (Kirkegaard, 1956b, 1961). The description of the former species, based only on the tube, is quite inadequate, but nevertheless the species is clearly assignable to the Polybrachiidae, an interesting conclusion for a species from the West Coast of America. The discovery of the second of these species in the Gulf of Panama was also remarkable, for it is undoubtedly a species of *Lamellisabella*. The amphi-Pacific nature of the distribution of the genus *Lamellisabella*, however, seems feasible, since the pogonophoran faunae of the eastern parts of the Bering Sea and the Aleutian Trench remain unknown. Hartman (1961) has recently described *Siboglinum veleronis* from deep water off California and several finds of pogonophores have been made off Oregon. In 1959 the R.V. *Vityaz*' found several new species, including species of *Birsteinia*, *Heptabrachia* and *Galathealinum*, in the north-eastern part of the Pacific Ocean. One of these species has now been described—*Galathealinum brachiosum* Ivanov (1961c), from the west coast of Canada and the coast of Oregon.

Only two species have been described from the Indian Ocean—*Diplobrachia belajevi*, collected by the Soviet Antarctic Expedition of R.V. *Ob*' to the east of Maskaren Island at a depth of 580 m, and *Siboglinoïdes dibrachia*, which has been collected at a number of stations from the entrance to the Gulf of Aden, the Arabian Sea, South of Bali Straits, South of Java and in the Timor Sea. R.V. *Vityaz*' has collected not less than 25 new species in the Indian Ocean, including representatives of *Siboglinum*, *Galathealinum*, *Polybrachia* and *Lamellisabella*.

The study of the pogonophoran fauna of the Atlantic has only just begun. In 1956 Jägersten described *Siboglinum ekmani* from the Skagerrak. In the following year he reported the presence of another species of *Siboglinum* (still undescribed) from the same area (Jägersten, 1957). In the summer of 1957 Kirkegaard also collected abundant material of *S. ekmani* from various points in the Skagerrak and has since collected much more, keeping some of the specimens alive for six weeks (Kirkegaard, 1958, 1961). At the same time the Southwards collected three species of *Siboglinum* at a few stations, situated to the south-west of Great Britain, dredged by R.V. *Sarsia* (Southward and Southward, 1958a; A. J. Southward, 1958), and N. A. Holme rook an undescribed species of *Siboglinum* in 160 m off the west coast of Ireland (A. J. Southward, 1958). Amongst these Atlantic species *S. atlanticum* (Southward and Southward (1958b)) is closely related to *S. taeniaphorum* from the Molucca Islands, while *S. caulleryi* was first described from the Sea of Okhotsk. The eastern Atlantic has yielded two new species, *Oligobrachia ivanovi* and *Polybrachia capillaris*, from deep water off the coasts of England and Spain (E. C. Southward, 1959).

Several new species of *Siboglinum* have been taken in the Norwegian Sea near the Shetland Isles and off the coasts of Norway and Iceland by the Russian ship R.V. *Lomonosov.* In 1959 Brattström collected a species of *Siboglinum* (probably *S. ekmani*) in one of the Norwegian fjords and he has since found abundant material of this same species, together with another undetermined species in all the deep water fjords of the Norwegian coast (Brattström and Fauchald, 1961). It is truly remarkable to find pogonophores in what are virtually inland waters.

No pogonophores have been recorded yet from the wesertn Atlantic* and only one from the southern basin of this ocean—*Heptabrachia talboti* E. C. Southward (1961b) from the coast of South Africa.

In the North Polar Basin several finds of pogonophores have been made. In 1949 Ivanov described *Polybrachia gorbunovi* (as *Lamellisabella gorbunovi*), which was collected by the Arctic Research Expedition of R.V. *Sadko* in the East Siberian sector of the Arctic Ocean. In 1956 the Soviet Arctic Expedition of R.V. *Ob'* found *Siboglinum hyperboreum* near the east coast of Greenland. A new species, at first thought to belong to *Diplobrachia* but now described under the name *Nereilinum murmanicum* Ivanov (1961), has been found in the Barents Sea near Murmansk (Moskalev, 1961), where it seems to be abundant. Southward (1962) has described a new species of *Galathealinum* from the Canadian Arctic and future research in the Polar Basin will undoubtedly bring to light other new species of pogonophores.

At present only *Siboglinum meridiale* is known from the Antarctic, where it appears to be widely distributed throughout the Atlantic sector together with fragments of several undeterminable species. This material was obtained during recent summers by the Soviet Antarctic Expedition of R.V. *Ob'*.

It is obvious that we possess only fragmentary information about the pogonophoran fauna of the oceans, so to present any kind of general conclusion about the geographical distribution of the group would be premature. It is, however, possible to list, with some degree of confidence, the following regularities:

1. Coastal seas and regions off the coasts of continents and large islands are far richer in Pogonophora than are the floors of the open ocean, though finds on the continental shelf are equally rare. It is possible that in places very far from land Pogonophora may generally be absent.

2. The fauna of each of the inshore seas of the Pacific Ocean is characterized by a different assemblage of pogonophores.

3. Trenches situated near to continental land-masses and near to coastal waters have their own specific pogonophoran fauna containing a large proportion of endemic species.

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* But see Bayer (1962).

CHAPTER 14

Systematic Position of the Pogonophora and Evolution within the Class

Are they related to the Annelida?

All the studies of the organization of the Pogonophora which have been published in recent years (Caullery, 1944; Ivanov, 1952, 1955a, b, c, 1957b, 1958a, b, 1960a; Jägersten, 1956, Johansson, 1937, 1939) do not leave any doubt of their oligomerism, or, more precisely, of their trimerism. It is not surprising, therefore, that all zoologists who have deliberated upon their systematic position have begun from the premise of their oligomeric nature (besides the above authors I might mention: Reisinger, 1938; Ushakov, 1940, 1953; Hempelmann, 1943, Beklemishev, 1944, 1951, 1952, 1957, 1958; Dawydoff, 1948; Ulrich, 1950; Boettger, 1952; Dogel', 1954, 1960; Zenkevich, Birshtein and Belyaev, 1954; Abrikosov *et al.*, 1955; de Beer, 1955; Petrunkevitch, 1955; Kirkegaard, 1956a; Alvarado, 1957a, b; Borradaile, Eastham, Potts and Saunders, 1958; Manton, 1958; Southward and Southward, 1958b). The only exception has been Hartman (1954), who looked upon the Pogonophora as polychaetes, regarding them as having changed from a polymeric structure to oligomerism by way of reduction of the dissepiments under the influence of a tubicolous way of life. In her opinion the adhesive papillae of Pogonophora were nothing but a variety of parapodia and their cuticular plaques corresponded to parapodial setae.

There is no need to go into a lengthy critique of these ideas.* Their complete inadequacy is clear from all the fore-going discussion. Neither in their basic body plan nor in their embryological development do the Pogonophora show anything in common with the Annelida.

And if that is so, then the question arises of how we are to regard the similarities with the annelids, which are undoubtedly present in some details of the organization of pogonophores. Amongst such morphological traits we may mention the toothed platelets of the girdles, the provisional bristles of the embryo and some features of the genital system.

The external similarity of the toothed platelets on the girdles of Pogonophora to the uncini of sedentary polychaetes, first noticed by Caullery (1944), can easily be explained by their similar mode of life. Cuticular hooks and

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* Such a critique is given by Ivanov (1955b, c).

teeth, as is well known, are developed in very different animals where they are necessary for steadfast attachment to the substratum. On the contrary, it would have been surprising if a tubicolous animal, which lacks any organic connexion with the tube and which withdraws its front end in a flash when disturbed, did not possess any special provision for securely attaching the hind end of the body deep in the tube.

The profound differences in their mode of formation underline the independent origins of the toothed bristles of pogonophores and the uncini of polychaetes. The former, as we have seen (p. 38), are each secreted inside a single cell, while the latter represent cuticular material secreted outside the cells. There can thus be no homology between the formation of the two.

The parapodia-like tufts of bristles on the metasoma, possessed by the nearly fully formed embryos of *Siboglinum* and *Oligobrachia*, might also suggest an affinity with the annelids. These structures, however, do not show any similarity of detail with the parapodia of annelids. Indeed, in Pogonophora, each provisional bristle is produced inside a multicellular or syncytial sac, all of whose cells take an equal part in the operation: there is no one cell amongst them specialized for this work such as we find in annelids. Hence the bristle sacs of embryonic Pogonophora and the parapodia of Polychaeta can be regarded as no more than analogous structures. To be sure, despite the marked distinction, it is impossible not to remark on the great similarity between them. This is hardly surprising, for in a number of groups of the animal kingdom there are frequently close analogies in many structural details.

Thus, for example, some Brachiopoda, especially Lingulidae, *Chlidonophora chuni* and others, possess numerous setae along the edge of the folds of the mantle. These setae or bristles are enclosed in deep cutaneous invaginations and each one is formed within a single giant cell which clasps its base (Blochman, 1900). The whole structure is very similar to the bristle sac of the parapodia. The likeness is increased by the similar finely fibrous structure of the setae of Brachiopoda and Polychaeta. Moreover, the larvae of some articulate brachiopods (*Argiope*, *Terebratulina*, etc) are furnished with provisional bristles or setae. Kovalevskiŏ (1874) pointed out that these are astonishingly like the parapodia of larval polychaetes. Nevertheless, despite the possession of these parapodia-like structures in both larva and adult, no one would pretend that the Articulata have anything in common with the Annelida. And the analogous bristles of Pogonophora give just as little foundation for any phylogenetic connexion with the polychaetes.

The genital system of Pogonophora seems at first glance to have more in common with that of the Annelida than with that of the Deuterostomia. In the Pogonophora the gonads are closely bound up with the coelomic walls and the germinal cells occupy a retroperitoneal position. In the female the eggs tumble out into the coelom through rupture of the coelomic wall of the ovary. In the male, maturation of the germ cells takes place in the sperm sacs, i.e. in essence in the coelom also. The genital products are passed to the exterior from the coelom through the coelomoducts. These are all characters which are shared with the annelids.

In Hemichordata and Acraniata, on the contrary, the gonads are separated from the general body cavity. It is, however, well known that the gonocytes in these animals too make their first appearance retroperitoneally and only later are the genital organs cut off from the coelom (Spengel, 1893; Zarnik, 1905). In the Echinodermata also the genital primordium is developed in association with the coelom. Finally, in the vertebrates the gonad is formed on the wall of the common coelomic cavity and the genital products fall into the coelom. Thus no significant distinction exists in those aspects which interest us between the genital apparatus of the annelids and the deuterostomic phyla. It is a mark of their extremely primitive condition that the gonad in the Pogonophora is not separated from the coelom, and in this sense they are formally nearer to the annelids than to the Hemichordata, but at the same time they stand on a par with the vertebrates. The similarity with the vertebrates is perhaps a reflexion of their common possession of trunk coelomoducts through which the genital products are discharged from the coelom.

Thus it is clear that in the question of the phylogenetic position of the Pogonophora the genital system gives no grounds for prefering annelid relationships over deuterostomic.

Are they related to the Phoronidea?

The question whether the Pogonophora might be related to the Phoronidea was raised by Johansson (1937, 1939), who immediately answered his own question in the negative. To our eyes the differences between the groups are more profound than Johansson showed. We may note the principle differences, looking first at the promorphological distinctions.

It is well known that the body of *Phoronis* is first formed as an outgrowth from the antero-ventral surface of the actinotroch larva, i.e. the Phoronidea are true Podaxonia (in the sense of Ray Lankester) and the adult body is not in any sense comparable with the body of such protaxonal animals as the Pogonophora. But if, nevertheless, we do compare the various organ systems we can find no grounds for associating the Pogonophora with the Phoronidea. The tentacular crown of *Phoronis*, which at first glance so closely resembles that of Pogonophora, is borne on the mesosoma, while the tentacles of the latter group are protosomal structures. The nephridia of the Phoronidea, in distinction to the protosomal coelomoducts of the Pogonophora, belong morphologically to the metasoma. The blood-vascular and nervous systems of the two groups are sharply distinguished in their fine structure. It has been pointed out by Reisinger (1938) and Johansson (1939) that the median cephalic lobe of Pogonophora might be compared to the epistome of *Phoronis*. It is impossible, however, not to agree with Jägersten (1956) that the foundations for this comparison are as slight as for the recognition of an epistome in the Enteropneusta.

Are they related to the Deuterostomia?

Johansson, recognizing that *Lamellisabella* belonged to a separate class Pogonophora, ascribed it to the superphylum Vermes Oligomera adopted first by Bütschli (1910) and later by Krumbach (1937). It is gradually becoming clear, however, that Bütschli had lumped together too heterogeneous and artificial a group to form the Oligomera. Johansson pointed out the impossibility of associating the Pogonophora with the Phoronidea and that their common inclusion in the Tentaculata would not bear examination, since in the composition of the Oligomera Bütschli also included the Chaetognatha and the Branchiotrema (= Hemichordata), groups which are totally diverse.

One of the essential defects of the Bütschli-Krumbach system is the unjustified break between the Hemichordata and the Echinodermata and Chordata to which they are clearly related. The proximity of the Hemichordata to the prototypes of the echinoderms and chordates, and the essentially common path of embryonic development in these groups, which led to their being united under the name Deuterostomia, was already obvious by the time of Hatschek (1888) and Grobben (1904) and was particularly well demonstrated by the work of MacBride (1914), Fedotov (1923) and Beklemishev (1951). Each of these three groups possesses its own structural plan and, within the Deuterostomia, merits the rank of an independent phylum.

A few zoologists, while not objecting in principle to the division of the Metazoa into Protostomia and Deuterostomia, reckon on formal grounds that these terms are themselves inappropriate. Thus Manton (1958), in her report of the work of Ivanov (1957b) on the embryology of Pogonophora, used in place of the name Deuterostomia the term preferred by many English authors—"the echinoderm-chordate stem". In her opinion the fate of the blastopore does not sufficiently characterize the Protostomia and Deuterostomia, since within the same stem there are groups with different blastoporal fates. The same might be said about such features as the nature of cleavage and the mode of formation of the coelomic mesoderm. It must be stated, however, that all these exceptions to the general rule are merely the results of secondary changes. In other words it is impossible to deny that the fundamental ontogenetic pathway of all the primitive Deuterostomia was: radial indeterminate cleavage, the blastopore associated with the anus, secondary formation of the mouth and enterocoelic origin of the coelom; and in the structure of the adult the common feature has been the trisegmental body plan. [The precise term we use to express this fundamental unity is immaterial, but] there is no real basis for abandoning the terms Deuterostomia and Protostomia.

The current status of our knowledge of the embryological development of the Pogonophora (Ivanov, 1957b) allows us to draw a few conclusions about the systematic position of the group despite the many gaps in our knowledge. As we have seen (pp. 103–119), the embryology of pogonophores in general shows clear evidence of secondary modification—in the bilateral symmetry of the egg and cleavage stages, the lack of an invaginated gastrula and correspondingly of a blastopore and an epithelial archenteron, and in the absence of a pelagic larval stage, so that development is direct. Even the earliest cleavage stages give no information about the primitive mode of cleavage: by the third division, when it usually first becomes clear whether cleavage is spiral or radial, *Siboglinum* has already diverged sharply from either of these modes of development.

Primitive features are, however, still preserved in later stages of development allowing one to compare the embryogenesis of Pogonophora with that of some other animals. Thus the coelomic mesoderm forms by enterocoely and in particular closely resembles the formation of the coeloms in those Enteropneusta which have an egg rich in yolk (*Saccoglossus pusillus*). This alone argues strongly in favour of assigning the phylum Pogonophora to the Deuterostomia. An essential point of similarity with the Deuterostomia lies in the fact that the protocoele is unpaired from the very beginning.

In place of a dipleurula larva Pogonophora produce an elongated embryo whose body is quickly dissected into three segments. In general it recalls the early stages of metamorphosis of Enteropneusta, particularly in those forms with direct development, such as *Saccoglossus kowalewskyi* and *S. pusillus*.

It is interesting that these enteropneusts, like pogonophores, possess an egg rich in yolk and lack a pelagic larva.

The trunk segment or metasoma, moreover, which later becomes the largest part of the body, is at first quite insignificant in size in both Pogonophora and Enteropneusta. In representatives of both groups the trunk then grows apace in length and in the adult animal it reaches a considerable size. Essentially the same thing happens in the development of the Acraniata. It is well known that in *Branchiostoma* most of the body is formed by growth in length of the third or trunk segment whose coelom becomes secondarily segmented.

Finally, the provisional ciliated bands and the ciliated patch on the mesosoma of the embryonic pogonophore must be regarded as rudiments of the ciliary locomotory system found in free-swimming dipleurula larvae.

Thus all the primitive features of embryological development encountered in Pogonophora are in accordance with the idea of their deuterostomic affinities.

Many significant features of the structural plan of the adult pogonophore also point to their location amongst the Deuterostomia, and in particular to their relationship with the phylum Hemichordata, in which the chief marks of the trisegmental deuterostomic archetype are preserved in the adult structure. This relationship was remarked by Dawydoff (1948), Ivanov (1955c) and Jägersten (1956) and particularly clearly stated by Beklemishev (1951). The intervening years have seen a great advance in our knowledge of the organization of the Pogonophora and it is now possible to list the following points of similarity with the Hemichordata:

1. The trisegmental body plan;
2. The unpaired first coelom;
3. The pair of coelomoducts by which the first coelom communicates with the exterior;
4. The possession of a pericardium (though the anatomical nature of this organ remains unclear);
5. The situation of the gonads in the metasoma;
6. The possession of a mid-dorsal nerve trunk running the whole length of the body;
7. The tendency for the dorsal nerve trunk to sink down, in the mesosomal region, to form a neural trough.

A further similarity between the two groups is the tendency towards secondary metamerism of the elongated trunk segment, though this affects more kinds of organs in the Pogonophora.

These features, however, are shared by all the lower Deuterostomia and afford no grounds for including the Pogonophora within the phylum Hemichordata. We must reach the opposite conclusion if we consider the following list of the features of organization which are peculiar to the Pogonophora:

1. The development of tentacles on the protosoma. We do not meet this peculiarity in other Deuterostomia, where tentacular outgrowths—such as the lophophores of Pterobranchia, the ambulacral outgrowths of Echinodermata or the oral cirri of Acraniata—are always attached to the second segment.
2. The great development of the coelomoducts in the trunk segment. Trunk coelomoducts are only otherwise developed in Vertebrata, unless we include the problematical atrio-coelomic funnels of *Branchiostoma* and do not accept the conclusion of Felix and Bühler (1906) that the gonads of Acraniata are homologous with coelomoducts. The Pogonophora are distinguished from the Hemichordata, moreover, by the absence of mesosomal coelomoducts.
3. The development of the chief ganglionic nerve centre in the protosoma.
4. The primitive nature of the genital system as expressed in the close association of the gonad with the coelom and in the trunk coelomoduct's functioning as a genital duct. This is, of course, also found in the vertebrates.
5. The differentiation of a muscular heart on the ventral vessel. No homologue is possessed by other Deuterostomia.
6. The strongly cuticularized skin.
7. The complete absence of any gut, and its function being taken over by the tentacular apparatus.
8. The possession of spermatophores.
9. The greatly modified embryological processes, with no trace of an invaginated gastrula, a blastopore, secondary mouth or pelagic larva.

The absence of gill slits and stomochord or notochord might be no more than consequences of the secondary reduction of the whole gut.

The ability of Pogonophora to produce their own chitinous tube further distinguishes them from other Deuterostomia. But Hyman (1958) correctly remarked that the distribution of chitin throughout the animal kingdom can hardly be regarded as a phylogenetic pointer. The only other group amongst the Deuterostomia in which chitin might possibly occur is the Hemichordata. The evidence is by no means clear upon the constitution of the coenoecia of *Rhabdopleura*, *Cephalodiscus* and the Graptolithoidea. Rudall (1955) could find no trace of chitin in the tube of *Rhabdopleura*. [I have found no trace of

N-acetylglucosamine or glucosamine in hydrolysates of the coenoecia of *Rhabdopleura* and *Cephalodiscus*, while the organic remains of graptolites, like the tubes of Pogonophora, yielded these substances upon enzymic and acid hydrolysis respectively—D.B.C.]

Many of the features of the organization of pogonophores were undoubtedly acquired under the influence of their sedentary way of life. Under this head we may include such features as the replacement of the gut by a tentacular system developed on the front end of the body, performing the functions of food collecting, digestion and absorption. We may also include the secretion of a chitinous tube, whose possession is associated with the extraordinary elongation of the body, and the adaptations which enable the animal to move up and down within it—the bridle, adhesive papillae and girdles of toothed bristles. The adhesive papillae were possibly primitively scattered higgledy-piggledy all over the trunk. Then, in connexion with the nature of their function, they become partially metamerically arranged, a common adaptation to tubicolous life.

We cannot in the long run escape the conclusion that pogonophores are an independent phylum within the Deuterostomia (Ivanov, 1955c; Beklemishev, 1944, 1957)*.

In this connexion it is worth paying attention to the fact that secondary metamerism of the trunk is fairly common amongst the Deuterostomia. It is well known that in Enteropneusta the gill slits, gastro-intestinal pores, branchial blood vessels, hepatic caeca and gonads are all metameric. And metamerism of the Acraniata and vertebrates is also essentially confined to the third of the three primitive segments. In the embryological development of *Branchiostoma*, as is well known, there is a stage when it clearly shows the ancestral trisegmental body plan (MacBride, 1914; Fedotov, 1923; Beklemishev, 1952). The anterior (proboscis) coelom and the middle ("collar") pair of coelomic cavities of the embryo play a very modest part in the organization of the adult *Amphioxus*. But the hind pair of coeloms of the embryo homologous with the third pair of coelomic sacs of the dipleurula and with the coeloms of the trunk of Hemichordata and Pogonophora, form almost all the mesoderm of the adult animal. As the embryo develops the hind pair of coeloms elongate rapidly and undergo secondary metamerization by dividing into somites. This process goes on to produce the metameric musculature of the adult Amphioxus and the consonant metamerism of the nervous system, gonads, gill slits, blood vessels and excretory organs.

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* A. M. Obut (1957) regards the Pogonophora as a subphylum of the Hemichordata. His arguments cannot, however, be taken seriously.

Thus the secondary metamerism of the trunk of Pogonophora is of the same nature as that found in the Enteropneusta and Acraniata, and consequently in the Vertebrata also. A tendency to metamerization of the trunk is evidently characteristic of the Deuterostomia. In the various groups it has appeared independently, involving a variety of organs, but only ever developing in the elongated trunk segment (Ivanov, 1952).

Evolutionary development within the class

When attempting to understand the phylogenetic relationships of the families and genera of Pogonophora, we must place major emphasis upon the structure of the tentacular apparatus and on the degree of secondary metamerism of the trunk.

The general body plan is remarkably constant in the various orders and families of Pogonophora, though the tentacular apparatus presents great variability of form. Because of the great physiological importance of the tentacles (p. 84) the evolution of pogonophores must have been bound up from the first with the progressive development of the tentacular apparatus. This appears to be the key organ system in the phylogenetic development of pogonophores (Ivanov, 1960a). Its structure, therefore, is of major importance for the characterization of the different families and orders.

In general, evolution of the tentacular apparatus has been accompanied by:

1. A gradual increase in the number (polymerization) of tentacles from 6–8 to 200 or more;

2. An increasing number of absorptive pinnules;

3. The formation of a permanent intertentacular cavity, through fusion of adjacent tentacles, replacing the temporary cavity of the more primitive forms.

[It should be noted, however, that the opposite tendencies—towards reduction of tentacles below the primitive half dozen and reduction or loss of the pinnules—have occurred more than once in the evolution of various groups—D.B.C.]

The origin and development of the metamerism of the adhesive papillae and their cuticular plaques have been set out above (pp. 20–25). Here I will only remark that to all appearances the start of the metamerism and its progressive development have taken place independently in different groups. An equal degree of metamerization in two genera is, therefore, no sign of their relationship. A small number of metameric papillae, however, may be taken as indicating a primitive condition.

When we consider the relationship between the different groups of Pogonophora we must pay attention to many other features of organization, such as the secondary fusion of the protosoma with the mesosoma. Such fusion is certainly a manifestation of the growing integration of the more specialized higher forms, but it has arisen independently in different phyletic lines.

Of the two orders of Pogonophora the Athecanephria must be accounted the more primitive. Their tentacular apparatus consists of a few free tentacles each bearing no more than two rows of pinnules. They possess a pericardium, which is lost in the Thecanephria. Physiological contact between the excretory coleomoducts of the protosoma and the blood system is less perfect than in the Thecanephria and takes a more primitive form (pp. 66–70).

The most primitive known athecanephrian genus is, without any doubt, *Oligobrachia*. The small number of free tentacles, the external division between the protosoma and the mesosoma and whole series of other features vouch for this. *Oligobrachia*, moreover, has no sign of any metameric papillae whatever in the preannular region of the metasoma, and the metameric dorsal glandular patches on the postannular region of the trunk are hardly discernible. [Perhaps the nearest genus to *Oligobrachia* is *Nereilinum*, which likewise has no metameric papillae in the anterior part of the trunk. It differs from *Oligobrachia* chiefly in the secondary reduction of the number of tentacles to two. The third genus of the family Oligobrachiidae—*Birsteinia*—differs from *Oligobrachia* in the opposite way, that is to say by increasing the number of tentacles.] *Oligobrachia* has six to nine, *Birsteinia vitjasi* has 12 tentacles. They have a series of features in common which suggest that they should be included together [with *Nereilinum*] in the one primitive family Oligobrachiidae (Ivanov, 1957b). *Birsteinia* is distinguished chiefly in the development of metamerism in the anterior part of the trunk. *B. vitjasi* has 50–55 pairs of metameric papillae furnished with weakly developed cuticular plaques.

Well-developed metameric papillae are found also in [the second athecanephrian family—the Siboglinidae]. Thus *Siboglinum caulleryi*, for example, has 50–75 pairs of papillae (without plaques). *Birsteinia* and the Siboglinidae, however, represent independent branches of development, for the former genus characteristically has a number of tentacles while [*Siboglinoïdes* has only a single pair and] *Siboglinum* has lost all but the first right tentacle (p. 25, 116). Thus the metamerization of the papillae in these two lines has taken place independently. [The reduction in tentacle number to two also seems to have taken place independently in *Nereilinum* and *Siboglinoïdes* (Ivanov, 1961a)].

Within the limits of the one genus *Siboglinum* somewhat different phyletic lines have diverged. Thus it is possible that species with a bipectinate pinnular arrangement—species which are also characterized by a pretentacular groove on the protosoma and a tendency for the rings of the tentacle to form doublets (*S. plumosum*, *S. fedotovi*, *S. ekmani*, *S. pinnulatum*) may form a separate group of species. And *S. atlanticum* and *S. taeniaphorum* are undoubtedly related and sharply distinguished from the remaining species.

Some species of *Siboglinum* are distinguished by their lack of pinnules (*S. inerme*, *S. pellucidum*, *S. hyperboreum*, *S. bogorovi*, etc.). The organization of animals of the genus *Siboglinum* is in general somewhat simplified in comparison with other forms and this is to some extent bound up with the small size of the body. It is interesting that all the species we have just mentioned are amongst the smallest in the genus and the lack of pinnules may be a result of this further reduction in size. The job of absorbing food substances in these species must be taken over by the tentacles themselves. Analogous reduction of physiologically important organs associated with small body size is well known in a variety of animals. Thus some small crustaceans (copepods and others) lack gills and a blood system. Bryozoa have lost their blood system, undoubtedly in association with their small body size which in its turn is associated with the formation of colonies. Whether species of *Siboglinum* which lack pinnules may be accounted near relatives is a moot point. It is possible that reduction of the pinnules has taken place independently in various small forms.

Amongst the Thecanephria the most primitive family is undoubtedly the Polybrachiidae in which the protosoma and mesosoma are divided (except in *Zenkevitchiana*), the tentacles are free and their bases are arranged in the primitive horse-shoe. [If we except *Diplobrachia* and *Sclerolinum*] the smallest number of tentacles (five to eight) is found in *Heptabrachia*, which in this regard is like *Oligobrachia*. In other respects also *Heptabrachia* is primitive. The cephalic lobe is not divided from the protosoma by a secondary ring and the number of metameric papillae in the preannular region is still small (14–20 pairs). Thus we may take *Heptabrachia* as lying near the common stem of the Thecanephria. It is doubtful whether this genus is derived from primitive Athecanephria of the type of *Oligobrachia*; it is more likely that both orders had a very ancient origin and sprang from a common distant ancestor.

Diplobrachia [and *Sclerolinum*] with two tentacles hold the same place amongst the Thecanephria as *Siboglinum*, [*Siboglinoïdes* and *Nereilinum*] amongst the Athecanephria. They are distinguished by their small body size, and, apparently in association with this, by secondary oligomerization of the tentacles. [This seems to have taken place independently in the two genera.]

The evolution of the rest of the Polybrachiidae is characterized chiefly by the progressive multiplication of the tentacles and consequent changes in the arrangement of the horseshoe base of the tentacular crown (p. 26). Thanks to the increase in the number of tentacles and in the number of longitudinal rows of pinnules on each of them, the functional efficiency of the tentacular crown is enhanced; its filtering capacity is improved and the absorptive surface is greater. All Polybrachiidae, except *Diplobrachia* [and *Sclerolinum*], fall into a morphological series in which the number of tentacles increases from five to eight in *Heptabrachia* to more than 200 in *Galathealinum brachiosum*. But the genera of the Polybrachiidae do not form a single line of

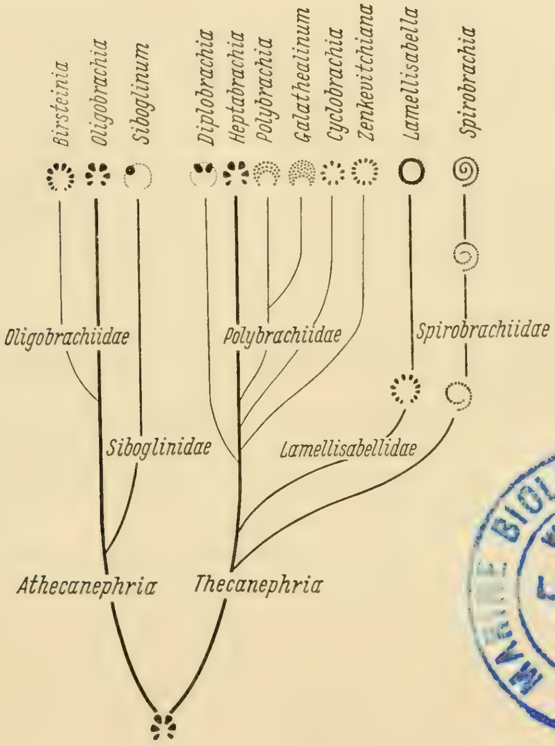


Fig. 88. Diagram of the phylogenetic relationships of the Class Pogonophora, showing also the evolution of the base of the tentacular crown.

development. Thus *Polybrachia* is distinguished by the secondary separation of the cephalic lobe, *Galathealinum* by the formation of ventral, and *Cyclobrachia* by that of dorsal mesosomal outgrowths. It is interesting that among the Polybrachiidae a circular arrangement of the tentacles is already developed in some genera—a feature which is especially pronounced in the Lamellisabellidae. The tentacle base forms a circle in *Heptabrachia beringensis*, *Cyclobrachia* and *Zenkevitchiana*.

The two higher families of the Thecanephria—the Lamellisabellidae and the Spirobrachiidae—have from the very beginning apparently followed a separate phyletic path from the more primitive forms exemplified by *Heptabrachia*. Both these families have the protosoma united with the mesosoma to form a unified fore-part of the body, and each tentacle fused firmly to the next. The evolution of the tentacular apparatus in these two families has, however, followed different paths. A tentacular cylinder is formed in the Lamellisabellidae, while in the Spirobrachiidae the asymmetrical spirally coiled tentacular plate is supported on a special corkscrew-shaped lophophore (p. 27).

My current ideas on the phylogenetic relationships within the Pogonophora are set out in Fig. 88.

CHAPTER 15

Methods of Investigation

The larger species of Pogonophora, possessing comparatively thick tubes, are relatively easily found in the contents of the trawl, dredge, grab or bottom corer. Sometimes, it is true, they may look like the tubes of sedentary polychaetes at first glance, but attentive examination under the binocular microscope soon reveals their true nature. The smaller very fine species, especially some of the tinier *Siboglinum*, might escape detection, but they too are recognizable in most cases upon examination under the higher powers of binocular microscope from the characteristic rings and "segmentation" of the tube. Tubes of pogonophores are rarely preserved whole; usually they are broken or torn. It is therefore desirable to collect all the longest specimens carefully, even if they are empty. Only in this way is it possible to gain some idea of the overall length of the whole tube and details of the structure of the various parts. Separate animals or parts of their bodies can sometimes be found out of their tubes amongst the contents of the dredge or in the washings from sifted soil. Such specimens are particularly valuable, since extraction of the animal from the tube (particularly in some small species) is not always successful. Epibionts (actinians, bryozoans, serpulids, *Scalpellum* and other animals), frequently dwelling on the tubes of some pogonophores, should be fixed without being detached from the tube, since they give one the opportunity of judging something of the way of life of the pogonophore. The greatest scientific interest would attach to any collection showing stages of embryological development in pogonophores. It is therefore well worth while to put on one side any which possess eggs or embryos in the tube. In looking for these tubes one should examine the material under the binocular by transmitted light.

Extraction of the animal from the tubes which have been collected can only be accomplished with great difficulty. It can be carried out by using magnifying spectacles or under the binocular microscope and demands much patience and time. All the material to be dissected should be kept in bowls of sea water cooled with ice, but even under these conditions the animals should not be kept for more than $1\frac{1}{2}$–2 hr before fixation. [*Siboglinum* spp. have been kept alive for six weeks or more in the cold room, but they are light-shy. It seems probable that, as with many deep-sea creatures, the mere actinic rays of light are lethal and they can only survive if sheltered from light. It goes without saying that only intact animals can be kept alive—D.B.C.]

Consistency, rigidity and elasticity vary enormously in the different forms, and it is difficult therefore to indicate any method which might be suitable for the extraction of all animals. Thick rigid tubes are sometimes comparatively easy to remove in bits by chipping or scratching away with a fine sharp scalpel. In some small species, *Siboglinum caulleryi* for example, the tube can be removed rather easily if it is torn lengthwise by means of a pair of mounted needles. In many cases, however, it is not generally possible to extract the animal from its tube without serious damage—for example, the delicate *Siboglinum minutum* from its hard brittle tube, or the very soft *Zenkevitchiana longissima* from its elastic easily torn tube. If, therefore, dissection cannot be accomplished at one stroke, the pogonophore should be fixed in the tube. A few species are generally easier to dissect after fixation when the body has been hardened by alcohol.

For the study of the very fine *Siboglinum* and *Diplobrachia* in particularly stiff tubes, the material may first be soaked in diaphanol. After a few hours the tube is so soft that it may easily be removed. At the same time it becomes completely bleached and transparent, and one may study the external morphology of the animal without removing it from the tube. It is necessary to remember, however, that under diaphanol treatment the cuticular structures—the keels of the bridle, adhesive plaques and toothed bristles of the girdles—are attacked and might be deformed.

Animals still in the tube should be fixed in 70% alcohol only if the consistency of the tube is sufficiently stiff. The alcohol should be changed after 24 hr. Thin soft tubes of *Siboglinum* and the elastic tubes of *Zenkevitchiana* and other forms should be fixed in 2–3 per cent formaldehyde since they shrink or become flattened in alcohol because of the rapid extraction of water and the animal inside is grossly distorted.

For histological fixation Bouin, Zenker, Helly or Stief may be recommended, or a saturated solution of mercuric chloride with acetic acid. These fixatives should also be used for eggs and embryos, extracted from the tube or still in a piece of it.

The simplest fixative for neurohistology appears to be 4–10 per cent neutral formaldehyde in which the material may be stored for up to three months.

For a complete systematic study we need not only the animal itself but its tube too. The external morphology can be studied on fixed material under the binocular or standard microscope, depending on the size. Measurements can be made with dividers or an eyepiece micrometer. The adhesive plaques and the toothed bristles of the girdles can most conveniently be studied on unstained whole mounts in glycerine jelly. In order to study the spermatophores, whose size and shape are important systematic pointers, they should be removed from the anterior part of the spermduct of the male, then, after staining with haemalum, mounted in glycerine jelly or Canada balsam. [I would recommend phase or "Anoptral" contrast for spermatophores—E.C.S. The polarizing and interference microscopes are also useful—D.B.C.]

Study of the internal anatomy and histology of Pogonophora is only possible in sections; whole mounts show very little. Small species may be embedded in paraffin wax and sectioned while still in the tube (e.g. *Siboglinum caulleryi*, *S. ekmani*, etc.). To obtain good sections it is no doubt far better to use proper histological fixatives, but on many occasions alcohol has given quite good results. Sections may be stained differentially with borax carmine, iron haematoxylin, Mayer's haemalum, Mallory's triple stain or azocarmine. [I have found it difficult to section material which is still in the tube without softening the tube first by some means. Diaphanol has the usual drawbacks of grossly damaging the tissues and is not really suitable for anything except whole mounts. I have been successful in using enzymic digestion of the chitin of the tube (Carlisle, 1960)—D.B.C.]

PART II

Systematic Account

Class POGONOPHORA JOHANSSON, 1937

The Pogonophora are marine animals of sedentary habit, mainly inhabiting the abyss, where they dwell in distinctive protective tubes, consisting chiefly of chitin.

The bilaterally symmetrical body consists of three segments—a small protosoma furnished with a cephalic lobe and tentacles, a larger mesosoma, and a very long metasoma—and internally the coelom is subdivided to correspond with the outward segmentation. The unpaired coelomic sac of the protosoma, the protocoele, communicates with the exterior by means of a pair of coelomoducts, which fulfill an excretory function, and coelomic canals lead from it into the tentacles. The mesocoeles, a pair of coelomic sacs lacking coelomoducts, are situated in the mesosoma, and the paired metacoeles in the metasoma. The metacoeles, unlike the mesocoeles, have strongly developed coelomoducts, acting as gonoducts.

The nervous system is primitive, lying wholly within the dermal epithelium. The central part, the "brain", is situated in the protosoma, and from it run a median dorsal nerve trunk and tentacular nerves.

There is no alimentary canal, mouth or anus whatsoever, and digestion is performed by the distinctive tentacular apparatus.

The vascular system forms a closed circulation, consisting of dorsal and ventral vessels which communicate anteriorly through the system of tentacular vessels, and posteriorly by means of transverse vessels. That part of the ventral vessel which lies at the base of the tentacles is differentiated into a muscular heart, which in some Pogonophora is bordered by a pericardial sac.

The sexes are separate, without sexual dimorphism, and the single pair of gonads lies in the metasoma. The sperm are confined within membranous spermatophores which are furnished with long, thin filaments. The eggs, rich in yolk, develop within the protection of the maternal tube. Cleavage is total, unequal and bilateral, and neither a blastopore nor a secondary mouth is formed. The coelom is formed enterocoelically. There is no free-swimming larva and no metamorphosis.

The class Pogonophora has two orders, the Athecanephria and the Thecanephria.

Key for the determination of orders, families and genera of Pogonophora

1 (10) Metameric dorsal shields, or more or less metameric glandular portions of the integument, are present in the postannular region of the trunk. Transverse rows of cuticular plaques are usually absent from the postannular region. The spermatophores are spindle-shaped. The tentacles are always free. The anterior part of the tube is always flimsy.
1. Order Athecanephria (p. 154).

2 (7) Usually 6–10 tentacles; if only 2 tentacles then the anterior part of the trunk is without pronounced metamerism.
I. Family Oligobrachiidae (p. 154).

3 (6) Less than 10 tentacles. Anterior part of the trunk has no paired metameric papillae.

4 (5) Tentacles 6–9, bearing pinnules. *1.* Genus *Oligobrachia* (p. 154).

5 (4) Two tentacles; no pinnules. *2.* Genus *Nereilinum* (p. 162).

6 (3) Twelve tentacles. The anterior part of the trunk bears more or less metameric paired papillae, which sometimes carry cuticular plaques.
3. Genus *Birsteinia* (p. 169).

7 (2) Not more than two tentacles. Paired metameric papillae are present.
II. Family Siboglinidae (p. 174).

8 (9) One tentacle. *1.* Genus *Siboglinum* (p. 174).

9 (8) Two tentacles. *2.* Genus *Siboglinoïdes* (p. 325).

10 (1) The postannular region of the trunk lacks metameric dorsal shields or glandular areas, and carries metameric transverse rows of adhesive cuticular plaques. The spermatophores are leaf-shaped. The tentacles may be free, or neighbouring ones may adhere at the base. The anterior part of the tube may either be flimsy or end in a hard funnel.
2. Order Thecanephria (p. 331).

11 (24) Tentacles free. Cuticular plaques in the anterior part of the trunk, if any are present at all, lie directly on the papillae. The anterior part of the tube is flimsy, with walls which collapse easily.
I. Family Polybrachiidae (p. 332).

12 (21) Tentacles 2–14. The cephalic lobe merges into the protosoma.

13 (18) The protosoma is divided from the mesosoma by a groove. The anterior metameric papillae possess cuticular plaques.

14 (17) Tentacles 5–13. The keels of the bridle are simple.

15 (16) The base of the tentacular crown is horseshoe-shaped. The cuticular plaques on the anterior papillae are round or oval, with crescentic front edges. There are not more than 30 pairs of metameric papillae. The toothed platelets of the girdles lie in 1–3 rows. The tube may have regular or irregular rings. *1.* Genus *Heptabrachia* (p. 332).

16 (15) The base of the tentacular crown is in the form of a circle. The cuticular plaques of the anterior papillae are kidney-shaped, with hoop-shaped front edges. There are more than 100 pairs of metameric papillae. The toothed platelets of the girdles lie in 3–4 rows. The tube is not ringed. *2.* Genus *Cyclobrachia* (p. 365).

17 (14) Tentacles 2–4. The keels of the bridle consist of an axis, to which, from behind on the ventral side, are attached cuticular rodlets. *3.* Genus *Diplobrachia* (p. 370).

18 (13) The protosoma is not divided from the mesosoma. The anterior metameric papillae lack cuticular plaques.

19 (20) Two tentacles. The mesosoma is not divided from the metasoma. The tube is ringless, unsegmented, transparent, colourless or yellow and has very thick rough walls. *7.* Genus *Sclerolinum* (p. 418).

20 (19) More than 10 tentacles. The mesosoma is clearly divided from the metasoma. The ringless tube is segmented, opaque and white, with smooth walls. *4.* Genus *Zenkevitchiana* (p. 388).

21 (12) Tentacles not less than 18. The cephalic lobe is divided from the protosoma by a pretentacular groove, or at least in some measure (in individuals with the body extended) the two are sharply distinguished by the colour and character of the integument.

22 (23) The mesosoma in front of the bridle is ringed with transverse grooves and lacks wing-shaped cutaneous folds. Tentacles 18–70 or more. Each papilla bears a single cuticular plaque. *5.* Genus *Polybrachia* (p. 393).

23 (22) The mesosoma in front of the girdle is not ringed and possesses wing-shaped cutaneous folds. Tentacles 78–268. Some papillae in the non-metameric part of the trunk bear several plaques each. 6. Genus *Galathealinum* (p. 403).

24 (11) Each tentacle adheres to the next. The cuticular plaques in the anterior part of the trunk lie on pulvilli, situated on the papillae. The mouth of the tube is stiff and funnel-shaped.

25 (26) Tentacles 10–31, fused into a hollow cylinder. The cuticular plaques on the front part of the trunk are shaped like horseshoes.
II. Family Lamellisabellidae (p. 421).
1. Genus *Lamellisabella* (p. 421).

26 (25) Tentacles 39–223, fused into a tentacular plate which is rolled up into a spiral. Cuticular plaques in the front part of the trunk shaped like brackets or hoops.
III. Family Spirobrachiidae (p. 445).
1. Genus *Spirobrachia* (p. 445).

1. Order ATHECANEPHRIA IVANOV, 1955

The first coelom is sac-shaped, and its coelomoducts are wide apart, with their excretory sections closely adjoining the lateral cephalic vessels. There is a pericardium close to the dorsal part of the heart, and the protosoma is separate from the mesosoma. There may be only one tentacle (in the genus *Siboglinum*), or if there is more than one they are always separate. On the dorsal side the postannular region of the metasoma bears metamerically arranged glandular sections of the epidermis or solitary glandular shields, and on the ventral side there may be a solitary large papilla opposite each of these. The spermatophores are spindle-shaped. The greater part of the tube is ringed and sometimes also segmented, while the anterior section is flimsy, with delicate, growing walls which collapse easily.

The Athecanephria includes two families, the more primitive Oligobrachiidae, and the unitentaculate Siboglinidae, characterized by secondary simplification.

I. Family Oligobrachiidae Ivanov, 1957

[The recent discovery of *Nereilinum* and *Siboglinoïdes* has necessitated revision of the diagnosis of the Oligobrachiidae. The revised diagnosis is given here instead of the one given in the Russian edition of this book.

The Oligobrachiidae are Athecanephria with a small number of tentacles, usually six to twelve, but sometimes reduced to a single pair. The base of the tentacular crown is horseshoe-shaped, and the pinnules lie along the tentacles in two rows. Papillae are not usually developed in the preannular part of the trunk, nor is there any sign of secondary metamerism in this region (except in *Birsteinia*). There are three genera – *Oligobrachia*, *Birsteinia* and *Nereilinum*. Type of the family: *Oligobrachia* Ivanov.]

1. Genus *Oligobrachia* Ivanov, 1957

Ivanov, 1955a: 177 (nom. nud.); Ivanov, 1955b: 382 (nom. nud.); Ivanov, 1955d: 173, 174 (nom. nud.); Ivanov, 1956b: 1864 (nom. nud.); Ivanov, 1956c: 165, 169 (nom. nud.); Abrikosov, 1957: 236; Alvarado, 1957b: 495; Ivanov, 1957a: 433–9, 490, 491, 493, 495–8; Ivanov, 1957b: 1127, 1128, 1134–8; Beklemishev, 1958: 367; Dajoz, 1958: 231, 232, 234, 235; Ivanov, 1958a: 1369; Ivanov, 1958b: 1682; Ivanov, 1958d: 1; Ivanov, 1958e: 1070, 1075–8; Manton, 1958: 750; Ivanov, 1960a: 1528, 1530, 1531, 1535, 1538, 1539, 1541, 1550, 1560, 1573, 1590, 1593, 1601, 1603, 1606, 1614, 1620; Ivanov, 1960c: 5, 11, 12, 15, 19, 24, 27, 37, 48, 60, 76, 87, 89, 91, 98, 105, 106, 107, 114, 115, 116, 220.

There are 6–9 tentacles on which the pinnules lie in double alternating rows. The cephalic lobe is not demarcated, but the protosoma is separated from the mesosoma by a slanting groove. There are no plaques. The preannular region of the trunk lacks any trace of metameric papillae, but, instead, there are continuous lateral glandular ridges. A trace of metamerism is visible on the postannular region, however, where irregular glandular areas of the dorsal integument are arranged more or less in this way. The spermatophores are spindle-shaped and the tube is unsegmented, with regular rings.

The absence of metamerism in the anterior part of the trunk, the mere trace of it in the postannular part and the small number of free tentacles, arranged in a horseshoe at their base, show that *Oligobrachia* is the most primitive genus among the Pogonophora (p. 141).

Type of genus: *Oligobrachia dogieli* Ivanov.

Key for the identification of the species of the genus *Oligobrachia*

1 (2) The papillae of the zone of thickening bear semilunar plaques, about 30–35μ across, thickened along the front edge. The cephalic lobe and the part of the mesosoma behind the bridle are glandular. There is a pair of longitudinal stripes alongside the dorsal ciliated band. The tube is black and the rings stick out above its surface. *O. ivanovi* (p. 160).

2 (1) There are no plaques on the papillae of the zone of thickening. The cephalic lobe and the mesosoma are not glandular. There are no longitudinal dorsal stripes. The brown rings of the tube are not protuberant. *O. dogieli* (p. 155).

1. Oligobrachia dogieli Ivanov (Figs. 89–92)

Ivanov, 1957a: 434–9, 490–3, 495–7, Figs. 1–5, 59; Alvarado, 1957b: 495; Ivanov, 1957b: 1127, 1128, 1134–8, Figs. 2, 12–14; Dajoz, 1958: 231, 235; Ivanov, 1958a: 1369; Ivanov, 1958b: 1682, Figs. 1, 4: Ivanov, 1958d: 1; Ivanov, 1958e: 1070, 1075–8, Figs. 6–8; Manton, 1958: 750, Figs. 17, 20, 22; Ivanov, 1960a: 1531, 1536, 1542, 1550, 1562, 1567, 1592, 1593, 1600, 1604, 1606, 1608, 1611, 1612, Figs. 1397, 1399, 1424, 1428, 1432, 1452, 1460, 1462, 1463 Pl. VII; Ivanov, 1960c: 5, 9, 10, 15, 19, 22, 36, 50, 54, 78, 85, 89, 91, 92, 93, 95, 96, 105, 116, 145, 265, Figs. 15, 17, 43, 48, 52, 71, 79–81, 87, 89–92, Pl. II.

The length of the anterior section (the protosoma together with the mesosoma) is 8 times greater than the breadth. The small protosoma is limited behind by a deep groove whose ventral ends do not meet, while the dorsal part makes a backwardly directed right-angle, overlapping the dorsal end of the bridle (Fig. 89*A*, *B*). Thus the protosoma is much shorter on the ventral than on the dorsal side. The cone-shaped cephalic lobe is not divided from the protosoma (Fig. 89*A*, *B*), and the crown of tentacles is attached at

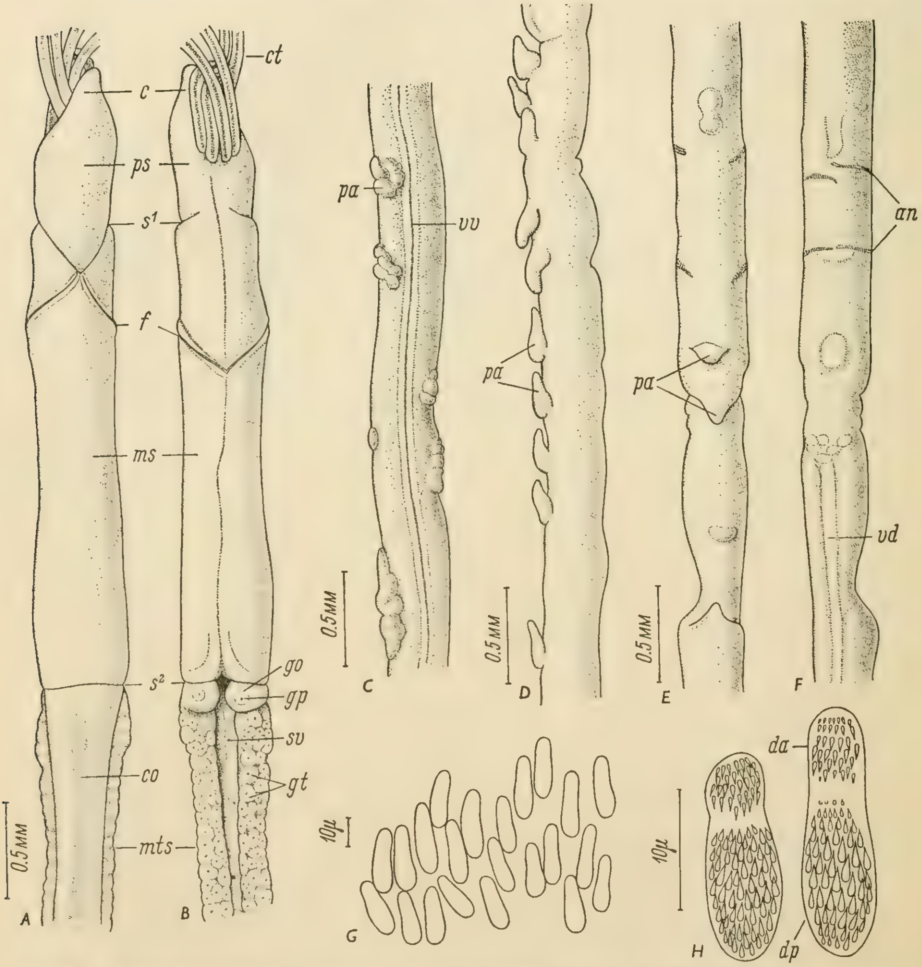


Fig. 89. *Oligobrachia dogieli*: *A* – front part of the body of a male in dorsal view; *B* – the same in ventral view; *C* – a portion of the middle part of the preannular region in ventral view; *D* – zone of thickened papillae from the left side; *E* – region of the girdles in ventral view; *F* – the same from the dorsal side; *G* – part of a girdle; *H* – toothed platelets.

an – girdles of toothed platelets; *c* – cephalic lobe; *co* – dorsal ciliated band; *ct* – tentacular crown; *da* – anterior group of teeth; *dp* – posterior group of teeth; *f* – keel of the bridle; *go* – genital papilla; *gp* – genital pore; *gt* – pyriform glands seen by transparency; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *vd* – dorsal blood vessel seen by transparency; *vv* – ventral vessel seen by transparency. (*A*, *B*, *C*, *E*, *F* – after Ivanov, 1957a.)

its base. The tentacles, whose number varies from 6 to 9, are attached in a single row, horseshoe-wise, whose ends turn inwards on the ventral side and almost close up into a full ring. The tentacles are 6–10 times longer than the anterior section of the body, and each of them bears on its inner side two rows of very delicate pinnules, 0·75 mm long, so arranged that they alternate with one another (Fig. 90). Microscopic study of living tentacles clearly reveals afferent and efferent blood capillaries running together at the tip of each pinnule, while groups of granular gland cells are visible in the tentacles themselves.

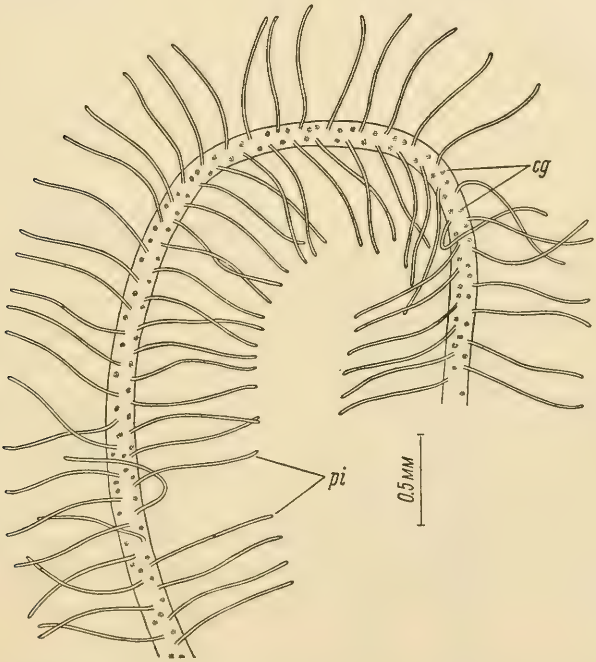


Fig. 90. *Oligobrachia dogieli*: Part of a tentacle *in vivo*. *cg* – gland cells; *pi* – pinnules. (After Ivanov, 1957a.)

On the ventral surface of the cylindrical mesosoma runs a narrow median furrow (Fig. 89*A*, *B*), and the delicate yellowish keels of the bridle, lying on cutaneous folds, are continuous on the ventral side, but broken dorsally, where their ends become thinner.

The front part of the metasoma, or trunk, has a well-marked ventral groove, which is bounded on each side by a wide ridge, through whose integument may be seen numerous pyriform glands, crowded together higgledy-piggledy, cheek by jowl with one another (Fig. 89*B*). This part of the trunk is remarkable for the lack of papillae and cuticular plaques, so that there is no trace whatever of the metamerism so characteristic of this region in other Pogonophora. In the male a pair of rounded genital papillae are placed ventrally at the front end of the metasoma (Fig. 89B). The dorsal ciliated organ (Fig. 89*A*) is visible as a narrow tract, blunt at its front end and beginning not far from the circular groove dividing the mesosoma from the metasoma. The ventral groove continues for some way along the metasoma and then flattens out, the body becomes more or less cylindrical and the lateral ridges gradually disappear, disintegrating into irregularly spaced glandular regions of rather indefinite form (Fig. 89*C*). This section of the trunk is of considerable length, making up the greater part of the body, and it is interesting that here, too, adhesive plaques are absent. For detailed study, the zone of thickened papillae was taken from a female (Fig. 89*D*). It was found to possess ten large transparent conical papillae, spaced out in a single ventral row.

There are two closely contiguous girdles, which are broken ventrally, while the foremost is also split on the dorsal side (Fig. 89*E*, *F*). The yellowish toothed platelets, 16–23μ long, are arranged in three, or sometimes two, irregular rows (Fig. 89*G*). Individually they are elongated in form, somewhat narrower at the front end and bear two groups of teeth. The anterior group, directed backwards, is confined to an area approximately one-third the size of the space occupied by the posterior teeth, which are directed forwards (Fig. 89*H*). Two papillae, devoid of cuticular plaques, lie in the mid-ventral line behind the girdles. The dorsal side of the long postannular part of the trunk is more or less uniform, except for broad glandular regions spaced at rather wide intervals and resembling the dorsal glandular shields of *Siboglinum* (Figs. 14, 112) but more weakly developed. There are no cuticular plaques.

In one of the individuals studied (a female) the whole body was preserved, except for the tentacles. The overall length of this specimen was 12 cm, almost all of which was taken up by the trunk, the preannular part accounting for about 9 cm and the postannular part for about 3 cm. To judge by other individuals whose tentacles were preserved, these latter would reach about 16 mm. The anterior section of the body is 2·8–3·3 mm in length and 0·3–0·4 mm in breadth. The breadth of the trunk in the anterior region is 0·3–0·5 mm. The ratio of length to breadth of the body is thus approximately 400 : 1.

The spermatophores (Fig. 91) are greatly elongated spindles, pointed at one end, while from the other springs out a long thread, at whose base the delicate membrane of the spermatophore forms a pair of wing-like expansions. The proximal part of the thread is comparatively stout for a significant length, then the thread gradually diminishes in thickness, passing into a delicate long distal part.

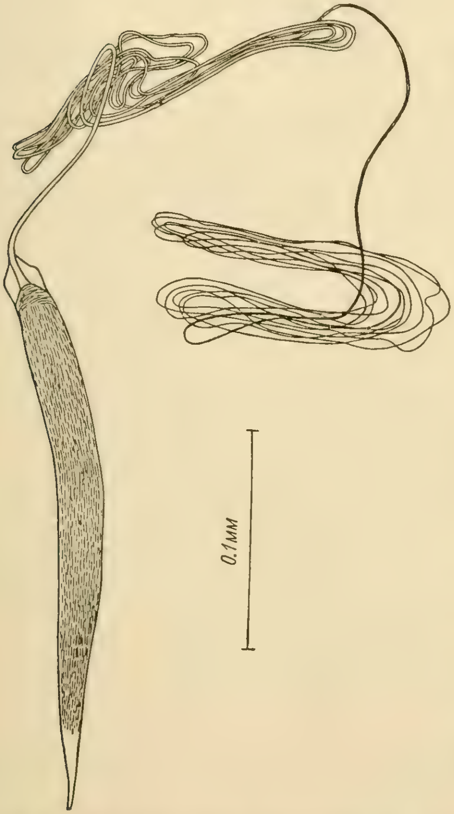


Fig. 91. *Oligobrachia dogieli*: Spermatophore. (After Ivanov, 1957a.)

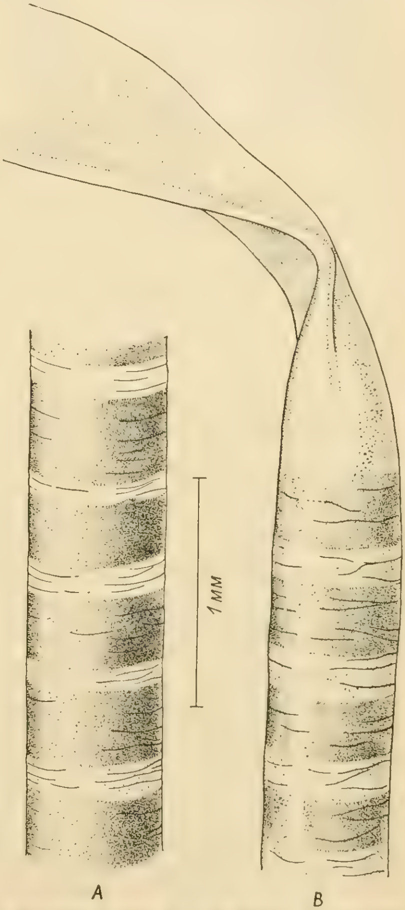


Fig. 92 *Oligobrachia dogieli*: Tube: *A* – middle part; *B* – anterior part. (After Ivanov, 1957a.)

The ringed tube (Fig. 92) is very firm but elastic, and dark-brown in colour. The length of the equal regular brown rings is about one-half to two-thirds of the diameter of the tube and they are separated by narrow transparent spaces. Both the rings and the spaces are transversely folded and wrinkled. Towards the front end of the tube the rings gradually become paler and finally vanish, so that the anterior extremity is membranous, very delicate, colourless and transparent, with walls which collapse rather easily (Fig. 92*B*). Towards the hind end also, the rings vanish and the tube becomes semi-transparent (in preserved material generally of a yellowish tint), but, in contrast to the front end, the walls here are very firm, and the surface is covered in weak longitudinal ribs or folds. The biggest known fragment of tube measures 25 cm and the anterior membranous part of another specimen reaches 3 cm in length. The diameter of the tube near the front end varies between 0·5 and 9·62 mm.

Material: part of 16 individuals, all incomplete, and a few dozen torn-off empty tubes.

Localities: the sub-littoral and semi-abyssal zones of the western and northern parts of the Okhotsk Sea in depths of 119–572 m. One example was taken also from farther east, south of Kamchatka, in abyssal depths (2532 m). In addition two fragments of empty tubes were discovered in the abyssal zone of the Japan Sea at 2850 m depth.

2. *Oligobrachia ivanovi* E. C. Southward (Fig. A92)

E. C. Southward, 1959; 38, 439-41, 444, Fig. 1.

[This species was unknown to Ivanov at the time of publication of the Russian edition of this book, and the following description is quoted almost verbatim from Dr. Southward's original description. In order to bring this description into line with the others in this monograph I have taken the liberty of transposing paragraphs and sentences so that the various parts of the body shall be described in the same order, and to the same end I have altered the nomenclature slightly. I am grateful to Dr. Southward and to the Council of the Marine Biological Association of the United Kingdom for granting permission to reproduce both the description and the illustration — D.B.C.]

"Only one specimen of this species has been found . . . collected on 28 November, 1958, at 48°26′N 10°8′W on a cruise of R.V. *Sarsia*. It has been named after Prof. A. V. Ivanov. The animal is 95 mm long, and since only 10 mm of the postannular region of the trunk is present the complete animal must have been considerably longer. Its diameter is about 0·5 mm and its colour is greenish brown with brown tentacles and red blood. There are 7 tentacles, coiled together, which are 12 mm long. Each has a double row of pinnules along the inner side (the length of the pinnules being about equal to the diameter of the tentacle) and a band of brown spots on the outer side (Fig. A92*D*). The tentacles are joined to the protosoma in a circle just in front of a slight transverse groove (Fig. A92*B*). The protosoma is about 0·8 mm long and is separated from the mesosoma by an oblique groove which reaches the anterior point of the bridle on the dorsal side. Patches of white glands are present on the proto- and mesosoma and their positions are shown in Fig. A92*B* and *C* by heavy stipple.

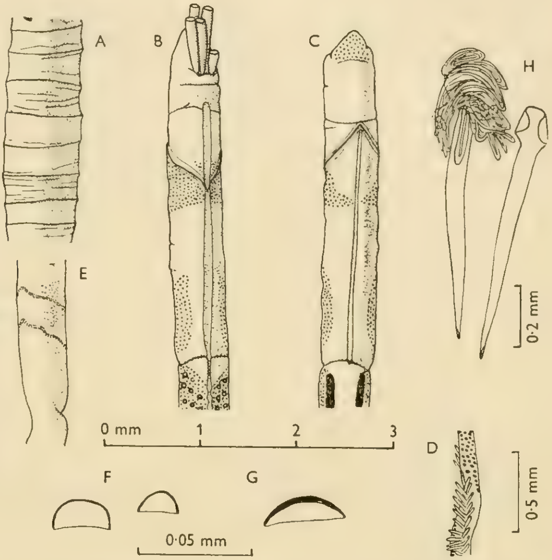


Fig. A92. *Oligobrachia ivanovi: A* – part of the tube (surface view); *B* – anterior end, ventral view; *C* – anterior end, dorsal view; *D* – part of tentacle; *E* – girdle region; *F–G* – adhesive plates from smaller and larger papillae of trunk; *H* – spermatophores, filament removed from one.

"The anterior part of the metasoma or trunk, called the metameric region in other genera, has white epidermal glands arranged in 2 lateral bands separated by a deep sulcus ventrally and by 2 dark brown stripes dorsally. Between the brown stripes lies the dorsal ciliated band which is pinkish white. The white bands are spotted with 3 to 4 rows of clear patches which mark the openings of internal pyriform glands. These patches lie in regular oblique lines and show up clearly because they are surrounded by brown rings. This glandular region of the body is 10 mm long. The second region of the metasoma lacks epidermal glands but bears numerous small papillae arranged in 2 irregular rows along the ventral side for about 50 mm. The rows of small papillae are followed by large papillae, arranged in 3–4 rows, extending for 10 mm, the zone of thickened papillae, while the last 5 mm of the preannular region is devoid of all but a few small papillae. Both large and small papillae are armed with half-moon-shaped adhesive plaques (Fig. A92*G*), but the plaques are difficult to see because they are almost colourless. There are 2 girdles (annuli), which both encircle the body completely, and each is made up of 2 to 3 rows of platelets. The last 10 mm of the body has no papillae, plaques or epidermal glands and is broken off abruptly.

"The preannular part of the trunk contains spermatophores which are 0·85 mm long and spindle-shaped. When the filament is removed the filamentar end of the spermatophore is seen to be flattened and drawn out into 2 flaps, which are usually folded inwards (Fig. A92*H*).

"The tube is black and completely opaque, and was 25 cm long before being broken to remove the animal. The diameter of the tube varies along its length from 0·5 to 0·9 mm. The wall is stiff and is made of several layers of brown material with a transparent lining layer; its outer surface has narrow raised rings at fairly regular intervals (Fig. A92*A*).

"*O. ivanovi* differs from *O. dogieli* in having plaques on the trunk papillae, and in this respect it resembles *Birsteinia vitjasi* and confirms Ivanov's hypothesis that the 2 genera are closely related. The spermatophores of *Oligobrachia dogieli* and *O. ivanovi* both have wing-like flaps at the filamentar end while there are no such flaps in *Birsteinia* or any other pogonophore yet described. Other characters in common between the 2 species of *Oligobrachia* are the curious patches or spots on the tentacles, and the comparatively long pinnules. The tentacles in *Birsteinia* have very short pinnules and, apparently, no spots or glands of any sort (Ivanov, 1952a)."

Material: one male, lacking most of the postannular region.

Locality: off the mouth of the English Channel (48°26′N 10°8′W).

Depth: 1335–1425 m.

TABLE A1

Characteristics of the species of *Oligobrachia*

	O. dogieli	*O. ivanovi*
Breadth/length ratio of fore-part	$\frac{1}{8}$	$\frac{1}{6}$
Number of tentacles	6–9	7
Pretentacular groove	—	+
Keels fused dorsally	—	+
Cuticular adhesive plaques	—	+
Girdles	Broken	Complete
Length of toothed platelets (μ)	16–23	?
Breadth of mesosoma (μ)	300–400	500
Length of spermatophore (μ)	240	850

2. Genus *Nereilinum* Ivanov, 1961

Ivanov, 1961a: 388; Ivanov, 1961b: 138–9.

The genus consists of Oligobrachiidae with two tentacles and a pronounced secondary metamerism of the metasomal pyriform glands. These glands, at the anterior end of the metasoma, are not set in papillae. The bridle is simple and its keels lack any accessory rodlets. There are no adhesive plaques. The postannular region of the metasoma bears metameric ventral papillae and dorsal shields. The tube is ringed but not segmented.

There is a single species, the type of the genus: *Nereilinum murmanicum.*

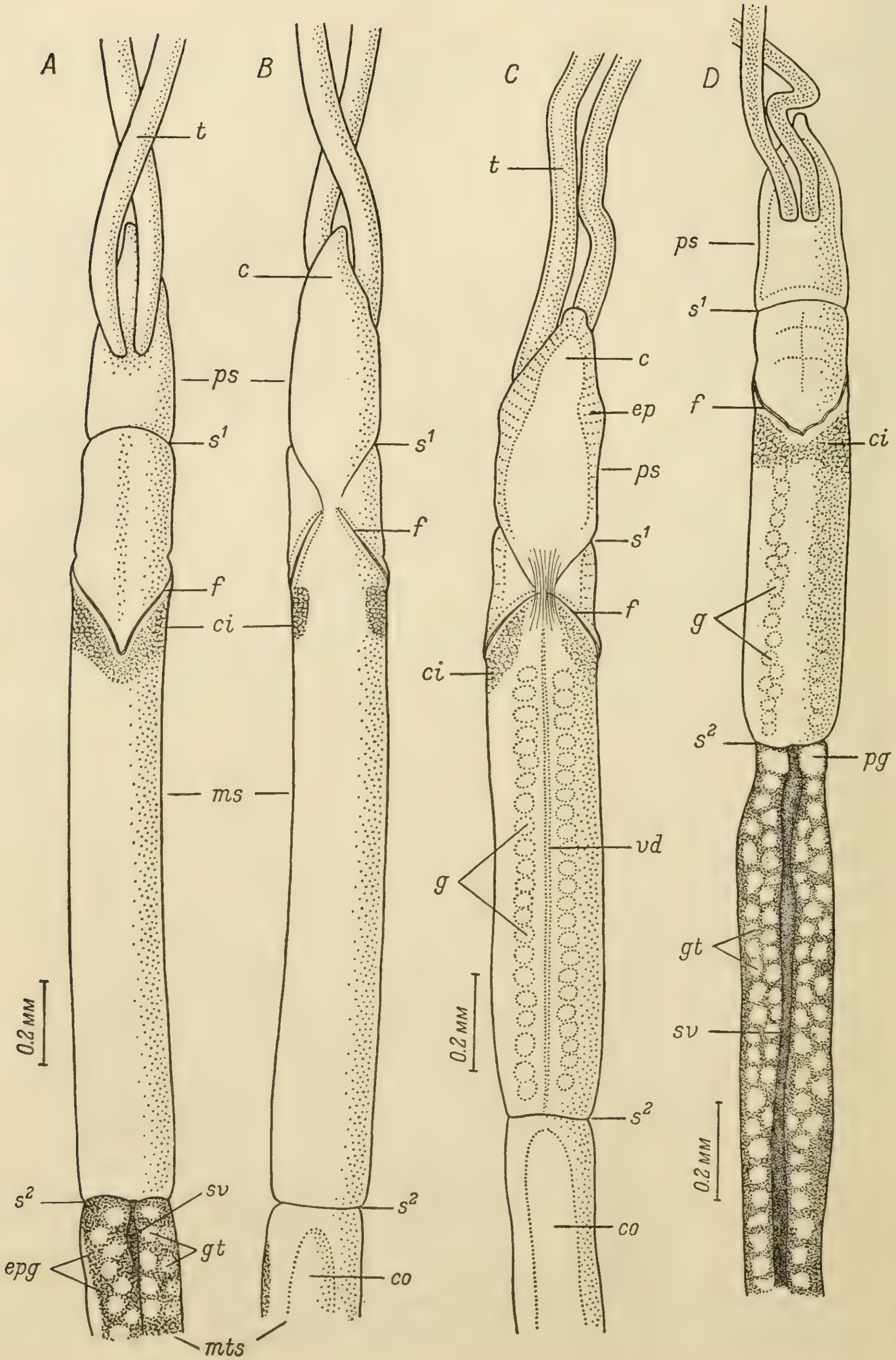
1. Nereilinum murmanicum Ivanov, 1961 (Figs. B, C, D, 92)

Ivanov, 1961a: 381–388, 396, Figs. 1–3; Ivanov, 1961b: 138, Fig. 1; Moskalev, 1961.

Pogonophora have recently been discovered in the Barents Sea (Moskalev, 1961) near to the Murmansk Institute of Marine Biology, where they have been kept alive in the laboratory. Material sent to me from this laboratory proved to be a new species which was named *Nereilinum murmanicum.*

The body is slender, no more than 0·32 mm in diameter. The fore-part of the body is cylindrical and smooth with a length to breadth ratio of 6 : 1 to 10 : 1 according to the degree of contraction of the body (Fig. B92). The bridle is placed at the end of the first third of the fore-part of the body. The groove between the protosoma and the mesosoma runs straight across the ventral side but dorsally it turns backwards to meet the dorsal ends of the keels of the bridle (Fig. B92*A*, *B*, *C*). The protosoma is thus much longer on the dorsal than on the ventral side. The small conical pointed cephalic lobe is not separated from the protosoma by any groove. Two tentacles are attached halfway between the anterior tip of the body and the hind end of the protosoma. They are long and delicate and lack pinnules. The epidermis of the tentacles is rather thin. The bridle is furnished with simple thin brownish keels which join on the ventral surface and just fail to meet dorsally. The epidermal ridges of the bridle are narrow but readily visible. Behind the bridle and in contact with it is a half ring of glandular tissue which is broken on the ventral side. In the majority of specimens the dorsal and ventral blood vessels and the round epidermal glands of the mesosoma are visible by transparency. The glands are only to be found behind the bridle where they form a more or less regular avenue on either side of the mesentery (Fig. B92*C*, *D*). The boundary between the mesosoma and metasoma is marked by a simple circular groove (Fig. B92).

The well-marked ventral sulcus of the anterior part of the metasoma is flanked by a pair of latero-ventral epidermal ridges inside which the clear pyriform glands can be seen by transparency. There are no adhesive papillae or plaques, and the glands are distributed in a rather haphazard manner, especially in the anterior region, where they usually are ranged two or three deep (Fig. B92*A*, *D*). Farther back, however, in certain specimens they become gradually more regular in their distribution, becoming reduced to a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single row in each ridge and often placed two by two. The glands hardly increase in size towards the back of this "metameric region". I have counted the number of "metameric" glands on ten specimens and found them to vary between 62 and 95 on each side of the body. The epidermis of the latero-ventral ridges is extraordinarily rich in gland cells: by transmitted light it is completely obscured because of the presence of a granular secretion in these cells. Thanks to this opacity the transparent pyriform glands stand out very plainly. This glandular epidermis of the metameric region of the metasoma is very like that found in some species of *Siboglinum* (e.g. *S. taeniaphorum* and *S. atlanticum*), where, however, it is confined to a longitudinal glandular band outside the papillae, whereas in *Nereilinum murmanicum* it covers the whole latero-ventral surface. The broad dorsal ciliated band is plainly visible and starts almost at the very beginning of the metasoma (Fig. B92*B*, *C*).

The "metameric region" only occupies a relatively short stretch of the preannular region; the greater part of this section of the body bears numerous glandular epidermal warts or papillae, very variable in shape and size (Fig. C92*A*). A zone of thickened papillae is present, formed of 5 to 10 large conical papillae disposed in a single row on the ventral side, one behind the other (Fig. B95*B*). They do not bear cuticular plaques. The part of the metasoma between this region and the girdles has no noteworthy features.

The two girdles are situated close together and both are widely broken ventrally. On each girdle the toothed platelets form two irregular rows (Fig. C92*C*, *D*, *E*). Behind the second girdle lies a large conical ventral papilla, lacking a cuticular plaque (Fig. C92*C*). The yellowish toothed platelets of the girdles are appreciably narrower at the front end. The anterior group of teeth is well developed but occupies no more than a quarter of the area of the platelet (Fig. C92*F*), and behind it runs a narrow transverse band. The posterior teeth are much larger and arranged in 8–10 oblique rows (Fig. C92*F*). The platelets are between 15 and 18μ long.

The postannular region of the metasoma is long and thin. In most individuals it was macerated and it was preserved in only a few specimens. Along

Fig. B92. *Nereilinum murmanicum.* The front ends of 3 specimens: *A*, *B* – a female in ventral and dorsal view; *C* – a female in dorsal view; *D* – a male in ventral view.
c – cephalic lobe; *ci* – glandular ring of the mesosoma; *co* – dorsal ciliated band; *ep* – epidermis; *epg* – concentration of epidermal gland cells; *f* – bridle; *g* – mesosomal glands; *gt* – metasomal pyriform glands; *ms* – mesosoma; *mts* – metasoma; *pg* – male genital papilla; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle; *vd* – dorsal blood vessel. (Ivanov, 1961*a*.)

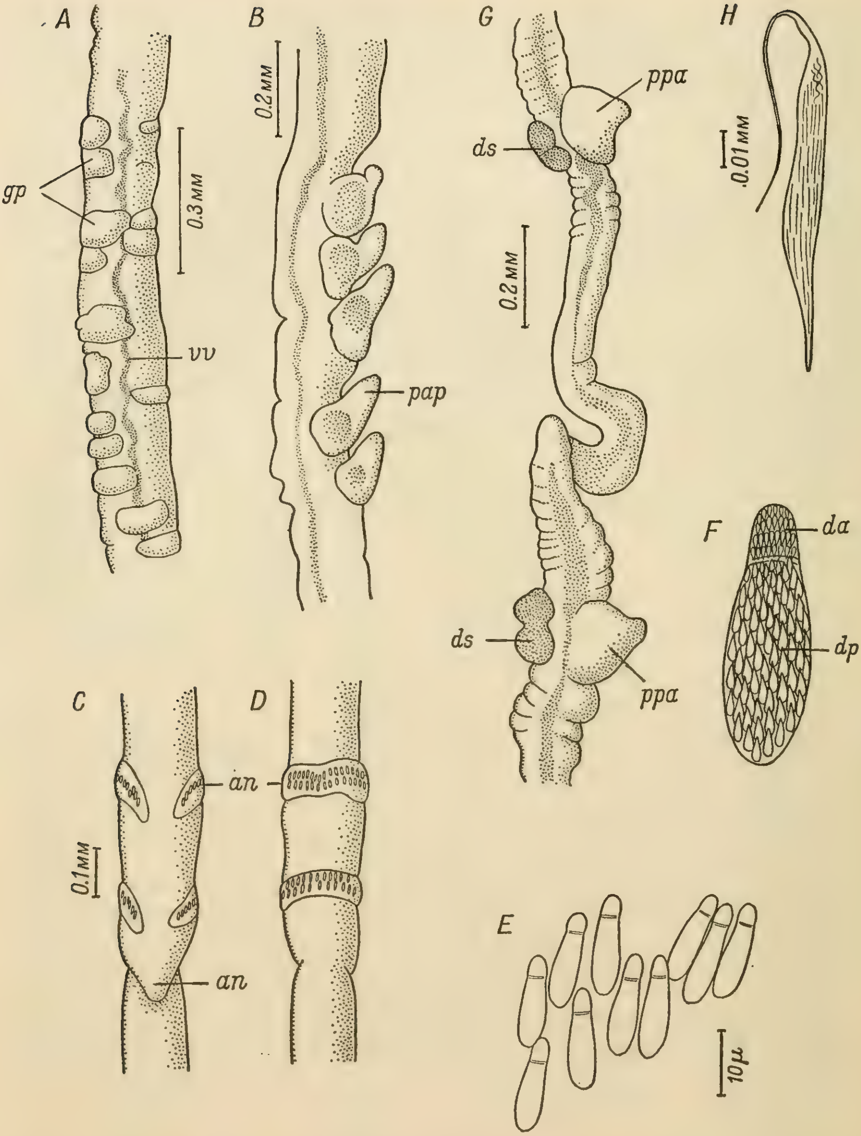

Fig. C92. *Nereilinum murmanicum*. *A* – the middle part of the preannular region; *B* – zone of thickened papillae from the right side; *C*, *D* – girdle region from ventral and dorsal sides; *E* – part of a girdle; *F* – toothed platelet; *G* – part of the postannular region from the right side; *H* – spermatophore.
an – girdle; *apa* – papilla of the girdle region; *da* – anterior teeth; *dp* – posterior teeth; *ds* – dorsal glandular shield; *gp* – preannular glandular warts; *pap* – papillae of the zone of thickening; *ppa* – postannular ventral papillae; *vv* – ventral blood vessel. (Ivanov, 1961a.)

its ventral side it bears, one behind the other, a series of large conical papillae, spaced at equal intervals (Fig. *C*92*G*). On the dorsal side, opposite each papilla a glandular shield, shaped like a figure-of-eight, projects slightly.

The range of sizes (in mm) amongst the specimens available is as follows:

Length of tentacles	8–23
Length of the fore-part of the body	1·4–3·4
Breadth of the mesosoma	0·15–0·32
Length of the metameric region	3·5–11·0
Length of the preannular region	14–52
Length of the postannular region	up to 45
Total length of the body without tentacles	up to 80 mm
Total length of the body including tentacles	up to 103 mm

In one male I have found a large number of cigar-shaped spermatophores about 0·1 mm long (Fig. C92*H*). The filament is very long and fine.

The yellowish brown ringed tube is unsegmented. The front part is limp, transparent and yellowish, and contains circular fibres in its walls (Fig. D92*A*). Then, little by little, grey-brown rings appear, about as long as the tube is wide. They are rather regular and have a matt surface. The interspaces between the rings are colourless and transversely wrinkled (Fig. D92*B*). The longest tube reached 236 mm; the diameter near the front end varied between 0·24 and 0·275 mm.

At first glance, from the development of two tentacles, one might place this species in the genus *Diplobrachia*. Several important features, however, argue against placing it in this genus which belongs to the

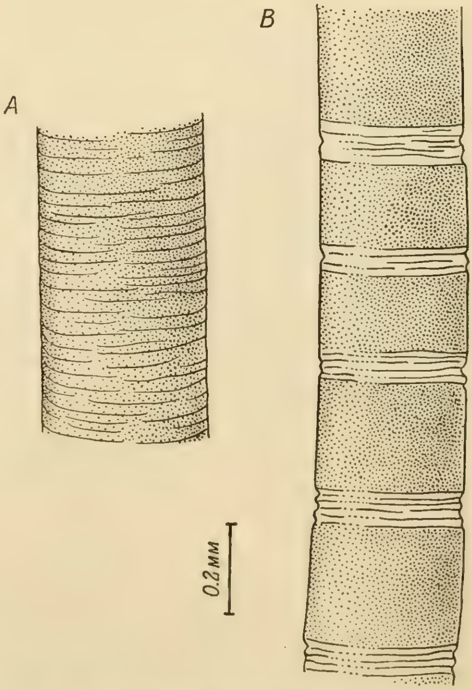

Fig. D92. *Nereilinum murmanicum*. Tube. *A* – front end; *B* – middle part. (Ivanov, 1961a.)

Thecanephria. *Nereilinum murmanicum* possesses metameric dorsal glandular shields and isolated ventral papillae in the postannular region, and also fusiform spermatophores. These are the principal external characters of the Athecanephria and in the absence of any study of the internal anatomy one can only conclude that it must be ascribed to this order. It should further be noted that it differs from *Diplobrachia* in the structure of the bridle, which lacks the cuticular rodlets attached behind the keels, and in the absence of cuticular plaques.

When *Nereilinum murmanicum* is compared with the other species of Athecanephria it is easily seen that it shares certain features with *Siboglinum* and *Oligobrachia*. But it differs from *Siboglinum* in possessing two tentacles instead of one, and in lacking adhesive papillae and any trace of metamerism in the front part of the metasoma. Particular importance must be attached to the latter trait which it shares with *Oligobrachia*, but whereas in *Oligobrachia* the pyriform glands are scattered at hazard throughout the latero-ventral ridges of the metasoma, without any trace of regularity, in *Nereilinum murmanicum* they are more regularly arranged and take on a metameric disposition in the posterior part of this region. The shape of the protosoma, and in particular the way in which its posterior border sweeps back on the dorsal side to meet the keels of the bridle, closely recalls the condition in *Oligobrachia dogieli* and in the more primitive species of *Siboglinum* (e.g. *S. caulleryi* and *S. japonicum*), so that we may consider this a primitive feature. The short oval eggs of *Nereilinum* closely resemble those of *Oligobrachia* and are very different from the long eggs of *Siboglinum*. In other ways *Nereilinum* approaches *Siboglinum*. The form of the cephalic lobe, the glandular belt of the mesosoma, the zone of thickened papillae which lack cuticular plaques, the structure of the girdle region and of the toothed platelets, the postannular region with its metameric papillae and dorsal glandular shields—all these are found in various species of *Siboglinum*. One can attach no importance to the absence of pinnules, since some species of *Siboglinum* possess them while others do not. The metamerism in the postannular region sharply demarcates the species under consideration from *Oligobrachia*, but the tubes are very similar.

In summary, one may say that the main features of *Nereilinum murmanicum* are all primitive and that it occupies a place intermediate between *Oligobrachia* and *Siboglinum*. From the absence of adhesive papillae in the anterior part of the trunk it must be placed in the Oligobrachiidae.

Material: about 100 fragments of tubes, 28 containing whole animals and one containing embryos.

Locality: the southern part of the Barents Sea at a number of stations in the area 69°–75°N 35°–40°E.

Depth: 170–325 m.

Substratum: sand or sandy mud.]

3. Genus *Birsteinia* Ivanov, 1952

Ivanov, 1952: 377, 388, 389; Hartman, 1954: 184; Ivanov, 1954b: 72, 76; Zenkevitch, 1954: 76; Zenkevitch, Birstein and Belyaev, 1954: 68; Ivanov, 1955a: 177; Ivanov, 1955b: 382; Ivanov, 1955d: 173, 174; Ivanov, 1955e: 224; Ivanov, 1956b: 1864; Ivanov, 1956c: 165; Jägersten, 1956: 238; Kirkegaard, 1956b: 186; Abrikosov, 1957: 236; Ivanov, 1957a: 435, 439, 468, 490–3, 495; Vinogradova, 1958: 112; Dajoz, 1958: 231–3, 235, 237; Ivanov, 1960a: 1573, 1607; Ivanov, 1960c: 5, 19, 23, 24, 27, 31, 37, 60, 92, 105, 114, 120.

The protosoma is continuous with the cephalic lobe, but divided from the mesosoma by a deep groove. The 12 free tentacles, arranged in a horseshoe at their base, have double alternating rows of pinnules. The preannular region of the metasoma has numerous metameric papillae provided with cuticular plaques, a proportion of which lie on pulvilli. The postannular region and the girdles themselves are unfortunately unknown. The spermatophores are spindle-shaped. Two erroneous statements were made in the original description of this genus (Ivanov, 1952). Firstly, it was stated that the base of the tentacular crown was in the form of a ring, whereas it is, in fact, horseshoe-shaped, and, secondly, a peculiar segment—the brachyophore—was described at the base of the tentacles; when I re-examined the material I found that this was absent (Ivanov, 1957a). My former opinion (Ivanov, 1952) that *Birsteinia* belonged to the Polybrachiidae has likewise turned out, after reinvestigation, to be incorrect. By the arrangement and development of the coelomoducts of the protosoma *Birsteinia* must take its place in the Order Athecanephria (Ivanov, 1957a), whereas the Polybrachiidae appear typical representatives of the Order Thecanephria.

The genus *Birsteinia* has only one species.

Type of the genus: *Birsteinia vitjasi* Ivanov.

1. Birsteinia vitjasi Ivanov (Figs. 93–95)

Ivanov, 1952: 377–9, Figs. 7–12; Ivanov, 1954b: 72, 76, Figs. 3, 8; Zenkevitch, 1954: 76, Figs. 5, 9; Zenkevitch, Birstein and Belyaev, 1954: 68, Fig. 10; Ivanov, 1955e: Pl. LXV, Fig. 3; Kirkegaard, 1956b: 186, Fig. 4; Abrikosov, 1957: 236, Fig. 6; Ivanov, 1957a: 439, 468, 491, 492, 495–7, Fig. 59; Dajoz, 1958: 233, 235, 237, Fig. 6; Vinogradova, 1958: 112; Ivanov, 1960a: 1537, 1538, 1541, 1546, 1552, 1608, 1612, 1620, Fig. 1399; Ivanov, 1960c: 5, 19, 22, 92, 96, 105, 120, 210, 263, Figs. 17, 87, 93–95.

The protosoma is two-fifths of the length of the mesosoma, getting somewhat narrower towards the front and rimmed at the back by an edging which takes the form of a circular cutaneous fold (Fig. 93*A*, *B*, *C*). The conical cephalic lobe is somewhat flattened dorso-ventrally and limited behind by a slight ridge. The tentacular crown consists of 12 tentacles, and not of 13, as was incorrectly stated earlier (Ivanov, 1952), and they are attached in the form of a horseshoe, with the ends drawn together ventrally. On the inner surface of each tentacle the short pinnules are arranged in two alternating rows.

Along the ventral side of the protosoma and mesosoma runs a sharply marked median groove, or furrow, which closes to a narrow slit in front of the bridle, and then opens out again on the protosoma where the edges fork to either side. The keels of the bridle are very delicate and joined to each other ventrally (Fig. 93*A*, *B*, *C*). On the ventral side it can readily be observed that the hind edge of the mesosoma is bilobed and overhangs the deep groove which divides it from the trunk (Fig. 93*B*).

The metameric part of the trunk is dorso-ventrally compressed (Fig. 93*A*, *C*, *F*), and the ridges bounding the ventral sulcus are moved rather far onto the sides of the body, thus appearing almost lateral, instead of ventral, and enhancing the flattening of this region. The papillae of the metameric region are rather sharply detached and delimited from one another, and the front ones are relatively short, becoming larger only farther back. In consequence of the lateral position of the ridges and papillae which bear them, pulvilli with cuticular plaques often lie on the side of the body (Fig. 93*F*). The total number of metameric papillae is 50–55 pairs and they contain numerous pyriform glands which are readily visible through the integument. A wide dorsal ciliated organ runs along the length of the metameric region, ending at the level of the 45th to 47th pair of papillae. The genital papillae of the males are oval, and approach one another at the front end, where they overhang the hind part of the mesosoma (Fig. 93*D*). The plaques are small and oval, measuring about 20μ across, and have crescentic thickenings along

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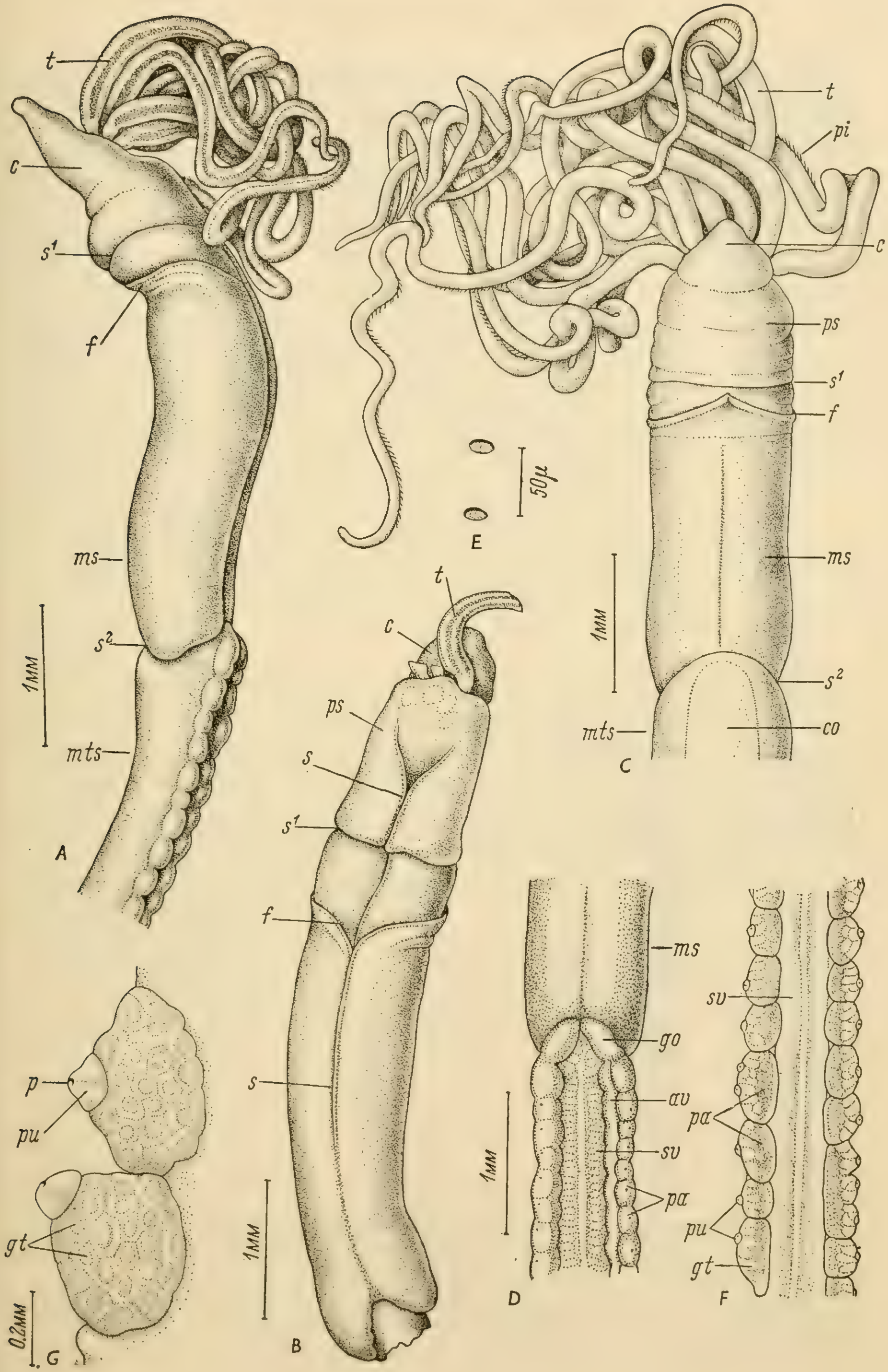
Fig. 93. *Birsteinia vitjasi*: *A* – front part of body of a male from the right side; *B* – the same in ventral view; *C* – the same in dorsal view; *D* – hind part of the mesosoma and front part of the metasoma of a male in ventral view; *E* – cuticular plaques from the metameric part of the preannular region; *F* – metameric part of the preannular region in ventral view; *G* – two metameric papillae from one side.

av – ridge beside ventral sulcus; *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – keel of the bridle; *go* – genital papilla; *gt* – pyriform gland seen by transparency; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaque; *pa* – papillae; *pi* – pinnule; *ps* – protosoma; *pu* – pulvilli; *s* – median ventral furrow; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle. (*A*, *B*, *D*, *E*, *F* – after Ivanov, 1952; *A* and *B* somewhat modified.)


t
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the front edge (Fig. 93*E*). They lie on cone-shaped pulvilli (Fig. 93*G*), whose dimensions, like those of the papillae, which bear them, increase considerably towards the posterior part of the metameric region.

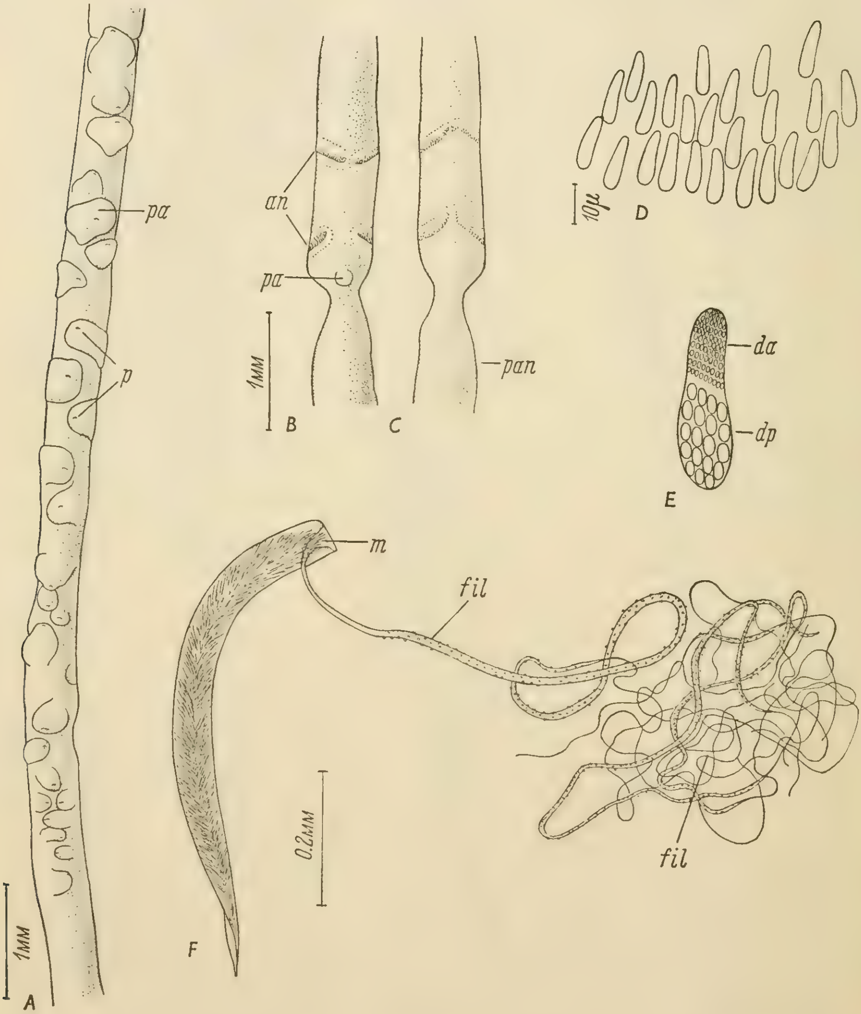

Fig. 94. *Birsteinia vitjasi*: *A* – zone of thickened papillae in ventral view; *B* – girdles of toothed platelets in ventral view; *C* – the same from the dorsal side; *D* – part of a girdle of toothed platelets; *E* – a toothed platelet (only the bases of the teeth are indicated); *F* – spermatophore.
an – girdle; *da* – anterior teeth; *dp* – posterior teeth; *fil* – filament of spermatophore; *m* – thickened base of filament; *p* – cuticular platelet; *pa* – papilla; *pan* – postannular region. (*E* – after Ivanov, 1952.)

The non-metameric part of the trunk is characterized by sparse, large, unpaired, lateral, glandular papillae. It was possible to observe in one specimen that in the zone of thickened papillae there were more than 20 very large papillae arranged on the ventral side of the trunk in a double alternating row (Fig. 94*A*), and carrying small hoop-shaped plaques on their tips. In this specimen also, the two contiguous girdles of toothed platelets were particularly well-preserved. Both of them were interrupted on the ventral side as well as on the dorsal side (Fig. 94*B*, *C*), and behind them lay a small ventral papilla. The toothed platelets, arranged in an irregular triple row (Fig. 94*D*), measure about 12–18μ in length and are appreciably narrower at the front end. Almost the whole of the front half of each platelet is occupied by teeth which are directed backwards, while the much larger teeth on the hinder part of the platelet are directed forward (Fig. 94*E*).

The postannular region is unknown and only males have been seen.

The tentacles are not less than 4 mm long. The protosoma and mesosoma together reach 4·5–5·0 mm in length and 0·75 mm in breadth. The length of the metameric part of the preannular region of the metasoma is about 10 mm.

The spermatophores of *Birsteinia vitjasi* are spindle-shaped, greatly elongated, somewhat curved, pointed at one end and almost round in cross-section (Fig. 94*F*). On one end the transparent casing of the spermatophore is elongated into a rapidly tapering flat appendix, which bends over at the base. The appendix is prolonged into an extraordinarily long thread whose first part is rather stout and covered with granules of some substance. More distally the thread becomes very slender and the granules on it disappear. However tangled the thread may be, the rather long thickened portion is visibly covered with granules of secretion. The length of the spermatophore is 0·75 mm, the breadth 0·06 mm.

The tube is firm and stiff, and its black surface is coarsely granular (Fig. 95*A*). On the whole it is rather rough, with quite opaque thick walls. Outside a dark layer contains coarse transverse fibres and when this is removed an inner layer is revealed, consisting of a transparent, dark brown substance,

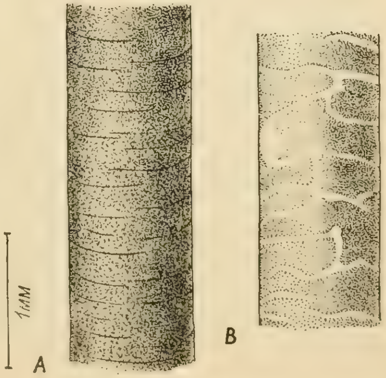

Fig. 95. *Birsteinia vitjasi*: Tube: *A* – middle part; *B* – the same after removal of the outer dark layer. (After Ivanov, 1952.)

crossed by irregular transverse light stripes (Fig. 95*B*). The diameter of the tube reaches 1·05 mm, the length of the greatest fragment 15 cm.

Material: 10 incomplete specimens and a number of torn-off tubes.

Locality: the western part of the Bering Sea at depths of 3260–3857 m.

II. Family Siboglinidae Caullery, 1914

[The recent discovery of the genera *Nereilinum* and *Siboglinoïdes* has necessitated revision of the diagnosis of the Siboglinidae. The original disgnosis given in the Russian edition of this book has been replaced by a revised version.

The Siboglinidae are Athecanephria with the number of tentacles reduced to two or only one. There are never more than two rows of pinnules on each tentacle and they may be reduced to only one row or be absent altogether. The anterior part of the preannular region of the trunk bears well-developed adhesive papillae, without cuticular plaques, arranged in a metameric fashion. The tube is flexible, ringed, sometimes also segmented. There are two genera – *Siboglinum* and *Siboglinoïdes.*

Type of the family: *Siboglinum* Caullery.]

1. Genus *Siboglinum* Caullery, 1914

Caullery, 1914: 2014; Caullery, 1944: 1–26; Caullery, 1948: 495–9; Dawydoff, 1948: 141–63; Beklemishev, 1951: 267–9; Ivanov, 1951: 739–42; Beklemishev, 1952: 295–8; Ivanov, 1952: 372, 374, 389, 390; Ushakov, 1953: 179; Dogiel, 1954: 250; Hartman, 1954: 184, 185; Ivanov, 1954a: 100; Ivanov, 1954b: 69, 79; Zenkevitch, Birstein and Belyaev, 1954: 66, 68; Abrikosov, *et al.* 1955: 472; Ivanov, 1955a: 177; Ivanov, 1955b: 382; Ivanov, 1955d: 175; Ivanov, 1955e: 223; Günter, 1956: 187; Ivanov, 1956b: 1863, 1864, 1867, 1870; Ivanov, 1956c: 165, 166, 168; Jägersten, 1956: 211–252; Kirkegaard, 1956a, 79, 82; Kirkegaard, 1956b: 186; Abrikosov, 1957: 232, 233–6, 238, 239; Alvarado, 1957a: 553; Beklemishev, 1957: 397; Ivanov, 1957a: 431, 433, 434, 439, 440–61, 490–7; Ivanov, 1957b: 1127–44; Obut, 1957: 13; Borradaile, *et al.* 1958: 714–16; Dajoz, 1958: 225–7, 229, 231–5, 237, 238; Ivanov, 1958a: 1363, 1369, 1371; Ivanov, 1958b: 1682, 1688–90; Ivanov, 1958c, 1; Ivanov, 1958d: 1–2; Ivanov, 1958e: 1070–86; Jägersten, 1958: 367; Kirkegaard, 1958: 1086, 1087; Manton, 1958: 748, 751; Marcus, 1958: 49; Southward, A. J. and Southward, E. C., 1958a: 1607; Southward, E. C. and Southward, A. J., 1958b: 627–32; Vinogradova, 1958: 112; Ivanov, 1960a: 1530, 1531, 1533, 1534, 1535, 1537, 1538, 1539, 1541, 1543, 1552, 1567, 1570, 1572, 1573, 1574, 1580, 1583, 1588, 1590, 1592, 1593, 1597, 1604, 1605, 1606, 1607, 1609, 1610, 1611, 1614, 1616, 1620, 2165; Ivanov, 1960b: 7–9, 12, 14–16, 18, 19, 23, 24, 27, 28, 47, 54, 57, 59–61, 63, 66, 69, 75, 76, 78, 79, 82, 87–96, 97, 98, 102, 105–110, 114, 124, 162, 183, 215, 219.

The protosoma is divided from the mesosoma by a more or less distinct groove, which may be simple or curved backwards on the dorsal side. The conical or paddle shaped cephalic lobe is often divided from the protosoma by a pretentacular groove, absent in related species some of which may possess instead a post-tentacular groove behind the base of the tentacle. Not infrequently, however, the protosoma is undivided. The long tentacle, which is capable of twisting into a tight corkscrew spiral, usually bears one or two rows of pinnules, but in some small species these are absent.

The mesosoma, as a rule, lacks secondary rings, but in some species there are one or two transverse grooves in front of the bridle. The keels of the bridle may be well marked or very faint, with tiny cuticular rods laid across them, and behind them is often a more or less complete glandular, epidermal girdle, while sometimes long, ventral, longitudinal glandular stripes are developed.

The metameric part of the trunk carries a large number of more or less paired papillae, devoid of cuticular plaques, while the papillae of the zone of thickening are generally few and, for the most part, arranged in a single ventral row. Their number and the extent of their development appear to be good diagnostic characters. The dorsal ciliated band is well developed. The number and arrangement of the girdles vary. Often there are two of them close together, but they may lie separated from each other; when three girdles are present the front two usually lie close together, far separated from the hindmost. The platelets or toothed bristles are usually arranged along the girdles in 1 or 2 rows, rarely in 3 or 4. On each platelet the teeth of the anterior group (much more weakly developed than the posterior) are more or less rudimentary or even absent, but in some few species they take up nearly as much space as the posterior group and are almost as well-developed. The postannular part of the trunk carries a series of metameric dorsal glandular shields, on which may be seen the pores of pyriform glands and opposite each shield, on the ventral side, lies a large conical papilla, sometimes carrying at its tip a slight thickening of the cuticle or even a cuticular plaque.

The spermatophores are spindle-shaped.

The tube is ringed, with simple or anastomosing rings, and in a number of species it is segmented.

Type species of the genus: *Siboglinum weberi* Caullery, 1914.

At the present time the genus *Siboglinum* contains 38 known species. This is a very extensive genus, whose various species are wide-spread throughout all the oceans of the world.

Key for the identification of the species of the genus *Siboglinum*[*]

[*] The following species have not been included in this partially revised version of the key given in the Russian edition:

Siboglinum cinctutum var *subtile*
S. macrobrachium
S. debile
S. timorense
S. veleronis
S. subligatum
S. concinnum
S. arabicum
S. silone
S. ceylonicum
S. exile
S. sumatrense
S. zanzibaricum
S. sergeevi
S. lacteum

1 (38) The keels of the bridle are fused on the ventral side or come close together.

2 (5) The keels of the bridle are fused on the dorsal side.

3 (4) The keels of the bridle are very stout and their ventral ends merge imperceptibly into one another. The pinnules are arranged in a single row. Behind the bridle there is a somewhat prominent glandular ridge, interrupted dorsally and ventrally. There are about 10 large papillae in the zone of thickened papillae, arranged in a single row and bearing weak, round cuticular plaques. There are two girdles of toothed platelets lying close together, with platelets 10–11μ long. The tube is thick-walled, with slightly brownish regular rings. 9. *S. frenigerum* (p. 213).

4 (3) The keels of the bridle are moderately thick and their ventral ends are closely fused together. There is no prominent glandular girdle behind the bridle. The pinnules are arranged in two rows. The papillae are placed at random in the zone of thickening and bear hoop-shaped cuticular plaques. There are two girdles of toothed platelets lying close together, with platelets 11–13μ long. The tube is thick-walled, with regular whitish rings. 7. *S. vinculatum* (p. 203).

5 (2) The keels of the bridle are not fused together on the dorsal side.

6 (7) The protosoma has a pair of lateral protuberances at the base of the cephalic lobe. The very delicate keels of the bridle are crossed by the finest of cuticular rodlets (use a microscope!). The toothed platelets, 10–11μ long, are arranged in a single row in each of the two adjacent girdles. The rings of the tube are irregular and brown with reddish tints. 20. *S. minutum* (p. 248).

7 (6) The protosoma lacks paired lateral protuberances at the base of the cephalic lobe.

8 (23) Pinnules are present.

9 (16) The pinnules form two rows. A pretentacular groove is present.

10 (13) The dorsal ends of the keels of the bridle are somewhat thickened. The groove between the protosoma and the mesosoma is simple.

11 (12) There is a glandular girdle behind the bridle, interrupted dorsally and ventrally. The pinnules of the bipectinate tentacle are very thin. The toothed platelets of the girdles are 17–23μ long. The tube is segmented, with 12–18 rings per segment, and a large part of it carries double, more or less anastomosing rings. 4. *S. fedotovi* (p. 193).

12 (11) There is no glandular structure behind the bridle. The pinnules of the bipectinate tentacle are thickish. The toothed platelets of the girdles are 10–11μ long. The tube is segmented, with 8 rings per segment; the rings are nowhere double. 3. *S. pinnulatum* (p. 190).

13 (10) The dorsal ends of the keels of the bridle are not thickened. The groove between the protosoma and the mesosoma is curved.

14 (15) The groove between the protosoma and the mesosoma lies at a considerable distance from the bridle and is strongly curved backwards on the dorsal side. The keels of the bridle are very thin, gradually getting finer towards the dorsal side. The tentacle is not bipectinate, but has two rows of delicate pinnules lying close together. The unsegmented fibrous tube has coarse brown rings which do not anastomose and are nowhere split into double rings. 6. *S. japonicum* (p. 200).

15 (14) The groove between the protosoma and mesosoma runs near to the bridle and curves backwards on the dorsal side. The keels of the bridle are stout, not becoming finer towards the dorsal side. The tentacle is obviously bipectinate, with large curved pinnules. The regular rings, which are sometimes joined by bridges or split into pairs, number seven or rarely six per segment of the segmented tube. 2. *S. ekmani* (p. 185).

16 (9) There is a single row of pinnules and no pretentacular groove.

17 (20) There is a post-tentacular groove near the base of the tentacle. The toothed platelets form a single row.

18 (19) The post-tentacular groove is complete. The pinnules are as long as the tentacle is wide. The keels of the bridle are brown. There are two girdles near together and the toothed platelets are 11–12μ long. The ventral postannular papillae have no cuticular plaques. 11. *S. pusillum* (p. 221).

19 (18) The post-tentacular groove is visible only on the ventral side. The pinnules are twice as long as the tentacle is wide. The keels of the bridle are colourless. The two girdles are a long way apart and the toothed platelets are 12–15μ long. The postannular papillae bear bent rod-like cuticular plaques. 1. *S. weberi* (p. 181).

20 (17) There is no post-tentacular groove. The toothed platelets are arranged in two or three rows in each of the two closely adjacent girdles.

21 (22) The groove between the protosoma and the mesosoma is simple. A prominent glandular girdle, broken on the ventral side, lies behind the bridle. The keels of the bridle are thick and black. The cephalic lobe is triangular and flattened. There are about ten conical papillae in the zone of thickened papillae, arranged in a single row and each bearing a bow-shaped cuticular plaque. The tube has regular whitish or slightly muddy rings. 8. *S. cinctutum* (p. 207).

22 (21) The groove between the protosoma and the mesosoma curves strongly backwards on the dorsal side. There is no bulging glandular girdle behind the bridle. The keels of the bridle are fine and brownish. The cephalic lobe is conical. There are five papillae in the zone of thickened papillae, arranged in a single row and lacking cuticular plaques. The tube has very regular brown rings. 10. *S. caulleryi* (p. 216).

23 (8) Pinnules are absent.

24 (25) The distance from the tip of the cepahlic lobe to the base of the tentacle is one fifth of that from the tip of the cephalic lobe to the bridle. The toothed platelets, 10–13μ long, are arranged in one or two rows. The unsegmented fibrous tube has regular short yellowish or brownish rings. 14. *S. meridiale* (p. 231).

25 (24) The distance from the tip of the cephalic lobe to the base of the tentacle is a half to a third of that from the tip of the lobe to the bridle.

26 (35) There is an incomplete glandular girdle behind the bridle.

27 (34) There are three girdles of toothed platelets, at least in some individuals.

28 (29) The two anterior girdles of toothed platelets lie at a considerable distance from the hindmost. The toothed platelets measure 8–10μ long. The keels of the bridle lie on brownish cuticular folds, crossed by dark transverse rodlets. The unsegmented tube is fibrous, with split, brown rings. 17. *S. tenue* (p. 238).

29 (28) The three girdles of toothed platelets all lie close together and the platelets are 11–15μ long. The keels of the bridle are simple.

30 (31) The glandular girdle behind the bridle is broken both dorsally and ventrally, and a long mid-ventral furrow runs in front of the bridle. The toothed platelets, 10–12μ long, are arranged in a single row in each of the two or three girdles. The unsegmented tube has close irregular brown rings very variable in length. 25. *S. inerme* (p. 268).

31 (30) The glandular girdle behind the bridle is broken only on the dorsal side. There is no mid-ventral furrow in front of the bridle.

32 (33) There is a circular groove behind the base of the tentacle. The toothed platelets, 11–12μ long, are arranged in a single row in their girdles. The tube is fibrous, with rings made up solely of thickened fibres. 13. *S. microcephalum* (p. 227).

33 (32) There is no circular groove behind the base of the tentacle. The toothed platelets, 10–15μ long, are arranged in two to four rows in their girdle. The tube has fibres only in the anterior part and the rather long rings stand out from an homogeneous ground substance. 21. *S. norvegicum* (p. 251).

34 (27) There are two girdles of toothed platelets (three in some individuals).

34a (34b) There are always two girdles of toothed platelets. The front edge of the mesosoma has a slight cutaneous thickening, making a sort of girdle. The toothed platelets, 9–12μ long, are arranged in a single row. The segmented tube has regular brown rings, sometimes anastomosing. 18. *S. variabile* (p. 241).

34b (34a) There are usually two, occasionally three girdles of toothed platelets close together. The toothed platelets, 10–12μ long, are arranged in a single row. The unsegmented tube has brown rings very variable in length. 25. *S. inerme* (p. 268).

35 (26) There is no glandular structure behind the bridle.

36 (37) There is a circular post-tentacular groove. The keels of the bridle are in one piece, unbroken. There are three girdles of toothed platelets, with the front two lying some distance from the hindmost. The toothed platelets, 13–14μ long, are arranged in two rows. The unsegmented tube is fibrous, with simple or split (double) rings. 16. *S. hyperboreum* (p. 236).

37 (36) A post-tentacular groove is lacking. The keels of the bridle are broken, i.e. formed of many isolated pieces. The toothed platelets, 9–12μ long are arranged in a single row in each of the two widely

spaced girdles. The unsegmented tube is not fibrous, but very limp and transparent, with regular rings. 15. *S. pellucidum* (p. 233).

38 (1) The keels of the bridle are divided on the ventral side.

39 (40) The dorsal ends of the keels of the bridle merge into one another. There is no post-tentacular groove. The pinnules are disposed in a single row. The spatulate toothed platelets, reaching 18μ in length, are arranged in a single row in each of the three girdles, of which the front two lie at a considerable distance from the hindmost. The tube is transparent, with brownish rings. 12. *S. buccelliferum* (p. 224).

40 (39) The dorsal ends of the keels of the bridle are separated.

41 (48) The mesosoma has more or less strongly developed glandular regions of integument.

42 (47) Pinnules are present.

43 (44) The pinnules are arranged in two rows and the tentacle is bipectinate. A pretentacular groove is present. The cephalic lobe is rounded. The glandular structures of the mesosoma are represented merely by a girdle, which is interrupted dorsally and ventrally and lies close to the bridle. The metameric part of the metasoma lacks lateral glandular tracts. The tube has very short irregular rings, formed from split double rings. 5. *S. plumosum* (p. 197).

44 (43) The pinnules are arranged in a single row and the tentacle is not bipectinate. A pretentacular groove is absent. The cephalic lobe is conical. In front of the bridle there are two ventral glandular regions, and behind it the lateral elements of the glandular girdle are elongated on the ventral side into an obvious pair of glandular tracts reaching backwards to the end of the mesosoma. There is a long glandular tract also above the papillae of the metameric region of the trunk on each side of the body.

45 (46) The zone of thickened papillae has only three papillae arranged in a single row. There are two girdles of toothed platelets, and the platelets measure 11–13μ long. The ventral papillae of the post-annular region of the trunk have no cuticular plaques. The thick-walled tube is segmented in front, with white semi-transparent complete or broken rings, often anastomosing with one another. 23. *S. taeniaphorum* (p. 257).

46 (45) There are many papillae placed at random in the zone of thickened papillae. The toothed platelets, 14–18μ long, are arranged in three contiguous girdles. There are more than 130 pairs of papillae in

the metameric region of the trunk. The ventral papillae of the postannular region carry hoop-shaped cuticular plaques. The thick-walled tube has complete, or partially incomplete, short brownish grey rings, sometimes anastomosing with one another.

24. *S. atlanticum* (p. 263).

47 (42) Pinnules are absent. A post-tentacular groove runs at the very base of the tentacle. A narrow glandular girdle, interrupted dorsally and ventrally, lies behind the bridle. Many small papillae are randomly placed in the zone of thickened papillae. The toothed platelets, 11–12μ long, are arranged in a single row in each of two widely separated girdles. The tube has long rings, some of them blotched or consisting of two or three secondary rings.

19. *S. bogorovi* (p. 244).

48 (41) The mesosoma lacks any glandular region of integument. There is a post-tentacular groove. The toothed platelets, 16–19μ long and shaped like the sole of a shoe, are arranged in three girdles, of which the front two lie close together, some distance from the hindmost. The delicate transparent tube has very short brownish rings looking like barrel hoops. 22. *S. robustum* (p. 254).

1. Siboglinum weberi Caullery (Figs. 1*A*, 96)

Caullery, 1914: 2014, Figs. 1–6; Caullery, 1944: 1–26, Figs. 1–89; Caullery, 1948: 495–9, Figs. 117–20; Dawydoff, 1948: 141–63, Figs. 1–12; Ivanov, 1951: 742; Ivanov, 1952: 372; Zenkevitch, 1954: 77, Fig. 9; Zenkevitch, Birstein and Belyaev, 1954: 66, 68, Fig. 10; Ivanov, 1954b: 69; Hartmann, 1954: 184, 185; Ivanov, 1956b: 1863; Jägersten, 1956: 212, 227, 230, 231; Kirkegaard, 1956a: 79, 82; Kirkegaard, 1956b: 186, Fig. 4; Abrikosov, 1957: 232, 233, 236, 238, Fig. 1; Ivanov, 1957a: 431, 444, 458, 459, 491, 494; Ivanov, 1957b: 1127; Borradaile *et al.*, 1958: 714–16; Vinogradova, 1958: 112; Dajoz, 1958: 225, 234, 237, Fig. 6; Ivanov, 1958a: 1363; Ivanov, 1958b: 1682, 1689, 1690; Ivanov, 1958d: 1; Ivanov, 1958e: 1070; Ivanov, 1960a: 1524, 1525, 1529, 1531, 1549, 1559, 1562, 1567, 1592, 1606, 1607, 1611, Fig. 1436; Ivanov, 1960c: 5, 7, 12, 14, 35, 46, 50, 54, 92, 93, 96, 125, 126, 128, 129–31, 136, 145, 158, 265, Figs. 1, 56, 87, 96; Southward, 1961: 2, 3–5, 21, Fig. 1 (revised description).

To all appearances, the various peculiarities mentioned by Caullery in his description of *S. weberi* belong to at least two different species, whose diagnosis is not at present possible. The form of the anterior division of the body, for instance, and the relative proportions of its parts, vary in different individuals to an extent that is difficult to explain as mere differences of degree of shrinkage upon fixation (Caullery, 1944; Figs. 6, 9). Some specimens, to all appearances, have distinct glandular belts on the mesosoma (Caullery's

Fig. 8), while others have none. The diameter of the tube, also, varies from individual to individual within very wide limits (a variation of 0·9–0·91 mm), in a way that is not found in other species of *Siboglinum.* Though the investigations of Caullery are of extraordinary value and interest, being of great importance for the understanding of the Pogonophora, they are, unfortunately, of little use as regards the accurate diagnosis of the species of *Siboglinum.*

[Since the publication of the Russian edition of this work Dr. Eve Southward has had the opportunity of examining Caullery's original specimens from the *Siboga* Expedition and has published a monograph on this material, which she has shown to contain not less than 16 species belonging to 4 or more genera. She writes:

"In deciding which species should provide the type specimen (lectotype) of *Siboglinum weberi* I have considered that it should be common in the collection, should provide sufficient material for a complete description, and should possess, as far as possible, all the characters noted as typical by Caullery (1914, 1944). I have chosen a small species which has tubes about 0·1 mm in diameter, with regular coloured rings on the walls. These rings are often arranged in pairs. The animal has all the characters of *Siboglinum* as described by Caullery, including two girdles of platelets around the trunk. This species is the one shown in Caullery's Figs. 9 and 10, and may be the one shown in his Fig. 3 (Caullery, 1944)." (Southward, 1961).

The following description and the accompanying figure (Fig. 96) are reproduced from Dr. Southward's monograph, by kind permission of the author and the publisher, E. J. Brill. Paragraphs and sentences have been transposed to bring the description into line with the form adopted here.

"The fore-part of the body is from 0·6 to 1·2 mm long (the average for 23 specimens is 0·9 mm), and this length is 7 to 12 times the diameter of this part of the body. The protosoma has a small, slightly pointed cephalic lobe and the tentacle is attached about 0·1 mm behind the tip (Fig. 96*D*, *E*). This tentacle is often coiled into a spiral but where it is not coiled the diameter is only about 30μ; it bears one row of pinnules, each about 60μ long (Fig. 96*F*). The row of pinnules begins close to the head of the animal and continues to the tip of the tentacle. There is no pretentacular groove visible but there is a slight transverse groove just behind the base of the tentacle, on the ventral side only. A little farther back there is a fairly well-marked annular groove separating the protosoma and mesosoma, which is followed by an annular or semi-annular groove just before the bridle. In some specimens there is a shallow longitudinal furrow between the third groove and the ventral part of the bridle (Fig. 96*E*). The bridle itself is difficult to see in many specimens: there is no ridge, only very thin, colourless keels, which fuse in a smooth curve on the ventral side and approach one another fairly closely, without joining, on the dorsal side (Fig. 96*D*, *E*). Just behind the bridle there is a small, ventral patch of glandular epidermis (Fig. 96*E*), which is not visible in all specimens.

"The groove between the mesosoma and the metasoma is shallow ventrally but deep dorsally and the dorsal side of the mesosoma often projects backwards, as shown in Fig. 96*G*. The first 2 mm of the trunk bears 24 to 45 pairs of small papillae, with a rather shallow ventral sulcus between the two rows.

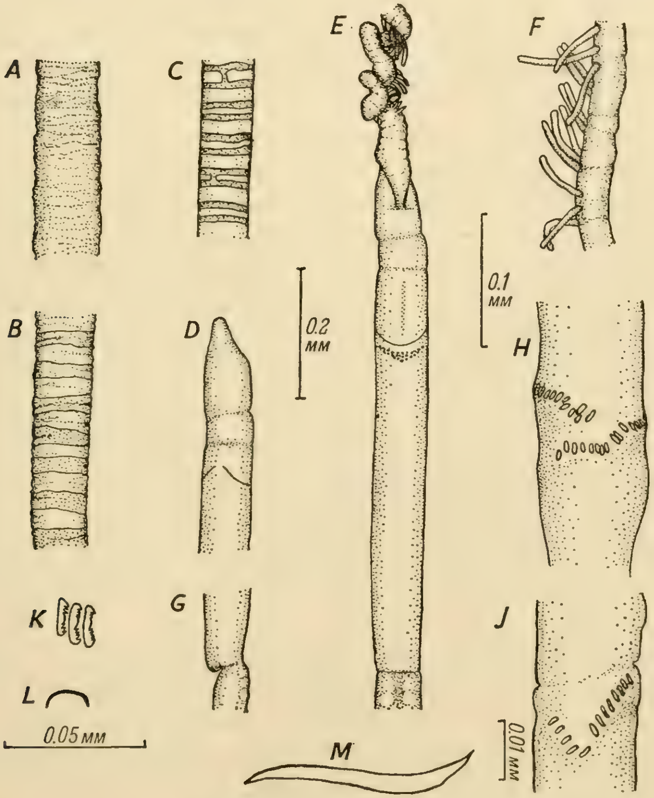

Fig. 96. *Siboglinum weberi*: *A*, *B*, *C* – anterior, middle and posterior parts of tube; *D*, *E* – anterior end of animal, dorsal and ventral views; *F* – part of tentacle; *G* – junction of mesosoma and metasoma, side view; *H* – first girdle; *J* – second girdle; *K* – toothed platelets, side view; *L* – cuticular bar from a postannular papilla; *M* – shape of spermatophore. Heavy stipple shows the position of epidermal glands. (After Southward, 1961.)

The part of the trunk between the metameric and girdle regions seems to be devoid of any sort of papillae, and the whole preannular region is only 4 to 9 mm long. There are two girdles, usually forming incomplete rings, 0·85 to 1·2 mm apart (Fig. 96*H*, *J*). In the space between them there are, in some specimens, a few large papillae without adhesive plaques. Each girdle has a single, regular row of toothed platelets, each of which is 12 to 15μ long and has its teeth arranged in two approximately equal groups (Fig. 96*K*). The postannular part of the trunk is up to 8·5 mm long. On it can be seen occasional large papillae, crowned with adhesive plaques in the form of curved bars about 15μ long (Fig. 96*L*).

"Most of the specimens contain gametes, and there seem to be about twice as many males as females. The spermatophores are remarkably small, always being about 40μ long, and their filaments have not been seen (Fig. 96*M*). One female has developing larvae in the anterior part of the tube.

"A more or less complete male specimen, 14 mm long, has been chosen as the lectotype of *S. weberi*, from among the specimens from sta. 212.

"The tubes of this species are among the finest in the material. All are broken, and the biggest fragment is 3 cm long. The diameter is fairly constant for any one tube, but in different individuals it ranges from 0·10 to 0·135 mm; though it is only rarely over 0·12 mm. The wall of the tube is thin, wrinkled outside and smooth inside (Fig. 96*A*). At the anterior end it is limp and colourless for a few mm, then narrow brown rings appear, separated by whitish interspaces, and the tube becomes stiffer, though the walls remain thin (Fig. 96*B*). Farther back the rings become lighter in colour and split into pairs; the wall gradually becomes smoother towards the posterior end, and has narrow yellow rings, usually in pairs, which sometimes form a more complex pattern with spots or bars between them (Fig. 96*C*).

"The animals inhabiting these tubes are up to 17 mm long and have a single tentacle up to 4·2 mm long. The fore-part of the body is from 0·6 to 1·2 mm long.

"*S. weberi* as described above, is rather similar to *S. pusillum* Ivanov, which occurs in the N.W. Pacific Ocean. There is a strong likeness between the tubes of the two species and some points of similarity between the animals. The tubes are wrinkled and provided with rather narrow (often double) brown rings in both species, but in *S. pusillum* there are also fine transverse fibres in the tube walls; these have not been seen in *S. weberi*.

"The animals differ in the following ways: (i) the length of the pinnules is equal to the diameter of the tentacle in *S. pusillum* but is twice the diameter of the tentacle in *S. weberi*; (ii) there is a complete post-tentacular groove in

S. pusillum; (iii) the length of the fore-part of the body is 0·6 to 0·8 mm in *S. pusillum*, whereas it averages 0·9 mm in *S. weberi*; (iv) the preannular region of the body is over twice as long in *S. pusillum* as in *S. weberi*, indeed the whole animal is twice as long; (v) the keels of the bridle are brown and well developed in *S. pusillum* but colourless and very fine in *S. weberi*; (vi) the girdles are close together in *S. pusillum*, but far apart in *S. weberi*; (vii) the postannular papillae have no adhesive plaques in *S. pusillum*." (E. C. Southward, 1961.)

Material: about 100 occupied tubes, of which 23 specimens have been examined in detail.

Localities: Malay Archipelago: *Siboga* stations 48 (8°4′S 119°4′E—Bali Sea), 52? (9°3′S 119°56′E—Bali Sea), 175 (2°37′S 130°35′E—Ceram Sea), 208 (5°39′S 122°12′E—Flores Sea), 212 (5°54′S 120°19′E—Java Sea; here most specimens were taken), 271 (5°46′S 134°E—Arafura Sea), 295 (10°35′S 124°27′E—Timor Sea).

Depth: 462–2060 m.]

2. *Siboglinum ekmani* Jägersten (Figs. 97–99)

Jägersten, 1956: 211–252, Figs. 1–8, Pls. 1–3; Jägersten, 1957: 67; Ivanov, 1957a: 431, 434, 494; Dajoz, 1958: 233, 237; Ivanov, 1958a: 1363; Ivanov, 1958b: 1682, 1688; Kirkegaard, 1958: 1086, 1087, Figs. 1, 2; Southward, A. J. and Southward, E. C., 1958a: 1607; Southward, E. C. and Southward, A. J., 1958b: 627, 628, 631, 632, Fig. 1; Ivanov, 1960a: 1524, 1541, 1547, 1559, 1561, 1562, 1567, 1582, 1583, 1606, 1611, Fig. 1466; Ivanov, 1960c: 4, 5, 9, 27, 37, 45, 50, 54, 69, 78, 92, 97, 105, 126, 131–4, 136, 140, 142, 145, 174, 188, 196, 265, Figs. 86, 87, 97–99.

Jägersten based his description of this species upon only two incomplete specimens, which lacked the region of the girdles and the postannular section. He directed his attention chiefly to the internal structure and only dissected parts of the tentacle out of the tube. His description of the appearance of the body is thus based on the study of sectioned material. His specimens were collected in 1933, by a Swedish expedition from Uppsala University, in the Skagerrak at a depth of 487–650 m, and included many empty fragments of tubes.

Not long after Jägersten's account was published, Kirkegaard very kindly presented me with a few individuals of *S. ekmani* taken by him in 1957 in the Skagerrak at a depth of 640 m (Kirkegaard, 1958). This material made it possible to supplement the description given by Jägersten.

The length of the dorso-ventrally compressed fore-part of the body is six to nine times the width of the mesosoma, depending upon the degree of contraction of the animal (Fig. 97*A*, *B*). A barely discernible transverse groove runs a little in front of the bridle, parallel to the keels, arching forward on the dorsal side and making a sharp backward bend in the mid-ventral line (Fig. 97*A*, *B*), while the protosoma bears a pretentacular groove, which curves backward on the dorsal side (Fig. 97*B*). The long stout tentacle is furnished with a double row of comparatively large, bow-shaped bent pinnules (Fig. 98*A*, *B*), but on the proximal part they are absent. The cephalic lobe is small and conical.

The bridle is placed near the front end of the mesosoma and its brownish keels are rather prominent and uniform in thickness. They are joined together ventrally, but not on the dorsal side, where, however, they very

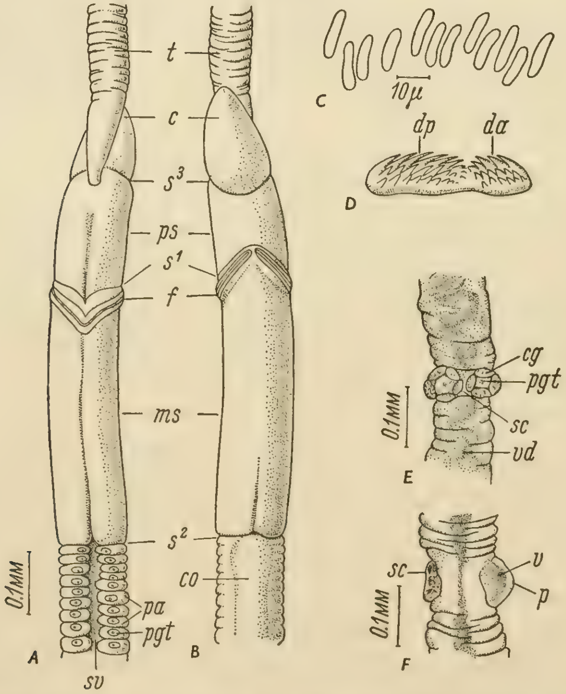

Fig. 97. *Siboglinum ekmani*: *A* – front end of the body of a female in ventral view; *B* – the same from the dorsal side; *C* – part of a girdle of toothed platelets; *D* – a toothed platelet from the side; *E* – part of the post annular region in dorsal view; *F* – the same from the left side.
c – cephalic lobe; *cg* – gland cell; *co* – dorsal ciliated band; *da* – anterior group of teeth; *dp* – posterior group of teeth; *f* – keel of the bridle; *ms* – mesosoma; *p* – cuticular plaque; *pa* – papillae; *pgt* – pore of pyriform gland; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; s^3 – pretentacular groove; *sc* – dorsal glandular shield; *sv* – ventral sulcus; *t* – tentacle; *v* – ventral papilla; *vd* – dorsal blood vessel.

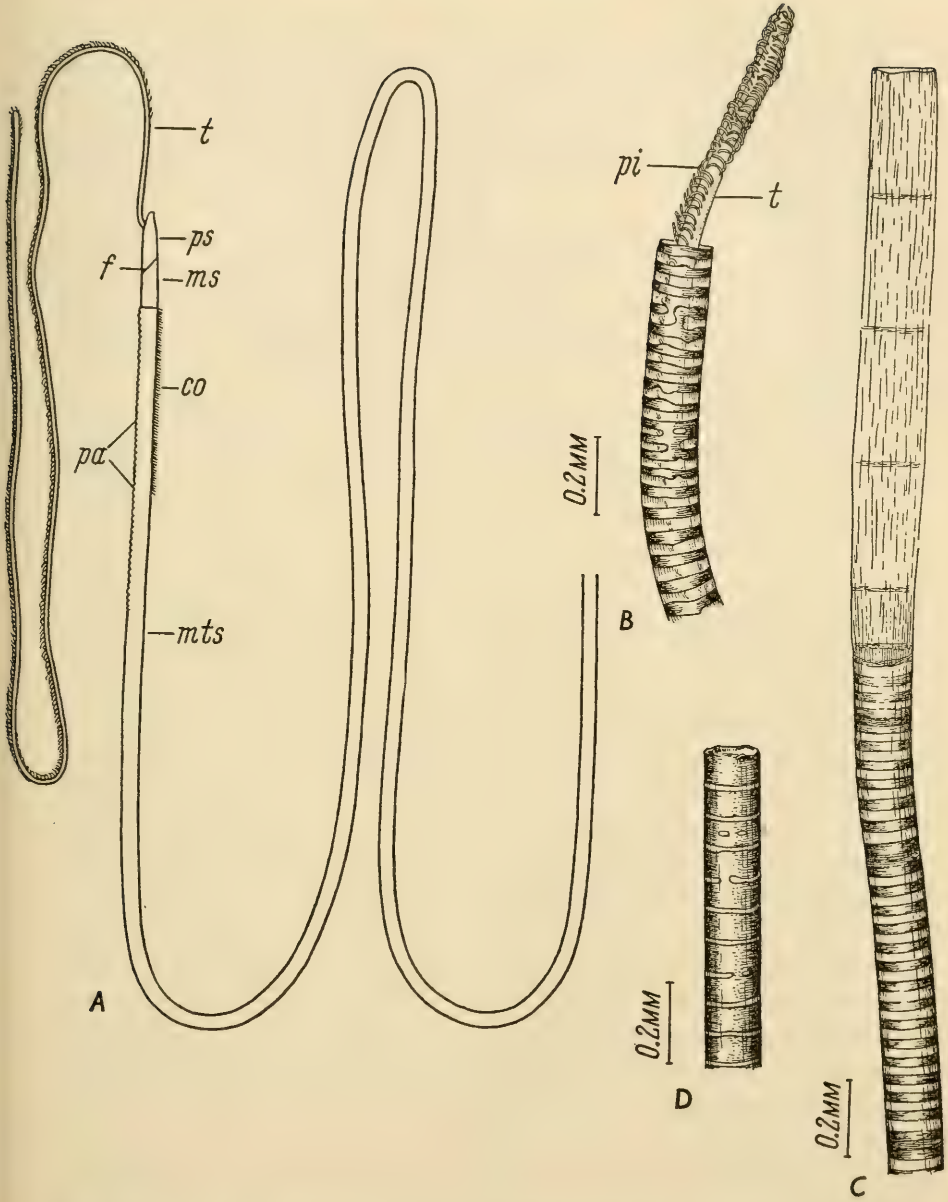

Fig. 98. *Siboglinum ekmani*: *A* – the body of an individual from the left side (hind part of the metasoma omitted); *B* – distal end of the tentacle sticking out of the tube; *C* – anterior part of tube; *D* – hind part of tube.
co – dorsal ciliated band; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae of the metameric part of the preannular region; *pi* – pinnules; *ps* – protosoma; *t* – tentacle. (After Jägersten, 1956, with modifications.)

nearly meet. They lie on a cutaneous fold (Fig. 97*A*, *B*), and the dorsal ends are almost the same thickness as the rest. No perceptible glandular formation whatever is to be found behind the bridle. The hind edge of the mesosoma is straight except for hardly noticeable notches on the dorsal and ventral sides. The ventral surface of the protosoma and mesosoma is marked by a weak median furrow.

The metameric part of the preannular section of the metasoma is roughly twice as long as the anterior division of the body (Fig. 98*A*). The transversely oval papillae are arranged in a regular double row, bounding the ventral sulcus rather tightly and pressed more or less closely together (Fig. 97*A*). In one particular specimen examined there were about 45 pairs. A single pyriform gland with a prominent duct can be seen by transparency in each papilla. Farther back the papillae increase noticeably in size and become irregularly placed. The wide dorsal ciliated band begins at the front end of the mesosoma and is expanded slightly at its origin. The external morphology of the nonmetameric part of the preannular region remains unknown. Jägersten described and figured the toothed platelets of the girdles and to judge by his drawings (Jägersten, 1956, Fig. 7*A*) they are arranged in a single row. He states that they are brownish in colour and measure about 13μ long, with the anterior group of teeth weakly developed. The material placed at my disposal, however, has enabled me to extend Jägersten's observations. I was able to observe the girdles in two individuals, in each of which there were three girdles, the front two close together at a considerable distance from the hindmost. The toothed platelets were pale yellow in colour, somewhat curved (Fig. 97*C*) and $12–16\mu$ long. The area occupied by the anterior group of teeth was about a third of the entire platelet.

In three individuals, furthermore, it was possible to observe the postannular region. The small, transversely elongated, spatulate dorsal shields each contained a pair of pyriform glands, with prominent pores around which were arranged, in two rosettes, a few large epidermal gland cells (Fig. 97*E*). A large conical papilla, lacking any visible cuticular thickening, lay opposite each shield on the ventral side (Fig. 97*F*). [There may be two or even three – E.C.S.]

The dimensions of the various parts of the body (on the basis of four individuals) are as follows: length of tentacle, 7–8 mm; length of anterior division of the body (protosoma + mesosoma), 0·75–1.05 mm; length of preannular region of the metasoma, 17–45 mm; length of the whole body, 41–93 mm.

The membrane of the spindle-shaped spermatophores is distinguished by a clear yellowish coloration, and at one pole it is continued into a very long filament, whose base is noticeably thickened. The sperm are arranged parallel to the length of the spermatophore, filling its whole space (Fig. 99). The length of a spermatophore is 0·15 mm.

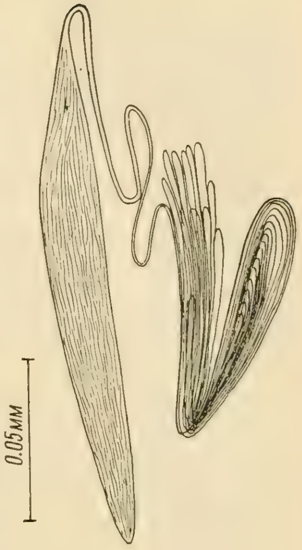

Fig. 99. *Siboglinum ekmani*: Spermatophore.

The tube consists of close-set, brilliant, golden-brown or brown rings, regularly alternating with transparent colourless intervals. The rings are somewhat longer than the intervals, sometimes much longer, and then their brown colour becomes darker. They may be irregular in form or incomplete, or their edges may be uneven. Not infrequently two adjacent rings may anastomose, and in the hinder part of the tube they may run into one another (Fig. 98*D*). The material of the rings is brittle. The anterior limp part of the tube is transparent and segmented, with the boundaries between the segments rather prominent. In the ringed part of the tube each segment covers seven rings (Fig. 98*C*), but exceptionally, in the posterior part of the tube, segments may sometimes be found containing six or even five rings. The largest known fragment of tube measures 213 mm long, and the diameter varies from 0·12 to 0·16 mm.

S. ekmani is allied to *S. fedotovi*, *S. plumosum* and *S. pinnulatum* by several characters, namely, the arrangement of the pinnules in a double row, the presence of a pretentacular groove and the tendency for the rings of the tube to coalesce. With the last of these species, moreover, *S. ekmani* is connected by the absence of any trace of a glandular belt in the mesosoma, and by the presence of three girdles in the metasoma. Three girdles of toothed platelets (two anterior and the third some way back) are, however, likewise found in *S. buccelliferum*, *S. hyperboreum* and *S. tenue* (the last two species lack pinnules). *S. ekmani* is distinguished from all known species by the peculiar form of the pretentacular groove, by the form of the groove between the protosoma and the mesosoma, and particularly by the dorsal shields of the postannular region of the trunk.

Material: I have had at my disposal four complete and a few incomplete individuals, and also some fragments of tubes, from Kirkegaard in collections from the Skagerrak. Jägersten had two incomplete specimens from the

Skagerrak and Southward had abundant material from southwest of Great Britain.

Localities: Skagerrak, and also from southwest of Great Britain.

Depth: 340–1250 m.

3. *Siboglinum pinnulatum* Ivanov (Fig. 100)

Ivanov, 1960c: 5, 18, 19, 96, 105, 126, 134–6, 140, 142, 145, 170, 196, 265, Figs. 87, 100.

One specimen of this species was taken in a trial dredging made in August, 1957, by R.V. *Vityaz*' off the north coast of Morotai (in the Molucca Islands) at a depth of 260 m.

The comparatively short fore-part of the body bears characteristic constrictions behind the bridle and on the rear edge of the mesosoma (Fig. 100*A*). The boundary between the protosoma and the mesosoma is distinctly visible in front of the bridle, and the protosoma narrows noticeably from this point towards the front end, where it passes imperceptibly into the dorsoventrally flattened, triangular cephalic lobe. The extraordinarily stout tentacle is covered with numerous circular wrinkles (probably in consequence of strong contraction upon fixation) and very densely furnished with long pinnules (up to 0·15 mm long) arranged in a double row (Fig. 100*A*). The general appearance of the tentacle with its numerous pinnules rather recalls that of *S. weberi* as figured by Caullery (1944, Fig. 10), but in *S. pinnulatum* the pinnules start almost at the base of the tentacle.

A median furrow runs between a pair of ventral swellings which lie on the mesosoma in front of a well-developed bridle. The brown keels of the latter are fused together ventrally and become gradually thicker towards the dorsal ends (Fig. 100*A*, *B*). Behind the bridle, on the dorsal side, stretches a narrow median groove.

The metameric part of the preannular region of the trunk has a row of large papillae on each side of the deep ventral sulcus (Fig. 100*A*.) There are three girdles of toothed platelets, the first two situated close together at a

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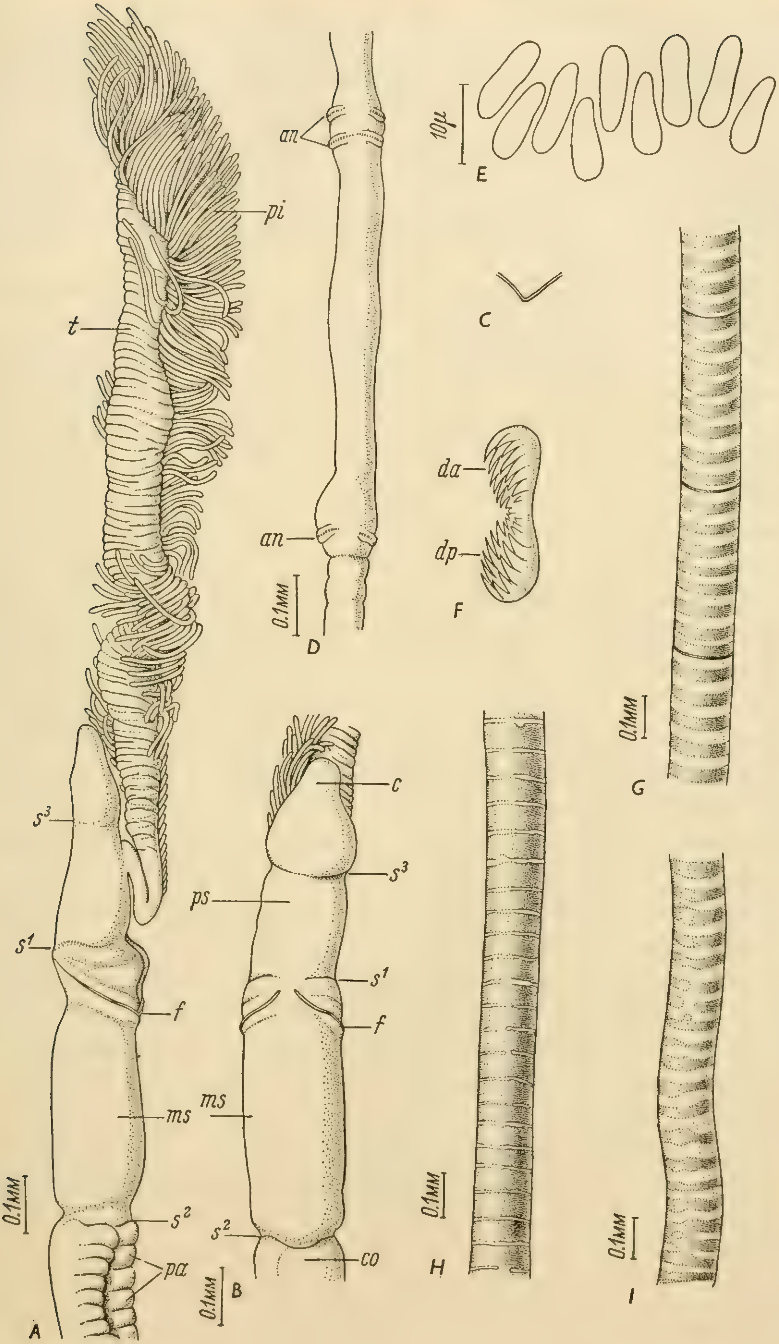
Fig. 100. *Siboglinum pinnulatum*: *A* – front end of the body from the side; *B* – the same from the dorsal side; *C* – the ventral fusion of the keels of the bridle; *D* – part of the metasoma with the girdles in ventral view; *E* – part of a girdle of toothed platelets; *F* – a toothed platelet from the side; *G* – front part of tube; *H* – middle part of tube; *I* – hind part of tube.
an – girdles of toothed platelets; *c* – cephalic lobe; *co* – dorsal ciliated band; *da* – anterior teeth; *dp* – posterior teeth; *f* – keel of the bridle; *ms* – mesosoma; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between protosoma and mesosoma; s^2 – groove between mesosoma and metasoma; s^3 – pretentacular groove; *t* – tentacle.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considerable distance from the third. The first and third girdles are interrupted ventrally, the second dorsally (Fig. 100*D*). The yellowish toothed platelets, arranged in a single row in each girdle, are shaped like elongated ovals, and the majority are pinched in at the middle (Fig. 100*E*). The anterior and posterior groups of teeth are almost equal (Fig 100*F*) and each consists of 6–7 obliquely transverse rows of teeth. The length of a platelet is 10–11μ, the breadth up to 4μ. The postannular region of the trunk has not been satisfactorily dissected out.

The length of the front section of the body is 0·85 mm, the breadth of the mesosoma 0·17 mm, the thickness of the tentacle 0·10 mm.

The tube is rather hard, brown and ringed. Its front part is flimsy and transparent, with walls that collapse readily, and it is distinctly segmented. Some way back yellow rings gradually appear, eight to a segment. Their length is about one-quarter the diameter of the tube and the light interspaces between them are the same size (Fig. 100*G*). In the middle part of the tube the segmentation disappears and the rings become closer together, darker in colour and about twice as long, so that the clear intervals between them are mere lines and, not infrequently, neighbouring rings anastomose (Fig. 100*H*). In the hind part of the tube the pattern of rings becomes less regular, the rings are considerably shorter, often no bigger than those of the anterior end of the tube, their boundaries become uneven, and sometimes neighbouring rings may anastomose with one another by irregular bridges (Fig. 100*I*). The longest, incomplete, fragments of tube measured 38–40 mm in length. The diameter of the tube was 0·18 mm at the front and 0·13 mm in the middle.

This species is distinguished from the closely related species (*S. ekmani*, *S. fedotovi* and *S. plumosum*) by the very numerous, closely packed long pinnules and by the posterior constriction of the mesosoma. The lack of any glandular element in the mesosoma and the peculiarities of the tube bring *S. pinnulatum* close to *S. ekmani*, while the characteristic thickening of the dorsal ends of the keels of the bridle is reminiscent of *S. fedotovi*, in which this peculiarity is well marked. Very characteristic of *S. pinnulatum* is the equal size of the areas occupied by the anterior and posterior groups of teeth on the toothed platelets.

Material: one specimen and two fragments of tube.

Locality: off the northern coast of Morotai Island (2°30′N 129°E) in the Moluccas.

Depth: 260 m.

4. Siboglinum fedotovi Ivanov (Figs. 6, 84A, 101, 102)

Ivanov, 1957a: 449, 453–9, 491, 495–7, Figs. 23–7, 59; Ivanov, 1960a: 1541, 1612, Figs. 1388, 1445, 1465; Ivanov, 1960c: 5, 12, 14, 92, 96, 105, 126, 134, 136, 137–40, 142, 145, 154, 167, 188, 196, 269, Figs. 6, 65, 87, 101–2.

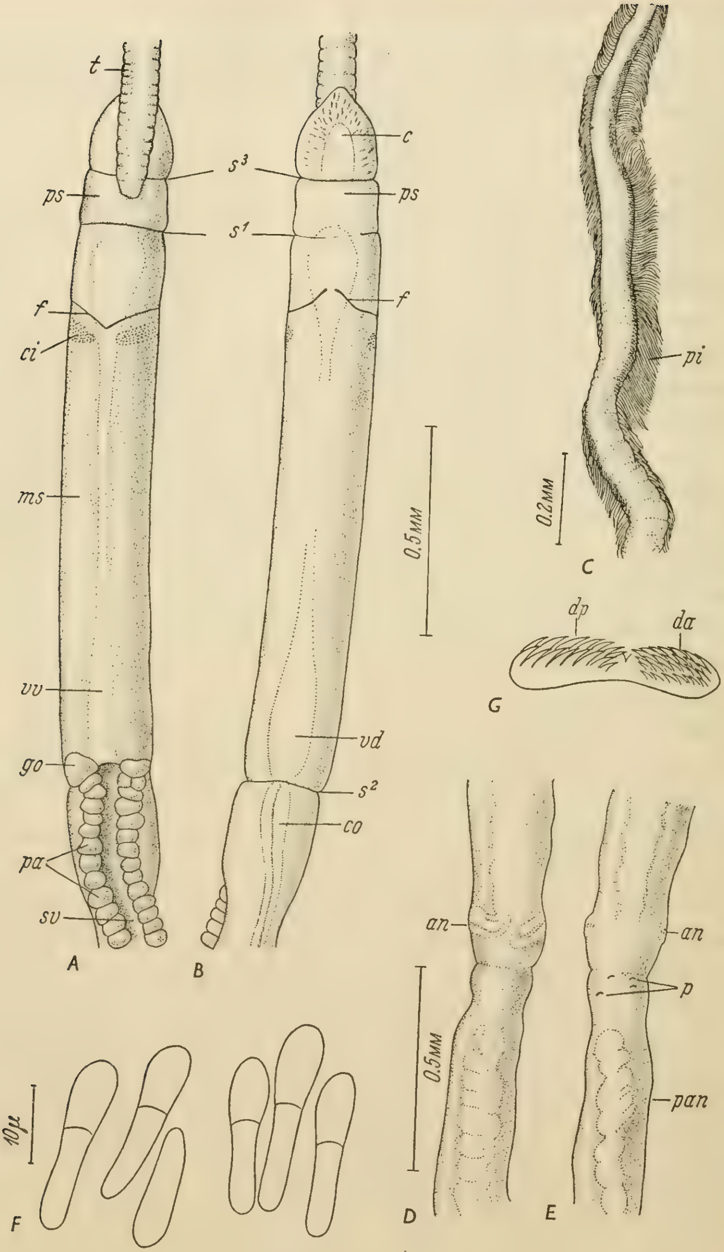
S. fedotovi is one of the few Pogonophora characteristic of the south-western parts of the Bering Sea. This species is in the collection of R.V. *Vityaz'* which was made along the line of stations east of Kamchatka and north of the Komandorski Islands.

The comparatively great length of the fore-part of the body is striking, reaching seven to ten times its breadth (in individuals fixed inside the tube), though the protosoma and cephalic lobe together account for only about one-fifth of this length (Fig. 101*A*, *B*). The protosoma is reduced to a mere girdle, whose breadth is considerably greater than its length. It is divided from the mesosoma by a circular groove, while another groove cuts it off from the cephalic lobe. The latter is somewhat bigger than the protosoma and a little thickened, with a pointed tip. Around its periphery, on the dorsal side, single-celled glands are visible by transparency (Fig. 101*B*). The tentacle is attached to the front edge of the protosoma and bears along most of its length two dense rows of fine, long pinnules (Fig. 101*B*). In fixed specimens it is often strongly contracted.

The bridle is placed near the front of the cyclindrical mesosoma (Fig. 101*A*, *B*). Its keels are joined together ventrally, but just fail to meet dorsally, a fact which often can be observed only under the microscope. They are generally the same thickness throughout their extent, but sometimes they may even become thicker towards the dorsal ends. Immediately behind the bridle lie a pair of transverse glandular tracts, tinted brown and situated latero-ventrally.

The metasoma is delimited by a circular groove, which curves slightly backwards on the ventral side, while the rather narrow dorsal ciliated band begins immediately in contact with it at the front end of the trunk (Fig. 101*B*). The metameric adhesive papillae are rounded, lacking in plaques and becoming larger in size and irregular farther back. In one individual studied there were about 80 pairs. In the male the larger genital papillae are situated in front of the first pair of the series (Fig. 101*A*).

In the original description of *S. fedotovi* (Ivanov, 1957a, pp. 453–9) I stated erroneously that this species was peculiar in having only one girdle of toothed platelets. I was, in fact, observing the hindmost of the three girdles which it actually possesses, as I have discovered more recently in examining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three new specimens. As in related species (*S. hyperboreum*, *S. robustum*, etc.), the first two are placed close together at a considerable distance from the third, the first girdle is interrupted ventrally, the second dorsally and the third both ventrally and dorsally, so that it consists of two half hoops. The dorsal ends of these half-hoops sometimes turn forwards and outwards, while the ventral ends may hardly reach round the sides of the body on to the belly (Fig. 101*D*, *E*). All the girdles lie on muscular folds, and in each of them the toothed platelets are attached in a single irregular row. In contrast with the bigger Pogonophora, the transparent yellowish toothed platelets of this species are broader at the front instead of the hind end (Fig. 101*F*). They are further remarkable in that the anterior group of teeth is twisted round obliquely almost as much as the posterior group (Fig. 101*G*). The anterior teeth are more broadly based than the posterior, but shorter and fewer, and between the two groups a transverse groove may be noticed dividing the platelet into two equal parts, the anterior broader and the posterior narrower (Fig. 101*F*). Most of the platelets are between 17 and 23μ long, but occasionally one may see under-developed ones only 13–15μ long. At the very beginning of the postannular region, on the ventral side, lie a few small, transverse, adhesive plaques, shaped like brackets (Fig. 101*E*).

The tentacle is 12 mm long, the anterior section of the body 1·1–1·7 mm long and *c.* 0·2 mm broad. The preannular region may be up to 65 mm long, but in one mature individual it was only 6 mm.

The very characteristic spermatophores (Fig. 65*A*) are cigar-shaped, broader at one end than the other. From the broader, rounded end runs the delicate filament of the spermatophore. The peripheral region of the spermatophore is cut off from the central region as a sort of cortex, free of sperm. The length is 0·2 mm.

A considerable length of the front part of the tube is transparent and colourless, with very soft, limp membranous walls and clear segmentation. Soon very soft, brownish rings begin to appear, 12–17 or even 18 per

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Fig. 101. *Siboglinum fedotovi*: *A* – front part of the body of a male in ventral view; *B* – the same from the dorsal side; *C* – part of the tentacle; *D* – the posterior girdle and the front part of the postannular region in dorsal view; *E* – the same from the ventral side; *F* – part of a girdle of toothed platelets; *G* – toothed platelet from the side.
an – girdle of toothed platelets; *c* – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *da* – anterior teeth; *dp* – posterior teeth; *f* – keel of the bridle; *go* – genital papilla; *ms* – mesosoma; *p* – cuticular plaques; *pa* – papillae; *pan* – postannular region; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; s^3 – pretentacular groove; *sv* – ventral sulcus; *t* – tentacle; *vd* – dorsal blood vessel seen by transparency; *vv* – ventral vessel seen by transparency. (*A*, *B*, *C*, *D*, *E* – after Ivanov, 1957a.)

segment (Fig. 102*A*). A little farther back the intervals between the rings grow shorter until they are little more than chinks, and the rings thicken and gain a dark muddy or brown tint. In each segment, moreover, a few of the anterior rings anastomose with one another to a greater or lesser extent, and between them only tiny, irregular clear patches remain, looking like slots (Fig. 120*B*). Still farther back from the mouth of the tube the segmentation breaks down, the intervals between the rings become greater, and each ring splits into two. This part of the tube with split rings (Fig. 102*C*) is very long, as is also the next portion which is characterized by incompletely fused

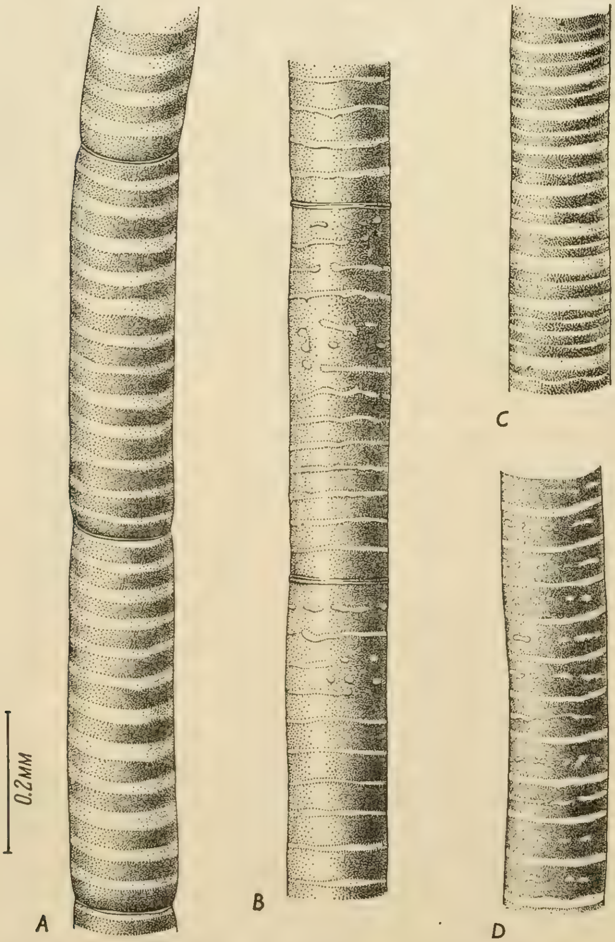


Fig. 102. *Siboglinum fedotovi*: Tube: *A* – front part; *B* – a little farther back; *C* – middle part; *D* – hind part. (*C* and *D* – after Ivanov, 1957*a*.)

doublets (Fig. 102*D*). In the intervals between the rings the walls of the tube are colourless and transparent. Then, in the hindmost part of the tube, the pattern of rings gradually breaks down and the walls become structureless, thin and transparent. The tube may be up to 25 cm long and 0·25 mm in diameter.

From related species, which also possess a bipectinate tentacle and a pretentacular groove, *S. fedotovi* is distinguished by the shortness of the protosoma, by the very long mesosoma, by the delicate pinnules, by the comparatively large toothed platelets of the girdles and by the detailed structure of the tube. The tube is like those of *S. ekmani* and *S. pinnulatum* in the segmentation, and like that of *S. plumosum* in the splitting of the rings to form doublets.

Material: many tubes, some containing animals.

Locality: the southwestern part of the Bering Sea.

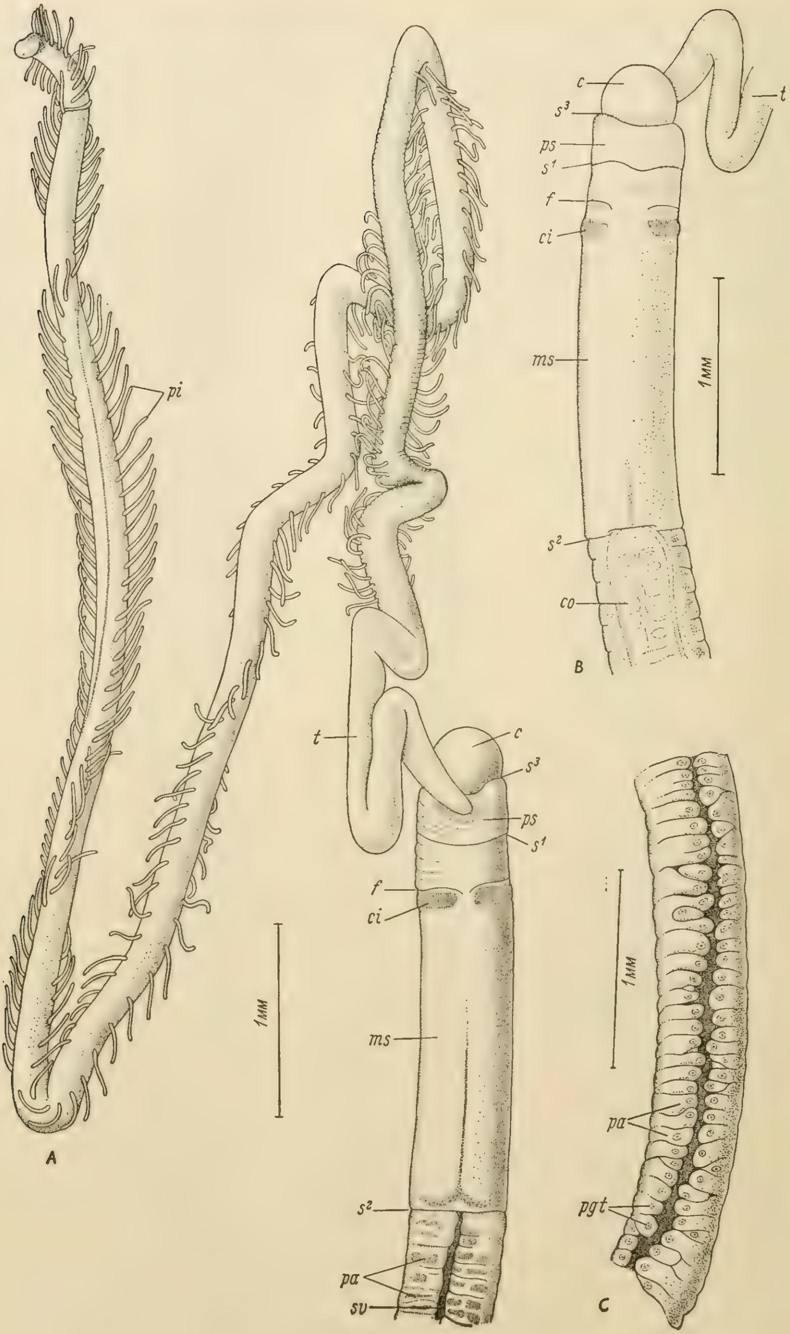
Depth: 2995–3875 m.

5. *Siboglinum plumosum* Ivanov (Figs. 19B, 103–4)

Ivanov, 1957a: 456–61, 491, 495–7, Figs. 28–30, 59; Ivanov, 1960a: 1607, 1612, 1613; Ivanov, 1960c: 5, 12, 14, 27, 92, 96, 105, 128, 134, 136, 140–2, 145, 196, 265, Figs. 19, 87, 103–4.

A near relative of the preceding species, to all appearances, is *S. plumosum*, one of the very largest species of this genus, which was taken in a trawl in the Sea of Okhotsk to the east of the coast of Sakhalin. Unfortunately, the only known specimen lacks the girdles and the postannular region.

The fore-part of the body is comparatively shorter than in *S. fedotovi*, with a length to breadth ratio of 5 : 1. The fore-part, however, and also the tentacle, is evidently strongly contracted, as may be seen from the numerous cross wrinkles, and also from the way the keels of the bridle lie in a transverse line. The protosoma is broader than it is long (Fig. 103*A*, *B*) and is divided by annular grooves from the mesosoma and from the cephalic lobe, which last is narrower than the protosoma and somewhat irregularly rounded. The rather stout, long tentacle bears two rows of comparatively large pinnules, which are absent only from its proximal part, and they are arranged alternately in the right and left rows (Fig. 103*A*). The cylindrical mesosoma is divided from the trunk by a simple transverse groove. The bridle lies near the front of the mesosoma and its keels are not fused on the ventral side and are wide apart on the dorsal side. Behind the bridle lies a pair of lateral glandular belts, more strongly developed than in *S. fedotovi*.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In the front part of the trunk the strongly compressed and hence laterally elongated papillae (Fig. 103*A*), which closely limit the deep narrow ventral sulcus, are irregularly shaped and show incomplete metamerism. Inside each one may be seen a rounded pyriform gland, but there are no cuticular plaques. In the hind portion of the metameric part, the papillae become rounded (Fig. 103*C*) and here, on the surface of each papilla, may be noticed the aperture of a pyriform gland forming a pore in the centre of a rosette. The broad dorsal ciliated band (Fig. 103*B*) begins immediately at the front edge of the trunk and stretches the whole length of the metameric region.

The parts of the body have the following dimensions: the length of the fore-part, 2·5 mm; its breadth, 0·5 mm; the length of the tentacle, 19·5 mm.

The dirty-brown thick-walled firm tube is rather rough, with an uneven surface, and consists of narrow, dark yellow ochre rings, separated by very narrow clear belts (Fig. 104). In the middle of each ring are irregular clear blotches, strung out in transverse rows, seeming to indicate that the rings are formed by the fusion of neighbouring pairs of rings. The length of the tube, torn off at both ends, is 27·5 cm, and its diameter 0·6 mm.

S. plumosum belongs to the group of species characterized by possessing a bipectinate tentacle and a pretentacular groove (*S. ekmani*, *S. pinnulatum* and *S. fedotovi*). To all appearances it is particularly closely related to *S. fedotovi*, with which it is linked by the structure of the tube also: in both species this shows a tendency for the rings to form doublets. *S. plumosum* is distinguished from all these species by the absence of any sign of a ventral fusion of the keels of the bridle.

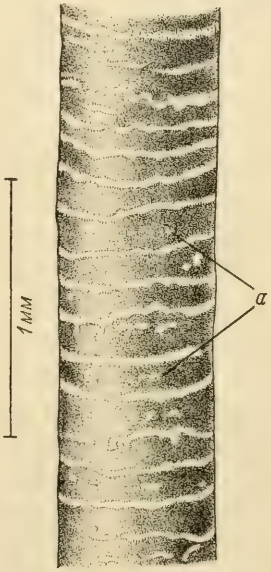


Fig. 104. *Siboglinum plumosum*: Tube. *a* – remains of the spaces between fusing rings. (After Ivanov, 1957a.)

Fig. 103. *Siboglinum plumosum*: *A* – front end of a female from the ventral side; *B* – the same from the dorsal side; *C* – middle section of the metameric part of the preannular region in ventral view. *c* – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *f* – keel of the bridle; *ms* – mesosoma; *pa* – papillae; *pgt* – pores of pyriform glands; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; s^3 – pretentacular groove; *sv* – ventral sulcus; *t* – tentacle. (After Ivanov, 1957a.)

Material: one female and one empty tube.

Locality: the Sea of Okhotsk, to the east of the coast of Sakhalin Island (52°N 144°30′E).

Depth: 119–342 m.

6. *Siboglinum japonicum* Ivanov (Fig. 105)

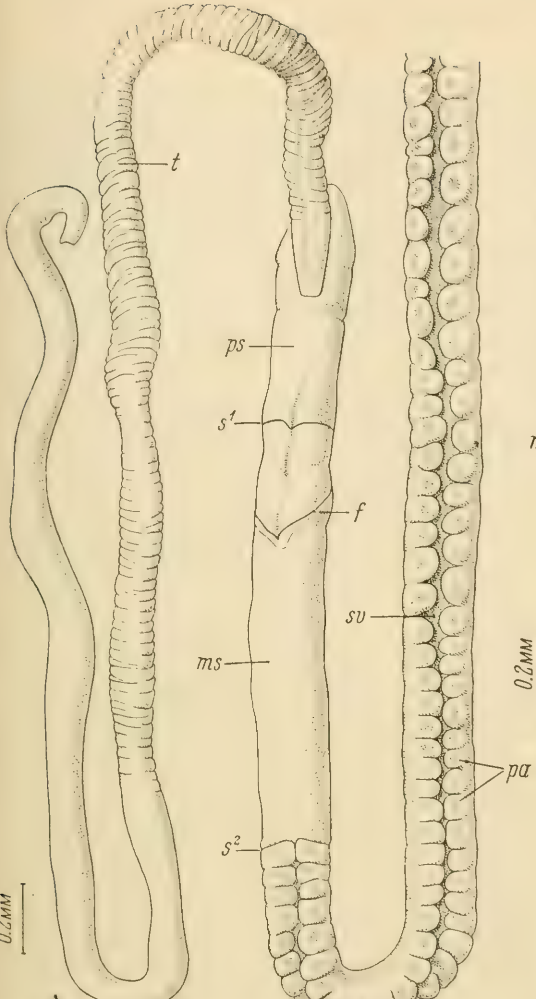
Ivanov, 1960c: 5, 94, 96, 126, 142–5, 158, 196, 264, Figs. 87, 105.

To all appearances this species forms a characteristic element of the abyssal fauna near the east coast of Japan. A few tubes of *S. japonicum* were taken amongst many of *Diplobrachia japonica* (p. 370) on a cruise of R.V. *Vityaz'* in the spring of 1957, and three of the tubes contained animals.

The long fore-part of the body is cylindrical or slightly flattened dorsoventrally (Fig. 105*A*, *B*). In one specimen its length was eight times its breadth, while in another, preserved in a strongly contracted condition, the ration was 6 : 1. The keels lie in the middle of the fore-part and the front of the mesosoma is marked by a groove which curves strongly back on the dorsal side and almost reaches the dorsal ends of the keels of the bridle (Fig. 105*B*). The protosoma is long and the cephalic lobe large, short and conical, and in one individual a transverse, pretentacular groove was noticed on the dorsal side (Fig. 105*B*). In all three individuals the stout but long tentacle was strongly contracted and to a considerable extent covered in abundant transverse wrinkles. The tentacle is attached in the mid-ventral line, just about at or a little in front of the middle of the protosoma (Fig. 105*A*) and pinnules are absent from its basal part. More distally, there are two closely adjacent, alternating rows of slender pinnules, each *c.* 0·1 mm long (Fig. 105*C*). The very delicate, brownish keels of the bridle are fused ventrally but wide apart dorsally, and the ridges of the bridle are weakly developed. In front of the bridle is a weak median ventral furrow, while behind the bridle may be made out a weakly developed brownish glandular belt, which is interrupted on the dorsal side. The boundary between the mesosoma and the metasoma takes the form of a simple annular groove Fig. 105*A*, *B*).

Fig. 105. *Siboglinum japonicum*: *A* – front end of a female in ventral view; *B* – the same part of another individual from the dorsal side; *C* – part of the tentacle; *D* – spermatophore; *E* – anterior filmy part of tube; *F* – anterior part of tube; *G* – middle part of tube.

c – cephalic lobe; *ci* – lateral part of glandular girdle; *f* – keel of the bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between protosoma and mesosoma; s^2 – groove between mesosoma and metasoma; s^3 – groove between cephalic lobe and protosoma; *sv* – ventral sulcus; *t* – tentacle.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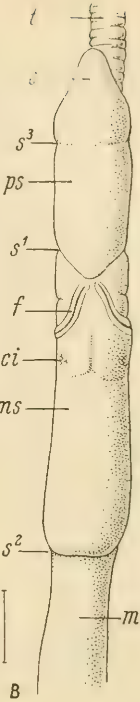
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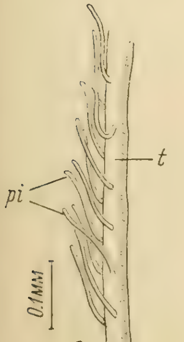
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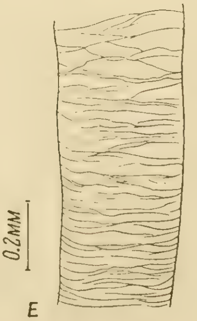
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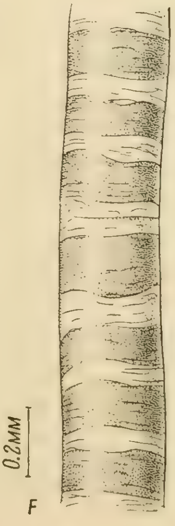
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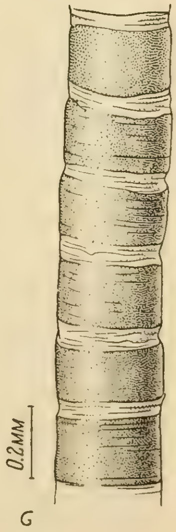
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G

The broad dorsal ciliated band begins at the front edge of the metasoma. The 65–70 pairs of metameric papillae of the trunk are large and more or less rounded, and the ventral sulcus between them is narrow (Fig. 105*A*). In each papilla may be seen a single pyriform gland. In the hind part of the metameric region the papillae become larger for a stretch and then the region of the trunk possessing small rounded disorderly papillae begins immediately. The genital papillae of the male are not large, but nevertheless meet in the mid-line. The zone of thickened papillae, the girdle region and the post-annular section remain unknown.

The tentacle is not less than 8 mm long; the fore-part of the body is 1·4–1·85 mm long; the breadth of the mesosoma is 0·2–0·25 mm; the length of the metameric part of the preannular region is *c*. 6 mm.

The spermatophores are shaped like narrow spindles, almost parallel-sided for the greater part of the length, then gradually tapering down to a point at the opposite end from the filament. This latter is very long and slender, but has a thickened base (Fig. 105*D*). The spermatophore is about 0·2 mm long, with a greatest breadth of about 0·014 mm in the middle.

The rings of the unsegmented tube are rather coarse. The front filmy ringless portion is colourless, transparent and limp. Then, in the walls of the tube appear, little by little, numerous transverse fibres (Fig. 105*E*). The walls gradually become thicker and turn brown, and rings begin to appear. The main part of the tube has well-developed, not very regular, coarse, muddy-brown rings, whose edges are uneven, and in the stouter tubes the rings are very dark brown and coarse. They vary noticeably in length, but are always shorter than the diameter of the tube (Fig. 105*F*). The narrow clear interspaces between them are transversely wrinkled, and possess coarse, brownish transverse fibres (Fig. 105*G*). The largest fragment of tube is about 100 mm in length and 0·28–0·32 mm in diameter.

The arrangement of the pinnules and the development of a pretentacular groove suggests that *S. japonicum* must be closely related to those species possessing a bipectinate tentacle (*S. ekmani*, *S. pinnulatum*, *S. fedotovi* and *S. plumosum*). The backward curve of the front border of the mesosoma, however, reaching back to the dorsal ends of the bridle, is not found in any of these other species. This characteristic feature, besides in *S. japonicum*, is found in *S. caulleryi*, in the primitive *Oligobrachia dogieli* (p. 155) and also in *Nereilinum murmanicum*. Another feature, moreover, which it shares in common with *Siboglinum caulleryi* appears to be the unsegmented tube with simple rings, while the development of fibres in the walls closely recalls the tube of *S. pusillum*.

Material: 30 fragments of tubes amongst which were three with animals in them.

Locality: the Pacific Ocean to the east of the northern part of Honshu, Japan.

Depth: 1660 m.

7. *Siboglinum vinculatum* Ivanov (Figs. 106–7)

Ivanov, 1960c: 5, 12, 16, 19, 97, 125, 145–8, 151, 196, 264, Figs. 87, 106–7.

In trial dredgings made by R.V. *Vityaz'* in January, 1958, in the Tasman Sea, near the coast of New Zealand, at depths of 1740 and 1225 m, were found two white ringed tubes, recalling those of *S. cinctutum* (p. 207) and *S. frenigerum* (p. 213). In both tubes were discovered animals undoubtedly belonging to no known species. One of these individuals, which turned out to be a male, was considerably larger than the other, which, to all appearances, was a young female. The proportions of the various parts of the body in the male seemed, at first glance, to differ considerably from those of the female, but this difference, in all likelihood, could be ascribed to the female's having been fixed in a strongly contracted condition. The most characteristic feature of this species is the presence of three annular grooves between the base of the tentacle and the bridle, giving it a cross-banded appearance, and it is to this that *S. vinculatum* owes its name [Latin *vinculum*, a band, hence, *vinculatum*, banded].

The length of the fore-part of the body in the male is seven times, and in the female five times the breadth (Fig. 106*A*, *B*, *C*). The second of the three annular grooves corresponds in position to the boundary between the protosoma and the mesosoma. On the ventral side it arches a little forward, while on the dorsal side it has a small median notch, pointing backwards. The last annular groove has a similar median notch on the ventral side, and the first groove lies immediately behind the base of the tentacle (Fig. 106*A*, *B*, *C*). The large, somewhat dorso-ventrally flattened, cephalic lobe is shaped like an equilateral triangle, and through its integument the median and lateral cephalic blood vessels can faintly be made out (Fig. 106*B*). The comparatively stout, cylindrical tentacle is furnished with a double, alternating row of pinnules, 75–80μ long (Fig. 106*A*, *D*), within which the afferent and efferent capillaries may readily be observed (Fig. 106*E*).

The cylindrical mesosoma has a narrow median ventral furrow in front of the bridle, which latter lies in the centre of the fore-part of the body. Its rather stout, yellowish keels are fused ventrally and gradually taper towards

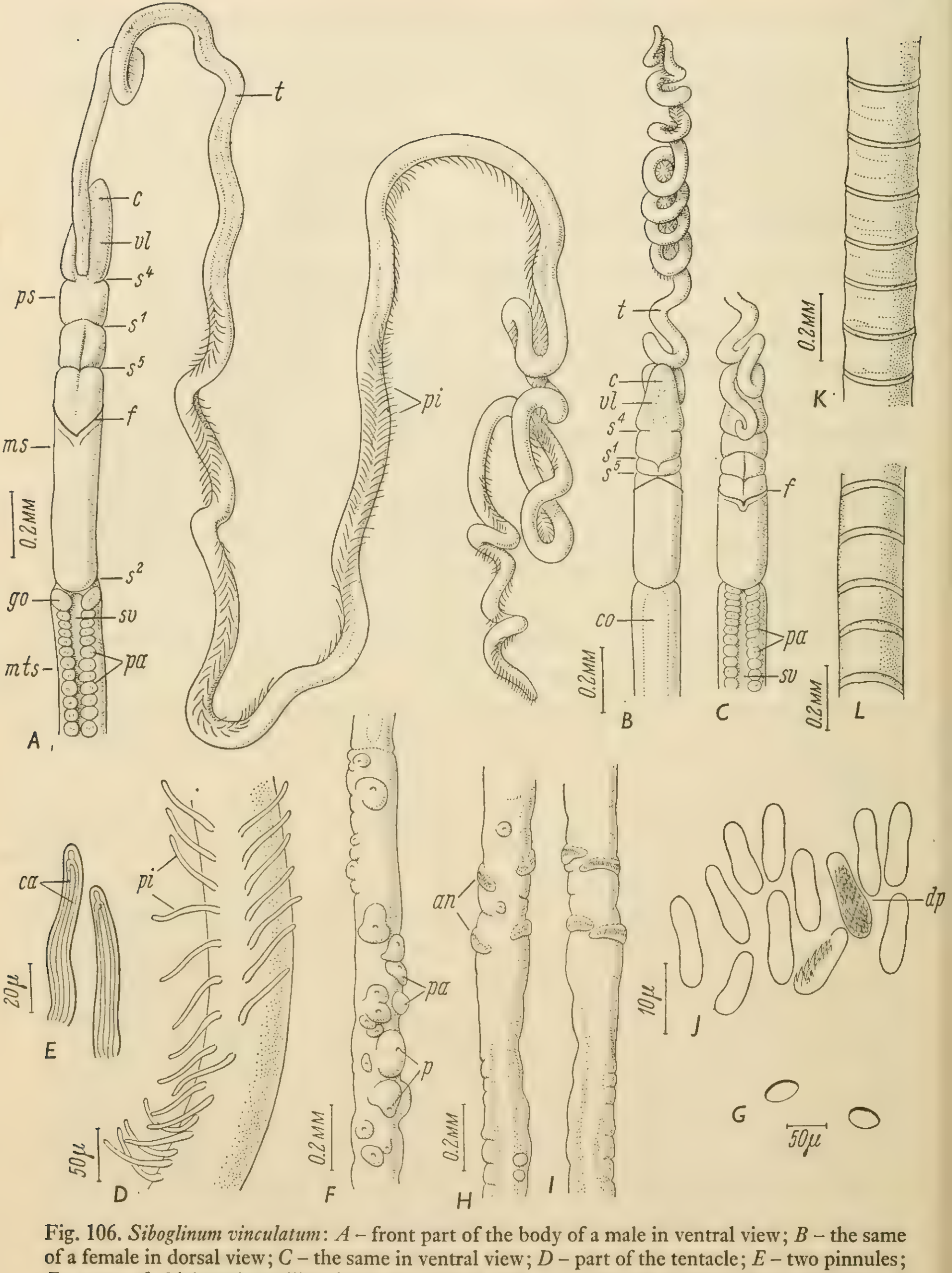

Fig. 106. *Siboglinum vinculatum*: *A* – front part of the body of a male in ventral view; *B* – the same of a female in dorsal view; *C* – the same in ventral view; *D* – part of the tentacle; *E* – two pinnules; *F* – zone of thickened papillae from the ventral side; *G* – cuticular plaques from the zone of thickening; *H* – the region of the girdles in ventral view; *I* – the same from the dorsal side; *J* – part of a girdle; *K* – anterior part of the tube; *L* – a more posterior part of the tube.

the dorsal side, where, once more, they fuse with each other (Fig. 106*B*). There is no trace of any glandular tissue behind the bridle. The hind end of the mesosoma is curved both dorsally and ventrally.

The metasoma is as broad as the mesosoma or, in the male, a little broader even, and the correspondingly broad dorsal ciliated band begins at the front of the trunk (Fig. 106*B*). The small transverse, oval or rounded metameric papillae have each a pyriform gland visible inside, and the ventral sulcus between them is distinct. The genital papillae of the male are rather large and oval (Fig. 106*A*). The zone of thickened papillae was dissected out in the female specimen and found to possess about ten large and ten small, higgledy-piggledy, rounded papillae (Fig. 106*F*) with characteristic oval cuticular plaques, some 35–40μ across, with crescentic thickenings along the front edge (Fig. 106*G*). The two girdles, situated close together, are both interrupted dorsally as well as ventrally. The gap, however, is much wider on the ventral side and very slight on the dorsal side. A few rounded papillae, with the same kind of cuticular plaques as in the zone of thickened papillae, are situated in the region of the girdles (Fig. 106*H*, *I*). The toothed platelets are arranged in two or three irregular rows in each girdle, and in shape they are elongated ovals, with a slight constriction in the middle. The front end is as broad as the back or only a little narrower. A characteristic feature of the platelets appears to be the absence of any anterior group of teeth, so that all the teeth point the same way—sharply forwards (Fig. 106*J*). The platelets are 11–13μ long. The postannular region of the trunk remains unknown.

The dimensions (in mm) of the various parts of the body are as follows:

	Male	Female
Length of the tentacle	10·7	4·5
Length of the fore-part	1·25	0·64
Breadth of the fore-part	0·17	0·15
Breadth of the metasoma	0·15	0·15
Length of the preannular section	145·0	—

The spindle-shaped spermatophores are greatly elongated and the end opposite the base of the filament gradually tapers to a lancet-like appendix,

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an – girdles; *c* – cephalic lobe; *ca* – capillaries of pinnule; *co* – dorsal ciliated band; *dp* – posterior group of teeth; *f* – bridle; *go* – genital papilla; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaques; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; s^4 – post tentacular groove; s^5 – secondary groove of the mesosoma; *sv* – ventral sulcus; *t* – tentacle; *vl* – lateral cephalic vessel seen by transparency.

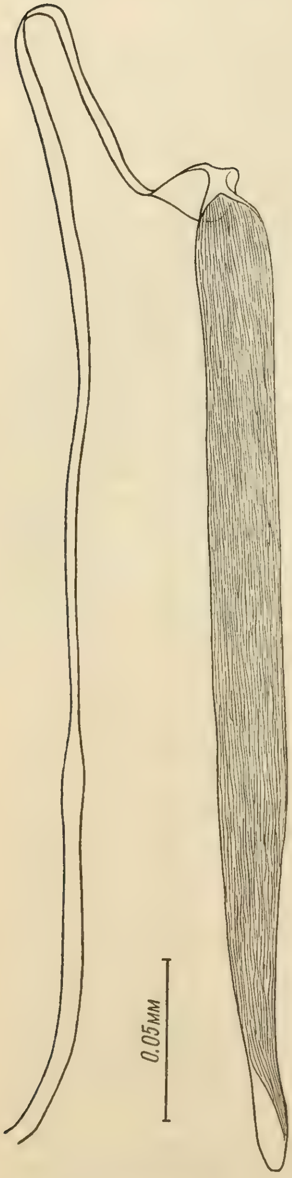


Fig. 107. *Siboglinum vinculatum*: Spermatophore (only the proximal part of the filament is figured).

free of sperm. The sperm are arranged parallel to the axis of the spermatophore. The base of the filament, springing from the rounded end, is constricted, then swiftly expands into a rather broad plate, which soon runs into the ribbon-like basal part of the filament (Fig. 107). The spermatophores are about 0·3 mm long and a little more than 0·02 mm broad.

The stoutish, coarse tube consists of lack-lustre white rings divided by narrow transparent interspaces (Fig. 106*K*, *L*). The rings are a little longer than broad, and in the front part of the tube each ring is just perceptibly constricted in the middle (Fig. 106*K*). The longer tube, that of the male, is 14·5 cm long, but it is torn off at both ends. The tube of the female, in two fragments, is 11·6 cm long. This tube may be distinguished from the slightly brownish tubes of *S. cinctutum* p. 207) and of *S. frenigerum* p. 213) by its absolute whiteness.

The major characteristic features of *S. vinculatum* are as follows: the possession of three annular grooves between the base of the tentacle and the bridle, the fusion of the dorsal ends of the keels of the bridle, the arrangement of the pinnules in two rows, the higgledy-piggledy placing of the papillae of the zone of thickening and their possession of cuticular plaques, the absence from the toothed platelets of any teeth pointing backwards, and the most characteristic shape of the spermatophores.

S. vinculatum is most closely related to *S. cinctutum*, from which it may be distinguished by the pattern of secondary rings on the fore part of the mesosoma, by the double row of pinnules, and by the dorsal fusion of the keels of the bridle. The peculiar whiteness of the rings of the tube links *S. vinculatum* with *S. cinctutum* and with *S. frenigerum*.

Material: two specimens in tubes, a mature male and a young female.

Locality: the Tasman Sea to the west of New Zealand.

Depth: 1925 and 1740 m.

8. *Siboglinum cinctutum* Ivanov (Figs. 108–9)

Ivanov, 1957a: 446–9, 458, 459, 490, 491, 496, 497, Figs. 14–16, 59; Ivanov, 1950a: 1541; Ivanov, 1960c: 5, 14, 27, 96, 127, 145, 148–51, 160, 264, Figs. 87, 108, 109.

Only two specimens of this species are known. The fore-part of the body is comparatively short, only about four and a half times as long as broad (Fig. 108*A*, *B*). The boundary between the protosoma and the mesosoma is a simple transverse groove, and the mesosoma is twice as long as the protosoma, which is not separated from the equilateral triangle of the cephalic lobe. The slender tentacle was broken across in both specimens and the distal part

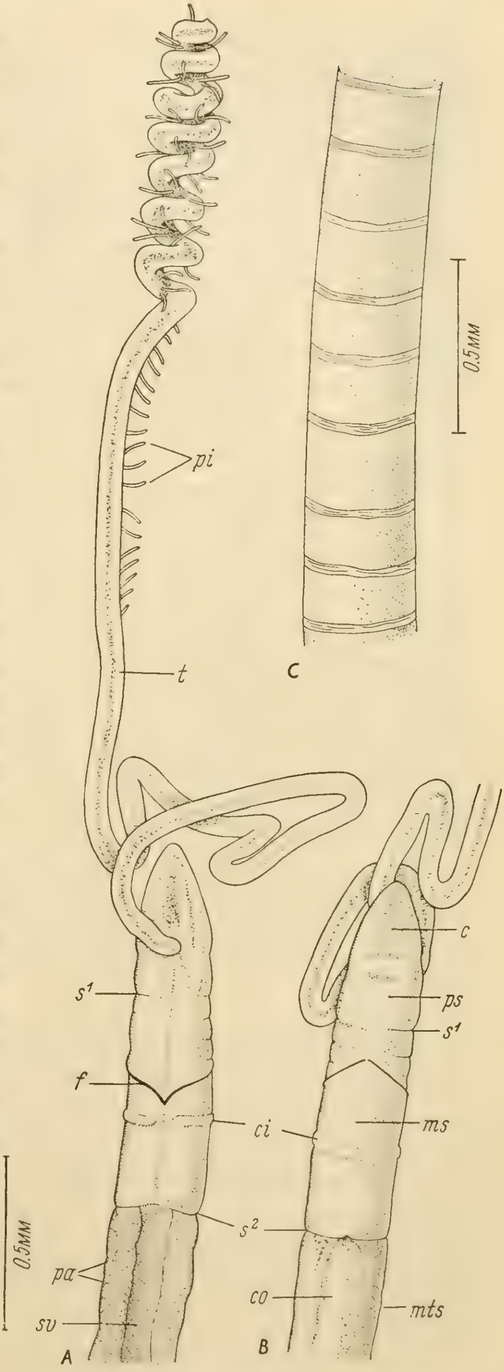


Fig. 108. *Siboglinum cinctutum*: *A* – front part of the body of a female in ventral view; *B* – the same from the dorsal side; *C* – the tube.
c – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *f* – keels of the bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle. (After Ivanov, 1957a.)

missing, but pinnules are present on the distal part of what is left, arranged in a single sparse row. The bridle is well-developed, its rather stout black keels fused together on the ventral side and almost meeting dorsally. The cutaneous ridges of the bridle are imperceptible, and behind the bridle the mesosoma bears an epidermal glandular ridge, forming a belt which is interrupted on the ventral side (Fig. 108*A*, *B*).

The metameric part of the preannular region is rather long, with a pronounced ventral sulcus and a broad, dorsal ciliated band beginning at the very front of the metasoma (Fig. 108*A*). The numerous metameric papillae, forming flat even lateral ridges, are strongly compressed and hence much elongated from side to side. They are obviously glandular and lack cuticular plaques. In one individual the zone of thickened papillae of the nonmetameric part of the trunk was dissected out for investigation. Here, eleven large conical papillae were immediately obvious, arranged in a single ventral row (Fig. 109*A*). On the tip of each papilla was a slightly curved transverse plaque, about 30–35μ across. The region of the girdles differs greatly in the two individuals. In one of them, to all appearances the more typical individual, the girdles lie on well-marked transverse ridges and are interrupted on the ventral side (Fig. 109*B*, *C*). The toothed platelets are arranged in two or, in places, three rows (Fig. 109F). Between the girdles lies a small unpaired papilla, and three similar papillae, bearing plaques, are to be found behind the girdles. In the other individual the girdles are rather strongly stretched (Fig. 109*D*). Each forms a broad arch on the dorsal side with the convexity directed forward. The toothed platelets, moreover, are placed in no sort of order, but at the same time are clearly more or less two deep in each girdle. The total effect is of a very strange girdle, quite unlike anything which has been seen in any other species of pogonophore, and, to all appearances, this must represent an extreme individual variant, for it cannot be an artefact of fixation.

The transparent and almost colourless toothed platelets are elongated and compressed at the front end. Their surface is covered with sharp teeth, pointing straight backwards and arranged in numerous regular oblique rows. On the front end of a proportion of platelets, however, may be observed a small feeble detached portion, which represents the area of the anterior group of teeth and is furnished with small sharp teeth pointing backwards (Fig. 109*G*). Sometimes this part is far lighter in colour than the rest of the platelet. The platelets are 12–19μ long by 4–5·5μ broad. The long slender postannular region of the trunk carries, at equal intervals, a series of large broad dorsal glandular shields (Fig. 109*D*).

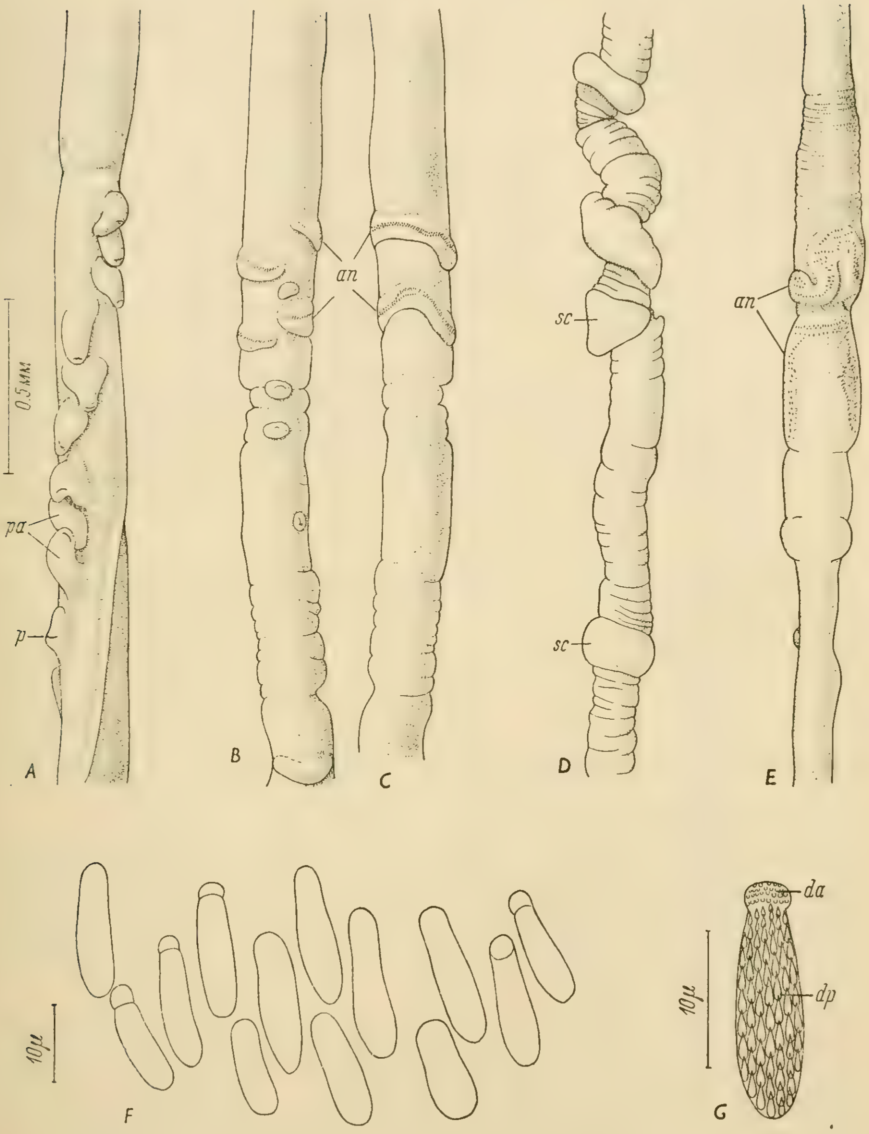


Fig. 109. *Siboglinum cinctutum*: metasoma: *A* – zone of thickened papillae; *B* – region of the girdles in ventral view; *C* – the same from the dorsal side; *D* – postannular region in dorsal view; *E* – region of the girdles (in an aberrant specimen) from the dorsal side; *F* – part of a girdle of toothed platelets; *G* – toothed platelet.
an – girdles; *da* – anterior group of teeth (only the bases of the teeth indicated); *dp* – hind group of teeth; *p* – cuticular plaque; *pa* – papillae; *sc* – dorsal shield. (*A*, *B*, *C*, *D* after Ivanov, 1957a.)

The length of the body, in all likelihood, is not less than 60 mm; the forepart of the body, including the cephalic lobe, is 1 mm long by 0·25 mm broad.

The spermatophores are unknown, since both individuals appear to be females.

The walls of the tube are stout, elastic and so soft that they may be easily cut with a sharp scalpel. At the same time the tube possesses the characteristic whiteness which recalls those of *S. vinculatum*, *S. frenigerum* and *Zenkevitchiana longissima* (pp. 203, 213 and 388). It is made up of regular rings, consisting of a firm opaque white substance, and of narrow transparent delicately pleated intervals (Fig. 108*C*). The longest tube is 15 cm long by 0·3 mm in diameter.

The large protosoma, the single row of pinnules, the strongly developed bridle and glandular belt, and the characteristic unsegmented white tube are the most important features distinguishing *Siboglinum cinctutum*. For the features by which it may be separated from *S. vinculatum* see under that species (p. 206).

Material: two females.

Locality: the northwestern part of the Pacific Ocean to the east of Hokkaido Island, Japan.

Depth: 3420 m.

[*8A. Siboglinum cinctutum* Ivanov var. *subtile* Southward (Fig. A109)

Southward 1961b: 9–11, 21, Fig. 5.

This variety was found by Dr. Southward in her re-examination of the *Siboga* material and was originally included by Caullery (1914, 1944) in his species *S. weberi*. The following description is by Dr. Southward (1961) and is reproduced by kind permission of the author and the publisher, E. J. Brill.

"The animals are . . . incomplete and are up to 25 mm long, with a tentacle over 4·5 mm long. The tentacle is not very thick, 50 to 80μ in diameter, and it bears one row of fine pinnules, 120 to 150μ long. The cephalic lobe of the protosoma is rather short and there is no pretentacular groove visible, but behind the base of the tentacle there is a semi-annular groove on the ventral side and a second semi-annular groove, also on the ventral side, before the bridle (Fig. A109*A*). The bridle is only slightly raised; its narrow brown keels are joined in a point on the ventral side but separated by a small gap on the dorsal side. There is a slight longitudinal furrow on the ventral side between the bridle and the tentacle (Fig. A109*A*, *D*). Behind the bridle there is a narrow ring of epidermal glands, complete except for a small gap on the ventral side. The fore-part of the body is 0·89 to 1 mm long, while the diameter of the mesosoma is 0·17 to 0·23 mm and the ratio of the two measurements is 5 : 1.

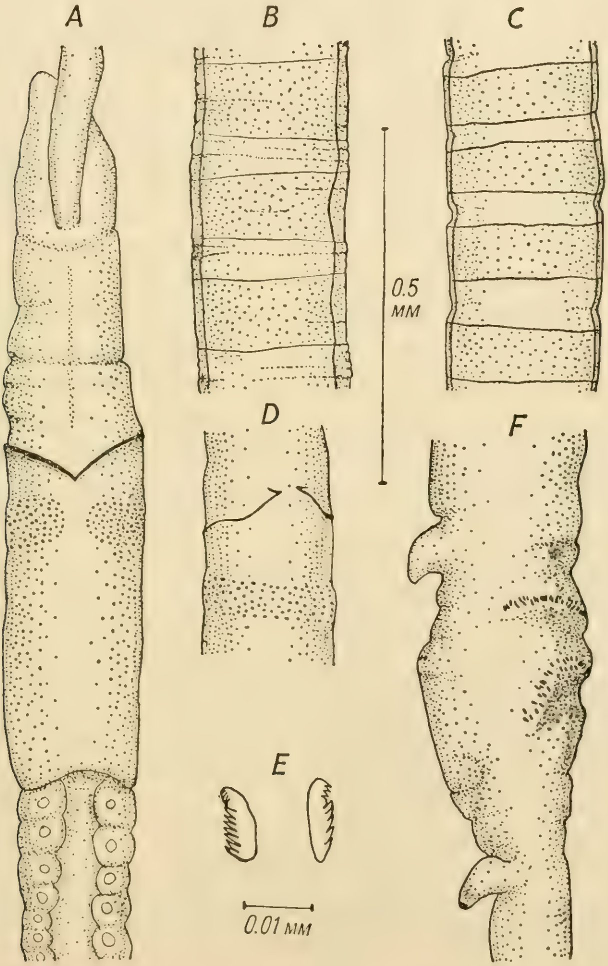


Fig. A109. *Siboglinum cinctutum* var. *subtile*: *A* – anterior end of animal, ventral view; *B*, *C* – middle and anterior parts of tube; *D* – dorsal view of bridle; *E* – toothed platelets, lateral view; *F* – girdles. Heavy stipple shows the position of the epidermal glands. (After Southward, 1961b.)

"The metameric region of the trunk is up to 3 mm long and contains about 80 pairs of small papillae in two even rows, separated by a wide ventral sulcus. In two specimens the rest of the preannular region can be seen clearly; it bears about 10 large papillae with curved cuticular bars 15 to 20μ long at their tips. The preannular region is 11 to 16 mm long. The two girdles are semiannular and lie close together; each one bears 1 to 3 very irregular rows of toothed platelets, which are about 12μ long and have a small anterior group of teeth and a larger posterior group (Fig. A109*E*, *F*). There are some large postannular papillae, with plaques like the preannular ones, fairly widely separated from one another.

"None of these specimens is sexually mature, but some slides of transverse sections prepared by Caullery, with no station number but, according to his text, from sta. 48 (Caullery, 1944, p. 23, Figs. 87–89), show the genital region of a male animal in a tube 0·22 mm in diameter, which could be this species. The spermatophores, in transverse section, are about 30μ in diameter.

"The tubes are whitish and transparent with fairly thin walls. The ends of the tubes are ringless and have thinner limp walls but the middle parts are stiffer and have rings which are whitish by reflected light and greyish in transparency, and are narrower near the anterior end of the tube than near the posterior end (Fig. A109*B*, *C*). One fragment, 5 cm long, is completely ringless. None of the fragments is longer than 5 cm and the diameter ranges from 0·17 to 0·29 mm in different individuals, though it is usually at least 0·22 mm.

"The specimens described here differ from Ivanov's (1957, 1960a) descriptions of *S. cinctutum* in only a few respects: the tube is not more than 0·29 mm in diameter, instead of 0·34 mm; the pinnules are rather longer; the bridle keels are brown, not black; the adhesive plaques (bars) are 15 to 20μ long, not 30 to 35μ. I do not think that these differences are sufficient to separate a new species, but they do justify the placing of the *Siboga* specimens in a new variety, at least until some intermediate form is discovered. This variety, *S. cinctutum* var. *subtile* is so named because of the smaller size of the tubes and animals."

Material: 13 fragments of tubes, ten occupied.

Localities: Malayan Archipelago: Siboga Stations 52 (Bali Sea, 9°3′S 119°56′E), 212 (Java Sea, 5°54′S 120°19′E).

Depth: 462 and 960 m.]

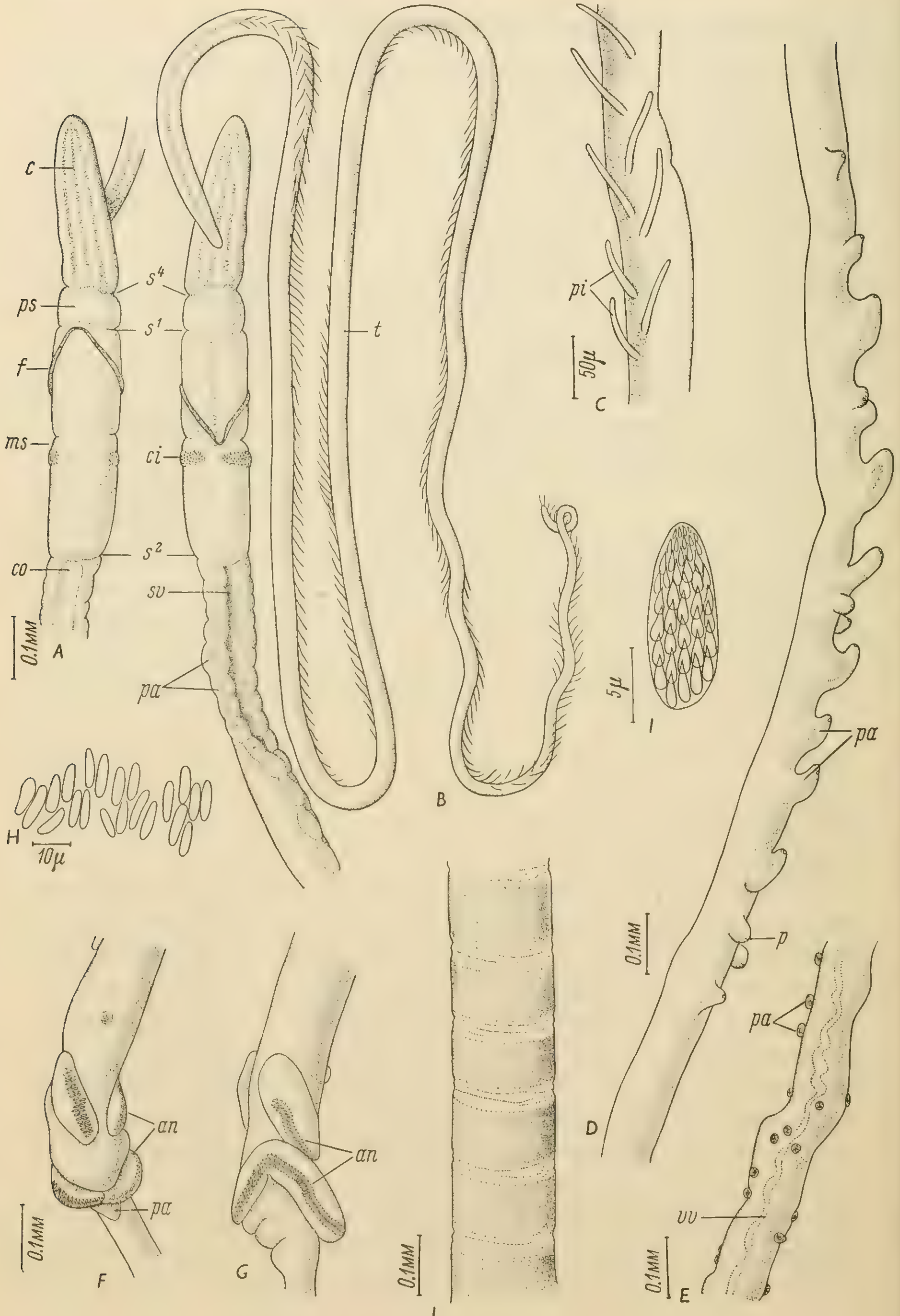
9. *Siboglinum frenigerum* Ivanov (Fig. 110)

Ivanov, 1960c: 5, 12, 96, 125, 145, 148, 151–3, 186, 196, 264, Figs. 87, 110.

This species was taken, together with *S. buccelliferum* and *S. robustum*, near Treasury Island, in the northern part of the Coral Sea, at a depth of 960 m, in January, 1957 by R.V. *Vityaz*'. Two females were collected, both with characteristic white ringed tubes, at first glance recalling those of *S. cinctutum* and *S. vinculatum*. Another female was taken by R.V. *Vityaz*' in November, 1959, in the Indian Ocean off the south coast of Sumatra. The extraordinarily strong development of the keels of the bridle affords grounds for naming this species *S. frenigerum* [Latin *frenum*, a bridle, *gerere*, to bear.]

The length to breadth ratio of the fore-part of the body is 7 : 1. In front of the bridle are 2 simple annular grooves, the first being half-way between the tentacle and the hind groove (Fig. 110*A*, *B*). The blood vessels in the large conical cephalic lobe are readily visible by transparency. The basal part of the very long, comparatively stout tentacle, which is attached in the mid-ventral line, is free of pinnules (Fig. 110*B*). More distally, pinnules about 0·07 mm long, are attached rather sparsely in a single row, but with a slight tendency to form a double row (Fig. 110*C*). The muddy-brown, very broad keels of the strongly pronounced bridle are fused together both dorsally and ventrally and reach their greatest thickness at the sides of the body (Fig. 110*A*, *B*). The ridges of the bridle are particularly well-developed on the ventral side. Behind the bridle is a protuberant glandular girdle, interrupted both ventrally and dorsally, and between the bridle and this girdle a weak constriction is discernible, forming a sort of waist. The back edge of the mesosoma is curved on the ventral side.

The metameric part of the trunk is a little narrower than the mesosoma and the papillae here are rather large, each with a pyriform gland visible inside it. Farther back they become somewhat drawn out and elongated. There are 60–64 pairs of metameric papillae. The dorsal ciliated band is much as usual (Fig. 110*A*). Behind the female genital apertures, in the region of the thickened papillae, are 13–16 large conical transparent papillae arranged in a more or less ventral row. On the tip of each one lies a very small thickening of the cuticle—a sort of rudimentary plaque (Fig. 110*D*). Then, between the zone of thickened papillae and the girdles, the trunk bears numerous darkish warts of a glandular character, placed higgledy-piggledy (Fig. 110*E*). Of the two girdles, which lie close together (Fig. 110*F*, *G*), the first is weakly developed and arranged as a pair of oblique lateral half-hoops, not meeting either dorsally or ventrally, while the second, lying on a broad ridge, is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interrupted only on the ventral side (Fig. 110*F*). The toothed platelets of each girdle, arranged in two irregular rows (Fig. 110*H*), are yellowish elongated ovals, covered with comparatively large teeth pointing forwards. The teeth of the anterior group are poorly developed and few in number (Fig. 110*I*). The platelets measure 10–11μ by *c.* 3μ. The anatomy of the postannular trunk has not been investigated.

All the known animals are females of almost identical size, and their dimensions are as follows: length of the tentacle, up to 6 mm; length of the fore-part of the body, 0·67 and 0·75 mm; breadth of the mesosoma, 0·1–0·15 mm; length of the preannular region of the trunk, 27 to 46 mm; length of the postannular region up to 33 mm. The overall length of the body, including the tentacle, is not less than 86 mm.

The ringed tube is distinguished by its whiteness. The very regular, lack-lustre rings, a little shorter than the diameter of the tube, are colourless or slightly mud-coloured, and the narrow colourless intervals between them are smooth and glassily transparent (Fig. 110*J*). In all individuals the remaining fragment of tube was almost 20 cm long, with a diameter of almost 0·17 mm near the front end.

The characteristic features of the species are as follows: the two simple, annular grooves between the base of the tentacle and the bridle, the "waist" behind the bridle, the extraordinarily strongly developed keels of the bridle (in this respect *S. frenigerum* is different from all other species of *Siboglinum*), the fifteen or so conical papillae of the zone of thickening, the two girdles, each with two rows of platelets, the considerable reduction of the front group of teeth on the platelets of the girdles, and the whiteness of the tube.

Material: three almost complete females.

Locality: The Coral Sea near Treasury Island in the British Solomon Islands (8°S 155°E) and off the coast of Sumatra.

Depth: 620–960 m.

Fig. 110. *Siboglinum frenigerum*: *A* – front part of the body of a female from the dorsal side; *B* – the same in ventral view; *C* – part of a tentacle; *D* – zone of thickened papillae from the right side; *E* – part of the trunk in front of the girdles in ventral view; *F* – girdles from the ventral side; *G* – the same from the dorsal side; *H* – part of a girdle of toothed platelets; *I* – toothed platelet; *J* – tube.

an – girdles; *c* – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *f* – keel of the bridle; *ms* – mesosoma; *p* – cuticular plaque; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; s^4 – post-tentacular groove; *sv* – ventral sulcus; *t* – tentacle; *vv* – ventral blood vessel seen by transparency.

10. Siboglinum caulleryi Ivanov (Figs. 3, 8, 10, 12, 14, 85, 111–13)

Ivanov, 1951: 740, 742, Fig. 1 (as *S. weberi*); Ushakov, 1953: 179 (as *S. weberi*); Abrikosov, 1957, 234, 236, Fig. 3; Alvarado, 1957b: 495; Ivanov, 1957a: 434, 440–6, 456, 458, 459, 490–3, 495–8, Figs. 6–13, 59; Ivanov, 1957b: 1127–44, Figs. 1, 3–10, 12, 14; Brunet and Carlisle, 1958: 1689; Dajoz, 1958, 231; Ivanov, 1958a: 1363, 1369, Fig. 10; Ivanov, 1958b: 1682, 1688, 1689, Fig. 2; Ivanov, 1958d: 1; Ivanov, 1958e: 1070–86, Figs. 1–4, 6, 8; Manton, 1958: 748–51, Figs. 1–22; Ivanov, 1960a: 1528, 1529, 1537, 1541, 1542, 1545, 1548, 1549, 1559, 1562, 1566, 1567, 1592, 1600, 1608, 1609, 1612, Figs. 1390, 1392, 1394, 1396, 1403, 1411, 1413–14, 1418, 1448, 1451, 1453–8, 1461, 1463–4, 1468, Pl. VI; Ivanov, 1960c: 5, 11, 22, 27, 28, 34, 44, 50, 53, 55, 91, 93, 94, 96, 105, 108, 127, 145, 153–8, 160, 196, Figs. 3, 8, 10, 12, 14, 22, 30, 32–3, 38, 67, 70–7, 81–2, 85, 87, 111–13, Pl. I.

The cylindrical fore-part of the body is six or seven times as long as it is broad (Figs. 3, 8, 111*A*, *B*, *C*). The groove dividing the protosoma from the mesosoma runs straight across the ventral side, but on the dorsal side it curves strongly backwards to meet the dorsal ends of the keels of the bridle. The mesosoma is three times as long as the protosoma. The comparatively large, more or less conical, cephalic lobe is not delimited from the protosoma and it is pointed at the tip. The slender and extraordinarily long tentacle (Fig. 3) is furnished with very small pinnules arranged in a single longitudinal row, with slight traces of a tendency to form two rows (Fig. 111*D*). The proximal part of the tentacle for a considerable length is free of pinnules. In the living animal the tentacle is coiled into a tight corkscrew, which sometimes persists to a greater or lesser degree in preserved material. [This is probably true of all species of *Siboglinum*, when the animal retracts into its tube and is not feeding; but in life the tentacle can protrude from the mouth of the tube to a considerable length, and probably this always happens when the animal is feeding—D.B.C.]

The bridle lies in the front half of the mesosoma and at the middle of the anterior section of the body. Its very slender cuticular keels are situated on slightly raised cutaneous ridges (Fig. 111*A*, *B*, *C*), and the ventral ends are fused together in the mid-line, but dorsally they just fail to meet each other. In some individuals a narrow transverse glandular patch of integument, whitish in colour, may be detected just behind the bridle. The trunk (metasoma—Figs. 3, 8, 111*A*, *B*, *C*) is divided from the mesosoma by an oblique groove and in its front part it is perceptibly flattened dorso-ventrally. The narrow, dorsal ciliated band begins a short distance behind the start of the metasoma. The pronounced ventral sulcus is bordered by rounded, metameric papillae which lack cuticular plaques and possess instead a glandular character (Figs. 3, 8, 111*A*, *C*). Their metamerism is incomplete

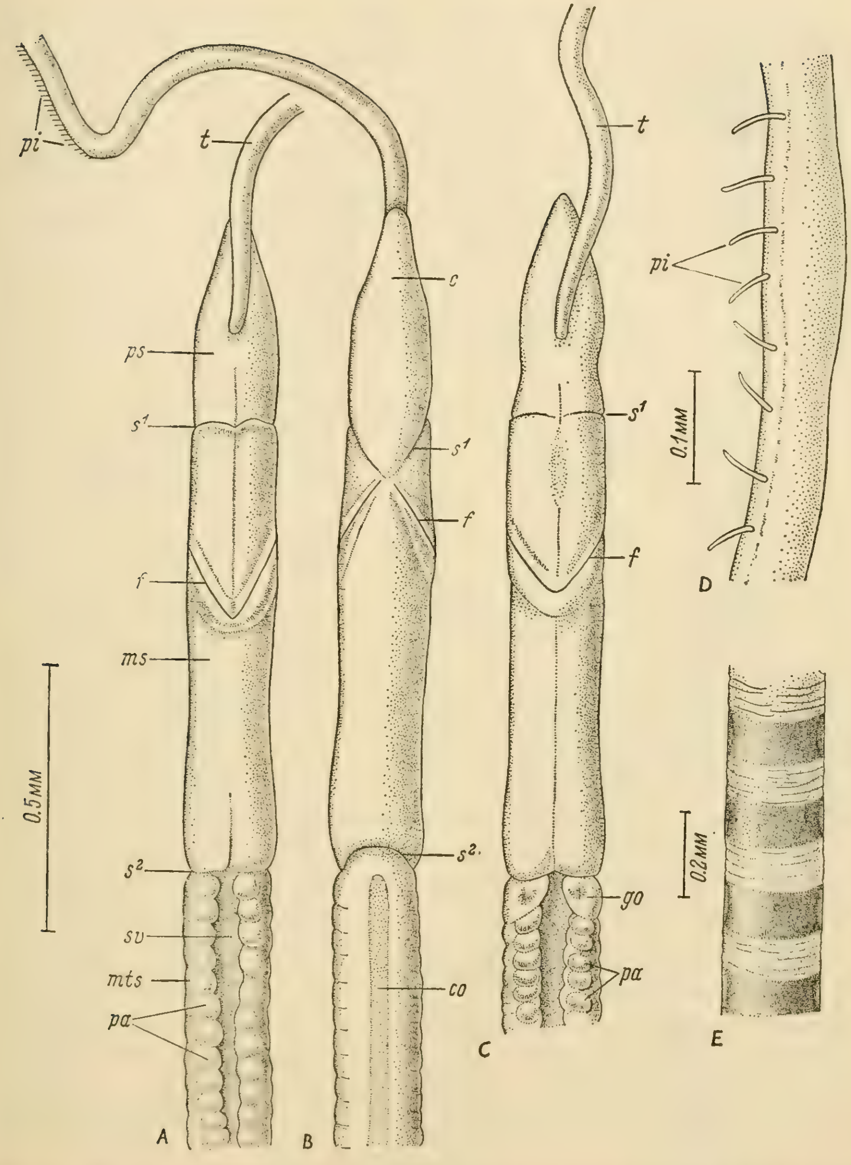
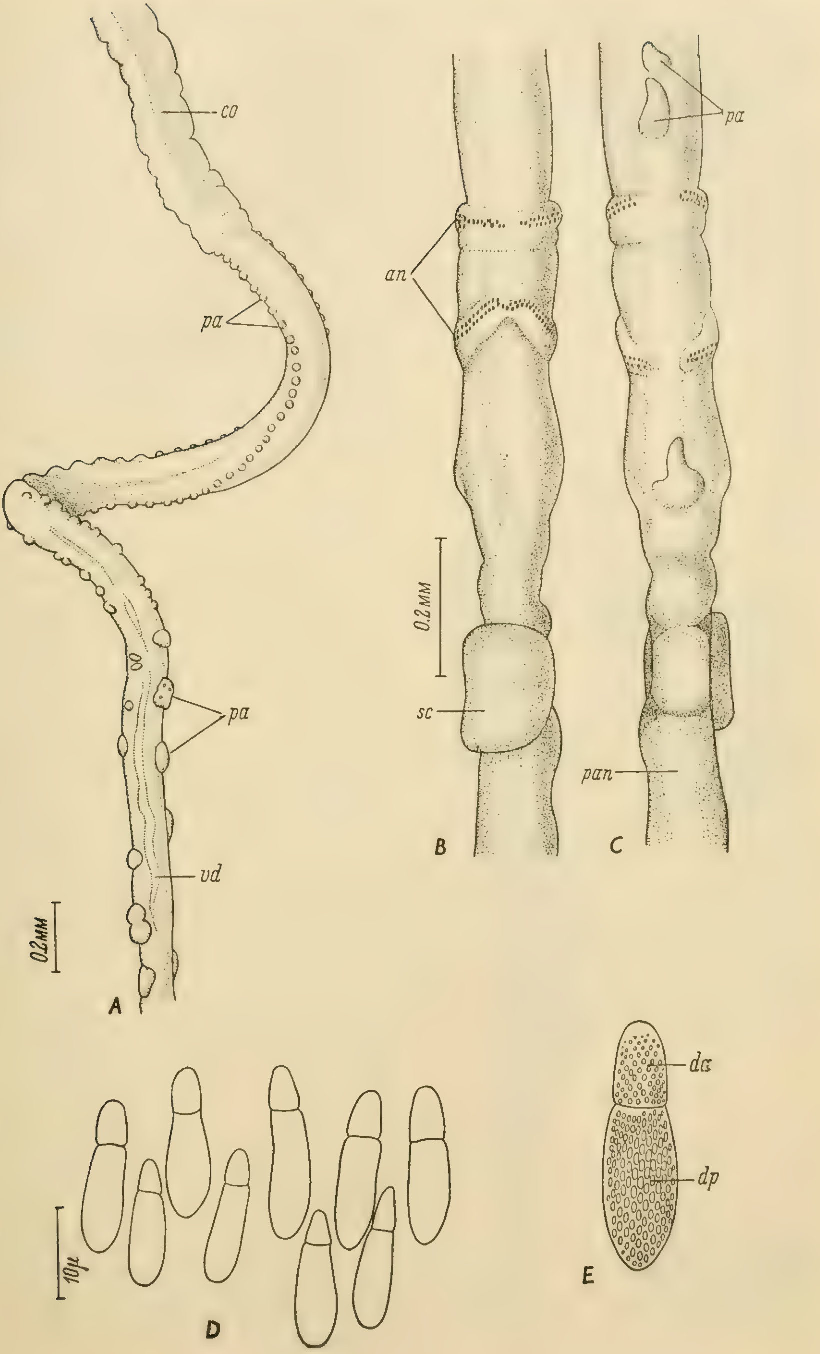


Fig. 111. *Siboglinum caulleryi*: *A* – front part of the body of a female in ventral view; *B* – the same from the dorsal side; *C* – a male in ventral view; *D* – part of the tentacle; *E* – an anterior portion of the tube.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – keel of the bridle; *go* – genital papilla; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle. (*A*, *B*, *C*, *D* after Ivanov, 1957a.)

and subject to very great individual variation, and their number fluctuates between 50 and 75 pairs. In the males the large genital papillae are prominent (Fig. 111*C*). Farther back the ventral sulcus vanishes and the papillae become smaller and move onto the sides of the trunk (Figs. 8, 112*A*). Then they quickly become larger again and move onto the dorsal side, at the same time losing any trace of metameric arrangement (Figs. 8, 112*A*). The character of the trunk hardly changes after this until the girdles are reached, except that at a considerable distance in front of them, in the zone of thickened papillae, are located five prominent long tongue-shaped soft papillae, closely spaced in a short median row on the ventral side (Fig. 10).

The number, shape, arrangement and dimensions of the nonmetameric glandular papillae are all subject to very great individual variation. Indeed, it is literally impossible to match any two individuals which might be identical in all these respects. In particular, between the zone of the median ventral papillae and girdles, in many individuals the dorsal papillae are laterally elongated, while in others this is not so. The two girdles (Figs. 12, 112*B*, *C*), lying on well-developed muscular ridges, are both interrupted on the ventral side and the first on the dorsal side also. In front of the girdles are two rather large conical papillae, lying on the ventral side in the mid-line, one behind the other, while a similar ventral papilla lies behind the girdles. The soft transparent toothed platelets, arranged in two dense rows (Fig. 112*D*), are faintly tinged yellow and noticeably constricted in the middle. The whole surface of each platelet is covered with numerous, very small teeth, of which the front group, covering less than one-third of the platelet, is divided from the hind group by an obvious transverse line (Fig. 112*E*), just as in the platelets of *S. fedotovi* and *S. robustum* (Figs. 101*F* and 127*E*). The platelets measure 15–20μ long by 4–5μ broad. The postannular region of the trunk is very long, as a rule considerably longer than the preannular region and sometimes exceeding it two-fold. Towards the hind end it tapers imperceptibly, and at more or less equal intervals along it are situated large glandular dorsal shields (Fig. 8), with a protuberant cushion-like papilla opposite each one on the ventral side. The first dorsal shield, which varies in size, is placed right behind the hindmost girdle (Fig. 112*B*). In general each

Fig. 112. *Siboglinum caulleryi*: *A* – trunk in the transitional region between the metameric and nonmetameric portions, mainly in dorsal view, with part twisted to show the ventral side; *B* – region of the girdles in dorsal view; *C* – the same from the ventral side; *D* – part of a girdle; *E* – toothed platelet (only the bases of the teeth indicated).
an – girdles; *co* – dorsal ciliated band; *da* – anterior group of teeth; *dp* – posterior group of teeth; *pa* – papillae; *pan* – postannular region; *sc* – dorsal glandular shield; *vd* – dorsal blood vessel seen by transparency. (*B*, *C* after Ivanov, 1957a.)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shield is divided into front and back halves by a slight transverse groove (Fig. 14).

The length of the whole animal, excluding the tentacle, is up to 9·6 cm, while the breadth of the body reaches 0·25 mm. If it is stretched out the tentacle may reach from 13 to 25 mm in length, depending upon the degree of contraction. The anterior part of the body is 1·0–1·8 mm long.

In the living animal the body is more or less transparent, so that the blood vessels, filled with red blood, are clearly visible.

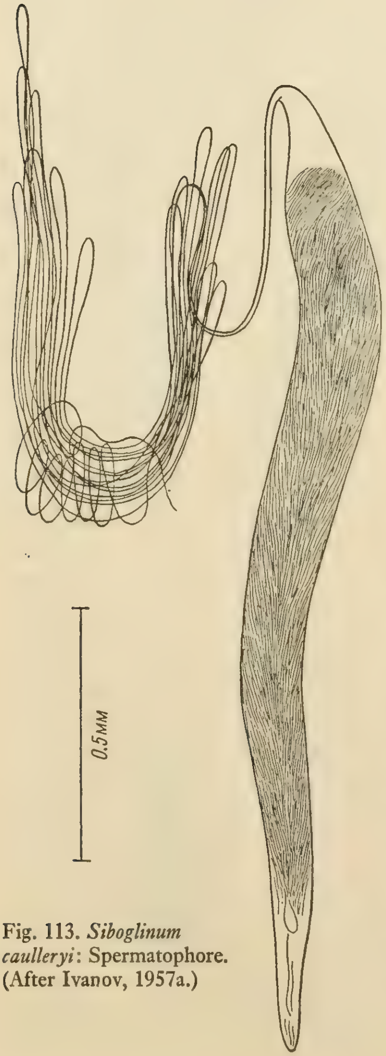


Fig. 113. *Siboglinum caulleryi*: Spermatophore. (After Ivanov, 1957a.)

The spindle-shaped spermatophores, round in cross-section, taper gradually towards one end (Fig. 113), and from the slightly broader end an appendix continues into the base of the extraordinarily long and slender filament. The spermatophores are 0·18 mm long.

The ringed tube is semi-transparent and very flexible. In a fresh condition, and also after fixation in formalin or alcohol, it appears greenish to the naked eye or under a hand lens, but under higher magnification the tube is brownish. The rather dense, brown regular rings are about half to two-thirds the diameter of the tube in length (Fig. 111*E*), but exceptionally one may come across rings considerably shorter. They are separated by light transparent intervals of the same length, which consist of a softer material; transverse wrinkles often appear on their surface and then they become considerably shorter. For a considerable distance the front part of the tube lacks rings. It is here completely transparent, colourless, very flexible and usually flattened into a sort of ribbon (Fig. 85). The walls are membranous in this part, then, passing backwards, the tube runs into the ringed portion. The hindmost part of the tube, also lacking rings, is structureless and transparent, but it has comparatively firm unbending walls. The longest fragment of tube reaches 20 cm, but amongst a great number of tubes only one was found which was not torn across. The length of the hindmost transparent portion is therefore uncertain. In a few cases it extended for 2 cm before the break. The front membranous part of the tube reaches not less than 2·5 cm.

Caullery (1944), in describing the tube of *S. weberi*, stated that it was completely cylindrical and untapered. In *S. caulleryi*, as in all other Pogonophora, it tapers towards the hind end, though very gradually. Thus a fragment 20 cm long measured 0·3 mm in diameter at the front end and 0·2 mm at the hind end, i.e. a taper of 0·05 mm in 10 cm, or 5μ/cm. Very nearly the same result has been obtained from measurements on other fragments. All the broken tubes are almost equal in diameter, measuring 0·2–0·3 mm at the front end.

The major specific characters distinguishing *S. caulleryi* from other species are as follows: the arrangement of the pinnules in a single row, the dorsally curved groove between the protosoma and the narrow dorsal ciliated band, the five mid-ventral papillae of the zone of thickening, and some features of the tube. One of the species closest to *S. caulleryi*, to all appearances, is *S. japonicum* (p. 200).

Material: many tubes, some with animals and some empty.

Localities: *S. caulleryi* is a typical representative of the benthic fauna of the Sea of Okhotsk, occurring in massive numbers to the east and northeast of the Shantarski Islands (55°N 137°E) at a depth of 90–150 m. It occurs also in Sakhalin Gulf (54°N 141°E) at 22–3 m, to the south of Tauiskaya Bay (59°N 150°E) at depths of 71 and 168 m, to the east of Cape Elizaveti (54°N 143°E—Cape Yelizavety in some atlases) at depths of 365 and 1518 m and near the west coast of Kamchatka at 355 m, all localities in the Sea of Okhotsk. A typical individual of the species was also taken in the Kuril-Kamchatka Trench at a depth of 8164 m. From these figures can be seen the enormous bathymetric range of *S. caulleryi*.

11. Siboglinum pusillum Ivanov (Fig. 114)

Ivanov, 1960c: 5, 126, 145, 158–60, 162, 197, 264, Figs. 87, 114.

A characteristic species of the northwestern part of the Pacific Ocean appears to be *S. pusillum*, collected in rather large numbers by R.V. *Vityaz'* in 1953 to the east of the northern Kuril Islands. Specimens of this species were at first mistakenly ascribed to *S. minutum* (Ivanov, 1957a) from the similarity of the tubes of the two species. The description of *S. pusillum* is based on five specimens.

The fore-part of the body is slightly compressed from side to side, and its length exceeds the breadth of the mesosoma seven or eight fold (Fig. 114*A*, *B*, *C*). The more or less triangular cephalic lobe is slightly flattened dorso-ventrally. Behind the base of the tentacle runs an obvious annular groove, and the tentacle itself is attached a little to the right of the mid-ventral line. The rather short pinnules, present in the middle and distal parts of the tentacle, are arranged in a single row (Fig. 114*D*). In one individual they were found to be exceptionally short, rather few and far between, and developed only on the distal half of the tentacle. The keels of the well-developed bridle, looking like delicate dirty-brown bands, are fused together ventrally, but the dorsal ends are a considerable distance apart (Fig. 114*B*). Behind the bridle in a few individuals it is possible to observe weakly developed glandular portions of the integument, forming rudiments of a glandular girdle. The back edge of the mesosoma arches slightly forwards on both dorsal and ventral sides.

A pyriform gland is visible inside each of the numerous small rounded paired papillae of the metasoma, and the ventral sulcus between them is comparatively narrow, limited by the latero-ventral ridges on which the papillae stand (Fig. 114*A*). The dorsal ciliated band is also narrow (Fig. 114*B*). The greater part of the preannular region of the metasoma remains unknown. There are two girdles lying close together and each bearing but one row of elongated toothed platelets (Fig. 114*E*), which are evenly rounded at the ends and, for the most part, bent. The front end of each platelet is a little narrower than the back, but the front group of teeth is only a little less developed than the hind group (Fig. 114*F*). The yellowish platelets are 11–12μ long. The very long and slender postannular region of the trunk is furnished with small, button-like, dorsal, glandular shields, arranged in a metameric series at a considerable distance from one another. The ventral papillae opposite the shields are conical and lack cuticular thickenings or plaques (Fig. 114*G*).

Measurement of the parts of the body in four individuals gave the following results: length of the tentacle, *c.* 4 mm; length of the fore-part of the body, 0·6–0·85 mm; breadth of the mesosoma, *c.* 0·1 mm; length of the preannular region of the metasoma, *c.* 20 mm; length of the postannular region, 20–26 mm; overall length of the body, including the tentacle, 43–49 mm.

The filmy transparent, slightly greyish fore-part of the tube has transverse fibres sticking up above the surface of the tube wall. The very front part of the filmy section has very sparse, soft fibres, but farther back they increase

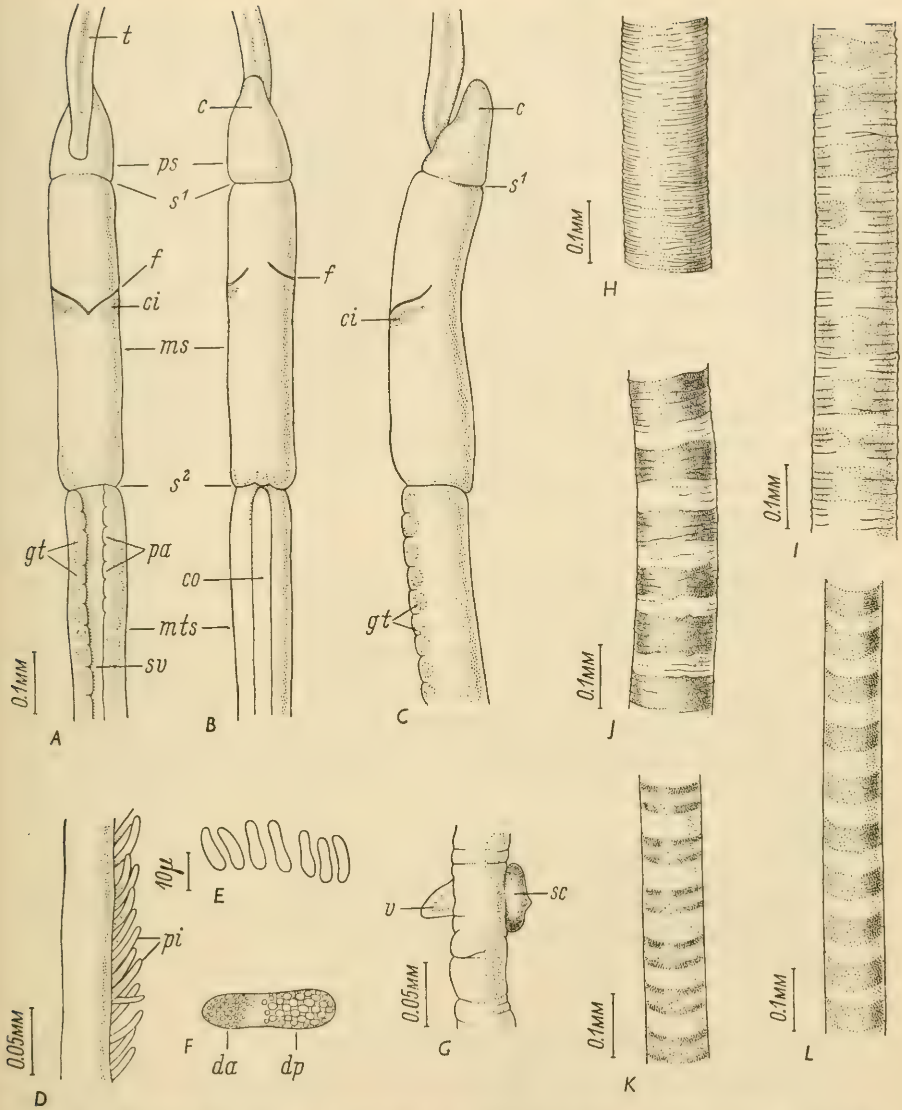


Fig. 114. *Siboglinum pusillum*: *A* – front part of the body of a female in ventral view; *B* – the same in dorsal view, and, *C* – from the left side; *D* – part of the tentacle; *E* – part of a girdle; *F* – toothed platelet (only the bases of the teeth are indicated); *G* – part of the postannular region from one side; *H* – front part of the tube; *I* – the tube a little farther back; *J* – the middle part of the tube; *K* – tube close to the hind end; *L* – hindmost part of the tube.

c – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *da* – anterior teeth; *dp* – posterior teeth; *f* – keel of the bridle; *gt* – pyriform glands seen by transparency; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sc* – dorsal glandular shield; *sv* – ventral sulcus; *t* – tentacle; *v* – ventral papilla.

rapidly (Fig. 114*H*); then yellowish or dirty-brown rings appear, at first very irregular and often incomplete (Fig. 114*I*). In the middle part of the tube the rings become coarse, dark and regular, though the edges always remain uneven. Just as in the rings, the clear spaces between them contain rather coarse sparse transverse fibres. The rings vary in length, but are always considerably less than (sometimes only half) the diameter of the tube (Fig. 114*J*). In the hind part of the tube the fibrous structure disappears, the rings become regular, and each splits into two secondary rings. The overall length of the doublet thus formed is much less than half the diameter of the tube (Fig. 114*K*). Still farther back the rings gradually become simple again, instead of double, and turn pale (Fig. 114*L*). The terminal part of the tube is delicate, transparent and structureless. The front filmy part of the tube is up to 20 mm long; a more or less complete tube may be about 12 cm long. The diameter near the front is up to 0·12 mm, but at the back of the ringed section it reaches only 0·08 mm.

S. pusillum is linked with *S. caulleryi* and *S. cinctutum* by the arrangement of the pinnules in one line and by the possession of two adjacent girdles, but it is distinguished from them by the arrangement of the toothed platelets in a single row, the development of their anterior group of teeth and by the development of a post-tentacular groove. In the latter respect it recalls certain species lacking pinnules, namely *S. tenue*, *S. microcephalum*, *S. hyperboreum* and *S. bogorovi*. In the development of the double rings in the hind part of the tube *S. pusillum* is like *S. variabile* and especially like *S. tenue*.

Material: some dozens of fragments of tubes, half containing animals.

Locality: northwestern part of the Pacific Ocean, between Onekotan (49°N 155°E) and the northern part of the Kuril-Kamchatka Trench.

Depth: 5529 m.

12. Siboglinum buccelliferum Ivanov (Fig. 115)

Ivanov, 1960c: 5, 12, 18, 19, 96, 128, 134, 151, 160–3, 174, 186, 188, 197, 265, Figs. 87, 115.

S. buccelliferum was taken in July, 1957, in the northern part of the Coral Sea near Treasury Island in the British Solomon Islands, by R.V. *Vityaz*'. In washing through the muddy silt taken by a dredge at a depth of 960 m a few tubes of *Siboglinum* were found, amongst which were two brownish ringed tubes of an undescribed species. Both tubes contained animals.

The fore-part of the body is comparatively short, with a length to breadth

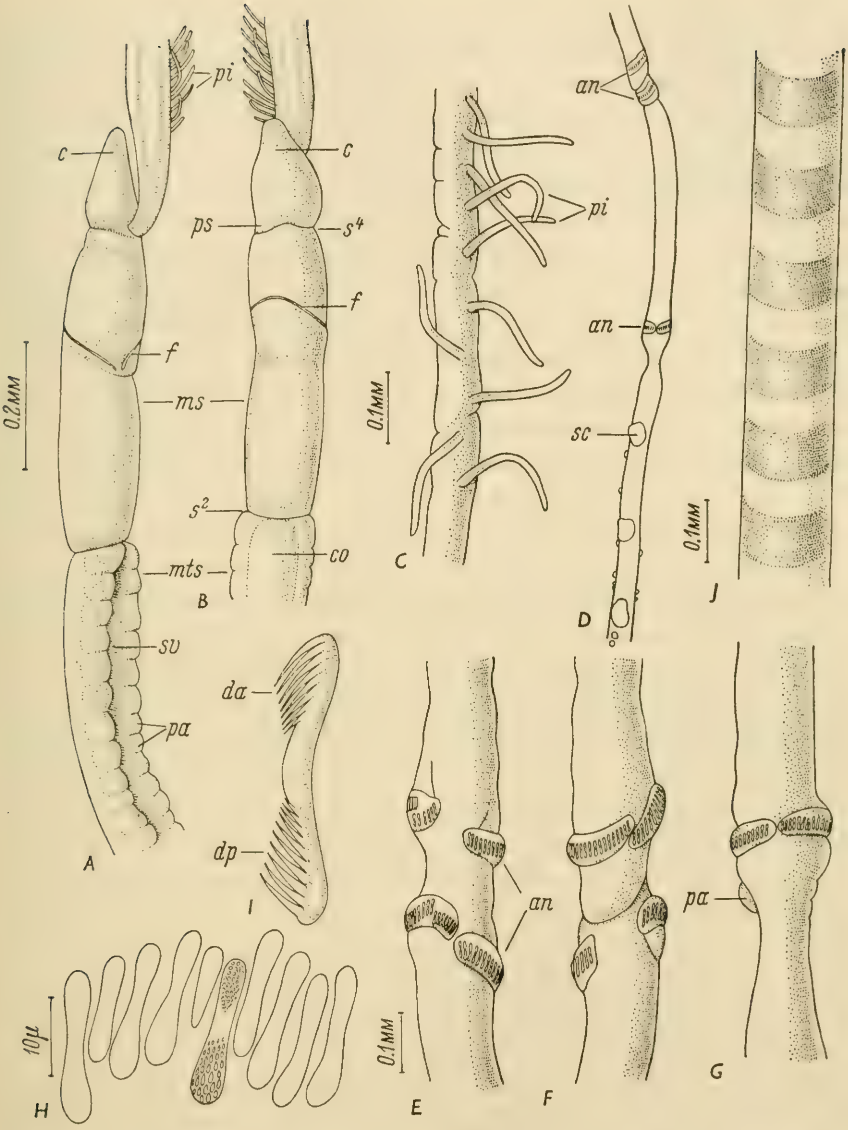


Fig. 115. *Siboglinum buccelliferum*: *A* – front part of the body of a female from the right side, and, *B* – from the dorsal side; *C* – part of tentacle; *D* – region of the girdles and the beginning of the postannular region; *E* – anterior girdles in dorsal, and, *F* – in ventral view; *G* – hindmost girdle from the dorsal side; *H* – part of a girdle; *I* – toothed platelet from one side; *J* – tube.
an – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *da* – anterior teeth; *dp* – posterior teeth; *f* – keel of the bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^2 – groove between the mesosoma and the metasoma; s^4 – post-tentacular groove; *sc* – dorsal glandular shield; *sv* – ventral sulcus.

ratio of 5 : 1. An annular groove runs behind the base of the tentacle, curving slightly backwards on the dorsal side of the body (Fig. 115*B*). The protosoma is tiny and the cephalic lobe conical and comparatively small. The mesosoma narrows towards both ends and also in the middle, behind the bridle, noticeable in side view (Fig. 115*A*). The yellowish or dirty-brown keels of the bridle are fused together dorsally but do not meet ventrally—the converse of the usual situation (Fig. 115*A*, *B*). The tentacle is rather stout, but it is capable of great extension, and the large pinnules (up to 190μ long), which characteristically begin almost at the base of the tentacle (Fig. 115*A*), are arranged in a single row, but with a slight tendency towards doubling up (Fig. 115*C*). Within them the blood capillaries may be seen (Fig. 115*B*).

The metameric region of the metasoma bears large, rounded and, anteriorly at least, more or less paired papillae (Fig. 115*A*). In one individual studied there were about 27–30 pairs, but in others there were many more. The ventral sulcus of the metasoma is broad and the dorsal ciliated band well-developed (Fig. 115*B*). The zone of thickened papillae remains unknown. *S. buccelliferum* has three girdles of toothed platelets, the two in front placed close together, with the third a considerable distance behind, after which the trunk takes on the character of a postannular region (Fig. 115*D*). All the girdles lie on muscular ridges and each consists of two halves. The ventral ends of the first girdle are separated by a broad gap, while the dorsal ends meet in the mid-line. The two parts of the second girdle, on the contrary, meet in the mid-line on the ventral side, but are far apart dorsally (Fig. 115*E*, *F*). The hindmost girdle hardly extends onto the ventral side at all, and its two halves are located wholly on the dorsal side, where they almost meet in the mid-line (Fig. 115*G*). The yellowish elongated toothed platelets, arranged in a single row (Fig. 115*H*), are rounded at the ends and rather strongly waisted in the middle, in consequence of which they take the form of that type of biscuit known as *langue de chat*, whence is derived the name *S. buccelliferum* [Latin *buccella*, a small mouthful, a morsel, whence late camp-Latin, *buccellatum*, a soldier's biscuit; *ferre* to bear]. The front part of each platelet is noticeably narrower than the hind part, and, as seen in profile (Fig. 115*I*), the teeth are very long and thin. The pinched-in middle part is free of teeth (Fig. 115*H*). The group of teeth in front of this bare patch, with their points directed backwards, are characteristically well developed, but both in size and in number they are considerably less than those of the back half of the platelet. Most of the platelets are 16–18μ long, with a few shorter, 12–14μ, but occasionally one may come across under-developed platelets only about 10μ long. Their greatest breadth (near the front end) is 4μ. The very long postannular region carries a more or less regular series of metameric, dorsal glandular shields (Fig. 115*D*), but it has not been possible to study these in detail because of the bad state of preservation.

Measurements made on the two specimens yielded the following results: length of the tentacle, not less than 9 mm; length of the anterior section of the body, 0·62 mm, breadth, 0·12 mm; length of the preannular section of the metasoma, *c.* 15 mm; distance between the second and third girdles, 2 mm; length of the postannular section of the body, not less than 8 mm; overall length of the body, including the tentacle, not less than 35–40 mm.

The spermatophores are not known.

The stoutish soft transparent tube has pronounced regular muddy-brown rings, whose length is half the diameter of the tube or a little more. The interspaces between the rings are large, completely transparent and colourless (Fig. 115*J*). The diameter of the tube in the front half is 0·13 mm, and the biggest fragment is about 20 cm long.

S. buccelliferum belongs to the group of species with only one row of pinnules, but it differs from the rest of this group in the absence of any glandular patches on the mesosoma, in the dorsal fusion of the keels of the bridle, in the development of three girdles, and in the possession of an annular groove immediately behind the base of the tentacle. This last feature, however, it shares with *S. pusillum.* The spatulate, "buccellate" form of the toothed platelets, with their strongly developed front group of teeth, is most characteristic of *S. buccelliferum.*

Material: 2 specimens.

Locality: the northern part of the Coral Sea, near Treasury Island in the British Solomon Islands (7°30′S 154°15′E).

Depth: 960 m.

13. Siboglinum microcephalum Ivanov (Figs. 116–17)

Ivanov, 1960c: 5, 96, 127, 160, 163–6, 167, 180, 197, 198, 264, Figs. 87, 116–17.

Amongst the washings from a trial dredging taken by R.V. *Vityaz*' in August, 1957, in the northern part of the Coral Sea at a depth of about 2000 m, was found a most distinctive tube of *Siboglinum* containing an entire animal. At first glance even, it was obvious that this belonged to no known species. Study of the external morphology confirmed this opinion. From the most characteristic feature, the very small cephalic lobe, this species derives its name, *S. microcephalum.*

The rather long fore-part of the body, with a length to breadth ratio of 6·5 : 1, is noticeably flattened in the dorso-ventral direction. The boundary between the protosoma and the mesosoma is unclear, but there is an annular groove immediately behind the base of the tentacle (Fig. 116*A*, *B*, *C*). The tentacle is attached so near the front end of the body that the cephalic lobe takes up a quite inconsiderable fraction, about one-ninth, of the total length

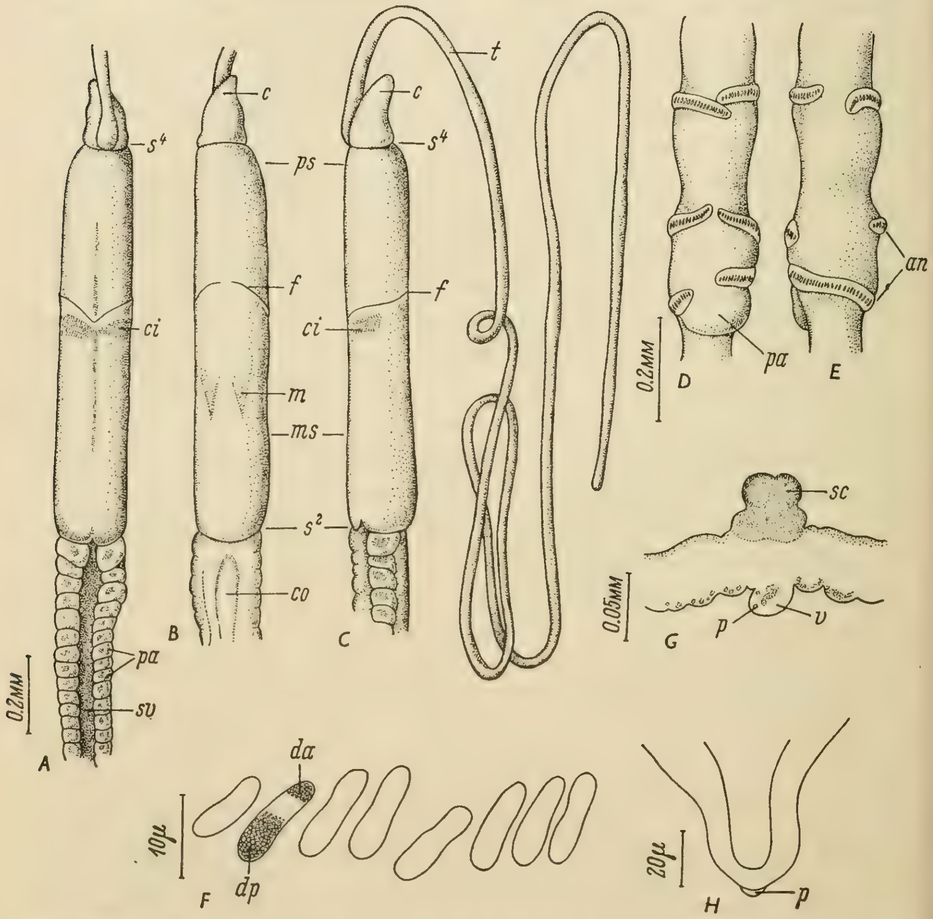


Fig. 116. *Siboglinum microcephalum*: *A* – front end of the body in ventral view, *B* – from the dorsal side, and, *C* – from the left side; *D* – the region of the girdles in ventral view, and, *E* – in dorsal view; *F* – part of a girdle (on one of the toothed platelets the bases of the teeth are indicated); *G* – part of the postannular region of the metasoma with a dorsal shield; *H* – ventral papilla of the postannular region.

an – girdles; *c* – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *da* – anterior group of teeth; *dp* – posterior group of teeth; *f* – keel of the bridle; *m* – bundle of muscle fibres seen by transparency; *ms* – mesosoma; *p* – cuticular plaque; *pa* – papillae; *ps* – protosoma; s^2 – groove between the mesosoma and the metasoma; s^4 – post-tentacular groove; *sc* – dorsal glandular shield; *sv* – ventral sulcus; *t* – tentacle; *v* – ventral papilla of the post-annular region of the metasoma.

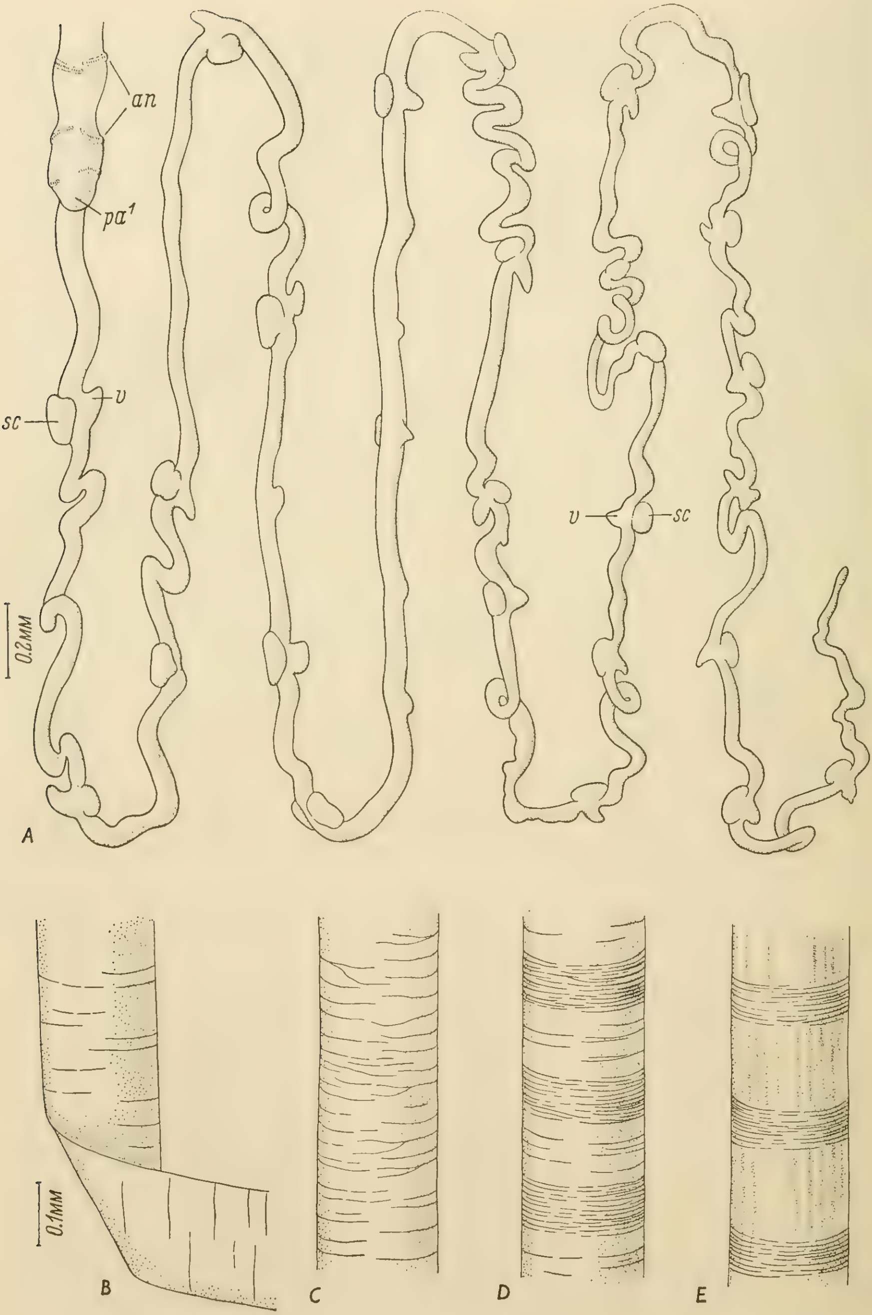
of the anterior section. At its very base the tentacle is a little swollen, but this may well be an artefact. The tentacle itself is very long and slender and devoid of pinnules (Fig. 116*C*). The protosoma is the same diameter as the mesosoma. The very delicate crests or keels of the bridle are fused together ventrally but do not quite meet dorsally, and the ridges of the bridle are almost imperceptible. Behind the bridle is a glandular girdle, widely interrupted on the dorsal side. The hind end of the mesosoma is curved and notched in the mid-ventral line (Fig. 116*A*, *B*, *C*).

The comparatively large, round, metameric papillae number about 70–80 pairs. The ventral sulcus between them is rather broad, unlike the dorsal ciliated band which begins a short distance from the front of the metasoma (Fig. 116*B*). The three girdles are all placed close together; the first two are interrupted both dorsally and ventrally, but the last only ventrally (Fig. 116*D*, *E*). The elongated oval toothed platelets, arranged in one row, have a noticeable waist in the middle. The front end is a little narrower than the back (Fig. 116*F*), and the front and back groups of teeth are separated by a considerable naked area. While the anterior teeth are relatively few they are well developed. The platelets are yellowish and 11–12μ long, with just a few as short as 10μ; most of them are about 3μ broad. The very long and slender postannular part of the trunk (Fig. 117*A*) bears well-differentiated metameric dorsal shields, shaped like cottage loaves (Fig. 116*G*). On the ventral side opposite each shield lies a conical papilla with a small transparent cuticular thickening on the tip (Fig. 116*G*, *H*).

The only specimen is a male, to judge by the rather large anterior papillae of the metameric part of the preannular region, but there is no sign of spermatophores.

The tentacle is 14 mm long, the fore-part of the body is 2·3 mm long and 0·18 mm broad; the preannular part of the trunk is 9·5 mm long, and the postannular part 21 mm; the overall length including the tentacle is *c*. 57 mm.

The front part of the unsegmented tube is very soft, filmy, transparent and limp (Fig. 117*B*), then, in the walls of the tube, yellowish transverse fibres begin to make an appearance (Fig. 117*C*). Farther back these form local condensations or agglomerations, thus giving rise to muddy brown, fibrous rings (Fig. 117*D*), while between them the walls of the tube remain completely transparent. The rings are half as long as the diameter of the tube, and the clear intervals between them are the same length, but towards the hind end of the tube the rings become shorter and the intervals considerably longer (Fig. 117*E*). The tube is 118 mm long and 0·19 mm in diameter near the front end.


an
pa1
sc
v
0.2MM
v
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A
0.1MM
B
C
D
E

Material: one tube containing a complete animal.

Locality: the northern part of the Coral Sea (the Solomon Sea) near the south coast of New Britain (6°S 150°E), in the British Solomon Islands.

Depth: 2028 m.

14. Siboglinum meridiale Ivanov (Fig. 118)

Ivanov, 1960c: 5, 27, 98, 127, 166–7, 197, 264, Figs. 87, 118.

A common representative of the genus *Siboglinum* in Antarctic waters is undoubtedly that described under the name *S. meridiale*. Tubes of this species were amongst the collections of Pogonophora made in 1957 by R.V. *Ob*', and were found at several stations in dredgings taken in the Indian Sector of the Antarctic at depths of 200–1200 m. Amongst a number of tubes, only three were found containing animals, and unfortunately these were so badly preserved as to make it impossible to describe them fully. Certain features, however, obvious even in defective material, and also some peculiarities of the tube, make it possible confidently to give a diagnosis of this species.

The fore-part of the body is long, eight or nine times as long as broad, and the boundary between the protosoma and the mesosoma is not apparent. The cephalic lobe is small and the long slender tentacle, lacking pinnules, is attached not far from the front end of the body (Fig. 118*A*). The extraordinarily long, delicate, light yellow keels of the bridle, which lies at or just in front of the middle of the anterior section, are fused ventrally but do not meet dorsally. The boundary between the mesosoma and the metasoma is marked by a simple transverse groove, and the front part of the metasoma carries small adhesive papillae, without plaques (Fig. 118*A*). The number of girdles of toothed platelets is not clear, but the platelets themselves are arranged for the most part in a single row, with an occasional one out of line (Fig. 118*B*). The front end of each platelet is a little narrower than the back, and the middle is slightly constricted. The small teeth, of which the anterior group is well developed, are numerous (Fig. 118*C*). The platelets are 12–15μ

Fig. 117. *Siboglinum microcephalum*: *A* – girdles and postannular region of the metasoma (girdles figured in ventral view); *B* – front, filmy part of tube; *C* – tube near the beginning of the rings; *D* – ringed part of tube; *E* – hind part of tube.

an – girdles; *pa*¹ – ventral papilla lying behind the girdles; *sc* – dorsal glandular shield; *v* – ventral papilla.

long. The morphology of the remaining parts of the body has not been open to investigation.

In one individual studied the tentacle was 19 mm long and the fore-part of the body *c*. 2 mm long. The overall length of the body, excluding the tentacle, in another individual was *c*. 50 mm.

The front, filmy part of the flexible ringed yellowish or slightly brownish

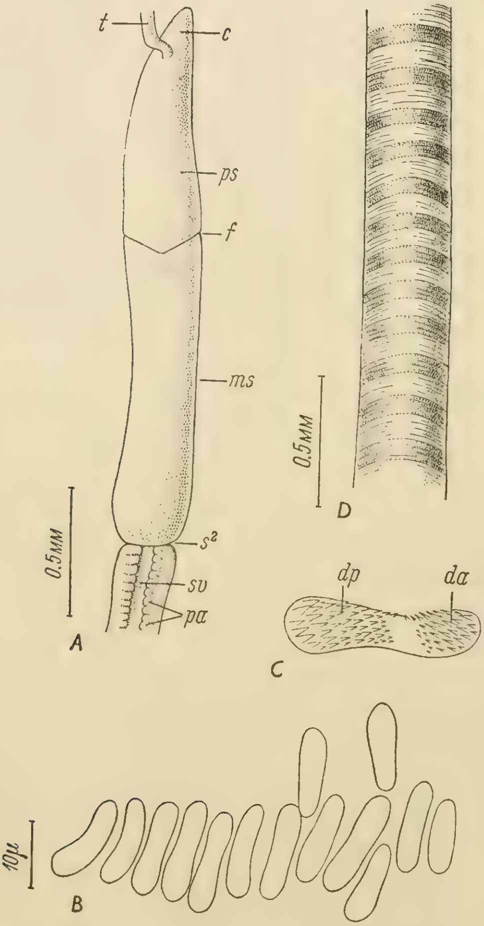

Fig. 118. *Siboglinum meridiale*: *A* – front end of the body in ventral view; *B* – part of a girdle; *C* – toothed platelet; *D* – tube.
c – cephalic lobe; *da* – anterior group of teeth; *dp* – hind group of teeth; *f* – keel of the bridle; *ms* – mesosoma; *pa* – papillae; *ps* – protosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle.

tube is unsegmented, colourless and transparent, with weak transverse fibres, except in one individual which had no fibres at all. Then just discernible yellowish rings gradually begin to appear, separated by narrow, colourless, transparent intervals. The length of the rings is about a quarter the diameter of the tube in this region, and the fibrous structure is distinct. In the middle of the tube the rings gain a light muddy-brown colour and a lustrous surface, their boundaries become clearer and the fibres coarser (Fig. 118*D*). The longest fragment of tube is 140 mm long, and the fragments are up to 0·34 mm in diameter near the front end.

S. meridiale may be distinguished from other species by the long fore-part of the body, by the almost colourless, ventrally fused, delicate keels of the bridle, by the slender tentacle, and by the very small cephalic lobe. In this last respect *S. meridiale* recalls *S. microcephalum* (p. 227), but it is easily distinguished from it by the nature of the tube.

Material: seven broken-off tubes, three of which contained badly preserved animals.

Locality: the Indian Sector of the Antarctic Ocean.

Depth: 200–1200 m.

Substratum: silty clay, sometimes with an admixture of pebbles, fine gravel or sand.

15. Siboglinum pellucidum Ivanov (Figs. 20, 119)

Ivanov, 1957a: 449–51, 458, 459, 491, 495–7, Figs. 17–19, 59; Ivanov, 1960a: 1529, 1541, 1616; Ivanov, 1960c: 5, 10, 12, 27, 96, 105, 128, 167–70, 180, 185, 197, 265, Figs. 20, 87, 119.

The small *S. pellucidum*, whose delicate tubes were found in the south-western part of the Bering Sea, is evidently one of the species characteristic of the abyssal zone of that sea, and is usually found in company with *S. minutum*, *S. fedotovi*, *Heptabrachia gracilis* and *Polybrachia annulata*.

The protosoma and the mesosoma are equal in length (Fig. 119*A*, *B*). The transverse groove between them curves backwards on the ventral side and is interrupted on the dorsal side. Tapering gradually towards the front end, the protosoma merges imperceptibly into the small conical cephalic lobe, while the very long and slender tentacle lacks pinnules. The cylindrical mesosoma is scored by weak median furrows on both dorsal and ventral sides (Fig. 119*A*, *B*). The delicate keels of the weakly developed bridle, lying at the front end of the mesosoma, are usually interrupted by a series of gaps, making them look like lines of dashes. As in larger species of *Siboglinum*, their ventral ends are fused together but their dorsal ends do not meet.

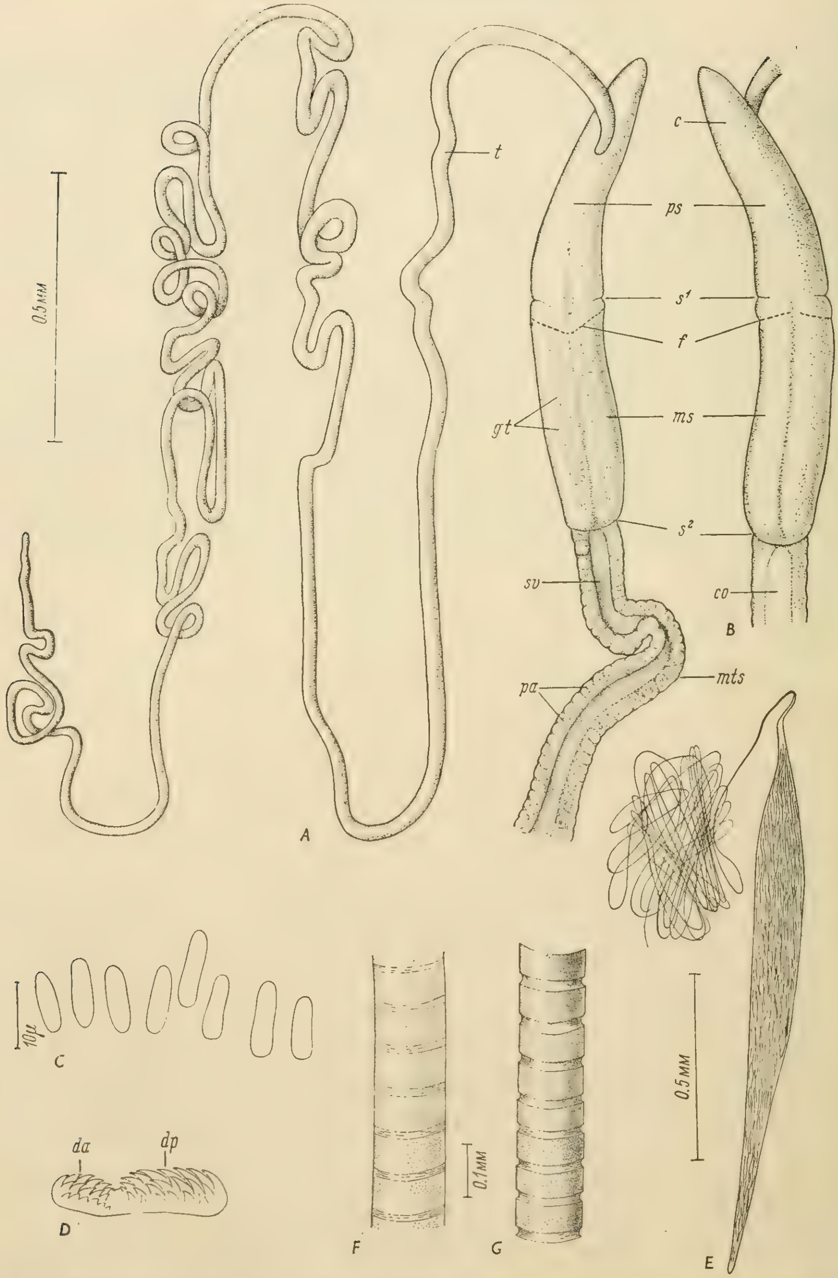

Fig. 119. *Siboglinum pellucidum*: *A* – front end of a female in ventral view, and, *B* – from the dorsal side; *C* – part of a girdle; *D* – toothed platelet from one side; *E* – spermatophore; *F* – anterior part of tube; *G* – hind part of tube.

c – cephalic lobe; *co* – dorsal ciliated band; *da* – anterior teeth; *dp* – posterior teeth; *f* – keel of the

The metameric part of the preannular region of the metasoma is thinner than the fore-part of the body (Fig. 119*A*), and the deep ventral sulcus is bordered by regular rows of oval glandular papillae, devoid of chitinoid plaques. The well-developed dorsal ciliated band begins at the front of the metasoma. Two girdles of toothed platelets lie far apart, with as much as 3 mm between them. The elongated platelets, tapering slightly towards the front end, are uniserial (Fig. 119*C*), and their surface is covered with comparatively large teeth of which the first group occupies about one-third of the total area of each platelet (Fig. 119*D*). The platelets are 9–12μ long. Nothing is known of the postannular region of the trunk.

The tentacle is *c.* 10 mm long; the fore-part of the body is 0·9 mm long by 0·14 mm broad, while the front part of the metasoma is only 0·1 mm broad; the preannular region of the trunk in one individual studied was 31 mm long and the postannular region *c.* 60 mm. The overall length of the body, including the tentacle, must, therefore, reach about 10 cm.

The spindle-shaped spermatophores, tapering gradually towards the end without the filament (Fig. 119*E*), are at least ten times as long as broad, and reach a length of 0·14 mm.

The first half of the tube is very soft, colourless, glassily transparent and limp. Then very regular transparent colourless rings begin to appear, whose length is half the diameter of the tube. The interspaces between the rings are short and covered with delicate transverse wrinkles (Fig. 119*F*). The hind part of the tube is distinguished by slightly denser, but still transparent, pale yellow rings, whose length is only one-third of the diameter of the tube, and which possess a smooth shining lustrous surface. The intervals between these rings take the form of thin, flexible membranes, usually constricted (Fig. 119*G*). A considerable length of tube at the very end is devoid of rings and as transparent as the front part. The longest fragment of tube reached 10 cm in length, of which 6 cm was taken up by the front colourless part. The diameter near the front end is 0·15 mm.

Amongst the species lacking pinnules *S. pellucidum* is distinguished by the absence of both post-tentacular groove and glandular girdle in the mesosoma. As in *S. bogorovi*, there are two girdles of toothed platelets close together. *S. pellucidum* may be distinguished from *S. bogorovi* by the fusion of

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bridle; *gt* – globular glands of the mesosoma seen by transparency; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *ps* – protosoma; s^1 – groove between the protosoma and the metosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle. (*A*, *B*, *E*, *F*, *G* after Ivanov, 1957a.)

the keels of the bridle and by the absence of double rings in the tube.

Material: *c.* 15 tubes, some containing animals.

Localities: the southwestern part of the Bering Sea, to the east and southeast of Cape Olyutorski (60°N 170°20′E) and also to the east of the Komandorski Islands (55°N 166°E).

Depth: 1693–4811 m.

16. Siboglinum hyperboreum Ivanov (Fig. 120)

Ivanov, 1960c: 5, 27, 30, 98, 105, 128, 134, 160, 170–2, 174, 177, 185, 188, 197, 263, Figs. 87, 120.

In August, 1957, at a depth of 215 m in the Greenland Sea, R.V. *Ob'* took a rather large number of tubes of *Siboglinum*, shown by immediate study as all belonging to the same undescribed species. The fore-part of the body is four and a half to five times as long as it is broad and possesses two annular grooves, one immediately in front of the bridle, and the other a little behind the point of attachment of the tentacle (Fig. 120*A*, *B*, *C*). This latter is long and rather slender, and quite devoid of pinnules. The conical cephalic lobe is not large. The keels of the bridle are of medium thickness, fused together ventrally and with a wide gap between their dorsal ends (Fig. 120*B*). Under the microscope it may be observed that along the light-brown cuticular strip of the bridle stretches a very delicate dark linear crest (Fig. 120*D*), similar to that found in *S. tenue*. The mesosoma broadens out towards its hind end, where its hind edge is curved backwards on the dorsal and notched in the mid-ventral line.

The transversely oval papillae of the metameric part of the trunk are small, and the ventral sulcus between them is deep and narrow. The dorsal ciliated band, of the usual width, begins at the very front of the metasoma (Fig. 120*B*). Of the three girdles, the first has a broad gap on the ventral side, the second is broken dorsally, while the third, lying a considerable distance behind the other two, is interrupted both dorsally and ventrally (Fig. 120*E*, *F*). All three lie on well-developed, muscular ridges, and a few rounded papillae with crescentic plaques on their tips are situated near the last girdle. The yellowish spatulate biserial toothed platelets have the anterior group of teeth only a little less strongly developed than the back group, and between the two groups lies a considerable interval bare of teeth (Fig. 120*G*). The platelets for the most part are between 13 and 14μ long and up to 4μ broad, but occasionally one may find an aberrant platelet only 10μ long.

The tentacle is more than 5 mm long, the fore-part of the body 0·6–0·9 mm

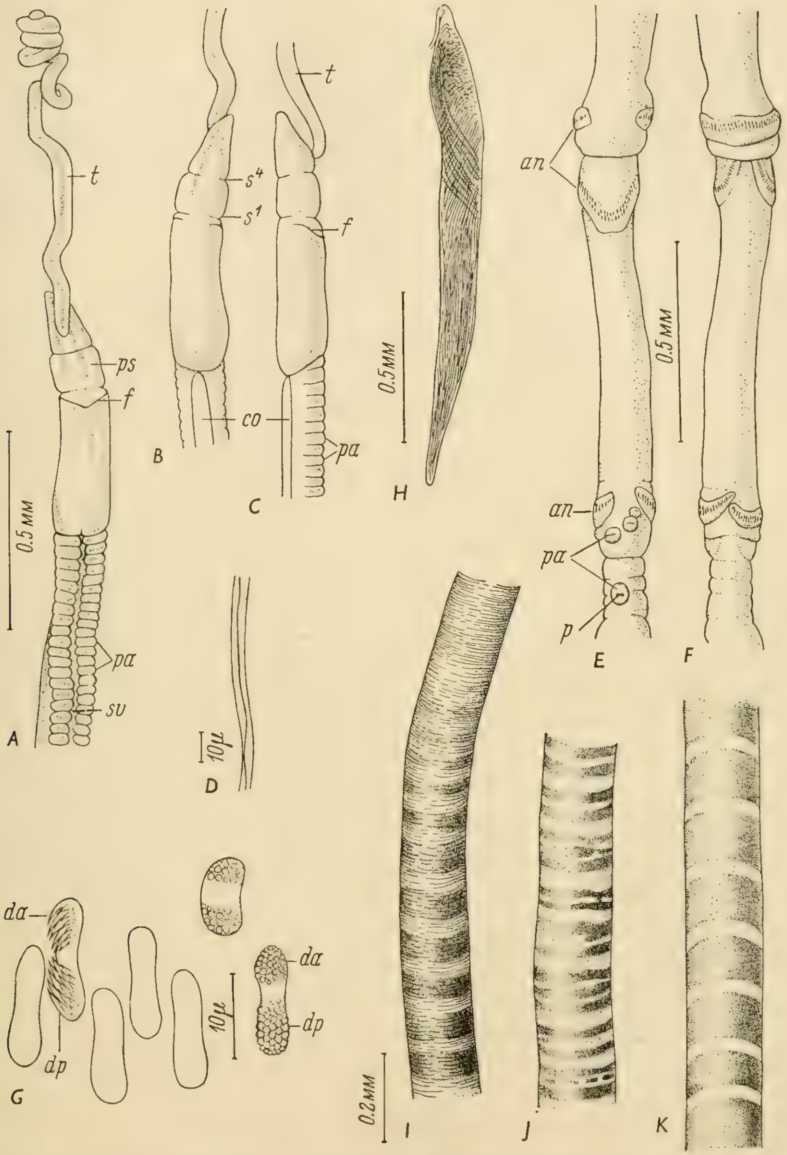


Fig. 120. *Siboglinum hyperboreum*: *A* – front end of a female in ventral, and, *B* – in dorsal view, and, *C* – from the right side; *D* – part of a keel of the bridle under high magnification; *E* – region of the girdles in ventral, and, *F* – in dorsal view; *G* – part of a girdle (on two platelets the bases of the teeth are indicated); *H* – spermatophore (filament omitted); *I* – tube (transitional region between the filmy part and the ringed part); *J* – tube, about halfway along; *K* – tube near the hind end.
an – girdles; *co* – dorsal ciliated band; *da* – front group of teeth; *dp* – hind group of teeth; *f* – keel of the bridle; *p* – cuticular plaque; *pa* – papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^4 – post-tentacular groove; *sv* – ventral sulcus; *t* – tentacle.

long and *c*. 0·15 mm broad; the preannular section of the trunk is 20–30 mm long, and the postannular section 20–25 mm.

The spindle-shaped spermatophores are 0·16 mm long, with a maximum breadth of 0·015 mm. The end bearing the filament is a little broader than the opposite pole, and the spermatophore tapers down gradually in this direction, but does not come to a sharp point. The base of the filament is rather narrow and ribbon-like (Fig. 120*H*).

The front part of the unsegmented tube is colourless and transparent except for numerous transverse fibres. The middle part of the tube is fibrous and ringed with brown or mud-coloured, rather regular rings, in length about half to two-thirds the diameter of the tube, while the narrow intervals between them are clear and transparent (Fig. 120*I*). Farther back the transverse fibres disappear and the rings anastomose into very short doublets, sometimes irregular in structure (Fig. 120*J*). In the hindmost part of the tube the rings become simple and regular once more, with a length about two thirds or, rarely, one-half of the diameter of the tube (Fig. 120*K*). The largest fragments of tube are about 20 cm long, and 0·15–0·2 mm in diameter near the front end.

Though a species of the high arctic seas of the western hemisphere, *S. hyperboreum* is nevethless most closely related to the more southerly species of the Pacific Ocean, namely *S. tenue*, *S. bogorovi* and *S. variabile*. Besides the absence of pinnules, all these species share the following features in common: the presence of a post-tentacular groove (except in *S. variabile*), the strong degree of development of the anterior teeth of the platelets of the girdles, and the possession of double or even of triple rings in the tube. In the structure of the bridle *S. hyperboreum* and *S. tenue* are very similar. *S. hyperboreum* may be distinguished from *S. variabile* by the presence of not two but three girdles, and by the unsegmented tube, and from *S. bogorovi* by the three girdles and by the ventral fusion of the keels of the bridle.

Material: some dozens of tubes, some containing animals.

Locality: the Greenland Sea to the east of Lambert Land (79°N 20°W).

Depth: 217 m.

Substratum: brown silt with pebbles.

17. Siboglinum tenue Ivanov (Fig. 121)

Ivanov, 1960c: 5, 27, 30, 127, 134, 160, 172–4, 177, 180, 188, 197, 264, Figs. 87, 121.

In a collection of benthos taken on a cruise of R.V. *Vityaz*' in 1958 near the east coast of the North Island of New Zealand, amongst tubes of *S. variabile* and of *S. bogorovi* were found a number of delicate tubes readily distinguishable by their double rings. Some of them contained animals, obviously belonging to a different species, here named *S. tenue.* This species is distinguished by the comparatively short, cylindrical fore-part of the body which is only five times as long as broad. The conical cephalic lobe is very rich in gland cells. The stout tentacle, attached a little to the right of the mid-ventral line, lacks pinnules, and behind its base runs a distinct transverse groove. The bridle lies about one-third of the way back along the mesosoma. Its keels, as seen under the microscope, are rather distinctive, each consisting of a rather broad, just perceptibly brown strip of cuticular material, crossed by short dark delicate transverse lines; and along the length of each strip runs a very dark slender cuticular thread, standing up slightly above the surface (Fig. 121*A*). The cutaneous ridges of the bridle are developed only on the dorsal side, and behind the bridle lies a pair of lateral patches of epidermal gland cells, forming a rudimentary glandular girdle. From the sides of the body these extend chiefly onto the ventral surface, where they almost meet in the mid-line, and hardly run onto the dorsal surface at all. The hind edge of the mesosoma is somewhat oblique, with the ventral side a trifle in advance of the dorsal (Fig. 121*C*).

The first part of the trunk is noticeably narrower than the mesosoma and the rather narrow dorsal ciliated band begins at its front edge. Each of the comparatively large, rounded adhesive papillae contains a large pyriform gland (Fig. 121*C*). It has not proved possible to investigate the middle part of the trunk because of the difficulty of dissecting it out of the very fine tube. *S. tenue* possesses three girdles, of which the first two, lying close to each other, are at a considerable distance away from the third, which is situated at the beginning of the postannular region (Fig. 121*D*). In this regard *S. tenue*, is comparable with *S. ekmani*, *S. fedotovi*, *S. hyperboreum*, *S. buccelliferum*, *S. pinnulatum* and *S. robustum.* The girdles lie on pronounced ridges, which in turn lie on muscular folds of the trunk. The first and last girdles are interrupted ventrally and the second dorsally (Fig. 121*D*), and the toothed platelets in each girdle are arranged in a single row (Fig. 121*D*, *E*). They are comparatively few, almost colourless and elongated, without any constriction in the middle, and bear two well-developed groups of teeth. The anterior teeth, pointing backwards, are rather numerous and comparatively well developed (Fig. 121*F*). The platelets are between 8 and 10μ long. The long delicate postannular section of the trunk carries a series of regularly spaced, metameric dorsal glandular shields, and, lying on the ventral side opposite each shield, papillae, which are devoid of any cuticular thickening at the tip.

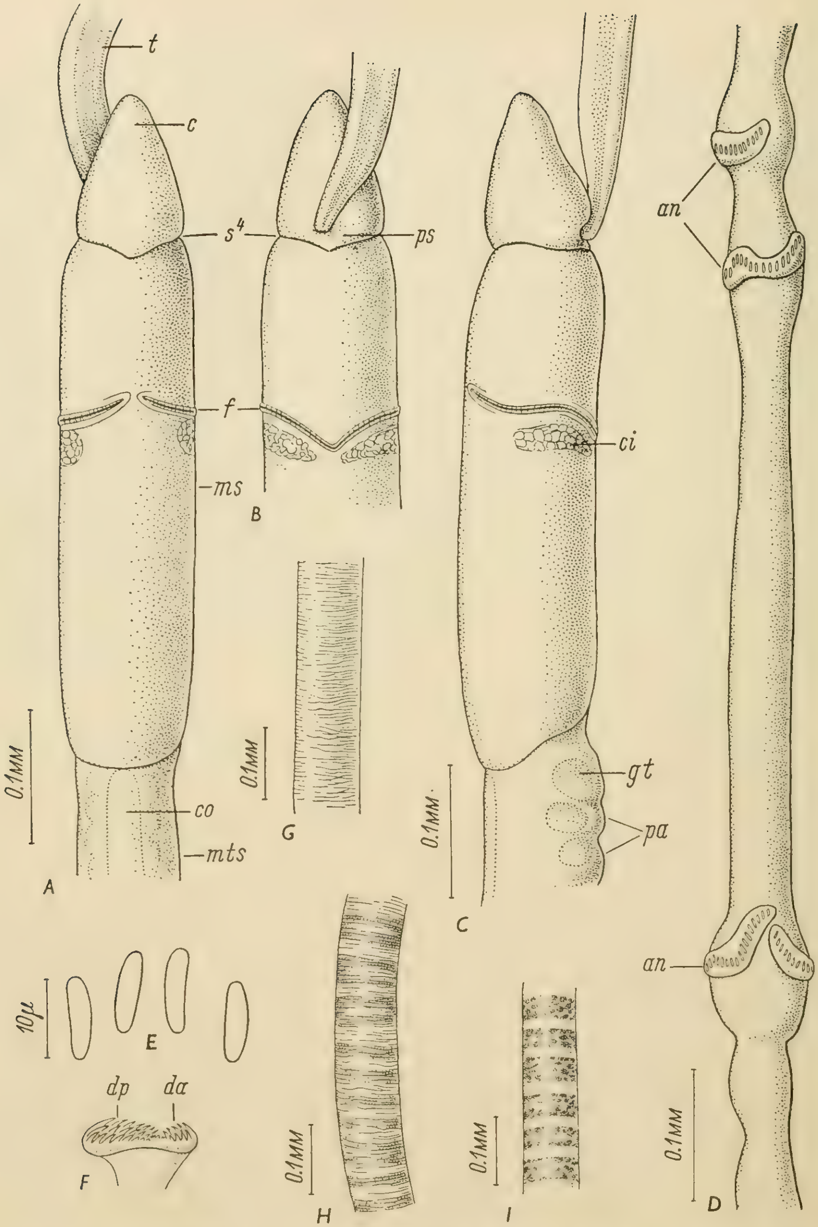


Fig. 121. *Siboglinum tenue*: *A* – front end of a female in dorsal, and, *B* – in ventral view, and, *C* – from the right side; *D* – region of the girdles; *E* – part of a girdle; *F* – toothed platelet from one side; *G* – front part of the tube; *H* – middle part of the tube; *I* – hind part of the tube. *an* – girdles; *c* – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *da* – anterior group of teeth; *dp* – posterior group of teeth; *f* – keel of the bridle; *gt* – pyriform glands seen by transparency through the integument; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *ps* – protosoma; s^4 – post-tentacular groove; *t* – tentacle.

S. tenue is one of the smaller species. The length of the anterior section of the body is no more than 0·5 mm and the breadth of the mesosoma 0·1 mm. The front part of the trunk is 0·075 mm broad and the distance separating the first two from the last girdle is 0·5 mm.

The rings of the unsegmented tube are most characteristic. Towards the hind end of the filmy, transparent front part of the tube, very numerous, soft delicate transverse fibres begin to appear (Fig. 121*G*). The greater part of the tube is characterized by a somewhat coarser fibrous structure and possesses double, dirty-brown rings, with indistinct edges (Fig. 121*H*). In the hinder part of the tube, the fibres disappear and the double rings come to consist of incompletely commingled, brownish blotches of an opaque dense substance (Fig. 121*I*). The longest tube reached 85–90 mm, and the diameter near the front of the middle section is *c*. 0·1 mm.

Among the species lacking pinnules, *S. tenue* is nearest to the Arctic form *S. hyperboreum*, with which it is linked by the possession of a post-tentacular groove, by the fusion of the keels of the bridle, by the development of three girdles in the metasoma and by the common characters of the tubes. It has also features in common with *S. variabile* (p. 241) and with *S. bogorovi* (p. 244). The diagnostic features of *S. tenue* are the following: the broad cuticular bands of the keels of the bridle (in *S. hyperboreum* they are much narrower), the rudiments of a glandular belt in the mesosoma, the arrangement of the toothed platelets in a single row, their comparatively small size and the rather weak development of their anterior teeth, and, finally, the blotchy double rings in the hind part of the tube.

Material: 26 broken tubes, some with animals.

Locality: Pacific Ocean to the east of the North Island of New Zealand.

Depth: 2072 and 3013 m.

Substratum: calcareous clay or a silty clay sediment.

18. Siboglinum variabile Ivanov (Fig. 122)

Ivanov, 1960c: 5, 27, 160, 172, 174, 175–7, 187, 265, Figs. 87, 122.

This species was taken in 1958 at a station of R.V. *Vityaz'* situated near the east coast of the North Island of New Zealand. Only two individuals, a male and a female, were extracted from the rather numerous tubes collected. One of the peculiarities of this species appears to be the considerable variability of the tube, which gives rise to the name *S. variabile*.

The anterior section of the body is comparatively short, with a length to breadth ratio of 5 or 6 : 1. The short protosoma is sharply divided from the cylindrical mesosoma by an annular groove which lies nearer to the base of the tentacle than to the bridle. The cephalic lobe is small and conical and the point of attachment of the long tentacle (which is naked of pinnules) lies a little to right of the mid-ventral line. The front edge of the mesosoma is scarcely, but nonetheless perceptibly, thickened, forming a sort of annular rim (Fig. 122*A*, *B*), and the bridle lies one-third of the length of the mesosoma back from this. Its delicate keels, fused together ventrally, lie on narrow but distinct cutaneous ridges (Fig. 122*A*) and they reach their greatest thickness in their lateral and dorsal parts, while on the ventral side they are considerably thinner. Their dorsal ends are separated by a wide gap (Fig. 122*B*). A glandular belt in the form of a pair of latero-ventral, muddy-brown areas of epidermis immediately adjoining the hind edge of the bridle, encompasses the mesosoma, while the ventral surface is scored by a perceptible, but shallow median furrow. The hind edge of the mesosoma has a mid-ventral notch and arches backwards on the dorsal side (Fig. 122*A*, *B*).

The metameric section of the metasoma carries large rounded papillae without plaques. In the male there were 51 of these on the right side and 50 on the left, while in the female there were 57 and 62 respectively. Through their walls the ducts of pyriform glands are visible, two per papilla for the most part, towards the front, but there is only one gland in each papilla farther back (Fig. 122*A*). The well-developed dorsal ciliated band begins at the front edge of the metasoma (Fig. 122*B*). In the female a few small scattered rounded papillae without plaques are situated behind the genital aperture (Fig. 122*C*), and these papillae differ in no way from those just in front of the girdles. In the male, however, in the zone of thickened papillae, two slightly prominent papillae may be discerned. Clearly there is no sharply defined zone of thickened papillae in this species. The two adjacent girdles are of the usual kind and both are interrupted on the dorsal as well as on the ventral side (Fig. 122*D*). The yellowish elongate-oval toothed platelets are just a little narrower at the front, without any noticeable central constriction. They are arranged in one or two rather irregular rows (Fig. 122*E*) and possess both groups of teeth, though the anterior group is only feebly developed (Fig. 122*F*). The platelets measure 9–12μ by 3–4μ.

The tentacle is not less than 2·5 mm long, and the fore-part of the body *c.* 0·8 mm; the breadth of the mesosoma is 0·13–0·16 mm; the metameric part of the preannular region of the metasoma is 3 mm long, the whole preannular region, 7–8 mm.

The tube is rather hard for most of its length, with firm walls, but the very front and back parts are flexible. The transparent front section, with soft

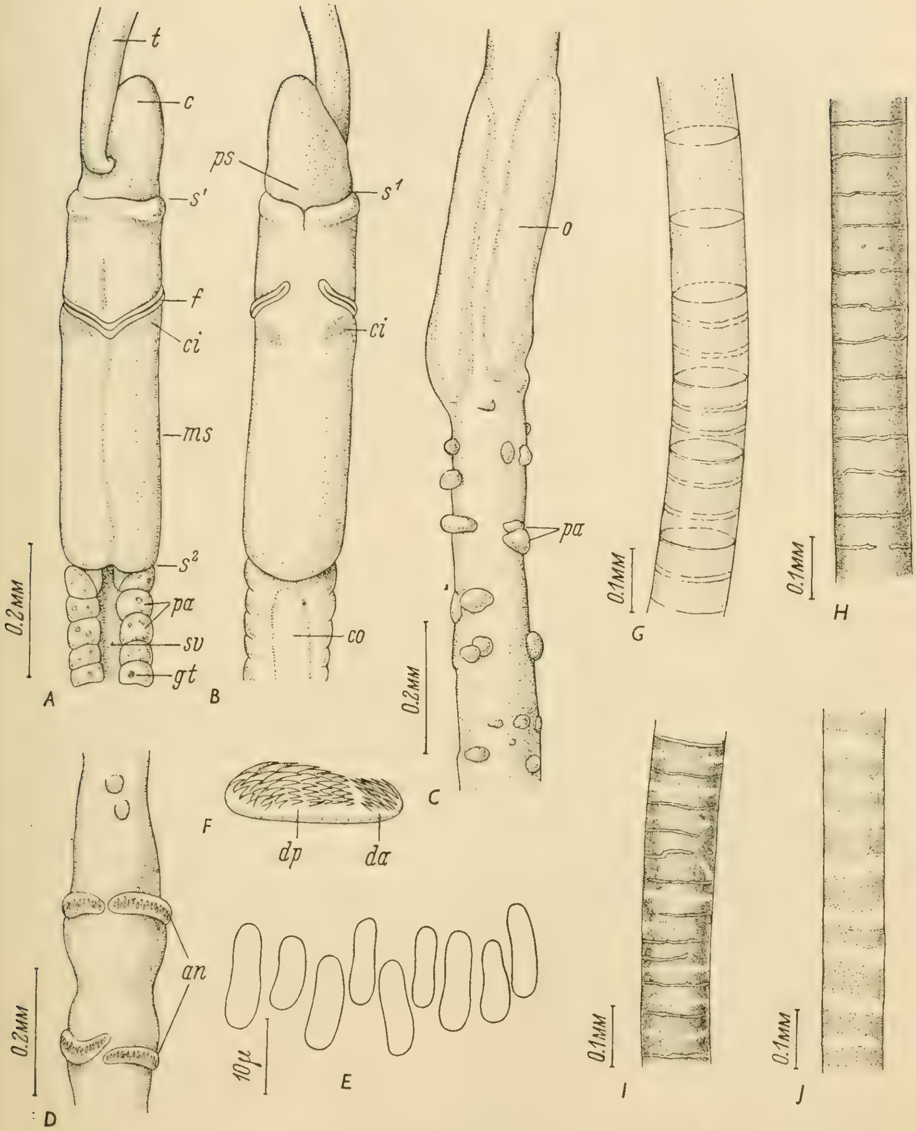


Fig. 122. *Siboglinum variabile*: *A* – front end of the body in ventral, and, *B* – in dorsal view; *C* – region of thickened papillae in ventral view; *D* – region of the girdles in ventral view; *E* – part of a girdle; *F* – toothed platelet viewed obliquely from one side; *G* – tube at the beginning of the ringed region; *H* – middle part of tube; *I* – hind part of tube; *J* – tube near the hind end.
an – girdles; *c* – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *da* – anterior group of teeth; *dp* – posterior group of teeth; *f* – keel of the bridle; *gt* – pyriform glands seen by transparency; *ms* – mesosoma; *o* – egg seen by transparency, lying in the oviduct; *pa* – papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle.

limp walls, is distinctly segmented and the boundaries between the segments take the form of delicate, brown lines. Then gradually, in each segment, three slight brown rings appear (Fig. 122*G*). The rings gradually increase in length and become darker, until only narrow clear interspaces are left between them. In this region the tube diameter is two and a half to three times the length of the rings. The number of rings per segment appears to be inconstant, and may be considerably more than the usual three. In one tube, indeed, there were as many as nine rings per segment. Very soon the boundaries between the segments begin to be irregular and the rings come closer together, so that the interspaces are mere slits. In a short space the rings begin to anastomose by means of narrow bridges or even to fuse in pairs, wholly or partially. The walls of the rings increase considerably in thickness and the tube becomes rigid (Fig. 133*H*). In the last third of the tube hazy, clear blotches appear in transverse rows in the middle of each ring. Sometimes these run into one another, thus dividing the ring into two narrower secondary rings (Fig. 122*I*). Still farther back the edges of the rings become diffuse, the rings themselves grow pale and the intervals between them longer (Fig. 122*J*), and finally the rings disappear. The biggest fragments of tubes are 75 mm long; the diameter varies between 1·12 and 0·2 mm, but near the hind end it may be only 0·1 mm.

S. variabile is distinguished from related species also without pinnules (*S. tenue*, *S. bogorovi* and *S. hyperboreum*), by the sharp division between the protosoma and the mesosoma, by the swollen, ridge-like front edge of the mesosoma, by the noticeable lateral and dorsal thickening of the keels of the bridle compared with the thinner, ventral part, by the absence of any groove immediately behind the base of the tentacle, by the possession of two girdles of toothed platelets lying close together, by the weakly developed anterior group of teeth on each platelet, and by the segmented tube.

Material: about 20 fragments of tubes, some with animals.

Locality: to the east of the North Island of New Zealand.

Depth: 2072 and 3013 m.

Substratum: calcareous clay and silty clay.

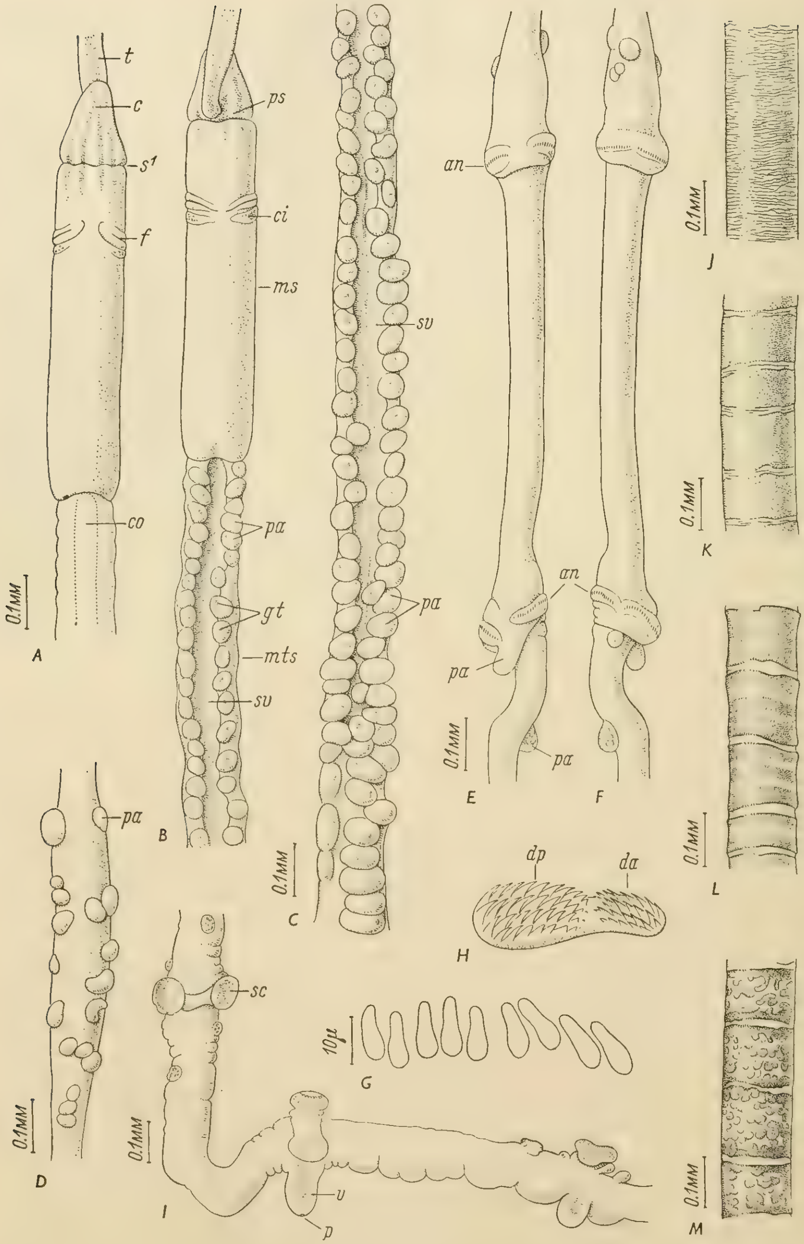
19. Siboglinum bogorovi Ivanov (Fig. 123)

Ivanov, 1960c: 5, 18, 27, 97, 105, 129, 160, 170, 172, 174, 177–80, 197, 264, Figs. 87, 123.

S. bogorovi was found in 1958, during a cruise of R.V. *Vityaz'*, near the east coast of New Zealand. Amongst five tubes three contained animals. This species is named after Prof. V. G. Bogorov, organizer and leader of the Pacific Ocean cruises of R.V. *Vityaz'*. The cylindrical fore-part of the body is five to six times as long as broad (Fig. 123*A*, *B*), and possesses a distinct annular groove behind the base of the tentacle. The conical cephalic lobe is not large and the long rather slender tentacle has no pinnules. The delicate keels of the bridle, which is situated in the front part of the mesosoma, are not fused ventrally and nowhere near meet dorsally, but are situated on slightly raised cutaneous ridges. Weakly developed lateral glandular regions are found behind the bridle (Fig. 123*A*, *B*). The hind edge of the mesosoma is slightly concave on both dorsal and ventral sides.

The rather long, metameric part of the preannular region of the trunk has small rounded papillae, each showing the dark pore of a pyriform gland (Fig. 123*B*). In the hind part of the metameric region the papillae become larger and their arrangement somewhat irregular (Fig. 123*C*). In one individual in which they were counted there were 53 on the left side and 63 on the right. The ventral sulcus of the metasoma is rather wide (Fig. 123*B*, *C*), and the dorsal ciliated band in no way remarkable (Fig. 123*A*). In the zone of thickened papillae there are about 20 comparatively large, higgledy-piggledy papillae on the ventral side (Fig. 123*D*), but these do not bear cuticular plaques. In this species, as in so many others, there are two girdles of toothed platelets, but they are unusual in being situated rather far apart, lying on muscular ridges. Each consists of two halves, which are separated by a wide gap ventrally, while dorsally they meet (Fig. 123*E*, *F*). Behind the second girdle lies a large ventral finger-shaped papilla (Fig. 123*E*). The uniserial, yellowish toothed platelets (Fig. 123*G*) are very characteristic, with the front end only half as wide as the back part. The surface of each platelet is covered with comparatively large, sharp teeth, of which the first group, with teeth pointing backwards, is quite well developed but only occupies a half to one-third the area of the hind group (Fig. 123*H*). The platelets are about 11–12μ long, 5μ wide at the back and 2–3μ near the front. The very long postannular section of the trunk is furnished with more or less metameric small, dorsal, glandular shields, shaped like dumb-bells draped across the width of the trunk. In each of the lateral expansions of the shields may be seen the duct of a pyriform gland, from which it may be inferred that there is a pair of glands in each shield. Opposite each shield lies a conical ventral papilla with a small cuticular thickening at the tip. The postannular region bears in addition numerous small scattered wart-like glandular papillae.

A typical individual of *S. bogorovi* has the following dimensions: length of the tentacle, 5 mm; the anterior section of the body, 0·8 × 0·14 mm; breadth of the body at the level of the girdles, 0·15 mm; distance between the girdles, 0·9 mm; overall length of the body, *c.* 25 mm.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The tube is most characteristic. In the limp walls of the very long, soft transparent filmy front part are numerous obvious fine transverse wavy fibres (Fig. 123*J*). This part of the tube then runs more or less gradually into the ringed portion, in which, characteristically, the rings form three separate zones. For most of the length of the tube the rings are as long as the tube is wide, or just a little less. In the first zone, between the muddy-brown homogeneous rings with uneven edges, are narrow clear interspaces with transverse fibres (Fig. 123*K*). Then, in the succeeding zone, the fibres disappear from the interspaces, and each ring becomes sub-divided into three or occasionally two, shorter secondary rings, between which are semi-transparent spaces, the whole forming a triplet or doublet (Fig. 123*L*). In the third zone the division into secondary rings disappears and the rings lose their homogeneity, and come to consist of irregular brownish dense patches with clear spaces between them, so that they here acquire a blotchy appearance (Fig. 123*M*). Towards the hind end of the tube the rings gradually grow paler and then rather quickly disappear. The largest fragment of tube reaches 118 mm in length, with a diameter near the front end of 0·2 mm. The front filmy part is not less than 45 mm long; the middle, ringed portion reaches 50–55 mm; the hindmost, ringless, filmy part not less than 25 mm. The whole tube must, therefore, be not less than 150–200 mm long.

S. bogorovi is distinguished from related species, also lacking pinnules, by the absence of any ventral fusion of the keels of the bridle. The post-tentacular groove is a feature shared with *S. hyperboreum*, *S. tenue* and *S. microcephalum*. The characteristic features of *S. bogorovi* include also the irregular arrangement of the papillae in the zone of thickening, the narrow front ends of the toothed platelets, the dumb-bell shaped dorsal glandular shields of the postannular region, and certain peculiarities of the tube, namely, its fibrous front part and the possession of a zone of blotchy rings. This last feature it shares in common with *S. tenue*.

Fig. 123. *Siboglinum bogorovi*: *A* – front end of a female in dorsal, and, *B* – in ventral view; *C* – metameric part of the preannular region from the ventral side (continuation of the part of the body shown in Fig. *B*); *D* – region of thickened papillae in ventral view; *E* – region of the girdles from the ventral side; *F* – the same from the dorsal side; *G* – part of a girdle; *H* – toothed platelet from a little to one side; *I* – part of the postannular region; *J* – front, filmy part of the tube; *K* – an anterior part of the tube; *L* – middle part of the tube; *M* – hind part of tube.
an – girdles; *c* – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *da* – anterior teeth; *dp* — posterior teeth; *f* – keel of the bridle; *gt* – pyriform glands seen by transparency; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaque; *pa* – papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma (post-tentacular groove); *sc* – dorsal glandular shield; *sv* – ventral sulcus; *t* – tentacle; *v* – ventral papilla.

Material: five tubes, of which three contained animals.
Locality: the Pacific Ocean to the east of the North Island of New Zealand.
Depth: 3013 m.
Substratum: silty clay.

20. Siboglinum minutum Ivanov (Figs. 4, 124–5)

Ivanov, 1957a: 449, 451–3, 458, 459, 491, 496, 497, Figs. 20–22, 59; Ivanov, 1958a: 1369; Ivanov, 1960a: 1541, 1542, 1545, 1550, 1587, 1606, Figs. 1386, 1405; Ivanov, 1960c: 5, 10, 19, 27, 35, 75, 91, 92, 108, 126, 158, 167, 180–3, 197, 266, Figs. 4, 87, 124–5.

This species, encountered in abundance in a few places in the abyssal zone of the Bering Sea, is one of the very smallest representatives of the genus *Siboglinum*. Its hair-like, very slender tube is distinguished by its characteristic appearance and its red-brown colour. The small diameter of the tube, the hardness and brittleness of its walls and the softness of the animal itself, all contribute to make it almost impossible to dissect it out. For this reason, despite the abundance of the material available, not all the parts of the animal have been extracted from the tube. The anterior section of the body, a little flattened dorso-ventrally, is four and a half to five times as long as broad (Fig. 124*A*, *B*). The small size of the protosoma and its peculiar shape are very characteristic, and the annular groove, limiting it behind, runs immediately behind the base of the tentacle. The mesosoma is five or six times as long as the protosoma, if the cephalic lobe is not taken into account. The protosoma, moreover, is made up of three parts: a triangular central part, including the base of the tentacle, and two swollen lateral parts, which are particularly sharply delimited on the ventral side of the body (Fig. 4, 124*A*, *B*). The conical cephalic lobe is like-wise very small, and because of the peculiar shape of the protosoma it is difficult to determine how far it is cut off from the latter. The long slender tentacle apparently has no pinnules, but this has not been determined for sure, because of inadequate fixation of the material. The keels of the bridle, which is situated a little in front of the middle of the mesosoma, lie on low cutaneous ridges, and are fused ventrally and almost meet dorsally. Under the miscroscope it is evident that each consists of a delicate cuticular thread, along which is arranged a series of very delicate transverse parallel rodlets, whose axes lie at right angles to the thread

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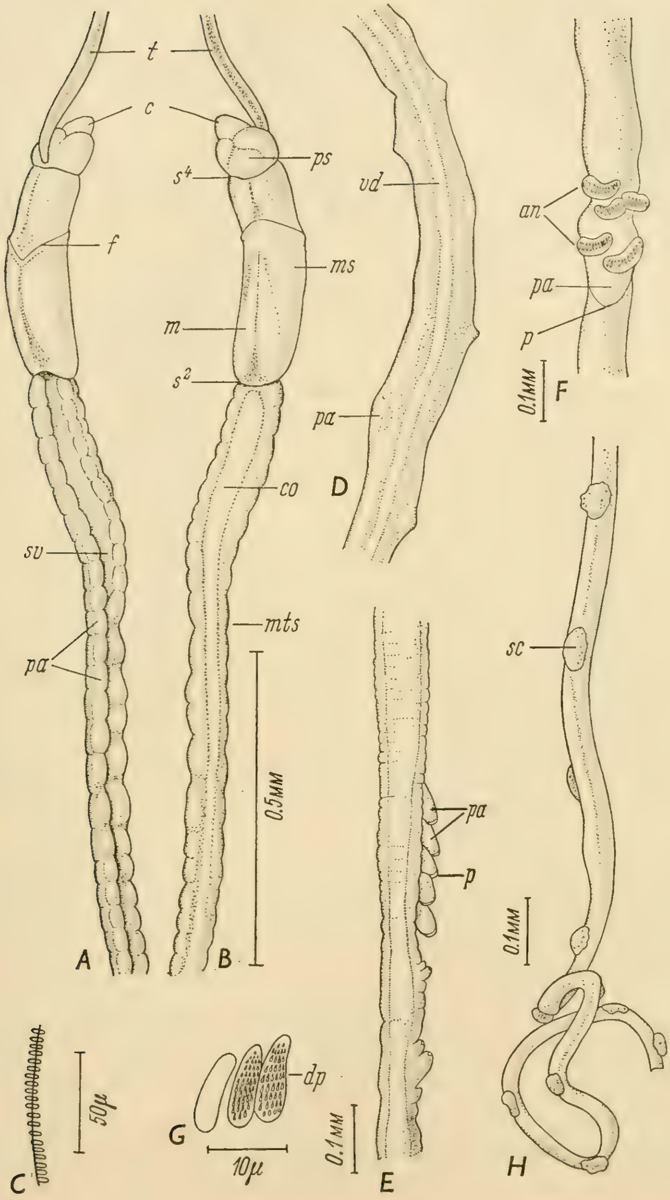
Fig. 124. *Siboglinum minutum*: *A* – front end of a female in ventral, and, *B* – in dorsal view; *C* – keel of bridle under high magnification; *D* – a portion of the non-metameric part of the preannular region; *E* – region of thickened papillae; *F* – region of the girdles; *G* – part of a girdle; *H* – part of the postannular region.
an – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *dp* – hind group of teeth; *f* – keel of the



bridle; *m* – bundle of muscle fibres seen by transparency; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaque; *pa* – papillae; *ps* – protosoma; s^2 – groove between the mesosoma and the metasoma; s^4 – post-tentacular groove between the protosoma and the mesosoma; *sc* – dorsal glandular shield; *sv* – ventral sulcus; *t* – tentacle; *vd* – dorsal blood vessel seen by transparency through the body wall. (*A*, *B*, *C* after Ivanov, 1957a.)

(Fig. 124*C*). Behind the bridle, on the dorsal side of the mesosoma, a pair of long, triangular bundles of longitudinal muscle fibres may be made out, under the skin (Fig. 124*B*). The hind edge of the mesosoma is arched backwards on the dorsal side and slightly concave ventrally.

The anterior metameric portion of the trunk is somewhat less flattened dorso-ventrally than the mesosoma. The ventral sulcus is bounded by comparatively large, elongated papillae, devoid of plaques (Fig. 124*A*). The front end of the well-developed dorsal ciliated band is wider than farther back (Fig. 124*B*). The middle nonmetameric part of the trunk bears scattered pointed lateral glandular papillae (Fig. 124*D*), while in the mid-ventral line, in the zone of thickened papillae, lies a single row of five transparent, conical papillae, placed close together, one behind the other, each bearing on the tip a noticeable thickening of the cuticle (Fig. 124*E*). The two girdles of the metasoma lie close together on muscular ridges (Fig. 124*F*). The uniserial colourless toothed platelets are narrow at the front end and lack the anterior group of teeth (Fig. 124*G*). They are 10–11μ long. The very long, slender postannular region of the trunk is furnished with metameric button-like dorsal glandular shields, but is devoid of papillae (Fig. 124*H*).

The parts of the body have the following dimensions: length of the tentacle, *c.* 4·5 mm; length of the anterior section of the body, 0·35–0·45 mm; breadth of the mesosoma, 0·1 mm; overall length of the body, including the tentacle, 50–55 mm.

The cigar-shaped spermatophores taper evenly towards both ends, and the filament has an expanded base (Fig. 125*A*). They are about 0·11 mm long.

The unsegmented tube, rather dark red-brown in colour, possesses very stout walls, as may easily be seen in optical section (Fig. 125*B*). It consists of irregular rings of a dark material, with narrow, clear intervals between them. In the hind part of the tube the rings are very much shorter and the intervals between them correspondingly longer, and often constricted or pinched in (Fig. 125*C*). The material of the tube is very hard and brittle. The longest fragments reach 15 cm in length and 0·1–0·12 mm in diameter. The transparent ringless front part of the tube is not less than 1·5 cm long, and the hindmost part, also unringed and transparent, reaches 1 cm in length. The tube tapers very little, losing only 10μ in diameter for each 4 cm, i.e. a taper of 2·5μ/cm.

S. minutum is sharply distinguished from all other species by the small protosoma, with its pair of lateral swellings. Not less characteristic are the following features: the very small, conical, cephalic lobe, the peculiar nature of the keels of the bridle, the absence of a glandular girdle, and the structure of the tube.

Material: masses of tubes, some with animals and some empty.

Locality: the Bering Sea, to the southeast of Cape Olyutorski (60°N 170°20′E).

Depth: 3740–3802 m.

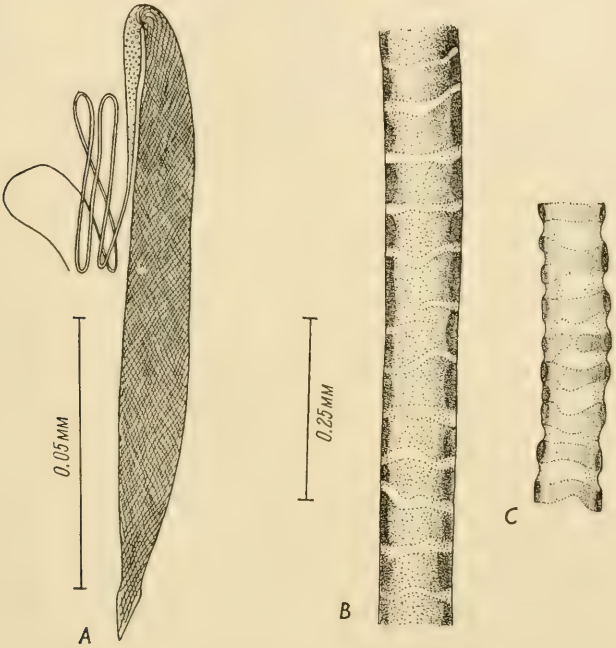


Fig. 125. *Siboglinum minutum*: *A* – spermatophore; *B* – middle part of tube; *C* – hind part of tube. (After Ivanov, 1957a.)

21. Siboglinum norvegicum Ivanov (Fig. 126)

Ivanov, 1960c: 5, 27, 127, 183–6, 197, 265, Figs. 87, 126.

The presence of *Siboglinum* in the northern part of the Atlantic Ocean, in the Norwegian Sea, is of great zoogeographical interest. In 1958, the Polar R.V. *Sevastopol* found tubes of several species of *Siboglinum* on the continental shelf near the Shetland Isles, in the eastern part of the sea, and, in deeper water, to the east of the coasts of Iceland. In these collections, the tubes most frequently encountered were characteristic delicate transparent tubes, with regular rings, belonging to none of the few known Atlantic species. In two of these tubes animals were found, in one an almost mature female, and in the other the front half of the body of a male. This species has been named *S. norvegicum.* The more or less cylindrical fore-part of the body is seven times as long as broad. The groove between the protosoma and the mesosoma lies a little in front of the bridle. Ventrally it is distinct, but on the dorsal side it becomes indiscernible or disappears altogether (Fig. 126*A*, *B*). The strikingly large protosoma is three-quarters the length of the mesosoma and, in the female, a little narrower than the mesosoma. The small, conical, cephalic lobe is not divided from the rest of the protosoma, and the long slender tentacle, free of pinnules, is attached not far from its tip. The delicate, muddy-brown keels of the bridle, located on the front end of the mesosoma, are fused together on the ventral side, where they are noticeably thickened, but between their dorsal ends lies a considerable gap (Fig. 126*A*, *B*, *C*). The small portion of the mesosoma lying in front of the bridle has a narrow crack-like median ventral furrow. Behind the bridle is a well-developed epidermal glandular girdle, widely interrupted on the dorsal side and only narrowly continuous on the ventral side (Fig. 126*C*). A large part of the mesosoma behind the glandular belt is occupied by two rows of internal glands, which may be seen through the body-wall by transmitted light. The boundary between the mesosoma and the metasoma is an annular groove, only slightly arched backwards on the dorsal and ventral sides (Fig. 126*A*, *B*).

The rather long, metameric front part of the metasoma is only a little less broad than the mesosoma, and the numerous small paired papillae are strongly compressed together (Fig. 126*A*). In each of the first few papillae one or two pyriform glands are present. The ventral sulcus is narrow, and the dorsal ciliated band begins immediately at the front edge of the trunk (Fig. 126*B*). The nonmetameric part of the preannular region of the trunk is unknown. There is no sharply defined zone of thickened papillae behind the genital aperture in the female. The three girdles of toothed platelets lie on three muscular thickenings of the trunk (Fig. 126*D*), and the first girdle is noticeably narrower than the others. The distance between it and the second girdle is about one and a half times that between the second and third. The first and second girdles are interrupted only on what appears to be the ventral side, but the third girdle is interrupted both ventrally and dorsally. The toothed platelets, arranged in 2–4 rows (Fig. 126*E*), are shaped like shoe-prints and each possesses a well-developed front group of teeth, occupying about one-third of the surface of the platelet. The anterior teeth are considerably smaller than the posterior, and between the two groups runs a narrow but noticeable interval clear of teeth (Fig. 126*F*). The platelets are 10–15μ long.

The female has the following dimensions: length of the tentacle, 11 mm; length of the fore-part of the body, 1·42 mm, of which the protosoma accounts for 0·6 mm and the mesosoma for 0·82 mm; breadth of the mesosoma, 0·2 mm; length of the trunk, *c*. 37 mm. The fore-part of the body of the male is the same size and of almost the same proportions.

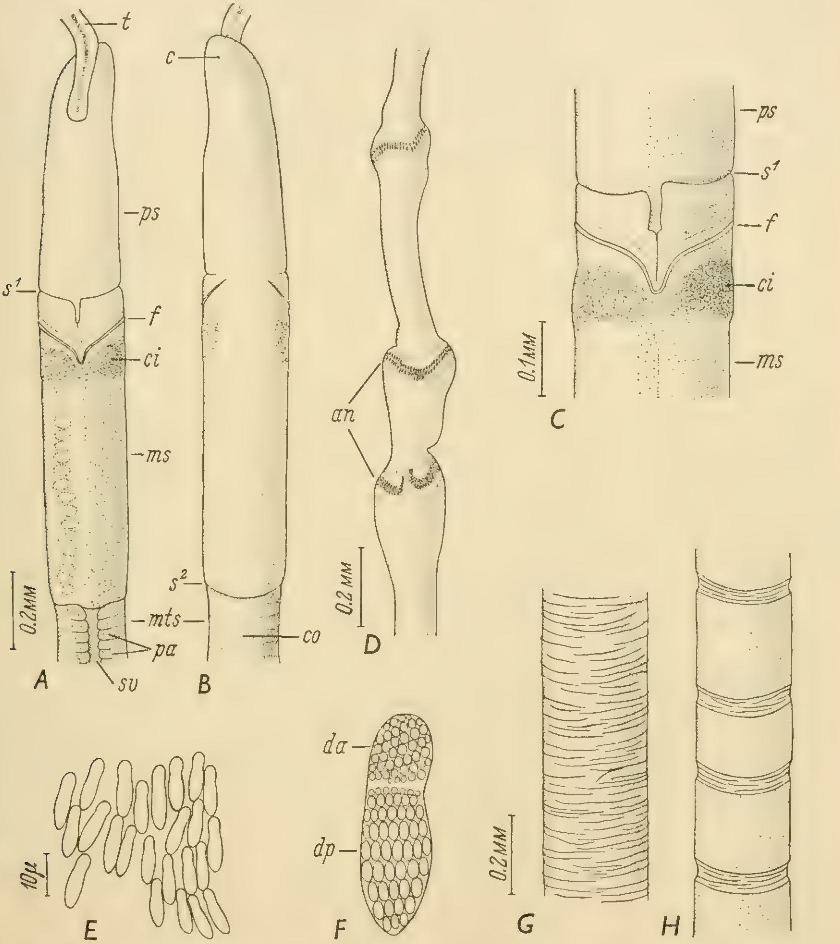


Fig. 126. *Siboglinum norvegicum*: *A* – front end of a female in ventral, and, *B* – in dorsal view; *C* – ventral view of the region of the bridle under higher magnification; *D* – region of the girdles from the ventral side; *E* – part of a girdle; *F* – toothed platelet (only the bases of the teeth are indicated); *G* – front part of tube; *H* – middle part of tube.
an – girdles; *c* – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *da* – front group of teeth; *dp* – hind group of teeth; *f* – keel of the bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle.

The spermatophores are unknown.

The front part of the unsegmented tube has transparent, filmy walls, containing transverse fibres (Fig. 126*G*). The middle part of the tube is free of fibres and ringed with smooth regular transparent almost colourless rings, with even edges (Fig. 126*H*). For the most part, they are as long as the tube is wide, but occasionally one may encounter longer or shorter rings. In the hind part of the tube, rings predominate which are one and half to two times as long as the diameter of the tube. The transparent interspaces between the rings are small, and the walls of the tube are here covered with transverse wrinkles and lightly constricted between rings. The largest fragments of tubes reach 74–78 mm in length and 0·23–0·25 mm in diameter near the front end.

S. norvegicum somewhat recalls *S. pellucidum* from the Bering Sea, but it is distinguished from it by the more highly developed, continuous, uninterrupted keels of the bridle, by the presence of a glandular girdle in the mesosoma, by the many-rowed arrangement of the toothed platelets in the metasomal girdles, by the longer rings of the tube, and by the fibrous structure of the anterior part of the tube. *S. norvegicum* is related to many species lacking pinnules by the possession of a glandular girdle, but it is distinguished from them by the relatively long protosoma. The chief distinctions from *S. hyperboreum* lie in the absence of any post-tentacular groove, in the different structure of the bridle, in the weaker development of the front teeth of the platelets, and in the structure of the tube. It may be distinguished from *S. inerme* by the greater development of the glandular girdle, by the length of the protosoma, by the arrangement and peculiarities of the toothed platelets, and by the structure of the tube.

Material: 6 tubes, of which 2 contained animals—one male and one female.

Locality: the Norwegian Sea to the west of the Shetland Isles; at a depth of 120 m, and to the west of the Norwegian coast at a depth of 1165 m.

22. *Siboglinum robustum* Ivanov (Fig. 127)

Ivanov, 1960c: 5, 12, 18, 129, 151, 154, 174, 186–8, 197, 264, Fig. 87, 127.

One of the most clearly distinguished species of *Siboglinum* is *S. robustum*, a single specimen of which was found together with *S. buccelliferum* and *S. frenigerum* in a trial dredging made by R.V. *Vityaz*' in 1957, in the northern part of the Coral Sea. The fore-part of the body is a little flattened dorsoventrally and comparatively short, with a length to breadth ratio of 4½ : 1 (Fig. 127*A*, *B*). The bridle lies a little in front of the middle of the anterior section, and a short way in front of it runs the transverse groove dividing the protosoma from the mesosoma. This is strongly marked on the ventral side and notched in the mid-ventral line, where the tip of a lappet points forwards (Fig. 127*B*), while the groove dies out towards the mid-dorsal line. Behind the point of attachment of the tentacle is another transverse groove. The comparatively large protosoma tapers towards the front end (Fig. 127*A*, *B*) and the tentacle, the greater part of which has not been preserved, is attached in the mid-line. No pinnules are present on the part of the tentacle which remains. The conical cephalic lobe is not large. The mesosoma is three times as long as broad, and narrows slightly behind the bridle. It then broadens out again, only to taper once more towards the hind end, which is curved at the sides and just perceptibly concave on the ventral side (Fig. 127*A*, *B*). The delicate keels of the well-developed bridle, lying on the front edge of low cutaneous ridges, are not fused ventrally, and the gap between their dorsal ends is very wide (Fig. 127*A*). The ventral surface of the mesosoma has a shallow median furrow.

The front section of the metasoma has pronounced lateral ridges bounding a rather narrow ventral sulcus, and the large metameric papillae have hazy outlines (Fig. 127*B*). The broad dorsal ciliated band begins at the front edge of the metasoma. The region of the thickened papillae is unknown. There are three girdles, the first two lying some way in front of the third. The first is interrupted on the dorsal side, the other two on the ventral side, and their well-defined ridges bear uniserial toothed platelets (Fig. 127*E*) of characteristic shape. Each platelet is divided by a transverse line into two parts, the front part smaller and narrower, with teeth pointing backwards, and the hind part larger and broader, with teeth pointing forwards. In profile the platelets appear very slim, and the central zone can be seen to lack teeth. The ratio between the sizes of the front and back parts varies: sometimes the front part is only a little less than half the area of the platelet, but for the most part it occupies about a third of it (Fig. 127*F*). Most of the platelets are 17–18μ long, exceptionally 16 or 19μ; their breadth in the middle is *c.* 5μ.

Since the only specimen is incomplete it is not possible to determine more than a few of the dimensions of the body: length of the fore-part of the body, a little more than 0·9 mm, breadth, 0·2 mm; the metasoma is the same breadth; in the region of the girdles the trunk reaches 0·15 mm in diameter; the distance between the second and third girdles, 0·3 mm.

The distinctive, thin-walled, soft transparent tube possesses very regular muddy-brown rings, whose length is about a quarter the diameter of the tube, while the completely colourless, glassily transparent interspaces between

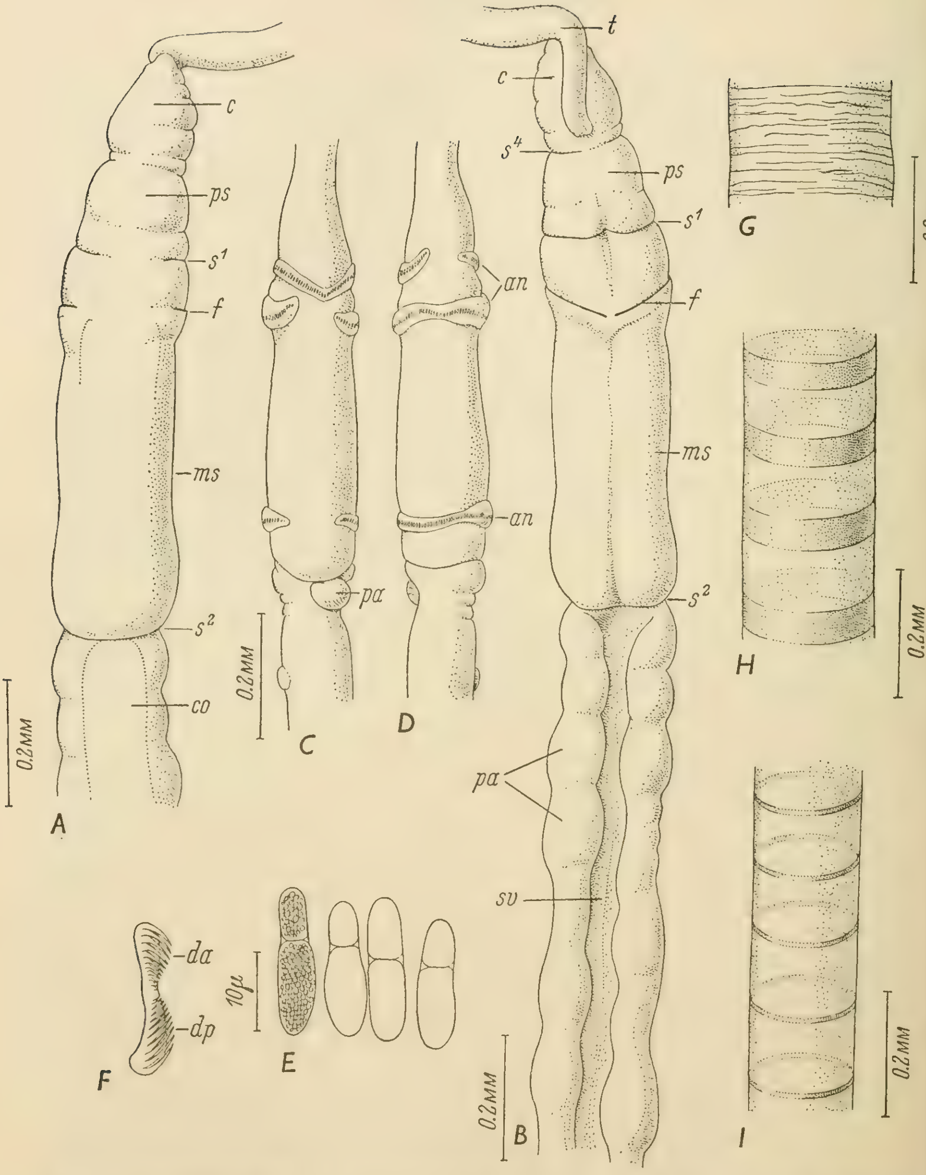


Fig. 127. *Siboglinum robustum* : *A* – front part of the body from the dorsal, and, *B* – from the ventral side; *C* – the region of the girdles from the ventral, and, *D* – from the dorsal side; *E* – part of a girdle (on one platelet the bases of the teeth are indicated); *F* – a toothed platelet from one side; *G* – part of the anterior, flimsy, region of the tube; *H* – middle part of the tube; *I* – hind part of the tube.

an – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *da* – anterior group of teeth; *dp* – posterior group of teeth; *f* – keel of the bridle; *ms* – mesosoma; *pa* – papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; s^4 – post-tentacular groove; *sv* – ventral sulcus; *t* – tentacle.

them are twice as long as the rings (Fig. 127*H*). In the hind part of the tube the rings become so short as to be quite insignificant, while the interspaces remain the same length as before (Fig. 127*I*). The transparent filmy front portion of the tube, 1·5 cm long, has limp walls in which it is possible to make out very faint transverse fibres. The only fragment of tube is 15 cm long; the diameter of the front filmy part is 0·25 mm, of the ringed part 0·2 mm near the front and a little more than 0·15 mm near the back; in other words, the tube tapers rather more rapidly than usual.

To all appearances *S. robustum* stands rather on its own amongst the species of *Siboglinum*. In some ways it recalls *S. buccelliferum*, for both species have a gap between the ventral ends of the keels of the bridle, both have three girdles, arranged in the same way, and they have rather similar toothed platelets. The first two of these characters, however, are not of any great significance, being found also in species of a very different nature. Thus, *S. atlanticum* and *S. taeniaphorum* also have a gap between the ventral ends of the keels of the bridle, but they clearly belong to quite a different group of species, while three girdles are also found in species with a bipectinate tentacle (*S. ekmani* and *S. fedotovi*) and also in species lacking pinnules (*S. hyperboreum* and *S. tenue*).

Material: a single incomplete specimen in a tube.

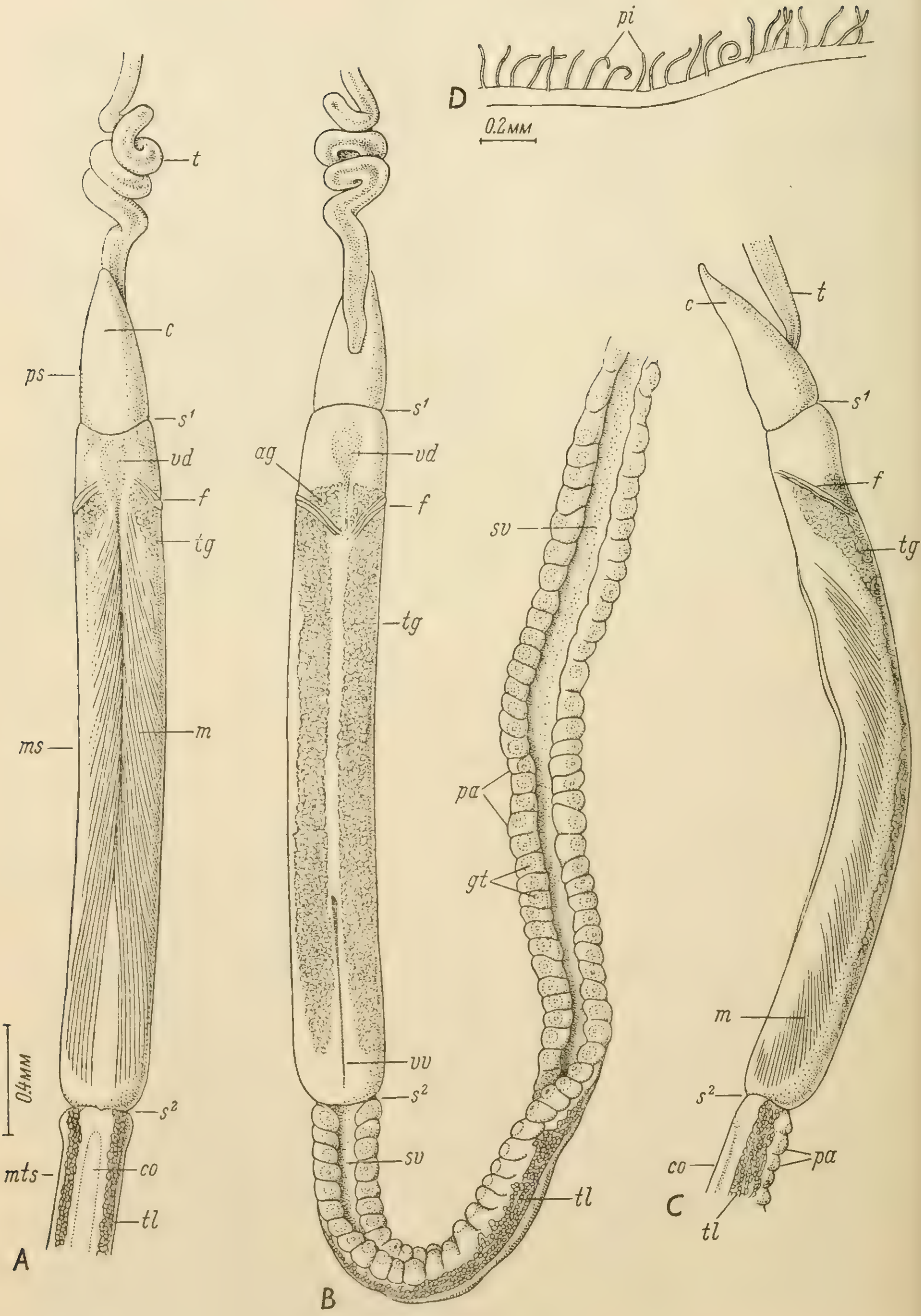
Locality: the northern part of the Coral Sea near Treasury Island (7°30′S 154°15′E) in the British Solomon Islands.

Depth: 960 m.

23. *Siboglinum taeniaphorum* Ivanov (Figs. 128–30)

Ivanov, 1960c: 5, 12, 14, 18, 28, 96, 98, 105, 128, 188–92, 195, 197, 263, Figs. 87, 128–30.

In August, 1957, during a cruise of R.V. *Vityaz'*, a few trial dredgings were taken near the north coast of Morotai in the Molucca Islands, at a depth of *c.* 300 m. Amongst the washings from the silty soil was found a transparent white tube, containing an intact female, sharply distinguished from all other species. From the possession of longitudinal glandular ribbons on the mesosoma, so obvious even at first glance, this species has been named *S. taeniaphorum* [Greek ταινία, Latin, *taenia*, a ribbon, Greek φόρον, a bearer]. A little flattened dorso-ventrally, the fore-part of the body is uncommonly long, with a length to breadth ratio of 10 : 1. The small protosoma is divided from the mesosoma by a distinct annular groove (Fig. 128*A*, *B*, *C*), and in front it runs gradually, without interruption, into the pointed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conical cephalic lobe. The long slender tentacle carries a single, rather sparse row of soft pinnules (Fig. 128*D*). The mesosoma is the same breadth all along, and the delicate muddy-brown unobtrusive keels of the bridle, which lies at its front end, are widely separated both dorsally and ventrally, extending along the surface of low, rather narrow ridges (Fig. 128*C*). Immediately in front of the bridle on the ventral side is a pair of triangular patches of glandular epidermis (Fig. 128*B*), while behind it extends a pair of rather broad, lateral glandular strips, homologous with the glandular girdles of many other species of *Siboglinum*, consisting of groups of epidermal cells, filled with granular secretion. On the ventral side of the body, however, the strips turn backwards and extend as broad parallel ribbons almost to the hind end of the mesosoma (Fig. 128*A*, *B*, *C*). Between these ribbons runs only a narrow mid-ventral strip of unmodified integument (Fig. 128*B*). A similar development of these glandular formations of the mesosoma is found also in *S. atlanticum*. The hind edge of the mesosoma is curved in the usual manner.

The fore-part of the trunk is considerably narrower than the mesosoma and the adhesive papillae in this region are shortish. In each of them can be seen a single pyriform gland with its secretory duct (Fig. 128*B*), and not less than 60 pairs of these more or less metameric papillae border the moderately wide ventral sulcus. The narrow dorsal ciliated band begins a little behind the front edge of the metasoma, and between it and the rows of metameric papillae run a pair of longitudinal lateral ribbons of glandular integument (Fig. 128*A*). The middle part of the preannular section of the metasoma is richly crowded with single-celled epidermal glands, situated laterally and more especially on the ventral side. Here and there they nearly coalesce to form two almost uninterrupted lateral rows. In the region of the female genital apertures and oviducts these glandular accumulations disappear, so that here, through the body wall, elongated eggs may be seen lying in the oviducts. A little farther back, in the zone of thickened papillae, the glandular tracts of integument begin afresh, on the dorsal side as well as ventrally, but

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Fig. 128. *Siboglinum taeniaphorum*: *A* – anterior end of a female from the dorsal, *B* – from the ventral, and, *C* – from the right side; *D* – part of the tentacle.
ag – anterior ventral glandular area; *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – keel of the bridle; *gt* – pyriform gland seen by transparency; *m* – muscle bundles seen by transparency; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae of the metameric section of the preannular region; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle; *tg* – ventral glandular ribbon of the mesosoma; *tl* – lateral glandular ribbon of the metasoma; *vd* – dorsal blood vessel seen by transparency; *vv* – ventral blood vessel seen by transparency.

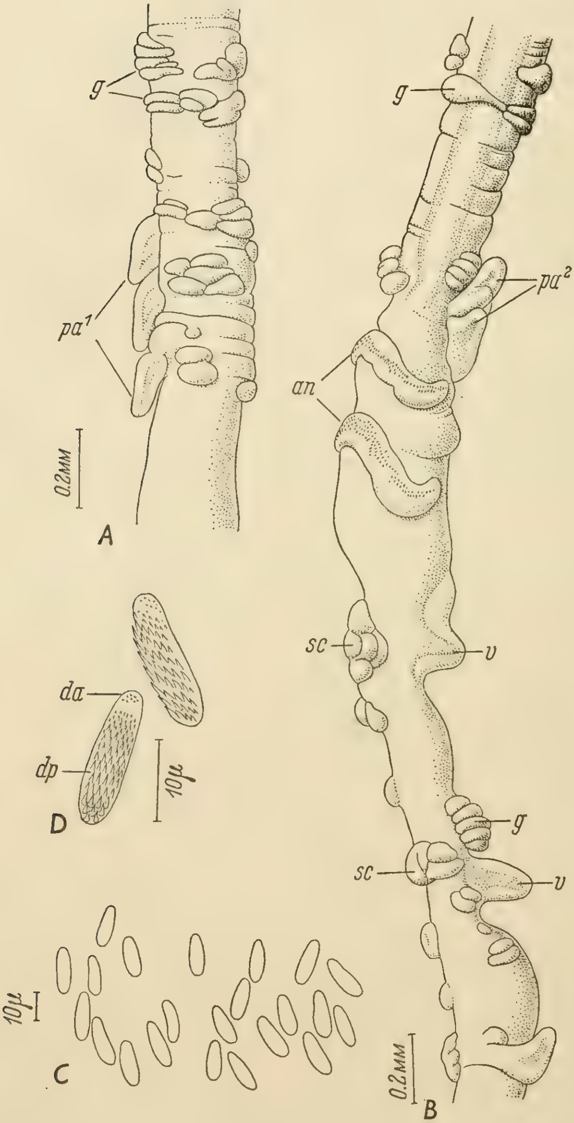

Fig. 129. *Siboglinum taeniaphorum*: *A* – zone of thickened papillae from the left side; *B* – girdles and the beginning of the postannular region from the right side; *C* – part of a girdle; *D* – toothed platelets.
an – girdles; *da* – front group of teeth; *dp* – rear group of teeth; *g* – glandular parts of the integument; *pa*^{1} – three papillae of the zone of thickening; *pa*^{2} – papillae lying in front of the girdles; *sc* – glandular dorsal shield; *v* – ventral papillae of the postannular region.

they are more disorderly in disposition. In the zone of thickening three large conical transparent papillae lie in the mid-ventral line one behind the other (Fig. 129*A*). Two girdles of toothed platelets lie on rather stout muscular ridges and both are interrupted on the ventral side only. Immediately in front of the first girdle lie three conical ventral papillae, one behind the other (Fig. 129*B*). The pale yellow, toothed platelets, arranged in three, four or in places in five rows, are elongated ovals, without any constriction in the middle (Fig. 129*C*). They measure 11·5–13μ long by *c.* 2·5μ wide, and the front group of teeth is rudimentary (Fig. 129*D*). The very long postannular region of the metasoma is covered in numerous scattered button-like groups of epidermal gland cells. A metameric series of papillae extends down the ventral side, and opposite each of them, on the dorsal side, is a glandular area of irregular outline, not distinguishable in appearance from the scattered glandular warts (Fig. 129*B*), but nevertheless representing extremely weakly developed dorsal glandular shields.

Our complete specimen has the following dimensions: length of the tentacle, *c.* 15 mm; fore-part of the body, 3·1 mm by 0·36 mm; breadth of the middle part of the metasoma, 0·23 mm; length of the preannular section, 34 mm; length of postannular section, 17 mm; overall length of the body, 69·1 mm.

In the living animal a number of organs show up coloured or opaque against a colourless and semi-transparent background. Thus the blood vessels filled with red blood may be seen in the mesosoma, the metasoma and the tentacle. The many-celled pyriform glands of the mesosoma and metasoma show whitish through the integument, while the glandular tracts and longitudinal ribbons of the epidermis are yellowish, as are the ovary and eggs in the oviduct. The wart-like groups of epidermal gland cells of the metasoma, in both the preannular and postannular parts are a lustreless creamy white. The conical ventral papillae, in the zone of thickening, in front of the girdles, and in the postannular section of the trunk, are all, by contrast, glassily transparent.

The tube is elastic, white, translucent and rather stout-walled. The front part is whitish with a faint dirty-brown tinge and distinctly segmented, with segments only a little longer than the diameter of the tube. Here and there in the walls of the tube are soft transverse fibres (Fig. 130*A*). Then the fibrous structure becomes denser and a little coarser, and the succeeding part of the tube has white semi-transparent rings, many of them short and broken or irregularly shaped. The intervals between them are not large, but so transparent that the rings on the other side of the tube can easily be seen through them. Numerous transverse fibres run in the interspaces (Fig. 130*B*). The black half of the tube has the same general nature, but the rings here are longer and the intervals between them lack fibres, but instead are thrown into deep transverse wrinkles (Fig. 130*C*). The length of the only available scrap of tube is 150 mm, with a diameter near the front end of 0·37 mm and near the back end, 0·3 mm.

Fig. 130. *Siboglinum taeniaphorum*: Tube: *A* – anterior part; *B* – middle part; *C* – hind part.

S. taeniaphorum is very closely related to *S. atlanticum* but at the same time clearly distinct from it. Both species share in common, in contrast with all other representatives of the genus, the following features: a very long mesosoma, seven to ten times as long as broad, the possession of ventral glandular areas of integument in front of the bridle, and the development of long paired glandular tracts on the ventral side of the mesosoma, behind the bridle and along the fore-part of the metasoma, above the metameric papillae.

There is also a characteristic reduction of the anterior group of teeth on the toothed platelets in both species and, moreover, both of them are among the larger representatives of the genus. *S. taeniaphorum* is nevertheless readily distinguished from *S. atlanticum* by the possession of 3 papillae in the zone of thickening, arranged close together, one behind the other, by the development of papillae in front of the girdles, by the lesser degree of differentiation of the dorsal glandular shields in the postannular region of the trunk, and by the fewer pairs of metameric papillae. *S. taeniaphorum* and *S. atlanticum* undoubtedly form a close-knit group of species within the genus *Siboglinum*, which makes it more remarkable that they should be so isolated from one another geographically, since *S. taeniaphorum* comes from near the Molucca Islands in the Pacific Ocean and *S. atlanticum* from the Atlantic, near the coasts of Northern Europe.

Material: 1 tube containing an intact animal.

Locality: the western Pacific near the north coast of Morotai Island (2°130′N 129°E) in the Molucca Islands.

Depth: 260 m.

24. Siboglinum atlanticum E. C. Southward and A. J. Southward (Figs. 131–2)

Southward, E. C. and Southward, A. J., 1958b: 627–30, Figs. 1, 2; Ivanov, 1960a: 1531; Ivanov, 1960c: 4, 5, 14, 28, 98, 105, 128, 188, 190, 192–5, 197, 264, Figs. 87, 131–2.

Recently E. C. Southward and A. J. Southward (1958b) described an interesting species, *S. atlanticum*, which was found in the Atlantic Ocean to the southwest of the British Isles, together with *S. ekmani* and *S. inerme*. The material, consisting of 20 tubes, from which were extracted parts of 14 animals, was taken in 1957 and 1958 on cruises of R.V. *Sarsia* of the Marine Biological Association of the United Kingdom, Plymouth. I was able to become better acquainted with *S. atlanticum* through a well-preserved female specimen, the generous gift of Dr. Eve C. Southward. The description given here is based on that of the Southwards, supplemented by my own observations.

The fore-part of the body is greatly elongated with a length to breadth ratio of 9–12 : 1, and the protosoma and cephalic lobe together account for only a fifth to a quarter of this (Fig. 131*A*). The large conical cephalic lobe, pointed at the tip, is not divided from the protosoma, but between the latter and the mesosoma runs a simple annular groove, interrupted on the dorsal side. The rather stout, very long tentacle, attached at the bottom of a mid-ventral furrow, is rather constricted at its base (Fig. 131*A*), and bears two dense, closely adjacent rows of pinnules. The delicate, brownish keels of the bridle, which lies at the front end of the mesosoma, are fused neither ventrally nor dorsally, and in front of the bridle lie a pair of triangular, ventral, clearly marked patches of glandular epidermis (Fig. 131*A*). Behind the keels, and almost parallel to them, are further glandular epidermal tracts, corresponding in their antero-lateral parts to the glandular girdles of some other species. Their ventral ends, however, turn backwards and extend far back to the hind edge of the mesosoma as a pair of ventral glandular ribbons (Fig. 131*C*). The fore-part of the body bears narrow mid-ventral and mid-dorsal furrows, and in the hind part of the mesosoma two rows of large internal sacculate glands may be seen by transparency. The dividing groove between the mesosoma and the metasoma has a forward-projecting lappet on either side of the mid-dorsal line.

The long metameric part of the trunk bears numerous paired papillae, numbering (in my female specimen) 153 on the right and 166 on the left side of the body. The rather large, densely packed papillae run along the sides of the narrow ventral sulcus (Fig. 131*C*) and each contains a single pyriform gland. The narrow dorsal ciliated band begins a short way behind the front edge of the metasoma (Fig. 131*B*). In the zone of thickened papillae lie 30–40 large higgledy-piggledy ventral papillae (Fig. 131*D*), many of them bearing on their tips weak cuticular thickenings, whose dimensions vary greatly, while there are on a few papillae oval or hoop-shaped adhesive plaques reaching 30–40μ across.

In two more or less complete individuals studied by Southward and Southward, one had two and the other three girdles of toothed platelets, whilst in a third specimen I found two girdles and a very weak additional

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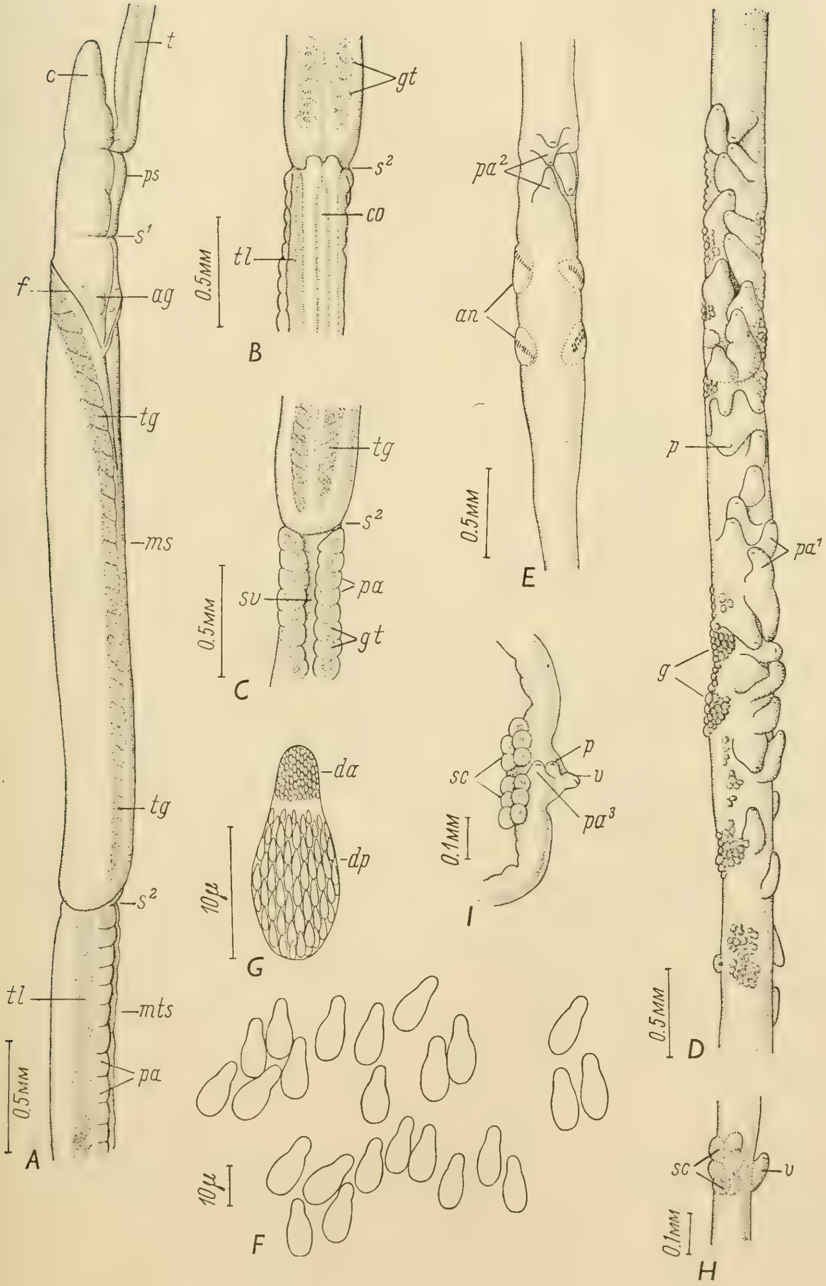
Fig. 131. *Siboglinum atlanticum*: *A* – front end of the body of a female from the right side; *B* – the hind part of the mesosoma and the beginning of the metasoma from the dorsal, and, *C* – from the ventral side; *D* – the region of thickened papillae from the ventral side; *E* – the region of the girdles from the ventral side; *F* – part of a girdle; *G* – toothed platelet; *H* – dorsal glandular shield and ventral papilla of the postannular region in dorso-lateral view; *I* – the same from one side. *ag* – anterior ventral glandular area of epidermis; *an* – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *da* – anterior group of teeth; *dp* – hind group of teeth; *f* – keel of the bridle; *g* – glandular part of the integument; *gt* – pyriform glands seen by transparency; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaque; *pa* – metameric papillae; pa^1 – papillae of the zone of thickening; pa^2 – papillae in front of the girdles; pa^3 – supplementary postannular papilla; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sc* – dorsal glandular shield; *sv* – ventral sulcus; *t* – tentacle; *tg* – ventral glandular ribbon of the mesosoma; *tl* – lateral glandular ribbon of the metasoma; *v* – ventral postannular papilla.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girdle lying behind them. In this same specimen a characteristic group of four ventral cone-shaped papillae lay in front of the girdle (Fig. 131*E*). The toothed platelets, which lie in three or four rows (Fig. 131*F*), are rather broad, slightly narrower, in the front third, and rounded at the ends. The well-developed front group of teeth occupies about a quarter of the surface of each platelet, and is considerably less in area than the better developed hind group. The platelets are 14–18μ long by 4–6μ broad. Southward and Southward did not describe the toothed platelets, contenting themselves with a figure, which did not show the anterior teeth. The postannular region of the trunk is long and slender and the metameric glandular shields well developed but irregularly shaped. Each consists of four to six or more, densely packed, rounded protuberances, in each of which lies a single pyriform gland, while the tip of each protuberance is marked by the aperture of the gland (Fig. 131*H*, *I*). The large conical ventral papilla lying opposite each dorsal shield widens out transversely towards the base and is invariably furnished with rather coarse, curved or rod-shaped brownish cuticular plaques, up to 40–60μ across. Occasionally, to judge by my one specimen, on each side of the papillae smaller supplementary papillae are sometimes developed, also bearing cuticular plaques (Fig. 131*I*). In a sense these form the rudiments of a transverse row of papillae, very reminiscent of the metameric postannular rows of papillae in the Thecanephria.

According to the data given by Southward and Southward the dimensions of the parts of the body are as follows: length of the tentacle, 20 mm; length of the protosoma, 0·68–0·87 mm; length and breadth of the mesosoma, 2·5–2·9 mm and *c.* 0·36 mm, respectively; length of the metameric part of the preannular region, 15–20 mm; length of the nonmetameric part of the trunk, *c.* 50–60 mm, of which the distance between the front edge of the zone of thickened papillae and the girdles accounts for 8 mm and the length of the postannular section for 28 mm; overall length of the body, excluding the tentacle, 112 mm.

The spermatophores (Fig. A131) are very long and narrow, pointed at both ends, and measure 500μ × 30μ.

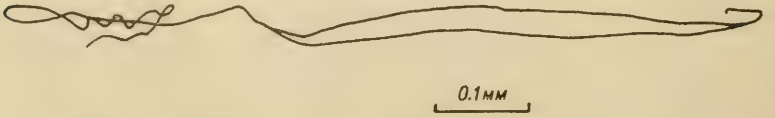


Fig. A131. *Siboglinum atlanticum:* spermatophore. (E. C. Southward.)

The rings of the pale brownish-grey unsegmented tube are no longer than a third the diameter of the tube, and for the most part possess even edges, but often one may encounter rings irregularly shaped or with uneven edges. The intervals between the rings are transparent and transversely wrinkled, but free of fibres (Fig. 132*A*, *B*). The front and hind ends of the tube are transparent. The longest tubes are 32 and 40 cm long. As noted by Southward and Southward they have one very distinctive feature, in that they are narrower in front than in the middle, in total contrast to the usual even backward taper: the diameter in the front part of the tube is *c.* 0·42 mm, and in the middle part 0·5 mm.

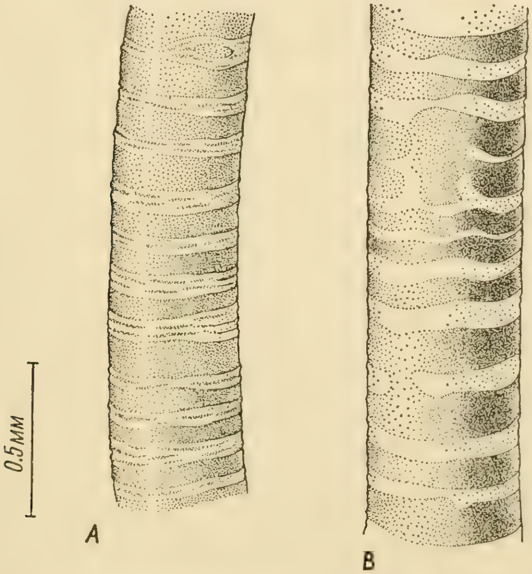


Fig. 132. *Siboglinum atlanticum*: Tube: *A* – front part; *B* – middle part.

S. atlanticum is undoubtedly very closely related to *S. taeniaphorum* (pp. 263 and 259), but distinguished from it in a number of ways: by the two rows of pinnules, by the numerous, disorderly papillae of the zone of thickening (*S. taeniaphorum* has only three), by the bigger and broader toothed platelets, whose anterior group of teeth are not rudimentary, by the development of cuticular plaques on the papillae of the zone of thickening and on those of the postannular region, and, finally, by certain features of the tube, especially its lack of segmentation.

Material: 20 tubes, 14 containing parts of animals.

Locality: the Atlantic Ocean to the southwest of the British Isles (48°28′N 10°04′W; 48°32′N 10°10′W; 48°31′N 10°11′W; 47°50′N 8°08′W).

Depth: 950–1685 m.

Substratum: mud with an admixture of sand, Foraminifera, gravel and stones.

25. *Siboglinum inerme* E. C. Southward and A. J. Southward (Figs. 133–A133)

Southward, E. C. and Southward, A. J., 1958b: 627, 628, 630, 632, Figs. 1, 3 (as *S. inermis*); Southward, E. C., 1959: 444 (orthography corrected); Ivanov, 1960a: 1541 (as *S. inermis*); Ivanov, 1960c: 5, 27, 78, 105, 185, 195–8, Figs. 87, 133 (as *S. inermis*).

This species, collected on cruises of R.V. *Sarsia* in the Atlantic Ocean to the southwest of the British Isles, was described by Southward and Southward, who had then 20 tubes at their disposal, some containing animals.

[At the time of the Russian edition of this book Professor Ivanov had not seen this species and he gave a description based entirely on the account and the drawings by Southward and Southward. The account given below has been amplified on the basis of notes provided by Dr. E. C. Southward upon her original specimens and upon a few more collected in 1960. In life the animal is largely colourless and transparent, but the cephalic lobe is brownish and the glandular patches behind the bridle are whitish. The blood is red because of the presence of haemoglobin.

The fore-part of the body is cyclindrical and the mesosoma is four or five times as long as the protosoma and divided from it by an obvious transverse groove, which is continuous on the ventral side and interrupted on the dorsal side (Fig. 133*A*, *B*). The smallish cephalic lobe is a little flattened dorso-ventrally, and the tentacle, as seen in the living animal, lacks pinnules. A post-tentacular annular groove is always present, but it is not always complete dorsally. The narrow keels of the bridle are always well separated dorsally and usually joined ventrally, but sometimes just separate (Fig. 133*A*, *B*), and in front of them runs a mid-ventral furrow which is not always well marked. Immediately behind the bridle are situated lateral glandular patches of epidermis, representing a glandular girdle interrupted both dorsally and ventrally. These patches are readily visible in the living animal but rarely seen in preserved specimens. The groove dividing the mesosoma from the metasoma is simple and the dorsal ciliated band begins just a little behind it. The rather broad ventral sulcus (Fig. 133*A*, *B*) is bounded by up to 47 pairs of metameric papillae, but more usually there are between 30 and 40.

There is no definite zone of enlarged papillae but some moderate-sized papillae are scattered in the region in front of the girdles; similar papillae are to be found in the genital region. There are normally two girdles, but very rarely three may be seen. This condition is probably brought about by overlapping of the two halves of the first girdle, because each normally consists of two lateral semi-circular bands, sometimes slightly overlapping.

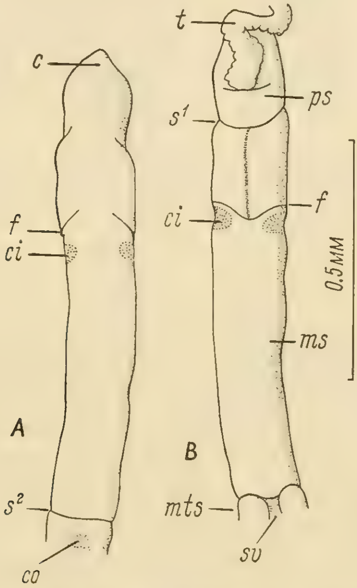


Fig. 133. *Siboglinum inerme*: *A* – front end of the body from the dorsa , and, *B* – from the ventral side.
c – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *f* – keel of the bridle; *ms* – mesosoma; *mts* – metasoma; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle. (After E. C. Southward and A. J. Southward, 1958b.)

Whatever the situation the girdles are always close together, and each has a single row of toothed platelets 10–12μ long. These each bear two groups of teeth, the anterior group smaller than the posterior (Fig. A133*D*). The post-annular region possesses dorsal shields and solitary ventral papillae.

The tentacle is 3 mm long; the fore-part of the body reaches a length of 0·7–0·96 mm; the breadth of the mesosoma is *c.* 0·15 mm; the overall length of the body varies from 13·5 to 25 mm; the metasoma in one female was 14 mm long, of which the preannular region occupied 5 mm.

The spermatophores are 50–60μ long.

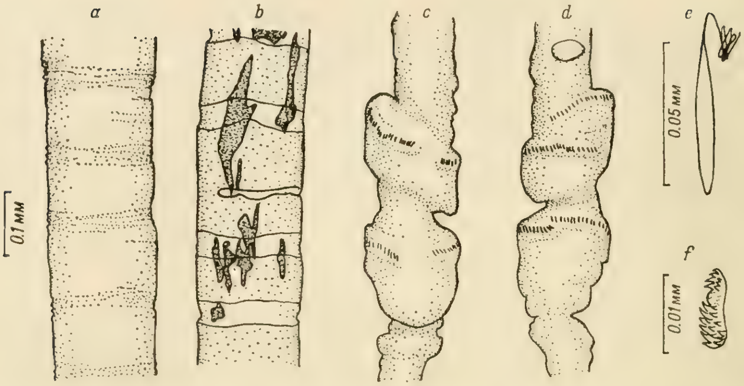


Fig. A133. *Siboglinum inerme*: *a* – part of anterior end of tube; *b* – middle part of tube; *c* – girdle region, dorsal view; *d* – girdle region, ventral view; *e* – spermatophore; *f* – toothed platelet. (E. C. Southward).

The first 1–2 cm of the tube is colourless, wrinkled and limp. The middle 2–4 cm has brown, opaque, irregular rings, which vary in length from half to twice the diameter of the tube, separated by colourless interspaces. The posterior part is paler with yellowish rings. Nearly all the tubes are encrusted outside with patches of a brown substance which obscures the interspaces in some places. An apparently complete tube is 50 mm long, while another broken piece of tube reached 65 mm. The diameter is 0·13–0·18 mm.

The characteristic features of *S. inerme* appear to be as follows: the presence of a median ventral furrow in front of the bridle, and the gap between the front edge of the mesosoma and the beginning of the dorsal ciliated band. In the occasional development of three adjacent girdles *S. inerme* is like *S. microcephalum*.

Material: more than 20 tubes, many containing animals.

Locality: the Atlantic Ocean to the southwest of the British Isles and near the west coast of Europe (48°28′N 10°04′W; 47°50′N 7°45′W; 48°54′N 10°54′W).

Depth: 500–1280 m.

Substratum: mud mixed with stones and shells of Foraminifera.]

[*26. Siboglinum macrobrachium* Southward (Fig. B133)

Southward 1961b: 5–7, 21, Fig. 2.

This species forms part of the *Siboga* material, originally included in *S. weberi*. It is probably the subject of Caullery's Figs. 65–70 (Caullery, 1944).

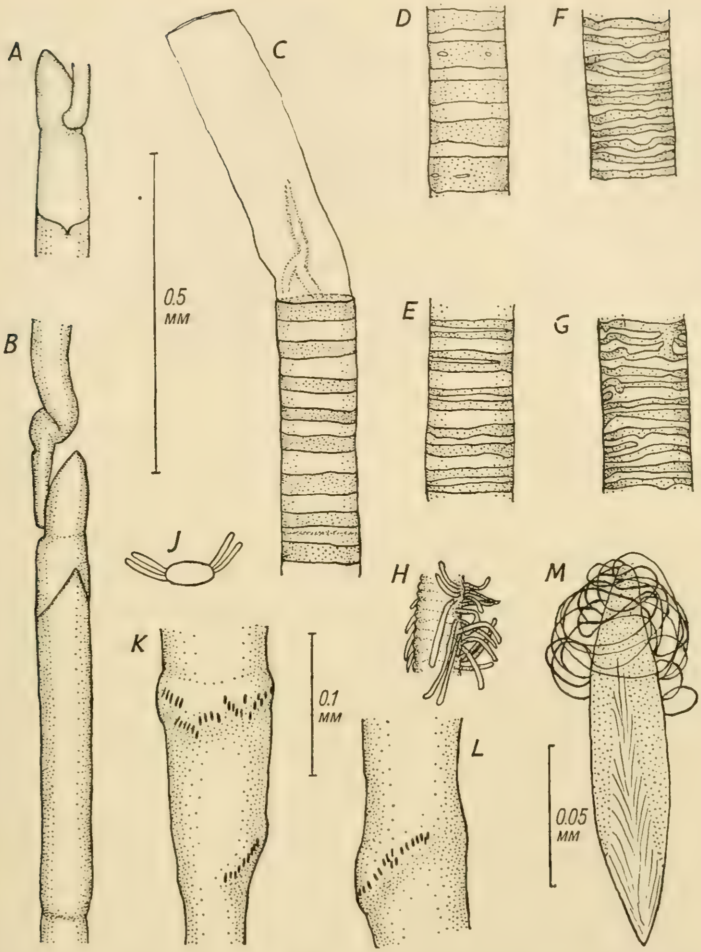


Fig. B133. *Siboglinum macrobrachium*: *A*, *B* – anterior end of animal, ventral and dorsal views; *C*, *D*, *E*, *F*, *G* – anterior and middle parts, and three variations of the posterior part of the tube; *H* – part of tentacle; *J* – diagrammatic transverse section of tentacle and pinnules; *K* – first and second girdles; *L* – third girdle; *M* – spermatophore. (After Southward, 1961b.)

The following description is transcribed from Southward (1961b), by kind permission of the author and the publisher, E. J. Brill. Paragraphs and sentences have been transposed to bring the description into the form adopted here.

"The animals are up to 48 mm long with a tentacle 6·8 mm long, which is usually coiled into a spiral. The tentacle is rather thick, its diameter being about half that of the tube at the proximal end. It becomes a little thinner distally. The pinnules, which are numerous and rather long (80μ), are arranged in two double rows and give the tentacle a bushy appearance (Fig. B133*H*, *J*). The cephalic lobe of the protosoma is rather small and there is no pretentacular groove. There is a complete but shallow groove around the body just behind the base of the tentacle, and this is the only groove in front of the bridle. The bridle consists only of the narrow keels, but these are pale yellow and easier to see than those of *S. weberi* (Fig. B133*A*, *B*). The keels join together to form points on both sides of the body (except in one specimen where there is a small gap between their ends on the dorsal side). The fore-part of the body is usually 0·6 to 1·1 mm long. The diameter of the mesosoma is 0·09 to 0·11 mm and is thus one-sixth to one-tenth of the length of the whole fore-part.

"The metameric papillae are not very well marked; they form two slight ridges each containing a single row of 40 to 50 pyriform glands, and extend for about 2 mm. Behind the metameric region the trunk is smooth until just before the girdles, where there is a row of at least three papillae crowned with fine, curved, cuticular bars about 10μ long. The preannular region is 14 to 26 mm long and the three girdles extend over at least 1 mm. The first and second girdles lie close together and are made up of rather irregular single rows of platelets, while the third lies 1·0 to 1·5 mm behind the second and is more regular (Fig. B133*K*, *L*). The platelets are 10 to 12μ long and have two approximately equal groups of teeth. The postannular region is up to 12 mm long but no papillae have been seen on it.

"Spermatophores are present in six of the specimens examined; they are relatively large for such a small species—120 to 190μ long and 25 to 30μ in diameter.

"The tubes of this species are easily confused with those of *S. weberi*, being much the same diameter and colour. The longest tube (broken) is 5·5 cm long. The diameter of different tubes varies from 0·10 to 0·135 mm and the majority are slightly larger than the majority of *S. weberi*. The tube walls are thin and smooth, and for the first few mm they are limp and colourless. This colourless part and at least some of the rest of the tube is marked into segments by occasional wrinkled rings, as in *S. ekmani* Jägersten (1956). Most of the tube is ringed, first with rather narrow brown rings which become gradually wider. Here the segments are 6–7 rings long. Farther back the rings are divided to form double rings, as in *S. weberi*, and at the posterior end there is a complex pattern of narrow yellow rings (Fig. B133*C*–*G*).

"*S. macrobrachium* is rather similar to *S. buccelliferum* Ivanov, which was collected near the Solomon Islands, but differs in the shape of the bridle, the number of rows of pinnules on the tentacle and the rings on the tube. *S. pinnulatum* Ivanov is another species with much in common with *S. macrobrachium*, but again they differ in the arrangement of the pinnules, the lack of a pretentacular groove in *S. macrobrachium*, the form of the bridle, and the thickness and arrangement of the rings on the tube. The large spermatophores resemble those of *S. fedotovi* Ivanov and the tube, though smaller, also resembles that of *S. fedotovi*."

Material: 18 occupied tubes plus at least 20 more tubes, some occupied.

Locality: Java Sea: *Siboga* station 212 (5°54′S 120°19′E).

Depth: 462 m.]

[*27. Siboglinum debile* Southward (Fig. C133)

Southward 1961b: 7–8, 21, Fig. 3.

This is another species of the *Siboga* material, originally included in *S. weberi*. The following description is transcribed from Southward (1961b), by kind permission of the author and the publisher, E. J. Brill.

"The animals are up to 14 mm long, with a tentacle up to 7·7 mm long and 30 to 50μ in diameter. There is one row of rather long pinnules (60 to 80μ) on the tentacle. The fore-part of the body varies in length from 0·7 to 1·6 mm and the ratio of its length to its diameter varies from 5 : 1 to 11 : 1. The cephalic lobe is flattened dorso-ventrally and ends in a point; the surface of the protosoma and mesosoma seems to be smooth, without any definite grooves (Fig. C133*A*, *B*). The bridle is a well-marked ridge, cross striated in appearance, surmounted by pale yellow keels which join in a point on the ventral side but are well separated on the dorsal side (Fig. C133*B*).

"The mesosoma and metasoma are separated by a very shallow transverse groove; the papillae and ventral sulcus of the metameric region are rather indefinite and extend for 1·3 to 2 mm. The whole preannular region is 6·5 to 11 mm long and seems to lack all but metameric papillae. There are two girdles which lie fairly close together (0·05 to 0·25 mm apart), each of which is made up of one or two irregular rows of toothed platelets (Fig. C133*C*). About 5 mm of the postannular region has been seen but details of it could not be made out. All the specimens seem to be immature.

"The tubes are whitish but transparent, with thin, limp, unringed walls. The biggest is 4 cm long, and the diameter varies from 0·1 to 0·135 mm, but it is difficult to measure accurately, as most of the tubes are flattened and twisted to a much greater extent than is usual for *Siboglinum* tubes.

"*S. debile* is distinct from all other species of *Siboglinum* in the lack of ornamentation of the tube, but otherwise belongs to the group of small species with one row of pinnules on the tentacle. These are: *S. cinctutum* Ivanov, *S. frenigerum* Ivanov, *S. caulleryi* Ivanov, *S. pusillum* Ivanov, *S. buccelliferum* Ivanov and *S. weberi* Caullery. The striated bridle is similar to those of *S. minutum* Ivanov and *S. tenue* Ivanov, but other characters do not agree.

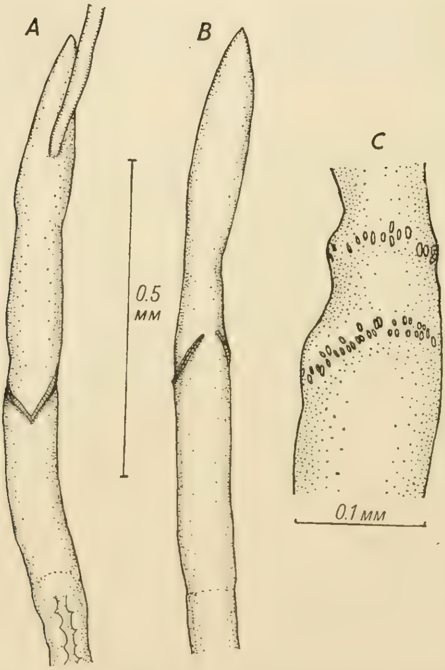


Fig. C133. *Siboglinum debile*: *A*, *B* – anterior end of animal, ventral and dorsal views; *C* – girdle. (After Southward, 1961b.)

"It is possible that these unringed tubes are merely the anterior ends of some more normal tubes, but the sample in which they occur contains a large number of specimens of different species in various tubes, and none of the animals are like those described above as *S. debile*."

Material: 20 fragments of tube, eight occupied.

Locality: Java Sea: *Siboga* Station 212 (5°54′S 120°19′E).

Depth: 462 m.]

[28. *Siboglinum timorense* Southward (Fig. D133)

Southward 1961b: 8–9, 21, Fig. 4.

This is another species of the *Siboga* material, originally included in *S. weberi*. The following description is by Southward (1961b), by kind permission of the author and the publisher, E. J. Brill.

"Seven of the tube fragments are in alcohol but have dried out at some time so that details of their contents cannot be distinguished. The other two are mounted on one of Caullery's slides and together contain the well-preserved anterior half of a species of *Siboglinum*.

"The two mounted fragments contain parts of an animal totalling 30 mm with a coiled tentacle 4·4 mm long (this is the specimen on which Caullery's Fig. 2 was based). The tentacle is very thick, contracted, and provided with a band of fine pinnules (Fig. D133*D*). This band is apparently five to seven pinnules in width for most of its length, and each pinnule is about 70μ long and only 5μ in diameter. The tentacle is joined to the protosoma at the bottom of a slight depression. The cephalic lobe is rather long and its anterior end is rounded; there is no pretentacular groove. Between the base of the tentacle and the bridle there are three transverse grooves (Fig. D133*A*, *C*), the second complete one is oblique; it touches the dorsal points of the bridle and probably separates the protosoma and mesosoma. Just in front of the bridle is a short, deep, longitudinal furrow. The bridle itself is a slight ridge crowned by prominent dark keels, which are fused into a point ventrally but just separate dorsally (Fig. D133*A*, *C*). Close behind the bridle there is a broken ring formed of two bands of epidermal glands which are just separate on the ventral side and far apart on the dorsal side. Together the protosoma and mesosoma are 1·43 mm long, with a maximum diameter of 0·23 mm.

"The metameric region of the trunk has about 70 pairs of papillae, on definite ridges separated by a deep ventral sulcus, and the epidermis of these ridges has a distinctly glandular appearance (Fig. D133*A*). The metameric region is 4·25 mm long. The following 15 mm of the preannular region lacks papillae but the last 10 mm bears at least 20 large papillae, irregularly arranged, with a curved bar (adhesive plaque) 20μ long on each. The girdles and the postannular region are missing. Some sections, prepared by Caullery, are from the genital region of this specimen and contain small oocytes.

"The largest fragment of tube is 7 cm long, and the diameter is much the same for all tubes, at between 0·32 and 0·34 mm. One end of the tube is unringed and colourless but the remainder is ornamented with wide greyish brown rings (Fig. D133*B*). The tube wall is thick (30μ) and at the narrow colourless interspaces it is swollen to twice the normal thickness (Fig. D133*B*).

"*S. timorense* is named after the nearest island . . . It is very similar to *S. japonicum* Ivanov, which was described from three incomplete specimens. They are separated by a few rather minor differences, which are: the absence of transverse fibres in the tube of *S. timorense*, together with slight differences in the appearance of the tubes, and an apparent difference in the disposition of the pinnules on the tentacle. The wide band of pinnules in *S. timorense* may have been produced from a narrower band, by contraction of the tentacle. The thickness of the tube wall and its enlargement between the rings is very

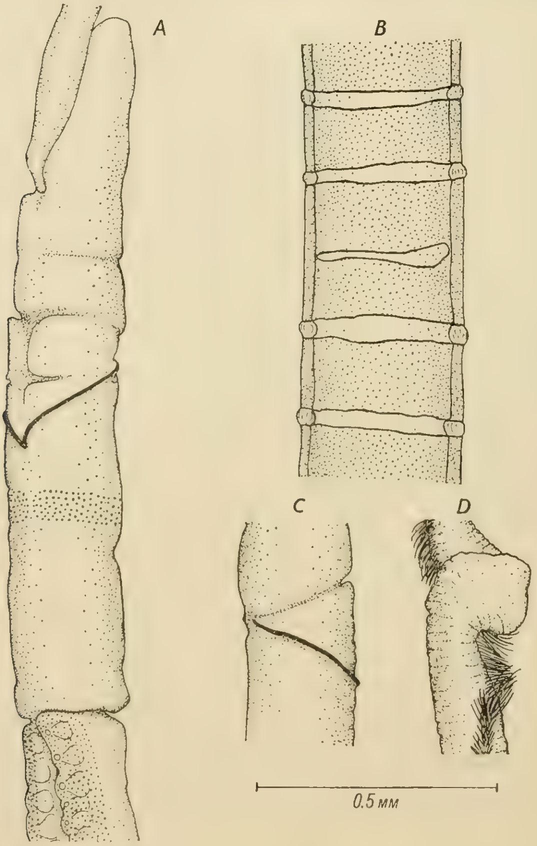


Fig. D133. *Siboglinum timorense*: *A* – anterior end of animal, latero-ventral view; *B* – middle part of tube; *C* – latero-dorsal view of bridle; *D* – part of tentacle. Heavy stipple shows the position of epidermal glands. (After Southward, 1961b.)

characteristic of *S. timorense*. Further material from the Pacific, when available, should help to elucidate the relationship between these species."

Material: nine fragments of tube, seven in alcohol which had dried out, and two mounted on a slide.

Locality: Timor Sea: *Siboga* Station 295 (10°35′S 124°27′E).

Depth: 2050 m.]

[*29. Siboglinum veleronis* Hartman (Fig. E133)

Hartman, 1961: 542–6, Figs. 1–9.

This species was taken in 1960 by M.V. *Velero IV* during the continuing surveys of the offshore faunae of Southern California, conducted by the Allan Hancock Foundation. The description which follows is reproduced from Hartman (1961) by kind permission of the author and of the editors of *Pacific Science*. Slight alterations have been made in the nomenclature to bring it into line with that adopted here and paragraphs have been transposed.

"The animal lies usually some distance within the ringed region of the tube; none has been found partly or wholly out of the tube. With the aid of a stereoscopic microscope the specimen can be seen through the wall of the tube and oriented with respect to the anterior and posterior regions, the tentacle in front directed forward, and the annular band or girdle of toothed platelets marking the approximate middle region of the body. However, dissection is necessary to study the animal more completely. Slitting the tube lengthwise has been found least destructive to the soft-bodied specimen; by using a razor-sharp, finely pointed knife and inserting it into the distal end of the tube, then extending the cut lengthwise for the length of the contained individual, one can then lift it out intact from the shell of the tube.

"The tentacle is less than half as wide as the body and extends forwards for a length nearly two and a half times that of the mesosomal length. Its insertion marks the ventral side of the body as here interpreted, as well as the posterior end of the first body region or protosoma. The three body regions are not sharply separated from one another. The separation between the first and second regions is behind the tentacular insertion and is vaguely indicated by a faint line extending obliquely forward around the body to the mid-dorsum. The second region, or mesosoma, is about four times longer and is separated from the third region, or metasoma, by a transverse groove located just in front of the paired glandular papillae (see Fig. E133*E*, *F*). The third region is much the longest and comprises most of the length of the body.

"The tentacle is extended forward nearly straight in some specimens and is loosely to closely coiled in others, or only a short distal end is coiled. Most of the length has lateral filiform branches or pinnules, inserted in two nearly regular rows along the ventrolateral edge (Fig. E133*D*); those nearest the distal end are more dispersed, whereas those nearer the base (Fig. E133*C*) are closer together and tend to be curled toward the midventral line. Each pinnule is very slender and longer than the tentacle is thick.

"The protosoma or anterior-most region of the body is short, subconical, tapers forward and lacks markings; its posterior end is indicated on the ventral side of the body by the insertion of the tentacle. This fusion is firm, so that the two are not easily severed.

"The second body region, the mesosoma, is considerably longer than the first and is cylindrical in shape; near its anterior end it is obliquely crossed by the bridle or frenulum. It is separated from the third region, or metasoma, by a transverse groove. A pair of cylindrical pores is located at the sides, just behind the frenulum (Fig. E133*F*)." Hartman believed these to be the external apertures of coelomoducts of the mesocoele, but since no such coelomoducts have been seen in any species examined it is more likely that they are the pores of flask-shaped glands – D.B.C.

"The anterior end of the metasoma is characterized by the presence of ventrolateral paired glandular papillae; they are so arranged that the two members of a pair are separated from the successive ones by a space about equal to that of the distance between the brown rings on the tube. It thus seems obvious that these papillar glands are directly concerned with tube secretion. This region is followed by the much longer gonadal region, characterized by sparsely and irregular dispersed epithelial papillae. About halfway along the length of the body two transverse series of toothed platelets indicate the position of the annular region . . . The annulae are of particular interest because they bear hard chitinized platelets in transverse series. Those of the anterior row are incomplete and number about 38, while those in the posterior row are more numerous, numbering about 44. All the toothed platelets are of one kind and terminate distally in a single row of denticles (Fig. E133*H*), numbering 9–13. Each toothed bristle is distally recurved so that the teeth of successive bristles tend to overlap. Seen from the end the the denticles form an arcuate row (Fig. E133*J*). The basal or embedded stems are not chitinized but taper rapidly to very tenuous strands, and are so prolonged that all those of one transverse series are brought together as a fascicle and carried obliquely forward to attach to the body wall. They may function to anchor the animal within the tube at selected places.

"An entire animal measures 15 mm long to the annular region, which is near the middle, making the total length about 30 mm. The body is nearly uniform in width but is widest in the mesosomal region where it measures 0·065 mm; the postannular region gradually becomes slenderer and tapers posteriorly. The tentacle is less than half as wide as the body and extends forwards for a length nearly two and a half times that of the mesosomal length.

"Individual tubes measure 50–65 mm long by 0·13 mm across. Others are longer or narrower, having a length to width ratio of 450—720 : 1. Each tube is usually slender cylindrical, pale to dark straw-coloured and crossed by alternating dark brown rings and pale bands (interspaces). The brown rings are typically paired (Fig. E133*B*), so that both of a pair are nearly twice as long as one pale interspace. An occasional irregularity in this pattern results when the two dark rings are so close together as to appear fused, or are incomplete on one side to form a broader than usual, incomplete, pale interspace. The greater length of the tube is crossed by these alternating cross bars; only the distal anterior and posterior ends (Fig. E133*A*) are pale and usually collapsed.

"*S. veleronis* was recovered from a quantitative sample covering a surface area less than half a square metre. The animals contained in the mud, without tubes, weighed about 6·4 g (moist weight)." The haul included more than 428 specimens of more than 30 species, of which *S. veleronis* accounted for more than 100 specimens, 22 species of polychaetes for more than 200 specimens and various molluscs for most of the rest.

Material: more than a hundred specimens.

Locality: off the coast of Southern California, *Velero IV* station 7049: the axis of La Jolla canyon near its convergence with the San Diego trench (32°49′37″N 117°35′12″W).

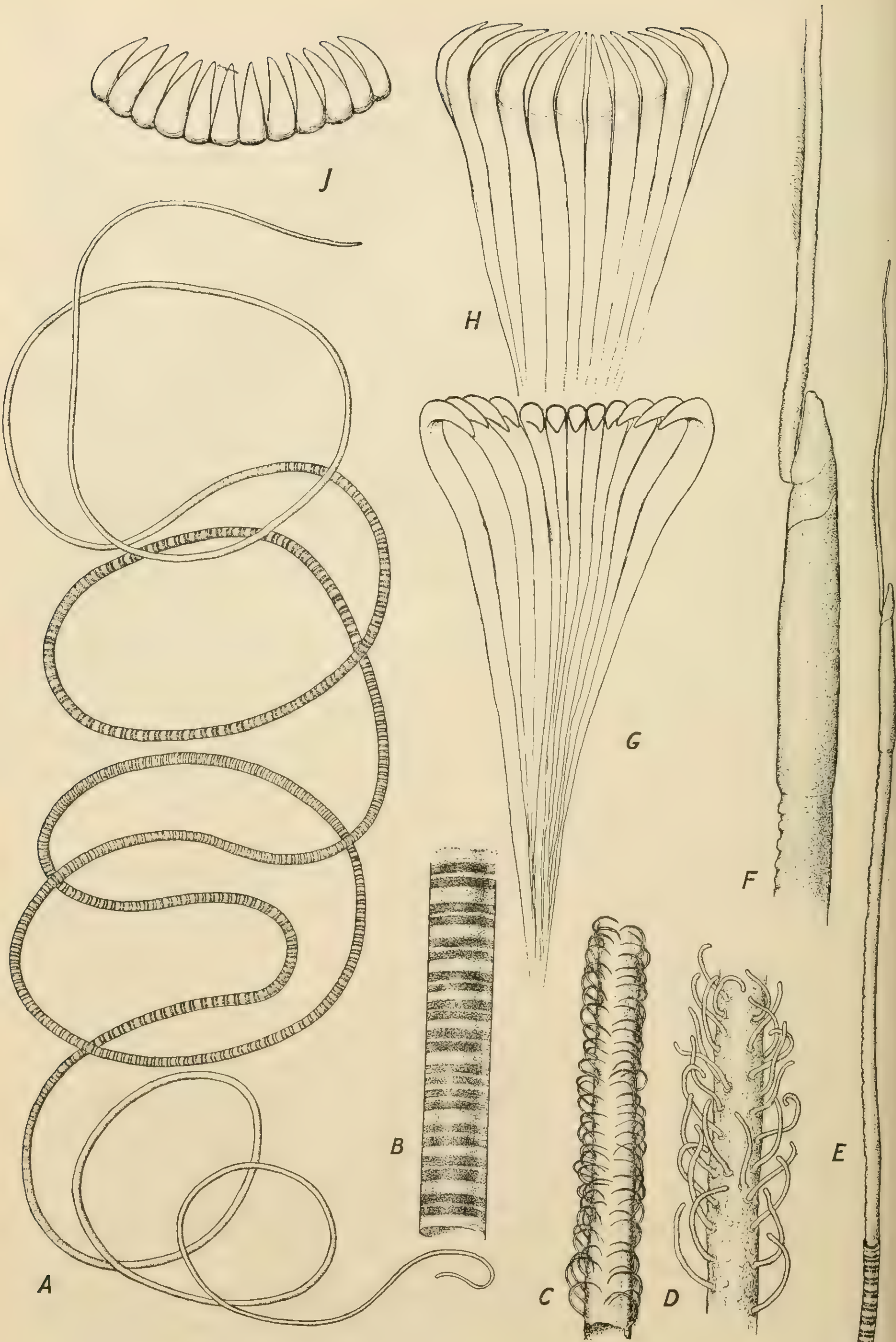
Depth: 976 m.

Substratum: grey sand and green mud.]

[*30. Siboglinum subligatum* sp. nov. Ivanov (Figs. AA133–DD133)

I took this species, which inhabits a characteristic whitish tube, on 21st December, 1960, in the trawl on board R.V. *Vityaz*', in the western part of the Indian Ocean in the area of the Cargados Carajos Islands (north of Mauritius). The material was generally in a good condition, allowing an unusually thorough investigation of the external morphology of the animal, and embryos were found in some of the tubes.

The mesosoma, as a rule, reaches a breadth of 0·2 mm. The fore-part of the body, sharply delimited from the metasoma, is greatly elongated, being eight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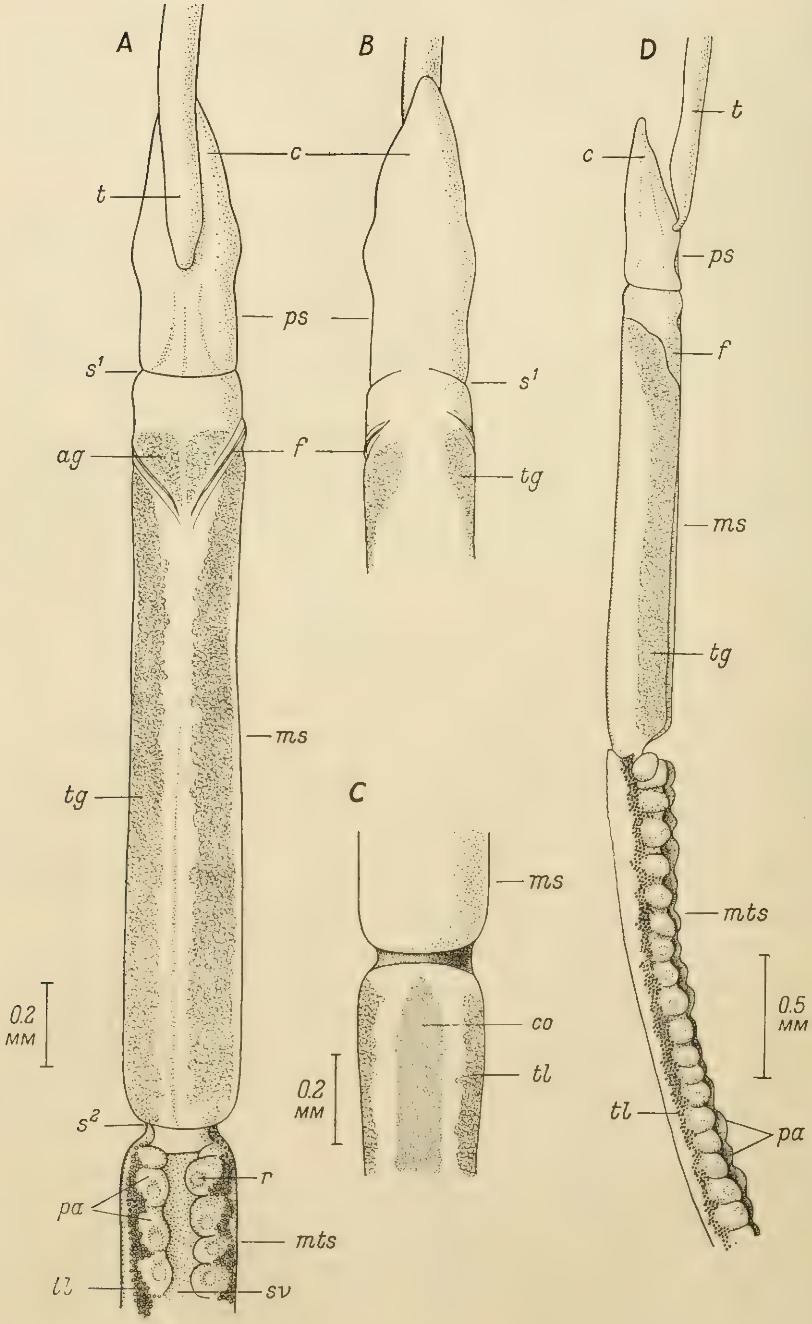
to ten times as long as broad. The boundary between the protosoma and mesosoma is a simple annular groove lying a little in front of the bridle. The comparatively short protosoma is cylindrical. The large conical cephalic lobe is pointed at the tip and is directed straight forward. The point of attachment of the tentacle lies a little nearer to the hind edge of the protosoma than to the tip of the cephalic lobe (Fig. AA133*A*, *D*).

The tentacle is moderately long but rather thick, often attaining a diameter of 0·1 mm, though it tapers gradually towards the end. In all individuals it seems to be in a state of contraction, though its surface almost always lacks wrinkles. There are no pinnules. It is most characteristic that the tentacle shows no tendency to coil into a corkscrew, such as we find in so many species of *Siboglinum.*

The bridle is found at the front end of the mesosoma. Its delicate keels, lying on narrow epidermal ridges, are simple and colourless. There is a broad gap between their dorsal ends, and the ventral ends gradually taper but do not meet (Fig. AA133*A*, *B*). On the ventral side of the mesosoma, between the ridges of the bridle and a little in front of them, the integument forms two small triangular glandular areas with clearly marked borders (Fig. AA133*A*). Behind the bridle and adjacent to it on the lateral surfaces of the body, begin the pair of broad longitudinal glandular ribbons of the mesosoma, which are whitish in reflected and opaque in transmitted light. They then turn onto the ventral side of the body and extend backwards parallel to one another to the hind end of the mesosoma (Fig. AA133). When they are sufficiently large they give the impression of consisting of large flat glandular epidermal cells filled with a small-grained secretion. Sometimes the nucleus may be observed in these cells as a small light area. The dorsal surface of the mesosoma has no special features.

The boundary between the mesosoma and metasoma is marked by a characteristic wasp-waist, from which the species is named (Lat. *subligatus*—bound or laced in). The mesosoma narrows suddenly on the ventral side, forming a sort of short stalk which joins it to the metasoma and which is particularly well seen when the animal is viewed from the side (Fig. AA133*D*).

Fig. E133. *Siboglinum veleronis. A* – entire tube containing animal, × 22; *B* – part of tube showing paired dark alternating with pale bands, × 89; *C* – part of tentacle from near base, showing pinnules curled toward midventrum, × 228; *D* – another part of tentacle from another invidual, with pinnules nearer tip of tentacle, × 228; *E* – animal with tube partly dissected away, in left lateral view, × 25·5; *F* – anterior regions, including protosoma, mesosoma with bridle and part of glandular metasoma, in left lateral view, × 83; *G* – a toothed platelet from the annular zone, seen from the denticled side, × 5,720, *H* – one seen from the opposite side, and *J* – from the top showing arcuate arrangement of denticles. (After Hartman 1961.)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The metameric section of the metasoma is very long and the moderately broad dorsal ciliated band begins at its front border. The plaqueless metameric papillae are well differentiated. They are more or less rounded, similar in size and closely pressed together (Fig. AA133*D*). A single pyriform gland can be made out inside each papilla, and on the surface of the papilla a small clear ring represents the rosette of gland cells surrounding the external pore of the pyriform gland (Fig. AA133*A*, *D*). A tract of glandular epidermis, whitish in reflected and opaque in transmitted light, extends along the bases of the papillae on the external side of each row (Fig. AA133*A*, *C*, *D*). Towards the hind end of the metameric region the papillae become considerably larger and sparser. In general the number of metameric papillae lies between 75 and 105 pairs.

The nonmetameric part of the trunk is several times longer than the metameric section and characterized by the unusually strong development of the granular gland cells of the epidermis. In reflected light this part stands out because of its intense whiteness, which in turn depends on the granular secretion of the glands. The lateral glandular tracts of the metameric region extend, gradually broadening out, far backwards along the whole or almost the whole length of the pre-annular region. The glandular epithelium in places covers almost the whole surface of the trunk, which lacks gland cells only along narrow mid-dorsal and mid-ventral strips (Fig. BB133*A*).

There is no definite zone of thickened papillae, but three to five large conical papillae are present immediately in front of the girdles. They do not bear plaques and are arranged in a single row along the ventral side close to each other (Figs. BB133*B*, CC133*A*).

In all the specimens which have been investigated I have found two girdles. Both are broken by a wide gap on the ventral side only (Figs. BB133*B*, CC133*A*). Behind the girdles there is always a conical ventral papilla which likewise bears no plaque (Figs. BB133*B*, CC133*A*). The yellowish toothed platelets are arranged on the surface of the more or less broad protuberant ridges of the girdles in two or sometimes in three or four

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Fig. AA133. *Siboglinum subligatum*: *A* – fore-part of the body in ventral view; *B* – protosoma from the dorsal side; *C* – region where the meso- and metasoma meet, in dorsal view; *D* – fore-part of the body from the left side.

ag – ventral glandular region of the mesosoma; *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *ps* – protosoma; *r* – rosette of gland cells around the pore of a pyriform gland; s^1 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and metasoma; *sv* – ventral sulcus; *t* – tentacle; *tg* – glandular ribbon of the mesosoma; *tl* – lateral glandular tract of the metasoma.

irregular rows (Fig. BB133*C*). The platelets are much narrower at the front end, and their anterior section, bearing the anterior group of teeth, is only a quarter the length and half the breadth of the hind section (Fig. BB133*D*). The toothed platelets are 14–16μ long.

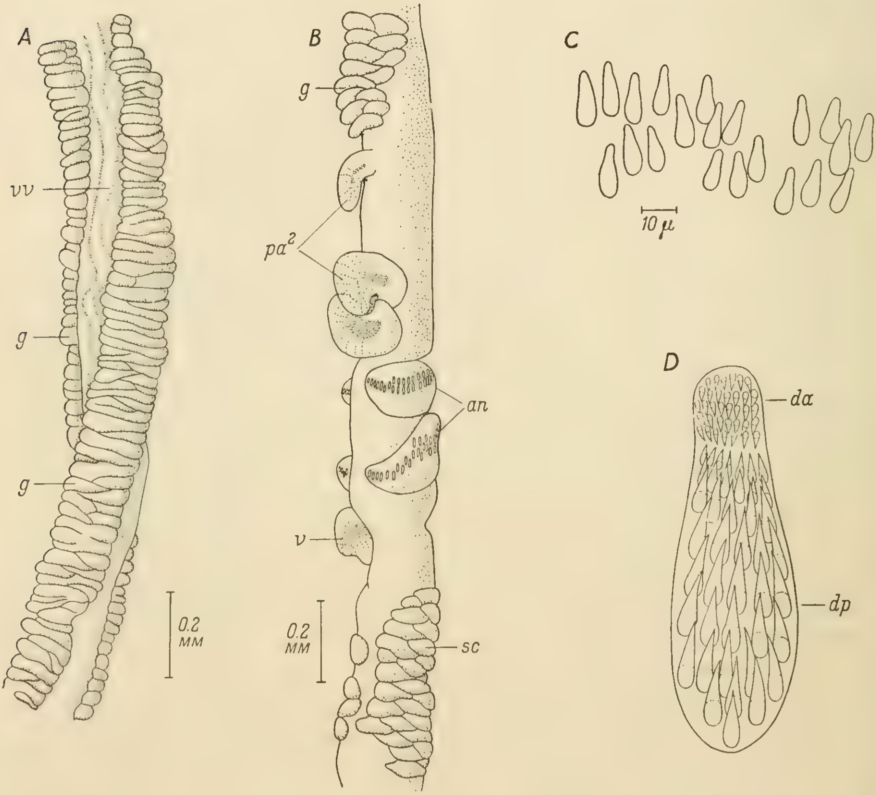


Fig. BB133. *Siboglinum subligatum*: *A* – part of the nonmetameric region of the trunk, from the ventral side and a little to the left; *B* – region of the girdles from the left; *C* – part of a girdle; *D* – toothed platelet.
an – girdles; *da* – anterior group of teeth; *dp* – posterior group of teeth; *g* – glandular portion of integument; *pa*² – papillae in front of the girdles; *sc* – dorsal glandular shield; *v* – ventral papilla behind the girdles; *vv* – ventral blood vessel seen by transparency.

The postannular region begins without the usual stalk-like waist. Single large conical plaqueless ventral papillae are spaced along its whole length at more or less equal and rather large intervals (Fig. CC133*B*). The epidermis near each papilla is distinguished by the rich whiteness (in reflected light) of its granular gland cells like those of the preannular region of the trunk.

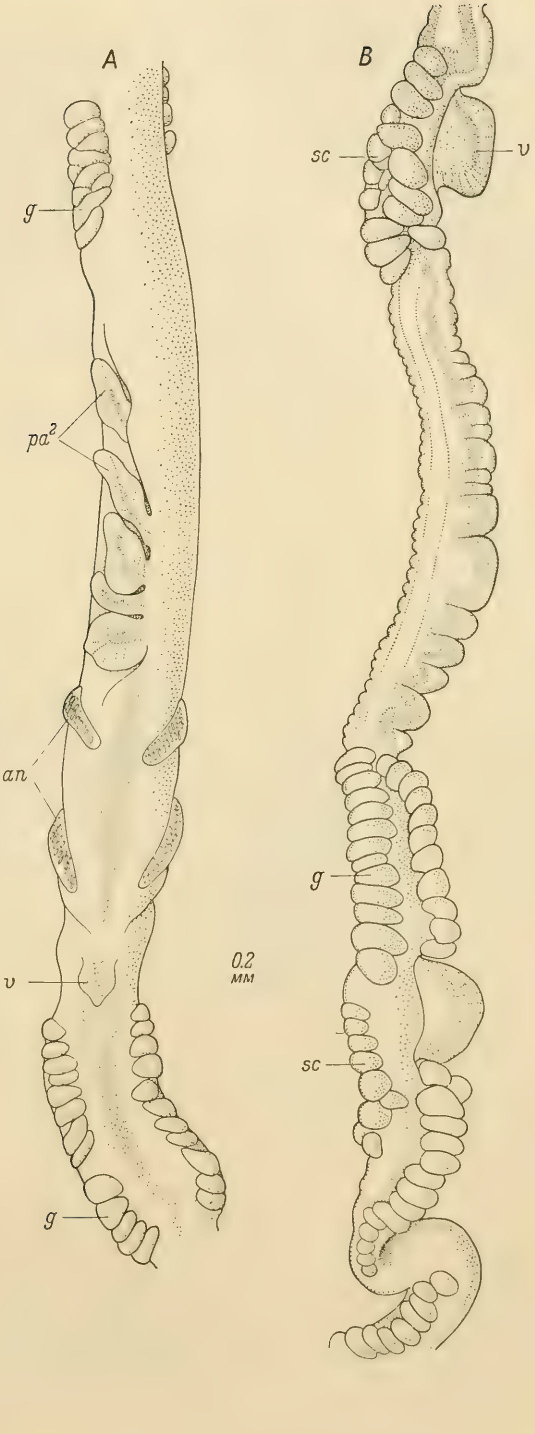


Fig. CC133. *Siboglinum subligatum*: *A* – region of the girdles in ventral view; *B* – part of the postannular region.
an – girdles; *g* – glandular portion of integument; *pa*² – papillae in front of the girdles; *sc* – dorsal glandular shield; *v* – ventral papillae.

On the dorsal side of the body these cells form a sort of primitive dorsal shield, but more often they extend·right round onto the ventral side as well (Fig. CC133*B*).

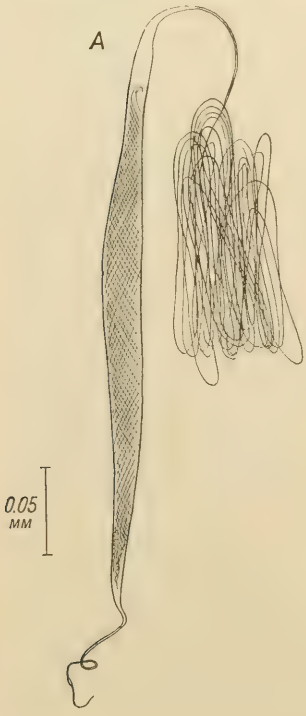
To gain a clear idea of the size and proportions of the various parts of the body I measured 25 individuals. The hind part of the animal, however, was unfortunately missing in most of the animals and only in three individuals was there a more or less complete postannular region. The sizes of the parts of the body vary as follows (dimensions given in millimetres):

Length of tentacle	4·5 – 8·8
Length of the fore-part of the body	1·8 – 2·9
Breadth of the mesosoma	0·16– 0·27
Length of the metameric part	8·0 –12·5
Length of the preannular section	up to 84
Length of the postannular part	probably not less than 30.

The overall length of the body, including the tentacle, may reach 125 mm.

The spermatophores of *Siboglinum subligatum* are very characteristic. They are very thin and shaped like elongated spindles or cigars. One end of the spermatophore is drawn out into the base of the filament, the other forms a very thin and rather long "tail-piece". The sperm are arranged parallel to one another (Fig. DD133*A*). The spermatophores are 0·3–0·35 mm long, not counting the "tail-piece", and the greatest breadth is 0·02–0·03 mm.

The white lustrous flexible thick-walled tube is unsegmented and ringed. The membranous transparent front end of the tube has



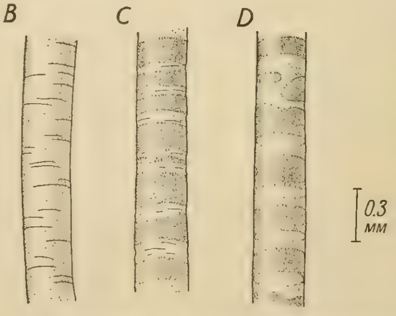


Fig. DD133. *Siboglinum subligatum*: *A* – spermatophore; *B–D* – successive parts of the tube.

superficial transverse wrinkles and folds (Fig. DD133*B*). The rings are greyish or, in transmitted light, brownish. They are more or less regular and their length varies between a third and a half of the diameter of the tube (Fig. DD133*C*, *D*). One often encounters irregularities in their development. The longest tube I have seen was 200 mm long. The diameter of the tube near the front end varies from 0·25 to 0·33 mm.

S. subligatum belongs to the group of species typified by *S. taeniaphorum*, which form a discrete and increasing group within the genus. The species are characterized by the following features:

1. Longitudinal glandular ribbons of the mesosoma and anterior part of the trunk;
2. A pair of triangular ventral glandular areas in front of the bridle;
3. Two or three girdles lying close together;
4. The very small size of the anterior group of teeth on the toothed platelets;
5. The characteristic whitish tube which for the most part is ringed and thick-walled.

Besides *S. taeniaphorum* and *S. subligatum* this group of species includes *S. atlanticum*, *S. concinnum* sp. nov., *S. lacteum* sp. nov., *S. elongatum* sp. nov. and *S. arabicum* sp. nov. Exceptionally great resemblances link *S. subligatum* with the last of these species, which also lacks pinnules. It is distinguished from *S. arabicum*, however, by the very clear boundary between the protosoma and mesosoma, the continuity and breadth of the glandular ribbons of the mesosoma, and in particular by the stalk-like waist between the fore-part of the body and the trunk, and also by a series of minor features, such as the size of the toothed platelets, the strong development of the epidermal glands of the trunk and some features of the tube.

Material: 75 tubes with animals (some fragmentary) and many empty tubes, besides 18 tubes with embryos.

Locality: *Vityaz'* station 4652 (31st cruise): the western part of the Indian Ocean to the north of the Cargados Carajos Islands (North of Mauritius) on the western slopes of the Nazareth Bank (*c.* 18°S 60°E).

Depth: 1740 m.]

[*31. Siboglinum concinnum* sp. nov. Ivanov (Fig. EE133)

In March 1960, while working on an oceanographical expedition on board R.V. *Vityaz'*, a little off the East African coast, I found one small white ringed tube. In it was a well-preserved front half of the body of a nondescript species of *Siboglinum*. I have named this species *Siboglinum concinnum* (Lat. *concinnus*—pleasing, shapely, elegant).

The fore-part of the body is very long and cylindrical, with a length to breadth ratio of 9 : 1. The protosoma is bounded behind by a distinct annular groove, farther from the bridle than in *S. subligatum* sp. nov. (p. 281). It is noticeably narrower than the mesosoma and rather short, passing imperceptibly into the cephalic lobe in front. The latter is very small, conical and pointed at the tip. The tentacle is attached rather nearer to the hind end of the protosoma than to the tip of the cephalic lobe (Fig. EE133*A*, *B*). It is thin and moderately long, and sparsely furnished with pinnules (175μ long) arranged in one row. The proximal part of the tentacle lacks pinnules. A rather thick transparent cuticle can be seen, under the microscope, covering the tentacle (Fig. EE133*C*).

The bridle is situated near the front edge of the mesosoma. Its clear transparent but comparatively thick keels lie on slightly protuberant ridges. It is remarkable that the ventral ends of the keels are no thicker than the rest; there is a small gap between them. The pair of ventral glandular patches in front of the bridle look like low pear-shaped cushions, separated in the mid-line only by a narrow longitudinal furrow. Behind the bridle are the whitish longitudinal glandular ribbons of the mesosoma. They are rather broad and begin on the lateral surfaces of the body just behind the ridges of the bridle, running at first parallel to the latter onto the ventral side, then extending backwards to the hind end of the mesosoma. At the very hind end each ribbon makes a short bend on the ventral side (Fig. EE133*A*, B, *D*). The boundary between the mesosoma and metasoma has no waist but is a simple annular groove.

The dorsal ciliated band of the metasoma is well developed. The ventral sulcus is narrow. The metameric papillae are rounded and densely packed together. The very anterior ones are a little larger, and towards the hind end of the metameric section they become, as usual, a little larger once more. There are about 70 pairs. A longitudinal band of glandular cells containing a granular secretion runs along the external side of the bases of the papillae on each side. In reflected light these bands appear light and, in transmitted light, opaque (Fig. EE133*D*).

The rest of the body is unknown.

The broken fragment of the animal is 32 mm long, of which the tentacle accounts for 6·9 mm, the fore-part of the body 2·1 mm and the metameric section of the trunk 9 mm. The mesosoma is *c.* 0·2 mm in diameter.

The tube of *S. concinnum* is very like that of *S. subligatum*. Its surface is

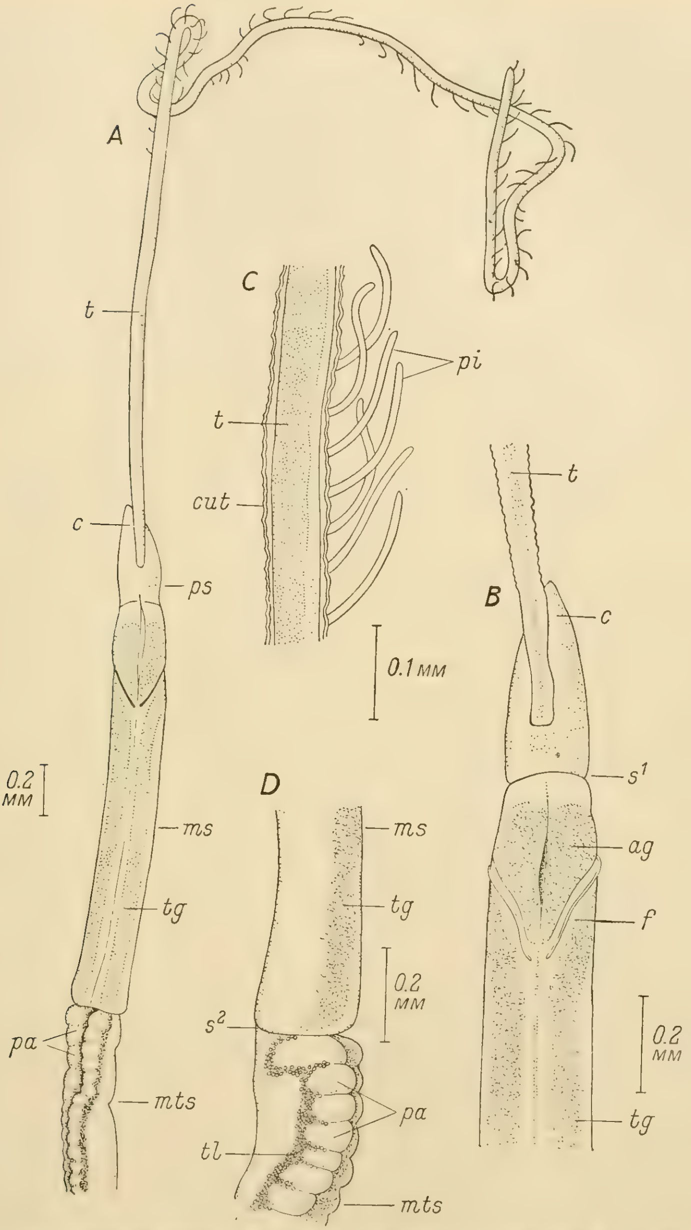


Fig. EE133. *Siboglinum concinnum*: *A* – fore-part of the body in ventral view; *B* – a portion of the fore-part in ventral view; *C* – part of the tentacle; *D* – region where the meso- and metasoma meet. *ag* – ventral glandular part of the mesosoma; *c* – cephalic lobe; *cut* – cuticle; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and metasoma; *t* – tentacle; *tg* – glandular ribbon of mesosoma; *tl* – lateral glandular tract of metasoma.

smooth and lustrous, its colour just perceptibly yellowish. The limp part of the tube lacks wrinkles, but in the anterior part of the tube there are fine circular ridges overlying superficial fibres. In the middle part, the tube is thick-walled (30μ) and rather tough. The rings are more or less regular, rather long and light greyish-brown. The one incomplete tube which we possess is 80 mm long and 0·3 mm in diameter near the front end.

Amongst the related "ribbon-bearing" or "taeniaphorous" species, *S. concinnum* is nearest to *S. taeniaphorum* and *S. atlanticum*, with which it is linked by the possession of a single row of pinnules. It is distinguished from these two species, however, by the pear-shaped outline of the glandular areas of the mesosoma and particularly by the unthickened ventral ends of the keels of the bridle.

It is interesting to compare the longitudinal glandular ribbons of mesosoma of these three species. In *S. atlanticum* they are clearly chopped up into metameric sections which thus represent discrete areas of gland cells. In *S. taeniaphorum* the ribbons present only traces of metamerism (and sometimes do not reach the hind end of the mesosoma). Finally, in *S. concinnum* they are continuous and homogeneous. If we bring the other taeniaphorous species into the comparison as well, we may note that in *S. subligatum* sp. nov. the longitudinal ribbons of the mesosoma are also homogeneous, and in *S. arabicum* sp. nov. they broaden out at the hind end and break up into small separate parts (isolated cells even) and do not reach the hind end of the mesosoma.

Material: one tube with front half of an animal.

Locality: *Vityaz*' station 4680 (31st cruise): Indian Ocean near the coast of East Africa to the east of Mafia Island, near Zanzibar.

Depth: 802 m.]

[*32. Siboglinum arabicum* sp. nov. Ivanov (Fig. FF133)

Amongst the washings from a muddy bottom, brought up with bottom-sampler or grab from a depth of 2385 m in the Arabian Sea at the mouth of the Gulf of Aden in April 1960 (31st cruise of R.V *Vityaz*') I found one transparent tube of *Siboglinum*. It contained an incomplete animal belonging to the group of species possessing a pair of glandular mesosomal ribbons, but it was clearly distinguished from all the known "taeniaphorous" or "ribbon-bearing" species.

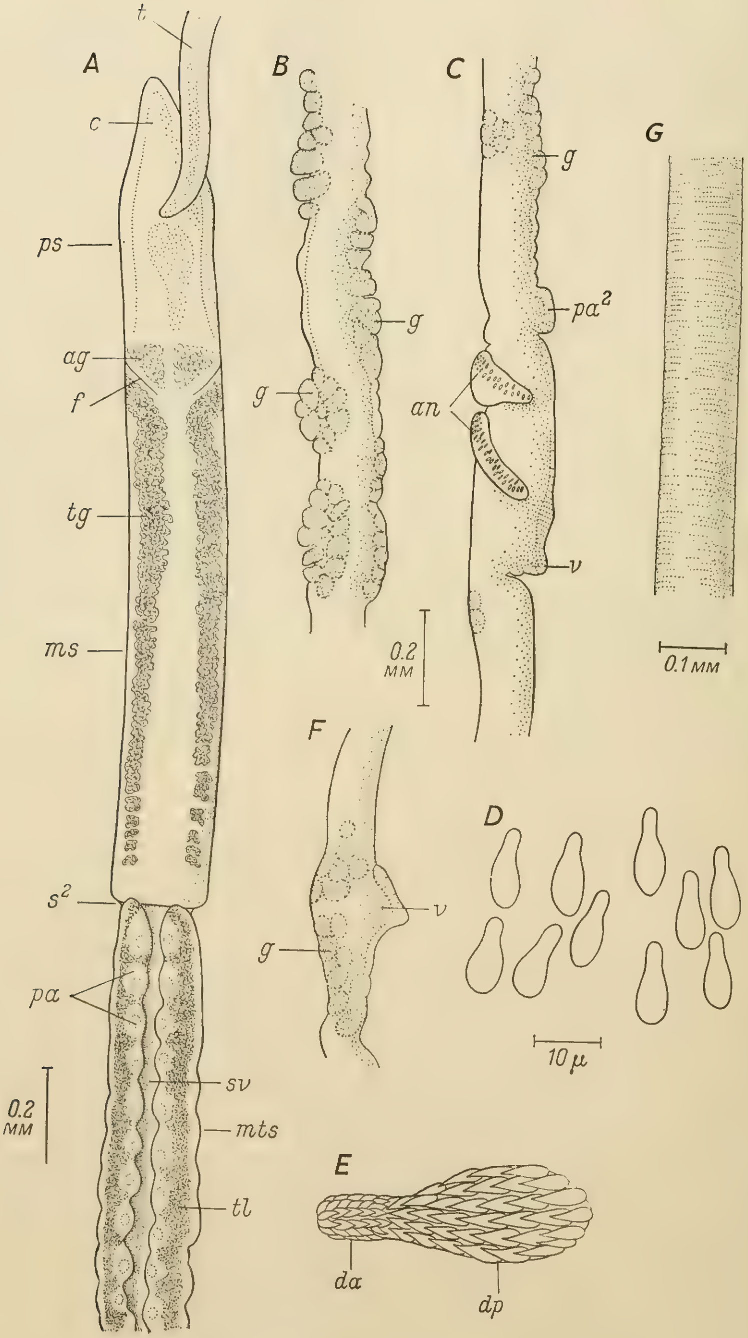
The fore-part of the body of *S. arabicum* is cylindrical and eight and half times as long as broad (Fig. FF133*A*). The distance from the front end to the bridle is half that from the bridle to the hind end of the fore-part. No transverse groove can be observed in front of the bridle, that is to say, there is no external boundary between the protosoma and mesosoma. The protosoma runs imperceptibly into the conical cephalic lobe which is pointed at the tip (Fig. FF133*A*). The tentacle is attached at the base of the cephalic lobe. It is long and rather delicate and along its whole length I can find no trace of pinnules. Its surface is smooth (Fig. FF133*A*).

The keels of the bridle are very delicate and hardly noticeable. Both dorsally and ventrally their ends taper and are broadly separated (Fig. FF133*A*). Two smaller triangular glandular patches lie in front of the bridle on the ventral side. The longitudinal glandular ribbons of the mesosoma are well developed. They begin on the lateral surface of the mesosoma where they run obliquely back, parallel to the keels of the bridle. Then they approach one another on the ventral side and run back parallel to one another to the hind end of the mesosoma, gradually tapering as they do so. At the hind end the glandular ribbons break up into a series of small areas, which probably consist of separate gland cells (Fig. FF133*A*). The ribbons do not reach as far as the front edge of the metasoma. In reflected light they appear whitish. Oblique muscle fibres of the mesosoma can be distinguished between them through the integument.

The metameric part of the trunk is rather narrower than the mesosoma. The ventral sulcus is rather deep and the paired papillae on either side of it are crowded so tightly together that they almost merge into one another. Each of them encloses a single clear pyriform gland (Fig. FF133*A*). Towards the hind end of the metameric region the papillae become larger. In each row they number about 65 in all. Alongside each row, on the lateral surface of the trunk, extends a very broad glandular tract which is whitish in reflected and opaque in transmitted light (Fig. FF133*A*). The nonmetameric region has numerous irregular accumulations of large protuberant gland cells containing a granular secretion (Fig. FF133*B* – *g*).

There are two girdles, both widely broken on the ventral side. Their protuberant ridges bear double rows of toothed platelets, 12–13μ long (Fig. FF133*C*, *D*). Large plaqueless ventral papillae lie immediately in front of and behind the girdles. The waist between the preannular and postannular regions of the trunk is represented by a deep transverse groove on the ventral side (Fig. FF133*C*). The toothed platelets are bottle-shaped. Their front section, bearing the anterior group of teeth, is narrow like the neck of a bottle; it is only a third the width and a quarter the length of the rest of the platelet (Fig. FF133*D*, *E*).

The postannular region is thin and probably long, and plaqueless conical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papillae lie at even intervals along its ventral side (Fig. FF133*F*). Numerous epidermal gland cells are found near each papilla, especially on the dorsal surface of the trunk where they form a primitive dorsal glandular shield (Fig. FF133*F*). These cells are very like the epidermal gland cells of the preannular region.

No sexual products have been observed in this animal.

The tentacle is 11 mm long, the fore-part of the body 1·65 mm long and the mesosoma 0·2 mm broad. The metameric part is 6·5 mm long and the whole preannular region 20 mm long. The preserved part of the postannular region is 6 mm long. The whole animal, including the tentacle, is about 39 mm long though, since a considerable part of the postannular region seems to be missing, the real length must be greater.

The torn-off tube from which the animal was extracted is 95 mm long and 0·13 mm in diameter. The tube is very soft and elastic, comparatively colourless transparent and structureless, lacking both rings and segmentation. Its front part is wrinkled with soft transverse ridges (Fig. FF133*G*).

S. arabicum is like *S. subligatum* in lacking pinnules, but it is distinguished from it by the lack of a waist between the mesosoma and metasoma, by the rather greater development of the glandular patches of epidermis and by the unringed tube.

Material: One tube containing an animal.

Locality: *Vityaz*' station 4726 (31st cruise): Indian Ocean, Arabian Sea at the entrance to the Gulf of Aden, to the northwest of Socotra Island.

Substratum: brown-grey mud.

Depth: 2385 m.]

[*33. Siboglinum silone* sp. nov. Ivanov (Figs. GG133–LL133)

This interesting species was first found in the Arabian Sea to the west of the South Indian coast, together with *Diplobrachia southwardae* sp. nov. and *Lamellisabella minuta* sp. nov. Later it was also found in the Gulf of Aden. I have had four complete specimens at my disposal, together with seven

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Fig. FF133. *Siboglinum arabicum*: *A* – fore-part of the body in ventral view; *B* – nonmetameric part of the trunk; *C* – region of the girdles from the right side; *D* – part of a girdle; *E* – toothed platelet; *F* – a postannular ventral papilla from the right side; *G* – tube.
ag – ventral glandular region of the mesosoma; *an* – girdles; *c* – cephalic lobe; *da* – anterior group of teeth; *dp* – posterior group of teeth; *f* – bridle; *g* – glandular portion of integument; *ms* – mesosoma; *mts* – metasoma; *pa* – metameric papillae; *pa*^{2} – papilla in front of the girdles; *ps* – protosoma; *s*^{2} – groove between the mesosoma and metasoma; *sv* – ventral sulcus; *t* – tentacle; *tl* – lateral glandular tract of metasoma; *tg* – glandular ribbon of the mesosoma; *v* – ventral papilla.

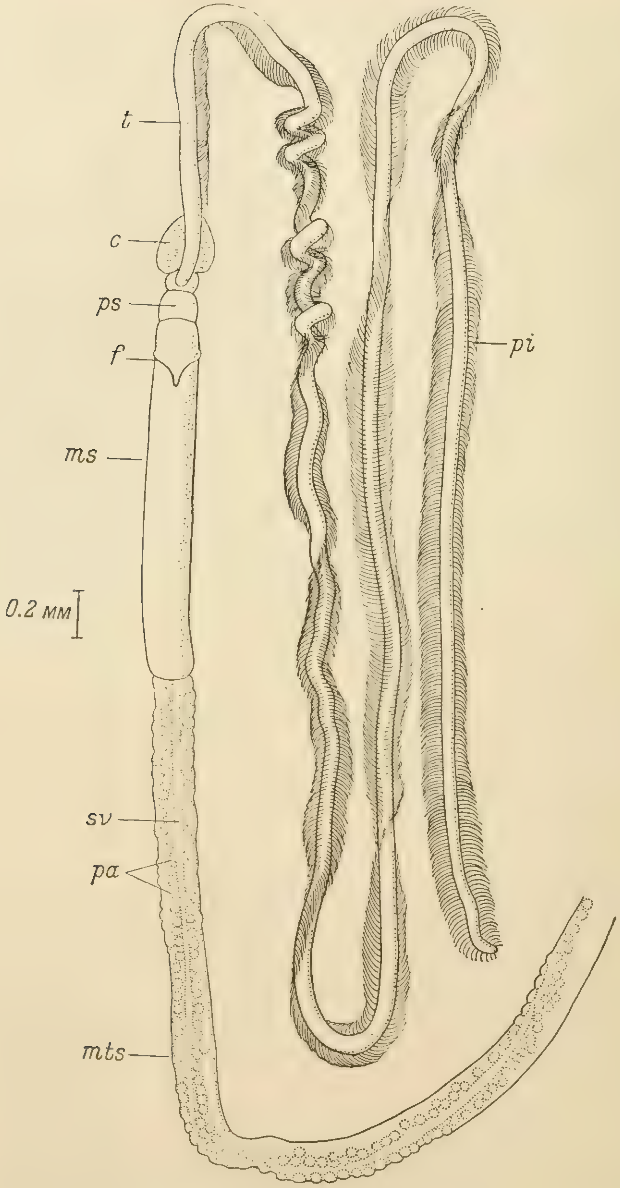


Fig. GG133. *Siboglinum silone*: Fore-part of the body seen from the ventral side. *c* – cephalic lobe; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; *sv* – ventral sulcus; *t* – tentacle.

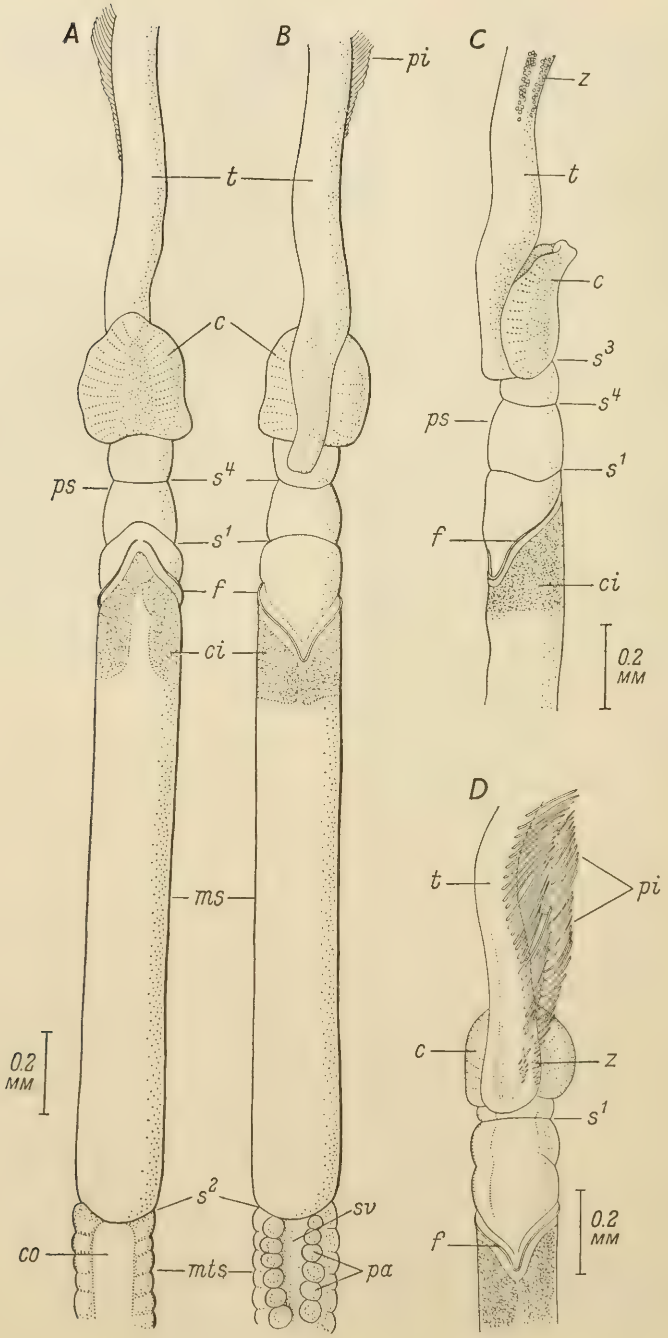
consisting of the greater part of the body, besides five small scraps of tubes containing parts of animals. I have named this new species *Siboglinum silone* from its most characteristic feature—the broad flattened cephalic lobe (Lat. *silonis*—flat-nosed, pug-nosed).

The fore-part of the body is long and cylindrical and the protosoma is clearly delimited. Its length to breadth ratio is usually 10 or 11 : 1 (Figs. GG133, HH133*A*, *B*), but in one specimen it was only 7 : 1.

The short protosoma is considerably narrower than the mesosoma, and bears a sharp post-tentacular groove (Fig. HH133*A–C*). The cephalic lobe, limited behind by a clear pretentacular groove, has an extraordinary shape. It is dorso-ventrally flattened, very broad and leaf-shaped. It hardly tapers to a proper tip and is sometimes even disc-like. In many individuals it is as broad as long and exceeds twice the diameter of the protosoma. The epidermis, particularly on the lateral expansions of the cephalic lobe, consists of very tall large cells of a glandular nature (Fig. HH133). The tentacle is long, but when it is contracted its proximal half is thickened (Figs. GG133, HH133*B–D*). The delicate pinnules, 150–350μ long (obviously they can expand and contract), are arranged in two dense rows along the whole length of the tentacle (Figs. GG133, JJ133*A*); but in a few individuals the proximal part of the tentacle has no pinnules (Fig. HH133*A–C*). The zone of formation of the pinnules lies on the ventral surface of the tentacle to the left at its very base (Fig. HH133*D*). Pinnule rudiments and small pinnules are arranged at first in two parallel bands each formed of three dense parallel rows (Fig. JJ133*B*). Then, as the pinnules grow longer and differentiate, each band opens out into a single longitudinal row (Fig. HH133*D*). The afferent and efferent capillaries are particularly visible in this species.

The anterior border of the mesosoma is an annular groove which runs straight across the ventral side and runs forward in an arch on the dorsal side (Fig. HH133*B*). The bridle is found in the front part of the mesosoma. Its keels are yellowish, their ventral ends fuse and their dorsal ends are separated by a small gap (Fig. HH133). Behind the bridle the epidermis of the mesosoma forms a rather large glandular area—a kind of broad glandular girdle, interrupted or almost interrupted on the dorsal side (Fig. HH133). The rest of the mesosoma has no outstanding peculiarities. In the coelom of the mesosoma, behind the bridle, there are numerous small round flask-shaped glands. The boundary between the mesosoma and metasoma is a simple groove (Fig. HH133*A*, *B*). In the male a pair of large rounded genital papillae lie on the ventral side in this region.

The anterior part of the preannular region—the metameric section of the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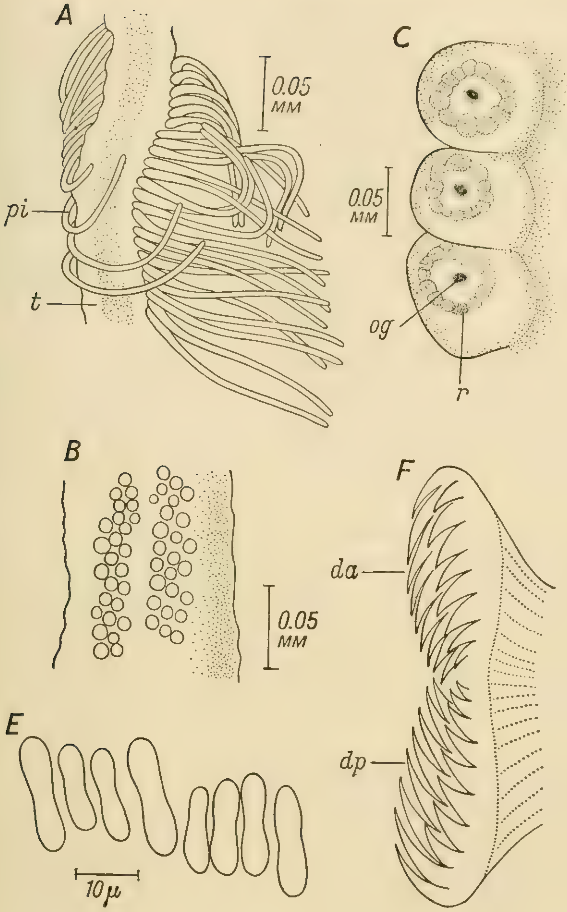


Fig. JJ133. *Siboglinum silone*: *A* – part of the tentacle; *B* – arrangement of the beginning of the pinnules in the basal part of the tentacle; *C* – three papillae of the metameric part of the trunk, in ventral view; *D* – the region of the girdles in ventral view; *E* – part of a girdle; *F* – toothed platelet from the side.
an – girdles; *da* – anterior group of teeth; *dp* – posterior group of teeth; *og* – aperture of a pyriform gland; *pan* – postannular region; *pi* – pinnules; *r* – rosette of gland cells; *t* – tentacle; *v* – ventral papilla.

Fig. HH133. *Siboglinum silone*: *A* – fore-part of the body from the dorsal, *B*, from the ventral, and C, from the left side; *D* – the anterior portion of the fore-part from the ventral side.
c – cephalic lobe; *ci* – glandular girdle; *co* – dorsal ciliated band; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and metasoma; s^3 – pretentacular groove; s^4 – secondary mesosomal groove; *sv* – ventral sulcus; *t* – tentacle; *z* – zone of growing pinnules.

trunk—has a dorsal ciliated band and a narrow ventral sulcus (Fig. HH133*A*, *B*). The adhesive papillae here are round and small, though often they become pressed together and correspondingly change their shape. They are arranged in rather regular rows on either side of the ventral sulcus and have no plaques. I have counted these 'metameric' papillae in seven specimens and found them to vary between 36 and 45 pairs. There is a single pyriform gland in each one. Attentive examination of the surface of the papilla reveals a small pore—the aperture of the canal of the pyriform gland—surrounded by a halo of epidermal gland cells which contain a small-grained secretion (Fig. JJ133*C*).

The nonmetameric region of the preannular section is several times longer than the metameric region. It bears small scattered contracted papillae which in places may be wart-like, and also large longitudinal (along the dorsal side?) bands of glandular epidermis, consisting of big flat cells with a granular secretion.

There are three girdles, the front two lying close together and the hindmost 0·7–2·2 mm behind. Each girdle is formed of a protuberant ridge bearing a single row of toothed platelets. The anterior girdle has a broad gap on the dorsal side, the second on the ventral and the third a narrow gap on both sides of the body. A small median papilla is found behind the last girdle, bearing on its tip a distinct crescent-shaped cuticular plaque (Fig. JJ133*D*).

The yellowish toothed platelets are elongated and have a rather distinct, if slight, constriction in the middle (Fig. JJ133*E*, *F*). The two groups of teeth—anterior and posterior—are equally developed. The platelets are mostly 15--22μ long, but sometimes smaller ones may be encountered 12 or 14μ long.

The postannular section starts with a clearly defined constriction (Fig. JJ133*D*). Its small conical ventral papillae, arranged at regular intervals, bear colourless plaques on their tips. There are no dorsal shields, but instead only a small glandular patch of epidermis opposite each ventral papilla.

Measurement of 11 specimens gave the following results (mm):

Length of tentacle	up to 11
(Length of tentacle when contracted	5 or 4)
Length of the fore-part of the body	0·7–1·57
Breadth of mesosoma	0·2–0·25
Length of preannular section	12–20
Length of postannular section	up to 25

Spermatophores, 300–380μ long, were found in the spermducts of three males. They are cigar-shaped and quite regular in outline. The filament begins with the ribbon-like proximal section shown in the figure (Fig. KK133).

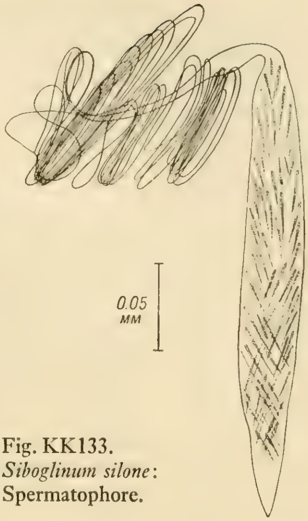


Fig. KK133.
Siboglinum silone:
Spermatophore.

The tube is at first the colour of straw, then brown; it is lustrous thin-walled elastic segmented and ringed. The anterior part is transparent, with clearly defined segments which have fine constrictions and transverse wrinkles between them. Each segment is five or six times as long as the tube is wide (Fig. LL133*A*). The rings appear gradually, first in the hind part of each segment, then over the whole length of the segment. They are brown in colour and very short – no more than a tenth or at the most a fifth of the diameter of the tube. Often the edge of each ring is dense and thick so that the rings appear almost double. Very often, though not invariably, there are numerous irregularities in the development of the rings. The number of rings in one segment may vary from 16 to 40, but is usually within the range 18–25. The first and last rings in a segment are usually longer and thicker than the others (Fig. LL133*B*).

In the middle part of the tube the segments become irregular and the rings longer and thicker. At first they usually appear double (Fig. LL133*E*), then they become single (Fig. LL133*F*), and they frequently become irregular. At the hind end of the tube the rings become shorter (narrower), irregular and sometimes double (Fig. LL133*G*) and finally they fade (Fig. LL133*H*).

S. silone most closely recalls *S. fedotovi.* These two species share the following features: a long mesosoma and small protosoma; a pretentacular groove delimiting the hind end of the cephalic lobe; a bipectinate tentacle; three girdles, two anterior and one farther back; and the strong development of the anterior group of teeth on the comparatively large toothed platelets. In both species the hindmost girdle is broken both dorsally and ventrally. The tubes of *S. silone* and *S. fedotovi* are also very similar, but in the latter species there are less rings per segment.

The possession of a pretentacular groove is a very important character. Besides *S. silone* and *S. fedotovi* this character is shared by *S. ekmani*, *S. pinnulatum*, *S. plumosum* and *S. japonicum.* All these species also possess bipectinate tentacles (at least when it is possible to make out the structure), three girdles and lingulate toothed platelets with strongly developed anterior teeth (this last point has been investigated in only the first two species).

The most distinctive features of *S. silone* are the shape of the cephalic lobe and protosoma and certain peculiarities of the tube.

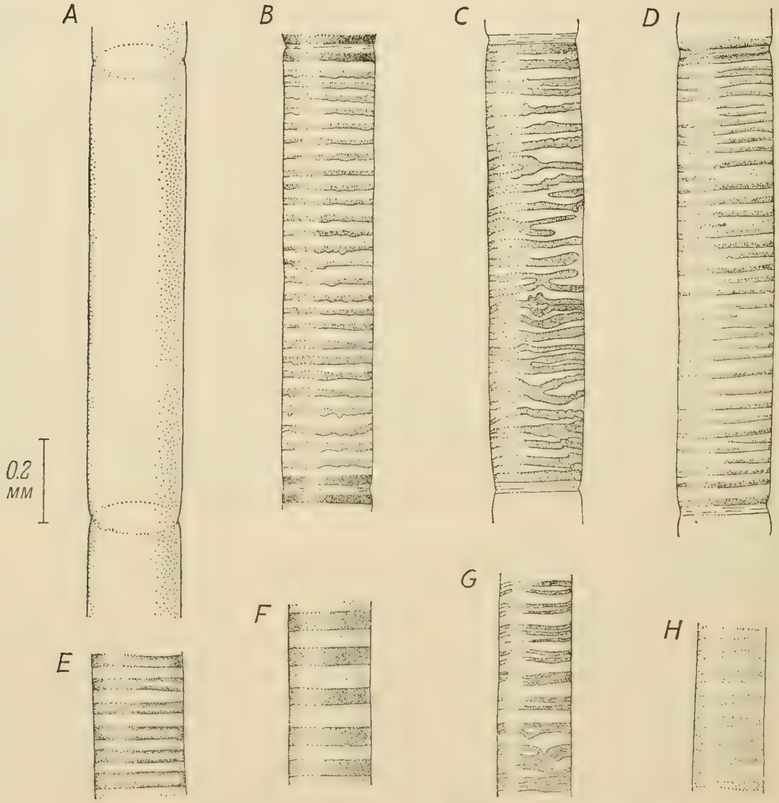


Fig. LL133: *Siboglinum silone*: Tube: *A* – the anterior unringed part; *B–D* – different variants of the anterior part of the tube; *E–H* – succeeding parts of the tube.

Material: 16 tubes with animals or parts of animals and 21 empty tubes.

Localities: *Vityaz'* stations 4620 and 4328 (31st cruise): Indian Ocean, to the west of the coast of southern India, and the Arabian Sea in the Gulf of Aden off the coast of Somalia near Cape Guardafui (12°N 51°E).

Depth: 1300 and 900 m.]

[*34. Siboglinum ceylonicum* sp. nov. Ivanov (Figs. MM133–OO133)

I found a few specimens of this species at the end of January, 1960, whilst investigating the abyssal fauna on board R.V. *Vityaz*' in the Indian Ocean, between Ceylon and the Maldive Islands. In a haul taken with a Sigsby trawl and in three dredgings we took 16 fine-ringed tubes each containing the greater part of an animal. *Siboglinum ceylonicum* is one of the smaller species of the genus—its body is no more than 0·2 mm across.

The fore-part of the body is very long, with a length to breadth ratio, in most individuals, of 7 or 8 : 1, but in one specimen, which appeared to be immature, the fore-part was only four times as long as broad. A characteristic feature is the lack of any clearly defined groove between the protosoma and mesosoma; in front of the bridle there is only a pretentacular groove, cutting off the cephalic lobe. The latter is rather large but no broader than the protosoma. It is longer than broad, it tapers rather rapidly towards the tip and it is somewhat flattened dorso-ventrally. The epidermis of the cephalic lobe consists of tall cells which contain a clear secretion (Fig. MM133*A*). The anterior part of the protosoma, immediately behind the pretentacular groove, has a rather broad continuous glandular girdle, which appears opaque in transmitted light (Fig. MM133*A*, *B*). The tentacle, attached at the hind edge of this girdle, has a narrow base, but soon broadens out and then for a considerable length it is remarkable for its stoutness, reaching 0·15 mm—hardly less than the diameter of the body of the animal. The surface of the tentacle is covered with numerous coarse wrinkles, indicating that it is strongly contracted (Fig. MM133*A*, *B*). In the distal part of the tentacle, however, where the circular epidermal folds disappear, it is still frequently 0·1 mm in diameter. Pinnules (200μ long) are arranged in two rows along the whole length of the tentacle (Fig. MM133*C*). Under the microscope the two capillaries in each one are clearly visible. There is a well-marked zone of rudimentary pinnules, similar to that in *S. silone* sp. nov. (see p. 293), at the base of the tentacle. It forms two thick rows of progressively sprouting pinnules.

In some individuals the protosoma is slightly constricted behind the point of attachment of the tentacle. The bridle is situated a little in front of the middle of the fore-part, and its colourless keels, lying on clearly protuberant cutaneous ridges, are moderately stout and thickened towards the dorsal ends but do not meet. On the ventral sides of the body each keel turns forward in a characteristic manner, the ends taper slightly and then fuse together (Fig. MM133*A*, *B*). In transmitted light it can be seen that behind the bridle the coelom of the mesosoma contains numerous rather small spherical glands

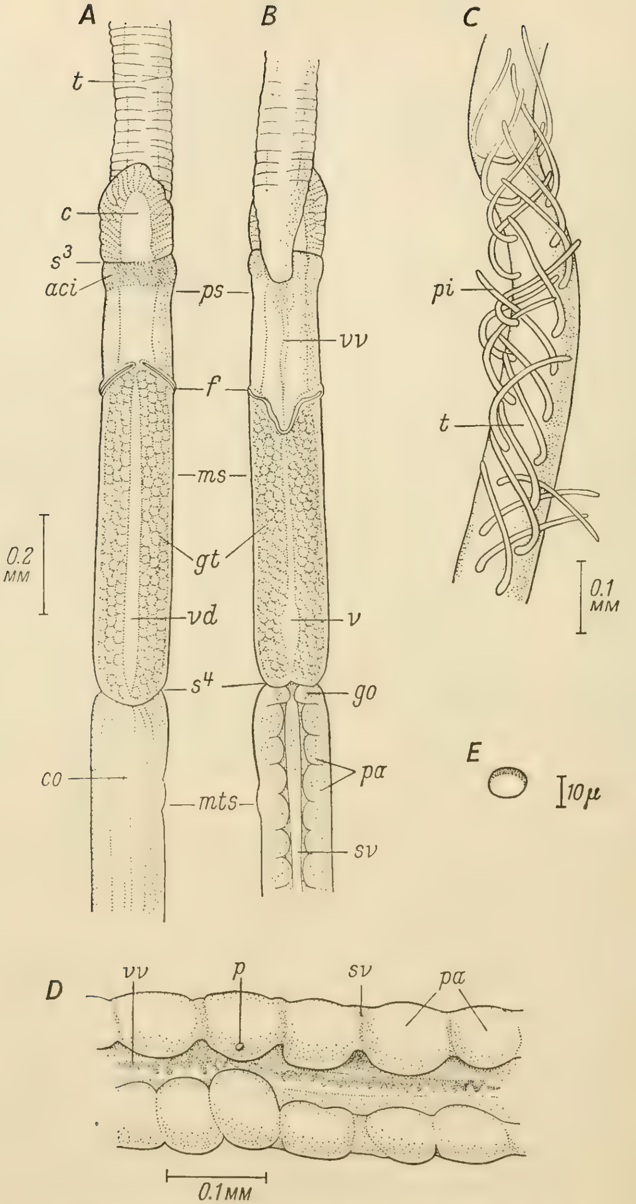


Fig. MM133. *Siboglinum ceylonicum*: *A* – fore-part of the body from the dorsal, and *B*, from the ventral side; *C* – part of the tentacle; *D* – part of the metameric region of the trunk from the ventral side; *E* – cuticular plaques from the metameric region.
aci – pretentacular glandular girdle; *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *go* – male genital papilla; *gt* – flask-shaped glands; *ms* – mesosoma; *mts* – metasoma; *p* – plaque; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^2 – groove between the mesosoma and metasoma; s^3 – pretentacular groove; *sv* – ventral sulcus; *t* – tentacle; *vd* – dorsal blood vessel; *vv* – ventral blood vessel seen through the body wall.

(Fig. MM133*A*, *B*). The boundary between the mesosoma and metasoma is arched forward on the dorsal side and forms a small median nick on the ventral side (Fig. MM133*B*).

The metameric part of the trunk is moderately long. The dorsal ciliated band begins at the front edge of the metasoma (Fig. MM133*A*). The ventral blood vessel can often be seen along the bottom of the well-marked ventral sulcus (Fig. MM133*D*). The papillae at the sides are comparatively large and rounded, and lie close together. Each encloses a single pyriform gland which is visible through the skin. On many papillae there is a tiny cuticular plaque, oval in shape with a dense blackish front rim (Fig. MM133*D*, *E*). These are about 15μ across. The number of papillae in the metameric part varies between 50 and 70 pairs. In the male a pair of small rounded genital papillae, which meet in the mid-ventral line, is situated almost on the boundary between the mesosoma and metasoma (Fig. MM133*B*).

The nonmetameric section of the trunk is very long and furnished with small contracted irregularly spaced papillae. No zone of thickened papillae has been observed. There are three girdles—two anterior and one much farther back. Each girdle is represented by a rather narrow annular ridge on which the toothed platelets are arranged in a single row (Fig. NN133*B*, *C*). The first girdle is broken dorsally, the second ventrally and third has a broad ventral gap (Fig. NN133*A*), but in one individual the first girdle is almost complete, while the second makes more than a complete turn around the trunk. There are no papillae within the girdle region, but where the postannular region begins, at the point of constriction of the trunk, there is a small plaqueless papilla (Fig. NN133*A*).

The shape of the toothed platelets varies enormously. In one individual they are greatly elongated and most of them have the hind end narrower (instead of the usual condition, which is the reverse). Often there is a transverse line cutting the platelet into two almost equal parts, one bearing the anterior and the other the posterior group of teeth (Fig. NN133*C*, *D*). The anterior group of teeth is usually the more poorly developed, though the reverse may occur. In the former case the front half of the platelet is not only broader than the hind half but also thicker and sometimes even inflated (Fig. NN133*B*). The platelets are 10–17μ long. Sometimes one may encounter anomalous short platelets, bearing only one group of teeth.

The postannular region of the metasoma is unfortunately only known in part from three individuals. It is furnished with metameric conical ventral papillae, near which the integument of the trunk is rich in large glandular cells. In one individual there is a slight colourless thickening of the cuticle on the tip of each postannular papilla.

The tentacle reaches 12 mm long and it may possibly be capable of much greater elongation. The fore-part of the body is 0·74 to 1·2 mm long. The

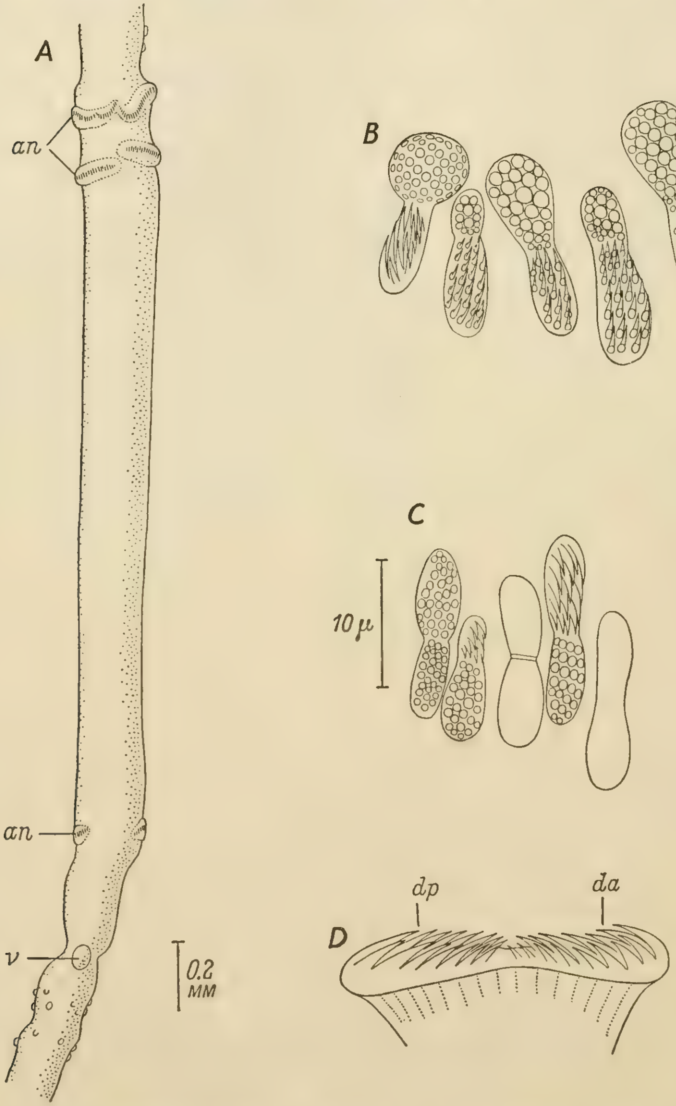


Fig. NN133. *Siboglinum ceylonicum*: *A* – region of the girdles from the ventral side; *B* – platelets of the first girdle; *C* – platelets of the hind girdle; *D* – toothed platelet from the side. *an* – girdles; *da* – anterior group of teeth; *dp* – posterior group of teeth; *v* – ventral papilla.

metameric part of the trunk is 2 to 5 mm long and the whole preannular region was 21 mm long in one specimen, but is usually more than 40 mm and in one specimen it is 79 mm long. The mesosoma is 0·15–0·18 mm broad. A complete specimen, including the tentacle, may possibly reach 80–100 mm long.

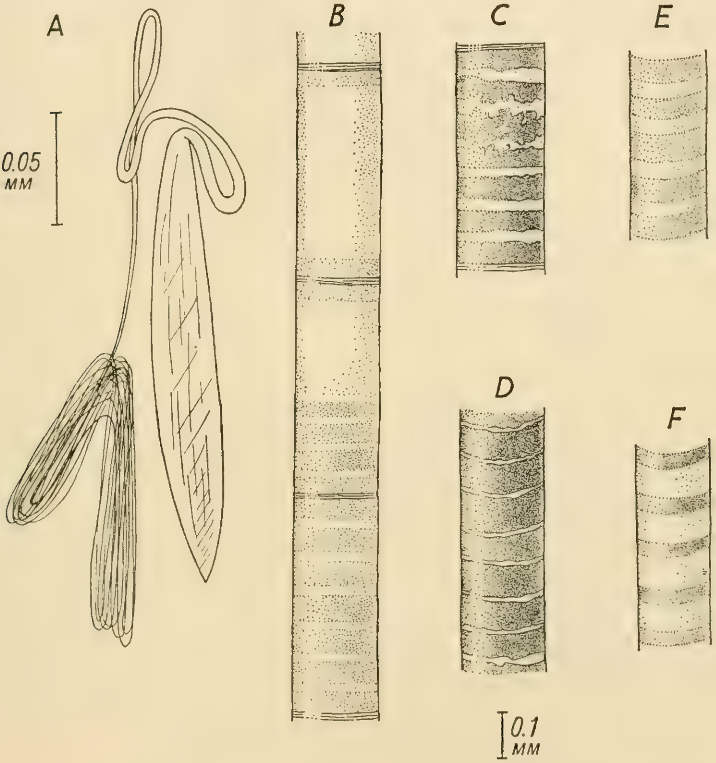


Fig. OO133. *Siboglinum ceylonicum*: *A* – spermatophore; *B–F* – successive parts of the tube.

In three males I have found numerous cigar-shaped spermatophores (Fig. OO133*A*). The base of the filament of the spermatophore is rather thick, but the greater part, as usual, is very thin. The filiform sperm are hard to see; they are very delicate and thin, lying parallel to the length of the spermatophore in the anterior half and arranged spirally in the posterior half. The spermatophore is 0·22 mm long by *c*. 0·03 mm broad.

The brown flexible thin-walled tube is segmented at the front end and ringed. Its surface is smooth and lustrous. The anterior filmy portion of the tube is transparent and colourless, but it has clearly defined segments. Then the tube becomes brown, and within each segment clear slightly raised rings appear, at first only in the two ends of the segment and then gradually appearing also in the middle (Fig. OO133*B*). The fully formed segments may have seven to ten rings each, but the most usual number is eight. The second, third and fourth rings in each segment are frequently very irregular. In the middle part of the tube the segments disappear, the rings become considerably longer and denser, brown-grey and homogeneous. They are a third to a half as long as the tube is wide. The narrow interspaces between the rings are transparent, with a golden glitter (Fig. OO133*D*). The tube retains this character for a great length. Towards the hind end of the tube the rings gradually pale and the clear interspaces grow longer in comparison with the length of the rings (Fig. OO133*E*). In the hindmost part of the tube the very delicate rings possess diffuse edges and become very short, so that they look like narrow belts. The interspaces are here rather long (Fig. OO133*F*).

S. ceylonicum belongs to the group of species with a bipectinate tentacle, a pretentacular groove, three girdles, a strongly developed anterior tooth-group on the toothed platelets and a segmented tube. Others of this group are *S. pinnulatum*, *S. fedotovi*, *S. ekmani*, *S. silone* sp. nov. and *S. plumosum*. Most of all this new species recalls *S. pinnulatum*, from the western part of the Pacific Ocean. In the latter each segment of the tube also has eight rings. *S. ceylonicum* is like *S. fedotovi* (known from the northwestern part of the Pacific Ocean) in the nature of its toothed platelets. It may readily be distinguished from all these species, however, by the following characters:

1. The presence of a pretentacular glandular girdle;
2. The characteristic curve of the keels of the bridle;
3. The very thick tentacle;
4. The somewhat greater development of the anterior group of teeth on the toothed platelets.

Material: six tubes with more or less complete animals, four tubes with parts of animals and six empty tubes.

Locality: *Vityaz'* station 4618 (31st cruise): between Ceylon and the Maldive Islands.

Substratum: grey mud and Foraminifera.

Depth: 1920–2970 m.]

[35. *Siboglinum exile* sp. nov. Ivanov (Figs. PP133–SS133)

In a dredge haul brought up from a depth of 626 m by R.V. *Vityaz'* in the Indian Ocean near the south coast of Sumatra, I found three species of *Siboglinum*, including that described here as *Siboglinum exile* (Lat. *exilis*—thin, lean). Out of seven tubes five contained animals.

The body of *S. exile* is very fine—*c.* 0·1 mm in diameter. The fore-part

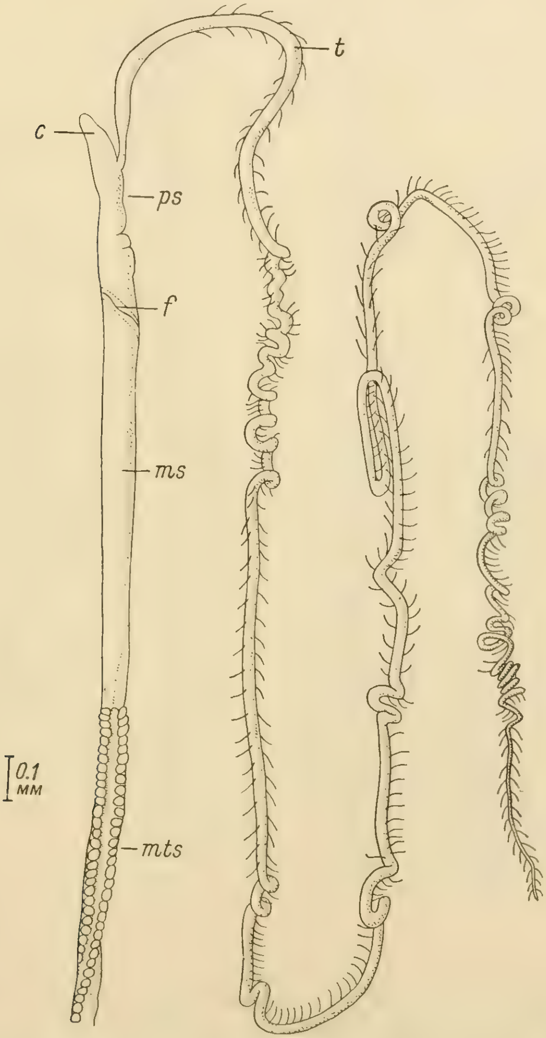


Fig. PP133. *Siboglinum exile*: The fore-part of the body viewed from the right side. *c* – cephalic lobe; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *ps* – protosoma; *t* – tentacle.

is thin, but thickens a little in the middle. Its length to breadth ratio is 8 or 9 : 1, but in one individual, which had an extended fore-part, it was no less than 18 : 1 (Fig. PP133). The protosoma is limited behind by a distinct annular groove, lying a short distance in front of the bridle. Towards the front end the protosoma tapers imperceptibly and runs into the small

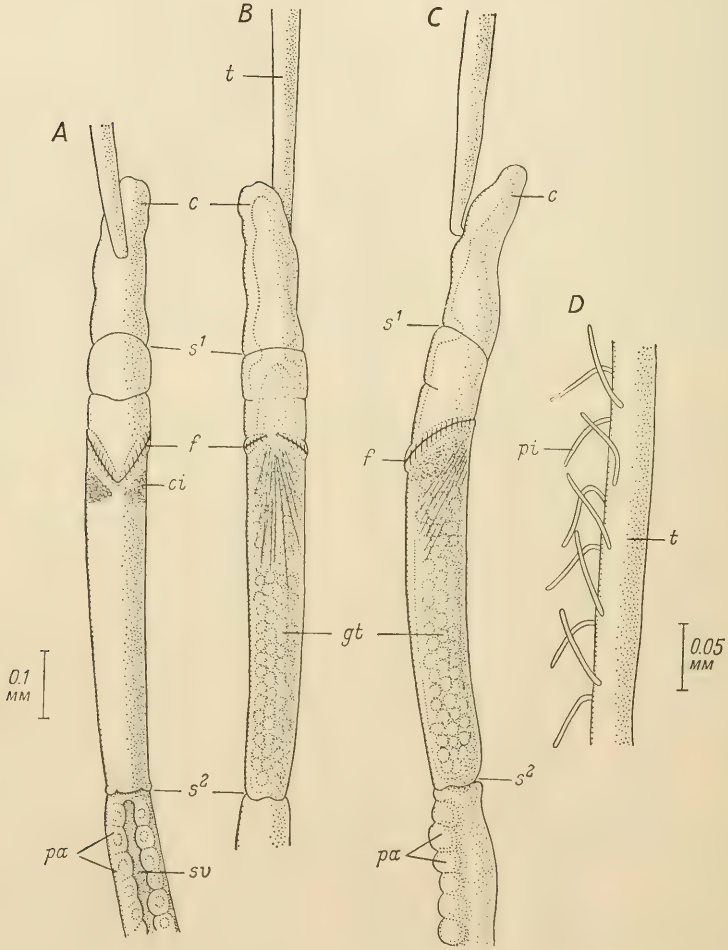


Fig. QQ133. *Siboglinum exile*: *A* – the fore-part of the body from the ventral, *B*, from the dorsal, and *C*, from the left side; *D* – part of the tentacle.
c – cephalic lobe: *ci* – glandular girdle; *f* – bridle; *gt* – flask-shaped gland; *pa* – papillae; *pi* – pinnules; s^1 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and metasoma; *sv* – ventral sulcus; *t* – tentacle.

cephalic lobe, which has a blunt tip. The epidermis of the cephalic lobe is not especially rich in gland cells. The long thin tentacle is attached much nearer to the tip of the cephalic lobe than to the hind edge of the protosoma. The comparatively short pinnules (75μ long) are arranged in two longitudinal rows at some distance from one another (Fig. QQ133*D*).

The distance between the tip of the cephalic lobe and the bridle is approximately half that between the bridle and the hind edge of the mesosoma. The part of the mesosoma in front of the bridle is divided into two almost equal parts by a slight transverse ventral groove (Fig. QQ133*A*–*C*). The keels of the bridle, which lie on ridges, are almost colourless, thin and tapering. On the dorsal side the keels do not meet, but on the ventral side they fuse. Characteristically, the keels are crossed by thin grey cuticular rodlets (Fig. QQ133*A*–*C*). There is a pair of small indistinct glandular patches on the ventral side in front of the bridle, and flask-shaped glands, visible through the body wall, occupy the whole mesocoele behind the bridle (Fig. GV133*B*, *C*). The boundary between the mesosoma and metasoma is a simple transverse groove.

In the metameric section of the metasoma there are 60–70 pairs of more or less equal papillae. The anterior ones are comparatively small, rounded and crowded close together (Fig. QQ133*A*, *C*); they increase in size towards the end of the series. There is one pyriform gland per papilla and no plaque. The nonmetameric section of the trunk is long and its epidermis is rich in gland cells, forming glandular areas and patches which are whitish in reflected light. Here and there one encounters roundish contracted papillae (Fig. RR133*A*).

There are three girdles, two lying about 1–2 mm in front of the third. The first and third girdles are widely broken on the ventral side, the second on the dorsal (Fig. RR133*B*, *C*). Immediately behind the last girdle is found a large plaqueless conical ventral papilla (Fig. RR133*C*). The toothed platelets lie in a single row on broad cushion-like ridges. They are elongated and lingulate ('biscuit-shaped'—see p. 226) (Fig. RR133*D*). The anterior and posterior groups of teeth are equally well developed (Fig. RR133*E*). Most of the toothed platelets are 11–17μ long, but there are sometimes small underdeveloped platelets.

The postannular region of the trunk is long. The metamerically repeated ventral papillae are small and lack plaques. Opposite each papilla there is a small but well-defined glandular dorsal shield (Fig. RR133*F*).

All five individuals turned out to be females and one of them appeared to be a young immature animal. Mensuration gave the following results (mm):

Length of the tentacle	up to 10·5
Length of the fore-part of the body	0·8–1·5
Breadth of the fore-part	0·08–0·1
Length of the metameric section of the trunk	2·0–3·5
Length of the whole preannular section	up to 18·5
Length of the postannular section	up to 15·0
Overall length including tentacle	25–40

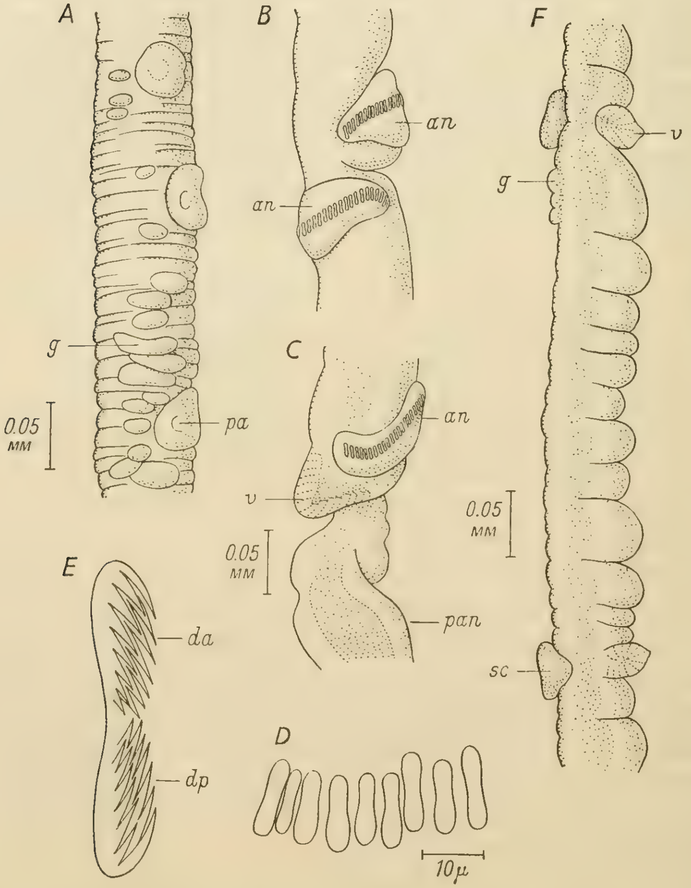


Fig. RR133. *Siboglinum exile*: *A* – part of the nonmetameric region of the trunk from the right side; *B* – first and second girdles from the left side; *C* – the third girdle, from the left side; *D* – part of a girdle; *E* – toothed platelet from the side; *F* – part of the postannular region from the right. *an* – girdles; *da* – anterior group of teeth; *dp* – posterior group of teeth; *g* – glandular portion of the epidermis; *pa* – papillae; *pan* – postannular region; *sc* – dorsal shield; *v* – ventral papillae.

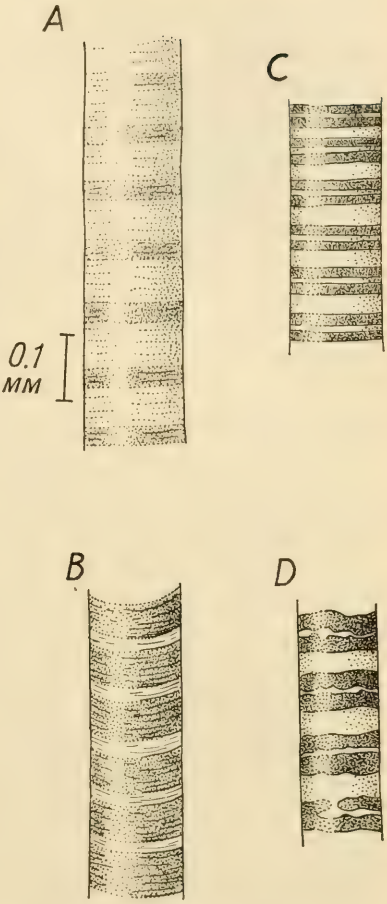


Fig. SS133. *Siboglinum exile*: *A–D* – successive portions of the tube.

The tube of *S. exile* is thin, brown, elastic, lustrous and thin-walled. In front it is fibrous. It is unsegmented but ringed and there are very characteristic double rings in the middle part of the tube. A considerable length of the anterior end of the tube is transparent and colourless, with soft flimsy walls. Then follows a still colourless but fibrous part. Brown rings gradually appear, forming from local accumulations of transverse fibres. The interspaces between the rings are large and clear, but still fibrous; they are half as long as the tube is wide, and the rings are only half this—a quarter the diameter of the tube (Fig. SS133*A*). Then, a little farther back (but still in the anterior part of the tube), the rings become denser and darker, remaining, as before, fibrous. In this region they are a third to a half as long as the diameter of the tube. The interspaces are narrow and clear (Fig. SS133*B*). A considerable region in the middle of the tube is characterized by double rings. In general the length of each doublet, taken as a whole, is about a quarter the diameter of the tube, and the interspaces are the same length. The fibrous nature of the rings here disappears and the colour is golden-brown (Fig. SS133*C*). In the hind part of the tube the double rings are preserved, but both the rings and the interspaces are longer, and the strict regularity of the rings disappears (Fig. SS133*D*). The very longest tube is 85 mm, the anterior diameter is 0·135 mm and the posterior 0·06 to 0·09 mm.

S. exile has much in common with a whole series of species, including the possession of a bipectinate tentacle, three girdles, and a strongly developed anterior tooth-group on the platelets of the girdles. It is distinguished from all such species, however, by the oblique cuticular rodlets of the bridle, the unsegmented, very fibrous tube, and the well-differentiated dorsal shields in the postannular region of the trunk. The tube of *S. exile* resembles that of *S. weberi* (inhabiting the Indo-Malaysian region), *S. hyperboreum* (from the North Atlantic) and *S. tenue* and *S. pusillum* (both from the Pacific Ocean). In other respects, however, it is considerably different from all these species.

Material: seven tubes, five with animals, all females.

Locality: *Vityaz*' station 4543 (31st cruise): Indian Ocean near the southern tip of Sumatra to the west of the entrance to Sunda Strait.

Substratum: muddy sand.

Depth: 626 m.]

[*36. Siboglinum sumatrense* sp. nov. Ivanov (Figs. TT133, UU133)

One tube containing an animal and fragments of empty tubes of this species were found together with *S. exile* sp. nov. off the coast of southern Sumatra in the Indian Ocean.

The fore-part of the body is cylindrical and the protosoma clearly defined. The length to breadth ratio of the fore-part is 9 : 1. The protosoma runs imperceptibly into the small brief conical cephalic lobe. The thick tentacle is attached one-third of the length of the protosoma from its tip (Fig. TT133*A*). It bears rather dense pinnules (*c*. 70μ long) arranged apparently in two rows (Fig. TT133*C*).

The bridle lies one-third of the way along the mesosoma. Its thin keels are colourless and neither taper nor thicken towards the ends. They meet neither dorsally nor ventrally (Fig. TT133*A*, *B*). The mesocoele is filled behind the bridle with flask-shaped glands. There is nothing to remark about the boundary between the mesosoma and metasoma (Fig. TT133*A*, *B*).

The ventral sulcus of the metasoma is sharply defined. The metameric papillae are poorly differentiated—within the lateral ridges which bound the ventral sulcus paired metameric pyriform glands can be distinguished, which in the anterior metameric region stick up just a little as slight humps (Fig. TT133*B*). There are no cuticular plaques.

There are two girdles lying close together. The toothed platelets, 13–14μ long, are uniserial (Fig. TT133*D*). They are somewhat narrower at the front end where they bear the small anterior group of teeth. This part is only a third the length of that which bears the posterior teeth (Fig. TT133*E*).

The postannular region is well differentiated, bearing small ventral papillae and dorsal glandular shields at rather short regular intervals (Fig. TT133*F*). The former are furnished with a transparent thickening of the

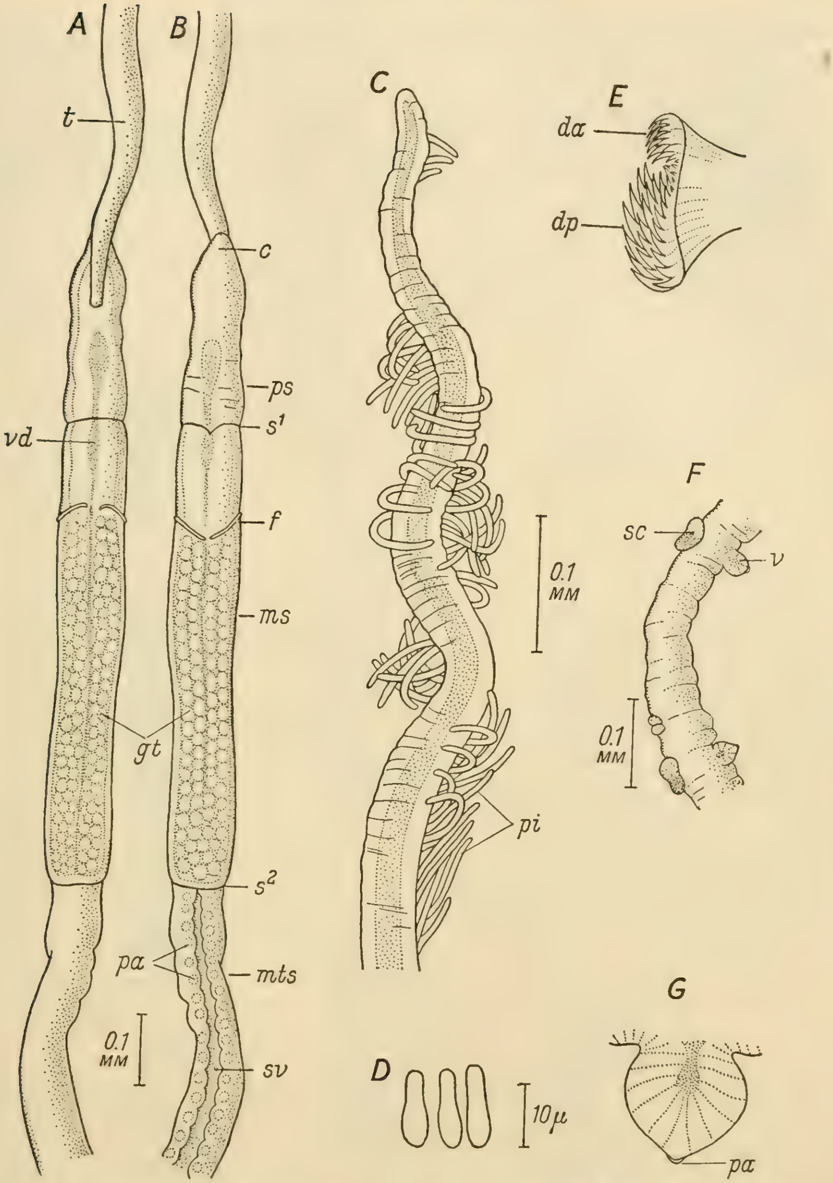


Fig. TT133. *Siboglinum sumatrense: A* – fore-part of the body from the dorsal, and *B*, from the ventral side; *C* – the distal part of the tentacle; *D* – part of a girdle; *E* – toothed platelet from the side; *F* – part of the postannular region; *G* – ventral postannular papilla.

c – cephalic lobe; *da* – anterior teeth; *dp* – posterior teeth; *f* – bridle; – *gt* – flask-shaped glands; *ms* – mesosoma; *mts* – metasoma; *p* – plaque; *pa* – papillae; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and metasoma; *sc* – dorsal shield; *sv* – ventral sulcus; *t* – tentacle; *v* – ventral papilla; *vd* – dorsal blood vessel; *vv* – ventral vessel seen by transparency.

cuticle at the tip (Fig. TT133*G*), and the latter are shaped like small warts or buttons.

The tentacle is 15 mm long, the fore-part of the body 0·97 mm. The mesosoma is 0·09 mm broad. The preannular section is 9 mm and the post-annular 10 mm long. The overall length of the body, including the tentacle, is 35 mm.

The thin elastic tube is lustrous, dark brown and thin-walled. The whole front part of the tube is divided into segments which are two or two and a

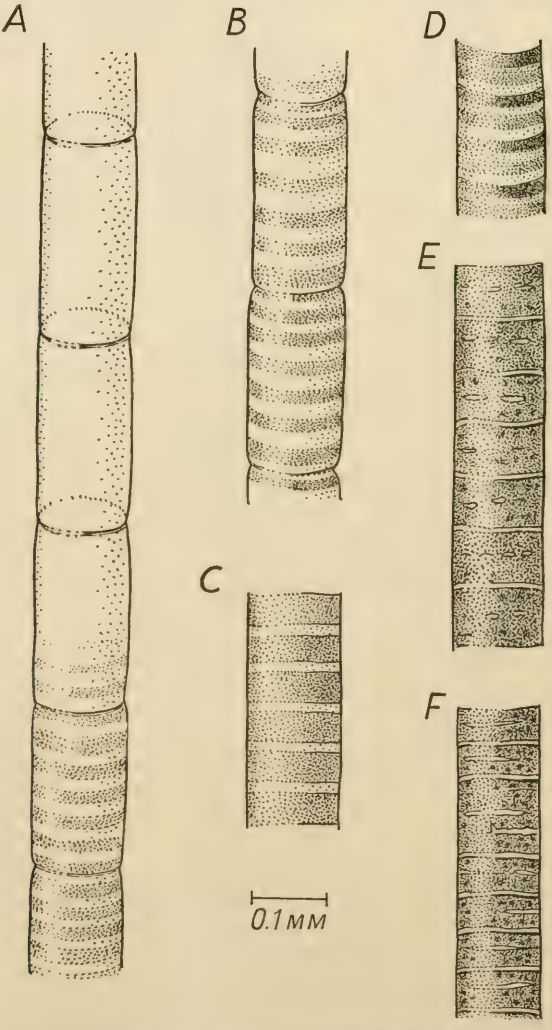


Fig. UU133. *Siboglinum sumatrense*: *A–F* – successive parts of the tube.

half times as long as the diameter of the tube. Seven rings gradually appear in each segment, beginning in the hind part of each one (Fig. UU133*A*). The ring-length is a fifth to a quarter of the diameter of the tube and the clear interspaces are the same length (Fig. UU133*B*). The segmentation soon breaks down and the rings become longer. They are very regular and brown with a lustrous surface (Fig. UU133*C*). In the middle of the tube clear streaks appear down the centre of each ring, dividing it into two secondary rings of which the anterior is darker than the posterior (Fig. UU133*D*). In the final third of the tube the rings are longer (half the diameter of the tube), but each has a clear central streak of "chinks" and "openings". The substance of the ring, moreover, is not homogeneous, but consists of small dark conspicuously more compact patches or blotches (Fig. UU133*E*.) This peculiarity increases towards the hind end of the tube (Fig. UU133*F*). The hindmost part of the tube is torn off. The length of the tube is 90 mm, its anterior diameter 0·135 mm and its posterior 0·09 mm.

The various features of *S. sumatrense* are all encountered separately in different representatives of this genus, but the species is sufficiently characterized by their combination. The most noticeable specific peculiarities *S. sumatrense* are the even width of the keels of the bridle and their dorsal and ventral separation, the absence of any glandular girdle behind the bridle, the poor differentiation of the metameric papillae and the nature of the tube. Though the tube of *S. sumatrense* is very like that of *S. ceylonicum* sp. nov. (p. 301), it is distinguished from the latter species by the poorly developed anterior group of teeth on the platelets of the girdles.

Material: one tube with an animal and one empty fragmentary tube.

Locality: *Vityaz*' station 4543 (31st cruise): Indian Ocean near the south coast of Sumatra near the entrance to Sunda Strait.

Substratum: grey muddy sand.

Depth 626 m.]

[37. *Siboglinum zanzibaricum* sp. nov. Ivanov (Figs. VV133, WW133)

One specimen of this rather large species of *Siboglinum* was found in the contents of a dredge haul taken by R.V. *Vityaz*' on 17 March, 1960, to the east of the Islands of Zanzibar and Pemba at a depth of 2173 m.

The fore-part of the body is very short, probably as a result of strong contraction when the fixative was added. It reaches its greatest breadth in the region of the bridle and gradually tapers from there to the tip of the cephalic lobe (Fig. VV133*B*, *C*). The length to breadth ratio is 3·5 : 1. The small cephalic lobe is triangular and much flattened dorso-ventrally. Behind the base of the tentacle there is a clearly defined annular groove which hardly appears to be the hind border of the protosoma (Fig. VV133*B*, *C*). The rather thin long tentacle has a single dense row of pinnules (*c*. 170μ long) only on the distal half: the proximal half has none (Fig. VV133*A*).

The front third of the mesoma is laterally compressed. The bridle lies a little in front of the middle of the mesosoma and its dark-brown keels,

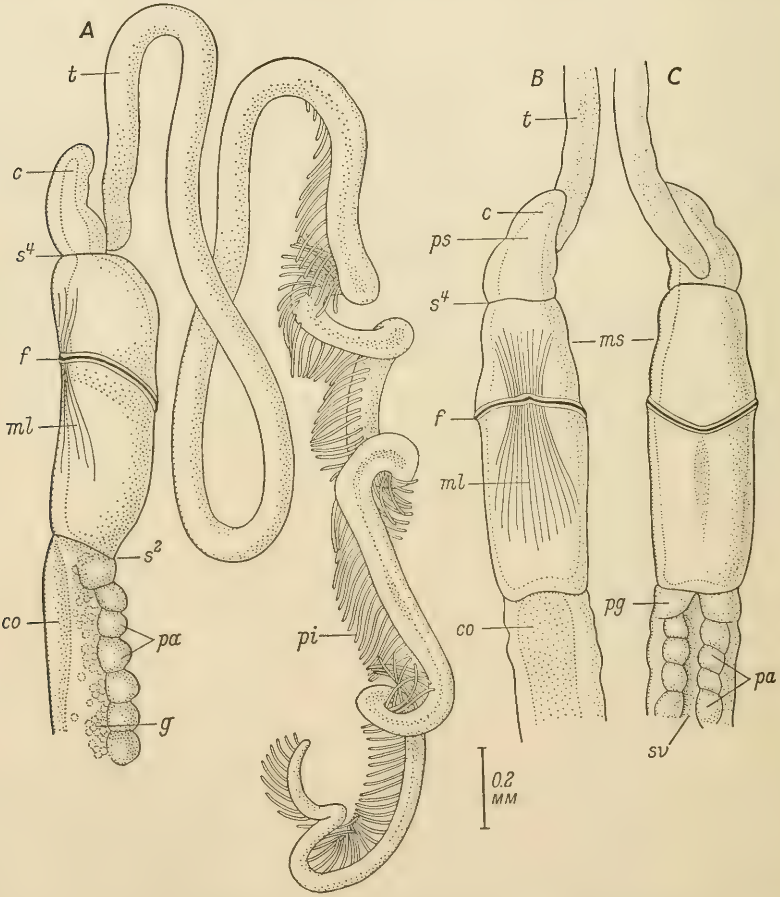


Fig. VV133: *Siboglinum zanzibaricum*: *A* – fore-part of the body from the right, *B*, from the dorsal, and *C*, from the ventral side.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *g* – glandular portion of integument; *ml* – longitudinal muscle fibres; *ms* – mesosoma; *pa* – papillae; *pg* – genital papilla; *pi* – pinnules; *ps* – protosoma; s^4 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle.

lying on narrow ridges, fuse both dorsally and ventrally. There is no sign of flask-shaped mesosomal glands behind the bridle. On the dorsal side of the mesosoma it is possible to make out bundles of longitudinal muscle fibres, at the level of the bridle (Fig. VV133*A*, *B*, *C*).

The boundary between the mesoma and metasoma is simple and the broad ciliated band begins immediately behind it (Fig. VV133*B*). The metameric part of the metasoma has about 50 pairs of rounded plaqueless papillae, tightly packed together, each containing a single pyriform gland (Fig. VV133*A*, *C*). Outside the papillae, on the lateral surface of the metasoma, the epidermis is very rich in granular gland cells, forming a pair of longitudinal glandular tracts like those of the "taeniaphorous" species (*S. taeniaphorum*, *S. altanticum* etc.—see p. 287) (Fig. VV133*A*).

The region of the girdles and the postannular section of the trunk remain unknown, since the body of our only specimen (which appears to be a male) is torn off in front of the girdles. The genital papillae are rather large (Fig. VV133*C*), but there is no sign of spermatophores.

The tentacle is 8·4 mm long and the fore-part of the body 1·05 mm. The greatest breadth of the mesosoma is 0·3 mm. The metameric section of the metasoma is 5 mm long and the remainder of what survives of the preannular region 26 mm. The overall length of the fragment of the animal (including the tentacle) is *c*. 40 mm.

The smooth lustrous ringed but unsegmented tube is yellow, shading to yellow-brown at the front. The anterior flimsy membranous transparent part of the tube has the end torn away; what is left of this part is some 7 mm long. Gradually golden-brown rings appear, a half, a third or a quarter as long as the diameter of the tube. The interspaces between

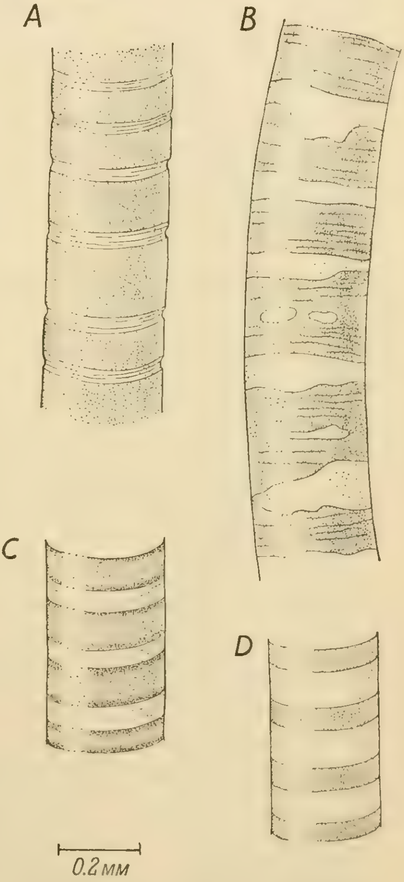


Fig. WW133. *Siboglinum zanzibaricum*: *A–D* – successive portions of the tube.

them are clear and creased (Fig. WW133*A*). In the next part of the tube the rings are very irregular, "chinks" appear in them and they anastomose with one another (Fig. WW133*B*). Then the rings regain their regularity but become much shorter. Their edges are a little darker in colour (Fig. WW133*C*). In the hind part of the tube the rings gradually fade and disappear, and finally the tube becomes glassily transparent (Fig. WW133*D*). The fragment of tube is 115 mm long, with an anterior diameter of 0·32 mm and a posterior of 0·27 mm.

S. zanzibaricum is distinguished by several unique features. Usually when the pinnules form two longitudinal rows they are thick-set, while a single row of pinnules is sparse. In *S. zanzibaricum* the thick-set pinnules are uniserial. Other peculiarities of the species appear to be the short fore-part, the extraordinarily small protosoma and the fused keels of the bridle.

Material: one individual in a tube.

Locality: *Vityaz'* station 4686 (31st cruise): Indian Ocean to the east of the Islands of Zanzibar and Pemba.

Substratum: sandy mud.

Depth: 2172 m.]

[*38. Siboglinum sergeevi* sp. nov. Ivanov (Figs. XX133–ZZ133)

A new species of *Siboglinum* was found in a dredge haul taken by R.V. *Vityaz'* on 17 October, 1959, in the Ceram Sea at a depth of 4774 m. Unfortunately only a single specimen was found, but it was excellently preserved. I have named the new species after Captain I. V. Sergeev, commanding officer of R.V. *Vityaz'*, to whom Soviet oceanology owes so many of its achievements and who was unfailing in his courteous assistance of my work on board R.V. *Vityaz'*.

The very short fore-part of the body is slightly compressed from side to side. Its length to breadth ratio is about 3 : 1 and the bridle lies at about its middle. An annular groove in front of the bridle, sharply defined ventrally and disappearing dorsally, represents the boundary between the protosoma and mesosoma (Fig. YY133*A*, *B*). The tentacle is inserted a little nearer to this groove than to the tip of the cephalic lobe. There is a post-tentacular groove, equally well defined on both sides of the body. Anteriorly the protosoma runs imperceptibly into the short conical cephalic lobe (Fig. YY133*B*). The long thin tentacle has no pinnules (Fig. XX133).

The mesosoma is no more than twice as long as it is broad. There is a short mid-ventral furrow in front of the bridle, and behind it a transverse fold or groove. The bridle is very like that of *S. zanzibaricum* sp. nov., but its keels do not fuse dorsally, as they do in the latter, but instead merely approach one another. The keels are brown and lie on a narrow ridge, so that, although they are delicate, they are very noticeable. Their ventral

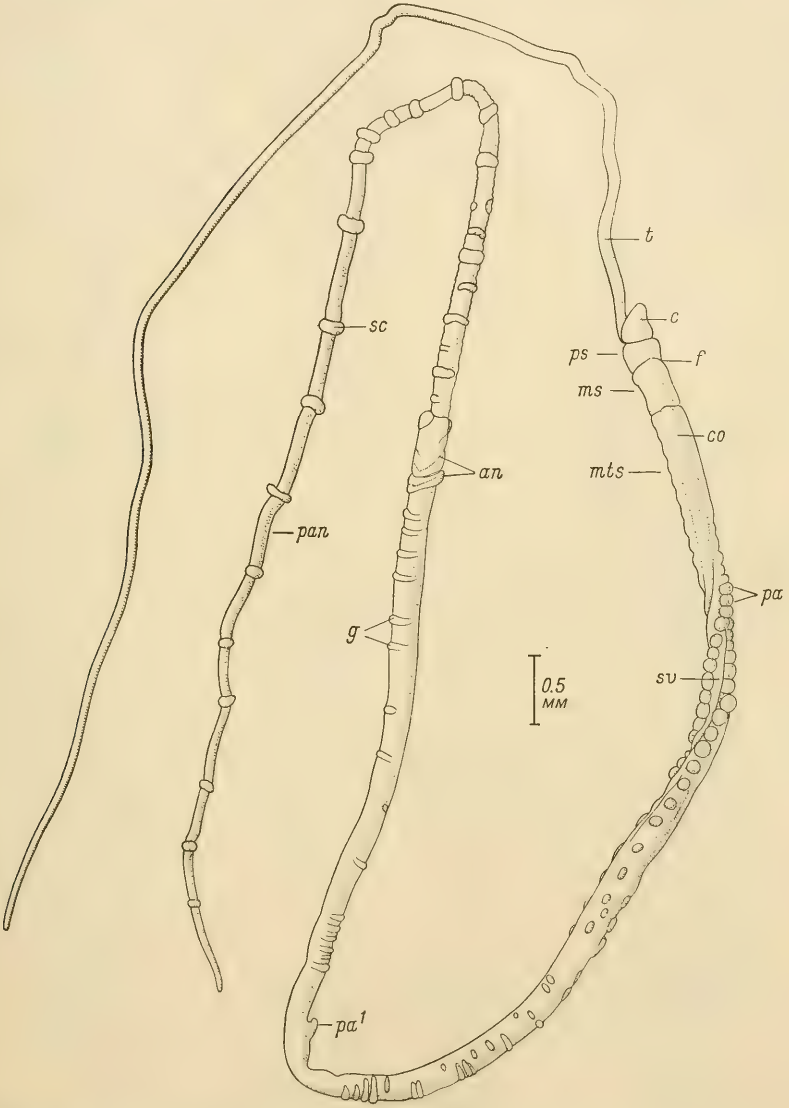


Fig. XX133. *Siboglinum sergeevi*: General view.
an – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *g* – glandular area; *ms* – mesosoma; *mts* – metasoma; *pa* – papillae; *pa*[1] – papilla of the zone of thickening; *pan* – postannular region of the trunk; *ps* – protosoma; *sc* – dorsal shield; *sv* – ventral sulcus; *t* – tentacle.

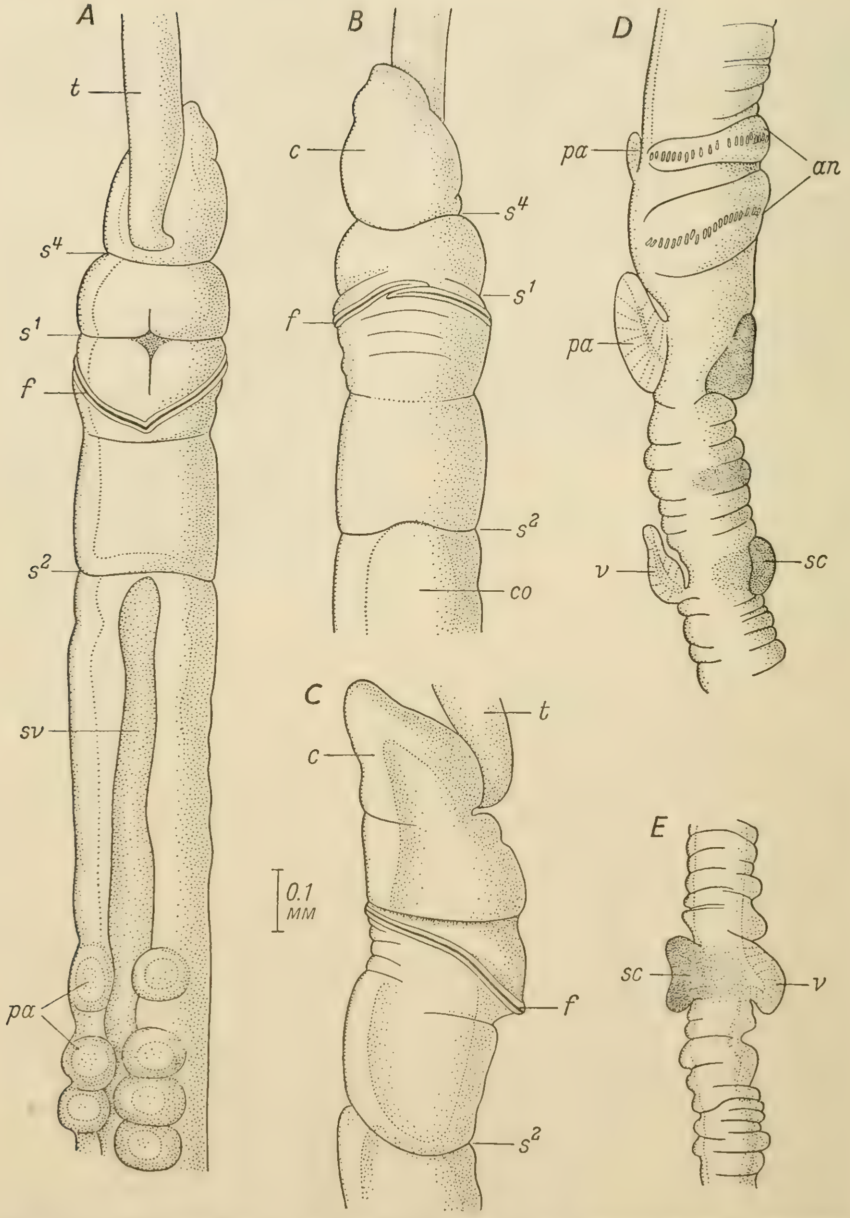


Fig. YY133. *Siboglinum sergeevi*: *A* – front end of the body from the ventral side; *B* – fore-part of the body from the dorsal, and *C*, from the ventral side; *D* – region of the girdles from the left; *E* – part of the postannular region from the right.
an – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *pa* – papillae; s^1 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and metasoma; s^4 – posttentacular groove; *sc* – dorsal shield; *sv* – ventral sulcus; *t* – tentacle; *v* – ventral papilla.

ends fuse (Fig. YY133*A*). No flask-shaped gland has been observed in the mesosomal region. Except for a forward excursion in the mid-dorsal line, the groove between the mesosoma and metasoma is simple (Fig. YY133*B*).

The very front end of the metasoma lacks papillae. For some 0·5 mm the deep ventral sulcus is bounded only by smooth lateroventral ridges (Fig. YY133*A*). The broad dorsal ciliated band, however, begins at the very front edge of the metasoma (Fig. YY133B). When the metameric papillae finally begin they are small, rounded, tightly-packed and plaqueless, and each contains a single pyriform gland (Fig. YY133*A*). Towards the caudal end of the region, where they become less regular, their size increases a little. There are 15 papillae on the left and 16 on the right.

The nonmetameric part of the trunk is approximately twice as long as the metameric (Fig. XX133). It bears scattered papillae and glandular patches of epidermis, the latter especially on the dorsal side. In the zone of thickening there is only one large conical plaqueless ventral papilla (Fig. XX133). It is situated almost in the middle of the nonmetameric region, indicating that the front half of the preannular region is somewhat underdeveloped—a sign of the immaturity of our specimen.

There are two girdles, both broken on the ventral side (Fig. XX133). At the level of the first girdle there is a small ventral papilla and a second larger one lies behind the second girdle. Both lack either plaques or cuticular thickenings at their tips. The girdles lie on broad protuberant ridges (Fig. YY133*D*). The toothed platelets, narrower at the front end, are arranged in one row (Fig. ZZ133*A*). The anterior group of teeth is feebly developed (Fig. ZZ133*B*). The platelets are 14–18μ long.

The postannular section is almost the same length as the preannular, but considerably thinner and it tapers gradually towards the hind end of the body (Fig. XX133). It bears metameric dorsal glandular shields which are shaped like buttons (Fig. YY133*E*), or else stretched out irregularly sideways (Fig. XX133). A tongue-like transparent plaqueless ventral papilla is situated opposite each shield (Fig. YY133*E*).

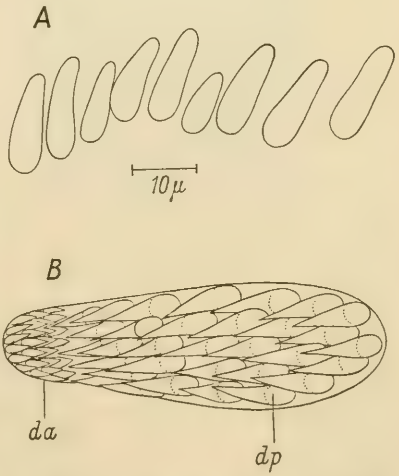


Fig. ZZ133. *Siboglinum sergeevi*: *A* – part of a girdle; *B* – toothed platelet. *da* – anterior group of teeth; *dp* – posterior group.

The tentacle is 12·2 mm long, the fore-part of the body 0·8 mm, with a greatest breadth of 0·25 mm. The metameric part of the trunk is 3·5 mm long, the nonmetameric 8·5 mm and the postannular region 10·2 mm. The overall length of the body, including the tentacle, is *c.* 37 mm. As we have seen, our specimen appears to be a young animal, and no sexual products have been seen.

The tube is very soft, colourless, thin-walled and structureless. Its whole front half is flimsy. It is 94 mm long with an anterior diameter of *c.* 0·3 mm.

S. sergeevi recalls *S. zanzibaricum* sp. nov., but it is distinguished from it by the presence of a sharply defined boundary between the protosoma and mesosoma, the absence of pinnules, the dorsal separation of the keels of the bridle, the underdeveloped anterior metameric papillae and the structureless tube.

Material: one tube with an entire animal.

Locality: *Vityaz*' station 4492 (31st cruise): the southern part of the Ceram Sea to the north of the Island of Buru.

Substratum: grey-green clayey mud.

Depth: 4774 m.]

[*39. Siboglinum lacteum* sp. nov. E. C. Southward (Fig. YX133, Pl. IV).

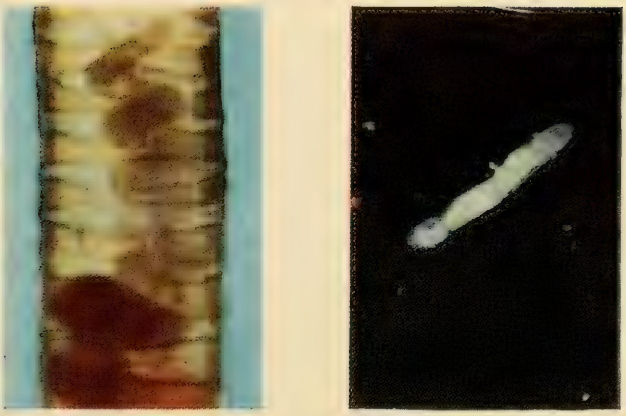
One specimen of this species has been collected; it was fortunately complete and in good condition and was photographed while alive (see Plate IV).

The animal is an immature female about 50 mm long but the coiling of the posterior part of the body made exact measurement difficult. Fragments of the tentacle are present, having a diameter of 50μ and bearing one semi-double row of pinnules (Fig. YX133*B*), each 50 to 80μ long.

The fore-part is 2·4 mm long and 0·25 mm wide, without any obvious transverse groove between proto- and mesosoma. The conical cephalic lobe is rather small and sharply pointed (Fig. YX133*E*, *F*). The ventral surface is transversely grooved in front of the tentacle base, but this groove could be an effect of contraction rather than a permanent feature of the species. Behind the tentacle two ridges run alongside the mid-ventral furrow to the point of the bridle and there is a slight notch in each a little before the bridle, which may represent the groove between proto- and mesosoma. The mid-ventral furrow continues a short way behind the bridle. The keels of the bridle lie on a slight ridge, almost touching one another on the ventral side but well separated dorsally (Fig. YX133*D*, *E*). In front of the bridle there are two white patches of epidermal glands, and behind the bridle two ribbons of the same glands extend back almost to the end of the mesosoma (Fig.

(a) *Siboglinum lacteum*
Fore-part of the body inside tube

(b) *Siboglinum lacteum*
Region of the girdles inside tube



(c) *Siboglinum atlanticum*
Coiled tentacle inside tube

(d) *Siboglinum inerme*
Living larva

Plate IV. Photographs of living Pogonophora. By courtesy of A. J. Southward.

YX133*D*). Similar glands are also present in long bands down the metameric part of the trunk, between the dorsal ciliated band and the openings of the internal glands of the papillae. Farther back, patches of glands are associated with the other papillae of the trunk. About 75 pairs of poorly differentiated papillae occupy the 7·5 mm of metameric region, and the remaining 27 mm of the preannular region has only occasional small papillae and diffuse patches of glands until 14 mm before the first girdle. Here there are two enlarged papillae tipped by cuticular bars about 40μ long, and a similar large papillae lies just in front of the first girdle (Fig. YX133*G*, *H*). In the zone of the two enlarged papillae the dorsal epithelium is ciliated (Fig. YX133*G*). As far as I am aware, cilia have not been noted in this region before, but they occur in another species (undescribed) of *Siboglinum* from the Atlantic, and may perhaps be found in others.

The two girdles lie close together, the first consisting of two unequal parts while the second is continuous round three-quarters of the circumference. The toothed platelets are arranged in irregular double or triple rows (Fig. YX133*H*). Each platelet is 15 to 18μ long and has a small group of a few teeth at the anterior end and a larger group of teeth posteriorly (Fig. YX133*C*).

The postannular region of the trunk occupies 15 mm of the tube and is 20 to 25 mm long, being closely coiled up. It bears small dorsal shields of epidermal glands, not well differentiated, opposite fairly large papillae, flanked by smaller papillae, so that there are 3 or 4 papillae opposite each shield. The cuticular bars crowning the papillae are about 15μ long.

The tube is 10 cm long and 0·27 mm wide. The walls are faint milky-white in colour, transparent, soft, unringed and unsegmented. They are slightly wrinkled on the outside (Fig. YX133*A*). The anterior end of the tube is closed, as it can be in some specimens of *S. atlanticum* (Southward & Southward, 1958).

The specific name *lacteum* records the milky appearance of the tube and the animal.

This new species belongs to the sub-group of the genus *Siboglinum* which contains *S. atlanticum*, *S. taeniaphorum*, *S. arabicum*, *S. concinnum* and *S. subligatum*. These are species with epidermal glands in front of the bridle and in bands behind the bridle and along the anterior metasoma. *S. lacteum* resembles *S. atlanticum* in having a mid-ventral furrow from the base of the tentacle to the point of the bridle, but differs from it in lacking a transverse groove between proto- and mesosoma and in having only two enlarged papillae instead of a large number. Other distinctive characters are the unringed tube, the presence of a pretentacular furrow, the presence of pinnules

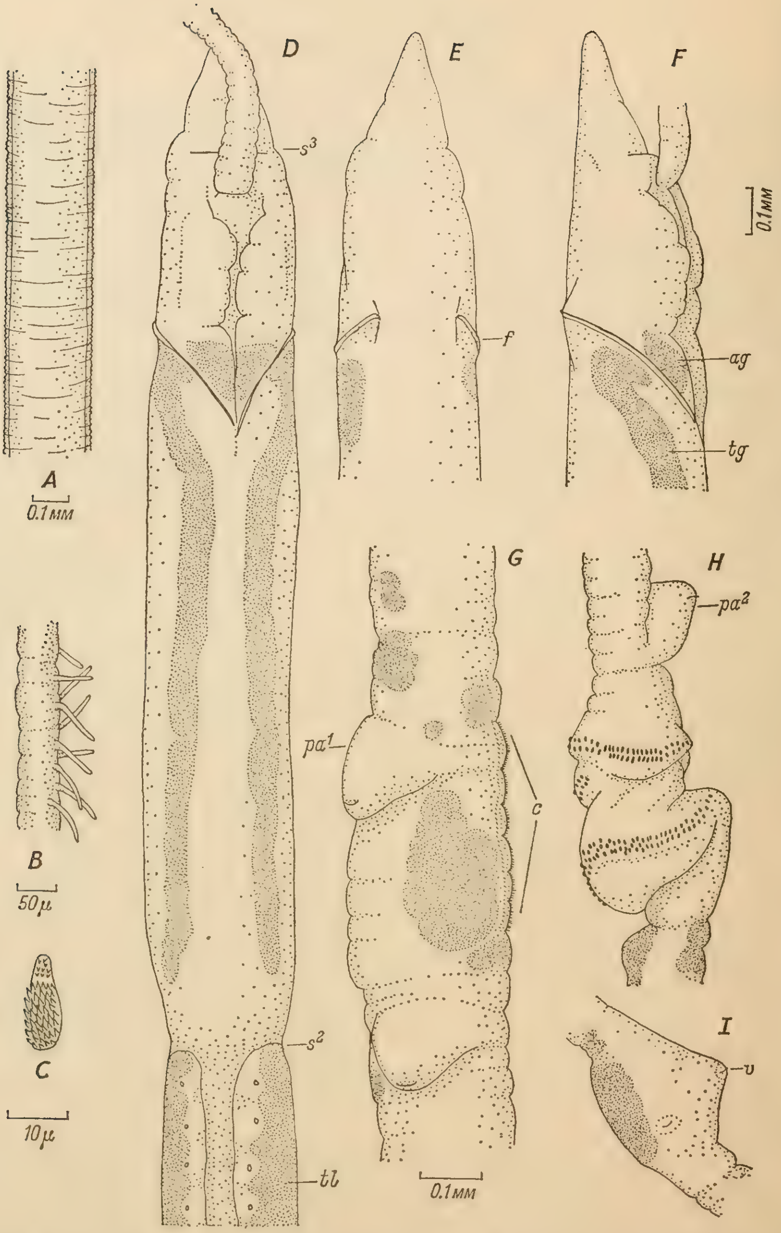


Fig. YX133. *Siboglinum lacteum* sp. nov. E. C. Southward. *A* – part of tube; *B* – part of tentacle; *C* – toothed platelet; *D* – anterior end, ventral view; *E* – anterior end, dorsal view; *F* – anterior end, side view; *G* – region with enlarged papillae and cilia; *H* – girdle region; *I* – postannular shield and papillae.

ag – anterior glandular patch; *c* – cilia; *f* – bridle; *pa*¹ – papilla of zone of thickening; *pa*² – papilla of girdle region; *s*² – groove between mesosoma and metasoma; *s*³ – pretentacular groove; *tg* – glandular tract of mesosoma; *tl* – lateral glandular ribbon of metasoma; *v* – ventral papilla of postannular region.

D, *E*, *F*, *G*, *H*, *I* all to the same scale.) (E. C. Southward.)

Table 2

Characteristics of the species of *Siboglinum*

	1. *S. weberi*	2. *S. ekmani*	3. *S. pinnulatum*	4. *S. fedotovi*	5. *S. plumosum*	6. *S. japonicum*	7. *S. vinculatum*	8. *S. cinctutum*	8a. *S. cinctutum* var. *subtile*	9. *S. frenigerum*	10. *S. caulleryi*	11. *S. pusillum*	12. *S. buccelliferum*	13. *S. microcephalum*
Breadth/length ratio of fore-part	$\frac{1}{7-12}$	$\frac{1}{6-9}$	$\frac{1}{5}$	$\frac{1}{7-10}$	$\frac{1}{5}$	$\frac{1}{6\ 8}$	$\frac{1}{5-7}$	$\frac{1}{4\cdot 5}$	$\frac{1}{5}$	$\frac{1}{7}$	$\frac{1}{6-7}$	$\frac{1}{7-8}$	$\frac{1}{5}$	$\frac{1}{6\cdot 5}$
Presence of pinnules	+	+	+	+	+	+	+	+	+	+	+	+	+	—
Number of rows of pinnules	1	2	2	2	2	2	2	1	1	1	1	1	1	
Pretentacular groove	—	+	+	+	+	+	—	—	—	—	—	—	—	—
Keels fused ventrally	+	+	+	+	—	+	+	+	+	+	+	+	—	+
Keels fused dorsally	—	—	—	—	—	—	+	—	—	+	—	—	+	—
Glandular girdle on mesosoma	+	—	—	+	+	+	—	+	+	+	+	+	—	+
Glandular strips on mesosoma and metasoma	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Number of papillae in zone of thickening	?	?	?	?	?	?	20	11	10	12	5	?	?	?
Number of girdles of toothed platelets	2	3	3	3	?	?	2	2	2	2	2	2	3	3
Number of rows of toothed platelets	1	1	1	1	?	?	2–3	2–3	1–3	2	2	1	1	1
Length of toothed platelets (μ)	12–15	12–16	10–11	17–23	?	?	11–13	12–19	12	10–11	15–20	11–12	16–18	11–12
Breadth of mesosoma (μ)	90	100–150	170	200	500	250	170	250	200	100	250	100	120	180
Length of spermatophore (μ)	40	150	?	250	?	230	300	?	?	?	180	?	?	?

	14. *S. meridiale*	15. *S. pellucidum*	16. *S. hyperboreum*	17. *S. tenue*	18. *S. variabile*	19. *S. bogorovi*	20. *S. minutum*	21. *S. norvegicum*	22. *S. robustum*	23. *S. taeniaphorum*	24. *S. atlanticum*	25. *S. inerme*	26. *S. macrobrachium*
Breadth/length ratio of fore-part	$\frac{1}{8-9}$	$\frac{1}{6-7}$	$\frac{1}{4\cdot 5-5}$	$\frac{1}{5}$	$\frac{1}{5-6}$	$\frac{1}{5-6}$	$\frac{1}{4\cdot 5-5}$	$\frac{1}{7}$	$\frac{1}{4\cdot 5}$	$\frac{1}{10}$	$\frac{1}{9-12}$	$\frac{1}{6-7}$	$\frac{1}{6-10}$
Presence of pinnules	—	—	—	—	—	—	—	—	?	+	+	—	+
Number of rows of pinnules							—		?	1	1		2(?4)
Pretentacular groove	—	—	—	—	—	—	—	—	—	—	—	—	—
Keels fused ventrally	+	+	+	+	+	—	+	+	—	—	—	+	+
Keels fused dorsally	—	—	—	—	—	—	—	—	—	—	—	—	+
Glandular girdle on mesosoma	?	—	—	+	+	+	—	+	—	+	+	+	—
Glandular strips on mesosoma and metasoma	—	—	—	—	—	—	—	—	—	+	+	—	—
Number of papillae in zone of thickening	?	?	?	?	?	20	5	?	?	3	30–40	?	3
Number of girdles of toothed platelets	?	2	3	3	2	2	2	3	3	2	2–3	2–3	3
Number of rows of toothed platelets	1–2	1	2	1	1	1	1	2–4	1	2–4	2–4	1	1
Length of toothed platelets (μ)	12–15	9–12	13–14	8–10	9–12	11–12	10–11	10–15	16–19	11–13	14–18	10–12	10–12
Breadth of mesosoma (μ)	150	100	150	100	160	140	100	200	200	360	360	150	100
Length of spermatophore (μ)	?	140	160	?	?	?	110	?	?	?	500	50	190

	27. *S. debile*	28. *S. timorense*	29. *S. veleronis*	30. *S. subligatum*	31. *S. concinnum*	32. *S. arabicum*	33. *S. silone*	34. *S. ceylonicum*	35. *S. exile*	36. *S. sumatrense*	37. *S. zanzibaricum*	38. *S. sergeevi*	39. *S. lacteum*
Breadth/length ratio of fore-part	$\frac{1}{5-11}$	$\frac{1}{7}$	$\frac{1}{10}$	$\frac{1}{8-10}$	$\frac{1}{9}$	$\frac{1}{8\cdot 5}$	$\frac{1}{7-11}$	$\frac{1}{7-8}$	$\frac{1}{8-9}$	$\frac{1}{9}$	$\frac{1}{3\cdot 5}$	$\frac{1}{3}$	$\frac{1}{10}$
Presence of pinnules	+	+	+	—	+	—	+	+	+	+	+	—	+
Number of rows of pinnules	1	1(5)	2	—	1	—	2	2	2	2	1	—	1
Pretentacular groove	—	—	—	—	—	—	+	+	—	—	—	—	—
Keels fused ventrally	+	+	?	—	—	—	+	+	+	—	+	+	—
Keels fused dorsally	—	—	?	—	—	—	—	—	—	—	+	—	—
Glandular girdle on mesosoma	—	+	?	+	+	+	+	—	+	—	—	—	+
Glandular strips on mesosoma and metasoma	—	+ (met.)	?	+	+	+	—	—	—	—	—	—	+
Number of papillae in zone of thickening	?	?	?	0	?	?	?	0	?	?	?	1	2
Number of girdles of toothed platelets	2	?	2	2	?	2	?	3	3	2	?	2	2
Number of rows of toothed platelets	1	?	?1	2–4	?	2	?	1	1	1	?	1	2–3
Length of toothed platelets (μ)	?	?	?7–8	14–16	?	12–13	?	10–17	11–17	11–12	?	14–18	15–18
Breadth of mesosoma (μ)	100	230	65	270	200	200	250	180	100	90	300	250	200
Length of spermatophore (μ)	?	?	?	350	?	?	?	220	?	?	?	?	?

on the tentacle and the comparatively narrow glandular ribbons of the mesosoma.

Locality not known exactly: within 10-mile radius of 48°30′N., 10°0′W. Depth 1100–1250 m.—E.C.S.]

[2. Genus *Siboglinoïdes* Ivanov, 1961

Ivanov, 1961a: 388, 394–5; Ivanov, 1961b: 138.

The genus consists of Siboglinidae with two tentacles. The coelom of the mesosoma is occupied by flask-shaped glands both in front of and behind the bridle. There are four or five girdles of toothed platelets in two groups, an anterior and a posterior. There are metameric adhesive papillae on the anterior part of the preannular region. There are no cuticular plaques. The postannular region possesses ventral papillae and dorsal glandular shields. The tube is segmented, with three rings per segment.

Type of the genus: *Siboglinoïdes dibrachia* Ivanov.]

The only species so far described is the type species, but a second one has been studied and its description is in the press.

[1. *Siboglinoïdes dibrachia* Ivanov (Figs. X-Z133)

Ivanov, 1961a: 388–393, Figs. 4–6; Ivanov, 1961b: 138, Fig. B.

The following description is based on that of Ivanov (1961a), by kind permission of the Editors of *Cahiers de Biologie marine.*

In many parts of the Indian Ocean one comes across small fine segmented tubes which regularly have three rings per segment. During 1959 and 1960 I have been able to collect some of these tubes while working on board R.V. *Vityaz*' on her 31st cruise, in the Timor Sea, south of Java and the Arabian Sea. Unfortunately we only found six tubes, one of which was empty. The animals extracted from the tubes possessed two tentacles (Fig. X133).

The body of *Siboglinoïdes dibrachia* is very fine: the diameter of the mesosoma is no more than 125μ. The fore-part of the body is very short, only four to five times as long as broad. It is at its widest in the region of the bridle which lies just about the middle of the fore-part (Fig. Y133*A*, *B*, *C*). The protosoma is separated from the mesosoma by an unusually distinct groove which dips sharply backwards in the mid-ventral line. The cephalic lobe, which is separated from the protosoma, is heart-shaped or triangular, rather short, rounded at its tip and noticeably broader than the protosoma. With the protosoma it accounts for a quarter of the fore-part of the body. By transparency one can clearly make out the structure of the epidermis of the cephalic lobe and protosoma, which consists of tall cylindrical cells with numerous gland cells filled with clear secretion scattered amongst them (Fig. Y133*B*).

The two tentacles are attached to the body side by side and the right tentacle is sometimes perhaps a little thicker than the left (Fig. Y133*A*). They are very long and furnished with sparse short pinnules attached in a single longitudinal row (Fig. X133). The basal part of the tentacles lacks pinnules. The tentacular epidermis is rather thick.

The mesosoma tapers towards its hind end. The part lying in front of the bridle has an epidermis as thick as that of the protosoma; the rest has a thin epidermis. The keels of the bridle are thin and colourless. They are situated on distinct ridges, which taper towards their dorsal ends and become much wider on the ventral surface. The keels are fused ventrally but do not meet dorsally (Fig. Y133*A*, *B*, *C*).

The strong development of the multicellular flask-shaped glands in the coelom of the mesosoma can be regarded as a most distinctive character of this species. Contrary to those of many other species of Pogonophora, these glands are developed not only in the posterior part of the mesosoma, but also in front of the bridle where they are readily seen by transparency (Fig. Y133, *A*, *B*, *C*). The boundary between the mesosoma and metasoma is marked by a deep groove which is transverse on the dorsal side but curves backwards on the ventral side (Fig. Y133*A*, *B*, *C*).

The metameric region of the metasoma is two or three times as long as the fore-part of the body (Fig. Y133*A*). The ventral sulcus between the metameric glandular papillae is plainly marked. The papillae are rounded and lack adhesive plaques. They become larger towards the hind end of the region. Each one contains a single large pyriform

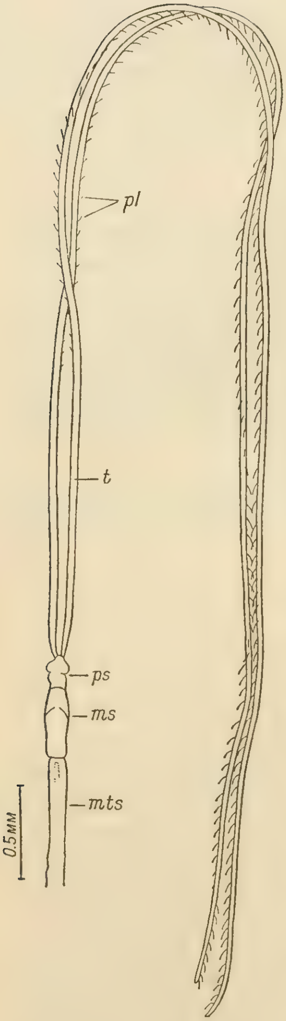


Fig. X133. *Siboglinoïdes dibrachia:* Front end of the body from the dorsal surface.
ms – mesosoma; *mts* – metasoma; *pi* – pinnules; *ps* – protosoma; *t* – tentacle. (After Ivanov, 1961a.)

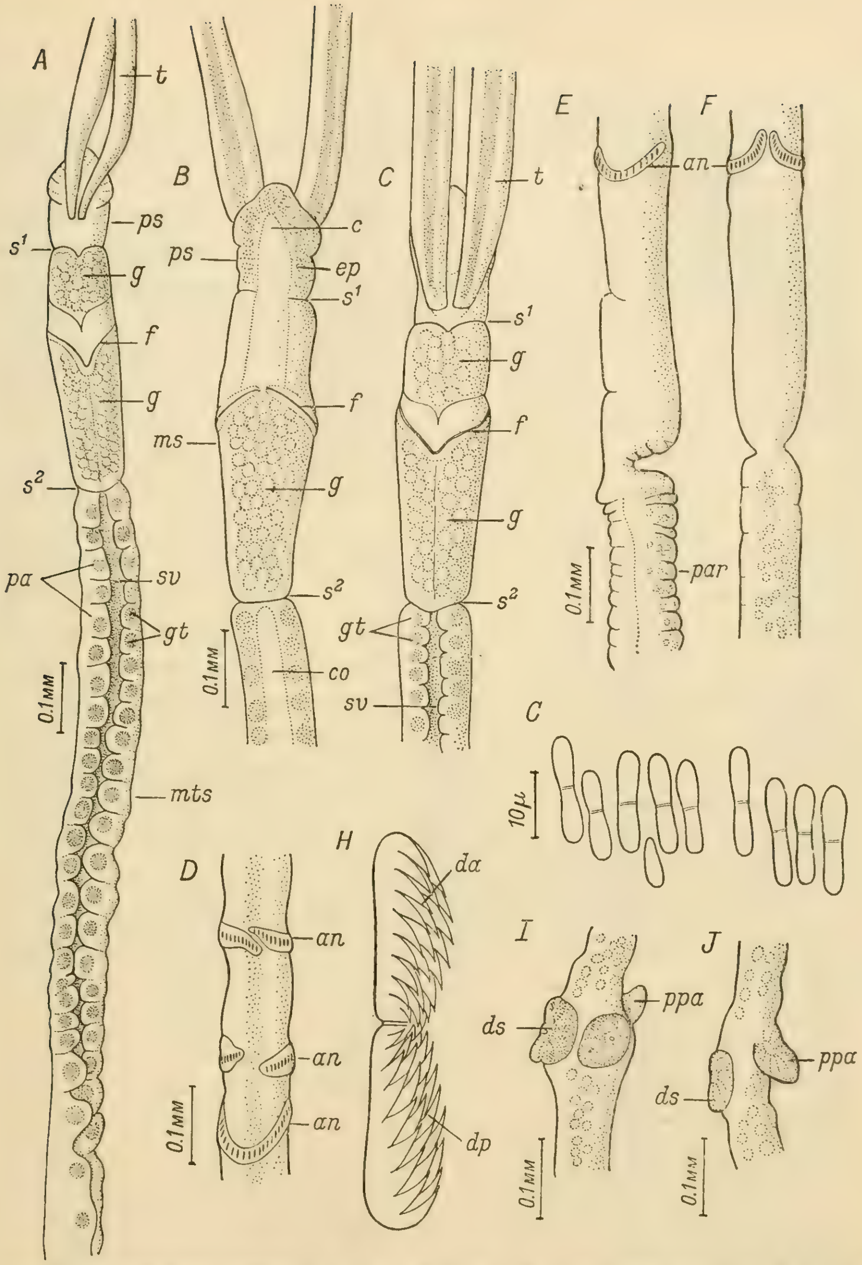


Fig. Y133. *Siboglinoïdes dibrachia : A* – front end of the body from the ventral side; *B*, *C* – the fore-part of the body in dorsal and in ventral view; *D* – the anterior group of girdles; *E*, *F* – the posterior girdle from the right side and in dorsal view; *G* – part of a girdle; *H* – toothed platelet; *I* – a postannular dorsal shield and papilla from the dorsal and, *J*, from the right side.
an – girdle; *c* – cephalic lobe; *co* – dorsal ciliated band; *da* – anterior teeth; *dp* – posterior teeth; *ds* – dorsal glandular shield; *ep* – epidermis; *f* – bridle; *g* – mesosomal flask-shaped glands; *gt* – metasomal pyriform glands; *ms* – mesosoma; *mts* – metasoma; *pa* – metameric papillae; *par* – postannular region of the metasoma; *ppa* – postannular ventral papilla; *ps* – protosoma; *s*^{1} – groove between the protosoma and mesosoma; *s*^{2} – groove between the mesosoma and metasoma; *sv* – ventral sulcus; *t* – tentacle. (After Ivanov, 1961a.)

gland. In one specimen 27 metameric papillae were counted on the right side and 26 on the left. The dorsal ciliated band starts at the very beginning of the metasoma.

This species differs from other Pogonophora in possessing four or five girdles arranged in two groups which are 1·5 – 2 mm apart. The first group, situated at the hind end of the preannular region (the region which contains the oviducts in the female), is composed of three girdles lying close together one behind the other (Fig. Y133*D*). A fourth ring, broken on the dorsal side, lies some way farther back (Fig. Y133*E*, *F*). Of the two specimens in which I have been able to study the girdle region, one possessed also a fifth girdle, with a broad gap on the ventral side, immediately behind the fourth. Shortly behind the last girdle there is a deeply indented wasp-waist (Fig. Y133*E*, *F*). Each girdle bears a single regular row of toothed platelets, shaped like "langue de chat" biscuits. The narrow middle part of the platelet is crossed by a clear transverse line which divides it into two almost equal parts (Fig. Y133*G*) occupied by the two groups of teeth which point in towards the transverse line. The length of the toothed platelets varies between 15 and 17μ.

The postannular region of the trunk is very long and tapers gradually. At long regular intervals solitary conical papillae occur on the ventral surface (Fig. Y133*I*, *J*); they have no cuticular plaques. Opposite each papilla the dorsal glandular shield is normally made up of a pair of swollen cushions, right and left. Each cushion is composed of a rosette of large epidermal cells surrounding the tiny pore of the multicellular flask-shaped gland within.

All the specimens studied were females and some contained ripe eggs.

Measurement of the parts of the body of our specimens gave the following results (mm):

Length of tentacles	Up to 6
Length of fore-part	0·45–0·58
Breadth of mesosoma	0·09–0·125
Length of preannular part of metasoma	Up to 27
Length of postannular region of metasoma	Up to 26
Overall length of body (including tentacles)	Up to 60

The tube is golden-brown in colour. It is smooth, glossy, segmented and ringed. The front end of the tube is transparent and a light yellowish colour soon giving way to the colour of straw. The limits between the segments are sharp; by reflected light they appear white and glistening. The walls of the tube in this region are very thin and homogeneous (Fig. Z133*A*). Then dark rings appear rather rapidly, three per segment. The middle ring of the three is often a little shorter than the others. The colour in this region is a pale brown, or rather brownish, and glistening (Fig. Z133*B*). Then the walls become thicker and darker, taking on a characteristic lustre and a golden brown tint. The interspaces between the rings are narrow and pale gold in colour (Fig. Z133*C*, *D*). In the hind part of this region of the tube the rings often become doublets (Fig. Z133*E*). Still farther back the outlines of the rings begin to break down and become very irregular, and neighbouring rings

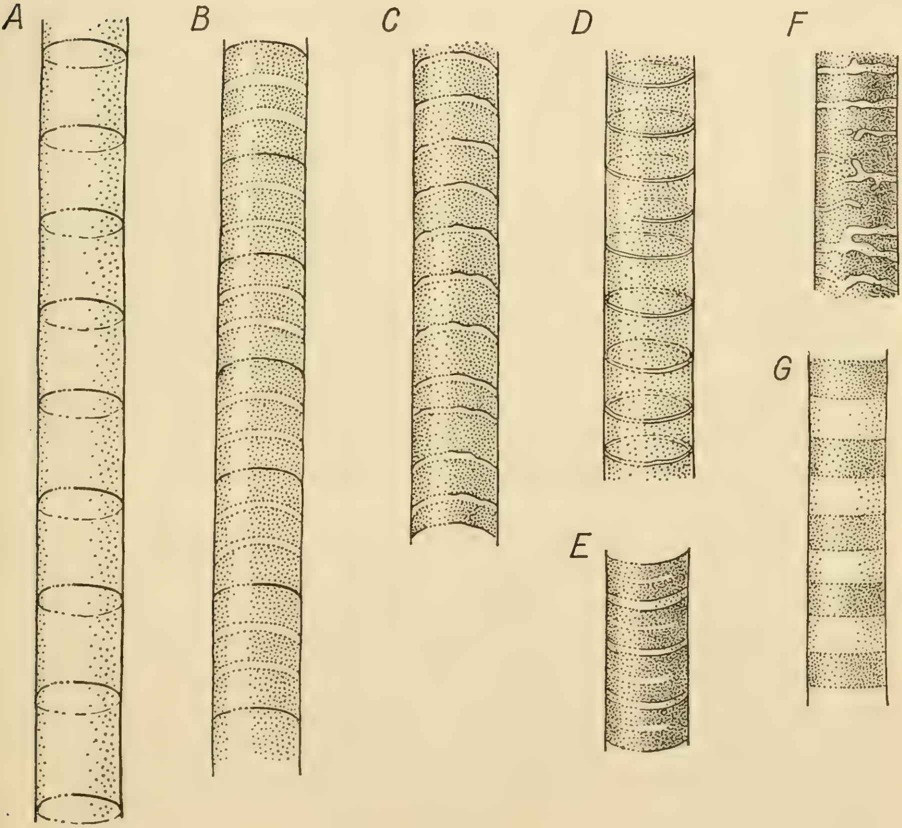


Fig. Z133. *Siboglinoïdes dibrachia :* Tube: *A*–*G* – successive parts starting at the front end. (After Ivanov, 1961a.)

may anastomose (Fig. Z133*F*). The hindmost part of the tube has thin walls. It is pale brown with dark rings some distance apart (Fig. Z133*G*). The longest tube we have had at our disposal was 217 mm long. Its anterior diameter varied from 120 to 135μ and its posterior was 105μ.

It is natural to enquire if the two athecanephrian species with two tentacles —*Nereilinum murmanicum* and *Siboglinoïdes dibrachia*—could perhaps be placed in the same genus. This is, however, impossible. *S. dibrachia* is very close to the genus *Siboglinum* and if it did not possess two tentacles it would be almost impossible to find any serious reason against its inclusion there. It is true that the possession of four or five girdles is not characteristic of the genus *Siboglinum*, but the disposition of the girdles into an anterior and a posterior group is a feature most characteristic of this genus and not encountered anywhere else. A more fundamental difference is the development of flask-shaped glands along the whole length of the mesosoma. This has not been observed in other pogonophores, in which, so far as we know, they are not developed in front of the bridle. All the other features of *Siboglinoïdes* turn up sporadically in different species of *Siboglinum*. Above all, the strong development of the anterior group of teeth on the toothed platelets is otherwise encountered only in a few species of *Siboglinum*, notably in *S. pinnulatum*, *S. fedotovi*, *S. buccelliferum*, *S. hyperboreum* and *S. robustum*. The postannular dorsal glandular shields of *Siboglinoïdes dibrachia* recall of those of *Siboglinum ekmani* (Fig. 97*D*, *E*). The form of the cephalic lobe, the nature of the bridle, and the differentiation and arrangement of the anterior papillae of the trunk are what one expects to find in species of *Siboglinum*. In brief, one could, almost without hesitation, class this species as a *Siboglinum* with two tentacles.

What can be argued against this idea? From what we know about the ontogeny of the tentacular apparatus we can be certain that the single tentacle of *Siboglinum* is the end point of a process of reduction of the tentacular crown, which has left these animals with only the first right tentacle. It is inconceivable that the left tentacle of *Siboglinoïdes* has been added to the right to complete a pair, for this would imply that the direction of evolution had been reversed. We must conclude that in comparison with *Siboglinum* the presence of two tentacles in *Siboglinoïdes* is a primitive character marking a stage in the reduction of the tentacular crown. We cannot derive *Siboglinoïdes* from *Siboglinum* by the addition of another tentacle, but must derive it from a multi-tentaculate ancestor by the reduction of tentacles. From the systematic point of view then, *Siboglinum* and *Siboglinoïdes* must be regarded as separate genera.

We have already noted that *Siboglinoïdes* is much nearer to *Siboglinum* than to *Nereilinum*. The characters which distinguish *Siboglinoïdes* from *Nereilinum* are as follows: in *Siboglinoïdes* the absence of the deep backwards dorsal sweep which the groove between the protosoma and the mesosoma makes in *Nereilinum*, the absence of a glandular girdle behind the bridle and of the masses of glandular cells from the epidermis of the anterior part of the trunk, the presence of four or five girdles arranged in two groups, the strong development of the anterior groups of teeth on the toothed platelets, the presence of flask-shaped glands in front of the bridle and the presence of pinnules on the tentacles. Perhaps the most important distinction is that *Siboglinoïdes* has fully developed secondary metamerism of the papillae of the anterior part of the metasoma, while metamerization of this region has hardly begun in *Nereilinum*, and there are not even any distinct papillae. Since the lack of papillae and of secondary metamerization of the anterior part of the trunk are characteristic of the family Oligobrachiidae, it is evident that *Siboglinoïdes* must be placed in the family Siboglinidae.

Material: six tubes of which one was empty.

Localities: Timor Sea to the south-west of Roty Island (11°30′S, 122° 30′E); Indian Ocean south of the Straits of Bali (9°05′S, 114°14′E); south of Java (8°56′S, 108°22′E); the western part of the Arabian Sea to the north-west of the Island of Socotra at the entrance to the Gulf of Aden (12°48′N, 52°38′E).

Depth: 2080 m to 3300 m.]

2. Order THECANEPHRIA IVANOV, 1955

In the Thecanephria the first coelom is horseshoe shaped, but in the Spirobrachiidae its right half is somewhat drawn out and twisted into a corkscrew, in correlation with the development of the spiral lophophore. The excretory sections of the coelomoducts of the protosoma approach the boundary of the mesosoma in the median plane, where they lie in sac-shaped ventral extensions of the dorsal blood vessel. The tentacles are sometimes fused together. The postannular region of the metasoma has transverse ventral adhesive papillae, bearing cuticular plaques, but it has no dorsal glandular shields. The spermatophores are more or less leaf-shaped. The tube may be ringed or segmented, its front part either filmy, or ending in a hard, funnel-shaped mouth.

The order Thecanephria has three families: Polybrachiidae, Lamellisabellidae and Spirobrachiidae, of which the first is the most primitive.

Fig. YZ133. Map of the geographical distribution of the more recently described species of Pogonophora.

I. Family Polybrachiidae Ivanov, 1952

The Polybrachiidae are Thecanephria with free tentacles. The base of the tentacular crown is a horseshoe, but the ends may be bent round to complete the ring. The pinnules on the tentacles form two or more rows.

The family includes the following genera: *Heptabrachia*, *Cyclobrachia*, *Diplobrachia*, *Zenkevitchiana*, *Polybrachia* and *Galathealinum*. The genus *Krampolinum* (p. 393) may also be regarded as belonging to this family.

1. Genus *Heptabrachia* Ivanov, 1952

Ivanov, 1952: 375, 387–90; Zenkevich, 1954: 76, 80; Zenkevich, Birstein and Belyaev, 1954: 68; Ivanov, 1954b: 72, 75, 76, 79; Hartman, 1954: 185; Ivanov, 1955a: 177; Ivanov, 1955d: 173, 174; Ivanov, 1956b: 1864, 1868; Ivanov, 1956c: 165, 169; Jägersten, 1956: 238; Kirkegaard, 1956b: 186; Abrikosov, 1957: 233; Ivanov, 1957a: 439, 449, 461–9, 470, 475, 490–7; Vinogradova, 1958: 112; Dajoz, 1958: 231; Fell, 1958: 46; Ivanov, 1960a: 1528, 1538, 1539; Ivanov, 1960c: 5, 11, 23, 24, 106, 114, 199, 215, 220.

There are 5–13 free tentacles forming a horseshoe at the base (the earlier report, Ivanov, 1952, 1957a, that *Heptabrachia abyssicola* had its tentacles arranged in a ring, is incorrect (Ivanov, 1960c)). The cephalic lobe is not divided from the protosoma, but the latter is divided from the mesosoma by an annular groove, and in a few species secondary transverse grooves are present on the mesosoma in front of the bridle, whose keels may be either fused on the ventral side or some distance apart. The front part of the trunk has round or oval cuticular plaques. The spermatophores are small and leaf-shaped, tapering from one end to the other. The tube is ringed.

Eight species are known: *Heptabrachia abyssicola* Ivanov, *H. gracilis* Ivanov, *H. subtilis* Ivanov, *H. beringensis* Ivanov, *H. talboti* Southward 1961, *H. ctenophora* Ivanov 1962, *H. canadensis* Ivanov 1962, and *H. celebensis* (Southward 1961).

Key for the identification of the species of the genus *Heptabrachia*

1 (10) In front of the bridle the mesosoma is scored by one or two secondary annular grooves. The adhesive cuticular plaques are oval.

2 (7) The ventral ends of the keels of the bridle fuse or touch. There are four to eight tentacles.

3 (6) There is a single secondary mesosomal groove. The plaques of the metameric papillae are about 20μ across.

4 (5) There are three to five papillae in each transverse row in the post-annular region. The front edges of the plaques on the metameric papillae are smooth. The toothed platelets are 16μ long. The tube has regular rings which are very unequal in length.

2. *H. gracilis* (p. 338).

5 (4) The postannular papillae are solitary. The front edges of the plaques of the metameric section are slightly serrated. The toothed platelets are up to 20μ long. The tube is segmented, with obvious funnels on the front rims of the segments; the regular rings are all equally short. 6. *H. celebensis* (p. 354).

6 (3) There are two secondary mesosomal grooves. The cuticular plaques on the metameric papillae are about 30μ across. There are about 15 papillae in disorderly confusion in the zone of thickened papillae. The toothed platelets are 11–12μ long. The rings at the front end of the tube are very short, but in the middle part of the tube they become very irregular in length. 8. *H. canadensis* (p. 365).

7 (2) The ventral ends of the keels of the bridle do not meet. There are more than ten tentacles. There are two secondary mesosomal grooves.

8 (9) The keels of the bridle look like combs, consisting of a long cuticular axis down the front edge and a broad membrane behind in which dark rod-like thickenings, like the teeth of a comb, are embedded. There are about 13 pairs of metameric papillae. The plaques are 30–40μ across and the toothed platelets up to 18μ long. The tube has short, sometimes irregular rings. 7. *H. ctenophora* (p. 360).

9 (8) The keels of the bridle are simple. There are 24–26 pairs of metameric papillae. The plaques are 25–35μ across and the toothed platelets up to 14μ long. The tube has regular rings which are not very long. 4. *H. beringensis* (p. 347).

10 (1) There are no secondary annular rings on the mesosoma in front of the bridle.

11 (12) The plaques of the metameric papillae are round, about 20μ in diameter. The dorsal ends of the keels of the bridle do not meet. The tube has irregular rings with no fibrous external layer. 1. *H. abyssicola* (p. 335).

12 (11) The plaques of the metameric papillae are oval and about 20–40μ across. The keels of the bridle fuse dorsally.

13 (14) The keels of the bridle fuse ventrally. There are less than ten tentacles. The plaques of the metameric papillae are about 20μ across. The tube has irregular rings and an external fibrous layer. 3. *H. subtilis* (p. 342).

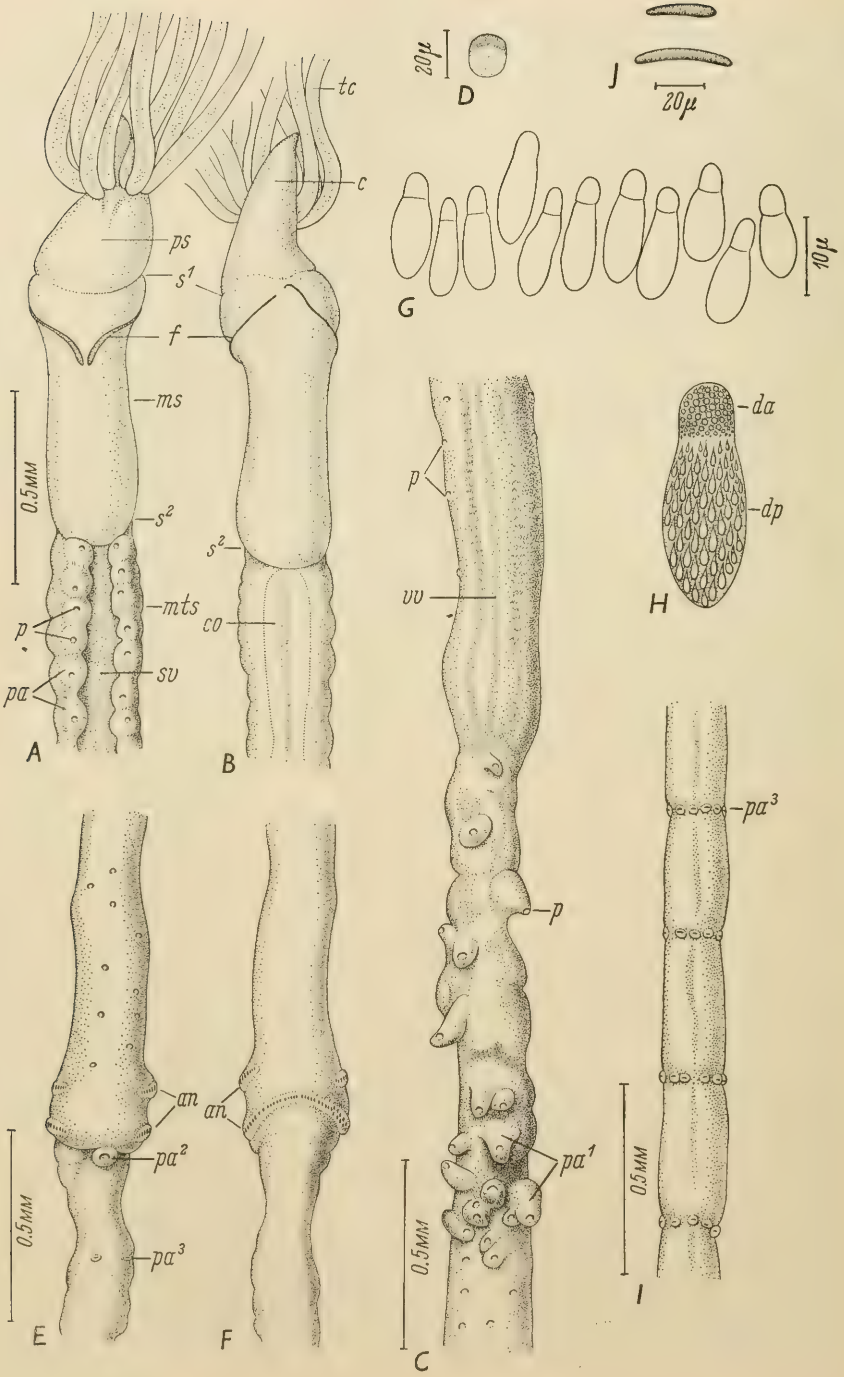
14 (13) The keels of the bridle do not meet ventrally. There are more than ten tentacles. The plaques of the metameric papillae are 30–40μ across. The tube has more or less regular rings, but lacks a fibrous external layer. 5. *H. talboti* (p. 350).

1. *Heptabrachia abyssicola* Ivanov (Figs. 134–5)

Ivanov, 1952: 375–7, 388, Figs. 2–6; Zenkevitch, Birstein and Belyaev, 1954: 68, Fig. 10; Zenkevitch, 1954: 76, 80, Figs. 4, 8; Hartman, 1954: 185; Ivanov, 1954b: 72, 76, Figs. 2, 8; Kirkegaard, 1956b: 186, Fig. 4; Abrikosov, 1957: 233; Ivanov, 1957a: 463, 464, 468, 469, 491, 493, 496, 497, Fig. 59; Vinogradova, 1958: 112; Dajoz, 1958: 233, 236, 237, Fig. 6; Ivanov, 1960a: 1553; Ivanov, 1960c: 5, 16, 20, 22, 37, 93, 199, 200–3, 204, 211, 214, 266, Fig. 87, 134–5.

The cylindrical fore-part of the body, which has a length to breadth ratio of 5–6 : 1, has a simple groove dividing the protosoma from the mesosoma. The conical cephalic lobe is pointed (Fig. 134*A*, *B*). The bases of the seven or eight very long tentacles are arranged horseshoe-wise; the pinnules have not been investigated. The yellow keels of the bridle, lying in front of the middle of the fore-part of the body, do not meet ventrally, where they are perceptibly thicker (Fig. 134*A*), and taper towards the dorsal ends. A faint median furrow is sometimes noticeable on the ventral surface of the fore-part of the body, while the hind edge of the mesosoma is curved.

The comparatively small, rounded, adhesive papillae of the front part of the metasoma number 14–20 pairs, each with a round cuticular plaque (Fig. 134*A*). This metameric part makes up a tenth of the whole preannular region of the trunk, and the ventral side of the succeeding, cylindrical, non-metameric part carries numerous disordered adhesive papillae. The dorsal ciliated band is well developed, especially its front portion, which begins immediately at the boundary between the mesosoma and the metasoma (Fig. 134*B*). The male genital papillae are small. The zone of thickened papillae consists of approximately 20 large conical disordered papillae, occupying the ventral side of the trunk (Fig. 134*C*). The cuticular plaques in the front metameric part of the trunk are 20μ across and very soft. The front edge of each plaque is thickened into a sort of sickle-shaped rim, the remaining part forming a delicate membrane (Fig. 134*D*). Similar plaques are found also on the papillae of the non-metameric part of the trunk (Fig. 134*C*), but on those of the zone of thickening the plaques are noticeably bigger. There are two girdles, both widely interrupted ventrally and the first girdle dorsally also (Fig. 134*E*, *F*). The yellowish toothed platelets, mostly between 10 and 15μ long, are uniserial, but occasionally the beginnings of two rows may be seen (Fig. 134*G*). The teeth of the front group are very small and the front part of the platelet, which they occupy, is somewhat narrower than the rest, colourless and often distinctly demarcated by a transverse line (Fig. 134*H*). A single large ventral papilla, with an especially large cuticular plaque, lies behind the second girdle (Fig. 134*D*). The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I
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very long postannular region of the trunk has on its ventral side about 40 transverse metameric rows, each of 7–8, of small papillae, arranged rather regularly at more or less equal intervals (Fig. 134*I*). The transverse cuticular plaques, 35–40μ long, on the papillae are rod-shaped and curved just a little forward (Fig. 134*J*).

Measurements made on two individuals gave the following results: length of the fore-part of the body, 1·1–1·7 mm; breadth of the mesosoma, 0·23–0·25 mm; overall length, excluding the tentacle, 59·7–71·1 mm; ratio of length of whole body to its breadth, *c.* 270:1. The preannular region of the trunk is one and a half times as long as the postannular section, and the metameric part accounts for only a fifteenth of the whole length of the trunk.

The spermatophores are shaped like flat leaves, drawn out into a long point at one end and rounded at the other (Fig. 135*A*). The transparent membrane of the spermatophore is very thin and delicate and inside it lie the numerous thread-like sperm with the head ends towards the rounded end of the spermatophore and fanning out to lie perpendicular to the wall in this part. A cortical zone at the broad end of the spermatophore is free of sperm. The filament which one would expect to find attached to this end has not been observed (Ivanov, 1952), but there is little doubt of its existence, the more so as it has been described in *H. gracilis* (Ivanov, 1957a). The spermatophores are 0·34 mm long.

The anterior part of the slender semi-transparent light-brown tube has irregular brown rings (Fig. 135*B*), and farther back they become longer and diffuse (Fig. 135*C*). The longest fragment measured 122 mm, but the total length of the tube must be not less than 200 mm, with a diameter of 0·33 mm.

Like *H. subtilis*, *H. abyssicola* has no secondary grooves on the mesosoma in front of the bridle, but it is distinguished by the large cuticular plaques (a feature not encountered in other species) and by the unfused keels of the bridle.

Material: 4 specimens in broken tubes.

Locality: the Kuril-Kamchatka Trench. Depth: 6475–8164 m.

Fig. 134. *Heptabrachia abyssicola*: *A* – front end of a female from the ventral, and, *B* – from the dorsal side; *C* – region of thickened papillae from the ventral side; *D* – cuticular plaque from the front part of the metasoma; *E* – region of the girdles from the ventral, and, *F* – from the dorsal side; *G* – part of a girdle; *H* – toothed platelet; *I* – part of the postannular region from the ventral side; *J* – hoop-shaped plaques from the postannular region.
an – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *da* – anterior group of teeth; *dp* – hind group of teeth; *f* – keel of the bridle; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaque; *pa* – metameric papillae; *pa*^{1} – papillae of the zone of thickening; *pa*^{2} – ventral papilla behind the girdles; *pa*^{3} – papillae of the postannular region; *ps* – protosoma; *s*^{1} – groove between the protosoma and the mesosoma; *s*^{2} – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *tc* – tentacular crown; *vv* – ventral blood vessel seen by transparency.

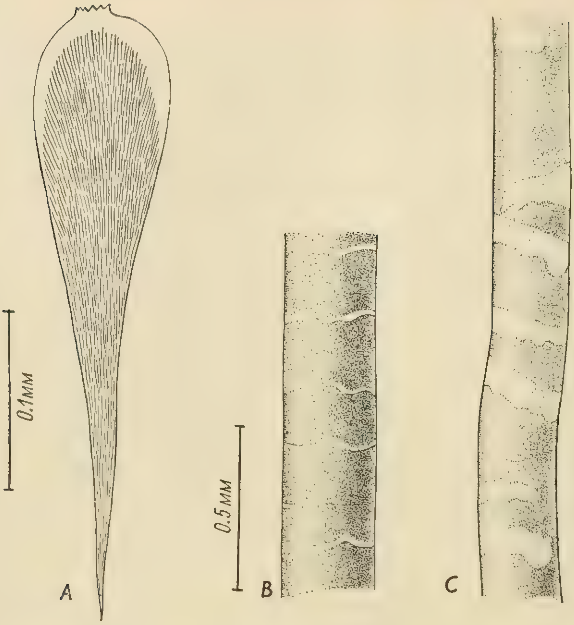


Fig. 135. *Heptabrachia abyssicola*: *A* – spermatophore (filament omitted); *B* – middle part of tube; *C* – hind part of tube. (After Ivanov, 1952.)

2. *Heptabrachia gracilis* Ivanov (Figs. 136–7)

Ivanov, 1957a: 449, 461–5, 469, 493, 495–7, Figs. 31–4, 59; Dajoz, 1958: 236; Ivanov, 1960a: 1531, 1537, 1612, Fig. 1394; Ivanov, 1960c: 5, 12, 16, 20, 22, 96, 199, 200, 203–6, 211, 214, 215, 266, Figs. 87, 136–7.

The fore-part of the body is cylindrical and the protosoma is only a quarter the length of the mesosoma, from which it is divided by a clear annular groove (Fig. 136*A*, *B*), while the broad, more or less triangular cephalic lobe is not divided from it at all. The very long tentacles, attached in a horseshoe, number five to seven. Their pinnules have not been studied because of the bad state of preservation of the material. A noteworthy feature of the mesosoma is a transverse groove in front of the bridle, as a result of which the front section of this segment looks like a broad girdle divided down the mid-ventral line by a deep furrow (Fig. 136*A*). Similar secondary mesosomal grooves are found also in *H. beringensis* and in *Polybrachia*, which latter, however, possesses not one but several mesosomal girdles (pp. 347 and 393). The stout greyish, weakly cuticularized keels of the bridle, situated just a

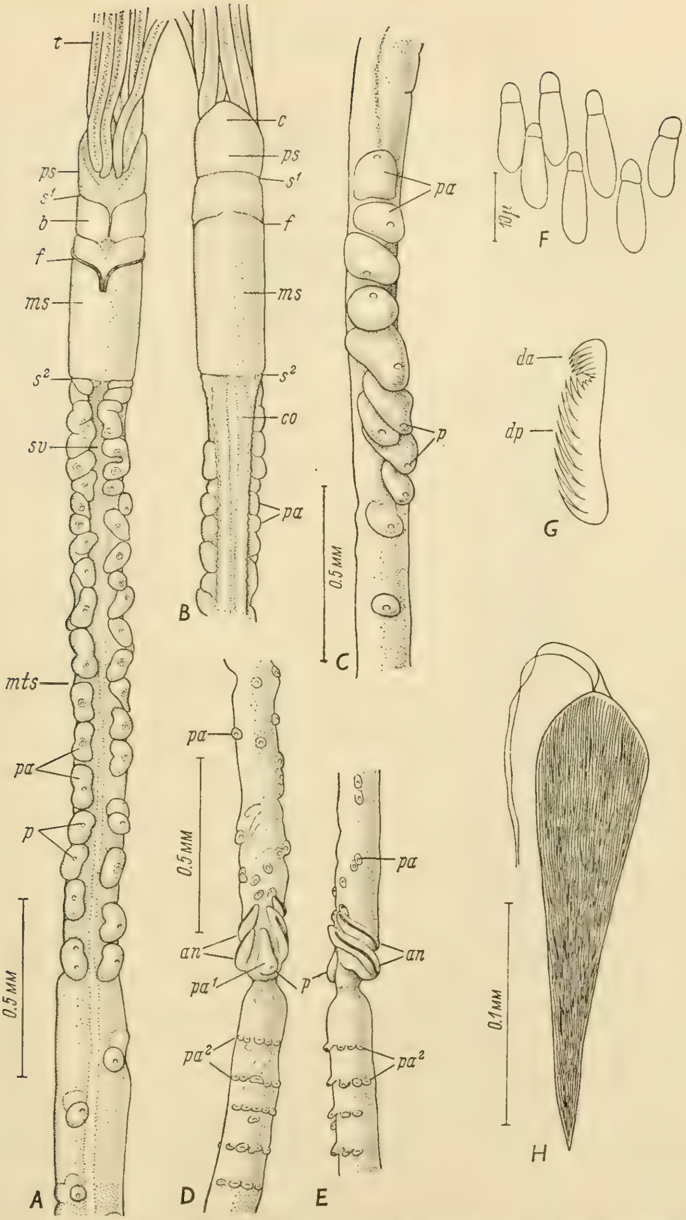


Fig. 136. *Heptabrachia gracilis: A* – front part of the body of a female from the ventral, and, *B* – from the dorsal side; *C* – zone of thickened papillae from the ventral side; *D* – region of the girdles from the ventral side; *E* – the same from one side; *F* – part of a girdle; *G* – toothed platelet from one side; *H* – spermatophore.

an – girdles; *b* – secondary annulus of the mesosoma; *c* – cephalic lobe; *co* – dorsal ciliated band; *da* – front group of teeth; *dp* – hind group of teeth; *f* – keel of bridle; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaques; *pa* – papillae; pa^1 – ventral papilla behind the girdles; pa^2 – metameric rows of postannular papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacles. (*A*, *B*, *C*, *D*, *E*, *H* after Ivanov, 1957*a*.)

little in front of the middle of the mesosoma (Fig. 136*A*, *B*), are fused ventrally and just fail to meet dorsally. The annular groove between the mesosoma and the metasoma is straight.

The short metameric part of the preannular region of the trunk is not more than two to two-and-a-half times the length of the mesosoma, and the ventral sulcus is feebly developed (Fig. 136*A*). The 17–18 pairs of comparatively big, metameric papillae are variable in shape, but often transversely elongated. Cuticular plaques are absent from the first one or two pairs of papillae, but on the remainder they look like broadly oval, transverse scales with dark crescentic thickenings along the front edge (Fig. 136*A*). As in *H. abyssicola*, where, however, they are round, these scales reach 20μ in greatest diameter. The dorsal ciliated band is so broad that it takes up the whole dorsal surface, beginning immediately at the front end of the trunk (Fig. 136*B*). The very long, cylindrical non-metameric part of the trunk is furnished with sparse scattered rounded adhesive papillae, mainly sited on the ventral side (Fig. 136*A*). Shortly behind the centre of this region they are larger, then become smaller again and characterized by somewhat smaller cuticular plaques, *c.* 15μ across. The well-developed zone of thickened papillae has 12–13 large, conical papillae arranged in a dense, mid-ventral row (Fig. 136*C*). The oval plaques here are about 25μ across. The two girdles, lying close together on well-marked ridges, are bow-shaped, arching backwards, and interrupted on the ventral side with the ends turned forward (Fig. 136*D*, *E*). In most specimens the first girdle is interrupted dorsally also, but in one individual there was no dorsal gap. The mainly biserial yellowish toothed platelets of the girdles, up to 16μ in length, are comparatively narrower than in *H. abyssicola*, but furnished with larger and longer teeth. The small group of anterior teeth is clearly demarcated from the hind group (Fig. 136*G*). The very long, cylindrical postannular region of the body begins with a pronounced waist immediately behind the second girdle, and then all along it small adhesive papillae are developed, arranged on the ventral side in transverse metameric rows of 3–5 each (Fig. 136*D*, *E*). Each papilla bears a transverse, rod-shaped, slightly curved, adhesive plaque.

To judge by one very nearly complete individual, the body must reach a length of 10 cm. The tentacles are 3 mm long; the fore-part of the body 0·8 mm long by 0·2 mm broad; the metameric portion of the trunk is not more than 2 mm long.

The spermatophore is shaped like that of *H. abyssicola*, but smaller by at least a third, and, as in the rest of the Pogonophora, it is furnished with a very long, slender filament, with a ribbon-like, transparent base. The spermatophores look like tiny flat narrow leaves, 0·2 mm long, gradually tapering towards one end and rounded at the other, filamentary end (Fig. 136*H*). The thread-like sperm are crowded parallel to each other along the length of the spermatophore.

A considerable length of the front part of the tube is transparent, with delicate thin limp walls. The greater part of the tube, however, is muddy brown, rather rigid and ringed. A characteristic of the tube is the very uneven length even of adjacent rings, so that an exceedingly short one may lie cheek by jowl with a very long ring (Fig. 137*A*). Short clear intervals separate the rings in this part. Towards the hind end of the tube, however, the intervals become longer, and the rings, which are here no longer than the diameter of the tube, become much paler in colour and their edges uneven (Fig. 137*B*). The hindmost part of the tube lacks rings altogether and the walls are here white and parchment-like (Fig. 137*C*). One of the longest scraps of tube measured 18 cm long, with a diameter of 0·25 mm near the front end and 0·19 mm near the hind end. A comparison of the lengths of the different sections of the tube, however, suggests that the overall length cannot be less than 25 cm. The anterior transparent section reaches 5–6 cm in length, and the hind parchment-like section is at least as long, if not longer.

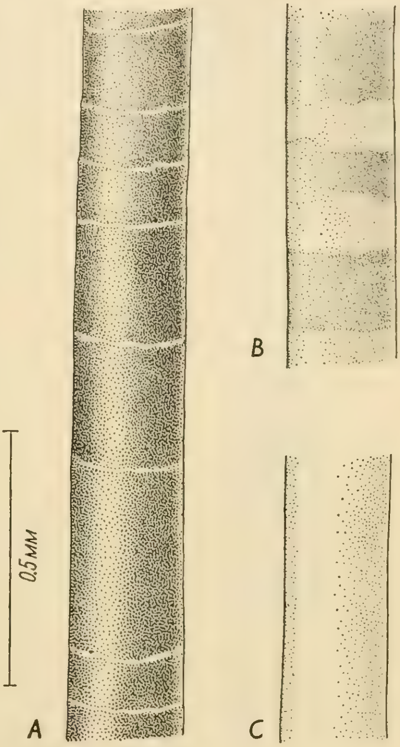


Fig. 137. *Heptabrachia gracilis*: Tube: A – middle part; *B* – hind part of ringed region; *C* – hindmost membranous section. (After Ivanov, 1957*a*.)

H. gracilis is distinguished by a number of features from other species of the same genus. The most important of these are the following: the possession of a single secondary annular groove cutting off the very front part of the mesosoma; the uniserial papillae of the zone of thickening; and the comparatively large number (3–5) of papillae in each of the transverse metameric rows of the postannular region. In addition, as may be seen from Table 3, facing p. 368, there are characteristic distinctions in the relative dimensions of the protosoma, the number of tentacles, the development of the keels of the bridle, the shape and dimensions of the cuticular plaques, the dimensions of the toothed platelets, the number of metameric papillae and of the papillae of the zone of thickening, the dimensions of the spermatophores, etc.

Material: many tubes, some with animals.

Locality: the Bering Sea to the east, southeast and south of Cape Olyutorski (60°N 171°E), and also to the east of the Komandorski Islands (55°N 166°E). Depth: 1693–4811 m.

3. *Heptabrachia subtilis* Ivanov (Figs. 138–41)

Ivanov, 1957a: 465–9, 491, 494, 496–8, Figs. 35–40; Dajoz, 1958: 236; Ivanov, 1960c: 6, 11, 12, 23, 92, 93, 199, 200, 203, 207–211, 214, 263.

Only two females of this species are known. The slender fore-part of the body is almost cylindrical (Fig. 138*A*, *B*). The protosoma is half the length of the mesosoma and the sharp groove between them runs straight across the ventral side and arches forward dorsally. The elongated cephalic lobe, which is not divided from the protosoma, is slightly flattened dorsoventrally. In front of the base of the tentacular crown lies a broad depression in the protosoma but this is most probably an artefact resulting from the strong contraction of the base of the tentacular crown into the body at the moment of fixation. The tentacles are long and thin. Their number has been studied only in sections, in which seven were found in one

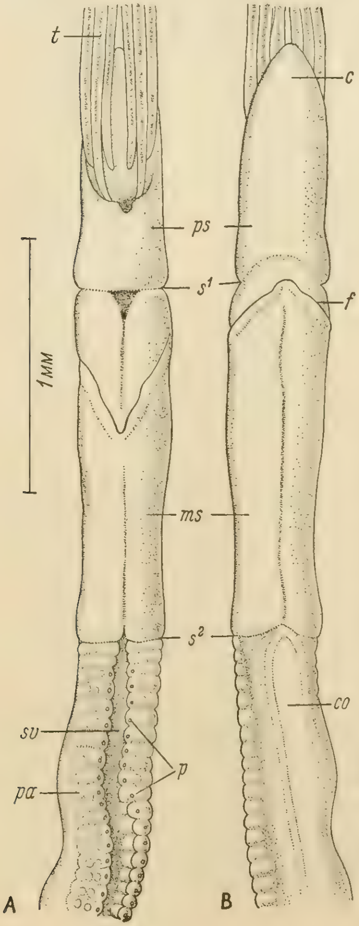


Fig. 138. *Heptabrachia subtilis*: Front end of a female. *A* – in dorsal, and, *B* – in ventral view.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – keel of the bridle; *ms* – mesosoma; *p* – cuticular plaques; *pa* – papilla with pyriform glands visible by transparency; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacles. (After Ivanov, 1957*a*.)

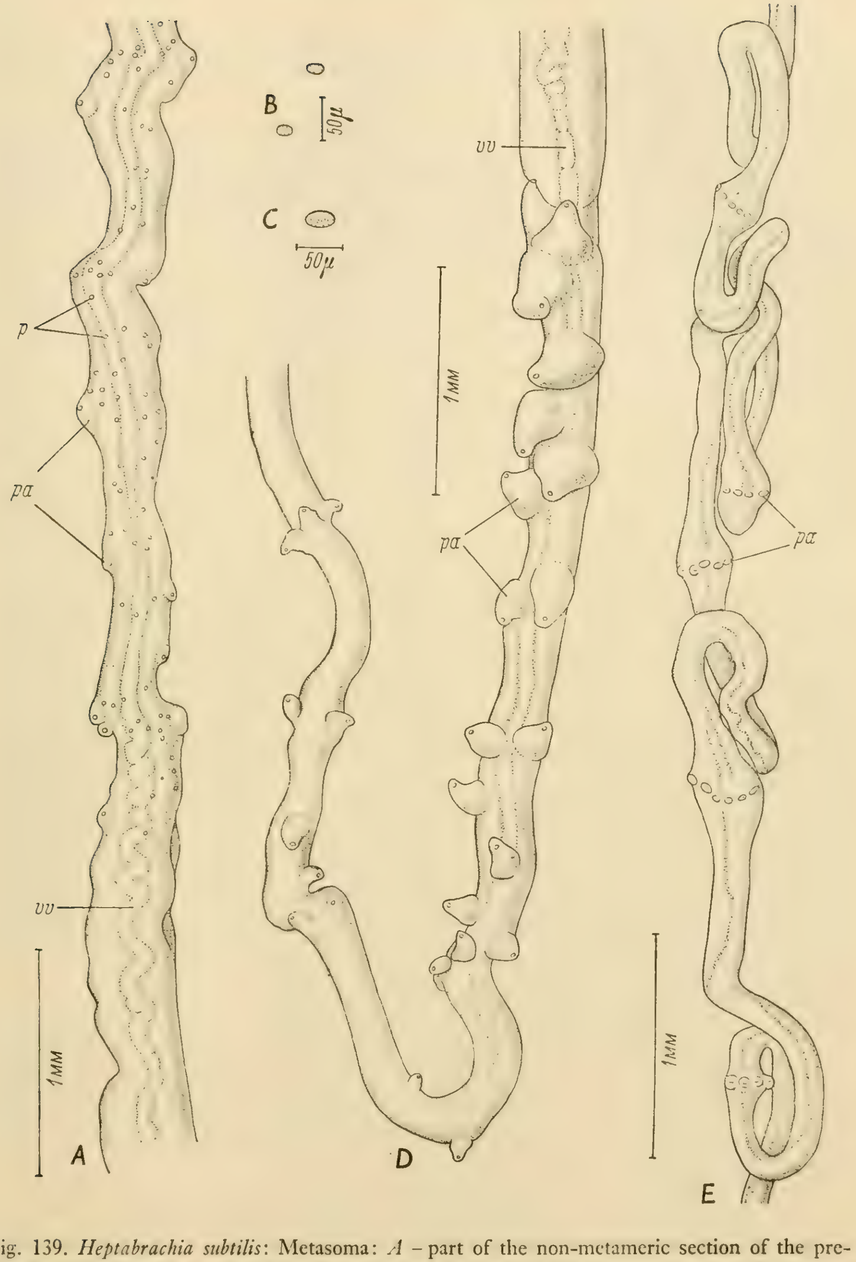


Fig. 139. *Heptabrachia subtilis*: Metasoma: *A* – part of the non-metameric section of the pre-annular region from the ventral side; *B* – cuticular plaques from the metameric region; *C* – plaques from the zone of thickened papillae; *D* – zone of thickened papillae from the ventral side; *E* – part of the postannular region in ventral view.
p – plaques; *pa* – papillae; *vv* – ventral blood vessel seen by transparency. (After Ivanov, 1957*a*.)

individual and eight in the other. The mesosoma has a ventral furrow. The very slender keels of the bridle are fused both ventrally and dorsally (Fig. 138*A*, *B*).

The front part of the trunk has a pronounced ventral sulcus and a broad fringed dorsal ciliated band, beginning at the very front edge of the metasoma. The regular oval metameric papillae are crowded together and each bears a small oval cuticular plaque with a thickened front edge (Fig. 138*A*). The succeeding, very long part of the trunk (Fig. 139*A*) bears conical or oval papillae, placed chiefly on the sides of the body, more or less at random. The muddy-brown oval plaques on their tips are 35–40μ across (Fig. 139*C*) and numerous similar plaques are scattered all over the dorsal and ventral surfaces of the trunk. The next, rather prominent part of the trunk, in which are situated the oviducts, is filled with eggs showing through the distended body wall. Papillae and plaques are absent from this region, which, however, is immediately followed by the zone of thickened papillae, where 15–18 very large, conical papillae are irregularly localized on the ventral side (Fig. 139*D*). Each bears on its tip an oval cuticular plaque up to 35μ across. Backwards from this region the papillae gradually grow smaller and the whole succeeding part of the trunk, as far as the girdles, has small scattered conical papillae. The two girdles, of the usual kind, lie on muscular swellings (Fig. 140*A*, *B*). Both are interrupted ventrally and the first dorsally also. The yellowish toothed platelets, 10–14μ long, are biserial, or in places triserial (Fig. 140*C*). They are comparatively broad, narrowing towards the hind end. The front group of teeth is well marked, and the part of the platelet occupied by them is colourless and clearly demarcated from the rest (Fig. 140D). A large median papilla with no plaque lies behind the girdles (Fig. 140*B*). The long slender postannular region of the trunk has metamerically repeated glandular thickenings, each of which bears an almost complete ring of 5–7 small conical papillae, with oval plaques 35μ across (Fig. 139*E*).

Both the available specimens proved to be females. The body of the larger, whose hind end was torn off, was 15 cm long, of which the postannular region accounted for more than half. The tentacles were not less than 4 mm long, the fore-part of the body 2·3 mm, the protosoma *c.* 1 mm long, and the trunk *c.* 0·4 mm broad.

The firm yellow tube is formed of very irregular muddy-brown rings with clear intervals between them (Fig. 141*B*). A considerable length at the front, however, is clad externally with a peculiar peripheral layer which is easily stripped off with a sharp scalpel (Fig. 141*A*). This rather thin, brownish layer contains coarse transverse fibres, often branching and interlacing, and

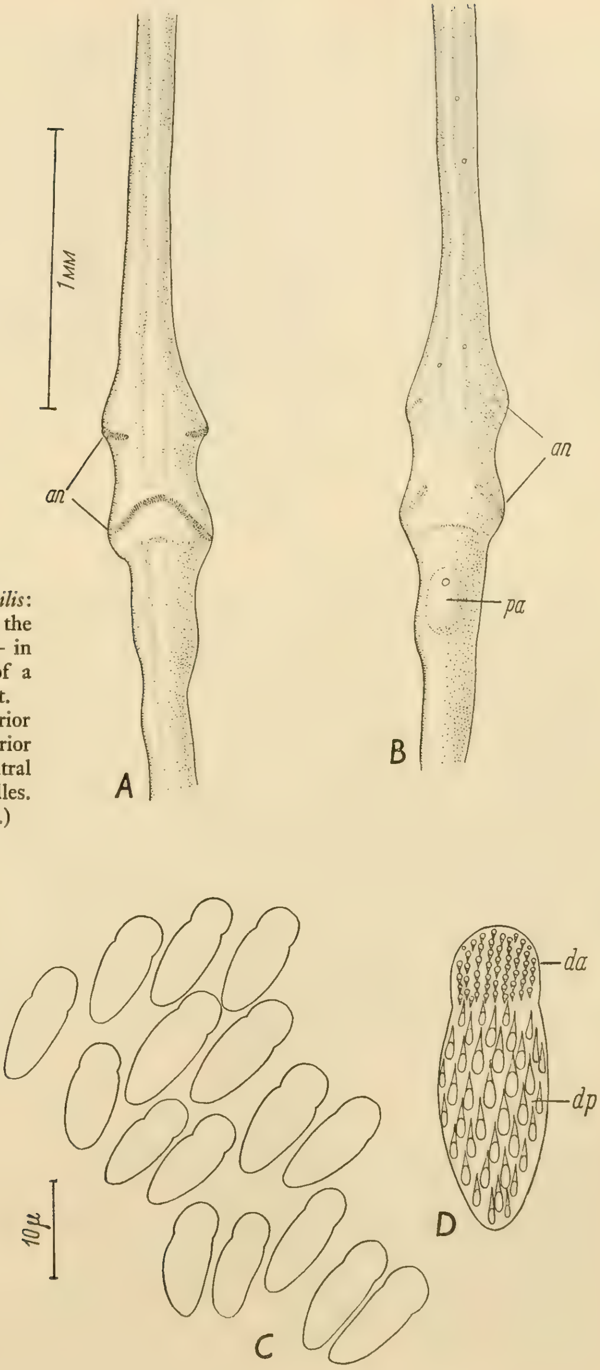


Fig. 140. *Heptabrachia subtilis*: Girdles: *A* – region of the girdles in dorsal, and, *B* – in ventral view; *C* – part of a girdle; *D* – toothed platelet. *an* – girdles; *da* – anterior group of teeth; *dp* – posterior group of teeth; *pa* – ventral papilla behind the girdles. (*A*, *B* – after Ivanov, 1957*a*.)

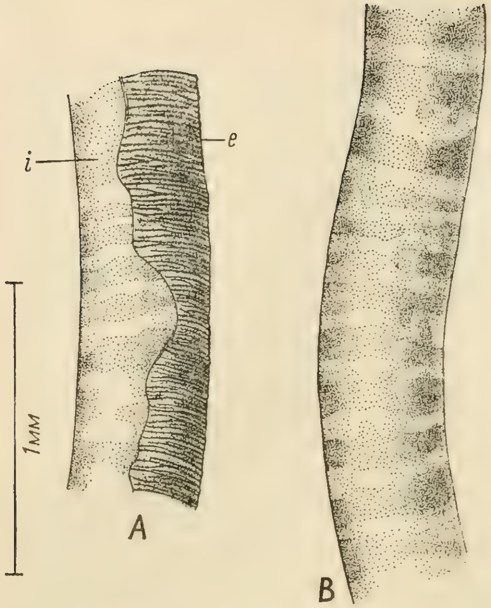


Fig. 141. *Heptabrachia subtilis*: Tube: *A* – part of the front half of the tube (external layer partly removed); *B* – hind part.
e – outer fibrous layer; *i* – inner layer. (After Ivanov, 1957*a*.)

slightly raised up on the surface of the tube, giving it a delicately wrinkled or ridged appearance. An analogous structure, to all appearances, is encountered in *Birsteinia vitjasi*, in which, however, the similar peripheral fibrous layer is distinguished by its noticeably greater thickness and frequently by its black tint (Ivanov, 1952). The very front part of the tube of *Heptabrachia subtilis* is transparent, with membranous, limp walls. In the hind half of the tube the external fibrous layer vanishes (Fig. 141*B*), and the hindmost end of the tube has homogeneous, transparent walls, muddy-brown and rather firm in consistency. To judge by the available fragments the overall length of the tube cannot be less than 25 cm, with a diameter of 0·5 mm near the front end and 0·17 mm near the back end.

The diagnostic features of *H. subtilis* are as follows: the absence of any secondary grooves of the mesosoma (a feature shared by *H. abyssicola*), the fusion both dorsally and ventrally of the keels of the bridle, the higgledy-piggledy papillae of the zone of thickening, the possession of 5–7 papillae in each transverse row of the postannular section, the oval shape of the adhesive plaques (as in *H. gracilis*, *H. beringensis* and *H. talboti*), and the development of the peculiar external fibrous layer of the tube. The characters of the seven species of *Heptabrachia* are compared in Table 3, (facing p.368).

Material: two females and one empty tube.

Locality: the Japan Trench to the northeast of Ogasawara Gunto (or the Bonin Islands) (29°N 143°E).

Depth: 9715–9735 m.

4. *Heptabrachia beringensis* Ivanov (Figs. 142–4)

Ivanov, 1960c: 5, 9, 14, 20, 24, 106, 199, 200, 203, 211–5, 265, Figs. 87, 142–4.

Amongst the abundant pogonophoran material collected in the semi-abyssal zones of the southern part of the Bering Sea were two tubes containing well-preserved animals of a hitherto unknown species of *Heptabrachia*. The cylindrical fore-part of the body of *H. beringensis* is six times as long as it is broad, while the short, lappet-like cephalic lobe is flattened dorso-ventrally. The very short protosoma, which is sharply divided from the mesosoma by a straight annular groove, bears a circle of 12–13 free tentacles, each with seemingly triserial pinnules (Figs. 142, 143*A*, *B*). The mesosoma has two secondary, annular grooves in front of the bridle, intersected by a

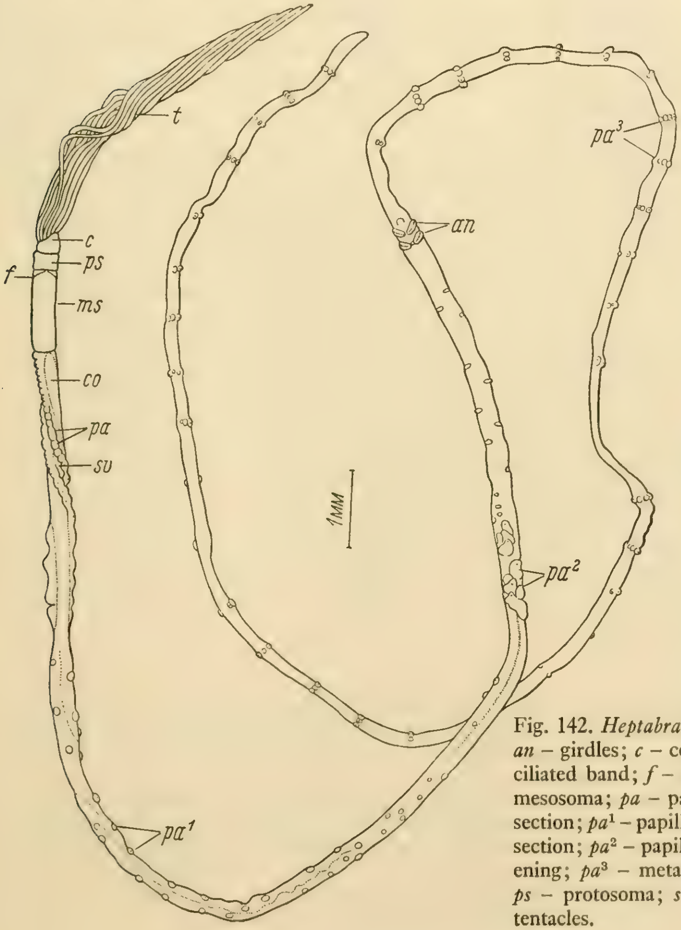


Fig. 142. *Heptabrachia beringensis*: Female. *an* – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – keel of the bridle; *ms* – mesosoma; *pa* – papillae of the metameric section; pa^1 – papillae of the non-metameric section; pa^2 – papillae of the zone of thickening; pa^3 – metameric rows of papillae; *ps* – protosoma; *sv* – ventral sulcus; *t* – tentacles.

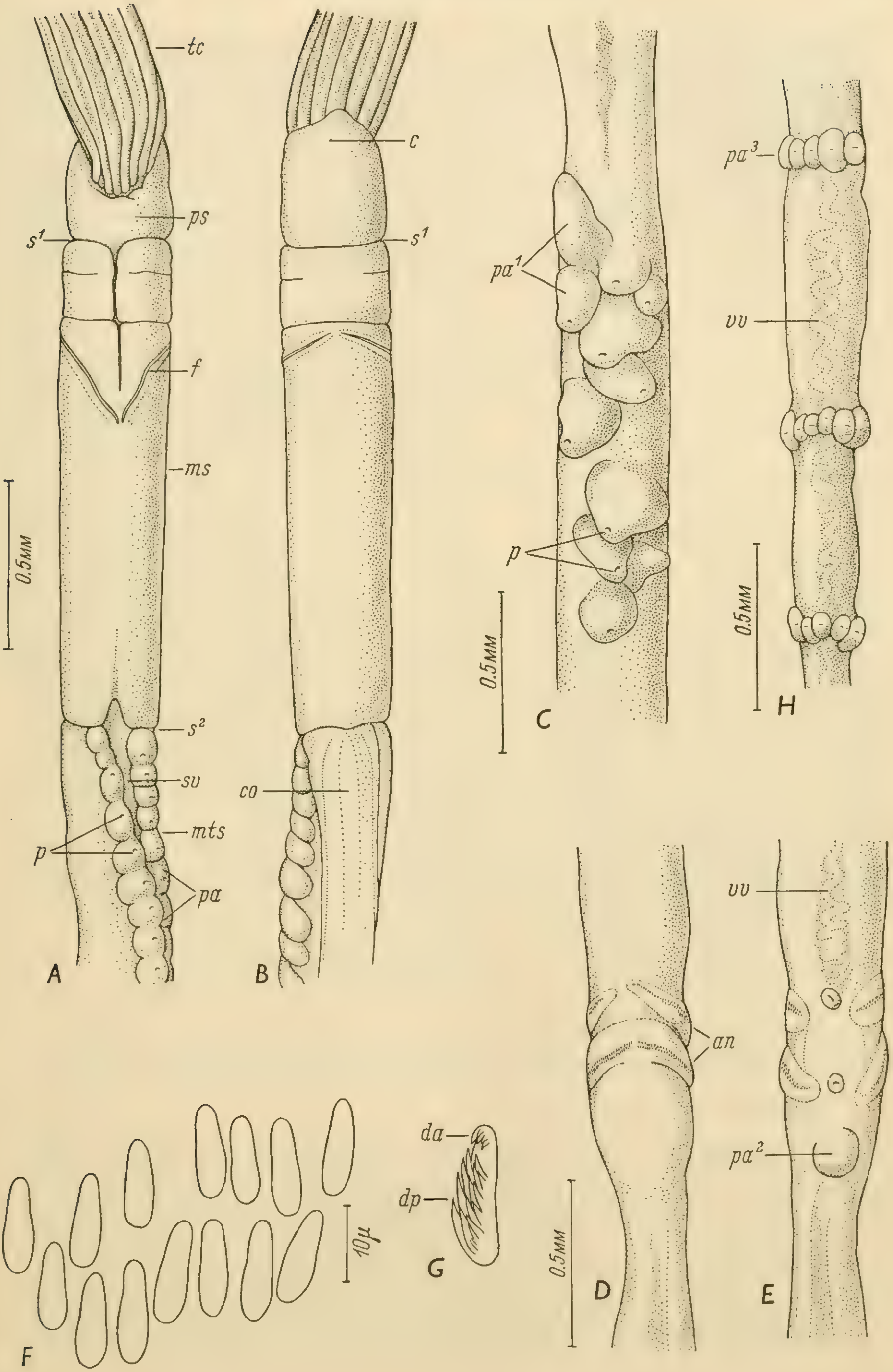
narrow, mid-ventral furrow (Fig. 143*A*). The pale, narrow keels of the bridle are fused neither ventrally nor dorsally, while the ridges on which they lie are but weakly developed (Fig. 143*A*, *B*). The strongly bevelled hind edge of the mesosoma is notched in the mid-ventral line (Fig. 143*A*).

The anterior metameric part of the trunk is short (Fig. 142), and the comparatively small, rounded papillae along the sides of the narrow ventral sulcus (Fig. 143*A*) number 24–26 pairs. Towards the hind end of the metameric section they grow larger and come to occupy a lateral situation so that the trunk widens here and the ventral sulcus opens out. The oval cuticular plaques have dark crescentic thickenings along their front edges and measure 25μ across (Fig. 144*A*). The dorsal ciliated band is well developed along the whole length of the metameric part (Fig. 143*B*). The succeeding very long, non-metameric part of the trunk bears scattered rounded papillae, mainly on the ventral side (Fig. 142). In both specimens the zone of thickened papillae is formed of eleven large ventral papillae crowded together in disorder (Fig. 143*C*), each of which has an oval cuticular plaque 32–35μ across (Fig. 144*B*). Two girdles of the usual appearance lie on well-defined ridges. The first girdle is interrupted both dorsally and ventrally, the second only on the ventral side (Fig. 143*D*, *E*). Between the ventral ends of each girdle is a single rounded papilla with a plaque, while behind the girdles lies a large spherical papilla with no plaque (Fig. 143*E*). The biserial toothed platelets (Fig. 143*F*) narrow a little towards the front end. Each is furnished with a small but well-developed anterior group of teeth, and measures 11–13·5μ long. The very long postannular region of the metasoma is noticeably broader than the preannular section (Fig. 142), and bears on its ventral side up to 36 transverse metameric rows of adhesive papillae, each row consisting of 4–6 papillae (Fig. 143*H*). The latter are rounded and crowded together, and each bears a rod-shaped plaque 35–45μ long (Fig. 144*C*).

The various parts of the body have the following dimensions: length of tentacular crown, 5 mm; length of the fore-part of the body, 1·5–1·8 mm;

Fig. 143. *Heptabrachia beringensis*: *A* – front end of a female from the ventral, and, *B* – from the dorsal side; *C* – zone of thickened papillae from the ventral side; *D* – region of the girdles in dorsal, and, *E* – in ventral view; *F* – part of a girdle; *G* – toothed platelet from one side; *H* – part of the postannular region in ventral view.

an – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *da* – anterior group of teeth; *dp* – posterior group of teeth; *f* – keel of the bridle; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaques; *pa* – metameric papillae; pa^1 – papillae of the zone of thickening; pa^2 – ventral papilla, lying behind the girdles; pa^3 – postannular papillae; *ps* – protosoma; s^1 – groove between protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *tc* – tentacular crown; *vv* – ventral blood vessel seen by transparency.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breadth of the mesosoma, 0·32–0·4 mm; length of the metameric part of the metasoma, 3·6 mm; length of the total preannular region of the metasoma, 20 mm; length of the postannular section, 27·5 mm; overall length of the body, 54 mm.

The rings of the elastic, pale golden-brown tube are almost regular, with more or less even edges, and often anastomose with each other. Their length is about a third to half the diameter of the tube, while the clear, more or less transparent intervals between them are much narrower (Fig. 144*D*). An incomplete tube is *c.* 100 mm long, with a diameter of up to 0·45 mm.

H. beringensis is distinguished by the comparatively large number of tentacles (12–13). It is like *H. gracilis* in possessing secondary rings on the front part of the mesosoma, but differs in having not one but two of these, and also in the disorder of the papillae of the zone of thickening. As in the majority of species of *Heptabrachia*, the cuticular plaques of the adhesive papillae are oval.

Material: two females.

Locality: the southwest part of the Bering Sea.

Depth: 1693 and 3789 m.

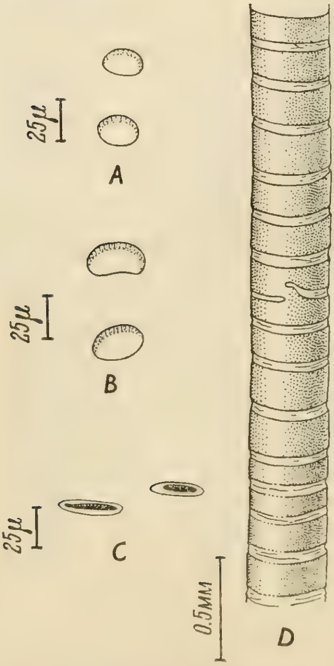

Fig. 144. *Heptabrachia beringensis*: *A* – cuticular plaques from the metameric part of the preannular region of the metasoma; *B* – the same from the zone of thickened papillae; *C* – the same from the postannular region of the metasoma; *D* – tube.

[5. *Heptabrachia talboti* (E. C. Southward) (Figs. A, B144)

Southward, 1961b: 47–52, Figs. 1, 2.

The tubes are brown and stiff anteriorly, white and soft posteriorly. Their diameter is a little greater at the anterior end. The tube of the holotype is 0·46 mm in diameter at the anterior end and 0·41 mm posteriorly, while the variation among the empty tubes is from 0·34 to 0·56 mm. The longest tube is not complete and is 13 cm long. The anterior part of the tube is marked with wide brown rings, separated by narrower yellow rings (Fig. A144*A*), but towards the middle part of the tube the brown rings become narrower and less distinct (Fig. A144*B*) and finally disappear. The posterior part of the tube is whitish and its rather thick walls are encircled by slightly wrinkled marks about 1 cm apart. One short fragment of tube with stiff, transparent, yellow walls may be the extreme anterior end of one of the tubes of this species, although other species of *Heptabrachia* have the anterior end of the tube colourless, with thin, limp walls (Ivanov, 1957).

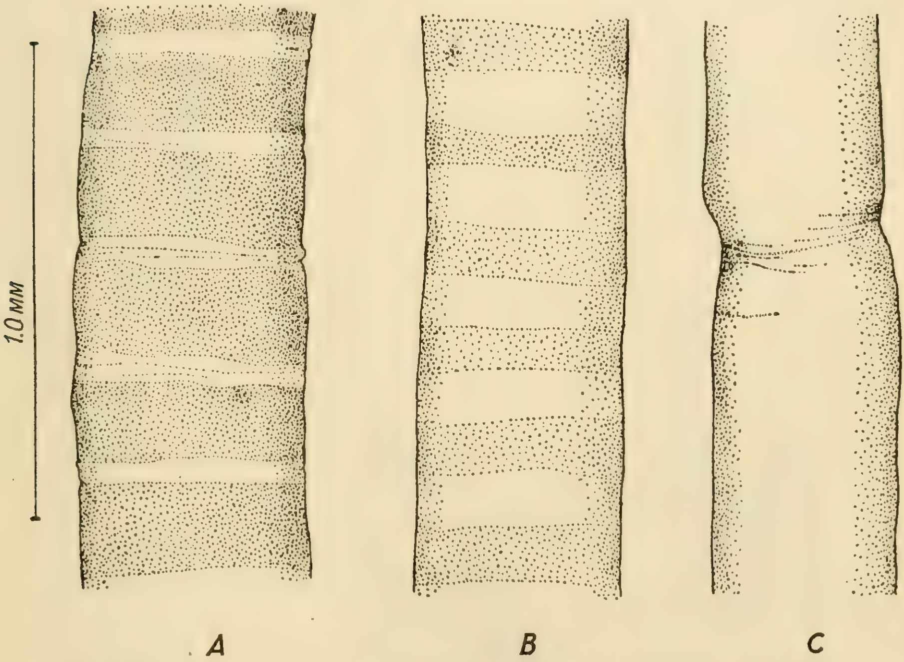

Fig. A144. Tube of *Heptabrachia talboti* n. sp. *A* – anterior; *B* – middle; *C* – posterior (After Southward, 1961b).

The animal has lost the distal parts of the tentacles and much of the posterior part of the body. Although parts of the specimen are crushed the following details can be seen. At the anterior end about 15 tentacles were attached to the cephalic lobe of the protosoma, or first segment (Fig. B144*A*, *B*), and about half of these tentacles were lying along the mesosoma (an unusual position which may have been produced during fixation). These backward-pointing tentacles had to be removed to expose the mesosoma (Fig. B144*A*) and this procedure slightly damaged the anterior part of the specimen, so that it is difficult to decide how the bases of the tentacles were arranged. In this specimen it is not possible to see any pinnules on the tentacles, but many pogonophores have them and they may be found in other specimens.

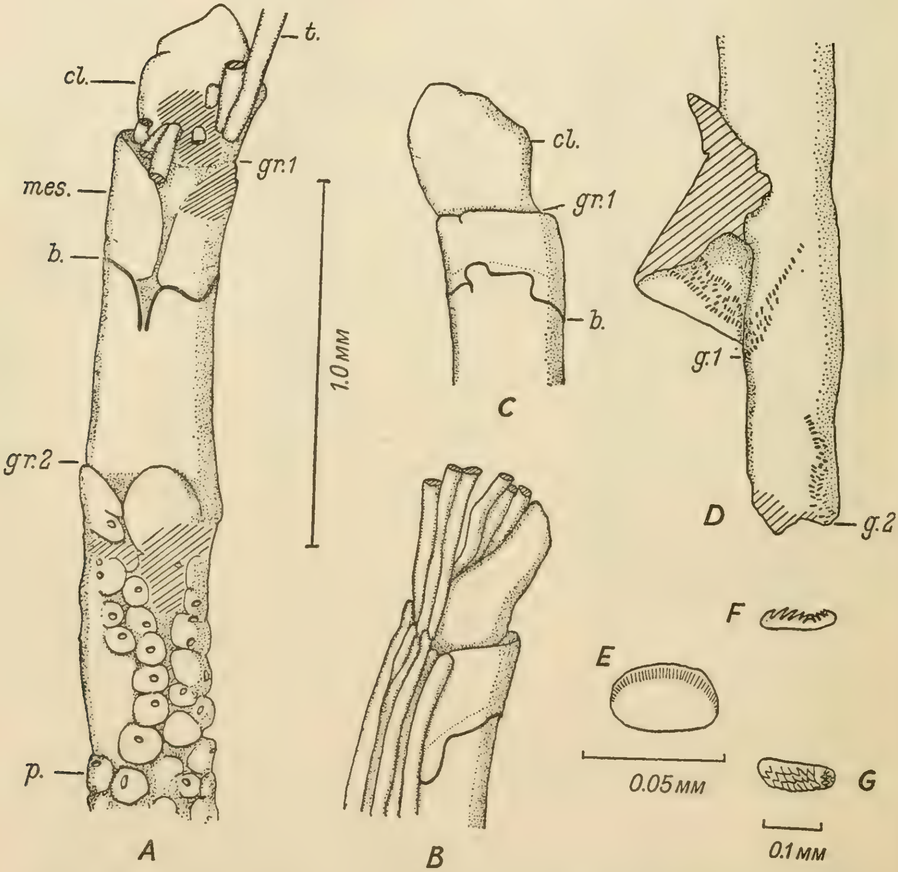

Fig. B144. *Heptabrachia talboti* n. sp. *A* – anterior end, tentaculate side, after removal of tentacles; *B* – anterior end, before removal of tentacles; *C* – anterior end, non-tentaculate side; *D* – girdle region of metasoma; *E* – adhesive plate; *F*, *G* – side and surface views of girdle platelet. Diagonal hatching indicates damaged surfaces.
b – bridle; *cl* – cephalic lobe; *g* – first girdle; *g. 2* – second girdle; *gr. 1* – groove between proto- and mesosoma; *gr. 2* – groove between meso- and metasoma; *mes* – mesosoma; *p* – papilla; *t* – tentacle (After Southward, 1961b).

The protosoma is separated from the mesosoma by a circular groove, behind and over which the anterior mesosoma is drawn out into a collar-like flap (Fig. B144*A*, *C*). On the tentacular side* the collar is divided by a deep groove which extends back, with a flap on each side, as far as the bridle. This bridle is a ridge of thickened cuticle which encircles the mesosoma except for a small gap on the tentacular side (Fig. B144*A*, *C*). Behind the bridle the mesosoma is smooth. Together the protosoma and mesosoma are 1·52 mm long and the greatest width of either is 0·32 mm. The third, last, and longest segment of the body is the metasoma, which in this specimen is 12 mm long and certainly not complete. The first part (1·7 mm) is very much contracted and twisted, and the closely packed papillae on the tentacular side (Fig. B144*A*) are probably normally arranged in two rows separated by a longitudinal groove, as they are in many other pogonophores. The paired arrangement of the papillae on this part of the body in other pogonophores has earned it the name of the 'metameric' region. In the present specimen each papilla is crowned with an oval adhesive plate with one thickened border (Fig. B144*A*, *E*). Behind the metameric region is a muscular region bearing a few scattered papillae, with adhesive plates (in a mature specimen this is the region which contains the gonads), extending for about 10 mm and ending with two girdles of small toothed platelets (Fig. B144*D*). The specimen is broken off at the second girdle and is also damaged at the level of the first, so that the extent and shape of the girdles in the complete animal are not known. Each girdle is made up of several irregular rows of platelets (Fig. B144*F*, *G*), of the shape and form found in many other pogonophores. The part of the metasoma behind the girdles (postannular region) is missing; in other species it is often as long as the preannular region.

For a complete description it will be necessary to have a specimen with the metasoma in good condition, in order to discover the true arrangement of the papillae in all parts, and to clarify the arrangement of the girdles. Complete tentacles are needed for measurement of their length and for investigation of their pinnules, if present.

However, with the material available, it is possible to place the species, with reasonable certainty, in the genus *Heptabrachia* Ivanov 1952, and to conclude that it is unlike any of the four species so far known. *H. abyssicola*, *H. gracilis*, *H. beringensis* and *H. subtilis* were all described by Ivanov and he has summarized their characteristics in a table (Ivanov, 1960, p. 214).

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* The tentacular side of the animal is ventral according to Ivanov (1955), dorsal according to Jägersten (1956).

H. gracilis is the closest in general appearance to *H. talboti*, but, in addition to differences in size and the number of tentacles, they differ in the size of the adhesive plates which are 15 to 20μ long in *H. gracilis* and 30 to 40μ long in *H. talboti*. Examination of more specimens of *H. talboti* might disclose more differences, since all four of Ivanov's species have, on part of the preannular metasoma, an area or row of large papillae set close together, whose arrangement and number varies with the species. In *H. talboti* some large papillae are visible in the correct region but their arrangement cannot be seen clearly. Another useful specific character in this genus is the arrangement of the papillae on the postannular region, which has been lost by the present specimen.

Material: one occupied tube (holotype) and twelve empty fragments.

Locality: West coast of S. Africa, 33°26′S, 16°33′E, 33°50′S, 17°21′E, 33°50′ S, 16°30′E.

Depth: 1097–2890 m. — E.C.S.]

[6. *Heptabrachia celebensis* (Southward) (Fig. D144)

Southward, 1961b: 15–16, 21, Fig. 9 (*Polybrachia celebensis*).

This species forms part of the *Siboga* material, originally included in *Siboglinum weberi*. The following description is transcribed from Southward (1961), by kind permission of the author and the publisher, E. J. Brill. This species must be ascribed to the genus *Heptabrachia* because of the small number of tentacles, the presence of a pretentacular groove, the presence of a secondary groove on the mesosoma and because of the general character of the tube.

"Two fairly complete animals are available, 21 and 35 mm long; one has four tentacles, 8·5 mm long, and the other has six shorter ones. In the latter the tentacles seem to be attached in two groups of three (Fig. D144*G*) but in the former the arrangement of the tentacles is not at all clear. There is a band of pinnules on each tentacle, apparently three or four pinnules wide; each pinnule is about 0·1 mm long, which is the same as the diameter of the tentacle. The fore-part of the body is contracted in one specimen (Fig. D144*D*, *E*, *F*) and extended in the other (Fig. D144*G*) and the total lengths of the protosoma and mesosoma in the two specimens are 0·78 and 1·5 mm respectively. In both, the cephalic lobe is rather short and somewhat spoon-shaped (Fig. D144*F*, *G*). A shallow annular groove between the protosoma and mesosoma is followed by a second annular groove just in front of the bridle (Fig. D144*D*, *E*). Slight ventro-lateral ridges are present on the protosoma and anterior mesosoma, but these are scarcely visible on the stretched specimen (Fig. D144*G*). The bridle consists of a wide ridge bearing narrow keels which are joined on the ventral side but separated by a very small gap on the dorsal side (Fig. D144*D*, *E*).

"The metameric region of the trunk is 4 mm long and at its anterior end the papillae are joined together to form lateral ridges of apparently glandular epidermis with slight humps around the aperture of each pyriform interior gland, but in the last 2 mm the ridges disappear and the paired papillae become more spread out. They finally become irregular and merge into the region of unpaired papillae, which are rather small and scattered along the

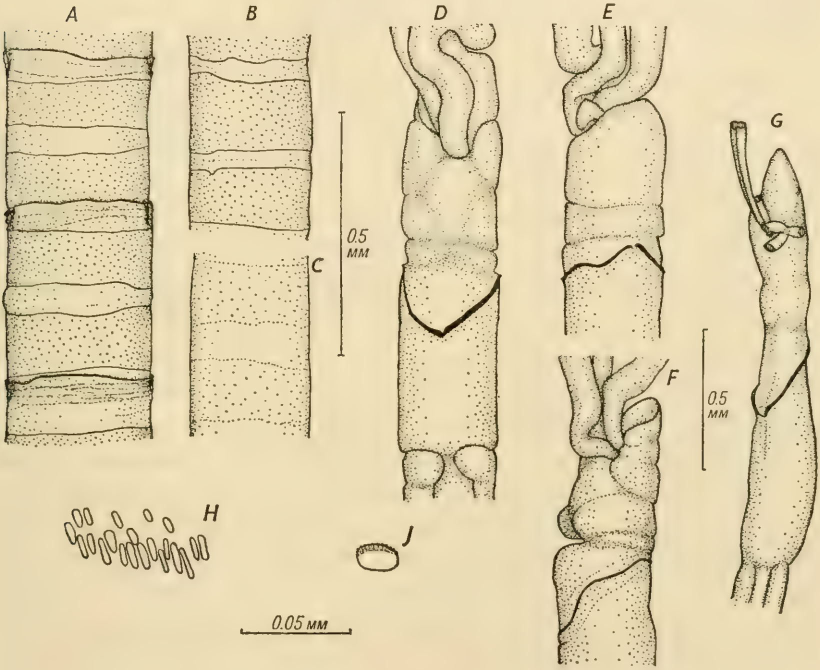


Fig. D144. *Polybrachia celebensis*: *A* – anterior part of the tube with rings and collars. *C*, *B* – middle and posterior parts of the tube; *D*, *E*, *F* – ventral, dorsal and lateral views of the anterior end of a contracted animal; *G* – ventral view of the anterior view of an extended animal; *H* – arrangement of plateletes in part of a girdle; *J* – an adhesive plaque from a preannular papilla. AfterIvanov (1961 c).

rest of the preannular region. Most of the paired and unpaired papillae are crowned with transparent oval adhesive plaques, 20μ long (Fig. D144*J*) with slightly serrated edges. The preannular region is about 17 mm long in both specimens, and the two girdles lie very close together. The toothed platelets are 10 to 20μ long and are arranged in semi-double rows (Fig. D144*H*). Their teeth are numerous and small, but difficult to distinguish. The postannular region, 16 mm of which are present in one specimen, bears some large papillae, which seem to be single, rather than in transverse rows; their adhesive plaques are like those of the preannular papillae. In one specimen some closely packed spermatophores are present. They are about 150μ long but their shape cannot be clearly seen.

"The tubes are up to 10 cm long and their diameter is a little greater at the anterior end than the posterior, being between 0·27 and 0·32 mm. A very short anterior section of about 1 mm is colourless limp and transparent, while the next 10 mm is yellowish, stiffer and formed of slightly overlapping segments (Fig. D144*A*). Towards the end of this part faint brown rings appear and the middle part of the tube has brown rings, yellow interspaces but no overlapping collars (Fig. D144*B*). Farther back the rings become paler and finally the whole tube is whitish with faint grey rings (Fig. D144*C*). Except for the first 1 mm and the last few mm the tube is fairly stiff, though the walls are only about 20μ thick.

"The overlapping collars and limp anterior end of the tube place this species in the family Polybrachiidae, though the single postannular papillae suggest some affinity with the Oligobrachiidae. Probably the poor condition of the posterior end has made it difficult to see details, and there may be more papillae present. If they really are single then they may represent very reduced 'rows' rather than the condition found in the Oligobrachiidae and Siboglinidae.

"*Heptabrachia* (*Polybrachia*) *celebensis* is named after the island of Celebes, near which it was collected."

Heptabrachia celebensis somewhat recalls *H. gracilis*, in possessing one secondary annular groove on the mesosoma, a small number of tentacles, the same shape and size of cuticular plaques on the metameric papillae. It is, however, distinguished from other species of *Heptabrachia* by the serrated front edge of the cuticular plaques and by the segmented tube. The rudimentary funnels on the latter recall the tubes of *Polybrachia*.

Material: two occupied and two empty tubes.

Locality: Java Sea: *Siboga* station 212 (5°54′S, 120°19′E).

Depth: 462 m.]

[7. *Heptabrachia ctenophora* Ivanov (Figs. E144-G144)

Ivanov, 1962b: 893–7, Figs. 1–3.

Two new species of *Heptabrachia* were collected by Z. A. Filatov in November, 1958, when on board R.V. *Vityaz*' working in the Pacific Ocean off the coast of Canada and the U.S.A.

Amongst the washings from clayey mud, brought up from a depth of 1376 m at a point a little to the north of Cape Blanko, about 40 miles from the coast of Oregon, two ringed tubes were found. One of them contained a complete animal of the genus *Heptabrachia*. I have named this species *H. ctenophora* because of its most remarkable feature—the comb-like structure of the keels of the bridle.

The fore-part of the body is more or less cylindrical (Fig. E144*A*, *B*). The very short protosoma is delimited from the mesosoma by a deep annular groove, which dips backwards on the ventral side as a small median notch (Fig. E144*A*). The small conical cephalic lobe is not cut off from the protosoma (Fig. E144*B*). The tentacular crown consists of 17 free tentacles which bear pinnules, some 100μ long, arranged in four dense longitudinal rows with the pinnules alternating in adjacent rows (Fig. F144*A*). The base of the crown forms a horseshoe.

In front of the bridle the mesosoma is scored by two weak annular grooves, as in *H. beringensis* (p. 347), and these are cut across by a mid-ventral furrow. The bridle is well-developed; its keels are almost colourless and meet neither dorsally nor ventrally. The ventral ends are considerably expanded and their structure is very characteristic. The front edge of each keel is an homogeneous transparent rather thick cuticular tract, with a broad transparent cuticular membrane attached behind. The latter is crossed by numerous rod-like darker thickenings, perpendicular to the front edge, whose distal ends push out just a little beyond the hind edge of the keel like a ridge of little hillocks (Fig. F144*B*). The epidermal ridges of the keels are feebly developed.

The groove between the mesosoma and the metasoma is sharp and has small but clear mid-ventral and mid-dorsal notches directed forward. The metameric section of the preannular region of the metasoma is short, with 13 adhesive papillae on each side of the ventral sulcus (Fig. E144*A*). The latter is wide and the ventral blood vessel is visible through its integument. The papillae are smallish and rounded; they are elongated ovals in shape or else bean-shaped. Each encloses several rounded pyriform glands. The first four pairs of papillae have no cuticular plaques but the rest bear a single small oval plaque each. The broad dorsal ciliated band begins at the front edge of the trunk (Fig. E144*B*).

The very long cylindrical nonmetameric part of the preannular region has numerous scattered papillae bearing oval cuticular plaques. At the front end of the nonmetameric region the papillae are sparse, then they increase considerably in number, especially on the sides of the trunk where they become numerous (Fig. E144*C*). Finally, in front of the zone of thickening the number of papillae falls again. In many places in this part of the trunk the dorsal and ventral blood vessel and the pyriform glands lying in the coelom are visible through the integument. The zone of thickening, lying a considerable distance in front of the girdles, consists of ten large conical papillae crowded together higgledy-piggledy on the ventral side (Fig. F144*D*). Behind them the preannular region of the trunk continues with small scattered papillae.

The cuticular plaques of the metameric papillae are oval with a dark

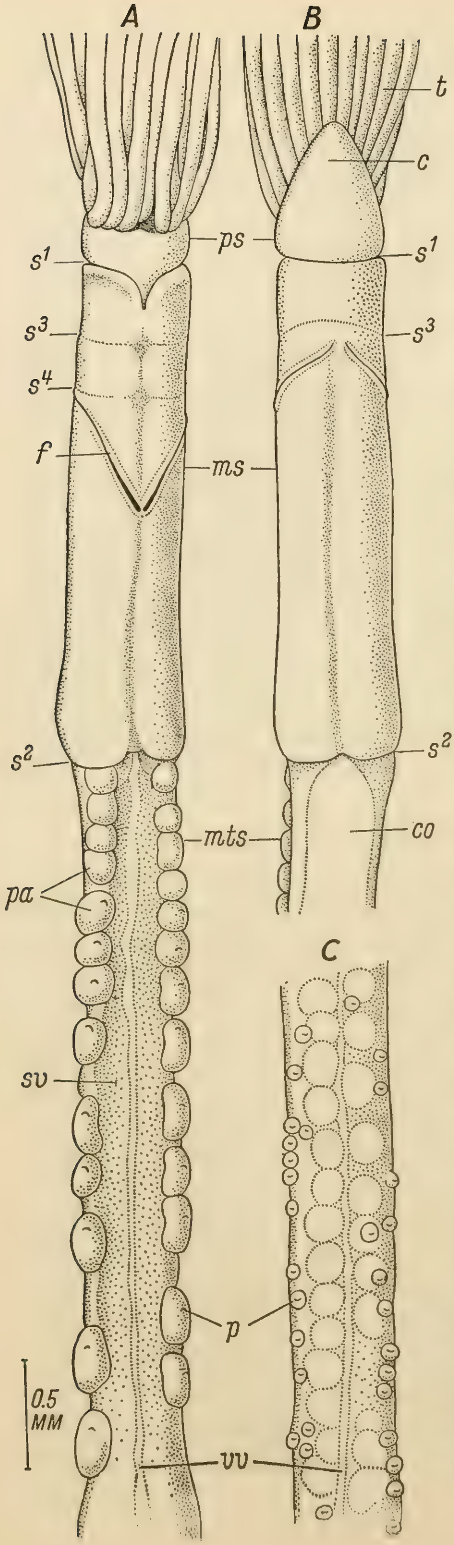


Fig. E144. *Heptabrachia ctenophora*. *A* – forepart of the body from the ventral and, *B*, from the dorsal side; *C* – part of the non-metameric region of the trunk from the ventral side.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaques; *pa* – papillae; *ps* – protosoma; s^1 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and metasoma; s^3, s^4 – secondary mesosomal grooves; *sv* – ventral sulcus; *t* – tentacles; *vv* – ventral blood vessel seen by transparency. (After Ivanov, 1962b.)

thickened anterior rim crossed by thin streaks perpendicular to the edge. Their greatest diameter varies from 30 to 40μ (Fig. F144*E*). On the papillae of the zone of thickening the plaques are much the same size, except that they are more expanded from side to side (Fig. F144*F*).

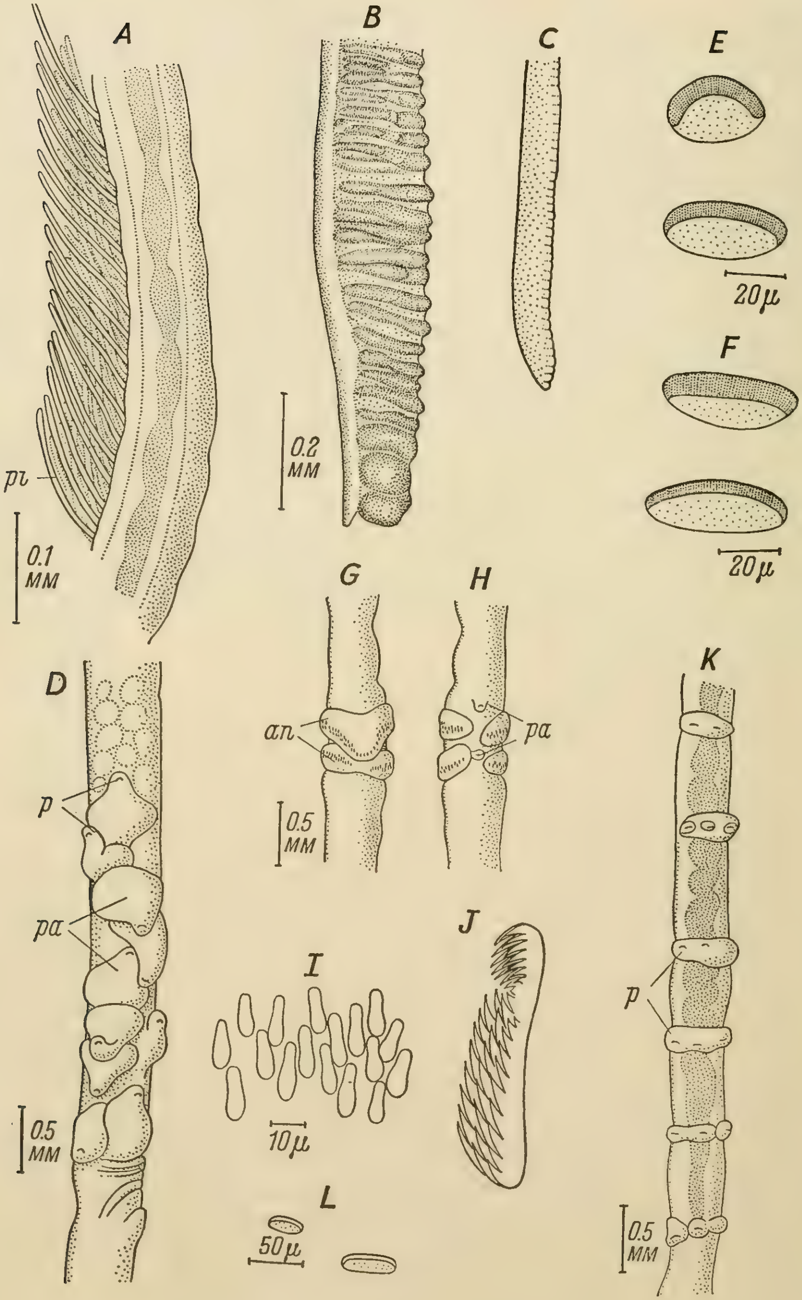
The two girdles, looking like thick transverse ridges, lie close together. Both have a wide gap on the ventral side and the posterior is broken dorsally also (Fig. F144*G*, *H*). The front girdle dips backwards in an arch on the dorsal side. Several small ventral papillae with cuticular plaques are found in the region of the girdles. The yellowish toothed platelets of the girdles form two or three rows (Fig. F144*I*). They are very like those of *H. gracilis* and each bears a small group of teeth pointing backwards on the narrower front end (Fig. F144*J*). The platelets are 11–18μ long.

The postannular region of the trunk is long and slender. The transverse rows of ventral papillae lie on metameric dermal ridges situated at rather frequent intervals (Fig. F144*K*). The cuticular plaques here, in contradistinction to those of other species of *Heptabrachia*, are not rod-shaped but oval (Fig. F144*L*). Their greatest diameter varies from 20 to 50μ.

This description is based on a single individual, a female, whose dimensions are as follows (mm):

Length of the tentacles	17·5
Length of the fore-part of the body	2·8
Breadth of the mesosoma	0·5
Length of the preannular region of the trunk	71·6
Length of the postannular region of the trunk	more than 25
Overall length of the body, including the tentacles	*c.* 120

The dark brown lustrous ringed but unsegmented tube is rather coarse and stiff in the middle region. Its anterior part (not less than 20 mm long) is membranous and transparent and the walls collapse easily. The rings appear very gradually; at first they are hardly noticeable, pale brown with hazy uneven outlines and incomplete (Fig. G144*A*); then, more caudally, they become brown or dark brown and their edges more even, but frequently here, as farther forward, one encounters irregularities—fusion of adjacent rings or underdevelopment of individual rings. Anteriorly the rings are a fifth or a quarter as long as the tube is wide, in the middle part of the tube a quarter or a third. The clear interspaces between the rings are rather broad. The hind third of the tube has more or less regular coarse dark brown rings each with a darker posterior border (Fig. G144*B*). Their length here is a half to a third the diameter of the tube. The clear interspaces between the rings are here very narrow, in places almost


A
pr
0.1 MM
B
0.2 MM
C
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20μ
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disappearing. The hind end of the tube has irregular clear rings outlined by narrow dark borders (Fig. G144*C*). The one inhabited tube was 281 mm long, its anterior diameter *c.* 0·7 mm and its posterior 0·5 mm. The empty tube was 225 mm long and 0·5 mm in diameter.

Heptabrachia ctenophora shares many features with *H. beringensis* including: the approximately equal size of the body, the comparatively large number of tentacles (12–13 in *H. beringensis* and 17 in *H. ctenophora*), the possession of two secondary annular grooves around the mesosoma in front of the bridle, and the small number (10–11) of papillae in the zone of thickening. There are many similarities too in the structure of the tubes. The new species, however, is readily distinguished from *H. beringensis* by the poorer development of the metameric part of the trunk and especially by the extraordinary structure of the keels of the bridle (compare Fig. F144*B* with F144*C*).

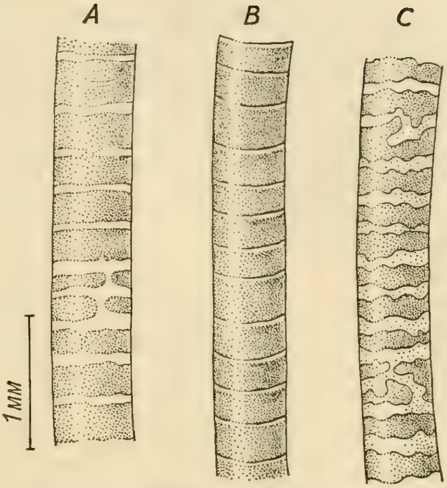

Fig. G144. *Heptabrachia ctenophora*: the tube. *A* – near the front; *B* – in the middle; *C* – near the hind end. (After Ivanov, 1962b.)

The strange comb-like structure of the keels of the bridle distinguishes *H. ctenophora* from the majority of Polybrachiidae. Something similar is found only in the bridle of *Diplobrachia*, *Lamellisabella ivanovi*, *Siboglinum tenue* and *S. minutum*. In these species, however, transverse cuticular rodlets are attached to the hind edge of the main cuticular band of the bridle (Figs. 149*E*, 152*A*, 169*F*), or they lie across it (Figs. 121*A–C*, 124*C*). In *Heptabrachia ctenophora*, on the other hand, the rodlets are completely enclosed in an homogeneous cuticular membrane.

Fig. F144. *Heptabrachia ctenophora*: *A* – part of a tentacle; *B* – the ventral end of a keel of the bridle; *C* – the same in *H. beringensis*; *D* – the zone of thickened papillae from the ventral side; *E* – cuticular plaques from the metameric region of the metasoma, and *F*, from the zone of thickened papillae; *G* – the region of the girdles from the dorsal and, *H*, from the ventral side; *I* – part of a girdle; *J* – a toothed platelet from the side; *K* – part of the postannular region from the ventral side; *L* – plaques from the postannular region.
an – girdles; *p* – plaques; *pa* – papillae; *pi* – pinnules. (After Ivanov, 1962b.)

H. ctenophora is distinguished from *H. gracilis* and *H. celebensis* by possessing not one but two secondary mesosomal grooves.

Material: one complete female and one empty tube.

Locality: off the Pacific coast of North America, a little to the north of Cape Blanko about 40 nautical miles off the coast of Oregon (43°N, 125°W). Substratum: clayey mud.

Depth: 1376 m.]

[8. *Heptabrachia canadensis* Ivanov (Figs. H144, J144).

Ivanov, 1962b: 897–9, Figs. 4, 5.

A single tube of this species, containing an almost complete animal, was taken in a Sigsby trawl north-west of Queen Charlotte Island, opposite the mouth of Dixon Entrance (off the Pacific coast of Canada) at a depth of 2500–2600 m. In some respects the animal was like *Heptabrachia gracilis*, in others like *H. abyssicola*, but differed from both in several ways.

The fore-part of the body is cylindrical. The mesosoma is four and a half times the length of the protosoma including the cephalic lobe (Fig. H144*A*–*C*). The latter is small and triangular. The crown of tentacles is badly damaged and only the basal part of the tentacles remains. There are apparently six to eight tentacles but the precise number and arrangement are not clear. Their length is unknown.

In front of the bridle the mesosoma is scored by two transverse grooves, as in *H. beringensis* and *H. ctenophora*. The anterior groove (Fig. H144*A*) cuts off the front part of the mesosoma as a separate region which is twice as broad as it is long. This groove almost disappears on the ventral side. The second groove runs immediately in front of the bridle and, unlike the first, is more strongly marked on the ventral side (Fig. H144*A*–*C*). The bridle has rather thick keels which do not meet on the dorsal side but are fused together ventrally. The ventral ends are strongly thickened and blackish (Fig. H144*D*), though the remaining part of the keels is colourless.

The boundary between the mesosoma and the metasoma is very distinct. The metameric part of the trunk is not large; it is furnished with 17 papillae on one side and 18 on the other. The first pair of papillae, lacking cuticular plaques, is larger than the rest and they appear to represent the male genital papillae (Fig. H144*A*). The rest of the metameric papillae are rounded (Fig. H144*A*) and each bears an oval cuticular plaque with a dark thickened anterior rim (Fig. H144*E*). The transverse diameter of the plaques is 30–33μ.

The nonmetameric part of the preannular region of the trunk bears scattered rounded papillae whose plaques differ neither in shape nor in size. Somewhat similar oval plaques of almost the same size (Fig. H144*F*) lie on the tips

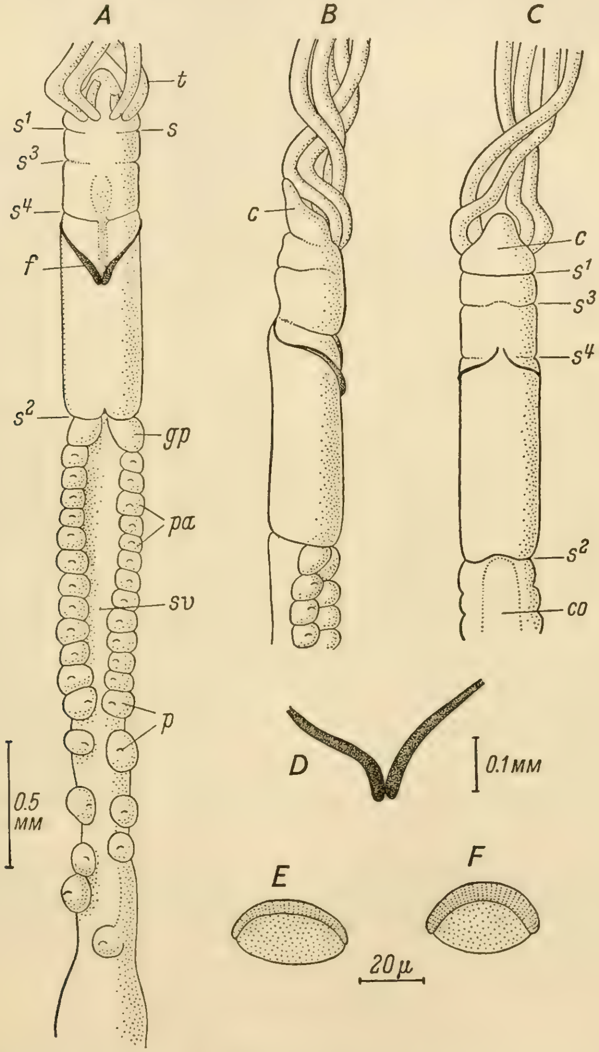

Fig. H144. *Heptabrachia canadensis*. *A* – the fore-part of the body from the ventral, *B*, from the right and, *C*, from the dorsal side; *D* – the ventral part of the keels of the bridle; *E* – a plaque from the metameric region of the trunk and, *F*, one from the zone of thickened papillae.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *gp* – genital papilla; *p* – plaques; *pa* – papillae; s^1 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and metasoma; s^3, s^4 – secondary mesosomal grooves; *sv* – ventral sulcus; *t* – tentacle. (After Ivanov, 1962b.)

of the 15 large conical papillae of the zone of thickening which are densely packed together in disordered confusion on the ventral side (Fig. J144*A*).

There are two girdles, the first of which has broad dorsal and ventral gaps, while the second is broken only on the ventral side (Fig. J144*B*, *C*). The toothed platelets are arranged in a single row (Fig. J144*D*). As in other species of *Heptabrachia* they have a small but well developed anterior group of teeth (Fig. J144*E*). The platelets are 11–12μ long. In the girdle region there are several small ventral papillae with plaques, and the large unpaired papilla at the boundary of the postannular region.

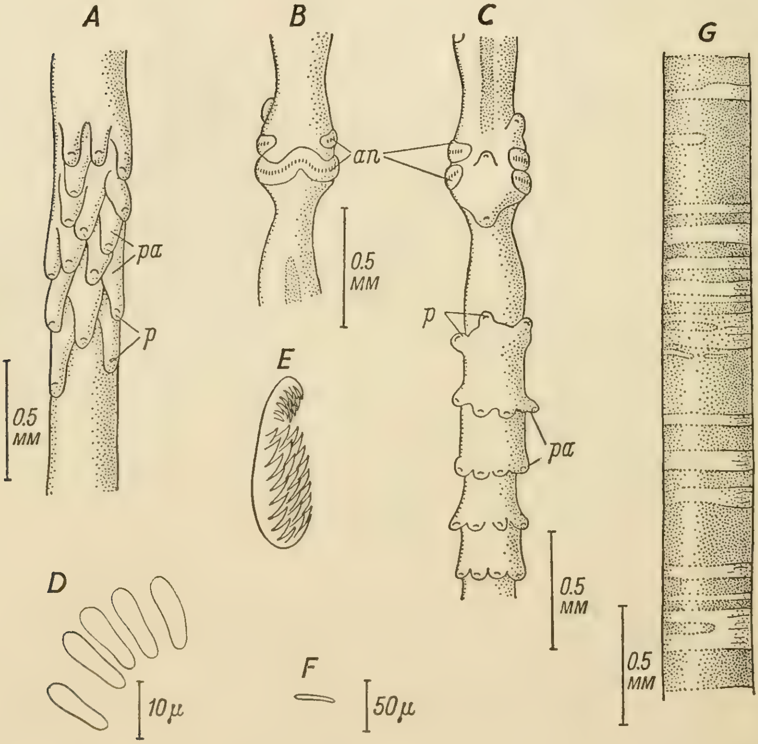

Fig. J144. *Heptabrachia canadensis*: *A* – zone of thickened papillae in ventral view; *B* – the region of the girdles in dorsal view; *C* – the same region with part of the postannular region in ventral view; *D* – part of a girdle; *E* – a toothed platelet from the side; *F* – a plaque from the postannular region of the trunk; *G* – tube.
an – girdles; *p* – plaques; *pa* – papillae. (After Ivanov, 1962b.)

The postannular region has a closely spaced series of transverse metameric ventral rows of small papillae, four or five per row (Fig. J144*C*). Their small plaques are rod-like (Fig. J144*F*).

No spermatophores have been observed.

The dimensions of the body are as follows (mm):

Length of the fore-part of the body	1·5
Breadth of the mesosoma	0·35
Length of the metameric part of the mesosoma	*c*. 2
Length of the whole preannular region	14
Length of the existing part of the postannular region	*c*. 0·8
Overall length, excluding the tentacles	not less than 25

The ringed and unsegmented tube of *H. canadensis* is the colour of straw, turning brownish in parts, transparent and lustrous. The front and hind ends are broken off. In the anterior part of the tube the rings are brownish and short, not very regular at first, but more or less uniform in length. Very quickly, however, in the hinder part of the tube, their length becomes extremely irregular. One may frequently encounter very long rings one and a half, two or even three times as long as the tube is wide, though the majority of rings are in fact much shorter (Fig. J144*G*). The walls of the tube are thin and rather brittle. The overall length of the fragment is 118 mm; the diameter near the middle is 0·3 mm.

In several features, such as the nature of the tube, the number of tentacles and of metameric papillae, *H. canadensis* recalls *H. gracilis*. It is, however, distinguished by the larger cuticular plaques, the smaller heads of the toothed bristles of the girdles and the disordered confusion of the papillae in the zone of thickening. Like *H. beringensis* and *H. ctenophora*, *H. canadensis* has two secondary mesosomal grooves.

Material: one almost complete individual, probably a male, in an incomplete tube.

Locality: the north-eastern Pacific off the coast of Canada, near the mouth of Dixon Entrance north-west of Queen Charlotte Island (54° N, 134° W).

Depth: 2500–2600 m.]

2. Genus *Cyclobrachia* Ivanov, 1960

Ivanov, 1960c: 6, 24, 106, 107, 114, 199, 215.

Amongst the new species that I collected while working on board R.V. *Vityaz*' in Pacific equatorial waters during the summer of 1957, one of the most interesting was *Cyclobrachia auriculata*. This species was found together with two still undescribed species of *Siboglinum* in a trawl taken at a depth of *c.* 8000 m in the region of the New Britain Trench to the south-west of Bougainville Island (6°S, 155°E) in the British Solomon Islands. The genus is characterized by the following features: the protosoma, sharply divided from the mesosoma, is very small and possesses a post-tentacular groove; there are only a few tentacles, which are always free, but the base of the tentacular crown forms a closed circle; the metameric section of the pre-annular region of the trunk supports a large number of paired papillae; the cuticular adhesive plaques are kidney-shaped and their front, thickened edges are bowed with rounded ends; the toothed platelets of the girdles are arranged in a few rows; paired epidermal, auricular lappets are developed on the dorsal side of the mesosoma; the tube is simple, without either segmentation or rings; the spermatophores are like those of *Heptabrachia* and *Polybrachia.* Almost all the features enumerated suffice to distinguish the genus from *Heptabrachia*, and almost the only feature they appear to have in common (apart from the common characters of the family) is the small number of tentacles. Important distinctions are the following: the circular area of attachment of the tentacles, the numerous paired metameric papillae, the multi-serial disposition of the toothed platelets of the girdles, and the structure of the tube, which in *Heptabrachia* is always ringed. *Cyclobrachia* is distinguished from *Polybrachia* and from other related genera not only by the small number of tentacles but also by the circular base of the tentacular crown, by the post-tentacular groove, and by the structure of the tube. The circular base of the tentacular crown appears to be a feature shared by *Heptabrachia beringensis*, *Zenkevitchiana* and *Lamellisabella.* Particular interest attaches to the length of the secondary metamerism of the pre-annular region of the trunk in *Cyclobrachia.* This feature is not general amongst the Polybrachiidae as a whole. Indeed, in number of metameric papillae (more than 100 pairs) *Cyclobrachia* is equalled only by *Spirobrachia.* Thus, in *Cyclobrachia* a primitive feature — the small number of tentacles, is coexistent with an advanced character. It is also note-worthy that the cuticular plaques of the papillae in *Cyclobrachia* are very similar to those of the Spirobrachiidae and distinguished from those of the other Polybrachiidae in which they are never bordered at the front by thick bows with rounded ends. As regards the dorsal auricular lappets of the mesosoma, something similar has been described only in *Galathealinum* where they lie on the ventral side in front of the bridle (Kirkegaard, 1956a).

Type of genus: *Cyclobrachia auriculata* Ivanov.

1. Cyclobrachia auriculata Ivanov (Figs. 145–7)

Ivanov, 1960c: 6, 93, 97, 215, 216–19, 266, Figs. 87, 145–7.

Amongst 13 fragments of tube of this species, unfortunately only a single animal was found, a male with a badly damaged tentacular crown of which only the base remained. The specific name *Cyclobrachia auriculata* refers to the possession of auricular lappets on the dorsal side of the mesosoma. The rather short, massive fore-part of the body is perceptibly stouter in the front half of the mesosoma (Fig. 145*A*, *B*, *C*), and the protosoma is considerably narrower than the mesosoma and divided from it by a very obvious groove. There is, in addition, a dorsal post-tentacular groove, and as may be seen in a side view, there are only nine tentacles arranged in a single series to form a closed circle. The small cephalic lobe forms an equilateral triangle. The brownish keels of the well-developed bridle, situated in the front half of the mesosoma, are rather stout, especially on the ventral side where they are fused together (Fig. 145*A*, *C*). The cutaneous ridges of the bridle are pronounced and on the dorsal side they expand to run into the swollen bases of the cutaneous auricular lappets. These latter are very characteristic and are not found in any other pogonophores. Each lappet is a triangular outgrowth pointing forwards and there is a moderate-sized gap between them (Fig. 145*B*). The keels of the bridle do not reach into the mid-dorsal region and in the single available specimen the two dorsal ends are differently situated, due, in all likelihood, to an individual variation from the norm. On the left the keel makes an S-bend at the base of the lappet before running on to it, while the right keel is situated just in front of the lappet, outside its limits, on the surface of the mesosoma (Fig. 145*B*). The front part of the mesosoma in front of the auricular lappets has both a clear, mid-dorsal furrow, which forks into two behind the lappets to outline a slightly swollen dorsal area (Fig. 145*B*), and a shallow longitudinal depression on the ventral surface (Fig. 145*A*). The boundary between the mesosoma and the metasoma is a straight transverse groove, which, on the ventral side, is masked by a pair of large male genital papillae (Fig. 145*A*, *C*).

The ventral sulcus in the front part of the metasoma is very broad, but not deep, and each of the comparatively small, rounded adhesive papillae, which run along each side, carries a dark-brown cuticular plaque (Fig. 145*A*). A prominent feature is the large number of these papillae, amounting to 113 on the left and 109 on the right. The cuticular plaques in this part of the trunk are kidney-shaped and the front thickened edge of each one is a broad dark-brown curved bow, with rounded ends. The remaining part of the plaque is very thin and transparent (Fig. 145*D*). The whole plaque measures

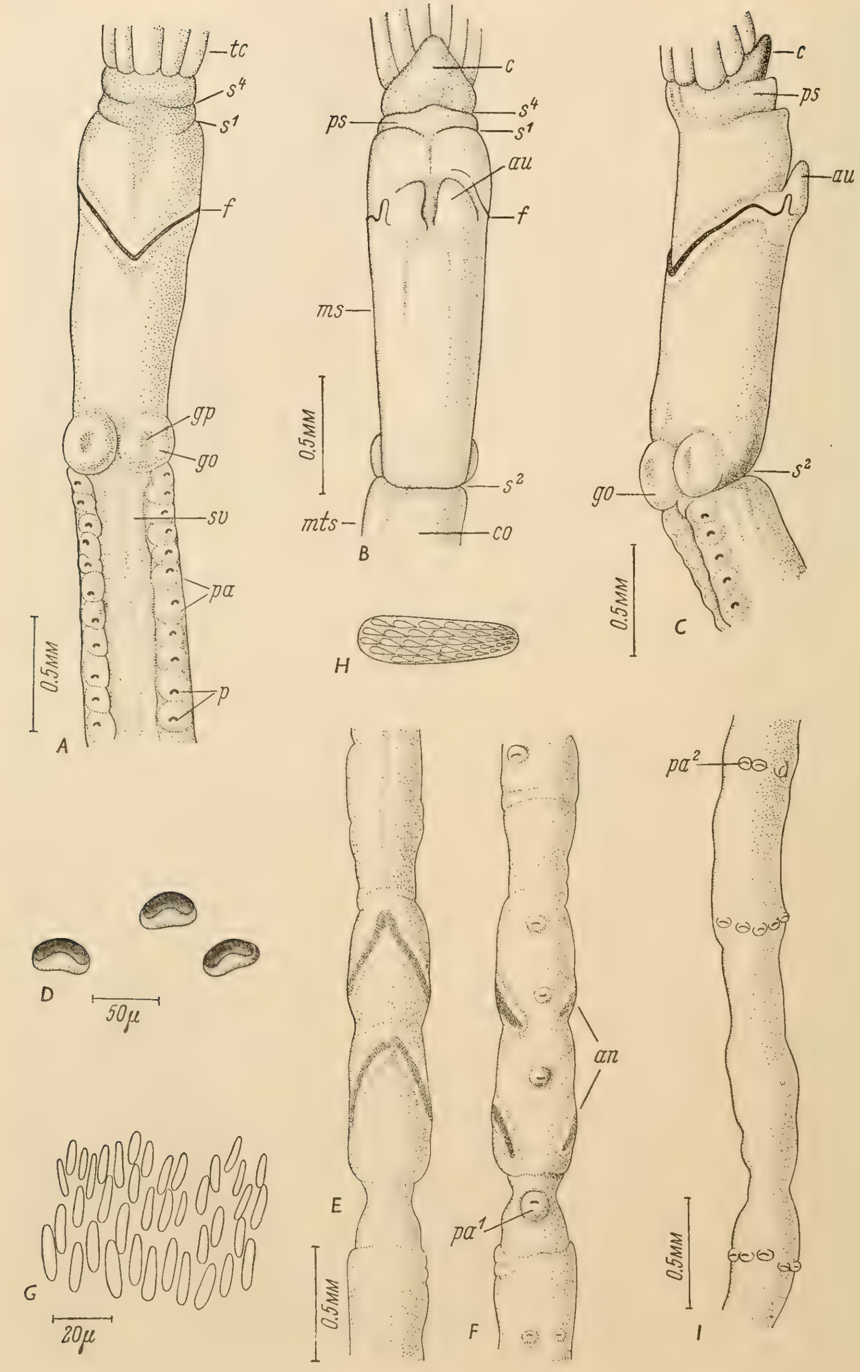
tc
s^4
s^1
f
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TABLE 3

Characteristics of the species of *Heptabrachia*

	H. abyssicola	*H. gracilis*	*H. subtilis*	*H. beringensis*	*H. talboti*	*H. celebensis*	*H. ctenophora*	*H. canadensis*
Ratio of lengths of protosoma + cephalic lobe to mesosoma	1 : 3	1 : 4	1 : 2	1 : 3	1 : 2·5	1 : 2·5	1 : 3·5	1 : 4·5
Number of tentacles	7–8	5–7	7–8	12–13	*ca* 15	4–6	17	6–8
Secondary mesosomal grooves	—	+	—	+	—	+	+	+
Fusion or contact of keels	—	ventral	ventral and dorsal	—	dorsal	ventral	—	ventral
Number of pairs of metameric papillae	14–20	17–18	?	24–26	?	?	13	17
Shape of cuticular plaques	Round	Oval	Oval	Oval	Oval	Oval	Oval	Oval
Diameter of cuticular plaques (μ):								
from metameric papillae	20	20	20	25	30–40	20	30–40	30–33
from nonmetameric papillae	20	15	35–40	25	?	20	40	30
from thickened papillae	25	25	35	32–35	?	?	40	30
Arrangement of papillae in zone of thickening	Random	One row	Random	Random	?	?	Random	Random
Number of papillae in zone of thickening	*ca* 20	12–13	15–18	11	?	?	10	15
Length of toothed platelets (μ)	10–15	16	10–14	11–13·5	*ca* 14	10–20	11–18	11–12
Number of papillae per transverse row in postannular region	7–8	3–5	5–7	4–6	?	1	3	4–5
Length of body (excluding tentacles) (mm)	Up to 71	70	*ca* 150	Up to 54	?	*ca* 35	*ca* 120	*ca* 25
Breadth of body (mm)	0·25	0·2	0·4	0·4	0·32	*ca* 0·2	0·5	0·35
Length of spermatophores (mm)	0·34	0·2	?	?	?	0·15	?	?
Diameter of tube (mm)	0·33	0·25	0·5	0·45	0·46	0·27–0·32	0·7	0·4

45μ across, and the tips of the bow are a little less than 40μ apart. The broad dorsal ciliated band begins at the front edge of the metasoma (Fig. 145*B*). In the hind part of the preannular region of the trunk are scattered papillae also furnished with plaques. The well-developed girdles are both interrupted dorsally and ventrally. The ventral ends are wide apart and point backwards, while the dorsal ends almost meet (Fig. 145*E*, *F*). A few round mid-ventral papillae lie in the neighbourhood of the girdles, with a prominent larger one behind the second girdle. The toothed platelets, 15–26μ long and 5–8μ across, are arranged in 3–5 rows (Fig. 145*G*). The front end of each is a little narrower, and the whole surface is covered with teeth which point forwards; the anterior group of teeth is thus absent (Fig. 145*H*). The postannular section of the metasoma begins with a nipped-in waist, on which lies the large ventral papilla mentioned above. Each of the well-marked, metameric, transverse rows of papillae consists, as a rule, of five small, rounded papillae bearing transverse, cuticular plaques which are slightly bent with the ends slanting backwards (Fig. 145*I*).

The fore-part of the body is 2 mm long; the front part of the mesosoma is 0·55 mm broad, and the back part 0·43 mm; the metameric part of the preannular region is 38 mm long, the total preannular region 58 mm, and the postannular 57 mm. The metameric part is thus two-thirds of the total preannular region, and the overall length of the body, excluding the tentacles, is 117 mm.

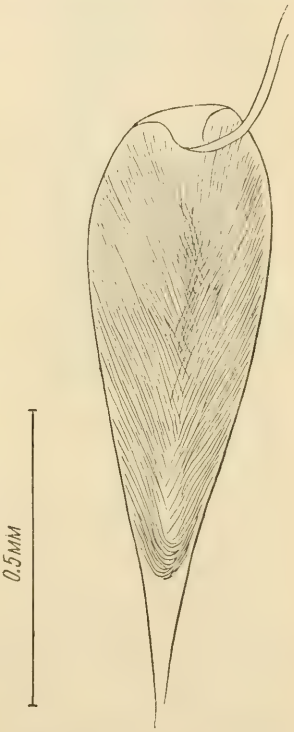


Fig. 146. *Cyclobrachia auriculata*: spermatophore.

Fig. 145. *Cyclobrachia auriculata*: *A* – front end of the body of a male from the ventral, *B* – from the dorsal, and, *C* – from the left side; *D* – cuticular plaques from the metameric papillae of the preannular region of the metasoma; *E* – region of the girdles in dorsal, and, *F* – in ventral view; *G* – part of a girdle; *H* – toothed platelet; *I* – part of the postannular region.
an – girdles; *au* – dorsal ear-shaped lobes; *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – keel of the bridle; *go* – genital papilla; *gp* – genital aperture; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaques; *pa* – papillae; *pa*[1] – ventral papilla lying behind the girdles; *pa*[2] – transverse rows of papillae of the postannular region; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; s^4 – post-tentacular groove; *sv* – ventral sulcus; *tc* – crown of tentacles.

The spermatophores are flat and leaf-shaped, about 1 mm long by 0·3 mm broad. The filamentary end is broad and rounded, the opposite end tapering evenly to a point (Fig. 146). The filament begins by bending down towards the spermatophore as a broad basal plate, before dwindling rather quickly into the ribbon-like proximal part of the filament. The surface of the very firm, dark tube of *C. auriculata* is smooth and the walls are structureless and slightly translucent. There are neither rings nor segmentation (Fig. 147), except that on a few fragments of moderate diameter very faint traces of segmentation were detected. The biggest fragments of tubes reached 70 mm in length, but the total length must be much more. The diameter of the thickest fragment is a little more than 1 mm.

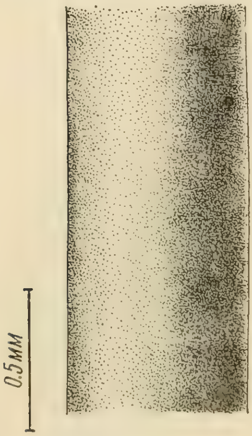


Fig. 147. *Cyclobrachia auriculata*: part of tube.

Material: one male and 13 scraps of tube.

Locality: New Britain Trench, to the south-west of Bougainville Island in the Coral Sea.

Depth: 7974–8006 m.

3. Genus *Diplobrachia* Ivanov, 1960

Ivanov, 1960c: 6, 24, 106, 107, 114, 199, 219–20, 252.

In a trawl-haul taken by R.V. *Vityaz'* in the spring of 1957 in the region of the Japan Trench at a depth of 7500 m were found numerous slender brown tubes of a pogonophore, very like those of *Siboglinum*; so like them, in fact, that they were so described in the log. They were found, however, to belong to a new genus, *Diplobrachia*, which, without doubt, belongs to the order Thecanephria. An unexpected and very distinctive feature of this genus is the possession of two to four tentacles. Its thecanephrial affinities may be judged from the development of transverse, ventral rows of papillae, bearing cuticular plaques, on the postannular section of the trunk, and from the characteristic leaf shape of the spermatophores, while the absence of any connexion between the tentacles and the distinctive protosoma suggest that amongst the Thecanephria this animal lies nearest to the Polybrachiidae. In spite of the reduction in numbers of the tentacles *Diplobrachia* scarcely merits the erection of a separate family, since it is distinguished from typical Polybrachiidae by but few characters. The genus *Diplobrachia* may be defined by the following features: the fore-part of the body is distinctly divided externally into protosoma and mesosoma; the protosoma carries two to four free tentacles, which, to all appearances, are homologous with the foremost tentacles of *Heptabrachia* and *Oligobrachia*; the keels of the bridle each consist of a cuticular axial rod, to which are attached, behind, a series of cuticular rodlets; all the papillae of the metasoma have adhesive papillae.

There are four species: *Diplobrachia japonica* Ivanov, *D. belajevi* Ivanov, *D. capillaris* (Southward), and *D. southwardae* Ivanov.

Type of the genus: *Diplobrachia japonica* Ivanov.

Key for the identification of the species of the genus *Diplobrachia*

1 (6) The whole front part of the metasoma bears adhesive papillae. There are usually two tentacles, sometimes three or four.

2 (5) The keels of the bridle do not meet dorsally. The cuticular plaques in the front part of metasoma are 20–25μ across.

3 (4) There are six to thirteen pairs of papillae in the metameric part of the metasoma, of which all but the anterior papillae bear round plaques. There are two to four tentacles. The tube is segmented with three irregular rings in each segment. 3. *D. capillaris* (p. 378).

4 (3) There are not less than 18 pairs of papillae with oval plaques in the metameric section of the metasoma. There are two tentacles. The tube is segmented, usually with seven very regular rings in each segment. 1. *D. japonica* (p. 371).

5 (2) The keels meet dorsally. The cuticular plaques in the anterior part of the metasoma are about 12μ across. There are more than 20 pairs of metameric papillae. There are two tentacles. The tube is ringed but unsegmented. 2. *D. belajevi* (p. 376).

6 (1) Paired adhesive papillae are absent from the frontmost region of the metasoma. There are three or four tentacles. The keels of the bridle do not meet dorsally. The plaques on the papillae of the front part of the metasoma are 25μ across. The tube is segmented, usually with five rings in each segment. 4. *D. southwardae* (p. 381).

1. Diplobrachia japonica Ivanov (Figs. 148–51)

Ivanov, 1960c: 6, 92, 93, 97, 220–3, 226, 263, Figs. 87, 148–51.

The fore-part of the body is rather long. The length to breadth ratio, depending upon the state of contraction, varies between 4·5 : 1 and 7 : 1. It is generally more or less cylindrical (Fig. 149*A*, *B*, *C*, *D*), but in one specimen the front half was found to be considerably narrower than the back half, probably as a result of unequal contraction of the musculature. It is always perceptibly flattened dorso-ventrally. A very distinct, straight, annular groove, dividing the protosoma from the mesosoma, is situated a little in front of the bridle (Fig. 149*A*, *B*, *C*, *D*). In many specimens, moreover, it is possible to observe a more or less evident post-tentacular groove (Fig. 149*D*). The large, pointed cephalic lobe is roughly triangular and slightly flattened. The very long tentacles are attached symmetrically, close together (Fig. 148*A*, 149*A*, *B*, *C*, *D*). They may be equal, or in a few individuals the left is a little thinner than the right (Fig. 149*D*). The very fine, delicate pinnules are arranged in two rows close together on each tentacle (Fig. 148*B*), except on the basal part, where they are absent. The rather stout, almost colourless keels of the bridle, which is situated in the front part of the mesosoma, lie on weakly developed cutaneous ridges and are fused neither dorsally nor ventrally (Fig. 149*A*, *B*). Each consists of a basal axis, tapering towards both ends, and a row of cuticular rodlets fitting close behind (Fig. 149*E*). The latter are developed only along the ventral half of the bridle. The hind end of the mesosoma is rounded and slanting in side view, so that on the dorsal side the mesosoma is a little longer than on the ventral side. The groove dividing it from the metasoma is very sharp, particularly on the dorsal side. Sometimes a very weakly marked mid-dorsal furrow may be detected behind the bridle.

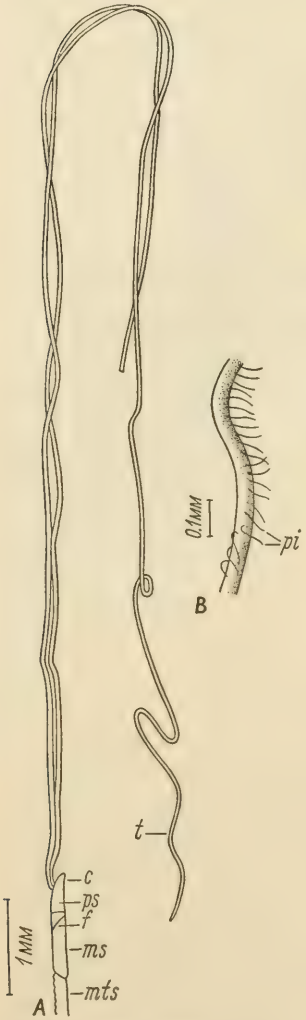


Fig. 148. *Diplobrachia japonica*: *A* – the front end of the body from the left side (the distal part of one of the tentacles is missing); *B* – part of a tentacle.
c – cephalic lobe; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *pi* – pinnules; *ps* – protosoma; *t* – tentacle.

The first part of the metasoma bears between 18 and 32 pairs of densely packed,

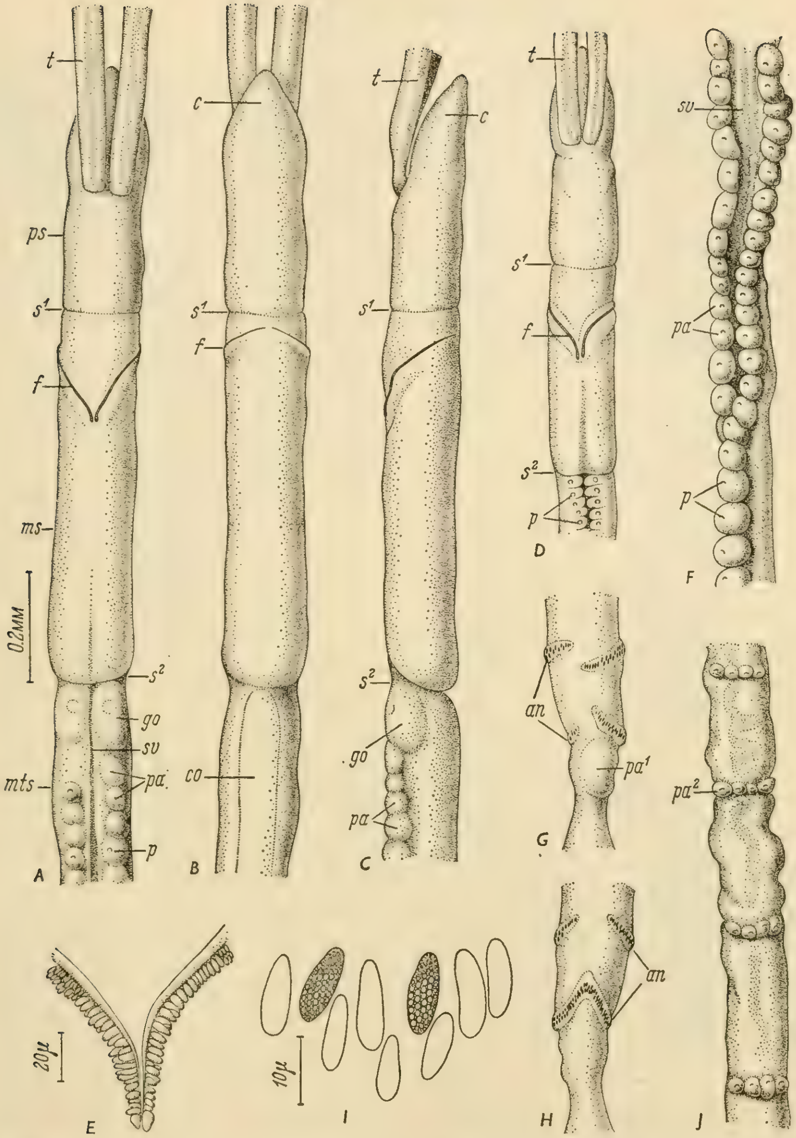


Fig. 149. *Diplobrachia japonica*: *A* – front end of a male from the ventral, *B* – from the dorsal, and, *C* – from the left side; *D* – front end of a female from the ventral side; *E* – ventral parts of the keels of the bridle under high magnification; *F* – part of the metameric section of the preannular region of the metasoma; *G* – the girdles from the ventral, and, *H* – from the dorsal side; *I* – part of a girdle (the bases of the teeth are outlined on 2 of the platelets); *J* – part of the postannular region from the ventral side.

an – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – keels of the bridle; *go* – genital papilla; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaques; *pa* – metameric papillae; pa^1 – ventral papilla lying behind the girdles; pa^2 – postannular papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle.

rounded metameric papillae (Fig. 149*F*). Each papilla contains two or three pyriform glands, and the ventral sulcus between them is rather narrow, whereas the dorsal ciliated band, which begins at the front edge of the trunk, is broad (Fig. 149*B*). In the males the slightly protuberant and large genital papillae lie vertically at the front end of the metasoma (Fig. 149*A*). The cuticular plaques of the metameric papillae are transversely oval, with dense sickle-shaped thickenings along the front edge, on which may be observed, under sufficiently high magnification, numerous fine striations perpendicular to the edge (Fig. 150*A*). The plaques are 25μ across. The non-metameric part of the preannular section has comparatively small, scattered papillae, also bearing plaques (Fig. 150*B*). The latter are hardly different from those of the metameric papillae. In the zone of thickened papillae about ten comparatively large, irregularly situated ventral papillae are present. The plaques lying on them are distinguished by very dark, homogeneous bow-shaped thickenings along the front edge (Fig. 150*C*) and by their smaller size (*c*. 17–18μ across). The remaining part of the trunk in front of the girdles lacks papillae. Two girdles lie one close behind the other; both are interrupted on the ventral side and the first on the dorsal side also. The ridges of the girdles are hardly discernible (Fig. 149*G*, *H*). The toothed platelets are yellowish, narrow ovals, whose front ends are narrower; they measure 10–13μ long and are arranged in two rows in each girdle (Fig. 149*I*). The numerous teeth on the surface of the platelets all point forwards and the front group of teeth is almost non-existent. The very long postannular region of the metasoma has characteristic transverse ventral rows of adhesive papillae placed at more or less equal intervals (Fig. 149*J*), with four or five papillae in each row. The plaques here are transverse rods, bent slightly forward and fringed with a narrow membrane (Fig. 150*D*). These rods are 40–50μ long.

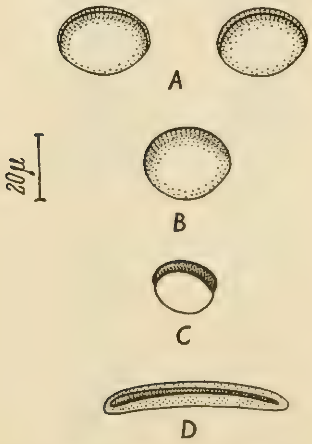


Fig. 150. *Diplobrachia japonica*: *A* – cuticular plaques from a metameric papilla; *B* – cuticular plaques from the non-metameric part of the metasoma; *C* – the same from the zone of thickened papillae; *D* – the same from the postannular section of the metasoma.

Nine individuals, a few of which were incomplete, were measured, giving the following figures for the dimensions of the various parts of the body: length of the tentacles, 8–14 mm; the fore-part of the body, 0·8–1·5 mm long by 0·16–0·18 mm broad; length of the metameric part, 2·5–3·0 mm; length of the whole preannular region, 17·5–30 mm; postannular region, 16–25 mm; overall length of the body together with the tentacles in a few individuals reaches 72 mm.

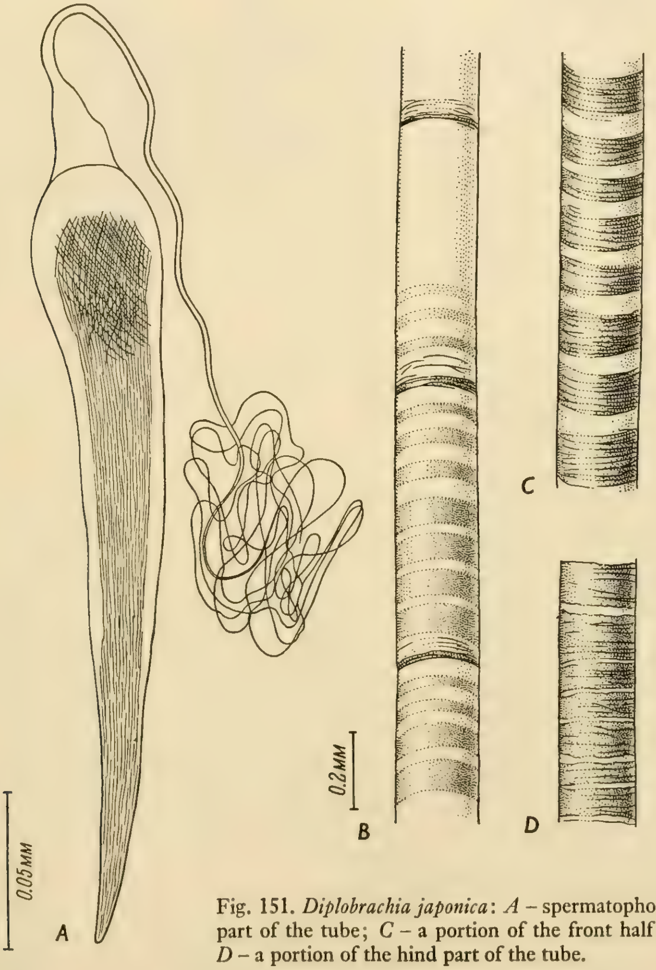


Fig. 151. *Diplobrachia japonica*: *A* – spermatophore; *B* – front part of the tube; *C* – a portion of the front half of the tube; *D* – a portion of the hind part of the tube.

The filamentary end of the very narrow, leaf-shaped spermatophores is rounded; the opposite end is pointed (Fig. 151*A*). The broadest part is near the base of the filament, about one-ninth of the way along. From there to the afilamentar end it tapers gradually and evenly.

A cortical zone free of sperm extends from the base of the filament down the edges of the spermatophore, not, however, reaching the pointed end, which is completely filled with sperm. The filament begins as a large triangular membrane which rapidly tapers into the stout basal part of the filament proper. The spermatophores are 0·25 mm long with a maximum breadth of 0·04 mm.

The front part of the flexible yellow-brown ringed tube is colourless, transparent, membranous and limp, with segments three and a half times as long as the tube is broad. Each segment has a few thin transverse fibres in the hindmost part, then gradually in each segment six or seven brownish rings appear (Fig. 151*B*). The greater part of the tube lacks perceptible boundaries between segments and possesses fibrous, muddy-brown rings whose length does not equal the diameter of the tube (Fig. 151*C*, *D*). The tube may be up to 95 mm long, with a diameter of 0·17–0·22 mm at the front end of the ringed part.

Material: many tubes, some with animals.

Locality: the Japan Trench to the east of Honshu.

Depth: 7450–7520 m.

2. *Diplobrachia belajevi* Ivanov (Fig. 152)

Ivanov, 1960c: 5, 97, 220, 223–6, 265, Figs. 87, 152.

A second species of *Diplobrachia* was found in the Indian Ocean a little to the east of Rodriguez Island by R.V. *Ob*' in 1956. The material, consisting of fourteen small fragments of tubes, was collected in a trial dredging taken at a depth of 580 m, and three incomplete animals were found in the tubes. This species, named after Dr. G. M. Belyaev, possesses a comparatively short, somewhat dorso-ventrally flattened fore-part of the body, whose length is 5–6 times its breadth (Fig. 152*A*, *B*). A simple annular groove defines the forward limit of the mesosoma in front of the bridle, and the protosoma in front of it is rather large, a little narrower than the mesosoma at its hind end but widening out forwards before passing imperceptibly into the broad, triangular or conical, more or less round-ended cephalic lobe (Fig. 152*A*, *B*). The long equal tentacles are attached side by side in the middle of the protosoma (Fig. 152*A*). The pinnules on the tentacles have not been preserved. The bridle is situated in the front part of the mesosoma. The basal axes of its keels are strongly developed, broad, colourless and irridescent under incident light. On the ventral side of the body, arranged in a single row behind the axes and touching them, are the cuticular rodlets (Fig.

152*A*). The ventral ends of the keels touch each other but do not fuse, while the dorsal ends are fused together. The groove between the mesosoma and the metasoma is slanting, as in *D. japonica*.

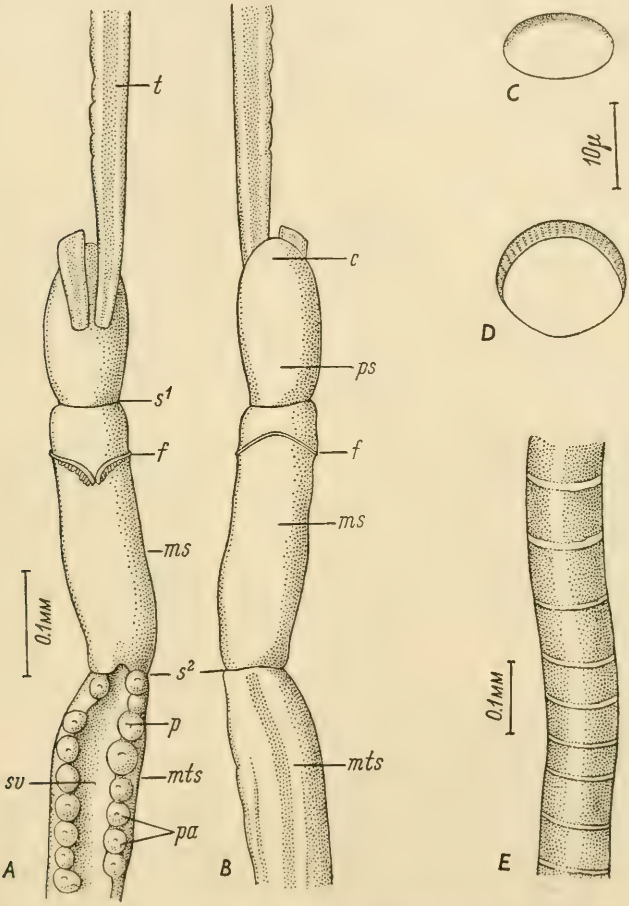


Fig. 152. *Diplobrachia belajevi*: *A* – front end of the body from the ventral side; *B* – the same from the dorsal side; *C* – cuticular plaque from a metameric papilla, and, *D* – one from the zone of thickened papillae; *E* – tube.
c – cephalic lobe; *f* – keel of the bridle; *ms* – mesosoma; *mts* – metasoma; *p* – plaque; *pa* – papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *t* – tentacle.

The rounded medium-sized metameric papillae of the trunk (Fig. 152*A*) have not been counted, but they certainly exceed 20 pairs in each specimen. On the surface of each lies a very delicate cuticular plaque which has its front edge slightly thicker and darker than the rest (Fig. 152*C*). These plaques are 12μ across. On the remaining part of the trunk the ventral papillae vary in size and lie in no sort of order. In the zone of thickening there are few papillae, the plaques of which are distinguished by their round shape and somewhat exceed in size those of the metameric region, reading 13–15μ across. A broad, darkish, crescentic thickening along the front edge of each plaque is crossed by numerous lines perpendicular to the edge (Fig. 152*D*). The region of the girdles and the postannular section of the trunk remain unknown.

The tentacles (in 1 specimen) are *c*. 3 mm long, the fore-part of the body 0·5–0·8 mm long, and the mesosoma 0·08–0·16 mm broad.

The pale rings of the elastic yellow-brown fibreless tube are regular, with even edges. Their length varies, but never exceeds the diameter of the tube. The interspaces between the rings are clear but narrow (Fig. 152*E*). The biggest scrap of tube measures 4·5 cm long and 0·17 mm in diameter.

This species is distinguished from *D. japonica* by the smaller size of the body, the powerful development of the bridle, the dorsally fused keels, the smaller size of the cuticular plaques (12μ across instead of 25μ), the round plaques of the zone of the thickening, and the absence of transverse fibres from the walls of the tube.

Material: 14 small pieces of tubes, four with incomplete animals.

Locality: the Indian Ocean to the east of Rodriguez Island (20°S 63°E).

Depth: 580 m.

[*3. Diplobrachia capillaris* (Southward) (Fig. A152)

Southward, 1959: 441–3, Fig. 2.

The tubes are dark chestnut brown and look very much like hairs; the specific name *capillaris* refers to this likeness. The tube wall is stiff and, in the anterior part at least, is made up of short overlapping segments (Fig. A152*A*). Occasionally the colourless lining layer extends a few mm beyond the first segment. The first few segments are pale brown and unringed; the later segments and the unsegmented part of the tube are marked with regular light and dark brown rings (Fig. A152*A*), or half rings. The posterior end of the tube is yellow; the wall is thinner, but still ringed, and is occasionally surrounded by short segments of a darker outer layer. The diameter is constant along any individual tube and may be from 0·12 to 0·17 mm in different individuals, but is usually between 0·13 and 0·14 mm.

It is difficult to assess the length of the complete tube or animal, since all the specimens seem to be broken, but the longest fragment of tube is 12 cm long. The animal itself may possibly reach 55 mm. A specimen (from the Spanish material) that seems to be nearly complete has been chosen as the type and its measurements are given below, followed by the range, in parentheses, found in other specimens: diameter 0·12 mm (0·10–0·12); total

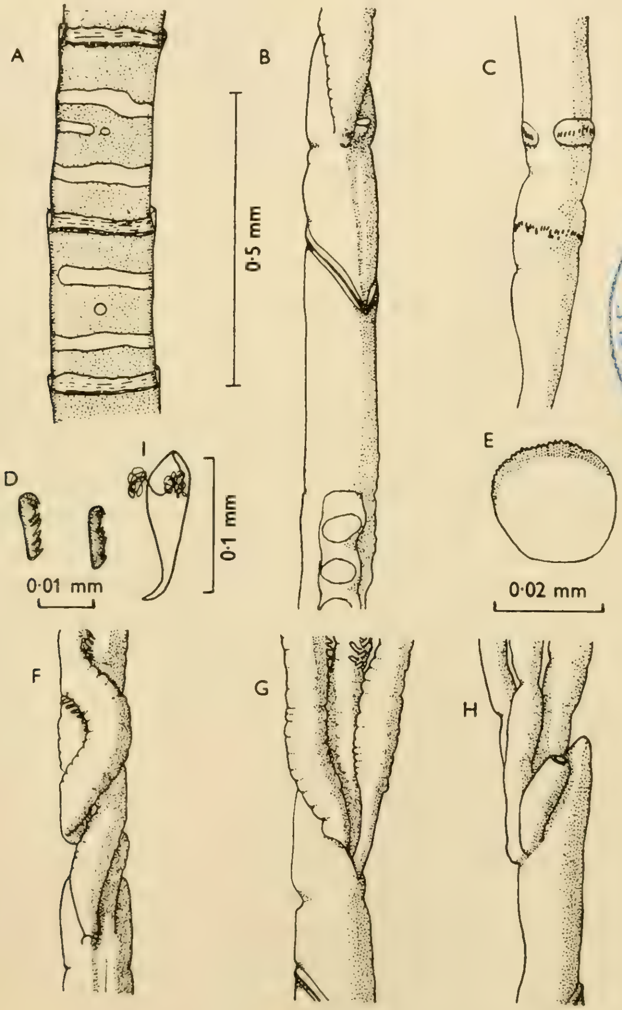


Fig. A152. *Polybrachia capillaris*: *A* – part of tube; *B* – anterior end of type specimen, ventral view; *C* – girdle region; *D* – girdle platelets (uncini), side view; *E* – adhesive plate; *F*, *G*, *H* – anterior ends of specimens with 2, 3 and 4 tentacles; *I* – spermatophore. (After Southward 1959.)

length 30·6 mm; length of pre-annular part 10 mm (5–15); length of post-annular part 20·6 mm (up to 39); length of proto- and mesosoma together 0·75 mm (0·5–1·0); length of coiled tentacles 1·5 mm (0·5–2·2).

The preannular part of the body grows longer as the gonads and gametes begin to develop. It is less than 7 mm long in immature specimens; 7–10 mm long in females and 10–15 mm long in males.

There are from two to four tentacles but two is the most common number (11 specimens have 2, 3 specimens have 3, 2 specimens have 4) and the type specimen has two; they are coiled together into a tight spiral inside the tube and each one has a double row of pinnules (Fig. A152*F*, *G*). Specimens with two tentacles often have a small swelling behind the base of one of them, which may be the first sign of the development of a third. The protosoma is very short (about one-quarter to one-fifth the length of the mesosoma) and is separated from the mesosoma by a shallow groove on the ventral side only (Fig. A152*B*). The bridle lies on a broad ridge and is not complete on the dorsal side, but on the ventral side the two halves are sometimes separate (Fig. A152*B*) and sometimes joined. There is a wide groove along the ventral side between the base of the tentacles and the bridle.

The septum between the mesosoma and metasoma can be seen through the body wall, but there is no external groove. The metameric region is short and has only 6–13 pairs of glandular papillae (7 in the type specimen). The first 4 or 5 of these papillae are devoid of adhesive plates, but all the other papillae on the metasoma bear small round plates (Fig. A152*E*). Behind the paired papillae is a long region bearing occasional isolated papillae and ending in a close row of up to 15 large papillae just before the girdles. The two girdles are made up of single or semi-double rows of small toothed platelets (Fig. A152 *C*, *D*). The post-annular region bears transverse rows of two or three papillae at intervals of about 1 mm.

Mature males contain flat, leaf-like spermatophores, with very fine filaments (Fig. A152*I*).

D. capillaris has the following characters in common with species of *Polybrachia*: part of the tube is built up of short overlapping segments; the tentacles bear pinnules; both paired and unpaired trunk papillae bear adhesive plates; the post-annular papillae are arranged in transverse rows, and the spermatophores are of similar shape to those so far described for *Polybrachia*. There are some differences which suggest that the new species might belong to a separate, new, genus: the number of tentacles is small compared with 18–73 in other species; there are no circular grooves on the proto- and mesosoma, apart from the incomplete one separating the two segments; the new species is only about half the size of the smallest species previously known. For the present it seems best not to propose a new generic name for a species obviously closely related to *Polybrachia*.—E.C.S.]

[Ivanov (*in litteris*) has moved this species to his subsequently everted genus *Diplobrachia*—D.B.C.]

D. capillaris has been collected at six stations, which are listed below:

Date	Position		Depth (fm)	No of specimens
16. v. 58	47° 56′ N	7° 57′ W	340–350	1 empty tube
16. v. 58	47° 50′ N	7° 57′ W	300–450	3 (and 1 empty)
6. viii. 58	43° 43′ N	4° 02′ W	680–970	12 (and many empty)
28. xi 58	48° 26′ N	10° 08′ W	730–780	2 (and 2 empty)
30. xi. 58	48° 39′ N	9° 50′ W	750–850	2
30. xi. 58	48° 40′ N	9° 48′ W	600–680	1

[*4. Diplobrachia southwardae* sp. nov. Ivanov (Figs. D152–G152)

An interesting new pogonophore was found in February, 1960, by R.V. *Vityaz*' in the Arabian Sea east of the coast of southern India. Together with *Lamellisabella minuta* sp. nov. (p. 436) and *Siboglinum silone* sp. nov., a Sigsby trawl brought up, from a depth of 1300 m, many characteristic segmented tubes containing a pogonophore with three or four tentacles. When these were examined closely it was apparent that they belonged to an undescribed species of the genus *Diplobrachia*, which, in honour of the English student of pogonophores Dr. Eve C. Southward, I propose to name *Diplobrachia southwardae*.

The fore-part of the body is six to eight times as long as broad. The very long cylindrical protosoma is divided from the mesosoma by a sharply defined transverse groove lying a little in front of the bridle (Figs. D152*A*, *B*; E152*A*). The very small rounded cephalic lobe is dorso-ventrally flattened and partially enveloped the base of the tentacles. It is separated from the main part of the protosoma by a post-tentacular groove (Fig. E152*A*, *B*). Most of the individuals investigated had three tentacles, but one had four. When three tentacles are present two are attached on the right side of the protosoma and the third on the left (Figs. D152*B*; E152*A*). In the individual with four tentacles two appeared to be on the right and two on the left. The tentacles are very long and have narrow bases. They are furnished with pinnules arranged in a single row, in which, however, traces of an incipient biserial arrangement can be detected (Fig. D152*C*). The pinnules are thick-set and about 140μ long, but near the base of the tentacle they are shorter and yet more thick-set.

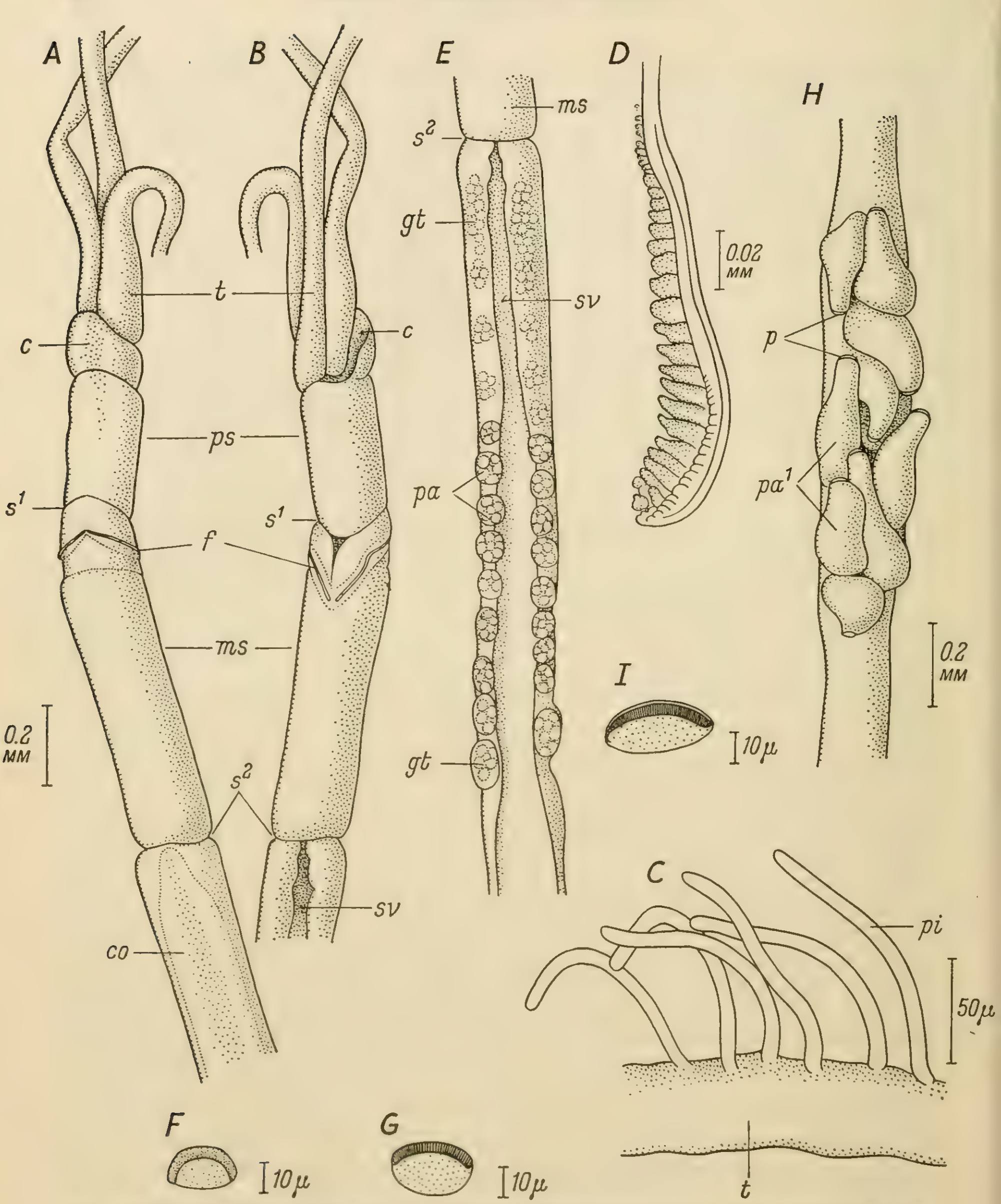


Fig. D152. *Diplobrachia southwardae*: *A* – front end of the body from the dorsal, and *B*, from the ventral side; *C* – part of a tentacle; *D* – the ventral part of a keel of the bridle; *E* – the metameric part of the metasoma from the ventral side; *F* – a plaque from the metameric region; *H* – the zone of thickened papillae from the ventral side; *I* – a plaque from the zone of thickening.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *gt* – pyriform gland; *ms* – mesosoma; *p* – plaque; *pa* – papillae; pa^1 – papillae from the zone of thickening; *pi* – pinnules; *ps* – protosoma; s^1 – groove between the protosoma and mesosoma; s^2 – groove between the mesosoma and metasoma; *sv* – ventral sulcus; *t* – tentacle.

The bridle lies a little in front of the middle of the fore-part of the body. Its thin keels fuse neither dorsally nor ventrally (Fig. D152*A*, *B*). Under sufficiently powerful magnification their structure can be observed: on the ventral side of the body a row of cuticular rodlets is attached to the posterior side of the narrow homogeneous colourless main axis of the keels (Fig. D152*D*)—an unexpected character to find in a species of the genus *Diplobrachia*, but one encountered in a few other forms (e.g. in *Heptabrachia ctenophora* and *Lamellisabella ivanovi*). There is a rather sharp mid-ventral furrow in front of the bridle (Figs. D152*B*, E152*A*), and behind it a slight waist (Fig. D152*A*). The coelom of the mesosoma contains numerous flask-shaped glands, but none lies in front of the bridle. The mesosoma is divided from the metasoma by a simple annular groove.

The metameric section of the trunk is very short but has a well-developed dorsal ciliated band (Fig. D152*A*) and ventral sulcus. In its front half the latter is narrow and bounded at the sides by broad smooth ridges; farther back the sulcus opens out and the ridges disappear (Fig. D152*E*). Adhesive papillae are developed only in the hind half of the region. It is possible to observe the pyriform glands, lying within the lateral ridges, assembled at the front end into longitudinal tracts which break up farther back into rounded metameric groups of glands. There are usually three or four pairs of such groups, each containing four to six glands. A little farther back again these gland-groups become located within well-differentiated oval or round papillae, projecting above the surface of the ridges (Fig. D152*E*). The number of papillae, to judge from six individuals, varies from

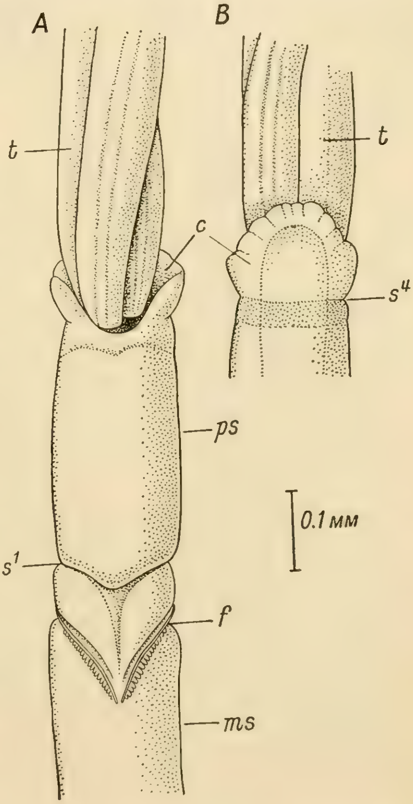


Fig. E152. *Diplobrachia southwardae*: *A* – the protosoma from the ventral side; *B* – the cephalic lobe from the dorsal side.

c – cephalic lobe; *f* – bridle; *ms* – mesosoma; *ps* – protosoma; s^1 – groove between the protosoma and mesosoma; s^4 – post-tentacular groove; *t* – tentacle.

five to sixteen pairs. The papillae bear small semilunar or oval yellowish cuticular plaques with a hoop-like dark thickening along the front edge (Fig. D152*F*). The plaques are 23–25μ across. There are no plaques in the front part of the metameric region.

In the succeeding nonmetameric part of the metasoma there are scattered papillae, also bearing plaques, which are distinguished only by a slight transverse streaking of the hoops and by their slightly greater size (30μ across) (Fig. D152*G*).

There is a well-developed zone of thickened papillae, consisting of 9–15 very large conical papillae, pressed tightly together willy-nilly on the ventral side of the trunk a little in front of the girdles (Fig. D152*H*). Each papilla bears an oval plaque on the tip with a streaky dark thickened rim in front of which there is a very narrow clear border (Fig. D152*I*). They are 40–45μ across.

The two contiguous girdles (Fig. F152*A*) consist of broad protuberant ridges on which the yellowish toothed platelets, 11–12μ long, are arranged for the most part in a double row (Fig. F152*B*). The front girdle has wide dorsal and ventral gaps, but the posterior girdle is only broken on the ventral side. There is a large conical ventral papilla with a tiny (not more than 5μ) transparent cuticular plaque immediately behind the girdles (Fig. F152*A*). The toothed platelets of the girdle are much narrower at the front end. The anterior part of the platelet, with small irregularly backward-pointing teeth, is only half the breadth and a quarter of the length of the posterior section (Fig. F152*C*).

The postannular region of the trunk begins with the characteristic short waist. It is very long but somewhat narrower than the rest of the trunk. On its ventral side it bears metameric transverse rows of conical ventral papillae, three or four in a row (Fig. F152*A*). The papillae bear plaques like oval scales with a rod-like thickening (Fig. F152*D*). The diameter varies from 10 to 25μ, the larger plaques being on the median papillae of a row.

The lengths of the various parts of the body, as measured in six individuals, are as follows (mm):

Tentacles	10·5–17·2
Fore-part of the body	1·3–1·8
Metameric part of the trunk	1·6–3·0
Entire preannular region	up to 30·0

In all the individuals examined only anterior parts of the postannular region remained. The breadth of the mesosoma varied from 0·20 to 0·25 mm.

Out of six nearly complete specimens two were mature males. The filamentar end of the leaf-shaped spermatophores is evenly rounded. This is the broadest part of the spermatophore which tapers gradually towards the other end. The sperm are arranged parallel to one another along the axial

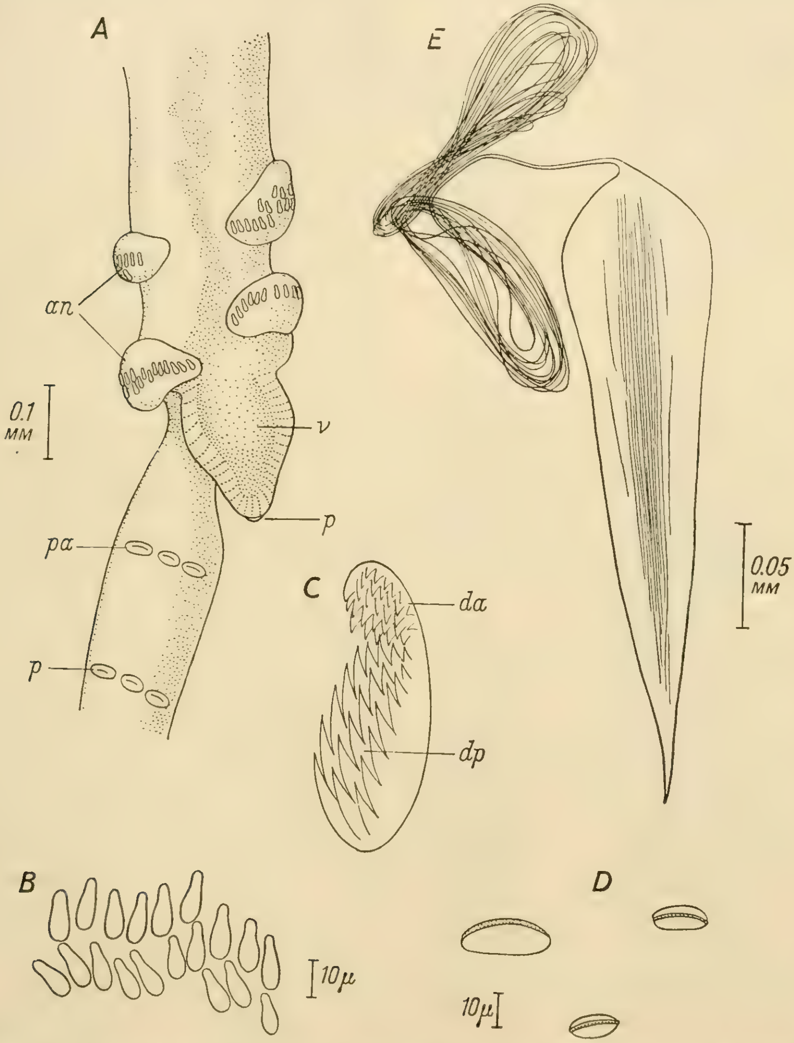


Fig. F152. *Diplobrachia southwardae*: *A* – region of the girdles from the ventral side; *B* – part of a girdle; *C* – toothed platelet seen somewhat from the side; *D* – plaques from the postannular region; *E* – spermatophore.
an – girdles; *da* – anterior group of teeth; *dp* – posterior teeth; *p* – plaques; *pa* – papillae; *v* – ventral papilla.

part of the spermatophore (Fig. F152*E*). The length of the spermatophore is 0·3 mm and the greatest width 0·075 mm. The filament is extraordinarily long and thin.

The brown elastic thin-walled tube is segmented and ringed. Its surface is lustrous. The segments are noticeable only in the anterior part of the tube and each contains, as a rule, five rings (Fig. G152*A*), but it is not rare to come across segments with four, six or even seven rings. The first and last rings in a segment are usually longer and a little darker than the others. The anterior part of the tube is flimsy and transparent. The rings are brown, regular, homogeneous and transparent, and their length is usually a third to a half the diameter of the tube, but occasionally almost equal to it. The interspaces between the rings are clear and transparent. The segments gradually disappear and the greater part of the tube is characterized by noticeably shorter rings (Fig. G152*B*). In the hind part of the tube they become muddy brown, opaque and somewhat fibrous, with darker edges (Fig. G152*C*). Still nearer the end the distance between the rings becomes greater and the rings themselves become irregular with crooked edges (Fig. G152*D*). In the hindmost part of the tube the rings gradually fade and ultimately disappear. The tube is up to 140 mm long and the anterior diameter 0·2–0·3 mm.

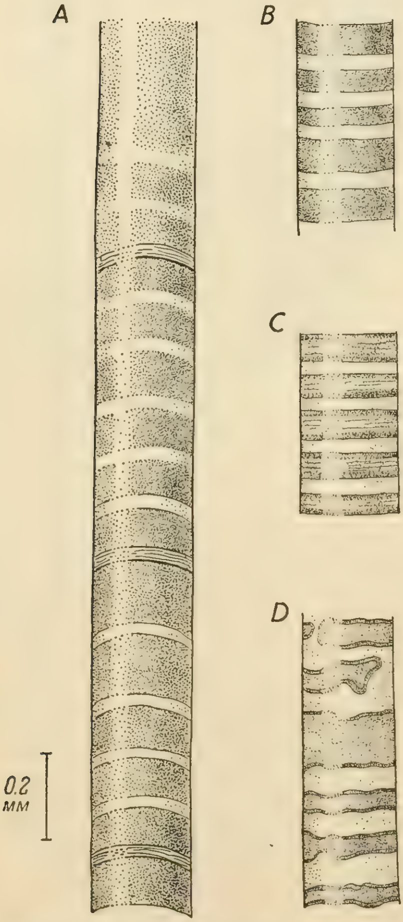


Fig. G152. *Diplobrachia southwardae*: *A–D* – successive parts of the tube.

D. southwardae is distinguished from other species of this genus by its large size, which is possibly connected with the increase in number of the tentacles to three or even four. The chief distinctions of this species, however, appear to be the very small size of the cephalic lobe and its lappet-like shape, and the poor development of the metameric region of the trunk. Particularly striking is the absence of adhesive papillae from the anterior part of the metameric region, where instead we see a pair of undivided tracts of pyriform glands. This first stage in the development of secondary metamerism tallies with what we have observed along the whole of the anterior 'metameric' section of the trunk in *Oligobrachia dogieli*. Finally, *Diplobrachia southwardae* possesses somewhat larger cuticular plaques than the other species of the genus, particularly on the papillae of the zone of thickening, and a characteristic spermatophore.

Material: 11 tubes with animals or fragments of animals and 21 empty tubes.

Locality: *Vityaz'* station 4620 (31st cruise): Arabian Sea to the west of the coast of southern India.

Depth: 1300 m.]

TABLE 4

Characteristics of the species of *Diplobrachia*

	D. japonica	*D. belajevi*	*D. capillaris*	*D. southwardae*
Number of tentacles	2	2	2–4	3–4
Length of the fore-part (mm)	0·8–1·5	0·5–0·8	0·5–1·0	1·3–1·8
Breadth of the mesosoma (mm)	0·16–0·18	0·08–0·16	0·10–0·12	0·20–0·25
Breadth/length ratio of fore-part	$\frac{1}{5\text{–}8}$	$\frac{1}{5\text{–}6}$	$\frac{1}{5\text{–}8}$	$\frac{1}{6\text{–}8}$
Fusion of the keels	Absent	Dorsal	Ventral in some specimens	Absent
Shape of the cephalic lobe	Triangular, pointed	Rounded	Pointed	Rounded
Number of pairs of metameric papillae	18–32	More than 20	6–13	5–16
Dimensions of the cuticular plaques (μ):				
from the metameric papillae	25	12	20	23–25
from the nonmetameric papillae	25	*ca* 12	?	30
from the papillae of the zone of thickening	17–18	13–15	?	40–45
Shape of the cuticular plaques on the papillae of the zone of thickening	Oval	Round	Round	Oval
Segmentation of the tube	+	—	+	+
Maximum diameter of tube (mm)	0·22	0·17	0·17	0·30
Length of spermatophores (μ)	400	?	120	300

4. Genus *Zenkevitchiana* Ivanov 1957

Ivanov, 1957a: 439, 448, 470–5, 483, 490, 492, 493, 496, 497; Abrikosov, 1957: 238; Dajoz, 1958: 236; Ivanov, 1960a: 1528, 1531, 1539, 1558, 1620; Ivanov, 1960c: 6, 11, 15, 24, 37, 92, 94, 106, 108, 114, 199, 215, 226–7.

The protosoma is continuous with the mesosoma and the cephalic lobe is not separated from the protosoma. The tentacular crown consists of a comparatively small number of tentacles. The front part of the trunk lacks cuticular plaques and the adhesive papillae are glandular. The tube is segmented, without funnel-shaped frills to the segments, and the segments in the front part are white and flexible. The inclusion of this genus among the Polybrachiidae is at first glance contradicted by the merging of the protosoma and the mesosoma into a single united fore-part of the body, a feature not found in other genera of Polybrachiidae, but, on the contrary, characteristic of the Lamellisabellidae and Spirobrachiidae. In the present case, however, a more important indication would seem to be the possession of free tentacles, while the fusion of the two anterior segments appears increasingly in the more highly evolved species of Thecanephria and must have arisen independently in the Polybrachiidae, *Lamellisabella* and *Spirobrachia*. The absence in *Zenkevitchiana* of any cuticular plaques in the fore-part of the trunk may be a result of their reduction, and thus cannot be considered to hinder the ascription of this genus to the Polybrachiidae (Ivanov, 1957*a*).

Type of the genus: *Zenkevitchiana longissima* Ivanov.

1. *Zenkevitchiana longissima* Ivanov (Figs. 9, 34, 153–5)

Ivanov, 1957a: 439, 448, 470–5, 483, 490, 492, 493, 496, 497, Figs. 41–45, 59; Abrikosov, 1957: 238; Brunet and Carlisle, 1958: 1689; Ivanov, 1960a: 1538, 1542, 1606, 1607, 1613, Figs. 1391, 1415; Ivanov, 1960c: 6, 10, 22, 91, 94, 97, 108, 151, 227–30, 266, Figs. 9, 34, 87, 153–5.

This species is characteristic of the Kuril Trench, where in places more than 9000 m deep it occurs in enormous numbers. The fore-part of the body is cylindrical, with a length to breadth ratio of 6 : 1 (Fig. 153*A*, *B*). The region of the protosoma is very small, strongly compressed and not divided from the mesosoma. In the mesosomal region masses of small round sacculate glands may often be seen through the body wall. The small cephalic lobe is somewhat flattened and rounded at the tip. The 14 very long, unfused tentacles are arranged in a complete ring and each bears an apparently single row of very small pinnules. The very delicate, pale keels of the bridle, which lies in the front half of the fore-part, almost meet dorsally and fuse together ventrally. In front of the bridle runs a sharp mid-ventral furrow. The forepart of the body is divided from the trunk by a slanting, annular groove, the ventral part of which lies a little in front of the dorsal (Fig. 9). The anterior, metameric part of the trunk has a well-marked ventral sulcus (Fig. 153*B*) running between lateral ridges on which are arranged the more or less metameric, paired papillae. These may be round or oval and the front ones are smaller (Fig. 153*B*), increasing in size several-fold farther back (Fig. 154*A*). Inside each of them several pyriform glands may be discerned through the integument, but they lack cuticular plaques. In one individual 40 papillae were counted on the left, 38 on the right. The rather broad, dorsal ciliated band begins at the front end of the trunk (Fig. 153*B*). The large genital papillae of the male are laterally compressed and project forward (Figs. 9, 153*B*). The very long, cylindrical non-metameric part of the trunk is dotted with small ventral or lateral, glandular papillae which bear adhesive plaques (Fig. 154*B*). The

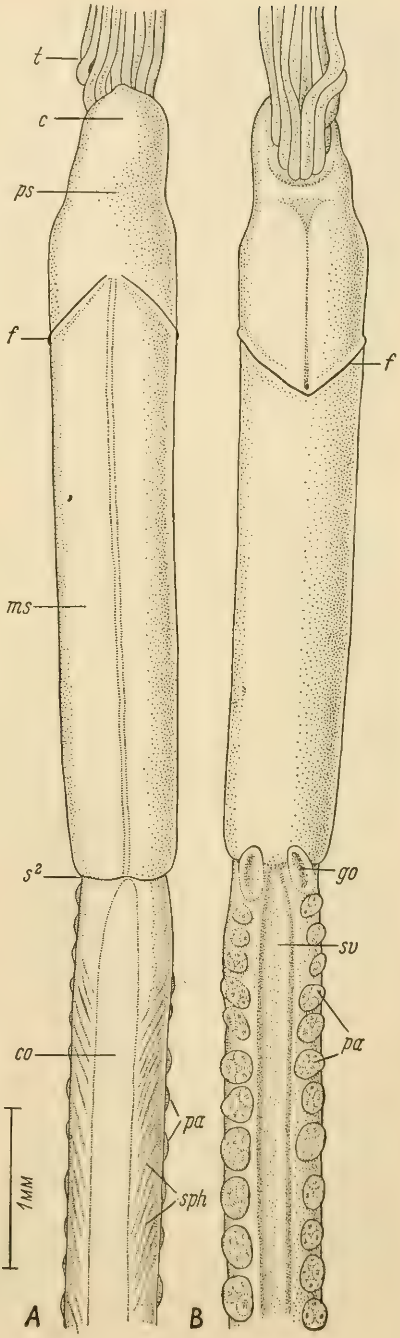
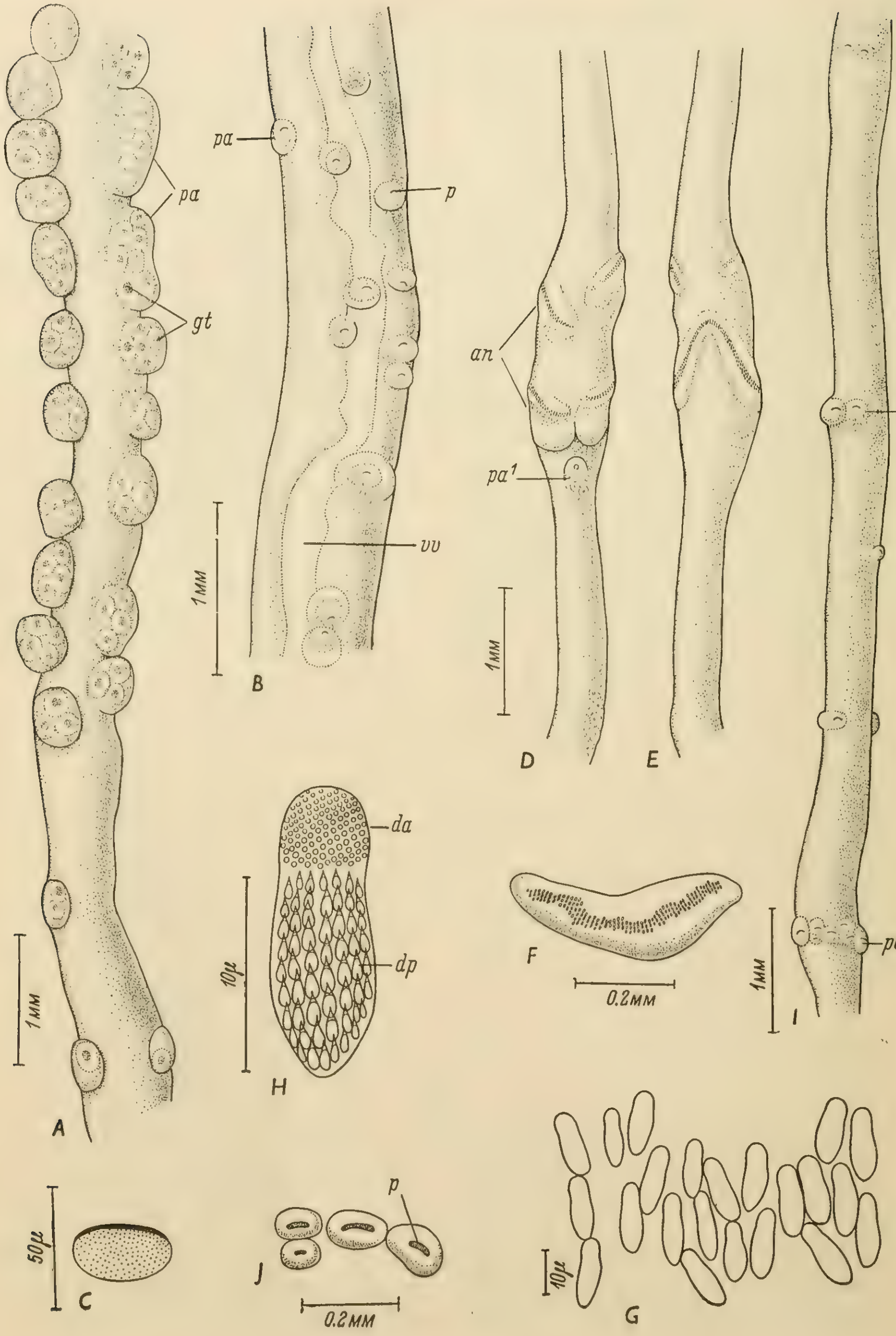


Fig. 153. *Zenkevitchiana longissima.* Front end of a male; *A* – in dorsal, and, *B* – in ventral view. *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – keel of the bridle; *go* – genital papilla; *ms* – mesosoma; *pa* – papillae; *ps* – protosoma; s^2 – groove between the mesosoma and the metasoma; *sph* – spermatophores, seen by transparency through the body wall; *sv* – ventral sulcus; *t* – tentacle. (After Ivanov, 1957*a*.)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0.2 MM
10μ
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latter, oval in shape and reaching 40–60μ across, are thin and delicate, but have a thickened front edge (Fig. 154*C*). The girdles, lying on muscular ridges, are interrupted ventrally and the first girdle dorsally also (Fig. 154*D*, *E*), while the hind girdle arches sharply forwards on the dorsal side. The yellowish oval toothed platelets, 13–17μ long, form three to four rows in each girdle (Fig. 154*F*, *G*). About a third of each platelet is covered by the numerous very small teeth of the anterior group, while those of the posterior group are comparatively large, but fewer (Fig. 154*H*). Behind the girdles lies a mid-ventral papilla (Fig. 154*D*) with a very small plaque. The postannular region of the trunk is also very long and cylindrical and the small adhesive papillae are here arranged on the ventral side in transverse metameric rows, with eight in each row (Fig. 154*I*). Variants not infrequently occur, however, with a smaller number of papillae in each row, with the papillae not in a straight line, or with single isolated papillae between the rows. Each papilla has a slightly bent, rod-shaped plaque not more than 80μ long (Fig. 154*J*).

In two individuals of medium size the length of the body, including the tentacles, amounted to 36 cm in the male and 35·5 cm in the female. The tentacles are usually 5–6 cm long and in one specimen reached 9·1 cm. The fore-part of the body is up to 5 mm long, with a breadth, at the level of the bridle, of up to 0·8 mm.

The spermatophores are much elongated, gradually tapering towards the afilamentar end and with the greatest breadth quite near the filamentar end (Fig. 155*A*). They resemble the spermatophores of *Spirobrachia grandis* and *S. beklemischevi*, except that they are much narrower. The basal part of the very long filament is stout and has a granular structure, but gradually tapers. The whole spermatophore is *c.* 1·5 mm long.

The tube of *Zenkevitchiana longissima* is rather peculiar. It is white, rather flexible and elastic, and the walls are very stout, consisting of a dense semi-transparent substance, which is easily cut with a sharp scalpel. Almost the

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Fig. 154. *Zenkevitchiana longissima*: Metasoma: *A* – hind part of the metameric section of the preannular region in ventral view; *B* – part of the non-metameric section of the preannular region in ventral view; *C* – cuticular plaque; *D* – region of the girdles in ventral view; *E* – the same in dorsal view; *F* – one half of a girdle under high magnification; *G* – part of a girdle; *H* – toothed platelet (in the front part of the platelet the bases only of the teeth are indicated); *I* – part of the postannular region in ventral view; *J* – ventral papillae of the postannular region.
an – girdles; *da* – anterior group of teeth; *dp* – posterior group of teeth; *gt* – pyriform glands seen by transparency; *p* – cuticular plaque; *pa* – papillae; pa^1 – papillae lying behind the girdles; pa^2 – transverse row of papillae; *vv* – ventral blood vessel seen by transparency.

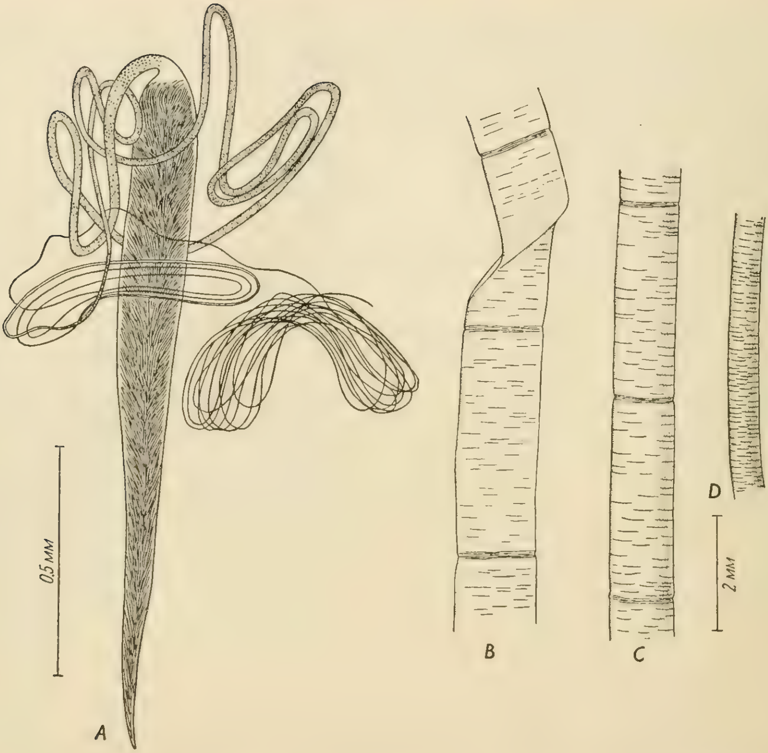

Fig. 155. *Zenkevitchiana longissima*: *A* – spermatophore; *B* – anterior membranous part of the tube; *C* – middle part of the tube; *D* – hind part of the tube. (After Ivanov, 1957*a*.)

whole tube, with the exception of the hindmost part, is segmented. The boundaries between the rather long segments are detectable only by careful inspection and look like clean superficial formations, or narrow belts, covered with transverse lines (Fig. 155*C*). The front end of the tube is transparent, limp and delicate, but the segmentation is visible here also (Fig. 155*B*). At the hind end the tube gradually becomes much more stiff and brown, while the hindmost end of all is dirty-grey with the firmest walls (Fig. 155*D*). The tube may be up to 150 cm long and the anterior membranous part up to 15 cm. The diameter of the front end may reach 1·6 mm, but is more often *c*. 1·0 mm; the diameter near the hind end is *c*. 0·4 mm.

Material: a great many tubes, some with animals and some empty.

Locality: Kuril Trench.

Depth: 4840–9950 m.

5. Genus *Polybrachia* Ivanov

Ivanov, 1952: 379–83, 388–90; Zenkevitch, 1954: 77, 78, 80; Zenkevitch, Birstein and Belyaev, 1954: 68; Hartman, 1954: 184, 185; Ivanov, 1954b: 73, 74, 77, 79; Ivanov, 1955a: 177; Ivanov, 1955b: 382, 383; Ivanov, 1955d: 173, 174; Ivanov, 1955e: 224; Ivanov, 1956b: 1864, 1868; Ivanov, 1956c: 165; Jägersten, 1956: 238; Kirkegaard, 1956b: 185, 186; Abrikosov, 1957: 234; Ivanov, 1957a: 431, 435, 439, 442, 449, 460, 461, 470, 475, 481, 490, 492, 494–7; Ivanov, 1957b: 1139; Vinogradova, 1958: 112; Dajoz, 1958: 231–3, 236, 237; Fell, 1958: 45, 46; Ivanov, 1958a: 1363, 1369, 1371, 1372; Ivanov, 1960a: 1528, 1529, 1531, 1538, 1539, 1550, 1552, 1572, 1580, 1583, 1606, 1607, 1620; Ivanov, 1960c: 6, 11, 12, 14, 24, 36, 37, 43, 57, 59, 66, 69, 75, 92, 94, 114, 199, 203, 215, 230–1, 237; Kirkegaard, 1960: 226.

The protosoma is divided from the mesosoma and the cephalic lobe from the protosoma by a transverse groove. The mesosoma has several secondary annuli in front of the bridle. There are never less than 18 tentacles, but the base of the tentacular crown does not form a complete circle but a horseshoe. The fore-part of the trunk bears cuticular plaques. The tube is segmented with funnel-like frills or collars to each segment.

There are at least three species: *Polybrachia annulata*, *P. barbata*, *P. gorbunovi.*

Type species: *Polybrachia annulata* Ivanov.

In all likelihood *Krampolinum galatheae* Kirkegaard belongs to this genus. This species was described by Kirkegaard (1956b), from a collection taken at a depth of 2950–3190 m in the Gulf of Panama in the eastern Pacific Ocean, on the basis of two tubes and a very badly preserved fragment of one individual, which did not permit any determination of the systematic position of the animal. The delicate pale clear tube is frequently speckled and transversely striped. The middle part of the tube has membranous frills, whereas the upper part has a close series of broad funnels (Kirkegaard, 1956b). Kirkegaard believes that this peculiarity of the tube is sufficient to afford grounds for establishing a separate genus within the family Polybrachiidae. The various characters enumerated are, however, all found in species of *Polybrachia*. It would thus seem that *Krampolinum galatheae* is a species of this genus, *Polybrachia galatheae* (Kirkegaard). *P. capillaris* Southward is better ascribed to *Diplobrachia* and is so described here.

Key for the identification of species of *Polybrachia**

1 (2) There are not more than 20 tentacles. The length of the fore-part of the body is not more than 1 mm, and the breadth not more than 0·3 mm. 3. *P. gorbunovi* (p. 400).

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* Excluding *P. galatheae.*

2 (1) There are not less than 26 tentacles, often many more. The fore-part of the body is not less than 2·5 mm long.

3 (4) There are between 26 and 39 tentacles. The mesosoma bears three secondary transverse grooves in front of the bridle, whose keels are black, with thickened ventral ends which meet. The fore-part of the body is *c*. 3 mm long, and less than 1 mm broad. 1. *P. annulata* (p. 394).

4 (3) There are about 70 tentacles, and two secondary grooves on the mesosoma in front of the bridle whose keels are thin and delicate and do not meet ventrally. The fore-part of the body is *c*. 4 mm and more than 1 mm broad. 2. *P. barbata* (p. 398).

1. *Polybrachia annulata* Ivanov (Figs. 7, 11, 13, 17*C*, 156–8)

Ivanov, 1952: 379–382, 389, Figs. 13–18; Zenkevitch, 1954: 77, Figs. 6, 9; Zenkevitch, Birstein and Belyaev, 1954: 68, Figs. 9, 10; Hartman, 1954: 185; Ivanov, 1954b: 73, 77, Figs. 4, 8; Ivanov, 1955e: 224, Pl. 65, Fig. 4; Jägersten, 1956: 238; Kirkegaard, 1956b: 185, 186, Fig. 4; Ivanov, 1957a: 442, 449, 481, 490, 492–7, Fig. 59; Ivanov, 1957b: 1139; Vinogradova, 1958: 112; Dajoz, 1958: 233, 236, 237, Figs. 2 (wrongly labelled), 6; Ivanov, 1958a: 1363, 1369, Figs. 11, 12; Ivanov, 1958b: 1682, 1687, 1689, Figs, 2, 5, 6; Ivanov, 1958e: 1078, 1079; Southward, 1959: 443; Ivanov, 1960a: 1534, 1538, 1540, 1541, 1558, 1565, 1606, 1608, 1609, 1612, 1613, Figs. 1389, 1393, 1399, 1410, 1416–17, 1429, 1437, 1449–50, 1465; Ivanov, 1960c: 6, 12, 22, 23, 25, 27, 51, 76, 92, 94, 96, 167, 231–5, 237, 240, 250, 266, Figs. 7, 11, 13, 17, 29, 35, 36, 40, 49, 57, 68–9, 84*B*, 87, 156–8.

In front of the bridle the mesosoma is ringed with three secondary grooves (Fig. 156*A*). The cephalic lobe is an equilateral triangle with gently rounded corners and it is divided from the protosoma by a transverse groove, most noticeable on the dorsal side (Fig. 156*B*, *C*). A deep, mid-ventral furrow on the mesosoma in front of the bridle cuts across the secondary rings, while behind the bridle stretches a cutaneous ridge which gradually broadens towards the hind end of the mesosoma. The tentacles vary in number from 26 to 39, forming a very long crown (Fig. 7) whose base is a horseshoe, opening towards the ventral side (Fig. 156*A*). In the dorsal part of the crown the tentacles are arranged in two rows, laterally they form three rows, while on the ventral side only one row (Fig. 17*C*). The numerous pinnules form four to five dense rows on each tentacle.

The metameric division of the front part of the trunk is about two or three times as long as the whole fore-part of the body and accounts for about a tenth of the overall length of the preannular region. The ventral sulcus, distinguished by its considerable breadth (Fig. 156*A*), is bounded by rather narrow ridges. The dorsal ciliated band is well developed and continues into the hind part of the preannular region. The metameric region carries 22–28 pairs of adhesive papillae, while within the very long non-metameric region five distinct zones may be distinguished with differing densities of adhesive papillae: (1) the adhesive papillae are very small and widely spaced; (2) the papillae are rather frequent; (3) the papillae are sparse; (4) the papillae are mostly on the ventral surface, almost touching each other in places—this is the zone of thickened papillae; (5) the papillae are moderately dense. The lengths of these five zones have the ratio: 12 : 6 : 2 : 1 : 2. In the females, in which the ova and oviducts may be seen through the body wall of the non-metameric region, the gonads end at the boundary between the third and fourth of these zones, i.e. in front of the zone of thickened papillae, where the boundary is usually very sharp (Figs. 11, 156*F*). The girdles are situated on muscular ridges (Fig. 156*G*), which are separated by considerable ventral gaps wherein lie a few small papillae with rod-shaped plaques. The first girdle, unlike the second, is interrupted only ventrally and not dorsally. In specimens collected from the Sea of Okhotsk the toothed platelets lie in three to four rows (Fig. 156*H*), while in specimens from the Bering Sea there are usually four to six rows in each girdle (Fig. 156*I*). The elongated oval platelets are a little narrower in the middle, and the front end is noticeably narrower than the back. Almost a third of the platelet is occupied by the fine teeth of the anterior group, the rest being occupied by the comparatively large, not very numerous, teeth of the posterior group (Fig. 156*J*). In specimens from the Sea of Okhotsk the platelets are 15–18μ long, in Bering Sea specimens 12–15μ.

The total number of adhesive papillae in the whole trunk is very great, certainly not less than several hundred. The oval adhesive plaques are very small, only 21–28μ across in the metameric region of the trunk, while those lying in the posterior zones of the preannular part are 35–40μ across. The plaques are membranous except for the thickened crescent along the front edge (Fig. 156*E*). In the postannular section of the trunk the plaques are rod-like, 35μ long, placed transversely, a trifle bent, and, for the most part, fringed in front and behind by a narrow membrane.

A medium-sized, adult female has the following dimensions: length of the tentacles, 16 mm; the fore-part of the body, 3 mm long and up to 0·75 mm broad; length of the metameric region, 6·5 mm; non-metameric region, 64·5 mm long; length of the body as far as the girdles, 90 mm; the post-annular region, *c.* 40 mm long; overall length of the body, 130 mm.

The flat, leaf-shaped spermatophores are like lance points packed with thread-like sperm (Fig. 157). One end of the spermatophore gradually

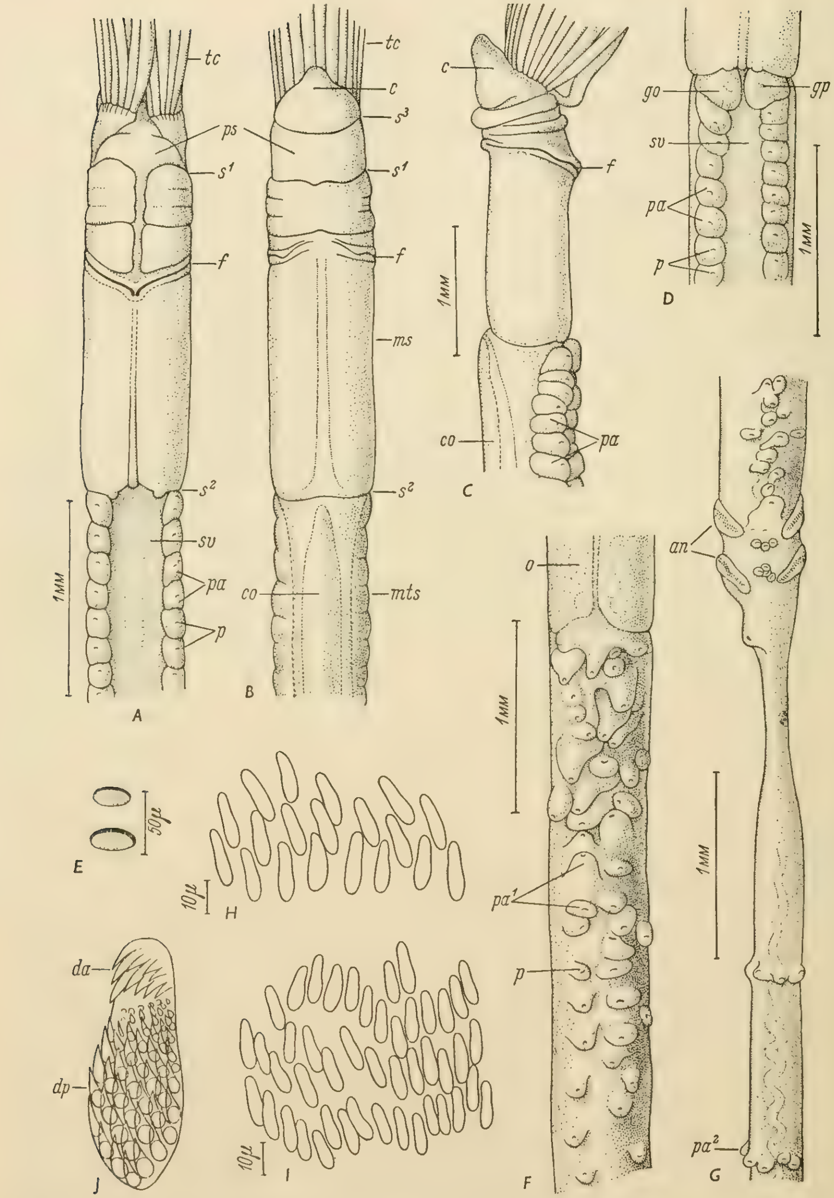

Fig. 156. *Polybrachia annulata*: *A* – front end of a female from the ventral, *B* – from the dorsal, and, *C* – from the right side; *D* – hind part of the mesosoma and the beginning of the metasoma of a male in ventral view; *E* – cuticular plaques from metameric papillae; *F* – zone of thickened papillae in ventral view; *G* – region of the girdles from the ventral side; *H* – part of a girdle from an individual from the Sea of Okhotsk; *I* – part of a girdle from an individual from the Bering Sea; *J* – toothed platelet.

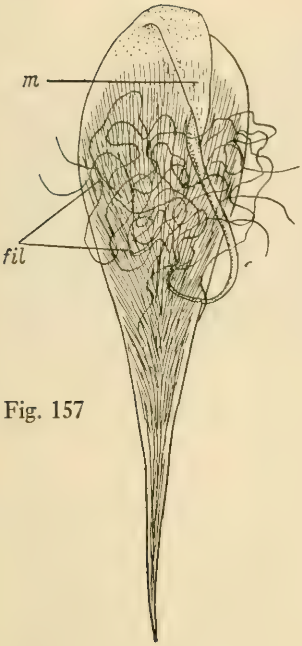

Fig. 157

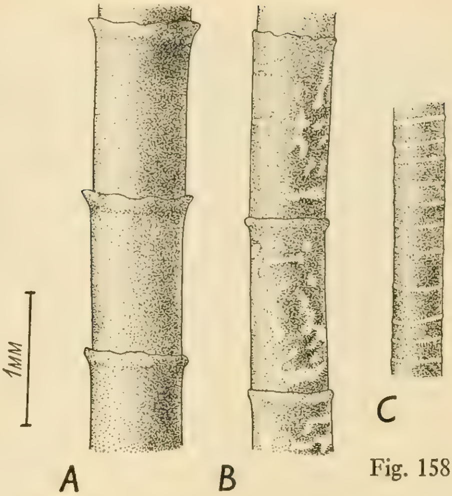

Fig. 158

Fig. 157. *Polybrachia annulata*: Spermatophore. *fil* – filament of spermatophore; *m* – base of filament. (After Ivanov, 1952.)

Fig. 158. *Polybrachia annulata*: Tube: *A* – middle part; *B* – a portion from about two-thirds back; *C* – near the hind end. (After Ivanov, 1952.)

tapers into a long point, the other end is rounded and supports a delicate, ribbon-like outgrowth, which always bends down at the base to run along one of the flat sides of the spermatophore before tapering into the very long slender filament. Excluding the ribbon-like outgrowth, the spermatophore is 0·6 mm long and has a maximum breadth of 0·17 mm.

The very firm, opaque tube of *P. annulata* is brown or brown-black. The length is not less than 50–60 cm and at the front end the diameter reaches 1·16 mm. The oldest narrowest part of the tube—the hind end—consists of dark rings alternating with narrow clear intervals (Fig. 158*C*), but the greater part of the tube is segmented, and each segment carries on its front edge a filmy funnel-like frill or collar (Fig. 158*A*), usually rather tattered. In the middle part of the tube the segments have clear transparent irregular blotches,

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an – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *da* – front group of teeth; *dp* – hind group of teeth; *f* – keel of the bridle; *go* – genital papilla; *gp* – genital aperture; *ms* – mesosoma; *mts* – metasoma; *o* – egg seen by transparency; *p* – cuticular plaque; *pa* – metameric papillae; pa^1 – papillae of the zone of thickening; pa^2 – postannular papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; s^3 – pretentacular groove; *sv* – ventral sulcus; *tc* – tentacular crown. (*E*, *F*, *G* – after Ivanov, 1952.)

a few of which may run together to form more or less complete rings (Fig. 158*B*).

P. annulata is distinguished from other species by the possession of three secondary grooves on the mesosoma and by the solid coarse keels of the bridle. In the number of tentacles this species occupies an intermediate position between *P. gorbunovi* and *P. barbata*.

Material: many tubes, some with animals.

Localities: *P. annulata* is encountered both in the abyssal zone of the Sea of Okhotsk, where it occurs together with *Lamellisabella zachsi*, and in the abyss of the southwestern part of the Bering Sea, of which it is especially characteristic.

Depth: 1440–5000 m.

2. *Polybrachia barbata* Ivanov (Figs. 17*D*, 159)

Ivanov, 1952: 383–4, 388, 389, Figs. 19–22; Zenkevitch, 1954: 78, 80, Figs. 7, 9; Zenkevitch, Birstein and Belyaev, 1954: 68, Fig. 10; Hartman, 1954: 185; Ivanov, 1954b: 74, 77, Fig. 5; Ivanov, 1955e: 224, Pl. LXV, Fig. 5; Jägersten, 1956: 238; Kirkegaard, 1956b: 186, Fig. 4; Abrikosov, 1957: 234, Fig. 4; Ivanov, 1957a: 492, 496, Fig. 59; Vinogradova, 1958: 112; Dajoz, 1958: 233, 236, 237, Figs. 2 (incorrectly labelled), 6; Ivanov, 1960a: 1530, 1539, Fig. 1399*D*; Ivanov, 1960c: 6, 12, 231, 235–7, Figs. 17, 87, 159.

Two transverse secondary grooves, which cross the mesosoma in front of the bridle (Fig. 159*A*, *B*), are intersected by a rather broad mid-ventral furrow which is very broad at the front and, in contrast with the analogous furrow in *P. annulata*, does not reach back as far as the bridle. The cephalic lobe is like that of *P. annulata*, with a blunt tip and delimited behind by a transverse groove (Fig. 159*A*). The tentacles are very long and numerous, numbering 71 in the only known specimen. The surface to which they are attached is shaped like a horse-shoe with incurved ends and the base of the tentacular crown covers the whole area of this horse-shoe, with the tentacles arranged in several rows (Fig. 17*D*). The very delicate, slender keels of the bridle, which lie on low ridges (Fig. 159*A*, *B*), do not run close to each other either dorsally or ventrally. The back end of the mesosoma is slightly compressed dorso-ventrally and ends in two small dorsal protuberances.

The ventral sulcus of the metameric part of the trunk is broad (Fig. 159*B*) and the dorsal ciliated band is well developed. The whole of the remainder of the preannular part and the entire postannular region remain unknown. The small oval cuticular plaques of *P. barbata* are interesting in that many of them are clearly double, consisting of two in tandem (Fig. 159*C*). The front plaque of such a pair is always well developed, the posterior plaque sometimes

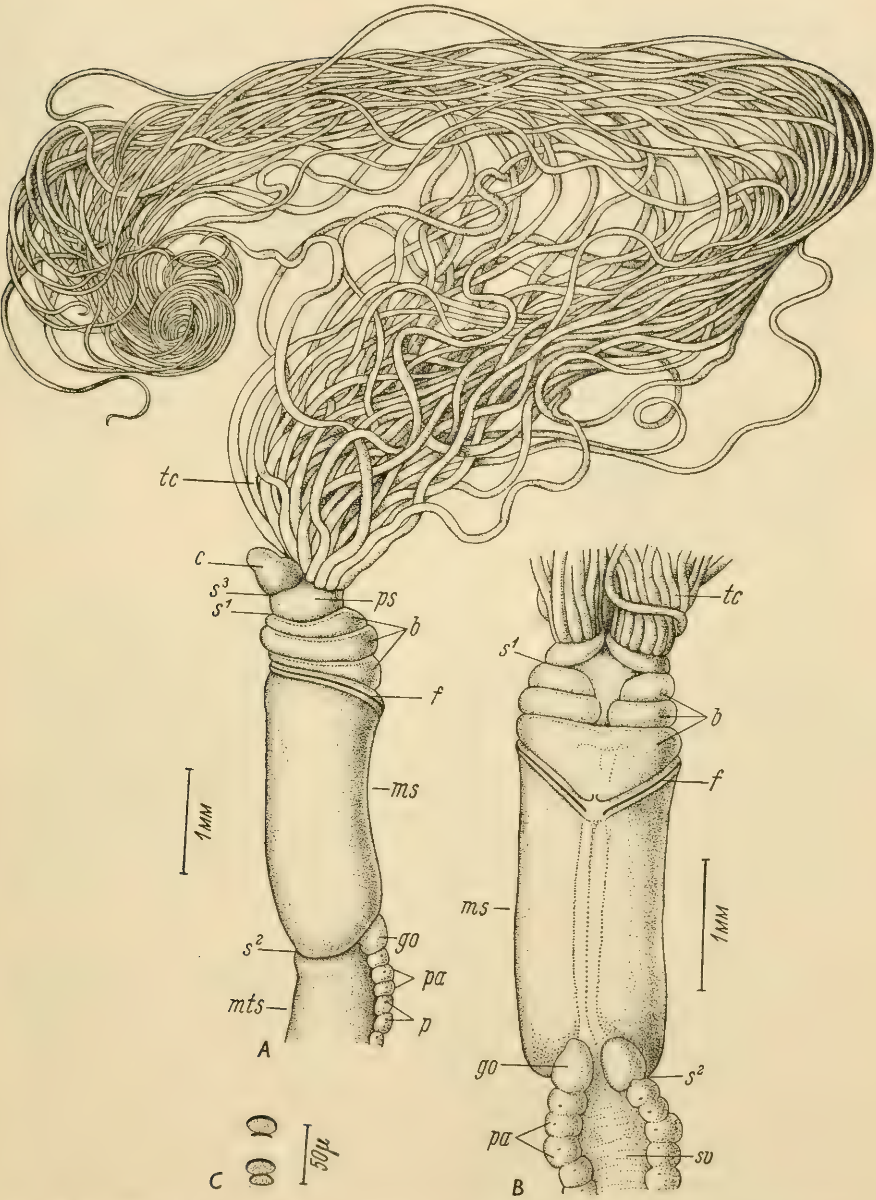

Fig. 159. *Polybrachia barbata*: *A* – front end of a male from the right side; *B* – the same in ventral view; *C* – cuticular plaques.

b – secondary mesosomal rings; *c* – cephalic lobe; *f* – keel of the bridle; *go* – genital papilla; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaques; *pa* – papillae; *ps* – protosoma; s^1 – groove between the protosoma and the mesosoma; s^2 – groove between the mesosoma and the metasoma; s^3 – pretentacular groove; *sv* – ventral sulcus; *tc* – tentacular crown. (After Ivanov, 1952.)

a little under-developed or even reduced to a mere detached fragment. The transverse plaques of the metameric papillae are *c*. 25μ across. The only known specimen is a male in which the large genital papillae overhang the back edge of the mesosoma and slant towards each other at the front (Fig. 159*B*). Spermatophores have not been found in the sperm ducts.

The various parts of the body have the following dimensions: length of the tentacles, 20 mm (in a strongly contracted condition); length of the forepart of the body, 4 mm; breadth of the mesosoma, 1·3 mm.

The tube is unknown.

The comparatively weakly developed, delicate, slender keels of the bridle, which do not meet ventrally, easily distinguish *P. barbata* from other species of this genus. In contrast with *P. annulata* there are only two secondary grooves on the mesosoma. The large number of tentacles is also diagnostic.

Material: one incomplete specimen.

Locality: the southwestern part of the Bering Sea.

Depth: 3792–3802 m.

3. *Polybrachia gorbunovi* (Ivanov) (Fig. 160)

Ushakov, 1940: 77 (as *Lamellisabella zachsi*); Ivanov, 1949: 79–84, Figs. 1, 2 (as *Lamellisabella gorbunovi*); Ivanov, 1952: 372 (as *L. gorbunovi*); Zenkevitch, 1954: 77, Fig. 9 (as *L. gorbunovi*); Zenkevitch, Birstein and Belyaev, 1954: 66, 68, Fig. 10 (as *L. gorbunovi*); Hartman, 1954: 185 (as *L. gorbunovi*); Ivanov, 1954b: 69, 79 (as *L. gorbunovi*); Kirkegaard, 1956a: 79 (as *L. gorbunovi*); Kirkegaard, 1956b: 186, Fig. 4 (as *L. gorbunovi*); Ivanov, 1957a: 431, 492, 494, Fig. 59 (as *Polybrachia gorbunovi*); Vinogradova, 1958: 112 (as *P. gorbunovi*); Dajoz, 1958: 225, 236, 237, Fig. 6 (as *Lamellisabella gorbunovi*); Ivanov, 1960a: 1611 (as *Polybrachia gorbunovi*); Ivanov, 1960c: 6, 8, 98, 231, 235, 237–8, 239, 266, Figs. 87, 160 (as *P. gorbunovi*).

This species was described by Ivanov (1949) from one badly preserved specimen under the name of *Lamellisabella gorbunovi*. When the material was sectioned, however, the structure of the tentacular crown and other features indicated that it should be ascribed to the genus *Polybrachia* (Ivanov, 1957a). The cuticular plaques and the tube also lend credence to this ascription, but such characteristic features of *Polybrachia* as the possession of an external division between the protosoma and the mesosoma, a separate cephalic lobe, and secondary grooves in the front part of the mesosoma, could not be observed because of the bad state of preservation of the material. In the original description of this species (Ivanov, 1949) there were several errors which were later corrected on the basis of the study of the sectioned material (Ivanov, 1957a).

The tentacular crown consists of 18 free tentacles disposed in a horse-shoe. The fore-part of the body is a regular cylinder and the cephalic lobe a triangle (Fig. 160*B*). The keels of the bridle, situated in the front half of the fore-part of the body, are rather weakly developed, with tapered ventral ends

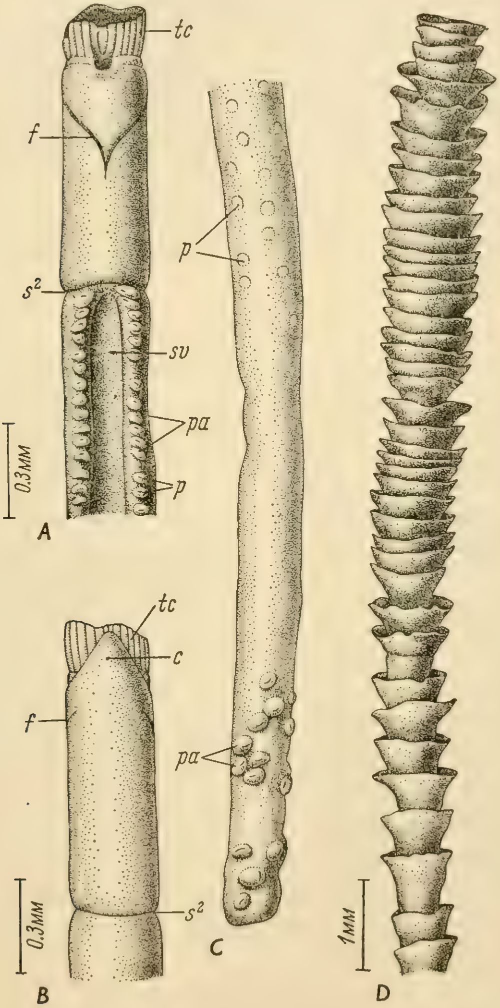

Fig. 160. *Polybrachia gorbunovi*: *A* – front end of the body in ventral, and, *B* – in dorsal view; *C* – non-metameric part of the metasoma in the zone of thickened papillae from the ventral side; *D* – tube.
c – cephalic lobe; *f* – keels of the bridle; *p* – plaques; *pa* – papillae; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *tc* – tentacular crown. (After Ivanov, 1949.)

which come into close contact with each other, though they are wide apart dorsally (Fig. 160*A*, *B*). The boundary between the mesosoma and the metasoma is a straight annular groove. The first part of the preannular section of the metasoma has *c*. 23 pairs of small, regular adhesive papillae and the ventral sulcus between them is well marked (Fig. 160*A*). In the zone of thickened papillae the 15–20 higgledy-piggledy ventral papillae are furnished with plaques *c*. 40μ across, while the oval plaques on the metameric papillae of the front part of the trunk are *c*. 30μ across. They are the usual delicate membranes with a thick dark crescent along the front edge. In the nonmetameric region of the trunk they assume a rounded outline and become somewhat bigger, reaching 40μ in diameter. The region of the girdle and postannular section of the metasoma are unknown.

The brown-black tube is quite extraordinary, consisting of a series of

TABLE 5

Characteristics of the species of *Polybrachia*

	P. annulata	*P. barbata*	*P. gorbunovi*
Number of tentacles	26–39	71	18
Number of secondary grooves on mesosoma	3	2	?
Keels of the bridle	Strongly cuticularized	Soft and thin	Weakly cuticularized
Ventral ends of the keels	Almost touching	Far apart	Touching
Diameter of the cuticular plaques (μ):			
on the metameric papillae	21–28	25	*ca* 30
on the nonmetameric papillae	30	?	*ca* 40
on the papillae of the zone of thickening	35–40	?	*ca* 40
Shape of the plaques of the nonmetameric papillae	Oval	?	Round
Number of pairs of metameric papillae	22–28	?	*ca* 23
Number of thickened papillae	40–70	?	15–20
Length of the fore-part of the body (mm)	3	4	0·9
Breadth of mesosoma (mm)	0·75	1·3	0·29
Length of toothed platelets (μ)	12–18	?	?
Maximum diameter of the tube (mm)	1·16	?	0·5
Length of spermatophore (μ)	600	?	?

funnels so stacked that each encloses the next. The dimensions and shape of the funnels are subject to considerable variation: in the front section of the tube they are larger and thicker (Fig. 160*D*), in the middle part they gradually grow smaller and ultimately, in the hindmost part, they are separated by considerable smooth intervals and are hardly perceptible. Since in general they are rather thin this is probably a consequence of their having worn away. The largest fragment of tube is 45 mm long and 0·5 mm in diameter at the narrowest part of the funnels.

The diagnostic features of *P. gorbunovi* are as follows: the small number of tentacles and the short intervals between the successive funnels in the tube.

Material: a few fragments of tubes from which one incomplete animal was extracted.

Locality: the Arctic Ocean, in the Laptevykh Sea (or Laptev Sea, in some atlases).

Depth: *c.* 3700 m.

6. Genus *Galathealinum* Kirkegaard, 1956

Kirkegaard, 1956a: 82; Kirkegaard, 1956b: 186; Jägersten, 1956: 76; Ivanov, 1957a: 431, 460, 461, 492, 494; Dajoz, 1958: 236, 237; Ivanov, 1960a: 1525, 1529, 1531, 1539, 1620; Ivanov, 1960c: 6, 9, 12, 14, 24, 107–8, 115, 239, 266; Ivanov, 1961c: 1378, 1384.

[The diagnosis given for the genus *Galathealinum* in the Russian edition of this book (Ivanov, 1960c) was based on the data of Kirkegaard (1956). One very important feature to which no attention had been paid concerns the multiplicity of cuticular plaques on the adhesive papillae. In his drawing (reproduced here as Fig. 161), Kirkegaard represented two plaques on most of the papillae of *G. bruuni*. In *G. brachiosum* there are usually four or five plaques on each papilla and sometimes as many as ten. In all the remaining Pogonophora the papillae have only one plaque each, if plaques are present at all, that is. Only in *Polybrachia barbata* have double plaques been described (p. 398); in this species on some papillae one plaque lies immediately behind another, with the hind one often underdeveloped. Another very characteristic feature found only in the genus *Galathealinum* is the external felt-like fibrous layer of the tube, from which the funnel-like frills of each segment are formed.

A revised diagnosis of the genus *Galathealinum* is given below.

The anterior part of the trunk has two or more plaques on each papilla. The plaques lie on oval or round cutaneous eminences. Each papilla in the nonmetameric part of the preannular region bears many plaques. The cephalic lobe is separated from the protosoma by a dorsal groove. The mesosoma lacks secondary rings. In front of the bridle there are two longitudinal dermal lappets or folds which in front turn onto the dorsal side of the protosoma where they fuse with each other. In known species there are 78–268 tentacles arranged on a horse-shoe-shaped base. The segmented tube has a funnel-like frill on the front edge of each segment, covered with a thin felt-like layer of rather coarse fibres.

Type of the genus: *Galathealinum bruuni* Kirkegaard.

Three species have been described—*Galathealinum bruuni* Kirkegaard, *G. brachiosum* Ivanov and *G. arcticum* Southward.]

Key for the identification of the species of the genus *Galathealinum*

1 (2) Each metameric papilla bears a single cuticular plaque; there are no large papillae of the second order, bearing several plaques each, on the metameric section of the metasoma. The hind part of the mesosoma has a mid-ventral furrow. The dorsal ends of the keels of the bridle meet or fuse. The cephalic lobe is triangular, truncated at the tip. The plaques on the metameric papillae are about 30μ across, those on the non-metameric papillae about 50–65μ. The fibres of the external layer of the tube are 1–2μ thick. 3. *G. arcticum* (p. 414).

2 (1) There are large papillae of the second order in the metameric section of the trunk, each bearing several cuticular plaques. There is no mid-ventral furrow in the hind part of the mesosoma. The dorsal ends of the keels of the bridle do not meet.

3 (4) The metameric papillae of the second order for the most part bear two plaques. The plaques of the metameric papillae are about 40μ across, those of the non-metameric papillae about 60μ. The fibres of the external layer of the tube are 2–4μ thick. 1. *G. bruuni* (p. 404).

4 (3) The metameric papillae of the second order bear two to ten plaques each. The plaques of the metameric papillae are 60–90μ across, those of the non-metameric papillae about 80μ. The fibres of the external layer of the tube are 7–12μ thick. 2. *G. brachiosum* (p. 407).

1. Galathealinum bruuni Kirkegaard (Figs. 161–2)

Kirkegaard, 1956a: 79–82, Figs. 1, 2; Kirkegaard, 1956b: 186, Fig. 4; Ivanov, 1957a: 431, 460, 461, 492, 494, Fig. 59; Jägersten, 1957: 76; Dajoz, 1958: 236, 237, Fig. 6; Ivanov, 1960a: 1611; Ivanov, 1960c: 6, 24, 96, 239–41, Figs. 161–2; Ivanov, 1961c: 1382–4, Fig. 6.

Kirkegaard described this genus and species on the basis of only two incomplete specimens and nine fragments of tube. The material was collected by the Danish *Galathea* Expedition in the southwest part of the Celebes Sea at a depth of 5090–5110 m. The following description of *G. bruuni* is based mainly on that given by Kirkegaard but I have made slight additions regarding the plaques of the postannular region of the trunk from a small fragment of this part of the body found in a tube kindly given me by Dr. Kirkegaard.

The tentacular crown is formed of numerous long tentacles (Fig. 161*A*,*B*). Kirkegaard gives the number as 105, but he indicated that in all likelihood some had been lost. The tentacles are attached horse-shoe-wise. On the fore-part of the body a deep groove in front of the bridle separates off the cephalic lobe, while a little farther back on the ventral side in front of the bridle are two wing-like folds or lappets, which extend laterally, where their edges run parallel to the bridle (Fig. 161*B*), to meet dorsally. The adhesive plaques of the fore-part of the trunk are oval, with a crescentic thickening along the front edge, and reach 40μ across. The metameric paired papillae are apparently numerous and densely packed

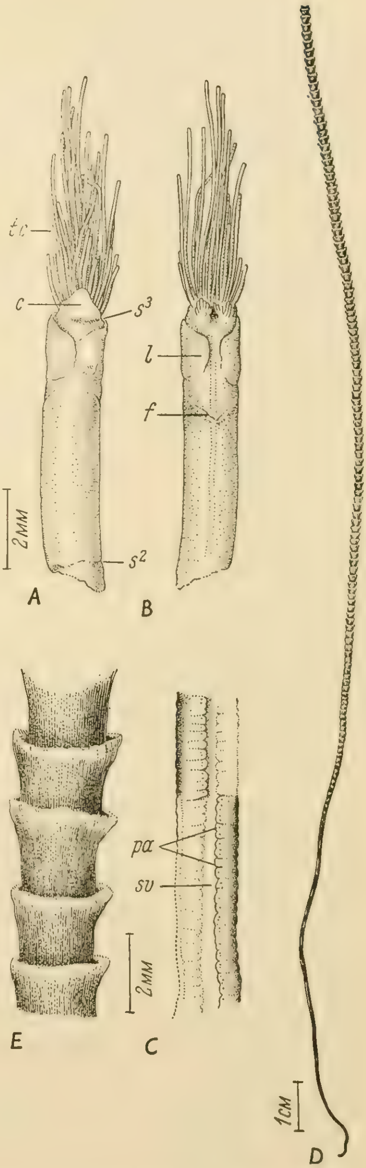

Fig. 161. *Galathealinum bruuni*: *A* – front end of the body in dorsal, and, *B* – in ventral view; *C* – part of the metameric section of the preannular region from the ventral side; *D* – tube; *E* – part of the tube.

c – cephalic lobe; *f* – bridle; *l* – ventral lappets of the mesosoma; *pa* – papillae; s^2 – groove between the mesosoma and the metasoma; s^3 – pretentacular groove; *sv* – ventral sulcus; *tc* – tentacular crown. (After Kirkegaard, 1956*a*.)

together (Fig. 161*C*). The fore-part of the body is 7 mm long and 1 mm broad. The ventral papillae of the nonmetameric part of the preannular region have many transversely oval cuticular plaques, each with a strong crescentic thickening along the front edge (Fig. 162*A*, *B*); they are between 40 and 60μ across.

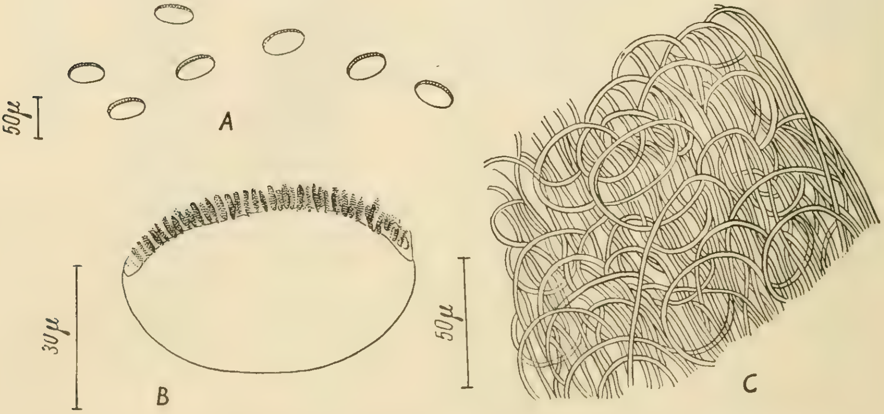

Fig. 162. *Galathealinum bruuni*: *A* – cuticular plaques from a papilla of the preannular region. *B* – the same under higher magnification; *C* – a piece of one of the funnel-shaped broadenings of the tube under high magnification.

The tube is slender at the base, which lacks any opening and is about 0·8 mm across. The rest of the cylindrical tube somewhat recalls that of *Polybrachia annulata* but it is distinguished from it by the lesser distance between the funnels (Fig. 161*D*, *E*). The tube is 2 mm across at the top and dark brown. A very peculiar feature of the tube, which does not appear to have been noticed by Kirkegaard is the development on its surface of a rather friable, felt-like layer which is absent from the tubes of other Pogonophora. Under the microscope this layer may be seen to consist of dense, interlacing, rather coarse fibres, the main mass of which are orientated parallel to the length of the tube. Many, if not all, of the fibres curl back at the front end (Fig. 162*C*). The fibrous layer is attached rather weakly to the tube proper, and the funnels of the tube consist exclusively of this layer, a portion of which is depicted in Fig. 162*C*. The biggest fragment of tube measured 37 cm long.

Material: Kirkegaard had nine fragments of tubes and two animals.

Locality: the Celebes Sea, 1°50′N, 119°30′E.

Depth: 5090–5110 m.

[2. *Galathealinum brachiosum* Ivanov, 1961c (Figs. A-F162)

Ivanov, 1961c: 1378–1384, Figs. 1–6.

In 1959 Ivanov received new pogonophoran material collected by an expedition of the Institute of Oceanology of the Academy of Sciences of the U.S.S.R. on board R.V. *Vityaz*', to the west coast of North America. The material he received, collected by Dr. Z. A. Filatova in late 1958 and early 1959 at stations near the west coast of Canada, U.S.A. and Mexico, consisted of fragments of tubes of various genera and species. Amongst this collection a few comparatively complete animals could be distinguished, forming a series of undescribed species of the genera *Galathealinum*, *Birsteinia*, *Heptabrachia* and *Siboglinum*. The description of *Galathealinum brachiosum* given below is a translation of that given in Ivanov (1961c).

Tubes of this very large species were taken twice by R.V. *Vityaz*', first on 11 November, 1958 off the coast of Canada and then on 4 December, 1958 off the coast of Oregon, U.S.A. Unfortunately, only one tube contained an animal, which lacked the hind part of the body. A series of features in the structure of the mesosoma and metasoma, and peculiarities of the tube indicate its position in the genus *Galathealinum*. The animal is clearly distinguished from *G. bruuni* and the very large number of tentacles has suggested the name *Galathealinum brachiosum*.

The protosoma and mesosoma are cylindrical (Fig. A162). The latter is three to four times longer than the former. The boundary between them takes the form of a sharp transverse groove which is most pronounced on the sides of the body a little in front of the bridle (Fig. B162). Between this groove and the bridle the epidermis is covered with numerous wrinkles and forms a pair of latero-dorsal wavy furrows. The epidermis on the ventral side of the protosoma also has a wrinkled surface. In front of the bridle a depression may be observed which gradually broadens into a median ventral sulcus. In the region of the protosoma this is bordered at the sides by two low cutaneous folds which run up onto the sides in the middle part of the protosoma and then onto the dorsum where they fuse with one another. The broad contracted cephalic lobe is rounded at the tip (Fig. B162). It is divided from the protosoma by a deep dorsal groove which is considerably arched backwards.

The tentacular crown is very long. It consists of 268 free tentacles disposed in a horseshoe at the base (Fig. B162). Each tentacle bears a few (not more than three or four) densely packed rows of short pinnules.

The bridle lies in the front third of the mesosoma (Fig. B162). Its keels are

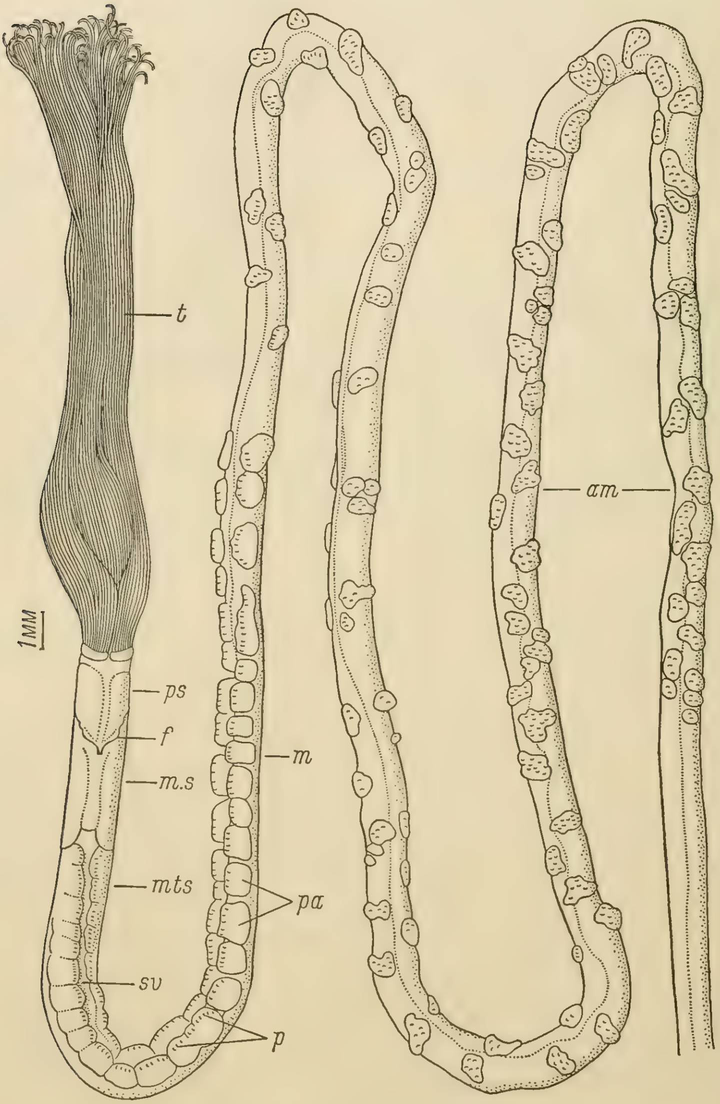

Fig. A162. *Galathealinum brachiosum*: ventral view.
am – the non-metameric section of the preannular region of the metasoma; *f* – bridle; *m* – metameric section of the preannular region; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaques; *pa* – adhesive papillae; *ps* – protosoma; *sv* – ventral sulcus; *t* – tentacle. (After Ivanov 1961c.)

thin and dark-brown, and on the ventral side where they touch one another they are pressed close together. The dorsal ends of the keels are very thin and do not meet. The dermal ridges of the bridle are feebly developed. The dorsal and ventral sides of the mesosoma have broad median tracts of light epidermis. The hind edge of the mesosoma is clearly delimited and dips forward on the dorsal side.

The metasoma has a well-developed ventral sulcus (Fig. B162*A*). At the sides it is bordered by rows of very large glandular adhesive papillae occupying the greater part of the ventral surface of the trunk and lying cheek by jowl. Most frequently each papilla bears four or five small cuticular plaques arranged in a more or less straight longitudinal row along its ventral edge. On a few papillae, however, the number of plaques may be as low as three or even two, or as high as ten. Their arrangement is also subject to variation. Each plaque lies on a small oval or round dermal eminence which is light in colour. Twenty-seven metameric papillae can be counted on the right side and 24 on the left.

The cuticular plaques in this region of the metasoma are scale-like regular ovals with a dark thickened front rim (Fig. D162*A*). The very front edge has a narrow clear uniform border and the thick rim just behind it may be seen under high magnification to consist of rows of dense cuticular rodlets. The hind edge of this anterior thickening of the plaque is not clearly delimited. The plaques are 80–90μ across and 50–55μ long.

The dorsal ciliated band of the metasoma is broad and pronounced, extending to the hind end of the metameric section of the trunk (Fig. B162*B*).

The next part of the metasoma is furnished with large nonmetameric papillae of irregular shape lying on the ventral side of the trunk (Fig. C162*B*, *C*). The length of this region is more than four times that of the metameric part. Each papilla bears between two and thirty cuticular plaques arranged in no fixed pattern. The size and shape of the plaques vary considerably more than those on the anterior part of the trunk. Oval plaques are most common but one may also encounter round plaques right alongside. The thickened anterior rim of the plaque, moreover, has its sharpest contour not in front but behind and has a coarser microscopic structure (Fig. D162*B*, *C*). The plaques are *c*. 80μ across and up to 60μ long.

Then follows a comparatively short part of the trunk completely without adhesive papillae. All the rest of the body is missing in our specimen. Near the break, however, there is a single large conical ventral papilla with one cuticular plaque at its tip which differs from those described above. This is

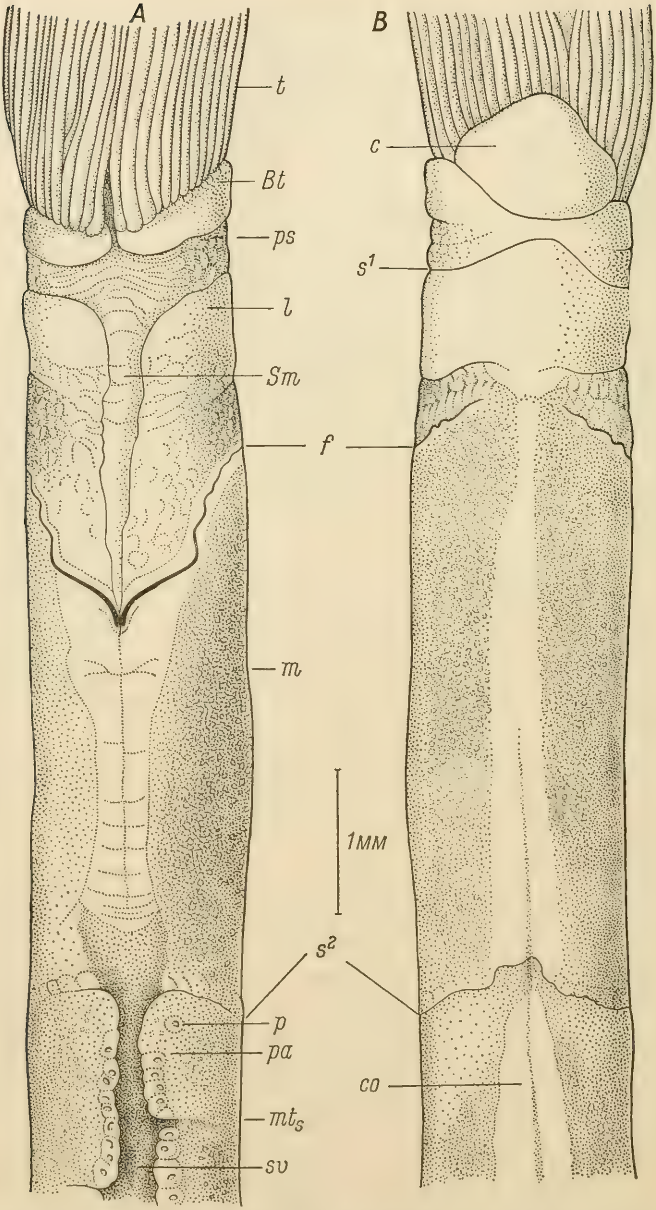

Fig. B162. *Galathealinum brachiosum*: fore-part of the body, *A* – from the ventral and, *B* – from the dorsal side.
bt – base of the tentacular crown; *c* – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *l* – lateral glandular ribbon; *m* – mesosoma; *mts* – metasoma; *p* – plaques; *pa* – adhesive papillae; *ps* – protosoma; s^1 – groove between the protosoma and mesosoma; *sv* – ventral sulcus; *t* – tentacle. (After Ivanov, 1961c.)

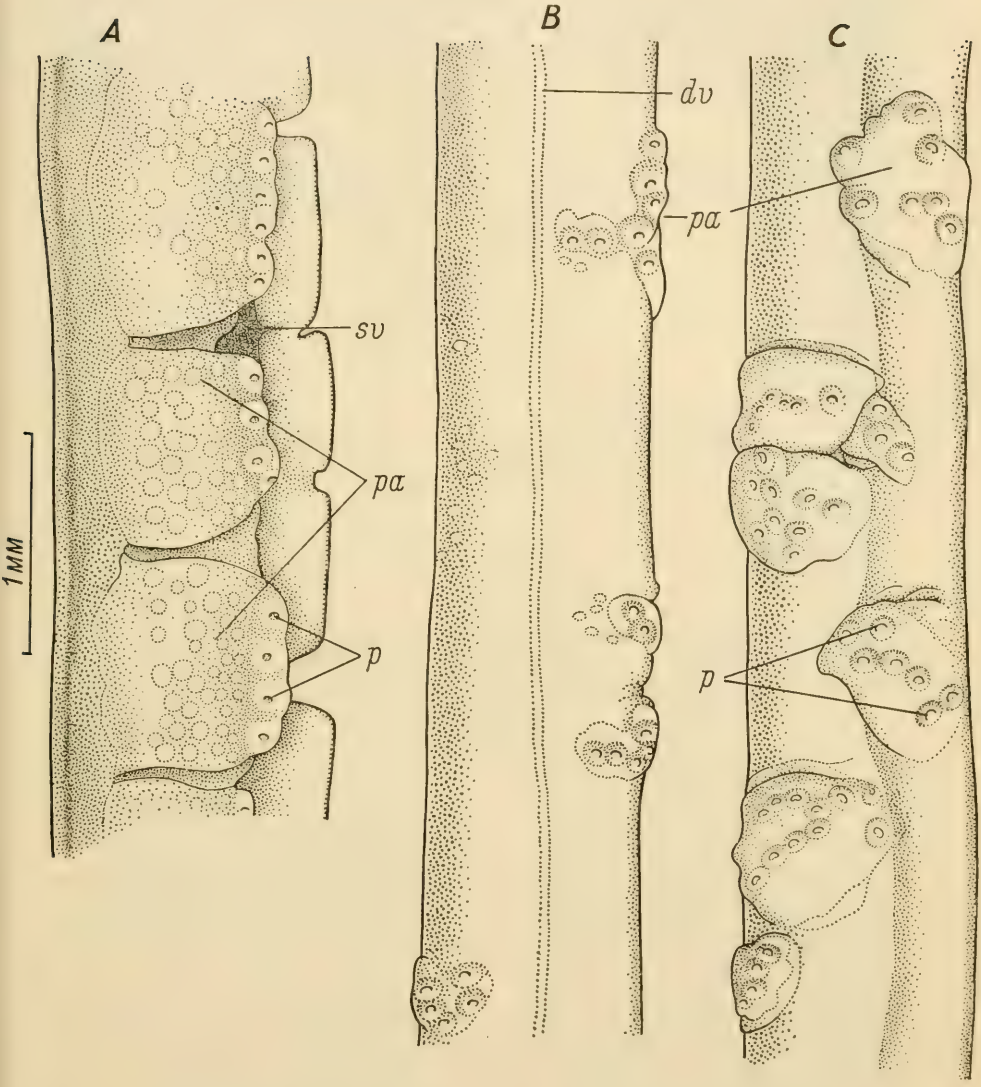

Fig. C162. *Galathealinum brachiosum*: preannular region of the metasoma.
A – part of the metameric section from the left side; *B* – part of the non-metameric section from the dorsal side; *C* – the same from the ventral side.
dv – the dorsal blood vessel; *p* – cuticular plaques; *pa* – adhesive papillae; *sv* – ventral sulcus.
(After Ivanov, 1961c.)

undoubtedly the first papilla of the zone of thickened papillae. The plaque has approximately the same width as the others but is much shorter—not more than 30μ long. The dark front border is similar to that of some plaques of the nonmetameric region of the trunk, but considerably narrower (Fig. D162*D*).

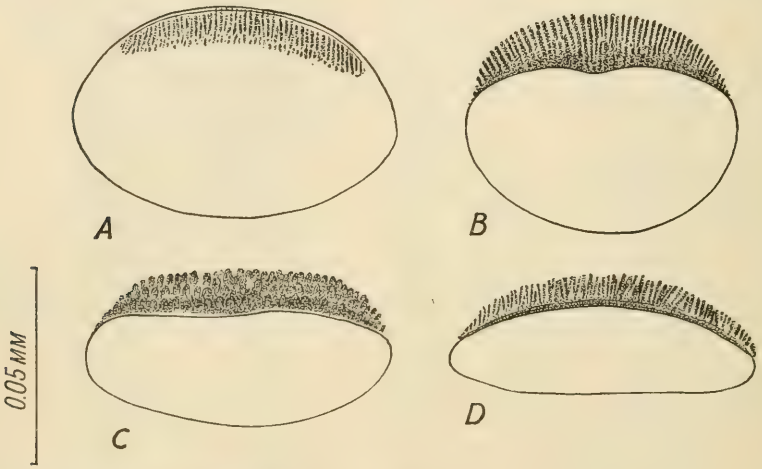

Fig. D162. *Galathealinum brachiosum*: cuticular plaques.
A – from the metameric section of the preannular region; *B*, *C* – from the non-metameric section.
D – from the zone of thickened papillae. (After Ivanov 1961c.)

Our specimen proved to be a female. The various parts of the body had the following dimensions: length of tentacles, 18 mm; length of protosoma, 1·5 mm; length of mesosoma, 4·5 mm; length of metameric part of the metasoma, 27 mm; length of the rest of the trunk as far as the zone of thickened papillae, 115 mm; breadth of mesosoma 1·5 mm. *Galathealinum brachiosum* appears to be one of the very longest species amongst the Pogonophora. The greatest length so far recorded is 36 cm in *Zenkevitchiana longissima*.

The tube is very like that of *G. bruuni*. For almost its whole length it consists of short segments whose length is for the most part equal to the diameter of the tube. The front edge of each segment is drawn out into a narrow funnel-like frill (Fig. E162). The tube is a dark earthy brown, almost black. The surface is thrown into small creases and is somewhat glistening. The funnels are soft and pliant; they consist entirely of the external fibrous layer of the tube (Fig. F162*A*), which is more strongly developed than in *G. bruuni*. The fibres of this layer are thicker too, reaching 7–12μ, while in *G. bruuni* they are only 2–4μ in diameter.

I have had no complete tubes of *G. brachiosum* at my disposal. The longest fragment of tube, the one which contained the animal, was 238 mm long. At its front end the diameter was 2·6 mm and at its hind end 2·0 mm.

Galathealinum brachiosum is distinguished from *G. bruuni* by the much greater number of tentacles, the shape of the cephalic lobe, the larger cuticular plaques and the greater number of them on each papilla. The body of *G. brachiosum*, moreover, is considerably larger. As regards the number of pairs of metameric papillae in *G. bruuni*, we must rely on Kirkegaard's (1956) drawing (reproduced here as Fig. 161). He has illustrated only a small fraction of the metameric region of the trunk, but this includes no less than thirty pairs of papillae and the total number must be much greater. *G. brachiosum* has only 24–27 pairs. The papillae of *G. bruuni* also seem to be much smaller than those of *G. brachiosum*. It seems clear that *G. brachiosum* has fewer but larger papillae than *G. bruuni*.

The differences between the species are laid out in Table A5.

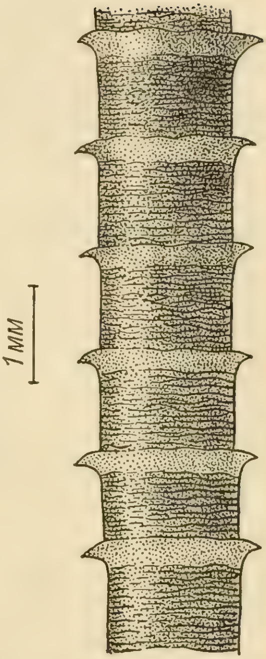

Fig. E162. *Galathealinum brachiosum*: part of the tube. (After Ivanov 1961c)

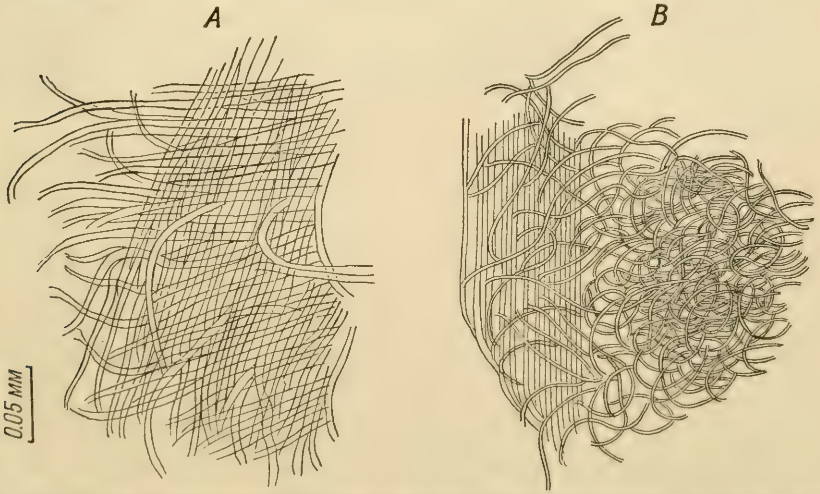

Fig. F162. The felt-like structure of the funnel-like frills of the tube in two species of *Galathealinum* at the same magnification.
A – *G. brachiosum*; *B* – *G. bruuni*. (After Ivanov 1961c.)

Material: several fragmentary tubes, one of which contained an incomplete specimen.

Localities: the eastern Pacific Ocean, off the west coasts of Canada (54°23′N, 134°41′W) and Oregon, U.S.A. (42°40′N, 124°59′W).

Depth: 1233–2607 m].

[*3. Galathealinum arcticum* Southward (Fig. G162)

Southward, 1962: 385–389, Figs. 1–10.

This first pogonophore to be recorded from the Canadian Arctic was collected in 1960 by Mr. J. G. Hunter of the Fisheries Research Board of Canada and sent to Dr. Eve C. Southward who described it in the Canadian Journal of Zoology (Southward, 1962). The following description is reproduced from her paper, by kind permission of the author and publishers. The material consisted of two incomplete specimens, one male, one female, in their tubes.

"The general colour of the animals (preserved in formalin) is a pinkish brown with lighter brown to cream-coloured epidermal glands.

"The tentacular crown is complete in the female and consists of 126 tentacles attached to the protosoma in several concentric horseshoe-shaped rows with the opening on the posterior side (Fig. G162*B*, *D*). The tentacles of the male were broken while it was being removed from its tube but there are at least 78 of them. Each tentacle has a band of pinnules along its inner side, starting near the head as a triple row of small pinnules (Fig. G162*F*) and narrowing to a double row of much longer pinnules towards the distal end (Fig. G162*E*). There is a band of cilia on each side of the row of pinnules.

"The flattened cephalic lobe is roughly triangular in outline, with a truncated apex in both specimens. On the dorsal side, a curved groove divides the cephalic lobe from the rest of the protosoma, and the dorsal point of the bridle reaches forward nearly to this groove. A second groove encircles the body just in front of the bridle (Fig. G162*C*). On the ventral side a longitudinal groove runs from between the tentacle bases back to the point of the bridle, dividing the ventral surface into two lateral lobes (Fig. G162*B*, *D*). The thin dark-brown keels of the bridle lie on a low ridge of slightly glandular epidermis, flanked by narrow dark-brown lines. The keels meet at a point on each side of the body, but whether they actually fuse is not clear. From behind the bridle to the posterior end of the mesosoma the epidermis is speckled with light-coloured gland cells, some of which are

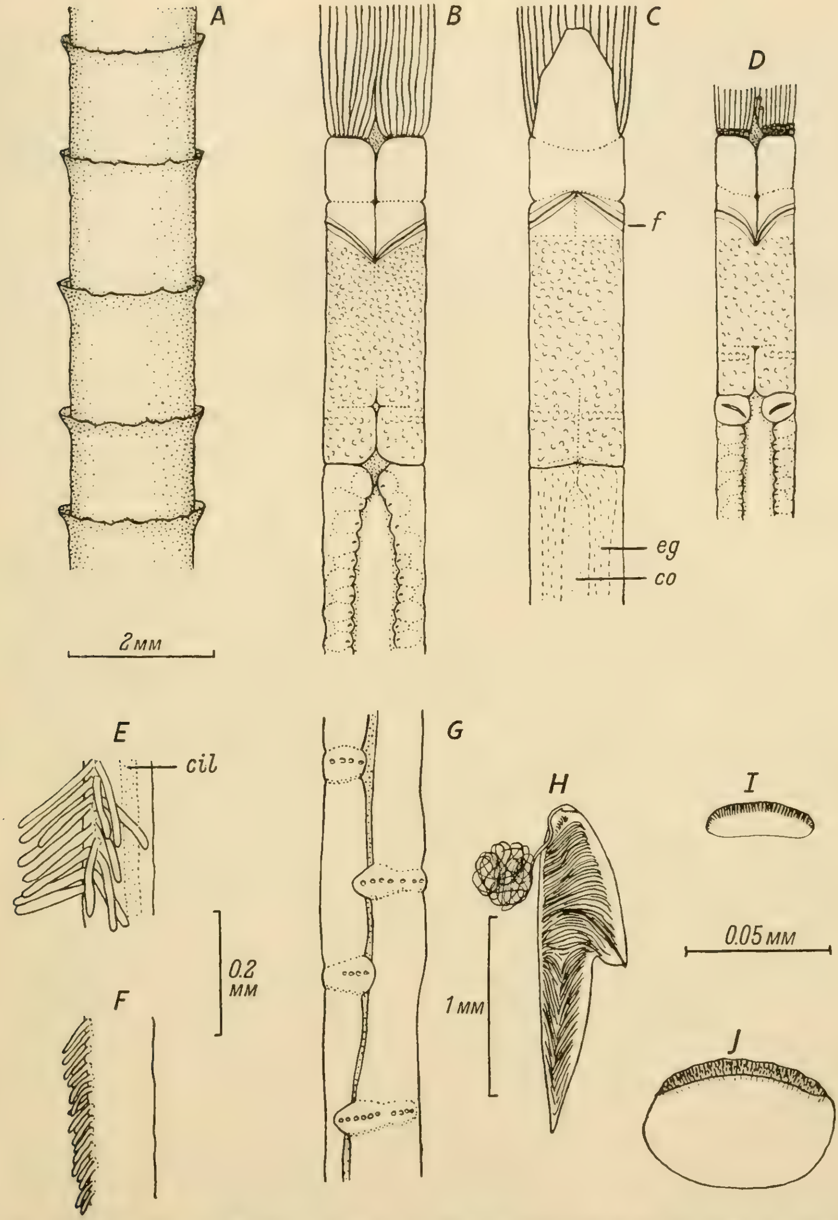

Fig. G162. *Galathealinum articum*: *A* – part of the segmented region of the tube; *B* – anterior end of female, ventral view; *C* – anterior end of female, dorsal view; *D* – anterior end of male, ventral view; *E* – tentacle, distal part; *F* – tentacle, proximal part; *G* – part of nonmetameric region of metasoma; *H* – spermatophore; *I* – plaque from metameric papilla; *J* – plaque from nonmetameric papilla.
cg – epithelial glands; *cil* – ciliated band of tentacle; *co* – dorsal ciliated band; *f* – bridle. (After Southward, 1962.)

concentrated into a whitish band near the posterior end of the mesosoma, encircling the body but most marked on the dorsal side. Just in front of this line on the ventral side there is a short transverse groove and from it a longitudinal groove extends back to the end of the mesosoma (Fig. G162*B*, *C*, *D*).

"The metameric region of the trunk (metasoma) bears sharp latero-ventral ridges, separated by a deep mid-ventral groove. Small papillae, each bearing a small adhesive plaque (Fig. G162*I*), lie along the crests of the ridges, and associated with each one is a patch of glandular epidermis on the outer surface of the ridge (Fig. G162*B*, *D*). Five to ten small dark spots on each patch mark the openings of internal pyriform glands. The arrangement of alternate large and small patches shown in Fig. G162*B* and *D* continues fairly regularly to the end of the metameric region. A ciliated band, flanked at its anterior end by bands of glandular epidermis, extends all along the dorsal side of the metameric region.

"The nonmetameric part of the trunk that follows the metameric part has a very regular arrangement of papillae. They lie alternately on either side of a narrow mid-ventral groove at intervals of 1–3 mm (Fig. G162*G*). Each elongated papilla covers about one-third of the circumference of the body and bears a row of five to fifteen adhesive plaques 50 to 65μ in diameter, with raised and striated anterior borders (Fig. G162*G*, *J*). These papillae continue to the posterior end of each specimen and the girdles and postannular regions of the trunk are missing.

"The larger tube belongs to a female about 50 cm long and 1·33 mm in diameter. The length of the fore-part of the body (protosoma plus mesosoma) is 6·08 mm, of the metameric region of the metasoma 35 mm, and of the tentacles 29 mm. The male is 13·5 cm long and 1·0 mm in diameter, with the fore-part 4·95 mm, the metameric region 40 mm and the tentacles about 20 mm long. In many pogonophores the preannular and postannular regions are approximately equal in length, so the complete adult female of this species may, quite possibly, be a metre long, and its tube may be longer still.

"The oviducts of the female, containing oocytes up to 150μ in diameter, run throughout the trunk. The trunk of the male is similarly occupied by ducts full of spermatophores. The spermatophores are flattened and leaf-like as in other members of the family Polybrachiidae, but their asymmetrical outline and curved superficial ridge (Fig. G162*H*) are entirely unknown in other Pogonophora.

"The dark-brown tubes are 34 and 50 cm long but still incomplete. The longest tube has a maximum diameter of 1·95 mm at the anterior end, the other tube is a little narrower, and both tubes taper slightly towards the posterior end. The first 10 to 20 cm of each tube is made up of small funnel-shaped segments 1·5 to 2 mm long, overlapping slightly (Fig. G162*A*). The thick wall is many layered, with an outer dark-brown layer of felted fibres. Individual fibres are only 1–2μ in diameter, but they are mostly aggregated into bands 50 to 500μ wide. The inner layers contain fewer fibres and are not uniformly coloured. Brown rings 0·5 to 1 mm long are separated by narrower colourless interspaces. The posterior part of the tube is unsegmented and all the layers of its wall are ringed, though the outer layer is whitish and its rings are not very distinct."

G. arcticum has most of the characteristics given by Ivanov in the diagnosis of the genus, "except that its metameric papillae bear single adhesive plaques, rather than groups of two or more (see Table A5).

"*G. arcticum* is distinguished from both of the other species in having single adhesive plaques on the metameric papillae and in having the keels of the bridle touching on the dorsal side. It differs from *G. brachiosum* in having a smaller number of tentacles, a differently shaped cephalic lobe (this may be only an effect of fixation), smaller adhesive plaques, especially on the metameric papillae and finer fibres in the tube wall. It has more in common with *G. bruuni*, but differs from it in the absence of a mid-dorsal groove in front of the bridle. All three species have been described from specimens which lack posterior ends. They are apparently all very long, and it is obviously difficult to collect the whole of an animal perhaps a metre long if it is deeply buried in the bottom deposit. To judge from the epifauna attached to the present tubes, all but the top 5 cm was buried in the deposit.

"Most pogonophores have been found in depths of more than 500 m, but *Siboglinum caulleryi* is known from 22 m in the Sakhalin Gulf, *Oligobrachia dogieli* occurs in 119 m in the Sea of Okhotsk and a few other species are known from between 100 and 500 m, always in cold waters. Thus this new record from 36 m adds to the evidence now accumulating to show that members of the Pogonophora are restricted to waters of low temperature than to those of great depths alone.

"Material: two incomplete specimens, one male, one female, in their tubes.

"Locality: Thetis Bay, Herschell Island, Yukon (Canada): 69° 32′ N, 138° 57′ W.

"Depth: 36 m."]

TABLE A5
Characteristics of the species of *Galathealinum*

	G. bruuni	*G. brachiosum*	*G. arcticum*
Number of tentacles	More than 105	268	78, 126
Shape of cephalic lobe	Triangular	Rounded	Triangular with truncated apex
Diameter of cuticular plaques (μ):			
on metameric papillae	40	60–90	30
on nonmetameric papillae	60	80	50–65
on thickened papillae	?	80	?
Length of fore-part (mm)	7	6·25	4·95, 6·08
Breadth of mesosoma (mm)	1	1·5	1·0, 1·33
Number of pairs of metameric plaques	?	*c.* 140	*c.* 130
Number of pairs of metameric papillae of second order	Several dozen	24–27	—
Number of plaques on each metameric papilla of second order	2	2–10	—
Thickness of fibres in funnels of tube (μ)	2–4	7–12	1–2
Diameter of tube (mm)	2	2·6	1·95

[7. Genus *Sclerolinum* Southward, 1961

Southward, 1961: 16, 18.

The genus includes Pogonophora in which the protosoma, mesoma and metasoma are not separated by grooves from one another, the cephalic lobe is separated by a groove from the rest of the protosoma; the metameric region has paired lateral ridges rather than individual papillae and lacks adhesive plaques, while the nonmetameric papillae have adhesive plaques. The tube is also characteristic: it lacks segmentation and rings, its walls are very thick except at the anterior end, where it is thin and limp, and most of its wall is also very much wrinkled.

Type of the genus and sole species: *Sclerolinum sibogae* Southward, 1961.]

[*1. Sclerolinum sibogae* Southward (Fig. H162)

Southward, 1961a: 16–18, 21.

This species forms part of the *Siboga* material, originally included in *Siboglinum weberi*. The following description is quoted from Southward (1961a) by kind permission of the author and the publisher, E. J. Brill.

"The tubes are very brittle and all attempts to extract the animals have failed. The following description is based on what can be seen through the wall of the tube, with the help of various clearing agents and stains.

"The longest fragment of an animal is 30 mm long, without a posterior end. There are six specimens in which the anterior end can be seen clearly and in all these there are two tentacles, from 0·5 to 2·0 mm long, attached side by side by very narrow basal portions (Fig. H162*B*, *C*, *D*). The rest of the tentacle is fairly thick, wrinkled and without pinnules. The small cephalic lobe is divided from the rest of the protosoma by a dorsal groove at the level of the tentacle base (Fig. H162*C*). The separation of protosoma, mesosoma and metasoma is not very clear, as there are no external grooves, and apparently no internal septa. The internal glands seem to be the most useful criterion of their distinction. From the base of the tentacles to about the level of the bridle there are numerous small spherical glands; behind the bridle the glands are still numerous but larger, and after a short distance they give way to two rows of much larger pear-shaped glands. Sometimes an oblique band of muscle is visible between the last two types of glands, perhaps homologous with the meso-metasoma septum of other genera. Using these criteria the total length of the protosoma and mesosoma is 0·5 to 0·85 mm. In one specimen the dorsal band of cilia can be seen to begin a little behind the dorsal part of the bridle, some way in front of the start of the largest glands (Fig. H162*B*). The bridle itself is scarcely raised above the body surface, and its keels are very fine, colourless and often broken up into short curved sections (Fig. H162*B*, *C*). The course of the keels around the body varies from one specimen to another; in some the dorsal points are anterior (Fig. H162*B*) to the ventral points while in others they are posterior (Fig. H162*D*). The keels are sometimes fused (Fig. H162*E*) and sometimes separate in the mid-line both dorsally and ventrally.

"Most of the metameric region of the trunk is slightly furrowed longitudinally between the two latero-ventral rows of glands. There are no very definite papillae, but there are up to 45 pairs of internal glands, which occupy the first 1·3 to 2·5 mm of the trunk. They do not bear adhesive plaques. The rest of the trunk has small single papillae, each bearing an oval or circular adhesive plaque, with a thickened edge (Fig. H162*F*), 15 to 30μ in diameter. These small papillae are scattered irregularly along the trunk and no large papillae have been seen. Girdles are absent even from the longest specimen, which indicates that the preannular region must be at least 30 mm long, which is an exceptional length in a pogonophore only about 0·07 mm in diameter. Two specimens contain leaf-shaped spermatophores about 0·10 to 0·15 mm long (Fig. H162*G*).

"The tubes are brownish and thin, like those of *Siboglinum weberi* and *S. macrobrachium* with which they are mixed in the collection from *Siboga* station 212. They all seem to be broken up and none is more than 5 cm long. Most of them are about 0·13 mm in diameter but they vary between 0·10 and 0·15 mm. The tube wall is light brown or yellow, very thick (15μ), very stiff and deeply wrinkled (Fig. H162*A*). The first 1 to 2 mm. of the tube has thinner limp and colourless walls. The tubes are very brittle and all attempts to extract the animals have failed.

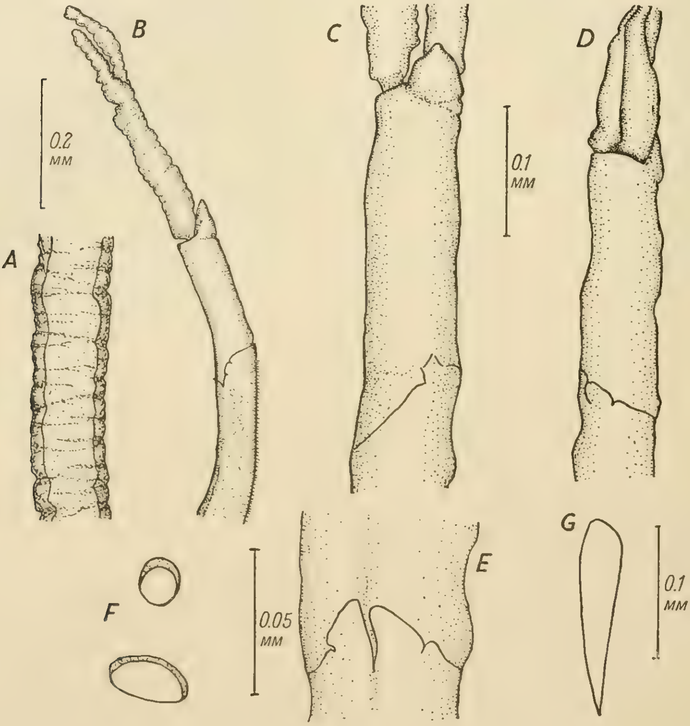

Fig. H162. *Sclerolinum sibogae*: *A* – part of tube; *B* – anterior end of animal, latero-ventral view; *C*, *D* – dorsal and ventral views of anterior end of animals; *E* – ventral view of bridle; *F* – adhesive plaques from preannular papillae; *G* – shape of spermatophore. (Southward, 1961a.)

"In spite of the absence of girdles and postannular region this species can be seen to be unlike any known genus. It appears to belong to the Polybrachiidae because it possesses the following combination of characteristics: the wall of the tube is thin and limp at the anterior end; the tentacles are not joined together; the protosoma is not divided from the mesosoma; and there are adhesive plaques on some of the preannular papillae. Of the genera in this family the species seems to be most closely related to *Zenkevitchiana*, which it resembles in the following ways: the tube is thick-walled and lacks overlapping collars; the protosoma is not separated from the mesosoma; the tentacles do not have pinnules; there are adhesive plaques on the nonmetameric papillae but not on the metameric papillae; the adhesive plaques are oval or round; and the preannular region is comparatively long.

"There are several differences which suggest that the species does not belong to the genus *Zenkevitchiana*: the tube is very wrinkled and is not divided into segments; the cephalic lobe is separated from the rest of the protosoma by a transverse groove; the mesosoma is not separated from the metasoma; there are two latero-ventral ridges containing separate glands instead of separate metameric papillae each containing several glands; and there are only two tentacles.

"I have decided to establish a new genus to include this species. I should have liked to name it after Professor Caullery but unfortunately the suitable names are preoccupied. I have therefore named it *Sclerolinum*, which is descriptive of the stiff thread-like tube."

Material: 30 fragments of tube, more than half occupied.

Localities: Ceram, Flores, Java and Arafura Seas: *Siboga* stations 175, 210A, 212, 271 (2°37′S 130°35′E, 5°28′S 123°18′E, 5°54′S 120°19′E, 5°46′S 134°E).

Depth: 462–1914 m.]

II. Family Lamellisabellidae Ushakov, 1933

The name Lamellisabellidae was first used by Ushakov (1933) to designate a new subfamily of sedentary polychaetes (as he thought) of the family Sabellidae, to which, he believed, belonged the species he described as *Lamellisabella zachsi*. In 1951 Ivanov assigned this name to a family of Pogonophora. The tentacles are arranged in a circle and fused together into a hollow cylinder. Only one genus is known, *Lamellisabella*.

1. Genus *Lamellisabella* Ushakov, 1933

Ushakov, 1933: 205–8; Johansson, 1937: 23–6; Reisinger, 1938: 49; Johansson, 1939: 253–68; Ushakov, 1940: 76, 77; Hemplemann, 1943: 78; Beklemishev, 1944: 257–9; Ivanov, 1949: 79–84; Ulrich, 1950: 3–25; Beklemishev, 1951: 267–9; Hartman, 1951:

379, 380; Ivanov, 1951: 739–42; Beklemishev, 1952: 289, 295–8, 386, 395, 457, 613; Boettger, 1952: 292–3; Ivanov, 1952: 372–4, 388, 390; Ushakov, 1953: 179; Zenkevitch, 1954: 75, 77, 78; Zenkevitch, Birstein and Belyaev, 1954: 66, 68; Hartman, 1954: 183–5; Ivanov, 1954b: 69–71, 79; Abrikosov *et al.*, 1955: 472; Ivanov, 1955a: 177; Ivanov, 1955b: 382, 383; Ivanov, 1955c: 595; Ivanov, 1955d: 171, 176, 177; Ivanov, 1955e: 224; Ivanov, 1956b: 1864, 1868; Ivanov, 1956c: 165, 166, 169; Jägersten, 1956: 212, 220, 228, 229, 230, 233, 234, 238; Kirkegaard, 1956a: 79; Kirkegaard, 1956b: 183, 185, 186; Abrikosov, 1957: 232, 233, 235; Alvarado, 1957a: 556; Beklemishev, 1957: 396, 397; Ivanov, 1957a: 431, 475, 476, 478, 480, 483, 485, 490, 492, 494–8; Ivanov, 1957b: 1127, 1139; Beklemishev, 1958: 34, 45; Vinogradova, 1958: 112; Dajoz, 1958: 225, 226, 230–3, 236, 237, 238; Fell, 1958: 44–6; Ivanov, 1958a: 1363–70; Ivanov, 1958b: 1682, 1687–9; Ivanov, 1960a: 1528, 1539, 1540, 1541, 1546, 1549, 1550, 1552, 1553, 1554, 1561, 1569, 1572, 1574, 1580, 1581, 1583, 1588, 1607, 1610, 1616, 1625; Ivanov, 1960c: 6, 8, 9, 11, 14, 23, 24, 26, 30, 31, 34–8, 43, 48, 56, 59, 61, 66, 67, 69, 75, 92, 97, 98, 101, 107, 115, 215, 227, 241–2, 252.

Ten to 31 tentacles enter into the composition of the tentacular cylinder and the pinnules upon them are triserial. The protosoma is joined to the mesosoma and the cephalic lobe to the protosoma. The pronounced keels of the well-developed bridle taper strongly towards the dorsal ends. The cuticular plaques of the fore-part of the trunk appear horseshoe-shaped with the ends pointing backwards, and each one lies on a separate pulvillus. The entire plaque consists of a thin round membrane with a horseshoe-shaped thickening from which a pair of powerful apodematous outgrowths penetrate into the papilla. The spermatophores are leaf-shaped and broad. The tube may be smooth or segmented, with no filmy section, but instead with a broad, funnel-like mouth.

Type of the genus: *Lamellisabella zachsi* Ushakov.

There are four known species: *Lamellisabella zachsi*, *L. johanssoni*, *L. ivanovi* and *L. minuta*.

Key for determining the species of *Lamellisabella*

1 (2) The ventral ends of the keels of the bridle are fused together. The keels possess prominent crests and are not less than 120μ broad. There are 18 tentacles. The transverse horseshoe-shaped plaques are *c.* 70μ across. The girdles of toothed platelets are interrupted dorsally. The tube is segmented. 2. *L. johanssoni* Ivanov (p. 429).

2 (1) The ventral ends of the keels of the bridle are not fused, the keels have no sharp crests and are considerably less than 120μ broad.

3 (4) There are ten tentacles. The mesosoma is less than 0·5 mm in diameter. The keels of the bridle each consist of a thin colourless cuticular axis and an attached brown band which breaks up into a

row of cuticular bodies on the ventral side. The keels are 60μ wide at the widest part. The transverse horseshoe-shaped plaques are 34μ across. The golden-brown tube is segmented at the front ends.
4. *L. minuta* sp. nov. (p. 436).

4 (3) There are 22–31 tentacles. The diameter of the mesosoma is at least 1 mm.

5 (6) There are 22 tentacles. The keels of the bridle consist of clear bars with small dark cuticular bodies attached to them behind. The keels are *c.* 110μ broad. The transverse horseshoe-shaped plaques are *c.* 75μ across. The tube is segmented.
3. *L. ivanovi* Kirkegaard (p. 434).

6 (5) There are 28–31 tentacles. The dark-brown or black, homogeneous keels of the bridle are 60–70μ broad. The transverse horseshoe-shaped plaques are 60μ across. The tube is unsegmented.
1. *L. zachsi* Ushakov (p. 423).

1. *Lamellisabella zachsi* Ushakov (Figs. 1*B*, 2, 17*E*, 19*A*, 163–5)

Ushakov, 1933: 205–8, Figs. 1, 2; Johansson, 1937: 23–6, Figs. 1–4; Reisinger, 1938: 49; Johansson, 1939: 253–68, Figs. 1–7, Pl. 1; Ushakov, 1940: 76, 77, Fig. 1; Hempelmann, 1943: 78; Beklemishev, 1944: 257–9; Ivanov, 1949: 79–83; Ulrich, 1950: 3–25, Figs. 1; Beklemishev, 1951: 267, 268, Figs. 9, 10; Ivanov, 1951: 740–2, Fig. 1; Hartman, 1951: 379; Beklemishev, 1952: 297, Fig. 142; Ivanov, 1952: 372–4, Fig. 1; Ushakov, 1953: 179; Zenkevitch, 1954: 75, 77, 78, Figs. 3, 9; Zenkevitch, Birstein and Belyaev, 1954: 66, Fig. 10; Hartman, 1954: 183–5; Ivanov, 1954b: 69–71, Fig. 1; Abrikosov *et al.*, 1955: 472, Fig. 467; Ivanov, 1955b: 381–3, Figs. 1, 2; Ivanov, 1955d: 176, 177, Figs. 2, 3; Ivanov, 1955e: 224, Pl. LXV, Fig. 1; Ivanov, 1956b: 1865; Ivanov, 1956c: 166; Kirkegaard, 1956a: 79; Kirkegaard, 1956b: 185, Fig. 4; Abrikosov, 1957: 232, 233, 235, Fig. 2; Alvarado, 1957a: 556; Bruun, 1957: 666; Ivanov, 1957a: 431, 476, 478, 480, 481, 483, 492, 495–7, Fig. 59; Ivanov, 1957b: 1127, 1139; Beklemishev, 1958: 88; Vinogradova, 1958: 112; Dajoz, 1958: 225, 226, 230, 233, 236–8, Figs. 1, 5, 6; Ivanov, 1958a, 1363–70, Figs. 2–8; Ivanov, 1958b: 1682, 1687–9, Fig. 8; Ivanov, 1960a: 1524, 1530, 1531, 1538, 1541, 1559, 1560, 1565, 1570, 1576, 1586, 1590, 1593, 1607, 1608, 1611, 1612, 1613, Figs. 1384, 1399, 1401, 1402, 1404, 1406–7, 1409, 1412, 1416, 1426, 1427, 1428, 1430, 1433–5, 1438, 1440–4, 1468, Pl. 8; Ivanov, 1960c: 6, 7, 8, 10, 14, 24, 25, 27, 44, 49, 51, 56, 57, 76, 78, 92, 94, 96, 235, 241, 242–7, 248, 250, 251, 252, 266, Figs. 1, 2, 17, 19, 21, 23, 25–6, 28, 31, 35, 45–8, 50, 53–5, 58, 60–4, 87, 163–5, Pl. III; Ivanov, 1960c: 1378.

L. zachsi was first described by Ushakov (1933) from incomplete specimens collected in the Sea of Okhotsk. Considering *Lamellisabella* to be a polychaete of the family Sabellidae, Ushakov regarded the crown of tentacles as branchiate filamentar palps, the fore-part of the body as the sabellid collar, and the cuticular plaques of the metasoma he homologized with the chaetal parapodia of annelids. The dorsal side of the body he interpreted as ventral and he mistakenly described a fusion of the hind end of the body with the walls of the tube. The postannular region of the body was unknown to Ushakov.

In 1952 this species was redescribed in detail and figured by Ivanov, as an example to illustrate the external morphology of the Pogonophora. As stated earlier (p. 15), the Class Pogonophora was erected by Johansson (1937) on the basis of his studies of the organization of *Lamellisabella zachsi.*

The fore-part of the body is short and cylindrical, its length varying between two and three times its breadth, depending on the state of contraction (Figs. 163*A*, *B*, *C*, 164*A*). The cephalic lobe forms a much-flattened equilateral triangle (Figs. 163*A*, *C*, 164*A*), and the base of the tentacular crown is sharply separated from the region of the protosoma, consisting of 28–31 tentacles (Figs. 2, 163*A*, *C*, 164*A*). Ushakov (1933), in his original description, suggested that the tentacles were united by a very delicate membrane, but in reality there is no such membrane, the tentacles being firmly united to one another by means of a common cuticle, such as is also found in *L. johanssoni* and in *Spirobrachia* spp. Ushakov is also mistaken in his statement that "large cartilage cells" were present in the tentacles. Between the bases of the two ventral tentacles there is always a small orifice which puts the intertentacular cavity into communication with the exterior (Fig. 163*B*). The distal ends of the tentacles are free for a considerable length and the internal surface of the tentacular cylinder bears a dense thicket of long pinnules, which are absent only from the basal part of the crown. On each tentacle the pinnules are arranged in three longitudinal rows and alternate regularly with the pinnules of the neighbouring rows. The bridle has pronounced ridges and the black keels are strongly thickened at the ventral end where they may reach 60–70μ in width. On the lateral sides of the body they taper quickly and on the dorsal side become very thin indeed (Fig. 163*B*, *C*). Neither ventrally nor dorsally do the keels fuse. In front of the bridle on the ventral side there is often a more or less broad but shallow dorsal furrow in which the epidermis presents an uneven surface. The hind edge of the fore-part of the body is a simple annular groove with a small dorsal notch and with a more or less deep ventral bay (Fig. 163*B*). The male genital papillae are large and rounded.

The metameric division of the trunk has more or less metameric, paired papillae, each bearing a pulvillus with a horseshoe-shaped cuticular plaque (Figs. 2, 163*B*). As noted by Ushakov (1933) the number of "horseshoes" varies between 17 and 22 pairs in different individuals, but if all the more or less paired papillae are counted, both those with horseshoes and those with simple plaques, then the number of metameric papillae reaches 27–30 pairs. The broad ventral sulcus (Figs. 2, 163*B*) stretches between them to the hind end of the metameric part. As in *Lamellisabella johanssoni* (p. 429), the cuticular plaques consist of thick, black horseshoes, each with an apodematous outgrowth projecting inwards and a delicate membrane surrounding it, *c.* 60μ across. The plaques lie on heart-shaped pulvilli, each of which has a

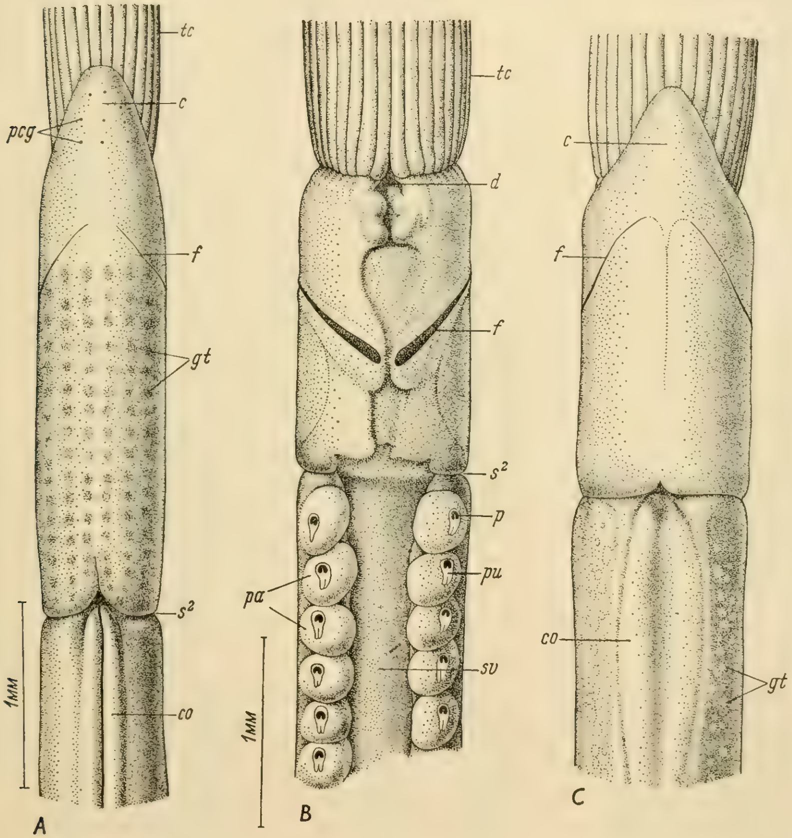

Fig. 163. *Lamellisabella zachsi*: *A* – front end of a weakly contracted individual from the dorsal side; *B* – the front end of a strongly contracted female from the ventral, and, *C* – from the dorsal side.

c – cephalic lobe; *co* – dorsal ciliated band; *d* – opening at the base of the tentacular cylinder, putting its cavity in communication with the external environment; *f* – keel of the bridle; *gt* – globular and pyriform glands seen by transparency; *p* – cuticular plaque; *pa* – papillae; *pcg* – pores of single-celled epidermal glands; *pu* – pulvillus; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *tc* – tentacular crown.

slight split along the narrow backward-pointing end (Fig. 163*B*). In the hind part of the metameric section the black horseshoes give way to thin, transverse plaques. As noted by Ushakov (1933) the change-over from one type of plaque to the other may be abrupt in one individual, while in another it may be gradual, so that one may observe an alternation of horseshoes and simple transverse plaques. In one individual, for example, with 22 pairs of horseshoes, on one side of the body there were 20 horseshoes in sequence, then in succession came a plaque, a horseshoe, two plaques, another horseshoe and then simple plaques; on the other side there were 16 horseshoes, then a regular alternation of plaque with horseshoe until the full 22 horseshoes had been reached. The simple plaques are transverse oval membranes with a heavily thickened front edge which takes the form of a bent bow whose ends are, as it were, lopped off. They are about 60–65μ across. The dorsal ciliated band is well developed (Fig. 163*C*) and the non-metameric division of the trunk is very long and characterized by scattered papillae which are furnished with simple plaques but no pulvilli (Fig. 2). There is no zone of thickened papillae. The girdles are well developed, but unusual, since there is no dorsal gap and they are interrupted only on the ventral side (Fig. 164*B*, *C*).* There are five to seven rows of elongated, oval toothed platelets in each girdle (Fig. 165*A*). The platelets are much narrower at the front end, which thus assumes the appearance of a small, colourless head-piece, bearing oblique rows of very small teeth all pointing backwards (i.e. the anterior group of teeth). The greater part of the platelet is brownish and its surface is covered with oblique rows of large teeth pointing forwards (Fig. 165*B*). The platelets are 13–23μ long. The long and slender postannular region of the trunk is cut off from the girdles by a narrow waist (Fig. 164*B*, *C*) and bears on its ventral side numerous transverse metameric rows of papillae. In one complete specimen there were 59 such rows (Fig. 2) arranged at more or less regular intervals, the length of which, to all appearances, varies with the state of contraction of the dermal musculature. On the papillae lie transverse, rod-like plaques up to 100μ long.

The average dimensions of the body, to judge by measurements made on a number of more or less complete specimens, are as follows: length of the tentacular cylinder, 26 mm; length of the fore-part of the body, 2·5 mm; breadth of the mesosoma, 1·2 mm; length of the metameric part of the preannular region, *c*. 30 mm; length of the non-metameric part, *c*. 60 mm; length of the postannular region, *c*. 57 mm; overall length of the body, *c*. 175 mm.

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* Ushakov (1933) described them as "curved chitinous bands".

The highly flattened spermatophores form rectangular plates with parallel sides, suddenly tapering to a point at the filamentar end (Fig. 165*C*). The base of the filament is a broad, flat triangle, bent down parallel to one of the flat sides of the spermatophore. It then tapers rapidly into the very slender and extraordinarily long filament, which forms a characteristic horseshoe-shaped skein, fitting closely on to the flat surface of the spermatophore. The sperm may be seen to lie within the spermatophore in two longitudinal rows, orientated with axis across the rows. The spermatophores are 1 mm long and 0·45 mm across.

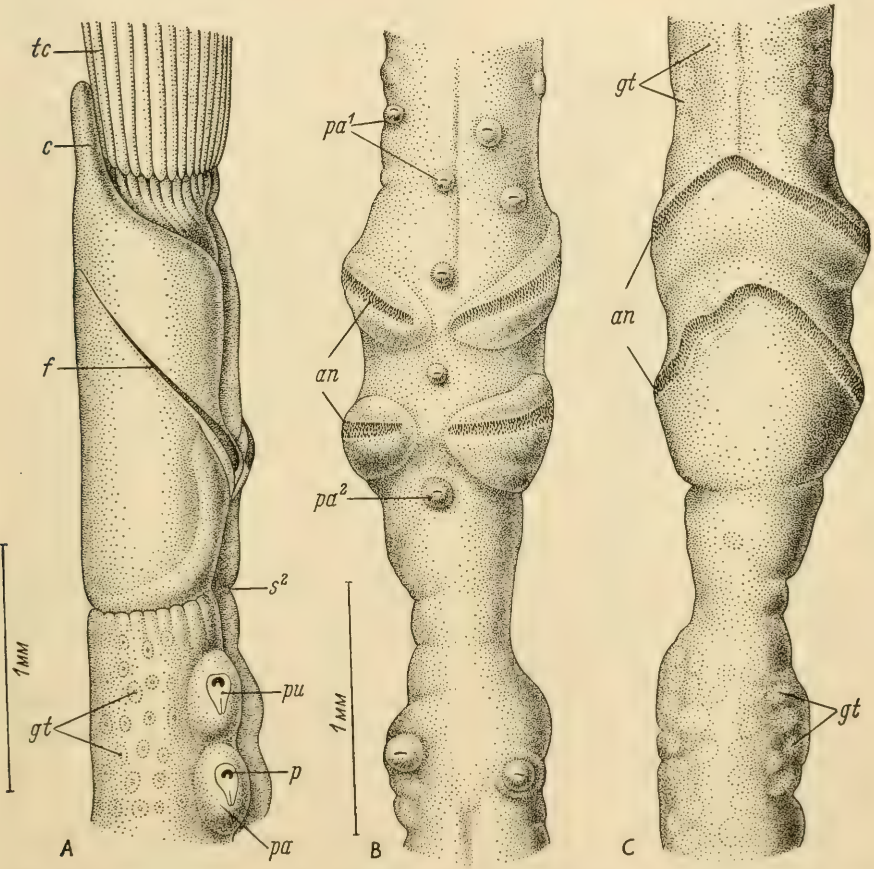


Fig. 164. *Lamellisabella zachsi*: *A* – front end of a female from the right side; *B* – region of the girdles from the ventral, and, *C* – from the dorsal side.
an – girdles; *c* – cephalic lobe; *f* – keel of the bridle; *gt* – pyriform glands seen by transparency; *p* – cuticular plaque; *pa* – papilla; *pa*¹ – papillae of the non-metameric part; *pa*² – papilla lying behind the girdles; *pu* – pulvillus; *s*² – groove between the mesosoma and the metasoma; *tc* – tentacular crown.

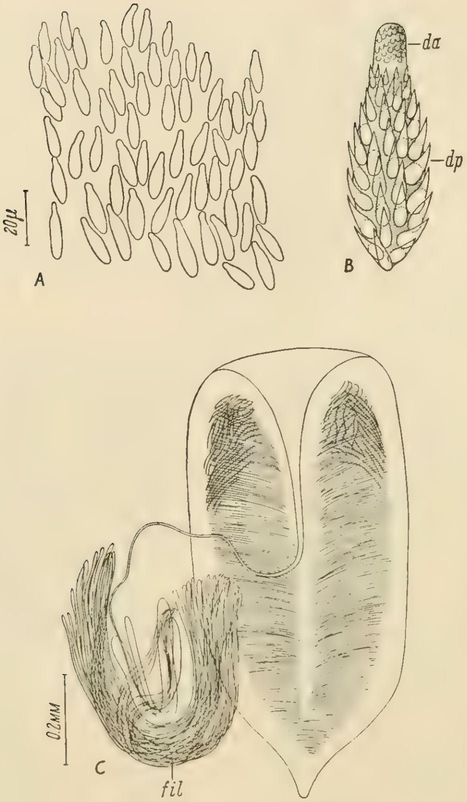


Fig. 165. *Lamellisabella zachsi*: *A* – part of a girdle; *B* – toothed platelet; *C* – spermatophore. *da* – anterior group of teeth; *dp* – posterior group of teeth; *fil* – filament of spermatophore.

The firm thick-walled tube is brown or black, with an even surface and no segments. Probably, as in *L. johanssoni*, the front end is furnished with a rigid oral funnel, though up to the present this has not been observed. The longest fragment is 30 cm long and up to 1·6 mm in diameter.

This species is distinguished from *L. johanssoni* by the greater size of the body, by the considerably larger number of tentacles and by the ventral gap between the narrower keels of the bridle, which do not form sharply raised crests.

Material: many tubes, some with animals, were taken in 1932 by P. V. Ushakov in the Sea of Okhotsk; a few specimens were collected later in far eastern seas.

Localities: the southern part of the Sea of Okhotsk and the western part of the Bering Sea.

Depth: 2917–3500 m.

2. *Lamellisabella johanssoni* Ivanov (Figs. 34*A*, *B*, *C*, 65*B*, 166–8)

Ivanov, 1957a: 475–83, 485, 492, 496–8, Figs. 46–52, 59; Dajoz, 1958: 236; Ivanov, 1960a: 1531, 1534, 1538, 1545, 1607, 1613, Figs. 1415, 1446, 1465, 1468; Ivanov, 1960c: 6, 12, 24, 30, 92, 94, 97, 242, 244, 246, 247–51, 252, 266, Figs. 34, 65, 84, 87, 166–8.

The comparatively short fore-part of the body, which is slightly flattened dorso-ventrally, has a length to breadth ratio of $2\frac{1}{2}$–$3\frac{1}{2}$: 1 (Figs. 166, 167*A*, *B*, *C*). On its ventral side runs a shallow median furrow, interrupted in the middle by the keels of the bridle and running into the ventral sulcus of the trunk at its hind end. The cephalic lobe is small and triangular. The powerful coal-black keels of the bridle run forward and quickly taper on the dorsal side. The very thick ventral ends are fused in the mid-line and rise sharply into a crest. Their greatest width reaches 0·135 mm. The dorsal ends of the keels are thin and do not meet in the mid-line. The groove dividing the fore-part of the body from the trunk is pronounced on the dorsal side but imperceptible ventrally. The tentacular crown, in the four specimens in which it is intact, consists of 18 tentacles fused together into a hollow cylinder (Fig. 166). The distal ends of the tentacles are, however, free for a short length, where dense masses of very thin pinnules about 0·13 mm long may be

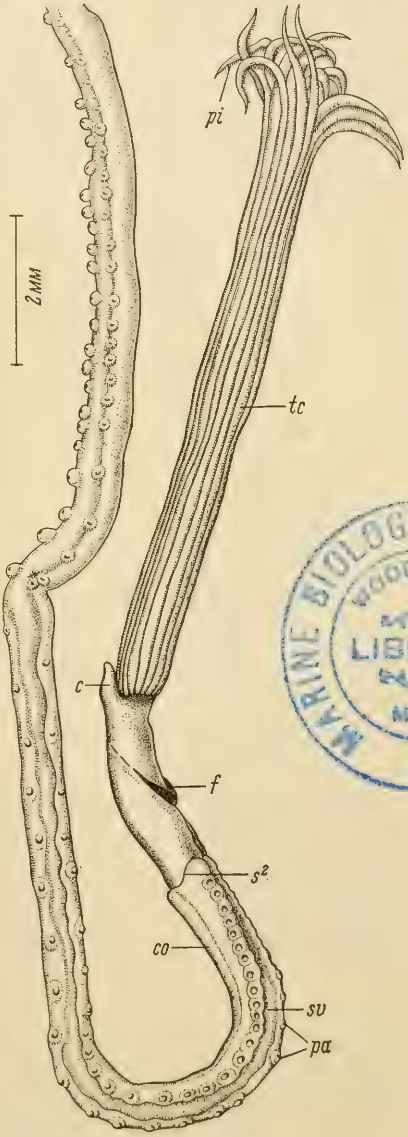
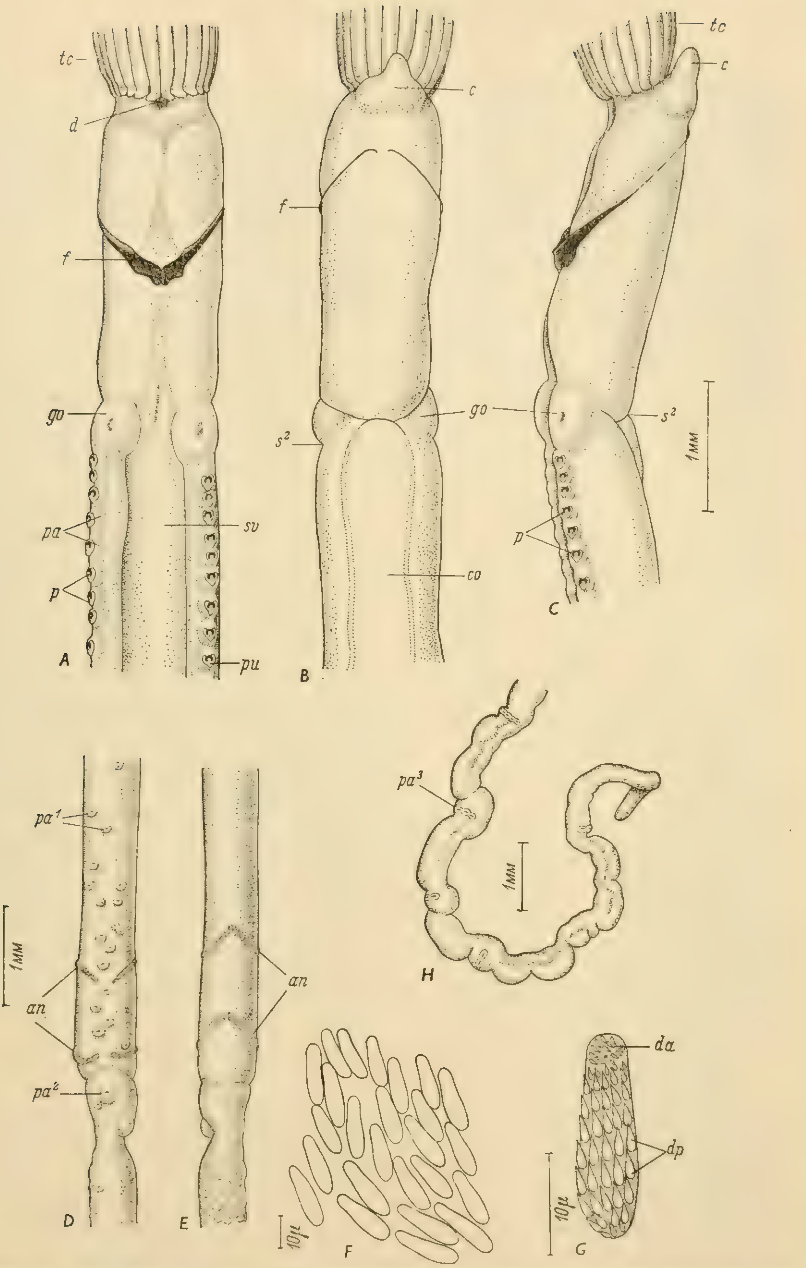


Fig. 166. *Lamellisabella johanssoni*: Front part of the body of a female.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – keels of the bridle; *pa* – papillae; *pi* – pinnules; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *tc* – tentacular crown. (After Ivanov, 1957*a*.)

observed. The tentacles themselves are four to five times as long as the fore-part of the body, and at their base, in the mid-ventral line, may be noticed an aperture which places the intertentacular cavity into communication with the exterior (Fig. 167*A*). The metameric part of the preannular region of the trunk, like the fore-part of the body, is somewhat compressed dorso-ventrally. The broad ventral sulcus (Fig. 167*A*), which has a smooth surface along the bottom, runs between pronounced lateral ridges which bear the adhesive papillae. The latter are rounded projections, touching one another in front but more widely separated farther back (Fig. 166). On each papilla lies a small heart-shaped pulvillus whose narrow end points backwards and which bears in its turn an adhesive plaque (Fig. 34*A*). In the fore-part of the trunk these are similar to those of *L. zachsi* (p. 423), but distinguished from them mainly by the slightly larger size of the horseshoe, which is 70μ across and black in colour. Towards the hind end of the metameric region they become simpler and semi-lunar in shape. Attentive observation reveals that at the same time the pulvilli also become simpler in shape and more or less rounded in outline. The simple, semi-lunar plaques are smaller than the horseshoes. The metamerism of the adhesive papillae of the front part of the trunk is far from complete, as may be seen in Figs. 166 and 167*A*, and subject to great individual variation. The number of papillae in this region varies from 47–60 pairs of which the anterior 22–30 pairs bear horseshoe plaques. The large rounded genital papillae of the males lie at the front end of the trunk (Fig. 167*A*, *C*). The dorsal ciliated band is well developed, beginning straight away at the intersegmental groove and stretching back along the greater part of the metameric region (Figs. 166, 167*B*). The non-metameric part of the preannular region of the trunk is very long and characterized by the absence of any ventral sulcus and by the irregular scattering of numerous adhesive papillae, lacking pulvilli, along the ventral surface. The cuticular plaques in this region are simple hoops 60μ across (Fig. 34*B*). A little in front of the girdles is a weakly marked zone of thickened ventral papillae, represented by five to ten rounded, scattered papillae. The broad girdles lie on muscular ridges which are sometimes flattened out and imperceptible. Both the girdles are interrupted dorsally and ventrally, but in a single individual the second girdle had no dorsal break, while the first girdle had a broad dorsal gap.

Fig. 167. *Lamellisabella johanssoni*: *A* – front end of a male from the ventral, *B* – from the dorsal, and, *C* – from the left side; *D* – region of the girdles in ventral, and, *E* – in dorsal view; *F* –part of a girdle; *G* – toothed platelet; *H* – hind end of the body.



an – girdles; *c* – cephalic lobe; *co* – dorsal ciliated band; *d* – opening putting the intertentacular cavity into communication with the outside environment; *da* – anterior group of teeth; *dp* – hind teeth; *f* – keel of the bridle; *go* – genital papilla; *p* – cuticular plaques; *pa* – metameric papillae; pa^1 – non-metameric papilla; pa^2 – papilla lying behind the girdles; pa^3 – transverse rows of post-annular papillae; *pu* – pulvillus; s^2 – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *tc* – tentacular crown. (*A*, *B*, *C*, *D*, *E* – after Ivanov, 1957a.)

Usually the dorsal ends turn somewhat forwards and run near to each other (Fig. 167*D*, *E*). The toothed platelets of the girdles are very numerous and crowded together into many rows (Fig. 167*F*). They are oblong, with a narrower front end which forms a sort of head-piece bearing the anterior group of teeth (Fig. 167*G*). This head-piece is not, however, sharply defined as it is in *L. zachsi.* The platelets are yellowish, but those which lie on the hind edge of the girdle may be blackish instead in some individuals. They measure 16–22μ long. Immediately in front of the girdles may be observed a cluster of adhesive papillae, lying in disorder on the ventral side (Fig. 167*D*). Between the girdles lie one to five small papillae with plaques on them, while there is always a solitary large mid-ventral papilla behind the girdles in the front part of the postannular region. All the papillae are furnished with somewhat bent, transverse rod-like plaques. The long postannular region of the trunk differs little from that of *L. zachsi.* The papillae are arranged in transverse metameric rows on the ventral side (Fig. 167*H*), and in each row there are, for the most part, seven small papillae, each of which has a thin, slightly bent, transverse rod-like plaque, 30–45μ long. In the hindmost rows there may be up to nine papillae and on the hind end of the body the papillae are not individually formed but run into one another (Fig. 167*H*).

All known specimens of *L. johanssoni* are nearly equal in body size. Therefore, though not one of them is complete, we may gain a good impression of the proportions of a normal adult. Thus, the overall length of the body, including the tentacular crown, must be *c.* 15–16 cm. The maximal lengths of the parts of the body are as follows: the tentacular crown, 12 mm; the fore-part of the body, 3 mm; the preannular region of the trunk, 80 mm, of which the metameric part accounts for 20–24 mm; the postannular region 60 mm. The breadth of the fore-part of the body and that of the front end of the trunk are both about 1 mm.

The living animals are whitish and through the body wall the red blood may be seen in the blood vessels.

The spermatophores are strongly flattened and leaf-like, rounded at the filamentar end and pointed at the opposite end (Fig. 65*B*). The filament of the spermatophore is broad at first, then rapidly tapering into the base of the very long, slender part. The sperm are thread-like and lie inside the spermatophore parallel to each other, forming two main bundles between which lies a narrow clear strip free of sperm. The spermatophores are 0·52 mm long by 0·24 mm broad.

The straight thick-walled unbending tube is very rigid and varies in shade from light to dark brown or almost black. It has a smooth surface and consists of a succession of segments each bearing on its front edge a barely perceptible, narrow membranous frill or collar. The length of a segment is just a little less than the diameter of the tube (Fig. 168). In general the tube strongly recalls that of *Polybrachia annulata*, but it is distinguished from it by the weakly developed frills of the segmental margins. The mouth of the tube is a broad thick-walled funnel (Fig. 168*A*). Amongst a large number of fragments of tubes a few were found with two to five such funnels developed not far from each other near the front end of the tube (Fig. 168*B*, *C*). It is not known how far this appearance may be considered normal. We may suppose that the function of the mouth of the tube, as shown in Fig. 168*B*, is served at first by the lowest funnel. Then the tube has increased in length by renewed growth and completed a new funnel-like mouth. Following this, after renewed growth of the tube, yet another funnel has been formed, and yet more. Finally after the formation of five funnels, subsequent growth has occurred in a different manner, by means of the deposition of new layers of tube material on the inner surface of the oral funnel, forming a multiple funnel. It is possible, however, that the whole series of funnels was formed in a continuous operation, without interruption, while the tube was growing in length. Some such mechanism as this must be invoked to account for the front end of the tube illustrated in

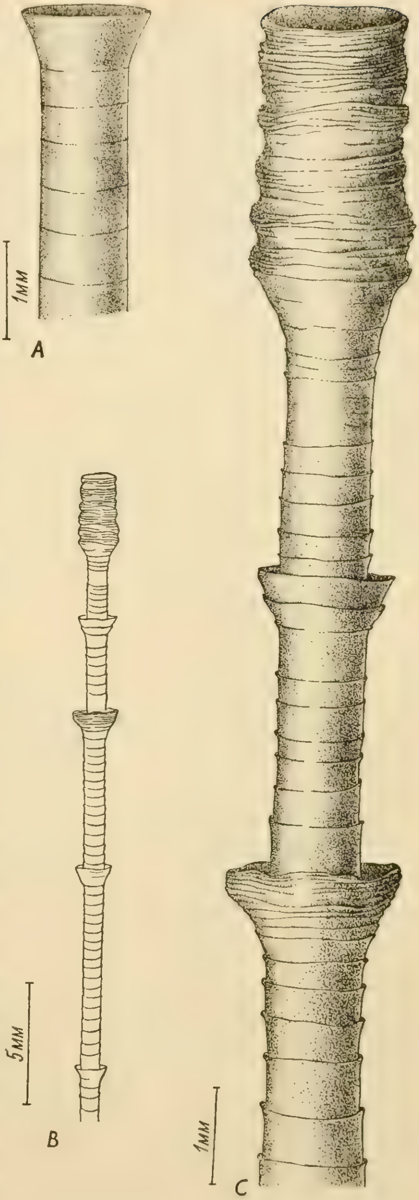


Fig. 168. *Lamellisabella johanssoni*: Tube: *A* – front end; *B* – front end with supplementary funnels; *C* – the same under higher magnification. (After Ivanov, 1957*a*.)

Fig. 168*C*. The longest fragments of tube reach 34 cm in length, but the whole tube must be much longer. The stoutest tube of all is 1·7 mm in diameter at the front end and 0·125 mm at the hind end.

The 18 tentacles of the tentacular crown contrast with the 29–31 found in *Lamellisabella zachsi* and the 22 in *L. ivanovi*. The exceptionally powerful bridle catches the eye immediately, and its keels are almost twice as broad and considerably higher than in *L. zachsi*, and, moreover, they are fused together on the ventral side, in contrast with their condition in the latter species. Again in contrast with *L. zachsi*, both the girdles are narrowly broken on the dorsal side. The spermatophores of *L. johanssoni* are sharply distinguished in shape from those of *L. zachsi* and are only half their size. The sperm, moreover, are arranged obliquely and not longitudinally as in *L. zachsi*. The tube of *L. johanssoni* is segmented while that of *L. zachsi* is smooth. Other distinctions between the species are presented in Table 6.

Material: nine specimens (amongst which four were semi-decomposed), together with a great number of pieces of tubes.

Locality: the northern part of the Japan Trench.

Depth: 6156–6207 m.

3. Lamellisabella ivanovi Kirkegaard (Fig. 169)

Kirkegaard, 1956b: 183–4, Figs. 1, 2 (as *L. zachsi*); Kirkegaard, 1961: 7–10, Figs. 1–3; Ivanov, 1960c: 4, 97, 242, 251–3, 266, Fig. 169.

[Because of an unfortunate delay in the publication of Kirkegaard's paper (1961) Ivanov's description of this species was the first to appear under this name, for he had been instrumental in pointing out to Kirkegaard that his material did not in fact belong to *L. zachsi*, as first described (Kirkegaard, 1956b) but formed a new species. These authorities were thus in correspondence and Ivanov was able to examine Kirkegaard's material and to read his manuscript. He incorporated the following description in his book in the full belief that Kirkegaard's description would appear first.]

This species is known from a single, badly preserved, incomplete specimen found by Kirkegaard in a collection of benthos from the Bay of Panama in the eastern Pacific Ocean and ascribed by him to *L. zachsi* (Kirkegaard, 1956b). As shown, however, by comparison with the other species of *Lamellisabella*, the Panamanian specimen appeared to be distinct (Kirkegaard, 1961).

L. ivanovi is distinguished by the possession of 22 tentacles and by the peculiar structure of the keels of the bridle, which consist of a pair of clear cuticular rods with a row of dark cuticular bodies attached behind them

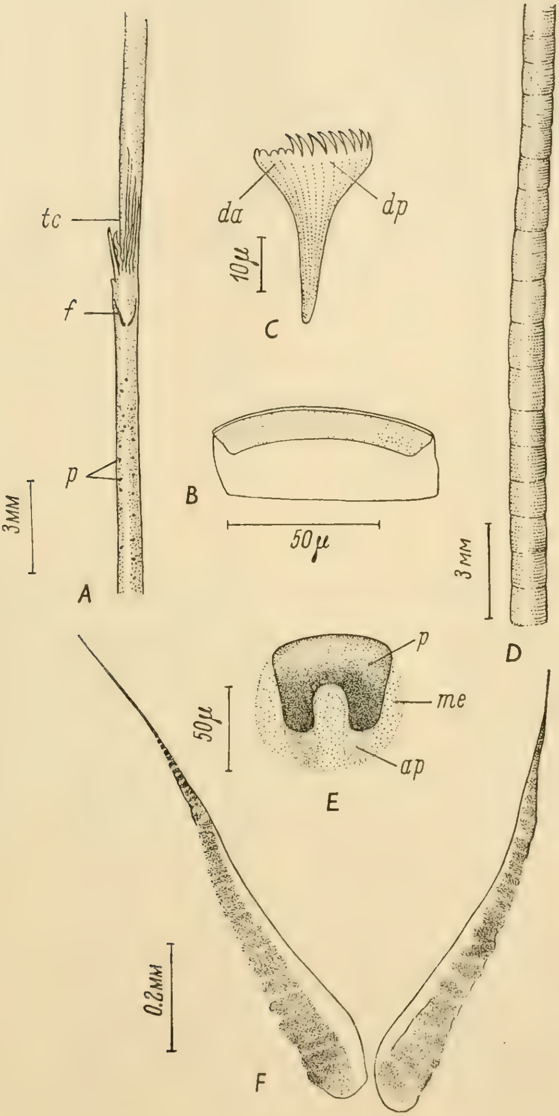


Fig. 169. *Lamellisabella ivanovi*: *A* – front end of the body in ventral view; *B* – cuticular plaque from the middle of the metasoma; *C* – toothed bristle in side view; *D* – part of the tube; *E* – cuticular plaque of a metameric papilla; *F* – keels of the bridle.
ap – apodeme of the plaque; *da* – front group of teeth; *dp* – hind teeth; *f* – bridle; *me* – membrane of the plaque; *p* – cuticular plaques; *tc* – tentacular crown. (*A*, *B*, *C*, *D* – after Kirkegaard, 1956b.)

(Fig. 169*F*). In this regard it is very like the genus *Diplobrachia* (pp. 369, 372). *Lamellisabella ivanovi* is like *L. zachsi* in many features: thus, in both species, the ventral ends of the keels of the bridle are not fused together and there is no sharp, upstanding crest on the keels. The keels, however, are almost twice as broad as in *L. zachsi.* The panamanian species is similar to *L. johanssoni* in the comparatively small number of tentacles, in the composition of the tentacular cylinder and in the segmentation of the tube. The characteristics of the species of *Lamellisabella* are compared in Table 6.

The tentacular crown is 12 mm long, the fore-part of the body *c.* 3 mm; the mesosoma is 1 mm broad; the horseshoe-shaped plaques are 75μ and the toothed platelets 21μ long.

The tube is dark, opaque, stout-walled and distinctly divided into segments which are as long as the tube is wide, or just a little larger.

Material: Kirkegaard had a single incomplete, badly preserved specimen.

Locality: Gulf of Panama (5°44′N, 79°20′W).

Depth: 2950–3190 m.

[*4. Lamellisabella minuta* sp. nov. Ivanov (Figs. A169–E169)

In February, 1960, R.V. *Vityaz*', working off the southwest coast of India, found, at a depth of 1300 m, a new species of *Lamellisabella*, which in view of its surprisingly small size I propose to call *Lamellisabella minuta.* The material consists of two almost complete animals in rather long tubes, and five small fragments of tubes, two of which contained scraps of the trunk.

The cylindrical fore-part of the body lacks any external boundary between protosoma and mesosoma (Fig. A169, B169). In comparison with that of other species of this genus it is greatly elongated, with a length to breadth ratio in one individual of 5 : 1 and in the other 6 : 1. The small cephalic lobe is somewhat dorso-ventrally flattened and shaped like an equilateral triangle (Fig. B169*B*, *C*). The cylindrical tentacular crown consists of ten tentacles, each stuck lengthwise to the next (Fig. A169). Inside the crown there is a wide intertentacular cavity, into which project the small pinnules, which are arranged in very thick-set rows along the inner sides of the tentacles.

The bridle lies in the middle of the fore-part of the body. Each keel consists of a thin colourless cuticular axis with a broad yellow-brown band attached behind it on the ventral side. This band broadens out gradually towards the ventral end of the keel and consists of a row of cuticular bodies which merge into one another (Fig. C169*A*). The very thin curved dorsal

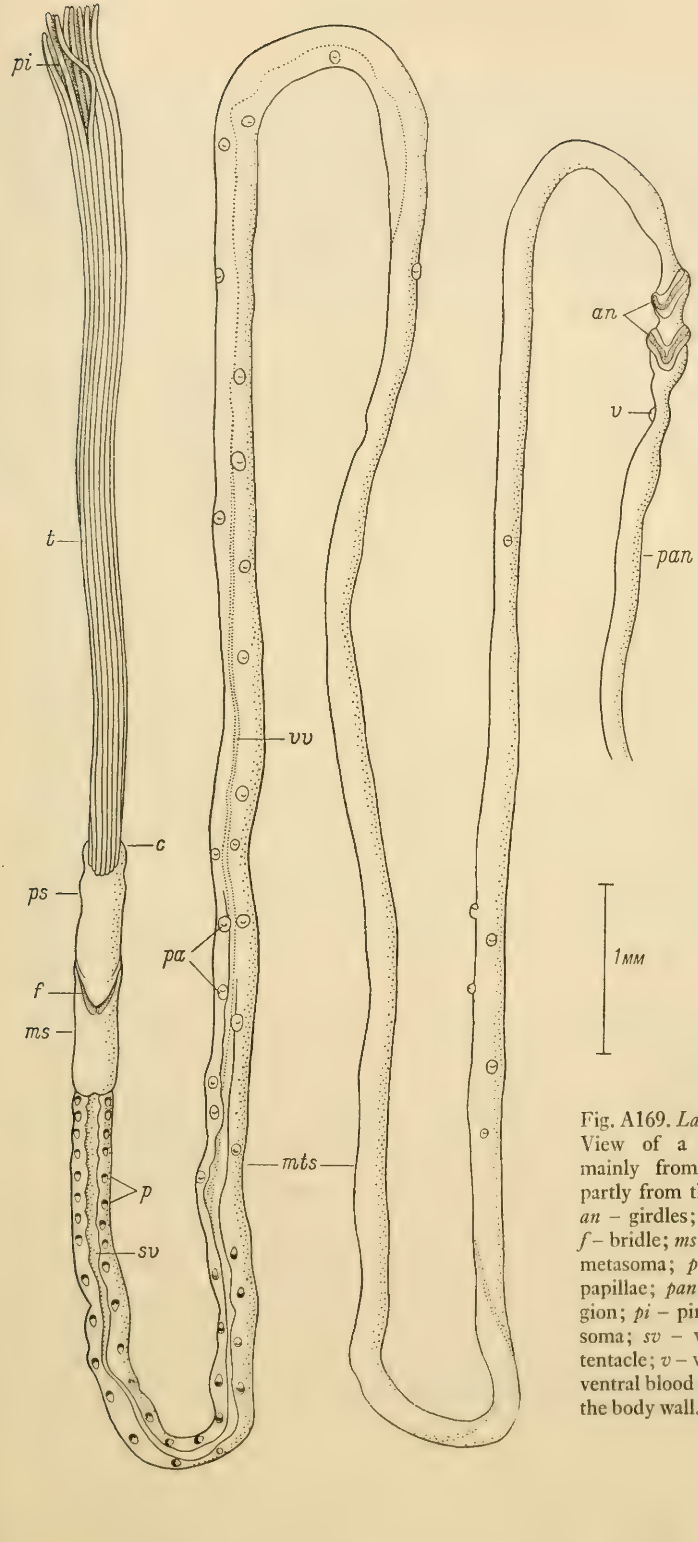


Fig. A169. *Lamellisabella minuta*: View of a twisted specimen mainly from the ventral and partly from the dorsal side.
an – girdles; *c* – cephalic lobe; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *p* – plaques; *pa* – papillae; *pan* – postannular region; *pi* – pinnules; *ps* – protosoma; *sv* – ventral sulcus; *t* – tentacle; *v* – ventral papilla; *vv* – ventral blood vessel seen through the body wall.

ends of the keels do not meet (Fig. B169*B*), nor do the ventral ends which are raised up above the surface of the body as tall crests (Fig. B169*C*). This is a peculiarity shared with *L. johanssoni*, and the complex structure of the keels recalls those of *L. ivanovi*. The ridges of the bridle are rather narrow and only discernable on the lateral and dorsal sides of the body (Fig. B169*B*, *C*). There is no median furrow either in front of or behind the bridle.

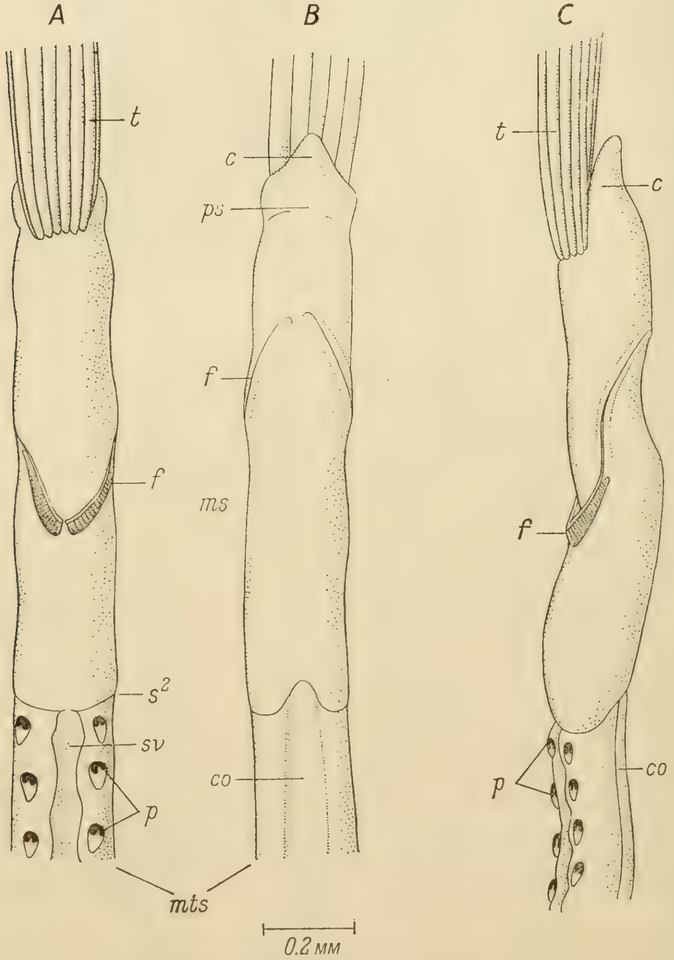


Fig. B169. *Lamellisabella minuta*: Fore-part of the body: *A* – from the ventral side; *B* – from the dorsal side; *C* – from the left.
c – cephalic lobe; *co* – dorsal ciliated band; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *p* – plaques; *ps* – protosoma; s^2 – groove between the mesosoma and metasoma; *sv* – ventral sulcus; *t* – tentacle.

The boundary between the mesosoma and metasoma is a somewhat bevelled groove, which takes a dip forward in the mid-dorsal region. The dorsal ciliated band starts in this dip and extends backwards to the end of the metameric part of the metasoma. There is a comparatively narrow but deep ventral sulcus running between lateral ridges (Fig. B169*A*) which bear the metameric pulvilli of the adhesive plaques. The adhesive papillae themselves hardly project from these ridges. As in other species of *Lamellisabella*, their metamerism is very imperfect. Thus in one specimen the papillae are arranged in more or less regular metamerism in the anterior part of the metameric region, but farther back this regularity breaks down so that the sixteenth plaque on the right is opposite the seventeenth on the left and the twenty-third on the right opposite the twenty-fifth on the left (Fig. A169). The metameric part of the second individual is much the same, as is one of the fragments which includes this part.

The strongly contracted pulvilli of the plaques in the anterior part of the metameric region are equilateral triangles with chamfered corners (Fig. C169*B*), but in the hind part of the region they become round (Fig. C169*C*). The plaques, as in all known species of *Lamellisabella*, appear horseshoe-shaped. Attentive examination, however, shows that they are in fact round, but enormously thickened at the front as a sort of dark-brown horseshoe-shaped catch, whose short ends stick out backwards like a ratchet (Fig. C169*B*, *C*). The ends of the horseshoe reach to the middle of the plaque and the remaining part is a sort of thin flat transparent roundish scale (Fig. C169*B*, *C*). Thus the structure of the horseshoe plaques is the same as in other species of *Lamellisabella* (Ivanov, 1957; Kirkegaard, 1961; see p. 47). The horseshoes in *L. minuta* are 34μ across and the plaques themselves vary from 44 to 52μ.

The horseshoe plaques are limited to the metameric part of the preannular region, but, as in *L. zachsi* and *L. johanssoni*, here and there simpler 'bow-shaped' plaques without apodemes replace the horseshoes. In one specimen, which has 23 plaques on the right and 25 on the left in the metameric region, the nineteenth pair of pulvilli are the last to bear horseshoes, but the fifteenth and seventeenth pulvilli on the left bear 'bows'. In the other individual, which has 25 pulvilli on each side of the body, the seventeenth pair bear the hindmost horseshoes, but the seventh and tenth pulvilli on the left and the fifteenth on the right have 'bows'. The oval plaques with the 'bows' have their major axis athwart the body and the dark bow-shaped thickened rod reaches 40μ across (Fig. C169*D*).

The nonmetameric section of the preannular region of the metasoma is very long and characterized by small round papillae (or pulvilli) sparsely scattered at random over the ventral side of the body (Fig. A169), so sparsely in fact that considerable parts of the trunk here completely lack papillae.

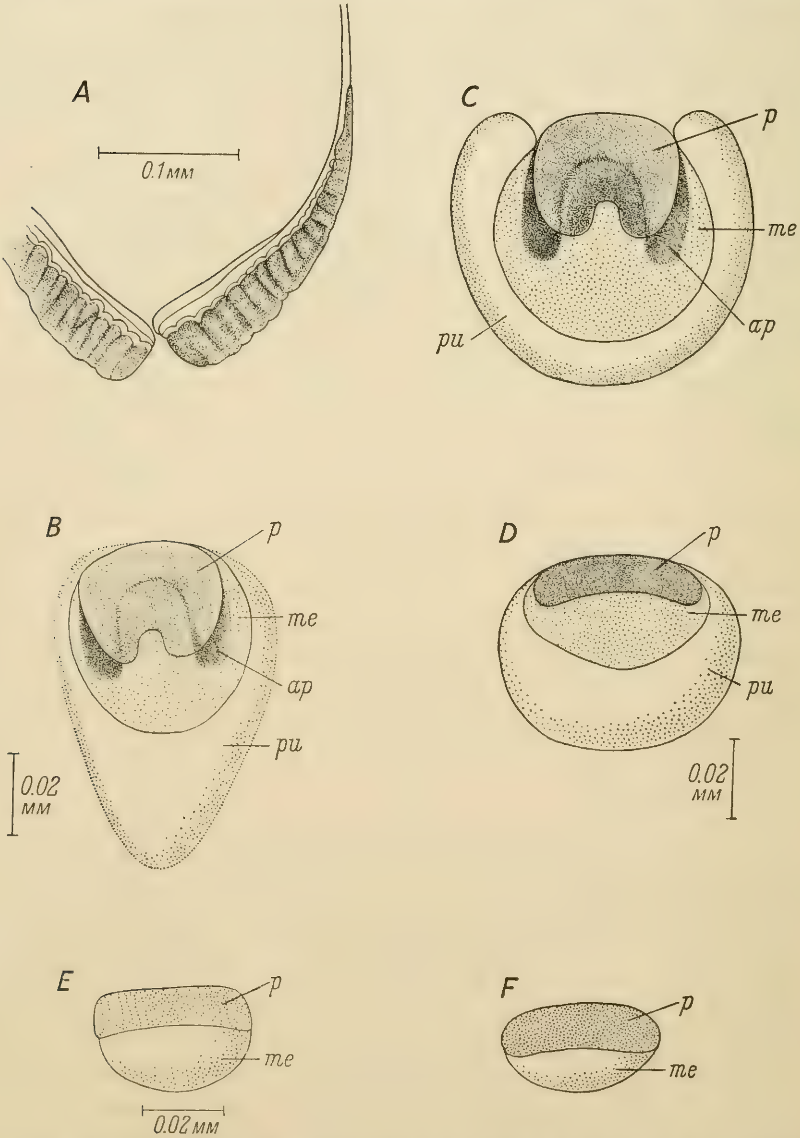


Fig. C169. *Lamellisabella minuta*: *A* – ventral ends of the keels of the bridle; *B–D* – plaques of the metameric region; *E*, *F* – plaques from the nonmetameric part of the trunk.
ap – apodemes of the plaques; *me* – membrane of the plaques; *p* – thickened part of the plaque; *pu* – pulvillus.

The papillae bear oval cuticular plaques with a dark bow-shaped or straight thickening, usually measuring about 40μ across (Fig. C169*E*, *F*). There is no zone of thickened papillae.

There are two girdles of toothed platelets (Figs. A169, D169), both broken only on the ventral side (Fig. E169*A*, *B*). The yellowish toothed platelets, 15–23μ long, are arranged in two, or in places three, irregular rows (Fig. E169*C*). They are greatly elongated and their shape is characteristic. The front part of the platelet, bearing the anterior group of teeth, is small and rather sharply detached; it usually takes up only a fifth of the total length of the platelet (Fig. E169*D*).

The postannular region of the metasoma has frequent metameric transverse rows of three to five conical ventral papillae (Figs. D169, E169*B*), of which the median papilla is larger than the others. The plaques take the form of dark transverse cuticular rods, slightly bent forward and measuring 26–32μ across (Fig. E169*E*).

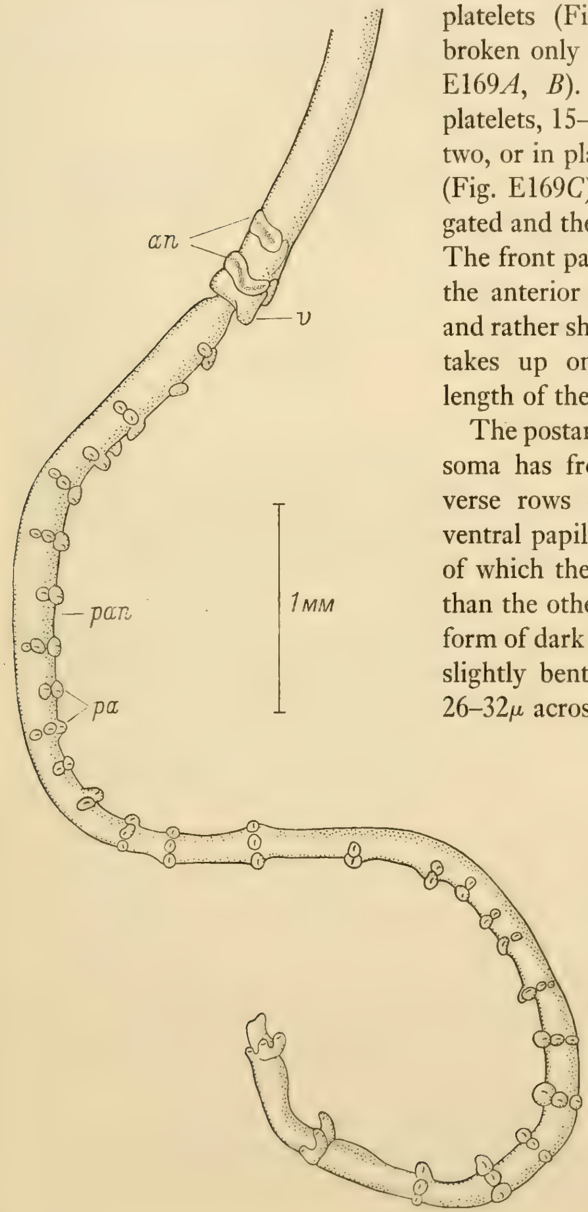


Fig. D169. *Lamellisabella minuta*: the region of the girdles and the front end of the postannular region, from the right.
an – girdles; *pa* – papillae; *pan* – postannular region; *v* – ventral papilla behind the girdles.

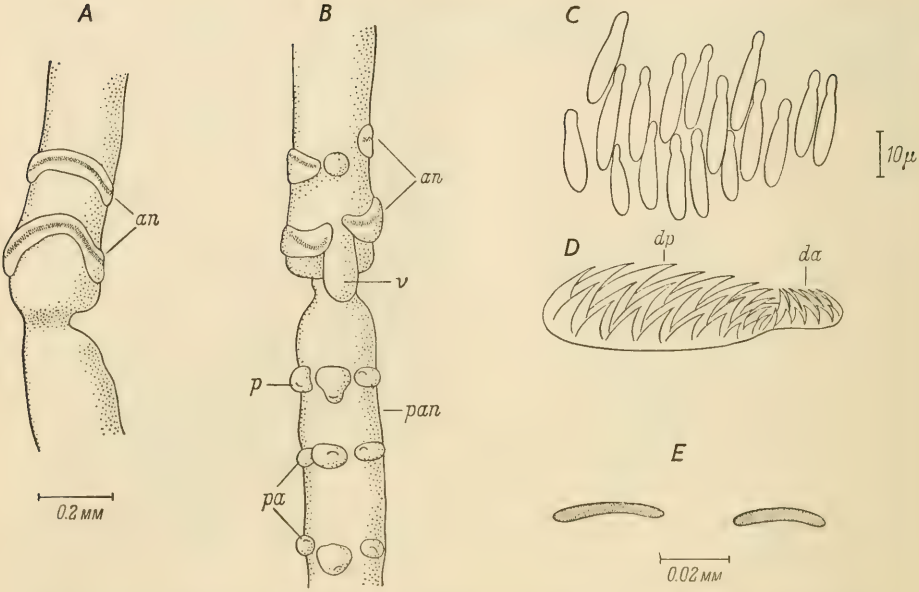


Fig. E169. *Lamellisabella minuta*: *A* – the girdles from the dorsal, and *B*, from the ventral side; *C* – part of a girdle; *D* – toothed platelet from the side; *E* – plaques from a postannular papilla. *an* – girdles; *da* – anterior teeth; *dp* – posterior teeth; *p* – plaque; *pa* – papillae; *pan* – postannular region; *v* – ventral papilla behind the girdles.

I have measured the different parts of the body in the two almost complete specimens (only the hindmost end of the postannular region is missing), and obtained the following results (mm):

	First specimen	Second specimen
Length of tentacles	5·1	3·4
Length of the fore-part of the body	1·6	1·2
Breadth of mesosoma	0·3	0·27
Length of the metameric region	6·5	3·0
Length of the nonmetameric region	24·0	7·5
Overall length of preannular section	30·5	10·5
Length of surviving fraction of postannular section	22·0	7·5

The second individual is considerably smaller than the first and may possibly be a juvenile. This is most strikingly suggested by the underdeveloped preannular region, which is only a third as long as that of the first specimen. The overall length of the latter is probably between 55 and 60 mm.

No spermatophores have been found.

The tube of *L. minuta* is very characteristic. Its mouth opens out as a broad funnel, like that of *L. johanssoni* (Ivanov, 1957, 1960c), and indeed, like the latter species, the front end of the tube has a series of funnels stacked one inside the other. The front ends of the two tubes are shown in Fig. F169. Each funnel corresponds to a single segment and the tube appears in essence to be segmented, but they very rapidly disappear as we pass backwards from the mouth of the tube, and then right to the end it is completely uniform and homogeneous (Fig. F169*C*).

A small distinct part of the tube (with funnels and segments) is brown, thin-walled and transparent. Then the tube gradually becomes lighter, turning a pale yellow-brown, and still more transparent. The hind half of the tube (or perhaps even more than a half) is whitish transparent and soft. Finally, the hindmost part has colourless laminated limp walls.

The incomplete tube (lacking the hind end) of the larger individual is 147·5 mm long, the one with young animal 119 mm. The anterior diameter of the tubes are respectively 0·4 and 0·35 mm.

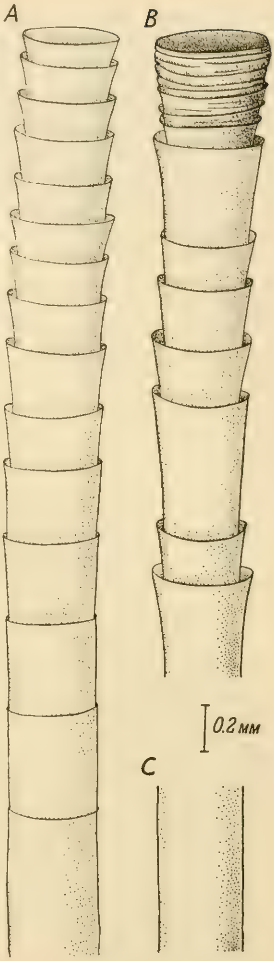


Fig. F169.
Lamellisabella minuta: *A–C* – successive parts of the tube.

L. minuta is sharply distinguished from the other species of this genus by the small size of the body. The most reliable measure of the size of a pogonophore is the breadth of the mesosoma. In this species the diameter is only a quarter to a third of that in the other species. Other important distinctions are the small number of tentacles, the structure of the keels of the bridle and the size of the cuticular adhesive plaques. The horseshoes on the metameric region of the metasoma in *L. minuta* have shorter ends than in the other species. A number of features of the four species of *Lamellisabella* are compared in Table 6.

In conclusion we may remark that the geographical distribution of the genus *Lamellisabella* is very wide. *L. zachsi* inhabits the southern part of the Sea of Okhotsk and the Bering Sea. *L. johanssoni* lives in the Japan Trench and the third species. *L. ivanovi*, has been found on the opposite side of the Pacific Ocean in the Gulf of Panama. Finally, *L. minuta* lives in the Indian Ocean off the coast of India.

Material: four tubes with animals or fragments of animals and three broken empty tubes.

Locality: *Vityaz*' station 4620 (31st cruise): Arabian Sea to the west of the coast of southern India.

Depth: 1300 m.]

Table 6

Characteristics of the species of *Lamellisabella*

	L. zachsi	*L. johanssoni*	*L. ivanovi*	*L. minuta*
Number of tentacles	29–31	18	22	10
Length of tentacular crown (mm)	Up to 27	Up to 12	12	Up to 5·1
Length of fore-part of body (mm)	2·5–3	2–3	*c.* 3	1·2–1·6
Breadth of mesosoma (mm)	Up to 1·3	Up to 1·0	1·1	0·3
Fusion of ventral ends of keels	—	+	—	—
Maximum width of keels (μ)	60–70	125	110	0·60
Shape of keels	Swollen	With a sharp crest	Swollen	With a sharp crest
Structure of keels	Homogeneous	Homogeneous	Complex	Complex
Diameter of horseshoe-shaped plaques (μ)	60	70	75	34
Maximum length of preannular region (mm)	110	80	?	30
Maximum length of postannular region (mm)	80	60	?	22
Length of toothed platelets (μ)	13–23	16–22	21	15–32
Size of postannular cuticular plaques (μ)	60–100	35–40	?	26–32
Maximum length of body (mm)	220	160	?	60
Size of spermatophores (mm)	1 × 0·45	0·55 × 0·24	?	?
Tube	Unsegmented	Segmented	Segmented	Segmented

III. Family Spirobrachiidae Ivanov, 1952

In this family the animals possess numerous tentacles fused together into a tentacular plate, which is then rolled up into a spiral, not unlike a scroll, so that the tentacular crown is asymmetrical. A considerable proportion of the tentacles is supported on a cork-screw-shaped lophophore, which is an outgrowth of the protosoma.

A single genus: *Spirobrachia.*

1. Genus *Spirobrachia* Ivanov, 1952

Ivanov, 1952: 384–90; Zenkevitch, 1954: 79, 80; Zenkevitch, Birstein and Belyaev, 1954: 67, 68; Hartman, 1954: 184, 185; Ivanov, 1954b: 75, 77, 79; Ivanov, 1955a: 177; Ivanov, 1955b: 382, 383; Ivanov, 1955d: 173, 174, 176; Ivanov, 1955e: 225; Ivanov, 1956a: 20; Ivanov, 1956b: 1864, 1868; Ivanov, 1956c: 165, 166, 169; Jägersten, 1956: 238; Kirkegaard, 1956b: 186; Abrikosov, 1957: 233, 238; Beklemishev, 1957: 399; Ivanov, 1957a: 474, 475, 483–9, 490, 492–97; Ivanov, 1957b: 1139; Vinogradova, 1958: 112; Dajoz, 1958: 231–3, 236, 237; Fell, 1958: 46; Ivanov, 1958a: 1369, 1370; Ivanov, 1958b: 1682, 1687, 1688; Ivanov, 1960a: 1528, 1534, 1537, 1539–41, 1549, 1550, 1552, 1561, 1569, 1572, 1574, 1580, 1581, 1607; Ivanov, 1960c: 6, 11, 18, 20, 23, 24, 25–27, 34–37, 43, 46, 48, 56, 59, 61, 66, 67, 75, 92, 115, 227, 244, 253–4.

In the known species the tentacular spiral consists of 39–223 tentacles. The turn of the spire is anti-clockwise, as looked at from in front and starting at the outermost tentacle, and the lophophore is likewise twisted into an anti-clockwise spiral. The protosoma is combined with the mesosoma and no cephalic lobe is separated off. A crack-like median furrow runs along the dorsal side of the mesosoma. The bridle is well-developed. The cuticular plaques in the front part of the metasoma are shaped like bows or hoops and lie on pulvilli. The spermatophores are leaf-like, with long pointed ends. The tube has a rigid, funnel-like mouth.

There are two species: *Spirobrachia grandis* and *S. beklemischevi.*

Type of the genus: *Spirobrachia grandis* Ivanov.

Key for the identification of the species of *Spirobrachia*

1 (2) The crown consists of more than 100 tentacles, though from the outside, in ventral view, only 30 may be visible. The keels of the bridle meet ventrally. The hoop-shaped plaques of the metameric papillae are 110–190μ across. The brown-black tube is opaque and up to 2·8 mm in diameter. 1. *S. grandis* (p. 446).

2 (1) The crown consists of not more than 100 tentacles of which only 20 may be visible from the outside in ventral view. The keels of the bridle do not meet ventrally. The hoop-shaped plaques of the metameric papillae are only 55–75μ across. The tube is transparent and up to 1·4 mm in diameter. 2. *S. beklemischevi* (p. 450).

1. Spirobrachia grandis Ivanov (Figs. 5, 17*F*, 18, 59, 170–3)

Ivanov, 1952: 384–7, 388, Figs. 23–7; Zenkevitch, 1954: 79, 80, Figs. 8, 9; Zenkevitch, Birstein and Belyaev, 1954: 67, 68, Figs. 9, 10; Hartman, 1954: 185; Ivanov, 1954b: 75, 77, 79, Figs. 6, 7; Ivanov, 1955e: 225, Pl. LXV, Fig. 6; Ivanov, 1956b: 1864, 1868; Ivanov, 1956c: 166, 169; Kirkegaard, 1956b: 186, Fig. 4; Abrikosov, 1957: 238; Beklemishev, 1957: 399, Fig. 146; Ivanov, 1957a: 483, 484, 489, 492, 493, 495–7, Fig. 59; Vinogradova, 1958: 112; Dajoz, 1958: 233, 236, 237, Figs. 3 (incorrectly labelled), 6; Ivanov, 1958a: 1369, 1370; Ivanov, 1958b: 1682, 1687, 1688, Figs 3, 7; Ivanov, 1960a: 1530, 1538, 1541, 1543, 1546, 1559, 1570, 1576, 1588, 1591, 1606, Figs. 1399, 1400, 1408, 1419, 1420, 1422, 1425, 1431, 1439, 1468; Ivanov, 1960c: 6, 10, 12, 22, 27, 30, 57, 61, 75, 76, 91, 92, 96, 228, 254–8, 261, 262, 266, Figs. 5, 17, 18, 27, 37, 39, 41, 44, 51, 59, 87, 170–3.

The fore-part of the body is a little compressed dorso-ventrally. The cephalic lobe is also compressed and is shaped like an equilateral triangle. The keels of the bridle, situated on the surface of cutaneous ridges, run close together on the ventral side, while their dorsal ends fuse. Narrow median furrows run along both the dorsal and the ventral side of the mesosoma (Figs. 5, 170, 171*B*). The tentacular apparatus consists of very numerous tentacles, and in one specimen, a female, 223 were counted. The whole tentacular plate makes not less than six rather close turns of spire (Figs. 17*F*, 18, 59), and its external free edge is attached to the body considerably farther down than the next turn, thus further emphasizing the asymmetry of the crown. The point of attachment of this edge lies on the right side in the female (Fig. 171*A*) and on the ventral side in the male (Fig. 172*A*). In both sexes the lophophore begins on the right side of the protosoma with a broad base, pointing forwards, gradually tapering and describing 3–4 turns around the main axis of the body (Fig. 18). Beginning from the outermost free edge of the tentacular plate, ventrally or on the right side of the body, the line of attachment of the tentacles runs first on to the left side, making a half or a little more than a half revolution. Then the tentacles extend on to the base of the lophophore and then on to the lophophore proper, describing a corkscrew on its outer side right up to the tip (Fig. 18). The pinnules are arranged along the inner side of the tentacles in four rows on each.

The metameric part of the trunk bears a large number of adhesive papillae: in a female about 220 pairs of more or less metameric papillae were counted (Fig. 170). For a considerable length the metamerism is rather strict, but falters after a time, so that while the 66th papilla on the left lies opposite the 66th on the right, the 139th on the right lies opposite the 138th on the left. Farther back the metamerism begins to break down completely. The papillae are crowded close together (Fig. 171*A*) and in the hind part of the metameric region they form conical mammillae, rather sharply delimited from the surface of the trunk (Fig. 172*C*). On their tips they bear round or pear-shaped pulvilli with cuticular plaques (Fig. 172*B*). The ventral sulcus does not extend to the end of the metameric part but peters out at the level of the 95th–100th pair of adhesive papillae. The dorsal ciliated band is broad (Fig. 171*B*) and extends in the female to the level of the 61st pair of papillae. The cuticular plaques are large (110μ across) and their anterior thickened part is represented by a flat curved hoop, whose ends are cut off square (Fig. 172*D*). In the second half of the metameric region the plaques are larger still (up to 190μ) and their hoops are more drawn out (Fig. 172*E*). The region of the girdles and the postannular section of the body remain unknown.

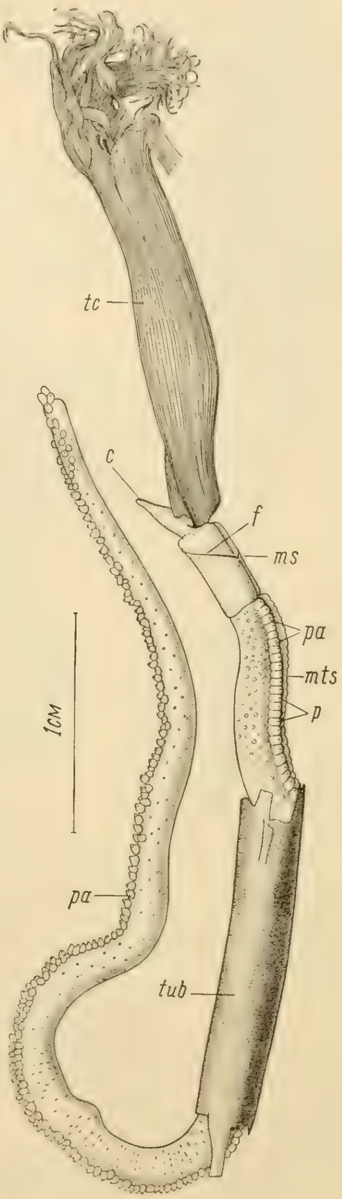


Fig. 170. *Spirobrachia grandis*: Front end of a female from the right side. Part of the tube has not been dissected away.

c – cephalic lobe; *f* – bridle; *ms* – mesosoma; *mts* – metasoma; *p* – cuticular plaque; *pa* – metameric papillae; *tc* – tentacular crown; *tub* – part of the tube. (After Ivanov, 1952.)

Two specimens were studied: a male, fixed while still inside its tube, and a female, which was removed from the tube while still alive and fixed in a state of strong contraction. They have the following dimensions (in mm):

	♂	♀
Length of the tentacles	27·0	24·5
Length of the fore-part of the body	5·1	4·2
Breadth of the fore-part of the body	1·2	2·5
Length of the metameric part of the metasoma	—	66·0

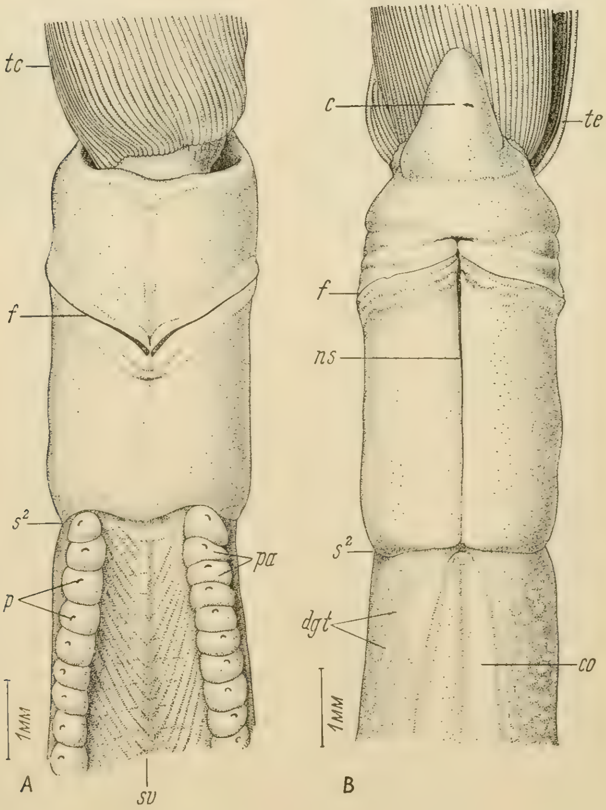


Fig. 171. *Spirobrachia grandis*: *A* – front end of a strongly contracted female in ventral, and, *B* - in dorsal view.
c - cephalic lobe; *co* – dorsal ciliated band; *dgt* – ducts of pyriform glands seen by transparency; *f* - keel of the bridle; *ns* – dorsal nerve furrow; *p* – cuticular plaques; *pa* – metameric papillae; s^2 - groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *tc* – tentacular crown; *te* - external tentacle of the tentacular plate.

Fig. 172

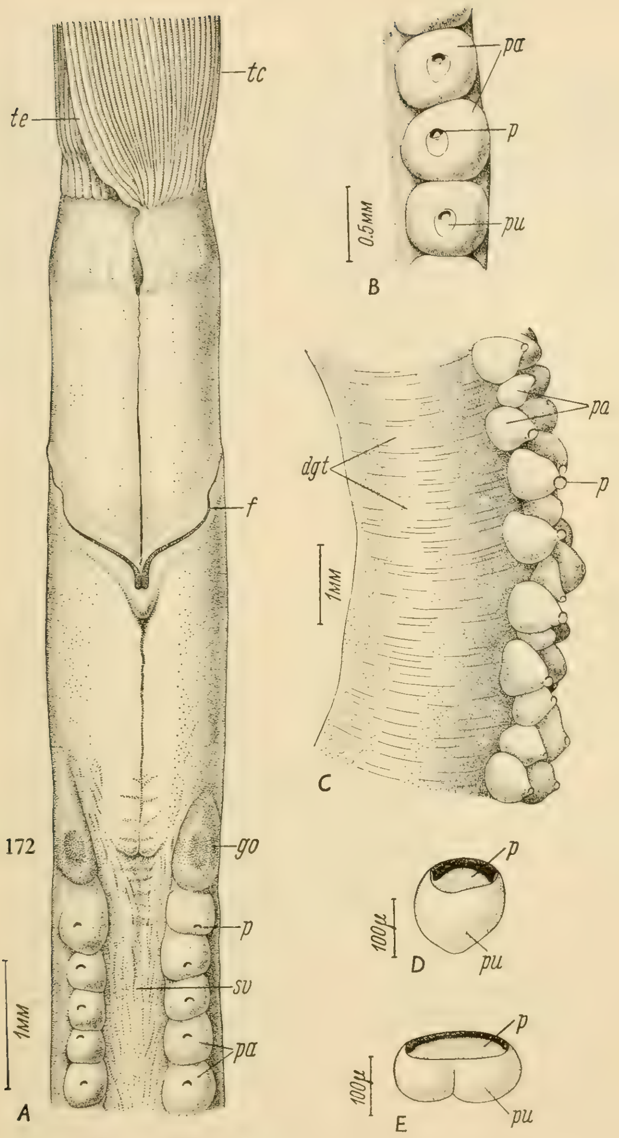


Fig. 173

Fig. 172. *Spirobrachia grandis*: *A* – front end of a fully extended male from the ventral side; *B* – metameric papillae; *C* – part of the metameric section of the metasoma of a female from the right side; *D* – pulvillus with a cuticular plaque from the front part of the metameric section, and, *E* – one from the hind part of the same section.
dgt – ducts of pyriform glands seen by transparency; *f* – keel of the bridle; *go* – genital papilla; *p* – cuticular plaque; *pa* – papillae; *pu* – pulvillus; *sv* — ventral sulcus; *tc* – tentacular crown; *te* – external tentacle. (*D* and *E* – after Ivanov, 1952.)

Fig. 173. *Spirobrachia grandis*: Spermatophore.
fil – filament of spermatophore. (After Ivanov, 1952.)

The colour of the living female after removal from the tube was brick-red.

The flattened, leaf-like spermatophore is very large (2·5 mm long by 0·35 mm broad at the widest part). One end is drawn out into a long, gradually tapering point, while the other broader end forms a flat outgrowth from which springs the rather stout filament (Fig. 173). The latter turns down at the base to run along one of the flat sides of the spermatophore where it forms a thick skein. The filament is very long and tapers gradually right up to the very end.

The tube has a smooth, somewhat lustrous surface and is a dark black-brown colour (Fig. 170). In the female its diameter near the front end reaches 2·8 mm, but fragments are known up to 3 mm across.

Material: three specimens (two males and a female).

Locality: the southwestern part of the Bering Sea.

Depth: 3260 m.

2. *Spirobrachia beklemischevi* Ivanov (Figs. 16, 174–6)

Ivanov, 1957a: 474, 483–9, 490, 492–4, 496, Figs. 53–9; Ivanov, 1957b: 1139; Abrikosov, 1957: 238; Dajoz, 1958: 236; Ivanov, 1958b: 1687; Ivanov, 1960a: 1538, 1540, 1542, 1613, Figs. 1387, 1398, 1465, 1468; Ivanov, 1960c: 5, 10, 22, 23, 25, 92, 94, 97, 228, 254, 258–62, 266, Figs. 16, 84, 87, 174–6.

The fore-part of the body is cylindrical and comparatively short, with a length to breadth ratio of 2–2½ : 1 (Fig. 174*A*, *B*, *C*). The large, flattened cephalic lobe is round in front. The bridle lies at the centre of the fore-part of the body and its narrow brownish keels are situated on ridges which are especially pronounced on the dorsal side (Fig. 174*A*). The ventral ends of the keels are somewhat club-shaped and do not meet, nor do the thinner dorsal ends. A shallow median furrow runs along the ventral side of the fore-part of the body, while a narrow dorsal furrow, broadening at its front end,

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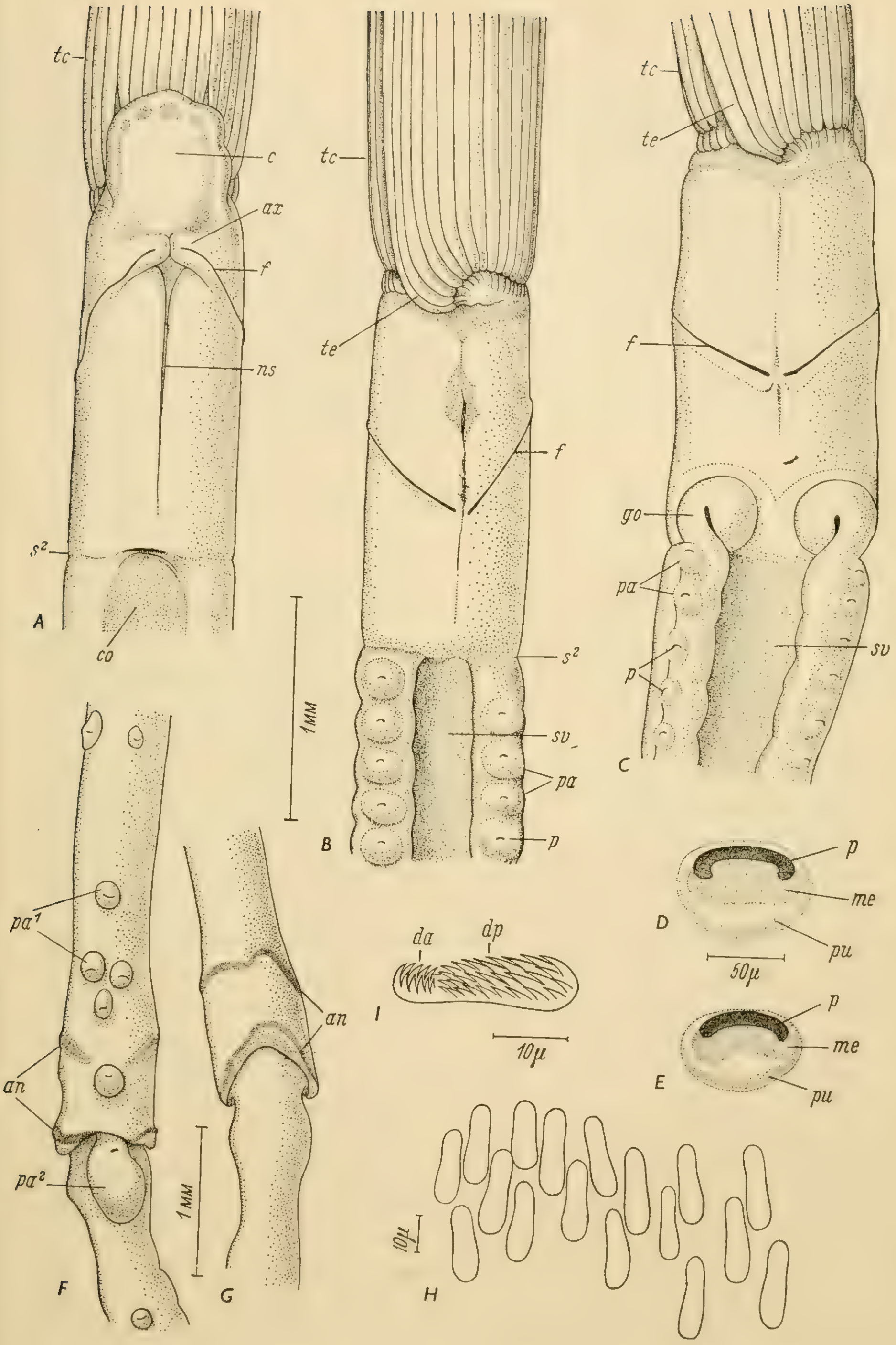
Fig. 174. *Spirobrachia beklemischevi*: *A* – front end of a female from the ventral, and, *B* – from the dorsal side; *C* – front end of a male in ventral view; *D* – pulvillus and plaque from a metameric papilla; *E* – pulvillus and plaque from the hind part of the metameric section of the metasoma; *F* – region of the girdles from the ventral, and, *G* – from the dorsal side; *H* – part of a girdle; *I* – toothed platelet in side view.

an – girdles; *ax* – ridge of the bridle; *c* – cephalic lobe; *co* – dorsal ciliated band; *da* – front teeth; *dp* – back teeth; *f* – keel of the bridle; *go* – genital papilla; *me* – membrane of plaque; *ns* – nerve furrow; *p* – cuticular plaques; *pa* – metameric papillae; *pa*¹ – non-metameric papillae; *pa*² – papilla lying behind the girdles; *pu* – pulvillus; *s*² – groove between the mesosoma and the metasoma; *sv* – ventral sulcus; *tc* – tentacular crown; *te* – external tentacle of the tentacular plate. (*A*, *B*, *C*, *D*, *E*, *F*, *G* – after Ivanov, 1957a.)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extends behind the bridle (Fig. 174*A*). The tentacular apparatus is very like that of *S. grandis*. The external free edge of the tentacular plate (Fig. 174*B*, *C*) is attached to the body in the mid-ventral line, but away from its attachment it turns outwards until the distal end of this part of the crown comes to lie on the right side, sweeping around the next turn of the spiral. As may be seen in transverse section the tentacular plate consists of 39–72 tentacles (up to 223 have been counted in *S. grandis*), and it makes three to four revolutions. The lophophore is much more feebly developed than in *S. grandis* and makes two or three revolutions in all. The tentacles of the internal turns of spire are arranged in a corkscrew along the surface of the lophophore and, as in *S. grandis*, the spiral is anti-clockwise, looked at from in front and starting from the outer free edge of the tentacular plate. On the inner side of each tentacle runs a dense line of fine, comparatively short pinnules, which, as a rule, all stick out into the narrow space between the successive turns of the tentacular spiral.

The fore-part of the body is divided from the trunk by a simple annular groove (Fig. 174*A*, *B*, *C*). The metameric part of the trunk is notable for its considerable length, while the succeeding non-metameric part is short (Fig. 16). The sharply marked ventral sulcus (Fig. 174*A*, *B*, *C*) continues to the end, or almost to the end, of the metameric part (Fig. 16). Usually there are 160–180 pairs of more or less paired adhesive papillae, situated on lateral ridges, but in one individual there were only 120–130. Their metamerism is not perfect; thus, in the individual illustrated in Fig. 16, the 15th papilla of the right side is opposite the 14th of the left side, the 76th opposite the 80th and the 125th of the right side opposite the 128th. The papillae are rounded and vary considerably in size. They bear flattened pulvilli (Fig. 174*D*), which in turn bear adhesive plaques. These latter are thin, oval cuticular scales, with a much thickened front edge. In the front part of the metameric region they measure 55–65μ across and in the hind part 75μ, and are thus only half the size of those of *S. grandis*. The dark-brown thickened front edge may take the form of a bow or hoop. The dorsal ciliated band is broad, with a firm edge (Fig. 174*H*). The genital papillae of the male are large and protuberant, overlapping the hind edge of the ventral surface of the fore-part of the body, and bear oblique slit-like genital apertures (Fig. 174*C*). The non-metameric part of the trunk, as stated above, is several times shorter than the anterior part (Fig. 16), whereas in most other Pogonophora the proportions are the reverse. On the ventral side a few scattered papillae may be found in this region, but their exact number cannot be stated because of the vague way in which the metameric part of the trunk turns into the non-metameric part.

The rather wide individual variation in their number is, however, very noticeable. Thus in one individual, for instance, there were about 15 such papillae, while in another there were not less than 50. There is no distinct zone of thickened papillae, and all the papillae of the whole preannular region have the same structure, while the plaques of the hinder part of this region are distinguished only by their slightly larger size.

The considerable predominance of the metameric over the non-metameric part of the trunk in *S. beklemischevi* is undoubtedly the result of the evolutionary process whereby the papillae have become increasingly more ordered in their arrangement (p. 21). It seems likely, moreover, that this feature may be shared by *S. grandis*, in which, however, the non-metameric part of the trunk has not been observed.

Two girdles, interrupted ventrally, but continuous dorsally, lie on feebly developed ridges (Fig. 174*F*, *G*). The yellowish elongate-oval toothed platelets are disposed in two to four rows in each girdle (Fig. 174*H*). The front end of the platelets is fractionally narrower than the hind end and the front group of teeth, though not big and occupying only a quarter to a fifth of the area of the whole platelet (Fig. 174*I*), is well developed. The platelets are 20–25μ long and 6–8μ broad.

The very long postannular section of the trunk (Fig. 16) usually starts with a sharp waist, which, however, is absent in a few individuals. Behind the girdles there is always a large ventral papilla with a plaque (Fig. 174*F*). Farther back the papillae, which lie only on the ventral side, are concentrated into transverse metameric rows, situated at more or less equal intervals (Fig. 16). There are five to seven papillae in each row, and here and there, between the rows, one may encounter solitary papillae. The plaques here are slightly curved, bow-shaped or rod-like.

The length of the animal, including the tentacles, may reach 13 cm. The parts of the body have the following dimensions: length of the tentacular crown, 7–10 mm; breadth of the crown, 1–1·3 mm; length of the fore-part of the body, 1·5–4 mm; breadth of the fore-part, 0·75–1·3 mm; length of the metameric part, 48·5–58 mm; length of the non-metameric part, 10–12 mm; length of the postannular region, 40–45 mm; overall length of the body 117–129 mm. *S. beklemischevi* is one of the least elongated of the Pogonophora, for its length is only a hundred times its breadth.

The flat, leaf-shaped spermatophores are much broader at the filamentar end and sharply pointed at the afilamentar end (Fig. 175). The basal part of the filament is rather stout for a considerable length. Around the broad end of the spermatophore extends a cortical zone free from sperm. The

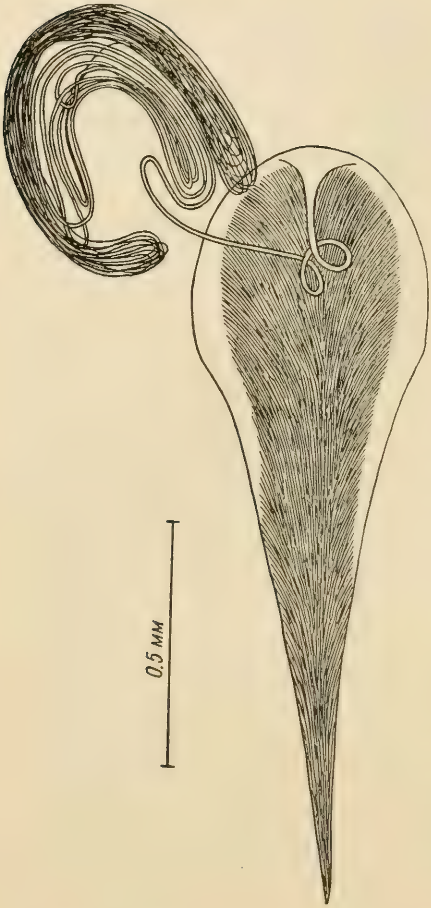

Fig. 175. *Spirobrachia beklemischevi*: Spermatophore. (After Ivanov, 1957a.)

spermatophores are 1·5 mm long and 0·5 mm broad at the widest part, and in general they are like those of *S. grandis*, but considerably smaller.

The mouth of the tube is a broad funnel with coarse stout lamellated walls (Fig. 176*A*). The funnel and the neighbouring parts of the tube are firm and light brown in colour. Then very quickly the tube becomes straw-coloured and the walls considerably thinner, flexible, and transparent (Fig. 176*B*). The surface of the tube is smooth and lustrous. In the hind third, the tube, though remaining transparent, gradually darkens until it is a dark brown; the walls become much thickened and acquire a considerable rigidity, but are still smooth and lustrous. Finally, near the hindmost end the tube becomes segmented, with segments exactly the same length as the tube's width (Fig. 176*C*). A peculiarity of the tube of *S. beklemischevi*, obvious at first glance when compared with other Pogonophora, is the relatively great length of tube which has a rather large diameter followed by the rapid taper of the hind end. Thus in one female in which the tube was 15·5 cm long the diameter at the front was 1·1 mm and at the hind end 0·45 mm, i.e. a taper of more than 40μ per cm, and a halving in thickness in less than 15 cm. To all appearances the maximum length of the tube is not less than 30 cm, the diameter across the funnel up to 1·75 mm, the diameter at the front end, just behind the funnel, up to 1·4 mm, and the diameter at the hind end 0·2 mm.

As may be seen in Table 7, the main diagnostic features of *S. beklemischevi*, as compared with *S. grandis*, appear to be the considerably smaller number of tentacles and the lesser development of the tentacular spiral and of the lophophore. Important distinctions from *S. grandis* appear also to be the absence of dorsal fusion of the keels of the bridle, the smaller plaques, the shape and size of the spermatophores, and the considerably smaller body size.

Material: many tubes, mostly containing animals.

Locality: Kuril Trench.

Depth: 9000–9050 m.

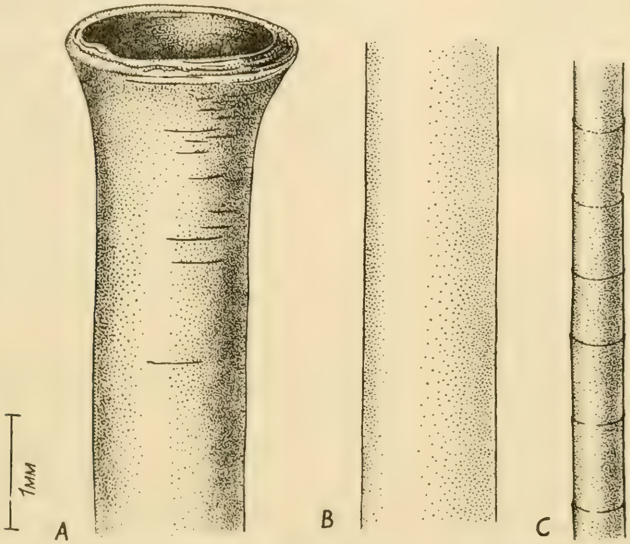

Fig. 176. *Spirobrachia beklemischevi*: Tube: *A* – front end; *B* – middle; *C* – hind part. (After Ivanov, 1957a.)

TABLE 7

Characteristics of the species of *Spirobrachia*

	S. beklemischevi	*S. grandis*
Number of tentacles	39–72	Up to 223
Length of tentacular crown (mm)	7–10	24–27
Number of turns of spire of tentacular plate	3–4	6–7
Number of turns of lophophore	2–3	3–4
Length of fore-part (mm)	1·5 –4·0	4·2–5·1
Breadth of fore-part (mm)	0·75–1·3	1·2 –2·5
Dorsal fusion of keels	—	+
Ventral meeting of keels	—	+
Length of metameric region (mm)	48–50	66
Number of pairs of metameric papillae	120–180	*c.* 220
Diameter of plaques of metameric region (μ)	55–75	110–190
Size of spermatophore (mm)	1·5 × 0·5	2·5 × 0·35
Maximum diameter of tube (mm)	1·4	2·8

Key for the identification of the species of Pogonophora from their tubes*

1 (74) The anterior part of the tube is flimsy, transparent, and very soft, with walls which collapse easily.

2 (5) For a considerable length of the tube there is a peculiar external layer, supporting coarse, circular fibres, and removable with a sharp scalpel.

3 (4) The diameter of the tube reaches 1 mm. Under the dark fibrous layer the wall of the tube is a transparent dark brown, with light, irregular, mainly transverse stripes *Birsteinia vitjasi* (p. 169).

4 (3) The diameter of the tube is not greater than 0·5 mm. Under the muddy-brown fibrous layer, the wall of the tube has short, irregular rings with light intervals between them. *Heptabrachia subtilis* (p. 342).

5 (2) There is no external layer of circular fibres. If fibres are present they do not form a separate layer. Sometimes there is a superficial felt-like layer.

6 (65) The tube is ringed for most of its length.

7 (24) Eye-catching brown circular fibres are present in the walls of the tube.

8 (9) The rings of the tube are formed exclusively from agglomerations of thickened fibres. *Siboglinum microcephalum* (p. 227).

9 (8) The rings of the tube consist of a dense substance, in which transverse fibres may run.

10 (11) The rings are colourless or whitish, and transparent. Many rings are incomplete or irregularly shaped and anastomosing with one another. Their edges are always even. The front part of the tube is segmented, and reaches a diameter of 0·35 mm. *Siboglinum taeniaphorum* (p. 257).

11 (10) The rings are yellow or brown and more or less opaque.

12 (13) The front part at least of the tube is segmented, with 6–7 rings per segment. The muddy-brown, regular rings are no longer than the diameter of the tube, which is 0·17–0·22 mm thick. *Diplobrachia japonica* (p. 371).

* The following species have been omitted from this key: *Oligobrachia ivanovi*, *Nereilinum murmanicum*, *Siboglinum inerme*, *S. macrobrachium*, *S. debile*, *S. timorense*, *S. veleronis*, *S. subligatum*, *S. concinnum*, *S. arabicum*, *S. silone*, *S. ceylonicum*, *S. exile*, *S. sumatrense*, *S. zanzibaricum*, *S. sergeevi*, *S. lacteum*, *Siboglinoïdes dibrachia*, *Heptabrachia talboti*, *H. celebensis*, *H. ctenophora*, *H. canadensis*, *Diplobrachia capillaris*, *D. southwardae*, *Sclerolinum sibogae*, *Polybrachia barbata*, *Krampolinum galatheae*, *Galathealinum brachiosum*, *G. arcticum* and *Lamellisabella minuta*.

13 (12) The tube is unsegmented.

14 (21) The rings are homogeneous.

15 (18) In the hind part of the tube the rings become double or triple.

16 (17) Side by side with double there are also triple rings. The diameter of the tube is 0·15–0·22 mm. *Siboglinum hyperboreum* (p. 236).

17 (16) There are no triple rings. The diameter of the tube is 0·12 mm. *Siboglinum pusillum* (p. 221).

18 (15) The rings in all parts of the tube are simple.

19 (20) The rings are very short, never more than one quarter the diameter of the tube, yellow or brownish. The diameter reaches 0·34 mm. *Siboglinum meridiale* (p. 231).

20 (19) The rings are long, but not longer than the diameter of the tube, coarse and dark brown or mud-coloured. The diameter of the tube is 0·28–0·32 mm. *Siboglinum japonicum* (p. 200).

21 (14) The rings in the hind part of the tube are inhomogeneous, i.e. consisting of irregular blotches of dark material with light irregular spaces between them. In the hind part of the tube the rings disintegrate into two or three secondary rings.

22 (23) For the greater part of the tube the rings are double. The length of the rings is much less than the diameter of the tube, which is about 0·1 mm. *Siboglinum tenue* (p. 238).

23 (22) Part of the tube has triple as well as double rings. The length of the rings is about equal to or only a little less than the diameter of the tube, which is about 0·2 mm. *Siboglinum bogorovi* (p. 244).

24 (7) The tube is not fibrous; if there are a few fibres then they are almost imperceptible.

25 (30) The rings are white or just slightly brownish. The walls of the tube are stout and rather soft (easily cut with a sharp scalpel). The rings are almost as long as or only a little less than the diameter of the tube.

26 (27) The diameter of the tube is 0·3–0·4 mm. *Siboglinum cinctutum* (p. 207).

27 (26) The diameter of the tube is about 0·2 mm.

28 (29) The rings are white, and in the front part of the tube just a little narrower in the middle. The diameter of the tube is slightly more than 0·2 mm. *Siboglinum vinculatum* (p. 203).

29 (28) The rings are just noticeably brownish, and not constricted in the middle. The diameter is a little less than 0·2 mm. *Siboglinum frenigerum* (p. 213).

30 (25) The rings are mud-coloured, or more or less colourless, but not white. The walls of the tube are not stout, but dense.

31 (34) The length of the rings is not more than one quarter the diameter of the tube, except that divided rings may reach one third the diameter of the tube.

32 (33) The rings are regular, complete and very short, recalling narrow barrel-hoops; their length does not exceed one quarter the diameter of the tube. The interval between successive rings is very large. *Siboglinum robustum* (p. 254).

33 (32) The rings are often irregular, incomplete or anastomosing with one another; their length rarely reaches one third the diameter of the tube which is 0·4–0·6 mm. *Siboglinum atlanticum* (p. 263).

34 (31) Most of the rings are longer than one quarter the diameter of the tube.

35 (42) The front part of the tube is segmented.

36 (37) There are 12–18 rings per segment. The anterior rings in each segment anastomose more or less tightly with one another. Along the greater part of the tube the rings come close together and partly fuse to form double rings. The diameter reaches 0·25 mm. *Siboglinum fedotovi* (p. 193).

37 (36) There are less than 10 rings per segment.

38 (39) In the hind part of the tube the rings anatomose in pairs by means of bridges, or coalesce forming secondary rings, whose length is a little more than half the diameter of the tube. There are usually seven rings per segment, rarely five or six. The diameter of the tube is 0·12–0·16 mm. *Siboglinum ekmani* (p. 185).

39 (38) The rings do not anastomose or coalesce.

40 (41) There are 3–9 rings per segment. The intervals between the rings in the front part of the tube are very narrow, like mere chinks. The diameter of the tube is 0·12–0·20 mm. *Siboglinum variabile* (p. 241).

41 (40) There are 8 rings per segment. The intervals between the rings are narrow but not chink-like. The diameter of the tube is 0·13–0·14 mm. *Siboglinum pinnulatum* (p. 190).

42 (35) The tube is unsegmented.

43 (46) The rings split into two or coalesce into double rings, forming secondary rings.

44 (45) The rings have even edges. Adjacent rings are divided by light intervals or run into one another. The length of the secondary

rings equals the diameter of the tube, which may be more than 0·2 mm. *Siboglinum weberi* (p. 181).

45 (44) The rings have uneven edges. Between the elements of the fused double rings are retained only sparse, irregular clear areas. The length of the secondary rings is no more than one quarter the diameter of the tube which is 0·6 mm. *Siboglinum plumosum* (p. 197).

46 (42) The rings are simple for the whole length of the tube.

47 (60) The rings are regular, with equal front and back edges.

48 (59) The diameter of the tube is not more than 0·5 mm.

49 (54) The diameter of the tube is not more than 0·15 mm.

50 (51) The rings are transparent, colourless or yellowish, with a glittering surface. The length of the rings is just a little more than half the diameter of the tube. The tube is very soft and thin-walled. *Siboglinum pellucidum* (p. 233).

51 (50) The rings are muddy-brown or yellowish brown and more or less opaque.

52 (53) The rings are equal in length, each one about half the diameter of the tube. *Siboglinum buccelliferum* (p. 224).

53 (52) The rings vary in length, but are never longer than the diameter of the tube. *Diplobrachia belajevi* (p. 376).

54 (49) The diameter of the tube lies between 0·2 and 0·5 mm.

55 (58) The diameter of the tube lies between 0·2 and 0·3 mm.

56 (57) The rings are dark brown, almost black, and about half to two thirds the diameter of the tube in length. *Siboglinum caulleryi* (p. 216).

57 (56) The rings are brownish or almost colourless, and almost equal in length to the diameter of the tube, but in part they may diverge to one side or other of this length. In the hind part of the tube the rings are only half to two thirds as long as the diameter of the tube. *Siboglinum norvegicum* (p. 251).

58 (55) The diameter of the tube is up to 0·45 mm. The rings are golden brown and their length is one third to a half the diameter of the tube. *Heptabrachia beringensis* (p. 347).

59 (48) The diameter of the tube lies between 0·5 and 0·7 mm. The rings are muddy-brown, some of them with darker edges. *Oligobrachia dogieli* (p. 155).

60 (47) The rings are irregular with uneven edges.

61 (62) The tube is up to 0·12 mm in diameter. The stoutish rings are brownish with reddish tints. *Siboglinum minutum* (p. 248).

62 (61) The diameter of the tube lies between 0·2–0·4 mm.

63 (61) The rings vary greatly in length. Generally in the front half of the tube, side by side with exceedingly short rings are found some which are several times as long as the diameter of the tube. Nearer the hind end of the tube the rings become more or less regular and not longer than the diameter of the tube, while the edges of some of them seem eroded. The diameter of the tube is up to 0·25 mm. *Heptabrachia gracilis* (p. 338).

64 (63) The rings are all more or less equal in length, and become very irregularly shaped in the hind part of the tube, whose diameter may reach 0·33 mm. *Heptabrachia abyssicola* (p. 335).

65 (6) The tube is not ringed; if there are any rings present they are only in the very hindmost part.

66 (67) The tube is white and elastic, and only the hindmost part may be dirty brown or blackish. It is segmented, and between the segments are narrow clear intervals. The diameter may be up to 1·6 mm and the length as much as 1·5 mm. *Zenkevitchiana longissima* (p. 388).

67 (66) The tube is dirty brown or black, firm and unbendable.

68 (69) There is no obvious segmentation. The diameter is about 1 mm. *Cyclobrachia auriculata* (p. 367).

69 (68) The tube is clearly segmented. The front edge of each segment has a filmy border forming a sort of funnel (sometimes not preserved).

70 (73) The diameter of the tube is not more than 1·2 mm. The surface of the tube is devoid of any felt-like layer.

71 (72) In the front part of the tube the funnel-shaped borders of the segments are placed very close to one another, looking almost like a pile of saucers. The diameter of the tube is 0·5 mm. *Polybrachia gorbunovi* (p. 400).

72 (71) In the front part of the tube the funnel-shaped borders of the segments are rather far apart. *Polybrachia annulata* (p. 394).

73 (70) The diameter of the tube is about 2 mm. The surface of the tube is covered with a felt-like layer. The funnels occur at frequent intervals. *Galathealinum bruuni* (p. 404).

74 (1) The front end of the tube is firm, with a funnel-shaped mouth.

75 (78) The tube is segmented.

76 (77) The length of the segments is rather less than the diameter of the tube, which is about 1·7 mm. *Lamellisabella johanssoni* (p. 429).

77 (76) The length of the segments is equal to or more than the diameter of the tube, which is 1·5 mm. *Lamellisabella ivanovi* (p. 434).

78 (75) The tube is devoid of segments or segmentation occurs only at the hind end.

79 (80) The tube is transparent. The front and back sections are brownish and firm. The middle section is thin-walled, flexible and straw-coloured. The diameter is not more than 1·4 mm. *Spirobrachia beklemischevi* (p. 450).

80 (79) The tube is opaque, stout-walled, more or less the same all along its length and dirty brown or black.

81 (82) The diameter of the tube is up to 2 mm. *Lamellisabella zachsi* (p. 423).

82 (81) The diameter of the tube reaches 2·8 mm. *Spirobrachia grandis* (p. 446).

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