

BRITISH MUSEUM (NATURAL HISTORY)

A SYNOPSIS OF THE SIPHONOPHORA

BY

A. K. TOTTON

assisted by

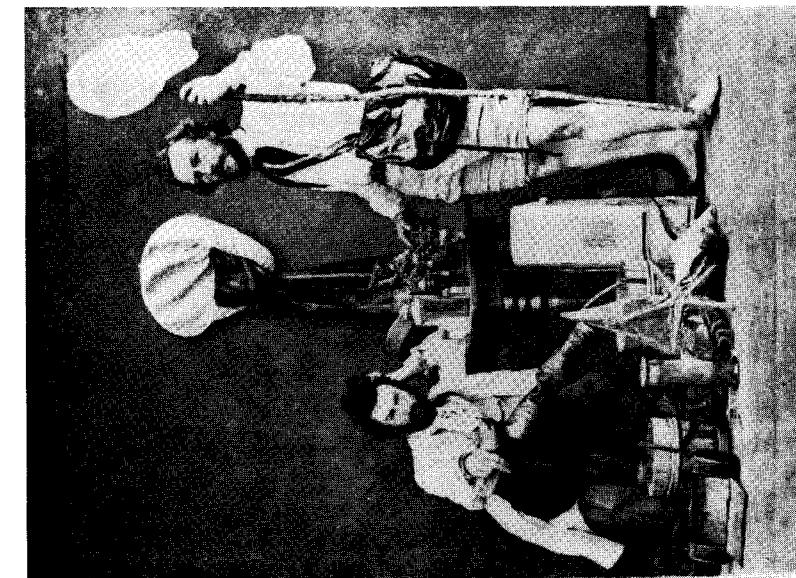
H. E. BARGMANN

With 153 figures in the text and 40 plates

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Frontispiece

OLD AND NEW METHODS OF COLLECTION



Left: Ernst Haeckel and Miklugo-Maclay at Lanzarote, Canary Islands, 1867. Haeckel is holding a Müller-net

Right: Aqualung divers of Professor Dubuisson's Collecting Expedition at Villefranche, 1963, with their leader. Aqualung divers use plastic bags for collecting siphonophores

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PREFACE

'In biology,' as Pantin (1963) has said, ' . . . the first essential is to know what you are talking about.' This synopsis attempts to show what actual species of siphonophora we have to deal with. To add to my own observations, I have tried to gather in one place the morphological descriptions contained not only in larger works but also in scattered papers.

The fact that some species have received more lengthy treatment than others is due to the opportunity that offered itself to make good some of the gaps in our knowledge of the Siphonophora. Very few species are well known.

Because the plate- and text-figures have been drawn from many different sources the lettering is not uniform. To re-letter them would have resulted in improvement of the general appearance of the illustrations, but would have entailed further delay.

The plates show the whole animal where possible in the Cystonectæ and Physonectæ, and the polygastric and eudoxid phases in the Calycophoræ.

I am very greatly indebted to Dr. Helene Bargmann for giving untiring help in organizing the account and for seeing it through the press.

A. K. TOTTON.

24 October, 1963

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INTRODUCTION

This synopsis attempts to gather together our knowledge of the anatomy and ontogeny of the various species of siphonophores, and to throw light on their characteristic organization and their probable origin. As this is a synopsis and not a full length monograph, no sections on Histology and Physiology have been included. Furthermore, there is no section on the distribution of the group, although in the course of sorting plankton collections, voluminous data on distribution have been recorded. But the completion of the synopsis has been considered a matter of some urgency, and therefore time and opportunity to work out these data have not been permitted to me.

The decision as to which so-called 'species' to include and which to exclude is based not so much on published descriptions, which are often inadequate for identification, as on my own knowledge of the animals themselves. For this reason I have given a rather longer treatment to some hitherto less well known forms on which I have been working in recent years. There are very few known species, individuals of which I have not examined myself, which are not represented in the unrivalled collection that I have built up at the British Museum (Natural History). It should be stated at once that the basis of the collection is the very extensive accumulation of plankton, still partly unexamined, made by the ships of the 'Discovery' Committee (collections now incorporated in the National Institute of Oceanography).

It should be borne in mind too that it has only been possible to review the vast literature at first-hand because of the proximity of the magnificent library at the Museum. It is fitting here to pay my tribute to the illustrious workers of the past in this special field. On the foundation of their pioneering work we are now able to build. Among living specialists from whose work I have profited most, I would mention especially Dr. H. B. Bigelow and his co-worker Dr. Mary Sears, and also Dr. E. Leloup. There seem to be all too few of these specialists to-day. This is due, no doubt, to the difficulty of obtaining adequate material. Vast collections of plankton, of which siphonophores generally constitute a large part, in Canada, America, England and elsewhere are still awaiting the attention of specialists, but unfortunately there seems to be no adequate organization for sorting this material. It is only exceptionally that comparatively complete specimens of forms other than diphyids are taken. In the majority of species there are still large gaps in our knowledge of the life-cycle.

The relatively few species of siphonophores fall obviously into one of three sub-orders:

- (1) Cystonectae Haeckel, 1888;
- (2) Physonectae Haeckel, 1888; and
- (3) Calycophorae Leuckart, 1854.

In order to understand the mature form of these complex marine animals, it is very necessary to look at their simple, larval or post-larval growth stages. I have spent some years searching for these larvae, both in the preserved plankton samples taken by the Royal Research Ships 'Discovery', 'Discovery II' and 'William Scoresby', as well as in tow-nettings I have made at Villefranche and off Lanzarote. On several occasions, not always successful, at Villefranche, I have tried to obtain larvae by fertilizing the eggs of various siphonophores.

My studies of larval and adult siphonophores, both alive and preserved, justify the recording of my conclusions about the general nature of these animals. First of all I will attempt a definition. The Siphonophora are holoplanktonic, asexual (larval) hydrozoan zooids or polyps that have a single tentacle, probably oral.* By giving rise to buds the zooids become asexual, larval nurse-carriers† (paedophores) of other polyps (larvae) and of the sexual (adult) medusoids as well as of other asexual (adult) medusoids (nectophores) that provide propulsion of the whole, or of separate parts, in all three sub-orders. The Order does not include the disconanth genera, *Velella*, *Porpema* and *Porpita*, in which there are no oral tentacles.

Thus a fully grown siphonophore is essentially an overgrown hydrozoan, oozooid polyp that remains juvenile and asexual, but carries around with it large numbers of other asexual, juvenile polyps (gastrozooids and palpons) as well as sexual adults (medusoid gonophores) and asexual adults (medusoid nectophores), all budded either from the original and often very much elongated oozooid, or from other juveniles. The adults may separate and become independent, usually in association with one or more of the secondary juveniles and with a protective buoyancy device (bract).

I first put forward this theory in 1960, in my 'Discovery' Report on *Physalia*, as the Paedophore Hypothesis. Furthermore, I think that the Siphonophora are only one of the groups of Hydrozoa, which have arisen during a comparatively recent radiation after a new type of neotenic organism, the actinula, had been evolved from the larvae of some proto-hydroid.

As far as I can ascertain from personal observation and a study of the vast literature, there are only about one hundred and thirty known species of Siphonophora. One can never be sure when and where to find living specimens. There are a few forms taken only once in the Canaries and off Ceylon by Haeckel, of which no preserved specimens are known, and which have never been seen again. In 1955 I followed in Haeckel's footsteps to Lanzarote, but was not lucky enough to find any of those particular, rare forms upon which he reported. The only 'Challenger' Expedition material still in existence consists of specimens of rhodaliids. I had never come across any other rhodaliid specimens until a few years ago the British Museum (Natural History) received from Dundee University one of the most perfect rhodaliid specimens known. Its great importance lay in the fact that it possessed bracts. The specimen had been lying at Dundee unknown to specialists for fifty years. An account of it (*Stephalia corona*) will be found on page 92.

The best known siphonophores, apart from *Physalia*, are those that can be found at the surface at places like Messina, Naples and Villefranche, generally at Villefranche after an upwelling of waters from about 200 metres to the surface.‡ The temperature of this upwelled water at say 20 metres in December is about 15·1 °C–16 °C, and the salinity about 37·8‰. This is one of the only clues we have to the conditions in which these animals live, apart from deductions made from the data given in 'Discovery' Station Lists where closing nets captured siphonophores.

Species found after upwelling in the Mediterranean include *Apolemia uvaria*, *Forskalia edwardsi*, *Physophora hydrostatica*, *Agalma elegans*, *Halistemma rubrum*, *Nanomia bijuga*, *Hippopodius hippopus*, *Rosacea cymbiformis*, and *Sulculeolaria quadrivalvis*. For similar knowledge about the rest of the siphonophores, except those that are commonly found near the surface in all oceans, like *Lensia subtilis*, *Chelophyses appendiculata*, *Sphaeronectes* spp. and *Abylopsis tetragona*, we are dependent upon closing net-hauls, in which, unfortunately, siphonophores usually occur broken into fragments.

* Libbie Hyman (1940, p. 370) disagrees.

† It is interesting to note that Kühn (1913) used the term 'Amme' (nurse) in connection with the polypoid phase in the Hydroida.

‡ See Halim, Y. (1959). *Observations sur l'hydrologie de la baie et du canyon de Villefranche-sur-mer*. *Vie et Milieu ix*, fasc. 3, 1958.

HISTORICAL REVIEW OF THE CHIEF WORKS ON THE ORDER

The phylum to which the Siphonophora belong is known to-day as Cnidaria, a name and group-conception introduced in 1888 by Hatschek, who excluded from it the Sponges and Ctenophora which had been included in Leuckart's (1847) group Coelenterata. Cuvier had already in 1817 separated the cnidarians as part of two out of the five classes of the last four primary groups, Zoophytes or Radiata, in the 1812 sketch of his celebrated arrangement of the animal kingdom, and in 1829 Eschscholtz had reorganized the various coelenterate groups included in Cuvier's third class, Acalephae. Eschscholtz separated the Ctenophora and Siphonophora, in the latter of which he still included the Chonodrophora of Chamisso & Eysenhardt, 1821, from the Medusae proper (Discophorae). He dealt with about twenty species of siphonophores. For every one of the one hundred and thirty years that have elapsed since Eschscholtz published his 'System', on an average not more than one new (good) species has been described.

Some other of the early detailed systematic work on siphonophores was done by Eschscholtz (1825-9), Risso (1826), Milne Edwards (1841), Vogt (1851, 1854), Leuckart (1847, 1851, 1853), Gegenbaur (1853a, b) and Kölliker (1853), all of them working on living Mediterranean forms at Nice, Villefranche and Messina. But, of course, many of the earliest names and figures are taken from the Atlases of Voyages of the older naturalists like Lesson (1826) (*Voyage . . . la Coquille*, 1822-25), Péron (1807) and Quoy & Gaimard (1824) (*Voyage . . . L'Uranie et la Physicienne*, 1817-20). We must also thank Sars (1846) and Will (1844) for early contributions. It was the latter's work which alone was available to Huxley during his voyage in H.M.S. *Rattlesnake* (1859). Further information about early work can be found in the bibliography of Haeckel (1888b). Others of the great siphonophore systematists, each publishing papers in the last hundred years, have been Claus (publications from 1860-89), A. Agassiz (1865-1902), Fewkes (1879-89), Haeckel (1887-8), Chun (1882-1913), Bedot (1882-1909), Schneider (1896-1900), Bigelow (1904-37), Lens & van Riemsdijk (1908), Moser (1917-25), and Leloup (1932-54).

It may be helpful to new students of the siphonophores to have some comments on the larger works of the last hundred years by one who has made a prolonged study of this group. It is interesting to note the gradual increase in the number of species dealt with by systematists. This rose from twenty-six (Huxley, 1859), thirty (Haeckel, 1888), thirty-two (Lens & van Riemsdijk, 1908), fifty-two (Bigelow, 1911) to fifty-seven (Moser, 1925). This number is about one-third of the species that we know to-day.

HUXLEY

I start with Huxley's 'Oceanic Hydrozoa' (1859), which dealt with twenty-seven siphonophores, three of which he had not seen, and four of which I cannot certainly identify. Like others before him, Huxley was struck by the simple sac-like form of the Hydrozoa, composed as they are of two membranes to which Allman (1853) had given the names ectoderm and endoderm. (O. & R. Hertwig (1882) showed that often a mesenchymal mesoderm separated the two.)

The first part of Huxley's work – sections 1 and 2 – dealt with the general morphology of the class Hydrozoa. The morphology of the siphonophores had, of course, been dealt with previously in some detail by Leuckart (1853, 1854) and by Gegenbaur (1854). Little need be said about Huxley's section

1 except his sub-section 7 (p. 16) on reproductive organs. He stated that throughout the Hydrozoa these consisted of *spermaria* and *ovaria*, portions of the tissue of the wall of the *hydrosoma* (defined on p. 2 as the 'entire double walled body of the Hydrozoan . . . (e.g.) an *Agalma* three feet long') and 'more particularly of the ectoderm metamorphosed into spermatozoa or ova'. They are found, he said, in *Hydra*, *Lucernaria*, in many medusae, in *Hydractinia*, *Coryne pusilla* and *Plumulariae* in their simplest form, as pouches or sacs (called gonophores by Allman (1859)) containing a diverticulum of the somatic cavity. 'The reproductive organs of both sexes in *Cordylophora*, the female organs of *Stephanomia*, *Agalma*, *Athorybia*, *Forskalia*, *Apolemia* and the male (*sic*) organs of *Physalia* exhibit,' he said, 'an interesting series of transitions from the simplest to the most complex condition of the genital apparatus in the Hydrozoa. For we find that in all these cases the reproductive organ is no longer simple, but that its investment has acquired more or less the structure of a nectocalyx, from whose walls those of the actual genital sac, the manubrium of Allman,* tend to become independent.'

Huxley said that he had identified in each order of Hydrozoa both sperms and eggs. The oocytes(?) measured from 0.004 inches to 0.005 inches in diameter. Fertilization in all those examined appeared to follow the description of Gegenbaur (1854) for Calycophorae and 'Physophoridae'. Huxley rightly appeared to doubt Gegenbaur's deduction that the larval nectophore in Calycophorae persisted as the distal (? posterior) one of the adult.†

Of ontogeny in 'Physophoridae' (Physonectae and Cystonectae) he said little was known except for some post-larvae of *Physophora*, *Forskalia* and *Agalma* described by Gegenbaur, and the larva of *Physalia* described by himself. He then proceeded to draw attention to the laws which in general govern the development of appendages upon the coenosarc. He compared the budding of new polypites, at or near the distal end in Hydroida with the budding on the proximal side of the old ones of new polypites, nectocalyses (nectophores) and reproductive organs and branches of tentacles of 'Physophoridae'; and of the same buds, excepting nectocalyses, in Calycophoridae, for instance in the Hippopodiidae.‡

Huxley outlined the simple development of gastrozooids and tentacles, palpons, nectocalyses (nectophores) and gonophores from buds. He repeated his idea, which seems now to be a mistaken one, that the course of evolution of gonophores has been towards the medusa stage instead of a regression from it. He cited only the Calycophorae and (footnote p. 27) *Agalma elegans* as the siphonophores which retain ('perfect') a free medusiform gonophore.

In section 2 Huxley summarized the seven ways in which these organs are grouped together in order to define seven groups of Hydrozoa, viz.: (1) *Hydra*, (2) Corynid hydroids, (3) Sertularian hydroids, (4) Calycophoran siphonophores, (5) Physophoran siphonophores, (6) Lucernariidae and (7) Craspedote medusae. As a scheme of classification to-day it is, of course, not good, particularly as it included Scyphozoa (Lucerneriidae) in the Hydrozoa.

Section 3 dealt with reproduction, and was written at the same time as Allman was preparing for publication two papers on the reproductive organs of the hydroids. Huxley adopted Allman's terminology as far as possible, though he made certain modifications in it. Twelve years later, Allman (1871)

* Allman evidently used the term gonophore originally for the gonadial tissue (in the form of a sac, for example, on the radial canal or stomach of a medusa). To-day, however, the term gonophore has come to denote a reduced or vestigial medusa. Even a sporosac is a reduced medusa, and it is not homologous with a gonadial pouch on the radial canal of a medusa as Huxley supposed. Allman in his Ray Society Monograph on the Hydroida (1871, p. 21, fig. 1) had introduced his generalized conception of a hydroid as if it were an adult, with a 'generative sac' emitted as an external bud from its side. By implication Allman seemed to suggest that a sac-like gonad evolved into a medusa. In fact the reverse is more likely to be true (see Libbie Hyman, 1940, p. 367). The regressive stages have been dealt with at length by Kühn (1913).

† We know now that in many it is caducous. I have evidence however, that it persists as the anterior nectophore in Abylidæ.

‡ The buds of new nectophores in *Hippopodium* arise from the foot stalks of the older ones, and in consequence they arise proximally and not distally as Huxley maintained. In my view those of physonects do the same thing, i.e. they bud from the foot stalks of predecessors.

published his large monograph of the gymnoblastic hydroids, in which he made much use of Huxley's terminology. Thus these two pioneers were working on Hydrozoa at about the same time and benefiting from one another's work. Allman's (1871) monograph is, of course, of equal value in studying the early history of any cnidarian, including that of the Siphonophora.

Huxley's fourth section dealt briefly with interesting historical facts: Cuvier's generic name *Diphyes*, and how he thought the two nectophores were two temporarily united animals, possibly in copulation; the setting-up by Eschscholtz (1829) of the group name *Siphonophorae* and three family names, *Diphyidae*, *Physophoriidae* and *Vellellidae*; and the proposal by Leuckart to substitute the name *Calycophoridae* for *Diphyidae* (invalid since there is no generic name *Calycophora*). Huxley realized, as did Sars, Vogt, and Leuckart, that special generic and specific names for eudoxid phases (which he called diphyozoids) were provisional, and would be suppressed in the course of further investigation. Then followed a summary of the classification and descriptions of the eighteen species of calycophoran siphonophores.

The fifth section dealt with the history of physonect and cystonect literature. As Huxley pointed out the systematic arrangement of these groups is beset with difficulties, which are partly due to the nature of the animals themselves, but still more to the confusion introduced by the mistakes of systematists. He mentioned the three distinct Mediterranean species dealt with by Forskål (1775) and four by Péron and Lesueur (1807), including *Stephanomia uvaria* Lesueur (?) 1811. He then recalled how Eschscholtz (1829) separated the last species and made a new genus, *Apolemia*, for it; united *Physophora rosacea* Forskål and *Rhizophysa heliantha* Q. & G. as *Athorybia rosacea*; changed the generic name of Forskål's *Rhizophysa filiformis* to *Epibulium* (thinking it must have had nectophores) and separated it from Péron's *Rhizophysa planestoma*, with which it is probably identical; and restricted the genus *Physophora*.

Huxley then recalled how Lamarck (1835-45) reunited Péron's *R. planestoma* and Forskål's *P. filiformis* as *Rhizophysa filiformis*, but in error included Forskål's *P. rosacea* (= *Athorybia*); set up the new physophorid genus *Agalma*; and wrongly included Quoy & Gaimard's *Hippopodius*, *Discolabe* (= *Physophora*) and *Physalia* in the family *Physophoridae*. Huxley eulogized Eschscholtz and said that his work was far ahead of Quoy & Gaimard, Lesson and de Blainville, the first two of whom he said introduced the most lamentable confusion.

Huxley next mentioned that the work of Milne Edwards (1841) and Sars (1846) inaugurated a new epoch in the study of siphonophores. Huxley succeeded in disentangling the '*Agalmopsis*' confusion of Sars and saw that Sars was dealing with two separate forms. This led him to restrict the name *Agalma* to forms whose tricornuate tentilla had a median sac and two lateral filaments, and to establish the new generic name of *Halistemma* for forms with unicornuate tentilla.

He then gave a systematic arrangement of the 'Physophoridae', i.e. Physonectae, Cystonectae and Disconantha, which appeared to him to be in accordance 'with our present knowledge'. The siphonophores were placed in six families, 'Apolemiidae, Stephanomiidae, Physophoriidae, Athorybiidae, Rhizophysiidae and Physaliidae'. Of the sixteen species listed under these families he then dealt systematically with eight physonects and two cystonects, as well as with the disconanths, *Velella* and *Porpita*. Subsequent changes in nomenclature result in the following list of siphonophores discussed and figured by Huxley:

TABLE I
Huxley's names

Modern names

A. Calycophorae

- Diphyes dispar* (Cham. & Eysen.)
- D. bojani* (Esch.)
- D. chamissonis* Huxley

- D. dispar*, *Eudoxia lessonii* (Esch.)
- Eudoxia bojani* (Esch.)
- D. chamissonis* sp.n.

TABLE I *continued*

Modern names	Huxley's names
<i>A. Calycophorae</i>	
<i>Chelophyses appendiculata</i> (Esch.)	<i>Diphyes appendiculata</i>
<i>Eudoxoides mitra</i> (Huxley)	<i>Diphyes mitra; Eudoxoides sagittata</i>
<i>Muggiae kochi</i> (Will)	<i>Diphyes kochii</i>
<i>Abylopsis tetragona</i> (Otto)	<i>Abyla pentagona</i>
<i>A. eschscholtzii</i> (Huxley)	<i>Aglaismoides eschscholtzii. A. elongata</i>
<i>Bassia bassensis</i> (Huxley)	<i>Abyla bassensis, Sphenoides australis</i>
<i>Enneagonum hyalinum</i> (Q. & G.)	<i>Abyla vogtii, Cuboides vitreus, Enneagonoides quoyi</i>
<i>Abyla sp.</i>	<i>Abyla trigona</i>
<i>Abyla sp.</i>	<i>Amphiroa alata</i> Lesueur
<i>Abyla ? sp.</i>	<i>Amphiroa angulata</i> sp.n.
<i>Ceratocymba leuckarti</i> (Huxley)	<i>Abyla leuckartii</i>
<i>Sphaeronectes gracilis</i> (Claus)	<i>Sphaeronectes köllikeri</i> gen. n., sp.n.
<i>Rosacea cymbiformis</i> (Chiaje)	<i>Praya diphyes?</i>
<i>Hippopodius hippocampus*</i> (Forskål)	<i>Hippopodius gleba*</i>
<i>Vogtia pentacantha*</i> (Kölliker)	<i>Vogtia pentacantha*</i>
<i>Sulculeolaria</i> sp.	<i>Galeolaria filiformis†</i>
<i>B. Physonectae</i>	
<i>Apolemia uvaria</i> (Lesueur)	<i>Stephanomia amphitridis†</i>
<i>Halistemma rubrum</i> (Huxley)	<i>Halistemma rubrum</i>
<i>Forskalia edwardsi*</i> (Kölliker)	<i>Forskalia edwardsii*</i>
<i>Agalma okeni</i> (Esch.)	<i>Agalma breve</i> sp.n.
<i>Physophora hydrostatica</i> (Forskål)	<i>Physophora</i> (sp. ?)
<i>Athorybia rosacea</i> (Forskål)	<i>Athorybia rosacea</i>
<i>C. Cystonectae</i>	
<i>Rhizophysa eysenhardtii</i> Gegenbaur	<i>Rhizophysa filiformis</i>
<i>Physalia physalis</i> (L.)	<i>Physalia utriculus</i> (Esch.).

† I have not identified Huxley's *Galeolaria filiformis* (posterior nectophore of *Sulculeolaria* sp.), nor his *Stephanomia amphitridis* (the siphosome only of a physonect). * Species not seen by Huxley.

This famous Ray Society monograph closes with Huxley's remarks on doubtful genera and species; a note on the terminology of hydrozoan organs; a bibliography; and twelve plates and their descriptions.

HAECKEL

It is a difficult task even for a specialist to sort out Haeckel's muddled classification, contained in his report (1888b) on the Siphonophora of the 'Challenger' Expedition, but this must be done before any discussion of his views on the morphology of the group can be appreciated. The difficulty is further enhanced by the fact that, as Lens & van Riemsdijk (1908) have already pointed out, 'of the Challenger siphonophores the British Museum contains no remnants other than a certain number of specimens of *Rhodalia miranda* Hkl. Of all the other species described in Haeckel's bulky volume – also of his own private collection – no traces are left'. Bigelow (1911b) went so far as to say (p. 176) 'Haeckel's monograph . . . with many new species beautifully figured but none of them critically studied from the systematic standpoint, cannot be used as a manual of the group'.

Haeckel divided the Siphonophora into four orders: Calyconectae, Physonectae, Cystonectae and Auronectae. The last of these was shown by Lens & van Riemsdijk (1908) and by Bigelow (1911b) to be a family of Physonectae. The following analysis of his classification of the Calycophorae may serve to illustrate the difficulties of working with Haeckel's system:

TABLE II

Haeckel's classification	Modern equivalent
<i>Class Siphonophora</i>	<i>Order Siphonophora</i>
<i>Order Calyconectae</i>	<i>Sub-order Calycophorae</i>
<i>Sub-order Monogastricae</i>	Eudoxid phase of species of Families: Diphyidae <i>pro parte</i> Abylidiae <i>p.p.</i> Prayidae <i>p.p.</i> Sphaeronectidae <i>p.p.</i>
<i>1st Family Eudoxidae</i>	Eudoxid phase of species of Families: Diphyidae <i>p.p.</i> Prayidae <i>p.p.</i> Sphaeronectidae <i>p.p.</i>
<i>1st Sub-family Diplophysidae</i>	
<i>2nd Sub-family Aglaismidae</i>	Eudoxid phase of species of Family: Abylidiae <i>p.p.</i>
<i>2nd Family Ersaeidae</i>	Eudoxid phase of species of Family: Diphyidae <i>p.p.</i>
<i>Sub-order Polygastricae</i>	Polygastric phase of species of Families: Diphyidae <i>p.p.</i> Abylidiae <i>p.p.</i> Prayidae <i>p.p.</i> Sphaeronectidae <i>p.p.</i>
<i>3rd Family Monophyidae</i>	
<i>4th Family Diphyidae</i>	Polygastric phase of species of Families: Diphyidae <i>p.p.</i> Abylidiae <i>p.p.</i> Prayidae <i>p.p.</i>
<i>5th Family Desmophyidae</i>	Polygastric phase of species of Family: Prayidae <i>p.p.</i>
<i>6th Family Polyphyidae</i>	Family: Hippopodiidae

Let us first consider the Calycophorae = Calyconectae Haeckel (*see* Table II). Following Lesson (1843), whom he said could not distinguish the natural groups critically, Haeckel made two sub-orders, the Monogastricae, for some forms which we now call the eudoxids or monogastric phases, and the Polygastricae, for those we now call the polygastric phases of the same animals, although as long ago as 1853 two men, Gegenbaur and Leuckart, independently had discovered the connection between the two phases, and although Haeckel himself had listed them on page 102 of his report.

If we now pass to the next systematic part of Haeckel's classification we find less difficulty in his treatment of the Physonectae, although he had the fixed idea that the pneumatophore represented the umbrella of a medusa – his Medusome Theory – and the reiteration of this hypothesis makes the descriptions difficult to follow unless it is disregarded.

He erected a special order, Auronectae, for forms that are now regarded as members of the physonect family Rhodaliidae, and of the eight families of his Physonectae the first two must be regarded with great caution: *Circalia stephanomia* (Circaliidae) has not been seen again – it might conceivably be a young Rhodaliid – and *Athoria larvalis* (Athoriidae) appears to be of very doubtful authenticity because of the sub-umbrella cavities said to be present at the tips of the bracts. Haeckel made the same claim for the bracts of the 'Athorula' larva of *Agalma elegans*; this has been dealt with by Garstang (1946), the so-called subumbrella or nectosac being merely a pocket of nematocysts, as anyone can see who examines this common larva. *Athoria larvalis* has not been seen again, and

Haeckel's *Athoria bractealis* is a *nomen nudum*. His third, fourth and fifth families, Apolemiidae Huxley, Agalmidae Brandt and Forskaliidae Haeckel still stand. *Nectalia loligo* (Nectaliidae) is, I feel sure, a juvenile form and not of generic or family significance. His family Discolabidae is now known as Physophoridae; in spite of Garstang's (1946) comments on *Discolabe*, I believe that there is only one physophorid, namely *Physophora hydrostatica*. Haeckel's last physonect family, Anthophysidae, is known as Athorybiidae.

Haeckel and others have stated that Cystonectae possess no nectophores. I have shown (1960) that nectophores are budded on the gonodendra of *Physalia physalis* and *Rhizophysa* species, though none are budded directly from the proximal part of the cystonect oozooid as in most Physonectae. Haeckel's English text says that the only 'organ of swimming' is the large apical pneumatophore. I think that the translator should have said 'organ of floatation'.

In Haeckel's treatment of the Cystonectae, he recorded how the species included in this group had not been separated from the Physonectae until the year 1835 when Brandt had then set up two sub-families: 1. Rhizophysidae for two species of *Rhizophysa*, one of which Brandt called *Epibulia*, and 2. Physaliidae (which we now consider to contain a single species *Physalia physalis*). Haeckel dealt with the three species of these two genera and a third, *Pterophysa conifera* Studer, as if there were thirty of them, grouped into fourteen genera. In addition to Brandt's two families, Haeckel erected three more, Cystalidae, Epibulidae,* and Salaciidae, all of which should be treated with caution. *Cystalia larvalis* might be a juvenile form of *Epibulia ritteriana*, in spite of the fact that its pneumatophore does not possess hypocystic villi. Haeckel's Salaciidae for *Salacia polygastrica* (*Salacia* was pre-occupied and *Salacella* was substituted by Delage & Hérouard in 1901) should be dropped. I have mentioned (1954) the difficulty of accepting *S. polygastrica*. Of Haeckel's rhizophysid genera, *Auropysa* and *Linophysa* are bathyphysids; *Cannophysa*, *Nectophysa* and *Pneumophysa* are synonyms of *Rhizophysa*. His three sub-families of Rhizophysidae, Cannophysidae and Linophysidae are therefore valueless.

Medusome Theory

The section (p. 21) headed 'Fundamental Form (Promorph)' begins with a discussion of the theories as to the organization of siphonophores. The two older interpretations which Haeckel thought to contain a mixture of truth and error are, of course, as Hadzi (1918), Garstang (1946), Leloup (1954) and other reviewers have mentioned, (1) the poly-person theory, held by most of the workers from 1848 to 1882, which regarded siphonophores as colonies of polyps, and (2) the poly-organ theory which, briefly, regarded the siphonophore organization as homologous with that of a budding medusa like *Sarsia prolifera*. After this discussion Haeckel then proceeded to expound his *Medusome Theory*. This theory (p. 3) was presumably based, without acknowledgement, on original views published twenty-three years earlier by Alexander Agassiz on dislocation of medusa parts (in A. Agassiz, 1865, p. 211). It is based on the false premise that all the parts of a physonect - float, nectophores, bracts, palpons, gastrozooids as well as gonophores (but not palpacles nor tentacles) - which were acknowledged as organs, are dissociated parts of a medusa or secondarily budded medusae. For instance, Haeckel added together the bract of a eudoxid (which probably represents a palpon) and a gastrozooid (both of them probably secondarily budded larvae) to form the umbrella and manubrium of a medusa or medusome. He thought that in siphonophores the constituent parts of an original medusa could exist as dissociated parts. He seems to mean three different things by 'medusomes': 1. medusoid gonophores; 2. sterile medusomes, eudoxids consisting of bract and gastrozooid but without gonophores; 3. any appendages except tentacles - all derived from medusae, sometimes by repetition or dislocation of parts.

* For a discussion of the 'Epibulidae', see page 44.

I have never seen a detailed criticism of the thirteen points of Haeckel's theory. Points 1, 2, 4, 6, 7, 8, 9, and 13 are grossly erroneous in statement of facts. Points 10, 11 and 12 are observational or terminological, and hardly find room in theory. Points 3 and 5 do not refer to *Siphonophora sensu stricto*. All thirteen points refer to larvae as medusae ('medusomes') and point 7 summarizes the theory in stating that 'all the parts which arise by budding from the primary larva of the Siphonophorae ("always a simple medusa", see point 1) are either medusiform persons or special organs of the same'.

It is really astonishing that Haeckel, who made a great study of medusae, should have concluded that the larva of *Physophora hydrostatica* was a medusa. It is not organized like one and the resemblance is very superficial. It is a particularly active little larva and was beautifully depicted by Vogt (1854); it occurs abundantly at Villefranche, where I have examined numerous living specimens (see text-fig. 47, p. 85) in various growth stages. I am convinced as the result of my own observations – Garstang (1946) had already drawn attention to Haeckel's mistaken deductions – that what Haeckel (1869) took for a split medusan umbrella is really the bract-homologue of a tentacle of an actinuloid larva.

Siphonula larva of the Siphonanthae (= Physonectae)

Haeckel erroneously called the siphonula larva 'medusiform' although he rightly says that it is bilaterally symmetrical. He said that 'the original circle of tentacles on the umbrella-margin had disappeared; in all cases only a single capturing filament (Fangfaden) persists, the *primary unilateral larval tentacle*, which in consequence of the ventral umbrella-cleft has been shifted centripetally to the base of the gastral tube. The primary umbrella itself (Protocodon) has, in consequence of this unilateral development, become bilateral; it develops in the Calyconectae (or Calycophoridae) into the primary swimming-bell, in the other three orders (Physonectae, Cystonectae and Auronectae) into the pneumatophore' (pp. 5–6).

As to the 'ventral umbrella-cleft', Haeckel mistook the larval bract of *Physophora* – homologous with an actinuloid tentacle – for the cleft umbrella of a medusa. What he called the 'primary umbrella (Protocodon)' is really the pneumatocyst, which in *Physophora* he wrongly thought was part of the bract – an error of observation.

The only significant and true facts that he gave about the siphonula larva are: (1) the different siphonulas are very similar; (2) the primary gastrozooid develops into the stem (there are no mono-gastric physonects) from which all the other persons of the colony proceed by lateral budding; (3) the 'whole structure . . . suggests the closest relationship with the Anthomedusae, and especially with the family Codonidae'; some of his reasons for this opinion are perhaps unsound, for instance that this relationship is corroborated by the marked tendency of many Anthomedusae to form medusa by direct budding from the gastral tube.

Corm and Cormidia

Under this heading Haeckel made the rather misleading suggestion that siphonophores are pre-eminently characterized by the development of a 'corm' or colony composed of several 'individuals proper'. Many people have erroneously thought a siphonophore arose from the union of separate individuals. In fact Haeckel himself talked of a *Cormus compositus* 'formed from the union of several individual groups of persons'.

'Ordinate Cormidia, Dissolved Cormidia'

Haeckel defined *ordinate cormidia* as 'metameres of the jointed stem or cormaxis', and by *dissolved cormidia* he meant those individual gonophores, for instance in *Agalma elegans* which appear to bud separately from the stem, instead of forming part of a complex gonodendron, as for example in

Physalia. I believe that this sort of phenomenon is due to a secondary masking of a more primitive arrangement, as Haeckel seemed to suggest.

Dislocation and Multiplication of Organs

This section starts with the proposition 'If our medusome theory is correct'. It is not! We need not follow his deduction from this false premise that nectophores, bracts and groups of palpons are replacement organs. However, he made the sound statement that he viewed each separate gonophore as a medusoid person which has lost mouth-opening and tentacles.

Haeckel then returned to the question of cormidia, 'monogastric and polygastric'. Here he introduced, as he loved to do, some rather useless terms not used since: Eudoxome, Ersaeome, Rhodalome, Athorome and Crystallome, all for cormidia which are either set free or not. One category, Ersaeome, is interesting since this type (which we now call an eudoxid) bears a 'special swimming-bell', i.e. an asexual medusoid.

Stem or Trunk

Here Haeckel compared a siphonophore with a hydroid, starting with the false premise that the siphonophore 'body' is a medusoid person. He rightly said that it was not logical to describe the stem of the Siphonophora as 'unbranched', but that forking or dichotomous ramification is absent.

Nectosome and Siphosome

This section contains the shocking suggestion that the nectosome in general represents the umbrella of a simple medusoid person and that the siphosome is the manubrium.*

Nectosomes of the Five Orders

Here the translator has not done Haeckel justice by writing of the pneumatophore as the 'swimming-bladder' instead of the 'float-bladder'. Although Haeckel correctly stated that a nectophore is the umbrella of a hydromedusa, he is quite wrong in stating that the pneumatophore is an invaginated and much modified umbrella. Garstang (1946) pointed out this error. Haeckel described briefly the arrangement of nectophores and pneumatophore in his five sub-orders. In his last sub-order, Auronectae, which we now regard as a family (Rhodaliidae) of the Physonectae, he gave an erroneous interpretation of the 'aurophore'. Lens & van Riemsdijk (1908) gave the correct one (see p. 91).

Nectophores or Swimming-bells

Haeckel gave a simple description of structure, followed by a bad interpretation in terms of his 'Medusome Theory'.

Pneumatophore or Swimming-bladder

Haeckel gave a simple description of the morphology, nomenclature and origin and went on to say that it is on the presence in some physonects of septa uniting the endoderm of the pneumatocodon and the pneumatosaccus that Metschnikoff (1874) based his opinion that the entire air-chamber is to be regarded as an invaginated swimming-bell. Haeckel himself stated that the radial pockets between the septa represent the radial canals of a simple medusoid umbrella; this view is quite erroneous. He added that Leuckart (1875),† Claus (1878) and Chun (1887) regarded the 'air-chamber' (pneumatophore) as an independent medusoid person supposed to originate as a bud from the primary larva, which it certainly does not do. The antithesis between these two opinions culminates in the

* I traced the origin of nectosome and siphosome and discussed their significance in 1956 in a description of the ontogeny of *Agalma elegans* to which the reader is referred.

† I cannot trace this reference.

interpretation of the air-sac, he said. According to the first theory, the air-sac (*pneumatosaccus*) is the *exumbrella* of a medusoid disc, according to the second it is the *subumbrella*. The latter opinion, Haeckel rightly thought is entirely erroneous, the former in a certain sense admissible. In the siphonula larva of the physonects the air-sac lies excentrically beside the apex. The whole pneumatophore is not, he said correctly, a secondary medusoid person, but the modified disc of the primary medusoid larva. But, of course, the larva is not medusoid.

Aurophore or Air-bell

In this short section Haeckel stated correctly that the air-bell is a voluminous gas-gland, but he was mistaken in thinking that it had developed out of a medusiform swimming-bell.

Siphosome or Nutritive Body

Haeckel made some erroneous statements in this section. He claimed a great distinction between what he called monogastric siphonophores which he said have no gastrozooids other than the protozooid – I do not know of any such forms – and the rest of the siphonophores, polygastric. He was quite mistaken in thinking that the mouth of the protozooid rarely persists, and that the protozooid itself does not survive. In my experience it is only missing from damaged specimens. He then interpreted *stem* – bracts, gonophores, gastrozooids, palpons and ‘gonostyles’ – in terms of (1) the polyorgan, (2) the poly-person and (3) his Medusome Theory. All three interpretations are in my opinion wrong.

Siphons or Suctorial Tubes

Haeckel also called these gastrozooids and this is what we call them to-day. His description is simple, but of the two alternative interpretations the first – that a gastrozooid is homologous with an entire polyp – is sound; the second – that it is homologous with the manubrium of a medusa – is false.

Monosiphoniae or Monogastric Siphonophores

Haeckel here included the eudoxid phases of Calyconectae, but these are really separated groups of secondary buds of polygastric forms. He said that monogastric forms (unspecified) might be regarded as ‘sexually mature larvae’ (neotenic) but, in true Haeckelian form, that ‘in more accordance, however, with the phylogeny is the reverse interpretation, that those larvae of the Polysiphoniae repeat according to the fundamental biogenetic law, the structure of their Monosiphoniae ancestors’.

Polysiphoniae or Polygastric Siphonophores

We read more about Haeckel’s interpretation of the budding of the secondary gastrozooids in this section. His statement that they arise from the ventral middle line of the primary siphon is sound, but he soon introduced his Medusome Theory to confuse what is, otherwise, a simple description of the formation of cormidia and eudoxids. He pointed out that the secondary stem-bracts are subordinate organs, though he had erroneously homologized the primary ones with the umbrella of medusae.

Palpons or Tasters

Haeckel made a distinction between palpons, which he said, wrongly in my experience, are mouthless, and cystons which he deals with in a short section, ‘*Cystons or Anal Vesicles*’, which follows. Palpons he claimed, are distinguished by (1) the absence of a distal opening, (2) by the absence of glandular villi and hepatic stripes in the stomach region. He thought their function is mainly if not exclusively, sensory. Here he repeated an error of observation in his description of the palpons of *Athorybia*: he reported the presence of a lens in a sickle-shaped pigment spot on the upper surface

of the apex and which he calls an *ocellus*. I have failed to see this structure in the only species of *Athorybia*, but I did observe at Villefranche in a living specimen of *A. rosacea* some metacercariae that Haeckel may have mistaken for lenses. Then follows a speculation on the otocyst function of the distal part of the palpon of 'some Agalmidae', in which a crystalline otolith is kept in rotary movement by a ciliated epithelium. This rotary movement I have often seen in palpons of *Forskalia edwardsi*, but I do not believe that any siphonophore produces otoliths or otocysts.

Cystons or Anal Vescicles

I doubt if special palpons can be distinguished for this category with which Haeckel dealt next. I have observed the tips of palpons in *Nanomia bijuga* flatten out and with a peristalsic-like movement eject granules from the opened distal end. I have reported (1960) on palpons of *Physalia* with opened tips. Normally the tips are closed and there is no sign of a potential opening.

Tentacles or Capturing Filaments. Palpacles or Tasting Filaments

It is not until we read these two sections that we are told of the usual arrangement of lateral branches or tentilla on the tentacles of the gastrozooids, and the simple palpacles of the palpons. Haeckel did not suggest what I believe to be the truth either that gastrozooids are more highly evolved palpons or *vice versa* that palpons are reduced gastrozooids. In *Apolemia* tentacles and palpacles are alike.

Bracts or Covering Pieces

These are interpreted in terms of the Medusome Theory as (1) displaced, (2) reserve, (3) partial umbrellas of medusoids. Haeckel talked of the direct transition of nectophores into bracts to be observed in the 'Athoriidae' and Anthophysidae. The whole interpretation is erroneous as pointed out by Garstang (1946). The section closes with a mention of the apophyses of the bracteal canals of Calycophorae. The homologizing of the four apophyses in the various bracts of different genera is a matter of considerable interest, but is not mentioned by Haeckel.

Gonostyles or Reproductive Stalks

Here Haeckel discussed a subject about which there are still differences of opinion. He added in brackets (Blastostyles, Gonoblastidia, Gonodendra, Klinozoooids). He began by saying that the 'gonophores or "medusiform reproductive persons" of the Siphonophorae sometimes develop directly . . . as buds on the gastral wall of the primary siphon or stem'. 'Much more frequently' he added, 'the buds arise from the stomach-wall of secondary polypoid persons . . . better designated sexual palpons. . . . These sacs frequently branch . . . so that the numerous gonophores . . . form large clustered masses (. . . gonodendra).' He used the term *Strophogenesis* for this relation of medusoid buds to the polypo-persons in terms of the poly-person theory, and called each gonostyle a medusa-manubrium in terms of the poly-organ theory.

Gonophores or Reproductive Persons (Sexual-Medusoids, Gonozooids)

Haeckel did admit in this penultimate section of his general introduction that 'among all parts of the siphonophoral organism, the gonophores are always those members which most distinctly preserve the original character of the medusoid person'. Haeckel rightly compared the siphonophore medusoids with codonid medusae, and points out that reduction to sporosacs often takes place. He said most siphonophores are monoecious but that others are dioecious. Among the monoecious he distinguished monoclinous and diclinous forms in respect of individual cormidia. His statement that some gonodendra are distylic, the basal part of the single branched gonostyle bearing female and the distal part male gonophores, needs careful checking. He added that gonophores which form both spermatozoa and ova are not known.

Fundamental Form (*Promorph*)

This final section does not appear in his paper in *Zeitschrift für Naturwissenschaft*, Jena 22 (1888a). He first mentioned that radial structure is found in the gonophores, and that bilateral structure occurs in all siphonophores proper. This bilateral arrangement he claimed 'is partly inherited from the bilateral Medusae, which we regard as the ancestors of the Siphonanthae (*Protomedia*) . . . but partly the bilateral type is produced by adaptation . . .'. 'To get a clear conception of these difficult promorphological relations, we must distinguish' he said, 'firstly the fundamental forms of the entire cormus and of the single persons . . . and secondly the different promorphological development in the two independent legions of the Class, the Disconanthae and the Siphonanthae'. In his sub-section 'Promorph of the Corms in the Siphonanthae', he gave a simple description of a siphonanth (physonect) larva – obviously that of *Physophora hydrostatica*, but mistakenly in terms of his Medusome Theory referred to its 'manubrium' (protozooid) and its 'primary umbrella' (bract) with 'its deep ventral cleft'. He then defined its different axes. In all this discussion of 'difficult promorphological relations' Haeckel remarked rather amusingly, if I may say so without irreverence, that the 'bilateral promorph of the Siphonanthae (has been) very unnaturally described by many authors'. (!) In his short discussion on orientation he erroneously stated that the larval nectophore of a calyconect occupies the apical pole. As to the distinction between right and left he claimed that it is clear when the ventral side is defined. To me it appears that it is also necessary to define anterior and posterior, which Haeckel failed to do. No wonder then he complained that the right and left halves are 'often confounded by different authors and described in striking contradiction'. Haeckel did, however, call the upper, pneumatophore pole of a physonect apical and the opposite one basal. I have always been taught to regard the oral end as anterior. His last words contain – alas – the erroneous statement that the radial pouches of a physonect-float are comparable to the radial canals of a medusa.

Before starting on his *Description of the Families, Genera and Species* Haeckel gave a 'Definition of the Class' in which, of course, he included the Disconanthae. I have suggested a new definition on page 2.

LENS & VAN RIEMSDIJK

This report by Lens & van Riemsdijk (1908) on the Siphonophora of the 'Siboga' Expedition with its rather crude illustrations dealt with thirty-two good species, mostly under synonyms of current names; ten of them were new, two indeterminate. It may, therefore, be useful to give in parallel columns the authors' and the current names.

TABLE III

Modern names	Lens & van Riemsdijk's names
1. <i>Chelophyes contorta</i> (L. & v. R.)	<i>Diphyes contorta</i> sp.n.
2. <i>Diphyes dispar</i> (Cham. & Eysen.)	<i>Diphyes dispar</i> Cham. et Eys. <i>D. Nierstrassii</i> 'sp.n.' <i>Diphyopsis campanulifera</i> Q. & G. <i>Ersaea lessoni</i> Huxley <i>Diphyopsis anomala</i> 'sp.n.' <i>Diphyes indica</i> 'sp.n.' <i>Diphyes (Diphyopsis) Malayana</i> 'sp.n.' <i>Diphyes (Diphyopsis) Gegenbauri</i> 'sp.n.' <i>Doromasia pictoides</i> 'sp.n.' <i>Ersaea bojani</i> Esch.
3. <i>Diphyes bojani</i> (Esch.)	<i>Diphyopsis diphycoides</i> 'sp.n.' <i>Eudoxia campanula</i> Hkl.
4. <i>Eudoxoides mitra</i> (Huxley)	<i>Diphyes (Diphyopsis) subtiloides</i> sp.n.
5. <i>Lensia subtiloides</i> (L. & v. R.)	<i>Galeolaria quadrivalvis</i> Les.
6. <i>Sulculeolaria quadrivalvis</i> (Blain.)	<i>Galeolaria biloba</i> M. Sars
7. <i>Sulculeolaria biloba</i> (Sars)	

TABLE III *continued*

Modern names	Lens & van Riemsdijk's names
8. <i>Sulculeolaria monoica</i> (Chun)	<i>Galeolaria monoica</i> Chun
9. <i>Sulculeolaria chuni</i> (L. & v. R.)	<i>Galeolaria Chuni</i> sp.n.
10. <i>Enneagonum hyalinum</i> (Q. & G.)	{ <i>Halopyramis adamantina</i> Chun <i>Cuboides adamantina</i> Chun
11. <i>Abylopsis tetragona</i> (Otto)	{ <i>Abyla pentagona</i> Q. & G. <i>Aglaisma cuboides</i> Lkt.
12. <i>Abylopsis eschscholtzii</i> (Huxley)	<i>Abylopsis quincunx</i> Chun
13. <i>Bassia bassensis</i> (Huxley)	{ <i>Abyla bassensis</i> Huxley <i>Sphenoides australis</i> Huxley
14. ? <i>Abyla trigona</i> (Q. & G.)	{ <i>Abyla trigona</i> Q. & G. <i>Amphiroa alata</i> Les.
15. <i>Abyla haeckeli</i> (L. & v. R.)	<i>Abyla Haeckeli</i> sp.n.
16. <i>Ceratocymba leuckarti</i> (Huxley)	{ <i>Abyla leuckarti</i> <i>Ceratocymba asymmetrica</i> 'sp.n.'
17. <i>Ceratocymba sagittata</i> (Q. & G.)	<i>Diphyabyla Hubrechti</i> 'gen.n.' and 'sp.n.'
18. <i>Clausophyes galeata</i> L. & v. R.	<i>Clausophyes galeata</i> gen. et sp.n.
19. <i>Chuniphyes multidentata</i> L. & v. R. V.	<i>Chuniphyes multidentata</i> gen. et. sp.n.
20. ? <i>Rosacea plicata</i> (?Q. & G.) (Bigelow)	? <i>Lilyopsis diphyses</i> Vogt.
21. [sp.indet.]	[? <i>Praya maxima</i> Ggbr.]
22. <i>Hippopodius hippocampus</i> (Forskål)	<i>Hippopodius luteus</i> Q. & G.
23. [Forskalia sp.indet.]	[<i>Forskalia contorta</i> M. Edw.]
24. <i>Forskalia edwardsi</i> (Köll.)	<i>Forskalia edwardsi</i> Köll.
25. <i>Erenna richardi</i> (Bedot)	<i>Erenna Bedoti</i> 'sp.n.'
26. <i>Halistemma cupulifera</i> L. & v. R.	<i>Halistemma cupulifera</i> sp.n.
27. <i>Physophora hydrostatica</i> (Forskål)	<i>Physophora hydrostatica</i> Forskål
28. <i>Athorybia rosacea</i> (Forskål)	<i>Anthophysa formosa</i> Fewk.
29. <i>Archangelopsis typica</i> L. & v. R.	<i>Archangelopsis typica</i> gen. et. sp.n.
30. <i>Rhizophysa filiformis</i> (Forskål)	<i>Rhizophysa filiformis</i> Forskål
31. <i>Rhizophysa eyenhardti</i> (Ggbr.)	<i>Rhizophysa Eysenhardtii</i> Ggbr.
32. <i>Pterophysa grandis</i> (Fewk.)	<i>Pterophysa grandis</i> Fewk.
33. <i>Pterophysa studeri</i> L. & v. R.	<i>Pterophysa (Bathyphysa) Studeri</i> sp.n.
34. <i>Bathyphysa sibogae</i> L. & v. R.	<i>Bathyphysa Sibogae</i> sp.n.
35. <i>Physalia physalis</i> L.	<i>Physalia utriculus</i> Lamartinière

The authors suppressed Haeckel's 'order' *Auronectae*, having demonstrated that the aurophore was only an evaginated part of the pneumatophore. They took the trouble to examine any specimens of former expeditions that had been preserved, as well as live specimens at Naples while undertaking the work, but the report is mostly of a descriptive nature and gives the impression that it was the authors' only experience of the animals. Nevertheless we owe descriptions of ten new species to them and some important observations on *Erenna*, which have enabled me to add more to what was known of these animals. They took great pains to seriate developmental stages of *Agalma okeni*, to which they referred as *Crystallomia* sp., and they published useful information on bathyphysids.

BIGELOW

Of Bigelow's (1911b) report on the Siphonophores of the 'Albatross'; the first thing to be said of course is that it is the most useful single systematic report on the siphonophores that has ever been written; and that the figures are superb. It deals with fifty-two species, about one-third of those now known. It is a key-work for checking synonymies and references to all works up to that date, and contains reviews of past work under each sub-order and family, and a section on geographical distribution.

It must be read in conjunction with his later work, especially his joint report (1937) with Dr. Mary Sears on the 'Thor' expedition to the Mediterranean, where he modified his earlier scheme for

placing in one group all the Calycophores with a single nectophore. This 'Thor' report contains some of Bigelow's most beautiful siphonophore drawings, and it is here that can be found Bigelow's final scheme of classification. The 'Albatross' descriptions and figures of each species are most valuable, though inevitably there have taken place some of those annoying changes in nomenclature. My only comments on Bigelow's section (p. 267) on the 'Physophorae', to which he did not add in subsequent papers, are (1) that the Anthophysidae should be referred to as Athorybiidae, because of past confusion between *Anthophysa* and *Athorybia*. On pages 268-9 I think that the identity of the genus named *Athorybia* is really *Melophysa* and that of '*Anthophysa*' is *Athorybia* as properly understood; and (2) that *Nectalia* Hkl 1888 probably refers to a juvenile growth stage of an Agalmid, so that no special sub-family or family group is needed. We really know rather less about physonects than about other siphonophores. Bigelow's subsequent work (1913, 1918, 1919, 1931, 1937) must also be studied in conjunction with his 'Albatross' report. I doubt if we shall see its like again.

MOSER

Another important and more recent work on siphonophores is the bulky volume by Fanny Moser on the specimens brought back by the German South Polar Expedition, sent to press in August 1914 but not published until 1925. It is concerned chiefly with the Calycophorae, of which she described nine new species, one of them *Diphyes antarctica*, confined to the Antarctic, but also contains descriptions of at least two new physophores, both Antarctic forms, *Stephanomia convoluta* and *Pyrostephos vanhoffeni*. Hitherto no work had been published on antarctic siphonophores.

Ninety-two of the four hundred and fifty-three pages that deal with siphonophores proper are taken up with general considerations of terminology, ontogeny, classification and phylogeny. Garstang (1946) has already published adverse criticisms of parts of those sections which were repeated in Kükenthal's Handbuch der Zoologie (Moser, 1924b). Nevertheless there is a great deal of information contained in the systematic part and in that dealing with distribution. Moser described about one-third of the species that we know to-day, fifty-one calycophores and six physonects. I am unable to do full justice to her report because of the paucity of my knowledge of the German language. Her comment on Haeckel's (1888b) monograph was (Haeckel's) 'Arbeit bildet auch heute noch einen Markstein in der Siphonophoren-Forschung'. In an interesting supplementary note dated February 1920 (p. 498) Moser (1925) recorded how in the interval that had taken place since finishing her work in February 1914, three of the remaining great authorities on siphonophores, Chun, Metschnikoff and Haeckel had passed away, leaving only Bigelow, who fortunately is still with us as I write this, thirty-four years later. I have been unable to ascertain what was the subsequent fate of Dr. Fanny Moser; nor do I know what happened to her report on Doflein's collection of siphonophores from Japan which she had begun, but feared (as she stated) might never be finished.

GARSTANG

The most important contribution to the understanding of siphonophore morphology and relationships made in Garstang's (1946) characteristically stimulating paper appear to me to be as follows:

The general direction of siphonophore evolution has probably been from Cystonectae with a large float and no nectophores (in the usual sense) —> Physonectae with nectophores and a small float —> Calycophorae with nectophores and no float. Garstang suggested that through atrophy the calycophore larva may have discarded a previously possessed float in favour of a precocious nectophore.

He visualized the phylogeny of siphonophores as having passed through three stages, comparable with those found in other groups, which originated from sessile stocks and became pelagic, e.g. Hydromedusae and Tunicata. These stages are (1) a locomotory larva, which metamorphoses into

fixed adult, which buds; (2) the addition of yolk to the egg leading to postponement of fixation and precocious larval budding; and (3) fixation abandoned, metamorphosis abbreviated and production of a nondescript oozooid nurse-carrier of secondary larvae which produce adults. He stated (p. 134) 'that there are grounds for thinking that a sequence of this kind has profoundly affected the character and organization of Siphonanth colonies. For budding begins in the earliest larval stage, the eggs of all Siphonanths are exceptionally large, and in Physophores only one egg is produced at a time – a feature which in Hydroids is associated with the formation of Actinula larvae. . . . It seems possible, therefore, that the original larva of Siphonanth ancestors was not a Planula but an Actinula, and that the Planuloid appearance of Siphonanth larvae is due to the precocity of budding before the typical Actinuloid characters have developed'.

This assumption led Garstang to suggest (p. 144) that siphonophore bracts are 'neither modified polyps nor modified medusoids, but represent the persistent tentacles of the original Actinula larvae more fully adapted for the locomotive and other functions (protective) which . . . they discharge'. Garstang revived Schneider's (1896) hypothesis that the primary (larval) bract, already verging on disappearance, in physonects, became secondarily fused with the larval nectophore in the Calycophorae, and he deduced that in the earliest stages of their history calycophores, as well as physonects, possessed larval bracts, probably before nectophores were evolved.

With increasing precocity, the first or larval bract was transformed into a transitory gelatinous shield over the budding area and in physophores the locomotor function was handed over to its successors (nectophores), while in calycophores, locomotive bracts became superfluous, and the primary bract was incorporated in the nectophore. I myself am inclined to think that in physonects the precocious bract was suppressed by the precocious nectophore *on that side*, so that the definitive nectophores were budded from the opposite side. It is not quite true that, as Garstang said, in siphonophores budding takes place in one meridian only, due to the early development of a thick muscular layer elsewhere. For it has been established that in most physonects (not apparently in *Forskalia*) the budding meridian for nectophores is on the side opposite that of siphosomal buds. The origin of this arrangement appears early on (*see* text-figs. 19 and 20 of the larvae of *Agalma elegans*) before the thick muscular layers are formed.

In this important paper Garstang gave a critical review of the opposing theories on siphonophore morphology held up to the year in which he wrote, and noted the confusion resulting in errors which had been perpetuated in text-book after text-book. He also included a very useful Glossary of Terms.

LELOUP

After many years of morphological research on Siphonophora some of us – Bigelow wisely is an exception – like to indulge in the luxury of a little stimulating speculation on phylogeny. Leloup published his thoughts on the subject in 1954, and the following review of it may be useful. Leloup (1954) summarized the published views of those who have been most interested in Siphonophora on the nature of these animals – whether they are individuals or colonies – and on their origin and phylogeny. It would perhaps have been less confusing if he had considered the disconanths (Chondrophora) apart from the siphonophores proper. Leloup is the first to have drawn attention to Hadzi's (1918 and 1944) speculation on the origin of these animals. I will here deal with what appears to be the most interesting or debateable features in Leloup's treatment of the subject. The minor criticisms I have to offer are included in square brackets.

Leloup maintained that siphonophores are derived from littoral gymnoblastic hydroids connected with the family Tubulariidae. He supported his general argument by a comparative study of the larvae of both groups (p. 674) and a study of pelagic tubularians which he called homologues of

tachygenic actinulas, and suggested that they still have a link,* however temporary, with the benthos. The Siphonophora, said Leloup, demonstrate the evolution of a planktonic group which has tended to abandon progressively a passive life and to take on an active one with a transition towards an alternation of generations. [The last statement refers, I suppose, to the formation of a free-swimming eudoxid phase, one which is more properly, I think, to be regarded as the setting free of a group of buds, both larval and adult.] There will be general agreement with Leloup that the change from a fixed, benthic way of life to a planktonic one must have taken place during a larval phase.

Leloup felt forced by a study of embryology and comparative anatomy to divide siphonophores into four groups – ‘Chondrophorides’ [which I prefer to consider as a separate order Chondrophora (Chamisso & Eysenhardt, 1821)], ‘Cystonectides, Physonectides and Calycophorides’. He calls the first three together ‘Physophorides’, without commitment to views on relationships. Quoting Moser (1925) he pointed out that there are no intermediate forms. What was capable of transformation has disappeared in the process. In default of palaeontological evidence we have to depend on embryology, where there is great condensation; and on morphology and ethology. A logical and objective hypothesis he said, postulates a common actinuloid larva in which at first the float (an invagination of the aboral pole of the larva) and trunk had equal importance, but in which, later on, they had evolved in opposite directions, that is towards predominance of trunk (siphosome) in ‘Physophorides’ and towards a nectosome [how is this related to the float?] in the ‘Calycophorides’. For all siphonophores, he says, can be related to an initial form, derived from an actinula larva, the *siphonula*.† [I would stress the fact that Leloup’s figure 4D represents a hypothetical form. We are familiar with all too few complete physonect or cystonect larvae. The best known are those of *Physophora hydrostatica*, *Agalma elegans*, *Agalma okenii*, *Nanomia bijuga* and *Physalia physalis*. Published figures of them are not always a good guide, and I would not venture to combine them into a common hypothetical form, as Leloup has done in his figure 4D.]

Leloup argued that, since a *siphonula* is found ‘in its characteristic form’ in the physonects, it is incontestable that the physonects appeared before the ‘Calycophorides’, whose larva, the *calyconula*, has evolved further than and can be derived from this *siphonula*. [I think that we must be careful that we really understand the morphology of the larvae of these two groups, and that we do not base our arguments on incorrect, schematic ‘morphological types’.] Leloup went on to say that he has already established the relationship between the cystonect larva – the *cystonula* [and the larva of the Chondrophora – the *ratarula*] and this *siphonula*, but confessed that the one cannot be derived from the other. He then reviewed the attempts that have been made to relate his four groups. He stated his own hypothesis (p. 681) that although the larvae of the four groups can be derived from the same type of larval ancestor the *siphonula* [?] one cannot link together the Chondrophora and ‘Cystonectides’ of to-day with present day ‘Physonectides and Calycophorides’. [Of course, the difficulty disappears when the Chondrophora are recognized as the odd group out, as it was by Haeckel (1888b) and Chun (1897a).] On his phylogenetic tree he labels a lower branch ‘Cystonectidae’ (and another ‘Chondrophoridae’).

He repeated his agreement with the view of Korschelt & Heider (1890) and myself (1932) – but omits Garstang’s (1946) – that ‘Calycophorides’ are descended from ‘Physophorides’, and mentioned the differentiation of nectophores that has taken place in ‘Calycophorides’. He thought that the ‘grandes formes’ [? Prayidae] were not the most complex, but that their structure was simple and repetitive, easily capable of giving rise to the ‘formes petites’ [? diphyids] with their complicated

* A fact verified by Werner (1954), whose paper on *Margelopsis haeckeli* was still in the press.

† It seems to have been Haeckel (1888b), who first introduced the term *siphonula* to indicate the young larva of *any* siphonophore. Here Leloup (1954, pp. 655 sqq.) uses the term in a *restricted* sense for a physonect larva. Is *siphonula* perhaps a *lapsus linguae* for *physonula*, a term that he nowhere employs? Throughout this work I have avoided the use of Haeckel’s terms (*siphonula*, *cystonula*, *physonula* and *calyconula*) for they would seem to indicate that the larval phase is *transitory*, whereas in my view it is *permanent*.

structure. He thought that the possession of only one nectophore is due either to tachygenesis or to a tendency to reduce the number of organs in order to increase speed.

In section IIIa Leloup dealt with 'Physophorides' (*sensu* Eschscholtz, 1829, that is including Chondrophora). Though the adults of his three groups differ from one another so much, Leloup said that their ontogeny was so similar that he dared not separate them.

On page 682 Leloup stated that a study of ontogeny proved that the larva of Chondrophora, the *ratarula*, had an organization more ancestral than the 'larve siphonula' of the cystonects, and that the *ratarula* presented a mixture of primitive characters and of more highly evolved ones by comparison with the *actinula* larva of certain present day hydroids. [I must point out that the only certainly known cystonect larva is that of *Physalia*. No reliance should be placed, except with great reserve, on certain figures of Haeckel's purporting to be of this nature. Leloup reproduced them in his figure 3 as larvae of a cystonect, *Cystalia monogastrica*. This specific name is applicable only to figure 5 of Haeckel's (1888b) plate XXII. The larvae which he took in a tow-net Haeckel thought might belong to this species. Certainly no phylogenetic arguments should be based on larvae of such doubtful parentage and identity. It is true that Leloup's figure 3B shows a larva not unlike that of *Physalia*. But I have grave doubts about the existence of Haeckel's Epibuliidae. As already stated (p. 8), *Epibulia* is a synonym of *Rhizophysa*, and has been used also for *Sulculeolaria quadridentata*.] Leloup (p. 682) said that a distant ancestor of the 'Physophorides' resembling an *actinula* with a float must have evolved in two directions. One group, keeping its aboral tentacles (*ratarula*) and expanding laterally, gave rise to the surface-living Chondrophora. Another group lost its aboral tentacles (*siphonula*) and subsequently lengthened. 'Adults' [physonects] have colonized even the great depths. [I have adopted Leloup's idea that the siphonophore tentacle represents one of the oral ones.]

On page 683, starting with the ancestral stage of a lengthening *siphonula*, Leloup postulated development of cystonects through a middle-zone proliferation which produced groups of polymorphic buds – the cormidia – accompanying the 'reproductive organs' which groups he said remained attached to the stem [in reality they finally break away].

In certain other siphonulas a second budding region, the nectosome, was formed for modified medusae, the nectophores. From these he derived the physonects, of which he regarded the Forskaliidae, as most primitive. He briefly described their families and organization.

In section IIIB Leloup tackled the phylogeny of the 'Calycophorides', showing that some authors have considered forms with a single nectophore – [the classification of Monophyidae, Diphyidae and Polyphyidae is outmoded] – as primitive [a proposition with which I dealt in 1932] and that other authors have thought that the polyphyids were the founders of the 'Calycophorides': Chun (1897b) and Moser (1925) thought that monophyids had given rise to diphyids, and these in turn to polyphyids. He quoted the systematic arrangement of the calycophorids adopted by Chun, Moser, Lameere (1929), Delage & Hérouard (1901), Schneider (1898) and my own tentative suggestions of 1932.

Finally in section IIIB2 Leloup gave his *conception personnelle* of the phylogeny of the 'Calycophorides', which he derived from an ancestor shared by the 'Physonectes' and resembling the *siphonula* [? *physonula*], the difference being that in the 'Calycophorides' the first formed nectophore rapidly acquires a power sufficient to move the colony along at a progressively increased speed. He thought that the Hippopodiidae were the most primitive. Where, amongst the siphonophores, the fully developed buds ('les éléments adultes') are restricted in number, the phenomenon of a very complicated organization indicates an advanced stage of evolution. [I think the Prayidae are more primitive, and the Hippopodiidae are more complicated.]

The behaviour of the animals throws light on their phylogeny and evolution. Siphonophores have rid themselves of a life of slow locomotion ('Prayomorphes') and have adopted a rapid one ('Diphyo-

morphes') with occasional returns to a passive one (Sphaeronectidae). [I know of no one who has described their movements, and personal observation does not suggest that sphaeronectids are active movers.] Colonies tend to become small, and this reduction affects the two zones of proliferation – a progressive limitation in numbers of nectophores. Sometimes, Leloup thought, the retention of only a single nectophore has arisen through tachygenesis. [I suspect that the single nectophore of *Sphaeronectes* spp. is the larval one retained.] Reduction affects the siphosome by precocious formation of eudoxids which lighten the colony and gives it greater speed. This is the origin of the *generation alternante*.

Where the stem is long and carries many cormidia (Hippopodiidae) Leloup said that the definitive (réserves) nectophores ejected the old ones, whilst where the stem is shortened by precocious liberation of eudoxids the 'reserve' bells were fewer and even disappeared completely (Monophyides). [From personal observation I doubt Leloup's statements about the comparative lengths of stems. That of *Chelophyses appendiculata* can be astonishingly long. I doubt if the lengths have been recorded with sufficient detail to judge.] Leloup then drew attention to the progressive stream-lining of nectophores in diphyids. The change in arrangement of nectophores from opposite rows to a fore-and-aft one favours ability to move (déplacement) rapidly. With this tendency arises another towards protection of the stem-buds both of the nectosome and siphosome. [Leloup gave an interpretation of the evolution of the hydroecium which I do not find very satisfying. A great deal depends on whether the anterior nectophore of Abylidæ, Chuniphyidae and some Diphyidae is, as I suspect, the larval one retained.]

Leloup then discussed briefly the specific gravity of the whole calycophore and of its separate parts, but without mention of the work of Jacobs (1937). 'Calycophores' with numerous similar nectophores arranged in two sub-opposite rows, the Hippopodiidae were, he thought, the most primitive. The position of the desmophyids [I know of only one species], Leloup says is ill-defined, as is that of the stephanophyids, whose four adult nectophores are arranged in a tight spiral: '*le long d'une hélice à tours très serrés*'. These polyphyids, which move fairly rapidly, were followed, he said, in his evolutionary story by the Prayidae, which gave rise to two evolutionary lines. One led either to neotenous monophyids – Sphaeronectidae [which in my view are descended from precursors of abyliids. I agree with Leloup that the single nectophore of *Sphaeronectes* is probably the larval one retained. For some years I have been collecting progressively earlier larval stages and think I now have critical stages to prove it] or to a line that culminated in degenerate diphyids (*Amphicaryon* [= *Mitrophyses*]) and degenerate monophyids, *Nectopyramis* spp. The second line diverging from Prayidae led on, he thought, to the Clausophyidae. [There is a somatocyst in the posterior nectophore as well as in the anterior, which I believe to be the larval one retained. A somatocyst in the posterior nectophore seems to me to be a primitive feature.] Leloup thought that the Clausophyidae led on to the Diphyidae [which in my view at present form a catch-all group. The anterior nectophore of species of the genus *Diphyes* will prove, I believe, to be the larval nectophore retained. I collected a number of very early growth-stages of *D. dispar* at Arrecife in 1955 and I hope that they will prove the point. The same thing holds true, I believe, for Clausophyidae, Chuniphyidae and Abylidæ]. Leloup's brief characterization of all these groups does not, I think, throw much light on Phylogeny, but we are all indebted to him for a great deal of very useful research work on the group. I regret to say that I do not consider that the suggested lines of descent shown on pages 692–4 are, in general, very probable. A great deal of further research is needed before we can really judge.

GROSS MORPHOLOGY

As already stated on page 2, a fully grown siphonophore is essentially an over-grown oozooid polyp that remains juvenile and asexual, but which carries round with it large numbers of other unseparated, asexual, juvenile polyps (gastrozooids, palpons and bracts) as well as sexual adults (medusoid gonophores) and asexual adults (medusoid nectophores), all budded from the original and often much elongated oozooid, or from other juveniles. Examination of the younger growth stages reveals three general patterns of organization, at first sight very complex, but in essence closely resembling each other in the very youngest stages: I in the Cystonectae, II in the Physonectae and III in the Calycophorae.

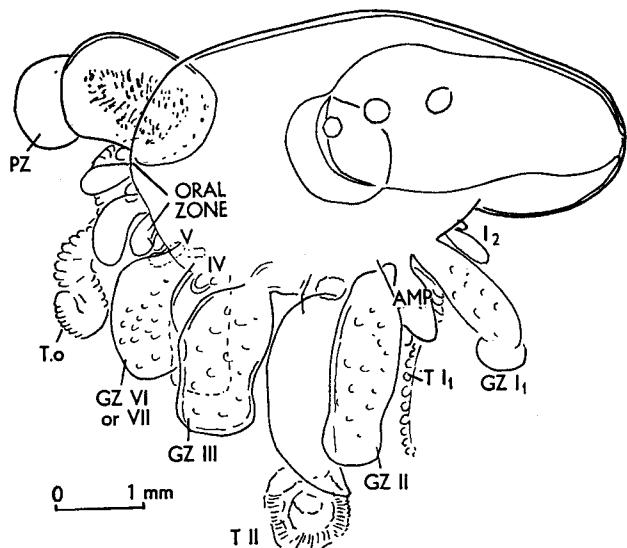


FIG. 1. Cystonect larva: *Physalia physalis*
 PZ = protozooid; T.o = tentacle of protozooid;
 GZ I₁-VII = secondary gastrozooids; T I₁, T II =
 tentacles of secondary gastrozooids; AMP = ampulla
 (basigaster); I₂ = second group of cormidium. (from
 Totton, 1960, fig. 24C).

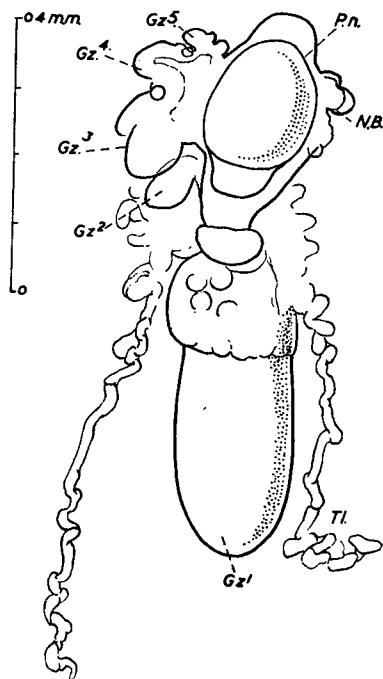


FIG. 2. Physonect larva:
Nanomia bijuga
 Pn = pneumatophore; Gz¹ =
 protozooid; Tl = tentacle of pro-
 tozooid; Gz²⁻⁵ = secondary gas-
 trozooids; N.B. = nectosomal
 budding zone (from Totton, 1954,
 fig. 3B).

A study of these patterns shows that in I, the Cystonectae (text-fig. 1), there is a floating larval polyp, the *oozooid*, with its *protozooid* (primary gastrozooid), a single, highly contractile tentacle and an aboral air-float (*pneumatophore*) on one side of which buds of secondary larval polyps (gastrozooids) appear. These buds may eventually give rise by further budding to groups of more larval polyps and adult medusoids to form very complex *cormidia*, as in *Physalia*. In II, the Physonectae (text-fig. 2), a condition can be seen which is very similar to that found in simple cystonects, except that the *siphosome*, the budding zone of the larval polyps, arises on one side of the float, and that a second budding zone, the *nectosome*, appears on the opposite side and gives rise only to adult asexual *nectophores* (medusoids). As in I, the larval polyp buds give rise to cormidia, and in addition some of the buds develop into protective or buoyant bracts. In III, the Calycophorae (text-fig. 3), the aboral part of the larva is atrophied and there is no float, but in other respects it can be compared with II. The larval polyp gives rise to two budding zones (as in II), *siphosome* and *nectosome* (text-fig. 4), but in addition a *larval nectophore*, which may or may not be lost later on, develops precociously as a

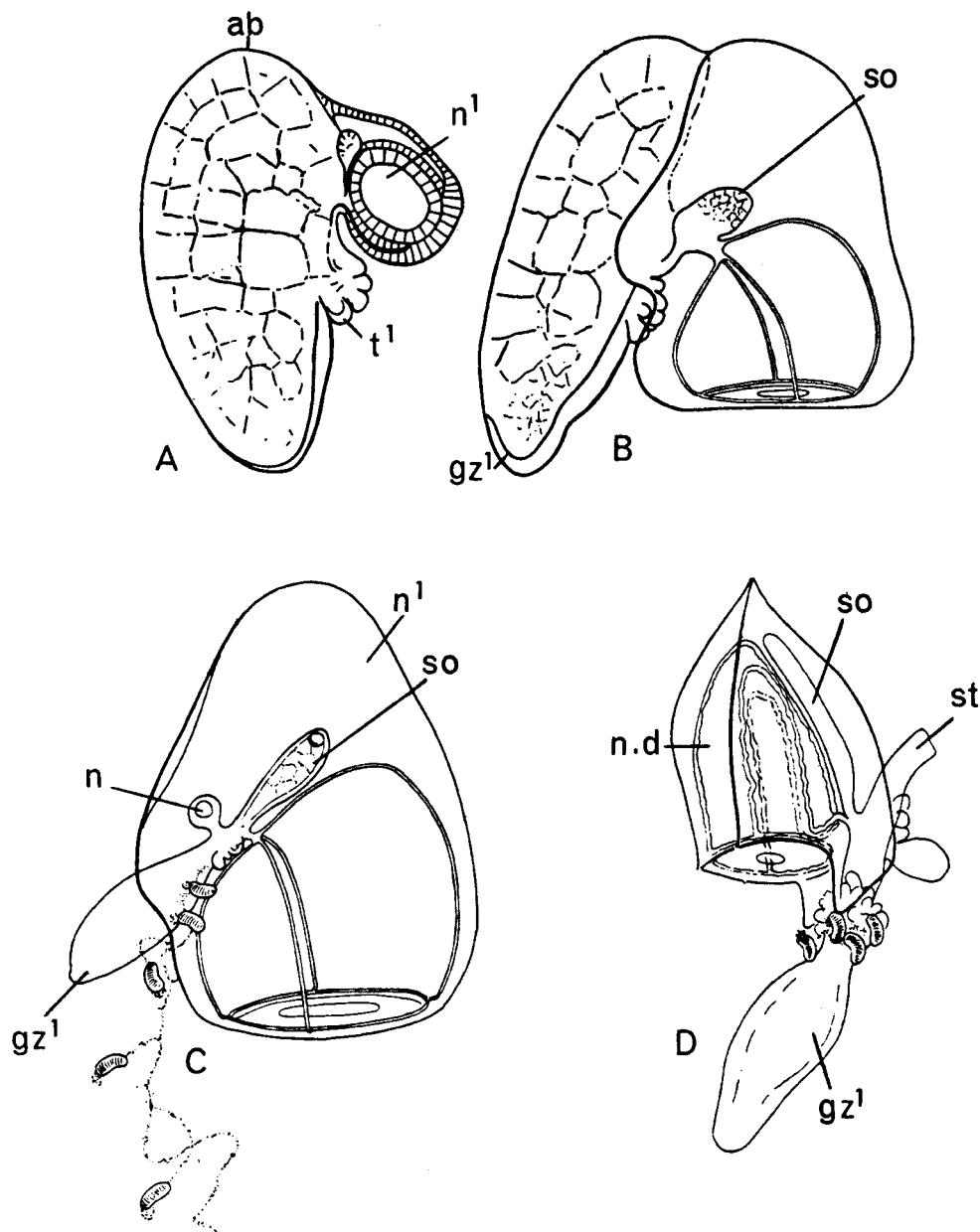


FIG. 3. Calycothore larvae: *Muggiae atlantica*

A, ca. 36 hours old; B, less than 48 hours old, both reared in the laboratory at Plymouth, $\times 150$; C, a larval nectophore 1.3 mm high taken in the plankton, $\times 150$. The bud, n, of the definitive nectophore, n.d, can be seen; D, the young definitive nectophore and stump, st, from which the larval one has separated, $\times 150$. ab = aboral end; n¹ = precocious larval nectophore; so = somatocyst; t¹ = larval tentacle; gz¹ = protozooid (from Russell, 1938, figs. 3, 5, 6).

protective housing for the siphosome, which hangs down inside and is retractable within the hydroecium. The budding zone of the nectosome remains short and near that of the siphosome, instead of being carried upwards, farther and farther away from it as in some physonects.

From these three basic patterns the full grown forms found in the three sub-orders of the Siphonophora arise. From the first, the *larval cystonect*, the budding zone either develops into a long stem (Pl. I, fig. 3), depending from the aboral float and carrying the cormidial groups, as in *Bathyphysa* and *Rhizophysa* (the earliest developmental stages of which are unknown), or the budding zone is

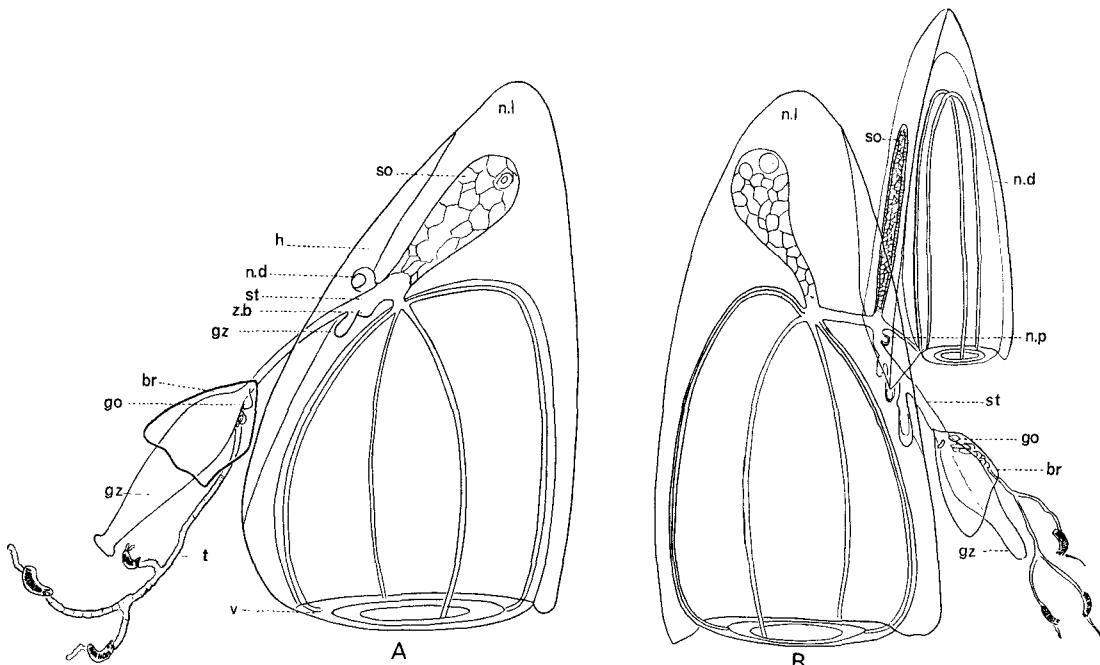


FIG. 4. Calycophore larvae: A, *Sulculeolaria quadrivalvis*, larval nectophore stage; B, *Chelophyses appendiculata*, larval and first definitive nectophores, and two budding zones, $\times 150$
 n.d = first definitive (anterior) nectophore; n.p = bud of second (posterior) nectophore; so = somatocyst; st = stem;
 gz = gastrozooids; br = bracts; go = gonophore; z.b = budding zone; t = tentacle (after Lochmann, 1914, Pl. VII,
 figs. 1, 4).

confined to the so-called ventral surface of the float, as in *Physalia physalis* (Pl. I, fig. 1). (The morphological pattern of the full grown *Physalia* resembles most closely the larval pattern, basic to all the categories I, II and III.) The cormidia each consist of branches carrying further groups, each group consisting of gastrozooid, tentacle and gonodendron (text-fig. 5). The gonodendra are complex structures which are formed by the successive budding of palpons (modified gastrozooids) from the foot-stalks of their predecessors, the original ones having been budded from the oozooid. The final series of palpons bud off the little adults proper in the form of (1) sexual medusoid gonophores, (2) asexual medusoid nectophores, and (3) in *Physalia* only, reduced, asexual medusoid nectophores (text-fig. 6) the 'jelly-polyps'. The terminal gonodendron groups may become detached and the nectophores function for propulsion.

From the second, the *larval physonect*, growth of the two budding zones in long-stemmed forms results in the formation of the two regions of the siphonophore: (a) the upward growing *nectosome*, terminated by the aboral float and carrying nectophores only, and (b) the *siphosome* carrying the cormidial groups of gastrozooids, palpons and gonophores with their buoyant bracts; the two regions are separated from one another by a zone of minimal growth (text-fig. 7). The nectosome serves to support and propel the siphonophore as a whole. The youngest nectophores are found immediately below the aboral float and the original larval polyp-group terminates the siphosome. This terminal group consists of the original gastrozooid, the protozooid, with its larval tentacle, and the secondarily budded palpons and larval bracts, but has no gonophores. The cormidial groups are budded from the siphosome stem, between the zone of minimal growth and the terminal, primary polyp-group. Each cormidium consists of a gastrozooid with a tentacle, branched (except in *Apolemia*), surrounded by bracts and palpons, and male and female gonophores. Sometimes one of these medusoid gonophores is asexual – a nectophore. The cormidia do not exhibit the same degree of branching and sub-branching as in the Cystonectae, nor do they break away as a whole and become free-swimming, except in *Apolemia uvaria*.

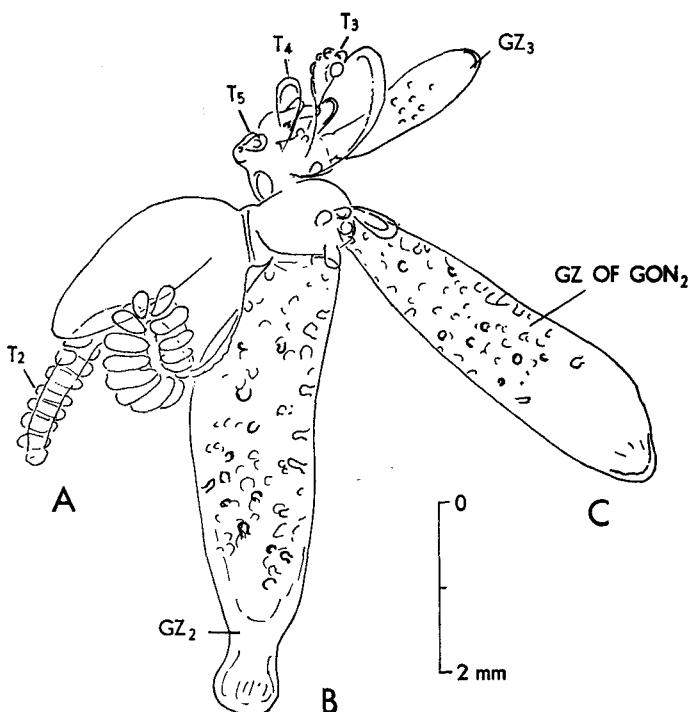
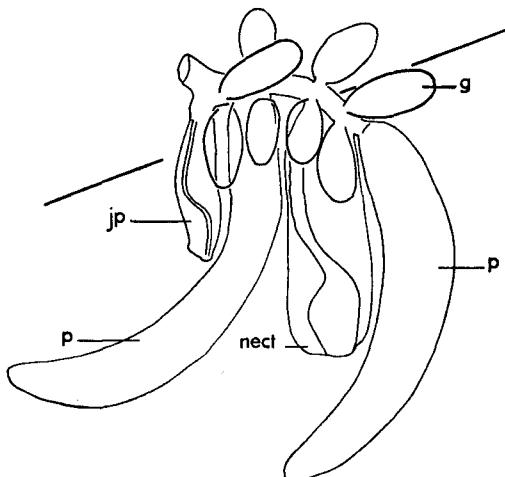


FIG. 5. Young cormidium: *Physalia physalis*. Cormidium 5 (oral zone) less group 1, to show budding. GZ_2, GZ_3 = gastrozooids; $GZ\text{ OF GON}_2$ = secondary gastrozooid: initial growth-stage of a gonodendron; T_{2-5} = tentacles (from Totton, 1960, fig. 15).



Physalia physalis
FIG. 6. Terminal part of a gonodendron: $\times 15$
 g = styloid gonophore; jp = jelly-polyp;
 $nect$ = nectophore; p = palpon (from Totton, 1960, fig. 29).

Not all the Physonectae are long-stemmed forms. Progressive shortening or perhaps failure to lengthen, of both nectosome and siphosome occurs, sometimes accompanied by enlargement of the aboral float. An extreme example of these changes in form is seen in *Stephalia corona* (Pl. XVIII, fig. 1) where the distended float lies above a circle of nectophores. In *Physophora hydrostatica* (Pl. XV, figs. 1, 9) the siphosome is hypertrophied to form a sac and in *Athorybia rosacea* (Pl. XVII, fig. 1) all the nectophores have been lost.

From the third type of larva, the *calycophore*, the nectosome gives rise to a varying number of asexual nectophores, each budded from the foot-stalk of its predecessor. They lie at the aboral pole of the siphonophore. There may be a single nectophore as in *Muggiaeae* (Pl. XXXII, fig. 1); two nectophores as in abylids (Pl. XXXVIII, figs. 1-3), one being the persistent larval nectophore; several, in a circle as in *Stephanophyes* (Pl. XXV), or alternating and closely arranged as in *Hippopodius* (Pl. XXVIII). In forms where the larval nectophore is caducous, the adult nectophores are replaceable by budding from the nectosome.

The siphosome, the second budding zone on the opposite side of the calycophore larva, gives rise to the stem-groups. Three growth phases generally occur in the further development of the calycophore: (1) the *polygastric* (text-fig. 8), (2) the *eudoxid* (text-fig. 9), and (3) the *mature free adult medusoid phase* (text-fig. 10). The first phase is called polygastric because the middle stem-part of the animal carries a succession of gastrozooids and tentacles, each gastrozooid accompanied by a single bract and medusoid gonophores. This phase is comparable with the condition found in a long-stemmed physonect, where palpons, gonophores and bracts are grouped with a gastrozooid to form a succession of cormidia, except that in the calycophore there are usually no palpons. In the second phase, the *eudoxid*, the stem-groups become free-swimming through fragmentation of the stem

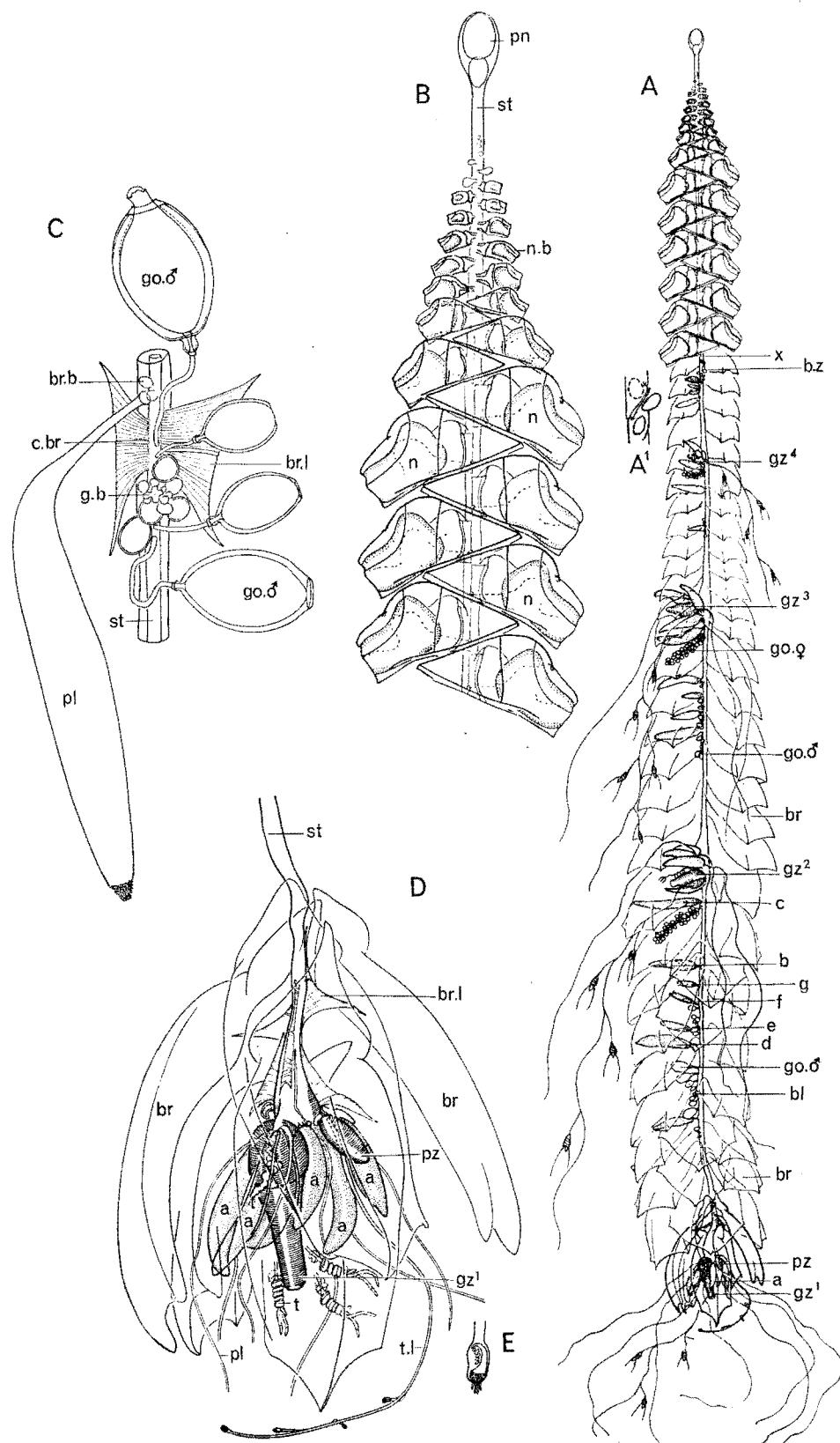


FIG. 7. A young physonect: *Agalma elegans* (Sars)

A, whole animal showing nectosome, siphosome with five cormidia and the protozooid, $\times 1.8$; A¹, to show twisting of the nectosome for convenience of representation; B, nectosome enlarged, $\times 5$; C, cormidial budding, male gonophores only, $\times 13$; D, enlarged drawing of the distal end showing the protozooid and the first definitive gastrozooid with their associated

palpons and bracts, $\times 7$; E, tentillum of the protozooid, $\times 35$

a-g = 1st to 7th series of palpons; *pz* = protozooid; *gz¹⁻⁴* = secondary gastrozooids; *br* = bract; *br.b* = bud of bract; *br.l* = bracteal lamella; *c.br* = bracteal canal; *go.♂*, *go.♀* = gonophores; *n* = nectophore; *pl* = papacle (fig. C); *pl* = papacle (fig. D); *pn* = pneumatophore; *t* = tentacle; *t.l.* = larval tentacle; *st* = stem; *n.b* = nectophore bud; *bl* = blastostyle; *g.b* = gonophore bud; *b.z* = budding zone of siphosome; *x* = zone of minimal growth (after Totton, 1954, frontispiece).

(Pl. XXII, figs. 2, 6). Each eudoxid consists of one gastrozooid and tentacle, with its accompanying medusoid gonophores, the whole generally covered by a protective and buoyant bract (the Hippopodiidae forming the exception). The eudoxid is capable of budding additional gonophores. One of the medusoids may lose its sexual function and become what is known as a special swimming-bell, or a sexual medusoid can function for propulsion. In the third final phase, the gonophores generally break away and swim free. The phenomenon of fragmentation probably has a selection value in that it ensures cross-fertilization. Certainly the Calycophorae are the most numerous and the most highly evolved of the siphonophores.

The conclusion I have drawn from the study of the siphonophore larvae is that, as Garstang (1946) supposed, they are generally comparable with the actinulae of certain gymnoblastic hydroids (text-fig. 11). In this group of hydroids the larvae usually become fixed by the aboral pole and develop into polyps, which give rise asexually by budding to more polyps and gonophores (blastostyles), which latter bud off free-swimming sexual medusae. In some species however, *Margelopsis* and *Pelagothys*, the polyp-stage is mostly pelagic, though Werner (1954) has shown that *Margelopsis* has a seasonal, benthic, larval phase. In the Siphonophora, the typical actinuloid pattern of development has been suppressed, no larval fixation takes place, although the power to bud off polyps and medusoids has been retained. It is possible, however, to homologize a certain larval structure in the siphonophore, the *somatocyst*, with that of the actinuloid tentacle (text-fig. 3b).

Those siphonophore structures derived from polyp- or medusoid buds will now be discussed.

1. *Polyp derivatives* are essentially in a larval or juvenile phase. They include the following: *Gastrozooids* or feeding polyps which retain one larval tentacle – the tentacle may be modified by branching to form a series of *tentilla*. *Palpons* or reduced gastrozooids, with simple tentacles or *palpacles*. And lastly, *Bracts* (Pl. IX, figs. 4–6). Gastrozooids may bud off more gastrozooids, palpons or bracts from the foot-stalks which join them to the stem of the siphonophore. In my opinion *bracts* are either modified palpons or gastrozooids. Schneider (1896, pp. 615–6, Taf. 44, figs. 11, 15, 18, 21–2) demonstrated clearly the origin of bract and accompanying gonophore as a twin bud on the foot-stalk of a gastrozooid. The bracteal canal does not branch from a common pedicel as in a medusoid; it represents the reduced cavity of a polypoid-zooid.

2. *Medusoid derivatives* are essentially in the adult phase and usually show their medusoid derivation in the retention and arrangement of the circular and radial canals. They include the following structures, which may be either functional or reduced, sexual gonophores and asexual nectophores.

(1) *Sexual gonophores* (text-figs. 7C, 10) can be homologized with those on the blastostyles of actinulae. They are budded from the foot-stalks of the secondary (juvenile) polypoids, which arise on the siphosome, and through gradual elongation of the siphonophore stem these groups of zooids come to lie farther and farther from the aboral pole. They retain

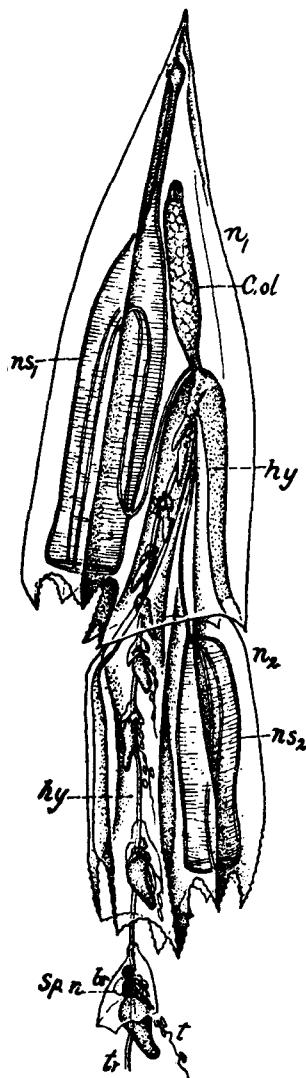


FIG. 8. Polygastric phase of a calyphore: *Diphyes dispar*
C.col = somatocyst; hy = hydroecium; br = bract;
 n_1n_2 = first and second nectophores; ns₁ns₂ = nectosacs of
nectophores 1 and 2; sp.n = special, asexual nectophore;
t = tentacle; tr = stem (from Kawamura 1915, pl. xii, fig.
21).

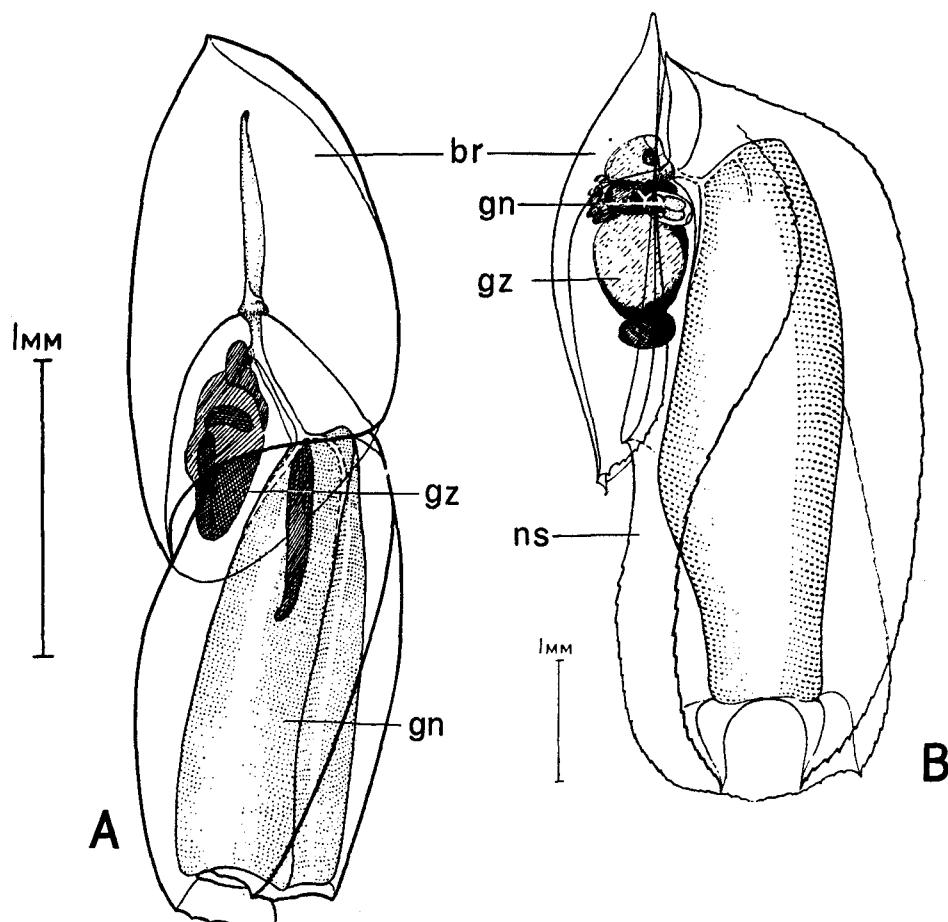


FIG. 9. Eudoxid phase of calycophores: A, *Chelophyses appendiculata*; B, *Diphyes bojani*
br = bract; *gn* = gonophore; *gz* = gastrozooid; *ns* = special asexual nectophore (from Totton, 1932, figs. 25, 22B).

the medusoid characters to a varying degree. In the Physonectae, they are small medusoids of the codonid type, with sexual products developed on the mouthless manubrium, but without marginal tentacles. In the Calycophorae, they are also codonid, but are larger and accompanied by a floatation-bract (a modified polypoid); in the most highly evolved forms, the Abylididae, they become largest of all and most complex in their development of ridges and prominences. In the Cystonectae, on the contrary, the gonophores are vestigial and styloid.

- (2) *Asexual nectophores* lack a manubrium and sexual products. There are two categories: (a) nectophores which arise (often precociously) on the nectosomal budding zone of the oozoooid (text-fig. 7B), and (b) those which arise on the siphosome in the same way as do the gonophores (text-fig. 9B). In the Physonectae, the nectophores are all of the first category and function only as swimming-bells. In the Cystonectae, the nectophores are of the second category and occur in the cormidia on the terminal branchlets of the gondendra. Some are reduced to mere vestiges, the 'jelly-polyps' (see p. 40 and text-fig. 6). In the Calycophorae, nectophores of both categories occur. The first nectosomal nectophore appears precociously, budded from the larva, and is often shed later on. The succeeding aboral nectophores are budded in varying numbers from the foot-stalks of their predecessors. These nectosomal nectophores are associated with a somewhat puzzling

structure, the *somatocyst*, a caecal diverticulum of their pedicels (text-figs. 3, 4). I hold the view, already stated on page 25, that this structure is the homologue of an ancestral actinuloid tentacle. Garstang (1946) dealt with earlier interpretations. Nectophores of the second category of ectophores form part of the stem-groups. Thus, medusoid gonophores and ectophores may occur together in the same stem-group or in the same eudoxid as (a) small somewhat reduced gonophores, and (b) a larger special swimming-bell.

In *Rosacea cymbiformis*, for example, the sexual kind (a) may at first contain only a rudiment of a manubrium and sexual products, while it intermittently propels its still unseparated eudoxid during full extension of the stem. Only shortly before fragmentation of the stem and separation of the eudoxids does it become sexually mature, but it is still capable of propulsion. In *Lilyopsis* spp., the special swimming-bell (b) has not even a rudiment of a manubrium from the start and is entirely asexual (text-fig. 71). It is accompanied by the much smaller type of gonophore (a) just described.

In view of the fact that these codonid medusoids, some of which are so small that they tend to be overlooked, are the true siphonophore adults, it may not be out of place here to refer readers who are not medusologists to an account by Kühn (1913, pp. 153–73) of the development and basic organization of Anthomedusae.

Chun (1891–97) in Bronn's *Tierreich* had already distinguished *medusae* from *medusoids* by the presence or absence of a mouth on the manubrium. Kühn accepted this definition. He pointed out (*loc. cit.*, p. 3) that in the Hydrozoa the gonozooids could be true free-swimming medusae, but that

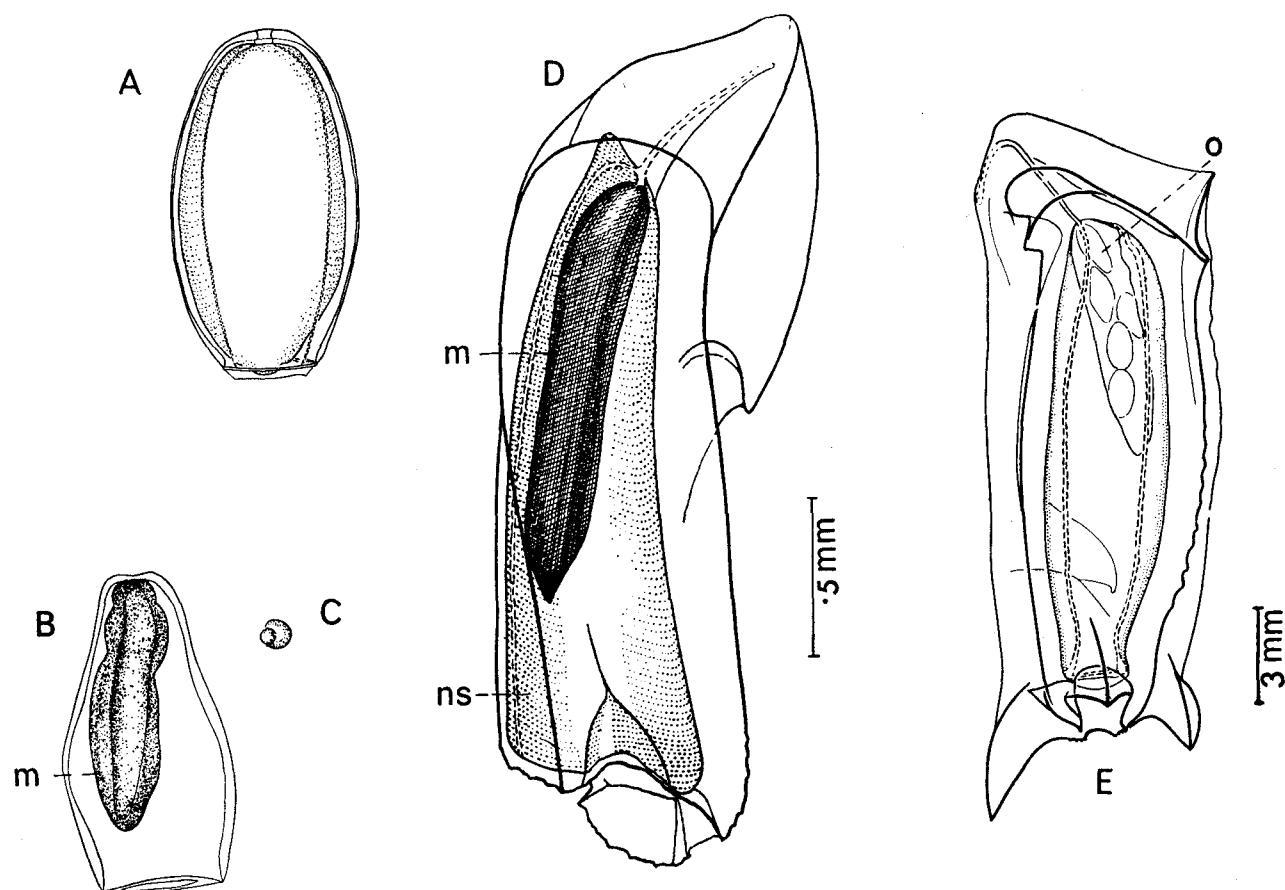


FIG. 10. Adult medusoids: A, B, *Halistemma rubrum*, ♂, $\times 12$ approx.; C, a sperm head from the same, $\times 600$ (from Vogt, 1854, Pl. X, figs. 29–31); D, *Chelophysa appendiculata* ♂ (from Totton, 1932, fig. 26A); E, *Ceratocymba dentata* ♀ (from Totton, 1954, fig. 81A).

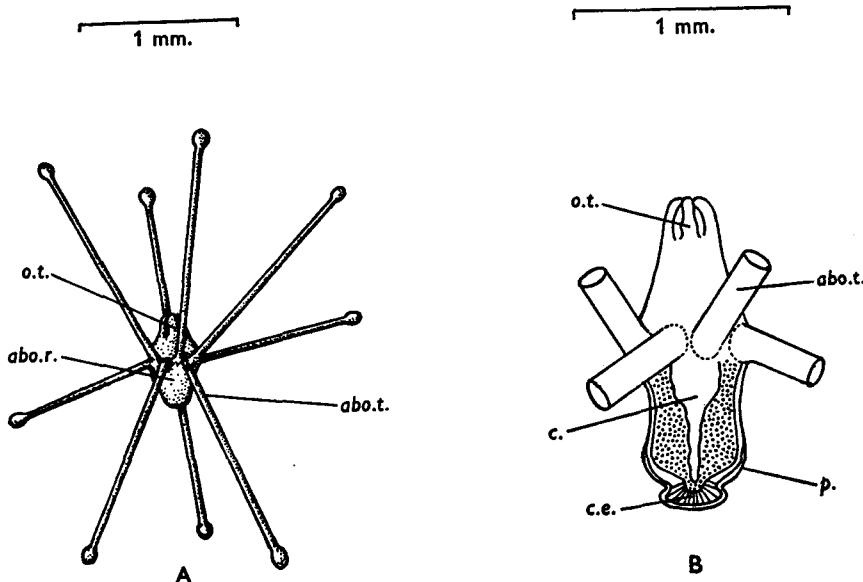


FIG. 11. Actinula larva of a gymnoblastic hydroid, *Tubularia larynx*
abo.r. = aboral region shown in optical section in B (semi-diagrammatic);
abo.t. = aboral tentacle; *c.* = coelenteron; *c.e.* = columnar ectoderm; *p.* =
 perisarc; *o.t.* = oral tentacle (from Pyefinch and Downing, 1949, fig. 1).

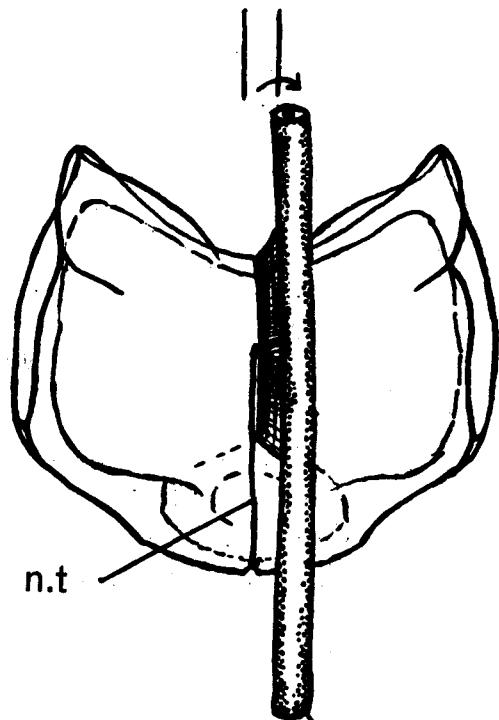


FIG. 12. Nerve-tract of a nectophore of *Nanomia bijuga* $\times 42$ (by permission of G. O. Mackie)

The stem is bent to one side to show the attachment lamella and the course of the exumbrella nerve-tract, *n.t.*

the gonophores frequently remained attached to the individuals from which they are budded, and that then the medusa-structure is modified to become medusoid. A similar sequence of events occurs in the Siphonophora, except that the free-swimming phase is always *medusoid*. I do not recall ever seeing the manubrium of siphonophore gonophores ingesting food, not even in the eudoxid phase of the caly-cophores. Kühn recognized five special types of medusoids in the Hydriida; only one of these, the *styloid* occurs in siphonophores, in the Cystonectae (text-fig. 6).

To sum up: these various polypoid and medusoid persons are associated in different combinations in the three sub-orders of the Siphonophora, in both the larval and in later growth phases:

A. Cystonectae and Physonectae have cormidial groups. A cormidium (except in *Apolemia* (text-fig. 13, p. 46)) is a non-separating stem-group consisting of secondary polyps – gastrozooids, palpons and bracts (when present) – and gonodendra, carrying nectophores in the Cystonectae, or gonophores generally with no nectophores in the Physonectae. The cystonect larval phase comprises the oozooid before there is any complex branching of cormidia. The physonect larval phase shows larval bracts covering the pneumatophore of the oozooid, and buds of gastrozooids and palpons on one side

of the oozooid and generally buds of nectophores on the other side (text-fig. 19, p. 55, and Totton (1956), fig. 1).

B. *Calycophorae*. Four growth phases are found:

1. Larval phase comprising the whole oozooid with its precocious nectophore (text-figs. 3, 4).
2. Polygastric phase – the growth stage between larva and eudoxid, comprising nectosome and siphosome with still attached groups of gastrozooids, palpons (in *Stephanophyes* Pl. XXVI, fig. 1, only), bracts when present, and buds of gonophores (text-fig. 8, and Pl. XXX).
3. Eudoxid phase – the last growth stage before the setting free of the mature individual gonophore medusoids, when the groups have separated (text-fig. 9).
4. The mature free adult medusoid phase – the free-swimming gonophores (text-fig. 10).

The two poles – oral and aboral – of the mature siphonophore, even when the stem reaches a length of fifty metres or more as it may in *Apolemia*, are precisely those of the original oozooid now immensely elongated, namely the mouth of the protozooid and in cystonects and physonects the apex of the pneumatophore, or in the calycophores the upper end of the stem. Although the various polyps and medusoids may move or feed independently, or groups of them break away and lead a free existence, yet there is co-ordination of the whole nurse-carrier. Examples of this can be seen when an agalmid, a forskaliid, a prayid or a diphyid contracts and initiates an evasive swimming-movement; when the stem of a prayid relaxes and the medusoids swim all together to extend the drift-net-like expanse of tentacles; or when, on stimulating the pneumatophore of a *Physophora*, the heavily armed tips of the ring of palpons are thrown up to the spot, probably in a defensive movement (Pl. XV, fig. 10). Again a small diphyid like *Chelophyses appendiculata*, which in a resting position is orientated with its long axis vertical, makes occasionally a few slow contractions of the nectosac of the larger nectophore to overcome the effect of sinking, and when stimulated makes a long series of co-ordinated contractions of both nectophores which provides a high-speed evasive mechanism. Another example is provided by *Physalia*. The stimulation of a wounded fish causes many gastrozooids to become active, open their mouths and attach them, spread-out, side by side on to the surface of the fish which is then digested. *Physalia* alone among the siphonophores is a passive drifter at the surface of the sea. The physonect *Athorybia* can swim up to the surface by co-ordinated movement of its paddling bracts, while other physonects swim by co-ordinated movements of the series of nectophores; the direction of the propulsive jets made by these nectophores can be changed to bring about a reversal of the main direction of progression. The nerve that initiates this change was first observed by Dr. G. O. Mackie (text-fig. 12).

REPRODUCTION

I should like to repeat here that the fully grown siphonophore is an over-grown, larval nurse-carrier (paedophore) that does not itself become sexually mature. The nurse-carrier gives rise to adult medusoid gonophores of both sexes, though each *single* gonophore is either male or female. Only one example of a unisexual siphonophore is known, *Physalia physalis*, in which all the adults are of one sex only in each animal. In the Physonectae, gonophores of both sexes occur in any cormidium. In *Nanomia*, there is an arrangement of particular interest, the sexes of the groups of gonophores (borne in pairs at the bases of the palpons) alternating from side to side as successive palpons are budded (text-fig. 36, p. 71). In the Calycophorae, where also there is repetitive budding of stem-groups (later

freed as eudoxids), the first budded gonophore of a single group may be of one sex and the second budded of the other sex; or all the gonophores of a single group may be unisexual (text-figs. 83, 84, pp. 145–146).

These medusoid adults, the gonophores, may be either free-swimming codonid medusae, as in physonects and calycophores, or reduced cryptomedusoid or styloid medusoids which are not individually freed, but may possibly become freed as the terminal part of the complex gonodendra of the cormidia, as in cystonects.

I have observed ripe male gonophores of a freely swimming diphyid emitting a continuous jet-stream of sperms into the water, until the manubrium of the gonophore shrank to a vestige. No detailed description or good figures of the spermatozoa or their maturation are known to me. Vogt (1854) figured the head only in plate 10, figure 31. I was fortunate in February 1963 to obtain a specimen of *Halistemma rubrum*, two feet long, with ripe male gonophores and I was able with great difficulty to examine the live sperms. I could see that the tail was fifteen times as long as the head, and that Vogt's figure of the head is a good representation of its appearance (text-fig. 10C).

The siphonophore egg is spherical, transparent and contains a large quantity of yolk. Often gonophores produce only one egg. The diameter of the eggs of *Halistemma rubrum*, in the specimen just mentioned, was about 0·7 mm. Early cleavage and development of the siphonophore eggs has been described by Haeckel (1869), Metschnikoff (1874), Chun (1882), Lochmann (1914) and more recently by Russell (1938) in a beautifully illustrated paper on the ontogeny of *Muggiae atlantica*.

From the work of these authors, it appears that the development of the egg up to the appearance of the rudiment of the larval bract, or of the precocious nectophore takes place rather more slowly in the Physonectae than in the Calycophorae. The development of the egg in the Cystonectae has not been studied; the earliest known larval stages are those of *Physalia* (Totton, 1960). In all the species of physonects and calycophores examined, segmentation is regular and results in the formation of an elongated, ciliated, planuloid-actinula larva. According to Haeckel (1869), this process in the physonects *Physophora*, *Agalma* and *Athorybia* takes place about the third day and by the fifth day a larval bract is well developed in the first two species, but in *Athorybia* this occurs about the seventh day. Metschnikoff (1874) studied *Agalma* and *Nanomia*, and the calycophores *Sulculeolaria* and *Hippopodius* as well. His results coincide with those of Haeckel for *Agalma*, and he pointed out that in *Nanomia* no larval bract is developed, and that by the sixth day rudimentary siphosomal buds have appeared. In *Sulculeolaria* and *Hippopodius*, the precocious nectophore appears about the fifth day, but in the calycophore *Muggiae*, its development is more rapid. Two species, *M. kochi* and *M. atlantica*, were studied, the first by Chun (1882) and the second by Russell (1938), and the latter stated that the course of development was the same in both. By the third day in *atlantica*, 'all signs of the original planula*' have disappeared and the primary nectophore is fully developed, with somatocyst, siphon, tentacle . . . and the rudiment of the secondary nectophore' (Russell, *loc. cit.*, p. 433) (see text-fig. 3). Once the rudiments of buds have been developed, the ensuing sequence of events results in the formation of the physonect or calycophore larva described on pages 20–25.

PHYLOGENY

The structural homologies between hydrozoan polyps and medusae are explained in any good textbook. The two phases have evolved from one another at different rates in different groups. It may be that originally the larval polyp metamorphosed into the adult medusa, and that later in ways not visualized as yet the sexually mature medusa arose by budding from the asexual larva. I myself imagine that all polyps of a hydrozoan stock once gave rise by budding to medusae; that then certain

* Except its oral half which develops into the protozooid.

polyps alone came to retain this function; that these polyps were reduced during the growth of the medusoid gonophores finally to vestigial blastostyles. The last stage of this reduction process may be represented perhaps in physonects like *Agalma elegans*, where, although in the mature state individual gonophores appear to arise singly from the stem, in earlier growth stages it can be seen that they arise from certain loci, which may be the final vestiges of blastostyles. As growth and elongation of the stem takes place, the points of attachment of the gonophore-pedicels can also be seen to separate from one another.

Much has been written on this subject since Huxley's (1859) and Allman's (1871) days, and it is necessary to consult their work to ascertain what exactly they meant by such terms as *gonoblastidium*, *ectotheca*, *perigonium*, *gonangium*, *sporosac*, *planoblast*, *gonocheme*, *gonophore*, *zooid*, *hydranth*, *blastocheme* and *blastostyle*. Various opinions about the interpretation of these structures have been put forward by such workers as Weissmann (1883), Goette (1907), Kühn (1910, 1913), Goto (1910), Delsman (1911) and others. Here it is necessary only to quote Allman's (1871, p. xv) definition of the term *blastostyle*: 'a columniform zooid destined to give origin to generative buds' and perhaps amend it to read: 'the base of a columniform zooid . . .'

It is not appropriate here to re-examine the Hydrozoa, nor to give a review of the voluminous literature, but there is abundant evidence for deducing that in that Order there has been reduction of the free-swimming, sexually mature medusa-phase to a sessile sac that still shows signs of varying amounts of medusoid organization – the view held by Kühn (1913). I hold the opinion that it is quite unrealistic to deduce all sessile sporosac- and other medusoid-gonophores from stages in the evolution of free-swimming medusae.

In 1946, Garstang pointed out that the actinula of the gymnoblastic hydroids is 'merely a planula with precocious adult character'; that it is 'provided with additional yolk so that it develops some at least of the future polyp tentacles as well as a mouth before its liberation' (p. 144). He went on to suggest that the original larva of the siphonophore ancestors was an actinula.* My own study of the larvae of representatives of all the major siphonophore groups has led me to endorse Garstang's work. Furthermore, as already stated on page 2, I think that the Siphonophora was only one of those groups which arose, during a comparatively recent radiation, after this new type of neotenic organism, the actinula (text-fig. 11), had been evolved from the larva of some proto-hydroid. This view was first put forward by me in 1960 as the Paedophore Hypothesis. It is, of course, axiomatic that forms alive to-day cannot be derived from one another, but only from precursors in the past, which unless they have survived as rare forms, are likely to have evolved into something different.

In my view, therefore, it is essential to bear in mind that the fully grown siphonophore oozooid is really an over-grown asexual polyp, which never itself takes on the adult hydrozoan form – the sexual medusa – but gives rise to it by budding. The reverse phenomenon is never seen in the Hydrozoa: a medusa never† truly gives rise by budding to a polyp, which always develops from an egg or from another polyp, thus demonstrating, in my view, the polyp's larval character. It is permissible to call both polyps and medusae 'zooids', but I retain the word polyp when I wish to stress the larval significance.

It is essential also to understand that the long axis of a fully grown physonect, even many metres long, carries at one end the original larval mouth of the oozooid (text-fig. 7D, p. 24), and its invaginated aboral float at the other. The word 'colony' is misleading when applied to the Siphonophora for it calls to mind the creeping, branching colonies of the hydroids.

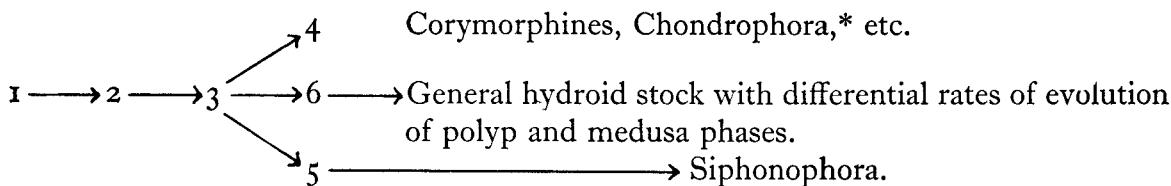
* See pages 15–16 for a fuller discussion of Garstang's views.

† The only exception known to me came to light after writing this. Kramp published in *Vidensk. Medd. dansk. naturh. Foren. Khb.*, 124, 1962, p. 344; figures of a peculiar polypoid structure growing out of the stomach-wall of the limnomedusan *Proboscisidactyla ornata* (McCrary).

My own view of the course that hydrozoan evolution has probably taken may be briefly summarized as follows:

- Stage 1. Continuous metamorphosis: planula → polyp → medusa.
- Stage 2. Very simple fixed larval polyp giving rise by budding to a well developed medusa.
- Stage 3. Advanced (complex) fixed polyp-phase with a well developed medusa-phase.
- Stage 4. Larva of polyp as in 3 retained by the medusoid-stage instead of being shed as either an ovum or a planula, and becoming an actinula with reduction of the medusa-phase.
- Stage 5. Larva of this new type of polyp-phase adapted for permanent planktonic life (Siphonophora), medusa-phase reduced to gonophores.
- Stage 6. Larva of 3 becoming, contemporaneously with 4 still more advanced with further reduction of the medusa-phase.

This summary may be represented in the form of a diagram, the numbers referring to the above stages:



During the course of evolution it would appear that in the Siphonophora neoteny has played an important part, if we can apply this term to the attainment of sexual maturity by an animal while it is still in a larval stage.

With regard to the phylogenetic trends within the Order itself, in my opinion the Cystonectae and Physonectae are more closely allied to one another than to the more highly organized Calycophorae. Although they are divided into two sub-orders, cystonects and physonects appear to form a natural group A, while the calycophores by reason of their greater specialization fall into a second group B. The main differences between these two groups are as follows:

1. In A there is a gas-filled float; in B none – it has probably been lost.
2. In A the gonophores are budded from the bases of reduced gastrozooids (palpons); in B there are no reduced gastrozooids (except in *Stephanophyes*), unless they are represented by the bracts from which the gonophores are budded, bract and gonophore together forming a twin bud from the peduncle of the gastrozooids. In A, especially in the cystonect *Physalia*, there is repeated secondary budding from the foot-stalks of the gastrozooids, palpons and gonophores. In B the process is shortened up, though Moser (1925, Taf. VII, fig. 5) has shown that in *Diphyes dispar* there may be a series of at least five gonophores, each budding from the foot-stalk of its predecessor. Chun (1892, p. 66, fig. 1) has figured the same origin for bract and gonophore in *Muggiae kochi*. In the Hippopodiidae the process is shortened up still further and the bract is eliminated, leaving a group of half-a-dozen gonophores budding from the peduncle of the gastrozooid, as shown by Bigelow (1911b, Pl. 15, fig. 8).

* The Reviewer in *Nature* (1961) of my 1960 paper on *Physalia* expressed surprise that I had not mentioned in my discussion of siphonophore phylogeny Picard's views on the phylogeny of the Chondrophora. This was an irrelevant issue to introduce into a review of a siphonophore paper because Chondrophora are not Siphonophora. Nor is this the place to state why, in any case, I cannot accept Picard's view. The Reviewer is mistaken in thinking that I hold that siphonophores have evolved from capitate hydroids.

3. In A there are numerous bracts, possibly homologous with palpons, but no one bract appears to be specially associated with a gonophore. In B there is only a single bract in each stem-group, surrounding the base of the gastrozooid and gonophores.
4. In A the cormidia as a rule do not separate from the terminal part of the stem, except perhaps in *Apolemia*. In B the stem-groups do separate except in the Hippopodiidae and are set free as eudoxids.
5. In A the individual gonophores are numerous, somewhat reduced and perhaps do not always separate from the cormidia. In B they are fully formed functional medusoids, which break away from the freed stem-groups, the eudoxids, when the eggs and sperms are ripening, and lead a free existence as sexually mature adults.

To sum up: in Cystonectae and Physonectae reduction has taken place in the medusoid-bearing secondary larvae (palpons) and in the adult medusoids (gonophores); also the cormidia do not separate but remain as the stem or middle part of the nurse-carrier; and lastly the stem bracts have multiplied. In the Calycophorae the float has disappeared; none of the gastrozooids as a rule are reduced (unless the bract is such a person), but each in turn breaks away with a single bract and functional medusoids (gonophores), which in their turn become detached from the stem-groups to lead a free sexually adult life.

All this indicates that there have been, so to speak, many changes of tack in the course of phylogeny, and it is exceedingly difficult to try to reconstruct the course. It would seem that the failure to separate on the part of the cormidia in Cystonectae and Physonectae is a secondary condition, which has led to permanent stem-formation with increase in the number of stem-bracts and reduction of gastrozooids to form a new type of polyp (essentially in the larval phase), the Palpon, which bears the adults, the Gonophores; whereas in the Calycophorae the gonophores are borne on the bases of unreduced gastrozooids. If the bract is interpreted as a former palpon, and gonophore and palpon as arising as a twin bud, this difference would not be fundamental, because both bract and palpon can be regarded as reduced gastrozooids.

PARASITES

Parasites of two groups – trematodes and dinoflagellates – are known to infest calycophore siphonophores. There is also an amphipod parasite.

I have described (1954) how a specimen of *Hippopodius hippopus* taken at Villefranche bore fifty trichocercous cercariae (with eyes), probably the larval stage (*Cercaria setifera* Monticelli) of the trematode *Lepocraedium album* Stossich. They made tubular tunnels into the mesogloea and lost their tails.

Of the second group, Rose & Cachon (1951) described the infestation of siphonophores by an interesting peridinian. In 1953 Cachon described the life-cycle of this animal, *Diplomorpha paradoxa* Rose & Cachon. Dr. Cachon has a great deal of unpublished information on these parasites.

TERMINOLOGY

The Siphonophora exhibit the highest degree of polymorphism of all the Hydrozoa. Both polypoid and medusoid persons occur, but none of them correspond fully to the typical hydroid forms. Both polypoid and medusoid persons are budded from the oozoid, which is the larval form developed from the fertilized egg.

A. *Oozooid* consists primarily of:

1. *Protozooid* – primary, terminal gastrozooid. This is the term usually applied to the gastrozooid at the *oral end* of the juvenile siphonophore, and in the mature cystonect and physonect.
2. *Pneumatophore or Float* – when present, it forms the invaginated, aboral organ, with an outer wall, the *pneumatocodon* and an inner wall, the *pneumatosaccus*, *pneumatocyst* or *air-sac*, which contains the *gas-gland*. The apex of the pneumatophore is either closed, or guarded by a sphincter muscle. A baso-lateral pore may be present, e.g. *Physophora*, Rhodaliidae.
3. *Stem* – the budding zone of the proximal part of the protozooid from which arise the polyps and medusoids. It can be in two parts, generally on opposite sides of the float – the *nectosome* (which may be very short, e.g. Diphyidae) from which are budded the *nectophores*; and the *siphosome*, from which are budded the *gastrozooids*, *palpons*, *bracts* and *gonophores*.

As development proceeds, the following polypoid and medusoid persons are budded from the oozooid, or from secondary polyps:

B. *Secondary polyps* – larval forms.

1. *Gastrozooids* (Siphons) – feeding polyps with only a single *tentacle* arising from the base of the gastrozooid. The tentacle is long, contractile with (except in *Apolemia*) lateral branches, or *tentilla*, each forming a sub-terminal battery of nematocysts. The base of the gastrozooid is enlarged into a nematocyst producing area, the *basigaster*.
2. *Palpons* (feelers, tasters) – reduced gastrozooids with a simple tentacle, a *palpacle*.
3. *Gonozooids*, *Gonopalpons* – gastrozooids or reduced gastrozooids associated with a gonodendron, but with no tentacle. Rather an imprecise category.
4. *Bracts* – perhaps modified palpons with enlarged mesogloea, for protection and buoyancy.
5. *Gonodendron* – a complex, derived by budding from an original palpon, of other palpons, gonophores and sometimes (e.g. Cystonectae) asexual nectophores.

C. *Medusoids* – the real adults.

6. *Gonophores* – small male or female medusae, functional or reduced, without tentacles; codonid-like, or styloid.
7. *Nectophores* (nectocalyces) – swimming-bells, asexual medusoids; sometimes reduced to
8. ‘*Jelly-polyps*’ – vestigial nectophores, found only in *Physalia*.

There remain some terms relating to the Siphonophora which it may be useful to define more fully.

i. *Pneumatophore* or Float and associated parts.

- i. *Pneumatocodon* (Luftschirm) – the outer three-layered wall of the invaginated float.
- ii. *Pericystic cavity* – the space between the pneumatocodon and the pneumatocyst, often traversed by septa.
- iii. *Pneumatocyst*, *Pneumatosaccus* (Luftflasche, Luftsac) – the three-layered, invaginated gas-containing part of the float, lined above by chitin, and below by secondary ectoderm that grows up from the gas-gland and lies over the chitinous lining.
- iv. *Pneumadenia* – the three-layered gas-gland of the invaginated pneumatocyst – a specialized part of the wall of the pneumatosaccus.
- v. *Pneumatochone* (air-funnel, Lufttrichter) – the basal cylindrical part of the chitinous lining of the pneumatosaccus, with the enclosed part of the pneumadenia.
- vi. *Hypocystic villi* – outgrowths containing giant ectodermal cells, said to have a diameter of up to 2 mm, arising from the pneumadenia and often penetrating the septa that cross the pericystic cavity.

2. *Nematocysts* and associated stinging apparatus.

- i. *Tentillum* – a side branch of a tentacle; either simple, or branched, e.g. in some cystonects; or consisting of a pedicel, involucrum (when present) and either a spirally twisted (unicornuate) cnidoband, a tricornuate body with a pair or more of lateral horns with or without a median terminal vehicle, e.g. in Agalmidae; or a closed sacculus containing elastic bands, cnidoband and other nematocysts, together with a terminal filament often provided with a disc-shaped sinker.
- ii. *Involucrum* – a fold round the base, or the whole, of a tentillum.
- iii. *Cnidoband* (Cnidotaenia, urticating band, Nesselband) – rows of sabre-shaped nematocysts forming the chief part of most stinging organs. It is often flanked basally by two rows of larger, bean- or sabre-shaped nematocysts.
- iv. *Cnidosac*, *Cnidobattery* (Sacculus, Nesselknopf, Bouton urticant) – pedicellate type of enclosed stinging organ formed by the tentilla of the Calycophorae.
- v. *Angle-bands* (Elastische Bände) – extensile structureless filaments connecting the basal mesogloea of the cnidosac with the base of the terminal filament. On activation (?) by ~~hydrolysis~~ they cause the folded cnidoband to straighten and slap itself with its larger flanking nematocysts on to its prey.

3. *Nectophores* and associated structures.

- i. *Nectosac* – the sub-umbrella cavity of a medusoid.
- ii. *Ostium* – the velar end of a nectophore.
- iii. *Hydroecium* – the hydrocial cavity (when present) in the nectophores of Calycophorae for housing the retracted stem with its associated structures. It lies on the ventral side.
- iv. *Somatocyst* – a caecal part of the common gastric cavity found in calycophoran nectophores. It is now thought to be a vestige of an original actinuloid tentacle (or bract) which has united with the nectophore. It may branch, e.g. in *Praya* spp.
- v. *Canal System* of nectophores and gonophores.

Pedicular canal – arises from the point of origin in the stem.

Radial canals – four meridional canals running from the pedicular to the circular canal.

Circular canal – uniting the distal ends of the radial canals.

Mantle canal (Mantelgefäß) – upper and lower diverticula of the pedicular canal at the point of entry into a nectophore or gonophore, e.g. in *Rosacea* spp. The muscular pedicular lamella is attached to its proximal wall. Very occasionally it lies embedded farther within the mesogloea of an agalmid nectophore. (See text-fig. 56, p. 104 of young nectophore of *Forskalia leuckarti*.)

Pallial canal – sometimes used for Mantle canal of a nectophore, sometimes for an apical part of it – thought to be homologous with the somatocyst.

Other terms used in this work are:

- 1. *Peduncle*, *Pedicel* – interchangeable terms used for the foot-stalk of attachment of gastrozooids, palpons, nectophores and gonophores. The *pedicel* of a *nectosac* is the apical canal from which arise the four radial canals.
- 2. *Phyllocyst*, *Bracteal canal* – part of the common gastric cavity occluded in some mature bracts.
- 3. *Central Organ* – of uncertain origin. The central part of a larva of Hippopodiidae and Prayidae. Also the remains of the fragment of stem in an eudoxid, e.g. Prayidae.
- 4. *Nectostyle* – area of attachment of larval type bracts of Physonectae, e.g. in *Athorybia*, and subsequent budding zone of the siphosome.

CLASSIFICATION

Classification of the Siphonophora is based not on the sexual, adult medusoids but on the asexual, larval nurse-carriers. In the Hydroida, a dual classification has been made in the past.

My views upon the probable course of evolution of siphonophores into three sub-orders, Cystonectae, Physonectae and Calycophorae, have been expressed on pages 32-33. These sub-orders with their general characteristics will be treated in this sequence, one which appears to show generally increasing complexity, although it must be borne in mind that there may be secondary simplification inside a group, following such events as the appearance of a neotenic form, as for example in the physonect, *Athorybia*.

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SYSTEMATIC SECTION

Sub-order I: *Cystonectae* Haeckel, 1887

Pneumatophoridae Chun, 1882

Siphonophores with a budding zone (siphosomal) on only one side of the base of the aboral float. There are no bracts. The tentacles are generally simple, and the cnidoblasts are not concentrated in batteries on the side branches, when these are developed.

There are only five cystonect species currently recognized, so that to review all that has been written on their division into sub-orders, families, sub-families and genera appears to be unimportant. Recent treatment of siphonophores by systematists like Lens & van Riemsdijk, Bigelow, Moser and Leloup have none of them included diagnoses of families and genera.

Two families are recognized to-day: the Physaliidae with a horizontal float, and the Rhizophysidae with an apical, vertical float. Haeckel's family Epibulidae is problematic (*see* p. 44).

The monotypic genus *Physalia* is obviously distinguishable by its large float or pneumatophore from the remaining four species, which have been divided into two genera of two species each, *Rhizophysa* and *Bathyphysa*. The criterion for distinguishing between these two is that in *Bathyphysa* spp. the young gastrozooids have lateral wings or *ptera* – they disappear in later growth stages – while in *Rhizophysa* spp. there are no *ptera*.

Family I: PHYSALIIDAE

Physalia physalis (L) 1758

Plate I, figure 1

The genus *Physalia* is monotypic and has been given a lengthy morphological treatment in Volume XXX of the Discovery Reports (Totton, 1960).

The *oozooid* develops as usual in Siphonophores into an asexual nurse-carrier, up to about one foot in length, with an anterior mouth at one end and the apical pore of the pneumatocyst at the other.

The larva at first swims below the surface, where it has been taken in tow-nets, but when about a millimetre in length it surfaces with the single tentacle of the protozooid (gastrozooid) either to one side or the other of its now horizontal body (hence the enantiomorphism). Thus two mirror-images are found, right-handed or left-handed *Physalia*. From this time onwards the gas-gland comes to lie asymmetrically on the lower side of the pneumatocyst, and outpocketings from the upper side begin to develop into finger-like processes that erect the crest.

The apical pore end, the posterior half of the animal, is free of secondary buds, which are developed in two anterior zones, main and oral, with a slight gap between. The secondary buds form *cormidial groups* (text-fig. 5) usually seven groups in each zone, which arise on the same side as the tentacle of the protozooid. Of these secondary buds the first to appear are the gastrozooids; each gastrozooid usually comes to be associated with a tentacle and a gonodendron, but *Physalia* differs from most siphonophores in that the tentacle becomes separated from its basigaster in later growth stages. The need for very numerous nematocysts in dealing with the fishes on which the animal feeds has led to much enlarged seats for their development, the *basigasters* (text-fig. 1 *amp*).

Budding is very profuse and new gastrozooids are budded off from the bases of their predecessors, together with further gonodendra, but in the course of successive budings, the gastrozooids gradually change into tentacle-less palpons. At the bases of the terminal palpons are developed the very much reduced medusoid gonophores. One gonophore of each terminal branchlet becomes an asexual nectophore; another, the so-called 'jelly-polyp', appears to be a vestigeal nectophore (text-fig. 6). The functional gonophores of each *Physalia* are of one sex only. Early developmental stages of the larva are unknown.

In young growth stages up to about two millimetres in length, the float-length is almost half the whole. In the oldest stages the protozooid appears as a small appendage of the enormously enlarged float. At this late stage the long axis of the whole lies horizontally at the surface of the sea. When the animal is being drifted along, at an angle of about 45° right or left of the down-wind direction, the tentacles lie near the surface and are extended perhaps to seventy times their contracted length.

Family 2: RHIZOPHYSIDAE Brandt, 1835

Rhizophysidae Huxley, 1859

The history of the literature of the sub-order Rhizophysaliae Chun, 1882, of the family – originally sub-family – Rhizophysidae and sub-families Rhizophysinae, Epibuliinae and Bathyphysinae has been dealt with by Bigelow (1911b).

It seems to me that if there are such animals as Epibuliinae (*Epibulia ritteriana* Hkl., 1888b) they could not be included in the Rhizophysidae because of the alleged possession of a ring of palpons below the float. I am inclined to suggest that the description of this animal by Haeckel was based on a misconception of a specimen of *Athorybia rosacea*, and that Haeckel's figure is unrealistic and idealized, though beautifully executed. If such animals exist no doubt one will be found again.

None of the Rhizophysidae commonly come into the hands of systematists, though the hands of fishermen suffer from their stings, since their tentacles often adhere to cordage and nets by their nematocysts. No doubt these animals are abundant in deep water. One species in particular, *Bathyphysa conifera*, is frequently found adhering to the hemp of the grappling lines used by cable-ships. Some special fishing device is probably needed to catch them for study, because specimens are naturally damaged when grappling lines and dredge-wires to which they may have adhered are taken inboard over a sheave.

It is more knowledge of actual specimens that is needed rather than further discussion of the literature.

Genus: **RHIZOPHYSYA** Périon & Lesueur, 1807

Distinguished from *Bathyphysa* by the absence of *ptera* on the walls of the gastrozooids in all growth-stages.

Lens & van Riemsdijk (1908) gave an account of the history of this genus and Bigelow (1911b)

another. Morphology, particularly that of the gas-secreting apparatus, was discussed by Schneider (1898), who gave the following generic diagnosis: 'Cystonects with long, fine stems, whose gastrozooids have no lateral wings or ptera.' The rest of his diagnosis was applicable to all cystonects.

***Rhizophysa filiformis* (Forskål, 1775)**
Plate I, figure 2; Plates II, III and IV

Physsophora filiformis Forskål, 1775

Rhizophysa gracilis Fewkes, 1882b

Cannophysa murrayana Haeckel, 1888b

Cannophysa eysenhardti Mayer, 1894

?*Cannophysa filiformis* Mayer, 1894

Rhizophysa filiformis Lens & van Riemsdijk, 1908

This species was described and figured by Gegenbaur (1853a, b) from specimens up to one and a quarter feet in length taken at Messina. Fewkes (1883) recorded one from Bermuda that measured over three feet in length. Fewkes (1879) examined three specimens taken at Villefranche, and gave a good figure of a whole specimen. He also figured developmental stages of the tentilla and gonodendra. Small specimens 2–4 cm in length with 4–6 cormidia often occur in spring off Algiers in hauls from about 400 m.* These animals sting sharply.

Apical pneumatophore: 12 mm long, 6 mm diameter (Chun, 1897b), very muscular. No septa surrounding it, but very obvious hypocystic villi containing giant gas-gland cells (Pl. II, fig. 2), each from 1·5–2 mm in length are present in the secondary ectoderm. Chun measured their nuclei as being from 0·25–0·27 mm in diameter. A cap of red pigment round the apical pore.

Gastrozoid: The colour of living specimens at Villefranche was pale green. They are 1–1½ inches apart with a tentacle at the upper side of the base. *Tentilla* of three types: (a) the most abundant form, the *tricornuate*. There is a hitherto undescribed web connecting each lateral branch to the central one (see Pl. IV, fig. 2). Ten or twelve tricornuate tentilla separate two of the next type (b) the *dendritic* or *palmate*, a developmental series of seventeen or more of which can be followed back on a single tentacle. Previous descriptions have not indicated the extent to which branchlets of the dendritic tentilla can expand (see Pl. IV, fig. 6). At one side of the distal end of the enlarged body of the dendritic tentillum, between the bases of the branches, is a hemispherical pigmented boss, reddish-brown in colour and covered with hair-like processes, resembling those that cover the ectoderm of the whole tentacle and the pedicels of all the tentilla. At the other side is an extensive opaque area of the ectoderm (c). The third type, known as the *bird-headed* or *beaked* tentillum (see Pl. IV, fig. 4) bears a bunch of rather longer processes with central enlargements, resembling those of the tentilla of the larval tentacle of *Agalma elegans*. I have seen as many as twenty-one tentilla of this type on a single tentacle of a young, 8 cm. long specimen. The tentacle bore five developed palmate and thirty-eight trifid ones. In five cases there were two successive tentilla of the bird-beaked type. The palmate tentilla did not expand in magnesium chloride as much as those of tentacles of larger specimens, and both the palmate and trifid tentilla bore areas of a light pink colour.

Gonodendron: Kawamura (1910) stated that as distinct from *Rhizophysa eysenhardti* the gonodendron is attached directly to the underside of the gastrozoid and not isolated between two. I find that this is not so. Developed as subsequently elongating ovoid buds from the stem, halfway between two gastrozooids, the gonodendra give rise to about two dozen branches, each terminating in a palpon and a sub-terminal nectophore (Pl. II, fig. 3; Pl. III, fig. 4). There is no sub-terminal branchlet as in *Physalia*. There are half-a-dozen or so gonophores around each of the nectophores. It seems probable that the (reduced) jelly-polyp and its accompanying palpon in *Physalia* are homologous

* Personal communication from Dr. J. Cachon.

with the nectophore and palpon in *Rhizophysa*. The finer structure and behaviour of the mature gonodendra in the two cystonects is remarkably similar. It is not known whether each specimen is unisexual as in *Physalia*.

Habits. In captivity in a tank specimens live for several days. They take up a vertical position with the pneumatophore at the surface. There is constant and repeated contraction of the stem which pulls down the pneumatophore and pulls up the lower end, followed by relaxation to a pendent position. The tentacles frequently shorten up too. This habit is reminiscent of *Physalia*.

Gegenbaur (1853, p. 325) described fully extended specimens peacefully drifting and writhing about at the surface of a calm sea. The elongated gastrozooids were actively searching for prey, while the tentacles sank into the depths like long fishing lines.

Rhizophysa eysenhardtii Gegenbaur, 1859
Plate I, figures 3, 3a; Plate V, figure 1; Plate VII

Rhizophysa eysenhardtii Gegenbauer, 1859

Rhizophysa filiformis Huxley, 1859 (*non* Gbr); Lens & van Riemsdijk, 1908

?*Rhizophysa inermis* Studer, 1878

Rhizophysa eysenhardtii Fewkes, 1883; Lens & van Riemsdijk, 1908

Nectophysa wyvillei Haeckel, 1888b; Agassiz & Mayer, 1902

Distinguished from *R. filiformis* by the possession of filiform tentilla (Pl. I, fig. 3a). Up to 50 cm long in formalin.

Pneumatophore: Up to 18 mm long, 11 mm diameter (in formalin), pale pink in colour like the stem, with a very deep red patch of pigment round the apical pore.

Stem: Several metres long when expanded (Kawamura, 1910) contracting to 30 cm; diameter 0.5–1.5 mm.

Gastrozoid: Half an inch long with short endodermal villi, pedicellate. Tentacle an inch long in contraction, extending to two or three inches, like a slender thread. Unilateral tentilla extending to half an inch. Spheroidal nematocysts 0.084 mm in diameter. Colour of tentilla claret or colourless.

Gonodendron: On the thread-like pedicels 1.5 cm long; side branches each with a single palpon, and asexual nectophore and several gonophores. *Colour:* Golden, pale reddish brown (Kawamura, 1954).

Genus: ***BATHYPHYSA*** Studer, 1878

A monotypic genus for *B. abyssorum* Studer, 1878.

Distinguished from *Rhizophysa* by the presence of *ptera* on the walls of the gastrozooids in early growth-stages, and absence of hypocystic villi.

Leloup (1936) made a thorough review after examination of type specimens of the various species. His conclusion, with which I agree, was that there are only two species, *B. sibogae*, L. & v. R., with characteristic tentilla on the tentacles and *B. conifera* (Studer) without tentilla.

The most likely method of obtaining bathyphysan material is through the services of the staff of a cable-ship. Specimens adhere to the hemp of the grappling wires. As the wire comes up over the bow-sheave fragments are scattered on the deck.

***Bathyphysa conifera* (Studer, 1878)**

Plate V, figure 3; Plate VI, figures 1-4

Rhizophysa conifera Studer, 1878*B. abyssorum* Studer, 1878*Pterophysa grandis* Fewkes, 1884*B. grimaldii* Bedot, 1893a; Kawamura, 1954*Pterophysa (Bathyphysa) studeri* Lens & van Riemsdijk, 1908*Pterophysa grandis* Lens & van Riemsdijk, 1908

Stem: Measured length of 3·7 m (in formalin: Lens & van Riemsdijk, 1908). The elongated cylindrical *pneumatophore* may measure 2 cm long and 0·5 cm diameter.

Gastrozooid: The secondary gastrozooids, each bearing a simple, tubular tentacle in the later but not earlier growth stages, are budded from a region close to the pneumatophore. In early growth-stages the sessile gastrozooids bear two longitudinal ridges or *ptera*. Later on these disappear.

Gonodendron: Associated with each gastrozooid is a gonodendron of cystonect type with palpons, gonophores and asexual nectophores. In early stages of growth the gonodendron is sessile and globular. In later stages it becomes pedunculate and elongated. Parts of it break away when mature, but few details are known of its structure and breakdown. The various growth-stages were illustrated by Leloup (1936, Pl. I, fig. 6).

B. conifera differs from the only other well-known species *B. sibogae* in having simple tentacles. It was beautifully illustrated by Lens & van Riemsdijk (1908, Pl. XIX) – as *Pterophysa grandis*.

Beautifully preserved gastrozooids and pieces of stem (Pl. VI, fig. 4) were collected by the method already described, in 1948 on board the cable-ship 'Monarch' working in depths of from 914 m to 4,489 m at the following localities: 01° 35'S, 31° 35'W, 914–2,743 m; 2° 40'S, 3° 05'W, 4,489 m; 20° 25'N, 21° 47'W, 4,189 m; 6° 19'N, 27° 23'W, 1,097 m.

Kawamura (1954) published some interesting observations and figures of preserved specimens which purported to show branches of the stem. My tentative interpretation is that these branches are gonodendra. The fact that they bear gastrozooids may perhaps be explained in the following way: Physonect gonodendra develop by successive budding of palpons from the bases of their predecessors. These palpons are reduced gastrozooids. In *Bathyphysa* gonodendra appear to develop from unreduced gastrozonoids, though there is a terminal gonopalpon on the ultimate branchlets.

***Bathyphysa sibogae* Lens & van Riemsdijk, 1908**

Plate V, figure 2

Only two specimens, the types of Lens & van Riemsdijk, are known, one 72 cm, and the other 10 cm in length. The *pneumatophore* of the longer one measured 9 mm × 4 mm. The hypocystic villi are small, and there is an apical pore. The gastrozooids, after fixation, measured up to 30 mm × 3 mm, and bear the usual two *ptera* or wings.

Gastrozooid: There is no peduncle to the gastrozooid (Leloup, 1936). Gastrozooids up to 25 mm in length, one bearing tentacles 40 mm in length with tentilla. The tentilla terminate in a central, short filament and two lateral excrescences, not unlike those of the trifid type in *Rhizophysa filiformis*. They were figured by Lens & van Riemsdijk (1908, Pl. XXIII).

Gonodendra borne on a peduncle resembling that of *B. conifera*.

Cystonectae : Species inquirendae

Under this heading I group the following: *Bathyphysa japonica*, Kawamura, 1943 and the family Epibuliidae, Haeckel, 1888.

Bathyphysa japonica Kawamura, 1943

B. japonica, Kawamura, 1954, Plate VI, figure 3; Plate VII, figures 8, 9

Kawamura described 'stem branches' as in *B. conifera* (q.v.). I tentatively offer the same explanation as I gave for that species.

? **EPIBULIDAE** Haeckel, 1888? **EPIBULIINAE** Bigelow, 1911***EPIBULIA*** Eschscholtz, 1829; non ***EPIBULIA*** Vogt, 1854 (= ***SULCULEOLARIA***)

Rhizophysa chamissonis, Eysenhardt, 1821, one of the two species – the other was *R. filiformis* – for which Eschscholtz created the genus *Epibulia*, was chosen by Haeckel (1888b) as the type species. No specimens of this animal are known to be preserved. If there are such animals alive in the sea no doubt some will eventually be captured. Meanwhile all we have for basic consideration are the two crude figures, and a very poor latin description by Chamisso published by Eysenhardt (1821). On account of the presence of a ring of what look like palpons underneath the float it seems best to regard the animals, if they exist, as forming a quite separate family Epibulidae Haeckel.

Thus, *Epibulia chamissonis* (Eysenhardt, 1821) is a problematic animal-name. It might conceivably apply to a *Bathyphysa* species, the alleged palpons being really young gastrozooids. Eschscholtz cannot have had a very clear concept of '*Epibulia*' since he seemed inclined to include in it a physophore *Cupulita boodwich* Q. & G., 'on account of its red tentacles'. The use of the same name *Epibulia* by Haeckel (1888b) for his *E. ritteriana* had not really any sound reasoning behind it. His figure and description will be dealt with under that name.

Epibulia chamissonis (Eysenhardt) 1821

Rhizophysa chamissonis Eysenhardt, 1821

A species *inquirenda*. There is supposed to be a ring of palpons below the float. But it seems to be improbable that there is in existence an animal that would correspond with the poor description and figures, rather than with one that has been properly described under another name.

Epibulia ritteriana Haeckel, 1888

? *Athorybia rosacea* (Forskål) 1775

I am not satisfied of the existence of a siphonophore such as was figured by Haeckel. If it was indeed a cystonect it could hardly have a ring of palpons under the float. The description is incomplete and unconvincing. It seems possible that Haeckel had worked up notes and sketches of an incompletely examined specimen of *Athorybia rosacea*.

Sub-order II: ***Physonectae*** Haeckel, 1888

Siphonophores whose larvae develop a budding zone on either side of the base of the apical float or pneumatophore. (*Forskalia* is an exception in that the budding-zone and siphosome appear to be on one and the same side.) From one zone, the nectosome (absent in *Athorybia*) bud the nectophores which propel the whole animal. From the other, the siphosome, the stem develops as either a long stem or a relatively short globular structure. It carries the gastrozooids, palpons, bracts and gonophores (text-fig. 7).

Seven families of physonects are recognized: Apolemiidae, Agalmidae, Pyrostephidae, Physophoridae, Athorybiidae, Rhodaliidae and Forskaliidae. The only new family since Bigelow's (1911b) 'Albatross' paper was published is the Pyrostephidae of Moser (1925).

Family 3: APOLEMIIDAE Huxley, 1859

Diagnosis: A family with a single monotypic genus *Apolemia*. Physonects with a unique kind of tentacle (probably larval) in small tufts below each muscular attachment of the nectophores. Each gastrozooid bears a filiform tentacle.

APOLEMIA Eschscholtz, 1829

Monotypic genus for *A. uvaria* (Lesueur, ?1811).

Apolemia uvaria (Lesueur, ?1811)

Plate VIII, text-figures 13-17

Agalma punctata Vogt, 1854

?*Dicymba diphyopsis* Haeckel, 1888b

For fuller synonymy see Bigelow, 1911b

HISTORICAL

This is one of the most interesting, most difficult to study and least understood of the Physonects.

Our first knowledge of it is due to Lesueur who took it with Péron when they were exploring the invertebrate marine fauna at Nice in 1809. Lesueur made a wonderful drawing of it which he partly engraved. After the death of Péron he published it in a rare work about 1811. This work bears a similar title to the better known two volumes of text edited by Péron, and, after his death, by Freycinet and the atlas of plates by Lesueur and Petit, published from 1807 to 1816. When Péron died he left his manuscripts to Lesueur, amongst them an almost completed *Histoire complète des Méduses* (see p. 447 of vol. 2 of the *Voyage*). The work of (?)1811 published by Lesueur was probably based on this, but was meant to be only a beginning. He said (p. 4) 'l'histoire de chaque genre (des Radiaires molasses composés) et les descriptions des espèces . . . devant êtres consignées dans un assez long Mémoire, j'ai cru devoir me borner à publier pour le moment quelques exemplaires de la planche (*Stéphanomies à grains de Raisin, (Uviformis)*) qui doit l'accompagner, avec cette courte description'.

This figure (Pl. VIII) has been referred to, often erroneously, and was copied in part by Blainville (1834, Pl. III). Kölliker (1853, p. 18) implied that an account of it had been published in the *Journal de Physique* for 1813. But I have found this suggestion to be erroneous. Volume 77 of that Journal for the latter half of 1813 carried a paper by Lesueur (p. 119) on some of the animals they took at Nice, but no description is made of any siphonophore, and there are no accompanying figures. Volume 76 of the same journal for the earlier half of 1813 carries no paper by Lesueur. Haeckel (1888b, p. 204) said '*Apolemia* was first observed in the North Atlantic by Lesueur who in 1813 executed a large and excellent picture of it drawn and engraved by himself from life. He called it *Stephanomia uviformis* (not *uvaria*)'. Haeckel went on to say 'Eschscholtz observed the same animal in the Atlantic, and recognizing it in the unpublished (*sic*) plate of Lesueur founded upon it a new genus, *Apolemia uvaria* (1829, p. 143)'. Before mentioning how Haeckel then went on to cause confusion about the species it is necessary to state that Lesueur did publish the figure in a work, the only two copies of which I know (1) formed part of the Banksian Library, now in the British Museum Library; (2) is in the Library of the Musée d'Histoire naturelle in Paris. Haeckel caused confusion by stating (p. 205) that

Lesson copied the description of it (by Blainville) and named it *Apolemia Lesueuria*; and that he himself (Haeckel) obtained in 1878 at Paris, owing to the kindness of Professor Perrier, a copy of Lesueur's beautiful plate, and on comparing it with the Mediterranean *Apolemia uvaria* was convinced that these two forms were not identical as previous observers had supposed, but belonged to different species or even genera. By 'the Mediterranean *Apolemia uvaria*', Haeckel evidently meant the species as described by Kölliker, Vogt, Gegenbaur, Leuckart and Claus. But of course Lesueur's specimen too was taken in the Mediterranean, at Nice. Haeckel then submitted that what was virtually the type specimen from Nice differs from those taken by Vogt at Nice and by the others at Messina in various ways such as being monoecious, having no marked internodes and not being densely covered with innumerable bracts – which is nonsense. He then 'renamed' Lesueur's species *Apolemia uvaria*: *Apolemopsis lesueuria*.

Haeckel then referred to an apolemiid which Mertens observed and figured in the Caroline Islands, and which Brandt described in 1835 as *Apolemopsis dubia*. I have made several attempts to discover if this and other unpublished figures made by Mertens are still extant, but without success. Since the publication of the wonderful, partly engraved figure by Lesueur in (?) 1811, we have had accounts and figures by Eschscholtz (1829), an account by Risso (1826), accounts and figures by Costa (1836), Kölliker (1853), Leuckart (1853, 1854), Gegenbaur (1853), Vogt (1854) and Claus (1863) and the notes by Haeckel (1888). Since Haeckel's time there seems to have been no systematic work published on this interesting species except that of Iwantzoff (1896) on the nematocysts. We are still uncertain about some morphological details, especially about the brown palpons. I feel almost sure that Haeckel's (1888b) *Dicymba diphyopsis* is really the same animal.

Our detailed knowledge is derived almost entirely from a study of Mediterranean specimens. The pioneers who worked on living siphonophores all did so either at Messina or at Villefranche, where upwelling waters bring them up from the deeper water-masses. It is unfortunate for those who work at Villefranche, in particular, that these upwellings are so infrequent.* A prolonged stay there may be necessary if one wishes to see this species.

Since *Apolemia uvaria* may reach, *vide* Prof. A. Trégouboff (1957), a length of 20 metres or more and because only a part of such a specimen can be caught by the method hitherto adopted, namely by engulfing the specimen in a large glass vessel dipped under the surface, it seems probable that the part most likely to be taken in this way is the forward end carrying the float and nectocalyces. But it is just in this anterior region that the gonophores are not well developed. It is to be hoped that future collectors especially aqualung divers, will take the hindmost part where the gonophores are likely to be ripe. We know nothing about the larvae, which should be very interesting.

* Halim, Y., 1959: *Vie et Milieu IX*, fasc. 3, 1958, 278.

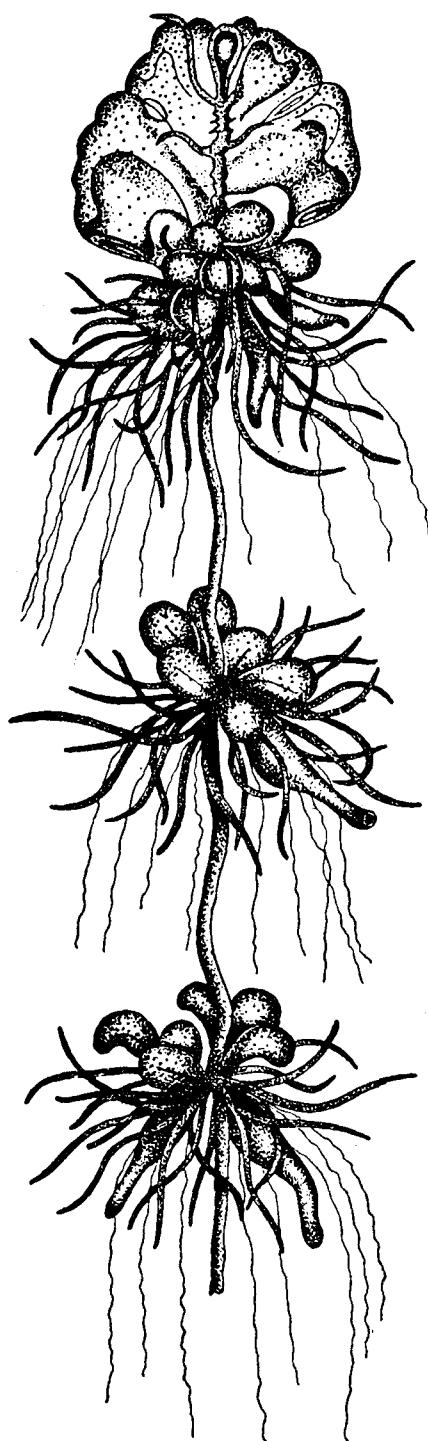


FIG. 13. *Apolemia uvaria* Lesueur
Whole animal, nat. size (after Gegenbaur, 1853b, from Totton & Fraser, 1955, fig. 3).

Indeed, if the gonophores (adults) were better known it might be possible to fertilize eggs and obtain larvae in the laboratory. The appendages are all budded from the ventral side of the stem in groups, separated by bare lengths of stem. These cormidial groups may suddenly separate.

To examine and make a drawing of a living specimen as Lesueur did in 1809 is a very arduous task. The vessel contains one writhing mass of palpons and tentacles. It is equally difficult to disentangle the parts and examine a fixed specimen particularly if it has been anaesthetized, when all the tentacles are expanded into very fine threads that cause one great tangle. Siphonophores soon become moribund in captivity.

The most significant and distinguishing character of *Apolemia*, as brought out in definitions by Leuckart (1854) and Claus (1863), is the presence of bunches of tentacles at the bases of the nectophores (text-fig. 15). These tentacles are quite unlike the single gastrozooid tentacle of other siphonophores which generally bears alternating side-branches (tentilla). They in fact probably represent the aboral tentacles of the progenitors of siphonophores rather than the characteristic siphonophore tentacles, which are probably oral in derivation, as suggested by Leloup (1954). They are found only in *Apolemia*. Their situation at the base of the muscular lamella of the nectophore seems to point significantly to a comparison with the somatocyst of calycophores, which too I have suggested represent bracteal canals or aboral tentacular canals. Another striking characteristic of *Apolemia* is the comparatively slight difference between the gastrozooids with their tentacles and the palpons with their palpacles. In these two ways *Apolemia* would seem to retain primitive features. The production of free cormidial groups constitutes the third striking character of *Apolemia*. This feature is found in no other Physonect.

Leuckart (1854), many of whose figures of details of siphonophores are very good, gave (pp. 313–320) a good account of this species, together with sketches of the air-sac, nectophores, gastrozooid, bract and female gonophores (Taf XII, figs. 6, 7, 10, 8 and 11). In the explanation of this plate on page 376 the numbering of figures 4–26 is erroneous. ‘Figure 4’ to ‘figure 25’ should read ‘figure 5’ to ‘figure 26’, and ‘figure 26’ should read ‘figure 17’ (bis.). There is no explanation of figure 4, which is a gastrozooid with basal tentacle (species unidentifiable). Leuckart on page 313 refers to a description of the animal by Lesueur in ‘*Journ. phys.*, 1813, p. 1’. This is an erroneous reference as I have already pointed out.

Leuckart’s brief preliminary description simply mentions the two most characteristic features, club-shaped bracts and tentacles (Tastern) (it must be stressed that they are not homologous with Tastern (palpons)) between the nectophores of the nectosome. He said it was as little related to species relegated to the genus *Stephanomia* as to species of *Agalma*, although Vogt had called it *Agalma punctata*. Leuckart (1854) said that he had only seen one complete specimen, a foot in length, at Nice, although he had on many occasions seen the isolated cormidial groups of appendages which appear easily to break off and, like eudoxids, continue their existence separately. His observations in general, he said, agreed with those of Gegenbaur (1853a, b), who gave another good account but did not observe the gonophores. Gegenbaur also commented on the ability of the whole colony to contract, and on the separate movement of the bracts. He mentioned that the longitudinal muscles of the stem occurred only on one side of the stem so that it took up a spiral form in contraction. Gegenbaur described at some length the fine structure of the stem and palpons.

The interesting red-brown palpons were not commented on by Gegenbaur, but both Leuckart (1853 and 1854) and Claus (1863) mentioned them. It is this feature about which we know least perhaps. Working on expanded material fixed in formalin I have not been able satisfactorily to determine their distribution in the cormidial groups. Nor am I certain that most palpons have not much of this brown pigment in their early developmental stages. This is a point on which to concentrate next time living material becomes available. I have never been stung by any Physonect, but Leuckart (1853), said that there was a pair of brown palpons distinguishable from the other palpons surrounding

each gastrozooid, and that the ectoderm is full of nematocysts, which cause a sharp burning pain. These nematocysts were distinguishable, he said from those of the tentacles partly through their globular form, and partly through the spiral winding on their strong threads. At the tips of the palpacles of these brown palpons Leuckart said that there were smaller nematocysts distributed in a special way – which he did not specify as far as I can understand. Claus (1863) described the following five kinds of nematocysts each of which, he said, had its fixed and characteristic distribution, and which he figured on his Plate XLVI: (1) small globular, 0.007–0.008 mm diameter, in the ectoderm of small palpons and at the mouth of gastrozooids (fig. 8b). (2) Large globular, 0.012–0.014 mm diameter without hampe (Zwischenstück), in the ectoderm of nectophores and gastrozooids, producing whitish spots also, forming the heavy armature of the red-brown palpons (fig. 8a). (3) Oval, with a twin-knobbed, simple thread, 0.012 mm diameter, 0.02 mm long, in the ectoderm of the tentacles (fig. 8c). (4) Longish, elliptical, 0.011 mm diameter, 0.023 mm long, with a cylindrical hampe bearing spirally wound spinelets, forming the chief part of the armature of the tips of the palpons. (5) Pear shaped, large 0.018–0.02 mm diameter, 0.022 mm long, with a long conical hampe which bears spinelets set across it, provided with an operculum, found at the tips of palpons.

Claus commented on the abundance of cnidocils. Iwantzoff (1896) confirmed the presence of Claus's category 2, to which Weill (1934, p. 86), who had not examined *Apolemia*, gave the name birhophaloïdes. Weill pointed out that according to Iwantzoff's and Claus's descriptions the two dilatations were on a *hampe*, but seemed doubtful of their existence, and said it was necessary to re-examine *Apolemia*. I have recently examined tentacles that had been extended in MgCl₂ before fixing in formalin-sea water, and have found many in which the nematocyst threads are devaginated. To my joy I found that the nematocysts were *birhophaloïdes*, just as Claus and Iwantzoff had described them. Actually they were first described and figured by Gegenbaur (1853b, Pl. 18, fig. 2). Subsequently in 1963 and 1964 I discharged numbers of these birhophaloïdes some of which I sent to Weill.

DESCRIPTION OF THE SPECIES

Nectosome: About a dozen nectophores (text-figs. 13, 14) are arranged as usual in two rows, each nectophore measuring from 13 to 19 mm in diameter or a little more. The axial side of each is deeply hollowed out. The two ridges on the latero-axial sides run up to form a rounded angle as shown (upside down) in Lesueur's figure 4 of an axial view. As described by Leuckart, the edges of these axial wings come together below to form a keel, but are wide apart above and embrace the

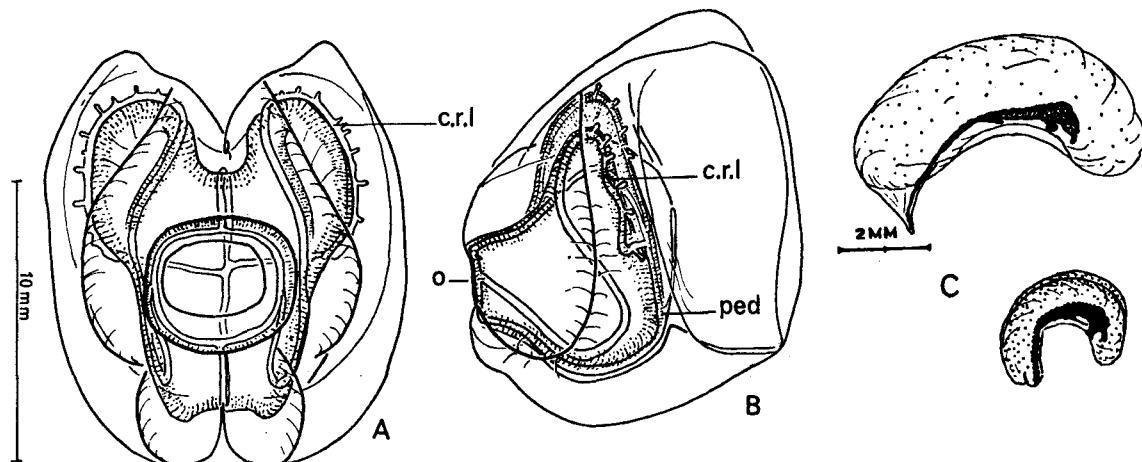


FIG. 14. *Apolemia uvaria* Lesueur. Nectophores and bracts
A, ostial view; B, lateral view of a nectophore; C, bracts (from Totton & Fraser, 1955, figs. 8a-c).

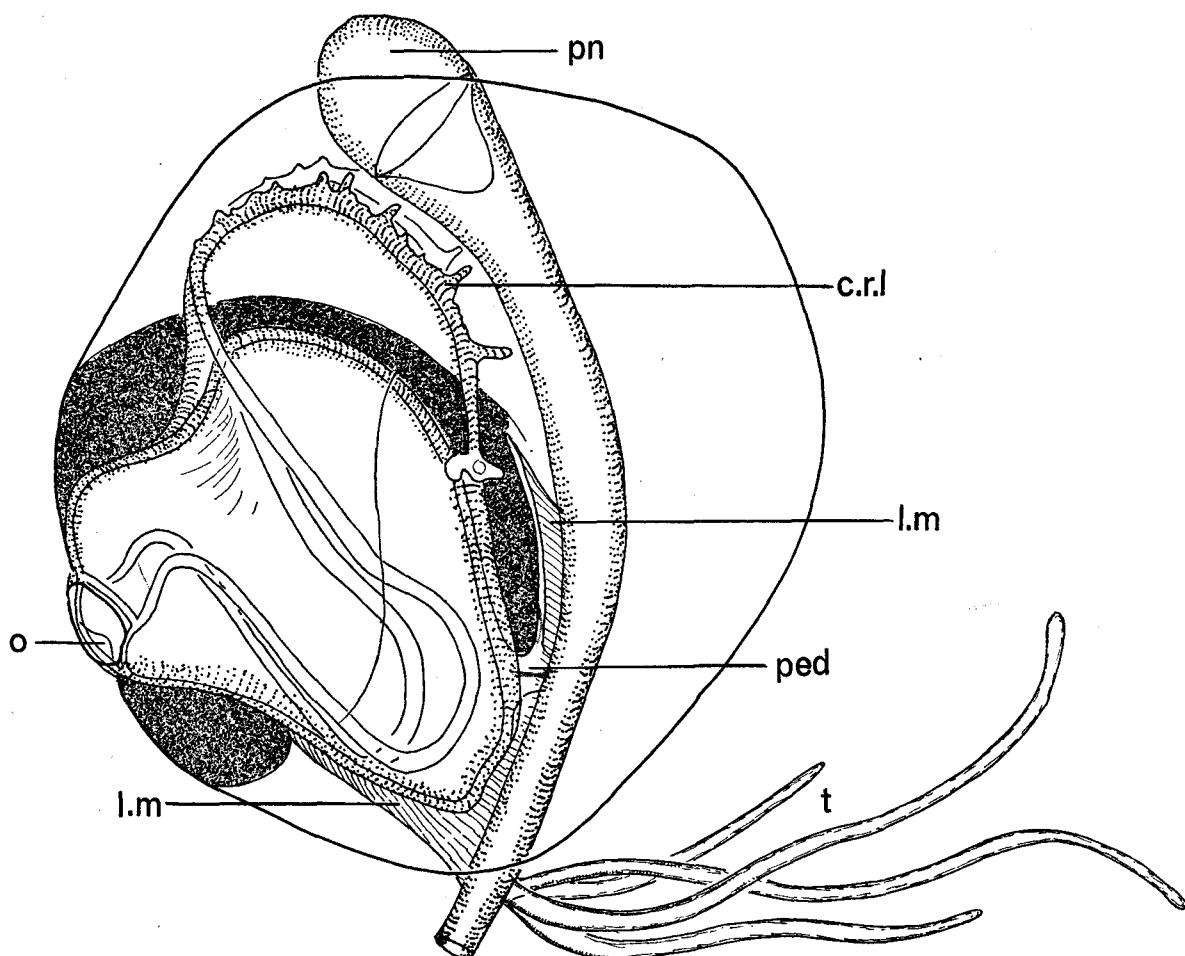


FIG. 15. *Apolemia uvaria* Lesueur. Upper part of the nectosome of a Villefranche specimen to show the peduncle of the nectophore, and the unique type of tentacle, $\times 8.3$
c.r.l. = lateral radial canal, showing spur canals; *l.m.* = muscular lamella; *o* = ostium; *ped* = peduncle;
pn = pneumatophore; *t* = tentacle.

lower part of the nectophore above. The uppermost of the fully formed nectophores embraces all the budding nectophores and the lower part of the pneumatocodon at the apex of the stem. The upper end of the muscular lamella, which as usual develops on the upper and lower sides of the nectophore-peduncle, reaches about half-way up the axial wall of the nectophore to a level a little above the point where the lateral radial canals branch off from the dorsal radial canal. The pedicular (peduncular) canal, which is rather difficult to locate (see text-fig. 15), is lower down and about half-way between the junction of the lateral radial canals and the lowermost part of the nectophore. The upper wall of this pedicular canal curves down gently from the dorsal canal to join the stem in a U-like curve. The lower wall of the pedicular canal is very short, and in separated nectophores is generally missing because the whole of the lower wall of the ventral radial canal, to which the lower half of the muscular lamella is attached, becomes torn away, leaving the exposed ventral canal in a long torn area at the base of the nectophore. This is confusing to anyone not familiar with the species.

Five or six special nectosomal tentacles (text-fig. 15), to which I have already referred, arise near the pedicular canal of each nectophore. The lateral radial canals form S-like bends. On the axial side of the upper bend of the S are a number of short irregular branches, found only in *Apolemia*.

Siphosome: May reach a length of 20 m, drawn up into a spiral when contracted, with numerous scaphoid *bracts* extending to the outer (dorsal) side, arranged in cormidial groups, up to 5 cms apart when the stem is extended. Each cormidium bears one or perhaps more *gastrozoooids* and fifty or more *palpons*, both having fine filiform tentacles of the same kind issuing from their bases. The palpons are very long and slender and very active in life. The bracts like the nectophores are covered with opaque patches of nematocysts on the outer side. Some of the palpons are shorter and more rigid, with much brown pigment and heavily covered with nematocysts which can sting the hands. These nematocysts are large and banana-shaped, 0.77 mm in length with a long barbed hampe. The tentacles of the gastrozoooids and palpons are armed with birhopaloïd nematocysts. A gastrozoooid tentacle severed from the upper part of the stem of a specimen taken at Villefranche and anaesthetized in $MgCl_2$, when straightened out measured 4 cm in length. My experience with siphonophore tentacles makes me estimate that in life this tentacle might have been three or four times as long or perhaps more. If an extended piece of tentacle is mounted on a microscope slide it can be seen to form internodes about $\frac{1}{10}$ mm in diameter separating nodes of twice this diameter. The nodes contain a pair of birhopaloïd nematocysts and appear to have a cap of gland cells, and there appears to be a 'double

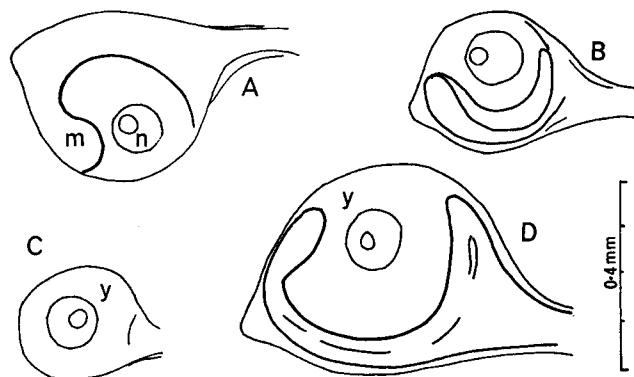


FIG. 16. *Apolemia uvaria* Lesueur
Detached monovon gonophores of a specimen from
Friday Harbour, California, Fontaine Coll. *m* = manu-
brium; *n* = nucleus; *y* = yolk.

fibre' down the centre of the tentacle. The gland cells and surrounding granules as well as the double fibre do not stain with borax carmine. The nematocysts appear to be associated with a pigment (see Vogt's fig. 1, Pl. 2). The 'double fibre' measures 0.01 mm in diameter. A specimen from Nanaimo, provisionally identified as *A. uvaria*, bore in addition on the tentacles and palpacles, oval nematocysts, $20-30\mu \times 19-20\mu$, whose devaginated spiral threads had no hampe.

Gonophores (text-figs. 16, 17) (see Leuckart, 1854, p. 319) are developed in bunches on the distal part of the stem. More information about them is needed. According to Claus (1863, p. 544) *A. uvaria* is dioecious.

Palpon nematocysts: The material used was the tip of a large palpon of a specimen of *Apolemia*(?) species from Nanaimo kindly sent me by Dr. G. O. Mackie of Alberta University.

A crush preparation showed several evaginated large banana-shaped nematocysts with a long hampe.

Maximum diameter	0.018 mm
Length	0.077 mm
Length of hampe	0.18 mm
Diameter of hampe	0.007 mm
Diameter of hampe including spines	0.013 mm

No thread was visible beyond the long hampe. These measurements do not correspond with those of Claus's (1863) figure 8d, Plate XLVI. The capsule and the hampe are much longer than those of Claus's specimen, who gave the length and diameter of his 'länglich elliptische Kapsel' as about 0.023 mm \times 0.011 mm. But his figure shows that the length of the capsule is nearly three times its diameter. My preparations of nematocysts made at Villefranche in 1964 could not be used in this synopsis.

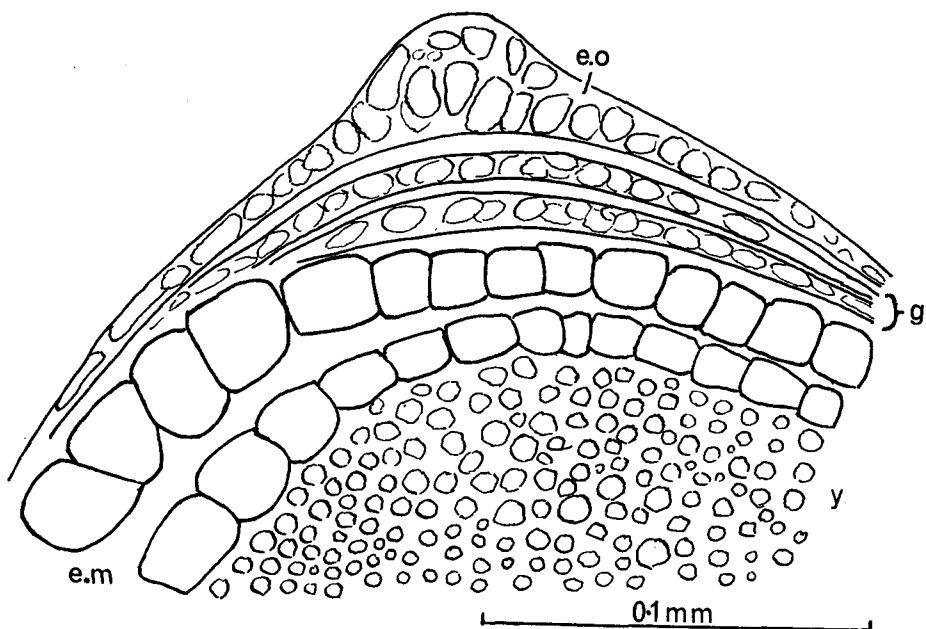


FIG. 17. *Apolemia uvaria* Lesueur. Distal end of female gonophore to show the laterally displaced manubrium lying wholly within the two-layered inner ectoderm. Radial canals are suppressed (semi-diagrammatic, based on a camera lucida sketch) *e.o* = outer ectoderm; *g* = inner ectoderm (Glockenkern); *e.m* = endoderm of manubrium; *y* = yolk.

Family 4: AGALMIDAE Brandt, 1835

This is a family of long stemmed physonects whose generally long series of nectophores are arranged in two rows on either side of the nectosome. The terminal part of the oozooid in the three well-known genera, *Agalma*, *Halistemma* and *Nanomia*, can be seen at the distal end of the stem, still surrounded by its larval palpons and bearing a larval type tentacle (text-fig. 7).

Only five of the sixteen species recognized in this Synopsis, which are grouped into eight genera, are well known as complete animals. Tabulated in the order in which they are treated in this Synopsis, Bedot (1896), in his academic review of the literature of the Agalmidae, recognized the following:

TABLE IV

Modern names of species

- Agalma elegans* (Sars, 1846)
- Agalma haackeli* Bigelow, 1911
- Agalma okeni* Eschscholtz, 1825

Bedot's names

- | | |
|--|-------------------------------------|
| <i>Agalmopsis sarsi</i> Kölliker | |
| <i>Agalma eschscholtzii</i> Haeckel (<i>non</i> Lesson) | |
| { | <i>Agalma okeni</i> Eschscholtz |
| | <i>Crystallomia polygonata</i> Dana |
| | <i>Agalma breve</i> Huxley |

TABLE IV (cont.)

<i>Modern names of species</i>	<i>Bedot's names</i>
<i>Agalma clausi</i> (Bedot, 1888)	<i>Stephanopsis clausi</i> Bedot
<i>Halistemma rubrum</i> (Vogt, 1852)	<i>Halistemma rubrum</i> Huxley
? <i>Halistemma amphytridoides</i> Huxley, 1859	<i>Cupulita amphitrites</i> Bedot
<i>Nanomia bijuga</i> (Chiaje, 1841)	{ <i>Cupulita picta</i> Haeckel
<i>Nanomia cara</i> Agassiz, 1865	{ <i>Cupulita canariensis</i> Haeckel
<i>Lychnagalma utricularia</i> (Claus, 1879)	{ <i>Anthemodes ordinata</i> Haeckel
	<i>Cupulita cara</i> Haeckel
	<i>Lychnagalma utricularia</i> Haeckel

Three of these species have been so rarely taken that I have never seen specimens, viz. *A. haeckli*, *A. clausi* and *Lychnagalma utricularia*.

To the eight sound (? *Stephanomia amphytridoides** excluded) species accepted by Bedot in 1896 must now be added:

<i>Halistemma cupulifera</i> Lens & van Riemsdijk, 1908	<i>Marrus orthocannoides</i> Totton, 1954
<i>Halistemma striata</i> sp.n.	<i>Marrus orthocanna</i> (Kramp, 1942)
<i>Cordagalma cordiformis</i> Totton, 1932	<i>Moseria gen.n. convoluta</i> (Moser, 1925)
<i>Marrus antarcticus</i> Totton, 1954	<i>Lychnagalma vesicularia</i> Haeckel, 1888

KEY TO GENERA OF AGALMIIDAE

1. Tentilla unicornuate	3
Tentilla with more than one terminal appendage	2
2. Tentilla multicornuate	<i>Lychnagalma</i> (p. 73)
Tentilla tricornuate	<i>Agalma</i> (p. 52)
3. Cnidoband very large, not spirally coiled	<i>Erenna</i> (p. 73)
Cnidoband small, spirally coiled	4
4. Cnidoband without basal involucrum	<i>Marrus</i> (p. 61)
Cnidoband with basal involucrum	5
5. Nectophores very flat. Antarctic species	<i>Moseria</i> (p. 67)
Nectophores thick, not Antarctic species	6
6. Mature specimens small, Gonodendra in pairs at bases of a series of palpons, sexes alternating from side to side	<i>Nanomia</i> (p. 68)
Mature specimens large, one ♀ gonodendron in each cormidium	<i>Halistemma</i> (p. 55)
7. Minute heart-shaped nectophores with unlooped lateral, radial canals	<i>Cordagalma</i> (p. 61)

Genus: *AGALMA* Eschscholtz, 1825

Type species *A. okeni* Eschscholtz, 1825.

Agalmopsis Sars, 1846; Kölliker, 1853

Crystallomia Dana, 1858; Kawamura, 1910/1911

Crystallodes Haeckel, 1869

Stephanopsis Bedot, 1896 (preocc. Cambridge, 1869)

Stephia Stechow, 1921

Agalmids with tricornuate tentilla, consisting of involucrate coiled cnidoband, terminal ampulla and paired lateral horns (Pls. IX, X).

*This indeterminate species is discussed on page 60.

Key to species of *AGALMA*

- 1. Distal border of bract very thick, obliquely truncated and faceted. Nectosac Y-shaped, viewed from above (Pl. IX, figs. 3, 11) *okeni*
- Distal border of bract thin, not truncated ²
- 2. Bracts with three unarmed, longitudinal ridges; nectosac triangular, viewed from above *elegans* (p. 54)
- Bracts with from three to five armed longitudinal ridges and red pigment spots *haeckeli* (p. 54)
- 3. Thick, oval, foliaceous bracts with red spots, two teeth on each side. Nectophores resembling those of *okeni* *clausi* (p. 53)

Agalma okeni Eschscholtz, 1825

Plate IX, figures 1-14; Plate XI, figure 3

Crystallomia polygonata Dana, 1858; Chun, 1897; Kawamura, 1910/1911*Agalma breve* Huxley, 1859*Crystallodes rigidum* Haeckel, 1869*Crystallodes vitrea* Haeckel, 1888*Crystallomia* sp. Lens & van Riemsdijk, 1908, figs.

A common species that occurs in the warmer regions of all three great oceans.

The nectosome is a dodecagonal body slightly tapered above, where lies the small egg-shaped pneumatophore with reddish-brown pigment at its apex. Eight lamellae stretch from pneumatosaccus to pneumatocodon. The nectophores and other details were figured beautifully by Bigelow (1911b, Pl. 17) and by Kawamura (1910/1911) reproduced here on Plate IX, figures 1-14.

Two types of nectophore are associated in plankton net hauls with the same kind of bracts and siphosome. One of these, which has two vertical ridges on the lateral facet on each side, is the mature form figured by Dana (1858) (Pl. IX, fig. 2). Nectophores produced in the early growth stages appear (see Totton, 1954, p. 54) to have only one ridge on each side (Pl. IX, fig. 10). To this type Kawamura (1910/1911) applied the name *Crystallomia polygonata* Dana.

The animal may reach a length of 13 cm and a width of 2, have eighteen nectophores on each side and from five to fifteen cormidia according to age.

Agalma haeckeli Bigelow, 1911*Agalma eschscholtzii* Hkl. 1888non *A. eschscholtzii*, 1843

Described and figured from a single, small specimen taken off Beligemma, Ceylon. Both description and figures are inadequate. As Bigelow (1911b) judged, this is not a well established species, but it is included here in the hope that someone will keep a look out for it.

The only recorded characters that might be regarded as specific are ribs, from three to five in number, on the bracts, and the patchwork of reddish pigment that they bear.

Agalma clausi Bedot, 1888*Stephanopsis clausi* Bedot, 1896*Agalma sarsi* Fewkes, 1881 (preocc. Kölliker, 1853). non *A. elegans* (Sars) 1846

This species was well figured and described by Bedot (1888) from three specimens taken at Villefranche, near Nice. It has not been recorded since then. Possibly it has escaped observation there because there is no copy of Bedot's paper in the Villefranche Station library. This paper by Bedot provides, perhaps, the most detailed description of any species of *Agalma*. But the nectophores were not described or figured adequately, so that I feel that there must be some doubt about the distinctiveness of the species. In some ways it resembles *A. okeni*, though the bracts are different. *A. clausi* has foliaceous bracts with parallel rows of red glands or pigment spots. The animal reaches a length of 24 cm and the stem is stiff and not contractile. There are thirteen nectophores or so on each side. They 'are like those of *A. elegans* and *A. okenii*', Bedot said, although the nectophores of these two species are unlike one another.

Agalma elegans (Sars, 1846) Fewkes, 1880

Plate X, figures 11–17; Plate XI, figures 1, 2; text-figures 7, 18–20

Agalmopsis elegans Sars, 1846 (partim)*Agalmopsis sarsi* Kölliker 1853; Leuckart, 1853*Agalma punctata*: Leuckart, 1853 (non Kölliker, 1853; Vogt, 1854)*Agalma clavata* Leuckart, 1853; 1854 (partim)*Agalma elegans* Fewkes, 1880a; 1881*Agalma sarsi* Fewkes, 1880a

Agalmopsis elegans Sars, was a compound species with two components, the second of which – form B – consisted of a trifid tentillum. The bulk of the description and all the rest of the figures referred to the other component, now known as *Nanomia cara*. Kölliker (1853) found specimens at Messina with trifid tentilla and called them *Agalmopsis sarsi*. Haeckel (1888b) restricted the name *elegans* to this species with the trifid tentilla, though he thought it different from *Agalmopsis sarsi* Kölliker.

Kawamura (1911b) gave a good figure of the whole animal (Pl. X, fig. 11) as well as figures of details. A figure of the whole animal and details were given by Totton (1954) reproduced here in text-figure 7.

Nectophores (text-figs. 7, 18): The nectosac, seen from above or below, is triangular in shape not Y-shaped as in *okeni*.

Bracts (Pl. X, figs. 14, 15): Foliaceous, 10 mm × 6 mm, in two latero-ventral rows, very thin at the distal margin which is tridentate. The upper convex surface bears three ridges on the distal half. The bracteal canal terminates, save occasionally for a fine vestigial extension, some distance short of the tip.

Tentacles (Pl. X, fig. 17): The cnidoband of the tricornuate tentillum is completely enclosed when mature in the involucrum. The lateral horns are up to 3 mm in length. The protozooid has tentilla with kidney-shaped cnidosacs.

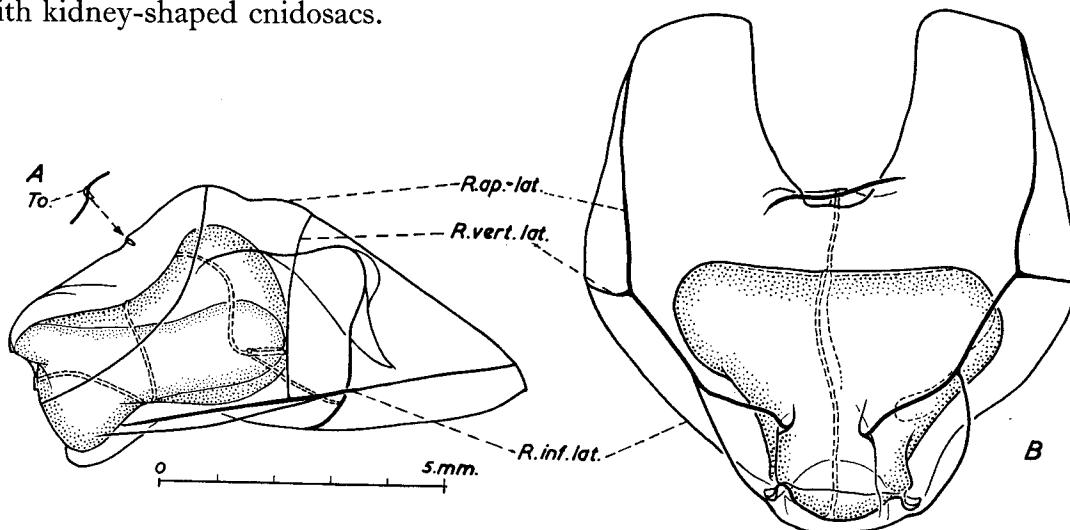


FIG. 18. *Agalma elegans* (Sars). Lateral, A, and upper, B, views of a nectophore from Villefranche,
× 8

R.ap.lat = apico-lateral ridge; R.inf.lat = infra-lateral ridge; R.vert.lat = latero-vertical ridge;
To = tooth (from Totton, 1954, fig. 24).

Gonophores: A female gonodendron at the proximal end of each cormidium. There is a gap along the stem between the insertion of this and the male gonophores, which with the palpons are scattered over more than half the length of each cormidial segment (text-fig. 7). Fewkes (1883) gave a good figure of the female gonophore and described the early development of the so-called ‘Athorybia larva’, of *A. elegans* (text-fig. 19). For the detailed description of the metamorphosis of this larva (text-figs. 19B and 20) see Totton (1956).

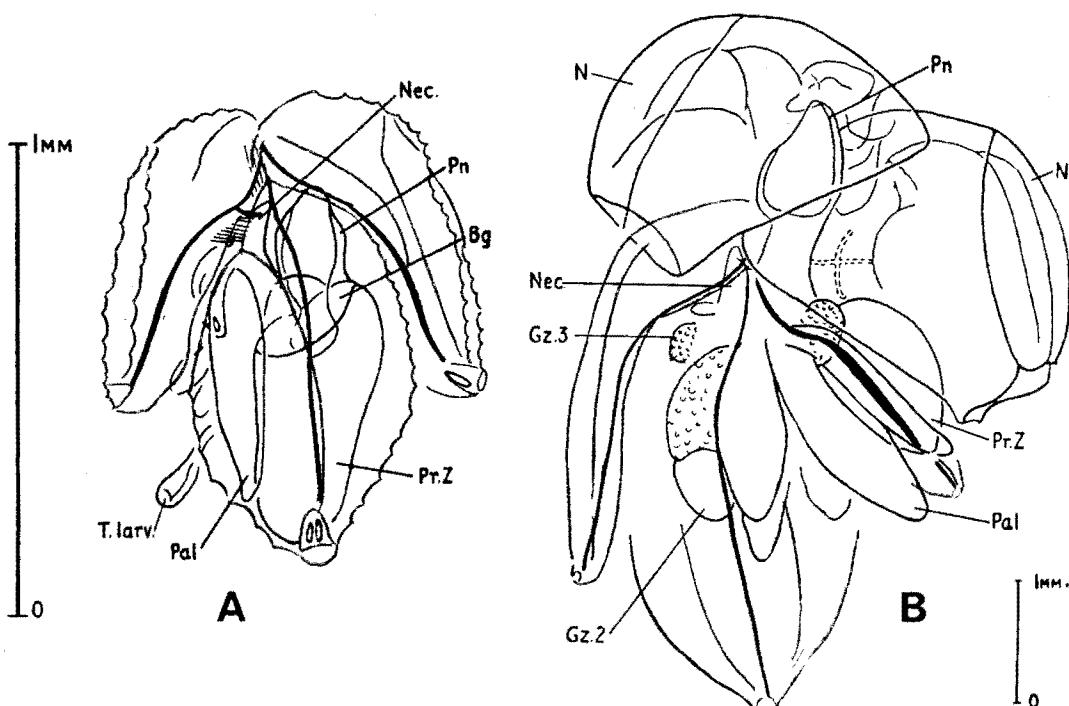


FIG. 19. *Agalma elegans* (Sars). 'Athorybia' larvae
A, an early larva, $\times 62$, showing bracts (coloured blue), bracteal canals (red), and the first of a ring of palpons; B, an early stage in metamorphosis, $\times 16$. That side of the upper end which carries the pneumatophore has elongated to carry the latter above the ring of coronal bracts. Two nectophores have developed and are functional. The protozooid has taken up a latero-terminal position leaving the second gastrozooid at the end

Pn = pneumatophore; *N* = nectophore; *T.larv.* = larval tentacle; *Gz2, 3* = secondary gastrozooids; *Nec* = nectostyle; *Bg* = basigaster; *Pal* = palpon; *Pr.Z* = protozooid (from Totton, 1956, figs. 2, 6).

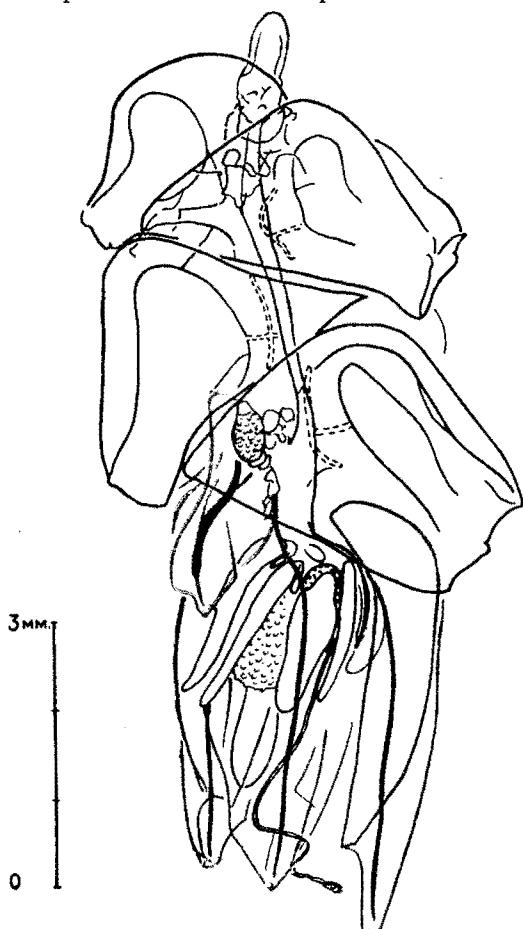


FIG. 20. *Agalma elegans* (Sars)
A juvenile specimen $\times 11$. Nectosome and siphosome have elongated in opposite directions. The nectostyle can still be seen opposite to the pedicel of the first nectophore. Note the small size of the protozooid. Definitive (secondary) stem bracts coloured green. Tentacles not shown except for part of the larval one of the protozooid (from Totton, 1956, fig. 9).

Genus: ***HALISTEMMA*** Huxley, 1859

Type species *H. rubrum* (Vogt) 1852.

Agalmidae with unicornuate tentilla whose cnidobands lack a marked basal involucrum. Only two species have hitherto been described, *H. rubrum* (Vogt) and *H. cupulifera* Lens & van Riemsdijk, but plankton samples sometimes contain nectophores of agalmids which somewhat resemble the large nectophores of *H. rubrum*, but with extra, vertical, lateral ridges. Such a specimen was taken in 1929 by Beebe off Bermuda, in about 1530 m (700 fathoms). It has been described under the name *H. striata* sp.n. on page 59 with others, which were taken at two Discovery stations, 81 and 704, in open nets fished obliquely from 231 m and 650 m to the surface. The nectophore is shown in text-figure 24.

***Halistemma rubrum* (Vogt, 1852)**

Plate XII

- Agalma rubra* Vogt, 1852; 1854
Agalmopsis rubra Leuckart, 1853
Agalma rubrum Leuckart, 1854
Agalmopsis punctata Kölliker, 1853
Halistemma rubrum Huxley, 1859
Agalmopsis rubra Schneider, 1899
Stephanomia rubra Bigelow, 1911b; Totton, 1954

A well-known Mediterranean species, studied in detail and beautifully illustrated by Vogt (1854, Tab. 7) but confused by him with juvenile specimens of *Nanomia bijuga* and with the 'Athorybia larva' of *Agalma elegans*, all of which he mistook for early growth-stages of *H. rubrum*.

The *nectosome* (up to 17 cm long) carries as many as thirty pairs of nectophores, which measure 13 mm in length and are 10.5 mm wide (text-fig. 21). The corresponding siphosome would be 176 cm in length. The stem is about 1.5 mm in diameter.

The *gastrozooids* are spaced about 2.5 cm apart, measure from 15–17 mm in length and 2 mm in diameter, and have an elongate ovate basigaster measuring 4.5 mm in length and 1.5 mm in diameter. The tentacle bears from four to six unicornuate, vermillion tentilla, coiled up in from eight to ten coils and 5 mm in length, on pedicels measuring 1 cm in length. At the junction of the pedicel with the cnidoband there is an inconspicuous expansion that probably represents the involucrum. The tentillum (see Korotneff, 1884; and Schneider, 1899) consists of a cnidoband loosely coiled ten or so times round the two cords that expand on activation and cause the apparatus to function like a mustard plaster. The bulk of the cnidoband consists of innumerable rows of sabre-shaped nematocysts which measure from 65–70 μ in length and 7 μ in width. On each side in the proximal region is a row of larger bean-shaped nematocysts of the same length but 20 μ in width. The terminal filament exceeds 2 cm in length and terminates in a cone-shaped coil of ten turns, 0.75 mm in length, faithfully depicted by Vogt (1854, Tab. 8, fig. 1).

The *palpons* are very active and vermiform in extension. They measure 11 mm in length and 2 mm in diameter. Their simple palpacles bear pairs of small nematocysts. Their arrangement and association with the gonodendra has not, as far as I know, been described hitherto. I observed the following arrangement in a specimen whose nectosome measures 10 cm in length, preserved in formalin after relaxation in MgCl₂. It was taken at Villefranche at 9.30 a.m. on March 31, 1949, and bore about forty gastrozooids.

On each cormidium there are proximally two or three palpons, probably derived from secondary budding. Distal to them there is a larger palpon with a palpacle that measures 15 mm in length, not fully

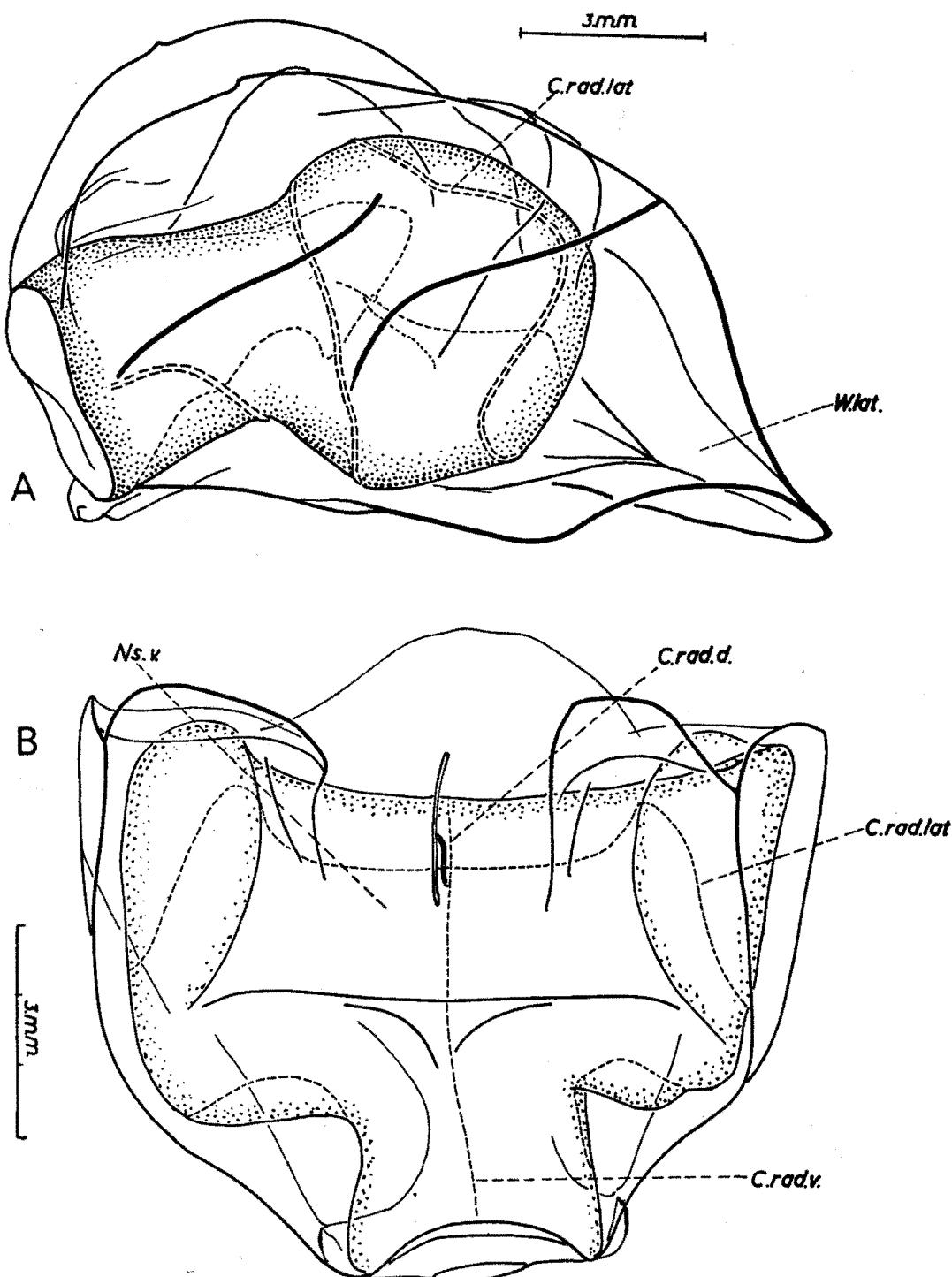


FIG. 21. *Halistemma rubrum* (Vogt). Nectophore, $\times 8$
 A, lateral view of specimen from Villefranche; B, underside of the same
C.rad.d., *C.rad.lat.*, *C.rad.v* = dorsal, lateral and ventral radial canals; *Ns.v* = ventral wall of
 nectosac; *W.lat* = lateral wing (from Totton, 1954, fig. 12B, E).

expanded. From the distal side of its base is budded, in the mid-ventral line, the wide muscular stemmed female gonodendron, with its branches and medusoid gonophores resembling a miniature bunch of grapes. When mature it is about 5 mm in diameter, and capable of a great deal of expansion and contraction. It is situated at about one-third the distance from the last gastrozoid to the next one, and bears a number of reinforcing rings in the stem-wall. Distal to the female gonodendron are three other large palpons with palpacles, occupying the middle region of the cormidium. On the distal side of the base of each and in the mid-ventral line of the stem is a reduced male gonodendron (text-fig. 22).

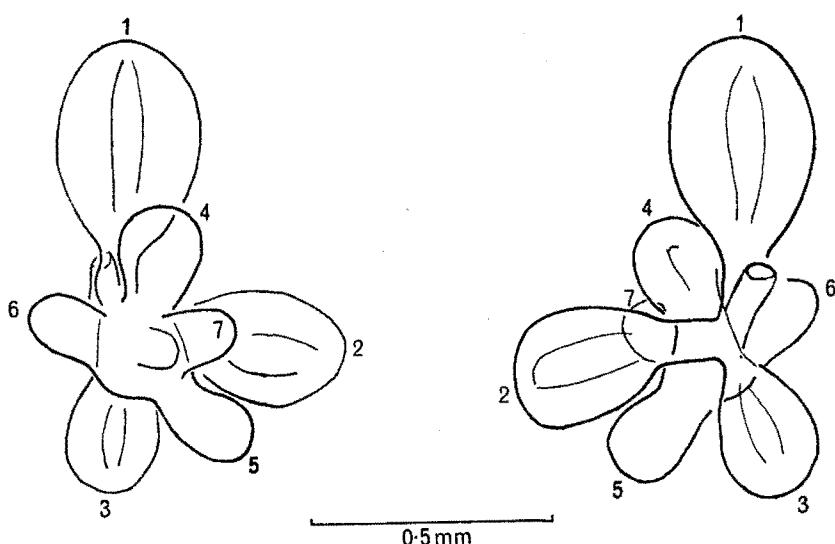


FIG. 22. *Halistemma rubrum* (Vogt)
Two views of an early growth stage of a male gonodendron, $\times 64$. The numerals refer to the order of budding.

It has not been sufficiently described hitherto. It can be seen that each of the male gonophores buds off at an angle of rather more than 120° in the transverse plane from the base of its predecessor to form a left-handed spiral. When mature the pedicels of the male gonophores grow to the comparatively enormous length of 5 mm. There may be present on each male gonodendron from eight to ten mature male medusoid gonophores, which start to pulsate whilst still attached, but finally detach themselves to swim away and shed their sperms. They are about 6 mm in length and lack tentacles. Each female gonophore – up to 0.7 mm in diameter – contains a single egg. In the distal region of each cormidium may be found two or three other palpons probably derived from secondary budding. It is not known whether they in turn develop gonodendra.

The *bracts* (text-fig. 23) are leaf-like, distally pointed, with two latero-terminal teeth and a short median terminal ridge. Overlying the tip of the bracteal canal there is a sagittal pad of nematocysts, which is most prominent in early growth-stages. The muscular lamella is attached a little below the proximal, pointed end, and the muscle is best seen on the under side of the pedicel.

Halistemma cupulifera Lens & van Riemsdijk, 1908
Plate XIII, figures 1-3

A partly known species described and figured from a single small fragment of a specimen, characterized by the terminal filament of the tentillum (Pl. XIII, fig. 2). This ends in an acorn-like appendage, whereas that of *H. rubrum* ends in a cone-shaped coil of ten turns, measuring about 0.75 mm

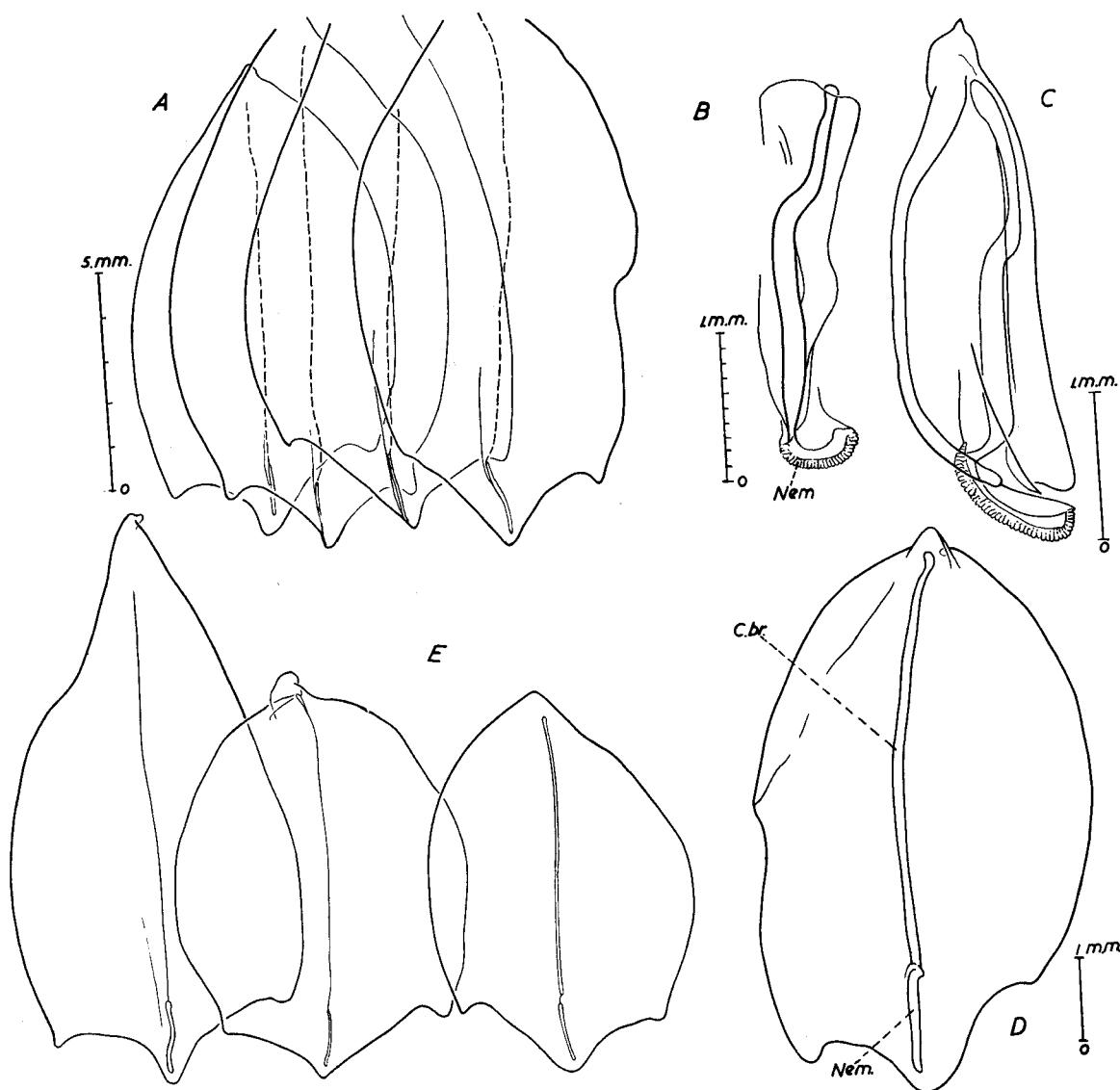


FIG. 23. *Halistemma rubrum* (Vogt). Bracts of specimen from Villefranche
B, C, young bracts, $\times 20$, to show the apical position of the pads of nematocysts. A, E, $\times 6$; D, $\times 11$
C.br. = bracteal canal; *Nem.* = apical pad of nematocysts (from Totton, 1954, fig. 14).

in length. There was said to be no involucrum, but that of *H. rubrum* is vestigial and has been missed by earlier observers. The rest of the original description is unsufficiently distinguishable from that of *H. rubrum*. It will be recognized again by its terminal filaments.

Halistemma striata sp.n.

Text-figure 24

The species is known only by very distinctive nectophores, which vary in width from 8 mm to 19 mm. The figured specimen is selected as the type. It was taken off Bermuda by W. Beebe.

Nectophore: There is a characteristic arrangement of four lateral ridges (text-fig. 24, *r, r, r, r*), which descend from the upper lateral ridge (*vk'* of Claus; see text-fig. 34) at an angle of about 30° from the vertical towards the ostial end of the base. The ridge at the ostial end bifurcates; the upper, inner branch runs down to and just below the ostial chromatophore (*c.o.*). The basal end of the lower

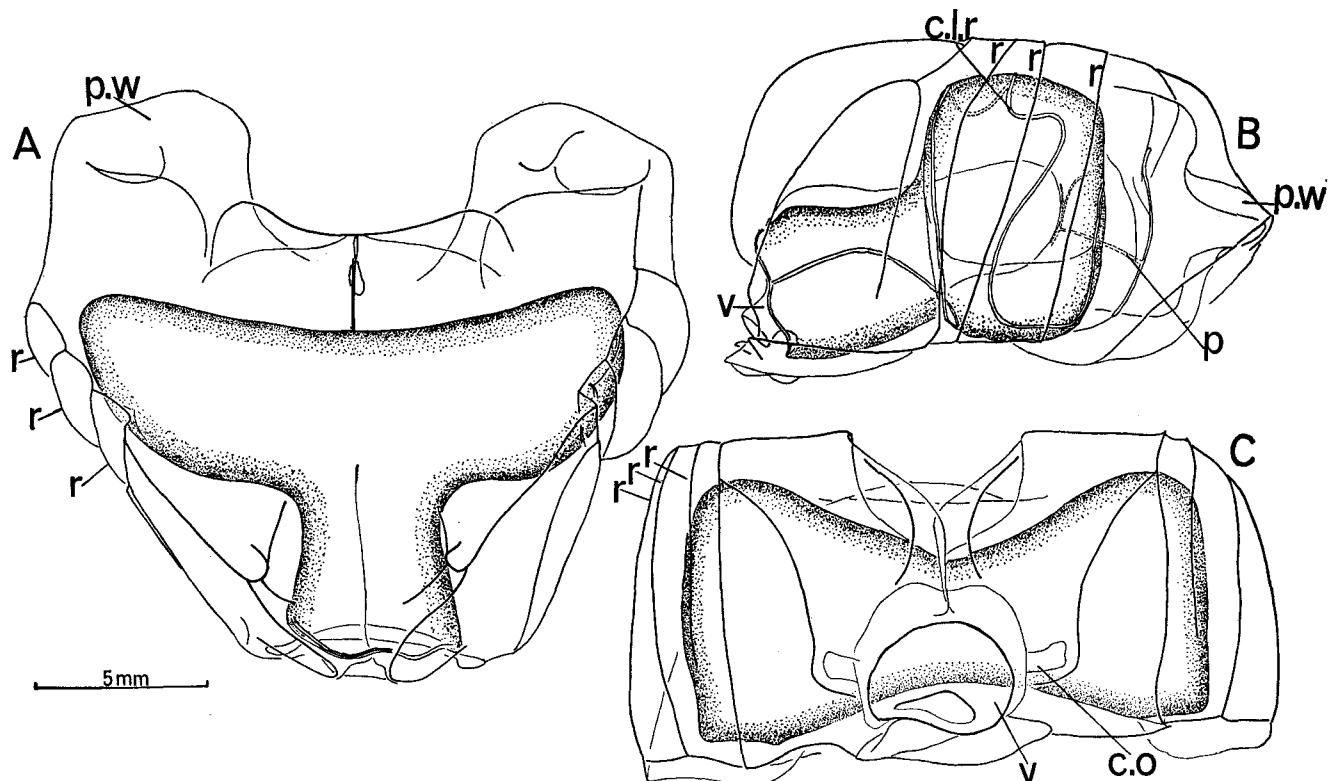


FIG. 24. *Halistemma striata* sp.n., from Bermuda, Beebe Coll. Three views of a nectophore to show ridges, $\times 4.9$
A, view from above; B, lateral view; C, ostial view

r = lateral ridges; c.o = ostial chromatophores; p = pedicular canal; p.w = wedge process; v = velum; c.l.r = lateral radial canal.

one is scarcely visible in a lateral view without staining. In text-figure 24B it is represented as incomplete.

There are prominent lateral wedge-processes (*p.w.*) at the stem end with marked articulation cavities and bosses.

The lateral radial canals run as shown in text-figure 24B. They rise above the horizontal after branching from the pedicular canal and then sweep down the outer and stem-side edge of the nectosac. There is a short, horizontal basal section, after which they sweep up just on the stem-side of the second ridge, to run ostiad half-way to the third ridge. Here they turn inwards over the shoulder of the lateral horn of the nectosac. They then sweep down the outer edge of the nectosac to the base, from which they run in obliquely to the circular canal at the ostium.

Known distribution: Bermuda (W. Beebe Coll.).

"Discovery" St. 81, $32^{\circ} 45' S$, $8^{\circ} 47' W$, 1 nectophore.

"Discovery" St. 704, $3^{\circ} 37.7' N$, $29^{\circ} 14' W$, 7 nectophores.

INDETERMINATE SPECIES

? *Halistemma amphytridis* (Lesueur & Petit), 1807

Stephanomia amphytridis Lesueur & Petit, 1807

? *Stephanomia amphitridis* Huxley, 1859

? *Stephanomia amphitridis* Bigelow, 1911b

One hundred and fifty-six years ago the name *Stephanomia amphytridis* was first used by Lesueur & Petit (1807) for the figured siphosome of a large unicornuate agalmid which at present cannot be

specifically identified. Fifty-two years later Huxley (1859) used the same name for a similar siphosome taken off the east coast of Australia, which he figured in some detail. Fifty-two years later still Bigelow (1911b) described and figured two similar siphosome fragments from the Eastern Tropical Pacific, both in beautiful condition, and with colour notes. These specimens are probably congeneric with species now referred to the genus *Halistemma*.

Even so, in the absence of data about the nectosomes of these four specimens, it is difficult to base a description of a species on them, although if a complete, well preserved specimen should ever be taken off the east coast of Australia, the details of whose siphosome corresponded with Huxley's (1859) and Bigelow's (1911b) figures and material, then we could firmly establish a species *Stephanomia amphytridis* Lesueur & Petit, 1807.

A great deal of similar material of both nectosomes and siphosomes collected off Bermuda by Beebe and also by the ships of the National Institute of Oceanography is known to exist, and it is to be hoped that yet another fifty-two years will not pass before it is examined more fully and described.

Genus: ***CORDAGALMA*** Totton, 1932

Minute agalmids with heart-shaped nectophores, whose lateral canals do not form sigmoid curves. Monotypic genus for *C. cordiformis* Totton, 1932.

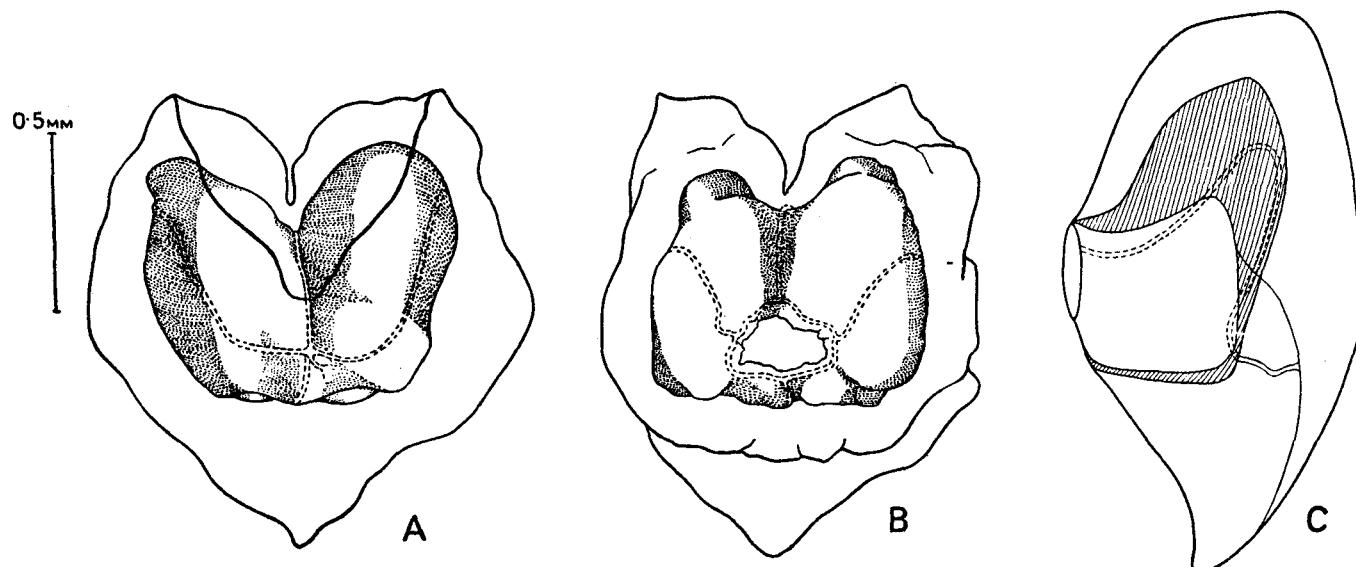


FIG. 25. *Cordagalma cordiformis* Totton

A, ventral and B, ostial view of a nectophore from the Great Barrier Reef, $\times 47$. C, diagrammatic optical section of a nectophore (from Totton, 1932, figs. 8, 9)

Cordagalma cordiformis Totton, 1932

Text-figure 25

Known only from its minute nectophores, this must be the smallest of Physonects, and has been generally overlooked, though reported by the author from the following localities, Great Barrier Reef; off St. Vincent, West Indies; Villefranche-sur-Mer, A.M., France; Gulf of Aqaba; East African coast.

The nectophores (text-fig. 25) measure $2.0 \text{ mm} \times 1.2 \text{ mm} \times 1.1 \text{ mm}$. They are heart-shaped when viewed from the ostial side and the lateral radial canals do not form sigmoid curves, but make one ascending loop on their way to the circular canal.

Genus: **MARRUS** Totton, 1954

Type species *Marrus antarcticus* Totton, 1954.

A group of three unicornuate Agalmidae known only from fragments, whose nectophores have straight (unlooped) lateral radial canals.

***Marrus antarcticus* Totton, 1954**

Text-figures 26, 27

A species associated with the antarctic zone and with water that has recently left the zone, or is in close proximity. A deep-water or mid-water species which is dioecious – an unusual condition for agalmids.

Pneumatophore: Carrot-shaped, 4·5 mm length, 1 mm diameter.

Nectophores (text-fig. 26): 17 mm × 15 mm × 9 mm. Lateral facets not cut off by a vertical lateral ridge. Ridges V K' and V K" (terminology of Claus, 1879) present though not easily seen without staining. Nectosac without musculature on its broad ad-axial face. Lateral radial canals straight, without sigmoid loops, pigmented deep, rich, orange-scarlet.

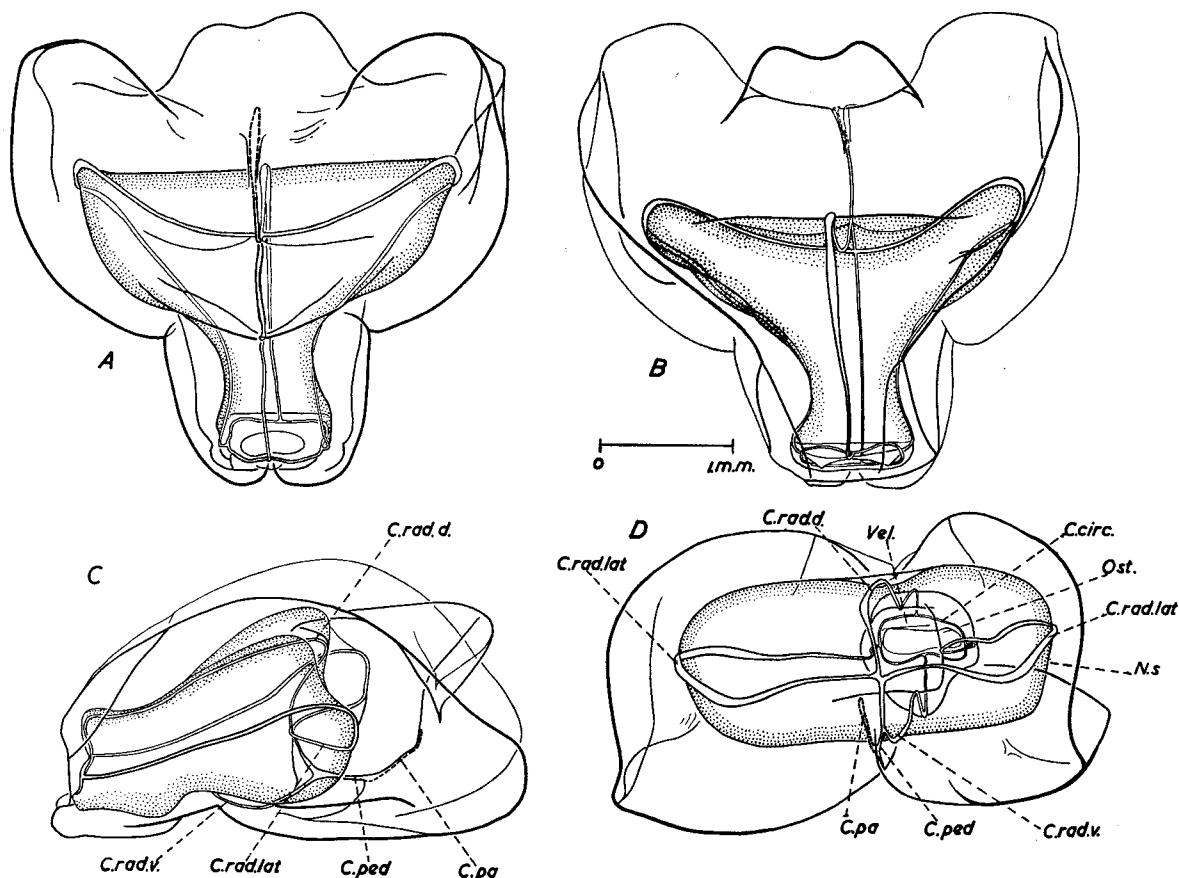


FIG. 26. *Marrus antarcticus* Totton. Nectophores

A, under side; B, upper side; C, lateral view; D, adaxial view, $\times 4.6$

C.circ., C.rad.d., C.rad.lat., C.rad.v. = circular, dorsal, lateral and ventral radial canals; C.pa = pallial canal; C.ped = pedicular canal; Ns = nectosac; Vel = velum; Ost = ostium (from Totton, 1954, fig. 20).

Stem: Deep, rich orange-scarlet in colour.

Gastrozoids and tentacles: Gastrozoids long and narrow, up to 30 mm in length, of which one-fifth to one-half is formed by the cylindrical basigaster. Tentilla unicornuate, without involucrum. Cnidoband in three coils, 0.9 mm to 2.5 mm in length. Pedicel of tentillum 0.8 mm in length, terminal filament 1-5 mm in length. Nematocysts of cnidoband in a dozen rows, about 5,000 in number, finger-shaped (?) anisorhizas, 40 μ long, 7 μ diameter. On either side are 125 large 'accessory' nematocysts, (?) mastigophores, measuring 50 μ long, 20 μ diameter. The terminal filament contains numerous smaller, ovoid, (?) isorhizas, measuring 18 μ \times 5 μ , as well as larger ovoid nematocysts measuring 18 μ \times 13 μ .

Palpons: Up to 30 mm length, slender, possibly lacking palpacles, borne on gonodendra.

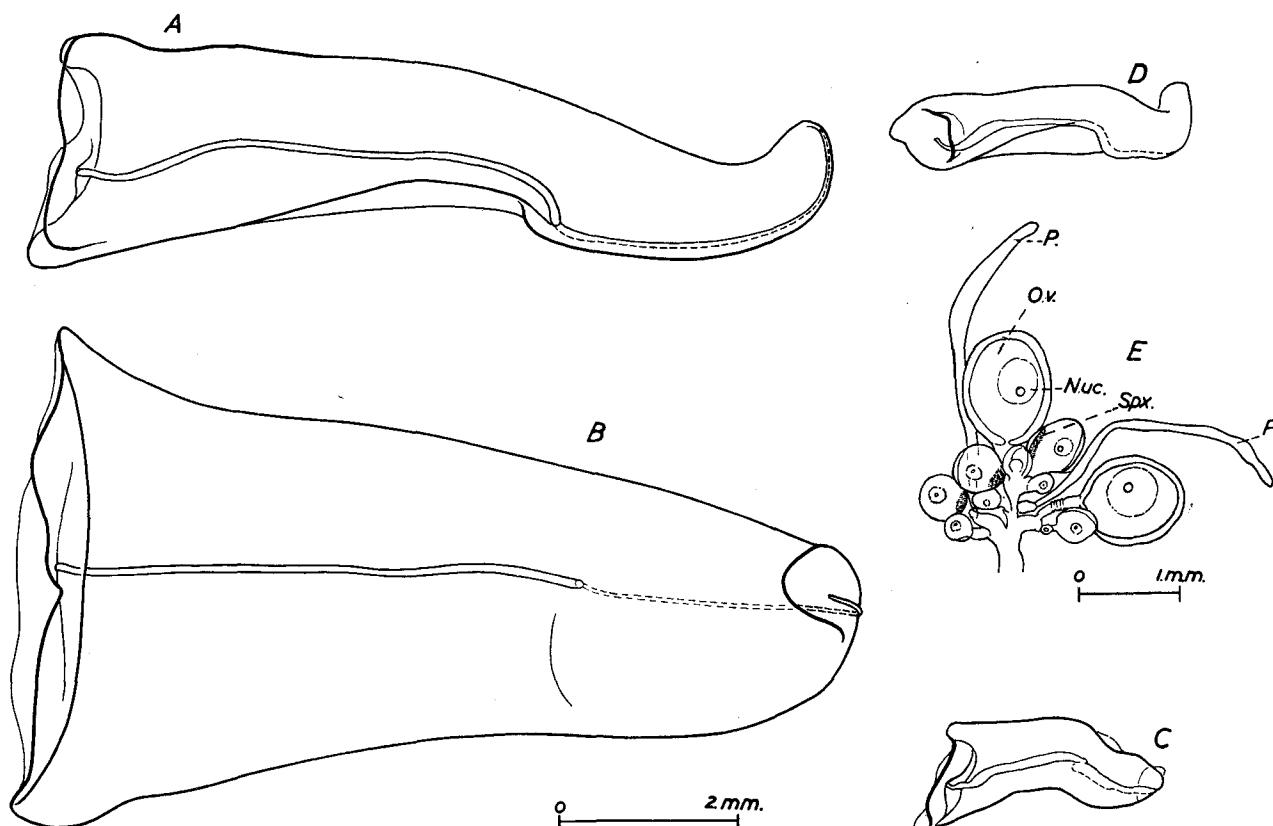


FIG. 27. *Marrus antarcticus* Totton. Bracts and gonophore

A, lateral view of an adult bract; B, upper view of same; C, D, lateral views of young bracts; E, gonophore. A, B, C,

D, $\times 12$, E, $\times 13$

Nuc = nucleus; Ov = ovum; P = palpon; Spx = spadix (from Totton, 1954, fig. 21).

Gonophores (text-figure 27E): (Female), much reduced, with four radial canals but no ostium, and monovon. Eggs up to 1.25 mm diameter, surrounded by irregularly branched spadix on one side only. A specimen from 'Discovery' Station 2010 is all male.

Bracts (text-fig. 27A-D): Flattened cone-shaped, truncated distally, bracteal canal terminating on papilla on this distal facet.

Marrus orthocannoides Totton, 1954

Text-figures 28, 29

A cold water form, whose nectophores differ in one important respect from those of the other two species in having no muscle-free adaxial wall to the nectosac. Known only from fragments.

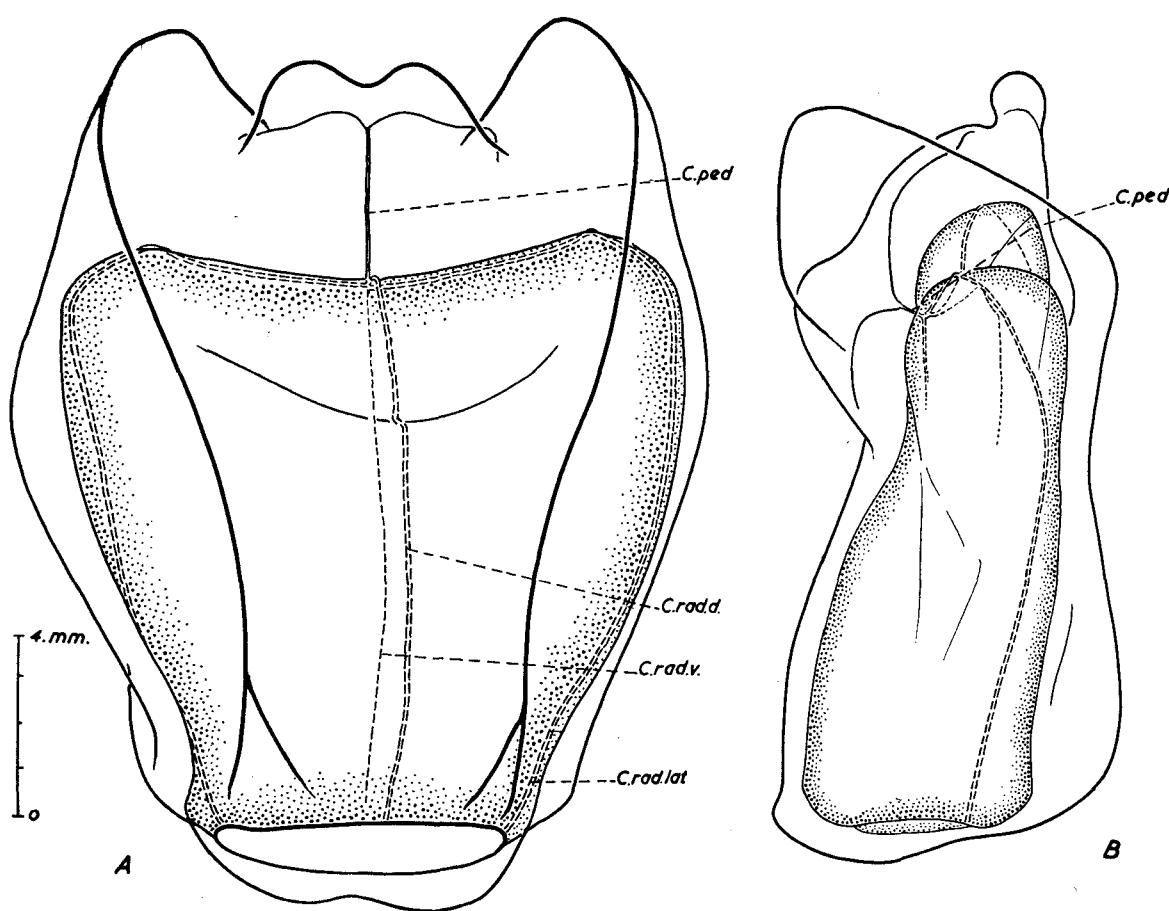


FIG. 28. *Marrus orthocannoides* Totton. Nectophores

A, upper side; B, lateral view, $\times 6$

C.ped = pedicular canal; C.rad.d, C.rad.lat, C.rad.v = dorsal, lateral and ventral radial canals (from Totton, 1954, fig. 22).

Pneumatophore: Oblong, 6 mm length, 2 mm diameter.

Nectosome: 14 mm \times 2 mm; strongly contracted.

Nectophores (text-fig. 28): Lateral facets undivided by ridges. Lateral radial canals straight, not forming sigmoid loops. No muscle-free ad-axial wall. A pair of ridges divides the upper surface from the lateral facets. They bifurcate near the ostium. The nectophores are borne on the same side of the stem as the gastrozooids.

Siphosome: 23 cm long, 3.7–4.6 mm diameter; stem strongly contracted.

Bracts (text-fig. 29): Thin and leaf-like, flanking the palpons up to 15 mm length \times 8 mm broad, ovate, without marginal teeth, distal end thickened, obliquely truncate, attached along proximal two-thirds of length, so that bracteal canal is only one-third the length of bract. The canal ends in the middle of one margin of the terminal facet.

Palpons: Very numerous, slender, 9.2 mm length, 0.2 mm diameter, on short pedicels; close set in four or five longitudinal rows, each with a fine palpacle.

Gonodendra: Fine, 4.6 mm length, two or three per cormidium, bearing a dozen or more male gonophores on very short pedicels. The species is dioecious.

Gonophores: (Male), globular, up to 1.1 mm diameter.

Gastrozooids and tentacles unknown.

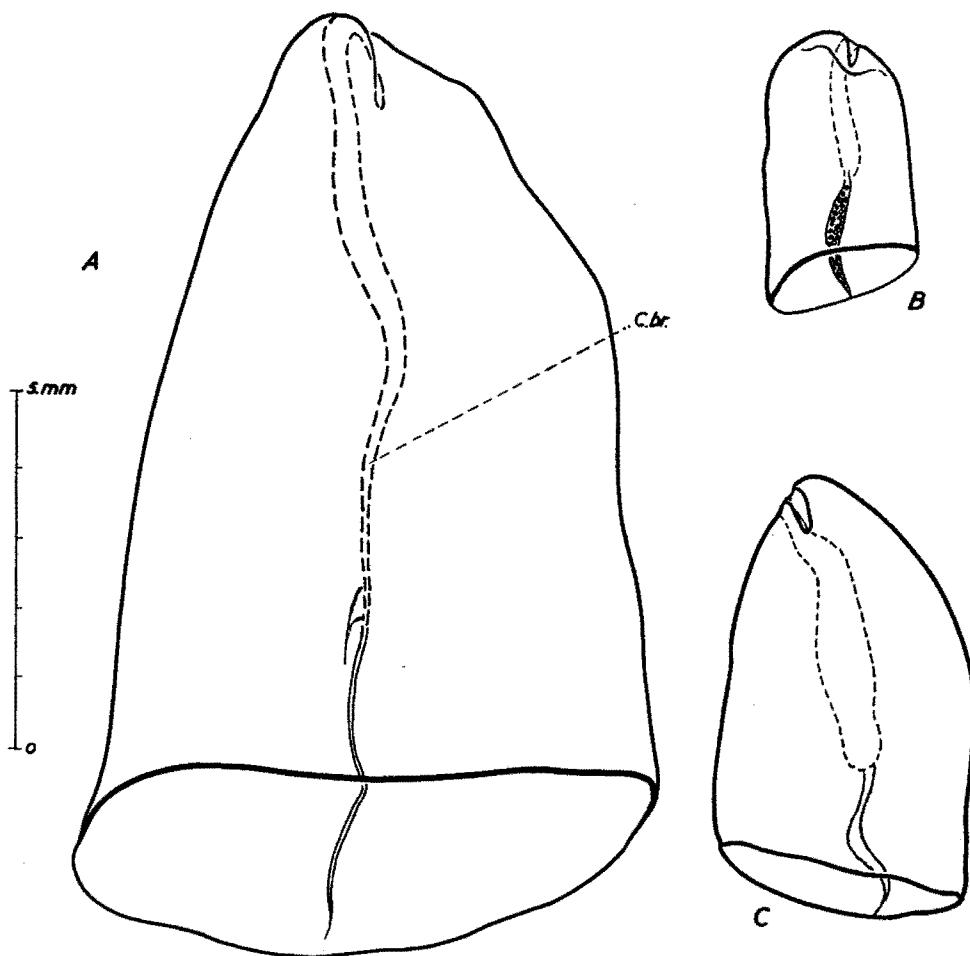


FIG. 29. *Marrus orthocannoides* Totton. Bracts
A, fully grown; B, C, young, $\times 10$. The pecked portion of the bracteal canal is the area
of attachment of the bracteal muscle
C.br = bracteal canal (from Totton, 1954, fig. 23).

***Marrus orthocanna* (Kramp, 1942)**
Text-figure 30

Stephanomia orthocanna Kramp, 1942

A large, high-arctic Agalmid from the deep water of Baffin Bay. Known from incomplete specimens. It has been found also penetrating south, west of the Faroes.

Pneumatophore: 4·5–5 mm long \times 2 mm diameter, flask-shaped.

Nectosome: Short.

Nectophores (text-fig. 30): Large, 13 mm wide, 15 mm long, 7·5 mm deep. Lateral radial canals without sigmoid loops (straight).

Stem: 2–3 mm diameter, bright scarlet in colour.

Gastrozooids: 15 mm long, spindle- or club-shaped.

Basigaster long, cylindrical, about equal in diameter to that of stomach, which has numerous villi. The cnidoband of the tentillum is slightly coiled, there is a single terminal filament and no involucrum.

Bracts (only one found): 5 mm long, 3 mm broad, 1 mm thick, quadrangular, distal and lateral angles almost rectangular, without protruding points or ridges.

Palpons and gonophores unknown.

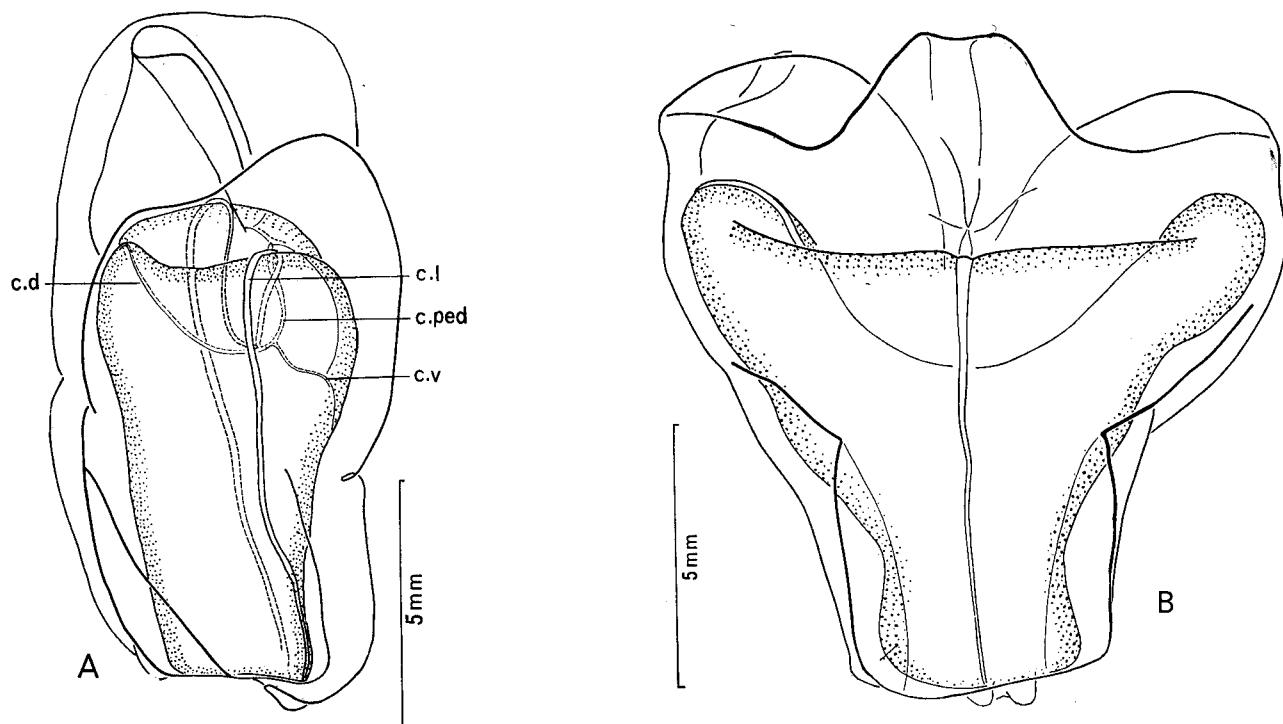


FIG. 30. *Marrus orthocanna* (Kramp). Nectophore
A, lateral view; B, upper view

c.d = dorsal, c.l = lateral, and c.v = ventral radial canals; c.ped = pedicular canal.

Genus: ***MOSERIA*** gen. n.

Monotypic genus for *Stephanomia convoluta* Moser, 1925.

As Moser (1925) suspected the type species has no close link with other species for which the name *Stephanomia* has been used.

A genus with only one little known antarctic species whose nectophores are exceptionally thin in comparison with length and breadth. The pneumatophore is of peculiar construction, consisting of two chambers besides the pneumatosaccus. The tentilla are involucrate and unicornuate, as in *Halistemma*.

At the time of going to press, when morphological research had to be terminated, it was thought that the material of *Moseria* available indicated the existence of two species. Unfortunately, the bulk of this material, whose generic identity is certain, is in a very poor state of preservation.

***Moseria convoluta* (Moser, 1925)**

Plate XIII, figures 4-10

Stephanomia convoluta Moser, 1925

The pneumatophore has no marked pedicel, and consists of the pneumatosaccus, a basal and a lateral chamber, all three intercommunicating, but cut off from the stem cavity.

Nectophores (text-fig. 31): Up to 15 mm × 16 mm, flat, heart shaped with deep apical incision at point of attachment, which is by a strong and broad muscular lamella which passes round the adcaudine side like a pair of callipers. The upper side is smaller in area than the under side so that the two narrow oblique lateral facets give a bevelled appearance to the sides. One of two young necto-

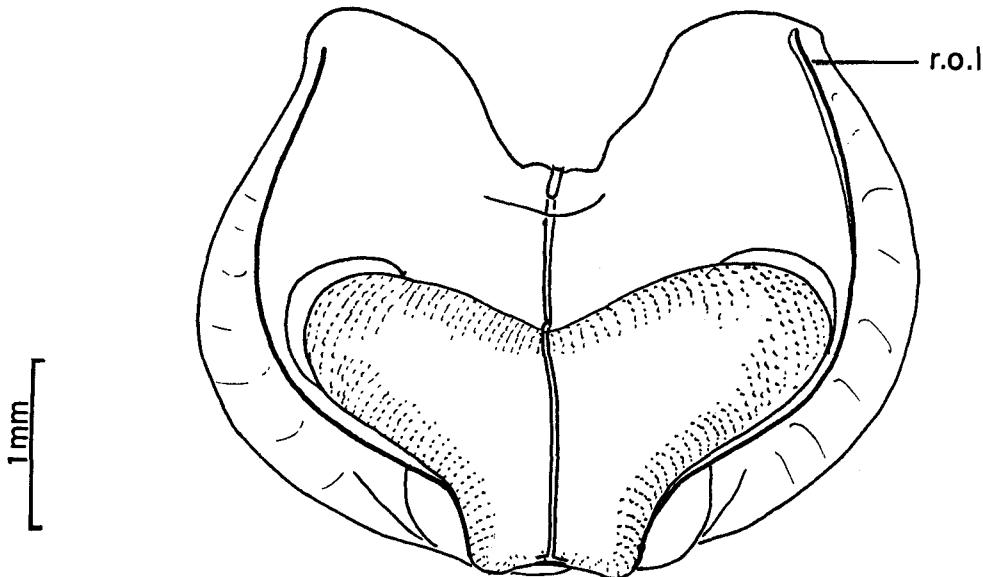


FIG. 31. *Moseria convoluta* (Moser). A young nectophore, 'Discovery' St. 1203, viewed from above, $\times 24$
r.o.l = oro-lateral ridge.

phores was found to have no radial canals, and in the other they appeared to be growing out from the pedicular canal. There is an oro-lateral ridge, clearly visible only in early growth-stages of the nectophore. The nectosac is Y-shaped.

Gastrozoid: Up to 9 mm long, with a very short peduncle and numerous liver-stripes.

Tentacle: The tentilla described and figured by Moser (1925) did not belong to this species. Both activated and non-activated tentilla of another type have been found in abundance on a specimen from 'Discovery' Station 1283. In early growth stages they are rod-like. In fully developed stages the involucrum is turned back along the pedicel – possibly a post-mortem effect. In the middle stages the involucrum covers one or two of the seven to eight coils of the unicornuate cnidoband, which in early stages can be seen to lap round three sides of the central tube. When coiling up takes place the tube is found on the inner side. It is thin walled with a large lumen. After activation it is found to have lost its lumen, to have shortened up and to be thick-walled. Cnidoband and terminal filament about 2.5 mm length. There are larger lateral nematocysts in the first three turns.

Palpons: 8.5 mm–10 mm length, 2–2.5 mm–5 mm diameter, without pedicel, drawn out into a short distal point, with palpacle.

Bracts (Pl. XIII, figs. 9, 10): These are well represented by Moser (1925, Taf. XXXI) and serve as a useful criterion in identification since they differ from those in the next species. Up to 6 mm length, broadest at one-third of length from attachment, which is by a broad vertical lamella that passes round the base on either side. The terminal part, divided by a transverse ridge on the upper side from the rest of the bract is bevelled off to a point on the under margin to form a new nematocyst battery on the end of the bracteal canal. A longitudinal pad of nematocysts stretches from this point to the transverse ridge.

Gonodendra: Male gonodendra 3 mm long, irregularly branched bearing more than eighty gonophores. Male gonophores (ripe) have a pedicel 1.7 mm long and measure 1.0 mm \times 0.68 mm. In them the radial canal are reduced to two or three. The female gonophores have four radial canals,

measure up to 1·34 mm \times 1·09 mm, and have shorter pedicels measuring up to 0·6 mm in length. It has not been ascertained whether the female gonophores are borne on gonodendra.

Genus: ***NANOMIA*** A. Agassiz, 1865

Type species *Nanomia cara* A. Agassiz (1865).

Agalmopsis Sars, 1846

Anthemodes Haeckel, 1869

The genus contains two species of small, brightly pigmented Agalmidae with unicornuate tentilla provided at the base with an involucrum. The arrangement of the gonodendra is characteristic, male and female alternating on either side in pairs at the bases of palpons.

The name *Nanomia cara* first appeared in print on page 181 of the Proceedings of the Boston Society of Natural History IX, for May 1863 (see p. 193 for date) in a résumé of the proceedings. This use of the name, without proper description or drawings, is insufficient to identify the species and constitutes a *nomen nudum*. *Nanomia cara* should date from 1865.

***Nanomia bijuga* (Chiaje, 1841)**

Plate X, figures 1–10; Plate XIV, figure 9; text-figures 32–6

Physsophora bijuga Delle Chiaje, 1841

Anthemodes canariensis Haeckel, 1869; Chun, 1888a

Halistemma picta Metschnikoff, 1870; Chun, 1888a

Stephanomia (Anthemodes) canariensis Metschnikoff, 1874

Stephanomia pictum Metschnikoff, 1874

Halistemma tergestinum Claus, 1878

Agalmopsis fragile Fewkes, 1882

Anthemodes picta Haeckel, 1888b

Halistemma fragile Haeckel, 1888b

Cupulita picta Haeckel, 1888b; Bedot, 1896

Cupulita tergestina Haeckel, 1888b

Cupulita fragilis Haeckel, 1888b

Cupulita canariensis Haeckel, 1888b; Bedot, 1896

Anthemodes ordinata Haeckel, 1888b; Bedot, 1896

Cupulita (Halistemma) pieta Chun, 1891

Cupulita bijuga Schneider, 1898

Anthemodes moseri Agassiz & Mayer, 1902

Stephanomia bijuga Bigelow 1911b

Nanomia bijuga Totton, 1954

The principal published figures of the whole animal are those of Metschnikoff (1870); Claus (1878); Chun (1891); Agassiz & Mayer (1902); Bigelow (1911b) and Kawamura (1911b).

Common in the Mediterranean; and in the Gulf of California (personal communication: Dr. Ahlström).

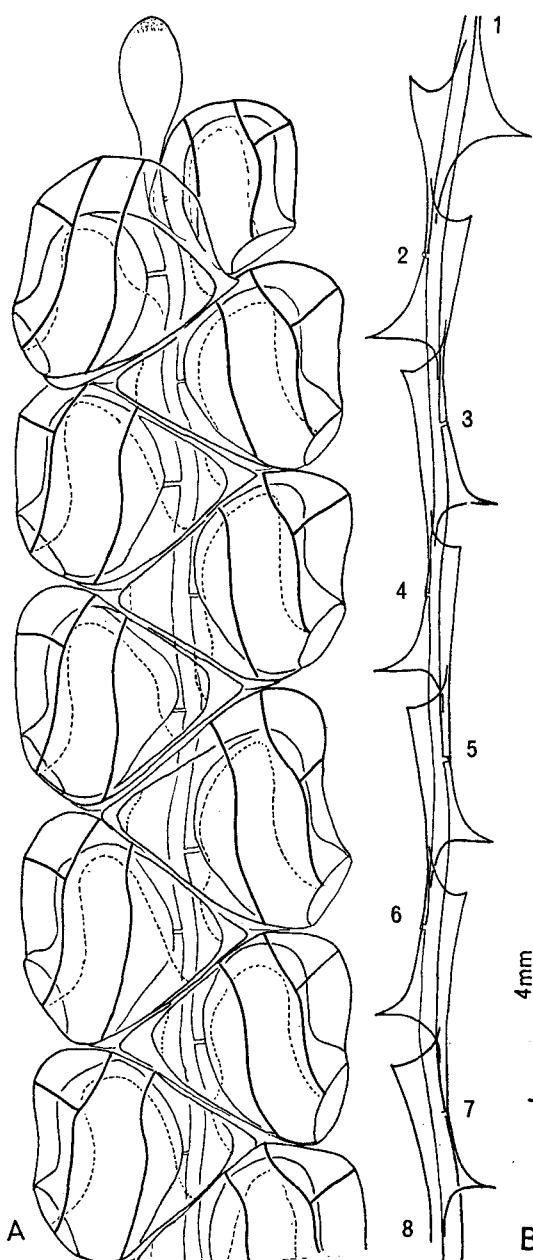


FIG. 32. *Nanomia bijuga* (Chiaje)
A, the nectosome to show the inter-locking of the tentacles; B, the stem of the nectosome to show arrangement of the muscular lamellae. The order of the tentacles starting from the apical one on the right is indicated by a numeral placed opposite to the origin of the pedicular canals. Camera lucida sketches of living animals at Villefranche.

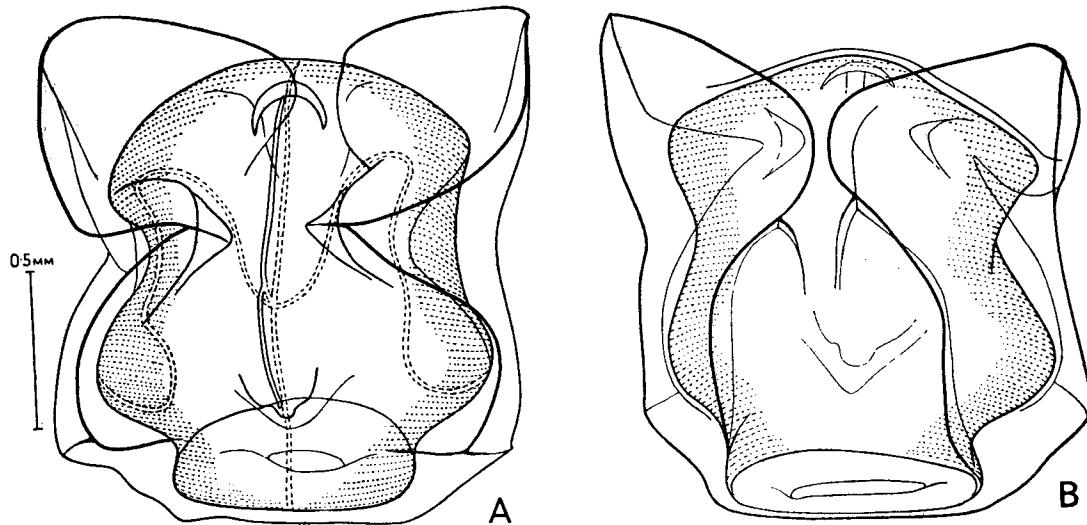


FIG. 33. *Nanomia bijuga* (Chiaje). Young nectophore
A, ventral view to show region of attachment, radial and pedicular canals; B, dorsal view of same to
show ridges, $\times 42$ (from Totton, 1932, fig. 6)

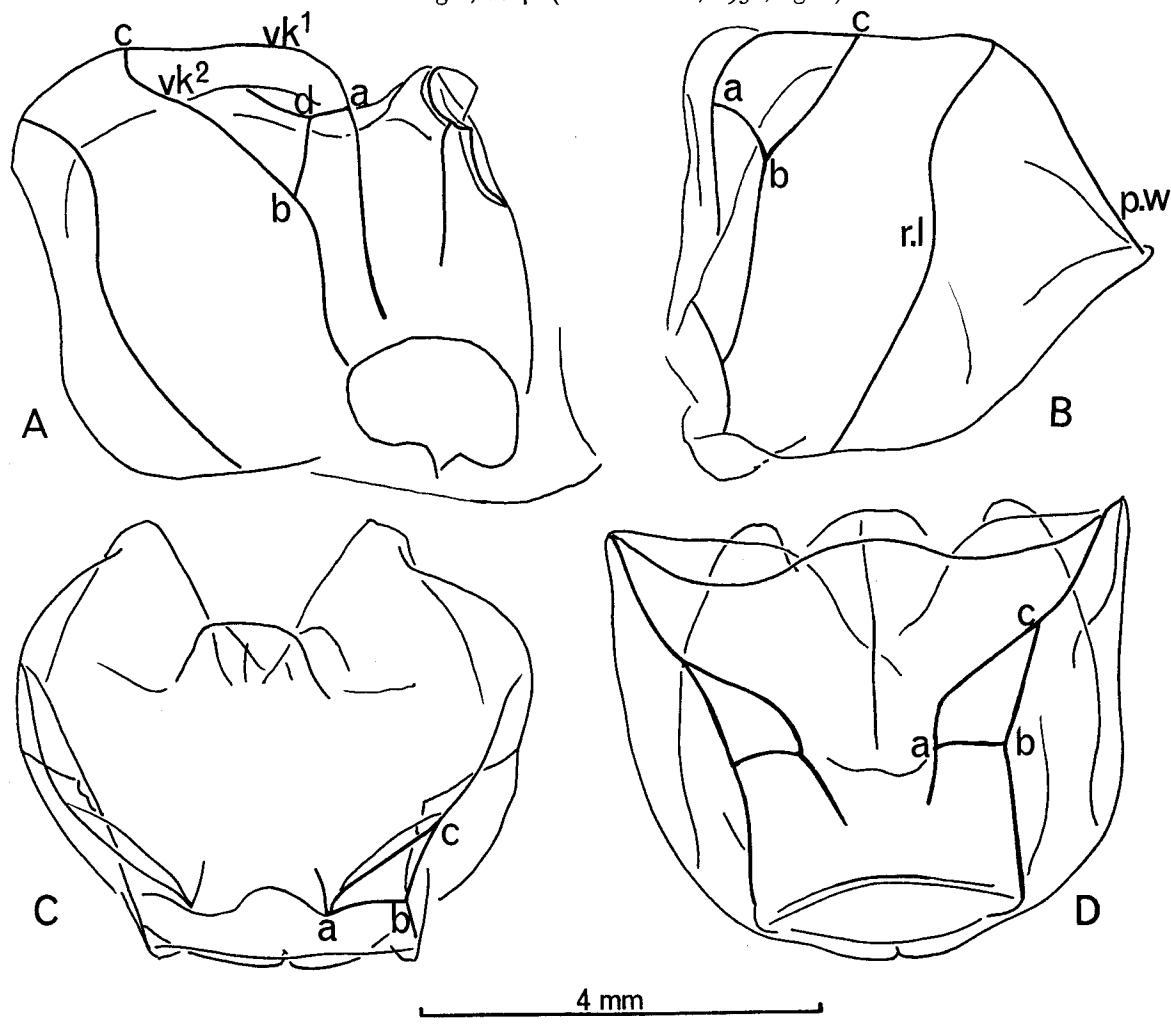


FIG. 34. *Nanomia bijuga* (Chiaje)
Four views of full grown nectophores (Villefranche specimens) of the auriculate variety.
A, fronto-lateral view; B, lateral view; C, view from above; D, ostio-superior view. Nectophore A is from
one specimen (B.M. Reg. No. 1953.7.2.45); B-D from another (B.M. Reg. No. 1953.9.23.604)
a-d = junctions of ridges. Junctions *a*, *b*, *d*, found only in auriculate varieties; *p.w* = wedge process;
r.l = lateral ridge; *vk¹*, *vk²* = vertical ridges named by Claus (1878).

Size: 10–45 cm long, according to state of contraction.

Pneumatophore: 1.8–2.0 mm long, 1–2 mm diameter. Eight septa. Light brown pigment spots at apex, which is surrounded by port-wine coloured polygonal cells. A temporary apical opening may appear.

Nectosome (text-fig. 32): One-fifth of total length. Nectophores in two rows of eight to twenty-five each; square in shape when viewed from abaxial or axial sides; length of sides 2–3.5 mm, with ear-like upper corners (text-fig. 33). The nectophores are flattened from stem-side to ostial side, an important field-mark. The upper outer angles are sometimes cut off by a ridge (text-fig. 34).

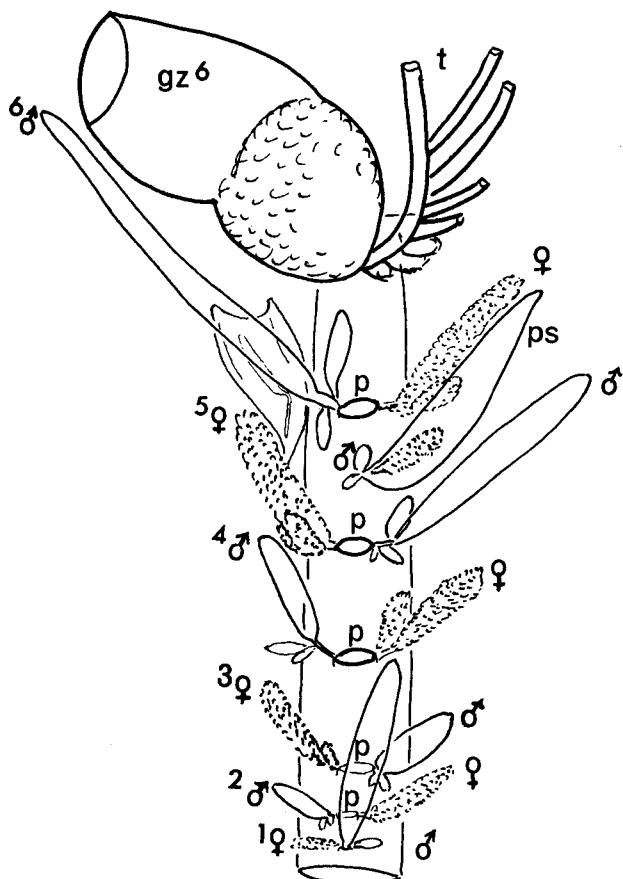


FIG. 35. *Nanomia bijuga* (Chiaje)
The whole internode shown in part in text-figure 36,
 $\times 15.6$. The proximal part lies below. *p* = primary series
palpons, or base from which a palpon has become de-
tached; *p.s* = the first of a secondary series of palpons;
t = tentacle; *gz⁶* = gastrozooid (distal end cut off);
♂, ♀ = male and female gonodendra.

Siphosome: Stem slender, highly contractile.

Gastrozooids: Twenty-four fully formed on stem 45 cm length, 3–6 mm in length. Cnidoband of tentilla 8 mm length, 2 mm diameter, in three coils, the upper half covered by an involucrum.

Palpons: Chun (1888a) gave a budding formula. There are six in a primary series, but others are budded subsequently. Arising from their bases are pairs of branching gonodendra (text-fig. 35).

Gonophores: Sexes alternate on each side of the pairs of gonodendra (text-fig. 36).

Bracts: Two categories: (1) large single, at base of each gastrozooid, thin leaf-like with three con-

spicuous cylindrical teeth at the distal end (Pl. X, figs. 5, 6); (2) leaf-like, shorter and wider, the three terminal processes not so distinct (Pl. X, figs. 7, 8). Some are spear shaped. Bracts attached in four longitudinal rows at sides of stem.

Colour: There are small, scattered, port-wine coloured blotches or flecks in the endoderm of both nectosome and siphosome.

Presence in the deep-scattering layer

There is, according to E. G. Barham (1963), a striking relation between the depths of recorded deep-scattering layers of the ocean waters and concentration of siphonophores. The abstract of his interesting paper reads: 'Bathyscaphe divers in the San Diego Trough have revealed a close spatial relation between siphonophores and the deep-scattering layer as recorded by precision depth-recording echo-sounders. Measurements of gas-bubbles* within the floatation structures of *Nanomia bijuga* captured in a closing-net in an ascended scattering layer indicated that these are very close to the resonant size for 12/kcy/sec. sound. Because such organisms are capable of making prolonged vertical migrations, and are widespread geographically, they are very probably the major causes of stratified zones of scattering throughout the oceans of the world.'

Specific identifications need confirmation.

* Dr. Barham (personal communication) and colleagues found concentrations of CO up to 90% on analysis of the gas.

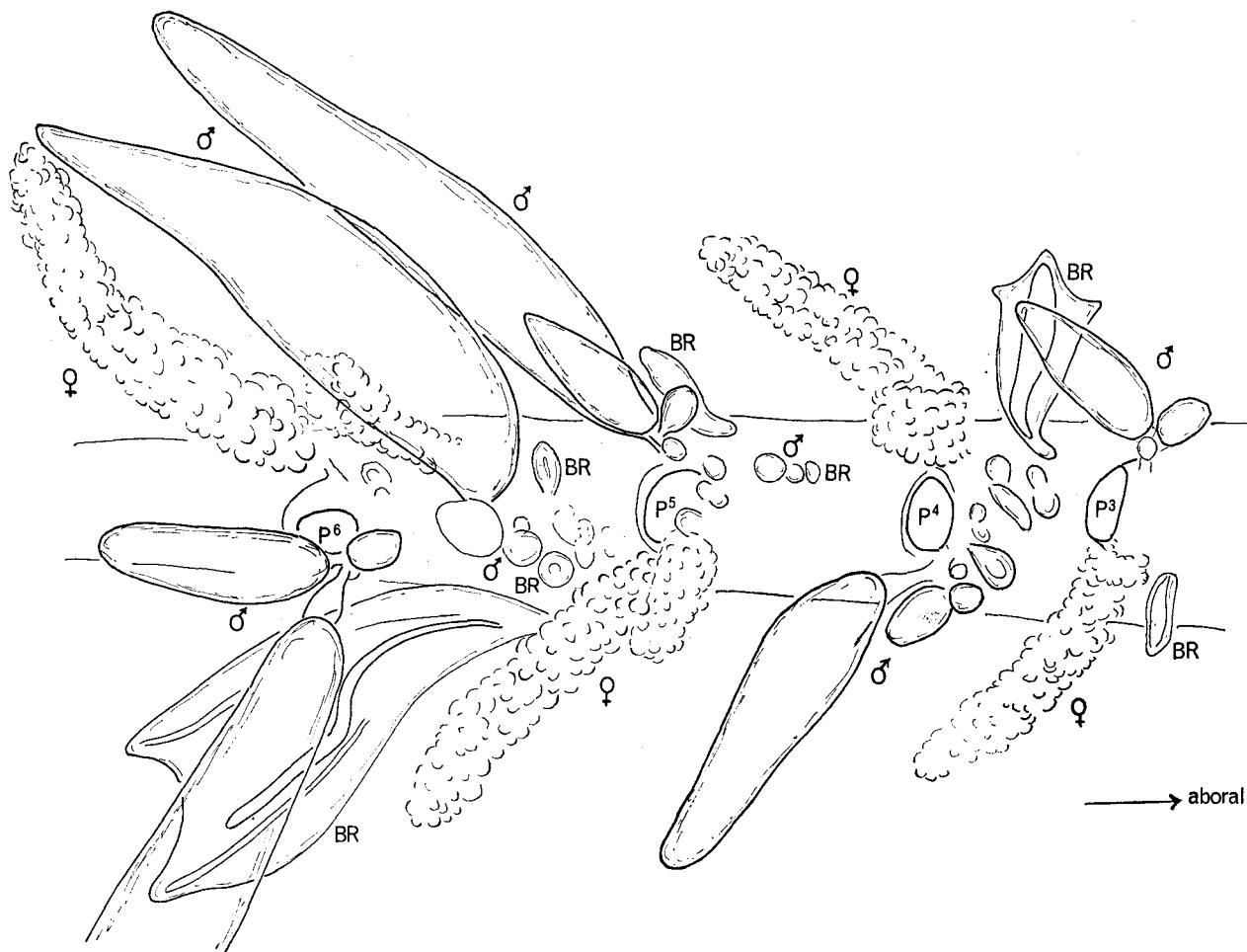


FIG. 36. *Nanomia bijuga* (Chiaje)

Part of an internode of the stem showing alternating ♂ and ♀ gonodendra arising from the bases of a series of palpons, $\times 39$. From Oak Bay Boat House, Victoria, B.C., March 16, 1959; W. G. Fields & A. R. Fontaine Coll. BR = bract; $p^3 - p^6$ = palpons of primary series (scars of detachment).

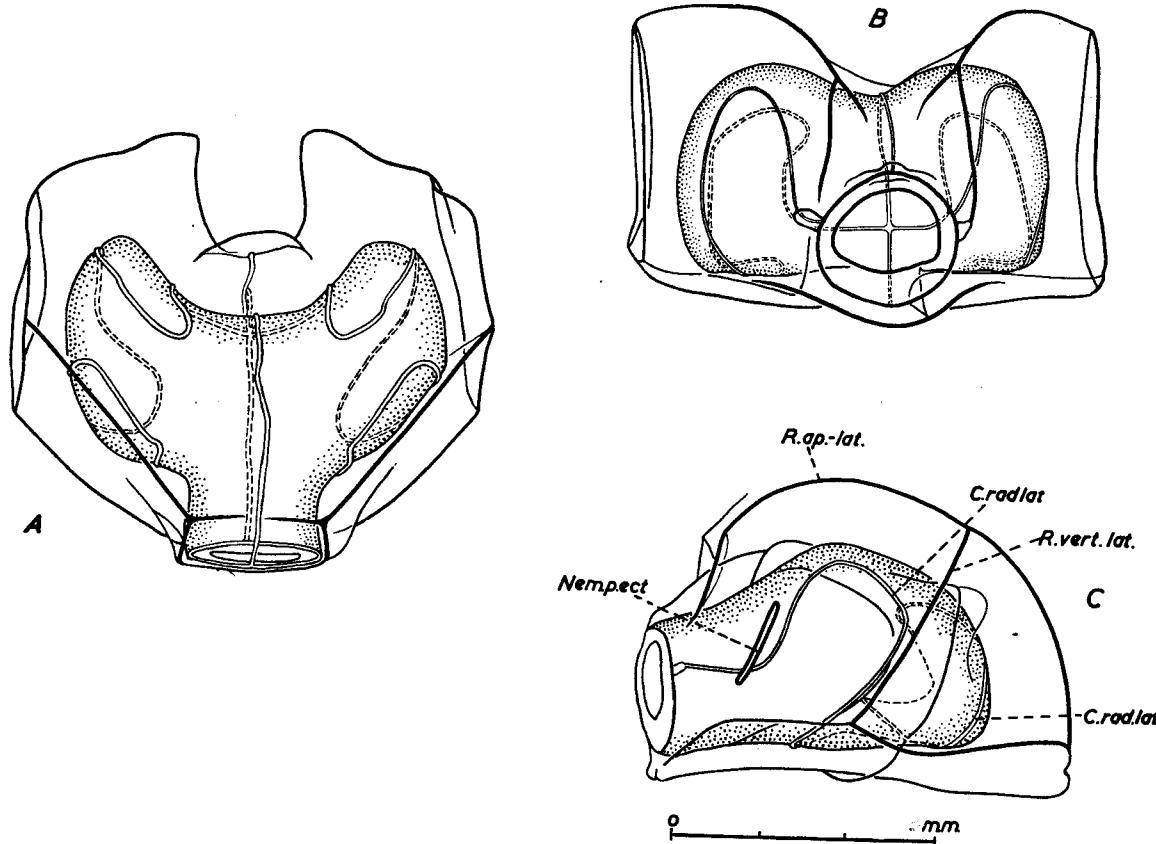


FIG. 37. *Nanomia cara* (A. Agassiz)

Nectophores from an Irish specimen. A, B, C, upper, abaxial and lateral views, $\times 12$
C.rad.lat = lateral radial canal; *Nem.p.ect* = ectodermal patch of nematocysts; *R.ap.lat* = apico-lateral ridge; *R.vert.lat* = lateral vertical ridge (from Totton, 1954, fig. 19).

Nanomia cara A. Agassiz, 1865

Plate XIV, figures 1-6

Agalmopsis elegans Sars, 1846 (partim: non form B = *Agalma elegans*)

Stephanomia cara Metschnikoff, 1874; Bigelow, 1911b

Halistemma elegans Claus, 1878

Nanomia cara Fewkes, 1880a; Totton, 1954

Cupulita sarsi Haeckel, 1888b; Browne, 1900

Cupulita cara Haeckel, 1888b; Romer, 1901; Vanhoeffen, 1906

This little known unicornate species was beautifully figured by its discoverer G. O. Sars in 1846 as *Agalmopsis elegans*, which name has since been restricted to a species, part of the tricornuate tentacle of which was included by Sars as 'form B' (see Pl. XIV, figs. 7, 8)

The species can be distinguished from *N. bijuga* by its nectophores (text-fig. 37) but to what extent the two species differ in other respects has not been determined.

Sars's specimen measured 51.5 cm in length, for 10.6 cm of which the nectosome accounts. The nectophores are flattened somewhat in the horizontal plane, whilst those of *N. bijuga* are compressed in the vertical one. The largest of Sars's specimens had fourteen or fifteen pairs of nectophores.

An analysis of the animal's locomotion, together with some good figures was published by G. O. Mackie in January 1964.

Genus: **LYCHNAGALMA** Haeckel, 1888

Type species *L. vesicularia* Haeckel, 1888b.

? *L. utricularia* (Claus, 1879)

Agalmidae with multicornuate tentilla consisting of involucrate cnidoband, terminal ampulla and a corona of eight radial horns or filaments.

***Lychnagalma utricularia* (Claus, 1879)**

Plate XVI, figures 1-7

Agalmopsis utricularia Claus, 1879

This very remarkable little agalmid was found several times at Messina by Claus, who described and figured it in some detail in a way that inspires full confidence, although his description and figures of the nectophores are difficult to follow, but detailed and painstaking. No one else has reported finding specimens.

Nectophores: Claus's ridge V K² does not join V K¹ (Pl. XVI, figs. 3, 4, 6) as it does in *Nanomia bijuga*. These two ridges are shown clearly in Haeckel's (1888b) figures of his new species *L. vesicularia*, but only doubtful reliance should be placed on them as he may have been unduly influenced by a fancied resemblance of his Ceylonese specimen to Claus's.

Gastrozooids and tentacles: The peduncles are exceptionally long, and the type of tentillum unique. The red cnidoband forms seven or eight spiral turns, the four or five proximal ones lying transversely, all enclosed in an egg-shaped involucrum. The proximal part consists of small cnidocysts, which are flanked by larger ensiform ones. The end of each tentillum forms a large egg-shaped vesicle 0.79 mm × 0.52 mm in size. From its base arise no less than eight fine terminal filaments which are carried upright (Pl. XVI, fig. 2).

Gonophores: The male gonophores 0.7-0.8 mm long have a distinct umbrella. With the female ones they are borne at the bases of the eight or nine palpons that occur between successive gastrozooids.

Bracts: Broad in proportion to length, which seems to be 1.5 mm. There are two or three distal points.

***Lychnagalma vesicularia* Haeckel, 1888**

? *L. utricularia* (Claus, 1879)

A doubtful species. It is not clear from Haeckel's description whether *vesicularia* differs from *utricularia*. It is to be doubted whether much reliance can be placed on Haeckel's beautifully idealized figures, or the record for geographical distribution.

Genus: **ERENNA** Bedot, 1904

Monotypic genus for *Erenna richardi* Bedot, 1904.

Nothing has been published about *Erenna* for thirty-seven years. The material on which its type species was based consisted of six remarkable, detached tentacles, taken between Portugal and the Azores, attached to the rope of a fish-trap. With the preserved specimens were included some large, detached gastrozooids. The animals themselves had been torn away.

A fragmentary siphonophore bearing what appear to be growth stages of such tentacles was taken in the East Indies by 'Siboga' at the beginning of the present century, and described and figured by Lens & van Riemsdijk (1908).

Three specimens of this type of siphonophore, exhibiting the basal parts of such tentacles have been

taken by 'Discovery II', the rest of the tentacles having been torn away, probably through their attachment to nets or trawls. The third 'Discovery' specimen was fortunately accompanied by twenty-seven large detached nectophores. This lucky chance has made it possible to prepare a description of a reconstruction.

Fragmentary specimens were recorded by Bigelow (1911b) from the Galapagos Islands, and by Moser (1925), in the Gulf of Gascony (Bay of Biscay).

In April 1963, M. Gostan brought back to the Station Zoologique at Villefranche from a cruise between Monaco and Corsica a small piece of a pink tentacle that one of his companions suggested might be part of a siphonophore and that came up with one of his water-samples. Having examined it and discovered its identity I obtained the information from him that these specimens were constantly found but were regarded as merely a nuisance. So the species is evidently common in the Mediterranean, though efforts to find specimens in the spring of 1964 were unsuccessful.

***Erenna richardi* Bedot, 1904**

Plate XIV, figures 10, 11

Erenna bedoti Lens & Riemsdijk, 1908

This rare siphonophore, an outline of the steps in the discovery of which has been given under the genus, has a quantity of black pigment in its endoderm, probably derived from feeding on pigmented, deep-sea fish.

Two specimens were taken by R.R.S. 'Discovery II' on August 21/22, 1959, in a 2 m, closing, young-fish trawl, fished at 1,200 m at Station 4230 ($12^{\circ} 30'W$, $40^{\circ} 09' 30''N$). On September 23, 1959, one larger and more complete animal was taken at Station 4255 in the Isaac Kidd mid-water trawl fished at 1,000 m for $2\frac{1}{2}$ hours from $36^{\circ} 31'N$, $11^{\circ} 24'W$ to $36^{\circ} 22'N$, $11^{\circ} 15' 30''W$.

A fragmentary specimen of a siphosome accompanied by three detached nectophores was taken in May 1937 by 'Discovery II' at Station 2061 at a depth of from 1,900–1,500 m.

The species probably occurs in Californian waters too. Dr. Ahlstrom of La Jolla has taken some thin nectophores with unlooped, pigmented lateral canals which appear to belong to this species; and Dr. William Beebe took nectophores of this type in deep water off Bermuda. Lens & van Riemsdijk figured (1908, Pl. XI, fig. 87) a young nectophore.

Nectophores (text-figs 38, 39): There is a muscle-free strip of the nectosac above and below the proximal, adcauline part of the unlooped pigmented lateral radial canals, and there may be a long, fine 'horn' canal at the outer end of this part. Nectophores measure up to $32\text{ mm} \times 25\text{ mm} \times 2\text{ mm}$.

Bracts: Elongated, up to 20 mm length, 3 mm broad and 1 mm thick, with a pair of short, hook-like processes 7 mm from the proximal end, and another pair at a distance of 3 mm from the distal end. Bracts commonly measure $12\text{ mm} \times 4.5\text{ mm}$. A characteristic feature is a terminal sphere of tissue containing nematocysts. The muscular lamella is attached to most of the length of the bract. The bracteal canal runs close to the adaxial surface except for the terminal 1 mm, which leaves the surface. The bracts are arranged in four rows on either side and five or six to a row in each cormidium.

~~Monotypic genus for *P. canhoeffii* Moser, 1925~~

Nematocysts: Two egg-shaped nematocysts that had been discharged from one of the terminal batteries of a bract measured $70\mu \times 23\mu$. The thread appeared to be ridged, but no spines could be seen with a $\frac{1}{2}$ inch objective.

Tentacles: Leloup (1936) reported that 'Princesse Alice II' took a tentacle 18 cm long on a 'palencre' (a long line) coming up from a depth of 2,032 m in the region of the Canaries, and numerous fragments also on a cable that had been down to 2,000 m in the Gulf of Gascony.

Through the courtesy of M. Testa of the Institut Océanographique, Monaco, I have been able to re-examine both Bedot's (1904) original material and also that recorded by Leloup (1936). The

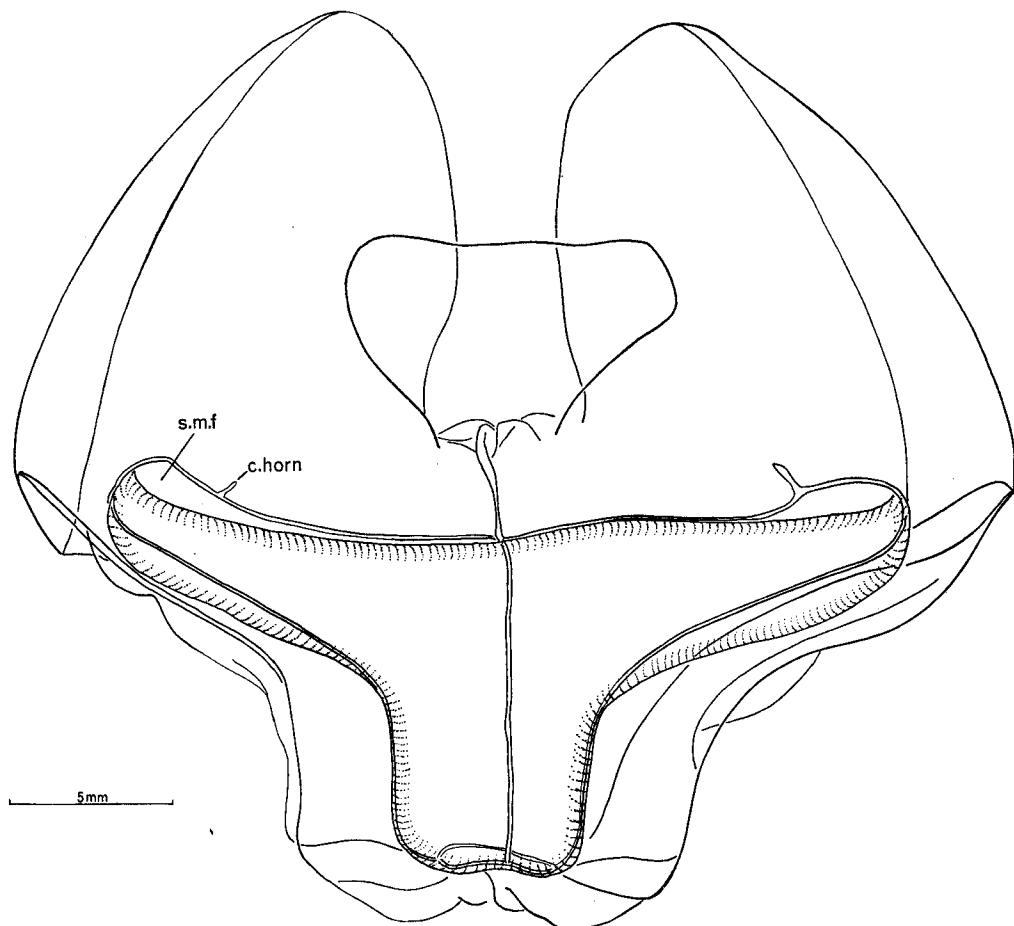


FIG. 38. *Erenna richardi* Bedot
Reconstruction of a nectophore from 'Discovery' St. 2061, S. Tropical Atlantic, $\times 3.5$.
s.m.f. = muscle free strip; c.horn = horn canal

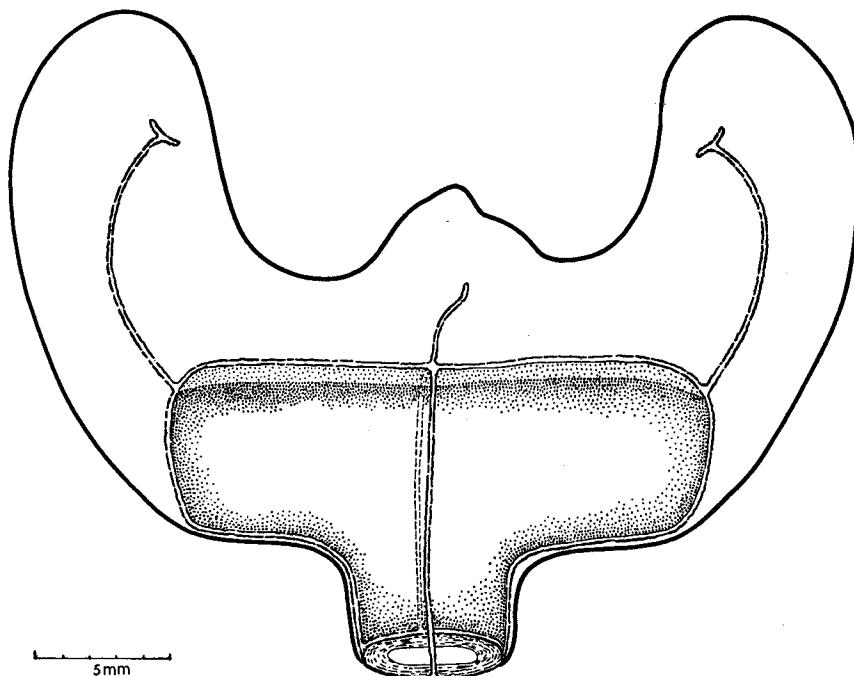


FIG. 39. *Erenna richardi* Bedot
Upper view of a nectophore, 'Discovery' St. 4255.

structure of the tentilla, so well figured and described by Bedot, at first sight so remarkable, can be homologized with that of the early growth stage of a tentillum of *Pyrostephos vanhoeffeni* (text-fig. 44). Bedot's *canal entodermal secondaire* appears to be what I have called the diverticular canal. What is so characteristic of *Erenna* is the hypertrophy of the cnidoband, which must be a very formidable stinging organ, and the mass of vacuolated endoderm surrounding the canals. Leloup's tentacle material is entangled with masses of discharged nematocysts.

Family 5 : PYROSTEPHIDAE

The characters of this family are those of the following genus, *Pyrostephos* Moser, 1925.

Moser's (1925) diagnosis of the genus – she unnecessarily erected a special family for it – is worthless: 'Nectosome long: Nectophores in more (?) than two rows. Siphosome long, with numerous oleocysts. Palpons wanting. Cormidia close together. Cnidosac *diphyes*-like, with a rope-like elastic band on either side. Terminal filament present.' The ectophores are not in more than two rows. The oleocysts are, as she suspected, the palpons. The two separated tentilla figured by Moser (1925, Pl. 30, fig. 6) do not belong to *Pyrostephos*, though the one shown in figure 7 does.

The characteristic features are as follows: Long nectosome (up to twenty pairs of ectophores). Lateral radial canals of nectosac arise separately from the dorsal and ventral canals, and have three lateral loops each. The ventral is straight or has a few minor bends; the dorsal has three or four more marked bends. The adaxial side of the nectosac lacks musculature and is deeply embayed towards the ostium, the embayment occupied by mesogloea. The inner ends of the pair of apico-lateral ridges usually make a sharp angle where bending of the wall takes place, just proximal to its bifurcation into the frontal and oro-lateral ridges. The gastrozooids have an almost cylindrical basigaster. Fifty or more tentilla to a tentacle. When fully formed the proximal part of the axial canal of the tentillum appears as a fine canal on one side of the widened diverticular canal that becomes the cavity of the saccus. The outer wall of the diverticular canal becomes the cnidoband. The bracts (23 × 15 mm) are three pointed, thick, flat below, conical above. Gonophores are budded one from another to form small gonodendra. Dioecious.

Genus: PYROSTEPHOS Moser, 1925

Monotypic genus for *P. vanhoeffeni* Moser, 1925

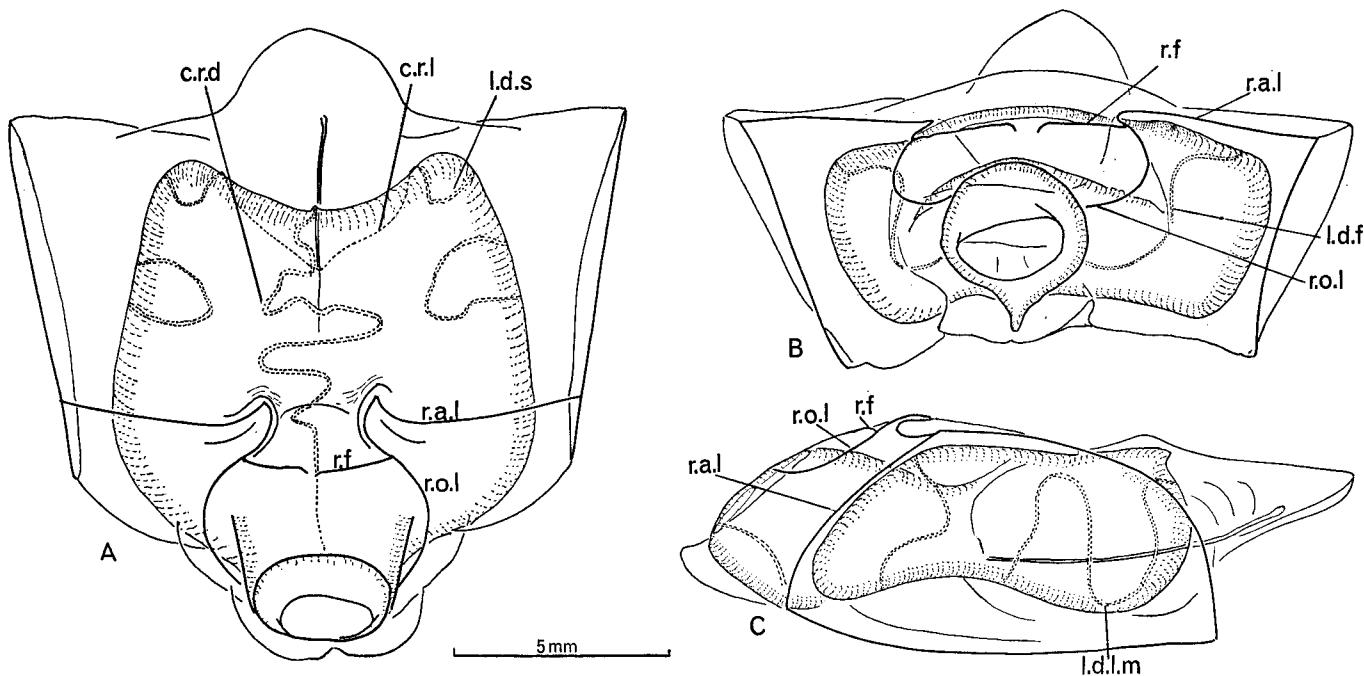
Pyrostephos vanhoeffeni Moser, 1925

Plate XVI, figures 8–10

Parts of this Antarctic siphonophore were first taken on February 25, 1902, by members of the German Southpolar Expedition in longitude 90°E, just off the Antarctic Continent. They took in all sixteen imperfect specimens of the whole animal. A year later parts of the animal were being taken through bore-holes, in the ice of the Ross Sea by members of Scott's National Antarctic Expedition, and fragments have been taken repeatedly since, though no complete specimen is likely to have been preserved. The stem contracts violently on preservation and the appendages are mostly shed.

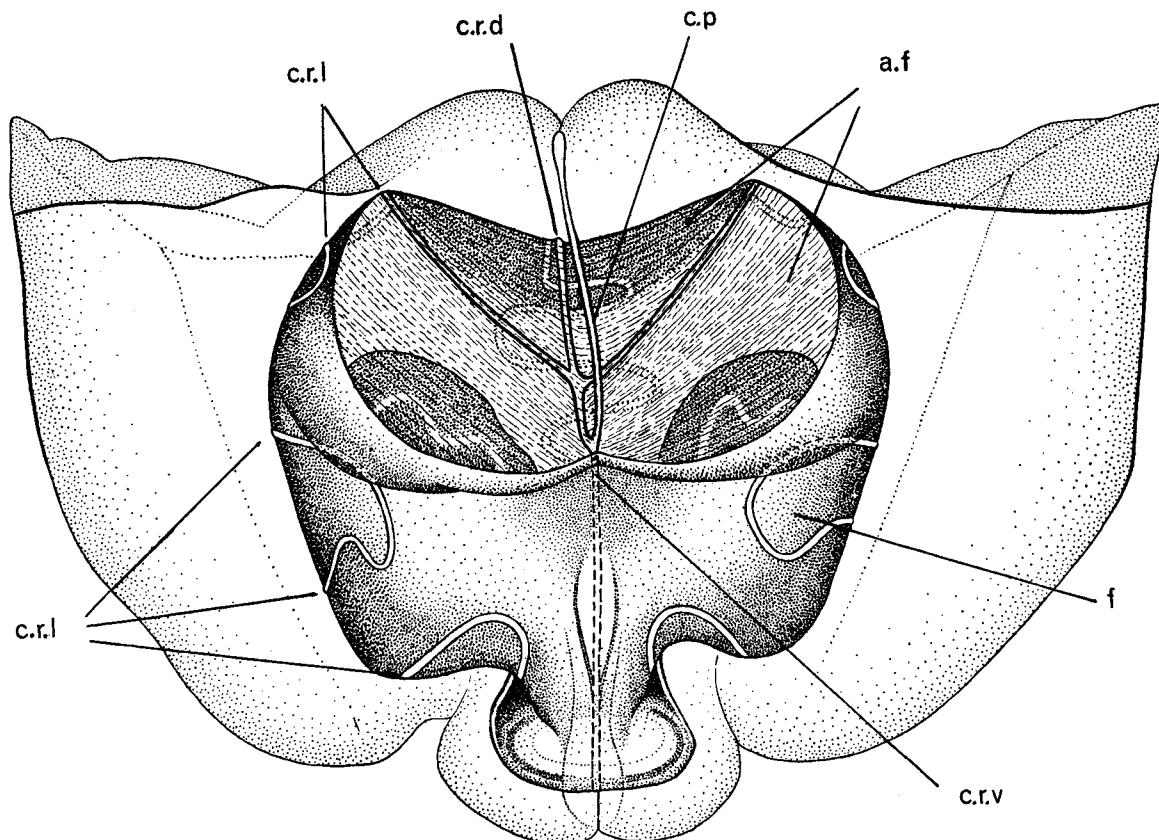
Mackintosh (1934) said that the species probably belonged only to Antarctic water, but occasionally strayed into sub-antarctic water. He found records of it everywhere from the Antarctic convergence to the most southerly 'Discovery' Stations in the Bellinghausen and Weddell Seas, but it was definitely more common in the colder than in the warmer parts of the Antarctic water. It seemed to be absent from the coastal regions of the South Orkneys, South Shetlands, and the Eastern Bellinghausen Sea. Mackintosh did not find any indications of a significant diurnal vertical migration.

For some time I could not find a specimen. But in 1971 I found a fragment of a specimen in the British Museum (Natural History) which had been collected by the RRS Discovery in 1903. It was a piece of the stem with a few tentacles attached.

FIG. 40. *Pyrostephos vanhoeffeni* Moser

Nectophore from 'Discovery' St. 1525 to show ridges and loops of the lateral radial canal. A, from above; B, ostial view; C, lateral view

c.r.d = dorsal radial canal; c.r.l = lateral radial canal; l.d.f = final downward lateral loop; l.d.l.m = main downward lateral loop; l.d.s = small downward lateral loop; r.a.l = apico-lateral ridge; r.o.l = oro-lateral ridge; r.f = frontal ridge.

FIG. 41. *Pyrostephos vanhoeffeni* Moser

Nectophore, adaxial view, 'Discovery' St. 331, $\times 11$

a.f = muscle-free area of nectosac wall; c.r.d, c.r.l, c.r.v = dorsal, lateral and ventral radial canals; c.p = pallial canal; f = fold in lateral wall of nectosac. The flag-line stops some 5 mm short of the fold.

The Greek generic name refers to its fancied resemblance to a fiery garland. It reaches a length probably of several metres.

Nothing descriptive has been published about it for thirty-five years, since Moser (1925) gave the first account of the species.

Colour: The long stem is orange coloured, or vermillion when juvenile; the nectophores, pink when young, appear later on to be tinged with wine red colour, their ostia with carmine; the gastrozooids are golden red with fiery red mouths. The cnidosacs are fiery red. A colour-note by Mr. Marr on a specimen taken at 'Discovery' Station 1989 off South Georgia at a depth between 1,500 m and 1,200 m stated that the gastrozooids were scarlet, transparent, and all separated when taken, and that the nectophores were transparent. Moser described the oleocysts (palpons) as brown-red. A colour-note accompanying a specimen taken by 'William Scoresby' at St. 555 said that the 'oleocysts were translucent, but appeared vermillion because of the colour of the stem, the nectophores pale pink and the stolon vermillion'.

Pneumatophore: Up to 8 mm in length, slender, tapering below. No pigment at the apex, generally broken off when preserved (see Moser, 1925, Pl. 30, fig. 2).

Nectosome: Relatively very long; two rows of nectophores, number uncertain but certainly up to twenty pairs and probably many more. Nectophores at least 20 mm in length, carried on rather narrow muscular lamellae, which are inserted into a long-bow shaped pallial canal that lies in a groove on the adaxial side of the nectophore. From a point almost at its base runs a very short and inconspicuous pedicular canal to the nectosac. This canal bifurcates almost at once to form the dorsal and ventral radial canals. The two lateral radial canals arise separately from the dorsal canal and take an outward and ascending course on the adaxial nectosac-wall to cross over onto the lateral wall of the same. Here each forms first a small downward loop (text-fig. 40A) and then the main downward, lateral loop (text-fig. 40C). After crossing under a fold in the lateral wall (text-fig. 41) each makes a final downward loop (text-fig. 40B) to run to the circular canal round the ostium. The ventral radial canal (text-fig. 41) is generally straight, but may have a few small bends. The dorsal canal usually has three or four more marked bends on the upper part of the nectosac (text-fig. 40A).

Moser said she had refrained from attempting to describe the nectophores because of their complexity and had relied on drawings to give the essential points. Her beautifully lithographed plate 29 (see Pl. XVI, figs. 8–10) was apparently based on colour-sketches and notes made by Vanhoeffen. But its figures of nectophores are difficult to recognize and give a very inadequate and often erroneous idea of their structure, which is, admittedly, difficult to represent in drawings. But once Moser's terminology of orientation is understood, her description of the nectosac and radial canals read in conjunction with my figures will give the specialist a fairly adequate conception of their peculiarities. Moser calls the upper side of the nectophore, which I call dorsal 'ventral' and the adaxial side 'oben'. The chief peculiarity is the inpushing of the adaxial side of the median part of the nectosac, and the absence of musculature from that part of its wall (text-fig. 42). The condition found in this area is reminiscent of the lens-shaped mass of jelly that projects inwards from the exumbrella of many medusae into the base of the manubrium. A similar arrangement is found in *Bargmannia elongata*. An absence of musculature in this area is found also in some other siphonophores such as species of *Marrus*.

Nectophores: The ridges can be identified and named with reference to the figures of nectophores of *Nanomia cara* (text-fig. 37).

The oral end of the nectophore can obviously move in towards the hemispherical plug of mesogloea on the adaxial side when contraction for propulsion takes place. The oral end of the apico-lateral ridge makes a sharp angle for bending just proximal to its bifurcation into the frontal and orolateral ridges. Seen in side-view the vertical-lateral ridge is much nearer the ostial end of the nectophore than in that of *N. cara*. Reference to text-figure 40C of *Pyrostephos vanhoeffeni* will make

further description unnecessary. It is useful to have found a basic arrangement of the ridges of a physonect nectophore to which descriptions can refer.

Siphosome: The large specimen figured by Moser shows the nectosome, which has lost its pneumatophore and the nectophores, as well as the siphosome which shows no gonophores.

The gastrozooids, when young, have an almost cylindrical basigaster and a conventional tentacle that springs from a point very close to the point of origin. The basigaster very often cannot be seen in preserved specimens, and most preserved gastrozooids lose the tentilla of their tentacles. For this reason large gastrozooids appear rather like palpons. Both Moser and myself nearly made this mistake. By dissection and section-cutting I have established the fact that the stem is not segmented as is usual in physonects with each segment terminating in a gastrozooid. In *Pyrostephos* there seems to be a continuous ventral line of budding of gastrozooids. A piece of a juvenile stem taken by 'Terra Nova' bore on each length of 1 mm no less than eleven or so gastrozooids, which fanned out on each side from the ventral surface.

The mature, spindle shaped gastrozooids measure about 15 mm \times 2 mm, and consist of three sections: (1) the basigaster, the ectoderm of which is usually lost in preserved specimens, leaving the narrow endoderm to look like a peduncle; (2) the main stomach and (3) a proboscis. The three parts

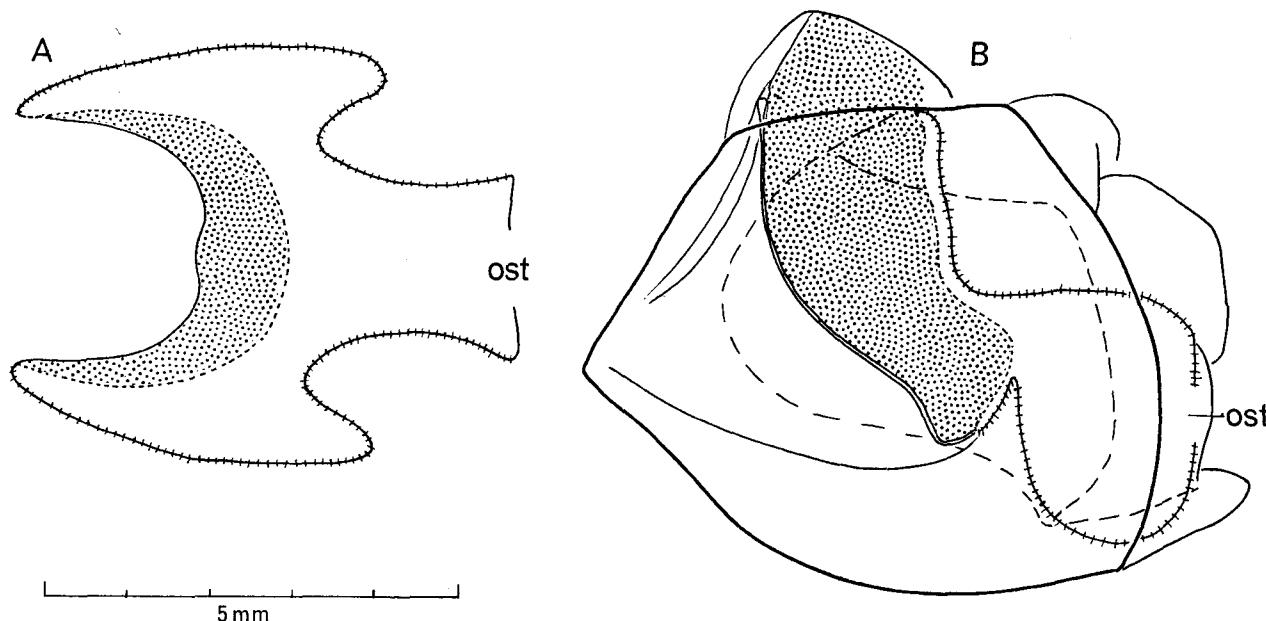


FIG. 42. *Pyrostephos vanhoeffeni* Moser

Nectophore from 'Terra Nova' Exped. St. 282, to show nectosac

A, horizontal section; B, sagittal section. The finely pecked line on the adaxial side shows the non-muscular wall which is pushed in by a thick dome of mesogloea (stippled). *ost* = ostium.

have lengths proportional to 6, 76 and 10. It can be seen at once on examination that there are some unusual features about their histology. Two kinds of lens-shaped or sub-spherical endodermal patches are visible through the stomach-wall, one transparent and a little larger than the other kind which appears darker than the rest of the endoderm. Inspection of sections and whole mounts of the endodermal wall with low magnification shows that it consists of four main types of cell. The endoderm is vacuolated, and scattered about are the larger transparent patches which are vacuoles about 0.07 mm in diameter. Each is surrounded by four or five smaller more irregularly vacuolated cells. In the interstices where several cell boundaries meet are small cylindrical cells which have produced

numerous secretion droplets. There are, scattered about, the darker sub-spherical cells already referred to. They are somewhat smaller in diameter than the large vacuoles, and their hemispherical surface, which projects into the lumen of the gastrozooid carries stiff cilia about 0.01 mm in length, which gives them the appearance of the back of a hedgehog (text-fig. 43). The whole cell may be likened to an ice-cream-cornet in shape. Rather similar absorptive cells were described by Willem (1894) in the palpons of *Apolemia*.

Tentilla of the tentacles. A single detached tentillum, mounted on a microscopical slide by Vanhoeffen, was figured by Moser (1925, Pl. 30, fig. 7), but the two shown in her figure 6 do not belong to this species. I have studied numerous tentilla still attached to tentacles. There may be fifty or more on one tentacle. The hypertrophy of the axial canal which develops thickened mesogloea walls, and appears to form the extensible part of the cnidobattery has not been noted in any other species.

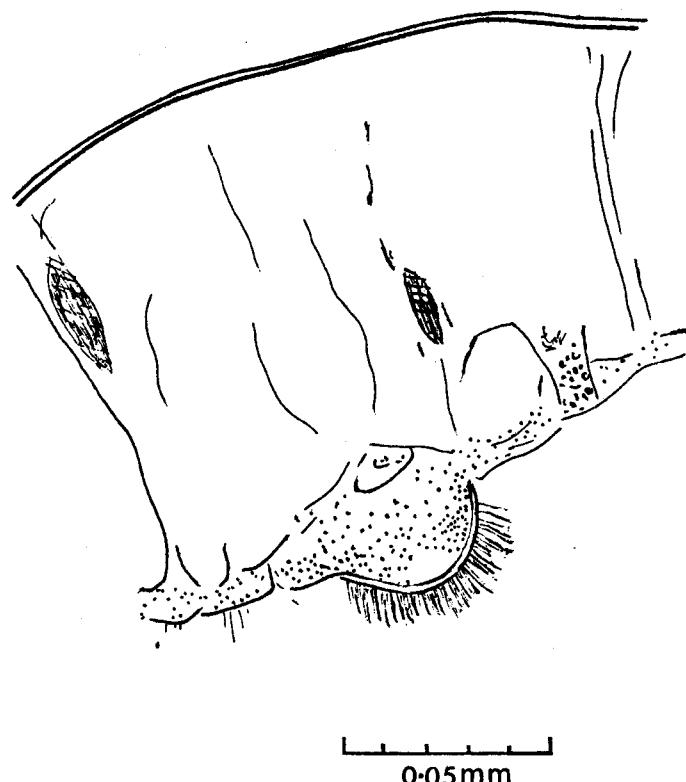


FIG. 43. *Pyrostephos vanhoeffeni* Moser

Transverse section of a mature gastrozooid to show a hedgehog cell of the endoderm. The ectoderm has been lost, leaving a narrow band of mesogloea on the outer side of the endoderm.

In an early growth stage the axial canal of a tentillum runs uniformly from tentacle-axis to the tip of the straight and short terminal filament. But at a point which marks the subsequent proximal end of the terminal filament a diverticulum of the axial canal, to which I shall refer as the diverticular canal, runs back towards the pedicel alongside the proximal part of the axial canal just described (text-fig. 44). Its epidermis, on the side opposite to the axial canal, forms the cnidoband.

As growth proceeds, the lumen of the diverticular canal, lying under the cnidoband, comes to exceed in diameter that of the axial canal proper, and forms the cavity of the saccus.

In the final growth stages the part of the axial canal that lies proximally to the terminal filament appears as a fine tube lying on the surface at one side of and opening into the dilated, diverticular canal at the point where the diverticulum originates. This same proximal part of the axial canal

develops thick mesogloal walls and becomes convoluted as it decreases in diameter towards the base of the terminal filament. It probably acts as an extensor on activation of the mechanism when the proximal end of the cnidoband breaks away from the pedicel and the whole cnidoband turns end for end and is flung on to the prey.

In most other siphonophores with the common type of tentillar cnidosac, the diverticular canal also becomes the cavity of the saccus, and the paired 'elastic bands' are probably formed from the lateral walls of the axial canal. These bands are, significantly, attached distally at the base of the terminal filament, at a point where the diverticulum just described originates. For this reason I believe the 'paired elastic bands' to be homologous with the lateral mesogloal walls of the proximal part of the axial canal. Their proximal ends are known to originate from the lateral mesogloal walls of the pedicel. The 'paired elastic bands' of the common type of cnidosac are probably more efficient and elaborate extensors than the axial canal of *Pyrostethos*.

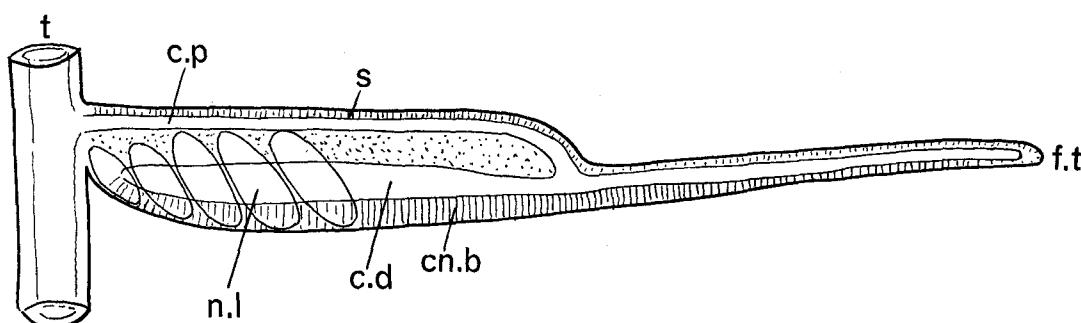


FIG. 44. *Pyrostethos vanhoeffeni* Moser

Schematic sketch of an early growth stage of a tentillum, $\times 50$
c.d. = diverticular canal; *c.p.* = pedicular canal; *cn.b.* = cnidoband; *f.t.* = terminal filament;
n.l. = lateral nematocysts; *t* = tentacle; *s* = saccus.

Thus *Pyrostethos* gives a clue as to the structure ontogeny and evolution of the hitherto puzzling and rather complicated tentillar knobs or cnidosacs that are found both in *Physonectae* and in *Calyco-phorae*. In this respect *Pyrostethos* seems to have retained a primitive feature. But in the still more primitive tentilla in species of *Nanomia* and *Forskalia* the axial canal never develops a diverticulum: there the axial canal remains simple, though it becomes spirally coiled throughout its length, and develops paired elastic bands. It seems that development of paired elastic bands in most siphonophores evolved prior to the development of the diverticulum.

At the base of the saccus there are from five to seven pairs of larger, lateral nematocysts. They do not enter the saccus-wall through the pedicel until the terminal filament, still in its straight uncoiled condition, is almost 0.5 mm in length. These large, ovoid, lateral nematocysts measure 0.04 mm \times 0.28 mm. They contain a large central structure, probably the hampe with spines, so that they possibly are heterotrichous heteronemes, euryteles or even stenoteles.

Bracts: The largest measure 23 mm \times 14 mm according to Moser. She described them as very thick, flat underneath, convex above, and proximally coming to a long point much broadened distally and irregularly toothed: the bracteal canal is fine, drawn out and ends some distance from the distal end. The basic pattern of the distal end seems to be three pointed. In early growth stages there is a shallow horizontal pocket on the upper side between the lateral pair of points.

Palpons (Oleocysts) (Pl. XVI, fig. 10): On a specimen taken on January 3, 1913, by 'Terra Nova' at Station 274 ($71^{\circ} 29' S$, $166^{\circ} 00' W$) in 80 m, the oleocysts seem to be arranged at the dorsal edges of the ventral tract of appendages as if to buoy up the stem.

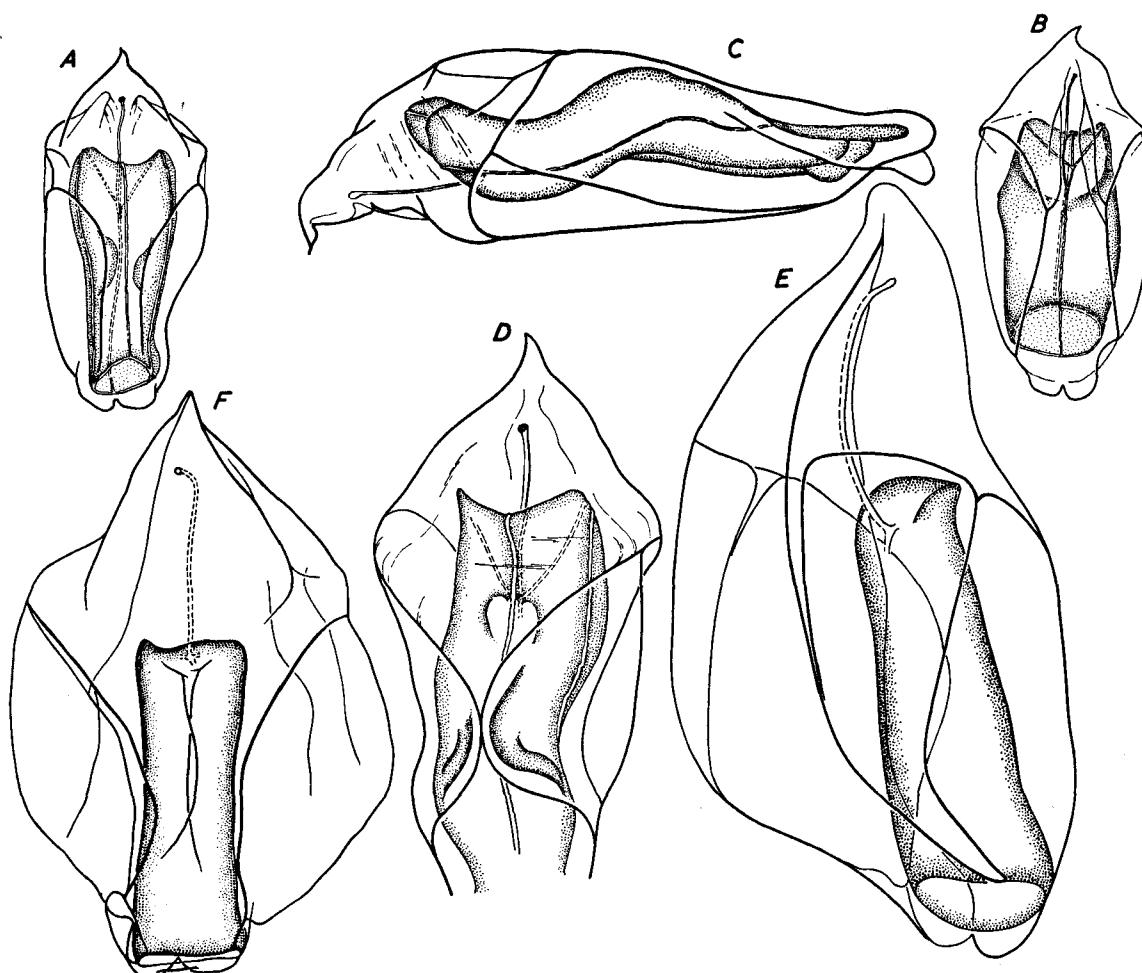


FIG. 45. *Bargmannia elongata* Totton. Nectophores
A, B, upper and under views, 'Discovery' St. 681, $\times 3.2$; C, D, lateral and upper views, 'Discovery' St. 699, $\times 6.3$; E, F, lateral and under views, 'Discovery' St. 1769 (1,000-750 m), $\times 3.5$. The muscular lamella is attached along the pecked lines in figs. E, F (from Totton, 1954), fig. 28).

Pyrostephos vanhoeffenii is dioecious.

Gonophores: The gonophores bud one from another to form small bunches. They were absent from the young specimens taken by 'Terra Nova' at St. 274 on January 3, 1913, but present in a smaller specimen taken on February 6, 1931, in 3-0 m at 'William Scoresby' Station 555. The males are sausage shaped, and when apparently mature measure 1.3 mm \times 0.5 mm. The females are ovoid, 0.5 mm in diameter, with from three to five eggs arranged meridionally to give the external appearance of the seams of a football.

Genus: **BARGMANNIA** Totton, 1954

Monotypic genus for *B. elongata* Totton, 1954.

Imperfectly known, chiefly from nectophores in which the lateral radial canals do not form loops.

Bargmannia elongata Totton, 1954

Text-figure 45

Nothing more has been published about this easily recognized species since I described the nectophores. The only new material I have identified came from 'Discovery' Station 4246 taken in a closing

net haul at 1,600 m on September 10, 1959. Unfortunately, there was on board no one interested in specially preserving siphonophores. There were many nectophores associated in the catch with fragments of an orange coloured stem and some large detached gastrozooids measuring up to 3 cm length \times 0.7 cm but no bracts were found, though the muscular siphosome, which is some 3 mm in diameter, carries a continuous series of the muscular bases of their lamellar attachments. A small two-chambered pneumatophore measures 6 mm \times 1 mm. The state of preservation is very bad and the ectoderm of the gastrozooids is wanting. Projecting into the lumen is a series of large irregular ridges and villi of mesogloea.

Well preserved nectophores in good shape are not generally found in plankton hauls. For the purposes of this synopsis I will not attempt a description but refer to my drawings which are reproduced here (text-fig. 45). Paradoxically, this is one of the least known but most easily recognized physonects.

Family 6: **PHYSOPHORIDAE** Eschscholtz, 1829 (*pro parte*)

PHYSOPHORIADAЕ Huxley, 1859

DISCOLABIDAE Haeckel, 1888

Genus: **PHYSOPHORA** Forskål, 1775

Monotypic genus for *P. hydrostatica* Forskål, 1775.

Physophora Forskål, 1775

Physsophora Forskål, 1775

Discolabe Eschscholtz, 1829

I recognize only one species of the only genus, *Physophora*, of this family of physonects. Characteristic of the family and genus is the fact that the spiral budding zone of the siphosome, instead of elongating, expands laterally into a spiral sac, on the outer rim of the under side of which are found the cormidial groups. The single palpons of each group are proportionately very large and form a ring of active 'feelers', capable of co-ordinated action, and stinging badly.

Physophora hydrostatica Forskål, 1775

Plate XV, figures 1-10

Physophora myzonema Péron & Lesueur, 1807

Physophora philippi Kölliker, 1853

Physophora borealis Sars, 1877

Discolabe quadrigata Haeckel, 1888b

Physophora hydrostatica Kawamura, 1911; Bigelow & Sears, 1937; Garstang, 1946; Totton, 1954

A distinctive short stemmed, almost cosmopolitan physonect that can be immediately identified from separated nectophores, palpons and tentacles, as well as from the denuded stem and pneumatophore. Its known temperature range extends from 3 °C to 21.1 °C. It was well figured – but the colours are incorrect – by Péron & Lesueur.

I am in no way satisfied by the evidence published by Haeckel (1888b) for the existence of a rather different species *Discolabe quadrigata*, alleged to have a quadriracial nectosome.

At first sight *Physophora* appears to be organized rather differently from long-stemmed physonects, but if the proximal end of the siphosome of one of the latter be examined, it will be seen that the budding zone either makes, by overgrowth, a similar sort of spiral, or makes several sinuous bends on the surface of the stem. In *Physophora* the proximal part of the protosiphon never elongates to form a stem, but instead becomes hypertrophied in the horizontal plane – to form a sac-like siphosome.

I would refer systematists to my earlier remarks (1954) on the species. There is a long description of the species by Vogt (1854), who gave an excellent figure of the larva (Tab. 6, fig. 24).

Pneumatophore: With plum coloured pigment at its apex, on a narrow mobile stalk (see Chun, 1898, p. 324, figs. 1-2 for details of the muscular lamellae). There is a basal pore.

Nectophores: Two rows of half-a-dozen or so, beautifully figured by Bigelow and Sears (1937, fig. 49) from the underside of a specimen 14.5 mm wide. Bigelow (1911b) had previously published photographs of young specimens and a good side-view of a nectophore (Pl. 16, fig. 8). Sars (1877) figured (Tab. VI, figs. 3, 4) the course of the radial canals as seen from both above and below. I show the upper side in text-figure 46B. The nectosac has sub-angular expansions at the ostial end of the

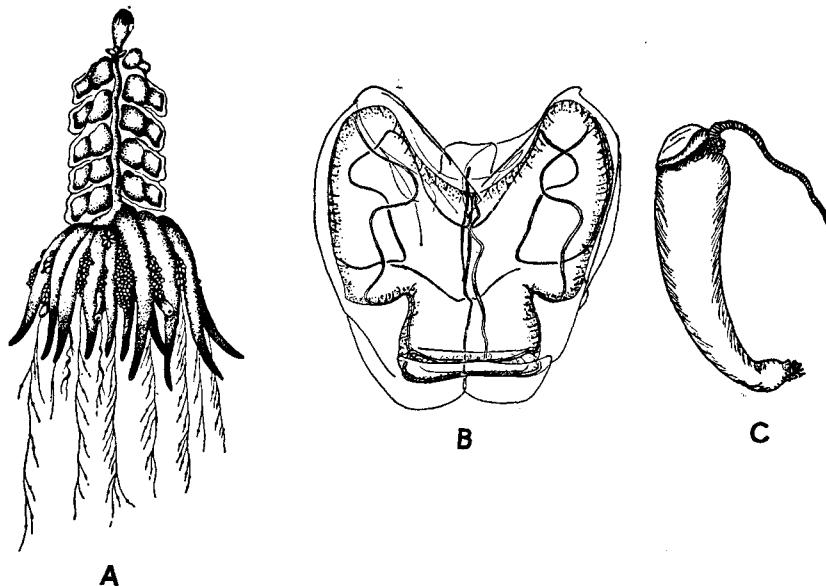


FIG. 46. *Physophora hydrostatica* Forskål
A, whole animal (after Gegenbaur, 1859), $\times 0.6$; B, nectophore from upper (outer) side, $\times 2$; C, palpon nat. size (from Totton & Fraser, 1955, figs. 1, 6a, 6b).

lateral sacs, and is embayed on the upper and adaxial side. The course taken by each lateral radial canal is as follows: From its common origin with the other three radial canals in the pedicel it runs a short distance outwards on the underside of the nectosac. It then turns 45° towards the ab-ostial end, though sometimes this change of course is not angular but gradual. It then forms an irregular loop round the ab-ostial half of the angle of the nectosac that separates the under and ad-axial sides of the 'lateral' wing of the nectosac, though not approaching the tip of the lateral sac. Having made this loop, it runs inwards and downwards parallel to the first two parts. So far my description can be followed in text-figure 46B. I have now described the course of the lateral radial canal to a point midway between the median longitudinal axial plane of the nectophore and the lateral face. Here it forms an acute bend outwards and runs irregularly round the lateral wall of the nectosac, and we can no longer follow its course in Bigelow's figure. It then runs an obliquely and slightly sinuous course upwards and inwards to form a loop at the same level, and on the opposite (outer) wall to that on which lies the first loop described, before it runs downwards and inwards to a level just above the junction of pedicular and radial canals, when the nectophore is viewed from the outer (or upper) surface. Here it makes a gradual right-angle bend outwards, then downwards, and again downwards and outwards to a point just inside the sub-angular ostial end of the lateral sac of the nectosac. Here it turns upwards along the ostial wall of the lateral sac, then down the lateral wall of the cylindrical section of the nectosac to terminate in the circular canal.

The *dorsal radial canal* makes three loops to each side on its course to the ring canal. The *ventral radial canal* makes two small loops to each side on its proximal half, and then runs direct to the ring canal.

The ad-axial side of the nectophore is hollowed out rather as in *Apolemia*. The hollow is limited on the ad-axial and under sides by rather fine edges, and also on the upper side by one running along the ad-axial end of the lateral sac of the nectosac to the median axis. Elsewhere the nectophore is more rounded than usual, and ridges are not apparent, except a basal one running from the divided mouth-plate to the ostial ends of the lateral sacs of the nectosac.

A median groove runs on the upper side of the nectosac between the lateral sacs, and curves round on the ad-axial side to the upper end of the muscular lamella of attachment. On the lower side is a great rounded mass of mesogloea, lying between the origin of the pedicular canal and the mouth-plate. The lower wall figures prominently in views from the ad-axial side. The ostial wall of this mass meets the lower outer wall of the cylindrical part of the nectophore at an angle of about 60° .

Tentacles: The cnido-batteries are of an unique kind. One side of the terminal part of the peduncle is hypertrophied to grow down alongside the coiled-up cnidoband. As a result the original distal end of the cnidoband is found near the upper part of the mature battery, and its original proximal end lies near the distal end of the battery. Growth stages of this complex apparatus have been figured several times (see Kefferstein & Ehlers, 1861, Taf. IV).

Palpons: Very characteristic are the large palpons, greenish-pink in colour and heavily armed at the tips with nematocysts that can inflict a very painful sting on the fingers. They are often called, mistakenly, 'tentacles'. Each bears a long, fine palpacle (Pl. XV, fig. 1, text-fig. 46C). When detached, the end of the palpon and the site of detachment are contracted, the latter showing a central papilla. The palpons show a characteristic concerted reaction to stimulation of the nectosome (Pl. XV, fig. 10), the tips being thrown up actively as far as the pneumatophore. In the swimming posture the tips are

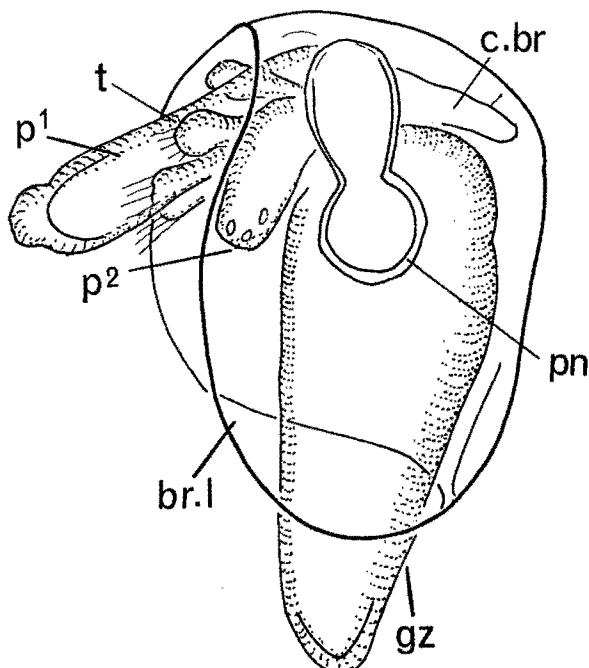


FIG. 47. *Physophora hydrostatica* Forskål
Larva, from life at Villefranche, March 3, 1954, $\times 20$.
br.l = larval bract; *c.br* = bracteal canal; *gz* =
gastrozooid; *p¹*, *p²* = first and second palpons;
pn = pneumatophore; *t* = tentillum.

approximated and traile aft. At all times when quiescent, the palpons obscure the gastrozooids and gonodendra.

Gonodendra (see Vogt (1854), Tab. 4, fig. 8; Garstang (1946), text-fig. 41): A male and a female gonodendron bud alongside each other in a whorl between the palpons and the gastrozooids. The male gonophores (see Vogt (1854), Tab. 6, fig. 19) are very much elongated. The tiny, ovoid, monovon, adult female differs in an interesting way from all other anthomedusae known to me as follows. The four radial canals do not join a ring-canal, but instead link up two and two distally to form two long lateral loops. The surface of the single egg is marked by meridional grooves corresponding with and probably impressed by the canals, making it appear at first sight as if there were four eggs. The medusoid – to adopt the terminology of Kühn (1913) – measures in formalin 0·4 mm × 0·32 mm. In this condition the egg does not completely fill the subumbrella, but appears to have shrunk a little. In the dozens of specimens stained with borax-carmine and examined under the binocular the nucleus measured 0·1 mm in diameter, and always lay close to one side of the umbrella between the two loops. At the end opposite the peduncle was a patch of tissue that stained well and contained nematocysts.

Ontogeny: Figures given by Haeckel (1869) suggest that the pneumatophore of the larva (text-fig. 47) lies *inside* the mesogloea of the great larval bract. In reality the float lies freely *outside* the bract. Vogt (1854, Pl. 6, fig. 24) gave a beautiful coloured sketch of the very active larva after the loss of its great larval bract.

Kawamura (1954) introduced, in my opinion unreasonably, two sub-species *major* and *minor*, depending chiefly upon the length of the peduncle of the tentillum. But observations of living Mediterranean specimens show that this varies enormously in one and the same animal.

Family 7: ATHORYBIIDAE Huxley, 1859

Anthophysidae Brandt, 1835
Pleophysidae Fewkes, 1888b

Two genera only are recognized – *Athorybia* and *Melophysa*. It appears that the main part of an athorybiid consists of an hypertrophied nectostyle carrying the larval-type bracts on groups of elongated muscular lamellae (pedicels), and groups of gonodendra with palpons and gonophores, as well as gastrozooids and their tentacles. The pedicel of the protosiphon never elongates downwards, as in long-stemmed forms, where successive cormidia are carried down with it, and no nectosome grows upwards in the opposite direction, except a very much reduced one in *Melophysa*. *Athorybia* never develops nectophores. Both types of organization may be compared with that of an '*Athorybia larva*' of *Agalma elegans* (text-fig. 19). These neotenous athorybiid animals finally take up a horizontal posture, lying on the nectostylar or ventral side from which the cormidal groups are budded.

In 'Discovery' Reports, Volume XXVII, 1954, I discussed the history of the family name and the significance of the morphology of the two species of physonects to which it applies. In systematic accounts there has been some confusion between the two. Neither is often found. I was lucky enough to have a living specimen of *Athorybia* to examine at Villefranche in 1950, on which I reported in 1954.

ATHORYBIA Eschscholtz, 1829

Monotypic genus for *A. rosacea* Forskål, 1775.
For synonymy see Totton (1954).

Athorybia rosacea (Forskål, 1775)
Plate XVII, figures 1–16, text-figure 48

- Physsophora rosacea* Forskål, 1775
Rhizophysa rosacea Lamarck, 1816
Rhizophysa heliantha Quoy & Gaimard, 1827
Rhodophysa helianthus Blainville, 1830
Rhodophysa rosacea Blainville, 1830
Athophysa rosea Brandt, 1835; Bigelow, 1911b, 1931; Leloup, 1941
Angela cytherea Lesson, 1843; (*Anga* nom. nov. Stechow, 1921, *Angela* preocc. Orthoptera)
Athorybia rosacea Kölliker, 1853; Huxley, 1859; Totton, 1954
Athorybia heliantha Gegenbaur, 1859
Athorybia formosa Fewkes, 1882; Schneider, 1898
Pleophysa agassizii Fewkes, 1888b
Diplorybia formosa Fewkes, 1888b
Athorybia californica Fewkes, 1888c
Anthophysa darwinii Haeckel, 1888b
Anthophysa formosa Chun, 1897b; Bedot, 1904; Lens & van Riemsdijk, 1908
Athorybia longifolia Kawamura, 1954
non Rhizophysa melo Quoy & Gaimard, 1827
non Rhodophysa melo Blainville, 1830
non Melophysa melo Haeckel, 1888b
non Athorybia melo Chun, 1897b
non Athorybia rosacea Bigelow, 1931 (= *Melophysa melo*)

Figured in colour by Quoy & Gaimard as *Rhizophysa heliantha*, by Kölliker as *Athorybia rosacea*, and as *Anthophysa darwinii* by Haeckel who gave three figures in monochrome on his plate XII. Bigelow (1911b) gave a beautiful detailed figure in monochrome and a description under the name *Anthophysa rosea*. Further notes on anatomy were given by Bedot (1904), Leloup (1941) and Totton (1954).

The organization of the animal is comparable with that of a young *Nanomia* or *Agalma* that has come to rest on its side. No nectophores are budded.

It is no easy matter to analyse the organization of the few available specimens of this species. My interpretation of the general organization differs from that of Leloup (1941 as *Anthophysa rosea*) in that Leloup describes two budding zones, the anterior (supérieure) of which 'en forme de mammelon' he homologizes with the nectosome of other physonects; I regard it as the nectostyle or budding zone of the siphosome. In Agalmidae it first appears on the opposite side to that on which the nectophores are budded (see Totton, 1956, fig. 1b). I maintain that there is only one budding zone in *Athorybia*, namely the nectostyle, from which the bracts (homologous with the larval bracts of the larvae of agalmids) and the cormidia are budded (as in agalmids).

It must be remembered that the name *Athorybia rosacea* has been applied to some descriptions and figures of specimens which are really *Melophysa melo*. If bracts are present it is very easy to distinguish between the two. Those of *Athorybia* are comparatively thin and smooth, those of *Melophysa melo* very thick with tuberculate ridges. *Melophysa* alone has nectophores and a shortly stalked pneumatophore.

The clue to the correct orientation and interpretation of the organization of both forms has been provided in a beautiful figure of *Melophysa melo* (as *Athorybia rosacea*) by Bigelow (1931, fig. 218). The morphological upper and lower poles of the long axis are marked in this figure, as in all physonects, by the pneumatophore and the protozooid (probably the smaller of the two gastrozooids shown).

The protozooid has always been found to be smaller and simpler than the secondary gastrozooids in all physonects so far examined on this point. I have discussed the basic organization further in notes on the family *Athorybiidae* on the opposite page.

Pneumatophore: Large, forming the bulk of the specimen. The thick secondary ectoderm was

figured by Bigelow (1911b, Pl. 21, as *Anthophysa rosea*) and by Leloup (1941, Pl. 11). Bigelow shows the giant cells in the septa connecting the saccus to the pneumatocodon. The long morphologically longitudinal axis is tilted over to the ventral side. I suspect that there is a basal *porus* as in *Physophora*, because I saw a living specimen emitting bubbles amongst the bracts and palpons. Its presence has not been noted in spite of the fact that Chun, Bedot, Bigelow and Leloup have all cut sections of specimens. Gas production must be rapid because I saw the same living specimen sink and rise again to the surface half a dozen times. Ten minutes or so elapsed between sinking and rising again. The apical end is half covered on one side by the enlarged nectostyle.

Bracts (text-fig. 48): These arise from the excentric nectostyle by pedicels, on the two sides of which broad based muscular lamellae arise. In maturity the bases of these lamellae form eight or nine groups of six or seven each, the newly budded one being more apical than the older ones.

The bracts themselves are capable of beating rhythmically in unison. I have seen them doing this when ascending to the surface, but particularly whilst being narcotized in magnesium chloride. They are three times as long as broad with a keel for attachment that is flattened laterally in the proximal part. The rest of the bract is flattened dorso-ventrally and convex on the upper side which bears seven inconspicuous longitudinal rows of nematocysts. The bracts form a complete corona and lie in several layers.

Gastrozooids: A protozooid marks the oral, anterior end. A young specimen may show only three or four gastrozooids, but in a specimen measuring 13 mm in length I counted eighteen. Their bases formed a line descending in a curve from the budding zone high up on the nectostyle towards and round the left and part of the broad underside. The curvature of this line in the growing zone is probably due to rapid, early hypertrophy. This occurs in most physonects, generally at the bases of all tentacles, especially in *Physalia*. The gastrozooids with their basigasters are of the usual Agalmid type. The tentacles have been described in great detail by Bedot (1904) and Bigelow (1911b). Bigelow decided that the trifid tentilla were of two main types, which he figured in his plate 20, figure 10 and plate 23, figure 4, an involucrate and a dendritic type, as described by Fewkes (1882) and by Haeckel (1888b). Bigelow said that some of Bedot's eight types were referable to stages of development of one type, and some to those of the other. My Villefranche specimen which measured about 1 cm in diameter, had seven tentacles and was carefully extended in magnesium chloride before fixation in formalin, bore five of the larger dendritic type of tentillum.

The preserved expanded tentacles, now measure about 3 cm in length. In life they were perhaps twice as long. There are from twenty-five to thirty tentilla on each, at distances apart of from 1-1.5 mm each pedicel measuring from 2 to 3 mm in length. There is a long thickened terminal part of each tentacle which is free from tentilla (see Leloup, 1941, Pl. 1, fig. 3).

The tentilla are of two kinds on this specimen. Each tentacle may bear one or two or none of the larger dendritic type (Pl. XVII, fig. 2; and see Bedot, 1904, Pl. 1, fig. 8δ). Those of the other involucrate type (Pl. XVII, fig. 3) are like those figured by Bedot on the same plate in figure 6β. Both are tricornuate.

The 'pendant' (Bedot) or 'dorsal spur' (Haeckel) of the dendritic type was long (1.25 mm). I saw no intermediates between this *delta* type and the *alpha* type of Bedot's figure 4. But I agree with Bigelow in thinking that there are two main types of tentilla and not eight as suggested by Bedot. My view is that the form of the 'spur' is probably very variable, rather than that one form grows into another.

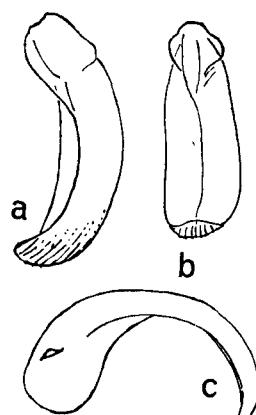


FIG. 48. *Athorybia rosacea* (Forskål)
Bracts a, oblique view; b, inner side;
c, side view (from Totton & Fraser,
1955, fig. 9 a-c), $\times 7$.

Measurement of δ form of tentillum (in mm)						
					length	diameter
Pedicel	6	0.03
Whole saccus	1.5	0.25
Lateral horns	0.5	
'pendant'	1.25	

Gonodendra: They originate as single gonopalpons from the pedicels of which secondary palpons up to nine or more in number are budded, together with a pair of gonostyles, ♂ and ♀, side by side. These gonostyles bear numerous gonophores (Pl. XVII, fig. 9), the actual 'adults' of this type of animal, the male ones with long pedicels. There is a pair of gonodendra to each gastrozoid, one on each flank of the animal. It is difficult to delimit the boundaries of the individual cormidia, and the exact relationships are not as yet understood. Each palpon bears, as usual, a palpacle or simple, reduced tentacle. The palpons themselves are long, vermiform, very active and heavily armed at their pink tips with nematocysts. I dealt with the Haeckelian myth of an ocellus in 1954.

Kawamura (1954) described and figured a single preserved specimen of *A. longifolia* from Sagami Bay. The possession of soft flexible bracts is due I suspect to the state of preservation and not to a specific difference. I have listed *longifolia* as a synonym.

Genus : *MELOPHYSA* Haeckel, 1888

Monotypic genus for *Rhizophysa melo* Quoy & Gaimard, 1827.

For the history of the name of this genus, see Totton, 1954 (p. 40).

Melophysa melo (Quoy & Gaimard, 1827)

Text-figures 49, 50

Rhizophysa melo Quoy & Gaimard, 1827

Rhodophysa melo Blainville, 1830

Stephanomia melo Quoy & Gaimard (1833), 1834

Athorybia melo Chun, 1897b

Athorybia rosacea Bigelow, 1931

Melophysa melo Totton, 1954

Bigelow (1931) confused *Athorybia rosacea* with *Melophysa melo*, but the only good account is his, though under the wrong name. He gave two beautiful text-figures of the whole animal as well as others of the tentilla. Detailed figures of nectophores are given in text-figure 50.

Specimens of this species can be distinguished quite easily from those of *Athorybia rosacea* by the presence of nectophores and bulky bracts which bear tuberculate ridges.

Pneumatophore: When mature, ovoid or pear-shaped, with septa containing giant cells, which are a part of the secondary ectoderm (see Chun, 1897b, Pl. IV, figs. 1, 7, 9); borne on a short nectosome which bears only a few (up to five) nectophores of a primitive kind. Bigelow suggested that only one at a time was functional (see Chun, 1897b, Pl. IV, fig. 3; and text-fig. 50). The post-larva has a more elongated, pear-shaped pneumatophore (see Totton, 1954, text-fig. 8).

Bracts (text-fig. 49): Thick and gelatinous borne in a corona on strong, contractile muscular lamellae. The nectostyle on which the larval bracts are borne cannot be distinguished in maturity, but is homologous with the whole of the bract-bearing side of the animal. The larval bracts are smooth surfaced, but like the later developed ones have a proximal keel of attachment. The mature bracts bear from eight to nine strong tuberculate radial ridges. In parts of the ridges, which may bear from six to twenty-seven tubercles, these have the form of conical papillae. In other parts they form more continuous crests. The bracteal lamellae are arranged in nine or more groups of three or four lamellae.

Gastrozooids and tentacles: Of the usual agalmid type, with thick walled basigasters, alternating radially with the lamellae. Bigelow counted eight gastrozooids. Tentilla tricornuate and involucrate. The cnidoband has seven or eight coils. The involucre may cover them or become contracted down to the base in preserved specimens.

Gonodendra: Both male and female on same specimen in pairs, each pair alternating radially with the gastrozooids. The detailed structure is not yet understood.

Palpons: There is a ring of nine palpons in the post-larva. Presumably these give rise to gonodendra.

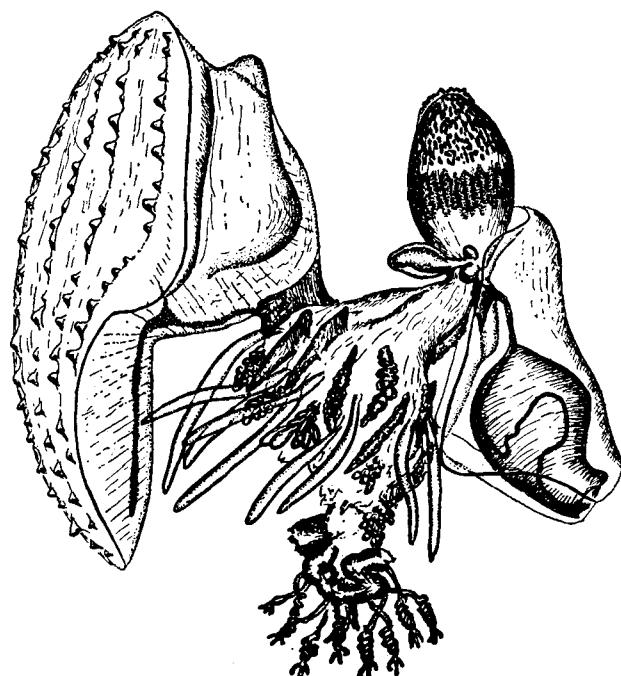


FIG. 49. *Melophysa melo* Q. & G.

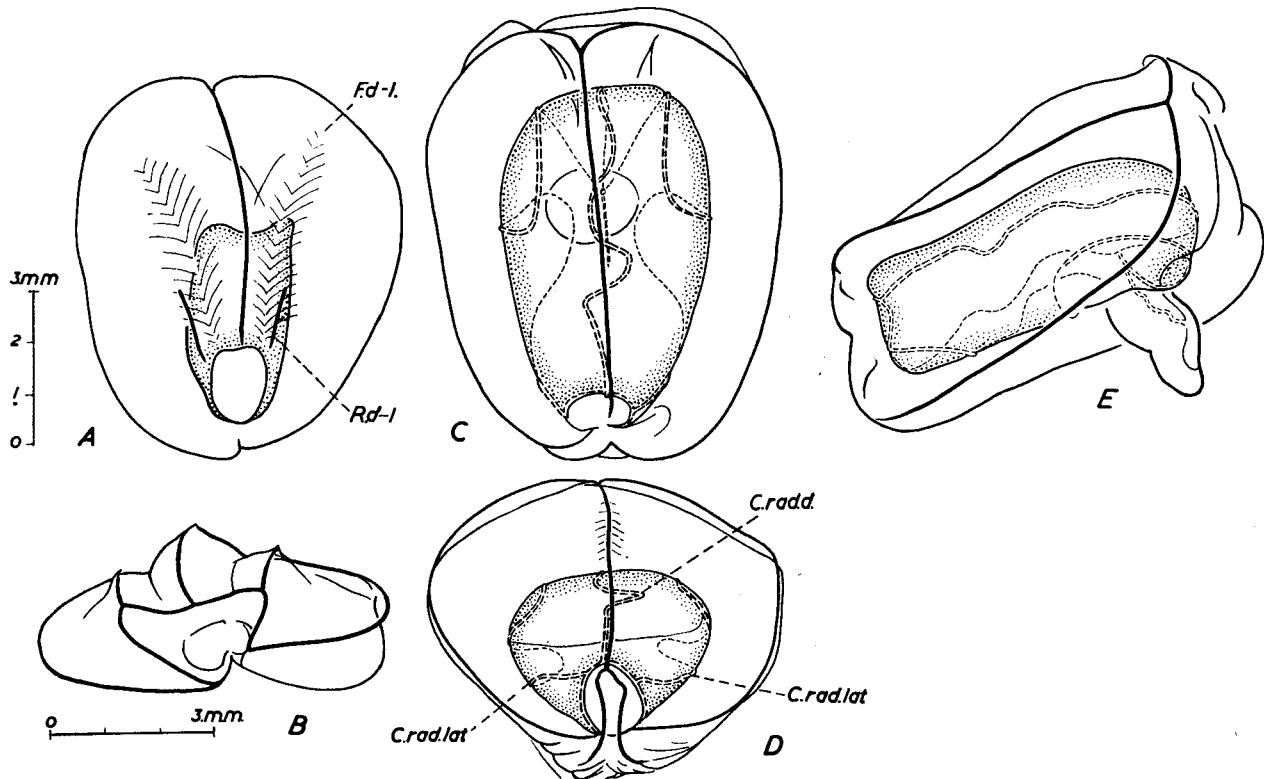
Whole animal, $\times 7$, with only one bract retained. The large nectophore has become twisted upside down (after Bigelow, 1931).

Nectophores (text-fig. 50): Probably only one functional at one time. They appear to be either rather primitive or reduced, somewhat flattened from above downwards, with a lateral ridge on each side and three longitudinal ridges on the upper side, best marked at the ostial end. There is a distinct pedicel as in agalmid buds of nectophores. The lateral radial canals form a loop on to the under side at mid-length. The dorsal radial canal is sinuous. In Bigelow's (1931) figure 217 the nectophore in my view has become twisted through 180° judging by the position of the ventral loop of the lateral radial canal, and the lateral ridges are somewhat contorted.

Very little material of this species has been reported in recent years. For this reason two additional records of identification of 'Discovery' specimens taken in the Peru Coastal Current (or Humboldt Current) are given here:

'William Scoresby' St. 707, $05^\circ 37'5''S$, $84^\circ 31'5''W$.

'William Scoresby' St. 713, $04^\circ 20'S$, $81^\circ 37'W$.

FIG. 50. *Melophysa melo* Q. & G. Nectophores $\times 7$

A, C, viewed from the upper side; B, D, from the ostial side; E, from the left side. A, from Bermuda, Beebe Coll.; B, 'Discovery' St. 692; C, D, E, 'Discovery' St. 1580
C.rad.lat = lateral radial canal; *C.rad.d* = dorsal radial canal; *F.d-l* = dorso-lateral fold; *R.d-l* = dorso-lateral ridge (from Totton, 1954, fig. 7).

Family 8: RHODALIIDAE Haeckel, 1888

Angelidae Lens & van Riemsdijk, 1908

Physonects in which an enlarged homologue of the pneumatophore or basal, gas secreting area of the pneumatosaccus protrudes on one side at the junction between the pneumatophore and the corm to form a characteristic structure, the aurophore. The nectosome and siphosome form a globular corm below the large pneumatophore. Both nectophores and bracts are developed, the simple sac-like nectophores forming a corona of one or more rows. The cormidia are borne on prominences. The zone of proliferation of the cormidia lies opposite to the aurophore.

The correct interpretation of the so-called aurophore was made by Lens & van Riemsdijk (1908) and by Bigelow (1911b).

The family name *Angelidae* Fewkes used by Lens & van Riemsdijk is unfortunate on nomenclatural grounds, as Bigelow (1911b) pointed out, for *Angela*,* Lesson (1843), is a synonym of *Athorybia* and is not as closely related as Fewkes supposed to his *Angelopsis*. Bigelow reviewed the family very thoroughly in his 'Albatross' report (1911b). Since then, very little additional material has been found. For this reason it seems to be unnecessary to summarize the review, which itself should be consulted.

When more specimens have been studied, it may be decided that *Rhodalia*, *Stephalia*, *Stephonalia*, and *Angelopsis* are congeneric.

It is difficult to extract from the descriptions of generally imperfect specimens of rhodaliidae what

* Stechow (1921) published a new name *Anga* for *Angela*, Lesson, 1843 (preoccupied by Serville, 1839 for Orthoptera). This would have necessitated writing *Angidae* for *Angelidae sensu* Fewkes.

characters are of generic and specific importance. The following descriptions are necessarily very imperfect and tentative.

Genus: **RHODALIA** Haeckel, 1888

Monotypic genus for *Rhodalia miranda* Haeckel, 1888.

The corm is in the form of a spongy mass and does not contain a large central cavity. The aurophore is smooth walled. A shallow hypocystic cavity of great breadth in the nectosome (Bigelow, 1911b, p. 309). Siphosome traversed by a network of innumerable small canals. General ground-substance cartilaginous in consistency as in *Angelopsis*.

Rhodalia miranda Haeckel, 1888

This specific name was based on four 'Challenger' specimens, three of which are still in the collection of the British Museum (Natural History), the sole remnants of this historic collection of siphonophores. The characters of the species are given above under *Rhodalia*.

The original specimens measured from 30–50 mm in diameter. The largest specimen bore a corona of from 50–80 (or more) nectophores in three alternating annular series, though the muscular lamellae form a single ring. Each cormidium of the siphosome consists of a conical mesogloal bulb bearing a single gastrozooid with a long tentacle and a clustered gonodendron bearing gonophores of both sexes and a single palpon.

Auralia profunda, a *nomen nudum* for a rhodaliid with nectophores arranged in a single circle, may have referred to a young specimen of *R. miranda*, in which case *Auralia* could be a synonym of *Rhodalia*.

Genus: **STEPHALIA** Haeckel, 1888

Monotypic genus for *S. corona* Haeckel, 1888b.

? *Stephonia* Haeckel, 1888b

? *Steleophysema* Moser, 1925

? *Sagamalia* Kawamura, 1954

The corm is bulbous and solid. The aurophore is smooth walled. Trefoil-headed, nail-like bracts are present on the cormidia.

Stephalia corona Haeckel, 1888

Plate XVIII, figures 1–4; text-figure 51

? *Stephonia bathyphysa* Haeckel, 1888b

? *Steleophysema aurophora* Moser, 1924b

? *Steleophysema auronecta* Moser, 1925

? *Sagamalia hinomaru* Kawamura, 1954

A most interesting specimen of a rhodaliid siphonophore in the D'Arcy Thompson collection, was presented in 1956 to the British Museum (Natural History) by Queen's College, Dundee, University of St. Andrews. It was taken nearly fifty years ago by F.C. 'Goldseeker' during North Sea Investigations by the Scottish Fishery Board in a fynnet on August 17, 1907, at a position 59° 35'N, 7° 00'W, just to the south of the Wyville Thomson Ridge at the entrance to the Faroe Channel. The depth given is 1,140 m, but the net was not a closing one. Apart from the 'Challenger' specimens of *Rhodalia miranda* the Museum has never possessed a rhodaliid specimen.

The particular interest of this specimen is that it still bears some beautifully preserved bracts of very distinctive shape (Pl. XVIII, fig. 4). In only two specimens of a rhodaliid hitherto has the pre-

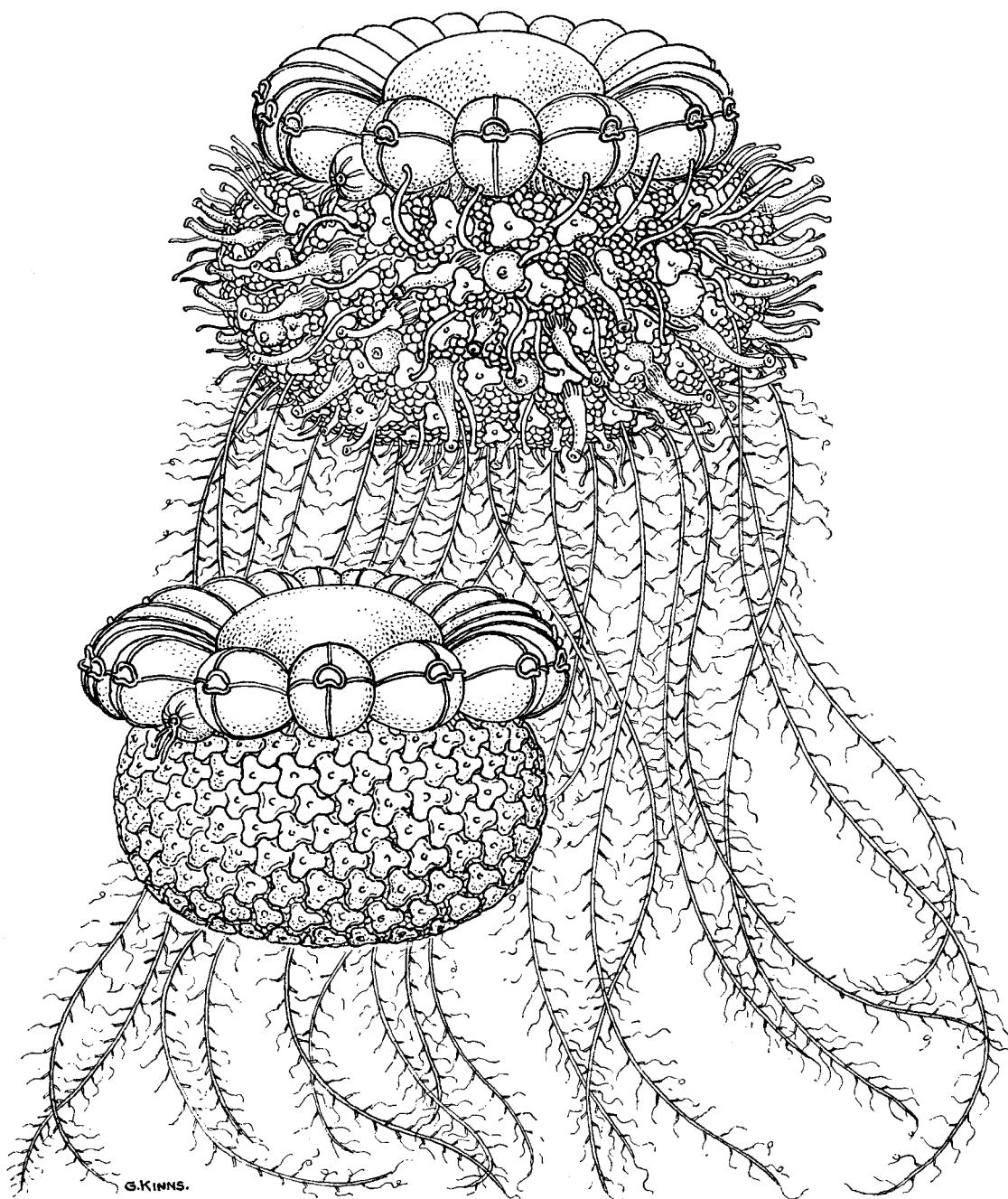


FIG. 51. *Stephalia corona* Haeckel
Reconstruction of the whole animal (Dundee specimen), expanded and contracted, $\times 3$

sence of bracts been noted. One was by Kawamura (1954) in a specimen described and figured as a new species of a new genus, *Sagamalia hinomaru*, taken by the boat of the Emperor of Japan in Sagami Bay in 1935 at a depth of 450 metres. Another Japanese specimen *Steleophysema aurophora* was briefly described by Moser (1924b, 1925).

The rhodaliid group is not well known, since specimens are rarely taken. When they are, they are usually defective. The only good review of the various species is that of Bigelow (1911b), to which the reader is referred. The specimen in question was labelled *Stephalia corona* Haeckel, and this may well be its proper name. But unfortunately none of the four specimens on which Haeckel (1888b)

based his account and figures of that species are known to be in existence. Two of them were taken in the Faroe Channel and Shetland Islands and were described as lacking tentilla on the tentacles and bracts, both of which are present in the 'Goldseeker' specimen, which was taken not far away to the south-west. The absence of tentilla and bracts may be due simply to the fact that the 'Triton' specimens were defective. So we have only Haeckel's idealized drawings and account of what were probably defective specimens as a guide to identification. The water masses in which the 'Triton' and 'Goldseeker' specimens were taken may well have had a common origin in the open North Atlantic, but certainly not in the Boreal region.*

Hitherto, we have had only one record of the male gonophores of a rhodaliid – they seem to be monoecious – and very interesting records by Brooks and Conklin (1891) and Moser (1924b, 1925) of the female ones. Apparently the eggs in this group develop in an egg-sac and migrate into the female medusoids singly, taking up a position between the ectoderm and endoderm of the manubrium. Being very yolked, one egg almost completely fills the gonophore. Secondary manubrial endoderm grows up inside the manubrial ectoderm to form finger-like processes which almost surround the egg and nourish it. The whole arrangement seems to have been wrongly interpreted by Haeckel (1888b).

The Dundee specimen is a male and hence of particular interest. Brooks and Conklin suggested that males might be widely different from female specimens, but I do not think this is likely. They made the same prediction about *Physalia* which has proved to be untrue. I myself think that they were unable to distinguish the two sexes in *Physalia*, and thought that all the specimens they handled were males.

Rhodaliids have been taken – never in closing-nets – from depths of perhaps 100 m, rather than from greater ones in the North, Tropical and South Atlantic; and North and Tropical Pacific; as well as the Malaysian region. Moser's *Steleophysema* was taken at the surface.

Systematists have used such characters as (1) presence or absence of tentilla on the tentacles – their absence only means loss; (2) nectophores in one or more rows; (3) solid bulbous corm or thin walled corm; (4) axial canal through corm or absence of it; (5) large or small hypocystic cavity; (6) aurophore smooth or papillated; (7) Pneumatophore smooth or papillated. Perhaps the most satisfactorily described species is *Dromalia alexandri* Bigelow, based on fifteen specimens, but even these had lost the nectophores. I think it possible therefore that nearly all described specimens of rhodaliids have been defective, and that perhaps they all originally bore bracts like the present specimen and Kawamura's one of *Sagamalia*. It may be that *Rhodalia*, *Stephalia*, *Stephonalia*, *Steleophysema* and *Angelopsis* are all congeneric, but we must await the capture of more material before arriving at a decision.

Meanwhile I shall regard the Dundee specimen as a well preserved male specimen of *Stephalia corona* with bracts still attached.

Description: The specimen measures 25 mm × 27 mm, and 21 mm in the axial direction. The smooth walled pneumatophore is 9 mm in diameter, and is surrounded by a corona, 20 mm in diameter, of eighteen thin walled nectophores. There is one detached one. In a gap at one end of the corona is the smooth walled aurophore, in another at the opposite end the budding zone, in which region are the only two small nectophores. The smallest of these lies not next to the gap, but between two of the large nectophores nearby, suggesting that a secondary row of nectophores might have arisen later on. Few mature gastrozooids are still attached but there are many stumps from which they have broken off and sixteen were lying in the bottom of the container. However, there are about three dozen immature ones, the distal ends just peeping out from the globular basigaster in a way characteristic of young gastrozooids. Fourteen bracts are still attached by the proximal half of one side to the outer sides of gelatinous prominences, the cormidia, and there are fifty-four detached ones.

* For this opinion I have to thank Dr. J. H. Fraser of the Marine Laboratory, Aberdeen.

The bracts are radially arranged so that their trifid, contiguous, truncated, interlocking outer ends appear to have formed a sort of carapace to the contracted living animal, at any rate in the equatorial region. A cormidium sometimes bears two or three bracteal lamellae. The palpons are numerous in places, but have been lost in others. The numerous pedunculate gonophores appear to be all male. There is no sign of an opening to the sub-umbrella. Radial and circular canals are visible in the gonophores. The numerous gonodendra are branched, and bear the palpons.

As in *Dromalia* and *Rhodalia* the cormidia appear to be slightly branched, new gastrozoooids growing from the base of older ones. The tentacles bear tentilla with a single terminal filament. The various appendages are so numerous and well preserved that it is hardly possible to ascertain whether there is a spiral arrangement as in *Dromalia*. The single specimen is at present too valuable to dissect, so that it is not known whether there is a single axial canal leading to the protozooid, which has not been located.

Kawamura (1954) cited the evidence of a coloured sketch of the living animal that the pneumatophore, circular and radial canals of the nectophores and the distal halves of the gastrozoooids were all brilliant red in colour.

He showed that the three distal corners of the bracts are heavily armed with nematocysts.

Genus: *ANGELOPSIS* Fewkes, 1886

Angelopsis Fewkes, 1889; Bigelow 1911b

Type species: *A. globosa* Fewkes, 1886.

Corm bulbous, the nectosome containing a 'hypocystic' cavity, the siphosome solid but traversed by a network of canals. General ground-substance cartilaginous, in consistency as in *Rhodalia*.

Angelopsis globosa Fewkes, 1886

The only known specimen was inadequately described and figured in 1886, but after the publication of Haeckel's monograph (1888b) in which he set up the group Auronectae, Fewkes (1889) re-described and refigured it in more detail (Pl. VII).

Pneumatophore: Spherical, 7–10 mm in diameter, smooth-walled.

Corm: Of same diameter as pneumatophore, globular, with central cavity. There is according to Fewkes (1889, Pl. VII, fig. 2) a wide hypocystic cavity, which may be part of the above mentioned central cavity.

Aurophore: Smooth-walled.

Angelopsis dilata Bigelow, 1911

Plate XVIII, figures 5–7

Pneumatophore: Voluminous, 5 mm in diameter, rounded and smooth-walled. No pigment has been recorded.

Corm: Dumbbell-like, nectosome narrow, siphosome globular, semicartilaginous, with network of canals. Zone of proliferation opposite to the aurophore. Cormidia forming a spiral, on conical gelatinous prominences, one to each prominence. Tentacles not described. Gonodendra on gelatinous stalks, with two branches, one bearing female gonophores. Palpons present on both branches.

Aurophore: Sac-like, smooth-walled, at junction of pneumatophore and corm.

Genus: ***ARCHANGELOPSIS*** Lens & van Riemsdijk, 1908

Monotypic genus for *Archangelopsis typica* Lens & van Riemsdijk, 1908.

***Archangelopsis typica* Lens & van Riemsdijk, 1908**
Plate XIX, figures 1, 2

Archangelopsis typica Bigelow, 1913

The corm forms a voluminous thin-walled sac. The aurophore bears numerous papilliform appendages on its surface.

Pneumatophore: 6 mm × 4 mm (the largest known specimen), flattened above, smooth.

Aurophore: With prominences on the surface. A well preserved specimen captured by 'Albatross' in the NW Pacific near Japan, was reported by Bigelow (1911b).

Corm: Sac-like, with one vast cavity, its walls not containing a network of canals (see Lens & van Riemsdijk, 1908, Pl. XVII, fig. 24); the cormidia were described by Bigelow (1913). They bear from one to three muscular lamellae to which bracts were probably attached.

Genus: ***DROMALIA*** Bigelow, 1911

Monotypic genus for *D. alexandri* Bigelow, 1911b.

The corm, is bulbous, its upper part or nectosome of considerable length. Pneumatophore flattened apically and bearing gelatinous prominences on its outer rim. The aurophore bears numerous papilliform appendages. No hypocystic cavity in nectosome.

***Dromalia alexandri* Bigelow, 1911**

Plate XIX, figures 3–6

Pneumatophore: Flattened apically; with eight to eleven triangular gelatinous prominences on its outer rim. Radial septa present between pneumatocodon and pneumatosaccus.

Aurophore: Sac-like, with numerous, hollow, papilliform appendages about 2 mm long on its surface, with terminal pores (see Bigelow, 1911b, Pl. 24, fig. 6).

Corm: Bulbous, its upper part or nectosome of considerable length. Zone of proliferation of nectophores and cormidia on the side opposite to the aurophore (see Bigelow, 1911b, Pl. 24, figs. 1–3). Cormidia arranged in a spiral (see Bigelow, 1911b, Pl. 23, fig. 11), on conical, gelatinous prominences (see Bigelow, 1911b, Pl. 23, fig. 9). A number of gastrozooids and gonodendra are carried on a common peduncle. From two to four palpons with gonophores at their bases to each of the gonodendra which bud from the pedicels of the gastrozooids.

Tentacles: With suspensorium at base. Tentilla tricornuate (Pl. XIX, fig. 6), probably with basal involucrum.

Family 9: **FORSKALIIDAE** Haeckel, 1888

Forskaliidae Bedot, 1893b

Haeckel established this family for four supposed genera, *Forskalia* Kölliker, *Forskaliopsis* Haeckel, *Bathyphysa* Studer and *Strobalia* Haeckel (*nom. nud.*). As typical of *Forskalia*, Haeckel cited *F. edwardsi* Kölliker. Typical of *Forskaliopsis* he cited '*F. ophiura* Leuckart' (= *F. edwardsi* Köll.), mentioning that in that form there were numerous 'tasting palpons' scattered between the nectophores. The only siphonophores which have tentacles *budded* from the nectosome are species of *Apolemia*. It is typical of *Forskalia* spp., as Bedot (1893b) pointed out, that the very long active palpons budded from the upper part of the siphosome habitually explore up among the nectophores, from between which their distal ends may protrude. Presumably Haeckel thought that such palpons were

budded from the nectosome. His *Forskaliopsis*, founded on this characteristic, may therefore be considered as a synonym of *Forskalia*.

Haeckel admitted that *Bathyphysa* was perhaps, as it obviously is, the representative of a separate family (see Rhizophysidae, p. 40). *Strobalia cupola* (*nomen nudum*) Haeckel said was observed living by him in 1881 in the Indian Ocean, and would be – but never was – described in his 'Morphology of the Siphonophorae'. He added that a fragment of a similar species '*Strobalia conifera*' (*nomen nudum*) was collected by 'Challenger' in the South Pacific (Station 288). '*Strobalia*' then is not a valid genus.

We are left with species of *Forskalia*, Koll, two of them easily identifiable.

Genus: ***FORSKALIA*** Kölliker, 1853

Type species: *Forskalia edwardsi* Kölliker, 1853.

Characteristic of *Forskalia* spp. is the cone-shaped or sometimes cylindrical nectosome of numerous, multiserial nectophores, all of which arise from one meridian of the coiled stem. In a contracted state the stem forms a close spiral, but it opens out very considerably on extension. The gastrozooids are borne on long peduncles that are covered with numerous bracts. These animals are well known to the Mediterranean fishermen. The oldest palpons readily eject a plum or orange coloured drop of liquid from their tips.

Associated in the older literature with descriptions and figures of obvious specimens of *Forskalia* spp. are seven valid specific names, four of them sunk in synonymy, two names for indeterminate species, one *nomen nudum*, one name of a mistakenly identified species (*Physophora hydrostatica* Forskål). Bedot substituted one new name for a prior name. In historical order these specific names are:

- (1) *Stephanomia ophiura* Chiaje, 1831
an indeterminate species
- (2) *Physophora mirabilis* Chiaje, 1841
an indeterminate species
- (3) *Stephanomia contorta* Milne Edwards, 1841
(the first species described in any detail) = *Forskalia leuckarti* Bedot, 1893
- (4) *Stephanomia prolifera* Milne Edwards, 1841
identifiable by its gonodendra as *F. edwardsi* Kölliker, 1853
- (5) *Stephanomia excisa* Leuckart, 1853
nomen nudum. Provisional name for *F. leuckarti* Bedot, 1893
- (6) *Forskalia edwardsi* Kölliker, 1853
the type species of *Forskalia*
- (7) *Forskalia formosa* Kefferstein & Ehlers, 1860, 1861
Syn: *F. leuckarti* Bedot, 1893
- (8) *Forskalia atlantica* Fewkes, 1882
Syn: *F. edwardsi* Köll. (fide Bedot, 1893b; Schneider, 1898)
- (9) *Forskalia tholoides* Haeckel, 1888
- (10) *Forskalia cuneata* Chun, 1888

I have not included *Forskalia hydrostatica* (Chiaje, 1830–31), because I think it was a case of mistaken identification on the part of Chiaje, and that the name was not put forward as that of a new species.

It can be seen that our basic information on members of this group of siphonophores was mostly published a century or more ago by Milne Edwards (1841), Kölliker (1853), Leuckart (1853, 1854), Vogt (1854) and Kefferstein & Ehlers (1861). Claus (1863) also contributed.

Because of their transparency and very active movements these animals are difficult to examine. So the older descriptions did not include details of the bracts (for which see Leuckart, 1854; Totton, 1954). But Kölliker's account of *F. edwardsi* and Vogt's of *Apolemia contorta* – one and the same animal – enable one to recognize with certainty this common Mediterranean species. It is the only species of *Forskalia* about which we can up to now obtain a tolerably complete picture. It can often be examined alive under laboratory conditions at Villefranche and Naples.

There is no doubt about the existence of a second species *F. leuckarti*, but it was known in recent years chiefly from detached nectophores. A complete specimen is described on page 107.

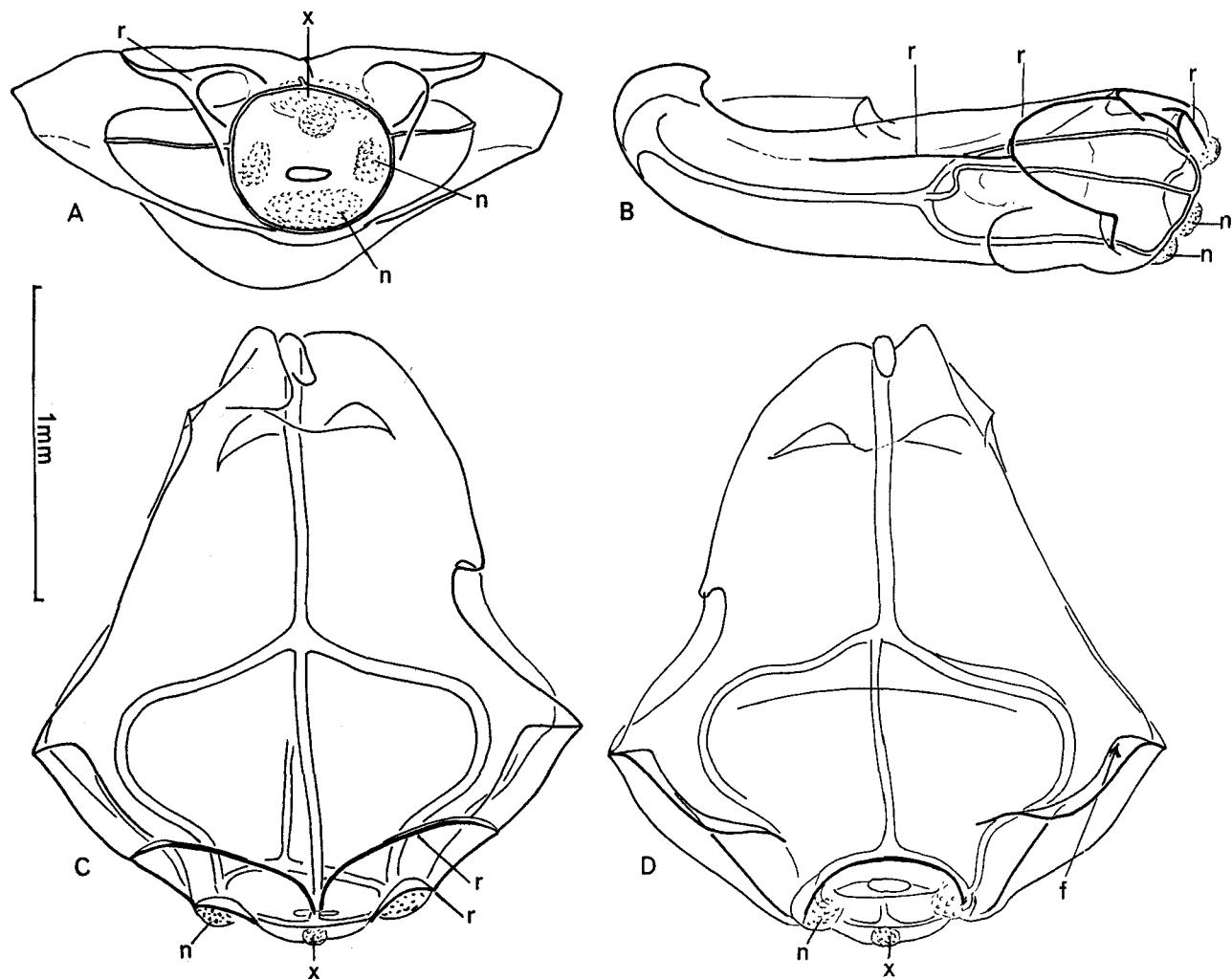
There was some doubt, which I hope I have dispelled, about the existence of a third alleged Mediterranean species, *F. contorta* Milne Edwards, 1841. I maintain that it can be recognized by its gonodendra to be what Bedot called *F. leuckarti*. It was considered by Bedot (1893b) to be a distinct species. *F. cuneata* and *F. tholoides* are doubtful species.

It will be seen that the conclusions to which I have come about speciation in *Forskalia* are rather different from those reached by Bedot (1893b). This is simply because I agree with Leuckart (1854) in thinking that the specimens he had before him in 1854 (but not in 1853) were indeed the *Stephanomia contorta* of Milne Edwards (1841). There are two criteria which make possible the identification of this species. Milne Edwards clearly indicated one – the gonodendra – while Leuckart clearly indicated the other – the *rete mirabile* in the pedicel of the nectophore. I was lucky enough to recognize at Villefranche a museum specimen, probably the only one in existence, which exhibits both characteristics. The prior name of this species is *contorta* Milne Edwards. But because of a great deal of confusion in the synonymy of this genus, Bedot renamed Leuckart's – and Milne Edwards's species – *leuckarti*. I retain this name since it appears to be the modern practice not to change a synonymy when it has remained unchallenged for a long period of years.

Larvae of species of *Forskalia* have not been described as such as far as I recollect, but Claus (1863, Taf. XLVIII, figs. 30–35) figured as young physophorids what I believe to be larvae of *Forskalia* spp. I have observed similar living larvae at Villefranche, where they are often taken in the plankton. They can be identified as such by their possession of orange coloured pigment.

Those physonect polyps that the German pioneers used to call 'Tastern' and are now called palpons seem to have originated as gastrozooids but to have become morphologically degraded. Their physiology has not been studied as far as I am aware, but they certainly do not ingest food. Their single tentacles are simple instead of bearing branches like all other tentacles of gastrozooids, except those of *Apolemia*. There are no palpons in the Calyconectae except in *Stephanophyes*; and in the other calyconects the gonophores bud from the bases of gastrozooids, whereas in the Physonectae it is from the bases of the palpons that the gonophores arise.

In 1960, I described the development of palpons and gonophores in the cystonect, *Physalia*, where it can be seen clearly how the gonophores arise as buds from the pedicels of the palpons. In 1954 I showed how in *Agalma elegans* the gonophores arise at first from small prominences near the bases of the palpons on the sections of the stem (*cormidia*). Later, after elongation of these sections of the stem, the gonophores become more scattered. In *Nanomia bijuga* I have shown (text-fig. 35) how the bunches of gonophores arise from the bases of the palpons. In *Forskalia* the arrangement is essentially similar, but in this genus the protuberances from the bases of the palpons may become very much elongated. At first sight it was not easy to correlate the conditions found in the two species, *F. edwardsi* and *F. leuckarti*. In *F. edwardsi* the male gonophores arise from a large protuberance of the distal palpon, and the female ones from smaller protuberances of the more proximal palpons. In *F. leuckarti* the two bunches of female gonophores appear to arise from an enormously extended, terminally bifurcated protuberance, whereas the male bunch arises from a much smaller protuberance at its base. But careful analysis shows that it is the smaller male branch that is formed from the base of the distal palpon, while the elongated base of the female gonophores actually arises from the

FIG. 52. *Forskalia edwardsi* Kölliker

A young nectophore of a Villefranche specimen. A, B, ostial and side views; C, D, upper and under side of the same
f = fold; *n* = patch of nematocysts; *r* = system of ridges; *x* = lemon-yellow spot.

penultimate and therefore more proximal palpon. It is almost incredible that the very elongate process that carries the two bunches of female gonophores is nothing but a protuberance from the peduncle of a proximal palpon, but that is the conclusion at which I have arrived: a conclusion that enables me to see a common pattern of budding of palpons and gonophores in those physonects in which these individuals have been studied.

There is always a tendency for palpons to bud repetitively and successively from the bases of their predecessors. In *Forskalia edwardsi* there is, as far as I have been able to discover, a single primary palpon (text-fig. 54). From its base when fully grown, buds a succession of smaller ones to form the gonodendron-complex. In *F. leuckarti* I have not been able to check the arrangement, but Leuckart (1854) described what appears to be an arrangement of up to four such groups. He used the terms 'Zwilling- und Drillingstaster' for such successions of palpons.

Kawamura (1954) published a paper in a journal which appears not to be taken in England, which contains a description and figures of an alleged new species *F. misakiensis*. The description and figures especially those of the bracts are not very detailed. I list it as a *species inquirenda*.

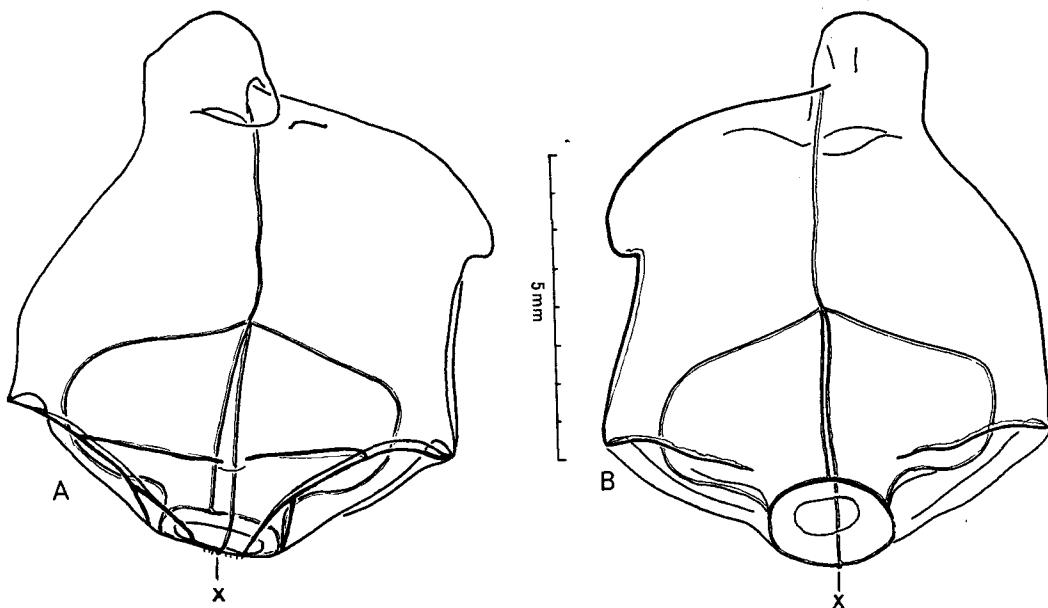
Forskalia edwardsi Kölliker, 1853

Plate XX, figures 1, 2

Stephanomia prolifera Milne Edwards, 1841*Stephanomia contorta* Leuckart, 1853*Forskalia edwardsii* Kölliker, 1853*Apolemia contorta* Vogt, 1854*Forskalia ophiura* Leuckart, 1854 ??*Forskalia ophiura* Sars, 1857*Forskalia edwardsii* Kefferstein & Ehlers, 1861*Forskalia* sp. 1 Claus, 1863 (p. 545, Pl. xlvi, fig. 16)*Forskalia edwardsi* Bedot, 1893b*Forskalia contorta* Leloup, 1935*Forskalia edwardsii* Totton, 1954

An abundant Mediterranean species whose appearance at the surface at places like Villefranche seems to depend on up-welling water. The stem, which may reach a length of seven or eight feet, may be coiled up closely during progression.

Nectophores (text-figs. 52, 53): The nectosome consists of a conical or more cylindrical structure of numerous nectophores, all budded from one meridian of the stem. The proximal portion of the nectophore (exumbrella) is elongate, flattened from above, tapering and without the marked incision

FIG. 53. *Forskalia edwardsi* Kölliker

A full grown nectophore of a Villefranche specimen. A, upper side; B, under side
x = lemon-yellow spot.

at the point of attachment of the muscular lamella found in *F. leuckarti*. There is a lateral basal projection and incision on the right side, and a projection on either side of the nectosac. A small sulphur-yellow pigment spot at the junction of the upper radial and circular canals is characteristic of the species, but there is no rete in the pedicular canal.

Gastrozooids: Very mobile, 16 mm in length, on long peduncles 37 mm in length, bearing numerous pairs of bracts.

Bracts (see Totton, 1954, p. 71, text-figs. 29, 30): Laterally compressed. *Stem bracts* leaf-like, pyramidal in outline, in pairs on each cormidium of the stem. *Peduncular bracts* of three types, in enantiomorphic pairs. At the base of the peduncle is a pair of bolster-shaped bracts, triangular in

cross-section. Other peduncular bracts have a knee-like bend, giving them the shape of a laterally flattened sock. All the bracts have a shallow pocket between the distal facet and the upper, dorsal facet. The pocket is very wide in the stem bracts. In the more distal peduncular bracts it is very narrow. There are two or three pairs of tooth-like projections on the distal half.

The peduncular bracts of *edwardsi* can be homologized with those of *leuckarti*. The outer angle is obtuse, otherwise the pattern is similar, but the flange on the inner side of the upper face which overlaps the next distal bracts is less marked, and the bracts are arranged in pairs which are mirror-images of one another. They are much less thick than in *leuckarti*, in which the pocket is much less evident. There is no little spur-canals at the bend of the bracteal canal such as is present in the bracts of *leuckarti*, and the bend in the canal itself is obtuse instead of being right-angled.

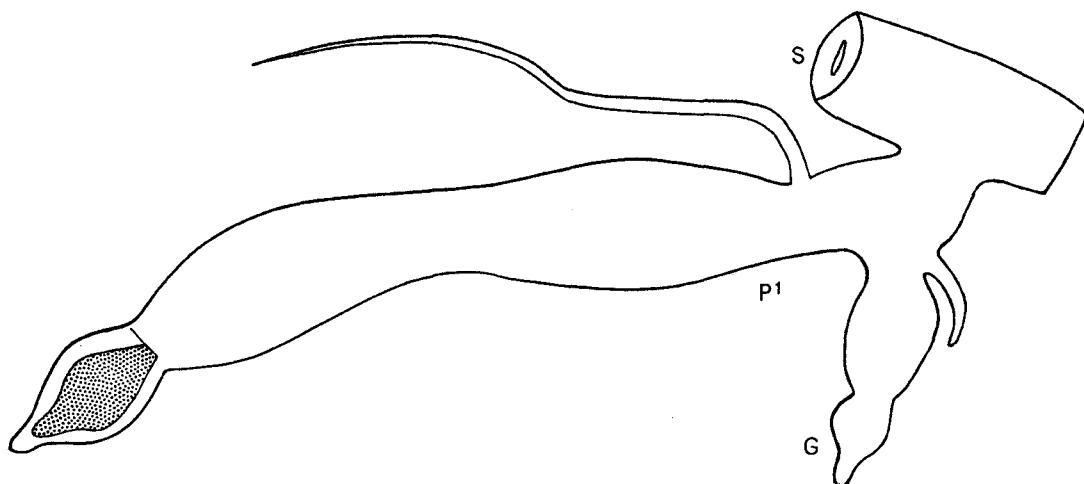


FIG. 54. *Forskalia edwardsi* Kölliker
A young growth stage of a gonodendron, $\times 12$ (after Leuckart, 1853)
s = stem; P¹ = palpon; G = gonodendron, initial growth-stage.

The arrangement of the bracts is as follows: In each cormidium there is a pair (*see* Totton, 1954, text-fig. 29a, b) attached immediately on each side of the ventral meridian by muscular lamellae, which extend from a point immediately distal to the gastrozoid of the previous cormidium to the base of the gonodendron. Their pedicular canals arise from the stem at about one quarter of the distance between gastrozoid peduncle and gonodendron. They are mirror-images of one another. The uppermost pointed ends of my figured bracts are aboral. The bolster shaped bracts (*id. fig. c*) are attached in pairs to the basal part of the peduncle of each gastrozoid on the side facing the gonodendron. The proximal edges of their muscular lamellae overlap somewhat the distal oral edges of the lamellae of the stem bracts. In figure 29c the pointed end of the bract is the proximal stem end. The bracts shown in my (1954) text-figure 30 a–e are arranged in an alternating, overlapping fashion on the peduncles of the gastrozooids, those at the base resembling figure c, those at the distal end – there may be a succession of ten – resembling figures d and e. The pedicular canals of these peduncular bracts issue from the peduncle close to the proximal end of the next distal broad muscular lamella. The lamellae lie nearly in one meridian of the peduncle, which may twist. I suppose that one of the functions of these peduncular bracts is to give buoyancy to the gastrozoid peduncle, which projects out nearly at right angles to the stem.

Gonodendra (text-figs. 54, 55): There is a single gonodendron between each two gastrozoid peduncles measuring 1 cm in length, of which the peduncle forms half. It is formed by a series of about six palpons, each with a palpacle, successively budded from the distal ends of the elongated

bases of their predecessors, and bearing bunches of gonophores on their bases. The terminal one bears male gonophores – about three bunches of fourteen, and the next proximal three bear bunches of smaller monovon female gonophores. No asexual medusoids – nectophores – are produced. The elongated bases of the successively budded palpons form the straight peduncle of the gonodendron. Though the distal bunch of male gonophores extends beyond the sixth palpon it may be regarded as an elongated extrusion from the base of the palpon.

Measurements: Length of peduncle, 4 mm

Male gonophore, length 1·3 mm; diameter 0·6 mm

Female gonophore, length 0·6 mm; diameter 0·37 mm

Behaviour: Leloup (1935) gave its rate of progression as 30–50 cm per minute. This rate seems a slow one. I regret that I have omitted to check it.

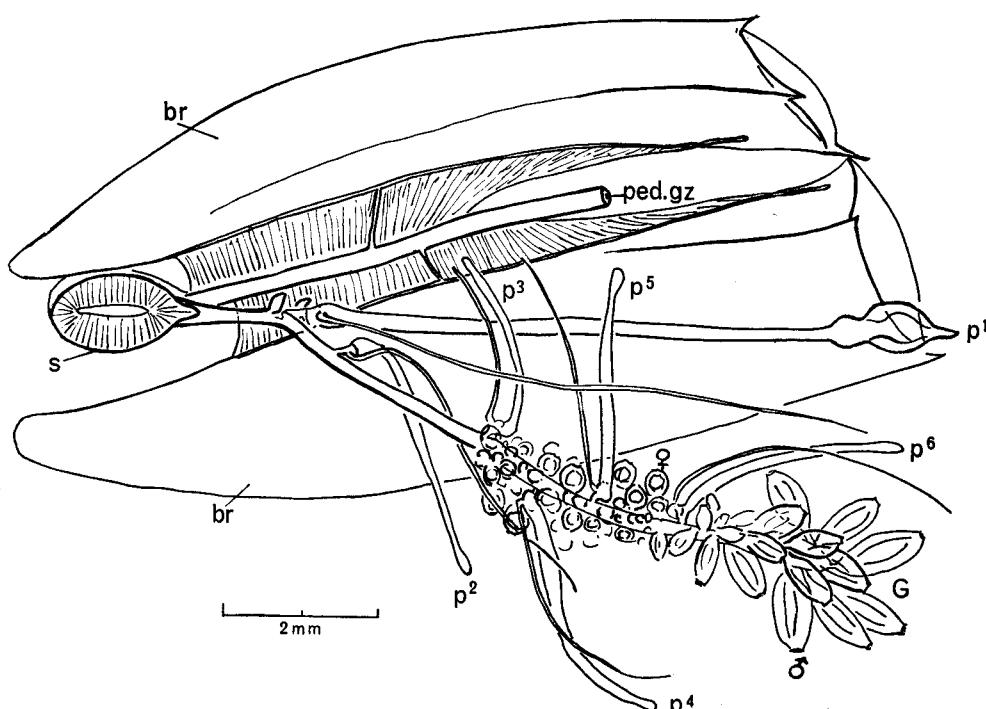


FIG. 55. *Forskalia edwardsi* Kölliker

A full grown gonodendron of a Villefranche specimen. In the background is the base of the pedicel of a gastrozoid.

br = bract; *g* = gonodendron; *p¹*–*p⁶* = palpons; *ped.gz* = peduncle of gastrozoid;
s = stem.

Forskalia leuckarti Bedot, 1893

Plate XX, figures 3, 4

Stephanomia contorta Milne Edwards, 1841

Apolemia edwardsii Lesson, 1843

Stephanomia excisa Leuckart, 1853

Forskalia contorta Kefferstein & Ehlers, 1860, 1861

Forskalia contorta Claus, 1863 (sp. 2, p. 545, Pl. xlvi, figs. 19, 21, 22)

Forskalia leuckarti Bedot, 1893b

A little known Mediterranean species. I know of only four sets of published figures of this easily identifiable species, characterized by the presence of a disc shaped pigmented *rete* in the pedicular canal of the nectophore.

The first set are those of Milne Edwards (1841, Pls. 7 and 8) showing the whole animal, the necto-

some, a nectophore, the female gonophores on the gonodendra, and some minor details. The second consists of figures by Leuckart (1854, *Taf.* XIII, figs. 8–17) of a nectophore, a bract and some buds. The third is by Kefferstein & Ehlers (1861, *Taf.* V, fig. 23), of a nectophore. The fourth is by Claus (1863, *Taf.* XLVII, figs. 21, 22 as *Forskalia* sp.2). In a footnote on page 545 Claus suggested that this specimen was one of *F. formosa* K. & E., of which species he wrongly alleged that no detailed description was given by Kefferstein & Ehlers. But these authors did give (1860, 1861) a diagnosis that was as adequate as usual in those days. It was a description of a specimen two feet in length taken at Messina. Claus figured a nectophore. In addition to these four sets of figures we also have long descriptions by Milne Edwards (1841) and Leuckart (1853, p. 38; 1854, p. 340).

Fortunately I recently recognized in the Musée at the Station Zoologique at Villefranche a well preserved specimen (No. 581) taken there in April 1927, and previously determined as *F. edwardsi*. Upon this specimen I can base a fresh, more detailed description, into which I have incorporated the salient features of the above descriptions and figures.

I agree with Schneider (1898, p. 157) in thinking that Leuckart's identification of his specimen with M. Edwards's *Stephanomia contorta* was correct. Bedot (1893b) asserted that it was incorrect. But Schneider had drawn attention to the *rete* in the pedicular canal of the nectophore of *S. contorta* figured by M. Edwards (1841, Pl. 8, fig. 4) and alluded to in M. Edwards's text (p. 221) as one of three little lobular appendices exhibited by the pedicular canal of the nectophore. (The other two are formed by the attachment of the muscular lamella of the pedicel.) And this discoidal *rete* is the criterion for identification of nectophores.

In his diagnosis, Leuckart says that 'the nectophores are incised at their point of attachment' – as they are in other species – 'and possess in the jelly of the umbrella a short distance from the nectosac a burning red pigment spot' – the *rete* which is one of the specific criteria – 'the cnidosacs and liver-stripes are similarly coloured bright-red'. To what extent particular shades of red will prove to be of systematic value we do not know. He continued, 'the bracts are either scaly or wedge-shaped with one thin and one thick edge and a bent central canal'. This tells us something of specific value about the bracts, but there the diagnosis ends. His further description deals mostly with generic rather than specific matters.

Kefferstein & Ehlers (1861) gave no description with their figure (Pl. XX, fig. 4) of the characteristic nectophore. Also they wrongly included in the synonymy Vogt's (1854) *Apolemia contorta* (= *F. edwardsi* Kölliker, 1853). Claus (1863, p. 545, footnote) made nine points in his brief description, including the critical one about the presence of a brick-red pigment spot in the pedicular canal, just short of the nectosac. His other points are of doubtful specific value.

My description is as follows:

Pneumatophore: Slim and small in size.

Nectophores (text-figs. 56, 57, 58): There are eight or nine right-hand spiral turns of the nectosome, each with nine or ten nectophores. The attachment to the muscular lamella lies in an incision, so that two dissimilar lobes are formed at the stem-end. This incision is deeper than in *F. edwardsi*. The nectophores are wider than deep and concave above. The mature nectophores I was able to examine only *in situ* (text-fig. 58), still attached to the nectosome, but I made detailed drawings of some detached immature ones. There is a deep, oblique lateral fold or inpocketing shown in text-figures A and B, which is much more pronounced than the one found in *F. edwardsi*. There is an incision on both right and left sides on the stem-side of and close to the lateral horns of the nectosac, instead of only one on the right-hand side in *F. edwardsi*. Leuckart gave the nectophore length from ostium to insertion of the peduncle as 7–9 lines (15–19 mm), width 7 lines (15 mm), thickness 3 lines (6·3 mm). I have assumed that Leuckart's line is equivalent to 2·116 mm.

There is a vertical, brick-red (fiery red), disc-shaped expansion, the *rete* of the pedicular canal of the nectophore measuring almost 2 mm in diameter. In early growth-stages it may not have developed

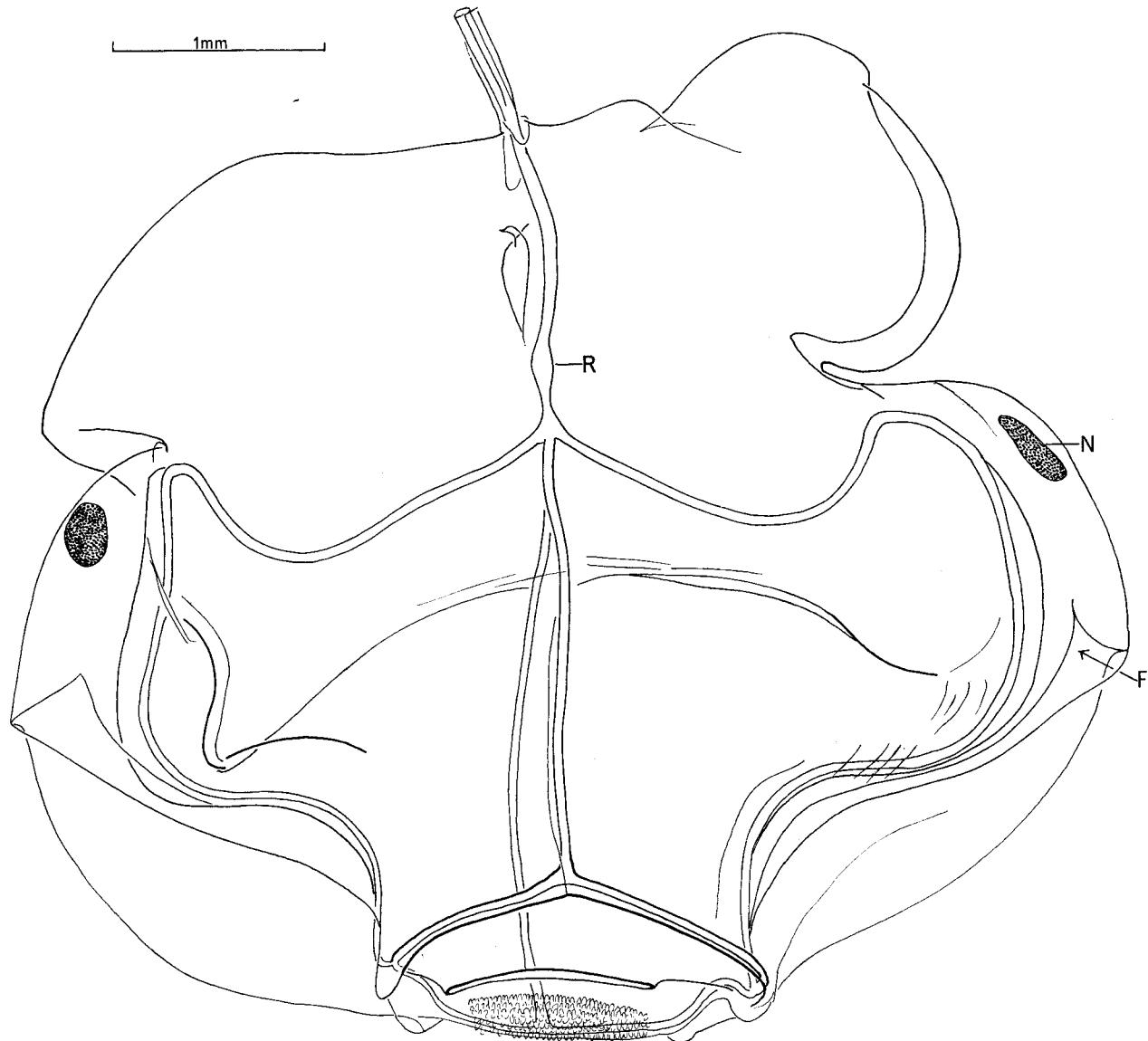
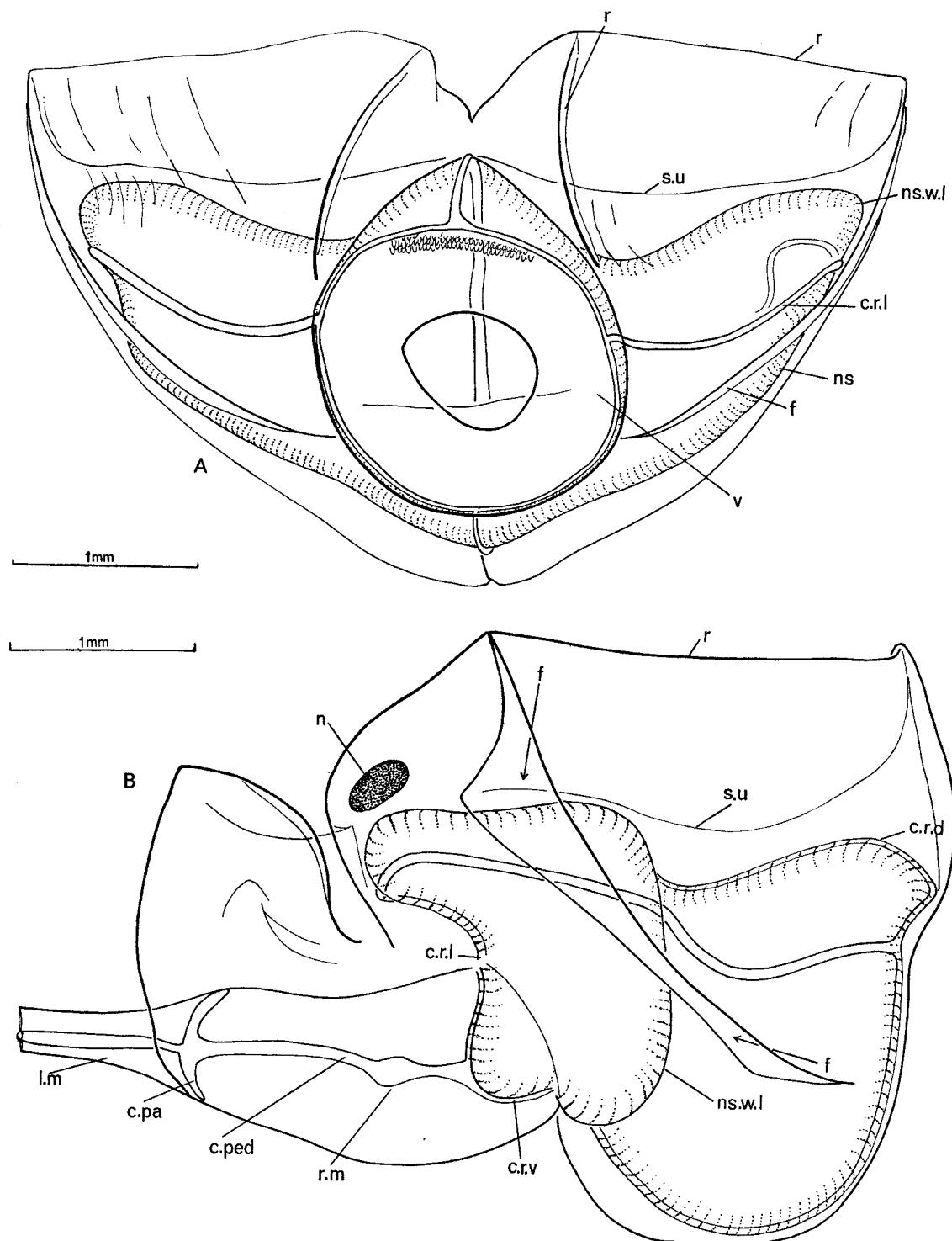


FIG. 56. *Forskalia leuckarti* Bedot
View of under surface of a young nectophore
F = fold; *N* = patch of nematocysts; *R* = future *rete mirabile*.

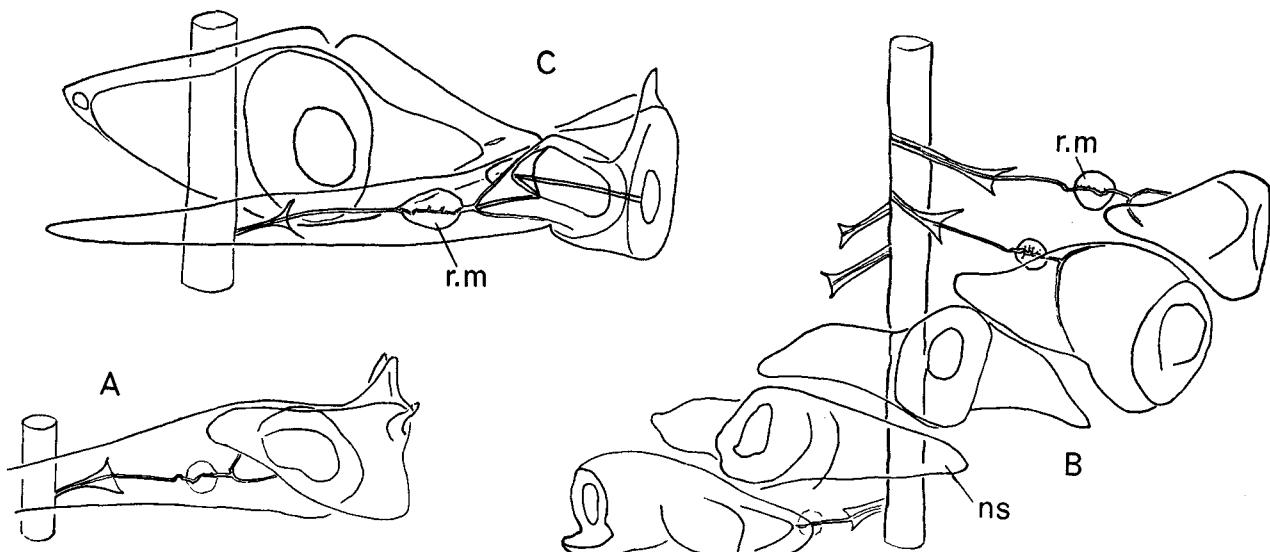
or appears only as a slight ovoid expansion of the pedicular canal. There is an oval patch of nematocysts just above the stem-side of the outer ends of the wings of the nectosac.

Gastrozooids: Forty to fifty on a 20 cm long specimen (contracted); from 10 to 19 mm in length. They are very mobile and are carried on long peduncles which measure 12 mm or more in length. There are from eight to twelve rose-red 'liver stripes' within the stomach. The cnido-band of the tentillum of the tentacle is fiery red in colour, with no involucrum and is spirally twisted into two to four turns. On either side of the cnidoband is a lateral row of bean-shaped nematocysts, 0.51 mm long and 0.16 mm broad. The long terminal filament carries short bean-shaped nematocysts, 0.003 mm in length. There are two pairs of folded cords in the tentillum, very much better developed according to Leuckart than in *Halistemma rubrum*.

Bracts (text-fig. 59): Very numerous, overlapping like shingles on a roof. When the peduncular bracts are lost the peduncles contract down to 2.1–3.2 mm in length. The majority of the peduncular

FIG. 57. *Forskalia leuckarti* Bedot

Nectophores of Villefranche Museum specimen No. 581, $\times 29$. A, ostial view; B, lateral view
c.r.d, *c.r.l*, *c.r.v* = dorsal, lateral and ventral radial canals; *c.pa* = pallial canal; *c.ped* = pedicular canal;
f = fold; *l.m* = muscular lamella; *n* = patch of nematocysts; *ns* = nectosac; *ns.w.l* = lateral wing of
 nectosac; *r* = ridge; *r.m* = *rete mirabile* (rudiment); *s.u* = upper surface of nectophore; *v* = velum.

FIG. 58. *Forskalia leuckarti* Bedot

Nectophores and nectosacs of Villefranche specimen 581, sketched *in situ*, $\times 6$. The aboral end of the stem is uppermost. A, part of a single nectophore; B, nectosacs of part of one turn of the nectosome; C, ostial view of one nectophore and (below) lateral view of a complete nectophore. ns = nectosac; r.m = rete mirabile.

bracts appear to be all of one kind, namely laterally flattened and triangular in outline. The length of both the upper side and of the perpendicular outermost side is about 1 cm. These two sides are thicker than the hypotenuse which has a comparatively sharp edge. These peduncular bracts form mirror-image pairs. The bracteal canal lies close to the inner face, and makes a right-angle bend corresponding to the angle made by the two thick edges or facets. At this bend in the bracteal canal is given off a short branch inclined inwards and towards the angle. The photograph (Pl. XX, fig. 3) shows how these closely approximated angular bracts appear in optical section.

Four or five large leafy bracts are attached to the stem cormidium and partially envelop the bases of the peduncles of the gastrozooids. There is a transition in shape from these towards the triangular bracts.

Leuckart stressed the difficulty of forming an idea of the shape of the bracts.

Gonodendra (text-fig. 60): As in *F. edwardsi* the gonodendra are formed by a series of palpons, each budding successively from the base of its predecessor. The gonophores are borne on secondary protrusions from these bases.

Leuckart (1854), like Milne Edwards (1841)* did not give a sufficiently precise description of the whole gonodendron-complex. I have been able to examine in detail only one gonodendron. It belonged to the complete specimen, No. 581, at Villefranche. Leuckart stated that there were up to four gonodendra between successive peduncles of gastrozooids. He deduced that they first appeared as a single pedunculate palpon with a simple palpacle. I reproduce (text-fig. 54) his drawing of an early growth-stage in *F. edwardsi*. That the primary palpon appears to bud from the gonodendron in the mature stage is only a question of relative growth. It can be seen at once that the mature gonodendron of *F. leuckarti* differs from that of *F. edwardsi* in that the basal extension of the simple palpon that bears the female gonophores is hypertrophied and overtops that bearing the male gonophores. It grows to a length of perhaps 30 mm, is probably highly contractile and is bifurcated at the distal extremity. There, each branch forms a globular terminal end, as shown in Milne Edwards's figure. They bear numerous female medusoid gonophores.

* It must be remembered that Milne Edwards was giving the first specifically recognizable figure of any species of *Forskalia*.

The larger, oval, male gonophores are borne on a smaller extension of the base of another palpon. The two palpons whose bases give rise to the bunches of gonophores were found in my specimen to be almost opposite one another, some 2 mm from the stem, and to bear no palpacle. It is possible that the palpon carrying the male gonophores is in origin distal to the other palpon carrying the female gonophores. In that case the gonodendra of the two species would be essentially comparable in spite of the impression given by a first inspection.

Milne Edwards (1841) figured this unique type of gonodendron in his plate 7, figure 1 (nat. size) and plate 9, figure 1 (twice nat. size). In both figures the globular bunches of female gonophores can be seen at the ends of bifurcated peduncles. The position of the bunches of male gonophores, however, is not so clearly indicated. Milne Edwards used the same term 'prolongements flabellaires' for both the peduncles of the bunches of female gonophores and for the palpacles of the palpons.

The palpons themselves are vermiform and very active. They measure from 3–5 mm in length – perhaps ten times as much when fully extended. The terminal part of the lumen of a palpon contains a red liquid which is readily freed on disturbance and then colours the surrounding water blood-red. The nematocysts of the palpacles are arranged in numerous groups of 4–5. They are rounded and measure 0.005 mm in diameter.

The canal system of the male gonophores consists of the usual four radials and a circular canal. The female ones frequently have four also, but just as frequently they are atrophied, branched or reticular. One, observed by Leuckart, had six radial canals, and one eight. He noticed pulsation only at the ostial ends of the gonophores, and doubted if they broke away to swim freely.

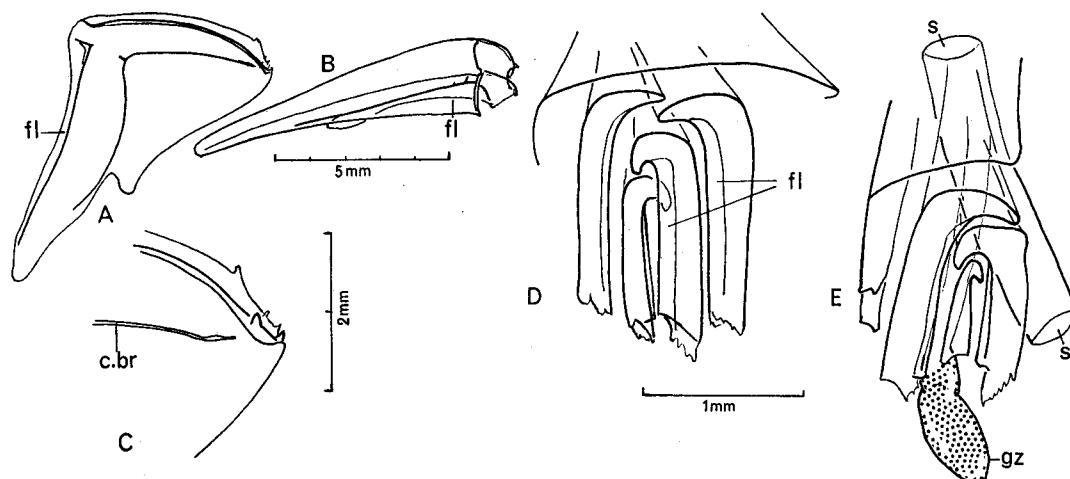


FIG. 59. *Forskalia leuckarti* Bedot
Bracts of Villefranche specimen 581. A, B, C, views from above; D, E, lateral views. A, B, D, E
 $\times 5$; C, $\times 11$
c.br = bracteal canal; *fl* = flange; *gz* = gastrozooid; *s* = stem.

The Villefranche specimen

My observations on this specimen are as follows: The overall length of the retracted specimen is now 11 cm, and the diameter (maximum) of the upper spire of bracts 2.1 cm. The length of the nectosome is 3.4 cm, excluding the overlap of the upper part of the siphosome by the distal ends of the lower nectophores.

The nectophores are arranged in a right-hand spiral of seven turns, each consisting of six or seven nectophores, whose maximum width at the ostium is 1.2 cm, and maximum depth 0.5 cm (see text-

fig. 58). The outer surface of the spiral succession of the series of bracts forms a cylinder which is a characteristic feature of the specimen and made me realize that it differed from *F. edwardsi*.

The peduncles of the gastrozooids measure (maximum) 8 mm, and bear half-a-dozen triangular bracts in two overlapping, enantiomorphic and imbricating rows. For illustrations of the bracts see text-figure 59. The gonodendra have been described earlier.

***Forskalia formosa* Kefferstein & Ehlers, 1860**
Plate XX, figure 5

? *F. leuckarti* Bedot, 1893b

A doubtful species. Without any pigment spots on nectophores.

Stem: Up to 2 feet in length.

Nectophores: The stem-side incision creates two unequal lobes.

Gastrozooids: On short peduncles hardly exceeding in length that of the rest of the gastrozooid. These peduncles are much shorter than the palpons. Liver-stripes burning brick-red in colour. Cnidobands of tentilla with from two and a half to three laevotropic spiral turns, bright brick-red in colour, 0·46–0·5 mm in length.

Reported only from Messina as single specimens.

***Forskalia tholoides* Haeckel, 1888**

A little known and doubtful species based on a beautiful idealized figure. Only three or four times recorded since Moser (1925, Taf. XXXII, fig. 1); Kawamura (1954, Pl. I, figs. 1, 3–6).

Nectophores: Stem side not incised but forming long and tapering peduncles, twice the length of the nectosac. Nectosac little expanded in lateral direction. Lateral facets ‘polygonal’.

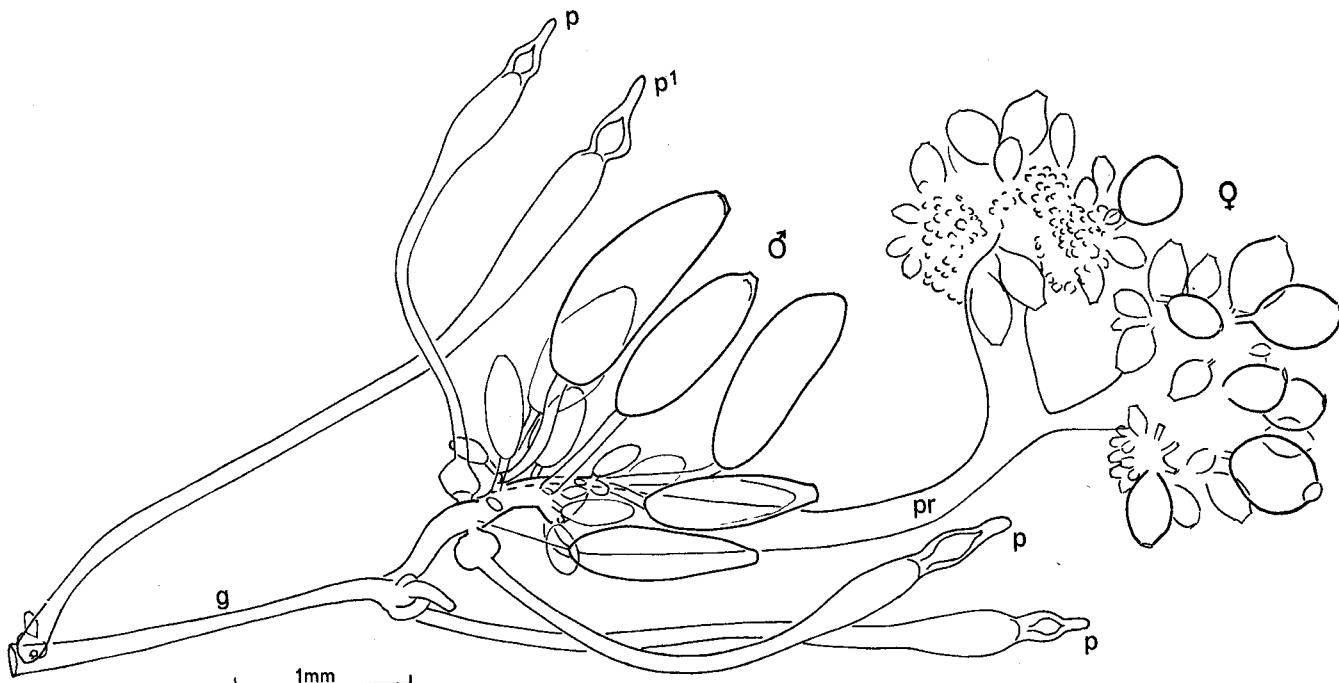


FIG. 60. *Forskalia leuckarti* Bedot
Gonodendron of Villefranche specimen 581, $\times 21$

g = gonodendron; *p* = palpon; *p*¹ = primary palpon; *pr* = secondary protrusion from base of a palpon; δ and ♀ = male and female gonophores.

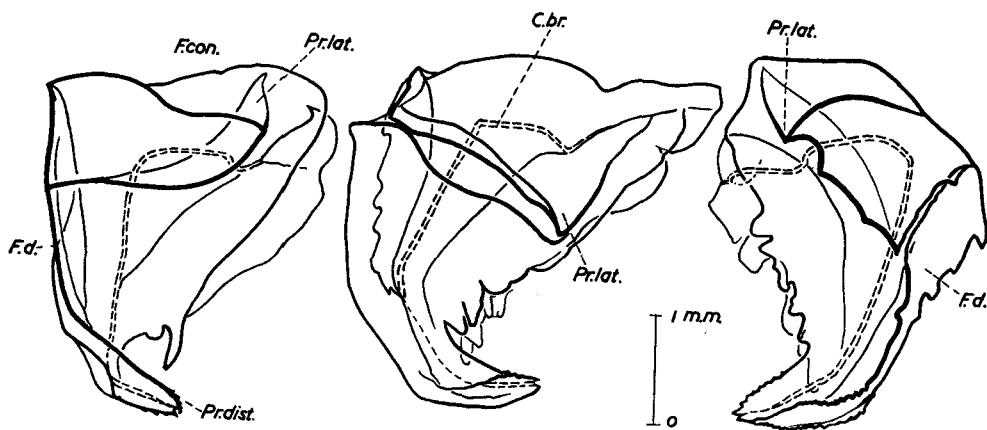


FIG. 61. *Forskalia cuneata* Chun
Bracts of 'Discovery' specimen, St. 1585, 1,400–700 m., $\times 15$ (from Totton, 1954, fig. 31)
C.br. = bracteal canal; F.con. = convex facet; F.d. = dorsal facet; Pr.lat. = lateral process.

Bracts: Said to be only four on each peduncle of gastrozooid. This is most doubtful. Described as three-sided prismatic, more or less asymmetrical, with a concave, smooth, lower or distal facet and a convex dentate upper or proximal one. The latter bears usually a strong dentate longitudinal crest, and the two lateral edges are also armed with a few teeth.

Gastrozooids: 10–15 mm long.

Forskalia cuneata Chun, 1888

Text-figure 61

Only once have specimens been recorded under this name. The two characteristics mentioned in Chun's original description (without figures) were (1) the presence in the sub-umbrella of the nectophore of from four to six red bands on each side; (2) the truncated outer ends of the bracts and the right-angled bend in the bracteal canal, (3) the particularly large gastrozooids. The largest specimen was only 7 cm in length.

Chun described the larval tentilla as acorn-shaped, deep red in colour and with numerous short sensory hairs. The only previous description of the larval tentilla of *Forskalia* spp. was that of Claus (1863, p. 557, Pl. XLVIII, figs. 30–35 as physophorid larvae, unnamed). I have seen larvae obviously belonging to some species of *Forskalia* (? *edwardsi*) judging by the colour and the fact that they were not those of any other known physophorids present at Villefranche. I recognize in Claus's figures similar larvae of *Forskalia* spp.

I have never seen nectophores of the type described by Chun. We look forward to another record of this sort from the Canaries region.

The bracts shown in text-figure 61 might possibly be those of such a species as Chun's *F. cuneata*.

SPECIES INQUIRENDA

Forskalia misakiensis Kawamura, 1954

Forskalia misakiensis Kawamura, 1954, p. 106, Pl. 1, figs. 2, 7–11

Described from a single preserved specimen from Misaki. The figure of a nectophore (Pl. 1, fig. 7) shows a quadrangular contour in upper view. If confirmation of the existence of a species with nectophores of this type in all stages of growth is forthcoming any doubt will be resolved.

The bracts figured in Kawamura's plate 1, figures 8, 9 are not of the same generic pattern as those of known species. All peduncular bracts, as these appear to be, are roughly triangular in cross section. These ones only resemble Kawamura's figures of bracts of *F. tholoides*. But they again are not of the generic pattern, which was clearly shown by Haeckel.

A fuller and more detailed description is needed.

Sub-order III: *Calycophorae* Leuckart, 1854

The Calycophorae have nectophores, and bracts – except in the Hippopodiidae – but no apical gas-filled float. It is now thought that they may have been evolved from forms which possessed a float (see Garstang, 1946). The stem-groups of the polygastric phase break away successively to form free-swimming eudoxids (the second phase), each consisting of one gastrozooid, a succession of gonophores (the third phase, see pp. 25–28) – one of which may be asexual and specialized for propulsion – but no palpons, except in *Stephanophyes*, where vestigeal ones are found.

Six families are recognized by me: Prayidae, Hippopodiidae, Diphyidae, Clausophyidae, Sphaernectidae and Abylidiae.

Family 10: PRAYIDAE Kölliker, 1853

Amphicaryoninae Chun, 1888a

Prayinae Chun, 1897b

Nectopyramidinae Bigelow, 1911b

Prayids are large slow-moving calycophores with a relatively great amount of mesogloea for the floatation of a large and heavy stem. When the mesogloea is massive the typically small somatocyst, in the form of a fine canal, may branch complexly.

The unusually large, ovoid, larval nectophore of the typical sub-family Prayinae is soon shed and is replaced by a short succession of larger heteromorph ones, usually a pair lying almost opposite one another, but in *Stephanophyes* several form a ring.

They are not noticeably staggered or superimposed one in front of the other as they are in the Diphyidae. The nectophores often support long stems of large eudoxids, whose bracts contain a canal-system which branches in a characteristic way (text-fig. 74). The eudoxids have large active gonophores or asexual nectophores, by the pulsation of which the stem can be rapidly extended and the tentacles spread like a drift net. It is hard to give a definition* that will apply to and differentiate such a varied group of species. It includes at one extreme neotenous, single-nectophored species like *Nectopyramis diomediae* and at the other *Stephanophyes superba*, with its ring of nectophores and in addition palpons. That prayids do form a natural group is now, however, agreed by systematists.

There are three sub-families: Amphicaryoninae, Prayinae and Nectopyramidinae. Moser (1925) distributed the members of these three sub-families amongst three of her four families of Calycophorae, thus making nonsense of her classification.

The nomenclature of the family is remarkably confused. Nine genera and fourteen species of prayids may be recognized provisionally. Only six species are at all common, namely *Amphicaryon*

* Chun's diagnosis (1897b) was as follows: nectophores rounded, opposed and nearly alike. He added that they seldom lacked reserve nectophores, which might either replace the first two or remain near them. This is no longer sufficient to include the Nectopyramidinae.

acaule, *Praya dubia*, *Rosacea plicata*, *Rosacea cymbiformis*, *Nectopyramis thetis* and *Nectopyramis diomedaeae*. The arrangement of species within the three sub-families is as follows:

	Page
1. Sub-family i: Amphicaryoninae Chun, 1888	111
Genus <i>Amphicaryon</i> Chun, 1888	111
<i>A. acaule</i> Chun, 1888	112
<i>A. peltifera</i> (Haeckel, 1888)	112
<i>A. ernesti</i> Totton, 1954	113
Genus <i>Maresearsia</i> Totton, 1954	113
<i>M. praecincta</i> Totton, 1954	113
2. Sub-family ii: Prayinae Haeckel, 1888	114
i. Genus <i>Rosacea</i> Quoy & Gaimard, 1827 (<i>sensu</i> Bigelow, 1911); Bigelow & Sears, 1937	115
<i>R. plicata</i> Quoy & Gaimard, 1827 (<i>sensu</i> Bigelow, 1911); Bigelow & Sears, 1937	116
<i>R. cymbiformis</i> (Chiaje, 1822)	118
ii. Genus <i>Praya</i> Blainville, 1834	121
<i>P. dubia</i> (Quoy & Gaimard, 1833)	122
<i>P. reticulata</i> (Bigelow, 1911)	123
Genus <i>Prayoides</i> Leloup, 1934	124
<i>P. intermedia</i> Leloup, 1934	125
iii. Genus <i>Stephanophyes</i> Chun, 1888	129
<i>S. superba</i> Chun, 1888	129
iv. Genus <i>Lilyopsis</i> Chun, 1885	126
<i>L. rosea</i> Chun, 1885	126
<i>L. gracilis</i> (Fewkes, 1883)	127
v. Genus <i>Desmophyes</i> Haeckel, 1888	127
<i>D. annectens</i> Haeckel, 1888	128
3. Sub-family iii: Nectopyramidinae Bigelow, 1911	130
Genus <i>Nectopyramis</i> Bigelow, 1911	130
<i>N. thetis</i> Bigelow, 1911	135
<i>N. natans</i> (Bigelow, 1911)	135
<i>N. diomedaeae</i> Bigelow, 1911	131
<i>N. spinosa</i> Sears, 1952	137

Sub-family i: **AMPHICARYONINAE** Chun, 1888

A characteristic feature of the eudoxid stage, in those species in which it is known, is the reduction of the bracteal canal-system to a pair of lateral hydroecial canals, the dorsal and ventral branches being absent. This reduction may be correlated with the reduction in mass of the bracts.

The larval nectophore appears to be retained, and the first heteromorph one is reduced or vestigeal.

Genus: **AMPHICARYON** Chun, 1888

Type species: *A. acaule* Chun, 1888.

The name *Mitrophyes* Haeckel (May, 1888a) has a few months priority over *Amphicaryon* Chun (November, 1888), but *Amphicaryon* should be entered on the list of *nomina conservanda*.

Bigelow (1911b) defined the genus as 'Prayidae with two nectophores of very unequal size, the older one degenerating', but I believe that it is the younger of the two which is vestigeal. Bigelow said that as far as he knew *Amphicaryon* had not been recorded between 1888 and 1911, the date of publication of his 'Albatross' report. He included *Mitrophyes peltifera* as a doubtful synonym *A. acaule*.

There are three known species.

Amphicaryon peltifera (Haeckel, 1888)

Text-figure 62

Mitrophyes peltifera Haeckel, 1888b, p. 131; Moser, 1924a, fig. 27; (1925, p. 401, Pl. 24, fig. 7)
Amphicaryon peltifera Bigelow, 1911b, p. 195

Polygastric phase

(Text-fig. 62.) In the past few decades I have come across specimens from time to time that correspond closely in the morphology of their nectophores with the figures given by Haeckel (1888b, Pl. 28, figs. 1-3). The radial canals of the reduced (vestigial) nectophore afford the characteristic field-marks of the species of *Amphicaryon*. In *A. peltifera* reduction has gone farthest and no nectosac remains, but only three reduced radial canals (see Moser, 1924a, fig. 27).

I saw this species alive in 1955, off Arrecife, Lanzarote, Canaries, when I made the rough sketch here reproduced (text-fig. 62). This is one of the species of which good figures are needed.

The only three recently published records that I know are in my 'Discovery' Report (1954).

*Eudoxid phase—unknown**Amphicaryon acaule* Chun, 1888

Plate XXI, figure 6

This species may now be described as common. Both the polygastric and eudoxid phases were beautifully figured by Bigelow (1911b, Pl. 4). The nectosac of the vestigial nectophore does not open to the exterior. Its four radial canals are distinct (Bigelow, 1911b, Pl. 4, fig. 4), and simple, like those of the larger nectophore. The vestigial nectophore is embraced by the larger one.

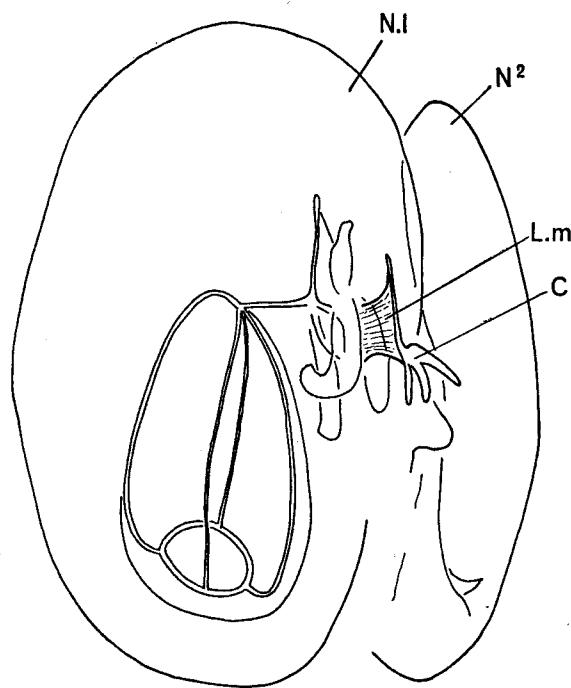
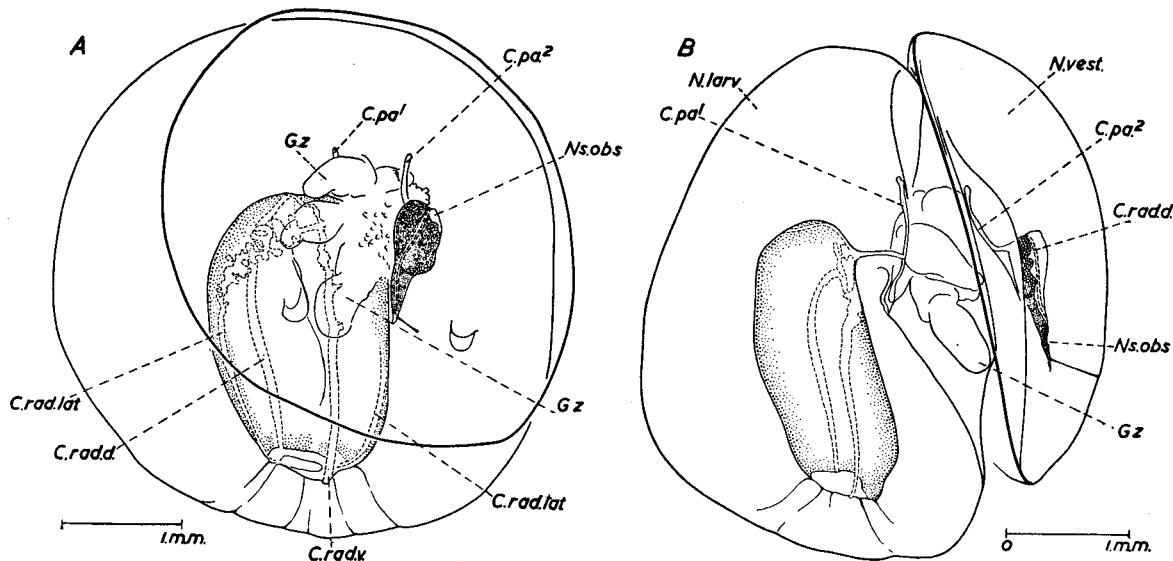


FIG. 62. *Amphicaryon peltifera* (Haeckel)
 Whole living specimen drawn from life by Totton at
 Lanzarote, 1955, to show the attachment (*L.m.*) of
 the second nectophore, and its vestigial radial canal
 system (*C*), $\times 2$. *N.1* = persistent larval nectophore;
N² = second nectophore.

FIG. 63. *Amphicaryon ernesti* Totton

Polygastric phase. Two views of the holotype specimen from 'Discovery' St. 2648, $\times 16$
C.pa¹, *C.pa²* = pallial canals; *C.rad.d*, *C.rad.lat*, *C.rad.v* = dorsal, lateral and ventral canals; *Gz* = gastro-zoid; *Ns.obs* = obsolescent nectosac; *N.larv* = larval nectophore; *N.vest* = vestigial nectophore (from Totton, 1954, fig. 44).

Amphicaryon ernesti Totton, 1954

Polygastric phase

The vestigial nectophore is not embraced by the larger one (text-fig. 63) whose lateral radial canals are branched in the proximal region. The former entrance to the vestigial nectosac lies at some distance from the surface, but is connected by a fine strand of tissue. Its ventral radial canal becomes a network covering the ventral wall of the nectosac, and its lateral radial canals have disappeared, leaving only the dorsal radial canal.

The known distribution was given by me in 1954.

Eudoxid phase—unknown.

Genus: *MARESEARSIA* Totton, 1954

Monotypic genus for *M. praecleara* Totton, 1954.

A new genus was erected for the large amphicaryonine described below because it seemed to differ more from all three known species of *Amphicaryon* than they did from one another. The genus was named after Dr. Mary Sears who has, with Dr. Bigelow, done so much work on siphonophores. The name *Searsia* was preoccupied and Dr. Sears graciously agreed to the present name. This dedication was unfortunately omitted in 1954.

Maresearsia praecleara Totton, 1954

Plate XXI, figures 2–5

Polygastric phase

The smaller nectophore is still functional, though its nectosac is smaller than that of the larger nectophore (text-fig. 64). There is some branching of the radial canals of both nectophores. The

pallial canal and somatocyst are much expanded, and the smaller nectophore is well sunken into the larger.

Eudoxid phase (shown on Pl. XXI, figs. 2–5)

So far the species has been recorded from the Atlantic, and from one 'Discovery' II Station 2636 in the Indian Ocean.

Sub-family ii: PRAYINAE Chun, 1897

In my view there are six groups of prayine species; (A) two well-known species with simple somatocysts or pallial canals and a pair of nectophores (with simple radial sub-umbra canals, the laterals meandering). In their polygastric and eudoxid phases they resemble each other more than either does other species, and so may be grouped under one generic name *Rosacea* (*sensu* Bigelow, 1911b). They are *R. cymbiformis* (Chiaje) and *R. plicata* (*sensu* Bigelow, 1911b); (B) two or more species

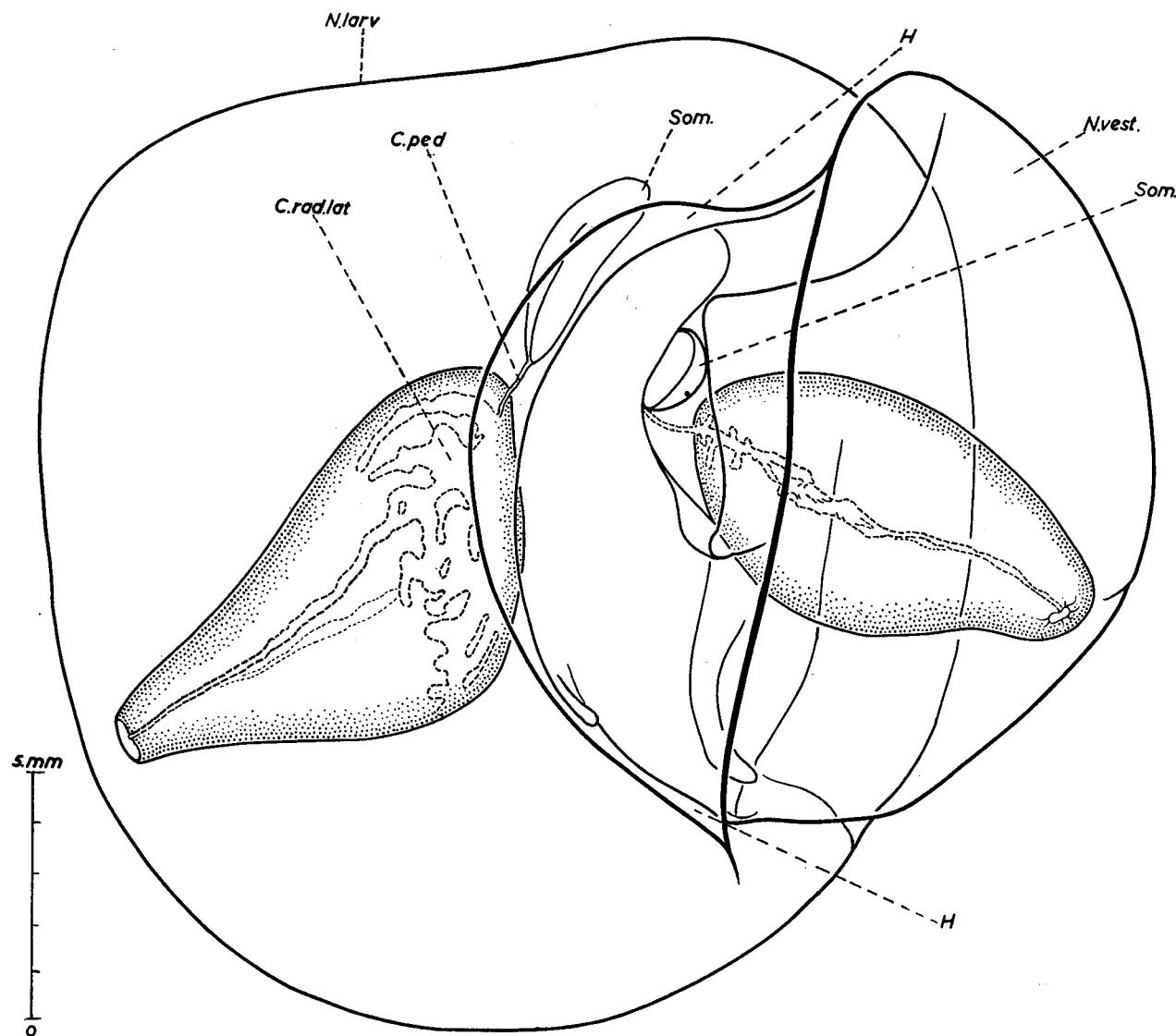


FIG. 64. *Maresearsia praecleara* Totton

Polygastric phase. Lateral view of two nectophores, $\times 6.6$, from Bermuda

H = hydroacium; Som = somatocyst; for other abbreviations see text-figure 63 (from Totton, 1954, fig. 46).

in which the nectophores have branched somatocysts and the nectosacs have multiform radial canals. They form a genus for which *Praia* Blainville, 1834 is the prior name, and their names are *P. dubia* Blainville and *P. reticulata* (Bigelow, 1911b); (C) an odd species with simple somatocyst and multi-form radial canals *Prayooides intermedia* Leloup, 1934; (D) an isolated species *Stephanophyes superba* Chun, 1888. It is the only calycophore to possess palpons and a second kind of cnidobattery (cnidosac), borne on the tentacle of the half-millimetre long, thick walled palpons, which appear singly or in groups of two or three on a single pedicel between the cormidia; (E) one or perhaps more species with a marked egg-shaped terminal dilation of the simple somatocyst as well as a relatively large, median, unpaired, egg-shaped or pyriform diverticulum of the bracteal canal-system of the eudoxid. Haeckel (1888a) introduced a new name for such a species, *Desmophyes annectens*. The first good description and figures of such a species were those of Kölliker (1853) and of Vogt (1854) for *Praya diphyses*; (F) there are left for consideration the little known species of *Lilyopsis* Chun. Some day it will have to be decided whether any of these should be grouped with (E) under *Desmophyes*.

KEY TO GENERA OF PRAYINAE

1. Nectophores biserial. Reserve bells may be present	2
Nectophores in corona. Palpons present	<i>Stephanophyes</i> (p. 129)
2. Nectophores biserial, somatocyst simple	3
somatocyst branched	<i>Praya</i> (p. 121)
3. Nectophores biserial, somatocyst simple, at surface of hydroecium	4
somatocyst simple, prolonged into mesogloea	5
4. Nectophores biserial, somatocyst simple, at surface radial canals simple	<i>Rosacea</i> (p. 115)
radial canals branched	<i>Prayooides</i> (p. 124)
5. Nectophores biserial, somatocyst simple, in mesogloea eudoxids; with central organ eudoxids with asexual nectophore but no central organ	<i>Desmophyes</i> (p. 127) <i>Lilyopsis</i> (p. 126)

Genus: *ROSACEA* *sensu* Bigelow, 1911

Praya Kölliker, 1853; Vogt, 1854 (non *Praya* Quoy & Gaimard, 1833)

Eodoxella Haeckel, 1888b (for eudoxid)

Huxleya Gravier, 1899

Type species *Rosacea plicata* Quoy & Gaimard *sensu* Bigelow, 1911b.

For the last fifty years the generic name *Rosacea* has been used, not in the sense in which its originators Quoy & Gaimard probably used it,* but for a better known species to which Bigelow (1911b) seems to have been the first to apply the name *R. plicata* Quoy & Gaimard, and to give a proper description. In order not to complicate further the very involved nomenclature of the Prayinae I propose that *Rosacea* shall continue in use in the sense of Bigelow, 1911b; and I designate *R. plicata* Quoy & Gaimard *sensu* Bigelow as its type species.

Generic diagnosis

Polygastric phase

Prayines with a pair of large, smooth nectophores which may be replaced by reserve bells of slightly different shape. The simple somatocyst does not lie as a free canal in the mesogloea but forms the pallial canal on the dorsal wall of the hydroecium. The lateral radial canals of the nectosac are sinuous.

Eudoxid phase

The bract of the eudoxid is convex on the proximal and concave on the distal side and contains

* Bigelow (1911b, p. 197) suggested that '*Lilyopsis diphyses*' (*sensu* *Praya diphyses* Kölliker, 1853 and Vogt, 1854) was the same species as *Rosacea plicata* (Quoy & Gaimard, 1827). This is probably true, though their figure is a very poor one. The strict application of the law of priority, unless debarred by a time clause, would necessitate the new use of *Rosacea* for *Desmophyes*.

four main bracteal canals, the branches of the phylloctyst. The gonophores are well developed medusoids, and there are no asexual nectophores in the eudoxid phase.

Rosacea plicata sensu Bigelow, 1911

Text-figures 65–67

Rosacea plicata Quoy & Gaimard, 1827; *sensu* Bigelow, 1911b; Bigelow & Sears, 1937

Polygastric phase

(Text-fig. 65.) Three categories of nectophores are known: (1) caducous, larval, up to 12 mm in length; (2) definitive nectophore number 1, up to 21 mm in length; (3) definitive nectophore number 2, up to 32 mm in length; they differ in shape from one another. This is probably true of *R. cymbiformis* too, but the succession has not been described in that species.

In the larval nectophore there is a short, circumscribed, slit-like orifice to the hydroecium as in Hippopodiidae. A constant character that distinguishes the larval nectophores of the two species of

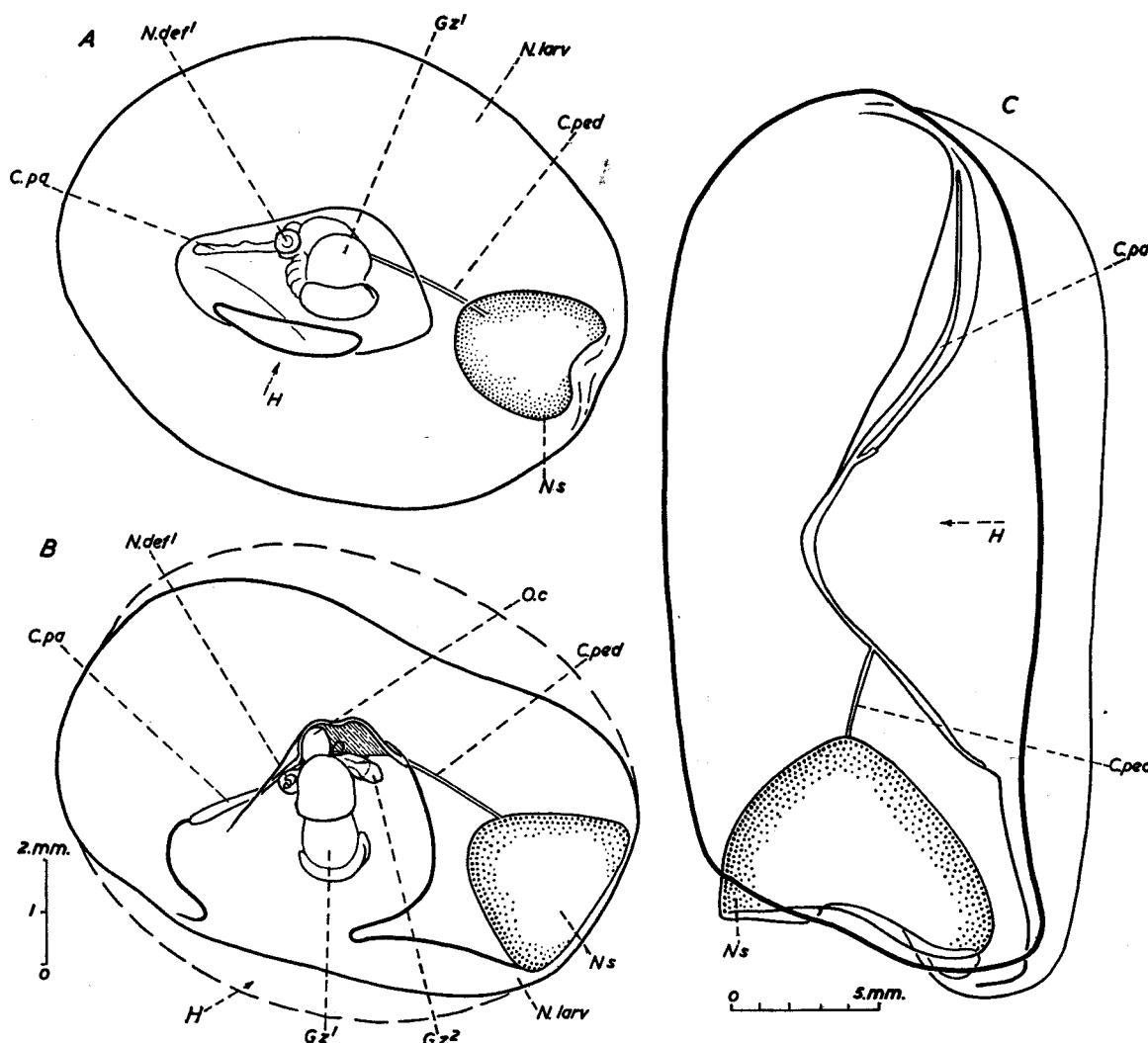
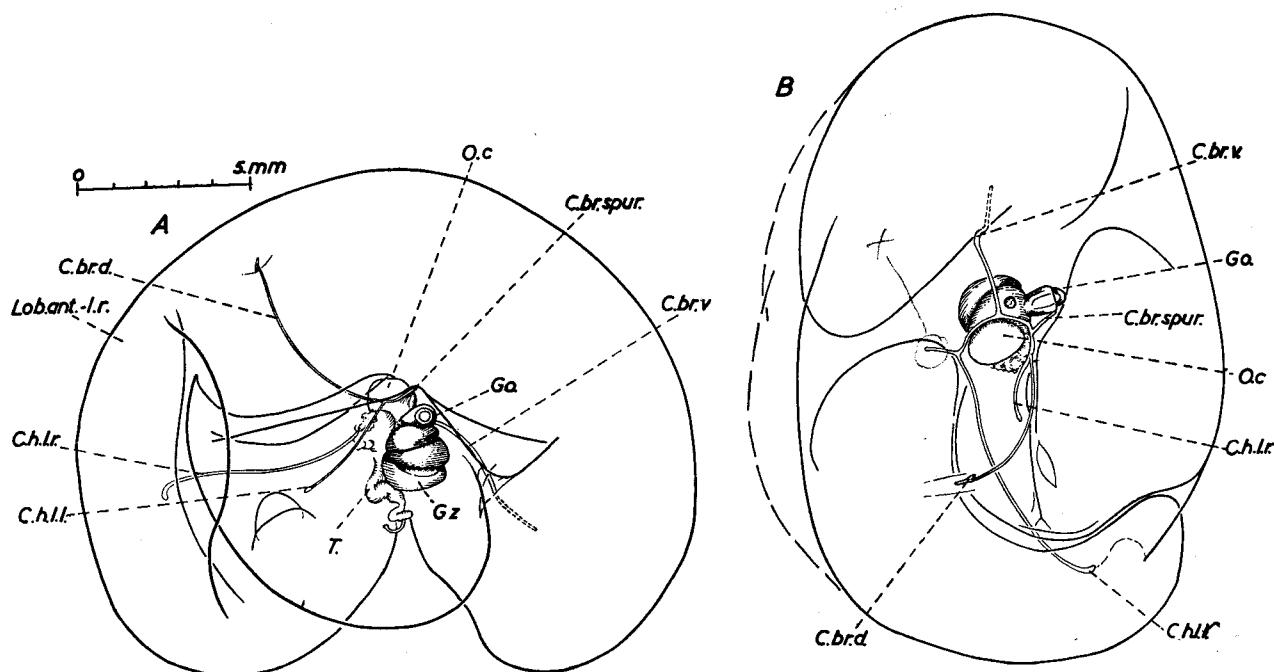
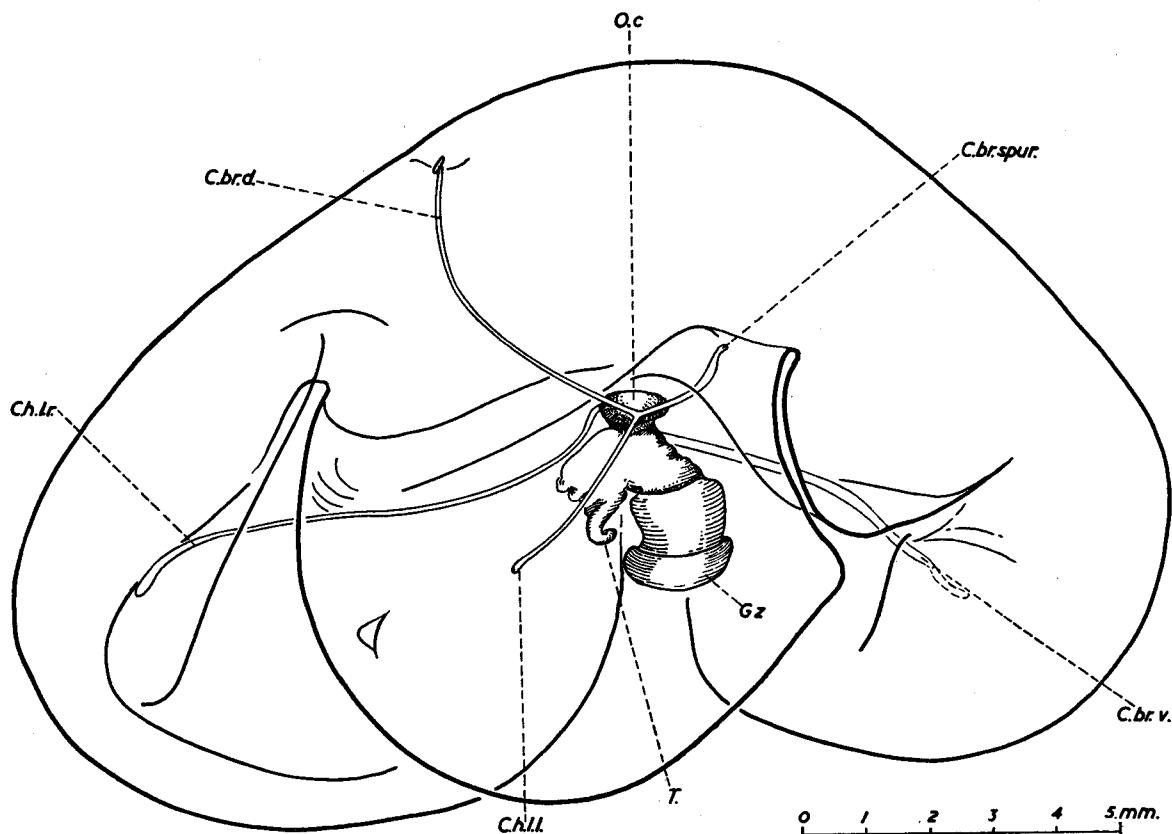


FIG. 65. *Rosacea plicata* Q. & G. Polygastric phase
A, lateral view of a larva, 'Discovery' St. 1617, 395–155 m, $\times 7$; B, the same to show the hydroecium in optical section; C, a second definitive nectophore from the same station, $\times 4.2$
C.pa = pallial canal; *C.ped* = pedicular canal; *H* = hydroecium; *Gz¹*, *Gz²* = gastrozooids; *N.def¹* = first definitive nectophore; *N.larv* = larval nectophore; *Ns* = nectosac (from Totton, 1954, fig. 43).

FIG. 66. *Rosacea plicata* Q. & G. Eudoxid phaseA, lateral view; B, view from above, 'Discovery' St. 1617, 395-155 m, $\times 4.5$

C.br.d, *C.br.v* = dorsal and ventral bracteal canals; *C.br.spur.* = bracteal spur canal; *Ch.ll*, *Ch.l.r* = left and right hydroecial canals; *Lob.ant.-l.r* = right antero-lateral lobe; *O.c* = central organ; *Go* = gonophore; *Gz* = gastrozooid; *T* = tentacle (from Totton, 1954, fig. 41).

FIG. 67. *Rosacea plicata* Q. & G.

Eudoxid from 'Discovery' St. 1617, 395-155 m, $\times 8.3$ (abbreviations as in text-fig. 66) (from Totton, 1954, fig. 42).

Rosacea from those of hippopodiids is the sharp bend of the pallial canal round the *central organ* in *Rosacea* spp (text-fig. 65A, B).

Beautifully executed figures of definitive nectophores have been made by Bigelow (1911b, 1913) and by Bigelow and Sears (1937). Definitive nectophore number 1 has a deeper shorter, circumscribed hydroecium, with a right-angled bend sometimes at the site of attachment of its muscular lamella. It is also shorter in length and larger in girth than number two. This second (later) definitive nectophore (text-figs. 65C, 66) also has a deep pocket for the attachment of the lamella, but the nectophore is comparatively larger, more closely resembling that of *R. cymbiformis*. The lateral radial canals of the nectosac meander as in *R. cymbiformis*. The corresponding canals of the larval nectophore take a sigmoid course which is much simpler.

Eudoxid phase

(Text-figs. 66, 67.) It is difficult to distinguish between the preserved eudoxids of *cymbiformis* and *plicata* except by comparison of the origin of the dorsal bracteal canal. In *plicata* it arises distally to the spur canal or the left hydroecial canal. The bract may reach a length of 18 mm. The tip of the right flap of the hydroecium which contains the longer (right) of the two longitudinal bracteal canals laps round the tip of the other flap (text-figs. 66, 67).

Rosacea cymbiformis (Chiaje, 1822)

Plate XXI, figure 1; Plate XXII, figures 1-3

Physalia cymbiformis Chiaje, 1822, 1841

Diphyes prayensis Quoy & Gaimard, 1833

Praya cymbiformis Leuckart, 1853, 1854; Huxley, 1859; Kefferstein & Ehlers, 1861; Graeffe, 1884; Schneider, 1896; Chun, 1897a; Bigelow, 1911b; Moser, 1924a

Praya maxima Gegenbaur, 1853b, 1854; Fewkes, 1880b; Chun, 1885, 1888b

Praya (Huxleya) californica Gravier, 1899

Praya galea Haeckel, 1888a, b

Good accounts of this species were given by Leuckart (1854), Gegenbaur (1853b, pp. 301-309 - extraordinarily detailed), Haeckel (1888b), Bigelow (1911b) and Bigelow & Sears (1937). Moser (1917) gave a diagnosis and (1924a) some new figures, one of which shows a specimen with the larval nectophore still attached as well as the first and second definitive nectophores.

Polygastric phase (Pl. XXII, figs. 1, 3)

Definitive nectophores (text-fig. 68C): Chun (1885) reported specimens with five reserve nectophores, and gave good figures of the buds of definitive nectophores. The first and second of these are usually found in pairs, the first one partially embracing the second in its hydroecium. They are up to 6 cm in length (No. 577, Musée, Villefranche), somewhat cylindrical or kidney-shaped, with a gutter-like hydroecial groove on the ventral side extending down beyond the ostium of the nectosac which is relatively small and faces outwards and downwards in the lower third of the nectophore.

The planes in which the two ostia of a pair of nectophores lie are nearly at right angles to one another, as shown by Gegenbaur (1853, Taf. XVII, fig. 1). The lateral canals take a meandering course (text-fig. 68) from the pedicel to the circular canal, a course well illustrated by Bigelow (1911b, Pl. 2, fig. 1).

The shape of the nectophores observed frequently by me at Villefranche is better represented by Bigelow & Sears (1937, figs. 6, 7) than by Bigelow (1911b, Pl. 2, fig. 1). The ostium of the nectosac is not at the ant-apical end as shown in the latter, but to the side of it. The distal end is formed by two rounded lobes as shown in figure 6 of Bigelow & Sears. I cannot confirm that the descending branch of the pallial canal extends beyond the nectosac. It terminates about the lower margin of the

nectosac, which has only a very narrow velum like the gonophore. The velum can only be seen in relaxed living specimens.

Larval nectophore: The only description is by Moser (1924a, Pl. 1, fig. 3). She illustrated a younger stage in figure 1 of plate 1, together with earlier growth-stages of the buds of definitive nectophores 1 and 2. This larva measured 5.5 mm in length. Its lateral radial canals are straight and not meandering, and a central organ (see Totton, 1954, text-fig. 43) is present as in *R. plicata*.

Eudoxid phase (Pl. XXII, fig. 2)

The bracts, which reach a maximum length of 9 mm, are convex proximally, slightly concave distally and almost hemispherical in outline dorsally. They are divided below the stem (when horizontal) on the proximal side into two lobes, with a third lobe on the concave distal side (the near side of fig. 4, Pl. 2, Bigelow, 1911b). This lobe forms the left side of the hydroecial cavity of the bract. The ectoderm of a living bract shows that it is formed of flat, polygonal cells measuring 0.25 mm in diameter, with conspicuous central nuclei. The walls appear to be lined with minute droplets. The dorsal horizontal branch of the phyllocyst runs up to but appears not to open into a conical depression of the surface. The eudoxid was beautifully figured by Bigelow (1911b, Pl. 2, fig. 4).

Haeckel's description (1888b, pp. 148–9) of the bracteal canal-system of *P. galea* (= *R. cymbiformis*) is obviously superficial. There is, when mature, no connection between the lumen of the stem and

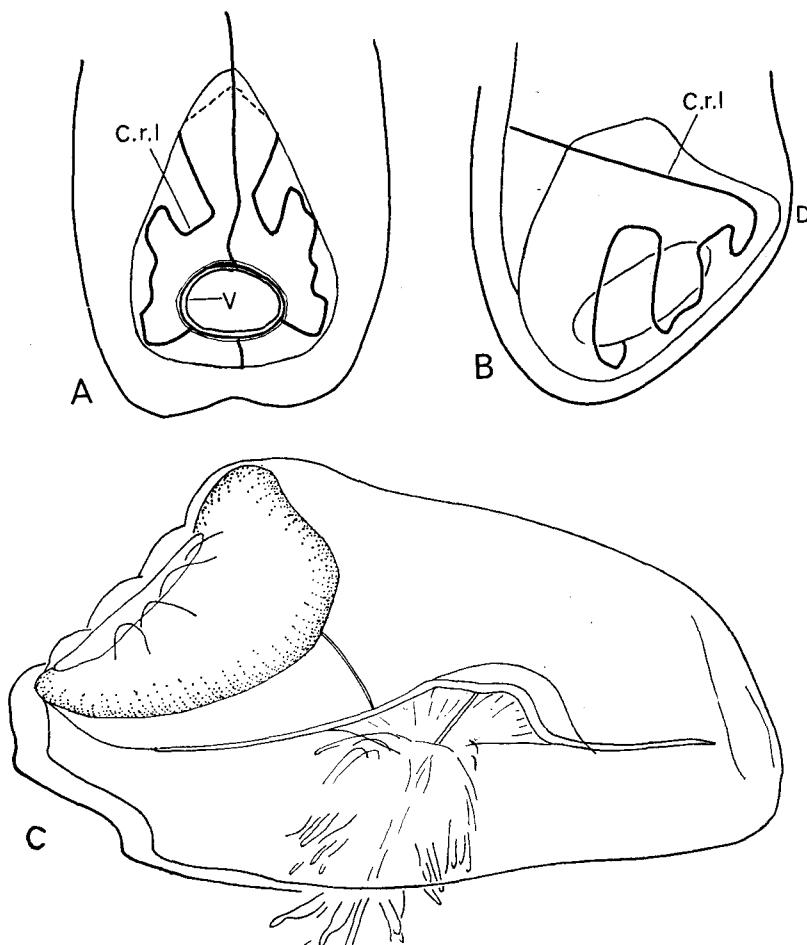


FIG. 68. *Rosacea cymbiformis* (Chiaje). Nectosac, $\times 7$

A, dorsal; B, lateral views to show the course of the radial canals
C.r.l = lateral radial canal; *d* = dorsal side; *v* = velum (from Totton & Fraser, 1955); C, polygastric phase from Villefranche; camera lucida sketch from a negative of a living animal

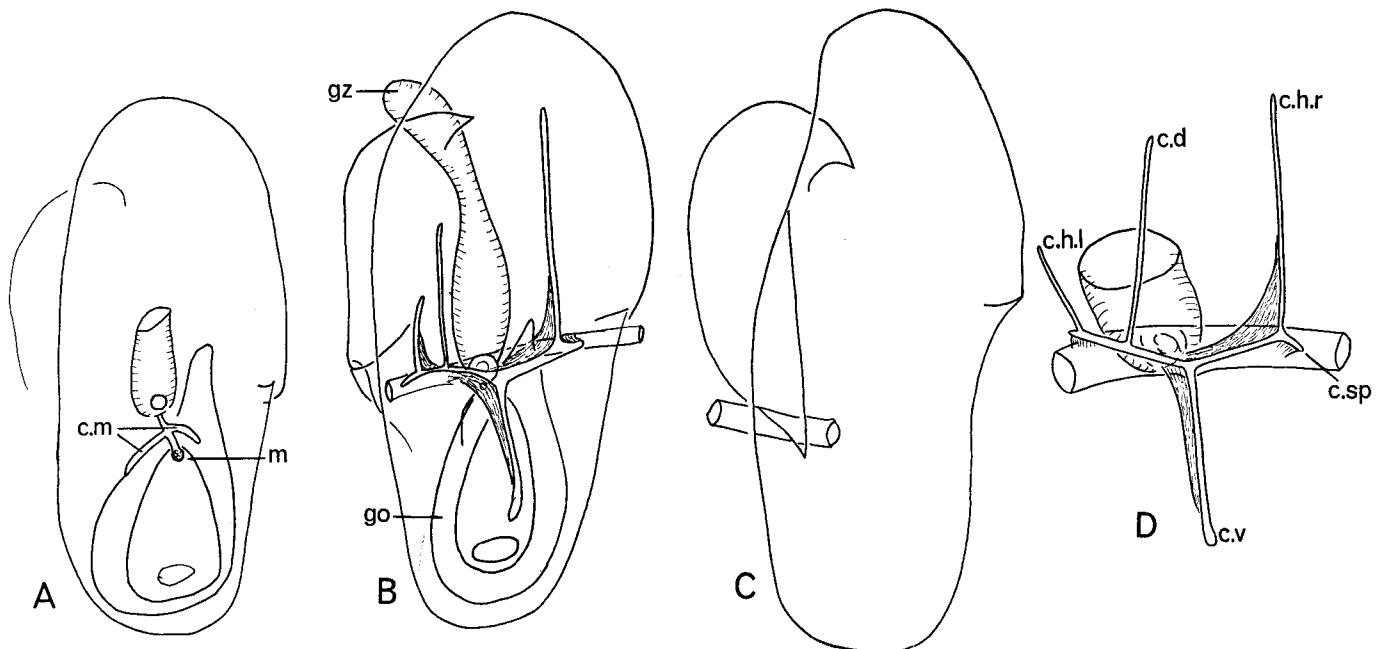


FIG. 69. *Rosacea cymbiformis* (Chiaje). Sketches of living stem-groups made at Villefranche 1962, $\times 20$
 A, to show a young gonophore; B, D, muscular attachment lamellae; C, upper view of bract
 $c.d$ = dorsal bracteal canal; $c.h.l$, $c.h.r$ = left and right hydroecial canals; $c.m$ = mantle canal; $c.sp$ = spur canal; $c.v$ = ventral canal; go = gonophore; gz = gastrozooid; m = manubrium.

that of the bracteal canals, no 'apical vessel' or peduncular canal (from the stem to apical part of the hydroecial cavity) and no short, spindle-shaped 'phyllocyst' (unless Haeckel was referring to one of the two short, lateral spur-canals). He did not describe the muscular attachment of the bract to the stem. The 'odd dorsal canal' does not 'run along the convexity of its basal and dorsal half'. Haeckel did not show nor mention that the dorsal canal reaches the surface of the bract. It does so as a closed vesicle.

The bract of *R. cymbiformis* differs from the bract of *R. plicata* in that the dorsal branch of the bracteal canal-system arises from a point on the left longitudinal (hydroecial) canal, proximally to the short (spur) branch, whereas in *R. plicata* the position is distal to this small lateral spur. A large triangular sheet of muscle stretches from a point half-way along the right (proximal) spur canal to the stem, and all along the stem to the base of the gastrozooid. A small muscle stretches vertically below the right spur canal to the horizontal stem. A long muscle extends from the stem in the region of the basigaster down most of the ventral canal (text-fig. 69).

The gonophores are budded from a point on the stem close to the base of the gastrozooid and on the side of it opposite to the tentacle. There is no special, asexual nectophore. Leuckart (1853) described and figured the young buds of two secondary gonophores close to the insertion of the first one, which he took to be an asexual nectophore. Six or so eggs can be seen in the rudimentary manubrium of the first gonophore from the start of its development, almost filling the closed sub-umbrella. This undeveloped, morula-like structure persists in older stages of development too. The eggs appear to develop more fully (see Bigelow, 1911b, Pl. 42, fig. 4) only shortly before the gonophore becomes detached. This has made observers uncertain whether the first medusoid was a gonophore or an asexual nectophore.

Male and female eudoxids are said to be found on the same stem. It seems likely therefore that the second gonophore bud may be male. There are two opposite longitudinal ridges on the exumbrella of the gonophore.

The gonophores pulsate actively, so that from time to time the stem relaxes and the eudoxids separate from one another as all the gonophores actively spread the stem into loops. This process extends the potential fishing-field of the tentacles, and is a beautiful phenomenon to observe. I have observed that the stem contracts again before the nectophores begin to pulsate. Gegenbaur said that the gonophores, after detachment, swam about for several days. He counted forty-six eudoxids on a three-foot long stem. There may be upwards of sixty tentilla from 4–5 mm apart when the tentacle is extended, in which condition it may be 27 cm long. The terminal filament can extend to 13 mm; it has a small disc-shaped terminal sucker edged with nematocysts. Thus a single animal may fish more than 35 m of armed line. I introduced some 4–5 mm long fish-larvae into a tank containing a specimen of *R. cymbiformis*. The fish generally avoided the 'net' but sometimes a filament attached itself to a tail. The fish usually broke away with a piece of filament attached and did not succumb. But one larva was observed being ingested head first by a gastrozooid, while the gastrozooid next but one was ingesting the tail of the same larva.

Attached bracts and detached gonophores and tentilla of *R. cymbiformis* provide good experimental material of siphonophores. When the inside margin of the ostium (velum) of the gonophore is touched with a needle, there follows a single contraction of the nectosac. When the needle is passed inside the umbrella cavity, without touching the ostium, until it touches the proximal surface of the nectosac a general tetanus occurs, together with a shortening and contraction of the whole gonophore. This tetanus can be terminated by another touch of the margin of the ostium. At this time there appears to be a tendency for the ectoderm to become sticky and to adhere to the bottom of the container. If the gonophore is placed between two electrodes (alternating current), a single pulse causes a similar spasm. It is probably the action of formalin on the nectosac that causes the contracted condition in which so much preserved material of nectophores and gonophores arrives in plankton samples.

I experimented with tactile and pressure stimuli on different areas of attached bracts of eudoxids. The region round the termination of the dorsal branch of the phyllocyst was unresponsive, but slight pressure over the terminal dilation of the median, longitudinal branch was followed by contraction of the muscular lamellae.

Genus: ***PRAYA*** Quoy & Gaimard in Blainville, 1834

Praya Auct pro parte

Praia Blainville, 1830, 1834

Nectodroma Bigelow, 1911b

Type species: *Praya dubia* (Quoy & Gaimard, 1833).

Blainville (1830) adapted Quoy & Gaimard's manuscript name *Praya*, taken from that of a beach in the Cape Verde Islands where these naturalists found the first prayid siphonophore. Subsequent authors have returned to the use of Quoy & Gaimard's original spelling in spite of the fact that *Praia* has priority of publication. According to the current code of nomenclature *Praya* must now be used. Blainville based his description on Quoy & Gaimard's actual specimen shown in their plate 5, figures 34–36, of which they say (pp. 105, 106), 'Nous avions fait de ce corps . . . notre genre *Praya* mentionné par M. de Blainville dans son *Traité des Zoophytes* . . .'

Generic Diagnosis:

Polygastric phase

Species with a pair of large, opposed, rounded nectophores (reserve buds may be present) with multi-form (branched) radial, subumbrial canals, a branched somatocyst and flattened, semi-circular bracts.

Eudoxid phase

The bracteal canal system has the typical four main branches but no median 'central organ' such as is found in *Desmophyes*.

There are two well-known species, *dubia* Quoy & Gaimard and *reticulata* (Bigelow). Their bracts have not been differentiated for certain owing to the fact that at stations such as 'Discovery' St. 2635 in $10^{\circ} 19'S$, $09^{\circ} 36.4'E$, where well preserved bracts have been found, nectophores of both species have been found also. It appears likely that in *P. reticulata* the tip of the right hydroecial (lateral) canal is recurved, and that the dorsal canal is longer and more recurved than in *P. dubia*. The bracts may measure up to 20 mm \times 10 mm, and 4 mm. The *Praya* type of tentillum was beautifully figured by Bigelow (1931, fig. 189), but the specific identification for this figure may be in doubt. The measurement of the large lateral nematocysts in this figure correspond well with those of similar ones from 'Discovery' St. 2635, namely 220μ long, 15μ diameter.

***Praya dubia* (Quoy & Gaimard, 1833) 1834**

Plate XXIII, figures 6, 7

Diphyes dubia Quoy & Gaimard, (1833) 1834, page 104, plate 5, figures 34-36

Praia dubia Blainville, 1834

Nectodroma dubia Bigelow, 1911b; Moser, 1925

Praya dubia Bigelow, 1931

The following description is taken largely from Bigelow (1911b).

Polygastric phase

Younger nectophore: About 40 mm long, 33 mm broad, obliquely truncate above, ventral wall extending below the level of the opening of the nectosac. Hydroecial groove deep, running the entire length of the nectophore, partially closed over above by a small gelatinous flap, and entirely enclosed below by two lateral flaps.

The somatocyst is extended by a system of branching canals. Below the point of origin of the pedicular canal it runs as a single unbranched tube along the dorsal wall of the hydroecium to a point slightly below the opening (ostium) of the nectosac. The ascending trunk, which may bear several short transverse branches, divides into three near the upper end of the nectophore. The simple median branch runs directly dorsad. The two laterals curve down with several minor, lateral branches, to terminate slightly above the apex of the nectosac. The sub-umbral (radial) canals number about twelve at the apex, branching distally to form about fifty at the margin. They are not interconnected as they are in *reticulata*.

Older nectophore: Up to 85 mm long, 50 mm broad. The somatocyst and radial canals are similar to those of the younger one. There may be at least three reserve nectophores.

Eudoxid phase

(Text-fig. 70.) Not hitherto recorded as such. I am inclined, however, to think that the bract figured by Bigelow (1931, fig. 185) coming from Monterey Bay, California (Bigelow & Leslie, 1930) and labelled *P. reticulata* really belongs to *P. dubia*.

The right hydroecial canal is not recurved at the tip as it is in *P. reticulata*, nor is the dorsal bracteal canal so long and recurved and the ventral bracteal canal C⁴ is not branched as in the original figure of the bract of *P. reticulata*.

TABLE V

Terminology of bracteal canals (see text-fig. 74, p. 132)

Chun (1891)	Bigelow (1911a)	Bigelow (1911b)	Totton (1954)	Present Usage
C.br.1, 4	Lateral Spur	Lateral Spur c ¹
C.br.2	C.4	C.br.3 C.B (<i>Bassia</i>)	C.4; ventral C.3; dorsal	Ventral c ⁴ Dorsal c ³
C.br.3	C.3	C.br.1; apical trunk		
C.br.5, 6	C.1; C.2	C.br.2; hydroecial	Longitudinal; hydroecial	Hydroecial c ^h

There are two surface grooves present on the bract: (1) a shallow transverse groove on the narrow dorsal margin. The dorsal bracteal canal comes to the surface in this groove; (2) a deeper lateral (right) and vertical groove near the free end of the hydroecium. In life this larger groove probably makes a passage for a tentacle.

Distribution: First taken – and studied alive – by Quoy & Gaimard near Adelaide, South Australia. Not recorded again until 1911, when Bigelow described a catch by 'Albatross' in the East Tropical Pacific. Moser (1925) described a specimen taken off Valparaiso in 1885, and lastly in 1931 Bigelow again recorded specimens taken in the East Tropical Pacific by 'Arcturus'. To these records must now be added catches by 'Discovery' and 'Discovery II' in the Atlantic and Pacific as follows:

TABLE VI

Praya dubia (Quoy & Gaimard)

Date	Station	Net	Depth in m.	No. of nectophores
28 x 1925	13° 25'N, 18° 22'W	N 450	0–900	2
17 viii 1927	286	TYF	125 (–0)	2
28 viii 1927	297	TYF V	200–300 (–0)	5
23 iv 1931	672	TYF B	200–0	2 (1 still attached)
11 v 1931	695	TYF B	370–0	2
12 v 1931	696	TYF V	250–0	2, and base of stem
12 v 1931	697	TYF B	460–0	1, and base of stem
11 iv 1931	2635*	TYF B	280–0	2, and bracts
17 x 1964	32° 36'N, 117° 31'W to 32° 30·6N, 117° 30·7'W	IKMT	330–(180)	6, and bases of two stems, etc.

Praya reticulata (Bigelow, 1911)

Plate XXIII, figures 1–4

Nectodroma reticulata Bigelow, 1911b, 1913, 1931? *N. reticulata* Bigelow & Leslie, 1930*Polygastric phase* (Pl. XXIII, figs. 1, 2, 4)

Nectophores: Sub-cylindrical, transversely truncate at the upper end, obliquely truncate below, reaching 55 mm in length and 20 mm in greatest diameter. The hydroecial canal which is deep and extends the entire length of the ventral surface may be entirely covered over by lateral flaps, or the flaps may be widely separate.

At about 1 cm or less from the upper end of the pallial canal (somatocyst) there is a median branch, which may have short lateral branches, extending dorsad at right angles to the pallial canal. The ascending and descending branches of the pallial canal (somatocyst) gives off short, lateral transverse branchlets, often bifurcated at the tip. They may be fewer in number (Bigelow, 1913) than shown in Bigelow's (1911b) figures here reproduced.

The nectosac is proportionately smaller than in *P. dubia*. The sub-umbrial canals are numerous and anastomose. At the apex of the nectosac there are about eight radial canals. They branch dichotomously.

* At this station was taken also a specimen of the only other species *P. reticulata*.

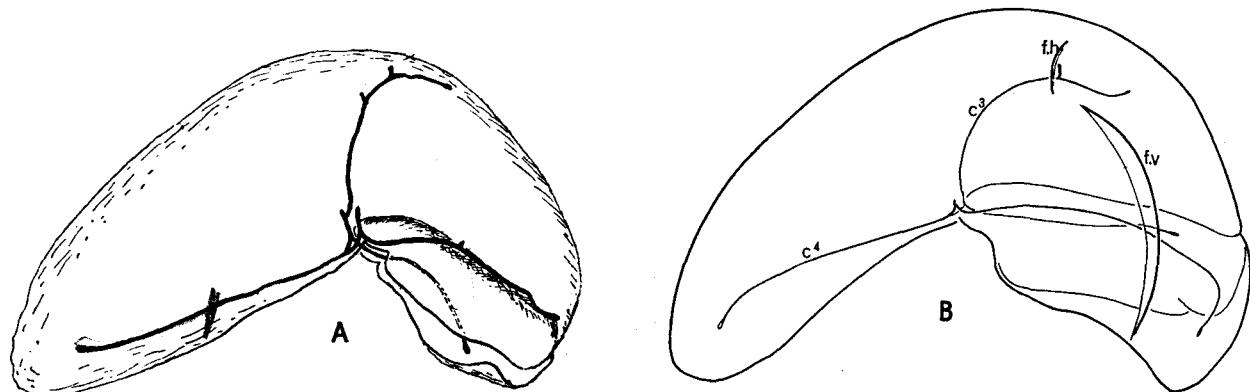


FIG. 70. *Praya dubia* (Q. & G.). Bracts of eudoxids
A, after Bigelow (1931) as *P. reticulata*, $\times 3$; B, from 'Discovery' St. 2635, $\times 2.6$
 c^3 = dorsal bracteal canal; c^4 = ventral bracteal canal; f.h. = horizontal fold; f.v. = vertical fold.

tomously at different distances from their points of origin. The resultant canals anastomose by means of short transverse canals to form an irregular *reticulum*.

Eudoxid phase (Pl. XXIII, fig. 3)

The bracts measure up to 20 mm in length, and are laterally flattened, convex above concave below. The dorsal bracteal canal is much recurved. The tip of the right hydrocial canal is longer than the other and recurved. The ventral canal C^4 may bear small lateral branches.

A magnificent specimen was taken in the Bay of Biscay, some thirty miles to the north of Santander in the Isaacs Kidd mid-water-trawl at 450 m by 'Sarsia' on May 22, 1957, and kindly submitted to the author by the Director of the M.B.A. Association, Plymouth. When the specimen was received in mid-July there were still traces of lemon yellow colour in the distal halves of the gastrozooids, and at the junction of tentacle and basigaster. The liver-stripes showed traces of a reddish-brown pigment. The two large transparent colourless nectophores became separated from the stem leaving a third, younger nectophore as well as two much smaller nectophore buds still attached. Ten pieces of stem, strongly contracted, measured 82 cm in total length. I estimate that the expanded stem might have reached a length of 3 m.

Distribution (see Bigelow, 1931, p. 535): Off Peru; South of Japan; Puget Sound; Galapagos – Panama Region; Monterey Bay, California – needs confirmation of specific identification.

New Records: 'Discovery' Stations 281, 964, 1690, 2365.

Station	Net	Date	Depth in m	Material
281	TYF	12 viii 1927	850 – 950 (- 0)	2 nectophores
964	N 70 B	15 ix 1932	125 (- 0)	2 nectophores
1690	N 70 B	8 iii 1936	520 – 200	2 nectophores still attached
2635	TYF B	11 iv 1939	280 – 0	2 nectophores, 1 attached with bud

Genus: *PRAYOIDES* Leloup 1934

Monotypic genus for *Prayoides intermedia* Leloup.

The name *Prayoides* was published for a 'groupe' of *Rosacea* Quoy & Gaimard. From a systematist's point of view this seems to be the equivalent of a sub-genus. It is best to raise the name to generic rank as I have done.

The distinguishing feature of this genus is that it appears to be intermediate between *Rosacea*,

with unbranched somatocyst and simple subumbral radial canals in the polygastric phase, and *Praya*, with branched somatocyst and branched radial canals.

Diagnosis: Prayines with simple, unbranched somatocyst and branched subumbral, radial canals. A single species *intermedia* was described by Leloup (1934).

***Prayoides intermedia* Leloup, 1934**

The only species known. The larger nectophore of the only complete specimen found measured 12 mm in length and 8 mm in breadth; the smaller 7.5 mm × 5 mm. There is a deep hydroecium in each. It was taken by 'Meteor' off Freetown, West Africa. A single nectophore was taken not far away off Cape Verde.

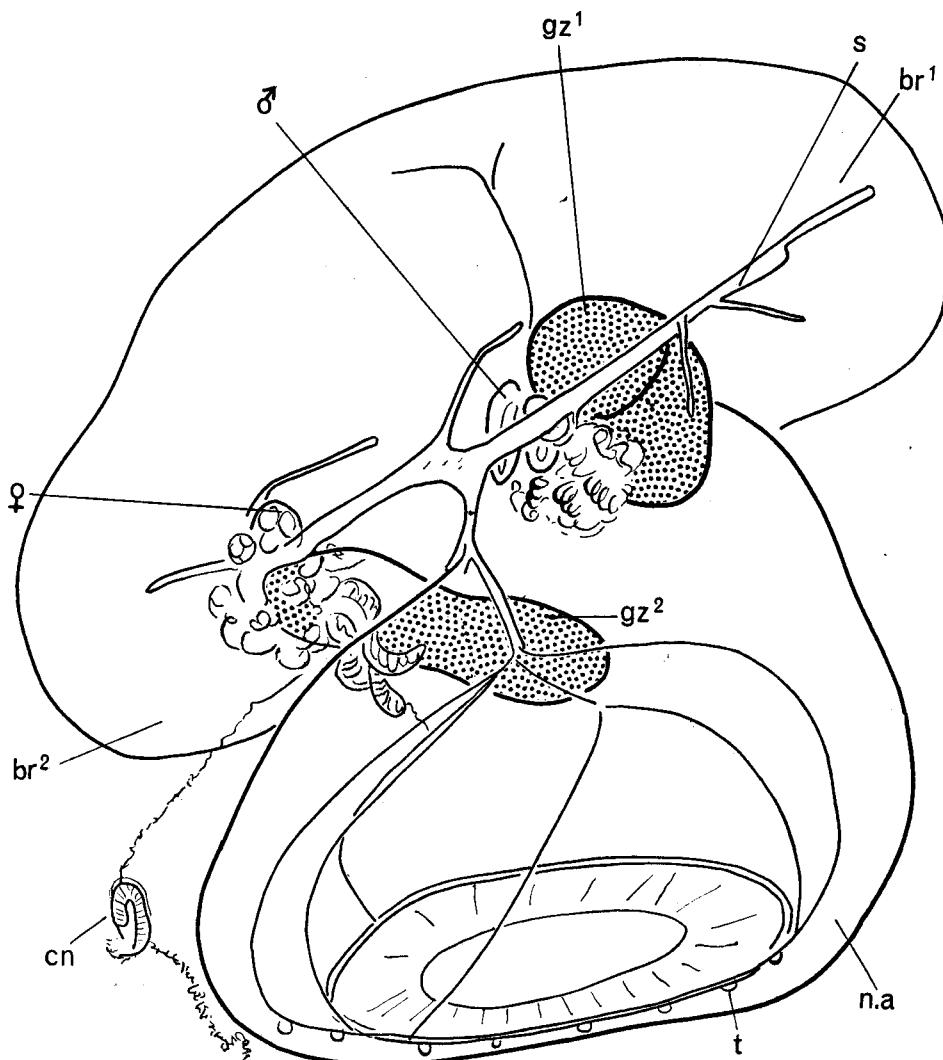


FIG. 71. *Lilyopsis rosea* Chun. Eudoxid phase
A complete male and an incomplete female stem-group, taken in the plankton, at
Villefranche and drawn by M. Carré, $\times 16$
 br^1 , br^2 = the two bracts; cn = cnidosac; gz^1 , gz^2 = the two gastrozooids; $n.a$ =
asexual nectophore; s = stem; t = tentacle-like process.

Genus: *LILYOPSIS* Chun, 1885

I designate as type species *Lilyopsis rosea* Chun, 1885.

Chun* included three species: (1) *L. diphyses* Vogt, *L. diphyses* Kölliker; (2) *L. medusa* Metschnikoff (? *L. rosea* Chun); and his new one (3) *L. rosea* Chun; *L. diphyses* of Vogt & Kölliker belongs to *Desmophyes*.

The type species was founded on two polygastric specimens with eudoxids borne on the stems.

We are very uncertain about the identity and morphology of species of this genus. No preserved specimens are known to exist, and the literature is very confused and descriptions and figures inadequate. A prolonged visit to Villefranche might enable a systematist to find specimens.

Chun did not mention the somatocyst in his *L. rosea* but in *L. medusa* it is figured as being prolonged into the mesogloea.

Lilyopsis rosea Chun, 1885

Plate XXVII, figure 1

'*Praya diphyses* Blainville' of Graeffe, 1860; non '*P. diphyses* Blainville' of Vogt, 1852 (= *Desmophyes annectens* Hkl.)

? *Praya medusa* Metschnikoff, 1870

Lilyopsis diphyses Moser, 1917, 1924a

Polygastric phase (Pl. XXVII, fig. 1)

Up to three reserve bells may be present. Nectophores of equal size, wedge-shaped in side-view with conspicuous, large nectosacs, whose lateral radial canals are meandering. Somatocyst simple, prolonged into mesogloea of ectophore. Chun did not mention ostial tubercles or pigment spots. But Metschnikoff did.

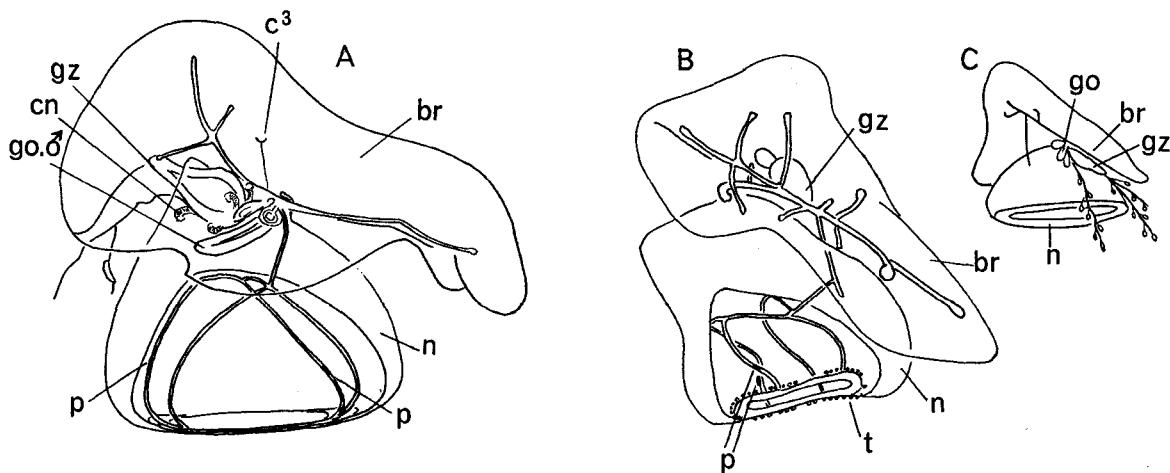


FIG. 72. *Lilyopsis rosea* Chun. Eudoxid phase

A, $\times 8.6$, after Chun (1885); B, $\times 22$, after Moser (1917); C, $\times 2.8$, after Graeffe (1860)
 br = bract; c^3 = dorsal bractal canal; cn = cnidosac; go.♂ = male gonophore; gz = gastrozoid; n = asexual nectophore; p = pigment spot; t = vestigial tentacles.

Eudoxid phase

(Text-figs. 71, 72.) Six bractal canals, but no pear-shaped 'central organ'. There is a large asexual nectophore with bright red pigment spots and tubercles on the ostial margin, whose radial canals arise in two pairs from the pedicular canal, and a bunch of small unisexual gonophores with reduced umbellae. Male and female eudoxids occur on the same stem.

* Chun (1891) said later on: 'Under the name *Lilyopsis* I included some Diphyids previously ascribed to *Praya*, characterized by the lack of sharp ridges on the rounded swimming bells and bracts, and by the occurrence of special swimming bells that ripen on the stem' (p. 559).

I am grateful to M. Claude Carré of the Station Zoologique, Villefranche, for permission to reproduce a sketch (text-fig. 71) of a complete male eudoxid and part of an attached female one, which he made a few years ago. The occasion was the first record of seeing this animal since 1917. In the spring of 1963 he showed me another living eudoxid. I was able to confirm the details of the nectophore, but the bract became detached and shrivelled before I could study the canal system.

In text-figure 72 are reproduced the figures of eudoxids by (A) Moser (1917); (B) Chun (1885); and (C) Graeffe (1860), the only figures known hitherto of the eudoxid. I have not so far succeeded in making a satisfactory interpretation of their sketches of the bracteal canal system. I am unable to indicate how it is homologous with those of other prayines shown in text-figure 74 p. 132.

Lilyopsis gracilis (Fewkes, 1883)

'*Praya sp.*' Fewkes, 1880a, page 146 (expl. of Pl. III), Plate III, figure 2
Lilyopsis gracilis Fewkes 1883, page 841

A doubtful species. It would be remarkable that there should be living in the Mediterranean two species *L. rosea* Chun and *L. gracilis* Fewkes, distinguishable only by the presence of meandering lateral radial canals in the nectosac of one, *rosea*, and straight ones in the other *gracilis*. This is a matter for confirmation or refutation by future observers.

In the meantime, since Fewkes in his only descriptive note (1880a) – appearing in the explanation of his plate III, figure 2 – specifically refers to the 'direct course from junction to circular vessel of the radial tubes', I must exclude this species *gracilis* from the synonymy of *L. rosea*. When the edge of the nectosac is rolled up it is not always easy to observe the course of the lateral radial canals, and it is possible that Fewkes was mistaken.

The name *gracilis* appeared, rather casually, three years later (1883) in the American Naturalist in his semi-popular paper, but obviously referred to the animal that he had previously figured. His figure shows that the somatocyst is missing from one nectophore. This is not of specific importance.

In other respects the specific description is the same as for *L. rosea*.

Genus: *DESMOPHYES* Haeckel, 1888

Praya auct (Kölliker, 1853; Vogt, 1854) non *Praia* Blainville, 1830
Lilyopsis auct (non *Lilyopsis* Chun, 1885)
Desmophyes Haeckel, 1888
Rosacea Kawamura, 1915 (non *Rosacea* sensu Bigelow, 1911)

Monotypic genus for *Desmophyes annectens* Haeckel, 1888.

The eudoxids of '*Praya diphyses*' Kölliker, 1853 and Vogt, 1854; of *Desmophyes annectens* Haeckel, 1888 and of '*Rosacea plicata*' Kawamura, 1915, have similar characteristics which separate them from the eudoxids of *Praya* spp. (sensu *Nectodroma* Bigelow), of *Rosacea* spp. (sensu Bigelow) and of *Lilyopsis* spp. Chun.

Two good figures of this different type of eudoxid appear in Kawamura (1915, Pl. VII, figs. 7–8) they are accompanied by a figure – 6 – of the associated polygastric phase of the animal. The figures appear to be original drawings of specimens taken at Misaki in 1907.

The polygastric phase associated with this type of eudoxid was beautifully figured by Vogt (1854, Tab. 6, as *Praya diphyses* Blainville).

Definition

Polygastric phase

Nectophores biserial, somatocyst simple, lying obliquely in the mesogloea. Lateral radial

canals straight, nectosac relatively small. There is a ring of minute red pigment flecks and tubercles round the ostium.

Eudoxid phase

The eudoxid has a large asexual nectophore and a group of unisexual reduced gonophores. There is a median pear shaped vesicle – the central organ – at the junction of the four main bracteal canals. Eodoxids of both sexes on one and the same stem.

Desmophyes annectens Haeckel, 1888

Plate XXII, figures 4–6; Plate XXIV, figures 1–9

Praya diphyses Kölliker, 1853; Vogt, 1854 (non *P. diphyses* Lesson, 1843) = *Rosacea cymbiformis* (Ch.)

Lilyopsis diphyses auct. Non *L. diphyses* Moser, 1917 = *L. rosea*

Praya filiformis (Ch.) Kefferstein & Ehlers, 1861

Desmophyes annectens Haeckel 1888b

Rosacea plicata: Kawamura, 1915 (non *sensu* Bigelow, 1911b)

The largest specimen found by Vogt had a stem one metre in length which bore one hundred eodoxids.

Polygastric phase (Pl. XXII, fig. 4; Pl. XXIV, figs. 1–3)

Nectophores: Rounded, wedge-shaped in lateral view, measuring up to 30 mm in length × 15 mm, soft and very transparent, and only loosely joined together, the younger one of the pair – several reserve nectophores may be present at the same time – being clasped only by the upper region of the hydroecium of the older. The somatocyst, simple and club-ended, lies obliquely in the mesogloea. The lateral radial canals are straight and do not meander as in *Rosacea*. The relatively small nectosac occupies only the lower part of the nectophore, its ostium directed downwards and outwards. Round the ostium is a ring of minute red pigment flecks and tubercles.

Eudoxid phase (Pl. XXII, figs. 5, 6; Pl. XXIV, figs. 4, 7)

The bract is rounded on the proximal side (above) and bounded below by two lateral, hydrocial flaps. There is a relatively large asexual medusoid and a bunch of smaller gonophores at its base, all of one sex in a single cormidium, but the sexes alternate from one cormidium to the next. A very characteristic feature not found in *Praya* or *Rosacea* spp. is a median, pear-shaped vesicle, the so-called central organ (Pl. XXII, figs. 5, 6; Pl. XXIV, fig. 4) which lies at the junction of the main bracteal canals. In addition, there are the four main canals found in *Praya* and *Rosacea* spp.

Kefferstein & Ehler's use of the name *filiformis* has priority, but is ruled out as a *nomen oblatum* by recent changes in the Rules of Nomenclature. It seems best, therefore, to use the name *annectens* of Haeckel (1888a, b). There would have been no possible doubt about the identity of Haeckel's form if only a single pair of nectophores had been described. But we know that in prayines there may be a succession of at least seven nectophores, although it is unusual to see six large ones all attached at the same time as shown by Haeckel. Therefore, I doubt if the presence of six nectophores is a specific characteristic of *Desmophyes annectens*, and we may use the name for specimens with only two fully formed ones such as Kölliker, Vogt, and Kefferstein & Ehlers have described.

Moser has introduced a great deal of confusion into the nomenclature by confusing specific identities.

Vogt (1854) reported that this species was not uncommon in the neighbourhood of Nice (Villefranche) but there are no records of it there since that time. This may be due to the fact that non-specialists could easily confuse it with the better known *Rosacea cymbiformis*. It is very desirable that

visiting planktonologists should keep a look out for this species at Villefranche and preserve in formalin some specimens relaxed in magnesium chloride because none are known to exist in museum collections.

Genus: ***STEPHANOPHYES*** Chun, 1888

Monotypic genus for *S. superba* Chun.

Definition

Polygastric phase

Prayines with four large nectophores forming a corona. Somatocyst with only one bifurcation in young stages of development, but in mature nectophores each of these branches may rebranch complexly about ten times, the tips of the branchlets being pigmented. When fully grown the nectosac's ostium lies nearly parallel with the long axis.

Eudoxid phase

The stem-groups bear in addition to the gastrozooids, nectophores, bracts and gonophores some characteristic reduced, mouthless gastrozooids or palpons growing singly or two to three on a single pedicel. They bear heteromorph tentacles. This is the only calycophore genus in which palpons are found. The lateral radial canals of the special swimming bells are meandering and not straight.

Stephanophyes superba Chun, 1888

Plate XXV, figures 1, 2; Plate XXVI, figures 1-3

Stephanophyes superba Chun, 1891

Lilyopsis diphyses (*pro parte*) Moser (1917, 1924a)

A very distinct species with a much branched somatocyst in the nectophores of the nectosome. It is the only known calycophore with a second kind of reduced gastrozooid, and a second, heteromorph kind of cnidobattery in the fully formed groups.

Polygastric phase (Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1-3)

Nectophore: Chun (1891) gave detailed figures of the various growth stages of the complexly branched somatocyst, which has only one bifurcation in the upper part of young specimens. It was probably one of those juvenile specimens that Moser (1917) described as '*Lilyopsis diphyses*', on page 734. In later stages the two lateral branches may subdivide about ten times each, not necessarily symmetrically. In the early growth stages the nectosac occupies the greater part of the nectophore, its ostium being directed obliquely outwards and downwards. In later stages the inner and upper end of the nectophore is relatively larger, and the ostium of the nectosac lies more nearly parallel with the stem. There are some small red tubercles on the ventral side of the ostium.

Eudoxid phase

(Text-fig. 73.) The stem-groups are closely set, and were stated by Chun not to separate off. Confirmation of this statement is needed. The bract has a canal system that can be related to those of species of *Rosacea* and *Praya*. There is (*see* Chun, 1891, Taf. III) a right and left hydroecial canal (c.rs.5, c.br.6), a right and left spur-canals (c.br.4, c.br.1), a dorsal canal (c.br.3) and a ventral canal (c.br.2). There is a large asexual swimming bell, whose lateral radial canals follow a meandering course to the ring-canal. The four radial canals do not branch together from the pedicel. There is, in addition to the special nectophore, a bunch of reduced medusoid gonophores close to the distal side of the

gastrozoid, or occasionally close to the reduced gastrozoids or (?) palpons. The radial canals of the gonophores take zig-zag courses to the ring canal and give off small lateral branches. Two or three male cormidia alternate with two or three female ones. There are some small red tubercles in the region of the circular canal of the asexual nectophore.

Palpons (Pl. XXVI, figs. 1, 3): Between successive stem-groups are found the characteristic reduced, mouthless gastrozoids or (?) palpons, growing singly or two or three to a single pedicel. They are thick walled, 0·5 mm in length, and bear heteromorph tentacles.

Because *Stephanophyes superba* has so seldom been recorded, Chun's account and figures have hardly been checked. It is worth remembering that Schneider (1899, p. 24) criticized Chun's figures of the cnidosacs. Schneider, who seems to have mistakenly thought *S. superba* and *Praya dubia* were the same species, denied the presence of Chun's lateral giant cells, and gave a different interpretation of them, and the structure of the cnidosac. The cnidosacs in the two species *S. superba* and *P. dubia* resemble each other basically in structure, as do those of most prayids, so that Schneider's comments are still valid.

Sub-family iii: NECTOPYRAMIDINAE Bigelow, 1911

A small group of four aberrant prayines, the nectophores of which instead of being smoothly rounded bear ridges, angles and serrations.

I include them in a single genus *Nectopyramis* Bigelow 1911a.

Genus: NECTOPYRAMIS Bigelow, 1911

Archisoma Bigelow, 1911b

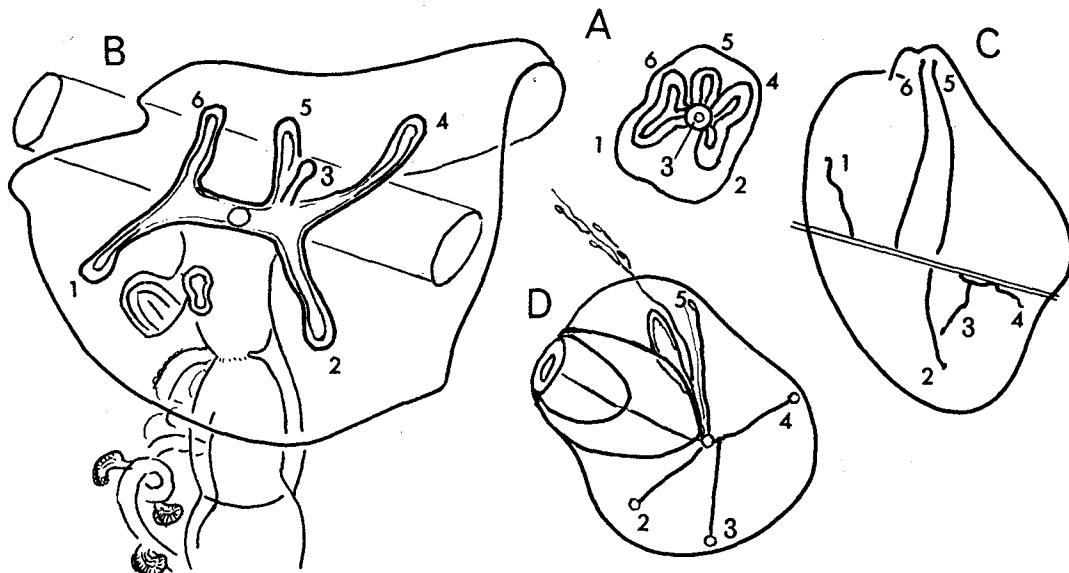
Type species: *Nectopyramis thetis* Bigelow, 1911a.

Four very distinct, aberrant, prayine species *N. thetis*, *N. diomedae*, *N. natans* and *N. spinosa* are included in a single genus *Nectopyramis*. This seems to be a better arrangement than recognition of three or four genera. *Nectopyramis* as originally defined had for fifty years contained a second species *diomedae*, and *natans* was at that time made the type species of a genus *Archisoma* Bigelow. *N. spinosa* Sears, 1952, was originally described and figured rather inadequately by Moser (1925) as *Hippopodius cuspidatus*. But it is not closely related to species of *Hippopodius*.

Polygastric phase

Nectophores of species of *Nectopyramis* are always taken singly, suggesting that only one nectophore – the larval one – is developed, except in *N. spinosa* where two types of nectophore are developed. One represents the caducous larval bell, and the other is a heteromorph definitive nectophore. Instead of being smoothly rounded as in other prayines there are in this phase in species of *Nectopyramis*, ridges, angles and serrations, or both together.

The somatocyst differs in the four species. In *natans* and *spinosa* it is simple, as in species of *Rosacea*. In *thetis* and *diomedae* it branches, complexly in *diomedae*, but there is a common basic pattern of branching in these two. It does not resemble the patterns of branching in the species of *Praya* and *Stephanophyes*. In 1954 I suggested what this pattern was like, but a textual error crept into the proof which was not corrected. It concerns the 'flagging' of a figure and made nonsense of the text. On page 84 of my 'Discovery' Report of that year, line 14 contained the words: 'C.pa², a right and left "dorsal" canal C.pa³, C.pa.² . . .' For C.pa² read C.pa¹, referring to the accompanying text figure 39A on page 85.

FIG. 73. *Stephanophyes superba* Chun. Eudoxid phase, $\times 50$

Growth stages of bracts of eudoxids to show the identities of the bracteal canals and the homologies with those of other prayid bracts shown in text-figure 74. The numbers are those of Chun's terminology (see table V, p. 123). A, young bract from stem-group immediately proximal to B, $\times 60$; B, stem-group from proximal part of a young specimen, $\times 60$; C, preserved bract, $\times 4$; D, stem-group, slightly magnified.

The pattern of branching of the somatocyst, common to *N. thetis* and *N. diomedae*, and indeed to all prayids, though some branches are lost (text-fig. 74) here and there, is as follows: Near the centre or apex of the hydroecial cavity are given off right and left dorsal (or lateral) branch-canals, each of which in turn sends a branchlet called the right and left hydroecial canals (C.h.r, C.h.l) to the flank of the hydroecium. In *N. thetis* these hydroecial canals are simple and symmetrical, but not in *N. diomedae*, where they are strangely twisted. In addition median branches are developed in *N. diomedae* – Bigelow's C.pa¹ and C.pa² (see Bigelow, 1911b, Pl. 1, fig. 1). These do not appear in the nectophore of *N. thetis*.

The four radial canals of the nectosac in species of *Nectopyramis* arise separately, but this phenomenon does occur in other prayines. There is a tendency towards reduction of the nectosac and stem, especially in *N. spinosa*. This is accompanied by an increase in the relative amount of mesogloea, indicating that specimens float passively.

Eudoxid phase

This is dealt with in detail in the specific descriptions (pp. 134–138).

Nectopyramis diomedae Bigelow, 1911

Plate XXIII, figure 5; Text-figure 75

The shape of the hydroecium and its slit-like ostium in the polygastric phase of this species resembles that found not only in larval prayines and amphicaryonines but also in hippopodiids. The tentilla, too, are of peculiar structure, resembling the larval type found in Physonectae. All this suggests that the species is neotenic. However, it has developed the most complex pattern of somatocyst-branching found in any prayid.

Only sixteen polygastric specimens have ever been recorded. No two of them look quite alike probably due to various degrees of shrinkage of the mesogloea. It is estimated that they live at a depth of from 650 m to 1600 m or so.

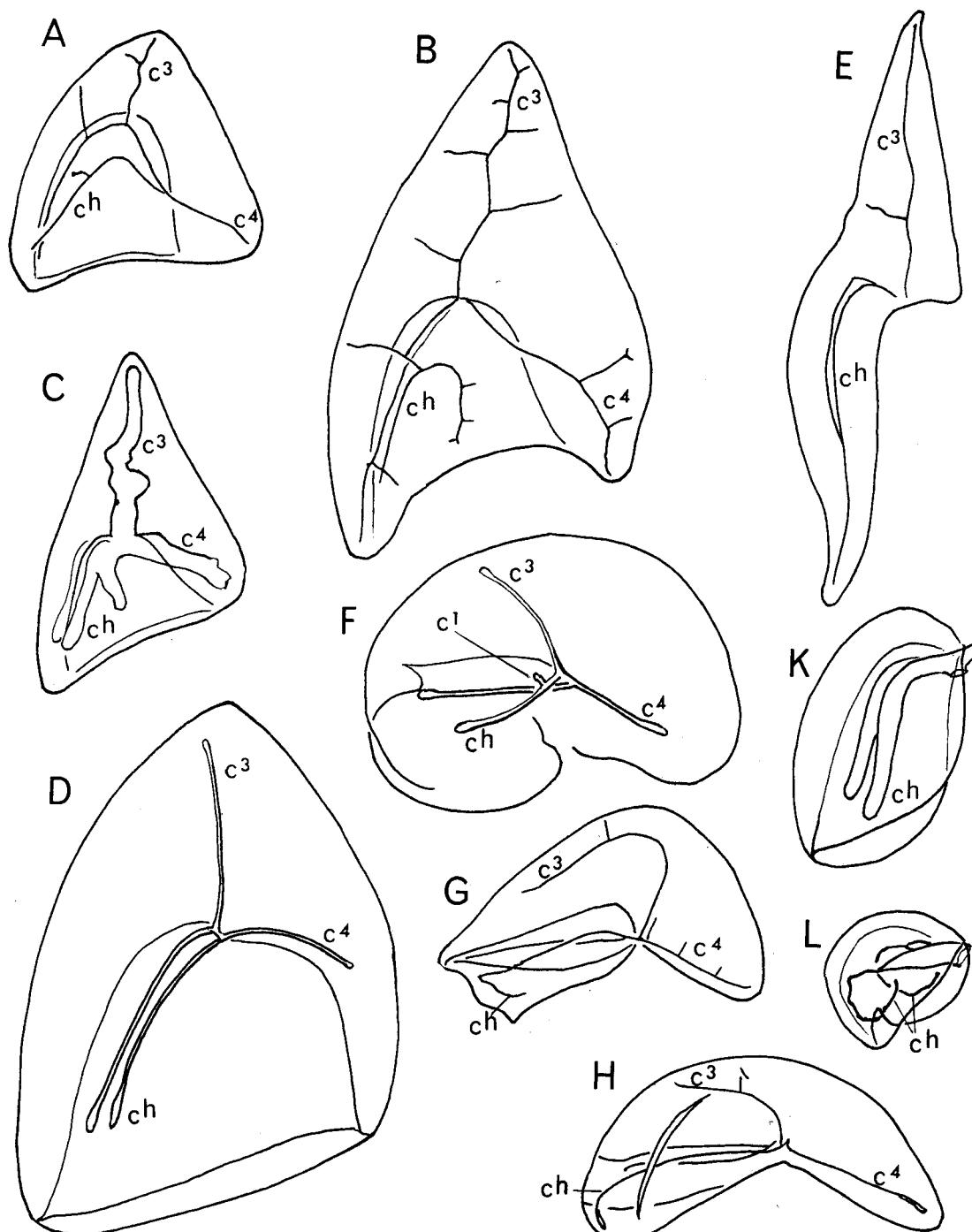


FIG. 74. Bracts of Prayidae
Some bracts of eudoxids to show how the branches of the bracteal canals may be homologized with one another:

- A, *Nectopyramis thetis* Bigelow (after Totton, 1954, fig. 36B), $\times 5.5$.
 - B, *N. diomedae* Bigelow, full grown bract (after Bigelow, 1911b, Pl. 1, fig. 5), $\times 3$.
 - C, *N. diomedae* Bigelow, juvenile bract (after Bigelow, 1911b, fig. A, p. 193), $\times 40$.
 - D, *N. spinosa* Sears, $\times 11$.
 - E, *N. natans* (Bigelow) (after Bigelow, 1911b, Pl. 20, fig. 6), $\times 3$.
 - F, *Rosacea cymbiformis* (Chiaje) (after Bigelow, 1911b, Pl. 2, fig. 4), $\times 15$.
 - G, *Praya reticulata* (Bigelow) (after Bigelow, 1911b, Pl. 3, fig. 6), $\times 3$.
 - H, *P. dubia* (Q. & G.), $\times 3$.
 - K, *Amphicaryon acaule* Chun (after Bigelow, 1911b, Pl. 4, fig. 5), $\times 50$.
 - L, *Maresearsia praecleara* Totton (after Totton, 1954, fig. 48A), $\times 9$.
- c.h = hydroecial canal; c¹ = spur canal; c³ = dorsal canal; c⁴ = ventral canal.

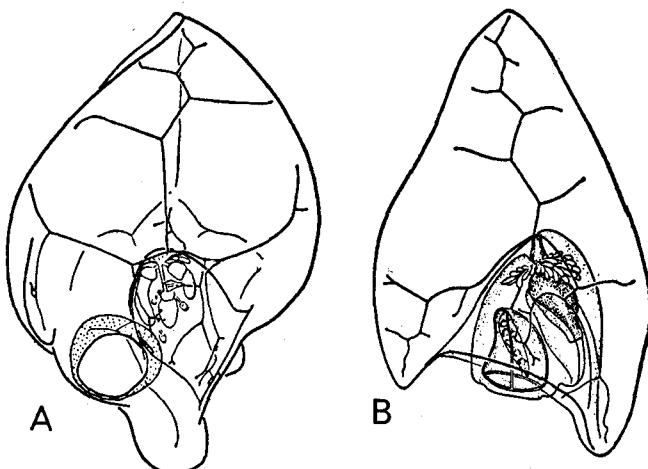


FIG. 75. *Nectopyramis diomedaeae* Bigelow
A, Polygastric phase, $\times 2.9$ and B, eudoxid phase, $\times 2$
(from Totton & Fraser, 1955).

Polygastric phase

Nectophore (text-fig. 75A): Rhomboid-ovate in outline, somewhat lens shaped, rather flatter on the dorsal side than the ventral, thin and pointed apically, up to 4.5 cm in length. The rather small nectosac with straight radial canals lies below with its ostium opening somewhat to the dorsal side. A little above the level of the nectosac or overlapping it is the deep, pocket-shaped hydroecial cavity. It opens by a curved slit-like ostium on the right edge, which here forms a narrow facet. The ostium is flanked by two ridges ending below in angular prominences. Below the lower lip of the ostium is a small flattened basodextral facet, bounded by two ridges, each with a basal angular process. The facet comes to a point below and is triangular in section. Into its mesogloea projects the basal end of the inferior branch of the pallial canal. The outline of the hydroecial cavity in optical section is flared at the ostium. Above it the dextral edge of the nectophore forms a fin-like ridge in some specimens. This runs right round the apical end and other side to terminate in an angular baso-sinistral prominence at the side of the nectosac. On the dorsal side in particular in some nectophores an apico-basal, rounded ridge can be seen, which bifurcates round the base of the nectosac. A lack of really well preserved specimens prevents a more complete description.

The complex somatocyst-canal-system, which is not always quite so complex as in the specimens figured by Bigelow (1911b) and Totton (1954) consists principally of a curved median pallial canal that runs round the apex of the hydroecial cavity at the point where the nectophore is attached to the stem, and then descends past the pedicel and radial canals of the nectosac to enter the baso-ventral prominence. The upper branch of this pallial canal is represented by the canal labelled by Bigelow (1911b) and Totton (1954) C.pa³. This canal, after giving off a downward branch on each side of the hydroecium ascends towards the apico-ventral angle of the nectophore. A second branched canal, C.pa², ascends from the apex of the hydroecium to the apex of the nectophore. A third, C.pa¹, runs out to the left edge of the nectophore.

During its phylogeny the nectophore of this species has become twisted and asymmetrical. Just what has happened it is not at all easy to deduce. But it looks as if figure 1 of plate I of Bigelow (1911b), and figure 2 of plate V of Totton (1954) show the dorsal side. The ostium of the hydroecial cavity seems to have become twisted round 90% to the right, and the original course of canal C.pa³ readjusted. Assuming that this is what has happened one can now attempt to homologize the canal systems of *N. thetis* and *N. diomedaeae*. Reference to figure 2 of Bigelow (1911a) shows the dorsal surface of *N. thetis* (polygastric phase). We see the longitudinal pallial canal extending from above

down beyond the radial canals of the nectosac. On either side is given off a right and left 'dorsal somatic canal'. Each sends a branch to the flank of the hydroecial cavity.

In *N. diomedae* I homologize Bigelow's C.pa³ with C.D.R. (right dorsal canal) in *N. thetis*, and his C.pa¹ with C.D.L. in *N. thetis*. In *N. diomedae* the right hand canal C.pa³ sends branches to both sides of the twisted hydroecium, and the left branch sends only small ones.

Eudoxid phase (Plate XXIII, figure 5; Text-fig. 75B.)

The large, flattened, triangular bract of the eudoxid in general somewhat resembles the polygastric nectophore and may be as much as 3·3 cm in length. Bigelow (1911b) figured both an early growth-stage and a mature one. In the former (fig. A, p. 193) is clearly typified the prayine pattern of branching of the somatocyst (text-fig. 74): a pair of hydroecial canals on the wall of the hydroecium, a ventral branch C⁴ on the opposite side, and dorsal branch C³. The hydroecial canals each give rise to a lateral branch. In later growth-stages all these branches rebranch in a complex way, the longitudinal ones asymmetrically. The large gonophore bears gonads in its manubrium, and is not an asexual swimming bell as in other species.

A well preserved eudoxid taken at 'Discovery' St. 3272, TYFB, 1000-0 m on 27.vi.1955 has three ridges on the side shown by Bigelow (1911b) in his plate 1, figure 6.

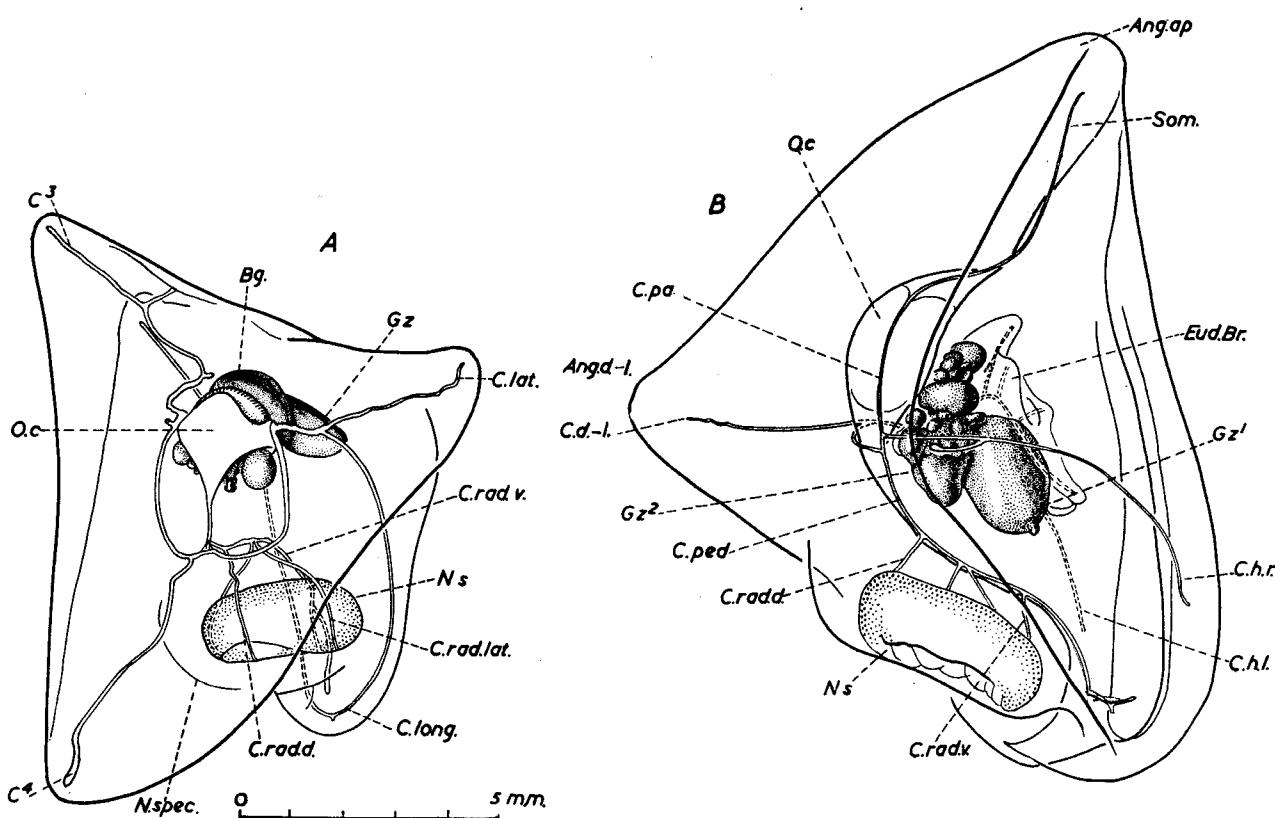


FIG. 76. *Nectopyramis thetis* Bigelow

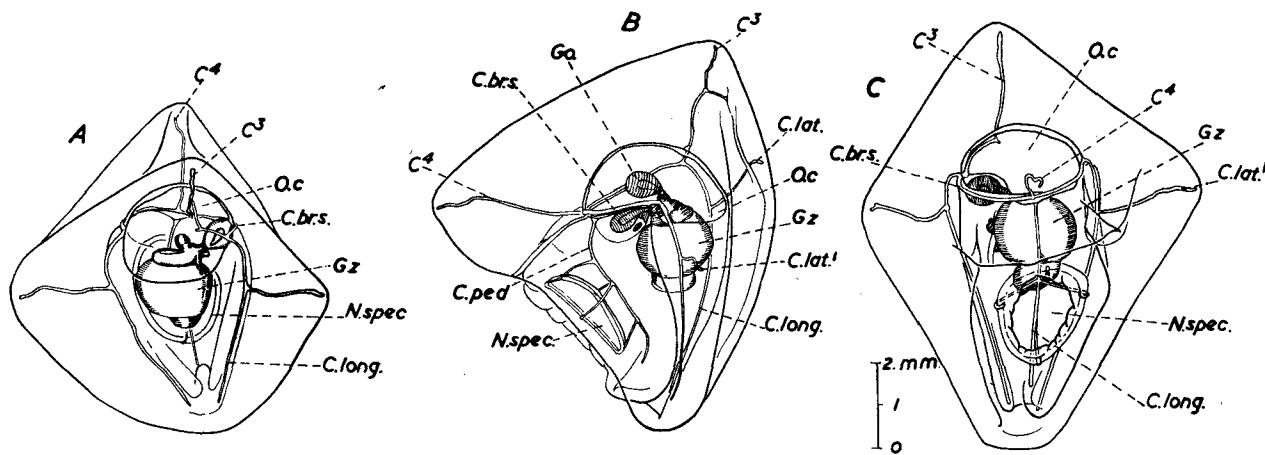
A, Eudoxid in dorso-lateral view, $\times 6.6$; B, Polygastric phase, dorso-lateral view, $\times 6.6$
ang.d-l = dorso-lateral angle; *Bg* = basigaster; *C³* = ascending canal; *C⁴* = descending canal; *C.br.s* = semi-circular bracteal canal; *C.d-l* = dorso-lateral canal; *C.h.r* = right hydroecial canal; *C.lat* = lateral canal; *C.lat¹* = branch of lateral canal; *C.long* = longitudinal canal; *C.pa* = pallial canal; *C.ped* = pedicular canal; *C.radd*, *C.rad.lat*, *C.rad.v* = dorsal, lateral and ventral radial canals; *Eud.br* = bract of eudoxid; *go* = gonophore; *gz¹, gz²* = gastrozooids; *Ns* = nectosac; *N.spec.* = special nectophore; *O.C* = central organ; *Som* = somatocyst (from Totton, 1954, fig. 37).

Nectopyramis thetis Bigelow, 1911

Text-figures 76, 77

Polygastric phase

Nectophore (text-fig. 76): The face opposite to the hydroecium, which may be called the dorsal face, is triangular, as may be seen in Bigelow & Sears, (1937) figure 2. But as shown in my figure 37B (Totton, 1954) this face can be seen to curve over below the level of the lateral angles into the face surrounding the nectosac. The deep hydroecium extends for the whole length of the nectophore. The upper median branch of the somatocyst or pallial canal extends up nearly to the apical angle, and the descending branch extends beyond the nectosac. Just below the level of the 'central organ' at the deepest part of the hydroecium a pair of hydroecial canals is given off to right and left. Near the origin of each arises a right and left dorsal canal running out to the prominent dorso-lateral angles. The four radial canals of the nectosac arise separately from one another.

FIG. 77. *Nectopyramis thetis* Bigelow. Eudoxid phase from Scotia St. 363

A, fore-shortened view from the dorsal end; B, lateral view; C, ventral view, $\times 5.5$ (for abbreviations see text-fig. 76)
(from Totton, 1954, fig. 36)

Eudoxid phase

(Text-fig. 77.) This also has two lateral, angular prominences and an apical angle. There is a very prominent 'central organ', which probably represents the remains of the piece of stem cut off when the eudoxid separated. At any rate I have ascertained that this is the origin of the central organ in *Rosacea plicata*. The canal system follows the usual prayine pattern, and consists of a dorsal canal C^3 , with a short branch to the surface, a pair of hydroecial canals, from each of which arises a lateral canal passing to the lateral angles, and on the opposite side a ventral canal C^4 . The four radial canals of the asexual swimming bell arise separately from the pedicular canal, which continues a little way beyond the nectosac.

Nectopyramis natans (Bigelow, 1911)

Plate XXVII, figure 4

Archisoma natans Bigelow, 1911b*Polygastric phase*

Nectophore (text-fig. 78): Only once recorded (Totton, 1954) the nectophore in general plan is not unlike those of species of *Rosacea*. But it is long-bow shaped, the hydroecium running the whole 2 cm of its length. It is pointed above, and truncated below. On the dorsal surface are three longitudinal ridges extending from the apex to the nectosac, which lies about a quarter of the total length above the truncate end. There is also a pair of lateral ridges extending the whole length. The simple

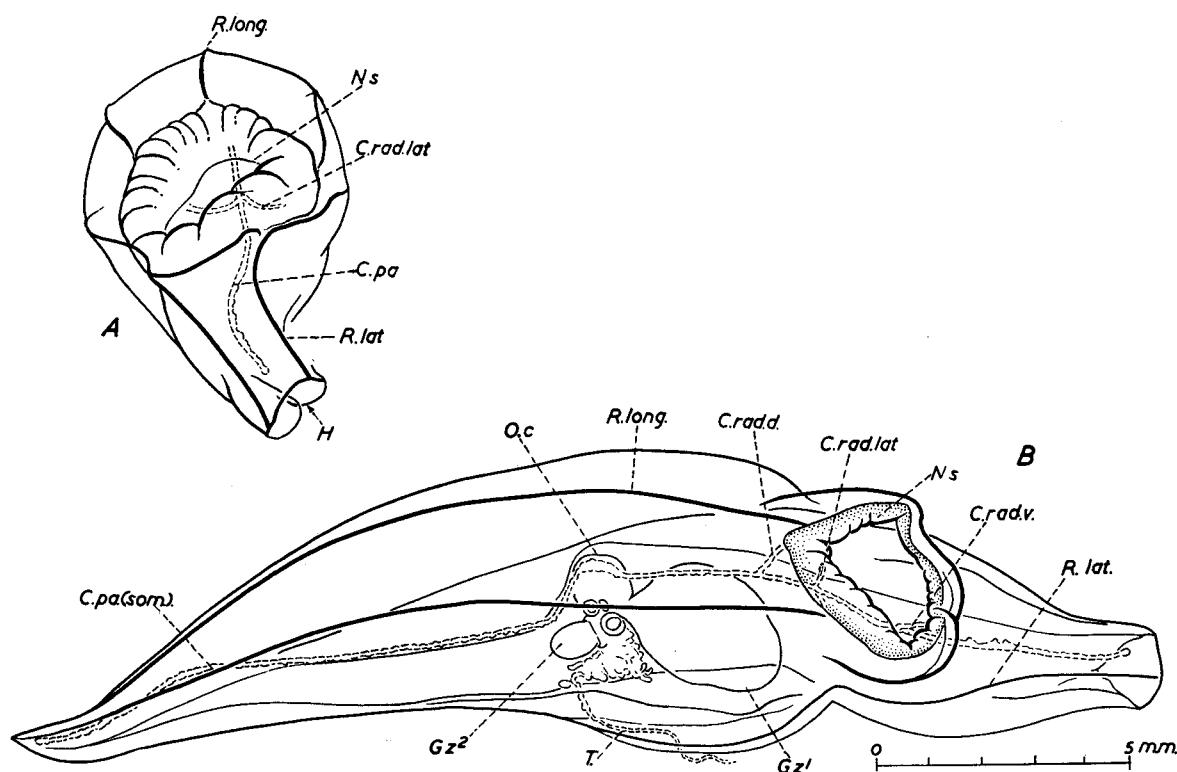


FIG. 78. *Nectopyramis natans* (Bigelow). Polygastric phase
A, fore-shortened view from the ostial end to show longitudinal ridges; B, dorso-lateral view, $\times 7$
 H = hydroecium; $R.lat$ = lateral ridge; $R.long$ = longitudinal ridge; T = tentacle; for other abbreviations see text-figure 76. (from Totton, 1954, fig. 38).

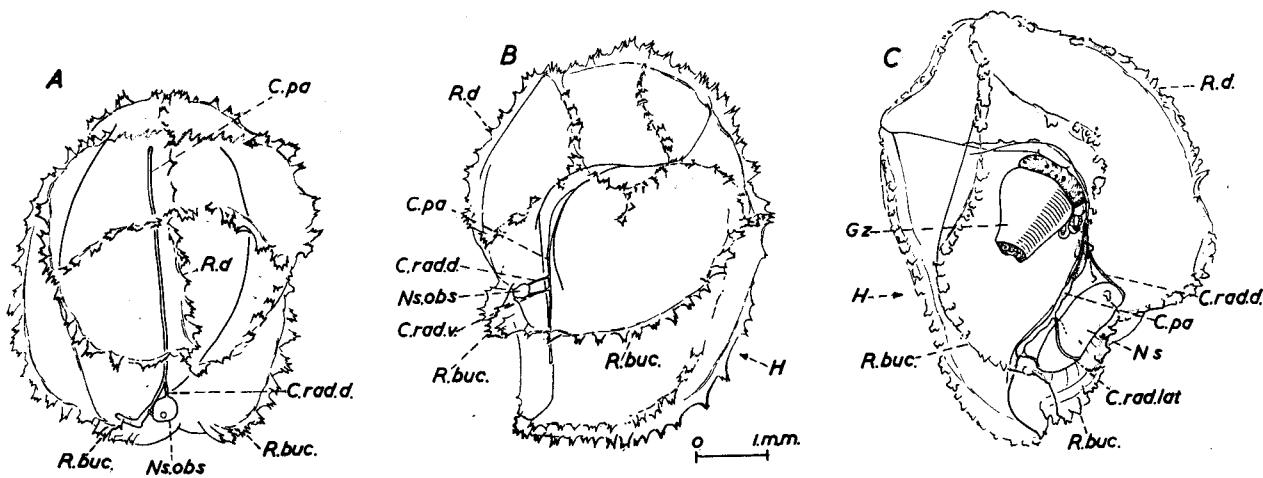


FIG. 79. *Nectopyramis spinosa* Sears. Polygastric phase
A, dorsal view; B, lateral view of the nectophore of the first type, with obsolescent nectophore, Scotia St. 363;
C, lateral view of a nectophore of the second type with a functional nectosac, 'Discovery' St. 1639, $\times 9.5$
 $C.pa$ = pallial canal; $C.rad.d$ = dorsal radial canal; $C.rad.lat$ = lateral radial canal; $C.rad.v$ = ventral radial canal;
 Gz = gastrozooid; H = hydroecium; Ns = nectosac; $R.buc$ = buccal ridge; $R.d$ = dorsal ridge (from Totton, 1954, fig. 40).

pallial canal or somatocyst extends from end to end. There is a sharp bend in its middle region round the central organ. The dorsal and ventral radial canals of the nectosac arise separately. The laterals arise opposite each other.

Eudoxid phase

The eudoxid, measuring about 54 mm in length has been described and figured by Bigelow, first in 1911b, then in 1919, and lastly in 1931. It is much elongated, triangular in section above the hydroecium which extends for little more than half its length, and is occupied by a very much elongated special swimming bell (asexual nectophore), with its nectosac in the middle of the outer, long, concave side. The pedicular canal, originates at the upper end and continues past the nectosac to the lower end. This special nectophore has a long hydroecial cavity. The radial canals of its nectosac arise as in that of the nectophore of the polygastric phase. The special nectophore measures about 31 mm in length. The bracteal canal-system is of the generalized prayine pattern. There is a long dorsal branch C³ giving off a short branchlet to the dorsal, slightly concave surface, which has two lateral, longitudinal ridges and a pair of hydroecial canals, one on each side of the hydroecium, which may unite below. But there are no spur canals and no branch C⁴. A bunch of small gonophores arises near the base of the gastrozoooid. The eudoxids are dioecious.

Nectopyramis spinosa Sears, 1952 Plate XXVII, figure 2

Hippopodius cuspidatus Moser, 1925

Hitherto two rather different types of nectophore have been described and figured (see Totton, 1954). I find that the one with the vestigial nectosac is the caducous larval one. I have found an early growth stage of the second type inside its hydroecium. The eudoxid which I describe below was hitherto unknown.

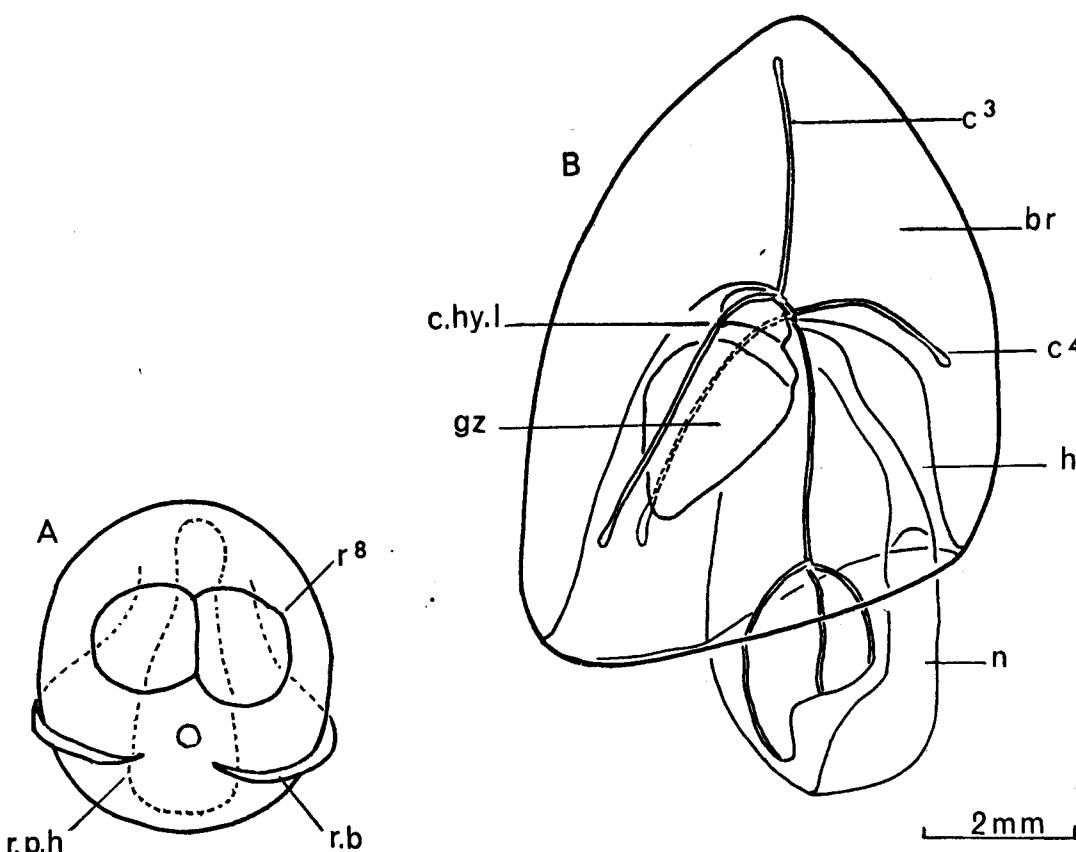
Polygastric phase

Nectophores (text-fig. 79): The larval one has a vestigial nectosac on one side, still supplied by two minute radial canals, which come off the pallial canal separately. The other type of nectophore has a larger, basal, functional nectosac whose radial canals come off separately from the lower branch of the pallial canal as in other species of *Nectopyramis*.

The nectophores of both types are characterized by the presence of a complex arrangement of spiny ridges, whose basic pattern (text-fig. 80A) I have been able to establish in one of the larval type. The hydroecial ostium is narrow, as in other larval types, and is edged by a spiny *peri-hydroecial* ridge. On the opposite side, just above the ostium of the vestigial nectosac is a horizontal *figure-of-eight* ridge. Running on either side horizontally from just below and outside the ostium of the nectosac, and bending up as they take their course towards the upper third of the perihydroecial ridge is a pair of *buccal* ridges. This is the basic pattern of ridges. Sometimes there are variants. The two buccals may almost meet at the ostium of the nectosac. There is often a connecting *dorsal* ridge joining the figure-of-eight and the peri-hydroecial ridges. Sometimes there is a *semi-circular* ridge between the figure-of-eight and the upper part of the perihydroecial. This arrangement was recognized in specimens from 'Discovery' Stations 4230 and 4254 both taken in the 'Young Fish Trawl' at 800 m.

Eudoxid phase

(Text-fig. 80B.) The bract, which measures 6 mm × 4 mm and is somewhat compressed laterally, is of the most generalized type found in the Prayidae; and can be homologized with the better known diphyid type. It has a deep hydroecial cavity, which has an oblique entire margin or ostium. The upper

FIG. 80. *Nectopyramis spinosa* Sears

A, Polygastric phase; schematic ostial view of the larval type nectophore to show the pattern of ridges; B, Eudoxid phase, hitherto unknown. Reconstruction of an eudoxid found in association with specimens of the polygastric phase at $31^{\circ} 00.5' N$, $116^{\circ} 37.5' W$, off the Mexican coast (Tebble coll.), $\times 16$

br = bract; *c³* = apical canal; *c⁴* = posterior canal; *c.hy.l* = left hydroecial canal; *gz* = gastrozooid; *h* = hydroecium; *n* = asexual nectophore; *r.b* = buccal ridge; *r⁸* = figure-of-eight ridge; *r.p.h* = perihydroecial ridge.

part is conical. The bracteal canal system is like that found in *Rosacea* species except that no spur canals are formed. There are two hydroecial canals running obliquely down one or either side of the dorsal wall of the hydroecial cavity. From the left-hand one of these arises the dorsal canal *C³* that does not send a branchlet to the surface, and there is present the usual ventral canal *C⁴*. The gastrozooid has a dark ring of pigment near the mouth; and the tentilla are well preserved. There is an asexual swimming bell. The small gonophores have long pedicels and mostly bear half-a-dozen large eggs.

Family 11, HIPPOPODIIDAE Kölliker, 1853

Hippopodiinae Kölliker, 1853

Polyphyidae Chun, 1882; Haeckel 1888b

Diagnosis: Calycophorae which may have a succession of up to twelve or more bells present at once, instead of the usual two. The stem is retracted up amongst the bells. In all species spines or protuberances are present at some stage, whether these are three serrations only as in *V. serrata* or two low protuberances as in *V. glabra*, but they tend to be less conspicuous in the later stages. In the ventral radial canal there is in young growth stages a large *rete mirabile* (dilation) which is smaller and perhaps absent in older ones. The cleft below the nectosac through which the muscular lamella

of the neighbouring bell protrudes varies in shape with the age and position ^{on} of the colony. The division into genera is not very sound: there is a single species of *Hippopodius* and four commonly called *Vogtia*. The stem-groups do not separate as eudoxids.

Hippopodiids are probably closely related to prayids. The definitive, heteromorph nectophores of hippopodiids resemble the larval type, common to both these families, in that there is no downward prolongation of the pallial canal beyond its junction with the pedicular canal of the nectosac. Hippopodiids have no bracts on the stem-groups. Sufficient buoyancy must be provided by the exceptionally thick, gelatinous mesogloea of the nectophores.

Chun (1897a) gave a good account of the relations between nectosome and siphosome. Owing to the fact that the upper part (nectosome) of the stem is deflexed and turned around the lower part (siphosome) in wide spiral turns, there would be little room for bracts in the comparatively narrow cylinder so formed when the siphosome is retracted into it (see Haeckel, 1888b, Pl. 29, fig. 7).

In hippopodiids, as probably in all Calycophorae, the larval budding zones (for nectosome and siphosome) remain close together, and growth proceeds in opposite directions, outwards from this point. By contrast in physonects growth proceeds in the same direction for each zone, so that in the Physonectae the two zones become separated by the length of the nectosome, the nectosomal zone being carried upwards relative to the other growth zone.

The history of the treatment and nomenclature of the family was given by Haeckel (1888b).

Genus: **HIPPOPODIUS** Quoy & Gaimard, 1827

Monotypic genus for *Hippopodius hippocampus* (Forskål, 1776).

I see no adequate reason for thinking that *Hippopodius hippocampus* should be regarded as generically distinct from *Vogtia* spp., but for the sake of maintaining stability in nomenclature I refrain from using one generic name for the five species, in spite of the fact that Schneider (1898) and Moser generally did so.

Hippopodius hippocampus (Forskål, 1776)

Plate XXVIII, figures 1-2; Plate XXIX, figures 1-3

Gleba hippocampus Forskål, 1776

H. neapolitanus Kölliker, 1853

Polyphyes unguilata Haeckel, 1888b

H. luteus Leloup, 1933

There have been many descriptions of the general morphology of specimens of this species and of their development. The sequence of developmental stages can be followed in the following sequence of figures: Metschnikoff (1874, Pl. XI, figs. 5-8); Chun (1888b, Pl. 2, figs. 1-3); Moser (1924a, Pl. 3, fig. 2); Chun (1913, figs. 5, 6; 1897a, figs. 6b, 6c; and 1913, figs. 7, 8). The relationship between the two budding zones in the fully developed animal was best illustrated by Chun (1897a, fig. 11) and Richter (1907, Pl. 28, fig. 27).

Nectophores: The larval nectophore is shed and its place taken by a series of secondary heteromorph ones, none of which are normally shed. The definitive nectophore (text-fig. 81, 1a-c) is horse-shoe shaped, up to about 19 mm in width, with four rounded dorsal knobs, varying in size and forming an arc above the ostium (see Bigelow & Sears, 1937, text-figs. 15-19). In life, the nectosac is not flat as has been suggested, but utilizes a considerable volume of water in forming a propulsive jet (see Totton, 1954, p. 99).

There is a large *rete* of unknown function in the ventral radial canal of recently budded nectophores, which is smaller in size or invisible in older ones. In its endoderm are found very striking multilobate nuclei (see Münter, 1912). The lateral radial canals arise from the dorsal radial canal near the upper margin of the nectosac, and are not easily seen in preserved material, owing to the rolling-up of the margin of the nectosac, unless the specimen has been treated with magnesium chloride. The mesogloea is sensitive to stimulation, upon which it may become opalescent in colour, with a subsequent return to its normal transparency. This blanching is accompanied by luminescence, a phenomenon demonstrated to me by G. O. Mackie at Villefranche in 1964. Each nectophore as it grows in the hydroecium of its predecessor does a 180° turn on its long axis.

Gastrozooid and Tentacle: The gastrozooid is borne by a short pedicel; about as long as a nectophore, with a sub-spherical basigaster. The tentacle is very long with a long terminal filament. Tentillum long with ellipsoidal cnidosac (see Haeckel, 1888b, Pl. 29, fig. 8; Bigelow, 1918, Pl. 7, figs. 6, 7). The cnidoband is curved round till its apical end lies near the base. On each side lie four large ensiform cnidocysts.

Gonophores, both male and female, arise from a point on the stem close to the pedicels of the gastrozooids. At maturity they break away and swim freely. In my own experiments, the female gonophores always swam directly downwards, indicating that the early stages of development take place in deep water. None of my many attempts to fertilize the eggs have been successful. Only Metschnikoff (1874) has achieved this. The manubria of the gonophores protrude freely from the ostia of the little medusac, which of course represent the adult phase of the animal.

Genus: *VOGTIA* Kölliker, 1853

For the history of the use of this generic name see Bigelow, 1918, pages 403–5. Bigelow maintains that species of this genus differ from the only species of *Hippopodius* in having an early growth stage of the cnidoband of the *tentillum saccus* in which it is coiled up. This is admittedly an almost universal phenomenon. In *H. hippocampus* the earliest growth-stage depicted by Bigelow (1918, Pl. 7, fig. 6) is also almost universally found. But in *H. hippocampus* the cnidoband is too short to coil up before it takes on its mature form. In my view this is a minor matter of degree and not one of generic importance.

Though Schneider and Moser both justifiably united *Vogtia* with *Hippopodius*, I am retaining *Vogtia* in order not to confuse further those who have to search the literature. There are four species. Bigelow & Sears (1937) defined their use of the name *Vogtia*. But in *V. pentacantha* there are sometimes spines around the base of the median dorsal prominence, so that the facets are not entirely smooth. There is a good deal of variation in the amount and kind of spinosity from specimen to specimen, and probably from the first to the last of a series of nectophores budded by any one specimen.

Vogtia spinosa Kefferstein and Ehlers, 1861

V. pentacantha Bigelow, 1918, plate 4, figure 1 (*non V. pentacantha* Kölliker, 1853)

A species with angular nectophores and spines on the facets as well as on the ridges. Organization is characteristic of all hippopodiids.

Definitive nectophores (text-fig. 81, 3): Short pentagonal prisms, the largest about 20 mm broad. The gelatinous tubercles or spines occur closely crowded not only on the ridges but on the lateral and dorsal facets. The oldest nectophores may be lacking spines. In young nectophores the *rete* in the ventral radial canal covers most of the upper surface of the nectosac, but later on in growth it decreases in size and may form two lateral wings (see Bigelow 1911b, Pl. 15, fig. 9). The nectosac is relatively large.

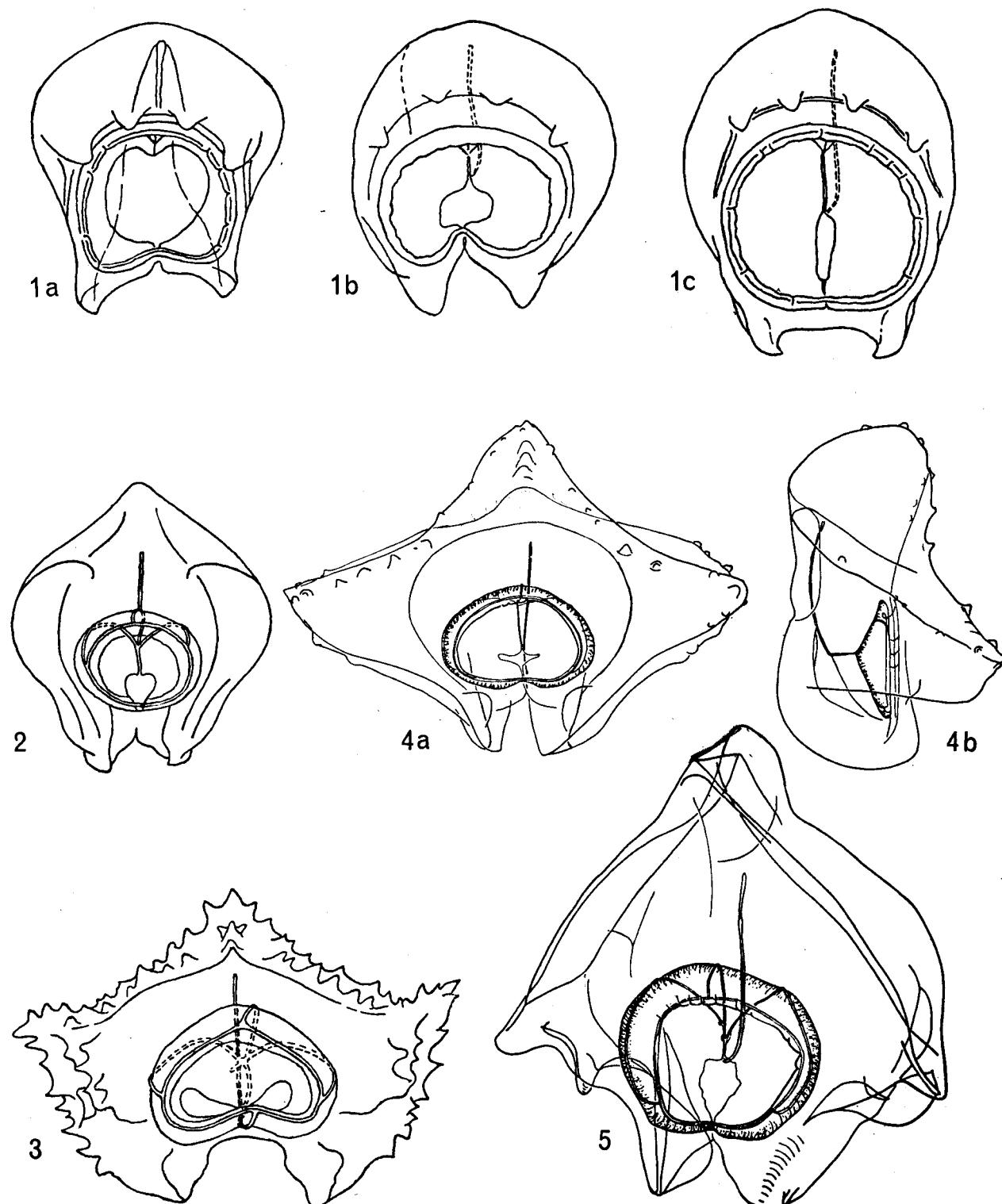


FIG. 81. Nectophores of 1. *Hippopodius hippopus* (Forskål), a–c, dorsal views, a, 8 mm, b, 10.5 mm, c, 19 mm. 2. *Vogtia glabra* Bigelow. 3. *V. spinosa* Kefferstein & Ehlers. 4. *V. pentacantha* Kölliker, a, dorsal, b, side view. 5. *V. serrata* (Moser).

Figures 1a, b, c, after Bigelow & Sears (1937); figure 2, $\times 2.7$ after Bigelow (1918); figure 3, $\times 3.5$ after Bigelow (1911b); figures 4a, b, $\times 6$; and figure 5, $\times 5.7$ from Totton & Fraser, 1955.

Both ♂ and ♀ gonophores are present in each cormidium. The tentilla vary from bright yellow to brick-red in life.

***Vogtia pentacantha* Kölliker, 1853**

This species is at once distinguishable from *spinosa* by the general absence of spines from the facets of the nectophores at all stages of development. Occasionally spines are found around the base of the median dorsal prominence. Otherwise the facets are entirely smooth.

Definitive Nectophores: Kölliker's (1853, Pl. VIII) figures 2 and 6 were badly drawn. For a more accurate representation see (text-fig. 81, 4a, b). Spines are found only on the edges of facets. The frontal-lateral wings have flat upper facets. The nectosac is relatively small.

***Vogtia serrata* (Moser, 1925)**

Plate XXVII, figure 3

V. pentacantha: Bigelow, 1913, plate 5, figures 7, 9 (*non V. pentacantha* Kölliker, 1853)

The large smooth, triangular nectophores of this species are easily recognized.

Definitive nectophores: Large, smooth and triangular, with hollows under the lateral corners (text-fig. 81, 5).

***Vogtia glabra* Bigelow, 1918**

Definitive nectophore: There are only two rounded prominences above the ostium (text-fig. 81, 2). Young nectophores are usually somewhat pointed, and their prominences more marked.

Family 12 : DIPHYIDAE Quoy & Gaimard, 1827

Galeolariinae Chun, 1897

Muggiinae Bigelow, 1911b (pars)

Diphyinae Moser, 1925

Bigelow (1911b) made a classical review of this family. The history of the treatment of members of the family will be found therein, as well as numbers of beautifully drawn figures and descriptions. He dealt with eleven of the thirty-nine forms now known. Moser (1925) wrote about the family at considerable length – some 250 pages – and described four new species, one of which is confined to the Antarctic. She dealt with nineteen of the thirty-nine forms we know to-day. Since then there have been no comprehensive reviews.

In earlier days calycophores which had two rather similar nectophores were called 'diphyids'. To-day we group together, because of the possession of a number of characters, thirty-nine species, some of which do not bud off a posterior nectophore. They are at present arranged in seven genera.

The first genus, *Sulculeolaria*, is separated off to form a monotypic sub-family, *Sulculeolariinae* (Totton, 1954). The old name *Galeolariinae* had regrettably to be changed when it became evident that *Sulculeolaria* and *Galeolaria* – itself changed by Stechow to *Galletta* – were synonymous.

Five of the other diphyid genera are treated as members of a sub-family *Diphyinae* which is a synonym of the older name *Diphyopsinae* Haeckel.

A seventh, monotypic genus, *Dimophyes*, which seems to be related to the diphyids, was regarded by Moser as forming a monotypic family, *Dimophyidae*.

The increase in the number of species known to-day is largely accounted for by additions to the number of species of *Lensia*, consisting of small specimens which had been overlooked previously.

I have separated off half-a-dozen mid-water forms, formerly regarded as diphyids, into a new family, Clausophyidae. Bigelow (1913) had already taken the first step when he set up a new sub-family, Clausophyinae, for *Clausophyes ovata* and *Cl. galeata*.

Sub-family i: SULCULEOLARIINAE Totton, 1954

Galeolarinae Chun, 1897b

Galettinae Stechow, 1921

Monotypic sub-family for *Sulculeolaria* Blainville, 1830.

Eudoxids of this sub-family have never been taken in plankton hauls, but they were set free from *S. quadrivalvis* in the aquaria of Miss M. J. Delap of Valencia, Ireland, who made many unpublished observations and drawings of siphonophores and other marine invertebrates from 1900–1930. Failure to release the eudoxids seems to be a primitive feature, found in what are now considered to be the more primitive siphonophores.

In the polygastric phase there is often a succession of both anterior and posterior nectophores, though it is only occasionally that a specimen is found bearing more than one anterior nectophore at a time. This phenomenon also appears to be an atavistic one.

Six species of the single genus *Sulculeolaria* are now recognized. A few species hitherto included under the old name *Galeolaria* have now been generically associated with *Lensia* spp.

Genus: SULCULEOLARIA Blainville, 1834

Galeolaria Blainville, 1830 (preoccupied Lamarck, 1818)

Galetta Stechow, 1921; Totton, 1932; Bigelow & Sears, 1937

Type species: *Sulculeolaria quadrivalvis* Blainville, 1834 (figured).

I have already dealt definitively with both the zoology and nomenclature of this genus (Totton, 1954, p. 101). My 1932 review was a tentative one. As Bigelow (1918) remarked: 'Successive studies progressively clarify the situation.' On Bigelow's work we chiefly depend.

Blainville's generic description of *Galeolaria* referred to fairly firm gelatinous, regularly and bilaterally symmetrical, sub-polygonal or oval animals, that each have a large posterior ostium; a velum and a two-winged sub-ostial lamella; a muscular sub-umbrella occupying much space inside; and a stem, borne on the anterior-superior face, that issues from a bilabiate hydroecium. This makes quite clear what genus of large diphyids he was dealing with.

In all the species of *Sulculeolaria* the lateral canals of the posterior nectophores make a loop from base to apex and back to the velar ring-canal, in contrast to the unlooped canals in species of *Lensia*. The surface of the anterior nectophore is always smooth and rounded rather than longitudinally ridged as in most other diphyids.

Sulculeolaria quadrivalvis Blainville, 1834

Plate XXIX, figure 4; Plate XXX, figures 1–4; Plate XXXI, figures 1–3; text-figure 82

Sulculeolaria quadridentata Quoy & Gaimard, (1833) 1834

Epibulia aurantiaca Vogt, 1851

Diphyes quadrivalvis Gegenbaur, 1853

Galeolaria aurantiaca Vogt, 1854

Galeolaria quadrivalvis Lens & van Riemsdijk, 1908; Bigelow, 1911b; Moser, 1925

The question whether *S. quadrivalvis* and *S. quadridentata* are synonyms of one and the same species was reviewed by Bigelow & Sears (1937) and by Totton (1954). I am of the opinion that they are synonyms.

My view is based on the fact that there is a great deal of variation of the denticulation round the ostium of the anterior nectophore, and that it is not a question merely of the number of teeth but the degree to which the dentate character appears, if at all.

The name *quadrivalvis* used to be applied (see Bigelow & Sears, 1937, p. 30) to anterior nectophores with only two dorsal ostial teeth, and *quadridentata* to those with two lateral as well as two dorsal teeth. After examination of hundreds of specimens from different areas I consider that these characters are not clear-cut, and that intermediate conditions are to be found (see Totton, 1932, p. 342), as well as specimens in which no lateral teeth are developed. All varieties are associated with indistinguishable posterior nectophores.

The species was well described and figured by Vogt (1851 as *Epibulia aurantiaca*) and by Gegenbaur (1853b). The whole living animal was first described by Vogt (1854) as *Galeolaria aurantiaca*.

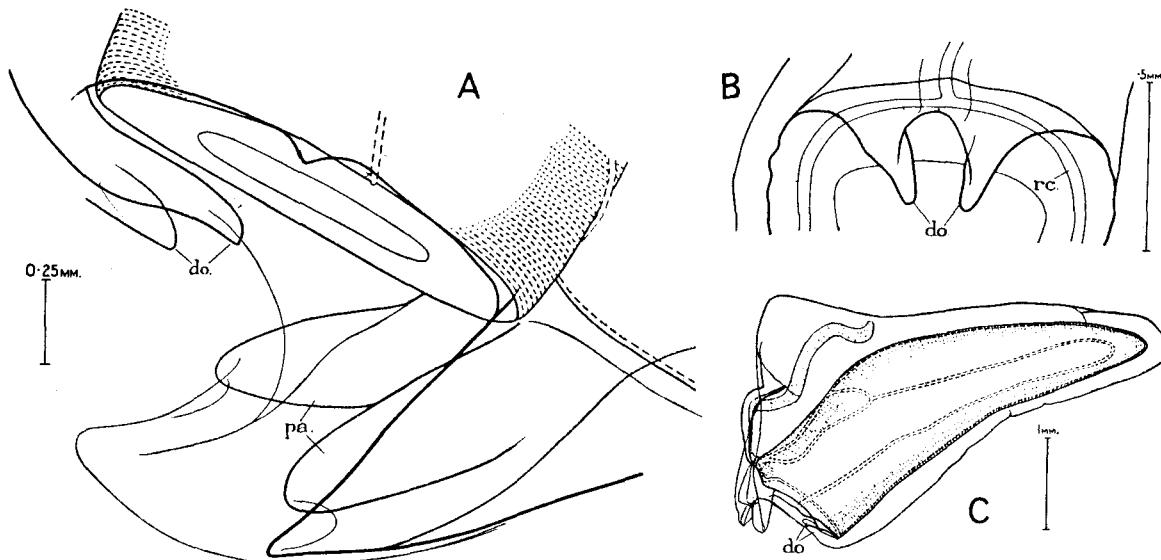


FIG. 82. *Sulculeolaria quadrivalvis* Blainville

A, base of the anterior nectophore, $\times 45$; B, ostial view of the nectosac, $\times 45$; C, lateral view of the anterior nectophore, $\times 12$, in the position for horizontal progression

do = dorsal teeth; *pa* = vertical pads on the inner sides of the two lamellae of the mouth-plate; *rc* = circular canal (from Totton, 1932, fig. 19).

Polygastric phase (Pl. XXX)

Anterior nectophore (see Bigelow, 1911b, Pl. 5, fig. 2; 1918, figs. 195–97; and text-fig. 82): Up to 18 mm long, not ridged, a feature common to all species of the genus. The somatocyst is long and fine reaching up to the middle of the dorsal side. Round the ostium there may be from two to four teeth of varying size. There are two baso-ventral wings (see Bigelow, 1911b, Pl. 5, fig. 4, not numbered on the plate). There is a deep division between the two wings (or halves of the mouthplate), not just a marginal notch. On the inner margins of the basal wings is an oval shaped pad with a vertical face. The course of the radial canals of the nectosac was described by Gegenbaur (1853b). Plate XXIX, figure 4 shows the budding zone of a specimen with one bud of an anterior nectophore and two other indeterminate buds.

Posterior nectophore (see Bigelow, 1911b, Pl. 5, figs. 1, 3): Up to 19 mm long. The nectosac has two characteristic constrictions at right angles to one another. There are two baso-ventral wings, and two large lateral and two dorsal teeth round the ostium.

M. Claude Carré has shown me sketches which he made on October 31, 1962, of a specimen bearing a short stem without gonophores, taken at Villefranche. Within a period of six days the first pair

of nectophores was shed, a second and third anterior and one posterior had developed and were shed, and a fourth anterior one was budded.

Eudoxid phase

(See Vogt, 1854, pp. 114–16.) Male and female gonophores are borne on separate ‘colonies’, according to Vogt (p. 112). He figured the saccus of the tentillum, and examined twenty-five specimens. The gonophores, which are in fact the adults, break loose from the attached cormidia and swim freely for several days.

Colour (see Vogt, 1854, p. 115): Male manubrium vermillion, female colourless.

Sulculeolaria biloba (Sars, 1846)

Text-figures 83–86

Galeolaria australis Bigelow, 1911b, plate 5, figure 8; Bigelow, 1918

Sars gave accurate figures; the last review was by Totton (1954) where further accurate figures are to be found. There has been much confusion between this species and forms called ‘australis’ by certain authors, making futile a study of much of the literature. For example, Bigelow & Sears’ (1937) *Galettea australis* is *Sulculeolaria turgida*. I have re-examined the material.

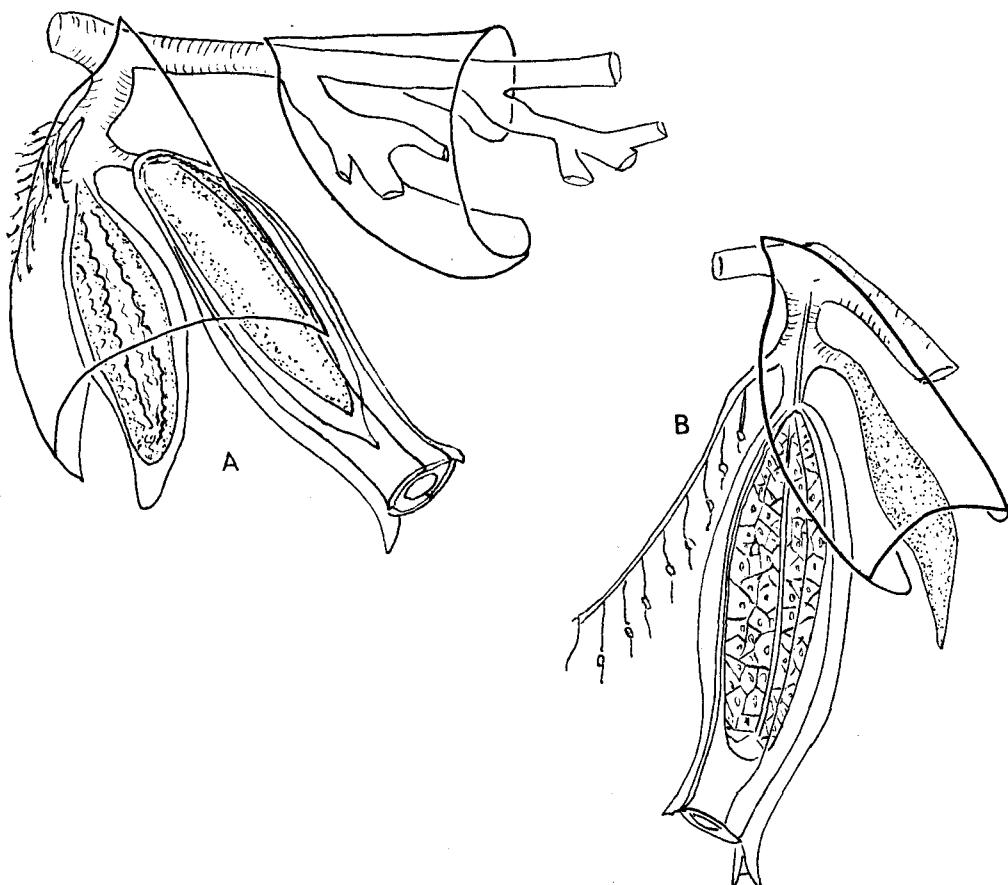
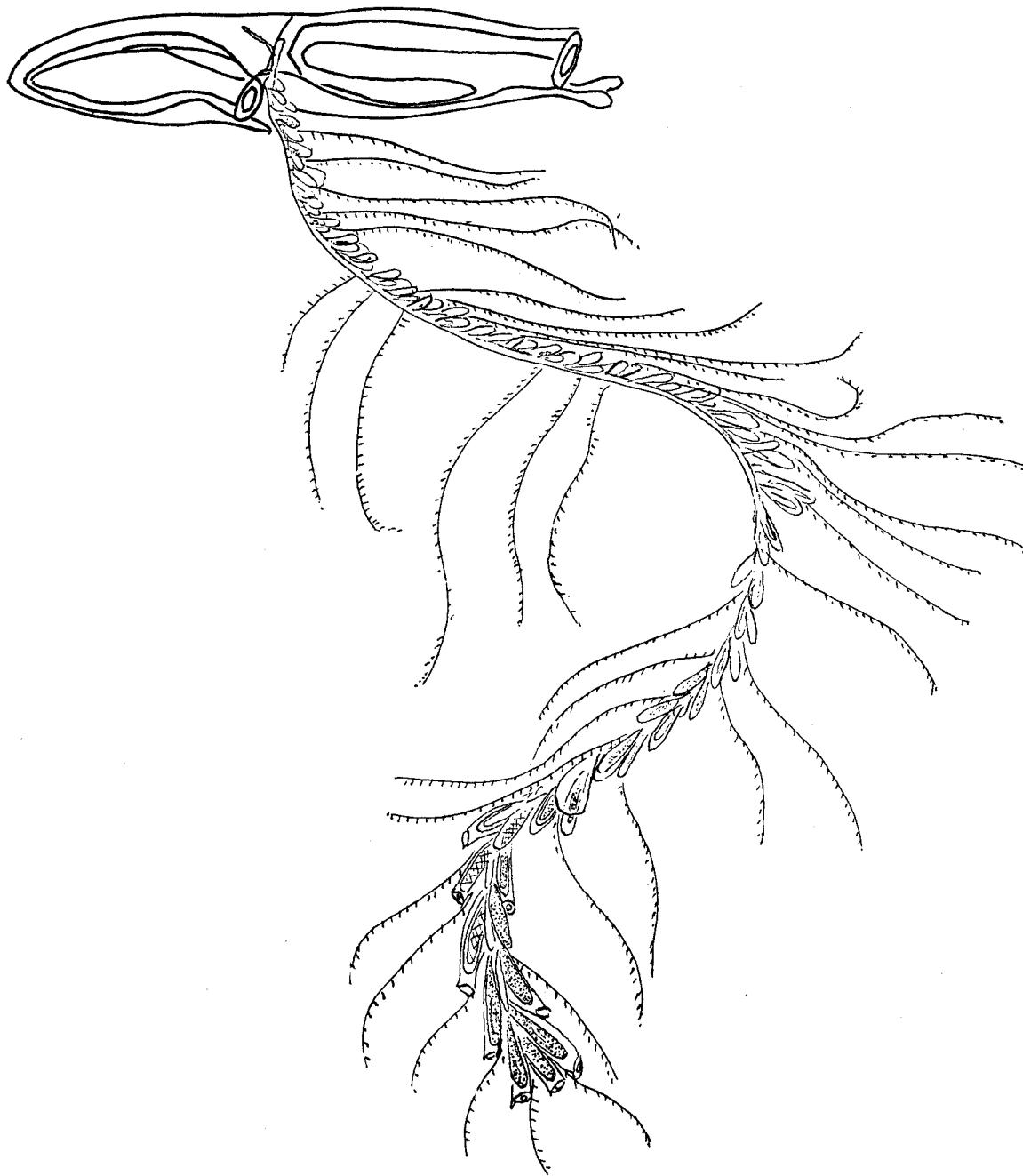


FIG. 83. *Sulculeolaria biloba* (Sars)

A, male and B, female stem-groups, $\times 10.4$. From pencil sketches from life by the late Miss M. J. Delap

FIG. 84. *Sulculeolaria biloba* (Sars)

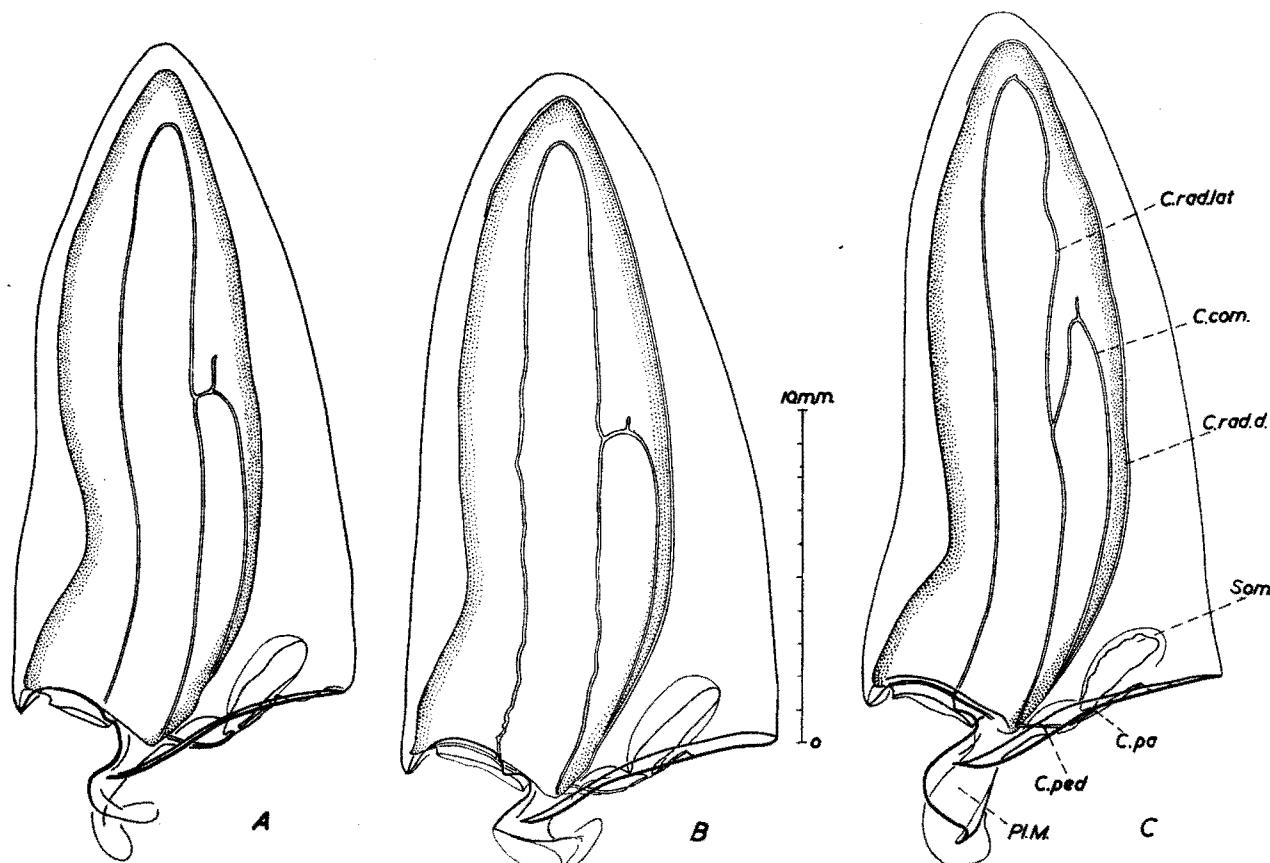
Original drawing of the whole polygastric phase, swimming, $\times 2.6$. From a pencil sketch by the late Miss M. J. Delap

Polygastric phase

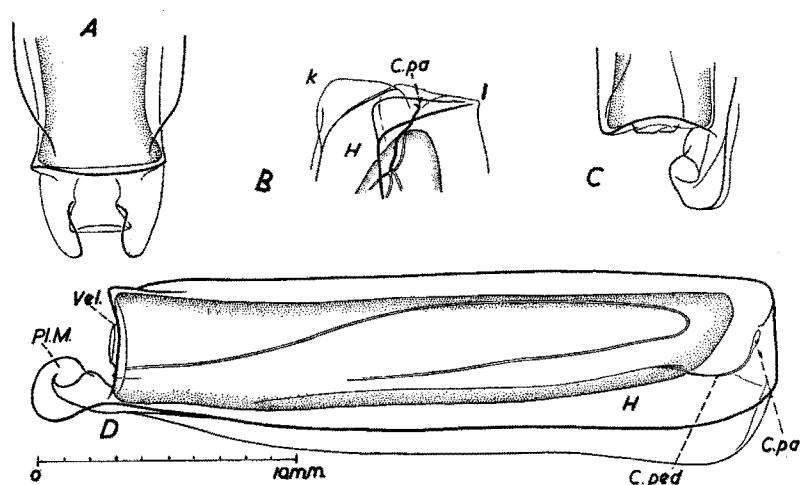
Anterior nectophore (text-figs. 84 and 85): Up to about 26 mm long. Somatocyst short, ovoid long axis oblique (in side view). There is a pair of commissural, lateral, radial canals running from a point close to the base of the dorsal radial to join the upward half of the looped lateral radial canals at mid-length of the nectophore.

I regret to find that a mistake was made in lettering and flagging my (1954) text-figure 50A: the lower pecked flag-lines to 'C.com' refer to ventral sides of the lateral radial canal loop.

Posterior nectophore (text-fig. 86): Up to 26 mm long and 6.5 mm wide. The upper end of the pallial canal, to which the posterior nectophore is attached, projects obliquely upwards into a small pocket in the base of the nectophore. This is a characteristic feature of the species (see Totton, 1954).

FIG. 85. *Sulculeolaria biloba* (Sars)

Three anterior nectophores from the Celtic Sea (M.B.A. Plymouth), A, B, C
C.com. = commissural canal; *C.pa* = pallial canal; *C.ped* = pedicular canal; *C.rad.d.*, *C.rad.l.* = dorsal and lateral radial canals; *Pl.m.* = mouth-plate; *Som.* = somatocyst (from Totton, 1954, fig. 49).

FIG. 86. *Sulculeolaria biloba* (Sars). Posterior nectophore from the Celtic Sea

A, C, dorsal and lateral view of the mouth-plate, $\times 2.5$; B, ventro-lateral view of the proximal end to show triangular articulating facets, $\times 3.5$; D, lateral view, $\times 3.5$

C.pa = pallial canal; *C.ped* = pedicular canal; *H* = hydroecium;
k-l = baso ventral sector; *Pl.m.* = mouth-plate; *Vel.* = velum (from Totton, 1954, fig. 51).

text-fig. 50). The detailed shape of the mouth-plate, which consists of two side pieces and a central thickening, is shown in figures A, C and D of the figure cited above.

There is a succession of buds. I have seen a pair, a larger posterior with a smaller anterior, as shown by Bigelow (1918, fig. 198). There was in addition a third rudiment on the base of the pedicel of the small anterior bud.

Tentilla: Of the basic calycocephoran pattern. The pedicel is folded concertina-wise in its distal part, next to the saccus. In the saccus it is continued by a single 'Angelband', also folded concertina-wise, larger in diameter distally where it is attached to the outer end of the saccus, at the junction of cnidoband, rowel (see 3 below) and terminal filament. There are three chief types of nematocysts, apart from those of the terminal filament:

	Length in μ	Diameter in μ
1. Two baso-lateral groups of three large ensiform	56–58	7–8
2. Small paliform, of cnidoband	19–24	3–5
3. Two bunches of three small pyriform nematocysts called the rowel, on branching fibre	9–11	7–8

Eudoxid phase – not identified

(See text-fig. 84 for stem groups.)

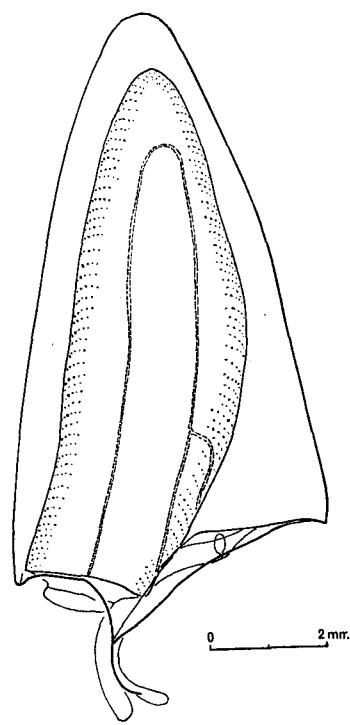


FIG. 87 *Sulculeolaria turgida* (Gegenbaur)
Anterior nectophore from the Adriatic.

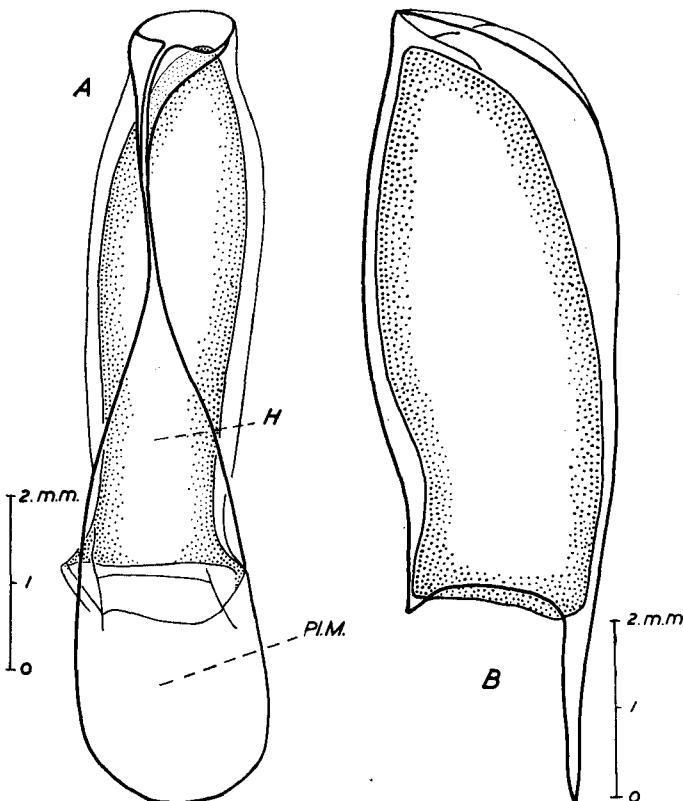


FIG. 88. *Sulculeolaria turgida* (Gegenbaur)
Posterior nectophore from 'Discovery' St., 1581, $\times 11$.
A, ventral view; B, lateral view.
H = hydroecium; PLM = mouth-plate (from Totton, 1954,
fig. 52).

***Sulculeolaria turgida* (Gegenbaur, 1853)**

Plate XXXI, figures 8-9

Diphyes turgida Gegenbaur, 1853b, page 344, Taf. XVI, figures 12-21*D. turgida* Gegenbaur, 1854, page 442, Taf. XXIII, figures 1-8*Galletta australis* Bigelow & Sears, 1937, page 35*Sulculeolaria turgida* Totton, 1954, page 107, text-figure 52

There was formerly doubt (see Bigelow & Sears, 1937) about this species, whose identity has been confused with that of other species, particularly '*Galeolaria australis*', including many forms from the Atlantic and Indian Oceans. Many specimens have been identified in recent years, following the capture of well preserved material from the Adriatic by Dr. T. Gamulin.

The most distinctive feature is the rounded and undivided basal lamella of the posterior nectophore (see Totton, 1954, text-fig. 52). The tiny somatocyst of the anterior nectophore can easily be overlooked (see Sears, 1950). It was not figured by Gegenbaur.

Polygastric phase (Pl. XXXI, fig. 8)

Anterior nectophore (text-fig. 87): With a very small somatocyst. Commissural canals are present. At the moment a description, that would distinguish it from the nectophore thought to belong (by association) to *S. angusta*, cannot be given unless it is the constant presence of commissural canals.

Posterior nectophore (Pl. XXXI, fig. 9; text-fig. 88): About 9 mm long, 2 mm wide, 3 mm deep, deeper, dorso-ventrally than wide with a 2 mm-long, thin, rounded, undivided mouth-plate. No lateral wings.

Eudoxid phase

Gonophores: Figured by Gegenbaur. Both sexes found on the same stem. Figures of developmental stages – egg to larva – were given by Gegenbaur (1853b, Taf. XVI, figs. 12-21) as *Diphyes sieboldi*, corrected to *D. turgida* on page 344.

***Sulculeolaria angusta* Totton, 1954**

Text-figure 89

The posterior nectophore is distinctive, but so far the anterior one cannot be distinguished from that of *S. turgida*, unless it proves never to develop commissural canals.

Polygastric phase

Anterior nectophore (text-fig. 89c): About 8 mm in length and 4 mm in depth. Somatocyst minute, but varying in size up to about 0.04 mm in length. The halves of the long mouth-plate have roundly pointed distal edges. No commissural canals.

Posterior nectophore (text-fig. 89a, b): Long and narrow 13.5 mm × 3.5 mm. Mouth-plate 3.25 mm long, thickened proximally with a small prominence in the lower edge of the thickening, thin and emarginate distally. In general shape the mouth-plate resembles that of *S. chuni* but is thicker proximally. No dorso-lateral ridge.

Eudoxid phase – not identified.

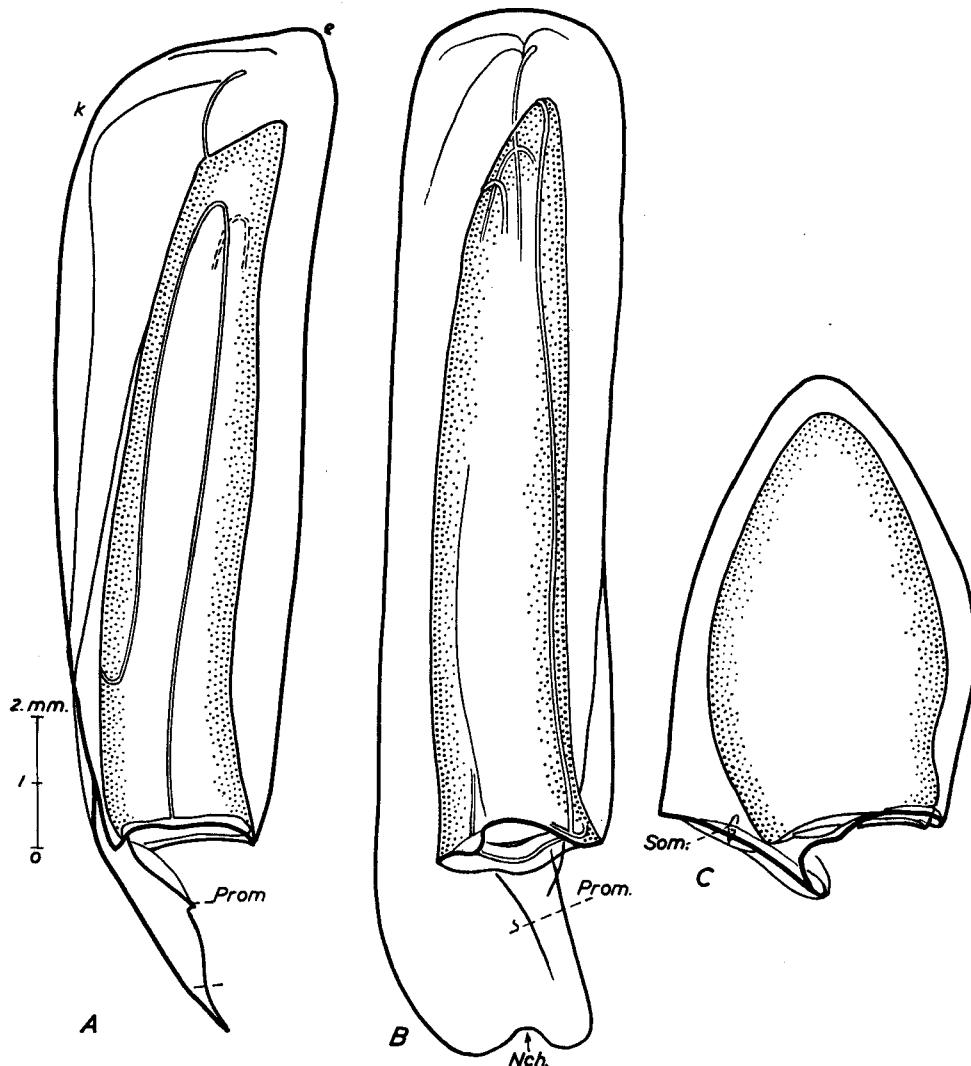


FIG. 89. *Sulculeolaria angusta* Totton. Polygastric phase
 A, B, lateral and dorsal views of the posterior nectophore, 'Discovery' St. 1586; C, lateral
 view of the anterior nectophore, Gulf of Aden, $\times 8.5$
Nch. = notch in the mouth-plate; *Prom.* = prominence on mouth-plate; *Som.* = somatocyst (from Totton, 1954, fig. 53).

***Sulculeolaria chuni* (Lens & van Riemsdijk, 1908)**
 Text-figure 90

Galeolaria chuni L. & v.R., 1908

Galella chuni, Totton 1932, text-fig. 20

Easily distinguishable by its possession of a long somatocyst and a thin emarginate lamella in the posterior nectophore.

Polygastric phase

Anterior nectophore: Up to about 6 mm in length \times 3 mm deep, without ostial teeth, with a long somatocyst (4 mm \times 0.3 mm). There are no commisural canals.

Posterior nectophore: Up to 9 mm long \times 2.75 mm deep, with thin emarginate mouth-plate or basal lamella, up to 25 mm long \times 2.75 mm wide. There are no dorso-lateral ridges.

Eudoxid phase – not identified.

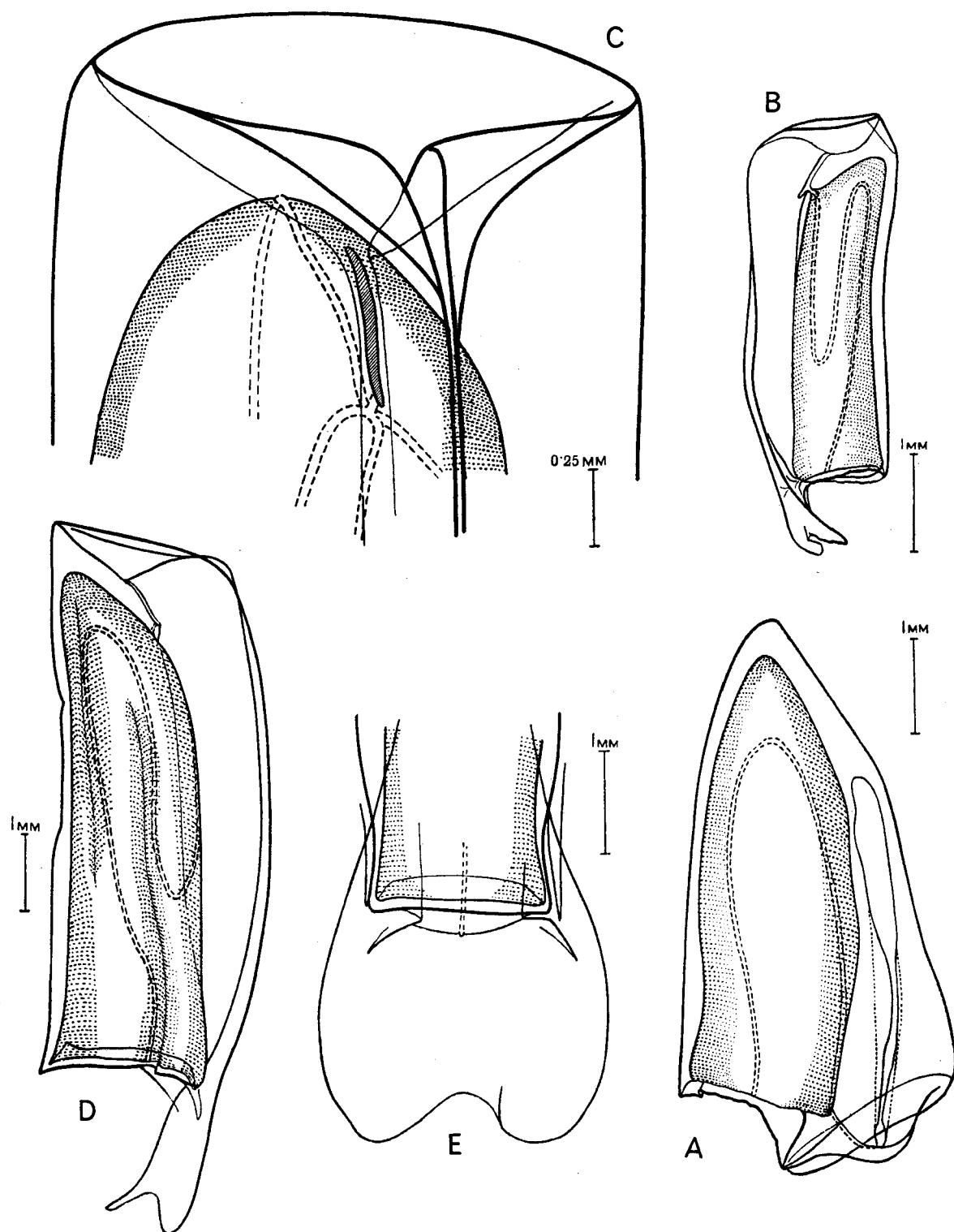


FIG. 90. *Sulculeolaria chuni* (L. & v. R.). Polygastric phase
 A, anterior nectophore, Gt. Barrier Reef, $\times 15.5$; B, posterior nectophore (apex damaged) Gt. Barrier Reef, C, ventro-lateral view of proximal part of the posterior nectophore from $6^{\circ} 10' N$, $24^{\circ} 5' W$, $\times 48$; D, lateral view of the same, $\times 12.5$; E, dorsal view of the mouth-plate of the same, $\times 17$ (from Totton, 1932, fig. 20)

***Sulculeolaria monoica* (Chun, 1888)**

Plate XXXI, figures 5-7, 10, 12

Epibulia monoica Chun, 1888b*Galeolaria monoica* Bigelow, 1911b, page 239, plate 6, figure 49

Easily distinguishable by the presence of three small dorsal teeth above the ostium in both nectophores in addition to a small pair of laterals. The somatocyst is minute.

Polygastric phase

Anterior nectophore (Pl. XXXI, figs. 5-6): Up to 10 mm in length \times 4.5 mm deep. Three fine dorsal and a pair of smaller triangular lateral teeth of varying size round the ostium. Somatocyst minute. Commissural canals present. Basal lamella or mouth-plate divided and bearing a pair of small teeth near the sagittal margin in the proximal part.

Posterior nectophore (Pl. XXXI, figs. 7, 10, 12): First described by Bigelow. Up to 10.1 mm long \times 0.35 mm wide. Ostial margin similar to that of anterior nectophore, with three dorsal and a pair of lateral teeth. Mouth-plate or basal lamella broadly truncate, with very slight emargination and two proximal teeth.

Eudoxid phase – not identified.***Sulculeolaria bigelowi* (Sears, 1950)***Galetta bigelowi* Sears, 1950

The only three known specimens consist of damaged anterior nectophores measuring from 3-4 mm in length. They were taken in the Marshall Islands.

Polygastric phase

Anterior nectophore: Apical and conical in both lateral and dorso-ventral views.

Somatocyst minute. Base very wide, and ventro-basal facet half as long as the nectophore, less mouth-plate, which is exceptionally wide. The ventral radial canal divides just before it joins the circular canal. No commissural canals present.

Posterior nectophore: Unknown.

Eudoxid phase – not identified.**Sub-family ii: DIPHYINAE**

In the polygastric phase of these Calyconects there are generally two nectophores, the posterior one sometimes reduced or suppressed altogether, of pentagonal cross-section, one placed behind the other. The anterior one is pyramidal; the posterior one either has a truncate forward end which articulates with the base of the anterior, or a prolongation which fits into the hydroecium.

Genus: *DIPHYES* Cuvier, 1817*Diphyopsis* Haeckel, 1888b

Type species: *Diphyes dispar* Chamisso & Eysenhardt, 1821, for *Salpa (bipartita) lancelota bipartita* Bory de St. Vincent, 1804, plate VI, figures 3A-C. Cuvier used no specific name.

There are four species of *Diphyes* (*sensu restricto* Totton, 1932); *dispar*, *bojani*, *chamissonis* and

antarctica. There is reason to believe that the anterior nectophore in these species is the larval one retained.

The anterior nectophore is five-ridged. Except in the isolated antarctic species, where the dorsal tooth is obscured, there are three conspicuous teeth round the ostium. The mouth-plate is undivided and the hydroecium deep. A posterior nectophore is produced except in *D. chamissonis*. There is a *rete mirabile* at the velar ends of all four radial canals of the anterior nectophores of *dispar*, *bojani* and *chamissonis*. It is found in a simpler form also in *antarctica*.

Polygastric phase

Species in which the large pentagonal anterior nectophore has a complete dorsal ridge extending from apex to ostium, three large ostial teeth and undivided mouth-plate with slightly prominent baso-lateral angles. Hydroecium deep. The lateral radial canals of the posterior nectophore, where developed, form an apical loop.

Haeckel (1888b, p. 152) purported to select what is now known as *Chelophyses appendiculata* as the type species. This is *ultra vires* since *Diphyes* Cuvier was monotypic.

Eudoxid phase

Details are given in the specific descriptions.

Diphyes dispar Chamisso & Eysenhardt, 1821

Plate XXXIII, figure 3

For synonymy see Moser, 1925, pp. 170–171. The following corrections and amendments should be made to her synonymy "Kolonie":

Diphyopsis compressa Haeckel, 1888, [read] p. 153

Doramasia picta Chun, 1892, [read] p. 91–8 T.VIII F.3, T.IX F.5 Canaren

Eudoxie:

Eudoxia lessonii Eschscholtz, 1829 [omit: ? = *Dimophyes arctica*]

Cucullus doreyanus Blainville, 1834, p. 131 [omit figure reference]

Ersaea lessonii Mayer, 1900, p. 75 T.XXVIII [read] F.96, 97 . . ."

The principal figures of the whole of this well-known animal, the first Calycophoran siphonophore to be described and figured, are those of Eschscholtz (1829, Taf. XII, fig. 6); Huxley (1859, Pl. I, fig. 1); Haeckel (1888b, Pl. XXXIII, fig. 1); Lens & van Riemsdijk (1908, Pl. VIII, fig. 63) and Kawamura (1915, Pl. XII, fig. 21).

Moser (1925) dealt with this species at very great length, but her theorizing has been judged to be unsound. Huxley gave the early history of the species, first described and figured by Bory de St. Vincent (1804). Since this is the species on which Cuvier founded his genus *Diphyes*, and since Bory's description is difficult to understand until one realizes that, as Huxley pointed out, Bory regarded the anterior nectophore as the posterior, I give a translation of part of Bory's description with an explanatory gloss in square brackets.

' . . . The anterior part [posterior nectophore] shows five projecting angles [ostial teeth] the dorsal side being carinate, the lower [ventral] on the contrary is furrowed. One recognizes in this part [posterior nectophore] two longitudinal cavities; from the upper one [hydroecium] emerges an artefact thread [a stem], often very long and rarely complete; it carries, when present, a mass of small bodies [gastrozooids, etc.] which resemble the pedicellate glands of many plants. The posterior part [anterior nectophore] is constricted at its extremity [apex] and has some similarities with the shape of a lancet; the upper [ventral] side, which is flat, is one-and-a-half lines thick. In this thick part is found an internal cavity [hydroecium], into which enters a sort of spur (pedicel of posterior nectophore) which terminates the anterior part [posterior nectophore]; and here is the only apparent union of the

two parts [nectophores] of the animal. There is also another lower cavity [nectosac] in the near half [anterior nectophore] of which the aperture, notched [toothed] at the point of junction of the two parts, forms a peg [dorsal tooth] at their union.' Bory's figures make the identity of his animal quite certain.

Polygastric phase

Anterior nectophore (text-fig. 8): Up to 35 mm length (see Lens & van Riemsdijk, 1908, Pl. VIII, fig. 63; also Bigelow, 1919, p. 341). Laterally compressed with five longitudinal ridges, the dorsal ones serrated, with a prominent reflexed dorsal tooth, larger than the laterals; ventral contour more convex than the dorsal one. The aperture of the hydroecial cavity is large and quadrilateral, occupying more than two-thirds of the basal width. The lateral edges are cut off very obliquely from the ventral side down to the mouth-plate, which according to Huxley is formed by two very broad quadrate overlapping wings (septal plates'). Huxley gives the following proportions for an inch long nectophore: Length 1, depth $\frac{1}{4}$, thickness $\frac{1}{4}$.

The hydroecium extends for about half the length of the nectophore. The somatocyst is narrow and sub-cylindrical and does not extend so far as the upper caecal extremity of the nectosac. The nectosac is wide and sub-cylindrical for most of its length, but towards the apex the lumen is suddenly occluded, leaving the narrow apical loop of the dorsal radial canal.

The peduncular (nectocalycine) canal descends vertically from the base of the somatocyst to a point near the circular canal so that the ventral radial canal is very short (see Huxley, 1859, Pl. V, fig. 3). Dorsal side of mouth-plate not denticulate but smooth.

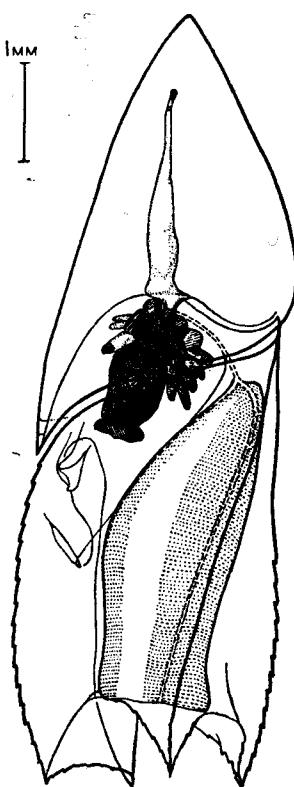


FIG. 91. *Diphyes dispar* (Chamisso & Eysenhardt)
Eudoxid phase, Gt. Barrier Reef. Lateral view, $\times 13$
(from Totton, 1932, fig. 21).

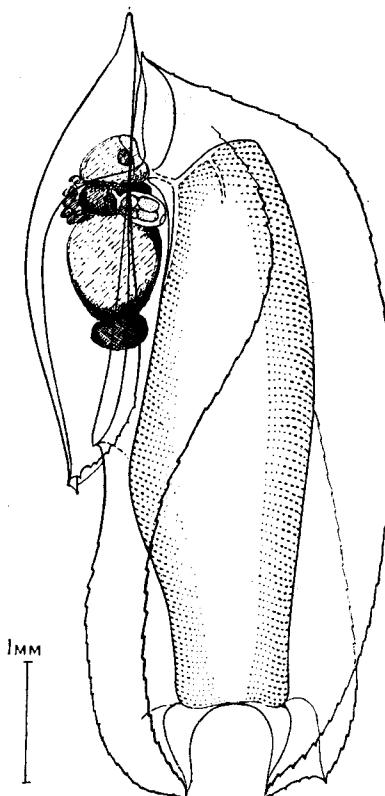


FIG. 92. *Diphyes bojani*
(Eschscholtz)
Eudoxid phase, Gt. Barrier Reef.
Lateral view, $\times 16$ (from Totton,
1932, fig. 22).

For many years I have collected the smallest anterior nectophores I could find in an attempt to discover whether the definitive one develops directly from the larval one – as I suspect – or is a secondary heteromorph one. A successful breeding experiment would settle this important question. Moser (1925, p. 192) refers to it as the definitive 'Einglockenstadium'. This is Chun's (1892) *D. picta*.

Posterior nectophore (see Huxley, 1859, Pl. 1, fig. 16C; Bigelow, 1911b, Pl. 10, fig. 1): A useful criterion for distinguishing the posterior nectophore of *D. dispar* from that of *D. bojani* is the comparatively larger size of the dorsal tooth. The mouth-plate is thick, and the two hydroecial flaps remain separated, and do not form a closed canal as in *Chelophyses* spp. Lateral basal edges and lateral hydroecial teeth smooth.

Eudoxid phase (Pl. XXXIII, fig. 3)

(Text-fig. 91.) About 7·5 mm long. Formerly identified with the *Eudoxia lessonii* of Eschscholtz (1825). For critical comments on this identification see Totton, 1932, page 346. The earliest recognizable figure is Huxley's (1859, Pl. III, fig. 6) of *E. lessonii*. The head-piece of the bract is 50% shorter than the neck-shield. The dorsal and sutural surfaces are nearly straight as seen from the side in optical section, and meet at an acute angle at the apex. The phyllocyst is broad at the base; tapers to an obtuse point above and has no lateral processes. It is equal in length to about two-thirds the distance from the apex of the bract to the apex of its basal cavity. The overall length of the bract is only a little less than the length of the asexual swimming bell. The relationship between the radial canals of this bell and the apex of its nectosac are constant (see my fig. *op. cit.*).

For a detailed description see Totton, *op. cit.*, page 348. All the gonophores of any single eudoxid are of one sex, but any two successively budded gonophores are mirror-images of one another.

Diphyes bojani (Eschscholtz, 1829) Text-figure 92

? *Diphyes serrata* Chun, 1888a, 1897b

For remainder of synonymy see Moser, 1925, p. 208. (There are some errors in the page and figure numbers quoted.)

This common species appears to be closely related to *D. dispar* though the bract of the eudoxid is very different. The best figures of the polygastric phase are: Bigelow, 1911b, plate 7, figures 2, 3; plate 9, figure 1; plate 10, figures 2, 3; and Moser, 1925, Taf. XIII, figure 1.

Polygastric phase

Anterior nectophore: Up to 14 mm in length; symmetrically pyramidal, five ridged, with some variation in the arrangement at the apex (see Bigelow, 1911b, p. 252), slender, pointed at the apex, the ridges often expanded in the apical third of their length. The serrations of the ridges are variable. The nectosac gradually narrows towards its apex, which lies close to the apex of the nectophore. The hydroecium is pointed above and reaches nearly to one-third of the height of the nectosac. The somatocyst is fusiform. A pair of large dorso-basal and latero-basal teeth. The dorsal tooth is not as prominent as it is in *D. dispar*, and is usually smaller than the laterals. The dorsal side of the mouth-plate bears a more or less marked median vertical crest of small teeth, first mentioned by Gegenbaur (1859, p. 370) and figured by Bigelow (1918, Pl. 8, figs. 3, 4).

Posterior nectophore: Up to 10 mm in length. Slender, but resembling that of *D. dispar*, the two lateral flaps of the hydroecium separated. Lateral basal edges and lateral hydroecial teeth serrated.

Eudoxid phase

(Text-fig. 92.) Characterized by its shield-like bract which lies in a plane parallel to the long axis of the large asexual swimming bell. The semi-annular phyllocyst of the young bract never develops

a secondary upstanding part as in most 'diphyid' bracts. The relationship of the articulating surfaces of bract and swimming bell in the apical region resembles that found in early developmental stages of the eudoxids of *D. dispar* and *D. chamissonis*. This surface is vertical. The cavity of the bract is very shallow. The ends of the phyllocyst grow out horizontally into horns.

The tiny mature gonophore has a cylindrical peduncle set on at an angle towards its right ventral side. It has no ridges, but vestiges of a dorsal tooth can be seen and a small elliptical mouth-plate. The manubrium which carries six or seven eggs in the female nearly fills the sub-umbrella.

The asymmetrical nectocalyx of the swimming bell has an enlargement in the middle of the left-hand side. For further details see Moser (1925, p. 214); Totton (1932, p. 350).

Diphyes chamissonis Huxley, 1859
Text-figures 93, 94

Diphyopsis weberi Lens & van Riemsdijk, 1908

A species not often taken in the open oceans, but very abundant in certain places offshore such as inside the great Barrier Reef. The then known distribution was given by Totton (1932, p. 351) who was the last reviewer.

Polygastric phase

Anterior nectophore (text-fig. 93): Up to 12 mm in length. Five longitudinal ridges, all reaching the apex. Apex not sharply pointed. At this point the ventral facet is twisted over a little to the right. The three ostial teeth of about the same size.

Hydroecium deep, reaching up to the mid length of the nectosac and extending well below the level of the ostium. Somatocyst short, fusiform.

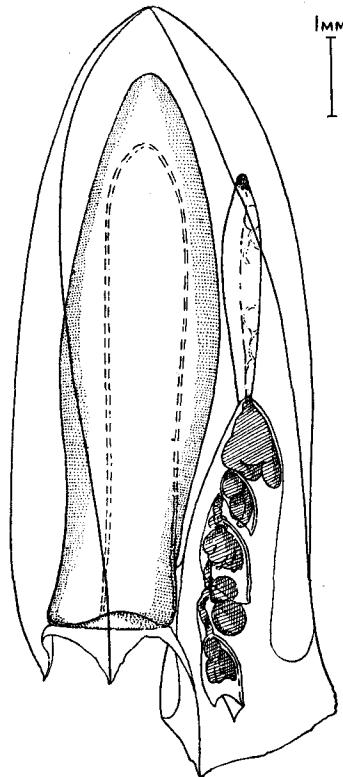


FIG. 93. *Diphyes chamissonis* Huxley Polygastric phase, Great Barrier Reef.
Lateral view of the solitary (anterior) nectophore, to show the asymmetrical twist of the ventral facet, fig. 23). $\times 10.5$ (from Totton, 1932)

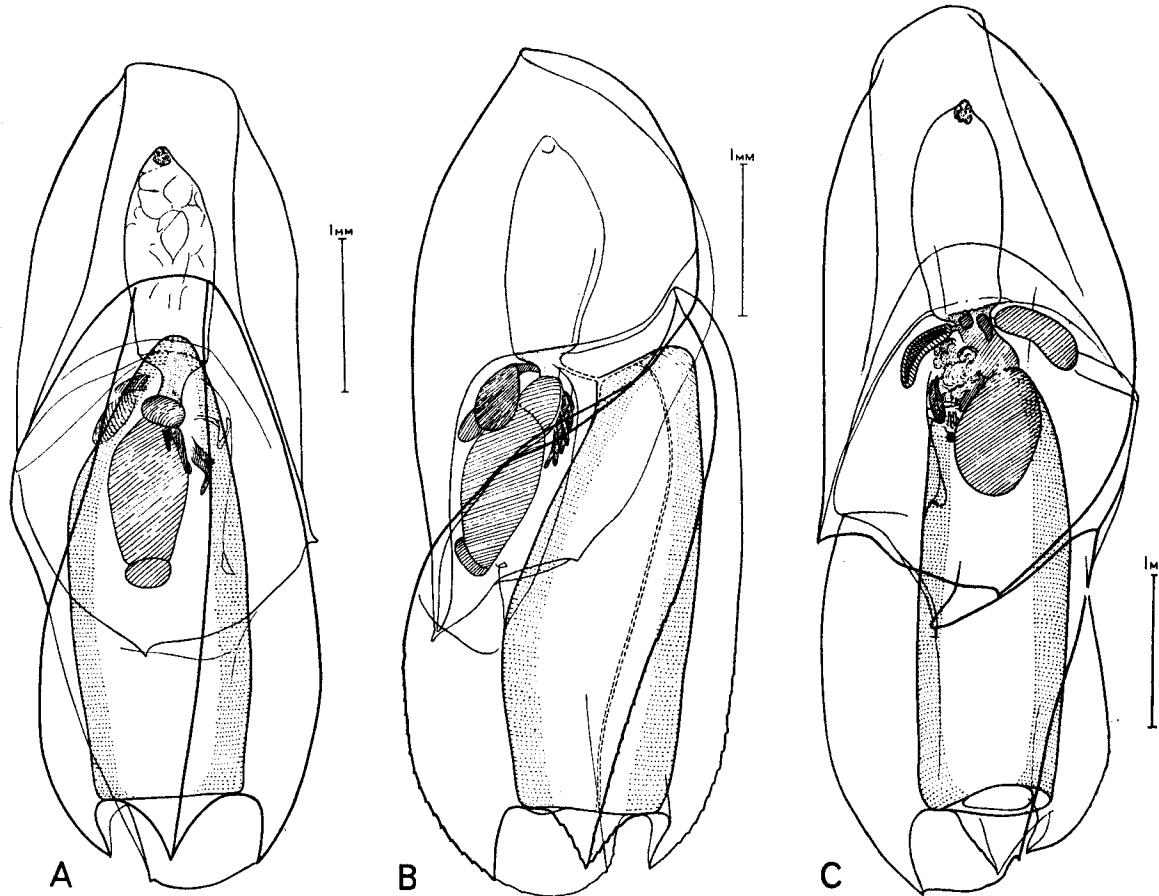


FIG. 94. *Diphyes chamissonis* Huxley. Eudoxid phase, Gt. Barrier Reef
A, ventral; B, lateral; C, dorsal view of the bract, $\times 20$ (from Totton, 1932, fig. 24)

Nectosac not constricted apically. There is a deep basal notch in the ventral wall of the hydroecium, and also in the mouth-plate.

Posterior nectophore: Not developed.

Eudoxid phase

(Text-fig. 94.) About 5.5 mm in length, the neck-shield of the bract is of about the same length as the head piece. The plane of articulation between bract and asexual swimming bell lies at about 45° to the long axis. The posterior (lower) part of the sutural surface is well rounded off. The dorsal and sutural surfaces, seen in optical section from the side, are rounded, and meet at the apex almost at right angles. The apical wall of the nectosac of the asexual bell is longer than in *D. dispar*. It is inclined at an angle to the long axis instead of being at right angles to it as in *dispar*. The pedicular canal of the bell is shorter than the apical wall of the nectosac. There is a rounded mouth-plate, and a small tooth on the hydroecial flap. Sexes are separate, the female manubrium bears from six to eight eggs. There are from six to seven simple, sac-like gonophores on each eudoxid. There appears to be no umbrella.

Diphyes antarctica Moser, 1925 Plate XXXIV

A form confined entirely to the Antarctic.

Polygastric phase (Pl. XXXIV, fig. 3)

Anterior nectophore (Pl. XXXIV, fig. 1): Up to 28 mm in length (see Moser, 1925, Pls. IX, X). Bilaterally symmetrical, with five longitudinal ridges.

At first sight there seems to be no dorsal tooth, but it is obscured only because its sides descend instead of rising towards the ostium. It is visible in optical section, but is very much shorter than the lateral teeth. The apex of the nectosac is not constricted. The mouth-plate is divided – one of the species' primitive features. The hydroecium scarcely reaches up to the middle of the nectosac. The somatocyst is short, spindle-shaped, and reaches up to a point on the nectosac about one-quarter of its length from the apex.

Posterior nectophore (Pl. XXXIV, fig. 11): Up to 28 mm in length (see Moser, *op. cit.*, Taf. IX, fig. 4). The dorsal tooth is obscured in the same way as described above for the anterior nectophore. The pedicel is long and fine, the proximal part of its ventral side concave where it articulates with the baso-dorsal part of the hydroecial cavity.

Eudoxid phase (Pl. XXXIV, fig. 12)

Up to 16 mm in length (see Moser, 1925, Taf. X). The margins of the bract which reaches a length of 3 mm are denticulate, but there is no large basal tooth. The phyllocyst is spindle-shaped or cylindrical, tapering at the apex. The sutural surface seen in optical section from the side makes almost a right angle with the adjacent part of the upper surface of the bracteal cavity. The gonophore, which is four ridged is truncate above, with an inconspicuous pedicel.

There is a square-shaped basal mouth-plate with a pair of lateral teeth, and two strong lateral ostial teeth. The dorsal tooth is obscured in the same way as described for that of the two nectophores. The manubrium reaches a length of 5–6 mm in a gonophore of 16 mm length. At a length of 4 mm a female gonophore has developed five eggs, but at maturity perhaps as many as thirty. There is no asexual swimming bell, but at least two secondary gonophores are budded.

The cnidosac of the tentillum measures about 0·27 mm in length and has a structureless horse-shoe-shaped covering (see Moser, 1925, Taf. X, figs. 5a, 5b) at its basal end where are found a pair of lateral groups of five larger spindle-shaped nematocysts measuring about 50 μ in length.

Genus: *LENSIA* Totton, 1932

Type species: *L. subtiloides* (Lens & van Riemsdijk, 1908).

Diphyes (*Diphyopsis*) *subtiloides* L & van Riemsdijk, 1908

Small diphyid calyconects in which the anterior nectophore of the polygastric phase is basically pentagonal in cross-section but may carry three, five, seven, fifteen, or even more longitudinal crests. The short mouth-plate is divided, its baso-lateral corners not produced into conspicuous projections. The radial canals have no commissures (*cf.* fig. 85C and fig. 99), and the somatocyst is relatively short. The hydroecium is generally shallow. The posterior nectophore, where known, is truncated proximally, has a rounded mouth-plate and no conspicuous teeth. The lateral radial canals of the smaller posterior nectophore are not looped, but run a slightly sigmoid course. The eudoxid has no special swimming bell. Its bract has a broad, rounded posterior margin without baso-lateral teeth, and its gonophores are truncated proximally, have a small, inconspicuous dorsal tooth, and a very narrow rounded mouth-plate.

Only a few of the eudoxid phases of species of *Lensia* have been described. The identification of a particular eudoxid can as a rule only be made if in a plankton haul one species predominates. Subsequent reviewers will doubtless remove certain groups of species like *L. fowleri*, *L. hardy* and *L. challengerii*, which resemble each other more than they do the type species, to form new genera. But all species of *Lensia* have the characteristic unlooped lateral radial canals in the posterior nectophores, so that if new generic groupings are made they should form a small sub-family.

Because specimens are often small and poorly preserved they have been neglected. I made a hurried review during the last war of the material I had been working on for years so that the results would

be recorded. Subsequent work has shown that my judgment was sound in delimiting species, and specimens can be identified from the figures in spite of the hurried descriptions. There are twenty-one described species. Some species have no crested ridges, some have three, some five, some seven, some are multicristate, and in one there is a ridged reticulation of the surface. The multicristate species probably do not form a distinct sub-group because one of them, *lelouveteau*, like the reticulate one *reticulata* appear to be related to *meteori* and *subtilis* neither of which are ridged.

Key to species of *Lensia*

Anterior nectophores

1.	Three non-crested ridges only (no ventro-lateral ridges between lateral and ventral facets)	3
	At least five ridges	2
2.	At least five longitudinal ridges, with reticulations	<i>reticulata</i> (p. 172)
	At least five ridges, without reticulations	4
3.	Three non-crested ridges; basal facet horse-shoe shaped; apex twisted	<i>campanella</i> (p. 165)
	Three non-crested ridges; basal facet horse-shoe shaped; apex not twisted	<i>cossack</i> (p. 166)
4.	Five crested longitudinal ridges only	7
	Five crested longitudinal ridges and two ventro-lateral crests: seven in all	5
5.	Seven crests, complete, apex to base	<i>havock</i> (p. 175)
	Seven crests some incomplete, apex to base	6
6.	Seven crests, some incomplete, ventro-lateral pair meeting mouth-plate	<i>hunter</i> (p. 164)
	Seven crests, some incomplete, ventro-lateral pair not meeting mouth-plate	<i>multicristata</i> (p. 164)
7.	Five non-crested ridges	8
	Five crested ridges	9
8.	Five non-crested ridges; somatocyst globular, on long pedicel	<i>subtilis</i> (p. 168)
	Five non-crested ridges; somatocyst on very short pedicel	<i>meteori</i> (p. 170)
9.	Five ridges, each with a single crest	10
	Five ridges, each with more than a single crest	17
10.	Five single-crested ridges; somatocyst elongated and lying above ostial level	11
	Five single-crested ridges; somatocyst at or below ostial level	15
11.	Five single-crested ridges; somatocyst above ostial level; base of lateral crests bending dorsad	<i>achilles</i> (p. 171)
	Five single-crested ridges; somatocyst above ostial level; base of lateral crests continuing basad	12
12.	Base of somatocyst above ostial level	13
	Base of somatocyst below ostial level	14
13.	Mouth-plates one half as long as somatocyst	<i>leloupi</i> (p. 161)
	Mouth-plates one-third as long as somatocyst	<i>subtiloides</i> (p. 159)
14.	Length of somatocyst equal to one half the length of the nectophore	<i>conoidea</i> (p. 162)
	Somatocyst short and oblique. Lateral ridges reaching ostium	<i>hotspur</i> (p. 167)
	Somatocyst short and oblique. Lateral ridges not reaching ostium	<i>tottoni</i> (p. 168)
15.	Five single-crested ridges; spheroidal somatocyst, and peak-shaped basal extension of dorsal wall	<i>challengeri</i> (p. 166)
	No peak-shaped basal extension of dorsal wall	16
16.	Hydroecium not extending below somatocyst	<i>fowleri</i> (p. 174)
	Hydroecium extends below somatocyst	<i>hardy</i> (p. 173)
17.	Five two-crested ridges and a horizontal basal (velar) ridge	<i>grimaldi</i> (p. 178)
	Five ridges each with more than two crests, and a velar ridge	18
18.	Five multicristate ridges and a velar ridge	19
	Five multicristate ridges but no velar ridge	20
19.	Five multicristate (3) ridges and a velar ridge	<i>exeter</i> (p. 176)
	Five multicristate (3-7) ridges and a velar ridge	<i>lelouveteau</i> (p. 172)
20.	Five multicristate ridges; no velar ridge; crests extending to ostium	<i>hostile</i> (p. 177)
	Five multicristate ridges; no velar ridge; crests not extending to ostium	<i>ajax</i> (p. 179)

Lensia subtiloides (Lens & van Riemsdijk, 1908)

Text-figures 95, 96, 97B

Diphyes (Diphyopsis) subtiloides Lens & van Riemsdijk, 1908

The Great Barrier Reef Expedition 1928-29 found this to be a very abundant species at from 8-

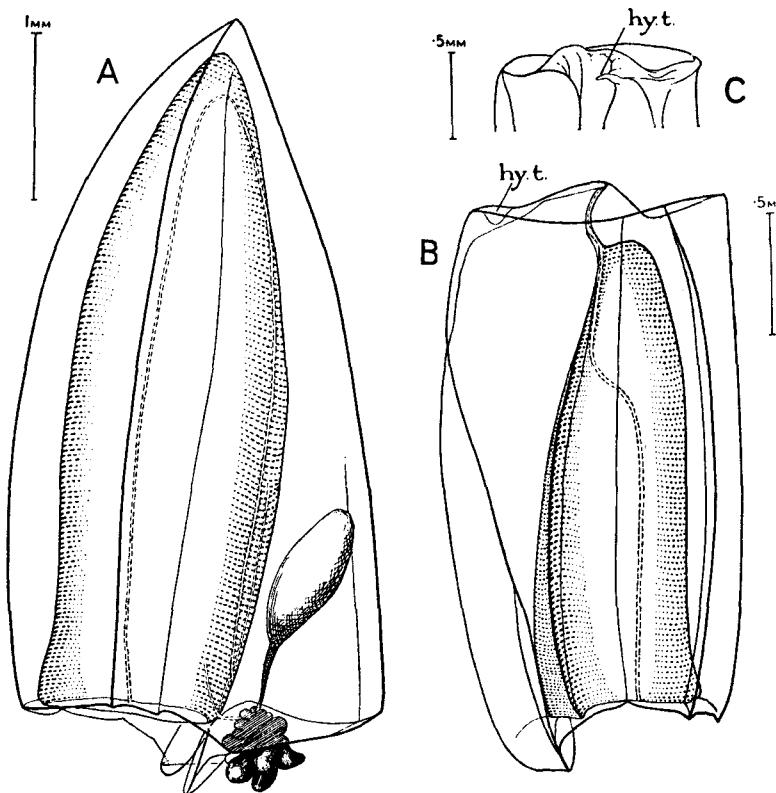


FIG. 95. *Lensia subtiloides* (L. & v. R.). Polygastric phase, Gt. Barrier Reef

A, anterior nectophore, $\times 22$; B, posterior nectophore, $\times 32$; C, ventral view of the proximal end of the posterior nectophore, $\times 23$. hy.t. = tooth at the apex of the right hydroecial fold (from Totton, 1932, fig. 32).

12.5 m depth, especially from December to the middle of February, in water of comparatively low salinity inside the Barrier Reef.

Polygastric phase

Anterior nectophore (see Lens & van Riemsdijk, 1908, Pl. VII, fig. 59; and text-fig. 95): Up to 5 mm in length and 2 mm deep, five ridged with shallow hydroecium and an oblique ovoid stalked somatocyst about 1.2 mm in length, the ovoid part varying from 0.54 to 0.66 mm in length, and from 0.23 to 0.28 mm in diameter. The loop of the lateral canals reaches within a distance of 0.20 mm from the anterior end of the nectosac and of 0.37 mm of the apex of the nectophore. The two halves of the mouth-plate are of almost equal size, rounded and slightly projecting below the base. The anterior wall of the hydroecium extends forward to the level of the ostium. The basal end of the dorsal ridge does not form a marked tooth-like projection.

Posterior nectophore: There is no projection of the nectosac anterior to the entry of the pedicular canal. There is a small tooth at the apex of the right hydroecial fold.

Eudoxid phase

(Text-fig. 96.) There are no projections on the posterior margin of the bract. The phyllocyst is club-shaped.

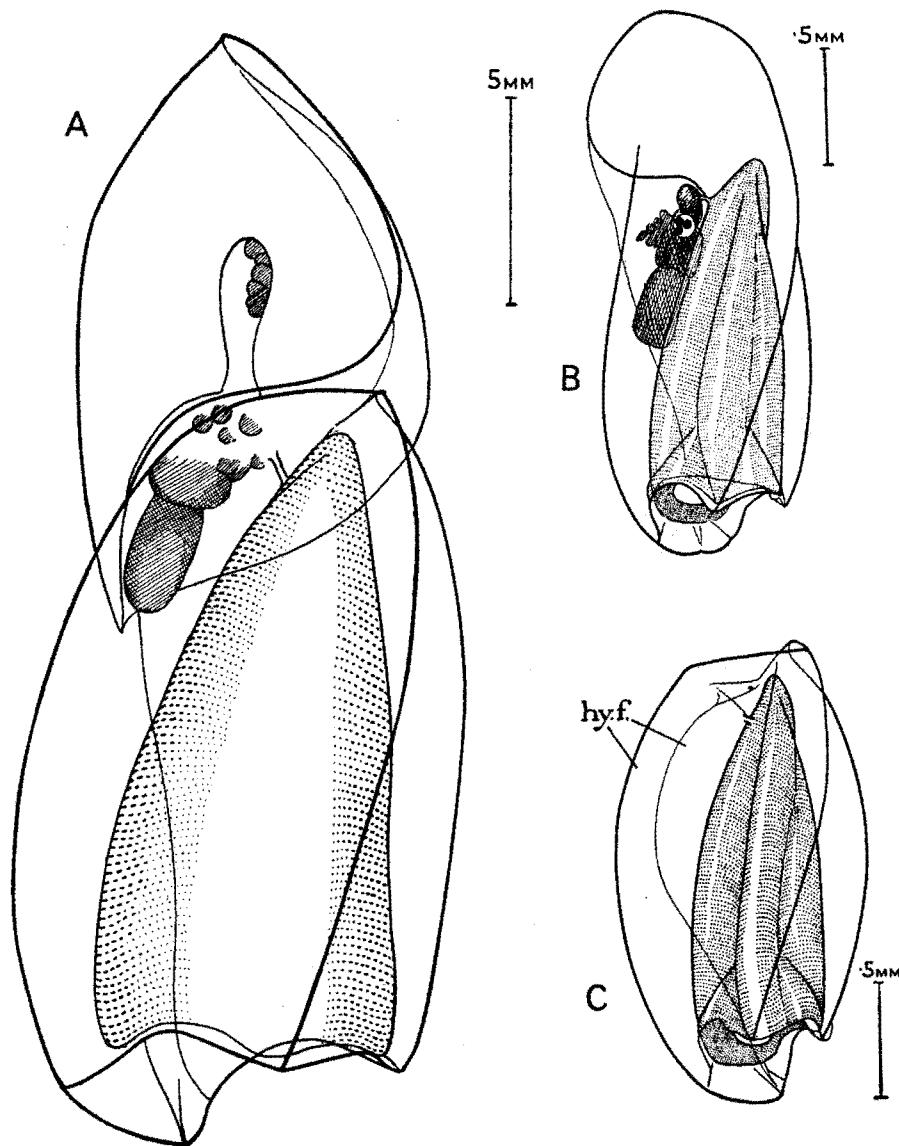


FIG. 96. *Lensia subtiloides* (L. & v. R.). Eudoxid phase, Gt. Barrier Reef
A, lateral view of the whole eudoxid, $\times 55$; B, right lateral view of a detached
gonophore with abnormal proximal end, $\times 31$; C, similar view of a normal
gonophore
hy.f. = hydroecial fold (from Totton, 1932, fig. 33).

***Lensia leloupi* Totton, 1954**

Text-figure 97A

Resembling *L. subtiloides* in general, but larger and with deeper hydroecium.

Polygastric phase

Anterior nectophore (text-fig. 97A): About 5 mm in length, and 2.5 mm deep; five-ridged. The pedicel arises further away from the nectosac than does that of species of *Muggiaeae*, of which genus it might otherwise be thought to belong. The mouth-plate is longer than in *L. subtiloides*. Somatocyst narrow. Apex of nectosac lies close to apex of nectophore. Hydroecium nearly half a millimetre deep.

Posterior nectophore: Unknown.

Eudoxid phase – unknown.

Like *L. subtiloides* it is found in water of comparatively low salinity, inshore. Locality: Near Cape Lopez, Gulf of Guinea ('Discovery' Station 277).

A very similar but larger species (anterior nectophore up to 10 mm long) is to be described shortly. It occurs commonly in coastal waters off Vancouver, B.C. The somatocyst is spindle shaped and distended. The ostial end of the prominent lateral ridge turns ~~distad~~ (see fig. 98). ~~distad~~

These three species all occur in coastal waters, and appear to be closely related.

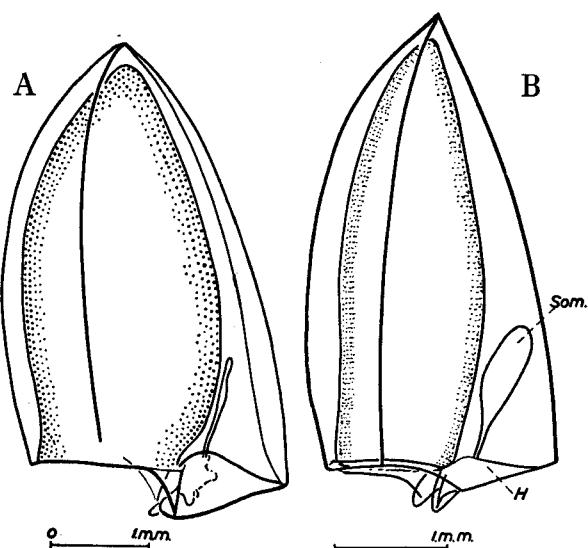


FIG. 97. A, *Lensia leloupi* Totton. Polygastric phase anterior nectophore, 'Discovery' St. 277, $\times 16$. The ostial end of the lateral ridge, though scarcely visible, reaches the ostium without turning ~~distad~~. ~~distad~~
B, *Lensia subtiloides* (L. & v. R.) Polygastric phase, Great Barrier Reef, anterior nectophore, $\times 18$. H = hydroecium; Som = somatocyst (from Totton, 1954, fig. 55C, D).

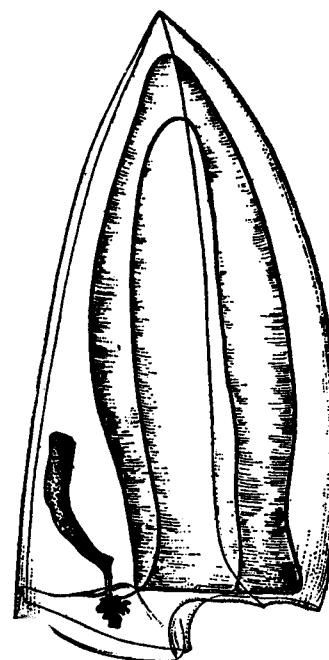


FIG. 98. *Lensia* sp. aff. *leloupi* Totton
Lateral view of the anterior nectophore from the coasts of British Columbia,
 $\times 5$ (after Bigelow (1913) as *Diphyes truncata*).

Lensia conoidea (Kefferstein & Ehlers, 1860)

Plate XXXI, figure 11; text-figure 99A

Diphyes conoidea Kefferstein & Ehlers, 1860, 1861

Diphyes truncata Sars, 1846 non *D. truncata* Quoy & Gaimard, 1827

Lensia truncata Totton, 1932

Lensia conoidea Bigelow & Sears, 1937

Well known since 1846. The name *truncata* has been used sometimes uncritically for other small Diphids. Moser (1925, p. 154) wrongly cited as synonymous *Diphyes fowleri* Bigelow, *D. subtiloides* Lens & van Riemsdijk and *D. sieboldii* Lochman, 1914 (= *Chelophyses appendiculata*). Great caution is needed, therefore, in the use of published lists of synonyms of this species. This is an easily recognizable species first well described and figured as *Diphyes* sp. by Stuwitz (1836) from dead specimens taken in Christianiafjord in May 1835. Sars (1846) gave a wrong reference to this paper.

Polygastric phase

Anterior nectophore (text-fig. 99A; see also Bigelow & Sears, 1937, fig. 33): It reaches a length of 20 mm, is of firm substance and has five longitudinal ridges. The distal end of the dorsal ridge is prolonged on to a small lip or projection distal to the general level of the ostium. The base was well

figured by Bigelow & Sears (*op. cit.*, figs. 29, 30 and 31—not fig. 32). The length of the somatocyst of Sar's original specimens was about 45% of that of the total length of the nectophore. The right-hand (*sensu* Bigelow & Sears) wing of the mouth-plate overlaps (is dorsal to) the other.

Posterior nectophore (see Bigelow & Sears, *op. cit.*, fig. 34; *non* 35): May reach a length of 18 mm. The apical end of the nectosac (*diverticulum*, Totton, 1932, p. 367) extends anteriorly beyond the entry of the pedicular canal. There are five longitudinal ridges. The basal wing or mouth-plate is indented in the mid-line. The left lobe is a little longer than the right. Specimens from the Irish Sea, the Indian Ocean and 'Discovery' Station 100C differ from the one figured by Bigelow & Sears (*op. cit.*, fig. 35) in that the articular surface of the right hydroacial wing of this figure 35 is square (see Totton, 1954, fig. 56) and not acute-angled as it is in *L. fowleri*.

Eudoxid phase (Pl. XXXI, fig. 11)

Well known from association, in catches, with the polygastric phase. First figured by Sars, it was figured again by Moser (1925) and described by her on page 162. But since Moser confused other species with *conoidea* this account should be checked. The eudoxid is relatively large, has a conical apex and a long phyllocyst. But systematists have not so far attempted to define the differences between the eudoxis of all the various species of *Lensia*. The gonophores, which are up to 4.5 mm long, have a mouth-plate 0.35 mm long with a slightly convex distal border. They are enantiomorphic, since either the right or the left hydroacial ridge may be the deeper. There is a corresponding difference in the twisting of the hydroecium.

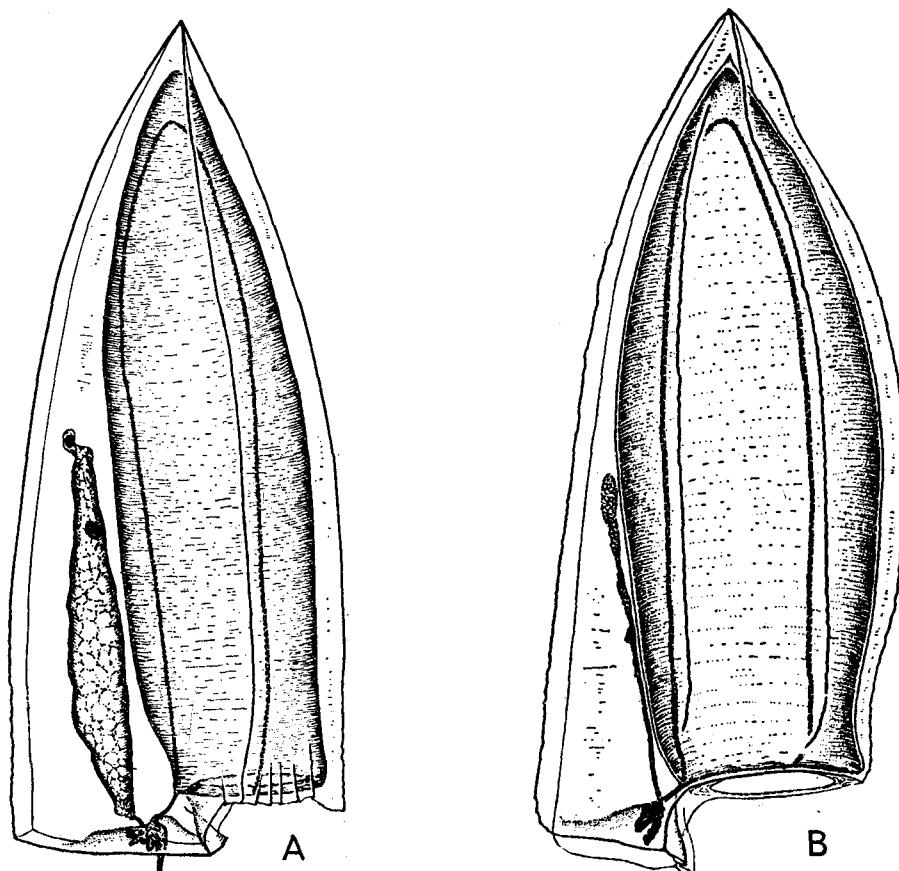


FIG. 99. A, *Lensia conoidea* (Kefferstein & Ehlers) lateral view of the anterior nectophore from Thor St. 36, $\times 5.2$ (after Bigelow & Sears, 1937, fig. 27); B, *Lensia multicristata* (Moser)—lateral view of the anterior nectophore, Thor St. 217, $\times 7.1$ (after Bigelow & Sears, 1937, fig. 40)

Sars (1846, p. 44) described how the eudoxids broke loose from the stem and swam freely.

The saccus of the tentillum was figured by Kefferstein and Ehlers (1861, Taf. III, fig. 10). The figure shows that there is a pair of lateral groups of four larger nematocysts near its base measuring about $53\mu \times 7\mu$.

For the benefit of any field worker in the Mediterranean, the eudoxid of this species may be distinguished from the common eudoxid of *Chelophyses appendiculata* by its larger size; the fact that the bract of the eudoxid of *conoidea* lacks the distinct cavity found in *appendiculata*, the fact that the gonophore of *conoidea* has a truncate articulating end and lacks the long peduncle of *appendiculata*.

Colour: Gastrozooids and tentilla sacs are rose-red.

Progression: Sars recorded that the two nectophores provided rapid propulsion. Each contraction propelled the animal forward for from 10–12.5 cm. When stationary, the tentacles are relaxed and extended.

***Lensia multicristata* (Moser, 1925)**

Text-figure 99B

Galeolaria multicristata Moser, 1925

Diphyes bigelowi Browne, 1926

Lensia profunda Totton, 1936 *nomen nudum*

A comparatively large, common and easily recognizable seven-ridged *Lensia* well described and superbly figured by Bigelow (Bigelow & Sears, 1937, fig. 40–44). Some of the ridges may escape observation in unstained material (see Bigelow 1911b, Pl. 12, fig. 2, as *Muggiaeae kochii*). The last review was that of Bigelow & Sears (1937).

Polygastric phase

Anterior nectophore (text-fig. 99B): Seven longitudinal ridges. The ventro-laterals reach neither apex nor basal margin. The laterals terminate slightly above the basal margin. A small hydroecial cavity lying below the level of the ostium. Basal margin of ventral facet rounded. Both halves of mouth-plate have a small projection at the inner angle. Somatocyst (see Bigelow & Sears, 1937, p. 58, fig. 43) 'slim, fusiform or linear, usually with a more or less definitely defined and thread-like stalk'. Its length equals about 40–45% of the length of the nectophore measured from apex to ostium.

Posterior nectophore (see Leloup, 1934, p. 34, fig. 8): Five longitudinal ridges, the laterals not reaching the ostial margin. Hydroecium shallow distally. Mouth-plate wide, short rounded with a slight median notch. At the proximal end of the right hydroecial fold there is a small tongue-shaped projection. Lateral radial canals follow a somewhat sigmoid course.

Eudoxid phase – undescribed.

A large number of new records were published by Totton (1954, p. 117).

***Lensia hunter* Totton, 1941**

Text-figure 101B, C (p. 166)

Another seven-ridged *Lensia* easily separated from the last by its somatocyst. It has been found again on many occasions since first described.

Polygastric phase

Anterior nectophore (text-fig. 101B): The dorso-lateral ridges do not meet the ostial margin. The ventro-laterals do not reach the apex, but meet the lateral edges of the mouth-plate. The basal wall of the hydroecium on the ventral side of the pedicel of the somatocyst curves off gradually to the

ventral facet. The somatocyst is generally bilobed and asymmetrical (text-fig. 101C). It reaches a length of about 10 mm.

Posterior nectophore: Not recognizable yet.

Eudoxid phase – not identified.

***Lensia campanella* (Moser, 1925)**

Plate XXXI, figure 4

Galeolaria campanella Moser, 1925

Specimens are small, and the apical end is twisted (see below).

Polygastric phase

Anterior nectophore (text-fig. 100A): Up to 3·3 mm in length. Apex twisted. Mouth-plate very small indeed, divided. Longitudinal ridges hardly visible. The ventro-basal facet shows hardly any hydroecial cavity, and slopes off at about 45° into the ventral facet. The somatocyst is short, oblique and club-shaped. The musculature of the nectosac is nearly always well preserved.

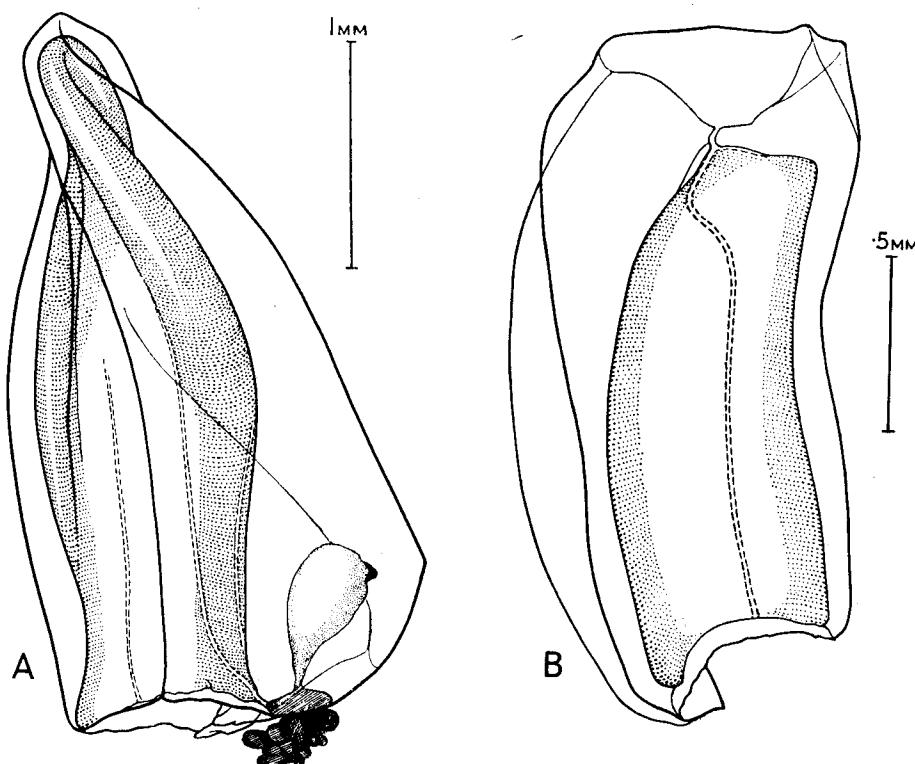


FIG. 100. *Lensia campanella* (Moser). Polygastric phase, Gt. Barrier Reef
A, left lateral view of the anterior nectophore, $\times 30$; B, right lateral view of the
posterior nectophore, $\times 46$ (from Totton, 1932, fig. 35)

M. Claude Carré of the Station Zoologique, Villefranche, has shown me sketches, which I hope he will publish, of several specimens of this species taken at Villefranche in November/December 1962. When alive the anterior nectophores did not show twisting of the apex; and both nectophores and gonophores had a fairly regular pattern of orange-red ectodermal pigment spots, three on the left side only of the anterior nectophore – one of them near the apex – and several in the ostial region. There were six or seven on the posterior nectophore, and an unrecorded number on the gonophore. They are useful field marks.

Posterior nectophore (text-fig. 100B).

Eudoxid phase – unidentified.

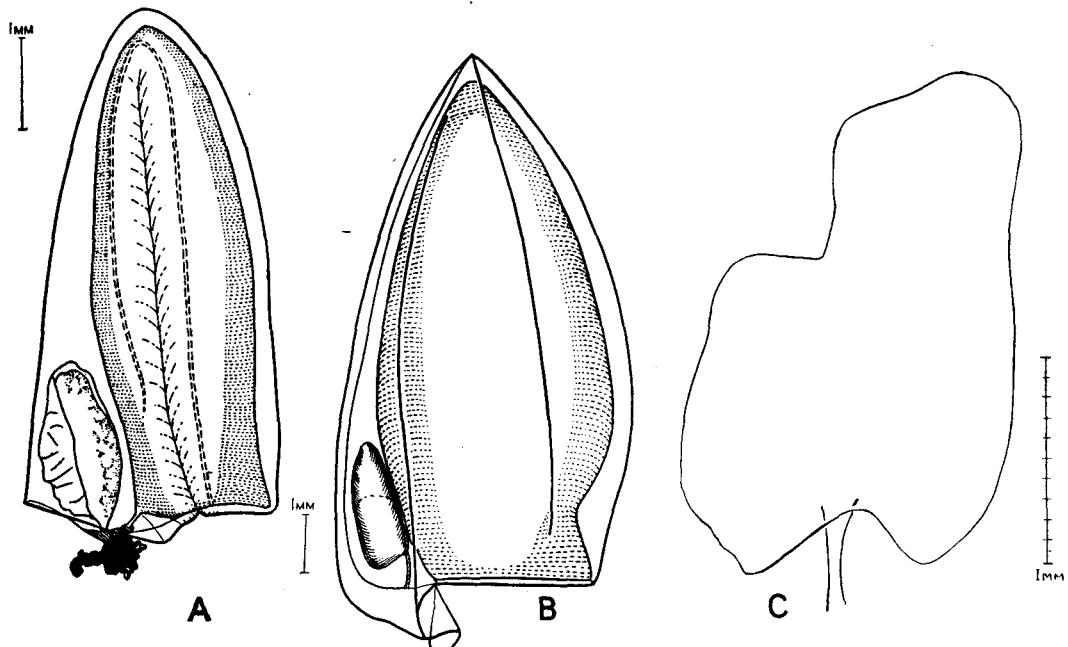


FIG. 101. A, *Lensia cossack* Totton polygastric phase; lateral view of anterior nectophore
B, C, *Lensia hunter* Totton (p. 164)

B, lateral view of anterior nectophore; C, ventral view of somatocyst (from Totton, 1941, figs. 8, 11, 12)

Lensia cossack Totton, 1941

Diphyes subtiloides Browne, 1926

Polygastric phase

Anterior nectophore (text-fig. 101A): Up to 11.6 mm in length. Four longitudinal folds, that enable the nectosac to contract and expand, divide the rounded exterior surface into four rounded longitudinal ridges, a dorsal, a pair of laterals and a ventral. There is a very slight median crest on the dorsal, and a pair of lateral vestigial ones may be present as well. The basal facet is horse-shoe shaped, and has a slight notch on the ventral side. There is virtually no hydroecial cavity. The mouth-plates are very short. The somatocyst is ovoid, oblique and measures, when well preserved, one-third of the length of the nectophore, the apex of which is not twisted.

Eudoxid phase – not identified.

Lensia challengereri Totton, 1954

Text-figure 102A, B (p. 166)

A form closely related to *L. fowleri* and *L. hardy*, occurring very abundantly off the Californian coast (see Totton, 1954, p. 111). The specimen figured by Totton (1941, fig. 13, as *L. hotspur*) belongs to *L. challengereri*.

Polygastric phase

Anterior nectophore: Up to 7.5 mm in length. Five longitudinal ridges. Somatocyst spherical, egg-shaped or flattened, lying at level of ostium. The hydroecial cavity does not extend below the ventral side. Baso-ventral margin entire. Mouth-plate on left (in dorsal view) much broader than the other (text-fig. 102B). Both halves of mouth-plate are much less deep than those of *L. fowleri* and *L. hardy*.

Posterior nectophore: Known but undescribed.

Eudoxid phase – known but undescribed.

Lensia hotspur Totton, 1941

Text-figure 102C-E

L. hotspur Totton, 1954 (Non *L. hotspur* Totton, 1941 figure 13 (= *L. challengerii*))*Polygastric phase*

Anterior nectophore (text-fig. 102C, D, E): Up to 4·5 mm long, five-ridged, with or without a shallow hydroecium that lies below the level of the ostium. The somatocyst is oblique, ovate and very shortly stalked. In Red Sea specimens the base of the somatocyst sometimes projects down slightly below the baso-lateral margin, but there are intermediates. In 1954, when more material became available I excluded the specimen shown earlier (1941, fig. 13) from Carnegie Cruise VII, station 36 (see *L. challengerii*, p. 176).

Posterior nectophore: There is a rounded notch in the distal edge of the mouth-plate. The upper (articular) end of the left ventral wing is not square but angular.

L. hotspur occurs side by side with *L. subtiloides* in the Red Sea. *L. hotspur* can be distinguished at once by the fact that there is practically no pedicel to its relatively shorter somatocyst.

Eudoxid phase – not identified.

~~I feel some doubt about the validity of this species, but the authors have not sent me specimens to check.~~

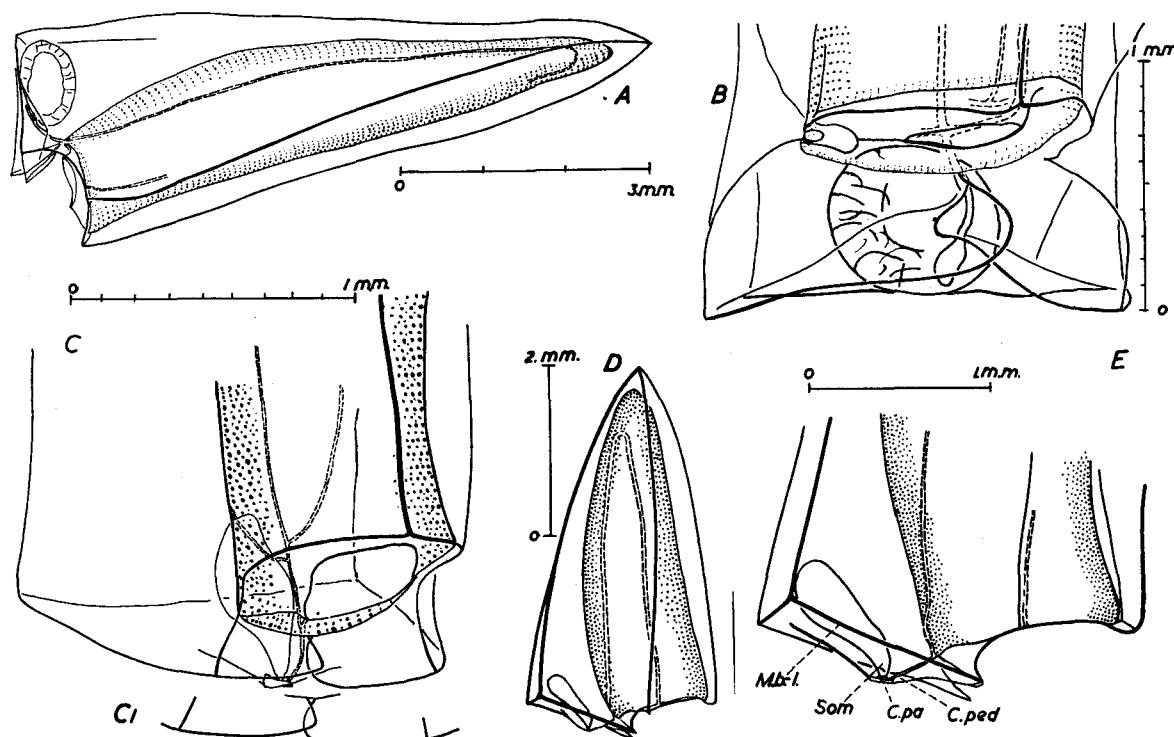


FIG. 102. *Lensia challengerii* Totton. Polygastric phase, Challenger St. 104 (1950)
A, lateral view of the anterior nectophore, $\times 12$; B, dorsal view of mouth-plate, $\times 40$

Lensia hotspur Totton. Polygastric phase, Gulf of Aqaba
C, anterior nectophore, antero-lateral view of the base, $\times 40$; D, lateral view, $\times 12$; E, lateral view of the base, $\times 25$
C.pa = pallial canal; *C.ped* = pedicular canal; *M.b.i* = baso-lateral margin; *Som* = somatocyst (from Totton, 1954, fig. 54).

Lensia tottoni Daniel, A. & Daniel, R., 1963

Text-figure 103

Polygastric phase

Anterior nectophore (text-fig. 103): Closely resembling that of *L. hotspur*, but with the following differences: The lateral ridges do not meet the ostium. The baso-ventral ridges are not quite so oblique as in *L. hotspur*, but almost at right angles to the ventrals. Only five specimens were recorded, but in all of them the base of the somatocyst lay well below the baso-ventral ridges, so that there was no hydroecium.

Posterior nectophore: Not known. *Eudoxid phase* – not identified.

I feel some doubt about the validity of this species, but the authors have not sent me specimens to check.

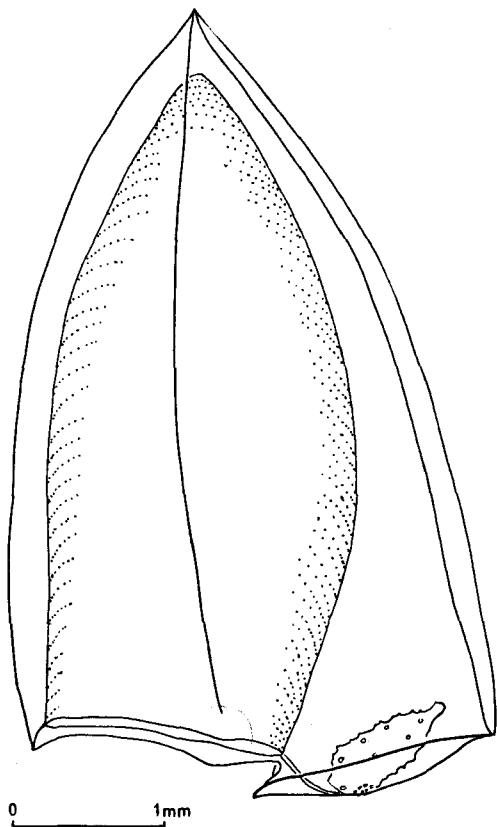


FIG. 103. *Lensia tottoni* Daniel & Daniel.
Polygastric phase, Bay of Bengal
Lateral view of the anterior nectophore, $\times 2$
(after Daniel & Daniel, 1963).

bud of an anterior nectophore replacement. It can grow from bud to active nectophore in 12 hours.

Posterior nectophore (see Chun, 1885, Taf. II, fig. 5, as *Monophyes gracilis*): About same length as anterior one, truncate proximally and five-ridged. The hydroecial cavity shallows out distally, where there is an inconspicuous, rounded mouth-plate. The lateral radial canals are sigmoid and not looped.

Eudoxid phase

Bract (text-fig. 105C-E): Length little more than 1 mm, rounded, with shallow basal cavity. Phyllocyst short, club-shaped.

Gonophore (text-fig. 105A, B): About 2.25 mm long. Hydroecial folds in proximal part only. Tip of manubrium yellow in colour (a useful field mark when making breeding experiments with diphyids in this region). The female gonophore bears twenty or thirty eggs. The gonophores become detached and swim freely.

Lensia subtilis (Chun, 1886)

Text-figure 104, 105

Monophyes irregularis Chun, 1885

Monophyes gracilis Chun, 1885

Diphyes subtilis Chun, 1886

A very abundant species at Villefranche, characterized when alive at all stages and in both phases by its yellow pigment.

Polygastric phase

Anterior nectophore (see Chun, 1885, Taf. II, fig. 3; Moser, 1925, Taf. IV, figs. 5-8; and text-fig. 104): Length up to 11 mm. Four longitudinal folds (inwards) divide the external surface when contracted into a dorsal, a pair of lateral and a ventro-longitudinal fold (uncrested ridges). The divided mouth-plate is small, each half being rounded distally. The basal, articular facet is oblique to the long axis, and is rounded off ventrally into the ventral facet. The best field-mark is the globular, long-stalked somatocyst. The stalk, in Mediterranean specimens, measures only 0.025 mm in diameter. The nectophore-bud often found at the base of the stem is probably the

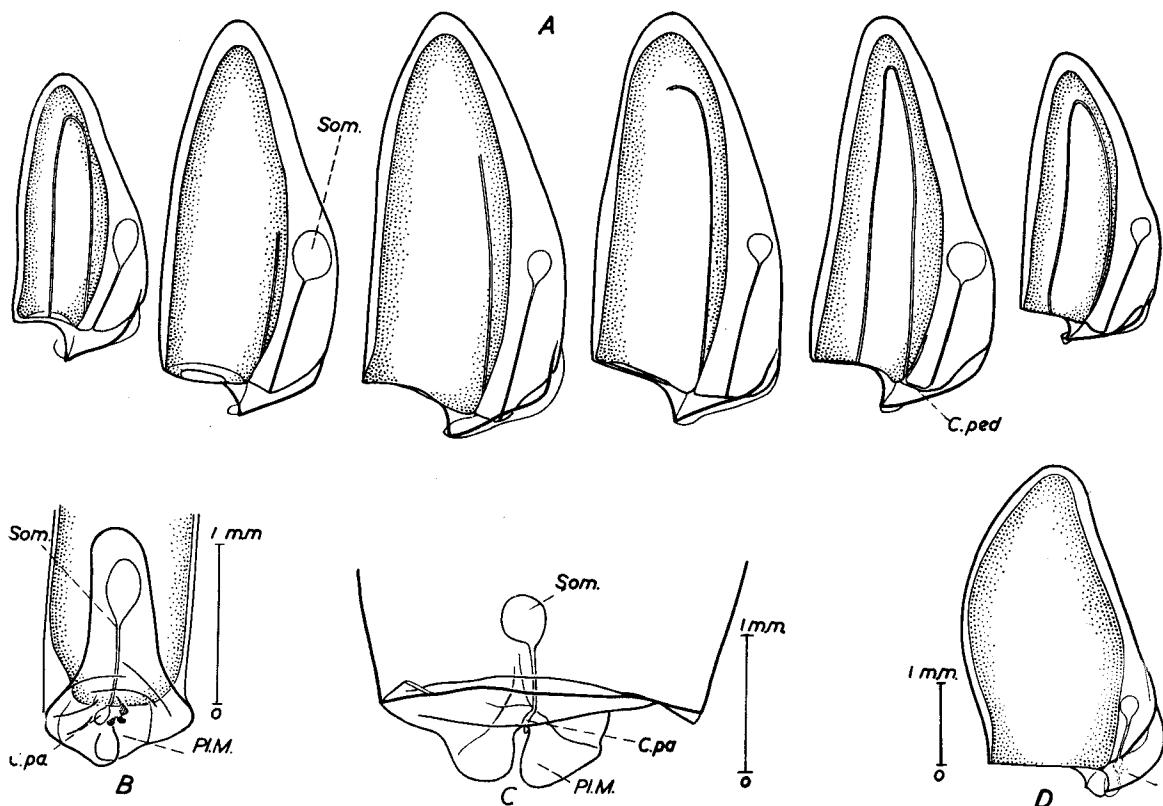


FIG. 104. *Lensia subtilis* (Chun). Polygastric phase. A, anterior nectophores, $\times 21$, Gulf of Aqaba; B–D, 'Discovery' St. 1587. B, $\times 21$; C, $\times 18$; D, $\times 11$. C.pa = pallial canal; Pl.m = mouth-plate (from Totton, 1954, fig. 57).

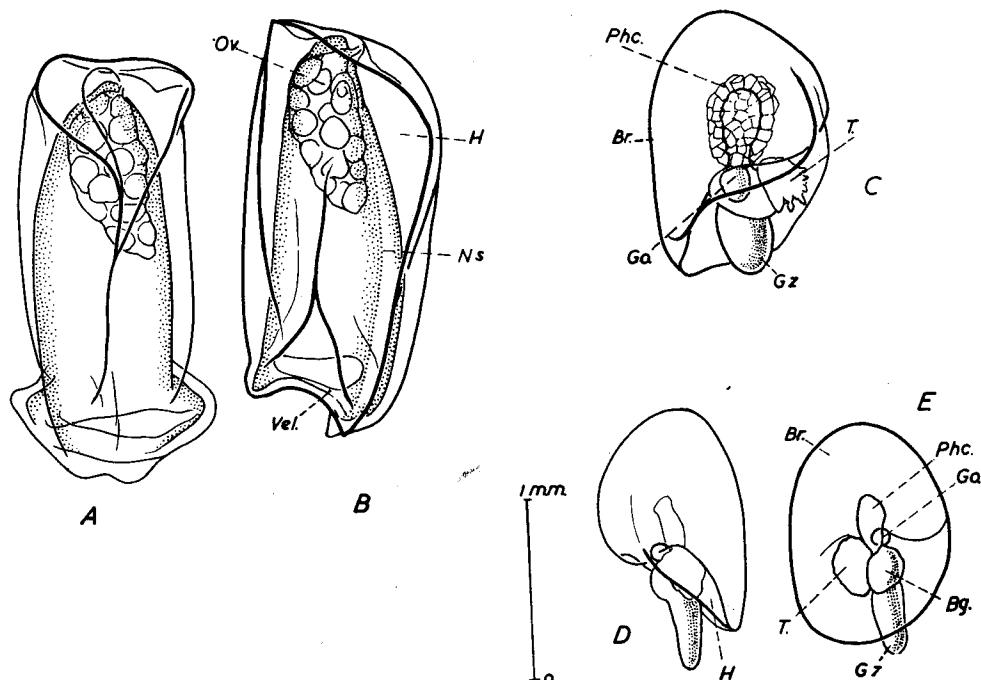


FIG. 105. *Lensia subtilis* (Chun). Eudoxid phase, Villefranche
A, B, female gonophore, $\times 24$; C, latero-ventral view of a young eudoxid, $\times 24$; D, E, bract, $\times 25$
Br = bract; Go = gonophore; Gz = gastrozooid; H = hydroecium; Ns = nectosac;
Ov = ovary; Phc = phyllocyst; T = tentacle; V = velum (from Totton, 1954, fig. 59).

***Lensia subtilis* var. *chuni* (*nom-nov.*)**

L. subtilis var. Totton, 1954, page 114

I gave figures (1954, fig. 57B, C, D) of some specimens that had shorter somatocyst pedicels than usual. These pedicels are, however, longer than in *L. meteori*. The general shape of the anterior nectophore resembles that of *subtilis* rather than of *meteori*.

***Lensia meteori* (Leloup, 1934)**

Text-figure 107

Galette meteori Leloup, 1934

Lensia meteori Totton, 1954

This species has been found on many occasions since Leloup described it.

Polygastric phase

Anterior nectophore (text-fig. 107): Up to 5 mm in length, resembling that of *L. subtilis* but the 'basal facet' is almost vertical, the mouth-plates much larger (see Leloup, 1934, fig. 6C); the pedicel of the somatocyst very short, and the somatocyst itself not globular but laterally produced.

Posterior nectophore: Unknown (if any).

Because the anterior nectophore so much resembles that of *subtilis* I refer the species to the genus *Lensia* in spite of the fact that no check on the lateral radial canals of the posterior nectophore (if any) can be made.

Eudoxid phase – not identified.

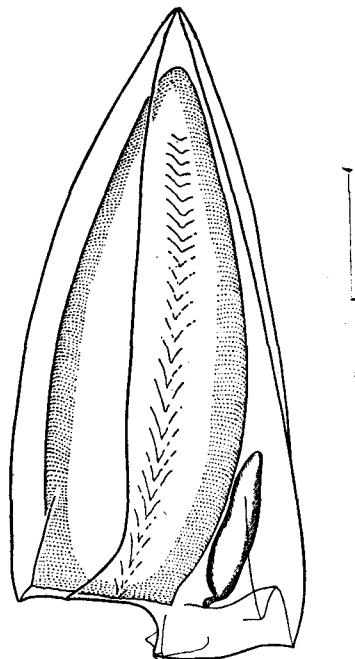
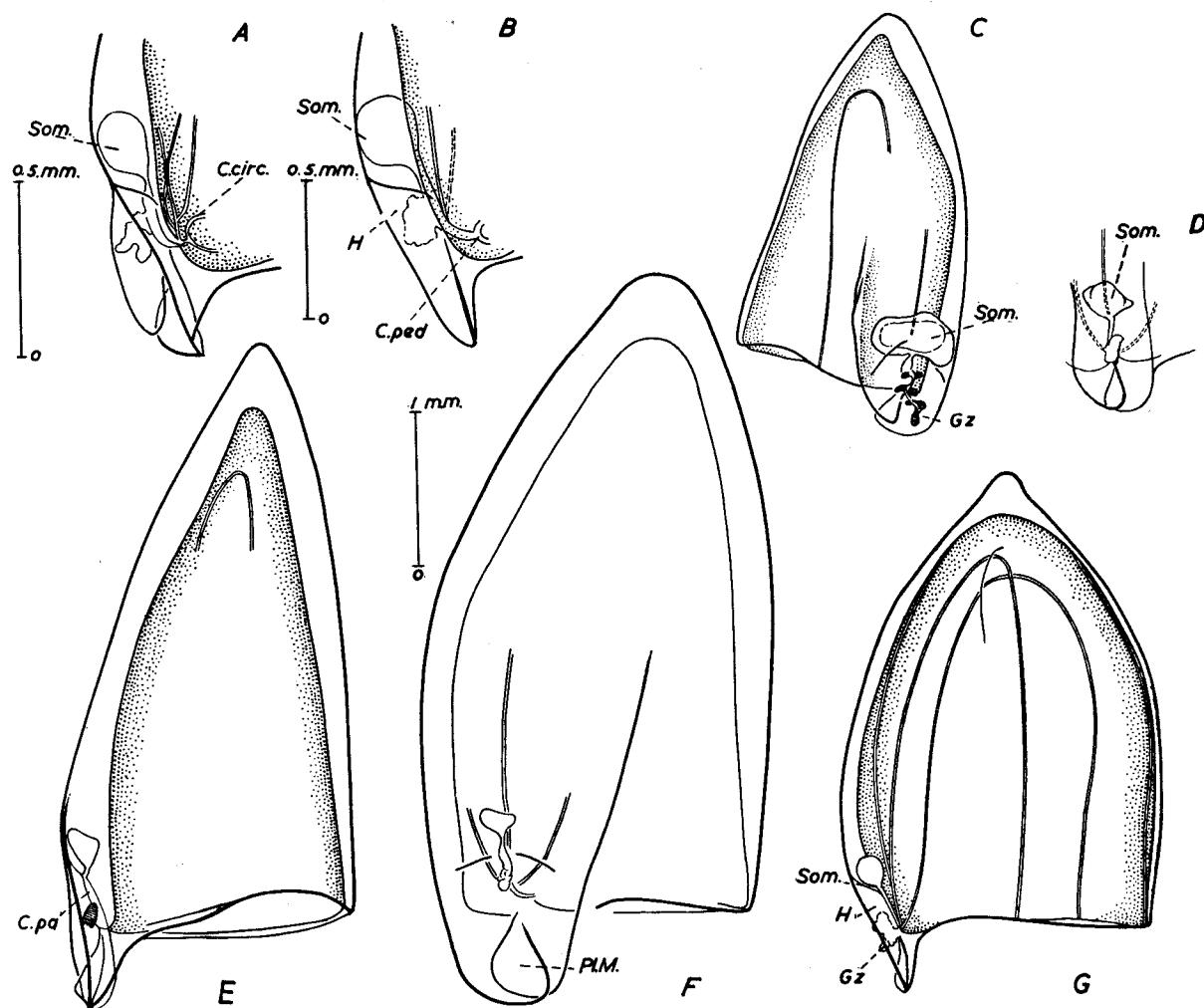


FIG. 106. *Lensia achilles* Totton
Lateral view of the holotype
anterior nectophore from 'Dis-
covery' St. 85, $\times 5$ (from Totton,
1941, fig. 6).

FIG. 107. *Lensia meteori* Leloup. Polygastric phase

A, B, D, somatocysts of anterior nectophores from the Adriatic; C, ventral view of a somatocyst from Port Sudan; E, F, anterior nectophores from S.W. Ireland; G, from 'Discovery' St. 1587. A, $\times 47$; B, $\times 38$; C, D, $\times 20$; E, F, G, $\times 20$
C.cir. = circular canal; *C.ped.* = pedicular canal; *Gz* = gastrozooid; *C.pa.* = pallial canal; *H* = hydroecium;
Som. = somatocyst (from Totton, 1954, fig. 60).

Lensia achilles Totton, 1941

Text-figure 106 (see p. 170)

A five-ridged, deep-water form, coloured deep or bright orange in life.

Polygastric phase

Anterior nectophore (text-fig. 106): Five complete ridges, the basal ends of laterals bending dorsad. Vault of hydroecium level with the ostium, with a deep notch on the baso-ventral margin. Somatocysts spindle-shaped. The nectophore shown by Bigelow (1913, fig. 2) almost certainly belongs to this species, but his descriptions of the two nectophores may refer to more than one species.

Posterior nectophore: The nectophore shown by Bigelow (1913, Pl. 6, figs. 3, 4) may belong to this species.

Eudoxid phase – undescribed.

Lensia lelouveteau Totton, 1941

Text-figures 108, 109

Lensia multicristata forme *grimaldii* Leloup, 1934

A very distinctive, rather rare little multicristate, mid-water species which somewhat resembles *L. meteori* in general outline and shape of somatocyst. Dr. Leloup very kindly allowed me to examine his 'Meteor' specimens in 1940. It has been taken in many 'Discovery' tow nettings.

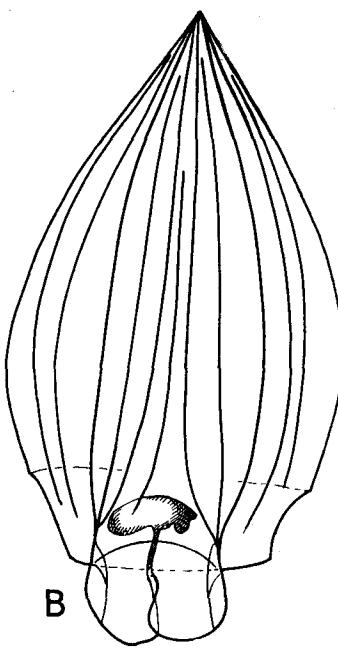
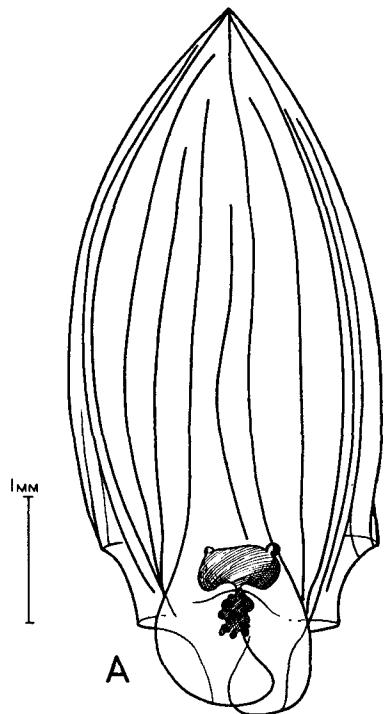


FIG. 108. *Lensia lelouveteau* Totton. Polygastric phase
Anterior nectophore, ventral view, $\times 10$, from Meteor Sts. 277, 246,
1,000–800 m (from Totton, 1941, fig. 24)

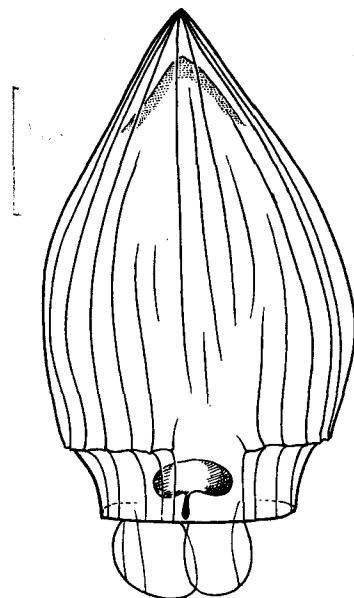


FIG. 109. *Lensia lelouveteau* Totton
Polygastric phase
Anterior nectophore, dorsal view,
 $\times 17$, from 'Meteor' St. 246 (from
Totton, 1941, fig. 23, part).

Polygastric phase

Anterior nectophore (see Leloup, 1934, fig. 9; and text-figs. 108, 109): The crests, not all of which reach the apex, are in five groups, three or more dorsal, seven or eight in each lateral group, and from four to six ventro-lateral ones. There is a cross-ridge (velar) about 0.75 mm above the ostium. The somatocyst is squat and kidney-shaped. The ventro-basal margins of the hydroecium are well rounded.

Posterior nectophore: (If any) unknown. *Eudoxid phase* – unknown.

Lensia reticulata Totton, 1954

Text-figure 110

A rare, small, multistriate form with cross-connecting ridges, and a velar ridge about 0.5 mm above the ostium. I am satisfied that the cross ridges are not due to shrinkage.

Polygastric phase

Anterior nectophore (text-fig. 110): About 2.75 mm in length.

The hydroecium is deep, with a notch on the ventral side. The baso-ventral margins rounded angular. The somatocyst is short and ovoid in shape. The horizontal velar ridge connects up the basal ends of half-a-dozen longitudinal ridges on either side as in *L. exeter*.

Posterior nectophore: (If any) unknown. *Eudoxid phase* – unknown.

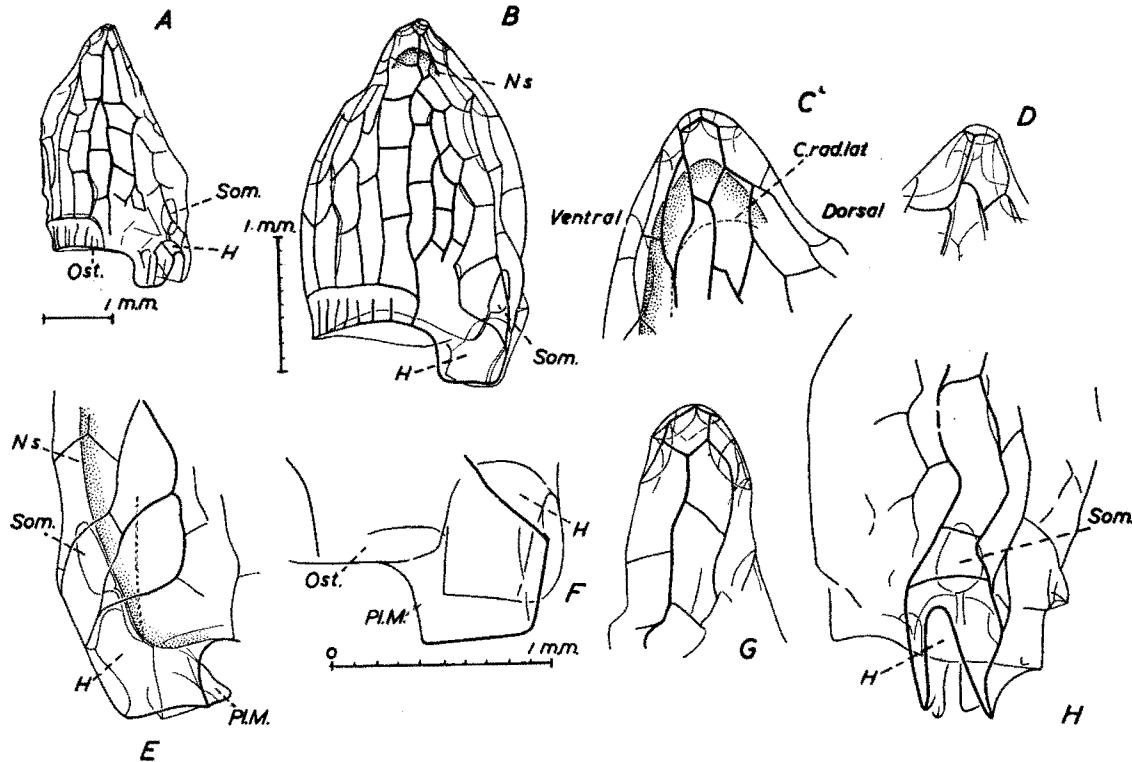


FIG. 110. *Lensia reticulata* Totton. Polygastric phase, anterior nectophores, 'Discovery' St. 1585, 1,400–700 m

A, D, F, the whole, the apex and the base of a larger specimen; B, E, H, C, G, the whole, two views of the base and two of the apex of a smaller specimen. A, $\times 9$; B, $\times 18$; C–H, $\times 29$
H = hydroecium; *Som* = somatocyst; *Ns* = nectosac; *C.rad.lat* = lateral radial canal; *Ost* = ostium;
Pl.M = mouth-plate (from Totton, 1954, fig. 61).

Lensia hardy Totton, 1941

Text-figure 111

A five-ridged form closely related to both *L. fowleri* and *L. challengeri*.

Polygastric phase

Anterior nectophore: Up to 14·5 mm in length. Hydroecium about 1 mm deep, extending below the base of the somatocyst, lying at the level of the ostium. No baso-dorsal tooth. Mouth-plates more than half the diameter of the ostium in length. There is an extensive notch in the baso-ventral ridge.

Posterior nectophore: Known but undescribed.

Eudoxid phase – known but undescribed.

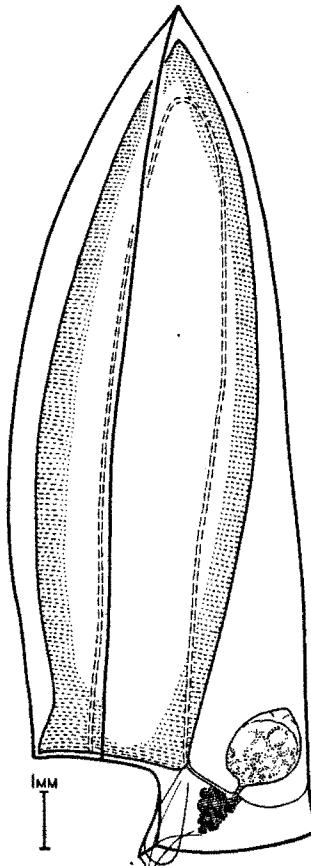


FIG. 111. *Lensia hardy* Totton
 Lateral view of the anterior nectophore, $\times 5$, 'Discovery'
 St. 672 (from Totton, 1941, fig. 10).

Lensia fowleri (Bigelow, 1911)
Text-figures 112, 113

Diphyes fowleri Bigelow, 1911a

For a good figure see Bigelow, 1911a, plate 28, figure 5.

A common five-ridged form whose globular somatocyst lies below the level of the ostium; first described from the Bay of Biscay, and taken in the Mediterranean (Bigelow & Sears, 1937, p. 139) at the rate of 250 per cu. metre of water. It resembles in general both *L. hardy* and *L. challengerii*, but is distinguished at once by the position of the somatocyst.

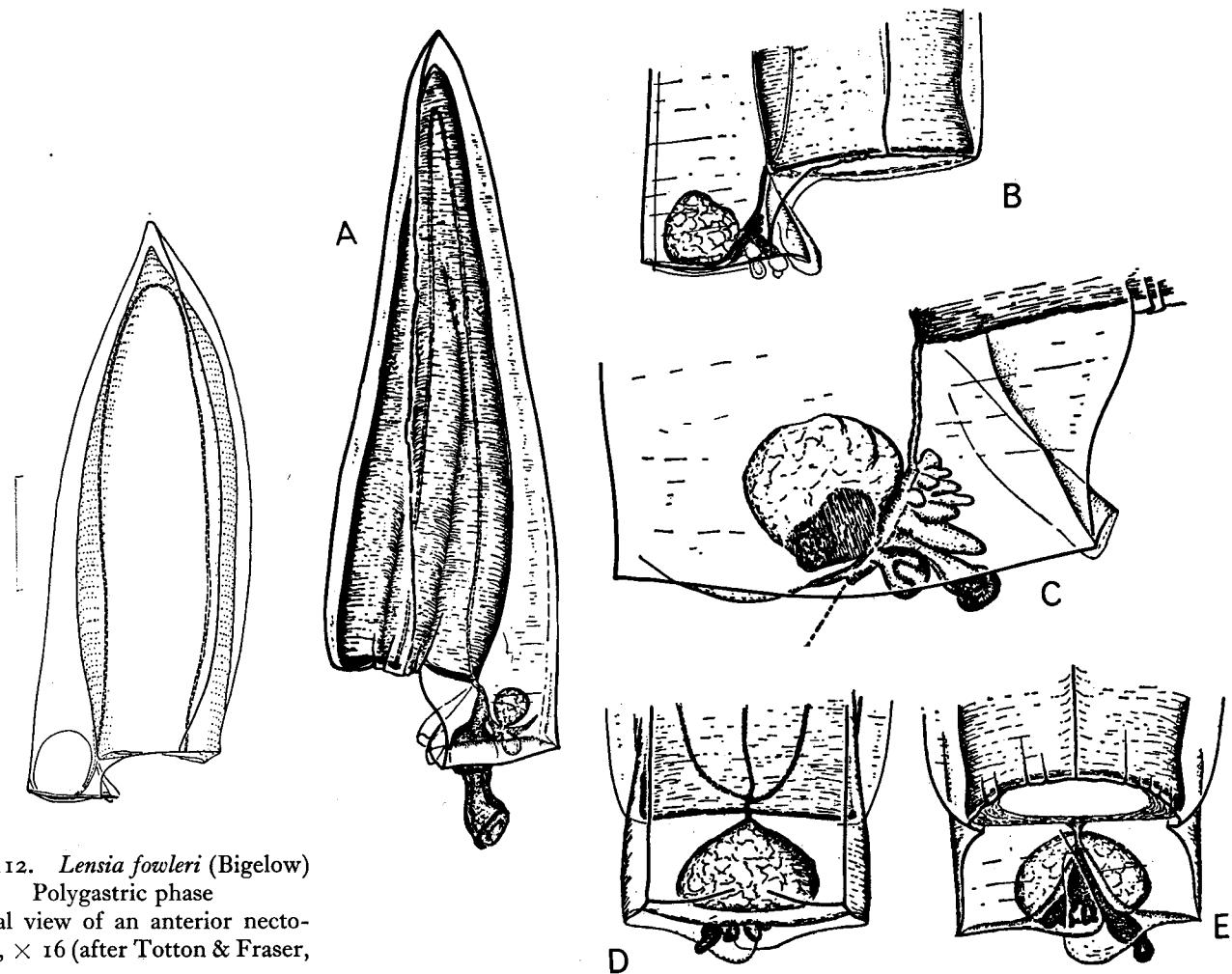


FIG. 112. *Lensia fowleri* (Bigelow)

Polygastric phase

Lateral view of an anterior nectophore, $\times 16$ (after Totton & Fraser, 1955).

FIG. 113. *Lensia fowleri* (Bigelow). Polygastric phase. Anterior nectophores
A, lateral view of a specimen from the Bay of Biscay, $\times 2.5$; B, basal part of another
specimen, 7.6 mm long; C, basal part of a large specimen, showing the bud of the
posterior nectophore; D, ventral view; E, dorsal view of the specimen shown in B
(after Bigelow & Sears, 1937, figs. 36-39)

Polygastric phase

Anterior nectophore (text-figs. 112, 113): Five longitudinal ridges, the bases of the laterals bending

ventrad. The ventro-basal area extends well below the ostium, and the globular somatocyst contained in it lies wholly below the level of the ostium, its pedicular canal descending almost vertically. There is no baso-dorsal tooth.

Posterior nectophore: Well known, but not described. About three-quarters the length of the anterior one. The apico-ventral corner of the right hydroecial wing, where it articulates with the anterior nectophore, is triangular in optical section as shown by Bigelow & Sears (1937 for *L. conoidea*) and not square as shown by me (1954, text-fig. 56 for *L. conoidea*). It slightly overhangs the hydroecium in the form of a rounded tooth.

Eudoxid phase: Not described hitherto. The elongated bract has a rounded tip. Only one of the sutural ridges is well marked. There is a notch in the margin of the neck-shield where it passes over one of the hydroecial ridges. The bract is about 4·5 mm long and nearly 2 mm in greatest diameter. The head-piece is twice the length of the neck-shield and its somatocyst is globular. The gonophores which are elongated, up to 5 mm in length and 1·3 mm in diameter, have no mouth-plate, whereas in *L. conoidea* one is present. The females bear about sixteen eggs. This description is based on specimens associated with those of the polygastric phase taken by Dr T. Gamulin in the Adriatic.

Lensia havock Totton, 1941

Text-figure 114

A seven-ridged form with a very deep hydroecium. It was taken in at least ten closing nets by 'Discovery' between 635 m and 300 m.

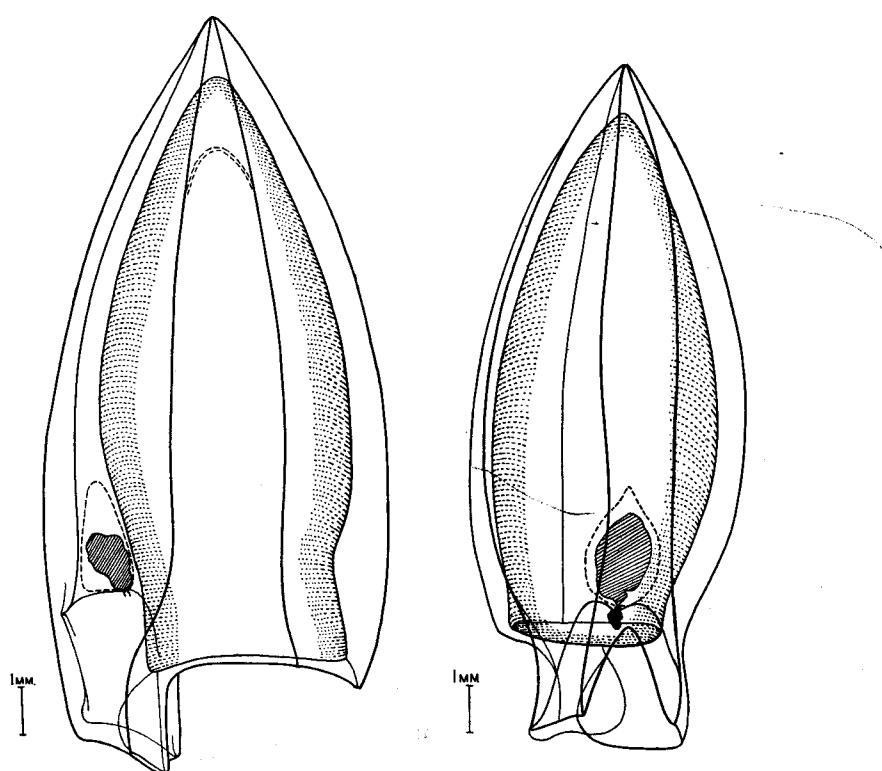


FIG. 114. *Lensia havock* Totton
Lateral and ventral views of an anterior nectophore, $\times 5$, 'Discovery' Sts. 1917, 100C, 1,400–100 m (from Totton, 1941, figs. 17, 18)

Polygastric phase

Anterior nectophore (text-fig. 114): Up to 16.5 mm in length. Seven complete ridges, the ventrolaterals bending ventrad basally to run onto the mouth-plate. The hydroecium which is very deep, extends well above the level of the ostium, and the ventral wall has a pronounced slit that extends nearly up to its upper limit. The somatocyst is short, spindle-shaped or club-shaped.

Posterior nectophore: Unknown.

Eudoxid phase – not identified.

Lensia exeter Totton, 1941

Text-figure 115

Polygastric phase

Anterior nectophore (text-fig. 115): Up to 9.5 mm in length, multistriate, five groups of three ridges. A transverse one on ostial ridge, distant 1 mm above ostium, connects the basal end of the lateral ridges of each side and runs down to the ostial margin near the dorsal side. The somatocyst is very long and spindle-shaped. The deep hydroecium is open on the ventral side.

Posterior nectophore: Unknown.

Eudoxid phase – not identified.

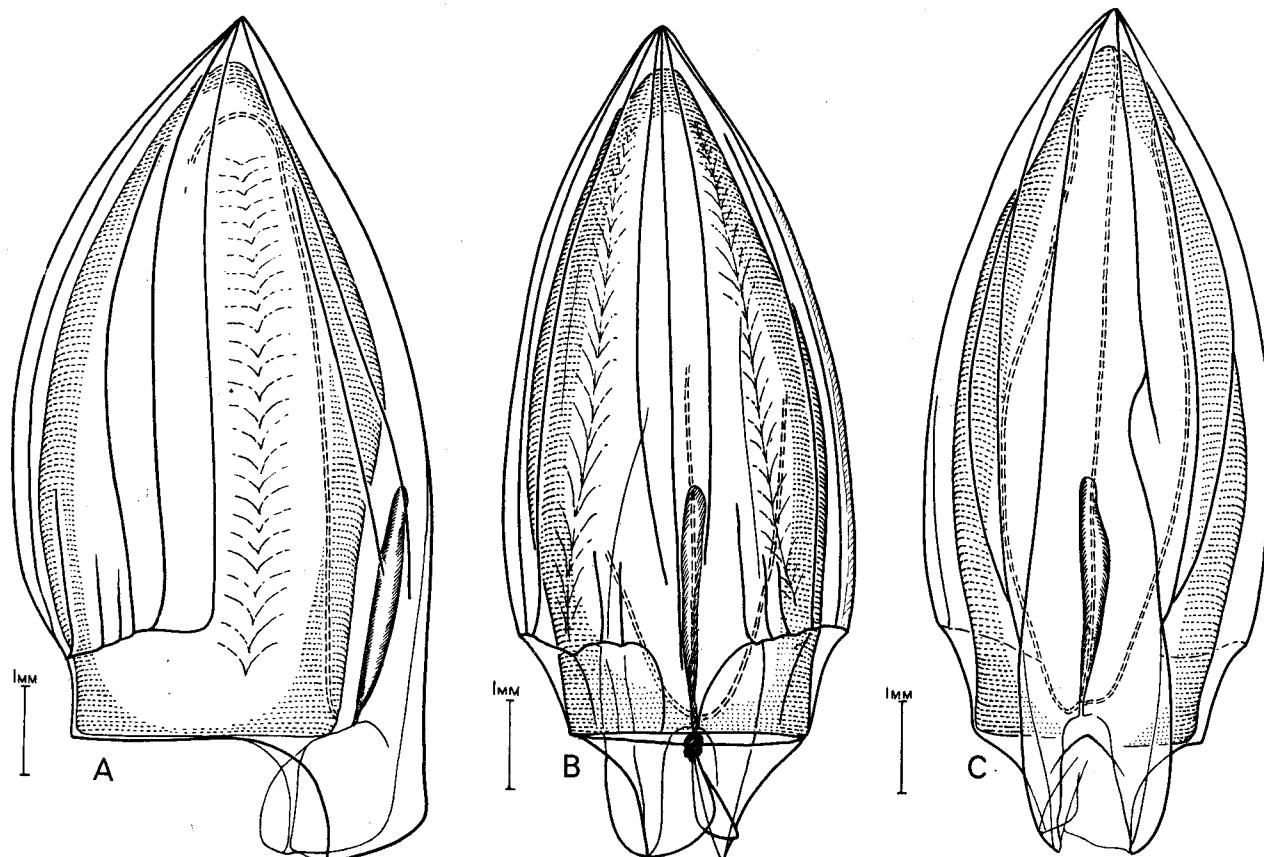
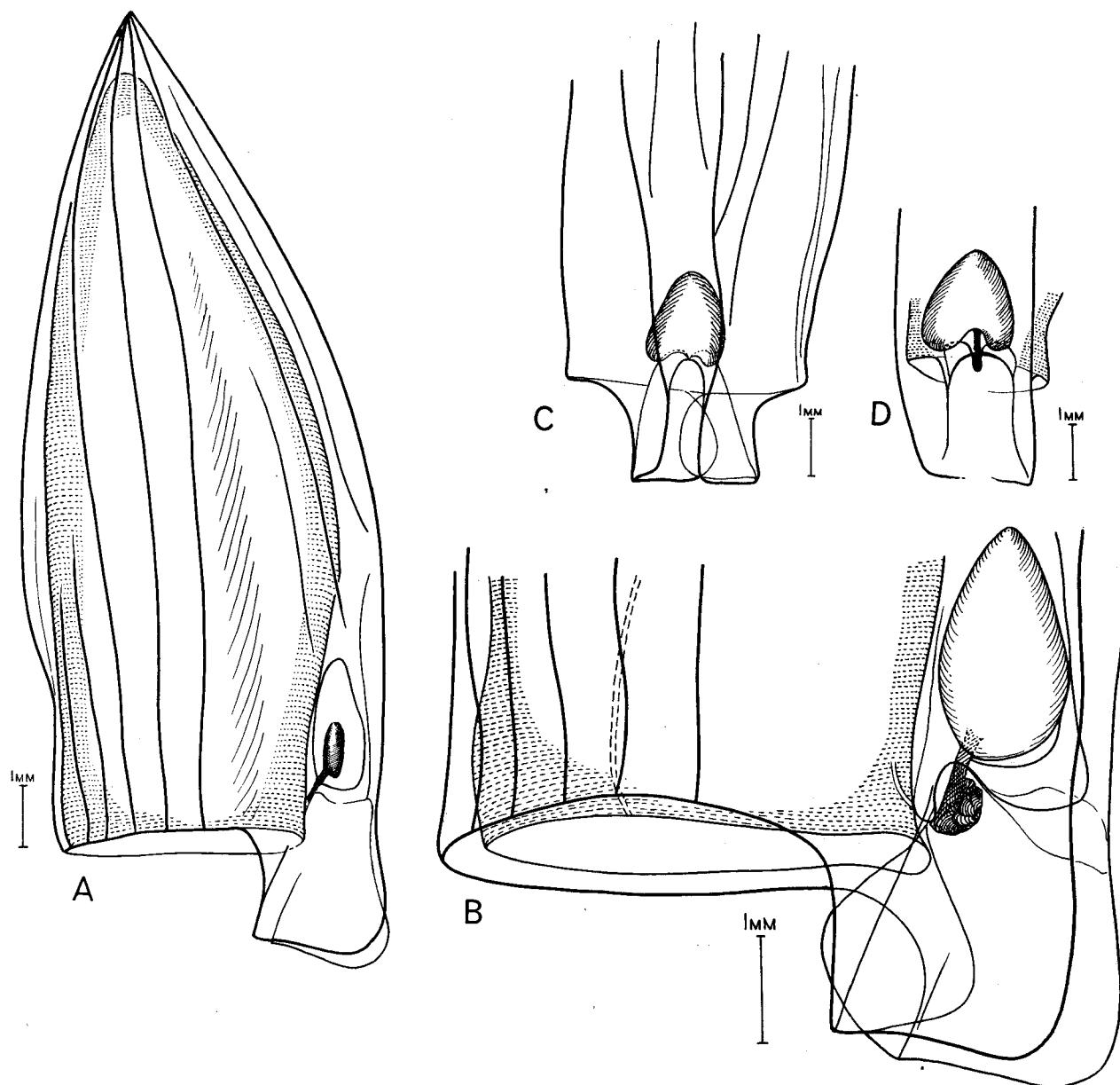


FIG. 115. *Lensia exeter* Totton

Lateral, dorsal and ventral views of an anterior nectophore, $\times 9$, from 'Discovery' St. 675, 750–500 m (from Totton, 1941, figs. 1–3)

FIG. 116. *Lensia hostile* Totton

A, lateral view of an anterior nectophore, $\times 5.5$, 'Discovery' St. 1743, 2,100–1,150 m; B, base of the same, $\times 10$; C, D, ventral views of the base of an anterior nectophore and of the hydroecium and somatocyst, $\times 5$, 'Discovery' St. 1571, 1,400–1,000 m (from Totton, 1941, figs. 20–22)

Lensia hostile Totton, 1941
Text-figure 116

Polygastric phase

Anterior nectophore (text-fig. 116): Up to 15.5 mm in length. Multistriate. There is a dorsal group of three or four longitudinal ridges cut off from reaching the ostial margin by two converging grooves; two dorso-lateral groups of three or four complete ridges; and two ventro-lateral groups of three or four incomplete ridges. The hydroecium is deep, with an open slit on the ventral side. The somatocyst is heart-shaped, apex uppermost.

Posterior nectophore: Unknown.

Eudoxid phase – not identified.

Lensia grimaldi Leloup, 1933

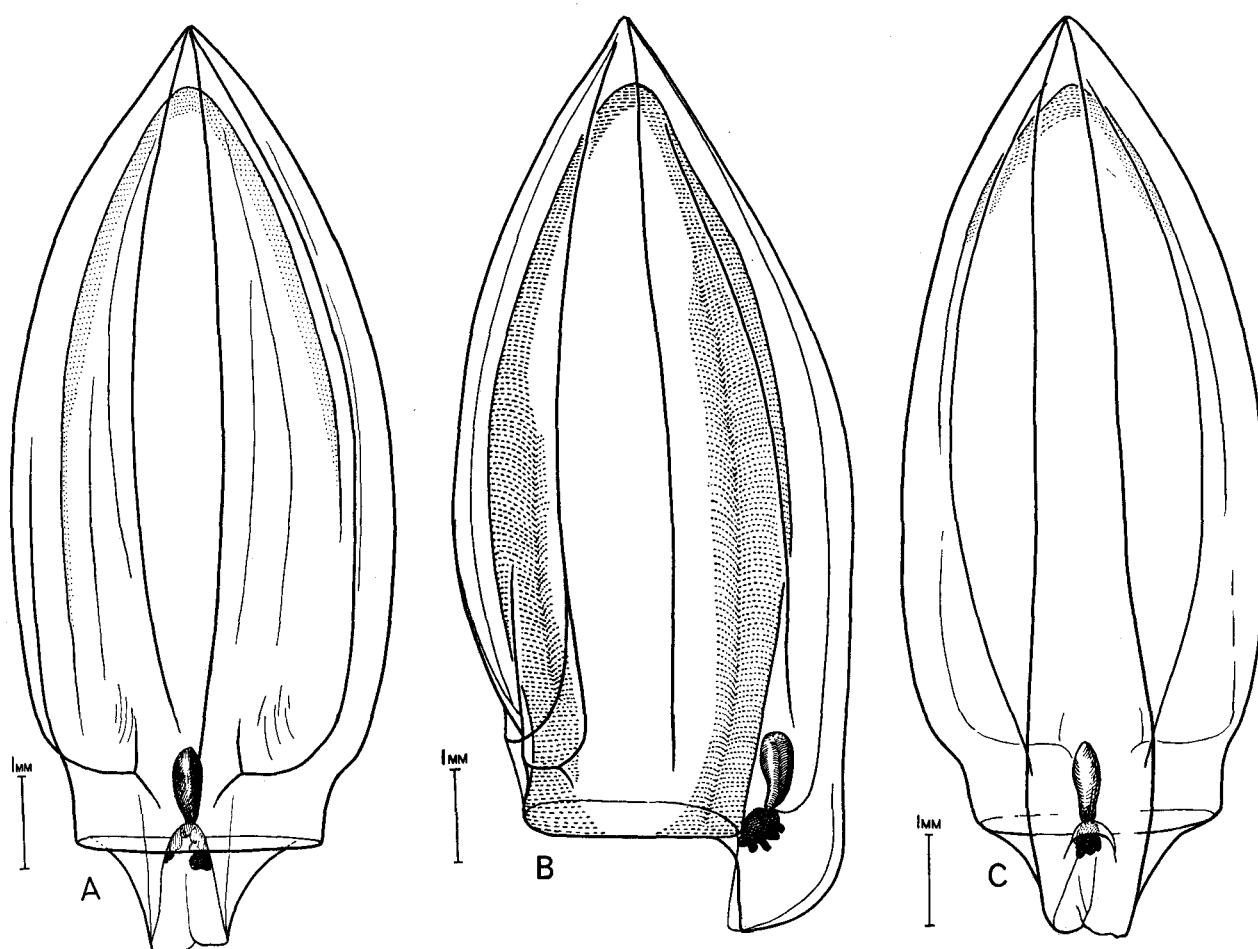
Text-figure 117

L. grimaldi Totton, 1941

A midwater form.

Polygastric phase

Anterior nectophore: Multistriate with a partial (dorsal region) ostial ridge. There is a dorsal ridge (or group) with a (sometimes a third incomplete one present) pair of longitudinal crests (see Totton, 1941, fig. 29); pair of lateral ridges (or group) with a pair of crests on each; and a ventral group of four crests. The bases of the dorso-lateral ridges run down dorsad to near the mid-dorsal point of the ostial margin. Just short of this point they join an incomplete (basal part of) dorsal ridge. The hydroecium is deep, not rising much above the ostial level, with a well rounded ventro-basal margin, and open ventrally. The somatocyst is short and club-shaped.

Posterior nectophore: Unknown.*Eudoxid phase* – not identified.FIG. 117. *Lensia grimaldi* (Leloup)Dorsal, lateral and ventral views of an anterior nectophore, $\times 9$, 'Discovery' St. 282 (from Totton, 1941, figs. 26–28)

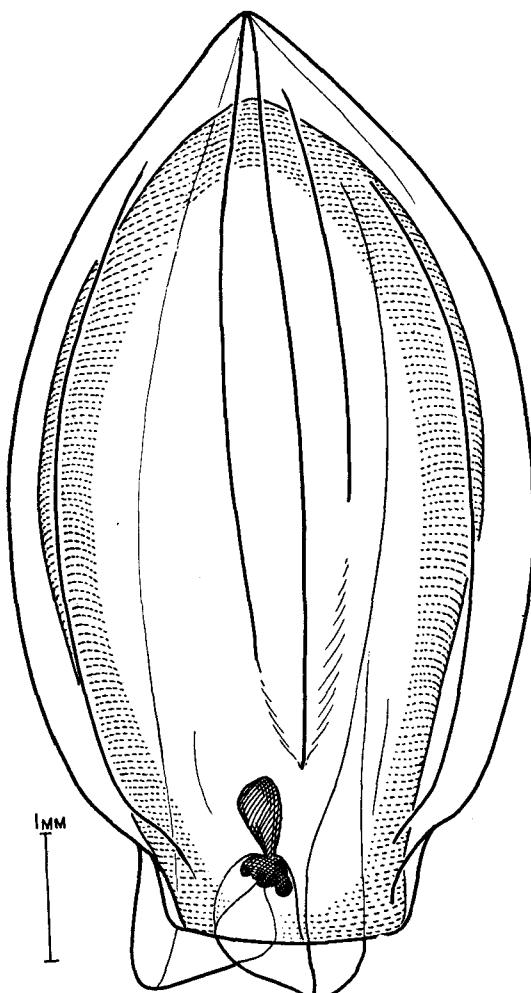


FIG. 118. *Lensia ajax* Totton
Dorsal view of an anterior nectophore, $\times 17$,
'Discovery' St. 282 (from Totton, 1941, fig. 4).

Lensia ajax Totton, 1941
Text-figure 118

Polygastric phase

Anterior nectophore (text-fig. 118): About 8 mm in length, with five groups of three (sometimes two and occasionally four) longitudinal ridges, without oral ridge. One of the dorsal group of three ridges is often incomplete basally or absent. A rudimentary ridge (or two) is present in the basal region between the dorsal and the lateral groups. The ridges of the two ventro-lateral groups are irregular and often incomplete. The somatocyst is short, oblique and club-shaped. The hydroecium does not extend above the level of the ostium, and is open on the ventral side.

Posterior nectophore: Unknown.

Eudoxid phase – not identified.

Genus: **MUGGIAEA** Busch, 1851

Type species: *Muggiae kochi* (Will, 1844).

Species in which the small pentagonal anterior nectophore develops a complete dorsal ridge, but no conspicuous ostial teeth. The mouth-plate is divided, its baso-lateral angles not produced. The hydroecium is deep. No posterior nectophore is produced. The comparative lengths of the hydroecium and somatocyst are specifically diagnostic. Two species are very common. Four in all have been described. *Muggiae bargmannae* occurs only to the southward of the Antarctic convergence, and in the Arctic.

I am inclined to think that *Dimophyes*, in whose only species the posterior nectophore is obsolescent, has affinities with *Muggiae*.

For the history of the systematic treatment of these forms see Bigelow (1911b); for references Moser (1925); for development, Chun (1882, 1913) and Russell (1938); for the occurrence of *M. atlantica* and *M. kochi* in the English Channel see Russell (1934); Southward (1962).

***Muggiae kochi* (Will, 1844)**
Plate XXXII, figures 1, 2

(1) *Polygastric phase*

Diphyes kochii Will, 1844; Busch, 1851; Claus, 1884; Stiasny, 1911a, 1912

Muggiae pyramidalis Busch, 1851

Muggiae kochii Chun, 1882, 1888a, 1892; Fewkes, 1884; Graeffe, 1884; Chun, 1885; Claus, 1885; Haeckel, 1888b; Schneider, 1898; Stiasny, 1911a, 1912; Moser, 1925; Russell, 1934.

Non *M. kochi* Bourne, 1889 (= *M. atlantica*); Murbach and Shearer, 1903 (= *D. chamissonis*); Bigelow, 1911a, 1911b
(= *Lensia multi-cristata*)

Monophyes primordialis Claus, 1874; Chun, 1882, 1885

(2) *Eudoxid phase*

Ersaea pyramidalis Will, 1844, Taf. II, figure 27

Eudoxia eschscholtzii Busch, 1851, Taf. IV, figures 7–10, Taf. V, figures 1–9; Leuckart, 1853; Chun, 1882, Taf. XVII,
figure 3; 1888a, 1892

Non *E. eschscholtzii* Johannsen & Levinsen, 1903 (= *Dimophyes arctica*)

A common and often described species which has received a good deal of attention at Plymouth from F. S. Russell (1934). Its development was studied by Chun (1882, 1913). For an account of the chequered history of the systematic treatment of the species and a good description see Moser (1925, p. 100). Chun (1882, p. 1171) referred to the larva as the first generation (*Monophyes primordialis*), to the definitive nectophore as the second generation (*Muggiae kochii*) and to the eudoxid as the third generation (*Eudoxia eschscholtzii*).

Polygastric phase

Anterior nectophore (text-fig. 119A): The nectophore is five-ridged, and the somatocyst spindle-shaped, and arises close to the nectosac as in the other species of the genus. Russell (1934) found that specimens preserved in formalin varied in length (ostium to apex) from 2·3 mm to 4·9 mm, the

majority lying between 2·7 and 4·0 mm. The relatively short somatocyst measured from ostium to summit 51–52% of the height of the nectosac measured from the ostium, and the depth of the hydroecium measured 15–16% of the height of the nectosac.

Posterior nectophore: Not developed.

Eudoxid phase

Figures were published by Will (1844); Busch (1851); and Chun (1882, Taf. XVII, fig. 3). It is not known how to distinguish these eudoxids from those of *M. atlantica*. They are unisexual.

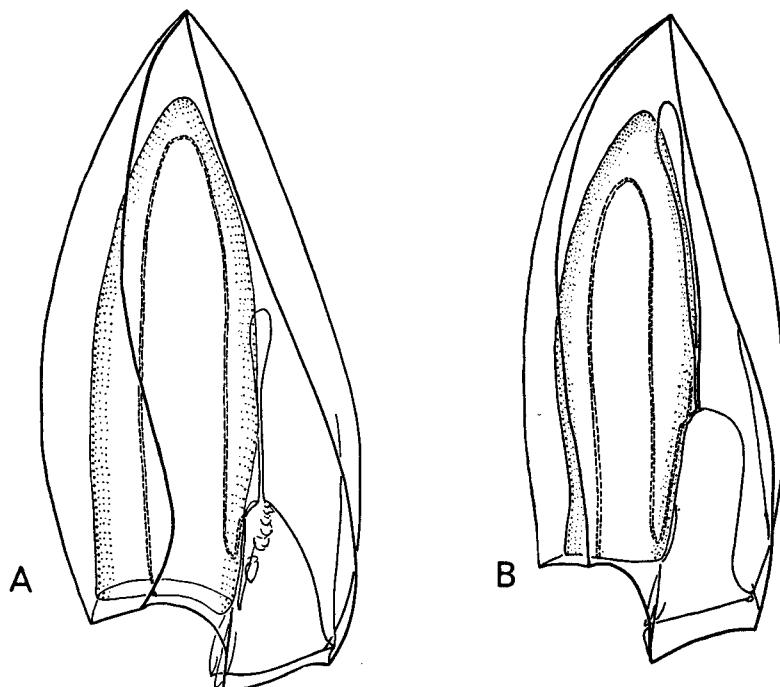


FIG. 119. A. *Muggiaeae kochi* (Will), $\times 15$
B. *Muggiaeae atlantica* Cunningham, $\times 15$
Lateral views of the polygastric phase (from Totton & Fraser, 1955)

***Muggiaeae atlantica* Cunningham, 1892**

Plate XXXII, figure 3

Probably a neritic form like *M. kochi*. It was first noticed by Cunningham off the Eddystone in September 1891. Russell (1934) recorded that it occurred there for an unbroken series of years from 1913 to 1924 (excepting 1915) but that in 1925 its place was taken by another species *M. kochi*. Its distribution in the English Channel and Irish Sea in 1904 was worked out by Gough (1905). The last review of its distribution was made by Bigelow & Sears (1937, pp. 99–101). Both species are warm water forms. *M. atlantica* has a longer somatocyst and deeper hydroecium.

Polygastric phase

Anterior nectophore (text-fig. 119B; see also Cunningham, 1892, figs. 1-2; Bigelow, 1911b, Pl. 7, fig. 1): Cunningham's specimens measured from 3-7 mm in length. Moser (1925, p. 106) said that the ridges were more or less strongly serrate. The hydroecium reaches up a third of the height of the nectosac. The somatocyst is long and tubular, and overtops the apex of the nectosac.

Posterior nectophore: Not developed.

Eudoxid phase

(See Russell (1938, figs. 1, 2).) Russell said that in their grosser features these eudoxids are indistinguishable from those of *M. kochi*. He gave their measurements as: total length usually 2·5 mm. His description was 'The bract is cone-shaped with a broad flat sutural surface, whose edges are raised into slight flanges. The right edge is continued downwards into a sweeping curve, while the left edge cuts away horizontally at its lower end. There is a slight cavity on the lower surface in which the somatocyst is centrally placed. The largest bract ever seen had an overall height of 1·9 mm. The gonophore bell is cylindrical and has four longitudinal ridges running from the apex to the velar opening with a spiral twist to the right. The two ventral ridges are prolonged below the velar opening and join to form a short curved mouth-plate. The right ventral ridge is more strongly developed than any of the others. Specimens with left-handed twisting or "mirror images", are common and are

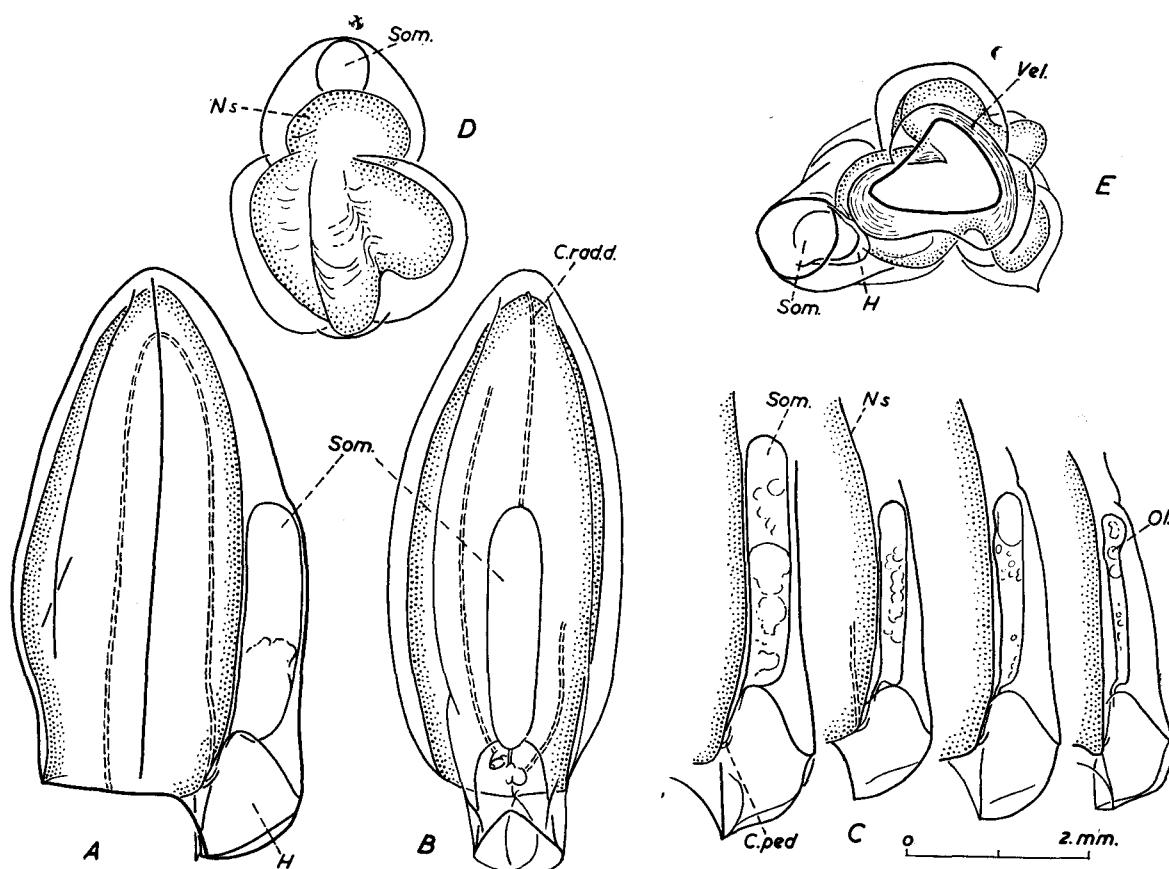


FIG. 120. *Muggiaeae bargmannae* Totton

A, B, lateral and ventral views of the holotype, 'Discovery' St. 2012, 100-50 m; C, baso-ventral parts of four paratypes from the same station, lateral view; D, E, apical and basal views of the holotype
Som. = somatocyst; *Ns.* = nectosac; *C.radd.* = dorsal radial canal; *H.* = hydroecium; *Ol.* = oil; *Vel.* = velum. All figs. $\times 12$ (from Totton, 1954, fig. 63).

presumably the second gonophores to be budded. The edges of the ridges are quite smooth, although some may show very faint traces of irregularity. The manubrium in fully developed gonophores extends more than two-thirds the length of the sub-umbrella cavity and has a pink tip. The radial canals follow the spiral courses of the ridges. One eudoxid was seen with twenty-one nematocyst batteries on its tentacle.'

***Muggiaeae bargmannae* Totton, 1954**

Text-figure 120

One of the five Antarctic and Arctic siphonophores, formerly confused with *Dimophyes arctica*, to which it bears some superficial resemblance in the preserved plankton hauls.

Polygastric phase

Anterior nectophores (text-fig. 120): The convex longitudinal folds which form on contraction of the nectosac are not surmounted by crests as they are in *atlantica* and *kochi*. There is only a small gap between the apex of the nectosac and that of the whole nectophore. Near the ostium the base of the dorsal fold is nearly obliterated by the approach towards each other of the lateral longitudinal folds. The somatocyst is relatively short, tubular, or sausage-shaped, varying in diameter from 0.14 mm to 0.5 mm according to its content, and equals in length half the distance from apex of hydroecium to apex of nectosac. The hydroecium is shallower than that of *M. kochi*; may reach a depth of 1.75 mm and has a deep notch in the ventral wall; the base of the mid-line of this wall lies at about the same level as the ostium. There are two rounded overlapping mouth-plates about 0.9 mm length.

Posterior nectophore: Not developed.

Eudoxid phase – not identified.

Some associated gonophores from the Arctic have been examined, but at present their characteristics cannot be differentiated for description.

Distribution: *M. bargmannae* has been recorded in the Antarctic from twenty-three closing net hauls made by R.R.S.S. 'Discovery' and 'Discovery II'. At a typical station (2017) the hauls containing it were made as follows: 100–50 m; 250–100 m; 500–250 m; and 750–500 m. One specimen was identified in each haul. Thanks to Dr. Martin W. Johnson of Scripps Institution of Oceanography, La Jolla, I was able on July 3, 1962, to identify small specimens taken in the Arctic in hauls from 1,500, 1,000, 500 and 100 m to the surface. I had no details of the exact localities of these Arctic hauls. There were from one to four small nectophores in each haul, all except one being in a poor state of preservation.

It is interesting to find this species occurring in association with *Dimophyes arctica*, with which it can be easily confused, in both the Arctic and Antarctic.

Unlike *Dimophyes arctica* it has not, so far, been found in Atlantic bottom water.

***Muggiaeae delsmani* Totton, 1954**

Text-figure 121

Found in the low salinity water of the Java Sea with two other species that are characteristic of a similar environment.

Polygastric phase

Anterior nectophore (text-fig. 121): Five-ridged with shallower hydroecium than in *M. kochi*.

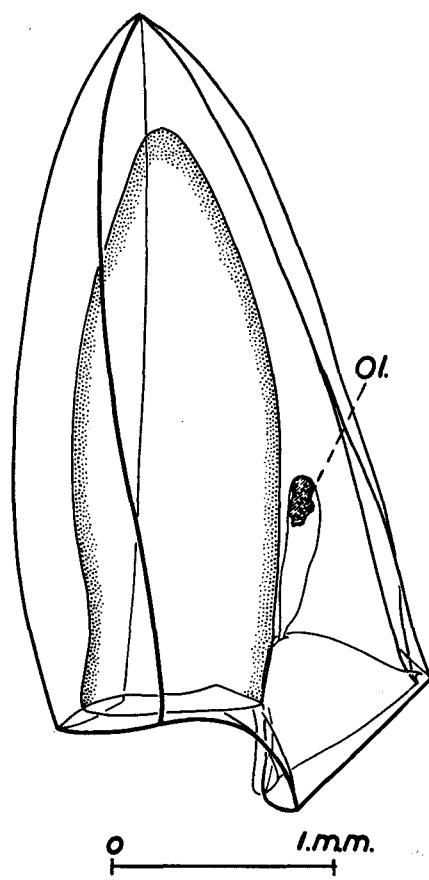


FIG. 121. *Muggiaeae delsmani* Totton
Lateral view of the holotype, $\times 19$,
from the Java Sea. *ol* = oil-drop in the
somatocyst (from Totton, 1954, fig.
55B).

such as those of the Bellinghausen and Weddell Seas, and found that it never approached the Antarctic convergence. Moser reviewed its distribution data in 1925.

Polygastric phase

Anterior nectophore (see Chun, 1897b; Moser, 1925, Pl. XXVI, fig. 5; and text-fig. 122): Up to at least 13 mm in length. The most characteristic feature is the hydroecium, where the dorsal side (mouth-plate) is undivided and the ventral side is wide open. Except for its shallow, apical end it lies below the level of the ostium. From it arises a broad spindle-shaped somatocyst, broad at the base, tapered at the apex, which reaches up to a point about one quarter of the way from the apex of the nectosac to the ostium.

Posterior nectophore (see Moser, 1925, Taf. XXVI, fig. 2): Obsolescent and reduced, with a rounded, truncated articulating surface; and an hydroecium bounded by two wings, deep proximally but shallow distally. The plane of the ostium is vertical rather than horizontal.

Eudoxid phase

(See Chun, 1897b, p. 21; Taf. 1, fig. 6.) About 9 mm in length.

Bract: Characterized by the presence of the fine basal horn of the phyllocyst in the thin, broad

The upper wall of the hydroecium is more nearly horizontal than it is in *M. kochi*. Somatocyst short, its length equal to less than one-third of the distance from apex of hydroecium to apex of nectosac; its base lying close to the nectosac.

Posterior nectophore: Not developed.

Eudoxid phase – not identified.

Genus: *DIMOPHYES* Moser, 1925

Monotypic genus for *Dimophyes arctica* (Chun, 1897b).

The genus *Dimophyes*, was regarded by Moser as forming a monotypic family Dimophyidae, but there is only one species, which seems to fall naturally into the family Diphyidae as at present understood. The posterior nectophore is reduced, half enclosed in the hydroecium, and appears to be obsolescent. The dorsal side (mouth-plate) of the hydroecium of the anterior nectophore is undivided.

Dimophyes arctica (Chun, 1897)

Plate XXXIII, figures 1, 2, 7

Diphyes arctica Chun, 1897b

Dimophyes arctica Moser, 1925; Totton, 1954

For references see Moser, 1925, page 389

This form occurs in both the Arctic and Antarctic water masses and their derivatives. Its established range of temperature is from minus 1.13° to 13.26°C , being plentiful between 1° and 2°C . Mackintosh (1934) regarded *D. arctica* as one of the species of animals typical of the coldest Antarctic regions

and long neck-shield. The head piece is broadly conical and contains the large globular main part of the phyllocyst with its apical horn.

Gonophore: Simple, about 7 mm long. There is scarcely any hydroecium. Estimated number of eggs from eighty to one hundred.

Cnidosac (see Chun, 1897b, Taf. 1, fig. 9): Kidney-shaped 0.53 mm in length. Two lateral groups of about twelve needle-shaped nematocysts 0.28 mm in length.

Genus: *CHELOPHYYES* Totton, 1932

Type species: *Diphyes appendiculata* Eschscholtz, 1829.

Diphyinae in which the medium sized anterior nectophore develops a dorsal ridge that extends only a short distance from the ostium towards the apex. It is thus quadrangular in the apical region. There are no conspicuous ostial teeth. The hydroecium is of medium depth, and claw-shaped when seen in profile. The mouth-plate is divided, its baso-lateral angles not markedly produced. The lateral radial canals of the posterior nectophore form an apical loop. There are only two species, which resemble each other more than either resembles other species.

Chełophyes appendiculata (Eschscholtz, 1829)

Plate XXXII, figure 4; Plate XXXIII, figure 6

(1) *Polygastric phase*

Diphyes appendiculata Eschscholtz, 1829; Bigelow, 1911b

D. elongata Hyndman, 1841

D. sieboldii Kölliker, 1853; Kefferstein & Ehlers, 1861; Moser, 1925

D. acuminata Leuckart, 1853; Gegenbaur, 1859

D. gracilis Gegenbaur, 1854

D. bipartita Costa, 1836; Chun, 1888b; Mayer, 1900

D. elongata Haeckel, 1888b

Chełophyes appendiculata Totton, 1932, 1954; Bigelow & Sears, 1937

(2) *Eudoxid phase*

Eudoxia campanula Leuckart, 1853; Chun, 1888b; Müller, 1870–71; Lens & van Riemsdijk, 1908

E. messanensis Gegenbaur, 1854

Eudoxoides sagittata Huxley, 1859

Eudoxia russelli Totton, 1932

Chełophyes appendiculata Totton, 1954, plate IV, figures 1, 3

Non *Diphyes appendiculata* Bigelow, 1911b, plate XI, figure 9 (= *Eudoxoides mitra*)

The most abundant and best known diphyid. Its seasonal and geographical distribution in the Mediterranean was reviewed by Bigelow & Sears (1937). Its metamorphosis was described by Lochmann (1914, p. 273).

Polygastric phase

Anterior nectophore (text-fig. 123): Only three ridges at the apex, two of them ventral. The right lateral (*sensu* Bigelow) twists in the apical region to lie dorsally. The left lateral ridge does not reach

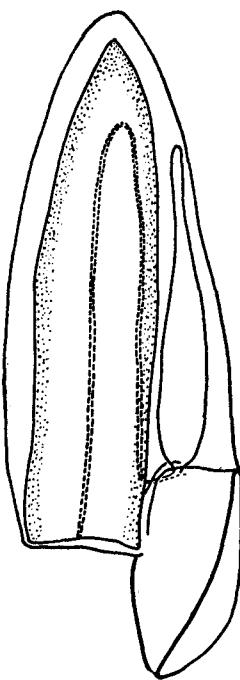


FIG. 122. *Dimophyes arctica* (Chun)
Lateral view of the anterior nectophore, 7 × 8 (from Totton & Fraser, 1955).

the apex (see Bigelow, 1911b, Pl. VIII, figs. 7, 8). Dorsal ridge very short, in the ostial region only. There are no baso-dorsal nor lateral teeth.

Posterior nectophore (see Bigelow 1911b, Pl. X, fig. 6): The basal ends of the ventral ridges end in strong teeth, the left (*sensu* Moser) always one-third longer than the other. There is a minor tooth on each at about the level of the ostium. Inside the left-hand (*sensu* Bigelow) side-wing of the hydroecial cavity is a long flap, comparable with the comb found in a similar position in species of abylopsids. It reaches over to meet the other wing and so covers in the hydroecial cavity completely. In Moser's (1925) figure 3 of a young nectophore the arrangement is different. A full description can be found in Moser (1925, p. 244).

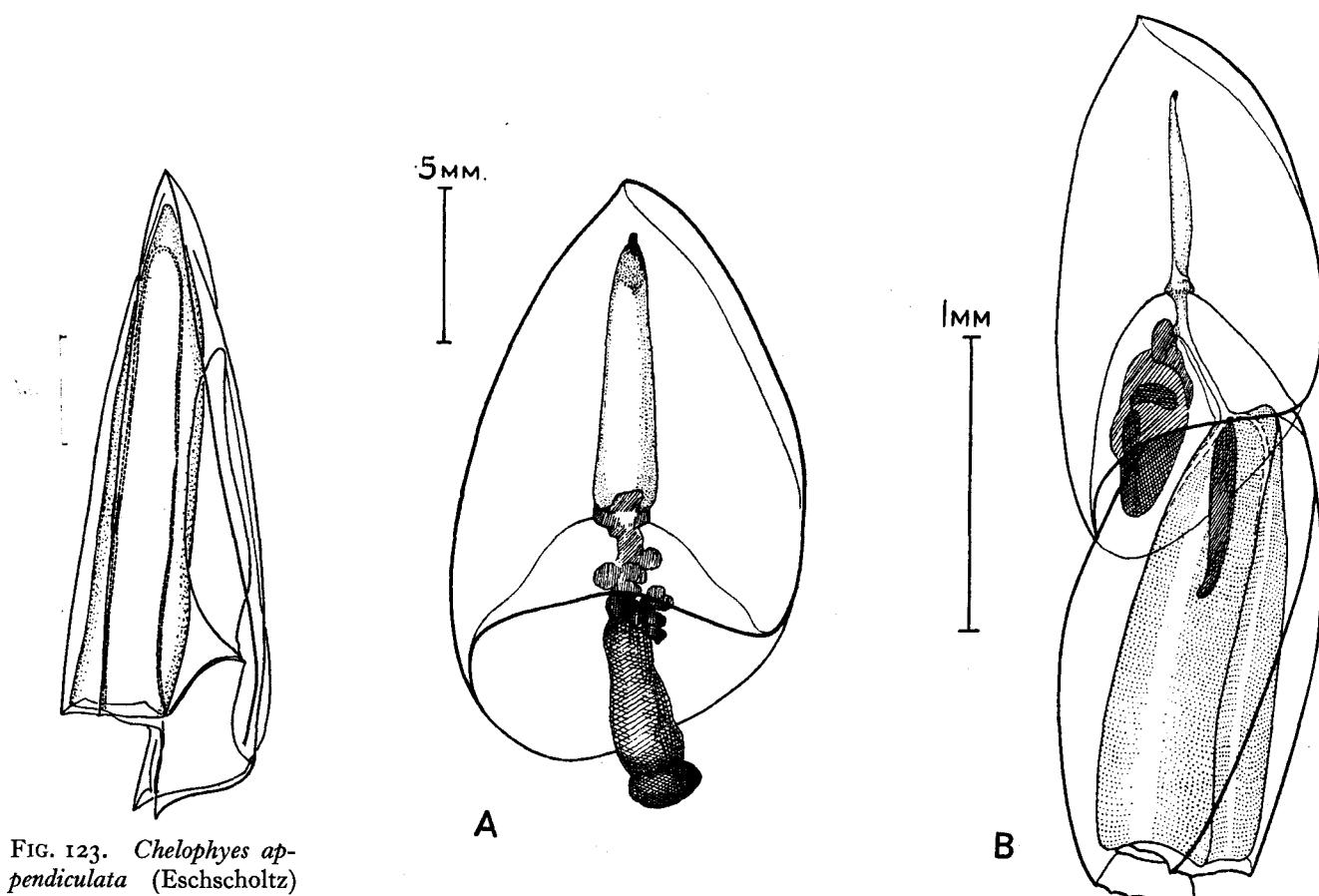


FIG. 123. *Chelophyses appendiculata* (Eschscholtz)
Lateral view of the anterior
nectophore (from Totton
& Fraser, 1955).

FIG. 124. *Chelophyses appendiculata* (Eschscholtz). Eudoxid phase
A, bract, $\times 41$; B, the whole eudoxid, $\times 39$, from Gt. Barrier Reef (from Totton,
1932, fig. 25, as *Eudoxia russelli*)

Eudoxid phase

(Text-fig. 124; see also Leuckart, 1853, Taf. 111, fig. 18; Totton, 1954, Pl. IV, figs. 1-3.) 5-6 mm long.

Eudoxids can easily be obtained from living animals at Villefranche, so that there is no longer any doubt as to their morphology. There is a deep bracteal cavity, the ventral surface meeting the sutural surface at an angle of about 75° . The somatocyst is cylindrical with a tapered apex; it reaches nearly to the apex of the sutural surface. The margin of the neck-shield of the bract is evenly rounded and smooth. The peduncle of the gonophore lies completely within the bracteal cavity, and there is no articulation between it and the margin of the bract.

Male and female gonophores are borne by different eudoxoids. The second gonophore to be budded is the mirror-image of the first. The whole eudoxoid and the male gonophore were described and figured in detail by Totton (1932, text-figs. 25, 26) as *Eodoxia russelli*. Although Leuckart's (1853) description and figure of his *Eodoxia campanella* differ in some respects (see Totton, 1932, p. 356), I now consider them to be synonymous. It was a common eudoxoid found by Leuckart at Nice. *Eodoxia messanensis* of Gegenbaur (1854) is not synonymous; it is probably the eudoxoid of *Lensia conoidea*. I discussed the literature of this in 1954 (pp. 128–29).

Progression: Notes on my observations will be found in Totton (1954, p. 129).

***Chelophyses contorta* (Lens & van Riemsdijk, 1908)**

Plate XXXII, figures 7, 8

Diphyes contorta Lens & van Riemsdijk, 1908

D. contorta Bigelow, 1911b

This species is not often taken by oceanographical expeditions. There are grounds for thinking that it may be a neritic form (see Totton, 1954, p. 130).

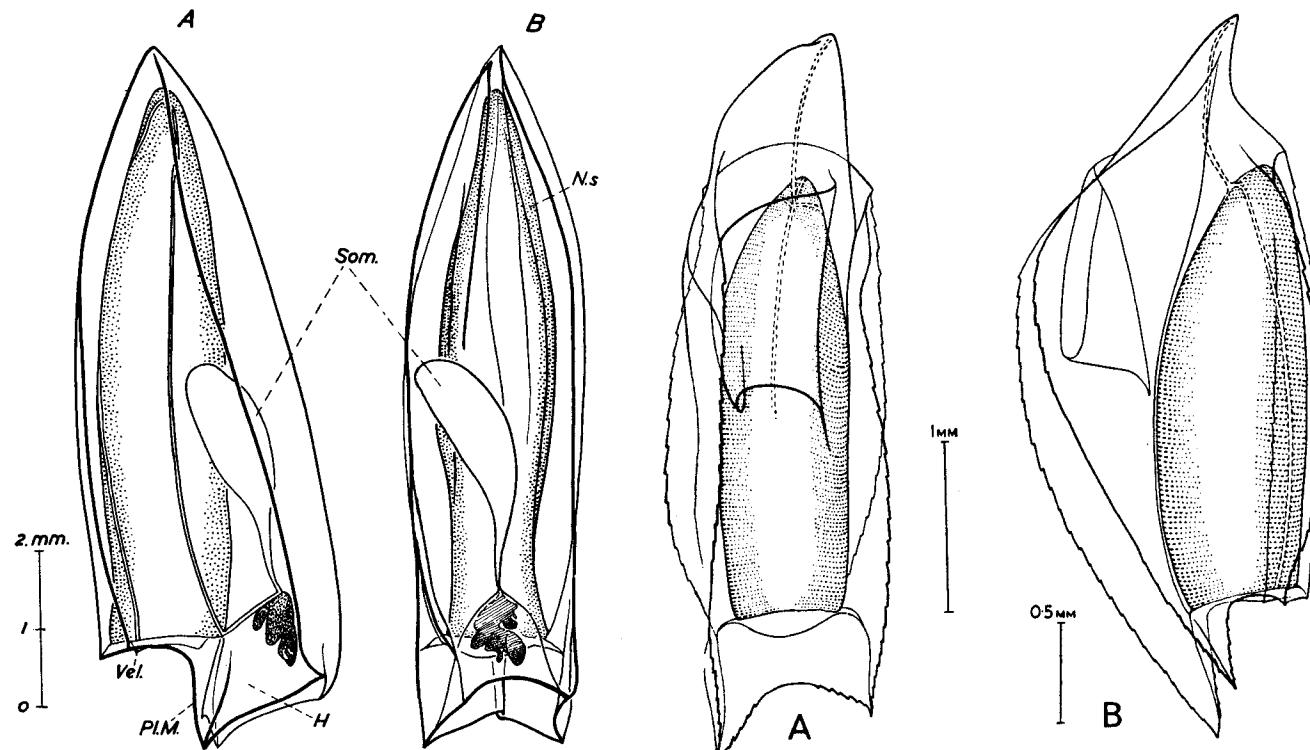


FIG. 125. *Chelophyses contorta* (L. & v. R.)
Polygastric phase. Lateral and ventral views of the
anterior nectophore, $\times 10.5$, from the Gulf of Aden.
H = hydroecium; *N.s* = nectosac; *Pl.M.* = mouth-
plate; *Som* = somatocyst; *Vel* = velum (from
Totton, 1954, fig. 65).

Polygastric phase

Anterior nectophore: About 7 mm in length (see Bigelow, 1911b, Pl. 7, fig. 8; Pl. 8, fig. 3; Moser, 1925, Pl. XIII, fig. 5; and text-fig. 125). Resembles that of *Ch. appendiculata*, but the ventral facet is twisted and the somatocyst too turns sharply to the right (*sensu* Bigelow). The right-ventral ridge

FIG. 126. *Chelophyses contorta* (L. & v. R.)
Ventral and lateral views of the posterior nectophore,
 $\times 25$, Gt. Barrier Reef (from Totton, 1932, fig. 27).

(*sensu* Bigelow) does not reach the apex. The hydroecium is shallower than that of *appendiculata*, hardly extending above the level of the ostium. The mouth-plate, as I have observed it, is always divided, although Bigelow (1911b, p. 255) says that it is not. The dorsal ridge is short and confined to the basal end as in *appendiculata*.

Posterior nectophore (text-fig. 126): It resembles that of *Eudoxoides mitra*, but lacks the dorso-apical notch found in that species.

Eudoxid phase

Very similar to that of *C. appendiculata*.

Genus: **EUDOXOIDES** Huxley, 1859

The generic name was used by Huxley for the eudoxid of *E. mitra*, which is the type species. Species in which the small pentagonal anterior nectophore has a complete dorsal ridge, but no conspicuous ostial teeth. The mouth-plate is divided, its baso-lateral angles produced into lancet-shaped wings. The lateral radial canals of the posterior nectophore form an apical loop.

Eudoxoides mitra (Huxley, 1859)

Plate XXXIII, figures 4, 5

Diphyes mitra Huxley, 1859

Diphyes gracilis Bedot, 1896 (non *D. gracilis* Gegenbaur, 1853 = *Chelophyes appendiculata*)

Diphyopsis diphoides Lens & van Riemsdijk, 1908

Diphyopsis mitra Bigelow, 1911b

Eudoxoides mitra Totton, 1932

A well-known species.

Polygastric phase (Pl. XXXIII, fig. 4)

Anterior nectophore: Up to 12 mm in length (see Bigelow, 1911b, Pl. 7, fig. 9). Not spirally twisted, with five serrate longitudinal ridges, all reaching the apex where they become smooth. There is a small baso-dorsal tooth but no laterals. The length of the part of the hydroecium below the ostial level is much greater than that of the part above. The hydroecium is truncate above, and the somato-cyst is relatively short and pear-shaped. It reaches only to the mid-level of the nectosac. The mouth-plate is divided into two serrate wings, the outer angles acute, the distal edges concave. The left-hand (*sensu* Bigelow) wing is longer than the other and bears a secondary triangular flap or tooth (see Bigelow, 1911b, Pl. 9, fig. 4).

Posterior nectophore (see Bigelow, 1911b, Pl. 10, figs. 4, 5): There is a characteristic notch between the apex and the pedicel – the apico-dorsal notch. The hydroecial canal is open except near the upper end where a broadening of the right hydroecial flap lies over a longer tongue-shaped broadening of the left to bridge the canal. There is a short basal prominence or tooth on the right, and a longer one on the left (*sensu* Bigelow). There is a prominence on the edge of each hydroecial flap about one-third of its length measured from the basal teeth.

Eudoxid phase (Pl. XXXIII, fig. 5; text-fig. 127)

About 8 mm in length (see Lens & van Riemsdijk, 1908, Pl. VII, fig. 62; Bigelow, 1911b, Pl. 11, fig. 9 – as *D. appendiculata*). Some criticisms of published figures can be found in Totton, 1932, page 359. The bract has a deep cavity and a pear-shaped phyllocyst.

The sutural surface of the bract forms an acute angle with the dorsal wall of the hydroecial cavity, so that the pedicel of the gonophore is correspondingly long. The serrate left sutural ridge curves

away to a tooth at the distal edge. From this point to the base of the other sutural ridge it is smooth and somewhat concave. The gonophores (there is no special swimming bell, though the manubrium almost vanishes after shedding sperms or eggs) have two dorso-lateral teeth and a mouth-plate with concave edge and two lateral teeth.

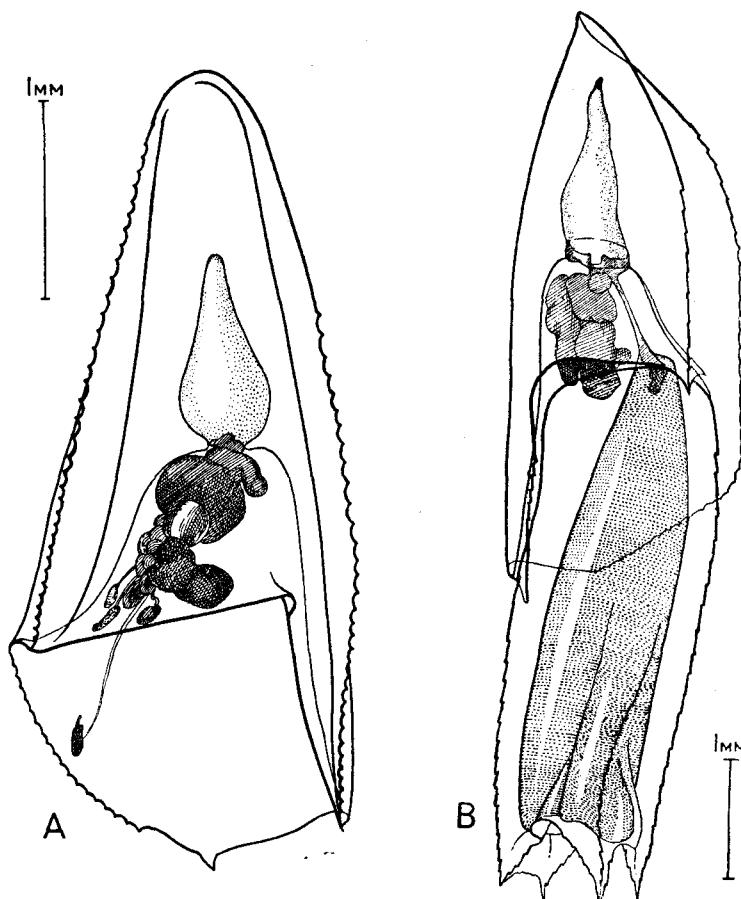


FIG. 127. *Eudoxoides mitra* (Huxley). Eudoxid phase
A, Bract, $\times 26$; B, whole animal, $\times 16$, Gt. Barrier Reef (from Totton, 1932, fig. 28)

***Eudoxoides spiralis* (Bigelow, 1911)**
Plate XXXII, figures 5, 6

Diphyes spiralis Bigelow, 1911b

Muggiae spiralis Moser, 1925

Eudoxoides spiralis Totton, 1932; Bigelow & Sears, 1937

Similar to *E. mitra*, but twisted. No posterior nectophore is produced. Common and easily recognized.

Polygastric phase

Anterior nectophore (text-fig. 128): Up to 11 mm in length (see Bigelow, 1911b, Pl. 7, fig. 4; Pl. 8, figs. 1, 2; Moser, 1925, Taf. 1, fig. 6). There are five twisted longitudinal ridges, but the left ventral ridge meets the right before it reaches the apex at which point there are in consequence only four ridges. The basal ends of the two ventral ridges are dissimilar. That of the right ventral ridge runs down to a deep notch in the ventral wall of the hydroecium. The basal end of the left ventral

ridge curves towards the mid ventral line and stops short at the level of the ostium. There are no dorsal or lateral teeth at the level of the ostium. The hydroecium is rather short and pointed at its apex, not truncated as in *E. mitra*. Its base is markedly asymmetrical. Its baso-lateral margins are concave (see Bigelow, Pl. 8, fig. 1), and each ends dorsally in a pronounced tooth. The mouth-plate is divided into two lanceolate wings of which the right-hand (*sensu* Bigelow) is much the larger (see Bigelow, Pl. 9, fig. 3). The left-hand wing bears a triangular flap or tooth as in *E. mitra*. The somatocyst is cylindrical, rather more than half as long as the nectosac, and lies obliquely to the right of the main axis (see Bigelow, Pl. 8, fig. 2).

Posterior nectophore: Not developed.

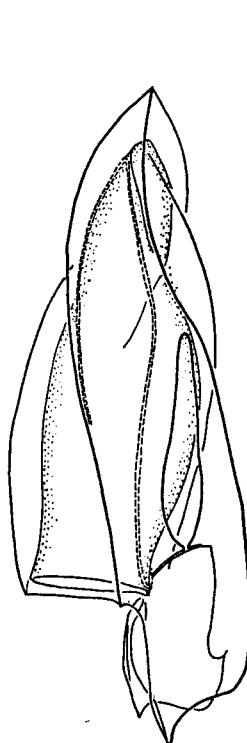


FIG. 128. *Eudoxoides spiralis* (Bigelow) Polygastric phase, $\times 10$ (from Totton & Fraser, 1955).

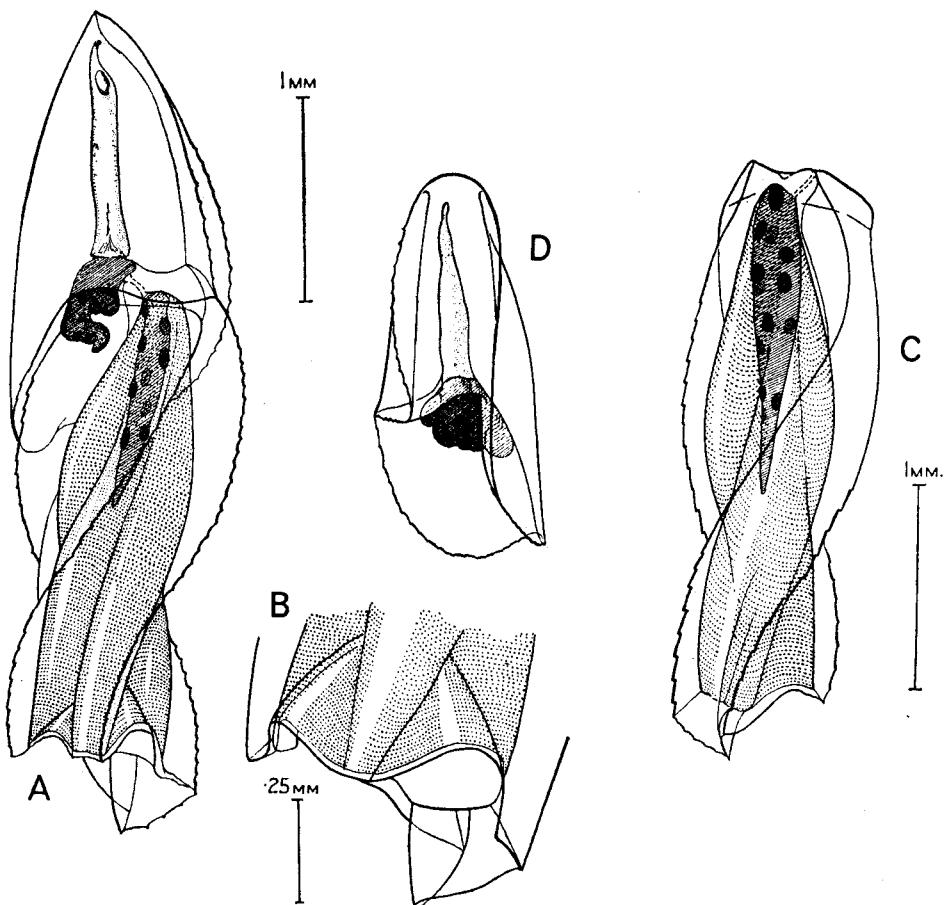


FIG. 129. *Eudoxoides spiralis* (Bigelow). Eudoxid phase
A, lateral view of the whole animal, $\times 27$; B, enlarged view of the base of A, $\times 54$;
C, lateral view of a detached female gonophore, $\times 27$; D, ventral view of the bract,
 $\times 27$ (from Totton, 1932, fig. 30)

Eudoxid phase

(Text-fig. 129.) About 6 mm in length. The bract is similar to that of *E. mitra*, but the somatocyst is relatively longer and cylindrical, and there is no basal tooth on the margin of the neck-shield. The sutural surface of the bract forms at its base a right angle with the dorsal wall of the hydroecium, so that the hydroecial cavity is not as deep as it is in *E. mitra*. In consequence the gonophore does not develop a long pedicel but is truncate at its upper end. It is spirally twisted rather more than one quarter of a turn to the left or right according to the order of budding. An extended description is to be found in Totton (1932, pp. 362-3).

In the Bay of Algeciras I noted that polygastric specimens moved rapidly and intermittently with a darting motion. Their course was an open spiral one.

***Eudoxia macra* Totton 1954**

Text-figure 130

Tentatively included in the Diphyidae is an eudoxid of unknown parentage, often found in plankton samples and easily recognizable from the figures. A description of the species must await the identification of the polygastric phase.

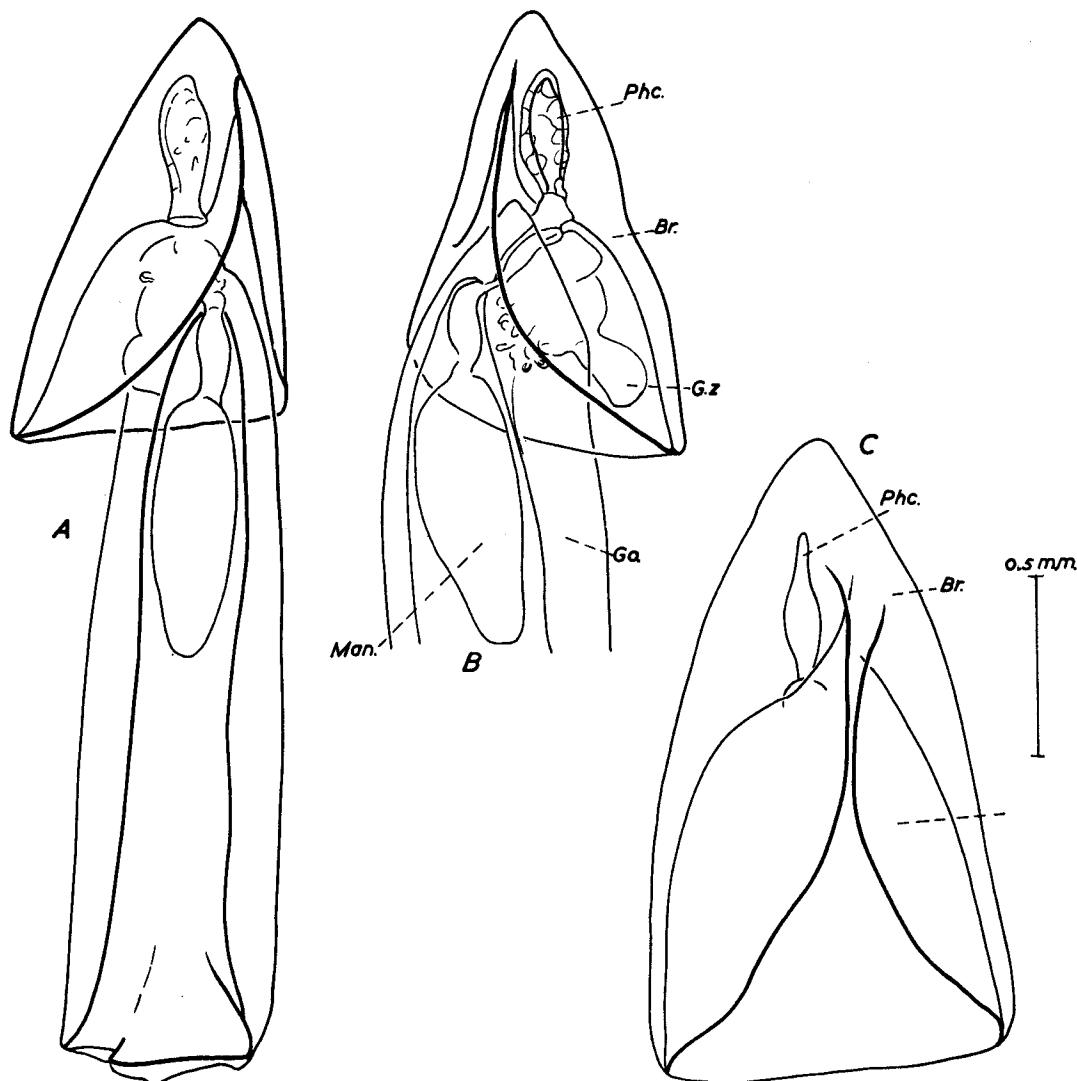


FIG. 130. *Eudoxia macra* Totton. Eudoxid phase, $\times 46$, 'Discovery' St. 1588, 250–100 m

A, whole eudoxid; B, another view of bract of same; C, bract of a second specimen
Br = bract; *Go* = gonophore; *Gz* = gastrozooid; *H* = hydroecium; *Man* = manubrium;
Phc = phyllocyst (from Totton, 1954, fig. 62).

Eudoxid phase

(Text-fig. 130.) The length overall is about 3·2 mm.

Bract: 1·25 mm long, with a rounded conical tip. Headpiece small. In optical section the head-piece and the neck-shield resemble those of *D. bojani*. The sutural surface is in a groove, its edges tending to overlap one another.

Gonophore: 2·5 mm long. Two dorso-lateral and two ventro-lateral canals. Two slight rounded ridges overlie the dorsal pair. There are two closely opposed hydrocial folds, one deeper than the other. Neither mouth-plate nor teeth present. Proximal end rounded and not articulating with the bract. From 14–16 eggs. The tip of the gonophore is deeply pigmented.

Family 13: **CLAUSOPHYIDAE Fam.n.**

Clausophyinae Bigelow, 1913

Heteropyramidinae Moser, 1925

Chuniphyinae Moser, 1925; Totton, 1954

Thalassophyinae Moser, 1925

Crystallophyinae Moser, 1925

There are only about half-a-dozen midwater species altogether in these five sub-families.

Moser's classification and theorizing appear to me to be very unsound. Her Heteropyramidinae and Thalassophyinae, each based on a single species which will probably prove to be one and the same, she placed – the former in queer company – in distant parts of her systematic arrangement. She still retained the old idea of classification according to the number and relative position of nectophores, using the categories Monophyidae, Diphyidae – Tribus Superpositae, Tribus Intermediae and Tribus Oppositae – and Polyphyidae. I am setting up the family Clausophyidae for her Diphyidae Tribus Intermediae and her Heteropyramidinae, all of which seem to be more closely related to one another than to the Diphyidae. One distinguishing morphological character of the Clausophyidae is the possession of a somatocyst by the posterior nectophore, as well as by the anterior one. Another is that, in species whose eudoxid phase is known, there are two longitudinal horns or branches of the phyllocyst lying in the neck-shield of the bract.

Genus: **CLAUSOPHYES** Lens & van Riemsdijk, 1908

At one time it was thought (*see* Chun, 1897b) that *Clausophyes* formed a link connecting the two families Prayidae and Diphyidae, but Bigelow (1913, p. 71) pointed out that *Clausophyes* was really an offshoot of the Diphyidae. He reached this conclusion chiefly because the anterior and posterior nectophores of *C. galeata* were unlike, and also because, the somatocyst of the posterior nectophore was structurally like that of the anterior one in being a special organ deeply embedded in the gelatinous substance, whereas in the Prayids he maintained that it was merely a slightly thickened extension of the canal system. I fear that the second reason may not be valid, but it seems reasonable to maintain a special sub-family for those diphyids with a somatocyst in the posterior nectophore. It seems to be probable that the anterior nectophore of the Clausophyidae is the larval one retained, so that it is understandable that the first definitive heteromorph one the posterior nectophore develops a somatocyst, though those of abylids do not. The Clausophyidae seem to be more primitive than the abylids.

Only two species of *Clausophyes* have been described. They appear to be distinguished chiefly by the character of the distal margin of the posterior nectophores and of the size of the basal end of the right-hand hydrocial fold. For evidence of the existence of a third *see* Totton (1954, p. 133). The present state of their specific diagnoses is unsatisfactory.

Clausophyes ovata (Kefferstein & Ehlers, 1860)

Plate XXXV, figures 1, 4-10

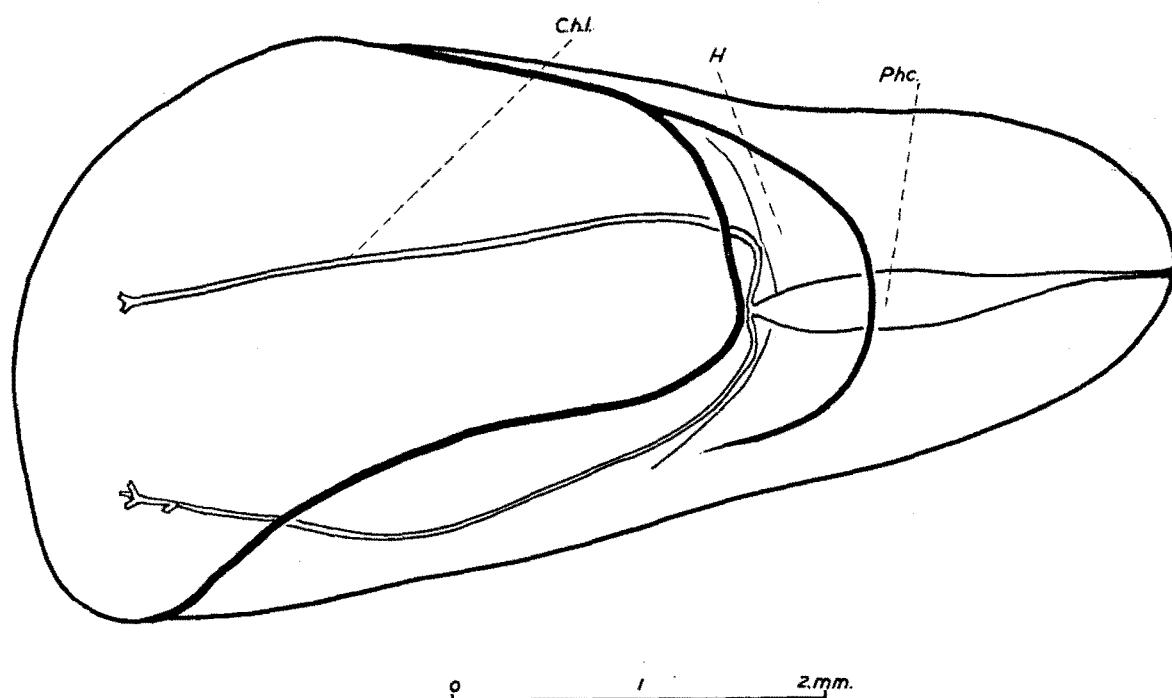
Diphyes ovata K. & E., 1860, 1861*Galeolaria ovata* Chun, 1897a

A species that appears to be found in deeper water. It was taken in twenty-three closing nets by R.R.S. 'Discovery II' at depths ranging from 3,000-2,000 m to 310-260 m.

Polygastric phase (Pl. XXXV, figs. 1, 4, 5)

Anterior nectophore: Up to 20 mm in length (see Moser, 1925, Taf. XXIV, fig. 4). Laterally compressed, generally smooth, blunt, rounded at apex, soft in consistency, pear-shaped *en profile*, with oblique ostium, smaller than posterior nectophore. The open hydroecium is bounded by two broad baso-ventral wings, whose rounded basal ends project down below the level of the ostium. It extends half-way up the nectophore. The somatocyst is long with a spindle-shaped expansion in the region of the apex of the nectosac. It extends as a narrow cylinder from there to the apex of the nectophore. The junction of pedicular canal, base of somatocyst and stem is at a point one-third of the distance from the base of the nectophore to the apex, so that the ventral radial canal of the nectosac is relatively long. The whole nectophore is reminiscent of a larval diphyid nectophore, as it probably is, retained.

Posterior nectophore: Up to 30 mm in length (see Moser, 1925, Taf. XXV, figs. 3, 4). With an open hydroecium extending the whole distance from apex to base. The point of attachment is at mid-length. The nectosac has a well rounded apex, and the lateral radial canals are looped. There is a long somatocyst which has a terminal spindle-shaped swelling. The distal end of the mouth-plate is truncated and has no lateral teeth.

FIG. 131. *Clausophyes ovata* (Kefferstein & Ehlers). Eudoxid phaseBract, $\times 25$, 'Discovery' St. 1567

C.h.l. = left hydroecial canal; H = hydroecium; Phc = phyllocyst (from Totton, 1954, fig. 67).

Eudoxid phase (Pl. XXXV, fig. 6)

Bract (text-fig. 131): With rounded apex. From the base of the phyllocyst, which reaches the apex, arise a pair of fine canals which extend basad to the bracteal margin. Gonophore unknown. The still attached stem-groups have been mentioned and figured only by Kefferstein and Ehlers (1861, Taf. V, figs. 2-5). These figures show what appears to be an asexual swimming bell, but no gonophores.

Clausophyes galeata Lens & van Riemsdijk, 1908

Plate XXXV, figure 11

C. galeata Bigelow, 1913 (*Lapsus calamae* for *galeata*)

A little known species described originally from the posterior nectophore only. The only other mentions and/or figures are by Bigelow (1913) and Totton (1954).

Polygastric phase (Pl. XXXV, fig. 11)

Anterior nectophore: At present not to be distinguished from that of *Clausophyes ovata*.

Posterior nectophore: Similar to that of *C. ovata* but the mouth-plate has two lateral teeth, smooth edged, triangular, of equal length.

Eudoxid phase – not identified.

Genus: ***CHUNIPHYES*** Lens & van Riemsdijk, 1908

Type species *Ch. multidentata* L. & van R., 1908

Moser treated as another species the *chuniphyid* eudoxid *Chuniphyes problematica* Moser, 1925, having already stated that she did not know if *Chuniphyes* produced eudoxids. A second species *moserae* Totton was described in 1954. We are not yet in a position to differentiate between the eudoxids of the two species. It was Leloup (1934, p. 51) who first determined that *Ch. problematica* was an eudoxid, and gave good figures of the bract and gonophore.

Chuniphyes multidentata Lens & van Riemsdijk, 1908

Text-figure 132B

Chuniphyes multicristata (*lapsus calamae*) Bigelow & Sears, 1937

A bathypelagic species widespread in all the great oceans. The last important review of this species was that of Bigelow and Sears (1937, p. 60). For full descriptions see Bigelow (1911b), and Moser (1925). Bigelow (1911b, Pl. 8, fig. 9), gave a good figure of a whole chuniphyid under the name of this species, but from the shape of the somatocyst it appears to represent the other species *Ch. moserae* Totton.

Polygastric phase

Anterior nectophore (text-fig. 132B): Up to 36 mm in length. For a full description see Bigelow (1911b, pp. 262-3). There are four ridges at the apex. The ventral ridge runs undivided to the opening of the hydroecium. The dorsal and pair of laterals branch dichotomously at from 5 mm to 7.5 mm below the apex in a specimen 3 cm in length overall (see Bigelow, 1931, figs. 208, 209). The dorso-lateral ridges end in prominent teeth, the two dorsals and two ventro-laterals in minor ones. There is a prominent tooth in the basal margin of each lateral wall of the hydroecium. The hydroecium

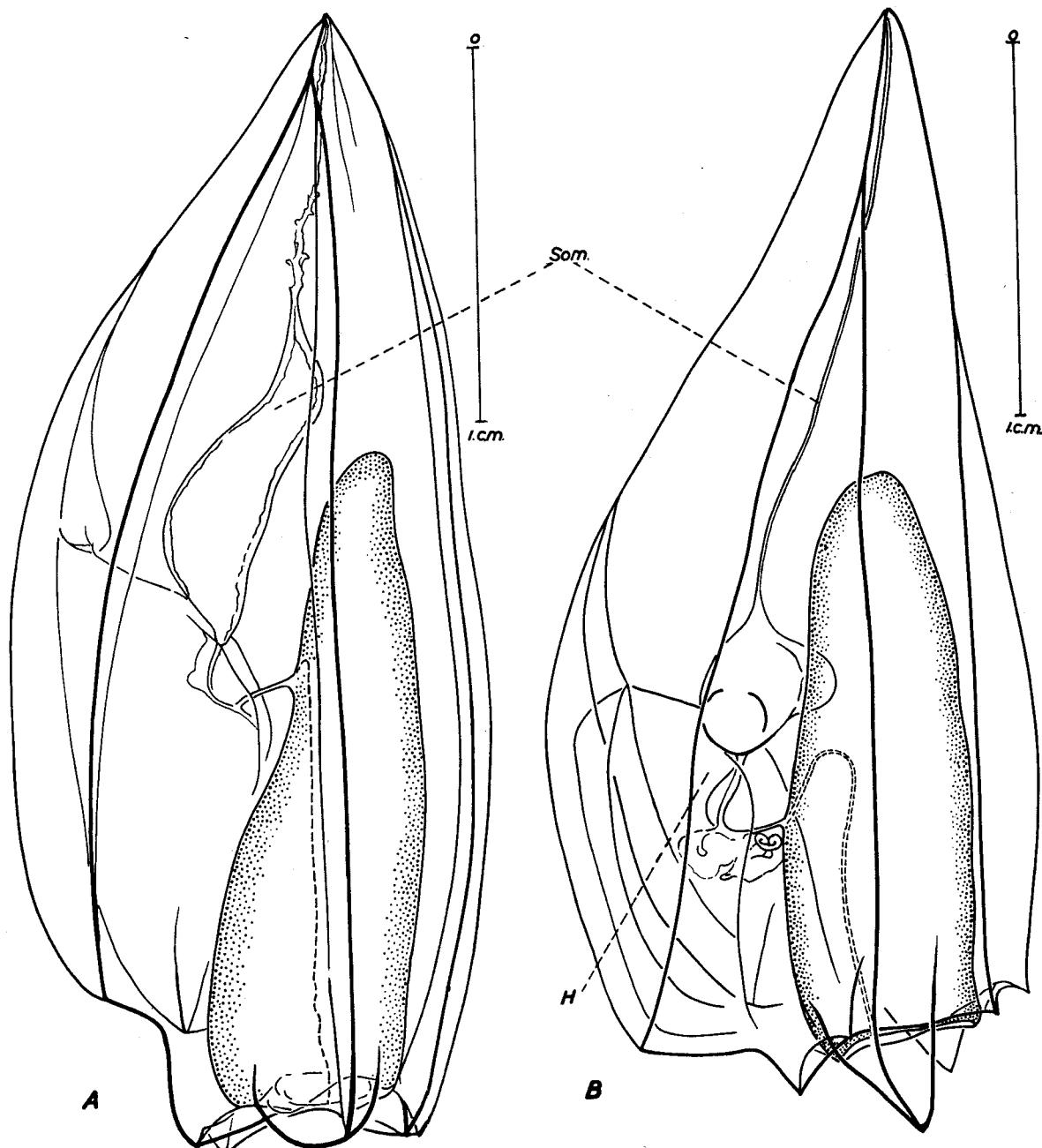


FIG. 132. *Chuniphyes moserae* Totton
A, lateral view of the holotype, polygastric phase, $\times 5$, 'Discovery' St. 1639, 2,400-1,150 m

Chuniphyes multidentata L. & v. R.
B, Polygastric phase, $\times 5$, 'Discovery' St. 407, 800-900 m
 H = hydroecium; Som = somatocyst (from Totton, 1954, fig. 66).

forms a deep cleft in the ventro-basal region. Its upper end reaches only two-thirds of the way up the nectosac. The stem is attached at its junction with the base of the pedicel of the somatocyst and the base of the pedicular canal on a rounded prominence at two-thirds of the height of the hydroecium. The somatocyst is divided into a broad two winged basal part that lies below the level of the apex of the nectosac, and a very fine long simple and terminal tube that reaches nearly to the apex of the nectophore.

Posterior nectophore: Up to 40 mm length (see Bigelow & Sears (1937, fig. 48)). The differences between that of *multidentata* and *moserae* have not been determined with certainty since there appear to be posterior nectophores of two kinds. One has markedly asymmetrical ventro-basal teeth and thick mesogloea separating the hydroecium from the nectosac. This will probably prove to belong to *Ch. multidentata*. There are three ridges at the apex, one dorsal and a pair of ventro-laterals, each of which divides dichotomously lower down, so that in the lower region there are six longitudinal ridges and six basal teeth. The dorsal ridge divides (see Bigelow & Sears, 1937) at a point 8% of the distance from apex to base. Each ventro-lateral divides at about 25% of the distance, apex to base, the lateral member of each pair continuing to run directly to the base, but the ventral member bending at first abruptly ventrad, then abruptly towards the base. In the upper region there is a pair of overlapping flaps, borne by the hydroecial wings, that close that part of the hydroecial canal. The pedicular canal, leading to the junction of the four radial canals, is given off some 5 mm below the junction to the 'Stiel-canal', and the pallial canal is continued below this point for about 6 mm (in a 30 mm long nectophore).

Eudoxid phase

The eudoxids of the two species cannot be identified and distinguished from one another. But the general shapes of bract, somatocyst and gonophore were described and figured by Leloup (1934, pp. 46–51, figs. 12–13). Both bract and gonophore are flattened dorso-ventrally. The somatocyst has a pair of longitudinal horns and a large median portion. The bract measures about 4 mm in length × 1.5 mm and its sides are recurved.

The pentagonal, flattened, gonophore measures about 7 mm in length × 4 mm. There is a dorsal (ventral *sensu* Leloup) ridge terminating in a minor tooth, and a pair of well developed laterals terminating in prominent teeth. The two ventral ridges form the sides of a shallow, gutter-like hydroecium and may sometimes unite in the apical region. The middle region of these ventral wings is little elevated. Above they form rounded projections seen *en profile*; below they are less marked, and end in small teeth a short distance above the ostium.

Chuniphyes moserae Totton, 1954 Plate XXXV, figure 2; text-figure 132A

Polygastric phase

Anterior nectophore (text-fig. 132A): Similar to that of *Ch. multidentata*. Moser evidently had a specimen of this species as a model for her (1925) Pl. 23, figure 1. Prior to 1954 differences between somatocysts had been noted, but not considered of specific significance. The criterion for specific identification is the somatocyst which in *Ch. moserae* is not expanded horizontally on its basal region, but is fusiform or spindle-shaped. The terminal part of the somatocyst is relatively shorter than in *multidentata* and bears short irregularly shaped side-branches. The hydroecium extends up nearly to the apex of the nectosac, and the enlarged basal part of the somatocyst generally overtops this apex. The dorso-lateral teeth may not be relatively so long as in *multidentata*. The points where the lateral and dorsal ridges diverge is relatively nearer to the apex of the nectophore in *moserae*.

Posterior nectophore: Not at present distinguishable with certainty from that of *multidentata*.

Eudoxid phase

Not at present distinguishable.

Genus: ***CRYSTALLOPHYES*** Moser, 1925

Chrystallophyes Moser (*lapsus calamae*), 1925, p. 356

A monotypic genus for *C. amygdalina* Moser, 1925.

Crystallophyes amygdalina Moser, 1925

Text-figures 133, 134

Described originally from three nectophores found off the Antarctic continent. Reported again by Leloup (1934) (two specimens from S. Georgia) and Totton (1954, seventy-two anterior and twenty-three associated posterior nectophores). It is evidently a mid-water form.

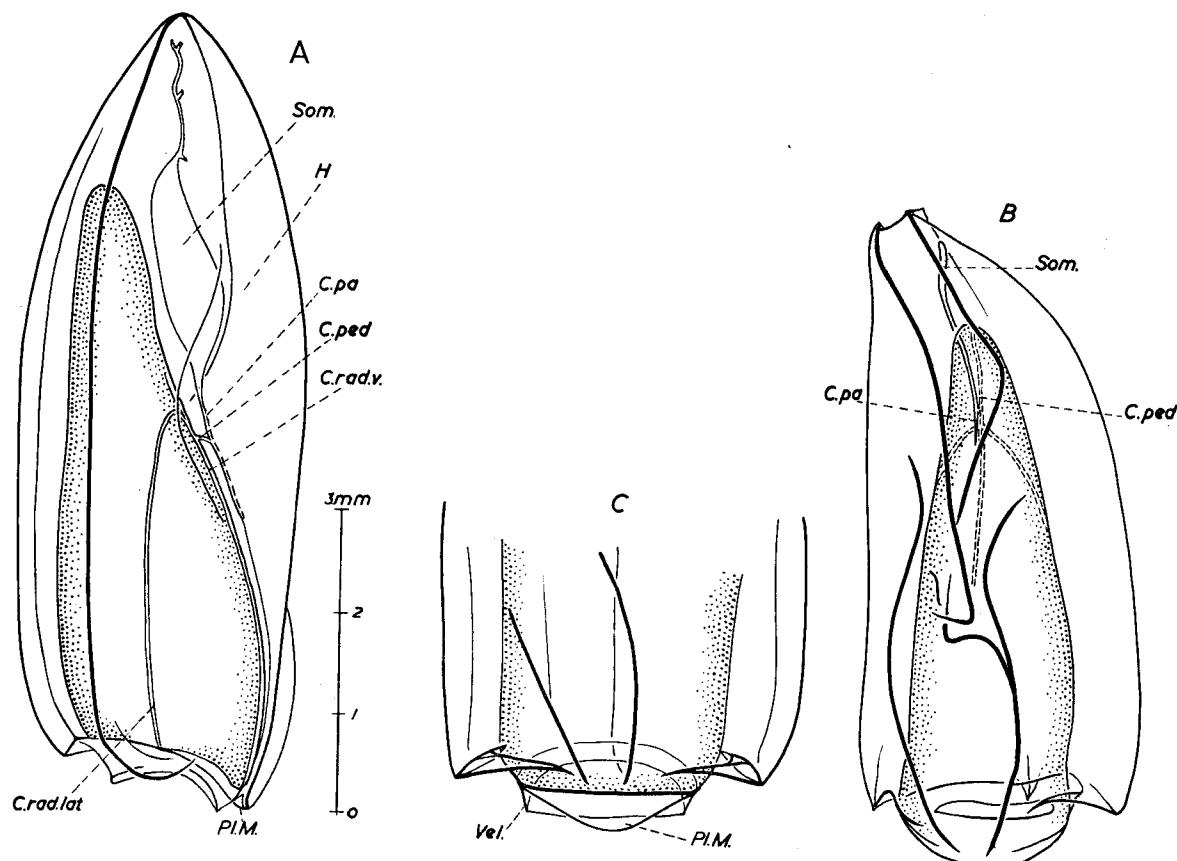


FIG. 133. *Crystallophyes amygdalina* Moser. Polygastric phase

A, lateral view of the anterior nectophore, 'Discovery' St. 663, 1,000-750 m; B, C, ventral views of posterior nectophores; B, 'Discovery' St. 129, 500-250 m; C, 'Discovery' St. 663, 750-500 m, $\times 14$

C.pa = pallial canal; C.ped = pedicular canal; C.rad.lat, C.rad.v = lateral and ventral radial canals; H = hydroecium; Pl.M = mouth-plate; Som = somatocyst; Vel = velum (from Totton, 1954, fig. 69).

Polygastric phase

Anterior nectophore (text-fig. 133A): The five longitudinal ridges do not divide into two in the basal region as they do in *Chuniphyes*. The hydroecium extends up almost to the apex. In the ostial

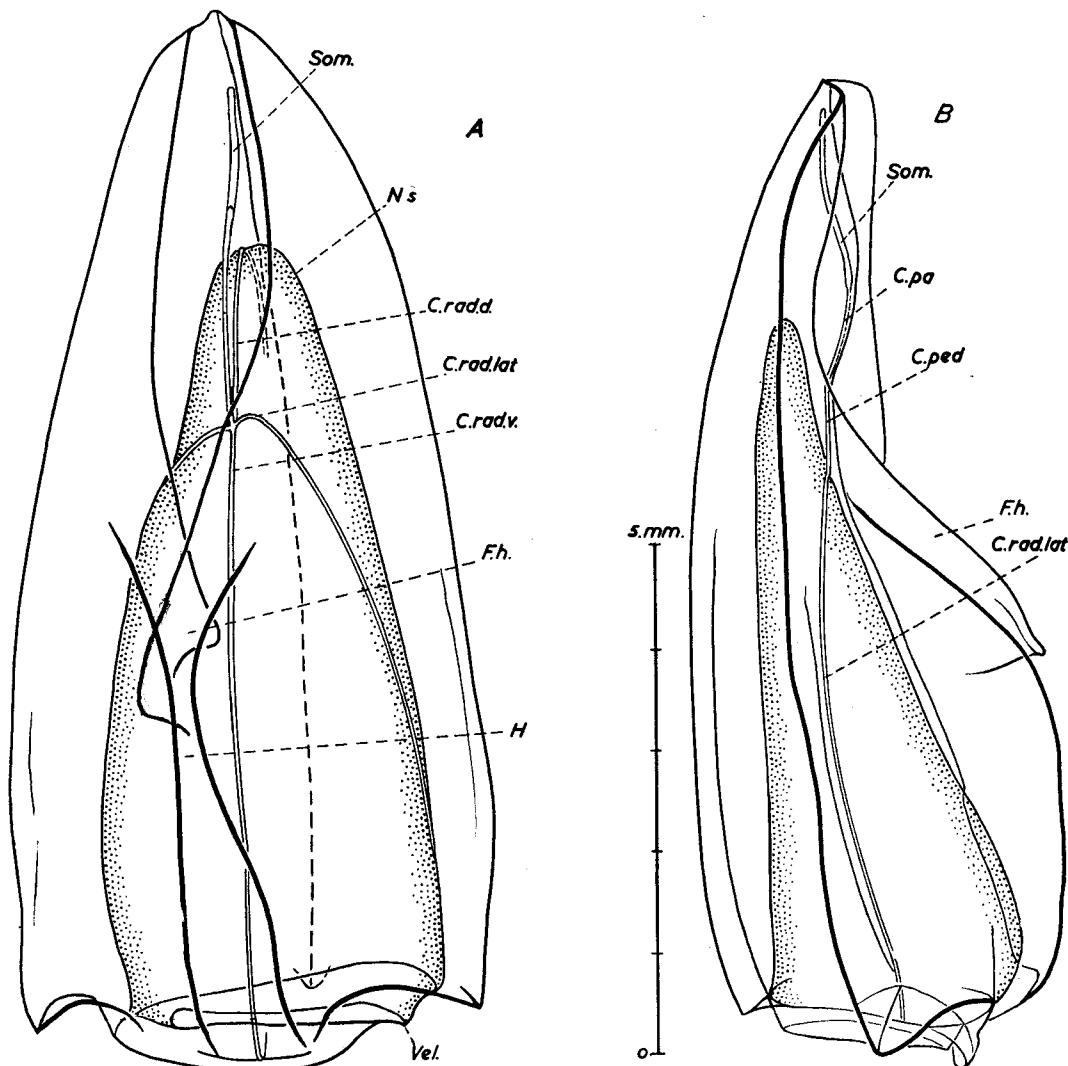


FIG. 134. *Crystallophyes amygdalina* Moser. Polygastric phase
Posterior nectophore. A, ventral; B, lateral view, $\times 13$, 'Discovery' St. 357, 750–500 m
N.s = nectosac; F.h = hydroecial fold; for other abbreviations see text-figure 133 (from Totton, 1954, fig. 68).

region its side walls almost disappear. The ostial ends of the lateral ridges are characteristically curved. The curved mouth-plate is very minute.

Posterior nectophore (text-figs. 133B, C and 134): Flattened dorso-ventrally in the apical region, where the five longitudinal ridges do not meet in a point. The ventrals join the laterals a short distance below the apex. The laterals have prominent pointed teeth at the ostial end. The lateral radial canals leave the junction of canals at a point about a quarter of the distance from apex to ostium of nectosac, and scarcely form an upward loop at all. The hydroecium runs from apex to ostium. There is a pair of small pointed flaps on the inner edges of the hydroecial folds (ventral ridges) at mid-length. There is a fine somatocyst, 3.5 mm in length.

Eudoxid phase – unrecorded.

Genus: **HETEROPYRAMIS** Moser, 1925

? *Thalassophyes* Moser, 1925

A monotypic genus for *H. maculata* Moser, 1925. Its relationships were not understood by Moser, who treated it with *Nectopyramis*, *Sphaeronectes* and *Muggiaeae* as parts of a family Monophyidae.

***Heteropyramis maculata* Moser, 1925**

Text-figure 135

Only a dozen or so spotted nectophores of this obscure mid-water form have been recorded since 1925, by Leloup (1934) and Totton (1954).

It is possible that this form with its opaque spots will prove eventually to be conspecific with the unspotted *Thalassophyes crystallina* Moser.

Polygastric phase

Anterior nectophore (see Moser, 1925, Taf. 2, figs. 1-3; and text-fig. 135D): Up to 13 mm in length, pyramidal, five-ridged at apex. The deep hydroecium, which extends up nearly two-thirds of the distance to the apex is delimited by two small, incomplete, ventro-lateral ridges. At present a series of opaque spots on the dorso-lateral ridges is taken as a criterion for specific identification. They vary in number and situation (see Totton, 1954, text-fig. 70) but are often nine in number, one each at the apical and basal ends of each dorso-lateral ridge, and from two to four intermediate ones.

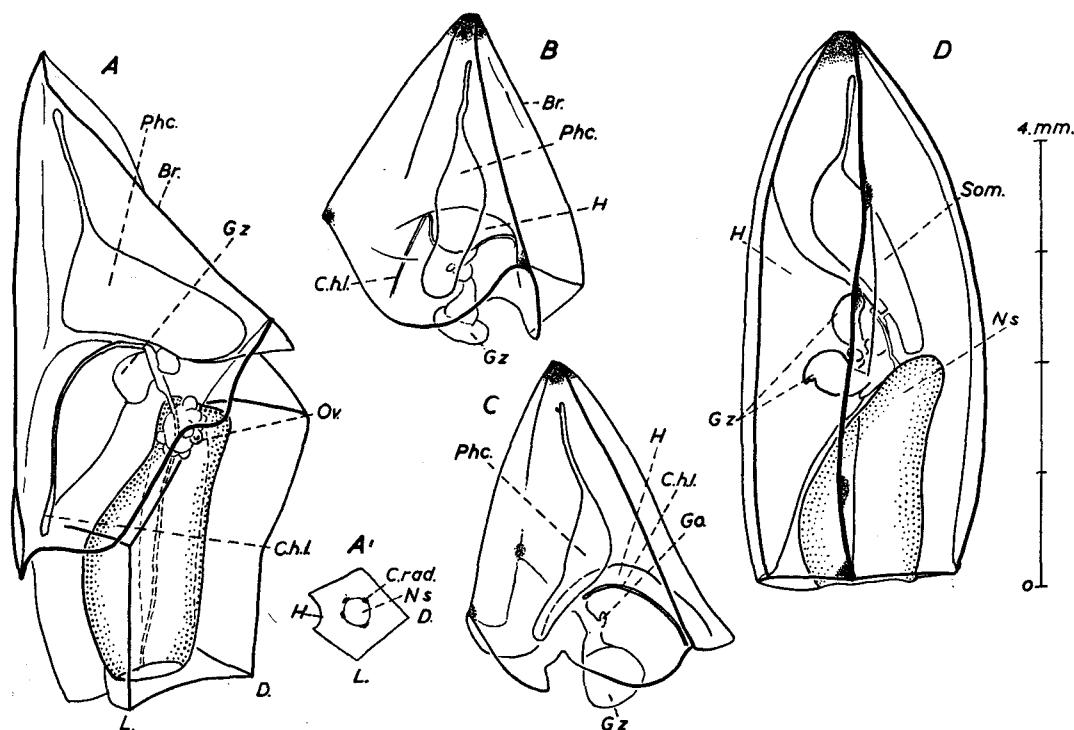


FIG. 135. *Heteropyramis maculata* Moser

A-C, Eudoxid phase; D, Polygastric phase; all $\times 15$

A, whole eudoxid, 'Discovery' St. 127, 950-780 m; A', diagrammatic transverse section of a gonophore; B, C, bract of the eudoxid, 'Discovery' St. 2927, 750-500 m; D, anterior nectophore

'Discovery' St. 2927, 750-500 m

Br = bract; C.h.l. = left hydrocial canal; C.rad = radial canal; D = dorsal; Go = gonophore; Gz = gastrozooid; H H' = hydroecium; L = left; Ns = nectosac; Ov = ovum; Phc = phylloctyst; Som = somatocyst (from Totton, 1954, fig. 71).

Well preserved specimens are not available, and figures such as those of Moser (1925, Taf. 2, figs. 1-3) must be used with caution. The pear-shaped nectosac is barely half the length of the nectophore, and lies wholly below the somatocyst, which is spindle-shaped below and lies obliquely to the main longitudinal axis. Apically the somatocyst is produced into a fine vertical tube.

Apart from the spots it is difficult to distinguish the anterior nectophore (with spots) from that of *Thalassophyes crystallina* Moser (without spots).

Posterior nectophore: Not recorded.

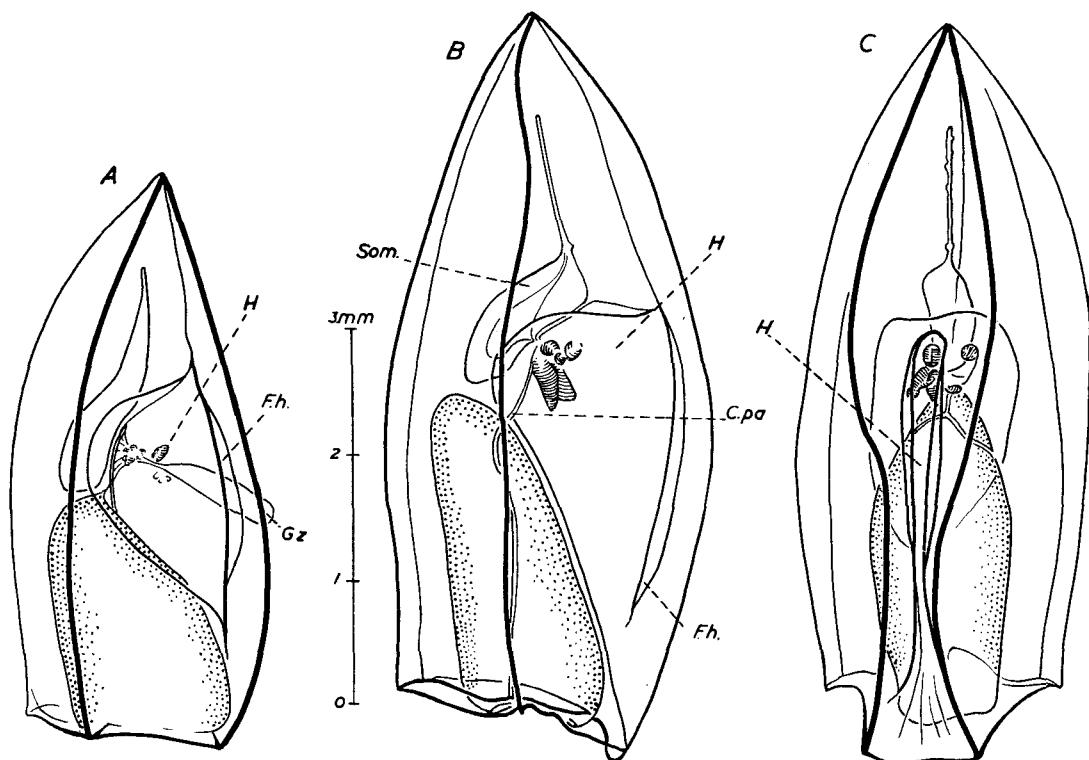


FIG. 136. *Thalassophyes crystallina* Moser. Polygastric phase
A, lateral view of the anterior nectophore, $\times 16$, 'Discovery' St. 1588, 500-200 m; B, C, lateral and ventral views, $\times 16$, of a specimen, 'Discovery' St. 102, 750-500 m
F.h = hydroecial fold; *H* = hydroecium; *C.pa* = pallial canal; *Som* = somatocyst (from Totton, 1954, fig. 72).

Eudoxid phase

(Text-fig. 135A-C.) Four-ridged with a neck shield, into which penetrate two lateral longitudinal horns of the somatocyst as in *Chuniphyes* spp., *Ceratocymba* spp. and some other Abylidæ.

The phyllocyst in general resembles the somatocyst, but the main part is relatively shorter and deeper as seen *en profile*, and the terminal part relatively longer. The gonophore is five-ridged, ~~and~~ dorsal ridge being added as in Abylinæ. The presence of opaque spots is the criterion for specific identification. There is an apical spot on the bract, a spot at the base of each dorso-lateral ridge of the bract, and a spot at each end of the two dorso-lateral ridges of the gonophore.

The phenomenon of opaque spots may prove to be comparable with blanching in *Hippopodius*.

Genus: **THALASSOPHYES** Moser, 1925

? *Heteropyramis* Moser, 1925

A monotypic genus for *T. crystallina* Moser, 1925.

It is quite probable that *T. crystallina* Moser will eventually prove to be the 'unspotted' form of

Heteropyramis maculata. Good specimens of the maculate form are rarely taken, but are indistinguishable from the unspotted form except for the spots, which vary in number and opacity.

***Thalassophyes crystallina* Moser, 1925**

? *Heteropyramis maculata* Moser, 1925

A little known mid-water species. Records of more than sixty specimens were published by Totton (1954).

Polygastric phase

Anterior nectophore (text-fig. 136; see also Moser, 1925, Taf. 23, figs. 5, 6): Hardly distinguishable from that of *Heteropyramis maculata* except for lack of spots. Pyramidal, five-ridged at apex. Hydroecium deep, with a pair of small incomplete ventro-lateral ridges. Nectosac, and somatocyst as in *H. maculata*.

Posterior nectophore: Not recorded. Indistinguishable from that of *H. maculata*.

Eudoxid phase

Not recorded. Indistinguishable from that of *H. maculata* except for absence of spots.

Family 14: SPHAERONECTIDAE Huxley, 1859

The family contains only one isolated genus of perhaps neotenetic forms. *Sphaeronectes* Huxley, 1859.

Bigelow (1911b) discussed a family Sphaeronectidae containing sub-families Sphaeronectinae, Muggiinae and Nectopyramidinae. In 1932 I suggested that this arrangement did not reflect natural relationships, and in 1937 Bigelow, in a joint paper with Dr. M. Sears adopted the suggestion that I there made. Bigelow (1911b) gave an excellent history of the genus and species.

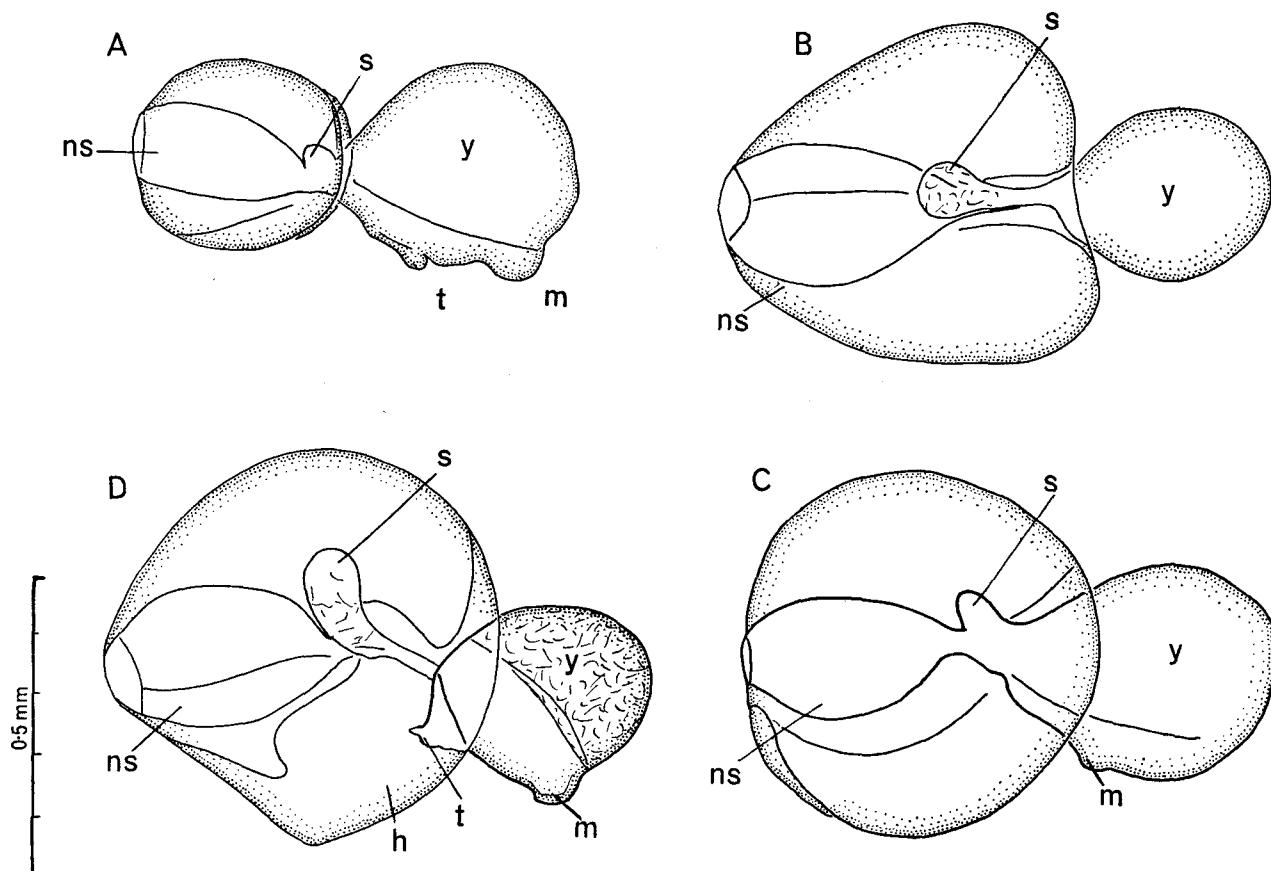
Genus: *SPHAERONECTES* Huxley, 1859

Diplophysa Gegenbaur, 1853b (eudoxid phase)

Type species: *S. gracilis* Claus, 1873.

It was this beautiful and remarkable little 'monophyid' in which the stem was supposed to arise from the exumbral pole of the nectosac that gave rise to the medusoid theory of siphonophore evolution. The mesogloea of the nectophore of both species is soft and the exterior surface rather adhesive. They were both unusually abundant at Villefranche in the spring of 1962 when I preserved very successfully many specimens. I had previously been able to rear larvae (text-fig. 137A-D) and am of the opinion that the larval nectophore is not caducous but develops into the definitive one. The work needs repetition. Because of the resemblance in some respects between the larval, caducous nectophores of Prayids, Diphyids and perhaps other forms and those of Sphaeronectids, I suspect that *Sphaeronectes* is a neotenous form. But its relationships are not yet clear.

Five differences between the nectophores of the two species were given on page 184 of Bigelow's (1911b) 'Albatross' Report. These are referred to under the descriptions of the species. In *S. gracilis* the apex of the somatocyst curves over towards the dorsal side. I am inclined to regard this phenomenon to be analogous with an early evolutionary stage of the condition found in most abylids and in *Ceratocymba*, though not in *Bassia* (see Totton, 1954, figs. 1, 2). In these abylids the main part of the somatocyst lies entirely on the dorsal side of the hydroecium.

FIG. 137. *Sphaeronectes* sp., ? *gracilis* Claus

Larvae bred from eggs of a 'Diplophysa' eudoxid taken on May 23 1950, at Villefranche. A, youngest larva; B, upper view; C, lateral view of slightly older stage; D, 6-day old larva, $\times 86$
 h = hydroecium; m = mouth; ns = nectosac; s = somatocyst; t = tentacle; y = yolk.

Sphaeronectes gracilis (Claus, 1873; 1874)

Plate XXXVI, figure 1

? *Ersaea truncata* Will, 1844 (eudoxid), Taf. II, figures 1-4

Diplophysa inermis Gegenbaur, 1853b (eudoxid), Taf. XVI, figure 3

For synonymy see Bigelow, 1911b, page 184 (as *S. truncata*)

This is the larger of the two species.

Polygastric phase

(Text-fig. 138.) The apex of the somatocyst usually curves over towards the dorsal side of the hydroecium, which is longer and less open on the dorsal side than in *S. irregularis*. The lateral radial canals are not bowed as they are in *S. irregularis*.

Eudoxid phase

The term 'Diplophysa' can be applied to the eudoxid of both species. Differences between the eudoxids of the two have not yet been made clear. The four branches of the somatocyst so frequently to be identified in only distantly related eudoxids are reduced to one in *Sphaeronectes*. Gegenbaur (1853b, Taf. XVI, fig. 3) gave a good figure of a 'Diplophysa', but I am not aware that its specific identity was established.

The species is said to occur generally in the tropical and sub-tropical regions of all three great oceans. It was abundant in Monterey Bay, California, in July 1928 (Bigelow & Leslie, 1930). It floats

in the position shown in Chun's (1885) figure (see Pl. XXXVI, fig. 1) ~~and in my text-figure 2~~, with the ostium downwards.

Measurements: Up to 8 mm in diameter (Bigelow, 1911b). Gastrozooid length 0·6 mm, diameter 0·15 mm. Pedicel of gastrozooid 0·35 mm long, with buds of bract and gonophore at proximal end, on the stem. Tentacle length, relaxed, 11 mm.

Variation: The somatocyst varies in shape, probably with age. Instead of curving over toward the dorsal side the tip may continue to grow spirally to form even more than one complete turn.

Sphaeronectes irregularis (Claus, 1873)

Monophyes irregularis Claus, 1873, 1874; Chun, 1888a, 1892, 1897b; Haeckel, 1888b; Bigelow, 1911b; Moser, 1925

Monophyes brevitruncata Chun, 1888a, 1892, 1897b

Sphaeronectes truncata Schneider, 1898

This is the smaller of the two species.

Polygastric phase

The somatocyst is short and straight, and the hydroecium is shorter and more open on the dorsal side than in *S. gracilis*. The lateral radial canals are bowed – another good diagnostic feature. The nectophore measures up to 5·7 mm in diameter and 7·1 mm in depth. The nectosac up to 4·3 mm in diameter and 2·8 mm in depth. The nectophore floats with the ostium downwards, as in *S. gracilis*.

Eudoxid phase

The 'Diplophysa' has not yet been shown to be distinct from that of *S. gracilis*, though M. Carré of Villefranche told me in April 1964 that he could distinguish two types.

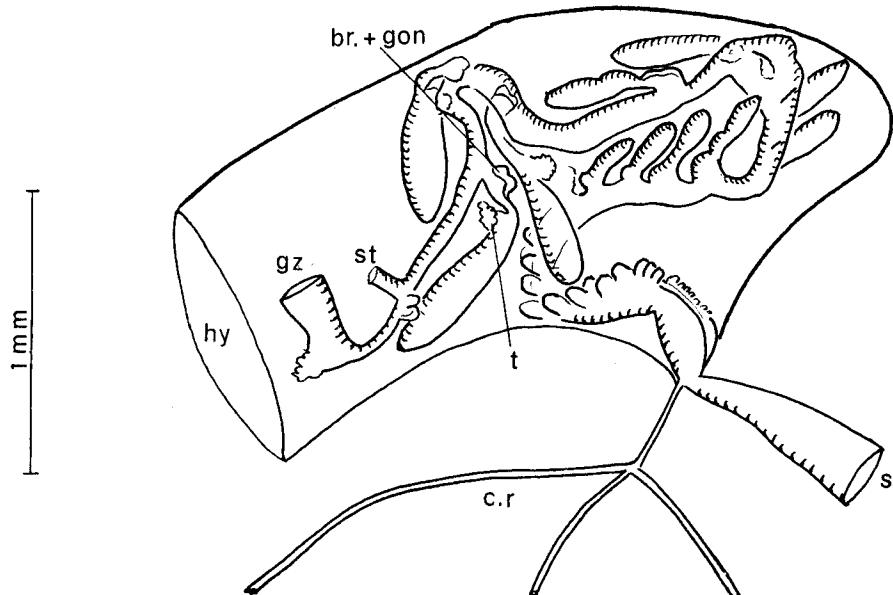


FIG. 138. *Sphaeronectes gracilis* Claus. Polygastric phase

Base of hydroecium with budding zone of the stem

br+gon = bracts and gonophores; *c.r* = radial canals; *gz* = gastrozooid;
hy = hydroecium; *st* = stem; *s* = somatocyst; *t* = tentacle.

Family 15: ABYLIDAE L. Agassiz, 1862

Abylidæ L. Agassiz, 1862; Haeckel 1888b; Totton, 1932; 1954

Abylinæ Lens & v. Riemsdijk, 1908; Bigelow, 1911b; Moser, 1925; Sears, 1953

There is a smaller anterior nectophore whose hydroecial cavity is closed in on the ventral side to form a tube that opens below. Also a larger, posterior, heteromorph, definitive nectophore, whose apophysis fits into the hydroecial tube (*Enneagonum* is an exception).

As Bigelow (1911b) pointed out the genera fall into two main groups, which I believe to be natural, based on the shape of the anterior nectophore. The posterior nectophore is not such a good guide.

In one sub-family, Abylinæ, the anterior nectophore has as a rule, a rectangular apical facet. In the other sub-family Abylopsinæ there is no apical facet, but a ridge, formed by the junction of two lateral facets (text-fig. 153).

The genera and species were very usefully reviewed with explanatory figures by Dr. Mary Sears in 1953. Into her revision she introduced a number of what I venture to consider to be confusing new synonyms for isolated and what appear to be pathological specimens. They seem to me to have suffered accidents in their development. On this account and with all respect to Dr. Sears, to whom I at once communicated my detailed comments, I have relegated them where possible to synonymy. Similar phenomena are well known to entomologists who adopt the same procedure. Abylids seem to occur abundantly, and so far we have not often depended on isolated specimens for our knowledge of species. The apparent freakishness of the specimens referred to is unlike the type of specific differentiation and variation that we have seen so far. It is, in my view, of a pathological rather than genetic kind.

In all abyliids except *Bassia*, the somatocyst has curved over to occupy a position on the ventral side of the hydroecium. What appears to be the commencement of development of such an arrangement can be seen in *Sphaeronectes gracilis*. *Sphaeronectes*, therefore, may possibly be a proto-Abylid, or perhaps a neotenic form.

The five genera appear to be natural groups, and nowadays are easily distinguishable.

Sub-family i: ABYLINAE L. Agassiz, 1862 s.str.

Cymbonectinae Haeckel, 1888b (*partim*); L. & v. R., 1908

Diphyabylinæ Lens & v. R., 1908

Ceratocymbinae Moser, 1925

Abylinæ Totton, 1932; 1954

Abylidæ, in the anterior nectophore of which there is as a rule a rectangular apical facet (see text-fig. 147a). I have restricted this sub-family to the genera *Abyla* and *Ceratocymba*.

Genus: CERATOCYMBIA Chun, 1888

Cymba Quoy & Gaimard, 1827

Nacella Blainville, 1830

Diphyabyla Lens & van Riemsdijk, 1908

Pseudocymba Sears, 1953

Type species: *Ceratocymba sagittata* (Quoy & Gaimard, 1827).

The chief diagnostic characteristics of this genus, as I stated in 1954, are that the eudoxid is a 'cymba' and the posterior nectophore has left and right dorso-lateral ridges terminating on the lateral teeth. There is a short median-dorsal ridge terminating in the dorsal tooth. The ventro-lateral facet of the anterior nectophore is not divided by a horizontal ridge as it is in *Abyla* (see text-fig. 147a).

Ceratocymba leuckarti (Huxley, 1859)
Plate XXXVI, figures 2-5, 7; text-figures 139, 141B, D

For synonymy see Sears, 1953, page 67

Polygastric phase (Pl. XXXVI, figs. 5, 7)

Anterior nectophore (text-fig. 139): Rectangular, not produced into a peak as in the other species. The apices of somatocyst hydroecium and nectosac are at the same level. Ventral facet very narrow. The lateral ridges run nearer the ventral side than in the other species, and near the base curve sharply dorsad, ending well above the lateral teeth, so that the dorso-lateral and ventro-lateral facets are incompletely and unequally divided.

Posterior nectophore: Three times as long as wide, fragile. For a description of minor details see Sears (1953, p. 67, fig. 20C). The ventral teeth are not so markedly disparate in length as are those of *C. sagittata*.

Eudoxid phase (Pl. XXXVI, figs. 2-4)

Bract: The left latero-dorsal ridge extends all the way from the basal margin to the apico-dorsal ridge. The apical facet is flat and quadrilateral (see Sears, 1953, text-fig. 20D).

Gonophores: The apico-lateral ridges, according to Sears (1953), are at the same level just above the tip of the nectosac. For minor differences from those of *C. sagittata* and *C. dentata* see Sears (1953, p. 68, text-fig. 20F). The dorsal ridge extends from the dorsal tooth more than half-way up the dorsal facet.

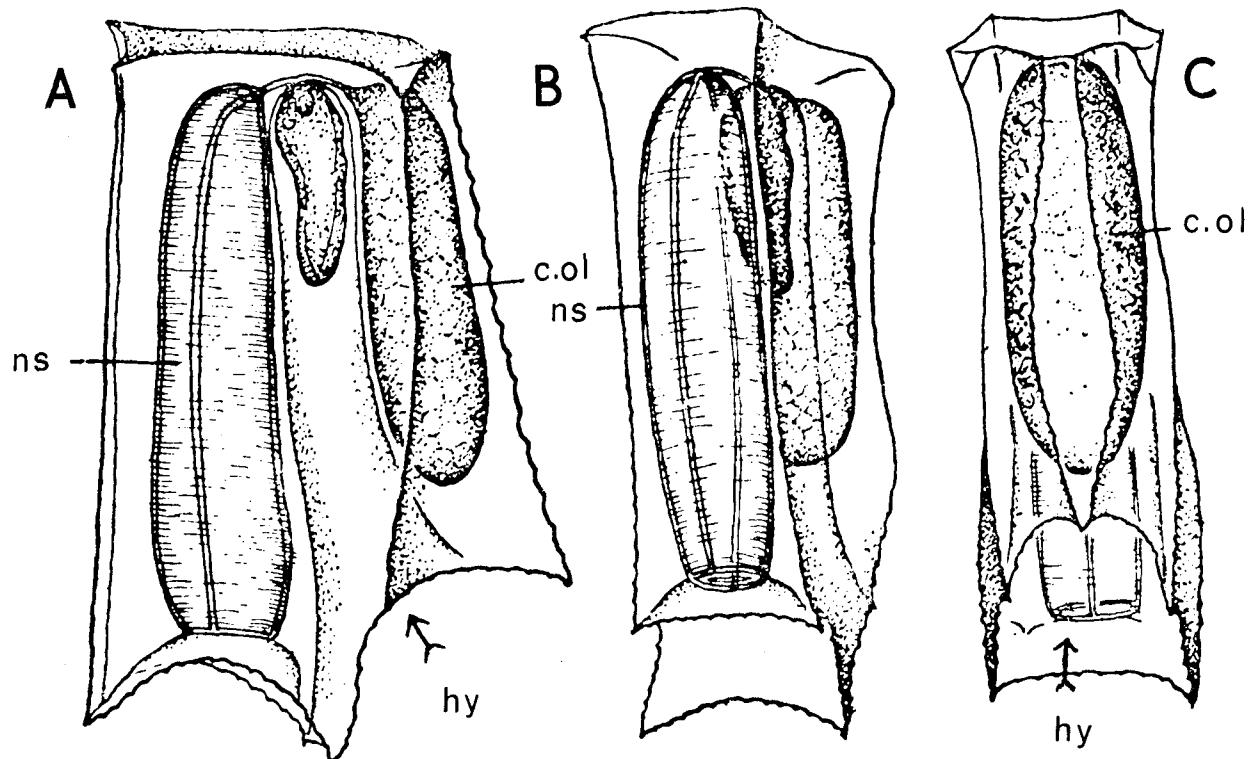


FIG. 139. *Ceratocymba leuckarti* (Huxley). Polygastric phase. Anterior nectophore, $\times 12$

A, lateral; B, oblique dorso-lateral; C, ventral view

c.ol = somatocyst; hy = hydroecium; ns = nectosac (after Kawamura, 1915, Pl. 15, figs. 29-31).

Ceratocymba sagittata (Quoy & Gaimard, 1827)
Plate XXXVII, figures 1-4; text-figures 140, 141A, C

For synonymy see Sears (1953), page 63

Polygastric phase (text-fig. 140)

Anterior nectophore: With a very long narrow pyramidal extension (E.P.) so that the apical facet characteristic of abylinines is not obvious. The nectosac is very long and tubular, about twice as long as the hydroecium, whose length is, according to Sears, about one-third of the overall length of the nectophore.

Posterior nectophore (text-fig. 141B, D): With a characteristic elongate left-hand (right *sensu* Sears, 1953) ventral tooth which is much longer than that of the opposite side. For an extended description see Sears (1953). The ventral teeth are not shown in the figure.

Eudoxid phase (see Sears, 1953, fig. 18B)

The bract has a concave apical facet and prominent lateral horns. It can readily be identified by the left lateral ridge which always joins the posterior margin. It usually does not reach the apico-dorsal ridge, though Sears (1953) has noted specimens in which it does so.

The *gonophore*, when well preserved, may be recognized according to Sears (1953) by: (1) the relatively small inconspicuous hook arising from the right ventral ridge and curved in toward the floor of the hydroecium; (2) the presence of serrations extending well above the level of this hook on the margin of the left ventral wing; (3) a very weak inconspicuous dorsal tooth; and (4) the lateral apical ridge next to the wall of the bract is deeper than the opposite exposed one.

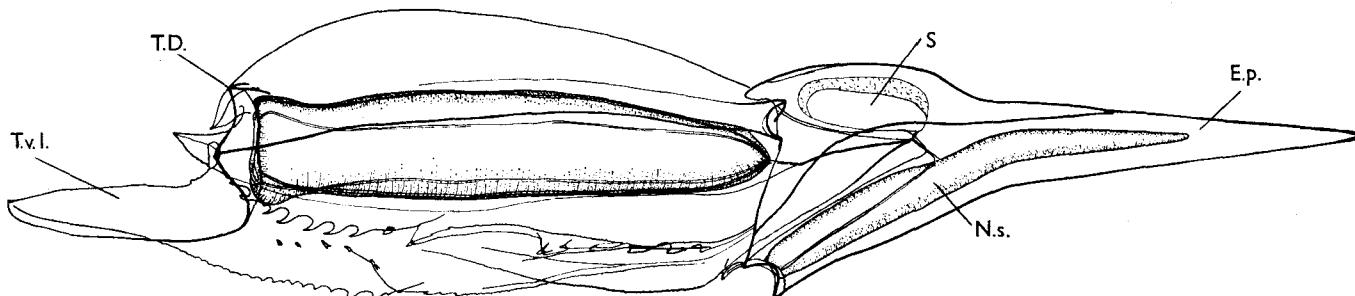
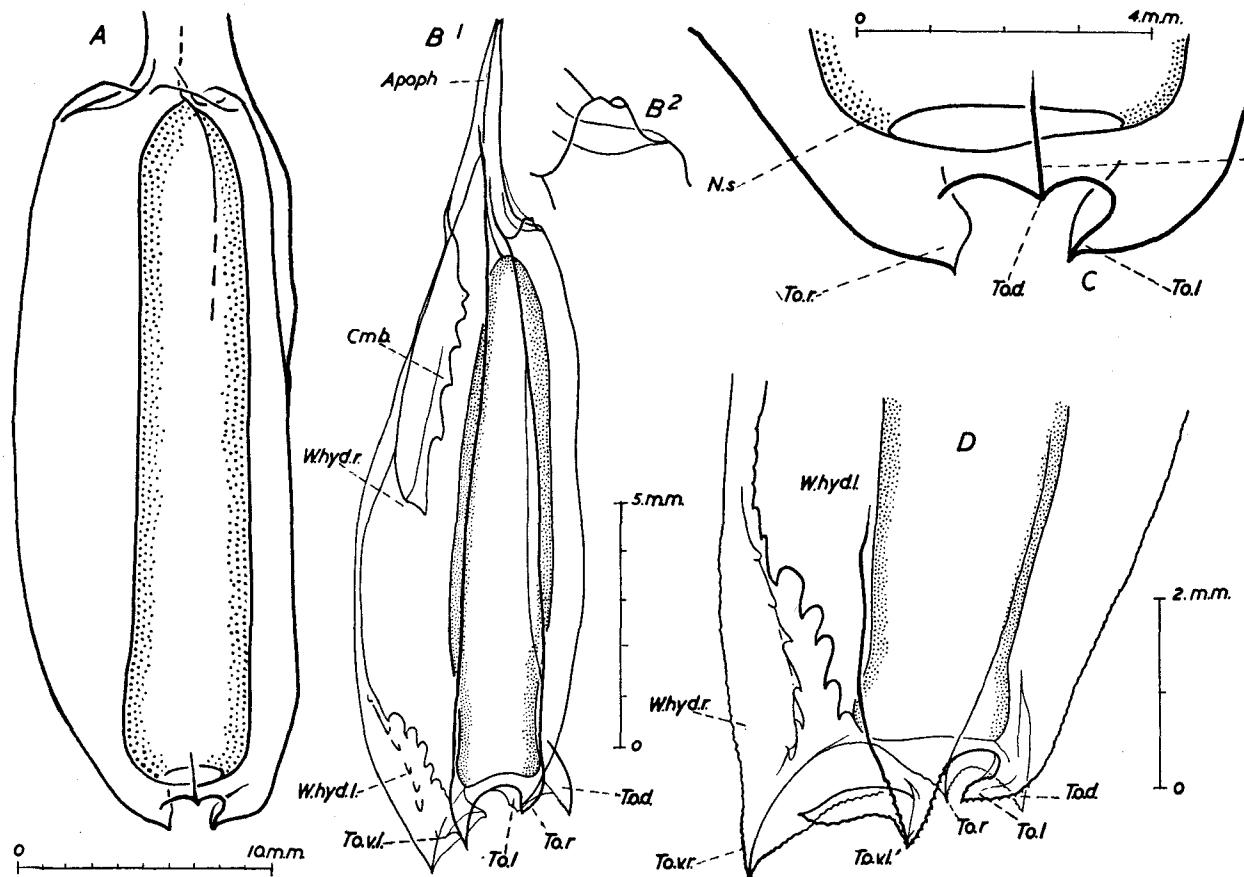


FIG. 140. *Ceratocymba sagittata* Q. & G. Polygastric phase. Two interlocking nectophores of a 45 mm long specimen, $\times 3.7$, 'Discovery' St. 284. E.p. = Pyramidal extension; N.s. = Nectosac; S. = Somatocyst; T.D. = Dorsal tooth; T.v.l. = Left ventral tooth.

Ceratocymba intermedia Sears, 1953

Although I feel very doubtful about the specific identity of this form I quote it on the authority of Dr. Sears who has stated her reasons for considering it as specifically different from *C. dentata* and *C. sagittata*.

Dr. Sears cites three specimens or figures: (1) Bigelow (1911b), plate 12, figure 7, anterior nectophore, 7 mm in length. Specimen no longer available. (2) Moser (1925), plate 15, figure 3, anterior nectophore, 5 mm in length. Whereabouts of specimen unknown. (3) Sears (1953), text-figure 22, anterior nectophore, 7 mm in length, mutilated, deposited in Universitets Zool. Mus. København: the type specimen. Sears argument appears to be that though (1) and (2) were naturally thought to be young specimens of *C. sagittata* yet in her experience of considerable numbers of young anterior nectophores of *C. sagittata* the definitive shape found in that species has been established in every case before reaching the length of 5 mm. I feel that specimens (1) and (2) may possibly be the exceptions. I cannot at this time give any data which would throw light on the subject. The question of associa-

FIG. 141. *Ceratocymba sagittata* Q. & G. Polygastric phaseA, Posterior nectophore, $\times 3.4$, 'Discovery' St. 676; C, ostial end of same, $\times 9.8$ *Ceratocymba leuckarti* (Huxley) Polygastric phase

B, Posterior nectophore, lateral view, $\times 6.5$; D, Postero-lateral view of same, $\times 2.5$, 'Discovery' St. 694
Apoph = apophysis; *Cmb* = comb; *Ns* = nectosac; *R.d* = dorsal ridge; *To.d* = dorsal (median) tooth; *To.l* = left dorso-lateral tooth; *To.r* = right dorso-lateral tooth; *To.v.l* = left ventral tooth; *W.hyd.l* = left hydroecial wing; *W.hyd.r* = right hydroecial wing (from Totton, 1954, fig. 79).

tion, if any, with larger specimens would have to be considered. We are largely dependent upon inferences of this sort in building up pictures of the various parts and phases of species.

Polygastric phase

Anterior nectophore: The chief diagnostic feature cited by Sears is that the hydroecium extends to about one-half the overall length instead of one-third as in *C. sagittata*, so that the apical prolongation is relatively shorter than in *C. sagittata*, though longer than in *C. dentata*.

Posterior nectophore and gonophore: Unknown.

Eudoxid phase – not identified.

Ceratocymba dentata (Bigelow, 1918)

Plate XXXVIII, figures 1–3

For synonymy see Sears, 1953, page 69

In a typical specimen ('Discovery' Station 2653 – see Totton, 1954) the anterior nectophore measured 11 mm in length and the posterior one 55 mm: its nectosac 45 mm \times 3–5 mm.

Anterior nectophore: The most distinctive features as described by Bigelow (1918) are (1) the

triangular dorsal facet with strongly bowed and serrated lateral margins and a deeply emarginated base; (2) its apex, into which the apex of the nectosac is extended, is produced into a short peak which extends beyond the apex of the somatocyst and hydroecium.

Posterior nectophore: At least three times as long as wide and opaque. Dorsal tooth larger than in the other species, and forward projecting. For detailed structure see Sears (1953, pp. 69-70, text-fig. 21); Totton (1954), Pl. X.

Eudoxid phase

Bract (see Totton, 1954, text-fig. 80): The finding of attached, well developed eudoxids enabled me in 1954 to publish confirmation of my deduction from associations of two phases in the same catches that the left lateral ridge always joins the apico-dorsal ridge, but not the posterior margin. This is the reverse of the condition found in *C. leuckarti*. Sears (1953) reported that this type of bract had been taken repeatedly with the polygastric stage of this species.

Gonophore: A larger female and smaller mirror image male usually found locked together under the bract (Totton, 1954, text-fig. 81). The structure of the gonophores is more complicated than that of any other species of siphonophore. The implication is that the genus is highly evolved.

Genus: *ABYLA* Quoy & Gaimard, 1827

Pseudabyla Sears, 1953, page 49, text-figure 16, 17

Type species: *Abyla trigona* Quoy & Gaimard, 1827.

Through the courtesy of the Musée d'Histoire Naturelle, Paris, both Dr. Sears and I have been able to make independent re-examinations of syntypes of the type species (see Sears, 1953, and Totton, 1954).

I regard the species of *Abyla* as the most variable of siphonophores, and the most highly evolved. The larval nectophore, however, appears not to be caducous but to persist as the anterior nectophore. As in all abylids except *Bassia* the somatocyst has curved over to occupy a position on the dorsal side of the hydroecium.

The generic characters were dealt with at length by Sears (1953). She made keys for nine species, and published many line drawings of the separate parts.

A great deal of material of *Abyla* spp. is available for the next reviewer.

Abyla trigona Quoy & Gaimard, 1827

Plate XXXVI, figures 9, 10

For synonymy see Sears, 1953, page 35

? Syn. *A. carina* Haeckel, 1888b

Polygastric phase (Pl. XXXVI, figs. 9, 10)

Anterior nectophore: Sears described four characteristics: (1) most of the ridges are heavily and irregularly serrated, the laterals of the dorsal facet especially so; (2) the apico-dorsal facet is sharply bent upward from the insertion of the lateral ridges to the transverse apical ridge*; (3) the lateral protrusions are somewhat sharper and more prominent than those of *A. carina*; (4) the facets of the nectophore as a whole are depressed below the ridges surrounding them. For figures see Sears (1953), text-figures 8B, 9B, 10B.

Posterior nectophore (text-fig. 142A, D, E): Sears described three characteristic features: (1) a smaller number (six to eight) of teeth on the comb than in *A. carina*; (2) the presence of two rows of teeth on the basal margin of the right ventral wing much as Haeckel (1888a, Pl. 35, figs. 8-9) showed them; (3) the heavier serration of the ostial teeth, more so than in any other known species of *Abyla*.

* Sears provided diagrammatic drawings to explain terminology. It should be noted that I continue to use the terms right and left in the sense opposite to that of Sears.

Eudoxid phase

At present we cannot distinguish between the eudoxids of the *A. trigona* group of species. There are no really satisfactory illustrations of these common animals.

Remarks: I suspect that *A. trigona* and *A. carina* will eventually prove to be synonyms of one species. For my comments on the statement by Sears (1953, p. 32) that both Quoy & Gaimard and Haeckel were confusing two species (the same two in each case) in their accounts of *A. trigona* and *A. carina*, see Totton (1954, pp. 148–151).

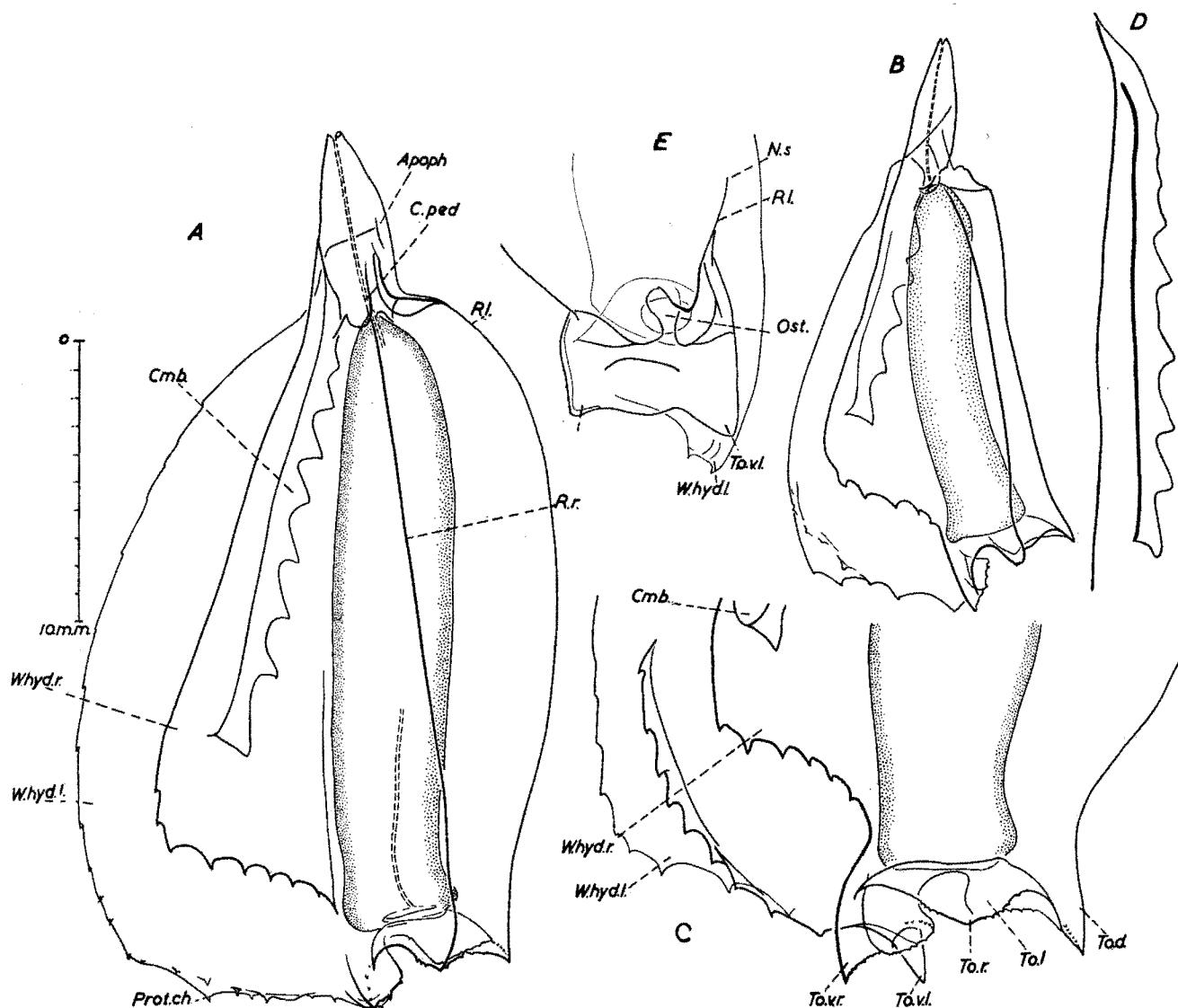


FIG. 142

A. *Abyla trigona* Q. & G. Polygastric phase. Posterior nectophore, lateral view, $\times 4.2$, 'Discovery' St. 2067

B. *Abyla carina* Haeckel. Posterior nectophore, Challenger Expedition

C. *Abyla tottoni* Sears. Basal part of the posterior nectophore, $\times 5.2$, 'Discovery' St. 1178

D. *Abyla trigona* Q. & G. Comb of right hydroecial wing of posterior nectophore, part of the type material
(Mus. d'Hist. Nat., Paris)

E. Dorsal view of the base of the posterior nectophore of the same, $\times 5.5$

C.ped = pedicular canal; Ost = ostium; R.I. = left ridge; R.r = right ridge; for other abbreviations see text-figure 141 (from Totton, 1954, fig. 75).

Abyla carina Haeckel, 1888

Text-figure 142B

I suspect that eventually it will become clear that *A. carina* is a synonym of *A. trigona* Quoy & Gaimard. In my experience, species of *Abyla* are very variable and few in number. Sears (1953) stated that *A. carina* shows in its anterior nectophore a number of distinguishing features, so that for the present I treat it as a separate species and cite the distinguishing features alleged by Sears.

Polygastric phase

Anterior nectophore (text-fig. 142B; see Sears, 1953, figs. 8A, 9A, 10A): (1) In lateral view the lower edges of the sides of the basal facet are diagonal (i.e. form an acute angle with the horizontal and only slightly curved because the dorsal teeth do not protrude below it as they do in *A. trigona*). (2) In side view the apico-dorsal-dorsolateral ridges of the apicodorsal facet form a diagonal to the dorsal facet.* I am not sure what Dr. Sears means, but I do not think that a distinction can be made in this type of nectophore between a *trigona* and a *carina* pattern of ridges. (3) The transverse apical ridge may be slightly elevated above the surface of the apical facets. (4) The lateral protrusions as seen in ventral or dorsal view are not prominent. (5) The ridges as a whole are not raised above the facets. (6) Most of the basal ridges are slightly serrated. (7) The nectophore is more massive than that of *trigona*.

Posterior nectophore: Sears admitted that the general shape is not sufficiently characteristic to separate it from that of *trigona*, but notes some differences. These appear to me to be of a kind that is very variable.

Eudoxid phase

It has not been determined whether the eudoxids are characteristically different from those of *trigona*.

Abyla haeckeli Lens & van Riemsdijk, 1908

Plate XXXVI, figures 6, 8

For synonymy see Sears, 1953, page 39

Polygastric phase (Pl. XXXVI, figs. 6, 8)

Anterior nectophore: There is a horizontal ridge dividing off from the ventral facet – as found in *trigona* (see Bigelow 1911b, fig. 3) – an apicoventral facet (see Bigelow, 1911b, Pl. 13, fig. 1 and Sears, 1953, fig. 3).

I have re-examined the nectophore I described in 1932, which Sears said might equally well be that of *ingeborgae*. My identification was correct.

Posterior nectophore (young specimens): (1) the lateral teeth round the ostium lie closer to the dorsal tooth than to the ventral ones. (2) There are only two or three teeth on the comb. We need a figure of a mature specimen.

Eudoxid phase

Bract: The ‘cleft’ shown in my (1932) text-figure was as I stated, an artefact, which distorted the basal facet. Apparently Sears excluded my specimen from *haeckeli* thinking that this was of a specific nature.

Gonophore (see text-fig. 143).

* For nomenclature of ridges and facets see Sears (1953, fig. 3). Since the lateral ridges of the apicodorsal facet may be said to be divided into two at their junction with the lateral ridge – the one between the apical ventrolateral facet and the dorsolateral facet – I have distinguished between the two parts by naming the facets between which the particular part runs.

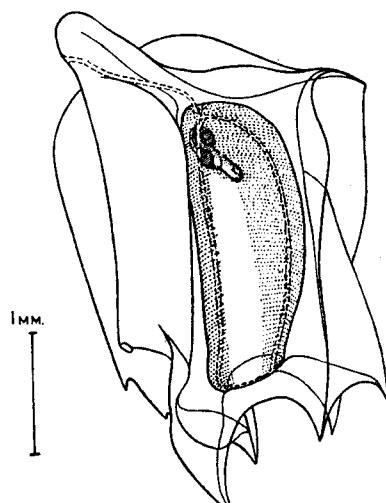


FIG. 143. *Abyla haeckeli* L. & v. R. Eudoxid phase. Gonophore, $\times 16$, Gt. Barrier Reef (from Totton, 1932, fig. 13).

than basal ventrolateral. (5) Dorsal facet is almost a perfect rectangle (not tapered at top as in *schmidti* or bowed on sides as in some species). (6) The only serrations are at the base of dorsal wall of hydroecium.

Posterior nectophore (text-fig. 145A, B): (1) Comb has five teeth. (2) Basal border of right (*sensu* Sears) ventral wing 'more nearly triangular' (? straight) than concave. (3) Dorsal tooth smaller and less prominent than in *haeckeli*. (4) Right lateral tooth almost as large as left, with a well defined ridge (in *haeckeli* right tooth is the smaller). (5) Ventral extent of basal margin of right (*sensu* Sears) ventral wing not delimited by strong teeth, and ventral margin not as thickened as in *haeckeli*.

In my experience all such characters are very variable.

Eudoxid phase

Bract resembles that of *haeckeli* with conspicuous dorsal tooth and ridge.

Abyla bicarinata Moser, 1925

Plate XXXVIII, figures 4-7

A. bicarinata Sears, 1953

A. brownia Sears, 1953

This species is characterised by the width of the nectophores. A complete polygastric specimen was taken on October 16, 1951, at 'Discovery' Station 2893 in a haul from 92 m to the surface. The following description is taken from Sears (1953).

Polygastric phase (Pl. XXXVIII, figs. 4-7)

Anterior nectophore: Wider than long, lateral ridges forming wing-like expansions. Edges of the facets rounded and tumid. There is no depression or furrow ventral to transverse apical ridge. Owing to the peculiar arrangement of facets and ridges, in a lateral view, the whole of the somatocyst may be seen through the ventrolateral facet.

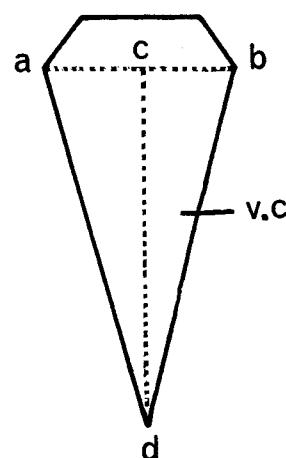


FIG. 144. *Abyla ingeborgae* Sears Polygastric phase. Anterior nectophore (schematic).
v.c = ventral facet; for other lettering see text.

Posterior nectophore: As wide as long. Left (*sensu* Sears) lateral ridge as conspicuous as right one: both much expanded. Right ventral wing almost semi-circular. Ostial teeth strong and prominent. Comb with four to seven teeth, six teeth on inner, basal part of right ventral wing.

The alleged posterior nectophore figured by Moser (1925, Pl. 19, figs. 7-9) does not belong to *bicarinata*, as pointed out by Sears. It may belong to *schmidti*.

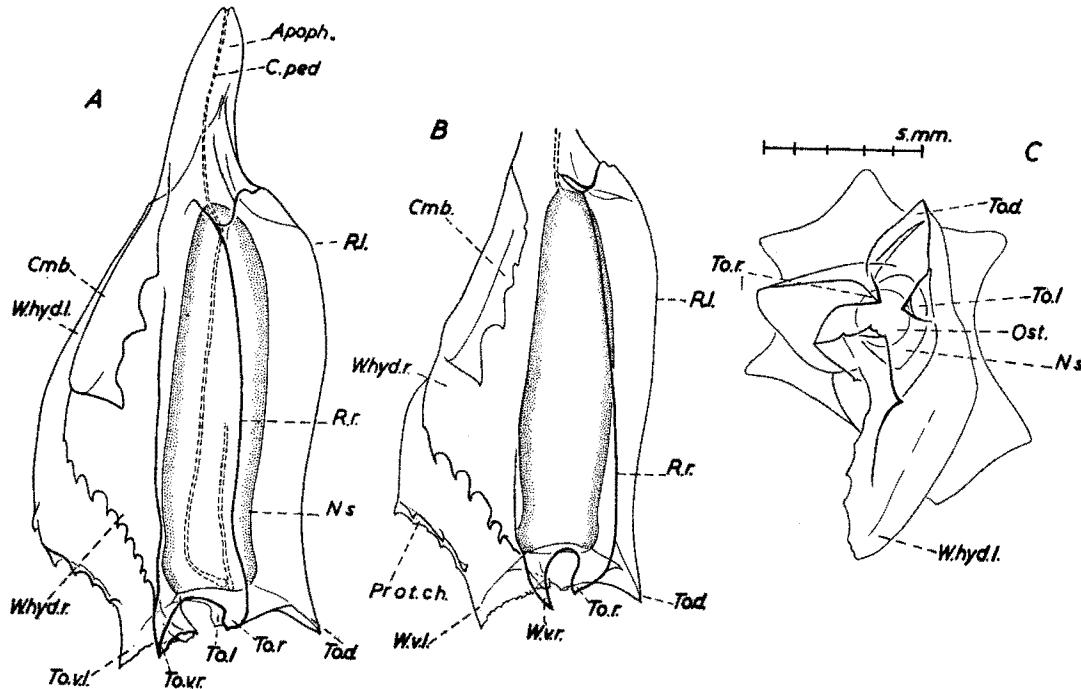


FIG. 145

A, B. *Abyla ingeborgae* Sears. Polygastric phase. Posterior nectophores, $\times 3.8$, 'Discovery' Sts. 706, 2639, 1,200-600 m. Each was associated with anterior nectophores of the species

C. *Abyla schmidti* Sears. Basal view of the posterior nectophore of ~~the imago~~, $\times 4$, 'Discovery' St. 1581

Apoph = apophysis; *C.ped* = pedicular canal; *Cmb* = comb; *Ns* = nectosac; *Ost* = ostium; *R.l* = left ridge; *R.r* = right ridge; *Prot.ch* = chin-shaped protuberance; *To.d* = dorsal tooth; *To.l*, *To.r* = left and right tooth; *To.v.l*, *To.v.r* = left and right ventral tooth; *W.hyd.l* = left hydroecial ridge; *W.hyd.r* = right hydroecial ridge; *W.v.l* = left ventral wing; *W.v.r* = right ventral wing (from Totton, 1954, fig. 78).

Eudoxid phase - not identified.

In view of the known variability of species of *Abyla* I do not think that there is reason to regard the one anterior nectophore named *A. brownia* by Sears (1953) as sufficient evidence of the existence of a separate species.

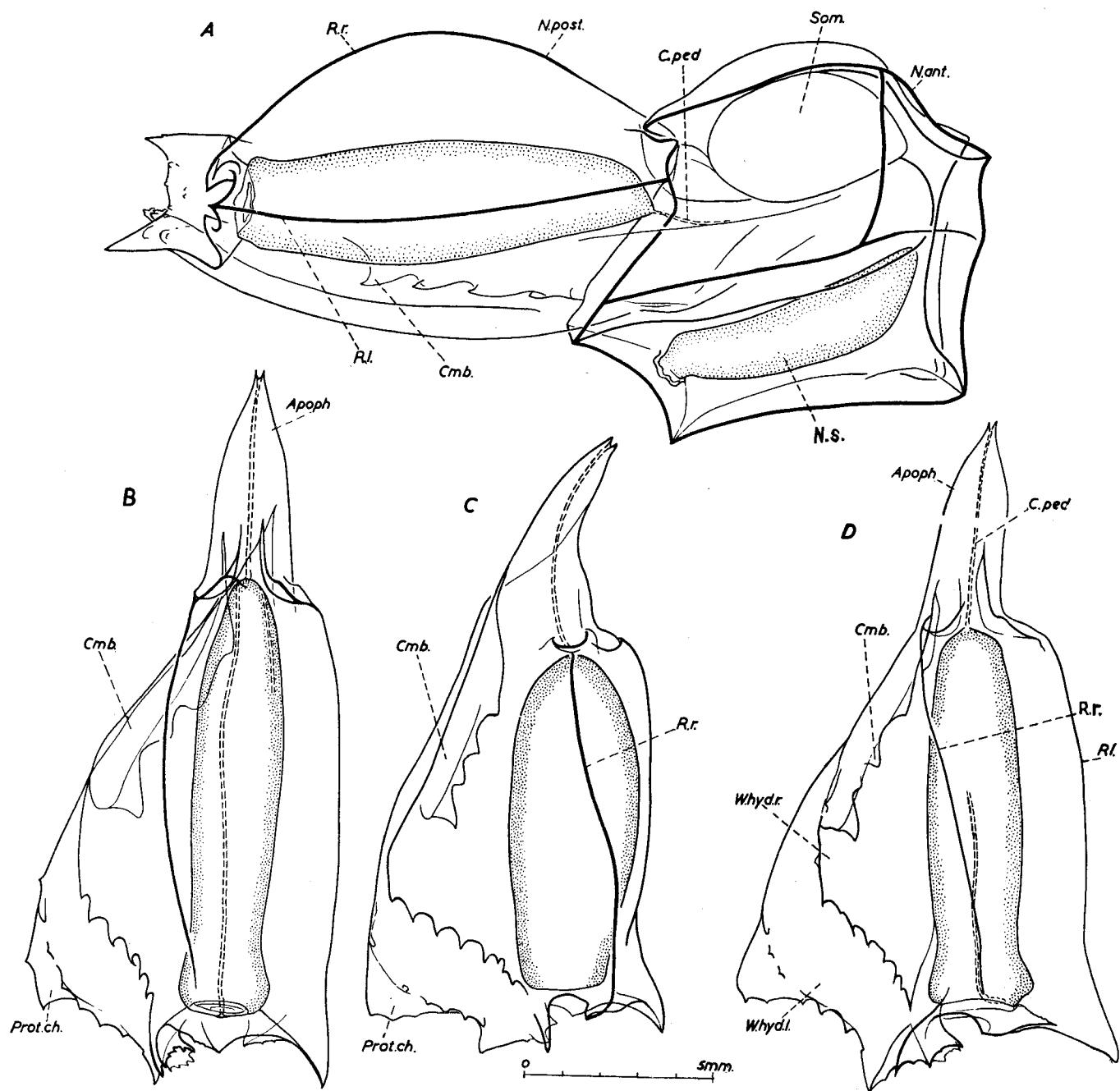
Abyla schmidti Sears, 1953

Text-figures 145C, 146, 147, 148

Abyla schmidti Totton, 1954

Polygastric phase (Text-fig. 146A, 148A.)

Anterior nectophore (text-figs. 147A-D, 148B, C): According to Sears it is differentiated by its proportionately larger apicodorsal facet, and a dorsal facet that tapers toward the base, rather than bulges in the middle as in *A. trigona/carina*.

FIG. 146. *Abyla schmidti* Sears. Polygastric phase

A, whole specimen, 'Discovery' St. 1581, $\times 6.4$; B, C, D, posterior nectophores. B, $\times 6.4$, 'Discovery' St. 1587; C, $\times 6.4$, N.W. Indian Ocean; D, $\times 6.4$, 'Discovery' St. 1585. In D a break in the pedicular canal indicates a shortening of the apophysis

Apoph = apophysis; *Cmb* = comb; *C.ped* = pedicular canal; *N.ant.*, *N.post.* = anterior and posterior nectophores; *N.s* = nectosac; *Prot.ch* = chin-shaped protuberance; *R.l*, *R.r* = left and right ridge; *W.hyd.l*, *W.hyd.r* = left and right hydroecial wings (from Totton, 1954, fig. 73).

Posterior nectophore (text-figs. 146B-D, 147E-G, 148D): Right ventral wing expanded, with a triangular protrusion between the two basal rows of teeth below which it hangs; the inner row strongly developed. Left ventral wing with from four to five large teeth.

Eudoxid phase

The bracts and gonophores have so far not been found to be specifically distinguishable.

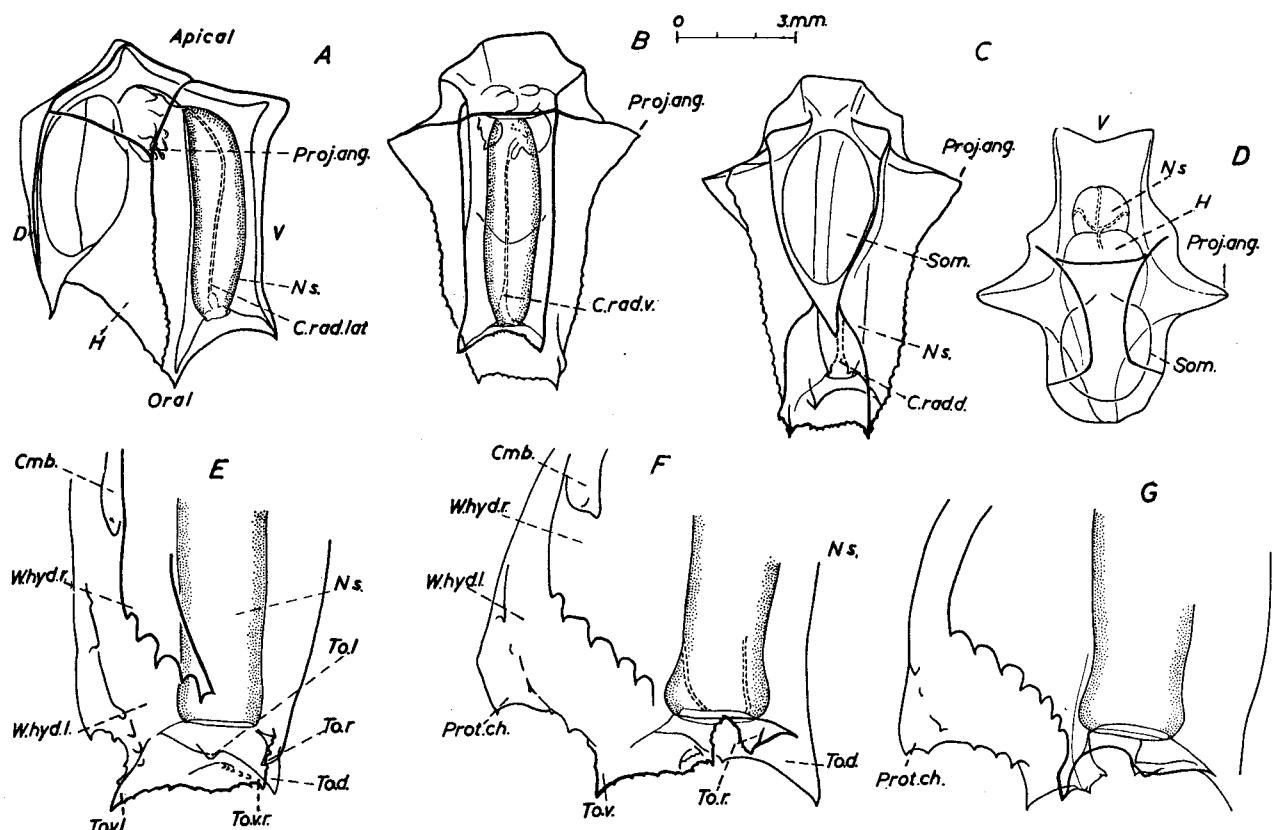


FIG. 147. *Abyla schmidti* Sears. Polygastric phase
A-D, anterior; E-G, posterior nectophores, $\times 5.5$. A-D, 'Discovery' St. 1588, 250-100 m; E-G, three views of the
ostial end of a specimen from 'Discovery' St. 1587 (from Totton, 1954, fig. 76)
Proj.ang = angular projection; other lettering as in figure 145.

Abyla tottoni Sears, 1953

Plate XXXIX

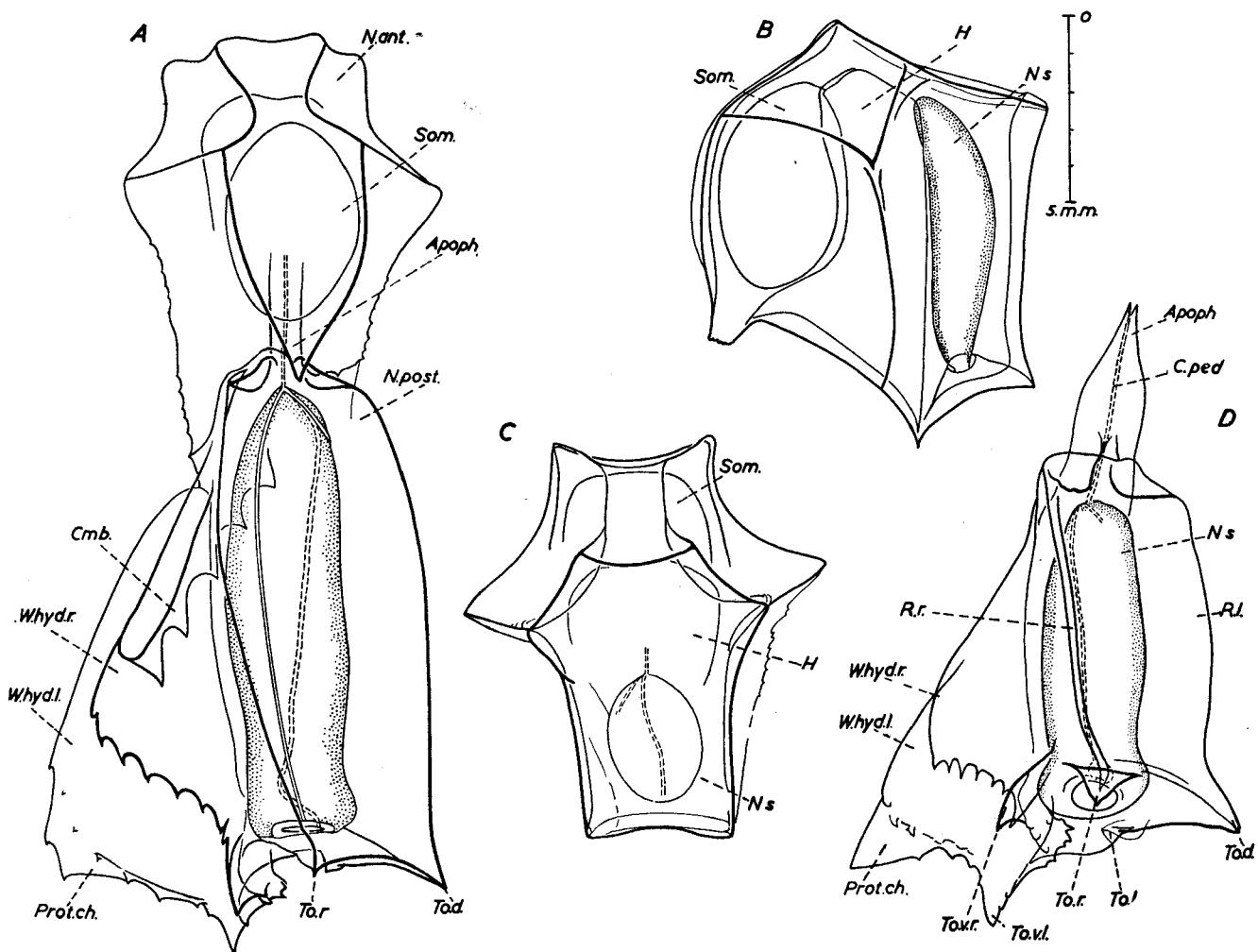
A. tottoni Totton, 1954 (text-fig. 75C, Pl. IX)

The following description is largely based on that of Sears.

Polygastric phase

Anterior nectophore: Nearly as wide as high, tumid, the ridges indistinct. The lateral protrusions more marked than in those of species with expanded lateral ridges. At the insertion of the horizontal ridge the width of the ventral facet nearly equals its length from that point to its basal tip. There is a deep depression just ventrad to the transverse apical ridge.

Posterior nectophore (text-fig. 142C): Three-quarters as wide as long (exclusive of apophysis). The 'dorsal' ridge (really the left ridge) is so expanded towards the apex that it curves sharply before merging with the dorsal tooth. The whole margin of the left (right *sensu* Sears) ventral wing may be

FIG. 148. *Abyla schmidti* Sears. Polygastric phase

A, whole specimen, $\times 5.5$, 'Discovery' St. 1581; B, lateral view of the anterior nectophore, $\times 5.4$, N.W. Indian Ocean; C, view of A from above, $\times 5.5$; D, baso-lateral view of the posterior nectophore, $\times 5.6$, 'Discovery' St. 1586; abbreviations as in figures 141, 142, 147 (from Totton, 1954, fig. 77)

serrated, and there may be from twelve to thirteen teeth on its inner basal margin. There may be from twelve to thirteen teeth on the base of the smaller wing, the ventral corner of which may be more rounded than shown in Sears figure 15B. On the comb there may be eleven teeth including two lesser ones between 1 and 2, and 2 and 3 of Sear's figure 15B.

Eudoxid phase – not identified.

Abyla peruana Sears, 1953

Described from a single anterior nectophore. Whether it will prove to be a distinct species time will show.

For a description and figure see Sears, 1953, page 45, figures 8D, 9D, and 10D.

The posterior nectophore and eudoxid are unknown.

Sub-family ii: ABYLOPSINAE Totton, 1954

This sub-family contains four species belonging to the genera *Abylopsis*, *Enneagonum* and *Bassia*. *Enneagonum* has only one species, like *Bassia*, and in it no posterior nectophore is ever developed. On this account it used to be included in another family. But its affinities with *Abylopsis* spp. were pointed out thirty years ago by Totton (1932). In these three genera the anterior nectophore has no apical facet but a ridge, formed by the junction of two lateral facets. The most characteristic feature in which the polygastric phase of abylopsines differs from that of abylines is the way in which anterior and posterior nectophores articulate with one another. In abylines the posterior nectophore, after issuing from the tunnel-like hydroecium, hangs below or follows after with its long axis in line with the long axis of the hydroecium and nectosac of the anterior nectophore. But in abylopsines these two long axes of the anterior and posterior nectophores form an angle of about 45° to each other (cf. Totton, 1954, text-figs. 73A and 82). As a consequence, when the animal is swimming horizontally, the dorsal facet of the anterior nectophore of abylines is on the underside; whilst in abylopsines it is nearly vertical, and the apical end of the posterior nectophore (excluding the pedicel or apophysis, which lies in the hydroecium) articulates with almost the whole of the ventral facet of the anterior nectophore. In abylines this ventral facet, which lies uppermost during horizontal progression, ends, as a rule, in a posterior tooth which hooks over the dorsal facet of the posterior nectophore. The ridge, which in abylines separates the dorso-lateral and ventro-lateral facets of the anterior nectophore, is represented in abylopsines by an elongated homologue the 'horizontal ridge'. Having no longitudinal lateral ridge to join onto, as in abylines, this horizontal ridge is produced till it meets the lateral margins or ridges of the dorsal facet. Anterior nectophores of abylopsines have no apical facets. Instead the apices of the pentagonal dorsal and ventral facets are joined together by a ridge. The dorsal facet itself in *Abylopsis* and *Bassia* is shaped as in *Ceratocymba dentata* and *C. sagittata*. But in *Enneagonum* it bears a ridge as in the Diphyinae. The posterior nectophore, in those abylopsine species where one is developed differs from those of Abylines in having a flap on the inner side of both right and left ventro-lateral ridges or wings.

The abylopsine eudoxid phase also differs from that of abylines, so that the division of abyliids into two sub-families seems to be a natural one. I have already (1932) pointed to the affinities between *Enneagonum* and the other three abylopsines.

Genus: *ABYLOPSIS* Chun, 1888

Type species: *Abylopsis tetragona* (Otto, 1823).

It was Chun who substituted the present name *Abylopsis* for the old one *Calpe* (preocc. Lepidoptera).

The somatocyst of the anterior nectophore extends well over to the ventral side of the hydroecium, whose lower walls are extended beyond both ventral and basal facets. The apical part of the nectosac extends well up between the somatocyst and the dorsal facet. The dorsal facet is flat and bears no median ridge. A posterior nectophore is produced. In the bract of the eudoxid the phyllocyst has well developed ventro-lateral branches. There is a rectangular apical bracteal facet.

Abylopsis tetragona (Otto, 1823)

Plate XL, figures 1, 3

For synonymy see Bigelow, 1911b, page 224

One of the very abundant and well-known 'Diphyids'.

Complete specimens of the polygastric phase of this species can be readily recognized by the

relatively long posterior nectophore, which is about three times as long as wide, whereas in *Abylopsis eschscholtzi* the posterior nectophore is a little less than twice as long as wide. I described in 1932 how the main propulsive jet is made by the posterior nectophore, and how the intermittent and more rapid contraction of the anterior nectosac serves to alter course. These observations were repeated by Dr. D. A. Boag at Naples in 1961.*

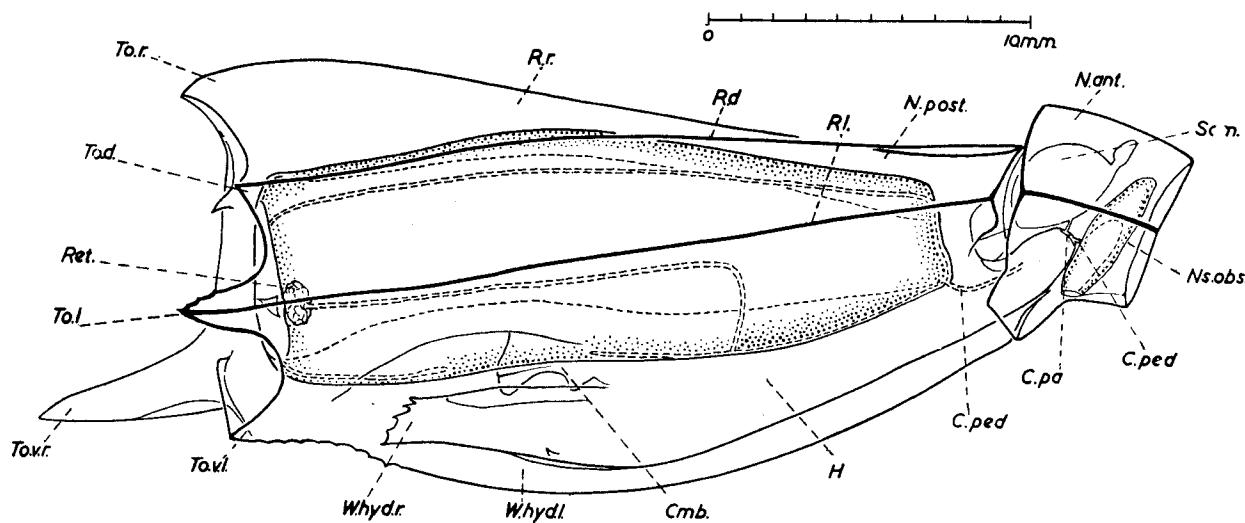


FIG. 149. *Abylopsis tetragona* (Otto). Polygastric phase

The two nectophores rigidly locked together as in life, $\times 4.2$. Abbreviations as in figures 141, 142, 147 (from Totton, 1954, fig. 82)

Polygastric phase

Anterior nectophore (text-fig. 149): The most reliable way of distinguishing it from that of *eschscholtzi* is, as a rule, to examine the lateral radial canals. In *tetragona* these canals rise towards the apex of the nectosac in an ascending loop before running down to the circular canal. In *eschscholtzi* they do not. The figures given by Bigelow (1911b, Pl. 14, figs. 6 and 1) are excellent and make this point quite clear. The other distinguishing features are more subtle and less reliable.

Posterior nectophore (text-fig. 150): About three times as long as broad. There is a peculiar arrangement of the radial canals which virtually increases the number from four to four-and-a-half (see Pl. XL, fig. 1; and Sears, 1953, fig. 25D – a ventral view – and Totton, 1954, text-fig. 83A). From the *rete* at the junction between the circular (ostial) canal and the ventral radial canal there arises towards the left a blind canal, separated at its apex from a short, blind down-growth from the left lateral radial canal, at a point where it is deflected to the left. The new half canal lies under the left ventral ridge.

The upper half of the hydroecial canal is covered by a flap of the left hydroecial wing or left ventral ridge. A comb or 'Leiste' bearing nine teeth arises from the upper half of the inner side of the right hydroecial wing or right ventral ridge. In *Abyla* this comb arises from the outer part of the wing. The outer reflexed part of the left hydroecial wing is locked in position between the comb and a small mamma-like projection from the middle of the hydroecial wing (text-fig. 150). The apical wall of the posterior nectophore articulates with almost the whole of the ventral wall of the anterior nectophore.

* Communicated *in litt.* to author.
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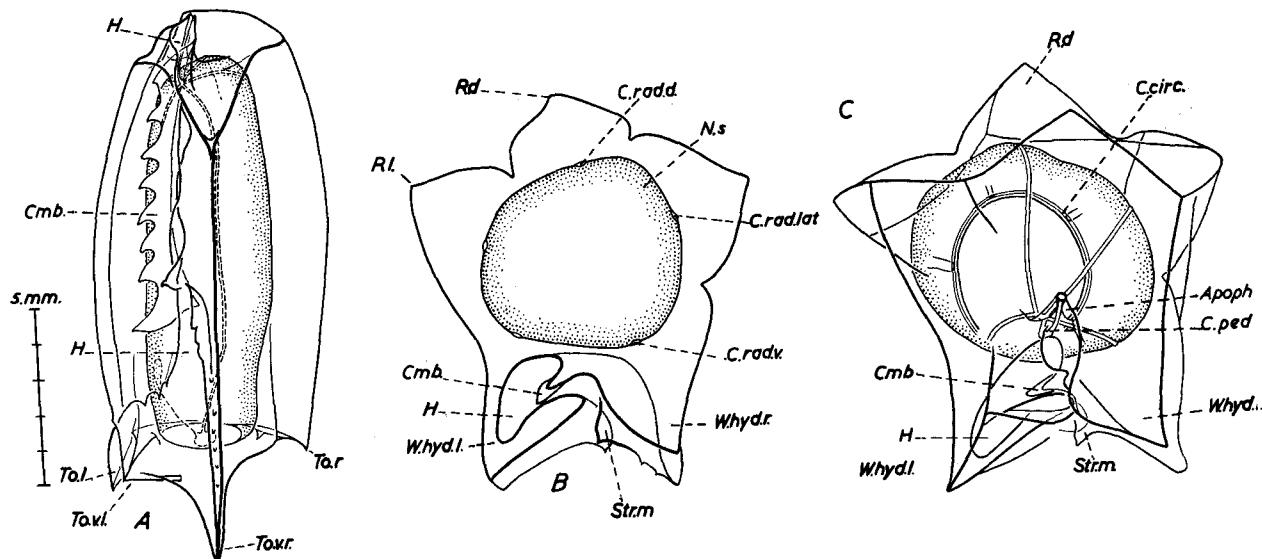


FIG. 150. *Abylopsis tetragona* (Otto). Polygastric phase. Posterior nectophore
A, latero-ventral view, $\times 5$; B, a section across the same, just above the locking tooth of the right wing, $\times 8.8$;
C, apical view, $\times 8.8$. Abbreviations as in figures 141, 142, 147 (from Totton, 1954, fig. 83)

Eudoxid phase (Pl. XL, fig. 3)
(Totton, 1932, text-fig. 17C).

Nomenclature: It is called an '*Agalaisma*' (an old synonym of *Abylopsis*).

Bract: The lateral facets are deep, so that the basal cross ridge (see Totton, 1932, text-fig. 17C ab) lies far below the level of the large lateral branches of the phyllocyst. The basal-sagittal ridge is very short.

Gonophore: Comparatively narrow and elongate with shallow ridges and long teeth. For further details see Sears, 1953, page 83.

Abylopsis eschscholtzii (Huxley, 1859)
Plate XL, figures 2, 4, 6

Aglaismoides eschscholtzii Huxley, 1859

Less commonly taken than *A. tetragona*.

Polygastric phase (Pl. XL, fig. 2)

A specimen of the polygastric phase is relatively shorter than one of *A. tetragona*.

Anterior nectophore (Pl. XL, fig. 4): The apex of the nectosac does not extend as far as the apex of the main part of the somatocyst and the bases of the lateral radial canals do not form an upward loop. The ridges are more marked and serrated than are those of *tetragona*.

Posterior nectophore (Pl. XL, fig. 6): Considerably less than twice as long as broad. Only four, regular radial canals. The apophysis relatively a little larger than in *tetragona*. Each hydroecial wing or ventrolateral ridge has in the hydroecial region a secondary flap. Their inner edges meet and fuse along the proximal half of their length to roof over a hydroecial tube. There may be from four to eight teeth on the ventrobasal curve of the left-hand (Sears' right) flap, and three or four in the same region of the smaller right-hand one, in the same region indicated by a dotted line by Sears (1953, fig. 25E). This smaller flap is the homologue of the comb in *tetragona* (see Sears, 1953, fig. 25C, E). The basal rim of the hydroecial cavity is much more simple than in *tetragona*. It is a simple, serrated semi-circular rim with two ventro-lateral teeth.

Eudoxid phase

Bract: The basosagittal ridge is much longer than that of the bract of *tetragona*, the basal cross ridge of the lateral facet higher up, and the lateral ridges of the dorsal facet slope in towards the apical facet instead of being vertical as in *tetragona* (see Bigelow, 1911b, Pl. 15, fig. 1, and Sears, 1953, fig. 2C, D).

Genus: **BASSIA** L. Agassiz, 1862

Sphenoides Huxley, 1859

A monotypic genus for *B. bassensis* (Quoy & Gaimard, (1833) 1834), an abundant species well described and figured by Huxley (1859), Gegenbaur (1859) and Haeckel (1888b).

The eudoxid phase is called a 'sphenoides' from a prior name of Huxley, 1859.

The edges of the ridges of specimens of *bassensis* are opaque by reflected light.

The somatocyst of the anterior nectophore does not extend over to the ventral side of the hydroecium. The apex of the nectosac does not extend up between the somatocyst and the dorsal facet. In the eudoxid phase the bract has an apical ridge and its phyllocyst lacks ventro-lateral branches. The ventral facet of the anterior nectophore has no median ridge.

The generic name *Bassia* was first published by Blainville (1830) for a manuscript name (nomen nudum) of Quoy & Gaimard. *Sphenoides* Huxley seems to have priority over it, but is a *nomen oblatum*.

***Bassia bassensis* (Quoy & Gaimard, (1833) 1834)**

Plate XL, figure 5

For synonymy see Bigelow, 1911b

Polygastric phase

(Text-fig. 151A.) The posterior nectophore may be replaced by a reserve bud.

Anterior nectophore (text-fig. 151B): Resembling that of *Abylopsis eschscholtzi* but the somatocyst has no apical projection and it does not extend into the apico-ventral part of the nectophore. The basal part of the hydroecium does not project below the basal (ostial) facet. The apex of the nectosac, which is small, does not extend much above the apex of the hydroecium or the base of the somatocyst. The hydroecium is rather shallow and has a flared opening.

Posterior nectophore (text-fig. 152; see also Sears, 1953, fig. 28C): Resembling that of *Abylopsis*

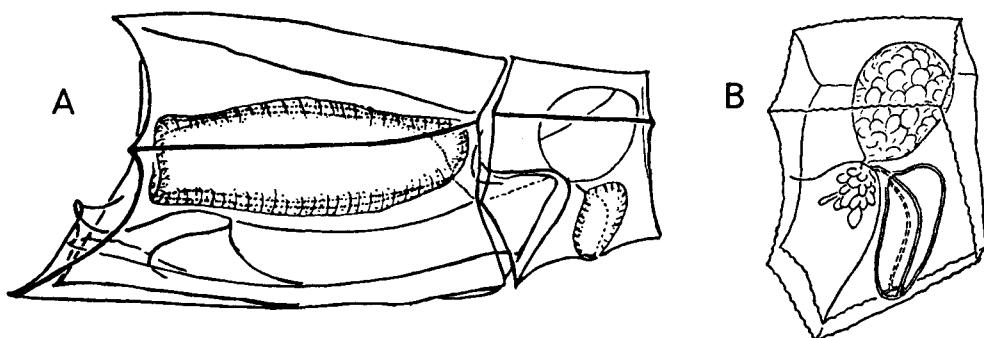


FIG. 151. *Bassia bassensis* (Q. & G.). Polygastric phase
A, whole specimen; B, lateral view of the anterior nectophore (from Totton & Fraser, 1955)

eschscholtzii. The median-dorsal ridge is suppressed (see my 1932 fig. 18). The ostial end is twisted so that the posterior end of the right lateral ridge and the keel-like tooth of the left ventral ridge come to lie almost in the sagittal plane. The inner flaps of the ventral wings or ridges appear to be fused to roof over the hydroecium in the proximal half of its length. The broadened basal end of the left ventral flap and the basal rim of the hydroecium are serrated.

Eudoxid phase (Pl. XL, fig. 5)

Bract: There is a long baso-sagittal ridge as in *Abylopsis eschscholtzii* but an apical ridge replaces an apical facet.

There are no lateral branches of the phyllocyst, but there is a large apical and a long narrow basal branch.

Genus: **ENNEAGONUM** Quoy & Gaimard, 1827

Cuboïdes Q. & G., 1827

Cuboïdes Bigelow, 1911b

Monotypic genus for *E. hyalinum* Q. & G., 1827.

If a suitable specimen of *E. hyalinum* – there is some variation – is orientated as in my (1932) text-figure 16 it will be seen that its features are homologous with those of *Abylopsis* and *Bassia* spp., except for the presence of a dorsal ridge. This was emphasized by Sears (1953), having been previously referred to by Huxley (1859) and Totton (1932). No posterior nectophore is produced.

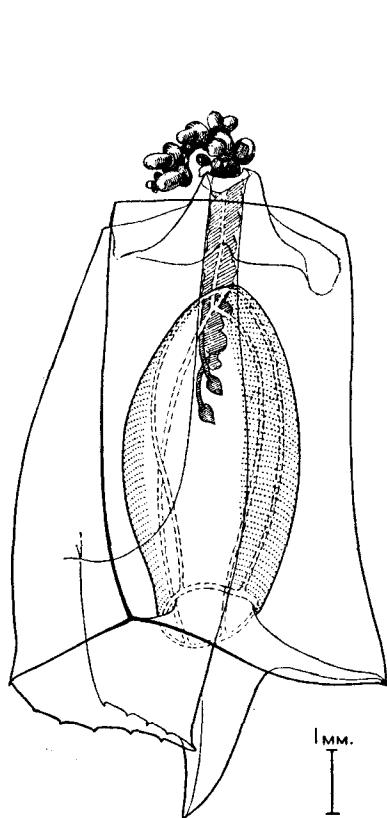


FIG. 152. *Bassia bassensis* (Q. & G.)
Polygastric phase. Dorsal view of the
posterior nectophore, $\times 8.5$ (from
Totton, 1932, fig. 18).

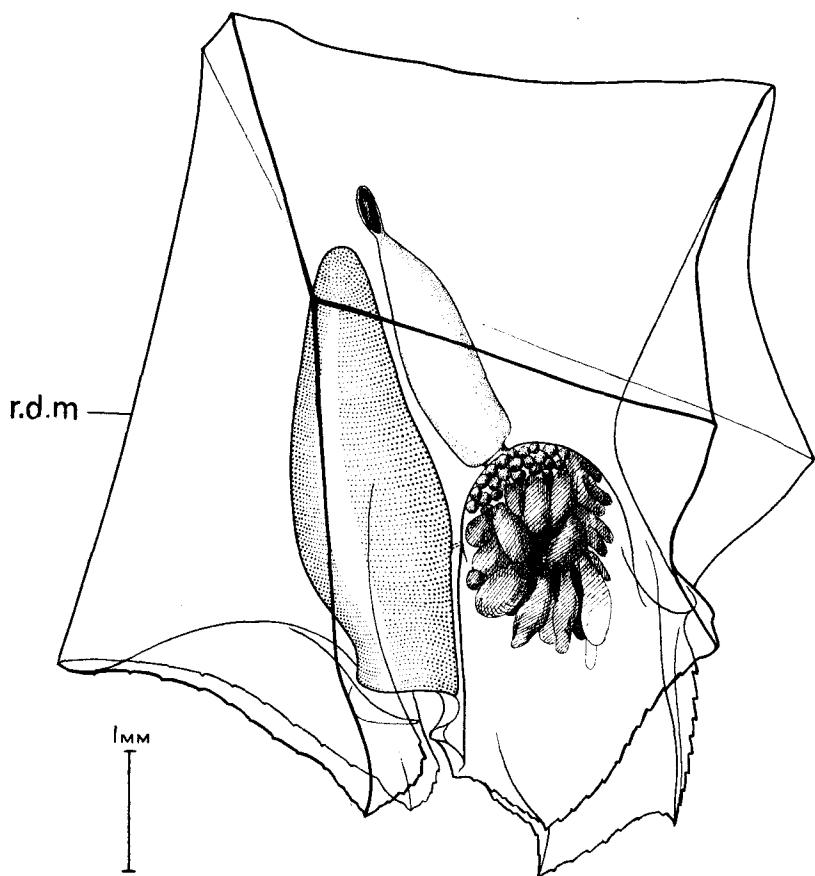


FIG. 153. *Enneagonum hyalinum* Q. & G. Polygastric phase
Lateral view, $\times 8$ (from Totton, 1932, fig. 16)

***Enneagonum hyalinum* Q. & G., 1827**

Text-figure 153

Cuboides vitreus Q. & G., 1827; Bigelow, 1911b*Abyla vogtii* Huxley, 1859*Enneagonum hyalinum* Totton, 1932*Polygastric phase*

(Text-fig. 153.) No posterior nectophore is budded.

The distinguishing features are the dorsal ridge and the elongated somatocyst. For minute details see Sears (1953, p. 99).

*Eudoxid phase**Bract:* Cubical, the basal ridge being the homologue of the cross ridge (Totton, 1932, text-fig. 17d) of *Abylopsis tetragona*. The baso-sagittal ridge has disappeared, as has the basal branch of the phyllocyst.*Gonophore:* This has been well described and figured by Sears (1953, fig. 29).

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A SYNOPSIS OF THE SIPHONOPHORA

PLATE I

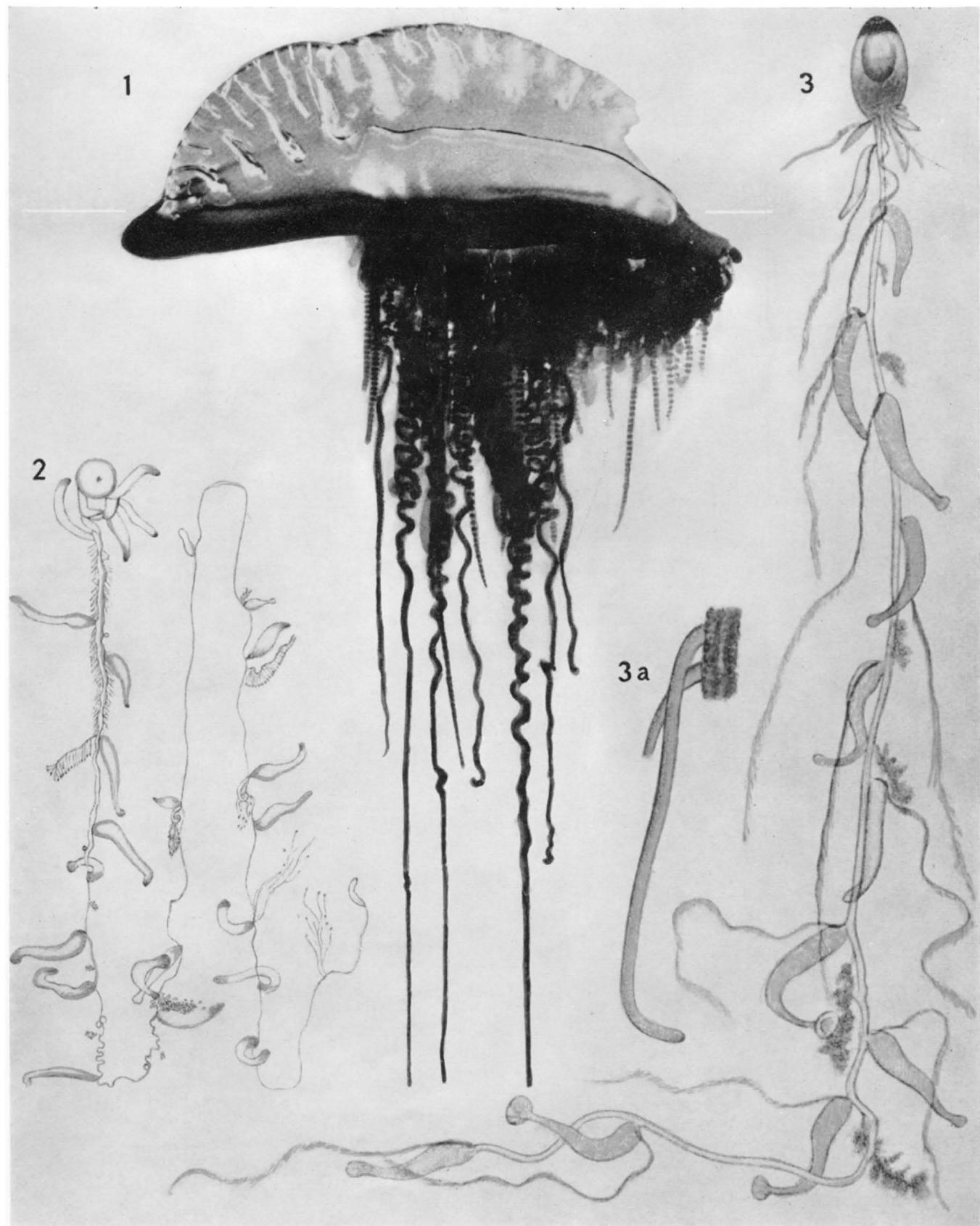
FIG. 1. *Physalia physalis* (L.). A medium sized, right-handed living specimen in a tank at Miami Marine Laboratory. By courtesy of Dr. Charles E. Lane.

FIG. 2. *Rhizophysa filiformis* (Forskål). From Lens & van Riemsdijk, 1908, plate 21, figure 151.

FIG. 3. *Rhizophysa eysenhardtii* Gegenbaur. From Kawamura, 1910, plate 14, figure 1.

FIG. 3a. Tentillum of the same, $\times 15$. From Kawamura, 1910, plate 14, figure 3.

PLATE I



A SYNOPSIS OF THE SIPHONOPHORA

PLATE II *Rhizophysa filiformis* (Forskål)

Photographs of living specimens from Villefranche, 1963

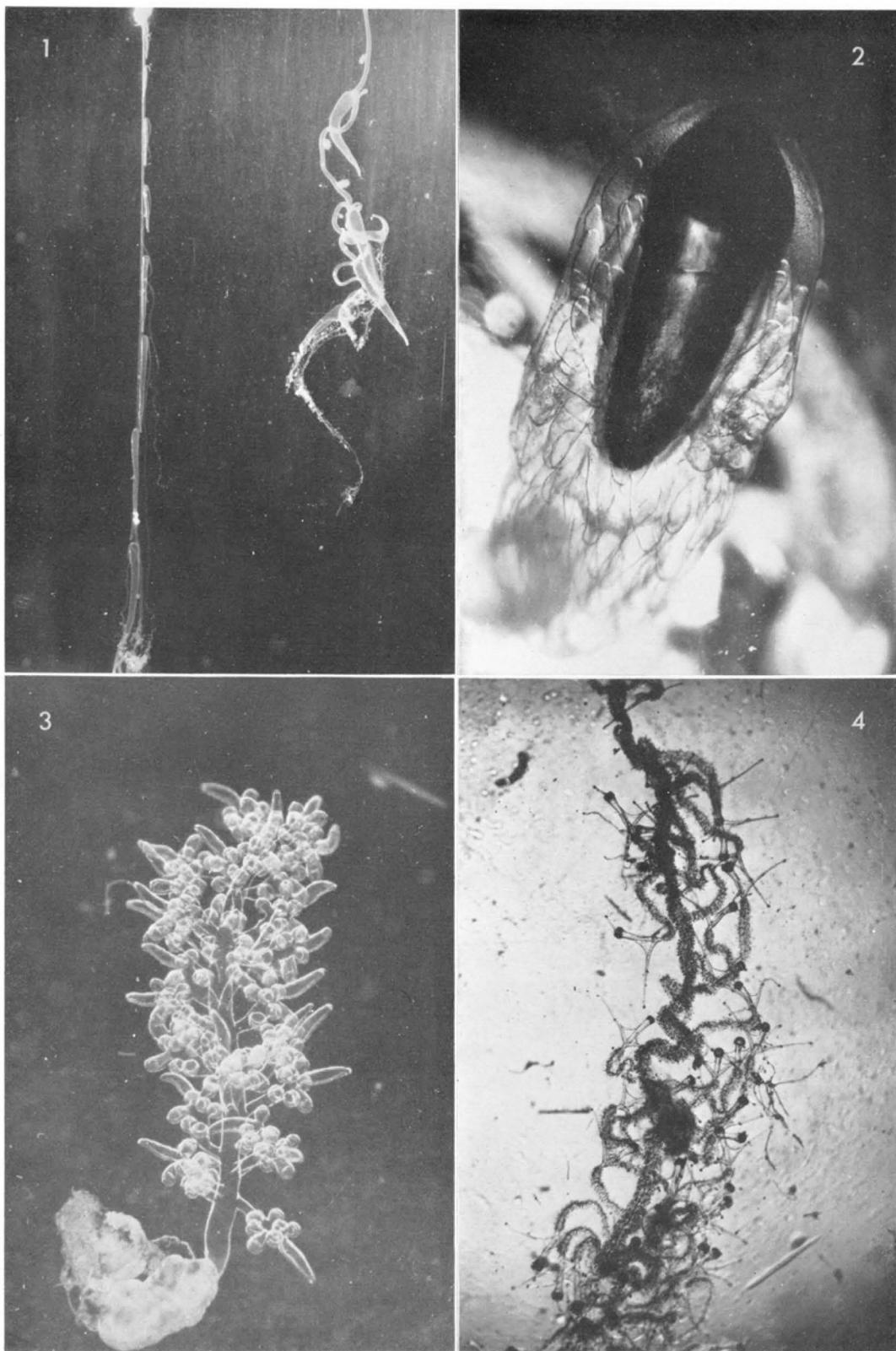
FIG. 1. Parts of two specimens, natural size.

FIG. 2. Pneumatophore, $\times 100$.

FIG. 3. Gonodendron in the middle stage of development, $\times 100$.

FIG. 4. Part of tentacle, $\times 100$.

PLATE II



A SYNOPSIS OF THE SIPHONOPHORA

PLATE III *Rhizophysa filiformis* (Forskål)

Photographs of living specimens from Villefranche, 1963

FIG. 1. Part of the upper region of the stem to show young stages of budding gonodendra.

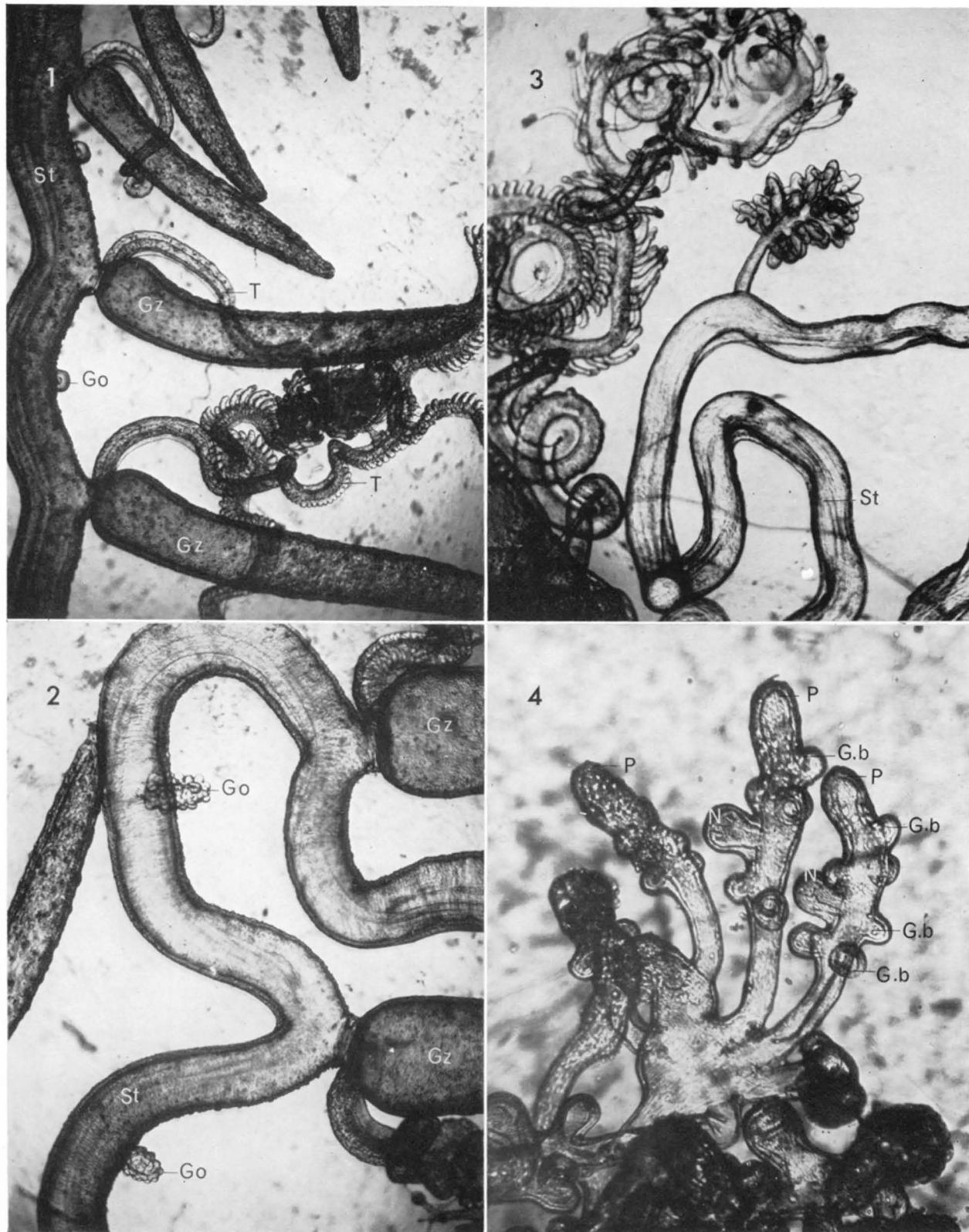
FIG. 2. Part of the upper region of the stem to show two early growth stages of gonodendra.

FIG. 3. The same, a little later.

FIG. 4. Part of a farther developed gonodendron.

G.b = gonophore bud; *Go* = gonodendron; *Gz* = gastrozooid; *N* = nectophore; *P* = palpon;
St = stem; *T* = tentacle.

PLATE III



A SYNOPSIS OF THE SIPHONOPHORA

PLATE IV *Rhizophysa filiformis* (Forskål)

Photographs of living specimens from Villefranche, 1963

FIG. 1. Two pieces of one tentacle. Below (left), some 4 cm from the proximal end showing early buds of tentilla into which some of the nematocysts have entered from the ectoderm. The longitudinal muscle band can be seen on the lower side. Above (right), a piece of tentacle some 2 cm nearer the proximal end. Only one tentillum has been entered by a single nematocyst.

FIG. 2. A tricornuate tentillum showing the web between the branches.

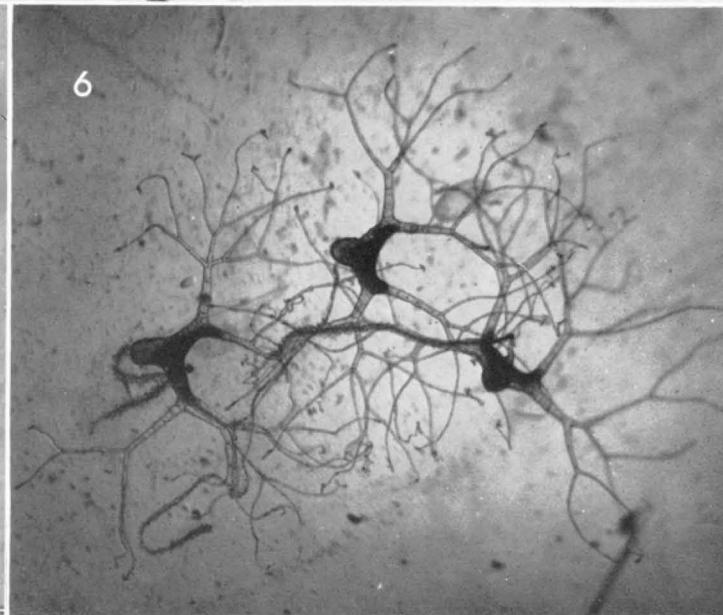
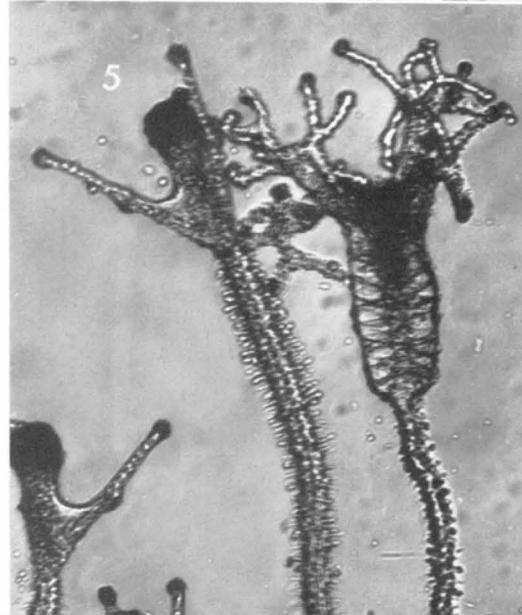
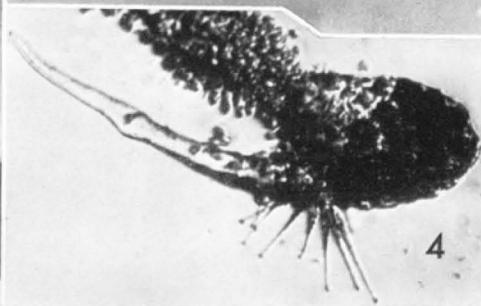
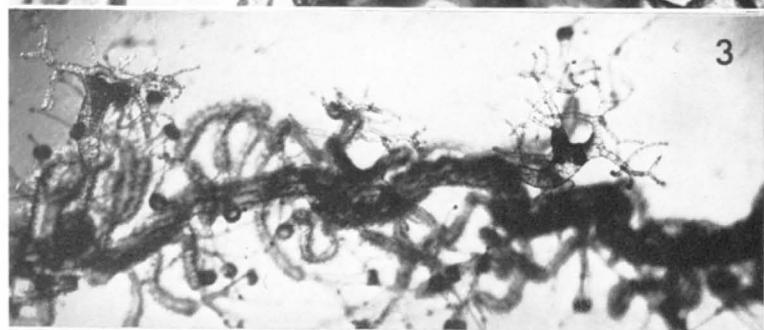
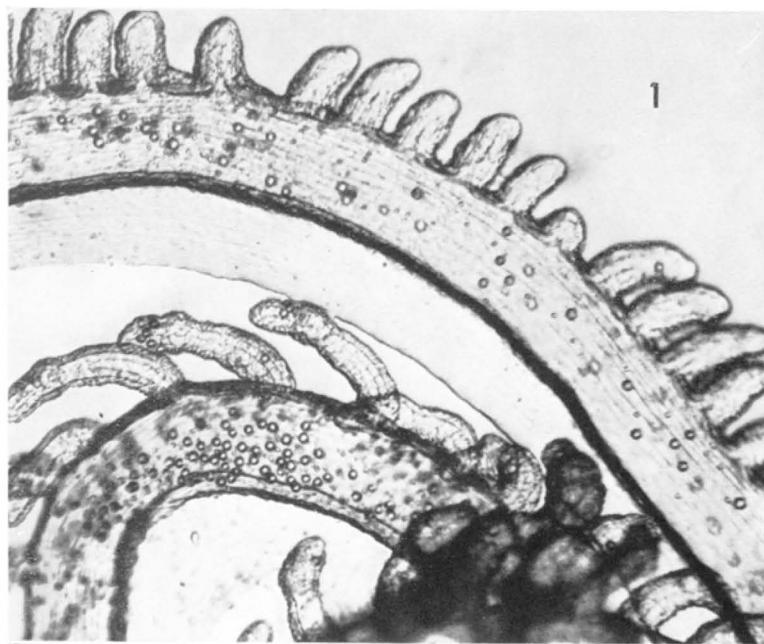
FIG. 3. View of a tentacle focused on two dendritic tentilla, partly expanded.

FIG. 4. A bird-headed or beaked tentillum.

FIG. 5. Partly expanded tricornuate and dendritic tentilla.

FIG. 6. Three fully expanded dendritic tentilla showing opaque areas.

PLATE IV

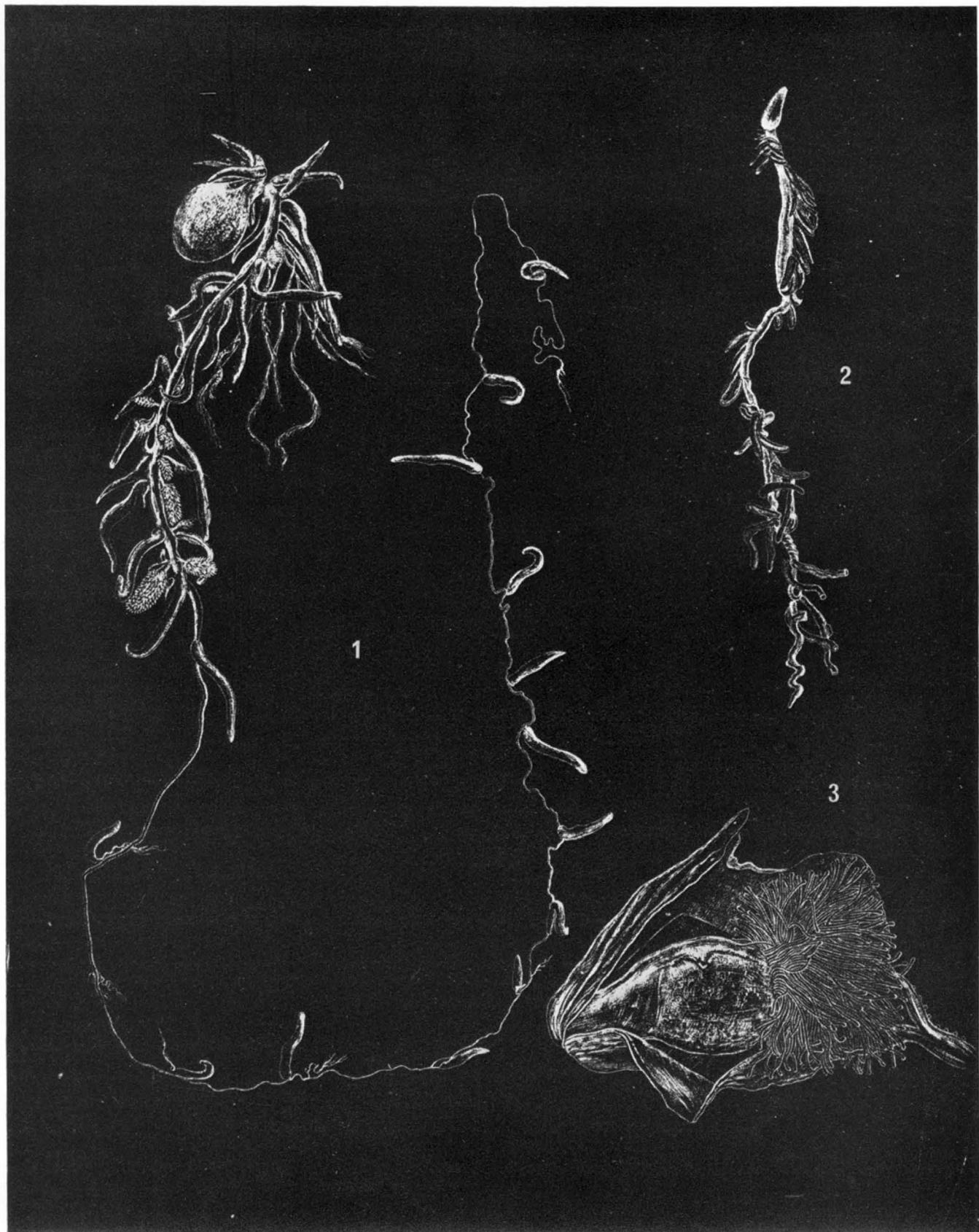


A SYNOPSIS OF THE SIPHONOPHORA

PLATE V

- FIG. 1. *Rhizophysa eysenhardtii* Gegenbaur. From Lens & van Riemsdijk, 1908, plate 20, figure 147.
- FIG. 2. *Bathyphysa sibogae* L. & van R. loc. cit. above, plate 20, figure 148.
- FIG. 3. *Bathyphysa conifera* (Studer). loc. cit. above, plate 20, figure 149.

PLATE V



A SYNOPSIS OF THE SIPHONOPHORA

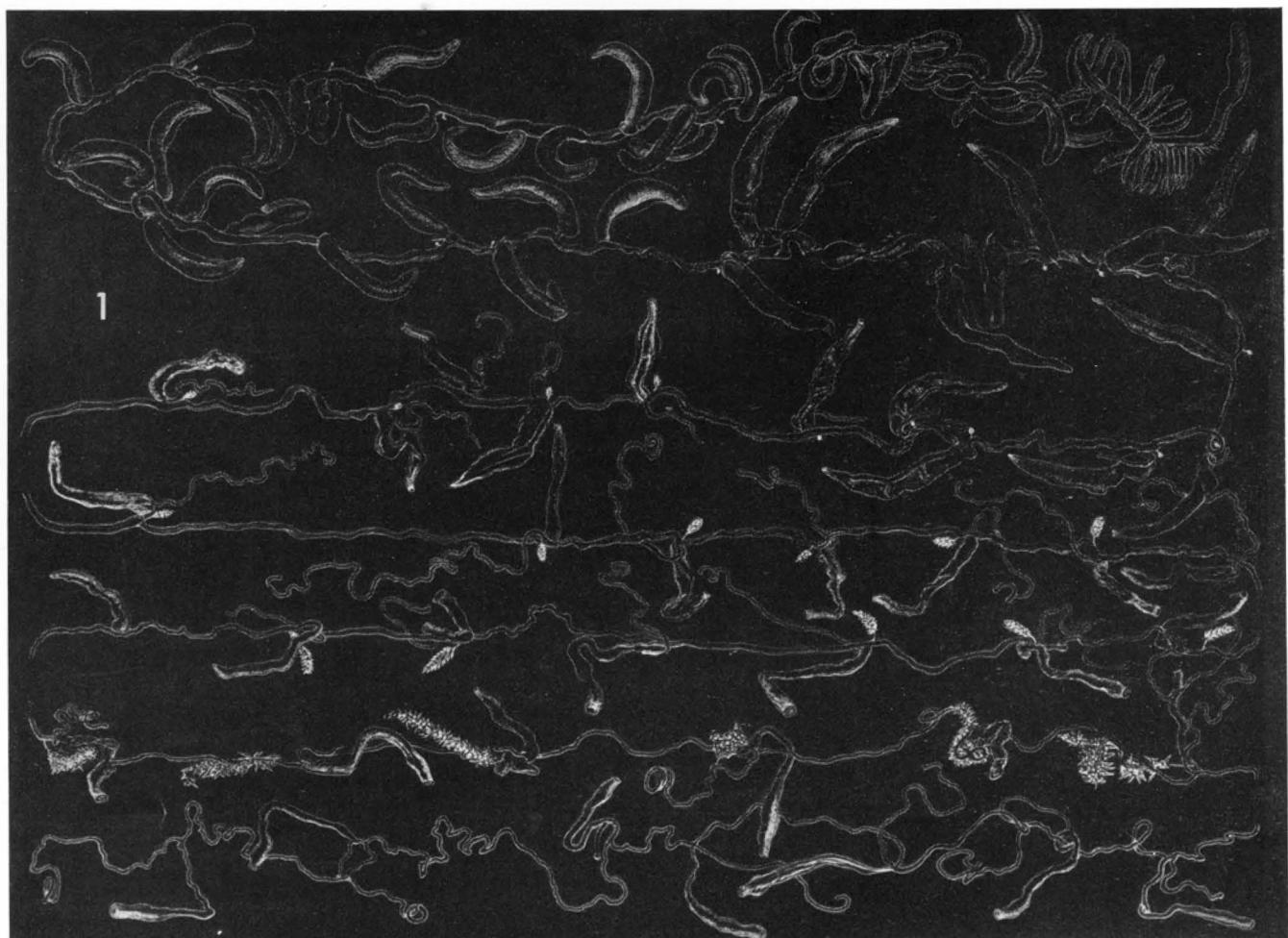
PLATE VI *Bathyphysa conifera* (Studer)

FIG. 1. From Lens & van Riemsdijk, 1908, plate 19, figure 146.

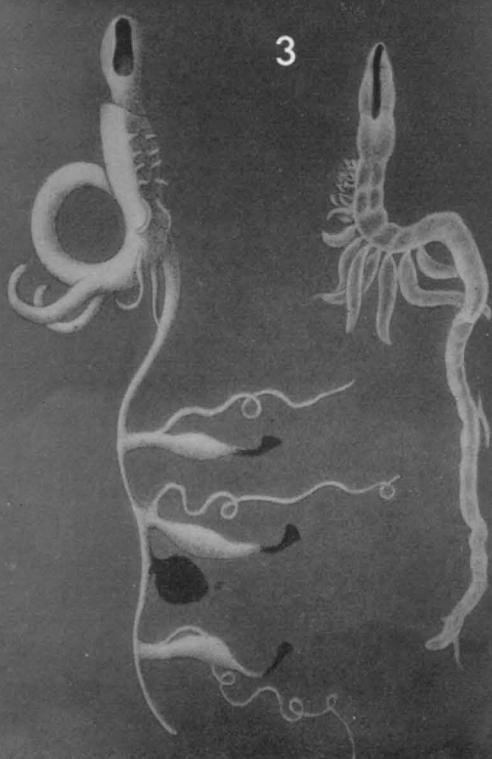
FIGS. 2, 3. From Studer, 1878, plate 1, figures 1, 2.

FIG. 4. Specimen (Brit. Mus. Reg. No. 1949.2.2.4) taken by the cable ship 'Monarch' on a grappling iron wire at $6^{\circ} 19'$ N, $27^{\circ} 23'$ W in 600 fathoms.

PLATE VI



2



3



4

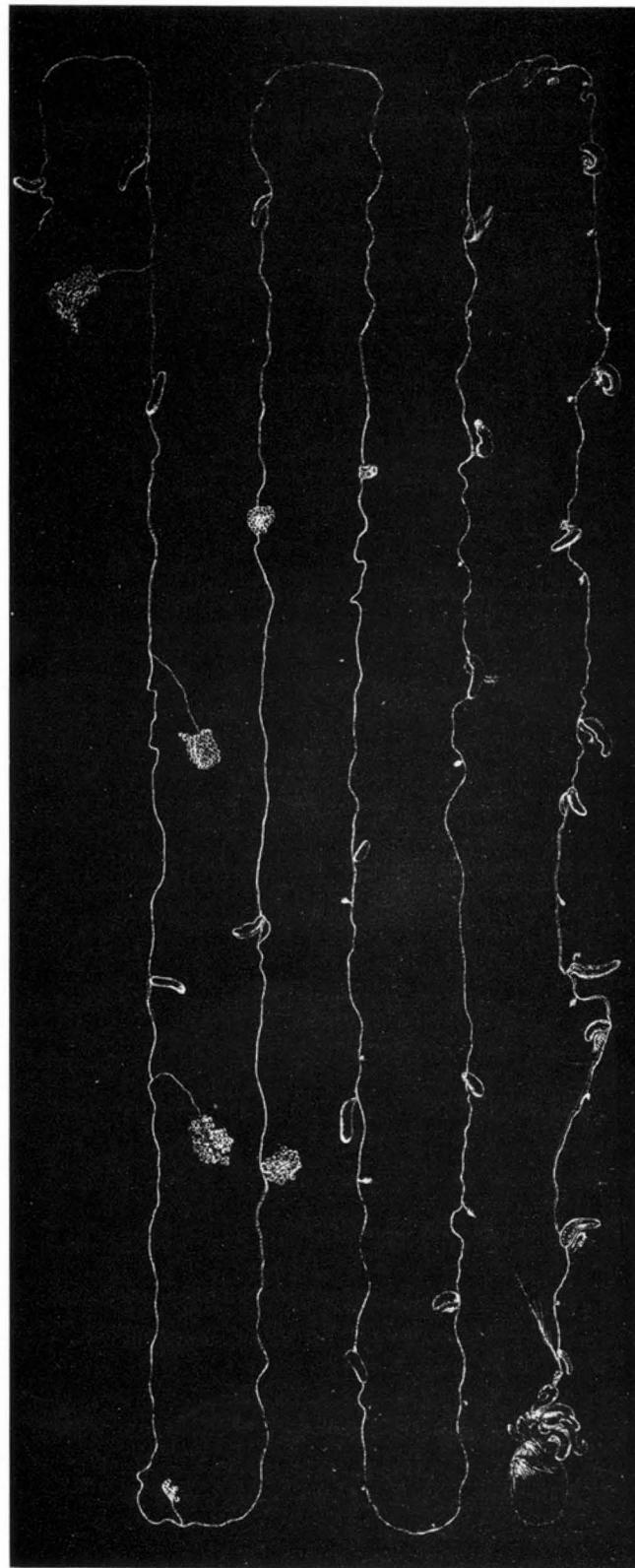


A SYNOPSIS OF THE SIPHONOPHORA

PLATE VII *Rhizophysa eysenhardtii* Gegenbaur

From Lens & van Riemsdijk, 1908, plate 21, figure 150

PLATE VII



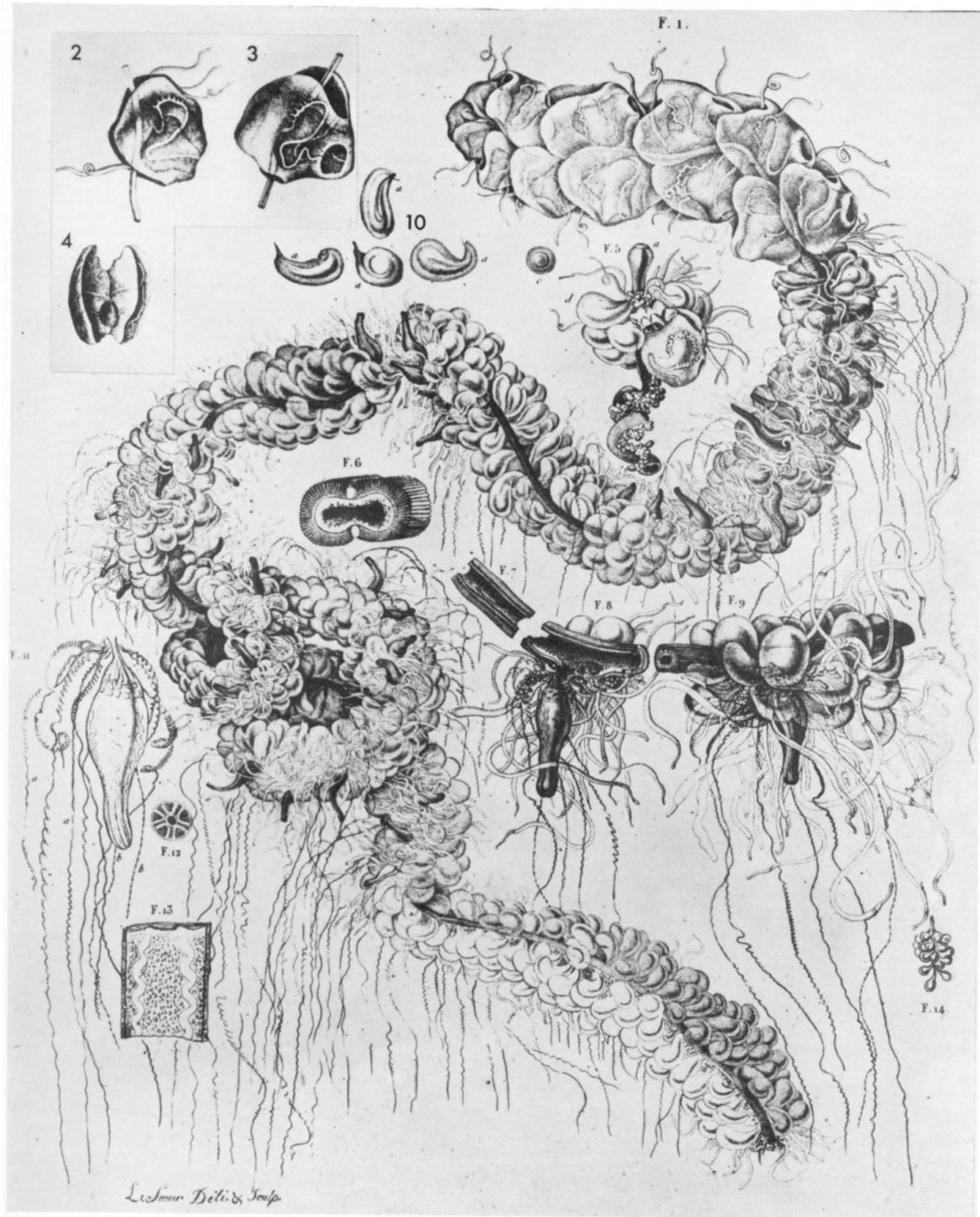
A SYNOPSIS OF THE SIPHONOPHORA

PLATE VIII *Apolemia uvaria* Lesueur

An engraving by Lesueur of a specimen taken in 1809 at Nice by Péron & Lesueur. It forms part of a rare work published by Lesueur about 1811, evidently an extract of a projected paper based on a manuscript left to him by Péron, entitled 'Histoire complète des Méduses'. Part of this engraving was copied and published by Blainville in 1834.

- FIG. 1. Part of the whole animal.
- FIGS. 2-4. Nectophores, showing tentacles.
- FIG. 5. Apex of the stem, enlarged, showing the pneumatophore and young replacement nectophores. *a.c* = pneumatophore; *d* = bract.
- FIG. 6. Transverse section of the stem.
- FIG. 7. Longitudinal section of the stem.
- FIG. 8. Cormidial group.
- FIG. 9. Part of the stem, enlarged. *a* = palpon.
- FIG. 10. *a, a.* Bracts.
- FIG. 11. Gastrozooid, with *a* palpacle and *b* gastrozooid.
- FIG. 12. Gastrozooid in transverse section.
- FIG. 13. Stem opened to show musculature.
- FIG. 14. Gonophores.

PLATE VIII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE IX

Agalma okeni Eschscholz.

From Kawamura, 1910-11, plate 16

Figures 1-8. Mature form

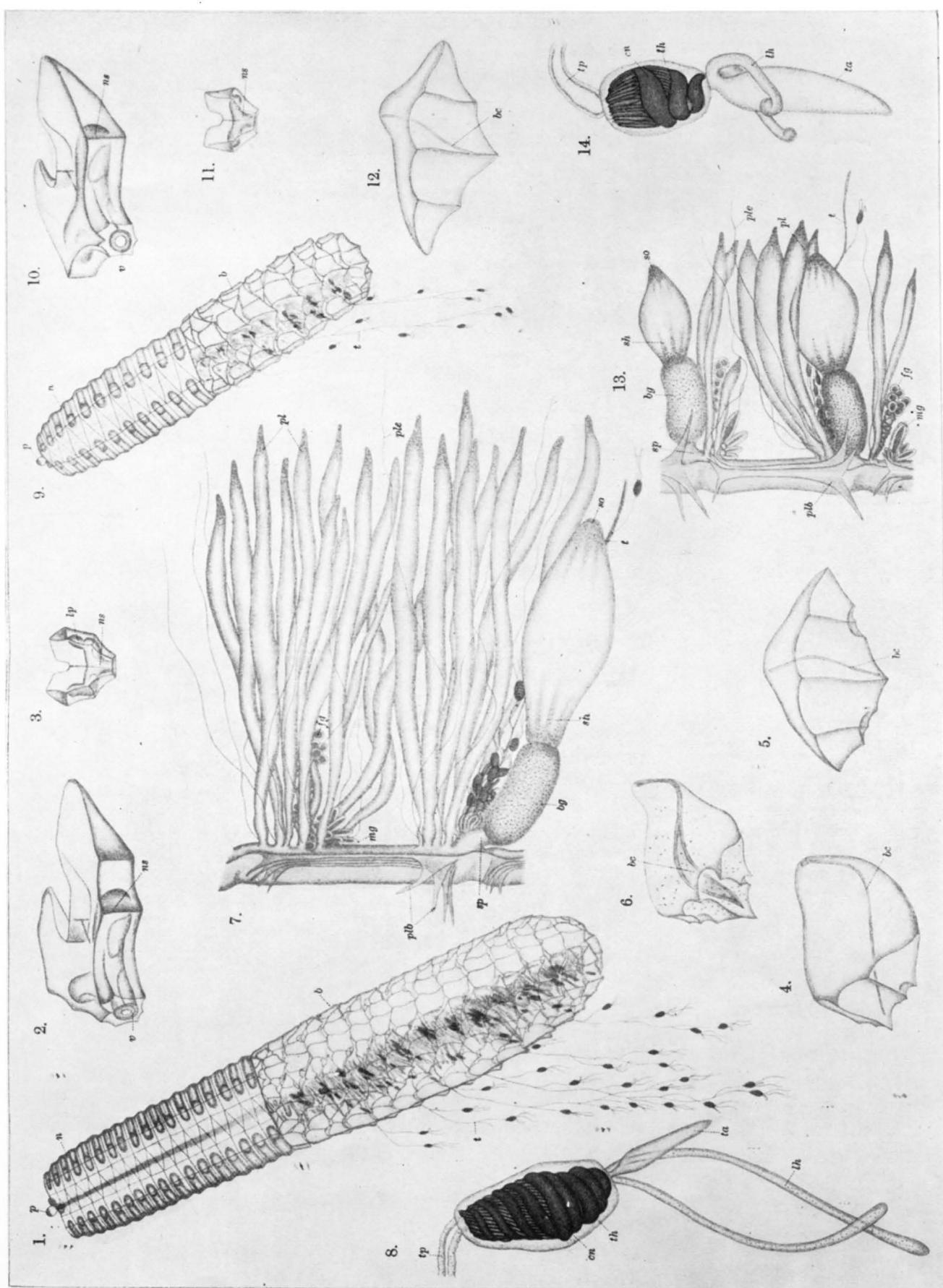
- FIG. 1. Whole animal, lateral view, natural size.
- FIG. 2. Nectophore viewed obliquely from above, $\times 3$.
- FIG. 3. Young nectophore from above, $\times 3$.
- FIG. 4. Bract, lateral view, $\times 3$.
- FIG. 5. Bract, viewed from distal end, $\times 3$.
- FIG. 6. Young bract, diagonal lateral view, $\times 3$.
- FIG. 7. Cormidium, without bracts, right view, $\times 8$.
- FIG. 8. Terminal cnidoband of a tentillum, $\times 15$.

Figures 9-14. Young form (as *Crystallomia polygonata* Dana)

- FIG. 9. Whole animal, lateral view, natural size.
- FIG. 10. Nectophore, diagonal view from above, $\times 3$.
- FIG. 11. Young nectophore from above, $\times 4$.
- FIG. 12. Bract, from ridged side, $\times 3$.
- FIG. 13. Cormidium, without bracts, right view, $\times 3$.
- FIG. 14. Terminal cnidoband of a tentillum.

b = bract; *bc* = bracteal canal; *bg* = gastrozooid (basigaster); *cn* = cnidoband; *fg* = female gonophore; *lh* = lateral horn; *p* = inflated pouch of left and right radial canals; *mg* = male gonophore; *ns* = nectosac; *n* = nectosome; *p* = pneumatophore; *pl* = palpons; *plb* = bracteal lamellae; *ple* = palpacle; *sh* = gastrozooid (digestive part); *so* = gastrozooid (apical part); *sp* = gastrozooid stalk; *t* = tentacle; *ta* = terminal ampulla; *th* = involucre; *tp* = peduncle; *v* = velum.

PLATE IX



A SYNOPSIS OF THE SIPHONOPHORA

PLATE X

Nanomia bijuga (Chiaje)

From Kawamura, 1910-11, plate 7, figures 1-10

FIG. 1. Whole animal, $\times 1\frac{1}{2}$.

FIGS. 2-4. Nectophores, $\times 7$.

FIGS. 5, 6. Bracts, $\times 7$.

FIG. 7. Internodal bract, $\times 15$.

FIG. 8. Young bract, $\times 15$.

FIG. 9. Tentillum, $\times 15$.

FIG. 10. Cormidia, $\times 2\frac{2}{3}$.

Agalma elegans (Sars), (1846), figures 11-17

FIG. 11. Whole animal, $\times \frac{2}{3}$.

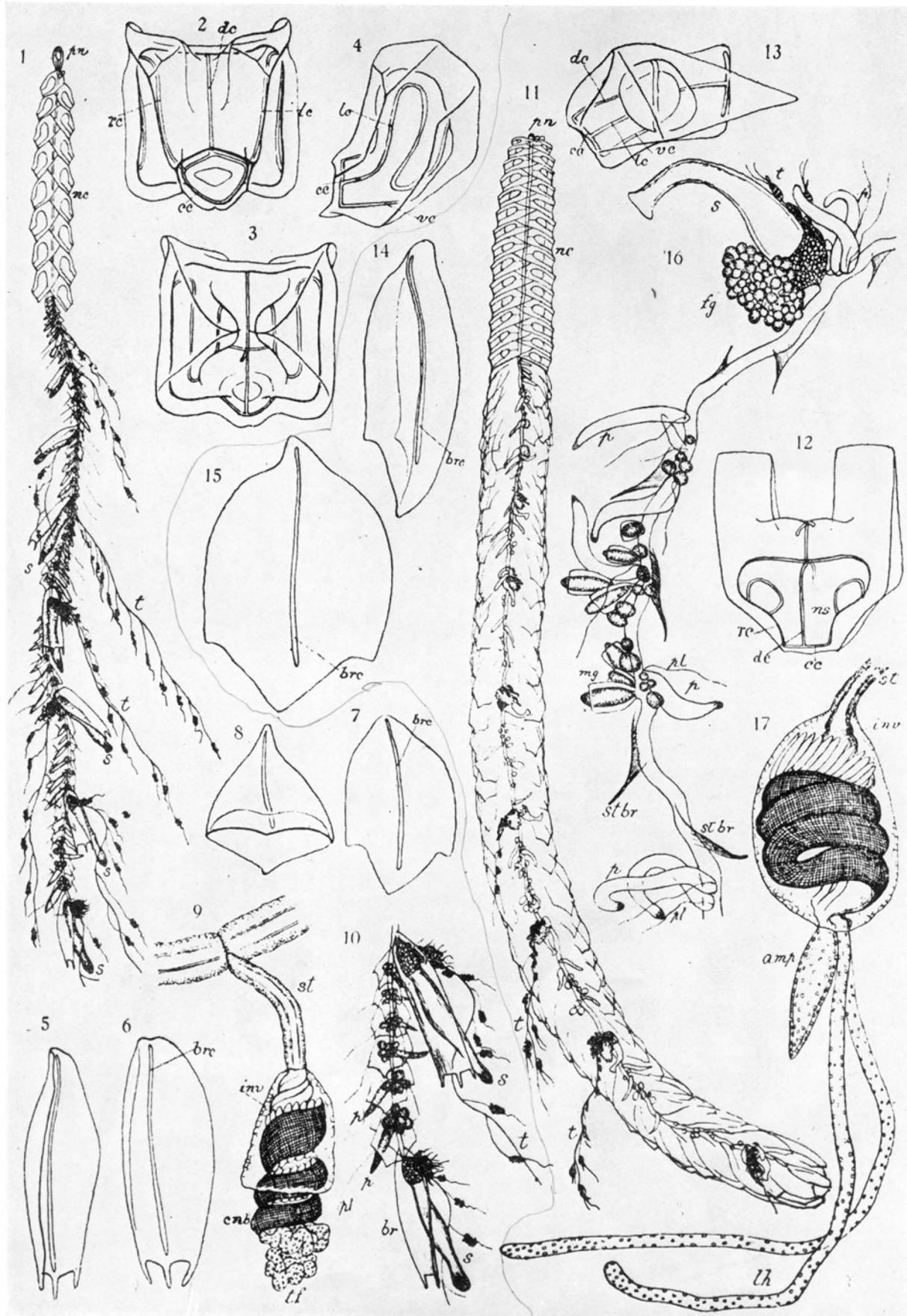
FIGS. 12, 13. Nectophores, $\times 6$.

FIGS. 14, 15. Bracts, $\times 4$.

FIG. 16. Cormidium, without bracts, $\times 4$.

FIG. 17. Tentillum, $\times 15$.

amp = ampulla; *br* = bract; *brc* = bracteal canal; *cc* = circular canal; *cnb* = cnidoband; *dc* = dorsal canal; *fg* = female gonophore; *inv* = involucre; *lc* = lateral canal; *lh* = lateral horn; *mg* = male gonophore; *nc* = nectophore; *ns* = nectosac; *p* = palpon; *pl* = palpacle; *pn* = pneumatophore; *rc* = radial canal; *s* = gastrozooid; *st* = peduncle; *st.br* = peduncular lamellae; *t* = tentacle; *t.f* = terminal filament; *vc* = ventral canal.



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XI

Agalma elegans (Sars)

Figures 1, 2. Post-larvae, preserved, from Villefranche

FIG. 1. To show the nectostyle (centre left), upward growth of the nectosome and the larval-type tentilla of the protozooid.

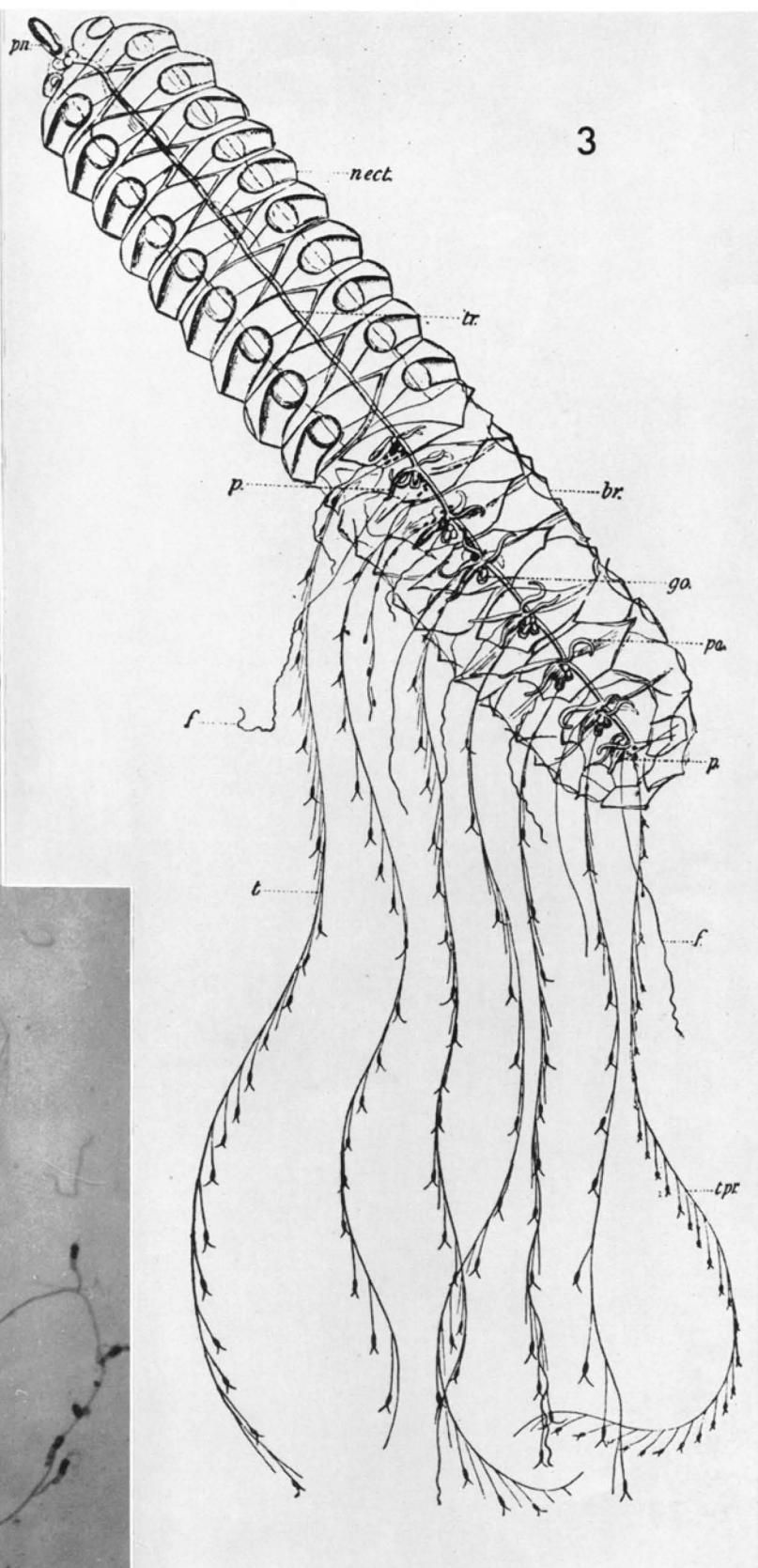
FIG. 2. To show the nectostyle, commencement of the upward growth of the nectosome and the larval-type tentilla of the protozooid.

Agalma okemi Esch.
From Chun, 1897, figure 18

FIG. 3. Whole animal, $\times 1\frac{1}{2}$ approx.

br = bract; *f* = palpacles; *go* = gonophores; *nect* = nectophores; *p* = gastrozooids; *pa* = palpons;
pn = pneumatophore; *t* = tentacles; *t.pr* = tentacle of protozooid; *tr* = stem (of nectosome).

PLATE XI



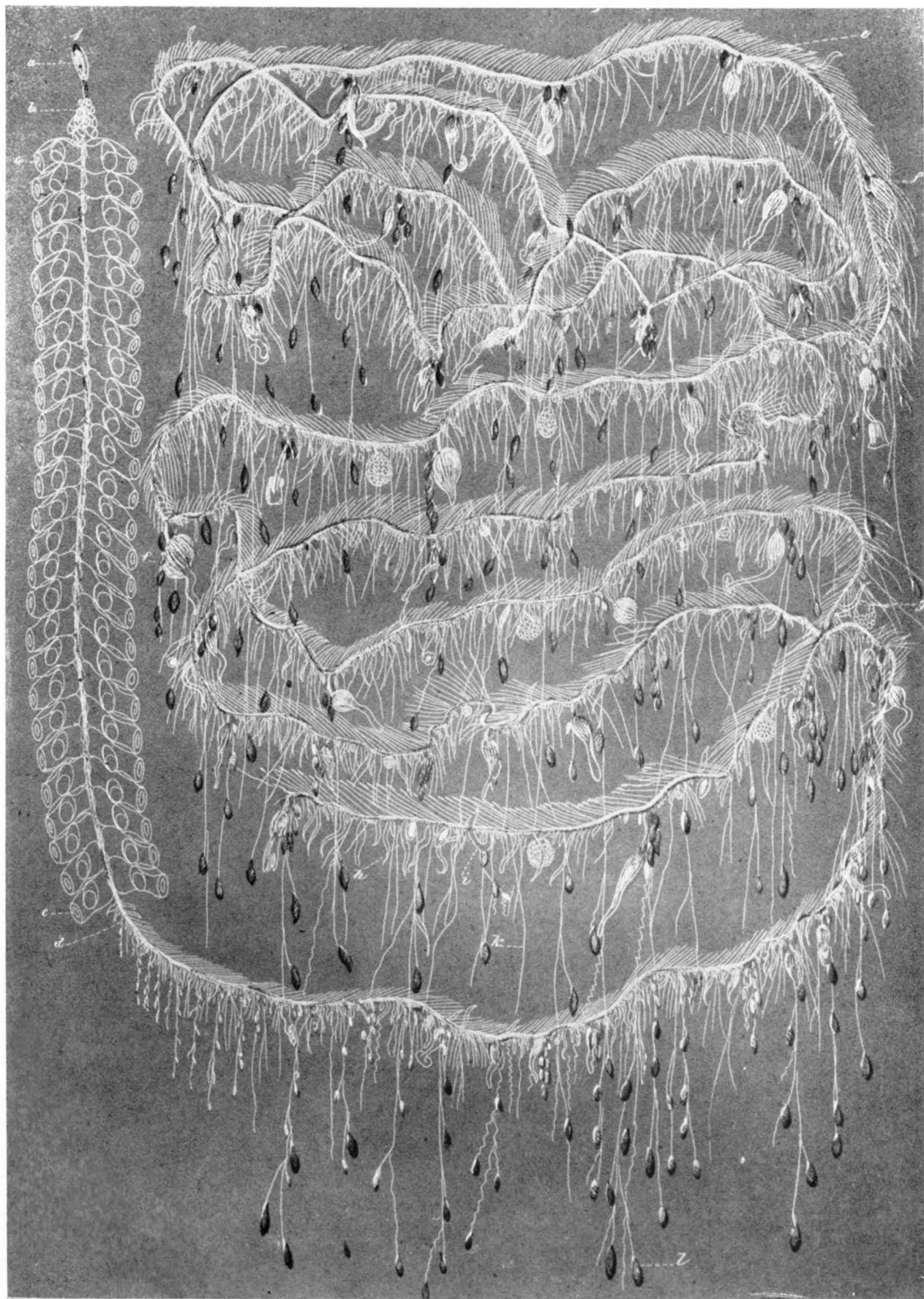
A SYNOPSIS OF THE SIPHONOPHORA

PLATE XII *Halistemma rubrum* (Vogt)

From Vogt, 1854, plate 7

a = pneumatophore; *b,c* = nectophores; *d* = buds of cormidial groups; *e* = bracts; *f* = gastrozooids;
g = female gonodendra; *h* = ripe ♂ gonophore; *i* = palpon; *k* = palpacle; *l* = cnidosac.

PLATE XII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XIII

Halistemma cupulifera L. & v. R.

From Lens & van Riemsdijk, 1908, plate XVI, figures 116-118

FIG. 1. Whole animal, $\times 11$.

FIG. 2. Tentillum, = 7.

FIG. 3. Tip of tentillum, $\times 130$.

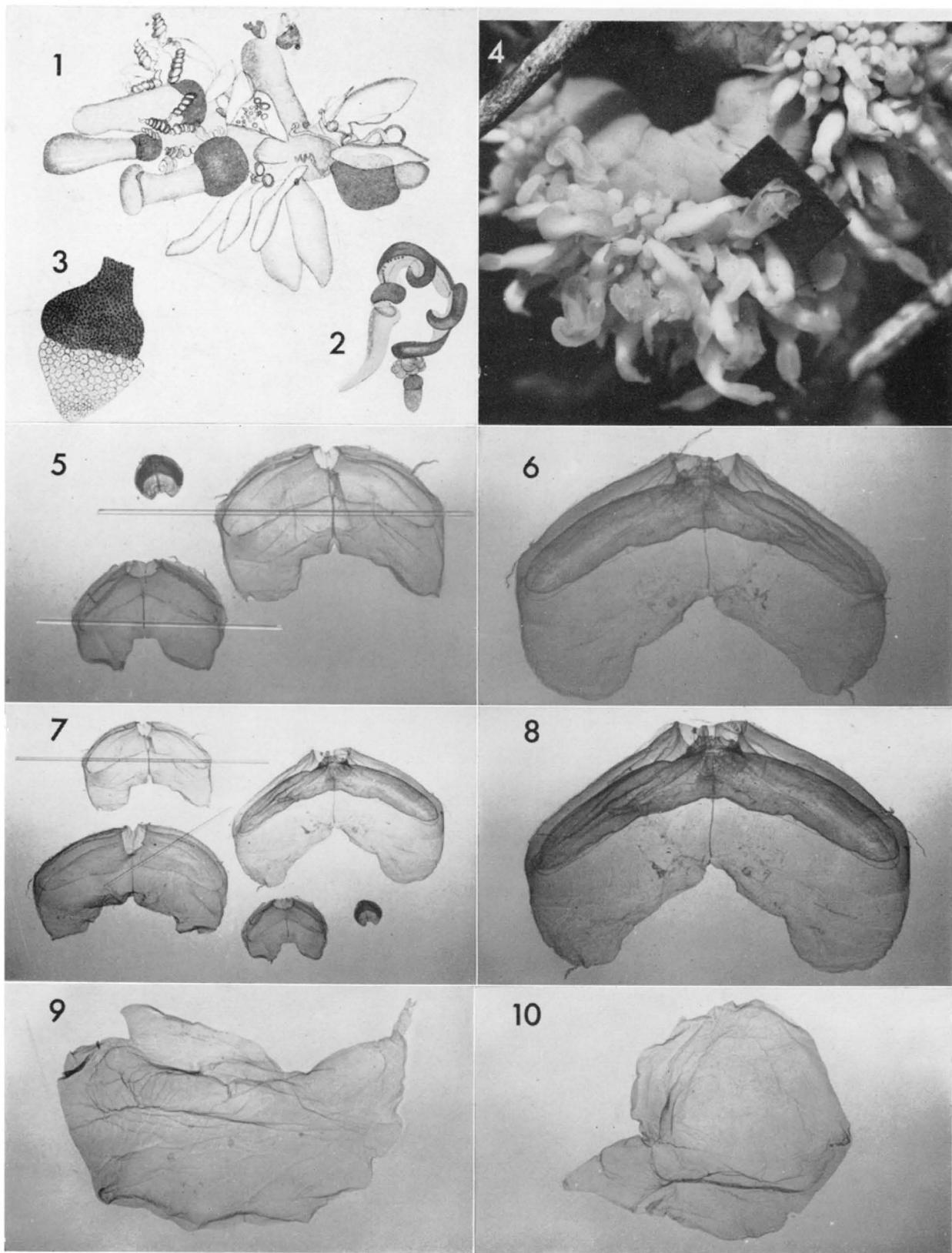
?*Moseria convoluta* (Moser)

FIG. 4. Part of the siphosome, $\times 7$, 'Discovery' St. 2023, $47^{\circ} 46'$ S, $00^{\circ} 28.6'$ E,
1500-1000 m, to show young bracts.

FIGS. 5-8. Nectophores, $\times 2$.

FIGS. 9, 10. Bracts.

PLATE XIII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XIV

Nanomia cara A. Agassiz

From Sars, 1846, plate 5, figures 1-8

FIG. 1. Whole animal

a = pneumatophore; b = nectophore; c = stem of nectosome; d = buds of nectophore; e = bract; f = gastrozooid; g = palpon; h = gonophore ♂; i = contracted tentacle.

FIG. 2. Part of siphosome

a = gastrozooid; b = contracted tentacle; c = stem; d = bract; e = palpon; f = gonophore ♂; g (no guide line) = unripe gonophore ♂; h = gonodendron ♀.

FIG. 3. Siphosome enlarged, bracts removed. a-h see figure 2

FIG. 4. Gonophores

a = peduncle of gonodendra ♀; b = gonophores ♀.

Figs. 5, 6. Tentilla, enlarged

a = pedicel of tentillum; b = involucrum; c = cnidoband; d = end filament.

Figs. 7, 8. *Agalma elegans*: tentilla. It was the inclusion of this different species which caused the confusion described in the text
a-c as in figures 5, 6; d = ampulla; e = terminal filament.

Nanomia bijuga (Chiaje)

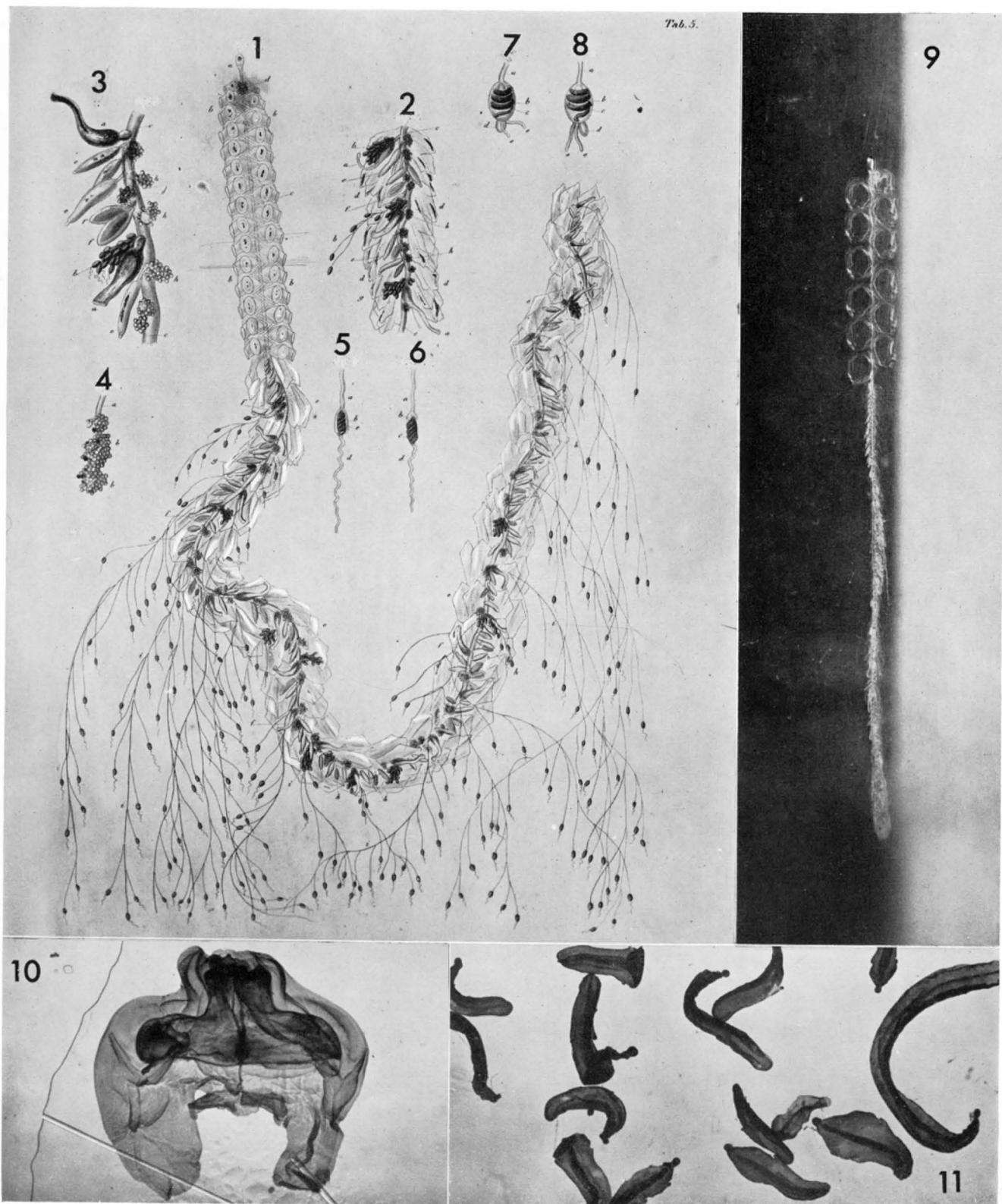
FIG. 9. Photograph of a living specimen 4 cm in length from Villefranche

Erenna richardi Bedot

FIG. 10. Nectophore, $\times 1.8$

FIG. 11. Bracts, $\times 2$

PLATE XIV



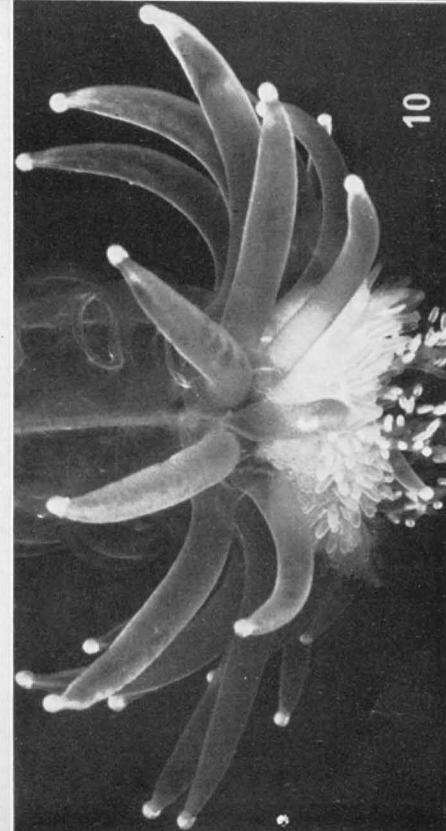
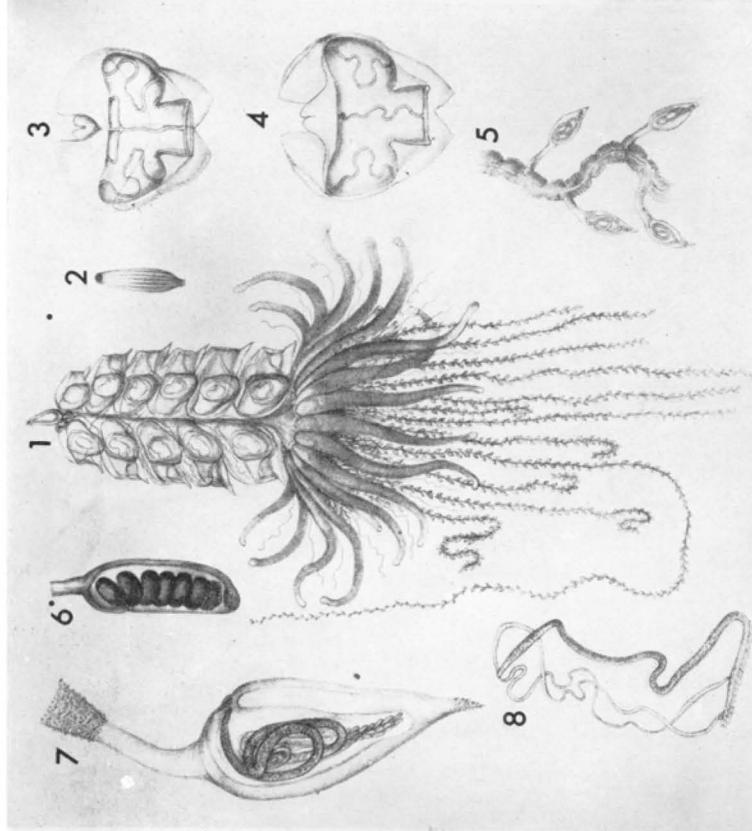
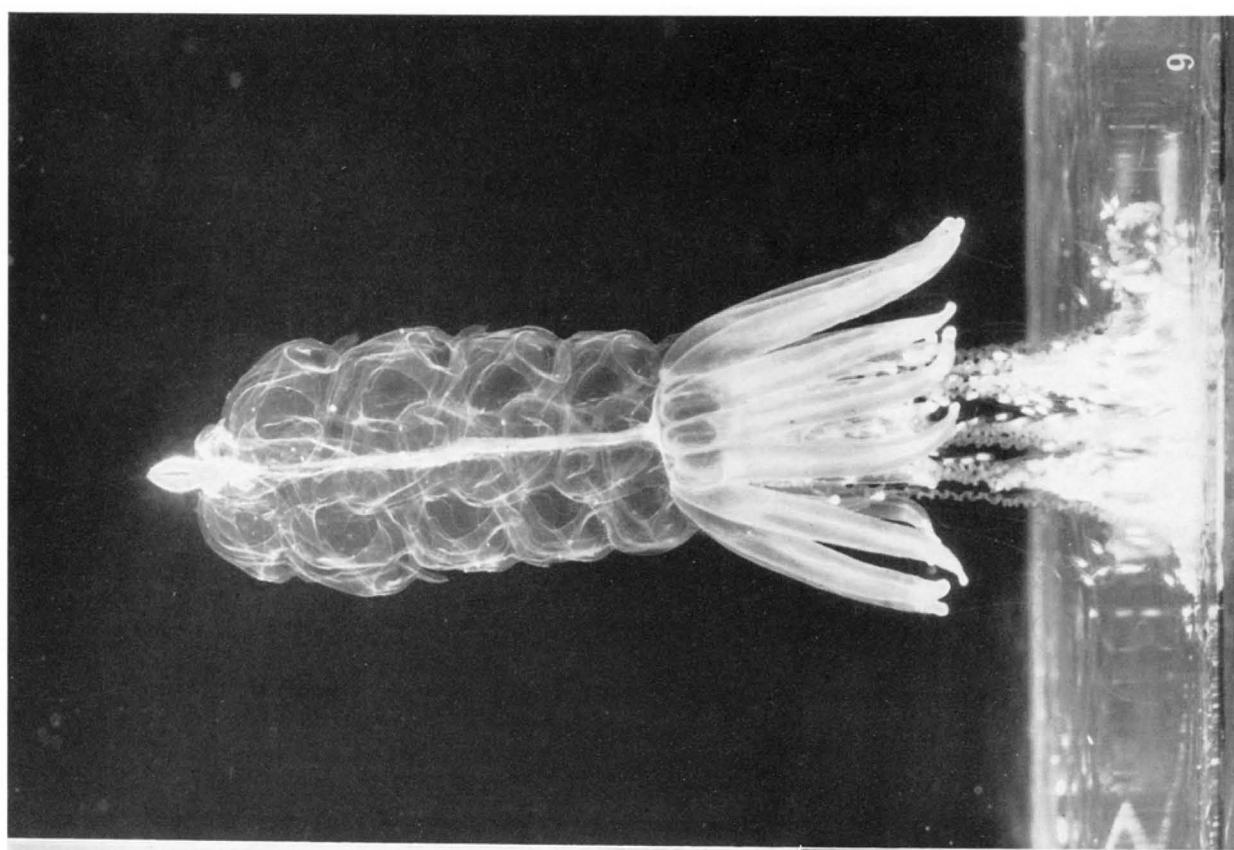
A SYNOPSIS OF THE SIPHONOPHORA

PLATE XV *Physophora hydrostatica* Forskål

Figures 1-8 from Sars, 1877, plate VI

- FIG. 1. Whole animal.
- FIG. 2. Gastrozoid.
- FIGS. 3, 4. Nectophores.
- FIG. 5. Part of a tentacle.
- FIG. 6. Tentillum, early growth stage.
- FIG. 7. Tentillum, late growth stage.
- FIG. 8. Activated cnidoband and elastic cords.
- FIG. 9. Photograph of the living animal, taking-off from the bottom of a tank, at Villefranche.
- FIG. 10. Another living animal reacting to a touch on the pneumatophore. The previously hidden gonophores can be seen.

PLATE XV



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XVI

Lychnagalma utricularia (Claus)

From Claus, 1879, plate 1, figures 1, 2, 5a, b, c, d, f

- FIG. 1. Whole animal.
- FIG. 2. Tentillum.
- FIG. 3. Dorsal view of an upper nectophore (ventral view in Claus's terminology).
- FIG. 4. Ventro-ostial view of a lower nectophore (lower and ventral view in Claus's terminology).
- FIG. 5. Lateral view of same.
- FIG. 6. Dorsal view of same (ventral view in Claus's terminology).
- FIG. 7. Ventral view of an upper nectophore (dorsal view in Claus's terminology).

All the following terms, except the last, are translations of those used by Claus: *SK* = lateral ridge; *DK* = dorsal ridge; *VK¹* = medial-lateral ridge; *VK²* = ventro-lateral ridge; *UK* = lower ridge; *TK* = transverse ridge; *KF* = wedge-shaped process; *Z* = socket (for stem); *DF* = dorso-lateral facet; *VG* = dorsal radial canal.

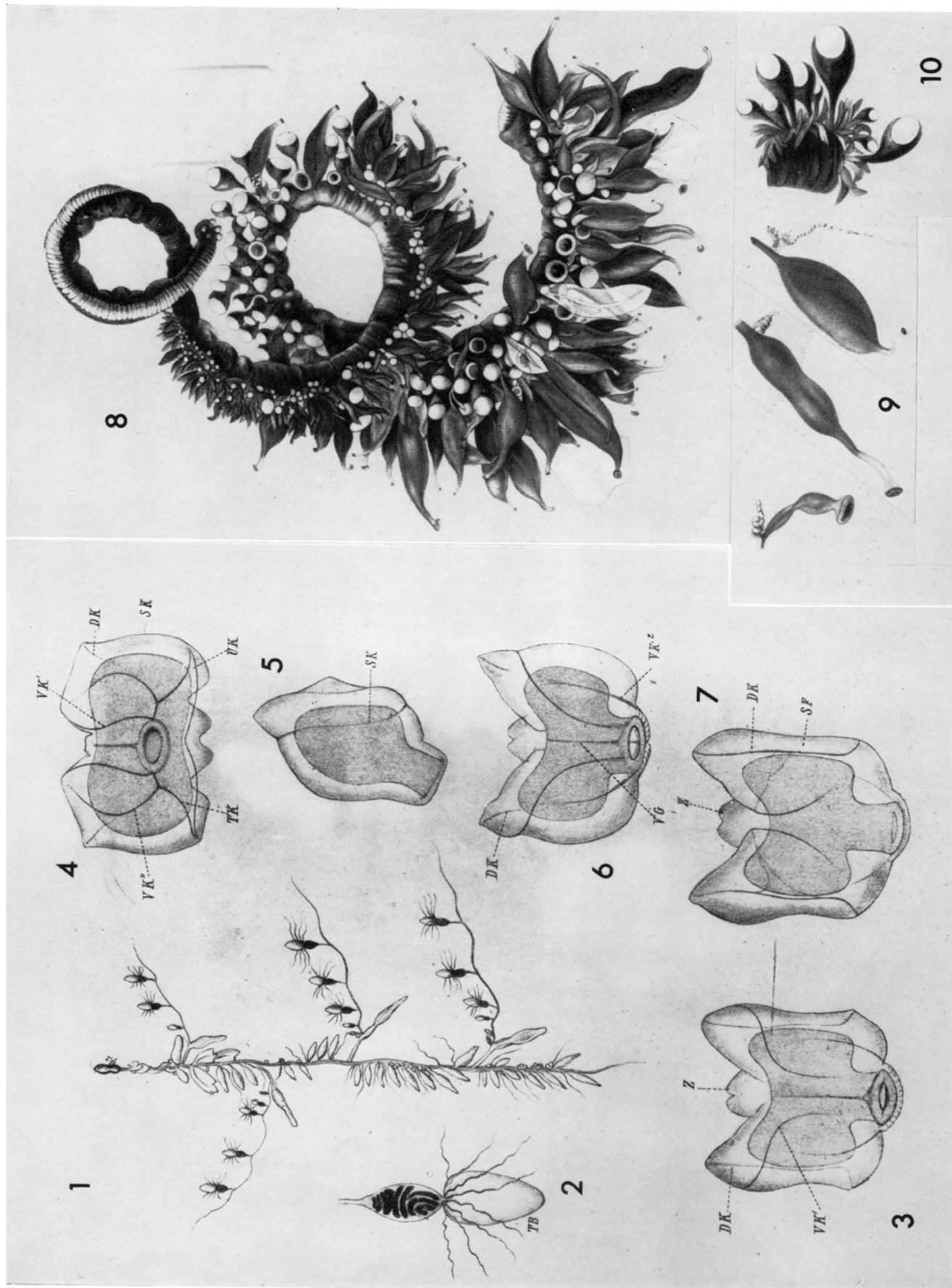
Pyrostephos vanhoeffeni Moser

From Moser, 1925, plate 29, figures 1, 10, 11

- FIG. 8. Reconstruction by Moser of a large specimen showing the nectosome (less the pneumatophore and nectophore) and part of the siphosome (less most of the bracts), $\times 2$.

FIG. 9. Three gastrozooids, $\times 2.3$.

FIG. 10. Part of the stem to show palpons, $\times 3$.



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XVII *Athorybia rosacea* (Forskål)

Figures 1-5 from Bigelow, 1911b, plate 20, figures 7-11

FIG. 1. Whole animal, less bracts.

FIG. 2. Tentillum, dendritic type, half grown.

FIG. 3. Tentillum, involucrate type, fully grown.

FIG. 4. Palpon and base of palpacle.

FIG. 5. Tentillum, tricornuate type, young growth stage.

L.Mu = muscular lamellae of bracts; *Am* = ampulla; *l* = involucre; *X* = marginal spur of involucre; *F* = (fig. 4) = palpacle; *F* (fig. 5) = lateral horn.

Figures 6-16 from Kölliker, 1853, plate 7, figures 1-11

FIG. 6. Whole animal.

a = pneumatophore; *b* = palpon; *c* = bract; *d* = gastrozooid; *e* = tentacle.

FIG. 7. Part of tentacle, enlarged.

a = tentacle; *b* = tentillum; *c* = cnidoband; *d* = lateral horns; *e* = terminal ampulla; *f* = part of cnidosac (marginal spur of involucre). The division between *e* and *f* is an artifact. Cf. figure 3.

FIG. 8. Tip of palpon.

a = lumen; *b* = ciliated endoderm; *c* = ectoderm; *d* = nematocysts; *e* = extensile tip.

FIG. 9. Female medusoid gonophore.

a = ectoderm; *b* = endoderm; *c* = velum; *d* = ostium; *e* = radial canal; *f* = pedicular canal; *h* = ovum; *i* = spadix of manubrium.

FIG. 10. Female and male gonophores.

FIG. 11. Spermatozoa.

FIG. 12. Distal end of a bract.

FIG. 13. A large nematocyst from the base of the cnidoband.

FIG. 14. Lateral view of bract.

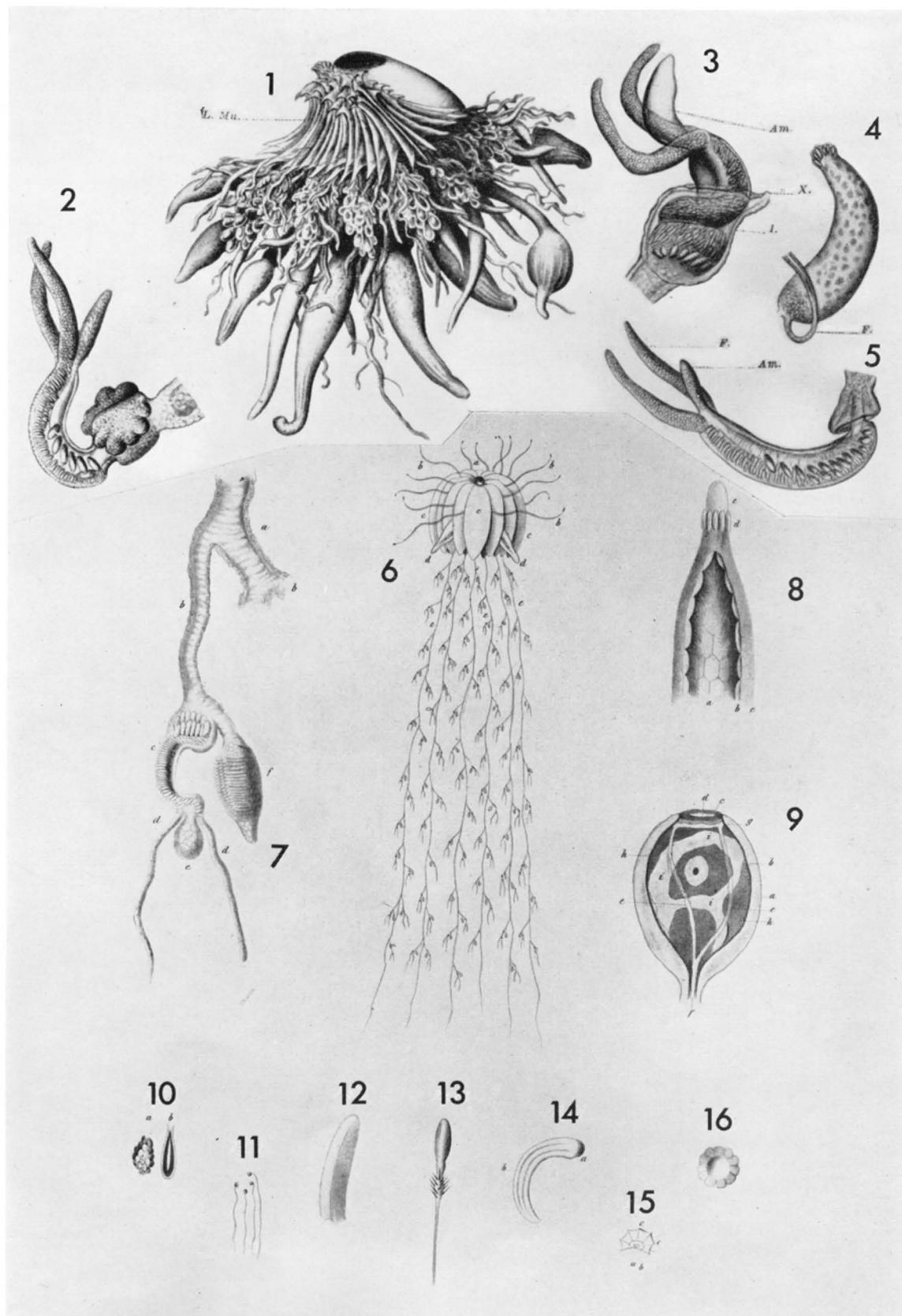
a = base; *b* = longitudinal ridge.

FIG. 15. Proximal view of a bract.

a = bracteal canal; *b* = attached side; *c* = longitudinal ridge.

FIG. 16. Endoderm cells of a gastrozooid.

PLATE XVII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XVIII

Stephalia corona Haeckel

- FIG. 1. Whole animal (Dundee specimen) to show the pneumatophore and corona of nectophores.
FIG. 2. Under surface of the same to show cormidial groups, gastrozooids and palpons.
FIG. 3. Lateral view, enlarged to show gonophores.
FIG. 4. A bract of the Dundee specimen.

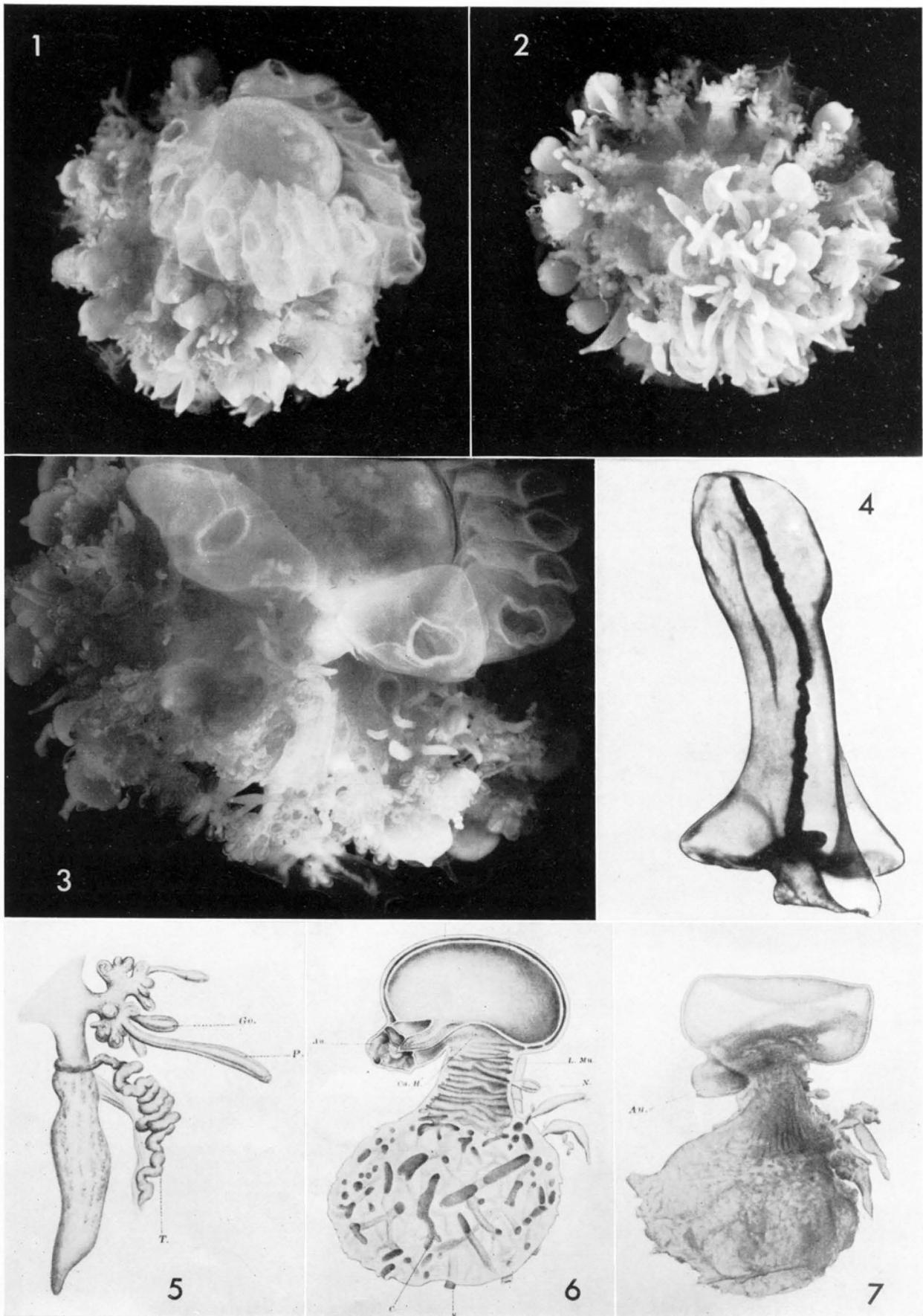
Angelopsis dilata Bigelow

From Bigelow, 1911b, plate 21, figures 6-8

- FIG. 5. A cormidium.
FIG. 6. Whole animal, radial section through the float.
FIG. 7. Photograph of the whole animal.

Au = aurophore; *C* = network of canals; *Ca.H* = hypocystic chamber; *Go* = gonophore; *L.Mu* = muscular lamella of the nectophore; *N* = nectophore; *P* = palpon; *Pn.c* = pneumatocodon; *Pn.S* = pneumatosaccus; *S* = gastrozooid; *T* = tentacle.

PLATE XVIII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XIX

Archangelopsis typica Lens & van Riemsdijk

FIG. 1. Whole animal. From Lens & van Riemsdijk, 1908, plate 18, figure 137.

pn = pneumatophore; *z.pr* = zone of proliferation; *s* = gastrozooid; *t* = tentacle; *n* = nectophore

FIG. 2. Whole animal. From Bigelow, 1913, plate 6, figure 1.

Dromalia alexandri Bigelow

From Bigelow, 1911b, plate 23, figures 6-9

FIG. 3. Whole animal.

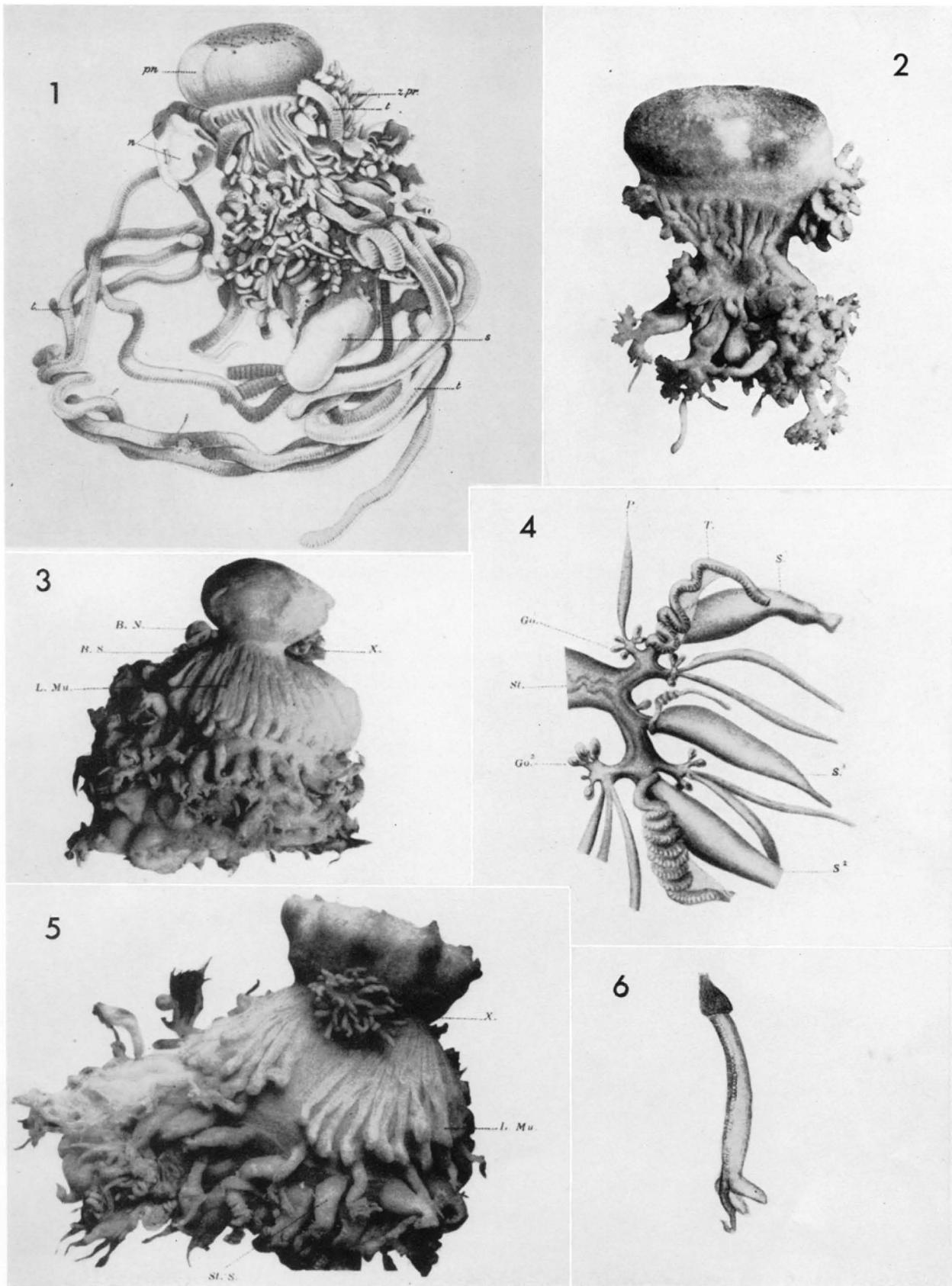
FIG. 4. Gonodendron.

FIG. 5. Whole animal.

FIG. 6. Tentillum.

X = aurophore; *L.Mu* = muscular lamellae of the nectophores; *B.S* = buds of gastrozooids; *B.N* = bud of nectophore; *St*, *St.S* = pedicel of cormidial group; *Go^{1, 2}* = gonodendra; *S¹⁻³* = gastrozooids.

PLATE XIX



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XX

Forskalia edwardsi Kölliker

FIG. 1. Whole animal. From Kölliker, 1853, plate 1, figure 1

a = pneumatophore; *a'* = buds of nectophores; *b* = nectophore; *b'* = stem of nectosome; *c* = buds of cormidial groups; *d* = gastrozooid; *e* = bract; *f* = gonodendra; *g* = palpon; *h* = tentacle; *i* = stem of siphosome.

FIG. 2. Part of the stem of a living specimen (nectosome hidden in the bottom left-hand corner).

Forskalia leuckarti Bedot

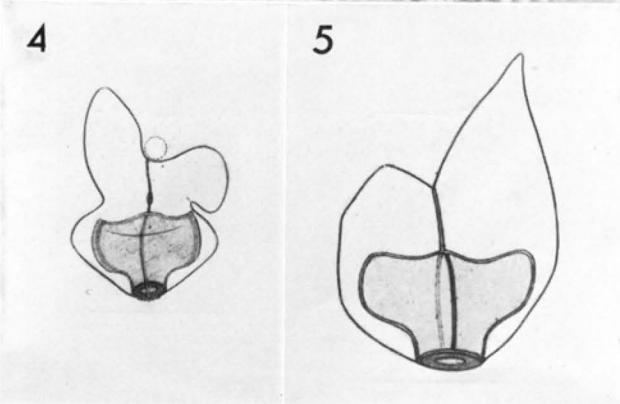
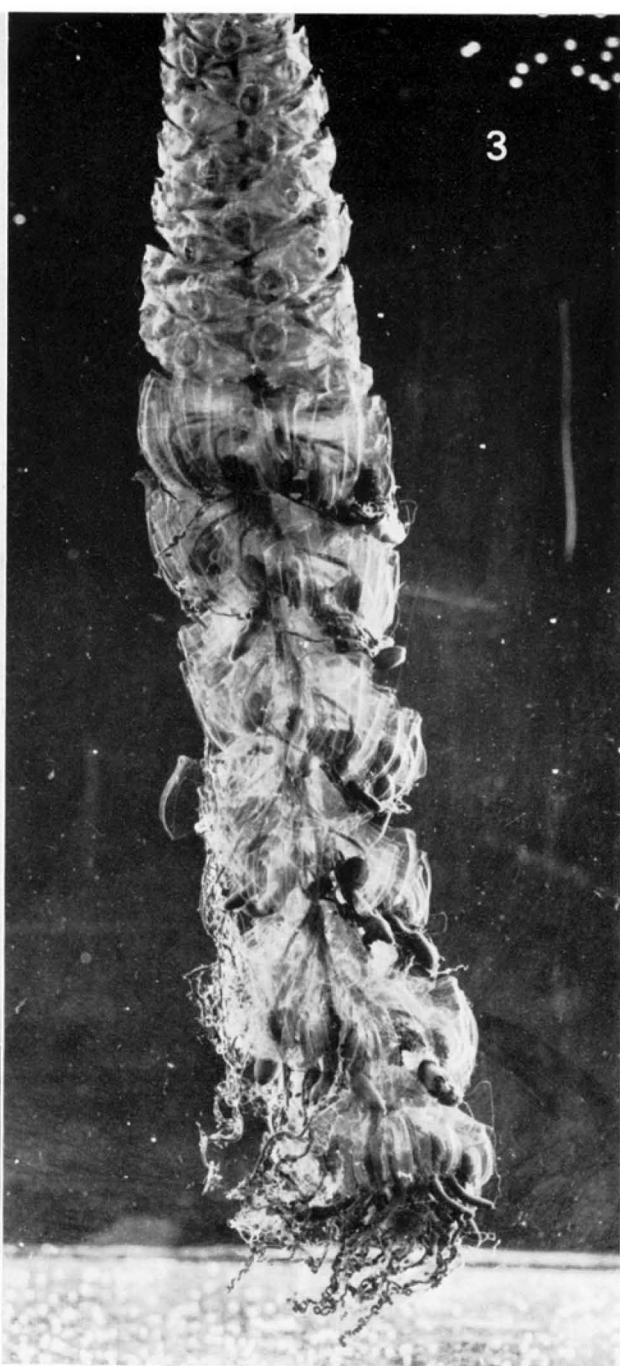
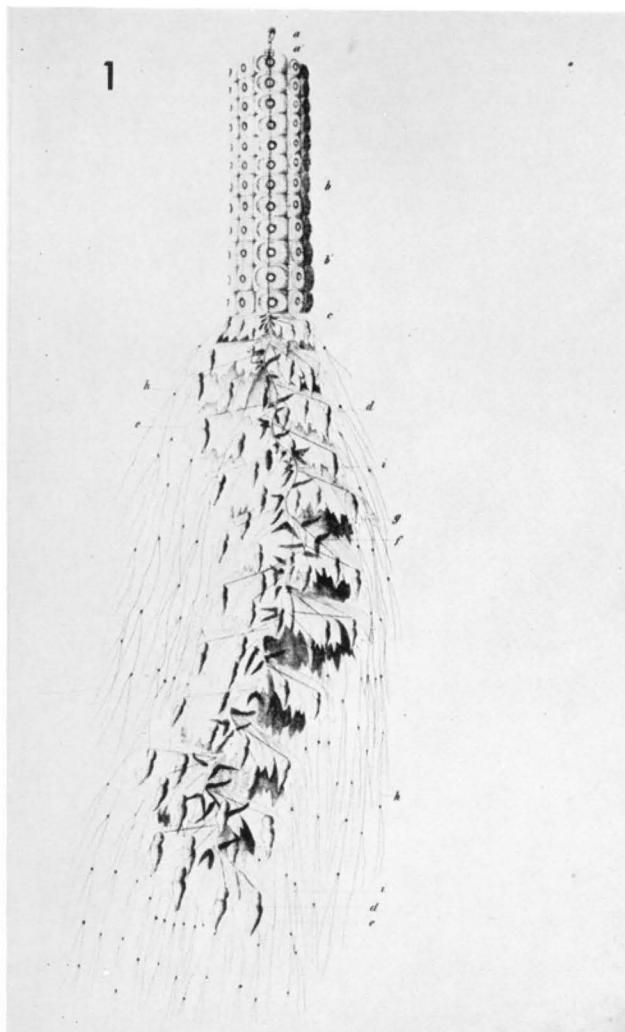
FIG. 3. Specimen from the Museum, Station Zoologique, Villefranche.

FIG. 4. Nectophore, from Kefferstein & Ehlers, 1861, plate 5, figure 23.

Forskalia formosa Keff. & Ehlers

FIG. 5. Nectophore from K. & E. loc. cit. plate 5, figure 22.

PLATE XX



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXI

Rosacea cymbiformis (Chiaje)

FIG. 1. Polygastric phase (one nectophore lost). Living specimen photographed at Villefranche.

Maresearsia praecleara Totton

From Totton, 1954, plate 7, figures 1-5

Figs. 2-5. Eudoxid phase.

FIG. 2. To show eudoxids still attached to the stem-groups.

FIG. 3. Complete eudoxid.

FIG. 4. Gonophores.

FIG. 5. Bract of eudoxid.

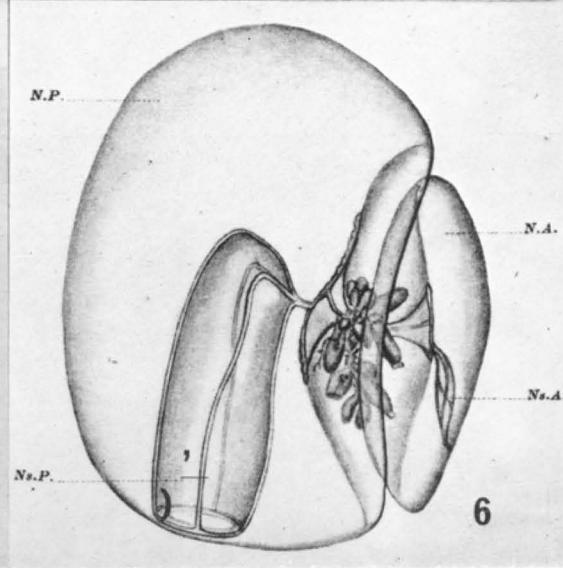
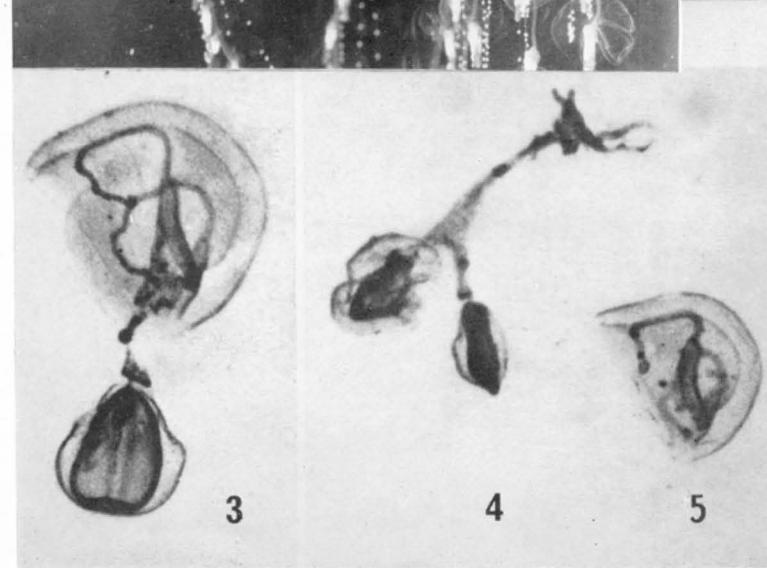
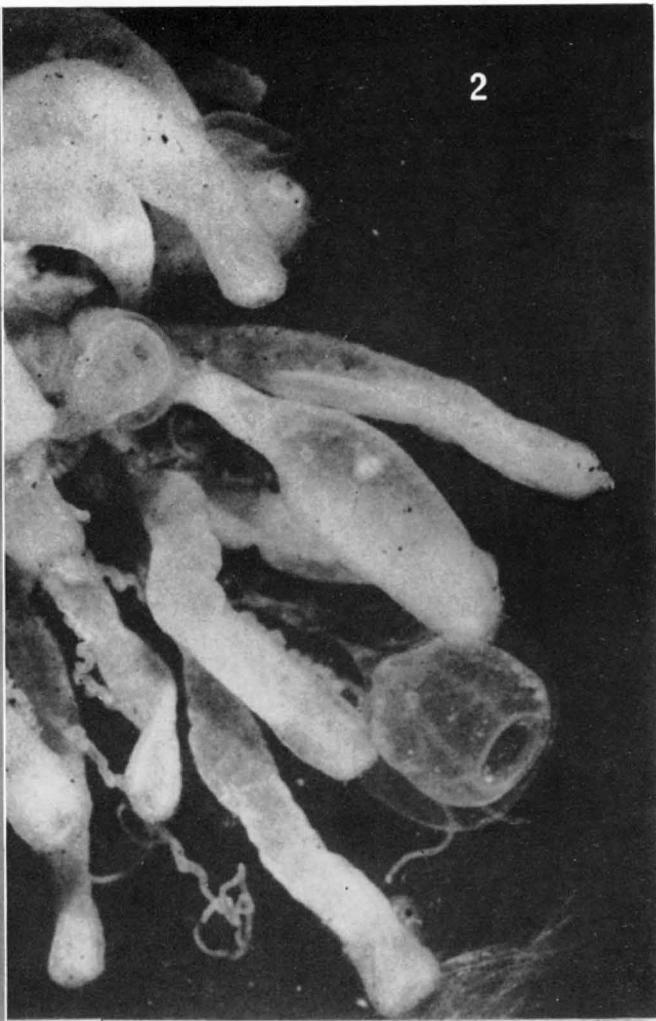
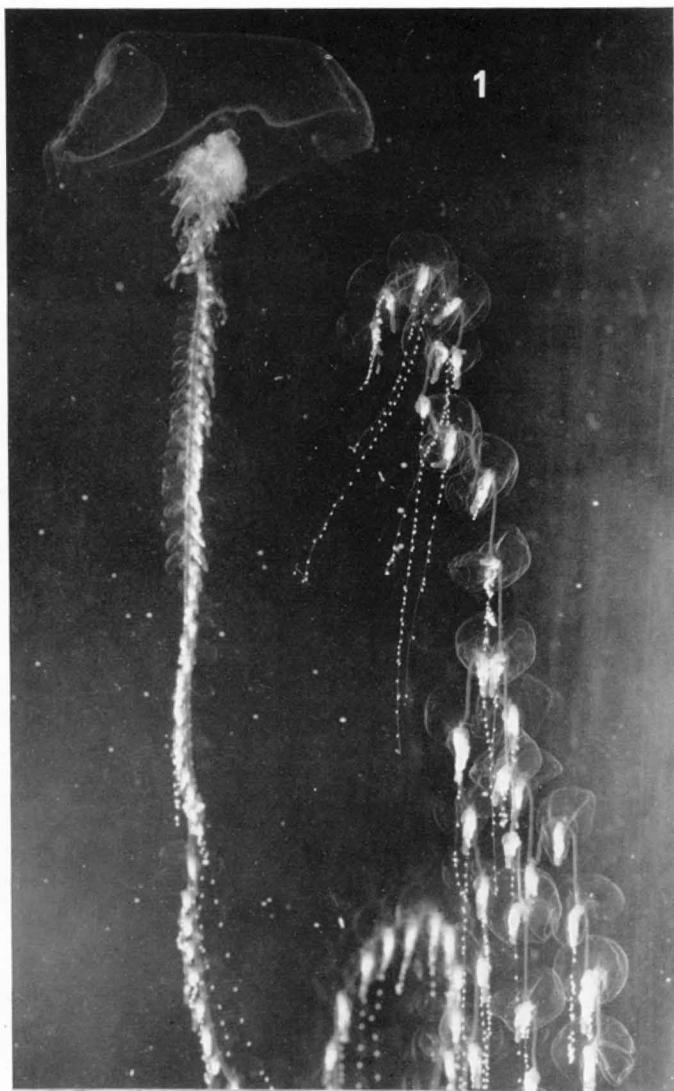
Amphicaryon acaule Chun

From Bigelow, 1911b, plate 4, figure 1

FIG. 6. Polygastric phase.

N.P. = older nectophore (*fide* A.K.T.); N.A. = younger nectophore; Ns.P., Ns.A. = the respective nectosacs.

PLATE XXI



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXII

Rosacea cymbiformis (Chiaje)

From Bigelow 1911b, plate 2, figures 1, 4

FIG. 1. Polygastric phase, $\times 2.5$.

FIG. 2. Eudoxid phase, $\times 15$.

N.P. = older nectophore; *N.A.* = younger nectophore; *St* = stem; *S* = gastrozoid; *Go* = gonophore; *H* = hydroecium; *T* = tentacle; *Te* = tentillum; *E* = egg; *C.br* = bracteal canal; *C.ped* = pedicular canal; *S.Ba* = basigaster of gastrozoid.

FIG. 3. Polygastric phase, from Kawamura 1915, plate 7, figure 4, $\times \frac{5}{8}$.

hy = hydroecium; *n₁₋₃* = nectophores; *ns₁* = respective nectosac; *C* = somatocyst; *br* = bract; *C.br* = central organ; *tr* = stem; *Sp.n* = special nectophore; *p* = gastrozoid.

Desmophyes annectens Haeckel

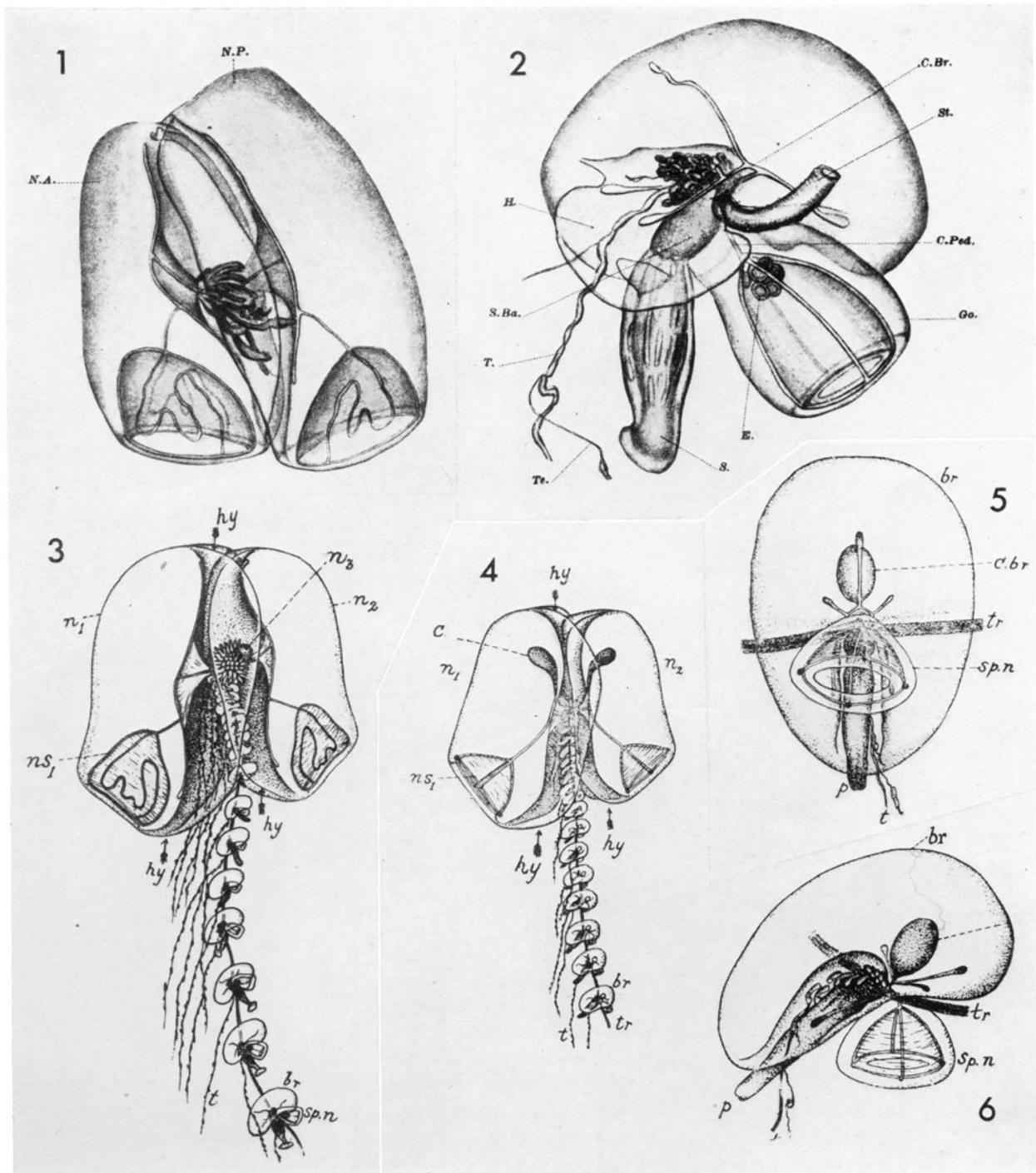
From Kawamura, 1915, plate 7, figures 6-8

FIG. 4. Polygastric phase, $\times 4$.

FIG. 5. Eudoxid phase dorsal view, $\times 16$.

FIG. 6. Eudoxid phase lateral view, $\times 16$.

PLATE XXII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXIII

Praya reticulata (Bigelow)

From Bigelow, 1911b, plate 3, figures 1, 2, 4, 6

FIG. 1. Polygastric phase, ventral view of nectophore, $\times 2$.

FIG. 2. Polygastric phase, lateral view of same, $\times 2$.

FIG. 3. Eudoxid phase, bract, $\times 3$.

FIG. 4. Polygastric phase. Oblique apico-ventral view of the nectosac, $\times 5$.

C.Br = bracteal canal; *C.pa* = pallial canal; *C.ped* = pedicular canal; *C.Su* = radial canal network;
H = hydroecium; *Ns* = nectosac.

Nectopyramis diomediae Bigelow

From Bigelow, 1911b, plate 1, figure 5

FIG. 5. Eudoxid phase. *C.Br¹*–*C.Br³* = bracteal canals; *Ns* = nectosac.

Praya dubia (Q. & G.)

From Bigelow, 1911b, plate 3, figures 8, 9

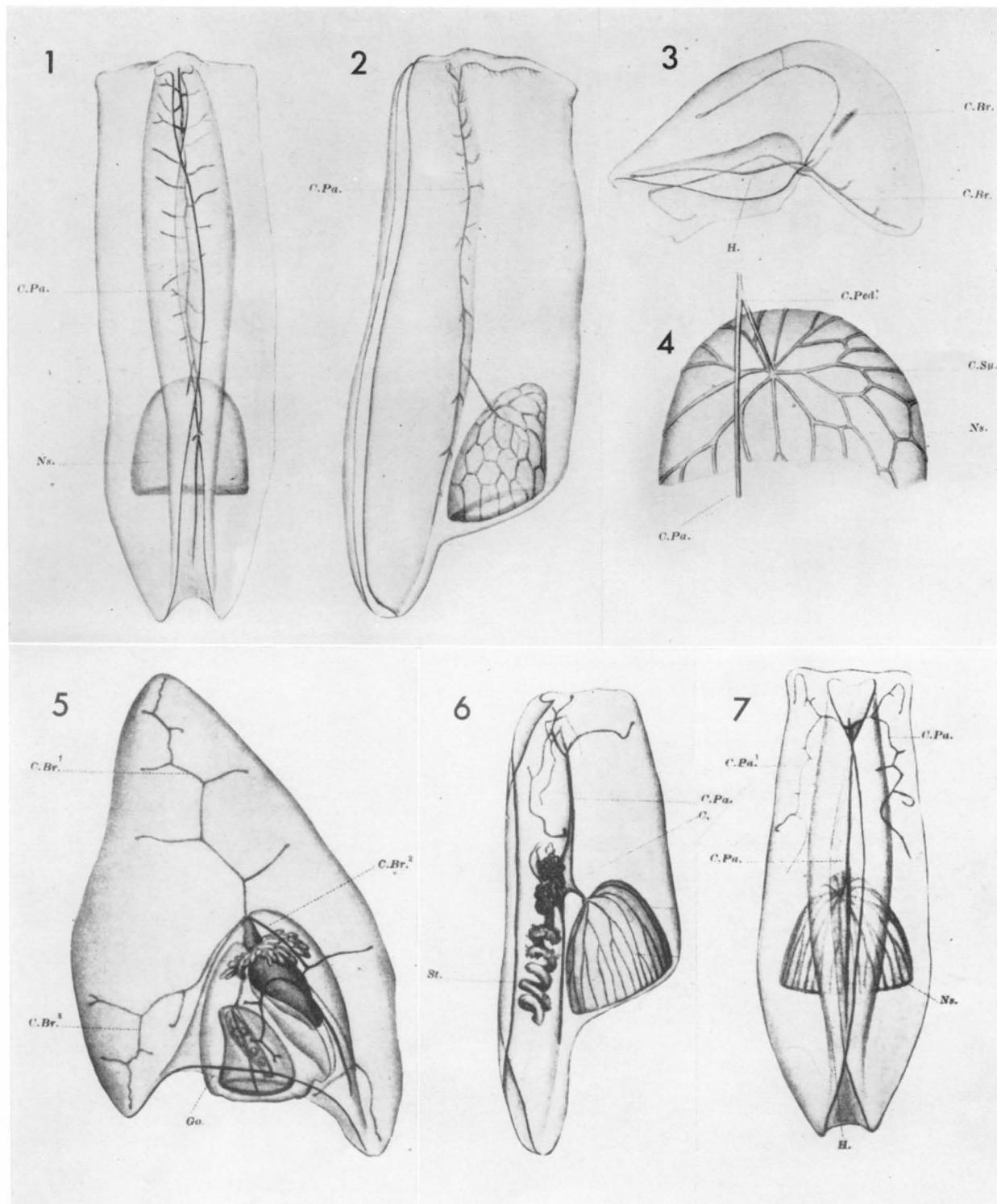
FIG. 6. Polygastric phase, lateral view of a nectophore, $\times 2$.

Ns = nectosac; *St* = stem; *H* = hydroecium; *C.pa* = pallial canal; *C* = pedicular canal; *C.su* = radial canal network.

FIG. 7. Polygastric phase, ventral view of nectophore.

C.pa¹, *C.pa²* = lateral branches of the pallial canal.

PLATE XXIII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXIV *Desmophyes annectens* Haeckel

FIG. 1. Polygastric phase. From Chun, 1897, simplified from Haeckel (1888b, Pl. 30).

br = bract; *go.♂, go.♀* = male and female gonophores; *n* = nectophore; *n.sp* = special nectophore; *p* = gastrozoid; *t* = tentacle.

FIG. 2. Polygastric phase, stem extended. From Vogt, 1854, plate 16, figure 1.

Figures 3-9 from Kölliker, 1853, plate 9, figures 1-8

FIG. 3. Polygastric phase.

a = nectophore; *b* = upper end of siphosome; *c* = pallial canal; *d* = somatocyst; *e* = pedicular canal; *f* = nectosac; *g* = bud of gastrozoid; *h* = gastrozoid; *i* = bract; *k* = nectophore of eudoxid; *l* = tentillum; *m* = siphosome; *n* = median pear-shaped vesicle or central organ.

FIG. 4. Eudoxid phase.

a = stem of siphosome; *b* = nectophore of eudoxid; *c* = gastrozoid; *d* = tentillum; *e* = central organ; *f* = bract; *g* = lateral canals; *h* = hydrocial canals; *i* = ventral canal.

FIG. 5. A lateral nematocyst from cnidosac, $\times 15$.

FIG. 6. Small nematocysts from the terminal filament.

FIG. 7. Bract of eudoxid.

a = hydroecium; *b* = central organ; *c* = lateral canal; *d* = hydrocial canal; *e* = ventral canal.

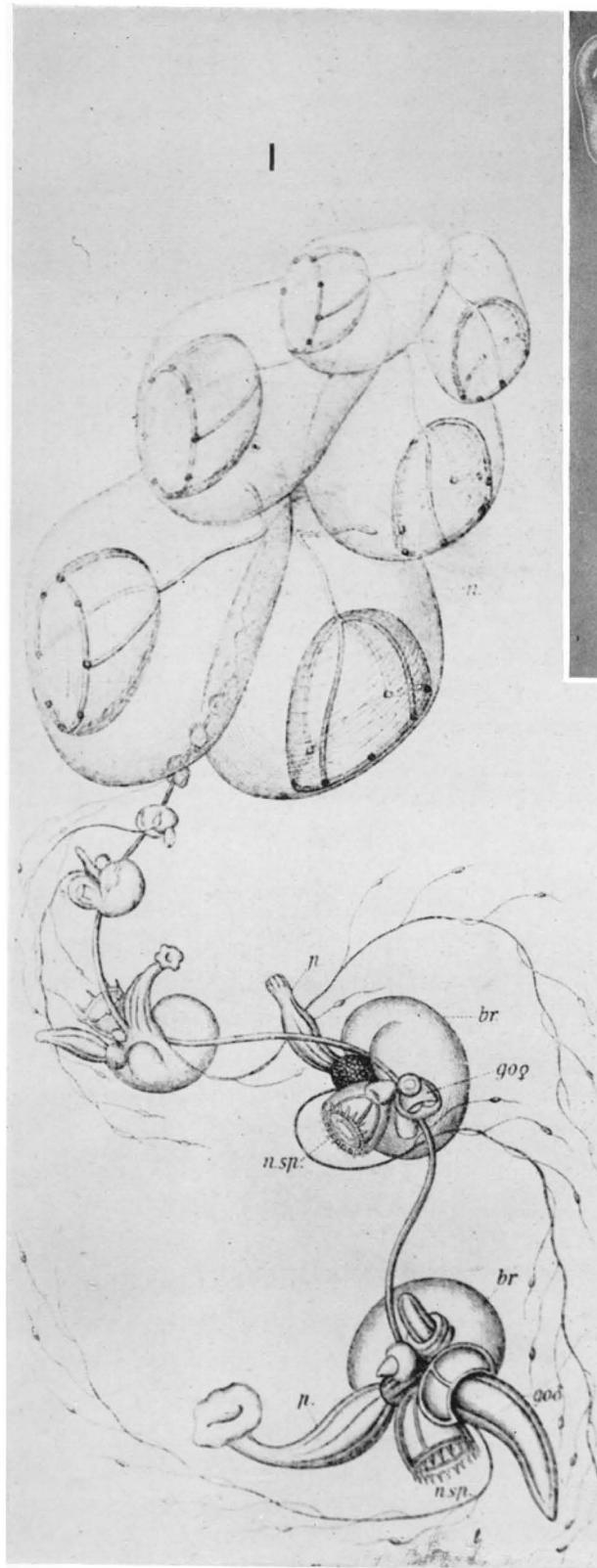
FIG. 8. Nectophore, dorsal view.

a = nectosac; *b* = ostium of same; *c* = somatocyst; *d* = pedicular canal.

FIG. 9. Tentillum.

a = pedicel; *b* = proximal end of elastic band; *b¹* = enlarged part of same; *c* = cnidoband; *d* = terminal filament.

PLATE XXIV



A SYNOPSIS OF THE SIPHONOPHORA

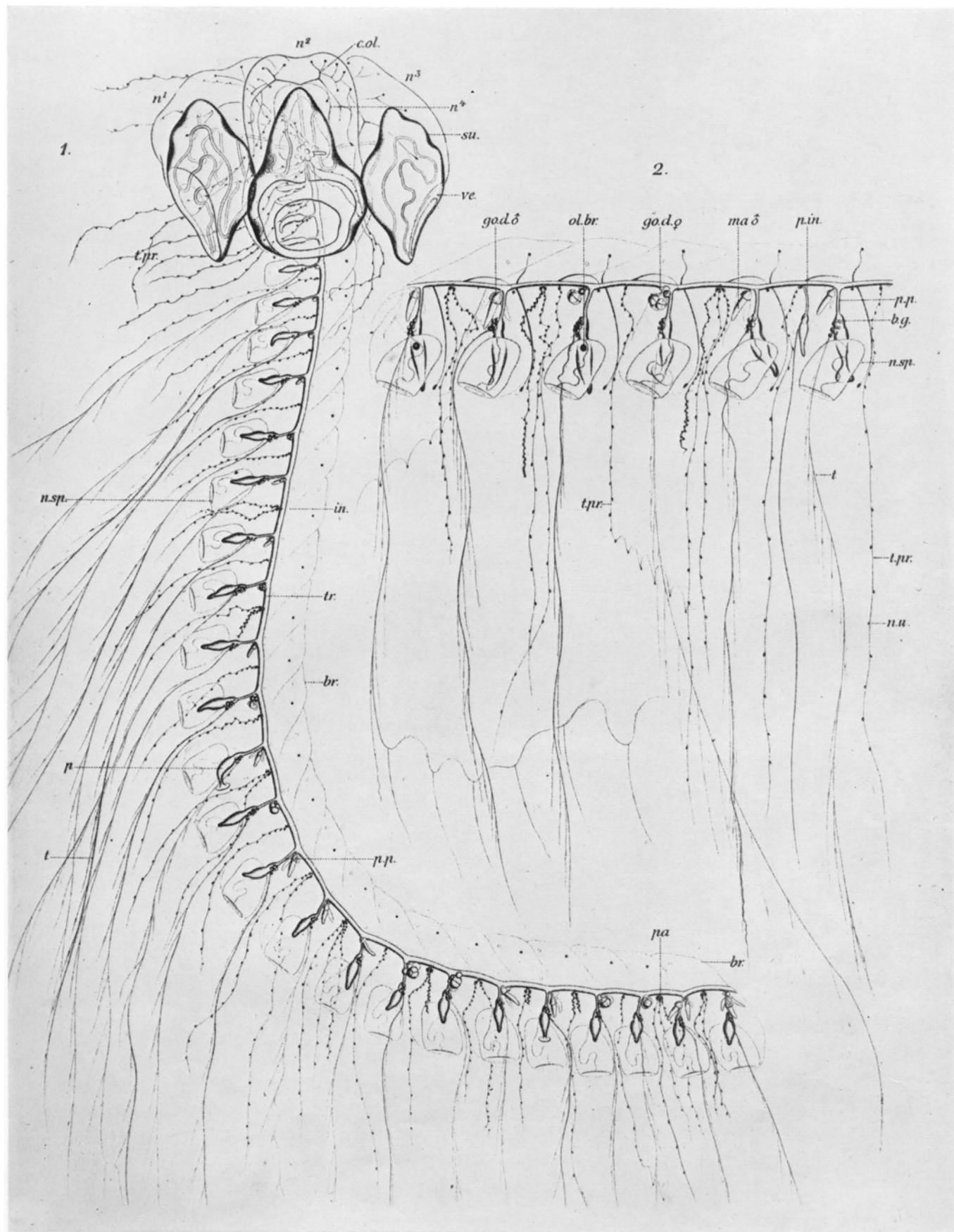
PLATE XXV *Stephanophyes superba* Chun

From Chun, 1891, plate 1.

FIG. 1. Polygastric phase, whole animal.

FIG. 2. Polygastric phase, part of the stem.

n^1-n^4 = nectophores; su = nectosac; $t.pr$ = palpacle; t = tentacle of gastrozooid; $n.sp$ = asexual nectophore of the eudoxid group; br = bract; pa = palpon; $ma.\delta$ = manubrium of ♂ gonophore; $n.u$ = tentillum of the palpacle; $ol(br)$ = oil-drop; $p.p$, $p.in$ = peduncle of gastrozooid; $go.d.\delta$ = male gonophore; $go.d.\varphi$ = female gonophore; $b.g$ = basigaster of gastrozooid; in = stem internode; ve = velum. Note the palpons in the stem internodes.



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXVI *Stephanophyes superba* Chun

From Chun, 1891, plate 3, figure 1

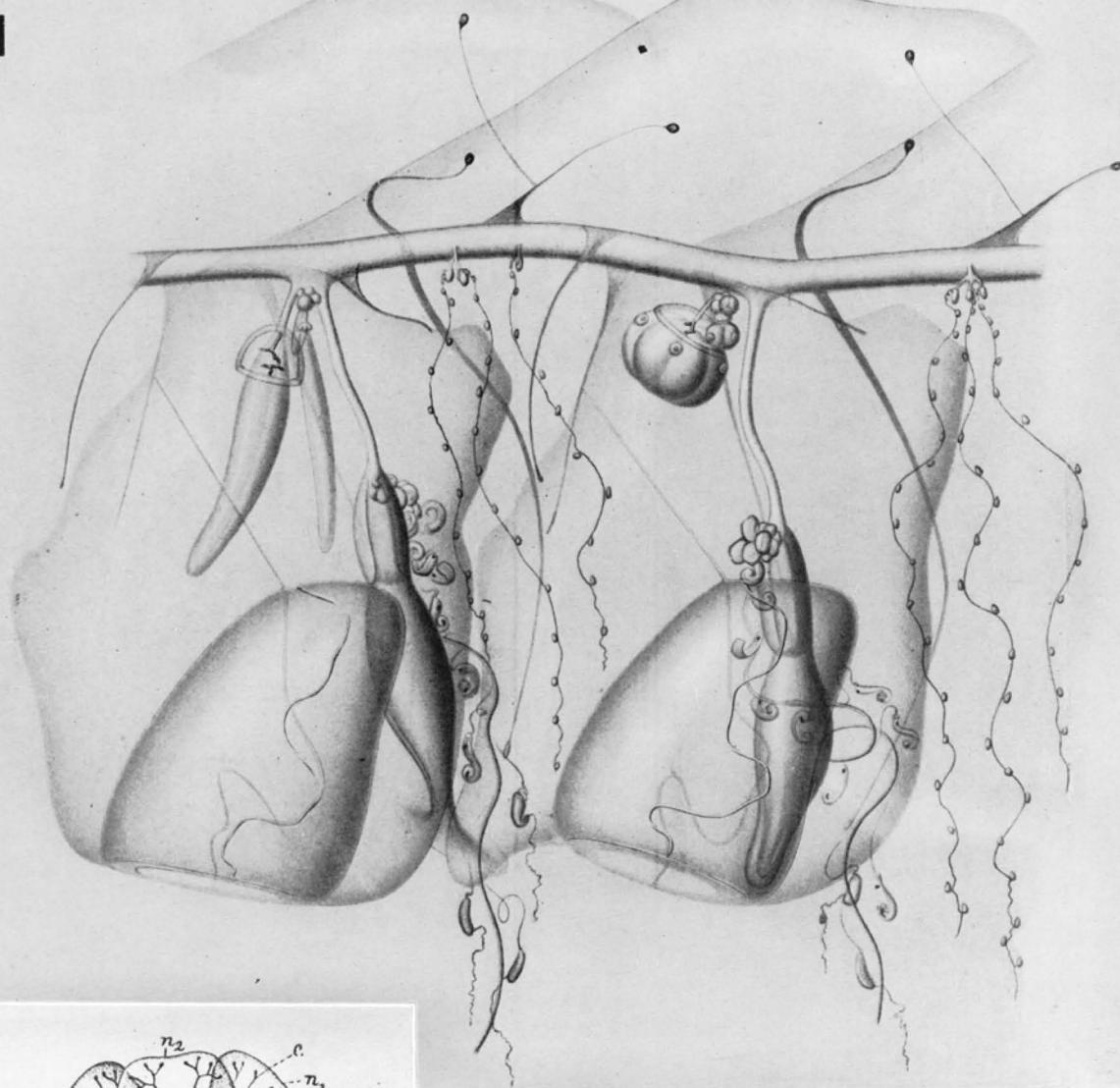
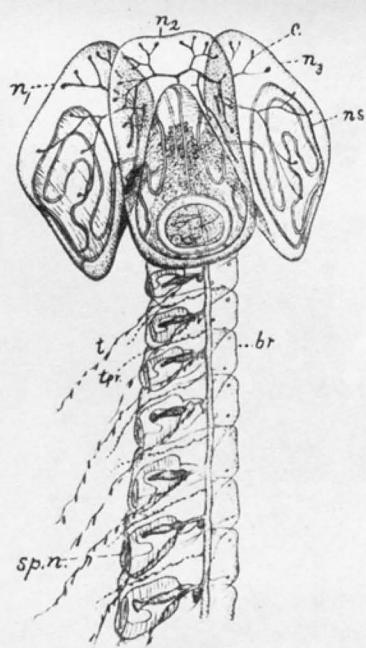
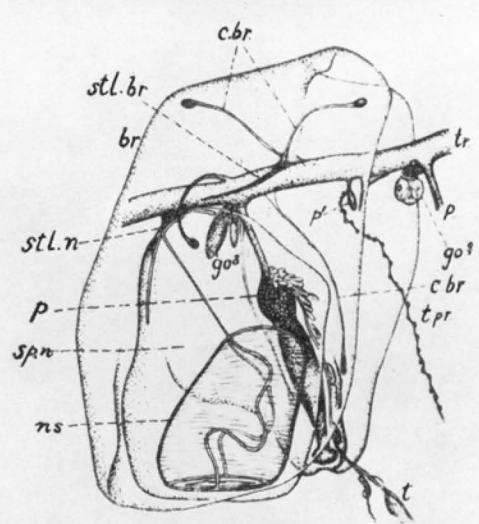
FIG. 1. Part of the stem showing two stem-groups of the polygastric phase with asexual nectophores, a male (on the left) and a female gonophore and a cluster of the unique palpons, each carrying a tentacle with many tentilla.

From Kawamura, 1915, plate 7, figures 9, 10

FIG. 2. Polygastric phase.

FIG. 3. A single stem-group of the same.

n^1-n^3 = nectophores; ns = nectosac; c = branch of the pallial canal (somatocyst); br = bract; t = tentacle; $sp.n$ = asexual nectophore; $c.br$ = bracteal canal; $st.l.br$ = muscular attachment of bract; tr = stem; p = gastrozooid; $st.l.n$ = muscular attachment of asexual nectophore of eudoxid; p' = palpon; $go.\delta$, $go.\varphi$ = male and female gonophores; $t.pr$ = palpacle.

1**2****3**

A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXVII

Lilyopsis rosea Chun
From Bedot, 1895, plate 12, figure 1

FIG. 1. Polygastric phase.

Nectopyramis spinosa Sears
From Totton, 1954, plate 5

FIG. 2. Polygastric phase showing obsolescent nectosac on the left, 'Discovery' St. 1179, 500-250 m.

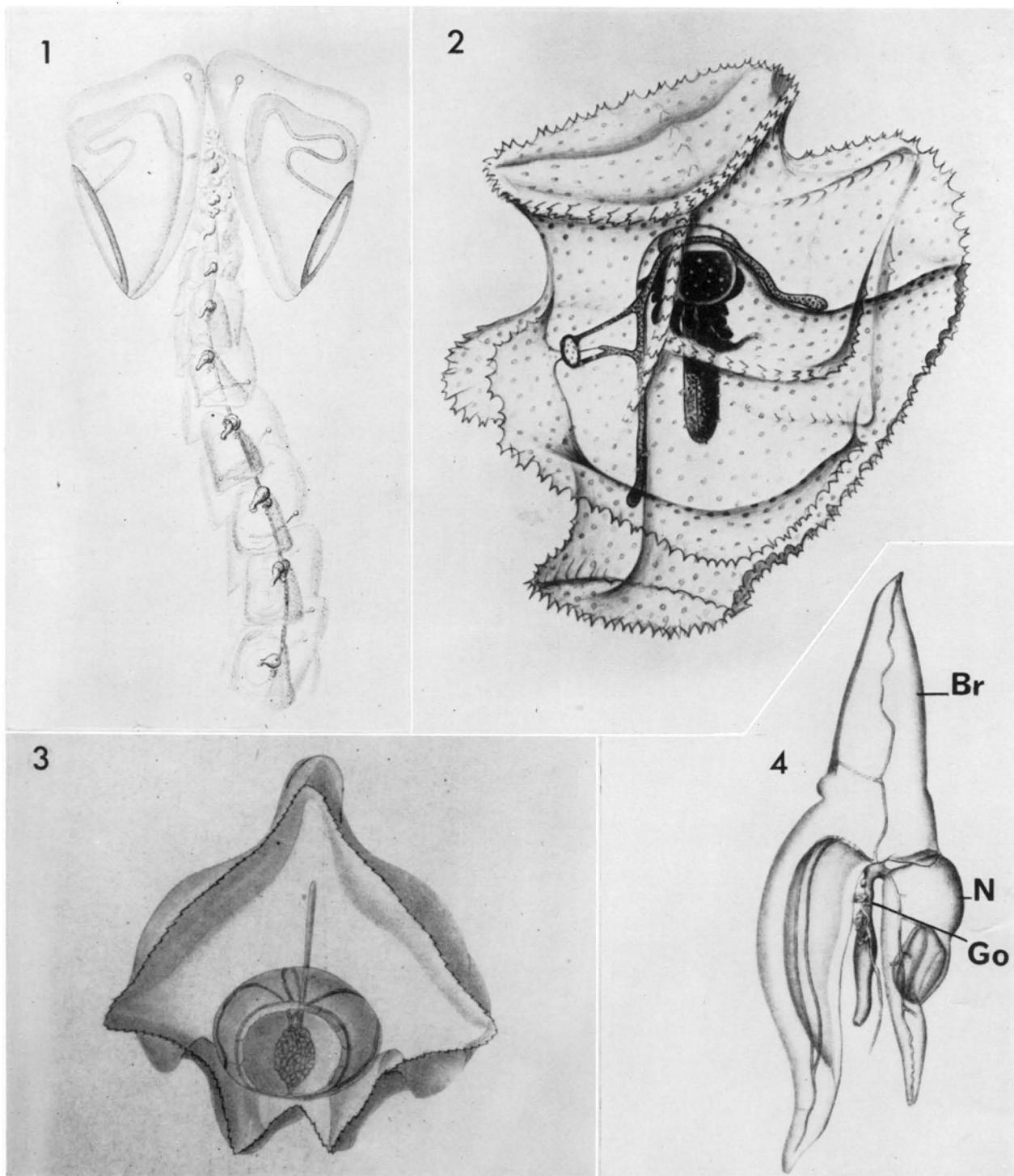
Vogtia serrata (Moser)
From Moser, 1925, plate 27, figure 7

FIG. 3. Nectophore.

Nectopyramis natans (Bigelow)
From Bigelow, 1911b, plate 20, figure 16

FIG. 4. Eudoxid phase. Br = bract; N = asexual nectophore; Go = gonophore.

PLATE XXVII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXVIII *Hippopodius hippopus* (Forskål)

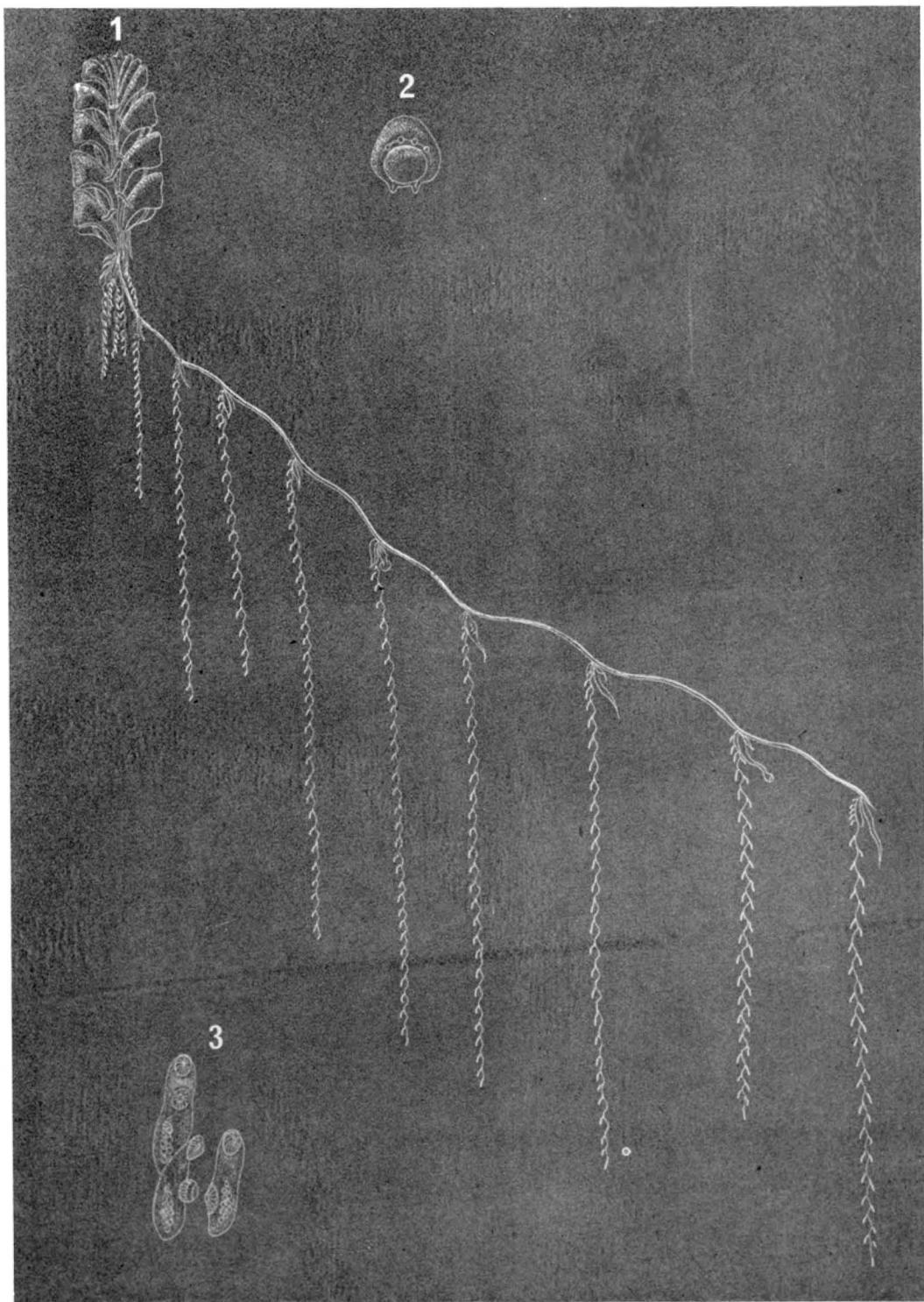
From Vogt 1854, plate 12, figures 1-3

FIG. 1. Whole animal.

FIG. 2. Nectophore.

FIG. 3. Parasitic trematodes.

PLATE XXVIII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXIX

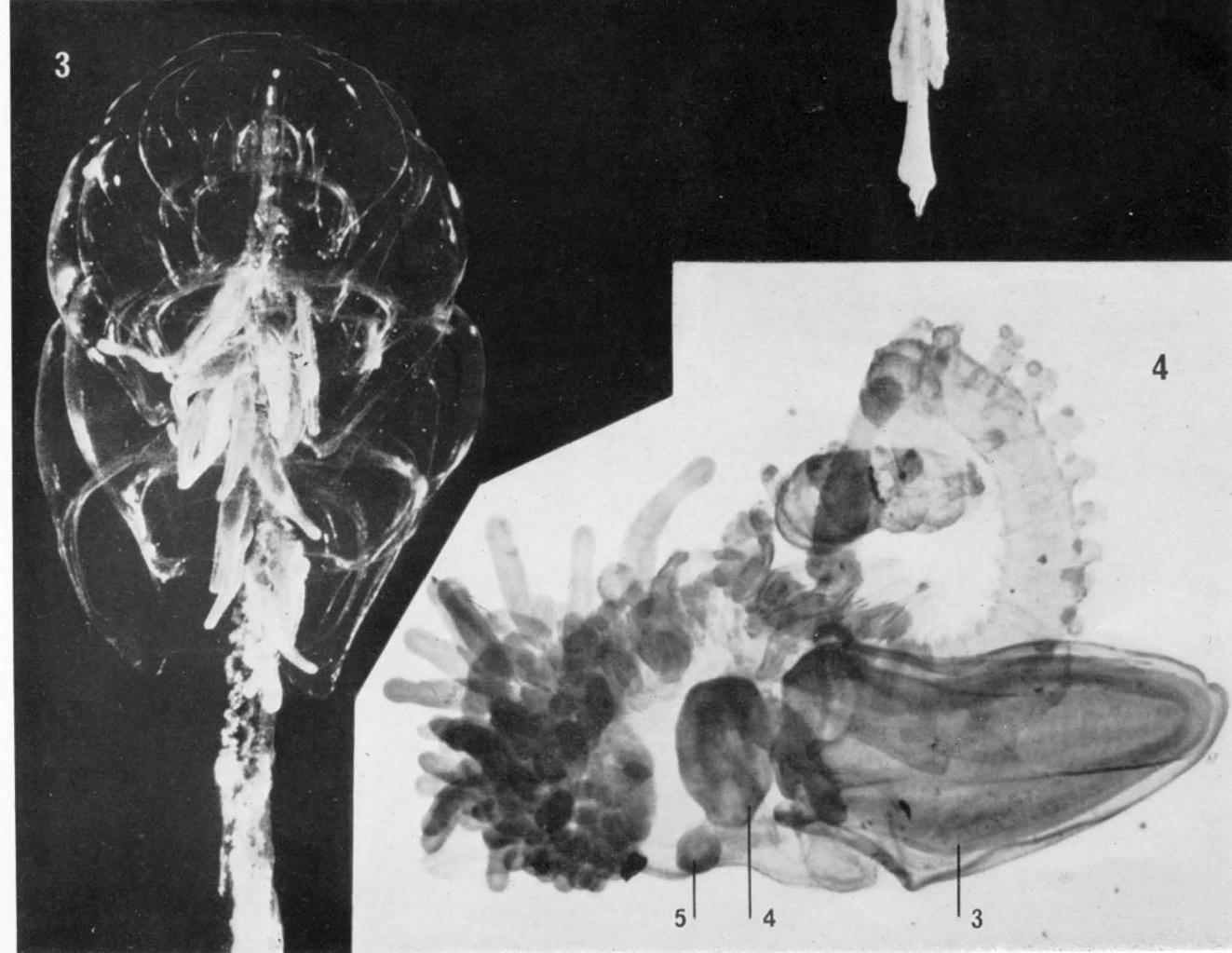
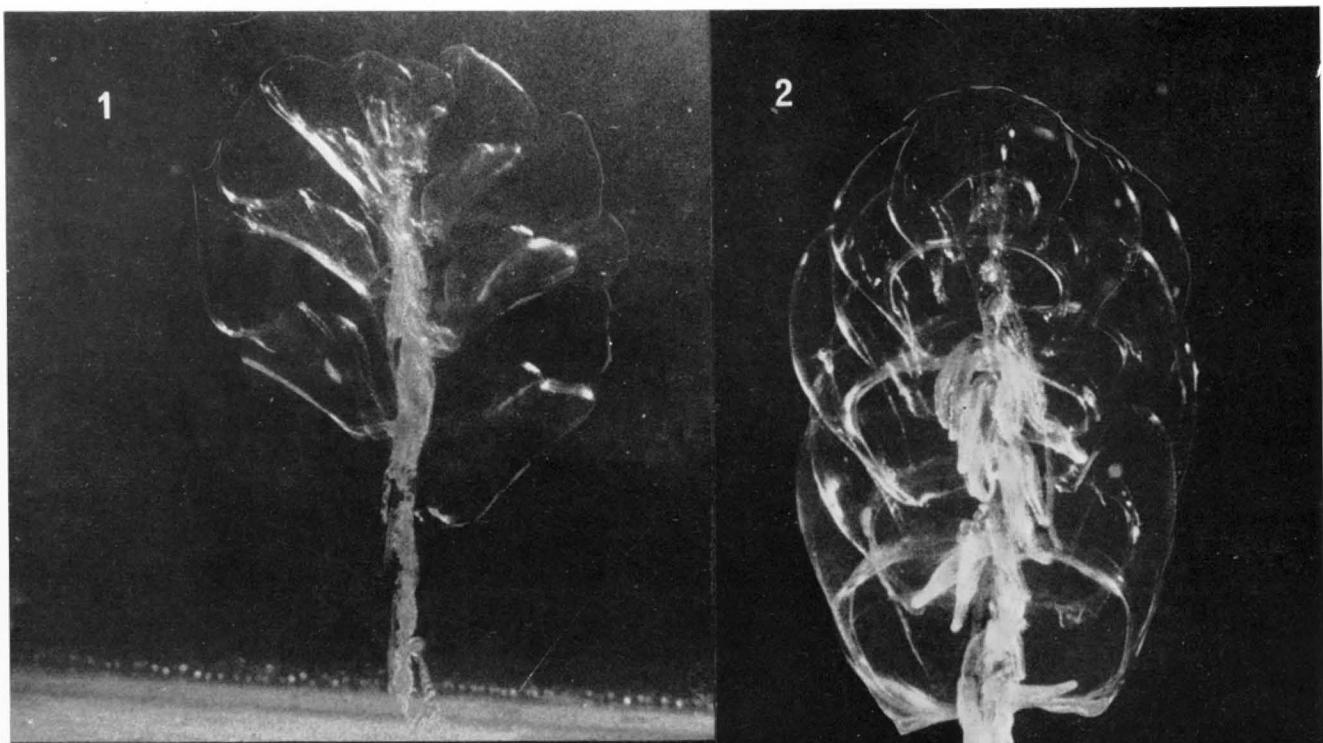
Hippopodius hippopus (Forskål)

FIGS. 1-3. Photographs of living animals, Villefranche, $\times 6$. The appendages of the contracted stem are viewed through the transparent nectophores. Figure 3 shows the sub-umbrella cavity fully expanded.

Sulculeolaria quadrivalvis Blainville

FIG. 4. Photograph to show 'reserve' buds of nectophores 3, 4, 5. The first and second definitive nectophores were removed to reveal the buds. Specimen taken by H.M. Survey Ship 'Challenger', 1950-51.

PLATE XXIX



A SYNOPSIS OF THE SIPHONOPHORA

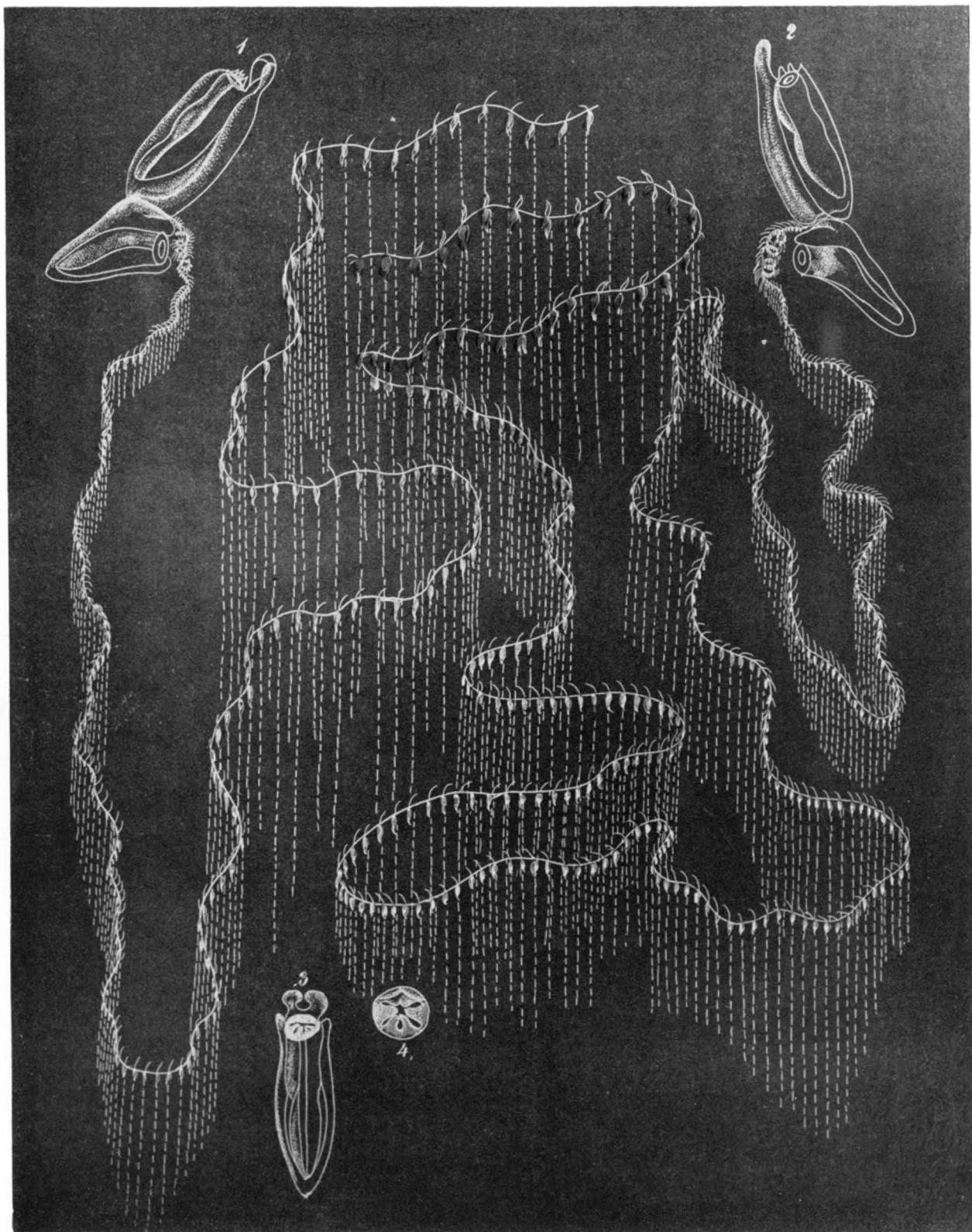
PLATE XXX *Sulculeolaria quadrivalvis* Blainville

From Vogt, 1854, plate 8

Figures 1-4 Polygastric phase

- FIG. 1. With female gonophores.
- FIG. 2. With male gonophores.
- FIG. 3. Posterior nectophore.
- FIG. 4. Posterior nectophore, ostial view.

PLATE XXX



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXXI

Sulculeolaria quadrivalvis Blainville

Figures 1-3 from Bigelow, 1911b, plate 5, figures 1-3

FIG. 1. Lateral view of the posterior nectophore, $\times 4.5$.

FIG. 2. Lateral view of the anterior nectophore, $\times 4$.

FIG. 3. Ostial view of the posterior nectophore, $\times 8$.

So = somatocyst; *To.D¹*, *To.D²* = dorsal teeth; *To.L* = lateral tooth; *W.V* = mouth-plates of basal wings.

Sulculeolaria monoica (Chun)

Figures 5-7 from Bigelow, 1911b, plate 6, figures 1, 6, 7

Figures 10, 12 from Bigelow, 1911b, plate 6, figures 4, 9

FIG. 5. Lateral view of the anterior nectophore, $\times 9$.

FIG. 6. Anterior nectophore, ostial view.

FIG. 7. Posterior nectophore, lateral view of the ostium, $\times 16$.

So = somatocyst; *To.L*, *To.D* = lateral and dorsal tooth; *W.V* = basal wing; *X* = secondary spines of basal wing.

FIG. 10. Posterior nectophore, lateral view, $\times 8$.

FIG. 12. Posterior nectophore, dorsal view of the ostium.

To.D = dorsal tooth; *To.L¹*, *To.L²* = lateral teeth.

Sulculeolaria turgida (Gegenbaur)

Figures 8, 9 from Gegenbaur, 1854, plate 23, figures 1, 3

FIG. 8. Whole animal, polygastric phase.

A = anterior nectophore; *B* = posterior nectophore; *a* = ostium; *b*, *b'* = mouth-plate; *c* = nectosac; *d* = lateral radial canal; *e* = stem of siphosome; *f* = eudoxid.

FIG. 9. Posterior nectophore of same.

Lensia campanella (Moser)

From Moser, 1925, plate 4, figure 1

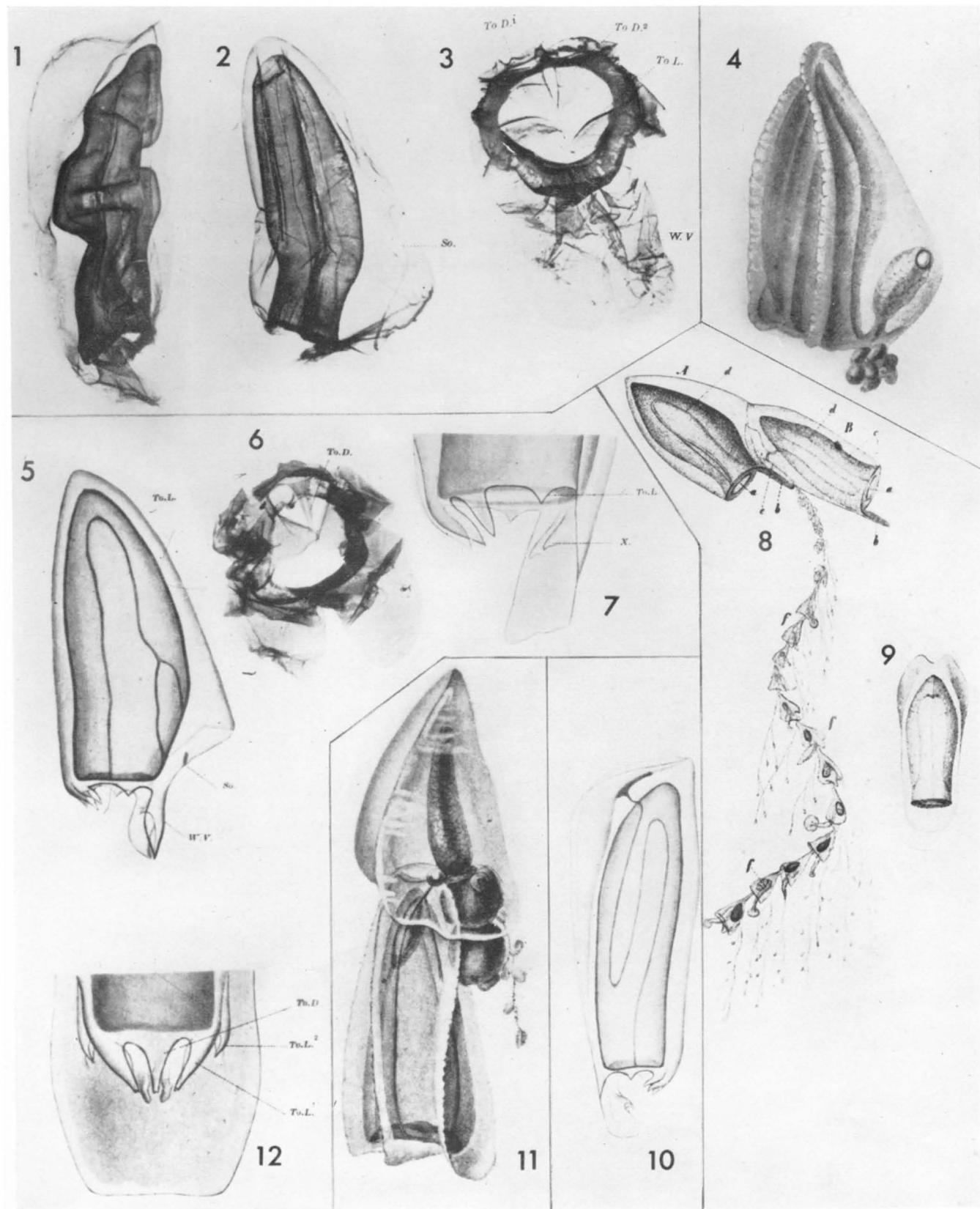
FIG. 4. Polygastric phase, anterior nectophore, $\times 6$.

Lensia conoidea (Keff. & Ehlers)

From Moser, 1925, plate 4, figure 3

FIG. 11. Eudoxid phase, $\times 18$.

PLATE XXXI



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXXII

Muggiaeae kochi (Will)

From Chun, 1883, plate 17, figure 2

FIG. 1. Polygastric phase, $\times 60$.

k = ridge; *s* = somatocyst; *m* = gastrozooid; *d* = bract; *g.sch* = gonophore; *x* = bud of second gonophore; *st* = stem.

FIG. 2. From Moser, 1925, plate 1, figure 1. Polygastric phase, $\times 12$.

Muggiaeae atlantica Cunningham

From Moser, 1925, plate 1, figure 5

FIG. 3. Polygastric phase, $\times 12$.

Chelophyses appendiculata (Eschscholtz)

From Lochman, 1914, plate 1, figure 1

FIG. 4. Polygastric phase with larval nectophore still attached.

l = larval nectophore; *B* = anterior nectophore; *br* = bract; *C* = bud of posterior nectophore; *c.ol* = somatocyst; *go* = gonophore; *p* = gastrozooid; *tr* = stem.

Eudoxoides spiralis (Bigelow)

From Bigelow, 1911b, plate 8, figures 2, 1

FIG. 5. Polygastric phase, ventral view of the anterior nectophore, $\times 20$.

FIG. 6. Lateral view of the anterior nectophore, $\times 20$.

H = hydroecium; *R.D* = dorsal ridge; *R.L* = left ridge; *R.V¹, R.V²* = right and left ventral ridges; *So* = somatocyst.

Chelophyses contorta (L. & v. R.)

From Moser, 1925, plate 13.

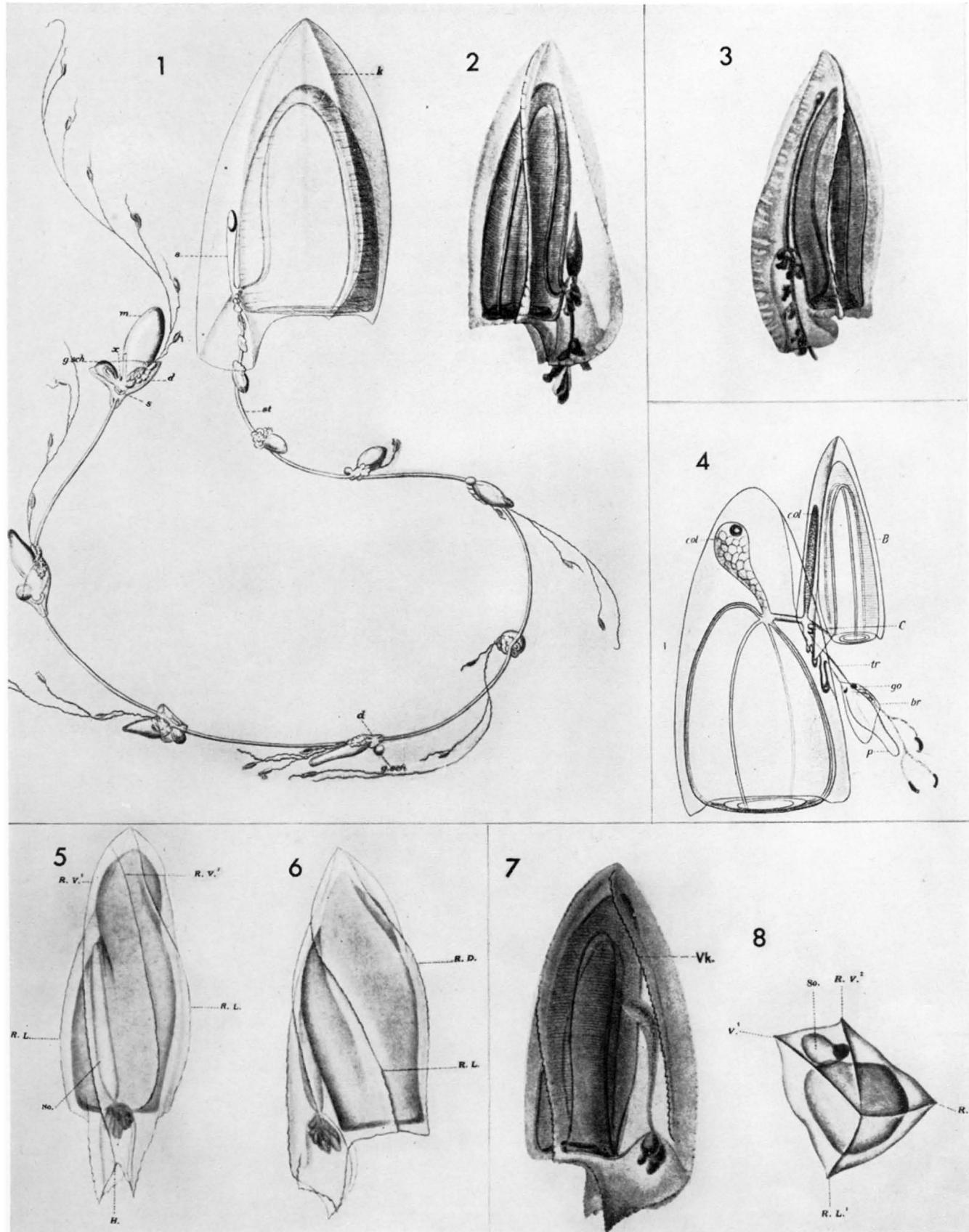
FIG. 7. Polygastric phase, anterior nectophore, lateral view, $\times 13$.

V.K = Ventral ridge.

From Bigelow, 1911b, plate 8, figure 3

FIG. 8. Anterior nectophore, apical view, $\times 12$.

So = somatocyst; *R.L¹, R.L²* = lateral ridges; *V¹, R.V²* = ventral ridges.



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXXIII

Dimophyes arctica (Chun)

From Moser, 1925, plate 26, figures 5, 1, 2

FIG. 1. Polygastric phase, anterior nectophore, juvenile, $\times 20$.

FIG. 2. Polygastric phase, whole animal, $\times 14$.

FIG. 7. Polygastric phase, posterior nectophore, $\times 19$.

UG² = bud of nectophore.

Diphyes dispar (Chamisso & Eysenhardt)

From Moser, 1925, plate 8, figure 2

FIG. 3. Eudoxid phase, to show the succession of gonophores, *Go¹*–*Go⁵*

x = vestige of the stem.

Eudoxoides mitra Huxley

From Moser, 1925, plate 13

FIG. 4. Polygastric phase, $\times 12$.

From Moser, 1925, plate 8

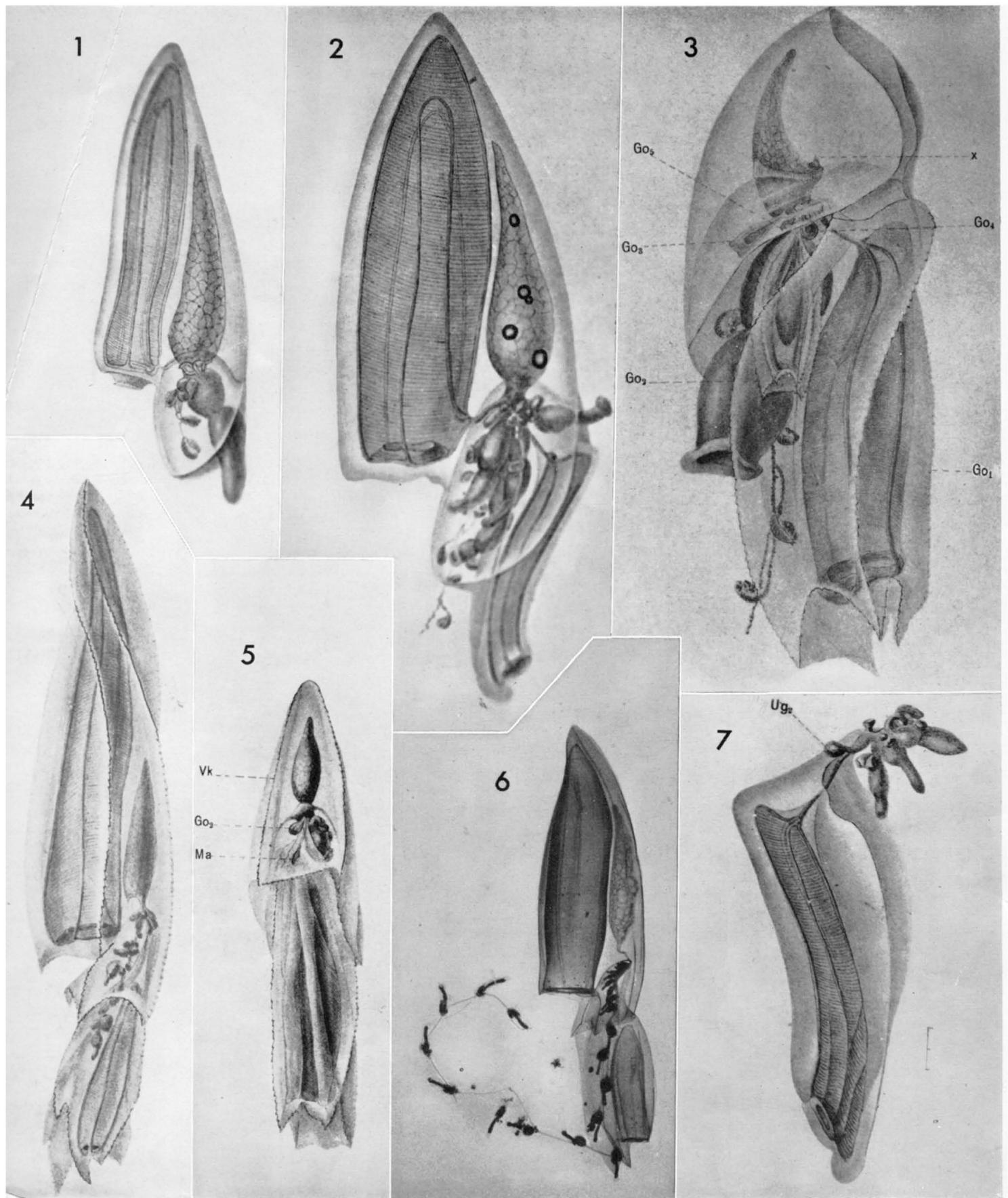
FIG. 5. Eudoxid phase, $\times 9$.

Vk = ventral ridge; *GO²* = bud of second gonophore; *Ma* = manubrium.

Chelophyses appendiculata (Eschscholtz)

FIG. 6. Polygastric phase, from Villefranche, $\times 3$.

PLATE XXXIII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXXIV *Diphyes antarctica* Moser

From Moser, 1925, plates 9, 10
Polygastric and eudoxid phases

- FIG. 1. Anterior nectophore, juvenile, $\times 10$.
FIGS. 2, 4. Schematic transverse sections of anterior and posterior nectophores.
FIG. 3. Whole animal, $\times 2.7$.
FIG. 5. Stem-group, $\times 18$.
FIG. 6. Bract of eudoxid phase.
FIG. 7a. Lateral view of the cnidosac, $\times 200$.
FIG. 7b. Ventral view of the same.
FIG. 8. Ostial view of the posterior nectophore.
FIG. 9. Whole animal, ventral view, $\times 2.7$.
FIG. 10. Gonophore, ♀, $\times 4$.
FIG. 11. Posterior nectophore, $\times 7.5$.
FIG. 12. Mature eudoxid, $\times 10$.
FIG. 13. Whole animal, dorsal view, $\times 2.7$.

Go = gonophore; *Go²* = bud of gonophore; *H* = hydroecium; *Lz* = lateral tooth; *Sb* = nectosac;
So = somatocyst; *W* = deeply coloured cap.

PLATE XXXIV

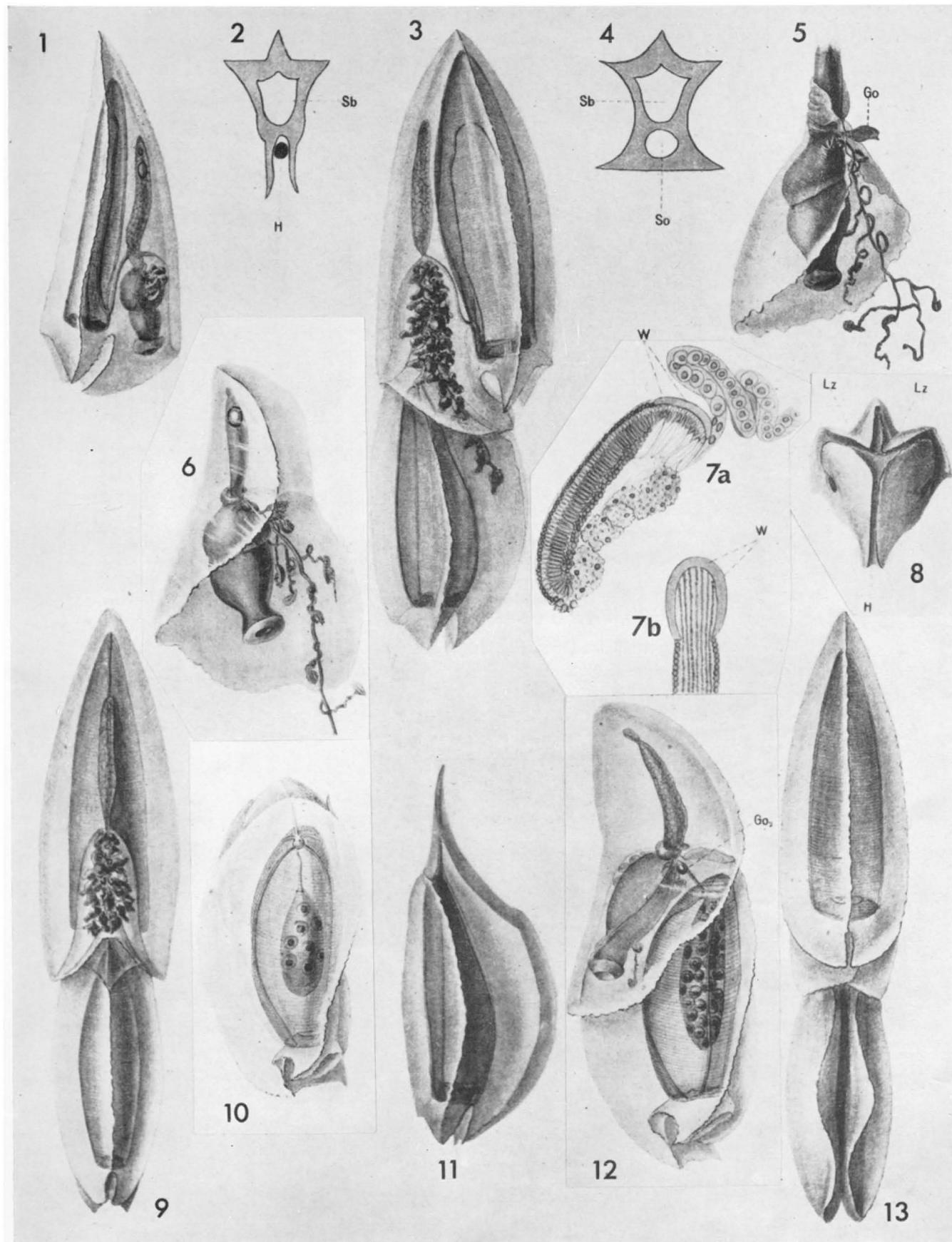


PLATE XXXV

Clausophyes ovata (Keff. & Ehlers)

Figures 1, 4, 5 from Moser, 1925, plate 24, figure 4, plate 25, figures 3, 4

FIG. 1. Anterior nectophore, $\times 5$.

FIG. 4. Posterior nectophore, $\times 9.5$.

FIG. 5. Posterior nectophore, $\times 4.2$.

Figs. 6-10. From Kefferstein & Ehlers, 1861, plate 5, figures 2, 3, 1, 4, 5.

FIG. 6. Eudoxid.

FIG. 7. Stem group.

FIG. 8. Whole animal.

FIG. 9. Stem groups.

FIG. 10. Stem groups.

g = bract (in K. & E's figure g flags bract in error for gonophore); p = gastrozoid.

Chuniphyes moserae Totton

From Bigelow, 1911b, plate 8, figure 9 (as *C. multidentata*)

FIG. 2. Polygastric phase, whole animal, $\times 2.5$.

D' = dorsal ridge; H = hydroecium; So = somatocyst; $R.L.$, $R.V.$ = lateral and ventral ridges.

Chuniphyes sp.

From Moser, 1925, plate 24, figure 3

FIG. 3. Bract of the eudoxid phase, $\times 18$.

Clausophyes galeata (L. & van R.)

From Bigelow, 1913, plate 6, figure 1 (as *C. galatea*)

FIG. 11. Polygastric phase, whole animal.

PLATE XXXV

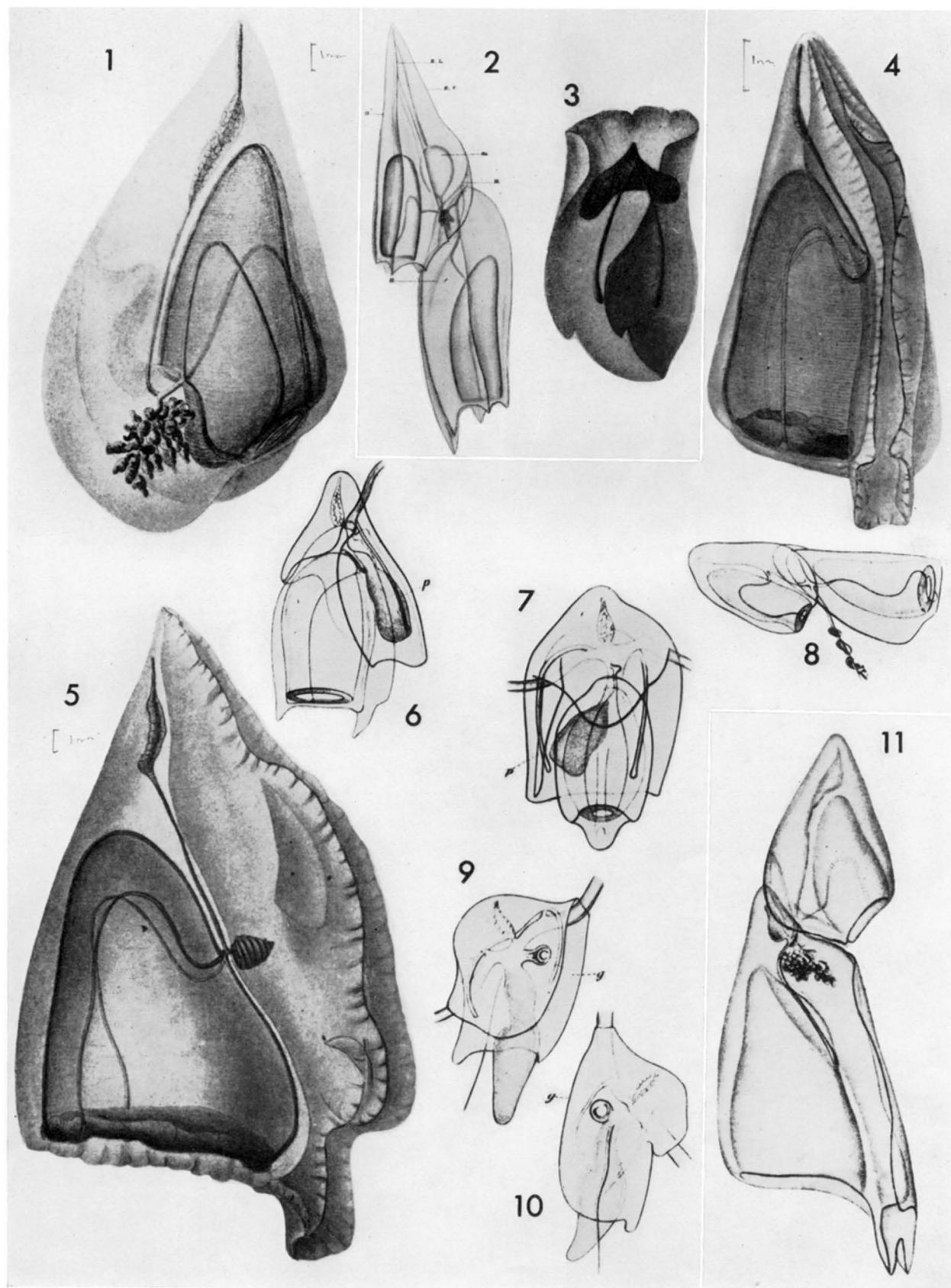


PLATE XXXVI

Sphaeronectes gracilis (Claus)

From Chun, 1885, plate 1, figure 1

FIG. 1. Polygastric phase, whole animal, $\times 6$.

Ceratocymba leuckarti (Huxley)

From Bigelow, 1911b, plate 13, figure 8

FIG. 2. Eudoxid phase, attached stem-group, $\times 30$.

C.B. = bracteal canal; *S* = gastrozooid; *T* = tentacle; *H.Go* = hydroecium of gonophore.

From Bigelow, 1911b, plate 15, figure 4

FIG. 3. Bract of eudoxid, dorsal view, $\times 4$.

From Bigelow, 1911b, plate 15, figure 3

FIG. 4. Lateral view of bract, $\times 4$.

From Bigelow, 1911b, plate 13, figure 6

FIG. 5. Posterior nectophore of specimen shown in figure 7, polygastric phase, $\times 30$.

H = hydroecium; *To.l* = lateral tooth.

From Bigelow, 1911b, plate 13, figure 5

FIG. 7. Polygastric phase, whole animal, $\times 10$. *So* = somatocyst.

Abyla haekeli L & v. R.

From Bigelow, 1911b, plate 13, figures 1, 7

FIG. 6. Polygastric phase, anterior nectophore, $\times 9$.

FIG. 8. Anterior nectophore, ventral view, $\times 9$.

Abyla trigona Q & G.

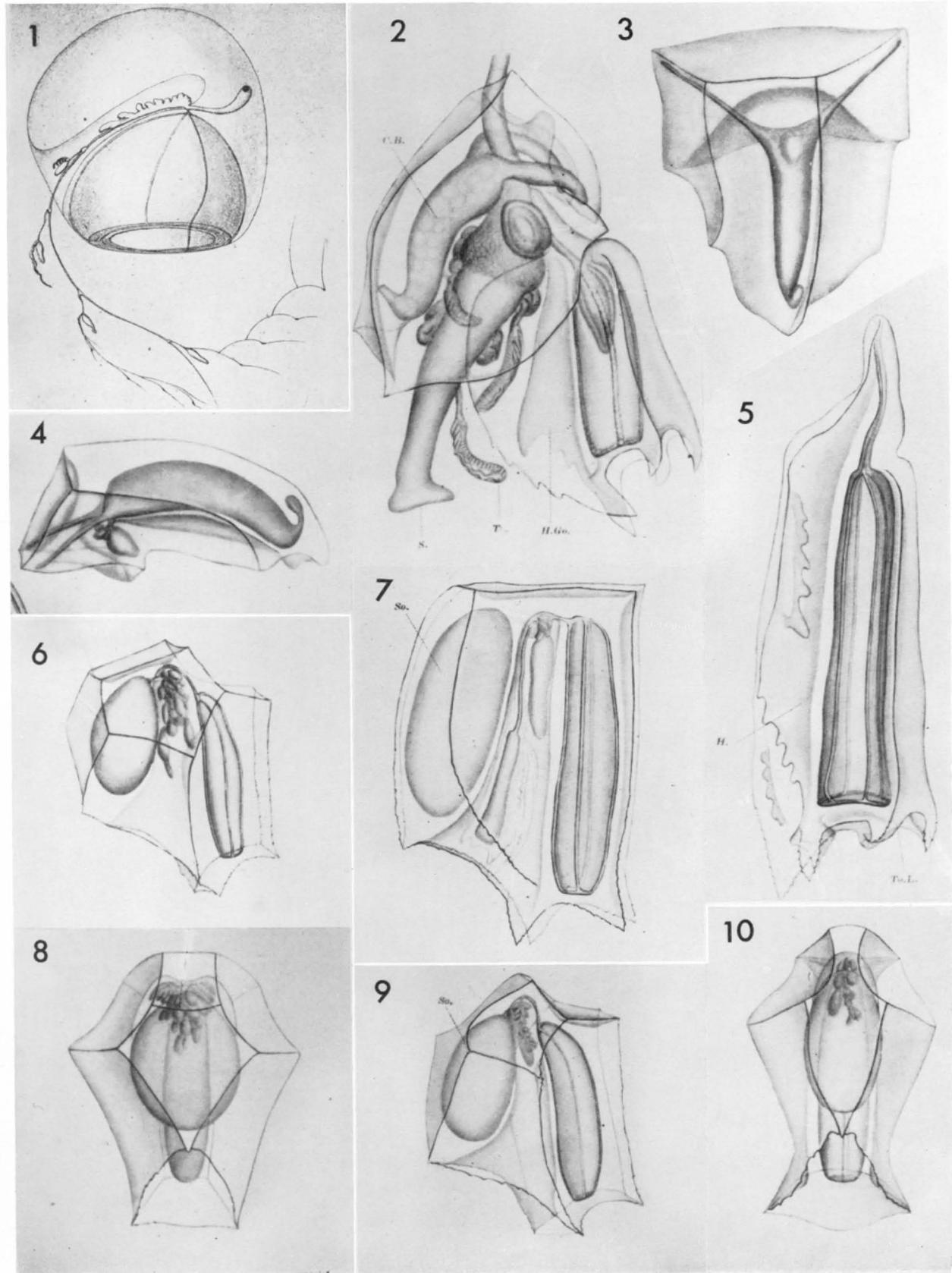
From Bigelow, 1911b, plate 13, figures 3, 4

FIG. 9. Polygastric phase, anterior nectophore, lateral view, $\times 9$.

So = somatocyst.

FIG. 10. Polygastric phase, anterior nectophore, ventral view, $\times 9$.

PLATE XXXVI

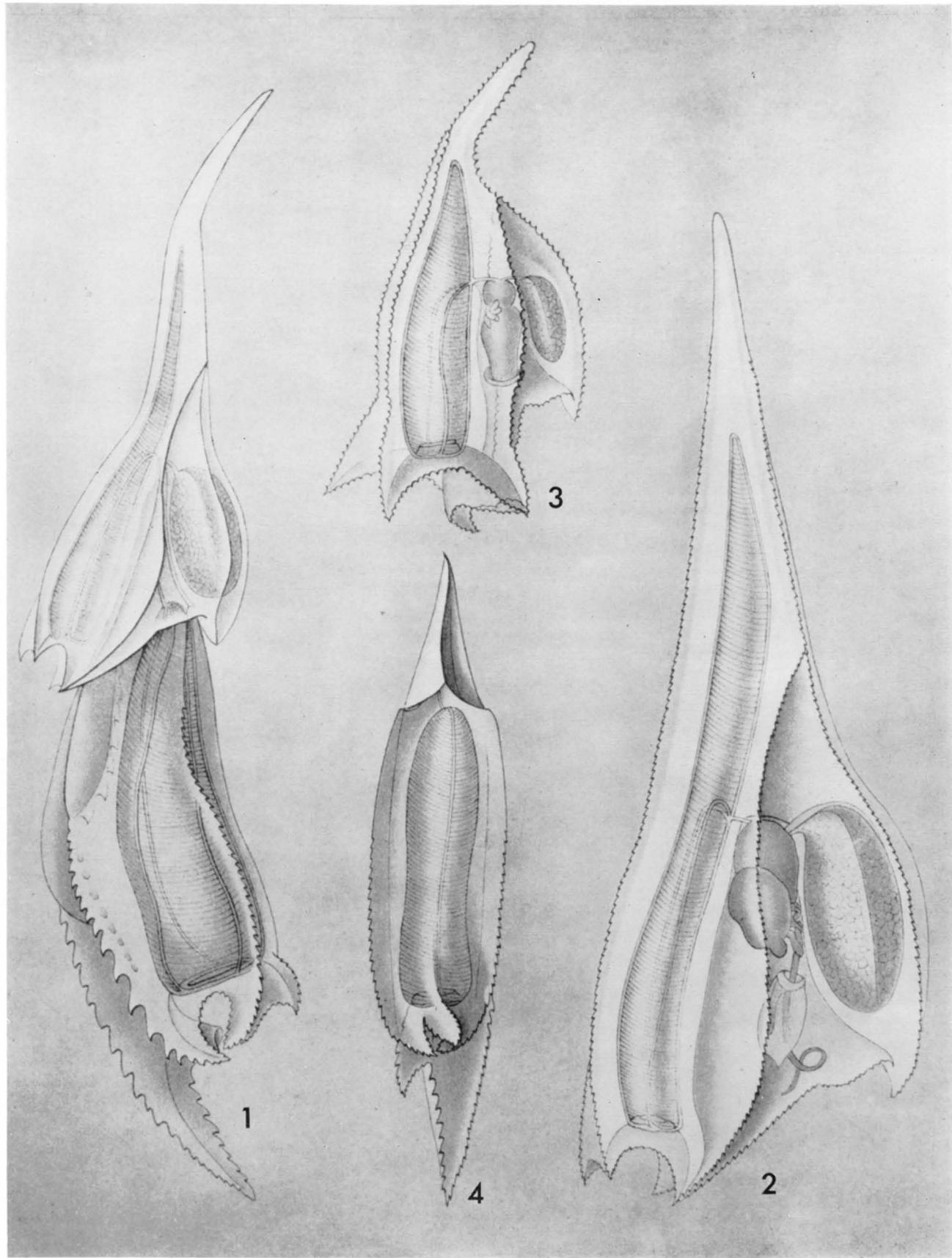


A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXXVII *Ceratocymba sagittata* Q. & G.

- FIG. 1. Polygastric phase, whole animal, $\times 3.7$.
FIG. 2. Polygastric phase, anterior nectophore, $\times 6.6$.
FIG. 3. Polygastric phase, young specimen, $\times 19$.
FIG. 4. Polygastric phase, posterior nectophore, $\times 4.2$.

PLATE XXXVII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXXVIII

Ceratocymba dentata (Bigelow) Figures 1-3
From Totton, 1954, plate 10, figures 1-3

Polygastric phase, whole animal, $\times 2$ to show the long cylindrical nectosac of the posterior nectophore and the obsolescent one of the anterior nectophore. Eudoxid groups can be seen in the hydroecium.

FIG. 1. View of the right side of the anterior nectophore and the ventro-left side of the posterior nectophore.

FIG. 2. Anterior nectophore, dorsal side; posterior nectophore, right side.

FIG. 3. Anterior nectophore, left side, posterior nectophore, ventro-right side.

Abyla bicarinata Moser. Figures 4-7
From Moser, 1925, plate 19, figures 3-6

Polygastric phase.

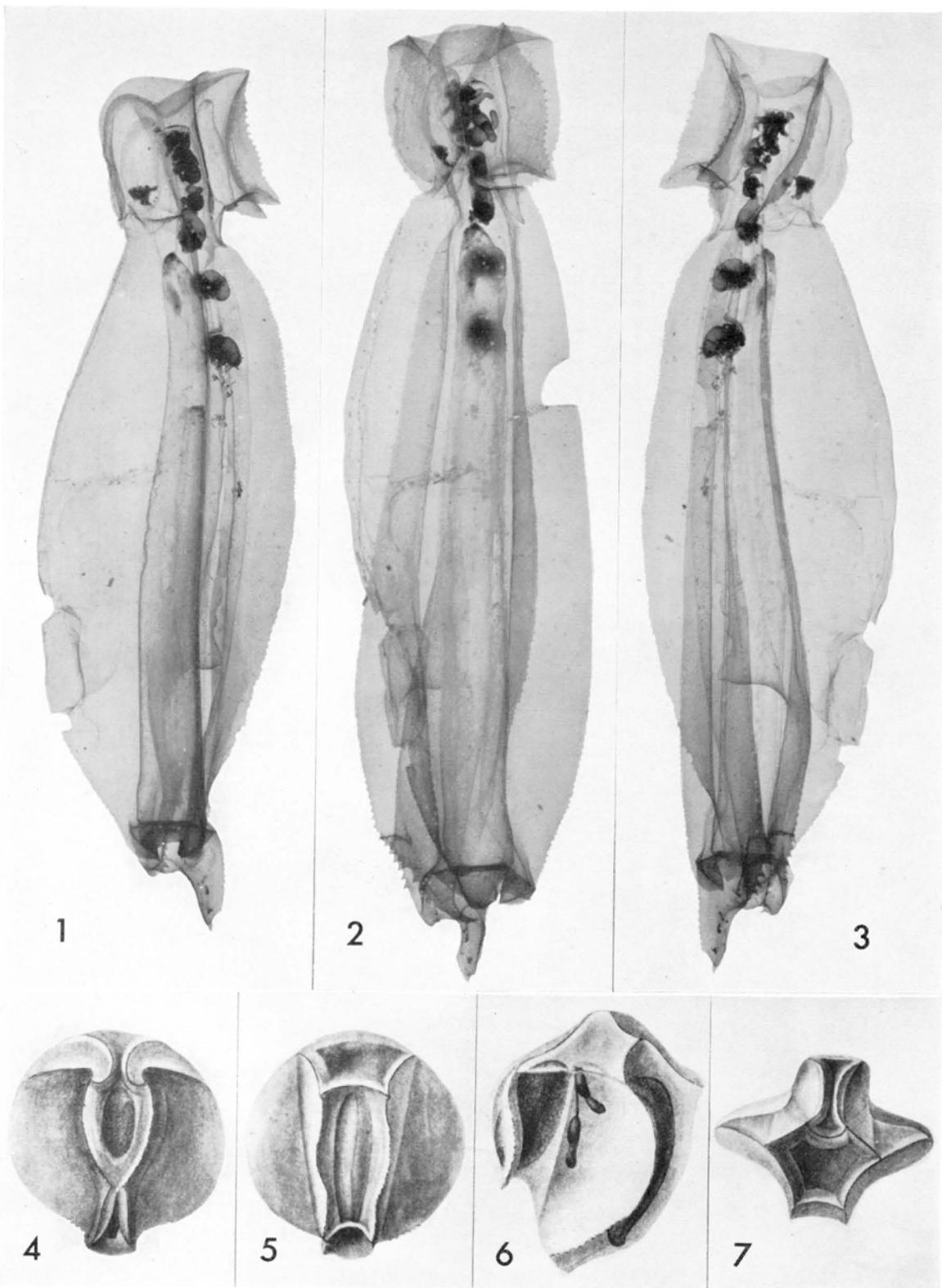
FIG. 4. Anterior nectophore, dorsal view, $\times 5.5$.

FIG. 5. Anterior nectophore, ventral view, $\times 5.5$.

FIG. 6. Anterior nectophore, oblique view of left side, $\times 5.5$.

FIG. 7. Anterior nectophore, from above, $\times 5.5$.

PLATE XXXVIII



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XXXIX *Abyla tottoni* Sears

From Totton, 1954, plate 9, figures 1-4

Polygastric phase, whole animal, $\times 4$.

FIG. 1. Apical view of the anterior nectophore with the large left hydroecial wing in the right background.

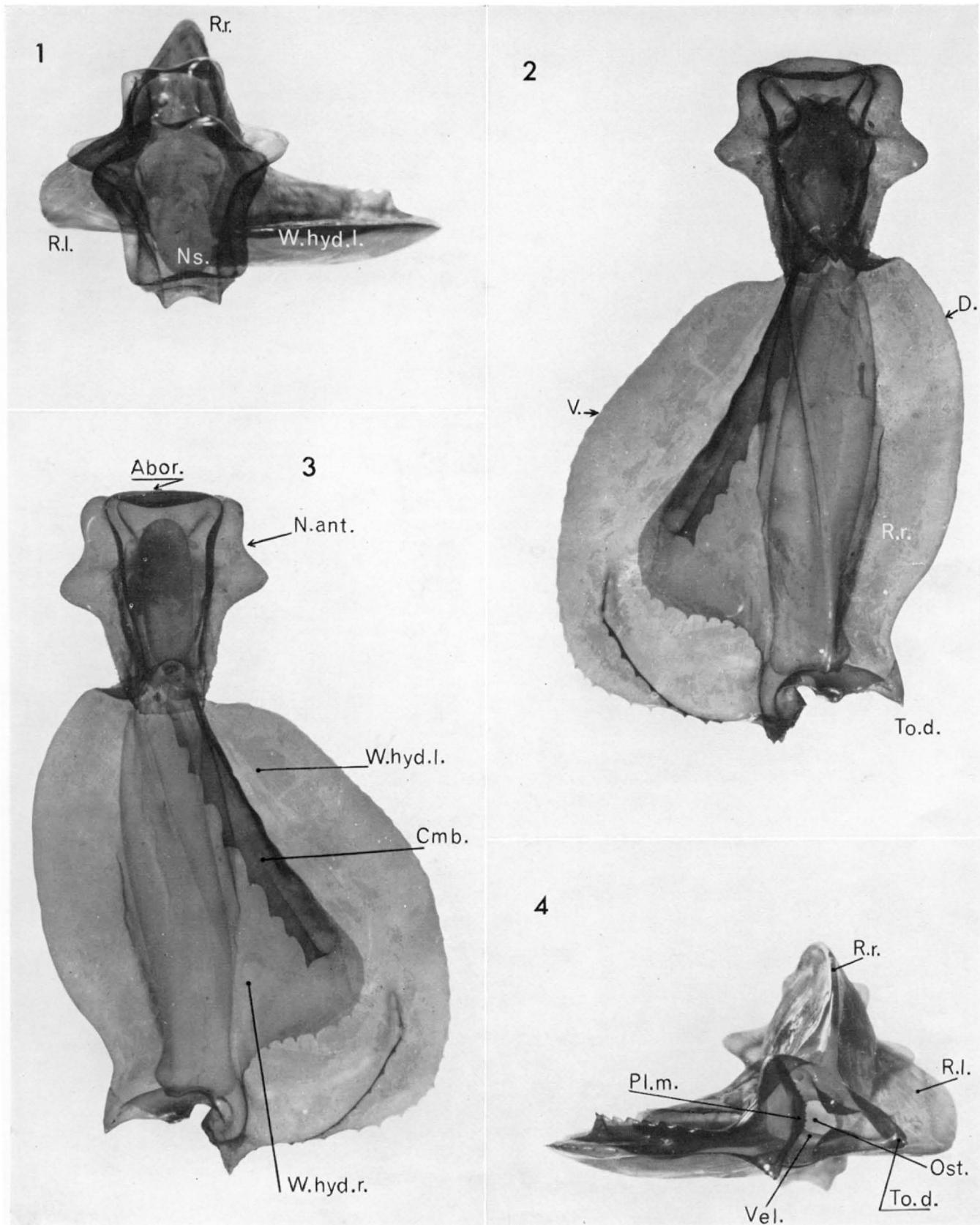
FIG. 2. Anterior nectophore, ventral side; posterior nectophore, right side.

FIG. 3. Anterior nectophore, dorsal side; posterior nectophore, left side.

FIG. 4. Ostial view.

Abor = aboral; *Cmb* = comb; *D* = dorsal; *N.ant* = anterior nectophore; *Ns* = nectosac; *Ost* = ostium; *R.r, R.l* = right and left ridge; *To.d* = dorsal tooth; *To.L* = lateral tooth; *V* = ventral; *Vel* = velum; *W.hyd.r, W.hyd.l* = right and left hydroecial wing.

PLATE XXXIX



A SYNOPSIS OF THE SIPHONOPHORA

PLATE XL

Abylopsis tetragona Otto

From Bigelow, 1911b, plate 14, figure 7; plate 15, figure 2

FIG. 1. Polygastric phase, posterior nectophore, $\times 4$.

FIG. 3. Eudoxid phase, $\times 8$.

C.d = dorsal canal; *C.l¹*, *C.l²* = radial canals; *C.v* = ventral canal; *x* = extra half canal.

Abylopsis eschscholtzi (Huxley)

From Lens & van Riemsdijk, 1908, plate 3, figure 1

FIG. 2. Polygastric phase, whole animal, $\times 15$.

From Bigelow, 1911b, plate 14, figures 1, 2

FIG. 4. Anterior nectophore, $\times 12$.

FIG. 6. Posterior nectophore, $\times 10$.

R.D = dorsal ridge; *R.L.* = left ridge (*sensu* Bigelow).

Bassia bassensis (Q. & G.)

From Bigelow, 1911b, plate 12, figure 8

FIG. 5. Eudoxid phase, $\times 12$.

C.b = bracteal canal; *Go.♂* = male gonophore; *Go.♀* = female gonophore; *S* = gastrozooid; *So* = somatocyst; *Te* = tentillum.

PLATE XL

