

FIGURE 1. *Rhodalia miranda* Haeckel, 1888. Reproduction of plate III from Haeckel's (1888b) *Challenger* monograph.
(a) Lateral view of the corm, somewhat diagrammatic. The triple corona of ectophores is interrupted in order to show the insertions of their lamellar pedicles, and the dorsal aurophore. Approximately 1.8 times natural size. (b) Dorsal view of the same corm, semidiagrammatic, showing the aurophore with its external opening, the aurostigma. For full legend see Haeckel (1888b).

BENTHIC SIPHONOPHORES:
A REVIEW OF THE FAMILY RHODALIIDAE
(SIPHONOPHORA, PHYSONECTAE)

BY P. R. PUGH

*Institute of Oceanographic Sciences (Natural Environment Research Council),
Wormley, Godalming, Surrey, GU8 5UB, U.K.*

(Communicated by N. B. Marshall, F.R.S. – Received 15 January 1982)

[Plates 1–16]

CONTENTS

	PAGE
1. INTRODUCTION	167
2. MORPHOLOGY	168
General morphology of the Physonectae	168
Morphology of the Rhodaliidae	171
Organization of the aurophore	174
3. HISTORY OF THE FAMILY RHODALIIDAE	177
The bathymetric distribution of rhodaliid siphonophores: historical	181
4. THE SYSTEMATICS OF THE FAMILY RHODALIIDAE	182
Genus: <i>Angelopsis</i> Fewkes	182
<i>A. globosa</i> Fewkes	184
<i>A. euryale</i> sp.nov.	189
Genus: <i>Stephalia</i> Haeckel	195
<i>S. corona</i> Haeckel	197
<i>S. dilata</i> (Bigelow)	207
<i>S. bathyphysa</i> (Haeckel)	211
Genus: <i>Sagamalia</i> Kawamura	215
<i>S. hinomaru</i> Kawamura	215
Genus: <i>Archangelopsis</i> Lens and van Riemsdijk	220
<i>A. typica</i> Lens and van Riemsdijk	220
Genus: <i>Rhodalia</i> Haeckel	227
<i>R. miranda</i> Haeckel	227
Genus: <i>Dromalia</i> Bigelow	238
<i>D. alexandri</i> Bigelow	238
Genus: <i>Thermopalia</i> gen.nov.	255
<i>T. taraxaca</i> sp.nov.	255
5. DISCUSSION	268
The systematics of the Rhodaliidae	268
Key to the genera and species of the family Rhodaliidae	273

The geographical and bathymetric distribution of rhodaliid siphonophores	273
The adaptations of rhodaliid siphonophores to their benthic existence	276
REFERENCES	298
GLOSSARY. LIST OF ABBREVIATIONS AND SYMBOLS USED IN CERTAIN FIGURES	300

This paper reviews the present state of our knowledge concerning a little known family of physonect siphonophores, the Rhodaliidae. The members of this family are unusual in that they are short-stemmed, with the cormidia basically arranged into spirals around the spheroidal corm, and with the nectophores forming a corona around the base of a greatly enlarged pneumatophore. Unique to these animals is the possession of a dorsal aurophore, a structure that contains the considerably expanded pneumatochone, or gas-secreting area, of the pneumatophore. These and other unusual aspects of the morphology of the rhodaliids are described and compared with those in the more typical, long-stemmed physonect siphonophore.

The history of the family Rhodaliidae is reviewed. The 37 specimens recorded in the literature, 15 of which belong to one species, originally were described under ten specific names. However, four of these names generally have been treated as synonyms of others, leaving six species within five genera. Whenever possible the extant material has been re-examined and, in addition, new specimens of five of the species have become available for study, as well as specimens of two new rhodaliid species. These studies, together with some additional information, have led to the suggestion that two of the original species, previously synonymized with another, should be resurrected as valid species, although a certain degree of intuitive reasoning is applied in one case, based mainly on differences in the geographical and bathymetric distributions of the relevant species. The systematics of the rhodaliid species is reviewed in detail and a key is provided for their identification.

Recently, observations have been made on two rhodaliid species *in situ*, and these have conclusively proven that these animals are unique among the siphonophores in that their habitat is not planktonic, as previous authors asserted, but benthic. The observations indicate that the animals float above the substratum, tethered to it, like hot-air balloons, by their tentacles. The re-adoption of a benthic existence has led to many unique features being evolved in the rhodaliids, and some of these are discussed. The extraordinary size of the pneumatophore, especially in comparison with the planktonic physonects, appears to be a necessity since the gas that it contains is required to offset the excess density of the corm and enable near-neutral buoyancy to be attained. In order that the huge volumes of gas may be secreted, sometimes at pressures exceeding 300 atm (3×10^7 Pa) the gas gland or pneumatadenia has become greatly enlarged and forms part of the peculiar structure, the aurophore. The role of both the pneumatophore and aurophore in buoyancy control is discussed in detail.

One other outstanding feature of the rhodaliid siphonophores is the possession of two types of gastrozooid on its cormidial units. Only one of these gastrozooids carries a tentilla-bearing tentacle. The arrangement is thought to be a result of the necessity to adopt a method of feeding different from the more usual fishing net set by the planktonic siphonophores. There is little doubt, therefore, that the rhodaliids are a fascinating and very unusual family of siphonophores.

1. INTRODUCTION

'The new and most interesting group of Auronectae, which is one of the most splendid discoveries of the Challenger... represents a new order which is adapted in a most remarkable manner to deep-sea life. The Auronectae differ from all other Siphonophorae in the peculiar structure of the bulbous cartilaginous trunk traversed by a peculiar network of canals, in the singular shortening of the vertical main-axis, and prolongation of the horizontal transverse axis. Upon this vertical depression of the trunk depends the peculiar development of the densely crowded cormidia. But the most striking peculiarity is the extraordinary development of the swimming apparatus, the voluminous pneumatophore, the powerful horizontal corona of radially expanded nectophores, and particularly the singular aurophore, wanting in all other Siphonophorae, and acting probably as an important gas-secreting gland or a pneumadenia. All these striking characters together make it very probable that the Auronectae are permanent deep-sea Siphonophorae, which may move up and down within certain limits of depth, but never come to the surface.' (Haeckel 1888b, p. 304)

The enthusiasm with which Haeckel (1888b) greeted the discovery of this peculiar group, the so-called Auronectae, has been passed on to most of the subsequent workers in this sphere of siphonophore studies. The extraordinary organization of these animals, particularly with regard to the enlarged pneumatophore and the extreme development of its gas-secreting area to form the aurophore, has given rise to much discussion as to their origins and mode of life. However, many of the statements, not least those made by Haeckel (1888b), are highly speculative, and the group remains little known and little understood. None the less, the beautiful illustrations of these animals that Haeckel provided in his *Challenger* monograph on the Siphonophorae (see, for example, figure 1, plate 1), frequently have been used in general textbooks on invertebrate zoology to demonstrate the complexity of organization of siphonophores, although not necessarily drawing any attention to the many unique features of these particular animals.

Haeckel (1888b) devoted a significant part of his *Challenger* monograph to describing his auronectid specimens. He placed emphasis on explaining their development and organization on the basis of his Medusome Theory, which suggests that all the parts of a physonect, except the tentacles, are dissociated parts of a medusa or secondarily budded medusae. Thus, he suggested (p. 283) that the aurophore was 'the modified umbrella of a medusome, or a peculiar medusoid person, which was originally a modified nectophore'. Subsequent authors, and indeed Haeckel himself in another part of his text, came to the conclusion that the aurophore was not such a 'singular' structure but was the true homologue of the gas-secreting area of the pneumatophore in physonect siphonophores. Consequently, the status of this group of animals has been reduced from that of an order, the Auronectae, to that of a family, the Rhodaliidae, within the suborder Physonectae of the order Siphonophora.

There are few parts of Haeckel's Medusome Theory that are considered now to have any validity, and Claus (1889) was one of many who criticized it severely. Another of Haeckel's assertions which provoked criticism from at least one other person was that which said that the auronectid (rhodaliid) siphonophores were 'one of the most splendid discoveries of the Challenger'. While it is true that the first known rhodaliid siphonophore was collected by H.M.S. *Challenger* in 1874, the first published description of one was given by Fewkes in 1886, from material

collected in 1883 by the U.S. Fish Commission Steamer *Albatross*. This fact was pointed out in no uncertain terms by Fewkes (1889). However, it is interesting to note that the *Challenger* and the *Albatross* have collected between them the majority of all the rhodaliid siphonophores that have been described, a total of 27 specimens. Until recently, there were records in the literature for only ten other specimens, and all but one of these had been collected before 1908. This absence of rhodaliid material in more recent collections probably is a reflection of the diversification of interests in biological oceanography. It is of particular significance when one considers the type of sampling programme carried out during the great expeditions of the late nineteenth and early twentieth centuries, and that of later expeditions. Currie (1972) reviewed the new developments in plankton research based on the work of Hensen which resulted in intensive investigations of the pelagic ecosystem, while studies on the benthos declined somewhat. Nevertheless the earlier expeditions had served to establish a supposed certainty as to which animals were planktonic and which were benthic, so that animals that were thought to be planktonic might have been rejected as contaminants if they had appeared in an open benthic net collection. Haeckel (1888b) conjectured that the rhodaliid siphonophores were bathypelagic organisms, but his arguments, especially with regard to the fact that they possessed a relatively enormous pneumatophore, were used by others to reach the opposite conclusion that a near-surface habitat was more likely. The discovery by Lens & van Riemsdijk (1908) of specimens at relatively shallow depths added fuel to this latter argument, but it transpires that rhodaliids inhabit neither the bathypelagic nor the neustonic zones of the oceans. Direct observations made from submersibles have enabled the actual depth distribution and habitat of some of these animals to be elucidated, and have proved that their mode of life is unique among siphonophores.

Our meagre knowledge of the rhodaliid siphonophores has been enhanced considerably, not only by these observations of the animals *in situ*, but by the collection of a considerable quantity of new material, of which over 40 specimens belonging to five rhodaliid species have been examined by the present author. In this paper it is intended to review the original descriptions of all rhodaliid species and, wherever possible, to enhance these with the information gleaned from a study of the new material. The taxonomic status of the species will be considered and the adaptations of these creatures to their unique mode of life will be discussed. First, however, it is appropriate to describe, in general terms, the morphology of a typical, pelagic physonect siphonophore so that the modifications that the rhodaliids have undergone can be better appreciated.

2. MORPHOLOGY

General morphology of the Physonectae

All physonect siphonophores possess an apical (aboral), gas-filled float or pneumatophore (figure 2a, b). The pneumatophore is formed by an invagination of the superficial cell layers at the apical pole of the physonect larva. It does not have a medusoid origin as was supposed by several early researchers, including Haeckel (1888a). The two-walled structure that results has its central, gas-filled cavity lined by ectoderm. The endoderm of the outer wall (pneumato-codon) becomes separated from that of the inner wall (pneumatosaccus) by the pericystic cavity, which is in communication with the main gastrovascular system of the animal (figure 2b). The pneumatophores of some physonect species possess a pore situated either apically, as in *Nanomia bijuga* (Chiaje, 1841), or basally, as in *Physophora hydrostatica* Forskål, 1775. These pores

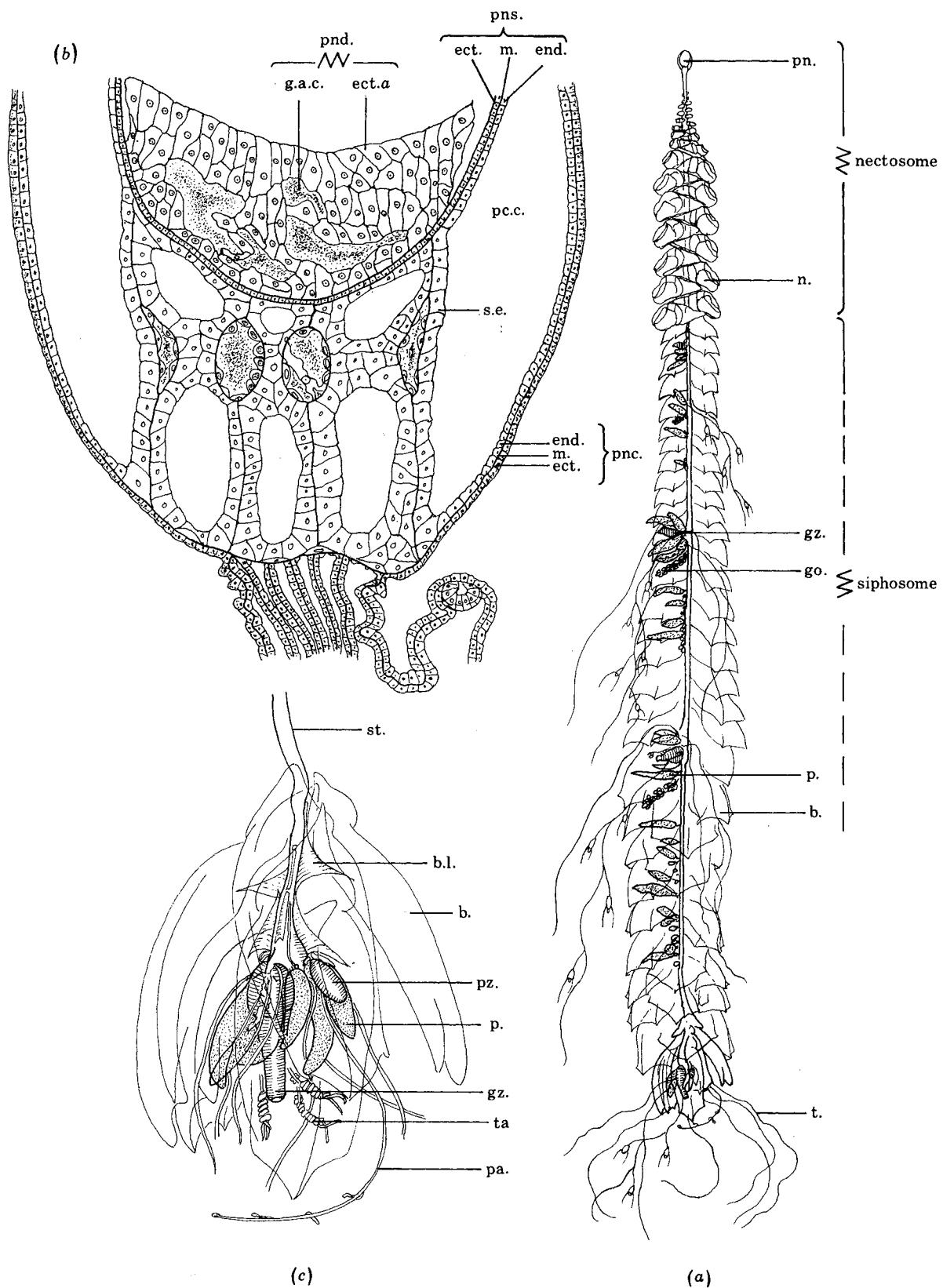


FIGURE 2. General morphology of a long-stemmed physonect siphonophore. (a) *Agalma elegans* (Sars). Whole animal, showing the apical pneumatophore, nectosome and siphosome. (Magn. $\times 1.8$.) (b) *Nanomia bijuga* (Chiaje, 1841). Parasagittal section of the basal part of the pneumatophore, showing the main cell layers, the gas gland and the endodermal septa. (Magn. \times ca. 120.) (c) *A. elegans*. Detail of the distal end of the siphosome, showing the protozooid and first definitive gastrozooid. (Magn. $\times 7$.) (a) and (c) are redrawn from the frontispiece of Totton (1954), and (b) is redrawn from Carré (1969, fig. 7 b). A list of abbreviations used in the figure is given in the Glossary.

may be used to vent excess gas, and the importance of such a role will be returned to later (see p. 278). However, it should be noted that there is some doubt as to whether there is a direct connection between the gas cavity and the exterior, via the basal pore, in *P. hydrostatica*. None the less, the ability to control the volume and pressure of gas in the pneumatophore may be of great importance not only to those physonects that undertake diurnal vertical migrations, but also to the rhodaliids, whose mode of life requires that they have an efficient means of buoyancy control.

The gas in the pneumatophore, which contains an unusually high percentage of carbon monoxide (see, for example, Pickwell *et al.* 1964), is secreted by a specialized, basal part of the pneumatosaccus called the pneumadenia or gas gland (figure 2*b*). The gas gland is formed by a massive, secondary development of the ectodermal cells, which spread, internally, over the basal part of the chitinous lining (pneumatocyst) to the gas cavity (see figure 4). Carré (1969) describes how, in *Nanomia bijuga*, the endodermal layer of the pneumatosaccus in this region also becomes highly developed and produces septa that traverse the pericystic cavity and unite with the endoderm of the pneumatocodon (figure 2*b*). These septa are well developed in the rhodaliid aurophores, as is the gas gland which, together with the chitinous layer surrounding it, forms an enlarged pneumatochone (figure 4*b*).

Beneath the pneumatophore physonect siphonophores usually possess two distinct regions arranged one above the other on a long stem. The more apical region, the nectosome, carries the asexual (medusoid) nectophores or swimming bells, while the polyps and sexual medusoids arise on the basal siphosome (figure 2*a*). The constituent parts of these two regions are budded off respectively from two zones of proliferation which originally arise, in most physonect larvae, on opposite sides of the pneumatophore (Totton 1965). However, as development proceeds they become separated from one another as the two distinct regions of the stem are differentiated. Immediately below the pneumatophore, in the mature animal, lies the ventral budding zone of the nectophores. These swimming bells are displaced basad as new buds appear, so that the oldest are at the oral end of the nectosomal region (figure 2*a*). The structure of the nectophores is usually a good systematic character in physonect siphonophores.

A zone of minimum growth (figure 2*a*) separates the nectosomal region from the siphosome, and the budding zone of the latter lies immediately below this. In the long-stemmed physonects the siphosome consists of a long, narrow tube, enclosing the gastrovascular canal, and from the walls of which, on the ventral side, arise the polypoid and medusoid structures. The main trunk can stretch out to many metres in length. The constituent bodies of the siphosome are grouped together into cormidia, with the original, larval cormidium terminating the siphosome at its basal or oral end. Each cormidium usually is comprised of a gastrozooid, with a tentacle, a variable number of bracts and palpons, and the gonodendra which bear the male and/or female sexual bodies or gonophores (figure 2*a, c*). Many physonect siphonophores are monoecious, in that the gonophores of both sexes are developed on the same stem, while others are protandrous and a few are known to be dioecious. With regard to the polypoid structures, Totton (1965) considered that the palpons were reduced gastrozooids, and often they carry reduced tentacles or palpacles. The palpons most probably have an excretory function, but may also have a sensory one, as they are often referred to as feelers or tasters. The bracts surround the stem of the siphosome and primarily have a protective function, in that the other cormidal elements can be retracted beneath them. In addition they can contain large volumes of mesogloea and, thereby, may effect the major role in the buoyancy control of the animal.

Jacobs (1962) has shown that the removal of the pneumatophore in some physonect species has little effect on their specific gravity, merely causing a slight change in the orientation of the animal. In the genus *Athorybia* Eschscholtz, 1829, nectophores are not developed and a limited means of propulsion is provided by the coordinated movement of the bracts.

Not all the physonect siphonophores are long-stemmed, and in three of the seven families a shortening, or failure to lengthen, of either/both the nectosome or/and siphosome has occurred. In *Physophora hydrostatica*, the only representative of the family Physophoridae, the siphosome has hypertrophied to form a bag-like structure around which the cormidia are arranged. Garstang (1946) suggested that the siphosomal arrangement in the rhodaliids arose in a similar but more highly developed manner. In another family, the Athorybiidae, several divergences from the more typical physonect pattern have taken place. The siphosome, in *Melophysa melo* (Quoy et Gaimard, 1827) and *Athorybia rosacea* (Forskål, 1775), has the appearance of a hypertrophied nectostyle, the area of the attachment of the larval bract. The nectosome is reduced or absent so that *M. melo* probably carries only a single functional nectophore, while in the genus *Athorybia* nectophores are absent. Whereas in *A. rosacea* the siphosome is hypertrophied, in *A. lucida* Biggs, 1978 it has elongated in a horizontal plane, with the pneumatophore remaining central. Initially it had been supposed that the zone of proliferation for the cormidia lay in the centre of the sac-like siphosome which would result in the cormidia being budded off in two directions, which is similar to the mode of formation of the nectosome in the rhodaliids. However, on close examination it was found that the zone lay at one end of the siphosome and thus that the cormidia were budded off in only one direction. None the less, many of the unusual features in the organization of the rhodaliid siphonophores are paralleled to some extent in other physonects, and further instances will be considered in the following section, where the general morphology of the rhodaliids is described.

Morphology of the Rhodaliidae

The unusual organization of the rhodaliid siphonophores can be seen in Haeckel's (1888b) figures of *Rhodalia miranda* Haeckel, 1888, two of which are reproduced in figure 1. The whole structure is compressed so that the nectosome and siphosome form a globular corm below the pneumatophore. The pneumatophore is greatly enlarged as compared with other physonects, although that of *Athorybia rosacea* appears relatively large owing to the reduction in the siphosome and the absence of a nectosome. The enormous pneumatophore of the pleustonic, cystonect siphonophore, *Physalia physalis* (L., 1758), the Portuguese Man O'War, clearly gives positive buoyancy to the animal and enables it to maintain its position on the sea surface. Similarly the pneumatophore of the rhodaliid confers some degree of positive buoyancy on the animal but, as is discussed later (p. 182), the mode of life is entirely different. Although *Physalia* has a relatively large gas-secreting area, in the rhodaliids this region is greatly developed and projects out from the pneumatophore, on the dorsal side in the nectosomal region, to form the characteristic structure, the aurophore (figure 4a, b). Details of the organization of the aurophore are given in the next section.

The nectosomal region in rhodaliid siphonophores surrounds and extends below the pneumatophore in such a way that the nectophores are arranged to form a corona, except that immediately below the dorsal aurophore there is a naked zone (figure 1b). The oldest nectophores lie on either side of this, while the youngest are budded off on the ventral side of the nectosome. The nectophores are relatively simple and sac-like, having no pronounced ridges,

and, with their arrangement in a circle, might be suggested to have a feeble locomotive ability, although Haeckel (1888b) conjectured the opposite. Haeckel also believed that, by their mutual compression, the nectophores in some species were arranged into a double or multiple corona. He used this feature as a systematic character and its validity as such will be returned to when the descriptions of his species are considered in detail.

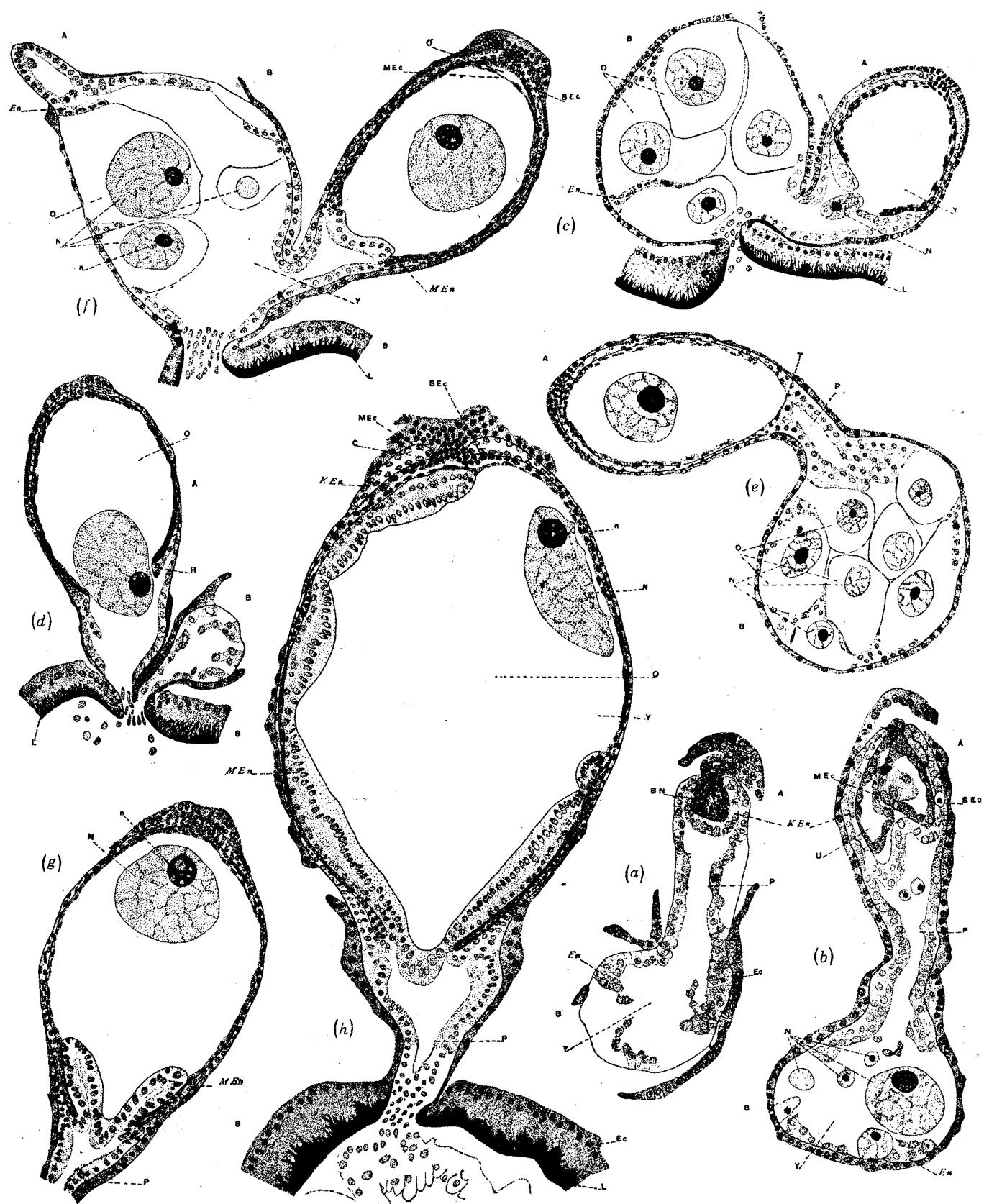
The budding zone for the nectophores, and that for the siphosomal cormidia, lies apically on the ventral side of the nectosome, that is on the opposite side to the aurophore. The two zones of proliferation do not become separated as in most other physonects but remain in close apposition. The nectophores are budded off in two directions, so as to give rise to the corona, but it is not clear whether their budding zone has become split into two entirely separate parts or whether the newly formed nectophores move away from a single site in alternate directions. The zones of proliferation in *Dromalia alexandri* Bigelow, 1911 are illustrated beautifully by Bigelow (1911, pl. 24, figs 1–3; as reproduced in figure 25a–c). Bigelow describes the presence of a well marked ridge or blastocrene in this region, on which the young appendages are born. The young nectophores lie on either side of this ridge, while directly below is a single row of young cormidia.

The young cormidia are carried basally down the ventral side of the nectosome and, on reaching the siphosomal region, usually become arranged into spiral whorls on the surface of the corm. Garstang (1946) asserted that the rhodaliid corm developed in a similar fashion to the inflated siphosome of *Physophora hydrostatica*, but the rigid and broad connection between the nectosome and siphosome in some rhodaliids is difficult to reconcile with this interpretation. The mode of formation of the rhodaliid corm will be discussed later, after the structure of the individual species has been discussed, and attention will also be drawn to the fact that there are exceptions to the basic spiral arrangement of the cormidia.

The cormidia themselves normally are carried on gelatinous protuberances and the typical constituent parts, i.e. gastrozooid with tentacle, bract and gonodendra, are present. The specific characters of the various organs are described later, but a general description of the development of the female gonophores will be given here. Haeckel (1888b) described the animals as monoecious, although he devoted only a few lines to a description of the androphores or male gonophores, which compared markedly with his detailed account of the structure and development of the female gonophores or gynophores. However, Brooks & Conklin (1891), while studying the development of the female gonophores in another rhodaliid specimen, concluded that the animals were dioecious and that Haeckel had mistaken for androphores some long, spindle-shaped gynophores. They criticized Haeckel's assertion that there were two basic types of female gonophore, both of which were stated to be medusoid in origin, and showed that the so-called 'Polyovone gynophores', which contained a variable number of developing ova, were merely pouches from the gonodendral stem, and, thereby, were not

DESCRIPTION OF PLATE 2

FIGURE 3. Stages in the development of the female gonophore of a rhodaliid siphonophore. Longitudinal sections, magn. \times ca. 250. This plate is reproduced from Brooks & Conklin (1891) and bears the original annotations, which are: A, gonophore; B, egg pouch; BN, bell nucleus; C, circular canal; Ec, ectoderm; En, endoderm; K En, cathamal endoderm; L, supporting lamella; M Ec, manubrial ectoderm; M En, manubrial endoderm; N, egg nucleus; n, nucleolus; O, ova; P, pedicel; R, rupture of endoderm and lamella; S, stem or gonostyle; S Ec, subumbrella ectoderm; T, reunion of ruptured endoderm and lamella; U, umbrella cavity; Y, yolk.



Conklin, del.

FIGURE 3. For description see opposite.

(Facing p. 172)

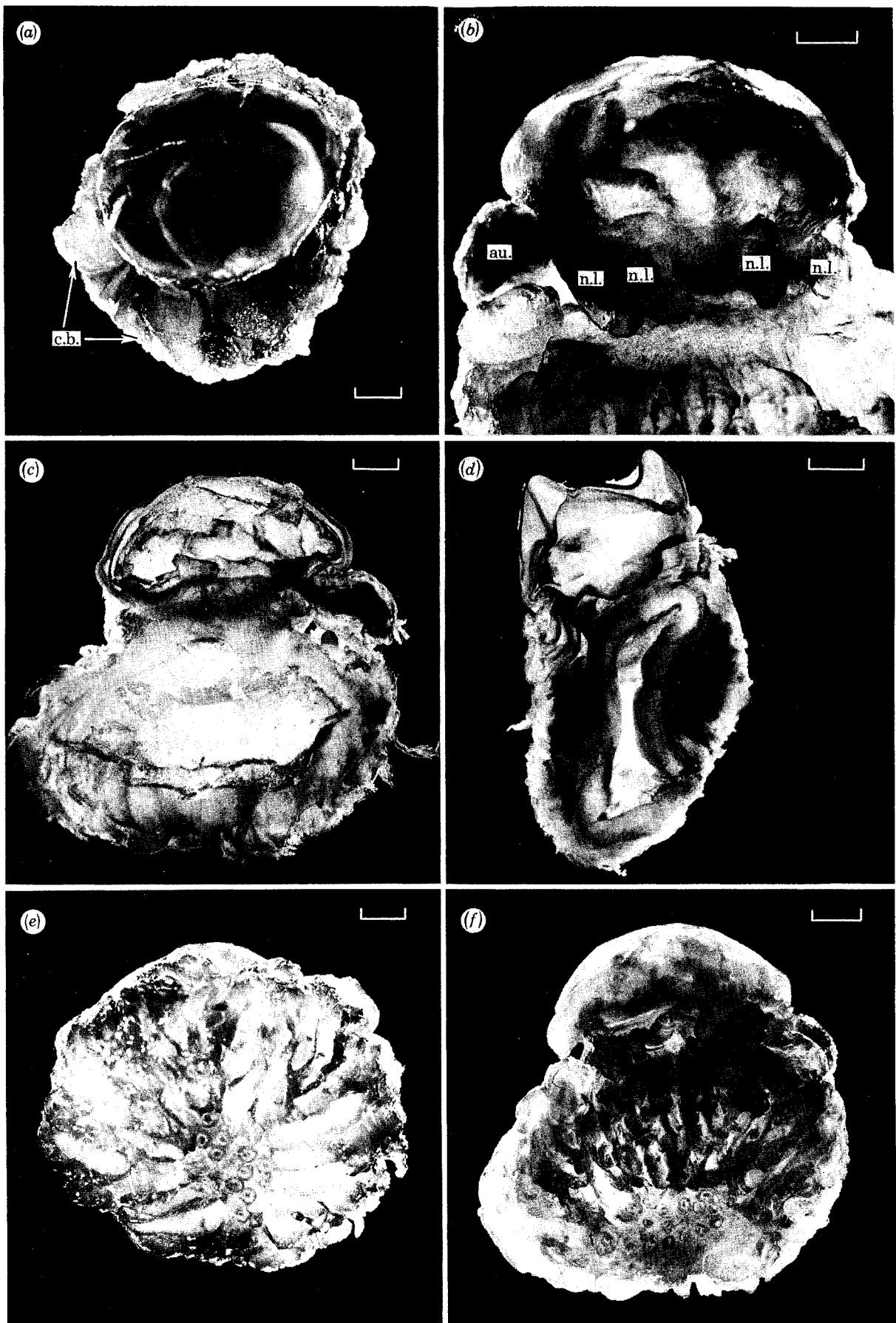
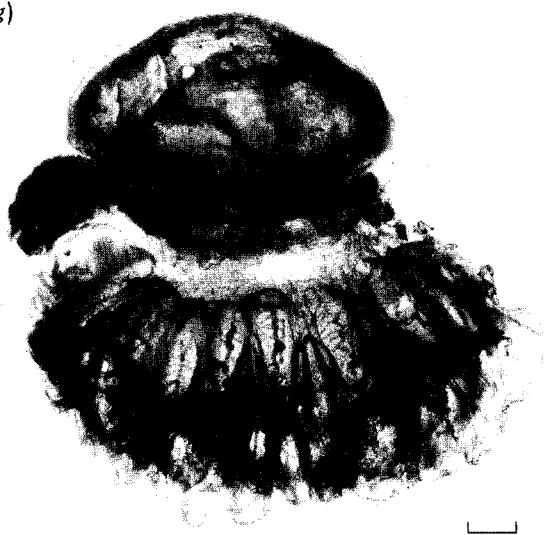


FIGURE 6*a-f*. For description see opposite.

(g)



(h)

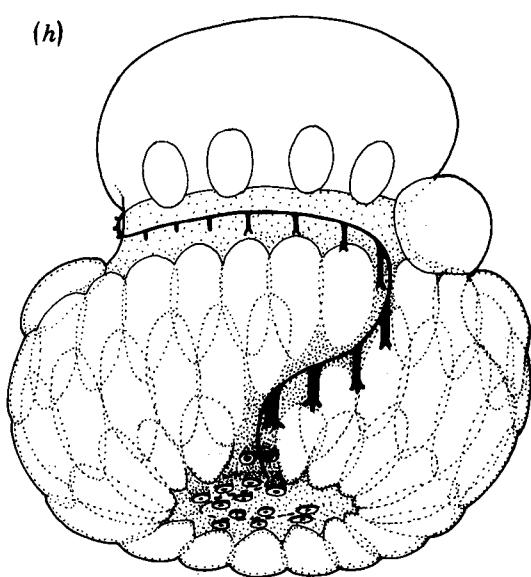


FIGURE 6. *Angelopsis euryale* sp.nov. (a) Apical view of specimen 1. Note the two pyriform cormidial bases (c.b.). (b) Side view of the apical part of specimen 2. Note the absence of a series of young cormidial bases in the gap below the four large nectophoral lamellae (n.l.), and the enlarged cormidial base below the aurophore (au.). (c) Sagittal section through specimen 2, showing the elongated aurophore and the large siphosomal cavity. (d) Sagittal section through specimen 3, with the distorted pneumatophore. (e) Base of the corm of specimen 1, showing the paired series of holes believed to be the scars left after the detachment of some type I gastrozooids. (f) Side and basal view of specimen 2, showing the series of scars. (g) Side view of the other half of specimen 2. (h) Diagram showing the arrangement of the series of young cormidial units on the side of specimen 1, from their origin in the zone of proliferation to the point where they connect up with the biserial arrangement of scars on the base of the corm. See text for details. Scale bars, 2 mm.



FIGURE 7. For description see page 173.

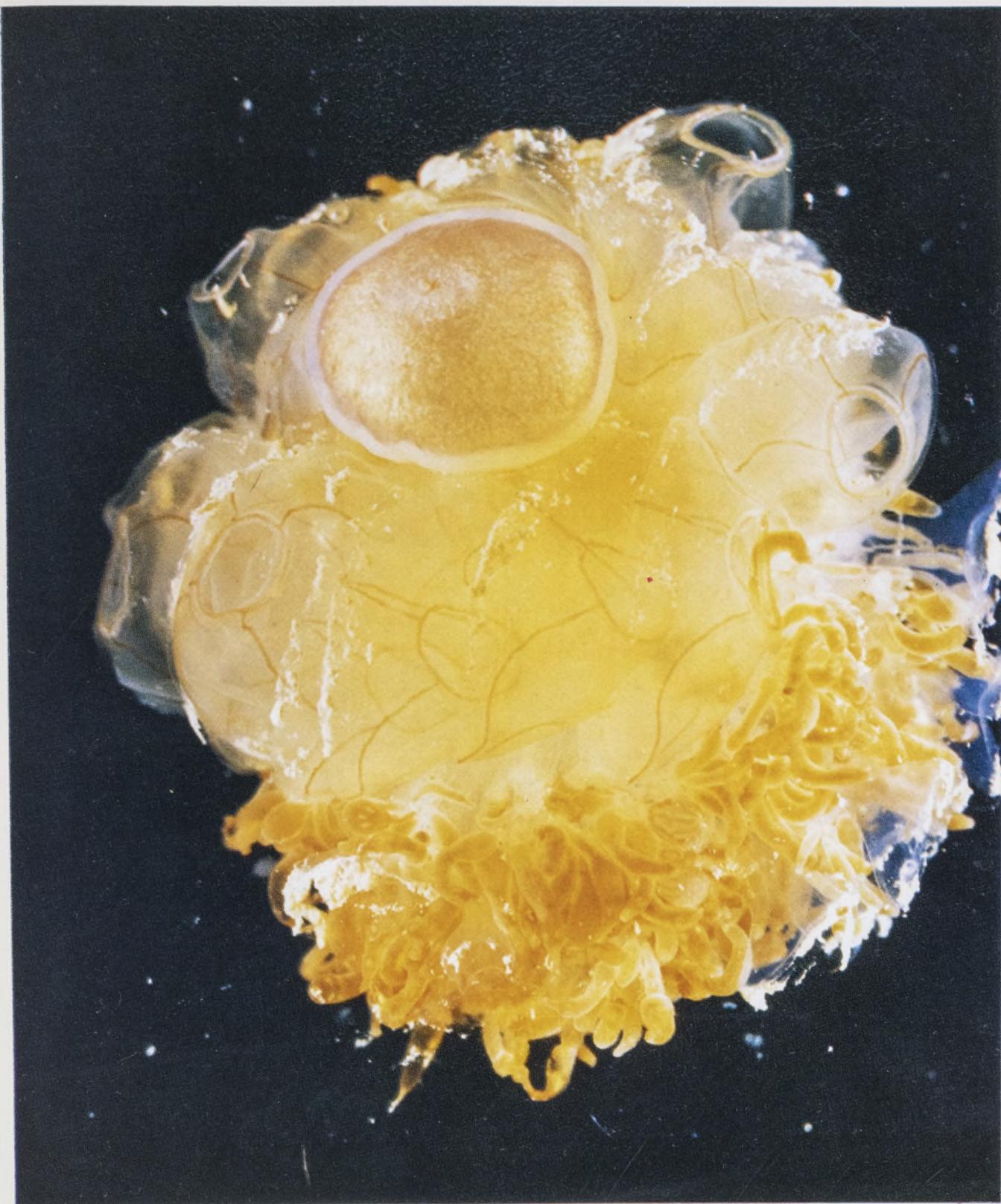


FIGURE 8. For description see page 173.

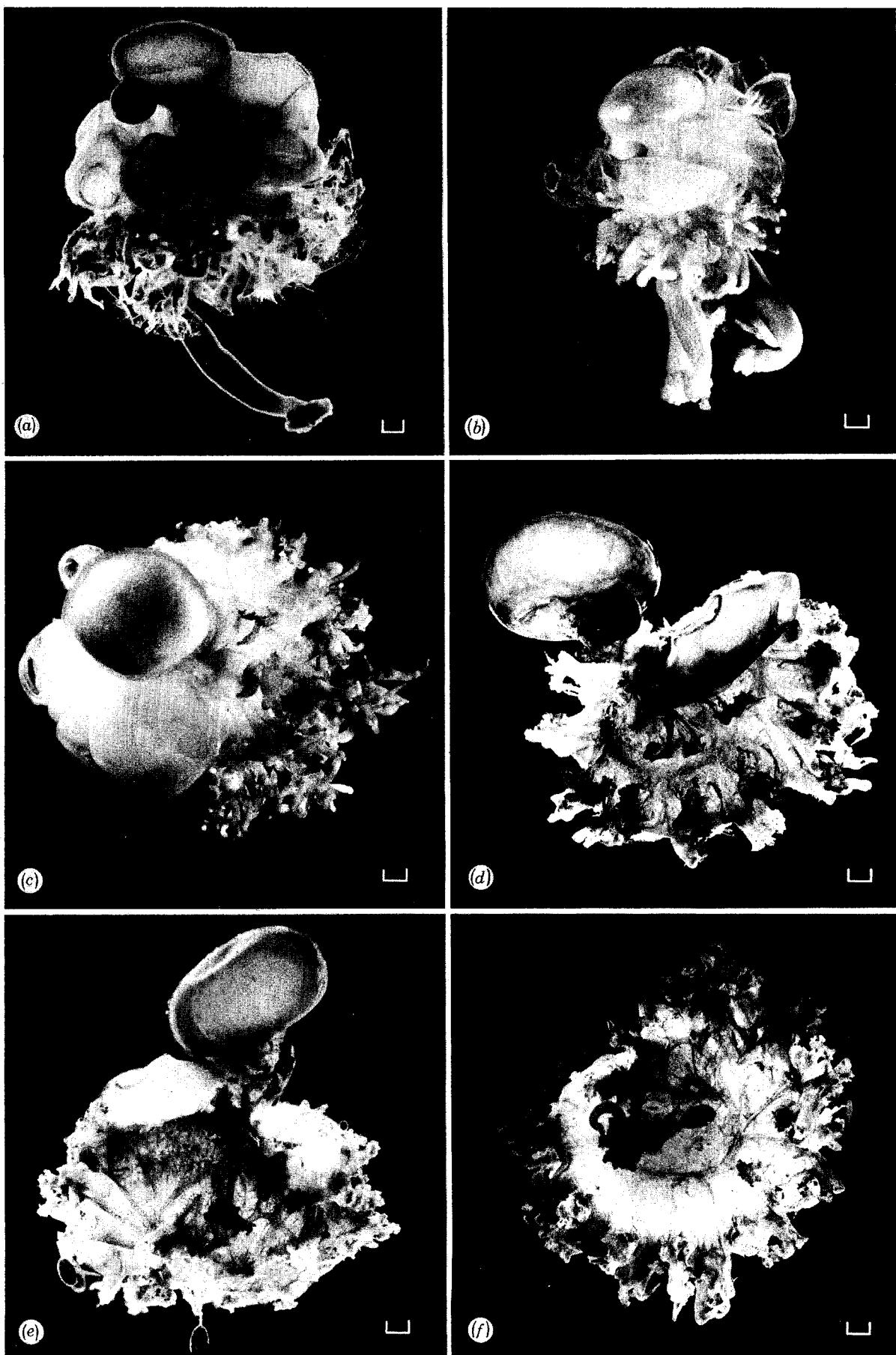
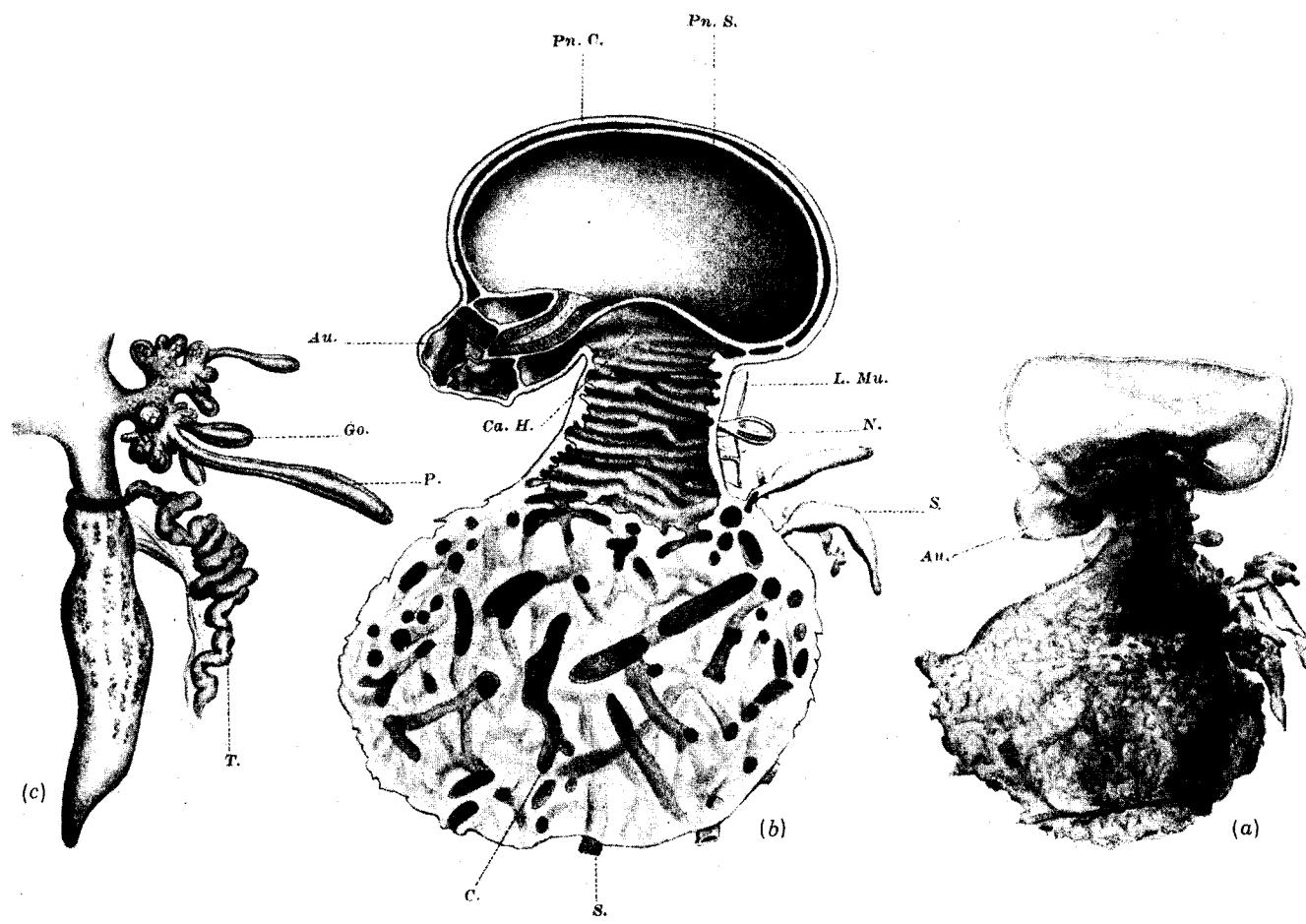
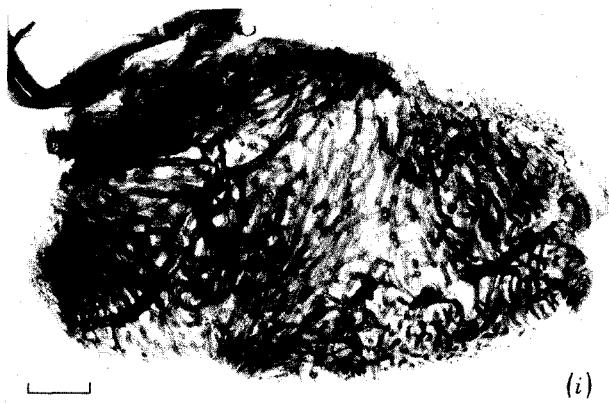
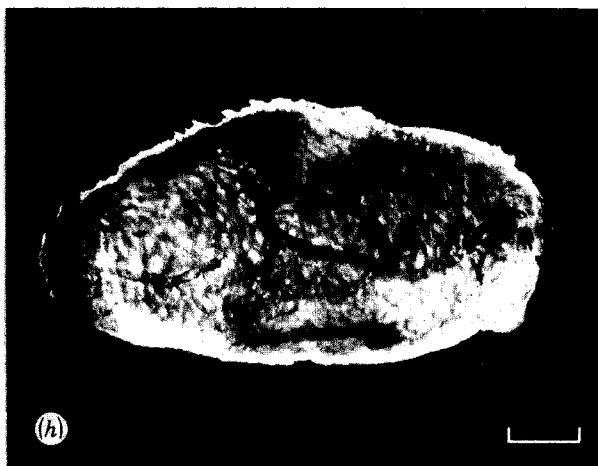


FIGURE 9*a-f*. For description see page 173.



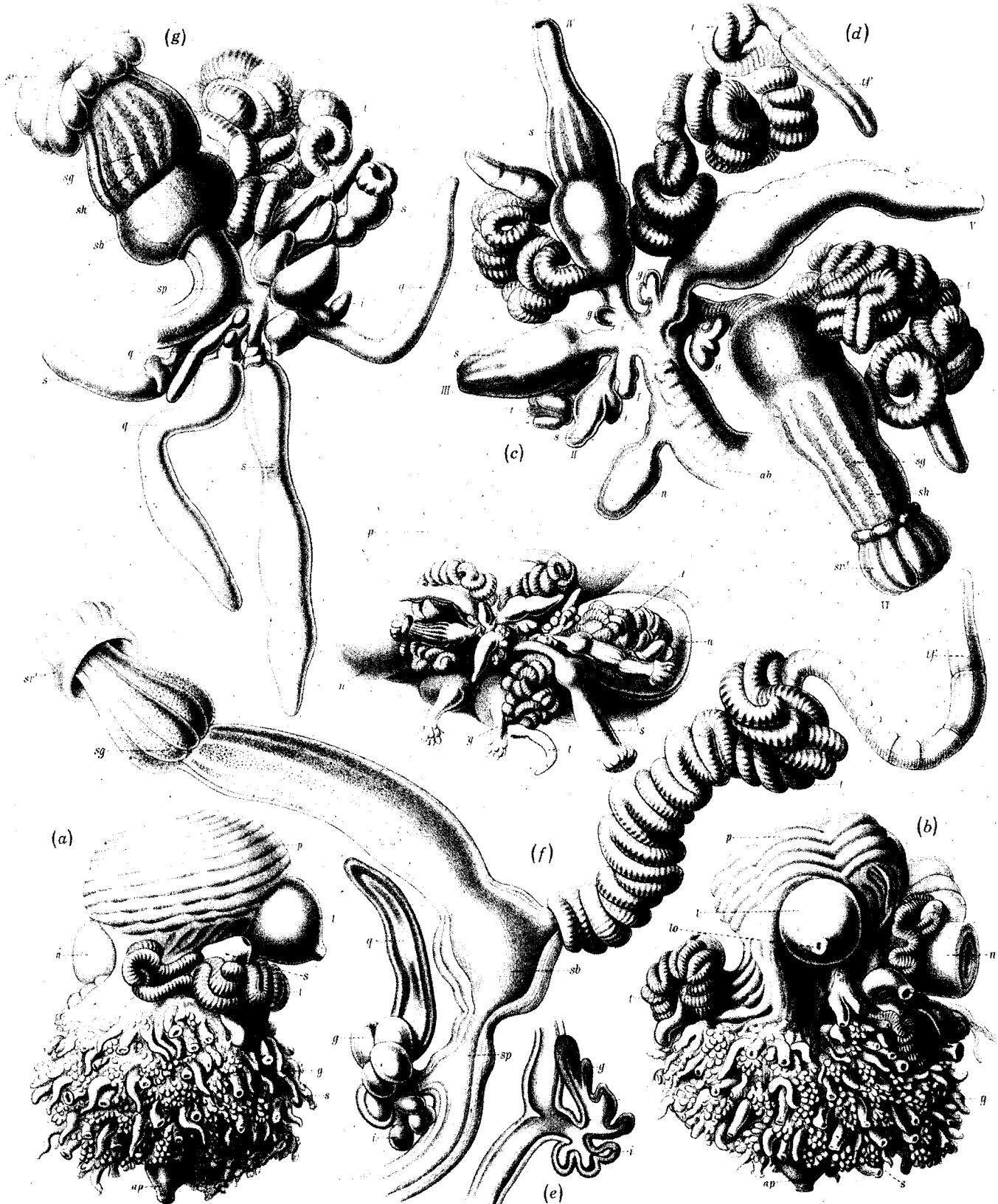


FIGURE 14. For description see opposite.

DESCRIPTION OF PLATE 5

FIGURE 7. *Stephalia corona* Haeckel (a-f) and *Rhodalia miranda* Haeckel (g-h and ?i-l). A reproduction of Haeckel's (1888b) plate vii (figs 39-50). Reference should be made to the *Challenger* monograph for the complete legend and the glossary of terms used. Note that the figures are not referred to here in the same order as they appear on the original plate. The original figure numbering is given in square brackets in the following description.

Stephalia corona. (a) [Fig. 39.] Lateral view of a young specimen, showing the aurophore (l) with a distinct pore (lo). (Magn. $\times 10$.) (b) [Fig. 40.] Sagittal section through the same corm. Note the axial canal (ca), with numerous anastomizing branches (ac). (Magn. $\times 10$.) (c) [Fig. 41.] The distal part of another specimen, showing the mouth opening (ao) of the protozooid (ap). (Magn. $\times 20$.) (d) [Fig. 48.] Lateral view of a further specimen. (Magn. $\times 5$.) (e) [Fig. 49.] A single cormidium with its siphon (s) and gonodendron (ga), supposedly bearing both female (f) and male (h) gonophores. (Magn. $\times 50$.) (f) [Fig. 50.] A section through the auronula larva, showing the protozooid and its tentacle (td), which apparently is attached dorsally in the region of the aurophore. (Magn. $\times 10$.)

Rhodalia miranda. (g) [Fig. 42.] A gastrozooid with the proximal part of its tentacle. Note the four regions of the gastrozooid; proboscis (sr), stomach (sg), basigaster (sb) and pedicle (sp). (Magn. $\times 10$.) (h) [Fig. 46.] (?) A mature male gonophore. (Magn. $\times 50$.) (i) [Fig. 43.] An undischarged (A) and discharged (B) ensiform nematocyst. (Magn. $\times 400$.) (j) [Fig. 44.] Nectophoral bud in longitudinal section (Magn. $\times 100$.) (k) [Fig. 45.] Nectophoral bud in transverse section. (Magn. $\times 100$.) (l) [Fig. 47.] The muscle epithelium on the outside of the pneumatophore. (Magn. $\times 300$.)

DESCRIPTION OF PLATE 6

FIGURE 8. *Stephalia corona* Haeckel. One of the specimens collected at *Discovery* st. 7846, shortly after it had been brought to the surface. (Magn. $\times ca. 8$.) The plate is reproduced by kind permission of Mr P. M. David.

DESCRIPTION OF PLATES 7 AND 8

FIGURE 9. *Stephalia corona* Haeckel. (a) Lateral view of specimen (no. 1) from *Discovery* st. 7853. Note: the extensive attachment of the aurophore to the pneumatophore; and the single, large type I gastrozooid. (b) Lateral view of another specimen (no. 2, st. 7853), with several type I gastrozooids attached to its base. (c) Apical view of st. 7853 specimen no. 1. (d) Latero-apical view of specimen (no. 2) from st. 7846, showing the course of the ectodermal band, with branches passing to the cormidial bases. (e) Ventro-basal view of the same corm showing the deep gutter below the zones of proliferation. The ectodermal band and part of the major branching gastrovascular canal system are visible. (f) Basal view of the same corm. At the termination of the ectodermal band a scar can be seen which represents the opening of the spiralling, branching gastrovascular canal system. (g) Sagittal section through a denuded corm (st. 9018 specimen), showing the shallow hypocystic cavity and part of the main canal system. (h) Part of the siphosome of the same specimen, showing the branching and spiralling course of the major gastrovascular canals. (i) A median, radial segment from the same specimen, showing the plethora of small gastrovascular canals and parts of the major branches. Scale bars, 2 mm.

FIGURE 13. *Stephalia dilata* (Bigelow). A reproduction of plate 21, figures 6-8 from Bigelow (1911), to which reference should be made for the full legend. (a) Lateral view of the denuded corm, showing the aurophore (Au.). (Magn. $\times 6$.) (b) Sagittal section of the corm, showing the hypocystic cavity (Ca. H.) in the nectosome, and the network of canals (C.) in the siphosome. (Magn. $\times 9$.) (c) An individual cormidium, with a gastrozooid (S.) and tentacle (T.), and a gonodendron bearing some gonophores (Go.) and gonopalpons (P.). (Magn. $\times 25$.)

DESCRIPTION OF PLATE 9

FIGURE 14. *Stephalia bathyphysa* (Haeckel). A reproduction of Haeckel's (1888b) plate vi (figs 32-38). Reference should be made to the *Challenger* monograph for the complete legend and glossary of terms. (a) [Fig. 32.] Lateral view of a corm showing the circular thickenings on the pneumatophore. (Magn. $\times 4$.) (b) [Fig. 33.] Dorsal view of the same corm, showing the additional radial thickenings on the pneumatophore. (Magn. $\times 4$.) (c) [Fig. 34.] Lateral view of the second specimen, showing a (?) spiral series of young cormidia. Note the smooth-walled pneumatophore. (Magnification not given.) (d) [Fig. 35.] Supposedly a group of six cormidia, numbered I-VI. Note the bud (n), and see text for details and discussion. (Magn. $\times 20$.) (e) [Fig. 36.] A very young (?) cormidium. (Magn. $\times 20$.) (f) [Fig. 37.] A single cormidium, with a well developed gastrozooid and tentacle, and a small gonodendron bearing gonophores (g) and a gonopalpon (q). (Magn. $\times 20$.) (g) [Fig. 38.] A well developed cormidium, to the base of which Haeckel suggested was attached a cluster of incipient cormidia. See text for discussion. (Magn. $\times 20$.)

medusoid structures. The only true sexual medusoids were the 'Monovone gynophores' which contained a single, large ovum. Brooks & Conklin (1891) gave a very detailed account of the development of the female gonophores and their set of illustrations is reproduced in figure 3, plate 2. A brief summary of their description is given here. The gonophores proper appear as small buds on the egg pouches ('Polyovones') (figure 3f, A). The distal ends of these buds invaginate, first as a solid mass of ectodermal cells (figure 3a, BN), but later develop into the typical umbrella structure of a medusoid (figure 3b, U) and a manubrium. At this stage (figure 3b) an egg in the egg pouch begins to develop and later it migrates into the gonophore and comes to lie in its final position between the ectoderm and endoderm of the manubrium (figure 3c-e). Large ectodermal folds appear at the proximal end of the gonophore and these have a secretory function so that the egg is supplied with yolk and rapidly increases in size (figure 3e-h). Brooks & Conklin suggested that the egg pouches also might supply nourishment to the egg as these pouches tend to degenerate as the gonophores develop. This results in the mature gonophores arising directly from the stem of the gonodendron (figure 3d, h) after the pouches have become totally resorbed.

Brooks & Conklin (1891) pointed out that most siphonophores were monoecious and that the dioecious state of the rhodaliids was unusual, although such is the case in, for instance, *Physalia physalis*. This led them to suggest (p. 89) that 'The fact that only female gonophores have been found on this "Albatross" specimen... suggests that the male may be widely different in form. And it is highly probable that the female of *Physalia* is so different from the male, which alone has been found, that if ever described, it has probably been classed as a wholly different genus'. Totton (1965) pointed out that this prediction was unfounded and he believed that Brooks & Conklin were unable to distinguish the two sexes of *Physalia*. This does not call into question their well illustrated description of the female gonophores of a rhodaliid, and the fact that Totton himself examined a well preserved male specimen of the rhodaliid, *Stephalia corona*, indicates that in this family too there are no gross morphological differences between specimens of either sex.

Finally, the internal structure of the corm is specifically variable and ranges from the situation where one vast cavity occupies the whole of the nectosomal and siphosomal regions, to one where the corm is solid, with a cartilaginous constituency, and is penetrated, to a variable extent, by an anastomizing network of canals forming part of the gastrovascular system. The internal configuration of the corm has been used extensively in this review as a systematic character, but it should be noted that several authors, including Schneider (1898), have conjectured that the extent of the infilling of the internal cavity is an ontogenetic character and, thus, has no systematic significance. The evidence against this latter assertion is referred to later (see p. 271).

Organization of the aurophore

Bigelow (1911) gives an excellent review of the structure and origin of the aurophore in rhodaliid siphonophores. He draws attention to the fact that the aurophore is nothing more than an enlarged, evaginated homologue of the pneumatochone or gas-secreting area of the pneumatophore. It is not a specialized medusoid structure as Haeckel (1888a) suggested and all the cell layers of the pneumatophore can be followed into it. The outer wall, the pneumatocodon, is separated from the inner one, the pneumatosaccus, by the pericystic cavity, which typically is in direct communication with the main gastrovascular canal system of the trunk (figure 4a). The chitinous lining to the pneumatophore cavity, the pneumatocyst, becomes

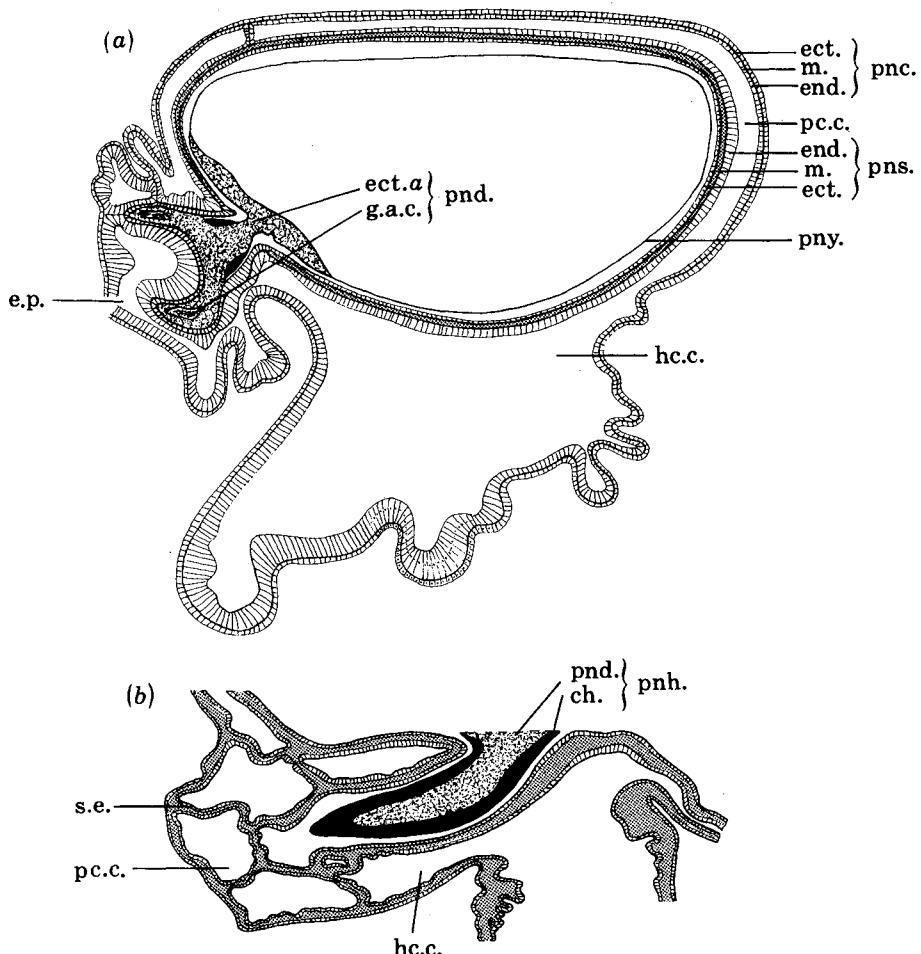


FIGURE 4. Sections through the rhodaliid aurophore. (a) *Archangelopsis typica* Lens and van Riemsdijk. A reconstruction of a median longitudinal section. (Magn. \times ca. 10.) Redrawn from Lens & van Riemsdijk (1908, pl. xvii, fig. 124). (b) *Stephalia dilata*. A reconstruction of a median longitudinal section. (Magn. \times 10.) Redrawn from Bigelow (1911, pl. 22, fig. 4). A list of abbreviations used is given in the Glossary.

much thickened in the aurophore and forms a distinct, thick-walled cylinder which encloses the secondary ectoderm of the pneumatocystis (figure 4b). Lens & van Riemsdijk (1908) observed that the gas secreted by the pneumatocystis formed vesicles between the secondary ectodermal cells, and that these gradually coalesced and finally burst, releasing their gas into the primary cavity of the pneumatophore. Their diagram of a section through the pneumatophore and aurophore in *Archangelopsis typica* Lens and van Riemsdijk, 1908, has been redrawn and is shown in figure 4a. In this particular specimen the chitinous ring in the pneumatophore is not as highly developed as it is in other specimens, e.g. *Dromalia alexandri* (see figure 25) and *Angelopsis dilata* Bigelow, 1911 (figure 4b).

During development of the physonect pneumatophore, as described by Carré (1969) for *Nanomia bijuga*, septa are formed which traverse the pericystic cavity (figure 2b). These septa are lined by two layers of endoderm, originating from the pneumatocystis, with a supporting layer of mesogloea between them. Such septa also are seen in the aurophores of rhodaliid siphonophores (figures 4a, b, 13g, 25f-h). In the pneumatophore, cavities are formed that Chun (1897) described in *Physophora hydrostatica* as being giant amoeboid cells ('Riesenzellen')

(see figure 42*b*), but Carré (1969) suggested that they were actually cavities, lined by ectodermal cells, which contained heavily staining granules (figure 2*b*). However, more recently Carré (personal communication) has made more histological studies and concluded that they are giant cells, whose nucleus is of aberrant form. During the development of the pneumatophore, at least in *P. hydrostatica* and *N. bijuga*, these cells extend into the developing, largely endodermal, radial septa, and later they become cut off from the original cells in the pneumatophore (figure 2*b*). Bigelow (1911) noted the presence of these cells in the pneumatophore of his rhodaliid specimens, but no author has observed them within the radial septa that traverse the pericystic cavity of the aurophore. The exact function of these cells has not been established.

Haeckel (1888*b*) believed that there was a central canal, or pistillum, in the aurophore which passed through the pneumatophore and connected the main cavity of the pneumatophore directly with the exterior (see figure 20*c*). Bigelow (1911) discounted this interpretation and suggested that the supposed canal was nothing more than one of the radial septa connecting the pneumatosaccus to the pneumatocodon and, thus, that no central canal was present. His representation of the construction of the aurophore in *Angelopsis dilata* is shown in figure 4*b*. However, he did not doubt Haeckel's observation of an excretory pore that connected the pericystic cavity with the exterior, and such pores were observed by him in another rhodaliid siphonophore. Similarly, the external pore can be seen (figure 4*a*) in *Archangelopsis typica*. Since this pore only connects the gastrovascular canal system with the exterior its function would appear to be that of an excretory pore. A similar function has been ascribed to the basal pore in *Physophora hydrostatica*, but there is some confusion here as, for instance, Leloup (1941) believed that there was a distinct connection from the gas cavity to the exterior, as in Haeckel's interpretation of a pistillum in rhodaliids.

The fact that this excretory pore on the aurophore lies in a dorsal position on the stem while that in *P. hydrostatica* is ventral has given rise to much discussion as to whether these two structures are homologues. For instance, Chun (1897) was unable to reconcile the dorsal position of the aurophore with the fact that it represented an enlarged pneumatophore. He suggested that the aurophore represented the distal part of the pneumatosaccus of the pneumatophore, while the voluminous cavity was equated with the pneumatophore. There is now no doubt that this interpretation was wrong. Bigelow (1911) explained the apparent anomaly between the situation in *Physophora* and that in the rhodaliids by suggesting that *Physophora*, with its ventral pneumatophore, was unlikely to be the direct ancestor of the rhodaliids, but that both were descended from some agalmid physonect stock whose primitive pneumatophore lay neither ventrally nor dorsally, but was axial. However, A. K. Totton (personal communication) pointed out that, although the pore was ventral in position, the pneumatophore itself simply lies at the base of the pneumatophore and is itself axial. The question remains as to whether the pore is purely an excretory one or whether gas can be vented from the pneumatophore cavity through it, since no apical pore is present in rhodaliid siphonophores. These points will be discussed later (p. 278) but it should be noted that buoyancy control must be an important factor in enabling the rhodaliid siphonophores to adopt their unique mode of life and it would appear imperative that these animals have some means of controlling the volume and pressure of gas in the pneumatophore, although this does not necessarily require the expulsion of gas.

3. THE HISTORY OF THE FAMILY RHODALIIDAE

Although the first known specimen of a rhodaliid siphonophore was collected in 1874 by H.M.S. *Challenger* and described by Haeckel in 1888, the first published description of one belongs to Fewkes (1886) under the name *Angelopsis globosa* Fewkes, 1886. Fewkes stated (p. 972) that 'Among the medusae collected by the Albatross is a pair of specimens which are considered the closest allies yet found of *Angela* [Lesson, 1843]... On account of its supposed affinities it is placed in a new genus of doubtful relationship to which is given the name *Angelopsis*'. Fewkes erected a new family, the Angelidae, to incorporate the two genera and took *Angela cytherea* Lesson, 1843 as its type species. Even before this time the genus *Angela* had been subjected to some doubt, for, as Huxley (1859, p. 133) stated, 'All the author [Lesson] of this genus really knows of it is, he says, derived from a drawing, "communiqué par M. Rang sans nom et sans renseignements." Under such circumstances, it is hardly worthwhile quoting his definition'. Fewkes himself (footnote, p. 974) stated, 'There are so many incongruous statements in Lesson's description that one suspects the whole account. About the only things which *Angelopsis* and *Angela* have in common is the very large float, the absence of the axis, and the basal tentacles. The propriety of my new name may be questioned, and it may seem better to form a generic name of different etymology. I have, however, retained in part the name given by Lesson, since this genus seems to me to occupy the place which he supposed *Angela* does, and as he expresses it, "fait le passage des physophores aux physales".'.

Bigelow (1911) discussed Lesson's description of *Angela cytherea* and considered for the most part that it corresponded so closely with earlier descriptions of '*Anthophysa [rosea]* Brandt, 1835' that he had no hesitation in synonymizing *A. cytherea* with it. Bigelow was himself confused in regard to the synonymies of the genus *Anthophysa* and, as Totton (1954) points out, the name *Anthophysa rosea* is a synonym of *Athorybia rosacea*, while Bigelow's *Athorybia rosacea* is synonymous with another athorybiid, *Melophysa melo*. This is a prime example of how confused much of the taxonomy of the siphonophores is, and we should be grateful to Totton for having set so much of the house in order. In this case, Totton (1965) drew attention to that fact that Stechow (1921) had found the name *Angela* to be pre-occupied by Serville, 1839 for a genus of Orthoptera, and so the name *Anga* Stechow, 1921 was proposed to replace it. This was, however, history as this meant that *Anga* became another synonym of *Athorybia*.

Haeckel (1888a) gave first notice of his new order, the Auronectae, in his 'System der Siphonophoren'. He established a single family, the Rhodalidae, and two subfamilies, the Stephanidae and Auralidae [sic], within this order, and gave brief notice of three new specific names: *Stephalia corona*, *Auralia profunda* Haeckel, 1888, and *Rhodalia miranda*. In the context of his genus *Auralia*, Haeckel (1888a, p. 43) stated, 'Vielleicht gehört hierher *Angelopsis globosa*, Fewkes, 1886?'. Later that year, when his *Challenger* monograph was published, Haeckel (1888b) made some slight alterations to his system of classification of the auronectids, and included a fourth species, *Stephanalia bathypysa* Haeckel, 1888, which he had previously confused with *S. corona*. He established a new family, the Stephanidae, to include these two latter species and dispensed with the earlier subfamily names. He also severely criticized Fewkes's (1886) description of *Angelopsis globosa*, but again included it provisionally in his genus *Auralia*. These statements prompted a riposte from Fewkes in 1889, a paper that is well worth reading if only for its vehemence of expression. Fewkes (1889) did enlarge on his original description and re-illustrated his specimens, but it is clear that the material in his possession

was not in good condition and little information of significance can be gained from either paper.

Haeckel (1888b) devoted 24 pages and seven plates to a description of his order Auronectae but, as was mentioned in the Introduction, much of the detail is open to doubt. His interpretation of the morphology of the siphonophores on the basis of his Medusome Theory, which has been criticized by several subsequent authors, e.g. Claus (1889), is no longer considered to have any significance. For instance, Haeckel (1888b, p. 284) stated that 'The remarkable structure of the single parts of the aurophore... makes it probable that the aurophore is a modified nectophore, transformed into a pneumadenia; in this case it has the morphological value of a medusoid person'. However, to his credit Haeckel did continue on to give the correct interpretation of the aurophore by stating that 'On the other hand, it is possible that it was originally only a secondary organ of the pneumatophore, a basal apophysis of the air funnel'. Haeckel (1888b) also drew attention to the similarities between his auronectid siphonophores and another species, *Circalia stephanoma* Haeckel, 1888, which he included in a new physonect family, the Circalidae. The single specimen of *C. stephanoma* that Haeckel described would appear to be a larval form as it has only one gastrozooid, but interest in the specimen lies in the fact that it possessed a single corona of nectophores. That is, however, where any similarity with the rhodaliids appears to end and, despite Schneider's (1898) suggestion that it might be a larval rhodaliid, for the present purposes this extremely doubtful species, which has never been re-described, will not be considered further.

The question of the systematic position of Haeckel's Auronectae was dealt with by many authors towards the end of the last century, as is reviewed by Bigelow (1911). Claus (1889) united Haeckel's genus *Stephonalia* with *Stephalia*, although he did not appear to discuss the reasons for this. Chun (1897) and many later authors accepted this reduction and the specific characters of *Stephonalia bathyphysa*, which will be discussed later, were ignored. Although Chun's (1897) interpretation of the organization of the pneumatophore and aurophore was wrong, as mentioned earlier, he did reduce the Auronectae to a family within the order Physonectae, the Auronectidae Haeckel, 1888 (Chun 1897, p. 8) or the Auronectae Haeckel, 1888 (Chun 1897, pp. 104, 112). However, as was pointed out later, the use of either of these names is untenable because they are not derived from a generic name. Schneider (1898) made even more sweeping reductions to Haeckel's classification. He reduced the Auronectae to a family, the Angelidae Fewkes, 1886, within the suborder Physophorae Eschscholtz, 1829. Further he lumped all four of Haeckel's species, together with *Circalia stephanoma* and *Angelopsis globosa*, into two species of the genus *Angela* taking, in accordance with Fewkes (1886), another species, *A. cytherea* Lesson, 1843 as its type. Thus he synonymized *Stephalia corona*, *Stephonalia bathyphysa* and *C. stephanoma* with *Angela corona* (Haeckel, 1888) and *A. globosa*, *Rhodalia miranda* and *Auralia profunda* with *Angela globosa* (Fewkes, 1886). He considered, for instance, that *S. corona* and *S. bathyphysa* represented nothing more than different growth stages of the same species. *A. corona* was distinguished from *A. globosa* by the presence, in the former, of a central canal in the siphosome, but Schneider (1898, p. 156) stated further, 'Ich möchte übrigens die Ansicht äussern, dass vielleicht sämmtliche von Haeckel beschriebene Auronecten nur verschiedene Altersstadien einer einzigen Art darstellen'. However he did not go so far.

Although the family name Angelidae was retained by Lens & van Riemsdijk (1908), Bigelow (1911, p. 300) pointed out that it was, 'unfortunate on nomenclatural grounds', since the supposed close relation between *Angela* i.e. *Athorybia*, and *Angelopsis* was not valid. Thus the

family name Angelidae must be abandoned 'according to the International rules of nomenclature (Art. 4) . . . [and] To replace it the name Rhodaliidae . . . must be used.' (Bigelow 1911, p. 301).

After Haeckel's description of his four auronectid (= rhodaliid) siphonophores in his *Challenger* monograph, there was a 20 year gap before another new species, *Archangelopsis typica*, was described by Lens & van Riemsdijk (1908). However, in the mean time Brooks & Conklin (1891) had in their possession a new rhodaliid specimen, which they intimated was closely related to *Rhodalia miranda*. Although they described in detail the development of the female gonophores on this specimen, they deferred a description of the whole animal to a later publication. Unfortunately this publication never appeared and the true identity of the specimen remains in doubt, as will be discussed later (p. 210).

Lens & van Riemsdijk (1908) made a detailed study of the histology of their three specimens of *Archangelopsis typica*, which were collected during the *Siboga* Expedition (1899–1900) to the Dutch East Indies. However, they gave little attention to the external morphology of the animals, particularly the cormidia. *A. typica* was the first rhodaliid species to be described that possessed papilliform appendages on the aurophore. The presence of these papillae confused Lens & van Riemsdijk, who interpreted them as representing the zones of proliferation of the nectosome and siphosome, in complete opposition to the interpretation given by Haeckel (1888b). Bigelow (1911) was able to correct their mistake and to show unequivocally that Haeckel's interpretation was correct, in that the aurophore and budding zones lay on opposite sides of the pneumatophore. Bigelow's review of the Rhodaliidae is excellent and did much to clarify the previous misconceptions regarding this family of physonect siphonophores. He decided, for instance, that Schneider's (1898) taxonomical reductions had been too sweeping and pointed out that *Angelopsis* clearly could be distinguished from *Rhodalia* by the presence of a very large hypocystic cavity, the cavity below the pneumatophore (figure 4b), and thus he resurrected the latter generic name. In addition, he gave detailed descriptions of two new species of rhodaliid siphonophores, *Dromalia alexandri* and *Angelopsis dilata*, the former of which also possessed papilliform appendages on its aurophore. In a later publication Bigelow (1913) described the external morphology of a further specimen of *A. typica*, taken by the *Albatross*, and so was able to enhance considerably our knowledge of this species. For instance, Bigelow noted on this specimen the presence of some lamellae on the bases of the cormidal stalks, to which, he suspected, bracts once were attached. This was the first mention of the fact that rhodaliid siphonophores might possess bracts, an assertion that subsequently proved correct.

Bigelow (1911) came to the conclusion that the following five genera and six species of rhodaliid siphonophore should be recognized.

Angelopsis with a very large hypocystic cavity; smooth-walled aurophore and pneumatophore

A. globosa synonym *Auralia profunda*

A. dilata

Rhodalia with a solid corm penetrated by an anastomizing network of canals; smooth-walled aurophore and pneumatophore

R. miranda

<i>Stephalia</i>	with a permanent axial canal in the siphosome; smooth-walled aurophore and pneumatophore
<i>S. corona</i>	synonym <i>Stephonalia bathyphysa</i>
<i>Archangelopsis</i>	corm a voluminous thin-walled sac; aurophore with papilliform appendages; pneumatophore smooth-walled
<i>A. typica</i>	
<i>Dromalia</i>	with a solid corm penetrated by a network of canals; aurophore with papilliform appendages; pneumatophore with several gelatinous protuberances
<i>D. alexandri</i>	

It is apparent that Bigelow (1911) based much of his classification of the rhodaliid siphonophores on two major morphological features, namely the external morphology of the aurophore and the internal structure of the corm. He chose to ignore the suggestion made by Schneider (1898) that the variability in the internal structure might be simply an ontogenetic factor, except that he continued to unite *Stephonalia* with *Stephalia*. Bigelow's works, particularly his 1911 monograph, represent milestones in the study of siphonophores, and for the rhodaliids little information has been published since. Moser (1924) presented two illustrations of parts of the cormidium of a new rhodaliid species, *Steleophysema aurophora* Moser, 1924, and a brief description of the animal appeared in a later publication under the name *Steleophysema auronecta* Moser, 1925. The single specimen was taken during the Doflein Expedition to Japan. One of the illustrations in Moser (1924) is of particular interest as it figures a bract attached to a cormidium. This was the first record for the presence of bracts in the rhodaliids and proved Bigelow's (1913) contention.

A further 30 years elapsed before another record of a rhodaliid siphonophore appeared in the literature. Kawamura (1954) described a specimen, again taken in the region of Japan, under the name *Sagamalia hinomaru* Kawamura, 1954. This specimen was in good condition when collected and possessed a large number of bracts. Later, Totton (1965) briefly reviewed the family Rhodaliidae and added a further record for *Stephalia corona*. This was probably the most complete specimen of any rhodaliid siphonophore yet collected, and Totton described its external morphology and paid particular attention to the presence of a large number of characteristically shaped bracts. Totton (1965) was in complete agreement with Bigelow's (1911) system for the classification of the rhodaliids in all but one respect. He considered that *Auralia* might be a young, post-larval stage of *Rhodalia* and thus, doubtfully, synonymized *Auralia* with this latter genus. He retained *Angelopsis globosa* as a separate, valid species. The two species that have been described since Bigelow's (1911) monograph, Totton included as doubtful synonyms of *Stephalia corona* so that he retained the same six species and five genera as Bigelow. Totton also resurrected Schneider's (1898) contention and proposed that *Rhodalia*, *Stephalia*, *Stephonalia*, *Steleophysema* and *Angelopsis* might all prove to be, at least, congeneric, but he pointed out that no decision really could be made until some new material became available. Since Totton, only one or two other records of rhodaliids have appeared in the literature. Alvarino (1971) mentioned briefly some new specimens of *Dromalia alexandri* and some *in situ* observations made on this species by Dr E. W. Fager. Recently some further specimens and observations have come to my notice, including the so-called 'Galápagos dandelions', a new rhodaliid species which will be described here.

The bathymetric distribution of rhodaliid siphonophores: historical

The mode of life of rhodaliid siphonophores has been a matter of contention ever since the first specimens were described. Nevertheless none of these earlier authorities even guessed at what is known now to be the actual niche that these animals occupy. In the introduction to the paper that contained the original description of *Angelopsis globosa*, Fewkes (1886, p. 928) commented that 'we are hardly able to definitely state the peculiar characteristics or limits of different bathymetrical zones, as far as those animals which do not live on the bottom are concerned'. He commented on the fact that the specimens had been collected in open nets and concluded (footnote, p. 972) that, 'If my interpretation of organs in this genus [*Angelopsis*] is correct it is probably a "surface jelly-fish"'.

Haeckel (1888b) took a different approach and reasoned that the striking and unusual characters in these animals made it probable that they were bathypelagic organisms. Fewkes (1889, pp. 148–149), in his later paper, took exception to Haeckel's statements and commented that 'Among the peculiarities referred to by him are "the extraordinary development of the swimming-apparatus, the voluminous pneumatophore, the powerful horizontal corona of radially expanded nectophores, and particularly the singular aurophores, wanting in all other Siphonophorae, and acting probably as an important gas-secreting gland or a pneumadenia". It is certainly difficult to see how any of the above-mentioned features "make it probable that the Auronectae are permanent deep-sea Siphonophorae (which may move up and down within certain limits of depth) but never come to the surface." One might even suggest that exactly the reverse conclusion might be drawn and that some of these features imply life at or near the surface'. Fewkes (1889) drew particular attention to the relatively enormous size of the pneumatophore and considered that such a structure would be unlikely to be found on a bathypelagic siphonophore.

Lens & van Riemsdijk (1908, p. 92) agreed with Fewkes's assertions and referred to the fact that their specimens of *Archangelopsis typica* had come from depths of 100 and 112 m. They stated, 'It seems therefore...that the extraordinary development of the pneumatophore and of the nectophores...indicates life at or near the surface of the water'. Sensibly Bigelow (1911, p. 316) remarked, 'Respecting the bathymetric range of the Rhodaliidae I may point out that all the hauls from which they have been recorded were made with open nets and therefore afford no real clue to the depths from which the specimens in question came'. He did reject, however, Haeckel's suggestion of a bathypelagic habitat. Similarly Moser (1925, p. 504) stated that her specimen of *Steleophysema aurophora* had been collected at the surface and suggested that all rhodaliids floated at that interface. Unfortunately, we do not know what type of net was used to collect her specimen. Finally, Totton (1965) reiterated the fact that none of the specimens had been collected in a closing net and suggested that these animals lived at depths down to, but no deeper than, 100 m. He was anxious to obtain further specimens of rhodaliids and it was a puzzle to him as to why none had been found among the vast collections of *Discovery* material (P. M. David, personal communication).

The capture of five specimens of *Stephalia corona* in two epibenthic sledge hauls made during *Discovery* cruise 45 (February–April 1972) really came too late for Totton to take an active interest in them. However, the present author's interest was stimulated and led to a check being made on the method of collection for all the previous specimens. With very few exceptions it was found that the specimens recorded in the literature had been collected in benthic nets or trawls,

and that these nets had reached the sea floor as a variety of benthic organisms had been recorded in the catches. The few exceptions to this scheme will be discussed in the following descriptive sections. However, the majority of the records for the capture of rhodaliid specimens strongly suggests that this group of animals is unique among the siphonophores in that they are neither surface-dwelling nor bathypelagic in their habitat, but that they are truly benthic. Fortunately, this conclusion does not have to remain speculative, as new evidence, which will be presented in this paper, shows. The *in situ* observations on specimens of *Dromalia alexandri* and the 'Galápagos dandelions' are particularly relevant in this context. A preliminary review of the rhodaliid siphonophores, incorporating some of the new information on *D. alexandri*, was given by the present author at the Third International Symposium on Coelenterate Biology, which was held in Victoria, British Columbia, Canada, during May 1976.

4. THE SYSTEMATICS OF THE FAMILY RHODALIIDAE

The systematics of the family Rhodaliidae have been subjected to many changes during its brief history, as was discussed earlier. Totton (1965) points out that, because of the dearth of material, it is difficult to decide which of the morphological characters have any generic or specific importance. To date the 37 rhodaliid specimens recorded in the literature, excluding those mentioned but not enumerated by Alvarino (1971), have been described under ten specific names. For the purposes of the present paper the original rhodaliid material has been re-examined whenever possible and, in addition, new information has become available for some species through observations on recently collected material. From all these observations it has been concluded that the current classification (see, for example, Totton 1965) of the family Rhodaliidae is inadequate and a revised classification is presented here. The order in which the specific descriptions are treated is a matter of convenience and has no other significance.

Genus: Angelopsis Fewkes

- | | |
|-------------------|--|
| <i>Angelopsis</i> | Fewkes 1886, pp. 971–974; 1889, pp. 146–155 |
| | Bigelow 1911, pp. 300–303, 309–310 (<i>partim</i>) |
| | Totton 1965, p. 95 (<i>partim</i>) |
| <i>Auralia</i> | Haeckel 1888a, p. 43; 1888b, pp. 301–302 |
| <i>Angela</i> | Schneider 1898, p. 157 |

Diagnosis. Rhodaliid siphonophore with smooth-walled aurophore and pneumatophore; with an extensive cavity in the siphosome, the thickened walls of which are penetrated by a network of canals, although this network may be restricted to the peripheral regions.

Type species. *Angelopsis globosa* Fewkes, 1886.

Discussion. Bigelow (1911, p. 309) defined the genus *Angelopsis* Fewkes, 1886 as 'Rhodaliidae with solid bulbous siphosome traversed by a network of numerous canals; with smooth-walled aurophore lacking papilliform processes; with very voluminous hypocystic cavity extending to or below the lower end of the siphosome [?nectosome]. Tentilla present (?)'. It is apparent that this definition is not only contradictory in itself, but does not agree with the structure of the type species. First, if the siphosome is solid then the hypocystic cavity cannot extend into it; it certainly cannot extend below it and so it is assumed that the 'siphosome' in the above statement should be corrected to 'nectosome'. Secondly, the siphosome of *A. globosa* is not solid, but contains a very large cavity. Bigelow also included Haeckel's *Auralia profunda* in this

genus although this species too has a wide, central cavity in the siphosome. Further, he pointed out that the conformation of the hypocystic cavity was probably significant in the classification of the rhodaliids, and certainly he used that reasoning to distinguish *Angelopsis* from *Rhodalia*.

With the above in mind it is interesting to note that Bigelow (1911) decided to include a new species, *Angelopsis dilata*, in this genus even though its hypocystic cavity was restricted to the nectosomal region, as it is in *Rhodalia* and *Stephalia*. Since his specimen was in a somewhat fragmentary state, Bigelow (p. 310) remarked, 'We have here another of those cases, so commonly encountered by the student of the pelagic Coelenterata, where it is difficult to decide whether the cause of science is best served by creating a new species, by referring the specimen to an old species on doubtful grounds, or by leaving it without specific identification. The difference in the hypocystic chamber is probably sufficiently important for recognition and may therefore justify a new species. But I must add the warning that research on better material may well prove it unfounded; therefore it should not be used as an instance of geographic distribution until tested further'.

Confusingly, Bigelow (1911) in one place (p. 310) remarks that his single specimen of *Angelopsis dilata* 'agrees in general structure with *A. globosa*' but later (p. 311) states, 'In general appearance the specimen resembles the figure given by Haeckel for *Stephalia* ('88b, pl. 6, fig. 32), except that there is no large central primary siphon'. It is considered, for reasons discussed below (p. 207), that Bigelow's *A. dilata* does more closely resemble *Stephalia corona* than *A. globosa*, although the configuration of the hypocystic cavity might represent an intermediate evolutionary stage between these two species. Accordingly, *A. dilata* here is removed to the genus *Stephalia*.

The presence, within the siphosome, of a large cavity that is surrounded by a thickened wall consisting of an amorphous layer of mesogloea penetrated by an endodermal canal system is one of the major morphological characters that distinguishes the genus *Angelopsis* from the other rhodaliid genera. A siphosomal cavity is present in some other rhodaliids, but in these the configuration of it is quite different. In *Archangelopsis* the cavity is large, but thin-walled and, besides, there are papilliform appendages on the aurophore in this latter genus; while in the so-called 'Galápagos dandelions', a new rhodaliid species described later (p. 255), the cavity is axial, narrow and relatively thin-walled. In two other rhodaliids, *Sagamalia hinomaru* and *Stephalia (Stephonalia) bathypysa*, the internal structure of the corm is described inadequately, but one can infer that the overall arrangement is different from that in *Angelopsis* as, in this latter case, the configuration is too obvious to be missed.

Some of the new specimens of rhodaliid siphonophores that have been examined were found to possess a large siphosomal cavity surrounded by a thickened wall, and have thus been assigned to the genus *Angelopsis*. As this new material is in an incomplete state it will be necessary to discuss in some detail the descriptions of *A. globosa* given by Fewkes (1886, 1889) in order to illustrate the inherent ambiguities and inconsistencies which make it difficult to ascribe any new material to this particular species. However, despite these difficulties, it is felt that there are sufficient morphological differences between the new material and that described for *A. globosa* to warrant the establishment of a new species. This conclusion could prove unfounded if the original specimens of *A. globosa* were available for further study.

Angelopsis globosa Fewkes (figure 5)

- Angelopsis globosa* Fewkes 1886, pp. 971–974, pl. x, figs 4, 5; 1889, pp. 146–155, pl. viii, figs 1, 2, 3
 Lens & van Riemsdijk 1908, pp. 89–99
 Bigelow 1911, p. 300–303, 309–310
 Totton 1965, p. 95
Auralia profunda Haeckel 1888a, p. 43; 1888b, pp. 301–302
Angela globosa Schneider 1898, p. 157

Type material. Two specimens from *Albatross* station (st.) 2105, 6. xi. 1883, taken at $37^{\circ} 50' N$, $73^{\circ} 03' 50'' W$, off the east coast of U.S.A. The net used to collect the specimens was a beam trawl which sampled the benthos at a depth of 1395 fm (2553 m). The bottom substrate was globigerina ooze.

Diagnosis. Rhodaliid siphonophore with a smooth-walled aurophore and pneumatophore. The siphosome contains a wide, central cavity, the thickened walls of which are penetrated (?) throughout by a network of canals. The siphosomal cavity may (?) have a connection with the hypocystic cavity in the nectosomal region. The number of nectophores once present may (?) have been in excess of 16; the cormidial stems may (?) have arisen from pronounced, thickened bases.

Discussion. It has not proved possible to trace the whereabouts of the original specimens of *Angelopsis globosa*. They are not present in the collections of the Museum of Comparative Zoology, Harvard (M.C.Z.), the U.S. National Museum of Natural History, Smithsonian Institution (U.S.N.M.) or the Peabody Museum of Natural History, Yale. Fewkes (1886) quotes a catalogue number of 6565 for his specimen of *A. globosa* and, according to Dr W. D. Hartman, this might have been a Peabody Museum number, but the catalogue entry for the number is blank. For Haeckel's (1888a, b) *Auralia profunda*, which is treated here as a synonym of *A. globosa*, the whereabouts of the single specimen also is unknown. It is presumed to have disintegrated like most of Haeckel's siphonophore collection (see p. 227).

Neither of Fewkes's (1886, 1889) descriptions of *Angelopsis globosa*, nor Haeckel's (1888b) description of *Auralia profunda* are satisfactory, and it will be necessary to study the information in some detail to see what may be gleaned from it. Fewkes's (1886) original description was none the less the first for any rhodaliid siphonophore, a point that he made with some force of expression in his later publication. A brief summary of it is given below, together with some examples of his descriptive vagueness. The original illustrations have been redrawn in figure 5a, b.

Pneumatophore. 'This medusa has a spherical region above which is considered a float, on the underside of which is clustered a number of small bodies resembling tentacles' (Fewkes 1886, p. 973). The pneumatophore was relatively large in size, 7–10 mm in diameter, and was smooth-walled without protuberances or an apical pore. The walls were said to be thin, but this might have been a relative statement in comparison with the thickness of the siphosomal wall.

Nectosome. Fewkes (1886, p. 973) described in this region some 'spherical bag-like structures (gm) of unknown function [figure 5a]. These bodies recall in appearance the larger float, from which they hang, and suggest the possibility that they are buds from the outer walls... so closely [do they] resemble the larger float that the supposition that they are new individuals budding from the thickened region of the bell seems highly probable... In cutting open one of the

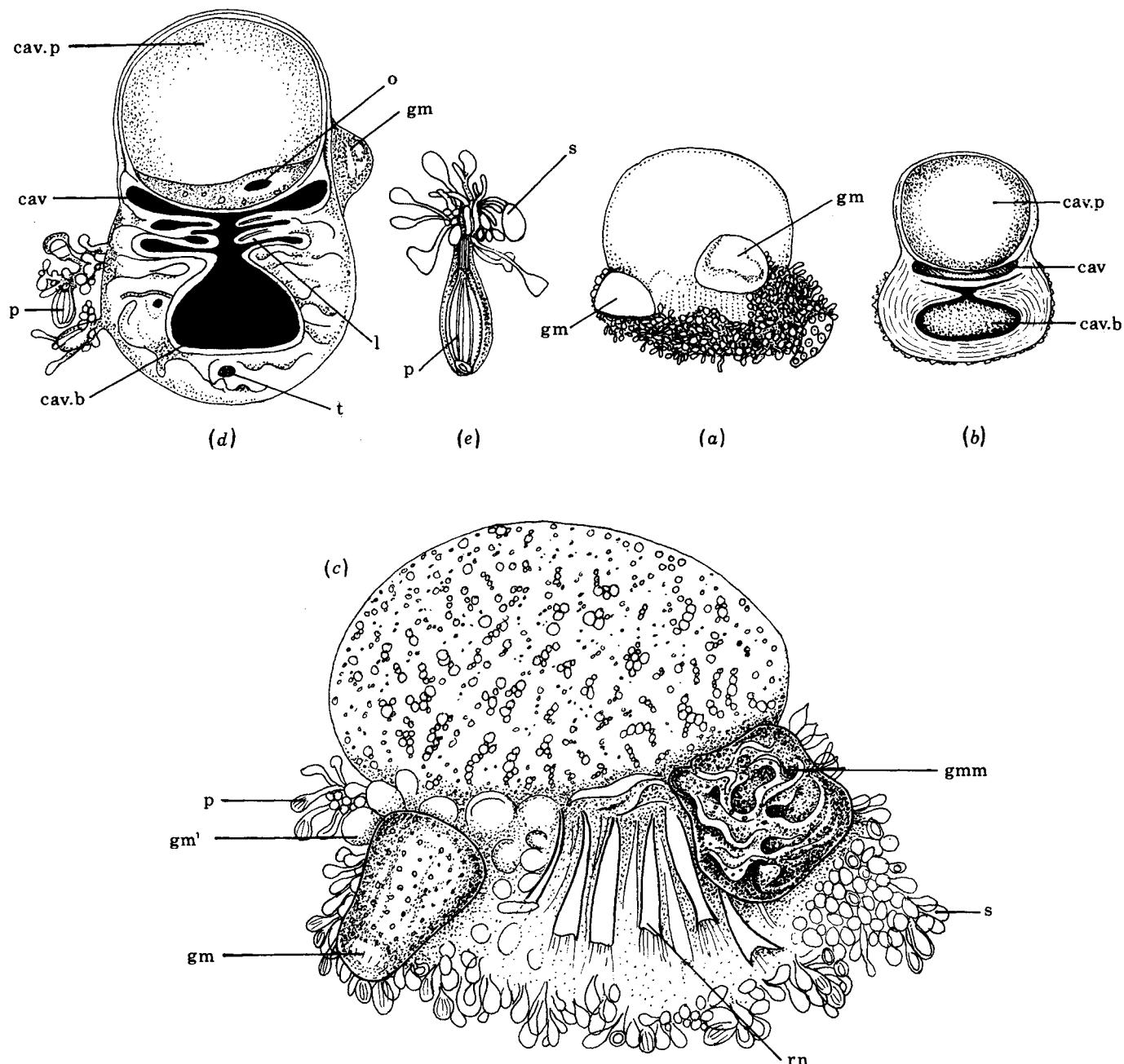


FIGURE 5. *Angelopsis globosa* Fewkes. (a) Lateral view of the denuded corm, showing the two 'globular enlargements' (gm). (b) Median section through the corm, showing the pneumatophoral cavity (cav.p), the hypocystic cavity (cav) and the siphosomal cavity (cav.b) all as separate entities. (c) Side view of the larger specimen which 'is distorted'. Note the globular bodies (gm, gmm) and some young buds (gm¹); the nectophoral lamellae (rn), plus some gonophores (s) and ?gonopalpons (p). (d) Median section through the corm, showing the arrangement of the cavities. Note that the hypocystic cavity (cav) here is in direct communication with the siphosomal cavity (cav.b), although partially separated by some folds (l) of a cartilaginous plate. The thickened walls of the siphosome are penetrated by a ramifying network of canals (t). The bud (gm) has an opening (o) into the pneumatophoral cavity. (e) A gonodendron. Diagrams (a) and (b) are redrawn from Fewkes (1886, pl. x, figs 4, 5); (c)–(e) are redrawn from Fewkes (1889, figs 1–3). In neither paper are the magnifications given.

small spherical bodies (gm) . . . I found it filled with a granular mass, which had some resemblance to the botryoidal clusters on the lower hemisphere of the medusa'. It is important to discover the identity of these two 'bag-like structures' and for the most part Fewkes's description at this point is extremely confusing. However, it is apparent that he was under the misapprehension that the pneumatophore was of medusoid origin.

Siphosome. It is difficult to unravel any details of significance from this part of Fewkes's (1886) description, but he appears to have described clusters of gonophores on the gonodendra, although he ascribes a grasping function to them. Fewkes, finally, went on to discuss the affinities of *Angelopsis*, first with *Pectyllis* (Pectyllidae = Ptychogastridae, Trachymedusae) but on rejecting this hypothesis he looked for 'allies of *Angelopsis* [among the] Physophores like *Physalia*', and commented, 'but even here we meet great difficulties.' (p. 974).

While it is evident that Fewkes's (1886) description of *Angelopsis globosa* is both confusing and inadequate, it is more substantial than the information given by Haeckel (1888b) for his species *Auralia profunda*. Actually Haeckel deferred the description of *A. profunda* to a later publication, his 'Morphology of the Siphonophorae', which unfortunately was never published and so all that is known of the genus *Auralia* is the definition given by Haeckel (1888b, p. 301), namely, 'Rhodalidae with a simple corona of nectophores, arranged in a single circle. Trunk of the siphosome with a wide central cavity, surrounded by a peripheral reticulum of trunk canals. The genus *Auralia* may be regarded as the older and inferior form of Rhodalidae, more closely allied to the preceding Stephanidae than the succeeding *Rhodalia*'. No specific description of *A. profunda* was given, but Haeckel suggested that *A. globosa* might belong to the genus *Auralia*. He added (p. 302), 'Fewkes' description, however, is so inaccurate, and the examination so superficial, that it is impossible to identify with any certainty his *Angelopsis* and my *Auralia*'. Since Haeckel did not describe his species it is apparent that Totton's handwritten margin comment on his copy of the *Challenger* monograph, 'pot calling kettle black' is distinctly appropriate. Haeckel (1888b) also gives no data as to where the specimen was collected, except to say that it was taken in the depths of the Atlantic Ocean. Moser (1925, p. 505) stated that the specimen was collected from a depth of 510 fm (933 m), but the source of this information is obscure. If one presumes that *A. profunda* was collected during the *Challenger* Expedition, then the only record for an Atlantic *Challenger* station in 510 fm of water was st. 109B, off St Pauls Rock, but this was a sounding station and no mention is made of any animal coming up attached to the line. This lack of station data is unfortunate as it might have given some indication as to the identity of the specimen for, although the information is scant, individual species of rhodaliid siphonophores do appear to have fairly restricted ranges of geographical distribution, as is discussed later (p. 274).

The comments made by Haeckel (1888b) concerning *Angelopsis globosa* initiated a further paper from Fewkes (1889). As well as providing some additional descriptive information on *A. globosa*, this later paper also contained some extremely scathing remarks about Haeckel and his *Challenger* monograph, and to give redress the following statements are worth quoting: 'The author [Haeckel] mentioned was unable "with any certainty" to identify his *Auralia* and my *Angelopsis*. I find the same difficulty, but the cause of my difficulty is not wholly the same as his.' (footnote to p. 150); 'Haeckel simply says that the corona of nectocalyces (nectophores) is simple in *Auralia*, but gives no information about them in this genus. He gives no account of their anatomy, whether they are sessile or pedunculate, or *any detail of any scientific value about them*.' (footnote to p. 149).

Fewkes (1889) quotes in full his earlier description, but then gives some additional information which clarifies in part some of the obscurities in the 1886 paper, in that he adopts the terminology that Haeckel introduced. Fewkes also provided three new illustrations and these are redrawn in figure 5c–e. One of the major points of discussion was whether the ‘spherical bag-like structures’ might be nectophores, as Haeckel (1888b) had suggested. Fewkes stated categorically that no nectophores were present, but he pointed out that the radial, muscular attachment lamellae (rn) could be seen clearly (figure 5c). He rejected the idea that the structures gm, gmm (figure 5c) might be nectophores on the basis that they had neither ostial openings nor radial canals. He did allow that they might be homologous with the aurophore, but stated that no external openings could be found. He failed to remark here that, as there is only a single aurophore on each individual rhodaliid, it is impossible that both these structures might be aurophores, or that both necessarily would have the same internal structure. Thus the fact that he dissected one and found it to contain a granular mass resembling the ‘botryoidal clusters on the lower hemisphere’ does not mean that the other need have the same structure. However, in the legend to his figures, Fewkes (1889) did suggest that the bud gm (figure 5c) somewhat resembled an aurophore, while the bud gmm was very much shrunken in preservation. Fewkes (1889) made another jibe at Haeckel, while commenting on the fact that his own illustrations were accurate outline drawings of badly preserved specimens, when he commented (p. 148) that ‘The system of “restoration” by which “semidiagrammatic” figures are constructed and “missing parts supplied from a knowledge of the form of the same in other Medusae” does not wholly recommend itself to the author’.

It is impossible to decide with certainty what these bag-like structures might be without a re-examination of the original material, which has not proved possible. However, a tentative explanation will be offered, based in part on the examination of some recent material which is described in the next section as a new species of *Angelopsis*. It is suggested that, if one of the buds (gm, gmm, figure 5c) is the aurophore, then it is more likely to be the bud gmm, rather than the bud gm as Fewkes (1889) concluded. It should be noted that the specimens were distorted in preservation, as Fewkes stated, and one can assume that there had been a shrinkage or folding of the nectosome which might result in the siphosomal region apparently coming to lie immediately below the pneumatophore. Such distortions have been observed in specimens of other rhodaliid siphonophores.

In his figure of the sagittal section of *Angelopsis globosa* (figure 5d) Fewkes (1889) shows the bud gm as being closely applied to the side of the pneumatophore. Also, Fewkes stated that the structure o, shown in this latter figure, was the opening of the bud gm into the cavity of the float. Lens & van Riemsdijk (1908) drew attention to this opening, and to the elliptical area that surrounded it. They considered that o actually represented the cavity that remained after a gas bubble had burst, as they had observed similar cavities in their specimens of *Archangelopsis typica*. The elliptical area surrounding it would then represent the cushion of secondary ectoderm which extended into the aurophore as the pneumadenia. On the basis of this the bud gm would have to represent the aurophore. Fewkes (1886) stated that both of these bodies hung from the pneumatophore, but in his later report he was more tentative and stated that they ‘hang from the neighbourhood of the float’ (1889, p. 153). From an examination of Fewkes’s (1889) illustration (figure 5c) it would appear that the structure gmm is attached directly to the base of the pneumatophore, as nectophoral lamellae stretch beneath it, while the other, gm, is attached lower down the corm. In this figure the protuberance, gm, is shown to be surrounded

by many protuberances and immature buds (gm^1), whose function was not apparent to Fewkes, although he suggested that they might represent undeveloped nectophores. This is considered unlikely as such a large number of nectophoral buds have never been observed in other rhodaliids. However, if one does consider them to be buds of nectophores and/or cormidia, then it must be remembered that the zones of proliferation lie on the ventral side of the corm, while the aurophore is dorsal. In this case the structure gm could not be the aurophore. A solution to this dilemma might be to suggest that Fewkes (1889) made a mistake in the labelling of his figures. This is not impossible for it should be noted that in the original illustrations (figure 5a, b) both of the buds are labelled gm , and it could be that this notation was only partially altered for the later publication. Also, since Fewkes's (1889) figure (figure 5d) appears to represent a sagittal section of the specimen that he illustrated entire (figure 5c), then it is strange that he did not show, in the former, the cluster of young buds (gm^1) which surround gm in the latter.

Thus, because of its position on the corm, as shown in figure 5c, the bud gmm is considered more likely to be the aurophore. In this figure a distinct nectosomal region, which is devoid of nectophores but characterized by the presence of their muscular lamellae, is discernible between the two bodies gm and gmm . These lamellae appear to extend beneath gmm , which might argue against it being the aurophore for, in that case, there should be a naked zone below it. However, as Bigelow's (1911, pl. 23, fig. 7) figure of *Dromalia alexandri* shows, these muscular lamellae often do extend beneath the lateral margins of the aurophore, and the naked zone becomes obscured by the overhang of the aurophore itself. In this region, the distortion of Fewkes's specimen again is apparent as structures that are clearly siphosomal in origin are shown not only below but also to one side of the body gmm .

Because the bag-like structure gm (figure 5c) is shown to be surrounded by young buds (gm^1) it is suggested that it originated not in the nectosomal region, but in the siphosome. It is unlikely, however, to be a cormidial component, such as a bract or a gastrozoid, as these are easily detached and one would assume that Fewkes could have recognized them as such. The structure gm appears to be rigidly attached to the corm and so it is suggested that it represents an enlarged cormidial base. These bases are seen as protuberances on the denuded corms of several species of rhodaliid siphonophore, and not least in the specimens of the new species of *Angelopsis* (see figure 6a, b), as is described in the next section. In this case there is a striking resemblance between the shape of the cormidial bases of the latter and the protuberance, gm .

There are several other anomalous statements in Fewkes's (1889) expanded description of *Angelopsis globosa*. One such confusion, which is of great significance, concerns the internal structure of the corm. Fewkes (1886) illustrated (figure 5b) the cavity of the siphosome as being completely separated from the hypocystic cavity, in the nectosome, by a 'muscular floor', whereas in the later publication these two cavities are shown (figure 5d) to be in direct communication. Since the internal organization of the corm will be established as an important systematic feature in rhodaliid siphonophores, this particular ambiguity in Fewkes's descriptions makes it very difficult to assign the name *A. globosa* to any new material, and is one of the primary reasons why the new specimens, which belong to the genus *Angelopsis*, will be described under a new specific name. In fact it is very difficult to glean any satisfactory additional information from Fewkes's (1889) re-description of *A. globosa*, but in this paper he does make one last plea for recognition when he states (pp. 154–155), 'My description [1886] which was the first printed account of an Auronectid, the revelation of which Haeckel styles "one of

the most splendid discoveries of the 'Challenger,'" was the first account of these strange Medusae'.

Finally, it is necessary to consider the relations between *Angelopsis globosa* and *Auralia profunda*. Bigelow (1911, p. 310) remarked, in regard to Haeckel's (1888b) account of *A. profunda*, 'This brief notice is of course entirely insufficient for specific diagnosis. But as it applies perfectly well to *A. globosa*, so far as it goes, and inasmuch as there is no geographical barrier between the localities of capture of the two, it is probably better to unite them'. Totton (1965), however, considered that *A. profunda* was probably a young specimen of *Rhodalia miranda*, possibly with regard to the fact that Haeckel (1888b) had placed these two species in a separate family, the Rhodalidae [sic]. Totton also stated that the specific name, *A. profunda*, was a *nomen nudum*, presumably because of the insufficiency of Haeckel's description. However, this statement would not seem to be justified entirely according to Article 16a(vi) of the International Code of Zoological Nomenclature.

In the absence of the specimens of both species, one can compare only the descriptions given. It is construed that both had smooth-walled aurophores and pneumatophores, as any papilliform appendages or gelatinous protuberances would surely have been noted. Haeckel's (1888b) definition of the genus *Auralia* was quoted above, and when writing of *A. profunda* (p. 301) he states, 'Its external appearance is similar to that of *Stephalia corona*...; but the nectophores of the simple corona are more numerous and the tentacles are of the same shape as in *Rhodalia*'. This latter statement presumably means that the tentacles were annulated but, as is shown later, this is a general feature of rhodaliid siphonophores and has no systematic significance. Besides, no useful information is available concerning the tentacles of *Angelopsis globosa*. In regard to the number of nectophores, Haeckel (1888b) stated that from eight to 16 were present on his specimens of *S. corona* and so, from the above statement, *A. profunda* should have had in excess of 16. The number of nectophores of *A. globosa* is not known, but might be estimated from Fewkes's illustrations. In figure 5c at least six muscular lamellae are shown in a region that would appear to represent from one-quarter to one-third of the whole nectosome. This would, by extrapolation, give a total nectophore count of the same order as that in *A. profunda*. However, the most important character described for both species is the internal structure of the corm. Both possess a wide central cavity in the siphosome, the thickened walls of which are penetrated by a network of canals. Although the exact configuration of this cavity is in doubt, no other rhodaliid siphonophore so far described has an internal organization of the corm that in any way resembles this. Thus it can be concluded that *A. globosa* and *A. profunda* are congeneric and, on the basis of Bigelow's statement quoted above, *A. profunda* is synonymized with *A. globosa*.

Angelopsis euryale sp.nov. (figure 6)

Type material. Three specimens collected at *Discovery* st. 9132 no. 5, 24. xi. 1976, at 20° 50.1' N, 18° 55.5' W, off the coast of Mauretania, NW Africa. The net used was a Marinovich Otter Trawl which was fished to and on the sea floor at a depth of 3109–3089 m. One specimen, described in this text as specimen 1, has been designated the holotype and has been deposited in the collections of the British Museum (Natural History) under catalogue no. 1982–2–2–1.

Diagnosis. Rhodaliid siphonophore with a smooth-walled aurophore and pneumatophore. The aurophore is a distinct elongated structure attached, at its proximal end alone, to the basal part of the dorsal surface of the pneumatophore. Eight to ten thickened, widely spaced

nectophoral lamellae are present on the nectosome. The siphosome contains a wide, central cavity, the walls of which are greatly thickened with a layer of amorphous, mesogloal ground substance. The network of gastrovascular canals is restricted to the periphery of this layer, except for a series of radial canals which penetrate through it and connect the central cavity with the cormidial stalks. These cormidial stalks are borne on expanded bases. The hypocystic cavity occupies most of the nectosomal region and is separated from the siphosomal cavity by a thick wall, although a small canal system may form a connection between the two.

Description. All three of the specimens are in a very poor condition. The cormidial elements and nectophores have been stripped off, by the action of the netting, leaving only the basic corm with a few denuded cormidial stalks. It is, therefore, impossible to give a full description of the specimens, but it is believed that there are sufficient morphological characters remaining to establish their specific individuality. The denuded corms measure from 14 to 17 mm in maximum diameter, and from 12 to 17 mm in height. However, the compression and distortion of the specimens makes difficult the true assessment of their size.

Pneumatophore. The pneumatophore is relatively large, in comparison with the overall size of the corm, and measures approximately 10 mm in diameter (figure 6, plates 3 and 4). It is smooth-walled, bearing no external protuberances or any apparent pigment spots. It is normally hemispherical but owing to damage appears flattened in one specimen (figure 6d). The pneumatocodon, or outer wall of the pneumatophore, is greatly thickened by a rigid, amorphous layer of mesogloea. This thickening is not uniform over the entire surface of the pneumatophore, being about 0.45 mm in thickness at the sides and thinning to 0.25 mm at the apex (figure 6c). Numerous fine, radial strands of endoderm penetrate through the mesogloea of the pneumatocodon. Such processes were noted by Haeckel (1888b) in his specimens of *Rhodalia miranda* and they will be mentioned further in the section on this latter species. No septa were seen to connect the pneumatocodon to the pneumatosaccus, or inner wall, but these fine structures are not always apparent without a detailed histological study. The pneumatosaccus is comparatively thin-walled over most of the pneumatophore, except in the region of the aurophore and basally where it overlays the hypocystic cavity (figure 6c, d). In this latter region it can reach a thickness of 0.2 mm. A fragile layer lines the cavity of the pneumatophore and, except in the region of the aurophore, shows no obvious connection with the pneumatosaccus, although it is presumed to be the chitinous layer secreted by the primary ectoderm of the latter (figure 6c). This chitinous layer is overlain, at least in the region of the aurophore, by the secondary ectoderm of the pneumadenia. The volume of gas in the pneumatophore was estimated geometrically to be approximately 240 mm³.

Aurophore. The aurophore is a distinctive, smooth-walled, elongated structure. It is attached, by its proximal end alone, to the base of the pneumatophore, just above the dorsal junction of the latter with the nectosome (figure 6b-d). This mode of attachment is in marked contrast to the arrangement in *Stephalia corona* or *Stephalia dilata*. The poor state of preservation of the present material made it difficult to make any detailed studies of the internal organization of the aurophore, but its basic structure conforms with that known from studies on other rhodaliid species (see, for example, Bigelow 1911). The mesogloal layer of the pneumatosaccus, which extends into the aurophore, is thickened and forms part of a distinct, cylindrical wall which surrounds the pneumatochone. Many large cavities are present in the pneumadenia and these probably contained the gaseous secretions of the secondary ectoderm. Similarly, in the distal region of the pneumadenia, where the primary and secondary ectodermal layers merge, many

so-called 'giant amoeboid cells' can be discerned. In this region the ectodermal layers are expanded greatly and spread out over the distal end of the chitinous cylinder to produce a mushroom-like structure (figure 6c, d). Here the mesogloea of the enclosing pneumatosaccus layer is much thinner. Although septa connecting the pneumatosaccus to the pneumatocodon were clearly present in the aurophore, it was not possible to assess their number or organization. The pericystic cavity of the aurophore was presumed to be connected to the exterior by a pore, although the damaged state of the specimens made this feature difficult to verify.

Nectosome. The nectosomal region is quite shallow and forms a neck between the pneumatophore and the siphosome (figure 6g). The hypocystic cavity occupies the upper two-thirds of the nectosomal region, being delimited above by the thickened pneumatosaccus of the pneumatophore and below by the extremely thick wall which separates it from the siphosomal cavity (figure 6c, d). Laterally, the walls are relatively thin and the nectosomal region may be foreshortened by their contraction during preservation.

The zones of proliferation lie on the ventral side of the nectosome, immediately beneath the overhang of the pneumatophore, and some very young buds of nectophores and cormidia are present thereon. No other nectophores were present, but between eight and ten nectophoral, muscular lamellae were noted. This would indicate that remarkably few nectophores were present considering the size of this rhodaliid siphonophore. These muscular lamellae are well developed (figure 6b), which again contrasts with the more usual thin tissue sheets seen in other rhodaliids. Since there are so few lamellae, there are large gaps between them. However, the oldest lamellae, on either side of the aurophore, extend well beneath the latter, and together with the overhang of the aurophore give the impression that the naked zone is absent. A single gastrovascular canal passes through each of these lamellae and connects with a system of horizontal canals which lie in the upper part of the wall beneath the hypocystic cavity. A large number of striations are apparent beneath the surface of the lamellae (figure 6b), and similar ones are seen on the cormidal bases. In the latter case, at least, these striations probably are similar to or identical with the thickened rings of longitudinal muscle fibres, ectodermal in origin, that are arranged in a radial series on either side of corresponding bands of mesogloea in the stem of most long-stemmed physonect species (see Garstang 1946, p. 137).

Siphosome. The whole siphosomal region is almost totally devoid of any cormidial components. No mature cormidia remain, but a few young buds and some denuded stems are still attached. However, there are various aspects of the organization of this region that are of interest. The corm is flattened basally and the arrangement of cormidia in this region is completely different from that on the sides (figure 6e, f, h). The fully developed cormidia on the sides of the corm once were situated on broad, gelatinous bases, before being stripped off on capture. These bases are arranged into at least two major whorls, although the pattern is complicated by the fact that the younger cormidia and bases, on the upper whorl, are inserted between the older ones below (figure 6g). The cormidal bases in the upper whorl are the most prominent and usually they are expanded apically so as to produce an inverted, pyriform structure (figure 6a, g). The growth of their basal halves is restricted by the presence of the older cormidia of the whorl below. The bases of the cormidia of the lower whorl(s) are not expanded but appear as long, narrow processes running down the side of the siphosomal corm. As many as eight of these bases may be present between those of the upper whorl, but from two to four is more usual (figure 6g). The whole arrangement is confused and, if the cormidia were originally arranged in a spiral fashion, then this pattern has become obscured.

One or two gastrovascular canals open on the apices of the gelatinous cormidial protuberances, and these canals, in the upper whorl of cormidia, also give off a few blind-ending branches (figure 6*g*). This arrangement is in marked contrast to that in several other rhodaliid species, where a complex system of branching and anastomizing canals is present. On the bases in the upper whorl, a superficial T-shaped scar can be discerned, with the major gastrovascular canal ending at the half-way point on the vertical. It would appear that the cormidial stalks radiated out from this point, as indicated by the scar tissue, but it is not possible to conjecture what their organization might have been. No bracteal scars could be seen on either the cormidial bases, cf. *Dromalia alexandri*, or on the occasional denuded cormidial stalks that remained attached.

On the flattened base of the corm a totally different arrangement prevails. A whorl of about thirteen gelatinous, cormidial bases delimits a central area that is totally devoid of such structures. In their place a series of apparently paired, rounded scars is present which spirals out from the centre and eventually penetrates between two of the surrounding cormidial bases (figure 6*e,f*). It is fortunate that a study of some new specimens of *Stephalia corona* reveals what was most probably attached to these scars. It is believed that these scars, in the centre of each of which is a wide gastrovascular canal opening, represent the points of attachment of some specialized gastrozoooids. No other cormidial components are developed. In *S. corona* (figure 9*a,b*, plate 7), a series of enlarged gastrozoooids are seen attached to the base of the corm, and these gastrozoooids have a different structure from the more usual ones found on the fully developed cormidia (see figure 11*a*). These enlarged gastrozoooids are referred to here as type I, and their specialized function will be discussed later (p. 292).

The origin of these type I gastrozoooids also is of interest, as is revealed from an examination of the zones of proliferation and the youngest cormidia in the specimens of *Angelopsis euryale*. It has been observed in some species of rhodaliid siphonophore, e.g. *Dromalia alexandri*, that the young cormidia, having passed down through the nectosomal region, become organized as part of a dextotropic, spiral whorl of cormidia. On searching for such an arrangement of the youngest cormidia in the specimens of *A. euryale* none could be found (see figure 6*b*). In contrast, for two of the three specimens, the tract of young cormidia, with an underlying gastrovascular canal, was found immediately below the nectosome to the left of the ventral surface (figure 6*h*). This tract was followed around the corm to a point just before it would have passed under the overhanging aurophore but, instead of continuing to form a complete apical whorl, it turned abruptly downwards (basally) and slightly back on itself, i.e. away from the dorsal line. It passed down between pairs of well developed cormidial bases and eventually reached the basal region of the corm, where it joined up with the biserial, spirally arranged scars of the detached type I gastrozoooids (figure 6*f,h*). In the third specimen, the tract of young buds also was found to connect with these basal scars but, instead of first passing round the apical part of the siphosome, it travelled straight down between the cormidial bases immediately below the zone of proliferation. Such an arrangement of the young cormidia, or a reduced part thereof, has not been described for any other specimens of rhodaliid siphonophores and certainly confounds any theory as to the mode of growth of these animals (see p. 292).

Internal structure of the corm (figure 6*c,d*). In essence the internal structure of the corm of *Angelopsis euryale* consists of a very large, thick-walled cavity in the siphosome, and a large hypocystic cavity in the nectosome. These two cavities are separated by a thick wall, which consists for the most part of a transparent, rigid, amorphous mesogloea layer, lined on either

side by endoderm. The hypocystic cavity, as described above, appears somewhat compressed, although this may be due to the collapse of its relatively thin external, nectosomal walls. The wall separating the two cavities is an extension of the thick wall that entirely surrounds the siphosomal cavity. This siphosomal cavity, as part of the gastrovascular system, is connected to the canals in the cormidial bases by a series of large radial canals (figure 6d). No other canals penetrate the thickened mesogloal wall, except in the region immediately below its outer, ectodermal lining, where a reticulum of canals is present. Branches from the radial canals do connect in with this superficial system but the general impression is that the two canal systems are quite separate. The superficial system appears to have a very regular arrangement, although it may be difficult to discern this among the plethora of canals. Certainly it bears very little resemblance to the jumbled mass of branching and anastomizing canals seen in *Rhodalia miranda* and *Stephalia corona*, for example. In *A. euryale* there are a number of widely spaced, large canals which are arranged longitudinally (i.e. circumferentially in the vertical plane) around the corm. Arising from these, and joining one to the next, is a closely knit system of latitudinal (i.e. in the horizontal plane) canals which are much smaller in size (figure 6d). These latter canals may branch to form a reticulum but the extent of this branching is small and, in general, the whole arrangement can be likened to a mesh.

This superficial canal system extends into the apical region of the wall that forms the floor of the hypocystic cavity, and some canals evidently open into that cavity. No distinct radial canals traverse this wall, thereby connecting the two cavities, and, in one of the two specimens that have been sectioned sagittally, there would appear to be no direct connection at all. In the other specimen an ill defined narrow canal was seen to pass obliquely upwards from the siphosomal cavity and join up with the horizontal network of canals on the apical part of the wall and ultimately, thereby, with the hypocystic cavity. It is certain that there is no distinctive opening connecting the two cavities.

Histological sections of the siphosomal wall of *Angelopsis euryale* show that there is a well developed endodermal lining to the central cavity of the siphosome. The mesogloal layer is extraordinarily thickened and its inner region is completely homogeneous. Its outer region is penetrated by the peripheral network of canals, also lined by endodermal cells, and external to these canals the mesogloea is divided into radially arranged columns. It is construed that these columns may be lined by the longitudinal ectodermal muscle fibres that Garstang (1946) commented on in the siphosomal stems of other physonect siphonophores. A large radial canal is seen to penetrate through the mesogloea in one section. This canal is lined by endoderm and it is destined to connect with the canal system of a cormidial base. This radial canal does give off branches, some of which probably connect with the peripheral canal system.

Discussion. The presence of a large, thick-walled cavity in the siphosomal region is taken here as a characteristic of the genus *Angelopsis*. Since the corms of the specimens of *Angelopsis euryale* are so denuded, the internal configuration of the corm must be taken as one of the major systematic characters and the question arises as to whether there is sufficient morphological evidence to distinguish the present species from *A. globosa*. In his original description of *A. globosa* Fewkes (1886, p. 973) clearly stated, 'The thickened region [siphosome] is found to have a cavity within (cav.b) [see figure 5b] and to be separated...from another cavity (cav.l) [cav., hypocystic cavity] just below the inner air sac [of the pneumatophore]'. However, in his expanded description Fewkes (1889, p. 154) stated, 'The interior is hollow, forming a [single] cavity which is destitute of an external orifice. This cavity is divided into regions and is lined

by a more or less cartilaginous plate... Directly below the air float the cavity of the polyp-stem forms a thin, disk-shaped recess, the upper walls of which are formed by the float, the lower by lamellar folds of the cartilaginous plate which lines the cavity of the polyp stem. A large orifice or communication leads from this vestibule into the main cavity (cav.b) [see figure 5d] of the polyp stem'.

Thus there is a complete contradiction in these descriptions, one having the nectosomal and siphosomal cavities completely separated, and the other having them joined by a large orifice. It is, of course, impossible to assess the true situation without a re-examination of the original material. However, one feature of Fewkes's illustrations, taken at their face value, is that the siphosomal wall of *A. globosa*, especially in the upper region, is much thicker than that seen in *A. euryale*, and the siphosomal cavity correspondingly smaller. However, a further difficulty in comparing the internal structure of these two species arises over the canal system in the siphosomal wall of *A. globosa*. Fewkes (1886) made no mention of any canal system, but in his 1889 paper he stated (p. 153), 'the polyp stem is thickened and its walls penetrated by a network of canals, which seem to ramify in all directions through it'. It is interesting to contemplate how much of Fewkes's later paper might have been coloured by Haeckel's description of the Auronectidae. Although Fewkes was vehement in his attacks on Haeckel, none the less he looked for and described all the morphological features that Haeckel had considered as relevant. Since Haeckel described a peripheral network of anastomizing trunk canals in the siphosomal walls of *Auralia profunda*, then perhaps Fewkes's observations of a similar arrangement in *A. globosa* was an attempt to validate the synonymy of the two species. Fewkes's figure (figure 5d) shows at least one canal (t) in cross section, while others are said, in the legend, to run longitudinally. If this arrangement of a network of anastomizing canals throughout the siphosomal wall is indeed present then it would contrast markedly with the organization of the gastro-vascular canal system in *A. euryale*. In this latter species the thickened siphosomal wall is, for the most part, devoid of any such network of canals and is only penetrated by radial canals.

There is one other morphological character by which one can infer that *Angelopsis euryale* is distinct from *A. globosa*, as far as the inadequate description of the latter species allows. This character concerns the number of nectophoral lamellae present in the nectosomal region. In *A. euryale* there are from eight to ten widely spaced, well developed lamellae present. Fewkes makes no mention of their number in *A. globosa* but, as was discussed earlier, one can infer that there were at least 15 of them and probably more. In figure 5c, these muscular lamellae appear as thin tissue sheets and this, together with the disparity in numbers, would indicate a difference between *A. globosa* and *A. euryale*. However, it is not absolutely clear how useful these differences in the organization of the nectosome are as systematic characters, although it should be noted that the specimens of the two species were of approximately the same size.

Finally, it is interesting to compare Fewkes's figure (figure 5c) of *Angelopsis globosa* with the photograph of *A. euryale* (figure 6a). Two distinct protuberances (c.b.) can be seen in the latter, both of which are cormidial bases. These protuberances bear a striking resemblance to those illustrated by Fewkes as 'globular bodies', gm and gmm. This is most apparent with the one labelled gm (figure 5c) and the cormidial base to the right of the pneumatophore in figure 6a. One could also infer a resemblance between the body gmm and the other base in these respective illustrations, but it is still preferred to associate gmm with the aurophore (e.g. figure 6b). It should be noted that in the present specimens of *A. euryale* not all the gelatinous cormidial bases, in the upper whorl, are as pronounced as others (figure 6a). This would be

consistent with the fact that only one or perhaps two were illustrated on Fewkes's specimen of *A. globosa*, the present interpretation of their function being correct.

Because of the inadequacies in the descriptions of *Angelopsis globosa* given by Fewkes (1886, 1889), it is concluded that it may prove impossible to identify any new material with that species. The present material is assigned to a new species within the genus *Angelopsis* partly for this reason and partly on the basis of certain specific differences in the internal structure of the corm and the organization of the nectosome. These conclusions may prove unfounded if some new material in better condition is collected or if the original specimens of *A. globosa* become available for re-description.

Genus: Stephalia Haeckel

Stephalia Haeckel 1888a, p. 43; 1888b, pp. 297–298

Bigelow 1911, pp. 300–302

Totton 1965, pp. 92–95

Stephonalia Haeckel 1888b, pp. 299–300

Angela Schneider 1898, pp. 156 (*partim*)

Angelopsis Bigelow 1911, pp. 309–313 (*partim*)

Diagnosis. Rhodaliid siphonophore with smooth-walled aurophore and pneumatophore; with the hypocystic cavity occupying the majority of the nectosomal region; with a solid siphosome traversed by a network of canals, which includes a major branching canal system.

Type species. *Stephalia corona* Haeckel, 1888.

Discussion. Haeckel's (1888b, p. 296) definition of his family Stephalidae was, 'Auronectae with a permanent central canal in the axis of the bulbous trunk, opening at the basal pore by the permanent primary mouth. Tentacles simple, filiform, without lateral branches'. He included two species within this family, namely *Stephalia corona* and *Stephonalia bathyphysa*. Claus (1889) synonymized these two species and, indeed, Haeckel (1888a) himself had failed to distinguish them. Since that time *S. bathyphysa* has been synonymized with *S. corona* almost invariably. However, for reasons that are discussed later the specific name, *bathyphysa*, has been resurrected and, for convenience, this species is included in the genus *Stephalia*, although the description given by Haeckel (1888b) probably is too inadequate even to be sure of its generic status.

Haeckel (1888b) believed that his specimens of *Stephalia corona* were all preserved in a good condition as most gastrozooids were still attached to the corm. He did not, however, note the presence of bracts. Using these specimens he was able, in his opinion, to study the general organization of rhodaliid siphonophores and this allowed him 'to restore the anatomy of *Rhodalia*' (p. 290) and to present his reconstruction of *R. miranda* (see figure 1). 'At the same time this experience teaches afresh the lesson that much care and critical judgment must be employed in the anatomical examination of preserved specimens of Siphonophorae' (Haeckel 1888b, p. 290)!

One of the original specimens of *Stephalia corona* was a monogastric post-larva, which Haeckel (1888b) called an *auronula*. This larva was described (p. 298) as 'a single medusome, the modified umbrella of which is the large, flatly spheroidal pneumatophore...; the manubrium a single large central siphon'. This is a prime example of how Haeckel's 'judgement' in interpreting the anatomy of rhodaliid siphonophores has been coloured by his adherence to his Medusome Theory. For further example, in regard to the supposed presence of a central canal in the siphosome, Haeckel (1888b, p. 288) stated that 'There can be no doubt in my opinion

that this important axial canal is the gastral cavity of the protosiphon, or the primary siphon of the larva, which is the manubrium of the original medusome. Its distal opening is the original Medusa-mouth. This explanation becomes evident by the comparison with the youngest larva observed (*Auronula*...). The entire siphosome is here represented by the single primary siphon. By thickening of its wall and development of nutritive canals in it arises the vascular bulbous trunk of the Auronectae. It corresponds to the basal protosiphon at the distal end of the Physalidae, and to the sterile central siphon of the Disconectae [Chondrophorae].

There is little reason to go into further detail as to how Haeckel's Medusome Theory is largely based on false assumptions, particularly as it is discussed by Totton (1965). Totton does agree, however, that the siphosomal stem arises from the budding zone in the proximal region of the primary gastrozooid (protosiphon or protozooid). As more buds appear this region of the protozooid becomes elongated and the older cormidial elements, together with most of the primary gastrozooid, are displaced basad. Superficially this might appear to corroborate Haeckel's statement, quoted above, but such a conclusion should be treated with caution. Haeckel considered that the gastrozooid could be divided into four sections: the proximal pedicel or stalk; the basigaster to which the tentacle is attached; the stomach or gastral cavity; and the proboscis with its distal mouth opening. As Totton (1965) shows, the protozooid, with its larval tentacle, always is retained at the oral end of the physonect siphonophore and it is the pedicel of this that elongates to form the stem on which the cormidia are borne. Haeckel, however, appeared to believe that it is the whole protozooid of the *auronula* larva that develops into the siphosome of the adult rhodaliid, with only the proboscis and mouth segment remaining, basally, as the opening of the central, gastral cavity. If this interpretation were correct one wonders where Haeckel would have attached the larval tentacle to the mature corm!

It will be shown that the basic tenets by which Haeckel (1888b) established his family Stephanidae, and distinguished the two genera within this family, are totally unfounded. There is no permanent central canal, representing the gastral cavity of the protosiphon, running through the corm. The opening on the basal part of the corm, if such exists, is not the mouth of this larval gastrozooid, nor are the remainder of the cormidia budded off from the walls of it. Thus, as Haeckel's overall concept is considered to be wrong, it is open to question as to whether he gave an accurate account of the internal structure of the corm in *Stephalia corona* and *Stephonalia bathypysa*, or whether he was using his 'judgement' in fitting the facts to the theory. In this instance it is believed that the latter is more likely.

Two species, as well as *Stephonalia bathypysa*, were included by Totton (1965) as doubtful synonyms of *Stephalia corona*. These species are *Steleophysema aurophora* Moser, 1924 = *S. auronecta* Moser, 1925, and *Sagamalia hinomaru* Kawamura, 1954. It will be established (p. 215) that *S. hinomaru* is a distinct species and, according to present definitions, belongs to a separate genus. *S. aurophora* will be included as a doubtful synonym of *S. hinomaru* although its description is probably insufficient for specific diagnosis. Thus the genus *Stephalia* is considered to comprise three species, *S. corona*, *S. bathypysa* and *S. dilata*. These three species, as far as one can judge, possess a hypocystic cavity that is confined to the nectosomal region, and have a solid siphosome that is traversed by a major canal system and an anastomizing network of smaller canals that branch from it. However, this characterization of the genus *Stephalia* may be of questionable significance, for it should be noted that the three species included therein have widely disparate geographical distributions. If additional material were available it might be possible to show that the similarities between the species were the result of convergent rather than

divergent evolution and, thereby, that the species might be better placed in separate genera. At the same time one should take account of Totton's (1965) statement that all the rhodaliid siphonophores with smooth-walled aurophores and pneumatophores may prove to be congeneric once sufficient information is at hand.

Stephalia corona Haeckel (figures 7–9, plates 5–8; figures 10–12)

Stephalia corona Haeckel 1888a, p. 43; 1888b, pp. 297–298, pl. VII (*partim*)
Bigelow 1911, pp. 300–302

Totton 1965, pp. 92–95, fig. 51; pl. 18, figs 1–4

Angela corona Schneider 1898, p. 156

Type material. Four specimens collected at two stations, two specimens at each, during the expedition of H.M.S. *Triton* in 1882: *Triton* st. 106, 22. viii. 1882 at 60° 18' N, 6° 15' W, and *Triton* st. 118, 24. viii. 1882 at 59° 40' N, 7° 21' W. Both stations are in the vicinity of the Wyville Thomson Ridge, northwest of Scotland. A trawl was used at both stations and the bottom sediment was mud. The depths of collection were given as 640 fm (1170 m) for st. 106, and 516 fm (945 m) for st. 118.

Material examined. Unfortunately none of the original specimens of *Stephalia corona* appear to be in existence (see p. 227). However, the additional specimen described by Totton (1965) is housed in the British Museum (Natural History), catalogue number 1973–5–9–5. This specimen was collected by the F.C. *Goldseeker* on 17. viii. 1907 at a very similar locality to the *Triton* specimens, namely 59° 35' N, 7° 00' W, at a depth of 1140 m. The date of collection given by Totton (1965) corresponds with *Goldseeker* st. 53, although the position given in 'D. Liste planktoniques pour l'année 1907–1908 (*Bulletin Planktonique*, Conseil Permanent International pour l'exploration de la Mer)' for this station is minutely different, i.e. 59° 36' N, 07° 00' W. The net used was a fry net which was described in the same journal (p. 72) as 'Nr. 4: fry-net, opening 4' 8" by 6' 3" [ca. 1.4 m by 1.9 m]: gauze?'! On p. 27 of this journal a list of species caught in the two fry-nets fished at st. 53 is given. The specimen of *S. corona* is not mentioned, but many of the animals caught in the net fished to 1140 m, particularly among the amphipods, are definitely benthic organisms (M. H. Thurston, personal communication). This, and the fact that the water depth at this locality is slightly in excess of 1000 m, indicates that the fry net fished the bottom fauna.

In the past few years, several more specimens that are structurally identical to Totton's (1965) specimen of *Stephalia corona* have been collected in benthic, non-closing, nets fished from R.R.S. *Discovery* at certain stations off the northwest African coast. The station data are as follows.

st. no.	date	position		depth m	gear	number of specimens
		N	W			
7846	24. iii. 1972	23° 53.0'	17° 26.9'	1500–1501–(0)	BN2.4	2
7853	26. iii. 1972	25° 51.7'	16° 02.4'	1503–1518–(0)	BN2.4	3
9018	18. viii. 1976	29° 20.2'	12° 35.1'	1635–1658–(0)	O.T.S.B.	1

BN2.4 is a bottom net with a 2.4 m² opening and with 5 mm mesh netting.

O.T.S.B. is a Marinovich otter trawl.

Diagnosis. Rhodaliid siphonophore with smooth-walled aurophore and pneumatophore. The apical part of the aurophore shares a common pneumatocodon wall with the dorsobasal part

of the pneumatophore. The hypocystic cavity is shallow, lying immediately beneath the pneumatophore in the narrowed part of the nectosome. Below it, the remainder of the nectosomal region is occupied by a series of chambers delimited by septa from the nectosomal wall. The siphosome is filled with the mesogloal ground substance through which the gastrovascular canals penetrate. There is a system of major canals which are arranged helically within the corm. These give off branches which pass out to the cormidial bases. A network of branching and anastomizing smaller canals is present throughout the corm. The cormidial bases, which are arranged in a distinctive spiral pattern, bear characteristically shaped bracts. A cluster of type I gastrozoooids, without tentacles, is developed on the base of the corm.

Description. The size of the whole animal will depend on its completeness in preservation. Thus Totton (1965) found that his *Goldseeker* specimen of *Stephalia corona*, to which many complete cormidia and bracts were still attached, measured 25 mm × 27 mm, and 21 mm in height. The *Triton* specimens of Haeckel (1888b) varied in size from 3 mm × 4 mm for the *auronula* larva to 15 mm × 20 mm for the most mature specimen. The smallest of the *Discovery* specimens measured 9 mm in width and 11 mm in height, while the largest was 20 mm by 18 mm respectively. Haeckel's figures of *S. corona* are reproduced in figure 7 (*partim*), and a photograph of one of the specimens taken at *Discovery* st. 7846, immediately after it reached the surface, is shown in figure 8. (Note. It is not absolutely clear how many of the figures in figure 7 (Haeckel 1888b, pl. vii) refer to *S. corona*. Figure 7(g, h) are certainly parts of another species, *Rhodalia miranda*, and presumably figure 7(i) is also, since Haeckel found no tentilla on his specimen of *S. corona*. Figure 7(j-l) do not appear to be referred to in the text, but from the organization of the legend to this plate one can construe that they belong to *R. miranda*.)

Pneumatophore. The pneumatophore varied in diameter from 5 mm in a *Discovery* st. 7853 specimen to 11 mm in a st. 7846 specimen, excepting in the *auronula* larva, where it measured 2.5 mm. It is smooth-walled and generally rounded, although sometimes flattened apically (figure 9a-c). Its colour is an orange-red (figure 8), except for a translucent ring around its widest point, which appears white in this photograph. This ring corresponds with a thickening of the mesogloal layer of the pneumatocodon, which can form a distinctive corona to the pneumatophore. Below this thickened ring, which is more obvious in some specimens than in others, the diameter of the pneumatophore decreases rapidly.

The pneumatocodon or outer wall of the pneumatophore is considerably thicker than the inner pneumatosaccus, except where the latter forms the ceiling to the hypocystic cavity (figure 9g). The thickening of the pneumatocodon is more pronounced laterally than apically. This agrees with Haeckel's (1888b) statements in his general introduction to the Auronectae (*sic*), where he described a twofold difference in the thickness of the pneumatocodon over the surface of the pneumatophore. It is not apparent in his illustrations (figure 7b, f). Fine, radial strands of endoderm were seen to penetrate through the mesogloea of the pneumatocodon. They are similar to those seen in *Angelopsis euryale* and such strands are presumed to be present in most rhodaliid siphonophores. The construction of the pneumatophore has not been studied histologically and it was not possible to determine the disposition of any septa that might traverse the pericystic cavity and connect up the two walls of the pneumatophore. The internal, gas-filled cavity of the pneumatophore was lined by a distinct, chitinous layer (figure 9g) and it is presumed that this was overlain, in the region of the aurophore, by a pad of secondary ectoderm from the pneumadenia. On the basal surface of the pneumatophore, immediately

above the hypocystic cavity, the mesogloea of the pneumatosaccus is greatly thickened and is lined below by a well developed endodermal layer (figure 9g).

Aurophore. The aurophore is a smooth-walled globular structure attached by much of its apical surface to the underhang of the pneumatophore (figure 9a-c). It is bright orange, as can be seen in figure 8, although somewhat obscured by the overlying nectophores. The diameter of the aurophore is approximately one-third of that of the pneumatophore. Its external form is very similar to that illustrated by Haeckel (see figure 7a, d) and it has a pronounced external pore (figure 9a). Because the apical part of the aurophore shares a common pneumatocodon wall with the pneumatophore (figure 7b) it appears more as a process of the pneumatophore than the distinctive structure seen in *Angelopsis euryale*. Internally, a thickened, open-ended, chitinous cylinder can be seen to traverse the aurophore and to connect in with the layer of chitin that forms the pneumatocyst in the pneumatophore. The distal opening of this cylinder was very distinct but the organization of the secondary ectoderm of the pneumadenia within it was not obvious in the specimens examined. It appears to be restricted to within the cylinder, as is shown by Haeckel (see figure 7b), excepting that no pistillum is present. No mushroom-like expansion of this ectoderm was noted (cf. *A. euryale*). Numerous septa could be seen connecting the pneumatosaccus to the pneumatocodon. The hypocystic cavity was in direct communication with the pericystic cavity of the aurophore. Unfortunately the crude sagittal sectioning that was done, by the author, on two of the specimens virtually destroyed both aurophore regions and these, therefore, cannot be illustrated. It was considered prudent to retain intact the remaining, more complete, specimens rather than sacrifice them also to such butchery. It is hoped that in the future an expert will section one of these for histological purposes.

Nectosome. The apical region of the nectosome is, in some specimens, extraordinarily narrow (figure 9d), so that the pneumatophore has a very flimsy connection with the remainder of the corm. This may be due to the collapse and contraction of this region during preservation, as those specimens that still have several nectophores attached have a more rigid appearance (figure 9c). Below this neck the nectosomal region extends down to occupy a broad area on the surface of the main body of the corm. The zones of proliferation lie ventrally in the more apical part of the nectosomal region. Totton (1965) remarked that in the *Goldseeker* specimen there were two nectophoral buds in the region of the zone of proliferation, one of which appeared to be inserted between two larger nectophores, suggesting that a second corona of nectophores was being developed. No signs of this arrangement could be discerned when the specimen was re-examined, although it is not now in such a good condition as Totton's photograph showed it once to be. The two nectophoral buds that were found were closely applied to their zone of proliferation.

The muscular lamellae of the nectophores are long and narrow, stretching from the lower surface of the pneumatophore to a point approximately one-third of the way down the main corm (figure 9c, d). Haeckel (1888b) appears to have been confused as to how many nectophores were once present on his specimens. In his description of *Stephalia corona* (p. 298) he states that from ten to 12 were present, but earlier (p. 286) he remarked on eight to 16. Some of the *Discovery* specimens were too denuded to allow a count of their nectophoral lamellae, but in the others a range of 17-22 was noted. The *Goldseeker* specimen had 19. The nectophores are flimsy, featureless bags which show a pale orange tinge in life (figure 8). The radial and circular canals are distinctly orange (figure 8). The specimens collected at *Discovery* st. 7846 and 7853 were still alive when examined on board ship and the nectophores were seen to be

extended into long cylinders, whose feeble musculature did not allow the active contraction of the whole nectosac. Peristaltic waves of contraction were seen to pass along the nectophores from their bases. There was no apparent synchrony in these contractions and, since they were using their jet-propulsive action in a radial direction, the result was to counteract the effects of the nectophores on the opposite side of the corm. Thus no actual movement of the animal was accomplished. However, the observations on the 'Galápagos dandelions' (see later) show that active and coordinated movement can be achieved.

The hypocystic cavity within the nectosomal region is described below.

Siphosome. Most of the cormidia are arranged in two dexiotropic spirals around the sides of the corm (figure 9d, e), while a few others on the base of the corm appear to be inserted in a different fashion (figure 9f). A distinct, superficial, dark band, believed to consist of a thickened ectodermal layer, is seen to unite the apical whorl of cormidia to the nectosomal region (figure 9d) and, thereby, represents the zone where these two regions of the corm have fused. Branches from this band form thickened ridges which pass downwards to connect with the cormidial bases of the apical whorl. These bands do not represent the course of the gastro-vascular (endodermal) canal system, which lies deeper in the corm at this level. It might be expected that this band of ectoderm would continue to spiral down the corm and be present between the two main whorls of cormidia on the sides of the corm. However, this is not so. Instead, having given off branches to the more apical whorl of bases, the band is found to pass down the corm, at a point immediately below the zones of proliferation on the ventral surface, and to spiral around the corm *below* the more basal whorl, giving off branches upwards to the cormidial bases in that whorl (figure 9e). Because of this arrangement, a distinct gutter appears between the cormidial bases of the upper two whorls which lie to the left and to the right of the ventral line. The second whorl of cormidial bases, which connect with this ectodermal band (figure 9f), is almost complete and the band is terminated, in the centre of the basal region of the corm, by a rounded scar which encircles an opening of the gastrovascular canal system. This scar might represent the original attachment point of the protozooid or larval gastrozoid, as is discussed later, but its arrangement bears no relation to that described by Haeckel (1888b).

The cormidia on the base of the corm do not appear to have any direct relation with those on the two main whorls, in that they may not represent the oldest whorl as would be expected from their basal position, but may be secondarily developed. Their bases either can be traced back to the region of the gutter, which lies immediately below the zone of proliferation (figure 9e), or are found to penetrate between the cormidial bases above and connect with the apical whorl to the right of the ventral line. These cormidial bases are less well developed than those in the major whorls. In addition they appear to be connected to a separate branch of the gastrovascular canal system. A major spiralling canal of this system is seen to lie close to the surface of the corm (figure 9e, f) and to give off branches to each of these cormidia. Although it is difficult to follow the path of this canal within the corm, it does not appear to give off any branches to other cormidial bases. The cormidial components that are attached to these bases and their possible origins will be discussed in detail later.

The major cormidial bases, apart from those on the base of the corm, become highly thickened and their distal regions bear many branches, so that it is difficult to discern the arrangement of their constituent parts. Figure 10 illustrates two quite young cormidial units from the apical whorl of cormidia close to the zone of proliferation. In this instance the arrangement of the

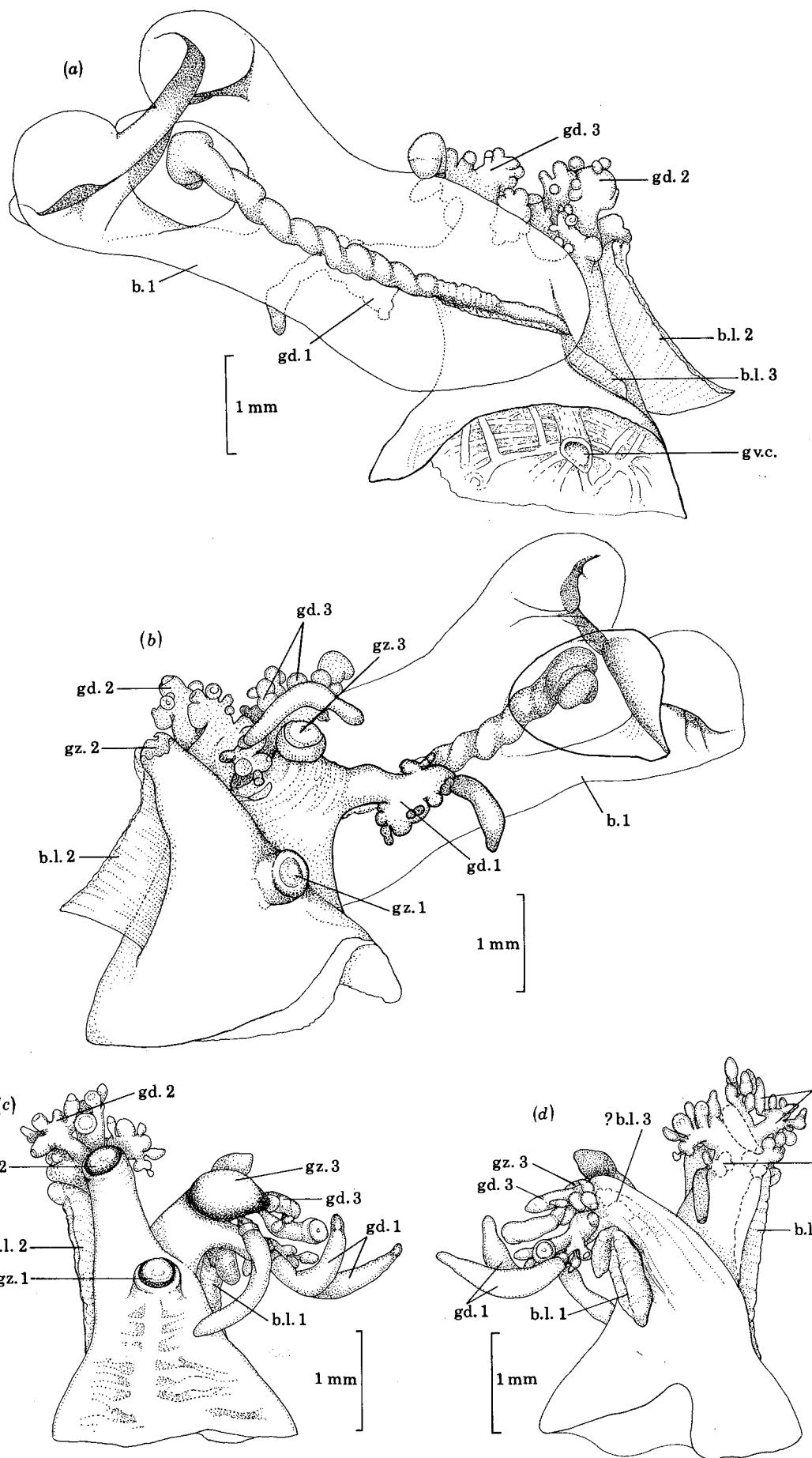


FIGURE 10. Cormidial units of *Stephalia corona* Haeckel. (a, b) Two aspects of a cormidial base from specimen 2 taken at Discovery st. 7846. (c, d) Two aspects of another, younger base from the same specimen. See text for discussion and Glossary for abbreviations.

cormidial elements corresponds, in principle, with that seen in other rhodaliid siphonophores. The cormidial stem contains a thickened mesogloal layer which encloses a major gastrovascular canal as well as a network of regularly arranged, smaller branch canals (figure 10a). At an early stage in development the cormidial unit splits into two very distinct branches, one of which, initially, bears the gonodendron (gd.1) of the first cormidium while the other carries the complete second cormidium. The first gastrozooid (gz.1) to be developed remains attached very low down on the cormidial base (figure 10b) and, as development continues and the base thickens, can become almost completely separated from this base. This gastrozooid is believed to be of type I, and is illustrated in figure 11a. The evidence for this assertion is discussed in the section on *Dromalia alexandri*. It is a simple, elongated structure whose regions, such as the basigaster and stomach, are not easily distinguishable. Some of the youngest of these gastrozooids are found to possess, at their bases, a very reduced, but annulated, tentacle, which bears no signs of having any tentilla (figure 11a). The older type I gastrozooids appear to lose this tentacle entirely, as is discussed later.

The type II gastrozooids are developed by all the succeeding cormidia that arise on each base. These are of typical shape (figure 11b), with a small proboscis and mouth, in the contracted state, an inflated stomach region, which is deep orange (figure 8), a basigaster and a narrow pedicle. Attached to the basigaster is a very large, annulated tentacle, which has a well developed suspensory ligament connected to its ventral groove. On the dorsal surface of the proximal segments of the tentacle, tentilla arise. Each tentillum (figure 11c) is a filiform structure on which three zones can be recognized. Proximally it is a simple tube, but its mid-region is thickened on one side to form the cnidoband, which is strongly armoured with large nematocysts. The terminal process usually is spirally coiled in the contracted, preserved state, but it is presumed that, as in other physonect siphonophores, it can be stretched out to a considerable length. This part of the tentillum bears numerous small nematocysts.

The gonodendra branch profusely and bear numerous bright orange gonopalpons (figure 8) and a multitude of gonophores, also orange. A cupular swelling sometimes is seen at the proximal end of the gonopalpons (figure 10c). Three of the *Discovery* specimens of *Stephalia corona* were found to bear female gonophores, one was male and the other two specimens were too denuded for their sex to be determined. Totton's (1965) *Goldseeker* specimen was male, while Haeckel (1888b) thought that his specimens were monoecious. Attached to the stalk of each gonodendron is a bract, the attachment lamellae of which are plain to see on most of the cormidial bases (figure 10d). It is uncertain whether all the bracts are retained on the mature cormidial bases, which bear at least four cormidia. The largest number found to be attached was two, but it is impossible to extrapolate this back to the living animal. The bracts are relatively enormous (figure 10a, b, 12), being about twice the height of a cormidial base. Totton (1965) described the bracts as being radially arranged so that their trifid, contiguous, truncated, interlocking outer ends appear to form a carapace to the contracted living specimen. Certainly the triangular distal facets of the bracts are suitably constructed so as to form an interlocking carapace, but it is not clear as to what extent the animal could use them as a protective barrier behind which the remaining cormidial elements are withdrawn (see later). Apart from these distal facets, the bracts are relatively featureless, being broad and containing large quantities of mesogloea. Among the rhodaliid siphonophores whose bracts are known, those of *S. corona* are by far the most robust. The bracteal canal is simple and is pale orange (figure 8). At the distal end of the bract this canal bends at a right-angle and passes ventrally into one of the facets (figure 12).

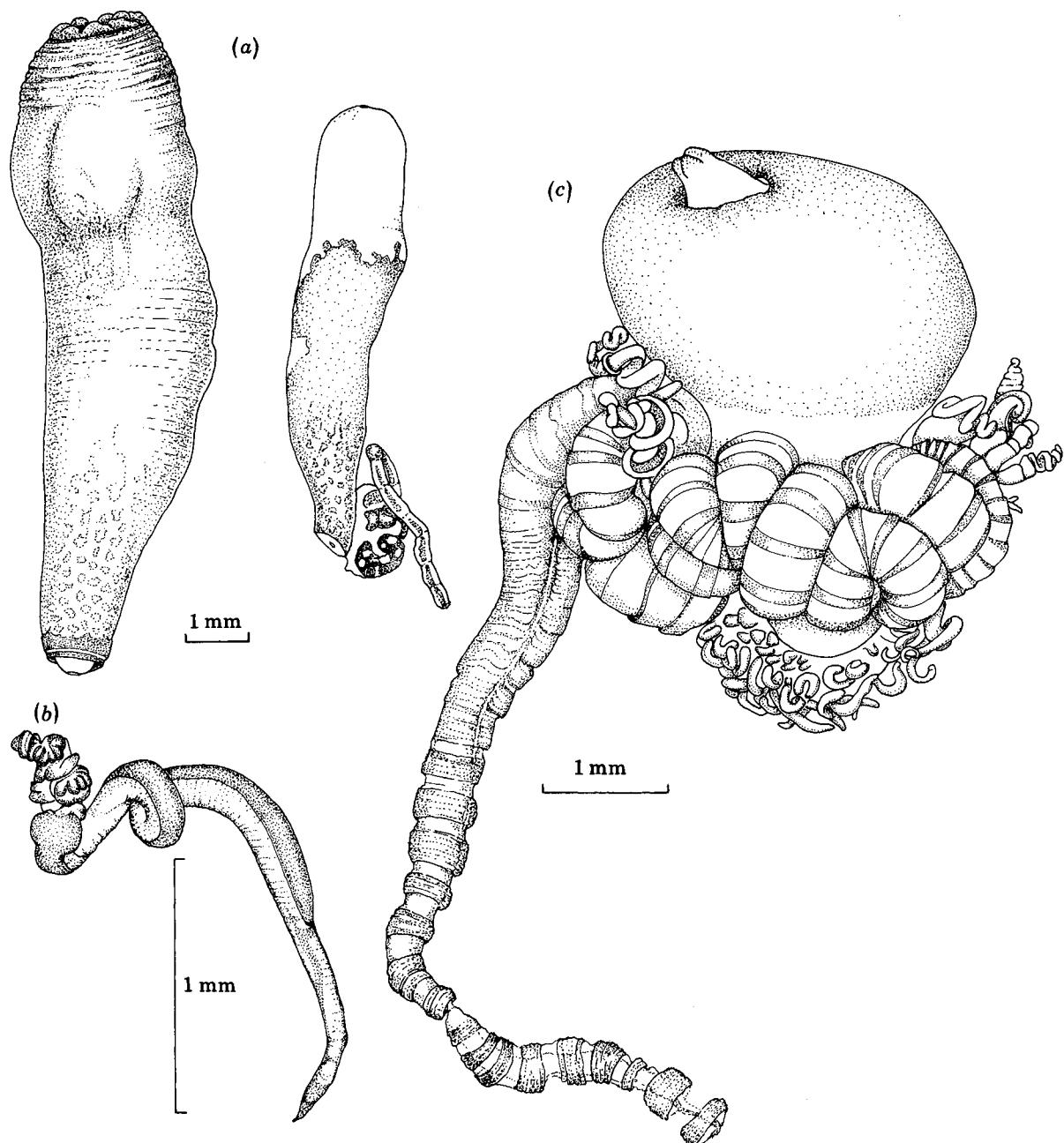


FIGURE 11. Gastrozooids of *Stephalia corona* Haeckel. (a) Two type I gastrozooids; the smaller, younger one still retaining its reduced tentacle. (b) A well developed type II gastrozooid and tentacle. (c) Detail of a tentillum from the tentacle of a type II gastrozooid.

In the developing bracts (figure 12b) the canal occupies a relatively large part of the bract. This canal runs along the ventral surface on the proximal half of the bract, indicating the area of attachment to the gonodendral stalk, before penetrating the mesogloea to form an axial canal distally.

As mentioned above, the deep division of the cormidial units (figure 10) arises at an early developmental stage, when the first gastrozooid (gz.1) becomes split off from the remaining

elements of the first cormidium. From the foot stalk of this gastrozooid, presumably, the second cormidium is budded off and soon overshadows the first, which becomes positioned basally on the side that is further away from the zone of proliferation, as would be expected. These elements form the more basal process of the cormidial unit. The exact point of origin of the third cormidium is uncertain, but it becomes associated with the more apical cormidial process,

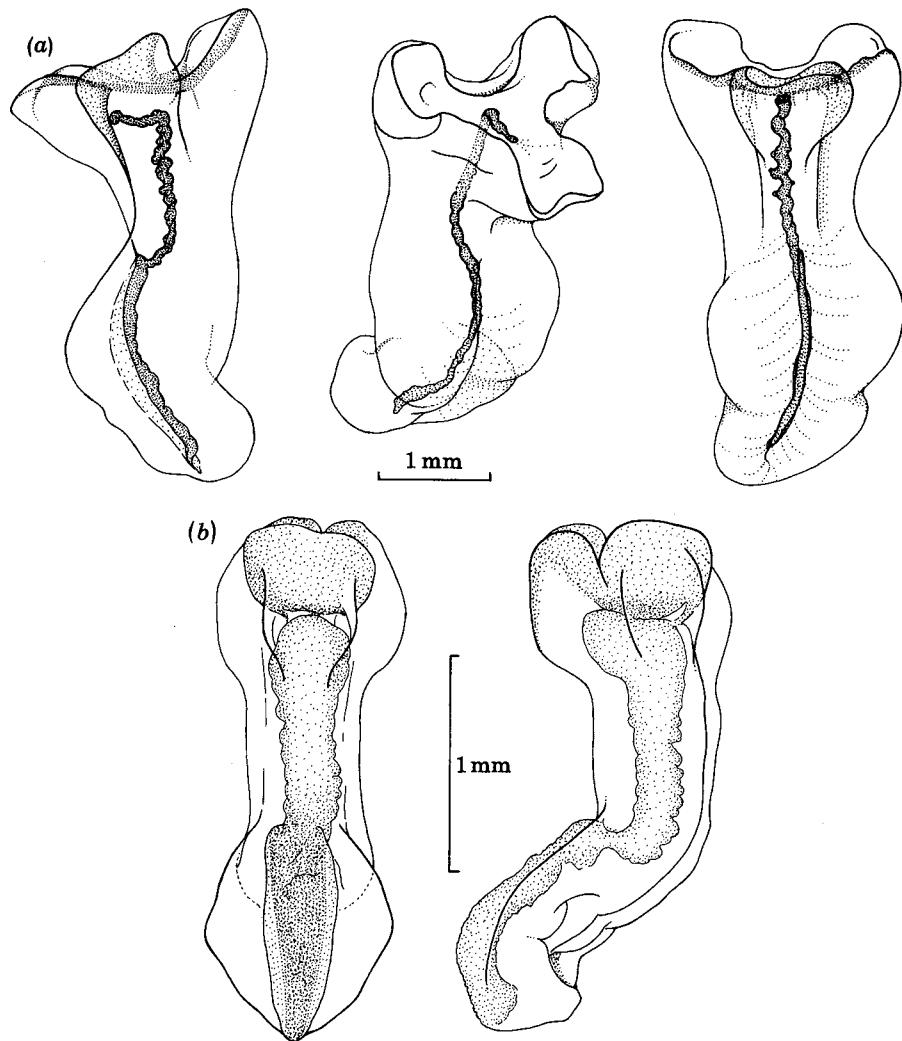


FIGURE 12. Bracts of *Stephalia corona* Haeckel. (a) Mature bracts; various aspects.
(b) Young bract; ventral and lateral aspect.

to which is attached the first gonodendron (gd.1). This is the situation illustrated in figure 10c, d. The bracteal lamellae (b.l.1 and b.l.2) of the first and second bracts can be clearly seen, and each is associated with its respective gonodendron (gd.1 and gd.2). The gonodendron (gd.1) of the first cormidium appears to be somewhat reduced, except for its bract (figure 10a, b), and soon is surpassed in size by the gonodendron (gd.3) of the third cormidium, even though the gastrozooid (gz.3) and tentacle of the latter may only be slightly differentiated as a mitten-shaped process (figure 10c, d). The fourth cormidium develops on the stalk of the second, although it is not certain whether it arises as a bud from the pedicle of the second gastrozooid.

In the young cormidial units illustrated in figure 10, this fourth cormidium is not well developed and its presence only can be inferred from some very small, darkly staining buds (c.4, figure 10*d*). The more mature cormidial units appear as two, almost separate, pyramidal processes connected by a narrow ridge, and with a bracteal lamella running down each of the sides closest to the zone of proliferation. This basic arrangement applies to most of the cormidial units found in the two main whorls on the sides of the siphosomal corm.

On the base of the corm, however, an arrangement of the cormidial units that is comparable with that in *Angelopsis euryale* can be discerned. It was remarked earlier that the band of ectoderm, which spirals around the corm, terminates in a rounded scar, within which an opening of the gastrovascular canal system is found. It is believed that a type I gastrozooid, possibly the protozooid, was attached at this point. Several other rounded scars are present on the base of the siphosome, and it is clear from figure 9*a, b* that type I gastrozooids were attached to them. The immense size of these gastrozooids, in comparison with the rest of the corm, is obvious and clearly these structures could not have been withdrawn behind the bracteal carapace. In the most complete specimen available (figure 9*b*) five such type I gastrozooids were present. None of these possessed any trace of a tentacle attached to them. The well developed tentacles, with tentilla, that can be seen in this photograph are attached to the smaller, type II gastrozooids of the main cormidial whorls. The two specimens (figure 9*a, b*) that still have these type I gastrozooids attached were taken at *Discovery* st. 7853. The general arrangement of these gastrozooids gives strong support to the earlier suggestion that such structures once were present in the specimens of *Angelopsis euryale*. The origins of these basal type I gastrozooids, from the gutter immediately below the zones of proliferation or from the apical whorl of cormidia, give credence to the suggestion that they are secondary developments, not forming part of the sequence of older cormidia in the two main whorls, and thus that their mode of development is comparable with that in *A. euryale*.

Internal structure of the corm. The hypocystic cavity forms a distinct, shallow cavity in the apical part of the nectosome, immediately below the pneumatophore (figure 9*g*). It is delimited from the latter by the thickened pneumatosaccus, which includes a well developed endodermal layer on its basal surface. A series of intercommunicating chambers, with a wide central canal, occupies most of the nectosomal region below this hypocystic cavity (figure 9*g*). This part of the internal structure of the corm corresponds with that illustrated by Haeckel (1888*b*) (see figure 7*b*), and could be interpreted as a partial infilling of the hypocystic cavity by horizontal septa developed from the nectosomal wall. However, in the siphosomal region, the arrangement of the gastrovascular canals is quite different from that described by Haeckel (1888*b*).

In the basal part of the nectosome some canals, of varying sizes, branch off from the central canal and pass outwards, horizontally, to supply the nectophoral lamellae and to link with the radial canals of the nectophores. The exact arrangement of these canals, however, is difficult to elucidate. The major central canal (figure 9*g*) continues basally into the siphosomal region before branching into three major semi-axial canals. Each of these latter canals then bifurcates to produce canals that pass outwards, at various levels, to supply the cormidial bases (figure 9*g-i*). Meanwhile numerous smaller canals branch off and these divide further and anastomize to form a dense network throughout the corm, and also penetrate into the cormidial bases (figure 9*i*). One of the three major canals is more fully developed than the other two and appears to follow a definite course through the siphosomal corm. It continues basally through the apical part of the corm and then divides into two further branches (figure 9*h*), which travel in a double

helical spiral downwards, each giving off side branches to the cormidial bases. It is possible, as mentioned above, that the more extensive of these branches might supply gastrovascular canals to the cormidia on the base of the corm, while the other supplies the cormidia in one of the major whorls on the sides of the corm. This basic pattern was noted in both the specimens that have been dissected, but in neither was it possible to assess their exact organization. It is evident, however, that there was no central, axial canal in the siphosome, as was described by Haeckel (1888b). Similarly the arrangement was not as a simple spiral canal, giving off side branches to the cormidia, as might be expected if the cormidia had arisen in an orderly sequence from their zone of proliferation. The presence of additional helical canals also might be evidence for the later development of the cormidia on the base of the corm.

Discussion. Haeckel (1888b) established his monotypic genus *Stephalia* on the basis of:

- (a) the presence of a permanent central canal in the siphosome, which connected with the mouth of the protozooid;
- (b) the presence of simple tentacles, without tentilla;
- (c) the presence of rudimentary gonopalpons; and
- (d) the arrangement of the nectophores into a single corona.

In the new *Discovery* material only the last character was found to be applicable, whereas there was no central canal, some of the tentacles possessed tentilla, and the gonopalpons were well developed. As was discussed earlier, in the introduction to this genus, it is felt that much of Haeckel's (1888b) description of his rhodaliid siphonophores was coloured by his desire to make it conform to his Medusome Theory and is, thereby, suspect. Any comparison of new material with his descriptions is made difficult and, as Totton (1965, p. 94) stated, 'we have only Haeckel's idealized drawings and account of what were probably defective specimens as a guide to identification'. It is fortunate that the *Goldseeker* specimen came into the hands of A. K. Totton although, because of its near perfect condition, he was loath to dissect it and so was unable to comment on its internal organization or compare it with Haeckel's description. The *Goldseeker* specimen came from an almost identical locality and depth to Haeckel's *Triton* specimens and this, together with the general similarities between the specimens, due allowance having been made for the probable errors in Haeckel's description, leaves little doubt that they all belong to the same species, namely *S. corona*.

Totton (1965) showed that the tentacles of the *Goldseeker* specimen of *Stephalia corona* were annulated and definitely possessed tentilla, and that well developed gonopalpons were present. The fact that Totton's specimen also possessed bracts, the presence of which Haeckel had never suspected in any of his rhodaliid siphonophores, was another indication that Haeckel's specimens were not preserved in such a good condition as he thought. Another important part of Totton's description was the verification of the assertion by Brooks & Conklin (1891) that each individual rhodaliid specimen was of a single sex, although he mistakenly used the term monoecious in this context.

Although the *Goldseeker* and *Triton* specimens came from a similar locality, northwest of Scotland, the *Discovery* specimens were all taken off the west coast of Africa, about 25° of latitude to the south. Several of these latter specimens possessed bracts that are identical with those of the *Goldseeker* specimen and this serves to identify them as specimens of *Stephalia corona*. It is noticeable that these *Discovery* specimens were collected at a depth (*ca.* 1500 m) somewhat greater than in the earlier records. However, an examination of these new specimens has allowed the clarification of several of the contentious parts of Haeckel's (1888b) original description, as has been pointed out in the sections above.

Haeckel's (1888b, pl. vii) illustrations of *Stephalia corona* are reproduced here in figure 7. The errors in the illustration of the internal organization of the corm (figure 7b) have been discussed already, and it is likely that the mouth opening of the primary siphon (figure 7c) merely represents one of the basal scars to which type I gastrozooids were attached (cf. figure 9f). In addition, it is doubtful whether the structure (h) shown in figure 7e is really an androphore or male gonophore since female gonophores clearly were present on the gonodendron. The so-called siphon or gastrozooid (s) in this figure also is considered to be a misconception and actually represents the stump or pedicle of the gastrozooid, the remainder of which had been detached.

Totton (1965) noted in the *Goldseeker* specimen the presence of several mature gastrozooids which had become detached and (p. 94) 'about three dozen immature ones, the distal ends just peeping out from the globular basigaster in a way characteristic of young gastrozooids'. A re-examination of this specimen shows that the mature gastrozooids, as referred to by Totton, are type I gastrozooids while the so-called immature ones are type II. The functions of the two types of gastrozooid are believed to be entirely different as the evidence from the *in situ* observations on the 'Galápagos dandelions' will show.

***Stephalia dilata* (Bigelow) (figure 4b; figure 13, plate 8)**

- Angelopsis dilata* Bigelow 1911, pp. 309–313, pl. 21, figs 6–8, pl. 22
 Totton 1965, p. 95, pl. xviii, figs 5–7
 ?*Rodalia* sp. Brooks & Conklin 1891, pp. 87–89, figs 1–8

Type material. One specimen from *Albatross* st. 4641, 7. xi. 1904 at 01° 34.4' S, 89° 30.2' W, ten miles south of Île Espaňola (Hood Island), the most southerly island in the Galápagos archipelago. The net used was a beam trawl, which sampled the benthos at a depth of 633 fm (1158 m). The bottom sediment was described as being light-grey globigerina ooze.

Diagnosis. Rhodaliid siphonophore with a smooth-walled aurophore and pneumatophore. The aurophore is globular and attached by most of its apical surface to the basal part of the pneumatophore. In the aurophore, the pneumatochone is elongated with a well developed chitinous sheath, and a few radial septa connect the pneumatosaccus to the pneumatocodon. The hypocystic cavity(?) occupies the whole of the nectosomal region as a free cavity, but basally it may be subdivided into a number of chambers by horizontal, transverse ridges. The nectosome forms a narrow neck to the specimen. The siphosome is solid and is traversed by a major network of canals, which may have a helical arrangement. The reticulum of small gastrovascular canals is restricted to the periphery of the corm.

Discussion. Bigelow (1911, p. 310) stated that he cut the specimen of *Stephalia dilata* in half longitudinally and then sectioned one half radially and the other transversely. This urge to section specimens of rhodaliid siphonophores seems to be derived from Chun's (1897) apparent criticism of Fewkes, as remarked upon by Lens & van Riemsdijk (1908), for failing to section his specimens of *Angelopsis globosa*. However, it seems incredible that all the type material of two rhodaliid species should have been subjected to such a fate (cf. *Archangelopsis typica*) and that the only means by which one can compare new material with the original is by means of a few photographs and illustrations, and the original description. Totton's (1965) judgement in refusing even to sagittally section his specimen of *S. corona*, being the only one in existence at that time, seems a more responsible attitude. To compound the situation it has not proved possible to trace the slide collection of the sections of *S. dilata*.

Another specimen of a rhodaliid siphonophore is included here, with reservations, under the name *Stephalia dilata*. This is the specimen on which the development of the female gonophores was described by Brooks & Conklin (1891). This paper mentions that the specimen was collected during the 1887–88 cruise of the *Albatross* at the locality 00° 46' S, 89° 42' W, which is south of San Christobel (Chatham) Island in the Galápagos archipelago. The coordinates correspond with *Albatross* st. 2817, 15. iv. 1888, where a small beam trawl was used and a bottom sediment of white sand was sampled at a depth of 271 fm (496 m). Brooks & Conklin (1891, p. 87) described the specimen as being ‘probably identical with the genus *Rodalia* [sic], described by Haeckel in his *Challenger Report*’, but they reserved the description of the whole animal to a future publication. This publication never appeared, and it has not been possible to trace the whereabouts of the specimen. It is not housed in the collections at the Museum of Comparative Zoology, United States National Museum, Virginia Institute of Marine Science, Chesapeake Bay Institute or the Johns Hopkins University. The reasons why this animal has been doubtfully ascribed to *S. dilata* are discussed later.

First, the description of *Stephalia dilata* given by Bigelow (1911) will be considered. Bigelow only described the basic anatomy of his single specimen of this species, as it was in a very poor condition with only two young nectophores and a few cormidia remaining attached to the corm. The type specimen measured 12 mm in height by 6 mm in diameter, and possessed the following characters.

Pneumatophore. The pneumatophore (figure 13a, b) was relatively voluminous, measuring 5 mm in diameter. It was smooth-walled and possessed no apparent pigmentation. The walls of the pneumatophore appear to be quite thin although, as in other rhodaliids, it is the pneumatocodon that is the thicker of the two. A few septa are seen to cross the pericystic cavity. It is evident that there was some thickening of the pneumatosaccus on the floor of the pneumatophore, above the hypocystic cavity (see Bigelow 1911, pl. 22, fig. 1), although Bigelow remarked that it was thin in comparison with the lateral walls of the nectosome.

Aurophore. The aurophore was sac-like and smooth-walled, with a single protuberance which, although not confirmed, probably represented the external opening of the pericystic cavity (figure 13a). The aurophore was damaged but the cell layers could be traced sufficiently to establish that the general structure was of the usual rhodaliid form. The pneumatochone, or air funnel (figure 4b), was relatively long and consisted of a thick chitinous cylinder surrounding a plug of secondary ectoderm, in which several large cavities were noted. Bigelow was not able to determine whether or not a disc-like expansion of the secondary ectoderm was present in the pneumatophore itself. The chitinous cylinder is illustrated as completely enclosing the pneumadenia (figure 4b, figure 13b), but Bigelow points out that lateral to this section a distal opening was present. Although no connection between the primary and secondary ectodermal layers could be seen in this region it was presumed that such was once the case. In comparison with *Dromalia alexandri*, Bigelow found that there were relatively few septa connecting the pneumatosaccus to the pneumatocodon. It is interesting to note that Bigelow’s figures show how the upper part of the aurophore and the pneumatophore have an integral pneumatosaccus wall. This is markedly different from the arrangement in *Angelopsis euryale*, but reminiscent of that in *Stephalia corona*.

Nectosome. The apical part of the nectosome was narrow, resulting in the whole of the corm having a dumbbell-like appearance (figure 13a, b). No nectophores were present but their muscular lamellae were obvious although, unfortunately, their number is not given and is

difficult to estimate from the figures given. On the ventral zones of proliferation two very young nectophores and some small cormidial buds were found. The nectophoral lamellae stretched down from the narrow part of the nectosome onto the inflated main body of the corm in a manner reminiscent of that seen in *Stephalia corona*.

Siphosome. The cormidia were situated on conical gelatinous prominences which were apparently arranged in a spiral fashion around the corm. Bigelow (1911) noted that on the youngest bases only a single cormidium was developed, but he did not rule out the possibility that the older ones bore additional cormidia. The gastrozooids were described (p. 311) as being 'of the usual type' and the tentacles were without, or had lost, their tentilla (figure 13c). The gonodendra were borne on gelatinous stalks and had two main branches each of which bore several gonopalpons. The gonophores whose sex could be determined were all female.

Internal structure of the corm. Bigelow (1911) described the hypocystic cavity as forming an extensive chamber extending down from immediately below the pneumatophore to the level where the nectosome joined the siphosome. Its lateral walls were thrown into numerous transverse, horizontal ridges which were traversed by a loose network of canals communicating with the nectophoral lamellae and with the hypocystic cavity. Although this is the configuration drawn by Bigelow (see figure 13b) it does not tally exactly with that shown in his photograph of a radial section of the specimen (Bigelow 1911, pl. 22, fig. 1). This section is from a little to one side of the mid- (dorsoventral) plane, as is indicated by the virtual absence of the pneumatophore in the aurophore. However, in this section the folds in the wall of the hypocystic cavity would appear to be more substantial than Bigelow indicated in his reconstruction (figure 13b), unless one assumes that the nectosomal region had collapsed and become extremely narrow. These folds seem to be organized into a series of cross septa which divide the lower part of the hypocystic cavity into a number of smaller chambers, which presumably communicate one with another. The hypocystic cavity *per se* would, if this interpretation were correct, be restricted to a small chamber immediately beneath the pneumatophore, and the general arrangement would be very reminiscent of that found in *Stephalia corona*, although specific differences are immediately obvious. Bigelow's illustration (1911, pl. 22, fig. 6), however, shows that only small folds are present in the internal wall of the nectosome, although this section is transverse to the aurophore. It is unfortunate that the internal construction of the nectosome cannot be re-investigated but it is most likely that Bigelow's description is accurate and that the section referred to above is misleading, owing to the collapse of the nectosomal wall.

Below the nectosomal region, the hypocystic cavity (or its basal chambers) communicates with a number of canals which branch to form a network ramifying throughout the semi-cartilaginous substance of the solid siphosome. The branching network is densest near the surface of the corm. Bigelow noted that the canals were not all of equal size, but was unable to identify any one as the primary, central canal that Haeckel described for *Stephalia corona*. As has been shown, such a canal does not exist in *S. corona* either and this would serve to negate Bigelow's (1911, p. 311) statement that 'In general appearance the specimen [described under the name *Angelopsis dilata*] resembles the figure given by Haeckel of *Stephalia* ('88b, pl. 6, fig. 32), except that there is no large central primary siphon'. It should be noted that Haeckel's (1888b) plate vi actually illustrates *Stephonalia bathyphysa* not *S. corona*, but it is presumed that Bigelow was treating the two species as synonyms.

It is tempting to interpret Bigelow's figure (figure 13b) as showing the presence of a major, non-axial canal system. The arrangement of the canals in radial section is similar to that seen in

Stephalia corona (see, for example, figure 9d) and, thus, it is suspected that a helical arrangement of these canals is present in *S. dilata*. The large branch canals that pass out to the cormidial bases can clearly be seen in Bigelow's plate 22 (figs 7, 8), together with the superficial network of branching and anastomizing smaller canals as in *S. corona*. However it is evident from another of his illustrations (pl. 22, fig. 1) that this smaller canal system is restricted to the outer regions of the corm for most of the siphosome is seen to be composed of mesogloea, with relatively few large canals. The network of canals in *S. corona* is much more extensive.

The internal configuration of the corm in *Stephalia dilata* differs markedly from that here taken as representative of the genus *Angelopsis*, where a large siphosomal cavity is present. Other features that indicate that Bigelow's specimen, which he described under the name *Angelopsis dilata*, bears a closer affinity to the genus *Stephalia* than to the genus *Angelopsis* are:

- (a) the general organization of the aurophore;
- (b) the narrowness of the nectosome;
- (c) the restriction of the hypocystic cavity, with or without transverse septa, to the nectosomal region; and
- (d) the general arrangement of the gastrovascular canal system in the otherwise solid siphosome.

Accordingly the species has been transferred into the genus *Stephalia*. *S. dilata* can be distinguished from *S. corona* by a variety of morphological features but particularly those concerned with the internal organization of the corm, as discussed above. The relationships with *S. bathyphysa* are discussed in the following section on that species.

The geographical distribution of the three species that here are included in the genus *Stephalia* may be useful in distinguishing them. The records for *S. corona* are all from the continental slope of the northeast Atlantic Ocean, while the single record for *S. dilata* is from the equatorial Pacific, off the Galápagos Islands. The specimen of *S. bathyphysa* came from off New Zealand, but with so few records it is impossible to say how valid are such arguments based on geographical distribution. However, this perhaps dubious reasoning will be used to speculate on the possible identity of the specimen on which the gonophores were described by Brooks & Conklin (1891). At that time only five species of rhodaliid siphonophores had been described, all of which had smooth-walled aurophores and pneumatophores. Haeckel (1888b) devoted the greatest space in the section on the Auronectae in his *Challenger* monograph to his description of *Rhodalia miranda* and this is the only one of his four species where much attention was paid to the structure of the gonophores. It is reasonable to assume that Brooks & Conklin would have best compared their information on the development of the female gonophores with that described for *R. miranda*. However, *R. miranda* was collected in the South Atlantic Ocean, a region from which new records for this species also are available, while the Brooks & Conklin specimen came from the Galápagos Islands. Thus, on these tentative grounds of geographical distribution it is considered that their specimen might be related to *S. dilata*, which was taken in the same region. Against this argument could be the fact that there is a disparity in the depths at which these two specimens were collected, and the possible relevance of this factor will be returned to later (see p. 276). Such statements are academic, however, as without a re-examination of the Brooks & Conklin specimen it can never be positively identified. The assignment of any specific name to it is impossible, but for convenience it has been discussed in this section.

Stephalia bathyphysa (Haeckel) (figure 14, plate 9)

<i>Stephonalia bathyphysa</i>	Haeckel 1888b, pp. 299–300, pl. vi
<i>Angela corona</i>	Schneider 1898, p. 156
<i>Stephalia corona</i>	Claus 1889, p. 197 (<i>partim</i>)
	Bigelow 1911, pp. 300–303 (<i>partim</i>)
	Totton 1965, pp. 92–95 (<i>partim</i>)

Type material. Two specimens from H.M.S. *Challenger* st. 166, 23. vi. 1874, at 38° 50' S, 169° 20' E, to the west of New Zealand. The net used was a bottom trawl which sampled the benthos at a depth of 275 fm (503 m). The bottom sediment was globigerina ooze.

Diagnosis. Rhodaliid siphonophore with smooth-walled aurophore and pneumatophore. The pneumatophore is said to have thickened walls and an unusual development of musculature consisting of eight equidistant radial muscles and *ca.* 12 strong circular muscles. Between 20 and 30 nectophores are present which are said to be arranged to form a double corona. The siphosome is said to contain a wide central axial canal. Two types of tentacles were present.

Discussion. Like so many of the early rhodaliid specimens, those of *Stephalia bathyphysa* have not been traced and are presumed to exist no longer (see p. 227). Haeckel (1888b) described his genus *Stephonalia* as being a close ally of the genus *Stephalia*, to such an extent that in his earlier publication (Haeckel 1888a) he had called his specimens of *Stephonalia bathyphysa* by the name *Stephalia corona*. This latter name still appears on plate vi in his *Challenger* monograph although the legend states '*Stephonalia bathyphysa*, n.sp., N.B. — Since this species was formerly confused by me with *Stephalia corona*, it bears the name of this species on the Plate'.

Haeckel (1888b) distinguished the genera *Stephonalia* and *Stephalia* on the basis of four criteria, namely:

- (a) the musculature of the pneumatophore;
- (b) the arrangement of the corona of nectophores;
- (c) the shape of the tentacles; and
- (d) the size of the gonopalpon.

These points will be considered during the following discussion of Haeckel's description of *S. bathyphysa*. Haeckel had in his possession two specimens that were said to be in good condition, although highly contracted and deformed in the preserved state. These two specimens measured 20 and 24 mm in height, by 16 and 20 mm in diameter, respectively. Haeckel's (1888b) illustrations of *S. bathyphysa* are reproduced in figure 14.

Pneumatophore. This was large, flatly spheroidal and distinctive in that there was an unusual development of musculature in its thickened walls. Eight equidistant radial muscles were said to run divergently from the apical centre to the basal periphery, and these were crossed by about a dozen strong muscle rings, of equal width, which encircled the pneumatophore. The illustrations of one of the specimens (see figure 14a, b) show the depressions in the pneumatophore which are presumably associated with this musculature, although the effects of the radial muscles can only be seen in the dorsal view (figure 14b). Neither radial nor circular constrictions are apparent in the illustration of the other specimen (figure 14c). However, while describing the general structure of the pneumatocodon of the auronectid pneumatophore, Haeckel (1888b, p. 283) mentioned that this peculiar development of parallel muscle rings was visible only on the inner surface of the pneumatocodon. It is possible that the general distortion of the specimens

might have produced this wrinkling in the pneumatophore, but such a pronounced effect has not been noted in the other rhodaliid siphonophores with smooth-walled pneumatophores, except perhaps in *Archangelopsis typica*. In one specimen of this latter species, Lens & van Riemsdijk (1908) noted that the pneumatophore was very muscular. It showed external lines and ridges but these were said to be simply thickenings of the pneumatocodon. The organization of these furrows is not symmetrical as it is in *Stephalia bathyphysa*, but it does raise the question as to whether the pattern described by Haeckel (1888b) can be used as a systematic character.

Aurophore. ‘The subspherical aurophore (l) [figure 14a, b] is about the same size as a nectophore’ (Haeckel 1888b, p. 300). This is the complete description given for the aurophore in *Stephalia bathyphysa*. It would appear, from the illustration, to be approximately the same size as that in *S. corona* and to have a similar mode of attachment to the pneumatophore. Although it is clear from the text that Haeckel did investigate the internal structure of his specimens, little detail and no illustrations are given on this subject.

Nectosome. Haeckel (1888b, p. 300) stated that ‘The number of nectophores in this species, judging from the insertions of their pedicles, may be twenty or thirty, and they seem to be arranged in a double corona... But the majority of the nectophores were detached in the two specimens examined, and a more accurate examination of their arrangement is required’. Haeckel did not describe the nectophores specifically and, from the statement quoted above, it is apparent that he himself was not convinced of their arrangement into a double or multiple corona. Haeckel seems to have found it necessary to arrange the nectophores of *S. bathyphysa* into a double corona to reconcile the fact that, in his specimens, the number of nectophoral lamellae was approximately double that found in *S. corona*, which possessed a single, tightly packed corona of nectophores. He used a similar argument in his description of the nectosome of *Rhodalia miranda*, and this point will be discussed in more detail in the section on that species (see p. 236). It is interesting to note that in Haeckel’s illustration of *S. bathyphysa* (figure 14c), which might be an idealized, semi-diagrammatic reconstruction, the nectophores would appear to be arranged in a single corona. Thus this criterion for distinguishing *S. bathyphysa* from *S. corona* is another that is based on Haeckel’s intuition rather than fact. However, if the nectophoral lamella count is accurate, then *S. bathyphysa* would appear to possess more nectophores than *S. corona*, at least in Haeckel’s specimens, although the more recent material of *S. corona* has up to 22 of them present.

No other details of the nectosome are given by Haeckel (1888b).

Siphosome. ‘The complete siphosome... is nearly spherical, and may be about the same size as the nectosome. The sagittal section is very similar to that of *Stephalia* [figure 7b]; but the central axial canal (ac) is wider, and the terminal protosiphon larger [figure 14a, b, (ap)]. The number of cormidia may be sixty to eighty, and they seem to be arranged in a condensed low spiral. The apical part of the trunk is surrounded by a corona of eight larger cormidia, distinguished by very large annulated tentacles, with a slender terminal filament [figure 7c-g]. The other cormidia have slender simple tentacles, similar to those of *Stephalia*. Each gonodendron (g) bears a large palpon (q)’ (Haeckel 1888b, p. 300). This description of the siphosome is rather vague, but a few additional details can be extracted from Haeckel’s general description of the morphology of the Auronectae. For instance, the larger tentacles are said (p. 291) to ‘appear elegantly annulated when examined by a weak lens; each prominent annulus is composed of densely crowded cnidocysts, wanting in the small constricted interval between each two rings’. (See figure 7d, f, g, t.)

No tentilla were found on the tentacles, and Haeckel used this as a criterion for subdividing his order Auronectae into two families, the Stephanidae without tentilla, and the Rhodalidae with them. Totton (1965) pointed out that tentilla were present in *S. corona* and considered that their presence or absence was merely a question of the completeness of the specimen. As was shown for *S. corona* this is not entirely accurate, as there are two types of tentacle, one of which possesses tentilla and the other does not. It should be noted, however, that Haeckel (1888b) is the only author to have described two types of tentacles on rhodaliid siphonophores. This observation has been totally ignored by all subsequent reviewers of this family. However, Haeckel's description of the thinner tentacles, as slender non-annulated tubes with equally disposed nematocysts, does not conform with either type of tentacle in *S. corona*. Since *S. corona*, and indeed several if not all rhodaliid species, has two types of tentacles then the third criterion, listed above, by which Haeckel distinguished *S. bathypysa* from that species is confuted. A similar fate also must befall the fourth criterion, the presence of a well developed gonopalpon in *S. bathypysa*, while those of *S. corona* were thought to be rudimentary, since large gonopalpons are present in the latter species.

Although Haeckel gave only a brief description of the cormidia, his illustrations (figure 14d-g) of them are very detailed. For instance, figure 14d illustrates a group of six cormidia, in varying stages of development, arising from a common stalk or pedicle (ab), while in figure 14g a single, well developed cormidium is drawn, to the base of which is attached a cluster of very young, incipient cormidia. It is suggested that both of these figures have been misinterpreted by Haeckel. Referring first to figure 14g, a well developed gastrozooid is seen which has been subdivided into its four main regions (sp, sb, sg and sr). Attached to the basigaster (sb) of this is a large, annulated tentacle, without tentilla. In addition to these parts, Haeckel illustrates some buds (i), and six major, elongated structures, three of which are referred to as young gastrozooids (s) and three as gonopalpons (q). The only morphological distinction between these two forms seems to lie in the cupulate processes on the proximal region of two of the gastrozooids, with the third having a everted distal end, while the gonopalpons are unadorned. However, such cupulate processes are frequently seen on the gonopalpons of various rhodaliid siphonophores, especially *S. corona* (see figure 10c) and, thus, it is suggested that all six of these structures are gonopalpons. Certainly they appear to be associated together into one major group on which the buds (i), presumably of gonophores, also are attached. Hence, figure 14g is thought to illustrate a single, but incomplete, cormidium composed of a large gastrozooid and tentacle, and a gonodendron with six gonopalpons and some gonophore buds.

This conclusion might also help in the interpretation of figure 14d, where six gastrozooids (labelled I-VI) are illustrated. Here one has to assume that an element of idealization has been applied to the figure. Of the six gastrozooids, four (III-VI) have been drawn with obvious tentacles attached, while another (II) appears to have the characteristic mitten shape of a developing gastrozooid and tentacle, and the last (I) is a bud. It would be somewhat unusual, but perhaps not impossible, to have six cormidia attached to one stalk, particularly such a narrow one, and so another interpretation is suggested. It is considered that gastrozooids VI, IV and probably III are true gastrozooids, while V and perhaps II are gonopalpons. The tentacle of V would have to become part of an extremely well developed one belonging to IV, the latter's tentacle, thereby, having been illustrated wrongly. Gastrozooid I is merely a bud and could be of anything. Attention is also drawn to the bud on the pedicle of the cormidia labelled n. In his glossary, Haeckel identifies n as a nectophore, but no mention is made in the

text to the presence of nectophores on the cormidia, and it is not considered very likely. It is suggested, again tentatively, that the bud might represent a developing bract. It is somewhat surprising, if this bud (n) is an incipient bract, that other bracts or their attachment lamellae were not observed, particularly as the gastrozoooids are so well developed. However, since Haeckel never suspected the presence of bracts on his rhodaliid siphonophores then such details might have been overlooked. Bracts are almost undoubtedly present on all complete specimens of these animals.

Of the four criteria that Haeckel (1888b) used to distinguish his *Stephonalia bathyphysa* from *Stephalia corona*, two, i.e. the structure of the tentacles and gonopalpons, have been shown to be untenable. A third, the arrangement of the nectophores into a double corona, is thought to be purely speculative; while the fourth, the musculature of the pneumatophore, might be a specific character or might simply be the result of the shrinkage and distortion of the specimen during preservation. It might appear, then, that Haeckel's description of *S. bathyphysa* is inadequate to distinguish this species from *S. corona*, and it is no wonder that Schneider (1898) considered that these two species were different growth stages of a single species. This conclusion has been subscribed to by most subsequent authors, but not in this paper. In contrast, it is suggested here that two features from Haeckel's description of *S. bathyphysa* may be of systematic significance. First, the number of nectophores, 20–30, is greater than that found in most specimens of *S. corona*. Secondly, Haeckel (1888b) indicated that the central, axial canal in *S. bathyphysa* was somewhat larger than that in his specimens of *S. corona*. Although it has been shown that no such axial canal exists in *S. corona*, one wonders if Haeckel actually had observed a truly axial cavity in the siphosome of *S. bathyphysa*, which led him to interpret a similar, but narrower, organization in *Stephalia corona*. This supposition is based on the fact that an axial cavity, although clearly not representing the cavity of the protozooid as Haeckel supposed, has been found in the 'Galápagos dandelions' (see p. 259). Nevertheless, unless the original material is found it would appear that the internal organization of the corm of *S. bathyphysa* will remain a mystery.

In conclusion, it has been shown that Haeckel's (1888b) description of his *Stephonalia bathyphysa* is most probably inadequate for specific recognition, unless the construction of the pneumatophore can be established as a true systematic character. Most of the morphological features of his specimens point to a close relationship with *Stephalia corona*, but it is felt that there might be sufficient justification to maintain them as two separate species within the genus *Stephalia*. This contention is based on the fact that, apart from the possible differences in the number of nectophores and the internal construction of the corm, the geographical distribution of these two species is very different. As was pointed out in the section on *S. dilata*, the dearth of data on rhodaliid siphonophores makes it difficult to establish the distributional ranges of the individual species. However, for the present, this argument again will be used as part of the evidence in establishing *S. bathyphysa* as a distinct species. It must remain an enigmatic one until further material is collected, but it should be pointed out that, if this material is found to have a narrow, axial cavity in its siphosomal region, then it would be necessary to remove the species from the genus *Stephalia*.

Genus: Sagamalia Kawamura

Monotypic genus for *Sagamalia hinomaru* Kawamura, 1954.

Sagamalia hinomaru Kawamura (figure 15)

<i>Sagamalia hinomaru</i>	Kawamura 1954, pp. 116–118, pl. 4, figs 1–9
? <i>Steleophysema aurophora</i>	Moser 1924, pp. 495, 501, figs 476b, 483
? <i>Steleophysema auronecta</i>	Moser 1925, pp. 503–505
? <i>Stephalia corona</i>	Totton 1965, pp. 92–95

Type material. One specimen taken by the boat of His Majesty the Emperor of Japan, on 23. viii. 1935, at Minami-Amadaiba, off Kurosaki in Sagami Bay, Kanagawa Prefecture, Japan. Approximate coordinates 35° 10' N, 139° 30' E. The net used was not mentioned by Kawamura (1954), but the depth of collection was said to be 450 m.

Material examined. His Majesty the Emperor of Japan graciously allowed me to examine the specimen of *Sagamalia hinomaru* which is housed in the biological collections at the Tokyo Palace.

Diagnosis. Rhodaliid siphonophore with smooth-walled aurophore and pneumatophore. The aurophore is very small and has an indistinct external pore. Approximately 12 or 13 nectophores are present. The siphosome is not a bulbous corm, but may be a narrow stem on which the cormidia are spirally arranged, or it may contain a large thin-walled cavity. Bracts of a characteristic shape are present.

Description. The description given here is based largely on that of Kawamura (1954), with a few additional remarks derived from a re-examination of the material. The corm measured ca. 22 mm in height by ca. 15 mm in width, although the nectosomal region, including the nectophores, measured ca. 20–23 mm in diameter. A sketch made of the specimen at the time of collection shows that the pneumatophore, the canals of the nectophores and the distal halves of the siphons were all a brilliant red.

Pneumatophore. A thin-walled, elliptical structure measuring 12 mm by 8 mm in diameter. The internal configuration was not investigated.

Auophore. Minute, spherical, smooth-walled; with an indistinct external pore. It is approximately 3 mm in diameter.

Nectosome. Twelve or 13 nectophores were present attached to the corm (figure 15a). These nectophores are long, ovate structures, up to 9 mm in length. Thin muscular lamellae attach them to the nectosomal region of the corm. Some buds of nectophores were noted on the ventral zone of proliferation. In the present state of preservation the pneumatophore and nectosome remain attached to each other, as in Kawamura's (1954, pl. iv, fig. 1) photograph, while the siphosome has become disassociated and only some individual cormidal components could be recognized.

Siphosome. The cormidal bases are not fused to form a bulbous corm, but the pyramidal cormidia appear to radiate out from a narrow stalk (figure 15b). Because the corm had fallen apart it was not possible to determine whether the cormidia were arranged into spiral whorls. The large, thick-walled gastrozooids had thick, muscular tentacles attached to them. The tentacles are annulated but no tentilla were noted, and are presumed to have been lost, unless all those tentacles present belong to type I gastrozooids. Kawamura (1954) stated that some of the tentacles were not attached to gastrozooids but bore lumps of gonodendra near their distal ends. This is rather confusing and one would suggest either that he had mistakenly

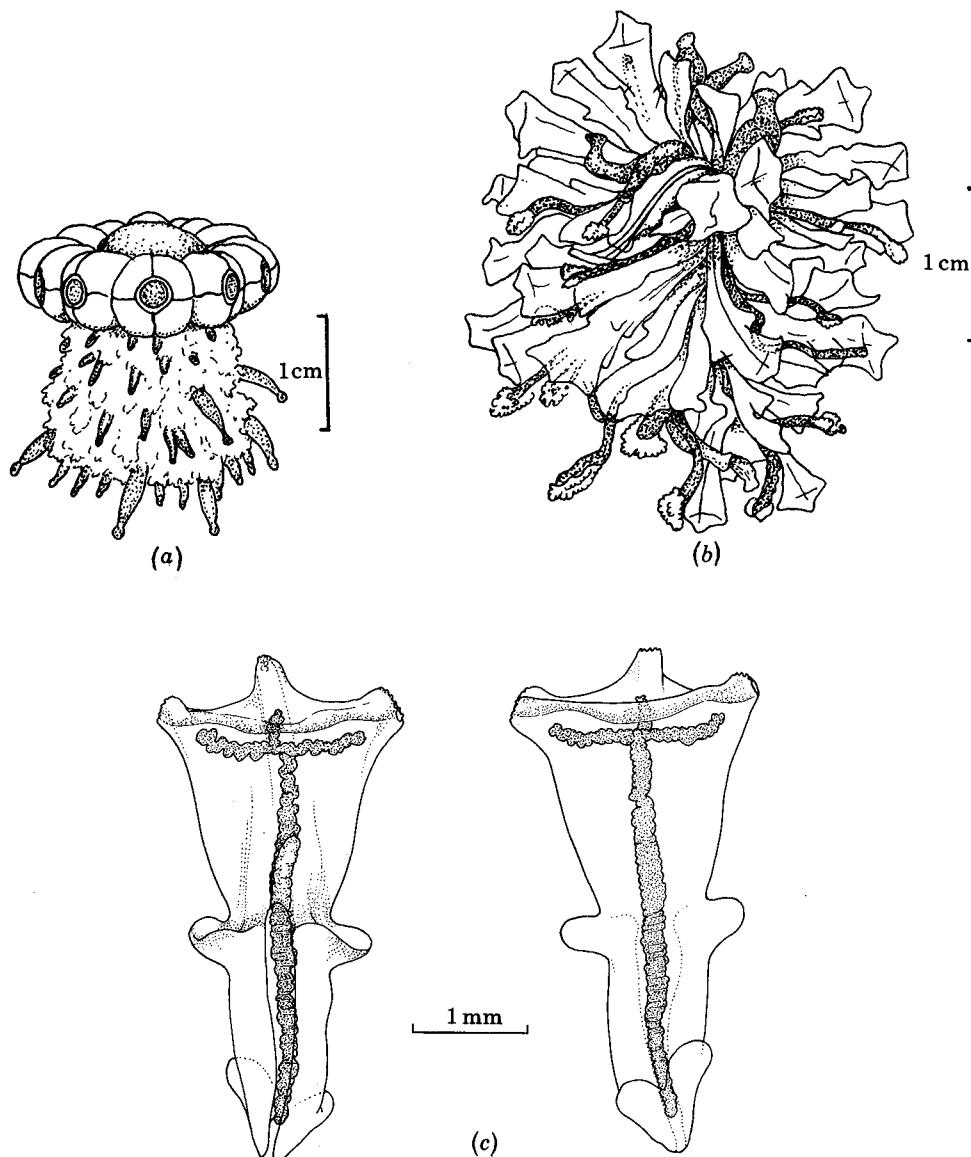


FIGURE 15. *Sagamalia hinomaru* Kawamura. (a) Sketch made of the animal before it was preserved. (b) An aboral view of the siphosome. (c) Ventral and dorsal views of a bract. Diagrams (a) and (b) have been redrawn from Kawamura (1954, pl. iv, figs 3 and 4 respectively, the former originally having been coloured).

identified some gonopalpons as tentacles or that some gonophores had become detached and had adhered to the broken off tentacles. This observation could not be verified on re-examination of the specimen. The gonodendra themselves were devoid of medusoid appendages.

A truly characteristic feature is the structure of the bracts (figure 15c), which are quite unlike those of *Stephalia corona*. Kawamura (1954) described these as being long, pyramidal, gelatinous structures, with triangular distal ends, the corners of which bore a pad of nematocysts. The lateral wings of the bracts were folded, ventrally, to form a deep groove which enclosed the cormidial stem. The bracts were arranged so as to diverge from the main trunk of the siphosome and to give a false impression of the diameter of the corm itself. From figure 15c some additional features of the bract are worth noting, as they have relevance to the

possible relationship of *Sagamalia hinomaru* with another species, *Steleophysema aurophora*, as is discussed later. The proximal part of the bract is not attached to the stem, but is thickened and recurved, dorsally, to form a distinct heart-shaped process. The simple bracteal canal arises above this proximal process and runs up the bract and lies immediately dorsal to the ventral groove, which represents the region of attachment of the bract to the cormidial stem. The canal is enlarged laterally and, in the proximal half of the bract, is thickened in the dorso-ventral plane. In the mid-region of the bract the canal bends abruptly through a right angle and travels towards the dorsal surface. Then it bends back onto its original plane and continues towards the distal process. At the distal end of the bract the canal divides into three branches, each of which terminates close to a corner of the triangular facet.

The internal organization of the corm was not investigated by Kawamura (1954) and when re-examined the siphosomal region had become so completely disassociated that it was impossible to assess what its organization might have been.

Discussion. Totton (1965) considered that *Sagamalia hinomaru* possibly was a synonym of *Stephalia corona*, and Kawamura (1954) himself remarked that at first glance he had believed his specimen to be allied to that species. However, the construction of the siphosome, in that it was not a solid, bulbous corm, convinced Kawamura that his specimen was unique. This conclusion has been confirmed, although there still remains the problem as to what is the internal organization of the corm. Kawamura's photograph (1954, pl. IV, fig. 2) of the siphosome of *S. hinomaru* is reminiscent of that structure in *Archangelopsis typica*, as illustrated by Bigelow (1913) (see figure 17, plate 10). The siphosomal corm of *A. typica* is known to be a voluminous, thin-walled sac, and it might be construed that the corm of *S. hinomaru* was organized in a similar manner, but that during preservation it collapsed and disintegrated. Conversely the corm may be a narrow stalk around which the cormidia are arranged in a spiral fashion, as seen in some of the 'Galápagos dandelions' (p. 259). However, to take the negative approach, the structure of the corm of *S. hinomaru* certainly bears no relation to that seen in the genus *Stephalia*, or to any other rhodaliid siphonophore with a smooth-walled aurophore. This would indicate, by inference, the distinctiveness of the genus *Sagamalia*. In addition, the structure of the bract appears to be a good systematic character and certainly serves to establish *S. hinomaru* as a distinct species. Unfortunately, since most specimens of rhodaliid siphonophores have been preserved in a poor condition, this character is not always available to facilitate identification and usually one has to rely on other morphological characters. The size of the aurophore in *S. hinomaru* might be of use in this context but the dearth of rhodaliid material makes it uncertain as to whether this is a good systematic character or a result of intra-specific variability. This point will be discussed later (p. 270). Incidentally, Kawamura (1954) stated that the name of his genus, *Sagamalia*, meant a corona from Sagami, the locality of collection, but it actually means Sagami Sea. The specific name, *hinomaru*, means in Japanese a red circle in the centre of a white area, as in the national flag of Japan, and alludes to the distribution of colour in the living specimen when viewed from above.

Another specimen of a rhodaliid siphonophore is included here as a doubtful synonym of *Sagamalia hinomaru*. Moser (1924), while describing the general morphology of siphonophores, referred to two figures where parts of a rhodaliid cormidium were illustrated under the name *Steleophysema aurophora*. No specific description was given, but in the supplement to Moser's (1925) monograph on the siphonophores of the German South Polar Expedition (1901–03) a description of a rhodaliid siphonophore, without illustration, was given under the name

S. auronecta, in remembrance of Haeckel's Auronectidae. Moser (1925) only mentioned a single specimen in this genus, *Steleophysema*, while making no reference to her earlier publication, and so it can be assumed that the name *S. auronecta* is an unjustifiable emendation and that the specimen should have been referred to under the name *S. aurophora*. This inconsistency probably arose because the 1925 monograph was actually finished in 1914, but the outbreak of war delayed its publication.

The single specimen of *Steleophysema aurophora* was taken during the Doflein Expedition, 1904–05. No station data are given and all that is known is Moser's (1925) statement that it was taken at the surface off Japan. Unfortunately it has not been possible to trace the whereabouts of this specimen. Moser's (1925) description, which is summarized below, is lacking in detail and in itself is inadequate to establish the specimen as a distinct species.

The aurophore and pneumatophore were smooth-walled, the walls of the latter being rigid. A narrow opening connected the pneumatocyst (*Luftflasche*) of the pneumatophore with the aurophore, and the aurophore possessed radial septa. The large, rounded, thin-walled nectophores were arranged in a single corona around the base of the pneumatophore. The cormidia were borne on very short, thickened stems, the branches of which terminated in dense tufts, presumably of gonophores. Large, well developed tentacles, which possessed tentilla, were present. The cormidia were described as being complete, in that they carried a complement of distinctive bracts, but the structure of these bracts was not described. The corm itself was said to be very short and thickened, but its internal structure was not investigated. The reproductive parts were thought to correspond substantially with those in *Rhodalia*. This refers presumably to Haeckel's (1888b) description as gonophores of both sexes were mentioned. Since the specimen was preserved intact it is puzzling that Moser was able to describe, albeit briefly, the internal organization of the aurophore and pneumatophore. Perhaps these regions had become transparent during preservation as has been noted in other species.

Moser (1925) suggested that her specimen was in some way related to the remarkable ('merkwürdige') *Rhodalia miranda* but she distinguished it principally by the fact that it possessed complete cormidia with bracts. She agreed with Schneider (1898) that *Stephalia corona* and *Stephonalia bathyphysa* represented different developmental stages of the same species, and suggested that *R. miranda* might also be included in this context. It is strange that she did not include her specimen of *S. aurophora* in this category as, apart from the possession of bracts, the characters that were described apply equally well to all the others. The presence of bracts on the cormidia is merely a concern of the completeness of the specimen and, without a comparison of the bracts in all species, has no systematic significance. It is no wonder that Totton (1965) doubtfully synonymized *S. aurophora* with *S. corona*.

The illustrations of parts of the cormidium of *Steleophysema aurophora* that Moser (1924) provided (redrawn in figure 16a, b) are difficult to reconcile with the structure of the cormidium that is known for other rhodaliid siphonophores. The legends to these illustrations indicate that Moser (1924) considered each cormidium (figure 16a) to be composed of a gastrozooid (gz.) with a (?)annulated tentacle (t.), a palpon (p.), male and female gonophores (Go.♂ and Go.♀) and a large bract (b.) with a distinct bracteal canal. The gonophores (figure 16b) are illustrated in a somewhat idealized form. The polyovan gonophores (P.Go.♀) or, more accurately, the egg pouches arise on short stalks from the stem, and Moser noted four stages in the development from those of the true monovan gonophores. The bud or evagination on the wall of the pouch (st.1) into which an egg begins to migrate (st.2), leads to the formation and further enlargement

to form a mature gonophore (st.3, st.4). New gonophores can arise on the stalks of the egg pouches or on the gonodendral stem itself, and some of these latter buds were thought to be male (Go. δ). This interpretation of the development of the female gonophores is inaccurate, as Brooks & Conklin (1891) had shown, and likewise the presence of male gonophores is considered unlikely.

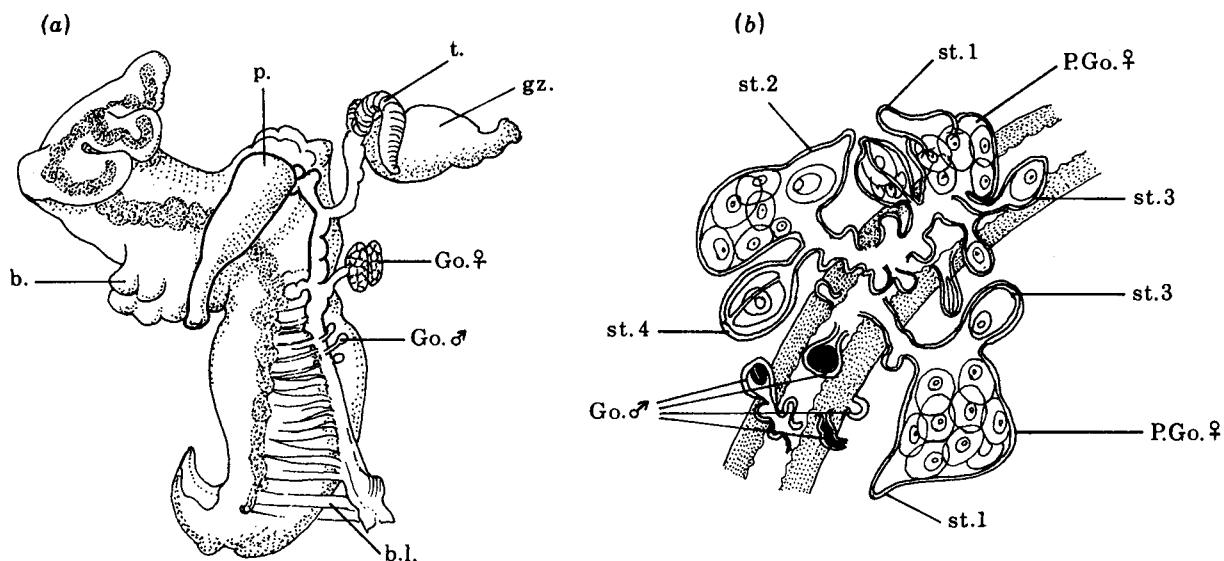


FIGURE 16. *Steleophysema aurophora* Moser ? = *Sagamalia hinomaru*. (a) A supposed cormidium. (b) The budding of the gonophores. See text for discussion of these figures, which are redrawn from Moser (1924, figs 476 and 483 respectively). No magnifications were given.

One of Moser's (1924) figures (figure 16a) was said to illustrate a complete cormidium, but there are several reasons why this is in doubt. First, the positioning of the palpon (p.), on a stalk next to the gastrozooid, is of interest as it does not appear to be directly associated with a gonodendron, i.e. it is not a gonopalpon. Haeckel (1888b) considered that gonopalpons normally were developed and noted no other types. Moser is, in fact, the only person to suggest the presence of palpons as distinct from gonopalpons in rhodaliid siphonophores. Secondly, Moser (1924) was the first person to demonstrate the presence of bracts in rhodaliids. The bract is shown attached to the main (?)cormidial stem, below the branches that bore the gastrozooid, palpon and some gonodendra. As will be shown, with the possible exception of *Archangelopsis typica*, the bracts of rhodaliids normally appear to be attached to the gonodendral stalk, although this attachment may spread down onto the cormidial base as the bracts develop as, for example, in *Dromalia alexandri* (figure 28). This factor also means that the gastrozooid (gz.) is attached in an unusual position to the cormidial stalk. In addition its tentacle (t.) is poorly developed and illustrated, although Moser (1925) states that they are very large. It is concluded from these comments that Moser (1924) has not illustrated a complete cormidium of *Steleophysema aurophora*, but only a gonodendron, with a bract attached to its stalk. The palpon would become a gonopalpon and a similar fate must befall the gastrozooid. To allow for the latter one must assume that the process (t.) is not a tentacle, but perhaps represents some developing gonophores or another, young gonopalpon. Kawamura's (1954, pl. IV, fig. 8) illustration also gives the impression that the bract is attached to the pedicle of the gastrozooid

but his figure 9 and the text indicate that the ventral groove of the bract is merely surrounding the base of the gastrozooid and that it is more likely to be attached to the gonodendron.

It is concluded that, at the time, Moser's (1924, 1925) illustrations and description of *Steleophysema aurophora* or *S. auronecta* were insufficient for specific diagnosis. Even now the true identity of the specimen could only be established if the original material were available for re-examination, but unfortunately its whereabouts have not been traced. It is apparent that Moser did intend to produce a fuller report on the siphonophores of the Doflein Expedition but, as she feared, this paper was never to appear. The only significant morphological features that Moser (1925) described are considered to be: the presence on her specimen of a smooth-walled aurophore and pneumatophore; the fact that the siphosome was very short and thickened; and that the cormidia bore bracts. Since all but two of the known rhodaliid species possess smooth-walled aurophores and pneumatophores then, without further details, these characters cannot be used to indicate the specific identity of her specimen. Further, the description of the construction of the cormidia is considered to be inaccurate and the presence of bracts only can be of significance if the bracts of other species, which undoubtedly were once present on all, can be compared. However, some clue as to the possible identity of Moser's specimen may come from a study of the structure of the bract that Moser (1924) illustrated (see figure 16a). It can be seen that most of the proximal half of the bract, excepting its basal extremity, is attached to the stem by a muscular lamella (b.l.). The distal half of the bract is free and bent away from the stem, although this may be due to distortion during preservation. In figure 16a, the features of the bract that are of particular interest are: (a) the folding back of the proximal end of the bract towards the dorsal surface; (b) the two median lateral processes; and (c) the three distal, digitate processes into each of which passes a branch of the bracteal canal. It will be apparent that all three of these features also are to be seen on the bracts of *Sagamalia hinomaru*, and such an organization has not been noted in the bracts of any other rhodaliid species, where these structures are known. In addition, Moser's description of the corm as being very short and thickened is reminiscent of the arrangement in *S. hinomaru*, and, further, both of these specimens came from the region of Japan. In conclusion, it is suggested that, because of these inferred similarities and taking into account the fact that Moser's description was insufficient for specific diagnosis, *S. aurophora* should be considered as a doubtful synonym of *S. hinomaru*.

Genus: Archangelopsis Lens and van Riemsdijk

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

Archangelopsis typica Lens and van Riemsdijk (figures 4a, 18; figure 17, plate 10)

Archangelopsis typica Lens & van Riemsdijk 1908, pp. 89–99, pls xvii, xviii, figs 137–140
 Bigelow 1911, p. 350; 1913, pp. 79–81, pl. 6, fig. 7
 Totton 1965, p. 96, pl. 19, figs 1, 2

Type material. Two specimens from st. 15 and one from st. 289 of the *Siboga* Expedition to the Dutch East Indies, 1899–1900. St. 15 was occupied on 15. iii. 1899 at 07° 02.6' S, 115° 23.6' E, close to Kangeang Island. The net used was a trawl which collected a sediment of fine coral sand from a depth of 100 m. St. 289 occurred on 20. i. 1900 at 09° 00.3' S, 126° 24.5' E, off the coast of Timor. The trawl collected a residue of mud, sand and shells from a depth of 112 m.

Material examined. Lens & van Riemsdijk made histological sections of all three of their specimens. The resultant slide collection has not been located, but some detached cormidia, nectophores, etc. from the two specimens collected at st. 15 are housed in the Zoological Museum of Amsterdam under catalogue number ZMA COEL 4921.

An additional specimen of *Archangelopsis typica* was described by Bigelow (1913). This specimen was taken by the *Albatross* at st. 4903 on 10. viii. 1906. The position was given as $32^{\circ} 31' 11''$ N, $128^{\circ} 33' 20''$ E, which is the Eastern Sea off Ose Saki lighthouse on the SW corner of Fukue Shima (Goto Island), the southern extremity of Japan. An 8 ft (*ca.* 2.4 m) Albatross-Blake beam trawl was used, and a bottom sediment of grey sand and broken shells was collected from a stated depth of 139 fm (254 m). It is suggested that at this *Albatross* station either the navigational or the bathymetric measurements were in error, as is also discussed for some records for *Dromalia alexandri*. Current Admiralty charts indicate a depth of water at the aforementioned position in the region of 60 fm (110 m), and definitely not in excess of 100 fm (183 m). A depth of 110 m is more in accord with the *Siboga* records, whose depth data are in agreement with the present day charts, for the given positions. Bigelow's specimen of *A. typica* is housed in the collections of the National Museum of Natural History, under catalogue number U.S.N.M. 32993. Thanks to the generosity and cooperation of both the U.S.N.M. and the Zoological Museum, Amsterdam, both sets of material have been made available for re-examination.

Diagnosis. Rhodaliid siphonophore with smooth-walled pneumatophore. The aurophore bears numerous papilliform processes on its external surface. The corm is a voluminous, thin-walled sac, on the siphosomal region of which are the (?) spirally arranged cormidia. The walls of the siphosomal cavity do not possess a network of gastrovascular canals. The monogastric cormidia are borne on stout stalks at the base of which a bract is developed. Secondary, (?) reduced cormidia also may bud from the base of these stalks.

Description. Neither Lens & van Riemsdijk (1908) nor Bigelow (1913) state the size of their specimens, but the *Albatross* specimen measured approximately 17 mm in height and had a maximum diameter of 10 mm. One of the *Siboga* specimens appeared to have been in good condition (see figure 17b), with a few nectophores and many large, annulated tentacles still attached. It is unfortunate that Lens & van Riemsdijk did not preserve it intact. The other two *Siboga* specimens were somewhat damaged. The *Albatross* specimen was denuded of nectophores and most cormidial elements (figure 17a). Although Bigelow (1913) stated that this last specimen had been preserved intact, subsequently it was sagittally sectioned and it now exists in four main pieces, the siphosomal halves having become detached from their nectosomal counterparts. The internal structure of the animals, especially the aurophore, was thoroughly investigated by Lens & van Riemsdijk (1908) as they sectioned all three of their specimens, with a total of 3134 sections, but little mention is made of the external morphological characters. These clearly were only given a cursory glance as is evident from some of the fragments of two of their specimens that are still in existence. These fragments comprise some well preserved gastrozooids and tentacles, some with tentilla attached, some gonodendral constituents and ten detached nectophores.

Pneumatophore. In all but one specimen the pneumatophore was smooth-walled and probably bore apical pigment spots. The exception was the specimen from *Siboga* st. 289 (see Lens & van Riemsdijk 1908, pl. xviii, fig. 138), whose pneumatophore was said to be very muscular, with lines and furrows on its apical surface which were the result of thickenings in the pneumatocodon. This arrangement calls into mind that described for *Stephalia bathypysa*, as was discussed

earlier. The sizes of the pneumatophore ranged from 4.5 mm × 2.5 mm to 10 mm × 6 mm in the *Siboga* specimens, while in the *Albatross* specimen it had a diameter of 9 mm. Both walls of the pneumatophore were relatively thin, with no pronounced thickenings in the mesogloal layers, although the Lens & van Riemsdijk diagram (figure 4a) shows that the mesogloea of the pneumatosaccus is thicker than that of the pneumatocodon. This would be an unusual feature among rhodaliid siphonophores, cf. *Angelopsis euryale* and *Dromalia alexandri*, for instance. Such a pronounced difference in the thickness of the pneumatophoral walls was not noticed in the *Albatross* specimen.

In the region of the aurophore the secondary ectoderm of the pneumadenia spreads over the chitinous lining (pneumatocyst) of the gas-filled cavity to form a disc-like pad. Lens & van Riemsdijk (1908, p. 95) made a cryptic comment that in one specimen, from *Siboga* st. 289, this secondary ectodermal layer was continuous over the whole interior of the pneumatocyst. They stated that a fuller description was to be given later in the text, but this does not appear to have occurred. This specimen also was not in a good condition and the histological study 'hardly shows any well-defined cells' (p. 93). Since in all other rhodaliid specimens that have been examined histologically the secondary ectoderm appears only as an outcrop in the immediate vicinity of the aurophore, the observation made by Lens & van Riemsdijk of a complete secondary ectodermal layer would seem unlikely.

Aurophore. The aurophore is of particular systematic significance as it is not smooth-walled, but instead its outer surface is covered with a large number of papilliform appendages (figure 17a). These appendages are outgrowths of the outer (pneumatocodon) wall of the aurophore and each is terminated by a pore which connects the pericystic cavity with the exterior. Lens & van Riemsdijk (1908) were convinced that the aurophore was absent from their specimens, and made several categorical statements to this effect. They believed, erroneously, that the aurophore represented, externally, the zones of proliferation and thus was ventral in position (figure 17b, z.pr.). However, they agreed that within this structure, which bore these so-called proliferation zones, was present the pneumatochone or gas-secreting area of the pneumatophore. Most of their text on *Archangelopsis typica* is devoted to a detailed description of their sections through the pneumatochone, and a summary of its structure was given earlier. Their reconstruction of a median longitudinal section has been redrawn in figure 4a. The pneumadenia appears to be strongly bifurcated although its chitinous lining is not so well developed as in other rhodaliids, cf. *Stephalia dilata* in figure 4b. Several giant amoeboid cells, containing numerous granulations, were present in the distal region of the pneumadenia. In other sections of the aurophore, Lens & van Riemsdijk (1908, pl. xvii, figs 124–133) found large cavities that once contained the gaseous secretions of the pneumadenia. These coalesced with each other and eventually burst, releasing the gas into the cavity of the pneumatophore. They drew attention to the similarity of the depression left by the burst bubble to the opening, o, which Fewkes (1886) illustrated in his section of *Angelopsis globosa*, as discussed earlier (see figure 5).

Several septa were found to connect the pneumatosaccus with the pneumatocodon of the aurophore.

Nectosome. The nectosome is a narrow, ill-defined zone below the pneumatophore. The zones of proliferation, despite Lens & van Riemsdijk's (1908) assertions, lie ventrally on the opposite side of the pneumatophore to the dorsal aurophore. In the *Albatross* specimen these zones were damaged and only a young nectophore and two cormidial buds could be discerned.

The ten nectophores, which are part of the remnants from the *Siboga* st. 15 specimens, are of the usual rhodaliid type, being flimsy, featureless, cylindrical tubes. The *Albatross* specimen was found to have about 24 nectophoral muscular lamellae (figure 17a) and the *Siboga* specimen (figure 17b) would appear to have about the same number. It would seem that the nectosomal region must have been greatly expanded in life in order to accommodate this large number of nectophores. The collapsed state in preservation is probably due to the fact that this region is thin-walled. The hypocystic cavity occupies the whole of the interior of the corm below the pneumatophore.

Siphosome. While making a preliminary examination of the *Albatross* specimen of *Archangelopsis typica*, Bigelow (1911) remarked that the cormidia might be arranged in a spiral fashion around the thin-walled siphosomal corm. However, in his 1913 paper he decided that the crowding of the cormidia, with the contraction of the corm, made impossible an assessment of the arrangement of the cormidia. The gastrovascular canals of the cormidia appear to be in direct communication with the vast central cavity of the siphosome and there is no obvious network of canals in its walls.

The individual cormidium (figure 18a, b) is borne on a stout, gelatinous stem which is penetrated by a simple canal. Each cormidial unit appears to be, for the most part, monogastric in that it carries a single gastrozooid, with its annulated tentacle, and a gonodendron whose branches bear the gonophores and well developed gonopalpons. Bigelow (1913) drew attention to the relatively large size of these units, in comparison with those of *Dromalia alexandri*, despite the fact that in the latter species the units were polygastric. The gastrozooids themselves show no unusual features and resemble in essence those of *Stephalia corona* (figure 11b). The tentacles which were attached to their basigasters were large, annulated structures with well developed suspensory ligaments. Simple, filiform tentilla arose on the dorsal surface of the tentacle. No involucrum was apparent on these tentilla, but their distal ends were sometimes spirally coiled. Several other tentacle fragments were present which were devoid of tentilla. This appears to be a general feature of the extremely long tentacles of rhodaliid siphonophores (see figure 17b). No gastrozooids with reduced tentacles devoid of tentilla, i.e. no type I gastrozooids, appeared to be present. The attachment point of the gastrozooid to the cormidial stem can clearly be seen in figure 18a, b.

Bigelow (1913) considered that each cormidium possessed at least two, and up to four gonodendra. Alternatively the arrangement shown in figure 18a, b could represent a deeply divided, single gonodendron, since the branches have a common stalk which continues beyond the point where the pedicle of the gastrozooid arises. The gonodendra are substantial and bear simple, thin-walled, but well developed gonopalpons. The gonophores of the *Albatross* specimen were all male, while those in the remnants of the *Siboga* st. 15 specimens were of both sexes, indicating that a specimen of each sex had been collected.

Bigelow (1913, p. 81) remarked, 'One of the most interesting features of the specimen... is that the stalks of the cormidia near the upper end of the bag-like siphosome usually bear from one to three small wing-like muscular lamellae on their outer sides, close to the base. At present there is nothing attached to any of these lamellae, but they are reminiscent, both in structure and in position, of the lamellae to which the bracts are attached in various Agalmids..., and therefore suggest the possibility that *Archangelopsis* may have bracts as well as nectophores'. This was the first reference to the possible presence of bracts in rhodaliid siphonophores, a fact that has subsequently been confirmed for several species. These lamellae can clearly be seen at the base

of the cormidial stem (figure 18*b*). On close examination of the *Albatross* specimen it was found that one of the cormidial units still had a very small bract attached to it (figure 18*a*). Little detail on this young, or vestigial, bract could be seen, except for its expanded distal process. Unfortunately, after illustration this bract became detached from the cormidium.

Figure 18*b* illustrates a more developed cormidial unit. It is concluded that the stalks of the gastrozooid and gonodendron have become united to form a common stem, as that of the gastrozooid appears as a swelling on the side of the gonodendral stalk. This feature also can be seen in the two cormidia on the left side of the corm in Bigelow's photograph of the *Albatross* specimen (figure 17*a*) and possibly these two branches were completely divided from each other at an earlier stage in development of the cormidium. At the base of the main cormidial stem (figure 18*b*) two bracteal lamellae are present and, arising from the axil between the primary lamella and the main cormidial stem, a thin stalk of what might be a second cormidium has been developed. This stalk bears at its distal end a cluster of gonophore buds. As Bigelow (1913) noted, it is not clear whether this stalk represents a second complete cormidium or whether it is solely gonodendral, as a gastrozooid or its scar has not been observed on any of them. It does develop a bract, however, as a bracteal lamella is found at its proximal end. The bracteal lamellae and this gonodendral stalk arise at the base of the main stem on the side that is associated with the primary gonodendron. In contrast to Bigelow's observations, a maximum of two bracteal lamellae was found on each cormidial unit in the *Albatross* specimen.

Discussion. *Archangelopsis typica* is one of the most easily distinguished of the rhodaliid siphonophores. The combination of a smooth-walled pneumatophore and an aurophore bearing external papilliform appendages is unique among the known species. Only one other species, *Dromalia alexandri*, has an aurophore with similar appendages but in this species the pneumatophore bears gelatinous protuberances, and there are many other morphological differences, both internal and external. The three specimens of *A. typica* described by Lens & van Riemsdijk (1908) were taken in the region of the then Dutch East Indies (Indonesia), while the *Albatross* specimen came from the southern tip of Japan. This represents a geographical distribution spanning over 40° of latitude which is the largest range of distribution for any of the rhodaliid species considered in this paper. There can be little doubt, however, that the specimens belong to the same species.

The interpretation by Lens & van Riemsdijk (1908) of the function of the aurophore is not entirely accurate. It appears to be based on an attempt to overcome Chun's (1897) difficulty in reconciling the dorsal position of the aurophore with the fact that it represents the enlarged pneumatophore, which was said to be ventral in some other short-stemmed physonects, e.g. *Physophora hydrostatica*. Chun took the step of interpreting the aurophore as the distal part of the pneumatophore and turned the main cavity of the rhodaliid pneumatophore into the pneumatophore. This interpretation, as discussed in an introductory section, was totally unjustifiable. Lens & van Riemsdijk were, however, in no doubt that the structure, which is now known to be the aurophore, was the pneumatophore but they placed it in a ventral position by misidentifying its papilliform appendages as young buds in the zones of proliferation. They criticized Haeckel's (1888*b*) interpretation of the arrangement of the aurophore and the zones of proliferation when they stated (pp. 90–91), 'It would seem to us, always judging by the facts, obtained in examining our own material, that Haeckel has often drawn too largely on his imagination. It appears to us he made one fundamental mistake and that, by not carefully comparing his material with the drawings of the *Auronectae* which he simultaneously intended for publication (the latter

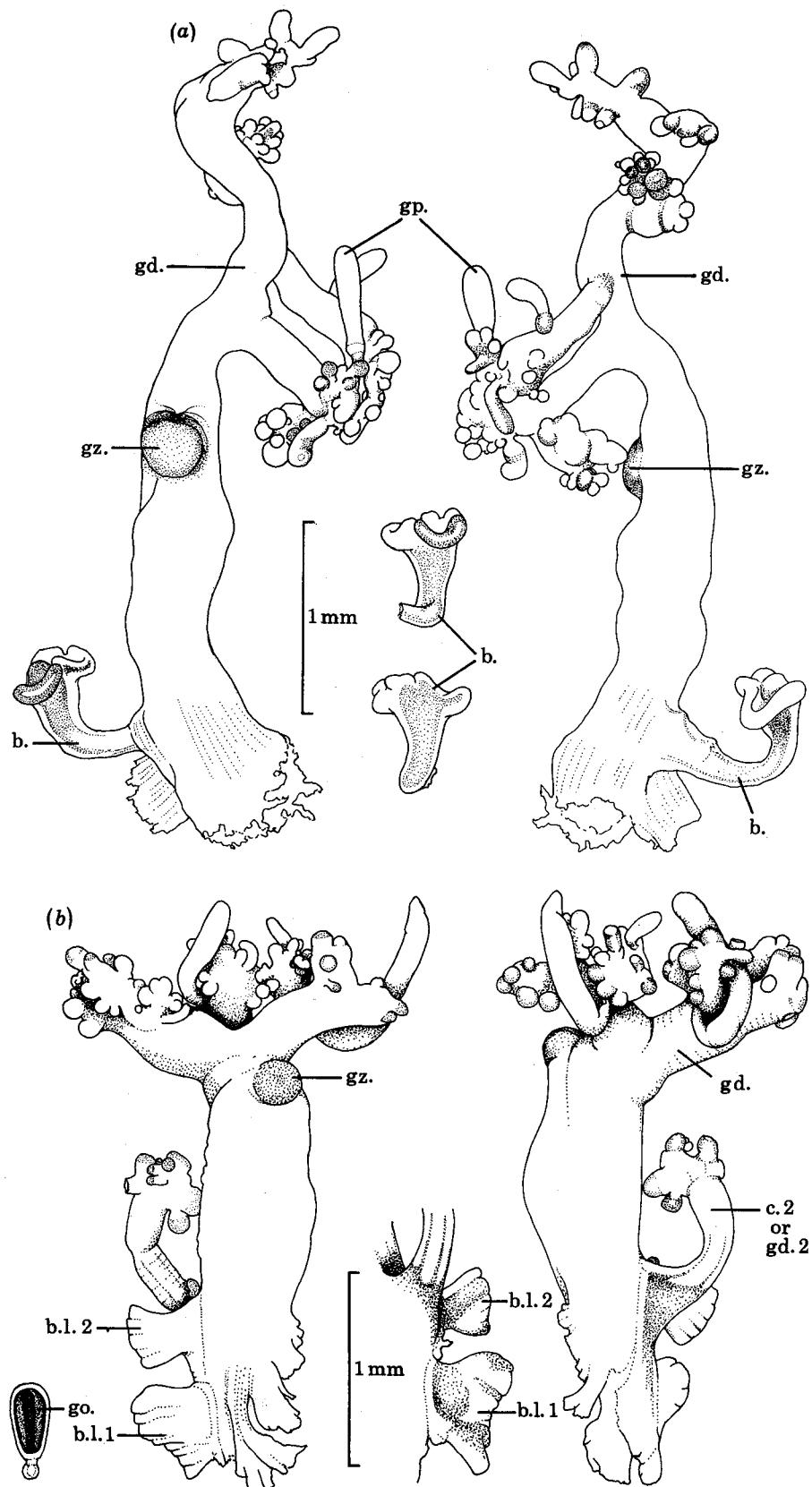


FIGURE 18. *Archangelopsis typica* Lens and van Riemsdijk. (a) Two aspects of a detached cormidial unit with a bract attached proximally. (b) Two aspects of another cormidial unit, showing the development of a second, (?) reduced cormidium. An individual male gonophore also is illustrated. See the Glossary for a list of abbreviations.

being perhaps not made by him but by Mr Giltsch) the mistake was inaugurated... This mistake concerns the position of the zone of proliferation...'. They concluded (pp. 93-94), '...there is no particular medusoid structure, no aurophore to be found in them. The so-called aurophore constitutes externally the modified outer wall of the bunch of youngest appendages, and contains interiorly an apparatus identical to the airfunnel or pneumatophore of *Physonecta*'. Lens & Riemsdijk (1908) claimed to have re-examined Haeckel's specimens of *Rhodalia miranda* and were unable to find the young buds of nectophores and cormidia on the opposite side of the pneumatophore to the aurophore. They could not have looked very hard for even today these buds can plainly be seen on the ventral surface of these specimens, while the aurophore is dorsal. However, they were correct in asserting that the aurophore is not a medusoid structure.

The organization of the cormidia of *Archangelopsis typica* also raises some interesting points. First, the fact that the cormidial units are for the most part monogastric. Most rhodaliids whose cormidial organization has been studied in any detail appear to have polygastric units, in that several complete cormidia are borne on the distal end of a thickened base. The presence, in *A. typica*, of a small gonodendral/?cormidial stalk at the base of the main stem is also unusual. Secondly, the attachment of the bract to the basal region of the stem has not been noted in other rhodaliids, except perhaps the 'Galápagos dandelions' (see p. 263). In the other species, the bract appears originally to be attached to the gonodendral stalk but with further development its attachment lamella tends to extend downwards onto the main cormidial stem (see, for example, figure 28, of *Dromalia alexandri*). It was noted earlier that the gonodendral and gastrozooidal branches appear to have been fused to form the common stem. This may help to explain the positioning of the bract in *A. typica* in that it was once attached to the separated gonodendral branch. Then, instead of the proximal region of the cormidial unit becoming elongated during development, it is the distal parts that have done so. In this way the bract would remain at the base of the stem.

The presence of a single gastrozooid on each cormidial unit poses another problem. In other rhodaliids, with polygastric cormidial units, it has been found that the first gastrozooid to be developed is of type I, whose tentacle is reduced and does not bear tentilla. This is discussed further in the section on *Dromalia alexandri*. However, all the detached gastrozooids of *Archangelopsis typica* possess well developed tentacles with tentilla, i.e. no type I gastrozooids appear to be present. It may be possible that, as in several other rhodaliid species, the type I gastrozooid of the first cormidium was attached low on the stem, or even to the siphosomal corm itself (cf. the 'Galápagos dandelions'), and subsequently has become detached or has regressed. In this way the small, basal side branch, which was considered above as a gonodendron of the second cormidium, might represent the reduced gonodendron of the first, and the major stalk belong entirely to the second cormidium. Such a reduction in the gonodendron of the first cormidium has been noted in some specimens of *D. alexandri*. This arrangement would also explain the presence of type II gastrozooids at the distal ends of the cormidial bases. However, no traces or scars of type I gastrozooids were noted. On the other hand the siphosome of *A. typica* might be organized along similar lines to that found in *Angelopsis euryale* but this is not apparent on the specimen of *A. typica* which is still in existence. It is to be hoped that further material will be collected, or observed, so that the organization of the animal, and in particular its siphosomal region, can be investigated more thoroughly.

Genus: Rhodalia Haeckel

Rhodalia Haeckel 1888a, p. 43; 1888b, pp. 281–304

Angela Schneider 1898, p. 157

Monotypic genus for *Rhodalia miranda* Haeckel, 1888, whose diagnosis is given in the following section.

Discussion. Haeckel (1888b) separated his family Rhodalidae [*sic*] from the Stephanidae [*sic*] on the basis that the former did not possess a permanent axial canal in the siphosome, while their tentacles bore tentilla. As was discussed earlier, both of these characters now are known to apply equally well to the so-called stephanid siphonophores, and Haeckel's classification no longer has any validity. Haeckel (1888b) included two species, in separate genera, within his Rhodalidae, namely *Rhodalia miranda* and *Auralia profunda*. The latter species was inadequately described in the *Challenger* monograph and, for convenience, has doubtfully been synonymized in this paper with *Angelopsis globosa*.

The genus *Rhodalia* was distinguished by Haeckel (1888b) on the basis of the presence of a solid siphosomal corm that was traversed by a reticulum of small, equally sized canals, and of his interpretation of a double or multiple corona of nectophores surrounding the nectosome. These points are discussed in the following section of *R. miranda*. Three of the four *Challenger* specimens of *R. miranda* appear to be the only rhodaliid siphonophores from this historic collection that are still in existence. A letter from Ernst Haeckel (dated 30 June 1903) addressed to R. Kirkpatrick, then the Curator of Coelenterates at the British Museum (Natural History), stated that the residue of the *Challenger* siphonophores had been returned to the Museum immediately after he had completed his monograph. Some *Challenger* material was entered into the B.M.(N.H.) catalogue as numbers 1889–12–6–1 to 1889–12–6–24 (later amended to 1889–12–6–1 to 1889–12–6–27 as three numbers had been duplicated). However, this material consists of specimens of only ten siphonophore species, under 13 of Haeckel's names, and was clearly only a small fraction of the total material. It appears from Haeckel's letter that most of the material was used for anatomical and histological studies and, thereby, was destroyed. Most of Haeckel's own collection of siphonophores was said to have disintegrated during preservation and this might explain why his promised 'Morphology of the siphonophores' was not produced. This is a pity as many of the descriptions of species that were only cursorily mentioned in the *Challenger* monograph were referred to this paper.

Rhodalia miranda Haeckel (figures 1, 7 (*partim*), 20–24; figure 19, plate 11)

Rhodalia miranda Haeckel 1888a, p. 43; 1888b, pp. 302–304, pl. I–V and VII (*partim*)

Bigelow 1911, pp. 300–303

Totton 1965, p. 92

Angela globosa Schneider 1898, p. 157

Type material. Four specimens taken at st. 320 of the H.M.S. *Challenger* Expedition, on 14. ii. 1876. The station was in the southwest Atlantic Ocean, off Argentina, at 37° 17' S, 53° 52' W. The net used was a bottom trawl which sampled the benthos, including corals, crinoids and asteroids, at a depth of 600 fm (1098 m). There is some confusion in the 'Cruise narrative' and 'Summary of results [zoology] of the Expedition' as to the nature of the bottom sediment. The 'Report on the deep-sea deposits' states that the sediments were of blue mud, green grey, fine grained, with a green residue.

Material examined. Three of the four original specimens of *Rhodalia miranda* are housed in the British Museum (Natural History) under catalogue number 1889-12-6-23. Of these three specimens, one is still intact, one has been sectioned sagittally and the third has been sectioned horizontally through the base of the pneumatophore. These specimens appear to be the ones on which Haeckel (1888b) based most of his studies of the morphology of the Auronectae (Rhodaliidae). The specimens of this species are wonderfully illustrated in the *Challenger* monograph, in which pls I-v, comprising 30 figures, plus (?) six figures on pl. vii (see p. 198) are devoted to them. One might presume that Haeckel had some excellent, complete material at his disposal, but a glance at the actual specimens in the B.M.(N.H.) shows that this is not the case. However, Haeckel (1888b, p. 303) does admit that many of his illustrations are semi-diagrammatic or are reconstructions.

The uncertain identity of the specimen of *?Rodalia [sic]* that was in the possession of Brooks & Conklin (1891) has been discussed in the section on *Stephalia dilata*. Apart from this unidentifiable specimen, there are no other records in the literature for specimens of *Rhodalia miranda*. However, thanks to the generosity of Dr Sofia Stepanyants and the Zoological Institute of Leningrad, I have been able to examine a further eleven specimens of *R. miranda*, all of which were collected at localities close to that of the original *Challenger* specimens, namely:

Six specimens collected at st. 1009 of the *Academician Knipovich* on 6. iv. 1967 at 51° 18' S, 56° 31.3' W. The net used was an otter trawl (no. 192), which also collected a residue of sand at a depth of 470–455 m.

Three specimens taken during the same cruise at st. 1021 on 8. iv. 1967 at 49° 00.8' S, 59° 07.6' W. The trawl (no. 204) collected pebbles and sandy mud at a depth of 525–515 m. Two specimens collected in a trawl by the *Zoond* on 18. v. 1974 at 46° 37' S, 59° 23' W from a depth of 1070 m.

DESCRIPTION OF PLATE 11

FIGURE 19. *Rhodalia miranda* Haeckel. (a) Sagittal section through the smaller of the *Zoond* specimens, showing the endodermal processes into the greatly thickened pneumatocodon of the pneumatophore, and the general internal arrangement of the corm. (b) Detail from the other half of the same specimen. Note the extremely long pneumatophore, pieces of which are present, which opens into the pneumatophore in a mid-basal position. (c) Sagittal section through a larger specimen from *Academician Knipovich* st. 1009. Here the opening of the pneumatophore (arrowed) into the pneumatophore is more towards the dorsal side, although the pneumatophore still is very long. (d) Ventral view of the smaller *Zoond* specimen, showing the young cormidial buds in the zone of proliferation. (e) Lateral view of the same specimen, showing the dorsal aurophore and ventral zones of proliferation, and the arrangement of the cormidia on the siphosome. (f) Basal view of the larger *Zoond* specimen, showing the arrangement of the cormidial bases. Scale bars, 5 mm.

DESCRIPTION OF PLATE 12

FIGURE 25. *Dromalia alexandri* Bigelow. A reproduction of Bigelow's (1911) plate 24, to which reference should be made for full legend and glossary. (a) Zones of proliferation with very young nectophores (B. N.); cormidial buds (B. S.) and the cormidial stalks (St. S¹, St. S²) from the two most apical whorls. The muscular lamellae of the nectophores (L. Mu.) are apparent. (Magn. × 4.) (b) An enlarged view of (a). (Magn. × 6.) (c) A further enlargement. (Magn. × 9.) (d) Radial section through a corm, showing the aurophore (X.) with its papilliform appendages (Pa. Pr.). Some large gastrovascular canals (C.) are apparent in the otherwise solid corm. (Magn. × 3.) (e) An enlargement of (d), with detail of the secondary ectoderm (Ec².) in the pneumadenia. (Magn. × 4.) (f) Radial section of the aurophore. Note the cavities in the pneumadenia, and the septa (Sm.) traversing the pericystic cavity. (Magn. × 20.) (g) Transverse median section of the aurophore. (Magn. × 20.) (h) Radial section of axial region of aurophore. (Magn. × 20.) (i) Radial section of the end of one of the papilliform appendages, showing the terminal pore (X.). (Magn. × 40.)

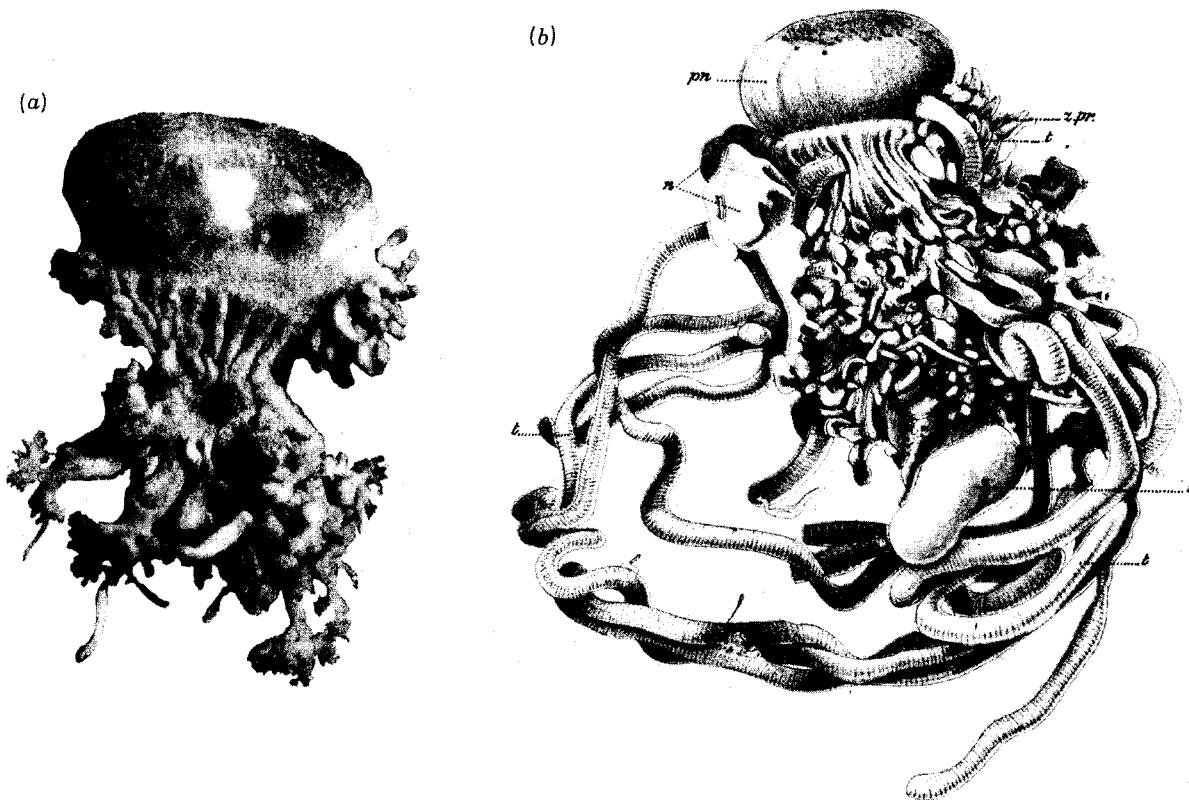


FIGURE 17. *Archangelopsis typica* Lens and van Riemsdijk. (a) Lateral view of the *Albatross* specimen. (Magn. $\times 4$.) Reproduced from Bigelow (1913, pl. 6, fig. 7). (b) Lateral view of the *Siboga* st. 10 A specimen. (Magn. $\times 1.5$.) Reproduced from Lens & van Riemsdijk (1908, pl. xviii, fig. 137). Note the misinterpretation of the papilliform processes on the aurophore as the zone of proliferation (z.pr.), and the large gastrozooids (s) with annulated tentacles (t).

DESCRIPTION OF PLATE 13

FIGURE 26. *Dromalia alexandri* Bigelow. (a) Lateral view of a small specimen (see item 18, table 1) with some very long type I gastrozooids, some of which have everted proboscis segments. (b) Other side of the same specimen. Note the cormidial buds in the zone of proliferation on the ventral (right) side, opposite to the papilliform aurophore. The ectodermal bands connecting each cormidial whorl are visible, as are some of the major gastrovascular canals. The more superficial canal system is barely developed. (c) Detail of the pneumatophore and aurophore from a young specimen (see item 5, table 1). Note the wide, cone-shaped space left after the removal of the pneumatocyste, and to the left of this the small hypocystic cavity (arrowed), which connects with the pericystic cavity of the aurophore. (d) Sagittal section through the pneumatophore of a larger specimen (see item 3, table 1), showing the gelatinous protuberances into which processes from the endoderm of the pneumatocyste penetrate. Note the absence of a hypocystic cavity below the pneumatophore. (e) Same sagittal section overall, showing the arrangement of the major gastrovascular canal system in the corm. (f) Detail of the surface of the corm in the same specimen, showing the superficial canal system, together with the larger, deeper-lying major system. The bracteal lamella of the first cormidium can be seen on the cormidial base to the right of the picture.

Scale bars, 1 mm.

DESCRIPTION OF PLATE 14

FIGURE 27. (a) *Dromalia alexandri* Bigelow. A partially denuded specimen that has recently been brought to the surface. Photograph kindly supplied by and reproduced with permission of Dr A. Fleminger. (b) *Dromalia alexandri* Bigelow. An *in situ* photograph taken during dive 422 of the submersible *Deepstar*. (c) *Thermopalia taraxaca* sp.nov. *In situ* photograph taken by and reproduced by kind permission of Dr J. B. Corliss. The photograph was taken in the Galápagos Rift during the 1977 series of dives. (d) *Thermopalia taraxaca* sp.nov. *In situ* photograph taken during *Alvin* dive 891 to the 'Garden of Eden' at the Galápagos Rift site. This photograph is reproduced by kind permission of Dr R. R. Hessler.

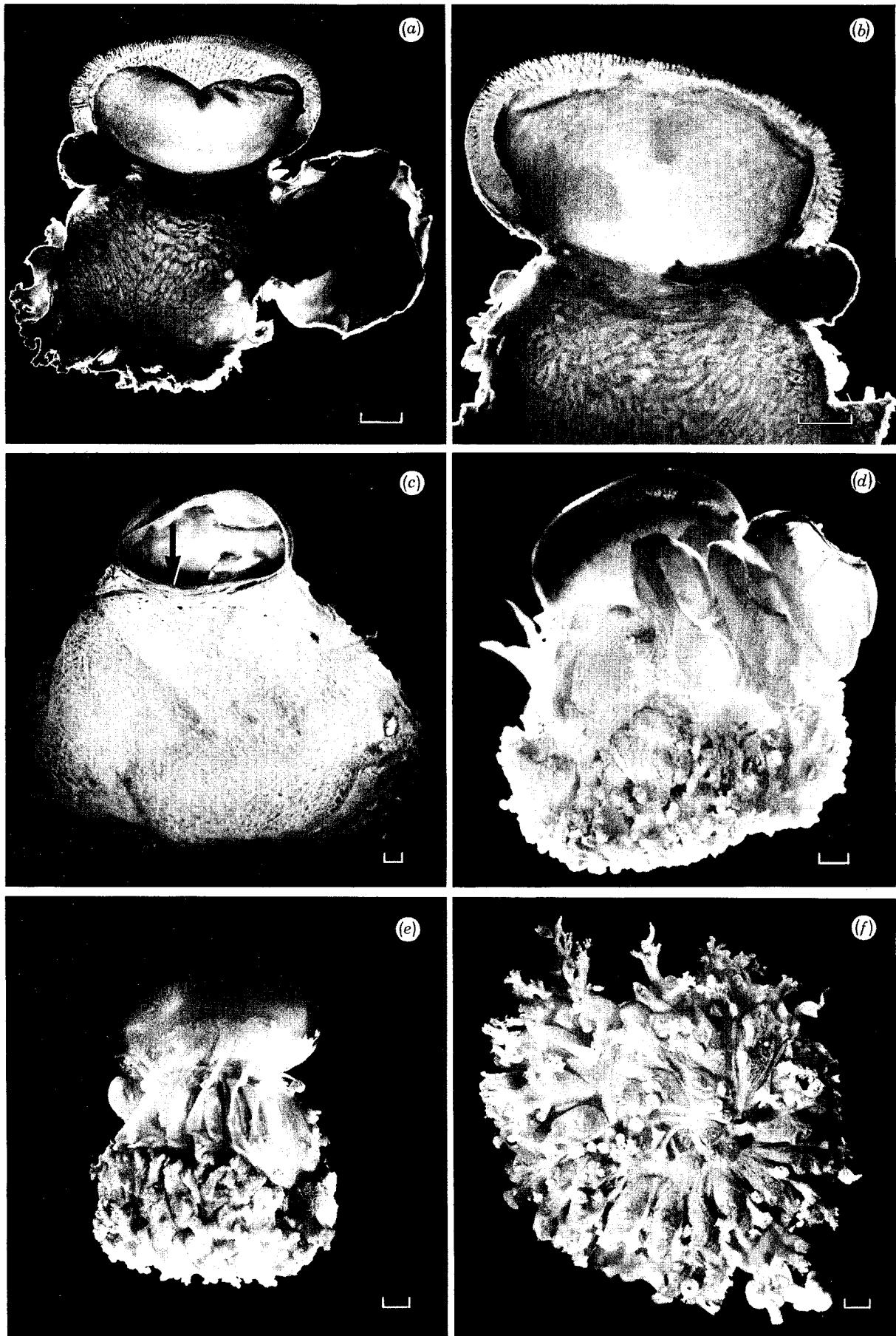


FIGURE 19. For description see page 228.

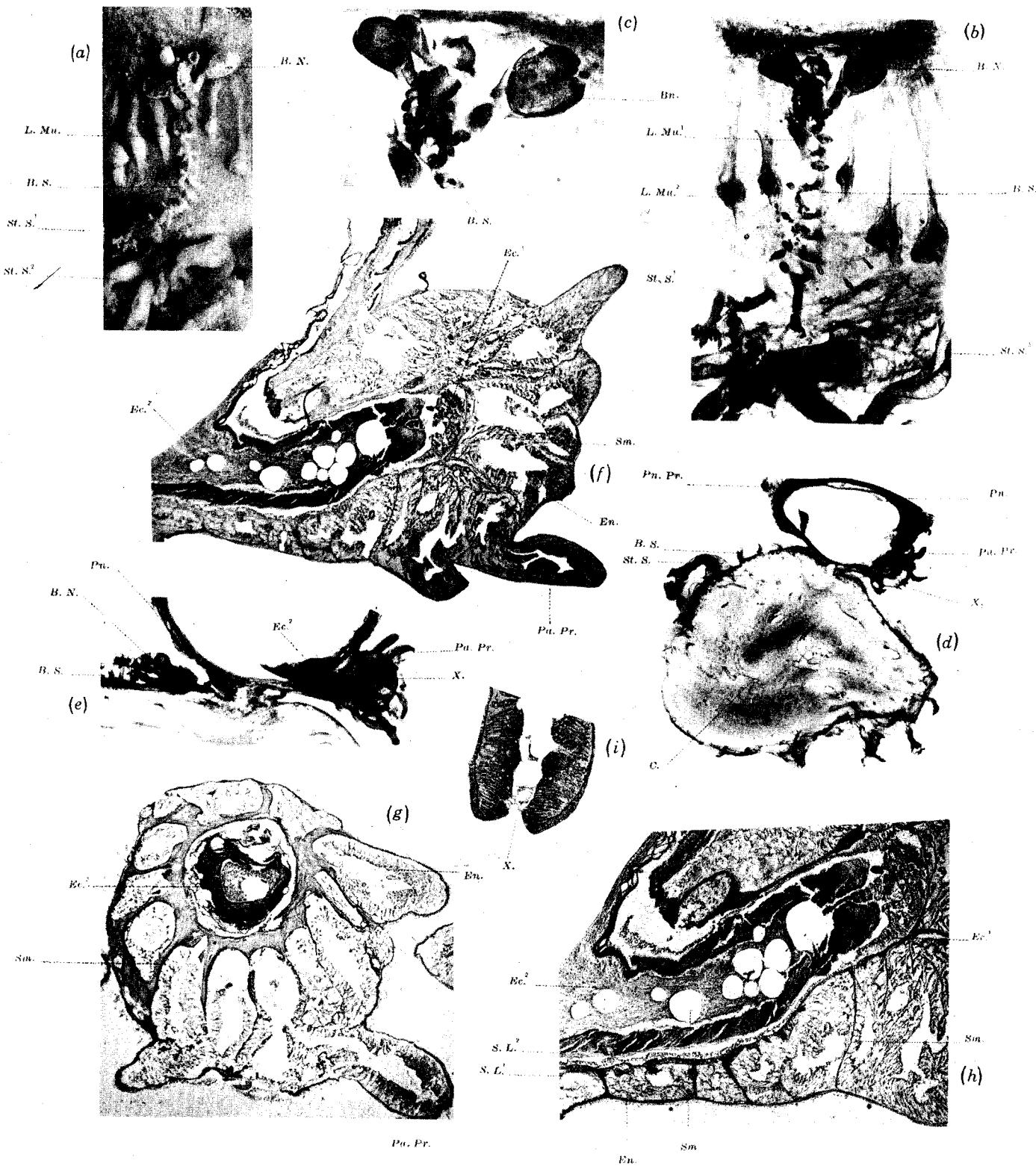


FIGURE 25. For description see page 228.

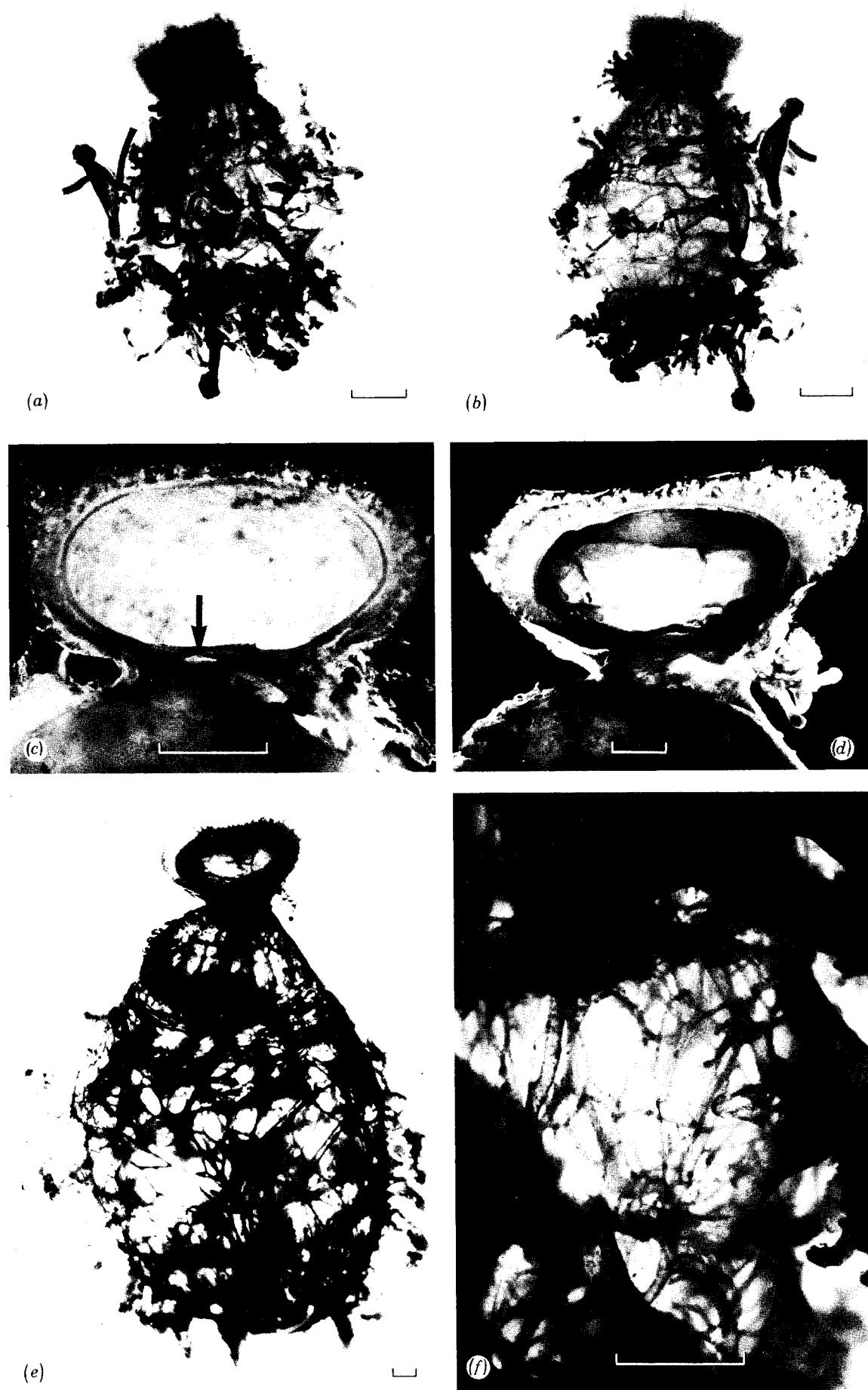


FIGURE 26. For description see plate 10.

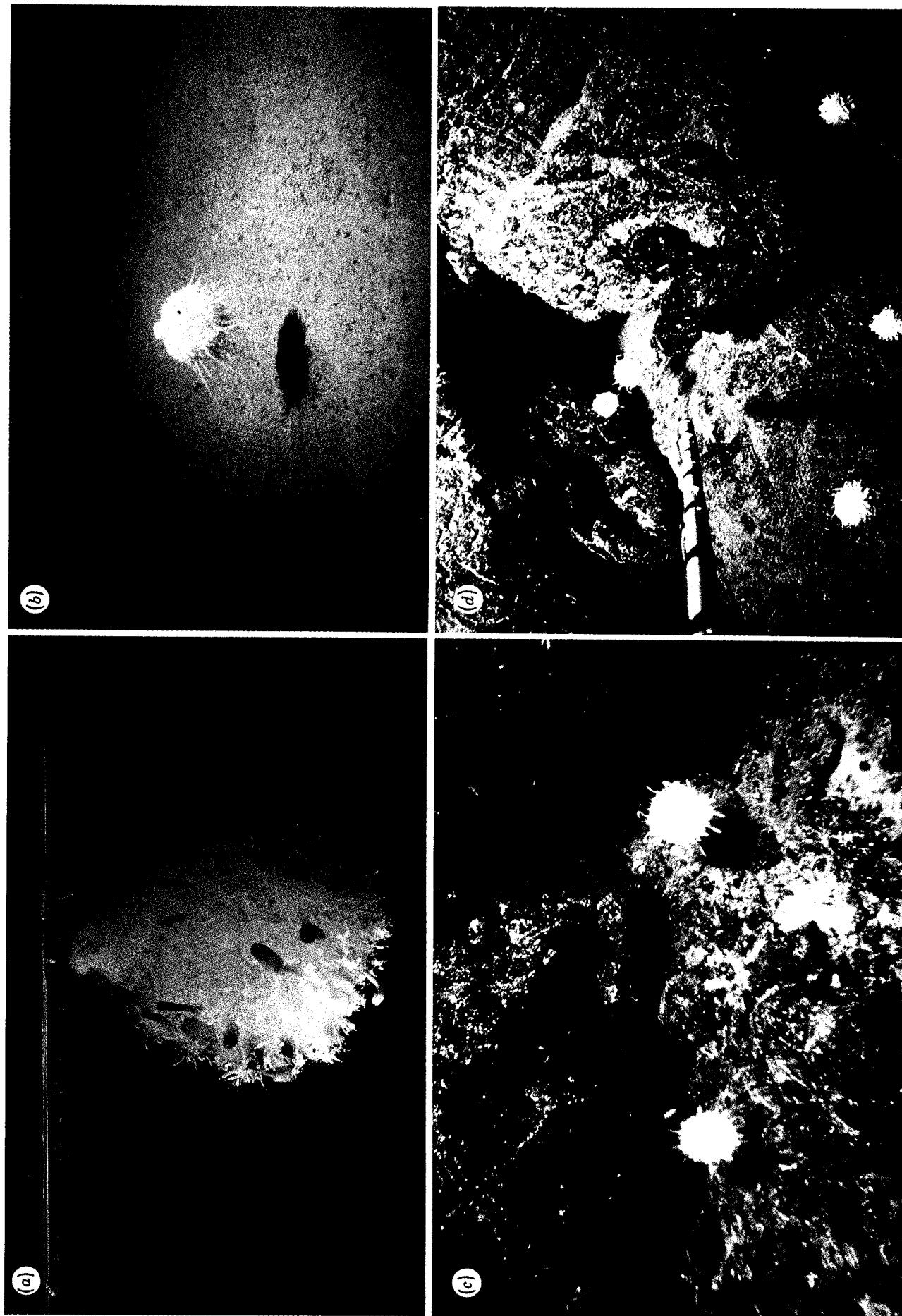


FIGURE 27. For description see plate 10.

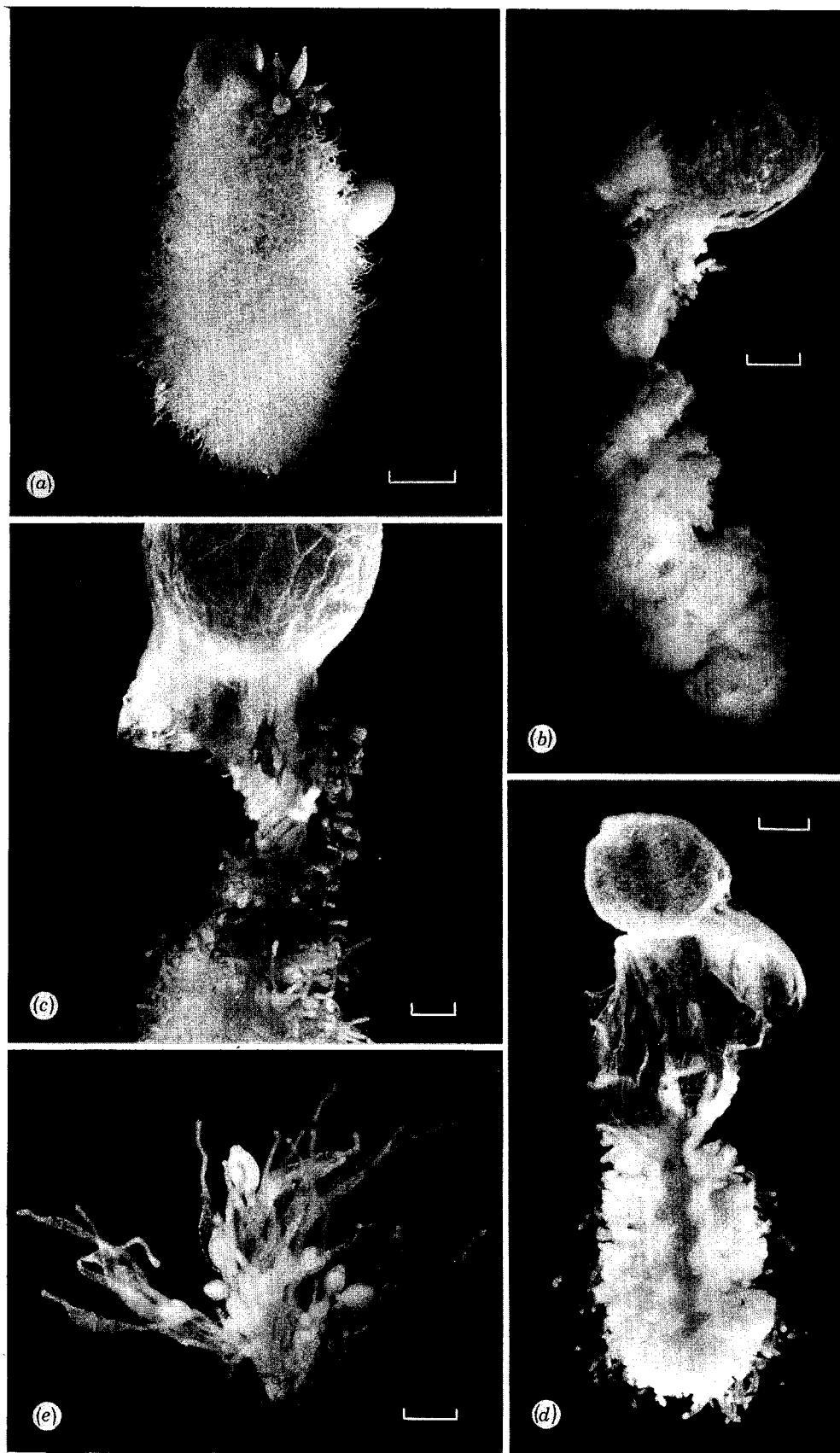


FIGURE 35*a-e*. For description see opposite.



FIGURE 35. *Thermopalia taraxaca* sp.nov. (a) Dorsal view of the type specimen. Note the smooth-walled pneumatophore and aurophore, the latter surrounded by young gastrozooids. A type II gastrozooid remains attached on the right side of the corm, while the latter's overall fuzzy appearance is caused by the stalks of the gonophores. The gonophores themselves mostly have become detached. (b) Lateral view of a young specimen from *Alvin* dive 884. Note the clear spiral arrangement of the cormidia around the siphosomal corm, together with their zone of proliferation on the ventral side of the nectosome, opposite to that of the aurophore. (c) More detailed view of the zone of proliferation and upper whorls of cormidia from an *Alvin* dive 878 specimen. (d) Sagittal section through an *Alvin* dive 884 specimen. Note: the thin-walled nectosome and large hypopycystic cavity; the basal sheet of tissue attaching the aurophore to the nectosome; and the axial cavity in the siphosome. (e) Part of a male gonodendron, showing the long gonophore stalks. (f) Median longitudinal section through the smallest specimen, from *Alvin* dive 884, showing the basal siphosomal cavity, above which are a series of cross septa.

Scale bars: (a) 5 mm; (b-f) 1 mm.

In addition, one specimen has been sent to me from the Oceanographic Sorting Center, Smithsonian Institution. This specimen was collected during Cruise 6 of the *Eltanin*, at st. 339, on 3. xii. 1962. The position given is 53° 05'-08' S, 59° 31'-24' W. An otter trawl was used to collect the specimen from a depth of 512-586 m. The specimen is housed in the U.S. National Museum of Natural History, Smithsonian Institution, and has the number 60424 in the coelenterate catalogue.

Diagnosis. Rhodaliid siphonophore with a smooth-walled aurophore and pneumatophore. The nectosomal region bears a large number of nectophores, usually between 50 and 80, which may, by their mutual compression, arrange themselves into a double or a multiple corona. The siphosome bears numerous, crowded cormidial units which possess characteristically shaped bracts. Internally, the hypocystic cavity is restricted to a very shallow, but broad, zone immediately below the pneumatophore. The remainder of the corm is composed of a spongy, cartilaginous ground substance which is penetrated throughout by a network of innumerable small canals. No major canal system is present.

Description. In comparison with most of the foregoing species, the specimens of *Rhodalia miranda* are large. Haeckel's (1888b) four specimens measured from 30 to 60 mm in greatest diameter and up to 40 mm in height. Most of the new specimens that have been examined were compressed in the axial direction and measured from 32 to 52 mm in diameter and from 18 to 40 mm in height. The two, smaller *Zoond* specimens were better preserved and measured 20 and 30 mm in diameter, and 24 and 28 mm in height respectively. The original coloration of the specimens is unknown but at present the corms are a pinkish-brown.

Pneumatophore. The smooth-walled pneumatophore is a large, very rigid structure. It varies in diameter from 13 mm, in the *Eltanin* specimen, to 22 mm, and the volume of gas that it contains would be in the region of 2000 mm³ for the larger specimens. Typically, the outer wall, the pneumatocodon, is considerably thicker than the pneumatosaccus (figure 19a-c). Its thickness varies from about 1.2 mm on the sides to 0.5-0.6 mm at the apex, irrespective of the size of the pneumatophore itself. The pneumatosaccus is slightly thickened basally where it overlies the hypocystic cavity. The chitinous layer, the pneumatocyst, completely lines the gas-filled cavity except in the region of the aurophore, where it is overlain by the pad of secondary ectoderm.

Haeckel (1888b) noted that the mesogloal layer of the pneumatocodon was pierced by a number of simple or branched radial cords which connected the endodermal layer with the covering ectoderm. These cords were endodermal in origin and Haeckel believed that they might also contain an extension of the pericystic cavity which, thereby, was able to open onto the external surface of the pneumatophore. These endodermal processes clearly can be seen in the present specimens of *Rhodalia miranda*, particularly the *Zoond* specimens (figure 19a, b), where they pass out radially from the endodermal lining of the pneumatocodon as simple cords which divide into three or four branches close to the outer surface. It would appear that these branches do make contact with the outer, ectodermal layer, although their organization has not been examined histologically. Some of these processes appear to have cavities within but it is thought that these are due to the loss of their endodermal cells rather than represent extensions of the pericystic cavity into them. These cords of endoderm are a general feature of the pneumatocodon of most rhodaliid siphonophores but their function is uncertain.

In the larger specimens a regularly spaced series of bands of thickened endoderm are seen to radiate out from the apex of the pneumatophore on the inner surface of the pneumatocodon.

It is not clear if they are bands of musculature but they are not comparable with the longitudinal or radial muscles that Haeckel (1888b) noted in the pneumatocodon as these were said to lie subjacent to the ectodermal epithelium, and presumably, had originated from that layer.

Aurophore. The aurophore is a small, smooth-walled, globular structure which is attached to the pneumatophore over most of its apical surface (figure 19a-c). It possesses a distinct external pore. Haeckel (1888b) considered that there was a duct, the pistillum, running through the aurophore, which connected the gas cavity with the exterior (figure 20c), as was discussed earlier. However, it is interesting to note that this duct is not illustrated in another of his figures (figure 20b). As Haeckel's (1888b) illustration shows (see figure 20c), the aurophore contains a very large pneumatochone which, in one of the *Zoond* specimens (figure 19a, b), extends beneath the pneumatophore before opening into the latter in the centre of its basal surface. In the larger specimens the point where the pneumatochone opens into the pneumatophore is shifted towards the dorsal surface (figure 19c), but none the less it is still a very long cylinder in comparison with that seen in other rhodaliid species. Large cavities, which once contained the gaseous secretions, can be seen in the pneumadenia at the proximal end of the pneumatochone.

The pneumatosaccus lining to the pneumatochone is well developed (figure 19a, b) and, in section, forms a distinct gutter. It does not connect with the pneumatocodon of the aurophore to form the so-called aurostigma, or opening of the pistillum as Haeckel (1888b) described and illustrated (see figure 20c), although an allusion of such an arrangement is apparent in figure 19(a, b) because there are very few radial septa in this particular region of the aurophore. The pericystic cavity in the remainder of the aurophore is interrupted by a large number of septa which connect the pneumatosaccus to the pneumatocodon.

Nectosome. The nectophores are attached over an extensive area of the surface of the corm, especially in the smaller specimens. Haeckel (1888b) estimated that the number of nectophores once present on his *Challenger* specimens was between 50 and 80 or more. These figures have been confirmed for the three of these specimens that are still in existence. Two have between 50 and 60 nectophoral muscular lamellae while the third, larger specimen has approximately 80. With regard to the new material, a count of the nectophoral lamellae was possible on only eight of the specimens. The number on the five larger ones was remarkably consistent, being between 50 and 55, while the *Eltanin* and one *Zoond* specimen had ca. 45, and the other *Zoond* specimen had as few as 27. Haeckel (1888b) suggested that the nectophores were arranged into three alternating horizontal rings (figure 1), but this cannot be verified unless the animals could be taken alive and intact. The nectophores themselves (figure 19a, d) are large, flaccid, featureless bags similar to those noted in other rhodaliid species.

The internal structure of the nectosome is described below.

Siphosome. Most of the cormidia are arranged into what appear to be dexiotropic spiral whorls around the surface of the siphosome (figure 19e), although this arrangement is not always obvious. Those cormidial bases that lie immediately below the zones of proliferation are well developed, even in the smallest specimen, and a series of developmental stages of these bases could not be followed. The thickened band of ectoderm, which represents the junction between the nectosomal and siphosomal regions, was discernable (cf. *Stephalia corona*) and the cormidial bases of the apical whorl connected with it. Some of these bases were inserted onto the corm below the others such as to produce an alternating, biserial arrangement.

The ectodermal band can be followed as it passes down the corm in a similar fashion to that described for *Stephalia corona*, except that it does not produce such a distinctive gutter below the

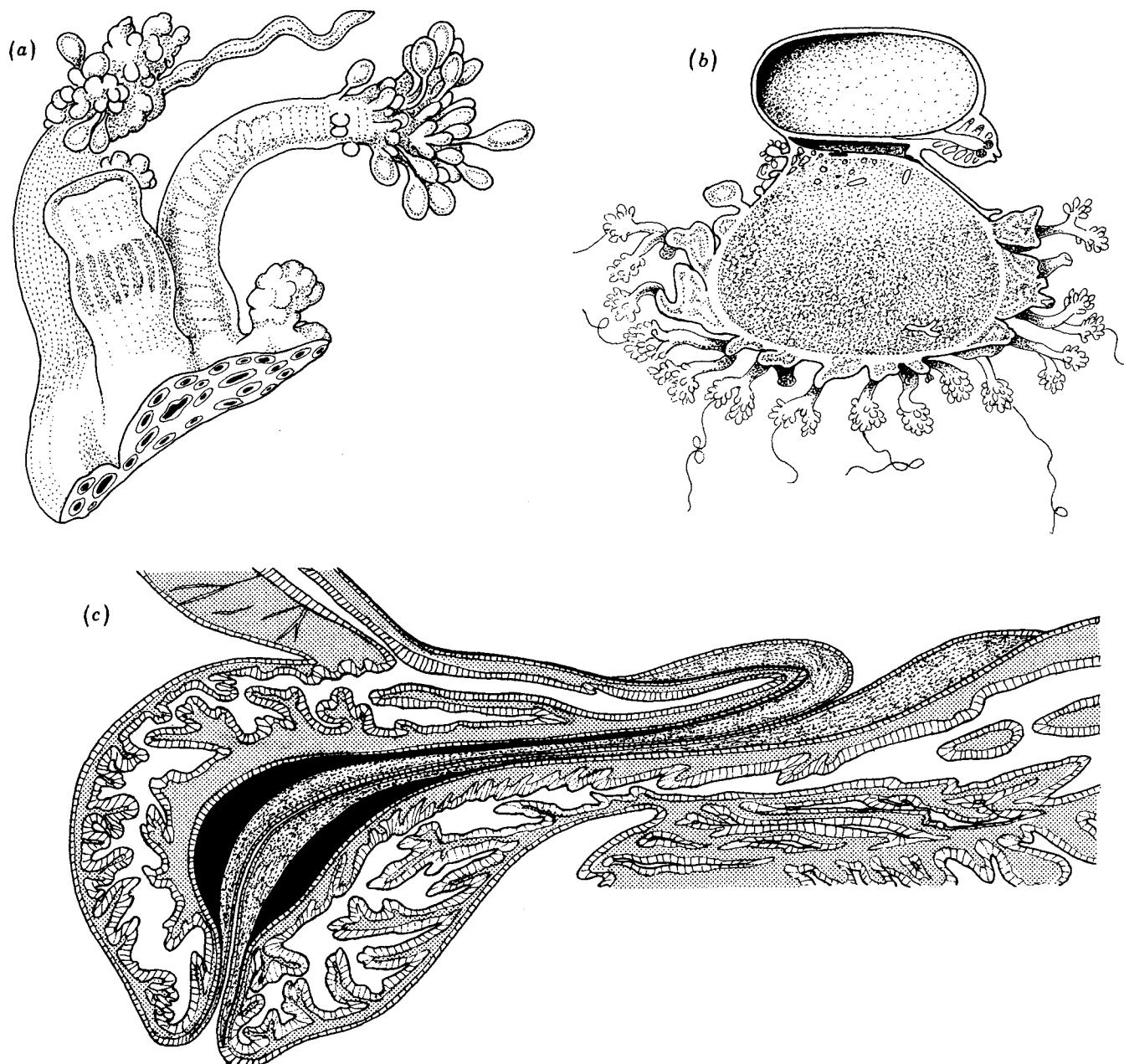


FIGURE 20. *Rhodalia miranda* Haeckel. (a) An individual cormidium, redrawn from Haeckel (1888b, pl. I, fig. 2). Haeckel illustrated the contracted pedicle of the gastrozoid, but considered that it was the entire gastrozoid. (Magn. $\times 15$.) (b) Sagittal section through the entire corm, redrawn from Haeckel (1888b, pl. IV, fig. 15). Note that the aurophore apparently does not possess an auroduct. (Magn. $\times 2$.) (c) A reconstruction of a section through the aurophore. Redrawn from Haeckel (1888b, pl. V, fig. 24). (Magn. $\times 15$ (?).)

zones of proliferation on the ventral surface. The cormidal bases of the second major whorl again connect basally with this band and, as in the apical whorl, these bases become arranged in a biserial fashion. Thus on the sides of the siphosomal corm, at least in the smaller specimens, there are four ranks of cormidal bases that appear to have arisen from only two whorls. On the base of the corm, in the *Zoond* specimens, the band of ectoderm spirals around once, giving

off the complete second whorl of cormidial bases, and then terminates in the centre (figure 19*f*). The arrangement of the cormidial bases in the older specimens is more difficult to follow owing to their poor state of preservation. However, it does appear that no new cormidial whorls have been added and that an increase in size results from the expansion of the corm itself and a corresponding increase in the size of the cormidial bases. Some of the cormidial units on the base of the corm originated directly from the tract of ectoderm where it passes downwards through the ventral furrow immediately below the zones of proliferation, but it was not possible to establish whether they were a secondary development as was suggested for the similar units found in *S. corona*. However, in one of the *Zoond* specimens, several large scars were noted on the basal region of the corm and it is suggested that type I gastrozooids once were attached to them.

Haeckel (1888*b*, pp. 288–289) stated that, ‘The cormidia are always monogastric and originally ordinate, arranged in regular circles or spiral coils... [but] sometimes the cormidia seem to arise united in small groups from a common pedicle, and if we regard one of these groups as a single cormidium of higher order... we may say that the cormidia are polygastric’. The cormidial bases are considered here to be the common stem of several cormidia and thus can be considered to be polygastric. Haeckel estimated the number of cormidia to be 50–80 or more, and in one of the *Zoond* specimens there are about 60 cormidial bases present. Since most of these bases carry two or more cormidia then the actual number of individual cormidia, each with a gastrozooid, would be in excess of 100. The common bases of these cormidia are greatly thickened structures which are penetrated by a main canal of the gastrovascular system and an extensive network of anastomizing branch canals. Some of the cormidial bases from the apical whorl, immediately below the zones of proliferation, are illustrated in figure 21. In this region the bases are closely applied one to another and may appear to have a common stem (figure 21*a*), but they become more widely separated as their development proceeds.

The arrangement of the cormidia on these bases conforms with the arrangement noted in other rhodaliid species, and each cormidium consists of a gastrozooid, with a tentacle, and a gonodendron to the stalk of which is attached a bract. Figure 21*c* illustrates a young cormidial base on which the second cormidium is still developing. All the parts of the first cormidium have become detached leaving the gonodendral (gd.1) and gastrozooidal (gz.1) stumps. The gonodendron (gd.2) of the second cormidium is somewhat denuded but it bears a small gonopalpon and a young bract (b.2). The developing second gastrozooid (gz.2), with its partially differentiated tentacle (t.), clearly can be seen. The gastrozooids of the two cormidia are developed very close to each other in a region towards the distal end of the common stem while the first gonodendron arises proximal to them. These gastrozooids are attached to the leading edge of the cormidial base, i.e. on the side furthest away from the zone of proliferation. The first gonodendron becomes deeply divided from the remaining cormidial components on the older cormidial bases. This situation contrasts with that seen in *Stephalia corona*, where the first gastrozooid is attached on the proximal part of the stem and in a basal position on the leading edge of the cormidial base.

Another cormidial base which was closely applied to the one described above is shown in figure 21*b*. It appears to be in a more advanced stage of development although its organization is difficult to interpret. The first gonodendron (gd.1) is assumed to be reduced and shows no indication of a bract or of a muscular lamella on its stalk, although it does bear a very large gonopalpon. The second gonodendron (gd.2) is well developed and has many denuded branches. The attachment lamella for the bract is apparent on its stalk. In the axil between the branches

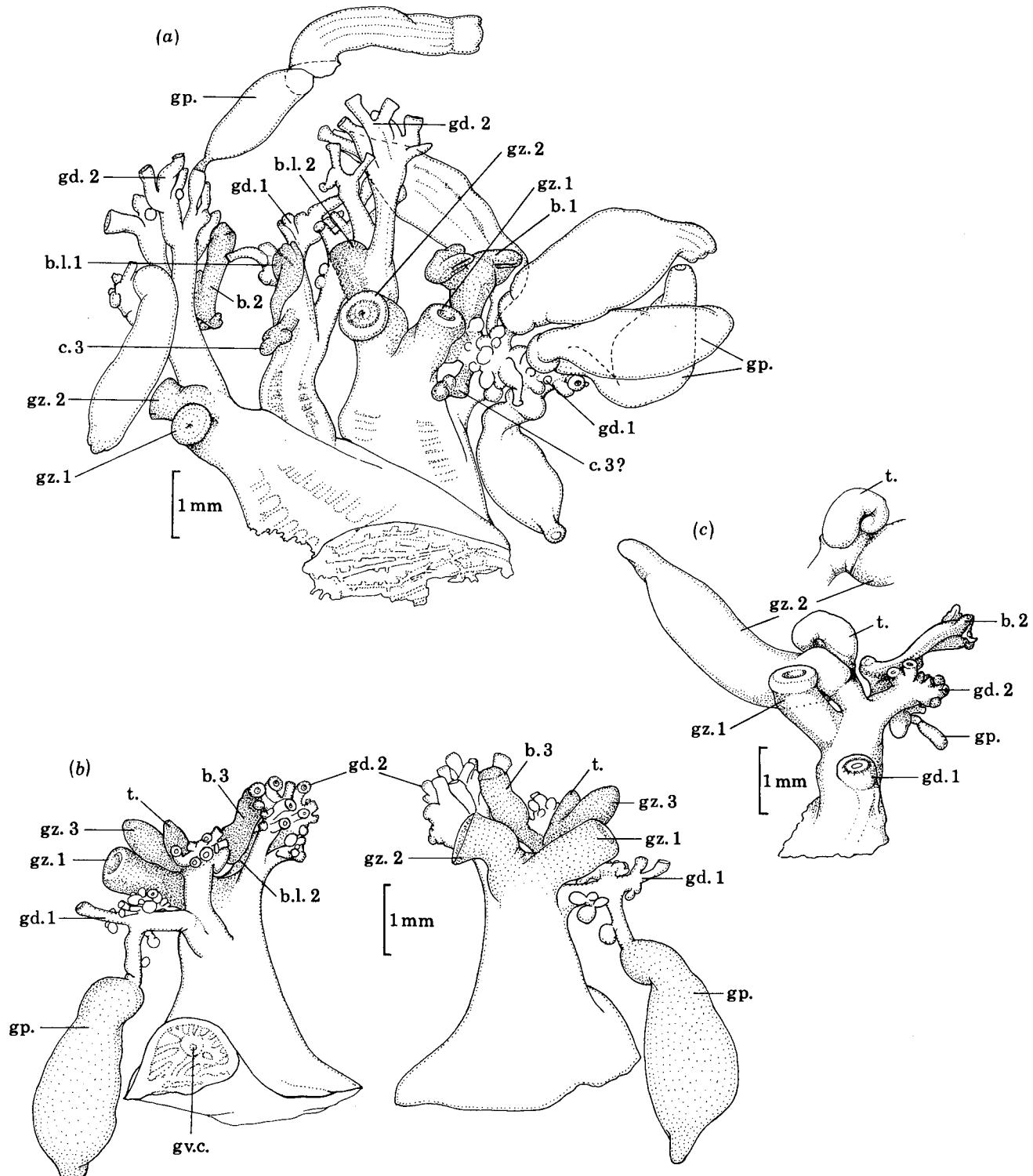


FIGURE 21. Cormidial units of *Rhodalia miranda* Haeckel. (a) Two developing cormidial units, each with two cormidia and (?) the bud of a third. See text for details. (b) Two views of a small, denuded cormidium. See text for details. (c) A very young cormidial unit with the second cormidium still developing, although all parts of the first have been lost.

bearing the gastrozoid and gonodendron of the first cormidium, a third cormidium has been developed, presumably from the pedicle of the first gastrozoid, whose gastrozoid (gz.3) and tentacle (t.) are slightly differentiated and appear as a mitten-shaped process. The gonodendron (gd.3) has several branches and a developing bract (b.3).

The two cormidial bases illustrated in figure 21a conform with the basic pattern described above, but it is unfortunate that in all these cases the gastrozooids have become detached. In figure 21a it can be seen that the first gonodendron (gd.1) on each cormidial base is deeply divided from the remaining components and that one of these bears a small, but well differentiated bract (b.1). Another bract (b.2) is attached to the second gonodendron (gd.2) on the other cormidial base, and the bracteal lamellae can be traced on the remaining two gonodendra that are present. Some peculiar buds (c.3?) were noted on the gonodendral stems of the first cormidium and it was thought that these might represent the origins of the third cormidia. However, their position relatively high up the gonodendral stalks might argue against this as Totton (1965) states that, in general, new gastrozooids, palpons and bracts are usually budded off from the stalk of an existing gastrozoid. However, it is in accord with the positioning of the third cormidium on the cormidial bases of *Stephalia corona* as described earlier, and can be compared with the situation on another unit that is illustrated in figure 21b. This point will be returned to when the development of the cormidia in *Dromalia alexandri* is discussed.

Most gastrozooids that have been found associated with the specimens are of type II (figure 22c). These closely resemble those found in *Stephalia corona* (figure 11b) except that they are somewhat larger. They have a globular stomach from which, in the contracted state, the proboscis segment protrudes distally. The annulated tentacle is very well developed and has a strong suspensory ligament attached to its ventral surface. The large tentilla are inserted at the distal end of each annulation on the dorsal surface. Tentilla were present only on the proximal part of the tentacle. They are large, filiform structures which, as Haeckel (1888b) described, can be subdivided into three sections. A short, proximal pedicle, which bears very small nematocysts, connects with a central cnidoband, spirally coiled in the contracted state and bearing a strong armoury of large ensiform nematocysts (figure 7h) on its ventral surface and small paliform nematocysts dorsally, and finally a slender terminal filament carrying roundish nematocysts. It is construed that these tentilla can be extended to a considerable length in life.

Haeckel (1888b) illustrated a gastrozoid of *Rhodalia miranda* (see figure 7g) whose tentacle carries tentilla and, thereby, would be type II. However, it does not resemble those type II gastrozooids that have been found on the new specimens. In fact it looks distinctly like some of the young type I gastrozooids that have been found, but the tentacles of these do not possess tentilla. Only a few type I gastrozooids have been found among the material examined, but two of these were in the Challenger material. One of these (figure 22a) had a proboscis-like extension distally and closely resembles Haeckel's illustration (compare figures 22a and 7g), except for the absence of tentilla on the tentacle. Another type I gastrozoid is illustrated in figure 22b and, unlike those seen in *Stephalia corona*, it possesses a well defined basigaster region from which arises the comparatively large tentacle. This tentacle, in the youngest examples, appears not to be annulated but older ones show that long, annular segments are present. Unfortunately no large type I gastrozooids were found and so it was not possible to investigate whether the tentacle is lost, as was the case for the mature type I gastrozooids of *S. corona*. Several large stumps were noted on the base of the corm of one Zoond specimen and, as mentioned above, it can be speculated that large gastrozooids once were attached to them.

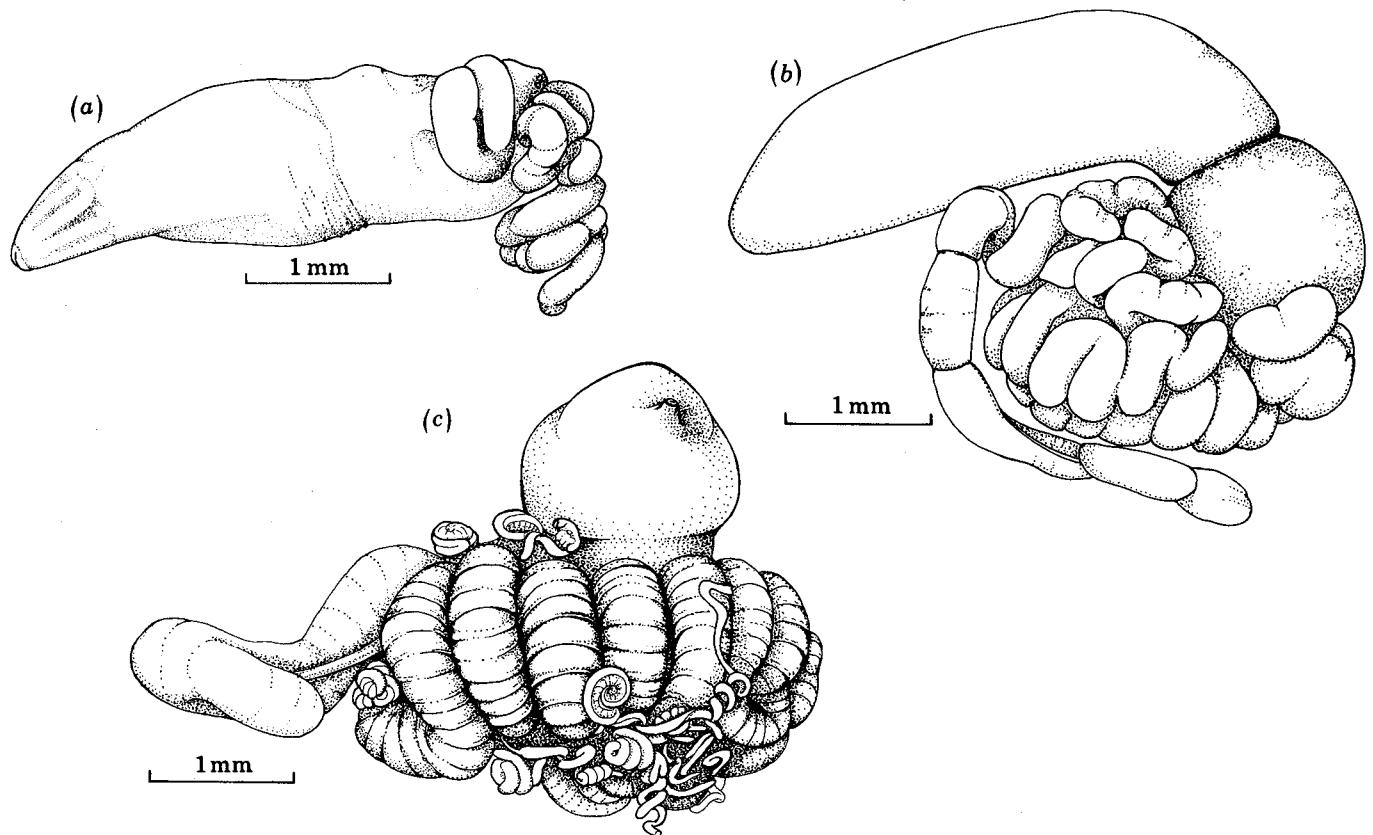


FIGURE 22. Gastrozooids of *Rhodalia miranda* Haeckel: (a, b) type I; (c) type II.

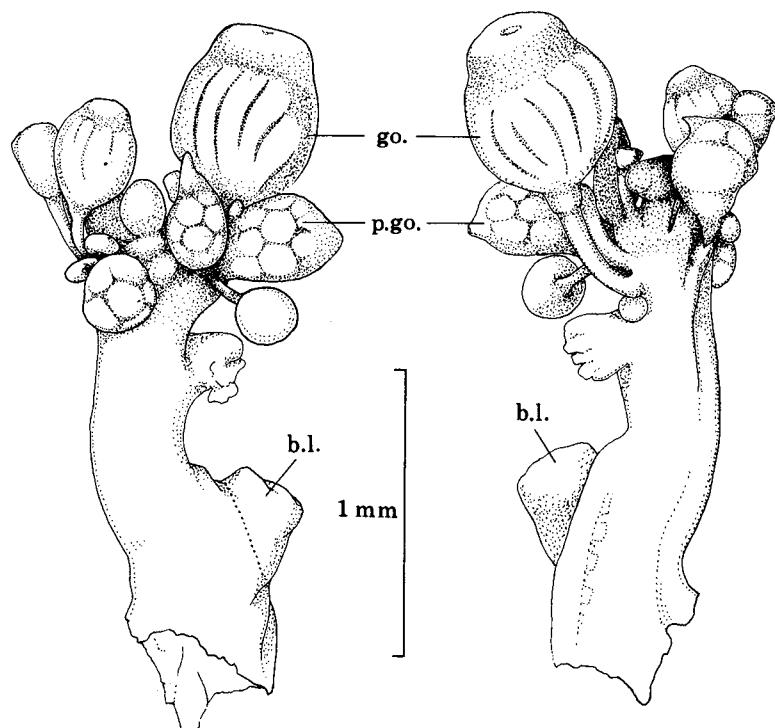


FIGURE 23. *Rhodalia miranda* Haeckel. Two aspects of a small female gonodendron.

The gonodendron is of the usual rhodaliid organization. The animals are dioecious and part of a female gonodendron is shown in figure 23. Ten of the 14 specimens that have been examined were found to be female, and the remainder male. Well developed gonopalpons are present (figure 21a), and some of these were noted to possess a distinct terminal chamber that opened to the exterior by a highly expandable mouth. As Mackie & Boag (1963) have shown, the terminal bulb of a palpon is a region specialized for the accumulation of waste matter, and it is probable that the rhodaliid gonopalpons have a similar function.

Relatively few bracts were found in the fragments associated with the material examined and most of these were young or reduced. These bracts (figure 24) are relatively simple in form, in comparison with those found in other rhodaliid species. They are triangular, with expanded, truncated, ovoid distal facets. Their proximal ends are recurved dorsally and slightly swollen to form processes reminiscent of those noted in *Sagamalia hinomaru*. The simple, broad bracteal canal passes straight up the bract and terminates in the centre of the distal facet without giving off any branches.

Internal organization of the corm. Haeckel's (1888b) illustration of the internal structure of the corm has been redrawn in figure 20b, and other sections are shown in figure 19a-c. The hypocystic cavity is a very shallow, but broad space lying in the nectosomal region, immediately below the pneumatophore. This cavity is in free communication with the pericyclic cavity of the aurophore. Immediately below the hypocystic cavity are a number of small chambers which are loosely associated. These chambers are delimited by outgrowths of the nectosomal wall, in its apical region. The remainder of the corm is 'solid' in that there are no major cavities. It is traversed throughout by a network of equally sized branching and anastomizing canals. There is no major system of large gastrovascular canals, except for a few large openings (figure 19c) which are apparent in sagittal section. These canals do not have any definite organization and like the central canals from the cormidial bases they rapidly become integrated into the general network.

Discussion. Haeckel (1888b) distinguished his family Rhodalidae [sic] on the basis of the absence of both a permanent central canal and a primary mouth at the base of the corm, and on the presence of tentacles with tentilla. *Rhodalia miranda* was distinguished by the presence of a solid siphosome that was traversed by a network of equally disposed canals, and by the arrangement of the nectophores into a double or multiple corona. The structure of the corm is the only one of these characters that is considered, at this moment, to have any systematic significance. The presence of a 'solid' siphosome traversed by a regular network of gastrovascular canals, but without a major canal system, adequately serves to distinguish the monotypic genus *Rhodalia* from the other rhodaliid genera. The other distinguishing characters that Haeckel (1888b) mentions are thought to be of lesser significance. All rhodaliid siphonophores possess tentilla on the tentacles of type II gastrozooids, and the arrangement of the nectophores into a multiple corona is a matter of conjecture. Haeckel suggested that such an organization of the nectophores was achieved as a result of their displacement by mutual pressure, since the attachment lamellae for the nectophores were arranged in a single corona. A study of the five nectophores that remain attached to one of the *Challenger* specimens does, however, give some indication of a biserial arrangement as their attachment lamellae are alternately elongated either basally or laterally. This might give some credence to Haeckel's statements except that the nectophores are loosely attached to the corm and it is probable that their arrangement has become distorted during preservation. The remaining muscular lamellae on this nectosome do not show an

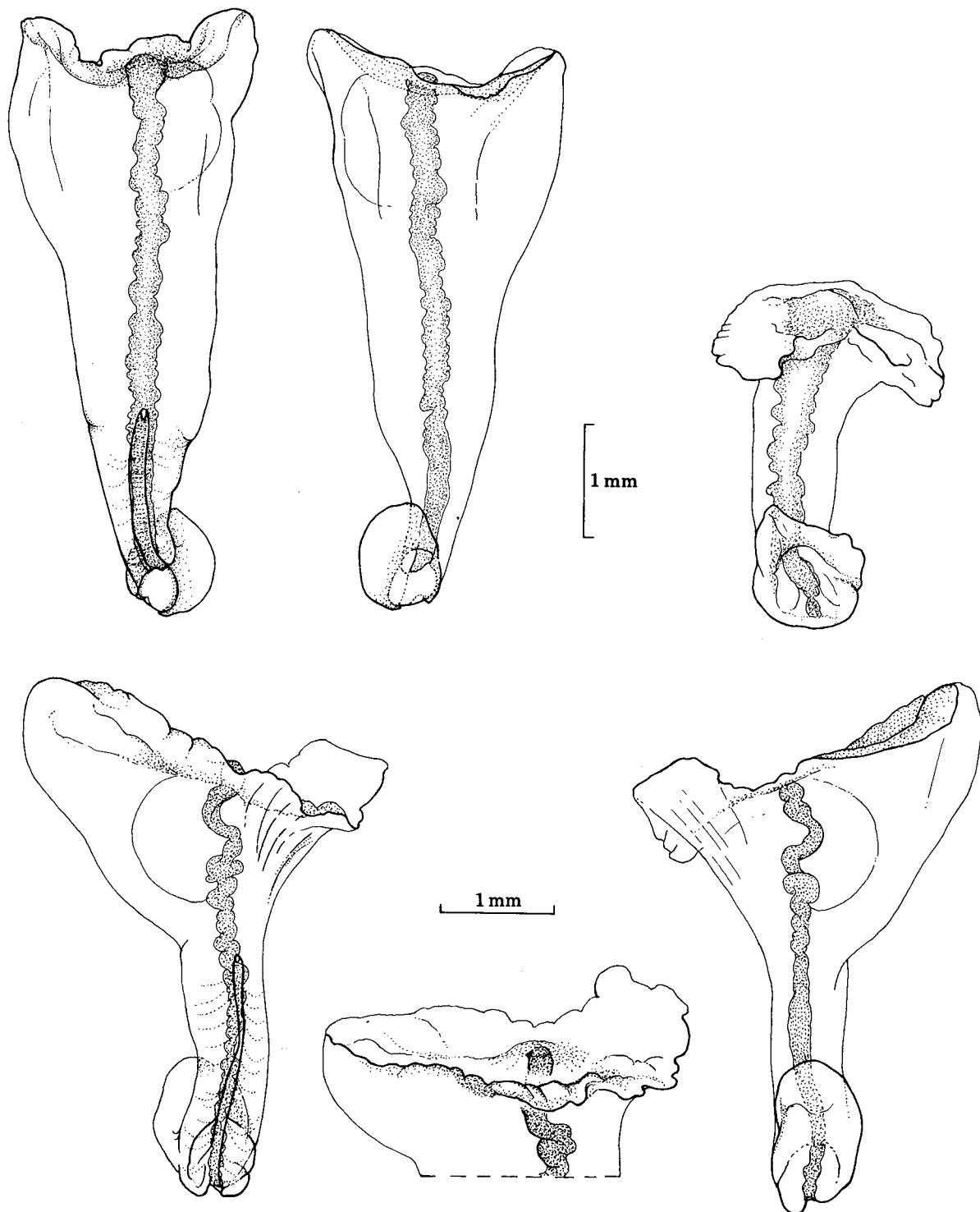


FIGURE 24. Bracts of *Rhodalia miranda* Haeckel.

alternating sequence, although many have been torn away completely. In contrast, one of the *Zoond* specimens had four nectophores attached that clearly were arranged in a single corona. However, this specimen possessed relatively few muscular lamellae, *ca.* 27, which might mean that there was not sufficient mutual pressure to force them into any other configuration. In the specimens of *Rhodalia miranda* the circumference of the nectosome is large in comparison with other rhodaliid species. Thus the distance between each nectophoral lamella would be similar to that in *Stephalia corona* despite the three- to fourfold difference in the number of nectophores present. Nevertheless, the arc into which the larger nectophores of *R. miranda* can expand obviously is smaller and this might result in crowding and their consequent dislocation from the single corona arrangement. It is to be hoped that some observations can be made on complete living specimens so that this factor can be investigated further.

Haeckel (1888b) appears to have based most of his studies on the morphology of the Auronectae (Rhodaliidae) on his specimens of *Rhodalia miranda*. As noted above these specimens are wonderfully illustrated (see figure 1), but, as Haeckel himself admitted, many of his figures are reconstructions or are semi-diagrammatic. There are several errors in these illustrations, as has been discussed already in the section on *Stephalia bathyphysa*, but further examples can be found among his figures of *R. miranda*. For instance, the legend to his pl. 1, fig. 2 (see figure 20a) states that, among other things, a complete gastrozooid is illustrated. It is apparent that this structure merely represents the pedicle or stalk of a gastrozooid and that the remaining elements, together with the tentacle, have been detached. Haeckel (1888b, p. 290) realized that these illustrations were in error when he stated, 'The basigaster is separated from the pedicle... by an annular constriction (sphincter). The basal sphincter is a very strong ring-muscle, and it is very probable that by its sudden contraction the three distal segments are frequently detached from the proximal pedicle. In my preliminary examinations... I saw only the pedicles of the siphons attached to the cormidia, and judged them to be highly contracted siphons... I was thus led into the same error as Gegenbaur thirty years before in *Stephanospira* [*Physophora*]'. It is a pity that the illustrations were not corrected on the basis of this re-examination of the material but it would appear that the chromolithographic plates were produced at an early stage in the preparation of the monograph.

Genus: Dromalia Bigelow

Dromalia Bigelow 1911, p. 303

Totton 1965, p. 96

Monotypic genus for *Dromalia alexandri* Bigelow, 1911, whose diagnosis is given below.

Dromalia alexandri Bigelow (figures 25–27, plates 12–14; figures 28–34)

Dromalia alexandri Bigelow 1911, pp. 303–309, pl. 23, figs 6–11, pl. 24

Totton 1965, p. 96, pl. 19, figs 3–6

Alvarino 1971, pp. 31, 257, 431

Type material. Fifteen specimens which Bigelow (1911, p. 303) stated were collected by the *Albatross* in 1887, at 21° 21' N, 157° 44' W, which is in the region of the Hawaiian Islands. The depth of sampling was said to be 293 fm (539 m) to the surface. On consulting the records for the cruises of *Albatross* in 1887 it was found that no sampling had been done in the vicinity of Hawaii. Thus the station data given by Bigelow are incorrect, as is discussed below, and the (?)correct information is listed in table 1.

TABLE 1. RECORDS FOR THE COLLECTION OR OBSERVATION OF *DROMALIA ALEXANDRI*

item no.	date	position†		depth‡	observation or		number of specimens
		N	W		m	net	
1	23. i. 1889	32° 43'	117° 51'	572 (?)	large beam trawl	15	
2	6. i. 1889	34° 00.5'	120° 29'	289	large beam trawl	1§	
3	28. i. 1965	off Pt La Jolla, California		64–183	otter trawl	4§	
4	28. i. 1965	off Pt La Jolla, California		311–183	otter trawl	1§	
5	22. v. 1971	28° 17.4'	115° 28.1'	329–311	6 ft (ca. 1.8 m) Sigsbee trawl	3§	
6	—	32° 56'	117° 20'	195–270	observations from submersibles		
		32° 58'	117° 22'	(mean 235)	on several occasions		
7	—	ca. 33° 11'	119° 30'	152–305	observation from <i>Nekton</i> submersible		
8	5. x. 1973	33° 41.8'	118° 21.6'	366	?trawl		
9	26. xi. 1973	33° 34.5'	118° 02.6'	137	?trawl		
10	8. v. 1974	33° 34.33'	117° 58'	139	?trawl		
11	10. xi. 1973	off Coronado Bank, Mexico		—	?trawl		
12	31. iii. 1976	off Pt Vicente		274	?trawl		
13	xii. 1966	off Santa Cruz I.		329	trawl	2§	
14	xii. 1966	off Gaviota		208	trawl	1§	
15	iii. 1967	N end Santa Cruz I.		201	trawl	3§	
16	21. viii. 1968	28° 34'	115° 34'	265 (max.)	observation from <i>Deepstar</i> dive 422		
17	—	8 n.m. S of Pt Dume		704	trawl	60	
18	—	14 n.m. SSE of Pt Fermin		485	trawl	7 (1§)	
19	—	3 n.m. SW of Long Pt		668–741	trawl	1	
20	—	4.5 n.m. S of Pt Fermin		563	trawl	5	
21	—	10 n.m. W of Catalina I.		407	trawl	1	
22	—	3 n.m. N of item 21		463	trawl	2	
23	—	Santa Monica Bay		752	trawl	4	
24	—	Tanner Bank		533	trawl	1	
25	—	Tanner Bank		216	trawl	10 (1§)	
26	—	Tanner Bank		244	trawl	1	
27	—	SSE of San Nicholas I.		584	trawl	3§	
28	—	S of San Nicholas I.		574	trawl	14	
29	—	S of Santa Rosa I.		584	trawl	2§	
30	—	S of San Miguel		463	trawl	4	
31	—	Pt Dume		541	photographic record		
32	—	Pt Dume		632	photographic record		
33	—	ca. 02°	119°	0–200 (?)	?epiplanktonic net		

† These positions (some approximate) are shown in figure 34, with the exceptions of items 5, 13, 15, 16 and 33.

‡ All these data, with the exception of item 33, also represent the depth of water.

§ Material examined.

|| The abbreviation n.m. stands for nautical miles.

Source of data

Item 1. Type material from *Albatross* st. 2927; see text for comment.

Item 2. Material from *Albatross* st. 2898; see text for comment.

Items 3–6. Information kindly supplied by Dr A. Flechsig, Scripps Institution of Oceanography; material supplied by Dr H. G. Snyder.

Item 7. Information kindly supplied by Dr J. W. Vernon, General Oceanographics, Newport Beach, California.

Items 8–10. Information kindly supplied by Dr J. Q. Word, South California Coastal Water Research Project, El Segundo, California.

Items 11–12. Information originating from Dr N. Westphal, Occidental College, by way of Dr J. Q. Word.

Items 13–15. Information and material kindly supplied by Dr F. G. Hochberg, Santa Barbara Museum of Natural History.

Item 16. Information kindly supplied by Dr E. Barham, Southwest Fisheries Center, La Jolla, California.

Items 17–32. Information and material kindly supplied by Dr J. Ljubenkov, University of Southern California, Los Angeles.

Item 33. From Alvarino (1971); see text for comment.

Material examined. One specimen of *Dromalia* sp., identified by F. M. Bayer in 1962, and housed at the United States National Museum, catalogue number U.S.N.M. 52452. This specimen was collected at *Albatross* st. 2898 on 6. i. 1889. The data for this cruise state the position of the station to be at $33^{\circ} 00' 30''$ N, $120^{\circ} 29'$ W, where a large beam trawl was used. The sampling depth was 158 fm (289 m), but a current bathymetric chart indicates the water depth at this position to be in excess of 1000 fm and it would be unlikely that a bottom trawl could have sampled the benthos at 158 fm. It is concluded that there is an error, or misprint, in the station data. On the basis of the positions given for the other stations visited on the same day and the statements made in the cruise narrative, it is assumed that the position for *Albatross* st. 2898 should have been 1° further to the north, namely $34^{\circ} 00' 30''$ N, $120^{\circ} 29'$ W. At this position the charts indicate a water depth of less than 100 fm (183 m), which is more consistent with the given sampling depth. It is assumed that errors (overestimates) could have been made in the estimation of the sampling depth as no actual soundings were made at this locality.

Eight specimens of *Dromalia alexandri* were kindly loaned to me by Dr H. G. Snyder of the University of California. Their station data are given in table 1, items 3–5. In addition, specimens were kindly loaned to me by Dr F. G. Hochberg of the Santa Barbara Museum of Natural History (see table 1, items 13–15), and a further seven were loaned by Dr J. Ljubenkov of the University of Southern California, Los Angeles (see table 1, items 18, 25, 27, 28).

Diagnosis. Rhodaliid siphonophore whose pneumatophore is flattened apically and bears several gelatinous protuberances around its outer rim. The aurophore bears papilliform appendages. The hypocystic cavity is very reduced or absent and the remainder of the corm is solid. A sparse system of gastrovascular canals penetrates through the translucent mesogloal ground substance of the corm and an anastomizing network of canals is present peripherally, just below the surface of the corm. The cormidia are arranged into distinct dexiotropic spirals around the surface of the siphosome and a developmental series can be discerned on the most apical (youngest) whorl. The mature cormidia are borne on thickened bases which are distinct one from another. Bracts, with a many branched bracteal canal system, are present. The tentilla are tricornuate and may possess a basal involucrum.

Description. Bigelow (1911) gave a detailed description of his specimens of *Dromalia alexandri* and some of his figures are reproduced in figure 25. Some additional information, however, has come to light from the examination of the new material and from observations of the animals *in situ*. Complete specimens have been estimated to measure up to *ca.* 100 mm in diameter, while the denuded corms of the specimens that have been examined ranged from 23 to 55 mm in height and from 18 to 36 mm in diameter. The corm of the living animal is salmon-pink (figure 27).

Pneumatophore. The structure of the pneumatophore in *Dromalia alexandri* is unique among the known rhodaliid species. It is not a smooth-walled, rounded structure but is flattened apically and bears a number of triangular gelatinous processes, of variable size, on its outer rim (figure 26a, b). In the specimens examined the pneumatophores varied between 9 and 18 mm in diameter and bore from ten to 13 gelatinous protuberances. The upper part of the pneumatophore is a distinct pink colour in life (figure 27).

Bigelow (1911) did not comment on the internal structure of the pneumatophore even though it shows many interesting characters. The pneumatocodon wall is extraordinarily thickened (figure 26c, d) over its entire surface and though slightly thinner at its apex it does not show the twofold variation in thickness noted in most rhodaliid siphonophores with smooth-walled

pneumatophores. The situation is complicated by the development of the gelatinous protuberances from the pneumatocodon wall. A large number of endodermal processes (figure 26c, d) penetrate throughout the mesogloal layer of the pneumatocodon, even into the gelatinous protuberances. These processes branch profusely and give rise to an extensive network. It is not clear whether they are purely endodermal in origin or whether they also include a canal extending from the pericystic cavity.

The pneumatosaccus too is relatively thick and rigid and is practically fused with the pneumatocodon so that the pericystic cavity is greatly reduced (figure 26c, d), although the presence of this cavity can be seen apically in one of Bigelow's sections (see figure 25d). Because of the close apposition of the pneumatocodon and pneumatosaccus, the hypocystic cavity below the pneumatophore becomes partially or totally obscured. Bigelow (1911) stated that this cavity was absent, but a small cavity can be seen below the pneumatophore in one of the smaller specimens that has been sectioned sagittally (figure 26c). This cavity does not extend across the whole of the nectosomal region but is situated on the dorsal side and is in direct communication with the pericystic cavity of the aurophore. In the older specimens this hypocystic cavity has virtually disappeared as the two endodermal layers have fused below the pneumatophore. The gas-filled cavity of the pneumatophore is lined by a very prominent chitinous layer (figure 26d) which is not rigidly attached to the ectodermal layer of the pneumatosaccus and consequently can easily be removed (note its absence in figure 26c). In the region of the aurophore, this chitin layer is overlain by the secondary ectoderm of the pneumadenia.

Aurophore. The aurophore was described and illustrated in detail by Bigelow (1911) (see figure 25). Much of Bigelow's discussion was concerned with establishing the true nature of the aurophore and with correcting some of the interpretive errors made by Lens & van Riemsdijk (1908). *Dromalia alexandri* and *Archangelopsis typica* are the only two known rhodaliid species that possess an aurophore bearing papilliform appendages on its external surface. These papillae (figure 25i) are each about 2 mm in length and are hollow with a pore connecting the pericystic cavity with the exterior. The pneumatochone, with its enclosing pneumatosaccus wall, is well developed and has a large opening into the cavity of the pneumatophore (figures 25f, 26c). Bigelow (1911) described the pneumatochone as being a thick-walled cylinder that is about five times as long as broad (figure 25f, h). However, in the new specimens, where the internal structure has been examined, the pneumatochone is shorter and more conical. Here the opening of the pneumatochone into the gas-filled cavity is very broad, especially in comparison with that in other rhodaliid species. The secondary ectoderm of the pneumadenia contains several large cavities (figure 25f, h), which contained the products of the gas-secreting cells. Bigelow also noted a number of giant amoeboid cells in the region where the primary and secondary ectodermal layers merged at the distal end of the pneumatochone. Numerous radial septa are present connecting the pneumatosaccus to the pneumatocodon (figure 25f-h).

Nectosome. Bigelow (1911) discussed the positioning of the zones of proliferation and of the aurophore and showed, beyond doubt, that they lay on opposite sides of the corm in the nectosomal region. The junction between the pneumatophore and the nectosome is narrow (figure 26c, d), but the nectophoral muscular lamellae spread down onto the main body of the corm. The zones of proliferation (figures 25a-c; 26a) are very distinct and the series of developing cormidia can be seen in most specimens as it passes down the nectosomal region. All the specimens examined were devoid of nectophores, apart from some young buds in the

zone of proliferation, and Bigelow (1911) makes no mention of them either. The U.S.N.M. 52452 material possessed one small detached nectophore which, typically, was a thin-walled, featureless sac with four straight radial canals. The muscular attachment lamellae of the nectophores also are flimsy structures which can be easily detached from the corm. Their number is quite variable, ranging between 30 and 50 in most specimens, with *ca.* 60 being present on the large U.S.N.M. 52452 specimen. These lamellae appear to be distributed asymmetrically on the nectosome and, in one extreme case, 31 were found attached to the right of the zone of proliferation while only nine were present to the left. This is an unusual arrangement as in the other rhodaliid species examined the number of lamellae on each side is approximately equal. This asymmetry might be due to the loss of some lamellae but even if allowance is made for this the numbers are still greatly disparate. Below the aurophore there is a naked zone, devoid of lamellae.

Within the nectosome the hypocystic cavity is greatly reduced or absent and the remainder of the region is filled by the mesogloal ground substance.

Siphosome. The organization of the cormidial bases on the siphosome of *Dromalia alexandri* is the most easily discernable of any rhodaliid siphonophore studied. The spiral whorls of these bases are distinct one from the next and a superficial band of ectoderm is seen to separate them (figure 26*b, e*). This is in marked contrast to the organization in some other rhodaliid species where the cormidial bases on one whorl frequently are inserted into gaps between those on an adjacent whorl, which results in a very confused picture. Further, in *D. alexandri* each cormidial base is a discrete entity and they are not crowded together, partially fused or overlapping. They are, however, in close apposition although some large gaps are occasionally noted between them. These gaps could either be the result of the loss of a base, which can be easily detached from the corm without leaving an obvious scar, or the spreading apart of the original sequence of bases.

The whole arrangement of the external surface of the siphosome is very ordered and the spiral of cormidial bases can be followed, without interruption, from their zone of proliferation down to the base of the corm. There are no signs of the insertion of additional, secondarily developed cormidia onto the corm as was construed to be the case in some other species, e.g. *Angelopsis euryale*, *Stephalia corona* and *Rhodalia miranda*, and unlike in those species it is clear that new whorls of cormidia are continually being added apically. Thus the number of cormidial whorls present will depend on the size, and presumably age, of the animal. In the specimens examined the number of whorls ranged from seven to 15, and in one of the larger specimens there were *ca.* 130 cormidial bases present but, as there were gaps between them, this number probably is an underestimate. Generally about 14 bases are present on each whorl except for the most apical, youngest one where there are up to 20.

In the specimens examined most of the cormidial components had been lost and all that remained were the gelatinous cormidial bases, which usually are greatly thickened (figure 28). These bases are penetrated by a canal which is in direct communication with the gastrovascular canal system within the corm. The reticulum of small canals, which lies below the surface of the corm (figure 26*f*), does not penetrate into these bases, but the central canal does give off some side branches (figure 28) in the distal regions of the mature bases. These branches do not form an anastomizing network and may, at most, bifurcate. They terminate on the outer surface of the stem beneath some pronounced ridges which represent the muscular lamellae to which the bracts of the cormidia once were attached. It is uncertain whether these

bracts are retained in life or whether they are caducous, but in all the specimens examined only one well developed bract was found and this was attached to a young cormidial base. However, these lamellae are extremely obvious on the older cormidial bases and it is strange that they were not noted by Bigelow (1911).

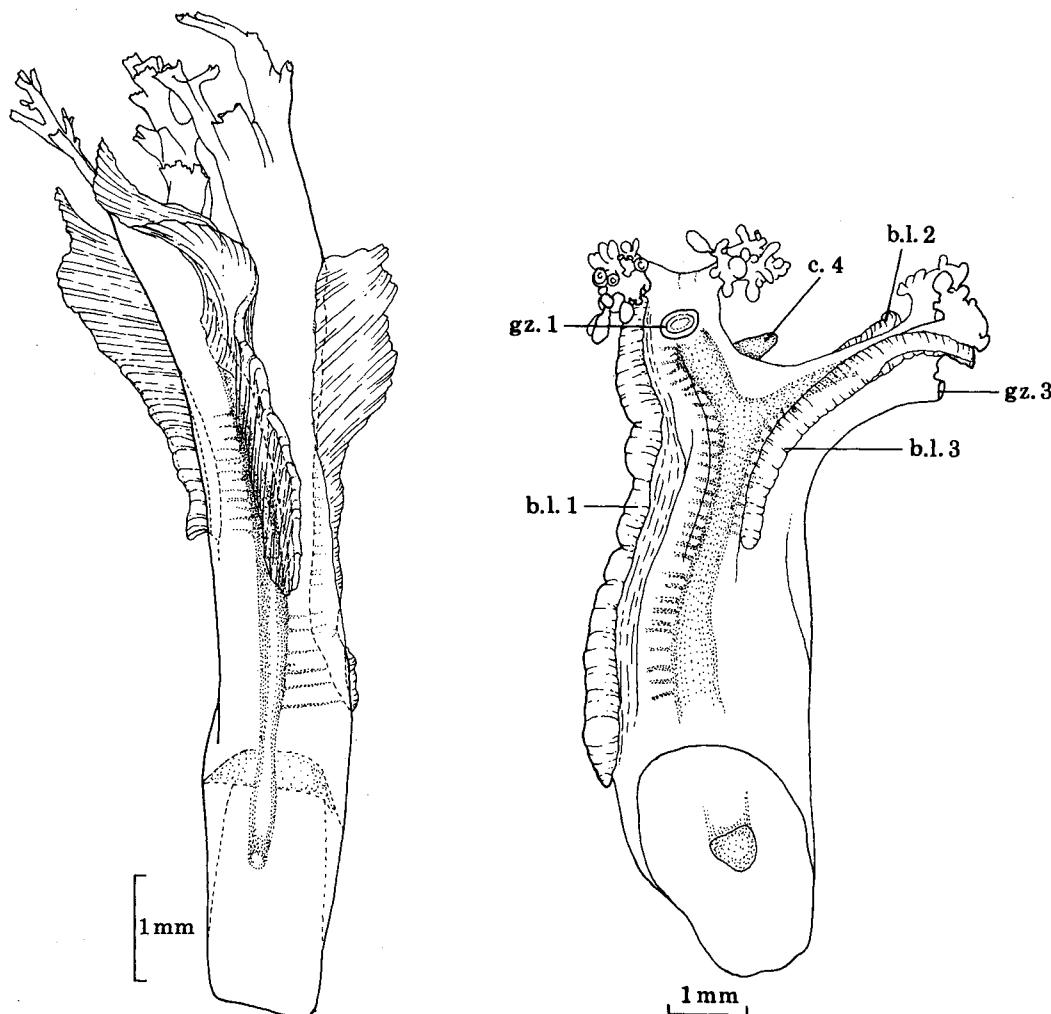


FIGURE 28. *Dromalia alexandri* Bigelow. Two old, denuded cormidial bases, showing the bracteal lamellae and the stumps left after the gastrozooids were detached.

The cormidial units in the apical, or most recently developed, whorl are all thin-stemmed and they exhibit a series of successive developmental stages according to their distance away from their origin at the zone of proliferation. This situation contrasts markedly with that described for *Rhodalia miranda* and *Stephalia corona* where even the units immediately below the zone of proliferation are at an advanced developmental stage. A close study of these young cormidial units on the specimens of *Dromalia alexandri* has been made and this has led to a better understanding of their formation and organization. The youngest unit in the apical whorl, which lies immediately below the ventral zones of proliferation, is a simple, thin-walled tube which carries at its apex a single, partially differentiated cormidium. On the next unit, to the right, the bud

of the second cormidium appears and by the third unit, illustrated in figure 29*a*, its component elements are visible. On this unit the components of the first cormidium still are at an early stage in their development. The gastrozooid (gz.1) carries a young, spirally coiled tentacle (t.1) which is little more than a simple tube. The annulations, so characteristic of older tentacles, only appear as slight emarginations on the surface, and there are no signs of the development of tentilla. The gonodendron (gd.1) bears a small bract (b.1) on its stalk, and distally a few young gonopalpons and gonophore buds. A mitten-shaped process represents the second gastrozooid (gz.2) and tentacle, and the second bract (b.2) is still only a bud. Even at this stage the second gonodendron (gd.2) is more fully developed than the first (gd.1), to judge by the number of gonophore and gonopalpon buds. Although it is difficult to assess accurately, it appears that the second cormidial bud is more closely associated with the gonodendral branch of the first cormidium rather than the gastrozooidal one.

The fifth, sixth and ninth cormidial units in the series of bases on the apical whorl of the same specimen are illustrated in figure 29*b-d*, respectively. In these the bract (b.1) of the first cormidium is quite well differentiated, as is the gastrozooid (gz.1) and its tentacle. This tentacle does not become clearly annulated until the ninth unit (figure 29*d*) but no tentilla have been developed. The basis components of the second cormidium have begun to differentiate, with buds of many gonophores and gonopalpons (gd.2) and the second bract (b.2), together with a young mitten-shaped gastrozooid and tentacle (gz.2). The first gonodendron (gd.1) still remains relatively undifferentiated. At this stage (figure 29*d*) the second cormidium is not borne on a separate branch of the stem but remains in close contact with the first.

As the development of the cormidial units proceeds some of the components of the first two cormidia become separated onto two short branches at the distal end of the common stem. This stem still remains a relatively thin-walled tube. The division of the stem does not result in the complete separation of each cormidium, as it is the gonodendron of the second cormidium which becomes bifurcated. Thus a small part of this gonodendron (gd.2*a*), and the second gastrozooid (gz.2) come to lie axially on the branch which also bears all the components of the first cormidium. The greater part of the second gonodendron (gd.2*b*), together with its bract (b.2), composes the other major branch. This arrangement does not become apparent until the third cormidium has begun to develop, and the stage in the developmental series at which this happens varies from specimen to specimen. In one series the bud of this cormidium appeared on the fifth cormidial unit away from the zone of proliferation while in another it did not appear until the twelfth. Figure 30*a* illustrates a cormidial unit which was fifteenth in the series and thus was situated about three-quarters of the way around the apical whorl. Here the branching of the second gonodendron has only just begun and the developing second gastrozooid (gz.2) lies in the axil between them. The first gastrozooid (gz.1) is a well developed elongated structure with a greatly distended mouth. Its tentacle (t.1) has clear annulations, but still show no sign of the development of tentilla. The first bract has been lost, leaving its pronounced muscular attachment lamella (b.1.1), while the second bract (b.2) is well differentiated but not fully developed. The components of the third cormidium (gz.3, gd.3 and b.3) can be seen attached to the side of the stem that carries the major part of the second gonodendron.

At about the same time as the differentiation of the third cormidium, the main stem of the cormidial base increases in length. This elongation occurs mostly at the distal end and results in the muscular lamellae of the bracts becoming extended down onto the main stem, below the gonodendral branches, as can be seen in figure 30*a*. The mesogloea of the main stem begins to

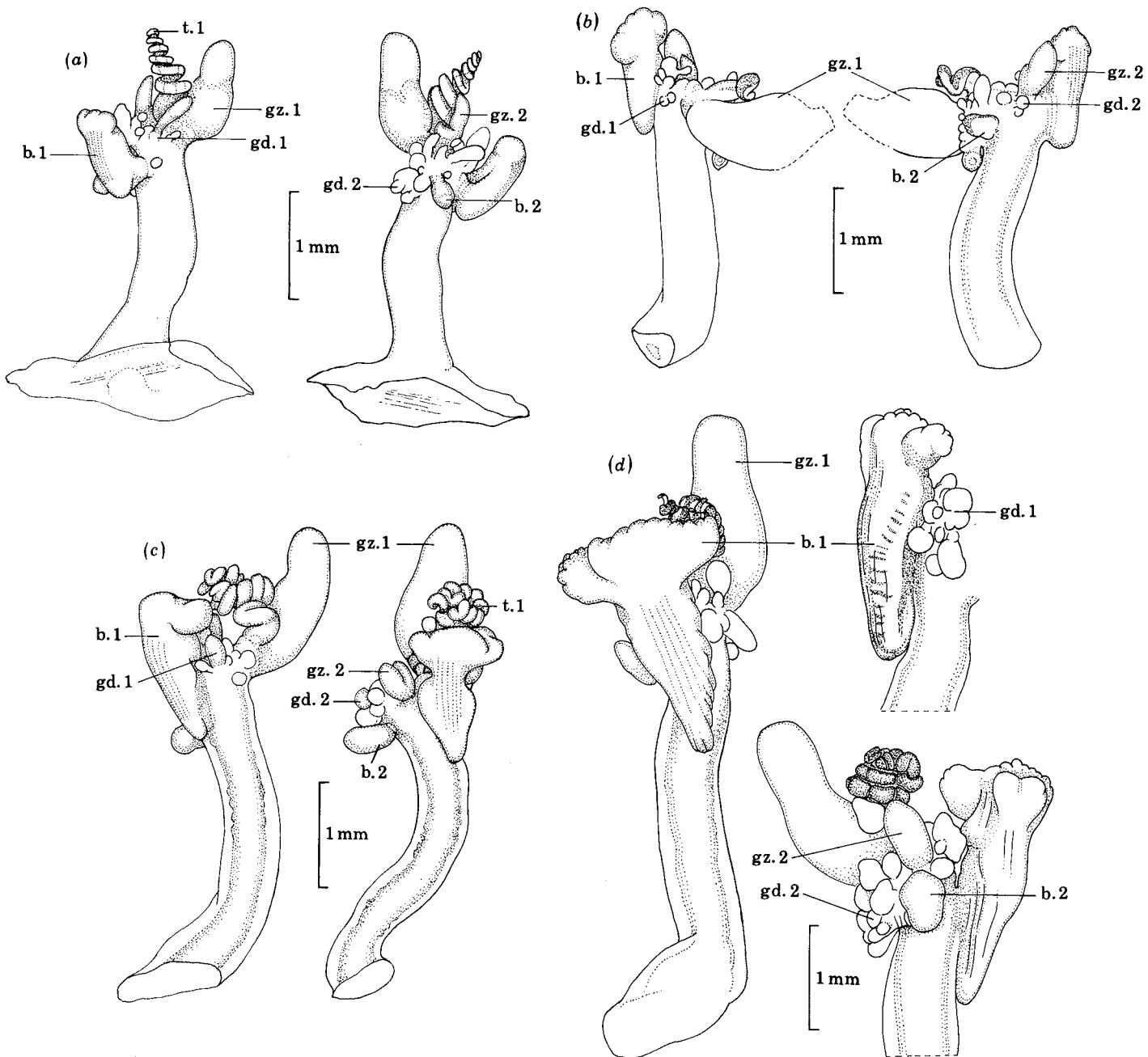


FIGURE 29. *Dromalia alexandri* Bigelow. (a-d) Stages in the development of the cormidial units.
See text for details and Glossary for list of abbreviations.

thicken at this stage and the diameter of the central gastrovascular canal is reduced. The branch canals which supply the bracteal lamella begin to appear, starting at the proximal end of the lamella but with the more distal ones appearing soon after (figure 30b). Ultimately the proximal part of the cormidial unit is shortened as it becomes greatly expanded so that the first bracteal lamella reaches almost to its base (figure 28), while the second and third lamellae are extended to a lesser extent. All three lamellae are supplied by a considerable number of canals from the gastrovascular system.

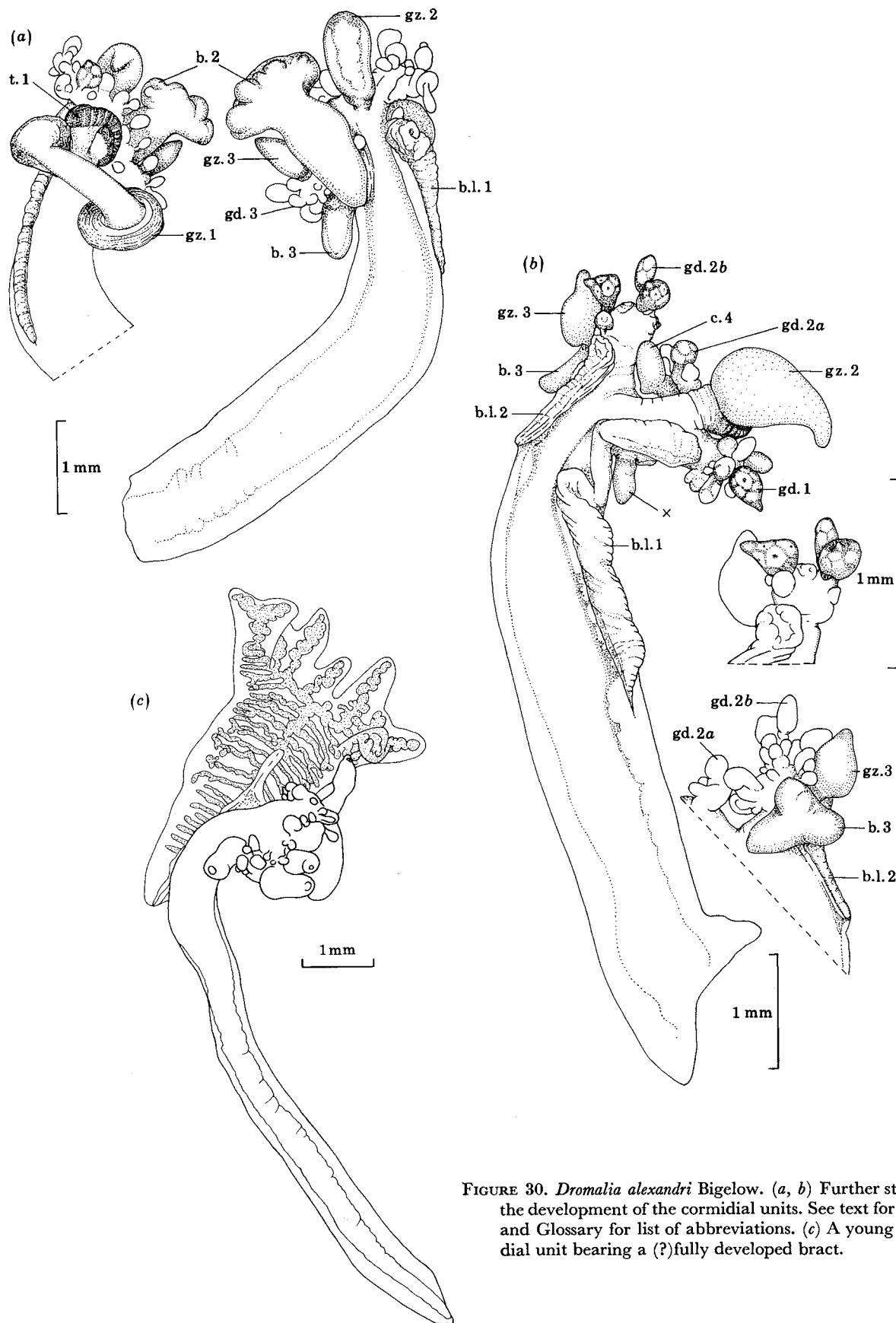


FIGURE 30. *Dromalia alexandri* Bigelow. (a, b) Further stages in the development of the cormidal units. See text for details and Glossary for list of abbreviations. (c) A young cormidal unit bearing a (?)fully developed bract.

The final stage that could be followed in the development of these young cormidial units was the appearance of the bud of the fourth cormidium. This stage is shown (figure 30*b*) by a unit which was twentieth in the series and was situated below the zone of proliferation, thereby representing the first unit in the second whorl. The branching of the second gonodendron is very pronounced and the second gastrozooid (gz.2) is seen attached apically to the branch that bore the first cormidial components. Unfortunately most of these components have become detached but the bracteal lamella (b.l.1) extends down from this branch to a point about half way down the main stem and is penetrated by a few canals. On the axial side of this branch there is a small gonodendral cluster (gd.2*a*). The other branch, which bears the major part of the second gonodendron (gd.2*b*) and the elongated attachment lamella of its bract (b.l.2), also has the components of the third cormidium attached to its outer surface. Thus this cormidium, at least, appears to have developed at the base of a gonodendron rather than as a prominence near the base of a gastrozooid, as Bigelow (1911) suggested. Similarly, the bud of the fourth cormidium (c.4) arises at the base of a gonodendron (gd.2*a*), but on the stalk that bears the second gastrozooid (gz.2). It was not possible to follow the further development of this cormidium as the older units were too denuded. However, the attachment lamella of the fourth bract could be discerned in the expected position (figure 28*b*). When these developing cormidial units first were examined it was thought that the small bud (figure 30*b*, \times) that lay between the stump of the gastrozooid and the bracteal lamella of the first cormidium was the precursor of the fourth cormidium, but this proved not to be so. The destiny of this bud is uncertain but it might represent the origin of a higher-order cormidium or of a replacement gastrozooid. Other such buds have been noted close to the bracteal lamellae of the second and third cormidia but no clearly defined structure was ever seen attached at these points. It is likely that, at most, four cormidia are developed on each base as this is the maximum number of bracteal lamellae that have been observed.

Although several developing bracts have been noted on the younger cormidial bases, in only one instance was a fully developed bract found (figure 30*c*). This bract has a unique construction. It is triangular in shape and flattened dorsoventrally. Its distal end is expanded and bears several folds and lobes, into each of which passes a branch of the bracteal canal. This canal is complexly divided with branches being given off throughout its length. It will be necessary to examine some more complete specimens of *Dromalia alexandri* in order to establish whether these bracts are retained on the older cormidial bases or whether they are caducous. The older bases bear the scars of the attachment lamellae but no loose bracts have been found in association with any of the specimens examined. The bract of the first cormidium is attached on the leading edge of the cormidial base, i.e. on the side furthest from the zone of proliferation (figure 26*f*).

Two types of gastrozooid have been found on the specimens of *Dromalia alexandri*. Like those of *Stephalia corona* and *Rhodalia miranda* the tentacle of the type II gastrozooid bears tentilla while that of the other (type I) does not. The type II gastrozooid (figure 31*a*) is an elongated structure with clearly defined proboscis, stomach and basigaster segments. Its long, annulated tentacle (figure 31*b*) has a well developed suspensory ligament attached along its ventral surface, particularly at the proximal end. The tentacle illustrated is devoid of mature tentilla but many young ones are seen developing at the proximal end. The shape of the annular segments was found to vary according to their position on the tentacle, and probably with the state of contraction of the tentacle on preservation. The segments in the proximal region (figure 31*b*, *i*)

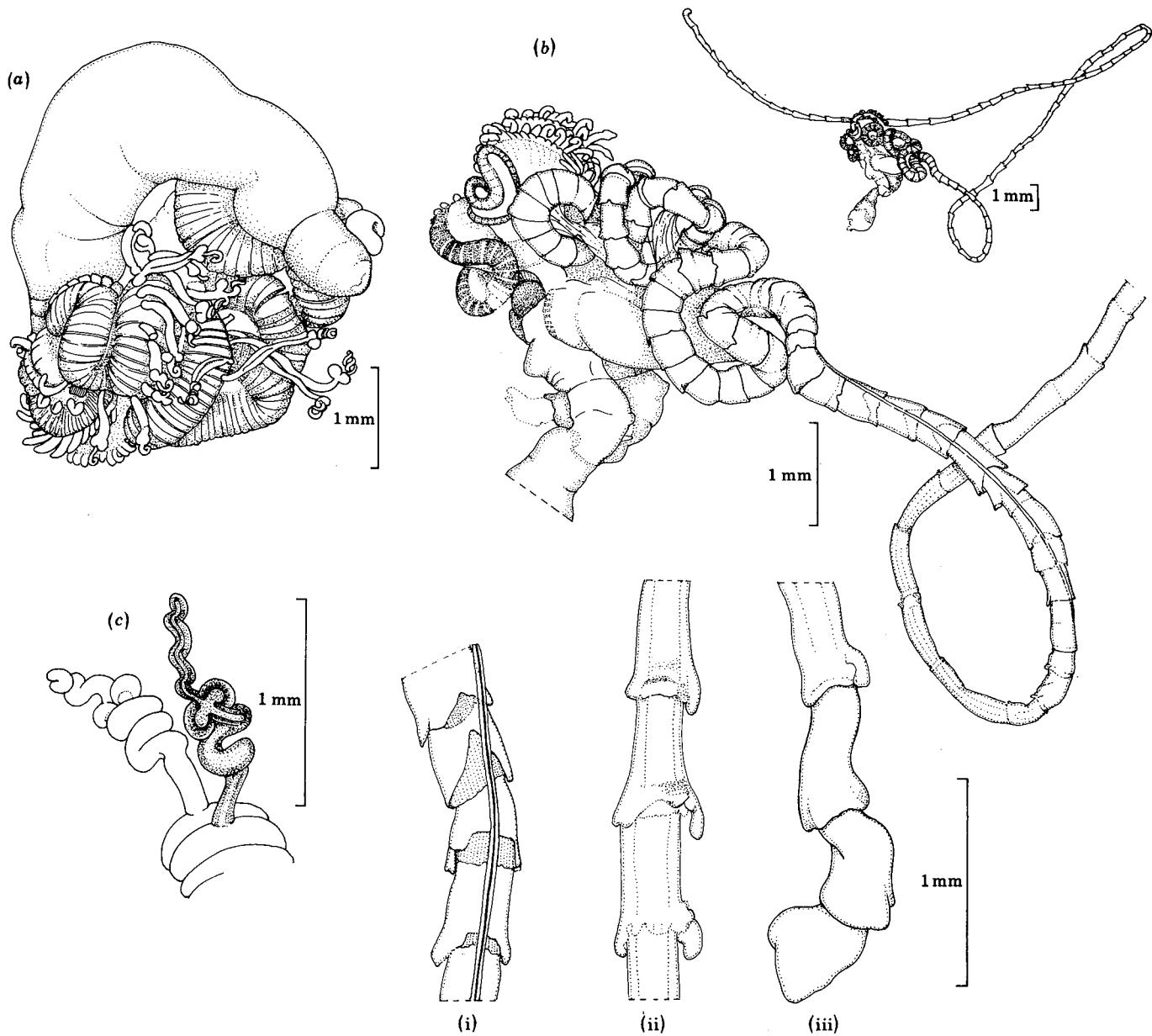


FIGURE 31. *Dromalia alexandri* Bigelow. (a) Type II gastrozooid bearing a well developed, annulated tentacle with tentilla. (b) A partially expanded tentacle from a type II gastrozooid with details of its proximal end. (b, i-iii) Detail of the segments at various positions on the tentacle. See text for details. (c) Detail of an individual tentillum.

are about as long as they are broad and the ventral attachment of the suspensory ligament is well defined. Each segment bears a distal, dorsal protuberance indicating where the tentillum was attached. Further along the tentacle the segments are more elongated (figure 31 b, ii) and their tentillar knobs are conspicuous. The distal end (figure 31 b, iii) of the tentacle, which may or may not be the terminal section as it is uncertain whether this has been broken off, bears thicker segments whose tentillar knobs are reduced. In another specimen these segments were very short and broad. It is probable that the distal tentilla were detached during life

and that the tentacle, as in other siphonophores, is continuously growing with new tentilla appearing at the proximal end. It is believed that the proximal tentilla play the important role in the feeding behaviour of the rhodaliid siphonophores.

Bigelow (1911) found only immature tentilla on his specimens but noted that their structure was the most complex yet seen on a rhodaliid siphonophore. He observed on them a basal thickening, which was reminiscent of a developing involucrum, and a tricornuate terminal process. A (?)mature tentillum is illustrated in figure 31c. There is no sign of a basal involucrum, but distally the tentillum bears two swollen, lateral processes and a central terminal filament of considerable length. It is presumed that the lateral swellings represent a modified cnidoband, which more usually expands down one side of the tentillum.

Some type I gastrozooids are illustrated in figure 32. The first to be noted were featureless, globular structures (figure 32a) to each of which was attached a long annulated tentacle devoid of tentilla. However, many others were later found and two extreme forms are shown in figure 32b, c. Here the gastral cavity is seen to be lined by a large number of digitate protuberances, and these are frequently exposed on the surface of the gastrozooid when its distal region becomes everted (figure 32c-e). In general these protuberances are of a similar size but in one case (figure 32e) a single large process was seen to project out beyond the rim of the everted mouth of the gastrozooid. Huxley (1859), for instance, noted the presence of numerous slender, conical, endodermal villi in the stomach region of the gastrozooids of several siphonophore species. These villi were most pronounced in *Physalia physalis*, where they reached a length of ca. 0.25 mm. Mackie (1960) considered that they played an important role in intracellular digestion as food fragments were found to be engulfed by their cells. The 'villi' in the gastral cavities of the type I gastrozooids of *Dromalia alexandri* appear to be extremely well developed, measuring up to 0.5 mm in length, and are very numerous. Whether they play some role in the intracellular digestion of food is uncertain, as the supposed feeding behaviour of the animals may not necessitate it. This latter conjecture has been reached from a study of the video tape-recordings of the 'Galápagos dandelions' *in situ*, as will be discussed later (see p. 292). None the less, a detailed study of these 'villi' in the type I gastrozooids will be necessary.

The question as to the organization of the two types of gastrozooids on the cormidial bases was raised in the section on *Stephalia corona*. The excellent series of stages in cormidial development found on the specimens of *Dromalia alexandri* has enabled this factor to be studied in detail. It has been found that the type I gastrozooids always are attached to the first cormidium (figure 32d, e) while the gastrozooids of all succeeding cormidia are of type II. This arrangement is shown clearly in the illustration (figure 33a) of a cormidial base to which three gastrozooids have remained attached. The gastrozooids of the first and second cormidia (gz.1 and gz.2, respectively) are large and fully developed while that of the third (gz.3) is only slightly differentiated. The tentacle of the first gastrozooid (figure 33b) is comparatively small but it is apparent that it carries no tentilla. In contrast, the tentacle of the second gastrozooid (figure 33c) is large and distinctly annulated. Numerous young tentilla are present at its proximal end and an occasional fully developed one is seen distally. Even the minute tentacle of the third gastrozooid (figure 33d) bears a few buds that represent the developing tentilla. Thus one would have expected to have seen some sign of them on the tentacle of the first gastrozooid, if they were to have been developed.

In *Dromalia alexandri* there does not appear to be any secondary insertion, onto the base of the corm, of reduced cormidia, comprising a type I gastrozooid, as was suggested for some

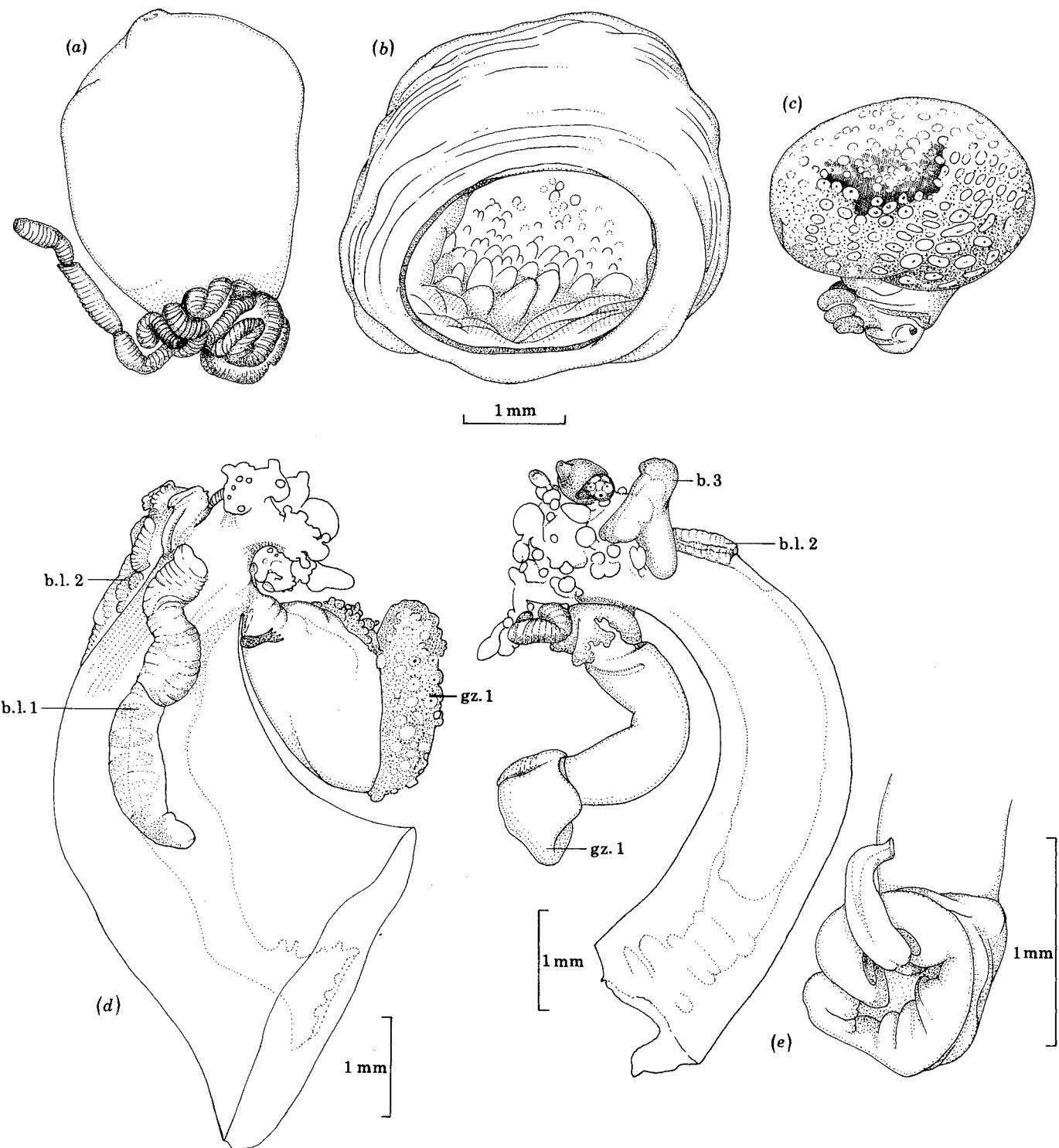


FIGURE 32. *Dromalia alexandri* Bigelow. (a-c) Type I gastrozooids. (d, e) Cormidial units with type I gastrozooids attached, and detail (in (e)) of a process from the mouth of such a gastrozooid. See text for details.

specimens of *Stephalia corona*, *Rhodalia miranda* and *Angelopsis euryale*. Whether new type I gastrozooids can be budded off on the individual cormidial bases is not known but the presence of some unaccounted for buds was noted earlier. The gastrozooids are a bright orange in life (figure 27) and this plate shows that the distal end of the type I gastrozooid frequently is everted. A young, somewhat denuded specimen (figure 26a, b), kindly loaned to me by Dr J. Ljubenkov, shows that the type I gastrozooids can reach relatively enormous lengths, reminiscent of the similar gastrozooids in *Stephalia corona*, but not as large. The older type I gastrozooids (figure 26a, b) bear no signs of the attachment of a tentacle, while the younger, thinner ones have narrow tentacles that, typically, do not bear tentilla. It is interesting to note that on the smaller specimens even the older cormidial bases are not greatly developed, and often only bear two well differentiated cormidia. Presumably growth of the siphosome is accomplished both by the addition of new cormidial bases apically, and by the expansion of the corm itself. The latter will allow more room for the individual cormidial bases to expand and, thereby, may allow further cormidial elements to be developed.

The remaining cormidial component, the gonodendron, shows no unusual features so far as can be discerned from the fragments that remain. Bigelow (1911) found that from two to four long, thin-walled gonopalpons were present on each. The specimens are dioecious and all but one of the present specimens that could be sexed were found to be male. A similar, but reversed, disparity in the sex ratio was found in the specimens of *Rhodalia miranda*, but it is impossible to suggest whether this has any ecological significance.

The internal structure of the corm. Bigelow (1911) concluded that the hypocystic cavity was absent in his specimens but, as discussed above, it is considered that it is present, at least in the younger specimens, but greatly reduced. The remainder of the interior of the nectosomal and siphosomal regions is filled by an almost transparent mesogloea ground substance. Bigelow stated that it was cartilaginous and extremely rigid, but again this is more apparent in the older specimens while in the younger ones the corm is quite spongy. The gastrovascular system can be divided into two sections: a system of large, uniformly sized canals which are relatively few in number but which form a network throughout the interior of the corm (figure 26e); and an extensive, reticulated network of canals of two sizes which is present immediately below the surface of the corm (figure 26f). Some of the canals in the major system within the corm have a spiral arrangement, particularly in the apical part of the siphosome. Also a large canal passes upwards from the siphosomal region and runs around at least half of the nectosome, giving off branches to the nectophoral muscular lamellae. The overall organization of these canals is complex and no obvious pattern could be elucidated. The superficial canal system, in the younger specimens, consists mainly of large canals that have relatively few branches (figure 26b). As the size of the specimens increases these larger canals branch more freely and an extensive reticulum of smaller canals is developed (figure 26f). This canal system does not penetrate into the cormidial bases as has been noted in other rhodaliid species. It can be seen that the band of ectoderm that separates the successive whorls of cormidial bases overlies the canal system and is in no way connected with it.

Discussion. *Dromalia alexandri* is the most distinctive species of rhodaliid siphonophore that has been examined. The presence of a flattened pneumatophore bearing several gelatinous protuberances is unique among the known rhodaliids and, as Bigelow (1911, p. 304) pointed out, would be of sufficient importance in itself to warrant the establishment of a new genus. In addition, only one other species, *Archangelopsis typica*, has an aurophore that bears papilliform

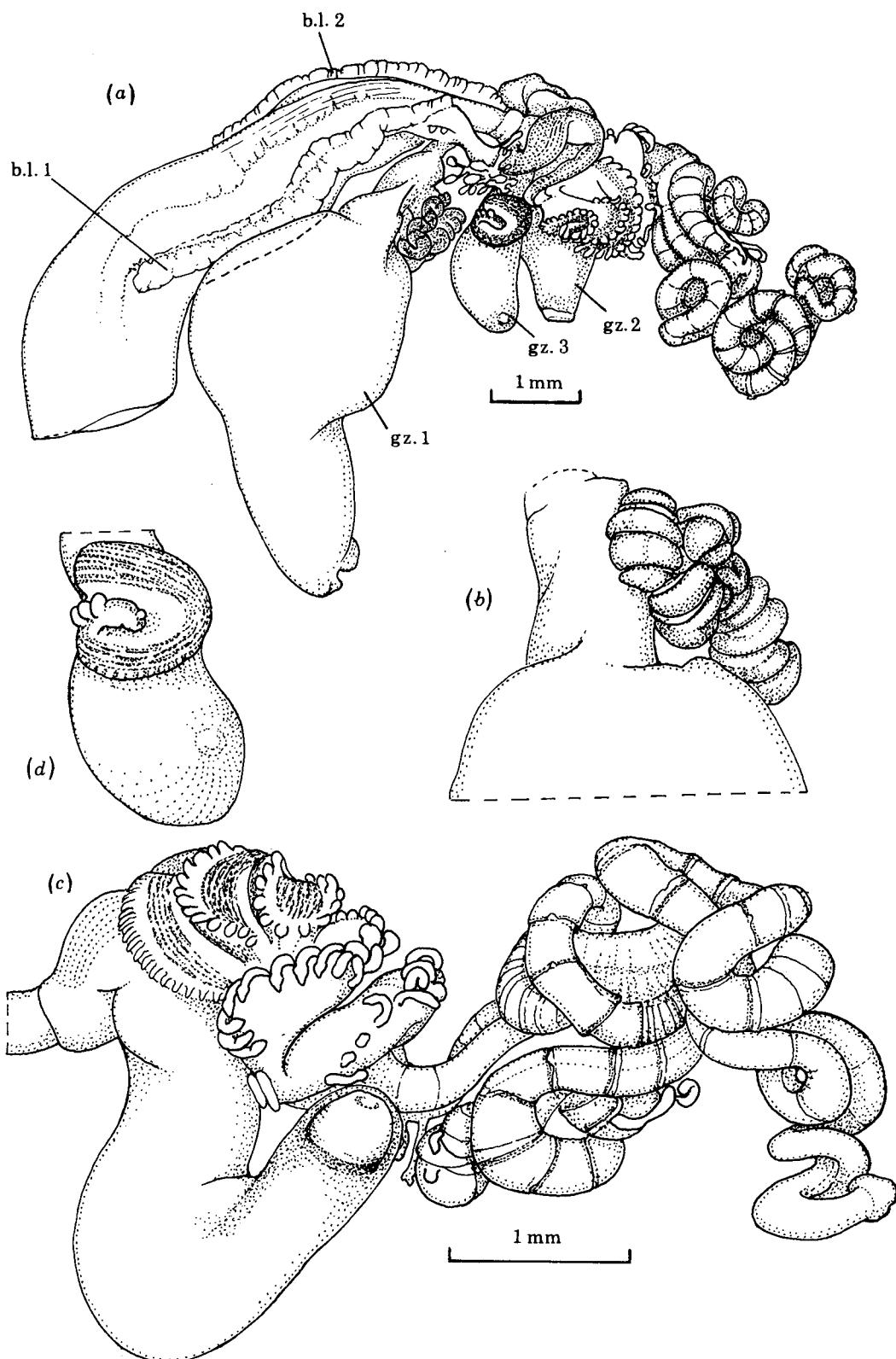


FIGURE 33. *Dromalia alexandri* Bigelow. (a) A cormidial unit with three gastrozooids attached. See text for details. (b) Detail of the basal region of the gastrozooid from the first cormidium. (c) The gastrozooid and tentacle from the second cormidium. (d) The developing gastrozooid and tentacle from the third cormidium.

appendages. The organization of the cormidial bases into discrete, regular whorls again is a feature that has not been noted in other rhodaliid species, and the structures of the bract and tentillum also are unique. Many other morphological characters, such as the virtual absence of a hypocystic cavity and the organization of the gastrovascular system, serve to establish the identity of this species without any difficulty.

The specimen of '*Dromalia* sp.' which was borrowed from the Smithsonian Institution (U.S.N.M. 52452) is, however, rather unusual. It is very large specimen whose siphosomal region has become flattened out in the form of a disc. The whole of the interior of the siphosome is missing and it is concluded that the specimen was dead on collection and that the base and interior of the corm had been eaten out by some predator or scavenger. In all other ways it resembles the other specimens of *Dromalia alexandri* that have been examined and, with due allowance for damage, there is thought to be no reason why the specimen should not be identified with that species.

Dromalia alexandri is the best known of any of the rhodaliid siphonophores although more *in situ* observations may have been made on the 'Galápagos dandelions'. Thirty-three records of its observation or collection have come to the author's notice and there are undoubtedly many more that have not. The records are listed in table 1 and their positions, where known, are plotted in figure 34, except for the three more southerly stations, and two others, from off Santa Cruz Island, where the information is too vague to allow the position to be plotted. In the process of establishing the geographical distribution of *D. alexandri* a few points arose that should be commented on. First, with regard to the original 15 specimens in Bigelow's (1911) possession, the dilemma (see p. 238) regarding the station data partially was solved by consulting the catalogue records for these specimens, all of which are still in existence. Eleven of the specimens are housed in the National Museum of Natural History, Smithsonian Institution, and the author is indebted to Dr M. Carpenter for supplying him with the following information: one specimen [TYPE] U.S.N.M. 29696 – *Albatross* st. 2927, collected off Southern California, 23. i. 1899 at a depth of 313 fm (572 m); ten specimens, U.S.N.M. 28326 – *Albatross* st. 2927, collected off San Diego, California in 1889 at the surface.

The remaining four specimens were transferred to the Museum of Comparative Zoology, Harvard University, and are catalogued as M.C.Z. 1594 and labelled "South Carolina, 1899; 'Albatross' st. 2927". The entry in the catalogue, however, gives the locality as Lower California.

It is evident that there is confusion with regard to both the year of collection and the locality, but all the entries have *Albatross* st. 2927 in common and this is taken to be accurate. This station was occupied on the 23. i. 1889 and is at $32^{\circ} 43' N$, $117^{\circ} 51' W$, which is off San Diego, California (figure 34). The net used was a large beam trawl which collected a bottom sediment of green mud at a stated depth of 313 fm (572 m). However, a current bathymetric chart indicates that the water depth at this locality is less than 200 fm (366 m), and it is assumed that the method used to estimate the original depth was in error. No actual soundings were made at this locality. Whether the ten specimens (U.S.N.M. 28326) were taken at the surface remains a mystery, but no mention was made of a surface collection in the cruise narrative and for other reasons too it is considered unlikely.

Another record for *Dromalia alexandri* was given by Alvarino (1971). She mentioned that some specimens had been collected in an epiplanktonic haul made in the eastern equatorial Pacific Ocean. However, in a list of records for *D. alexandri*, Alvarino (1971, p. 257) makes mention

only of Bigelow's (1911) specimens and to some unpublished data from the region off San Diego. It has not been possible to confirm this equatorial Pacific record and on the basis of the other information it is thought that it should be treated with some caution. The author is, however, indebted to the many people who kindly and generously supplied the remainder of the information given in table 1. All these records, apart from Alvarino's, point to a quite narrow geographical distribution for *D. alexandri* off the coasts of California, U.S.A., and Baja California, Mexico.

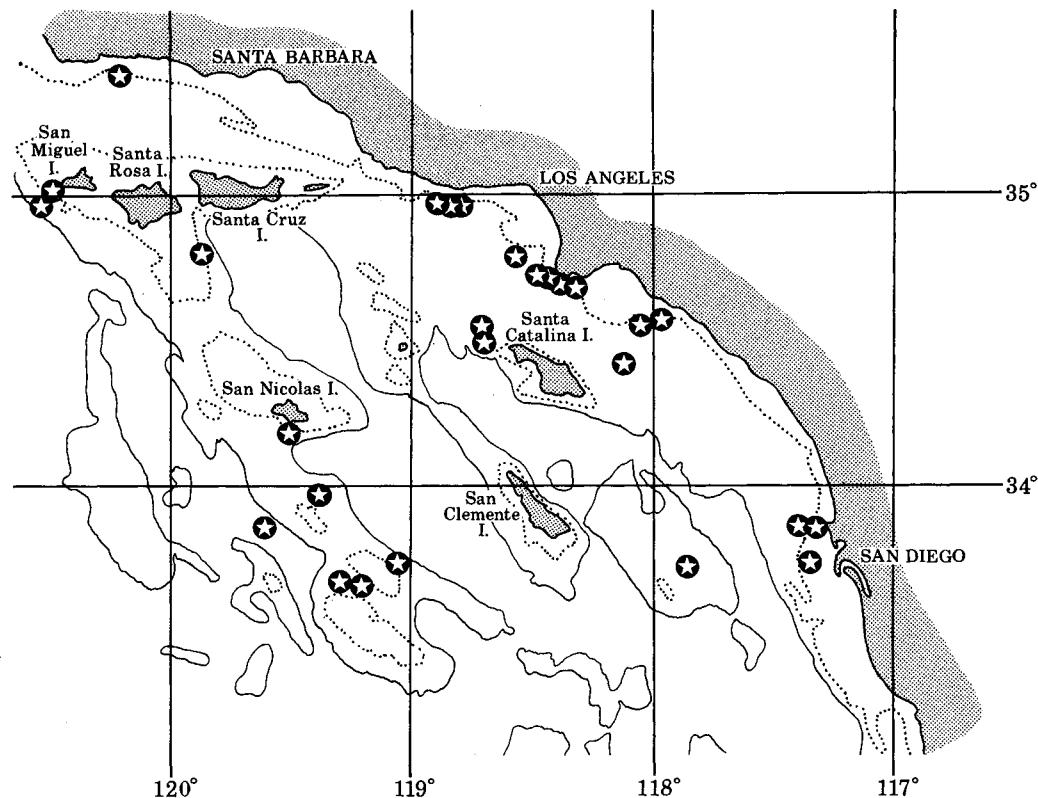


FIGURE 34. The geographical distribution of *Dromalia alexandri* Bigelow. Details of the positions are given in table 1. The depth contours are 100 fm (...) and 500 fm (—). 1 fm = 6 ft = 1.83 m.

The author also is greatly indebted to Dr E. W. Fager and Dr A. Flechsig of the Scripps Oceanographic Institution, and to Dr J. W. Vernon of General Oceanographics, Newport Beach, California, for making available their observations, from submersibles, on specimens of *Dromalia alexandri* *in situ*. It is these observations that definitely established that this species and, by extrapolation, all the other rhodaliids are benthic organisms. As is shown in figure 27, the animals are positively buoyant, principally by virtue of the gas in the enlarged pneumatophore, but remain tethered to the substratum, rather like miniature hot-air balloons, with the aid of their tentacles. The number of these tentacles attaching each specimen was estimated to range from as few as six to as many as three or four dozen, although these may be conservative estimates. There may be some correlation between the type of substrate and the number of attaching tentacles as those animals clinging to rocky surfaces used fewer than those on sedimentary bottoms. However, all the tentacles observed were used for attachment and none were

seen to be floating free. The tentacles themselves were greatly extended, being long, thin tubes with occasional small swellings and thickened portions along their length. Indeed, Dr J. Ljubenkov has supplied me with a picture of a specimen of *D. alexandri*, attached to a sandy bottom, whose tentacles extend to lengths of at least five times the diameter of the main corm. This contrasts markedly with the highly contracted, thickened tentacles seen on the preserved specimens (see, for example, figure 31a, b). On average the corm of each specimen was maintained at a height of 10–12 cm above the substratum, although heights of up to 30 cm were recorded. Occasionally, particularly if the animal was disturbed, the tentacles were contracted, thereby pulling the animal downwards to within 2–3 cm of the sea floor. If the animals were dislodged from their attachment then they floated smoothly upwards without any visible sign of propulsion: again the simile of the hot-air balloon. These observations might indicate that the animals were unable to swim using their nectophores, and certainly the presence of the latter was not noted by any of the observers. However, in these circumstances it is clear that the positive buoyancy of the animal would override any attempts at swimming, while under more natural conditions the buoyancy may be adjusted to near neutrality before detachment and active swimming takes place. The latter has been observed in the specimens of the 'Galápagos dandelions' which are described in the next section.

Although all of Dr Flechsig's observations indicated that *Dromalia alexandri* was attached to fine sedimentary material, Dr Vernon observed them attached to rocks. It was estimated from a series of photographs that the density of animals over the sea floor was $2.3 \pm 0.7 \text{ m}^{-2}$, but this might be biased on the high side since only the more interesting vistas were photographed. The animals were not seen to be actively feeding, but on one occasion Dr Fager observed the coordinated detachment and reattachment of a few tentacles which might serve as a means of 'walking' across the bottom. The overall depth distribution recorded for *D. alexandri* lies in the range 130–750 m (see table 1), but most of the records, including the *in situ* observations, lie in the 130–300 m depth range. The observations made by Dr Flechsig and Dr Fager showed that the animals were present between 195 and 270 m, with a mean depth of $235 \pm 7 \text{ m}$. However, in these instances the submersible spent relatively little time below 280 m. The information regarding the depth distribution of all the rhodaliid species will be reviewed later but it is evident that *D. alexandri* is one of the shallower-living species.

Genus: Thermopalia gen.nov.

Diagnosis. Rhodaliid siphonophore with smooth-walled pneumatophore and aurophore. The aurophore has a large basal attachment with the nectosomal region. There is a narrow, axial cavity within the siphosome. The cormidia, in the younger specimens, are arranged into obvious spiral whorls and are not borne on distinct, gelatinous bases. The gonodendra of the cormidia bear long-stalked gonophores, but gonopalpons are absent. The genus is monotypic.

Type species. *Thermopalia taraxaca* sp.nov.

Thermopalia taraxaca sp.nov. (figure 27, plate 14; figure 35, plates 15 and 16; figures 36–40)

Type material. One specimen (holotype) taken during dive 896 of the submersible *Alvin* on 21. ii. 1979 at a depth of approximately 2480 m. The type locality was $0^\circ 48.247' \text{ N}$, $86^\circ 13.478' \text{ W}$ in the region of the so-called 'Rose Garden' in the Galápagos Rift region. The device used to collect the specimen was a specially constructed container which was placed over the animal *in situ* and closed, by a magnetic catch, from below. This specimen is housed in the

United States National Museum of Natural History, Smithsonian Institution, and has the number 60425 in the coelenterate catalogue.

Material examined. The specimens collected during the 1979 Galápagos Rift Expedition have been examined, and I am grateful to Dr J. F. Grassle for placing them at my disposal. These specimens include the type material and:

Two specimens from *Alvin* dive 878, 19. i. 1979, at $0^{\circ} 47.92' N$, $86^{\circ} 13.5' W$, from a depth of ca. 2500 m. The dive was called 'The Search for Clambake'.

One specimen from *Alvin* dive 883 to the 'Garden of Eden' on 24. i. 1979 at $0^{\circ} 47.692' N$, $86^{\circ} 07.739' W$ and at a similar depth. This specimen has been designated a paratype and has been deposited in the British Museum (Natural History) collections as catalogue number 1982-2-2-2.

Five specimens from *Alvin* dive 884 to the 'Garden of Eden' on 25. i. 1979. Other station data as for dive 883. Histological sections, in the longitudinal plane, have been made using the smallest of these specimens.

In addition, numerous observations of these animals were made during the series of dives, and photographic records are available for *Alvin* dives 880, 883 and 891. The video tape-recordings of all the *Alvin* dives in this area include several sequences of the animals *in situ*. Details of the dives are given in the cruise report: Biological exploration of hydrothermal vents of the Galápagos Rift, 1979.

Diagnosis. Rhodaliid siphonophore with smooth-walled pneumatophore and aurophore. The pneumatophore is remarkably thin-walled with no obvious endodermal processes into the mesogloea of the pneumatocodon. The aurophore is a distinctive elongated structure that has a large, basal area of attachment to the dorsal region of the nectosome. The pneumatochone is surrounded by a highly thickened mesogloal layer, an extension from the pneumatosaccus. The chitin layer of the pneumatochone also is well developed. The cormidia, on the siphosome, are organized into distinct spiral whorls in the younger specimens, although this arrangement is obscured in the larger specimens. The cormidal elements are attached directly to the main body of the corm and are not mounted, distally, on pronounced bases. Two types of gastrozooid are present, and the type II form bears filiform tentilla. The gonodendra carry distinctive bracts and gonophores with elongated stalks. No gonopalpons appear to be present. Within the siphosomal corm there is a narrow, axial cavity. An anastomizing network of canals in the walls of this cavity is absent.

Description. The rhodaliid siphonophores observed and collected in the Galápagos Rift region originally were christened 'dandelions' by the participants in the series of dives made by the submersible *Alvin* in February and March 1977. The name was suggested by the appearance of the animals which resembled dandelions gone to seed (see, for instance, figure 27). In deference to this pseudonym, this new species of rhodaliid siphonophore, described here, has been named *Thermopalia taraxaca*, meaning the dandelion from the hot, sea vent hole. The description of *T. taraxaca* represents contribution number 15 of the Galápagos Rift Biology Expedition, which was supported by the National Science Foundation of the United States of America.

In the present state of preservation, almost all the gastrozooids, bracts and nectophores and many gonophores have been detached from the specimens. The denuded corms measure from 15 to 33 mm in height, and the siphosomal diameter ranges from 2.5 to 17.8 mm. The largest specimen here is designated the holotype. In life the size of the animals will obviously be

greater than the measurements given here since the type I gastrozooids, for instance, measure up to 17 mm in length in their contracted, preserved state. The overall colour of the animals *in situ* is bright orange (figure 27). Additional, more detailed photographs of the holotype *in situ* and shortly after having been brought to the surface are to be found in the '*National Geographic*' article by Ballard & Grassle (1979).

Pneumatophore. The pneumatophore is a large, smooth-walled structure which has a pinkish-orange colour in life. Its diameter, in the preserved material, ranges from 2.4 mm in the smallest specimen to 5.9 mm in the holotype. The walls of the pneumatophore are exceptionally thin, *ca.* 0.02 mm, and are of a uniform width over the whole surface, except for a slight thickening of the mesogloea of the pneumatosaccus basally, where it overlies the hypocystic cavity. The endodermal layers of both the pneumatocodon and pneumatosaccus are in frequent contact and so the pericystic cavity is somewhat reduced. In the histological sections, no processes from the endoderm of the pneumatocodon were seen to penetrate the mesogloal layer, as has been noted in many other rhodaliid species. The pneumatocyst, or chitinous lining to the gas-filled cavity, also is very thin, except in the region of the aurophore. There it is overlain by a distinct pad of secondary ectoderm which forms part of the pneumadenia.

Aurophore. The aurophore is a large, smooth-walled structure (figure 35a-d,f) which apparently bears a single external pore. The latter is not easily seen and could not be traced in the histological sections. The aurophore's diameter varies from 2.3 to 3.8 mm which, on average, is about half that of the pneumatophore. It is an elongated structure, somewhat resembling that in *Angelopsis euryale*, except that its basal surface is connected to the upper part of the dorsal surface of the nectosome (figure 35d,f; figure 36) by a thin tissue sheet which represents an extension of the nectosomal wall. The hypocystic cavity, which occupies the whole interior of the nectosome, is thus expanded dorsally into this lower region of the aurophore.

The pneumatochone is restricted to the apical part of the aurophore (figure 36). It is composed of a very thick, elongated, chitinous cylinder which connects with the pneumatocyst of the gas-filled cavity. It does not extend beneath the pneumatophore as was noted in *Rhodalia miranda*, for instance. In the sections, the chitinous cylinder appears, for the most part, to be made up of circumferential fibres, surrounded by a narrow band of disorganized fibres. This sheath is surrounded by a monolayer of regularly shaped ectodermal cells, the primary ectoderm of the pneumatosaccus, and then by a highly thickened, homogeneous layer of mesogloea (figure 36). The chitin layer has a constriction towards its distal end, before becoming expanded laterally. Within and throughout this chitin cylinder lies the secondary ectoderm of the pneumadenia. The ectodermal cells, for the most part, appear elongated and lie along the length of the cylinder. There are frequent gaps between these cells which, although they may be artificial, might allow the passage of gas through the pneumadenia. In addition there are several large cavities (figure 36) present which presumably once contained the gaseous products of the ectodermal cells. At the distal end of the pneumatochone, the chitinous cylinder is open, allowing the secondary ectoderm of the pneumadenia to connect with the primary ectoderm which extends out into the aurophore from the pneumatosaccus wall of the pneumatophore. This connection is difficult to follow in the histological sections, presumably because of its partial destruction during gas expulsion. Within the distal part of the pneumadenia some granulated cells, the so-called 'giant amoeboid cells', can be discerned.

Several radial septa traverse the pericystic cavity in the apical part of the aurophore. Basally, the aurophore contains only a cavity. The radial septa are lined by endodermal cells, which

surround a thin layer of mesogloea. There were no signs of the presence of pockets of ectodermal cells within the mesogloea, as Carré (1969) noted in the pneumatophore of the agalmid physonect siphonophore, *Nanomia bijuga*.

Nectosome. In several of the preserved specimens, the nectosome appears as a long, narrow neck to the corm (figure 35*b, c*), while in others it is greatly expanded (figure 35*d*). In the

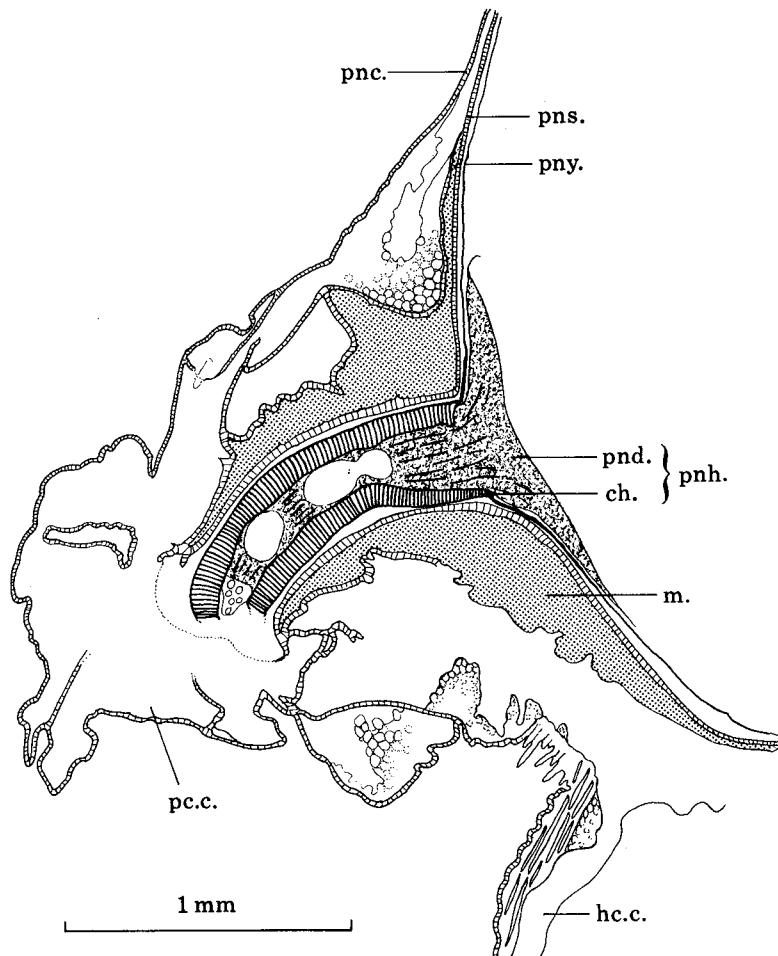


FIGURE 36. *Thermopalia taraxaca* sp.nov. A median section through the aurophore.
A list of abbreviations is given in the Glossary.

holotype (figure 35*a*) the nectosome is very short and difficult to characterize. It appears (J. F. Grassle, personal communication) that the nectophores are not always apparent in the living specimens, as also can be seen from the photographs of the holotype (see Ballard & Grassle 1979). Only when these animals are actively swimming can the nectophores be discerned. These observations would suggest that the nectosome is greatly contracted in life, with the nectophores somehow folded out of sight. However, if necessary, the nectosome can be expanded, possibly by pumping gastrovascular fluids into the hypocystic cavity, which might raise the pneumatophore clear of the rest of the corm and expose the nectophores so that they can become functional. The nectophores were a pale orange colour in life, with more darkly

coloured radial and ostial canals. They are of the usual rhodaliid type, being flimsy, thin-walled sacs with four straight radial canals.

The nectosome itself is thin-walled and surrounds the extensive hypocystic cavity. On its external surface are borne from 11 to 17 symmetrically arranged, thin muscular lamellae, to which the nectophores once were attached. The pedicular canals of the nectophores are in direct communication with the hypocystic cavity. On the ventral side of the nectosome, one or two nectophoral buds usually remain attached to their zone of proliferation (figure 35*b, c*). In this region a succession of five or six cormidial units, in a series of developmental stages, can be followed down the nectosome and these connect with the units on the most apical whorl in the siphosome.

Siphosome. In all but the largest (holotype) specimen, the cormidia are seen to be arranged into dextrotropic spiral whorls on the siphosome (see, for example, figure 35*b, c*). The number of whorls varies from four to seven according to the size of the specimen, and each whorl is separated from the next by an obvious gutter where the wall of the corm itself can be discerned. In these specimens, new whorls clearly are being added apically, while below the older whorls are expanding in size. This results in the siphosomal corms of some specimens having a cone-shaped appearance. There appears, from the *in situ* observations, to be a maximum size to which the animals grow and this point appears to have been reached by the largest (holotype) specimen (figure 35*a*). Here the siphosomal corm has become greatly expanded and the spiral arrangement of the cormidia obscured. As in other rhodaliid species, it appears that at this stage the growth of the corm is accomplished more by the development of new cormidial components on the existing cormidial units than by the addition, apically, of new units, although young cormidia still can be seen in the region of the zone of proliferation. Because of the excessive development of the cormidial components, particularly the gonodendra, in this largest specimen it is impossible to estimate the number of cormidial whorls that are present. This situation is compounded by the fact that the gutter-like depression that separated the whorls in the younger specimens has disappeared as the cormidial units have overgrown it.

Within the siphosome of the smaller specimens there is a narrow, irregular, axial cavity (figure 35*d*), which is surrounded by a wall of varying thickness. In the youngest specimen, which has been histologically sectioned, this cavity (figure 35*f*) is ill defined. The endodermal lining of the cavity is well developed and, apically, several septa of mesogloea, lined by endodermal cells, are seen to penetrate into or traverse the cavity. These septa are possibly the original linings to the gastrovascular canal of the younger siphosomal whorls which are gradually breaking up to produce a single cavity. This suggestion is consistent with the fact that, in the basal part of the corm, such septa are not so pronounced. In addition, these septa have, in sagittal section, a staggered arrangement that is indicative of a spiral arrangement on the corm as a whole. In a larger specimen (figure 35*d*) the central, axial cavity is better defined, although endodermal processes are still noticeable. The walls of the cavity in this case appear thickened but this is probably due to the contracted state of the bases of the cormidial elements rather than to an increase in the thickness of the wall itself.

The mesogloea in the wall of the siphosomal cavity is relatively thin, but it bears innumerable septal processes which extend outwards between the deeper layers of the ectodermal cells. These septa are lined by small, rounded ectodermal cells which presumably represent the longitudinal musculature as was noted also in the sections of the corm of *Angelopsis euryale*. External to these muscle fibres are some large ectodermal cells with darkly staining nuclei. The

cormidial elements connect directly with the central, axial cavity and no peripheral network of canals was noted. It is hoped to make a more detailed histological study of the corms of these animals in the future.

The actual organization of the individual cormidia has proved difficult to assess since the cormidial elements are attached directly to the main corm of the siphosome rather than being borne on pronounced cormidial bases as has been found in most other rhodaliid species. The very young cormidia, from close to their zone of proliferation, consist of a gastrozoid, which lies basally, and a gonodendron with a developing bract. At this stage there is a very short, common stem but the two elements are deeply divided one from another. The slightly older cormidial units already have a second cormidium developing on them, in the axil between the major branches of the first. Further stages in their development could not be followed, but it is presumed that the cormidial units on the main body of the siphosome are organized according to the general plan worked out earlier for either *Stephalia corona* or *Dromalia alexandri*. On the denuded corms, the large protuberances, which represent the pedicles of the gastrozooids, are very obvious, as are the highly branched gonodendra.

Some indication of the organization of the cormidial units may be given by the number of detached gastrozooids and bracts present in the residues of the samples, since attempts were made to collect the animals intact. The total residue for the five specimens taken during *Alvin* dive 884 contained 120 type I gastrozooids, 347 type II and 539 bracts. This indicates a ratio, in the above order, of approximately 1:3:4, which would be consistent with a conclusion that the mature cormidial units were made up of four cormidia, each with a bract on its gonodendron. The type I gastrozooids probably were attached to the first cormidium to be developed, as has been noted in other rhodaliid siphonophores. However, this conclusion is difficult to reconcile with the number of cormidial elements found in the residue of the type material from *Alvin* dive 896. In this case, the ratio, in the same order as above, is 1:10:5. This ratio can only be explained if one assumes both an excessive development of cormidia on the corm and a loss of bracts. Certainly the external surface of the corm in this specimen is very crowded and the bracts would appear to serve little purpose, especially for protection, as they would not extend out beyond the gastrozooids in the living animals.

The individual components of the cormidia easily can be recognized. The type I gastrozoid is a large, elongated structure, measuring up to *ca.* 17 mm in length in its contracted state (figure 37a). It is apparent that these gastrozooids can reach considerable lengths when extended in life (see photograph on p. 698 of Ballard & Grassle 1979, and figure 27 of the present paper), when they have the appearance of long, narrow tubes which actively move about among the tentacles. The stomach regions of these gastrozooids are bright orange, while the proboscis and basal segments are a pale yellow. The proboscis segment bears several longitudinal, pigmented striations, which are underlaid by endodermal ridges within. These ridges become convoluted in the stomach region, presumably as a result of contraction. Further down in the stomach region, the gastrozoid wall bears numerous endodermal villi (cf. *Dromalia alexandri*), some of which measure over 1 mm in height. None of the mature type I gastrozooids bears any signs of the attachment of a tentacle (figure 37a), but some of the younger ones do possess a very reduced structure (figure 37b). This tentacle is a short, narrow tube that bears long, ill defined annular segments which show no signs of the presence of tentilla.

The type II gastrozooids (figure 38) are of the usual rhodaliid type, having a bulbous stomach region, a small, narrow proboscis, and a slightly expanded basigaster to which the well

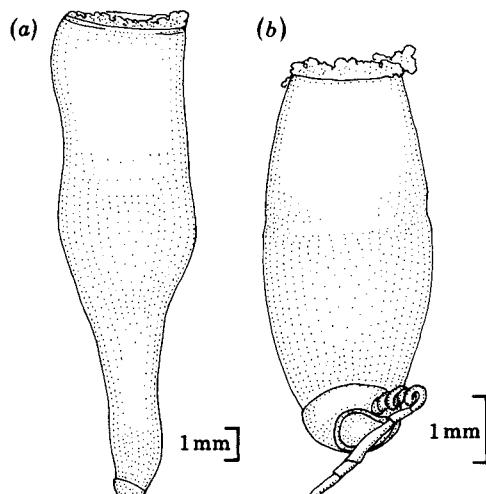


FIGURE 37. *Thermopalia taraxaca* sp.nov. Type I gastrozooids. (a) A well developed gastrozooid.
(b) A young gastrozooid, with a small, annulated tentacle attached.

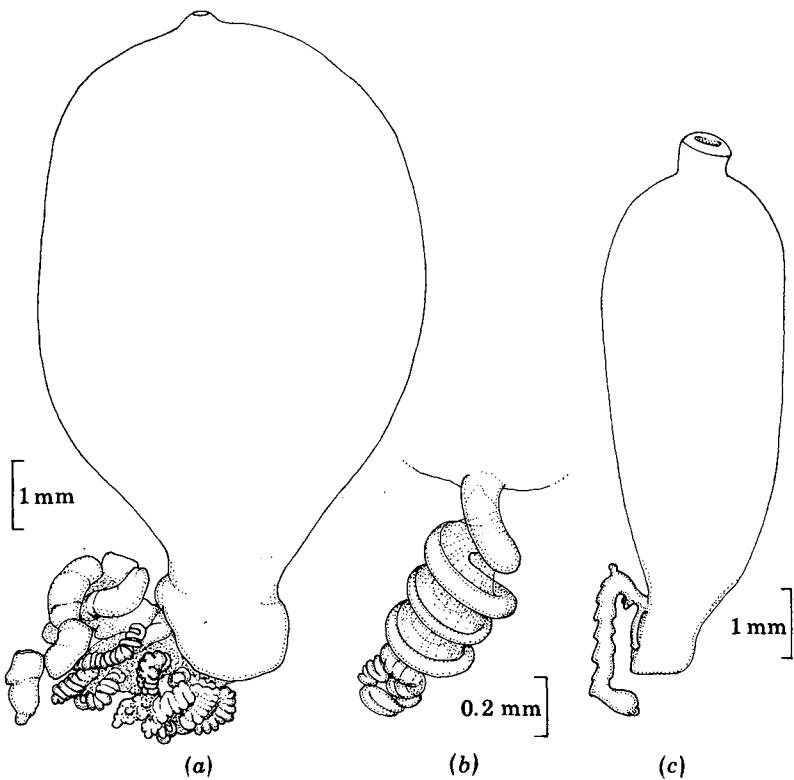


FIGURE 38. *Thermopalia taraxaca* sp.nov. Type II gastrozooids. (a) A mature gastrozooid with the proximal part of a well developed tentacle. (b) An individual tentillum. (c) A young gastrozooid with a developing tentacle.

developed tentacle is attached. The gastrozooids are a brownish-orange (see photograph on p. 698 of Ballard & Grassle 1979), flecked with whitish spots, and with five, sometimes six, whitish streaks symmetrically placed around the mouth opening. The *in situ* photographs show that these gastrozooids are elongated, not globular, in life, but they do not stretch out as far as do the type I form. The holotype possessed over 310 type II gastrozooids and clearly they are

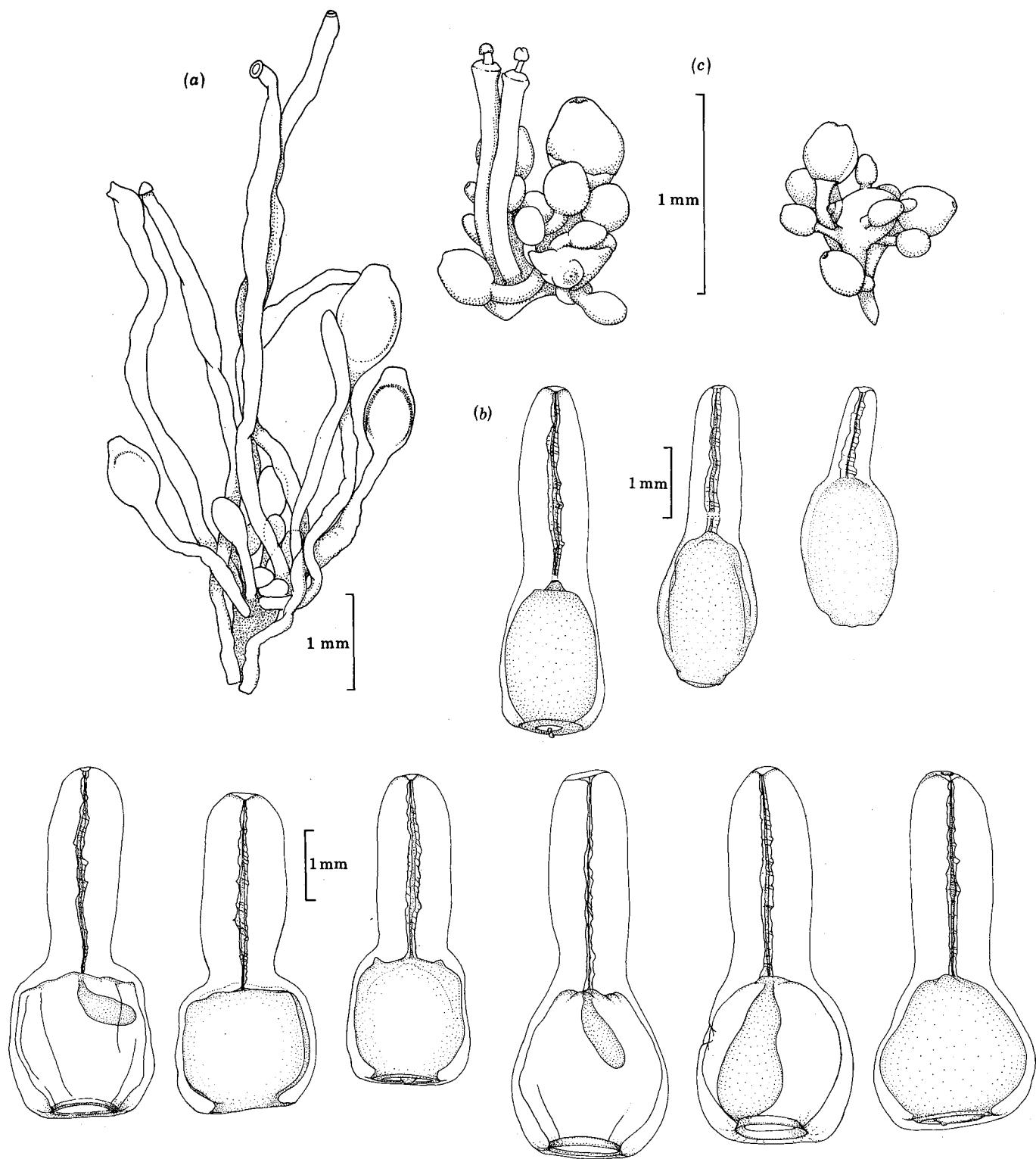


FIGURE 39. *Thermopalia taraxaca* sp.nov. (a) Part of a male gonodendron. (b) Various stages in the development of and forms of male gonophore. (c) Parts of a developing female gonodendron.

densely crowded on the corm. The contracted pedicles of these gastrozooids are very evident on the denuded corms (figure 35c, d), and a few detached gastrozooids were found with this section still attached. These pedicles were of a similar length to the gastrozooid itself and so, when extended in life, they can bear the gastrozooid well away from the main body of the corm.

A young type II gastrozooid (figure 38c) has a very small tentacle attached, whose annulations only appear as emarginations, but on which the buds of tentilla clearly can be seen. The fully developed tentacle is very long and is made up of many hundreds of annulated segments. These segments, in the preserved state, are about as broad as they are long, i.e. somewhat shorter in length than those of the tentacle on the young type I gastrozooids. No tentilla were found attached to the more distal segments, although their original points of attachment can be seen on the dorsal surfaces. There is a large suspensory ligament attached along the ventral surface at the proximal end of the tentacle, and in this region each annular segment bears a large tentillum (figure 38a). The tentillum (figure 38b) is a filiform structure, highly coiled in the preserved state, on which three regions can be recognized. The short, proximal pedicle connects with a long, spirally coiled cnidoband, which bears three types of nematocyst. Although these nematocysts have not been positively identified, they might be large euryteles or stenoteles, smaller anisorhizas and some small rhopalonemes or haplonemes. The anisorhizas are the commonest. The third section, the terminal filament, is long and thin and bears numerous rounded nematocysts, which are probably rhopalonemes or desmonemes.

None of the gastrozooids, either type I or II, that were cut open were found to contain any obvious prey fragments. However, since the animals were collected at least 1–2 h before they were examined and preserved, it is likely that the digestive processes would have been well under way by that time. The type I gastrozooids were found to contain very little material of any sort, while the type II ones usually were filled by an amorphous, mucoid mass, within which only a few undischarged nematocysts could be recognized.

The organization of the gonodendron (figures 35e, 39) is unusual among the known rhodaliid siphonophores, in that gonopalpons are not developed. The long, filamentous structures that cover the corm of the denuded specimens (figure 35a) were at first glance thought to be gonopalpons but on closer examination it was found that they were the very long stalks of the gonophores. The absence of gonopalpons is probably due to the fact that in other rhodaliid species they are developed at the distal ends of the gonodendral stem, but such a stem in *Thermopalia taraxaca* is either very short or non-existent. Also the tufts of gonophores are so densely crowded that there would be little room for the development of gonopalpons.

The specimens of *Thermopalia taraxaca* are dioecious, as has been found to be the case in other rhodaliid siphonophores. The type specimen is male, and the dense tufts of gonophoral stems can be seen all over the surface of the denuded corm (figure 35a). The individual male gonophores arise from a very short gonodendral stalk, very close to the main body of the corm (figure 35e, 39a) and possess extraordinarily long stems. Some stages in the development of these gonophores are shown in figure 39b. At an early stage in their development the gonophores are short-stemmed with a rounded umbrella region. This latter region gradually increases in size and the distal part of the stem becomes laterally thickened. Meanwhile the proximal region of the stem rapidly increases in length. The shape of the mature male gonophore is variable, some having squared umbrella regions while others remain rounded (figure 39b). The manubrium, on which the sexual products are borne, increases in size until it fills the entire sub-umbrella cavity. The thickened, distal part of the stem sometimes is notched.

In the female specimens, the stem of the gonodendron again is very short and the egg pouch is attached very close to the corm itself (figure 39c). The female gonophores are budded off from these pouches although, when mature, their stems may have moved down onto the short gonodendral stem, as was remarked upon, in another species, by Brooks & Conklin (1891). The mature female gonophores are borne on long stems (figure 39c). Because of the unusual organization of the cormidia, with all the elements attached very close to the main body of the corm, it is necessary for the pedicles or stems of all these elements to be of considerable length in order to reduce the effects of crowding.

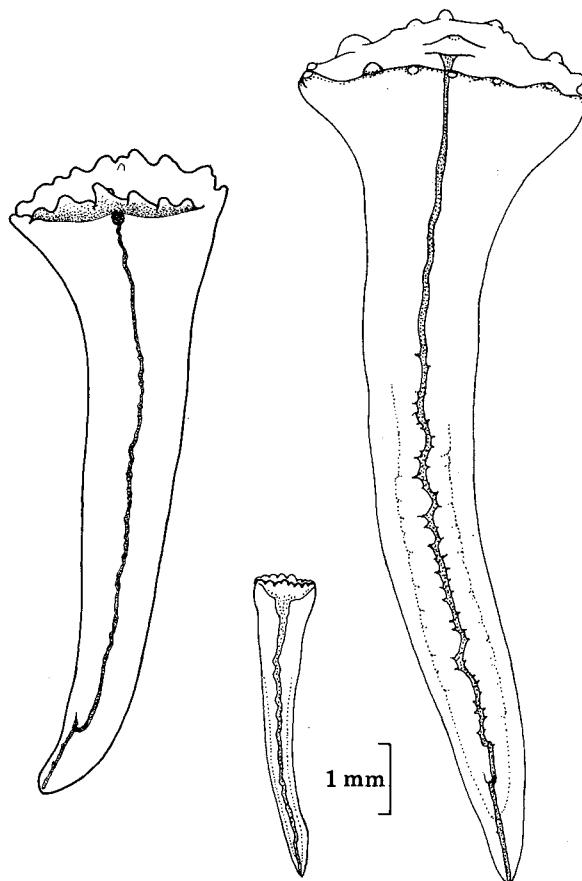


FIGURE 40. Bracts of *Thermopalia taraxaca* sp.nov.

It is difficult to observe the point of attachment of the bract to the gonodendron, but the fact that they are developed on this stem can be discerned from the young cormidial units in the zone of proliferation. It is evident that only the extreme proximal tip of the bract is attached to the stem as there the bracteal canal is seen to lie on the ventral surface (figure 40). The bract is a soft, flexible, triangular structure, which has an expanded, truncated, concave distal facet. The edges of this facet bear rounded, tooth-like projections, usually 16 in number but, depending on the size of the bract, their number can vary between 14 and 28 (figure 40). The bracteal canal is simple, without branches, and terminates in the centre of the distal facet, which is slightly swollen at this point. This canal is not pigmented (see photograph on p. 698 of Ballard & Grassle 1979).

Discussion. One of the major distinguishing features of the specimens of *Thermopalia taraxaca* lies in the construction of the siphosome. The fact that the cormidial elements are not borne distally on swollen or elongated, gelatinous bases has not been noted in any other rhodaliid siphonophore, with the probable exception of *Sagamalia hinomaru*. The absence of gonopalpons on the gonodendra also is an unusual feature as the other, better known species possess them. In addition, the presence of a narrow, axial cavity within the siphosome, whose walls are relatively thin and do not contain an anastomizing network of canals, is another characteristic feature. The only other species whose siphosomal cavity is similarly organized is *Archangelopsis typica*, but here the cavity is voluminous, and, further, this species is easily recognized on the basis of another character, the papilliform appendages on the aurophore. The exact nature of this cavity in *S. hinomaru* is uncertain, owing to the disassociation of the corm in the single available specimen, but it is possible that it might be found to resemble that of *T. taraxaca*. A cavity is present in the siphosome of the species in the genus *Angelopsis*, but there it is a large, thick-walled structure and an extensive, anastomizing network of canals is present in its walls. It was suggested earlier that *Stephalia bathyphysa* might possess a narrow, axial cavity, but this cannot be established until new material becomes available. However, the structure of the cormidia in *S. bathyphysa* would appear to be quite different, as far as one can gather from Haeckel's (1888b) meagre description. From the above it is apparent that there are several similarities in the organization of *T. taraxaca* and *S. hinomaru*. None the less the species are quite distinct as is established by the structure of the bracts and the presence of gonopalpons on the gonodendra of the latter. It may be, however, that these two species are more closely allied to each other than to any other known rhodaliid species.

The 'Galápagos dandelions', *Thermopalia taraxaca*, were first sighted during a series of dives, made by the submersible *Alvin*, in February and March 1977 during an expedition to the Galápagos Rift region. Photographs of specimens also were taken by using the deep-towed camera system ANGUS. At that time no specimens of the rhodaliid siphonophore were collected and the researchers were puzzled as to their identity, referring to them as perhaps being a new form of Protozoa (Corliss & Ballard 1977). Corliss & Ballard (1977) give a brief account of the results of the expedition, while a more detailed geological account of the area can be found in, for example, Corliss *et al.* (1979), Allmendiger & Riis (1979), van Andel & Ballard (1979) and Crane & Ballard (1980).

The Galápagos Rift is a region of divergence between the Cocos and Nazca plates, and it lies in a small valley, 3–4 km in width, which is bordered by steep escarpments. Within this valley is a continuous, east–west, axial ridge and several narrow, marginal ones. The axial ridge includes the youngest areas of volcanic activity in the valley as well as the hydrothermal vents. Topographic profiles, perpendicular to the rift axis, are given by van Andel & Ballard (1979). The presence of hydrothermal vents was of great interest to the geologists, and the scientists on the Expedition made a detailed investigation of five particular vents, called 'Clambake I and II', 'Garden of Eden', 'Oyster Bed' and 'Dandelions'. The early results (see Corliss *et al.* 1979) indicated that 'Clambake II' was no longer active, hydrothermally or biologically, but later investigations proved this not to be the case (Crane & Ballard 1980).

The hydrothermal vents were found to be located in areas where pillow lava was present, which was in contact with flatter lying flows, except at the 'Dandelions' vent. The vents lay close to small vertical scarp faults. The maximum temperature of the water issuing from these vents was found to range from 7 to 17 °C (Corliss *et al.* 1979), compared with an ambient

bottom water temperature of *ca.* 2 °C. The highest temperature anomaly observed was 20 °C, and the warmed water was found to be pluming from the vents at rates between 2 and 10 l s⁻¹. The effects of these warm water plumes were detectable at heights of 180 m above the vents, but here the anomalies were very slight. At another site of hydrothermal activity, in the East Pacific Rise (see later) it was found, by the RISE Project Group (1980), that the venting water, with temperatures of up to 23 °C, very quickly mixed with the bottom waters and that at a height of 10 m above the vent the anomaly was only 0.3 °C, while at a similar distance to the side the anomaly was as low as 0.1 °C. The water issuing from many of the vents contains high concentrations of hydrogen sulphide, up to 160 µM (Corliss *et al.* 1979), as well as large numbers of metabolically active bacteria. The plume waters, whether they contain hydrogen sulphide or not, were found to be anoxic, but the oxygen concentration increased rapidly as mixing occurred with the ambient bottom waters. Karl *et al.* (1980) have suggested that primary production by bacterial chemosynthesis, using the geothermally reduced sulphur compounds, is the basis of the food chain that sustains the dense populations of benthic organisms, particularly the filter feeders, that surround the vents. However, Enright *et al.* (1981) consider that chemosynthesis may not be the only source of food and that advection from the surrounding waters also may play a significant part. Both these potential sources of material were first mooted by Lonsdale (1977).

The preliminary biological results for the 1977 Galápagos Rift expeditions (see, for instance, Corliss *et al.* 1979; Crane & Ballard 1980) indicated that the benthic fauna that surrounded the vents was usually dominated, in biomass, by large vesicomyid clams, mytilid mussels, enormous vestimentiferan worms (?pogonophores) and numerous small serpulid worms. In general the different faunistic groups had distinctive arrangements around the vents (Galápagos Biology Expedition Participants 1979). Thus, as the hydrothermal vent region is approached the outer ring of benthic organisms is made up of crabs, enteropneusts ('spaghetti') and 'dandelions', *Thermopalia taraxaca*. The enteropneusts were draped on the rocks while the 'dandelions' occupy low, protected spots between them. Closer to the vent the area is dominated by clams, mussels, serpulid worms and small anemones; adjacent to the vents the worms predominate, while many galatheid crabs scavenge in the area. It is only these innermost regions where the temperature or the anoxic state of the plume waters might have any effect on the organisms.

Crane & Ballard (1980) give a more detailed description of the distribution of the benthic organisms around the five hydrothermal vents studied during the 1977 expedition. Whereas four of the vents had the usual population of benthic organisms around them, the fifth, 'Dandelions', had the rhodaliid siphonophores as the predominant organism. The explanation for this difference probably lies in the fact that the 'Dandelions' vent is the only site of hydrothermal activity where no hydrogen sulphide was found to be present in the plume water. The absence of large, filter-feeding organisms thus would be correlated with the absence of the chemotrophic bacteria, which also may give rise to the dissolved organic matter on which the enteropneusts and vestimentiferans feed. According to Crane & Ballard (1980) the 'Dandelions' patch had a thermal field of about 400 m². The 'dandelions', *Thermopalia taraxaca*, were attached to the rocks near the bases of the pillow lava. In one region (depth range 2472–2482 m) the average density of these animals was 3 m⁻², while at another (depth range 2486–2494 m) up to 11 animals per square metre were found. At the other vents, where the 'dandelions' occurred on the periphery of the thermal field the average density of these animals was *ca.* 2 m⁻².

In January and February 1979 a second expedition took place in the Galápagos Rift region.

It was during this expedition that the specimens of *Thermopalia taraxaca* were collected. A brief summary of the results is given in the 'National Geographic' article by Ballard & Grassle (1979). Immediately after this expedition another site of hydrothermal activity was discovered a little further north in the East Pacific Rise, at 21° N, ca. 109° W. The RISE Project Group (1980) reports on this expedition, which took place in March–May 1979. Some of the hydrothermal vents in this area were found to be ejecting water at temperatures as high as 380 ± 30 °C, while others, around which the biological communities were mainly clustered, had plume temperatures of ca. 20 °C. The water depth at these vents was slightly greater than at the Galápagos ones, namely 2600–2650 m. The fauna of the vent regions is similar to that of the Galápagos site, with vestimentiferan worms, large vesicomyid clams, and serpulid polychaetes. Although the RISE Project Group makes no mention of the presence of 'dandelions', the photographic records show that rhodaliids are present at that site (Dr W. Smithey, personal communication), but they are somewhat lighter in colour than the Galápagos ones. It is not yet known whether these animals are of the same or a different species. The RISE Project Group suggested that, because of the similarities in the populations, the vent communities are widespread and that the species are equipped with sophisticated dispersal mechanisms. In line with this idea Lutz *et al.* (1980) recently have suggested that the mytilid mussels found at the Galápagos site have a planktotrophic larval stage that is equipped to enable dispersion over large areas. These authors discuss the possibilities for behavioural adaptations to life in these geographically isolated regions of hydrothermal activity.

Each *Alvin* dive made during the 1979 Galápagos Rift Expedition was recorded on video tape, and there are several sequences showing the 'dandelions' *in situ*. As mentioned above, specimens of the 'dandelion', *Thermopalia taraxaca*, are most commonly found in crevices between the lava blocks for, since there is much biological activity in the region of the vents, it is advantageous for the 'dandelions' to avoid disturbances that might cause their detachment from the substratum. However, this is not to say that they never detach themselves deliberately, as active swimming has been observed (Dr J. F. Grassle, personal communication). Each 'dandelion' attaches itself to the rocks using its tentacles (figure 27). The large number of these tentacles is consistent with the abundance of type II gastrozooids, and over 310 of the latter were found attached to the holotype. Since it would appear that the animals are positively buoyant then, to avoid rising rapidly away from the sea floor, the animals must be able to adjust their buoyancy to near neutrality before releasing their grip. In this context, Dr Grassle has seen neutrally buoyant 'dandelions' swimming actively, with the nectophores clearly visible. The leading edge of the corm is tilted downwards so that the nectophores in this region exert their thrust in that direction. The other nectophores are able to push the animal along in a horizontal direction. Observations also showed that the 'dandelions' could swim up or down one of the collecting cylinders, again indicating both near-neutral buoyancy and a high degree of coordination in the use of the nectophores for locomotion.

It was noted earlier that the type I gastrozooids are extraordinarily elongated in life. The video tape recordings indicate that these gastrozooids move actively among the tentacles and in some cases it appears that the mouth region is placed directly onto the tentacle, when the gastrozooid is fully extended, and then pulled back along the tentacular surface until it reaches the base. In this way the gastrozooid may be searching for food items trapped, by the tentilla, on the tentacles. The individual tentilla probably are too fine to be resolved on the tape recordings, but some sequences indicated the presence of some elongated filamentous structures

which might be tentilla or perhaps the stalks of gonophores. Although the tape recordings indicate that the type I gastrozooids appear to be actively searching for prey it is not known what these animals feed on. It is unfortunate that none of the gastrozooids contain any distinct prey fragments, although pieces of polychaete worms, possibly the so-called 'Pompeii worms', *Alvinella pompejana* Desbruyeres and Laubier, 1980, were noted in association with the specimens. The type II gastrozooids were invariably packed with an amorphous, mucoid substance without any recognizable fragments. The possible mechanisms involved in feeding will be discussed later (see p. 292).

The many observations and tape recordings of the 'Galápagos dandelions', *Thermopalia taraxaca*, *in situ* are convincing proof of the benthic nature of these animals. The strange modifications that these animals have undergone, in comparison with their presumed long-stemmed ancestors, will be discussed later but it is clear that they are well adapted to their unusual mode of life. It will be interesting to know, as more areas of hydrothermal activity are investigated, just how widespread *T. taraxaca*, or its relatives, are along such fracture zones. In this context it is interesting to note that some recent expeditions to the Juan de Fuca Ridge in the Blanco Fracture Zone, ca. 44° 40' N, 130° 20' W, have shown that rhodaliid siphonophores are present at a depth of approximately 2500–2600 m. I am indebted to Dr John R. Delaney of the University of Washington for sending me some photographs of the specimens taken during the expedition. Unfortunately no specimens have, as yet, been collected and it is impossible to be sure of the identity of the rhodaliids from the photographs, but their presence in another fracture zone in the NW Pacific Ocean might lead one to suppose that these new records represent a further extension of the geographical range of *T. taraxaca*. There is still much to learn about these fascinating animals.

5. DISCUSSION

The systematics of the Rhodaliidae

In the previous sections, where the morphological characters of each rhodaliid species have been discussed, it has been suggested that the system of classification of this family used by earlier workers, e.g. Totton (1965), is too broadly based and that several specific names, previously synonymized with others, should be re-established as distinct species. The major morphological features that have been used previously to distinguish the rhodaliid species are:

- (a) the shape of the pneumatophore;
- (b) the shape of the aurophore;
- (c) the internal structure of the corm, including
 - (i) the configuration of the hypocystic cavity,
 - (ii) the arrangement of the gastrovascular canal system in the siphosome, and
 - (iii) the presence or absence of a cavity in the siphosome, and whether it is extensive or central and axial;
- (d) the arrangement of the nectophores into a single, double or multiple corona;
- (e) the presence or absence of tentilla on the tentacles;
- (f) the presence or absence of two types of tentacles; and
- (g) the general character and organization of the cormidia.

The first three of the characters listed above are considered here to be the major characters in the systematics of the Rhodaliidae. Before they are considered in detail, the other characters

will be reviewed briefly, together with the structure of the bract. Haeckel (1888b) used the presence or absence of tentilla on the tentacles as one of the major characters by which he subdivided his order Auronectae into two families, the Stephalidae and Rhodalidae [sic]. However, because of the defective state of almost all the specimens that have been described, the various diagnostic features that concern the presence or absence of certain external morphological characters, as listed above, generally have been discounted by more recent authors or are considered to have doubtful validity. For instance, Totton (1965) thought that the absence of tentilla on the tentacles was simply the result of their loss during collection, and indeed he found them to be present on his *Goldseeker* specimen of *Stephalia corona* whereas Haeckel (1888b) had not found them on his *Triton* specimens.

It appears that no author has commented on the extraordinary observation made by Haeckel (1888b) that two types of tentacle were present on his specimens of *Stephalia (Stephonalia) bathypysa*, albeit that both types were said to be without tentilla and that one was not annulated. This inadequately described species has been given little attention since its description and indeed within a year Claus (1889) had synonymized it with *Stephalia corona*, a precedence that has been followed up to now. The intuitive reasoning that has led to the re-establishment of *S. bathypysa* as a distinct species, probably within the genus *Stephalia*, has been discussed earlier. It now appears that the presence of two types of tentacles, one with and one without tentilla, but both being annulated, is a general feature of rhodaliid siphonophores, with the possible exception of *Archangelopsis typica*, owing to the unusual arrangement of its cormidia. Whether the tentacles, which previously had been described as being without tentilla, represent those belonging to the type I gastrozooids or whether the tentilla simply have been detached is uncertain, but it has now been established that at least five rhodaliid species possess two types of tentacle. Thus, this feature cannot be used as a specific character for *S. bathypysa*. The possible differences in the function of these two types of tentacle, and their associated gastrozooids, are discussed later.

Another of the morphological characters that Haeckel (1888b) used in distinguishing his four species was the arrangement of the nectophores into single, double or multiple coronas. The evidence for these specific configurations here is thought to be based on somewhat spurious evidence, and clearly the true nature of the nectophoral organization only can be established when observations are made on the live animals. At present, it does not appear to be a usable systematic character and will not be considered further. The structure of the nectophore itself, unlike in many other physonect siphonophores, is not a useful character as, in all species where they are known, the nectophores are flimsy, featureless bags with no apparent ridges or crests or differences in the pattern of the radial canals.

In contrast, the structure of the bracts here has been established as an excellent systematic character, so long as they remain attached to the corm during collection. In the original descriptions of most rhodaliid siphonophores, the presence of bracts was not considered and until now bracts have been described on only three rhodaliid specimens, although Bigelow (1913) had suspected that they were originally present on *Archangelopsis typica*. With the new material, and a re-examination of some of the original material, it has been possible to show that bracts definitely are present on six of the ten rhodaliid species that are currently recognized. Undoubtedly all the rhodaliid species possess them at some stage, although they may have been lost in life, as was suggested for *Dromalia alexandri*, or have been detached from the corm during collection. It has been shown that there are specific differences between the bracts, but it is

considered unwise to establish a system of classification based on their structure until the bracts of all the rhodaliid species have been studied. In a similar fashion, it is difficult to use the morphological differences in the cormidal organization of the various species as systematic characters, as the corms are usually collected in a highly denuded state. However, there are some obvious differences in the mode of attachment of the cormidia to the siphosomal corm, as is mentioned later. Nevertheless, it is apparent that the most useful morphological characters might be those which are almost invariably present despite the degree of mutilation of the specimen. Only three of the characters listed above appear to fill this role; namely the shape of the pneumatophore, and of the aurophore, and the internal construction of the corm. These features will now be considered in turn.

(a) *The shape of the pneumatophore*

Dromalia alexandri is the only species that can be distinguished immediately on the basis of this character alone. All the other known species possess smooth-walled pneumatophores while *D. alexandri* has an extremely thick-walled, flattened pneumatophore which bears several triangular, gelatinous protuberances. It is doubtful whether other features, such as the relative size of the pneumatophore, its mode of attachment to the nectosome and the presence of pigment spots can, as yet, be considered to have any real systematic value. The size of the pneumatophore clearly is a function of the growth stage of the animal as is evinced by the fourfold variation in its size among the specimens of *Stephalia corona*, if one includes the post-larval *auronula* stage. However, the extremely thin-walled pneumatophore of *Thermopalia taraxaca*, which does not have any endodermal processes into the mesogloea of the pneumatocodon, sets this species apart from many of the other rhodaliids, for instance those in the genera *Angelopsis*, *Rhodalia* and *Stephalia*.

(b) *The shape of the aurophore*

All but two of the known species have smooth-walled aurophores, with a single pore connecting the pericystic cavity with the exterior. The two other species, *Dromalia alexandri* and *Archangelopsis typica*, bear numerous, external papilliform appendages, each with a terminal pore. Since *D. alexandri* can be distinguished on the basis of its pneumatophoral structure, then *A. typica* is identified immediately by the combination of smooth-walled pneumatophore and papilliform aurophore. In the eight species with smooth-walled aurophores, the method of attachment of the aurophore to the dorsal side of the pneumatophore, and the relative size of the former, may possibly have some systematic significance. Certainly the elongated aurophore of *Angelopsis euryale*, which is attached only at its base, contrasts markedly with the globular structures in the genera *Stephalia* and *Rhodalia*, especially as in the latter much of the upper surface of the aurophore is united with the pneumatophore. In addition, the tissue sheet that connects the aurophore of *Thermopalia taraxaca* to the nectosomal region is unique among the known rhodaliid species. It would appear, from the little evidence available, that these characters do not have any ontogenetic variability. However, they deserve further attention once more material is at hand, but since more distinctive characters can be found, it would seem that, at present, the mode of attachment of the aurophore only need be used as corroborative evidence.

In addition, there appear to be specific differences in the relative size of the aurophore. Kawamura (1954) noted that the aurophore of *Sagamalia hinomaru* was minute in comparison with the nectophores, while Haeckel (1888b) observed a close similarity in sizes between the

aurophore and nectophores of *Stephalia corona*. The ratio of the diameter of the aurophore to that of the pneumatophore has been found to be fairly consistent in 12 of the specimens of *Rhodalia miranda* that have been examined, namely $0.312 \pm 0.005:1$, and this ratio shows no apparent trend according to the size of the specimen. Conversely the specimens of *Thermopalia taraxaca* showed a wider variation in this ratio (mean $0.54:1$, range $0.44\text{--}0.66$), which again bore no relation to the size of the animal. In *T. taraxaca*, the flimsy nature of the aurophore, with its tissue sheet connecting it to the nectosome, made the measurements less exact. In general, relatively small aurophores are found in *R. miranda* and *S. hinomaru* while larger ones are found in *T. taraxaca*.

Finally, the internal structure of the aurophore might be of systematic significance, e.g. in the number of radial septa, or the shape of the pneumatophore, but such information is known inadequately and difficult to ascertain without the destruction of the specimen. None the less, the extraordinarily elongated pneumatophore, particularly in the younger specimens, of *Rhodalia miranda* is distinctive, as is the internal organization of the aurophore in *Thermopalia taraxaca*, and possibly in *Angelopsis euryale*.

(c) *The internal structure of the corm*

Daniel (1974) provides the only published key to the genera of the family Rhodaliidae, and this key is based largely on the internal structure of the corm. It should be noted that this key is based on the generic diagnoses given by Totton (1965) and includes only those genera that Totton recognized. Schneider (1898) conjectured that all five of the rhodaliid species then described might be congeneric, and even might represent different growth stages of the same species. He considered that the internal, endodermal cavity of the siphosome disappeared progressively during ontogenetic development and that it was replaced by a richly developed supporting layer that was penetrated by a network of tubules. Although more recent authors have considered that up to three of the original species are valid, Totton (1965) reiterated the suggestion that they might prove to be congeneric. Totton drew attention to the difficulties involved in deciding which characters were of a generic or specific importance and it appears that he was uncertain as to the systematic significance of the internal structure of the corm.

To investigate further the variability in the internal structure of the corm in rhodaliid siphonophores, at least two specimens from five species have been sectioned sagittally. One of the other two species that have been examined, *Archangelopsis typica*, clearly has one large cavity within its corm, and its thin walls are not penetrated by an anastomizing network of gastrovascular canals. The internal organization of the other species, *Sagamalia hinomaru*, is uncertain but, by inference, differs from all other known rhodaliids, as discussed earlier. *A. typica* could only be considered as a young growth stage of *Dromalia alexandri*, on the basis of the fact that they both possess papilliform appendages on their aurophores, but it has been established that the organization of their cormidia for instance, particularly in the structure of their bracts, is entirely different. The bracts of *S. hinomaru* serve also to establish its specific identity in comparison with, for example, *Stephalia corona*.

The specimens that were sectioned sagittally were chosen to represent, whenever possible, the widest range in size and, thereby(?), age. One is torn between the necessity of establishing the variability, if any, of the internal structure of the corm and the propriety, perhaps misguided, of maintaining the better preserved material intact. However, it was found that the internal structure of the corm was specifically consistent while the interspecific differences were marked.

For instance, although the peripheral network of canals was less well developed in the younger specimens of *Dromalia alexandri* the basic arrangement was directly comparable with that in the older ones. Also, there were no differences in the internal organization of the specimens of *Rhodalia miranda* despite the large size difference between those from the Zoond collection and those taken by Challenger. Similarly, the corms of the specimens of *Angelopsis euryale* that have been examined showed little variation in their internal organization, as was the case with the specimens of *Stephalia corona*. There were some ontogenetic variations in the structure of the axial cavity in *Thermopalia taraxaca*, which could be reconciled with a gradual breakdown of the walls separating the individual cormidial whorls, but the basic arrangement bears no relation to that in any other rhodaliid species. Thus, it is felt that the internal organization of the corm is a good systematic character and that it can be used to distinguish almost all the rhodaliid species. Only in *Sagamalia hinomaru* and *Stephalia bathyphysa* is this organization of the corm imperfectly known.

The question remains as to whether the internal structure of the corm is of specific or generic importance. It is difficult to make a comparison with the classification of the other six families of physonect siphonophores as the systematic characters used in those are very different. The family Apolemiidae is distinguished by the presence of tentacles on the nectosome, the Physophoridae by the laterally expanded, sac-like siphosome, the Athorybiidae by their contracted form and hypertrophied nectostyle, the Forskaliidae by the arrangement of their nectophores into a multiple series, and the Agalmidae by the more general, long-stemmed appearance with biserial nectophores. Within these families, the genera and species are distinguished on the basis of their best or, in some cases, only known character. Such characters are usually the structure of the nectophore, or of the tentillum or gonodendron. Such characters have little significance among the rhodaliid siphonophores. No clear interspecific variations have been noted in the featureless nectophores, and in all but one species, *Dromalia alexandri*, the tentilla are filiform, although a more detailed study is warranted. As Bigelow (1911) pointed out, the tricornuate tentilla of *D. alexandri* are so distinctive that they alone would necessitate the establishment of a separate genus to include the species that bears them.

It is clear that some of the other nine rhodaliid species, apart from *Dromalia alexandri*, that are considered in this paper should be placed in separate genera despite the fact that they all possess filiform tentilla and similar nectophores. Other criteria must be brought into play. As discussed above, the combination of a smooth-walled pneumatophore and an aurophore with papilliform appendages must be sufficient to establish *Archangelopsis* as a separate genus. However, although there appear to be some differences in the structure of the aurophore in the remaining eight rhodaliid species, with smooth-walled aurophores and pneumatophores, this factor alone may not be sufficient for specific identification. It is necessary, in this context, to combine this character with others, such as the organization of the cormidia and the internal structure of the siphosome. In this way, particularly with reference to the absence of gonopalpons on the cormidia, the status of the genus *Thermopalia* can definitely be established. Similarly, although with an element of negative evidence, the genus *Sagamalia* can be separated off from all the other known rhodaliids.

Unfortunately, the cormidial organization in four of the remaining species, *Angelopsis globosa*, *A. euryale*, *Stephalia dilata* and *S. bathyphysa*, is inadequately known and so cannot, as yet, be considered as systematic evidence. However, there are clear similarities between the cormidial organization in *Rhodalia miranda* and *S. corona*, although that of the former is more complicated

than that of the latter. Whether all six of these species should be considered as congeneric depends on the relative significance of morphological characters, other than those of the aurophore and of the cormidia. The most obvious of these features is the internal structure of the corm and this character alone can be used to define three distinct groups among these six species, namely: (i) those with a large, thick-walled cavity in the siphosome (genus *Angelopsis*) ; (ii) those with a solid siphosome traversed by a major gastrovascular canal system and a network of smaller canals (genus *Stephalia*) ; and (iii) those with a solid siphosome traversed throughout by a reticulum of small, similarly sized canals (genus *Rhodalia*). These arrangements, together with the ontogenetic evidence mentioned above, are thereby taken to be of generic significance. They form one of the bases of the following key to the genera and species of the Rhodaliidae. This key is not wholly satisfactory, because of the lack of knowledge on the exact nature of the construction of the corm in certain species. It is to be hoped that new specimens will become available in order that some of these uncertainties can be cleared up.

Key to the genera and species of the family Rhodaliidae

- 1 (a) Pneumatophore and aurophore smooth-walled. 2
- (b) Pneumatophore smooth-walled, aurophore with papilliform appendages.
 - Genus *Archangelopsis* (*A. typica*)
 - (c) Pneumatophore apically flattened and bearing several gelatinous protuberances; aurophore with papilliform appendages. Genus *Dromalia* (*D. alexandri*)
- 2 (a) Hypocystic cavity restricted to nectosomal region; siphosomal corm possesses a reticulum of different-sized gastrovascular canals including a major canal system.
 - Genus *Stephalia* (see below)
 - (b) Broad hypocystic cavity restricted to region immediately below the pneumatophore; siphosomal corm without a major canal system. Genus *Rhodalia* (*R. miranda*)
 - (c) Hypocystic cavity throughout nectosomal region; cavity present in siphosome. 3
- 3 (a) Siphosomal cavity vast and thick-walled; aurophore a distinctive elongated structure. Genus *Angelopsis* (see below)
 - (b) Siphosomal cavity narrow and axial†; aurophore connected to nectosome by a thin tissue sheet. Genus *Thermopalia* (*T. taraxaca*)
 - (c) Siphosomal cavity either large or axial (exact configuration uncertain); aurophore minute; distinctive bracts present on cormidia. Genus *Sagamalia* (*S. hinomaru*)

Genus: *Stephalia*

- (a) Hypocystic cavity *per se* restricted to upper part of nectosome, the remainder of the nectosome being filled with many large, intercommunicating chambers; up to ca. 20 nectophores present which are arranged in a single corona; reticulum of small gastrovascular canals throughout siphosomal corm. *S. corona*
- (b) Hypocystic cavity probably occupies whole of nectosomal region; reticulum of small gastrovascular canals restricted to periphery of siphosome (number of nectophores not known). *S. dilata*
- (c) Internal structure of corm inadequately known but there is either an axial cavity or a system of gastrovascular canals that includes a very large canal; between 20 and 30 nectophores present, which may be arranged in a double corona. *S. bathyphysa*

† This character also may apply to *Stephalia bathyphysa*.

Genus: *Angelopsis*

- (a) Walls of siphosomal cavity penetrated only by radial gastrovascular canals, with a peripheral reticulum of longitudinal and latitudinal canals; connection between siphosomal and hypocystic cavities reduced or absent. *A. euryale*
- (b) Walls of siphosomal cavity (?) with a reticulum of gastrovascular canals throughout; (?) distinct opening connecting siphosomal and hypocystic cavities. *A. globosa*

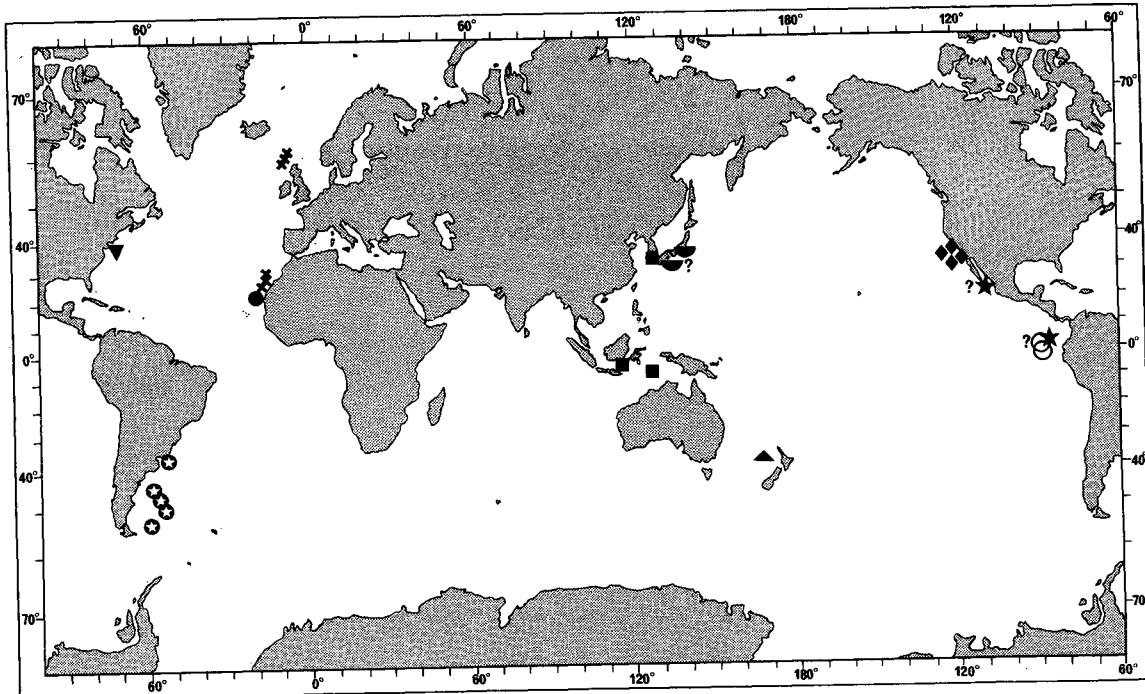


FIGURE 41. The geographical distribution of the species of rhodaliid siphonophore: ▼, *Angelopsis globosa*; ●, *A. euryale*; ✕, *Stephalia corona*; ○, *S. dilata*; ▲, *S. bathyphysa*; ■, *Sagamalia hinomaru*; ▨, *Archangelopsis typica*; ★, *Rhodalia miranda*; ◆, *Dromalia alexandri*; ★, *Thermopalia taraxaca*.

The geographical and bathymetric distribution of rhodaliid siphonophores

The previous authors who have studied specimens of the family Rhodaliidae have made various conjectures as to the bathymetric distribution of these animals, as discussed earlier (see p. 181). However, the overwhelming evidence, from *in situ* observations on two species, *Dromalia alexandri* and *Thermopalia taraxaca*, shows that none of these earlier conjectures are accurate and that, for the most part at least, the animals are benthic in habitat. The fact that almost all the known specimens were caught in benthic trawls or nets that sampled the benthos, by accident or design, lends credence to this statement. The rhodaliid siphonophores have been found at most depths throughout the coastal regions of the World's oceans. None the less, the distribution of each individual species occurs within a moderately localized area, and also depth range, although it must be recognized that there is a dearth of available data. The geographical distribution of the ten rhodaliid species that are recognized here is summarized in figure 41. The fact that the distributions are localized has been used as evidence that certain poorly known rhodaliids should be considered as separate species, and not synonymized with others, as previous authors have done.

The numerous records for *Dromalia alexandri* (see also figure 34 and table 1) conform with the generalized picture for the distribution of rhodaliid species. This species is one of the shallowest-living, although it has been recorded, on the bottom, over a depth range of 64–725 m, with a peak of abundance in the 150–300 m depth range. It is interesting to note that the other shallow-living species, *Archangelopsis typica*, like *D. alexandri*, possesses papilliform appendages on its aurophore. All the species with smooth-walled aurophores live at depths greater than 450 m, as far as is known, with most occurring below 900 m. *A. typica* also is the most widely distributed species, albeit only known from three localities. The specimens described by Lens & van Riemsdijk (1908) came from the East Indian Archipelago, at depths of 100 and 112 m, while Bigelow's (1913) record was from the southern tip of Japan. Bigelow gave 254 m as the depth of collection but, for reasons discussed earlier, this is considered to be an overestimate and it is thought that a depth closer to 100 m is more reasonable.

Another species, *Sagamalia hinomaru*, occurs in the region of Japan, but little is known about this animal as there is only one (?two) record for its existence. Kawamura (1954) said that the specimen was collected at a depth of 450 m, while Moser's (1924, 1925) specimen, which might belong to the same species, was said to have been collected at the surface, although no station data are available.

The evidence for *Stephalia bathyphysa* being a separate species, distinct from *Stephalia corona* with which previously it had been synonymized, rests on the fact that the single record for it comes from the west of New Zealand, at a depth of 503 m. *S. corona* meanwhile only has been found in the North Atlantic Ocean, and its depth distribution is markedly deeper. In the region of the Wyville Thomson Ridge, to the northwest of Scotland, *S. corona* has been found at depths of ca. 1000 m, while off the NW African coast it occurs somewhat deeper at ca. 1500 m. As for *Archangelopsis typica*, the two main sites where *S. corona* has been collected are widely separated and there are no records to connect them. This may, however, be a reflection on the areas at which benthic trawling surveys have been made. In the NE Atlantic the continental slope, in the 1000–1500 m depth range, is relatively steep for most of the region between NW Africa and the outer limits of the Celtic Sea, particularly in the Bay of Biscay. This factor would limit the possibilities of successfully trawling in these regions. None the less it should be noted that the continental slope is contiguous throughout the depth range in question, and it is surprising that no specimens have been found in the Porcupine Seabight, to the southwest of Ireland, where extensive work has been done recently by the biologists at the Institute of Oceanographic Sciences.

Another species, *Angelopsis euryale*, recently has been found, at a depth of ca. 3100 m, beneath the highly productive, upwelling waters off the NW African coast. This depth is the greatest for any known rhodaliid species, and it is extraordinary that such animals, with relatively large pneumatophores, can produce gases at pressures in excess of 300 atm (ca. 30 MPa). Indeed, some planktonic physonect siphonophores, albeit with much smaller pneumatophores, have been found at depths down to 4000 m (unpublished data). The other species within the genus *Angelopsis*, *A. globosa*, also occurs at great depth, namely 2553 m, and the single record for it comes from the western side of the North Atlantic Ocean. The differences between these two species have been discussed already and, although there are frequent records for the widespread distribution of benthic organisms that live in the deep abyssal zone (below 4100 m), such a distribution is less apparent among the shallower-living benthos. Thus it is considered unlikely that the two species may be synonymous.

One other species, *Rhodalia miranda*, has been found in the Atlantic Ocean, but all five records come from the slope region off Argentina (figure 41), at depths ranging from 455 to 1098 m. The record for ?*Rodalia* [sic] given by Brooks & Conklin (1891) came from the region of the Galápagos Islands, in the equatorial Pacific. If this specimen were to be referred to *R. miranda* then this species would have the widest geographical distribution of any rhodaliid, but this is considered unlikely and the specimen has been referred to another species, *Stephalia dilata*, which was taken at a similar locality. However, without a re-examination of both specimens the validity of this procedure can never be verified. It should be noted that whereas the Brooks & Conklin specimen was taken at a depth of 496 m, Bigelow's (1911) specimen of *S. dilata* came from a depth of 1158 m. These depths are similar to the maximum and minimum depths at which *R. miranda* has been collected but, as a general principle, although the data are scant, many individual rhodaliid species occur over a depth range of 500–600 m.

The remaining recognized rhodaliid species, *Thermopalia taraxaca*, has been found also in the region of Galápagos Islands, in the Galápagos Rift, and (?) additionally in the East Pacific Rise. It is the only species that has been recorded in association with a distinctive geological feature, the hydrothermal vents. However, as more research is done into such areas, the distributional range of this, and perhaps other species, may be greatly increased. Indeed some new records for a rhodaliid siphonophore that might be *T. taraxaca* have recently come to light from the Juan de Fuca Ridge region, further to the north in the NW Pacific. *T. taraxaca* has been found within the depth range 2450–2600 m, and for a semi-sedentary animal to exist at such depths, and in such numbers, must require a consistent supply of food. Whereas this is clearly the case in the area around the hydrothermal vents, such a conclusion also must be extrapolated to the other areas where the deep-living rhodaliids have been found. An abundant supply of energy to the benthic food chain, but not necessarily directly to the rhodaliids, will be found in the upwelling region off NW Africa, where both *Stephalia corona* and *Angelopsis euryale* have been found. However, it is difficult to make corresponding remarks about many of the other areas. In general the deeper-living rhodaliids are found on substrates that consist of globigerina ooze or mud, and Sokolova (1969) classifies such substrates as occurring in the more eutrophic regions of the ocean floor, where the benthic biomass varies between 0.1 and 1 g m⁻². None the less the lack of detailed distributional data for the rhodaliid siphonophores makes it difficult to draw any definite conclusions except to state a truism that these carnivorous animals can only exist where there is a sufficient supply of prey material.

The adaptations of rhodaliid siphonophores to their benthic existence

Phylogeny

The phylogeny of the siphonophores has given rise to much discussion and many misconceptions in the past for little, if any, fossil record exists (Scrutton 1979), and it is most probable that several divergent, and later convergent, lines of evolution have occurred. However, there is general agreement that the ancestral siphonophore was an advanced larval, polypoid stage of a benthic hydrozoan, which became adapted to a permanent planktonic life, aided by the development of the pneumatophore. This process may have included a phase when the larva became attached to the surface film, as an alternative to becoming transformed into the benthic, polypoid stage. At this former interface, the entrapment of an air bubble at the aboral end, followed later in the evolutionary process by the actual secretion of gas into a pneumatophore, may have been facilitated. It has been suggested that the pneumatophore appeared at an early

stage in siphonophore evolution but later was lost when the calycophoran species evolved, for it appears that the apical part of their larvae, which is the site of pneumatophoral development in the cystonect and physonect larvae, atrophies during development. This might lead one to consider one of these suborders to be phylogenetically primitive but, as Totton (1965) points out, various aspects of the organization of both groups appear to represent reductions from the predicted ancestral form so that it is impossible to distinguish an ancestral form from among the extant species.

Some of the theories of siphonophore evolution are summarized by Leloup (1954), although it should be noted that much of his discussion is concerned with the Chondrophoridae, which now are considered to be only distantly related to the siphonophores and have evolved quite separately. It should be remembered that, until recently, all siphonophores, with the exception of the pleustonic cystonect, *Physalia physalis*, were considered to be holoplanktonic animals, although Rottini (1974) had suggested that the calycophore, *Muggiae kochi* (Will, 1844) may have a benthic stage in its life history, when a young cormidium becomes detached from the stolon. It is known now that the rhodaliids also are an exception to this rule. In addition, most siphonophores are long-stemmed, sometimes reaching several tens of metres in length, and their organization is adapted to a free-swimming existence. There are very few brachystele siphonophore species, and (?) all of them are physonects. When considering the phylogeny of the physonect siphonophores, Leloup (1954) suggested that the long-stemmed (macrostele) forms were probably more primitive than the short-stemmed (brachystele) ones, and thus that the shortening of the stem occurred at a later evolutionary stage and culminated in the appearance of the species of the families Rhodaliidae and Athorybiidae. Garstang (1946) and Totton (1954), however, reached a different conclusion. They suggested that there was no reason to suppose that a short-stemmed form should have evolved from a macrostele ancestor, and that it was more likely for the reverse to be the case. Garstang supported this conclusion with a simplified analogy to the fishing potential of both brachystele and macrostele forms. He suggested that the tentacles and tentilla of short-stemmed forms, such as *Athorybia rosacea*, easily became entangled, but observations on such species show that this is not so and that their fishing behaviour is highly coordinated. Indeed, Garstang himself pointed out how little was known concerning the special adaptations of such siphonophore species.

It can be tacitly assumed that the ancestor of the rhodaliid siphonophores was some form of holoplanktonic physonect. Although the hydrozoan ancestor of the siphonophores was undoubtedly benthic, there is little to suggest that the specialized mode of existence that the rhodaliids have adopted is ancestral or even atavistic. Further, and despite previous assertions, there are several indications, which are discussed later, that the ancestor of the rhodaliid siphonophores was a long-stemmed, planktonic physonect. Nevertheless, there are similarities between the anatomy of the physophorids and rhodaliids that might suggest a close relationship. Whether one can extrapolate this fact to suggest that the other brachystele species are holoplanktonic forms whose ancestors once passed through a benthic '*rhodalia*' stage is a conjecture beyond the scope of this present work and, indeed, beyond the comprehension of the present author. But, whatever the origins of the rhodaliid siphonophores, whether from a macrostele or from a brachystele ancestor, there seems little doubt that many of the peculiar features that these animals display have appeared as a result of the readoption of a benthic way of life. For instance, the fishing behaviour of the holoplanktonic physonect species results in the tentacles being deployed in a variety of fashions (Biggs 1977), and Purcell (1980) has suggested that some

species may resort to aggressive mimicry to maximize their fishing effort. When a prey item is captured it is transferred to the mouths of the gastrozooids by the contraction of the tentacles. However, since the rhodaliid siphonophores are attached to the substratum by their tentacles, their feeding behaviour has had to undergo considerable change to adopt to this unique way of life among the siphonophores. Thus, it is of interest to summarize some of the features of rhodaliid siphonophores that may have resulted from their adaptation to a novel benthic existence.

Pneumatophore and aurophore

In comparison with those of all other physonect siphonophores, the pneumatophore of the rhodaliid species is enormous. In the largest known species, *Rhodalia miranda*, the pneumatophore may contain a volume of gas of 2000 mm³, compared with the 0.3–10 mm³ in most holoplanktonic physonects. Only in the pneumatophore of the pleustonic cystonect, *Physalia physalis*, is this volume exceeded, and in this case the buoyancy that it provides is necessary to maintain the animal at the air-sea interface. The gas is secreted by a specialized basal region of the pneumatophore which is called the gas gland or pneumadenia, and it is clear that the aurophore of the rhodaliid siphonophores represents an enlarged homologue of this region. The general structure of the aurophore has been described earlier (p. 174). The gas secreted by the secondary ectoderm of the pneumadenia appears to be largely, if not exclusively, carbon monoxide (see, for example, Pickwell *et al.* 1964). Wittenberg *et al.* (1962) have demonstrated that this gas is derived from the terminal carbon atom of L-serine by a process that involves tetrahydrofolates as cofactors. It is intriguing to know why the cytochrome system in the tissues is not adversely affected by the presence of carbon monoxide since in most organisms this gas has lethal effects even in very low concentrations. Further, the fact that several physonect siphonophores can live at depths greater than 3000 m must exacerbate the problem for at these depths the pressure of the gas must exceed 300 atm (*ca.* 30 MPa). It is probable that the chitinous lining, pneumatocyst, to the pneumatocyst wall may function to reduce the diffusion of gases and, thereby, to protect the living tissue.

The specialized nature and large size of the pneumadenia in the aurophore of the rhodaliids must be correlated with the large volumes and high partial pressures of gases that it is called upon to secrete. However, outwardly it would seem unnecessary for rhodaliids to have such enlarged pneumatophores since they are benthic organisms, and one can understand why most previous authors considered the animals to live near to the surface of the sea. Whereas the gas in the pneumatophore of the Portuguese Man O'War certainly must make the animal positively buoyant, it has been tacitly assumed by many earlier researchers that the pneumatophore of the holoplanktonic species functions to reduce the density of the animal so that it can become neutrally buoyant and thus maintain its relative position in the water column. However, several authors, including Jacobs (1937, 1962), noted that the pneumatophore contributed little to the overall buoyancy of several of the larger physonect species and that its removal resulted in only a slight change in orientation. In such physonects, as in the calycophoran siphonophores, it is the large quantities of mesogloea in the nectophores and bracts that enable neutral buoyancy to be achieved. Control of the ionic composition of the protoplasm plays a role here and heavy ions, such as sulphate, often are excluded as, for instance, Bidigare & Biggs (1980) have shown. The possibility that diurnal changes in the ionic composition aid the vertical migrations of some siphonophores was mooted by Pugh (1977). The fact that the pneumatophore may not play

a major role in the buoyancy control of these larger physonects led Moser (1924) to suggest that it might then have a sensory role, and more recent observations seem to concur with this conclusion.

In the smaller physonect species, however, it is quite possible for the pneumatophore to have a significant effect on buoyancy control, and it may also play a role in the diurnal vertical migrations that some undertake. If the animal was neutrally buoyant then for upward migration it would be necessary for the volume of the pneumatophore to be increased, since the density of the gas is negligible in comparison with the rest of the animal. Once the animal has become positively buoyant and has started to float upwards then the gases will expand as the pressure decreases and ultimately it will be necessary for gas to be removed to prevent the pneumatophore from exploding. It has been suggested, and indeed observed (Barham 1963) in *Nanomia bijuga*, that excess gas can be vented from the pneumatophore via a pore, although few physonect siphonophores are known to possess such a structure. In contrast, for downward migration it would be necessary for the volume of the pneumatophore to be reduced, and thence, once descent is underway, it would be necessary for gas to be secreted into the pneumatophore at a rate commensurate with the rate of volume compression in order to prevent its total collapse.

Barham (1963) believed that the longitudinal musculature around the pneumatophore of *Nanomia bijuga* was sufficient to cause, by its contraction, a reduction of the volume of gas, resulting in the release of a gas bubble from an apical pore. Similarly, Pickwell (1970) commented that the pneumatophore appeared quite elastic, and that the pressure of gas within it was close to the ambient pressure. However, Carré & Carré (1983), while commenting on the role of the pneumatophore in vertical migration, point out that the walls of the pneumatophore (in planktonic physonects) are quite thin and largely deprived of musculature, such that the latter would be unlikely to cause much reduction in the gas volume. Similarly, the chitin lining to the pneumatosaccus might prevent any considerable expansion in the volume. It may be misleading, however, to consider the expansion or contraction of the pneumatophore as a prerequisite to vertical migration. If one can extrapolate from the situation in a fish's swim bladder to that in a siphonophore's pneumatophore, then d'Aoust (1970) has pointed out that the diffusion rate of the gas (oxygen in the former case) from the bladder exceeded the volume change due to ascent rate of the fish and thus that the venting of gas would be unnecessary. This would, of course, depend on the particular depth range over which the animal was migrating. Even if the rate of diffusion was insufficient to counteract the increase in volume, and it must be remembered that carbon monoxide is about 1000-fold less soluble in water than oxygen, a change in the volume of the pneumatophore need not be the initializing force in vertical migration, but this force could be the active swimming of the animal. Any volume change caused by the alteration in the ambient pressure would then effect a passive migration without the need for further active swimming.

Although the expulsion of gas may be unnecessary during the upward migration of a physonect siphonophore, there are, none the less, several observations of active gas bubble formation. Totton (1949), for instance, observed the virtual collapse of the pneumatosaccus wall after the expulsion of a gas bubble from the pneumatophore of *Nanomia bijuga*. However, this species is the only physonect that is known to possess an apical pore. Such a pore exists in the cystonect species, including *Physalia physalis*, and in these the orifice probably represents the original opening of the invaginated cavity that, during larval development, becomes the

pneumatophore. In *N. bijuga* its apical pore is thought to be a neo-formation (Carré 1969), the original orifice having been blocked by a plug of tissue. However, a secondary basal pore is developed in some species, all of which are brachystele physonects. Whether this basal pore connects the exterior only with the pericystic cavity, i.e. penetrates through only the pneumatocodon wall, or represents a direct connection with the gas-filled cavity has been a matter of

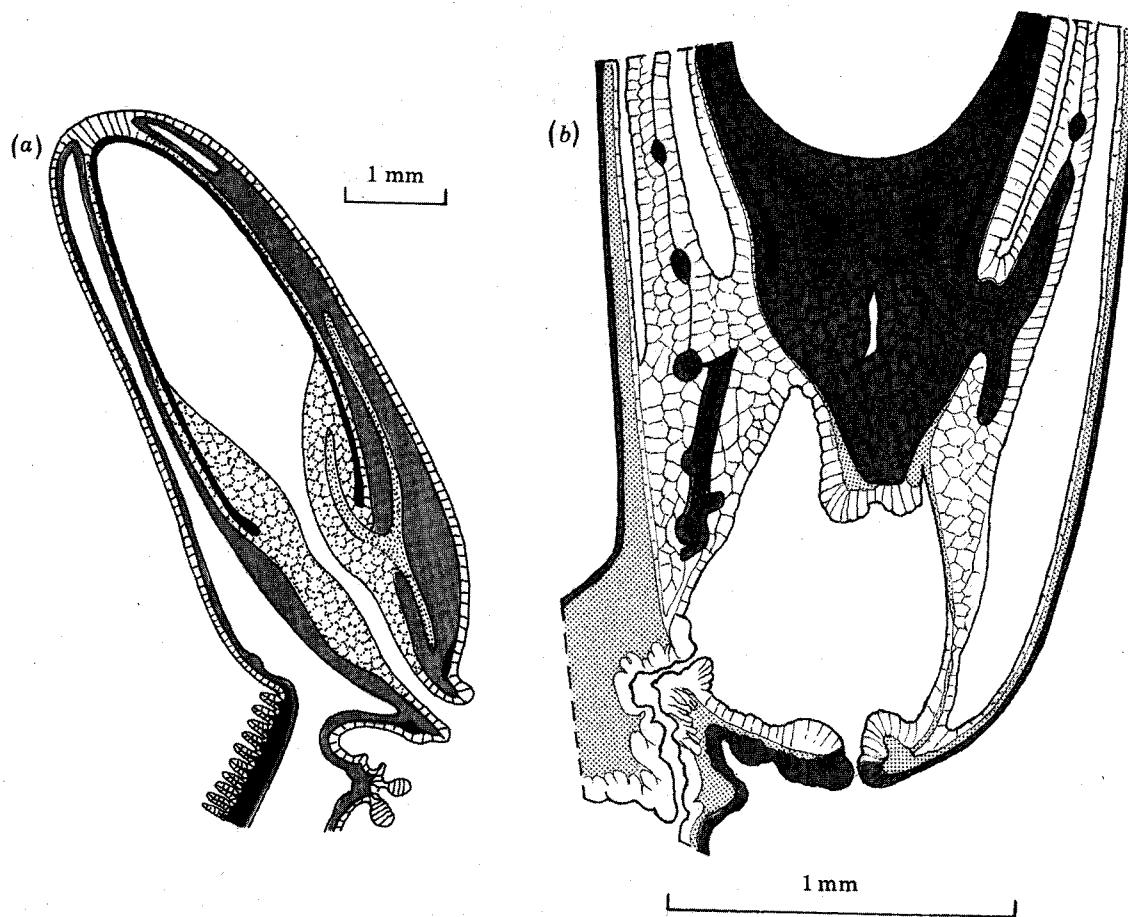


FIGURE 42. The organization of the pneumatophore in *Physopora hydrostatica* Forskål. See text for discussion.
 (a) Redrawn from Leloup (1941, fig. 1A). Leloup believed that a pneumatic duct was present. (b) Redrawn from Chun (1897, pl. II, fig. 8). Chun believed that only an excretory pore was present.

much concern to several authors. For the pneumatophore of *Athorybia rosacea* the evidence for a basal pore is only circumstantial. Totton (1954) observed how a specimen of this species, in captivity, released a number of small gas bubbles among its bracts and, thereby, was able to sink. Although it was presumed that the bubbles were released from a basal pore, Totton (1965) pointed out that the presence of such a pore has never been established even though several researchers have made histological sections of the region in question.

The release of gas from a basal pore in the pneumatophore of *Physopora hydrostatica* is much better documented. Keferstein & Ehlers (1861) observed both voluntary and stimulated expulsion of gas through such a pore, and noted further that the gas pressure in the pneumatophore was greater than the ambient pressure, as the volume of the released bubble frequently

exceeded that of the pneumatophore itself. Again it was observed that the release of gas caused a reduction in the float volume and resulted in the sinking of the animal. Several authors have made histological sections of the pneumatophore of this species, and several opinions as to its organization have been expressed. The controversy that reigned in this field also has a direct counterpart in the various descriptions of the structure of the aurophore in rhodaliids. The two most favoured arrangements that have been described for the pneumatophore of *P. hydrostatica* are shown in figure 42. Figure 42a exemplifies the school of thought that considers there to be a direct connection between the gas-filled cavity and the exterior, via a pneumatic duct. In this case, as Schneider (1898) pointed out, the pore would have the same function as the apical pore in the cystonect siphonophores. Almost all authors agree that the pore is situated on the ventral side of the stem, in the midline, immediately above the nectophoral buds. Haeckel (1869) believed that the pneumatic duct was only present in the adult animal, and he (1888b) also sought to homologize this pore with the opening of the pistillum in the aurophore of the rhodaliids (see figure 20c) by suggesting that it was situated dorsally. Bigelow (1911), however, considered that this pistillum was nothing more than one of the radial septa that traversed the pericystic cavity of the aurophore, and thus that no pneumatic duct was present. His interpretation of the relation between the aurophore and the pneumatochone of other physonects was discussed earlier (p. 176).

The second school of thought concerning the external pore in *Physophora hydrostatica* is that it represents an excretory pore that connects the exterior only with the gastrovascular space or pericystic cavity. The gas-filled cavity of the pneumatophore remains, under normal circumstances, completely enclosed. This is the arrangement noted by Chun (1897), as shown in figure 42b. The fact that gas is vented via this pore is, none the less, indisputable and Chun noted that, under exceptional circumstances, the basal part of the pneumatophore, in the region of the pneumatochone, became ruptured and allowed gas to pass into the gastrovascular space and thence to be vented to the exterior via the excretory pore. This rupturing was caused by violent contractions of the musculature in the pneumatoscoccus wall, and Chun drew attention to the thinness of the mesogloea in the central part of the pneumatochone. It is this interpretation that is most generally adhered to and with which the present author will concur. However, it should be noted that the dorsal aurophore of the rhodaliids contains both the pneumatochone and an excretory pore. Thus, the correspondence between the positions of these two structures may have some significance, although the two need not be directly connected. As Bigelow (1911, p. 314) points out, "it is by no means certain that the 'porus' in *Rhodalia* is accidental".

Chun's (1897) interpretation of the arrangement of the basal part of the pneumatophore in *Physophora hydrostatica* also can be compared with the situation that Lens & van Riemsdijk (1908) and Bigelow (1911) have found in the aurophore of certain rhodaliid siphonophores (see figure 4). In all but the animals studied by Haeckel (1888b), the gas-filled cavity of the rhodaliid pneumatophore has been found to be totally enclosed. However, it is quite probable that gas may be vented via the pneumatochone in a similar fashion to that which Chun (1897) described, and gas bubbles have been noted in the papilliform processes of the aurophore of *Dromalia alexandri* (figure 27c). Gas-filled cavities frequently have been noted in the pneumadenia, for example in *Thermopalia taraxaca* (figure 40) and *D. alexandri* (figure 25f, h). Indeed, in *T. taraxaca* the cells of the pneumadenia appear to be aligned in a longitudinal direction which might facilitate the extrusion of gas between the cells. It is also possible that the giant

amoeboid cells, which are frequently found at the distal ends of the pneumadenia, may play some role although their function remains uncertain.

It is very striking that the only physonect species that are known to have a basal pore are all brachystele forms, but whether this may represent some close phylogenetic relationship is uncertain. Although the venting of gas occurs via this basal pore, it would appear that the necessity to rupture violently the pneumatophore to release the gas is not an activity that the animal would want to use as a regular means of buoyancy control; but it could be used as an emergency measure. All the observations of gas expulsion by *Physophora hydrostatica* or *Athorybia rosacea* seem to suggest that the voluntary expulsion of gas occurred only when the specimens approached the surface of the container in which they were being kept. Thus gas expulsion might be an emergency reaction to avoid entering the turbulent surface realm. It would seem otherwise that the diffusive processes, or the resorption of gas would be sufficient to cause the necessary volume changes to effect downward motion, as was discussed earlier for the fish swim bladder. In this context several other physonect species have dramatic escape responses when they come in contact with the surface of a container.

Whatever the function of the pneumatophore in the holoplanktonic physonect species, it would appear that its function in the benthic rhodaliid siphonophores is, for the most part, to impart a positive buoyancy to the animal so as to enable it to float above the substratum, tethered, like an air balloon, by its tentacles. The observations on specimens of *Dromalia alexandri* (see p. 254) clearly show that this is the case. None the less, Dr Grassle (see p. 267) has noted that specimens of *Thermopalia taraxaca* apparently can adjust their buoyancy to near neutrality and that they can release themselves from the substrate and swim around close to the bottom. The fact that they could also swim up and down a tube is not necessarily indicative of fine buoyancy control as the jet propulsive action of the nectophores may overcome the slight density differences between the animal and the sea water. However, as has been conjectured for *Physophora hydrostatica*, it would seem that the rhodaliids too must have both a means of buoyancy control and a means of rapidly venting gas from the pneumatophore under emergency conditions. The latter would be necessary if the animal were accidentally dislodged from the substratum, whence, because of its positive buoyancy, it would float upwards and the gas in the pneumatophore would begin to expand, the rate depending on the relative changes in the partial pressure. It is under these circumstances that one would expect the pneumatophore tissue to be ruptured and for gas to pass, via the pericystic cavity, to the exterior. What is uncertain is the extent to which rhodaliid species may change the volume of the pneumatophore and whether musculature control plays some active role. Unlike the planktonic physonects, the walls of the rhodaliid pneumatophore, especially the pneumatocodon, are usually extraordinarily thickened (see figures 6c, d, 19a, c, 26c, d for examples). The pneumatosaccus wall is never as thick but would appear to be moderately rigid and has a well developed chitin lining or pneumatocyst, so that any volume change would appear to cause it considerable damage. However, as in the planktonic forms, the passive diffusion of gases from the cavity could act to reduce its volume. It is obvious that the pneumadenia must be able to secrete large volumes of gases at partial pressures in some cases in excess of 300 atm (*ca.* 30 MPa), and so some degree of inflation of the pneumatophore is possible.

The question remains as to what degree the volume of the gas phase will have to be regulated to effect the necessary changes to the buoyancy of the animal. Outwardly it would appear that the relatively enormous volume of gas in the pneumatophore would reduce the overall density

of the animal to such an extent that it would be impossible for neutral buoyancy to be achieved, even though the main corm of the animal is more substantial than that of planktonic physonects. However, using the volumes of the pneumatophore and corm of the type specimen of *Thermopalia taraxaca*, which are approximately 100 and 7000 mm³ respectively, one can calculate the density of the corm. If one assumes that the animal is neutrally buoyant, i.e. its overall density equals that of sea water, say 1.027 g cm⁻³, and that the density of the gas phase is negligible, then the density of the main corm would have to be ca. 1.0417 g cm⁻³. By using an average value for the density of the organic content of the corm, say that of 1.3 g cm⁻³ for protein, and assuming that the remainder is salt and water of density 1.027 g cm⁻³, it transpires that the organic content of the corm would have to be approximately 5 %. Beers (1966) found that the dry mass of planktonic siphonophores was, on average, only 3.85 % of the wet mass, and clearly most of this would be accounted for by salts, leaving only ca. 0.25 % organic matter. However, it would perhaps be more reasonable to compare the rhodaliids with a benthic coelenterate, e.g. a sea anemone, where the total organic matter can be in the region of 10 % of the wet mass (Nicol 1967). Thus the calculated values of 5 % organic matter for the rhodaliids would not seem to be too unreasonable. Although the volume of gas in the pneumatophore appears to increase proportionally with the size of the animal, for individual species, there is a great interspecific variation in the relative size of the pneumatophore with regard to the remainder of the corm. Such variations may be correlated with the variability in the internal structure of the corm, e.g. the presence or absence of a hypocystic or siphosomal cavity, or the extent of the 'ground substance'. These factors would affect the density of the corm itself and, thus, the volume of gas in the pneumatophore that would be necessary to bring the overall density of the animal to near neutrality.

From the above calculations it appears that the large volume of gas in the pneumatophore does not impart an excessive positive buoyancy to the animal, but instead it is a necessary prerequisite to the establishment of near-neutral buoyancy. But can the animals adjust their buoyancy? If in the normal state the tethered animal has an overall positive buoyancy, then can it reduce its density sufficiently that it can release itself and swim about close to the bottom? Unfortunately we do not know the magnitude of the density change required and it may be that the density difference can be overcome simply by the thrusts that can be exerted by the nectophores while swimming. However, the observations on *Thermopalia taraxaca* showed that the nectophores were exerting their thrust in either a horizontal or a downward direction, the latter of which would tend to indicate that the animal was negatively, rather than positively, buoyant.

As for planktonic siphonophores it is assumed that for a rhodaliid siphonophore to change its density it must alter the volume of gas in the pneumatophore, any possible rhythmic control of the ionic composition as mooted earlier being ignored. It was noted that many of the rhodaliid species have smooth-walled pneumatophores that are not hemispherical in shape, in preservation, but are flattened apically. One could conjecture that this is the stable state but given a sufficient pressure of gas, this part of the pneumatophore could be flipped up, despite the thickness of the walls, thereby increasing the gas volume. But what volume change would be necessary to affect the buoyancy of the animal to any extent, and could such a change be accomplished by the means outlined above? Alan Packwood, here at the Institute of Oceanographic Sciences, has kindly supplied some calculations on the terminal velocities of spheres of similar dimensions to the rhodaliids although, as he points out, the velocities would probably

be less for siphonophores as the drag coefficients would be expected to be greater. If one considers a sphere 3 cm in diameter, the values obtained for the terminal velocities based on various percentage volume changes in a theoretical pneumatophore, whose initial volume is 100 mm³, are shown in figure 43, as are the changes in the height of this pneumatophore needed to accomplish these volume changes. It can be seen that, for instance, to achieve a velocity of 1 cm s⁻¹ requires only a *ca.* 3 % change in the volume of the pneumatophore, which represents a 0.6 mm change in its height. Since it would seem unnecessary for the animal, under normal circumstances, to move vertically at such a rate, then it is apparent that sufficient control of the animal's buoyancy can result from relatively minor adjustments to the volume of gas in the pneumatophore.

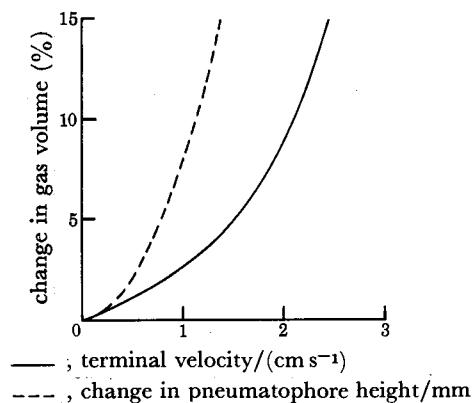


FIGURE 43. The resultant terminal velocity (—), or alteration to the height of the pneumatophore (---) caused by changes in the volume of gas in the pneumatophore. See text for details.

Clearly there are many physiological problems that need to be investigated with regard to buoyancy control in rhodaliid siphonophores. It could be considered that the thickness of the pneumatophore walls in many species helps to decrease the diffusion of gases from the cavity into the sea water, although fundamental to all arguments is the fact that carbon monoxide, if one assumes that this is the major constituent of the gas phase, is relatively insoluble in sea water. Consideration of this point is, however, beyond the scope of the present paper. The thickness of the pneumatophore walls also act to prevent the excessive expansion of the gases, if the animal is accidentally detached from the substratum, and to force the gas to be vented, via the weak link of the pneumadenia. Further, although the possibility of any consistent rupturing of the pneumadenia to make minor adjustments in the gas volume has been considered unlikely, the observations on *Thermopalia taraxaca* may be contrary to this concept. It was observed that there was a change in the orientation of the animals when swimming, in that they became tilted on their axes (see p. 267). Such a change may be caused by the variable directional thrust of the nectophores, but could be consistent with the appearance of an air bubble in the pericystic cavity of the aurophore. It could also be argued that such a change in orientation would be necessary to facilitate the venting of gas to the exterior since, under normal circumstances, the excretory pore opens on the basal side of the aurophore. There is also much inter-specific variation in the thickness of the pneumatophore wall which is not correlated with the depth, and thereby pressure, at which each species lives. Thus one shallow-living species, *Dromalia alexandri*, has a very thick pneumatocodon, while in another, *Archangelopsis typica*, the

pneumatocodon is relatively thin. Similarly in the deep-living species the pneumatophore walls of *Thermopalia taraxaca* are extraordinarily thin, while *Angelopsis euryale* has thickened walls. It is also interesting to note that the two shallow-living species mentioned above are the only known rhodaliid siphonophores that possess papilliform appendages on their aurophores. It can only be conjectured that these structures play some role in the control of gas expulsion, since the gas volume at these lower pressures will increase more rapidly over a given depth range if the animal is accidentally detached.

Nectosome

In most physonect siphonophores, the nectophores are arranged biserially, one above another, to form the typical long nectosomal region. The biserial arrangement is created by the alternate bending of the nectophores to each side from their point of origin in the mid-ventral line. Even the apparently complicated nectosome of the *Forskalia* species is derived from this basic arrangement of nectophores. However, the rhodaliid siphonophores are an exception in that the nectophores are arranged around the base of the enlarged pneumatophore to form a corona. Such an arrangement would appear to reduce the swimming capabilities of the animals, but it has been observed that coordinated swimming behaviour is possible. In *Stephalia corona* it was noted that peristaltic waves of contractions passed down the nectophore, but whether this is the basic jet-propulsive action or not is uncertain as the animals under observation clearly were considerably stressed. None the less, the rhodaliid nectophores are flimsy, featureless bags which would not appear to be capable of strong muscular contractions. Unlike the holoplanktonic physonects it would seem that the ability for coordinated locomotion is of lesser importance in the rhodaliids. If one assumes that the animals spend most of their time tethered to the substrate, and set their feeding web in this static state, then the necessity of a swimming-fishing behavioural cycle (Biggs 1977) is eliminated. As yet the observations are too few to indicate how often the animals do detach themselves and swim about, but even so few free-floating animals have been noted.

The infrequency with which the nectophores are used could also be correlated with the apparent ability of some species to retract them from out of sight, as in the specimens of *Thermopalia taraxaca*. This capability may be associated with the internal structure of the nectosome. In *T. taraxaca*, the thin-walled nectosome surrounds a large hypocystic cavity which may be collapsed to allow withdrawal of the nectophores, and re-inflated, by pumping in gastrovascular fluids, when it is necessary for the animals to swim about. In most other rhodaliid species the hypocystic cavity occupies part, if not all, of the interior of the nectosome and so one might predict that they too might withdraw their nectophores. Only in *Dromalia alexandri* is the hypocystic cavity so reduced as to be virtually absent, although in *Rhodalia miranda* it is very shallow, in the preserved state. *R. miranda* also has a large number of nectophores attached to the nectosome, purportedly arranged in a triple corona, and so these would be difficult under any circumstances to withdraw from sight. Although it has been shown that the internal configuration of the nectosome, in combination with that of the siphosome, has some systematic significance, it is not absolutely clear what benefit, if any, such variations in the arrangement might confer on any one species, although buoyancy control and the ability to withdraw the nectophores have been suggested here.

In the long-stemmed, holoplanktonic physonects the budding zone for the siphosome becomes separated from that of the nectophores by the nectosome itself (figure 44a). Thus, the

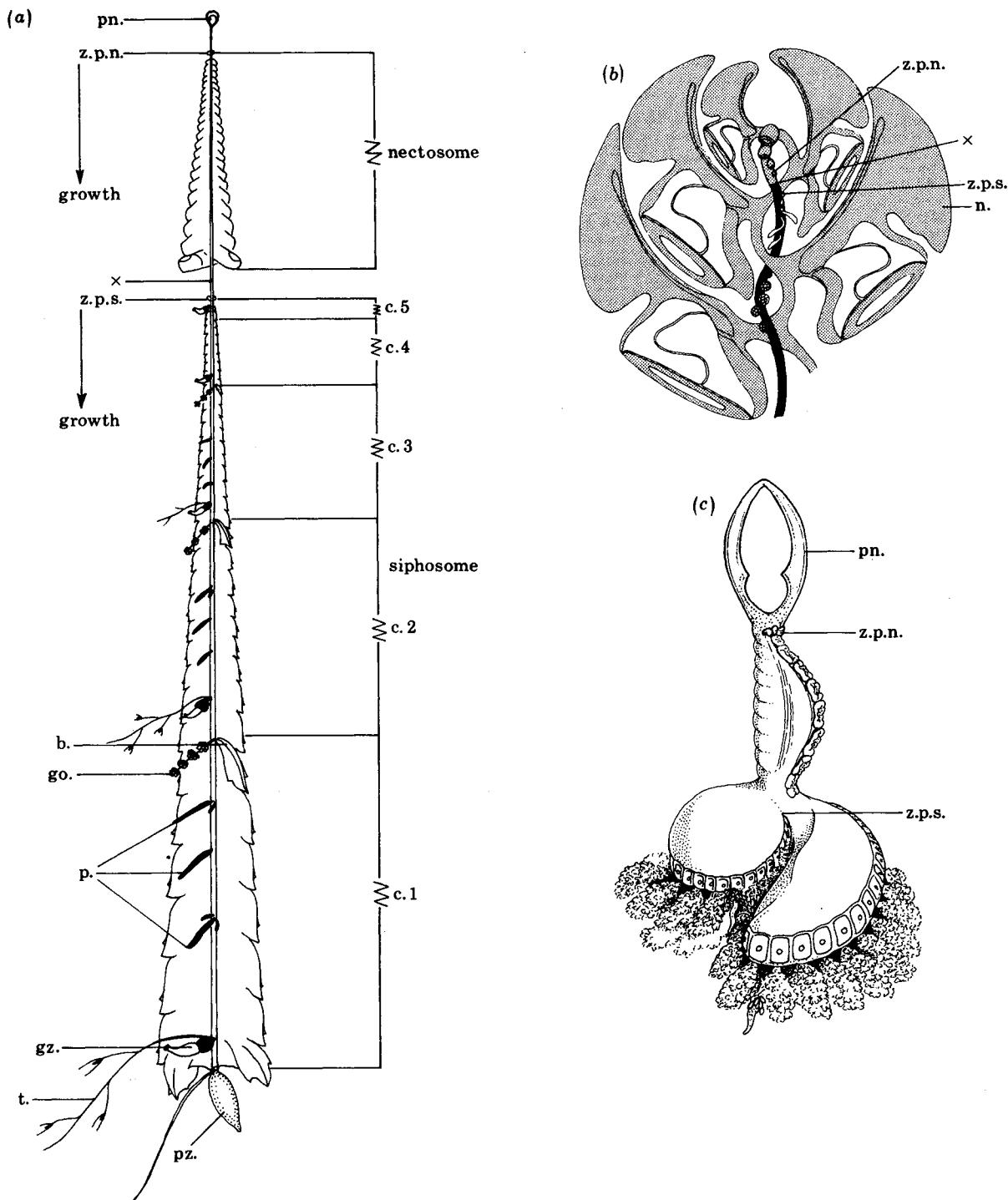
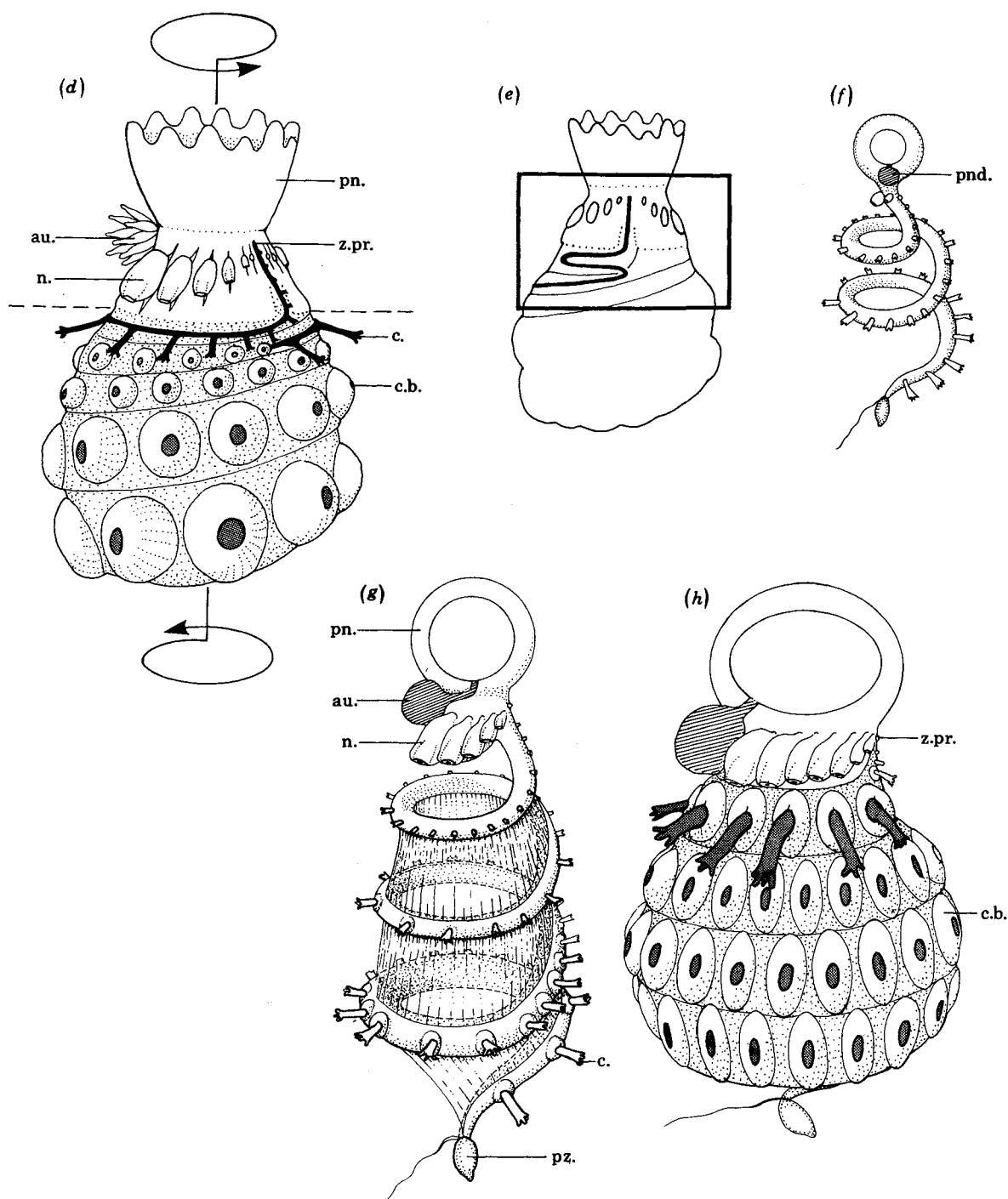


FIGURE 44. Schematic diagrams of the growth patterns of siphonophores. (a) A typical long-stemmed physonect, with the nectosomal and siphosomal regions expanding in the same direction. Adapted from the frontispiece of Totton (1954). (b) The calycothoracan, *Hippopodius hippocampus*, showing the nectosomal and siphosomal regions expanding in opposite directions. Adapted from Haeckel (1888 b) and Chun (1897). (c) The brachystele, *Physophora hydrostatica*. A schematic diagram showing the usual physonect nectosome, while the siphosome is formed into a bag-like structure around which the cormidia are arranged in a dextiotropic spiral. Adapted from Haeckel's (1888 b, pl. xx, fig. 10) figure of *Discolabe quadrigata* Haeckel, 1888. (d) The arrangement of the corm in a rhodalid such as *Dromalia alexandri*. Note the series of developing cormidal units on the



apical siphosomal whorls. Their presence indicates the possibility that the nectosomal and siphosomal regions are twisting relative to each other in the plane marked by the dotted line and in the directions indicated. (e) A hypothetical method for the growth of the siphosome in a rhodaliid such as *Dromalia alexandri*, where the siphosome and nectosome are firmly united and are unable to twist relative to each other. See text for discussion. (f-h) A hypothetical series of stages in the development and/or evolution of a rhodaliid corm. See text for discussion, but note the movement of the pneumadenia from an original axial position, below the pneumatophore, to a dorsal position where it enlarges and forms part of the aurophore. Note also the presence, in (h), of a well developed cormidial base immediately below the zone of proliferation, indicating that no new cormidial whorls are being formed. A list of the abbreviations used in these diagrams is given in the Glossary.

increase in the lengths of the nectosome and siphosome are in the same direction, and between the oldest nectophores and the siphosomal budding zone there lies a zone of minimum growth. In the rhodaliids, the zones of proliferation, or blastocrene, for both the nectosome and siphosome lie in very close proximity just below the pneumatophore in the mid-ventral line. This failure of the two proliferation zones to become separated is unusual among the physonects. However, in the calycophoran siphonophores, which lack a pneumatophore, the two budding zones develop and remain close to each other, such that the nectosome and siphosome increase in length in opposite directions (figure 44*b*). Totton (1954) pointed out that theoretically it was possible to derive the calycophoran pattern from the physonect one. He envisaged, after the disappearance of the pneumatophore, that the pedicel of the first nectophore grew continuously in length, as does the pedicel of the protozooid, and that successive nectophores were budded each from the foot stalk of its immediate predecessor. This system does not, however, appear to apply to the rhodaliids and it is doubtful whether they could be thought to represent an intermediary stage in such evolutionary processes. Indeed there is no known physonect where the nectosome and siphosome expand in totally opposite directions.

It is generally thought that the presence of a pneumatophore prevents the nectosome from expanding apically, but quite why the rhodaliid nectosome cannot or does not increase in length in a basal direction is less apparent. In the athorybiid physonects, another brachystele but planktonic family, the nectosomal region also has undergone considerable modification to such an extent that, in the genus *Athorybia*, it has totally disappeared. Whether this situation too is a result of a similar failure of the two budding zones to separate is uncertain, but in another athorybiid, *Melophysa melo*, a nectosome is still present although considerably reduced. In this case it appears that only a single nectophore is functional at any one time. However, the muscular lamellae of earlier, detached, nectophores can be seen arranged down the short nectosome, below which lies the budding zone of the siphosome. Another brachystele physonect, *Physophora hydrostatica* (figure 44*c*), bears a normal, fully developed nectosomal region while its siphosome is laterally expanded. Thus to explain the lateral expansion of the nectosome in the rhodaliids one again must resort to the theory that it was an evolutionary step associated with the adoption of the benthic habitat. This requires that once the animals have attached themselves to the substratum they should be able to secrete sufficient gas so as to become slightly positively buoyant. It was suggested earlier that a *pari passu* increase in the volume of the pneumatophore also was needed to offset the greater density of the siphosome as the latter began to solidify into a globular corm. One can then envisage that, with an increase in the size of the pneumatophore, the growth of the ventral surface of the nectosome in a lateral direction was facilitated or, more probably, necessitated in order to act as a support for the enlarged pneumatophore. Thus sufficient space became available for the nectophores to be displaced to alternate sides from the mid-ventral budding point and eventually to form a corona (figure 44*f-h*). The importance of the nectophores in jet-propulsive locomotion also was reduced by the adoption of the benthic habitat, and so their biserial arrangement down the nectosomal region was less essential. The nectophores of the rhodaliids are themselves reduced to weakly muscled tubes which contrast with the strongly muscled nectophores of many planktonic physonects.

Garstang (1946) considered that, as new nectophores were added to the corona, the horizontal or lateral expansion of the nectosome continued *pari passu*. Whether this is indeed the case is uncertain. However, in the three species where sufficient material is available for

study, there does not appear to be a close relation between the number of nectophores and the pneumatophore diameter. For instance, in some smaller specimens of *Thermopalia taraxaca*, whereas the pneumatophore diameter varied between 3.9 and 5.0 mm, the nectophoral count remained the same; while in the larger specimens, the number of nectophores increased sharply. Also the regular displacement of the nectophores to alternate sides of the nectosome may not be rigidly followed as is shown by the extreme asymmetry in their distribution in one of the specimens of *Dromalia alexandri*.

As discussed above, one considers the growth of the nectosome purely as an expansion of its ventral surface so that the whole of the corona, apart from the naked zone which typically lies below the aurophore, is ventral in origin. Evidence for this horizontal expansion can be found in the younger specimens of *Thermopalia taraxaca* where there is a marked narrowing in the basal part of the nectosome where it unites with the still loosely coiled siphosome (figure 35*b*). The positioning of the aurophore, with the pneumatochone, must be as a result of this extreme horizontal development. It was pointed out earlier that, although the excretory pore of the brachystele physonect *Physophora hydrostatica* is ventral in position, the pneumatochone, which in some way is associated with it, is most likely axial. Indeed, the young specimen of *Rhodalia miranda* (figure 19*a, b*) shows that the original point of insertion of the pneumatochone into the pneumatophore was in a median basal position. In this particular specimen the pneumatochone is extraordinarily long, but as the growth of the nectosome and the pneumatophore continues its relative length decreases and its point of insertion is moved dorsally (figure 44*f-h*). Since the zones of proliferation lie so close to the main body of the pneumatophore it is probable that an excretory pore could not be developed in the mid-ventral line and, like the pneumatochone, became displaced.

Many of the problems regarding the structure and orientation of the nectosome, aurophore and, indeed, siphosome might be answered if some very young specimens of rhodaliid siphonophores could be studied. Unfortunately, the only (?)larval form so far reported is the so-called *auronula* of *Stephalia corona* which Haeckel (1888*b*) briefly described. From the description it appears to be a remarkable animal in that it consists only of (*a*) a well developed aurophore and pneumatophore (see figure 7*f*) and (*b*) a protozooid with a simple tentacle. These two characters would appear to be incompatible in a larval physonect, and the absence of other larval features, such as bracts or nectophores, make the whole structure very puzzling. However, the early development of the radial septa in the aurophore led Haeckel to suggest that the latter was not perhaps the independent medusoid structure that earlier he had supposed it to be.

Siphosome

The structure and organization of the siphosome appears to be intimately related to the method of growth that the rhodaliid siphonophores have evolved. For instance, the arrangement of the cormidial units is unusual in comparison with the linear pattern found in the holoplanktonic macrostele physonects. The process of cormidial development has been most closely studied in specimens of *Dromalia alexandri*. In this species the apical whorl consists of a progressive series of developmental stages, distinct one from another, while in most other rhodaliids such a series is confused and difficult to study. Indeed, it will be conjectured later that *D. alexandri* is an exceptional species and may have a totally different pattern of siphosomal growth from all the other known rhodaliid species. However, the studies on *Stephalia corona*, for instance, show

that the basic cormidial organization is similar in most species, in that each cormidial unit is a distinct entity, with its component parts isolated at the distal end of a stalk. The major exception to this arrangement is *Thermopalia taraxaca*, where all the cormidial elements remain attached directly to, or at least very close to, the main corm.

Although the spiral whorls of cormidial units in *Dromalia alexandri* would appear to be equivalent to the linear series of cormidia, the further development of these units is unusual in that they become polygastric, i.e. additional, complete cormidia are budded off. It is presumed that the new cormidia in the rhodaliids bud from the pedicel of the preceding gastrozooid, but the pattern is not always easy to discern. Totton (1965) pointed out that the gastrozooids could bud off, from their pedicels, further gastrozooids, palpons and bracts; while the gonophores usually were budded from the pedicels of palpons. In addition, the gonodendra are complexes formed by numerous palpons and gonophores budded from the original palpon. This may not be the origin of the gonodendra in the rhodaliids, as they appear to be derived directly from the foot stalk of the gastrozooid. However, the great development of these structures may have concealed the identity of the original palpon, while the secondary palpons are retained at the distal ends of the branches as gonopalpons.

Totton (1965) comments that the gonopalpons are a rather imprecise category among the polypoid structures, but are distinguished from the true palpons by the absence of a palpacle, as well as their close association with the gonodendron. Totton (1960) summarized the more recent information on palpons in general, and noted that those of *Physalia physalis* were gonopalpons. In this case the gonodendron was developed when a normal gastrozooid budded off, from its pedicel, a series of gonozooids or secondary gastrozooids which lacked the characteristic type of tentacle. The bases of these gonozooids increased in length and budded off the genital clusters, which consisted of small palpons and the gonophores, plus jelly polyps and nectophores. Totton (1960) mentioned no other species that possess gonopalpons, and it is not clear whether there are any physonect species, apart from the rhodaliids, that possess such structures. Nevertheless one would not necessarily expect a precise agreement between the processes of gonodendral development in the rhodaliids and the cystonect siphonophores. Further, the presence of the gonopalpons and absence of other palpons in rhodaliids may have no phylogenetic significance, but again be the result of the animal's adaptation to the benthic existence. Because the basic cormidial elements are so closely crowded onto the corm it is probable that there would be insufficient space for the true palpons to develop and so some of their functions are taken over by the gonopalpons which are mounted distally on the gonodendra away from the corm. This is carried to the extreme in *Thermopalia taraxaca* where, because the cormidial elements are attached so close to the corm itself, the overcrowding has resulted even in the disappearance of the gonopalpons. It is also interesting to note that the rhodaliid siphonophores appear to be dioecious, in that the gonophores on all the gonodendra are of one sex. The monoecious state is more common in the holoplanktonic physonects, although insufficient evidence is available on many species. Whether the two-dimensional habitat plays any part in the selection for the single-sexed animal is uncertain but it is interesting, perhaps fallaciously, that *Physalia physalis* also is dioecious.

Schneider (1896) described how the gonophore and an accompanying bract were formed as a twin bud on the foot stalk of a gastrozooid. The arrangement of the cormidia in, for instance, *Dromalia alexandri* shows this close association between the bract and the main stalk of the gonodendron. However, it is construed, in the majority of cases, that the bract is a redundant

organ, and that the general reduction in its size is a result of this. In the holoplanktonic physonects the bracts have primarily a protective function, allowing the other organs to be withdrawn below them and thereby streamlining the body for effective escape, and secondarily they give buoyancy to the animal particularly in those species with relatively small pneumatophores. In the rhodaliids, with their relatively enormous pneumatophore, the necessity for the bracts in buoyancy control is obviated. Thus in most species the bracts are reduced, although in *Stephalia corona* they remain enlarged and robust. Totton's (1965, fig. 51) diagram suggests that the interlocking distal processes of the bracts in this species may allow the remaining cormidial elements to be withdrawn beneath them so that, at least, the bracts still retain a protective function. This would be suitable for a holoplanktonic organism as the withdrawal of the cormidial elements could also streamline the body for efficient movement. However, the predominantly static nature of the life style of the rhodaliids does not fit in so easily with this picture. *Thermopalia taraxaca* also possesses quite large, flattened bracts but the *in situ* photographs scarcely indicate their presence and it is unlikely that they could have any effective role. In other species it has been postulated that the bracts may be so reduced in function as to be vestigial or caducous, but because of the incomplete state of most rhodaliid specimens it is premature to speculate too deeply on the function and arrangement of their bracts.

One of the unusual features of the cormidia in the rhodaliids is that they usually become polygastric. The retention of such a budding function is thought to be connected with the growth pattern of the rhodaliid siphosome. It is considered that as the corm increases in diameter the space generated is filled by budding from the extant cormidia because the general rigidity of the whole structure prevents the shunting downwards of these cormidia to allow infilling by new cormidia apically. The fact that the additional gastrozooids differ in structure and form from the original, so-called type I gastrozooid, with its reduced basigaster and simple tentacle, also is of interest. An immediate comparison can be made with the development of some holoplanktonic physonects, where the protozooid or larval gastrozooid is a reduced structure which bears a simple tentacle, which may be fusiform or bear a few larval-type tentilla. Totton (1956) made a close examination of the post-larval development of *Agalma elegans* (Sars, 1846) and he noted that the second gastrozooid to be developed, bearing a tentacle with adult-type tentilla, replaced the smaller protozooid at the basal (oral) pole of the animal. In another species, *Nanomia bijuga*, the protozooid was so reduced as to be virtually vestigial. Totton concluded that this displacement of the protozooid represented some new line in evolutionary experiment marked by the appearance of the more highly evolved gastrozooids with well developed basigasters.

The type I gastrozooid of the rhodaliids would appear to resemble the larval protozooid of these other physonects, although no tentilla of any sort have been noted on the tentacle. Nevertheless it would be presumptuous to assume that they are definitely not developed as many such errors of judgement have been made in the past owing, most likely, to the imperfection of the specimens. However, in the Apolemiidae, which is thought to be the most primitive physonect family, the tentacles of both the gastrozooids and the palpons are simple filiform structures, as are the tentacles of some cystonect species. Even if the presence of the larval-type gastrozooid in each cormidium is a primitive character, the additional development of type II gastrozooids with adult-type tentacles must place the rhodaliids in a different phylogenetic position. In accordance with this the cnidome of the tentillum of *Dromalia alexandri* appears to be relatively advanced and outwardly resembles that of *Physophora hydrostatica*.

It was suggested earlier that, since the rhodaliids are tethered to the substratum by their tentacles, a different type of feeding behaviour from that of the holoplanktonic physonects has evolved. The number of tentacles that are used to tether the animal appears to be consistent with the number of type II gastrozoooids in *Thermopalia taraxaca*, although the reports for *Dromalia alexandri* might indicate the presence of unattached tentacles. The holoplanktonic species often set a complicated net to ensnare their prey (Biggs 1977), and on capture it would be brought to the mouth of the gastrozoooid mainly by the contraction of the tentacle, although the proboscis segment of the gastrozoooid would actively stretch out towards it. The fishing net of the rhodaliids, however, must be more rigid and static, and there is the added problem of transferring the food from the tentacles to the mouths. If the latter was undertaken by retraction of the tentacle then this would necessitate the release of one or more of the anchors, and in smaller specimens might make the whole attachment precarious.

The observations on *in situ* specimens of *Thermopalia taraxaca* suggest that the animals have adopted another approach to feeding. It was noted earlier that the type I gastrozoooids are extraordinarily elongated and appear to be moving actively among the tentacles, occasionally touching one of them and then brushing along its length as if to clean it or to search for food on its surface. These gastrozoooids frequently arch back and touch some cormidial element on the main body of the corm, as if to transfer something. Although the tentilla probably are too fine to be resolved in the photographs or video tape-recordings, the preserved material indicate that they are attached only at the proximal end of the tentacle. In this context, however, the video tape-recordings appeared to indicate the presence of some fine, filamentous structures, which arose from close to the main body of the corm (?the proximal end of the tentacles) of *T. taraxaca* and which might have been tentilla. The scars of tentillar attachment are visible further down (distally) the tentacle but it is thought that these are old attachment sites rather than that the tentilla have been torn off during collection. Thus it is suggested that the proximal tentilla are used to capture the prey which is then picked off by the mouths of the type I gastrozoooids and transferred to the type II gastrozoooids for digestion. The type I gastrozoooids may digest the prey themselves, and indeed they have been found to have very large gastric villi in *Dromalia alexandri* (figure 32), but no food items or even mucoid material have been found in those belonging to specimens of *T. taraxaca*. Clearly, however, further studies need to be made on the *in situ* feeding behaviour of the rhodaliids.

The supposition that the type I gastrozoooids of *Thermopalia taraxaca* play a role in the transfer of prey can be extrapolated to the same structures in other species. The enormous type I gastrozoooids of *Stephalia corona* (figure 9a, b) would easily fulfil the role suggested. There is a concentration of these gastrozoooids on the base of the corm in this species, and it has been suggested that other species, e.g. *Angelopsis euryale*, have a similar configuration. This positioning and their enormous size would appear to be ideal for searching the dangling tentilla over a large part of the tentacles. The *in situ* pictures of *Dromalia alexandri*, however, do not appear to show the presence of elongated gastrozoooids but quite large type I ones are known to be present. It would not be surprising if this species has evolved a different feeding behaviour from the other species since in many ways it is an exception to the general rhodaliid rule.

Growth of the siphosome

Garstang (1946) considered that the growth of the rhodaliid siphosome was merely an extension of the situation found in *Physophora hydrostatica* (figure 44c), although he did point

out that the growth of the rhodaliid nectosome was an exception to most rules. He also discussed the growth pattern in other brachystele forms, among which he included two species, *Epibulia ritteriana* Haeckel, 1888 and *Nectalia loligo* Haeckel, 1888, which now are considered not to be brachystele forms. The former is thought merely to be a contracted specimen of a cystonect, probably of the genus *Rhizophysa*, while the latter is a post-larval stage of a species of the genus *Halistemma*. Although the cormidial bases on the rhodaliid corm essentially are arranged into dexiotropic spirals, and might represent an extension of the situation in *P. hydrostatica* as Garstang suggested, other arrangements also exist and so it will be necessary to reconsider the various growth patterns of the rhodaliids. Equally, it should be noted that Totton (1954) disagreed with Garstang's interpretation of the growth of *P. hydrostatica* and, indeed, most of the great siphonophore experts have disagreed on that subject. Some of such discussion centres on whether the stem of the siphosome was spirally twisted. Garstang (1946) took great pains to dismiss such an assertion and he considered that the arrangement of the siphosome resulted from a predominant growth of the right side of the stem. However, Totton (1954), who drew some parallels between arrangement of the cormidia in *P. hydrostatica* and in the rhodaliids, considered that the peripheral margin to which the cormidia were attached corresponded to, but was not necessarily derived from, the ventral median line of a *twisted* macrostete stem. The failure of the proximal part of the pedicle of the protozooid to elongate contrasted with the origin of the siphosomal stem in the macrostete physonects, and this led Totton, like Garstang, to suggest that such an elongation was phylogenetically more likely than a failure to do so, i.e. macrosteles evolved from brachysteles rather than the reverse.

Since so few of the great experts can agree on the growth pattern in the relatively well known species, *Physophora hydrostatica*, it would seem inappropriate for anyone, including the present author, to speculate too deeply on such a pattern in the little known rhodaliid siphonophores. However, it might be appropriate to summarize the scant information that is available on the subject. Most of the earlier researchers on the rhodaliids assumed that the growth of the siphosome was a continuing process with the spiral arrangement of the cormidia being extended by the addition of new cormidia from the apical zone of proliferation. The present observations seem to suggest that, whereas that is almost certainly true for one species, there are several others where a more complicated pattern emerges. *Dromalia alexandri* is the one species that clearly and apparently unequivocably demonstrates the classical growth pattern of the siphosome. The cormidial elements are arranged spirally and each whorl is distinct from its neighbour with up to 15 or more being present. Each cormidial unit also remains a distinct entity, and a series of developing units can be found in the most apical whorl of the siphosome (figure 44d). In addition there are no signs of, nor apparent mechanism for, the insertion of type I gastrozooids onto the base of the corm as is suggested for other species. It is perhaps surprising, since there is such a regular arrangement of the cormidia, that there is no major canal of the gastrovascular system that spirals around the corm immediately beneath the cormidia. However, on reflection this would not be a very ergonomic system for a spheroidal body like the corm of a rhodaliid. The canal system is a complicated arrangement of branching and anastomizing canals in which it is difficult to discern any pattern, although there may be an underlying spiral arrangement in the more apical region. None the less it is suggested that the system of gastrovascular canals in *Dromalia alexandri* is probably a product of the growth pattern in these animals.

It remains problematic to explain exactly how new cormidial whorls are added to the apical part of the siphosome. Such additions cannot be merely a matter of the lateral expansion of the

stem so that the cormidia are sequentially moved away from the ventral line as Garstang (1946) suggested in *Physophora hydrostatica* (figure 44c) and, by extrapolation, the rhodaliids. In *Dromalia alexandri* the most apical whorl of extant cormidia is to all intents and purposes firmly connected to the nectosome, both externally and internally. Thus movement away from a point source, as may be the case in *P. hydrostatica*, with or without the twisting of the stem, would appear to be impossible unless the siphosomal region itself can twist relative to the nectosomal region (figure 44d) or unless some peculiarly shaped animal is to be produced. It does not seem reasonable either for the apical part of the siphosome to expand, apico-basally, so that new cormidia can be pushed out from the zone of proliferation over the surface of the corm to produce a new whorl. This should result in intermediate stages where incomplete whorls are present and, since the series of young cormidia bases must be joined both to the whorl below and to the zone of proliferation above, a double row would have to be present (figure 44e). Such partial whorls of young cormidia have not been noted in the available specimens of *D. alexandri* and their possible presence is not considered likely. Although a partial ring of young bases has been noted in specimens of *Angelopsis euryale*, the cormidial elements are not destined to form part of a new apical whorl but, in the present interpretation, will be inserted onto the base of the corm and become type I gastrozooids. The growth pattern here is quite different, as is discussed below.

The most obvious solution to the problem of how new cormidia can be continuously added to the spiral arrangement of the units around the corm in *Dromalia alexandri* is that the siphosomal region must be continually turning, in a clockwise direction, relative to the nectosome and the zone of proliferation, and despite the fact that the two zones appear to be permanently connected (figure 44d). As each new cormidial unit passes down from the proliferation zone and out of the nectosomal region it does not itself cause the sideways displacement of the previous unit but more likely the siphosomal stem elongates to allow for its positioning on the main trunk. This is precisely what happens in a normal macrostele physonect, where the stem, the derivative of the foot stalk of the original protozooid, elongates, bearing the new cormidia away from their budding zone. The process by which the necessary rotation of the siphosomal region relative to the zone of proliferation, and thereby the nectosome and pneumatophore, occurs is not clear. It may be that the pronounced bands of thickened ectoderm that separate the whorls result from the necessity for the whorls to slide over one another. The necessary tracking of this movement by an endodermal gastrovascular canal may give rise to the system's apparent spiral arrangement in the more apical regions, but presumably this is later rearranged in order to produce a more efficient circulatory system. It is not clear how this supposed method of siphosomal growth in *D. alexandri* will affect the other features of the internal organization of the corm. However, it is interesting to note that the hypocystic cavity in this species has virtually disappeared, whereas in the other rhodaliid species, which are believed to have a different method of growth, a cavity is still present. If the nectosomal and siphosomal regions are to twist relative to each other then the absence of this cavity in *D. alexandri* is somewhat surprising since the area of attachment between the two regions thereby is maximized.

Among the other rhodaliid species it is believed that at least four have a pattern of growth that is quite different from that envisaged for *Dromalia alexandri*. In these species it is suggested that there is not a continual addition of cormidial units to the apical whorl on the siphosomal surface, but that the number of whorls is limited and once these have been developed and the corm

solidifies, further growth generally is restricted to budding within each unit. However, in some species additional cormidial elements can be added to the corm from the zone of proliferation, but these elements do not form part of the basic spiral arrangement of cormidia, instead being moved down onto or close to the base of the corm where they probably develop into type I gastrozooids. The siphosomal organization of *Thermopalia taraxaca* may appear to represent an intermediate stage between the continual growth process, as seen in *D. alexandri*, and the extremely reduced growth pattern that is thought to be found in *Stephalia corona*, *Rhodalia miranda* and *Angelopsis euryale*, although it has much closer affinities with these last three species. In the younger specimens of *T. taraxaca*, the whorls of cormidia, which number from four to seven, are loosely associated one with another, and there is a narrowed neck between the most apical whorl and the nectosome above (figure 35b). One could compare this situation with that in *Physophora hydrostatica* (figure 44c), where the lateral expansion or spiral twisting of the siphosomal stem away from a point source of budding can give rise to whorls of cormidia. Figure 44f is a schematic diagram of a possible early developmental stage of an ancestral rhodaliid where the siphosome is organized into separate whorls while the two zones of proliferation remain close to each other. It may not be necessary for the whorls to be separated during development and, once the first whorl is formed, a link may be maintained between all subsequent ones so long as the growth of each whorl continues in proportion with that of the ones above and below it. Thus, at a later stage, both evolutionary and developmentally, one might expect the cormidial whorls to be loosely connected by tissue sheets, while the nectosome has expanded laterally, although it still maintains a narrow connection with the siphosome (figure 44g). This is similar to the arrangement found in the young specimens of *T. taraxaca*, and in this species it was considered that the addition of cormidia onto the spiralling corm continued until a critical number of whorls or size of corm was reached, at which time the whorls became closely united and the corm 'solidified'. At this stage it was considered that no new cormidial units were added apically to the corm and that the siphosomal zone of proliferation ceased to generate them. Such a situation appears to be present in the type specimen whereon it is impossible to distinguish the separate cormidial whorls, and the nectosome, although difficult to discern, is probably more firmly attached to the siphosome. The ontogenetic changes in the internal structure of the corm in *T. taraxaca* appear to be consistent with its suggested growth pattern, although that of the type specimen has not been investigated. In the youngest specimens the axial cavity is ill defined, with several oblique transverse septa present, which probably represent the original walls of the simple gastrovascular system. In the older specimens the cavity is more obvious, with only some remnants of cross septa. It is construed that the type specimen would have a distinctive siphosomal cavity, although some sort of cross septa may delimit this cavity from hypocystic cavity in the nectosome. However, the possibility of proving oneself wrong is resisted for the present and the type specimen is preserved intact.

The arrangement of the cormidial units appears to be very similar in *Stephalia corona*, *Rhodalia miranda* and, probably, *Angelopsis euryale*. In these species the units that lay immediately below the zone of proliferation were seen to be well developed and mature, and a series of developmental stages, as noted in the apical whorl of *Dromalia alexandri*, was absent. Also, particularly in the specimens of *S. corona*, only two closely associated and often interlaced whorls of units could be discerned on the side of the corm, with a distinct, thickened ectodermal band separating the nectosomal and siphosomal regions and delineating the bottom edge of the more basal whorl (figure 9e). A distinctive gutter was also found immediately below the zone of

proliferation, in the median ventral line. It was suggested that the additional type I gastrozoids were moved down through this gutter to be inserted onto the base of the corm, and in doing so they must have passed over the surface of the second cormidial whorl, presumably in a gap between two bases, although such bases probably are suppressed in the gutter region. Despite the fact that the corm of some specimens of *R. miranda* is relatively enormous, it was thought that again there were only two major cormidial whorls on the sides of the siphosome, although the expansion of the corm had allowed a biserial arrangement of the units to develop within each whorl. A furrow was discernable below the zone of proliferation (figure 19*d*), although it was not as pronounced as the gutter in *S. corona*, and it was believed that some of the cormidial elements on the corm base were connected with the band of ectoderm that passed down it. The presence of large, rounded scars on the base also indicated that type I gastrozoids probably once were attached there.

It is concluded that in these species, including *Angelopsis euryale*, the critical number of whorls has been reduced to two or three and that once these have been developed, in a similar fashion to that thought to have occurred in *Thermopalia taraxaca*, the corm solidifies and no further cormidia are added apically to the spiral. This is shown by the fact that the cormidial base immediately below and to the right of the zone of proliferation is well developed and mature. Any further growth of the corm is then by an expansion in its volume, with the gaps created being filled by additional cormidia developed on the existing cormidial bases. In addition, these animals retain the potential to insert new cormidial elements onto the bases of their corms. Because of the dearth or absence of specimens of the other rhodaliid species considered in this paper it is not possible to speculate on their growth pattern. It has been suggested that the cormidia on the siphosomes of *Archangelopsis typica*, and possibly *Sagamalia hinomaru*, are arranged into spirals; their arrangement in *Stephalia dilata*, *S. bathyphysa* and *Angelopsis globosa* remains obscure. For none of these species has any statement been made on the possibility that cormidial elements are inserted onto the base of the corm although this might be suspected in several species, particularly the last three.

In the earlier discussion it was suggested that the type I gastrozoids play an important role in the transference of food items from the tentacles to the type II gastrozoids. Clearly the enormous size of the type I gastrozoids in *Stephalia corona* must, by inference at least, indicate such a conclusion. However, it has also been found that these gastrozoids are produced only on the first cormidium within each unit and that all additional cormidia bear type II gastrozoids. It may be then that in *S. corona*, along with *Rhodalia miranda* and *Angelopsis euryale*, the original type I gastrozoids are easily detached or are reduced in size so that the insertion of additional such gastrozoids onto the base of the corm is an essential prerequisite for efficient feeding. Clearly, however, it is a specialized situation which may have arisen because of the reduction in the number of cormidial whorls.

The route via which these cormidial elements are passed down onto the corm base varies among the species studied. In *Stephalia corona* and *Rhodalia miranda* they appear to travel directly down from the zone of proliferation, while in *Angelopsis euryale* they may either pass directly downwards or form a partial whorl around the apical part of the siphosome before travelling obliquely downwards, between mature cormidial units, to the base of the corm (figure 6*h*). In the latter case, the presence of the partial whorl would not seem to indicate that the siphosome was able to rotate in relation to the nectosome, as is suggested for *Dromalia alexandri*, for the direction is laevotropic while the normal cormidial whorls are dexiotropic. It is proposed that

the method of growth necessary to move the cormidial elements down to the base of the corm is linked to the idea that no new cormidia are being added to the basic spiral arrangement and the nectosomal and siphosomal regions are permanently united and cannot rotate relative to each other, but that the siphosomal zone of proliferation retains the potential to produce new cormidial buds. One must consider the series of proliferating young cormidia as being attached along a small tube, which is equivalent to the stem of a macrostele physonect, and which has, at this stage, little or no connection with the remainder of the corm and is, in effect, being extruded over the latter's surface. The band of young cormidial bases (figure 6*h*) in *A. euryale* clearly demonstrates this concept; and it is not until the cormidial elements reach their final positions that a permanent connection with the corm is established. One can now conjecture that, as the budding continues in the zone of proliferation, the expansion of the tube in its usual, dextrotropic direction is blocked by the presence of the last cormidial base to be inserted into the now permanently fixed spiral arrangement. Thus the tube is forced to expand either vertically downwards or laterally away from, and to the left of, the zone of proliferation, thereby forming, respectively a -- or L-shaped branch in the gastrovascular canal system. The former branching would result, by further extrusion of the now blind-ending tube, in the cormidial elements being carried directly towards the base of the corm. The latter branching might arise if, by chance, the passage down the corm was blocked by the presence of a well developed cormidial base. However, what determined the point at which it eventually turns and travels towards the base is not clear.

Although *Stephalia corona*, *Rhodalia miranda* and *Angelopsis euryale* appear to have similar growth patterns as regards the cormidial units, it is interesting to note the divergences that have occurred in the internal structure of the corm. In *S. corona* a spiral arrangement of the major gastrovascular canals persists deep in the corm, although the canal that supplies the basal, reduced cormidia is a separate branch from the others. This arrangement may be indicative of the 'solidification' of the corm, in contrast to the continued growth in *Dromalia alexandri* where the spiral pattern is confused. In *R. miranda* the major canal system has disappeared and is replaced by a reticulum of smaller ones, without any apparent configuration. Finally, in *A. euryale* one large cavity has developed. This is probably a further development of the situation in *Thermopalia taraxaca*, with the mesogloal layer becoming extraordinarily thickened, causing the development of the radial canals that connect the cormidia with the cavity.

The fact that the growth pattern of *Dromalia alexandri* appears to be so different from those of all the other species again raises the question as to whether the origin of the rhodaliids was polyphyletic. *D. alexandri* differs in a large number of characters from all the other species, although *Archangelopsis typica* also has papilliform appendages on its aurophore. Nevertheless it is clear that there is still much to learn about the members of the physonect family Rhodaliidae, and that many questions might be answered if some larvae or post-larvae were available for study. Haeckel's (1888 *b*) description of the so-called *auronula* larva unfortunately is unsatisfactory, but it might at least indicate that the larvae are benthic since it appeared in the same catch as some adult specimens. However, with a more intensive study of the biology of such areas as the geothermal vents it is to be hoped that more complete specimens will be collected and perhaps more detailed *in situ* studies made of these fascinating animals which are unique, at this present state of our knowledge, among the siphonophores in having re-adopted the benthic way of life.

It is a pleasure to be able to acknowledge here the many people who have aided me during the long gestation period of this paper. Specimens of rhodaliids have been loaned to me from several museums, as noted in the text, and I am indebted not only to my correspondents at these places but also to many more at several other museums, where I have drawn an unfortunate blank in the search for certain rhodaliid specimens.

I wish to thank those people who have kindly allowed me to reproduce their excellent photographs in this paper, and the Trustees of the British Museum (Natural History) for permission to reproduce material from Totton (1965).

Several people have taken the trouble to acquaint me with their *in situ* observations on or provide me with information about some specimens of *Dromalia alexandri* and I am grateful for their help. In particular, I am grateful to Dr J. F. Grassle, at the Woods Hole Oceanographic Institution, not only for allowing me to describe the specimens of the 'Galápagos dandelions', *Thermopalia taraxaca*, but also for communicating his personal observations and for his efforts in obtaining for me some comparable video tape-recordings of the *Alvin* dives, thereby overcoming some previous difficulties concerning the inherent differences in the U.S.A.-U.K. colour television systems.

I have benefited greatly from conversations with, and the patience of, my colleagues at the Institute of Oceanographic Sciences, to all of whom I express my gratitude. In particular, I would thank Mr P. M. David for his constant interest in the project, for his helpful and deep-sighted discussions on a variety of aspects of rhodaliid biology, and for his critical readings of and useful suggestions on the text.

My special thanks also are due to Mrs C. E. Darter for her excellent standard of work in producing the line drawings, for her skill in bringing out and understanding the salient features of these illustrations, and for her general enthusiasm throughout the project. In addition, Mr A. F. Madgwick and his colleagues in the Photographic Department at I.O.S. have made sterling efforts to make the most of some rather poor photographs taken by me and have worked wonders in reproducing the plates of earlier texts by several authors, e.g. Haeckel (1888b), which have been used in this paper. I am grateful to all of them.

REFERENCES

- Allmendiger, R. W. & Riis, F. 1979 The Galápagos Rift at 86° W. 1. Regional morphological and structural analysis. *J. geophys. Res.* **84** (B10), 5379-5389.
- Alvarino, A. 1971 Siphonophores of the Pacific with a review of the World distribution. *Bull. Scripps Instn Oceanogr. tech. Ser.* **16**, 1-432.
- van Andel, T. H. & Ballard, R. D. 1979 The Galápagos Rift at 86° W. 2. Volcanism, structure and evolution of the rift valley. *J. geophys. Res.* **84** (B10), 5390-5406.
- d'Aoust, B. G. 1970 Physiological constraints on vertical migration by mesopelagic fishes. In *Proceedings of an International Symposium on Biological Sound Scattering in the Ocean* (ed. G. B. Farquhar), pp. 86-89. Washington, D.C.: Maury Center for Ocean Science.
- Ballard, R. D. & Grassle, J. F. 1979 Return to oases of the deep. *Natn. geogr. Mag.* **156**, 689-703.
- Barham, E. G. 1963 Siphonophores and the deep scattering layer. *Science, N.Y.* **140**, 826-828.
- Beers, J. R. 1966 Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. *Limnol. Oceanogr.* **11**, 520-528.
- Bidigare, R. R. & Biggs, D. C. 1980 The role of sulfate exclusion in buoyancy maintenance by siphonophores and other oceanic gelatinous zooplankton. *Comp. Biochem. Physiol. A* **66**, 467-471.
- Bigelow, H. B. 1911 The Siphonophorae. Reports of the scientific research expedition to the tropical Pacific. *Albatross* XXIII. *Mem. Mus. comp. Zool. Harv.* **38**, 173-401.
- Bigelow, H. B. 1913 Medusae and Siphonophorae collected by the U.S. Fisheries Steamer 'Albatross' in the northwestern Pacific, 1906. *Proc. U.S. natn. Mus.* **44**, 1-119.
- Biggs, D. C. 1977 Field studies on fishing, feeding, and digestion in siphonophores. *Mar. Behav. Physiol.* **4**, 261-274.

- Brooks, W. K. & Conklin, E. G. 1891 On the structure and development of the gonophores of a certain siphonophore belonging to the order Auronectae (Haeckel). *Johns Hopkins Univ. Circ.* **10**, 87–89.
- Carré, D. 1969 Étude histologique du développement de *Nanomia bijuga* (Chiaje, 1841), Siphonophore Physonecte, Agalmidae. *Cah. Biol. mar.* **10**, 325–341.
- Carré, D. & Carré, C. 1983 In preparation.
- Chun, C. 1897 Die Siphonophoren der Plankton-Expedition. *Ergebn. Plankton Exped.* **2.K.b.**, 1–126.
- Claus, C. 1889 On the organism of the Siphonophora and their phylogenetic derivation: a criticism upon E. Haeckel's so-called Medusome-theory. *Ann. Mag. nat. Hist.* (6) **21**, 185–198.
- Corliss, J. B. & Ballard, R. D. 1977 Oases of life in the cold abyss. *Natn. geogr. Mag.* **152**, 441–453.
- Corliss, J. B., Dymond, J., Gordon, L. I., Edmond, J. M., von Herzen, R. P., Ballard, R. D., Green, K., Williams, D., Bainbridge, A., Crane, K. & van Andel, T. H. 1979 Submarine thermal springs on the Galápagos Rift. *Science, N.Y.* **203**, 1073–1083.
- Crane, K. & Ballard, R. D. 1980 The Galápagos Rift at 86° W. 4. Structure and morphology of hydrothermal fields and their relationship to the volcanic and tectonic processes of the rift valley. *J. geophys. Res.* **85** (B 3), 1443–1454.
- Currie, R. I. 1972 Quantitative investigations in marine biology. *Proc. R. Soc. Edinb. B* **73**, 239–245.
- Daniel, R. 1974 Siphonophora from the Indian Ocean. *Mem. zool. Surv. India* **15** (4), 1–242.
- Enright, J. T., Newman, W. A., Hessler, R. R. & McGowan, J. A. 1981 Deep-ocean hydrothermal vent communities. *Nature, Lond.* **289**, 219–221.
- Fewkes, J. W. 1886 Report on the Medusae collected by the U.S. F.C. Steamer Albatross, in the region of the Gulf Stream, in 1883–'84. *Rep. U.S. Commr. Fish. for 1884*, pp. 927–980.
- Fewkes, J. W. 1889 On *Angelopsis*, and its relationship to certain Siphonophora taken by the 'Challenger'. *Ann. Mag. nat. Hist.* (6) **4**, 146–155.
- Galápagos Biology Expedition Participants 1979 Galápagos '79: initial findings of a deep-sea biological quest. *Oceanus* **22**, 2–10.
- Garstang, W. 1946 The morphology and relations of the Siphonophora. *Q. Jl microsc. Sci.* **87**, 103–193.
- Haeckel, E. 1869 Zur Entwicklungsgeschichte der Siphonophoren. *Natuurk. Verh. Prov. Utrechtsch Genoots* (i) **6**, 1–120.
- Haeckel, E. 1888a System der Siphonophoren. *Jena Z. Naturw.* **22**, 1–46.
- Haeckel, E. 1888b Report on the Siphonophorae collected by H.M.S. *Challenger* during the years 1873–1876. *Rep. Sci. Res. H.M.S. Challenger (Zool.)* **28**, 1–380.
- Huxley, T. H. 1859 The oceanic Hydrozoa; a description of the Calycophoridae and Physophoridae observed during the voyage of H.M.S. 'Rattlesnake', in the years 1846–1850. *Rep. Ray Soc.*, pp. 1–143.
- Jacobs, W. 1937 Beobachtungen über das Schweben der Siphonophoren. *Z. vergl. Physiol.* **24**, 583–601.
- Jacobs, W. 1962 Siphonophore structures help colonies maintain specific depth. *Nat. Hist., N.Y.* **71**, 23–27.
- Karl, D. M., Wirsen, C. O. & Jannasch, H. W. 1980 Deep-sea primary production at the Galápagos hydrothermal vents. *Science, N.Y.* **207**, 1345–1347.
- Kawamura, T. 1954 A report on Japanese siphonophores with special reference to new and rare species. *J. Shiga Prefect. jun. Coll. A* **2**, 99–129.
- Keferstein, W. & Ehlers, E. 1861 Beobachtungen über die Siphonophoren von Neapel und Messina. In *Zoologische Beiträge Gesammelt im Winter 1859/60 in Neapel und Messina*, pp. 1–34. Leipzig: Wilhelm Engelmann.
- Leloup, E. 1941 À propos du pneumatophore de *Physophora hydrostatica* (Forskål, 1775). *Bull. Mus. r. Hist. nat. Belg.* **17** (31), 1–11.
- Leloup, E. 1954 À propos des Siphonophores. In *Volume jubilaire, Victor van Straelen, 1925–1954*, vol. 2, pp. 641–699. Brussels: Institut Royal des Sciences Naturelles de Belgique.
- Lens, A. D. & van Riemsdijk, T. 1908 The Siphonophora of the Siboga Expedition. *Siboga Exped.* **9**, 1–130.
- Lonsdale, P. 1977 Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep Sea Res.* **24**, 857–863.
- Lutz, R. A., Jablonski, D., Rhoads, D. C. & Turner, R. D. 1980 Larval dispersal of a deep-sea hydrothermal vent bivalve from the Galápagos Rift. *Mar. Biol.* **57**, 127–133.
- Mackie, G. O. 1960 Studies on *Physalia physalis* (L.). Part 2. Behaviour and histology. *Discovery Rep.* **30**, 369–408.
- Mackie, G. O. & Boag, D. A. 1963 Fishing, feeding and digestion in siphonophores. *Pubbl. Staz. zool. Napoli* **33**, 178–196.
- Moser, F. 1924 Ordnung: Siphonophora. In *Handbuch der Zoologie*, vol. 1 (ed. W. Kükenthal & T. Krumbach), pp. 485–521. Berlin and Leipzig: Walter de Gruyter & Co. (1923/25).
- Moser, F. 1925 Die Siphonophoren der Deutschen Südpolar Expedition 1901–1903. *Dts. Südpol.-Exped.* **17** (zool. 9), 1–541.
- Nicol, J. A. C. 1967 *The biology of marine animals*. London: Pitman & Sons.
- Pickwell, G. V. 1970 The physiology of carbon monoxide production by deep-sea coelenterates: causes and consequences. *Ann. N.Y. Acad. Sci.* **174**, 102–115.
- Pickwell, G. V., Barham, E. G. & Wilton, J. W. 1964 Carbon monoxide production by a bathypelagic siphonophore. *Science, N.Y.* **144**, 860–862.

- Pugh, P. R. 1977 Some observations on the vertical migration and geographical distribution of siphonophores in the warm waters of the North Atlantic Ocean. In *Proceedings of the Symposium on Warm Water Zooplankton*, pp. 362-378. Goa: National Institute of Oceanography.
- Purcell, J. E. 1980 Influence of siphonophore behaviour upon their natural diets: evidence for aggressive mimicry. *Science, N.Y.* **209**, 1045-1047.
- RISE Project Group 1980 East Pacific Rise: hot springs and geophysical experiments. *Science, N.Y.* **207**, 1421-1433.
- Rottini, L. 1974 Identificazione in vitro di una probabile fase bentonica nel ciclo biologico di *Muggiae kochi* Will (Sifonoforo, Calicoforo). *Boll. Pesca Piscic. Idrobiol.* **29**, 149-155.
- Schneider, K. C. 1896 Mittheilungen über Siphonophoren. II. Grundriss der Organisation der Siphonophoren. *Zool. Jb.* **9**, 571-664.
- Schneider, K. C. 1898 Mittheilungen über Siphonophoren. III. Systematische und andere Bemerkungen. *Zool. Anz.* **21**, 114-133 and 153-173.
- Scrutton, C. T. 1979 Early fossil cnidarians. In *The Origin of major invertebrate groups* (ed. M. R. House), *Systematics Ass. spec. vol.* no. 12, pp. 161-207. London: Academic Press.
- Sokolova, M. N. 1969 Distribution of deep-sea benthic invertebrates in relation to their methods and conditions of feeding. In *The Pacific Ocean*, vol. 7 (*Biology of the Pacific Ocean, part II, the deep-sea bottom fauna*; ed. L. A. Zenkevich), pp. 210-233. Moscow. (English translation: U.S. Naval Oceanographic Office, Washington, D.C., translation no. 487 (1970).)
- Stechow, E. 1921 Neue Genera und Species von Hydrozoen und andere Evertebraten. *Arch. Naturgesch.* A **87**, 248-265.
- Totton, A. K. 1949 Pneumatocyst of the physophores. *Nature, Lond.* **164**, 877.
- Totton, A. K. 1954 Siphonophora of the Indian Ocean together with systematic and biological notes on related specimens from other oceans. *Discovery Rep.* **27**, 1-161.
- Totton, A. K. 1956 Development and metamorphosis of the larva of *Agalma elegans* (Sars) (Siphonophora Physonectae). *Pap. mar. Biol. Oceanogr., Deep Sea Res.* **3** (suppl.), 239-241.
- Totton, A. K. 1960 Studies on *Physalia physalis* (L.). Part 1. Natural history and morphology. *Discovery Rep.* **30**, 301-368.
- Totton, A. K. 1965 *A synopsis of the Siphonophora*. London: British Museum (Natural History).
- Wittenberg, J. B., Noronha, J. M. & Silverman, M. 1962 Folic acid derivatives in the gas gland of *Physalia physalis* L. *Biochem. J.* **85**, 9-15.

GLOSSARY. LIST OF ABBREVIATIONS AND SYMBOLS USED IN CERTAIN FIGURES

au.	aurophore	o.	opening
b.	bract	p.	palpon
b.l.	bracteal lamella	pa.	palpacle
c.	cormidium	pc.c.	pericytic cavity
c.b.	cormidial base	p.go.	polyovan gonophore or egg pouch
ch.	chitin	pn.	pneumatophore
e.b.	ectodermal band	pnc.	pneumatocodon
ect.	ectoderm	pnd.	pneumadenia or gas gland
ect. a	secondary ectoderm	pnh.	pneumatochone
end.	endoderm	pns.	pneumatosaccus
e.p.	excretory pore	pn.y.	pneumatocyst
g.a.c.	giant amoeboid cells	pz.	protozooid or larval gastrozooid
gd.	gonodendron	s.	siphon or gastrozooid
go.	gonophore	s.e.	endodermal septum
gp.	gonopalpon	st.	stem
g.v.c.	gastrovascular canal	t.	tentacle
gz.	gastrozooid or point at which it was attached	ta	tentillum
hc.c.	hypocystic cavity	×	zone of no growth
m.	mesogloea	z.p.n.	zone of proliferation of nectosome
n.	nectophore	z.pr.	zone of proliferation
n.l.	nectophoral lamella	z.p.s.	zone of proliferation of siphosome

(Where a number appears after an abbreviation, e.g. gd.2, this component belongs to a particular cormidium on a cormidial base.)