DISCOVERY REPORTS

VOLUME XXVII

DISCOVERY REPORTS

Issued by the National Institute of Oceanography

VOLUME XXVII

CAMBRIDGE
AT THE UNIVERSITY PRESS
1956

PUBLISHED BY
THE SYNDICS OF THE CAMBRIDGE UNIVERSITY PRESS
London Office: Bentley House, N.W. 1
American Branch: New York
Agents for Canada, India, and Pakistan: Macmillan

Printed in Great Britain at the University Press, Cambridge
(Brooke Crutchley, University Printer)

CONTENTS

SIPHONOPHORA OF THE INDIAN OCEAN. Together with systematic and biological notes on related specimens from other oceans (published 28th April, 1954)

By A. K. Totton

THE PELAGIC MOLLUSCA OF THE BENGUELA CURRENT. Part I. First Survey, R.R.S. 'William Scoresby', March 1950. With an account of the Reproductive System and Sexual Succession of *Limacina Bulimoides* (published 30th July, 1954)

By J. E. Morton, Ph.D.

THE CIRCUMPOLAR CONTINUITY OF ANTARCTIC PLANKTON SPECIES (published 30th July, 1954)

By A. de C. Baker

THE PLANKTONIC DECAPOD CRUSTACEA AND STOMATOPODA OF THE BENGUELA CURRENT. Part I. First Survey, R.R.S. 'William Scoresby', March 1950 (published 8th November, 1954)

By Marie V. Lebour, D.Sc.

THE DISTRIBUTION OF *SAGITTA GAZELLAE* RITTER-ZAHONY (Published 11th May, 1955)

By P. M. David

CUMACEA OF THE BENGUELA CURRENT (published 6th July, 1955)

By N. S. Jones, Ph.D.

THE WAX PLUG IN THE EXTERNAL AUDITORY MEATUS OF THE MYSTICETI (published 20th July, 1955)

By P. E. Purves

ALEPISAUROID FISHES (published 29th July, 1955)

By N. B. Marshall

EUPHAUSIACEA OF THE BENGUELA CURRENT. First Survey, R.R.S. 'William Scoresby', March, 1950 (published 30th August, 1955)

By Brian Boden

CESTODES OF WHALES AND DOLPHINS FROM THE DISCOVERY COLLECTIONS (published 17th October, 1955)

By S. Markowski

[*Discovery Reports. Vol. XXVII, pp.* 1–162, *Plates I–XII, April* 1954.]

SIPHONOPHORA OF THE INDIAN OCEAN

TOGETHER WITH SYSTEMATIC AND BIOLOGICAL NOTES ON RELATED SPECIMENS FROM OTHER OCEANS

By

A. K. TOTTON
British Museum (Natural History)

CONTENTS

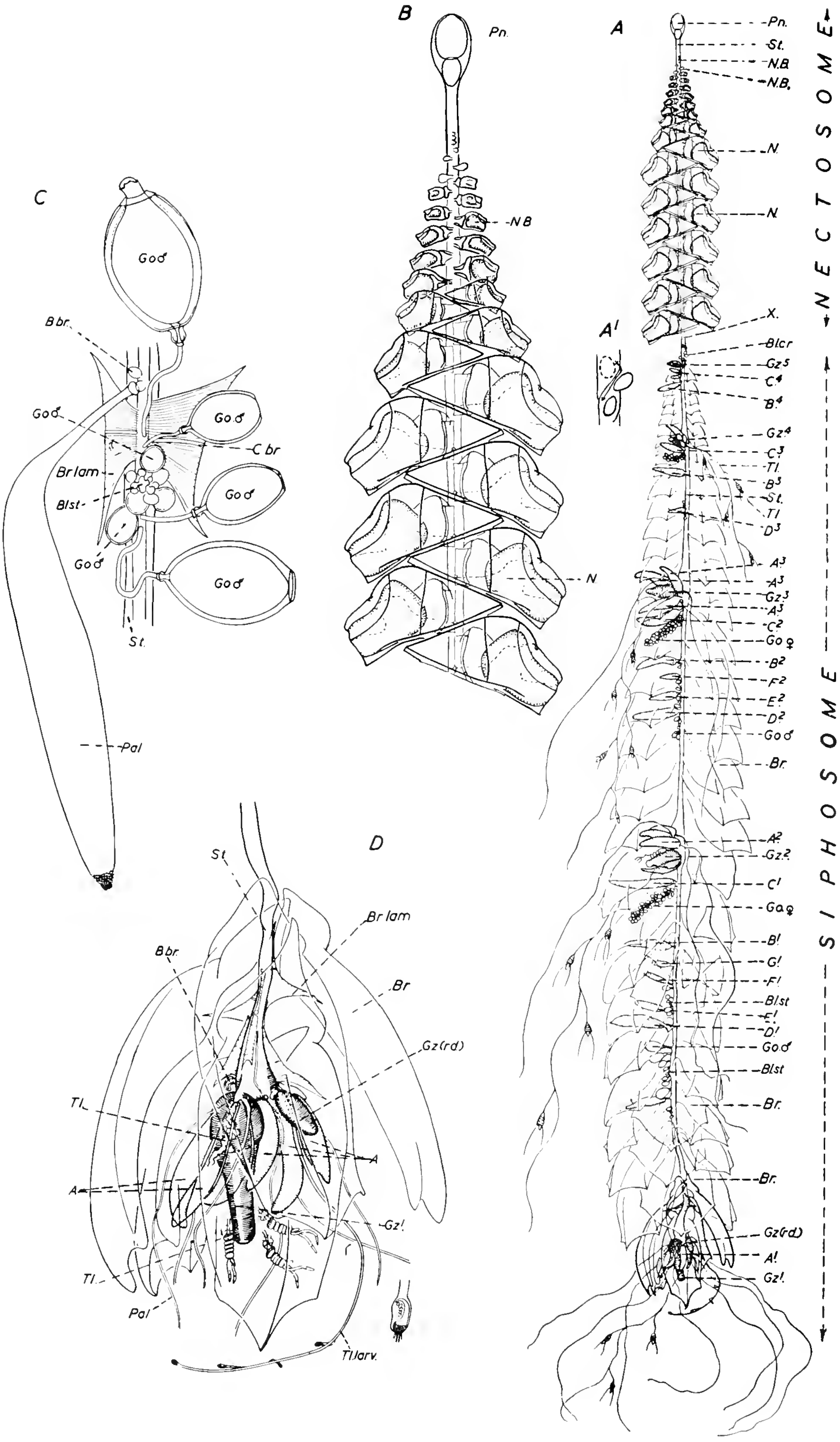


Diagram of a young Physonect Colony.

Legend to Diagram of a young Physonect Colony

A. The whole colony, showing the nectosome and the siphosome with five cormidia.

A′. This shows that the siphosome has been deliberately twisted to bring the ventral meridian to which the buds are attached from the underside (opposite to that of the nectosome) over to the left for the convenience of the artist.

B. Enlarged diagram of the nectosome to show (i) the budding zone of the nectophores, and (ii) how the muscular lamellae of the nectophores all arise in one meridian (dorsal) but bend alternately to left and right.

C. The stem in the region of a blastostyle to show the budding of the male gonophores, a palpon and two of the bracteal lamellae.

D. Enlarged diagram of the primary terminal gastrozooid.

The pneumatophore, *Pn.*, stem, *St.*, and terminal gastrozooid, $Gz.^1$, represent the original polypoid oozooid. The nectosome gives rise to asexual medusa-buds, and the siphosome to both polyp- and medusa-buds, so that the whole animal may be called a floating bud-colony, as suggested by Garstang (1946). The bracts, *Br.*, are probably neither polyp- nor medusa-buds, but are possibly homologous either with larval actinuloid tentacles, or with larval or adult appendages which have arisen *de novo.*

The nectosome with its apical organ—not a medusoid bud, but an air-secreting and air-releasing float (pneumatophore, *Pn.*)—carries only the propelling nectophores, *N.* (asexual medusae). The pneumatophore together with the budding-zone for nectophores, which in the larval stage originated on one side of it (Fig. 3), grows upwards (aborally) from the nodal point of minimum growth *X.*

The siphosome grows downwards (orally) from the same nodal point *X.* It consists in the juvenile stage illustrated, of five cormidia or groups of buds, which originated in the larval stage on the side of the pneumatophore opposite to that which gave rise to the budding zone of the nectophores (Fig. 3). The first formed gastrozooid (protozooid) $Gz.^1$, with its ring of palpons bearing simple tentacles (palpacles, *Pal.*) together with a reduced secondary gastrozooid, *Gz.(rd.)*, which bears a less highly elaborate 'larval tentacle', forms the terminal part of the oldest cormidium, and is surrounded by a whorl of larger bracts of larval origin. Four successively younger cormidia can be seen between this and the siphosomal budding-zone or blastocrene, *Bl.cr.*

Each cormidium consists of:

(1) A distal gastrozooid with branched tentacle, surrounded by
(2) A ring of bracts and palpons, the latter provided each with a simple tentacle and increasing in number with age.
(3) Several ventro-lateral rows of bracts.
(4) A number of intermediate palpons without palpacles, which increase in number with age.
(5) A number of male medusae (gonophores, androphores), *Go.* ♂, which become separated with age from their budding points (blastostyles), and lastly
(6) A grape-like bunch of female medusae (gonophores, gynophores) *Go.* ♀, which arises from the base of a gonopalpon at the proximal end of the cormidium.

A tentative analysis of the arrangement of palpons and gonophores in successive cormidia suggests that there is a separate growth-gradient in each cormidium and that new palpons and male gonophores are budded off at several loci, characteristic for each species. The order of the development of successive cormidia is indicated in the diagram by numerals added to the symbols, the explanation of which is as follows:

Symbol	*Explanation*
$A.^{1,2,3,4}$	The first series of gastric palpons, associated with $Gz.^1$, $Gz.^2$, etc., the first palpons to appear.
$B.^{1,2,3,4}$	Intermediate palpons, the second series of palpons to appear.
$C.^{1,2,3}$	Intermediate palpons, 3rd series of palpons to appear.
$D.^{1,2,3}$	Intermediate palpons, 4th series of palpons to appear.
$E.^{1,2}$	Intermediate palpons, 5th series of palpons to appear.
$F.^{1,2}$	Intermediate palpons, 6th series of palpons to appear.
$G.^1$	Intermediate palpons, 7th series of palpons to appear.
B.br.	Bracteal bud.
Bl.cr.	Blastocrene (budding-zone of siphosome).
Bl.st.	Blastostyle (gonodendron), a bud from the oozooid from which the gonophores bud.
Br.	Bract.
Br.lam.	Bracteal lamella.
C.br.	Bracteal canal.

Symbol	*Explanation*
Gz.^{1}	Protozooid (oldest gastrozooid or siphon), part of the oozooid.
Gz.^{2}	Second oldest gastrozooid (siphon), a bud from the oozooid.
Gz.^{3}	Third oldest gastrozooid (siphon).
Gz.^{4}	Fourth oldest gastrozooid (siphon).
Gz.^{5}	Fifth oldest gastrozooid (siphon).
Gz.(rd.)	Reduced gastrozooid, a bud from the oozooid.
Go.♂	Male gonophore (androphore), ? a bud from the oozooid, secondarily acquiring direct connexion with the oozooid.
Go.♀	Female gonophore (gynophore) ? a bud from the oozooid bearing medusoid-buds.
N.	Nectophore.
N.B.	Nectophore bud.
Pal.	Palpacle.
Pn.	Pneumatophore, apical organ of the oozooid.
St.	Stem, part of the oozooid.
Tl.	Tentacle, part of the gastrozooid.
Tl.larv.	Larval tentacle.
X	Nodal point of minimum growth.

See also Pl. IV.

SIPHONOPHORA OF THE INDIAN OCEAN

TOGETHER WITH SYSTEMATIC AND BIOLOGICAL NOTES ON RELATED SPECIMENS FROM OTHER OCEANS

By A. K. Totton
British Museum (Natural History)

With a frontispiece, chart, 12 plates, and 83 text-figures

INTRODUCTION

The original object of this report, based primarily on the very rich collections made by R.R.S. 'Discovery II', was to investigate the Siphonophore fauna of the Indian Ocean, which, by comparison with that of the Atlantic and Pacific, was little known. It soon became apparent that, as Bigelow had long suspected, members of the group have very wide distributions, and that it was, indeed, doubtful if any species is either confined to or excluded from some part of the Indian Ocean, except those few species that are confined to antarctic waters. The chief result then of the study of the collections has been to advance our knowledge of the morphology of many of the species concerned; and accordingly use has been made, in the systematic account, of some new and critical specimens taken in other waters, not only by ships of the Discovery Committee, but by other expedition ships as well.

Our knowledge of the Siphonophora does not increase as rapidly as it might, because the systematist can only, with few exceptions, obtain the material needed for study by laboriously picking it out of plankton hauls. Unfortunately man-power is insufficient for sorting. For this reason there are still some thousands of plankton net hauls among the Discovery Collections alone that have not been examined for Siphonophora, all of which are holoplanktonic animals; no one can tell what treasures these jars of plankton may contain. One may search for a very long time before being lucky enough to find a really well-preserved specimen, or a larval or other much desired stage, of some particular species, especially if it is a deep-water one. *Chuniphyes moserae* may be cited as an example. The rarely seen *Nectopyramis spinosa*, *N.* [*Archisoma*] *natans* and the Rhodaliids, of which I have never found a specimen, are others. There is also the inherent difficulty of dealing with fragmentary specimens. Again, many of the species occur in two phases, since the stems of most Calycophores eventually break up into free-swimming groups of buds called eudoxids, the successive gonophores of which in their turn may break away and swim as free medusae. I have been lucky enough to secure, anaesthetize and preserve for comparison with the fragments secured by nets, fairly complete specimens of *Forskalia edwardsii*, *Apolemia uvaria*, *Agalma elegans*, *Nanomia bijuga* and *Stephanomia rubra*—all of them available at times at Villefranche, some in large numbers.

The polygastric stages of Diphyiinae and most of their eudoxids, especially those which occur near the surface, as well as the polygastric and eudoxid stages of the Abylopsinae are now well known. The Prayidae are less well known; also the Physonectae, which are the most difficult to determine because they fall to pieces in the nets or in the bottles of plankton, and no one except Bigelow has had the patience to describe and figure accurately more than a few of the pieces. This is regrettable because the nectophores, bracts, gastrozooids and tentacles, siphons and gonophores, both individually and in their arrangement on the oozooid, all have very definite characters. As a rule it is far more worth while to figure accurately the details of these buds than to attempt to give a sketchy figure or description of the whole animal. Indeed, it is a most exacting task to make a figure of a live Siphonophore such as a *Forskalia* or *Apolemia*. Most of them are transparent, extremely complex in shape, and very active in movement as a whole, and in expansion and contraction of the stem, tentacles and nectophores. In addition to these difficulties, specimens as a rule quickly become moribund in captivity.

Much of the literature is full of names that only with grave doubt can be referred to zoological concepts. For many years now I have been occupied with the laborious task of picking out hundreds of thousands of fragmentary specimens from plankton samples and of trying to form some idea of how many species are represented, and then attempting to apply old specific names and, where none are available, giving new ones. Gradually specialists are building on the foundations laid by their illustrious predecessors and on their own early work, and are beginning to recognize the various species. The greatest stimulus to progress is given by field work, but unfortunately the opportunities afforded to me for this have been very limited.

The best known and most easily identifiable Siphonophores are perhaps those of the Mediterranean, a region where so much of the pioneer work on the group was done, and a region where many are often easily accessible at the surface, as long as the sea is calm and sea-temperature does not exceed 21° C. The least well known are those of the Indian Ocean, for which reason this report has been prepared with no little labour.

Many species are difficult to take with tow-nets, except in fragments, and it is probable that many species of a particular fauna of Siphonophores will always be missed by the nets. As an illustration of this fact, in intensive tow-netting campaigns from 1908 to 1910 in the Mediterranean, the 'Thor' missed not only all the common Physonects like *Agalma*, '*Stephanomia*', *Forskalia* and *Apolemia*, but also such abundant species as *Muggiaea kochii* and *Lensia subtilis*. Another explanation for the absence from 'Thor' catches of the last two species is that they may be neritic forms.

MATERIAL AND METHODS

Our knowledge of the Siphonophora of the Indian Ocean was summarized by E. T. Browne (1926) in his report on thirty-six species taken on the 'Sealark' Expedition by Stanley Gardiner. 'Sealark' ranged over the banks and slopes of the Chagos Archipelago, the Seychelles and the Mascarene Islands, in the tropical zone during the months May to October. The Siphonophores collected by 'Dana II' in the 1928–30 cruise are being worked out by Dr Mary Sears. Jesperson (1935) gives a summarized list of stations showing that a large number of plankton hauls were made in the Indian Ocean from the north point of Sumatra across to Ceylon and thence via the Seychelles to the north point of Madagascar and to Mombasa. Changing southwards, the route then passed through the Mozambique channel to Durban, thereafter following the coast-line down to Cape Town. The macroplankton on the line Ceylon-Madagascar-Mombasa appears to have been much richer than that on the stretch through the Mozambique channel down to Cape Town.

Dr Sears's 'revision of the Abylinae', published since this report went to press, contains records of Indian Ocean specimens of *Abyla bicarinata* Moser, *A. brownia* Sears (sp.n.), *A. carina* Haeckel [=*A. trigona* Q. & G.], *A. haeckeli* L. & van R., *A. ingeborgae* Sears (sp.n.), *A. schmidti* Sears (sp.n.), *A. trigona* Q. & G., *Ceratocymba dentata* Bigelow and *C. leuckartii* Huxley.

From September 1933 to May 1934, the John Murray Expedition with the 'Mabahiss' was working principally in the open West Tropical Indian Ocean, in the Somali and Arabian Basins, and brought back thirty-nine species of Siphonophores.

Since the return of the 'Mabahiss', our knowledge of the Indian Ocean siphonophore fauna has been supplemented by a study of eight more collections. The first was a rich collection made by R.R.S. 'Discovery II' which, in 1935, ran a line of stations up from Marion Island to the Gulf of Aden. From the plankton taken at these 'Discovery' Stations I have picked out and identified about 14,000 specimens. They fall into some 170 categories which represent the parts of polygastric and eudoxid colonies of seventy-six species. They were taken in forty-five tow-net hauls (Stations 1566–89), fished at various depths between the surface and 1900 m., all being closing-net hauls. These 'Discovery' Stations provide records of twenty-one known Siphonophores not previously recorded from the Indian Ocean, and not taken by the 'Mabahiss'. In addition a number of new species were taken at these 'Discovery' Stations: three of these have been known to me for a long time, though descriptions have not yet been published, and some others are new to me. There are a few other novelties which will not be mentioned until more is known about them. 'Discovery's' N70V series of nets in particular gave valuable results, and I have separated out no less than 11,000 Siphonophores, including larvae, from these catches.

The next collection was made in the Red Sea in 1935–6 by Cdr. J. H. Bowen, R.N., in H.M.S. 'Weston'.

Another line of stations across the Indian Ocean was made in 1936 by R.R.S. 'Discovery II' in lat. 32° S., at which thirty-five species of Siphonophora were taken in twenty-nine closing-nets.

A fourth collection was made between November 1948 and February 1949 in the Gulf of Aden by Mr A. Fraser-Brunner, while investigating the fisheries of the Aden Protectorate. Off Aden he fished a metre net both by day and night, by anchoring the boat and streaming the net out with the tide, allowing it to fish for half an hour and hauling it. Off Bulhar, Mukalla and Alayu he also fished the same net for half an hour just below the surface at a towing speed of about three knots (see Chart, p. 10). 'Discovery II' made four stations, Nos. 2679–82, in the Gulf of Aden in 1950. I have examined the oblique haul from 200 m. to the surface made at Station 2681. In 1951 she made another station there, No. 2900.

A fifth collection of 925 specimens was made in the Gulf of Aqaba by the British Museum (Nat. Hist.) Expedition in M.Y. 'Manihine'. Thirty-two stations were made between 31 December 1948 and 3 February 1949. Thirteen species of Siphonophora in all were present at thirty of the stations. The fact that not many species were present at any one station in the Gulf of Aqaba has had a useful systematic result, in that an Agalmid larva could be almost certainly identified as that of the species *Agalma okenii*; the eudoxid of *Chelophyes contorta* could be definitely identified for the first time owing to the absence of *C. appendiculata*; and the eudoxid of *Lensia hotspur* and its posterior nectophore could be identified, because, apart from *L. subtilis* whose eudoxid is known, it was the only other common species of *Lensia* present at the depth explored. The surface temperatures (21–22° C.) and salinities (40·6–40·8‰) were high, and no doubt the Siphonophores were at the lower limit of the vertical hauls rather than at the surface. Unfortunately, hauls could not be made from depths below 180 m. or more specimens might have been taken.

A sixth collection was made in the Red Sea off Port Sudan by M.Y. 'Manihine' in the winter of 1950–1. Three thousand eight hundred and thirty-seven specimens were removed from ten catches and identified, providing almost the first records of Siphonophores from that area.

A seventh collection, consisting of six bottles of plankton, was made in November 1951 with oblique hauls from 200 m. or so to the surface in the Red Sea by 'Discovery II' and was received in January 1952. This collection adds no species that were not taken there earlier by H.M.S. 'Weston' and by M.Y. 'Manihine', and in fact does not contain specimens of seven species taken by them, but it gives valuable corroborative evidence about the fauna of the area. More important, it has enabled me to conclude that *Sulculeolaria quadridentata* is identical with *S. quadrivalvis* (see Systematic Notes, p. 109).

Finally, I have picked out thirty-three species of Siphonophores from ten of the stations made in 1950–1 by 'Discovery II' along a line in longitude 90° E. The finding at Station 2895 in surface waters of *Sulculeolaria biloba* led to a long-needed revision of the old genus *Galetta* and its submergence in *Sulculeolaria*.

It is comparatively easy to preserve Siphonophora in good condition for morphological work, if not for exhibition. They can be engulfed at the surface of a calm sea in a bottle, or picked out with a dip-net, and they should be isolated unless very small. Two or three or more live specimens of a species such as *Rosacea cymbiformis*, if kept in a jar, soon become inextricably entangled. The use of an isotonic solution of magnesium chloride makes it possible to achieve a good deal of relaxation of muscles and consequent expansion before killing in formalin, which should contain at least 5% formaldehyde. It is advisable to add 2 lb. of hexamine (hexamethylenetetramine) to each gallon of 38–40% formaldehyde solution to buffer it. Before subsequent examination it is a good plan to stain for a day or two with dilute Grenacher's Borax-carmine. A little of this stain can be added to the jar in which the specimens are preserved. For examination of the external form of nectophores and bracts, brief staining in dilute Delafield's haematoxylin is effective, but if hexamine has been used the specimens must first be thoroughly washed or the stain will be precipitated.

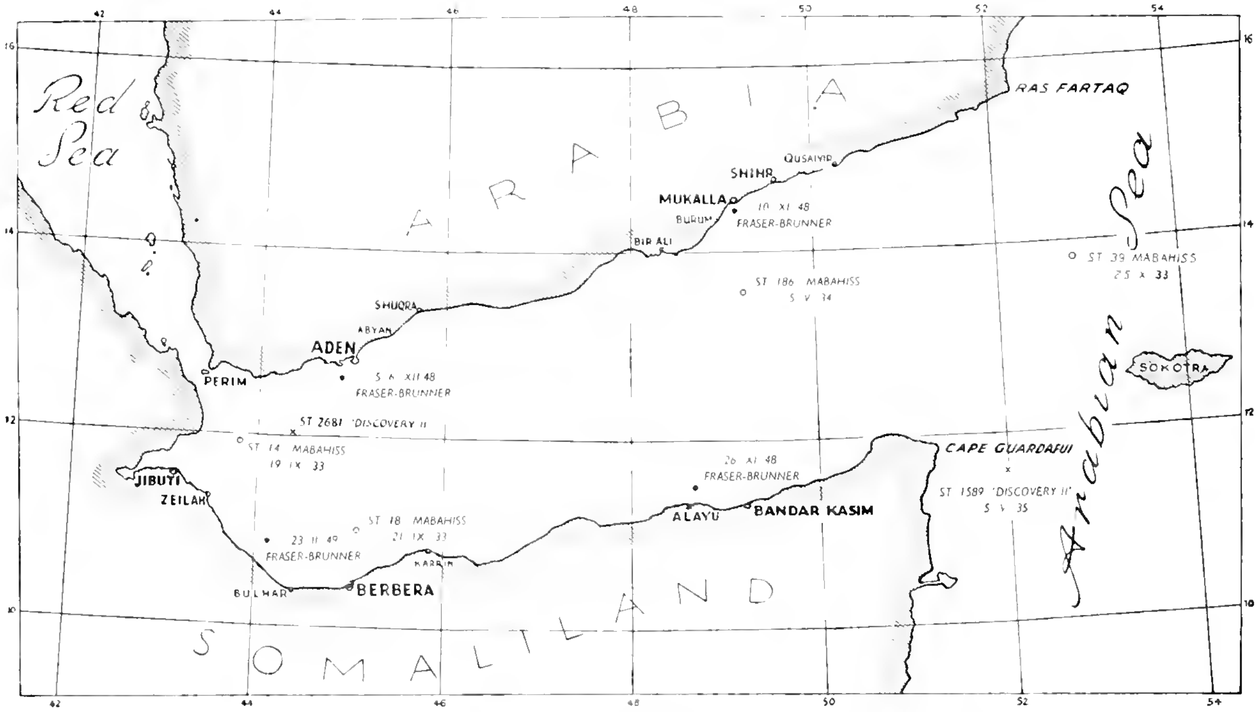


Chart. Stations in the Gulf of Aden occupied by 'Mabahiss', 'Discovery II' and Mr Fraser-Brunner.

To photograph them alive is exceedingly difficult because of the lack of contrast, the depth of the field that it is necessary to cover, and their constant change of form and position.

The text-figures, with the exception of a few diagrammatic ones, were all drawn by the author with the aid of a camera lucida. The inking in of the figures was done by Mrs Walker (*née* E. C. Humphreys) after demonstration and examination of the specimens. A subsequent check with the specimens was made by myself, or by both of us. In order to be able to make drawings of large specimens I removed the foot of a Leitz binocular and made the stage slide on a track, fixed at such a height above the bench that the drawing could be moved about underneath it. Thus by movements of the specimen on the stage, of the stage on the track, and of the drawing, it was possible to make large drawings, 18 in. or more across.

Preserved specimens were stained lightly with Delafield's haematoxylin and photographed in formalin. To obtain the view of the ostium of the nectophore of *Abyla tottoni* Sears (Pl. IX, fig. 4) the specimen was held in a vertical glass tube in a vessel of formalin. As well as light from the top, some was reflected upwards through the specimen. *Maresearsia praeclara* (Pls. VI and VII) was photographed with a Leitz 400 mm. Milar lens. The photomicrographs 4 and 5 of Pl. IV were made by Mr M. G. Sawyers, principal photographer, with a 3 in. Holos lens, and the others (unless otherwise stated) were made by Mr J. V. Brown of the Museum Staff, with a Leitz Summar 12 cm. lens.

Acknowledgements. I am grateful to Dr W. J. Rees for having read the draft of this report, and to Dr Helene Bargmann of the National Institute of Oceanography for a great deal of help.

SIPHONOPHORE FAUNA OF THE RED SEA

This report gives, for the first time,[1] a record of the Siphonophores which live in the Red Sea and in the Gulf of Aqaba. These are areas about whose Siphonophores we previously knew practically nothing. It is therefore satisfactory to be able to include in this work on the species from the Indian Ocean, material collected from these two localities. This fauna, to judge from the material so far available, does not include the following species found elsewhere in the Indian Ocean:

Porpita umbella
(?) *Physalia physalis*
Physophora hydrostatica
Rosacea cymbiformis
R. plicata
Hippopodius hippopus
Vogtia glabra
V. pentacantha
V. serrata
Chuniphyes multidentata
Clausophyes ovata
Sulculeolaria monoica
[*Galetta*] *S. biloba*
[*G.*] *S. turgida*
Dimophyes arctica
Diphyes bojani
Abyla haeckeli
A. trigona (sp. aff.)
A. leuckartii
Chelophyes appendiculata
Eudoxoides mitra
E. spiralis
Lensia achilles
L. campanella
L. conoidea
L. cossack
L. multicristata

Bigelow & Sears (1937) showed that there was a paucity of siphonophore species in the Mediterranean as compared with the Atlantic beyond, and noted that two of the reasons for this probably were (*a*) the excluding action of the deep outflow over the sill upon species which lived below that level, (*b*) the rather high minimum temperature (12–13° C.) of the Mediterranean deep water.

There appears to be an even greater paucity of siphonophore species in the Red Sea as compared with the Indian Ocean outside. Here again the deep outflow over the sill at the southern entrance of the Red Sea probably has an excluding action on deeper-water species, and the even higher (21·5–22° C.) minimum temperature of the Red Sea deep water would be unbearable for such species, even if they entered.

Sverdrup, Johnson & Fleming (1946), summarizing the work of Thompson and others on the water masses of the Indian Ocean, say that the entire basin of the Red Sea below sill depth (100 m.) is filled in winter with water which has a salinity of from 40·5 to 41·0‰, and a temperature between 21·5° and 22° C.: and that it has a very low oxygen content, less than 1 ml./L. in summer, a little more than 2 ml./L. at the end of the winter. The maximum surface temperature in summer is about 30° C. and

---

[1] Schneider (1898, p. 120) mentioned that Steindachner, scientific leader of the 'Pola' Expedition had handed over to him two Siphonophores from the Red Sea, now known as *Agalma okenii* and (possibly) *Melophysa melo*.

the minimum (February) about 18° C. A species like *Stephanomia rubra*, which leaves the surface waters of the Mediterranean when the temperature rises above about 21° C. and descends into deeper cooler water, appears to be living in the Red Sea in an environment that it can only just manage to tolerate. It is therefore interesting to find that the new records given in Table 1, show at least two dozen species of Siphonophores from the Red Sea.

Table 1. *List of Chondrophora and Siphonophora taken in the Red Sea.* (*New records*)

	R.R.S. 'Discovery II', 1951, St. 2905, N 70 B	R.R.S. 'Discovery II', 1951, St. 2905, TYF B	H.M.S. 'Weston', 1935–6, Kamaran Islands, Apr. 1936	M.Y. 'Manihine', 1950–1, Port Sudan, Jan. 1951	H.M.S. 'Weston', 1935–6, Port Sudan, Nov.–Dec. 1935	R.R.S. 'Discovery II', 1951, St. 2906, N 70 B	R.R.S. 'Discovery II', 1951, St. 2906, TYF B	R.R.S. 'Discovery II', 1951, St. 2907, N 70 B	R.R.S. 'Discovery II', 1951, St. 2907, TYF B	M.Y. 'Manihine', 1950–1, Koseir and Jaffatin Islands, Nov. 1950	M.Y. 'Manihine', 1948–9, Gulf of Aqaba, Jan. 1949	H.M.S. 'Weston', 1935–6, Safajin Islands, 26° 40′ N. 34° 0′ E., Jan. 1936	H.M.S. 'Weston', 1935–6, Aqaba, Feb. 1936
Winter or summer	W	W	W/S	W	W	W	W	W	W	W	W	W	W
South, central or north part of Red Sea	S	S	S	C	C	C	C	N	N	N	N	N	N
Velella velella	—	—	—	×	—	—	—	—	—	—	—	—	—
Forskalia sp. or spp.	×	×	—	×	—	×	×	—	—	—	×	—	—
Nanomia bijuga	×	×	×	$\times^c$	—	—	—	—	—	—	—	—	—
Stephanomia rubra	—	—	—	×	—	×	×	×	—	×	×	—	—
Agalma elegans	—	—	—	×	—	—	—	—	—	×	×	—	—
A. okenii	×	×	—	×	—	×	×	×	×	—	*L*	—	*L*
Athorybia rosacea	—	—	—	×	—	×	×	—	—	—	×	—	—
Amphicaryon sp.	—	—	—	—	—	—	—	—	—	—	$\times^1$	—	—
Cordagalma cordiformis	—	—	—	—	—	—	—	—	—	—	$\times^c$	—	—
Sulculeolaria chuni	×	×	—	×	×	×	×	×	—	×	×	—	—
S. quadrivalvis	×	$\times^c$	—	×	—	×	×	×	—	×	×	—	—
Diphyes dispar	—	×	—	2^c	—	—	—	—	—	—	—	—	—
D. chamissonis	2	2	2^c	2^c	2	—	—	—	—	—	—	—	—
Abylopsis eschscholtzii	—	—	2	—	—	—	—	—	—	—	—	—	—
A. tetragona	—	×	—	2^c	*E*	2	2	2	2	×	2	—	—
Bassia bassensis	—	—	2	2^c	—	*E*	—	—	—	—	—	—	—
Enneagonum hyalinum	2	2^c	—	2^c	P^1	—	—	—	—	—	—	—	—
Lensia campanella	—	—	—	P^1	—	—	—	—	—	*P*	—	—	—
L. fowleri	—	—	—	*P*	—	—	—	—	—	*P*	*P*	—	—
L. hotspur	—	—	—	×	—	×	×	2	2	×	2	—	—
L. meteori	—	—	—	P^1	—	—	—	—	—	—	*P*	—	—
L. subtilis	—	—	—	P^1	—	—	—	—	—	—	2^c	—	P^1
L. subtiloides	×	×	2^c	$\times^c$	×	—	P^1	—	P^2	—	—	×	—
Chelophyes contorta	×	×	—	2	P^1	2	2	2	—	×	2	—	—
Muggiaea atlantica	—	—	—	×	—	—	—	—	—	—	—	—	—
Sphaeronectes sp.	—	×	—	—	—	—	—	—	—	—	—	—	$\times^1$

Explanation of symbols:

× = present, stage and numbers not recorded.
— = absent.
P = polygastric stage.
E = eudoxid stage.
$\times^1$, P^1, P^2, P^3 = number of specimens.
c = common.
2 = both stages.
L = larval stage.

The almost cosmopolitan *Chelophyes appendiculata* has not, so far, been taken there, though its close ally *C. contorta* is common. The evidence for the occurrence of *Agalma elegans* depends on the identification of young nectophores and a few larval bracts, and needs corroboration. The rather uncommon, associated pair *Diphyes chamissonis* and *Lensia subtiloides* are abundant.

Comparison of the records from the northern, central and southern areas of the Red Sea, for what they are worth, show that there are eleven species in the southern, twenty-one in the central and seventeen in the northern. All the records are winter ones.

Red Sea records by the 'Manihine' for the ten following species show that they were living at the upper limit of their known temperature range: *Diphyes dispar*, *D. bojani*, *D. chamissonis*, *Lensia subtiloides*, *L. subtilis*, *Chelophyes appendiculata*, *Eudoxoides mitra*, *Abylopsis tetragona*, *A. eschscholtzii*, *Bassia bassensis*.

SIPHONOPHORES FROM THE GULF OF ADEN

From the Gulf of Aden, where forty-five 'Mabahiss' Stations were made, five hauls were made with plankton nets but only nine Siphonophores were captured. However, Mr Fraser-Brunner, who made some very rapid oblique hauls off Aden, Mukalla, Alayu and Bulhar on 10 and 26 November 1948, on 5 and 6 December 1948, and on 23 February 1949, respectively, showed that the water was teeming with Siphonophores. He took more than 9000 specimens, yet *Vogtia glabra* was caught by the 'Mabahiss' and missed by Fraser-Brunner, probably because it is not a surface species.

One station, No. 2681, was also made by R.R.S. 'Discovery II' in 1950 in the Gulf of Aden.

Table 2. *Siphonophore colonies from the Gulf of Aden. Analysis of catches made by 'Mabahiss'* (1933–4) *and by Fraser-Brunner* (1948–9)

	Fraser-Brunner, Alayu 26. xi. 48 ½ m. net 0 m. Night		'Mabahiss', St. 186 5. v. 34 2 m. net 952–0 m. Day		Fraser-Brunner, Mukalla 10. xi. 48 1 m. net 0 m. Day		'Mabahiss', St. 18 21. ix. 33 2 m. net 900–0 m. Day		Fraser-Brunner, Aden 6. xii. 48 1 m. net 0 m. Day		Fraser-Brunner, Aden 5. xii. 48 1 m. net 0 m. Night		Fraser-Brunner, Bulhar 23. ii. 49 1 m. net 0 m. Day		'Mabahiss' St. 14 19. ix. 33 Agassiz trawl 988 m.	
Nanomia bijuga	—		—		—		—		×		×		—		—	
Agalma okenii	×		—		—		—		× × ×		× ×		×		—	
Vogtia glabra	—		1		—		—		—		—		—		—	
Sulculeolaria chuni	4		—		—		—		—		—		—		—	
Sulculeolaria sp. indet.	2		—		—		—		—		—		—		—	
S. quadrivalvis	7		—		—		—		1		2		—		—	
	P	*E*	*P*	*E*	*P*	*E*	*P*	*E*	*P*	*E*	*P*	*E*	*P*	*E*	*P*	*E*
Diphyes dispar	27	188	—	—	506	748	1	—	36	6	20	16	5	2	3	—
D. bojani	—	2	—	—	—	—	—	—	—	1	2	1	3	1	—	—
D. chamissonis	12	4	—	—	226	155	—	—	7	5	16	61	—	—	—	—
Lensia subtiloides	26	—	—	—	—	—	—	—	15	2	6	0	—	—	—	—
Muggiaea atlantica	14	—	—	—	—	—	—	—	59	?	402	?	—	—	—	—
Chelophyes appendiculata	—	—	—	—	—	—	—	—	—	—	10	—	—	—	—	—
Ch. contorta	99	3	—	—	113	—	—	—	15	4	46	70	88	—	—	—
Eudoxoides mitra	3	4	—	—	—	—	—	—	0	3	—	5	10	18	—	—
Abylopsis tetragona	3	3	1	—	—	—	—	—	10	0	3	1	22	27	—	—
A. eschscholtzii	2	—	—	—	0	10	—	—	—	—	1	0	—	—	—	—
Bassia bassensis	20	33	—	—	1024	4820	—	—	15	47	260	888	31	5	—	—
Enneagonum hyalinum	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Abyla trigona sp. aff.	—	—	—	—	—	—	—	—	0	1	—	—	—	—	—	—

P = polygastric stage. *E* = eudoxid stage.

SALINITY TOLERANCE

Siphonophores evidently have a wide range of salinity tolerance as well as of temperature. Although Bigelow (1911 *b*) found that in the Eastern Tropical Pacific they are an almost negligible factor in the plankton from waters with a salinity less than 35‰, and that they are entirely absent where the salinity is below about 30‰, in the Gulf of Aqaba with surface salinities as high as 40·8‰ (Deacon, 1952), the records are far from scanty.

SIPHONOPHORES FROM THE INDIAN OCEAN

Table 3 gives a list of species from the Indian Ocean. It will be seen from the brief summary of the broad hydrographic conditions in these waters, given below, that in these regions they are living in surroundings very different from those obtaining in the Red Sea and the Gulf of Aqaba.

The penetration of water of high salinity from the Red Sea can be detected in the Indian Ocean at depths of about 500 m. in latitude 8° N. to depths of 1250 m. in latitude 20° S.

According to Sverdrup *et al.* (1946), the southern limit of the Indian Ocean is marked by the sub-tropical convergence in approximately latitude 40° S. To the north it is closed by the land-mass of Asia. The temperatures of the surface layers are uniformly high during the greater part of the year, varying between 25–29° C. In August the south-west monsoon causes upwelling of cold water along the East African and south-east Arabian coasts as far south as the Equator, and in February the north-west monsoon brings about the same phenomenon in the Bay of Bengal. Consequently, lower surface temperatures are met with in these regions in these months. Salinity values also show an annual variation because of these influences, but otherwise have a sub-tropical maximum of 35·4‰.

Below the surface-layers are three main water masses:

(1) Indian Ocean Central water, probably formed at the subtropical convergence by sinking, and having temperatures of 8–15° C. and salinities of 34·6–35·5‰.

(2) Indian Ocean Equatorial water formed by sub-surface mixing, and having temperatures of 4–17° C. and salinities of 34·9–35·25‰.

(3) Deep-water mass below depths of 2000 m. approximately, formed partly by antarctic intermediate water (temperature 2·2° C. and salinity 33·8‰) and partly by antarctic bottom water (temperature 2·0° C. and salinity 34·8‰). Their mixing produces deep water in the Indian Ocean of relatively high salinity 34·76‰ and temperatures about 2·5° C.

MORPHOLOGY AND RELATIONS OF SIPHONOPHORA

An outstanding event in the history of siphonophore literature was the publication in 1946 in the *Quarterly Journal of Microscopical Science* by Walter Garstang of his 'Morphology and Relations of the Siphonophora'. It is indeed, as John Colman has said, an admirable exercise in classical comparative morphology.[1] Try as one will it is difficult to escape from Garstang's main conclusions.

Written in less than two years as the last of his great papers, it has its roots deep in his personal history. He told me that he could never have tackled the larval development of the big groups Tunicata, Mollusca, Crustacea and Siphonophora had it not been his duty in the early years of the Plymouth Laboratory to make himself familiar with all branches of the Plymouth fauna, both as regards structure and habitat, an experience which taught him to turn easily from one group to another. No doubt Garstang was not familiar with more than a few Siphonophores, alive or preserved, and the paper itself is really a masterly review of the literature. It is very satisfactory for one who has spent more than twenty years making an intensive and fresh study of the Siphonophora, both preserved and alive, to find himself so much in agreement with Garstang's main conclusions.

---

[1] Personal communication.

Table 3. *List of species identified by the author in the Indian Ocean*

	Page	Whether previously recorded from Indian Ocean	Off south and east coasts of Africa, 'Discovery II' Sts. 1554–89	S.E. Indian Ocean (part of '90° E. Line') 'Discovery II', Sts. 2685–8, 2886, 2894–5	S. Indian Ocean 'Discovery II' Sts. 1736–66	N.W. Indian Ocean 'Mabahiss'	Gulf of Aden, 'Fraser-Brunner'	Red Sea, 'Discovery II'; 'Manihine'	Gulf of Aqaba, 'Manihine'
CHONDROPHORA									
Porpita umbella	33	×	×	—	—	×	—	—	—
Velella velella	34	?	—	—	×	—	—	×	—
SIPHONOPHORA: PHYSONECTAE									
A. CYSTONECTAE									
Physalia physalis		×	×	—	—	×	—	—	—
B. PHYSONECTAE									
Athorybia rosacea	38	×	—	—	—	—	—	×	×
Melophysa melo	41	?	×	—	—	—	—	—	—
Physophora hydrostatica	42	×	×	—	—	×	—	—	—
Stephanomia rubra	47	○	×	×	—	×	—	×	—
Nanomia bijuga	52	○	×	—	—	—	×	×	—
Marrus orthocannoides gen.n., sp.n.	59	○	×	—	—	—	—	—	—
Agalma elegans	61	×	—	—	—	—	—	×	×
A. okenii	64	×	×	—	×	×	×	×	×
Cordagalma cordiformis	69	○	×	—	—	—	—	×	×
Bargmannia elongata gen.n., sp.n.	69	○	×	—	—	—	—	—	—
Forskalia sp.	73	×	×	—	—	—	—	×	×
SIPHONOPHORA: CALYCOPHORAE									
SPHAERONECTIDAE									
Sphaeronectes sp.		×	×	—	—	—	—	×	—
PRAYIDAE									
Praia ? dubia		○	×	—	—	—	—	—	—
Nectopyramis thetis	78	○	×	×	—	—	—	—	—
N. natans	82	○	×	—	×	—	—	—	—
N. diomedeae	83	○	×	×	×	—	—	—	—
Rosacea cymbiformis	89	?	×	—	—	×	—	—	—
R. plicata	89	○	×	—	—	×	—	—	—
Amphicaryon acaule	92	×	×	×	—	—	—	×	?
A. ernesti sp.n.	94	○	×	—	—	—	—	×	—
A. peltifera	96	○	×	—	—	—	—	—	—
Maresearsia praeclara gen.n., sp.n.	97	○	×	—	—	—	—	—	—
HIPPOPODIIDAE									
Hippopodius hippopus	99	×	×	×	×	×	—	—	—
Vogtia glabra	100	○	×	×	×	×	×	—	—
V. pentacantha		×	×	×	×	×	—	—	—
V. spinosa		○	×	—	×	—	—	—	—
V. serrata		×	×	—	—	—	—	—	—

Table 3 (*continued*)

	Page	Whether previously recorded from Indian Ocean	Off south and east coasts of Africa, 'Discovery II' Sts. 1554–89	S.E. Indian Ocean (part of '90° E. Line'), 'Discovery II' Sts. 2685–8, 2886, 2894–5	S. Indian Ocean 'Discovery II' Sts. 1736–66	N.W. Indian Ocean, 'Mabahiss'	Gulf of Aden, 'Fraser-Brunner'	Red Sea, 'Discovery II'; 'Manihine'	Gulf of Aqaba, 'Manihine'
SIPHONOPHORA: CALYCOPHORAE (*continued*)									
DIPHYIDAE: SULCULEOLARIINAE									
Sulculeolaria biloba	104	○	×	×	—	×	×	—	—
S. turgida	107	○	×	×	—	?	—	—	—
S. chuni		×	×	×	—	×	×	×	×
S. angusta sp.n.	108	○	×	—	—	—	—	—	—
S. quadrivalvis	109	×	×	×	×	×	×	×	×
S. monoica		×	×	×	×	×	—	—	—
DIPHYINAE									
Lensia achilles		○	×	×	—	×	—	—	—
L. ajax		×	×	—	—	—	—	—	—
L. campanella		×	×	—	—	×	—	×	—
L. conoidea	114	○	×	×	×	×	—	—	—
L. cossack	112	×	×	×	×	×	—	—	—
L. exeter		×	×	×	—	—	—	—	—
L. fowleri		×	×	×	×	—	—	×	×
L. grimaldii		○	×	×	—	—	—	—	—
L. havock		×	×	×	—	—	—	—	—
L. hostile		×	×	—	×	—	—	—	—
L. hotspur	110	×	×	×	—	×	—	×	×
L. hunter		×	×	×	—	—	—	—	—
L. lelouveteau		○	×	—	—	—	—	—	—
L. meteori	117	○	×	×	—	—	—	×	×
L. multicristata	113	×	×	×	×	×	—	—	—
L. reticulata sp.n.	118	○	×	—	—	—	—	—	—
L. subtilis	114	×	×	×	—	×	—	×	×
L. subtiloides	112	○	×	—	—	×	×	×	—
Eudoxia macra sp.n.	118	○	×	×	—	—	—	—	—
Muggiaea atlantica	120	○	—	—	—	—	×	×	—
Dimophyes arctica	123	×	×	×	—	—	—	—	—
Chelophyes appendiculata	127	×	×	—	×	×	×	—	—
Ch. contorta	130	×	×	×	—	×	×	×	×
Eudoxoides mitra		×	×	×	×	×	×	—	—
E. spiralis		×	×	×	×	×	—	—	—
Diphyes dispar		×	×	×	×	×	×	×	—
D. bojani		×	×	×	—	×	×	—	—
D. chamissonis	130	×	×	—	—	×	×	×	—
CHUNIPHYINAE									
Chuniphyes multidentata	131	○	×	×	×	×	—	—	—
Ch. moserae sp.n.	131	○	×	×	—	—	—	—	—
Clausophyes ovata	133	○	×	×	×	×	—	—	—
Crystallophyes amygdalina	134	○	×	—	—	—	—	—	—
Heteropyramis maculata	137	○	×	×	—	—	—	—	—
Thalassophyes crystallina	141	○	×	×	—	—	—	—	—
ABYLIDAE: ABYLOPSINAE									
Abylopsis tetragona	155	×	×	×	×	×	×	×	×
A. eschscholtzii		×	×	×	×	×	×	—	—
Enneagonum hyalinum		×	×	×	—	×	×	×	—
Bassia bassensis		×	×	—	×	×	×	×	—
ABYLINAE									
Abyla schmidti	147	×	×	×	×	×	×	—	—
A. haeckeli	151	×	×	×	×	×	—	—	—
Ceratocymba sagittata		×	×	×	×	—	—	—	—
C. leuckartii		×	×	×	—	×	—	—	—

GARSTANG ON PHYLOGENY

Reduced to its elements Garstang's paper consists of some corrections of interpretation which permit a more satisfactory alignment of the orders, and support the idea that the pelagic habit of the Siphonophores results from a prolongation of a free-swimming larval phase, coupled with precocious development and sundry adaptations of the ancestral characters, including budding.

Garstang attractively rounded off his critical discussion of siphonophore phylogeny by suggesting that a myriotheline relationship of Siphonanths is indicated by the resemblance of their lateral, paddling (*sic*) bracts to the larval tentacles of the actinula of the hydroid *Myriothela*, which are aboral in position, locomotive in function and precociously developed. But he thought that this relationship of Siphonanths to *Myriothela* had to be reconciled with the corymorphine affinities of Disconanths before the common origin which he suspected could be firmly assured. He suggested that *Pelagohydra*, Siphonanths and Disconanths may in fact be independent pelagic offshoots from three different types of gymnoblastic hydroid, the larvae of which failed to attach themselves but succeeded in keeping afloat until their gonophores ripened. *Pelagohydra* absolutely, and Disconanths to some extent, may be said to have survived, he continued, by adaptive aggrandizement of their oozooids at the expense of their colonies, while Siphonanths, by precocious budding, elaborated the colony at the expense of the oozooid. Rather surprisingly, Garstang did not mention another floating tubularid hydroid, *Margelopsis haeckeli*; and had he been familiar with the little-known Siphonophore, *Apolemia uvaria*, I feel sure that he would have commented on the fact that the unique feature it presents, namely the presence of tufts of tentacles at various points on the nectosome, recalls the arrangement in *Pelagohydra*.[1]

RELATIONSHIPS BETWEEN SIPHONOPHORA AND HYDROIDA

Having noted Garstang's conclusions about the phylogeny of Siphonophora and their relationship with corymorphine and myriotheline hydroids, let us now take a brief look at this group of hydroids and the rest of the Hydroida (Anthomedusae) Capitata. Whenever these hydroids bud off medusae they belong to the old Haeckelian family Codonidae, considered by medusologists to be a simple and primitive group of Anthomedusae. The Capitata include hydroids which have two contrasting habits. In one the oozooid secretes a permanent tube, simple or branched, attached to the substratum at its basal end by a branching stolon. In the other we find either planktonic forms, or insecurely attached solitary forms anchored by hydrocauline processes to the sand or mud. It is perhaps natural to ask which of these two contrasting types appears to be primitive and which derivative.

Kramp (1949) gave a most interesting review of the corymorphine hydroids, including several of the less sedentary forms of which very little is known. He said that actinula larvae are unknown in this family, but both Hartlaub (1907) and Rees (1937) have shown that actinuloid larvae or polyp buds are indeed known. Kramp, who, in his important paper, nowhere mentioned either Garstang's (1946) work nor that of Grönberg (1898) on the canals of *Tubularia*, presented an outline of the course which he thinks has been taken in the phylogeny of a *Tubularia* line of hydroids and a *Corymorpha* line, and he derived the solitary, anchored forms like *Corymorpha* from those with fixed stolons like the Corynidae. From general considerations this seems to be most improbable, but I shall not attempt myself to speculate on the detailed phylogenies of genera of hydroids within the Capitata. Garstang's argument for the derivation of the sedentary forms like *Tubularia* and *Pennaria* with fixed stolons, from the free forms like *Corymorpha*, was based on good evidence from comparative morphology.

---

[1] I have re-examined the type specimen of the latter and have made efforts to find detached medusae referable to it amongst plankton hauls from the New Zealand region, but without success. I was interested to hear recently from Dr Elizabeth J. Batham that Canterbury Museum, Christchurch, New Zealand possessed a second specimen of *Pelagohydra*.

Kramp does not appear to have produced arguments of similar worth for concluding that evolution has proceeded in the reverse direction, nor did he anywhere refer to Garstang's work, as I have already mentioned.

ACTINULOID ANCESTORS

The question whether it is theoretically impossible for the ancestral Metazoa to have been pelagic is of critical importance.

A morphological character possessed by so many of the Corymorphidae is the presence on various parts of the stem of papillae and root-processes, which bear suggestive signs of homology with the larval tentacles of actinuloid animals. What are we to conclude from the fact that so many groups of Hydrozoa have actinuloid larvae—Trachymedusae, Narcomedusae, Chondrophora, (?) Siphonophora, Margelopsidae (*Margelopsis haeckeli*, *Pelagohydra*, *Climacocodon*), Corymorphidae, Myriothelidae, Tubulariidae, and Corynidae and allies? It must mean that the common ancestor of all these animals had an actinuloid larva. Garstang appears to have believed that, as in the Tunicata, this larva was a purely locomotive one, that it was followed by fixation, and then by an adult stage of feeding and growth, with budding last of all, but that in some forms fixation was postponed and finally abandoned altogether. I should like to think that the adult ancestor had always been planktonic, like the ancestral larva, and that fixation did not take place until much later in phylogeny. According to Carter (1949) who briefly reviewed Hadzi's (1944) Turbellarian theory of the Cnidaria, Hadzi believes that 'only the smaller Protista can float without either an elaborate structure adapted to enable them to do so or considerable expenditure of energy. We must think, then', he says, 'of the ancestral metazoan as a bottom-living form, and not as a floating spherical colony.... It would develop an intermediate cell-layer, a parenchyma, between the ectoderm and the endoderm, to give solidity and support to the body.' But if animals like the trachymedusan *Liriope*, whose youngest stages show neither elaborate structure, except a mesogloea, nor appear to be obliged or able to expend considerable energy, can live at the surface, it would seem that this argument is not valid.

The Trachylina are thought to be the most primitive Cnidaria. It is true that most Trachymedusae are well-marked bathypelagic forms, as are the Narcomedusae from northern latitudes, but in the warm seas the latter suborder are found in the surface layers.

POLYP AND MEDUSA

The argument for thinking of the medusa as the original adult form of Cnidaria rather than as a dispersal device was stated by Brooks (1886) following Bohm (1878) and Claus (1878). He advanced a theory that the polypoid generation in Hydromedusae is a persistent larval form, and that the adult ancestral hydrozoan was some sort of medusoid, perhaps (see Brooks, 1886, pl. 41, figs. 6–7) rather like the earliest medusa-stage of development of the trachymedusan *Liriope*, the adult stage of which has made only a slight advance beyond its larval polypoid stage (Brooks, fig. 8). The ancestral polypoids, as suggested by Brooks and supported by Libbie Hyman, developed the habit of budding before some of them took up a prolonged attached existence as polypoid oozooids or colonies. After this, instead of becoming metamorphosed directly into a medusoid, the actinuloid produced the medusoid by budding. Libbie Hyman (1940) pointed out that this view harmonizes with the development of Siphonophores, where the planula develops into the polypoid and buds off the medusoid.

LIBBIE HYMAN ON PHYLOGENY

Libbie Hyman, though repeating some outmoded theories about the interpretation of the morphology of Siphonophora, has given a more satisfactory account (pp. 636–40) of the probable phylogeny of the various groups of Cnidaria and Ctenophora than is found elsewhere. I find it hard to believe in that part of Hadzi's (1944) Turbellarian theory of Cnidaria which derives Anthozoa from Turbellaria. But then I have only a text-book knowledge of the Turbellaria, and if text-books on Cnidaria are any criterion, they can be grossly misleading.

SOMATOCYSTS AND BRACTS

Garstang (p. 143) boldly revived Schneider's contention that the Calycophoran somatocyst is homologous with the cavity of the cap-shaped bract of a larval Physonect. But whereas, as Garstang says, Schneider, Woltereck and Moser all realized this, they thought that the Calycophorae were primitive, and that in the Physonect (1) the primitive Calycophoran bract had secondarily become separated from the nectophore, (2) this separated nectophore had become the pneumatophore, and (3) the separated somatocyst had become the Physonect bract. The true significance of the homology according to Garstang is this: the Physonects are primitive and the independent primary bract of the Physonect (e.g. the larval bract of *Physophora*) has become secondarily fused with the precocious nectophore in the Calycophorae; and this shows that originally Calycophorae as well as Physonectae possessed larval, locomotive bracts, reminiscent of the larval tentacles of hydroid actinulae.

So Garstang put forward, and himself adopted what he called the illuminating view that the original larva of the Siphonophore ancestors was not a planula but an actinula, in which, before the typical actinuloid characters could be developed, precocious budding became established.

It is quite impossible to be sure that the somatocyst of Calycophorae represents a larval actinuloid tentacle at all and, in addition, that it represents a larval tentacle of the ancestor of a particular group of gymnoblast hydroids within the Capitata. In ontogeny it always arises, in my view, as an integral part of the precocious larval nectophore-bud, and may in reality have no more connexion with the larva than that. It may, in fact, be an oil-storing organ developed late in phylogeny which now appears early in ontogeny. I think that Garstang was probably right in believing that bracts were developed from actinuloid tentacles, though another possible explanation is that larval bracts are precociously developed adult bracts, developed late in phylogeny.

If a close study is made of the bracts of *Athorybia* and *Melophysa*, and they are compared with the larval bracts of *Agalma elegans*, and particularly of the larval and young stem bracts of *A. okenii*, it will be seen that the stem bracts of Physonectae in general are probably all homologous with larval bracts (see Text-figs. 8, 9 and 26).

ORIGIN OF NECTOPHORES

One of the most difficult questions to answer about siphonophore phylogeny has always been how nectophores were evolved. Judging by their simple nematocysts and tentacles, lack of nectophores, and structure of the pneumatophore, Cystonects are the most primitive group of Siphonophora. Long ago, Kawamura (1910) in an inaccessible[1] Japanese work, suggested a way in which the three-branched tentilla of *Rhizophysa filiformis* might have evolved from a simple unbranched tentacle. The process can be watched in the course of ontogeny. The great puzzle was how, if Cystonects are primitive, did the nectophores of Physonects originate? Garstang linked his explanation that they represented pre-siphonophore (i.e. hydroid) gonophores with an argument that does not appear to be very sound, namely that hydroid gonophores were originally produced on the hydrorhiza of the ancestral hydroids, and that only later did they invade the circumoral region via the hydrocaulus with which he homologizes the siphonophore stem.

Before proceeding with the discussion of Garstang's theory of the origin of nectophores it should be noted that Garstang made it somewhat difficult for a non-specialist to follow some of his arguments

---

[1] Through the good offices of Dr Mary Sears most of Kawamura's work on the Siphonophora has been translated from Japanese into English by Rodney Notomi.

by using what seems to be a faulty nomenclature—one that leads to a confusion of identities. He said much about two not very well-known Physonects which, like Bigelow, he called '*Anthophysa*' and '*Athorybia*'. The proper names of these two forms are *Athorybia* Forskål (for Garstang's '*Anthophysa*') and *Melophysa* (Haeckel) (for Garstang's '*Athorybia*'). The synonymies are explained in my systematic notes (p. 37). It is most unfortunate that these corrections must be made, since Garstang's paper will become a classic. But in places Garstang uses both names *Athorybia* and '*Anthophysa*' for one and the same animal, *Athorybia rosacea* Forskål: at other times he uses one of these names '*Athorybia*' for a distinct species *Melophysa melo* (Haeckel). The confusion in siphonophore synonymy is notorious.

According to Garstang's theory the rudimentary medusoid buds, discovered by Chun in '*Athorybia*' (=*Melophysa* Haeckel) and hitherto regarded as vestigial nectocalyces, are (bearing *Pelagohydra* in mind) tentatively claimed as obsolescent hydroid gonophores; in other families they are said to have been converted into nectocalyces; and in '*Anthophysa*' (=*Athorybia* Forskål) they are thought to have disappeared altogether. I have now collected and examined quite a number of these *Melophysa* nectophores (see Text-fig. 7). They may be more primitive in many ways than other nectophores, but show no obvious sign of being obsolescent gonophores, nor of being vestigial. In fact '*Anthophysa*' (=*Athorybia* Forskål) may never have possessed nectophores at all, being descended from an 'Athorybia larva'-like ancestor comparable with the stage in the ontogeny of an 'Athorybia larva'[1] before nectophores arise. In that case *Athorybia* would be neotenous. Garstang's '*Athorybia*' (=*Melophysa* Haeckel) is in my opinion another neotenous form descended from a similar 'Athorybia larva'-like ancestor, only it is comparable with a rather later stage in the ontogeny of an 'Athorybia larva' when nectophores have begun to develop. But of course we cannot be sure whether or not an 'Athorybia larva' represents an actinuloid larva with precocious gonophore (nectophore) buds. Even if it does it is probable that Garstang's '*Anthophysa*' (=*Athorybia* Forskål) arose at a stage in phylogeny before the appearance of the precocious buds which, in Garstang's theory, represent the obsolescent hydroid gonophores. Garstang tried to clinch his argument by saying that the nectocalyces of the nectosome of Physonects must represent the gonophores of pre-siphonophore (i.e. hydroid) ancestors because they are produced from the oozooid, which in Siphonophores remains sterile, whilst sexual siphonophore medusa buds are borne on secondarily budded gonopalpons.

The explanation of the fact that nectophores (sterile swimming medusae) arise from the oozooid is, I believe, that they were evolved later than the bud-borne, sexual medusae distributed along the stem of all Physonects, that they were developed precociously in the larvae of Physonects purely for swimming purposes, and were then further developed and carried into adult life—a curious case of adult retention of an organ that was originally transformed and developed precociously for larval use. That a medusoid gonophore bearing a sexual manubrium can lose this manubrium and be specially developed for swimming is proved by the transformation of gonophores into special swimming nectophores in the eudoxids of forms like *Diphyes dispar*, *D. bojani* and *D. chamissonis*.

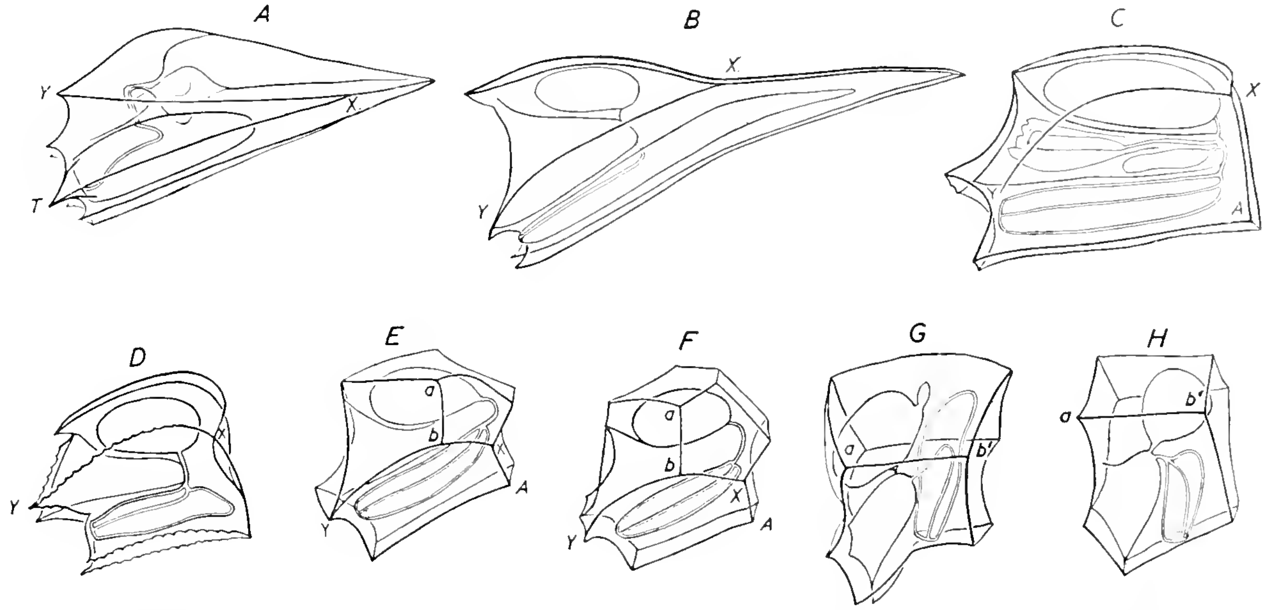
LARVAL AND DEFINITIVE NECTOPHORES

From a study of the ontogenies of many calycophore species of the genera *Rosacea*, *Hippopodius*, *Vogtia*, *Chelophyes*, *Muggiaea* and *Galetta*, we can deduce that as successive nectophores are budded off, so in the course of evolution they have become more and more specialized. For instance, the second definitive or adult (posterior or inferior) nectophore of *Chelophyes appendiculata* is very unlike the first definitive one, which replaces the original, caducous larval one. This type of ontogeny is typical

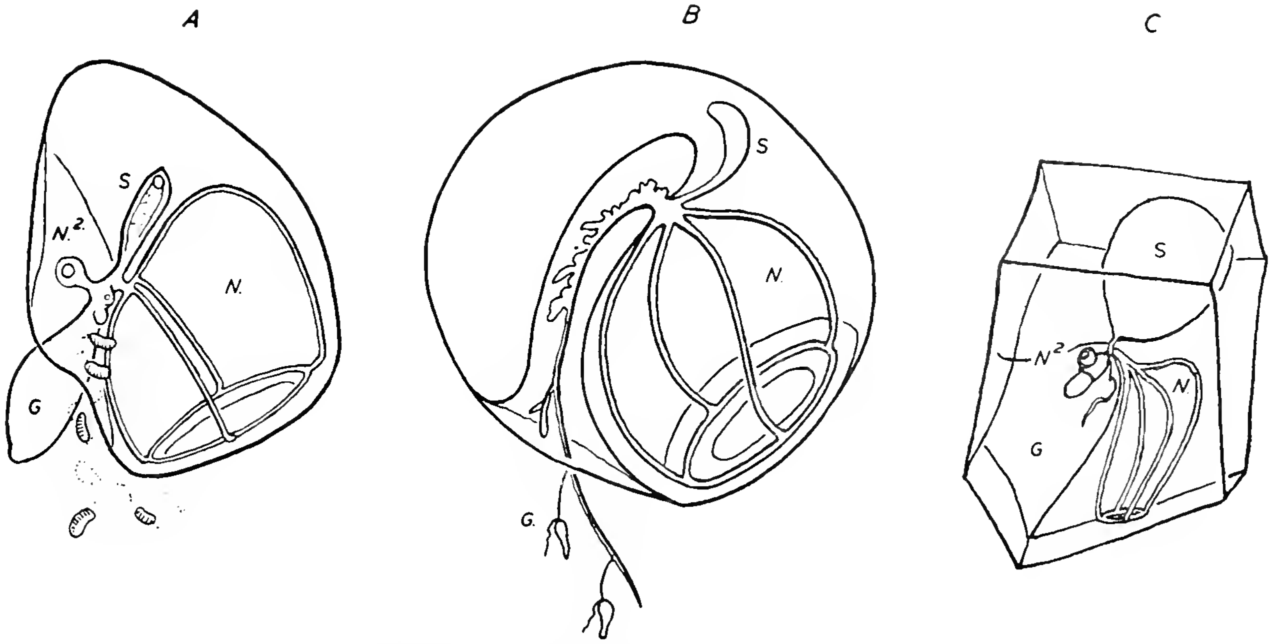
---

[1] The expression 'Athorybia larva' is used, not for the larva of *Athorybia rosacea*, but for the larvae of Physonects like *Agalma* spp., at the stage when they look rather like miniature specimens of *A. rosacea*.

of diphyine Diphyidae, but we know little of the ontogeny of any species of the Diphyidae Tribus-Intermedia of Moser, or of the Abylidae.



Text-fig. 1. Phylogeny of Abylids. Anterior nectophores (in position for horizontal progression) arranged in sequence to suggest evolutionary trend. Fig. 1 H will be seen, on comparison with Text-fig. 2, to resemble larval forms. A, *Chuniphyes multidentata*; the tooth *T* and ridge *XT* are missing in subsequent forms; B, *Ceratocymba sagittata*; C, *Ceratocymba leuckartii*; D, *Ceratocymba dentata*; E, *Abyla trigona*; F, *Abyla haeckeli*; G, *Abylopsis tetragona*; H, *Bassia bassensis*. Ridges *XY* and *ab* respectively are homologous. Ridge *ab*^{1} is an extension of ridge *ab*. Ridge *XA* in C, E and F is homologous.



Text-fig. 2. A, The larval 'calyconula' (*Muggiaea atlantica*, after F. S. Russell) representative of many Calyconects, compared with B, *Sphaeronectes* sp., and C, the anterior nectophore of *Bassia bassensis*. *N*, larval nectophore; N^2, first definitive nectophore; *S*, somatocyst, *G*, gastrozooid.

In tentatively reconstructing a phylogenetic sequence of forms, and in crudely using present-day forms as some sort of guide, it is often difficult to decide in which direction evolution has proceeded. So, for instance, the present-day species of the last two groups mentioned above may be arranged provisionally as a sequence, which suggests that evolution either started or ended with a *Bassia*-like form, as the first diagram (Text-fig. 1) shows. But there are to be found in the plankton very young stages of the anterior nectophore of Abylines and Abylopsines with a single gastrozooid, which suggests that they are larvae. I have accordingly arrived at the tentative conclusion that the anterior nectophore of Abylids is the persistent larval nectophore, and that the anterior nectophore of *Bassia* represents an initial rather than a late stage in evolution. It may be compared in the second diagram (Text-fig. 2) with larval nectophores of other Calycophorae, and with the nectophore of *Sphaeronectes*. I have bred one species of *Sphaeronectes* at Villefranche, and it is evident that the adult nectophore is the persistent larval one. It is interesting then, to see that although, as Garstang pointed out, the pioneers and the writer of one modern text-book, Moser, misconstrued the structure of *Sphaeronectes* as representing a medusa with an exumbral manubrium, they were not far wrong in thinking it was the nearest approach to an archetype of the Siphonophora, since the adult is at any rate most like what we imagine the ancestor of the Calycophorae to have been. Perhaps it is a neotenous form, like *Nectopyramis diomedeae*.

BUDDING ZONES

It is evident from a fresh study of living and preserved post-larvae that in such forms as *Nanomia bijuga*, *Agalma okenii* (Text-fig. 27), and to some extent also in *Physophora hydrostatica*, the budding zones for the nectosome and for the siphosome, where true gonophores are now budded, arise on opposite sides of the larval air-sac (Text-figs. 3–5), although the significance of this is not yet understood.[1] In the adult of *Forskalia edwardsii* the nectophores, siphons (gastrozooids) and gonophores appear all to be budded from the ventral side, as far as I have been able to ascertain. But even in an anaesthetized *Forskalia* there is so much crowding together of the siphosomal buds that it makes observation very difficult. In many Physonects whose siphosomal budding zone I have examined, there are indications that the successive gastrozooid-buds arise in a curved line that lies obliquely to the main axis or stem (Text-fig. 4) as in the nascent lobe of *Physophora hydrostatica* and in *Athorybia rosacea* (Text-fig. 5). Further work is needed on this point, for in both species of *Rhizophysa*, a contracted specimen shows that, though the budding zone of cormidia has always been thought to be single and ventral, it is only very close to the start of the budding zone that this can be seen to be true. As successive gastrozooids move distad they shift alternately to the right and left sides, leaving the gonophores between in the mid-ventral meridian. It is only further down the stem that they secondarily appear to arrange themselves in a single meridian again.

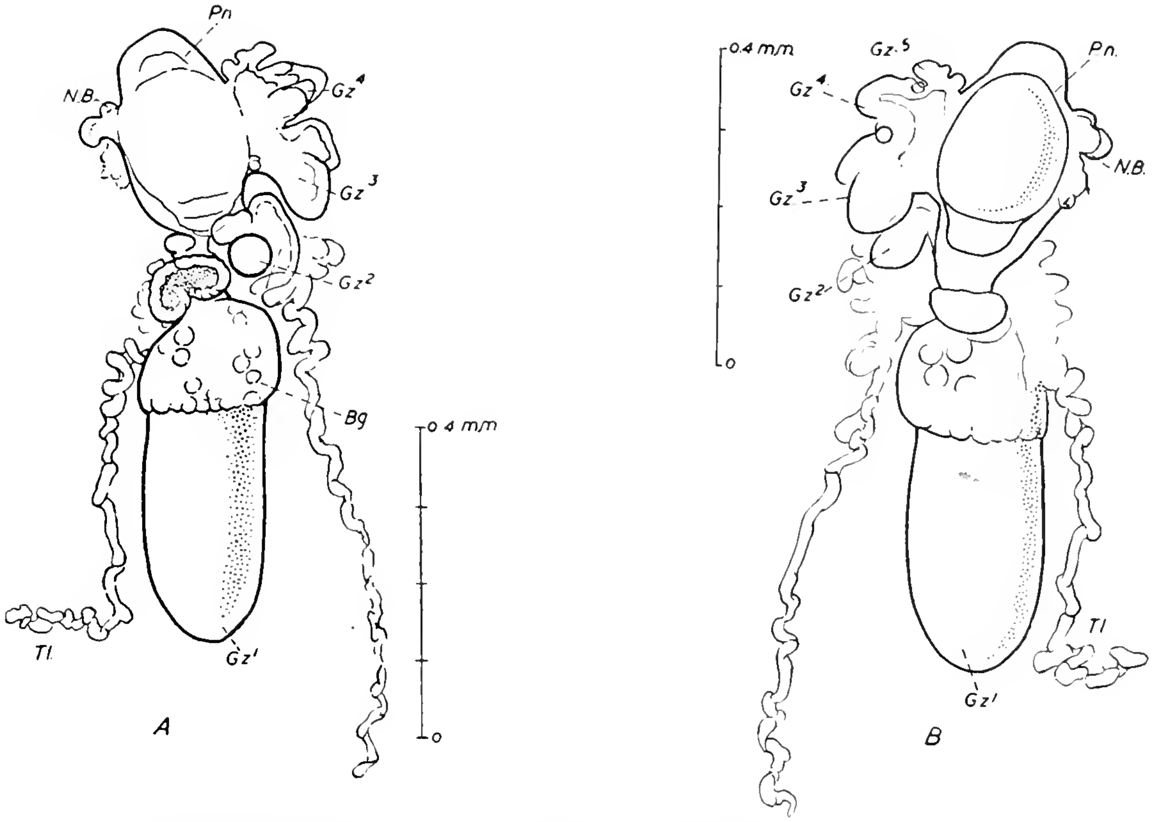
Although, as I shall show below, it is possible theoretically to derive the calycophoran budding arrangement from that of the Physonectae, no one, as far as I am aware, has drawn attention to the true nature of these budding arrangements and to the striking difference between the relationships of siphosome to nectosome in the two groups.

In a mature, long-stemmed Physonect such as *Nanomia* (*Stephanomia*) *bijuga* and *Stephanomia rubra* (originally known as *Agalma rubra* Vogt), the youngest proximal part of the siphosome is distal to the oldest part of the nectosome, so that the two parts of the stem must have increased in length in the same direction; and the budding zone of the siphosome must have been carried distad (in an oral direction) in the course of growth from the larval stage, with the result that nectosome and siphosome form a single pendant stem, and the nectosome separates the two budding zones.[2] Garstang's description of the arrangement (1946, pp. 106, 147) is misleading and gives the impression that the two budding zones lie close together between nectosome and siphosome in Physonectae—a statement which is true of Calycophorae but not of Physonectae.

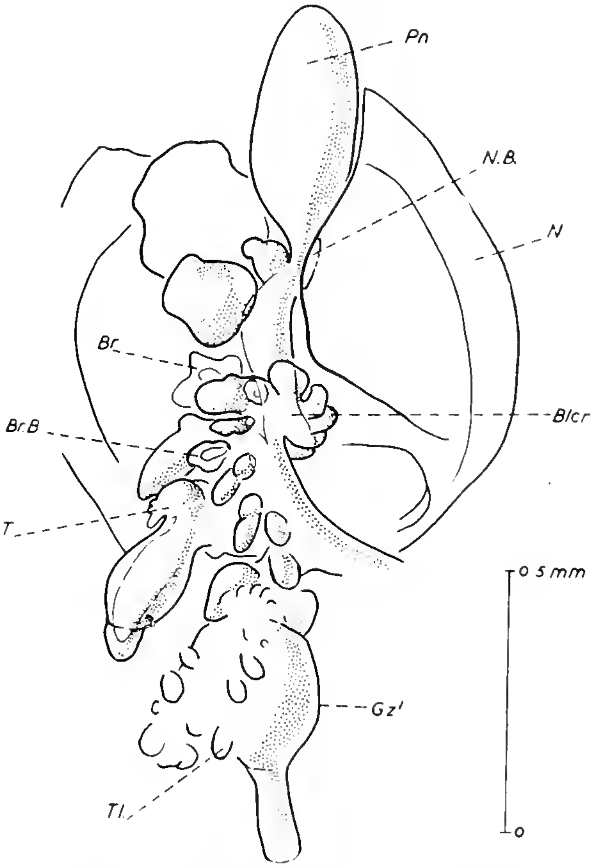
---

[1] Metchnikoff (1874) figured the two budding zones on opposite sides of the stem in the larvae of *Sulculeolaria quadrivalvis* ('*Epibulia aurantiaca*'), pl. 7, figs. 12–14, and in the post-larva of *Agalma elegans* ('*A. sarsii*'), pl. XI, fig. 2. Chun (1897*a*, fig. 6*c*) figured the two zones in a larva of *Hippopodius hippopus*.

[2] See frontispiece.

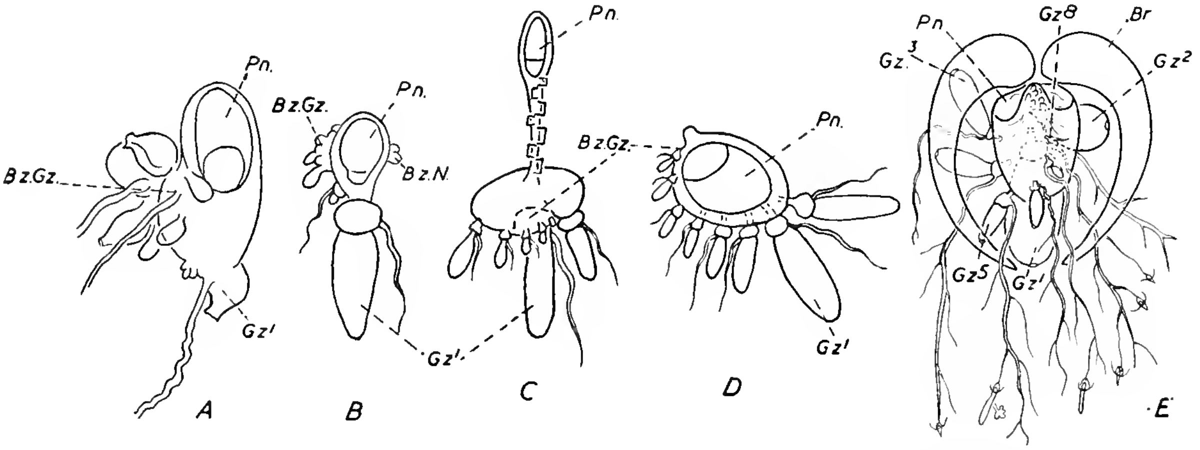


Text-fig. 3. Larva of *Nanomia bijuga* captured at the surface at Villefranche, 17 June 1949, to show budding zones for stem-groups and nectophores (*N.B.*). *Gz.*^{1}, protosiphon; *Gz.*^{2}, reduced secondary siphon budded from region near protosiphon; × 103.



Text-fig. 4. Upper part of young specimen of *Nanomia bijuga* taken at Villefranche, 0 m., 23 June 1949, to show budding zones of nectophores and of stem groups on opposite sides of stem. × 69.

The calycophoran condition is best seen in the Prayids and in the Hippopodiids. Here the budding zones arise and remain close to each other, and the increase in length of nectosome and siphosome takes place in opposite directions. This is particularly noticeable in Hippopodiids, where the region adjoining the joint budding zones forms an upper, progressively twisting loop, and the nectosome forms a spiral-shaped, pendant housing (hydroecium) for the siphosome, which hangs down inside and is retractable within it. In the early stages of Hippopodiid growth the larval nectophore is attached above the joint growing-zone, but is later cast off.



Text-fig. 5. A, larva of *Physalia physalis* (after Okada, 1932) for comparison with B, larva of *Nanomia bijuga*, C, young *Physophora hydrostatica* (diagrammatic) after elongation of nectosome, and D, adult *Athorybia rosacea* (diagrammatic), E, diagrammatic ventral view of D to show the succession of gastrozooids. In all four species there is a terminal protosiphon Gz^1, one or more secondary gastrozooids in a nearby group and a separate budding zone *Bz.Gz.* for the main succession of gastrozooids.

Leaving out of account the larval Hippopodiid nectophore, which is specialized precociously to support the bud-colony, it would be possible theoretically to derive the Hippopodiid condition from that of the long-stemmed Physonect by imagining that with the disappearance of the pneumatophore, the pedicel or foot-stalk of the first nectophore grew continuously in length like that of the protosiphon (first gastrozooid), and that each successive nectophore was budded from the foot-stalk of the one before. Thus the nectosomal budding zone would remain near the siphosomal one, instead of being carried upwards further and further away from it as it is in Physonectae. In this way the lengthening of nectosome and siphosome in Calycophorae would take place in opposite directions instead of in the same one (cf. frontispiece).

In both Prayids and Diphyids the definitive nectophores are reduced to a number which varies between four and one, but the arrangement of budding zones is difficult to see because it is not easy to anaesthetize the stem in that region, so that details are obscured by overcrowded buds.

PHYSONECTAE: PRIMITIVE OR DERIVATIVE

Once having been evolved, it is evident that the nectophores of Calycophorae and Physonectae are homologous structures, although the situation in Calycophorae is complicated by what Garstang supposes to be the addition of a bract, now represented by the somatocyst. The relationship of the budding zone of the nectophores with that of the siphosome in the two groups was discussed above. We now have to decide which group, Physonectae or Calycophorae, is primitive and which derivative. Garstang published the view which I myself have always held, namely, that the Physonect ancestors appeared first. In text-books the order in which the groups are dealt with implies that they appeared last. As Garstang said, it is the Calycophore which has undergone the most radical change, and it may even be that calycophoran larvae have discarded, in favour of a precocious nectocalyx, a previously possessed aboral float. He quite justifiably trounced the systematists for not having noticed the significance of the atrophy of the anterior end of the larval planula in Calycophorae. Moreover, although the early development of Hippopodiids is still not well known,[1] probably because it takes place in deep water, Metchnikoff's figures of early stages seem to indicate that the larval nectophore of *Hippopodius* is in fact produced by the aboral (anterior) part of the planula. I reminded Garstang of this some time after the publication of his paper, but by then he was approaching the end of his life's work and felt unable to go into the matter again.

The reduction in number and kind of appendages in the Calycophorae and their detachment in the form of highly specialized, free-swimming eudoxid groups is almost certainly an evolutionary advance, and their significance lies in the fact that this arrangement tends to increase the chances of cross-fertilization with all its attendant advantages. Also, the fact that calycophoran species are so much more numerous than physonect ones would suggest that the evolution of eudoxids had been followed by deployment of the group. And judging by the long tubular nectosac of the posterior nectophore of *Ceratocymba dentata* and the complex structure of the gonophores of its eudoxid, one would certainly think that evolutionary progress had gone furthest in the Calycophorae.

In considering which group is derivative, however, it has to be borne in mind that in Physonects the polyps are of two kinds, as Vogt realized long ago, each with a specialized function. First, there is the sterile gastrozooid with a large nematocyst factory (basigaster) for the highly evolved, branched tentacle. Secondly, there are the sexual palpons (with minute basigaster and simple tentacle), some of which bear at their base a prominence of varying length that carries the sexual medusae. This prominence ('stalk of the gonophore') is obviously not itself a polyp or gonopalpon because it has no tentacle: it is part of the base of a palpon, and is quite short as a rule in the male gonophore. In the Calycophorae, on the other hand, the gonophores generally arise from the base of polyps of the highly evolved, gastrozooid type. Does the absence of the palpon-type of sexual polyp in the Calycophorae mean that reduction has taken place, or does the presence of the gastrozooid type of sexual polyp, with a highly evolved kind of tentacle mean that in this respect Calycophorae are an advance on the Physonectae?

LARVAE

Since Garstang wrote his valuable thesis I have seen post-larvae of three forms related to *Hippopodius hippopus*, namely *Vogtia glabra*, *V. serrata*—also figured by Moser (1925)—and *Rosacea plicata* (see pp. 73–77). A study of these has convinced me that the adult *Nectopyramis diomedeae* is a neotenous form closely resembling in basic plan all these post-larvae. The Hippopodiids seem to have some characters more primitive than those of *Rosacea*.

CLASSIFICATION

The classification given by Moser (1924*b*) in Kukenthal's *Handbuch* almost completely obscures the natural relationships of the Siphonophora and should not be followed.

Libbie Hyman's text-book (1940) will be very widely used. Her classification of Siphonophora (pp. 370, 475) is:

Order *SIPHONOPHORA*
  Suborder CALYCOPHORAE
  Suborder PHYSOPHORIDA
    Group PHYSONECTAE
    Group RHIZOPHYSALIAE
    Group CHONDROPHORAE

---

[1] I failed in my attempts at Villefranche to breed Hippopodiid larvae (see Systematic Notes, p. 77).

The tentative scheme outlined by Garstang (1946, p. 190) treats the Chondrophora and the Siphonantha as two suborders:

I DISCONANTHA—Order *CHONDROPHORA*
II SIPHONANTHA
  A PHYSOPHORIDA
    (1) CYSTONECTA
    (2) AMPHINECTA (= PHYSONECTAE Haeckel)
  B CALYCOPHORIDA

On grounds of priority Eschscholtz's old name Physophorae should perhaps be retained in preference to Garstang's new one Physophorida, Haeckel's old name Physonectae for Amphinecta, and Calycophorae for Calycophoridae.

I doubt whether Garstang's Cystonecta (= Rhizophysaliae Chun) and Amphinecta (= Physonectae Haeckel) are more closely related to each other than are his Amphinecta and Calycophorida (= Calycophorae Leuckart). And I believe that the Chondrophora are as distantly related to the Siphonophora as the Margelopsid genera *Pelagohydra*, etc. So the outline of the revised classification I have adopted is:

Order *CHONDROPHORA* (Chamisso & Eysenhardt, 1821)
  = *DISCONANTHAE* Haeckel, 1888
  Genera *Velella*, *Porpita*, *Porpema*

Order *SIPHONOPHORA* (Eschscholtz, 1829, part)
  = *SIPHONANTHAE* Haeckel, 1888

  Suborder CYSTONECTAE Haeckel, 1888
    = 'PNEUMATOPHORIDEN' Chun, 1882
    = RHIZOPHYSALIAE Chun, 1897

  Suborder PHYSONECTAE Haeckel, 1888
    = PHYSOPHORAE Eschscholtz, 1829 (part)

  Suborder CALYCOPHORAE Leuckart, 1854

[Order *HYDROIDA*
  Suborder ANTHOMEDUSAE
    Family MARGELLOPSIDAE
      Genera *Pelagohydra*
        Margelopsis (*haeckeli*)
        Climacocodon]

Much more work and consideration is needed before a sound and detailed classification of Siphonophora can be arrived at, but for the sake of planktonologists and others who handle these animals, the following very tentative arrangement of Calycophoran genera is suggested. The first genus contains what are probably the most simply organized siphonophores, and the last the most highly evolved.

Suborder CALYCOPHORAE

  Family 1. SPHAERONECTIDAE
    Sphaeronectes

  Family 2. PRAYIDAE
    Nectopyramis
    Rosacea

- Family 2. PRAYIDAE (*cont.*)
  - *Praia*
  - *Desmophyes*
  - *Lilyopsis* (see p. 88)
  - *Stephanophyes*
  - *Amphicaryon*
  - *Marescarsia* gen.n. (see p. 97)
- Family 3. HIPPOPODIIDAE
  - *Hippopodius*
  - *Vogtia*
- Family 4. DIPHYIDAE
  - Sulculeolariinae
    - *Sulculeolaria* (= *Galeolaria*, *Galetta*)
  - Diphyinae
    - *Lensia*
    - *Muggiaea*
    - *Chelophyes*
    - *Eudoxoides*
    - *Dimophyes*
    - *Diphyes* (*dispar*, *bojani*, *chamissonis*, *antarctica*. These are probably proto-abylids)
  - Chuniphyinae (these are probably proto-abylids)
    - *Chuniphyes*
    - *Thalassophyes*
    - *Crystallophyes*
    - *Heteropyramis*
    - *Clausophyes*
- Family 5. ABYLIDAE
  - Abylopsinae
    - *Abylopsis*
    - *Bassia*
    - *Enneagonum*
  - Abylinae
    - *Ceratocymba*
    - *Abyla*

The relationships of the Cystonects are not at all certain. The gonophores of *Rhizophysa* arise in a longitudinal meridian on the lower part of the air-sac, and are flanked on either side by a meridional row of gastrozooid buds. Distally they all come to occupy a single meridional row. Each branchlet of the gonophore has a subterminal medusa-bud in which, presumably, the eggs are developed. But the early development of cystonects is quite unknown, except for *Physalia*. Hitherto they have been placed with the Physonectae because in both groups there is an air-sac or pneumatocyst. But it seems possible that the Physonectae have not passed through a Cystonect stage in their phylogeny, and that the Calycophorae may be more closely related to the Physonectae than either group is to the Cystonectae. The larva of *Physalia* would certainly seem to indicate a much earlier origin of the Cystonectae than that suggested by the larvae of Physonectae or of Calycophorae, namely at an ancestral stage in which nectophores had not developed (Text-fig. 5 A).

For the purpose of this report I have placed *Athorybia*, *Melophysa* and *Physophora* at the head of the list of Physonectae because they are probably neotenous forms, but the relationships between the others are not understood. In the list of Calycophorae, about the relationships of which, one with another, Garstang was silent, *Sphaeronectes*, as the ancestral type, comes first. It is followed by the Prayidae, which appear to be primitive in that the adults resemble the larvae fairly closely in their organization. The Hippopodiidae develop heteromorphous definitive nectophores, but their larvae are very similar to those of the Prayidae. These are followed in my list by Moser's group, the Tribus Diphyidae Intermediae, which appears to lead on to the genus *Diphyes* (*sensu stricto*) and to the Abylidae. The relationships *inter se* of the remaining Diphyidae are unknown, except that the species of Galettinae seem to be related to one another. It still remains to be ascertained whether, as I suspect, there is a fundamental difference between those species—included in the three groups Tribus Diphyidae intermediae, *Diphyes* (*sensu stricto*) and Abylidae on the one hand, and the remaining Diphyidae on the other, the suspected difference being, that in the former three groups, the larval nectophore is retained as the anterior, definitive one, whilst in the last group it is caducous and is followed by one or more heteromorphous ones.

NUMBER OF SPECIES

In his famous 'Challenger' Report Haeckel dealt with about sixteen species taken by 'Challenger', eleven of them very common, and two not seen since. In that report he described and figured altogether about thirty distinct species of Siphonophora. Haeckel listed 240 so-called species, of which not more than fifty are recognized as distinct to-day. Twenty-six of these 240 he called new species, which he promised to describe later. Four of them prove to be synonyms for known species and the rest are *nomina nuda*, since Haeckel never did describe them.

No one, as far as I know, has commented on the fact that there are so few species—something in the order of 150—of Siphonophores, which occur in great abundance in most seas. Is the small number of species due to the fact that so many of the species have very wide distributions and so consist of virtually single, interbreeding populations?[1] There is a second remarkable phenomenon, namely the existence of many genera with 'pairs' of species such as *Abylopsis tetragona* and *A. eschscholtzii*; *Diphyes dispar* and *D. bojani*, *Rosacea cymbiformis* and *R. plicata*, *Chelophyes appendiculata* and *Ch. contorta*, *Agalma okenii* and *A. elegans*, *Eudoxoides mitra* and *E. spiralis*, *Chuniphyes multidentata* and *Ch. moserae*, *Nanomia bijuga* and *N. cara*, *Rhizophysa filiformis* and *Rh. eysenhardtii*. The number of monotypic genera is also large, *Apolemia*, *Lychnagalma*, *Erenna*, *Nectalia*, *Physophora*, *Athorybia*, *Melophysa*, *Dromalia*, *Rhodalia*, *Physalia*, *Porpema*, *Porpita*, *Velella*, *Enneagonum* and *Bassia*. These two categories account for thirty-five out of the total of 150 species, but the analysis cannot be completed at present. There has appeared recently a note by C. B. Williams (1951) on the relative sizes of genera in the classification of animals and plants. 'One general principle', he said, 'of a mathematical nature, has several times been pointed out and discussed. In almost every classification the number of genera with one species is greater than with two, the number with two greater than with three, and so on; so that if we plot the classification in the form of a frequency curve, we get a "hollow curve" somewhat resembling a hyperbola.' He then proceeded to show that we can only recognize as real the scheme of relative specific and generic relationships commonly used by good systematists if we bear in mind that the point in time-past, at which to 'draw the line' or make

---

[1] If it can be shown that waste products play some part in causing mutation, it seems possible that there may be a connexion between the small number of species and the fact that waste products must quickly diffuse out into the surrounding sea-water.

a cross-section to demonstrate these relationships, is a matter of opinion, and that there must be consistency in the choice. Even if the phylogeny of a number of species were known, it might be quite correct to adopt any one of a number of generic groupings, according as to where in the past the cross-section was taken. Judge, then, of the systematists' difficulty when the phylogeny is not known.

THE PIONEER WORK OF HENRY B. BIGELOW

Many additions have been made to our knowledge of the Siphonophora since Bigelow, forty years ago, published his famous 'Albatross' Report, which has been a key-work on the group ever since. It was a study of this delightful work that first lured me to examine these animals and to build up an enormous collection at the British Museum (Nat. Hist.). Hardly a day passes when it is not necessary to refer to the work again. If in my systematic notes I often appear to criticize this classic, it is only with the desire to build firmly on sure foundations. Bigelow's figures of siphonophore structure in that, and subsequent reports, are unrivalled. Only he and Dr Mary Sears know how painstakingly he worked upon them. To orientate these animals, whose density is so nearly that of the media in which they have to be examined, and to hold them in position without movement for drawing is a major difficulty in the study of the group.

GENERAL CONCLUSIONS

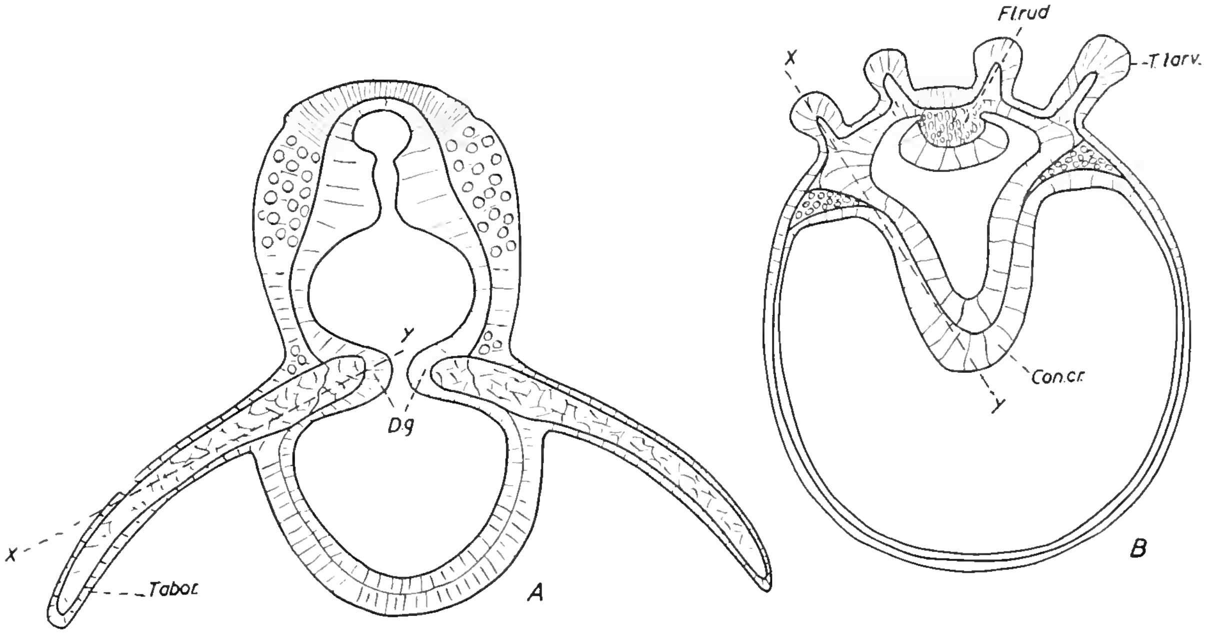
To sum up my tentative conclusions on the phylogeny of Siphonophora—reached, it has to be admitted, without full consideration of either Rhodaliids or Apolemids—there is evidence that leads to the deduction that siphonophore ancestors, like the primitive Trachylines, had an adult medusoid stage (medusoid gonophores, nectophores), as well as a larval polypoid one (present-day larvae, gastrozooids, palpons). In the course of evolution, and after the adoption of the budding process, the two phases instead of following one another, as in scyphomedusan and trachyline metamorphosis, appeared simultaneously in one and the same bud-colony (gastrozooids and gonophores) as, for example, in *Agalma*.

After the development of an aboral organ as a gas-secreting gland (pneumatophore), this gland was once again lost (Calycophorae), when medusoid gonophore-buds were developed precociously in the larval stage as swimming organs. The precociously developed and functionally altered (gonophore → nectophore) larval organs were then carried into adult life and improved upon as adult swimming organs (nectophores). But some of the larvae of these bud-colonies never adopted the device of using a precociously developed gonophore as a swimming organ and so the adults (e.g. Cystonects, and *Athorybia rosacea*) do not swim to-day by jet propulsion.

It should here be emphasized that this interpretation of a very complicated evolutionary story bears no resemblance to the old classical 'medusome' theory of Haeckel's, which was exploded by Garstang. It follows that acceptance of the conclusions set forth above is compatible with finding in Siphonophora much evidence of neoteny (*Physalia*, *Nectopyramis diomedeae*, *Sphaeronectes*, *Athorybia*). This phenomenon probably affords the explanation of the existence of both short-stemmed forms (brachysteles) and long-stemmed forms (macrosteles) among the Physonectae, the macrosteles having increased in length and the brachysteles having failed to lengthen in one or two directions. There seems to be every chance that in the future other unspecialized larvae will evolve on new neotenous lines.

We may, perhaps, in some ways compare the story of the siphonophore nectophore with that of the tail of the Ascidian tadpole, which appears to have been developed as a larval organ, is lost at metamorphosis by Ascidians, but is retained and developed in the adult stage of other Chordata. In the siphonophore story, of course, the organ (gonophore) adapted specially for larval use (as a nectophore) was originally an adult 'organ', or rather the adult (medusa) phase itself, produced by budding, and developed in the larva precociously (by heterochrony). It was then developed still further in the adult for the same purpose (swimming). Some adult Physonects took to swimming by jet propulsion, it might almost be said, because of an 'afterthought' on the part of an ancestral larva.

The old suborder Disconanthae contains three forms *Velella*, *Porpita* and *Porpema* that are really the floating Tubulariid hydroid-phases of inconspicuous adult Codonid medusae known as *Chrysomitra*. There is nothing in their morphology in the least like the Siphonanthae, and it is possible that their pneumatophore has been acquired independently. They form a separate Order Chondrophora. Garstang (1946) interpreted the *Conaria* larva, but omitted reference to important papers by Delsman (1923) on the *Conaria* larva of *Porpita* and its development, and by Leloup (1929), who, after studying *Velella* at Villefranche, pointed out the homology between the *Conaria* larva and the actinula of *Tubularia larynx*, showing that the peculiar 'crimson cone' of *Conaria* corresponded with the 'gastric diaphragm' of *Tubularia*. This work of Leloup appears not to have been known to Garstang. Text-fig. 6 will make this point clear. There is no need to endeavour, as Garstang did, to 'close the gap' between Disconanths and Siphonanths. The old order Siphonophora without doubt had a double origin, as Haeckel realized.



Text-fig. 6. A, Actinula of *Tubularia*. After Leloup (1929). B, Conaria of *Porpita*. Based on Delsman (1923, figs. 16, 17, 18). XY = homologous planes.

As to the position of *Pelagohydra*, one is struck by the origin of the tentacles between the axial parenchyma in the meshes between the endoderm canals, from which the gonophores (gonozooids now reduced) spring. In Chondrophora Bigelow's sections show that the tentacles arise from the canals themselves. The difficulty of exactly homologizing the structure of the two forms was stressed by Garstang (1946, p. 126), and of course *Pelagohydra* has no pneumatophore. Garstang maintained that the 'float' of *Pelagohydra* represents the hydrocaulus of *Corymorpha*, on account of the position of the gastric diaphragm, and that the gonophores are cauline. In the Chondrophora the gonophores are on the oral cone. Possession by hydroids of cauline gonophores is probably a later evolutionary stage than that of oral ones and in the opinion of my colleague Dr W. J. Rees leads on to a hydrorhizal position.

The Chondrophora appear to be aberrant, pelagic, tubularian Anthomedusae. They have lateral (radial) extensions of the walls of the aboral chamber, the edge of the extension being provided with mucus glands. They have radial extensions as well of the oral cone, which bears a large number of gonozooids. They possess too, rings of aboral tentacles, and large floats invaginated into the aboral end. They differ widely from Siphonophora, though the two groups, no doubt, had a common ancestor. The Chondrophora are so much more aberrant than the somewhat similar pelagic tubularian Margellopsinae, that they should be treated, perhaps, as a separate order, neither as Hydroida, with which Vogt, Kölliker and Agassiz were inclined to associate them, nor as Siphonophora, as has for long been customary.

TERMS USED IN THIS REPORT

I have used the same terms as those used by Bigelow (1911*b*) in his 'Albatross' report. A long-stemmed Agalmid is divided into the *nectosome* above, and the *siphosome* below. In the early larva or oozooid these two parts occupy opposite sides of the float or pneumatophore.[1] As growth proceeds the growing point of the nectosome, lying as it does just below the pneumatophore, is carried upwards from the level of the growing point or *blastocrene* of the siphosome, whose oldest *gastrozooid* (*protosiphon*) is thus carried downwards.[2] The outer wall of the *pneumatophore* is called the *pneumatocodon*, and the inner wall the *pneumatosaccus*. Libbie Hyman regards these as the exumbrella and subumbrella respectively of a medusa, a point of view that I hope will be abandoned after reading Garstang (1946) on the subject. The rhythmical contractions of the muscular lining (*nectosac*) of the *nectophores* provides jet-propulsion. The nectophores of the Calycophorae include a *somatocyst* which has vacuolated walls and usually contains a quantity of fat. It is in direct communication with the *stem* and all the buds (*blastozooids*) of the original larva (including the *protosiphon*) or *oozooid*. The whole forms a floating bud-colony of larval-type polyps or *zooids*, to which are added precociously the adult-type medusae or nectophores—for swimming only—without manubrium or mouth, and later the *gonophores* with manubrium but without mouth. At the base of the feeding zooid or *gastrozooid* is a swollen part, the basigaster, filled with growing *nematocysts*, from which arises the single *tentacle*. Its lateral branches or *tentilla* are provided with complicated nematocyst batteries or *cnidosacs*. The cnidosac is attached to a pedicel of the tentillum by two structureless, much folded, elastic bands (*angle-bands*). From this point a broad band (*cnidoband*) of probably adhesive nematocysts, often spirally coiled, is doubled back towards the pedicel and partially or wholly covered by an *involucre*. Distad to the attachment of the angle-bands may be a central *ampulla* and a pair of *lateral horns*. In the Calycophorae there is usually a distal patch of pear-shaped *nematoblasts*, and a (sub-terminal) *terminal filament* bearing numerous nematocysts. Flanking the inner end of the cnidoband of an unexploded *cnidosac* is a series of large penetrant nematocysts. Upon appropriate stimulation, whose nature, in spite of experiment, is still not understood, the inner end of the cnidoband is flung forward, its outer end anchored to the pedicel by the *elastic* bands.

The Calycophorae appear to have lost the aboral end of the larva after the precocious formation of nectophores. They now have no pneumatophore. Their nectophores differ from those of the Physonectae in that they include a *somatocyst*, about the significance of which there has been much speculation. Old authors sometimes referred to the other type of nectophore, found in Physonectae, as *pure nectophores*.

There is only one other type of zooid commonly called the *palpon*. In Physonectae it is generally much less developed than the gastrozooid. It does not feed, though its terminal end may occasionally open. Its basigaster is very reduced, and its tentacle or *palpacle* is simple.

In the Calycophorae there is no such distinction, or in other words there are no palpons. So that either Physonectae possess reduced or undeveloped zooids (palpons) or in Calycophorae the palpons are upgraded to gastrozooids or else have disappeared.

---

[1] Text-fig. 3.

[2] See frontispiece.

Calycophorae have made progress from an evolutionary point of view by freeing the segmentally repeated groups of gastrozooids, *bracts* and gonophores, in the form of *eudoxids*. In some cases one of the gonophores loses its manubrium and becomes an organ for jet-propulsion, the *special nectophore*. Bracts are found in larval Physonectae, and in the adult Physonectae they reach the peak of their development, being present in several ventro-lateral rows on the stem. They are not found in larval Calycophorae, unless their canals are represented by the somatocyst. In adult Calycophorae, as stated above, there is only one bract to each gastrozooid, and it eventually becomes the protective part of the free eudoxid.

Explanation of abbreviations used in figures

Abor.	aboral
Ang.ap.	apical angle
Ang.d.-l.	dorso-lateral angle
Apoph.	apophysis
Bg.	basigaster
Blcr.	blastocrene
Br.	bract
Br.B.	bract-bud
Br.lam.	muscular lamella of bract
B.z.Gz.	budding zone of gastrozooids
B.z.N.	budding zone of nectophores
C.br.	bracteal canal
C.br.d.	dorsal bracteal canal
C.br.s.	semicircular bracteal canal
C.br.spur	bracteal spur-canal
C.br.v.	ventral bracteal canal
C.circ.	circular canal
C.com.	commissural canal
C.d.	dorsal canal
C.d.-l.	dorso-lateral canal
C.desc.	descending canal
C.h.l.	left hydroecial canal
C.h.l.l.	left lateral hydroecial canal
C.h.l.r.	right lateral hydroecial canal
C.h.r.	right hydroecial canal
C.lat.	lateral radial canal
C.long.	longitudinal canal
Cmb.	comb
C.med.long.	median longitudinal canal
Con.cr.	crimson cone
C.pa.	pallial canal
C.pa.(som.)	pallial canal
C.ped.	pedicular canal
C.rad.	radial canal
C.rad.d.	dorsal radial canal
C.rad.lat.	lateral radial canal
C.rad.v.	ventral radial canal
d.	dorsal
D.g.	gastric diaphragm
Eud.Br.	eudoxid bract
F.con.	convex facet
F.d.	dorsal facet
F.d.-l.	dorso-lateral furrow
F.h.	hydroecial fold
Fl.rud.	rudiment of float
Go.	gonophore
Gz.	gastrozooid
Gz.rd.	gastrozooid (reduced)
Gz.m.	mouth of gastrozooid
H.	hydroecium
H.op.	hydroecial opening
L.musc.	muscular lamella
Lob.ant.-l.r.	right antero-lateral lobe
Man.	manubrium
M.b.-l.	baso-lateral margin
N.	nectophore
N.ant.	anterior nectophore
N.B.	bud of nectophore
Nch.	notch
Nec.	nectostyle
N.def.	definitive nectophore
Nem.	nematocysts
Nem.p.ect.	ectodermal patch of nematocysts
N.larv.	larval nectophore
N.post.	posterior nectophore
Ns.	nectosac
Ns.def.	nectosac of definitive nectophore
Ns.larv.	nectosac of larval nectophore
Ns.obs.	nectosac of obsolescent nectophore
N.spec.	special nectophore
Ns.v.	ventral wall of nectosac
Nuc.	nuclei
N.vest.	vestigial nectophore
O.c.	central organ
Ol.	oil
Ost.	ostium
Ov.	ovum
P.	palpon
Pal.	palpacle
Phc.	phyllocyst
Pl.M.	mouth-plate
Pn.	pneumatophore
Pr.dist.	distal process
Pr.lat.	lateral process
Prom.	prominence
Proj.ang.	projecting angle
Prot.ch.	chin-shaped protuberance
R.ap.	apical ridge
R.ap.-lat.	apico-lateral ridge
R.buc.	buccal ridge

R.d.	dorsal ridge
R.d.-l.	dorso-lateral ridge
Ret.	rete
R.inf.lat.	inferior lateral ridge
R.l.	left ridge
R.lat.	lateral ridge
R.lat.as.	asymmetrical lateral ridge
R.lat.l.	left (asymmetrical) lateral ridge
R.long.	longitudinal ridge
R.or.lat.	oral lateral ridge
R.post.	posterior ridge
R.r.	right ridge
R.vert.lat.	lateral vertical ridge
Som.	somatocyst
Som.N.def.	somatocyst of definitive nectophore
Som.N.larv.	somatocyst of larval nectophore
spx.	spadix
Str.m.	mamma-like structure
Surf.art.	articulating surface
T.	tentacle
T.abor.	aboral tentacle
Tl.	tentillum
T.larv.	larval tentacle
To.	tooth
To.d.	dorsal (median) tooth
To.int.	internal tooth
To.l.	left dorso-lateral tooth
To.r.	right dorso-lateral tooth
To.v.l.	left ventral tooth
To.v.r.	right ventral tooth
V.	ventral
Vel.	velum
W.hyd.l.	left hydroecial wing
W.hyd.r.	right hydroecial wing
W.lat.	lateral wing
XB	growing apex of pallial canal

SYSTEMATIC AND BIOLOGICAL ACCOUNT

CHONDROPHORA

Porpita Lamarck, 1801

Forty years ago Bigelow (1911*b*) reviewed the question of generic and specific limits in Porpitidae. I do not think further progress will be made by any survey of literature, but only by the fresh examination of all growth stages from both Atlantic and Pacific. On *a priori* grounds it seems unlikely that species of these surface animals from tropical and sub-tropical waters would be isolated in one or other ocean—that is, if our knowledge of distribution of other siphonophores, and if Sewell's (1948) views on transportation of planktonic copepods are any guide. Haeckel recognized no less than six genera and twenty species of Porpitids. Bigelow regarded many of Haeckel's forms as growth stages and provisionally recognized two genera and five species. Bigelow considered five points in the anatomy of *Porpita*: (1) the tubercles on the upper surface of the disc, (2) the arrangement of the stigmata, (3) comparative width of the limbus, (4) radial or branching arrangement of the canals of the limbus, and (5) the number of stalked tentacular nematocyst clusters on the tentacles, and from a study of these anatomical points, he came to the conclusion that an Atlantic form *Porpita umbella* could be distinguished from a Pacific form *P. pacifica*; but he doubted if a Pacific and Atlantic species of *Porpema*—the only other genus he recognized—could be distinguished.

I am inclined to think that there are only two Porpitids, *Porpita porpita* (L.) and *Porpema prunella* (Haeckel, 1888*b*), and that one genus *Porpita* is enough to contain them.

Porpita porpita (Linné), 1758.

(Synonymy in Bigelow, 1911*b*, p. 353.)

Porpita umbella (O. F. Müller), 1776.

(Synonymy in Bigelow, 1911*b*, p. 352.)

Porpita pacifica Lesson, 1826.

(Synonymy in Bigelow, 1911*b*, p. 333.)

Seven specimens were taken at the surface at 'Mabahiss' Stations 39 (see Chart, p. 10) and 99. It was on Indian Ocean material that Linnaeus based his *Medusa porpita*, to which the present material probably belongs. So far, a critical comparison of Indian Ocean, with Atlantic or Pacific material appears not to have been made, although Bigelow (1904) described and figured some from the Maldive Islands. Leloup (1934*b*) identified some taken off the Madras coast, stating that this species is common in the Indian Ocean, but without giving further details. I am unable, without good material of all growth stages from all three oceans, to make the desired critical comparison. Examination of such material and critical descriptions as are available, leads me to suspect that one species only is to be found in all three oceans. If so, it should bear the name *porpita* (Linné.)

A few counts of the stalked tentacular nematocyst clusters of the long rows gave the figure 21–24, and of the short rows 10–13. The numerous tubercles are obvious and have no connexion with the stigmata which are few and become covered not far from the inner edge of the limbus. The radial plications of the surface of the disc are slight. The limbus is comparatively narrow as in *Porpita pacifica*. In a specimen ('Mabahiss', 23. xii. 33, near St. 99) 3·9 cm. in diameter, the limbus measured 3 mm. In another 2·7 cm. in diameter, it measured 2 mm. The canals of the limbus are irregularly arranged and not radial. In all these respects the Indian Ocean and Pacific forms agree.

Velella velella (Linné), 1758.

Velella spirans Forskål, 1775; Chun, 1897*b*.

The development of the *Conaria*-larva, first described by Woltereck (1904, 1905) was interpreted by Leloup (1929) and Garstang (1946); and the further development of the *Rataria*- or *Ratarula*-post-larval stages are now fairly well known. Likewise the young medusae (*Discomitra* Haeckel, 1888*b*, p. 39, pl. 50, fig. 8) from the time when they arise as buds on the walls of the gonozooids to the time when they are shed, are well known. They are of the Tubulariid type, the tentacles, usually undeveloped, bearing four radial canals and four radial, exumbrellar rows of nematocysts. In the youngest stages these rows extend only half-way to the apex, but later reach all the way up. Such *Discomitra* medusae may be compared with the well-known Tubulariid medusae, *Hybocodon prolifer* and *Ectopleura dumortieri*, the earliest stage of the latter having only one tentacle, three and four being developed later on. The possession by *Velella* and *Porpita* of this type of medusa appears to confirm Garstang's view about the Tubulariid ancestry of the Disconanthae (Chondrophora).

Not so well known as *Rataria* and *Discomitra* is an apparently quite different type of medusa *Chrysomitra striata* (Gegenbaur), the genus founded by him in 1857 for a little free-swimming medusa *Phorcynia striata* (not *stricta*) described by Kölliker (1853*a*) with from thirteen to sixteen radial canals and one or two tentacles. This *Chrysomitra* medusa (not larva) is commonly said by writers of text-books to come from *Velella*, but I am not yet satisfied that this has been proved. It possesses exumbrellar nematocyst tracts, but in appearance differs from *Discomitra*. Its direct connexion with *Velella* was not observed by Gegenbaur, but on account of the nematocyst tracts and the 'yellow-cells' in the sub-umbrella in both forms, and the appearance of rudiments of further radial canals growing out from the stomach in some specimens of *Discomitra*, Gegenbaur thought it reasonable to assume their identity. That this is very probable has been shown by the micro-photograph by Ankel (1951) of living specimens of *Discomitra* recently freed by *Velella*. One of the medusae has a single small tentacle of the *Chrysomitra* type, but the rest of the medusae are in the *Discomitra* stage. Metchnikoff (1886) recorded that on two occasions in January and February 1883, he fished at Messina some sexually mature medusae of *Velella* and he gave good figures of the single amoeboid egg, the four testes, the sperm and the medusa itself. The medusa had only four radial canals and a single tentacle. He likened them to Keferstein & Ehlers' (1861) *Rhabdoon singulare*, but left any decision about their identity with Gegenbaur's *Chrysomitra* for future research to decide.

Bigelow (1911*b*) in his review of the genus mentioned that eleven so-called species have been described from the Indo-Pacific. Most recent authors have agreed that there is only one Indo-Pacific species of *Velella* and that it is distinct from the Atlantic one, but Schneider (1898), and Bigelow & Sears (1937) with whom I am inclined to agree, thought it was the same as the Atlantic one. Bigelow (1911*b*) found no features to differentiate more than one Pacific species, but was not prepared to unite it with an Indian Ocean one, because a critical review of Indian Ocean specimens was not then possible; but he believed that the separation of Pacific and Atlantic species was justified, the breadth in proportion to the length being greater in Pacific than in Atlantic specimens: in other respects he could find no constant difference.

Bigelow gave measurements of sixteen shells from the Atlantic and of the same number from the Pacific. The ratio of breadth to length of the Atlantic ones was from 32 to 37%, and of the Pacific ones 44 to 51%. For Mediterranean specimens, more than 8 mm. in length, Bigelow & Sears gave a mean ratio of 38·5%. It is convenient to call the long axis of a specimen of *Velella* the 'N./S.' one, and a specimen in which the sail runs 'N.W./S.E.' is called a 'N.W.' one and the type in which it runs 'N.E./S.W.' a 'S.W.' one.

Station 2669 (W. Mediterranean)			Stations WS 1057, WS 1058 (S. Atlantic)		
Length (mm.)	Breadth (mm.)	Height of sail from apex of liver (mm.)	Length (mm.)	Breadth (mm.)	Height of sail from apex of liver (mm.)
20	9	7	13	6	4
22	10	8	17	10	5
22	14*	10	18	10	6
23	9	9	27	16	8
25	9	9	—	—	—
26	13	9	—	—	—
27	13	8	—	—	—
28	13	10	28	17	9
28	12	10	28	14	11
29	12	8	28	16	10
29	12*	11	—	—	—
30	14	10	—	—	—
30	14	9	—	—	—
31*	14	8	—	—	—
32	15	12	—	—	—
32	15	10	—	—	—
33	15	12	—	—	—
33	12*	12	33	20	12
34	17	12	34	21	13
34	16	11	—	—	—
35	19	10	35	18	9
35	13	10	35	22	12
35	14	10	37	23	12
37	17	14	37	19	12
40	17	14	38	22	13
44	22	13	40	22*	10
45	21	14	41	24	15
Ratio average Br./L. 45%			Ratio average Br./L. 55%		

An asterisk indicates that the measurement is an estimate of an imperfect specimen.

The 'Discovery II' brought back a 'S.W.' specimen from Station 1738 in the South Indian Ocean that measured: length 33 mm., breadth 18 mm., height of sail from apex of 'liver' 9 mm. This gives a ratio of 54·5% for breadth and length.

The 'Discovery' collections also contain a series of twenty-seven 'N.W.' specimens from Station 2669 in the Western Mediterranean, as well as an interesting series of 'S.W.' specimens from Stations WS 1057 and WS 1058 made in the South Atlantic between St Helena and Tristan da Cunha. The ratio L/Br for these two groups of specimens is given in the table on p. 35. Only those specimens fit for measurement are listed.

Bigelow showed that the 'N.W.' condition of the sail was much more common in the Pacific *Velella lata* than in the Atlantic *V. velella*. More data are needed on proportions and direction of sail.

Distribution. In the Atlantic *Velella* extends from Cape Cod to at least 28° S.

Feeding. The specimen from Station 1738 was 'brilliant indigo-blue' in colour when fresh; 'the sail pale purple almost transparent'. Many of its gonozooids had been feeding on crustacea, which I have not attempted to examine or identify, and in many cases the mouths are still open. One gonozooid had extended its mouth to a width of 2 mm. in an attempt to engulf a Calanoid copepod (family Euchaetidae) which measured 2·5 mm. in length (excluding terminal setae).

SIPHONOPHORA

PHYSONECTAE

At least eleven Physonect species are represented in these Indian Ocean collections, an increase of 50% on numbers last reported by Browne (1926). So far, very few Physonects at all have been described and figured to the satisfaction of specialists, and though the systematic work on them is always going on, it is necessary to send this report to press before it has been possible to complete it. Quite apart from the morphological work entailed, the synonymy is very involved, as shown by the classical example of *Agalmopsis elegans* Sars, 1846. Sars himself realized later that he had based his name on two species. A discussion of the matter was published by Bigelow (1911*b*). The two species occur together commonly not only in Norwegian waters but off South-west Ireland and in the 'Celtic' Sea. Unfortunately each component, generally referred to as '*Agalma*' (trifid tentilla) and '*Stephanomia*' (filiform tentilla), has been renamed *sarsii*, the first by Kölliker (1853*b*); and the second by Haeckel (1888*b*) as *Cupulita sarsii*. And finally Bigelow (1911*b*) chose to use the name *elegans* for the minor '*Agalma*' component thinking that the major one was '*Stephanomia*' *bijuga*. My contribution to the discussion is to affirm, on the evidence of the nectophores (Sars, 1846, Tab. 6, figs. 3–4) and of the palpon (Tab. 6, fig. 11), that fig. 1 of both of Sars's plates 5 and 6 represented at the time a new genus and species, a species later redescribed from the Gulf of Maine by Agassiz (1865) and Fewkes (1888*a*) as *Nanomia cara* (see Text-fig. 19). The main concept that Sars had in mind when describing his novelty was the species represented in twenty-four out of twenty-six of his figures. *Agalmopsis elegans* obviously has priority as the name of the species to which they belong, but Haeckel (1888*b*, p. 234) chose to restrict *Agalmopsis* to the other species.

Two short visits to Villefranche have enabled me to study alive in the field six of eleven Physonects found in the Indian Ocean and here reported upon, viz. *Physophora hydrostatica*, *Stephanomia rubra*, *S. bijuga*, *Agalma elegans*, *Athorybia rosacea* Forskål (*non* Bigelow) and *Cordagalma cordiformis*, together with a species of *Forskalia*; and also to study alive the larvae of *Physophora hydrostatica*, *Stephanomia bijuga*, *S. rubra*, *Agalma elegans*, and *Forskalia* sp.

One of these species, *Cordagalma cordiformis* Totton, 1932, must be the smallest of all the Physonects. At Villefranche I found loose nectophores frequently, and some minute, colourless colonies that

I believe to belong to them. A similar stem was associated with many nectophores at one 'Manihine' Station in the Gulf of Aqaba. One of the eleven Indian Ocean Physonects, a new species (see p. 59) is of special interest because of its apparent relationship with the one and only known high-arctic Siphonophore *Stephanomia orthocanna* described by Kramp (1942). Kramp's species is characterized by the straight lateral canals of the nectophores. In the Antarctic there is a third Physonect of this group, also new, and the type species of a new genus which has been named (p. 55) after Mr J. W. S. Marr. It has very characteristic bracts with truncated distal ends and straight lateral canals in the nectophore. To this new genus both *S. orthocanna* and the two new species belong.

ATHORYBIADAE Huxley, 1859

Syn. ANTHOPHYSIDAE Brandt, 1835

Eschscholtz (1829) included in his genus *Athorybia*: (1) *Rhizophysa heliantha* Quoy & Gaimard; (2) *R. melo* Quoy & Gaimard; and (3) *Physsophora* (sic) *rosacea* Forskål. Haeckel (1888*a*) took *Rhizophysa melo* Quoy & Gaimard as the type of a new genus *Melophysa*. I now select *Physsophora* (sic) *rosacea* Forskål as the type of *Athorybia*[1] Eschscholtz. I believe that *Rhizophysa heliantha* Quoy & Gaimard is a synonym of *Athorybia rosacea* (Forskål). The two genera *Athorybia* and *Melophysa* are quite distinct. In the latter a distinct nectosome is found.

Schneider (1896, p. 590) suggested that *Athorybia* was really a sexually mature, larval (neotenous) form, with which I agree. I go further in suggesting that *Melophysa melo* represents a form that has similarly become sexually mature but at an early post-larval stage. This would account for the absence of nectophores in *Athorybia* and the presence of a single functional nectophore at any one time (?) in *Melophysa*. Furthermore, I consider an important point in this argument, to be the shape of the nectophore in *Melophysa*. In Bigelow's (1931) fig. 217, I suggest that the nectophore has become twisted through 180°, as so often happens, about one axis or the other,[2] even in a species like *Diphyes dispar*. I believe that in *Melophysa melo* the pedicular canal ascends and does not descend to the nectophore. Now the important point is that in young nectophores of *Agalma okenii* there is a very distinct inferior pedicel, a condition which I believe to be homologous with that in *Melophysa melo*. If Bigelow's nectophore were to be reversed, the loops of the lateral canal could also be homologized with those of Agalmids. The external features of the nectophore are unlike those of other Agalmids as my figures show (Text-fig. 7), a fact that once more suggests that *Melophysa*'s nectophore is a survival of an earlier stage of development of these organs.

Schneider (1896) gave no clue as to the identity of the form he was discussing except that it was evidently the larval form described by Haeckel (1869*a*). The identity of Haeckel's larvae can only be surmised. He took a unique specimen of *Athorybia ocellata* (syn. *rosacea*) at Lanzarote in 1876, and the larvae, which he was observing and describing at the same time, probably came from this same specimen.

Athorybia Eschscholtz, 1829

Anthophysa Brandt, 1835.
Angela Lesson, 1843.
Athorybia Kölliker, 1853*b*; Huxley, 1859; Gegenbaur, 1859; Fewkes, 1882; Haeckel, 1888*b*; Fewkes, 1888*b*.
Ploeophysa Fewkes, 1888*b*.

---

[1] Bigelow (1931, p. 579) discussing *Melophysa melo* said, 'it will never be possible to settle conclusively whether or not it was this same form *Athorybia rosacea* [Bigelow, syn. *Melophysa melo* Q. & G.] that Forskål described and pictured as *Physsophora* (sic) *rosacea*, for his figures and account would apply equally to any *Athorybia*'. But, as Haeckel says, Forskal was describing a typical Mediterranean form, which *Melophysa melo* is not.

[2] I have even witnessed in *Agalma elegans* the loss of one of a series of nectophores, shot off when the stem contracted, followed by the twisting round of a neighbouring nectophore to take its place.

Diplorybia Fewkes, 1888*b*.
Anthophysa Chun, 1897*b*; Bedot, 1904; Bigelow, 1911*b* (excl. synonymy); Totton, 1936; Leloup, 1941.
Athorybia Garstang, 1946, pp. 135, 140, 141, 190; *non* 147, 167, 175 (= *Melophysa melo*).
Anthophysa Garstang, 1946, pp. 141, fig. 45; 142, 147, 148, 167, 168, 170, 171, 172, 175; *non* 190 (= *Melophysa melo*).

Brandt (1835) established a genus *Anthophysa* based on unpublished figures and a manuscript description by Mertens. Haeckel (1888*b*) said that he had seen these and made a few comments on them, but his observations are not sufficiently critical to enable me to come to a certain conclusion about the generic identity of *A. rosea* Brandt. As far as I can judge it is congeneric with Kölliker's *Athorybia rosacea*, but not with Bigelow's (1931) *A. rosacea*. The species described and figured by Bigelow (1911*b*) as *Anthophysa rosea* is of the same genus as Forskål's *Physsophora* (sic) *rosacea* and Kölliker's *Athorybia rosacea*.

I hope that the selection of the lectotype of *Athorybia* will end this confusion of generic names.

Athorybia rosacea (Forskål), 1775. (Plates I–III.)

This Mediterranean species was figured in colour by Quoy & Gaimard in 1827 as *Rhizophysa heliantha*, by Kölliker in 1853*b* as *Athorybia rosacea* and again, probably, by Haeckel from the Canaries in 1888*b* under the name of *Athorybia ocellata*. Bigelow (1911*b*) gave a detailed description and figures of it under the name *Anthophysa rosea*. Finally, Leloup (1941) gave us the latest summary of our knowledge of this genus under the name *Anthophysa* Brandt, 1835, together with some notes on a specimen from the Gulf of Guinea. Leloup also plotted the distribution of the species. His figs. A–C (1941, pl. 1) are of interest for they tend to question the significance of Bigelow's similar photographs of a section of an alleged superior, gas-secreting, secondary ectoderm of the pneumatochone. In Bigelow's fig. 1 (1911*b*, pl. 23) the thickened secondary ectoderm reaches right across the vault of the pneumatosaccus, a condition unparalleled, as far as I know, in any Physonect. But the pneumatophore lies obliquely, and the section may have missed the apex of the pneumatosaccus. In Leloup's figures the condition is more normal. Further work on this point is needed. I recently studied *Athorybia* alive at Villefranche, where Sabine Baur made some excellent coloured sketches[1] of it. The only species of this genus *Athorybia* is characterized by having a large air-sac that forms the bulk of the specimen. It is half covered by what Fewkes called the hood. Haeckel called it the nectostyle or attachment of the bracts, which he claimed were used in swimming. There are no nectocalyces.

Behaviour. Whilst I was aboard the launch belonging to the Station Zoologique at Villefranche in May 1950 a living specimen, 12–14 mm. in diameter, was secured at about 9 a.m. after being detected by the keen eyes of the mechanic, M. Raibaud, as an inconspicuous floating object 'à peine rouge'. No specimens had been seen there in the last forty years. Observation soon showed that the animal could ascend and descend at intervals in the jar of sea-water, which I protected from the sun with a duster. Before sinking, with closed bracts, a number of small bubbles would appear amongst the bracts, and be removed by their movement. It was not possible to locate the pore from which the bubbles must have come, although my notes twice mention that they appeared to be released from the lower or basal part of the pneumatocyst, but I now believe that they must have come from an apical pore. After an interval of ten minutes the animal would begin slowly to leave the bottom of the jar again, after intermittent closure of the bracts that caused a slight rise followed by a falling back. The partially raised bracts were held motionless during ascent and not flapped in the manner described by Kölliker, except that when about an inch from the surface they opened somewhat and closed with a kick. This action had the effect of sending the animal downwards for an inch before rising again

---

[1] Mlle Baur has generously allowed me, with Professor Portman's permission, to publish reproductions of these unfinished drawings. I consider them of greater value as records than finished ones.

to rest at the surface. My desire to obtain sketches of the living animal, and then to anaesthetize and preserve it for detailed examination, as well as my fear that it might become moribund and lose all its bracts, forbade me to keep it under observation alive for more than two hours or so, but the ascent and descent with contracted tentacles were repeated some half-dozen times after capture. I watched the descent three times. When, finally, 7% magnesium chloride was added in three stages, after drawing off most of the sea-water, a slow beating of the bracts, which opened out at once, was seen for a long time.

Cook's first voyage. Whilst examining the third volume of Sydney Parkinson's unpublished water-colour drawings made during Captain Cook's first voyage, I came across a page of sketches of this animal which is reproduced here (Pls. II–III) since so few figures exist. It was 'painted from life in October 1768 between the tropicks', and appears to be the earliest record of the species. Perusal of a photographic copy of Banks's MS. Journal shows that the specimen was probably taken, with other invertebrates on 4 or 7 October, at a position which I estimate to have been about 9–12° N. and 22–23° W.

Haeckel's ocellus. Haeckel described near the tip of each palpon a red ocellus and figured it as if it had a small lens. I was interested therefore to observe in some of the living palpons small cercariae. The palpons had a pink spot, but none had a lens. It may be that Haeckel was deceived by the appearance of cercariae into thinking that there was a lens associated with the pink spot.

Anatomy. Haeckel claimed to have discovered, what he said previous observers had missed, the true nature of *Athorybia*. However, it seems that even Haeckel did not make the correct interpretation of its anatomy. My suspicion, gained from examining one or two better preserved specimens in the British Museum (Nat. Hist.) Collection, that the line of budding gastrozooids was not strictly median-ventral, as Haeckel had described it, but took a curved course from a 'kink' or 'hilum' at the upper right-hand side, down to the lower left-hand one (Text-fig. 5E), was recently confirmed by the examination of several more specimens taken by 'Discovery', 'Carnegie VII' and by Beebe, as well as of the Villefranche specimen, which is probably the most complete one to be found anywhere. In young specimens the ovoid pneumatophore rises with long axis vertically above the protosiphon, and its ventral side is covered by bracteal lamellae. There are, in a young specimen, in addition to the large protosiphon, three or four secondary gastrozooids on the right-ventral side, the youngest bud placed on a higher level. This arrangement is comparable with the stage at which the nectophores first appear in a larval *Nanomia bijuga* (Text-fig. 3). There is a corona of bracts attached to the 'nectostyle', which projects above the ventral side of the pneumatophore. Below the bracts there is, in an early stage, another corona of about six comparatively large palpons provided with palpacles, although these simple tentacles cannot always be seen. Later, more buds of secondary gastrozooids appear on the upper right-hand side, just in front of the nectostyle. In one full-grown specimen from Bermuda, 13 mm. in length, I counted eighteen gastrozooids, including buds. They form a staggered row, descending in a curved line running from the budding zone towards and round the left-hand side of the basal area (Text-fig. 5E), as in *Physophora* (Text-fig. 5C). By the time that they have all appeared the animal has 'toppled over' to the ventral side (or end) so that the original vertical axis is now at an angle, and the apex of the pneumatophore is nearly covered by the nectostyle.

The gonopalpons are produced on both right and left sides, in an order that has not yet been ascertained, and from each common, gonodendral stalk arise five or six palpons. In addition to the secondary gastrozooids already mentioned there is usually, I think, another gastrozooid budded near the protosiphon. The arrangement of the gastrozooids that I have described has not been noticed before. It is extraordinarily interesting because it links *Athorybia* not only with other Brachystelia (short-stemmed forms), especially *Physophora* but also with such Macrostelia as *Nanomia bijuga*.

It seems, then, that in *Athorybia* the pneumatophore is never carried up by a growing zone above the level of the young gastrozooids, and that an adult *Athorybia* is homologous in its general organization with a larva of *Nanomia bijuga* turned on its side. It is homologous also with a young *Physalia* in which the same turning has occurred, for the gastrozooids are in the same relative position to the pneumatophore as they are in a larval *Nanomia bijuga* (Text-fig. 5 A, B).

Bracts. The basal part, to which the muscle is attached, is flattened from side to side. The main part of the bract is flattened dorso-ventrally. There are seven slight longitudinal ridges of nematocysts on the dorsal surface. When the ectoderm is stripped off no ridges remain. Only the median row reaches the proximal end.

New Indian Ocean Records. 'Manihine' Aqaba Station 18, 1 example (juv.), bracts; Red Sea Station 10, 1 bract.

'Discovery II' Station 1589, 1 example (juv.), 1 bract.

Other new records. 'Terra Nova' Station 57 (Tropical Atlantic, 13 May 1913), 1 example.

'Discovery'. Four specimens were taken by dip-net on 16 October 1925 at a position 29° 56′ 50″ N., 15° 03′ 10″ W. and fixed in Schaudin. A note on the label by Professor A. C. Hardy reads 'small fish [14 mm. long] was caught clasped by one of the *Athorybia*, but separated on being transferred from net to fixative'.

'Discovery' Stations 281, 282, 284, 299. 'Discovery II' Stations 689, 697, 698, 2069, 2648.

Bermuda, Beebe Collection. Four specimens were recorded in a preliminary note under my name in 1936 as *Anthophysa formosa* Fewkes. Beebe took another specimen number 29453, net 267.

H.M.S. 'Rodney'; Kingstown, St Vincent, B.W.I., 20 February 1931 (Totton Coll.); 1 example.

Melophysa Haeckel, 1888

Type species *Rhizophysa melo* Q. & G., 1827

Eschscholtz (1829) included three species in his *Athorybia*. Of these, two—no doubt the same species—*Physsophora* (sic) *rosacea* Forskål and *Rhizophysa heliantha* Quoy & Gaimard belong to one genus *Athorybia* Eschscholtz, and the other *Rhizophysa melo* Q. & G. belongs to the quite distinct genus which Haeckel (1888*a*) named *Melophysa*. Bigelow (1911*b*) rejected this name *Melophysa* on the grounds that Haeckel in his 'Challenger' Report (1888*b*) referred to, but did not describe under this generic name, a single specimen taken in the Strait of Gibraltar in 1867. It was lost before Haeckel could draw it, but the form of its bracts was said to be similar to that in *Athorybia melo*, which Quoy & Gaimard had observed in the Strait of Gibraltar forty years before and figured in their 'Astrolabe' Atlas (pl. II, figs. 7–12). However, prior to publication of this 'Challenger' Report in 1888, Haeckel had published in December 1887 and again in May 1888 in his *System der Siphonophoren* the new name *Melophysa*, citing *Rhizophysa melo* Quoy & Gaimard as the only species. Perhaps this was overlooked by Bigelow, but, bearing it in mind, we can hardly agree that Haeckel set up a new genus for a problematical, undescribed and unfigured specimen that was soon lost. In fact I see no reason why Haeckel's name, *Melophysa* should not be used for Quoy & Gaimard's species, *Rhizophysa melo*.

The only good account of this species is by Bigelow (1931) under the name *Athorybia rosacea*. The probable origin of the confusion, both zoological and nomenclatural, is the fact that till figures were published by Chun (1897*b*) it was not realized that *Rhizophysa melo* had a distinct nectosome with nectocalyces and that there was a characteristic difference between the heavy, ribbed bract of *melo* and the light, striated bract of *rosacea*.

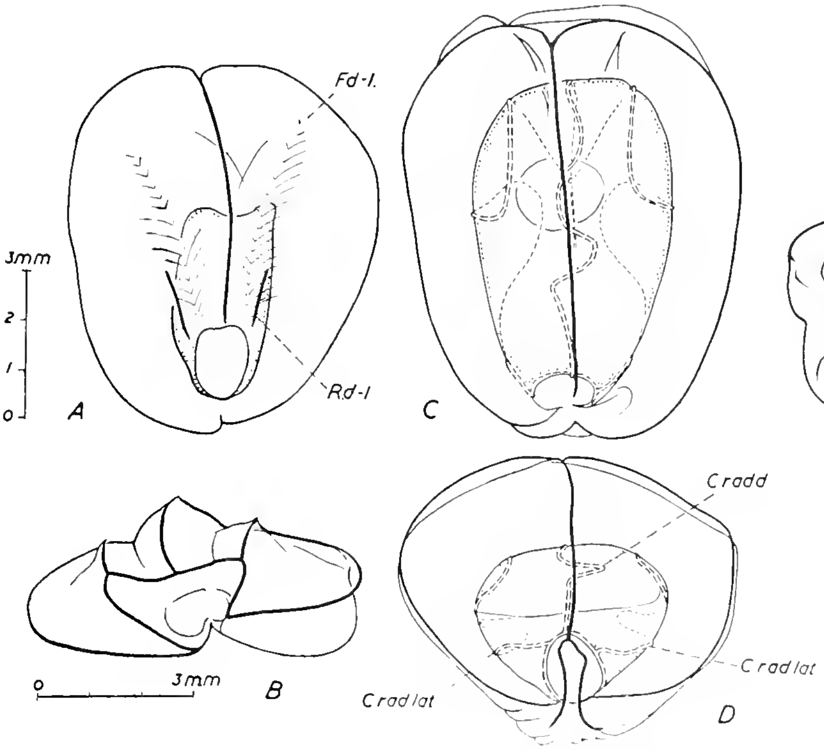
Melophysa melo (Q. & G.), 1827.

The nectophores are shown in Text-fig. 7; and the bracts are like that figured by Bigelow (1931, fig. 217).

New Indian Ocean records. 'Discovery II' Stations 1375, 1580, 1581, 1586, 1755, 1758, 1763.

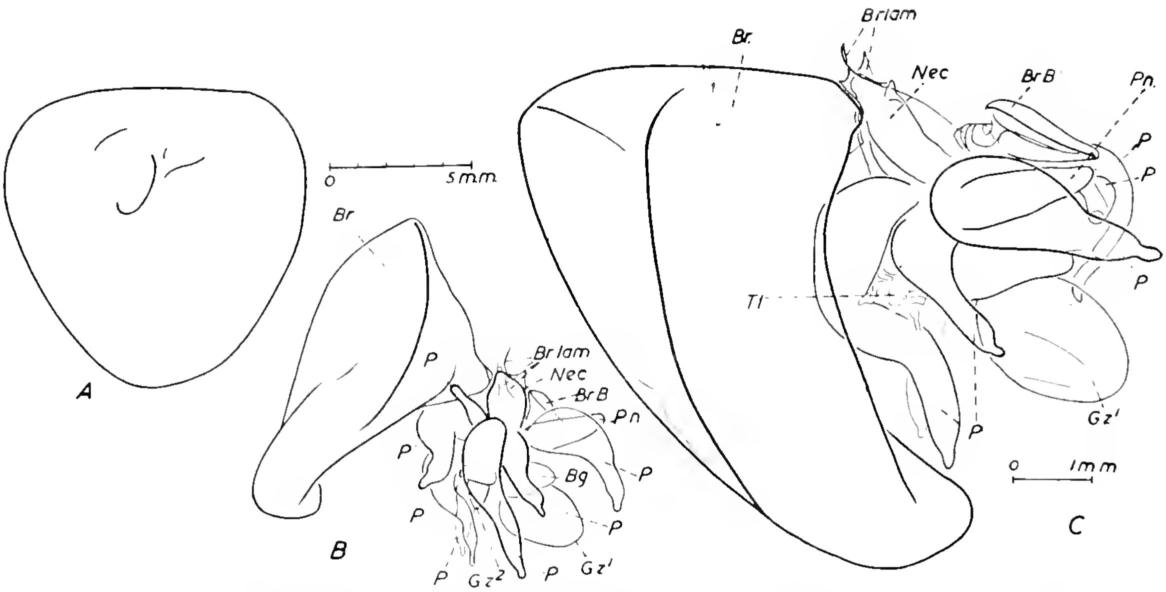
Other new records. 'Discovery' Stations 282, 284, 288; 'Discovery II' 692, 695, 701, 702, 2068, 2635, 2638.

Beebe Collection, Bermuda. Nos. 29,266; 29,270; 29,349; 29,400; 301,072; 301,427; 311,008; 312,067; 312,071. *Corrigendum.* Items 27, 28 in my (1936) list of Wm Beebe's siphonophore material taken at Bermuda in his 1931 Oceanographic Expedition refer to *M. melo* and not *Athorybia rosacea.* The name was used *sensu* Bigelow.

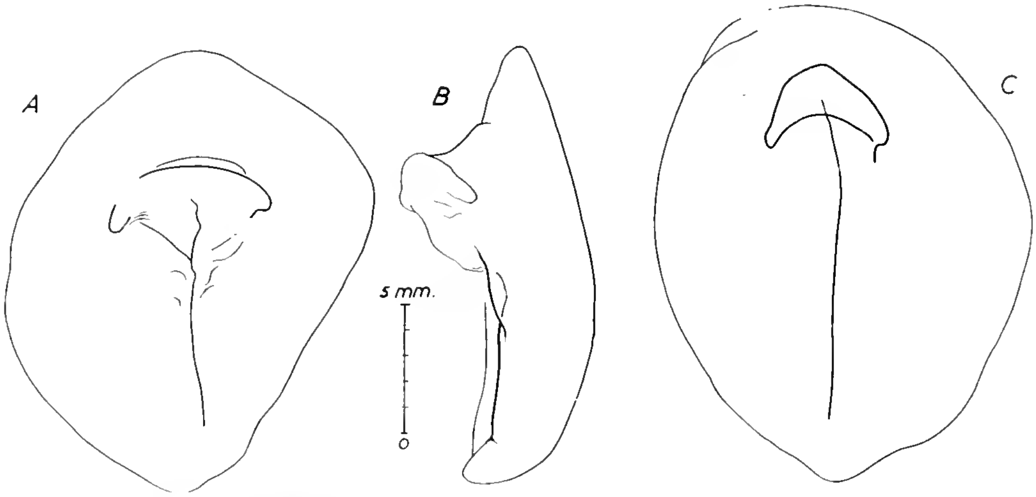


Text-fig. 7. Nectophores of *Melophysa melo.* ×7. A, C, viewed from upper side; B, D, from abaxial end; E, from left side. A, from Bermuda, Beebe Collection, 1463 m. B, 'Discovery II' St. 692, 350–0 m. C, D, E, 'Discovery II' St. 1580, 450–0 m.

A post-larval specimen (Text-figs. 8, 9) taken by H. B. Moore at Bermuda in 1938–9 bears two gastrozooids. It is particularly interesting because (1) it still bears an attached larval bract with smooth outer surface, (2) the larval bract is attached near the tip of a long, conical nectostyle whose axis is at right angles to that of the pneumatophore, and not overlapping it as in *A. rosacea.* Only about half a dozen bracts were attached to the upper parts of the nectostyle, and buds for younger ones are attached much lower down on the 'body' of the specimen. There appears to be a young nectophore bud at the base of the pneumatophore, but it is doubtful whether buds of different types can certainly be distinguished. The nectosome has not started to elongate. There is a ring of nine palpons. The length, from apex of nectostyle to mouth of protosiphon is 5 mm.; the length of the attached bract is 7 mm. The tentilla are like those figured by Bigelow (1931).



Text-fig. 8. Larva of *Melophysa melo*. A, dorsal view of the attached larval bract. B, C, lateral views of larva. A, B ×4; C ×10. Coll. H. B. Moore, Bermuda.



Text-fig. 9. Larval bracts of *Melophysa melo*. B, side-view of A. Coll. H. B. Moore, Bermuda. × 3·4.

Physophora hydrostatica Forskål, 1775.

This almost cosmopolitan species, which is especially common in the North Atlantic Gulf Stream area and the Mediterranean, has been shown by Kramp (1942) not to occur in the cold tracts of the Polar Currents. So far the only Indian Ocean record is that of Haeckel (1888*b*) from off Ceylon. There are records from the Malaysian region by Lens & van Riemsdijk (1908); off South Australia (43° 26′ S., 126° 37′ E.), by Huxley (1859); the North-eastern Pacific, Bigelow (1911*b*, 1931)—I have examined young specimens from La Jolla, California—and North-western Pacific, Bigelow (1913). Bigelow (1931) pointed out that it had not been recorded from as high latitudes in the Pacific as in the Atlantic. From the South Pacific (Station 967) 'Discovery II' took this species midway between New Zealand and South America at a temperature of 9·5° C., at the junction between the sub-antarctic South Pacific upper water and the eastern South Pacific central water. It was taken also at Station 943 off the east coast of New Zealand, at a temperature between 7·37° and 7·40° C. It was taken in the Pacific equatorial water by 'William Scoresby' in the Peru current (Sts. WS 687, 766) in 07° 20′ S. and 07° 42′ S. lat.

In the South Atlantic it was taken by 'William Scoresby' at several stations on the Patagonian Shelf between Magellan Straits and the Falkland Islands at temperatures of from 5° to 6° or 7° C.

On the eastern side of the South Atlantic 'Discovery' found the species at Station 104, about seven degrees south of the Cape, and south of the sub-tropical convergence in lat. 41° 33′ 30″ S. and long. 17° 58′ W.

Bigelow gave its known temperature range as between 7·2° and 21·1° C. Kramp (1942) gave records from South-west Greenland at temperatures between about 3° and 4·7° C. 'Mabahiss' took a small specimen at the surface, temperature 26·6° C, salinity 35·82 ‰ at Station 39, about 80 miles north-west of Sokotra on 25 November 1933. The fact that *Physophora hydrostatica* was at the surface at such a high temperature is in itself of interest. No specimen has ever been recorded from this part of the Indian Ocean before. The only other Indian Ocean records are those of Haeckel (*Discolabe quadrigata*), but there may be some doubt whether all his Ceylon specimens belonged to this species (Garstang, 1946). The so-called record by Quoy & Gaimard (1833) of *Physophora australis* is based on figures which do not for certain, in my opinion, represent *Physophora*.

The 'Mabahiss' specimen is small, about 15 mm. overall, and has five attached buds of nectophores and six detached, crushed and deformed ones. All the palpons are missing, but one half-grown gastrozooid with a half-grown tentacle is attached, as are three younger ones, each with only a rudiment of a tentacle. Some of the tentilla on the former are unmistakably characteristic of similar stages in *Physophora*. The nectophores and the course of their radial canals have been compared and correspond with those of good Mediterranean specimens. The nectophore was well figured in Bigelow & Sears's 'Thor' Report (fig. 49—a little masterpiece).

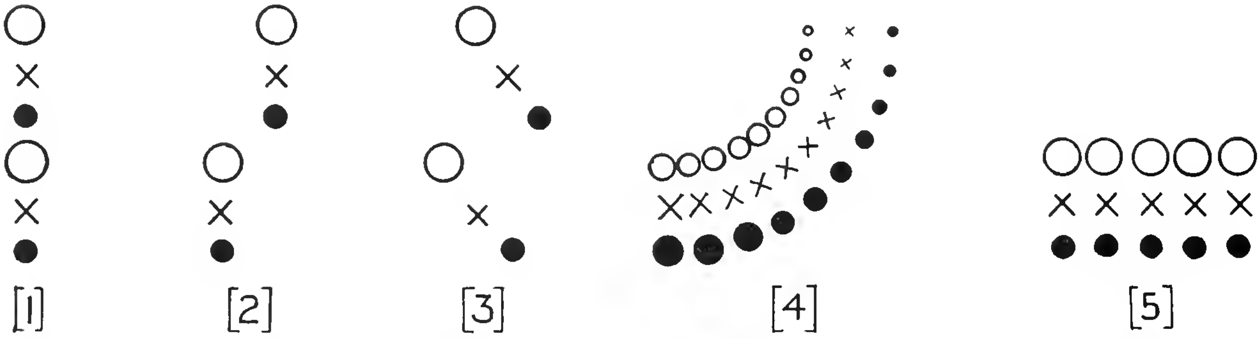
The 'Mabahiss' specimen is somewhat younger than that figured by Haeckel (1888*b*; pl. xx, fig. 13). Like it, the small discoidal siphosome exhibits a one-sided dextral proliferation of buds. There are one or two small buds proximal to the youngest gastrozooids which may be young gonophores. Though the specimen is poor, incomplete and difficult to study, I have not the slightest doubt about its identity.

A great deal more work is needed on the development and structure of this species. On 18 and 19 June 1951, 'Scotia' took three young specimens to the north-west of the British Isles in the region of 19° N., 12° W. It was these that first made me doubt whether there is such a regular, dextral sequence of cormidia arranged in vertical, trimorphic series as maintained by Garstang (1946). My own tentative view is that the peripheral margin of the disc to which the cormidia are attached does indeed correspond with the ventral median line of a twisted macrostele stem. This does not mean that that is its phylogenetic history. I made a large collection of larvae of the species at Villefranche, and studied alive, anaesthetized, and preserved two full-grown specimens. There is no time to complete the morphological study of the material now in the British Museum collection before submitting this report, but a cursory examination of the 'Scotia' specimens shows that the lower one of the two rows of palpons on the nascent lobe is a secondary one, and has not been caused by deformation, through squeezing, of a single row, as suggested by Garstang. It also suggests that the upper row itself is not a single sequence. This view is borne out by a study of the series of larvae. Garstang could not understand how the spiral winding of a uniserial trimorphic stem could, in theory, produce the parallel coronas 'as we see them' in *Physophora*, but I think that Claus's (1860, 1878) interpretation of homology is quite correct, though the *Physophora* condition is probably primitive and the macrostele is derivative.

Let us start with Text-fig. 10 [1], the generalized, uniserial, macrostele arrangement: theoretically this could give rise to, or be derived from [2] and [3]. In *Physophora*, omitting secondary palpons, we find the arrangement [4]. If the budding area is not studied closely we can easily get the impression, which Garstang seems to give, of an arrangement such as [5].

Arrangements [1] and [5] are at first sight incompatible. Further study of available pickled material should clear up this point, though it could be done best in the field where musculature can be relaxed. A study of old figures and diagrams will not help much. Haeckel's figures of larvae are not reliable. He would have us believe, for instance, that the pneumatophore arises as the basal part of the bracteal canal.

Physophora is an interesting animal to study alive: it is very active and responds readily to stimuli. If the air-sac is touched when the animal is at rest all the palpons are at once thrown up. Even a larva can be recognized by the irritability and activity of the palpons. In the adult they very often poke about amongst the nectophores, and their tips even enter the nectosacs. When swimming (Text-fig. 11 B) all the palpons are trained aft, their tips coming to a point outside the retracted tentacles. The air-sac on its relatively long neck turns vertically upwards, the main axis being horizontal. It is an active swimmer. A specimen measuring 6·5 cm. in length and having four pairs of fully developed nectophores moved about 5·0 cm./sec. The rate of contraction of the nectophores in a closed vessel at Villefranche on 28 April 1950 was about 1/sec. In horizontal progression half of the nectophores had their orifices facing upwards, and only these nectophores contracted in unison. The initial contraction when moving from the vertical resting position was made by the youngest nectophore.



Text-fig. 10. Diagrammatic representation of the possible steps in derivation of the '*Physophora*' arrangement of stem appendages [5] from that of *Agalma* [1] or vice versa. × = gastrozooid; ○ = palpon; ● = gonophore.

Text-fig. 11. *Physophora hydrostatica*. Sketches from life of A, resting position on bottom of glass vessel; B, swimming posture. Nat. size.

The simple tentacles of the palpons extended to about the same length as the palpons themselves, namely an inch or more. When the animal sank, the tentacles of the palpons trailed upwards. At rest they hung down inside the ring of palpons, which were of a rose-pink colour. The float was tipped with a plum-coloured pigment.

Garstang tried to analyse the structure and development of *Physophora*, one of five types of brachystele Physonects, *Rhodalia*, *Physophora*, *Athorybia*, *Epibula* and *Nectalia*. He had, perforce, to rely on very unsatisfactory, old and partly restored figures for developmental stages. Thanks to a generous grant from the Browne Fund which I received in 1949 from the Royal Society, I was able to study alive at Villefranche two mature and some dozens of developmental stages of this species. There was a great deal of other work to be done at Villefranche and it was only recently, after staining the anaesthetized and fixed larvae, and after examining young specimens from La Jolla and others taken in 1951 by 'Scotia' off North-west Ireland, that I was able to gain a more correct idea of the morphology and ontogeny. It would not be profitable to mention all the mistakes that have been made in the interpretation of the morphology and development of this species. Haeckel was not, I think, able to distinguish the different types of bud from one another, so that his figures of developmental stages do not make it clear which are palpon-, gastrozooid- and nectophore-buds. His 'Challenger' figures of larvae give the erroneous impression that the pneumatophore is contained in the mesogloea of the bract.

How to orientate the larva is a puzzle. In one place Haeckel calls the bracteal cleft dorsal, as does Garstang, and in another ventral. Perhaps the meridian in which the second gastrozooid is budded, close to that in which the first palpon is budded, and near the bracteal cleft, might be called ventral, and the region of attachment of the nectophore buds dorsal. The meridian, in which the tentacle of the protosiphon (first gastrozooid) and bract lie, would then be close to the ventral. But there are no two well-marked and opposite meridians. The function of the bract seems to be to provide cover for the retracted tentacle.

The picture Garstang gave of a young stage of development was that of a protosiphon hanging down from the middle of a basal stem surface. This consisted of a wide space surrounded by a ring of palpons. Round this open space he pictured the buds of siphons, gonodendra, and other palpons circulating, with much jostling and squeezing, as they advanced from a marginal budding zone in three parallel whorls, grouped into cormidia along the meridians. My own observations show that this is not a good picture of what takes place. There is no open space until after most of the appendages have been formed and have grown apart. The first palpons are not, I believe, budded regularly in one meridian, though the last formed ones may be. For instance, palpon II appears commonly to be budded to the right of palpon I, palpon III to its left and palpon IV between I and II. Later on, palpon-buds appear in other meridians, between and distal to earlier formed ones. The second gastrozooid is budded quite early on, when there are only two or three palpons. When the bract drops off, its position is taken by palpons, which by that time form a complete ring. The first palpons are budded from a region on the apical side of the constriction that separates the pneumatochone from pneumatosaccus, at a time when the pneumatochone extends down to the level of the distal end of the basigaster. As the growth of the budding zone of the nectophores carries the pneumatophore upwards and away from the ring of the palpons, the external wall, to which they are attached, increases in diameter, but not to an equal extent in all meridians. The radius of curvature increases steadily as we pass from the growing point. At first sight, it might be thought that the marginal area, to which palpons are attached, should be regarded as part of the nectosome, because of their relative larval position. But this area is not muscular like the nectosome proper. Since there is virtually no special growing zone between the level of attachment of the palpons and the base of the protosiphon, there is little to compare with the siphosome of Macrostelia. Any argument, therefore, as to whether the siphosome in *Physophora* forms a twisted stem round an imaginary central axis is unnecessary. But if the basal part of the protosiphon was extended by a growing zone, we should get something very like a macrostele stem. Examination of hundreds of larvae of *Nanomia bijuga*[1], a macrostele, shows that the budding zone of the

[1] Commonly known as *Stephanomia bijuga*.

siphosome bears a great resemblance to that in *Physophora*, and forms a pointed outgrowth (Text-fig. 3).

As Haeckel truly stated, the gonodendra develop on meridians between those on which the gastrozooids are found, but on their apical side. Haeckel's figure, on the contrary, would give the impression that successive groups of palpon, gonodendron and gastrozooid were each borne on one meridian.

The whole arrangement of the cormidia is very like that found in Rhodaliids, but whereas the nectophores, in that family, form a bilateral corona, in *Physophora* the budding zone of the nectophores is carried up in an apical direction. Whether their muscular lamellae are all attached to a single meridian or not needs further, careful determination. Successive lamellae overlap one another, but the pedicular canals may lie in one meridian. *Physophora* is a highly specialized form, and it is unlikely that its larva would tell one much about its phylogeny. I agree with Garstang in thinking that there is no reason why it should ever have had a macrostele ancestor. On the other hand the elongation of the proximal part of the protosiphon of one of its ancestors conceivably might have given rise to a macrostele type of Physonect.

'Stephanomia'

No one can be sure at present what is the identity of a siphosome originally figured by Lesueur & Petit (1807–11, Atlas) which they called *Stephanomia amphytridis*. Péron (1807–16) did not mention it by name in his text (Tome 1, p. 45) but gave a short description of the living siphosome, its feeding habits, its phosphorescence, and a reference to Lesueur's and Petit's figure. Strictly speaking, then, the name was published by Lesueur & Petit. I have found in Péron's text no clue as to where it was taken—Bigelow (1911*b*, p. 288) said, 'in the Atlantic'—but in Péron's narrative it was mentioned after that part of the text which dealt with arrival at Ile de France. It might, therefore, have been taken anywhere between Le Havre and Mauritius.

There are two courses open to systematists when dealing with this name and with long-stemmed Physonects that have single terminal filaments to their tentilla. The first is to use the name '*Stephanomia*' as a temporary convenience and to acknowledge that *S. amphytridis* of Lesueur & Petit is at present unidentifiable; and therefore cannot be the name of the type of a genus *Stephanomia*.

The second course is to abandon the generic name *Stephanomia* and to take instead one that can be used for a species of which topotype specimens, or a type specimen, can be re-examined—specimens, that is, of a long-stemmed form with single terminal filaments.

For the present I am taking the first course, but I am excluding and placing in a new genus named after Mr J. W. S. Marr three species found chiefly in the Arctic and Antarctic. In the present state of our knowledge, I think it would be unwise to attempt to identify specimens of '*Stephanomia*' (*sensu* Bigelow) unless they bear nectophores, for nectophores do, I believe, have constant specific characters which establish their identity. Lesueur's, Huxley's and Bigelow's famous specimens of *Stephanomia* lacked the nectosome, and no nectophores have even been described under the name of *amphytridis* or *amphitridis*. Indeed, there are few proper descriptions of the nectophores of any species of '*Stephanomia*'. Different species of Physonects may have nectophores that are superficially alike, so great care must be taken with their identification. It is generally necessary to stain[1] both the radial canals and the ridges. Figures of nectophores published long ago are not, as a rule, to be relied upon.

---

[1] I recommend the use of very dilute borax-carmine for the canals, and of Delafield's haematoxylin for ridges. (See p. 10.)

Stephanomia rubra (Vogt), 1852. (Text-figs. 12–18.)

Agalmopsis punctata Kölliker, 1853*b*.

This well known, but not well described or figured Mediterranean species, which I have examined alive at Villefranche, and of which there is a good deal of material preserved in the British Museum (Nat. Hist.) collections, was taken by 'Manihine' in the Gulf of Aqaba; and in the Red Sea and west Indian Ocean by 'Discovery II'.

Although specimens living at Villefranche are easy to identify from the sum of the characters, and because of the restricted fauna, it is not easy to establish the presence of this species in another fauna by deduction from the identification of loose nectophores taken in the tow-net. But this, as a rule, is the only sort of evidence that is available, and for many years past I have been working to achieve such an aim.

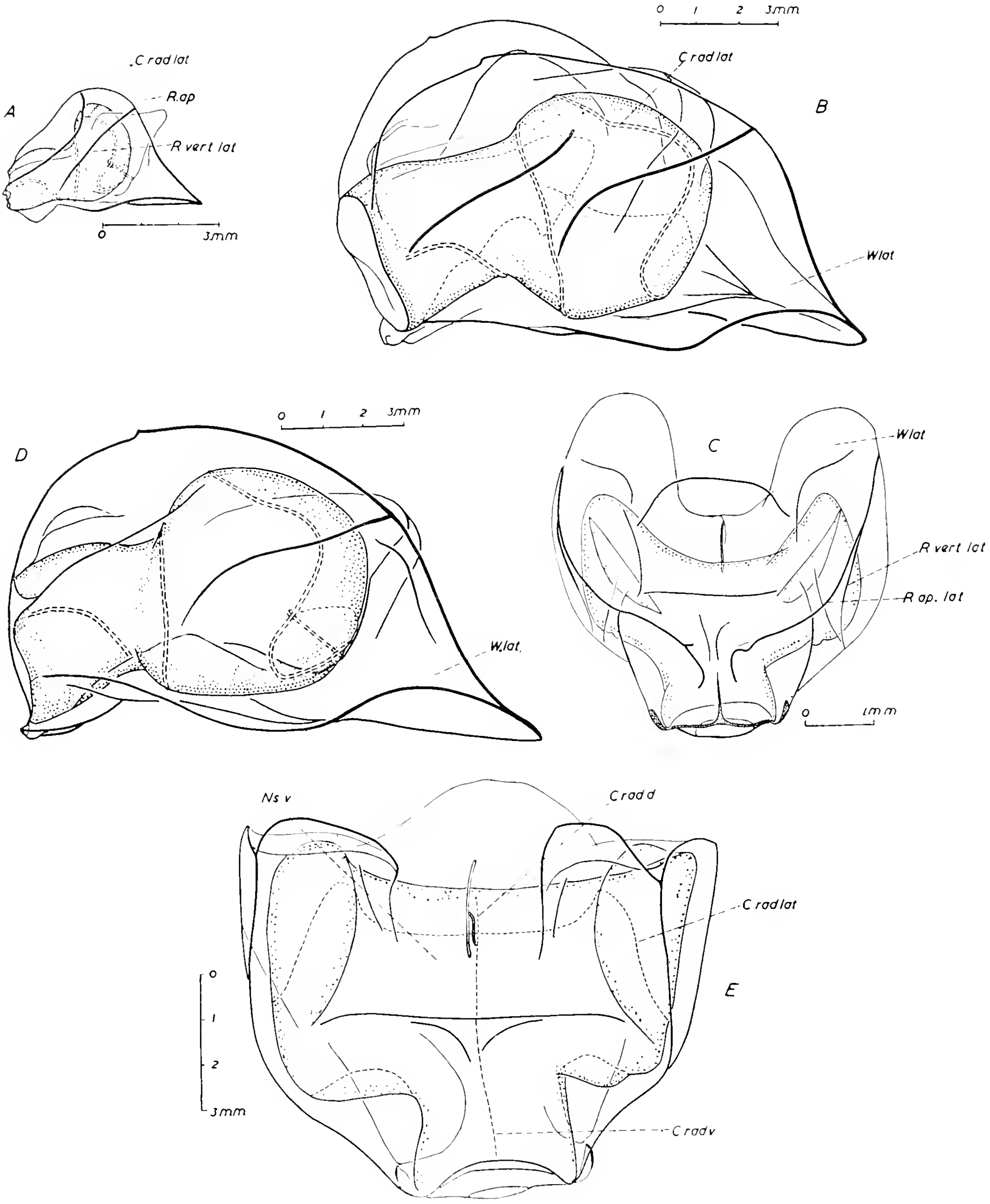
There is a species of Physonect whose nectophores can easily be confused with those of *Stephanomia rubra* by the less expert, and that is *Agalma elegans*. Of course the living or complete animal cannot be confused, on account of their very different tentacles. If we compare the nectophores of the two species, and bear in mind that fully grown nectophores look very different from young ones, we find the following distinctions:

1. *General shape of nectophores*. If nectophores of *A. elegans* and *Stephanomia rubra* are examined together as they lie, abaxial sides uppermost on the bottom of a watch-glass of formalin, it will be seen that the paired lateral wings or wedges of *Agalma elegans* are proportionately longer than those of *Stephanomia rubra*. It will also be noticed that on each side, on a level with the ventral (adaxial) wall of the nectosac of *Agalma elegans*, there is a vertical ridge that runs from the upper (apical abaxial) to the lower (oral adaxial) lateral ridge. In other words, the lateral facets, in *A. elegans*, have the 'latero-ventral (adaxial) triangle' cut off by a complete vertical ridge to form a separate facet. It will be seen, too, that in *A. elegans* the upper (apical, abaxial) lateral ridge forms a prominent tooth halfway between the ostium and the ventral (adaxial) wall of the nectosac. In *Stephanomia rubra* there is sometimes a slight prominence at this point, but usually not a well-marked tooth.

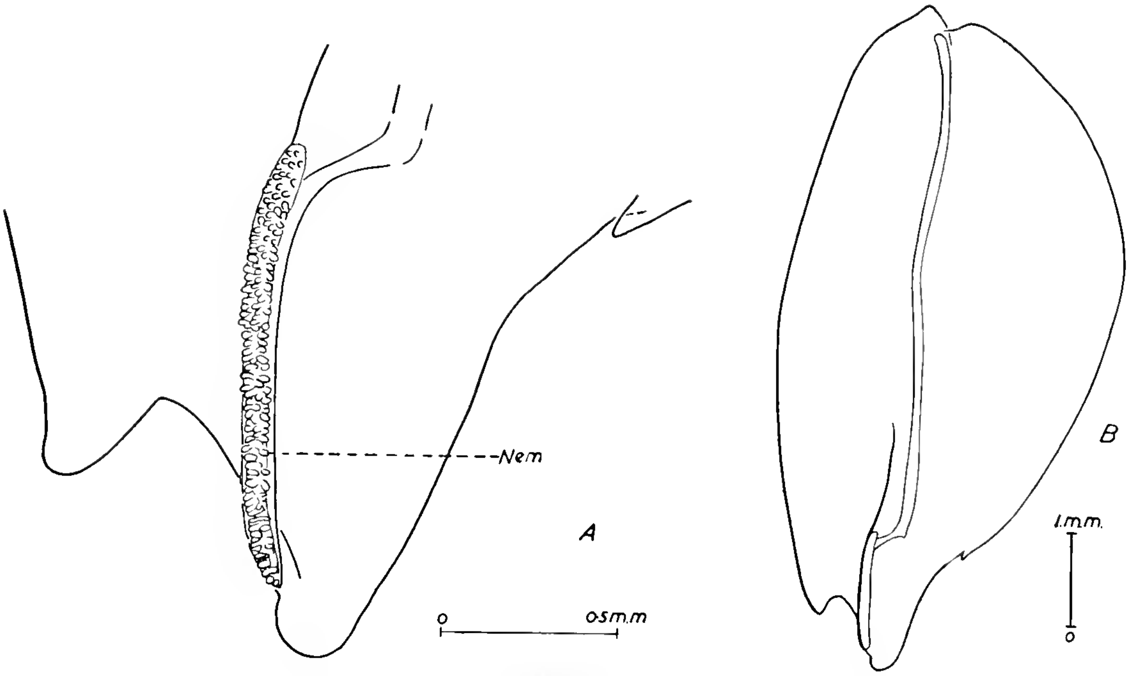
In a strictly lateral view of *Agalma elegans* (Text-fig. 24A) the vertical ridge, described above, can be seen, with appropriate staining, running down in line with the adaxial (ventral) wall of the nectosac: and it will be noticed that the upper part of the adaxial, median 'thrust-block' (in which runs the pedicular canal), does not project so far in *A. elegans* (Text-fig. 24B) as it does in *Stephanomia rubra* (Text-fig. 12C, B, D). The much greater length of the long (abaxial-adaxial) axis of the nectophore when compared with that of the vertical (oro-aboral) axis is another distinguishing feature of the nectophore of *Agalma elegans*.

2. *Lateral radial canals*. Another useful distinguishing feature of *Stephanomia rubra* is the way in which the lateral radial canal dips down as it runs on to the lateral face of the nectosac, before making its ascending, abaxial run to the semicircular dorso-lateral curve, and descent to the circular velar canal. In a strictly lateral view this dipping down of the lateral radial canal as it runs on to the lateral face of the nectosac takes it well below the level of the inner end of the pedicular canal, and below the horizontal part of the lateral canal that runs on the adaxial wall of the nectosac (Text-fig. 12D). In *Agalma elegans* the lateral canal does not dip down noticeably as it runs on to the lateral wall of the nectosac, but runs horizontally (Text-fig. 24A).

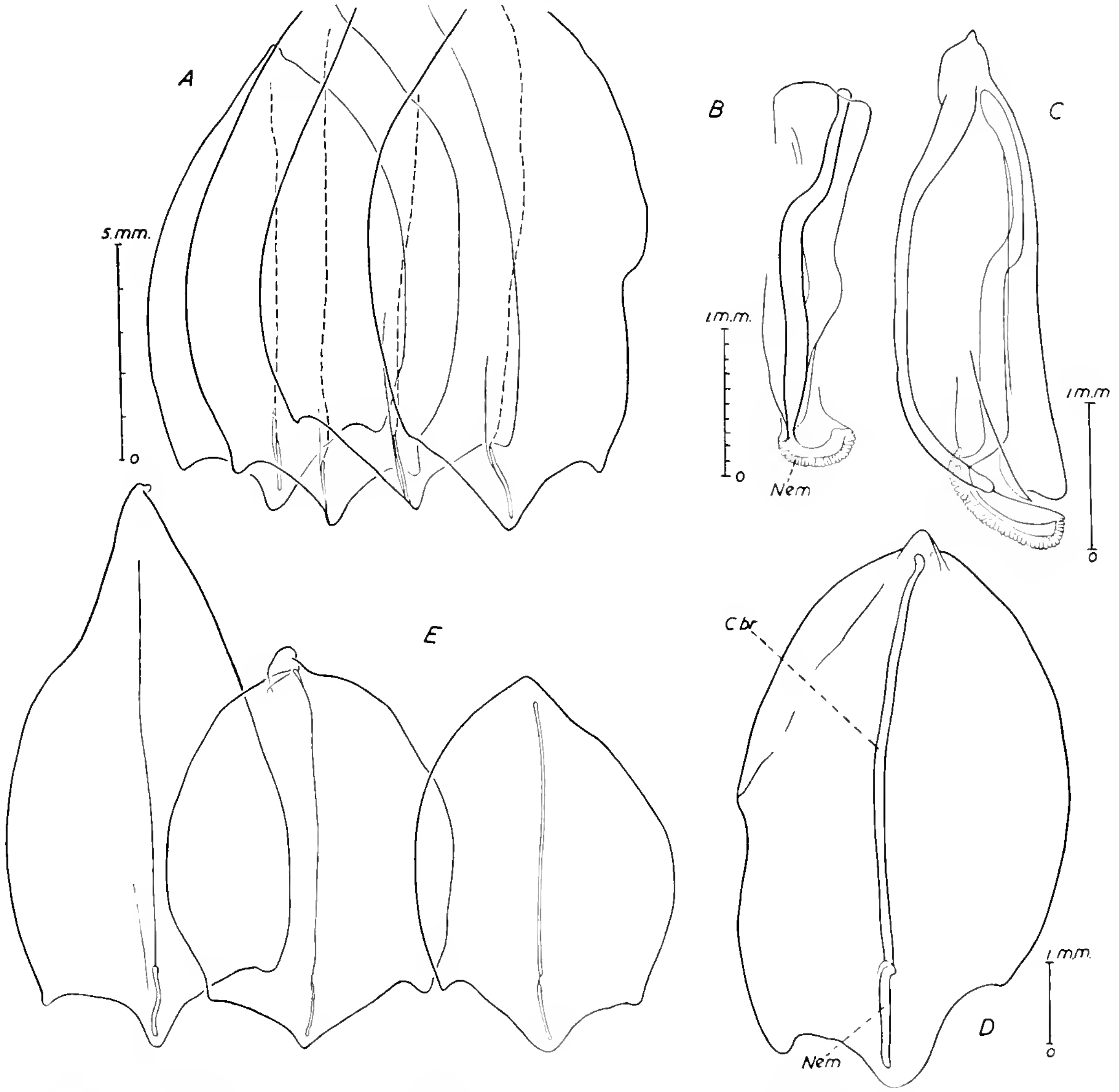
It should be pointed out that in both *A. elegans* and *Stephanomia rubra* and many other Physonects, immature nectophores, when viewed from above (apically), have the upper lateral ridges somewhat folded in towards the sagittal plane, so that care must be taken, when comparing nectophores, to allow for immaturity.



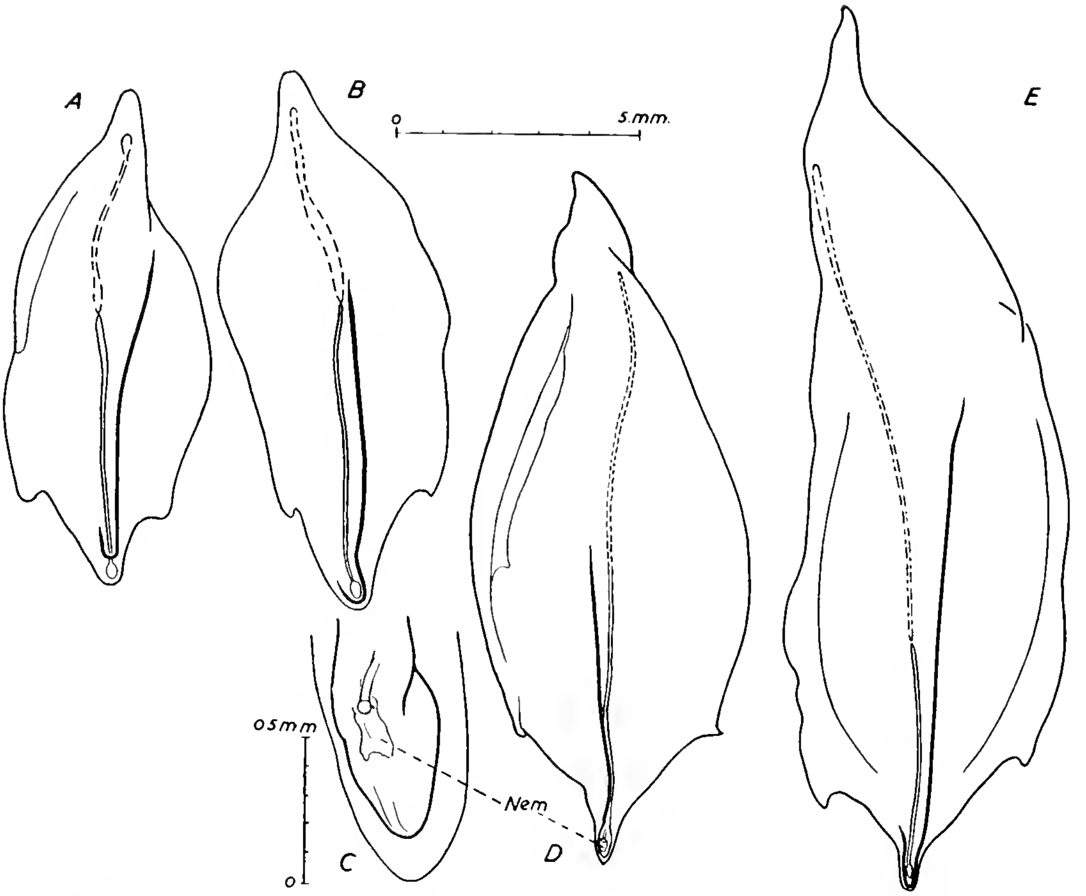
Text-fig. 12. *Stephanomia rubra.* A, C, side and upper view of nectophores from 'Manihine' Aqaba St. 1. A ×7; C ×12; B, D, side views of Mediterranean specimen from Villefranche, ×8; E, underside of nectophore of Mediterranean specimen, ×8.



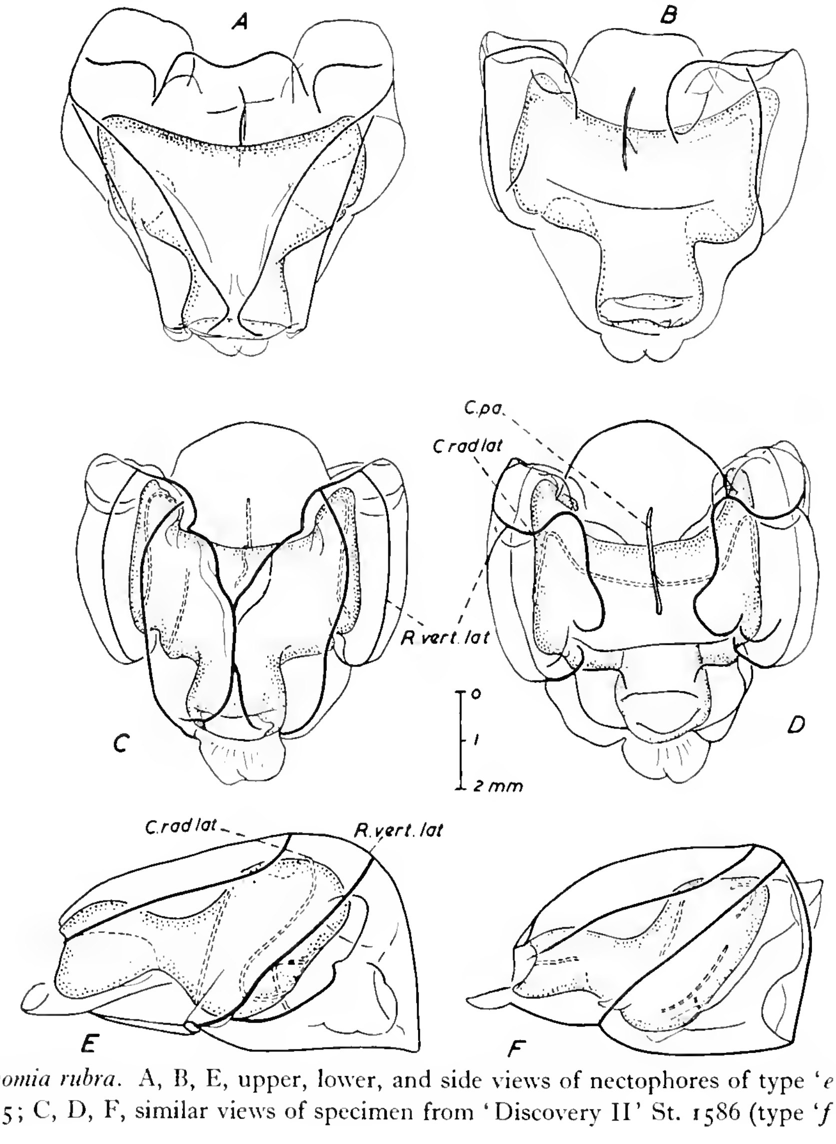
Text-fig. 13. *Stephanomia rubra.* Bract of a Mediterranean specimen from Villefranche, × 12. A shows the tip of B enlarged, × 47.



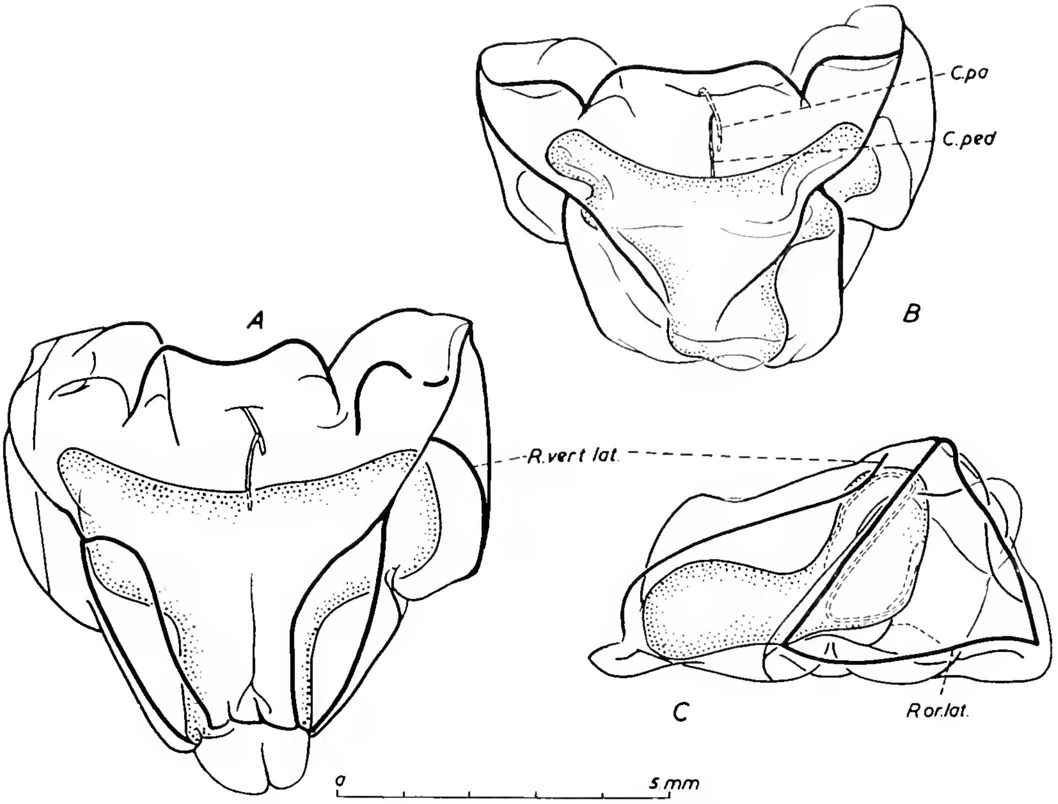
Text-fig. 14. *Stephanomia rubra.* Bracts of a Mediterranean specimen from Villefranche. B, C, young bracts, × 20, to show apical position of pad of nematocysts. A, E × 6; D × 11.



Text-fig. 15. *Stephanomia rubra.* Bracts from 'Discovery II' St. 1587. A, B, D, E × 7. C, tip of bract D, × 38. The pecked area of the bracteal canal shows the area of attachment of the muscular lamella.



Text-fig. 16. *Stephanomia rubra.* A, B, E, upper, lower, and side views of nectophores of type '*e*', from 'Discovery II' St. 1585; C, D, F, similar views of specimen from 'Discovery II' St. 1586 (type '*f*'). × 6·5.



Text-fig. 17. *Stephanomia rubra.* A, C, upper and side views of nectophore from 'Mabahiss' St. 145; B, upper view of nectophore from 'Discovery II' St. 1586. ×9.

Text-fig. 18. *Stephanomia rubra.* Bracts from 'Discovery II' St. 1586. ×6. The pecked area of the bracteal canal shows the area of attachment of the muscular lamella.

It is interesting to find such a close similarity between nectophores of *Agalma elegans* and *Stephanomia rubra* because their tentilla are so very different.

Bracts. In Mediterranean specimens the bracteal canal rises towards the dorsal (abaxial) surface near the tip and forms an enlarged subterminal, elongated, cylindrical vessel provided with about 200 nematocysts (see Kölliker, 1853*b*, Tab. IV). This subterminal section of the bracteal canal lies under a short ridge. In the youngest bracts the subterminal section is bent at right-angles to the main axis, and so is terminal (Text-fig. 14B, C).

In Indian Ocean collections, as indeed in those from the Atlantic, there are many small nectophores and bracts that closely resemble those of the Mediterranean species *S. rubra*, and also some more complete specimens that bear parts of both nectosome and siphosome. There are differences in shape between many of these nectophores and some well-preserved ones of *S. rubra* that I was able to anaesthetize at Villefranche. But in the present state of our knowledge it would be premature to establish a new species for the Indian Ocean forms.

For a long time it seemed possible to divide the Indian Ocean nectophores into two categories, one, type '*f*', appearing to be somewhat more compressed or shortened in the abaxial-adaxial axis than the other type '*e*'. The appearance of the two types of nectophore as they lie flat on the bottom of a watch-glass is quite different (cf. Text-figs. 16A, B, E—type '*e*', and C, D, F—type '*f*'). But if a different view-point is taken of the type '*f*' nectophore shown in Text-fig. 16C, we get the appearance shown in Text-fig. 17B, which is that of type '*e*'. Although in the Mediterranean form of *S. rubra* there is only a very small mouth-plate in the nectophore, if any at all, in these Indian Ocean nectophores the mouth-plate is often conspicuous. Their canal system is indistinguishable from that of *S. rubra*. Their bracts are very similar to those of the Mediterranean form but the bracteal canal does not rise up abruptly towards the terminal ridge as it does in the Mediterranean form. Tentatively I regard all these specimens as belonging to *S. rubra*.

New Indian Ocean records. 'Manihine' Aqaba Station 1; ten small but well-preserved nectophores. 'Discovery II' Stations 1567, 1568, 1585, 1586, 1587, 1589, 2688, 2907 (Red Sea).

Much more work must be done on the large amount of available Atlantic material before the size-range of specimens and the variation in form of nectophores and bracts can be determined. It is still uncertain whether there are other closely related species. The nectophores described and figured in my (1932) Great Barrier Reef report as *Agalma* sp. indet. belong to *Stephanomia rubra*.

Nanomia bijuga (Delle Chiaje), 1841.

This species has been mentioned a good deal in the literature under many names:

Physsophora bijuga Delle Chiaje, 1841.
Anthemodes canariensis Haeckel, 1869*b*.
Halistemma pictum Metchnikoff, 1870.
H. tergestinum Claus, 1878.
Agalmopsis picta Fewkes, 1880.
Cupulita picta Chun, 1897*a*; Kawamura, 1911*b*.
Stephanomia bijuga Bigelow, 1911*b* (see synonymy).

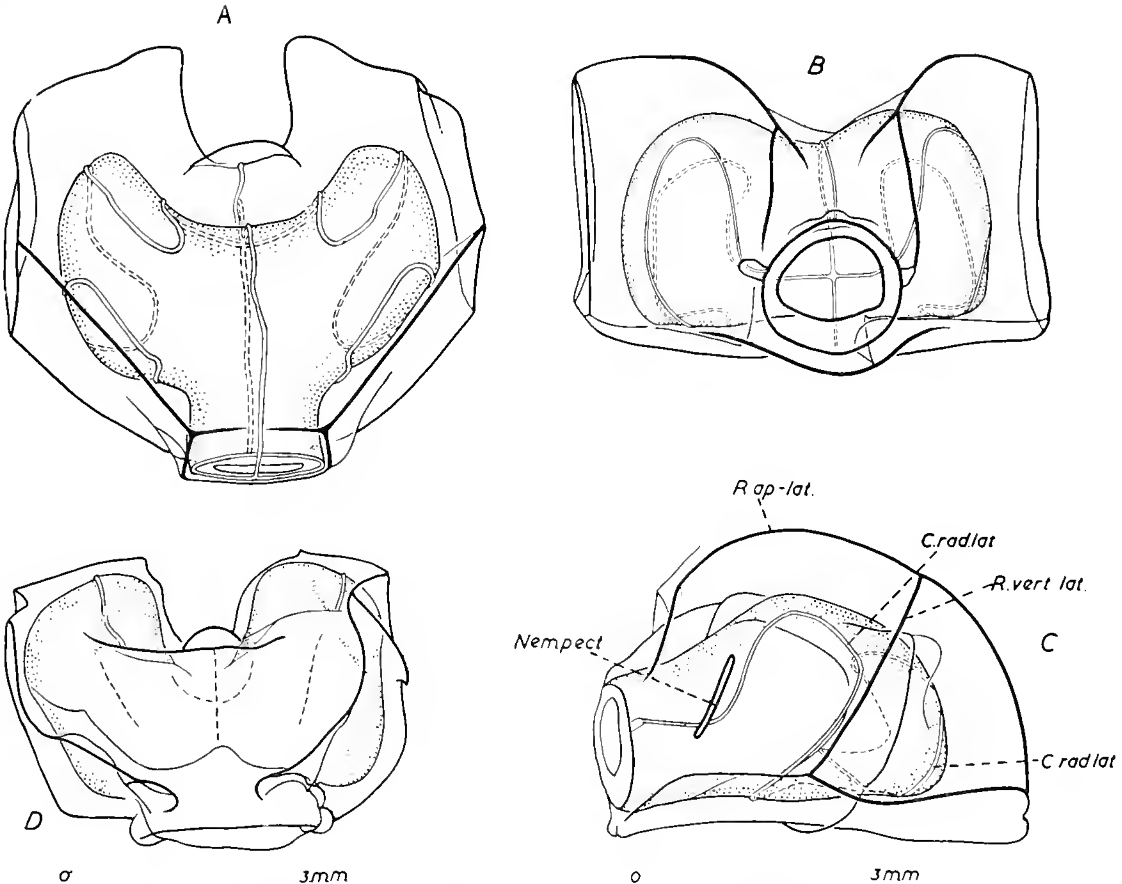
This species was not taken in the Indian Ocean either by 'Mabahiss' or by 'Manihine'. 'Discovery II' took only a very few, small nectophores as follows:

St. 1587	450–0 m.	TYF B	One nectophore.
St. 1587	450–0 m.	N 70 B	Two small nectophores.
St. 1589	600–0 m.	N 70 B	One small nectophore.

Attention may be called to Kawamura's excellent figures (1911*b*; pl. 7, figs. 1–10) of *Cupulita picta*, which have escaped mention in the synonymy lists. He took many specimens at Misaki in the months of January and February. He noted that they carried from ten to fifty nectophores and more than ten cormidia. The bracts and their distribution were described by Kawamura. He said they were generally in four longitudinal rows round the stem, each siphon having an extremely large and long bract close to it. The only colour he noted was that of the reddish cnidoband of the tentillum. He agreed that *Stephanomia bijuga* is not identical with Agassiz's *Nanomia cara*, but he had not resolved the confusion of at least two species under Sars's (1846) name *Agalmopsis elegans*, and in error said in his generic diagnosis that *Cupulita* had trifid tentilla. His description of *C. picta*, however, was good, and his figure of the whole animal is perhaps the best in existence. His figures of the nectophores are excellent and characteristic, and show that they are quite different from those of the species figured by Sars (1846; Tab. 6, fig. 3) and renamed by Haeckel (1888*b*) *C. sarsii*. The Siphonophore whose abundance at Salcombe, Devon, was noted by Berrill (1930) but not studied morphologically, was probably *C. sarsii* and not *Stephanomia bijuga*. The oil-filled diverticulum at the base of the palpon appears to be characteristic of *Cupulita sarsii*. Forty years ago Bigelow raised the question whether the southern *Stephanomia bijuga* (*Cupulita picta* Metchnikoff) was distinct from a northern form *Nanomia cara* Agassiz. I have examined specimens labelled *cara* by Bigelow and taken by 'Albatross II' (St. 21315) just north of Cape Cod, and other specimens that agree with them but differ from those of the Mediterranean species *bijuga*. These other specimens were collected (1) by Miss Delap at Valentia Island, Ireland, where I myself collected a mature specimen on 3 May 1951; (2) in the Celtic Sea between Ireland and Cornwall, and sent to me by the Marine Biological Association, Plymouth; (3) by 'Scotia' in 1951 to the north-west of the British Isles; (4) in Norwegian waters, a single nectophore. The nectophores of all these specimens agree with each other, and with the figure made by Sars, in being flattened at right-angles to the long axis of the whole animal. They differ from those of *Nanomia bijuga* (= *Cupulita picta*) which are flattened in a plane parallel with the long axis of the whole animal.

I have therefore come to the conclusion that there are two closely allied species (*a*) *Cupulita sarsii* Haeckel, 1888*b*, found in Norwegian and British waters, and probably identical with the North-west Atlantic form *Nanomia cara* Agassiz, and (*b*) a Tropical Atlantic, Mediterranean, West Indian, Indian Ocean and warm-water Pacific species, referred to by Bigelow (1911*b*) as *Stephanomia bijuga*. As to applying to these two related species the prior generic name valid for either of them, my opinion is as follows:

Stephanomia (1807) is the name of a monotypic genus, the identity of whose only species *amphytridis* Les. & Petit is exceedingly doubtful. *Cupulita* (1824) is also monotypic, and the identity of its only species, *bowditchii* Q. & G., is very doubtful. *Agalmopsis* Sars, 1846, was set up for two species; and was subsequently used by Kölliker (1853*b*) for the component with trifid tentilla. But most of Sars's account and all the figures, except for two of the tentilla of his form *b* (an *Agalma*) refer to my species (*a*). *Agalmopsis* was restricted by Haeckel (1888*b*, p. 234) to the other component with trifid tentilla. There seems to be little doubt that *Agalmopsis* is the prior and correct name of the genus in question. *Halistemma* (1859) was published by Huxley for a species from East Australian waters, represented only by the siphosome of a specimen. The identity of Huxley's species has not been established. And so we come to the name *Nanomia* Agassiz, 1863. The figures of nectophores and palpons given by Agassiz (1865) for *N. cara* show the relationship of this species to, and its differences from *bijuga*; and the differences of both species from species of other genera. I give three views of a nectophore of *N. cara* (*Cupulita sarsii*) taken by me in May 1951 on the ebb tide, off the landing stage of Valentia Island, Co. Kerry, Ireland; and a view of a nectophore of *Nanomia bijuga* taken at Villefranche (Text-fig. 19). In order to avoid confusion at the moment I shall use the name *Nanomia*.



Text-fig. 19. A, B, C, upper, abaxial and side views of nectophore of *Nanomia cara* from Valentia Harbour, Kerry, Ireland. × 12. D, upper view of nectophore of *Nanomia bijuga* from Villefranche for comparison with A.

There were colour differences between *N. bijuga*, as observed alive at Villefranche on 23 March 1949, and *Cupulita sarsii* as observed alive at Valentia Island, Co. Kerry, Ireland on 3 May 1951.

	N. bijuga	*N. cara* (*Cupulita sarsii*)
1. Tip of air sac	Plum coloured	Light red
2. Nectophores	Red patch on each side. Red patch in middle of upper side, with sometimes one or two red patches on either side of the dorsal patch	No pigment
(*a*) Young	Red pigment all the way round circular, velar canal	
(*b*) Oldest five pairs	Colour round velar canal lost or absent entirely	
(*c*) Elder dozen or more	Some or all of colour round velar canal lost or absent	
3. Stem of nectosome	Numerous irregular flecks (half bands) of red	Irregular flecks
4. Tentilla	Red	Red
5. Gonads	Red pigment round bases	
6. Gastrozooids	Irregular spots of red, six round mouth, two circlets above and below basal bulb	Small dark plum-coloured spot on side next to tentacle, in basal half only
7. Siphosome	Numerous irregular patches of red on stem	Irregular flecks
8. Palpons	Red pigment round base: band or patch of red round the terminal part	Red pigment round base of oil globule

The gastrozooids of *C. sarsii* appeared pink as the animals were carried along in the ebb tide off the pier at Valentia Island. Further observations on the pigmentation of this species are desirable. At times it is abundant at Valentia Island.

Marrus gen.n.

Type species *Marrus antarcticus* sp.n.
Holotype (in fragments) from 'Discovery II' Station 943

Species of this genus are known from fragments only. The lateral radial canals are unlooped, the tentilla are unicornuate.

Marrus antarcticus sp.n.

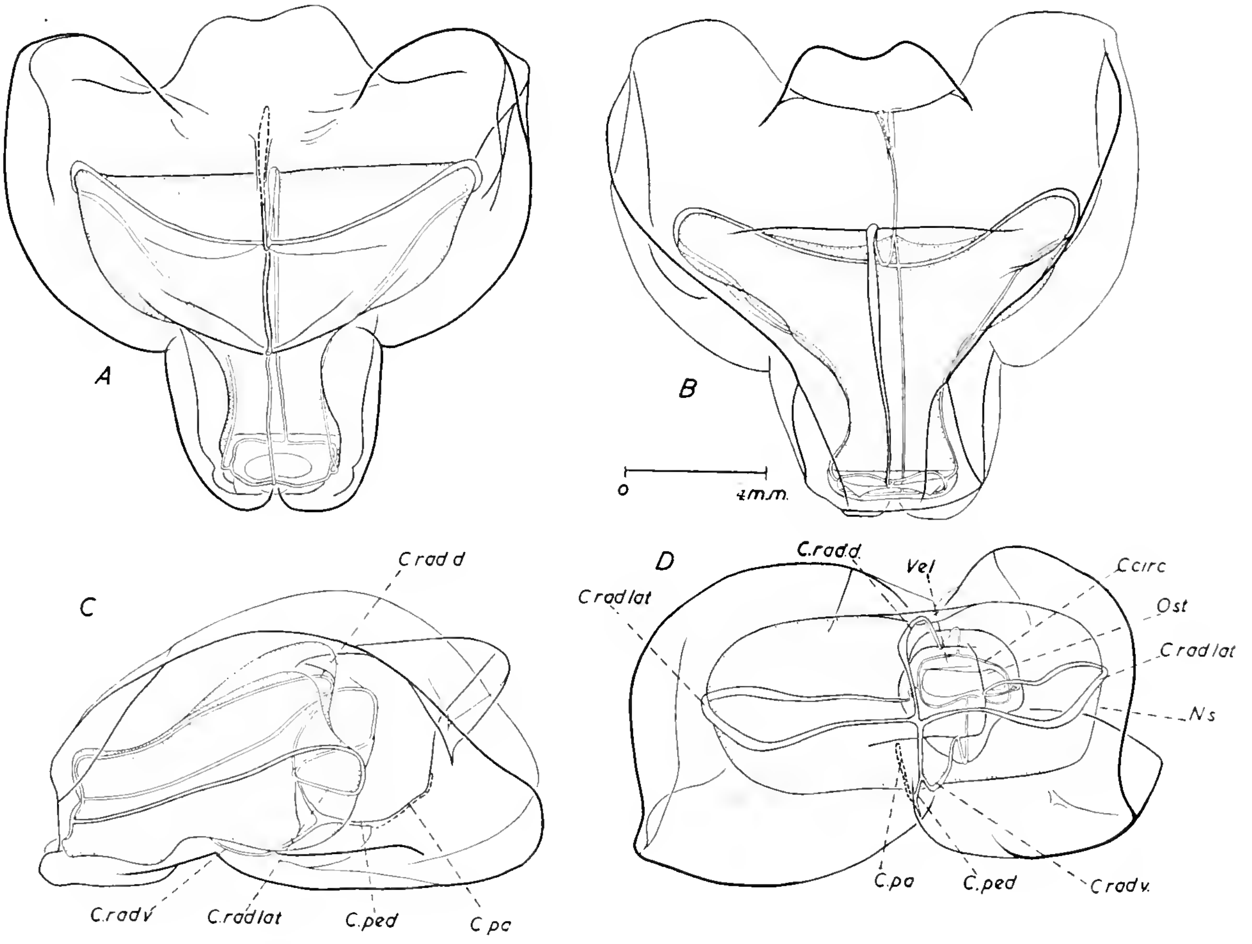
I have named the new genus to which this large Physonect from antarctic and southern sub-antarctic waters belongs after Mr J. W. S. Marr, who has had more than thirty years active association with the Antarctic and has always treated siphonophore material with loving care. He also made useful colour notes on this Siphonophore when it was alive. It appears to be closely related to a species '*Stephanomia*' *orthocanna* from deep cold water in Baffin Bay described by Kramp in 1942, and since collected by 'Scotia' at Station 688 in 1951 at 1100 m., some 5° W. of the south-west end of the Faroe-Shetland Channel.[1] Through the kindness of Kramp I have been able to compare nectophores, stems and siphons. The nectophores of both have straight lateral canals and their other details are very similar. The siphons of both have a long, cylindrical basigaster, and are in other respects similar. Unfortunately, the northern specimens, whose stems show numerous attachments of bracts, were not associated with either attached or unattached bracts except for one specimen which had one small attached one. As described by Kramp, the bract is of a different shape from those so characteristic of *Marrus antarcticus*. The specimens of the northern form had very few tentilla, so that a satisfactory description of them has not yet been made.

DESCRIPTION. **Nectosome** at present known only from loose nectophores. **Nectophores** measuring up to 17 × 15 × 9 mm., lateral facets triangular but not cut off by an oblique cross ridge; two broad lateral wedges, and broad median lappet (thrust block); dorso-lateral ridge bifurcated distally. These ridges are present, though not easily seen except after staining, also in '*Stephanomia*' *orthocanna*, but not figured by Kramp. **Nectosac** lacks musculature on its broad basal (adaxial) face as in '*S.*' *orthocanna*. The blind end extends in the form of two widely rounded lateral arms; lateral-radial canals unlooped. **Siphosome** long, coiled in tight turns when preserved, apparently unsegmented, about 6 mm. in diameter when contracted and preserved. The appendages are all budded from the ventral, non-muscular groove. **Gastrozooids** of a specimen from 'Discovery II' Station 2010, reached a length of 30 mm., of which about half is the cylindrical basigaster. Another gastrozooid (St. WS 552 E) measured 27 mm., the basigaster accounting for 5 mm. It was dilated with food at the distal end which measured 5 mm. in diameter. A third gastrozooid, 15·5 mm. in length, from the same 'William Scoresby' Station 552 E consists of three parts: (1) the basal, cylindrical basigaster, which measures 6·0 mm. in length and 1·0 mm. in diameter; (2) the stomach proper with 'liver streaks', which measures 7·25 mm. in length and 1·25 mm. in diameter; and (3) the oral section (closed) which measures 2·25 mm. in length and 0·5 mm. in diameter. Mature **tentilla** are unicornuate, have no involucrum and a simple, straight canal. The pedicel of a retracted tentillum measures about 0·8 mm., the cnidoband, in three coils, 0·9 mm. and the filament 1 mm. in length. A more extended tentillum

---

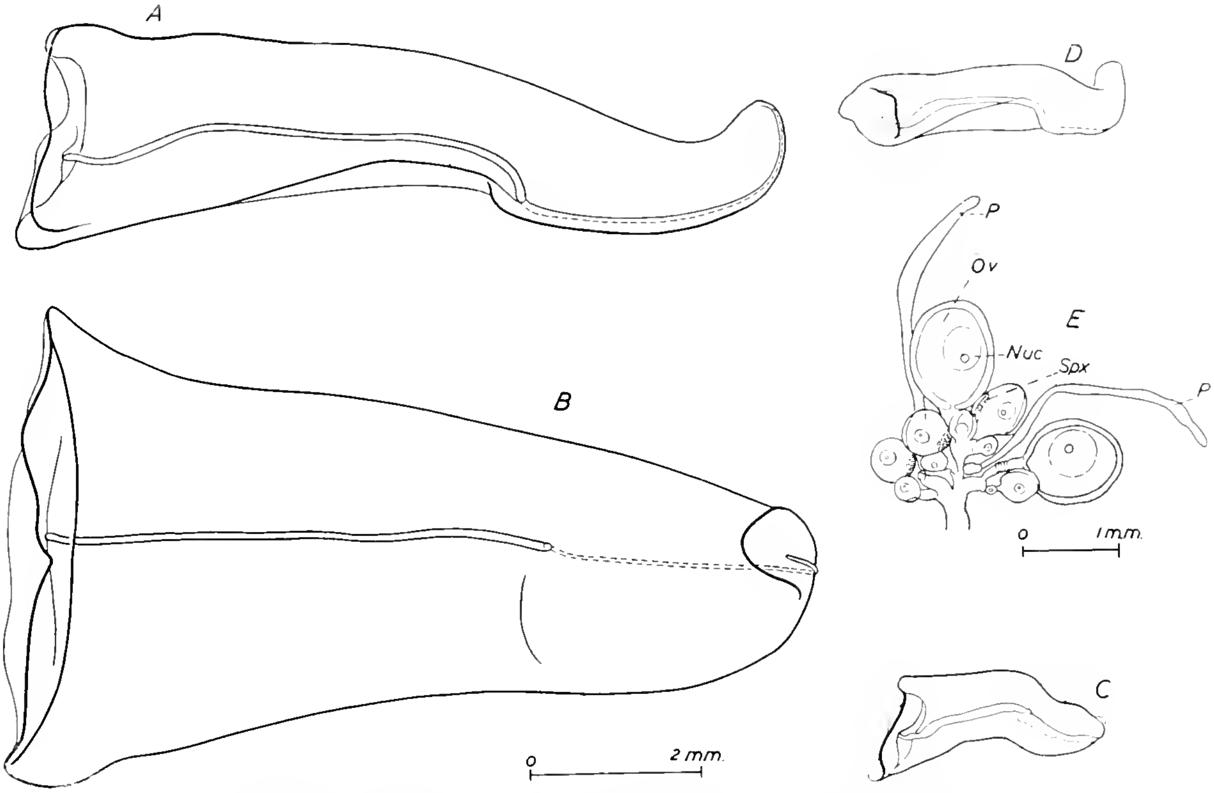
[1] Dr J. H. Fraser of the Scottish Fisheries Department has been kind enough to inform me that evidence from hydrographic data as well as from planktonic data would suggest that there is very little outflow, if any, into the Atlantic through the Faroe-Shetland Channel even in deep water. He thinks that it is much more likely that '*S.*' *orthocanna* and other cold-water plankton species taken in haul S 51/688 had penetrated southwards via the area west of the Faroes than through the channel.

measures: pedicel 1 mm., cnidoband 2·5 mm., filament 5 mm. in length. In young stages the tentilla are finger-shaped, with a patch of large, pavement-epithelial cells over the developing cnidoband: the three sections show histological differences at an early stage. The filament contains numerous smaller ovoid nematocysts (? isorhizas) measuring 18μ in length and 5μ in diameter, as well as larger ovoid nematocysts, type unidentified, measuring 18 × 13μ. The cnidoband has on each side a row of about 125 large nematocysts (? mastigophores) measuring 50 × 20μ. In between these are about 5000 finger-shaped nematocysts (? anisorhizas) regularly arranged in a dozen rows measuring 7μ in diameter and 40μ in length. Their outer ends, which form a pavement, are overlain by large polygonal, epithelial cells measuring 0·04 × 0·02 mm. Often the exploded cnidoband may be found on bracts. **Palpons** are of the same length as siphons, but more slender. No filament has been observed at the base. Some of them, probably all, arise from the gonodendra. **Gonophores** observed have all been female and monovon (Text-fig. 21 E). The largest eggs measure about 1·25 mm. in diameter. The position of the gonophores relative to the gastrozooids has not been determined. Dissection of female gonophores with a micro-manipulator showed that the endoderm of the outer thin coat (umbrella) forms four or more radial canals, and that there is no terminal opening. Inside this outer tunic is another, formed by the irregularly branched spadix (manubrium) (cf. Vogt, 1854, Tab. 10, fig. 25; and Huxley, 1859, pl. VI, figs. 13, 14; pl. IX, fig. 14) that is flattened out by the large ovum. When the ovum is partly grown the spadix grows up to one side of it and wraps branches



Text-fig. 20. *Marrus antarcticus* gen.n., sp.n., 'Discovery II' St. 943, 1000–750 m. Nectophore; A, underside; B, upper side; C, lateral view; D, adaxial view. × 4·6. The muscular lamella is attached along the pecked continuation of the pedicular canal.

round it, but leaves an oval area on the other side free. Under the spadix lies the nucleus. A similar condition was figured by Weismann (1883, Taf. XXII, and p. 203) for *Agalma rubrum* (*Stephanomia rubra*). **Bracts** are very characteristic in shape (Text-fig. 21). The bracteal canal terminates on a papilla on the concave terminal facet. The presence of young bracteal buds of this characteristic form is the criterion for identification of large pieces of the siphosome, and at once distinguish such pieces from those of another antarctic physonect *Stephanomia convoluta*, whose young bracts have a terminal sausage-shaped mass of nematocysts lying in the sagittal plane of the bracts, separating the two oblique, dorso-lateral, terminal facets. The muscular lamellae of bracts and buds of bracts are closely crowded together in at least six rows on either side of the gonophores in the contracted and preserved material, and most of the gastrozooids are detached.



Text-fig. 21. *Marrus antarcticus* gen.n., sp.n., WS St. 552 E. A, B, two views of adult bract; C, D, side of young bracts; E, gonophore, × 13. A, B, C, D × 12.

Colour. There are colour notes on Antarctic physonects by members of 'Discovery' staff made on four occasions on board while sorting the plankton. They related to specimens of two physonect species that turn out to be other than *Pyrostephos vanhoeffeni*.

It has been a difficult matter to apply these notes because on each of the four occasions (Sts. 890, 2001, 2006 and 2010) all three Antarctic physonects were present in the catch; but, bearing in mind that it is possible that I have made some mistake, the following collectors' notes appear to apply to *Marrus antarcticus*:

(1) Station 890, N 100 B. A large part of the siphosome (no nectosome) labelled '*Pyrostephos vanhoeffeni*'; 'typical deep brown colouring [probably applies to gastrozooids] central stalk portion bright pink'.

(2) Station 2001. 'Stolon deep orange crimson [this appears to refer to a specimen of the nectosome, without nectophores, of *Stephanomia convoluta*]. Coloured part of bells [*Marrus antarcticus*] very rich deep orange red.'

(3) Station 2006. 'Stolon [this appears to refer to two specimens of the nectosome, without nectophores, of *Stephanomia convoluta*] and coloured part of swimming bells [*Marrus antarcticus*] very deep rich scarlet orange.'

(4) Station 2010. Part of the siphosome and numerous appendages of *Marrus antarcticus*: 'Stolon milk white, tinged with a lovely rose pink, large tasters [? gastrozooids] deep purple brown: faint purple-red streak [canal] in bracts, also in swimming bells.'

Distribution:

A. Antarctic Zone

(1) Boundary depths between the cold bottom water (which must have a small northward creep as well as eastward movement) and the warm deep layer (in which the water must be assumed to have a small southward creep as well as eastward movement):

'Discovery II' Stations	Depth (m.)
661	1500–1000
663	1500–1000
2001	1750–1300
2006	1750–1400
2010	700–400

(2) Warm deep water:

'Discovery II' Stations	Depth (m.)
1728	800–350
WS 552	290–190

B.A.N.Z.A.R. Exp. Station	Depth (m.)
31	1000–0

(3) Boundary depths between the warm deep layer and the cold antarctic surface water:

'Discovery II' Station	Depth (m.)
890	240–110

B. Sub-antarctic Zone

(4) Water layer into which the antarctic surface water sinks when it sinks below the surface at the antarctic convergence:

'Discovery II' Stations	Depth (m.)
671	1000–750
943	1000–750

(5) Warm water below the sinking antarctic water:

'Discovery II' Station	Depth (m.)
2023	1500–1000

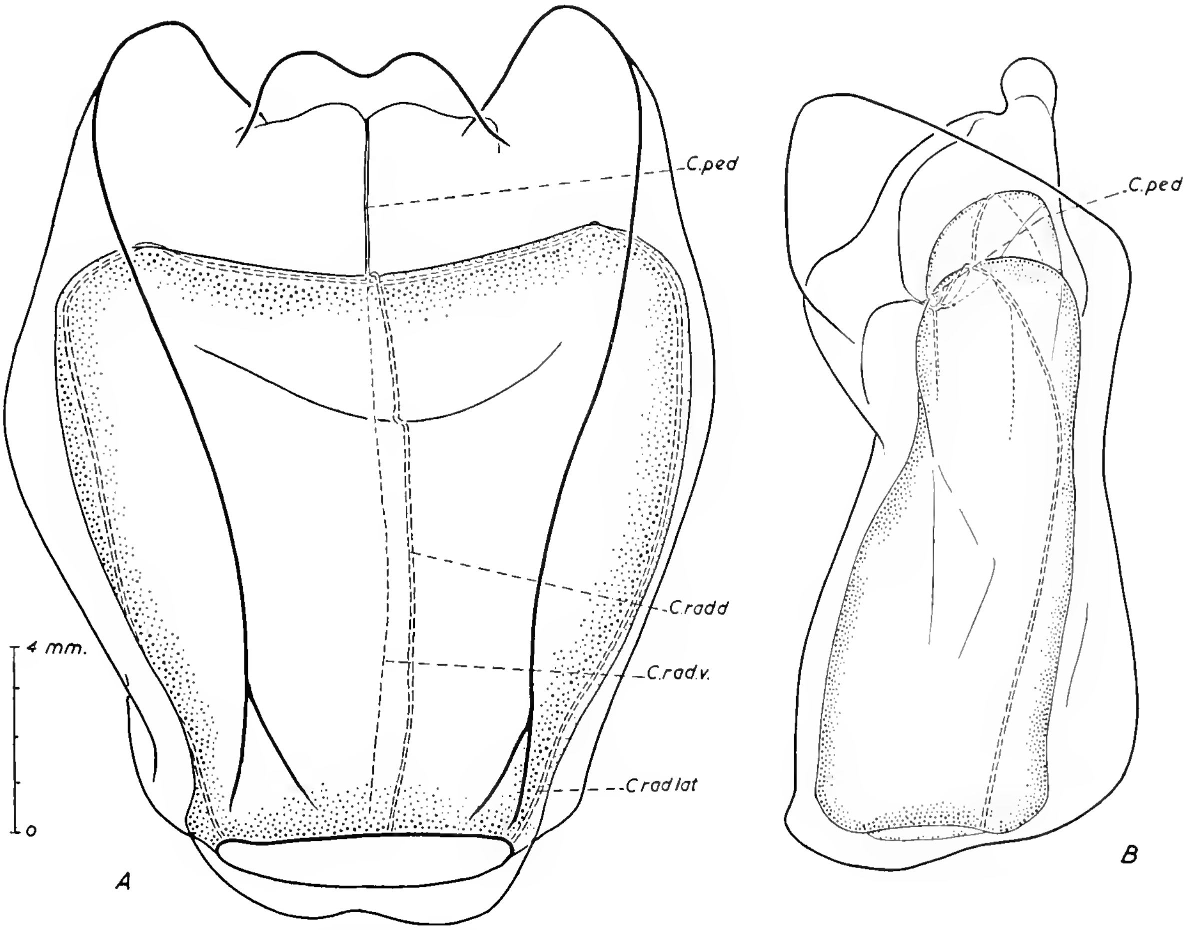
I am obliged to Dr G. E. R. Deacon for identifying the water-masses concerned, and for suggesting the generalization that *Marrus antarcticus* thus appears to be associated with the antarctic zone and with water that has recently left the zone, or to live in close proximity to such water. It appears to be a deep water or mid-water form; but a scarcity of very deep net hauls prevents the formation of conclusions about its distribution at great depths.

The figured holotype (a nectophore) came, with other fragments, from 'Discovery II' Station 943, and bears the Brit. Mus. (Nat. Hist.) Register No. 1952. 11. 19. 26 (Text-fig. 20).

Marrus orthocannoides sp.n.

A haul of the young fish trawl from 1400 to 700 m. at 'Discovery II' Station 1585 in the West Tropical Indian Ocean contained loose nectophores (Text-figs. 22, 23), bracts and denuded stems (nectosome and part of siphosome) of a new Physonect that appears to be closely akin to the high-arctic species '*Stephanomia*' *orthocanna* Kramp. Dr H. Bargmann of 'Discovery Investigations' has kindly made an approximate estimate of what would have been the temperature and salinity reading at the time and place of capture. Her figures are:

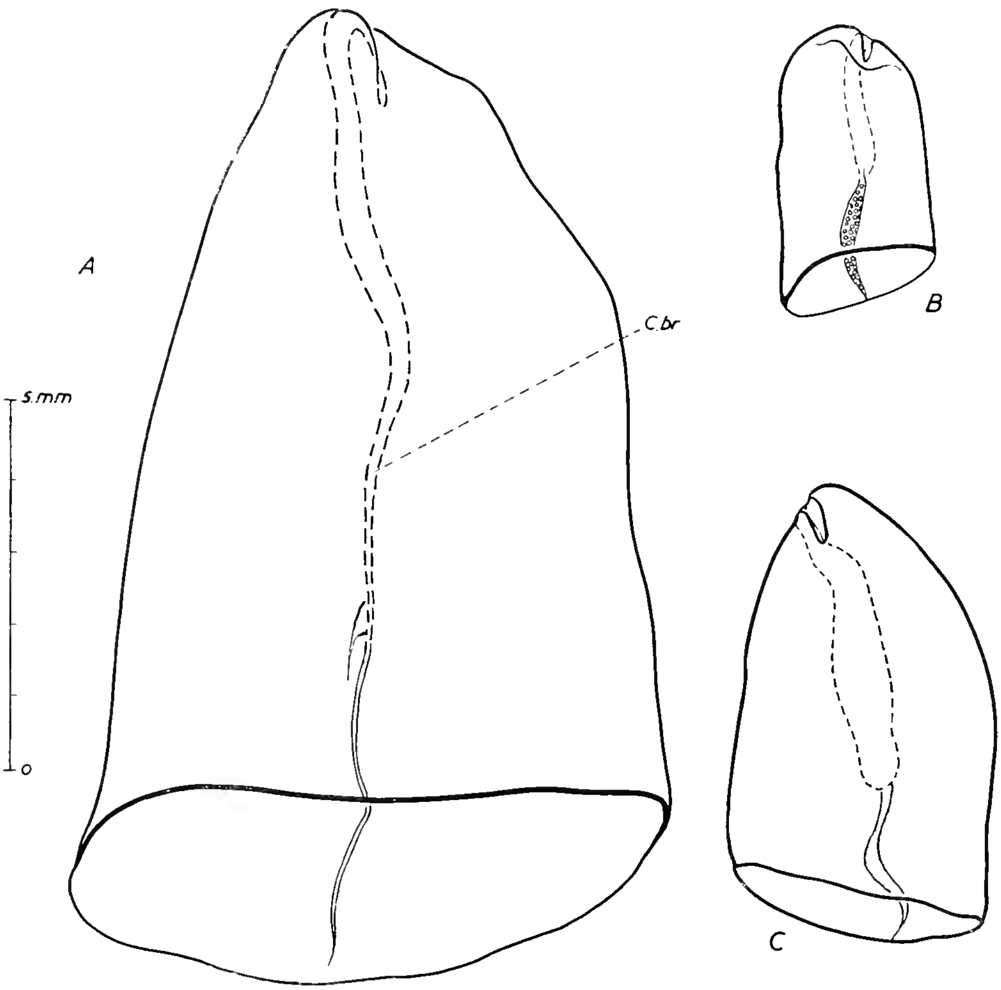
Depth (m.)	T. ° C.	S.‰
1400	4·85	34·84
700	8·35	34·98



Text-fig. 22. *Marrus orthocannoides* sp.n. Upper and side views of a nectophore from 'Discovery II' St. 1585, 1400–700 m. ×6.

I have already described (p. 55) a new antarctic Physonect which appears, in the present state of our knowledge, to be congeneric with '*S.*' *orthocanna*, and owing to the fact that, since the name '*Stephanomia*' is used in a loose way for a number of macrostele Physonects, whose tentilla have single terminal filaments, these three species have been placed in the new genus *Marrus*. The study of each of these three related species has been difficult because of the fragmentary condition of the material.

The nectophores of the three related species are characterized by the absence of any oblique ridge dividing the lateral facets. On the dorsal surface there is a pair of ridges dividing it from the lateral surface. Each divides again before reaching the ostium of the nectosac. These ridges are not shown in the figures by Kramp (1942) of '*Stephanomia*' *orthocanna*, but, after staining a nectophore kindly supplied by Kramp, I am satisfied that these ridges are present, though not well marked. In all three species the place of attachment to the muscular lamella is deeply sunk, as Kramp says, in a narrow longitudinal furrow. The lateral radial canals follow a straight course to the ring canal. There is a ventral, medianly cleft mouth-plate. Whilst in '*S.*' *orthocanna*, and in its antarctic counterpart mentioned on p. 59, the proximal side of the nectosac, bearing the junction of the canals, is free of muscular tissue, in *orthocannoides* it is not so, nor is the wall of the nectosac of *Marrus orthocannoides* sunken in as it is in those two species.



Text-fig. 23. *Marrus orthocannoides* sp.n. A, fully grown; B, C, young bracts, × 10. The pecked portion of the bracteal canal indicates the area of attachment of the bracteal muscle.

Bracts. In a row (? rows) flanking the palpons, thin and leaf-like, the largest about 15 × 8 mm., ovate, without marginal teeth. There are signs of thickened oblique truncate distal ends. The bracts' attachment to the muscular lamella takes place along the proximal two-thirds of its length, so that the terminal canal measures about one-third of the bract length. This canal appears to terminate in the middle of one margin of the end-facet, without any sign of a pit or other surface marking. All the bracts are detached.

Palpons. Very numerous, slender, 9·2 mm. long × 0·2 mm., on short pedicels, close set in four to five longitudinal rows, each with a fine tentacle.

Gonodendra. Fine, about 4·6 mm. long, two or three per segment of stem, bearing a dozen or more male gonophores on very short pedicels. The gonophores are globular, the largest measures 1·1 mm. in diameter. As the gonophores of *Marrus antarcticus* were all female, it appears that *Marrus* may be dioecious.

Stem (? contracted). Air-sac oblong, 6 × 2 mm.; nectosome 14 × 2 mm.; siphosome 23 cm. long, 4·6 mm. measured dorso-ventrally, 3·7 mm. side to side, very muscular, segmented. Gastrozooids and tentilla missing. Other appendages (not well preserved) in a ventral band 2·7–3·7 mm. wide.

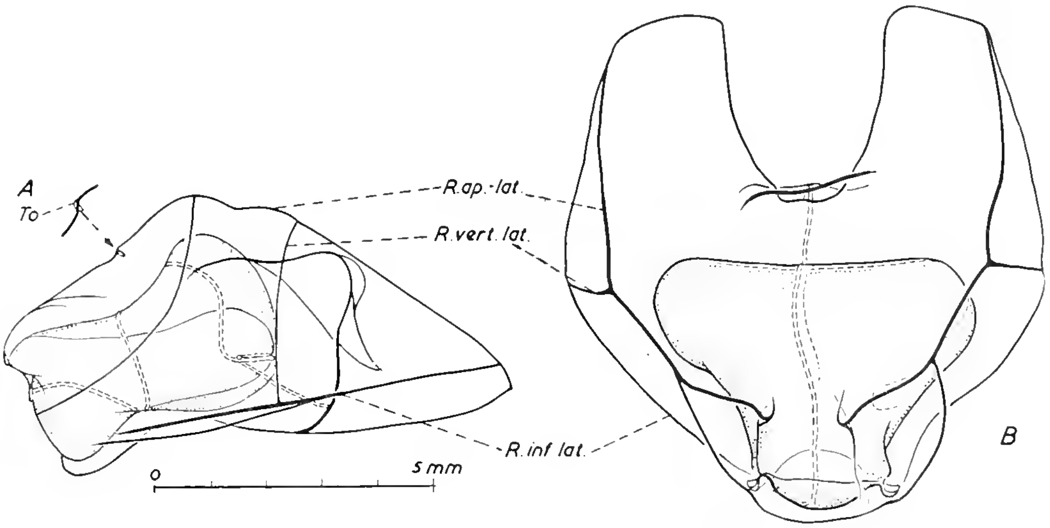
I take this opportunity to publish a second record of the capture of *Marrus* (*Stephanomia*) *orthocanna* Kramp by 'Scotia' on 31 August 1951 in haul 688. Locality: 59° 50′ N., 11° 24′ W., two loose nectophores, which I have compared with type material.

The figured holotype of *Marrus orthocannoides* bears the Brit. Mus. (Nat. Hist.) Register No. 1952. 11. 19. 4.

Agalma elegans (Sars), 1846.

Agalmopsis sarsii Kölliker, 1853*b*.

I have found no adult specimens, not even loose nectophores, of this species amongst the 20,000 siphonophore specimens that I have examined from the Gulf of Aden, or from the Somali or Arabian basins of the Indian Ocean. But in November 1950 and January 1951 'Manihine' took eighty-four small nectophores at five stations in the Red Sea (16–17 January 1951) at a distance of from 5 to 35 miles east of Sanganeb Lighthouse, off Port Sudan, where the temperature must have been about 21·5–22° C. Also 'Discovery II' took a young specimen at Station 2906 in the Red Sea. It had two gastrozooids (no tentilla are visible) and two nectophores 4 mm. in diameter, which I have compared carefully with Mediterranean specimens (Text-fig. 24). The only other specimens that I have found in the whole of the vast amount of 'Discovery' material from the Indian or Atlantic Oceans were some well-preserved young ones, of typical form taken at Station 273, differing in no way from those that I have examined from Villefranche, the Celtic Sea (M.B.A. Plymouth 'Mackerel Cruises'), Valentia harbour (E. T. Browne collection) and to the north-west of the British Isles ('Scotia' 1951, St. 683, 60° 18′ N., 12° 20′ W.). I must mention that Bigelow's figure (1911*b*; pl. 19, fig. 2) of a nectophore does not perhaps give a very good idea of the typical form. In fact for years this figure misled me into mis-identifying the juvenile nectophores of *Agalma okenii*, which have only one ridge on the lateral facet (see p. 64) as those of *A. elegans*. I give this warning because Bigelow's famous report is a standard reference work, and his figure is the only one likely to be used by planktonologists. Leuckart (1854; pl. 12, fig. 22) illustrated well the characteristic dorsal view, and showed its difference from that of *Stephanomia rubra*, which he illustrated on the same plate in fig. 12. Leuckart's drawing of the



Text-fig. 24. Side and upper views of nectophore of *Agalma elegans* from Villefranche, × 8.

lateral radial canals, however, is not very good. My new drawing of the nectophore (Text-fig. 24) is still not quite satisfactory.

From 'Discovery II' (East African line) Stations 1567, 1568, 1581, 1583, 1584, 1586 and 1587 come larvae with bracts typical of larvae thought to be those of this species. These bracts are identical in shape with those of larvae taken with adult specimens in the Celtic Sea, and also with those of a series of post larvae taken by 'Scotia' and kindly sent by Dr J. H. Fraser of Aberdeen. A study of the 'Scotia' specimens has enabled me to say that the well-known larval Agalmid stage (see Haeckel, 1888*b*; pl. XXI, fig. 12) in which larval bracts cover the air-sac and all buds, is followed by one in which the nectosome elongates and emerges from the whorl of larval bracts. The last of these, however, remain for a time attached by their muscular lamellae to their supporting prominence, and have been found in specimens 3 or 4 mm. in length, after the appearance of a second functional gastrozooid, and even in the terminal cormidium of a specimen 7 cm. in length. The buds of the nectophores now grow and begin to function. There is a second smaller gastrozooid and a ring of from four to eight palpons present at this stage, which is prior to the elongation of the siphosome in the reverse direction to that of the nectosome and to the appearance of a succession of secondary stem groups of buds. The stage before the appearance of secondary groups is reminiscent of the adult *Nectalia loligo*, and might be referred to as the 'Nectalia-stage' in the same way in which earlier stages are referred to as 'Athorybia-larvae' because of their resemblance to miniature specimens of *Athorybia rosacea*. In the 'Nectalia-stage' the terminal gastrozooids are surrounded, just as they are in *Nectalia*, by a number of long, trifid bracts of the general shape figured by Haeckel (1888*b*; pl. XIII, figs. 1, 9–12). They are very much like those of *Athorybia rosacea* and, since they are probably pre-cormidial as Garstang suggested, they may be homologous with them and with the larval bracts of *A. okenii*. It remains to work out in *Agalma elegans* the succession of bracteal types and their situation on the stem.

A slightly later stage at which four or five nectophores are functional, is represented by a series of beautiful specimens taken at 09.15 hr. at Villefranche on 28 March 1949 near the surface in a 1-m. net. In these, the larger of the two terminal gastrozooids described above for the 'Nectalia-stage' bears an adult-type tentacle (but with only two turns of the cnidoband, and the involucrum either covering it completely or only partially on one and the same tentacle), whilst the smaller one bears a tentacle with kidney-shaped (larval-type) tentilla.

If anyone was able to devote the spring of a year like 1949, when *Agalma elegans* was abundant at Villefranche, to watching the development of this species he would, I think, be able to confirm that in the course of its life-history it passed through successive stages reminiscent of *Athorybia*, *Melophysa* and *Nectalia*[1] and would therefore come to the conclusion that species of these genera have become neotenic at successively later evolutionary stages.

I take this opportunity of publishing the following data for a live specimen 12 cm. in length, taken at Villefranche on 14 April 1949. Nectosome: 3·5 cm. long, 1 cm. diameter; ten nectophores on one side and nine on the other, and buds. Siphosome: three complete gastrozooids, one young one. Gastrozooids 5 cm. apart. The terminal gastrozooid was surrounded by a ring of palpons. But the tentacle of one 'palpon' bore larval type tentilla so that it was probably the secondary gastrozooid. The rest had ordinary thread-like tentacles. The terminal gastrozooid bore a typical tentacle 12 cm.

---

[1] *Nectalia* Haeckel, 1888*b*, should be accepted with some caution, since specimens with the very peculiar tentilla that Haeckel figured have not certainly been seen again, and his figures are often not dependable. Bigelow's (1911*b*, pl. 20, figs. 4, 5) specimen may be a young stage of a long-stemmed form. I have examined many such specimens taken at Bermuda by Beebe, but a great deal more work has still to be done on the large amount of Agalmid material sent me by Beebe before the question can be resolved. I hope eventually to be able to link up these *Nectalia*-like specimens with a giant form that I provisionally called *Stephanomia amphitridis*. They have a new type of nectophore.

or more in length (expanded) with twenty-seven tentilla, 5 mm. apart when expanded. The expanded horns of the tentilla measured 3 mm. in length.

I have examined closely the arrangement of the gonophores in a specimen that I anaesthetized and fixed in formalin at Villefranche on 5 May 1949. The female gonophore is at the proximal end of each segment, just distal to the last gastrozooid. It has a plain stalk which subdivides distally. Following it is a gap, and then male gonophores and palpons are scattered over more than half the length of the segment. Another gap follows and then the gastrozooid and a group of palpons are found. A newly budded gastrozooid is accompanied by a single palpon. More are added in the course of growth in the region of the male gonophores. The general arrangement was shown quite clearly, if a little crudely, by Kölliker (1853*b*, pl. 3).

The pneumatophores of live specimens (7–12 cm. in length) varied in shape, presumably according to the state of air-secretion.

In jars of sea-water at Villefranche, specimens at rest took up a vertical position, but swam round horizontally at the surface. On 5 May 1949, the calm water off Cap Ferrat, Villefranche, was full of *Agalma elegans* and *Stephanomia rubra*, and six dozen of the former were picked out with dip-nets at 8.45 a.m. on this fine sunny morning (wind S.E., light). Specimens had fourteen to twenty nectophores a side, six gastrozooid groups, and were about 17 cm. in length (contracted). It may be noted that specimens like these can be lifted out of the water on a flat dip-net and jolted into jars of sea-water without damage.

Kawamura (1911*b*) studied alive a species which he identified as *Agalma elegans*. He captured and illustrated one perfect specimen 26 cm. in length at Misaki on 29 January 1910, and observed, without being able to catch them, a number of much larger specimens that were swimming at some depth from the surface. From a glance at Kawamura's figures (1911*b*, pl. 7) it will be seen that there are two important differences between the figure of a Misaki and a Villefranche nectophore. One is the abaxial shift in position of the vertical ridge in Kawamura's specimen, and the other is the way in which the lateral radial canal, in his fig. 13, crosses the lateral face of the nectosac. If these prove to be constant features of a Pacific form it will merit specific rank. But Kawamura's fig. 13 does not appear to have been so carefully drawn as others. The upper and lower vertical 'branches' of the pedicular canal described by Kawamura form the area of attachment of the muscular lamella. Kawamura commented on the length of the paired horns of the tentilla, and figured them as somewhat less than 1 mm. in length. I measured them in an expanded, live specimen and found them to be three times this length. I found also that specimens (from 7 to 12 cm. in length) were very susceptible to vibration and contracted violently.

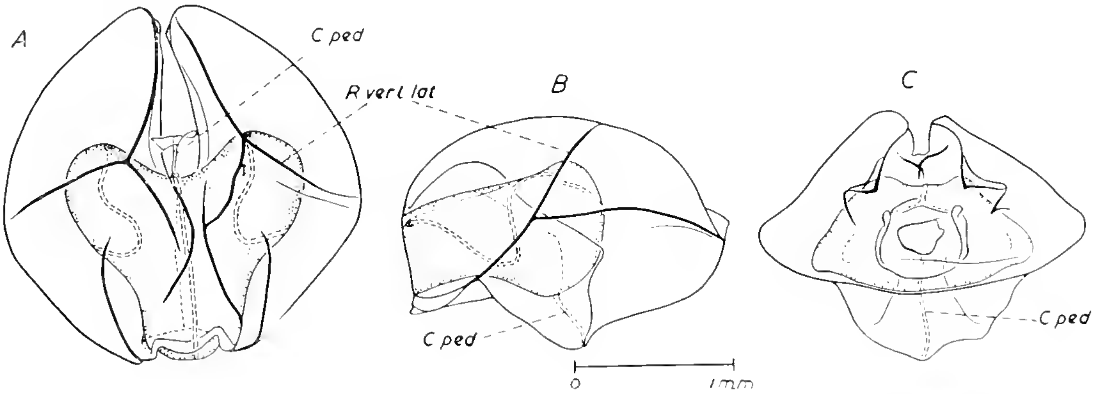
Agalma elegans was hitherto known to occur in the Indian Ocean only from Browne's (1926) record of a post larva with a couple of not very characteristic bracts, and without nectophores. It has a protosiphon, a ring of palpons, and many buds.

It is a pity that Haeckel (1888*b*, p. 234) restricted the name *Agalmopsis elegans* to that one of Sars's two species which had trifid tentilla, because nowhere did Sars describe or figure the rest of a specimen of that species. All his figures and most of his text, based on notes made during the eight years 1835 to 1842, is descriptive of what Agassiz (1865) later called *Nanomia cara*. Kölliker (1853*b*) had already given the Agalmid a new specific name *sarsii*. Haeckel seems, mistakenly, to have thought that the whole of Sars's plate 6 referred to the specimens with trifid tentilla. He seems, too, to have overlooked the fact that eight years before his description of *Agalmopsis* was published, Fewkes (1880, p. 135) restricted *Agalmopsis elegans* to the species (now *Nanomia cara*) that had a single terminal filament. But I dare not cause further nomenclatural havoc by putting these matters right now. The best thing to do is to have the name put on the list of *nomina conservanda*. We can be certain, however, of the identities of Sars's two species because of their frequent association in these northern waters.

Agalma okenii Eschscholtz, 1825.

Plethosoma cristalloides Lesson 1826; 1838. (For synonymy see Bigelow 1911 *b*.)

Kawamura (1911 *a*) studied specimens at Misaki in the winter. He observed, described and figured specimens of what he considered to be two separate species, *Agalma okenii* Eschscholtz and *Crystallomia polygonata* Dana. Specialists for the last forty years have thought that the two names were synonyms of one and the same species, but Kawamura's criteria are clearly set out and illustrated on his plate 16. Much research will be needed before his claim can be either supported or refuted. He considered one of the characters of the smaller *C. polygonata* to be that in its nectophores there is only one vertical ridge on the lateral facet, so that it has only two parts instead of the three found in *Agalma okenii*, though reference to Dana's (1858) original figure shows that the nectophores had two vertical ridges.



Text-fig. 25. Three views of a young nectophore of *Agalma okenii* from the Gulf of Aqaba, 'Manihine' St. 1, ×21. Only one ridge is developed on the lateral facet.

Meanwhile, I am able to contribute towards what I believe to be the solution of the problem of the existence of two types of nectophore associated with *okenii* type bracts, the two differing only in the number of the longitudinal ridges on the lateral facets. The solution is that Kawamura's smaller *Crystallomia polygonata* is a young stage of *Agalma okenii*. A long search through accumulated material of *A. okenii* at last revealed the presence of two young specimens of *A. okenii* each about 1·5 cm. in length having only two functional gastrozooids. A few larval type bracts were still attached, and the budding nectophores all possessed two longitudinal ridges on the lateral facets. But each specimen was associated with one or two nectophores, 8 mm. in diameter, that possessed only one longitudinal ridge. I tentatively suggest, therefore, that the earliest nectophores, like the larval bracts, may have only one ridge whilst the subsequently budded bracts and nectophores have more. The critical specimens upon which this view is based are:

'Terra Nova', 1910–13:

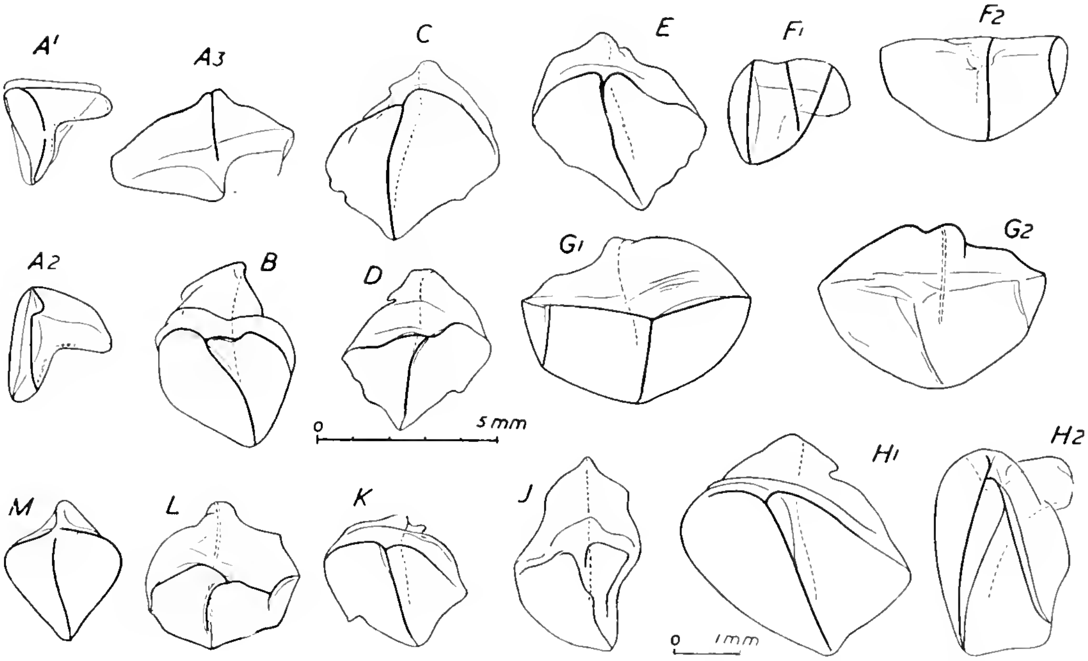
Station 32. A series of nine young specimens taken in the tropical Atlantic south of the Cape Verde Islands. The seven youngest specimens possess nectophores and buds of the 1-ridge type. The two elder ones possess nectophore buds of the adult (2-ridge) type.

Station 63. Two young specimens taken a little further south than the last. One of them had still attached to it a nectophore of the juvenile (1-ridge) type, and was associated with detached nectophores of the same (1-ridge) type. In the catch also were pieces of a larger specimen and detached nectophores of the adult (2-ridge) type.

Station 107. Three young specimens were taken off Three Kings Islands, North Island, New Zealand. One of these had nine attached nectophores of the juvenile (1-ridge) type as well as buds of the same type, but not of the adult type. There were present also detached nectophores of the adult (2-ridge) type.

Mr Fraser-Brunner's collection (Gulf of Aden). On the night of 26 November 1949, Mr Fraser-Brunner took at the surface, ten miles north-east of Alayu one young specimen (only two gastrozooids developed) that had still attached to it one nectophore of the larval (1-ridge) type, as well as a larval bract. It was associated with one detached nectophore of the adult (2-ridge) type.

'Discovery II' Station 1598, 460–300 m. (tropical Atlantic), 1 juv. ex. 1·5 cm. in length with one attached nectophore possessing a single longitudinal ridge on its lateral facets. It was associated with two more young specimens, one of which still had two bracts of the larval type attached near the penultimate gastrozooid. Four gastrozooids are present, a reduced terminal one—the protozooid, but no tentacle is visible—two functional gastrozooids and one well-developed bud. The bracts are similar to those shown in Text-fig. 26D, E.



Text-fig. 26. Larval bracts of *Agalma okenii* from the Gulf of Aqaba. A^1–J × 5; H^1, H^2 × 9. The numerals indicate that more than one view is given of a particular bract.

Dr W. Beebe's collection (Bermuda, where the species appears to be plentiful). A young specimen numbered 312117, net 1314, and 1·5 cm. in length, has some larval type bracts, and only two functional gastrozooids. There is no sign of larval type tentilla and the budding nectophores all possess two longitudinal ridges on the lateral facets. Associated in the phial with this specimen were two unattached nectophores, 8 mm. in diameter, and some unattached larval type bracts. One of these nectophores had only one ridge, the other had traces of a second.

H.M.S. 'Challenger' in October 1950 took some larvae and post-larvae about 30 miles off the Pacific coast of Costa Rica. There were in the catch small detached nectophores of the 1-ridge type. The temperature of the surface water, in which the larvae were probably living, though the tow was made at a depth of 27 m., was 26·6° C. Long ago Bigelow (1911*b*) dealt with Lens & van Riemsdijk's (1908) attempt to split the species *Agalma okenii* on the form of the tentillum, which is one of Kawamura's criteria.

The number of specimens taken by 'Discovery II' or 'Manihine' in the Indian Ocean was small when one remembers that, quantitative considerations apart, at a single station, No. 4600, in the Eastern Tropical Pacific 'Albatross' took fifty-seven complete specimens, as well as innumerable loose cormidia and nectophores. At three stations off the East African Coast, 'Discovery II' took four small specimens, fifty-six small nectophores and fifty-two bracts, while at six Aqaba stations 'Manihine' took two very small specimens, three small nectophores and a small bract, as well as seven specimens of what appears to be the little known larvae of this species, and twenty-one loose larval bracts. These bracts are the field-mark of these larvae. They differ considerably in shape from those of *A. elegans*. Mr Fraser-Brunner, however, took many specimens in the Gulf of Aden as indicated below.

Material. The following specimens belong to the stage in which the nectophores have a single ('equatorial') lateral, longitudinal ridge:

'Manihine'

Aqaba Station	Depth (m.)	Complete ex. and cormidia	Small loose nectophores	Small loose bracts	Post-larvae	Loose larval bracts
1	183	1	.	.	3	12
13	130–0	.	.	.	2	3
17	180–0	.	2	.	.	4
23	183	1	1	1	.	.
25	180–0	.	.	.	1	.
29	180–0	.	.	.	1	2

'Discovery' Stations: SS 43 (1 nectophore); 288 (2 juv. ex.); 299 (nects); 'Discovery II' 679 (1 ex. and nects); 689 (1 nect.); 690 (nects and bracts); 693 (part of ex. and cormidia); 694 (nects); 695 (2 ex. and nects); 696 (cormidia and nects); 698 (nects); 704 (nects); 705 (nects); 1372 (cormidia and nects); 1373 (1 ex., nects and bracts); 1567 (nects and bracts); 1580 (nects); 1581 (1 juv. ex., nects and bracts); 1585 (4 juv. ex., cormidia and nects); 1586 (nects and bracts); 1752 (1 ex., no nects); 2648 (nects).

'Terra Nova' 1910–13 Stations: 45, Atlantic (nectophores); 56, Atlantic (1 nectophore); 311, 35° 29′ S., 51° 21′ W. (1 nectophore).

The following specimens belong to the typical adult stage in which there is a second lateral, longitudinal ridge on the nectophores:

'Discovery II' Stations: 1375 (nects and bract); 1576 (1 ex.); 1580 (nects and bracts); 1585 (6 juv. nects); 1747 (1 ex. and cormidia); 1759 (nects and cormidia); 1760 (2 adult ex.); 2681 (6 adult ex.).

The specimens from Station 1760, where the surface temperature was 21·22° C. are from 5 to 6 cm. in length, and the siphosome consists of from ten to twelve segments. The terminal (? primary) gastrozooid is much smaller than those in the middle region, and has a reduced basigaster. The bracts are arranged in five rows on each side in the middle region and in three rows near the end.

Numerous specimens with nectophores of the 2-ridge type were taken in Bermuda by Beebe.

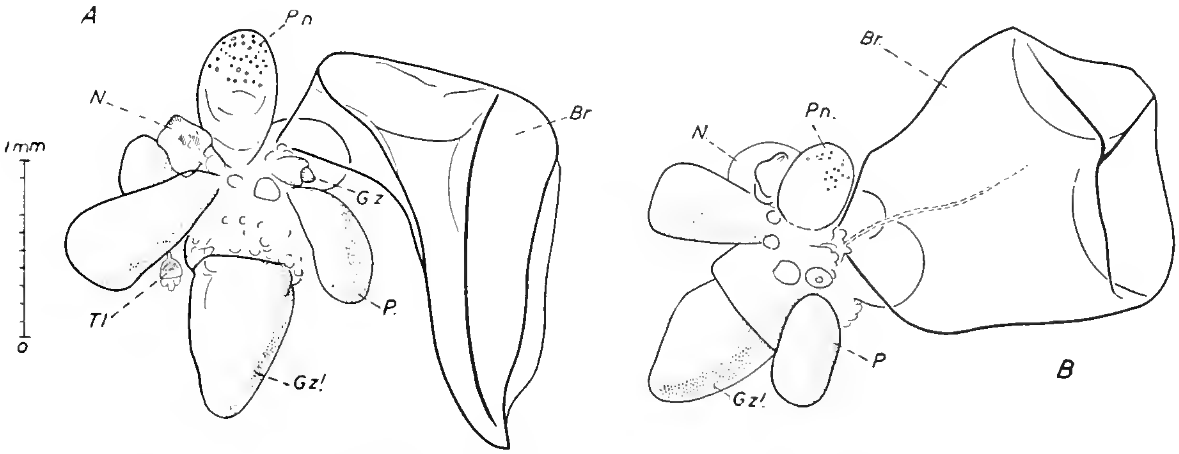
A fine specimen of *Agalma okenii* (siphosome only) from 'Discovery II' Station 1752 is nearly 6 cm. in length. Some of the tentilla have as many as sixteen turns of the cnidoband, and the involucre covers from six to nine of them. The first seven turns are larger in diameter, and are flanked by the larger, elongated type of nematocysts, whose threads can penetrate through at least 6 mm. of bracteal jelly. The terminal eight or nine turns, which are not so flanked, are smaller in diameter. In the absence of nectophores this specimen cannot be placed in either of the above groups of specimens, though it is typical of the species.

'Terra Nova' 1910–13 Stations: Station 46, 1 specimen possessing buds of nectophores and detached nectophores of the adult (2-ridge) type: 56 (1 nectophore); 59 (nectophores); 69 (nectophores).

Mr Fraser-Brunner's collection (Gulf of Aden). Off Aden (night, 5. xii. 1948) several adult specimens (and five larvae); off Aden (day, 6. xii. 1948) parts of several adult specimens; 20 miles north-west of Bulhar one small specimen with adult (2-ridge) type nectophores.

'S.V. Cap Pilar' (Seligman collection). At a position in 35° 21·5′ S., 66° 22·5′ E. (to the south of 'Discovery II' Station 1754) at the surface on 30 April 1937 an adult specimen was taken bearing twelve to thirteen gastrozooids.

Larvae. There is no record of larvae having been bred since Haeckel (1869*a*, *Crystallodes rigidum*) watched their development in the Canary Island of Lanzerote in the winter of 1866–7, though Lens & van Riemsdijk (1908) recorded what is probably a series of thirty-four post-larvae of this species under the name '*Crystallomia* spec. group I'. Twenty-three of these formed a series, specimens increasing gradually in length from 1·5 to 12 mm. Four of them were in the monogastric stage, but bore no larval bracts, except one which evidently had a bud of one. Lens & van Riemsdijk described the succession of types of tentilla. It will therefore be of interest to illustrate some post-larvae taken by 'Manihine' in the Gulf of Aqaba Station A 1 (Text-fig. 27). Their specific determination depends on the facts that they have trifid tentilla like *Agalma* spp. and that the bracts differ from those of the only other *Agalma* species *elegans*, but agree with those figured by Haeckel for *Crystallodes rigidum* (= *Agalma okenii*).



Text-fig. 27. Larva of *Agalma okenii* from the Gulf of Aqaba, 'Manihine' St. 1, × 23.

The three interesting monogastric larvae bearing larval bracts and a larval type of tentillum were taken at 'Manihine's' Aqaba Station A1 made on 31 December 1948 in 15 fathoms. The smallest of the tentilla measured about 0·2 × 0·13 mm., having three tiny processes at the distal end, one turn of the cnidoband, and a number of nematocysts (0·01–0·06 mm. long) set obliquely at the base (cf Lens & van Riemsdijk, 1908; fig. 98, pl. XIII, 'type 1').

Dawydoff (1928) has given a warning that accounts of siphonophore development prior to those of Metchnikoff must be treated with caution. This warning should be extended to Dawydoff's own short summary, which contains false statements as well as interpretations. The remarkable allegation by Haeckel (1869*a*) that the pneumatophore originated as a diverticulum of the common 'Primitivhole' was by implication denied in 1888*b*, when he said that in all cases the pneumatophore arose as a gland-like invagination of the exoderm. It is very difficult to see the structural details of these siphonophore larvae when they are alive, except in the early stages. I am concerned here only with the larval bracts figured by Haeckel. They have a shape that is characteristic, and is shown in lateral view by Haeckel's (1869*a*) plate VII, fig. 51. The upper and outer faces are nearly at right-angles to one another, and the outer face is divided by a longitudinal ridge into two facets (Text-fig. 27).

Material.

A. 'Manihine', Gulf of Aqaba Stations

Station	Date (Jan. 1949)	Hour	Depth (m.)	T. ° C.	S.‰	No. of nectophores (when counted)
1	15th	1300–1415	0	21·59	40·79	6
			137	—	40·78	—
			274	—	40·38	—
2	15th	1435–1500	0	21·65	40·78	—
			137	21·65	40·71	1
5	15th	1150–1410	0	21·61	40·72	1
			137	—	40·68	—
			274	—	40·80	—
6	16th	1010–1115	0	21·56	40·74	1
			137	18+	40·80	—
			274	18+	40·79	—
8	16th	1350–1440	0	21·72	40·79	3
9	16th	1455–1540	0	21·57	40·75	10
			274	—	40·79	—
			548	18+	40·66	—
11	17th	1105–1125	0	21·51	40·76	2
12	17th	1015–1045	0	21·53	40·77	13
13	17th	1240–1330	0	22·0	40·74	2
15	18th	0930–1000	0	21·35	40·71	6
18	18th	1310–1415	0	21·57	40·78	16
19	18th	1430–1530	0	21·58	40·78	3
			137	—	40·74	—
			823	18+	40·66	—
21	19th	1120–1200	0	21·56	40·70	1
			137	18+	40·74	—
			548	18+	40·64	—
24	19th	0900–0930	0	21·20	40·75	1
29	21st	1000–1030	0	21·5	40·66	4
30	21st	1100–1150	0	22·38	40·50	3
			137	18+	40·66	—
			548	18+	40·68	—

B. R.R.S. 'Discovery II'

Station	Date (Apr. 1935)	Hour	Depth (m.)	T. ° C.	S.‰	No. of nectophores (when counted)
1581	28th	1815	50	22·29	35·26	1
			100	17·21	35·30	—
1583	30th	0930	0	29·53	35·32	1
			50	27·18	35·37	—

I have re-examined Browne's 'Sealark' specimens from Mauritius and Farquhar (he did not keep them apart). They are well preserved and show stages of development a little later than those of the Aqaba ones. Two are post-larvae in the monogastric stage, one still bearing a larval bract, and the other one three larval bracts. They are about 3 mm. in length. A third specimen is 10 mm. in length, and two others about 18 mm. These last two have gastrozooids, and one has lost at least seven nectophores. All bear buds of nectophores, and two of them large ones. A sixth specimen is a single cormidium to which is attached three bracts. The largest of these is of adult type, 0·8 mm. broad, with four primary facets and two outer secondary ones.

The larva of *A. okenii* differs from that of *A. elegans* in having none of the simple, larval type of tentilla, so well known in *Nanomia bijuga*. The explanation of this is that this simple type of tentillum in *Agalma elegans* is borne by the tentacle of a reduced type of gastrozooid intermediate in type between an ordinary gastrozooid and a palpon, and that there is no gastrozooid of this type accompanying the normal, terminal gastrozooid in *A. okenii*. The larval bract of *A. okenii* is comparable with that of *A. elegans*, but its proximal end makes an angle with the distal one. In *A. elegans* six or seven bracts of this larval type, much enlarged, may still be attached to the terminal cormidium when the specimen has reached a length of 7 cm.

Cordagalma cordiformis Totton, 1932.

This must be the smallest of all Physonects, and it has been overlooked by everyone. I described it first in 1932 from the Great Barrier Reef of Australia. I have found it in daylight close to the surface in the West Indies, and on many occasions at Villefranche, and am now able to report its presence at sixteen of the 'Manihine' Aqaba Stations and at 'Discovery II' Stations 1581 and 1583 (see Tables A and B on p. 68). It was not taken by 'Mabahiss'.

My figure, published in 1932, will serve to identify the nectophores of this very obscure species, about which we know so little at present.

Measurements. A nectophore was taken at random from the catch made by 'Manihine' Station 18. Its length is 2·0 mm., breadth 1·2 mm., and thickness 1·1 mm. measured dorso-ventrally. The other nectophores are of similar size.

Bargmannia elongata gen.n., sp.n.[1]

This species has long been known to me by its very characteristic nectophores, and since they are very unlike those of species of known genera, I have made this species the type of a new genus.

Two views of a nectophore of this species from 'Discovery II' Station 681, which I had already prepared, are now published for the identification of this very characteristic nectophore, but no description will be attempted, beyond saying that the lateral canals do not form loops as they do so commonly. In this respect it resembles Kramp's (1942) '*Stephanomia*' *orthocanna* and related species.

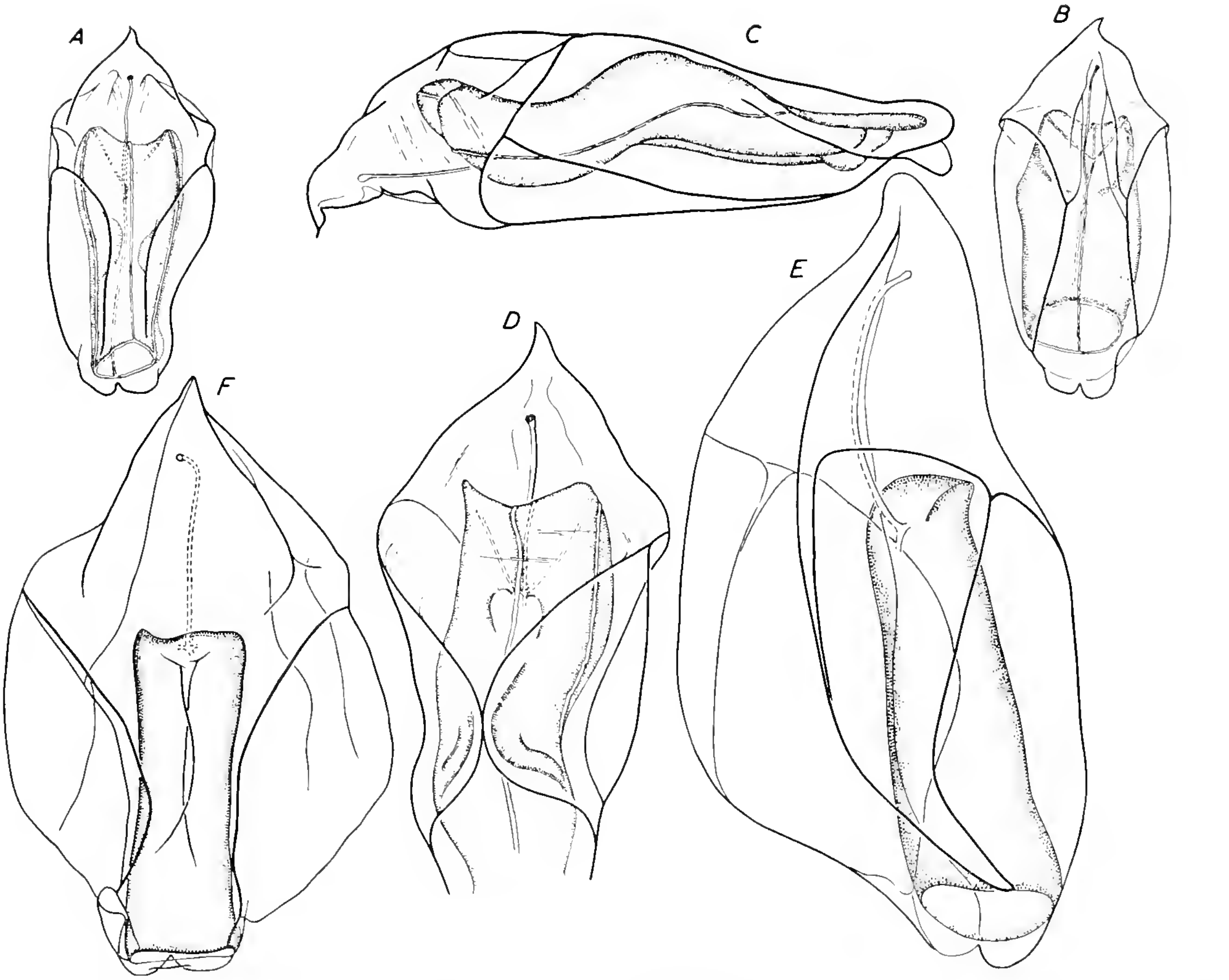
Distribution: 'Discovery' Stations 107, 'Discovery II' 681, 686, 698, 699, 701, 1554, 1585, 1586, 1587, 1589, 1769, 2061.

Holotype (Text-fig. 28D) and eighteen paratype nectophores Brit. Mus. (Nat. Hist.) Register No. 1952. 11. 19. 7–25 from 'Discovery II' Station 699, 370–0 m.

I have found a single nectophore in a tube of material submitted by Dr Leloup from 'Michael Sars' Expedition Station 58 (12–13 January 1910, 37° 37′ N., 29° 25′ W.).

---

[1] Named for Dr Helene Bargmann.



Text-fig. 28. Characteristic nectophores of a new Physonect *Bargmannia elongata*, the other parts of which are unknown. A, B, specimen 'Discovery II' St. 681, ×3·2; C, D, specimen from 'Discovery II' St. 699, 370–0 m., ×6·3; E, F, specimen from 'Discovery II' St. 1769, 1000–750 m., ×3·5. The muscular lamella is attached along the pecked line in figs. E and F.

Forskalia Kölliker, 1853*b*

Very little advance has been made in our meagre knowledge of species of *Forskalia* since Bedot (1893), who was familiar with living Mediterranean forms, reviewed the genus. He recognized five species, three of them Mediterranean ones. I am familiar with one living Mediterranean species, whose identification depends, as a field-mark, on a lemon-yellow coloured spot at the junction of the ventral radial and circular canals of the nectophores. This spot is not visible after fixation in formalin. Schneider (1898) maintained that this species should bear the name *ophiura* Delle Chiaje 1829. Bedot called it *edwardsii* Kölliker, 1853*b*. I have also often seen preserved nectophores of the *leuckarti* type, namely those with a small disc-shaped rete on the pedicular (apical) canal.

Very little information has been given in descriptions about the shape and disposition of bracts, but I believe that bracteal characters will prove to have great systematic value.

Leuckart (1854) gave the impression that, in *F. contorta*[1], the bracts on the polyp-stalk are very numerous. In *F. edwardsii* I estimate that there are ten, including the small distal buds. We really know very little about the different species.

That quantitative processes of change in animal tissues produce allometric growth-rates is well known. Child and others have done much classical work on the growth gradients in gymnoblast

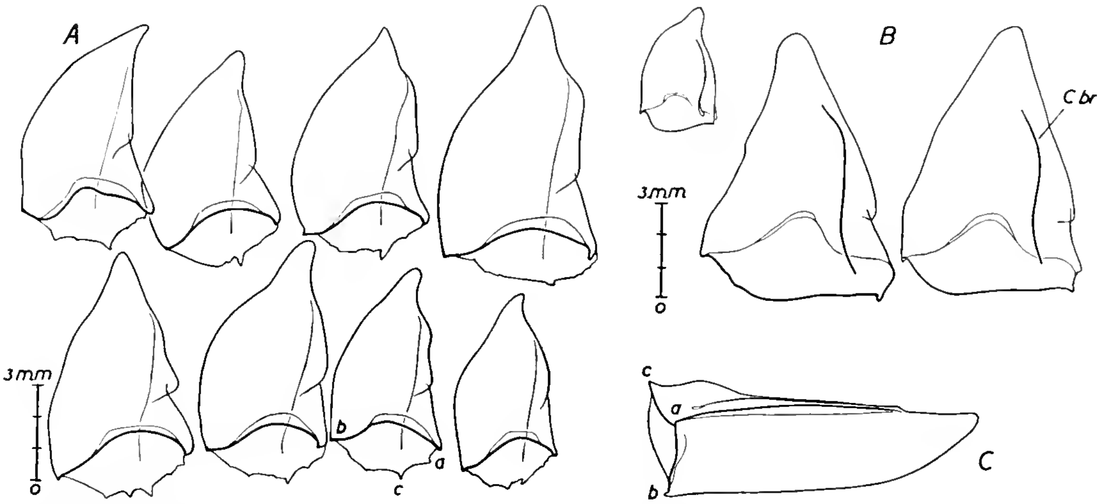
---

[1] Redescribed by Bedot (1893) as *F. leuckarti*.

hydroids, but I am not aware of any work that may have been done on gradient phenomena in other coelenterate bud-colonies. That such phenomena occur, for instance, in Aglaophenid hydroids becomes evident when the denticulation of the theca-margin from the stem-region to the tip of a hydrocladium is examined; and there are axial gradients, too, from top to base of the colony. Lately I have come across similar growth-gradient phenomena whilst making a tedious study of the bracts of *F. edwardsii*, the Mediterranean species with the lemon-yellow spot on the velum. In no account of any species of *Forskalia* can a satisfactory description or figures of the morphology be found, especially of the bracts.

Forskalia edwardsii Kölliker, 1853*b*.

In the spring of 1949, at Villefranche, I took the opportunity to anaesthetize and carefully preserve parts of thirty-two large colonies of *F. edwardsii*, and to obtain some photographic records[1] of the living animal (Pl. IV, figs. 4, 5, 8)—a very difficult procedure. Examination of a small, random sample of the loose, preserved bracts of a specimen of *F. edwardsii* showed that it was easy to pick out bracts of certain shape-categories, and that each category appears in two forms, one the mirror-image of the other. Further examination of the specimen after staining—the bracts are very transparent—showed that the stem bore leaf-like bracts, and that the long, muscular peduncles of the siphons, so characteristic of *Forskalia* spp., carried bracts of at least three other kinds, the proximal pair being of the most simple form (Text-fig. 29C). After making a series of camera-lucida drawings of numbers of each category, it was apparent that the shapes of bracts at different relative positions on the peduncle were fairly constant and characteristic. Finally I was able to homologize their structure. Though it appeared in life, while appendages, some of them almost invisible, were writhing about under the binocular, that there was no discernible ordered arrangement, it is now clear that all the bracts of *F. edwardsii* have essentially the same structure, but that their proportions in different positions on the stem and peduncles vary markedly. The change in form takes place suddenly in passing from stem to peduncle, but progressively from the proximal to the distal end of each peduncle. It remains to be seen whether there is further progressive change from the anterior to the posterior end of the whole bud-colony.

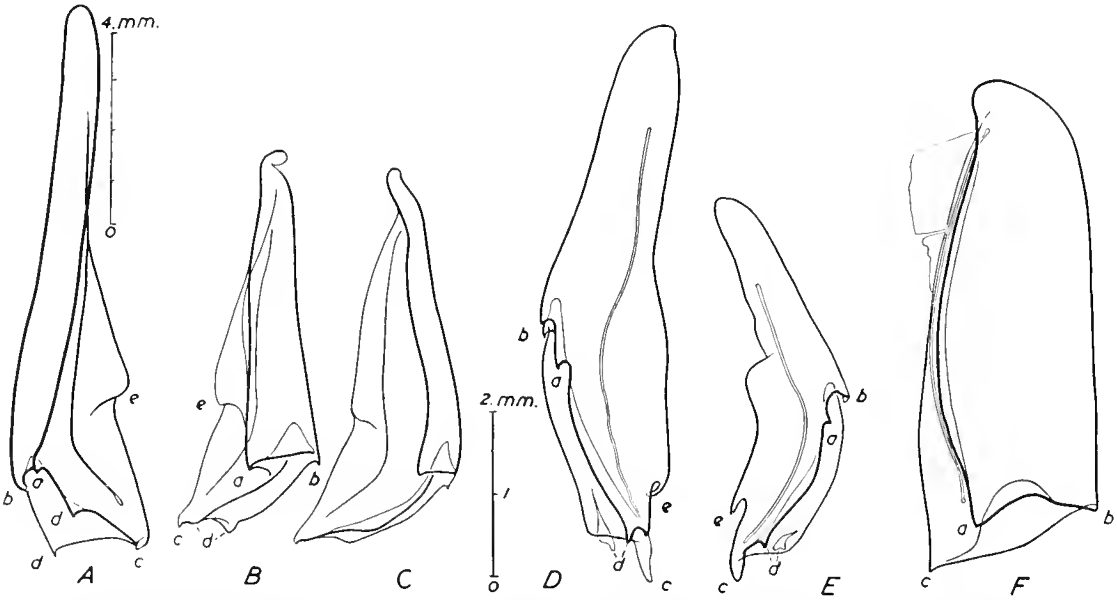


Text-fig. 29. *Forskalia edwardsii.* Bracts of a specimen captured at Villefranche, 31 March 1949, ×4. The three bracts, B, are of a kind found only on the stem. C, a bolster-shaped bract found only on the upper part of the pedicels of the gastrozooids. A, a series of eight stem bracts to illustrate constancy of shape. All bracts have enantiomorphs. Homologous points on the bracts are lettered *a*, *b*, *c*.

---

[1] I have to thank Dr W. G. R. Marden for co-operation in this difficult task.

The small *Forskalia* specimens occasionally brought back in plankton-collections are invariably strongly contracted. No doubt the sudden contraction in length of siphon-peduncles caused by formalin has the mechanical effect of tearing the long and delicate membranous, muscular attachments of the bracts. Sometimes a few distal bract-buds remain, but siphons and bracts are nearly always shed. In cross-section the long, peduncular bracts of *F. edwardsii* are triangular, and have a distal facet set on at varying angles. As a result the distal facet is of varying length, relatively short in the proximal pair, relatively long and oblique at the distal end. The feature of all the bracts, which makes it possible to homologize the various categories, is a shallow pocket between the distal facet and what I will call the dorsal facet. By labelling the two distal teeth of the dorsal facet *a* and *b* in the figures (Text-figs. 29, 30), and attaching other letters *c*, *d* and *e* to the distal tooth, the two median teeth of the distal facet and the penultimate tooth respectively, it is hoped to make the homologies clear.



Text-fig. 30. *Forskalia edwardsii*, Villefranche. A–E, knee-shaped bracts from pedicels of gastrozooids. F, bolster-shaped bract from base of pedicel. A–C ×6, D, E ×11, F ×9. Homologous points on the various bracts are lettered similarly, *a*, *b*, *c*, *d*, *e*.

It will be seen that in a cross-section of a stem-bract the longer transverse axis is from side to side, and the 'pocket' is very wide, whilst in the distal peduncular bract the longer transverse axis might be called dorso-ventral, and the 'pocket' is very narrow.

In January 1952 I received four bottles of plankton containing *Forskalia* material, taken in the Red Sea by 'Discovery II' in November 1951. The material is in better condition than usual, and although it cannot be worked up for this report it can be said that it corresponds well with specimens of *F. edwardsii* from the Mediterranean.

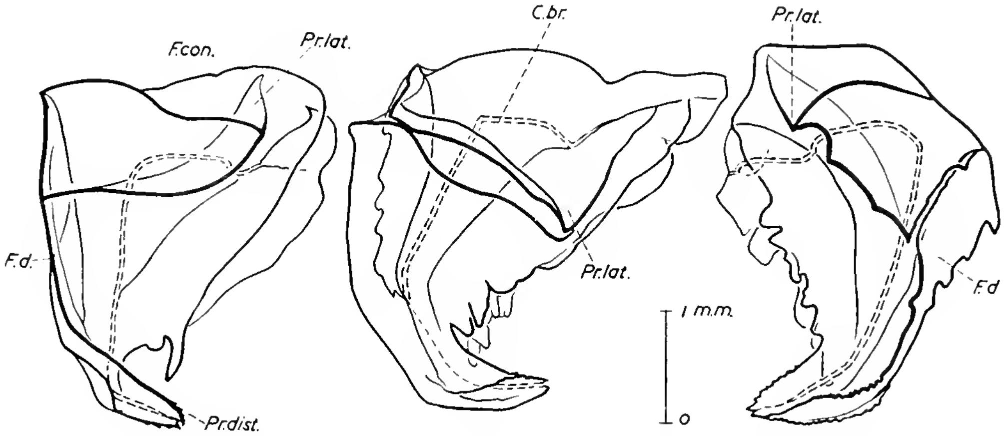
The material consisted of:

'Discovery II'	Net	Depth (m.)	Material
Station 2905	TYF B N 70 B	250–0	Two young colonies
Station 2906	TYF B N 70 B	200–0	Pieces of several colonies and young ones

Forskalia sp. or spp.

A species was taken at one 'Manihine' Aqaba Station and in the following 'Discovery II' hauls: 1375 (1 ex., no nectophores); 1568 (nectosome and 31 nectophores); 1573 (5 nectophores); 1581 (4 juv. nectophores); 1583, 100–50 m. (1 juv. nectophore); 1585, 1400–700 m. (11 nectophores), 500–0 m. (11 bracts); 1586, 1650–950 m. (1 nectophore); 1587 (1 ex., no appendages).

The above nectophores are unmistakably those of a *Forskalia* species and have the characteristically shaped nectosac, with straight radial canals. The flattened asymmetrical ventral process that carries the pedicular canal is also characteristic. But the pedicular canal itself is noteworthy for lacking the branched expansion in its middle region found in *F. leuckarti*.



Text-fig. 31. Knee-shaped bracts of a species of *Forskalia* from 'Discovery II' St. 1585, 1400–700 m., × 15.

Of the above bracts, five are similar (Text-fig. 31) in having a concave oval facet on the dorsal side, a cavity on the ventral side, a convex facet at right angles to the dorsal one, a three-cornered lateral process with a ridge and a canal that has a right-angled bend in the middle of its course. All the bracts are somewhat hollowed on one side and have a distal process, triangular in section, on which the canal ends. The knee-shaped bracts described above can be mirror images of each other, as the figures show.

At present we do not know enough about the morphology of species of *Forskalia* to be able to identify species from loose bracts and nectophores, unless they are of living Mediterranean specimens.

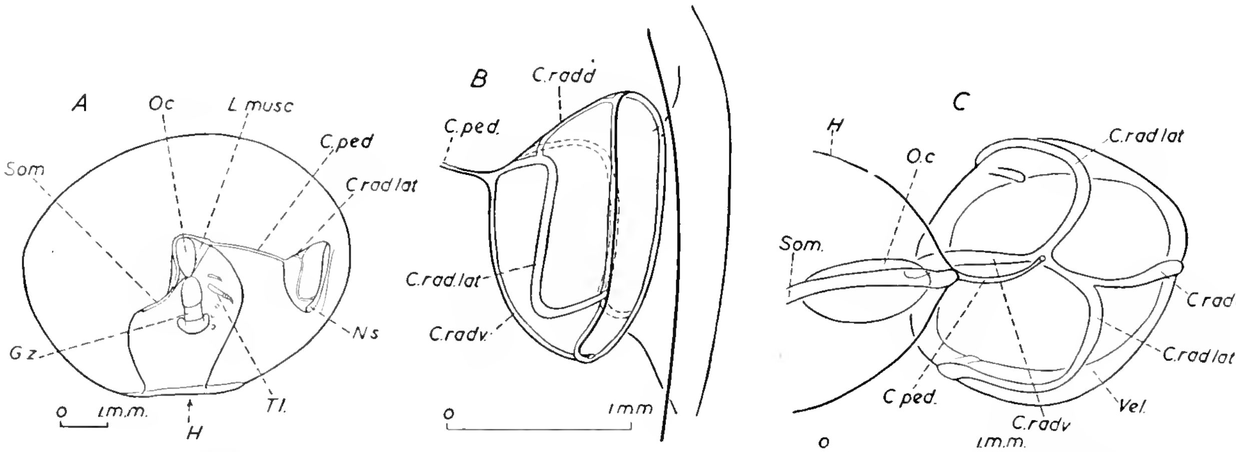
CALYCOPHORAE

Post-larvae of Prayidae and Hippopodiidae

It has long been recognized that Prayids and Hippopodiids more nearly resemble one another than either resembles the remainder of the Calycophorae. In both of the families there appears to be a similar larval, caducous nectophore, combined possibly with a bract, like the one first figured by Chun (1888*a*) for the Canary Islands *Hippopodius hippopus*.

Up the present time we have known very little about the larvae of any Prayid or Hippopodiid species, and as far as I am aware no one has succeeded in breeding any except Metchnikoff (1874). Eighty years ago he reared some larvae of *H. hippopus* at Villefranche, but could not keep them alive for more than ten days. The rest of our knowledge is based on larvae of unknown parentage captured in the sea. Great caution should be used in accepting identification of such larvae unless there is within the hydroecium a young, definitive nectophore of recognizable shape.

Quite recently, in June 1951, I was able to identify such larvae of a Hippopodiid and a Prayid from the Antarctic ice-edge. But we know only one Antarctic species of each family, so that after seriation of growth stages we can reasonably assume that these ice-edge larvae are those of *Vogtia serrata* and *Rosacea plicata*. These last grow to a considerable size, a diameter of 12 mm. The larvae of *Vogtia serrata* and *Rosacea plicata* can be separated by the shape of the somatocysts. Without attempting to go into detail it may be stated that in larvae of *R. plicata* the somatocyst is ovate or globular, whilst in *Vogtia serrata* it is elongated. There appears to be a much more pronounced angle in the dorsal wall of the hydroecium of the larval nectophore in *Rosacea plicata* than in *Vogtia serrata*. Both have comparatively straight lateral subumbral canals, those of *Rosacea plicata* being somewhat sigmoid in shape. The post-larva of *R. plicata* was recorded by Bigelow (1911*a*) as *Hippopodius hippopus* in his report on Biscayan Siphonophores. I have re-examined some of these 'larvae' from 'Research' Station 36K. One is an eudoxid, and three are post-larvae of *Rosacea plicata* (Text-fig. 32).



Text-fig. 32. *Rosacea plicata*. Larva from 'Research' (1900) St. 36*k*, Bay of Biscay. A, lateral view of whole larva, ×6; B, larval nectophore, ×24; C, view of nectophore from aboral end, ×22.

Thanks to the generosity of Dr Trégouboff, Director of the Station Zoologique at Villefranche, where so much of the pioneer work on Siphonophores was carried out, I have been able to examine a very well-preserved post-larva of *Vogtia glabra* (Pl. IV, fig. 2; Text-fig. 33). It is identifiable because within the hydroecium of the larval nectophore is a young, definitive, heteromorph nectophore characteristic of the species.[1] Its identification is important because the larval nectosac shows clearly that only dorsal and ventral radial canals are developed at this stage in *V. glabra*, if my identification is correct. Both types of shed larval nectophores, i.e. with two and with four radial subumbral canals, have been found from time to time in plankton samples, and would constitute distributional records for the species concerned. In Chun's (1888*b*) figures of Naples larvae he omitted the dorsal canal (inserted by Moser in a copy, 1925).

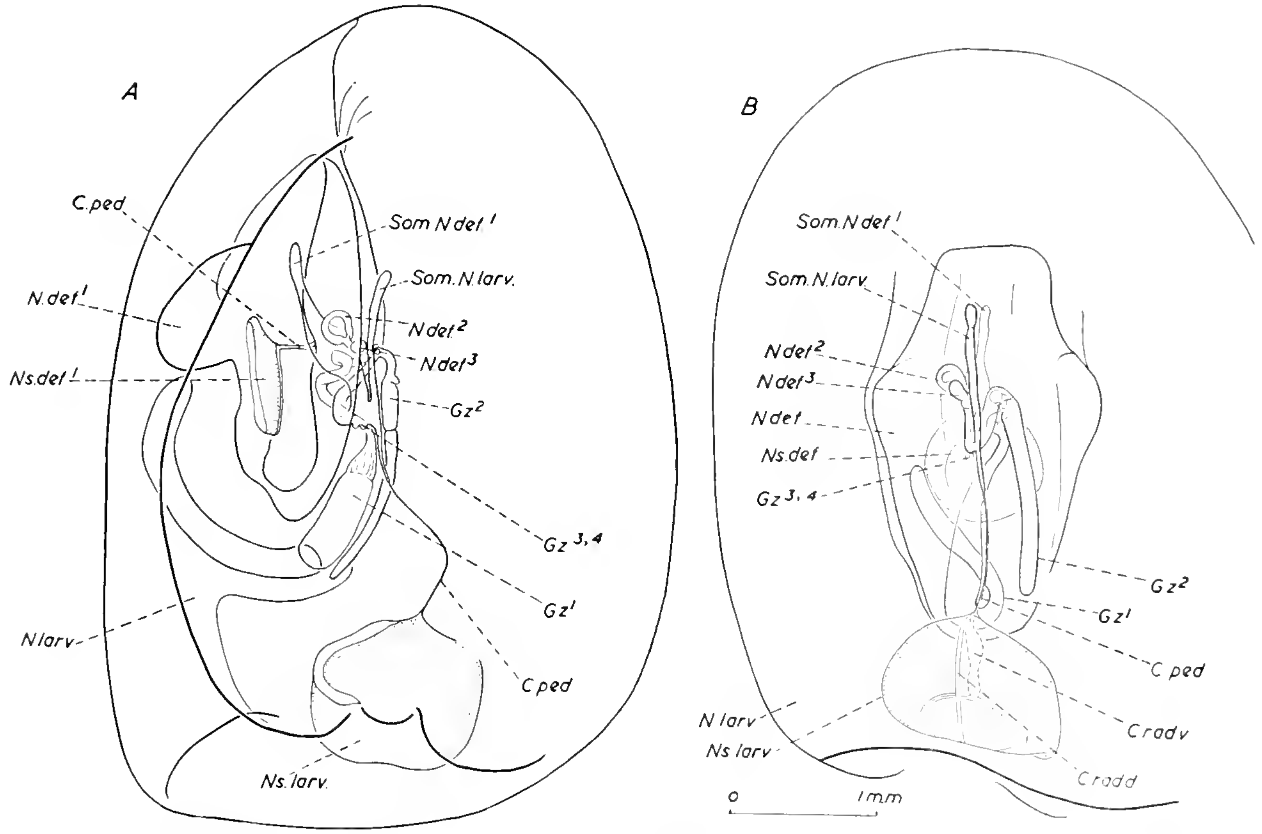
R.R.S. 'Discovery II' has taken many dozens of post-larvae of *Rosacea plicata* measuring up to 12 mm. in length. There is a clear discontinuity between these and the smallest definitive nectophores. From this fact I deduce that the larval nectophore of *R. plicata* is caducous, as in *Hippopodius*.

Moser (1924*a*) figured larval nectophores of *Rosacea cymbiformis*, *Vogtia serrata* and *V. pentacantha*. The subjects of her plates (pl. I, fig. 3; pl. II, fig. 5; and pl. III, fig. 4) contained a young definitive nectophore, but the last two cannot be identified with much certainty.

---

[1] Only two prominences are present above the nectosac and not four. In the larva from Orotava, attributed by Chun (1888*a*) to *Hippopodius hippopus*, he did not mention the number of prominences, but figured what looked like one of a pair only. But Chun's larva had four radial subumbral canals.

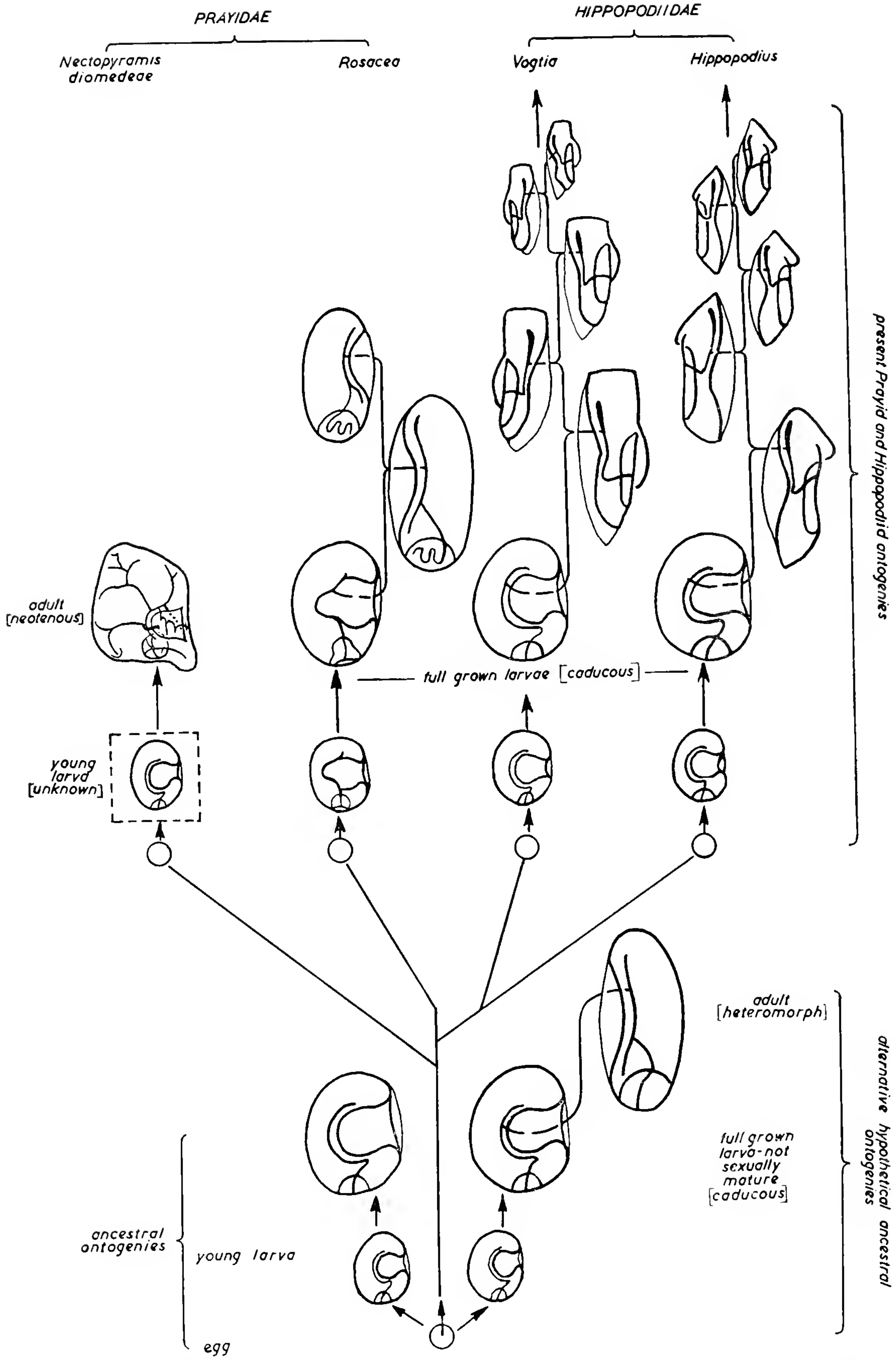
We are now in a position to see how closely alike are the larvae of two species of Prayidae and of three species of Hippopodiidae, for Chun (1888*a*, *b*, 1913) had already figured three larvae of *Hippopodius hippopus*. In all except *Rosacea cymbiformis* there is a deep, pocket-shaped hydroecium, and in none is there an extension of the somatocyst distad to the pedicular canal of the nectosac. All, except *Vogtia glabra*, where they are missing, have simple straight, lateral subumbral canals such as are found in *Desmophyes*. Reference to Bigelow's (1911*b*) figure of *Nectopyramis diomedeae* will show that these same features appear in the definitive nectophore of the species, which I consider to be a good instance of a neotenous form which has subsequently evolved on new lines. We do not, of course, know whether the common ancestor had a very different adult stage. Text-fig. 34 will make this discussion plain.



Text-fig. 33. *Vogtia glabra*. Prof. Trégouboff's larva from Villefranche, × 19·5. For photograph, see Pl. IV, fig. 2.

It may be mentioned at this point that the definitive nectophores of Hippopodiid species resemble the larval type common to Hippopodiidae and Prayidae in that there is no distal prolongation of the somatocyst beyond the pedicular canal of the nectosac.

There is present in Prayid and Hippopodiid larval nectophores an ovate or globular structure that lies between the pallial canal (somatocyst) and the gastrozooid. In older stages it is transformed or absorbed into the stalk canal that traverses the muscular lamella. It has been considered that the free end of the pallial canal in Prayids is homologous with the somatocyst in other Calycophorae, but the origin of the rest of the pallial canal is in doubt. Metchnikoff's figures of *Hippopodius hippopus* larvae show no sign of a homologue of the somatocyst, which appears so clearly in all other Calycophorae. The stalk canal of the larval nectophore (not the pedicular canal of its nectosac) must lie somewhere near the morphologically aboral end of the post-larva, and the curved pallial canal, so characteristic of Prayids, has probably arisen as an endodermal proliferation at the junction of the yolky larva proper and its enormous mesogloeal nectophore. This pallial canal terminates at the inner



Text-fig. 34. Phylogeny of Prayids and Hippopodiids, to show the nature and relationship of the nectophore of *Nectopyramis diomedeae*. In this diagram arrows are used to indicate growth stages, and long links to show how successive somatocysts are budded from their predecessors. A break in these links indicates that the larval nectophore is caducous.

end of the pedicular canal of the nectosac. In the definitive nectophore the pallial canal extends for some distance beyond this point, and is usually called the descending branch of the somatocyst. One is tempted to speculate as to why such large nectophores as those of *Rosacea* spp. appear to need no somatocyst of the type found in other Calycophorae. The somatocyst of Hippopodiids is of an intermediate type. The branched somatocyst of species of *Praya* and *Stephanophyes* seem to fulfil a circulatory rather than a flotational function, such as it is presumed to fulfil in other Calycophorae.

Garstang (1946) made the interesting suggestion that in Calycophorae the aboral end of the larva is aborted, and that for this reason Calycophorae do not develop the pneumatophore which he assumes that their ancestors possessed. But Metchnikoff's account of 9- and 10-day old larvae of *Hippopodius hippopus*, raised by himself at Villefranche eighty years ago, seems to show that it is from the aboral end of the larva that its united bract and nectophore develops, although the nectosac itself lies to one side.

It appears to be a matter of some importance to observe the early stages of development of either *H. hippopus* or *Rosacea cymbiformis*, both common Mediterranean species, so that the account of larval development can be completed.

In the spring of 1950 I made attempts at Villefranche to rear larvae of *Hippopodius hippopus*, but specimens were scarce during my short visit, and although I kept the actively swimming and apparently ripe female gonophore alive for ten days, and introduced active sperms to the eggs, I was unable to induce the gonophores to shed their eggs and obtained no larvae. Chun (1888*a*) reported that he, too, had tried in vain. Metchnikoff himself reported that he had great difficulty in getting the species to breed. My experiments were carried out in an improved Harvey 'rocker', consisting of a battery of sixteen 500 ml. beakers, in which plates of glass were kept rocking by a siphon-emptying water-can and counter weight. The air temperature of the *sous sol* of the Station Zoologique in which the rocker was installed was about 21° C., and subdued daylight entered from a small north window. The gonophores appear to be heavy, and no doubt sink to some depth in the sea, where the temperature would be lower.

PRAYIDAE

Nectopyramis Bigelow, 1911

Type species *N. thetis*

The two[1] deep-sea species described forty years ago under this generic name, *N. thetis* Bigelow (1911*a*) and *N. diomedeae* Bigelow (1911*b*) differ in several respects that are of some importance. First, the dorsal and ventral radial canals of the nectosac of *N. thetis* do not arise in common with the lateral pair, but are far separated. In this *N. thetis* agrees with *Archisoma natans*. Secondly, the eudoxid of *Nectopyramis thetis* resembles that of *Archisoma natans* and differs from that of *Nectopyramis diomedeae* in having a special swimming bell with similarly dissociated canals. Thirdly, *N. thetis*, unlike *N. diomedeae*, but like *Archisoma natans* (which, of the Nectopyramidinae, has the most simple somatocyst (canal system), consisting of one longitudinal canal), has an open hydroecial cavity extending the whole length of the polygastric stage of the animal. There is also a sharp bend in the middle region of *Nectopyramis thetis* and *Archisoma natans* near the base of the stem, as in *Rosacea plicata* and *R. cymbiformis*. In these three ways it would seem that *Nectopyramis thetis* and *Archisoma natans* are more closely related than the two so-called species of *Nectopyramis* are to each other. Bigelow & Sears (1937) accepted my suggestion that *Nectopyramis* is a Prayid genus, and gave some more excellent figures of the type species *N. thetis*. It would be best perhaps to include *Archisoma*

---

[1] Bigelow (1919) mentions a name *N. albatrossi*. I have failed to find it elsewhere, and it appears to be a *nomen nudum*, possibly the manuscript name he used for *N. diomedeae* before publication of his 'Albatross' Report.

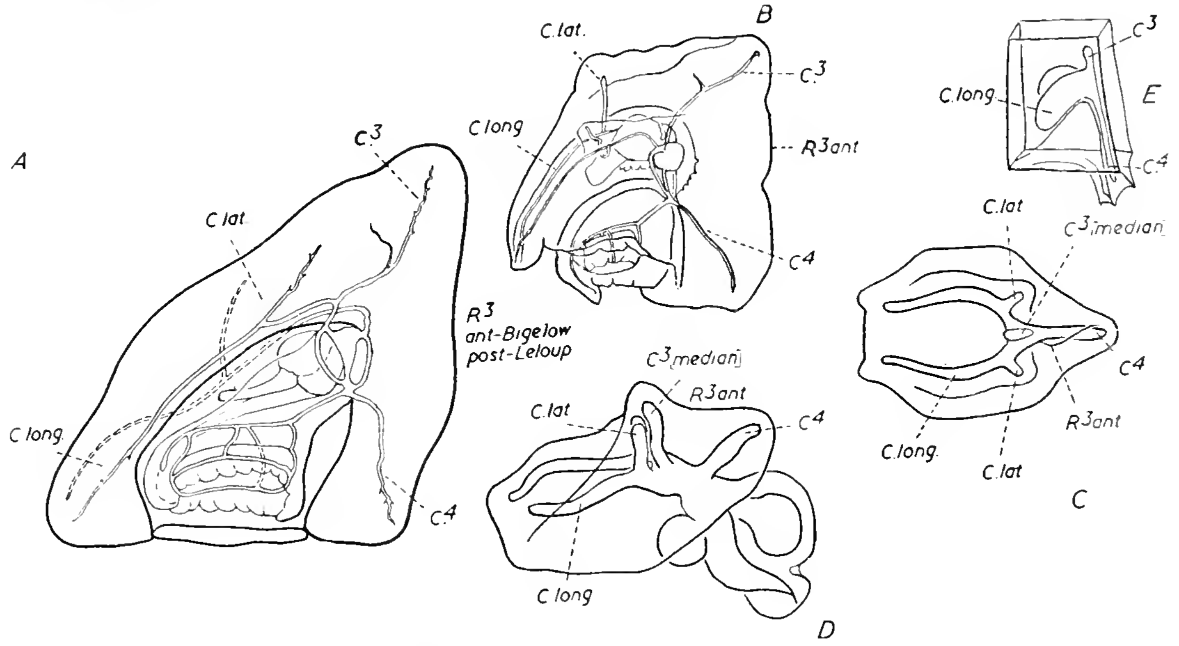
natans in the genus *Nectopyramis*, but we cannot exclude *N. diomedeae*, because the branches of the somatocyst of its polygastric stage can be homologized with those of *N. thetis* (see p. 84).

A new species *N. spinosa* was published by Sears (1952) after this report was written. I have dealt with it on p. 86.

Nectopyramis thetis Bigelow, 1911*a*.

Attention has been drawn on p. 77 to the apparent close relationship between this species and *Archisoma* (=*Nectopyramis*) *natans*, and to its differences from *Nectopyramis diomedeae*.

The eudoxids of *N. thetis* and *N. natans* each have a flattened dorsal (posterior *sensu* Bigelow, anterior *sensu* Leloup) surface (Leloup, 1932*b*, calls it 'une crête médiane'), up to which reaches a small branch of the ascending canal (not shown by Leloup). But whereas there are in the eudoxid of *N. thetis* two lateral projections of the margins of the facet, each served by a lateral (*sensu* Leloup, transverse *sensu* Bigelow) canal, in *N. natans* both projections and lateral canals are absent. But in *N.* ~~*pyramis*~~ natans also the branch of the ascending canal reaches the dorsal surface.



Text-fig. 35. *Nectopyramis thetis*. Growth stages of eudoxids and homologies of bracteal canals with those of Abylids: A after Leloup, B, C, D after Bigelow. E, *Abylopsis tetragona*.

The eudoxids, or stem groups, of the following Prayids are now known: *Praia dubia*, *P. reticulata*, *Rosacea cymbiformis*, *R. plicata*, *Maresearsia praeclara* sp.n. *Amphicaryon* spp. indet., *Nectopyramis thetis*, *N. diomedeae* and *N. natans*. They are all homologous, but *Amphicaryon* eudoxids, of which *Eudoxia tottoni* Leloup, 1934*a*, is one, appear to me much more primitive in that the bract is simple, helmet-shaped, and carries only a pair of longitudinal (*sensu* Leloup) bracteal canals running on each side of the bracteal cavity. But with this difference is correlated the fact that the bracts of *Amphicaryon* only extend on one side of the stem, whilst in all the rest of the genera they are attached athwart the stem, so that the half of each bract which corresponds with the whole *Amphicaryon* bract bears a similar pair of bracteal canals in the walls of the bracteal cavity. The ascending and descending bracteal canals, absent from the *Amphicaryon* bract, appear to have arisen as the bract extended on to both sides of the stem and increased in thickness above it. The ascending canal in each case arises from one of the longitudinal canals, though not on the same side in all Prayids. Bigelow (1911*a*) had at once noticed the homologies in the bracteal canals of *Nectopyramis thetis* and species of *Rosacea*. I know of no descriptions or figures showing exactly how the Prayid bract is attached by its muscular lamellae, and my own efforts to elucidate this point in the living specimens of *Rosacea cymbiformis* failed though I have lately found a canal linking the stem-cavity with the bracteal canal system in young, preserved eudoxids of *Rosacea cymbiformis*.

There is a superficial resemblance between the bracteal canals in Prayids and in Abylids, a quadripartite arrangement in each case. But whereas the paired longitudinal canals of the Prayid bract run athwart the stem, in the Abylid bract they clasp it. The resemblance can hardly be fortuitous.

It may be well to record a note on the homologies of the early growth stages of bracts of the eudoxid of *Nectopyramis thetis*, originally figured by Bigelow, and on figures of mature bracts by Leloup and by Bigelow (Text-fig. 35). Only the canals *C. lat.* (Text-fig. 36B, C) are wanting in the Abylids.

Bigelow (1911*a*) in his first figure (3) showed three crests or ridges R1, R2, and R3. I have studied similar bracts still attached to the stem lying in the hydroecial canal. R3, which runs down to the tip of canal C4 (labelled C3 in Bigelow's fig. 4) is what Bigelow later called the anterior side. The other two ridges are the margins of the dorsal facet (Bigelow's posterior side). They start from the prominence over the tip of the ascending bracteal canal (*C. lat.*), run over the tips of the two horizontal canals and down to Bigelow's postero-dorsal margin of the hydroecium.

In well-preserved bracts these ridges are preserved. In less well-preserved material they become rounded and obscure. In Bigelow's fig. 4 of his original paper (1911*a*) only one transverse canal can be seen, labelled C7. The other canal, shown nearby under a prominence, is the ascending canal C3. The descending canal C4 is labelled C3.

N. thetis was not amongst the specimens sent to me taken by Beebe in his many deep hauls off Bermuda in the years 1929, 1930, 1931. There are, so far, thirteen records in 'Discovery' hauls in the Tropical and South Atlantic and in the South Indian Ocean. Altogether, four polygastric and seventeen eudoxid specimens have been taken, in seven cases in closing hauls, as well as an eudoxid taken in 1951 and another in 1952 by 'Scotia' to the north-west of Ireland.

Hitherto only three polygastric specimens had been recorded (see Bigelow & Sears, 1937) and eight eudoxids, often in an unsatisfactory condition. They were taken in the Bay of Biscay, Bay of Cadiz and between the Azores and Canaries; always in open nets towed at considerable depths.

Now from Indian Ocean Stations I have to record the capture by R.R.S. 'Discovery II' of five polygastric specimens and eleven eudoxids.

'Discovery' Stations	Depth (m.)	Closing-net	Locality	Material
1567	1350–0		South-east of Cape of Good Hope, South Indian Ocean	1 E.
1568	1400–0		South-east of Cape of Good Hope, South Indian Ocean	4 E.
1571	500–0		Indian Ocean, between Durban and South Madagascar	1 E.
1573	800–0		Indian Ocean, between East African coast and South Madagascar	2 E.
1581	600–0		Indian Ocean, East African coast	2 P.
1585	500–0		Indian Ocean, East African coast	1 P.
1587	1250–800	×	Indian Ocean, East African coast	1 E.
1749	1050–600	×	South Indian Ocean	1 P.
1754	900–400	×	South Indian Ocean	1 P, 1 E.
1755	1700–0		South Indian Ocean	1 E.

P. = polygastric. E. = eudoxid stage. × = closing net.

Seven other captures, all made by 'Discovery' in the Tropical and South Atlantic are as follows:

'Discovery' Stations	Depth (m.)	Closing-net	Locality	Material
86	1000(–0)		South Atlantic, west of Cape of Good Hope	1 P., 1 E.
89	1000(–0)		South Atlantic, west of Cape of Good Hope	1 E.
100 B	900–1000	×	South Atlantic, west of Cape of Good Hope	1 E.
677	2000–0		South Atlantic	1 E.
2042	2800–2300	×	South Atlantic	1 E.
2063	1150–600	×	South Atlantic, west of Cape of Good Hope	1 P.
2639	1200–600	×	Tropical Atlantic, off west coast of Africa	1 P., 2 E.

P. = polygastric. E. = eudoxid stage.

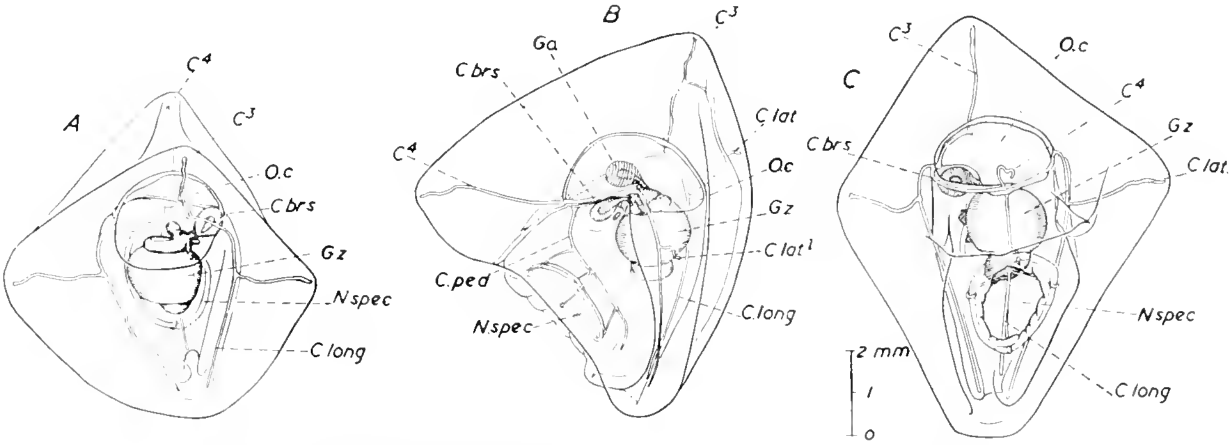
Recent 'Scotia' captures are:

'Scotia' Stations	Depth (m.)	Closing-net	Locality	Material
1951 Haul 363	1000–250	×	North-east Atlantic, north-west of Ireland	1 E.
1952 Haul 1305	500–0		58° 38′ N., 8° 21′ W.	1 E.
Haul 1197	700–0		55° 28′ N., 9° 42′ W.	2 P.

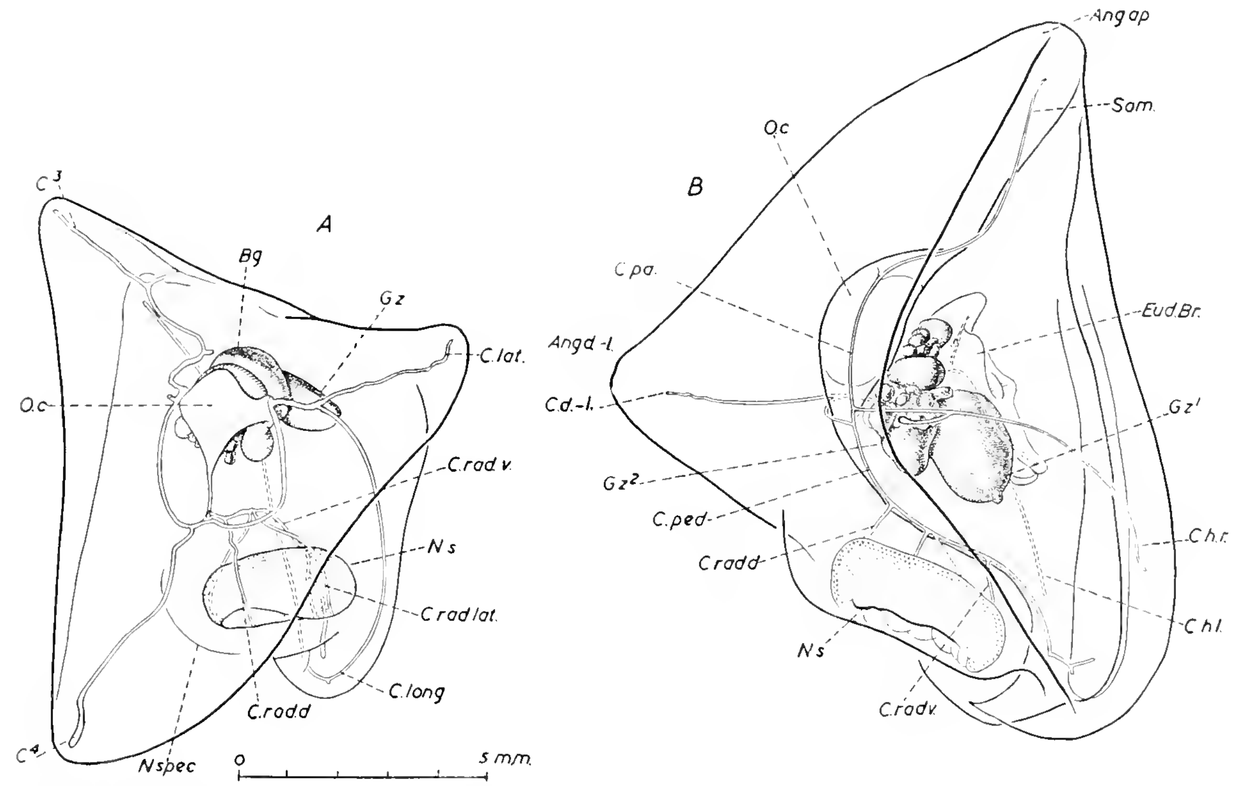
P. = polygastric. E. = eudoxid stage.

The characteristic relationship of Leloup's '*formation speciale*' (Bigelow's 'bilobed vesicle') with the bracteal and pedicular canals of the eudoxid is complex. I give two new figures which show that in the particular specimen figured, the pedicular canal of the special nectophore of the eudoxid arises from the ventral side of the central organ, and that all the 'canals' at this point do not meet at a point (Text- fig. 36B).

The 'central organ', which lies in the hydroecium, is substantially the same as figured in Leloup's diagram (1933, pl. 1, fig. 13), and in Bigelow & Sears (1937, fig. 5). I believe that it serves as a food reservoir. Its upper wall forms a pouch, which spreads over on to the base of the gastrozooid. In a recently captured specimen ('Scotia' 1951, haul 363) the bilobed vesicle figured by Bigelow can be seen clearly. There is a ring of deeply staining tissue (? Bigelow's pedicular plate) between the central organ and the basal bulb (basigaster) of the gastrozooid which unites everything together, and from which the gonophores spring. The special nectophore is attached by a long semicircular adhesion to the junction of what I will call the semicircular bracteal canal (Text-fig. 36, *C.br.s.*) and the central organ. But the cavity of the bracteal canal system is isolated from that of the stem in the fully formed eudoxids of Prayids. In young stages of *Rosacea cymbiformis* I have seen a canal connecting the bracteal canal system to the stem, but later that disappears. The pedicular canal of the special nectophore of *Nectopyramis thetis* does not arise, as it can appear to do, from the semicircular bracteal canal, but from the central organ itself. This is what might be expected since I have discovered that in *Rosacea plicata* the central organ of the eudoxid represents a development of the remains of the stem. The central organ of *Nectopyramis thetis* varies in its state of development. Where it appears triangular (Text-fig. 35A) I think it is ageing, and what looks like a descending canal is only a constricted part of the sac-like structure. Some of the better preserved eudoxids of *Rosacea plicata* from 'Discovery II' Station 1617 show a homologous central organ and central organ complex. The central organ in *R. plicata* is globular and is filled with a substance that may be of importance in controlling the density of the eudoxid. The post-larva of *R. plicata* is provided with a similar organ. In that species, as the nectophore grows, this part of the pallial canal decreases in size, and becomes the pedicular canal of the muscular lamella attaching the nectophore to the stem. A similar somatocyst-organ can be seen in my figure (Text-fig. 38) of the nectophore of *Nectopyramis natans*, and in Moser's (1924*a*) figure of the larva of *Rosacea cymbiformis*.



Text-fig. 36. Eudoxid of *Nectopyramis thetis*, from 'Scotia' 1951 St. 363. A, foreshortened dorsal view; B, lateral view; C, ventral view. × 5·5.



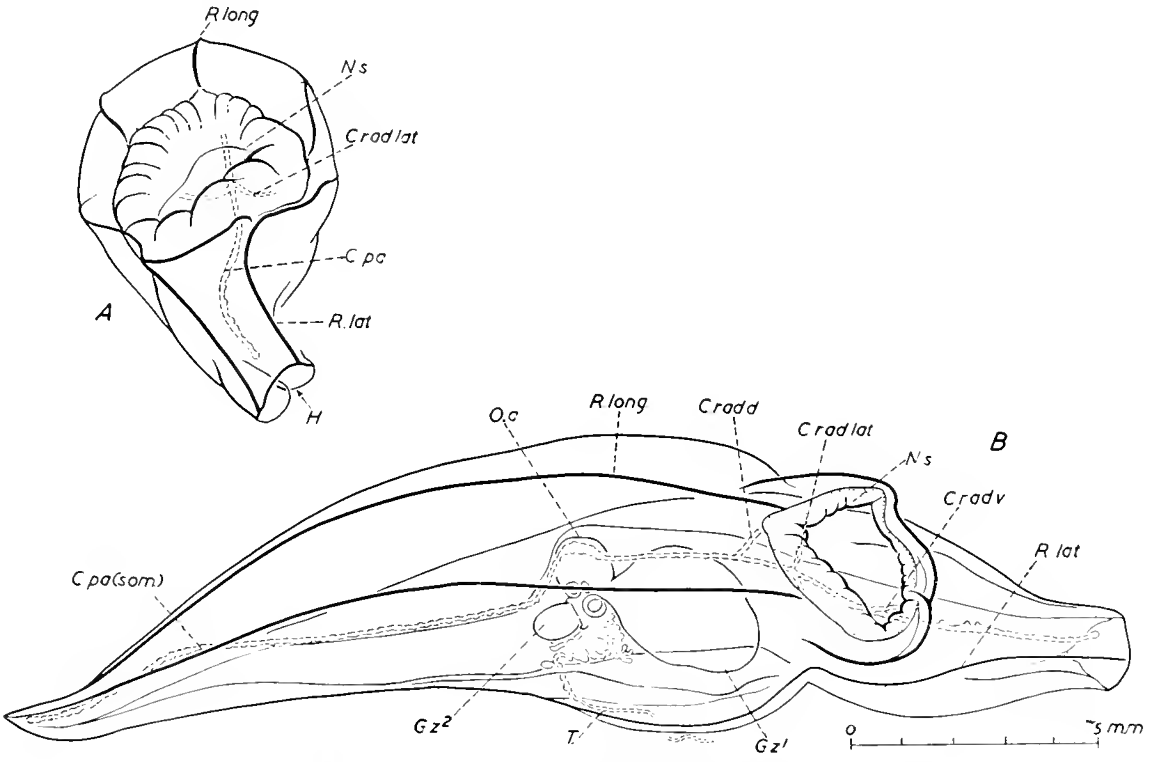
Text-fig. 37. *Nectopyramis thetis*. A, dorso-lateral (antero-lateral *sensu* Bigelow, postero-lateral *sensu* Leloup) view of eudoxid from 'Discovery' St. 89, to show central organ and canals. B, dorso-lateral view of polygastric stage. × 6·6.

In some Diphyid eudoxids there is, between the bracteal somatocyst and the basigaster of the gastrozooid, a cylindrical connecting piece (see Vogt, 1854; pl. 19, figs. 1, 12). In living specimens of *Chelophyes appendiculata* which I anaesthetized at Villefranche, it measures 0·6 mm. in length and 0·1 mm. in diameter. To its middle and distal half are attached the successively developed gonophores. This peduncle is the homologue of the central organ described above, and represents the remains of the part of the stem to which the gastrozooid was originally attached, or perhaps the peduncle of the gastrozooid.

Nectopyramis natans (Bigelow), 1911 *b*.

= *Archisoma natans* Bigelow, 1911 *b*.

An eudoxid of this interesting Prayid was taken by 'Discovery II' between 1650 to 950 m. at St. 1586, off Italian Somaliland. The polygastric stage has never been recorded. I take this opportunity, therefore, to mention two polygastric specimens, one taken by 'Discovery' at Station 101, off South-west Africa, in a closing net at a depth between 2480 and 2580 m.; and the other by S.Y. 'Rosaura' in 1937, at a depth between 750 m. and the surface, between St Paul and the Brazilian coast.



Text-fig. 38. *Nectopyramis natans*, polygastric stage. A, foreshortened view from lower end to show longitudinal ridges; B, dorso-lateral view. × 7.

The eudoxid was described and figured by Bigelow (1911 *b*, 1913), and has been taken several times since.

Curiously enough the polygastric stage has much the same long-bow shape as the eudoxid. The 'Discovery' polygastric specimen is 2 cm. in length, shaped like a long-bow, pointed above at one end, and truncate at the other. The hydroecium runs practically the whole length. At mid-length it contains the large gastrozooid and tentacle, and what are probably the buds of a second and third. On the dorsal surface are three longitudinal ridges extending from the apex to the nectosac, which lies about a quarter of the total length above the posterior truncate end. There is also a pair of lateral ridges running from the apex, past the nectosac to the truncated end. There is a single longitudinal canal, the somatocyst, running from end to end. It lies just underneath the dorsal wall of the hydroecium, except for the upper 5 mm. where it leaves the hydroecial wall and runs deeper in the mesogloea. In the middle region of the specimen the hydroecium is deepest, and the longitudinal canal has a corresponding bend, as in the better known *Rosacea*. Just at this point, and at the base of the primary gastrozooid, is an ovate structure found also in post-larvae of *R. plicata*, *R. cymbiformis* and *Hippopodius hippopus*. It is similar to the 'central organ' found in the aboral end of some Prayid eudoxids. It may act as a food reservoir or perhaps control density.

The dorsal and ventral canals of the nectosac arise independently, one at each end of the nectosac, and the lateral ones form a pair in the middle, as in the special swimming bell of the eudoxid. The lower edge of the nectosac is distinctly undercut. The structure of the tentacle of the polygastric specimen has not been well preserved, and the nature of the tentilla has not yet been elucidated.

Study of a well-preserved eudoxid from 'Discovery' Station 287 (800–1000 m.) off the west coast of Africa enables me generally to confirm Bigelow's (1931) account, and to add a little to it. The two longitudinal hydroecial canals which arise as in *Nectopyramis thetis*, one on each side of the central organ, join one another distally as in the type, though in another specimen from 'Discovery' Station 100 (2500–2000 m.) west from Cape Town they do not. There is a 'central organ' (Leloup's 'formation speciale') very similar to that in *N. thetis*, with a loop of the canal system—the semicircular bracteal canal—running round the ventral side. The central-organ sac has probably burst, so that its junction with the pedicular canal of the special nectophore[1] cannot be seen, but this pedicular canal arises in approximately the same place as in *N. thetis*. The chief difference between the eudoxids of *Nectopyramis natans* and *Nectopyramis thetis* is that in *N. thetis* there have grown out a ventral and two dorso-lateral processes of the bract, each served by a branch of the canal system. The tentilla of the eudoxid of *Nectopyramis natans*, viewed *in situ*, resembles those of *Nectopyramis thetis* and differ very markedly from those of *N. diomedeae*.

The relationship of this species have been dealt with above.

Nectopyramis diomedeae Bigelow, 1911*b*. (Plate V, figs. 2–3.)

Only three polygastric and eight eudoxid specimens have ever been recorded, all from the Eastern Tropical Pacific (Bigelow, 1911*b*, 1931). I can now report that the species occurs also in the Atlantic, where Beebe took seven polygastric and twelve eudoxid specimens off Bermuda. The specimens noted in my list of Siphonophora taken by Beebe in 1931 (*Nectopyramis* sp.nov.?) belong to the species *N. diomedeae*. 'Discovery II' took two more polygastric specimens in the South Indian Ocean, in 32° lat., at Stations 1749 and 1755; two more off South-east Africa at Stations 1567 and 1568; and two further polygastric specimens off East Africa at Stations 1585 and 1587. 'Discovery II' took eudoxids in the South Atlantic at seven stations between Station 679 at 26° S. lat. and Station 1555 at 39° S. lat.; and again at Station 1999 (64° S.) between South Georgia and the Ice Edge.

From the records so far available I estimate that the species lives at a depth of from 650 to 1600 m. or a little more. The polygastric stage has been taken, so far as we know at present, in only one closing net haul (1060–600 m.); the eudoxid in eight, varying in depth between 625–675 m. and 1500–2000 m. Beebe's seven hauls were open hauls to the surface after long horizontal hauls. His deepest net (1829 m.) contained a polygastric specimen when it came to the surface, as did his 1646-m. net, but there must be some doubt about the depth at which the captured specimens were living.

Polygastric stage. There is the usual Prayid plan of a median longitudinal canal (Text-fig. 39A, *C.med.long.*) that passes round the dorsal side of the hydroecium. Below, it gives off the pedicular

---

[1] The special nectophore bears a manubrium and eggs, and is therefore a gonophore. The second gonophore probably remains in a reduced condition as far as its general shape and subumbrella are concerned.

canal (*C.ped.*) of the nectosac and then continues distad along the face of the hydroecium. Above, it leaves the hydroecial wall and continues (*C.pa*^{2}) towards the apex of the bract, giving off four or more long, alternate lateral branches. At the point where *C.pa*^{2} leaves the hydroecial wall the longitudinal median canal forms on either side, as in *N. thetis*, a curved lateral canal, which runs on the wall of the hydroecium. On the left side it forks, one complicated branch (Bigelow's *C.h.l.*) running on the left wall of the hydroecium, and the other giving rise to *C.pa*^{3}, which very shortly after the fork gives off a downward branch (Bigelow's *C.h.r.*) on the right wall of the hydroecium.

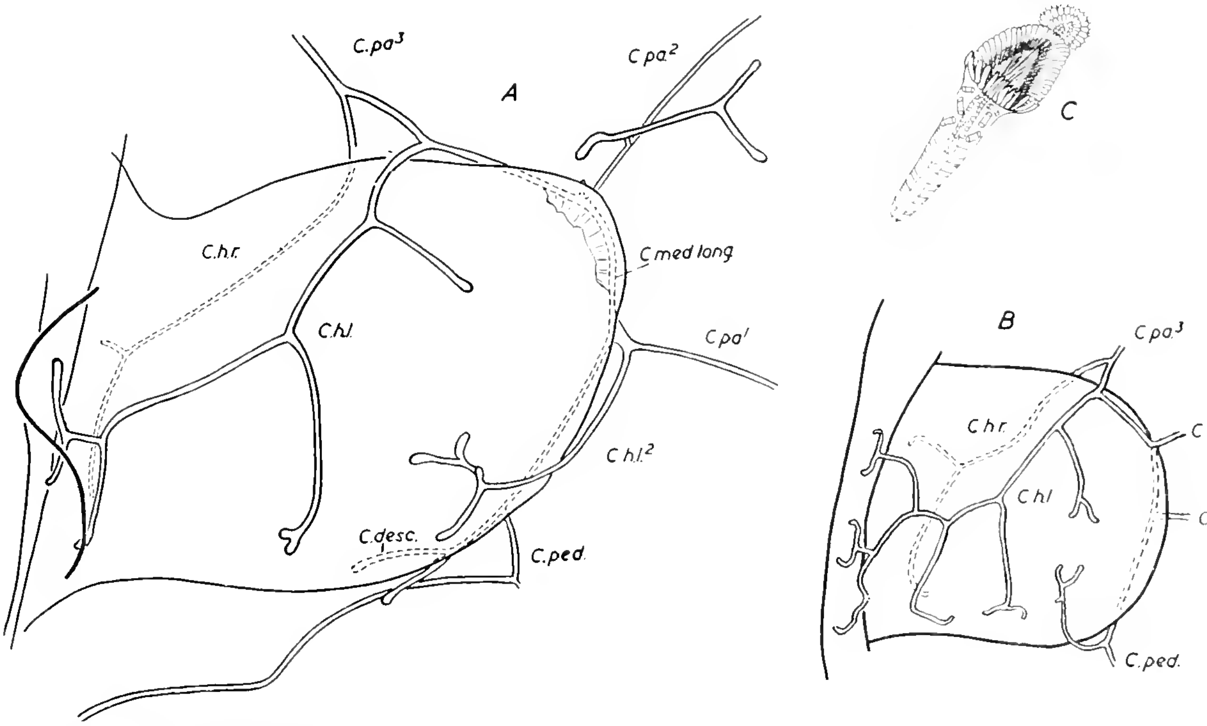
Returning again to the base of *C.pa*^{2}, the longitudinal canal, on the right side of *C.pa*^{2}, gives off *C.pa*^{1}, which almost at once gives off a descending branch, *C.h.l.*^{2}, that runs on the left wall of the hydroecium.

The problem is how to homologize the canal systems of *N. thetis* and *N. diomedeae*. My tentative solution is that the small *C.h.l.*^{2} in *N. diomedeae* is the true left hydroecial canal, and that Bigelow's *C.h.l.* is a secondarily developed canal. We should then see in both species a similar arrangement—an ascending canal *C.pa*^{2}, a right and left 'dorsal' canal *C.pa*^{3}, *C.pa*^{2}, and a right and left hydroecial canal *C.h.r.*, *C.h.l.*^{2}. In *N. diomedeae* the canal system is more complicated still, but the basic arrangement is similar to that in *N. thetis*.

The whole nectophore is twisted, so that the nectosac opens on one side instead of dorso-basally, and the branches of the somatocyst have become secondarily displaced. Bigelow's (1911*b*) description of the system, as far as the lower part and the free upper part of the longitudinal median canal is concerned, agrees with mine. After this Bigelow (1911*b*, p. 192) says, 'at the point at which it [the ascending canal] bends apically it gives off a branch which runs over the left-hand face of the hydroecium [his *C.h.l.* of fig. 4] and a short distance further on gives off a second trunk which passes over its right-hand face [his *C.h.r.*]. These two canals of the hydroecium...'. In my view only one of these, Bigelow's *C.h.r.*, is the homologue of an hydroecial canal (the 'right' hand one) in *N. thetis*. Bigelow did not figure or describe what I take to be the true, short, simple, left-hand hydroecial *C.h.l.*^{2}. The 'explanation' of Bigelow's (1911*b*) plate 1 (which does not mention fig. 6, part of the eudoxid) corrects certain lettering in figs. 3 and 4. It should be noted that the lettering *C.pa*^{1} and *C.pa*^{2} also in these figures should be transposed. The 'descending branch', to which Bigelow refers on p. 192, can be seen at the top on the right in his figs. 3 and 4, descending from *C.ped.* (marked on the plate *C.pa*^{3}). With these trifling corrections made it will be more easy to enjoy Bigelow's description and figures, and to understand the homologies of this complex canal system, which he figures so beautifully. To clarify my remarks, I give a new figure (39A) of part of the canal system, and reproduce a comparable one (39B) by Bigelow.

Since the adult nectophore of *N. diomedeae* retains in its nectosac the type of radial canals found in larvae of other Prayinae (its own larva is unknown), and its hydroecium has the pocket-shape so characteristic of larvae, it is reasonable to regard it as a neotenous form. Secondarily its somatocyst has become very much complicated (see Text-fig. 39).

The tentilla of *N. diomedeae* (Text-fig. 39C), though partly described by Bigelow (1911*b*), have never been figured. They are relatively large and of peculiar construction when mature, borne on long, loosely coiled pedicels. The apical part consists not of a terminal filament but, as in the larval tentillum of *Physophora hydrostatica*, of a small hollow cap of ovate nematocysts that appear to be stenoteles. This cap is from 0·2 to 0·25 mm. in diameter, and is perched on the apex of a large hemispherical cap of longer scimitar-shaped nematocysts. The larger cap measures from 0·35 to 0·4 mm. in diameter. Into it penetrates a tapered endodermal core, round which, externally to the cap, is twisted irregularly a long, double, structureless, elastic cord. Proximal to this cord is a thickened opaque length of ectoderm. It is not possible at the moment to make a further examination of the structure of these tentilla, but in the young tentillum the larger cap of the elongate nematocysts is narrower and one-sided, and it only secondarily acquires its final hemispherical shape. The smaller cap in its final form is provided with prominent cnidocils. In younger stages it is generally turned to one side. The tentilla of *Nectopyramis thetis* are totally different. There the main battery of nematocysts is confined to one side, and there is a long spirally coiled terminal filament. In *N. diomedeae* there are a number of irregular surface ridges which are shown on Pl. V, figs. 2 and 3.



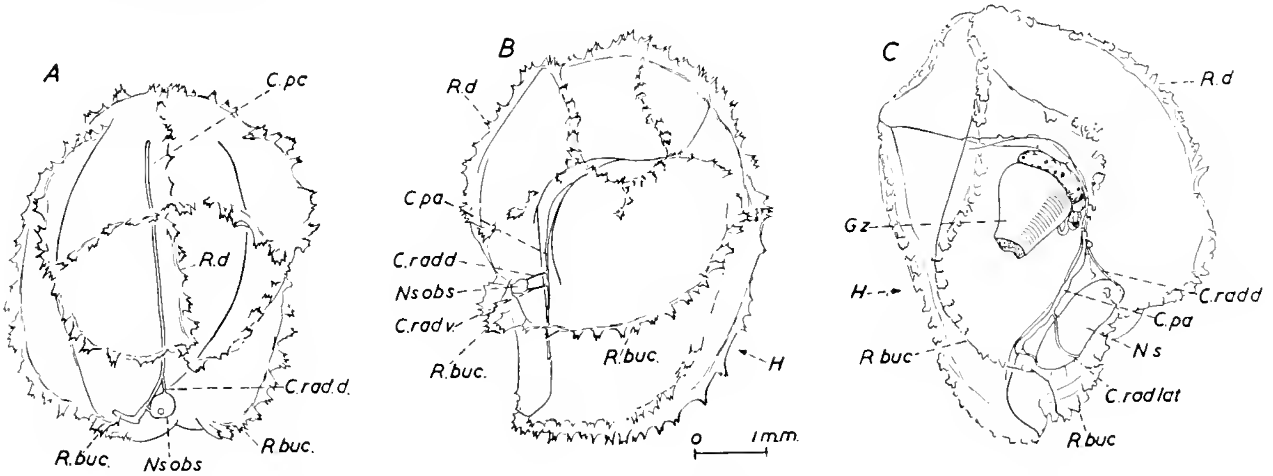
Text-fig. 39. *Nectopyramis diomedeae*. A, the branching somatocyst-complex in the region of the hydroecium of the polygastric stage. Specimen taken by Wm Beebe at Bermuda; B, the same, after Bigelow (1911 *b*, pl. 1, fig. 4) taken in Eastern Tropical Pacific; C, a tentillum.

Eudoxid. The 'central organ' is well figured by Bigelow (1911 *b*; pl. 1, figs. 5 and 6). In fig. 6 it can be seen quite clearly that the pedicular canal of the large nectophore arises from the central organ and not from the nematocyst canal system, which is a closed system in the full-grown eudoxids of Prayids. What cannot be seen so clearly in Bigelow's figures is that there is a semicircular bracteal canal as in *Rosacea*; that the hydroecial canal diverges from it at about the point marked in Bigelow's fig. 6 with a 'pointer' labelled *C.br.*; and that in some specimens at least the ascending canal lies on the wall of the hydroecium for a short distance before passing to the apex. Its point of origin from the semicircular canal is not directly opposite that of the ascending canal, which does not arise from the central organ. As usual in Prayids, the central organ is closely attached to the semicircular canal, and the fact that their lumina are quite separate is not easy to determine. This description will show at once that the bracteal canal system of *N. diomedeae* can be homologized with that of *N. thetis* and of *Rosacea* spp. In *Nectopyramis diomedeae* there are no lateral canals at the junction of the semicircular and hydroecial canals.

Nectopyramis spinosa Sears, 1952. (Plate V, fig. 1.)

?=*Hippopodius cuspidatus* Moser, 1925.

During a period of many years I have picked out from 'Discovery' catches three very curious Prayid nectophores, which I think may be what Moser (1925) described and rather inadequately figured as ? *Hippopodius cuspidatus*. A fourth was taken in a closing net fished from 1000 to 250 m. by 'Scotia' in 1951 to the west of Ireland in W. long. 17° 03′, and a fifth also by 'Scotia' in 54° 15′ N., 14° 32′ W. at the same depth. The nectophores are of two kinds, and there are three of the first and two of the second. The first has a very minute obsolescent nectosac (Text-figs. 40A, B) and the second a much larger functional nectosac (Text-fig. 40C). In both kinds the radial canals arise separately as in *Nectopyramis thetis*.



Text-fig. 40. *Nectopyramis spinosa* Sears. A, dorsal view; B, lateral view of nectophore of first type, with obsolescent nectosac, 'Scotia' 1951 Cruise, St. 363; C, lateral view of nectophore of second type, with functional nectosac, 'Discovery II' St. 1639. ×9·5.

Although there is some variation in the arrangement of spinose ridges in the first group of three nectophores with obsolescent nectosac, there are elements in their arrangement that can be compared with that in the second group of two nectophores with the larger nectosac. For instance we find the same dorsal-median and what I will call 'buccal' ridge in both groups; but more material is needed to complete the morphological account. *Nectopyramis* (including *Archisoma*) is the only Prayid genus known in which the nectophores bear ridges.

We may have here, in the existence of two types of nectophore, a phenomenon similar to that found in *Amphicaryon*, where one nectophore has an obsolescent nectosac. This would be of special interest seeing that other species of *Nectopyramis* have only one nectophore as far as we know, though presumably their ancestor had more. It is possible that one type of nectophore represents a caducous larval, and the other the definitive nectophore. In favour of this interpretation is the fact that the somatocyst or pallial canal is extended well beyond the obsolescent nectosac in the first group of nectophores. This extension is characteristic of larval Prayid nectophores. In the second group the pallial canal stops short at the ventral radial canal of the nectosac, just as it does at the pedicular canal in definitive nectophores of Prayids.

Since I wrote this note Dr Mary Sears has published (1952) a note on this siphonophore, of which 'Dana' took six specimens—one with the large and five with the obsolescent nectosac. Three were taken in the Indian Ocean, two in the South Pacific and one in the Tropical Atlantic. In none of them were the stem or appendages preserved. Dr Sears regards it as a new species, and in the light of the information at present available this is convenient, since there must remain doubt about the identity of Moser's specimen. At the same time the number of siphonophore species is not large; and the spinose condition is so unusual that there is some probability that Moser was really reporting (if not accurately describing) the same species.

Material.

	Depth (m.)	Material
'Discovery II' Station		
1179	500–250	1 nectophore of first type with gastrozooid and tentacle
'Scotia' 1951 Station		
363	1000–250	1 nectophore of first type
371	1000–250	1 nectophore of first type
'Discovery II' Station		
681	1000–750	1 nectophore of second type with gastrozooid, tentacle and bud
1639	2400–1150	1 nectophore of second type with gastrozooid and tentacle

Dr Sears and I have been exchanging information for some time—a fortunate circumstance in days when publication is so long delayed. As soon as Dr Sears informed me that she was publishing a note on a new species *N. spinosa* I guessed that she was referring to the spinose Prayid I had for so long been studying. I sent her a figure of a nectophore with obsolescent nectosac and she confirmed it. But at the same time she asked if I had the nectophore as well as the 'bract'; and in her account, which at the time was in the press, she again refers to the 'bract', by which she means the bract of the eudoxid. Describing its hydroecium she says that closely associated with it is a long tubular somatocyst, and adds that on two of her specimens two thread-like branches are given off dorsally and appear distally to have a 'globular connexion'. It is quite clear to me that the 'globular connexion' is the obsolescent nectosac, and that 'the two thread-like branches of the somatocyst' are the dorsal and ventral radial canals of the nectosac, so characteristically dissociated in *N. thetis*, instead of arising with the lateral radial canals from a common pedicular canal as in most Prayids.

In the very well-preserved specimen (Pl. V, fig. 1) from 'Discovery II' Station 1179, the opening of the obsolescent nectosac is visible as well as the ring canal.

In the three specimens to which the gastrozooids are still attached the 'central organ' to which I have referred (p. 81) in my notes on other Prayids, is visible. It is comparatively large in the specimen from 'Discovery II' Station 681, and spreads down on each side of the base of the gastrozooid. The tentilla of the same specimen are well preserved and show a peculiar spheroidal swelling at the junction of pedicel and saccus. They have been examined only with a binocular microscope under very bright illumination, because it is not advisable to dissect the only three complete specimens.

Rosacea [? Q. & G.] Bigelow & Sears, 1937.

After many years study of both living and preserved siphonophores and of the literature I have come to the conclusion that we only know two species of the genus which Bigelow (1911*b*) and Bigelow & Sears (1937) rightly or wrongly called *Rosacea*. The distinguishing features of these two species, *R. cymbiformis* and *R. plicata*, is that the eudoxids have large gonophores and no special nectophore, and a somatocyst canal system of the type figured by Bigelow (1911*b*, pl. 2, fig. 4). A third alleged species of *Rosacea*, referred to by Bigelow as *R. medusa* Metchnikoff (1870), belongs to a separate genus. I have re-examined the Russian[1] account and figures of Metchnikoff, and repeat some points of interest referred to in his Russian description.

Praya medusa is described as being the most transparent of siphonophores, and is very difficult to catch. It differs from *P. diphyes* Vogt, says Metchnikoff, in its smaller size, shape, as figured by him, and equality of development of the nectophores, which do not overlap as in *P. maxima*. There is less gelatinous substance and there is a wide velum. Most important is the mention of little tentacles and 'eye-spots' on the edge of the nectophores as well as on the edge of the special nectophores of the eudoxids, in the latter of which they number from twenty-five to thirty. Metchnikoff does not mention or figure the four radial subumbral canals of the main nectophores but says that the vascular system is 'the same as in other species'. There is a single (pallial) vessel running from top to base and ending in a small vesicle (somatocyst). The shape of the comparatively small gonophores can be seen in Metchnikoff's figures. Since this species was recorded from the Mediterranean, with whose fauna most of the siphonophore pioneers dealt, it may be useful to give my conclusions about the identity of the various Prayids found in the Mediterranean.

There appear to be at least six species belonging to four genera in the Mediterranean:

Genus A. **Rosacea** (Q. & G.) Bigelow, 1911*b*

Species 1. **R. cymbiformis** Delle Chiaje, 1822.
Species 2. **R. plicata** ([?] Q. & G.) Bigelow, 1911*b*.

Genus B (new name required). ?= **Desmophyes** Haeckel, 1888*a*
(A pyriform branch of the eudoxid's somatocyst present.)

Species 3. **Praya diphyes** Kölliker, 1853*b*.

Diphyes Brajae [sic] Vogt, 1851.
Praya diphyes Vogt, 1854 *not* pl. 16, fig. 3 = *R. cymbiformis*).
Praya diphyes Graeffe, 1860 (Taf. 1, fig. 2).
Praya diphyes Fewkes, 1880 (pl. III, fig. 1).
Praya filiformis Keferstein & Ehlers, 1861 (pl. V, figs. 8–11).

Genus C. **Lilyopsis** Chun, 1885

Species 4. *Lilyopsis rosea* Chun, 1885 (with meandering lateral canals in (main) nectophores).

Praya diphyes Graeffe, 1860 (Taf. 1, figs. 1*a*, *b*, *c*; eudoxids).
Lilyopsis diphyes Moser, 1917, 1924*b*.
? *Praya medusa* Metchnikoff, 1870.

Species 5. **Lilyopsis** sp. (Fewkes), 1880 (pl. III, fig. 2) (with straight lateral canals in (main) nectophores).

Genus D. **Stephanophyes** Chun, 1891

Species 6. **Stephanophyes superba** Chun, 1891.

Forms closely resembling species 3 (as '*Rosacea plicata*') and 6 are recorded also from Misaki by Kawamura[2] (1915); species 4 by Bedot (1896) from Amboina; and species 6 from the Canaries by Chun (1891).

In the course of many years during which I have been searching plankton samples for Siphonophora, I have found outside the Mediterranean—in the Atlantic, Indian and Antarctic Seas—many Rosacean

---

[1] I have to thank Dr S. B. Markowski for translating parts of Metchnikoff's paper.

[2] I have to thank Dr Mary Sears for having been instrumental in producing a valuable translation by Rodney Notomi of most of Kawamura's inaccessible Japanese work.

nectophores all of which, except a few of *Rosacea cymbiformis*, appear to belong to one species, *R. plicata*.

The only allied species that I know is the common Mediterranean one, *R. cymbiformis* (Delle Chiaje). In both species there are only four simple, subumbral radial canals, the lateral pair of which take a meandering course along the edge of the nectosac.

A (first definitive) nectophore of *R. plicata* from 'Discovery II' Station 1617, shows an interesting variation in the path of the lateral radial canals. Similar variations are not uncommon. This variation consists of irregular cross-branches connecting the major loop of the lateral radial canal with other parts of the subumbral canal-system. Sometimes only blind diverticula are seen. This variation is of particular interest in connexion with the description by Leloup (1934*a*) of *R.* (*Prayoides*) *intermedia*. Leloup's specimen (fig. 4A), which I select as the holotype of *R.* (*Prayoides*) *intermedia* Leloup, appears to show a larger larval nectophore—'larval' because there is no descending branch of the somatocyst—from which projects a first definitive nectophore with deep hydroecium. In the absence of any indication of the looped *Rosacea* type of lateral radial canal I am inclined to regard this form as too much unlike *R. cymbiformis* and *R. plicata* to be included in the same genus.

Moser (1925) described and figured a few nectophores from the Tropical Atlantic which she called *R. tuberculata*. Several poorly preserved specimens of *R. plicata* that I have seen look rather like Moser's figures, but I have never found a well-preserved one looking like these figures. I do not think '*tuberculata*' represents a distinct species.

The synonymies of the two species of *Rosacea*, are, in my opinion, in a state of confusion, a fact that is not surprising in view of the unsatisfactory nature of so many of the earlier figures and descriptions.

The first species, *R. cymbiformis*, was figured unmistakably by Delle Chiaje (1822, Tav. 50, fig. 3; 1841–4, Tav. 33, fig. 1); Leuckart (1854, pl. 11, figs. 18–24); Vogt (1854, pl. 16, fig. 3); and Haeckel (1888*b*, pls. 31, 32), though Haeckel's figures of nectophores are poor. I know of no recognizable old figures of the second species, *R. plicata*.

Rosacea plicata (? Q. et G.) Bigelow, 1911.

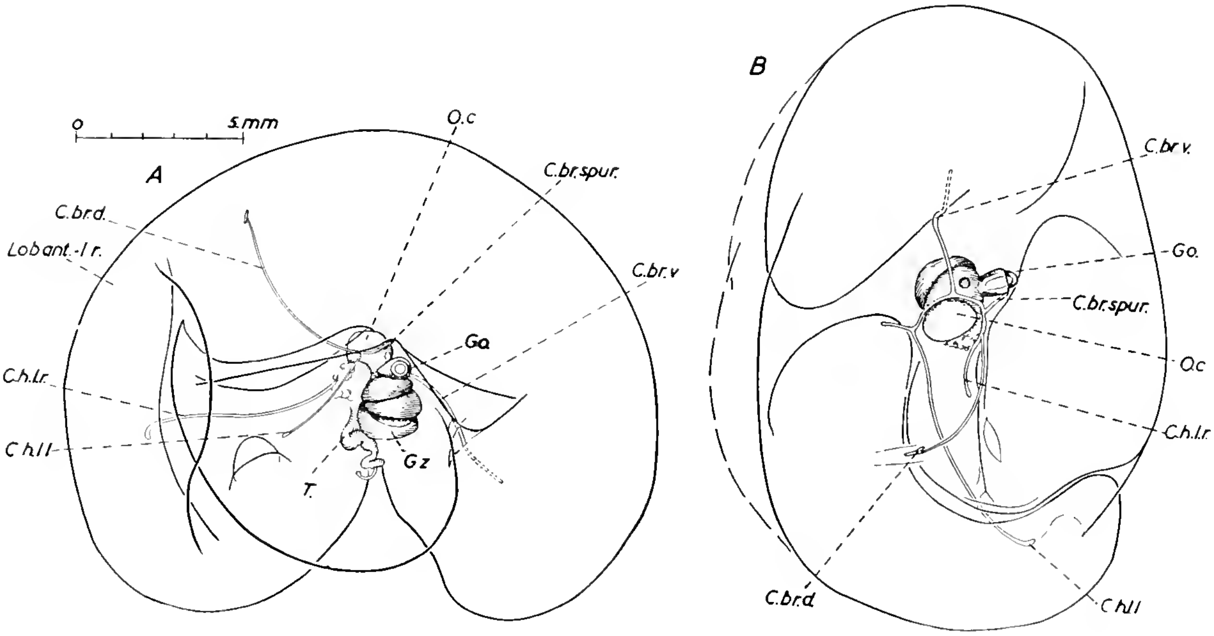
The nectophores of *R. plicata* fall into three categories: (1) larval caducous nectophores, in the hydroecia of some of which are to be found buds of (2) secondary (definitive) nectophores. Larger detached nectophores of this category are the ones most commonly found, and are those figured by Bigelow & Sears (1937, figs. 11, 12). In the hydroecia of a few have been found buds of (3) tertiary nectophores. Nectophores of category 3 have also been found detached. The species to which all these specimens belong appears to be the one that Bigelow & Sears figured and described so well in their 'Thor' Report (1937) on the Mediterranean siphonophores, and for which species, rightly or wrongly, they used the name *R. plicata* Quoy & Gaimard.

The eudoxids are large, up to 2 cm. in length, at first sight globular, and three-lobed, much as in *R. cymbiformis*.[1] The right antero-lateral lobe in *R. plicata* bends round distally to the left, and in front of the distal end of the left lobe—a feature not shown by Bigelow (1911*b*, pl. 2, fig. 4) in *R. cymbiformis*, although it often occurs in that species. In the early growth-stage it can be seen that the proximal side of the bract of *R. plicata* is convex, whilst the distal side is flattened, as in *R. cymbiformis*.

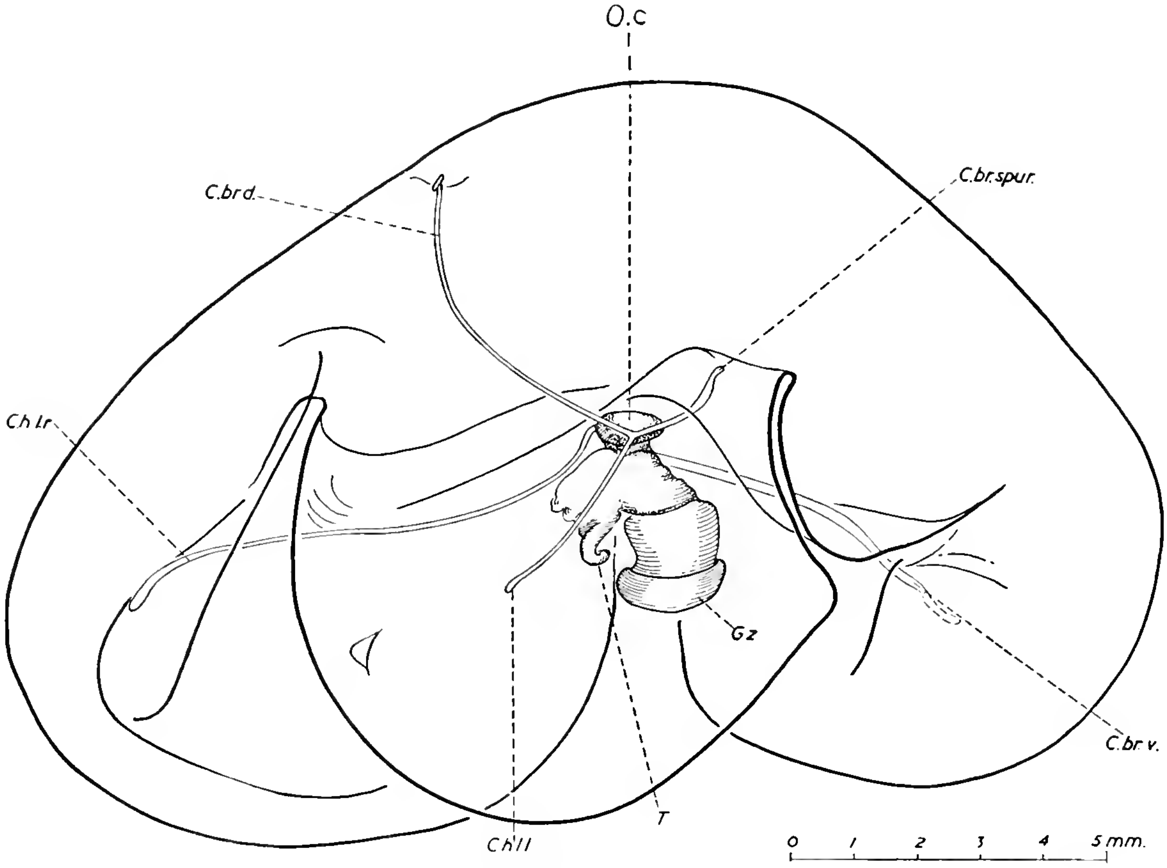
One noticeable and constant difference between eudoxids of the two species is in the position, on the shorter left, lateral hydroecial canal, from which the unpaired dorsal canal springs. In *R. cymbiformis* this position is proximal to the small lateral 'spur' canal, as clearly figured by Bigelow (1911*b*, pl. 2, fig. 4), whilst in *R. plicata* the position is distal to—in Bigelow's figure, to the left of—this small lateral spur.

---

[1] See Pl. IV, figs. 6–7.



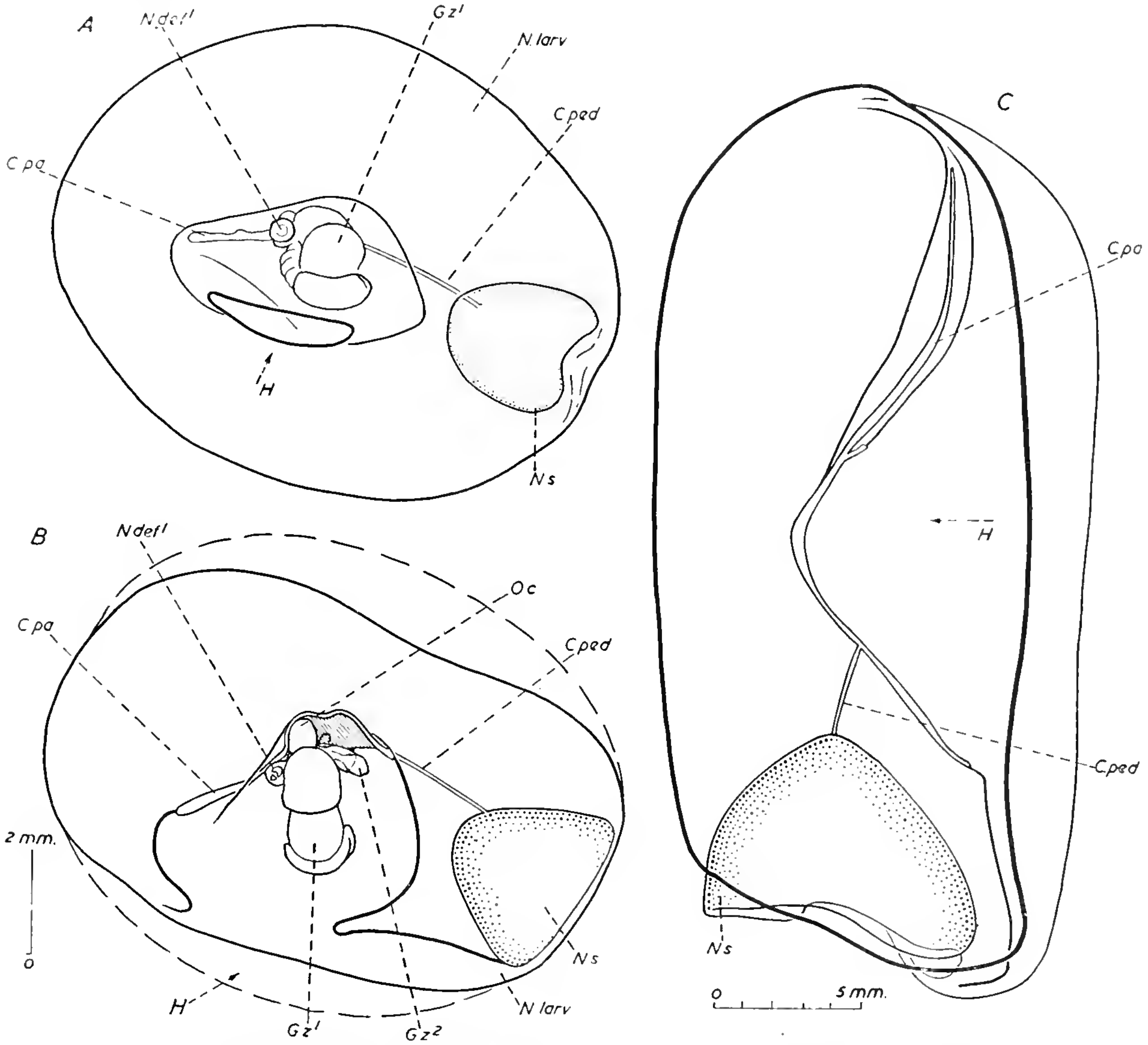
Text-fig. 41. *Rosacea plicata.* Two views of an eudoxid from 'Discovery II' St. 1617, 395–155 m., × 4·5.



Text-fig. 42. *Rosacea plicata.* Eudoxid from 'Discovery II' St. 1617, 395–155 m., × 8·3.

In *R. plicata* the right-hand longitudinal hydroecial canal of the bract is relatively much longer than the left.

The caducous, larval nectophores grow to a diameter of at least 12 mm. Some of the first known larvae of this species, together with at least one eudoxid, were taken by 'Research' in the Bay of Biscay in 1900; but all were recorded as larvae of *Hippopodius hippopus*. In the larval nectophores the lateral radial canals are somewhat sigmoid in shape and do not meander as in the definitive nectophores. Also there is no descending branch of the somatocyst, so that the attachment of the muscular lamella lies entirely above the junction with the pedicular canal that leads to the nectosac (see Text-fig. 32A).



Text-fig. 43. *Rosacea plicata*. A, B, two views of a larva from 'Discovery II' St. 1617, 395–155 m., ×7; C, a second definitive nectophore 32 mm. in length, from the same station, ×4·2.

The slit-like orifice of the hydroecium is less deep and narrower than its main cavity. The whole hydroecium is reminiscent of the hydroecium in the neotenous nectophore of *Nectopyramis diomedeae*. A constant character that distinguishes larval nectophores of this species (*Rosacea plicata*) from those of Hippopodiids is the kink caused by the 'central organ' in the dorsal side of the hydroecium. The nature of this central organ, which has very little affinity for haematoxylin, borax carmine or Sudan III, is uncertain, but seems unlikely to be yolky. It is very like the 'central organ' of the eudoxid, which appears to be a development of the small piece of stem that remains after separation of the individual eudoxids. The irregularly triangular shape of the gonophore in transverse section is due to the fact that it fits into a space between the gastrozooid and two lobes of the bract. There is no special swimming nectophore in the eudoxid, and no sign of vestigial tentacles on the edge of the nectosac of either the polygastric or eudoxid stage. Bigelow & Sears (1937) say that the location of the point of attachment of the pedicular ('stalk') canal of the 'inferior (older)' nectophores is characteristically much closer to the apex of the bell in *R. plicata* than in *R. cymbiformis*. I have not been able to confirm or refute this statement. But their fig. 9 shows a connected pair of first and second definitive nectophores that have been twisted back into their proper relative positions after fixation, and some tearing of tissue may possibly have taken place. It is not always easy to distinguish the 'stalk' canal from folds of the muscular lamella. What Bigelow & Sears call the 'inferior' ('older') nectophore appears to me to be the second definitive and therefore younger nectophore. The location of the point of attachment of the stalk-canal of the first definitive nectophore is just above the angular bend in the dorsal wall of the hydroecium, and not opposite the pedicular canal of the nectosac as figs. 9 and 12 of Bigelow & Sears seem to indicate. The eggs, which may number up to six, measure about 1·4–1·75 mm.

Hitherto unrecorded closing-net and upper-layer catches are listed on pp. 93 and 94. Only about 16% of the nets of these stations have been examined.

The depth at which the greatest number (23) of the seventy-seven 'Discovery' closing-nets took the polygastric stage of *Rosacea plicata* was about 300 m. The upper water-layers down to about 300 m. were fished at these stations three times as frequently (358) as the deeper water-masses (115), but only 16% of this total number of catches have been examined so far. At 'Discovery II' Station 1581, off the East Coast of Africa, the species was living in water at a temperature of 12–20° C. and salinity 34·88–35·26‰ at a depth of 50–0 m. At the Antarctic Ice Edge, Station 1639, where it also occurs, the temperature was about 0·18–1·36° C. at 2400–1150 m., and the salinity 34·68–34·74‰—a fairly wide range. On 28 June 1951 'Scotia' took a first definitive nectophore and two larvae in a closing-net between 1000 and 250 m. to the west of Ireland. This is the most northerly record for the species, which was also taken by H.M.S. 'Research' in 1900 in the Bay of Biscay, 300–0 m. and recorded as *Hippopodius hippopus*.

Amphicaryon Chun, 1888*a*

Nomenclature. It seems to be quite clear from a study of the original wrappers of the journals in which the generic names were published that *Mitrophyes* Haeckel dates from 29 May 1888, and *Amphicaryon* Chun from 15 November 1888. But since *Amphicaryon* has been in common use since 1911, it will be better to have the name entered in the list of *nomina conservanda* than to replace it by the little known *Mitrophyes*.

Bigelow (1911*b*) defines the genus as 'Prayidae with two nectophores of very unequal size, the older one degenerating...'. He adds that though we should expect the smaller enclosed nectophore of *Amphicaryon acaule* to be the younger, its relatively larger size in younger stages, when it overlaps the nectophore, which later encloses it, and its subsequent relative degeneration, shows that it is in reality the *older*, and that the younger overtakes it by its much more rapid growth. I believe that the vestigial nectophore is the younger, because in Prayids the buds of successive nectophores first appear inside the hydroecium of the older. No one has hitherto recorded the larval stages of *A. acaule*, but a series of three larvae of *A. acaule* mentioned (p. 95) shows that the larval nectophore is retained as the functional, adult one, and that the reduced, shield-shaped nectophore arises as a bud inside its hydroecium. I recognize three species of *Amphicaryon*, and am taking this opportunity to publish a new generic name *Maresearsia*[1] for a giant new Amphicaryonine from the Atlantic Ocean (see p. 97). It has recently been identified by me in the Indian Ocean too.

---

[1] Named after Dr Mary Sears.

'Discovery and Discovery II' Stations		Depth (m.)	Material		
			Polygastric	Eudoxid	Larval
8	N 200	600–700	×	—	—
100 A	TYF	625–675	×	—	—
100 B	TYF	900–1000	×	×	×
		1500–1550	×	—	—
100 C	TYF	260–310	×	×	×
		450–550	×	×	—
		2500–2000	×	×	—
102	N 70 V	500–250	×	×	—
		750–500	×	—	—
103	N 70 V	500–200	×	—	—
107	N 70 V	750–500	—	×	—
		500–250	—	×	—
		850–900	×	—	—
117	N 70 V	500–300	×	×	—
129	N 70 V	500–250	—	×	—
276	TYF	150–0	×	—	—
324	N 70 V	500–250	—	×	×
335	N 70 V	500–250	—	×	—
336	N 70 V	500–256	×	×	—
343	N 70 V	500–250	—	×	—
344	N 70 V	500–250	—	×	—
391	N 450 H	1200–1300(–0)	×	—	—
407	450 H	800–950	×	—	×
519	N 100 B	390–137	×	×	—
588	N 100 B	460–150	×	—	—
592	N 100 B	350–124	×	×	—
594	N 100 B	435–165	×	—	—
595	N 100 B	380–133	×	×	—
668	TYF V	500–250	×	×	—
		750–500	×	×	—
		1500–1000	×	—	—
671	TYF V	500–200	×	×	—
		750–500	—	×	×
		1000–750	—	×	—
679	TYF V	750–500	×	—	—
701	TYF B	242–0	×	—	—
848	—	270–196	×	—	—
892	N 100 B	220–100	×	×	—
946	—	270–120	—	×	—
970	—	380–110	×	×	—
1055	—	0–5	×	—	—
1571	—	1400–1000	×	—	—
1581	N 70 V	500–250	—	?	—
		50–0	×	×	—
1583	N 70 V	50–0	—	—	—
		100–50	?	—	—
		250–100	—	×	—
		500–250	—	?	—
1584	N 70 V	50–0	—	—	—
		100–50	—	?	—
		250–100	—	×	—
		500–250	—	—	—
1585	TYF B	500–0	×	—	—
		1400–700	—	?	—
1586	TYF B	530–0	×	—	—
		1630–959	—	—	—
	N 70 V	50–0	—	—	—
		100–50	—	—	—
		250–100	—	—	—
		500–250	×	—	—

'Discovery II' Stations		Depth (m.)	Material		
			Polygastric	Eudoxid	Larval
1587	TYF B	450–0	—	—	—
		1250–800	—	—	—
1588	N 70 V	50–0	—	—	—
		100–50	—	—	—
		250–100	—	—	—
		500–250	—	—	—
1589	N 70 V	50–0	—	—	—
		100–50	—	—	—
		250–100	—	—	—
		500–250	×	—	—
1616	N 70 V	250–500	×	×	—
		500–250	×	×	×
1617	N 100 B	395–155	×	×	×
1627	TYF B	580–400	×	—	×
1629	TYF B	350–220	×	×	×
1632	N 100 B	330–165	×	×	×
1633	N 70 B	1100–875	×	—	—
1635	TYF B	460–320	×	×	—
1636	N 70 B	380–150	—	×	—
1639	TYF B	2400–1150	×	—	—
1723	TYF B	800–500	×	—	—
1728	TYF B	800–350	×	×	—
1729	N 70 B	430–310	×	×	—
1730	N 100 B	420–230	—	×	×
1747	N 450	1200–400	×	—	—
1754	TYF B	900–400	×	—	—
1766	N 450 B	1200–600	×	—	—
2023	N 100 B	750–400	×	×	×
		450–150	×	×	×
2024	—	650–400	×	—	—
2025	N 100 B	750–400	×	—	—
2038	TYF B	1200–850	×	—	—
2059	N 450 B	1900–1400	×	—	—
2066	N 450 B	1900–1550	×	—	—
2636	TYF B	950–550	×	×	—
2639	—	1200–600	×	—	—
2646	TYF B	1500–800	×	—	—
'William Scoresby' Stations					
WS 61	N 70 V	500–250	—	×	—
WS 63	—	500–250	—	×	—
WS 69	—	750–500	×	×	—
'Scotia' Stations 1951					
363 54° N., 15° W. (approx.)	—	1000–250	×	—	×

× = present, — = absent.

Amphicaryon ernesti sp.n.

It has long been clear to me that two distinct species may have been confused under the name *A. acaule*. At the same time, except for two specimens from Tristan da Cunha and west of the Cape Verde Islands attributed to *Mitrophyes peltifera* by Moser (1925) (Haeckel's *M. peltifera*), a third species of *Amphicaryon*, has not, since his day, been recognized again, and has been regarded as a problematic species. Over a period of many years I have sorted out specimens of two species of

Amphicaryon. The first *A. acaule*, has been well figured by Bigelow (1911 *b*, pl. 4). The reduced nectophore is embraced by the larger one, and its atrophied nectosac has the characteristic shape illustrated by Bigelow. Its closed entrance is in contact with the surface, and its four radial canals are distinct. The upper parts of the lateral-radial canals of the larger nectophore are simple and not branched as in *ernesti* and *peltifera.*

In the second, a new species, to which I give the name *ernesti*,[1] the smaller nectophore is not partially enclosed by the larger one, whose lateral radial canals are branched in the basal region, and the entrance to its atrophied nectosac lies at some distance from the surface, but is connected by a fine strand of tissue. Its ventral radial canal becomes a network covering the ventral wall, and its lateral canals disappear and leave only the dorsal canal. These differences in the radial canals appear to be constant. The whole arrangement is often difficult to see, and sometimes looks rather like Haeckel's figure (1888 *a*, p. XXVIII, fig. 2) of *Mitrophyes peltifera.* For years I thought it must be *M. peltifera*, but in March 1952 I found (in a haul from 'William Scoresby' Station 459) an *Amphicaryon* specimen that is different from both *acaule* and *ernesti*, but closely resembles Haeckel's fig. 2 of *Mitrophyes peltifera.* All the radial canals of its larger nectophores are simple. In its shield-shaped second nectophore, whose outer wall is concave, can be clearly seen, on the ventral side, a three-branched canal, but there is no sign of a nectosac. Some days later I found two other exactly similar specimens in plankton from 'Discovery II' Station 1580, TYF B, 450–0 m. I feel hopeful, therefore, that one day more material of Haeckel's species will come to hand. Bigelow (1918) reported 30 specimens of '*A. acaule*' from the W. Atlantic. But they differ from that species as here recognized and agree with this new species in two of the main characters: (1) the smaller nectophore is not enclosed by the larger; (2) the lateral radial canals are branched. I suspect that he was dealing with *A. ernesti.*

A fourth, new, giant Amphicaryonine species from the West Coast of Africa is described below. Both its nectosacs are functional.

The eudoxid described by Leloup (1934 *a*) as *Eudoxia tottoni* is the eudoxid of a species of *Amphicaryon*, probably *A. acaule.*

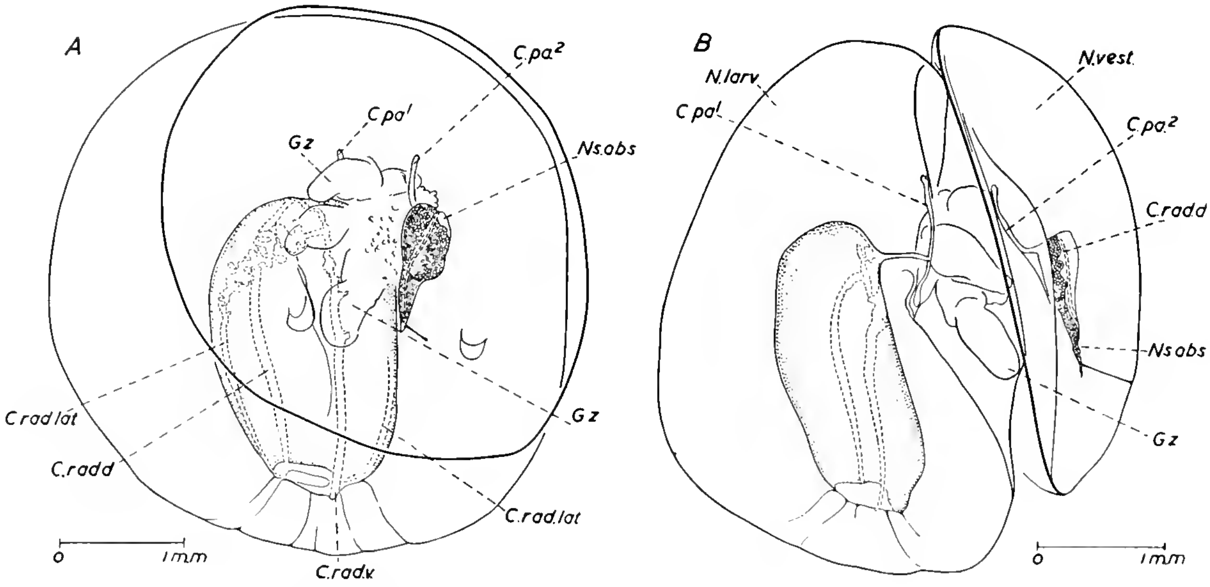
Material. 'Discovery II' Station 2648, 500–0 m. (Text-fig. 44, type specimen); Station 698, 470–0 m., 2 'larger' nects.; Station 702, 230–0 m., 4 ex., 1 larger nect.; Station 1374, 230–0 m., 1 ex., 1 'larger', 1 'smaller' nectophore; Station 1584, 100–50 m., 1 larva, 1·75 mm. in length (Text-fig. 45) Station 2679, 2 ex.

The larva is the first, as far as I know, of any species of *Amphicaryon* to be recorded. The lateral radial canals are similar to those of *ernesti* and are not simple as in *acaule.* The larval nectosac is similar in shape to that of the 'larger' of the adult nectophores. The pedicular canal is so short that it has almost disappeared. I think that the 'larger' nectophore in species of *Amphicaryon* must be the persistent larval one, and that it is not caducous as it is in *Rosacea.* A slightly older larva of *Amphicaryon acaule* from 'Discovery II' Station 1583 (550–250 m.) also shows the bud of the smaller (obsolescent) definitive nectophore growing out from the spot marked N^2B in Text-fig. 45 A. On the side of the central organ opposite to this bud, both larvae show the budding zone of gastrozooids. Both also show the median growing apex of the pallial canal or somatocyst, *XB.* Two other larvae of *A. acaule* from 'Discovery II' Station 1581 (600–0 m.) show quite clearly that the first nectophore bud becomes the obsolescent nectophore of the adult, and that the 'larger' nectophore of the adult is the persistent larval nectophore.

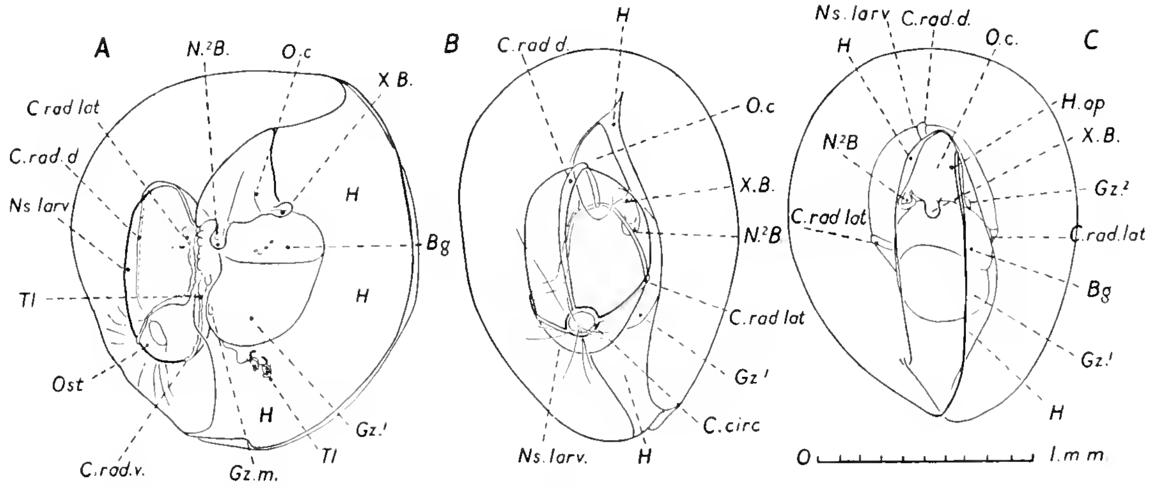
---

[1] In honour of my esteemed colleague Ernest White, who has given me invaluable assistance in all my work since 1918, and who has undertaken so much of the routine work involved in examining thousands of plankton samples and in sorting and curating enormous siphonophore collections. I have to thank him for very great assistance in preparing and checking the text of this report.

The figured holotype *A. ernesti* (Text-fig. 44) bears the Brit. Mus. (Nat. Hist.) Register No. 1952. 11. 19. 5.



Text-fig. 44. *Amphicaryon ernesti* sp.n. Two views of the holotype specimen, × 16.



Text-fig. 45. *Amphicaryon ernesti* sp.n. Three views of a larva from 'Discovery II' St. 1584, 100–50 m., × 29.

Amphicaryon peltifera (Haeckel, 1888).

Mitrophyes peltifera Haeckel, 1888*a*.

A single specimen was taken at 'Discovery II' Station 1584 in an open haul from 100–0 m.

All the radial canals of the larger nectophore are simple. There is no nectosac in the shield-shaped second nectophore, but the characteristic three-branched canal which distinguishes it from *A. acaule* and *A. ernesti* can be seen.

As mentioned above, it has seemed best not to use Haeckel's slightly prior name *Mitrophyes* for the genus since it has so long been out of use, but to attempt to have the well-known name *Amphicaryon* placed on the list of *nomina conservanda*.

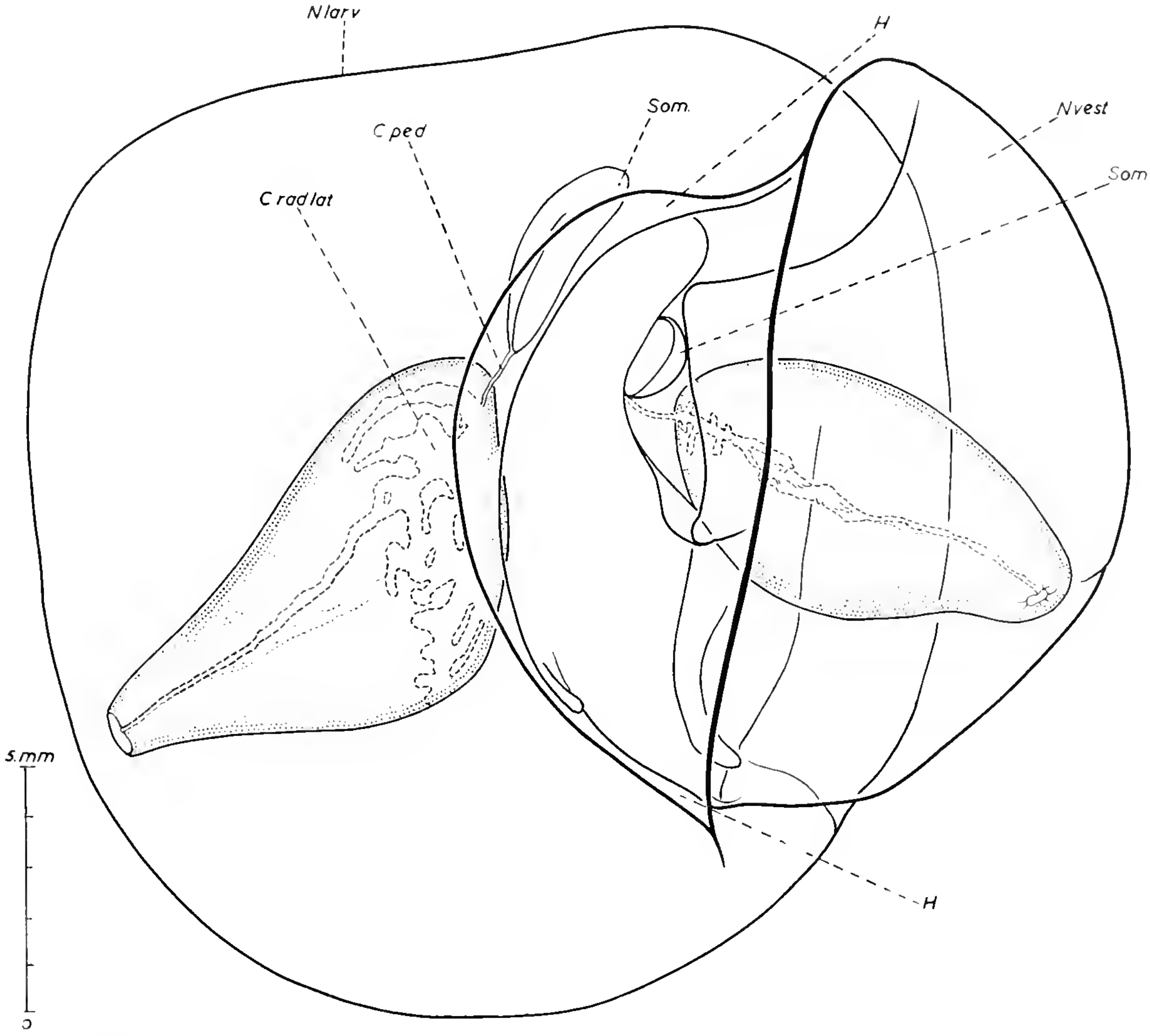
Three other specimens of this little-known species which I have had for study are from:

'Discovery II' Station 1580, 450–0 m., 2 ex.
'William Scoresby' Station 459, 135–0 m., 1 ex.

Maresearsia praeclara gen.n., sp.n.

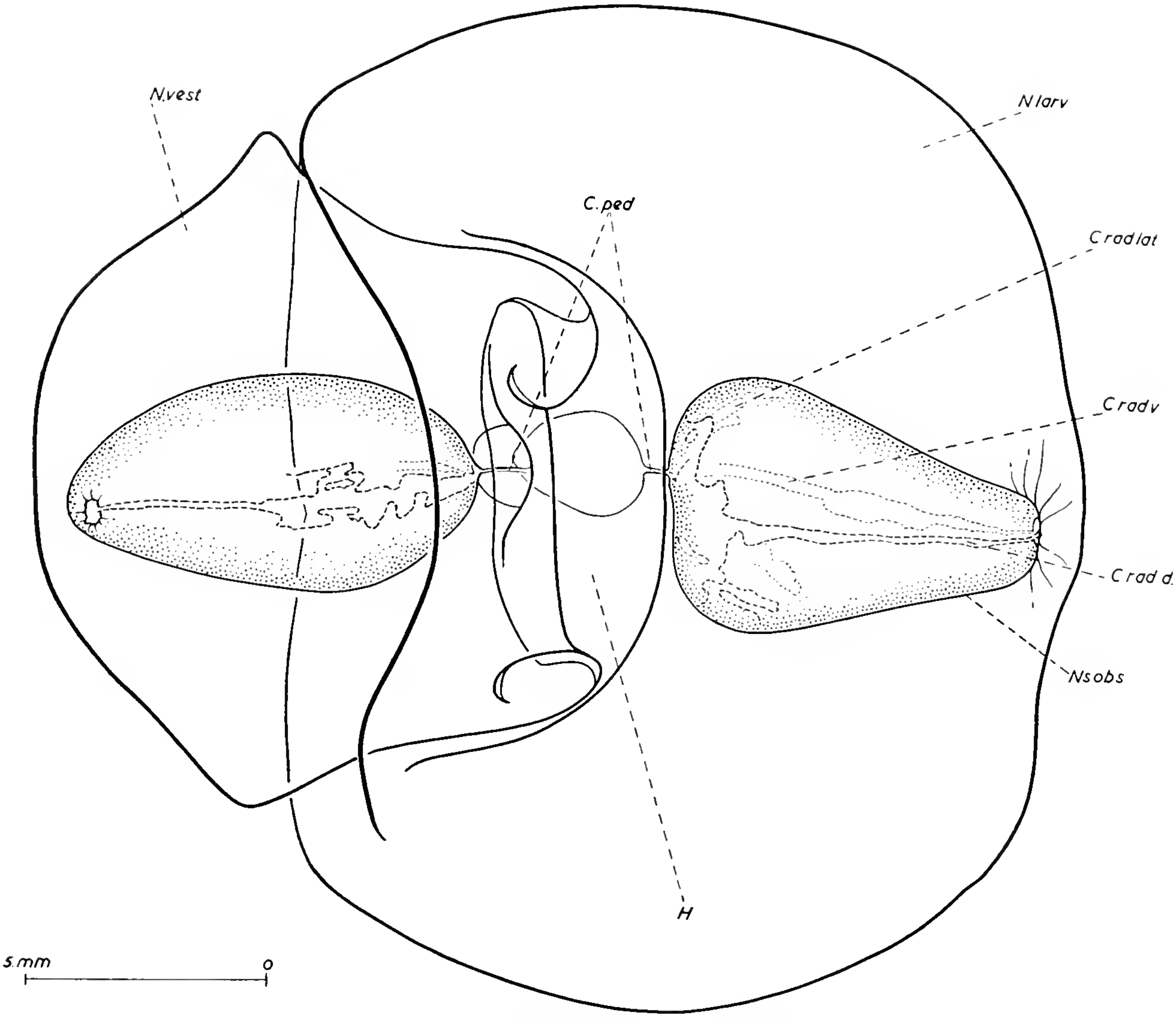
For many years past I have been familiar with a remarkable Prayid, obviously related to *Amphicaryon acaule* Chun and to the new species *ernesti*, as well as to Haeckel's *Mitrophyes peltifera*.

Polygastric stage. The two nectophores, both of which are functional, though one is somewhat reduced or less developed than the other, fit in to one another to form a globular mass about 2 cm. in diameter. The basal part of the lateral and radial canals of the nectosac are hypertrophied as in the other two species. The gastrozooids are large, and measure 3·5 mm. in length. A study of the figures (Pls. VI, VII fig. 1; Text-figs. 46, 47) will make an extended description of the nectophore unnecessary.

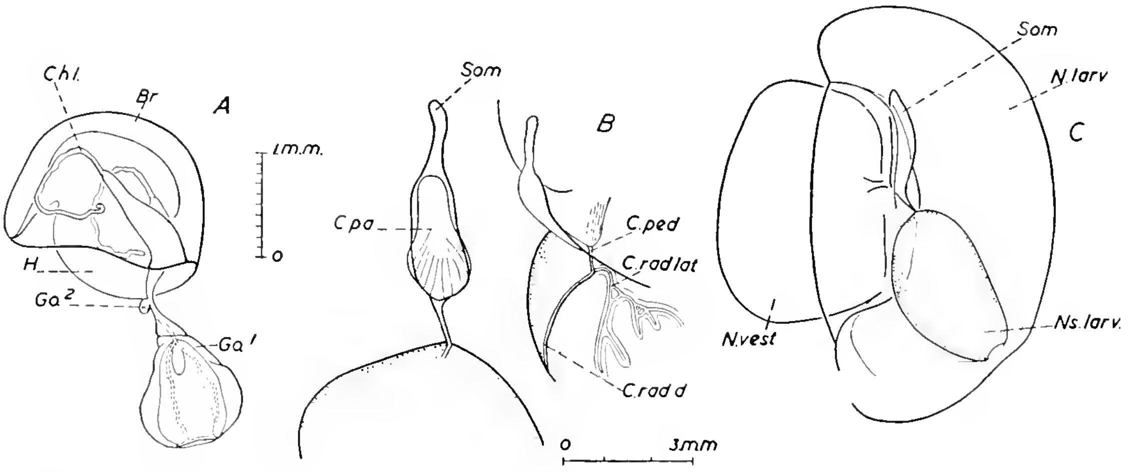


Text-fig. 46. *Maresearsia praeclara* gen.n., sp.n., lateral view, ×6·6. Beebe, Bermuda Oceanographic Expedition, 1929, 1828(–0) m. The smaller nectophore has been restored to its original position.

Eudoxid stage. Many eudoxids are still attached to the holotype by long stalks. The bract is similar to that found in *Amphicaryon acaule*, but there is a lateral notch, and the two hydroecial canals curve round on themselves in a nearly circular course. The gonophores are of a type usually found in Prayids and are too sac-like to warrant detailed description. A minute description of the eudoxid is unnecessary at this stage, and figures (Pl. VII, figs. 2–4; Text-fig. 48A) will be sufficient for its identification.



Text-fig. 47. *Maresearsia praeclara* gen.n., sp.n., view from above, × 6·8.



Text-fig. 48. *Maresearsia praeclara* gen.n., sp.n. A, eudoxid from holotype specimen taken at 'Discovery II' St. 2636, 950–550 m., × 13·5; B, pallial canal, somatocyst and attachment of muscle of polygastric stage, 'Discovery II' St. 2636, × 5·7; C, damaged polygastric specimen from 'Discovery II' St. 695, to show pallial canal and somatocyst.

Material. Bermuda, Coll. Wm Beebe; 1645–1828 m., two pairs of nectophores (separated), two large nectophores, one eudoxid.

'Discovery II' Station 695, 370–0 m., one connected pair, 1 cm. in diameter. Station 2636, 950–550 m., one pair of nectophores (separated) with stem groups. Station 2639, 1200–600 m., one pair of nectophores (separated).

Distribution. Hitherto the species had been found only in the Atlantic Ocean. 'Discovery II' Station 1580 (450–0 m.) in the Indian Ocean.

Holotype. One larger nectophore—a smaller, now detached, probably belongs—with attached stem groups, 'Discovery II' Station 2636 (Pls. VI, VII; Text-fig. 48A). Brit. Mus. (Nat. Hist.) Register No. 1952. 11. 19. 6.

HIPPOPODIIDAE

Hippopodius hippopus (Forskål), 1776.

The four peculiar teeth of the nectophore of *H. hippopus*, and probably the two of *Vogtia glabra* are homologous with, and vestiges of, more numerous teeth found in other more spiny species of *Vogtia*. Bigelow (1911 *b*, p. 211) states that the nectosome of *Hippopodius hippopus* is not effective as a swimming organ. Certainly, if retracted preserved nectophores alone are studied, this is an understandable deduction to make. But in life the upper, oral side of the nectosac has a very different appearance, and takes part in a scooping action (as it fills with water) reminiscent of a movement of the appendages of a cirripede. There is a reduplication of the dorsal part of the nectophore (see Chun, 1897*a*, fig. 11) which gives the thin upper wall of the nectosac freedom of movement. Observation with a lens showed me that it is chiefly the upper, dorsal half of the subumbrellar musculature that contracts. There is a distinct line of demarcation visible between the velum and subumbrella. The whole swimming action of the nectophore is reminiscent of *Rosacea cymbiformis*.

The contraction of the nectosac of *Hippopodius hippopus* appears to be an advance upon that of *Rosacea*. The extent of the living nectosac of *Hippopodius hippopus* would surprise an observer who is familiar only with preserved and contracted material. I refer elsewhere (p. 138) to the 'smoky' appearance assumed by nectophores of this species when they are stimulated, a phenomenon mentioned also by Korotneff (1884) and by Chun (1888*a*). When undisturbed the nectophores are quite transparent, a condition to which they return in about ten minutes after stimulation has ceased. The four teeth may show this 'smoky' appearance even when unstimulated. When the nectophores, some time after detachment, become moribund they finally become 'smoky'. The change appears to take place in the ectoderm, as Chun also observed. This species is one of the siphonophores most easy to keep in confinement. A specimen with six or more nectophores, taken at Villefranche at 9 a.m. 19 May 1949, was still alive and pulsating at 7.45 p.m. on 23 May, the room temperature being about 20° C. By 28 May it had given up swimming and had lost three nectophores but was still transparent and able to turn 'smoky' when removed (in one piece) to a watch-glass. At 7.25 p.m. on that day I dropped the specimen into Bouin fixative, whereupon one more nectophore became detached. Detached nectophores can swim for days.

The female gonophores were particularly active swimmers when detached, but as stated elsewhere (p. 77) I was unable to fertilize and rear the eggs.

A specimen of *H. hippopus* taken at Villefranche on 18 March bore fifty trichocercous cercariae (with eyes), probably the larval stage (*Cercaria setifera* Monticelli) of the trematode *Lepocreadium album* Stossich.[1] Some had made tubular tunnels into the jelly and lost their tails (metacercariae).

---

[1] See Dollfus, R.-Ph. (1925) and Palombi, A. (1937).

Chun (1888*a*) said[1] that the postembryonal stages of *Hippopodius* which he had previously observed from considerable depths in the Mediterranean, he had succeeded in capturing in an unbroken series at the surface near Orotava, Tenerife. He gave a good description of a stage that he had been able to study on three occasions in detail, and figured it well on p. 1150. He did not at that time figure the other stages of development because he intended shortly afterwards to publish a full description of the postembryonic development of *Hippopodius*. It was not, however, for twenty-five years that he did so (1913, p. 35), though he had meanwhile published two figures of young stages. The sequence of developmental stages can be seen in the following published figures: Metchnikoff (1874), pl. 11, figs. 5–8; Chun (1888*b*), pl. 2, figs. 1, 3; Moser (1924*a*), pl. 3, fig. 2; Chun (1913), figs. 5, 6; Chun (1897*a*), figs. 6*b*, 6*c*; Chun (1888*a*), p. 1150; Chun (1913), figs. 7, 8. The relationship of the two budding zones in the adult was best illustrated by Chun (1897*a*, fig. 11); and Richter (1907), pl. 28, fig. 27.

Vogtia Kölliker, 1853*b*

The four specific names *spinosa*, *pentacantha*, *serrata*, and *glabra* are used in the sense defined by Bigelow & Sears (1937), except that in *pentacantha* there are sometimes spines around the base of the median dorsal prominence, so that the facets are not entirely smooth. There is a good deal of variation in the amount and kind of spinosity from specimen to specimen, and probably from the first to the last of the series of nectophores on one specimen, but I agree that there are four species. None of the species were found in the Red Sea area, but *Vogtia glabra* was taken by Mr Fraser-Brunner in the Gulf of Aden.

Some notes on the larvae of *V. serrata* will be found on pp. 73–77 in the special section on post-larvae of Prayidae and Hippopodiidae.

Vogtia glabra Bigelow, 1918. (Plate IV, fig. 2.)

The following interesting observation on phosphorescence in this species was made by Mr P. M. David: 'When bringing the 70 cm. net inboard after the 1000–750 m. haul at 'Discovery II' Station 2890, an animal was observed phosphorescing on the $\frac{1}{4}$ in. netting above the closing band. It was seen to be part of a siphonophore, and was transferred to a small jar of sea-water. When taken into a dark cabin, it was seen to luminesce when prodded, or when the water in the jar was agitated; the light which was greenish-blue lasted several seconds before fading. The animal broke up after a while, but the component parts were still able to light up, the light seemed to be evenly spread throughout each part.'

The preserved specimen consisted of ten nectophores of definitive shape and four buds, three of them still attached to the contracted stem and appendages. All the nectophores, the largest of which measures 17 mm. in diameter, are now quite transparent.

The only other observation on luminescence in Hippopodiidae of which I am aware was made by Korotneff (1884, pp. 281, 282) on *Hippopodius hippopus*. He correlated luminescence by night with a smoky colour by day.

SULCULEOLARIINAE subfam. nom.nov.

Galettinae Stechow, 1921

Sulculeolaria Blainville, 1830 (no published specific names or figures cited).

Type species *S. quadrivalvis* Blainville, 1834 (figured).

Galeolaria Blainville, 1830 (preoccupied).
Galetta Stechow, 1921.

---

[1] English translation in *Ann. Mag. Nat. Hist. London* (6), III, p. 214, 1889.

Nomenclature. Blainville (1830) named one species of *Galeolaria* (preoccupied, renamed *Galetta*) *australis* without any indication as to its identity, except references to three names that were only manuscript names in 1830. Blainville's generic description of *Galeolaria* refers to fairly firm gelatinous, regularly and bilaterally symmetrical, subpolygonal or oval animals that have a large posterior ostium; a velum and a two-winged subostial lamella; a muscular subumbrella occupying much space inside; and a stem, borne on the anterior-superior face that issues from a bilabiate hydroecium. Various authors have since used the name *australis* for at least three separate species, *Diphyes biloba* Sars, 1846, *G. turgida* (Gegenbaur), 1853, *G. chuni* Lens & van Riemsdijk, 1908, and a new one to which I give (p. 108) the name *Sulculeolaria angusta* sp.n.

We are, however, faced with an insuperable difficulty in the use of the name *Galetta* Stechow, 1921 (nom.nov. for *Galeolaria* Blainville, 1830, preoccupied Lamarck, 1818), for any of these species.

One legalistic solution of the whole problem is as follows: The 'specific' names cited by Blainville under *Galeolaria* in 1830 were all manuscript names. Opinion 46, rendered by the International Commission on Zoological nomenclature, seems to be applicable here, and we have to ask ourselves what is 'the first species published in connexion with the genus' after 1830; for it will be this species that becomes *ipso facto* the type species of *Galetta* Stechow, 1921. The answer is:

(1) *Galeolaria australis* Quoy & Gaimard, 1833. But this is specifically indeterminable, as I will show on pp. 101–4, and therefore to be rejected.

(2) *G. quadridentata* Quoy & Gaimard, 1833. So that if we reject *G. australis* on the grounds that it is specifically indeterminable, *G. quadridentata* Quoy & Gaimard, 1833 becomes the type species of *Galeolaria* Blainville, 1830 (preocc., =*Galetta* Stechow, 1921).

But since I shall show (p. 109) that zoologically *G. quadridentata* Q. & G. 1833 is the same species as *Sulculeolaria quadrivalvis* Blainville 1834,[1] and since this species *S. quadrivalvis* Blainville, 1834, is, as I showed in 1932, the type species of *Sulculeolaria* Blainville, 1830, by virtue of opinion 46, International Rules of Nomenclature, it follows that *Galetta* Stechow, 1921, becomes a synonym of *Sulculeolaria* Blainville, 1830.

Zoology. From a zoological point of view this may be a good thing, for *Sulculeolaria* has been used lately for those species which have teeth round the ostium of the anterior nectophore, and *Galetta* for those that have none. But I shall show (p. 110) that sometimes *Sulculeolaria quadrivalvis* has no teeth; and my Text-fig. 50A, B, D shows that *Sulculeolaria* [*Galetta*] *biloba* has a peak on the dorsal side of the ostium, which really represents undivided dorsal teeth.

What generic name is the working systematist to use? I dislike upsetting the involved synonymy of siphonophores again, but regret that I must follow the logical course of using the name *Sulculeolaria* Blainville, 1830, for all the species, whether toothed or not. The subfamily will have to be renamed Sulculeolariinae.

I hope that systematists in future will find that the identification and naming of Sulculeolariine Diphyids is fairly easy. It certainly has not been so in the past. The next reviewer of the genus will have a sounder basis from which to start.

'Galetta australis'

G. australis Bigelow, 1911*b* (='*G.*' *biloba* Sars, 1846).
G. australis Bigelow & Sears, 1937 (='*G.*' *turgida* Gegenbaur).

'*G. australis*' auct. refers to several distinct species. More work is needed to confirm my views on how many are represented, and what is their morphology. Quoy & Gaimard's original 'Astrolabe'

---

[1] The *S. quadrivalvis* cited by Blainville in 1830 is only a manuscript name. Figures of it were published by Blainville in 1834, at which date it becomes a valid specific name.

specimen came from the Southern Indian Ocean (36° 32′ S. lat., long. unknown), so that the name of their species, if applicable at all, should be used for one that occurs there.

From the official narrative of the 'Astrolabe' expedition it is difficult to follow the track from Trinidad Island[1] in the South Atlantic, round the Cape to Albany, Western Australia. On 3 September 1826 'Astrolabe's' position was 37° 17′ S. lat., 27° W. long. On 13 September it was decided to make for Albany, and on 20 September she was following the parallel of St Paul Island in the South Indian Ocean, six or eight miles to the northward of which she probably passed on 21 September. Albany was reached on 7 October. As she met with particularly violent weather in the eastward passage of the Indian Ocean it seems unlikely that any collecting was done there although sea-temperature records were made. On the return journey the course taken was through Sunda Strait to Mauritius and Réunion and down to the Cape. It seems therefore more probable that the latitude, 36° 32′ S., given for the capture of the original '*G.*' *australis* was where the ship's track cut this parallel, somewhere off Algoa Bay, particularly as Quoy & Gaimard say that it was here and off Western Australia that plankton was abundant in the Indian Ocean.

An examination of hauls made by R.R.S. 'Discovery II' in this area, namely at Station 1567, 37° 50′ S., 35° 47′ E., and Station 1568, 34° 48′ S., 34° 28′ E., reveals the presence of at least three species of '*Galetta*' that systematists in general would report as '*G.*' *australis*. The differences are seen at once in the lamellae of the posterior nectophores, but it was only after completing this report that I was able to discriminate between anterior nectophores. One type of posterior nectophore can be distinguished by having a rounded, undivided lamella, as in the Mediterranean species '*G.*' *turgida*. The second has a thickened, notched lamella, as described below for ['*G.*'] *Sulculeolaria angusta* sp.n. The third kind of posterior nectophore is similar in profile to that figured by Bigelow (1911 *b*, pl. 5, fig. 9), and the lamella has the 'duplex curve', figured by Bigelow (1911 *b*, pl. 5, fig. 9 *bis*). This is the well known and adequately figured '*G.*' *biloba* (Sars), 1846 (see Text-figs. 49–51). Quoy & Gaimard's (1834) figure of '*G.*' *australis* might represent any one of the three. The absence of any indication of a somatocyst from this old figure may or may not be significant.

If given only the basal (articulating) end of a well-preserved posterior nectophore of '*G.*' *biloba*, '*G.*' *turgida* or '*G.*' *angusta*' it would now be possible for a specialist to identify it. If the lamella was in good shape too, any competent systematist could do so.

Bigelow & Sears (1937) gave a key for the identification of the anterior nectophores of the '*australis*' group of '*Galetta*'. My criticism of this is that Leloup's species *meteori* is more clearly related to *Lensia subtilis* and should be excluded. '*Galetta*' *chuni* is now so well known that it gives no trouble. '*G.*' *turgida*, common in the Adriatic, has a minute somatocyst and a divided 'basal wing' in the anterior nectophore and a rounded one in the posterior. The posterior nectophores are very characteristic, and each end exhibits characters that are very useful to the systematist. Bigelow & Sears (1937) found the task of identification of posterior nectophores more difficult than that of the anterior ones.

The morphological features of specimens attributed by various authors to this 'species' *australis*, and over which there has been some confusion, are as follows: The somatocyst of the anterior or superior nectophore may be minute or nearly as long as the 'mouth-plate' or lamella. The posterior nectophore may have a comparatively 'broad baso-ventral sector' when viewed laterally, or may be long and slender, and may or may not have lateral, longitudinal 'wings'. The 'mouth-plate' or lamella of the posterior nectophore may be long or short; notched, or have a 'duplex curve', or be convexly rounded at the end.

Bigelow (1911 *b*) is the authority for the use of the name *australis* in recent years, having provided (pls. 5 and 6) both good photographs and not such good drawings of a species of '*Galetta*' bearing

---

[1] Position: 20° 30′ S, 29° 20′ W.

that name in a work which is one of the standard references for the group. The legends to the figures do not indicate the locality of the particular specimens, but presumably they came from the Eastern Tropical Pacific. Much as I dislike having to criticize any part of Bigelow's delightful work which I admire so much, there is one drawing, beautiful in its execution, which I mistrust, fig. 1 of his plate 6. The only part of it which I query is the stiff base of the lamellar plates. The rest of the drawing appears to represent '*G.*' *biloba* (Sars), but in that species, as reference to my Text-fig. 50 of the base of the anterior nectophore shows, the dorsal end of the lateral surfaces for articulation with the posterior nectophore reaches well out below the ostium of the nectosac, in fact to a point not far short of its centre. This means that the basal portion of the lamella or mouth-plate of the anterior nectophore in '*G.*' *biloba* is much more rigid than the thin distal part, which in preserved specimens is usually bent back. Bigelow's fig. 1 of plate 6 does not show this feature, and is, I suspect, not correct. It is not at all easy to draw this region even with a camera lucida, because it is only rarely that a specimen is preserved in a satisfactory condition, and living material is not readily available. Then again this fig. 1 of Bigelow does not show the little pit in the roof of the base of the anterior nectophore that houses the tip of the stalk, a minor but a very characteristic feature of '*G.*' *biloba*. It is of course possible that Bigelow has accurately drawn a representative of a Pacific species that I have not seen, but we are finding more and more that most siphonophores have very wide distributions and my experience is based on hauls from a very extensive oceanic area. Besides, Bigelow's photograph 8 on plate 5, though not strictly a side-view, shows all the characters of '*G.*' *biloba* that I have mentioned. The somatocyst and the basal pit are diagnostic, though the somatocyst does not show very clearly.

Kawamura (1915, fig. 10) tried, unsuccessfully, to fit together drawings 1 and 3 of Bigelow's plate 6, but had to distort fig. 1, and left no space for the appendages.

Bigelow & Sears (1937) attributed 514 anterior and 673 posterior nectophores from the Mediterranean to this 'species', *australis*. All of the posterior ones showed (in lateral view) 'the broad baso-ventral sector' characteristic of both *biloba* and of *turgida* (see Bigelow, 1911*b*, pl. 5, fig. 9, lateral view—there are two figs. 9), and all had an undivided basal wing, which is a character of *turgida*. Bigelow & Sears's (1937) fig. 26 shows typical bases of *turgida* nectophores.

The great breadth of this baso-ventral sector in '*G.*' *biloba* and '*G.*' *turgida*, which carries, at the proximal end of each ventral wing, a long (dorso-ventrally) and rounded articulating surface, necessarily implies that the base of the corresponding anterior nectophore is equally broad dorso-ventrally and that the margins of the hydroecium are hollowed out to take these articulating surfaces which transmit the thrust of the posterior nectophore. This condition is particularly well marked in the Mediterranean species that I refer to below as '*G.*' *turgida*.

Bigelow & Sears (1937) also stated that these posterior nectophores from the Mediterranean have undivided basal wings, but not, as I have already remarked, whether they have the duplex curve mentioned on p. 35 of their 'Thor' report and figured by Bigelow (1911*b*, pl. 5, fig. 9 *bis*). This is important because in recent years Dr Gamulin has sent me from the Adriatic some well-preserved specimens of anterior and posterior nectophores of a '*Galetta*' of which the posterior ones possess a convexly rounded lamella, neither notched as in *chuni* nor with the duplex curve of Bigelow's figure of '*australis*', but like Gegenbaur's (1854) pl. XXIII, fig. 3. In fact I believe Gamulin's specimens are the '*G.*' *turgida* of Gegenbaur. The anterior nectophores have a much smaller somatocyst than Bigelow's figures (1911*b*, pl. 5, fig. 8; pl. 6, fig. 1) of *australis*, and resemble those in fig. 26 of Bigelow & Sears (1937), which are in fact specimens of '*G.*' *turgida* Gegenbaur.

At the end of September 1952, when the draft of this report had been completed, I was able to re-examine, through the courtesy of Dr Kramp of the Copenhagen Museum, a number of the anterior and posterior nectophores, separated into vials, from 'Thor' Stations 206 (1910) and 297 (1911).

As I suspected, they were all, with the exception of one rogue (*Sulculeolaria quadrivalvis*), representatives of *S. turgida* (Gegenbaur). I carefully examined, after staining, eighty-five posterior (inferior) nectophores from Station 297 and found that they all possessed the simply rounded, undivided lamella of *S. turgida* (Gbr). The fifty-five anterior (superior) nectophores that I examined from the same station all had the minute somatocyst and conformation of the base of the nectophore characteristic of *S. turgida*. The specimens were not in very good condition, and I did not check the presence, or run of the lateral commissural canals.

The problem has been to link up the anterior and posterior nectophores of the various '*Galetta*' forms so as to define species, and then to see if we can apply the specific name *australis* to any of them. But the natural desire to retain Quoy & Gaimard's name should not blind us to the danger of a perpetuation of the present state of confusion. This review of '*Galetta*' *australis*, then, shows that whilst it is possible that Quoy & Gaimard's specimen came from off Algoa Bay, this is by no means certain. Also that in this area are to be found three species of '*Galetta*' which can be separated by their posterior nectophores as well as by their anterior ones. Quoy & Gaimard only figured the anterior nectophore of '*G.*' *australis*, and that very inadequately. It seems doubtful on the whole whether it will ever be possible now to use the name *australis* correctly. I have now found the North Atlantic '*G.*' *biloba* (Text-figs. 49–51), with which I am well acquainted, in the Indian Ocean. It is worth while mentioning this to confirm Bigelow's statement that the identity of the Atlantic *biloba* with an Indo-Pacific species has been sufficiently established by comparison of series from the different oceans. It is a dioecious species which has been taken abundantly by the Marine Biological Association, Plymouth, in the Celtic Sea; by the Irish Fisheries Board; and at Valencia Island by Miss Delap, who noted its ability to jump out of the water, made interesting sketches of it and its developmental stages and presented specimens to the British Museum.

It is of interest to record that had it not been for a chance invitation to Robert Prescott of Latymer School, a member of the Museum's Junior Naturalist Club, to do some plankton sorting, the presence of '*G.*' *biloba* in the Indian Ocean might not have been demonstrated, and the whole question of '*Galetta*' species might have remained in confusion.

[Galetta] Sulculeolaria biloba (Sars), 1846.

Galeolaria australis Bigelow, 1911*b*, pl. 5, fig. 8; Bigelow, 1918.
Galeolaria australis Candeias, 1929 (part C, fig. 3).
Non *Galetta australis* Bigelow & Sears, 1937 (? = '*G.*' *turgida*).

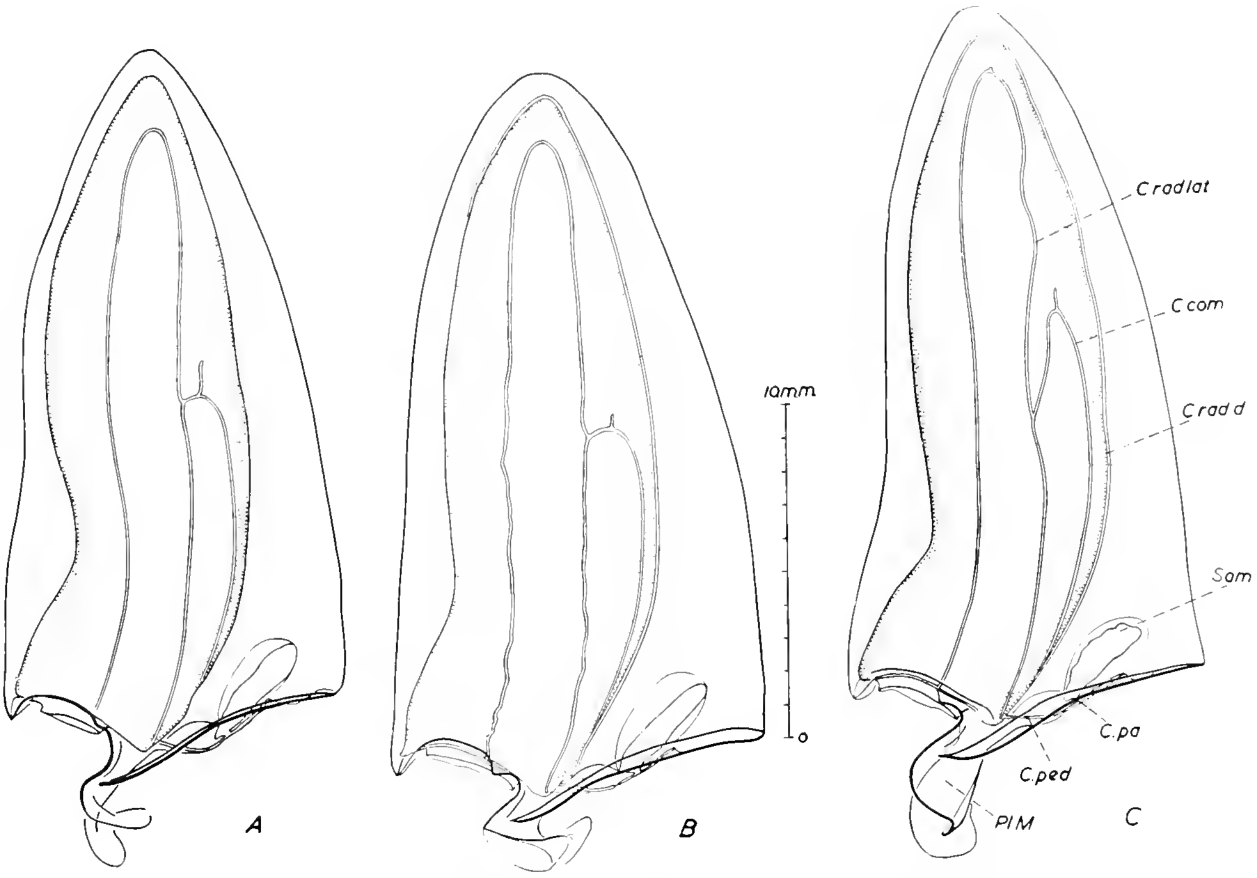
Sars's (1846) figures of this species are very accurate. His fig. 16 shows not only the characteristic somatocyst, but also the minute indentation in the base of the nectophore or roof of the hydroecium that houses the terminal end of the stem. Sars's fig. 17 of the young posterior nectophore shows, under a lens, the characteristic 'duplex curve' of the lamella. I feel obliged to discard the name *Galetta australis* which Bigelow has used for *biloba* as being impossible to apply to any zoological concept, and to use for this widely distributed and adequately figured species its original name *Sulculeolaria biloba* (Sars), 1846. Anyone who is familiar with the North Atlantic species would say at once of Sars's figure 'that is the species', whereas we shall probably always be in doubt about Quoy & Gaimard's *Galetta australis*,[1] which was figured in such a way that it might represent any one of several Sulculeolariine species known to-day.

Distribution. Under the name *G. australis* Q. & G. Bigelow (1918) reported on thirty specimens of this species from surface and intermediate hauls in the Western Atlantic; and could find no distinction between them and series from the North and South Pacific. Lens & van Riemsdijk (1908)

---

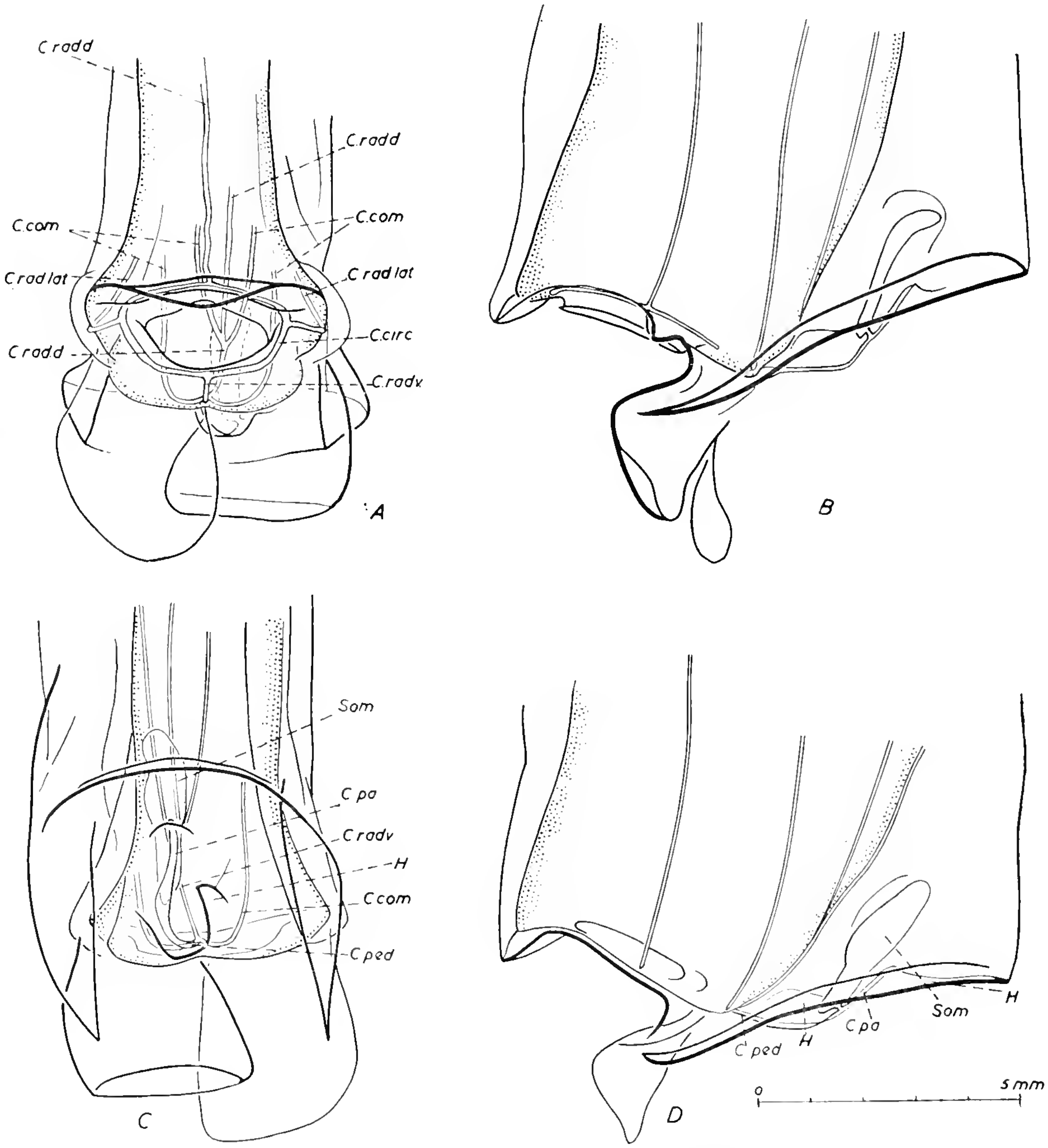
[1] Bigelow held the contrary opinion.

reported on a species under the name *G. biloba* Sars from the Malaysian area, but their figure is not good. Through the courtesy of Prof. Dr H. Engel, Director of the Zoölogisch Museum, Amsterdam, I was able to re-examine a little tube full of 'Siboga' specimens labelled '119 E 1 *Sulculeolaria biloba* Sars'. These must be Lens & van Riemsdijk's specimens, now in alcohol, from 'Siboga' Station 117A, lat. 1° 15′ N., 123° 37′ E. I could not recognize the figured specimen, but picked out seven anterior and seven posterior nectophores that were the best preserved. Most of the specimens were in very poor shape. The seven posterior nectophores had bilobed lamellae with a 'sigmoid curve'. One or two were preserved well enough for me to be able to decide that though small specimens they corresponded sufficiently well with those of *G. biloba* from the North Atlantic. I am satisfied that the seven anterior nectophores that I selected represented *G. biloba* Sars, though they were in poor condition. The somatocysts were not easily visible, but I think that I could just detect in each the characteristic arrangement of the somatocyst and the 'basal pit' for the proximal end of the stem, such as I have described. These seven anterior and seven posterior selected nectophores could hardly represent any other species known to me. 'Discovery II' took specimens at Stations 1567 and 1568 as reported above (p. 102) and very recently thirteen anterior and nineteen posterior nectophores were sorted out from a surface-haul from 'Discovery II' Station 2688 on the '90° E.' line of stations in lat. 20° 19′ S. The average length of the nectosac of these anterior nectophores is 8·8 mm. I am quite satisfied therefore that the Atlantic species *Sulculeolaria biloba* occurs in the Indian as well as the Pacific Ocean. It is possible that the North Atlantic specimens reach a greater size than the tropical Indian, but we have not sufficient data yet to be able to judge.



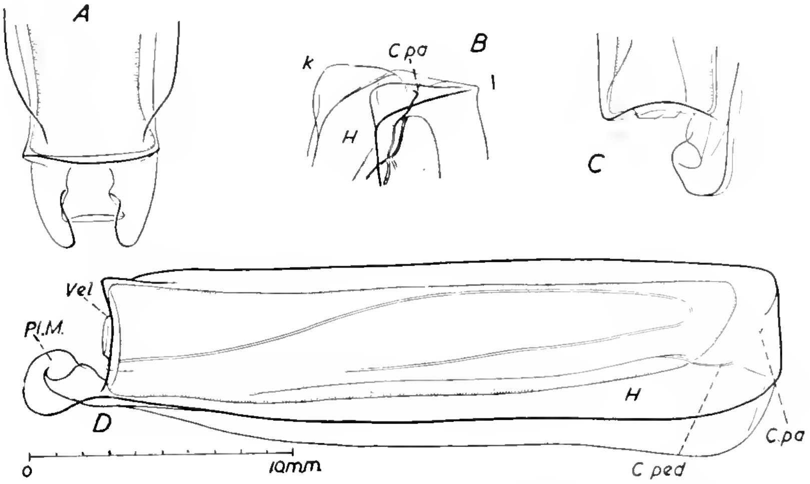
Text-fig. 49. *Sulculeolaria biloba*. Three anterior nectophores taken by M.B.A. Plymouth in Celtic Sea, July 1937. × 4·4.

Morphology. Lateral commissural canals are, I think, always present. In *S. turgida* they are sometimes absent. There are two inconstant characters about the commissural canals: (1) the position on the dorsal radial canal from which they spring—sometimes opposite each other, but usually the right-hand one given off before the left; (2) their course before junction with the lateral radial canals.



Text-fig. 50. *Sulculeolaria biloba*. Basal parts of anterior nectophores taken by M.B.A. Plymouth in Celtic Sea, July 1937. A, dorsal view; B, D, lateral views; C, ventral view. ×8.

The ventral side of these lateral radial canal-loops always springs from the pedicular canal-junction (Text-fig. 50C) of all four radial canals, and never from the ring canal as described by Bigelow & Sears for a Mediterranean species (? *S. turgida*) which they called *Galetta australis* (1937, fig. 26A). It is not easy to see this junction in a lateral view. One side (left) of the base of the posterior nectophore is higher than the other (Text-fig. 51B). In consequence the cavity round the central boss of the base of the anterior nectophore is asymmetrical, as can be seen in my Text-fig. 50C. The width of the base of the paired lamellae or mouth plates is greater than that of the base, and there is a groove between outer edge of lamella and base, shown in my lateral views. The somatocyst is probably ovate in life, as it is in the best preserved specimens. In those in which it is shrunken there is left an ovate outline in the jelly, seen perhaps only in certain lights. The upper end of the stem complex projects upwards into a small pocket in the base of the nectophore. This minor feature appears to be constant and characteristic, and was shown in Sars's original figure, as well as by Bigelow (1911 *b*, pl. 5, fig. 8). The base of the mouth-plate or lamella of the anterior nectophore is thicker than the terminal part, and projects out nearly to the centre of the ostium.



Text-fig. 51. *Sulculeolaria biloba.* Posterior nectophore from Celtic Sea, M.B.A. Plymouth 1937 Cruise, St. 6. A, C, dorsal and lateral view of the mouth-plate, × 2·5; B, ventro-lateral view of proximal end to show triangular, articulating facets, × 3·5; D, posterior nectophore, × 3·5. Bigelow's 'baso-ventral' sector indicated between *k* and *l* in fig. B.

[Galetta] Sulculeolaria turgida (Gegenbaur), 1854.

Gegenbaur (1854) described and figured (under the name *Diphyes turgida*) a species of '*Galetta* with no obvious somatocyst in the anterior and an undivided, rounded lamella to the posterior nectophore from the Straits of Messina. Candeias (1929) found the anterior nectophore of a similar species, and in 1932 I reported on similar specimens from the Great Barrier Reef. Since then I have often seen these forms. In recent years Dr T. Gamulin has been sending me fine specimens of both nectophores of this species from the Adriatic.

Since a species of this sort was long ago described from the Mediterranean and can still be recognized there, I think it well to retain the name *turgida* for it.

The two points about the alleged absence of a somatocyst and the undivided lamella of the anterior nectophore can both be explained, I still think, by the difficulties encountered in trying to see the details of these transparent animals. Dr Sears herself says 'both characters which make the species... unique...are such that they could have been overlooked easily'.

The most characteristic thing about the Mediterranean species is the rounded and undivided lamella of the posterior nectophore (Text-fig. 52), which Gegenbaur clearly figured.

The larva was figured by Gegenbaur (1853, pl. 16, fig. 20) and labelled in error, *Diphyes sieboldii*. On 15 April 1950 Dr Mary Sears published a paper on siphonophores from the Marshall Islands. In it appears a review of this subject and a description of the deformed anterior nectophore of a similar species under the new name *Galetta bigelowi* in honour of Dr H. B. Bigelow that great contributor to our knowledge of the group, and himself the foremost authority on it. I have found similar specimens and think it is a distinct species.

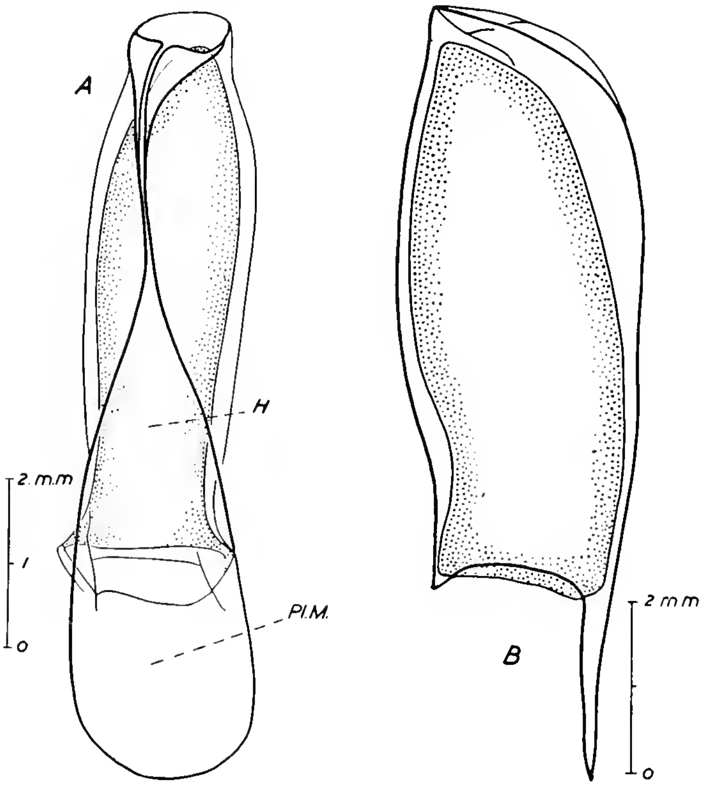
S. turgida occurred in the Indian Ocean as follows (depth in metres follows the number of the Station):

A. Off south-east and east coasts of Africa. 'Discovery II' Stations: 1371, 146–0; 1373, 135–0; 1374, 230–0; 1375, 210–0; 1568, 1400–0 and 5–0; 1573, 800–0; 1581, 600–0; 1585, 500–0; 1587, 450–0; 1589, 600–0.

B. On 90° E. line of 'Discovery II' Stations: 2688, 121–0; 2894, 142–0; 2895, 54–0.

C. In the hauls made on the 32° S. line of 'Discovery II' Stations 1736–66, *S. turgida* was not taken.

The species has been taken by 'Discovery' and 'Discovery II' in the Atlantic at the following Stations: 89, 100(–0); 100B, 0–5; 292, 110–0; 673, 340–0; 676, 290–0; 677, 420–0; 678, 360–0; 680, 260–0; 681, 500–250; 682, 375–0; 699, 370–0; 701, 242–0; 702, 236–0; 703, 358–0; 708, 208–0; 712, 224–0; 713, 200–0; 2635, 280–0; 2648, 500–0.



Text-fig. 52. *Sulculeolaria turgida*, posterior nectophore, 'Discovery II' St. 1581, × 11. A, ventral view; B, lateral view.

[Galetta] Sulculeolaria angusta sp.n.

The outline of the anterior nectophore (Text-fig. 53 C) has the general *Sulculeolaria* form. The halves of the long 'mouth-plate' or lamella of the anterior nectophore have a roundly pointed posterior edge as can be seen in a well-preserved specimen after staining.[1] The somatocyst is minute, but varies in size.

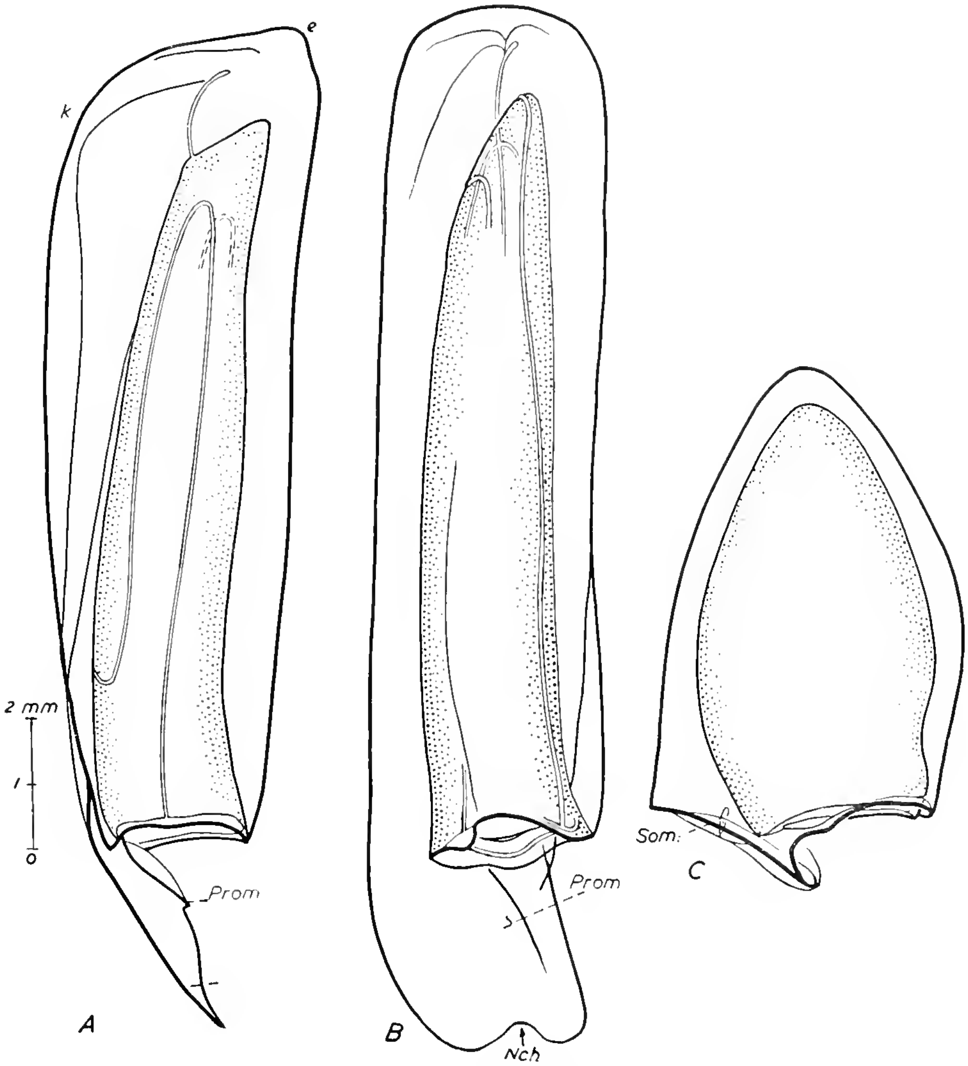
The profile of the posterior nectophore is long and narrow, without the 'broad baso-ventral sector' of Bigelow. The lamella of the posterior nectophore is roundly notched as in *Galetta chuni*, but is thicker in its basal half. About the centre of the mouth-plate appears a variable little prominence. It lies at the terminal end of the thick basal part of the lamella. Between this and the notch is a thinner area. No lateral ridges or wings have been seen, even on well-preserved specimens of the posterior nectophore.

---

[1] It is generally advisable to stain Sulculeolariinae. With specimens preserved in formalin which has been buffered with hexamine, this may be done fairly quickly, after one or two washes in distilled water, by adding two or three drops of Delafield's haematoxylin to a watch-glass of distilled water.

The type material was taken by R.R.S. 'Discovery II' at Station 1586 in an oblique haul from 550 m. to the surface, and consisted of twenty-seven anterior nectophores and twenty posterior, of which I select one posterior nectophore Brit. Mus. (Nat. Hist.) Register No. 1950. 6. 20. 1 as the holotype. It is not possible to select an anterior nectophore as well, because we do not know for certain whether any were connected in life with the holotype. Seven posterior nectophores were taken also at 'Discovery II' Station 1374 in an oblique haul from 230 m. (off the coast of Natal).

The posterior nectophore figured by Candeias (1929, fig. 6) probably belongs to this new species.



Text-fig. 53. *Sulculeolaria angusta* sp.n. A, B, lateral and dorso-lateral views of holotype posterior nectophore, Brit. Mus. Reg. No. 1950. 6. 20. 1., 'Discovery II' St. 1586, 550–0 m., × 8·5; C, anterior nectophore probably of this species, 'Mabahiss' St. 61, night, 0 m., × 8·5. *k–e* = baso-ventral sector.

Sulculeolaria quadrivalvis Blainville, 1830.

The question whether *Sulculeolaria quadrivalvis* and *S. quadridentata* are synonyms of one and the same species was last reviewed by Bigelow & Sears (1937).

They concluded (1) that there was an unbridged gap between the bidentate and the extreme quadridentate forms of the anterior nectophore; (2) that the bidentate form occurs in both sexes, and that the only quadridentate colonies of which the sex has been definitely determined chanced to be female; (3) that it is possible that the quadridentate form is a sport that appears more often in female than in male colonies; (4) that it seems wisest to recognize two species.

'Discovery II' took 144 well-preserved anterior nectophores of various sizes, together with a similar number of posterior ones on 11 November 1951 at Station 2905 in the Red Sea. Fifty-five are bidentate, and twenty-eight are of the extreme quadridentate form. Fifty-eight others have a pair of lateral teeth of various lengths (which I am unable to record at the moment). In my opinion they bridge the gap between the two forms satisfactorily. Three have no teeth at all but resemble this species more than they do *S. chuni*. My conclusions are that (1) it is not a question of the number of teeth but of the total development of the 'denticulate character'. For in bidentate forms the two teeth may be quite small, whilst in the four-dentate form they never are; and the inner distal corners of the mouth-plate of the bidentate form are generally rounded and not denticulate, whilst in the four-dentate form they are always denticulate, so that there is a gradual change from the condition where only two dorsal teeth are present and the mouth-plates are rounded, to the extreme four-dentate form with long dorsal and lateral teeth and 'denticulate' mouth-plates; (2) only one species is to be recognized. The name *quadrivalvis* has priority. It is possible that a genetical explanation of the variability in number and size of these periostial teeth might be found in a chromosomal deletion or in a preponderance of a suppressor gene. Fortunately this species is fairly abundant at times in the Mediterranean, and also in Valencia Harbour, Ireland, at either of which places genetical experiments might be tried in order to confirm the view that only one species is represented. *S. quadrivalvis* would then be established as one species of siphonophore whose characters were not so clear cut as most others.

Lensia Totton, 1941

Since writing on the species of *Lensia* in 1941, I have repeatedly found specimens of them all, including Leloup's interesting little *L. meteori*, which I had not at that time seen. My grouping into species appears to be sound in the light of twelve years' further work, and only three further new species have appeared. Nineteen of the twenty-one known species are found in the Indian Ocean, two having been previously recorded there. I have figured fourteen of these before (1932, 1941). Bigelow & Sears (1937) figured *L. conoidea*, *L. fowleri* and *L. multicristata*; and Leloup (1934*a*) figured *L. meteori*. My present identifications are in accordance with these figures and related descriptions.

Lensia hotspur Totton, 1941.

The syntypes from 'Discovery' Station 100 exhibited a very small hydroecial cavity which included the base of the somatocyst. In the Red Sea specimens the base of the somatocyst generally projects down slightly below the baso-lateral margins (Text-fig. 54 C–E). At 'Manihine' Aqaba Station 13 (135–0 m.) four well preserved anterior nectophores, between 4·0 and 4·5 mm. in length, were taken. Two of them are of this same type, and two of the type in which the base of the somatocyst does not extend below the baso-lateral margin. From 'Manihine' Red Sea Station 8 came 19 anterior nectophores containing both types and intermediates in which the base of the somatocyst is on a level with the baso-ventral margin. Associated with anterior nectophores from the Gulf of Aqaba were posterior nectophores and eudoxids, which unfortunately cannot be described and figured at the present time, except to say that the mouth-plate of the posterior nectophore has a rounded notch in its distal edge, and that the upper end of the left ventral ridge is not square but angular. Specimens of this species though abundant are nearly always in a poor condition. But systematists in future would do well to watch for variation in this respect, and to make certain that we are not dealing with more than one species. It is certainly clear now that the 'Carnegie' specimen drawn by me (1941, fig. 13) belongs to a different species, which has since been taken abundantly by H.M.S. 'Challenger' in the E. Tropical Pacific in October 1950. The new species I have named in honour of the ship. *L. hotspur* occurs side by side in the Red Sea with *L. subtiloides*, but can at once be distinguished by the fact that there is practically no stalk to its relatively shorter somatocyst.

Lensia challengeri sp.n.

Thirty anterior nectophores of what appears to be a distinct new species of *Lensia* were taken by Surgeon Lt. D. O. Haines, R.N. in H.M.S. 'Challenger' (Cdr. G. S. Ritchie, D.S.C., R.N.) off the coast of Southern California on 21 October 1950 at Station 104, 23° 51′ N, 112° 59′ W. The species occurred also at Stations 103, 105, 106, 107, 108, 109 and 114, the first being in 21° 41′ N., 111° 43′ W., and the last in 31° 12′ N., 117° 31′ W. At all these stations the specimens were in a layer of presumed plankton located by echo-sounding. Temperatures in the layer varied from 57° to 61° F., and the depths from 37 to 220 m. At night the presumed plankton layer was observed to remain at about 37–55 m. as seen on the echo-sounding recorder and by day the layer was occasionally seen on the trace at about 274 m. A number of bathythermograph temperature/depth records taken at the time all show a similar pattern—80–67° F. at the surface, a degree or so less at 27·5 m., 56·5–62° (once 72°) at 56 m. and 49·5–56° at 131 m.

Captures of *Lensia challengeri* sp.n., by H.M.S. 'Challenger' in the E/S layer of plankton off S. California in October 1951 are given in the following table. It shows the descent before sunrise.

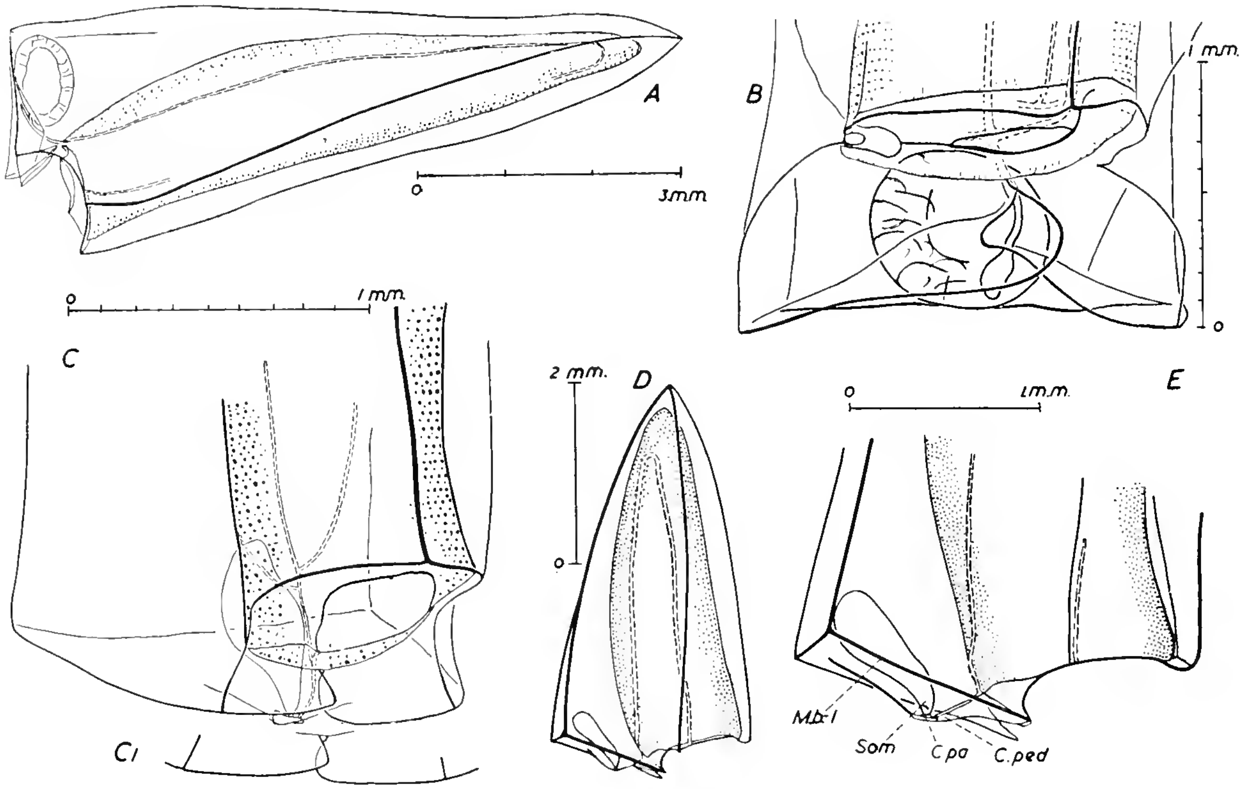
Sunset	Station	Depth of layer (m.)	T° F.	
			Surface	E/S Layer
+12 min.	114	73	67	53
+16	105	64–91	75·5	55·5
+22	108	91	69·5	52
+25	103	73	80	57·5
+30	109	101	69·5	52
+36	106	37–64	76	61·5
−30	107*	91*	70	57·5
Sunrise	104	220	78·5	—

* The haul at this depth was probably made a few metres above the E/S layer.

Commander Ritchie (1952) stated that migrations appear to depend on light, and not on various depth/temperature changes, though Moore (1943) makes the generalization that among Siphonophores there is a tendency in the Florida Current for a change in day level in relation to temperature, the animals there moving upward when cold water comes closer to the surface. Herdman (1953) too shows that there appears to be a certain measure of agreement between the depths at which temperature-discontinuities occur and those of the various echoes recorded. But he adds that it is a matter of conjecture whether this connexion depends entirely on the purely physical boundaries, or on possible concentrations of falling detritus or animal life checked in its fall by a sudden change in density. According to Cdr. Ritchie the rate of change of depth for descent averaged about 4·26 m. per minute, the movement being very regular over five days. The ascent in the evening was more ragged, small groups sometimes appearing to come up ahead of others, and speeds of ascent varied from 2·74 to 0·91 m. per minute. Open plankton nets were lowered into the mid-level of the E/S layer at night. No fish were caught, and the fine 'texture' of the echo-sounding record obtained led Cdr. Ritchie to believe that the echoes came from a vast layer of plankton rather than from fish feeding upon that plankton.

Lensia challengeri bears some resemblances to both *L. fowleri* Bigelow and *L. hardy* Totton. From *L. fowleri* it can be distinguished by a projection, shaped like the peak of a cap, that is found on the baso-dorsal margin of the anterior nectophore, which has the appearance in lateral view of a dorsal tooth (Text-fig. 54A). The hydroecium is less deep than that in both *L. fowleri* and *L. hardy*. The somatocyst, which alters shape, presumably in accordance with the amount of fat in store, may be spheroidal or egg-shaped, often much flattened, but its base remains close to the basal facet of the nectophore, and it usually reaches to the ventral facet. The canal leading immediately to the somatocyst is well on the baso-dorsal side. In dorsal view it will be noticed that the mouth-plate on the left (morphologically the right-hand one) is much broader than the other (Text-fig. 54B). Both halves of the mouth-plate are much less deep than in *L. hardy* and *L. fowleri*. It may be found advisable later on to include the three species *fowleri*, *hardy* and *challengeri* in a separate genus. The eudoxids of all are known but have not all been described and figured.

The holotype specimen (Text-fig. 54A, B) bears the B.M. (Nat. Hist.) Register number: 1953.8.11.1.



Text-fig. 54. *Lensia challengeri*, sp.n., anterior nectophore from 'Challenger' St. 104, Oct. 1950; A, lateral view, ×12; B, dorsal view of mouth-plate, ×35. *Lensia hotspur*, anterior nectophore, Gulf of Aqaba, Manihine St. 1; C, antero-lateral view of base, ×40; C^1, dorsal view of mouth-plate; D, lateral view, ×12; E, lateral view of base, ×25.

Lensia cossack Totton, 1941.

This species was reported by Browne from Chago, Mauritius, Farquhar and Amirante under the name of *Diphyes subtiloides*. I have re-examined eight of the eleven anterior and the two posterior nectophores which are now in the British Museum Collection.

Lensia subtiloides (Lens & van Riemsdijk), 1908.

The record by Browne from Chagos, Mauritius, Farquhar and Amirante is not for this species but for *Lensia cossack*. I have re-examined the specimens in the British Museum Collection.

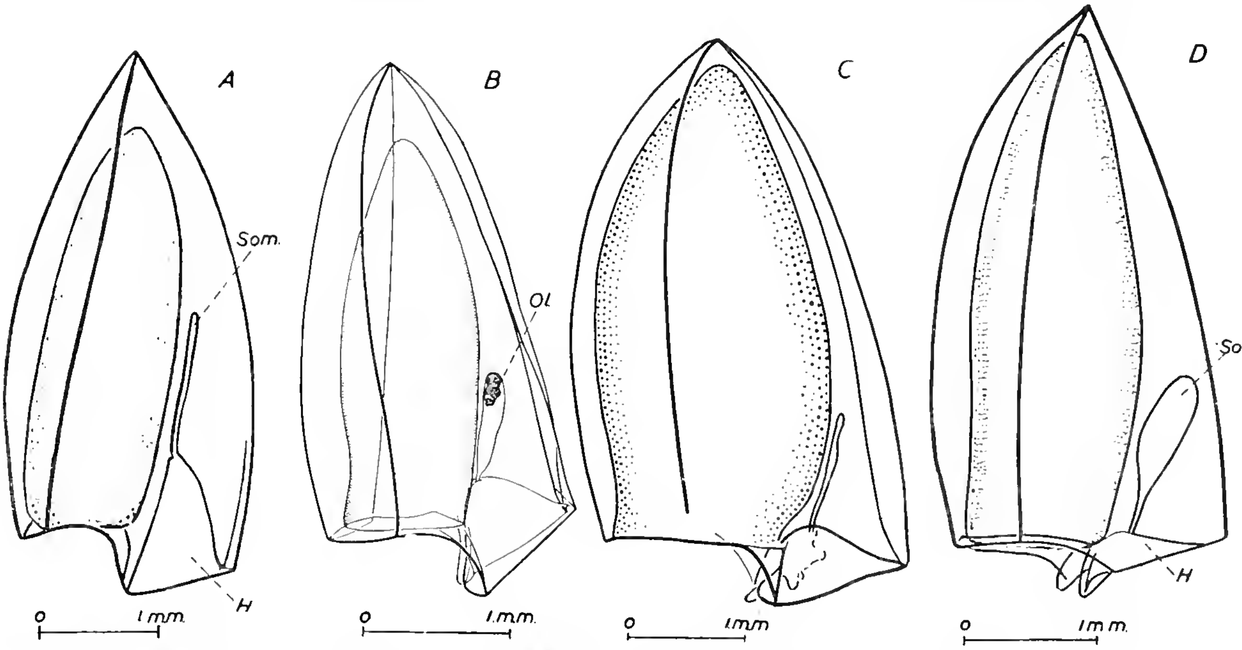
L. subtiloides and one of its associates, *Diphyes chamissonis* are not widely spread over the oceans. They were the only two really abundant Siphonophores that the Great Barrier Reef Expedition of 1928–9 found in the Barrier Reef lagoon, where *Lensia subtiloides* became relatively very rare when the temperature dropped below 24° C. In the Red Sea off Port Sudan, 'Manihine' found them associated in five out of ten hauls (Text-fig. 55 D).

H.M.S. 'Weston' took an abundance of specimens off Kamaran, Red Sea on 9 April 1936 at a surface temperature of 28° C. Once more the species was associated with *Diphyes chamissonis.* This species evidently thrives at a high temperature.

Lensia leloupi[1] sp.n. (Text-fig. 55 C).

Since there is a new species of *Lensia* with which *L. subtiloides* might be confused a description is now given of the anterior nectophore.

The nectophore differs from that of *L. subtiloides* in having a deeper hydroecium or longer mouth-plates. In other respects it is very similar, though larger. After comparison with *Muggiaea delsmani* it might be thought that *Lensia leloupi* was only another species of *Muggiaea* with still shallower hydroecium. But *Lensia subtiloides* and *L. leloupi* agree in (1) showing a notch on the edge of the left mouth-plate ('right' if viewed from the dorsal side, apex uppermost); (2) the origin of the somatocyst from a point on the hydroecial roof to the left of the highest point, and not nearly so close to the nectosac as in *Muggiaea* spp.; (3) the tip of the nectosac being so near to the apex of the nectophore. This third character is found in *M. bargmannae* but not in the other three *Muggiaea* species.



Text-fig. 55. A, *Muggiaea kochii*, off Plymouth; B, *M. delsmani* sp.n., Java Sea; C, *Lensia leloupi* sp.n., 'Discovery' St. 277; D, *Lensia subtiloides*, Great Barrier Reef. A, C × 16; B × 20; D × 18.

The type specimens of this new species *Lensia leloupi* were taken at 'Discovery' Station 277 near Cape Lopez in the Gulf of Guinea, and not far from the mouth of the Ogowe river. No salinities are recorded from this station, but at Station 279, closer still inshore, the salinity was 33·08 ‰ at the surface, a comparatively low salinity for Siphonophores to tolerate.

The figured holotype bears the Brit. Mus. (Nat. Hist.) Register No. 1952. 11. 19. 1.

Lensia multicristata (Moser), 1925.

This species was recorded by Browne from Chagos and Amirante under the name *Diphyes bigelowi.*

New Indian Ocean records: specimens of *Lensia multicristata* have been identified from the following 'Discovery II' Stations in the Indian Ocean: 847 (270–196 m.); 1743 (2100–1150 m.); 1566 (1350–

---

[1] Named for Dr E. Leloup.

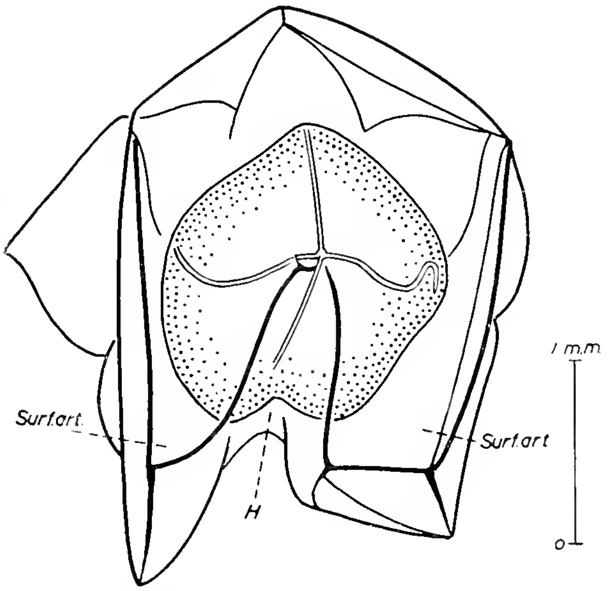
0 m.); 1568 (1400–0 m.); 1571 (500–0, 1400–1000 m.); 1581 (500–250, 1750–600 m.); 1585 (500–0, 1400–700 m.); 1586 (250–100, 550–0, 1650–950 m.); 1587 (450–0 m.); 1588 (500–200 m.); 1589 (600–0 m.).

The other new 'Discovery' records for the species are: Stations 87 (1000–0 m.); 89 (1000–0 m.); 100B (900–1000 m.); 100C (260–310, 2500–2000 m.); 102 (250–0 m.); 282 (300–0 m.); 297 (200–300–0 m.); 'Discovery II' 670 (470–0 m.); 671 (2000–0 m.); 673 (1500–1000, 750–500 m.); 675 (500–250 m.); 677 (1500–1000, 470–0 m.); 679 (750–500 m.); 681 (500–250, 250–0 m.); 682 (375–0 m.); 684 (750–500 m.); 690 (1500–0, 500–250, 460–0 m.); 693 (750–500, 500–250, 250–0 m.); 695 (370–0 m.); 696 (750–500, 500–250 m.); 697 (460–0, 450–0 m.); 698 (470–0 m.); 699 (500–250, 370–0, 250–0 m.); 702 (236–0 m.); 703 (358–0 m.); 845 (242–180 m.); 847 (270–196 m.); 848 (270–196 m.); 899 (350–0 m.); 965 (310–106 m.); 968 (250–106 m.); 969 (250–100 m.); 1178 (310–0 m.); 2068 (700–0 m.); 2635 (280–0 m.); 2636 (950–550 m.); 2639 (1200–600 m.); 2646 (1500–800 m.); 2647 (310–0 m.); 2648 (1450–950 m.); 716 (212–0 m.); 2084 (1500–800 m.); 943 (128–0, 250–100, 356–130, 500–0 m.); 944 (500–750 m.); 967 (306–145 m.).

The unfortunate nomen nudum *L. profunda* of Totton (1936, p. 235) refers to specimens of *L. multicristata* Moser from Bermuda (Beebe Collection).

Lensia conoidea Keferstein & Ehlers, 1861.

Bigelow & Sears (1937) published some fine figures of this species and valuable further notes. Their figure (fig. 35) shows the apical view of the posterior nectophore, but I find that in specimens from off the Irish Coast, from 'Discovery' Station 100C, and from 'Manihine' South-west Ireland Station 4, the apico-ventral corner of the right hydroecial wing is not like the left one, which is figured correctly. The right one is of a square section as shown here in Text-fig. 56.



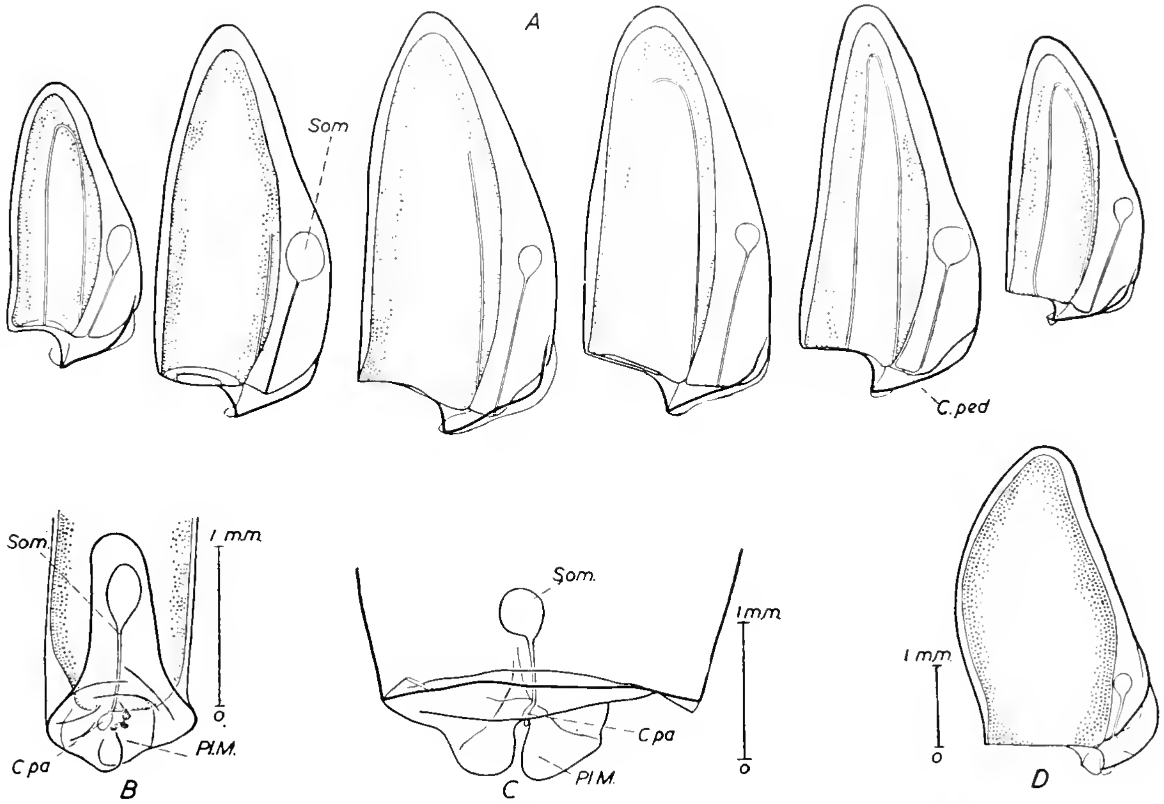
Text-fig. 56. *Lensia conoidea*. Apical view of posterior nectophore, × 34, to show the correct shape of the articulating surfaces. 'Manihine', South-west Ireland, St. 4.

Lensia subtilis *var.* (Chun), 1886.

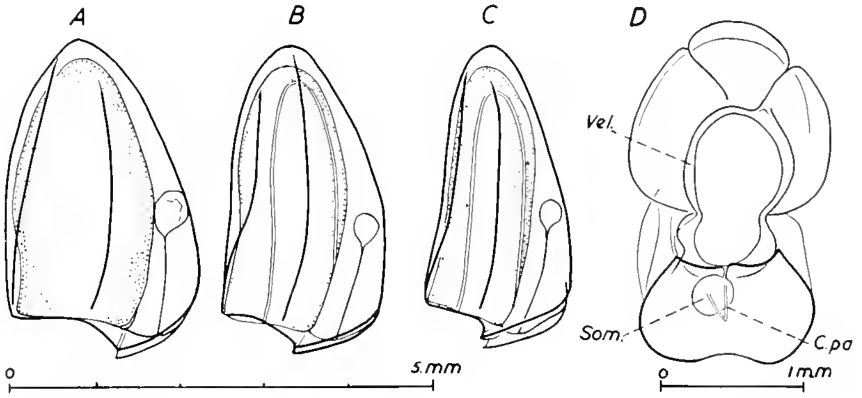
Quite arbitrarily I am referring to fourteen specimens (Text-fig. 57B, C, D) as a variety of this common species. They come from 'Discovery II' Stations 1585–7. The stalks of their somatocysts are relatively longer than in *L. meteori* (Text-fig. 60), and the wall of the hydroecium instead of being nearly vertical for most of its extent as in *L. meteori*, lies at 45° and more nearly approaches the condition found in *L. subtilis*. I report these specimens under the name *subtilis* var., pending the discovery of more specimens and hesitate to set up a new species. It may be significant that from 'Discovery II' Stations 1585 and 1586 at which eight of these intermediate type specimens were taken no other specimens of *L. subtilis* were found. Also at 'Discovery II' Station 1587, where two specimens of *L. meteori* were found as well as several of this intermediate type, again no other specimens of *L. subtilis* were found, although *L. subtilis* was common at most stations off the East African coast. The fourteen specimens were found at a rather greater depth than those of *L. meteori*, but there may be no significance in this.

I give sketches of six anterior nectophores of *L. subtilis* from Aqaba for comparison (Text-fig. 57A).

The stalk of the somatocyst of a Mediterranean specimen measured 0·025 mm. in diameter. The passage of an oil droplet up this canal may distend it. The expanded gastrozooids of the same specimen measured 0·6–0·8 mm. in length and 0·15 mm. in diameter. The diameter of the distal half, the proboscis, was only 0·08 mm. In one complete specimen there was a bud of a third nectophore.

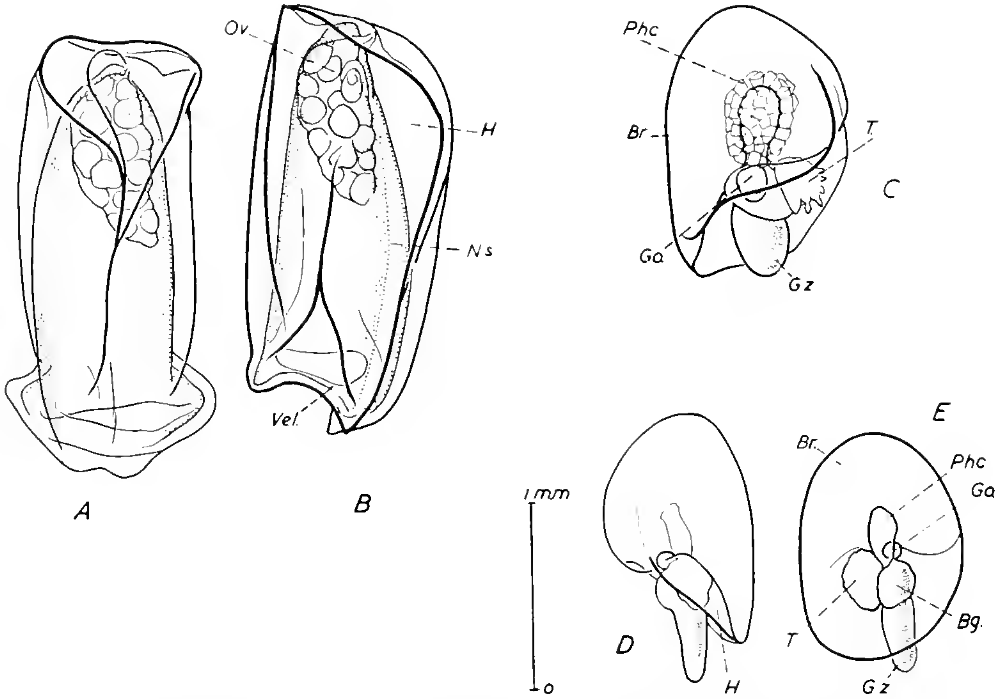


Text-fig. 57. *Lensia subtilis*, anterior nectophores. A, a series of six specimens from the Gulf of Aqaba, Red Sea, 'Manihine' St. 17, ×21; B–D, specimens from 'Discovery II' St. 1587. Magnification: B ×21; C ×18; D ×11.

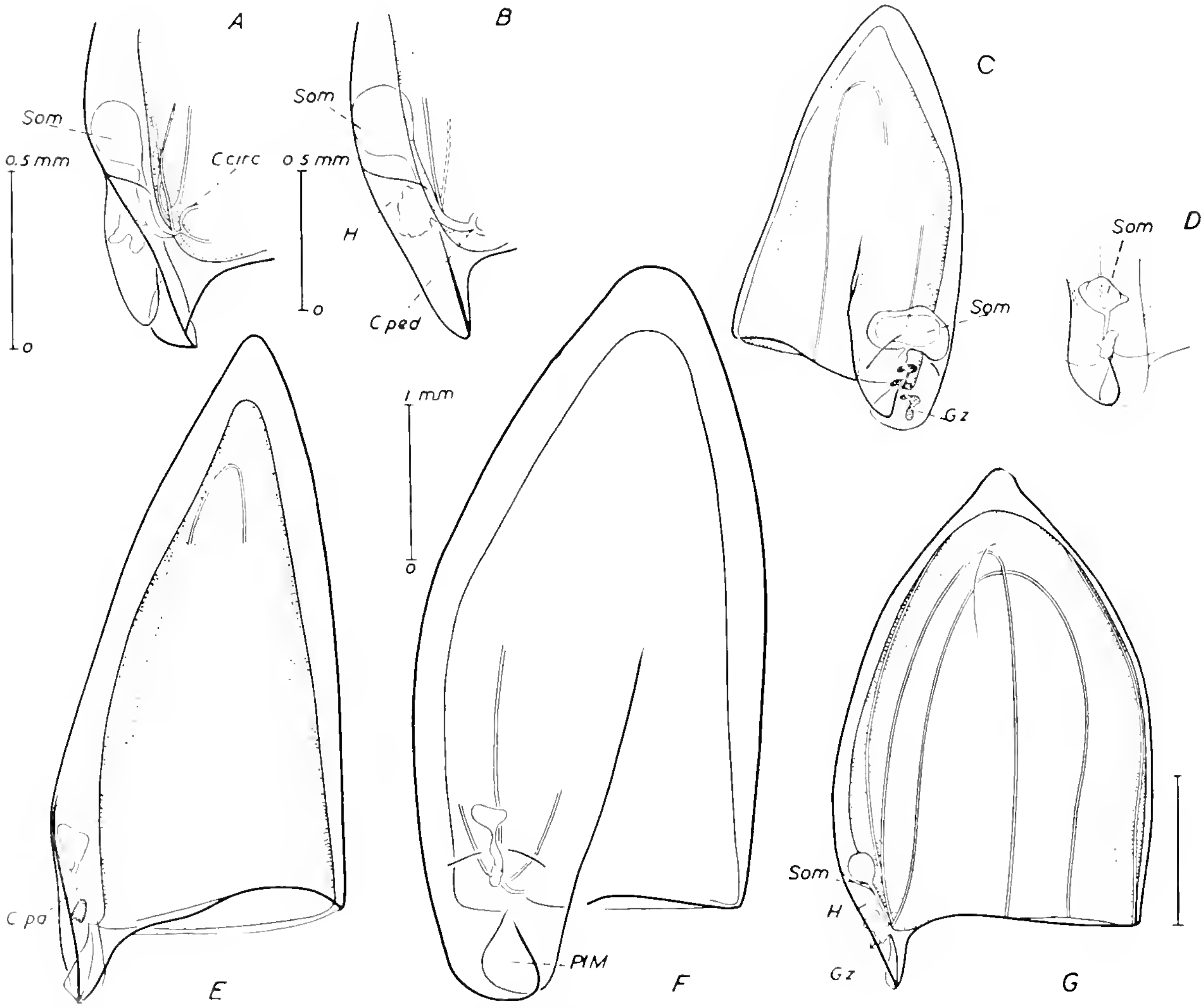


Text-fig. 58. *Lensia subtilis*, anterior nectophores from Villefranche. A, B, C, three stages in contraction of the nectosac, ×12; D, basal view of a nectophore, ×19.

In 1932 I reported that there was some doubt about the appearance of the eudoxids of this species. It is very abundant at Villefranche and I give a figure now (Text-fig. 59). A useful field mark at Villefranche for recognition of gonophores of this species is the yellow colour of the tip of the manubrium.



Text-fig. 59. *Lensia subtilis*, eudoxids from Villefranche. A, B, two views of a female gonophore, ×24; C, latero-ventral view of a young eudoxid, ×24; D, E, two views of a bract, ×25.



Text-fig. 60. *Lensia meteori*. A, B, D, somatocysts of Adriatic specimens (Dr Gamulin); C, ventral view of somatocyst of a twisted specimen from Port Sudan, 'Manihine'; E, F, specimens from South-west Ireland, 'Manihine' St. 4; G, specimen from 'Discovery II' St. 1587. Magnification: A ×47; B ×38; C–D ×20; E–G ×20.

Lensia meteori (Leloup), 1934*a*.

This charming but rather rare little species occurred at half of 'Discovery's' East African Stations, and was represented by a single specimen only at four 'Manihine' Stations off Port Sudan. I have found it once or twice in hauls from 100 m. or more at Villefranche, where Leloup also recorded it; and it occurs also off Split in the Adriatic, from which area Dr T. Gamulin has sent me specimens. It is a species that can easily be overlooked.

As mentioned earlier in these notes, I believe that Leloup's *meteori* is closely related to *L. subtilis*, and not to species of '*Galetta*', with which Bigelow & Sears (1937) linked it. *Lensia subtilis* has unlooped lateral canals in its posterior nectophores, as in all known species of *Lensia*, whereas in '*Galetta*' spp. the lateral canals are looped, or bend back on themselves.

It seemed at one time that *Lensia meteori* was a very distinct species, but at 'Discovery II' Stations 1585–7 fourteen specimens were found (Text-fig. 57B, C, D) which are intermediate between *L. meteori* and *L. subtilis*. They are dealt with as a variety of *L. subtilis* in my notes on that species.

Three anterior nectophores were taken by 'Manihine' in July 1950 off south-west Ireland.

A single anterior nectophore found by 'Manihine' off Port Sudan has a somatocyst which is produced laterally as shown in Text-fig. 60C.

Lensia meteori (Leloup)

New Records

	Station	Depth (m.)	Specimens
'Discovery II'	1567	1350–0	1
	1568	1400–0	1
	1581	100–50	1
		250–100	1
	1584	250–100	1
	1586	250–100	1
		500–250	1
	1587	450–0	2
	1588	250–100	1
		500–200	1
'Manihine', Gulf of Aqaba	5	183–0	1
	6	—	1
	10	183–0	1
	13	135–0	1
Port Sudan	11	366–0	1
S.W. Ireland, 50° 48′ N., 11° 4′ W.	4	183–0	3
'Michael Sars' 48° 1′ N., 39° 46′ W.	81A	(? 1000)	1

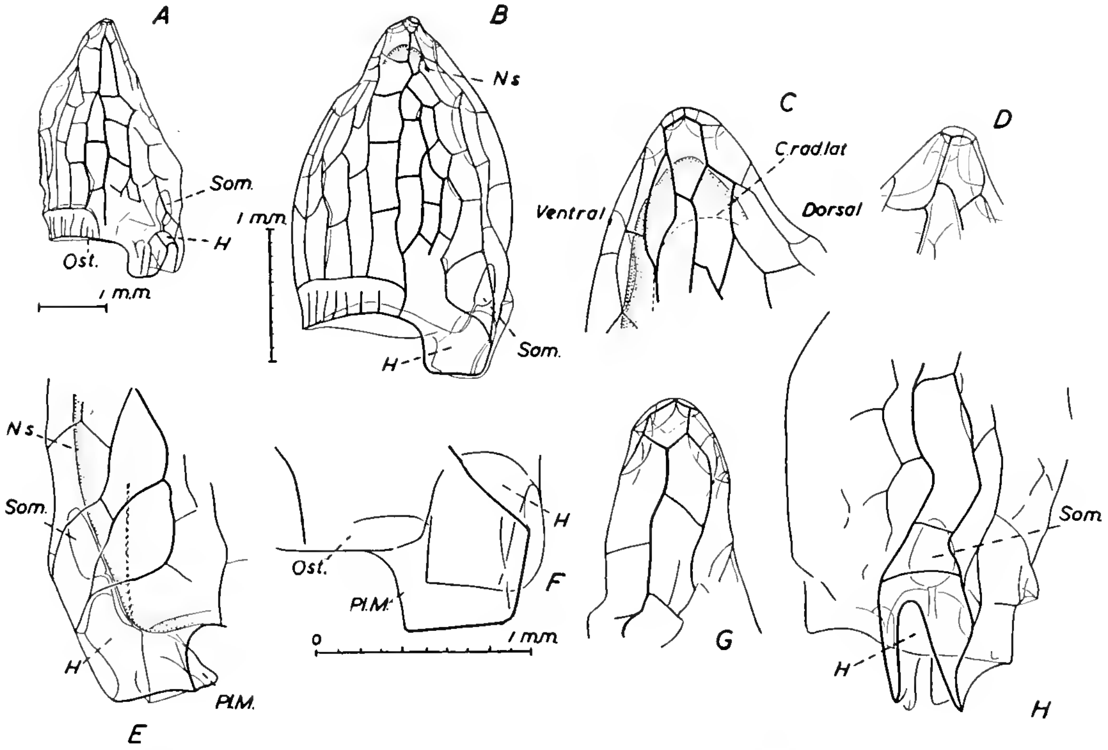
Lensia subtilis var. (→ *L. meteori*)

	Station	Depth (m.)	Specimens
'Discovery II'	1585	500–0	1
		1400–700	1
	1586	550–0	5
		1650–950	1
	1587	450–0	6

Lensia reticulata sp.n.

This is a small multistriate species with cross-connecting ridges, the whole pattern of ridges being somewhat irregular. The hydroecium is well formed and has a ventral slit; the somatocyst is short and ovate in outline, seen from the ventral side, but measures less across the dorso-ventral than across the latero-ventral axis. An aboral, dorso-lateral, horizontal ridge connects up the basal ends of half a dozen longitudinal ridges on either side of the nectophore as in *Lensia exeter*.

Material. Three anterior nectophores, two from 'Discovery II' Station 1585, 1400–700 m. (Text-fig. 61), the smaller of which is chosen as the holotype of the species, and one from 'Discovery II' Station 1586, 1400–0 m.



Text-fig. 61. *Lensia reticulata* sp.n. from 'Discovery II' St. 1585, 1400–700 m. A, D, F, the whole, the apex and the base of a larger specimen; B, E, H, C, G, the whole, two views of the base and two of the apex of a smaller specimen. Magnification: A ×9; B ×18; C–H ×29.

At first sight it might be supposed that the reticulation was due to shrinkage. I am quite satisfied that it is a specific character. Most of the facets are deeply concave, as can be seen from the sketches of the apical parts of two specimens (Text-figs. 61 C, D). The material, as is usually the case with small delicate specimens from the depths, is only moderately well preserved, and the reticulated ridges could only be examined after staining.

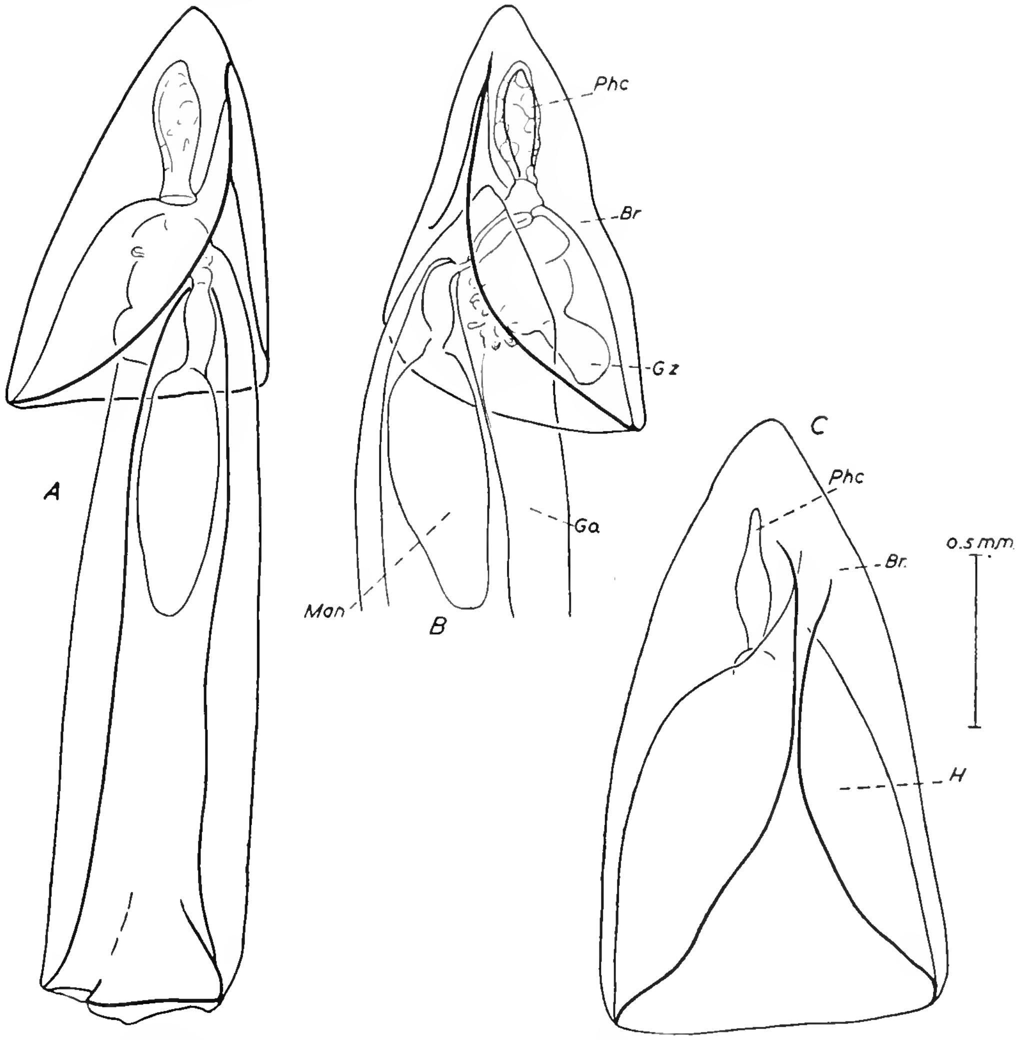
This is one of the three new species of *Lensia* to come to light since I reviewed the species in 1941. The figured holotype bears the Brit. Mus. (Nat. Hist.) Register No. 1952. 11. 19. 2.

Eudoxia macra sp.n.

This new eudoxid of unknown parentage is easily recognized by its peculiar bract and long gonophore which has no prominent teeth but a deeply pigmented tip to its manubrium.

Measurements of holotype. Length overall 3·2 mm.; length of bract 1·25 mm.; length of gonophore 2·5 mm.

Using again the terminology that I employed in 1932 (p. 318) the headpiece of the bract would be described as small, the phyllocyst comparatively small and near the apex. In optical section the head and neck shield resemble those of *Diphyes bojani*. The sutural surface is in a groove. In fact the whole bract has not evolved far beyond the developmental stage through which Diphyid eudoxid bracts pass. The edges of the sutural surface tend to lap over one another as if lapping round the stem. These ventral edges are cut away like the sides of a man's tail-coat till they meet the dorsal edge of the bract. The tip of the bract is rounded and conical, and the sutural surface does not reach the apex. The eudoxid, then, may be regarded as more primitive than that of a species such as *D. dispar*.



Text-fig. 62. *Eudoxia macra* sp.n., a new eudoxid from 'Discovery II' St. 1588, 250–100 m., whose complete polygastric stage is either unknown or has not been identified. C × 46.

The eudoxid has one characteristic, namely the rounded, conical tip of the bract, that recalls the apex of the anterior nectophore in *Clausophyes ovata*, and of the eudoxid figured (1861) by Keferstein & Ehlers. But *Clausophyes* is taken in much deeper water than this *Eudoxia macra*, and the eudoxid of *Clausophyes* appears to have longitudinal bracteal canals.

Gonophore. There are two dorso-lateral and two ventro-lateral radial canals, and two slight rounded ridges overlie the dorso-lateral pair. There are two closely opposed hydroecial folds, one deeper than the other. Distally these folds become less and less deep till they disappear as slight ridges before reaching the level of the velum. Neither mouth-plate nor teeth are present. The proximal end of the gonophore does not appear to articulate with the bract itself. It is sometimes rounded and shaped like the apex of the bract, and sometimes flattened on its ventral side. The female gonophore bears from fourteen to sixteen eggs.

There is not enough material for a study of the details of the tentilla.

Material. Two eudoxids, six bracts, fifty-four gonophores.

'Discovery' Station	Net	Depth (m.)	Material
100c	TYF	260–310	2 gonophores
702	TYF B	236–0	1 gonophore
1567	N 70 B	1350–0	1 eudoxid, 6 gonophores
1568	N 70 B	600–0	4 gonophores
1581	N 70 V	50–0	1 gonophore
		100–50	1 gonophore
1583	N 50 V	100–0	1 gonophore
1584	N 70 V	50–0	1 gonophore
		100–50	2 gonophores
1586	N 70 V	100–50	2 bracts, 3 gonophores
		250–100	1 bract, 3 gonophores
		500–250	1 gonophore
1587	N 70 V	450–0	8 gonophores
1588	N 70 V	100–50	1 bract, 2 gonophores
		250–100	1 eudoxid, 1 bract, 3 gonophores
		500–200	1 bract
1589	N 70 B	600–0	4 gonophores
2647	TYF B	310–0	9 gonophores
2929	N 70 V	750–500	2 gonophores

The complete eudoxid from 'Discovery II' Station 1588 is chosen as holotype. It bears the Brit. Mus. (Nat. Hist.) Register No. 1952. 11. 19. 3.

Muggiaea atlantica Cunningham, 1892.

Russell (1934) published interesting information on the occurrence of the two hitherto known species of *Muggiaea*. He thought that both are essentially inhabitants of less contaminated coastal waters, a fact which he suggested would account for their absence from the collections of Oceanographical Expeditions.

This species occurred abundantly near the surface off South Africa at 'William Scoresby' Stations 444–460.

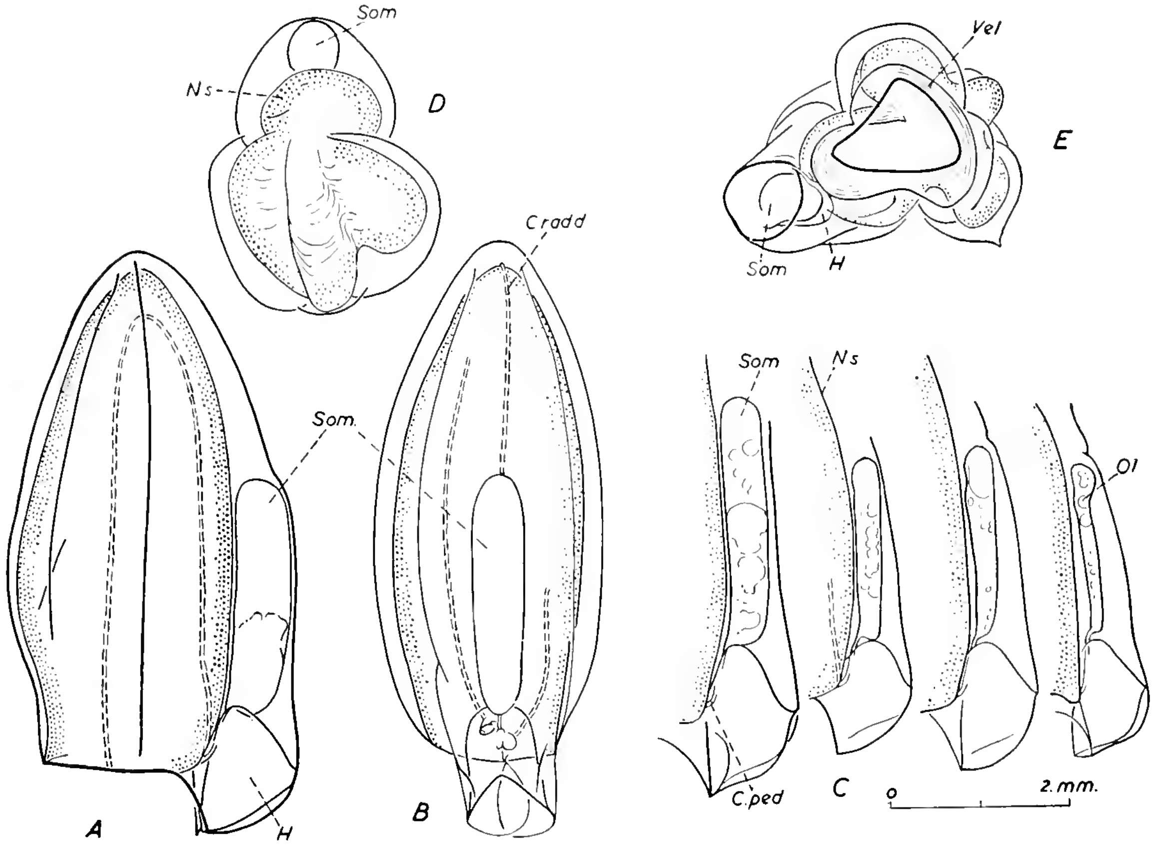
Bigelow & Sears (1937) most recently summarized our knowledge of the distribution of *M. atlantica*. The 'Thor' records made these authors think that it is definitely a neritic species, as are probably also *M. kochii*, *Diphyes chamissonis*, *Lensia subtilis* and *L. subtiloides*.

Fraser-Brunner took *Muggiaea atlantica* in the Gulf of Aden (Chart, p. 10) off Aden and Alayu, localities which bear out the idea that it is definitely a neritic species.

'Manihine' took a single nectophore at each of three stations, 10 miles, 35 miles and 40 miles east of Sanganab Lighthouse, off Port Sudan. All the hauls were made from depths of 365 m. to the surface in January 1951.

Muggiaea bargmannae[1] sp.n.

Many years ago I recorded in my manuscript notes on the distribution of Siphonophores along 'Discovery II's' 30° meridian line of stations the occurrence of a new species of *Muggiaea* at Station 663, in a haul from 500 to 250 m. Recently, whilst identifying Siphonophores from part of 'Discovery II's' 0° line of stations, I found this species again. I therefore re-examined much of the 'Discovery' material of *Dimophyes arctica*, which the new *Muggiaea* superficially resembles, and found in hauls from the Antarctic more specimens which had been confused with those of *Dimophyes arctica*. Unless material is well preserved or stained, confusion of this sort is quite easy, since the new species lacks the ridges found in *Muggiaea atlantica* and *M. kochii* (the apex of the nectosac is closer to the apical end of the nectophore than in those species). But the mouth-plate is divided, unlike its counterpart in *Dimophyes*, and the ventral slit in the hydroecial wall is in the mid-ventral line and is shorter than in *Dimophyes*, so that in lateral view the ventral wall of the hydroecium extends further towards the base, as in the other two species of *Muggiaea*. This point will be readily appreciated if comparison be made between the ventral view of *M. bargmannae* given in my Text-fig. 63 B and that of *Dimophyes arctica* given by Chun (1897*b*) in his fig. 4 of Taf. 1.



Text-fig. 63. *Muggiaea bargmannae* sp.n. A, B, holotype specimen, 'Discovery II' St. 2012, 100–50 m.; C, baso-ventral parts of four paratype specimens from same station; D, E, apical and basal views of holotype. All figures × 12.

With the knowledge of this new species I am inclined to think that *Dimophyes* whose affinities have always been obscure, is most closely related to *Muggiaea*, especially since its posterior nectophore is obsolescent. In *M. atlantica* and *M. kochii* the posterior nectophore has ceased to develop; and no posterior nectophore has so far been found associated with the new species, whose eudoxid has not yet been certainly identified.

---

[1] This species is named after Dr Helene Bargmann.

M. bargmannae differs from both *M. atlantica* and *M. kochii* and the other new species *M. delsmani* described below in that the tip of the nectosac approaches much nearer to the apex of the whole nectophore and also in that the convex longitudinal folds into which the nectophore is thrown on contraction of the nectosac are not surmounted by crest-like ridges. Another point to note is that towards the ostium of the nectophore the two lateral folds almost meet, so that the dorsal fold is most apparent in the apical two-thirds of its course. The length of the somatocyst is about half the distance between the tip of the nectosac and the tip of the hydroecium. In well-fed specimens such as that illustrated in Text-fig. 63A the somatocyst is sausage-shaped and its base projects ventrally over the top of the hydroecium. In this state it contains much oil. When not distended with oil, its diameter may measure only one-third or less, as shown in Text-fig. 63C. The hydroecium is shallower than that of *M. kochii*, but not as shallow as that of *M. delsmani*.

Records of capture of Muggiaea bargmannae *sp.n.*

	Stations	Depth (m.)	Nectophores
'Discovery'	117	250–100	1
	208	800–0	5
'Discovery II'	519	390–137	1
	663	500–250	3
		1000–750	2
	671	1000–0	1
	1048	340–140	15
	1772	520–250	1
	2010	100–50	5
		250–100	5
	2012	100–50	6 (including the figured holotype)
		250–100	1
		500–250	3
	2014	100–0	3
		100–50	1
		250–100	9
	2015	100–50	1
		250–100	14
		500–250	1
	2017	100–50	1
		250–100	1
		500–250	1
		750–500	1
	2024	250–100	1
		650–400	2
		750–500	1
'William Scoresby'	WS 550	121–0	7
	WS 551	121–0	70

Examination of 'Discovery II' hauls on both the 0° and 30° lines of stations showed that *M. bargmannae* occurred only to the southward of the Antarctic convergence. Of the other six records five are from the Antarctic, but Station 1772 was made in lat. 36° S., and the haul that contained one young specimen was made from 520 to 250 m. This record should be treated with reserve. The most southerly record I have at present is at 'William Scoresby' St. WS 551, in 68° 17½′ S., where it was taken in a haul from 121 m. to the surface in temperatures of from 0·84° to 0·30° C. and salinities of from 33·99‰ to 33·17‰.

The recognition of this new species of *Muggiaea* brings up the total of Siphonophores found in the Antarctic to fifteen. They are: *Pyrostephos vanhoeffeni*, *Marrus antarcticus* gen. et sp.n., *Stephanomia convoluta*, *Diphyes antarctica*, *Muggiaea bargmannae* sp.n., *Dimophyes arctica*, *Lensia havock*, *L. achilles*, *Rosacea plicata*, *Vogtia serrata*, *Thalassophyes crystallina*, *Crystallophyes amygdalina*, *Heteropyramis maculata*, *Chuniphyes multidentata*, and *Ch. moseri* sp.n. The first five and *Vogtia serrata* are confined to the Antarctic.

The figured holotype from 'Discovery II' Station 2012 bears the Brit. Mus. (Nat. Hist.) Register No. 1952. 3. 18. 1.

Muggiaea delsmani sp.n. (Text-fig. 55B.)

In December 1937 I received for identification from Dr H. C. Delsman of Hilversum a small collection of Siphonophores from the Java Sea. From a station at 5° 57′ S., 108° 23′ E. came specimens of *Diphyes chamissonis*, *Lensia subtiloides* and a new species of *Muggiaea* which I have named after Dr Delsman and describe below. An interesting point about the record is that the salinity was low for Siphonophores. Dr Delsman's note read 'salinity surface 32·7‰, bottom (45 m.) 31·6‰ . . . a few other stations where the salinity was slightly higher viz. about 33·3‰. All these salinities, however, have been determined with an areometer which possibly gave slightly too low values. At any rate the salinity in the Java Sea hardly ever surpasses the 34‰ and at an average is not higher than 33‰'.

M. delsmani can be distinguished at once from *M. kochii*, which also has a short somatocyst, by its shallower hydroecium, whose upper wall is more nearly horizontal than in *M. kochii*. As in other species of *Muggiaea* the base of the somatocyst lies close to the ventral wall of the nectosac. The usual five ridges are present, and the tip of the nectosac, as in *M. atlantica* and *M. kochii* does not come as close to the apex of the nectophore as it does in the new species *M. bargmannae*. The distal edges of the two mouth-plates are rounded, and there is no sign of a notch in one of them as there is in *Lensia subtiloides*.

Reference to Text-fig. 55B makes further description of the nectophore unnecessary. The eudoxid has not been recognized as yet.

The figured holotype bears the Brit. Mus. (Nat. Hist.) Register No. 1937. 12. 9. 1.

Dimophyes arctica (Chun), 1897.

The only previous records from the Indian Ocean are: (1) One complete polygastric specimen (not one eudoxid as stated by Browne, 1926) recorded by Moser (1925, p. 390). (2) One anterior nectophore from a locality 8° 16′ S., 51° 26′ E., between Providence and Alphonse; open net, 900–0 fm., recorded by Browne (1926).

The species was taken in seventeen of the forty-eight 'Discovery II' hauls that I have examined from the west Indian Ocean; it was probably breeding at eleven of them. Because of the possible value of this species as an 'indicator' of water masses the details of the catches are given on p. 124.

The species was not found further north than 06° 05′ N. lat. It was breeding in a depth not greater than 250 m. as far north as 07° 42·1′ S. lat. at a temperature somewhere between 11·7° and 17·21° C.

I have accumulated data on the temperature and salinity tolerances of *D. arctica* from 117 hauls of closing-nets made at sixty 'Discovery' stations (outside the Indian Ocean) as set out on pp. 125 and 126.

Using the higher temperature of the lowest range of any closing haul as the minimum and the lower temperature of the highest range as the maximum, I find that the known range of temperature is from −1·13° to 13·26° C.

Similarly the known range of salinity is from 34·08‰ to 35·33‰.

From data given for 179 'Meteor' hauls where *Dimophyes arctica* was taken I have computed a known range of salinity 34·14–36·57‰, and of temperature 0·14–22·05° C.

The data given on pp. 125–126 are representative, but not good enough perhaps, for drawing very definite conclusions. To do that it would be necessary to examine a much larger number of catches, and especially ones taken at all times of the year, such as those taken at full stations on the meridians of 0° and 20° E.

New records of catches of D. arctica *in the Indian Ocean (i.e. north of subtropical convergence)*

'Discovery II' Station	Net	Depth (m.)	Catch	By interpolation from values given in Station List	
				T. ° C.	S. ‰
1587	TYF B	450–0	1 anterior nectophore	—	—
1586	N 70 V	500–250	8 eudoxids	10·3–13·1	35·13–35·2
1586	N 70 V	250–100	1 eudoxid	13·1–23·60	35·2–35·63
1586	TYF B	1650–950	2 anterior nectophores	3·8–7·25	34·87–34·11
1586	TYF B	550–0	5 anterior nectophores	—	—
1585	TYF B	1400–700	2 eudoxids	—	—
1585	TYF B	500–0	5 anterior nectophores, ? 2 gonophores	—	—
1584	N 70 V	500–250	1 ? posterior nectophore, 1 bract of eudoxid	9·25–11·92	34·98–35·06
1584	N 70 V	250–100	8 anterior nectophores (juv.), 1 eudoxid	11·92–21·42	35·06–35·29
1583	N 70 V	500–250	1 anterior nectophore, 6 eudoxids	8·64–11·64	34·85–35·06
1583	N 70 V	250–100	1 anterior nectophore, 1 eudoxid	11·64–20·67	35·06–35·28
1581	N 70 V	500–250	? 4 gonophores	8·29–11·69	34·83–35·07
1581	N 70 V	250–100	2 anterior nectophores, 1 eudoxid	11·69–17·21	35·07–35·30
1581	TYF B	1750–600	1 anterior nectophore	3·09–7·68	34·76–34·77
1581	TYF B	600–0	4 anterior nectophores	—	—
1568	N 70 B	1450–0	2 eudoxids	—	—
1567	N 70 B	1350–0	5 anterior nectophores	—	—

The data indicate that *D. arctica* has a much greater range of tolerance than *Diphyes antarctica*, or at any rate that the habits of the two are quite different, for it would seem that the differences in their geographical distribution are mainly brought about by their resorting to different depths at various times, or at different stages in their life cycle, for this would bring them into currents which flow in different directions at various depths. But Mackintosh (1934) did not find any marked diurnal variation in the catches of the N 100 B nets, and there is probably little diurnal migration up or down of the polygastric stages upon which Mackintosh worked.

On 17 November 1952, after this report was prepared, I received from Dr Fraser of Aberdeen some siphonophores taken in June of this year, and amongst them an undoubted posterior nectophore of *Dimophyes arctica* taken in a horizontal tow at 20 m. at 'Scotia' Station 1199. The temperature and salinity recorded at that depth were 12·05° C. and 35·39‰.

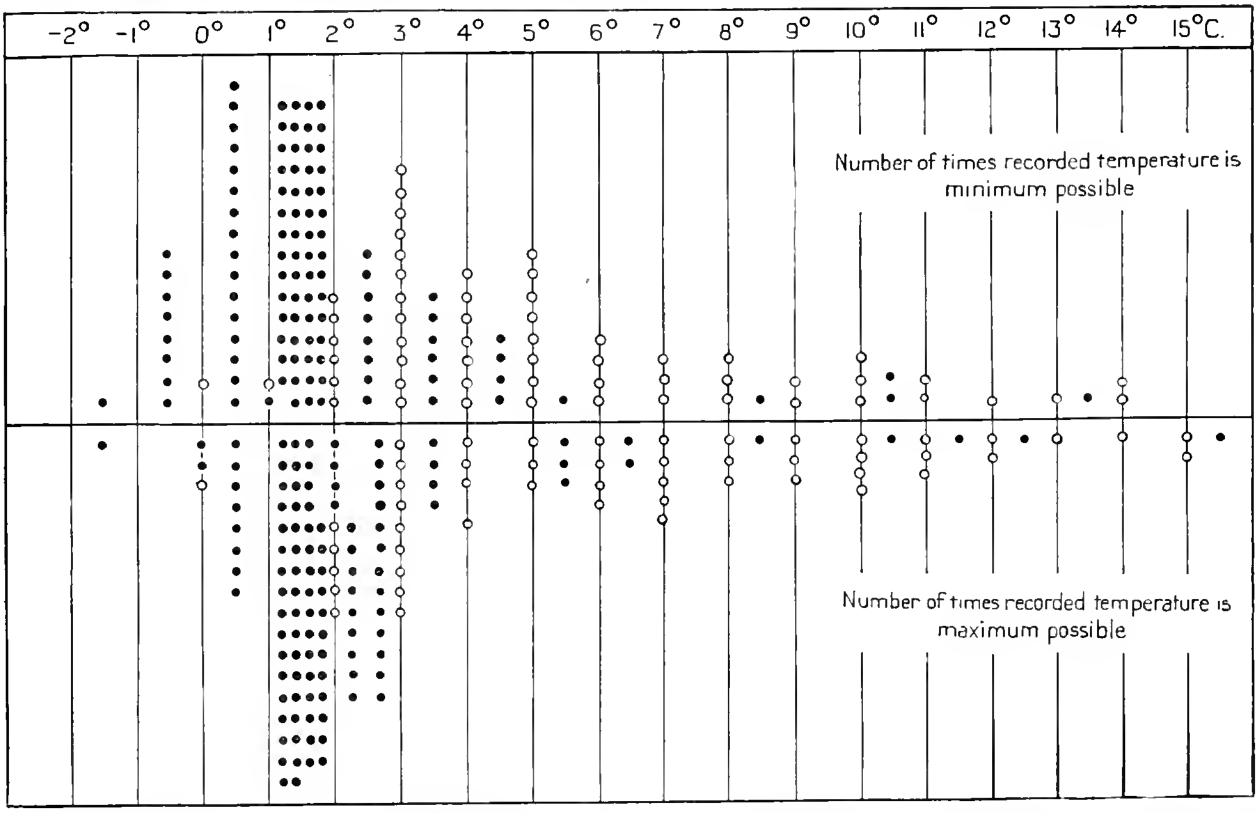
Bigelow & Sears (1937, fig. 81) plotted the frequency of capture of certain siphonophores, including *D. arctica* in 'Meteor' hauls in Atlantic water of known minimum and maximum temperature. The main distribution for *D. arctica* was from 2° to 14° C. with a maximum around 3° C. At the sixty 'Discovery' Stations mentioned on p. 125 the most frequent occurrence was between −1° and 6° C., with a very small marked maximum between 1° and 2° C. (Text-fig. 64).

Station	Net	Depth (m.)	Date	S. ‰	Temp. °C.
WS 22	70 V	1000–750	30. xi. 26	34·70–34·69	1·14/1·82
WS 26	70 V	500–250	18. xii. 26	34·57–34·30	2·48/1·00
WS 26	70 V	750–500	18. xii. 26	34·63–34·57	1·95/2·48
WS 29	70 V	500–250	19. xii. 26	34·56–34·40	2·02/1·33
WS 29	70 V	250–100	19. xii. 26	34·40–33·96	1·33/0·60
WS 30	70 V	250–100	19. xii. 26	34·43–34·95	1·55/−0·70
WS 30	70 V	500–250	19. xii. 26	34·60–34·43	2·04/1·55
WS 36	70 V	750–500	22. xii. 26	34·63–34·54	1·99/2·15
WS 38	70 V	750–500	22. xii. 26	34·69–34·58	1·90/2·00
WS 38	70 V	500–250	22. xii. 26	34·58–34·40	2·00/1·73
WS 44	70 V	500–250	8. i. 27	34·52–34·30	2·04/1·71
WS 61	70 V	250–100	18. i. 27	34·48–34·05	1·70/−0·06
WS 61	70 V	500–250	18. i. 27	34·67–34·48	1·95/1·70
WS 63	70 V	500–250	20. i. 27	34·54–34·33	2·09/1·86
WS 67	70 V	250–100	20. ii. 27	34·17–33·95	1·78/1·16
WS 67	70 V	1000–300	20. ii. 27	34·63–34·23	2·13/2·09
WS 69	70 V	500–250	22. ii. 27	34·18–34·12	2·42/3·11
WS 70	70 V	1000–750	23. ii. 27	34·28–34·20	2·94/3·25
WS 70	70 V	500–250	23. ii. 27	34·19–34·18	3·76/4·16
WS 70	70 V	250–100	23. ii. 27	34·18–34·16	4·16/5·01
WS 110	70 V	500–300	26. v. 27	34·60–34·39	2·07/1·88
WS 388	70 V	400–250	16. ii. 29	34·51–34·47	−1·13/−1·24
11	70 V	500–250	16. ii. 26	34·54–34·22	2·02/1·34
102	70 V	250–100	28. x. 26	34·81–35·03	10·28/12·36
102	70 V	750–500	28. x. 26	34·34–34·42	3·85/5·77
102	70 V	500–250	28. x. 26	34·42–34·81	5·77/10·28
102	70 V	1000–750	28. x. 26	34·46–34·34	3·24/3·85
103	70 V	500–250	30. x. 26	35·33–34·51	13·26/15·97
107	70 V	500–250	4. xi. 26	34·21–34·10	3·60/4·45
107	70 V	750–500	4 xi. 26	34·27–34·21	3·03/3·60
107	70 V	250–80	4. xi. 26	34·10–34·01	4·45/5·87
117	70 V	250–100	17. xi. 26	34·60–34·07	1·28/1·43
129	70 V	780–500	19. xii. 26	34·67–34·59	1·96/2·02
129	70 V	500–250	19. xii. 26	34·59–34·40	2·02/1·46
133	70 V	270–100	20. xii. 26	34·47–33·96	1·83/0·68
137	70 V	700–500	22. xii. 26	34·69–34·60	1·86/1·94
137	70 V	250–100	22. xii. 26	34·40–33·96	1·63/−0·20
138	70 V	500–250	22. xii. 26	34·66–34·47	1·98/1·83
138	70 V	750–500	22. xii. 26	34·71–34·66	1·82/1·98
138	70 V	1000–750	22. xii. 26	34·72–34·71	1·64/1·82
151	100 H	500–625	16. i. 27	34·60–34·64	1·84/1·85
151	70 V	750–500	16. i. 27	34·66–34·60	1·77/1·84
300	70 V	750–500	20. i. 30	34·72–34·65	1·84/1·85
300	70 V	500–250	20. i. 30	34·65–34·44	1·85/1·54
300	70 V	1000–750	20. i. 30	34·69–34·72	1·63/1·84
301	70 V	750–500	20/21. i. 30	34·71–34·63	1·85/1·92
301	70 V	500–250	20/21. i. 30	34·63–34·46	1·92/1·71
302	70 V	500–250	21. i. 30	34·59–34·34	1·90/1·19
302	70 V	250–100	21. i. 30	34·34–34·93	1·19/−0·22
303	70 V	750–500	21. i. 30	34·66–34·56	1·92/1·88
303	70 V	500–250	21. i. 30	34·56–34·41	1·88/1·35
303	70 V	1000–750	21. i. 30	34·72–34·66	1·69/1·92
304	70 V	1000–750	21. i. 30	34·69–34·67	1·75/1·93
304	70 V	500–250	21. i. 30	34·59–34·35	1·89/1·38
305	70 V	500–250	21. i. 30	34·58–34·36	1·98/1·51
305	70 V	750–500	21. i. 30	34·68–34·58	1·97/1·99
311	70 V	500–250	24. i. 30	34·49–34·29	1·97/1·60
320	70 V	750–500	30. i. 30	34·69–34·63	1·76/1·69

Station	Net	Depth (m.)	Date	S.‰	Temp. ° C.
320	70 V	500–250	30. i. 30	34·63–34·32	1·69/0·78
320	70 V	1000–750	30. i. 30	34·70–34·69	1·53/1·76
321	70 V	750–500	30. i. 30	34·69–34·62	1·74/1·84
321	70 V	500–250	30. i. 30	34·62–34·32	1·84/0·87
322	70 V	500–250	31. i. 30	34·60–34·35	1·91/1·34
322	70 V	1000–750	31. i. 30	34·71–34·69	1·67/1·83
323	70 V	500–250	31. i. 30	34·59–34·41	1·96/1·58
324	70 V	500–250	1. ii. 30	34·57–34·38	1·81/1·46
325	70 V	500–250	1. ii. 30	34·47–34·29	2·10/1·60
334	70 V	500–250	4. ii. 30	34·54–34·31	1·97/1·42
334	70 V	1000–750	4. ii. 30	34·71–34·67	1·89/2·02
334	70 V	750–500	4. ii. 30	34·67–34·54	2·02/1·97
336	70 V	500–250	5. ii. 30	34·54–34·34	1·96/1·60
336	70 V	250–100	5. ii. 30	34·34–34·04	1·60/0·32
336	70 V	750–500	5. ii. 30	34·68–34·54	1·96/1·96
337	70 V	750–500	5. ii. 30	34·68–34·57	1·97/1·96
337	70 V	500–250	5. ii. 30	34·57–34·36	1·96/1·60
339	70 V	250–100	5. ii. 30	34·27–33·96	1·20/1·30
342	70 V	500–250	7. ii. 30	34·65–34·48	1·86/1·67
343	70 V	500–250	7. ii. 30	34·65–34·49	1·98/1·60
344	70 V	500–250	7. ii. 30	34·59–34·41	2·00/1·48
344	70 V	750–500	7. ii. 30	34·66–34·59	1·94/2·00
345	70 V	180–100	8. ii. 30	34·30–34·10	1·07/0·38
353	70 V	750–500	9. ii. 30	34·66–34·57	1·95/1·96
353	70 V	500–250	9. ii. 30	34·57–34·31	1·96/1·27
354	70 V	500–250	9. ii. 30	34·64–34·44	1·97/1·74
354	70 V	250–100	9. ii. 30	34·44–34·05	1·74/0·28
354	70 V	750–500	9. ii. 30	34·69–34·64	1·88/1·97
355	70 V	500–250	9. ii. 30	34·64–34·48	1·91/1·77
355	70 V	250–100	9. ii. 30	34·48–34·07	1·77/0·00
355	70 V	750–500	9. ii. 30	34·67–34·64	1·73/1·91
355	70 V	1000–750	9. ii. 30	34·69–34·67	1·47/1·73
356	70 V	750–500	10. ii. 30	34·69–34·66	1·62/1·83
356	70 V	1000–750	10. ii. 30	34·70–34·69	1·37/1·62
357	70 V	750–500	10. ii. 30	34·67–34·61	1·84/1·91
357	70 V	500–250	10. ii. 30	34·61–34·44	1·91/1·62
358	70 V	1000–750	11. ii. 30	34·70–34·69	1·61/1·77
358	70 V	500–250	11. ii. 30	34·67–34·41	1·89/1·38
358	70 V	750–500	11. ii. 30	34·69–34·67	1·77/1·89
588	100 B	460–150	13. i. 31	34·71–34·43	1·61/0·30
661	TYF V	750–500	2. iv. 31	34·68–34·68	0·62/0·86
661	TYF V	500–250	2. iv. 31	34·68–34·60	0·86/0·59
661	TYF V	3000–2000	2. iv. 31	34·66–34·67	−0·15/0·00
661	TYF V	1000–750	2. iv. 31	34·67–34·68	0·46/0·62
663	TYF V	500–250	5. iv. 31	34·65–34·47	1·14/0·40
663	TYF V	1000–750	5. iv. 31	34·67–34·67	0·69/0·93
663	TYF V	750–500	5. iv. 31	34·67–34·65	0·93/1·14
663	TYF V	2000–1500	5. iv. 31	34·67–34·67	0·19/0·43
663	TYF V	1500–1000	5. iv. 31	34·67–34·67	0·43/0·69
666	TYF V	500–250	17. iv. 31	34·56–34·32	1·88/0·94
671	TYF V	1000–750	22. iv. 31	34·41–34·31	2·53/2·63
671	TYF V	1500–1000	22. iv. 31	34·63–34·41	2·51/2·53
671	TYF V	750–500	22. iv. 31	34·31–34·19	2·63/2·69
671	TYF V	500–250	22. iv. 31	34·19–34·23	2·69/4·94
673	TYF V	750–500	24. iv. 31	34·28–34·41	4·08/6·31
673	TYF V	1000–750	24. iv. 31	34·28–34·28	3·20/4·08
847	100 B	270–196	11. iv. 32	34·78–34·86	10·05/11·22
942	100 B	350–110	31. viii. 32	34·56–34·58	8·40/8·97
1048	100 B	340–140	30. xi. 32	34·65–34·35	0·70/−0·63

Mackintosh (1934) classed *D. arctica* as one of the species typical of the coldest Antarctic regions such as those of the Bellingshausen and Weddell Seas, where it was plentiful, and said that it rarely or never approaches the convergence. He gave the average number of anterior nectophores per haul between the mean summer isotherms −1·00° to −1·99° as 14·4, and between similar isotherms 6·00° to 6·99° as 1·40.

Compared with an abundant Antarctic species like *Calanus acutus* (1900 per haul) Mackintosh found that *Dimophyes arctica* was only moderately abundant in the Antarctic (1·90 per haul).



Text-fig. 64. Frequency of capture of *Dimophyes arctica* in water of known upper and lower limits of temperature by 'Discovery' closing-net hauls. Black tally-marks show (upper series of columns) the number of times that the indicated temperature was the minimum in which the specimens could have been taken; and (lower series) how often the temperature was the maximum possible for the same group of hauls (111). Superimposed, in the form of open circular tally-marks are some of Bigelow & Sears (1937, fig. 81) records (53) for 'Meteor' closing hauls that yielded this species (six of their records, covering temperatures ranging from 16° to 26° C., are omitted). The class boundaries used in the two sets of records are staggered by half a degree Centigrade. The reason for giving two series of columns is that each closing-net capture was made at an unknown depth in limited columns of water whose upper and lower levels were at different temperatures.

In June 1952 'Discovery II' took *D. arctica* in closing-nets in the North Atlantic at Stations 2927, 2929 and 2935 at depths between 1500–100 m., 1000–750 m. and 750–500 m. Dr Cooper informed me (in lit.) that the mean temperature at Station 2929 (44° N., 15° W. approx.) for depths between 746 and 977 m. was 10·19° C., and that the water was 'Mediterranean' or 'Gulf of Gibraltar' water, formed in the Atlantic west of Gibraltar by mixing of warm, deep, saline water from the Mediterranean with North Atlantic central water. *D. arctica* is not known to occur in the Mediterranean.

Chelophyes appendiculata (Eschscholtz), 1829. (Plate IV, figs. 1, 3.)

Although this is one of the most common Siphonophores it was, until lately, the only common diphyid that could not be associated in preserved plankton collections with an eudoxid. As Moser (1925) said, that there should still be doubt on this point was difficult to believe. But Bigelow, as long ago as 1911, said that the eudoxid was so well known as to require no description. The explanation of this paradox is that Bigelow mistook the eudoxid of *Eudoxia mitra* for that of this species.

In the Mediterranean *Chelophyes appendiculata* is very common. Its seasonal and geographical distribution was worked out by Bigelow & Sears (1937), although 'Thor' did not provide them with any material of the eudoxid stage.

On searching the literature for descriptions and figures of eudoxids that might be those of *Ch. appendiculata* we find first of all that Leuckart (1853) described and figured *Eudoxia campanula*, a common eudoxid which he found at Nice. I have found it near there too. The immature eudoxids he described and figured well in figs. 17 and 19 of his plate III, but the details of the loose gonophore (his fig. 19) are not so well shown. He came to the conclusion, without being able to prove it, that it could be the eudoxid only of his *Diphyes acuminata* (*Chelophyes appendiculata*). In this I agree with him.

Leuckart's paper was shortly afterwards followed by Gegenbaur's (1853) figure and description of *Eudoxia messanensis* from Messina. He does not mention *E. campanula* Leuckart because his work was already in the press when Leuckart's appeared, though he does refer to the paper in an appendix. The bract does not show the deep cavity, nor the gonophore the long apophysis that are characteristic of the eudoxid of *Chelophyes appendiculata*. I think that *Eudoxia messanensis* may be the eudoxid of *Lensia conoidea*; it is not that of *Chelophyes appendiculata*. *Eudoxia lessonii* Eschscholtz (1829) is neither convincingly figured nor does it form part of a well-defined fauna, so that we cannot be sure of its identity.

The identity of McCrady's (1857) *E. alata* has been discussed by Moser (1925). I agree that there seems no reason to believe that it is the eudoxid of *Chelophyes appendiculata*.

Schneider (1896, p. 581) copied Gegenbaur's figure (1853, pl. 16, fig. 20) of the larva of what is now known as *Galetta turgida* but was, in error, then called *Diphyes sieboldii* by Gegenbaur; and labelled it *D. appendiculata*. Five pages later he gives it its proper name, *D. turgida*. At the same time, on plate 45, Schneider figured an eudoxid of unknown parentage, apparently from Naples, as the eudoxid of *D. appendiculata*. The gonophore, from its size and the minuteness of the gonadial part, would appear to be spent. It can scarcely be the eudoxid of any Mediterranean diphyid except *Lensia conoidea*. The figure certainly does not represent the eudoxid of *Chelophyes appendiculata*.

Moser (1925), p. 245 says that the eudoxid of *Ch. appendiculata* so closely resembles, especially in its young stages, that of *Muggiaea kochii* that they are difficult to distinguish, but that it comes to exceed the latter in size. She notes in the eudoxid of *Chelophyes appendiculata* the presence of a relatively long, flattened apophysis to the gonophore, its freedom from the bract and the shallowness of its suture and of the cavity under the bract; her accompanying Text-fig. 39 is not characteristic of the eudoxid of *Ch. appendiculata* which has a deep bracteal cavity. She says (on p. 240) that since the eudoxid of *Muggiaea kochii*, *Galetta subtilis* and *G. truncata* (*Lensia conoidea*) were all found at Villefranche a determination of the differences was possible. She figured them on pls. I and IV. Her figure (pl. XII, fig. 8) is a good representation of the eudoxid of *Chelophyes appendiculata*.

Moser did not succeed in getting *Ch. appendiculata* to separate off its cormidia till the month of May, when one specimen gave off thirty eudoxids in two days. These remained alive under observation for ten days. Moser (1925) figured these immature eudoxids on pl. XII in figs. 4–7. In the oldest of the figured specimens the bract had metamorphosed into the eudoxid condition. Her fig. 8 of an eudoxid of unknown parentage taken in a plankton haul gives a good representation of the common Diphyid eudoxids that I found at Villefranche in March, April, May and June 1949, and which I believe to be those of *Ch. appendiculata*. These eudoxids were shedding their ripe, active gonophores at the end of June 1949. I have watched the detached gonophores extruding eggs, and have also observed the spent gonophores. My attempts to raise the polygastric generation from wild male and female gonophores, kept in an improved Harvey rocker (see Rees & Russell, 1937), failed in my 1949 and 1950 experiments at Villefranche. I described and figured a very similar, if not the same, eudoxid as *Eudoxia russelli* in 1932, from material brought back from the Great Barrier Reef of Australia. It occurred there on 20 September 1928 at one station at the Barrier Reef lagoon, and on 20 October 1928 at another station outside Trinity Opening. At these two stations the polygastric stages of both *Chelophyes appendiculata* and *Ch. contorta* were present. In December 1948 Fraser-Brunner took some more eudoxids off Aden, very similar to *Eudoxia russelli* in structure and associated with the polygastric stages of *Chelophyes contorta*. *Ch. appendiculata* was very much less common in Fraser-Brunner's catches, ten specimens in one catch against 359 of *Ch. contorta* in five. In the one catch both specimens occurred.

Using my 1932 terminology, the left sutural ridge of the eudoxid bract of *Ch. appendiculata*, taken wild at Villefranche, does not bear such a marked crest as the right, and the left ridge terminates before reaching the basal edge of the bract. Although a trivial character, this serves as a very useful field-mark for distinguishing between eudoxids of *Ch. appendiculata* and *Lensia conoidea* when breeding from wild eudoxids. Another such field-mark for use in the Mediterranean is the colour of the tip of the manubrium of the gonophore of an eudoxid. It is yellow in *L. subtilis* and pink in three species of *Muggiaea*. I have no written notes on the colour in *Lensia conoidea* or *Chelophyes appendiculata*.

Vogt (1854), a pioneer who made very valuable observations at Nice, figured three eudoxids of unknown parentage whose nature he did not understand. He thought that they had developed from eggs and that they would grow into polygastric specimens of his *Galeolaria aurantiaca* (= *Sulculeolaria quadridentata*). The largest one figured, without a mature gonophore, on his plate 21, probably presents the eudoxid of *Chelophyes appendiculata*.

Up to the present time, therefore, I think it fair to say that we have no detailed description or figure of the full grown eudoxid of *Ch. appendiculata* except for *Eudoxia campanula* Leuckart (1853); *Diphyes sieboldii* Moser (1925, pl. XII, fig. 8—an eudoxid caught at Villefranche); and *Eudoxia russelli* Totton (1932).

A Mediterranean calycophore whose eudoxids might be mistaken for those of *Chelophyes appendiculata* is *Lensia conoidea* (referred to by Moser and also Leloup as *Galetta truncata*). But it is much larger and the bract lacks the distinct cavity found in *Eudoxia campanula* and *E. russelli*, and the gonophore has a truncate articulating end, as in most species of *Lensia*.

There remains the task of differentiating between the eudoxids of *Chelophyes appendiculata* and *Ch. contorta*, which species were taken together, both by 'Mabahiss' and 'Discovery II' in the Indian Ocean.

The length of a free swimming, mature, male gonophore of *Ch. appendiculata* taken at Villefranche (28 March 1949) was found to be 4·5 mm. A full-grown bract measured about 2·5 mm. in length and 1·25 mm. in (maximum) diameter.

Observations on the behaviour of this very rapidly swimming species were made by me at Villefranche. When a complete, living, polygastric specimen sinks in a container of water it does so with its main axis vertical. The small posterior nectophore only is used to maintain vertical height, and contracts feebly at intervals to do so. The animal also cruises about slowly in a horizontal position in the same way without contracting its larger anterior nectophore until the high-speed 'escape action' is called for, when the anterior nectophore comes into use. It was not possible to see what the posterior nectophore was doing when the animal was travelling at speed.

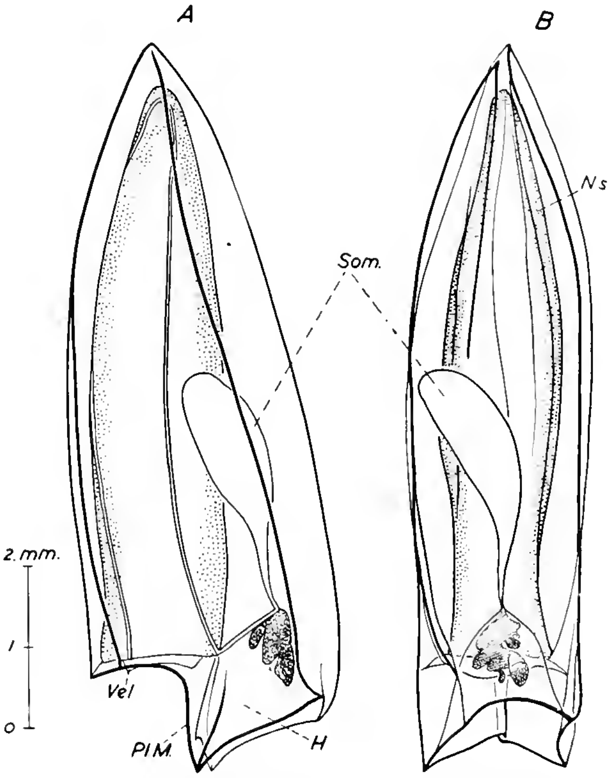
Moser (1925, p. 243) said that there was no ventral radial canal in this species. Actually there is a very short one, measuring about 0·1 mm. in length, which runs to the circular canal, for the latter lies that distance within the inner boundary of the velum. The first part of the lateral radial canals are somewhat irregular, with a tendency to branch, and run parallel with the circular canal before rising up towards the apex.

Chelophyes contorta (Lens & van Riemsdijk), 1908.

This species appears to be much more abundant in the West Tropical Indian Ocean than its ally *Ch. appendiculata*, though they occur side by side at most of the stations. During a recent examination of seven of the bottles of plankton brought back by M.Y. 'Manihine' from the Gulf of Aqaba I have identified young specimens of *Ch. contorta* and eudoxids of the *Eudoxia russelli* type. Since *Chelophyes appendiculata* was not found in the Gulf of Aqaba it is probable that these eudoxids are of the species *contorta*, but I have not yet been able to distinguish them from those of *Ch. appendiculata*. They are both of the type described by me (1932) as *Eudoxia russelli*.

This species is not often taken, but it was one of the common species taken by the Great Barrier Reef Expedition; and Russell & Colman (1935) showed that it could not apparently withstand the conditions of the environment in the Barrier Reef lagoon during the period of lower salinity. We find it in the Indian Ocean in some catches associated with *Enneagonum hyalinum*, one of the three Barrier Reef species that was definitely able to withstand lowered salinity, and so was possibly well suited for life in coastal waters.

New Indian Ocean records. 'Discovery II' Stations: 1567 (1350–0 m.); 1571 (500–0 m.); 1573 (800–0 m.); 1581 (50–0, 100–50, 600–0, 1750–600 m.); 1582 (1900–1850 m.); 1583 (50–0, 100–0, 100–50, 250–100 m.); 1584 (50–0, 100–50, 250–100, 500–250 m.); 1585 (500–0, 1400–700 m.); 1586 (50–0, 250–100, 550–0, 1650–950 m.); 1587 (450–0, 1250–800 m.); 1588 (50–0, 100–50, 250–100, 500–200 m.); 1589 (50–0, 100–50, 250–100, 600–0 m.).



Text-fig. 65. *Chelophyes contorta.* Two views of the anterior nectophore, × 12. Specimen from off Alayu, Gulf of Aden.

Diphyes chamissonis Huxley, 1859.

'Manihine' took *D. chamissonis* at six stations, fixed at 5, 10, 20, 35 and 40 miles east of Sanganab Lighthouse off Port Sudan, in open nets (366–0 and 183–0 m.), in January 1951. At Station 6, ten miles east of the Lighthouse, twenty-one nectophores and seven eudoxids were taken; the largest catch. At five stations it was associated with *Lensia subtiloides*, an association that has been noted before.

The species was previously recorded from the Red Sea by Leloup (1932*a*). He based his record on one nectophore and an eudoxid in the Zoologisches Museum, Hamburg. He recorded another nectophore in the same Museum from Ceylon. H.M.S. 'Weston' found this species (both stages) abundant off Kamaran, Red Sea, in April 1936, at a surface temperature of 28° C.

'Discovery II' records from the west Indian Ocean are: Station 1581, TYF B, one bract of eudoxid (1750–500 m.); 1589, TYF B, one anterior nectophore (600–0 m.); 1589, N 70 B, three anterior nectophores (600–0 m.). The species was not present in any of the catches made on the 32° S. line of Stations.

CHUNIPHYINAE subfamily nov.

Chuniphyes Lens & van Riemsdijk, 1908

For many years I suspected that I had been dealing with more than one species. A review of all the material after the chance finding of a well-preserved specimen from 'Discovery II' Station 1639 revealed that there are two quite distinct species, the well-known *multidentata* Moser, and a new species described below.

The interesting eudoxid stage (*Eudoxia problematica* Moser) of one or other species was first related to the polygastric stage by Leloup (1934*a*). It can now be said to be well known.

Lens & van Riemsdijk had for study only one very poorly preserved anterior and posterior nectophore. Very often specimens of these mid-water species arrive at the surface in a damaged condition, since the somatocyst frequently bursts into the subumbral cavity of the nectosac. Their description and figures leave very little doubt as to which species Lens & van Riemsdijk found and named *multidentata*. Moser (1925) appears to have had both species under examination since she says that the somatocyst may have either a cylindrical or a butterfly-shaped base. She figured (1925, pl. 23, fig. 1) the anterior nectophore of the new species under the old name.

Chuniphyes multidentata Lens & van Riemsdijk, 1908.

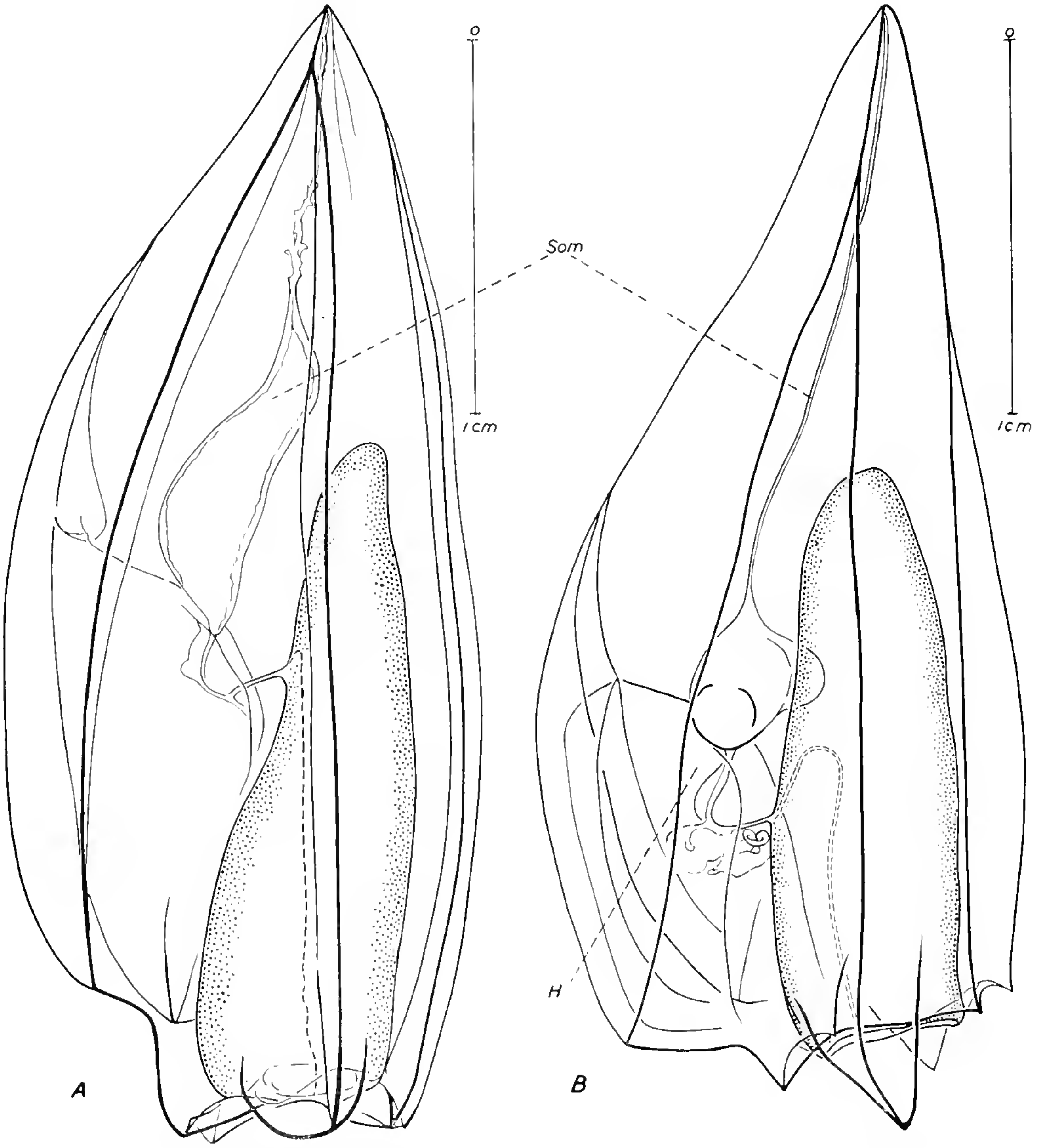
There are two characteristics of the anterior nectophore figured by Lens & van Riemsdijk which indicate that they had before them the species with the butterfly-shaped somatocyst-base, namely the location of the junction of the two lateral ridges at some distance from the apex, and the position of the rounded protuberance for the attachment of the posterior nectophore. This protuberance is nearer to the ostium of the nectosac than in the second species. I give a new figure of a well-preserved specimen (Text-fig. 66B).

Chuniphyes moserae sp.n. (Text-fig. 66A.)

The anterior nectophore of this species, which was figured quite characteristically by Moser (1925, pl. 23, fig. 1), shows the sub-apical junction of the lateral ridges and the location of the protuberance for the attachment of the posterior nectophore above the mid-level of the nectosac. Moser, however, regarded all specimens as belonging to one species, *multidentata* Lens & van Riemsdijk.

I will not attempt to give an expanded description of the new species here nor show how it differs from the already known one. My figures of the anterior nectophores of the two species will make this clear. That there are differences between the posterior nectophores as well is probable, since there appear to be posterior nectophores of *Chuniphyes* of at least two kinds. One has markedly asymmetrical ventro-basal teeth and thick mesogloea separating the hydroecium from the nectosac, and is the kind generally associated with *Ch. multidentata*. The other has sub-equal ventro-basal teeth and a thinner sheet of mesogloea between the hydroecium and the nectosac. It is this kind that I think will prove to belong to *Ch. moseri*. No doubt the matter will be cleared up one day when we are lucky enough to find well-preserved, complete specimens.

The holotype (anterior nectophore) was taken by R.R.S. 'Discovery II' at Station 1639 in lat. 58° 35′ S., long. 92° 06·2′ E. between depths of 2400 and 1150 m. and bears the Brit. Mus. (Nat. Hist.) Register No. 1951. 3. 24. 1. Twenty-seven anterior and twenty-three posterior nectophores were taken by Beebe in 1929 and 1930 off Bermuda in thirty-three open tow-nets that had been fished for some hours horizontally at depths varying between 900 and 1800 m. Nineteen of the anterior and fifteen of the posterior nectophores were taken between 1450–1650 m., and as many (7) at 1800 m. as (8) above 1450 m. The figures for *Ch. multidentata* off Bermuda are comparable. *Chuniphyes* spp. have been recorded from at least fifty-eight other 'Discovery' Stations, varying in depth between 250–100 and 2480–2580 m., but specific identifications have not been re-checked so far.



Text-fig. 66. A, *Chuniphyes moserae* sp.n., holotype, 'Discovery II' St. 1639, 2400–1150 m., × 5; B, *Chuniphyes multidentata*, 'Discovery II' St. 407, 800–900 m., × 5.

The contracted gastrozooids of a specimen from 'Discovery' Station 2006 are very small. A typical one measured 1·12 mm. in length and 0·37 mm. in diameter. The tentilla are minute and their structure has not been examined or described.

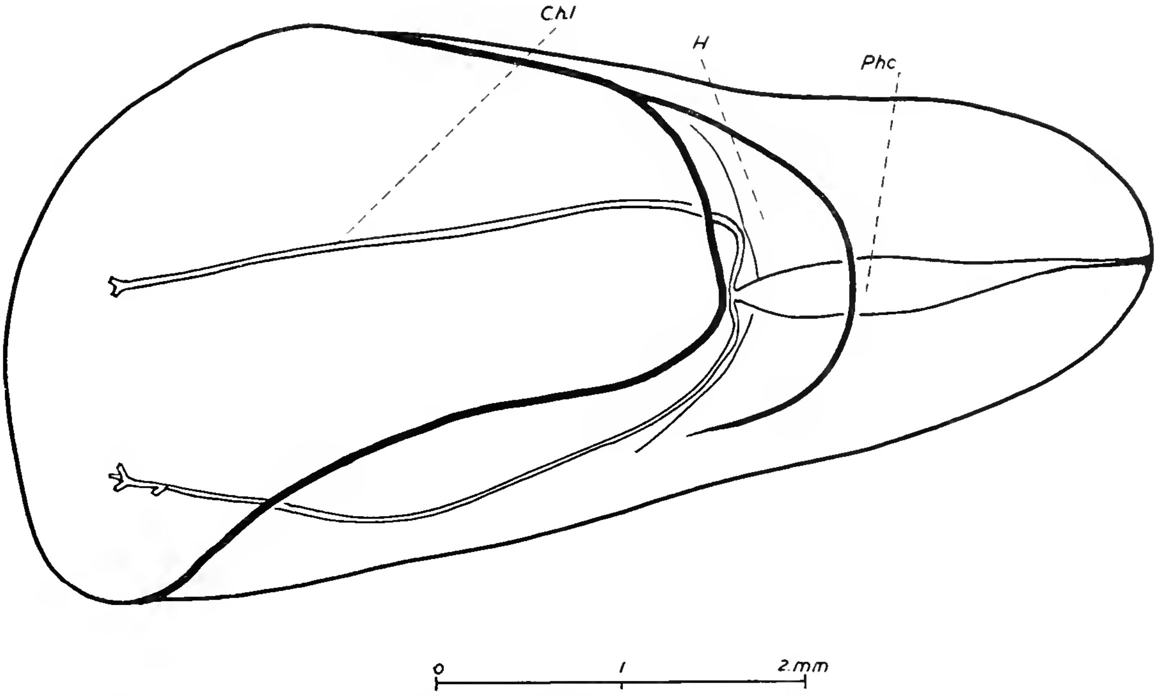
Occurrence in the Indian Ocean. 'Discovery II' Station 1587 off Italian Somaliland, 1250–800 m., two anterior nectophores; 1581, off Zanzibar, 1750–600 m., three anterior, two posterior nectophores.

Clausophyes Lens & van Riemsdijk, 1908

There appear to be two described species, *ovata* Keferstein & Ehlers, 1861 (figured), and *galeata* (not *galatea*) L. & van R., 1908, well figured by Bigelow 1913. I have also seen material of what appears to belong to a new species from 'Discovery II' Station 2084. *Clausophyes* has obvious affinities with *Chuniphyes*.

Clausophyes ovata (Keferstein & Ehlers), 1861. (Text-fig. 67.)

Eudoxid. 'Discovery II' (Station 1567) took two anterior and one posterior nectophore, all in very poor condition, in a haul from 1350 m. to the surface, together with an interesting though poorly preserved bract of an eudoxid. This eudoxid bract has a rounded apex, and from the phyllocyst arise a pair of bracteal canals. A free eudoxid of *Clausophyes* has never been described, and the stem groups have been figured only by Keferstein & Ehlers (1861), when they first described the polygastric stage. The presence of the pair of bracteal canals would seem to link this bract of a free eudoxid with those of Keferstein & Ehlers's attached stem-groups of *C. ovata*.



Text-fig. 67. *Clausophyes ovata*. Bract of eudoxid. 'Discovery II' St. 1567, 1350–0 m., ×25.

Material. 'Discovery II' has taken this species in twenty-three closing-nets so far examined, at depths ranging from 3000–2000 to 310–260 m. It seems to be characteristic of the deeper water.

My identification of *ovata* is based on the posterior nectophore which has a straight, not emarginate basal edge to the mouth-plate. The left hydroecial fold fits into a notch at the basal end of the right-hand fold. The notch is bounded on the inner side by a prominence which forms a good recognition mark.

In a new species from 'Discovery II' Station 2084, whose description I am unable to complete at the moment, the posterior nectophore is intermediate in size between the smaller *ovata* and the very large *galeata*. The right-hand hydroecial fold has a very large flap midway along its length, which I have never seen in *ovata* and *galeata*.

Here is a list of hitherto unpublished records of capture of *C. ovata* in closing-nets by R.R.S. 'Discovery' and R.R.S. 'Discovery II':

Station	Depth (m.)	Station	Depth (m.)
100 A	625–675	1753	2900–1400
100 C	2500–2000	2057	1450–700
	260–310	2059	1900–1400
101	850–95	2061	1900–1500
138	100–750	2063	1150–600
666	3000–2000	2065	1600–1400
671	2000–1500	2084	1500–800
675	2000–1500	2636	950–550
696	750–500	2639	1200–600
699	3000–2000	2646	1500–800
1639	2400–1150	2648	1450–950
1750	2000–1900		

Clausophyes galeata L. & van R., 1908.

Clausophyes galatea (sic) Bigelow, 1913.

'Discovery II' took a very well-preserved posterior nectophore of *C. galeata* at Station 1639 off the Antarctic Ice Edge in the Australian basin, in a haul from 2400 to 1150 m. The posterior end is thick and gelatinous. The emarginate mouth-plate being concave on the dorsal side and convex, with a pronounced median conical projection, on the ventral. The basal ends of the hydroecial folds extend further than in *ovata*. The basal end of the right hydroecial wing is thick and trihedral, and is overlapped by the smaller left-hand one. Inside the hydroecium, just below the group of appendages, there is on either side a finger-shaped projection not shown in Bigelow's figure. The musculature of the nectosac is not complete, but the radial canals can be seen in places. The laterals, after ascending obliquely, run down towards the circular canal but turn up again before reaching it to form a second parallel loop. They finally run down again near the ventral radial canal. This nectophore measures 43 mm. in length.

Crystallophyes amygdalina Moser, 1925.

The only published records of this rare mid-water species are those of Moser's three original types from off the Antarctic continent, and of two specimens from South Georgia reported by Leloup ('Meteor' Expedition, 1934*a*). 'Discovery' and 'William Scoresby' took seventy-three anterior nectophores and twenty-three specimens of an associated posterior nectophore in thirty-seven closing-nets at twenty-nine 'Discovery' stations. The posterior nectophore (Text-figs. 68, 69B, C) is undescribed and appears to belong to this species. 'Discovery II's' 'Atlantic Line' series of stations (661–99) showed that the species was present only at Stations 661, 663 and 671.

Like most small, deep-water siphonophores the specimens were usually in poor condition, but one or two better preserved specimens have enabled me to add to our knowledge of its morphology, especially of the previously unknown posterior nectophore.

Moser's (1925) figure of the anterior nectophore does not show the lateral ridges, but she does indicate the characteristic curved ostial end of one. The very minute mouth-plate (Text-fig. 69, *Pl.M.*) does not curve in under the velum as suggested in Moser's figure. There is a short pedicular canal, as shown in my figure, at the junction of the radial canals. In a well-preserved specimen, what appears to be the scar of attachment of the muscular lamella can be seen continuing for nearly 1 mm. distad to the pedicular canal. There is some variation in the arrangement of the junction of the ridges

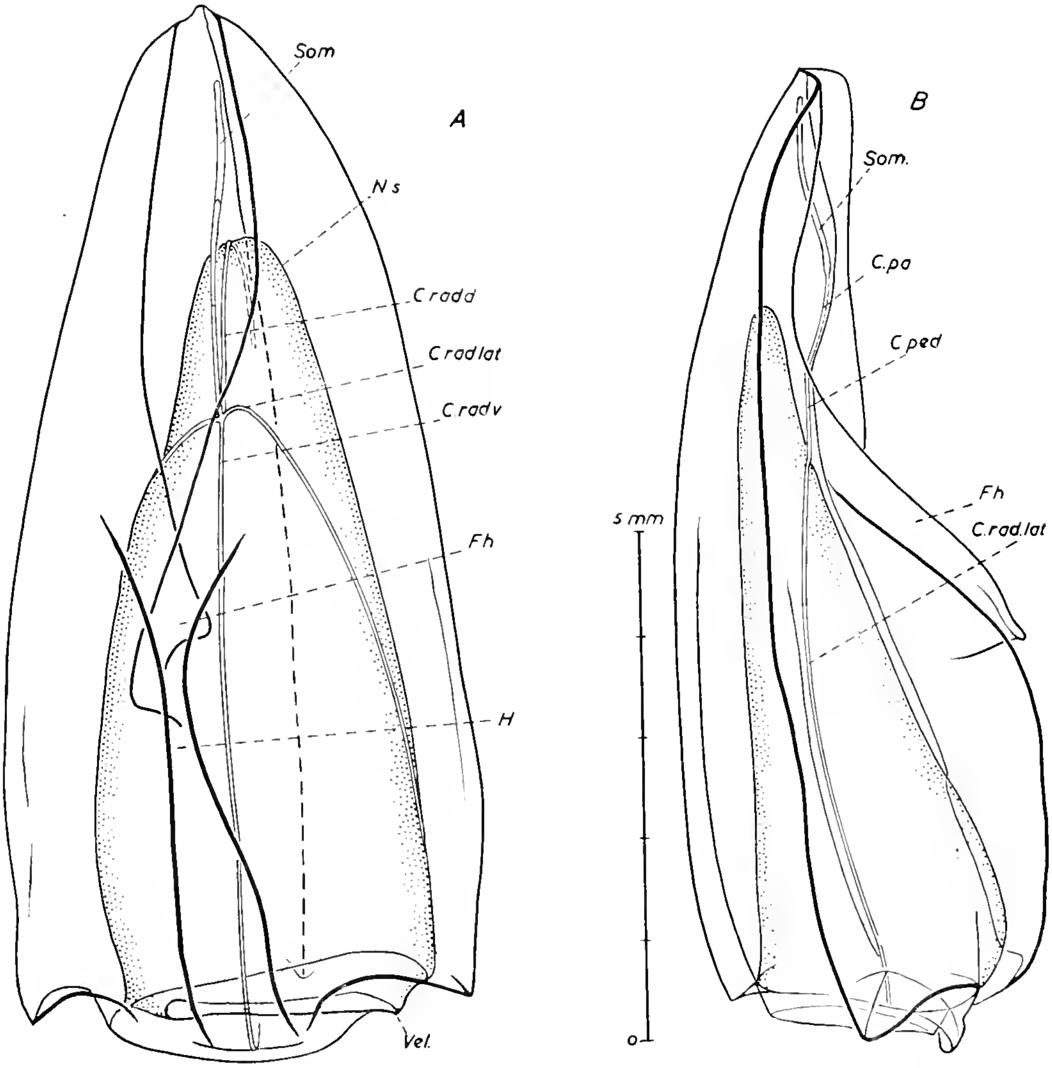
Records of capture of Crystallophyes amygdalina *in closing-nets by R.R.S. 'Discovery', 'Discovery II' and 'William Scoresby'*

[These records do not take into account some 30,000 plankton samples so far unexamined. Only one specimen was taken in each haul unless otherwise stated. Posterior nectophores have not been included.]

	Depth (m.)																
	3000–2000	2500–2000	2400–1150	2000–1500	1650–950	1500–1000	1450–950	1400–700	1000–750	800–500	800–350	750–500	500–250	460–320	390–137	395–155	380–150
'Discovery II' Stations 'Atlantic Line'																	
661	×	—	—	—	—	—	—	—	—	—	—	×	×3	—	—	—	—
663	—	—	—	×	—	—	—	—	×8	—	—	×18	×3	—	—	—	—
671	—	—	—	—	—	×3	—	—	×2	—	—	—	—	—	—	—	—
'Discovery' and 'Discovery II' other Stations																	
100 C	—	×4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
117	—	—	—	—	—	—	—	—	—	—	—	×2	—	—	—	—	—
125	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
129	—	—	—	—	—	—	—	—	—	—	—	×	×	—	—	—	—
151	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—
335	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—
337	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
355	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—
356	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
357	—	—	—	—	—	—	—	—	—	—	—	×3	—	—	—	—	—
358	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—
519	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×7	—	—
1616	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
1617	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	—
1635	—	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
1636	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×
1639	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1723	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—
1728	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—	—
2648	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
'William Scoresby' Stations																	
WS 30	—	—	—	—	—	—	—	—	—	—	—	×	×	—	—	—	—
WS 36	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—
WS 38	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
WS 67	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
'Discovery' Indian Ocean Stations																	
1585	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—	—
1586	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—

at the apex of the anterior nectophore. Sometimes all five meet in a point, but the junction of the dorsal and lateral ridges may be separated from that of the ventrals.

A comparison of the figure of *Chuniphyes moserae* (Text-fig. 66 A) and of the figure of *Crystallophyes amygdalina* will show an obvious relationship between the two. But in *Chuniphyes* the dorsal and lateral ridges divide below to the apex.

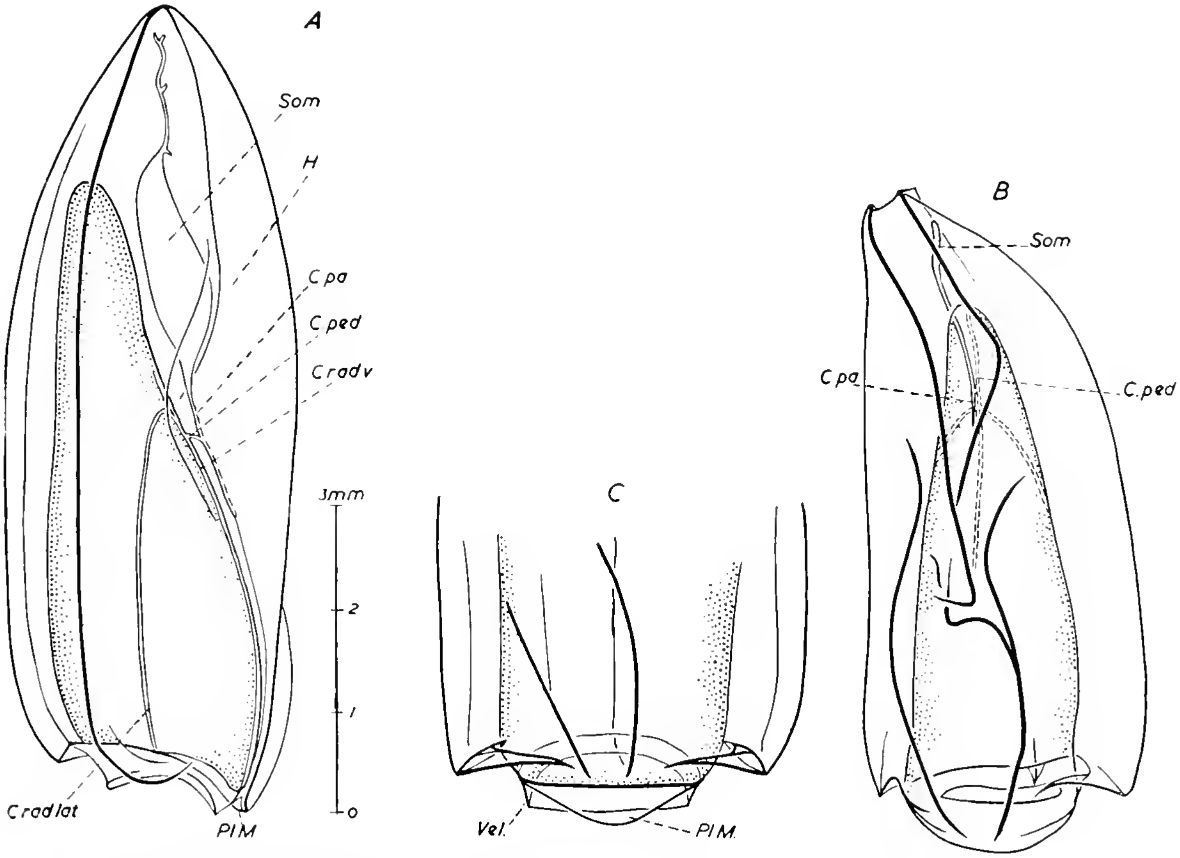


Text-fig. 68. *Crystallophyes amygdalina.* Lateral and ventral views of posterior nectophore, 'Discovery II' St. 357, 750–500 m., × 13.

The posterior nectophore of *Crystallophyes*, hitherto undescribed, is flattened dorso-ventrally in the apical region, and the five ridges do not meet in a point; the ventrals join the laterals at a short distance below the apex. The laterals form prominent pointed teeth at the base. The lateral radial-canals leave the dorsal and ventral radial-canals at a point about a quarter of its length distal to the apex of the nectosac.

Only after suitable staining is the nature of the ventral ridges apparent. At about the level of the mid-length of the nectosac, the ventral ridges form pointed flaps, between which and their distal continuations open grooves (Text-fig. 69 B) are found. We do not know at present how the anterior and posterior nectophores are articulated, but it would appear as if at some point there is a grasping of some part of the anterior by the posterior nectophore.

Quite recently, since this report was drafted, it has been found that *C. amygdalina* was present at 'Discovery II' Ice-Edge-Cruise Stations between 59 and 98° E., and at another Ice-Edge Station 1723.



Text-fig. 69. *Crystallophyes amygdalina.* A, lateral view of anterior nectophore, 'Discovery II' St. 663, 1000–750 m.; B, C, ventral views of posterior nectophores; B, 'Discovery' St. 129, 500–250 m.; C, 'Discovery II' St. 663, 750–500 m., × 14.

Heteropyramis maculata Moser, 1925. (Text-fig. 71.)

Moser described this species from specimens taken in seven open vertical hauls from deep water made between the Cape Verde Islands and Ascension Island. At one station on the equator 'Gauss' took a great number of nectophores in a vertical haul from 3000 m. Leloup (1934*a*) recorded it from the South Georgia region.

Moser commented on the strong dorso-ventral flattening of the nectophore, on the open hydroecium running the whole length of the nectophore, and on the long somatocyst seated on the apex of the nectosac, the apex of which only reached the middle of the nectophore. Moser also drew attention to a number of opaque (pigmented) patches found, one at the apex, one at the basal end of each lateral ridge, and from two to five more, according to size in between, on each lateral ridge. The lower two are sometimes small, as if in process of formation.

Such opaque spots are known only in the nectophore and the alleged eudoxid of this species. The phenomenon may be related to similar ones occurring in several other siphonophores. For example, *Bassia bassensis* has long been known to have opaque ridges.[1] Also in *Diphyes bojani* parts of the ridges of the special nectophore of the eudoxid are sometimes opaque, and in *Chuniphyes multidentata* the same phenomenon is common. It is probably related also to the phenomenon occurring in *Hippopodius hippopus* and in the anterior nectophores of some species of Abylids, where preserved nectophores

---

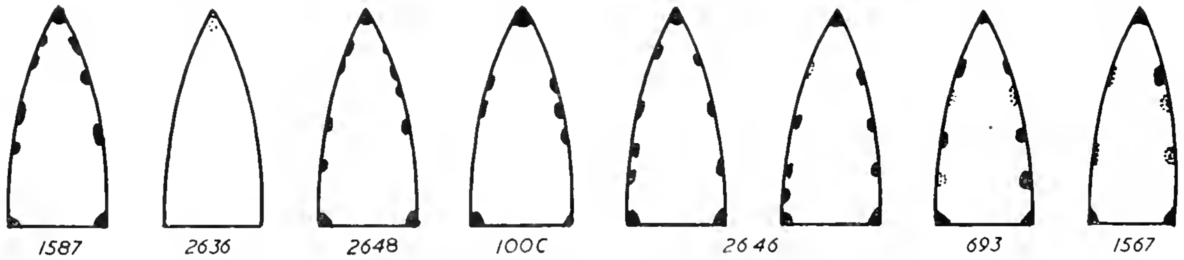
[1] Huxley (1859) said that they were dark blue when the animal was alive.

are commonly opaque. At Villefranche I have observed that the nectophores of undisturbed specimens of *H. hippopus* are quite transparent, but that when disturbed they immediately become opaque. After a rest they once more become transparent. As far as is known no research has been carried out upon this phenomenon. But I have recently found a description of this same phenomenon by Chun (1888*a*) which he observed whilst working in the Canaries. He said that the turbidity occurred in the ectoderm of *Hippopodius*, and added that a related phenomenon observed in the eudoxid of a *Ceratocymba* was due to the appearance of extremely fine granules in the neighbourhood of the horn-like canals of the somatocyst. These granules later spread throughout the mesogloea, but disappeared again in about half an hour if the eudoxid was left in repose.

In 'Discovery' hauls so far examined I have seen eleven 'spotted' anterior nectophores. Neither the number, size, degree of opacity nor symmetry of their opaque spots is constant, if my identifications of these small and ill-preserved nectophores are correct.

In the better preserved of these nectophores of *Heteropyramis maculata* examined, nine opaque spots can usually be seen, one each at the apex and basal end of each dorso-lateral ridge, and three intermediate ones on each of these ridges. I have observed as few as eight spots and as many as sixteen in all.

In the following diagram the kind of variation that exists in the opaque spotting is shown.



Text-fig. 70. *Heteropyramis maculata.* Diagram of distribution of pigment-spots in specimens from various 'Discovery' Stations.

A serious doubt has arisen in my mind as to whether *H. maculata* and *Thalassophyes crystallina*[1] are not really one and the same species. The difficulty is that the spotted form *Heteropyramis maculata* is rare, and the twelve nectophores that I have examined were none of them sufficiently well preserved to enable me to construct a very reliable drawing of the side-view. Moser, who described the nectophores as flattened dorso-ventrally did not attempt to draw such a lateral view. Consequently, it is difficult to compare her published figures of the nectophores of the two forms. The ventral facets are similar, and both have two small incomplete ventro-lateral ridges, one on each side of the opening of the hydroecium. I can see no significant external differences in shape or size. As to the somatocyst, the absence of opaque spots—in *Thalassophyes*—on the lateral ridges does seem to be associated with a large, well-preserved and vacuolated somatocyst, the proximal part of which lies obliquely to the main axis of the nectophore; the distal part, which is a fine tube, lies roughly at right-angles to the proximal part. In one or two of the spotted forms the somatocyst can be partially seen. It appears to be thin-walled, never well preserved and straighter. Perhaps the terminal part of the somatocyst of spotted forms approaches more nearly to the apex of the nectophore. Two nectophores from 'Discovery' Station 2636 have somatocysts of this second type, but no opaque spots other than small, faintly discernible opaque areas at the apex of each. It may possibly be found in future that opaque spots can be present or absent in nectophores of *Heteropyramis maculata*. In this connexion my observations on the temporary opacity of the nectophores of *Hippopodius hippopus* should be borne in mind. It seems to be all the more probable that in the nectophores, opaque spots may be present

---

[1] Text-fig. 72.

or absent, because that is just what is found in the very peculiar and characteristic eudoxids of *Heteropyramis maculata* (see Text-fig. 71) described and figured by Moser (1925), and since found again in some numbers. It is possible, but scarcely likely, that there are two eudoxids of the same remarkable shape but belonging to two distinct species, one with opaque spots and one without. We find eudoxids of both kinds associated in hauls with both the spotted nectophores of *H. maculata* and the unspotted ones of *Thalassophyes crystallina*. The chief reason why I shall continue for the present to recognize nectophores of two species is that often quite well-preserved specimens of *T. crystallina* are found, but none of them ever have spots, whereas the spotted nectophores of *Heteropyramis maculata* are always poorly preserved and usually twisted and deformed. It is possible of course that shrinking and deformation are correlated with opacity. But recently a good specimen of *H. maculata* was taken by Scot. Fish. Res. V. 'Scotia'. *Chuniphyes*, too, is frequently much deformed, and is well known for its opaque ridges. The externally well-preserved spotted nectophore of *Heteropyramis maculata* taken at the end of June 1951 by 'Scotia' in a closing-net—1000–250 m.—in lat. 54° 15′ N., long. 14° 32′ W., enables me to confirm the resemblance of *H. maculata* to *Thalassophyes crystallina*. The hydroecium is not open to the apex, as stated by Moser, and the nectophore is not flattened dorso-ventrally, but has the usual Diphyid pyramidal form. The ventral side of the nectosac of the 'Scotia' specimen is broken open, and the shape of the base of the somatocyst, which may have burst into the nectosac, is difficult to determine. The pedicular canal cannot be distinguished nor can the lateral radial canals. In profile the apex of the nectosac is very much like that of *Th. crystallina*. It is shown as pointed in Moser's figures. It may be noted that Moser kept these closely similar, if not identical, forms wide apart in two separate families of her artificial classification, calling the former a Monophyid and the latter a Diphyid. It is true that I have found no posterior nectophore that I can closely associate with the spotted nectophores called *Heteropyramis maculata*, but I think that the relationship between the two species must be a very close one, if indeed they are separate species.

From the Indian Ocean I have one nectophore, one bract and two gonophores of eudoxids, all bearing the characteristic opaque spots of *H. maculata*. The stations are given below:

	Station	Depth (m.)	Material
'Discovery II'	1584	500–250	1 bract, 1 gonophore
	1585	1400–700	1 gonophore
	1587	450–0	1 nectophore

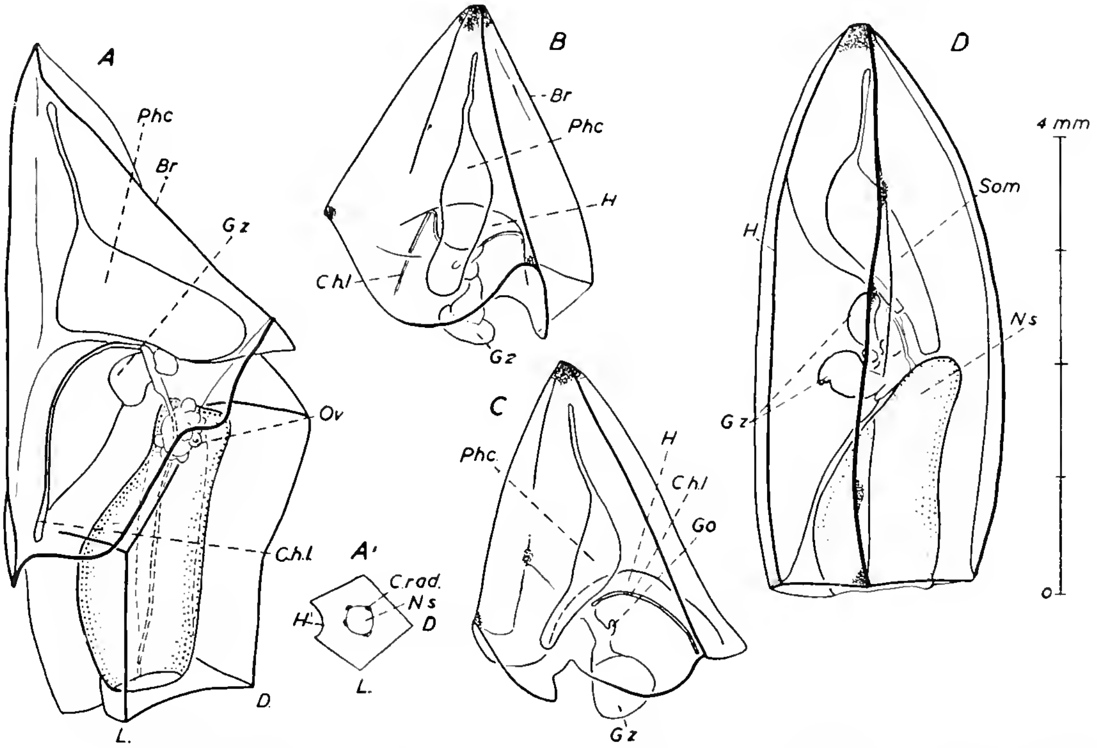
Further unpublished records (other than from the Indian Ocean) for this spotted species taken in closing-nets are:

	Station	Depth (m.)	Material
'Discovery' and 'Discovery II'	1000	450–550	1 nectophore
	693	500–350	1 nectophore
	696	500–250	2 nectophores
	699	500–250	1 bract of eudoxid
	2636	950–550	2 nectophores, 1 bract of eudoxid
	2646	1500–800	2 nectophores
	2927	750–500	2 nectophores, 2 eudoxids
'Scotia', 1951, 54° 15′ N., 14° 32′ W.		1000–250	1 nectophore

Similar records for this spotted species in open hauls are:

	Station	Depth (m.)	Material
'Discovery II'	1567	350–0	1 nectophore, 1 gonophore of eudoxid
	2648	500–0	1 nectophore
British Antarctic 'Terra Nova' Expedition 1910–13	285	600–0	1 bract of eudoxid
'Carnegie VII' 31° 54′ S., 88° 17′ W.	64	1000–0	1 nectophore

Moser (1925, p. 122) gave a complicated account of the gonophore, which in some respects does not fit the facts as I have checked them. It is important to separate descriptive matter from hypothesis about phylogeny. The simple fact seems to be that the dorsal and lateral radial canals of the nectosac of the gonophore do not underlie the respective ridges, but are disposed much as in abyline gonophores. It is quite unnecessary, therefore, to put forward such a fantastic hypothesis as that used by Moser.



Text-fig. 71. *Heteropyramis maculata.* A, eudoxid, 'Discovery' St. 129, 950–780 m.; A′, diagrammatic transverse section of gonophore, B, C, bract of eudoxid, 'Discovery II' St. 2927, 750–500 m.; D, nectophore, 'Discovery II' St. 2927, 750–500 m. All figures × 15.

She supposes that a four-ridged gonophore of Diphyid type (Moser's text-fig. 28 I) is rotated through 45° on its longitudinal axis and that the right ventral ridge then comes into collision with the stem and divides into two to give a five-angled gonophore. She denied what seems to be the truth that there is present an extra dorsal ridge as in Abylinae.

Both polygastric and eudoxid stages of *Heteropyramis* suggest affinities with *Chuniphyes* and Abylinae. In particular the gonophore has a median dorsal ridge, and the two interesting basal vessels of the phyllocyst not only can be homologized with the pair of basal vessels in the phyllocyst of the peculiarly small bract of *Chuniphyes* spp. but also with the 'horns' of the phyllocyst of *Ceratocymba* spp. and other Abylids.

On 8 June 1952, after the completion of this report, 'Discovery II' took two even more perfect specimens of *Heteropyramis maculata* together with two 'spotted' eudoxids at Station 2927. The accompanying Text-fig. 71 of one of these nectophores shows the very close similarity between nectophores of this species and those of *Thalassophyes crystallina*. In fact the only significant difference seems to be in the presence or absence of the spots. The distribution of opaque spots on the two eudoxids is as follows: an apical spot on the bract, a spot at the base of each dorso-lateral ridge of the bract, and a spot at each end of the two dorso-lateral ridges of the gonophore.

Thalassophyes crystallina Moser, 1925. (Text-fig. 72.)

Moser (1925) described this species from two anterior nectophores only, one from 2000 m., at 'Gauss' Station in the Antarctic, and the other from an unknown locality. It has not been recorded since except by Leloup (1934*a*), who identified one anterior nectophore taken at 'Meteor' Station 56, from a depth of between 800 and 600 m., to the north-west of South Georgia. It occurred at 'Discovery II' Stations 1568, 1585, 1588 and 1589, in the Indian Ocean. At Station 1585 it occurred in a closing-net haul made between 1400 and 700 m.; at Station 1588 in a closing-net haul made between 500 and 200 m.; and at Station 1589 in two open hauls from 600 m. to the surface. Since this is a little-known species, I give all the other unpublished records that I have accumulated:

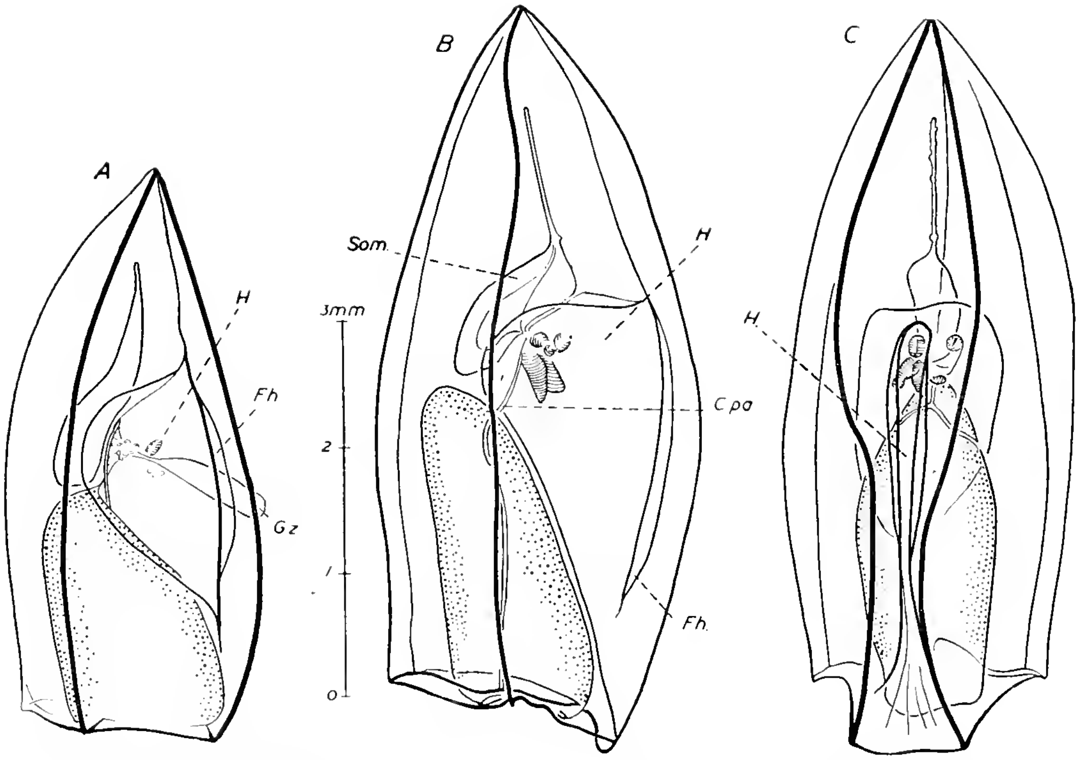
'Discovery' Stations, closing-net hauls. 100 A (625–675 m.); 100 C (450–550 m.); 102 (750–500 m.); 107 (1000–750 m.). *'Discovery II'* 300 (1000–750 m.); 311 (500–250 m.); 343 (500–250 m.); 344 (500–250 m.); 357 (750–500 m.); 661 (750–500, 1000–750 m.); 663 (750–500, 1000–750, 1500–1000 m.); 666 (1000–750 m.); 671 (1500–1000, 2000–1500 m.); 1617 (395–155 m.); 1624 (350–210 m.); 1627 (580–400 m.); 1633 (1100–875 m.); 1639 (2400–1150 m.); 1723 (800–500 m.); 2024 (650–400 m.); 2636 (950–550 m.); 2639 (1200–600 m.); WS 26 (1000–750 m.); WS 36 (750–500 m.).

Anterior nectophores have been taken in closing-net hauls:

Metres	'Discovery' Station	No. of specimens
2000–1500	671	3
1500–1000	663	2
	671	6
1400–700	1585	1
1000–750	300	1
	661	8
	663	1
	107	1
	WS 26	2
750–500	102	1
	357	2
	661	5
	663	2
	WS 36	1
675–625	100 A	3
650–400	2024	1
550–450	100 C	2
500–250	311	1
	343	1
	344	1
500–200	1588	1
'Scotia', 1951, Haul 363		
1000–250	—	1

In open hauls:

	Stations	Depth (m.)	Material
'Discovery'	87	1000(–0)	1 nectophore
	100	475(–0)	3 nectophores
	208	800(–0)	1 nectophore
'Discovery II'	669	2000(–0)	1 nectophore
	1589	600–0	2 nectophores
British Antarctic ('Terra Nova' Expedition), 1910–13	285	600–0	2 nectophores
Irish Fishery Board	SR 175 (40 miles N.W. of Eagle I., Co. Mayo, Ireland	1097–0	2 nectophores



Text-fig. 72. *Thalassophyes crystallina*. A, lateral view of specimen from 'Discovery II' St. 1588, 500–200 m., ×16; B, C, lateral and ventral views of a specimen from 'Discovery' St. 102, 750–500 m., ×16.

The nectosac in this species is only half the length of the nectophore, and the dorsal extension of the somatocyst is found just above its apex.

Comments have been made above, in the notes on *Heteropyramis maculata*, upon the close relationship between the two species.

ABYLIDAE

I recognize the family Diphyidae to be distinct from the Abylidae, which contains two subfamilies: (1) Abylinae (for *Abyla* and *Ceratocymba*), and (2) Abylopsinae (for *Abylopsis*, *Bassia* and *Enneagonum*).

On 15 June 1953, when I was awaiting the galley-proofs of this report, I received Dr Mary Sears's 'Revision of the Abylinae' of which she had already been kind enough to allow me to see an advance copy. I had tried to persuade Dr Sears not to publish the descriptions of what I believe to be eight abnormal specimens as the type material of new species and genera. The new names in question are: (1) *Pseudabyla irregularis*; (2) *Pseudabyla dubia*; (3) *Pseudocymba asymmetrica*; (4) *Pseudocymba* *anomala*; (5) *Abylopsoides ventralis*; (6) *Abylopsoides dorsalis*; (7) *Abylopsoides basalis*; (8) *Pseudabylopsis anomala*.

Judging by figures all the specimens so named belong to species of *Abyla*, *Ceratocymba* or *Abylopsis* whose development has been abnormal. I have come across such specimens very occasionally myself. They will be of interest to those who study organogeny, but I feel that it was unnecessarily confusing to give them new specific and generic names.

From what little attention I have been able to devote to their analysis I am inclined to believe that, for instance, in *Pseudocymba asymmetrica* (Sears's text-figs. 23 D, E) the sagittal area of the anterior nectophore has been suppressed, and that there has been an overgrowth of one of the sides bordering on it; and that in *Pseudabyla dubia* (Sears's text-fig. 17 F) one of the margins of the dorsal facet has been suppressed. But we have no knowledge, at present, of what organizers may have been upset during the ontogeny of the specimens. In my opinion if the specimens represented new species, we should find in anterior nectophores of known species just that sort of constant tendency towards variation which has the functional potentiality that seems to appear in the hydroecial folds of the posterior nectophores. Also specimens of *Abyla* spp., *Ceratocymba* spp. and *Abylopsis* spp. are very abundant, but these crazy specimens are very rare, and none of them have the appearance of normal healthy specimens: it is not their rarity alone that makes me think that they are freaks. I can only record my regret that Dr Sears finally decided to make this abnormal material into the types of new species and genera, since I fear it will cause much confusion amongst systematists.

Dr Sears has brought together much old and a great deal of new data on Abyline species, but the animals appear to be exceptionally variable, and this is only the starting point of our inquiries. The figures are very clearly drawn, but were not made, I understand, with a camera lucida. Those of anterior nectophores do not perhaps bring out the fact that asymmetry is the rule. My own analysis (p. 144) of the homologies of ridges in posterior nectophores leads me to affirm that in *Ceratocymba* spp. the dorsal ridge is present, whilst it is absent in *Abyla* spp. Dr Sears evidently holds the opposite view. For the sake of any systematist who tries to compare Dr Sears's descriptions with my own I should mention that in her very useful figure 5 (p. 14) the following synonyms must be borne in mind:

Dr Sears's terminology:	*Terminology of this report:*
Dorsal ridge	Left lateral ridge
Left lateral ridge	Right lateral ridge
Right ventral wing	Left ventral wing
Left ventral wing	Right ventral wing
Right lateral tooth	Left lateral tooth

Abundant material of Abylid eudoxids is available in the Brit. Mus. (Nat. Hist.) Collection. Systematists would be very grateful for a revision which would enable them to identify and relate them with their corresponding polygastric stages.

ABYLINAE

Abyla

The species of *Abyla*, as that name has been generally used, fall naturally into two groups, which should be given generic status. The chief characteristics of the two groups are as follows: in the species of the *Ceratocymba* group, namely *C. sagittata*, *C. dentata* and *C. leuckartii*, the eudoxid is a '*cymba*', and the posterior nectophore has left and right dorso-lateral ridges terminating on the lateral teeth. There is a short, median-dorsal ridge terminating in the dorsal tooth. In the species of the *trigona*-group namely *Abyla trigona*, *A. carina*, *A. haeckeli*, *A. bicarinata* and *A. schmidti*, the eudoxid, where it is known, is an '*amphiroa*'; and in the posterior nectophore, what appears to be the homologue of the left[1] ridge in the *Ceratocymba* group, runs down to the mid-dorsal tooth, and not to the left tooth. In species of *Abyla* (*sensu stricto*), but not in those of *Ceratocymba*, the ventro-lateral facet of the anterior nectophore is divided by a horizontal ridge.

As far as I can follow Moser (1925, p. 314) she said that the condition of the teeth and ridges at the distal end of the posterior nectophores of *C. sagittata* and *C. leuckartii* is the most primitive and most like *Diphyes*, and I agree with her. In *Ceratocymba dentata* she said that the median dorsal (Moser's ventral) ridge has shortened and is displaced to the right, together with the middle (dorsal) tooth. In *C. dentata* I have not seen such a displacement to the right, but I have seen a slight displacement towards the left. In *C. leuckartii*, however, the middle tooth is much closer to the left lateral than to the right lateral ridge. Moser appeared to believe that in the *trigona*-group the dorsal (Moser's ventral) ridge and dorsal tooth had disappeared altogether, that the tooth at the oral end of the left lateral ridge is the left lateral tooth, and that the tooth furthest to the left is a new structure, the 'pseudo-tooth'.

In reality I think that the middle tooth and the distal end of the left lateral ridge have come together so that the left lateral tooth has no corresponding ridge (Pl. IX, fig. 4). The beginning of the process can be seen in *C. leuckartii*, where the left ridge and middle tooth are close together. In fact, in *C. leuckartii* Moser's joint left and right ('ventral') dorsal facets are present just as they are in *C. dentata*. But the middle (median dorsal) tooth is at the left margin of this joint dorsal facet in the *trigona*-group instead of in its middle line as in *C. dentata*. One might almost say that in the *trigona*-group the reduced median dorsal ridge and tooth have coalesced with the left lateral ridge. Moser thought that the dorsal (her ventral) tooth had completely disappeared, together with its ridge, and that a 'pseudo-tooth' had been developed on the left side to compensate for this. But there is no need to invent a 'pseudo-tooth', for of course in all abylines there are three dorsal teeth at the distal end of the posterior nectophore, and it seems to be so much more probable that they are homologous structures in all species.

One of the most striking features of the nectophores of abylines is the peculiar angle between the dorso-ventral planes of the anterior and posterior nectophores. Viewed from aft (Pl. IX, fig. 4), the distal end of the posterior nectophore in some species is twisted clockwise through an angle of from 55° to 90° so that the dorsal sides of the two nectophores are no longer opposite one another. The twisting is accompanied by a progressive broadening of the left wing of the hydroecium in species of the *trigona*-group. Here, too, the distal edge of the broad left wing is marked by a double row of spines, an inner and an outer row as can be seen from a distal and ventral view. These two rows of spines are much better marked in *Ceratocymba dentata* (Pl. X, figs. 4, 5).

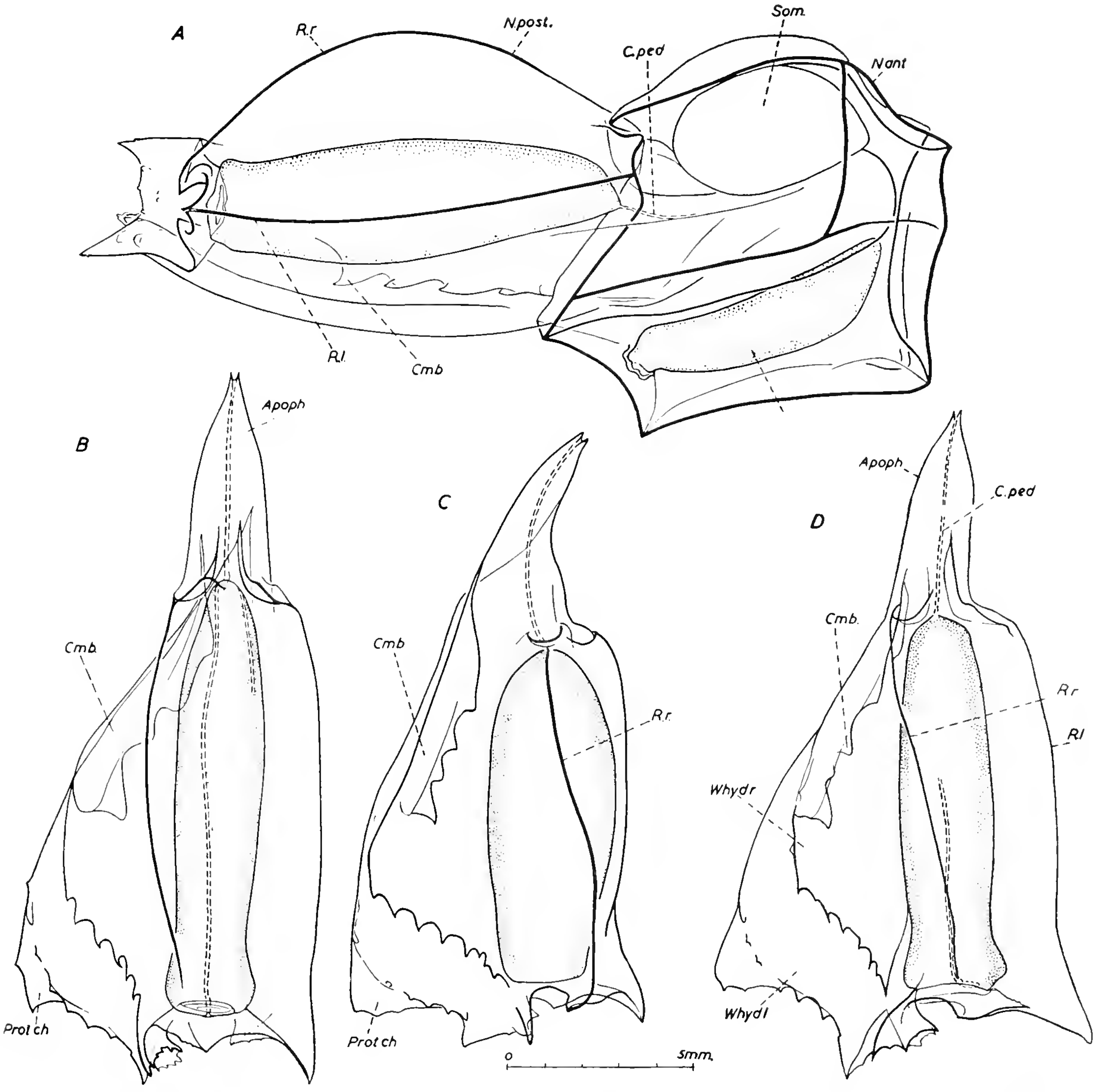
The starting-point of this evolutionary trend of axis-twisting and wing-broadening can best be seen in the homologous structures of the posterior nectophore of *Diphyes dispar*, where the distal edges of both right and left wings of the hydroecium are formed into a flattened area without any trace of spines. In that species the ventral edges of both hydroecial wings reach the level of the velum and then bifurcate, turning distad to form the flattened area just described.

No specimens of those species of the *trigona-carina* type occurring in the Atlantic have been found in the 'Discovery' material from the Indian Ocean, though Dr Sears (1953) has recorded the capture of *A. trigona* from that ocean at 'Dana' Stations 3920, 3921 and 3955. The specimens consisted of one

---

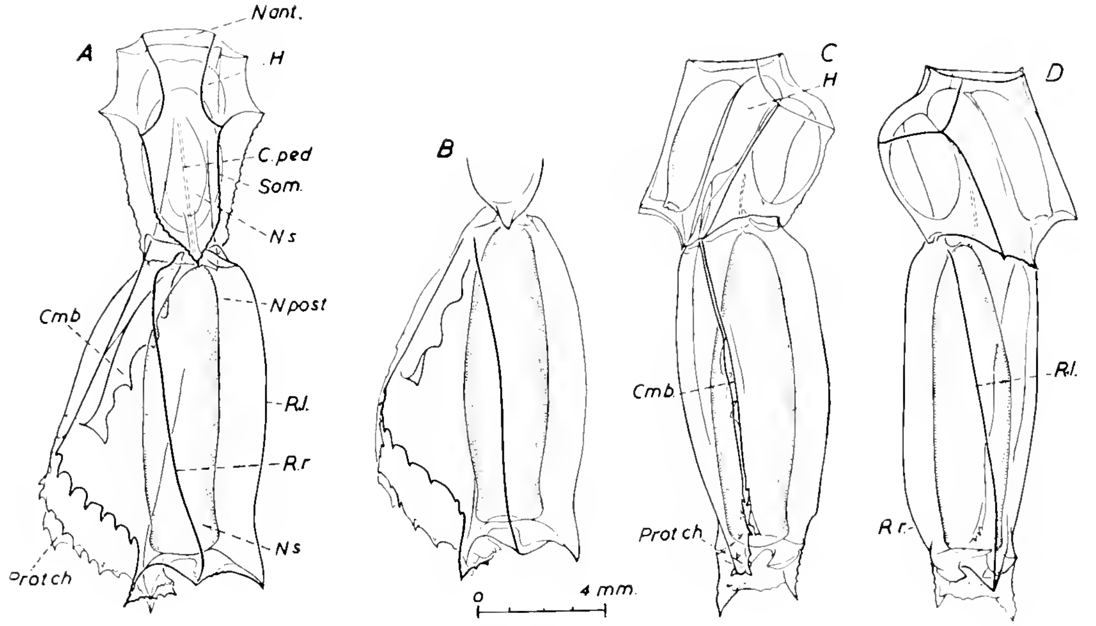
[1] My terminology differs from that of Bigelow & Sears (1937, p. 4) because I use the same orientation (oral and aboral) for an adult as for a larva, where it is self-explanatory. Unfortunately these animals progress with the aboral end forwards. By a very old convention the ventral side of a larva is the one on which budding first appears. 'Ventral' has thus become to be synonymous with adaxial, and 'dorsal' with abaxial. As far, then, as orientation of posterior nectophores of diphyids is concerned my 'left' and Moser's 'left' corresponds with Bigelow's 'right' and Sears's 'right'.

colony and seven anterior nectophores. In my opinion, anterior nectophores of *A. schmidti* cannot be distinguished with certainty from those of *A. trigona*. *Abyla schmidti* (Text-figs. 73, 76, 77), though common in the Tropical Indian Ocean has not been noted hitherto in the North Atlantic except at 'Dana' Station 4762. This record perhaps needs checking. There is however an allied form in the western South Atlantic (Text-fig. 74).

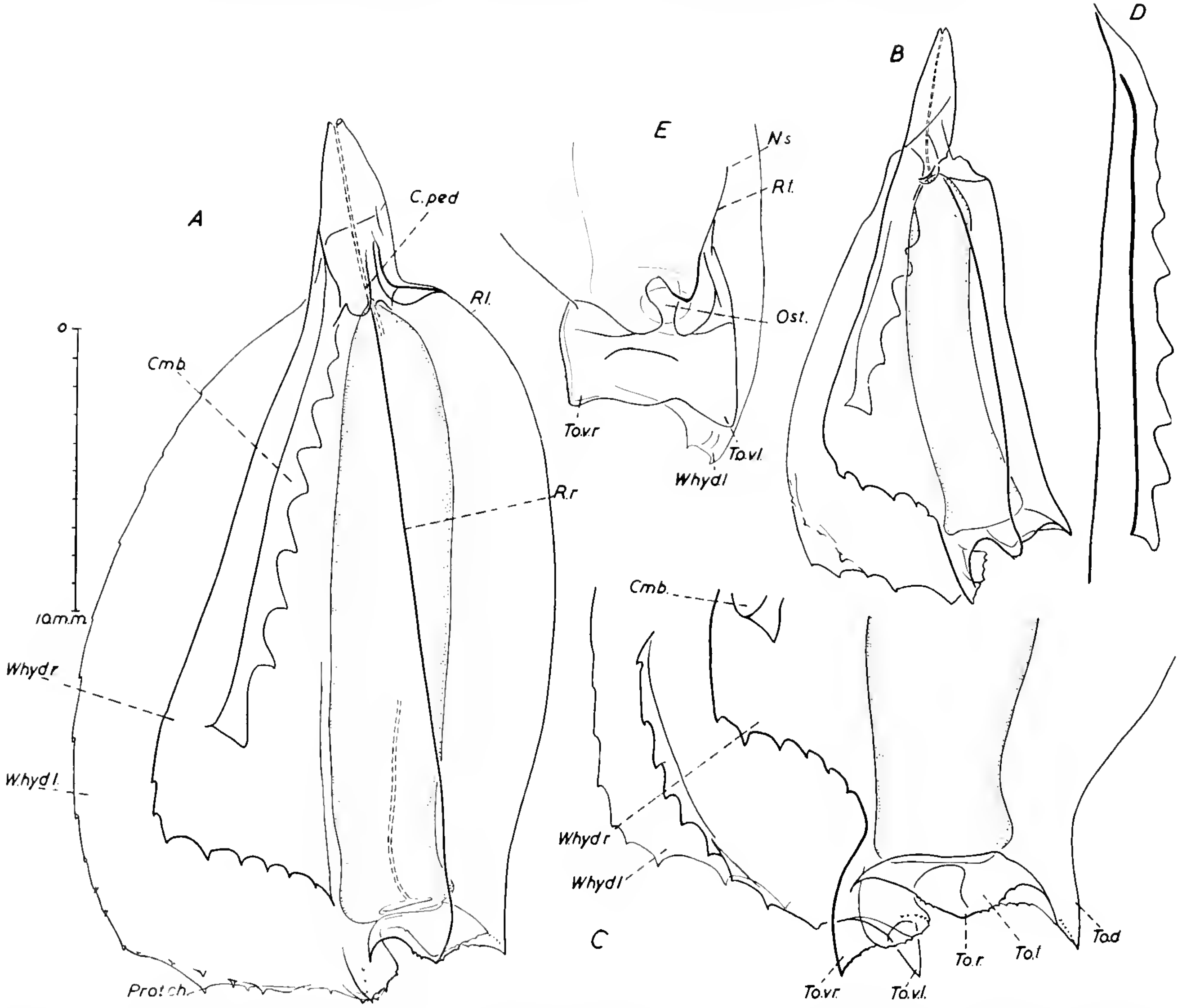


Text-fig. 73. *Abyla schmidti* Sears. A, specimen from 'Discovery II' St. 1581 (base of right-hand side slightly restored), ×6·4; B, C, D, posterior nectophores; B, 'Discovery II' St. 1587, ×6·4; C, 'Mabahiss' St. 131, ×6·4; D, 'Discovery II' St. 1585, ×6·4. In fig. D, the break in the apophysis indicates shortening of total length.

So far as I can tell at present, there appears to be more than one species of *Abyla* with anterior nectophores similar to those figured by Quoy & Gaimard (1827, pl. 2, *B*, figs. 1–8), Gegenbaur (1859),



Text-fig. 74. *Abyla* sp. aff. *trigona* from Tropical Atlantic. A, complete specimen from 'Discovery II' St. 711; B, C, D, different views of a specimen from 'Discovery II' St. 709. A–D × 4·2.



Text-fig. 75. A, *Abyla trigona*, posterior nectophore, 'Discovery II' St. 2067, Canaries, × 4·2; B, *Abyla carina*, part of 'Challenger' material, posterior nectophore; C, *Abyla tottoni*, basal part of posterior nectophore, × 5·2, 'Discovery II' St. 1178, eastern South Atlantic; D, *Abyla trigona* Q. & G., comb of right ventral hydroecial wing of posterior nectophore, part of type material (Mus. d'Hist. Nat. Paris); E, same, dorsal view of base of posterior nectophore to show ventral teeth, × 5·5.

and Bigelow (1911*b*) for *A. trigona*. Fortunately Quoy & Gaimard's types have been preserved at Paris (Text-fig. 75 D, E) and thanks to the good offices of the authorities there,[1] have been re-examined by both Dr Sears of Woods Hole and myself. At the moment, I have found no reliable criteria for separating the anterior nectophores of species of the *trigona*-group, though they are associated with several readily distinguishable types of posterior nectophores. As stated before, the distal (oral) end of the left (larger) hydroecial fold of the posterior nectophore of species in this *trigona-carina* group of species carries two marginal rows of spines. It appears that there is a tendency for the outer margin to overgrow the inner margin, so that a protuberance is formed as figured by Moser (1925) for *A. bicarinata*. The relative size and shape of this protuberance, together with the number of spines on the margins and the number of large spines or teeth on the infolded flap, '*Leiste*' or 'comb' of the right hydroecial wing, may well be found to have specific significance.

As a result of long and tedious work it appears that, in the Indian Ocean, there are six abyline species, *Ceratocymba dentata*, *C. leuckartii*, *Abyla haeckeli*, *A. trigona* and the two new ones *A. schmidti* and *A. ingeborgae*.

Dr Mary Sears kindly kept me informed in letters of her intention to publish a revision of the Abylinae and gave me some of her views on the subject. I sent Dr Sears copies of some of my figures, and also one or two specimens. Dr Sears also sent me copies of her figures and finally a copy of her text. Her paper (1953) reached me on 15 June when I was awaiting galley-proofs. In it, one of my supposed new species will be found described and named after Dr Johannes Schmidt.

Abyla schmidti Sears 1953. (Plate VIII).

Posterior nectophores resembling one taken by 'Gauss' to the south-east of Madagascar and figured by Moser (1925, pl. XIX, figs. 7–9) were taken at several East African 'Discovery II' Stations between lats. 7° S. and 11° 32′ N. With two detached anterior nectophores Moser named her posterior nectophore *A. bicarinata*. In one haul only ('Discovery II' Station 1581, 600–0 m.) an anterior nectophore was found still attached to a posterior one of this kind, and this complete specimen (Text-fig. 77A) I had designated the holotype of a new species, now *schmidti* Sears. Dr Sears has shown that Moser's figured anterior and posterior nectophores belong to separate species, the posterior one is *A. schmidti*. I now choose the larger of Moser's anterior nectophores as the holotype of *A. bicarinata* Moser.

Moser, did not, I think, figure the velar end of the posterior nectophore very critically, unless the specimen was a dead, disintegrating one such as one finds sometimes in the plankton; but her fig. 7 shows a characteristic, distal, chin-shaped protuberance of the left hydroecial wing. It extends considerably more distad than in any of the 'Discovery' specimens, even than in those which have begun to disintegrate and were presumably mature.

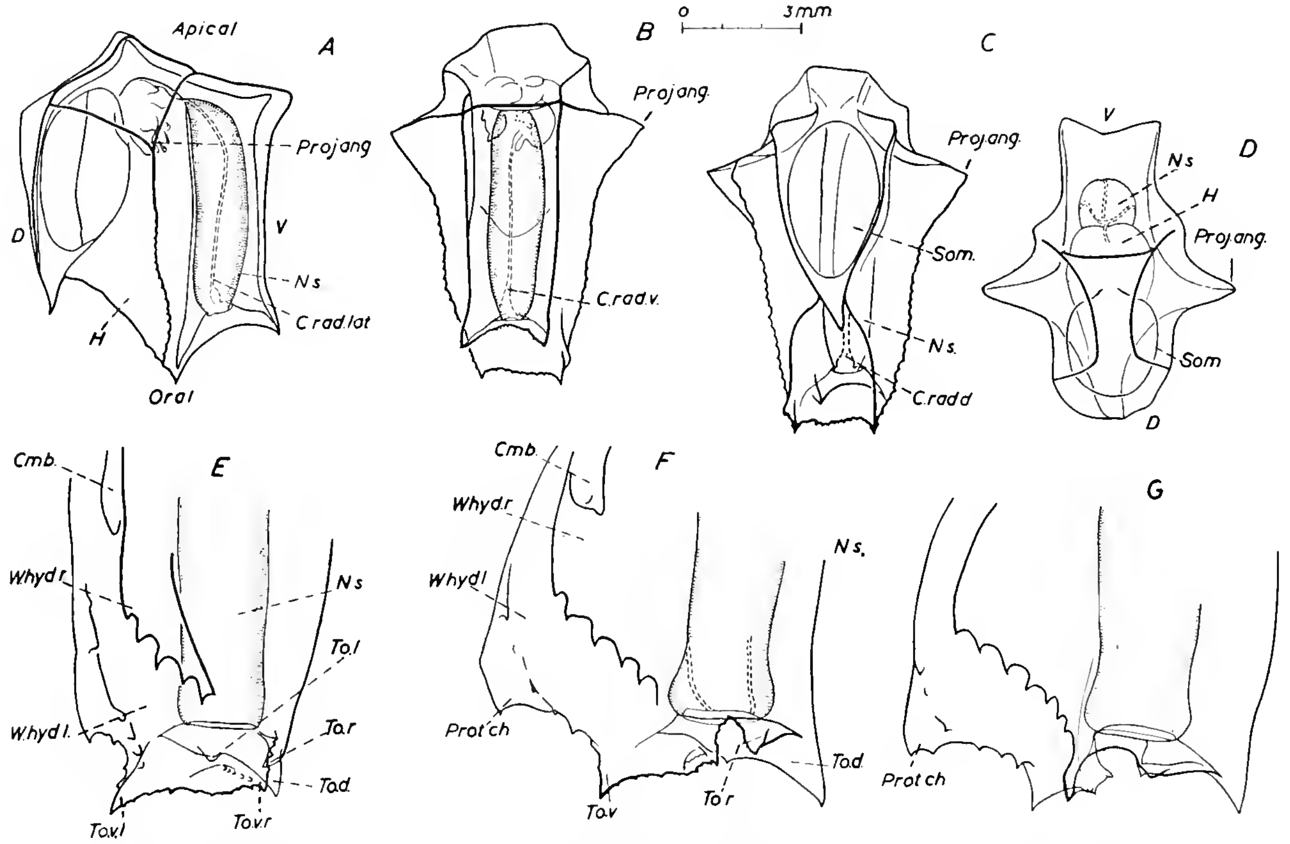
I have not so far found posterior nectophores like those described and figured above (Text-figs. 73, 76, 77) as *A. schmidti*, except in material from the Indian Ocean, and certainly not from the region of the Canaries, where the types of both *A. trigona* and *A. carina* were found. Specimens of those two species (probably one and the same) grow to a size much greater than any of the Indian Ocean specimens that I have seen. But specimens of an intermediate type (Text-fig. 74) were found in the Tropical Atlantic. Much *Abyla* material is now available for some student of the future.

Eudoxids. No entirely satisfactory figures have been published of the eudoxid (*Amphiroa* Blainville) of any species of the *trigona*-group of *Abyla* to which *A. schmidti* belongs. The earliest, Blainville's (1834) copy of Lesueur's unpublished drawing of a Bahaman specimen named *alata* by Blainville (1830), omits details of the hydroecial wings and folds or *Leisten*. Huxley's (1859) figures are more

---

[1] I have to thank Dr A. Franc for much help in this matter.

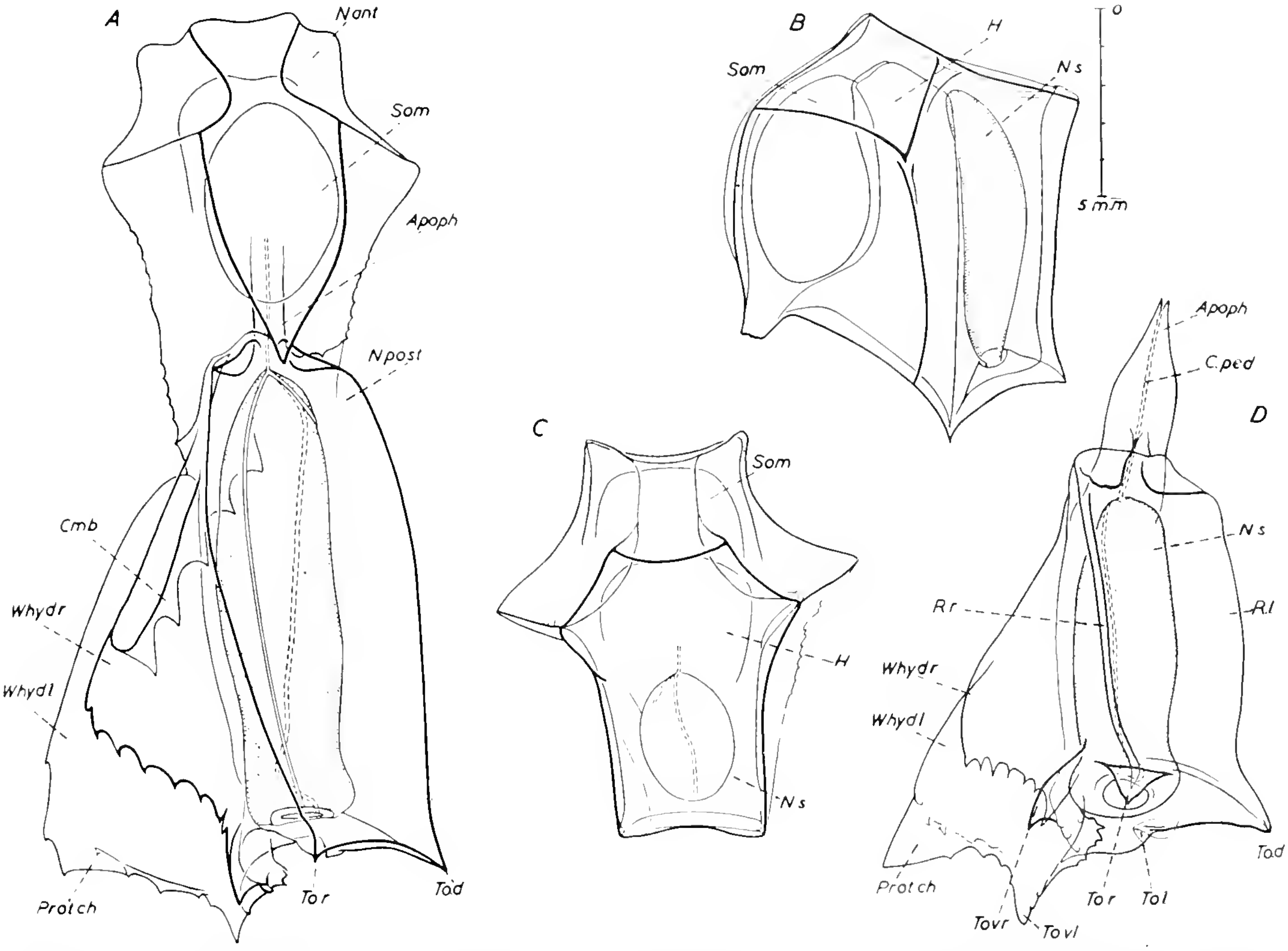
characteristic, whilst Gegenbaur's (1859) are not so satisfactory as Huxley's. Haeckel (1888*b*) gave more elaborate drawings of *A. carina*, but the gonophores were not shown with sufficient detail. Bedot (1896) figured the only bract he saw at Amboina, but not the gonophores. Lens & van Riemsdijk (1908) again failed to give details of gonophores. Moser (1925) was the first to give a detailed sketch of the gonophores, but did not show an optical section of the mouth-plate from the side, a detail that is necessary for specific identification. In Part v of Kawamura's (1915) paper on Caliconectid Siphonophorae (translated in typescript by Rodney Notomi, and a copy generously presented to me by Woods Hole Oceanographic Institute), there are some useful original figures of Abylines. Figs. 27 and 28 of plate xv, labelled *A. trigona* from Misaki are good, but these again omit essential details of the gonophores.



Text-fig. 76. *Abyla schmidti*. A, B, C, D, different views of a detached anterior nectophore from 'Discovery II' St. 1588 250–100 m., × 5·5. Note the slight asymmetry characteristic of all such nectophores; E, F, G, three views of distal end of a posterior nectophore from 'Discovery II' St. 1587.

For comparison with the new Indian Ocean species of *Abyla schmidti* I give figures of the following: (1) type specimens of *A. trigona* Q. & G., kindly lent by the Muséum d'Histoire Naturelle, Paris (Pl. XII); (2) type specimens of *A. carina* Haeckel (Text-fig. 75 B); (3) a specimen of *A. trigona* from 'Discovery II' Station 2067 (Text-fig. 75 A), all these three from the Canaries region of the Atlantic; (4) a specimen of a related species *A. tottoni* Sears from 'Discovery II' Station 1178 in the eastern South Atlantic (Text-fig. 75 C); (5) another related but unnamed new species from 'Discovery II' Stations 709 and 711 in the western South Atlantic (Text-fig. 74).

Dr Sears states that both Quoy and Gaimard and Haeckel were confusing two (the same two) species in their accounts of *A. trigona* and *A. carina*. Her argument is that (1) Quoy and Gaimard's type anterior nectophores were too small to have been linked to the type posterior nectophores, which probably do not belong to them, (2) Quoy and Gaimard's type anterior nectophores resemble (*a*) some of Haeckel's Challenger [not type] specimens, and (*b*) some 'Dana' specimens, some of both (*a* and *b*) of which have small inferior nectophores attached within the hydroecium. (3) These 'Challenger' and 'Dana' young inferior nectophores differ from those inferior nectophores amongst Quoy and Gaimard's types. (4) One of Haeckel's 'Challenger' colonies (complete) has an inferior nectophore resembling Quoy and Gaimard's types. (5) It thus seems certain that these are the same two species in both Quoy and Gaimard's and Haeckel's samples. But Dr Sears does specify the resemblances and differences alluded to. She goes on to say that (6) Lens and van Riemsdijk (1908) can be considered to have designated the superior nectophores of Quoy and Gaimard as the types of *Abyla trigona*, because they compared their specimens of anterior nectophores of '*Abyla trigona*' [in my opinion probably *A. schmidti*, A.K.T.] with those of Quoy and Gaimard and found them to be identical 'in all respects' [Dr Sears refers Lens & van Riemsdijk's posterior nectophores of '*Abyla trigona*' to *A. schmidti*]. (7) Since the inferior nectophores of Quoy and Gaimard's types apparently belong to the same species as the complete colony and three superior nectophores in Haeckel's 'Challenger' sample [in B.M. Coll.], she considers it appropriate to designate these as *carina*.



Text-fig. 77. *Abyla schmidti* Sears. A, specimen from 'Discovery II' St. 1581, × 5·5; B, lateral view of anterior nectophore, 'Mabahiss' St. 131, × 5·4; C, view from above of some specimen as A, × 5·5; D, baso-lateral view of posterior nectophore from 'Discovery II' St. 1585, × 5·6.

From this I gather that Dr Sears regards Haeckel's 'Challenger' anterior nectophores (but not the posterior ones) and Quoy and Gaimard's type posterior nectophores (but not anterior ones) as *Abyla* *carina*, nevertheless she regards Haeckel's *carina*, if I understand her correctly, as *trigona*, yet she uses Haeckel's figure of his type *carina* as one of her criteria for distinguishing the posterior nectophore of *carina*. As other criteria for separating the posterior nectophores of the species, Dr Sears refers to (1) the ventral teeth, elongate, heavily serrated, straight and sharp in *trigona* but 'stubby' in *carina*; (2) comb with 6–8 teeth in *trigona*, 9–10 teeth in *carina*; (3) margin of ventral wing with heavy and prominent teeth in *trigona*, but not so robust and jagged in *carina*, and scarcely more than strong serrations; (4) width of the nectophore half its length in *trigona* but nothing in its general shape to distinguish that of *carina*; (5) an overgrowth of the outer ventro-basal margin of the larger of the ventral wings in *carina*. In her own words 'the inner row of nine or ten small spines is parallel to the basal margin close to the two ventral teeth but ventrad it gradually swerves inwards a short distance from the margin crossing the inner surface to merge with the outer row at the ventral margin, much as is shown in one of Haeckel's drawings (1888*b*, pl. 35, fig. 1)'.

New records of Abyla schmidti

	Depth (m.)	Polygastric			Eudoxid		
		Complete	Anterior nectophore	Posterior nectophore	Complete	Bract	Gonophore
'Discovery II' Station							
1374	230–0	—	—	1	—	—	—
1581	100–50	—	1	—	—	—	—
	600–0	1	4	—	30	—	15
1582	1900–1850(–0)	—	7	4	—	—	—
1583	250–100	—	—	—	1	—	—
1585	500–0	—	4	1	10	—	10
	1400–700	—	—	—	—	—	1
1586	1650–900	—	2	1	—	—	—
	550–0	—	1	3	1	2	8
	100–50	—	—	—	1	—	1
	50–0	—	—	1	—	—	1
1587	1250–800	—	1	1	—	—	—
	450–0	—	4	2	1	1	1
	50–0	—	—	1	—	—	—
1588	250–100	—	1	1	—	—	—
1589	600–0	—	—	1	—	1	—
1750	1900–0	—	—	1	—	—	—
'Mabahiss' Station							
131D	2500	—	1	1	—	—	—
	1500	—	2	2	—	—	—
	500–0	—	1	—	2	—	1
131A	600–0	—	1	—	2	—	—

We know nothing of Haeckel's actual type specimens, though the 'Challenger' ones still exist at the Brit. Mus. (Nat. Hist.). Therefore we have to depend entirely for data on the 'Challenger' figures and description of the Lanzerote type specimens. I am not satisfied as yet that *A. carina* Haeckel is not a synonym of *A. trigona* Quoy and Gaimard. Chun (1888*a*) said that *A. trigona* occurred in great swarms in the Canaries at the end of February and in March. Even the eight anterior nectophores of Haeckel's type material show variation in the shape of the dorsal tooth and in other respects. In the adults of both species the general shape of the nectophores is the same, there are nine or ten teeth on the comb of the right ventral wing, and the shape of the ventral teeth is the same. It is true that in a young posterior nectophore of one of the 'Challenger' specimens of *A. carina* which is only just emerging from the hydroecium of the anterior nectophore, the ventral teeth are relatively longer, narrower and more spiny, but this difference is probably a matter of age and growth.

In order satisfactorily to delimit species of the *A. trigona* group, much statistical analysis will have to be made on large samples of swarms.

Dr Sears has already published a description of another new species of this group.

Abyla tottoni Sears, 1953. (Plate IX.)

Dr Sears recorded the capture in 1930 of 27 complete colonies, 30 anterior and 19 posterior nectophores of *Abyla tottoni* at three 'Dana' stations in the subtropical South Atlantic, as well as one anterior nectophore from between 'Timor and New Guinea'.

'Discovery II' took 12 complete colonies, five anterior and six posterior nectophores and three eudoxids of this species in 1933 at Station 1178 close to one of these 'Dana' stations; and a young specimen (post. nect. 15 mm. l.) some 1500 miles further west in the same region at Station 686.

The whole margin of the larger ventral wing may be serrated. There may be from 12 to 13 teeth on its inner basal margin, and from 11 to 13 teeth on the basal margin of the smaller wing, the ventral corner of which, between comb and base, is more rounded than shown by Dr Sears (fig. 15B). The number of comb teeth may be as large as 12. But it is difficult to count comb teeth at the apical end, and to agree on the number when there are smaller intermediate teeth, or the final apical one is not well marked.

This appears to be a distinguishable species, and I had already marked it as a new one.

Abyla haeckeli Lens and van Riemsdijk, 1908.

Until Dr Sears published her revision of the Abylinae I had assumed that all anterior nectophores of *Abyla*, in which the apico-ventral facet was subdivided by a transverse ridge, belonged to the species *haeckeli*. Whilst this report was in the press I re-examined my figured material. All the anterior nectophores from 'Discovery II' E. African stations are relatively small, and have the type of ventral facet described and figured by Dr Sears for *haeckeli*. All the specimens from 'Discovery II' Atlantic stations are relatively large, and have a ventral facet of the type described and figured by Dr Sears for *ingeborgae*. I am hoping that these two forms will prove to be quite distinct species, though Browne's specimens seem to be intermediate.

Dr Sears (1953) has published a figure of a young posterior nectophore for the first time. She appears to have examined 10 colonies, 553 anterior nectophores and 51 posterior nectophores from 38 'Dana' hauls. This should be a good sample, and it is hoped that some one will have time to establish the range of specific variation.

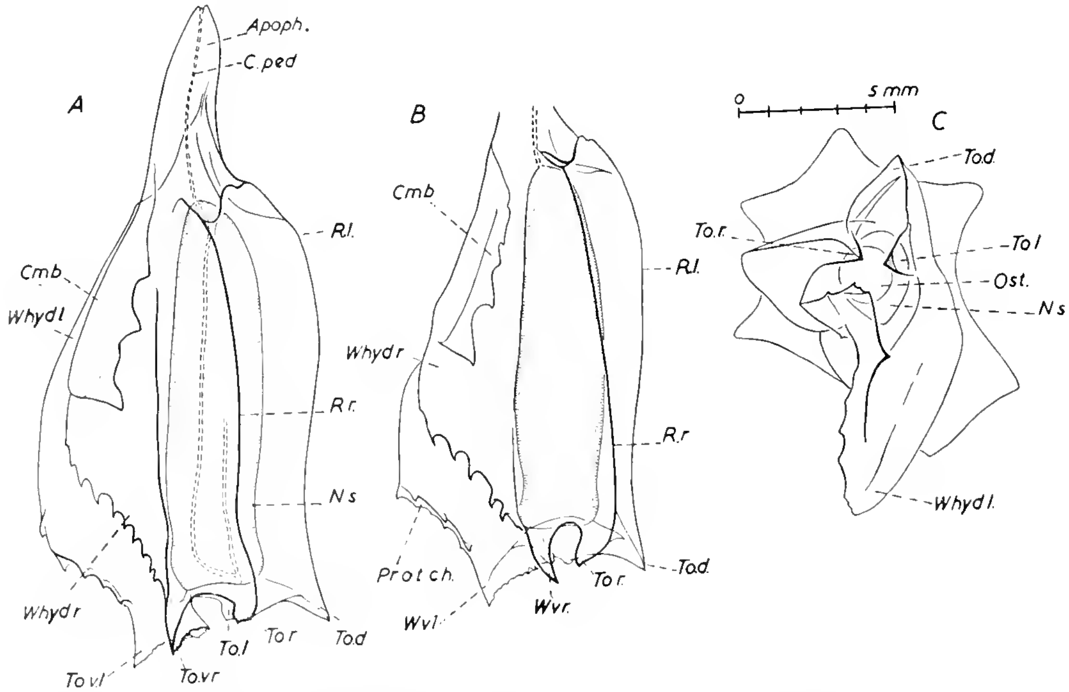
I have re-examined the three anterior nectophores described by Browne (1926). Two of them measure 6·1 mm. in length, the third measures 6·9 mm. One of these, specimen 'A' is 4·6 mm. wide, but two are rather squashed, and their width cannot be measured. Specimen 'A' is in good condition and the horizontal ridge in side view is only *slightly* above the middle of the somatocyst (1/1·1). Dr Sears's critical proportions of the pentagonal ventral facet, namely width-between-middle-corners/length-from-middle-corners-to-tip are as follows: 1/0·65, 1/0·75, 1/0·82. The proportions of the facet figured by Dr Sears (fig. 13D, E) for *A. haeckeli* were 1/0·57 and for *A. ingeborgae* 1/1·1. On the basis of these last two characters, as well as that of the ventral view, Browne's specimens are intermediate between Dr Sears's figs. 13D and E. The total size, the relative size of the apico-ventral facet, and the size and position of the lateral projections lead me to conclude that they belong to *A. haeckeli*.

It is certain however, that specimens of *Abyla* spp. will not all fit neatly into Dr Sears's proposed categories.

I have also re-examined the anterior nectophore recorded by me (1932) from the Great Barrier Reef. The proportions of the pentagonal facet are 1/0·63, and I confirm that it belongs to *A. haeckeli*. It happens to be another of those partly injured or disorganized freaks that Dr Sears has brought to notice.

Abyla ingeborgae Sears, 1953.

Complete specimens of this species at 'Discovery' Stations 295 and 297 and at 'Discovery II' Station 699, which enabled me to identify loose posterior nectophores (Text-fig. 78) from Stations 706 and 2639. Until the publication of Dr Sears's paper, I had identified all these Atlantic specimens as *A. haeckeli*, but anterior nectophores of the two types, *haeckeli* and *ingeborgae*, can sometimes be separated at once. A good figure of the full grown posterior nectophore of *A. haeckeli* is needed for comparison with that of *A. ingeborgae*.



Text-fig. 78. A, B, posterior nectophores of *Abyla ingeborgae* Sears, × 3·8, from 'Discovery II' Sts. 706 and 2639 (1200–600 m.) respectively, each associated with anterior nectophores of that type; C, basal view of posterior nectophore of holotype specimen of *Abyla schmidti* Sears from 'Discovery II' St. 1581, × 4.

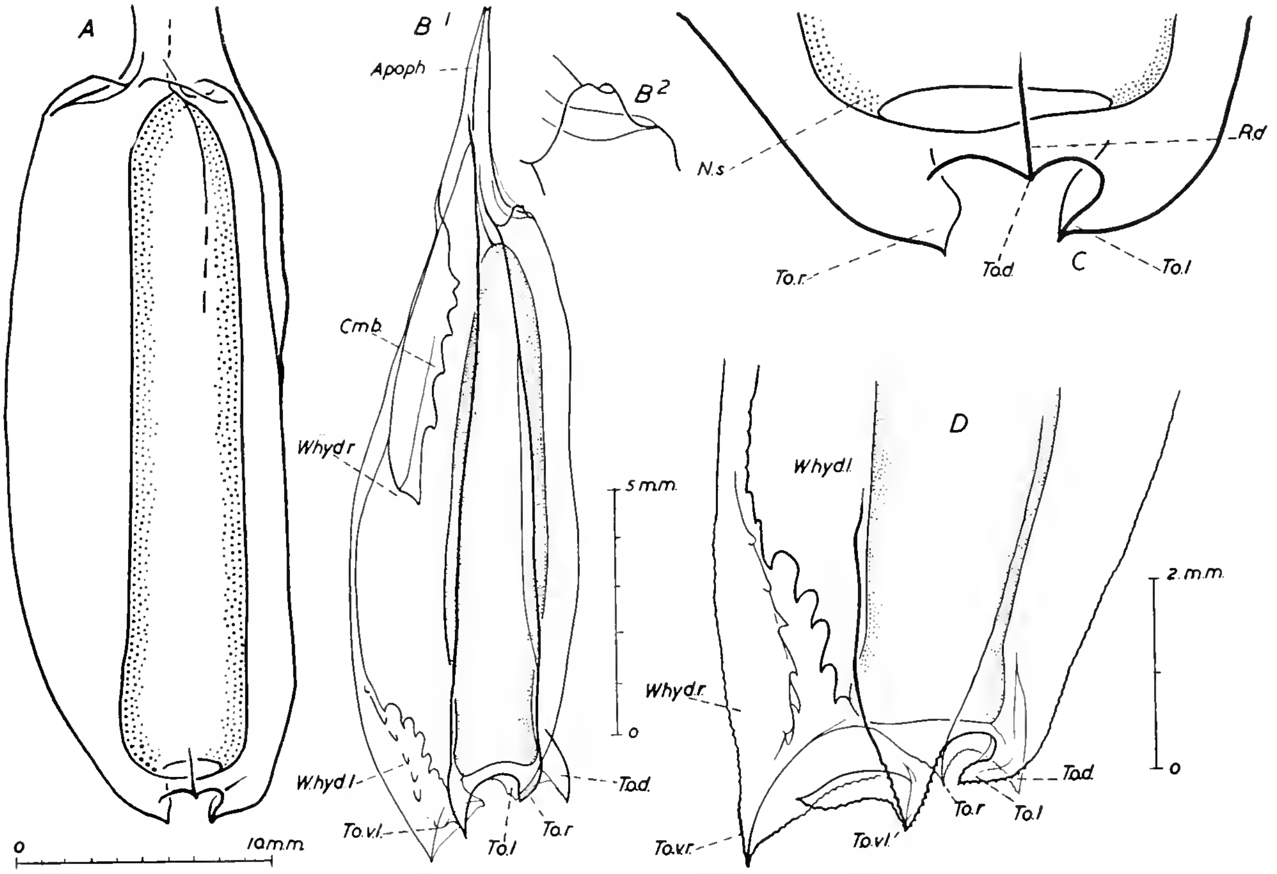
The solution of this question of a distinction between *A. haeckeli* and *A. ingeborgae* may lie in the fact that a species, whose distribution covers such a wide area as that including the N. Atlantic and Indo-Malaysian oceans, may appear as a larger form in the N. Atlantic, and that problems in allometric growth may be involved. *Sulculeolaria biloba* appears to be another such species.

Ceratocymba dentata (Bigelow), 1918. (Plates X, XI.)

This Abylid has been taken in the Indian Ocean only at 'Discovery II' Stations 1585 and 2696, though 'Discovery II' took it many times in the Atlantic. It has been recorded only by Bigelow (1918), who made the original record of the species from two North-west Atlantic Stations, about 32° N. lat. and 70–72° W. long., and by Moser (1925) west of the Cape Verde Islands under the synonym *Abyla quadrata*.

The only other known and still unrecorded, catches, are of eudoxids taken by Beebe at Bermuda; and of both stages taken by 'Discovery' at Stations in the South Atlantic. These 'Discovery' Stations lay between lat. 32° S. and the Cape Verde Islands. They include some Stations (280–298) on a line starting from the West Coast of Africa on the Equator and running westwards and northwards to the Cape Verde Islands; and Stations on another line running up the 30° mer. from 28° 30′ S. lat. to the Cape Verde Islands; as well as Station 81 at the same south latitude, but nearer the Cape.

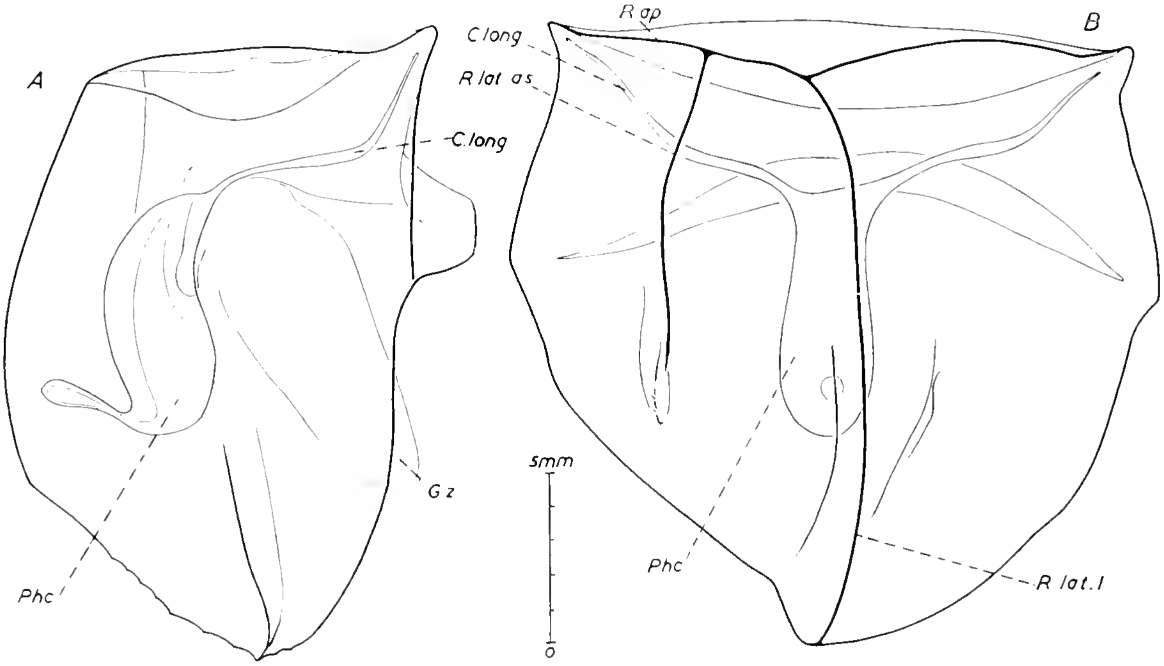
Also there has recently come to my notice a specimen of *Ceratocymba dentata* taken by Mr J. S. Colman in 1937 during a cruise in Lord Moyne's yacht 'Rosaura' in the Guinea current. The locality was 7° 27′ N. lat., 23° 08′ W. long. It was taken in a 2-m. stramin net fished from 1000 m. to the surface.



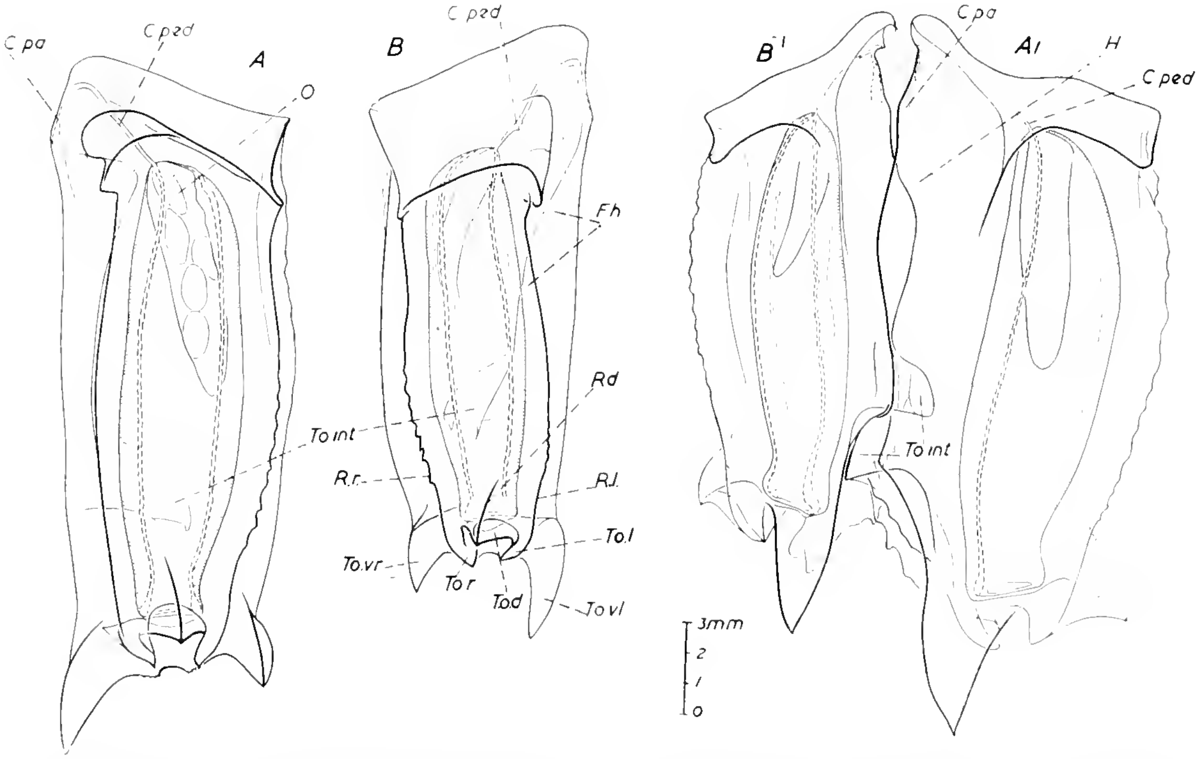
Text-fig. 79. A, C, *Ceratocymba sagittata*, a posterior nectophore from 'Discovery II' St. 676; A × 3·4; C × 9·8; B, D, *Ceratocymba leuckartii*, two views of a posterior nectophore from 'Discovery II' St. 694; B × 6·5; D × 12·5.

Polygastric stage. The lengths of the nectophores of a complete polygastric specimen from 'Discovery II' Station 2635, 280–0 m., measured from either end to the notch on the dorsal side of the posterior nectophore, where the ventro-basal tooth of the anterior nectophore locks the two in position, are: anterior nectophore, 11 mm.; posterior, 55 mm. The length of the nectosac of the posterior nectophore is 45 mm.; its diameter at the forward end is 3 mm., increasing to 4·5 mm. just before the terminal bulge, which measures 5 mm. in diameter. There are nine or ten functional stem groups, the terminal three of which show the growth of the eudoxid bract and two gonophores. On one of the bracts, still attached to the stem, in the long hydroecial canal of the posterior nectophore, can be seen the two ridges as found in the full-grown bract and shown in Text-fig. 80. The identity of loose bracts is therefore established. The temperature in which Moser's type of *quadrata* was taken at the surface on 7 November west of the Cape Verde Islands, must have been about 26° C.

The surface temperature at 'Discovery II' Station 2635 was 27·40° C. but it is uncertain at what depth and temperature the species was living, since even at 60 m. at a nearby Station (2640) five days later, there was a drop to 20° C.



Text-fig. 80. *Ceratocymba dentata.* Lateral and dorsal views of the bract of the eudoxid, × 4·4, from 'Discovery' St. 286 (see Text-fig. 81).



Text-fig. 81. *Ceratocymba dentata*, gonophores of eudoxid from 'Discovery' St. 286, × 4; A, B, dorsal views of female and male gonophores; A'B', the same gonophores locked together, viewed from side of attachment to bract (see Text-fig. 80).

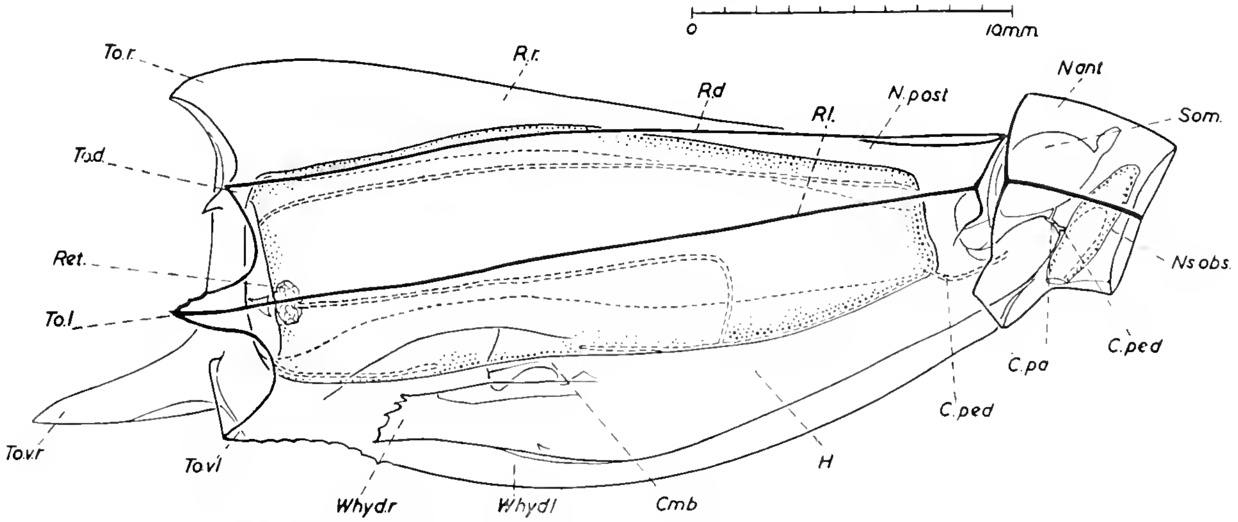
Eudoxid: A large bract, still bearing an immature female gonophore ('Discovery' Station 286) measures: length, 11 mm.; breadth, 19 mm.; depth, 14 mm. A pair of detached gonophores from the same haul (mirror images of each other) were possibly carried by the same bract. The larger is female and measures 23 mm. in length, the smaller, male, 20 mm. They fit accurately together, as shown in Text-fig. 81, the hydroecial wings of the larger clasping those of the smaller at the upper and lower sides of the whole eudoxid. The pedicular canals of the two gonophores arise near the forward end on the borders of their upper hydroecial wings, so that they must arise just below the forward end of the swan-shaped somatocyst[1]. In fact, scars of corresponding shape can be seen in this position on the bract. The hydroecial wings of the gonophores surround the gastrozooid and its tentacle. This combined hydroecial cavity narrows towards its after end, and at its periphery there are two large curved teeth, one above the other, and one belonging to each gonophore. These large teeth are in positions about two-thirds of the way down the obliquely running hydroecial folds, which bear a few more much smaller distal teeth. Such teeth are commonly found on the hydroecial fold or 'Leiste' of gonophores and of posterior nectophores of many genera and species. In the posterior nectophore of this species *dentata* there are about two dozen teeth on the left hydroecial fold, the terminal one as usual being the largest. Their function perhaps is to prevent entanglement of the numerous side branches of the tentacles, or to remove prey.

In structure the gonophores of *Ceratocymba dentata* are perhaps more complicated than those of any other species of Siphonophore, a fact that strengthens the belief that it is the most highly evolved Calycophore.

ABYLOPSINAE

Abylopsis tetragona (Otto), 1823.

In 1951, nine open hauls containing Siphonophores were made by 'Manihine', six of them during the night of 16–17 January between five miles and forty miles east of Sanganab Lighthouse, off Port Sudan, from either 183 or 366 m. to the surface. An examination of the catches showed that *A. tetragona* was abundant and actively breeding. At three other 'Manihine' Stations 1 (P), 2 and 3, further north, fifty-six polygastric specimens, and 276 eudoxids were taken.



Text-fig. 82. *Abylopsis tetragona.* The two nectophores locked rigidly together as in life. ×4·2.

Since the 'Manihine' catches appear to be some of the first records of Siphonophores from the Red Sea it was thought worth while to compare the absolute abundance per unit volume of water of this species in the Red Sea ('Manihine' records), in the Mediterranean ('Thor' records) and in the warm tropical Atlantic ('Meteor' records). Bigelow & Sears (1937) went into the question of the last two in some detail. Here I need only give the comparable figures and repeat the caution about accepting figures based on a small number of open hauls, where the straining efficiency of the net, the

---

[1] Clearly shown in Text-fig. 80.

speed of hauling and the occurrence of swarms are not known precisely. As far as 'Manihine' records are concerned it is assumed that an open 1 m. stramin net was hauled obliquely from either 183 or 366 m. to the surface whilst the ship went slowly ahead for about 100 metres.

Abundance of Abylopsis tetragona *per unit volume of water*

1. 'Thor', Mediterranean, western basin (Bigelow & Sears, 1937). Mean frequency of specimens, at the level of maximum abundance, at Stations where the species occurred:

	Polygastric	Eudoxid
Winter	1 per 180 cu.m.	1 per 1100 cu.m.
Late June	1 per 21 cu.m.	1 per 20 cu.m.
Late August	1 per 25 cu.m.	1 per 152 cu.m.
Maximum (late August)	1 per 2 cu.m.	1 per 0·2 cu.m.

2. 'Meteor', warm tropical Atlantic. Frequency at several levels, calculated from Bigelow & Sears's tables (based on those of Leloup & Hentschel, 1935):

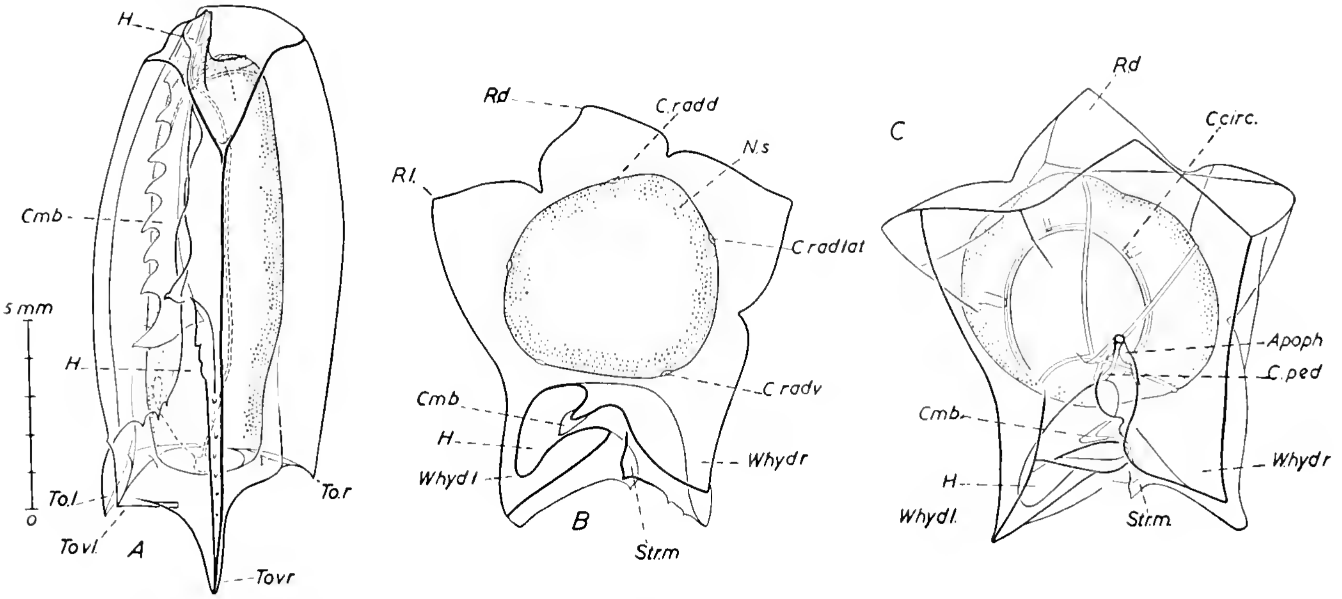
	Polygastric	Eudoxid
0–50 m.	1 per 75 cu.m.	1 per 60 cu.m.
50–400 m.	1 per 375 cu.m.	1 per 375 cu.m.

3. 'Manihine', Red Sea, off Port Sudan, 16/17 January 1951. (T. ° C. estimated at 21·5–22; equivalent to a late June surface temperature at Villefranche, West Mediterranean):

	Polygastric	Eudoxid
Mean frequency at six stations (183 or 366–0 m.)	1 per 4 cu.m.	1 per 1·4 cu.m.
Maximum frequency (St. 4, 183–0 m.)	1 per 2 cu.m.	1 per 0·4 cu.m.

It appears that Port Sudan would be a favourable spot at which to attempt to observe the species throughout its life cycle, an objective that has not so far been achieved. The importance of this is to ascertain whether the small anterior nectophore is the primary nectophore or a secondary heteromorphous one. Haeckel's attempt at Lanzerote in 1867 failed. So also did my own at Villefranche in 1950, where, at that time, there were never more than two or three ripe gonophores available on odd days, and then generally one sex or the other and not both at once.

Text-fig. 83 illustrates the arrangement of the two hydroecial folds, for comparison with the arrangement in *Abyla* spp. A distinctive character is that the broad, left-hand fold, the free edge of which Moser called the left, pseudo-dorsal ridge, is held in place at one point between two parts of the right-hand fold, i.e. between a mamma-like structure and the comb or 'Leiste', at a position just proximal to the terminal parting of the two folds. Moser's figure (1925, pl. xx, fig. 4) and her description (p. 330) does not make this clear. It should be remembered that owing to her fantastic 'Urmedusentheorie' she called the morphological dorsal side of a posterior nectophore 'ventral'. The 'Leiste' or comb, which Moser described as arising from the 'dorsal' wall of the nectosac should, I believe, properly be considered as part of the free, ventral margin of the right hydroecial fold, as can be seen at any rate proximally in the apophysis or portion of the posterior nectophore that is enclosed in the hydroecium of the anterior one. This comb or 'Leiste' is the homologue of the comb or 'Leiste' in *Abyla* spp. The hydroecium of the posterior nectophore has been displaced to the left side in the proximal half. I observed at Villefranche that the tip of the tentacle consists of a sinker in the form of a disc, around the edge of which are from 13 to 16 nematocysts. A similar sinker occurs at the tip of the tentacle of *Rosacea cymbiformis*.



Text-fig. 83. *Abylopsis tetragona*, posterior nectophore, to show how the left ventral hydroecial fold is held rigidly in place by the right. A, latero-ventral view, × 5; B, a section just above the locking tooth of the right wing, × 8·8; C, apical view, × 8·8.

REFERENCES

Agassiz, A., 1863. *On* Nanomia cara. Proc. Boston Soc. nat. Hist. IX, pp. 180–1.

—— 1865. *North American Acalephae.* Ill. Cat. Mus. comp. Zool. Harv. No. 11, pp. 201–13, text-figs. 331–50.

Ankel, W. E., 1951. Phyllirrhoe, Mnestra *und die Probleme der Gemeinschaften des ozeanischen Pleustals.* Verh. dtsch. zool. Ges. 1951, pp. 396–404, 6 text-figs.

Bedot, M., 1893. *Revision de la Famille des Forskalidae.* Rev. suisse zool. I, pp. 231–54.

—— 1896. *Les Siphonophores de la Baie d'Amboine.* Rev. suisse zool. III, pp. 367–414, pl. 12.

—— 1904. *Siphonophores provenant des campagnes du yacht Princess-Alice* (1892–1902). Résult. Camp. sci. Monaco, XXVII, pp. 1–27, 4 pls.

Berrill, N. J., 1930. *On the Occurrence and Habits of the Siphonophore,* Stephanomia bijuga (*Delle Chiaje*). J. Mar. biol. Ass. U.K. XVI, pp. 753–5, 1 text-fig.

Bigelow, H. B., 1904. *Medusae from the Maldive Islands.* Bull. Mus. comp. Zool. Harv. XXXIX, pp. 245–69, 9 pls.

—— 1911*a*. *Biscayan Plankton Collected during a Cruise of H.M.S. 'Research'*, 1900, Part XIII. *The Siphonophora.* Trans. Linn. Soc. Lond. (Zool.), X, pp. 337–58, pl. 28.

—— 1911*b*. *The Siphonophorae. Reports Sci. Res. Expedition to the Eastern Tropical Pacific...Albatross...XXIII.* Mem. Harv. Mus. comp. Zool. XXXVIII, No. 2, pp. 173–402, 32 pls.

—— 1913. *Medusae and Siphonophorae Collected by the U.S. Fisheries Steamer 'Albatross' in the North-Western Pacific*, 1906. Proc. U.S. nat. Mus. XLIV, pp. 1–119, 6 pls.

—— 1918. *Some Medusae and Siphonophorae from the Western Atlantic.* Bull. Mus. comp. Zool. Harv. LXII, pp. 363–442, 8 pls.

—— 1919. *Contributions to the Biology of the Philippine Archipelago and adjacent regions: Hydromedusae, Siphonophores and Ctenophores of the 'Albatross' Philippine Expedition.* Bull. U.S. nat. Mus. C, i, 5, pp. 279–362, 5 pls.

—— 1931. *Siphonophorae from the 'Arcturus' Oceanographic Expedition.* Zoologica, N.Y. VIII, No. 11, pp. 525–92, text-figs. 185–220.

Bigelow, H. B. & Sears, M., 1937. *Siphonophorae.* Rep. Danish oceanogr. Exped. Medit. II, Biology, H. 2, pp. 1–144, 83 text-figs.

Blainville, H. M. de, 1830. *Zoophytes.* Dict. sci. nat. Paris. LX, pp. 1–548, 68 pls.

—— 1834. *Manuel d'actinologie ou de zoophytologie*, pp. 1–694, 100 pls.

Bohm, R., 1878. *Helgolander Leptomedusen.* Jena. Z. Naturw. xii, pp. 68–203, 6 pls.

Brandt, J. F., 1835. *Polypus, Acalephas Discophoras et Siphonophoras, nec non Echinodermata continens. Prodromus descriptionis animalium ab H. Mertensio in orbis terrarum circumnavigatione observatum,* Fasc. 1, pp. 1–76. St Petersburg: Graeff.

Brooks, W. K., 1886. *The Life History of the Hydromedusae: A discussion of the Origin of the Medusae, and of the Significance of Metagenesis.* Mem. Boston Soc. nat. Hist. iii, No. 12, pp. 359–430, 4 pls.

Browne, E. T., 1926. *Siphonophorae from the Indian Ocean.* Trans. Linn. Soc. Lond. (Zool.) (2), xix, pp. 55–86.

Candeias, A., 1929. *Note sur quelques siphonophores Calycophorae de Madère.* Bull. Soc. portug. Sci. nat. x, No. 23, pp. 269–84, 12 text-figs.

Carter, G. S., 1949. *The Turbellarian Theory of the Cnidaria. Being a Review of 'Turbelarijska Teorija Knidarijev', by J. Hadzi.* Sci. Progr. Lond. xxxvii, No. 145, pp. 136–9.

Chamisso, A. de & Eysenhardt, C. G., 1821. *De animalibus quibusdam e classe vermium Linneana . . ., fasc.* 2. Nova Acta Leop. Carol. x, pp. 343–74, 10 pls.

Chun, C., 1882. *Über die cyklische Entwickelung und die Verwandtschaftsverhaltnisse der Siphonophoren.* S.B. preuss. Akad. Wiss. lii, pp. 1155–72, 1 pl.

—— 1885. *Über die cyklische Entwickelung der Siphonophoren.* S.B. preuss. Akad. Wiss. xxvi, pp. 511–29, 1 pl.

—— 1886. *Über Bau und Entwickelung der Siphonophoren.* S.B. preuss. Akad. Wiss. xxxviii, pp. 681–8.

—— 1888*a*. *Bericht über eine nach den Canarischen Inseln im Winter* 1887–1888 *ausgeführte Reise.* S.B. preuss. Akad. Wiss. xliv, pp. 1141–73.

—— 1888*b*. *Die pelagische Thierwelt in grösseren Meerestiefen und ihre Beziehungen zu der Oberflächenfauna.* Bibl. Zool. Stuttgart. 1, Heft 1, pp. 12–17, 1 pl.

—— 1891. *Die Canarischen Siphonophoren in monographischen Darstellungen.* 1. Stephanophyes superba *und die Familie der Stephanophyiden.* Abh. senckenb. naturf. Ges. xvi, pp. 553–627, 7 pls.

—— 1897*a*. *Über den Bau und die morphologische Auffassung der Siphonophoren.* Verh. dtsch. zool. Ges. vii, pp. 48–111, 29 text-figs.

—— 1897*b*. *Die Siphonophoren der Plankton-Expedition.* Ergebn. Plankton Exp. 2, K.b., pp. 1–126, 8 pls. Kiel and Leipzig.

—— 1913. *Über den Wechsel der Glocken bei Siphonophoren.* Ber. sächs. Ges. (Akad.) Wiss. lxv, pp. 27–41, 8 text-figs.

Claus, C., 1860. *Über* Physophora hydrostatica *nebst Bemerkungen über andere Siphonophoren.* Z. wiss. Zool. x, pp. 295–332, 3 pls.

—— 1878. *Über* Halistemma tergestinum *n.sp. nebst Bemerkungen über den feinern Bau der Physophoriden.* Arb. zool. Inst. Univ. Wien. 1, pp. 1–56, 5 pls.

Cunningham, J. T., 1892. *On a Species of Siphonophore observed at Plymouth.* J. Mar. biol. Ass. U.K. (N.S.) ii, No. 3, pp. 212–15, 2 text-figs.

Dana, J. W., 1858. *On a New Species of Medusa related to* Stephanomia, Crystallomia polygonata. Mem. Amer. Acad. Arts Sci. (N.S.) vi, pt. 2, pp. 459–60, 1 pl.

Dawydoff, C., 1928. *Traité d'embryologie comparée des invertébrés,* xiv + 930 pp., 509 text-figs. Paris.

Deacon, G. E. R., 1952. *The 'Manihine' Expedition to the Gulf of Aqaba. II. Preliminary Hydrological Report.* Bull. Brit. Mus. (Nat. Hist.) Zool. 1, No. 8, pp. 159–62, 4 text-figs.

Delle Chiaje, S., 1822. *Memorie sulla storia e notomia degli Animali senza vertebre del Regno di Napoli.* Atlas, 109 pls. Napoli.

—— 1829. *Memorie sulla storia e notomia degli Animali senza vertebre del Regno di Napoli.* iv, i–viii + 1–14 pp. Napoli.

—— 1841. *Descrizione e notomia degli Animali Invertebrati della Sicilia citeriore osservati vivi negli anni* 1822–30. vi–vii, Atlas, 181 pls. Napoli.

Delsman, H. C., 1923. *Beiträge zur Entwickelungsgeschichte von* Porpita. Treubia, iii, pp. 243–66, 28 text-figs.

Dollfus, R.-Ph., 1925. *Liste critique des cercaires marines à queue sétigère signalées jusqu'à présent.* Trav. Sta. zool. Wimereux, ix, pp. 43–65, 6 text-figs.

Eschscholtz, F., 1825. *Bericht über die zoologische Ausbeute wahrend der Reise von Kronstadt bis St Peter und Paul.* Oken's Isis, xvi, pp. 733–47, pl. v.

—— 1829. *System der Acalphen,* 1–190 pp. 16 pls. Berlin.

Fewkes, J. W., 1880. *Contributions to a Knowledge of the Tubular Jelly-fishes.* Bull. Mus. comp. Zool. Harv. vi, pp. 127–46, 3 pls.

—— 1882. *Notes on Acalephs from the Tortugas, with a description of New Genera and Species.* Bull. Mus. comp. Zool. Harv. ix, pp. 251–89, 7 pls.

—— 1888*a* *Studies from the Newport Marine Zoölogical Laboratory. On certain medusae from New England.* Bull. Mus. comp. Zool. Harv. xiii, pp. 209–40, 6 pls.

—— 1888*b*. *On a new Physophore,* Ploeophysa, *and its Relationships to other Siphonophores.* Ann. Mag. nat. Hist. (6), 1, pp. 317–22, 1 pl.

Forskal, P., 1775. *Descriptiones animalium...quae in itinere orientali observavit, post mortem editit Carsten Niebuhr.* Hauniae, 20+xxxiv+pp. 15, 1 map.

—— 1776. *Icones rerum naturalium...post mortem auctoris...editit Carsten Niebuhr.* Hauniae, pp. 15, 43 pls.

Garstang, W., 1946. *The Morphology and Relations of the Siphonophora.* Quart. J. micr. Sci. lxxxvii, pt. ii, pp. 103–93, 57 text-figs.

Gegenbaur, C., 1853. *Beiträge zur näheren Kenntniss der Schwimmpolypen (Siphonophoren).* Z. wiss. Zool. v, pp. 285–344, 3 pls.

—— 1854. *Ueber* Diphyes turgida *n.sp., nebst Bemerkungen über Schwimmpolypen.* Z. wiss. Zool. v, pp. 442–54, 1 pl.

—— 1857. *Versuch eines Systemes der Medusen, mit Beschreibung neuer oder wenig gekannter Formen; zugleich ein Beitrag zur Kenntniss der Fauna des Mittelmeeres.* Z. wiss. Zool. viii, pp. 202–73, 4 pls.

—— 1859. *Neue Beiträge zur näheren Kenntniss der Siphonophoren.* Nova Acta Leop. Carol. xxvii, pp. 331–424, 7 pls.

Graeffe, E., 1860. *Beobachtungen über Radiaten und Würmer.* Denkschr. schweiz. naturf. Ges. vii, pp. 1–59, 10 pls.

Grönberg, G., 1898. *Beiträge zur Kenntniss der Gattung* Tubularia. Zool. Jb. Anat. xi, pp. 61–76, 2 pls.

Hadzi, J., 1944. *Turbelarijska Teorija Knidarijev.* Dela mat. prir. Akad. Ljubljan. iii, pp. 1–239.

Haeckel, E., 1869*a*. *Zur Entwickelungsgeschichte der Siphonophoren.* Natuurk. Verh. Prov. Utrechtsch Genoots. i, vi, pp. 1–120, 14 pls.

—— 1869*b*. *Über Arbeitstheilung in Natur und Menschenleben*, pp. 1–40, 1 pl., 18 text-figs. Berlin.

—— 1888*a*. *System der Siphonophoren....* Jena. Z. naturw. xxii, pp. 1–46.

—— 1888*b*. *Report on the Siphonophorae.* Rep. sci. results H.M.S. 'Challenger' Zool. xxviii, pp. 1–380, 50 pls.

Hartlaub, C., 1907. *Craspedote Medusen*, 1 Teil, 1 Lief., *Codoniden und Cladonemiden.* Nordisches Plankton, Lief. 6, xii, pp. 1–135, 126 text-figs.

Herdman, H. F. P., 1953. *The deep scattering layer in the sea: Association with density layering.* Nature, Lond., clxxii, p. 276.

Huxley, T. H., 1859. *The Oceanic Hydrozoa...Voyage of H.M.S. 'Rattlesnake'*, pp. 1–143, 12 pls. London: Ray Society.

Hyman, L. H., 1940. *The Invertebrates: Protozoa through Ctenophora*, 1st ed., pp. 1–726, 221 text-figs. New York and London: McGraw-Hill Book Company, Inc.

Jesperson, P., 1935. *Quantitative Investigations on the distribution of Macroplankton in different Oceanic Regions.* Dana-Report, No. 7, pp. 1–44, 28 text-figs.

Kawamura, T., 1910. *'Bozunira' and 'Katsuwo no Eboshi'.* Rhizophysa *and* Physalia. Zool. Mag., Tokyo, xxii, pp. 445–54, 1 pl. and 5 text-figs.

—— 1911*a*. *Genus* Agalma *and* Crystallomia. Zool. Mag., Tokyo, xxiii, pt. 1, No. 267, pp. 1–10, 1 pl.

—— 1911*b*. *'Shidarezakura Kurage' and 'Nagayoraku Kurage'* Cupulita picta *Metschnikoff and* Agalmopsis elegans *Sars.* Zool. Mag., Tokyo, xxiii, pp. 359–63, 1 pl.

—— 1915. *Calycophorae III.* Zool. Mag., Tokyo, xxvii, pp. 317–24, 1 pl.

Keferstein, W. & Ehlers, E., 1861. *Beobachtungen über die Siphonophoren von Neapel und Messina. Zoologische Beiträge gesammelt im Winter* 1859–1860 *in Neapel und Messina*, pp. 1–34, 5 pls. Leipzig: Wilhelm Engelmann.

Kölliker, A., 1853*a*. *Bericht über einige im Herbste* 1852 *in Messina angestellte vergleichendanatomische Untersuchungen, Quallen.* Z. wiss. Zool. iv, pp. 306–15.

—— 1853*b*. *Die Schwimmpolypen oder Siphonophoren von Messina*, pp. 1–96, 12 pls. Leipzig: Engelmann.

Korotneff, A., 1884. *Zur Histologie der Siphonophoren.* Mitt. zool. Sta. Neapel. v, pp. 229–88, 6 pls.

Kramp, P. L., 1942. *The Godthaab Expedition* 1928. *Siphonophora.* Medd. Gronland, lxxx, 8, pp. 3–24, 5 text-figs.

—— 1949. *Origin of the Hydroid Family Corymorphidae.* Vidensk. Medd. dansk. naturh. Foren. Kbh. cxi, pp. 183–215, 9 text-figs.

Lamarck, J. B. P. A. de M. de, 1801. *Système des Animaux sans vertèbres.* Paris, 432 pp.

Leloup, E., 1929. *Recherches sur l'anatomie et le développement de* Velella spirans *Forsk.* Arch. Biol., Paris, xxxix, pp. 397–478, 3 pls., 6 text-figs.

—— 1932*a*. *Contribution à la Répartition des Siphonophores Calycophorides.* Bull. Mus. Hist. nat. Belg. viii, No. 11, pp. 1–30, 3 text-figs.

—— 1932*b*. *L'eudoxie d'un Siphonophore Calycophoride rare, le* Nectopyramis thetis *Bigelow.* Bull. Mus. Hist. nat. Belg. viii, No. 3, pp. 1–8, 5 text-figs.

—— 1933. *Siphonophores calycophorides provenant des campagnes du Prince Albert 1^{er} de Monaco.* Résult. Camp. sci. Monaco, Fasc. 87, pp. 1–67, 1 pl.

—— 1934*a*. *Siphonophores Calycophorides de l'Océan Atlantique Tropical et Austral.* Bull. Mus. Hist. nat. Belg. x, No. 6, pp. 1–87, 15 text-figs.

—— 1934*b*. *Siphonophores de Madras (Indes Anglaises).* Bull. Mus. Hist. nat. Belg. x, No. 9, pp. 1–5.

—— 1941. *A propos des Siphonophores du genre* Anthophysa *Brandt*, 1835. Bull. Mus. Hist. nat. Belg. xvii, No. 47, pp. 1–7, 1 pl., 2 text-figs.

Leloup, E. & Hentschel, E., 1935. *Die Verbreitung der calycophoren Siphonophoren im Südatlantischen Ozean.* Wiss. Ergebn. dtsch. atlant. Exped. 'Meteor', xii, 2, pp. 1–31.

Lens, A. D. & Riemsdijk, T. van, 1908. *The Siphonophora of the Siboga Expedition.* Siboga Exped. ix, pp. 1–130, 24 pls., 52 text-figs.

Lesson, R. P., 1826. *Voyage autour du monde...sur la Corvette de sa Majesté, 'La Coquille', pendant les années* 1822, 1823, 1824 *et* 1825....Atlas, Zoophytes, 16 pls.

—— 1838. *Voyage Autour du Monde, etc.* Zoologie, 2, part 2, 2nd division, pp. 155.

—— 1843. *Acalèphes. Histoire naturelle des zoophytes*, pp. 1–596, 12 pls. Paris: Librairie Encyclopédique de Roret.

Lesueur, C. A. & Petit, N., 1807–11. *Voyage de découvertes aux Terres Australes.* Atlas, 40 pls. Paris.

Leuckart, R., 1853. *Zoologische Untersuchungen.* 1. *Die Siphonophoren*, pp. 1–95, 3 pls.

—— 1854. *Zur näheren Kenntnis der Siphonophoren von Nizza.* Arch. Naturgesch. Jahrg. xx, 1, pp. 249–377, 3 pls.

Linné, C., 1758. *Systema naturae*....Ed. x, 1, 823 pp.

McCrady, J., 1857. *Gymnopthalmata of Charleston Harbor.* Proc. Elliott Soc. Sci. 1, pp. 103–221, 5 pls.

Mackintosh, N. A., 1934. *Distribution of the Macroplankton in the Atlantic sector of the Antarctic.* Discovery Reports, ix, pp. 65–160, 48 text-figs.

Metchnikoff, E., 1870. *Contributions to the Knowledge of Siphonophores and Medusae (Russian).* Mem. Soc. Amis Sci. nat. Moscou, viii, pp. 295–370, 6 pls.

—— 1874. *Studien über die Entwickelung der Medusen und Siphonophoren.* Z. wiss. Zool. xxiv, pp. 15–83, 11 pls.

—— 1886. *Medusologische Mittheilungen.* Arb. zool. Inst. Univ. Wien. vi, pp. 237–66, 2 pls.

5 Moore, H. B., 19~~4~~3. *Plankton of the Florida Current. II. Siphonophora.* Bull. mar. Sci. Gulf & Caribbean, ii, No. 4, pp. 559–73, 9 text-figs.

Moser, F., 1917. *Die Siphonophoren der Adria und ihre Beziehungen zu denen des Weltmeeres.* S.B. Akad. Wiss. Wien, Math.-nat. Klasse, Abt. 1, cxxvi, Heft 9, pp. 703–63, 4 pls., 1 text-fig. and 1 chart.

—— 1924*a*. *Die larvalen Verhältnisse der Siphonophoren in neuer Beleuchtung.* Zoologica, xxviii, 1 Lief., Heft 73, pp. 1–52, 5 pls., 35 text-figs.

—— 1924*b*. *Siphonophora in:* Kukenthal & Krumbach. *Handbuch der Zoologie*, 1, pp. 485–521, text-figs. 462–511.

—— 1925. *Die Siphonophoren der Deutschen Südpolar Expedition*, 1901–3. Dtsch. Südpol. Exped. xvii, Zool. 9, pp. 1–541, 36 pls., 61 text-figs.

Müller, O. F., 1776. *Beschreibung zweier Medusen.* Beschäft. Ges. naturf. Fr. Berlin, ii, pp. 290–8, 1 pl.

Okada, Yok, 1932. *Développement post-embryonnaire de la* Physalie *pacifique.* Mem. Coll. Sci. Kyoto, Ser. B, 8, No. 1, Art. 1, pp. 1–25, 11 text-figs., 1 pl.

Otto, A. W., 1823. *Beschreibung einiger neuen Mollusken und Zoophyten.* Nova Acta Leop. Carol. xi, pp. 273–314, 5 pls.

Palombi, A., 1937. *Il ciclo biologico di* Lepocreadium album *Stossich sperimentalmente realizzato. Osservazioni etologiche e considerazioni sistematiche sulla* Cercaria setifera (*non Joh. Müller*) *Monticelli.* Riv. Parassit. 1, 1, pp. 1–12, 1 pl., 2 text-figs.

Péron, F., 1807–16. *Voyage de découvertes aux terres Australes, exécuté...pendant* 1800–4...*et rédigé par M. F. Péron*..., 2 tom. [et Atlas]. Paris.

Quoy, J. R. C. & Gaimard, J. P., 1827. *Observations zoologiques faites à bord de 'l'Astrolabe', en mai* 1826, *dans le detroit de Gibraltar.* Ann. Sci. nat. x, pp. 5–21, 172–93, 6 pls.

—— —— 1833. *Voyage de découvertes de 'l'Astrolabe'...de M. J. Dumont D'Urville.* Zool. iv, pp. 1–390, Atlas, Zoophytes, Pls. 1–26. Paris.

Rees, W. J., 1937. *The development of the Hydroid* Corymorpha nutans *M. Sars from the egg.* J. Mar. biol. Ass. U.K. xxi, No. 2, pp. 743–6, 2 text-figs.

Rees, W. J. & Russell, F. S., 1937. *On rearing the hydroids of certain medusae, with an account of the methods used.* J. Mar. biol. Ass. U.K. xxii, pp. 61–82, 12 text-figs.

Richter, W., 1907. *Die Entwicklung der Gonophoren einiger Siphonophoren.* Z. wiss. Zool. lxxxvi, pp. 557–618, 3 pls. 13 text-figs.

Ritchie, G. S., 1952. *H.M.S. Challenger's Investigations in the Pacific Ocean.* J. Inst. Navig. v, No. 3, 251–61.

Russell, F. S., 1934. *On the occurrence of the Siphonophores* Muggiaea atlantica *Cunningham and* Muggiaea kochi (*Will*) *in the English Channel.* J. Mar. biol. Ass. U.K. xix, pp. 555–8.

Russell, F. S. & Colman, J. S., 1935. *The Zooplankton.* IV. *The occurrence and seasonal distribution of the Tunicata, Mollusca and Coelenterata (Siphonophora).* Sci. Rep. Gr. Barrier Reef Exped. ii, 7, pp. 203–76, 30 text-figs.

Sars, M., 1846. *Fauna littoralis Norwegiae*, 1, pp. 1–94, 10 pls. Christiania.

Schneider, K. C., 1896. *Mittheilungen über Siphonophoren.* II. *Grundriss der Organisation der Siphonophoren.* Zool. Jb. Abt. anat. ix, pp. 571–664, 3 pls., 32 text-figs.

—— 1898. *Mittheilungen über Siphonophoren.* III. *Systematische und andere Bemerkungen.* Zool. Anz. xxi, pp. 51–7, 73–95, 114–33, 153–73, 185–200.

Sears, M., 1950. *Notes on Siphonophores.* 1. *Siphonophores from the Marshall Islands.* J. Mar. Res. ix, 1, pp. 1–16, 2 text-figs.

—— 1952. *Notes on Siphonophores.* 3. Nectopyramis spinosa *n.sp.* Breviora, No. 3, pp. 1–4, 3 text-figs.

SEARS, M., 1953. *Notes on Siphonophores. 2. A revision of the Abylinae.* Bull. Mus. comp. Zool. Harv. 109, No. 1, pp. 1–119, 29 text-figs.

SEWELL, R. B. SEYMOUR, 1935. *Introduction and list of stations.* Sci. Rep. Murray Exped. No. 1, pp. 1–41, 1 chart.

—— 1948. *The free-swimming Planktonic Copepoda: Geographical distribution.* Sci. Rep. Murray Exped. VIII, No. 3, pp. 317–592, 24 text-figs. 2 charts.

STECHOW, E., 1921. *Neue Genera und Species von Hydrozoen und anderen Evertebraten.* Arch. Naturgesch. A. 87, 3, 248–65.

SVERDRUP, H. U., JOHNSON, M. W. & FLEMING, R. H., 1946. *The Oceans, their physics, chemistry, and general biology*, pp. 1–1087, 265 text-figs., 7 charts. New York: Prentice-Hall, Inc.

TOTTON, A. K., 1932. *Siphonophora.* Sci. Rep. Gr. Barrier Reef Exped. IV, No. 10, pp. 317–74, 36 text-figs.

—— 1936. *Plankton of the Bermuda Oceanographic Expeditions.* VII. *Siphonophora taken during the year* 1931. Zoologica, N.Y., XXI, 4, pp. 231–40.

—— 1941. *New species of the Siphonophoran Genus* Lensia, 1941. Ann. Mag. nat. Hist. (11), VIII, pp. 145–68, 29 text-figs.

VOGT, C., 1851. *Zoologische Briefe, etc.* I, pp. 138–41, 4 text-figs. Frankfurt.

—— 1852. *Über die Siphonophoren.* Z. wiss. Zool. III, pp. 522–5, 1 pl.

—— 1854. *Recherches sur les animaux inférieures de la Méditerranée.* 1. *Sur les Siphonophores de la Mer de Nice.* Mém. Inst. nat. génev. I, pp. 1–164, 21 pls.

WEISMANN, A., 1883. *Die Entstehung der Sexualzellen bei den Hydromedusen. Zugleich ein Beitrag zur Kenntnis des Baues und der Lebenserscheinungen dieser Gruppe*, pp. iii–xiii, 1–295, 24 pls., 21 text-figs.

WILLIAMS, C. B., 1951. *A note on the relative sizes of genera in the classification of animals and plants.* Proc. Linn. Soc. Lond. CLXII, 2, pp. 171–5, 2 text-figs.

WOLTERECK, R., 1904. *Über die Entwicklung der* Velella *aus einer in der Tiefe vorkommenden Larve.* Zool. Jh. Suppl.-Band VII, pp. 347–72, 3 pls., 6 text-figs.

—— 1905. *Beiträge zur Ontogenie und Ableitung des Siphonophorenstocks, mit einem Anhang zur Entwicklungsphysiologie der Agalmiden.* Z. wiss. Zool. LXXXII, pp. 611–37, 21 text-figs.

INDEX TO GENERA AND SPECIES

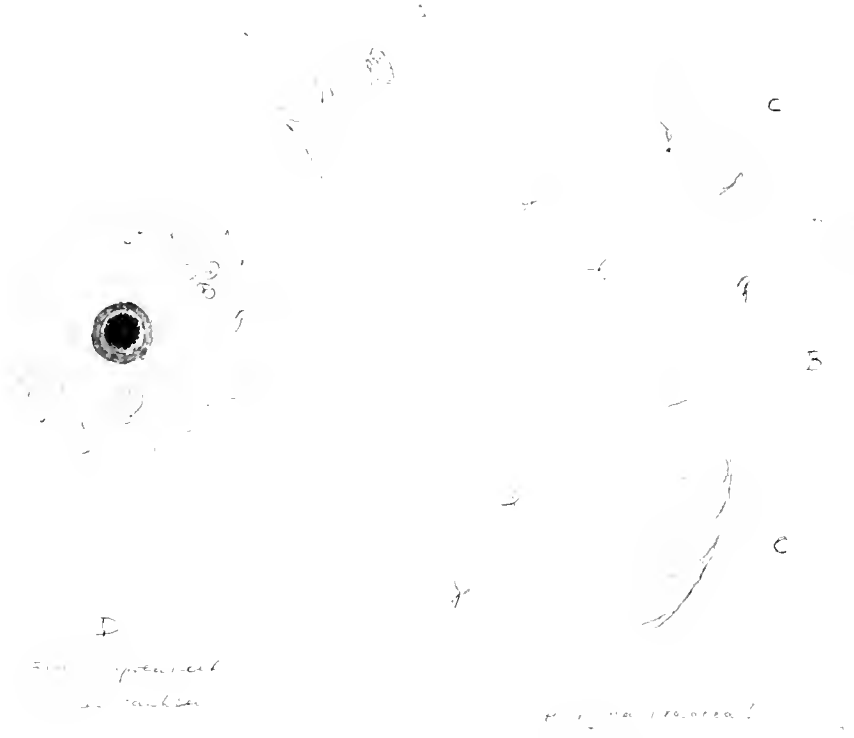
PLATE I

Athorybia rosacea Forskål

Villefranche, 0 metres, 9 May 1950

Unfinished sketches of the living animal by Mlle Bauer, by permission of Professor Portmann. A. Batteries of nematocysts on the tips of the palpons. B. A single palpon with its pink tip. C. Bracts.

ARTIST'S NOTES: *C.*, bract, fattish, delicate; *D.*, (apex of pneumatocyst) brownish stippling with green spots; *E.*, view from above (binocular); *F.G.*, naked eye sketches; *F.*, (pneumatocysts) metallic; *G.*, (centre) opaque. All the rest very transparent.



1

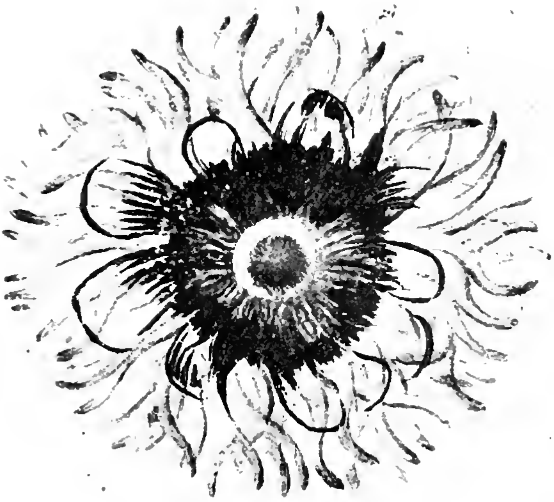
2

PLATE II

Athorybia rosacea Forskål

Water-colour sketch of a living animal, made by Sydney Parkinson in 1768, during Cook's first voyage. The specimen was taken two or three hundred miles south of the Cape Verde Is. The general colour used is cerise: outside the pneumatophore, reddish orange. The dark pigment outlining the topmost bracts and the lines of bracteal nematocysts was originally white. The white area on the outer edge of the pneumatophore represents the giant cells of the gas-gland. Nat. size right. Animal × 9. Tentacle × 20.

Plates II and III reproduced by kind permission of the Trustees of the British Museum (Natural History).



Medusa – rutilans.

voisine du Rhisophisa Rosacea – f. 1. – tableau des radiaires molles composées

PLATE III

Athorybia rosacea Forskål

Water-colour sketch of the living animal made by Sydney Parkinson in 1768 (see Pl. II). The tentacles are coloured pale yellow and the cnidosacs cerise. × 9.

Sydney Parkinson pinx^{t} ad vivum 1768.

PLATE IV

Figs. 1, 3, *Chelophyes appendiculata*. From the surface plankton at Villefranche, ×25. The left hydroecial wing of the separated gonophore lies to the left under the right wing (out of focus).

Fig. 2, *Vogtia glabra*. Larva taken at Villefranche by Dr Trégouboff, ×20. For explanation see legend to Text-fig. 33.

Figs. 4, 5, 8, *Forskalia edwardsii*. Species with the yellow spot on the velum, showing the helically coiled stem; photographed alive in the laboratory of the Station Zoologique at Villefranche. $\times\frac{1}{2}$, $\times\frac{1}{3}$, $\times\frac{1}{6}$.

Figs. 6, 7, *Rosacea cymbiformis*. Photographed alive in the laboratory of the Station Zoologique at Villefranche to show the extended stem and the eudoxids. $\times\frac{1}{6}$.

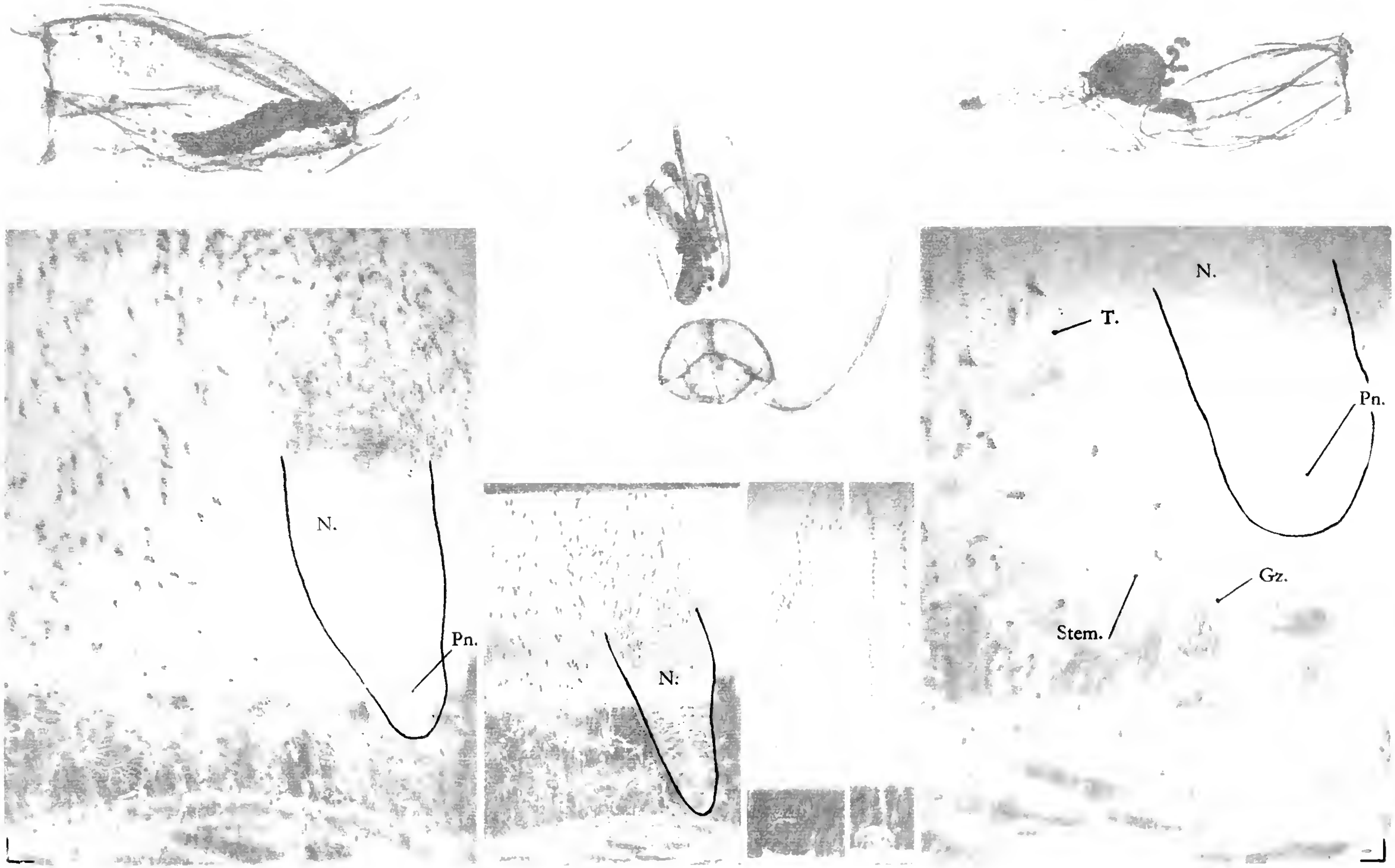

N.
Pn.
N:
T.
N.
Pn.
Gz.
Stem.

PLATE IV

Figs. 1, 3, *Chelophyes appendiculata*. From the surface plankton at Villefranche, $\times 25$. The left hydroecial wing of the separated gonophore lies to the left under the right wing (out of focus).

Fig. 2, *Vogtia glabra*. Larva taken at Villefranche by Dr Trégouboff, $\times 20$. For explanation see legend to Text-fig. 33.

Figs. 4, 5, 8, *Forskalia edwardsii*. Species with the yellow spot on the velum, showing the helically coiled stem; photographed alive in the laboratory of the Station Zoologique at Villefranche. $\times \frac{1}{2}$, $\times \frac{1}{3}$, $\times \frac{1}{6}$.

Figs. 6, 7, *Rosacea cymbiformis*. Photographed alive in the laboratory of the Station Zoologique at Villefranche to show the extended stem and the eudoxids $\times \frac{1}{6}$.

1

2

3

4

5

6

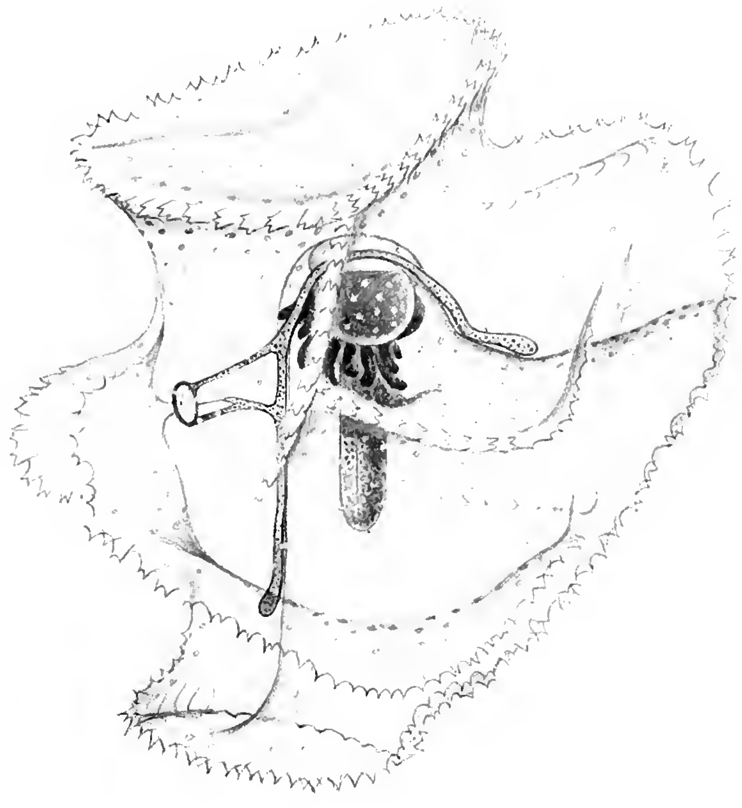
7

8

PLATE V

Fig. 1. *Nectopyramis spinosa* Sears, the nectophore with obsolescent nectosac, × 12. 'Discovery II' St. 1179, 500–250 m.

Figs. 2–3. *Nectopyramis diomedeae*, × 4·6, Bermuda, 1646 m. Beebe. See also Text-fig. 39.



1

2

3

PLATE VI

Maresearsia praeclara, gen.n., sp.n., larger nectophore, gastrozooids and eudoxids (still attached) of holotype specimen from 'Discovery II' Station 2636, 950–550 m. ×9·5.

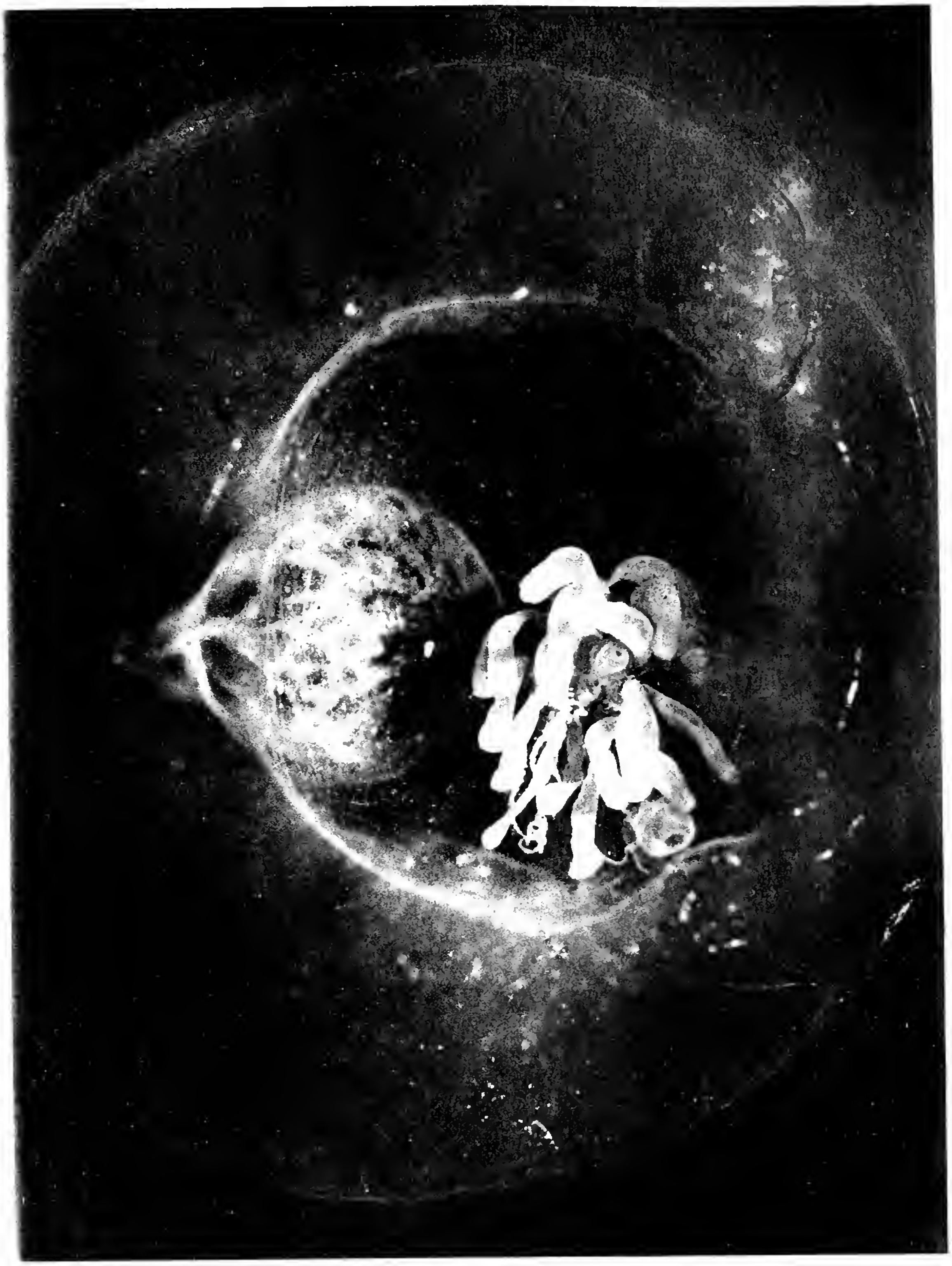


PLATE VII

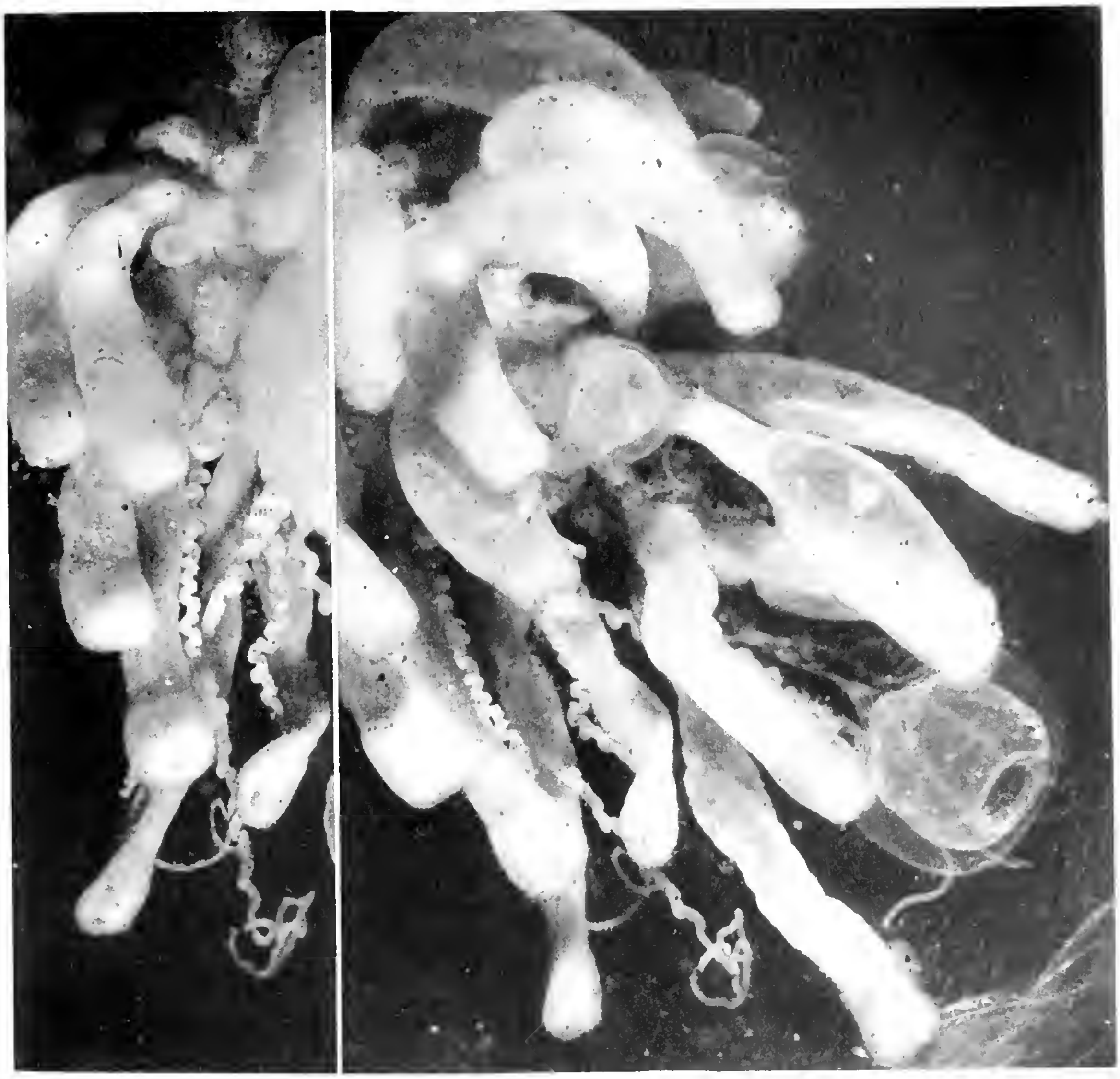
Maresearsia praeclara gen.n., sp.n.

Fig. 1. Gastrozooids and cormidia of holotype specimen. × 23.

Fig. 2. An eudoxid of holotype specimen showing first gonophore partly severed from bract, together with a bud of the second gonophore. × 17.

Fig. 3. A younger eudoxid, bract on the left, gonophore and bud on the right, borne on a peculiar stalk. × 17.

Fig. 4. The bract of a young eudoxid. × 17.



1

2

3

4

PLATE VIII

Abyla schmidti Sears, whole animal. 'Discovery II' St. 1581

Fig. 1. View showing ventral side of the anterior nectophore and right side of the posterior nectophore. × 7.

Fig. 2. End-on view, showing the ostium of the nectosac of the posterior nectophore, and its surrounding teeth. × 5·2.

Fig. 3. View showing the dorsal side of the anterior nectophore and the left side of the posterior nectophore. × 7.

Fig. 4. View showing the right side of the anterior nectophore and the postero-lateral aspect of the posterior nectophore. × 7.

Fig. 5. Apical view of the anterior nectophore, with the large left-hand, hydroecial wing of the posterior nectophore in the background. × 7.

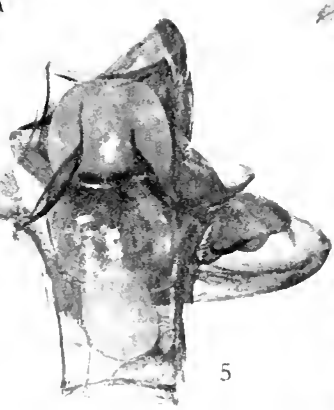
Fig. 6. View showing the left side of the anterior nectophore and the right side of the posterior nectophore. × 7.

1

2

3

4



5

6

PLATE IX

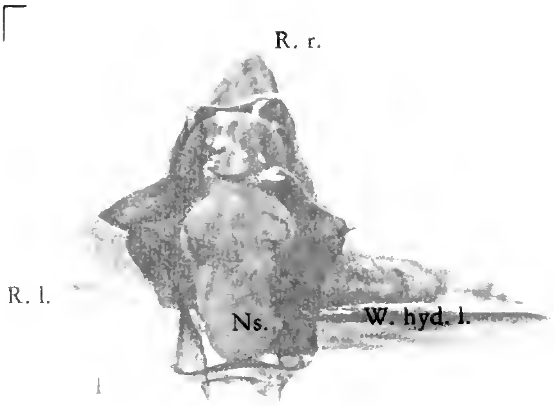
Abyla tottoni Sears, whole animal, × 4. 'Discovery II' St. 1178

Fig. 1. Apical view of the anterior nectophore, with the large left hydroecial wing in the right background.

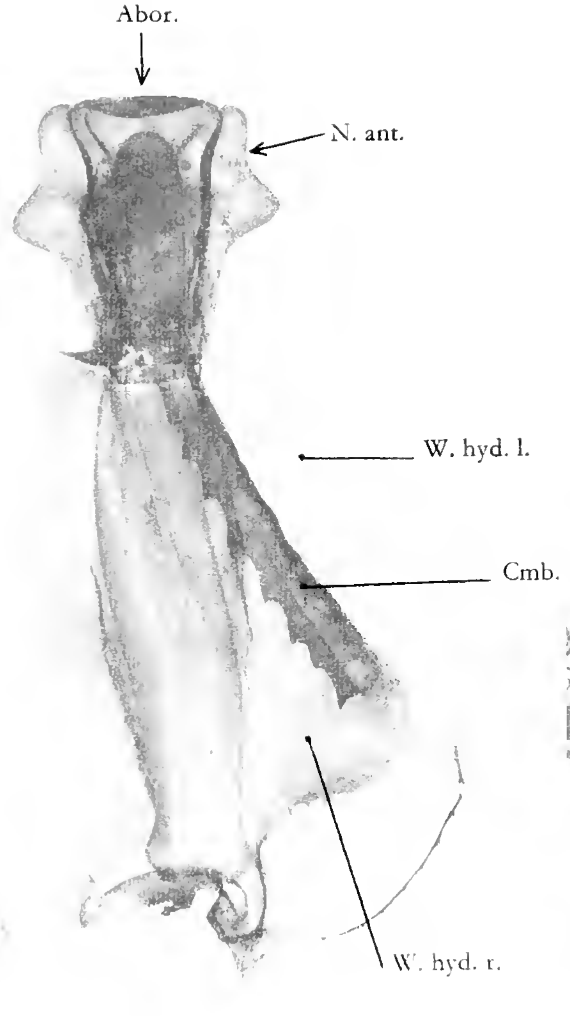
Fig. 2. View showing the ventral side of the anterior nectophore and the right side of the posterior nectophore. The left dorsal ridge is on the right running down to the median dorsal tooth.

Fig. 3. View showing the dorsal side of the anterior nectophore and the left side of the posterior nectophore. The strong teeth on the 'comb' (or inturned edge of the right hydroecial wing) can be seen lying under the larger left hydroecial wing.

Fig. 4. Basal view of the animal, showing the ostium of the nectosac of the posterior nectophore and its surrounding teeth. The large left hydroecial wing lies on the left, and on the right the left dorsal ridge can be seen joining the median dorsal tooth. The right dorsal ridge lies above, and parts of the anterior nectophore are seen in the background. Inset: the ostial region, showing (white pecked lines) the actual junction of the left ridge, *R.l.*, with the median tooth, *To.d.*, and its hypothetical former junction with the left tooth, *To.l.*


R. r.
R. l.
Ns.
W. hyd. l.


V.
D.
R. r.
To. d.


Abor.
N. ant.
W. hyd. l.
Cmb.
W. hyd. r.

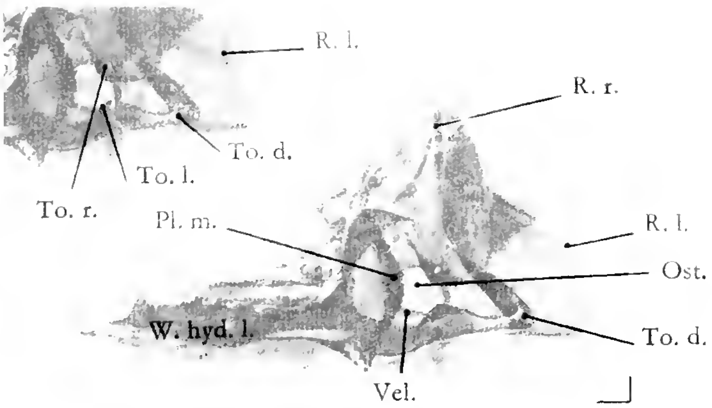

R. l.
To. d.
To. l.
To. r.
R. r.
Pl. m.
R. l.
Ost.
W. hyd. l.
To. d.
Vel.

PLATE IX

Abyla tottoni Sears, whole animal, × 4. 'Discovery II' St. 1178

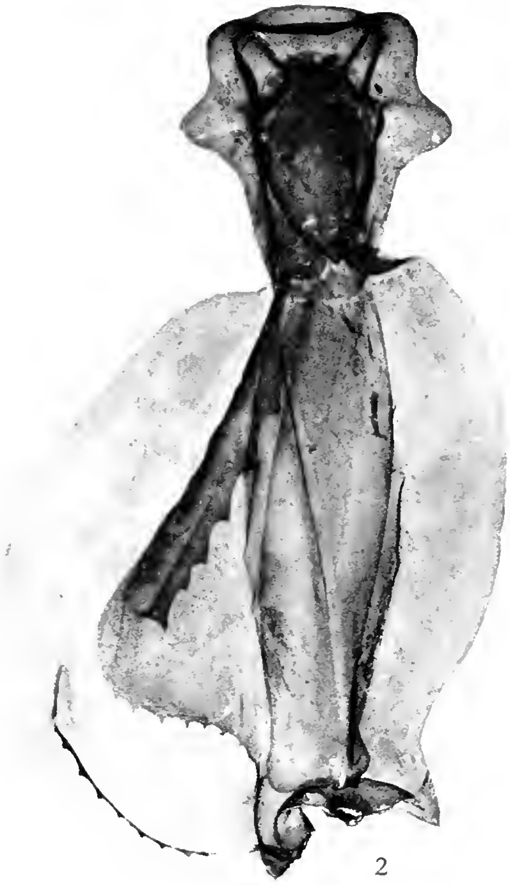
Fig. 1. Apical view of the anterior nectophore, with the large left hydroecial wing in the right background.

Fig. 2. View showing the ventral side of the anterior nectophore and the right side of the posterior nectophore. The left dorsal ridge is on the right running down to the median dorsal tooth.

Fig. 3. View showing the dorsal side of the anterior nectophore and the left side of the posterior nectophore. The strong teeth on the 'comb' (or inturned edge of the right hydroecial wing) can be seen lying under the larger left hydroecial wing.

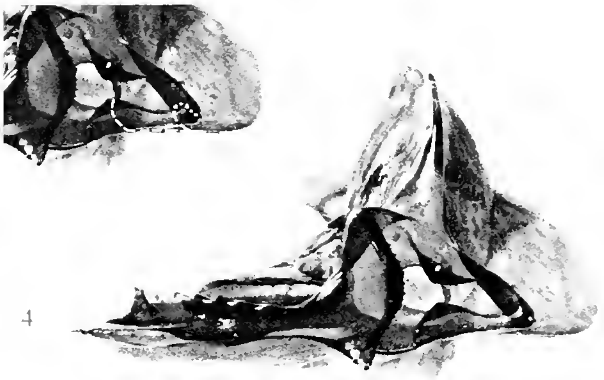
Fig. 4. Basal view of the animal, showing the ostium of the nectosac of the posterior nectophore and its surrounding teeth. The large left hydroecial wing lies on the left, and on the right the left dorsal ridge can be seen joining the median dorsal tooth. The right dorsal ridge lies above, and parts of the anterior nectophore are seen in the background. Inset: the ostial region, showing (white pecked lines) the actual junction of the left ridge, *R.l.*, with the median tooth, *To.d.*, and its hypothetical former junction with the left tooth, *To.l.*

1



2

3



4

PLATE X

Ceratocymba dentata, whole animal. 'Discovery II' St. 2635

Fig. 1. View showing the right side of the anterior nectophore and the ventro-left lateral aspect of the posterior nectophore, showing the remarkably long cylindrical nectosac of the posterior nectophore, and the obsolescent one of the anterior. × 2.

Fig. 2. View showing the dorsal side of the anterior nectophore and the right side of the posterior nectophore. × 2.

Fig. 3. View showing the left side of the anterior nectophore and the ventro-right lateral aspect of the posterior nectophore, showing the elongated left ventral tooth. Eudoxid groups can be seen in the hydroecium of figs. 1–3. × 2.

Fig. 4. Basal view of the animal showing the ostium of the nectosac of the posterior nectophore and its surrounding teeth. In the background parts of the anterior nectophore are seen. In the foreground above can be seen the left dorsal ridge of the posterior nectophore running down to join the left dorsal tooth, and on the left the right dorsal ridge running down to the right dorsal tooth, leaving the median dorsal tooth free. Below are the bases of the two ventral hydroecial wings. × 4.

Fig. 5. Basal part of the posterior nectophore to show the oblique flattened facets, the left-hand one bearing a double fringe of spines, at the base of the ventral hydroecial wings. × 3·5.

1

2

3

4

5

PLATE XI

Ceratocymba dentata, an eudoxid. 'Discovery II' St. 286

Figs. 1–2. Detached ♂ and ♀ gonophores from the upper (attached) side. Their respective median dorsal teeth are facing each other. × 4.

Fig. 3. Bract and gastrozooid of the eudoxid from the outer side, showing on the left the incomplete 'left' ridge. The complete ridge is the misplaced 'right' one. A third gonophore (♀) is still attached, 11 mm. in length. × 2·8.

Figs. 4–5. Detached ♂ and ♀ gonophores viewed from their ventral (opposed) sides, showing the large single teeth at the basal end of the left (and vice versa right) ventral hydroecial wings, also the unequal right and left ventral teeth. × 4.

Fig. 6. *Stephanomia rubra*. Part of a denuded cormidium to show how the nectophores (one young bud visible) are attached to one side (nectosome, on the right) and the appendages to the opposite side (part of the siphosome, on the left). × 17.

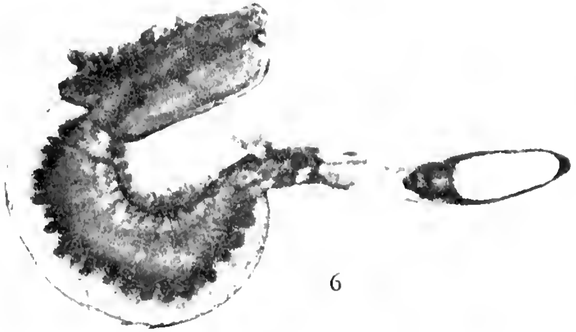
1

2

3

4

5



6

PLATE XII

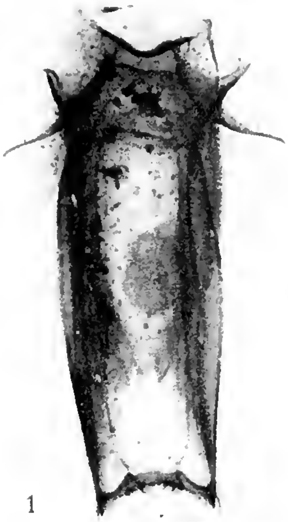
Abyla trigona Quoy and Gaimard, syntypes

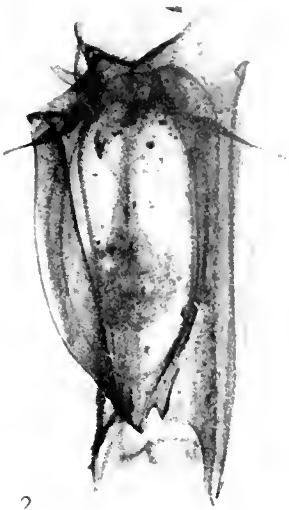
(Musée d'Histoire Naturelle, Paris)

Figs. 1–4. One of the anterior nectophores.

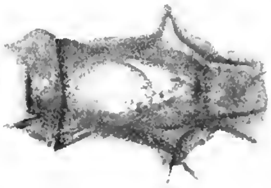
Figs. 5–7. A second anterior nectophore.

Figs. 8–10. A posterior nectophore. Fig. 8 by transmitted light, figs. 9–10 by reflected light.


1


2

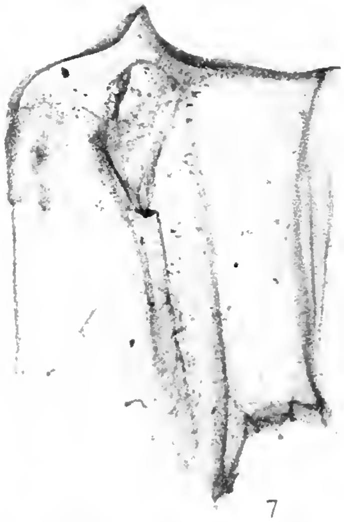

3

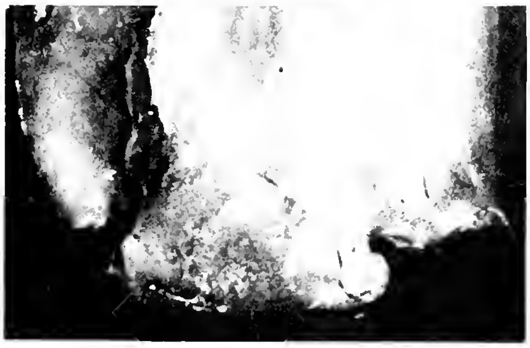

5


4


8


6


7


9


10

[*Discovery Reports. Vol. XXVII, pp.* 163–200, *August*, 1954.]

THE PELAGIC MOLLUSCA OF THE BENGUELA CURRENT

PART I. FIRST SURVEY, R.R.S. 'WILLIAM SCORESBY', MARCH 1950

WITH AN ACCOUNT OF THE REPRODUCTIVE SYSTEM AND SEXUAL SUCCESSION OF *LIMACINA BULIMOIDES*

By

J. E. MORTON, Ph.D.

CONTENTS

THE PELAGIC MOLLUSCA OF THE BENGUELA CURRENT

PART I. FIRST SURVEY, R.R.S. 'WILLIAM SCORESBY', MARCH 1950

WITH AN ACCOUNT OF THE REPRODUCTIVE SYSTEM AND SEXUAL SUCCESSION OF *LIMACINA BULIMOIDES*

By J. E. Morton, Ph.D.

(Text-figs. 1–17)

INTRODUCTION

The Mollusca collected by the R.R.S. 'William Scoresby' during the first of her two surveys of the Benguela Current off the coast of South West Africa (March 1950—Stations WS 964–1002) form a small collection, representing in all eleven species of pelagic gastropods, one larval gastropod, two lamellibranch post-larvae (one species in considerable numbers), and some cephalopod larvae. Of the gastropods the 'pteropods' are by far the largest group and they yielded two species of numerical importance, the gymnosome *Pneumodermopsis paucidens*, and—in special abundance at certain points—the thecosome *Limacina bulimoides*. The latter was taken at five offshore stations lying to the west of the continental shelf, and at two stations was the dominant zooplankton species. The material secured gives valuable information on the depth distribution, reproductive activity and sexual succession of this pteropod. Further, the fixation of the *Limacina* in 5% formalin was in many cases good enough to enable detailed morphological work to be carried out on this species, and the second section of this report has been devoted to an account of reproduction in *L. bulimoides*, in which the genital system has been described in detail and the sexual phenomena of this mollusc discussed.

Lamellibranch larvae occurred close inshore at Walfisch Bay, at the inshore station WS 989, and at the mouth of the Orange River. The cephalopod larvae, which were four in number, have kindly been examined by Dr W. J. Rees of the British Museum (Natural History) and I am grateful to him for allowing me to publish his comments on them. In addition to material from the South West African coast, one haul of *Ianthina* taken with a surface net in north equatorial waters off the north coast of the Gulf of Guinea is conveniently referred to here; while one of the cephalopods (from WS 1091) belonging to second survey material is included for comparative purposes in this report.

For full hydrological data, reference should be made to the detailed Station List already issued for the 1950 cruise of the 'William Scoresby' (*Discovery Reports*, XXVI, 211–58). Preliminary accounts of the hydrological results of the expedition and of the distribution of phytoplankton in the South West African area have already been published (Currie, 1953; Hart, 1953). A table of positions and dates together with surface temperatures and salinities from the stations which yielded mollusca during the first survey is given on p. 166.

ACKNOWLEDGEMENTS

I am indebted to Dr N. A. Mackintosh, C.B.E., of the National Institute of Oceanography for permission to report upon this material. I must also record my appreciation of the kindness of Dr T. J. Hart, at whose suggestion the work was placed in my hands, and who was personally responsible for the heavy task of sorting and classifying the molluscan material from the general bulk samples.

I am also grateful to Dr V. Fretter for a great deal of helpful discussion on reproduction in the Gastropoda, and to Dr H. E. Bargmann and Mr T. J. Evans for their careful and kindly criticism of the manuscript. The greater part of this paper was completed while I was the holder of the University of London Table at the Plymouth Laboratory of the Marine Biological Association, and I have to acknowledge the kindness throughout of Mr F. S. Russell, F.R.S., and others of the laboratory scientific staff.

Table 1. *Positions and hydrological data of stations yielding Mollusca**

Station	Position	Date	Surface temp. ° C.	Surface salinity S ‰
WS 976	From 22° 50′ S, 11° 38′ E to 22° 48′ S, 11° 35′ E	6. iii. 50	19·31	35·32
WS 978	22° 28′ S, 12° 42′ E	7. iii. 50	18·16	35·23
WS 980	22° 44′ S, 14° 08′ E	8. iii. 50	16·97	35·15
WS 981	22° 44′ S, 14° 20′ E	8. iii. 50	16·69	35·15
WS 986	From 22° 15′ S, 13° 06′ E to 25° 13′ S, 13° 08′ E	10. iii. 50	17·10	35·00
WS 987	25° 13′ S, 13° 43′ E	10. iii. 50	15·71	34·97
WS 988	25° 12′ S, 14° 22′ E	11. iii. 50	16·26	35·06
WS 989	25° 11′ S, 14° 39′ E	11. iii. 50	14·82	35·03
WS 996	From 28° 41′ S, 13° 25′ E to 28° 39′ S, 13° 23′ E	12. iii. 50	20·38	35·18
WS 997	From 28° 40′ S, 14° 06′ E to 28° 37′ S, 14° 08′ E	13. iii. 50	20·18	35·20
WS 998	28° 40′ S, 14° 43′ E	13. iii. 50	18·36	35·01
WS 999	From 28° 38′ S, 14° 59′ E to 28° 31′ S, 15° 00′ E	13. iii. 50	18·22	35·00
WS 1002	28° 40′ S, 16° 14′ E	14. iii. 50	14·23	33·64
WS 1091	20° 38′ S, 12° 18′ E	8. x. 50	15·6	—

* See *Discovery Reports, supr. cit.*

I. SYSTEMATIC

Class GASTROPODA

Subclass PROSOBRANCHIA

Order MESOGASTROPODA

Superfamily PTENOGLOSSA

Family IANTHINIDAE

Ianthina ianthina (Linnaeus)

1767 *Helix ianthina* Linn., *Syst. Nat.* ed. 12, 1246.
1798 *Ianthina violacea* Bolten, *Mus. Bolt.* 75.
1815 *Ianthina fragilis* Lmk., *Anim. sans Vertebr.* (earlier ed.).
1835 *Ianthina communis* Lmk., *Anim. sans Vertebr.* (ed. Desch.), 9, 4.
1850 *Ianthina planispirata* A. Ad. & Rve., *Zool. Voy. H.M.S. 'Samarang'*, p. 54, pl. xi, fig. 10.
1853 *Ianthina britannica* Leach in MS., Forbes and Hanley, IV, 260, pl. 133, fig. 1.
1858 *Ianthina balteata* Rve., *Conch. Icon.* XI, pl. 3, fig. 11.
1858 *Ianthina depressa* Rve., *Conch. Icon.* XI, pl. 3, fig. 14*a*, *b*.
1858 *Ianthina trochoidea* Rve., *Conch. Icon.* XI, pl. 2, fig. 10*a*, *b*.
1858 *Ianthina roseola* Rve., *Conch. Icon.* XI, pl. 1, fig. 1*a*, *b*.
1858 *Ianthina africana* Rve., *Conch. Icon.* XI, pl. 2, fig. 8, 8*a*.

Ianthina globosa Swainson

1822 *Ianthina globosa* Swainson, *Zool. Illustr.* II, pl. 85.
1828 *Ianthina nitens* Menke, *Synopsis*, 84.
1840 *Ianthina rotundata* Leach., MS. Dillwyn, *Contrib. towards a History of Swansea*, 59.
1840 *Ianthina pallida* Thompson, *Ann. Nat. Hist.* V, 96.
1844 *Ianthina patula* Phillipi., *Moll. Sicil.* II, 224, pl. 28, fig. 14.
1858 *Ianthina striolata* Rve., *Conch. Icon.* XI, pl. 5, fig. 24*a*, *b*.
1858 *Ianthina iricolor* Rve., *Conch. Icon.* XI, pl. 5, fig. 23*a*, *b*.

Two species of *Ianthina* are represented in this collection from the first survey, both occurring together at each of two places. On the second survey, specimens occurred at WS 1057 and WS 1058 in surface hand-nets. The samples consist of seven *I. ianthina* (of *planispirata-balteata* shape and markings) and four *I. globosa* (mauve-white to pale pinkish, and probably closest in form to Thompson's *pallida*).

From north equatorial waters (0·6° 10′ N, 11° 25′ W), on the northern edge of the Guinea Current, came another sample, four *I. ianthina*—of the typical *ianthina* form—and two large typical *I. globosa*. The Biological Log-book records the presence of the siphonphore *Porpita*, upon which the *Ianthina* were feeding. One *I. ianthina* carried an egg-raft.

These two species are very distinct, wide-ranging over most seas, and would seem very frequently to occur side by side.

The systematics of the genus *Ianthina* are at present in course of full revision by Dr Dan Laursen, who has worked on the extensive Dana material. I have not seen these results, and have therefore in the present account merely assigned the two Benguela species according to the currently accepted view of Iredale (1910), who regarded *Ianthina* as containing four widely distributed species. The first is *ianthina* (Linn.) in which Iredale groups *planispirata*, *trochoidea*, *britannica* and *depressa*. Oliver (1915) considered *violacea* Bolten to include both *communis* and *balteata*, and in addition to these species I have examined *roseola*, *africana* and *fragilis*, as represented in the Winckworth Collection at the British Museum, and would tentatively place all these forms in synonymy with *ianthina*.

In shell features, the distinctive characters of this species are evidently its angled periphery and strongly retracted, sharply triangular apertural sinus. Typical specimens of the form *ianthina* are paler bluish white, above the periphery, and deeper blue below; the chief colour variation in the species is the development of a white band at the central part of the base of the shell, giving the *planispirata-balteata* pattern, of pale blue above, deep blue around and below the periphery and white at the base. In shell height, *depressa* and *planispirata* are the most flattened, *africana* and *trochoidea* the most elevated and conical, distinctly higher than broad.

The second species, *globosa* Swainson, has a much more delicate shell; the whorls are rounded, the body whorl especially large, and bubble-shaped, with an extremely wide trumpet-shaped aperture in the largest adults. There are rather wavy growth lines and these are gently recurved at the periphery, to give a shallow apertural sinus, rounded or obtusely angled. In some forms, especially *pallida*, there may be low, rounded, longitudinal striae, best developed on the body whorl. The colour does not vary much, and is usually paler blue or mauve, and almost white in the form *pallida*.

The two remaining species recognized by Iredale are *exigua* and *umbilicata*. Neither is represented in the Benguela material.

I have provided outline sketches (Fig. 1) illustrating the leading shell characters of *ianthina* and *globosa*. All consideration of radula features, anatomy or life-history has been omitted. These aspects will be dealt with both by Dr Laursen, and also in a forthcoming paper by Professor Graham, on the results of a study of the animals of British *Ianthina* and the effects of growth on shell contour. These results will together give a clearer view of the interrelations of the various forms included in the species of *Ianthina*, and in particular of the influence of life-history on shell form.

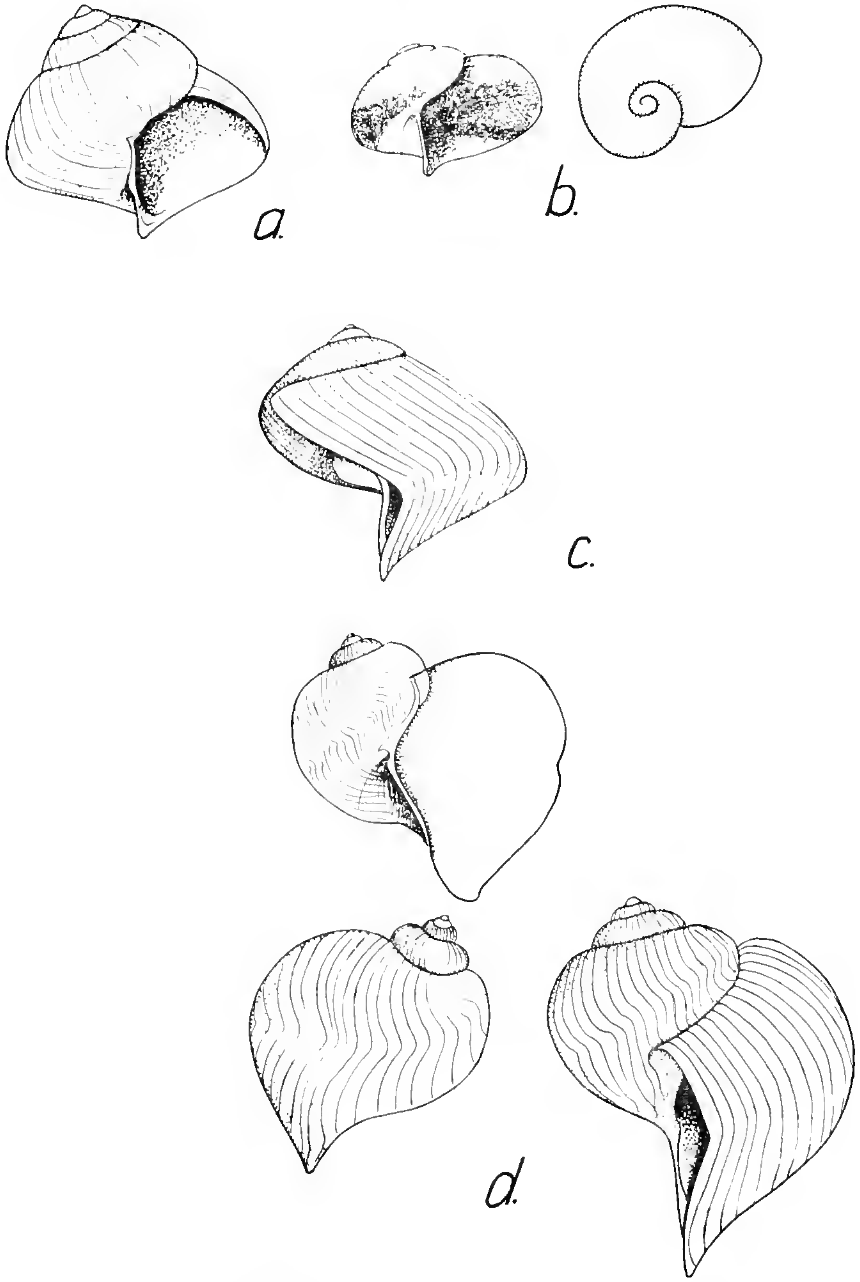


Fig. 1. Sketches of the shells of *Ianthina ianthina* (L.) (*a*, *b*, *c*) and of *I. globosa* Swainson (*d*) to show characteristic range of form. (*a*) *I. ianthina*. The typical *communis*-form (Winckworth Collection, Madras). (*b*) *I. ianthina*. The *planispirata*-form, view from above and in side view. (*c*) *I. ianthina*. View of the *balteata*-form, showing the periphery and strong labial sinus characteristic of the species (shell from WS 1057). (*d*) *I. globosa*. Three views of shells from the Winckworth Collection (Brit. Mus.).

Order MESOGASTROPODA

Unidentified prosobranch larval shells

The three sets of inshore stations, WS 980 and WS 981, off Walfisch Bay, WS 988 and WS 989 off Sylvia Hill, and WS 1002 at the mouth of the Orange River, each yielded shells of a gastropod veliger larva and of lamellibranch larvae. The gastropods at all three stations were of the same species, which—owing to the retraction or loss of the velar lobes and damage to the shell after preservation—were impossible to identify accurately. The largest shells were of 3–3½ whorls, turbinate, with globose, smoothly rounded whorls, the body whorl very large, and the aperture two-thirds the height of the shell, ovoid and entire. There were no special sculptural features, except for the presence in the body whorl of about six well-defined, close-spaced spiral cinguli, encircling the base of the whorl, well below the point of greatest diameter. Numerous earlier stages of various sizes were present. Dimensions of the largest individual: height *c.* 1·5 mm., diameter 1 mm.

Superfamily HETEROPODA

Family ATLANTIDAE

Atlanta peroni Lesueur

1817 *Atlanti peroni* Lesueur, *Journ. Ac. Nat. Sci. Philadelphia*, 1.
1852 *Atlanta rosea* Souleyet, *Voy. de la Bonité, Zoologie*, 11, 373, pl. 19, figs. 1–8.
1949 *Atlanta peroni* Tesch, *Dana Reports*, XXXIV, p. 16, fig. 9.

Table 2. *Occurrence of* Atlanta peroni

Station	Time	Depth (m.)	No. of animals
WS 996	1858 to 1610	50–0	1 adult, 22 juvenile
		100–50	6 juvenile
		500–250	1 juvenile
		1000–750	1 adult
WS 997	0105 to 0401	50–0	3 adults, 1 juvenile
		250–100	1 adult
		500–250	1 adult
		250–0 (extra sample)	5 adults
WS 998	0850 to 0810	175–100	1 adult

This is the only heteropod represented in the present collection. It is an abundant and widespread species, the commonest in Atlantic waters. Tesch (1949) discusses its distribution (p. 21). In the North Atlantic it dwindles south of 20° N and appears to avoid equatorial waters. In the Benguela material it was present on the southern line only, at three stations, WS 996, WS 997, WS 998. The largest specimens measured 4·5–5 mm., and there were in several hauls an abundance of juvenile shells, measuring up to 0·7 mm.

Subclass OPISTHOBRANCHIA

Order PTEROPODA[1]

Suborder THECOSOMATA

Superfamily EUTHECOSOMATA

Family LIMACINIDAE (= SPIRATELLIDAE)

The continued use of the generic name *Limacina* in this paper may be held to require justification. Sherborn (1930) accepted *Spiratella* de Blainville (1817), as displacing *Limacina* as proposed by

---

[1] The single order Pteropoda is employed here to include both the thecosomatous and gymnosomatous pteropods, in keeping with Thiele's system of classification (1931) which has been adopted throughout this section. It is not possible, however, to regard such an order as a natural grouping. Pelseneer (1887, 1888) conclusively demonstrated the separate origins of the two groups of pteropods, placing the Thecosomata at the end of the bullomorph series and regarding the Gymnosomata as being derived from an aplysiomorph stock. He based his classification of 1906 on this view. The present writer (1954*a*) has elsewhere pointed out—from a consideration of feeding and digestive mechanisms in the pteropods—that the reversion by Thiele and by Hoffmann (1938) to a single order Pteropoda cannot be defended on strict phylogenetic grounds.

Cuvier in *Le Règne Animal* (1817), apparently on the ground that the latter name was employed in the form 'les Limacines' and was nowhere in that work explicitly proposed in latinized form. A second pteropod generic name, 'les Pneumodermones', established by Cuvier was saved by the addition of the latinized parenthesis '(Pneumodermon)', which followed the usual practice upon introduction of new generic names in *Le Règne Animal*, but was omitted, evidently inadvertently, in the case of *Limacina*. Lamarck in 1819 validly proposed *Limacina* in conformity with Linnaean practice in the Latin form. Unfortunately de Blainville (1817) had already followed upon Cuvier with the introduction of the term *Spiratella*, which thus by two years antedates *Limacina* Lmk. as the first validly proposed name for these pteropods. Such a loss of the Cuvierian generic name would be particularly unfortunate, in view of its long-established currency and of the obviousness of the editorial slip in the proposition of the name. The general practice in the nineteenth and early twentieth century was to employ *Limacina* without question: thus—for example—Pelseneer (1888), Meisenheimer (1905), Bonnevie (1913) and Vayssière (1915). Following Sherborn (1930), however, two Continental works of first importance have adopted *Spiratella*—Hoffmann's opisthobranch treatise in Bronn's *Tierreiches* (1938) and Thiele (1931) in his authoritative systematic account. In British oceanographic literature the use of *Limacina* has continued unchanged, and the name was most recently employed by Tesch in his two extensive works (1946, 1948).

It is greatly to be doubted whether the progress of systematics is really assisted by excavations from the forgotten past. Here, one might have thought, was a name which could have rested secure and for which a suspension of International Rules might justly have been claimed. It is, however, one of the disadvantages of a rule of law that obedience is necessary even when the consequences appear most irksome. If it does not prove possible to add *Limacina* to the list of *nomina conservanda*, *Spiratella* must unquestionably take precedence of it and come into general use. In the meantime the familiar name *Limacina* is retained in use without apology in both the systematic and morphological sections of this paper.

Limacina inflata (d'Orbigny)

1836 *Atlanta inflata* d'Orbigny, *Voyage dans l'Amérique méridionale*, v, p. 174, pl. xii, 16–19.
1852 *Limacina inflata* Souleyet, *Voyage de la 'Bonité', Zoologie*, II, 216, pl. xiii, figs. 1–10.
1888 *Limacina inflata* Pelseneer, *Challenger Reports*, XXIII, ii, p. 17.
1905 *Limacina inflata* Meisenheimer, *Pteropoda, Wiss. Ergebn. D. Tiefsee-Exped. 'Valdivia'*, IX, 4.
1946 *Limacina inflata* Tesch, *Dana Reports*, v (28), p. 8, pl. i, fig. 1.

Table 3. *Occurrence of* Limacina inflata

Station	Time	Depth (m.)	No. of animals
WS 986	1118	50–0	4
		100–50	17
		250–100	6
		500–250	—
		750–500	1

This is the *Limacina* of the line to the north of the southernmost line; it occurred here at one offshore station, WS 986, and locally outnumbered *bulimoides*, which accompanied it in the 0–50 m. haul only. The species *inflata* was represented by a relatively small number of animals, the shells having been for the most part dissolved by the formalin preservative. But from the size and structural characteristics of the animal there can be little doubt that *inflata* is the species to which it belongs. Moreover, this *Limacina* has been reported several times as accompanying *bulimoides* in great numbers in the Sargasso Sea, and the warm temperate Atlantic. The depressed spire of the animal is of $1\frac{1}{2}$ turns only, and the edge of the mantle is strongly prolonged forward, as in the overarching margin of the shell aperture, most characteristic of this species. The umbilicus was open, and the aperture wide and oval. An operculum was obtained which did not agree very well with the only available figure (Souleyet, *loc.* cit.), being rather more circular in shape.

The depth distribution of *inflata* at this day-time station corresponds closely to what has also been established (see below) for *bulimoides*. It shows its greatest day-time concentration at 50–100 m., thinning out markedly below this level and also at the surface.

Limacina bulimoides (d'Orbigny)

1836 *Atlanta bulimoides* d'Orbigny, *Voyage dans l'Amérique méridionale*, v, p. 179, pl. xii, figs. 36–8.
1852 *Limacina bulimoides* Souleyet, *Voyage de la 'Bonité', Zoologie*, ii, 224, pl. xiii, figs. 35–42.
1888 *Limacina bulimoides* Pelseneer, *Challenger Reports*, xxiii, ii, p. 30.
1904 *Limacina bulimoides* Tesch, *Siboga-Exped. Repts.* 27, iv, p. 13.
1905 *Limacina bulimoides* Meisenheimer, *Pteropoda*, *Wiss. Ergebn. D. Tiefsee-Exped. 'Valdivia'*, ix.
1946 *Limacina bulimoides* Tesch, *Dana Reports*, v (28), p. 9, fig. 5, pl. i, fig. 4.

Table 4. *Occurrence of* Limacina bulimoides

Station	Time	Depth (m.)	No. of animals
WS 986	1118	50–0	8
WS 996	1858	50–0	93
		100–50	1542
		250–100	178
		500–250	25*
		750–500	90*
	1610	1000–750	6
WS 997	0410	50–0	1116
		100–50	468
		250–100	3142
		500–250	13
		750–500	82
	0105	1000–750	76
WS 998	0850	175–100	80
WS 999	1125	50–0	5
		100–50	1
	1200	150–100	29

* Many empty.

This species is one of the more abundant of tropical and subtropical Atlantic Limacinas, and its general distribution has been discussed by Tesch (1946). Of the high-spired species of the genus, *bulimoides* is distinguished from *retroversa* and *australis* by the oval aperture as distinct from the quadrangular. The umbilicus is constricted as in *retroversa*, and almost imperceptible as Pelseneer points out. From the subspecies *balea*, the taller form of *retroversa*, *bulimoides* is best distinguished by the smaller number of whorls, which never reaches ten as in the mature *balea*. The shape of the aperture is not always an easy character to interpret precisely: it may vary within a population with the age of the individual. In typical adult females (1·9 mm.) in the Benguela material the columella is always slightly concave towards the aperture; in earlier stages it may be straight or even convexly curved to the left. A good distinction, however, from all the taller forms of *retroversa* is the absence of a tentacular lobe on the anterior margin of the fin. From *trochiformis*, *bulimoides* is differentiated by its larger size, the presence of an apertural beak and the relatively longer spire. As Tesch says, the shell is tall and turreted and quite transparent, sometimes exhibiting faint longitudinal striae interrupted by growth lines on the last whorl. The aperture is drawn out in front into a beak or rostrum, rounded or more or less pointed. In the Benguela material this is especially well marked in the younger stages, while tending to be obscured in the mature females. A distinctive character is the frequent marking of the suture line with light chestnut brown, which may also be present at the columellar edge of the aperture and around the vestigial umbilicus. A figure of a shell (mature female—1·8 mm.) and of an operculum is given here (Fig. 2).

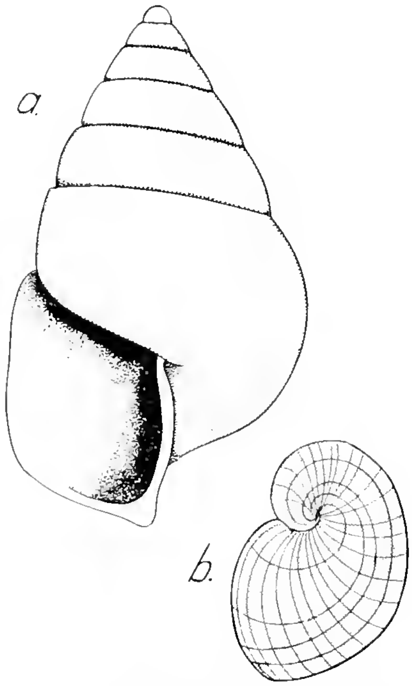


Fig. 2. *Limacina bulimoides*. (*a*) Shell of 'mature female' at stage **6**. Shell height approx. 1·9 mm. (*b*) Operculum, on slightly enlarged scale.

Recorded distribution. According to Tesch this species is very generally distributed in the tropical Atlantic, being nearly always present in large numbers. Its centre of abundance is probably in the Sargasso Sea area; it reaches the eastern United States seaboard and extends, according to Meisenheimer's chart, into the Mediterranean where, however, it is less abundant. Sparser records are from the Indian Ocean and the tropical Pacific. The Atlantic area of *Limacina bulimoides* appears to lie roughly between 40° N and 40° S. Comparing its distribution with that of *L. inflata*, Tesch found its greatest abundance per fishing unit in the upper 100 m. to be 243 against 280 of *inflata* in the Sargasso Sea. In the Benguela hauls of the first survey, this predominance is reversed and *inflata* is never present in large numbers. Off South West Africa *bulimoides* was never taken inshore and was confined in March to the five stations WS 986, WS 996, WS 997, WS 998 and WS 999, near the edge of the continental shelf. It is clearly an oceanic species avoiding the colder up-welled waters towards the coast.

ECOLOGY—DEPTH DISTRIBUTION

The samples from WS 996 and WS 997 were from an area poor in phytoplankton according to Dr Hart (1953).[1] There was some evidence of recent heavy grazing, though the abundant green faeces present were probably attributable to euphausiids. Whatever may have been the economics of this population of *Limacina*, its presence in such numbers must have made greedy inroads on the phytoplankton of the vicinity. Although presumably they had fed rather recently, the stomachs of almost all the numerous specimens sectioned were empty of recognizable contents. In one specimen, coccolithophores were present, which may represent an important part of the diet of this population, and which would, at *c*. 40 μ, be likely to be missed by the N 70 V. plankton net. Of predators probably feeding on *Limacina*, we may mention the abundance of *Pneumodermopsis paucidens* accompanying *Limacina* at a depth of 50–100 m. at WS 997, and a few large *Atlanta* at the same station and at WS 996. Partial exclusion of *Limacina* at 50–100 m. at WS 997 (night station) is evidently not to be explained by the action of predators or by existing hydrological features. An explanation has been ventured below after considering the pattern of depth migration of *Limacina bulimoides*.

Depth distribution. Stubbings (1937) regards the known facts of the diurnal depth migrations of thecosomatous pteropods as consistent with the idea of an optimum light intensity for each particular species. 'At dusk the animal follows the optimum towards the surface and after dark the stimulus to

---

[1] Also in personal conversation.

ascend is removed and the animals probably sink back to the water layers offering the best combination of other factors such as temperature and perhaps salinity. With the coming of dawn they rise to meet the optimum and follow it downwards.' Thus for many species of cavoliniids a double diurnal rhythm is established; those liking a low light intensity will rise very near the surface at night and those preferring a higher intensity will lose the stimulus earlier and sink. At dawn the reverse takes place, those liking a low intensity receiving the stimulus earlier and preceding the others to the surface.

Considering first the two stations WS 996 and WS 997, we find great abundance of *Limacina bulimoides* by day (4 to 6 p.m.) and by night (1 to 4 a.m.) (Fig. 3). At WS 996 the day-time distribution shows a maximum at 50–100 m. (1542) and relatively few (93) at 0–50 m. From 100–250 m. the numbers fall away markedly to 178, and the fall continues, decreasing fairly evenly down to 750–1000 m. where only six specimens were taken. The species is virtually excluded below 250 m., some of the shells counted here being dead. Of the three smaller day-time samples, no station yielded sufficient material to compare adequately with WS 996. At WS 986 (11 a.m.) (on the line immediately north of the southernmost one—the other four stations being on the southernmost line) there were only eight specimens taken and these were all at 0–50 m. At WS 999 at noon there was a small maximum (twenty-nine) at 100–150 m., and at WS 998 (8 a.m.) *Limacina* was found only at 100–175 m. where there were eighty. For the night distribution at WS 997 there were 1116 just below the surface (0–50 m.), many fewer (468) at 50–100 m. and the greatest number anywhere recorded (3142) between 100 and 250 m.

On the basis of much smaller samples than the above, Stubbings finds the vertical distribution of cavoliniids (with the exception of the abnormal *Creseis virgula* which he regards as not controlled by light intensity) to vary between 250 m. for *Creseis acicula* down to 650 m. for *Clio cuspidata* and 700 m. for *Diacria quadridentata*, with *Clio pyramidata*, *Cavolinia globulosa* and *Hyalocylia striata* at intermediate optima from 400 to 600 m. All show a well-marked surface migration by night, and well-developed diurnal depth behaviour (see Stubbings, 1937, fig. 1, p. 27).

When considering the depth distribution and light response of *Limacina*, it is important to keep its much smaller size in mind. A journey to the surface from 250 m. in the six hours after dusk would entail continuous travel at the rate of 2 ft. per minute, a performance greatly in excess of what I have found *L. retroversa* capable of maintaining for even a short time (Morton, 1954*c*). On grounds of size alone we should thus expect species of *Limacina* to be much less sensitive to changes in illumination than the larger cavoliniids, if only because they are not large or swift enough to swim away from regions of diurnal changes in light intensity. We might expect to find them remaining rather near the surface as grazers on phytoplankton and tolerant of strong light. If they abandon the surface too far by avoiding light during the day, they will be unable to reach it again by night. A similar reasoning may explain the preference for the upper layers of the two smaller and more slender cavoliniids *Creseis virgula* and *C. acicula*. These have a relatively tiny wing expanse and no doubt limited diurnal swimming powers. The cavoliniids occurring deepest are the larger and more robust ones. The greatest density of *Limacina bulimoides* by day at WS 996 is between 50–100 m. This is much nearer the surface than any optimum recorded for cavoliniids (with the exception of *C. virgula*), and this layer probably represents the maximum light concentration above which *Limacina* is not happy by day. With the doubtful exception of WS 886, *L. bulimoides* was never found predominantly in the upper 50 m. by day. The ninety-three individuals present at 0–50 m. at WS 996 were but a small portion of a population in very much greater concentration in the layer immediately below. The most numerous day-time samples came from 50 to 100 m., 100 to 150 m. and 100 to 175 m. Light response by large diurnal depth changes seems to be a feature that arose with the cavoliniids; the more primitive limacinids show it

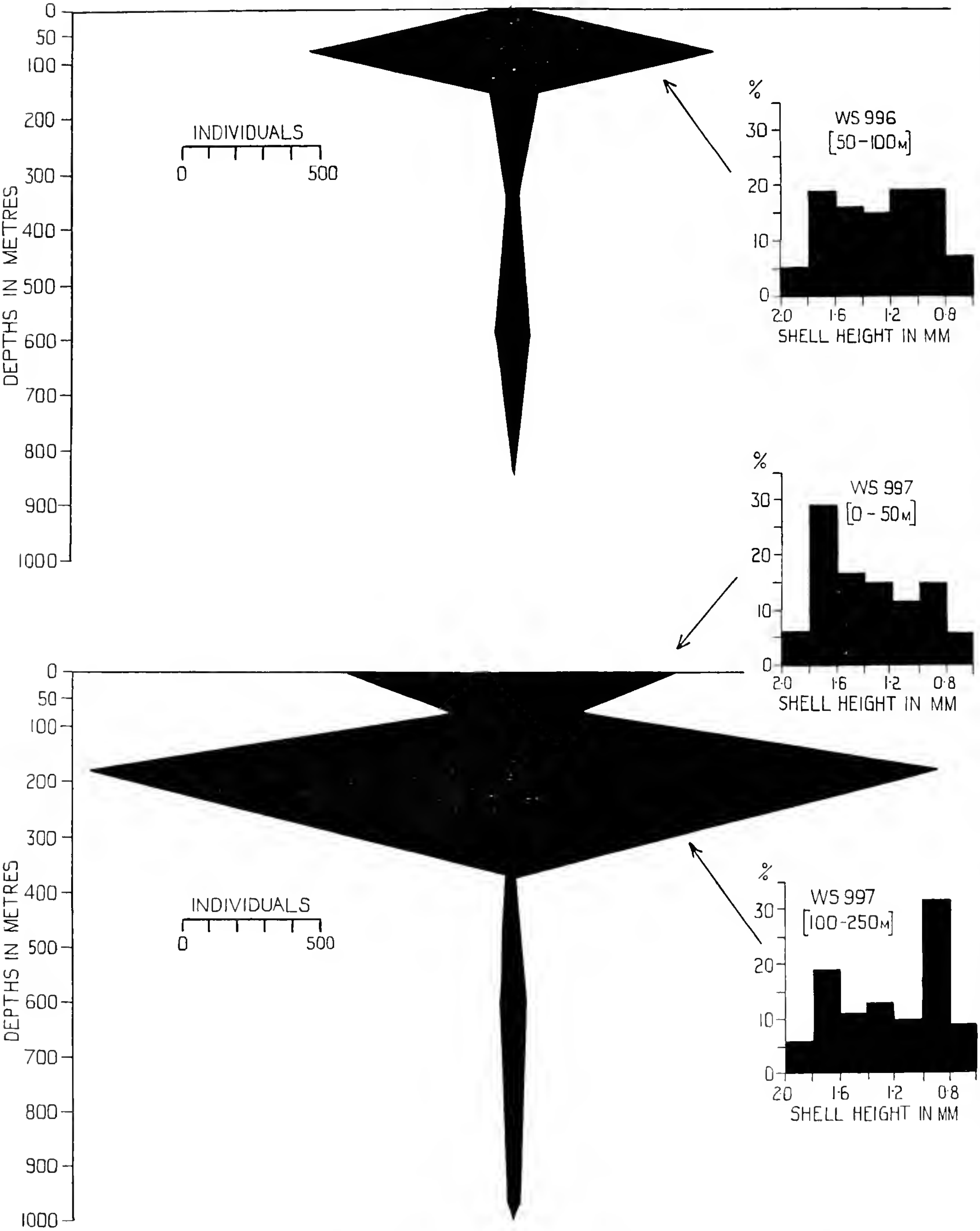


Fig. 3. *Limacina bulimoides*. Depth distribution diagrams for populations at the day-time station WS 996, and the night station, WS 997. (*Insets*) Histograms showing size composition of the population at WS 996 (50–100 m.), WS 997 (0–50 m.) and WS 997 (100–250 m.).

much less. It is perhaps worthy of note that *L. helicoides*, by far the largest species of *Limacina* (12·5 mm.) is also the only one found regularly at great depths (see Tesch, 1948).

It follows that at the night station WS 997, worked between 1 and 4 a.m., we should not expect to find a great concentration of the population at the surface. Those species accustomed to a high concentration of light should lose the impulse to come to the surface soon after dark, and would have begun to sink downwards by the early hours of the morning. Such a species will probably rise again early with the dawn, but hauls between 1 and 4 a.m. may be expected to coincide with the period of night when the stimulus to rise is weakest. From the greatest concentration by night at the 100–250 m. level, *L. bulimoides* would seem to show little upward movement—perhaps even a descent, from its day-time optimum. The greatest depth at night, however, is still less than that of any cavoliniid optimum (except *Creseis virgula*) by day, and the population of *Limacina* as a whole is probably not significantly responsive to light at all. There is an apparent tendency for a minority to rise to the surface at night. It is probable that only the larger individuals and strongest swimmers will be able to make this migration, and that these individuals will come not from the 250 m. level but from water layers of less than 100 m. depth. Further, the individuals at the surface at night may be expected to be mainly large ones.

How does the size composition of the population at various depths at WS 997 agree with this conclusion? By reference to the histograms (Fig. 3) for the levels 0–50 m. and 100–250 m., a great falling off is found in the percentage of small individuals near the surface—twenty-one as compared with forty-one for the added percentages of the two lowest size groups. Conversely there is an increase in the percentage of larger individuals at the top, thirty-five as compared with twenty-five for the added percentages of the two largest size groups. In the more homogeneous day-time population at WS 996, the comparative percentages are twenty-four for the two large groups and twenty-six for the two smallest groups. It may thus be possible to explain the constriction in the distribution diagram for WS 997; there is a tendency to depth division of the population at night, larger individuals tending to rise nearer to the surface. The bulk of the population including smaller individuals and those present in the deeper layers of the day-time distribution, are not able to reach the surface at night, and show little tendency to migrate at all. Perhaps with no light stimulus to hold them at day-time level, they tend to sink a short distance, which they do faster and more easily than they are able to compensate by swimming up. It would be interesting to look for similarly constricted distribution figures for the night behaviour of other planktonic organisms relatively feebly responsive to light.

Superfamily EUTHECOSOMATA

Family CAVOLINIIDAE

Superfamily PSEUDOTHECOSOMATA

Family CYMBULIIDAE

These two families, constituting the larger size thecosomatous pteropods, were rather poorly represented among the mollusca of the first survey, the first by small numbers of juvenile individuals of three species, and the second by a single juvenile individual.

Diacria trispinosa (Lesueur)

1821 *Hyalaea trispinosa* Lesueur, in de Blainville, *Dict. de Sci. Nat.* XXII, 65–83.
1905 *Diacria trispinosa* Meisenheimer, *Pteropoda*, *Wiss. Ergebn. D. Tiefsee-Exped. 'Valdivia'*, IX, 27.
1946 *Diacria trispinosa* Tesch, *Dana Reports*, XXVIII, p. 24, pl. iii, fig. 14.

This species occurred only at WS 986, represented by three individuals at 50–100 m., and two at 100–250 m. The three first specimens are the young form, the *Cleodora compressa* of Souleyet, terminating in a rounded embryonic shell (one of 2·5 mm. the other two of *c.* 1 mm.). The others are slightly older, representing 'stage B' of Tesch, 3 mm. in length. The species is, according to Tesch, eurythermic, ranging widely from the tropical into the temperate Atlantic.

Table 5. *Occurrences of Cavoliniidae and Cymbulidae*

Station	Time	Depth (m.)	No. of animals
		Diacria trispinosa	
WS 986	1118	100–50	3 juveniles
		250–100	2 juveniles
		Euclio pyramidata	
WS 986	1118	1000–750	1 juvenile
WS 996	1858 to 1610	500–250	2 juveniles
WS 997	0105 to 0410	50–0	2 juveniles
WS 997	—	750–500	1 juvenile
		Cavolinia inflexa	
WS 997	0105 to 0410	250–100	1 juvenile
		Cymbulia peroni	
WS 986	1118	100–50	1 juvenile

Euclio pyramidata (Linn.)

1767 *Clio pyramidata* Linnaeus, *Syst. Nat.* ed. 12, 1, pt. ii.
1905 *Clio pyramidata* Meisenheimer, *Pteropoda, Wiss. Ergebn. D. Tiefsee-Exped. 'Valdivia'*, IX, 21.
1946 *Euclio pyramidata* Tesch, *Dana Reports*, XXVIII, p. 14, pl. ii, fig. 11.

This is much the most numerous species of the genus, and is widely distributed throughout the Atlantic. Four records were obtained, all from the deeper layers and represented by a few very young specimens. They are not easy to identify after the erosion of the shell by formalin, and two measure only 1 mm., the larger ones about 3·5 mm. They are placed in *pyramidata*, since they show no trace of the enlarged foot characteristic of the rest of the species of the genus.

Cavolinia inflexa (Lesueur)

1813 *Hyalaea inflexa* Lesueur, *Mém. sur quelques Anim. Moll.* etc., *Nouv. Bull. Soc. Philom.* III, 281–5, figs. i–v.
1905 *Cavolinia inflexa* Meisenheimer, *Pteropoda, Wiss. Ergebn. D. Tiefsee-Exped. 'Valdivia,'* IX, 35.
1946 *Cavolinia inflexa* Tesch, *Dana Reports*, XXVIII, p. 30, pl. iii, fig. 21.

This species occurred at WS 997 only, represented by very young specimens—1 mm. long. It is to be regarded as a very common species from 40° N to 40° S—and it is worthy of remark that no more numerous or adult material of any of the above pteropods was available.

Cymbulia peroni de Blainville

1818 *Cymbulia peroni* de Blainville, *Dict. de Sci. Nat.* XII.
1946 *Cymbulia peroni* Tesch, *Dana Reports*, XXVIII, p. 37, pl. v, figs. 27, 28.

One juvenile specimen of the eastern Atlantic species *Cymbulia peroni* was taken, at 50–100 m. at WS 986.

Suborder GYMNOSOMATA (= PTEROTA)
Families THLIPTODONTIDAE and PNEUMODERMATIDAE

Table 6. *Occurrences of Gymnosomata*

Station	Time	Depth (m.)	No. of animals
	Thliptodon diaphanus		
WS 996	1610 to 1858	500–250	1
	Pneumodermopsis paucidens		
WS 996	1610 to 1858	100–50	82
		250–100	34
		500–250	2
		750–500	2
		1000–750	3
WS 997		50–0	7
		250–0	6

Thliptodon diaphanus Meisenheimer

1905 *Thliptodon diaphanus* Meisenheimer, *Pteropoda, Wiss. Ergebn. D. Tiefsee-Exped. 'Valdivia'*, IX, 59.
1926 *Thliptodon diaphanus* Pruvot-Fol, *Moll. Ptérop. gymnos. Rés. Camp. Sci. Monaco*, LXX, p. 28, pl. 3, fig. 79.
1942 *Thliptodon diaphanus* Pruvot-Fol, *Gymnosomata I, Dana Reports*, XX, 23, figs. 20–5.
1950 *Thliptodon diaphanus* Tesch, *Gymnosomata II, Dana Reports*, XXXVI, 22, figs. 10, 11.

Thliptodon diaphanus was the only gymnosomatous pteropod beside *Pneumodermopsis paucidens* to be taken by the first survey, and it occurred as one specimen only at 250–500 m. at WS 996. Its recorded distribution shows it to be an essentially oceanic species with a wide range over all the warmer regions. In the Atlantic Ocean (Massy, 1917) it reaches the west coast of Ireland (52° N) while in the Pacific it seems to attain its southernmost extreme at 45° S on the New Zealand coast. It is a species of the upper layers as well as of the deep sea.

The leading character of the genus *Thliptodon* is the enormously swollen head, which contains a pair of large bladders ('Schlundblasen') and two very roomy hook-sacs, in which lie a number of golden-coloured hooks. The number of these is of taxonomic importance. Otherwise the only reliable specific character is the radula. The fins form a pair of narrow outgrowths at the constriction between the enlarged head and the rest of the body, and frequently—as in this specimen—both they and the lobes of the foot are difficult to see, being withdrawn into folds of the baggy skin. In the specimen dealt with here, the number of hooks in either sac is about fifteen, decreasing in length inwards as is the case in *diaphanus*.

My figure of the radula does not perfectly agree with either of those of Pruvot-Fol (1926, 1942) or with that of Tesch (1950), but the differences are not hard to reconcile among these variant drawings. Pruvot-Fol's (1926) figure and my accompanying one (Fig. 4*a*) both show a narrow arcuate transverse bar, all that can be seen of the median tooth. Tesch (1950), however, is probably correct in figuring this tooth as a broader plate which is for the most part extremely thin, fragile and transparent, and impossible to see in my probably damaged specimen. The anterior edge of the tooth, however, is considerably more thickened than would appear from Tesch's figure, and I was able to detect a row of the finest denticulations, like those figured by Pruvot-Fol (1926). At the inner edge of the intermediate plate is a short but strong spine. In the specimen figured, this did not appear so strongly curved down as in Tesch's figure or in either of Pruvot-Fol's, and—as Tesch also claimed—the denticles are lacking from the spine of the intermediate plate. The rest of the antero-median margin is exactly as in Pruvot-Fol's first figure, and the three falciform laterals agree well with the previous illustrations.

Differences between this radula and that of *Thliptodon rotundatus* lie in the absence of the long curlew's bill spine at the inner end of the intermediate tooth, and the smaller width of the median. From both *schmidti* and *gegenbauri*, on the other hand, *diaphanus* is well distinguished by the greater width of the median tooth compared with that of the intermediate tooth.

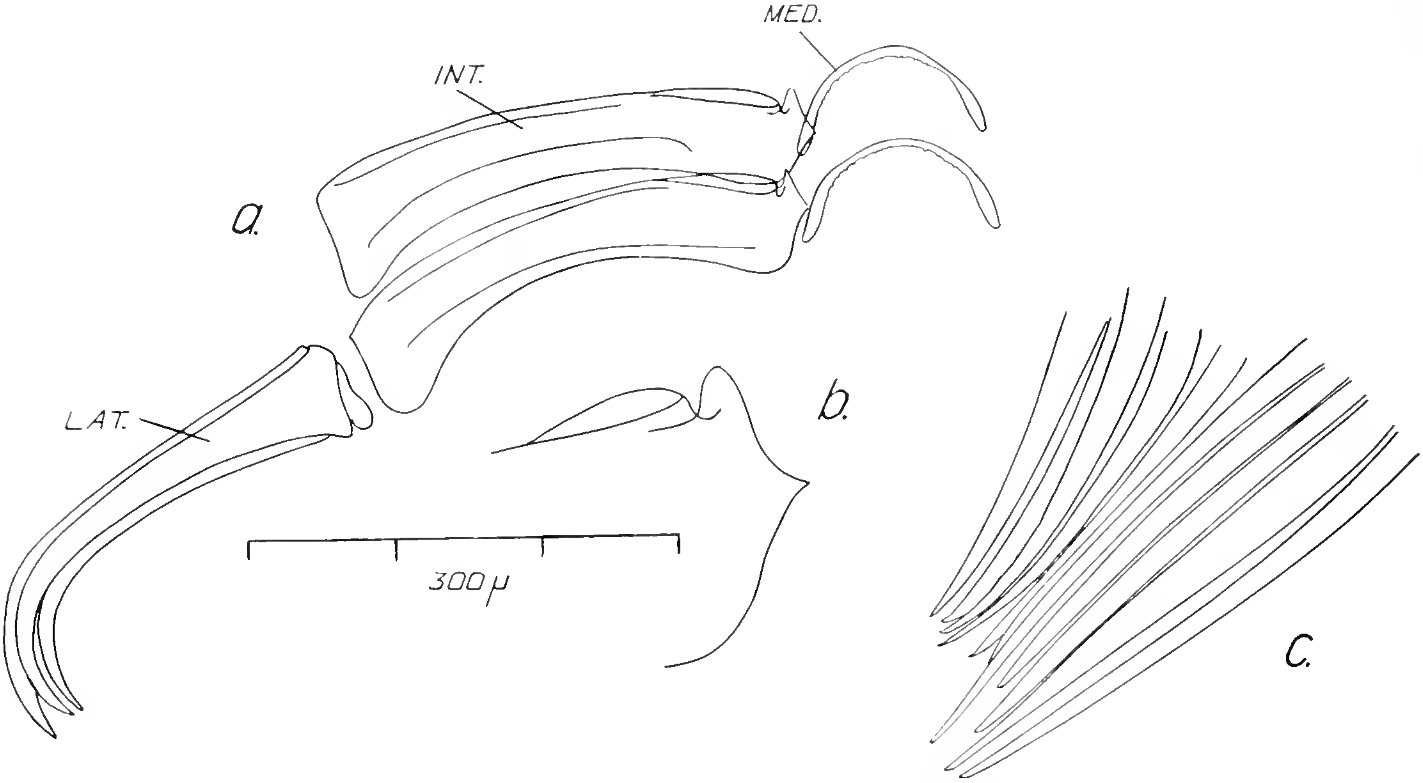


Fig. 4. *Thliptodon diaphanus*. (*a*) The radula, showing the median plate and the intermediate and lateral plates of one side. *INT.*, intermediate plate; *LAT.*, lateral plate; *MED.*, median plate. (*b*) Enlarged detail of the mesial edge of the intermediate plate. (*c*) A bundle of hooks from the hook-sac of one side.

Pneumodermopsis paucidens Boas

1886 *Pneumodermopsis paucidens* Boas, *Spolia Atlantica. Dansk. Vid. Selsk. Skrift.* IV, 160, pl. vii, figs. 105–6.
1887 *Dexiobranchaea paucidens* Pelseneer, '*Challenger*' *Reports*, XIX. *Pteropoda*, I, 17.
1926 *Pneumodermopsis paucidens* Pruvot-Fol, *Moll. Ptérop. gymnos. Rés. Camp. Sci. Monaco*, LXX, 12, pl. i, figs. 36–7.

This species was very local in its occurrence in first survey material. It was taken in considerable numbers at 50–100 m. and at 100–250 m. at WS 996, and makes a second appearance at WS 997, where it was rather sparsely represented. It turned up nowhere else. Its greatest abundance at WS 996 may be related to the heavy concentration of *Limacina bulimoides*, since it is chiefly upon small thecosomes that these Gymnosomata are thought to feed. A close agreement is apparent between the depth distribution of *P. paucidens* at station WS 996 (Fig. 5) and that of *Limacina* at the same station. The night station, WS 997, did not yield sufficient numbers of individuals for an adequate comparison, but the day-time distribution of this gymnosome is in agreement with Meisenheimer's conclusion (1905, p. 98) that the Gymnosomata ('Tagtiere')—unlike most of the thecosomes—approach the surface by day.

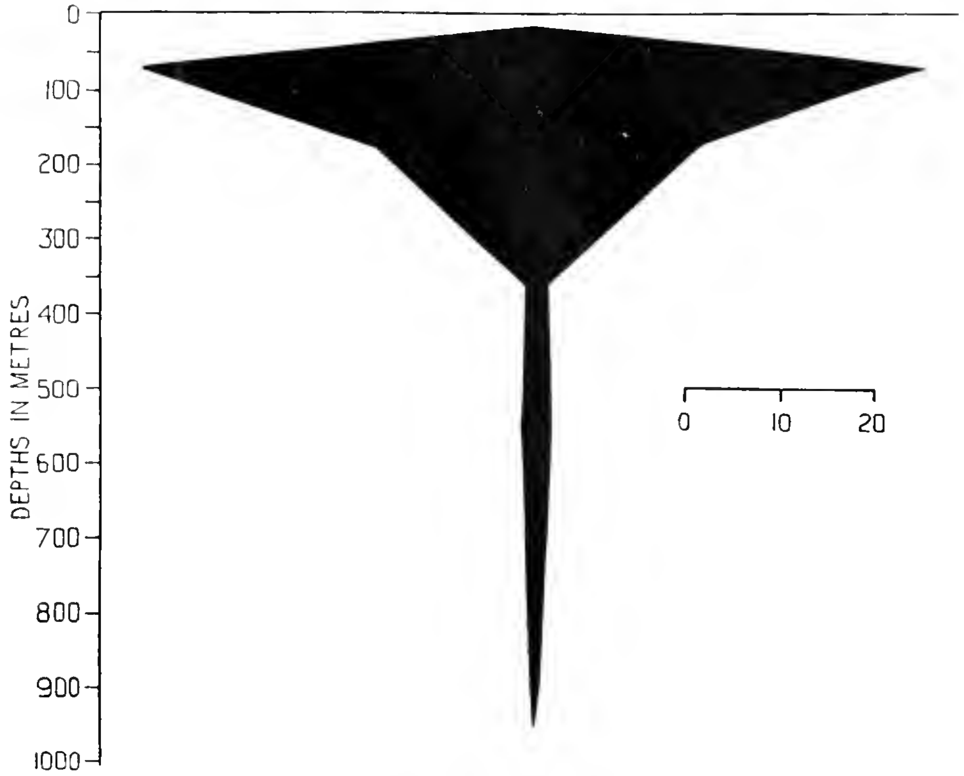


Fig. 5. Depth distribution of *Pneumodermopsis paucidens* at the day-time station WS 996.

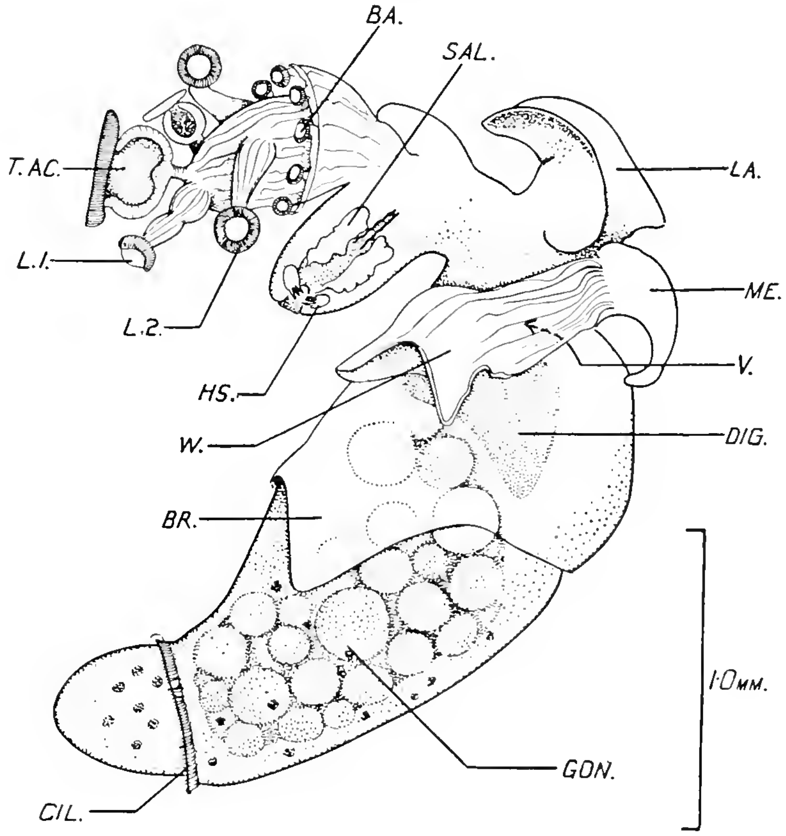


Fig. 6. *Pneumodermopsis paucidens*. The animal viewed from the right side, with the buccal apparatus fully extended. *BA.*, row of basal suckers; *BR.*, gill; *CIL.*, posterior ciliated circle; *DIG.*, area of digestive gland; *GON.*, gonad; *HS.*, hook-sac; *LA.*, lateral lobe of foot; *L.1*, lateral sucker of first pair; *L.2*, lateral sucker of second pair; *ME.*, median lobe of foot; *SAL.*, salivary gland; *T.AC.*, enlarged terminal sucker; *V.*, position of genital opening (female); *W.*, right wing.

The anatomy of the genus *Pneumodermopsis* has been best described by Pruvot-Fol (1924). The distinctive feature of the group is the presence of a membranous triangular outgrowth forming a lateral gill on the right side, somewhat beyond the point of greatest diameter. There is no posterior gill, and in some species—such as the present one—the posterior ciliated circle may persist long into adult life. The hook-sacs are extremely small, forming a pair of short, blunt outgrowths at the sides of the buccal mass, each containing a cluster of short chitinized hooks. The posterior (or median) lobe of the foot is long, tapering and slender. The species represented here is clearly *P. paucidens* Boas. Its chief distinguishing character is the number and arrangement of the suckers borne on the acetabuliferous appendages inserted on the dorsal wall of the buccal cavity. There is a long median arm with a single large terminal sucker, more than twice the size of the lateral suckers, and much larger indeed than might be deduced from the diagrammatic illustration of Tesch's key (1950). Two pairs

Fig. 7. *Pneumodermopsis paucidens*. Outline drawings of a representative group of twelve specimens from station WS 996, showing some of the variations of form encountered in preserved material.

of pedunculate lateral suckers are inserted upon the stalk of the large median sucker, and at the base of the stalk, inserted directly upon the wall of the buccal cavity and almost encircling it, is a single transverse row, consisting on either side of the middle line of five small, sessile suckers.

Species of *Pneumodermopsis* appear in general to be of rather restricted distribution. *P. paucidens* was first described from the tropical Atlantic (Boas, 1886) and Massy (1917) has recorded it as reaching the south-west coast of Ireland. Pruvot-Fol gives some further subtropical Atlantic localities, and mentions (1942) its occurrence in the Indo-Pacific.

The considerable amount of material obtained from the Benguela survey yielded several rather well-expanded specimens by which identification was greatly assisted, and it has been thought worthwhile to provide a figure (Fig. 6) for this species, since detailed illustrations appear to be altogether lacking. Like all the Gymnosomata, *P. paucidens* suffers great distortion upon preservation. The foot and wings are frequently lost from sight, disappearing into a roll of skin surrounding the middle of the body like a tyre. The buccal armature is but rarely well-extended. At times, however, even a misshapen specimen yields outlines rather characteristic of its species when preserved, and I have provided here a series of outline figures representing the size range and the more typical modes of distortion found in a series of specimens from the larger sample at WS 996 (Fig. 7).

Class LAMELLIBRANCHIATA

Order EULAMELLIBRANCHIATA

Two species of lamellibranch larvae occurred at the three sets of inshore stations. The first, lamellibranch larva 'A', was from WS 981, off Walfisch Bay, where 540 specimens were taken in 0–50 m. The second species, lamellibranch larva 'B', was present off Sylvia Hill, at WS 988 (two larvae at 0–50 m., one at 50–100 m.) and at WS 989 (six larvae in 0–50 m.), and, much more numerously, at the mouth of the Orange River where a sample of about 600 was secured at WS 1002 (0–50 m.).

The Station WS 1002, off Walfisch Bay, is in the area of an 'azoic zone' where the bottom deposit consists of a mud populated with sulphate-reducing bacteria (Currie, 1953; Marchand, 1928). It would appear that settlement of the larval lamellibranch taken in large numbers in the plankton hauls is scarcely possible on this ground, and Currie observes that during March oxygen depletion of the water was most marked near Walfisch Bay, water with less than 1·0 c.c. oxygen per litre extending in some places to the sea surface.

Lamellibranch larva 'A' (Fig. 8)

The largest individuals of this species consisted of a 'veliconcha' made up of the two 'prodissoconch' shell stages, and measuring 290–300 μ in length. The smallest members of the population were late stages of the 'D-shaped larva', still possessing the straight-line hinge along about half the visible dorsal margin, and measuring 150–180 μ in length. In neither of the species of lamellibranch larvae were details of the hinge-teeth easily available for examination; shells preserved in formalin were softened so that their shape became distorted on applying the methods for opening recommended by Rees (1950). Outline figures of the intact shells are, however, provided, in the hope that a further knowledge of lamellibranch larvae of this region or correlation with the occurrence of adults on shore may enable a more exact identification of this material.

Details of hinge-teeth were available by examination of the transparent intact shell of the late D-shaped or straight-hinged stage. Here, although there is already some differentiation of hinge-teeth, the hinge structure is unfortunately not advanced enough to justify comparison with the stages figured for the main superfamilies by Rees (1950). The provinculum at this stage appeared to bear no teeth at all, but a simple lateral hinge system was present. In the left valve, lateral teeth are developed in the form of solid triangular wedges, accommodated in shallow depressions in the right valve. These teeth lie at either end of the featureless provinculum, two smaller teeth posteriorly, one large tooth anteriorly.

Lamellibranch larva 'B' (Fig. 9)

This species—at the more advanced stages present—is of larger size than larva 'A'. Its shape is more orbicular with the beaks rather less prominent. The shell-length of the largest individuals is approximately 500 μ, and the smallest, which just passed the straight-hinged D-shaped stage, measure 150 μ in length.

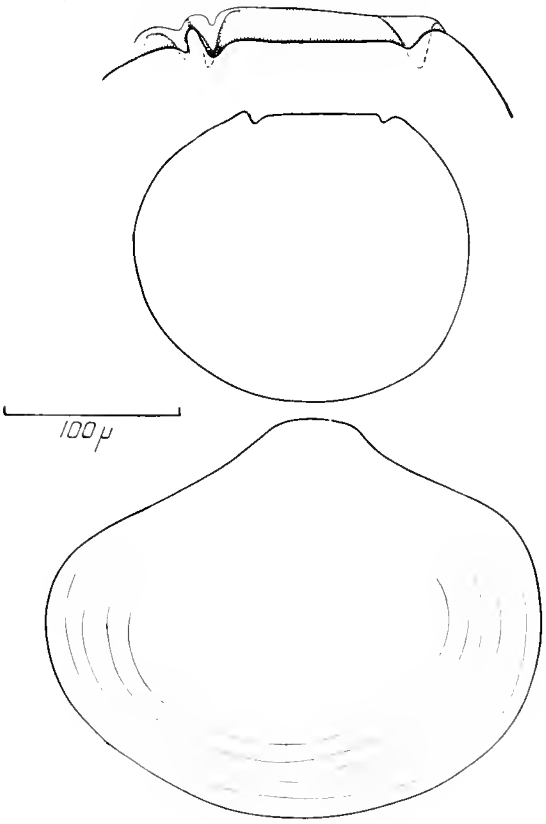


Fig. 8. Shell of lamellibranch larva 'A' from inshore station WS 981, off Walfisch Bay. (*Above*) The hinge-line of the late 'D-shaped stage', the right valve towards the observer.

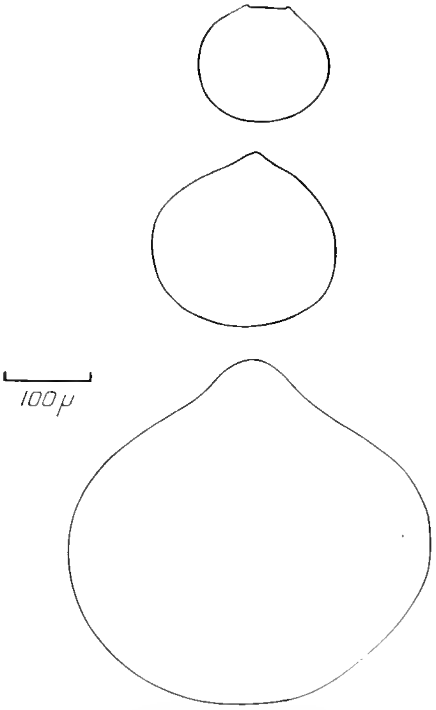


Fig. 9. Shell of lamellibranch larva 'B' from inshore station WS 1002, off Orange River.

Class CEPHALOPODA
Subclass DIBRANCHIA
Order DECAPODA
Superfamily ARCHITEUTHACEA

Four specimens of oigopsid larvae were present in the Benguela material, and—chiefly because of the incompletely known life-histories of oceanic decapods of the South Atlantic area—presented some difficulty in assigning to genera. Specific identification has not been ventured on, but by the kindness of Dr W. J. Rees, who has examined the material, I am able to provide the following notes.

1. A cranchiid larva, approximately 5 mm. in length, with the characteristic features of a bursiform body, very short series of eight sessile arms, and protuberant or pedunculated eyes. The body is unpigmented, and the eyes reddish brown. The specimen 'compares very favourably with the juvenile *Taonidium* figured by Chun (1910), Pl. 61, fig. 9'.

Occurrence. WS 976, 250–500 m.

2 and 3. Two very juvenile larvae, not long out of the egg. The body is colourless, the eyes sessile and the arms very short and subequal. Beyond the position of these larvae in the Architeuthacea, it is possible to establish very little about them.

Occurrence. WS 978, 350–500 m., one specimen, *c.* 3·5 mm.; WS 978, 250–500 m. (second haul), one specimen, *c.* 2·5 mm.

4. A larval histioteuthid, agreeing largely with the figure of a young stage of *Calliteuthis reversa*, given by Naef (1923), p. 355, fig. 174: 'Naef was working in the Mediterranean on two histioteuthids which he could separate because there are only two adult species known in that area. In the Atlantic there are at least six species which may have larvae of this kind.'

Occurrence. WS 1091, surface to 100 m., one specimen, *c.* 7·5 mm.

II. THE REPRODUCTIVE SYSTEM AND SEXUAL SUCCESSION OF *LIMACINA BULIMOIDES*

It is to the work of Hsiao (1939*a*, *b*) that we owe almost our whole knowledge of reproduction in *Limacina*. He gave an account of the reproductive system in *L. retroversa* and established that this animal is a protandrous hermaphrodite passing after a sexually undifferentiated period through a male stage, succeeded by a phase that is predominantly female. He worked with sufficiently large numbers to establish the incidence of sex phases among the size groups in a population at different times of the year. A knowledge of breeding in an ecological dominant like *Limacina* has two special advantages: we are able to trace the elements in a population made up of mixed components not always with the same relation between sex and size (see Redfield, 1939), and, with information about the mode of life and conditions of reproduction, we are able to predict the probable seasonal movements and activity of a given population. The Benguela material of *L. bulimoides* is especially good for the study of a large population of a single origin with an apparently uniform sexual sequence. We still lack comparative data for any other month, but—taken in the breeding month of March—the autumn Benguela material contains a good proportion of mature females and a complete section of other age groups. It is hoped in a second report to examine the late winter or early spring material from the second survey.

Hsiao gave a rather brief account of the structure of the reproductive system with little histological or structural detail. Unfortunately, from the literature then available he was not able to take a comparative view of *Limacina* in its relation to the other primitive opisthobranchs. The present material of *bulimoides*, though preserved in routine formalin, was found to be good enough in many cases for a study of histology and enabled a fuller report of the genital system to be prepared. The lack of living material was unfortunate, yet with such a large number of stages and with living British *retroversa* for comparison it was felt justifiable to redescribe the whole system.

Protandrous hermaphroditism may well have been the original condition in the Gastropoda. In prosobranchs at the most primitive level it has been found by Orton (1909) in *Patella* and by Bacci (1947*a*, *b*) in *Fissurella nubecula* and in *Patella coerulea*. In mesogastropods, hermaphroditism survives only in rather isolated cases, such as *Valvata* and *Crepidula*. We may regard the Mesogastropoda, especially in their frequent atypical spermatogenesis, as sexually specialized gastropods. In the pulmonates and opisthobranchs previously known, hermaphroditism is of the simultaneous type and it appears, as for example in *Helix* and in higher nudibranchs, that the stages have been telescoped together. Morton (1954*b*) presents evidence that the opisthobranchs and pulmonates came off close together from a prosobranch stock below the level of the present day Mesogastropoda, and in a study of the ellobiids he gives the first account of reproductive succession in a primitive pulmonate. In a single season there is a well-spaced successive hermaphroditism, male to female. *Limacina* represents the first primitive opisthobranch so investigated, and its life-history may be tentatively regarded in all respects as typical of the early gastropods. The specialization of atypical sperm-formation has not been developed. Hsiao looked for the representatives of 'nurse sperms' in *Limacina* and not surprisingly did not find them. The masses of residual cytoplasm observed by him are too indefinite to suggest any such anomaly and have not been found in *Limacina bulimoides* at all.

(i) THE GONAD AND GENITAL TRACT

We have now a description of a primitive genital tract in a pulmonate (Morton, 1954*a*) and in a primitive opisthobranch, from the earlier work of Guiart (1901), while a forthcoming account by Lloyd will make clear the condition in several bullomorphs. In *Limacina* we must look for features characteristic of primitive tectibranchs, with resemblances on the one hand to early pulmonates and on the other to prosobranchs. In primitive opisthobranchs we are probably near a point where the three major groups of gastropods draw very close together.

The gonad consists of a long, tubular sac occupying in the mature female $3\frac{1}{2}$ visceral whorls and the whole of the apex of the animal. It is not subdivided and bears in all its stages a general resemblance to that of *L. retroversa*. It leads forward alongside the liver into a narrow hermaphrodite duct. This opens into the glandular genital tract, which is the pallial genital duct of Fretter (1946), and lies on the floor of the mantle cavity, at later stages bulging strongly into it. It consists of an albumen gland and a mucous gland. From the albumen gland, in the mature female there runs back alongside the stomach a sausage-shaped receptaculum seminis, lying dorsally on the first visceral whorl and attaining almost the size of the stomach. The common genital aperture opens on the right side rather far forward in the pallial cavity, and from it a ciliated fold leads forward to the secondary male aperture on the head at the base of the right wing. The male aperture leads into a highly complicated invaginated penis in front of and quite separate from the pallial tract; and with the penis is closely associated a stout, tubular prostate gland.

Condition of the gonad and sexual stages

Hsiao (1939*a*) divided his population into those with sexually undifferentiated gonads, those with 'pure male' gonads (designated 'functional males'), 'functional hermaphrodites', and finally 'hermaphrodite females'. It was recognized that no clear line of demarcation separated the males and females, but that they merged into a continuous series. No pure females were found among *L. retroversa*, and functional females were held to be those where more than 75% of the gonadial contents were oocytes or eggs. In *bulimoides*, however, it is possible to recognize a pure female phase. The gonad in animals of more than 1·9 mm. shell height is usually cleared of all but a few lingering sperms. The female duct is now highly developed, the penis is lost and the sperm sac is full after copulation. The sexual succession is thus better spaced and the later stages further separated in *bulimoides* than in *retroversa*.

We may list in Table 7 the sexual phases and their characteristics as recognized in *L. bulimoides*.

For the three largest samples of *L. bulimoides* comprising 5800 individuals from stations WS 996 and 997, the following data were obtained (Table 8) for the percentage distribution of sexual stages with size. Seven size groups separated by 0·2 mm. intervals were obtained by breaking up the three samples by the use of graded and measured pipettes, and the results afterwards carefully checked by the measurement of representative samples from each group. From each size group a sample of approximately fifty individuals was then examined after bulk staining with Ehrlich's haematoxylin and clearing in xylol. The condition of the gonad could be ascertained by rapid inspection of the cleared animal, and each specimen assigned to its stage in Table 7. The results were checked by correlating the appearance of the stained gonad with the condition of the genital tract and gonad in a large series of sectioned specimens.

Table 7. *Stages in the sexual succession of* Limacina bulimoides

1. No sexual development at all. Gonad represented only by a small cap of undivided pregerminative cells.
2. Less than one gonadial whorl. An apical mass of lighter staining primary spermatogonia, which in lower part of gonad have begun to divide into darker-staining secondary spermatogonia.
3. Less than two gonadial whorls. Primary spermatocytes arranged in spherical clusters lying freely in the lumen of the gonad. Penis and prostate absent or very tiny.
4. More than two gonadial whorls. Gonad contains primary spermatocytes and spermatids. Stained appearance never shows lighter areas of bundles of sperm tails. Penis and prostate fairly large. Female ducts present, but usually non-glandular.
5. *Mature male.* Most of gonadial lumen occupied by platelets of mature sperms. Penis and prostate large. Oocytes which have now appeared, are increasing in size (*c.* 70–100μ) but still parietal and with no dark granular yolk inclusions. Epithelium of female duct filled with undischarged secretion. Receptaculum seminis usually not visible.
6. *Pure Female.* Gonad containing entirely (or almost entirely) oocytes, with at times a few clusters of sperms left behind. Spermatogenesis entirely ceased. Many ova discharged into lumen of gonad, and of large size (*c.* 130μ) with dark-staining yolk inclusions. Penis and prostate lost. Mucous gland large and distended with secretion. Receptaculum seminis large and tightly filled.

Table 8. *Percentage distribution of sexual stages among size groups in* Limacina bulimoides

Sexual stage (%)	Shell length in millimetres						
	over 1·8	1·8–1·6	1·6–1·4	1·4–1·2	1·2–1	1–0·8	Less than 0·8
1	—	—	—	—	—	11	85
2	—	—	—	—	6	89	15
3	—	—	—	11	69	—	—
4	—	8	41	89	25	—	—
5	17	61	50	—	—	—	—
6	83	31	9	—	—	—	—

The data of Table 8 have been expressed diagrammatically in Fig. 10 in a form easily comparable with Hsiao's diagram for *L. retroversa* (Hsiao, 1939*b*, p. 286). In Fig. 11 is further shown the distribution of the four sexual types, here designated females, mature males, developing males and sexually undifferentiated individuals, among the three largest samples from the March cruise. The form of the diagram should enable easy comparison with data obtained in the second survey, and with subsequent data obtained for this or other species of *Limacina* over the twelve months of the year.

(ii) THE GENITAL DUCTS (Fig. 12)

The animals used for description are chiefly those of stage **5** shortly before female maturity. The glandular genital duct already bulges into the pallial cavity, where later, at stage **6**, it becomes pressed closely against the pallial mucous gland (*PALL.G.*) on the roof of the mantle, and filled with masses of colourless secretion. As it appears in Fig. 12, looking down upon it lying on the pallial cavity floor, the mucous gland, which is the most obvious part of the genital tract, consists of two limbs. The largest is the descending tubular limb (*MUC.D.*), very thick-walled, tapering forward to the common genital aperture (*C.GEN.*). It acts as an hermaphrodite genital duct, as in primitive hermaphrodite gastropods, and sperms traverse it before the passage of eggs. It is translucent white in colour. The

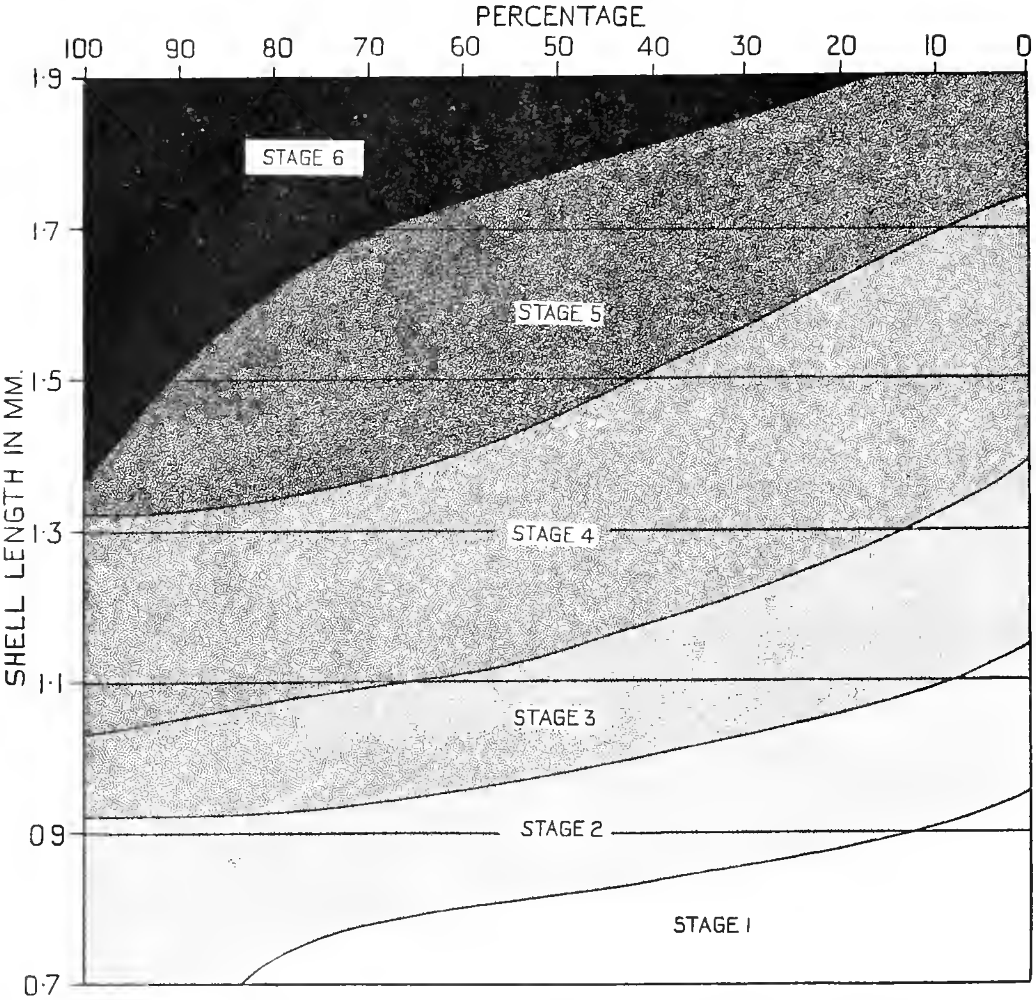


Fig. 10. *Limacina bulimoides.* Diagram showing the percentages of each sexual stage in the different size groups of the population. Combined data from the three largest samples at WS 996 (50–100 m.) and WS 997 (0–50 and 100–250 m.).

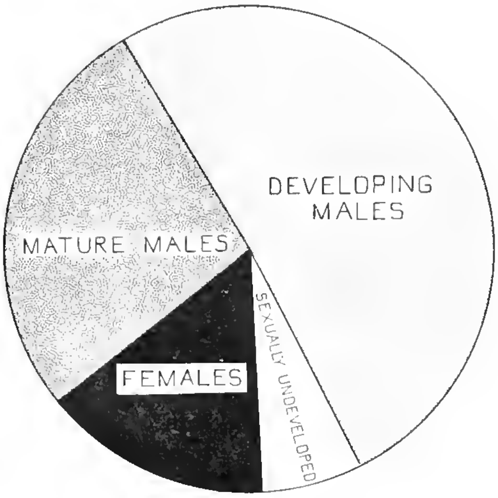


Fig. 11. *Limacina bulimoides.* March population at WS 996 and WS 997. Diagram showing the distribution of pure females, mature males, developing males and sexually undifferentiated individuals in the whole March population.

other limb of the mucous gland is a plump, horseshoe shaped crescent of glandular tissue (*MUC.AC.*) closest on the right side to the edge of the mantle cavity and the columellar muscle (*COL.*). Sperm would not appear to enter this part of the mucous gland and it forms an appendage to a deeper lying part of the genital duct. This deeper portion constitutes the albumen gland (*ALB.*), which consists of a wide atrium, thinner walled than the mucous gland. The non-glandular little hermaphrodite duct (*L.HERM.*) opens into it posteriorly. In front it leads forward between the two limbs of the mucous gland, into a thin walled pouch with very long cilia (*FERT.*). This pouch corresponds in position and in its histology to the fertilization pouch of primitive pulmonates, and forms an annexe to the albumen gland where the sperms come into contact with the egg.

The albumen gland is lined with a rather opaque white epithelium, contrasting in appearance with the mucous gland. It differs from the same gland of most primitive pulmonates in still forming an integral part of the duct traversed by the genital products, and bulging freely into the pallial cavity. In even the most primitive pulmonates, as also in the higher opisthobranchs, the albumen gland forms a diverticulum which becomes quite removed from the main channel of the genital tract, and is haemocoelic in position. After copulation, the albumen gland in *Limacina* contains isolated sperms suspended in mucoid secretion. Leading back from it, close alongside the little hermaphrodite duct, runs the short tubular duct of the receptaculum seminis (*REC.*). The receptaculum is well developed only at stage 6 when it becomes tightly distended with sperm and easily recognizable in cleared whole-mounted animals after staining. It forms a very spacious caecum, reaching a maximum diameter of more than 100 μ, and it apparently increases in size suddenly after one or more acts of copulation. It is thin-walled and lined with flattened squamous epithelium, entirely non-glandular and, so far as can be made out, non-ciliated. The large masses of sperm within it are arranged in rather wavy, parallel bundles, but they are never packed together in such distinct platelets as are seen in the lumen of the male gonad. The duct of the receptaculum is 15–20 μ across, consisting at first of flattened ciliated cells. Before its opening into the albumen gland, the duct itself becomes non-ciliated and albuminiparous. The whole sac is of the nature of an outgrowth from the albumen gland. It is homologous with the receptaculum of prosobranchs, and not with the bursa copulatrix, which is a separate structure opening from just within the common genital aperture, and forming the sperm storage sac in *Aplysia* (Eales, 1921) and in the majority of pulmonates. From the sketch given by Hsiao, the receptaculum in *Limacina bulimoides* seems to correspond to what he calls the 'vesicula seminalis' in *retroversa*, though this is a wrong name for it, since it does not store 'home' sperm derived from previous male gametogenesis. This is evident by its position as a diverticulum of the albumen gland, not as an outgrowth or distension of the little hermaphrodite duct as in the 'vesicula' of pulmonates or prosobranchs. In *Limacina* the whole of the stored sperm produced by the animal in its male phase evidently remains in bundles in the cavity of the ovotestis at stage 5; further, the receptaculum does not appear until after the penis of the same individual has disappeared. Of the sperm sac described by him in this position, Hsiao states that 'masses of mature spermatozoa can be seen inside this organ in the case of the mature *Limacina*'. His account of the origin of these spermatozoa whether from the gonad of the same animal or from a partner at copulation is non-committal.

Of the 'receptaculum seminis' described as such by Hsiao in *retroversa*, I can find no representative in *bulimoides*. Hsiao states that this sac is connected with the 'basal portion of the outgoing duct' and that it consists of two portions, the first thick-walled and much folded, containing sperms normal in structure and staining deeply with iron haematoxylin. The second is described as thinner walled and baggy in appearance; the sperms stain only very lightly and undergo degeneration. From the position of this diverticulum in Hsiao's figure and from the occurrence of sperm disintegration, it would appear to correspond to a true bursa copulatrix.

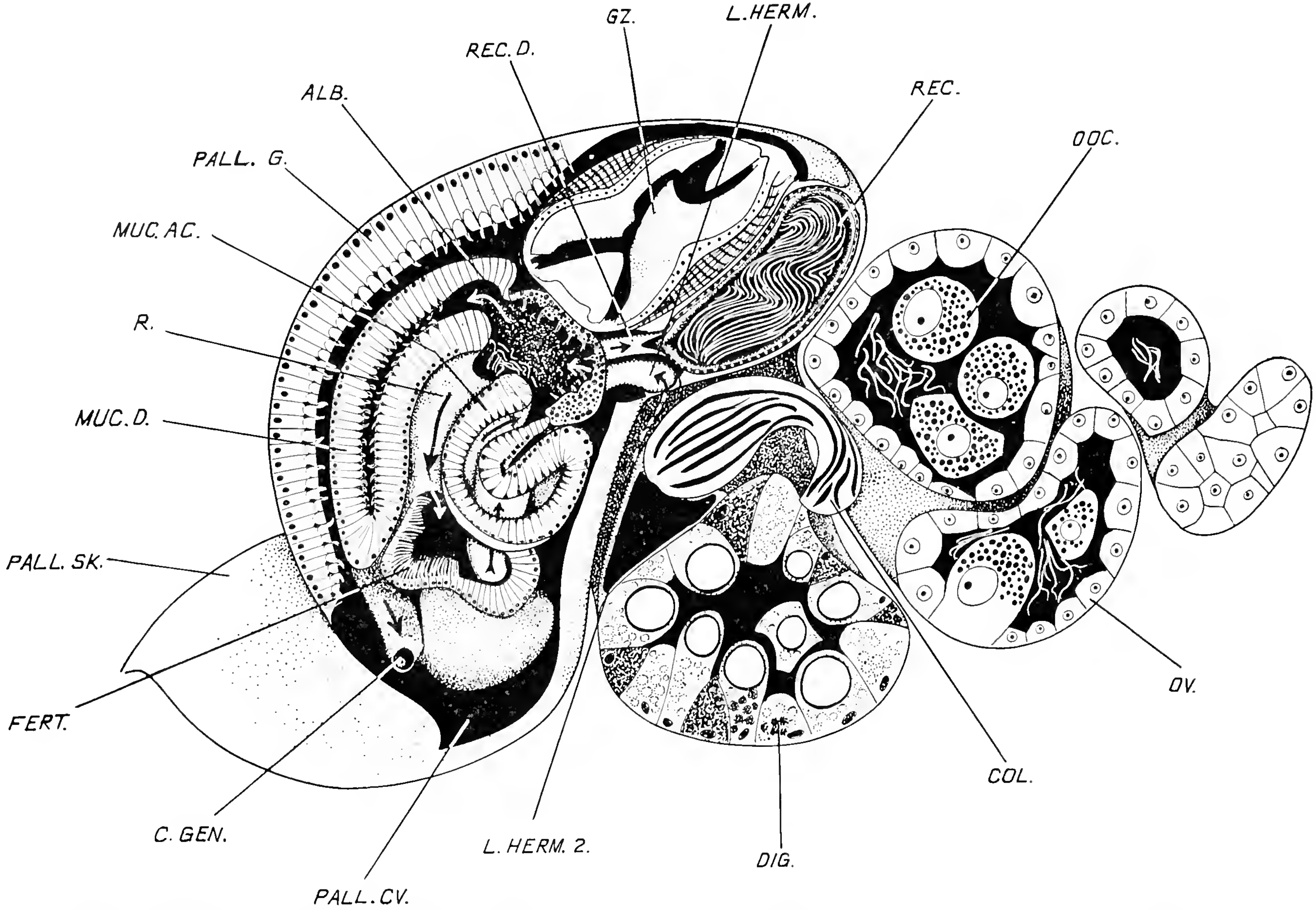


Fig. 12. *Limacina bulimoides.* Stereogram of the whole animal at the mature female stage **6** viewed from the left side in sagittal section to show the arrangement of the reproductive organs. The roof of the mantle has been removed, and the genital ducts, lying within the mantle cavity, have been opened horizontally to show their internal structure. The gizzard has been partly opened by a tangential section to disclose four of its teeth and the receptaculum seminis has been sectioned longitudinally. The head, foot and wings, lying anteriorly to the pallial skirt have been omitted. The figure is diagrammatic in that the glandular parts of the female tract are, for the sake of greater clarity, shown much less enlarged and distended with secretion, than is normally the case at stage **6**.

ALB., albumen gland; *C.GEN.*, common genital aperture; *COL.*, columellar muscle; *DIG.*, digestive gland; *FERT.*, fertilization pouch; *GZ.*, gizzard; *L.HERM.*, little hermaphrodite duct; *L.HERM.2*, portion of little hermaphrodite nearer the gonad, with sperms remaining; *MUC.AC.*, accessory lobe of mucous gland; *MUC.D.*, descending limb of mucous gland; *OOC.*, oocytes free in lumen of gonad; *OV.*, wall of gonad with parietal oocytes; *PALL.CV.*, pallial cavity; *PALL.G.*, pallial mucous gland; *PALL.SK.*, pallial skirt; *R.*, uncut roof of glandular genital duct; *REC.*, receptaculum seminis; *REC.D.*, duct of receptaculum seminis.

Of the histology of the glandular genital tract, which was not within the scope of Hsiao's paper, only a brief description is needed here. The epithelium of the albumen gland (Fig. 13*a*) reaches *c*. 50 μ in height at stage 6. Its free surface becomes rather ragged by the discharge of secretion and only a few cells remain typical and intact, with the rounded tips which represent the usual condition at stages 4 and 5. Ciliated cells are small and interposed at rather wide intervals between the gland cells. Their nuclei are smaller and darker than those of the glands, and the tufts of fine cilia become dislodged and carried away at the secreting stage. The nuclei of the gland cells are 6–7 μ in length, densely chromatic and rounded to sausage-shaped. The contents of the cytoplasm bear a considerable resemblance to those in the albumen cells of Ellobiidae (Morton, 1954*a*). The secretory inclusions form masses of tiny granules of varying but minute size. They stain golden brown with eosin-Orange G, and especially towards the base of the cell they become enclosed in clear, non-staining vacuoles. A group of vacuolated spherules is sometimes found enclosed by a single larger vacuole. The secreting cells of the mucous gland (Fig. 13*b*) increase in size from 20 to 30 μ at stage 5 to as much as 150 μ in the greatly distended gland at stage 6. Their nuclei are basal, in a single row, large and densely chromatic. Here again there is a close resemblance to the Ellobiidae. The contents of the cell stain deep purple with haematoxylin and are granular, and with the change to a secreting state, large ovoid, lightly staining droplets are formed, bulging from the cells into the lumen. The ciliated cells are extremely narrow; they fan out as triangular wedges at the free surface, and their small and dark staining nuclei are either compressed between the gland cells, or flattened closely against the top of a neighbouring cell.

No eggs of *bulimoides* were taken in the Benguela hauls, nor does Hsiao give a description of the egg mass. Lebour (1932) has, however, observed the oviposition of British *retroversa*, and has described and figured the eggs as planktonic, floating in small gelatinous strips with the eggs scattered and widely separated. Each strip measures about 2 mm. in length and 0·64 mm. in breadth and both the matrix (which is obviously the secretion of the mucous gland), and the eggs are perfectly transparent. Sometimes the strips are interconnected by a thread-like secretion which is presumably also a product of the glandular female duct.

The penis, as examined at stage 5, is perhaps the most complicated part of the reproductive system, and *Limacina*, with others of the thecosomatous pteropods, possesses probably the most elaborately constructed penis in the opisthobranchs. As pointed out by Hsiao this organ is practically independent of the rest of the reproductive system, both in position and in structure. The seminal groove does not continue as a closed tube towards the male aperture at the base of the right wing, but passes forward as the ciliated groove and becomes continuous with the interior of a large ovoid pouch the penial sac, lying in front of the rest of the reproductive organs and bulging into the pallial cavity just behind the head (Fig. 14). It is first visible at stage 4, especially large at stage 5 and lost at stage 6. The penial sac is involuted with a lining wall elaborately ridged and furrowed, and this lining, or a portion of it, constitutes the penis itself when evaginated. There is no muscular papilla traversed by a closed vas deferens as in even the earliest pulmonates. Associated with the penial sac is a tubular prostate gland. This is intricately involved in the folds and furrows of the sac, and the whole structure in the fixed and contracted condition is exceedingly difficult to make out clearly. A good deal can be seen from cleared whole-mounted individuals, but in the absence of living material serial reconstruction is necessary to determine its details. Hsiao does not attempt a description, and in the other Thecosomata, such as the cavoliniids, Meisenheimer gives few details. Bonnevie (1916) provides an account of the penis and its associated structures in *Cuvierina*, a cavoliniid, and there is a briefly labelled drawing of the penis in longitudinal section in his figure of *Cymbulia* (1905, Atlas, pl. 13). Vayssière (1915), figuring the opened penial sac, gives a picture of the folds of the interior without any interpretation. Tesch's

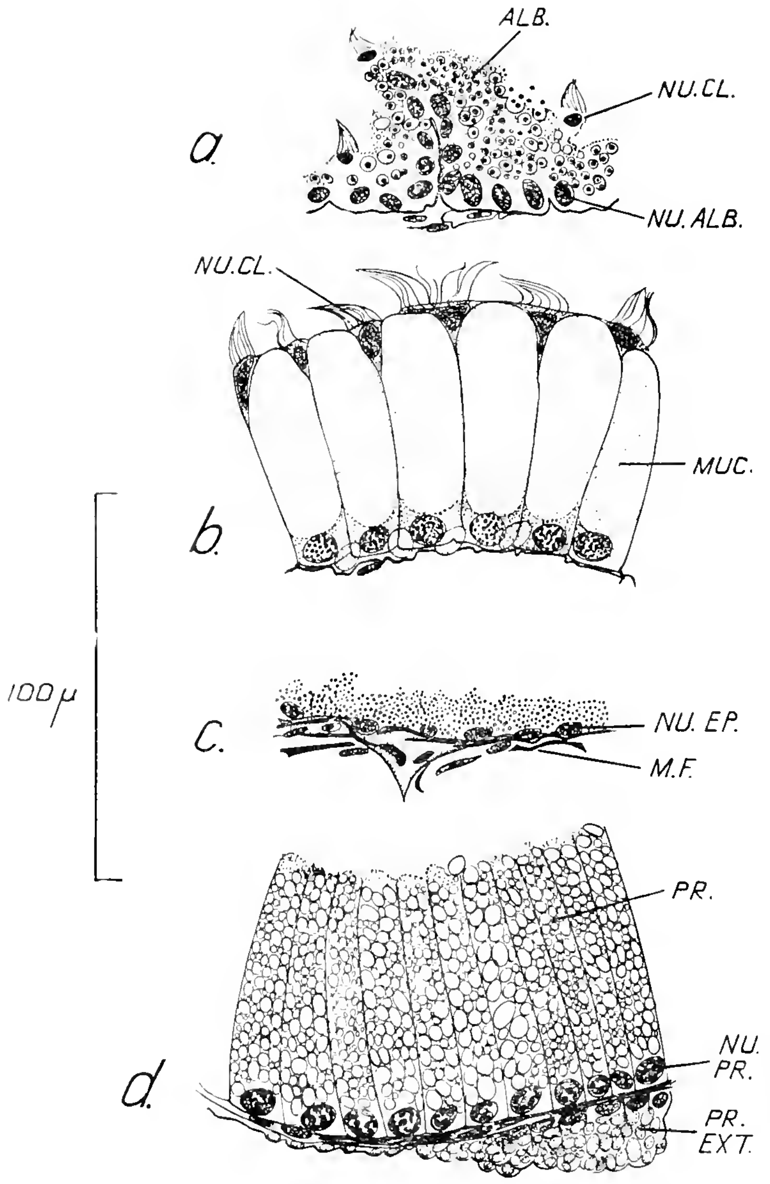


Fig. 13.

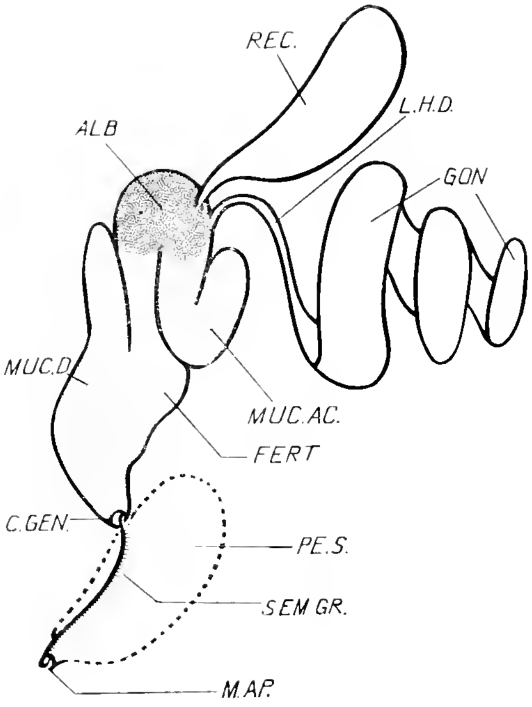


Fig. 14.

Fig. 13. *Limacina bulimoides.* Histology of the genital tract. (*a*) The albumen gland approaching the secretory condition at stage 6. (*b*) The mucous gland at stage 5, before the onset of secretory activity. (*c*) The short glandular epithelium lining the general cavity of the penial sac. (*d*) The prostatic epithelium, at stage 5, the cells opening into the prostate above, and the smaller cells forming part of the external epithelial sheath below.

ALB., albumen spherules beginning to pass from the free surface of the cell; *M.F.*, muscle fibre in wall of penial sac; *MUC.*, mucous contents of a secretory cell of the mucous gland; *NU.ALB.*, nucleus of albumen cell; *NU.CL.*, nucleus of ciliated cell; *NU.EP.*, nucleus of glandular epithelial cell; *NU.PR.*, nucleus of a prostatic cell; *PR.*, Prostatic epithelium; *PR.EXT.*, external sheath of prostatic cells.

Fig. 14. *Limacina bulimoides.* Diagram of the relations of the gonad, genital ducts and penial sac, for comparison with Fig. 12. The penial sac is shown in broken outline as it appears at stage 5; the receptaculum (*REC.*) in fact never appears until the penis is lost, at stage 6.

ALB., albumen gland; *C.GEN.*, common genital aperture; *FERT.*, fertilization pouch; *GON.*, gonad; *L.H.D.*, little hermaphrodite duct; *MUC.AC.*, accessory limb of the mucous gland; *MUC.D.*, descending limb of the mucous gland; *M.AP.*, male aperture; *PE.S.*, penial sac; *REC.*, receptaculum seminis; *SEM.GR.*, ciliated seminal groove.

figures of a dissection of the penis in *Limacina helicoides* are also wanting in detail. A prostate is nowhere mentioned by these authors, though Hsiao correctly points out its presence in *retroversa*.

Fig. 15 must serve to illustrate schematically the interior of the penis in *L. bulimoides*. It represents a stereogram of the whole sac opened longitudinally and slightly obliquely. The ciliated seminal groove enters at the male aperture (*M.AP.*) and through the same aperture the intromittent portion of the penis is extruded. The chamber of the sac into which the sperm flows from the seminal groove is to a large extent occupied by the thick tubular prostate, which is usually coiled in an S or doubled upon itself in the retracted and fixed condition. It is slung to the wall of the sac by a long, winding septum and the lumen of the penial sac consists of a series of narrow slits and spaces unoccupied by the prostate. The lumen of the prostate itself is a narrow slit, rounded or crescentic in cross-section. It receives the secretion from the lining cells and communicates apparently only at its proximal end with the sperm canal. So far as can be made out from reconstruction, the distal end of the prostate appears to end roundly and bluntly. At the bottom of the penial sac there is a flask-like expansion, with which the inner end of the prostate communicates, and towards which converge also the interstices of the sac surrounding the prostate. This flask-like expansion (*LU.PEN.*) is prolonged into a conical or pointed tube, perforate throughout and surrounded by a layer of vacuolated tissue, clear-staining and cartilage-like. While no doubt flexible, this structure appears to be the most rigid part of the male apparatus. It terminates at one side of the prostate, opening directly into the lumen of the penial sac, some distance inside the male aperture. Though in the absence of observations of copulation, it is difficult to reach a final conclusion, it would appear, from a comparison with similar 'cartilage'-supported structures in *Clione*, that this is the intromittent portion of the male apparatus. It is the only part that is not tied down by the insertion of the prostate and that is likely to be eversible from the male opening. Into it, as has been said, converge the folds leading the sperm inwards and between the coils of the prostate; and at its base opens the duct of the prostate itself.

The histological structure of this part of the penis is illustrated diagrammatically in Fig. 15. The main thickness of its wall is formed by a row of large wedge-shaped or columnar vacuolated elements. These are actually the 'cells' of molluscan cartilage, a modification of connective tissue, resembling a stiff parenchyma, developed—as in the buccal mass—in most regions where stiffness combined with flexibility is required. The lumen of this part of the penis is lined with a low epithelium of cubical cells of the same glandular type (see below) as cover the rest of the interior of the penial sac. At the base of the sac, and spreading along its wall from the intromittent portion of the penis runs an extension of the cartilage-like connective tissue.

It seems to be one of the characteristic features of the genital system of primitive tectibranchs that the 'prostate' develops as a long appendage to the penis quite separate from the rest of the glandular genital duct. Such a condition is in strong contrast to that of the primitive Pulmonata, where the prostate—as in the prosobranchs—retains a close relation with the anterior part of the pallial genital tract. Here at first it forms part of a common mucous-prostatic duct, possessing a single lumen conveying both eggs and sperm; later—in the higher pulmonates it becomes cut off as a separate male channel. In both pulmonates and opisthobranchs the nature of the prostatic glandular cells appears to be essentially similar. Their function is probably identical, and there would seem to be no good reason to restrict the descriptive term 'prostate', following the suggestion of Hubendick (1948), to the prosobranch or pulmonate type, and to exclude from this category the male accessory gland of tectibranchs. In *Philine*, according to the description by Guiart (1901), there is a tubular prostatic gland opening as an appendage from the base of the penis, with which it makes a double connection. 'Chez la *Philine aperta* la prostate se compose d'un long tube glandulaire qui forme de nombreux replis dans la cavité céphalique de l'animal, mais le canal central de cette prostate se trouve en rapport

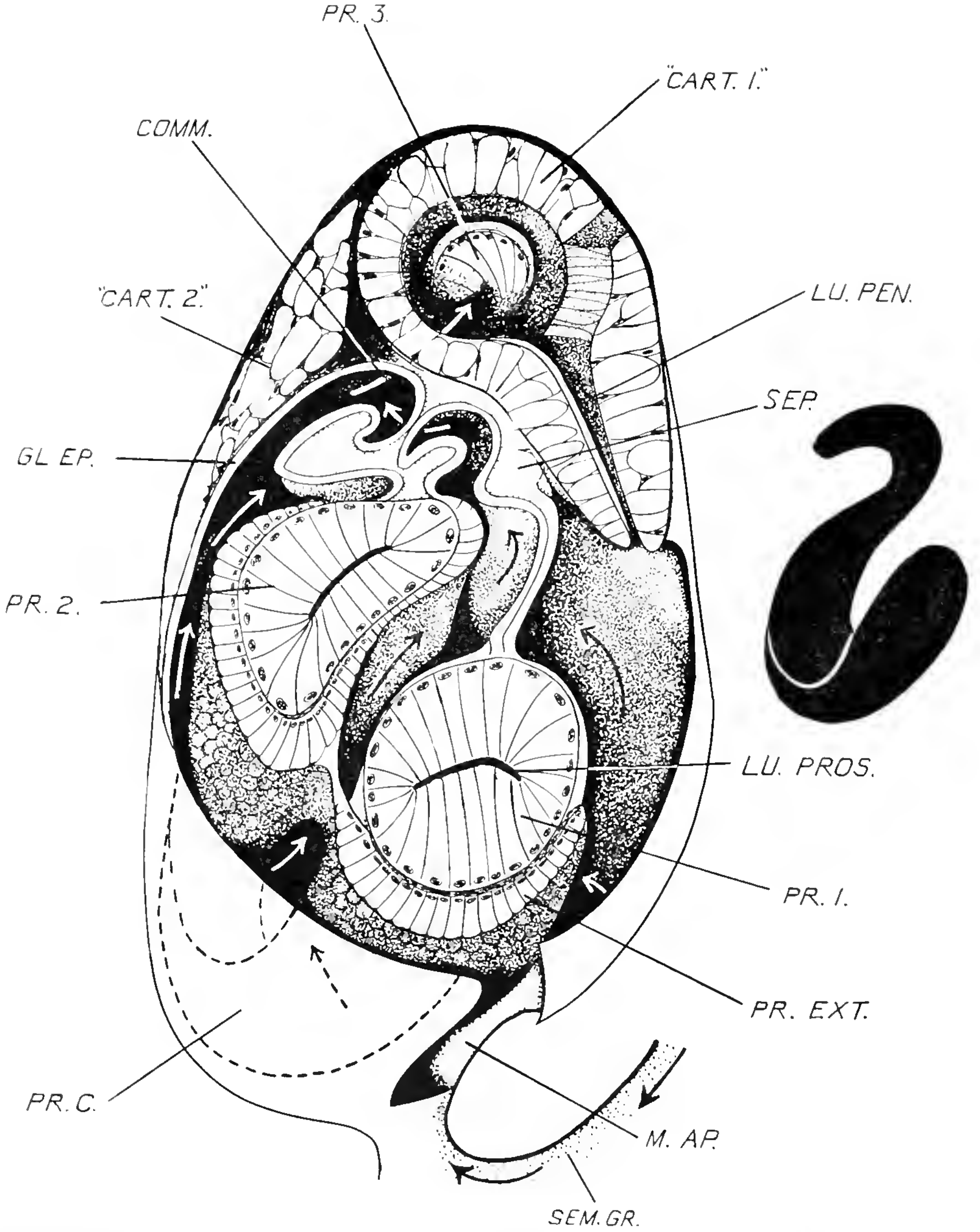


Fig. 15. *Limacina bulimoides.* The penial sac containing the coiled prostate gland illustrated as a stereogram by the opening of the sac in an obliquely longitudinal plane. The prostate is represented as having been cut transversely at three points, *PR.*1, which ends bluntly in the direction of the observer, and *PR.*2 which becomes continuous above the plane of the section with *PR.*3, forming the terminal part of the prostate lying at the base of the intromittent portion of the penis. The arrows suggest the course followed by the sperm from the seminal groove, through the interstices between the prostate and the wall of the penial sac, to the base of the intromittent portion. The inset diagram shows the shape of the intact prostate. '*CART.*1', vacuolated connective tissue, forming cartilage-like support of the intromittent portion of the penis; '*CART.*2', 'cartilaginous' connective tissue of the wall of the penial sac; *COMM.*, communication between the grooves of the penial sac and the base of the intromittent portion; *GL.EP.*, glandular epithelium forming the general lining of the penial sac; *LU.PEN.*, lumen of the intromittent portion of the penis; *LU.PROS.*, lumen of the prostate; *M.AP.*, male genital aperture at anterior end of penial sac; *PR.C.*, prostate as indicated by dotted lines through wall of penial sac; *PR.*1, *PR.*2, *PR.*3, prostate gland; *PR.EXT.*, investment of prostatic epithelium external to the tubular prostate gland; *SEM.GR.*, ciliated seminal groove, running from common genital aperture to male opening; *SEP.*, septum.

par un double conduit—d'une parte avec la gaîne du pénis par un conduit rélativement court et d'autre part avec le pénis par un tube excréteur formant une anse assez considérable.' In *Haminea*, *Doridium* and *Gastropteron* there is also a prostate of the appendage type, and a similar structure was described briefly by Tesch (1950) and further investigated by the writer (unpubl. obs.) in the gymnosomatous pteropod *Clione limacina*. It is apparently lacking in *Aplysia*, the pleurobranchomorphs and in the bullomorph *Acera*, and also in the primitive *Actaeon*, which in many features of its genitalia would seem to stand apart from other tectibranchs. The condition in the Thecosomata, with the prostate so closely involved in the actual penial sac, would appear to be unique. Its relations are likely to be much better understood after the examination of more species of pteropods, and especially after Lloyd's work has been published, which will give a full and detailed review of the genitalia in a wide range of opisthobranchs.

The histology of the prostate in *Limacina* (Fig. 13*d*) is relatively simple; there is one type of gland cell and at no stage could ciliated cells or cilia be identified at all. The glandular cells are columnar, at stage 5, 75 μ in length. The nuclei are large rounded and deeply staining, forming a single basal row. The inclusions in the cytoplasm vary in size extremely; the largest are about 10 μ across and the smallest extremely fine, much less than 1 μ. Their size in a given cell is relatively constant, and sometimes in a transverse section there appears a sector of cells containing smaller granules, very distinct from the rest. The free surface of the cells is flat or bulges slightly into the lumen—it is broken only by the passage of contents from the mature cell. The staining reaction is little if any with haematoxylin, pink in eosin, and orange after eosin-Orange G. The epithelium of the prostate lies on a very thin connective tissue sheath, sparsely muscular. Outside the prostatic tube, facing towards the lumen of the penial sac, there is another layer of glandular epithelium (*PR.EXT.*). The base of this layer lies against the base of the prostatic epithelium, forming a sleeve wrapped around about half the circumference of the prostate along the best part of its length. The secretion from these cells is similar to that produced by the prostate, and it is discharged directly into the lumen of the penial sac. The height of this layer reaches 10 μ, and the cell nuclei are rather flattened, only about half the size of the prostate nuclei. Towards the edge of the epithelial zone the height of the cells diminishes and they merge gradually with the very thin glandular epithelium, which seems to line the whole of the rest of the penial sac, being reflected both over the coils of the prostate and the ridges and furrows of the sac, and running through the intromittent portion of the penis itself. Here the cell height is less than 5 μ, and the cell boundaries are very indistinct. The cytoplasm is packed with tiny granules of secretion, some of them highly refractile, and staining like those of the prostate. The nuclei form a flattened basal row, and the free border of the cells, when fixed in formalin, tends to break away with the shedding of its contents. Whether it is ever ciliated is not easy to determine, but even in the best fixed material no cilia were detected anywhere in the prostate or penial sac. So far as is known, *Limacina* has never been observed in copulation, and our knowledge of pairing in a pteropod is restricted to the one species *Clione limacina*. It would be of great interest to examine the relations of the male organs in the everted condition and to find how the supposed intromittent organ is brought into use. We may, however, reasonably suggest from examination of the structure of the penial sac the course taken by the sperms, which are presumably liberated freely into the general cavity of the sac when brought to it by the seminal groove. Together with prostatic secretion they enter the intromittent organ at its base. The secretion of the prostate, and that of the general lining of the sac evidently contribute the nutritive portion of the semen, and the sperm finds its way through the lumen of the sac by several rather tortuous paths between the coils of the prostate, to the base of the penis. The arrows in Fig. 15 suggest the general course taken by the sperm after it is received into the sac and before ejaculation.

(iii) SEXUAL SUCCESSION

In the colder waters of the North Atlantic according to Hsiao, sexual differentiation in *L. retroversa* commences in the winter months and sexually differentiated individuals appear as in 'pure males' by the beginning of March. The predominance of pure males decreases towards the end of March and disappears in May, being replaced by a predominance of female animals. In April the percentage of females was forty and early in May the two sexual types were in equal numbers. Spawning had commenced by the end of April, which may be compared with Lebour's statement that in British waters the eggs are ripe for the greater part of the year, with a maximum in summer when each individual may apparently have had several broods. In *retroversa* from the Gulf of Maine the period of egg-laying thus reached its height at the end of the spring. The Benguela *bulimoides* were from autumn material. There were few cases of individuals having been spent in spawning and a relatively small number of very young individuals. The immature males may well belong to a component of the population resulting from spawning earlier in the spring of the same year. All sexual stages of the population were represented in the autumn material of the first survey and there is a very uniform correlation of successive sexual stages with increasing shell size throughout all the material examined. There is no indication, in the form of variable sex-size relations that this population was heterogeneous, as was demonstrated by Redfield (1939) in North Atlantic *retroversa*.

Several questions arise regarding *L. bulimoides* which probably can be answered after examining material from the second survey, with a spring population available for comparison. First, *Is there a differentiated breeding season in* L. bulimoides, *or does reproduction, as in the English* retroversa, *(as distinct from cold water Gulf of Maine material) take place all the year round?* In Hsiao's *retroversa* a spring breeding season commences by the end of April, with a fairly rapid maturation of oocytes and a change in sex predominance during the preceding month. In *L. bulimoides*, where an autumn breeding season has been shown to occur, it would seem likely that reproductive activity in March may have been preceded by breeding in spring, possibly continuing without interruption during the summer months. This leads to the query, *Are single individuals of* Limacina *able to undertake a second breeding season during the same year, or does the breeding life of a single* Limacina *extend beyond the first breeding year?* From the sex-size analysis of the autumn population of *bulimoides*, there seems to be a single peak within a definite size group for each successive sexual stage. As yet there is no evidence for this species that a restitution of the male phase is possible in individuals in which the oocytes are spent. Such a form of sexual alternation occurs, as shown by Orton (1926) in the oyster; and the present writer obtained evidence from a colony of the primitive pulmonate *Carychium*, which had laid eggs in June, that a restitution of sperm-producing tissue took place during the same year in the gonad of spent females.

Further, *Do seasonal differences occur in* Limacina bulimoides, *in the proportions of the various sexual stages at different sizes of the animal?* Hsiao (1939*b*) suggested that small individuals in the hermaphrodite female condition in his 'population B' did not pass through a protandric phase of noticeable length, though other specimens of the same population had a distinct 'young male phase' preceding the female. He concludes that 'during the warmer part of the year sexual differentiation takes place sooner than in colder times and that the sexual phases may be telescoped together when development is speeded up in the summer'. This is in agreement with observations made by Coe (1931) and Orton (1909; and other papers) on *Ostraea*. Such a trend towards the 'telescoping' of sexual stages in the warmer parts of the year points the way to the simultaneous hermaphroditism of higher opisthobranchs and pulmonates, where the female phase is pushed back until it is contemporaneous with the male and the two types of sexual product reach maturity at the same time in the common ovotestis.

In view of the probably uniform breeding season of the English Channel *retroversa* and the Benguela *bulimoides*, with but slight acceleration in summer, it is probable that variation in the rate of sexual succession is less pronounced in *Limacina* from warmer seas. Geographically, *Limacina* is divisible into two groups, the smaller-sized tropical species, *trochiformis*, *inflata*, *lesueuri* and *bulimoides*, and the larger species of higher latitudes like *retroversa* (which extends also into the warmer parts of the North Atlantic), *balea*, *helicina* and *antarctica*. The genus is well known to reach its highest development, as indicated by the size attained by the species, in colder seas. It is probable that in high latitudes the 'telescoping' of the sexual succession, occurring in the summer months, may be more advanced than the primitive condition of a fully extended sexual succession in warmer seas. For example, in *bulimoides* 'telescoping' of the succession appears hardly to occur at all; but in cold water

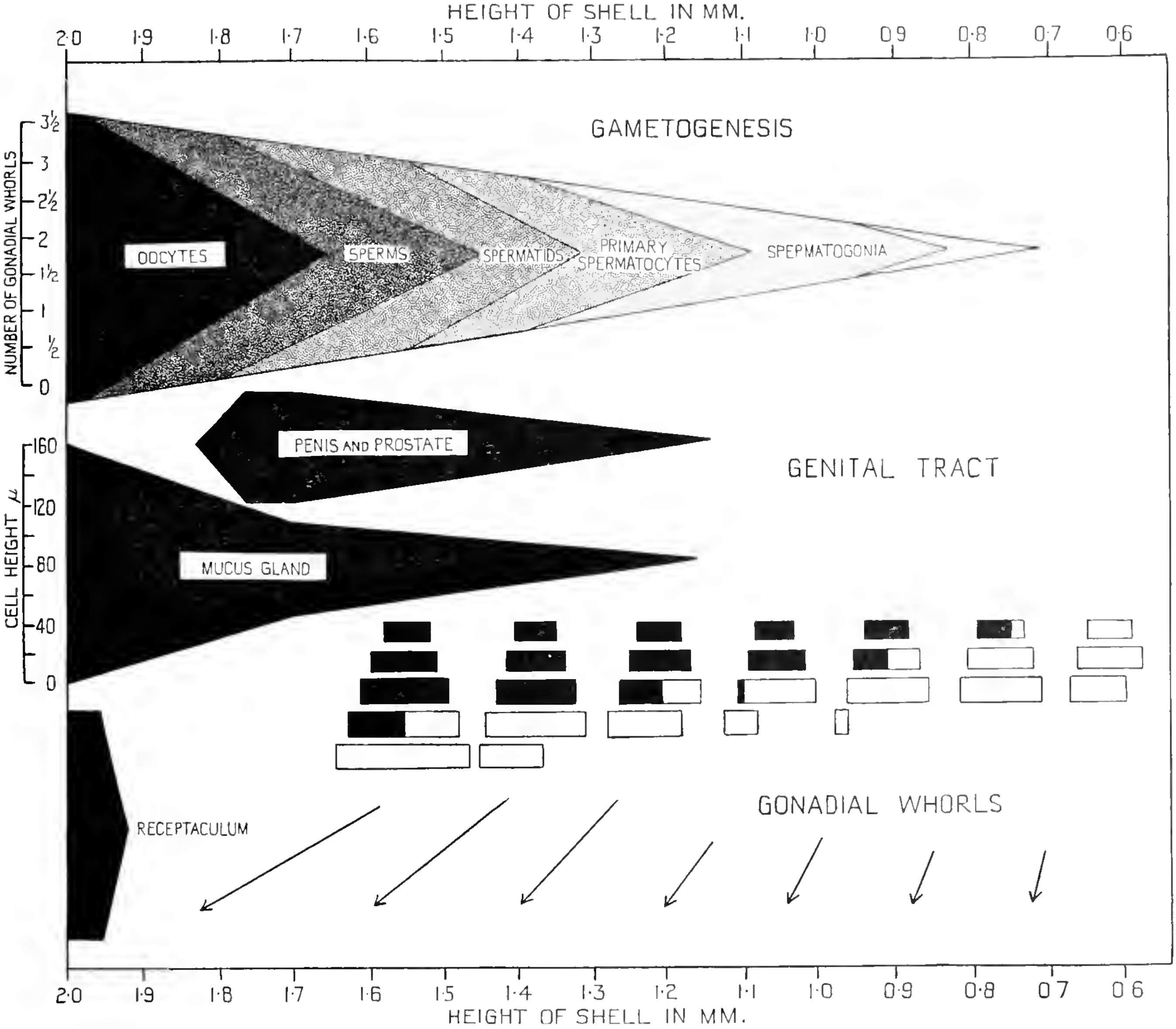


Fig. 16. Diagram to summarize the course of the sexual succession of *Limacina bulimoides*. The topmost panel represents the growth of the gonad, the scale showing the number of gonadial whorls. The successive stages in gametogenesis are indicated by the types of shading. At the centre of the figure is shown the development of the male organs, as indicated by the epithelial height of the prostate (see scale); and of the female tract, expressed by the cell height of the epithelium of the mucous gland. Below is represented on the left the increase in size of the receptaculum seminis (total diameter, by the same scale), and the increase in the number of whorls of the animal, gonadial whorls being represented in black.

retroversa, Hsiao at no time found any pure females. The final stage in succession has evidently been pushed back to occur simultaneously with the later part of the male phase, and the largest animals are 'hermaphrodite females'. In the autumn *bulimoides* there were as many as 15% of pure females with sperm absent, or present in the gonad only in the smallest traces. In these females, the penis is always lost. Such a condition may perhaps occur also in the 'hermaphrodite females' of *retroversa*, though this appears to be nowhere explicitly stated by Hsiao.

Within the family Limacinidae, it might be reasonable to expect that evolution—as in the great group of opisthobranchs as a whole—has moved away from complete protandry, towards a telescoping of the sexual succession in the direction of simultaneous hermaphroditism.

One remaining species of *Limacina*, which dwells in cold waters, the very large, abyssal-planktonic *helicoides*, which may reach a diameter of 12·5 mm., appears from Tesch's account (1946) to have developed reproductive specializations not elsewhere found in the family. This species, as first noticed by Bonnevie (1913), is viviparous and, at the female stage, developing eggs and small embryonic replicas of the adult are found in the distended coils of the mucous gland.

We may attempt to sum up the sexual development and succession in *L. bulimoides* in a diagram (Fig. 16) expressing the stages in the maturation of the gonad and the condition of the accessory genital apparatus against the growth of the shell. The lower panel represents the number of gonadial whorls in relation to the total number of whorls of the animal. This is a feature easy to determine by external inspection. The gonad shows a regular increase up to $3\frac{1}{2}$ whorls in the mature female at stage 6. It should be noted that because of the increase in size from the apical to the body whorl this relationship does not directly express the proportion of gonadial to other tissues. With practice in the examination of stained sections, the viewing of the gonads of cleared whole animals lightly stained in Ehrlich's haematoxylin yields accurate information as to the stage of sexual development. Parallel with gonad growth, Fig. 16 shows the stages in gametogenesis corresponding to the sexual phases established for this species in Table 7. The development of the male accessory organs is expressed in terms of the maturity of the prostate gland as determined by the height of its epithelial cells. In the female system, development is regarded as a function of the cell height of the epithelium of the mucous gland, while the total diameter of the tubular receptaculum is shown on the same scale—this organ increases in size not primarily by growth but by rapid inflation when the sperm is deposited at copulation.

(iv) DISCUSSION—SEX IN GASTROPODA

With the description of sexual succession in a primitive opisthobranch and in a primitive pulmonate and with a knowledge of the changes undergone by the gonad in some primitive prosobranchs, we may venture very tentatively to reconstruct the evolution of sexuality in gastropods (see diagram, Fig. 17). Let us suppose protandrous hermaphroditism to be the earliest condition in the gastropoda at the point where, from evidence given elsewhere (Morton, 1953*b*) the three great subclasses of gastropods draw closest together. We may suppose this to be somewhere near the archaeogastropod level of the prosobranchs. From such a condition, perhaps like that of Bacci's *Fissurella nubecula* today, and without any development of genital ducts, we first find among living and archaic archaeogastropods a tendency to the separation of the sexes in different individuals, which has probably been best realized in living trochids. Then, with the emancipation of the renal genital duct from its excretory function and the addition of a glandular genital duct developed from the pallial wall, the further advances are possible. In almost all the rest of living prosobranchs there is a tendency to complete separation of the sexes and bisexuality obtains in the great majority of species. Such cases of hermaphrodite prosobranchs as do remain (such as the Calyptraeidae and the Valvatidae), assumed in the past to be specialized, may on this interpretation be regarded as survivals of a primitive hermaphroditic condition. It is to be noted that in the great majority of mesogastropods—whether bisexual or hermaphrodite—there is a trend towards sperm dimorphism, and in some species the oligopyrenic sperms reach a grotesque size. [Fretter (1953)[1] has demonstrated huge giant sperms in *Clathrus* transporting vast numbers of attached normal sperms.] Parthenogenesis, too, appears to occur in at least one species, *Paludestrina jenkinsi.* The sexual condition in the mesogastropods as a whole is therefore too specialized to make them easily acceptable as ancestors of the pulmonates or the opisthobranchs. The two latter groups have probably originated close together at a higher archaeogastropod level and have retained their hermaphroditism. Each group began with a protandrous sexual succession and the succession also involves the pallial genital duct which, like the higher prosobranchs, these groups have acquired. The higher members of both subclasses have evolved in the direction of simultaneous hermaphroditism, with the sexual stages telescoped together and eggs and sperm produced side by side as in *Helix*, for example, or in separate acini of the ovotestis (higher nudibranchs). A similar but less well-marked trend seems to have been to cut out localized breeding seasons and to produce eggs and sperm simultaneously all the year round.

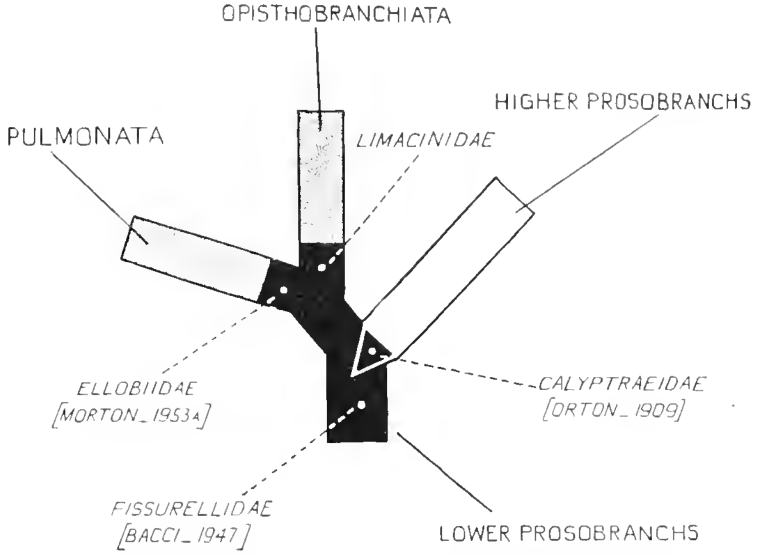


Fig. 17. Diagram to illustrate the theory of the evolution of sex in the Gastropoda discussed in this paper. Black indicates a condition of protandrous hermaphroditism, stipple simultaneous hermaphroditism and white separation of male and female individuals.

A more detailed discussion of the evolution of hermaphroditism in gastropods is intended in a later account, after the presentation of further work. It is already clear, however, that a study of *Limacina* is of great value for an understanding of the early condition with which the sexual evolution of many opisthobranchs and pulmonates would seem to have begun.

SUMMARY

The pelagic Mollusca collected during the Benguela Current Survey by the 'William Scoresby', in March 1950, comprise the following species: *Ianthina ianthina*, *I. globosa*, *Atlanta peroni*, *Limacina inflata*, *L. bulimoides*, *Diacria trispinosa*, *Euclio pyramidata*, *Cavolinia inflexa*, *Cymbulia peroni*, *Thliptodon diaphanus*, *Pneumodermopsis paucidens*, as well as two species of larval lamellibranchs, one prosobranch larva, and several larval cephalopods. The numerically important members of the plankton were the two lamellibranch larvae at stations close inshore, and the two pteropods, *Pneumodermopsis*

---

[1] Also in personal conversation.

paucidens and *Limacina bulimoides* offshore. The latter was by far the most abundant species and greatly outnumbered the related *L. inflata.* Its ecology and distribution are discussed. There is evidence that the diurnal depth migrations performed by the Limacinidae are very much shorter than in the Cavoliniidae already investigated, and there appears at night to be a size-depth division of the population, the larger individuals making a journey to the surface, and the smaller individuals remaining predominantly lower down as in their day-time distribution. The gymnosomatous pteropod *Pneumodermopsis paucidens* is a species that has not been found commonly in past collections, and a taxonomic description and fresh figures are given.

In the second part of this paper the reproductive system and sexual succession of *Limacina bulimoides* are described in detail. The genital ducts are typical of the lower level of evolution in both the opisthobranchs and the pulmonates, and consist of a little hermaphrodite duct and a glandular hermaphrodite tract comprising albumen gland, fertilization pouch and mucous gland. A receptaculum seminis forms a large diverticulum in the mature female. The penis is a complicated structure, and with it is associated a tubular prostate gland. These structures are for the first time described fully, with details of their histology. *Limacina* is a protandrous hermaphrodite and six sexual stages are recognized, all of which are present in the March population, ranging from sexually undifferentiated individuals of small size, through various stages of male development, to the pure females which are the largest individuals. A comparison is made between *L. bulimoides* and *L. retroversa* as reported upon by Hsiao, and a short discussion is added, dealing with the sexual succession in *Limacina* and the problem of the evolution of sex in the Gastropoda as a whole.

REFERENCES

Bacci, G., 1947*a*. *L'inversione del sesso ed il ciclo stagionale della gonade in* Patella caerulea *L.* Publ. Staz. zool. Napoli, xxxi, pp. 183–217.

—— 1947*b*. *Sull'ermafroditisma nell'Archaeogastropoda.* Arch. Zool. Ital. xxxii, p. 329.

De Blainville, 1817. Dict. Sci. Nat. ix, p. 407.

Boas, J. E. V., 1886. *Zur Systematik und Biologie der Pteropoden.* Zool. Jahrb. Jena, i, p. 311.

Bonnevie, Kristine, 1913. *Pteropoda.* Sci. Repts. 'Michael Sars' N. Atlantic Deep Sea Exped. 1910, 3, (1) Zoology.

—— 1916. *Mitteilung über Pteropoden. I. Geschlechts-apparat von* Cuvierina columnella *Rang.* Jena. Z. Naturw. liv, p. 245.

Chun, C., 1910. *Über Cephalopoden der D. Tiefsee-Expedition.* Zool. Anz. Leipzig, xxxiii.

Coe, W. R., 1931. *Spermatogenesis in the Californian Oyster* (O. lurida). Biol. Bull. Woods Hole, lxi, p. 309.

Currie, R., 1953. *Upwelling in the Benguela Current.* Nature, London, clxxi, p. 497.

Cuvier, G., 1817. *Le Regne Animal.* Paris, ii, p. 380.

Eales, Nellie B., 1921. *Aplysia.* L.M.B.C. Memoir, no. xxiv. Liverpool.

Fretter, Vera, 1946. *The Genital Ducts of* Theodoxus, Trivia *and* Lamellaria *and a discussion on their evolution in the prosobranchs.* J. Mar. biol. Ass. U.K. xxvi, p. 312.

—— 1953. *The Transference of Sperm in Gastropods.* Proc. Linn. Soc. London (in the Press).

Guiart, J., 1901. *Contribution à l'étude des gastéropodes opisthobranches et en particulier des céphalaspides.* Mém. Soc. zool. Fr. xiv, (5).

Hart, T. J., 1953. *Plankton of the Benguela Current.* Nature, London, clxxi, p. 631.

Hoffmann, H., 1938. *Opisthobranchia*, in *Bronn's Klassen und Ordnungen des Tierreichs.* Mollusca, II, vol. iii.

Hsiao, S. C. T., 1939*a*. *The reproductive system and spermatogenesis of* Limacina (Spiratella) retroversa. Biol. Bull. Woods Hole, lxxvi, pp. 7–25.

—— 1939*b*. *The Reproduction of* Limacina retroversa (*Flem.*). Biol. Bull. Woods Hole, lxxvi, pp. 280–303.

Hubendick, B., 1948. *The Anatomy of* Bulinus *with a discussion of the term Prostate and its sense in the* Basommatophora. Proc. Malacol. Soc. London, xxvii, pp. 186–96.

Iredale, T., 1910. *On Marine Mollusca from the Kermadec Islands and on the 'Sinusigera' apex.* Proc. Malacol. Soc. London, ix, p. 74.

Lebour, Marie V., 1932. Limacina retroversa *in Plymouth Waters.* J. Mar. biol. Ass. U.K. xviii, pp. 123–9.

Marchand, J. M., 1928. *Special Report No.* 5, *Fish. and Mar. Biol. Surv., Union of S. Africa.*

Massy, Anne L., 1917. *The gymnosomatous pteropods of the coasts of Ireland.* Sci. Proc. R. Dublin Soc. xv, p. 223.

Meisenheimer, J., 1905. *Pteropoda.* Wiss. Ergebn. Deut.-Tiefsee Exped. 'Valdivia', ix.

Morton, J. E., 1954*a*. *Studies on the Digestive and Reproductive Systems of the British Ellobiidae* (Leucophytia bidentata, Ovatella myosotis *and* Carychium tridentatum). (In the Press.)

—— 1954*b*. *The Evolution of the Ellobiidae with a discussion on the origin of pulmonates.* Proc. Zool. Soc. London (in the Press).

—— 1954*c*. *The Biology of* Limacina retroversa. J. Mar. biol. Ass. U.K. xxxiii, pp. 297–312.

Naef, A., 1923. *Die Cephalopoden. Teil II. Systematische Morphologie der inneren Organisation.* (*Vergleichende Anatomie und Organogenese.*) Fauna e Flora del Golfo di Napoli, Monografia, xxxv, p. 2.

National Institute of Oceanography, 1950. *Station List R.R.S. 'William Scoresby'* 1950. Discovery Repts. xxvi, pp. 211–58.

Oliver, W. R. B., 1915. *The Mollusca of the Kermadec Islands.* Trans. N.Z. Inst. xlvii, pp. 509–68.

Orton, J. H., 1909. *On the occurrence of protandric hermaphroditism in the mollusc* Crepidula fornicata. Proc. Roy. Soc. London, B, lxxxi, p. 468.

—— 1926. *Observations and Experiments on Sex-change in the European Oyster* (O. edulis). J. Mar. biol. Ass. U.K. xiv, p. 967.

Pelseneer, P., 1887. *Report on the Pteropoda collected by H.M.S. 'Challenger'. I. The Gymnosomata.* Sci. Repts. 'Challenger', Zoology, xix, (iv), pp. 1–69.

—— 1888. *Report on the Pteropoda... 'Challenger'. II. Thecosomata; III. Anatomy.* Sci. Repts. 'Challenger', Zoology, xxiii, pp. 1–132.

—— 1906. *Mollusca*, in *A Treatise on Zoology* (ed. by E. Ray Lankester, London), pp. 355.

Pruvot-Fol, Alice, 1924. *Étude de quelques Gymnosomes mediterr. des pêches de l'Orvet en* 1921–22. Arch. Zool. exp. gén. Paris, lxii, pp. 345–400.

—— 1926. *Moll. ptérop. gymnos. provenant des campagnes du Prince Albert I de Monaco.* Rés. Camp. sci. Monaco, lxx, pp. 1–60.

—— 1942. *Les Gymnosomes. I.* Dana Rept. xx.

Redfield, A. C., 1939. *The History of a population of* Limacina retroversa *during its drift across the Gulf of Maine.* Biol. Bull. Woods Hole, lxxvi, pp. 26–47.

Rees, C. B., 1950. *The Identification and Classification of Lamellibranch Larvae.* Hull. Bull. Mar. Ecol. iii, (19), pp. 73–104.

Sherborn, C. D., 1930. *Index Animalium*, 1801–1850. London, xxiii, p. 6093.

Stubbings, H. G., 1937. *Pteropoda*, in *Sci. Repts. John Murray Exped.* 1933–34, v, pp. 15–33.

Tesch, J. J., 1904. *The Thecosomata and Gymnosomata of the Siboga-Expedition.* Leyden, 27 (iv), p. 13.

—— 1946. *The Thecosomatous Pteropods. I. The Atlantic.* Dana Repts. xxviii.

—— 1948. *The Thecosomatous Pteropods. II. The Indo-Pacific.* Dana Repts. xxx.

—— 1949. *Heteropoda.* Dana Rept. xxxiv.

—— 1950. *The Gymnosomata. II.* Dana Repts. xxxvi.

Thiele, J., 1931. *Handbuch der systematischen Weichtierkunde*, (ii), Jena.

Vayssière, A., 1915. *Moll. euptéropodes.* Rés. Camp. sci. Monaco, xlvii.

[*Discovery Reports. Vol. XXVII, pp.* 201–218, *August*, 1954.]

THE CIRCUMPOLAR CONTINUITY OF ANTARCTIC PLANKTON SPECIES

By

A. de C. BAKER
National Institute of Oceanography

CONTENTS

THE CIRCUMPOLAR CONTINUITY OF ANTARCTIC PLANKTON SPECIES

By A. de C. Baker
National Institute of Oceanography

(Text-figs. 1–5)

INTRODUCTION

THE Southern Ocean is a continuous circumpolar belt, the greater part of which is drifting eastwards under the influence of the prevailing westerly winds. It is clear from the widespread soundings taken by many ships that there is an uninterrupted belt of deep water, and Deacon (1937), Clowes (1938) and Mackintosh (1946) have shown that there is a circumpolar continuity in the relative positions and movements of the main water masses,[1] in the distribution of nutrient salts and in the surface isotherms. As a general rule the physical features are arranged in zones (with local modifications and distortions) in which uniform conditions persist in east and west directions and changes or gradients occur from north to south. Since the distribution of pelagic species may be expected to extend as far as the environment is uniform, it would be surprising if the distribution of planktonic species were not also circumpolar.

Those who have examined collections of plankton from different parts of the Southern Ocean have observed that the familiar species can indeed be looked for in any longitude at least in the Antarctic zone, and the circumpolar distribution of the plankton is generally taken for granted. This, however, is a far-reaching assumption, and if it is true it may sometimes allow general conclusions based on samples from one sector of the Antarctic to be applied to other sectors. Although much diffuse evidence of circumpolarity may be found in the reports of various expeditions which have collected material during the past sixty years or so, it appears that no evidence has yet been assembled to show that circumpolarity is a general character of the distribution of the plankton of high southern latitudes.

The present paper sets out to show that at least the common species of the macroplankton animals and of the phytoplankton have a circumpolar distribution in the Antarctic zone, and that this circumpolar distribution is continuous in so far as, with sufficient sampling, they can be found at one time or another in all longitudes. It goes little further than this, but the point is considered to be of sufficient basic importance to form the subject of a separate paper.

MATERIAL AND METHODS

The material considered here includes the most numerous Antarctic phytoplankton species, and the commoner animals of the macroplankton in the Antarctic surface layer. Material could also be found in collections and publications for examining the circumpolar distribution of the smaller planktonic animals, those of the deeper layers, and the mammals, oceanic birds, fishes, and benthos; but such a comprehensive investigation would involve more complex problems, and the work entailed would at this stage be out of proportion to the particular question at issue.

---

[1] The Antarctic Bottom Water might be regarded as an exception. Although it can be traced all the way round, its potential temperature shows a gradient from west to east (Deacon, 1937, pl. XLIV) so that it does not have uniform circumpolar properties.

During the Discovery Investigations some thousands of plankton samples have been taken from stations spread over the whole of the Southern Ocean at all seasons of the year, the majority south of the Antarctic Convergence. For the present investigation an arbitrary selection of samples has been made from hauls between the surface and a depth of 250 m. in the Antarctic water, which means that they have been taken from within the limits of the Antarctic surface water (Deacon, 1933). Further particulars of the selection of samples are given below.

As explained on p. 209 the material used in this paper is largely derived from the work of other members of the staff of the National Institute of Oceanography and the former Discovery Committee, who for other purposes have identified the species in a large number of samples. I have had the advantage of advice from various specialists also in checking the identity of zooplankton species. Their names are mentioned below on p. 209. My own work has been to examine such additional samples as were necessary, to assemble the material, and to present the conclusions. For the phytoplankton, however, most of the work had already been done some years ago by Dr T. J. Hart, who has very kindly allowed me to use, in the section which follows, his own account of the phytoplankton, which he had prepared in anticipation of some more general study of circumpolar distribution. It is reproduced here with only slight modifications to adapt it to the present paper. Dr Hart has had much experience of the Antarctic diatoms and is confident of the specific identities of the forms listed in Fig. 2.

PHYTOPLANKTON

Among organisms other than diatoms, only *Phaeocystis* and *Distephanus* can be considered important in the plant population of the seas of the Antarctic zone. The general homogeneity of the vegetation is not always obvious from the results of a single voyage owing to seasonal changes in its constituents. Prolonged cruises by the research ships of the Discovery Committee have enabled us to distinguish between seasonal variation and differences in regional distribution with some certainty. In the course of this work it became so evident that all the more important species had a completely circumpolar distribution, that in a paper on phytoplankton periodicity in those seas Dr Hart stated it as a fact (Hart, 1942, p. 270). Nevertheless, no detailed exposition of common circumpolar distribution for Antarctic phytoplankton organisms has yet been made, and these notes are designed to supply one.

The observations available to the south of the Antarctic Convergence have been grouped into intervals of 20° longitude and found sufficiently numerous for the selection of ten representative summer stations in all but two of these eighteen sectors. Between 140° and 160° E. only eight observations are available and between 180° and 160° W. only nine. Much material obtained during the second and fourth commissions of the R.R.S. 'Discovery II' has not been fully examined, but the results presented here seem ample to prove the point at issue. In Fig. 2 the frequency of occurrence of each species in any one sector is shown, to the nearest 5%, as a percentage of the number of samples examined in that sector. The stations selected are listed in Table 3, p. 217.

In tabulating the results Dr Hart has considered all the more important phytoplankton species of the first four ecological groupings adopted in his paper on 'Phytoplankton Periodicity in the Antarctic' (1942). It will be realized that in most sectors all the observations were obtained under strictly oceanic conditions. This alone accounts for such gaps as occur in the observed distribution of diatoms of the neritic/ice-edge group. Other gaps are probably due mainly to the rather rigid time limit adopted to keep the observations in several sectors fairly comparable; for example, the inclusion of autumnal stations would doubtless show a more complete distribution of *Chaetoceros radiculum*, but would greatly diminish the percentage frequency of occurrence of other more important species.

The chief source of the observations is the series of qualitative counts from hauls with the Harvey

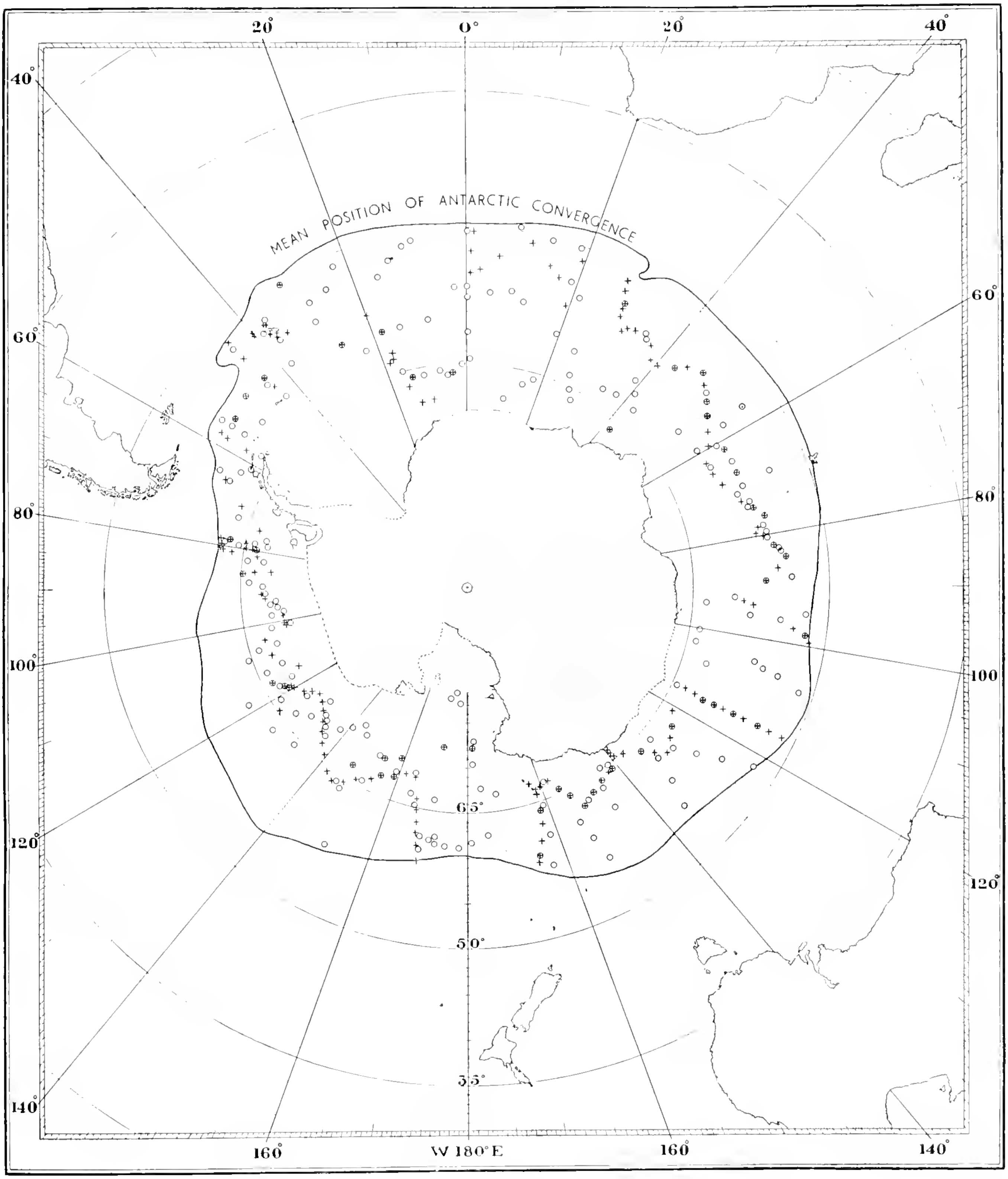


Fig. 1. Positions of the stations from which samples have been used to demonstrate the circumpolar continuity of the common phytoplankton and zooplankton species of the Antarctic surface water. +, Phytoplankton stations; ○, Zooplankton stations; ⊕, Phytoplankton and zooplankton stations.

apparatus (NHP) during the circumpolar cruise of the R.R.S. 'Discovery II' during the summer of 1937–8. This has been supplemented by published data from hauls with the Gran international net (N 50 V) obtained in 1929–31 by both the R.R.S. 'Discovery II' and the R.R.S. 'William Scoresby'; by centrifuge counts, usually from six depths at each station, obtained during the third commission of the R.R.S. 'Discovery II' (1933–5); and by some of Mr J. W. S. Marr's field notes obtained during the fourth commission (1935–7).

Taking the ecological groups in order:

Group I. Small oceanic pennate diatoms with *Distephanus*. Here it is seen at once that all three species have a very complete circumpolar distribution.

Group II. Large diatom species: the solenoids, large Chaetocerids and two elongated oceanic pennate forms, twelve categories considered. Here *Chaetoceros criophilum*, *Rhizosolenia alata*, *Dactyliosolen antarcticus*, both main phase groups of *Corethron* and *Synedra pelagica*, all show complete circumpolar distribution, and there is no doubt that a wider choice of stations within the relevant dates between 0° and 20° W. would complete the circle for that 'patchy' species, *Thalassiothrix antarctica*. The species of *Rhizosolenia*, other than *Rh. alata* have a gap here and there, but they would almost certainly show continuous distribution if further observations become available.

Group III. Neritic/ice-edge forms, seven categories considered. This group necessarily shows less continuous distribution than the others, for the majority of the observations were obtained under strictly oceanic conditions. It has already been shown (Hart, 1942, p. 285) that the importance of this group in the open Southern Ocean is confined to a particularly narrow time-interval immediately following the break up of the pack-ice. It is to this fact and the unavoidable absence of neritic observations in many sectors that the discontinuity of distribution shown here is due. *Asteromphalus parvulus* shows complete continuity, but this is the most nearly oceanic member of the group. *Thalassiosira* spp. and *Nitzschia closterium*, however, show only one gap each, and it is to be supposed that further work would show continuous distribution for the other species of this group also.

Group IV. Oceanic Chaetocerids of medium size, eight categories. Gaps in the circumpolar distribution of this group as represented here are almost certainly due to their time distribution. Dr Hart has shown (Hart, 1942, p. 293) that they reach their greatest relative importance during the post maximal midsummer decrease of the phytoplankton as a whole—*Chaetoceros radiculum* even later as already mentioned—and this fact made it impossible to select stations representative of the full spatial distribution of the group. Even so, there is very little doubt of the complete circumpolar distribution of all the categories. *Chaetoceros atlanticum* and *Ch. dichaeta* (type phase) show complete continuity from the present data. *Ch. castracanei* shows one gap, *Ch. chunii* and *Ch. schimperianum* only two each.

From the data presented here the following species show complete circumpolar distribution within the Antarctic zone: *Fragilariopsis antarctica**, *Nitzschia seriata*, *Distephanus speculum*, *Chaetoceros criophilum*, *Rhizosolenia alata*, *Dactyliosolen antarcticus*, *Corethron criophilum*, *Synedra pelagica**, *Asteromphalus parvulus**, *Chaetoceros atlanticum*, *Ch. dichaeta*.

The majority of these are also completely cosmopolitan species, occurring in polar and sub-polar waters of both hemispheres; most of them in specialized portions of the intervening sub-tropical and tropical waters as well, though not, as a rule, in the same phases. Only the species marked with an asterisk are rigidly confined to the far south, and even they 'overlap' occasionally into the sub-Antarctic zone, especially *Fragilariopsis*.

Turning to species of which the circumpolar distribution seems certain though not completely shown by the present data we can add: *Rhizosolenia antarctica**, *Thalassiothrix antarctica**, *Thalassiosira* spp., *Nitzschia closterium*, *Chaetoceros castracanei*.

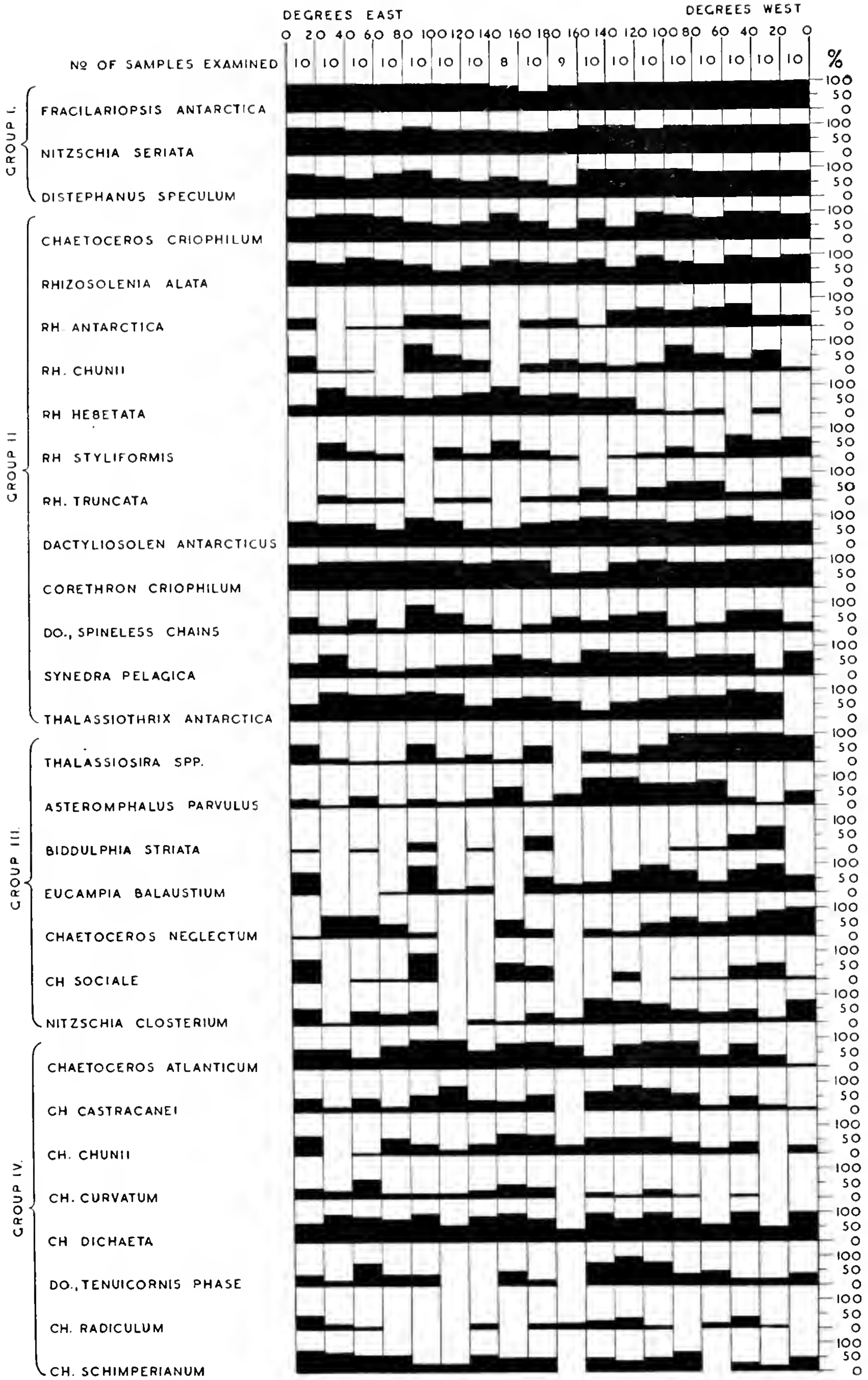


Fig. 2. Occurrence of species of phytoplankton in all longitudes around the Antarctic zone of the Southern Ocean, showing the percentage frequency of occurrence in samples taken within every 20° of longitude.

It is instructive to note the proportion of the species in the phytoplankton within the Antarctic zone. For the present purpose all the categories previously examined may be divided according to the measure of completeness of circumpolar distribution shown by the data examined here (Table 1). The figures tabulated with them are mean percentages by counts from 177 observations obtained in the three main oceanic regions of the Antarctic zone over the periods of the main increase during 1937–8 and 1938–9.

Table 1. *Probability of circumpolar distribution and mean percentages of each species in the phytoplankton population*

Circumpolar distribution					
Proved	%	Almost certain	%	Probable	%
Fragilariopsis antarctica	24·0	*Rhizosolenia antarctica*	0·1	*Rhizosolenia chunii*	0·2
Nitzschia seriata	11·8	*Thalassiothrix antarctica*	1·7	*Rh. hebetata*	1·3
Distephanus speculum	1·4	*Thalassiosira* spp.	2·4	*Rh. styliformis*	>0·1
Chaetoceros criophilum	6·5	*Nitzschia closterium*	1·3	*Rh. truncata*	>0·1
Rhizosolenia alata	1·9	*Chaetoceros castracanei*	1·3	*Biddulphia striata*	>0·1
Dactyliosolen antarcticus	1·8			*Eucampia antarctica*	0·5
Corethron criophilum	10·1			*Chaetoceros neglectum*	1·7
Synedra pelagica	0·9			*Ch. sociale*	3·8
Asteromphalus parvulus	0·4			*Ch. chunii*	2·3
Chaetoceros atlanticum	4·0			*Ch. curvatum*	0·4
Ch. dichaeta	4·5			*Ch. dichaeta, tenuicornis* phase	6·8
				Ch. radiculum	0·3
				Ch. schimperianum	1·3
	68·3		6·8		18·7

It will be seen that the rarer microscopic plants, not considered here, form only 6·2 % of the total phytoplankton; 68 % of the organisms captured by the NHP have been shown to have a completely circumpolar distribution, while it is very highly probable that a further 25 %, representing some eighteen species, are truly circumpolar also. It thus appears that the statement 'almost all the important species have a completely circumpolar distribution' is not exaggerated.

The only important plant not dealt with is *Phaeocystis brucei*. Dr Hart has already explained (Hart, 1942, p. 266) that this organism defies existing methods of estimating even its relative abundance; further, that it has a very limited time distribution as a first colonist when pack-ice disperses. Thus we cannot show the distribution of the species with the precision possible when dealing with diatoms. All our available records of *Phaeocystis brucei* plotted on a circumpolar chart are shown herewith (Fig. 3). From this it appears (at the least) highly probable that this species has a completely circumpolar distribution also.

ZOOPLANKTON

The material used for the investigation of the zooplankton consisted of samples collected by the R.R.S. 'Discovery II' between 1930 and 1951, and the R.R.S. 'William Scoresby' during the years 1928–31. These samples were taken with the 1-m. net hauled obliquely (N 100 B) from a depth of approximately 100 m. to the surface. The construction and operation of this net have been described by Kemp, Hardy & Mackintosh (1929). Where necessary the N 100 B material has been supplemented with samples from similar oblique hauls with the 70-cm. net (N 70 B) and from vertical hauls with the 70-cm. net (N 70 V) from 100–50 m. and from 50–0 m.

As in Dr Hart's treatment of the phytoplankton the circumpolar area has been divided into eighteen sectors, each of 20° longitude. The method was to choose about ten of the richer samples spaced as evenly as possible in each of these sectors, and to note which species were present. There were never less than ten samples available in each sector. If some species were absent, then a few more samples would be examined. Hence, as will be seen in Table 2, the number of samples examined from each sector varies between ten and sixteen. The total amounts to 230 and the positions of the stations at which they were taken is shown in Fig. 1. The station numbers are given in Table 3, p. 217.

Most of the samples used were taken during the southern summer (October–April) but in order to cover each sector satisfactorily it has been necessary to include twenty-eight winter stations. The sectors in which these occur and the relative numbers of winter and summer stations are shown in Table 2.

Table 2. *Proportion of winter to summer stations*

Sectors	0–20° E.	20–40° E.	40–60° E.	60–80° E.	80–100° E.	100–120° E.	120–140° E.	140–160° E.	160° E.–180°
Winter	6	1	0	0	0	0	8	3	0
Summer	10	10	12	14	13	12	2	12	12
Total	16	11	12	14	13	12	10	15	12

Sectors	180–160° W.	160–140° W.	140–120° W.	120–100° W.	100–80° W.	80–60° W.	60–40° W.	40–20° W.	20° W.–0°
Winter	0	1	2	1	0	2	0	1	3
Summer	15	13	10	12	11	11	11	10	12
Total	15	14	12	13	11	13	11	11	15

IDENTIFICATION OF SPECIES

During the years prior to the last war a large number of plankton samples were analysed by various members of the staff. This has greatly facilitated the present work, since just over half the data used here have come from samples in which the species were already identified. The methods (of fractioning, etc.) used in these analyses have been described by Mackintosh (1934), but it is necessary to give here some idea of the accuracy of identifications as they affect this present work.

Where a large number of plankton samples have to be examined it is essential that a technique should be developed that enables each to be dealt with comparatively rapidly. Descriptions and reference specimens of the common Antarctic zooplankton were provided by specialists, and it was found that with the aid of these in the first instance the worker very soon became familiar with the general appearance and one or two diagnostic features of the larger and more characteristic forms, which enabled them to be identified by the naked eye.

Thus it will be seen that the analyses are based on a familiarity with the species that are commonly found in the samples, and this obviously allows a slight risk of inaccurate identification where some of the forms are concerned. I have therefore made a further check on the identifications of the species. For this purpose specimens were taken from samples from each of the following four sectors of the Antarctic circumpolar area, 0–20° E., 80–100° E., 180–160° W. and 100–80° W. These specimens were then submitted to specialists for examination. As a result it was found that in all but two instances, which are considered below, the selected specimens had been correctly identified.

I would like to take this opportunity of thanking the specialists concerned for their assistance. Captain A. K. Totton of the British Museum very kindly examined the Siphonophores and Mr N. Tebble of the British Museum the Polychaets. I would particularly like to thank Dr J. P. Harding,

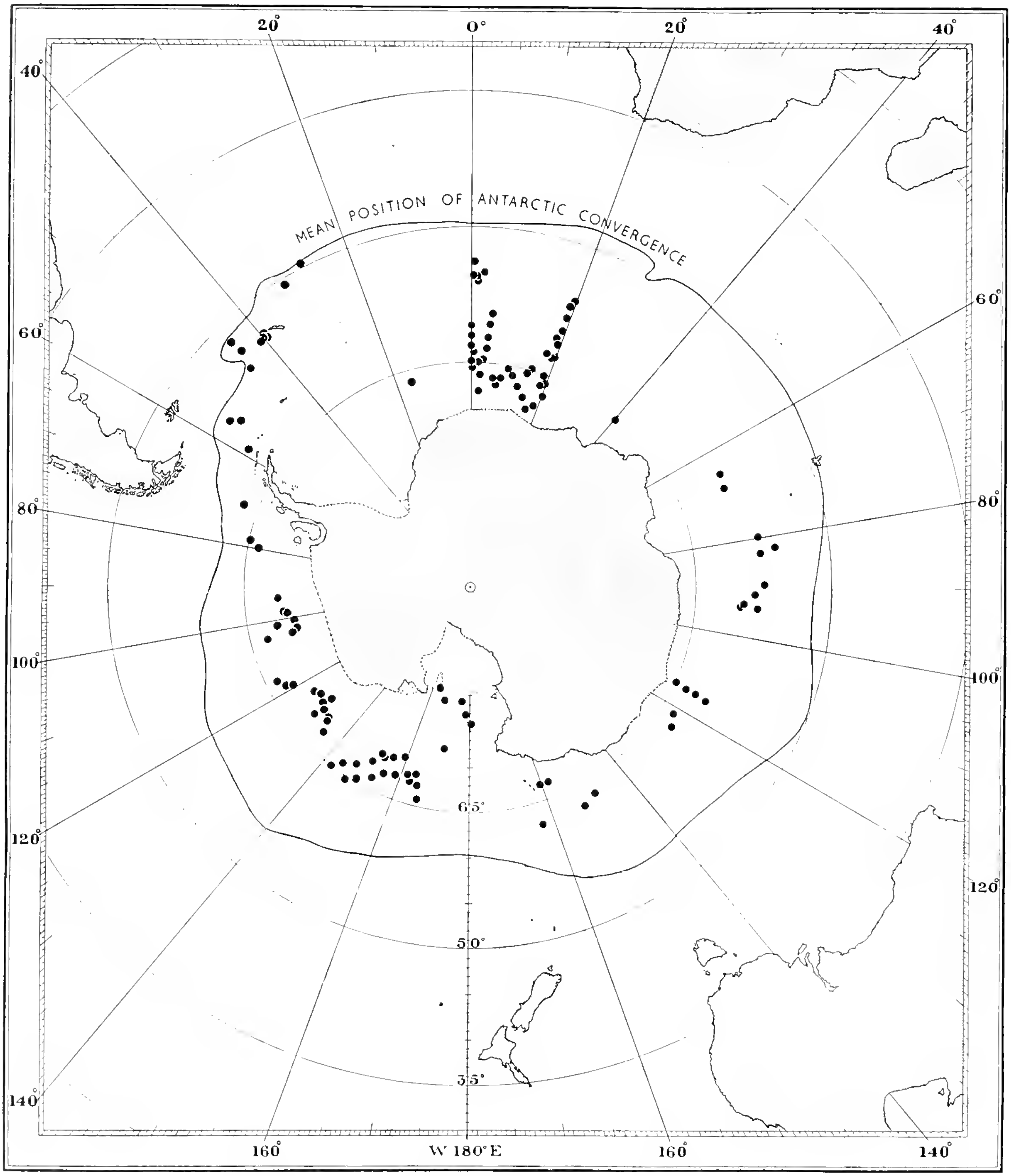


Fig. 3. Observed distribution of *Phaeocystis brucei* within the Antarctic zone of the Southern Ocean.

also of the British Museum, for his help with the Copepoda, a group that involved a great deal of work. Mr P. M. David of the National Institute of Oceanography examined the Chaetognatha and has been of assistance on several occasions, and Dr J. E. Morton of Queen Mary College has kindly examined the Mollusca. Dr T. J. Hart, as well as contributing a large part of this paper, has given me assistance with the Amphipoda. Mr N. B. Marshall of the British Museum has kindly read a draft of the paper and made some helpful comments. Finally I would like to thank Dr N. A. Mackintosh for his general guidance during this work.

The following is a list of genera and species identified:

SIPHONOPHORA
Diphyes antarctica Moser
Dimophyes arctica (Chun)
Pyrostephos vanhoffeni Moser

ANTHOMEDUSAE
Sibogita borchgrevinki E. T. Browne

POLYCHAETA
Vanadis antarctica (McIntosh)
Tomopteris spp.

CHAETOGNATHA
Sagitta gazellae Ritter-Záhony
S. planctonis Steinhaus
Eukrohnia hamata (Möbius)

ECHINODERMATA
Auricularia antarctica MacBride

OSTRACODA
Conchoecia hettaera Müller

COPEPODA
Calanus acutus Giesbrecht
C. propinquus Brady
C. simillimus Giesbrecht
Rhincalanus gigas Brady
Pleuromamma robusta (F. Dahl)
Metridia gerlachei Giesbrecht

COPEPODA (*cont.*)
Haloptilus ocellatus Wolfenden
H. oxycephalus Giesbrecht
Pareuchaeta antarctica Giesbrecht
Euchirella rostromagna Wolfenden
Heterorhabdus austrinus Giesbrecht
Candacia spp.

AMPHIPODA
Parathemisto gaudichaudi (Guérin)
Primno macropa Guérin
Vibilia antarctica Stebbing
Eusirus antarcticus (Thomson)
Cyllopus spp.

EUPHAUSIACEAE
Euphausia superba Dana
E. frigida Hansen
E. triacantha Holt and Tattersall
Thysanoessa spp.

MOLLUSCA
Cleodora sulcata (Pfeffer)
Limacina helicina (Phipps)
L. balea Möller[1]
Spongiobranchea australis d'Orbigny
Clione antarctica E. A. Smith

TUNICATA
Salpa fusiformis f. *aspera* (Chamisso)

The samples (or the notes made by those who had already analysed them) were examined for the presence or absence of the genera and species on the above list. It will be seen that four organisms are listed only by generic names. These have little real value compared with identified species but nevertheless it seems worthwhile to include them as they appear to have a circumpolar distribution when grouped as genera. In the samples examined these genera are probably represented by, at most, two species each. Two common species of *Tomopteris* occur in the Antarctic, *T. carpenteri* and *T. septentrionalis*. It is not easy to separate them except when the former is adult. *Thysanoessa* spp. includes *Th. macrura* and *Th. vicina*, and again no attempt has been made to separate these two owing to the difficulty of distinguishing the younger stages; *Cyllopus* spp. includes *C. lucasii* and *C. magellanicus*; these are only easily distinguishable when fresh. *Candacia* spp. possibly includes more than

---

[1] Dr J. E. Morton suggests that this is better referred to as *L. retroversa balea* (Fleming). The two forms intergrade very closely.

one species. Of these genera only *Thysanoessa* occurs in large numbers; the others, although they appear regularly enough to show a circumpolar distribution, are rarely represented by more than three or four specimens in one sample.

SIPHONOPHORA. Of the three Siphonophores included in the list the nectophores of *Diphyes antarctica* and *Pyrostephos vanhoffeni* are easily identified in the adult stage. The third, *Dimophyes arctica* was thought, until recently, to be equally straightforward, but Captain Totton (1954, p. 121) has found a new species which has previously been confused with *D. arctica*. It should be pointed out that the proportion of the new species to *D. arctica* is only small, only one being present among the twelve specimens presented to Captain Totton for examination, and that this by no means invalidates the conclusion that *D. arctica* has a circumpolar distribution.

ANTHOMEDUSAE. The single Medusan considered, *Sibogita borchgrevinki* is, as far as can be ascertained, the only species of this genus to be taken in the Antarctic.

POLYCHAETA. The *Tomopteris* species have been mentioned above. In addition, *Vanadis antarctica* is the only species found commonly in the Antarctic surface water.

CHAETOGNATHA. The three members of this group found in the Antarctic surface water are easily distinguishable by their general appearance. *Sagitta gazellae* is the only flaccid species; this prevents confusion with *Eukrohnia hamata* which is firm, more or less opaque,[1] has continuous lateral fins and has almost always a distinct oil globule in the gut (Fraser, 1952, p. 10). *Sagitta planctonis* is altogether a more rigid and opaque species with a stout tail region.

ECHINODERMATA. The pelagic Echinoderm larva found consistently in the Antarctic surface water is identified here as *Auricularia antarctica* but as the specimens have not been examined by a specialist it is not impossible that other species may be included under this heading.

OSTRACODA. The Ostracod *Conchoecia hettacra* would not at first sight appear to be easily and rapidly identified by the methods applied to the larger forms, and in fact because of its small size it has inevitably to be examined at least under a low-power lens. The shell shape and the arrangement of the shell glands then enable a confident identification to be made. This is not to say that all the members of this species including the young stages in the samples have been examined, but that sufficient specimens have been identified for the purpose of this work.

COPEPODA. On the whole the larger common Antarctic copepods are easy to recognize. *Calanus acutus* has a characteristic triangular shaped head when seen from the dorsal surface which prevents it from being confused with *C. propinquus* or *C. simillimus*. The two latter species of *Calanus* present certain difficulties. The adult *C. propinquus* is straightforward as it can be distinguished from *C. simillimus* by size alone, but to avoid confusion between *C. simillimus* and juvenile *C. propinquus* examination of the fifth thoracic limb is necessary. This causes little delay where only the presence or absence of a species is to be decided, as only a few specimens need be examined, but where a count is being made the delay may be considerable. Again *Parenchaeta antarctica* is readily identified when adult but confusion may occur between juvenile *P. antarctica* and *P. biloba*; similarly *Euchirella rostromagna* and *E. latirostris* may be confused in the younger stages. Thus these two species, *Parenchaeta biloba* and *Euchirella latirostris* are not included in the list of species under consideration. Of the remaining copepods only *Candacia* sp. presents any difficulty and as mentioned above this is listed only as a genus.

AMPHIPODA. The members of this group included in the above list of species are, with the exception of *Vibilia antarctica*, readily identified. There was some doubt concerning the correct identification of *V. antarctica* and it was intended to compare specimens with the type specimen, but unfortunately

---

[1] Remarks concerning the identification of organisms refer to their appearance after preservation in 10% sea water formalin.

this was not possible. However I have compared my specimens with those identified by Dr K. H. Barnard and as there is agreement the specific name *antarctica* has been used. As previously mentioned no attempt has been made to separate the two common species of *Cyllopus.*

EUPHAUSIACEA. The Antarctic species of *Euphausia* have formed the subject of a previous Discovery Report (John, 1936) and the descriptions and figures in this enable the adults of the various species to be identified with confidence and usually with little trouble.

MOLLUSCA. The five species from this group that have been taken into consideration are, provided they are not badly damaged, easily identified by their general appearance. The shells of the two species of *Limacina* are rather fragile and are often broken in the samples but they are usually present in such numbers, particularly *L. balea*, that sufficient complete specimens may be found.

TUNICATA. The only Tunicate considered here is *Salpa fusiformis* f. *aspera.* This is readily identified by the spinose ridges on the test. This characteristic is used by Thompson (1948) in a key to the Australian pelagic Tunicata as the distinguishing feature between *S. fusiformis fusiformis* and *S. fusiformis aspera.*

Excluding any possible errors inherent in the actual method of obtaining samples of the population with the nets, it will be seen from what has been said above that there are two sources of possible error in dealing with the plankton samples themselves. The first, the overlooking of smaller organisms, is generally corrected by the examination of additional samples. The second, error in identification, has been shown to be comparatively slight and usually to occur only in dealing with juvenile forms. Again, where only presence or absence is being considered, this has little effect, as there must be few samples containing nothing but juveniles of a species, and only one adult specimen is required for evidence of presence.

DISTRIBUTION

As in the section on phytoplankton, Figs. 4 and 5 show the frequency of occurrence of a genus or species in each sector expressed as a percentage of the number of stations examined in that sector. E.g. in the sector 0–20° E. *Diphyes antarctica* was present in twelve out of the sixteen samples examined and is thus shown as having a frequency of occurrence of 75 %.

When all the 230 samples had been examined it was found that eight species still showed gaps in their distribution of between 20° and 60° of longitude in certain areas, but it was thought that these gaps might be caused by insufficient sampling of a rather sparse population and not by their complete absence from those regions. Therefore additional samples were examined for the discontinuous species only, and, with the exception of *Eusirus antarcticus*, all such gaps disappeared. Where samples have been examined for only a few species these samples are not included under 'No. of samples examined' and the presence of a species is indicated in the histograms by a pecked line.

The purpose of the histograms is to show diagrammatically the circumpolar continuity of all the species whose distribution has been examined in this connexion, and this continuity is seen to hold good for all, except in so far as *Eusirus antarcticus* shows a gap of more than 20° of longitude.

The variations in the height of the histograms are of no great significance, for they merely show the frequency of occurrence of a species in those samples which happen to have been chosen from among those available in each 20° sector. The only reason why this percentage occurrence is indicated in the diagrams is that it shows some species to be more nearly ubiquitous than others. Thus it may be noted that the following species occur in over 80 % of the total samples examined: *Sagitta gazellae, Calanus propinquus, Eukrohnia hamata, Thysanoessa* spp., *Rhincalanus gigas* and *Calanus acutus.* This sequence represents the order of frequency in which they were found, *Sagitta gazellae* being present in 96·0 % and *Calanus acutus* in 83·5 % of the samples. Taking the lower range of frequencies, *Eusirus antarcticus* and *Sibogita borchgrevinki* occur in only 9·5 and 15·0 % of the samples respectively. The species which show the highest percentage occurrence are not necessarily the most abundant species but rather those which are more evenly distributed. Species with a 'patchy' distribution are liable to be absent from several samples even though they may be present in the sea not far from where the samples were taken. Again some species are confined either to the warmer or colder parts of the Antarctic water, and if, as in some instances, the available samples tend to be grouped in one part of the temperature range, a false impression is given of their occurrence in the sector as a whole.

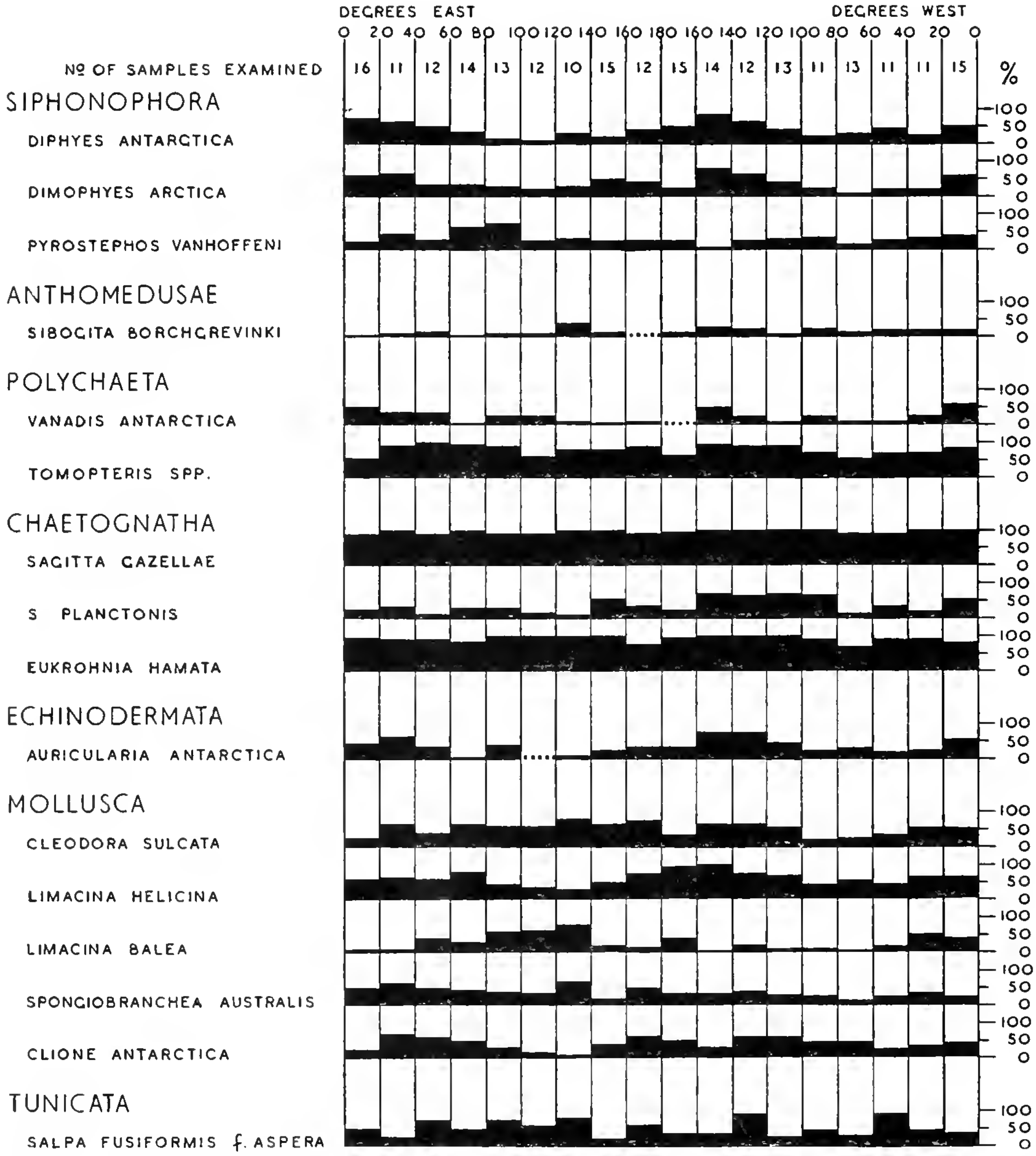


Fig. 4. Occurrence of species of zooplankton in all longitudes around the Antarctic zone of the Southern Ocean, showing the percentage frequency of occurrence in samples taken within every 20° of longitude.

CONCLUSIONS

The zooplankton can be taken first. To begin with it is not claimed that the species dealt with here include every oceanic species of the macroplankton existing in the Antarctic surface water, and it must be made clear that there has been no selection of those which happen to have a circumpolar distribution. For this it is probably enough to point out that these species include all except two of those definitely identified by Mackintosh (1937) and listed on his p. 372 in order of abundance and without reference to their circumpolar distribution. The exceptions are *Sagitta maxima* and *Euphausia vallentini*, and these are not usually found in the Antarctic surface water. We are thus dealing with all except the rare species and a few which happen to be difficult to identify.

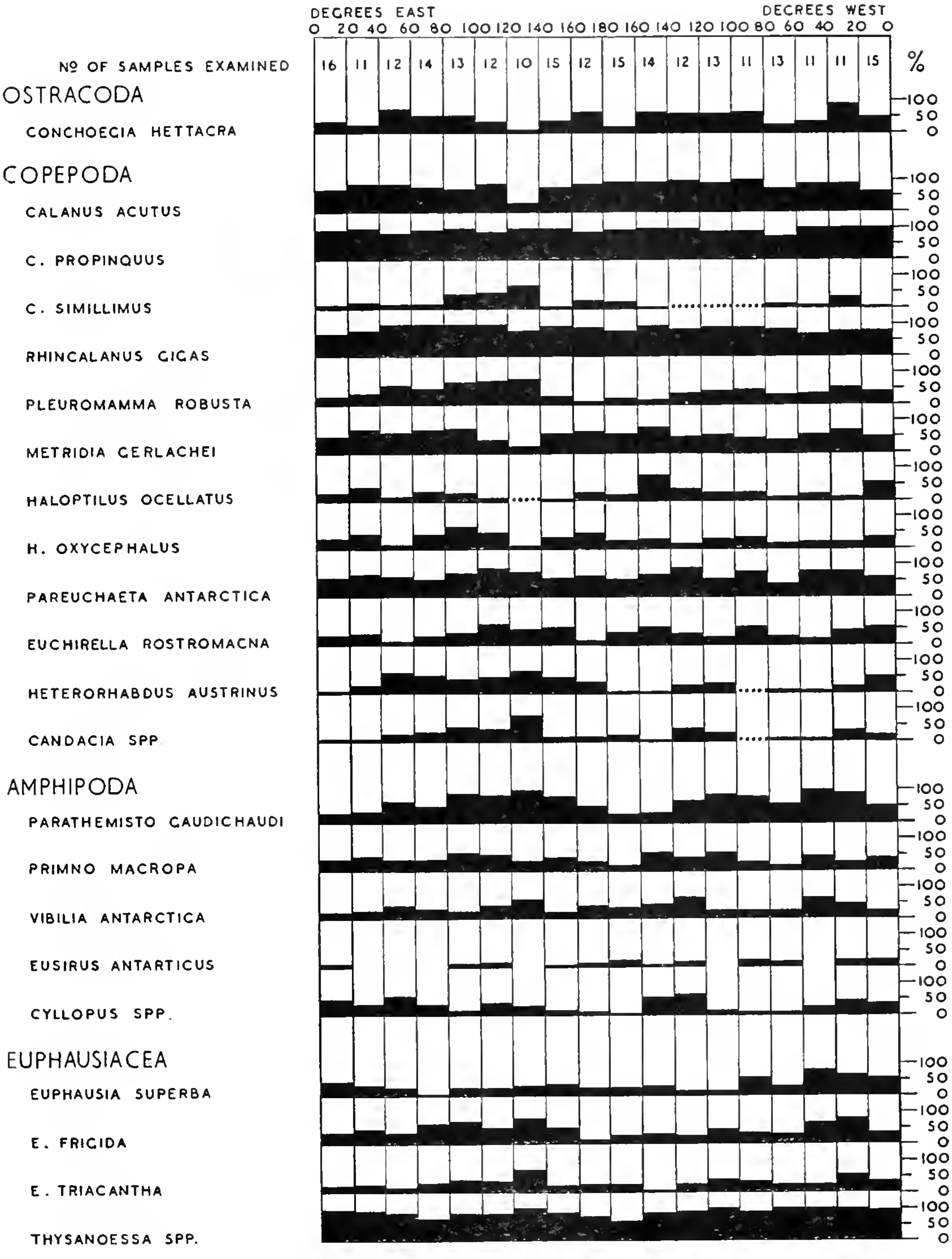


Fig. 5. Continuation of Fig. 4.

It has been shown that, with the exception of *Eusirus antarcticus*, each of these species has been found at one time or another at least once in every 20° sector round the whole circle of 360° south of the Antarctic Convergence. All of them, including *E. antarcticus* can properly be described as having a circumpolar distribution; and there can scarcely be any doubt that such gaps as appear in this species would be eliminated with further sampling. It is thus reasonable to infer that this circumpolar distribution is continuous in the sense that there are no longitudes from which the species are excluded. This is not quite the same as to say that each species is represented by a single completely continuous circumpolar population throughout the year, for it is not impossible that at a time of year when the numbers of a species are reduced in the surface layer the population becomes broken up into isolated local stocks. It seems safe, however, to conclude that there is no persistent discontinuity in any longitudes. The distribution of the samples in time and space hardly leaves room for the possibility of several discrete populations drifting round through all longitudes but remaining separate from each other, and in any case it would be difficult to conceive of any mechanism in the water movements by which they could be kept permanently isolated from one another.

To demonstrate on taxonomic grounds alone that there can be no reproductively isolated population of a species in different parts of the Antarctic it would be necessary to prove that there are no subspecific differences in different sectors; and in this connexion it must be remembered that in a widespread species distance alone may constitute a sufficient barrier to bring about genetic isolation and the development of subspecific differences between remote parts of the range, even in a continuous system of populations. No proof is offered here that the representatives of each species are everywhere subspecifically identical, but it can be said that no such differences have been observed, and in view of the uniformity of the properties of the Antarctic surface layer in a circumpolar direction, and the absence of any known environmental barriers which might interrupt the continuity, there is good reason to believe that each species has a circumpolar population forming a single unit in which little if any geographical variation can be expected. This does not of course rule out the possibility of two or more concentric circumpolar populations occupying different zones, partially isolated from one another and perhaps exhibiting subspecific differences.

Very much the same can be said of the species of phytoplankton. Here rather more gaps appear in the histograms (in Fig. 2) than in those for the zooplankton, as Dr Hart adopted a rather more rigorous method of selecting the samples. The distribution of all the species can be described as circumpolar, it is certainly or almost certainly continuous in most of them (at least in the period of relative abundance), and it is highly probable that apparent gaps in the remainder would disappear with further sampling.

The species dealt with in this paper do not include the smaller zooplankton forms, but they are an arbitrary selection of the total plankton in the sense that they are the common species taken in certain types of nets, and they include representatives of many taxonomic groups with different habits and modes of life. Evidence has been given that all of them are circumpolar, and there is at least a strong expectation that circumpolar continuity is a general rule for oceanic plankton species of the Antarctic surface layer.

SUMMARY

It has been suggested that, as the Southern Ocean is an uninterrupted circumpolar belt with more or less uniform conditions prevailing in east and west directions, the range of planktonic species of the Antarctic surface water may be expected to extend as far as these uniform conditions persist, i.e. to be circumpolar.

Dr Hart has shown this to be true of the important phytoplankton species and discusses the reasons for the few gaps that appear when the selected data are plotted.

The same is shown for the larger zooplankton species and an indication of the degree of accuracy of the specific identification is given.

Histograms are drawn which demonstrate the occurrence of each species in a circumpolar direction and show the percentage of samples in which the species occur.

Table 3. *Serial numbers of the stations on which Figs. 2, 4 and 5 are based*

0– 20° E.	20– 40 E.	40– 60 E.	60– 80° E.	80– 100 E.	100– 120 E.	120– 140 E.	140– 160 E.	160 E.– 180	180– 160 W.	160– 140 W.	140– 120 W.	120– 100 W.	100– 80 W.	80– 60 W.	60– 40 W.	40– 20 W.	20 W.– 0
Phytoplankton																	
2496	2089	1543	1627	2128	2159	2174	2187	1663	1283	1263	1255	571	566	1222	WS 470	479	WS 541
2498	2090	2101	1629	2129	2160	2175	2188	2198	2220	1265	2241	572	568	1223	WS 471	480	WS 543
2500	2091	2103	2116	2131	2161	2177	2189	2199	2221	1267	2242	1247	577	1224	1213	485	WS 547
2502	2092	2104	2117	2132	2162	2178	2190	2200	2222	2230	2244	1249	1241	1235	1214	486	WS 550
2504	2093	2106	2119	2134	2163	2180	2192	2201	2223	2232	2245	1251	1243	1236	1215	518	WS 552
2508	2094	2107	2122	2137	2164	2181	2193	2202	2224	2233	2247	1253	1245	1237	1491	523	WS 554
2511	2095	2109	2123	2138	2165	2183	2195	2204	2225	2235	2248	2254	1472	1239	1492	525	1513
2513	2096	2110	2125	2141	2166	2184	2196	2205	2227	2236	2250	2255	1473	1447	1493	1198	1515
2517	2098	2113	2126	2142	2167	2185		2206	2229	2238	2251	2256	1474	1449	1494	1212	1517
2519	2100	2114	2127	2143	2168	2186		2207		2239	2253	2258	1475	1450	1495	1510	1519
Zooplankton																	
452	1357	856	858	862	1720	883	904	1662	1270	1263	1254	WS 503	575	549	547	WS 310	WS 543
1161	1532	857	859	863	1725	884	905	1663	1271	1265	1255*	973*	975*	1216	613	362	461
1356	1533	1543	860	865	1726	885	906	1665	1273	1267	1256	1246	1240	1220	1213	532	1351
1521	1534	1546	861	1634	1727	886	1695	1667	1274	1287	1257	1248	1241	1221	1214	1198	1352
1525	1538	1547	1626	1642	1729	887	1697	1669	1282	1289	1258	1250	1242	1223	1326	1208	1383
1527	1540	1621	1627	2129	1722*	889	1700	1675	1283	1291	1259	1252	1244	1238	1327	1344	1385
1528	1548	1623	1628	2130	2161	890	1701	1677	1284*	1292	1294	1253	1306	1239	1328	1390	1386
1784	1550	2103	1629	2131	2163	891	2187	1679	1285	1293	1295	1301	1307	1314	1332	1501	1514
1785	2091	2106	1630	2134	2165	2175	2189	2201*	1647	2230	1296	1305	1309	1315	1337	1510	1515
1786	2097	2108	1631	2140	2166	2179*	2190	2202	1648	2232	1297	1464	1310*	1412	1492	1511	1519
1796	2374	2109	1633	2142	2169	2181	2191	2206	1651	2234	1299	2256	1311	1414	2298	2302	1520
1812		2110	2121	2810	2815		2192	2764	2758	2237	2835	2258	2269	2286			2006
2014			2123	2813	2816		2193	2767	2759	2741	2836	2260	2271	2287			2008
2016			2125				2195		2760	2832		2837					2009
2017							2197		2761								2309
2477									2763								

Note. Further particulars of these stations (excluding the more recent Stns. 2758–2837) can be found in the Station Lists published in the Discovery Reports, Vols. III, pp. 1–132, IV, pp. 1–232, XXI, pp. 1–226, XXII, pp. 1–196 and XXIV, pp. 1–422. Stations marked with an asterisk are those from which samples were examined for one or two species only (see p. 213).

BIBLIOGRAPHY

CLOWES, A. J., 1938. *Phosphate and Silicate in the Southern Ocean.* Discovery Rep., XIX, pp. 1–120.

DEACON, G. E. R., 1933. *A General Account of the Hydrology of the South Atlantic Ocean.* Discovery Rep., VII, pp. 171–238.

—— 1937. *The Hydrology of the Southern Ocean.* Discovery Rep., XV, pp. 1–124.

FRASER, J. H., 1952. *The Chaetognatha and other Zooplankton of the Scottish Area and their value as Biological Indicators of Hydrological Conditions.* Scottish Home Dept., Marine Research, 1952, No. 2, pp. 1–52.

HART, T. J., 1942. *Phytoplankton Periodicity in Antarctic Surface Waters.* Discovery Rep., XXI, pp. 261–356.

JOHN, D. D., 1936. *The Southern Species of the Genus* Euphausia. Discovery Rep., XIV, pp. 193–324.

KEMP, S., HARDY, A. C. & MACKINTOSH, N. A., 1929. *Discovery Investigations: Objects, Equipment and Methods.* Discovery Rep., I, pp. 141–232.

MACKINTOSH, N. A., 1934. *Distribution of the Macroplankton in the Atlantic Sector of the Antarctic.* Discovery Rep., IX, pp. 65–160.

—— 1937. *The Seasonal Circulation of the Antarctic Macroplankton.* Discovery Rep., XVI, pp. 365–412.

—— 1946. *The Antarctic Convergence and the Distribution of Surface Temperatures in Antarctic Waters.* Discovery Rep., XXIII, pp. 177–212.

THOMPSON, H., 1948. *Pelagic Tunicates of Australia.* Commonwealth Council for Scientific and Industrial Research, Australia (Melbourne).

TOTTON, A. K., 1954. *Siphonophora of the Indian Ocean, together with systematic and biological notes on related specimens from other oceans.* Discovery Rep., XXVII, pp. 1–162.

[*Discovery Reports. Vol. XXVII, pp.* 219–234, *October* 1954.]

THE PLANKTONIC DECAPOD CRUSTACEA AND STOMATOPODA OF THE BENGUELA CURRENT

PART I. FIRST SURVEY, R.R.S. 'WILLIAM SCORESBY', MARCH 1950

By

MARIE V. LEBOUR, D.Sc.

CONTENTS

THE PLANKTONIC DECAPOD CRUSTACEA AND STOMATOPODA OF THE BENGUELA CURRENT

PART I. FIRST SURVEY, R.R.S. 'WILLIAM SCORESBY', MARCH 1950

By Marie V. Lebour, D.Sc.

(Text-figs. 1–6)

INTRODUCTION

THE R.R.S. 'William Scoresby' made two surveys in 1950 of the Benguela Current off the coast of South-West Africa. The plankton hauls so obtained were sorted by Dr T. J. Hart, who handed the Decapoda and Stomatopoda over to me. The material from the first survey (March, Stations WS 977–1002) forms the basis of this report. The second survey will be dealt with subsequently.

The adult specimens consisted of two species of *Gennadas* and one of *Pasiphaea*. The rest were all larvae. One of the commonest of these was a species of *Callianassa* which occurred in several hauls, and the most frequent crab larva was a species of *Ebalia*, closely related to *E. tuberosa*. A pagurid larva was of special interest as it represents a type hitherto undescribed. It is here compared with one from Bermuda, very closely related and so far unknown.

The Stomatopod larvae all belong to one species and are almost certainly *Squilla armata* which is the commonest form in these regions.

ACKNOWLEDGEMENTS

My best thanks are due to Mr F. S. Russell, Director of the Marine Laboratory for allowing me to work at Plymouth.

SYSTEMATIC

PENAEIDEA

PENAEIDAE

ARISTEINAE

Gennadas gilchristi (Calman)

Calman, 1925, p. 6.
Balss, 1927, p. 261 (as *Amalopenaeus*).

OCCURRENCE. St. WS 997, 1000–0 m.

DISTRIBUTION. Known from near the Cape of Good Hope and in the East Atlantic.

Gennadas similis Stephensen

Stephensen, 1923, p. 12.
Balss, 1927, p. 256 (as *Amalopenaeus*).

OCCURRENCE. St. WS 996, 1000–750 m.

DISTRIBUTION. South-east and East Atlantic. The original locality is the Bay of Cadiz (Stephensen).

Gennadas sp., 1 protozoea

Heldt, 1938, p. 122.

OCCURRENCE. St. WS 997, 50–0 m.

Table 1. *List of Stations at which Decapods and Stomatopods were taken*

Station	Position	Date	Depth in m.	Species	Larvae
WS 977	22° 39′ S. 12° 16′ E. to 22° 33′ S. 12° 17′ E.	6/7. iii. 50	50–0	? *Sergestes cornutus*	1 elaphocaris I–II
				1 *Sergestes* (cf. *arcticus*)	1 mastigopus
WS 978	22° 28′ S. 12° 42′ E.	7. iii. 50	1000–750	*Acanthephyra acanthetelsonis*	1 late or post-larval
WS 979	22° 47′ S. 13° 35′ E.	7. iii. 50	50–0	*Callianassa*	15 larvae I–V
				Solenocera (cf. *membranacea*)	1 protozoea III
				Brachyrhyncha indet.	3 zoea I
				Hippolytid (cf. *Eualus* sp.)	2 larvae I and V
				Processa	1 larva VIII or IX
			100–50	1 *Pasiphaea semispina* (juv.)	
				Hippolytid indet.	1 larva
				Brachyrhyncha indet.	1 zoea II
				Callianassa	1 larva I
				Processa	1 larva IV or
WS 980	22° 44′ S. 14° 08′ E.	8. iii. 50	50–0	*Solenocera* (cf. *membranacea*)	1 protozoea II
				Solenocera (cf. *membranacea*)	2 protozoeae III
				Brachyrhyncha indet.	3 zoeae II, III and V
			100–50	*Callianassa*	2 larvae (early)
				Brachyrhyncha indet.	1 zoea I
WS 987	25° 13′ S. 13° 43′ E.	10. iii. 50	50–0	3 *Pasiphaea semispina*	
			250–100	1 *Pasiphaea semispina* (ovigerous)	
WS 988	25° 12′ S. 14° 22′ E.	11. iii. 50	50–0	*Brachyrhyncha* indet.	1 zoea I
WS 996	28° 41′ S. 13° 25′ E. to 28° 39′ S. 13° 23′ E.	12. iii. 50	100–50	*Periclimenes*? sp.	1 late larva
				Ebalia	1 zoea III or IV
			250–100	*Ebalia*	1 megalopa
		—		*Sergestes arcticus*	1 elaphocaris III
			1000–750	1 *Gennadas similis* (adult)	
WS 997	28° 40′ S. 14° 06′ E. to 28° 37′ S. 14° 08′ E.	13. iii. 50	50–0	1 *Sergestes* sp. (juv.) (cf. *diapontius*)	1 mastigopus (juv.)
				Gennadas sp.	1 protozoea
				Ebalia	4 megalopae
			250–100	*Ebalia*	1 zoea IV
				Ebalia	1 megalopa
			1000–750	*Ebalia*	1 zoea I
			1000–0	1 *Gennadas gilchristi* (adult)	
				Glaucothoë	2 larvae
WS 998	28° 40′ S. 14° 43′ E.	13. iii. 50	50–0	*Ebalia*	18 zoeae
				Ebalia	1 megalopa
				Brachyrhyncha indet.	2 zoeae
				Callianassa	25 larvae I–V
			100–50	*Callianassa*	1 larva I
				Crab indet.	1 megalopa
				Acanthephyra	1 larva
			175–100	*Callianassa*	1 larva I
				Ebalia	3 megalopae
WS 999	28° 38′ S. 14° 59′ E. to 28° 31′ S. 15° 00′ E.	13. iii. 50	50–0	*Ebalia*	1 megalopa
				Callianassa	9 larvae II–III
				Brachyrhyncha indet.	1 zoea IV
			100–50	Hippolytid (cf. *Eualus*)	1 larva *c.* IV
				Callianassa	1 larva III
			150–100	*Callianassa*	1 larva V
				Ebalia	1 megalopa
WS 1000	28° 40′ S. 15° 29′ E.	13. iii. 50	50–0	*Jasus*	4 phyllosoma I
				Stomatopod	2 larvae
WS 1001	28° 40′ S. 15° 56′ E.	14. iii. 50	50–0	Stomatopod	19 larvae
				Callianassa	28 larvae I–V
				Pagurid indet.	1 larva I
				? Hippolytid	1 larva I
				? *Eualas* sp. (cf. *lebourae*)	1 post larva
			100–50	*Callianassa*	4 larvae I–III
				Ebalia	1 megalopa
				Stomatopod	3 larvae
WS 1002	28° 40′ S. 16° 14′ E.	14. iii. 50	50–0	Portunid	1 megalopa (large)
				Callianassa	7 larvae I–IV
				Hippolytid (cf. *Eualus*)	3 larvae
				Stomatopod	4 larvae

SOLENOCERINAE

Solenocera membranacea (Milne-Edwards)

Heldt, 1938, p. 125.

OCCURRENCE. St. WS 980, 50–0 m., 1 protozoea, stage II; 2 protozoeae, stage III.

SERGESTIDAE

SERGESTINAE

Sergestes cornutus Kröyer

Gurney & Lebour, 1940, pp. 13–19.

OCCURRENCE. St. WS 977, 50–0 m., 1 elaphocaris, stage I changing to stage II.

Sergestes sp., cf. *arcticus* Kröyer

Hansen, 1922, p. 62.

OCCURRENCE. St. WS 977, 50–0 m., 1 mastigopus, late larval or juvenile.

Sergestes arcticus Kröyer

Gurney & Lebour, 1940, pp. 19–21.

OCCURRENCE. St. WS 996, 250–100 m., 1 elaphocaris, stage III.

Sergestes diapontius Bate

Hansen, 1922, p. 172.

OCCURRENCE. St. WS 997, 50–0 m., 1 mastigopus, late larval or juvenile, *c.* 15 mm. long.

The specimen agrees with *diapontius* in the shape of the third maxillipede. It is apparently intermediate between *diapontius* and *vigilax*. I am inclined to place it in *diapontius* as this species is known to have a more southerly distribution than *vigilax*.

CARIDEA

HOPLOPHORIDAE

Acanthephyra acanthetelsonis Bate

Kemp, 1939, p. 574.

OCCURRENCE. St. WS 978, 100–50 m., 1 larva, stage V; 1000–750 m., 1 post-larva or juvenile.

The specimen from 1000–750 m. is probably a post-larva as it closely resembles the post-larva of *Acanthephyra purpurea* Milne-Edwards from Bermuda (see Lebour, in Gurney & Lebour, 1941). It is, however, clearly distinguishable by the number of dorso-lateral spines (in this case fourteen each side), the number in *A. acanthetelsonis*, according to Kemp, ranging from thirteen to nineteen. The adult characters are not all present, but the dorsal spines on the third to the sixth abdominal somites and the large hump on the third, continuing in the dorsal carina, are conspicuous. There are five spines dorsally on the rostrum and one below as in the post-larval *A. purpurea*, and the rostrum hardly reaches to the end of the eyes. Holthuis (1951) has recorded this species from West Africa (Gold Coast and Liberia) and Kemp gives its distribution as 'Central and South Atlantic about 14° N. to 28° S.'

PASIPHAEIDAE

Pasiphaea semispina Holthuis

Holthuis, 1951, p. 9; 1952, p. 26.

OCCURRENCE. St. WS 987, 50–0 m., 3 specimens, *c*. 35–40 mm. long; 250–100 m., 1 specimen, *c*. 45 mm. long, in berry.

This species was described from a single male of 66 mm. by Holthuis (1951) from off Angola (7° 35′ S., 12° 38′ E., 235–460 m. depth, bottom mud, 17. iii. 46). Later, Holthuis (1952) recorded several more specimens, including females, from the South Atlantic. These records range from 5° 52′ S., 11° 43′ 30″ E. to 10° 45′ S., 13° E., therefore all came from much farther north than the 'William Scoresby's', which were collected between 20° and 26° S., thus greatly extending the known range of the species. The 'William Scoresby' specimens came from depths of 50–0 to 250–100 m. and were 35–45 mm. long; Holthuis's from 74–500 m. and measured up to 70 mm. in length. The species apparently does not inhabit great depths.

A young pasiphaeid, 7 mm. in length, occurred at St. WS 979, 100–50 m. It is almost certain that it belongs to this species for the spines on the fourth and sixth abdominal somites are beginning to show, the rostrum and appendages are similar and the merus of the first and second legs have no spines. The sixth abdominal somite is very long, a good deal longer than the fourth and fifth combined, but it frequently happens in decapod larvae that the length of this somite is longer in the young than in the adult. It seems likely that there are only a few stages between this and the newly hatched larva. The telson bears eight setae at its end but is slightly concave instead of convex at the margin.

HIPPOLYTIDAE

Several larvae are present but it is difficult to place the young stages, most of which resemble *Hippolyte* or *Eualus*. One first stage differs in having a distinct hump on the third abdominal somite and a very much elongated telson, and this may not be an Hippolytid at all (St. WS 1001, 50–0 m.).

Two Hippolytid larvae indet., cf. *Eualus* (St. WS 979, 50–0 m.) and one Hippolytid larva indet. (St. WS 979, 100–50 m.) are at stage I, with humps on the third abdominal somite and a long telson, as is the larva from St. WS 1001 (50–0 m.).

One Hippolytid post-larva, possibly *Eualus lebourae*, was described by Holthuis (1951) from West Africa. This is not unlike the post-larval stage of *E. occulta* (Lebour, 1936*a*). It is possible that the larva from St. WS 1001 may be a first young stage of this species (*occulta*) as the exopods have disappeared from the legs. There are two dorsal teeth on the rostrum, the telson has three pairs of dorso-lateral spines and three pairs at the end which is pointed. The second leg is incompletely segmented but there are three distinct divisions and an indefinite number (possibly four) not properly formed. The antennule is like that of *E. lebourae* but more elongated.

Three Hippolytid larvae, stages II–IV, possibly *Eualus*, occurred at St. WS 1002, 50–0 m.

PROCESSIDAE

OCCURRENCE. St. WS 979, 50–0 m. 1 *Processa* larva, stage VIII or IX. St. WS 979, 100–50 m. 1 *Processa* larva, stage IV or V.

These larvae are of the *Processa edulis* type with no dorso-lateral spines on the fourth abdominal somite (Lebour, 1936*b*). Holthuis (1951) describes several new species of *Processa* from the East Atlantic, not far from the present region. His *P. intermedius* seems to be the closest to *P. edulis*.

PALAEMONIDAE

PONTONIINAE

Periclimenes, sub-gen. **Periclimenes** sp.

OCCURRENCE. St. WS 996, 100–50 m., 1 late larval stage, Fig. 1.

This late larval stage of a pontoniid is very interesting and apparently belongs to a species of *Periclimenes*, sub-gen. *Periclimenes*. It bears a close resemblance to Gurney's 'larva of an unknown genus' (Gurney & Lebour, 1941, p. 117, fig. 9*m*, *n*) from 'Discovery' Station 278 off North Africa, and probably belongs to the same genus. These peculiar larvae have the very unusual feature of a long antennular flagellum which surpasses the length of the body. These two specimens, belonging to separate species and possibly to separate genera, are apparently the only known instance of such a phenomenon. Gurney included his figure in order to compare it with *Rhinchocinetes rigens*, which in the late larval stages possesses an extremely long *antennal* flagellum comparable with the present *antennular* flagellum. In Gurney's figure the flagella are figured in each case (fig. 9*h*, *m*) as loosely held at the side and behind, but in the live *Rhinchocinetes* larva observed by myself (Gurney & Lebour, 1941, p. 119) the *antennal* flagella, nearly four times the length of the body, were carried straight out in front, the two together closely approximated, and having a ram-like appearance. In the present larva here described, the *antennular* flagellum is carried straight in front in an exactly similar way (Fig. 1*a*). The purpose of these analogous organs is probably to help suspend the animal in the water-layer in which it habitually swims. Gurney's figure *m* and the present larva agree in many features besides the long antennular flagellum, and almost certainly belong to the same genus although they differ enough to be placed in separate species. The present larva is bent at the third abdominal

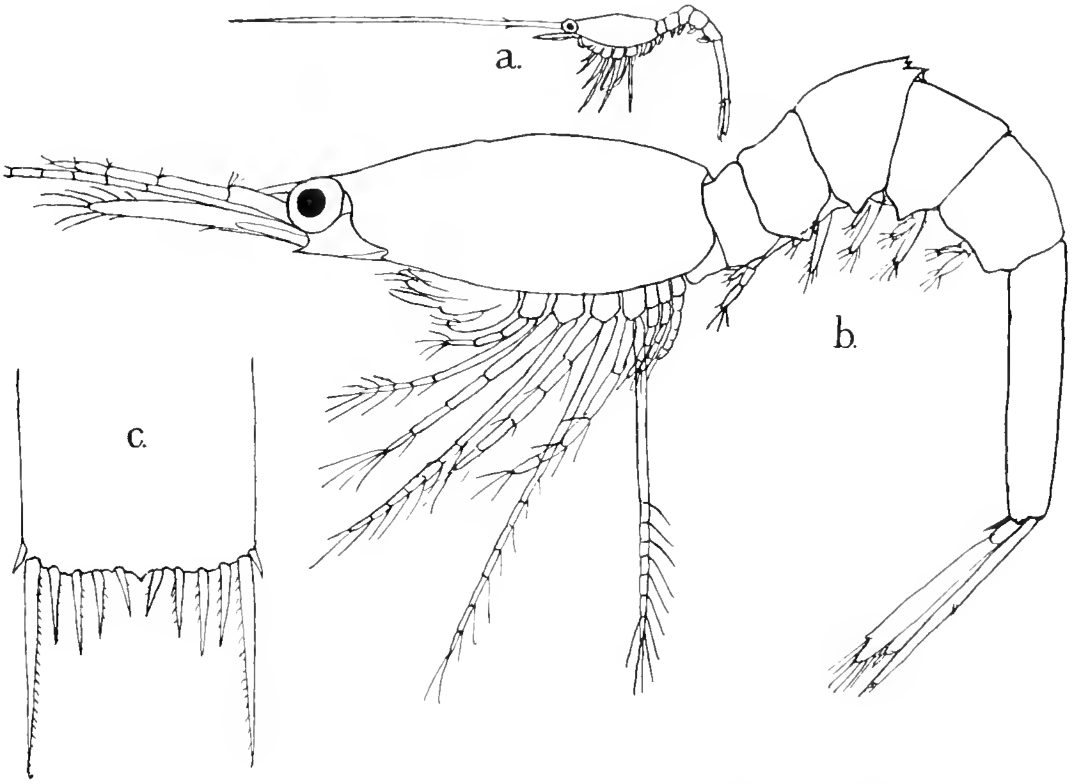


Fig. 1. *Periclimenes* sp., late larval stage, *c.* 10 mm. long. *a*, showing complete antennule; *b*, the same, enlarged, antennular flagellum cut off; *c*, telson.

somite, but the body is apparently straight in Gurney's larva. In both, the rostrum is slender and unarmed and reaches beyond the eyes for about the length of the eye, the antennal scale reaches nearly to the end of the inner antennular branch, there are as yet no chelae on the first and second legs, there are very long setose exopods on the third maxillipede and on legs 1 and 2, in all cases longer than the endopods, and there are no exopods on legs 3–5 which are as yet not fully developed but are all of about equal length. The pleopods are small buds in Gurney's larva, but are slightly setose in the present specimen which is at a later stage. The sixth abdominal somite is as long as the third to the fifth inclusive. The sides of somites 1–5 are slightly pointed. In the present larva the third abdominal somite has a small median tooth and just behind it another tooth. These are apparently not present in Gurney's larva. He gives no size for the latter. The present larva measures nearly 10 mm. in length from the tip of the rostrum to the end of the telson, the antennular flagellum measuring 12·45 mm. in length. The telson is nearly straight-sided, the end being slightly indented in the centre and rounded on each side. It is armed with two pairs of dorso-lateral teeth and six setae terminally on each side of a small knob, the outer tooth small, the inner teeth setose on the inside only.

A comparison with known larvae of this sub-genus shows that it must belong here. Very little is known of the larval stages of the sub-genus *Periclimenes*, genus *Periclimenes*. We do, however, know one, the last larval stage of a form attributed with a query to *Periclimenes* (*Periclimenes*) *longicaudatus* (Stimpson) (Gurney & Lebour, 1941, p. 146) which was followed through four moults to the third stage and was shown to belong undoubtedly to this sub-genus. Lebour (1949*a*) described the newly hatched larvae of *Periclimenes* (*Periclimenes*) *iridescens* Lebour.

These are the only larvae so far known which undoubtedly belong to this sub-genus, and the late larva differs much from *Ancylocaris* whose late larvae are also known. The features of these indicate that they belong to some species of the sub-genus *Periclimenes* of the genus *Periclimenes* and a comparison with the last larva of *P. longicaudatus*(?), shows certain features in common. For example, the body is bent at the third somite (as in the present larva), the fourth and fifth legs are short and similar and there are no exopods on legs 3–5. This last feature is, however, perhaps not of generic value as in many larvae of various genera, the number of exopods on the legs varies. The telson is of a palaemonid type and very like that of the larva of *P. longicaudatus*(?), and also like some of the larvae attributed in 1924 by Gurney to the Palaemonidae.

It is of course impossible to be sure of the place of this larva, but it seems almost certain that it is a palaemonid of the sub-family Pontoniinae and belongs to the genus *Periclimenes* sub-genus *Periclimenes*. There are several species of this sub-genus recorded from West Africa, but it may quite likely belong to a new species.

THALASSINIDEA

CALLIANASSIDAE

OCCURRENCE (Stations). WS 979, 50–0 m., 15 *Callianassa* larvae, stages I–V. WS 979, 100–50 m., 1 *Callianassa* larva, stage I. WS 980, 100–50 m., 2 *Callianassa* larvae, early. WS 998, 50–0 m., 25 *Callianassa* larvae, stages I–V. WS 998, 100–50 m., 1 *Callianassa* larva, stage I. WS 998, 175–100 m., 1 *Callianassa* larva, stage I. WS 999, 50–0 m., 9 *Callianassa* larvae, stages II–III. WS 999, 100–50 m., 1 *Callianassa* larva, stage III. WS 999, 150–100 m., 1 *Callianassa* larva, stage V. WS 1001, 50–100 m., 28 *Callianassa* larvae, stages I–V. WS 1001, 100–50 m., 4 *Callianassa* larvae, stages I–III. WS 1002, 50–0 m., 7 *Callianassa* larvae, stages I–IV.

A large number of *Callianassa* larvae (Fig. 2) were obtained, apparently all of the same species, but varying from stage I to stage V. They are of the type I of Gurney (1942) to which *C. subterranea* belongs (sub-genus *Cheramus*). The sub-genus *Trypaea* has a similar larva, those of *T. affinis* from

California (Lebour, 1938) and *T. australiensis* from New South Wales (Dakin & Colefax, 1940) being known from the parent. There are species from South Africa which apparently belong to *Trypaea* and which were recorded by Barnard (1950), but the only callianassid, *Callianassa guineensis*, which undoubtedly comes from the region of the Benguela Current, was recorded by De Man (1928), and this belongs to the sub-genus *Calochirus*, whose larva is of a different type (type II of Gurney). It would seem therefore that the present larvae must belong to a species of *Trypaea* or *Cheramus*, and one that is common in the region.

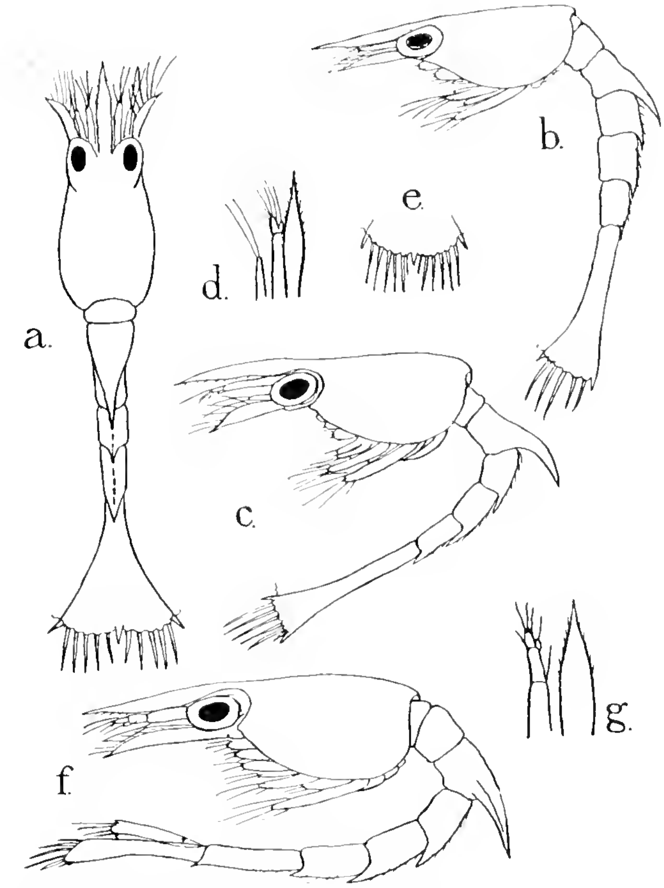


Fig. 2. *Callianassa* sp. St. WS 998, 3. x. 50. *a*, *b*, stage I, length 4·2 mm.; *c*, *d*, *e*, stage II, length 5 mm.; *f*, *g*, stage III, length 5·5 mm.

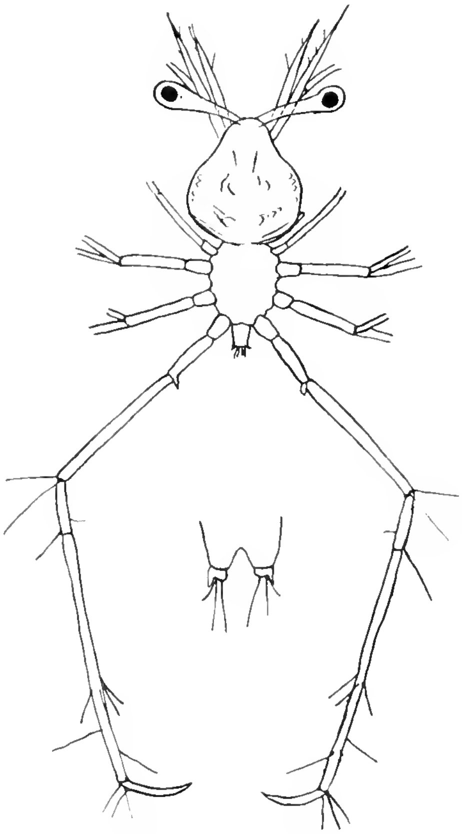


Fig. 3. *Jasus lalandii*, stage I, length 1·5 mm.

SCYLLARIDEA

PALINURIDAE

Jasus lalandii (Lamarck)

Gilchrist, 1916, p. 101.
Gurney, 1936, p. 416.

OCCURRENCE. St. WS 1000, 50–0 m., 1 phyllosoma, stage I. St. WS 992, 100–0 m., 1 phyllosoma, ?stage VIII.

Jasus lalandii is the common crawfish of the district. Phyllosoma, stage I, measured 1·5 mm. from the front to the end of the telson. It has been well described by Gilchrist (1916). A peculiarity of the phyllosomas of *Jasus*, unlike the other Palinuridae, is the absence of an exopod on the first maxillipede, except for a minute rudiment in some of the later stages. Gurney (1936) specially notes this as a character of all known phyllosomas of the Scyllaridae. The first stage of *Jasus* (which has been shown by Gilchrist to emerge from a naupliosoma) is very like some of the known first stages of *Scyllarus* and *Scyllarides*, so much so that one is inclined to regard them as very closely related. In 1949*b* I described and figured a phyllosoma from Bermuda which I attributed to *Scyllarides* sp., stage I. Although like *Scyllaris*, in many ways it was more developed, especially the antennae which were segmented and branched, the telson also being much more advanced. In many ways it resembled *Jasus* which has not been recorded from Bermuda, but the telson of *Jasus* is different and the antennae reach beyond the eyes, the two branches being much longer. The third leg is also much longer, the thorax broader than long (in the Bermuda species it is pear-shaped and longer than broad). At least two species of *Scyllarides* occur in Bermuda and it is probable that my *S. phyllosoma* B belongs to one of these. The similarity to the *Jasus* larva is, however, very striking.

Gurney's later stage of *Jasus* was 11 mm. long and was about stage VIII (Gurney, 1936, p. 421). He suggested that his specimen was about six weeks old. It was captured at a depth of 200–0 m. One of Gurney's specimens of this size was taken 900 miles from the nearest coast. The present specimen came from 93 miles off-shore (Fig. 3).

ANOMURA

PAGURIDEA

PAGURIDAE

Three species of pagurid larvae occur in the collection. The first represented by one damaged specimen only is of the *Eupagurus* type and is in the second stage (St. WS 1001, 50–0 m.). The second is represented by two larvae of the *Glaucothoë peronii* Milne-Edwards type (see Gurney, 1942, p. 259) (St. WS 997, 1000–0 m.).

It has been suggested by Bouvier (1905) and Thompson (1943) that these large Glaucothoës belong to the genus *Sympagurus*, the larva agreeing in many ways with the adult of this genus. It is probable that it belongs to some deep-water genus and not to a shore form.

The third larva represents a type of pagurid larva not hitherto described. Two specimens were obtained from St. WS 1001, 50–0 m., two specimens from St. WS 1047, 100–0 m., and three specimens from St. WS 1047, 100–0 m. The two last hauls were made during the second survey, the material from which has not yet been fully worked out. All these larvae are in the first stage.

One specimen only of a similar larva, but of a different species obviously closely related, was obtained in one of Dr Moore's hauls in Bermuda (100–150 fms.). These elongated larvae belong to some pagurid, but are not at present identifiable with any known adult. They are peculiarly interesting as they differ entirely from any known form and they are worth a detailed description. The drawings of the Bermuda specimen were shown to the late Dr Gurney who suggested that the larva might belong to one of the symmetrical genera.

The characters which these first larva have in common are the great length, elongated body, long rostrum, carapace rounded posteriorly with conspicuous grooves, antenna with a large spine at the base of the exopod, the endopod with three terminal setae, abdominal somites 2–5 with long curved latero-ventral spines directed backwards, telson deeply incised with the usual hair-like second seta of the pagurids and their allies, rounded knobs on rostrum and carapace, and on part of the abdomen and telson.

I shall call these larvae from the Benguela Current and from Bermuda, larva A and B respectively.

Larva A. Five specimens from the Benguela Current (Fig. 4). The colour does not show. Length of body 6 mm., transverse groove on carapace definite but imperfect. Rostrum reaching well beyond eyes for about twice the eye length, knobs on each side of the margin. Knobs scattered on carapace, not showing much on abdomen but present near the margin of the telson. Abdominal somites 2–5 with small teeth on each side above the large recurved spines. Telson deeply indented but not so broad as in larva B. Mandible, maxillule and maxilla of the usual pagurid type except that the posterior lobe of the exite of the maxilla has four setae, the end one on the posterior margin, which is unusually bare.

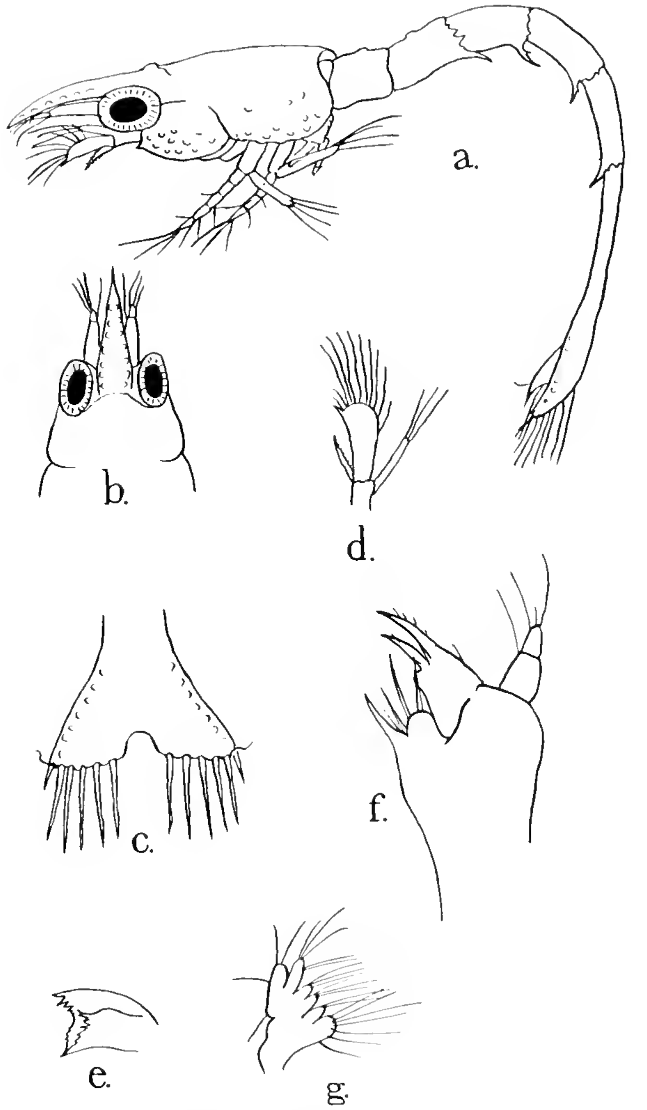


Fig. 4. Pagurid larva A, St. WS 1001–1, 50–0 m., 14. iii. 50, length 6 mm. *a*, side view; *b*, head; *c*, telson; *d*, antenna; *e*, mandible; *f*, maxillule; *g*, maxilla.

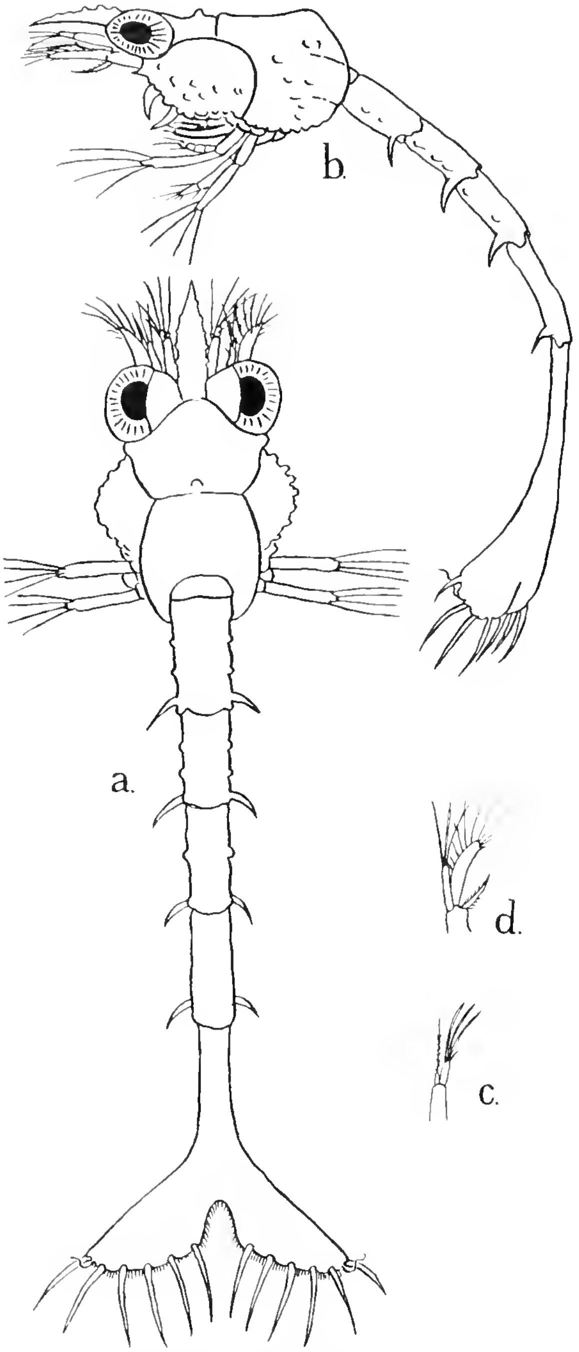


Fig. 5. Pagurid larva B, Dr Moore's cruise, St. 101, Dec. 1938, Bermuda, length 6 mm. *a*, dorsal; *b*, side view; *c*, antennule; *d*, antenna.

Larva B. From Bermuda. Length 6 mm. (Fig. 5). Colour brilliant red with the main background yellow (as this was preserved but examined soon after capture, the colour may be slightly different in life). Transverse grooves on carapace very conspicuous. Rostrum similar to larva A with knobs along the sides and along margin of carapace and also on the sides. Knobs less conspicuous than in larva A but here they are also along the abdomen. Telson more slender with a longer first spine, eye much larger. Abdominal somites pointed posteriorly but without small teeth above the lateral spines. Main spine of upper lobe of maxillule very conspicuous.

It seems certain that these larvae are pagurids but of a type hitherto unknown. Gurney (1924, p. 156, fig. 62) figured and described a larva attributed to the Laomediidae, but later (1938, p. 156) regarded by him as a pagurid, which has features in some way resembling the present larvae. The abdominal somites 2 and 3 have backwardly directed spines, the rostrum is not unlike, the telson deeply indented.

This larva of Gurney's is at stage III and therefore in many ways different, but the exite of the maxilla is armed on the posterior lobe in a similar way to the Bermuda larva.

These larvae all show the thalassinid characters well and seem to emphasize the resemblance, which Gurney pointed out (1938) between the *Upogebia* and the *Laomedia* type of thalassinid larvae and the pagurid larvae.

There are other pagurid larvae (at least three species) to be found in Bermuda, all of which have a deeply hollowed telson in the first stage and two of these are much alike. These were attributed to *Clibanarius*, as that is the commonest genus in Bermuda, moreover the *C. misanthropus* larva described and figured by various authors (Williamson, 1915; Hesse, 1876; etc.) is of this type. Although differing in many ways, especially in size, from the present larvae, they have certain features in common—telson much indented, rounded carapace, long and broad rostrum, endopod of antenna with three setae. It is probable that they all belong to the same group, and as *Clibanarius* belongs to the *Eupagurus* group, it follows that Gurney's remarks on the larvae do not apply here. We know too little of the pagurid larvae to divide them into groups with any certainty—and study of the newly hatched larvae of any known species is much wanted.

BRACHYURA

OCCURRENCE (Stations). WS 979, 50–0 m., 3 *Brachyrhyncha* zoeae indet, stage I. WS 979, 100–50 m., 1 *Brachyrhyncha* zoea indet., stage II. WS 980, 50–0 m., 3 *Brachyrhyncha* zoeae indet. These are peculiar in having a very large telson spine externally on the fork. WS 980, 100–50 m., 1 *Brachyrhyncha* zoea indet., stage IV. WS 996, 100–50 m., 1 *Ebalia* zoea, 3rd and 4th stages. WS 996, 250–100 m., 1 *Ebalia* megalopa. WS 997, 50–0 m., 4 *Ebalia* megalopae. WS 997, 250–100 m., 1 *Ebalia* zoea, 4th stage, 1 *Ebalia* megalopa. WS 997, 1000–750 m., 1 *Ebalia* zoea, 1st stage. WS 998, 50–0 m.; 18 *Ebalia* zoeae (1st to last), 1 *Ebalia* megalopa, 2 *Brachyrhyncha* zoeae indet., 1st stage. WS 998, 100–50 m., 1 *Brachyrhyncha* megalopa indet. WS 998, 175–100 m., 3 *Ebalia* megalopa. WS 999, 50–0 m., 2 *Ebalia* zoeae, 1 *Ebalia* megalopa, 1 *Brachyrhyncha* zoea indet., 4th stage. WS 999, 150–100 m., 1 *Ebalia* megalopa. WS 1001, 100–50 m., 1 *Ebalia* megalopa. WS 1002, 50–0 m., 1 large Portunid megalopa indet., having the last legs with setose swimming paddles.

A number of crab zoeae occur in the collection and some megalopae. The commonest of these, both zoeae and megalopae, belong to a species of *Ebalia*. The remainder are nearly all *Brachyrhyncha*, some of which can be identified as portunids.

Adult *Ebalia* live on the bottom and these larvae closely resemble *E. tuberosa* (Pennant), but differ from it in having more setae on the last pleopods of the megalopa (Lebour, 1928). No colour was present in the preserved specimen of the zoea and consequently it could not be distinguished from that species. *E. tuberosa* is widely distributed and has been recorded from the Atlantic as far as the Azores and Canaries. It may well be that the present form is closely related to it.

STOMATOPODA

Five adult *Squilla*, identified as *S. armata* Milne-Edwards and confirmed as such by Dr I. Gordon of the British Museum, were taken at St. WS 990, net. O.T.C., depth 128 m. Position: from 25° 35′ S., 14° 27′ E., to 25° 36′ S., 14° 24′ E., off west coast of Africa.

OCCURRENCE (Stations). WS 1000, 50–0 m., 2 larvae (intermediate stage). WS 1001, 50–0 m., 19 larvae (from first pelagic stage to latest seen, presumably stage IX). WS 1001, 100–50 m., 3 larvae (1 stage IV, 1 stage VII, 1 stage VIII). WS 1002, 50–0 m., 4 larvae (intermediate stages).

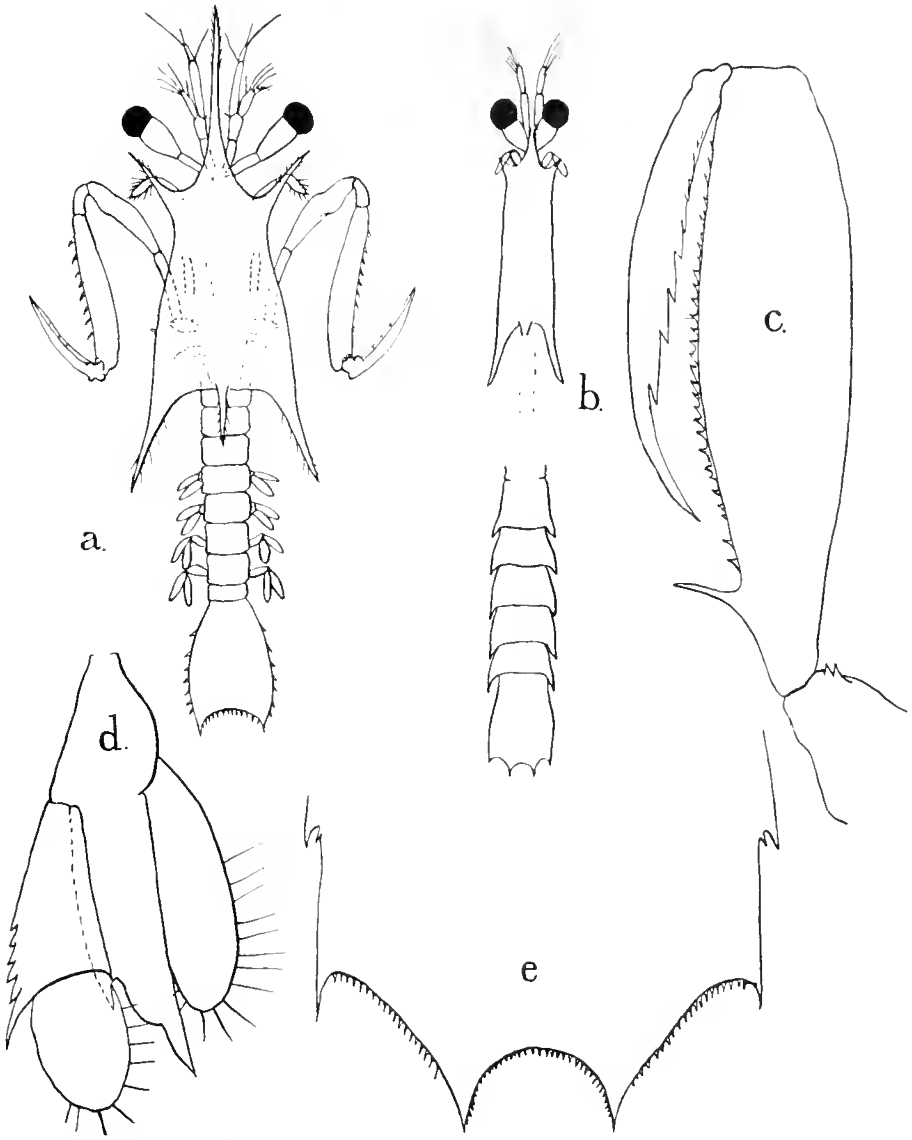


Fig. 6. *Squilla armata*?, St. WS 1001, 14. iii. 50, 50–0 m. *a*, alima, first pelagic stage, length 4·7 mm.; *b*, late alima, probably last (rostrum and posterior carapace spine broken), length 20 mm.; *c*, the same, raptorial claw; *d*, uropod; *e*, end of telson.

Several Stomatopod larvae were obtained in the plankton round about the area at which the adult *Squilla armata* occurred, and almost certainly belong to this species (Fig. 6). The oldest larva had the raptorial claw with seven teeth, some of which were still covered but were quite distinct. The uropods are also very like this species. The oldest larva, *c.* 20 mm. long, is either at the last or penultimate stage and no older specimens were seen. The other stages range from the first pelagic stage, through several intermediate stages to this late stage. They correspond very closely as a series to those of

Squilla desmarestii Risso, as described by Giesbrecht (1910), and are possibly identical with *Alima bidens* of Claus (1871) and of Brooks (1886) which, according to Gurney (1945), are probably synonymous with *A. longicaudata* Jurich (1904). The larvae are certainly much alike except that *A. bidens* has no dorsal spine on the carapace. (Only two specimens were described by Brooks, and it is possible that the spine may have been broken which seems to be a common occurrence, or alternatively it may have disappeared in the last stage.) Jurich's *A. longicaudata*, about stage VII, which was obtained in the Benguela Current, is almost certainly the same as the present form and we may presume that it belongs to *Squilla armata*.

Description of first pelagic stage (Fig. 6*a*)

Length 4·7 mm. Long spiny rostrum about equal in length to the carapace. Conspicuous anterior lateral spines, slightly spiny, about one-third the length of the rostrum. Posterior lateral carapace spines spiny, about half the length of the carapace. Posterior median spine on carapace short. Carapace covering two thoracic somites and a half. Five abdominal somites without lateral spines. Four pairs of setose pleopods. Raptorial claw with unarmed dactyl, except for a spine underneath the cuticle, the propod with fine spines internally. Telson with a series of teeth laterally, the first two separated by a space larger than the others, *c.* twenty-four spines internal to the terminal lateral spines.

The following stages progress in a manner similar to those of *Squilla desmarestii*. The latest seen which corresponds to stage IX of that species still has a small medium posterior spine on the carapace, the anterior lateral spines have dwindled and the rostrum and posterior lateral spine are shorter. None of them has spines. The carapace is about three times as long as broad. The thoracic limbs are all well developed and there are gills on maxillipedes 1–4. There are six abdominal somites and five pairs of setose pleopods, somites 1–5 with long lateral spines. The raptorial claw has a long spine and a series of small spines on the propod internally, and the dactyl has four free spines and three still covered. The telson has a small tooth just behind the lateral tooth and there are nineteen spines each side, between the intermediate and sub-median teeth, and thirty-six between the sub-median teeth. Length of larva from tip of rostrum to end of telson 20 mm. Uropods very like those of the adult *S. armata*.

As *S. armata* is the common *Squilla* of this district and has much the same distribution as *Jasus lalandii* and as only one *Squilla* larva occurred in the plankton hauls, and in one case together with a first larval stage of *Jasus lalandii*, it seems almost certain that these larvae belong to *Squilla armata*, which is known from a wide area including the region of the Benguela Current (Balss, 1938). It has been described by several authorities including Bigelow (1895) and Kemp (1913).

Although it is nearly certain that these larvae belong to *S. armata*, occurring as they do in exactly the same locality as the adult, it is just possible that they may belong to Calman's *S. africana* (Calman, 1916). His specimen of the adult came from the West African coast, from the Congo northwards, and he shows that Jurich's (1904) *S. empusa* from the Congo belongs to this species, as do other specimens from West Africa in the British Museum. All, however, are obtained farther north than the present specimens and it seems more probable that these latter belong to *S. armata*.

LITERATURE

BALSS, H., 1927. *Macrura der Deutschen Tiefsee-Expedition*, 3. *Natantia. Teil B.* Wiss. Ergeb. deutsch. Tiefsee-Expedition 'Valdivia', XXIII, pp. 247–75.

BARNARD, K. H., 1950. *Descriptive Catalogue of S. African Decapod Crustacea.* Ann. S. Afr. Mus. XXXVIII.

BOUVIER, E. L., 1905. *Nouvelles Observations sur les Glaucothoes.* Bull. Mus. Oceanogr. Monaco, no. 51, pp. 1–14.

CALMAN, W. T., 1925. *On Macrurous Decapod Crustacea collected in South African Waters by S.S. 'Pickle'.* Rep. Fish & Mar. Biol. Survey, IV. Special Report 3, pp. 1–26.

Dakin, W. J. & Colefax, A. N., 1940. *The Plankton of the Australian Coastal Waters of New South Wales*, Part I. Pub. Univ. Sydney, Part I of Zool. Monograph I, pp. 1–395.

De Man, J. S., 1928. *The Thalassinidae and Callianassidae collected by the 'Siboga' Exp.* 'Siboga' Exp. Rep. xxxix, *a*, *b*, pp. 1–183.

Gilchrist, J. D., 1916. *Larval and Post-larval stages of* Jasus lalandii (M.-Ed.). J. Linn. Soc. Lond. Zool. xxxiii, pp. 101–24.

Gurney, R., 1924. *Decapod Larvae.* Nat. Hist. Rep. 'Terra Nova' Exped. Zool. viii, No. 2, part ix, pp. 37–302.

—— 1936. *Larvae of Decapod Crustacea.* Part iii. *Phyllosoma.* 'Discovery' Reports, xii, pp. 400–40.

—— 1938. *Larvae of Decapod Crustacea*, Part v. *Nephropsidea and Thalassinidea.* 'Discovery' Reports, xvii, pp. 291–344.

—— 1942. *Larvae of Decapod Crustacea.* Ray Society Monograph, pp. 1–306.

Gurney, R. & Lebour, M. V., 1940. *Larvae of Decapod Crustacea*, Part vi. The Genus *Sergestes.* 'Discovery' Reports, xx, pp. 1–68.

—— —— 1941. *On the Larvae of Certain Crustacea Macrura, mainly from Bermuda.* J. Linn. Soc. Lond., Zool., xli (no. 277), pp. 89–181.

Hansen, H. J., 1922. *Crustacés Decapodes (Sergestides) provenant des campagnes des yachts 'Hirondelle' et 'Princesse Alice' (1885–1915).* Res. Camp. Sci. Monaco, fasc. lxiv, pp. 1–232.

Heldt, J. H., 1938. *La Reproduction chez les Crustacés decapodes de la Famille des Peneides.* Ann. Inst. océanogr. Monaco, n.s. xviii, fasc. 2, pp. 1–206.

Hesse, M., 1876. *Description des Crustacés rares ou nouveaux des côtés de France*, Arb. 5. Ann. Sci. Nat. Zool. (6), pp. 1–42.

Holthuis, L. B., 1951. *The Caridean Crustacea of Tropical West Africa.* 'Atlantide' Report, no. 2, Sci. Res. of the Danish Exp. to the Coasts of Tropical West Africa, 1945–6, pp. 7–187.

—— 1952. *Crustacés décapodes macrures.* Exp. Océan. Belge dans les Eaux côtières africaines de l'Atlantique sud (1948–1949). Rés. Sci. iii, fasc. 2, pp. 1–88.

Kemp, S., 1939. *On* Acanthephyra purpurea *and its Allies (Crustacea Decapoda: Hoplophoridae).* Ann. & Mag. Nat. Hist. ser. ii, iv, no. 24, pp. 568–79.

Lebour, M. V., 1928. *The Larval stages of the Plymouth Brachyura.* Proc. Zool. Soc. Lond. part 2, pp. 474–560.

—— 1936*a*. *Notes on the Plymouth Species of* Spirontocaris. Proc. Zool. Soc. Lond. pp. 89–104.

—— 1936*b*. *Notes on the Plymouth* Processa. Proc. Zool. Soc. Lond. pp. 609–17.

—— 1938. *The newly hatched larva of* Callianassa affinis *Holmes.* Proc. Zool. Soc. Lond. cviii, pp. 47–8.

—— 1949*a*. *Some New Decapod Crustacea from Bermuda.* Proc. Zool. Soc. Lond. cxviii, pp. 1107–17.

—— 1949*b*. *Notes on some larval Decapods (Crustacea) from Bermuda.* Proc. Zool. Soc. Lond. cxx, pp. 369–79.

Stephensen, K., 1923. *Decapoda Macrura.* Rep. Danish Oceanog. Exp. 1908–10, to the Mediterranean and adjacent Seas, ii, D 3, pp. 1–252.

Thompson, E. F., 1943. *Paguridae and Coenobitidae.* Sci. Rep. 'John Murray' Exp. 1933–34, vii, pp. 412–26.

Williamson, H. C., 1915. *Nordisches Plankton*, Lief. xviii, *Decapoden*, I. Teil (*Larven*). Kiel and Leipzig, pp. 315–588.

LITERATURE STOMATOPODA

Balss, H., 1938. *Stomatopoda.* In Bronn's Klassen und Ordnungen des Tierreichs. 5. Abt. i. Buch 6, Teil ii, pp. 1–178.

Bigelow, H. P., 1895. *Report upon the Crustacea of the order Stomatopoda collected by the Steamer 'Albatross' between 1885 and 1891, and on other specimens in the U.S. National Museum.* Proc. U.S. Nat. Mus. xvii, pp. 489–550.

Brooks, W. K., 1886. *Report on the Stomatopoda collected by H.M.S. 'Challenger' during the years 1873–76.* 'Challenger' Reports, Zool. xvi, pp. 1–116.

Calman, W. T., 1916. *A New Species of the Crustacean Genus* Squilla *from West Africa.* Ann. & Mag. Nat. Hist. ser. 8, xviii, pp. 373–6.

Claus, C., 1871. *Die Metamorphose der Squilliden.* Abh. Kgl. Ges. Wiss. Göttingen, xvi, pp. 111–63.

Giesbrecht, W., 1910. *Fauna und Flora des Golfes von Neapel. Stomatopoden*, xxxiii, pp. 1–239.

Gurney, R., 1945. *Notes on Stomatopod Larvae.* Proc. Zool. Soc. Lond. cxvi, pp. 133–75.

Jurich, B., 1904. *Die Stomatopoden der deutschen Tiefsee-Expedition.* Wiss. Ergeb. deutsch. Tiefsee-Exp. 'Valdivia', vii, pp. 361–408.

Kemp, S., 1913. *An account of the Crustacea Stomatopoda of the Indo-Pacific region.* Mem. Ind. Mus. iv, 1, p. 41.

[*Discovery Reports. Vol. XXVII, pp.* 235–278, *Plate XIII, April* 1955].

THE DISTRIBUTION OF *SAGITTA GAZELLAE* RITTER-ZAHONY

By

P. M. DAVID

CONTENTS

THE DISTRIBUTION OF *SAGITTA GAZELLAE* RITTER-ZAHONY

By P. M. David

(Plate XIII, text-figs. 1–27)

INTRODUCTION

ONE of the main objects of the plankton studies carried out by the Discovery Committee and the National Institute of Oceanography is to disclose the principles which underlie the distribution of oceanic organisms. Among the different species of pelagic zooplankton there are very wide contrasts in horizontal and vertical ranges, and in the relations between distribution, life cycle, and environment. Yet there are few oceanic species of which even the limits of distribution have been fully delineated, and fewer still whose life cycle has been adequately related to their distribution. To understand the basic factors it is clearly desirable to know how much the range of habitat and the life cycle vary among planktonic organisms, and to consider whether any types of distribution are associated with certain methods of reproduction or feeding habits, or with the phylogenetic position of the species. One method of approaching these problems is to work out as fully as possible the distribution of a number of species at all stages of their life history, so that those of different habits and from different taxonomic groups can be compared; and the present paper is intended as a contribution to this end.

The Discovery Committee's field of work was mainly in Antarctic and Subantarctic waters, and these regions were very widely sampled by the 'Discovery II' in five voyages before the war. During a sixth voyage, under the National Institute of Oceanography in 1950–51, much material was collected in the winter months, which had been insufficiently represented in the pre-war plankton samples. The collections are now well suited to studies of distribution since they cover the whole range of a number of southern species at all times of year. The closing nets provide good information on vertical distribution, and detailed hydrological data are available from most stations.

At present, a most exhaustive study of the life history and distribution of *Euphausia superba* by Mr J. W. S. Marr is nearing completion, and it is hoped that a study of a carnivorous species such as *Sagitta gazellae* will be of special interest when compared with a herbivorous species such as *Euphausia superba* which has wholly different habits.

Sagitta gazellae was chosen as an example of a carnivorous species for various reasons; experience had shown that it is widely distributed; it is easily recognized; it occurs in large, but not inconveniently large, numbers; the animal itself is of considerable size, and is thus easily picked out of samples; it is transparent and the state of its gonads can be determined without dissection. In addition to these points, very considerable data on this species had been amassed by Mr Marr during two pre-war commissions of 'Discovery II'.

Although in its distribution *S. gazellae* is restricted to the Southern Ocean, data from other areas concerning other species collected during the course of this work suggest that its habits are not unique and that *S. lyra*, a more cosmopolitan species, has, at least in the subtropics of the southern hemisphere, a very similar life history. It may well be that other species will be found to conform to a similar pattern.

ACKNOWLEDGEMENTS

I am particularly grateful to Mr Marr for advice and encouragement, and for permission to use the very large collection of data which he had assembled during the second and fourth commissions of R.S.S. 'Discovery II'.

The present study was suggested by Dr N. A. Mackintosh, C.B.E., who has given me advice and guidance during the whole time I have been engaged on it.

I should like to thank both Dr J. H. Fraser, F.R.S.E., who has read and corrected the typescript and given me a great deal of valuable advice during the preparation of this paper, and Dr H. E. Bargmann who read the first draft and made many helpful suggestions.

Mr E. Childs has assisted me in sorting a number of the samples required for this work, and my colleagues, Mr P. Foxton and Mr A. de C. Baker, have drawn my attention to any interesting specimens which they found while they were engaged upon work on the Discovery collections.

I wish to thank Professor T. Tokioka of the Seto Marine Laboratory, Japan, for kind permission to reproduce two of his figures (Figs. 9 and 13); Walter de Gruyter and Co. of Berlin for permission to reproduce four of Ritter-Zahony's figures (Figs. 1 and 11) from the Deutsche Süd-Polar Expedition Report; A. H. Pettifer of the Government Printing Office, Sydney, N.S.W., for permission to reproduce one of Johnston & Taylor's figures (Fig. 2) from the Australasian Antarctic Expedition Report; and the Council of the Linnean Society for permission to reproduce two of Fowler's figures (Figs. 3 and 4) from the Report on the Biscayan Plankton of H.M.S. 'Research'.

METHODS

All the material used in this investigation came from plankton samples in the Discovery collections. Most of the samples were taken from stations worked in the Southern Ocean, but in order to confirm that *S. gazellae* is confined to this area, the field examined was extended where possible by examination of tropical and subtropical stations.

It was the practice on board 'Discovery II' to make both vertical and oblique hauls at each full station, mainly with closing nets. (There are a number of stations at which only one or two nets were used, and some also at which plankton nets were not used at all. This accounts for many of the serial numbers 'excluded' in Tables 1 and 2.) At the great majority of full stations samples were taken with the standard 70 cm. vertical nets (N 70 V) from six or seven depths: 50–0, 100–50, 250–100, 500–250, 750–500, and 1000–750 m.; and on a good many occasions (especially on lines of stations on the 0° meridian) a haul from 1500 to 1000 m. was added. Except when this series was curtailed on account of bad weather or shallow water, the vertical nets covered a much greater range of depth than the oblique nets (N 100 B and N 70 B), which were normally towed through approximately 100–0 m. and occasionally also through deeper horizons. The oblique nets, however, usually take larger samples. Occasionally deep 2 m. and 4½ m. nets were used, and in many cases the resulting samples have been examined for *S. gazellae*, but owing to the irregularity with which these hauls were made, in time, position and depth, the material so obtained was only of use in anatomical comparisons.

For certain aspects of this work samples from a particular series of nets alone were examined, e.g. the vertical 70 cm. nets were used for the section on vertical distribution, but for other aspects, where it was necessary to obtain as many specimens as possible, all nets from any appropriate station were examined.

At the outset of this study a great deal of data were already available. These consisted of counts of *S. gazellae* present in the oblique 1 m. net hauls which had been analysed from time to time, and also in the 70 cm. vertical net hauls from lines of stations which had been repeated at different times of year in the meridian of 80° W. More detailed information was also made available through the kindness of Mr Marr who studied the Chaetognatha during the commissions of the 'Discovery II' in 1931–33 and 1935–37. These data consisted of measurements and numbers of chaetognatha from the 1 m. oblique nets (commission of 1931–33) and 70 cm. vertical nets (commission of 1935–37), and included notes on food, and observations on the state of maturity.

During the commission of the 'Discovery II' in 1950–51, I was able to count and measure all specimens of *S. gazellae* which were collected, and also made observations on food, and the development of the gonads.

Table 1 summarizes the stations from which information was thus available, and Table 2 summarizes the additional stations from which I have examined samples in order to cover the horizontal and vertical range of the species. It was not necessary for this purpose to examine all the plankton samples in the Discovery collections. For horizontal distribution I found it enough to use samples from a selection of lines of stations covering all areas of the Southern Ocean (see Fig. 17, p. 261), and have found enough hauls in subtropical and tropical latitudes to determine the northern limits of the species. The vertical series of hauls from lines of stations which have been repeated on a number of occasions in the meridian of 0° have been examined with the object of getting a picture of vertical distribution in one locality for most months of the year. These were long lines of stations covering Antarctic and Subantarctic waters. A series of deep vertical 2 m. net hauls, which extended from the Antarctic into the tropics in the meridian of 30° W., were also used to check the depth range and to examine the possibility of tropical submergence.

Table 1. *List of stations from which data were available at the commencement of this work*

	Counts only
N 70 V	Stations 1220–1229 1312–1320 1415–1421 1441–1450 1472–1476
N 100 B	Stations 1188–1258 (excluding 1191, 1192, 1194, 1196, 1207, 1230, 1231, 1234, 1247) 1331–1508 (excluding 1341, 1374–1379, 1398, 1432, 1457, 1459, 1477–1490, 1500)
	Counts and measurements
N 70 V	Stations 1608, 1609, 1610, 1612, 1614, 1616, 1617, 1620, 1622, 1624, 1628, 1632, 1636, 1687, 1688, 1689, 1690, 1691, 1692, 1694, 1696, 1699 1702, 1705, 1720, 1725, 1727, 1767, 1768, 1769, 1771, 1772, 1773, 1774, 1775, 1776, 1777, 1778, 1779, 1781, 1782 1805, 1806, 1807, 1808, 1809, 1810, 1812 2699–2704 (excluding 2700) 2736–2743 (excluding 2742) 2802–2812 (excluding 2809) 2817–2821 2834–2892 (excluding 2836, 2840, 2843, 2845–2847, 2854, 2856–2866, 2873, 2876–2879, 2881–2885)
N 100 B	Stations 725–923 (excluding 728, 730, 732, 734, 736, 738, 740, 742, 744, 747, 749, 752, 754, 756, 758, 762, 764, 767, 770–794, 796, 798, 800, 802, 805, 807, 809, 812, 814, 817, 821, 823, 826, 827, 832, 833, 835, 843, 846, 864, 874, 875, 876, 878, 888, 896, 897, 901, 907–910, 912–918) 942–1019 (excluding 944, 952–955, 957, 963, 979–982, 984, 987, 989, 991, 993, 997, 998, 1002, 1004–1012, 1014, 1016, 1018) 2699–2704 (excluding 2701) 2726–2731, 2736–2741, 2743, 2757, 2759, 2768–2770, 2785, 2794–2797 2802–2892 (excluding 2809, 2822, 2827, 2829, 2845, 2847, 2883–2885)

Descriptions of the nets employed by the expedition and the manner of fishing them may be found in Kemp, Hardy & Mackintosh (1929), Ommanney (1936) and Marr (1938). The positions and hydrological information for most of the stations which will be referred to, may be found in the various Discovery Station Lists. ('Discovery' Reports, Vols. IV, XXI, XXII and XXIV), but those from St. 2699 onwards will appear in the Station List for 1950–51 which is expected to be published shortly.

All the specimens were fixed, and preserved in neutralized sea-water formalin, in most cases in the whole plankton sample; this seems to give the best results. Chaetognaths removed from hauls before fixation and preserved separately often fix in a bent or distorted position, and if placed upon formalin-soaked blotting-paper to keep them straight, tend to get damaged. Specimens of *S. gazellae* preserved in large plankton samples are usually in good condition, and samples consisting mainly of copepods such as *Rhincalanus gigas* or *Calanus propinquus* nearly always contain perfect specimens of *Sagitta gazellae*. The material from 70 cm. vertical nets is the most perfect, and the 70 cm. oblique nets yield specimens in better condition than those from the 1 m. nets. Specimens from 2 m. and 4½ m. nets are often damaged, none being found with seminal vesicles intact, although the animals were of such a size and stage of maturity that these structures should have been present. However, for the examination of hooks, teeth and ovaries, material from large towed nets is quite satisfactory. The ovaries are sometimes inadequately preserved, especially in the larger specimens, and cannot be accurately measured, but this only occurs at the fourth stage of maturity (see p. 244) (when the ovaries are greatly swollen); the thin rod-like ovaries of the earlier stages are always adequately preserved. Thus the stage of maturity can always be determined, even if the degree of advancement of maturity within the stage cannot be.

Table 2. *List of stations from which data were obtained during the present work*

Counts and measurements

N70V	Stations 2010, 2012, 2014, 2015, 2017, 2018, 2020, 2022, 2023, 2024, 2025, 2026, 2027
	2311, 2313, 2316, 2318, 2320, 2322, 2355, 2356, 2357, 2358, 2359, 2361, 2385, 2386, 2387, 2389, 2391, 2393
	2424, 2425
	2492, 2494, 2495, 2496, 2498, 2501
	2530, 2531, 2532, 2533, 2535, 2538, 2541, 2543, 2545, 2547
N100B	Stations 414, 1774, 1775, 1776
	2312, 2313, 2316, 2318, 2320, 2322
	2355, 2359, 2361, 2374
	2385, 2386, 2387, 2389, 2391, 2393
	2424, 2425, 2426, 2428, 2430
	2459, 2460, 2461, 2463, 2465
	2492, 2495, 2496, 2498, 2500
	2531, 2535, 2538, 2541, 2543, 2545, 2547
	2606–2626
	2374–2379 (excluding 2376)
	1608–1625 (excluding 1613, 1620, 1622)
	1644–1664 (excluding 1649, 1650, 1656–1658, 1661)
	1687–1699 (excluding 1691, 1692, 1698)
TYF and N450 oblique	Stations 391, 395, 401, 405, 413
	1298
	1702, 1707, 1715, 1718, 1719, 1723
	1871, 1876, 1917, 1919, 1944, 1946, 1966, 1970, 1972, 1974, 1989, 1991, 1993, 1995, 2001, 2006, 2008, 2029, 2031, 2033, 2036, 2042
TYF vertical	Stations 661, 663, 666, 668, 669, 671, 673, 675, 677, 679, 681
	1154, 1156, 1158, 1160, 1165, 1167, 1173, 1175

Considerable shrinkage takes place in formalin-preserved material (George, 1952) and as measurements of freshly preserved material from the 1931–33 and 1935–37 commissions of 'Discovery II' were available it has been possible to gain some idea of the extent. Unfortunately the degree of shrinkage is not consistent, and it has not therefore been worth while making any corrections to measurements to allow for it. Measurements of 100 specimens ranging from 20 to 105 mm. (freshly preserved) show an average shrinkage of 7·25%.

In 1951 a few measurements were done on board ship to determine the extent of shrinkage during fixation. The same specimens were measured in 1952 and 1954, and although the number of observations is very small, the results are fairly consistent, and suggest that, disregarding the rather large difference which occurs between live and fixed animals, most of the shrinkage occurs during the first two years in preservative (Table 3). It is quite possible that anomalies in tables of head armature and tail percentages may be due to shrinkage, as the tail segment is often much less affected than the rest of the body. This is especially so in animals at stage II (those with their tail segments packed with sperms).

Bollmann (1934) remarks that preservation affects the appearance of the hooks in the closely allied species *S. lyra*, but no difference, other than a slight increase in opacity, has been observed between the hooks of live and dead specimens of *S. gazellae*.

Table 3. *Shrinkage of a series of specimens shortly after preservation and after several years in formalin*

(Each column of figures refers to one specimen.)

Date measured		Length in mm.								
25. viii. 51	Alive	93	92	92	—	88	—	83	—	—
26. viii. 51	Preserved	89	87	87	—	84	—	80	—	—
26. viii. 51	Alive	—	—	—	89	—	86	—	79	77
27. viii. 51	Preserved	—	—	—	85	—	82	—	77	73
1. x. 52	Preserved	86	85	84	83	83	81	77	76	71
1. x. 54	Preserved	85·5	85	84	83	83	81	77	76	71

Hooks and teeth (in animals over about 12 mm. long) have been examined and counted under a low-power binocular microscope; for animals below this length a monocular has been used. The head armature can best be seen if the animal is held by the pressure of a mounted needle just behind the corona; the anterior part of the head then faces the objective of the microscope, and by varying the pressure on the mounted needle the whole armature can be seen, and counted quite rapidly. Occasionally the use of methylene blue has helped in counting teeth, as it leaves an area free of stain at the base of each tooth.

All counts of hooks include the rudimentary ones. These are often very small, and may be only just projecting through the cuticle. They are only present in animals below about 30 mm. in length, and are usually easily seen, if strong reflected light is used; they are sometimes difficult to see by transmitted light.

A weak aqueous solution of methylene blue has been used to show the corona. As Thomson (1947) has observed, methylene blue fades rapidly, and animals stained with it can be returned to samples after examination. For permanent preparations a dilute solution of aqueous haematoxylin has proved fairly satisfactory, though it does not show the corona and sensory spots as distinctly as methylene blue.

The heads of some specimens have been boiled in caustic potash to verify the hook and teeth numbers counted under the binocular microscope. There were no discrepancies, but it is possible that among the large numbers of teeth counted, some immature ones may have been missed. It is unlikely, however, that the hook numbers are in error, as even the rudimentary ones are large in comparison with the smallest teeth.

STAGES OF MATURITY

Various systems for the classification of the stages of maturity of Chaetognaths have been proposed by Russell (1932), Kramp (1939), Thomson (1947) and Pierce (1951). Although the Chaetognatha are hermaphrodite some of these authors have based these stages only on the ovaries, but Kramp has used both testes and ovaries, and this I think provides a sounder basis; though no system of this kind seems universally applicable. Each species or closely related group of species tends to differ in the development of the gonads, and in dividing up the stages of *S. gazellae* I have adhered as nearly as possible to the system proposed by Kramp (1939) for *S. maxima*, a closely related species.

Specimens of *S. gazellae* at advanced stages of maturity are rarely taken, and there is no record of any in the literature; this rarity is due to the breeding migration to deep water (see p. 270). Even in the extensive Discovery collections there are few perfect mature specimens, and although I have examined a large number of deep hauls in the collection I have only ninety specimens in the later stages (III to V) of maturity.

Previous records of *S. gazellae* have been only of comparatively immature animals from the upper water layers, and the total absence of really mature stages led to the view that the most advanced stages then found (stage II) were nearer full maturity than in fact they were. Ritter-Zahony (1909), in the original description of the species, stated that the ovaries were knee-shaped and compressed, and gave an impression of maturity despite their shortness; he also remarked that the seminal vesicles were not observed, but evidently mature before the ovaries. In a later paper (1911), in which he redescribed the species, he said he had never observed a ripe specimen, and that the largest ovary (in an individual 66 mm. long) did not reach the anterior fin. Jameson (1914), describing an individual of 88 mm. in length from the 'Scotia' collections, said 'the reproductive organs are prominent, but they do not seem to be quite mature; the ovaries extend forward for a length of 16 mm.' Subsequent work on the species has not included any reference to any stages of maturity, and it is evident that only immature specimens have been taken.

Table 4. *Comparison of maturity stages for* Sagitta maxima *and* S. gazellae

	S. maxima (from Kramp, 1939)		*S. gazellae*	
Stage	♂	♀	♂	♀
I	Unripe	Unripe	Tail segment empty; rudiments of testes present	Ovaries not visible or rudimentary
II	Tail containing more or less sperm	All eggs small	Tail segment opaque; seminal vesicles may show as small protuberences	Ovaries short and thin; eggs small
III	Sperm evacuated, vesicles filled with sperm	All eggs small; seminal receptacles filled with sperm	Seminal vesicles fully formed; tail segment empty	Ovaries thin, but variable in length
IV	Sperm evacuated	Ovaries filled with ripe eggs	Seminal vesicles usually discharged	Ovaries thick and long; eggs enlarged
V	Sperm evacuated	Eggs evacuated	Sperm discharged	Eggs discharged; remnants of ovaries are irregular masses sometimes spread into the tail segment

Kramp (1939) has tabulated the development of the gonads in *S. maxima*. Consequently in this species the advanced stages are better known, and I have used Kramp's work as a basis for making a similar table for *S. gazellae*. The two are given side by side in Table 4, and the similarities between them are apparent.

Stage I. This is inevitably a wide category, covering a range of development from the larvae to those animals in which the ovary is quite recognizable and characteristically 'knee-shaped', and the testes quite large.

Stage II. The onset of stage II is sharply defined, and the complete filling of the tail segment with sperm was chosen as the feature of this stage, partly because it is immediately visible to the naked eye, and partly because its occurrence is so abrupt. Very few animals need be recorded as intermediate (stage I/II). Animals at stage II (Pl. XIII, fig. 1) can be picked out immediately by the complete opacity of their tail segments. The ovaries continue to grow during this stage as do the seminal vesicles, but the tail segment remains opaque.

The growth of the animal takes place during stages I and II, and before reaching stage III it has attained its full size. The relation between growth and the attainment of maturity is discussed on p. 272.

Stage III (Pl. XIII, fig. 3). The transfer of sperm from the tail segment to the now fully developed seminal vesicles marks the onset of this stage. The tail segment is once more translucent, and the seminal vesicles, as seen in the living animal, are chalky white and very conspicuous. Although the onset of this stage appears to be fairly sudden, several specimens have been taken which show an intermediate condition (Pl. XIII, fig. 2), and these have opaque tail segments with large opaque vesicles; these have been recorded as stage II/III. Stage III ovaries are thin rod-like structures, varying in length from 14 to 40% of the total body length. There is a reduction of the numbers of posterior teeth at this stage; these drop out in a haphazard manner from anywhere in the tooth row, and not in a regular manner from one end, as is usually the case in the reduction of the hooks. The loss of teeth coincides with the filling of the seminal vesicles and does not seem to be correlated with the size of the ovaries. At this stage there is a reduction in hook numbers, and the base of the hooks becomes slightly claw-shaped. Table 5 shows a series of Subantarctic specimens arranged according to the length of the ovaries calculated as a percentage of the total body length, and it gives the head armature, maturity stages and presence or absence of the vesicles. In this table animals in stages III and IV are arranged in order of ovary length, but the other stages (II and II/III) have been arranged according to the relative advancement of the male genital products. It will be noticed that the ovary percentage of some stage II animals exceeds that of some stage III animals.

Table 5. *A series of Subantarctic specimens of* S. gazellae *showing head armature and ovary size as a percentage of total body length*

Length (mm.)	Ovary (%)	Vesicles	Hooks	Ant. teeth	Post. teeth	Stage	
57	70	—	5/5	4/4	0/0	IV	—
57	68	—	5/5	6/5	0/0	IV	—
63	63	—	5/5	3/5	0/0	IV	—
47	55	Present	4/4	5/4	0/0	IV	—
48	44	Present	4/4	1/2	0/0	III/IV	Rather contracted
63	43	Present	3/3	4/4	0/0	IV	Hooks exceptional
56	35	Present	5/5	5/3	0/0	III	—
60	30	Present	5/4	5/4	0/0	III	—
62	21	Present	5/5	5/5	0/0	III	—
55	18	Present	5/4	5/4	0/0	III	—
45	17	Present	5/5	5/4	1/1	III	—
54	14	Present	6/4	6/6	0/0	III	—
54	14	Present	6/6	6/6	1/1	III	—
61	(28)	Present but tail segment opaque	6/5	6/6	4/?	II/III	Arranged in order of advancement of maturity based on tail segment
63	(22)	Present but tail segment opaque	6/5	5/5	3/1	II/III	
55	(22)	Tail segment opaque	6/6	7/7	7/8	II	
53	—	Tail segment opaque	8/8	7/7	10/10	II	

Stage IV (Pl. XIII, fig. 4). The fully developed seminal vesicles persist into stage IV, the ovaries swell and become longer, and the change from the thin rod-like ovary to the thick form marks the beginning of this stage. The eggs are not round, owing to pressure against each other in the ovary, but they are considerably larger than normal for stages II and III. It is easy to recognize this stage: in all cases the ovary has reached a length more than 40% of the total body length, and no animal in stage III has been found with the ovary in excess of this percentage, with the exception of the specimen marked as III/IV in Table 5 which has an ovary 44% of the total body length; this was a contracted specimen whose body length was probably several millimetres longer than is shown in the table.

The seminal vesicles discharge during stage IV. The sperms are apparently spread throughout the ovaries, and there is no conspicuous receptaculum seminis. The ovaries in living *S. gazellae* are conspicuous pale organs; their lateral margins and the interstitial material are pale yellow or straw coloured.

Table 6. *A comparison of the head armature of specimens in stages II and V of maturity*

Length (mm.)	Stage	Hooks	Ant. teeth	Post. teeth
83	V	5/6	6/6	0/0
83	II	6/6	6/6	9/9
76	V	3/4	5/6	0/0
76	II	7/7	6/6	10/10

Stage V. Kramp did not find any *S. maxima* at this stage, and presumed that they died after spawning. There are several specimens in the Discovery collections which may be referred to this stage, but they all appear to have been dead when caught. The eggs have been discharged, but the position of the ovary is occupied by an irregular mass of material which is sometimes not confined to the limits of the ovary but is spread throughout the body cavity and even extends down into the tail segment. The tail septum is sometimes broken, possibly by damage in the net, but perhaps by the effort of discharging the eggs, and the appearance of the animals in this state with opaque tail segments is suggestive of stage II. Examination of the head armature, however, immediately demonstrates the difference as is clear from Table 6.

No animals have been found which can be presumed to have spawned and begun to regenerate their gonads; nor does there seem to be a stage comparable with stage V in *Eukrohnia hamata* (usually described as var. *antarctica*) which is frequently taken in the deeper nets, and sometimes in the shallow ones. Evidently the spent *S. gazellae* die after spawning and sink below the range of the nets.

SYNONYMY

Sagitta gazellae Ritter-Zahony, 1909

Sagitta hexaptera (part) Steinhaus, 1900.
S. hexaptera (part) Fowler, 1907.
Sagitta innom. Fowler, 1908.
S. gazellae Ritter-Zahony, 1909.
S. gazellae Ritter-Zahony, 1911.
S. gazellae Germain, 1913.
S. gazellae Jameson, 1914.
S. lyra Johnston & Taylor, 1921.
S. gazellae Burfield, 1930.
S. lyra (part) } Bollmann, 1934.
S. gazellae }
S. maxima group (part) Thiel, 1938.
S. lyra (part) Thomson, 1947.

S. gazellae was originally described in 1909 by Ritter-Zahony from Subantarctic material taken by the 'Gazelle' expedition (1874–76). Unfortunately this description was incomplete, in that the fins were not observed owing to the long preservation of the specimens in alcohol; from other features the species was thought to be nearest to *S. hexaptera*. Ritter-Zahony did not consider possible confusion with *S. lyra* until later when he examined the well-preserved collection of the 'Gauss'. The specimens from this collection showed that the lateral fins were set on lateral fields as in *S. lyra* and that there was little resemblance to *S. hexaptera*. Ritter-Zahony therefore redescribed the species in 1911, but the description was still inadequate, owing partly to the fact that his collections contained no sexually mature individuals, and partly to an overlap in the tail segment percentages of *S. gazellae* and *S. lyra*, as shown in his tables on pages 9 and 11.

Germain (1913) and Jameson (1914) both recognized and recorded *S. gazellae* from Antarctic waters, though neither the 'Pourquoi pas?' nor the 'Scotia' collections contained any mature individuals.

Michael (1911), in a discussion on the species of chaetognaths not taken in the San Diego region, drew attention to the shortcomings of Ritter-Zahony's original description of *S. lyra* and *S. gazellae*, but, being unable to examine any specimens of *S. gazellae* himself, was prepared to let it stand as a separate species, and in a later publication (1919) included it in his key.

In 1921 Johnston & Taylor published their report on the Chaetognatha of the Australasian Antarctic Expedition in which they decided that *S. gazellae* was synonymous with *S. lyra*.

Despite Johnston & Taylor's opinion, Burfield (1930) felt justified in retaining *S. gazellae* as a separate species, although he pointed out that precise distinction was most difficult.

In the report on the 'Deutschland' collection, Bollmann (1934) also retained *S. gazellae*, but he evidently had much difficulty in distinguishing it.

Kuhl (1938) included *S. gazellae* in his key, but without special comment, and presumably regarded Bollmann's view, the most up-to-date opinion at that time, as correct.

The 'Meteor' must have taken specimens of *S. gazellae*, but Thiel (1938) has dealt with certain species in groups, and has included *S. maxima*, *S. lyra* and *S. gazellae* in his '*S. maxima* group' and has not therefore contributed to the problem of the synonymy. (Though these three species resemble one another in many anatomical features, their distributions are dissimilar and thus his picture of distribution of the group is of little value.)

This point in the history of *S. gazellae* is a most important one, for, up to 1939, most authors who wrote about the species had examined and described specimens from areas in which (as I shall show later) *S. gazellae* is found; whereas subsequent authors with one partial exception have examined and described specimens from areas in which *S. gazellae* is not found, and have in fact described variation in *S. lyra* Krohn. They have shown that certain forms of *S. lyra* resemble *S. gazellae*, and have claimed that intermediate forms exist which link *S. gazellae* with *S. lyra*. I have been unable to find any such intermediates in the Discovery collections. There is, however, a continuous series of intermediates between the extremes of variation of *S. lyra*, and I believe that the incorrect assumption that 'the cold water form of *S. lyra* Krohn is identical with *S. gazellae* Ritter-Zahony' has been responsible for much confusion.

In 1939 Tokioka described certain specimens of *S. lyra* closely resembling *S. gazellae*, from Japanese waters; these he called *S. lyra* "*gazellae*"-type to distinguish them from the typical *S. lyra*, which he named *S. lyra* "*lyra*"-type.

Thomson, in 1947, records the existence of both these forms in S.E. Australian waters and follows Johnston & Taylor and Tokioka in regarding *S. lyra* "*lyra*"-type and *S. gazellae* Ritter-Zahony as extremes of variation in one species; he regarded *S. gazellae* and the 'intermediate types' as *S. lyra* "*gazellae*"-type.

Ghirardelli (1950) found both varieties of *S. lyra* in the Mediterranean and informally applied the trinomial *S. lyra typica* to the form shown in his fig. 2 which appears to be identical with the *S. lyra* "*lyra*"-type Tokioka, and in a later paper has used the trinomial *S. lyra gazellae* to describe *S. lyra* "*gazellae*"-type Tokioka.

Furnestin (1953), in her report on the Mediterranean collections of the 'Théodor Tissier', has gone a stage further and formally returned to two separate species *S. lyra* (= *S. lyra* "*lyra*"-type Tokioka, Thomson = *S. lyra typica* Ghirardelli) and *S. gazellae* (= *S. lyra* "*gazellae*"-type Tokioka, Thomson = *S. lyra gazellae* Ghirardelli). As I shall show, *S. gazellae* Ritter-Zahony is a separate species and thus the name is preoccupied. The presence of 'intermediate types' recorded by Tokioka and Thomson which link the extremes of variation in *S. lyra* suggests that considerably more investigation will be needed before a decision can be reached as to whether the two extremes of variation in *S. lyra* may be regarded as separate species.

It is now pertinent to examine the characters which have led some previous authors to consider *S. lyra* and *S. gazellae* as separate species; these are summarized in Table 7.

Table 7. *A comparison of* Sagitta lyra *and* S. gazellae *according to previous publications*

Features	*S. lyra*		*S. gazellae*
	S. lyra "*lyra*"-type	*S. lyra* "*gazellae*"-type	
Hooks	Inner margin of shaft 'claw' shaped	Inner margin of shaft simple	Inner margin of shaft simple
Fins			
(*a*) Commencement of anterior fins	Close to ventral ganglion	Close to ventral ganglion	Away from ventral ganglion
(*b*) Lateral fields	Swollen—conspicuous	Usually inconspicuous	Usually inconspicuous
(*c*) Posterior end of anterior fin	Sharply curved in; Fig. 6	Sharply curved in; Fig. 6	Smoothly curved in; Fig. 6
(*d*) Junction of fins	Conspicuous	Inconspicuous	Inconspicuous
(*e*) Insertion of posterior fin	Sometimes present	Sometimes present	Not present
Tail segment (%)	Usually more than 15	Usually more than 15	Usually less than 15

DIAGNOSTIC CHARACTERS FROM PUBLISHED DESCRIPTIONS

Hooks. The significance of the shape of the base of the hooks of *S. lyra* and *S. gazellae* has been extensively discussed by Tokioka (1939) and Ghirardelli (1950); they claim that their findings confirm Johnston & Taylor's (1921) opinion that the shape of the base of the hooks has no specific value. However, examination of Johnston & Taylor's report reveals that the opinion was based upon a misunderstanding of Ritter-Zahony's report.

Ritter-Zahony (1911) described and figured a typical hook of *S. gazellae* and a 'secondary' hook of *S. lyra*, the former having a simple base, the latter a 'claw'-shaped base (see Fig. 1). On page 9 of his report he stated that the 'secondary' hooks occurred only in the more mature animals, the hooks of the younger individuals being 'typical', i.e. of the simple '*gazellae*' type. On page 12 he recorded that all his specimens of *S. gazellae*, even the largest (71 mm.), had 'typical' hooks, whereas 'secondary' hooks were sometimes found in specimens of *S. lyra* measuring as little as 15 mm.

Johnston & Taylor (1921), on page 7, state that 'Ritter-Zahony (1911, p. 8) said that in older specimens of *S. lyra* the jaws became claw-shaped. As will be seen from fig. 3 [Fig. 2], the tips of our specimens agree with his description of *S. lyra* in this respect, while the shaft of the jaw resembles his own figure of *S. gazellae* (1911, fig. 7).' Ritter-Zahony did not refer to the tips of the hooks in either *S. gazellae* or *S. lyra*, nor do his figures give any indication of claw tips. It appears, therefore, that

Johnston & Taylor assumed that the description 'claw'-shaped applied both to the tip and to the base of the hook, and thus the hooks of their specimens seemed to have *lyra* and *gazellae* characteristics; it is clear from Ritter-Zahony's report that the description 'claw shaped' applies only to the base of the hooks, and so, in this respect, Johnston & Taylor's specimens were *S. gazellae*.

Nevertheless, these authors had reason to doubt the validity of the shape of the base of the hooks as diagnostic of *S. lyra* owing to Ritter-Zahony's inclusion of *S. furcata* Steinhaus in the synonymy of *S. lyra*. One of the diagnostic features of *S. furcata* was the forked tail, and this is a feature which occurs in many species (possibly owing to damage). Undoubtedly many specimens of *S. furcata* were *S. lyra*, but it seems likely that others were not. Thus, the hook of *S. furcata* (Fowler, 1905, pl. 4, fig. 12) (Fig. 3) referred to by Johnston & Taylor as being of the simple *gazellae* type (yet from a species synonymous with *S. lyra*), may well have been taken from the specimen shown in Fowler (1905, fig. 7, p. 14) (Fig. 4) which appears to be *S. hexaptera*; or alternatively it may have come from a young specimen of *S. lyra* and still be correct. Neither the existence of claw tips in *S. gazellae* hooks nor the presence of simple type hooks in certain specimens of *S. lyra* affect the validity of Ritter-Zahony's statements.

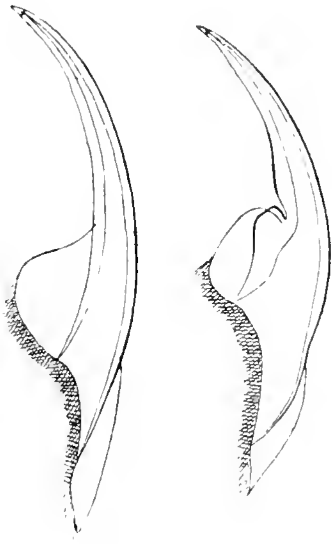


Fig. 1.

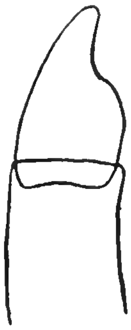


Fig. 2.


Fig. 3.


Fig. 4.

Fig. 1. A 'typical' hook from *S. gazellae* (*a*) and a 'secondary' hook from *S. lyra* (*b*). (From Ritter-Zahony, 1911.)
Fig. 2. The tip of a hook of *S.* '*lyra*'. (From Johnston & Taylor, 1921.)
Fig. 3. A hook of '*S. furcata*'. (From Fowler, 1905.)
Fig. 4. A specimen of *S. furcata*. (From Fowler, 1905.)

It is upon Johnston's & Taylor's evidence that the case put forward by Tokioka (1939) and Thomson (1947) for the inclusion of *S. gazellae* in the synonymy of *S. lyra* mainly depends, and this evidence has been wrongly interpreted.

Hamon (1952) has shown that there is no second generation of hooks (the 'secondary' hooks of Ritter-Zahony) in *S. lyra*, but that in sexually mature specimens the existing hooks become 'claw'-shaped. She has suggested that this type of hook is a secondary sexual character.

In *S. gazellae* a claw-type hook is found in the specimens at stages III, IV and V of maturity, but the claw shape is not nearly so pronounced as in *S. lyra*. There is no sign of a 'claw' in the inner margin of the hook, but only in the thin plate at the base, whereas both the inner margin and the base are 'clawed' in *S. lyra*. Comparison of Fig. 5*a–c* demonstrates this point.

The typical claw-type hook of *S. lyra* is characteristic and remains a useful feature in differentiating the species from *S. gazellae*.

Fins. An important feature of difference between the two species, and one which has not received the attention it merits, is the position of the commencement of the anterior fins. This is appreciably nearer the ventral ganglion in *S. lyra* "*lyra*"-type than in *S. gazellae*, but in *S. lyra* "*gazellae*"-type the lateral fields of the fins are often quite inconspicuous and thus the commencement of the fin is not easily visible. In such a case the angle between the two nerve cords from the posterior end of the ventral ganglion may be used as a guide, for the cords lead direct from the ganglion to the commencement of the fin. Although this feature is most useful, it is one which requires experience of the species to recognize with certainty and rapidity.

Fig. 5.

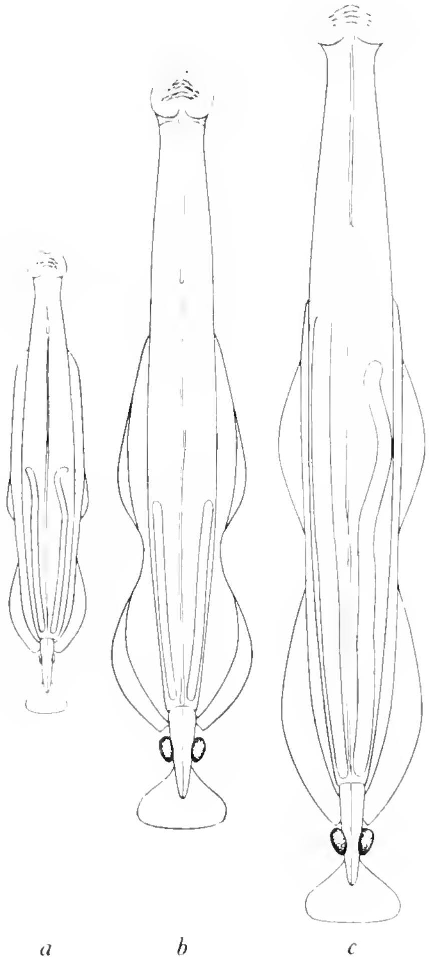


Fig. 6.

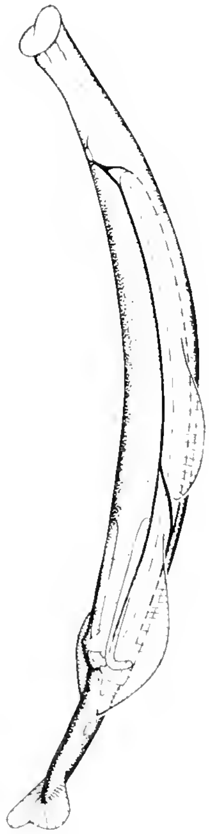


Fig. 7.

Fig. 5. Hooks from mature specimens of *S. gazellae* and *S. lyra*, traced from photomicrographs. (*a*) *S. gazellae* L.S. 85 mm. long at stage III; first hook. (*b*) *S. gazellae* S.N. 62 mm. at stage III; first hook. (*c*) *S. lyra* 31 mm. at stage III; first hook.

Fig. 6. Mature specimens showing relative length at maturity and the shape and position of the fins and seminal vesicles. (*a*) *S. lyra* at stage III. (*b*) *S. gazellae* S.N. at stage III. (*c*) *S. gazellae* L.S. at stage IV.

Fig. 7. *S. lyra* from its left side, showing the course of part of one of the ventral nerve cords across the lateral field between the anterior and posterior fins.

There are also several other points with regard to the position and shape of the fins. The appearance of the junction between the anterior and posterior fins has been discussed by Tokioka (1939) and Ghirardelli (1950); it is of no value in distinguishing *S. lyra* "*gazellae*"-type from *S. gazellae*. The appearance of the posterior end of the anterior fin is much more sharply curved in *S. lyra* than in *S. gazellae* (Fig. 6), but this is a difficult feature to see, and the delicate fins are often damaged. In *S. lyra* "*lyra*"-type the lateral fields present a swollen appearance. Tokioka (1940) gives a good illustration of this point, but again this only differentiates *S. lyra* "*lyra*"-type from *S. lyra* "*gazellae*"-type and *S. gazellae*.

The posterior fin of *S. lyra* is often shown with a forward 'insertion' into the anterior fin (e.g. Ritter-Zahony, 1911, fig. 3) and this appearance is often seen; it is due to part of one pair of lateral nerve cords crossing the lateral fields between the fins (Fig. 7), and I have been unable to detect a similar feature in *S. gazellae*; it is not, however, a particularly obvious feature in most specimens of *S. lyra*.

Tail segment. Another feature of difference which has been much discussed is the relative length of the tail segment. Ritter-Zahony's (1911) tables show an overlap of this feature in the two species, but this overlap may be due mainly to uneven shrinkage (see p. 240), and the method of compiling tables giving tail percentages and head armature formulae gives undue weight to exceptional specimens. For example, if in a series of ten specimens of similar length nine give tail percentages between 11 and 12% and one gives a measurement of 15% then the table will record the tail percentage for this size group as 11–15%, in no way taking into account the abnormality of the one specimen in comparison with the other nine. (This becomes even more apparent when dealing with hook numbers and, in Fig. 8, I have tried to avoid this difficulty by using a scatter diagram which shows all the observations including the abnormal ones, thus enabling the reader to assess the value of each one.)

The interpretation of the situation in regard to tail segment percentages given by Michael (1919) and quoted by Burfield (1930) is a fair statement: 'the tail segment percentage is *usually* less than 15% in *S. gazellae*, and *usually* more than 15% in *S. lyra*'.

It is evident from Table 7 and the preceding discussion that there are in fact recognizable differences between *S. lyra* and *S. gazellae*. The characters upon which those differences are based, however, cannot always be determined with sufficient precision to justify the retention of the two as separate species. However re-examination of *S. lyra* and *S. gazellae* has resulted in some further characters, some of which are reliable; these are summarized in Table 8 and are discussed below.

Table 8. *Diagnostic characters of* Sagitta lyra *and* S. gazellae *from re-examination of the species*

Features	*S. lyra*		*S. gazellae*
	S. lyra "*lyra*"-type	*S. lyra* "*gazellae*"-type	
Maximum length	42 mm.	42 mm.	105 mm.
Hooks	Maximum number 11	Maximum number 11	Maximum number 14
Corona	Simple pear-shaped, away from eyes	Simple pear-shaped, away from eyes	Complex, near to eyes
Width apart of eyes as percentage of head width	51·9	49·1	24·5
Seminal vesicles	Nearer to posterior fin	?	Mid-way between posterior and caudal fins
Receptaculum seminis	Conspicuous	Conspicuous	Inconspicuous
Distribution	Tropical and subtropical waters	Tropical and subtropical waters	Antarctic and subantarctic waters

DIAGNOSTIC CHARACTERS FROM RE-EXAMINATION OF THE SPECIES

Total length. S. gazellae reaches a maximum size of 105 mm. in Antarctic waters, and 68 mm. in Subantarctic waters; the largest specimen of *S. lyra* among 1593 specimens from the 'Discovery' collections was 42 mm. long. Previous records of *S. lyra* at a greater size than this are possibly due to confusion with other species; for example, Michael (1911) did not recognize *S. maxima* as a separate species (see p. 252), nor did Germain & Joubin (1916) report *S. maxima* in the Monaco collections, although it is common in the North Atlantic, but they recorded a specimen of *S. lyra* 48 mm. long: Thomson (1947) recorded *S. lyra* up to 50 mm., but these may well be *S. gazellae* from Tasmanian waters: Furnestin (1953) reported a specimen of *S. gazellae* (= *S. lyra* "*gazellae*"-type) 55 mm. long, but has informed me that this was in fact a damaged specimen of *S. hexaptera*.

Hooks. The maximum number of hooks present in *S. lyra* can be as high as 11, but more usually 10 is the figure (Fraser, 1952).

Ritter-Zahony (1911) gives 10 as the maximum number in *S. gazellae*, but in Subantarctic specimens of this species I have found as many as 14. This difference is due to the fact that Ritter-Zahony did not count the small hook rudiments on the dorsal side of the head, as I have done (see p. 241) (I have followed this practice in making counts of hooks in *S. lyra* but still find a maximum of 11 only), and to the fact that Ritter-Zahony's counts were on Antarctic specimens which have a rather lower maximum number than the Subantarctic ones (see p. 256).

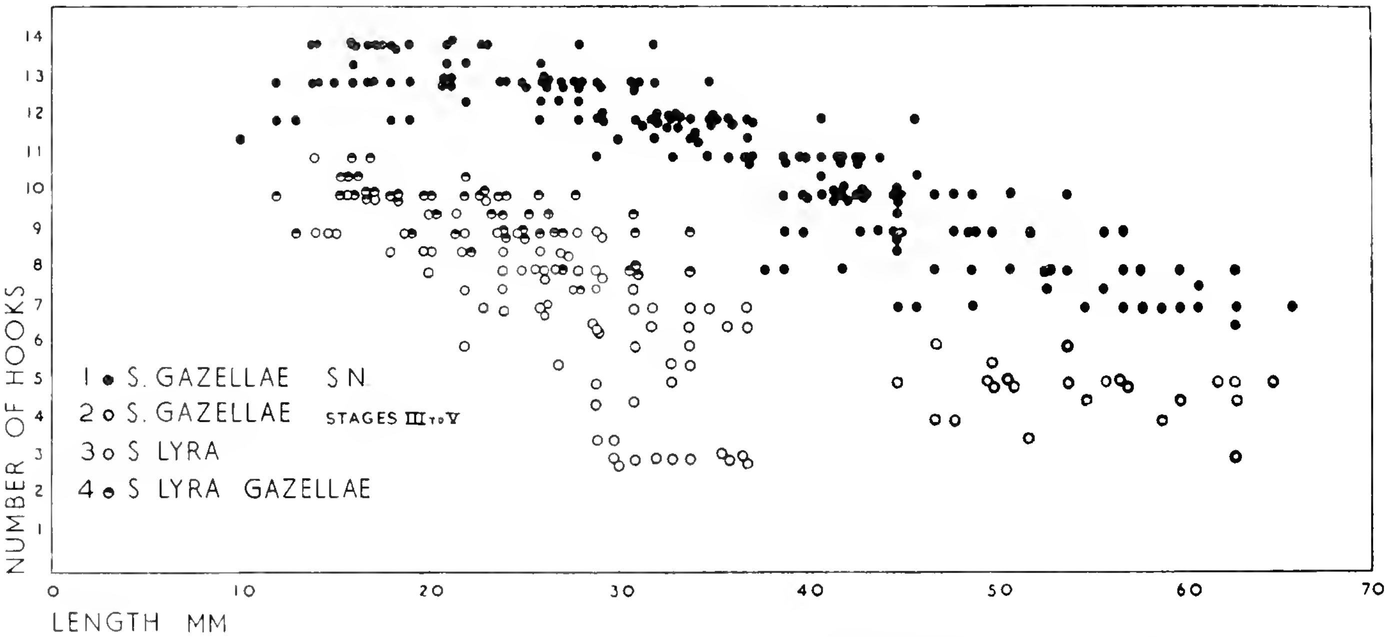


Fig. 8. The number of hooks plotted against length for *S. gazellae* S.N. race and *S. lyra*.

Johnston & Taylor (1921) record a specimen of *S. lyra* (= *S. gazellae*) with 13 hooks on each side, but other authors have agreed with Ritter-Zahony.

The larger number of hooks in Subantarctic specimens of *S. gazellae* is of considerable value in differentiating the species from *S. lyra*, and Fig. 8 gives a comparison of hook numbers and length in both species.

Corona. The shape of the corona in *S. lyra* is simple and pear-shaped. Fig. 9 (after Tokioka, 1940) shows it in a specimen of *S. lyra* "*lyra*"-type. I have examined this feature in a fairly large series of specimens of *S. lyra* "*gazellae*"-type and find it to be similar. Though exhibiting a range of variation (Fig. 10) it does not depart from the general pear shape.

Ritter-Zahony (1911) gives two illustrations of the corona of *S. gazellae* (fig. 6A, B) (Fig. 11). Fig. 11 *b* is the corona drawn directly from a specimen, and Fig. 11 *a* is a simplified representation of it, the latter was done because the author considered the sinuosities of outline to be due to contraction of the head muscles. Although the corona is often damaged or absent in preserved specimens of *S. gazellae*, I have been able to observe it many times among the very large number of specimens which are available in the Discovery collections, and the sinuosities of outline are always present except in very small specimens. I do not think they are due to contraction of the head muscles, for no evidence for contraction can be seen, and in specimens having the hood fully extended (Fig. 12*a*) the corona still exhibits a sinuous outline. The corona of *S. lyra* shows no sinuous outline, yet the head of such a similar species must be equally liable to muscular contraction. On the other hand, I have not found a perfectly symmetrical corona in *S. gazellae*, but this structure in any specimen of any species is seldom perfect, and the complexity of the *S. gazellae* corona makes it difficult to speculate as to the perfect outline. The features of the *S. gazellae* corona which serve to differentiate it from that of *S. lyra* are the marked sinuosities between the eyes (Fig. 12*a–d*) (this portion of the corona often remaining when the rest is absent); the close proximity of the eyes to the corona; and the straight cross-portion (Fig. 12*a*, *b*, *d*) at the posterior end, which is quite different from the continuous curve of the equivalent part in *S. lyra*. Although the difference in outline of the corona in the two species may be considered a valuable taxonomic difference, it is not a very practical one, owing to the delicacy of the structure and the consequent fact that it can so seldom be observed in specimens of *S. gazellae*.

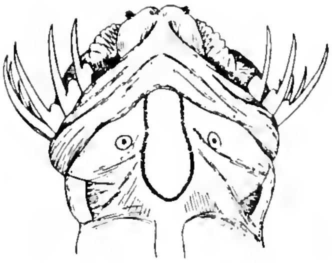


Fig. 9. Corona of *S. lyra*. (From Tokioka, 1940.)

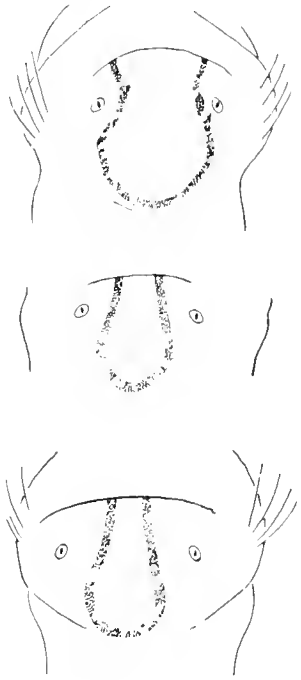


Fig. 10. Variation in the shape of the corona in *S. lyra* "*gazellae*"-type.

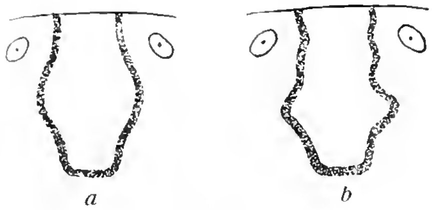


Fig. 11. Corona of *S. gazellae*. (From Ritter-Zahony, 1911.)

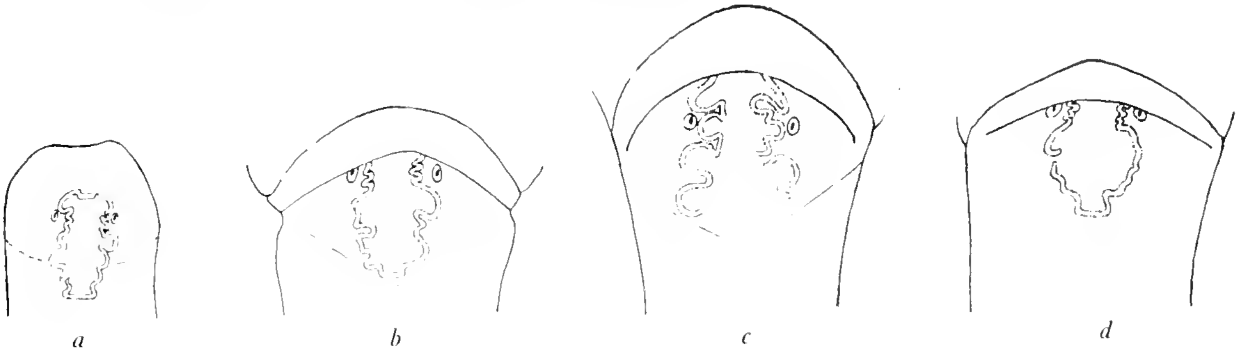


Fig. 12. Variation in the shape of the corona in *S. gazellae*.

Width between the eyes. This feature is perhaps the most convenient and precise of all. The width between the eyes is given as a percentage of the width of the head. Table 9 gives the data from fifty specimens of *S. lyra* "*gazellae*"-type and fifty specimens of the Subantarctic race of *S. gazellae*, to show the range of variation in the measurements. It can be seen that the average percentage for *S. lyra* "*gazellae*"-type is double that of *S. gazellae* for the same state of contraction of the head and the highest percentage for the latter species does not overlap the lowest percentage of the former. But it will be seen from Table 9 that the range for each species is considerable, and this is due to the position in which the head has been fixed. I have not found any overlap between the species; but it is quite possible that in specimens with very distorted heads this may occur. Therefore, when using this method, if specimens give a percentage between 30 and 40 the shape of the head should be noted; if the hooks are pointing in towards the mouth, and the hood is withdrawn, the head will be much wider than normal, and the specimen will be *S. lyra*; if, on the other hand, the hood is forward, and the hooks point straight forwards or outwards then the specimen is *S. gazellae*. As a general rule, however, specimens giving a percentage over 35 are *S. lyra* and under 35 are *S. gazellae*.

Reference to Tokioka's (1940) illustration of *S. lyra* ("*lyra*"-type) shows that the percentage of eye width to head width of the specimen illustrated is 60, which fits the range of *S. lyra* given in Table 9. Similarly, reference to Johnston & Taylor's (1921) illustration of one of the specimens which they describe as *S. lyra* shows that the percentage of eye width to head width is 16·7, which is within the observed range for *S. gazellae* given in Table 9.

Mature stages. The appearance of the seminal vesicles and the receptaculum seminis serves to distinguish between the species in mature specimens only. The use of these differences is limited by the fact that such specimens occur only at depths of 750 m. or more, and are therefore not commonly taken. Both *S. lyra* (Ramoult and Rose, 1946; Ghirardelli, 1950) and *S. gazellae* (see p. 270) breed in deep water.

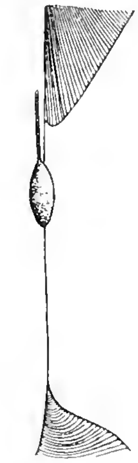


Fig. 13. Seminal vesicle of *S. lyra*. (From Tokioka, 1940.)

The seminal vesicles of *S. gazellae* occur midway between the posterior and caudal fins, whereas Fraser (1952) states that in *S. lyra* they lie 'nearest the posterior fin'. Those of *S. gazellae* appear to differ slightly in shape from those of *S. lyra* (Fig. 13), but are also of the '*enflata*-type' (Tokioka, 1939). Although I have examined fairly large numbers of *S. lyra* in varying degrees of maturity I have found none with perfect seminal vesicles, and must therefore depend upon published figures for comparison.

The receptacula seminis are conspicuous white objects in *S. lyra*, but are not visible in *S. gazellae*.

Two other features of difference in the mature animals may be noted. The number of hooks at these stages in *S. lyra* is nearly always three on each side, whereas in *S. gazellae* there may be from three to six (see Figs. 8 and 15). In *S. gazellae* the posterior teeth are reduced to none, or occasionally one on each side, whereas in fifty specimens of mature *S. lyra* I have never seen less than two, and usually three on each side.

Distribution. S. gazellae is confined to Antarctic and Subantarctic waters, whereas *S. lyra* is a species with a world-wide distribution in tropical and subtropical waters, and is found in both hemispheres. *S. lyra* has not been recorded from Arctic or Subarctic waters. Though Michael (1911) records *S. lyra* from very cold waters, he failed to differentiate it from *S. maxima*, and his table of measurements of twenty specimens of *S. lyra* appears to contain a number of specimens of *S. maxima* (nos. 1, 3, 5, 8, 11, 13, 14, 17, 18 and 19). On page 38 of his report he states 'it is possible that I may have obtained both *S. lyra* and *S. maxima* and confused them'; I think it is just such confusion which accounts for the records of *S. lyra* at very low temperatures, for Fraser (personal communication) informs me that he has never observed *S. lyra* in Arctic or Subarctic waters. If *S. gazellae* is merely a cold-water form of *S. lyra* (as some authors maintain) which has colonized the Antarctic and Sub-

Table 9. *A comparison of the width between the eyes calculated as a percentage of the width of the head in* Sagitta lyra "gazellae"-*type and* S. gazellae

Total length (mm.)	*S. lyra "gazellae"*-type		*S. gazellae*	
	Eye width/head width (%)	No. of specimens	Eye width/head width (%)	No. of specimens
56·5	—	—	32·3	1
49	—	—	25·0	1
48	—	—	22·4	1
45	—	—	25·9–33·3	2
44	—	—	26·9	1
42	—	—	28·6	1
39	—	—	22·2	1
38·5	—	—	28·0	1
38	—	—	20·8	1
37	—	—	27·3–30·3	2
36	—	—	26·1	1
35	—	—	25·0	1
34·5	—	—	20·0	1
34	50·0–53·3	2	28·6	1
33·5	—	—	21·7	1
33	—	—	23·8	1
31	50·0–53·3	5	29·4	1
30	57·1	1	27·9	1
29	—	—	26·9–27·8	2
28	50·0–53·3	2	—	—
27·5	—	—	27·7	1
27	50·0–65·3	3	24·4–25·0	2
26·5	46·7	1	21·1	1
26	46·7–46·8	2	21·9	1
25·5	46·2	1	25·0	1
25	50·0–58·3	2	21·1	1
24·5	—	—	22·2	1
24	46·2–58·2	6	22·2	1
23·5	50·0	1	20·0	1
23	50·0	3	20·0	1
22·5	—	—	25·0	1
22	42·8–50·0	2	21·4	1
21·5	44·5	1	—	—
21	—	—	20·0–27·3	3
20·5	46·2	1	—	—
20	60·0–62·5	2	16·7–23·8	2
19	50·0–55·5	2	20·0–27·3	2
18·5	50·0–55·6	2	—	—
18	45·4	1	19·2–33·3	2
17·5	—	—	23·1	1
17	44·5–50·0	3	20·0	1
16·5	42·9	1	—	—
16	50·0–62·5	3	18·2	1
15·5	50·0	1	—	—
14	—	—	25·0	1
13·5	—	—	22·2	1
13	60·0	1	—	—
12	40·0	1	28·6	1
	Av. 49·1	50	Av. 24·5	50

antarctic waters in profusion, then it might be expected that a similar colonization would have taken place in the Arctic, as there is ample opportunity for specimens to be carried north by the North Atlantic drift especially since the so-called 'intermediate' *S. lyra* "*gazellae*"-type has been reported from various parts of the northern hemisphere.

From the various points discussed above it may be concluded that *S. gazellae* Ritter-Zahony is a species in its own right, which can be distinguished from all the varieties of *S. lyra* Krohn.

RACIAL CHARACTERISTICS

The surface layers of the Southern Ocean are divided into two main areas, the Antarctic zone, and the Subantarctic zone. The line which divides these areas is the Antarctic Convergence, which is the point where the Antarctic surface water sinks beneath the Subantarctic surface water. The division is, in most areas, sharp and distinct, and is to some extent a faunistic boundary (Hart, 1934; John, 1936).

Examination of a series of hauls made from the Subantarctic across the Convergence and into the Antarctic zone, reveals striking differences in the appearance of *S. gazellae* on each side of the Convergence. In the Subantarctic, specimens are found at advanced stages of maturity when 60 mm. in length, whereas specimens of the same length in the Antarctic are found to be immature; in the Subantarctic surface waters no specimens are found at a length greater than 68 mm., yet in the Antarctic surface waters specimens of more than 90 mm. are quite common.

In an unpublished progress report written on board R.R.S. 'Discovery II', in 1932, Mr Marr suggested that the Antarctic and Subantarctic populations of *S. gazellae* are two separate races; and by a thorough study of the state of maturity of the various size groups was able to differentiate the two races in areas where they mixed, notably in the Scotia Sea (especially south-east of the Falkland Islands).

The stages of maturity which he used prove to be subdivisions of the stages which I have called I and II (pp. 242–3). Marr's stages are distinguished from mine by the use of arabic numerals 1 and 2, and letter X, whereas I have used roman numerals I, II, etc. Fig. 14 shows these stages diagrammatically.

There are three stages of maturity of the tail segment. Stage 1 includes specimens with small visible rudiments of the testes up to specimens in which these rudiments extend to the transverse septum. Stage 2 is usually characterized by the curl of the testes across the anterior end of the tail segment. Stage X is equivalent to my stage II (p. 243). The tail segment is full of sperm and is opaque. No further stage was found as no further development takes place in the surface layers (the deep-breeding habits of *S. gazellae* were not known at the time when this system was devised) though the presence of rudimentary seminal vesicles was noted in the most advanced specimens. Marr also noted the state of maturity of the ovaries. These stages depend on the relative sizes of the transverse to the longitudinal portions of the ovary. In *S. gazellae* the ovary opens on the dorsal surface, and its posterior part extends towards the ventral surface at right angles to the long axis of the animal before continuing ventrolaterally along towards the head of the animal. This is the characteristic 'knee-shape' described by Ritter-Zahony (1909, 1911).

Marr's stage 1 included animals which had visible rudiments of ovaries, and all intermediate stages up to the stage where the longitudinal part of the ovary equalled the transverse part in length. The upper limit of his stage 2 was reached when the longitudinal part was double the length of the transverse part, and so on up to stage 4. In the surface waters animals were seldom found with ovaries more mature than stage 4.

Marr often recorded these stages as 'weak' or 'strong', according to their degree of maturity within the stage. Animals in which no rudiments of the gonads were visible were recorded as immature, and given no stage number.

Marr referred to the races as Large Southern (L.S.), the Antarctic form, and Small Northern (S.N.) the Subantarctic form. I have also followed this practice.

Table 10*a*, *b* shows Marr's data from two hauls, one Antarctic, and the other Subantarctic, in which the stages of maturity and total lengths are compared. It is evident that there can be no confusion between the two races when the gonads are visible. In the Subantarctic race Marr's stage 1 begins at about 25 mm. total length, and it is only in specimens smaller than this that the gonads are not visible; thus below 25 mm. it is not possible to determine the race by the method just described. In practice this does not matter, as hauls are usually composed of one race or the other, and mixing only takes place in a few areas. However, it is possible in most cases to differentiate the immature forms by the number of hooks, although the method is not infallible, as there is slight overlap in the hook numbers, but in general it is satisfactory. I have found the basic number of hooks in the S.N. race to be 14 and in the L.S. race 12 (rarely 13). Comparison of Figs. 8 and 15 shows that below 25 mm. individuals of the L.S. race are likely to have 11 or 12 hooks, whereas individuals of the S.N. race are likely to have 13 or 14. The overlap is evident, but not extensive. Counts of hook numbers from individuals below 12 mm. are not reliable, as even with a high-power monocular it is difficult to be certain of the numbers present.

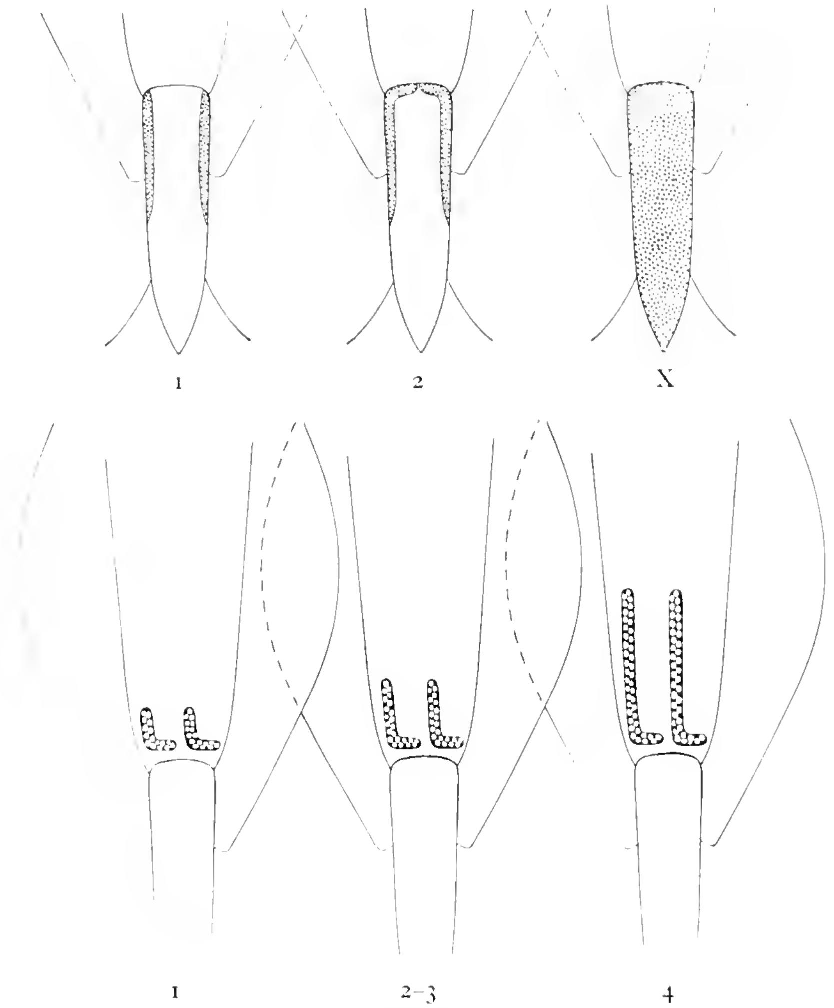


Fig. 14. Stages of maturity devised by J. W. S. Marr for differentiating the races of *S. gazellae*. The upper series show the stages of the testes and the lower series the stages of the ovaries. No ovaries have been drawn in the upper series, and no testes in the lower series, as no particular stage of maturity of the testes is necessarily combined with a particular stage of maturity of the ovary.

Figs. 8 and 15 also show that the L.S. race is, in its hook numbers, intermediate between *S. lyra* "*gazellae*"-type and the S.N. race. This is an interesting point, as it shows that the tendency in *S. gazellae* is to have less hooks in cold water than in warm, whereas the cold water form of *S. lyra* (*S. lyra* "*gazellae*"-type) has more hooks than the warm water *S. lyra* "*lyra*"-type. That the L.S. race is in this way apparently an intermediate form between *S. lyra* and *S. gazellae* is of no practical taxonomic significance, for the L.S. race seldom extends more than a hundred miles or so north of the Antarctic Convergence, and so could never be found mixed with *S. lyra*: indeed the whole Subantarctic area separates the two forms

Another feature in which the L.S. race resembles *S. lyra* is the occasional retention of posterior teeth at stage III and IV maturity. The total loss of posterior teeth is an almost invariable feature of the

Table 10*a*. '*Small Northern' form of* Sagitta gazellae

(Stages distinguished by J. W. S. Marr.)
Station 839

Length (mm.)	Stages		Remarks
	♀	♂	
61	4	X	Seminal vesicles* present but clear
53	4	X	Seminal vesicles* present but clear
52	4	X	Seminal vesicles* present but clear
50	4(3)	X	Seminal vesicles present, ovary only just 4
47	3	2	Ovary just 3
43	2	2	—
39	2	2	—
39	2	2	—
39	2	2	—
38	2	2	—
38	2	2	—
38	2	2	—
34	1	—	High limit ovary nearly 2
33	1	—	—
28·5	1	—	—
28	—	—	All immature
9–28	—	—	

* Rudimentary vesicles.

Table 10*b*. '*Large Southern' form of* Sagitta gazellae

(Stages distinguished by J. W. S. Marr.)
Station 825

Length (mm.)	Stages		Remarks
	♀	♂	
82	3	2	Very strong 3 approaching 4
77	3	2	—
74	3	2	—
63	2	2	Strong 2 approaching 3
62	2	Trace (1)	Strong 2 approaching 3
61	2	1	—
59	2	1	—
54	2	1	—
47	1	—	—
44	1	—	—
41	—	—	All immature
22–41	—	—	

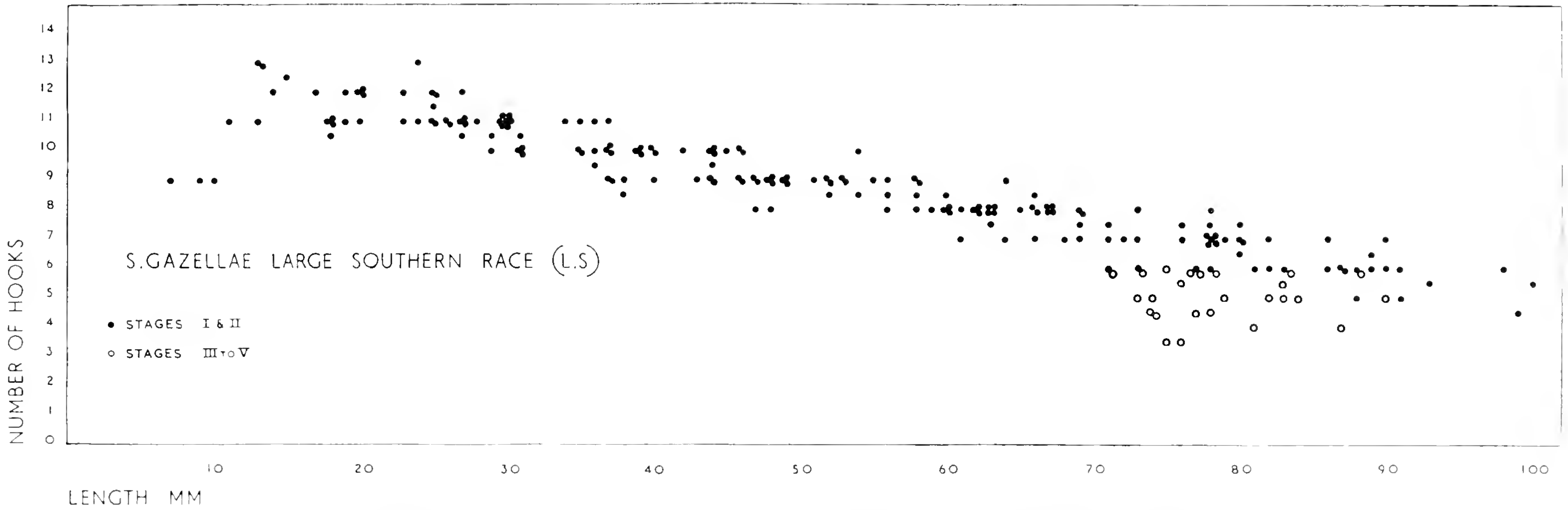


Fig. 15. The numbers of hooks plotted against length in *S. gazellae* L.S. race. (Compare with Fig. 8, p. 250).

S.N. *S. gazellae*, and as I have remarked (p. 243) mature *S. lyra* retain two or three teeth on each side at full maturity. Of fifty specimens of *S. lyra*, all had at least two posterior teeth on each side, and most had three; of thirty specimens of L.S. *S. gazellae*, sixteen had no posterior teeth, and fourteen had at least one tooth on one side, and in most cases on both sides; whereas of thirty specimens of S.N. *S. gazellae* twenty-five had no posterior teeth, and only five retained one tooth on one or both sides (all the specimens referred to here were at advanced stages of maturity). Fig. 16 shows a comparison of the teeth numbers of both races throughout their size ranges, and it can be seen that the numbers of posterior teeth found in the L.S. race are slightly higher than those found in the S.N. race.

In the form of the body, fins, seminal vesicles and corona, the L.S. race appears to be identical with the S.N. race.

Table 11. '*Very warm water' form of* Sagitta gazellae

(Stages distinguished by J. W. S. Marr.)

Length (mm.)	Stages		Remarks
	♀	♂	
52	4	X	Ovary as long as tail segment to insertion of caudal fin
50	4	X	
47	3	2	—
46	3	X	—
45	3	2	—
2/44	3	2	♂ strong approaching X in one of them
43	3	2	—
40	3	2	—
37	2	2	—
37	2	2	Low
37	2	2	Low
36	2	2	—
36	1	—	Peak
34	1	—	
31	1	—	—
31	1	—	Strong
31	1	—	
29	1	—	—
28	1	—	High
28	1	—	—
26	1	—	—

It can be seen from Fig. 8 that the hook numbers of the S.N. race tend to be scattered above 40 mm. total body length, and the size range of the mature forms is from 45 to 65 mm. or 31% of the total size range of the race. The S.N. *S. gazellae* living in the northern and warmer part of the Subantarctic tend to mature at a shorter total length than those living in the colder part of the area. Table 11 shows the sizes at the stages of maturity given at the beginning of this section, for a typical warm water haul, and comparison with Table 10*a* shows the differences within the Subantarctic zone. Fig. 8 shows, however, that up to 40 mm. the hook number and size relationship is the same for all the forms of *S. gazellae* in the Subantarctic. The differences in size at maturity are probably environmental, and phenotypic.

In the L.S. race there is a size range at maturity from 71 to 90 mm., or 19% of the total size range (this is considerably less than that found in the S.N. race), and Fig. 15 shows that the variations in the hook number to size range are much smaller, which suggests that there is less variation within the race. The ratio between maturity and size confirms this. The absence of intermediate forms linking the L.S. and S.N. races, and the fact that the two can be distinguished at most sizes suggest that they

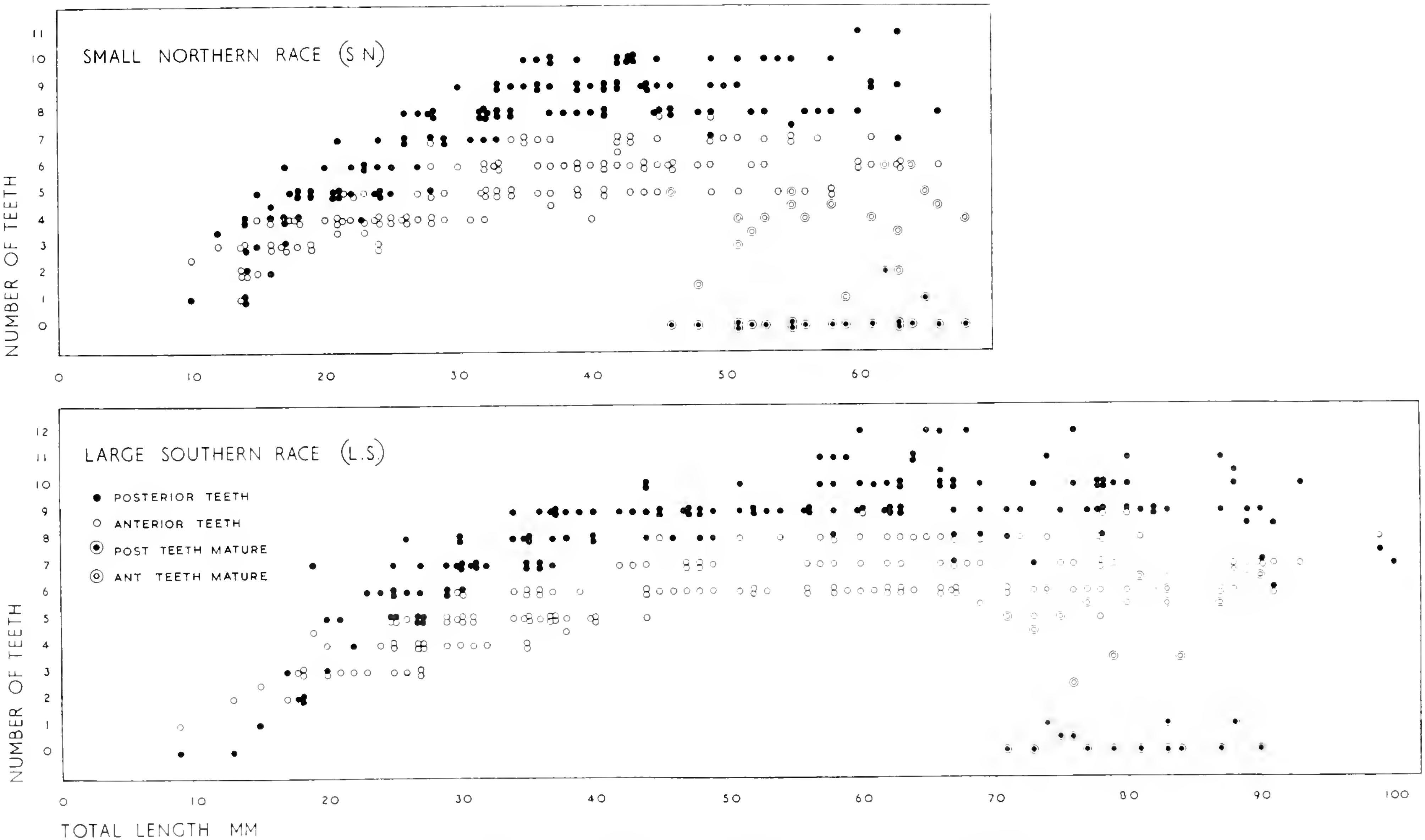


Fig. 16. The numbers of teeth plotted against length in both races of *S. gazellae*.

might be regarded as separate species, but the close anatomical similarity and an apparently common life history suggests that the two may be regarded as racially, rather than specifically, distinct. It is possible that the Antarctic Convergence is an isolating mechanism, and that the two races of *S. gazellae* represent an early stage in the formation of a new species. As individuals of both races are found, and can live, on the 'wrong' side of the Convergence one may suppose that the irregularity and rapidity of environmental changes in the region of the Convergence, more than the widely different, but stable, conditions on each side of it represent the real barrier.

Further, the distribution of the separate, though closely related, species *S. lyra* overlaps that of *S. gazellae* slightly in the region of the subtropical convergence. It might be postulated that individuals of the *S. lyra* "*gazellae*"-type crossed this convergence and successfully colonized the Subantarctic zone, giving rise to the specifically distinct Small Northern *S. gazellae* form, and subsequently these *gazellae* were equally successful in establishing themselves in the Antarctic zone, and produced the Large Southern form. The suggestion that colonization by *S. gazellae* of the Antarctic from the Subantarctic zone took place is supported by the evidence of its greater abundance in the Subantarctic (see Fig. 17). Although the colonization of the Subantarctic was sufficiently long ago to enable the Subantarctic population to become specifically distinct from the subtropical stock from which it originated, the time since the colonization of the Antarctic zone has only been sufficient for the formation of a new race.

HORIZONTAL DISTRIBUTION

S. gazellae is an oceanic species with a continuous circumpolar distribution in Antarctic and Subantarctic water; Baker (1954) records it as the most consistently occurring of the Antarctic zooplankton species which he has examined, being present in 96% of the hauls.

Fig. 17, which shows the horizontal distribution of density of the species, has been compiled from data from the 1 m. oblique nets (N 100 B) fished in the surface (100–0 m.) layer. Ommanney (1936) has discussed the significance of the variations in fishing depth of these nets, and concluded that they can be disregarded for most purposes. The shallow N 100 B is always fished for 20 minutes at a standard speed of hauling, and thus the symbols on Fig. 17 represent numbers per 20-minute haul.

It has not been necessary to take into account the time of day when the hauls were made, as Table 12 leaves little doubt that no diurnal migration takes place.

Although this species has usually been regarded as an Antarctic form (Ritter-Zahony, 1911), its main centre of abundance, as Fig. 17 shows, is in the Subantarctic zone, and no catch in excess of 200 individuals per 20-minute haul has been obtained from Antarctic waters. Many of the negative and very small hauls in Antarctic water shown on Fig. 17 were made in winter, and give the impression that the Antarctic population is sparser than it is; regrettably there are not sufficient data to make separate charts for winter and summer.

There is no evidence that the species 'swarms' or forms 'shoals', and the consistency of its occurrence suggests a fairly even distribution.

The northern limit of the distribution of the species is the region of the subtropical convergence; in making Fig. 17 the mean position of this convergence has not been used, but for each line of stations which has crossed it, its position has been found by reference to the continuous thermograph records; this convergence is a variable phenomenon, and the mean position given by Deacon (1937) is a simplified representation of it. In areas where tropical currents such as the Aghulas or the S.E. Australian current influence it, it is probably never stable, and the limits of the distribution of *S. gazellae* fluctuate in a similar manner. Even when a contemporary position for the subtropical convergence is used, some hauls of *S. gazellae* are occasionally taken north of it, for example at

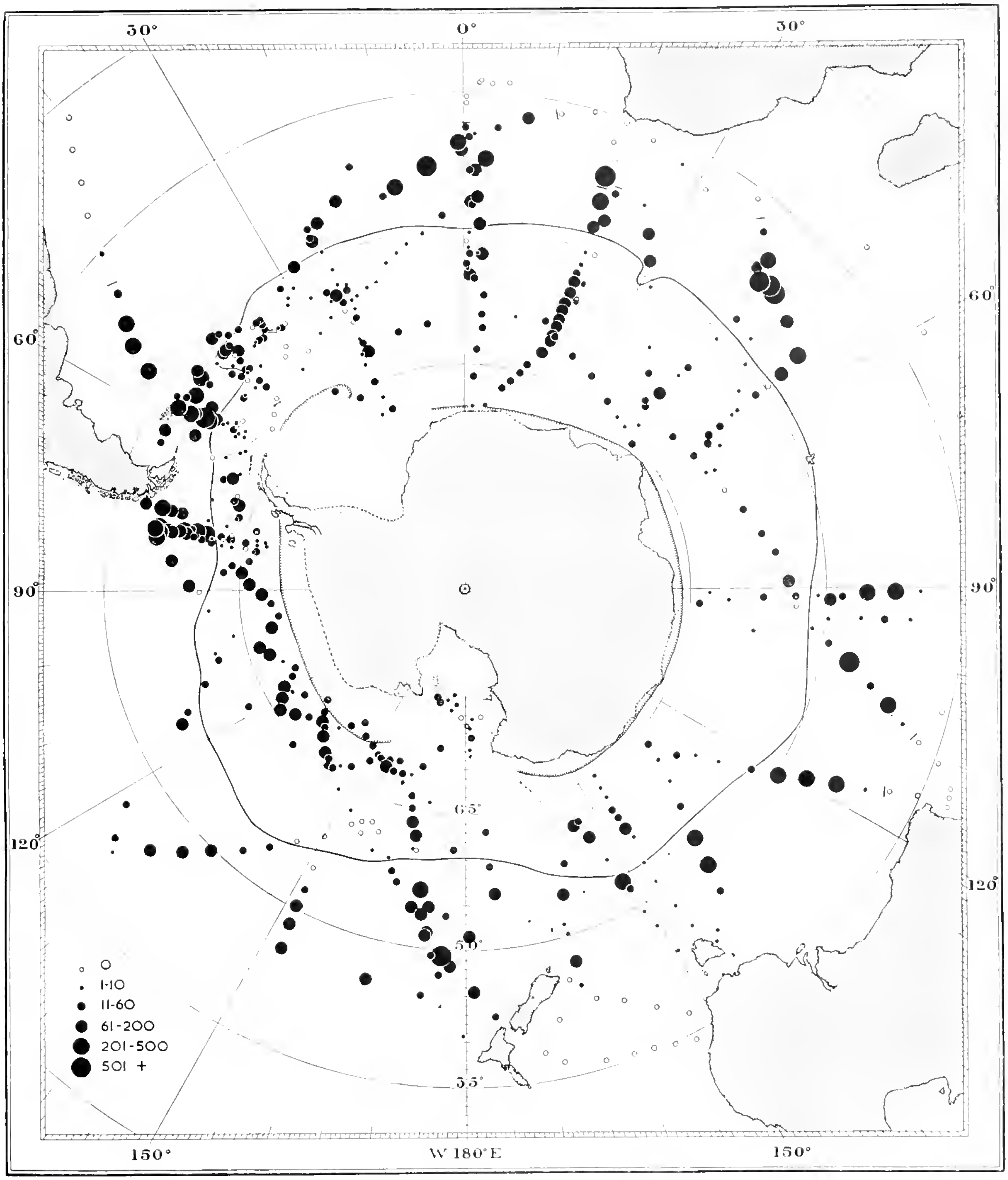


Fig. 17. The horizontal distribution of *S. gazellae* in the top 100 m. of water. Data from the shallow oblique 1 m. nets. The chart shows the Antarctic Convergence, and, closer to the continent, the normal position of the pack-ice edge in March. The subtropical convergence is shown as a short line at right angles to each line of stations which crossed it, and is the contemporary position found by reference to the continuous thermograph, and not a mean position.

Station 2625 (41° 49·7′ S., 18° 49·9′ E.). Reference to the hydrological data for this station shows that a northward extension of Subantarctic water was present between 50 and 100 m., and the net which fished from 93 to 0 m. may well have taken the majority of the catch from this layer. Similar penetrations below subtropical water are shown at Stations 1773 and 1774, and also at Station 2036 (Fig. 22).

It seemed possible that the penetration may be even farther north in the deeper waters, but examination of a line of 2 m. vertical nets in subtropical waters at Stations 675 (fishing depths 2750–2000, 2000–1500, 1500–1000, and 1000–750 m.), 677 (fishing depths 2000–1500, 1500–1000, 1000–750 m.) and 679 (fishing depths 2000–1500, 1500–1000, 1000–750 m.), has not revealed a single specimen, and it is therefore very unlikely that tropical submergence takes place. A series of hauls from stations off the limits of the chart shown in Fig. 17 have been examined for *S. gazellae*, and in all cases the results have been negative. The stations were made in the Peru current, the Benguela current, and on the meridian of 90° E. in the Indian Ocean.

Table 12. *A comparison of day and night vertical stations from various localities, and various months; numbers corrected for a 250 m. haul; percentage is the number at a particular horizon to the total for all depths*

Depth (m.)	Day			Night		
	No.	Percentage	Hauls	No.	Percentage	Hauls
50–0	325	23·3	35	420	21·5	35
100–50	715	51·4	35	1075	55·2	35
250–100	281	20·2	35	340	17·4	35
500–250	52	3·74	35	76	3·90	35
750–500	6	0·43	35	21	1·08	35
1000–750	10	0·72	35	13	0·68	33
1500–1000	2	0·14	14	4	0·20	24
Totals	1391	99·93	224	1949	99·96	232

The southern limit of distribution of the species is the Antarctic continent; and although it has not been possible owing to ice conditions to prove this in many areas, it can be said that where the Antarctic coastal waters have been reached, *S. gazellae* has been found. Owing to peculiarities of its life history (p. 270) it is improbable that it can breed in shallow shelf-waters, but even in the almost uniformly shallow Ross Sea it occurs in small numbers. In this area it averaged seven specimens per 20-minute haul in the month of January. In oceanic waters the average per 20-minute haul for the month was 47·7.

Discovery stations in the Weddell Sea have been infrequent, and were only made in the eastern end, owing to the treacherous ice conditions often encountered in the area; but Bollmann (1934) reported that the 'Deutschland' found *S. gazellae* in the Weddell Sea. Unfortunately he gives little indication of its frequency of occurrence.

Previous work on the distribution of the species has been somewhat confused by the inclusion of *S. gazellae* in the synonymy of *S. lyra*, and also by the existence of a form of *S. lyra* which closely resembles *S. gazellae*. This has been discussed on pp. 245–254.

Although *S. gazellae* was not described until 1909, there were several earlier records of *S. hexaptera* which have been attributed to the species. These are discussed by Ritter-Zahony (1911).

In his paper giving the original description of the species, Ritter-Zahony observes that although his specimens came from the South Indian and South Pacific Oceans, the Berlin Museum possessed a specimen from the Tonga islands; he does not refer to this specimen again, and, bearing in mind the fact that he was unable to determine the shape of the fins in his alcohol-preserved specimens, it seems likely that the Tonga specimen was not *S. gazellae*. In the *Revision of the Chaetognaths* (1911) he states that the distribution of *S. gazellae* is between 60° and 66° S. in the Antarctic, and that the most northerly catch was 35·5° S. He also states that it occurs in deeper water farther north; but I think this last statement is a reference to the catch from 35·5° S. rather than a suggestion of tropical submergence.

Subsequent records are mainly from Antarctic and Subantarctic waters, but there are a few exceptions.

Burfield (1930) records *S. gazellae* from Rio de Janeiro (23° S.) from the 'Terra Nova' hauls, but on p. 219 of his report remarks 'The horizontal range of the stations at which this form was captured extends from lat. 23° N. to lat. 77° 38° S.'. From the station numbers and distribution charts, it would appear that 23° N. is a misprint, and should be 23° S. Through the kindness of the British Museum (Natural History) I have been able to examine the original 'Terra Nova' hauls from Rio de Janeiro (Stations 39 and 40) and, although the specimens are in a bad state of preservation, it is evident from the position and shape of the seminal vesicles that they are *S. enflata* and not *S. gazellae*.

Tokioka (1939) records *S. gazellae* as a synonym of *S. lyra* in Japanese waters, but these specimens are almost certainly the cold water form of *S. lyra*.

Thomson (1947) found *S. gazellae* in Tasmanian waters, but followed the synonymy proposed by Johnston & Taylor (1921) and Tokioka (1939) and described them as *S. lyra*. The Discovery collections from Tasmanian waters contain specimens of *S. gazellae*, and their presence there may be due to vagaries of the subtropical convergence.

Furnestin (1953) reports *S. gazellae* from the Mediterranean, but has informed me that, after reading a typescript copy of part of this paper, she considers them to be *S. lyra* "*gazellae*"-type.

Table 13*a* gives the numerical data from 496 shallow oblique hauls. The year has been divided into four equal seasons, and the table is in two parts, one for the Subantarctic, and the other for the Antarctic zone.

The difference in size of the population for the two zones is immediately apparent, the average for 165 Subantarctic samples is 120·3 per 20-minute haul, as compared with 27·2 based on 331 Antarctic samples.

The striking decrease in numbers in the upper layers during the winter months is evidence of a seasonal migration, comparable with that described by Mackintosh (1937) for certain other Southern Ocean plankton species.

Though in the Subantarctic the total for August is rather exceptional owing to a single haul at Station 2869 of 502 individuals, three other hauls made at different times of the year in almost the same position (in the vicinity of the Crozet islands) all yielded very large numbers, and the presence of *S. maxima* in quite large numbers at the surface in this area suggests that some exceptional conditions exist there. The haul at Station 2869 is the only August haul in the collections which contains large numbers of *S. gazellae*, and if it is omitted the average for August becomes 48·0, and the winter average 66·3; these figures (shown in brackets in Table 13*a*) give a more accurate picture of normal conditions.

The Subantarctic winter average is low because a part of the population is at a depth of more than 100 m. In spring the average increases with the return of most of the population to the surface. The summer average is the highest owing to the appearance of young individuals at the surface. In autumn the average decreases for two reasons, the commencement of the winter vertical migration in April and May, and the extensive migration in March and the beginning of April in which the larger size groups of the population descend to the deeper layers to mature and breed. However this decrease is to some extent offset by the appearance in the surface layers in May of young from the March April breeding period.

The Antarctic population shows a similar rise and fall in numbers, but the peak appears to be later in the year, and the summer and autumn averages are almost the same. The low average in February may be due to the comparatively small number of hauls available in this month, and if this is so then possibly the summer total is rather too low.

The extent of the winter migration in the Antarctic can be seen by comparing the totals and averages for the months during which the animals are in deep water (May–September) with the totals and averages for the remainder of the year (Table 13*b*).

Table 13*a*. *Monthly and seasonal totals and averages per 20 min. haul with N 100 B in the surface layers*

(For explanation of figures in brackets see p. 263.)

Season	Month	Subantarctic			Antarctic		
		Total	Hauls	Average	Total	Hauls	Average
Winter	June	1,013	14	72·35	309	17	18·17
	July	461	6	76·8	18	6	3
	Aug.	886 (384)	9 (8)	98·4 (48·0)	179	25	7·1
		2,360 (1,858)	29 (28)	**81·3 (66·3)**	506	48	**10·5**
Spring	Sept.	3,989	28	142·4	196	37	5·3
	Oct.	1,519	15	101·2	634	29	21·8
	Nov.	2,916	25	116·6	1,430	52	27·5
		8,424	68	**123·8**	2,260	118	**19·1**
Summer	Dec.	1,595	7	227·8	926	31	31·0
	Jan.	685	7	97·8	2,292	48	47·75
	Feb.	1,887	14	134·7	204	14	14·5
		4,167	28	**148·8**	3,458	93	**36·7**
Autumn	Mar.	1,077	5	215·4	1,231	17	72·4
	April	616	12	51·3	1,105	35	31·57
	May	3,217	23	139·8	459	20	22·9
		4,910	40	**122·7**	2,795	72	**38·8**
	Totals	19,861	165	—	9,091	331	—

Table 13*b*. *A comparison of winter and summer totals from 1 m. oblique net hauls in Antarctic water*

Season	Months	Totals	No. of hauls	Average
Winter	May–Sept.	1,161	105	11·05
Summer	Oct.–Apr.	7,858	226	34·76

From this it can be seen that the surface population is three times larger in summer than in winter. Although this is due in part to the presence of many young broods, it must be remembered that there are very large numbers of young hatched in the autumn, and therefore a major part of the difference between the two seasons is due to migration.

The numbers of *S. gazellae* decrease in the vicinity of the Antarctic Convergence, and although this is not very apparent in Fig. 17, Fig. 18 shows some North to South lines with the stations plotted according to their distance in nautical miles from the Convergence, which demonstrate the point more clearly.

The position of the Antarctic Convergence fluctuates slightly, and it is likely that the sudden and violent changes in physical conditions brought about by these fluctuations are unfavourable to *S. gazellae* (*Eukrohnia hamata* is numerous in this area and is presumably not so sensitive to environmental fluctuations).

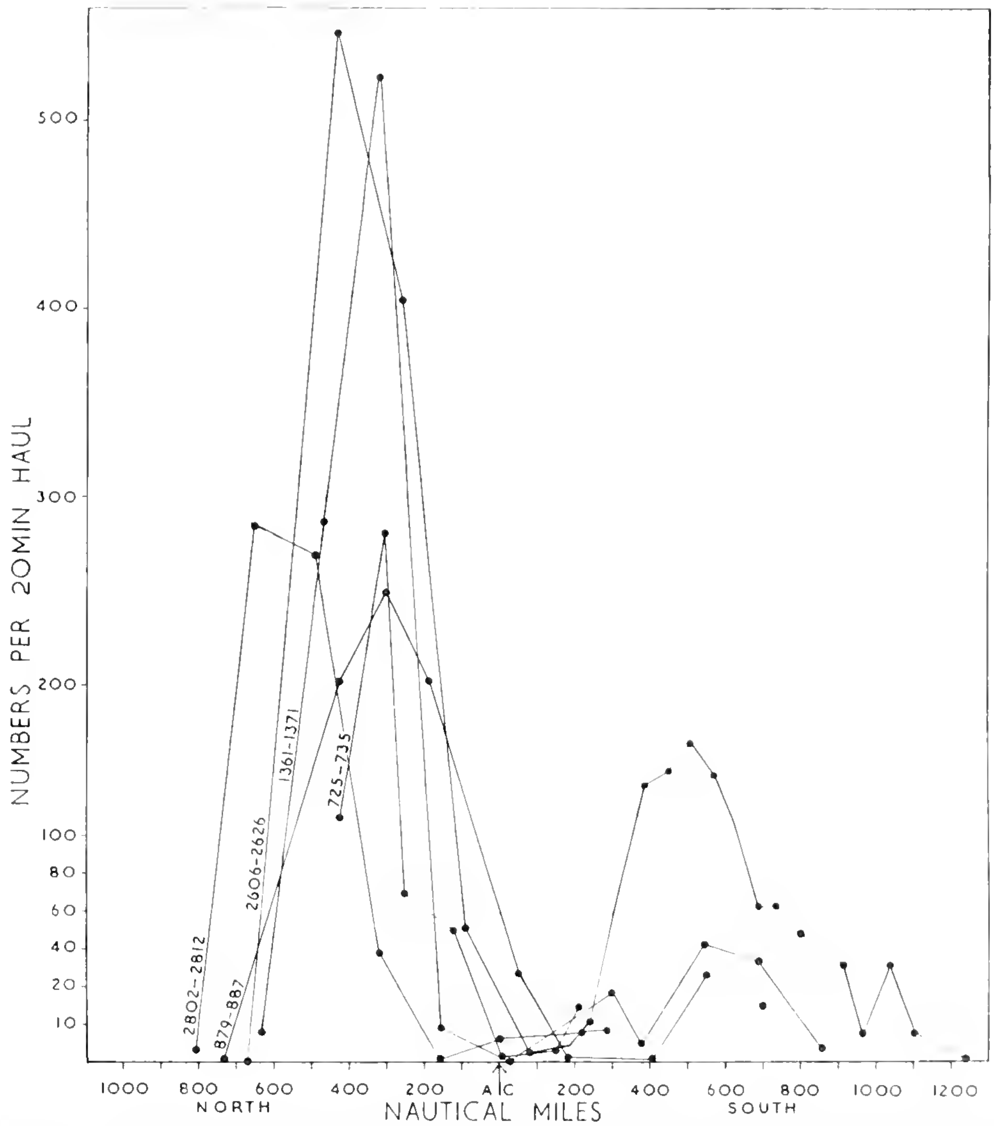


Fig. 18. A series of hauls from north-south lines of stations plotted by distance in nautical miles from the Antarctic Convergence. The position of the Antarctic Convergence has been determined by reference to the continuous thermograph record from each line.

VERTICAL DISTRIBUTION

Fowler's (1898, 1906) method of dividing the water column into three zones, the epiplanktonic, mesoplanktonic and hypoplanktonic is generally used in describing the vertical distribution of the chaetognatha. *S. gazellae*, as I shall show, is both epiplanktonic and mesoplanktonic according to the season of the year, and its state of maturity.

Fig. 19, which has been compiled from the numerical data from 129 vertical stations, shows the average depth distribution of *Sagitta gazellae* at all seasons in both the Subantarctic and Antarctic zones. Although these vertical hauls (made with the 70 cm. net) can be checked by the deeper oblique nets to determine whether the falling off in numbers below 100 m. is real or due to inaccurate sampling of larger size groups by a small, comparatively slow-moving net, it is not possible to check the difference between the 50–0 and 100–50 m. layers by the oblique hauls, as the shallowest layer normally fished is 100–0 m. Nevertheless, the vertical catches seem consistent.

The species extends in quite considerable numbers up to the surface, for although the horizontal surface nets have not been systematically examined, occasionally they have been observed to contain large numbers of *S. gazellae*. These are nets which have been towed at many stations at a depth of less than 5 m. below the surface.

Fig. 20 shows the size and numbers of individuals taken in the 1 m. oblique nets at Station 461 (56° 44′ S. 0° 23′ W, 21.x.30), a 24-hour station in Antarctic water, and it demonstrates that size increases with depth. The animals have been plotted on Fig. 20 by their length in mm. against the mean depth of each haul, e.g. the mean depth for a haul from 280 to 180 m. has been assumed to be 230 m. The scatter of the observations when plotted is considerable but, although there are a number of animals of the smaller size groups present in the deeper hauls, it must be noted that these were made with *flights* of oblique nets, and therefore the paying out of the nets must be halted from time to time for attachment of more nets; thus the deeper ones may have sampled shallow layers for short periods of time. As the small animals are present in the upper layers in large numbers, it is likely that many of the small animals in the deep hauls are due to this source of error.

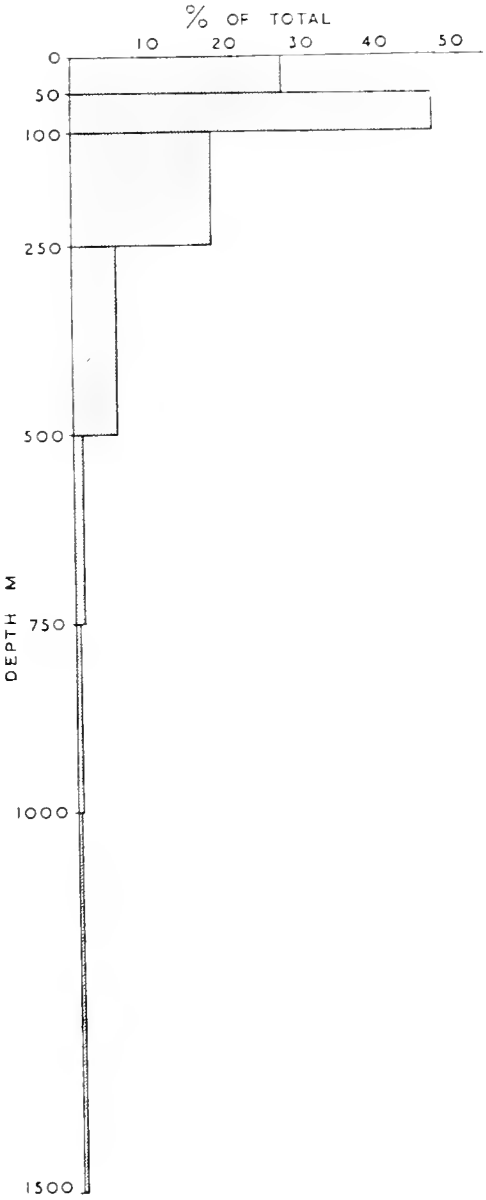


Fig. 19

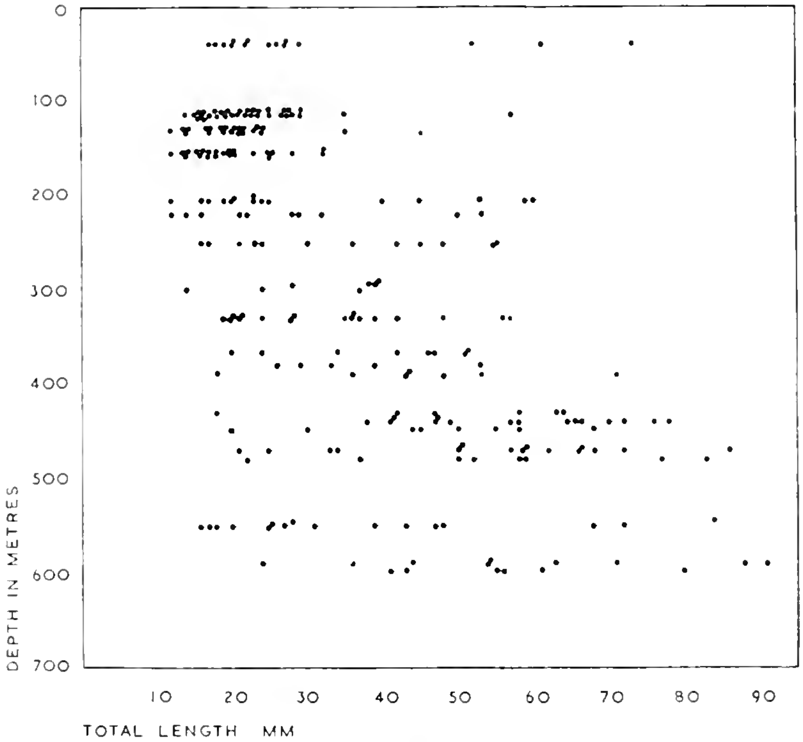


Fig. 20

Fig. 19. The vertical distribution of *S. gazellae* at 129 vertical stations: the numbers at each depth are represented as a percentage of the total for all depths.

Fig. 20. The vertical distribution of *S. gazellae* at Station 461 showing the increase in size with depth.

It is also evident from Fig. 20 and from Table 18, Appendix, which gives the numbers plotted on Fig. 20, that there is a considerable decrease in numbers with depth. This confirms the evidence from the series of vertical stations mentioned above.

The evidence from the vertical series suggests that the maximum concentration of *S. gazellae* is in the 100–50 m. layer, and this confirms Bollmann's (1934) statement for both *S. lyra* and *S. gazellae* (considered together). The data in Fig. 20, however, suggest that the main concentration is between 100 and 150 m. The numbers in this figure have been plotted against the mean depth of each haul and the concentrations between 110 and 135 m. may well have been taken at a depth of less than 100 m., as the nets which took them fished into the 100–50 m. layer. The data from the vertical nets may be considered to be more reliable in this respect. The depth range of the species obtained from the samples available extends down to 3000 m., but it is quite possible that its total range may reach to the bottom; at great depths specimens are rare.

Table 12 shows the numerical data from thirty-five daylight and thirty-five night vertical stations and suggests that there is no diurnal migration in the species; Fig. 21 shows the depth distribution during the 24-hour Station 461, and confirms the absence of diurnal migration.

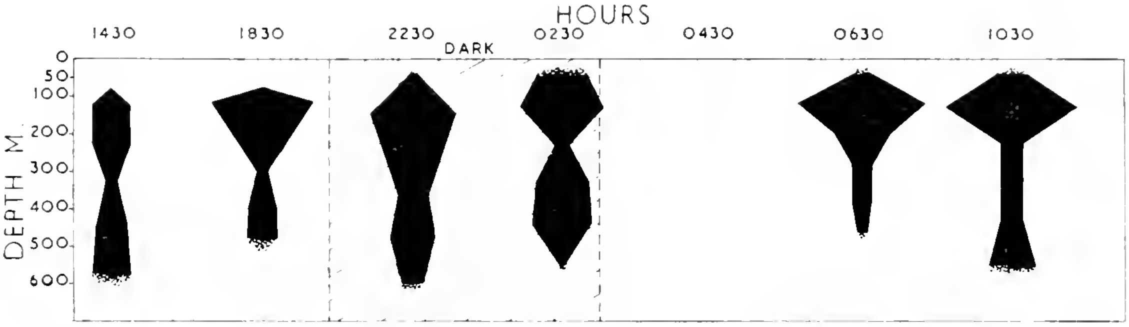


Fig. 21. The vertical distribution of *S. gazellae* at Station 461 showing absence of diurnal migration. Data from oblique 1 m. nets. Horizontal scale 1 mm. = 2 individuals.

Fig. 22, which has been constructed by the method described by Mackintosh (1934, p. 377), shows the monthly vertical distribution of the species in the meridian of 0°, and demonstrates the seasonal vertical migration in winter. Table 19, p. 278, gives the numerical data from which the figures were compiled. In the Antarctic (south of 51° on the meridian of 0°) this migration is into the warm deep layer (between approximately 150 and 1000 m) (Fig. 23*a*, *b* confirms this), but in the Subantarctic (north of 51°) the migration is not so great, and only in August does the centre of maximum abundance of the population move below 100 m. However, a study of the size-group percentages in the surface 100 m. as sampled by the 1 m. oblique nets in winter (Fig. 26, see p. 271) reveals that the population is mainly composed of one brood, hatched out in late March and early April; and as there is evidence that breeding has been taking place throughout the summer (see p. 274) one must conclude that the larger individuals have migrated to below 100 m. This is confirmed by the size of individuals taken in the N 70 V nets at this time of year, and also by Fig. 24 which is a comparison of size-group percentages from the shallow (100–0 m.) and deep (250–100 m.) oblique nets during the months of May and June.

Fig. 23*a*, *b* referred to earlier gives the numerical data from N 70 V nets from the 0° line plotted on a temperature-salinity diagram, and shows the shift of the Antarctic population from the surface water towards the warm deep water in winter. This would be more striking if it were not for the fact that the 250–100 m. nets pass through both the warm deep and the Antarctic surface layers; and although it is probable that the animals in a haul come from the warm deep and not from the Antarctic surface water (for example when there is a large number in the 500–250 m. net, but none in the 50–0 and

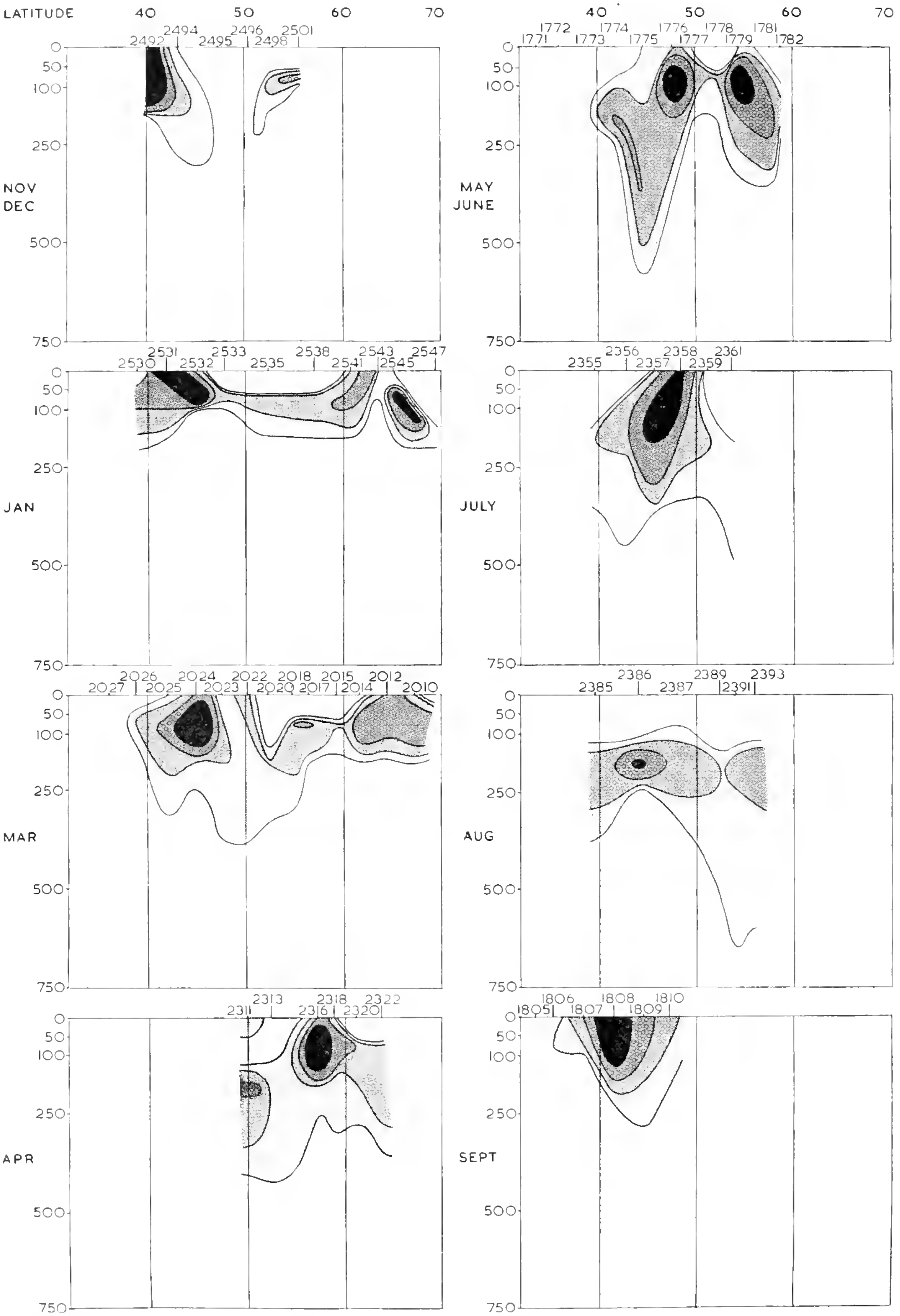


Fig. 22. The vertical distribution of *S. gazellae* for 8 months of the year on the meridian of 0°. The shading represents density per 250 m. haul: (i) (the darkest) >41 individuals, (ii) 21–40 individuals, (iii) 11–20 individuals, (iv) (the lightest) 5–10 individuals. Hauls containing less than 5 individuals have been disregarded. The mean position of the Antarctic Convergence on this meridian is 51° S. See Table 19, p. 278.

100–50 m. nets) it is still necessary to use the temperature and salinity data for the whole 250–100 m. horizon when calculating the mean for the haul, and this inevitably shifts it away from the warm deep layer.

The change in position of the Subantarctic population in winter is also evident in Figs. 23*a*, *b*, but not enough is known about the characteristics of the surface and subsurface waters in this area to draw any conclusions from these figures, other than to point out a movement down towards the Antarctic intermediate water, which bears out the data from oblique nets.

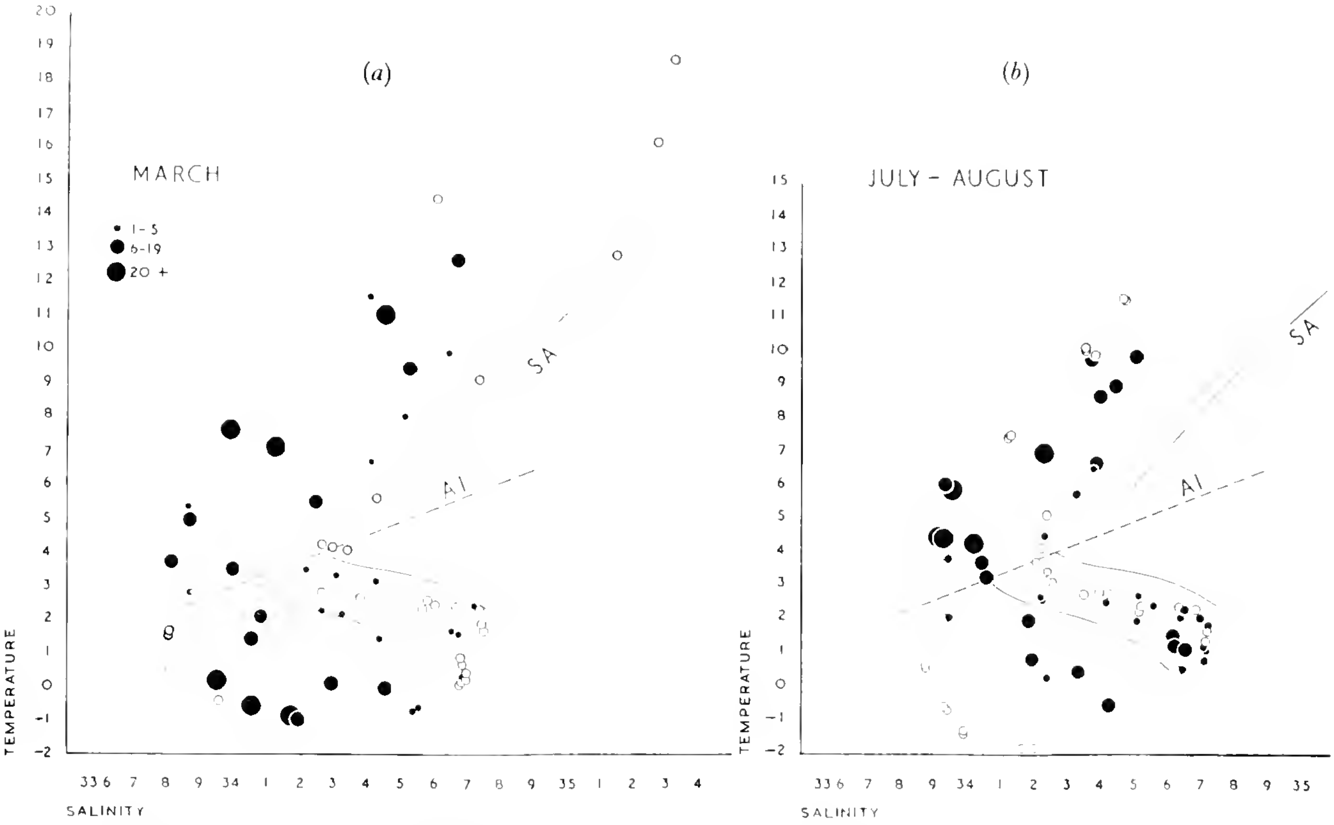


Fig. 23. The vertical distribution of *S. gazellae* in relation to temperature and salinity, based on three lines of stations on the meridian of 0°, one in summer and two in winter. The core of the South Atlantic Central water is marked S.A. and that of the Antarctic Intermediate water A.I. Above the Antarctic Intermediate water and to the left of the South Atlantic Central water is the Subantarctic surface water. Below the Antarctic Intermediate water, enclosed by two lines is the warm deep water, while to the left of this is the Antarctic surface water. Open circles represent hauls containing no *S. gazellae*.

Fig. 25, in which the animals at stage III and IV maturity from N70V hauls have been plotted against temperature and salinity, shows that they are concentrated in the warm deep layer. This is discussed further on pp. 270–1, but the fact must be mentioned here in order to obtain a complete picture of vertical distribution. These mature animals habitually migrate to deep water (750–2000 m.) to breed, and animals sinking down for this purpose are taken at intermediate depths.

It has been shown above that for most of its life, *S. gazellae* is an inhabitant of the surface waters, and is mainly concentrated in the 100–50 m. layer; but in the winter months in the Antarctic it sinks to the upper layers of the warm deep water between 250–100 and 500–250 m. At the same season in the Subantarctic, the population is about equally concentrated in the 100–50 and 250–100 m. layers, partly in Subantarctic surface water, and partly in Antarctic intermediate water.

In winter the smallest individuals form that part of the population which is nearest to the surface, the larger-sized animals occurring below, and increasing in size with increasing depth. In summer the larger-sized animals are mixed with the small in the surface layers, but large animals descending to breed are found in the deeper layers. The mature animals are normally only found below 750 m., in the warm deep water.

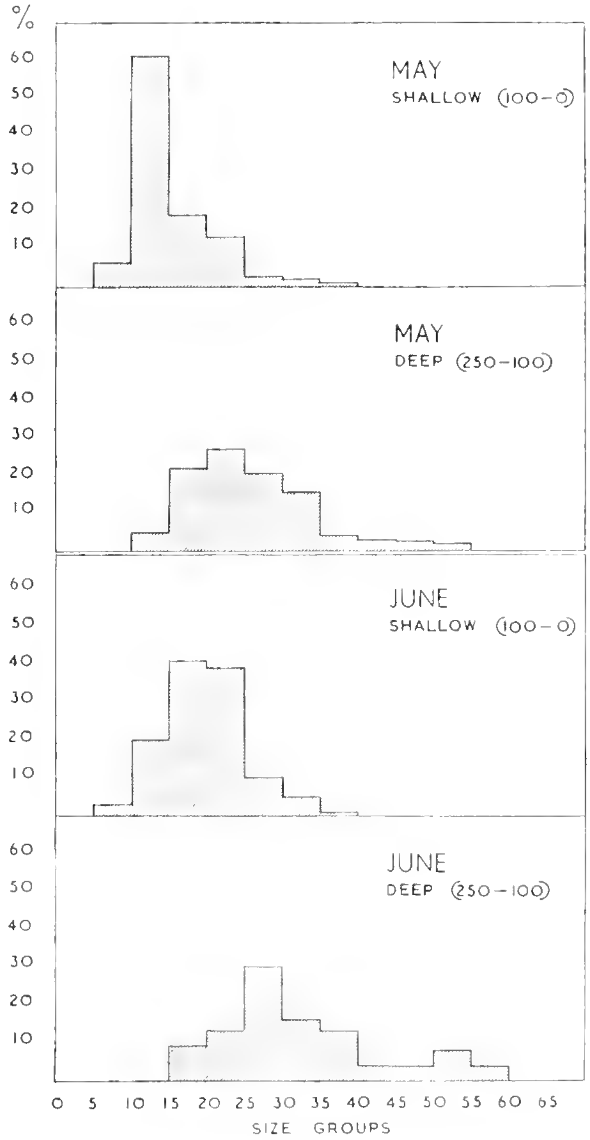


Fig. 24

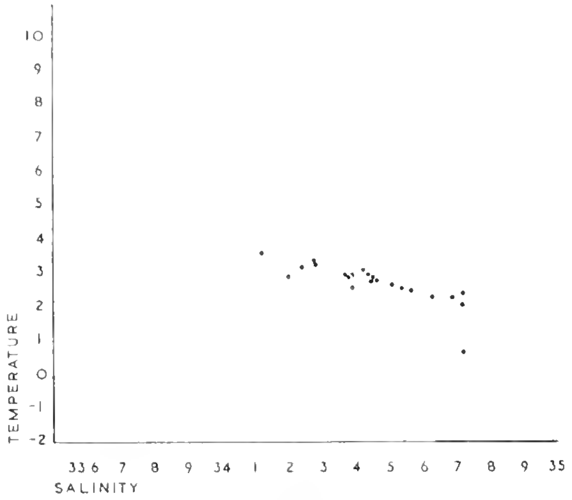


Fig. 25

Fig. 24. The vertical distribution of size groups of *S. gazellae* in early winter, from shallow and intermediate oblique 1 m. nets.
Fig. 25. The distribution of mature specimens of *S. gazellae* in relation to temperature and salinity.

VERTICAL DISTRIBUTION OF MATURE ANIMALS

Table 14 shows the depth distribution of all mature specimens taken in closing nets (N450, TYF, N100, N70). Here I class as 'mature' those specimens in which the seminal vesicles have grown to full size, and these include all in the stages of maturity from II/III to V. It is evident from the data that the advanced stages are very rare at depths above 750 m., and probably most common in the 1500–1000 m. layer. The number of hauls made below 1000 m. is small compared with the number made in the shallower layers, and therefore the one stage III individual taken in the top 250 m. is the only mature specimen from approximately 35,000 immatures observed from this layer, whereas the fifteen mature specimens from the 1500 to 1000 m. layer represent a high percentage of the total numbers taken in this layer. Deep hauls have been searched for mature specimens, and Table 15 has been compiled from ninety-three vertical stations, the number of individuals at each stage of maturity being expressed as a percentage of the total numbers in each horizon. Both races of *S. gazellae* are combined and the stations are from nearly all months of the year. It can be seen that in the deepest hauls (1500–1000 m.), the mature stages III and IV represent more than 50% of the total.

Stage I is the commonest in the 100–50 m. layer, though the difference in percentage composition in the three shallow layers is small.

Stage II reached a maximum in the 750–500 m. layer, falling off above and below this level.

Stage III appears in the 1000–750 m. layer, being as numerous as stage II at that depth.

Stage IV appears in the 1500–1000 m. layer, but is not as numerous as stage III.

Table 14. *Vertical distribution of mature specimens from closing nets*

Depth (m.)	Stages of maturity					
	II/III	III	III/IV	IV	IV/V	V
250–0	—	1	—	—	—	—
500–250	—	—	—	**1**	—	—
750–500	—	1	—	1	—	—
1000–750	4	5	—	4 **8**	1	1
1500–1000	2	11	1	4 **4**	—	**2**
>1500	—	1 **1**	**1**	2 **2**	—	3

(S.N. race, light type; L.S. race, heavy type.)

Table 15. *Vertical distribution of all stages at ninety-three stations—each stage given a percentage of the total for each depth (percentages in heavy type)*

Depth (m.)	Stages of maturity				
	I	II	III	IV	No. of hauls
50–0	1075 **96·4**	40 **3·5**	—	—	92
100–50	1990 **98·5**	30 **1·5**	—	—	92
250–100	695 **97·4**	19 **2·6**	—	—	93
500–250	141 **89·3**	17 **10·7**	—	—	93
750–500	30 **63·9**	17 **36·1**	—	—	90
1000–750	9 **47·4**	5 **26·3**	5 **26·3**	—	89
1500–1000	6 **30·0**	3 **15·0**	9 **45·0**	2 **10·0**	73

GROWTH RATE AND LIFE HISTORY

The seasonal vertical migration of *S. gazellae*, in which part of the population sinks below the horizon of the shallow oblique nets in winter, is the main factor which makes a study of the growth rate of the species possible. In summer months the range of size groups in the population is so great that it is not possible to identify, or follow the progress of, one particular brood among all the others. In winter, however, one brood is left within the horizon of the shallow (100–0 m.) oblique nets, and its progress can be observed from May when it first appears until September and October when it becomes mixed with other broods, and its individuality is lost. This, however, applies only to the Subantarctic zone, for in the Antarctic the seasonal migration carries the population almost entirely below the horizon of the shallow oblique nets, and in addition the ice conditions prevent a study of the southern part of the Antarctic zone during the winter months. Thus the growth rate and life history of the L.S. race can only be inferred from that of the S.N. race.

Fig. 26 shows the data from the shallow oblique (1 m.) nets fished in the Subantarctic zone during the months of May to November. The animals have been plotted in 5 mm. size groups, the numbers of each group calculated as a percentage of the total haul or set of hauls. Each haul or set of hauls has been plotted against the day or mean of the days on which they were made. Regrettably it has not been possible to utilize data from one area alone (or from one year alone) as the numbers available in the series of repeated stations on 0° have been insufficient by themselves. Thus Fig. 26 is composed of data from many localities taken in several different years. The results are, however, remarkably consistent, and this suggests that the general pattern of breeding and development is the same from year to year throughout the Subantarctic zone.

The variation in the upper size limit during the winter months may well be due to the variation in depth of the nets; for example the first set of June observations made at Stations 2824 and 2825 show a greater number in the larger size groups than the other June observations, because the net at Station 2824 was fished from 163 to 0 m., and thus sampled the older and larger-sized broods below 100 m. The smallest size groups are affected by the occasional presence of a small brood hatched later than the main one under consideration; this later brood seems to separate out in September.

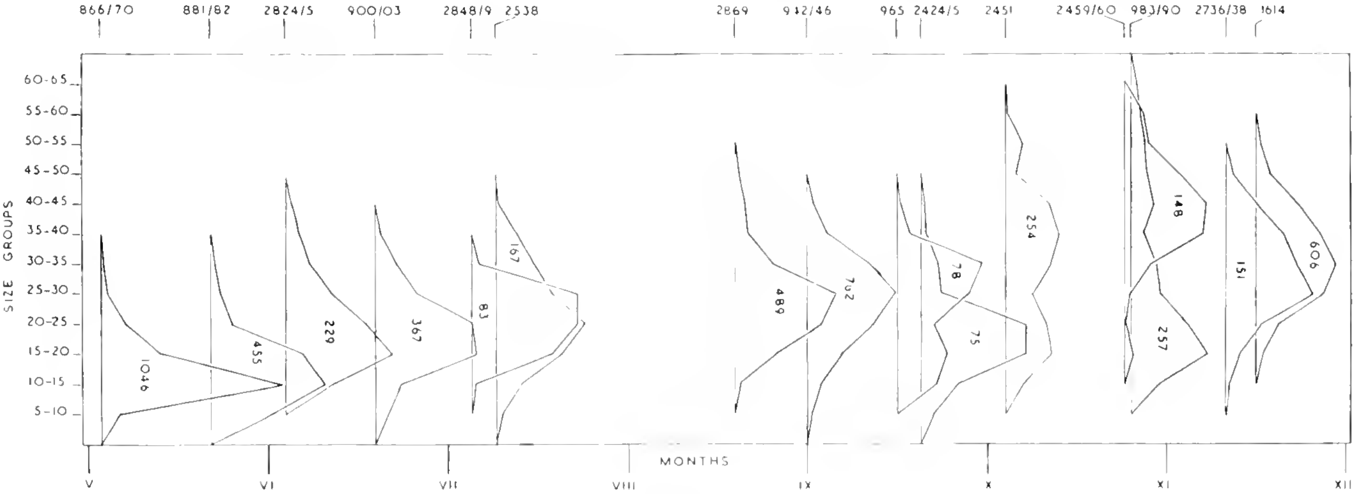


Fig. 26. The growth of *S. gazellae*, based upon counts and measurements of specimens taken in the shallow oblique 1 m. nets. The station numbers of the hauls used are given along the top and the number of individuals in each haul or set of hauls is enclosed in each figure.

The growth rate from May to October is shown by Fig. 26 to be about 5 mm. per month. This is evidently a low rate which is most probably higher in spring and summer, and which appears to be lowest during August. The normal size at maturity is 55–60 mm. and this would be reached in 12 months at a 5 mm. per month growth rate: Figs. 8 and 15 suggest that the maximum size is reached in the surface layers, for none of the mature animals (found in the deep layers) was larger than at stage II which is the most advanced stage found in the surface layers. Thus in considering the growth rate one must make allowance for both the time needed for the breeding migration, and the time taken for the maturation of the gonads. It has not been possible to discover how much time elapses between the commencement of the breeding migration and the shedding of eggs. If one assumes that for at least 1 month, and possibly 2, no growth takes place, then the summer growth rate must be somewhat higher to achieve a length of 60 mm. in 10 or 11 months. This seems a reasonable assumption, as the food supply is much greater in spring and summer.

There are certain stages in the life history of *S. gazellae* which I have been unable to find, but in most cases they can be inferred from other evidence, and it may be possible at some future date to fill in the gaps, now that it is known when and where to look for those stages.

I shall describe the life history of one particular brood, referred to as the March April brood, which is observed during the winter months in the surface 100 m. Then having established the pattern of its life history I shall proceed to discuss that of other broods.

Since the fully mature specimens are found only in deep water it can be assumed that the eggs are laid also in deep water, and that they, or the newly hatched young, rise to the surface. Certainly the youngest individuals taken in our nets occur in the surface layers. Judging by the growth rate indicated in Fig. 26 it seems likely that eggs are laid in about late March or early April. The youngest individuals are found between 250 m. and the surface in early May. Although at this stage they are mainly in the 10–15 mm. group, there are still quite a large number in the 5–10 mm. group; individuals at a length less than 5 mm. are rare at all times. It seems likely that hatching takes place in the top 250 m. as no very small individuals have been found below this depth (see Table 16), though specimens of other forms (*S. maxima*, *S. planctonis* and *Eukrohnia hamata*) are common in the deeper nets, at lengths from 2 to 5 mm. I have been unable to find the eggs, but judging from their size in the mature ovaries they must be very small when laid, and I do not know how to distinguish them from eggs of other species. Kramp (1939) states that some of the eggs of *Sagitta maxima*, a species which also breeds in deep water, rise to the surface to hatch. The ovaries of the living mature *S. gazellae* are pale yellow in colour, and this may be due to the presence of fat or oil which might help the eggs to rise.

Table 16. *Monthly distribution of* 0–10 *mm. size group, from seventy-one vertical stations*

Depth (m.)	Months												Total
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	
50–0	25	20	10	—	30	15	5	—	10	0	50	—	165
100–50	65	30	65	—	95	90	50	—	30	0	45	—	470
250–100	3	2	3	—	10	12	37	—	5	3	18	—	93
500–250	0	0	0	—	0	0	0	—	0	0	0	—	0
750–500	0	0	0	—	0	0	0	—	0	0	0	—	0
1000–750	0	0	0	—	0	0	0	—	0	0	0	—	0
1500–1000	0	0	0	—	0	0	0	—	0	0	0	—	0
No. of stations	9	6	10	0	13	6	11	0	6	6	7	0	71

From May to late July the March April brood is concentrated in the 100–50 m. layer. In late July and August they sink to the 250–100 m. layer (Fig. 22), and the upper layers are almost completely empty of this species (the haul at Station 2869 in August is quite exceptional (see p. 263) though very fortunate, as without it there would be no data for August in Fig. 26).

During the winter months the animals grow at a rate of 5 mm. a month, and by September are mainly in the 25–30 mm. group. The growth rate increases in the spring, and by the end of October specimens have reached the 35–40 mm. group, but the individuality of the brood is lost by mixture with other broods which have ascended from deeper water. The March April brood remains in the surface until February or March, and attains stage II maturity and full size. The breeding migration (p. 270) now commences, and the animals sink, passing from stages II to III at about 750–500 m., down to the 1000–750 m. layer, where they are usually at stage III, and on to the 1500–1000 m. layer where they are mainly at stage IV. Loss of the posterior teeth occurs between stages II and III at about 750 m., and the rest of the head armature also decreases. At the advanced stages of maturity the hooks are often damaged and broken, but the main reduction in hook numbers is effected by normal shedding from the ventral end of the hook rows. After leaving the surface the animals do not appear to increase in length; their food is presumably used almost entirely by the rapidly developing ovaries, which at stage III are thin rod-shaped structures, sometimes as little as 14 % of the total length but which at stage IV are thick swollen structures occupying as much as 70% of the total length. It is probable that fertilization takes place when the ovary/body length percentage is between 55 and 60, and that the eggs are laid when this percentage is about 70. No animals with seminal vesicles intact have been taken with the ovary/body length percentage in excess of 55, and none at all with this percentage in excess of 71.

Spawning takes place throughout the spring, summer and autumn, and perhaps to a small extent in winter. This prolonged breeding season is evident both from the fact that small-size groups are always present in the population, and from the almost complete overlapping of all size groups which makes the interpretation of a figure such as Fig. 26 impossible during the late spring and summer months.

Fig. 26, however, indicates the presence of several recognizable broods apart from the March/April one. Traces of a later brood, probably hatched in April/May, are evident at Station 965 in September, and this brood may account for the 5–10 mm. group at Station 2536 in July; the graph for Stations 2424 and 2425 is based mainly on this brood, which is still recognizable at Station 2451 in early October and at Stations 983–90 later in the same month; its individuality is lost in November. It is possible that with the advent of spring the larger animals of the March/April brood grow at a more rapid rate than do the smaller animals of the April/May brood, and thus for a month there is a noticeable gap between the peaks for the two broods.

At Station 2451 in October the large size groups appear. These are from broods hatched in late spring and summer of the previous year, and have spent the winter months in deep water. It is probable that the stock which gives rise to the earliest spring broods never ascends to the surface after its winter migration. These large animals are absent from the shallow hauls in November, and evidently begin their breeding migration early in that month (there are always at least a few large individuals in the shallow hauls in every month). The peaks of the November graphs are probably due to a combination of the March/April and April/May broods, the point of overlap of the size ranges of each brood giving a combined total in excess of the peak of either brood separately.

The areas of greatest density of population in the vertical sections (Fig. 22) for December to May are composed mainly of animals less than 20 mm. in length, and the apparent shift of the centre of density of the population southwards during the summer suggests that the earliest breeding takes place in the most northerly part of the Subantarctic zone, and as the summer progresses the centre of breeding moves southwards.

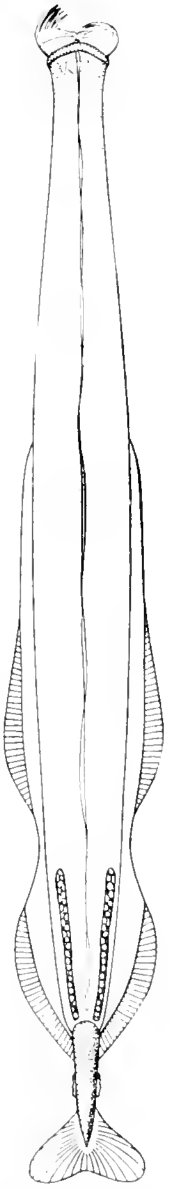


Fig. 27. A large non-breeding specimen of *S. gazellae* L.S. race, 100 mm. long.

It is not possible to say much about the life cycle of the L.S. race. The normal size at maturity is from 75 to 80 mm., and no mature animals in excess of 90 mm. have been recorded. If the growth rate is assumed to be 5 mm. per month, as in the S.N. race, then the time taken to reach full size will be 15–16 months. However, the growth rate may be expected to be considerably higher in summer, and a 12-month life cycle seems probable on these assumptions.

Although most of the mature specimens of the L.S. race have been taken in March, this is probably due to the greater number of deep towed nets fished in this month and hence the larger quantity of specimens available. The N70V net, though it obtains specimens in perfect condition, catches only a few of the smaller Subantarctic race, and it catches still fewer specimens of the large Antarctic race. The large deep-towed nets, which are the main sources of supply of specimens of the mature L.S. race, have not been regularly fished, and so no real indication of the frequency of breeding can be obtained from the catches of mature animals.

Very large individuals (>90 mm.) are found in the Antarctic zone; these are apparently non-breeding (Fig. 27), and are usually found at the surface in winter and spring; they do not appear to perform either a seasonal or a breeding migration. They are never found at a more advanced stage of maturity than stage II, and the largest specimen taken to date measured 105 mm. (fresh). This is probably not the largest, for preserved specimens of 99 and 100 mm. have been examined on several occasions, and taking shrinkage into account (see p. 240) the maximum length fresh is probably 108–110 mm. It is possible that in certain cases individuals have not been able to migrate to breed because they have been in shallow water, and have therefore continued to feed and grow at the surface; the large specimen of 105 mm., for example, was taken at Station 1007 where the sounding was only 152 mm. However, in many cases these large animals are found over deep water, and one must assume that there is another factor which operates to prevent both breeding and seasonal migration.

FOOD

S. gazellae is frequently taken with animals held in its jaws, but this is not necessarily any indication of its normal food, for often the animals which it has seized are far too large to be ingested—large medusae or fish for example—and not infrequently specimens are found which have bent back upon themselves and seized their own tails. While a net is being hauled the animals concentrated in the net bucket are swirled together, and evidently *S. gazellae* will seize anything it touches; during fixation also, the animals make convulsive movements which may have a similar result.

Observations have been made of specimens with food in the gut, and owing to the great transparency of the animal it has sometimes been possible to identify the species of food animal. These positive observations are however surprisingly few. In two commissions of 'Discovery II', during 1931–33 and 1950–51, only in forty-five hauls out of 667 examined were specimens of *S. gazellae* recorded with food in the gut; this does not mean only forty-five specimens, for in many cases there were a number of animals with food in their gut found in one haul, but even so the number is very low.

Table 17 shows that Copepods and Euphausians are the commonest food animals for the species, the third group, Chaetognaths, being but 13% of the total.

No mature *S. gazellae* has been found with food in the gut, but the total number of matures taken is small, and this may therefore be of no significance.

On one occasion a large specimen of *S. gazellae* was kept alive aboard ship for nearly 2 hours, and was given a live Euphausian to eat. The food was touched against the mouth of the chaetognath which promptly seized it and pushed it into the mouth by alternate movements of the hooks on each side; once in the mouth the food was passed rapidly down to the middle of the gut, this process taking about 10 minutes; from this point to the posterior end of the gut the passage of the food was much slower, and it reached the posterior end about 1 hour after ingestion. The animal died before it had defaecated. The behaviour of one specimen in far from natural conditions must of course be regarded with reserve.

Chaetognaths form part of the diet of many marine animals, notably of fish. Large pelagic fish are uncommon in the Southern Ocean, and so it is not likely that they represent major predators of *S. gazellae.* Dr T. J. Hart has observed a Cape pigeon (*Daption capensis*) holding a large sagitta in its beak, and from the position of the observation it is fairly certain that the sagitta was *S. gazellae.*

S. gazellae is probably eaten by most of the larger plankton-feeding organisms in the Southern Ocean, but no records are yet available.

Table 17. *Food organisms found in the gut of* Sagitta gazellae *arranged by groups in order of frequency of occurrence*

Species		Group	No.	Percentage
Calanus propinquus	2	Copepoda	19	42·2
Rhincalanus gigas	1			
Pleuromamma robusta	1			
Metridia gerlachii	1			
Calanus sp.	3			
Other Copepoda	11			
Thysanoessa macrura	2	Euphausiaceae	18	40·0
Thysanoessa vicina	1			
Thysanoessa sp.	5			
Euphausiid larvae	3			
Euphausiid spp.	7			
Eukrohnia hamata	2	Chaetognatha	6	13·3
Chaetognatha spp.	4			
Primno macropa	1	Other Crustacea	2	4·5
'Large red crustacean'	1			

SUMMARY

1. *Sagitta gazellae* has been examined from a series of stations made by ships of the Discovery Committee in the Southern Ocean.

2. The species is shown to be separate from *S. lyra* (Krohn) with which it has been considered synonymous in recent years.

3. Five stages of maturity based upon those of Kramp (1939) for *S. maxima* are outlined.

4. The population of *S. gazellae* in the Southern Ocean consists of two races divided by the Antarctic Convergence. The Northern or Subantarctic population matures at a shorter length than does the Southern Antarctic one.

5. The limits of horizontal distribution are shown to be, to the north, the region of the subtropical Convergence, and to the south, the Antarctic Continent. The region of maximum abundance of the species is in the Subantarctic zone.

6. The species has an observed vertical range of 3000–0 m., with a layer of maximum abundance between 100 and 50 m.

7. *S. gazellae* performs a seasonal vertical migration to deep water in winter, but does not perform any diurnal migration.

8. The Subantarctic race is shown to have a growth rate of 5 mm. per month during the winter and early spring. The growth rate is presumed to be higher in summer.

9. The species breeds only in deep water (>750 m.). The breeding season is very extended. The smallest individuals observed were taken in the upper 250 m.

10. *S. gazellae* feeds mainly upon copepods and small euphausians.

REFERENCES

Baker, A. de C., 1954. *The Circumpolar Continuity of Antarctic plankton species.* 'Discovery' Rep. xxvii, pp. 201–18.

Bollmann, A., 1934. *Die Chaetognathen der deutschen antarktischen Exped. auf der 'Deutschland' 1911–1912.* Int. Rev. Hydrobiol. (Leipzig), xxx, pp. 251–305.

Burfield, S. T., 1930. *Chaetognatha.* Brit. Antarct. Terra Nova Exped. (Zool.), vii(4), pp. 203–28.

Deacon, G. E. R., 1937. *The Hydrology of the Southern Ocean.* 'Discovery' Rep. xv, pp. 1–124.

Fowler, G. H., 1898. *Contributions to our Knowledge of the Faeroe Channel.* Proc. Zool. Soc. Lond. 1898, p. 545.

—— 1905. *Biscayan Plankton of H.M.S. 'Research'. Part III. Chaetognatha.* Trans. Linn. Soc. Lond. (Zool.), ser. 2, x, pp. 55–87.

—— 1906. *The Chaetognatha of the Siboga expedition.* Siboga Exp. Reps. xxi, pp. 1–86.

—— 1907. *Chaetognatha.* Nat. Antarctic Exped. 1901–1904, iii. Zoology and Botany, pp. 1–6.

—— 1908. *Notes on a small collection of Plankton from New Zealand, I.* Ann. Mag. Nat. Hist., ser. 8, i, pp. 240–1.

Fraser, J. H., 1952. *The Chaetognatha and other Zooplankton of the Scottish Area and their value as Biological Indicators of Hydrographical Conditions.* Scottish Home Dep., Marine Research, no. 2, pp. 1–52.

Furnestin, M. L., 1953. *Chaetognathes récoltés en Méditérranée par le 'Président Théodore Tissier'.* Travaux publiés par la Station d'Aquiculture et de Pêche de Castiglione. New ser. no. 4, pp. 1–44.

George, P., 1952. *A systematic account of the chaetognatha of the Indian coastal waters with observations on their seasonal fluctuations along the Malabar Coast.* Proc. nat. Inst. Sci. India, xviii, no. 6, pp. 657–689.

Germain, L., 1913. *Chétognathes.* Deuxième expédition Antarctique Française (1908–10). Sciences Naturelles: Documents scientifiques—zoologie, pp. 87–104.

Germain, L. and Joubin, L. 1916. *Chetonathes provenants des campagnes des yachts 'Hirondelle' et 'Princesse Alice', 1885–1910.* Res. Camp. Sci. Monaco xlix, pp. 1–118.

Ghirardelli, E., 1950. *Osservazioni biologiche e sistematiche sui Chetognati della Baie du Villefranche sur mer.* Boll. Pesca, Piscic. Idrobiol. xxvi, v (n.s.), Fasc. 1, pp. 1–27.

—— 1952. *Osservazioni biologiche e sistematiche sui Chetognati del Golfo di Napoli.* Pubbl. Staz. Zool. Napoli, xxiii, pp. 296–312.

Hamon, M., 1952. *Note complémentaire sur les Chétognathes de la baie d'Alger.* Bull. Soc. Hist. nat. Afr. N. xliii, pp. 50–2.

Hart, T. J., 1934. *On the phytoplankton of the South West Atlantic and the Bellingshausen Sea 1929–31.* 'Discovery' Rep. viii, pp. 1–268.

Jameson, A. P., 1914. *The Chaetognatha of the Scottish National Antarctic Expedition 1902–1904.* Trans. roy. Soc. Edinb. xlix, pp. 979–89.

John, D. D., 1936. *The Southern Species of the genus* Euphasia. 'Discovery' Rep. xiv, pp. 193–324.

Johnston, T. H. & Taylor, B. B., 1921. *The Chaetognatha.* Aust. Antarct. Exped. Ser. C, vi(2), pp. 1–17.

Kemp, S., Hardy, A. C. & Mackintosh, N. A., 1929. *The Discovery Investigations, Objects, Equipment and Methods.* 'Discovery' Rep. i, pp. 141–232.

Kramp, R. L., 1939. *The Godthaab expedition 1928. Chaetognatha.* Medd. Grönland, no. 80, part 5, pp. 1–44.

Kuhl, W., 1938. *Chaetognatha.* Browns Klassen. Ord. Tierreich iv(2), pp. 1–266.

Mackintosh, N. A., 1934. *Distribution of the Macroplankton in the Atlantic sector of the Antarctic.* 'Discovery' Rep. ix, pp. 65–160.

—— 1937. *The seasonal circulation of the Antarctic Macroplankton.* 'Discovery' Rep. xvi, pp. 365–412.

Marr, J. W. S., 1938. *On the operation of large Plankton nets.* 'Discovery' Rep. xviii, pp. 105–20.

Michael, E. L., 1911. *Classification and vertical distribution of the Chaetognatha of the San Diego Region.* Univ. Calif. Publ. Zool. viii, pp. 21–186.

—— 1919. *Report on the Chaetognatha of the Albatross expedition to the Philippines.* Bull. U.S. Nat. Mus. 100, 1, part 4, pp. 235–77.

Ommanney, F. D., 1936. *Rhincalanus gigas (Brady). A copepod of the Southern macroplankton.* 'Discovery' Rep. xiii, pp. 277–389.

Pierce, E. L., 1951. *The Chaetognatha of the West Coast of Florida.* Biol. Bull., Woods Hole, c, no. 3, pp. 206–28.

Ramoult, M. and Rose, M. 1946. *Récherches sur les Chétognathes de la baie d'Alger.* Bull. Hist. nat. Afr. N. xxxvi, pp. 45–71.

Ritter-Zahony, R., 1909. *Die Chätognathen der Gazelle-Expedition.* Zool. Anz. xxxiv, pp. 787–93.

—— 1911. *Revision der Chaetognathen.* Deutsche Südpolar Exped. xiii(5), pp. 1–71.

Russell, F. S., 1932. *On the biology of* Sagitta. *The breeding and growth of* S. elegans *in the Plymouth area 1930–31.* J. Mar. biol. Ass. U.K. xviii(1), pp. 131–45.

Steinhaus, O., 1900. *Chätognathen.* Ergebn. d. Hamb. Magalhaens. Sammelreise, iii, 10 pp.

Thiel, M. E., 1938. *Die Chaetognathen-Bevölkerung des südatlantischen Ozean,* xiii, no. 1. Wiss. Ergebn. dtsch. atlant. Exped. 'Meteor'.

Thomson, J. M., 1947. *The Chaetognatha of South-eastern Australia.* Bull. Coun. Sci. industr. Res. Aust. no. 222, pp. 1–43.

Tokioka, T., 1939. *Chaetognatha collected chiefly from the Bays of Sagami and Suruga with some notes on the shape and structure of the seminal vesicle.* Rec. Oceanogr. Wks. Jap. x, no. 2, pp. 123–50.

—— 1940. *A small collection of Chaetognaths from the coast of New South Wales.* Rec. Aust. Mus. xx, no. 6, pp. 367–79.

APPENDIX

Table 18. *Numbers of* Sagitta gazellae *taken in oblique* 1 *m. nets at a 24-hour station* (461)

461 *A*		461 *B*		461 *C*		461 *D*		461 *E*		461 *F*		Total
80–0	0	75–0	0	95–0	2	85–0	13	75–0	4	80–0	8	27
175–80	10	160–75	27	200–95	23	180–85	22	160–75	36	175–80	35	153
270–170	10	255–160	15	310–200	13	280–180	4	245–160	13	270–175	6	58
385–270	3	345–255	3	420–310	8	385–280	14	330–245	5	375–270	6	37
510–385	8	440–345	7	535–420	12	490–385	16	420–330	5	490–375	6	52
650–510	10	520–440	8	660–535	6	600–490	2	515–420	3	615–490	14	43

Table 19. *The numbers of* Sagitta gazellae *taken in the* 70 *cm. vertical nets on the meridian of* 0°, *numbers corrected for a* 250 *m. haul. Fig.* 22 *has been compiled from these data*

November–December

	2492	2494	2495	2496	2498	2501
50–0	60	5	0	0	0	0
100–50	125	10	0	0	15	30
250–100	3	10	0	0	2	0
500–250	0	1	0	4	2	0
750–500	0	0	0	1	1	0
1000–750	0	0	0	0	0	1
1500–1000	0	0	0	—	0	—

May–June

	1771	1772	1773	1774	1775	1776	1777	1778	1779	1781	1782
50–0	0	0	0	0	5	10	5	0	5	0	0
100–50	0	0	0	5	0	65	15	10	70	15	5
250–100	0	0	2	10	16	20	5	5	16	26	15
500–250	0	0	0	20	18	3	1	0	1	2	0
750–500	0	0	0	0	2	0	0	2	1	0	1
1000–750	0	0	0	0	1	0	0	0	0	0	1
1500–1000	0	0	1	0	1	0	0	1	—	0	0

January

	2530	2531	2532	2533	2535	2538	2541	2543	2545	2547
50–0	15	50	15	0	0	0	10	10	0	0
100–50	24	25	100	15	15	15	25	5	55	0
250–100	8	5	0	0	3	5	3	3	7	8
500–250	0	0	2	0	3	1	0	0	0	0
750–500	0	0	0	0	0	0	0	0	0	0
1000–750	2	1	0	0	0	1	0	0	0	0
1500–1000	1	1	—	1	1	—	0	0	0	0

July

	2355	2356	2357	2358	2359	2361
50–0	0	0	10	45	0	0
100–50	0	15	40	50	5	0
250–100	10	17	42	15	12	5
500–250	4	7	4	2	2	7
750–500	0	0	3	0	3	2
1000–750	0	0	0	0	3	1
1500–1000	1	0	0	1	0	1

March

	2027	2026	2025	2024	2023	2022	2020	2018	2017	2015	2014	2012	2010
50–0	0	0	5	30	5	15	0	0	0	0	0	30	10
100–50	0	10	25	90	10	5	0	20	20	10	35	35	35
250–100	0	3	12	8	10	7	10	12	7	3	3	3	5
500–250	0	1	2	1	1	5	3	1	0	1	0	1	0
750–500	0	0	0	0	0	0	2	2	0	0	0	0	0
1000–750	0	1	1	0	0	0	0	0	0	0	0	0	0
1500–1000	1	0	—	—	1	0	0	0	0	0	—	0	0

August

	2385	2386	2387	2389	2391	2393
50–0	0	0	0	0	0	0
100–50	0	0	5	0	0	0
250–100	17	40	17	9	12	19
500–250	5	0	1	7	6	1
750–500	0	0	0	3	0	0
1000–750	0	0	1	0	0	0
1500–1000	0	3	0	0	0	0

April

	2311	2313	2316	2318	2320	2322
50–0	5	0	20	10	0	0
100–50	0	0	95	15	20	10
250–100	22	5	7	7	9	17
500–250	6	9	1	4	1	3
750–500	1	5	0	1	0	0
1000–750	0	0	0	0	0	0
1500–1000	1	0	0	0	0	0

September

	1805	1806	1807	1808	1809	1810
50–0	0	0	20	60	25	10
100–50	0	5	15	60	25	10
250–100	0	0	0	15	10	5
500–250	1	0	0	0	1	0
750–500	0	0	0	0	0	0
1000–750	0	0	0	1	0	0
1500–1000	0	0	0	0	0	1

PLATE XIII

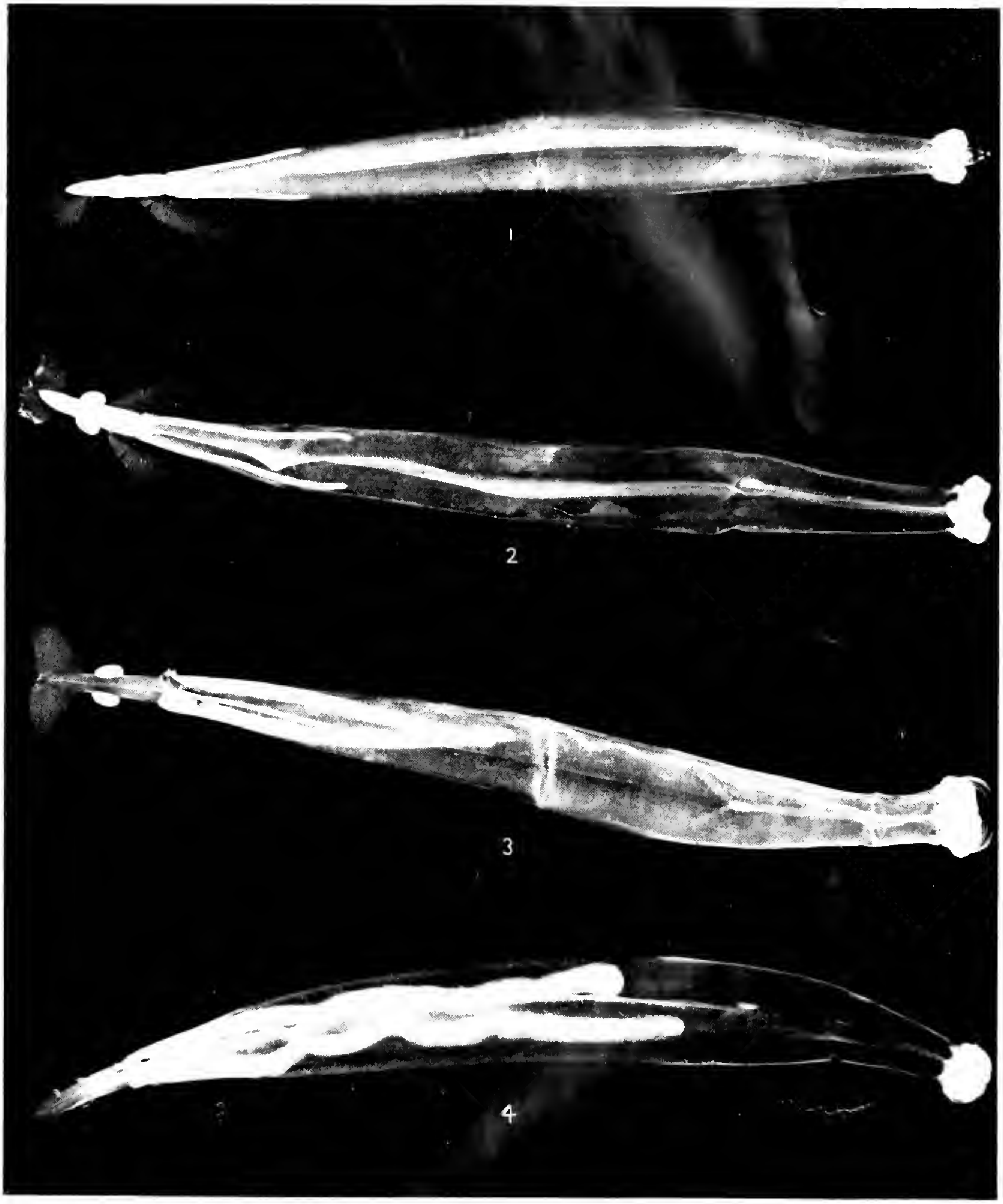
Development of the gonads in *Sagitta gazellae* Small Northern race.

Fig. 1. Late stage II, showing the opaque tail segment characteristic of the stage, rudimentary seminal vesicles and short thin ovaries.

Fig. 2. Stage II/III, a rare intermediate stage, the seminal vesicles are full sized but the tail segment is still opaque, the ovaries are still short and thin.

Fig. 3. Late stage III, the tail segment is empty and the seminal vesicles full, the ovaries are somewhat thickened.

Fig. 4. Late stage IV, the seminal vesicles have burst, and the ovaries are nearly fully developed.


1
2
3
4

[*Discovery Reports. Vol.* XXVII, *pp.* 279–291, *June*, 1955.]

CUMACEA OF THE BENGUELA CURRENT

By

N. S. JONES, Ph.D.
Marine Biological Station, Port Erin

CUMACEA OF THE BENGUELA CURRENT

By N. S. Jones, Ph.D.
Marine Biological Station, Port Erin

(Text-figs. 1–7)

INTRODUCTION

Through the kindness of Dr N. A. Mackintosh, Deputy Director of the National Institute of Oceanography, the Cumacea obtained by R.R.S. 'William Scoresby' during 1950 in the Benguela Current off the south-west coast of Africa were sent to me for examination. The ship made two surveys of the region in this year, in March and in September–October, and most of the material is from the first survey.

I am much indebted to Dr T. J. Hart of the National Institute of Oceanography for information and for sorting the Cumacea from the rest of the plankton.

The Cumacea described in this paper were obtained in the vertical plankton net hauls, but more specimens may be available when the horizontal catches have been sorted. Very large numbers of individuals—up to about 7700—were caught in some of the hauls. Cumacea were taken on the continental shelf at varying distances offshore, and in depths between 64 and 204 m. The rich hauls were all from depths of less than 150 m. and at distances of less than 30 miles from the coast. Full details are available in the Station List R.R.S. 'William Scoresby' (1950), 1953. Cumacea did not occur in nets fished at greater depths off the shelf. At all stations where oxygen determinations were made the O_2 concentration at the bottom was low.

The presence of Cumacea in large numbers in vertical nets was unexpected, and raises certain problems since they are normally bottom-living forms. When Cumacea have been caught in tow-nets at night, adult males have usually predominated, especially when attracted by artificial light, although in some recent records newly moulted adult or ovigerous females have outnumbered the males (Hale, 1953*b*). The hauls containing the largest numbers of specimens described here were made during the hours of darkness, but all stages and both sexes were present and there was not an unduly large proportion of adult males. It is possible that the presence of the animals in the upper layers was not due to normal vertical migration. Although the species present in these hauls may be able to live normally in the plankton, they show no special adaptations to this mode of life and their nearest relatives are coastal bottom-living forms and it may be that they have been forced up from the bottom by the low O_2 concentration, as Dr Hart has suggested to me. One would hardly expect them to inhabit the azoic mud which covers so much of the sea-floor in this region, but if they do not do so the alternative habitats are either the narrow bottom zone close inshore—which may be aerated by surf action—or else isolated patches surrounded by the so-called 'azoic zone' (Marchand, 1928; Currie, 1953; Copenhagen, 1953). On the other hand, the exceptionally large March haul of about 7700 individuals, which contained ovigerous females and adult males, as well as many juveniles, may represent a nuptial swarm (Forsman, 1938).

Five species were present, of which three are previously undescribed. They are *Bodotria glabra* sp.n., *Upselaspis* gen.n. *caparti* (Fage), *Iphinoe fagei* sp.n., *I. africana* Zimmer, and *Diastylis rufescens* sp.n. Of these, the two species of *Iphinoe*, particularly *I. fagei*, were much the most abundant and widespread.

The genus *Iphinoe* is apparently richest in species round the coasts of Africa. Of the seventeen so far described[1] the following occur on the west or south African coasts: *zimmeri* Stebbing, *robusta* Hansen, *brevipes* Hansen, *africana* Zimmer, *crassipes* Hansen, *hupferi* Zimmer, *brevidactyla* Hale and *truncata* Hale (Hale, 1953*a*), and *fagei* sp.n. described below. *I. trispinosa* (Goodsir), *inermis* G. O. Sars, *tenella* G. O. Sars, and *serrata* Norman are found in the Mediterranean and north-west European waters, and *trispinosa* and *tenella* have been taken off the Atlantic coast of Morocco (Fage, 1928). Only *I. sanguinea* Kemp from the Chilka Lake, *macrobrachium* Calman (possibly identical with *I. crassipes*) from the Gulf of Manaar, *calmani* Fage (Fage, 1945) from Assam, and *pellucida* Hale (Hale, 1944) from Tasmania and New South Wales have not been found near the African continent. It is probable, however, that further work will show the genus to be more widely spread in southern Asiatic waters also. Three species, *I. crassipes*, *brevipes* and *tenella*, have recently been reported from the coast of Travancore (Kurien, 1951).

Table 1. *Stations arranged from North to South, but not according to date*

Species	WS 970	WS 971	WS 980	WS 981	WS 982	WS 988	WS 989	WS 1063	WS 990	WS 1002	WS 1050
Bodotria glabra	7	2	—	—	—	—	—	—	—	—	—
Iphinoe africana	1	1	3	—	—	2	240	1	—	—	—
I. fagei	—	—	33	9	17	631	7450	88	24	—	—
Upselaspis caparti	—	—	—	42	1	—	—	—	—	—	—
Diastylis rufescens	—	—	—	—	—	—	—	—	—	26	3

There is evidently a succession of species from north to south among the Cumacea present in this collection (Table 1). *Bodotria glabra* occurred only at the most northerly stations at which Cumacea were caught, at 19° 44′ S, 12° 40′ E and 20° 11′ S, 12° 30′ E. *Iphinoe africana* also occurred at these stations and as far south as 25° 11′ S, 14° 39′ E. *I. fagei* was found from 22° 44′ S, 14° 08′ E to 25° 36′ S, 14° 24′ E. *Upselaspis caparti* was found only in the area of Walvis Bay, 22° 44′ S, 14° 08′ E., near to its original location reported by Fage. *Diastylis rufescens* was found only at the most southerly station, 28° 40′ S, 16° 14′ E, and it occurred in almost the same locality 8 months later.

Forsman (1938) described the stages in the life-history of *Diastylis rathkei* (Kröyer). The larger collections from the Benguela Current offer an abundant material for a study of this kind. I hope at a later date to compare the two *Iphinoe* species from this point of view with some other members of the genus in British waters.

SYSTEMATIC ACCOUNT

Family **BODOTRIIDAE**

Genus **Bodotria** Goodsir, 1843

Bodotria glabra sp.n. (Figs. 1 and 2).

OCCURRENCE:

St. WS 970, 100–0 m., 2♀♀ (1 ovig.), 5 juv., night station.
St. WS 971, 100–0 m., 1 ovig. ♀, 1 juv., night station.

Ovigerous female. Length 4·5 mm. Carapace about twice as long as high, $1\frac{1}{2}$ as long as broad; antero-lateral angle (antennal tooth) prominent and acute; dorsal carina faintly marked on carapace and pedigerous somites; lateral carinae slightly developed on each side of carapace, but not reaching to the posterior border; eye prominent, with lenses.

---

[1] Refer to Zimmer, 1942, except where other references are inserted.

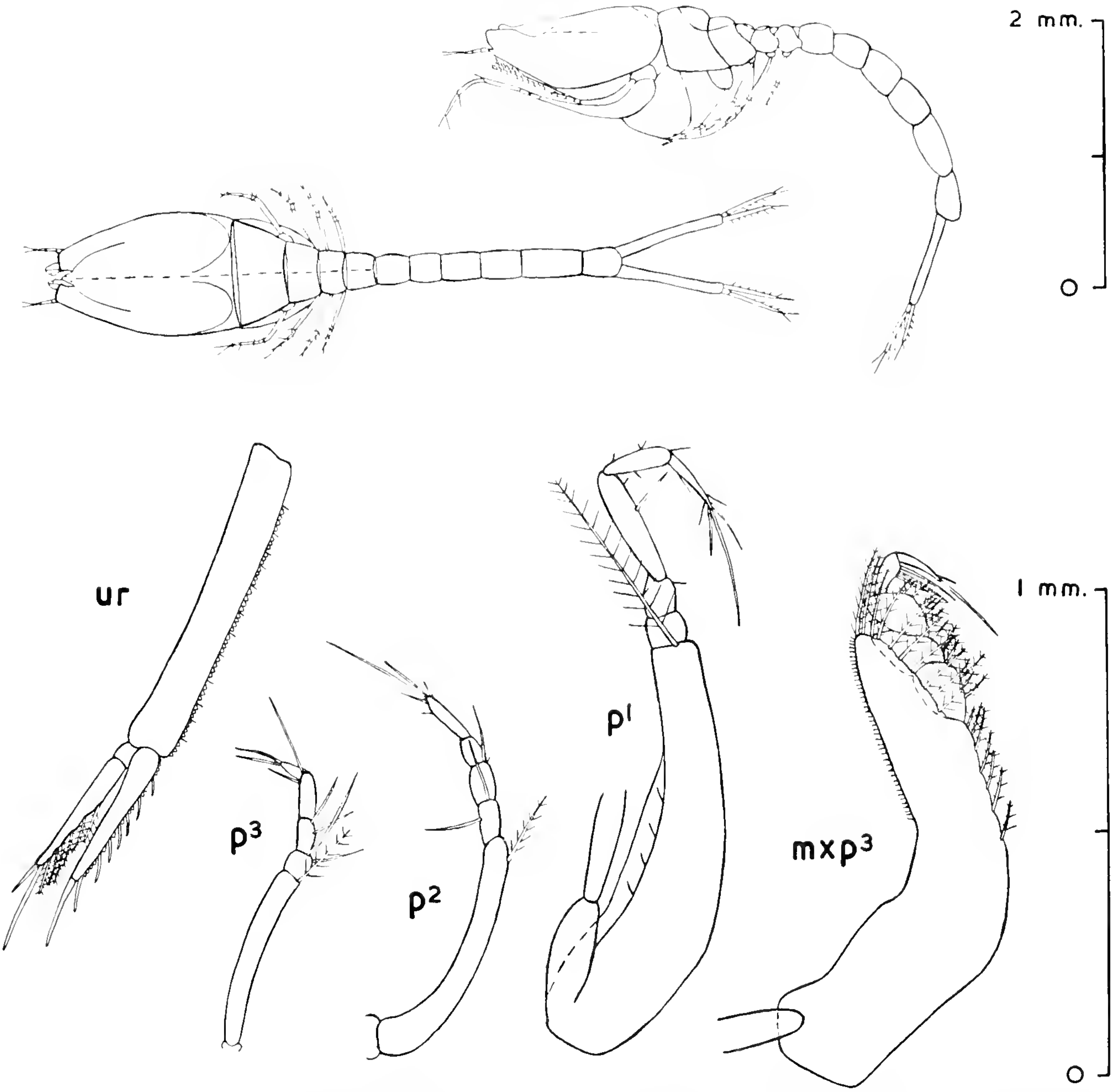


Fig. 1. *Bodotria glabra* sp.n. Paratype ovigerous female from the side and from above. p^1, p^2, p^3, first, second and third peraeopods; mxp^3, third maxilliped; *ur*, uropod.

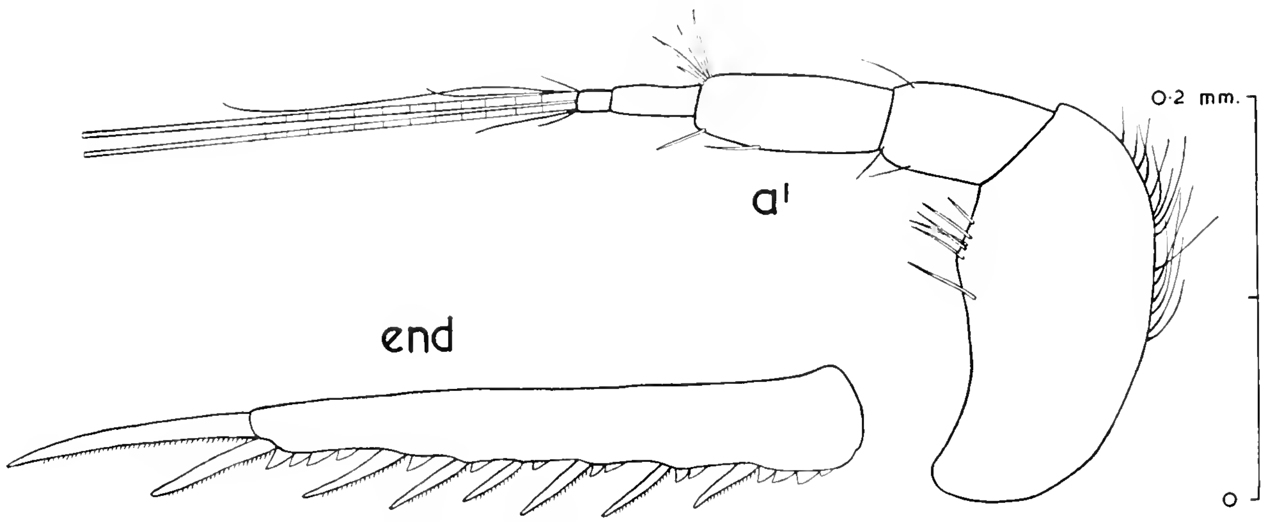


Fig. 2. *Bodotria glabra* sp.n. Paratype ovigerous female. a^1, first antenna; end, endopod of uropod.

First pedigerous somite concealed at the sides; the second somite long.

First antenna with two-jointed flagellum, bearing two aesthetascs; accessory flagellum rudimentary. Basis of third maxilliped twice as long as the remainder of the appendage, with its distal extension reaching to the end of the merus. First peraeopod with the last two joints reaching beyond the end of the pseudorostrum; basis about $1\frac{1}{4}$ as long as the remaining joints together; carpus nearly twice the length of the propodus, which is about the same length as the dactylus. Second peraeopod with six joints. Exopods present only on the first pair. Uropods slender, the peduncle about $2\frac{1}{4}$ as long as the rami, of which the exopod is slightly the longer; endopod one-jointed; the peduncle with hyaline serrations on the inner edge, interspersed with about twelve short setae; exopod with six plumose setae on the inner edge and ending in two spines; endopod with six spines interspersed with hyaline serrations on the inner edge, and two end spines.

Colour in alcohol, yellowish-white.

This species seems to be near to *B. siamensis* Calman, which it resembles in the absence of lateral ridges on the pedigerous somites, but the peduncle of the uropods is much longer in proportion to the rami and the second joint of the first peraeopod is longer than the rest of the appendage.

Genus **Upselaspis** gen.n.

Carapace smooth without carinae. First pedigerous somite not visible from above, the second not much longer than the following. First antenna with accessory flagellum. Only the first peraeopod provided with an exopod (male and female). The second peraeopod with the basis and ischium fused. The inner ramus of the uropod with two joints.

Upselaspis caparti (Fage).

Fage, 1951*b*, p. 5.

OCCURRENCE:

St. WS 981, 50–0 m., 19♂♂, 20♀♀ (2 ovig.), 3 juv., day station.
St. WS 982, 100–0 m., 1♂., day station.

This species was placed by Fage in the genus *Cyclaspoides* Bonnier, with the proviso that it might be necessary to propose a new genus for it when *C. sarsi* Bonnier became better known. I have examined three out of four specimens of *C. sarsi* from the British Museum (Natural History), for which I am indebted to Dr I. Gordon, and it seems to me that the differences between that species and Fage's species *U. caparti* are too great for them to be placed in the same genus. Fage lists a number of these differences (1951*b*, p. 9), to which may be added the following: *C. sarsi* is much more slender when viewed dorsally; the gut is coiled anteriorly, but is straight in *Upselaspis caparti*; the telsonic somite in *C. sarsi* is produced nearly half-way along the peduncle of the uropods, but is not produced in *U. caparti*; the endopod of the uropod in *C. sarsi* is one-jointed, ending in a spine much narrower than the breadth of the joint at its end, while I consider the endopod of *U. caparti* to be two-jointed, as Fage thought possible, because the second joint is almost as broad at its proximal end as the distal end of the first joint; its inner margin is finely serrated, and it ends in a spine, while in the male it bears two or three plumose setae on the inner edge proximally.

Generically the important difference between the two species is that in *Cyclaspoides sarsi* the first three pedigerous somites are fused with the carapace in both sexes, while in *Upselaspis caparti* only the first pedigerous somite is fused in the female and the first and second in the male.

Upselaspis is distinguished from *Cyclaspis* by the presence of six joints in the second peraeopod, and from *Bodotria* by the shorter second pedigerous somite.

The species was obtained in almost the same locality as the original find reported by Fage.

Genus **Iphinoe** Bate, 1865

Iphinoe fagei sp.n. (Figs. 3 and 4).

OCCURRENCE:

St. WS 980, 100–50 m., 2♂♂, 5♀♀ (2 ovig.), 9 juv.; 50–0 m., 2♂♂, 9♀♀ (1 ovig.), 6 juv., night station.
St. WS 981, 50–0 m., 1♀, 8 juv., day station.
St. WS 982, 100–0 m., 17 juv., day station.
St. WS 988, 100–50 m., 44 ♂♂, 237♀♀ (82 ovig.), 222 juv.; 50–0 m., 17♂♂, 70♀♀ (33 ovig.), 41 juv., night station.
St. WS 989, 50–0 m., 115♂♂, 36 ovig. ♀♀, *ca.* 7300♀♀ and juv., night station.
St. WS 990, 100–0 m., 1♂, 7♀♀, 16 juv., day station.
St. WS 1063, 50–0 m., 6♀♀, 82 juv., night station.

Ovigerous female. Length 8 mm. Body slender. Carapace rather less than twice as long as broad, slightly more than twice as long as high; upper surface slightly undulatory, with 0–5 small denticles set about one-third back from the front end; dorsal carina faint; pseudorostrum prominent in side view, rather blunt, with its edges slightly crenulated; antero-lateral angle prominent with a large tooth at the angle and several small teeth on either side; eyelobes broad, pointed in front, with distinct lenses, but not strongly pigmented.

The first antenna with the proximal joint the longest, the second longer than the third; the flagellum two-jointed, with one aesthetase and two long setae; accessory flagellum very small, one-jointed. Second antenna, mandible and maxillae as in *I. trispinosa* (Goodsir) (Sars, 1900). The third maxilliped with the basis more than $2\frac{1}{2}$ as long as the remaining joints together, with its prolongation reaching to the end of the prolongation of the merus.

Five pedigerous somites exposed. First peraeopod with the basis about as long as the remainder, its external border crenulated; the lower edge of the ischium with several small teeth. Second peraeopod about equal in length to the third, with the terminal joint longer than the two preceding joints. Last abdominal segment smoothly rounded posteriorly. The uropods longer than the last two segments of the abdomen; the peduncle longer than the subequal rami, with twenty-four spines on the inner border; the proximal joint of the endopod about half the length of the distal, with four and thirteen spines on their respective inner edges; the distal joint of the exopod armed on its inner edge with seven plumose setae and terminating in three spines.

Adult male. Length 7·5 mm. Carapace without teeth above, with the pseudorostrum less prominent than in the female; the antero-lateral corners rounded.

The second antenna reaching to the base of the uropods. The coxal plates of the first peraeopods with a smooth posterior border armed with several plumose setae, with a median tooth set just behind them on a broad tubercle on the second sternite. The basis of the second peraeopod with an internal spur. The third sternite with a broad median tubercle. The uropods relatively shorter than in the female, with a greater number of spines, more than forty, in two rows on the inner edge of the peduncle.

Colour, yellowish-white in alcohol.

This species resembles *I. trispinosa* in some respects, but is easily distinguished by its less slender carapace and blunter pseudorostrum; the dorsal teeth, when present, are set further forward on the carapace than in *trispinosa*; the eye is less prominent; the uropods in the female are more slender and have a greater number of spines on the peduncle; the prolongation of the basis of the third maxilliped reaches farther along the merus; in the male the armature of the thoracic sternites is more simplified (see Fage, 1951 *a*).

The other species of *Iphinoe* which have been recorded from the west coast of Africa comprise *I. africana* Zimmer and *I. brevipes* Hansen. The present species is at once distinguished from these

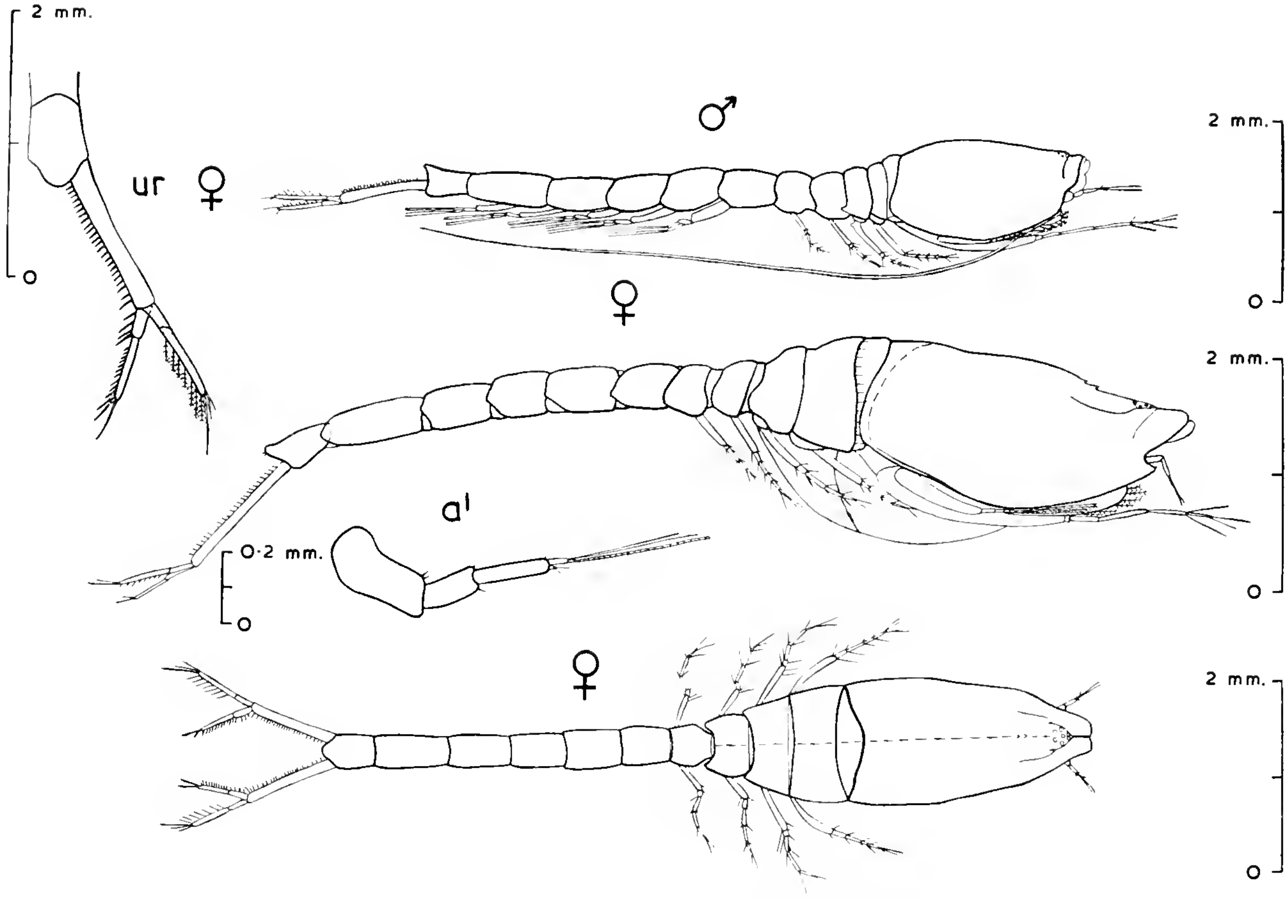


Fig. 3. *Iphinoe fagei* sp.n. Allotype adult male from the side; paratype ovigerous female from the side and from above. *a*¹, female first antenna; *ur*, female uropod.

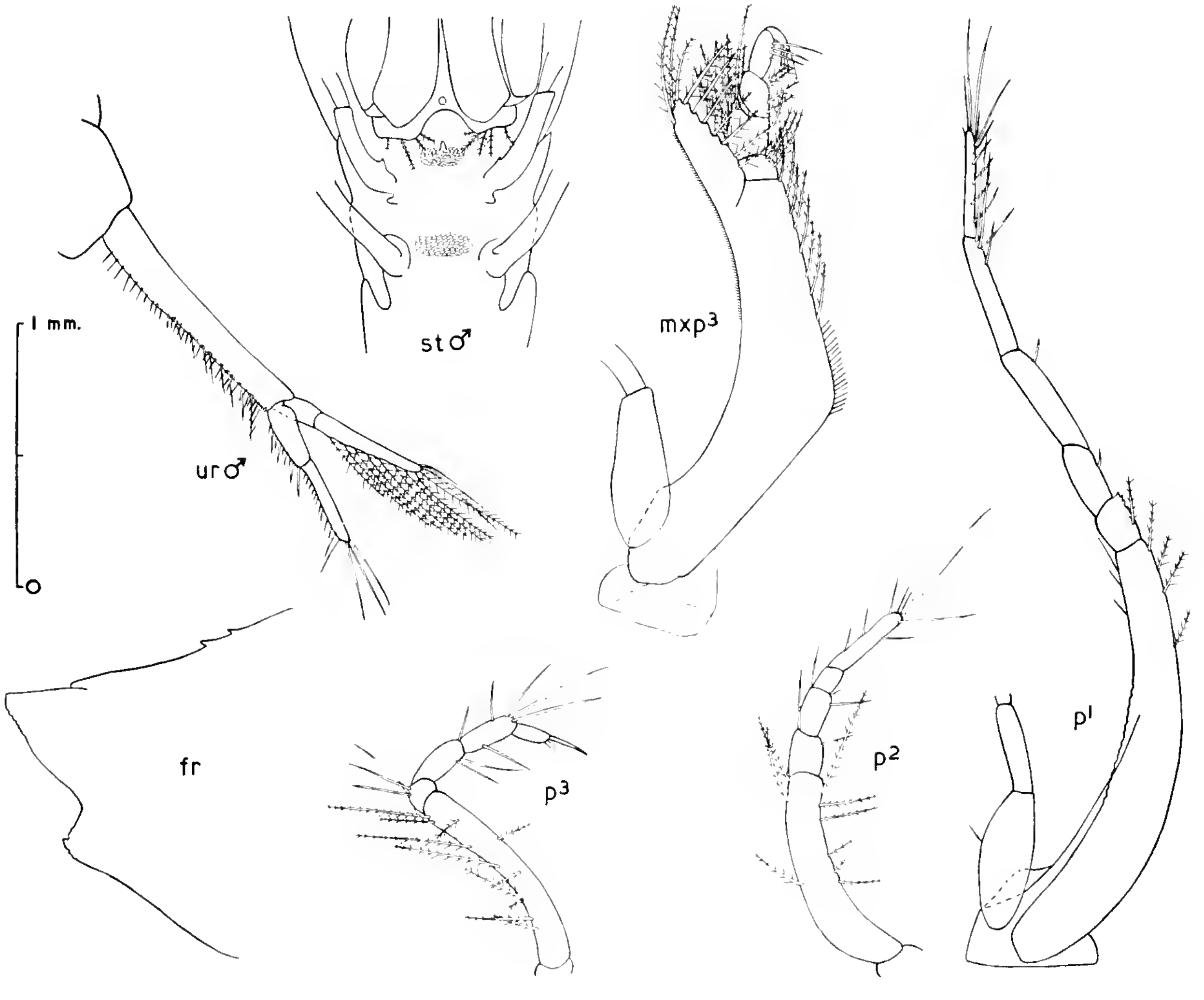


Fig. 4. *Iphinoe fagei* sp.n. Allotype adult male: *ur*, uropod; *st*, anterior thoracic sternites from below. Paratype ovigerous female: *fr*, front end of carapace from the side; *p*¹, *p*², *p*³, first second and third peraeopods; *mxp*³, third maxilliped.

by its second peraeopods, the shape of the pseudorostrum, and the telsonic somite. *I. crassipes* Hansen is peculiar in the development of the merus of the third maxilliped and in the proximal joint of the endopod of the uropod which is longer than the distal joint. *I. hupferi* Zimmer is a much smaller species (5 mm.) and has the proximal joint of the inner ramus of the uropod only a little shorter than the distal joint. *I. robusta* Hansen (female unknown) has in the male a number of lateral carinae on the thoracic and abdominal somites, while the pseudorostral lobes are very short. *I. zimmeri* Stebbing has only four free thoracic somites and is doubtfully referable to *Iphinoe*, and *I. brevidactyla* Hale and *I. truncata* Hale are both smaller species, *brevidactyla* having the endopod of the uropod with the first joint longer than the second, while in *truncata* the two joints are subequal.

The following key should enable the known species of *Iphinoe* to be distinguished from each other. Species which are doubtfully included in the genus, or about which further information is required, are enclosed within square brackets:

KEY TO SPECIES OF *IPHINOE*

1	Uropod with 1st joint of endopod shorter than 2nd.	2
	Uropod with 1st joint of endopod longer than 2nd or joints subequal.	13
2	Uropod with 1st joint of endopod only slightly shorter than 2nd.	3
	Uropod with 1st joint of endopod at most three quarter length of 2nd.	4
3	Antennal notch very shallow and antennal tooth of carapace not developed.	I. sanguinea
	Antennal notch and antennal tooth well developed, at least in ♀.	I. hupferi
4	Three pairs of lateral carinae present on last three pedigerous somites (♂).	[I. robusta]
	No lateral carinae.	5
5	Carpus of 3rd maxilliped widened distally on median side.	[I. zimmeri]
	Carpus of 3rd maxilliped not widened distally.	6
6	2nd peraeopod shorter than 3rd.	7
	2nd peraeopod as long as 3rd.	8
7	Pseudorostral lobes acutely produced anteriorly.	I. africana
	Pseudorostral lobes blunt anteriorly.	I. brevipes
8	Distal joint of 1st antenna with two aesthetascs.	9
	Distal joint of 1st antenna with one aesthetasc.	10
9	Exopod of uropod bearing setae on external side of distal joint.	I. calmani
	Exopod of uropod without setae on external side of distal joint.	I. serrata
10	Basis of 1st peraeopod shorter than remaining joints together.	I. tenella
	Basis of 1st peraeopod at least as long as remaining joints together.	11
11	Carapace less than twice as long as high.	I. inermis
	Carapace at least twice as long as high.	12
12	Prolongation of basis of 3rd maxilliped reaching to end of prolongation of merus.	I. fagei sp.n.
	Prolongation of basis of 3rd maxilliped not reaching to end of prolongation of merus.	I. trispinosa
13	Abdominal somites with lateral articular pegs.	I. pellucida
	Abdominal somites without articular pegs.	14
14	Merus of 3rd maxilliped produced in a broad lobe reaching beyond end of carpus.	15
	Merus of 3rd maxilliped not produced in a broad lobe.	16
15	Outer ramus of uropod shorter than inner.	[I. macrobrachium]
	Rami of uropods subequal.	I. crassipes
16	Dactylus of peraeopods 3–5 very short, about one-sixth length of carpus.	I. brevidactyla
	Dactylus of peraeopods 3–5 longer, about half length of carpus.	17
17	Carapace with mid-dorsal serrations.	I. tenella var.
	Carapace without mid-dorsal serrations.	I. truncata

The damaged specimen mentioned by Fage (1951*b*) may probably be referred to the new species described here.

Iphinoe africana Zimmer.

Zimmer, 1908, p. 163.

Occurrence:

St. WS 970, 100–0 m., 1♀, night station.
St. WS 971, 100–0 m., 1 juv., night station.
St. WS 980, 100–50 m., 1♀; 50–0 m., 1♂, 1♀, night station.
St. WS 988, 50–0 m., 1♂, 1 ovig. ♀., night station.
St. WS 989, 50–0 m., 8♂♂, 3 ovig. ♀♀, *ca.* 230♀ and juv., night station.
St. WS 1063, 50–0 m., 1♂, night station.

Stebbing (1913) considered *I. africana* to be synonymous with *I. brevipes* Hansen (Hansen, 1895). However, Zimmer (1942) pointed out that there were well-marked differences between the females, and Fage (1951*b*) was able to confirm these differences for the males. The females in these collections differ from Zimmer's description in that they have from 0–5 small teeth on the dorsal crest of the carapace, and not 13–14, but I am able to confirm the other differences mentioned by Zimmer between *brevipes* and *africana*, as I have examined several specimens of *brevipes* from the British Museum (Natural History).

Fig. 5. Front end of carapace from the side of *br*, *Iphinoe brevipes*, adult female, and *af*, *Iphinoe africana*, ovigerous female.

In *I. africana* the front of the carapace is distinctly toothed above the antero-lateral angle, and there are subsidiary teeth on either side of the central tooth on the hinder end of the telsonic somite. In *I. brevipes* the front of the carapace shows only slight serrations, while there are two central teeth on the telsonic somite. In addition the front of the carapace is a different shape in the adults of the two species (Fig. 5).

Family DIASTYLIDAE

Genus Diastylis Say, 1818

Diastylis rufescens sp.n. (Figs. 6 and 7).

Occurrence:

St. WS 1002, 50–0 m., 1♂, 8♀♀, 17 juv., night station.
St. WS 1050, 50–0 m., 1♂, 2♀♀, night station.

Adult female. Length 8·5 mm. Carapace similar in form to that of *D. laevis* Norman (Sars, 1900, as *D. rostrata*); surface smooth with scattered hairs; antero-lateral angle not very prominent, with fine serrations extending some distance posteriorly; carapace about $2\frac{1}{3}$ as long as high, $1\frac{1}{2}$ as long as broad. Eye well developed.

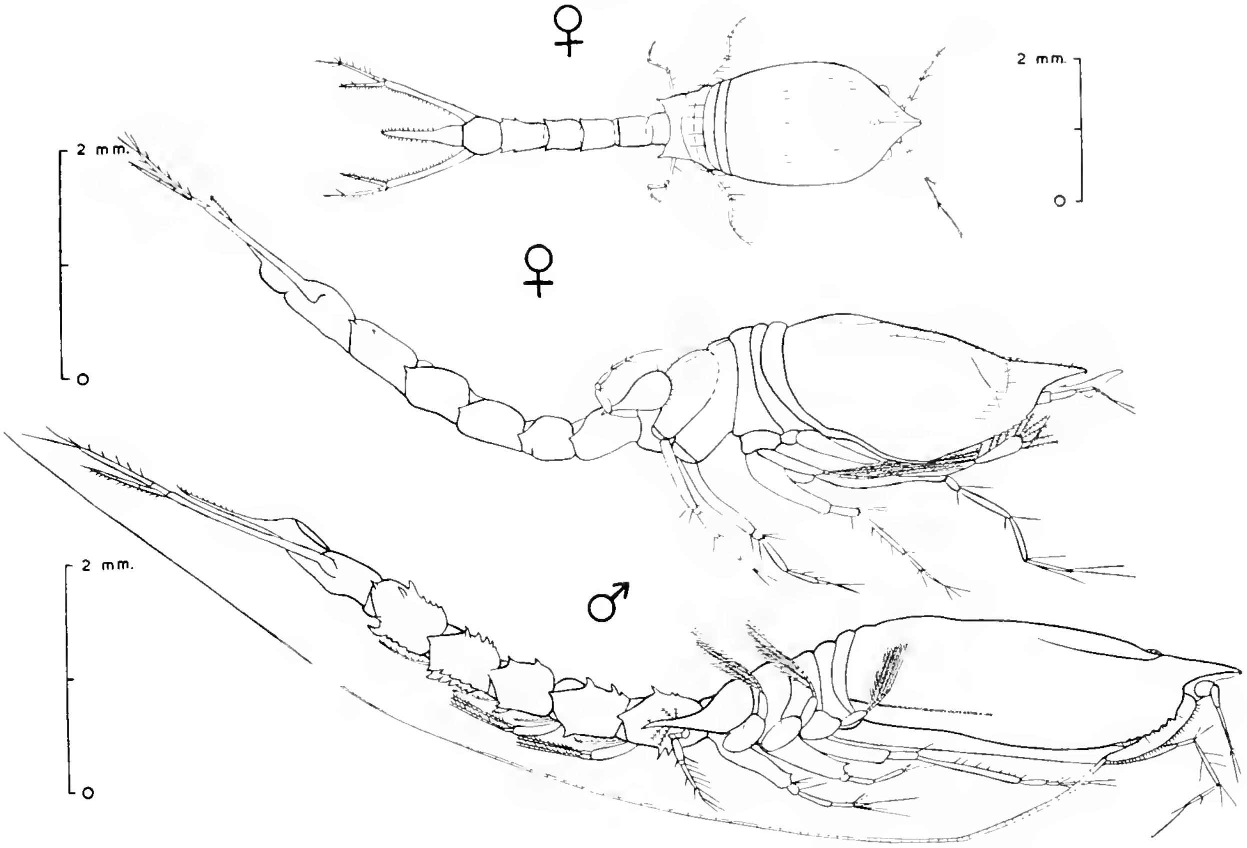


Fig. 6. *Diastylis rufescens* sp.n. Paratype adult female from above and from the side; allotype adult male from the side.

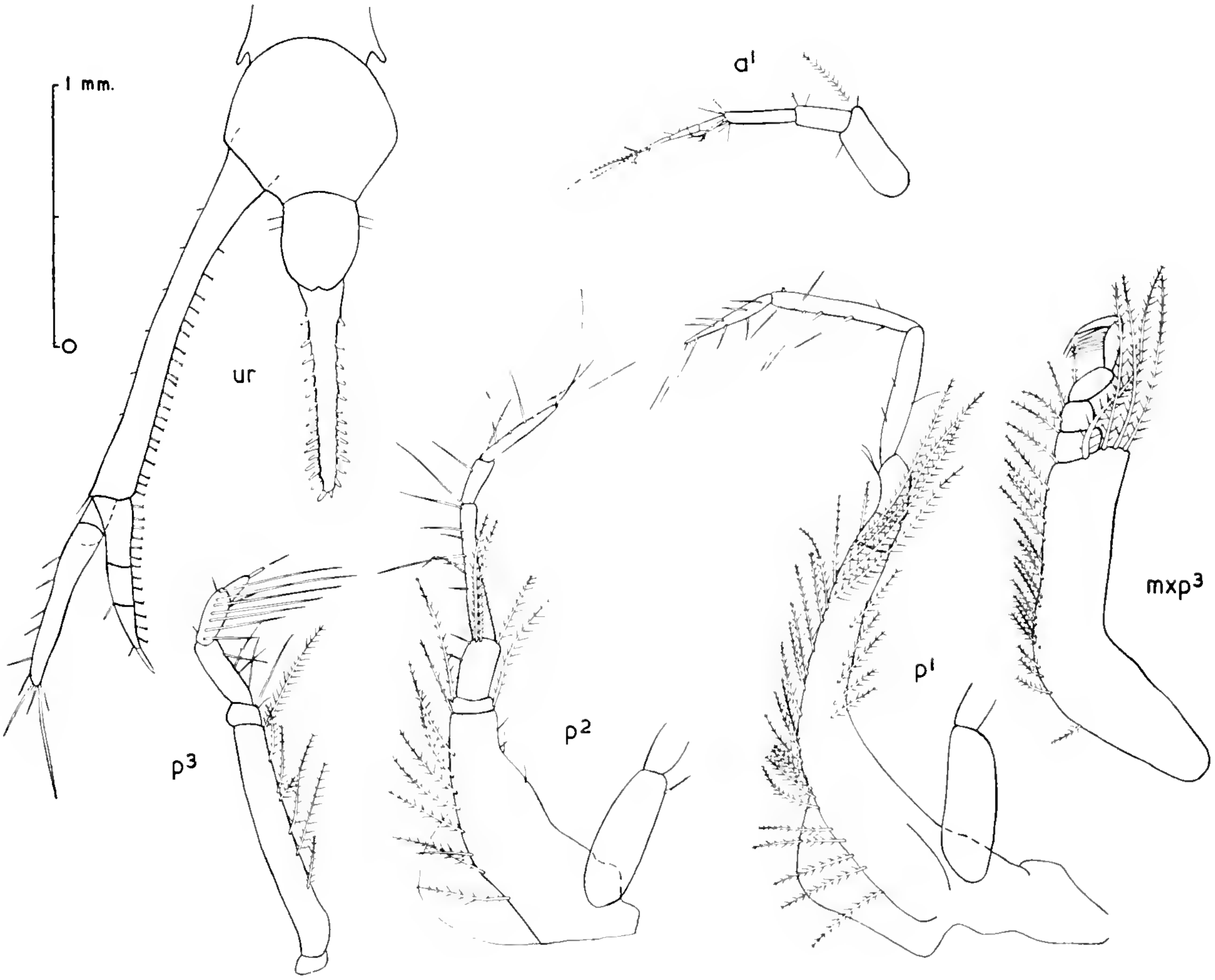


Fig. 7. *Diastylis rufescens* sp.n. Paratype adult female. a^1, first antenna; p^1, p^2, p^3, first second and third, peraeopods; mxp^3, third maxilliped; *ur*, telson and left uropod.

Third and fourth pedigerous somites divided dorsally only by a suture line, the fifth with its anterior border finely serrate, and with the sides acutely produced rearwards, reaching half-way along the first pleon somite.

Fifth pleon somite with the sides produced at the posterior end to form a prominent tooth, with one or two smaller teeth set on each side anteriorly. The telson about as long as the fifth and sixth pleon somites combined, the distal section twice as long as the proximal, with thirteen pairs of lateral and two terminal spines.

The first antenna with the second joint of the peduncle the shortest; principal flagellum with four joints, ending in two aesthetascs; accessory flagellum three-jointed. Second antenna and mouthparts as in *D. laevis*.

The first peraeopod with the second joint shorter than the rest of the appendage, without spines. The second peraeopod with the fifth joint about as long as the sixth and seventh combined; the third joint with two small teeth on the lower edge. No exopods on the third and fourth pairs. The peduncle of the uropods longer than the telson, with about twenty spines on the inner edge; the exopod longer than the endopod; the endopod with the first joint shorter than the second and third combined, with 7.3.3 spines on its inner margin.

Adult male. Length 10 mm. Carapace longer than in female, three times as long as high; anterolateral corners rather more produced, with about five more prominent teeth. On each side there is a carina extending forward about two-fifths of the length; carapace otherwise smooth, without oblique transverse folds. The fifth pedigerous somite more produced behind than in the female. The pleon somites armed with prominent spines. The flagellum of the second antenna reaching beyond the uropods.

Colour of the female yellowish-white; the male similar with reddish-brown pigment in the basal joints of the peraeopods, especially in the exopods, and in the pleopods, and with two lateral spots on the first pleon somite.

The species is rather similar in general form to *D. laevis*, but may easily be distinguished by the more prominent backward projection of the fifth pedigerous somite and by the spines at the sides of the fifth pleon somite; in the male it differs in the absence of oblique folds on the carapace and in the presence of pigment which is fast for some time in alcohol. From *D. algoae* Zimmer it is easily distinguished by the absence of an emargination in the pseudorostrum of the female, by the shape of the carapace, and by several details of the appendages.

REFERENCES

BATE, S., 1856. *On the British Diastylidae.* Ann. nat. Hist. (2), XVIII, p. 157.

BONNIER, J., 1896. *Edriophthalmes.* Rés. scient. Camp. du 'Caudan'. Ann. Univ. Lyon, XXVI, pp. 527–689.

COPENHAGEN, W. J., 1953. *The periodic mortality of fish in the Walvis region.* Fish. Div., Dept. of Commerce and Industries, Union of S. Africa, Invest. Rep. XIV, pp. 1–35.

CURRIE, R. I., 1953. *Upwelling in the Benguela Current.* Nature, CLXXI, pp. 497–505.

FAGE, L., 1928. *Cumacés de la côte atlantique du Maroc.* Bull. Soc. sci. nat. Maroc, VIII, pp. 173–81.

FAGE, L., 1945. *Les Cumacés du plancton nocturne des côtes d'Annam.* Arch. Zool. exp. et gén. LXXXIV, pp. 165–224.

FAGE, L., 1951*a*. *Cumacés.* Faune de France, LIV, pp. 1–136.

FAGE, L., 1951*b*. *Cumacés.* Exp. océanogr. Belge dans les Eaux côtieres africaines de l'Atlantique Sud (1948–1949), III, fasc. 1, pp. 1–9.

FORSMAN, B., 1938. *Untersuchungen über die Cumaceen des Skageraks.* Zool. Bid. fr. Uppsala, XVIII, pp. 1–161.

GOODSIR, H., 1843. *Description of the genus* Cuma *and of two new genera nearly allied to it.* Edinb. new phil. Journ. XXXIV, pp. 119–80.

HALE, H. M., 1944. *Australian Cumacea. No. 8. The family Bodotriidae.* Trans. Roy. Soc. S. Australia, LXVIII, pp. 225–85.

HALE, H. M., 1953*a*. *Two new Cumacea from South Africa.* Trans. Roy. Soc. S. Australia, LXXVI, pp. 45–50.

HALE, H. M., 1953*b*. *Australian Cumacea. No. 18. Notes on distribution and night collecting with artificial light.* Trans. Roy. Soc. S. Australia, LXXVI, pp. 70–6.

HANSEN, H. J., 1895. *Isopoden, Cumaceen u. Stomatopoden der Plankton-Expedition.* Plankton-Exp. II, pp. 1–105.

KURIEN, C. V., 1951. *The Cumacea of Travancore.* Bull. Central Res. Inst., Univ. Travancore, Ser. C. II, pp. 77–118.

MARCHAND, J. M., 1928. *The nature of the sea-floor deposits in certain regions of the West Coast.* Fish. and Mar. Biol. Surv., Union of S. Africa, Special Rep. No. 5, pp. 1–11, Rep. No. 6.

SARS, G. O., 1900. *Cumacea.* Crustacea of Norway, III, pp. 1–115.

SAY, T., 1818. *An account of the Crustacea of the U.S.* J. Ac. nat. Soc. Philad. I, pp. 313–19.

STATION LIST R.R.S. 'WILLIAM SCORESBY' 1950, 1953. Discovery Reps. XXVI, pp. 211–58.

STEBBING, R. T. R., 1913. *Cumacea (Sympoda).* Das Tierreich, XXXIX, pp. 1–210.

ZIMMER, C., 1908. *Die Cumaceen der Deutschen Tiefsee-Expedition.* Ergebn. Dtsch. Tiefsee-Exp. VIII, pp. 157–96.

ZIMMER, C., 1942. *Die Gattung* Iphinoe *(Ord. Cumacea, Fam. Bodotriidae).* Zool. Anz. CXXXIX, pp. 190–200.

[*Discovery Reports. Vol. XXVII, pp.* 293–302, *Plates XIV–XVIII, July*, 1955.]

THE WAX PLUG IN THE EXTERNAL AUDITORY MEATUS OF THE MYSTICETI

By

P. E. PURVES
Department of Zoology, British Museum
(Natural History)

CONTENTS

THE WAX PLUG IN THE EXTERNAL AUDITORY MEATUS OF THE MYSTICETI

By P. E. Purves

Department of Zoology, British Museum
(Natural History)

(*Received* 9 *March* 1955)

(Plates XIV–XVIII; Text-figs. 1, 2)

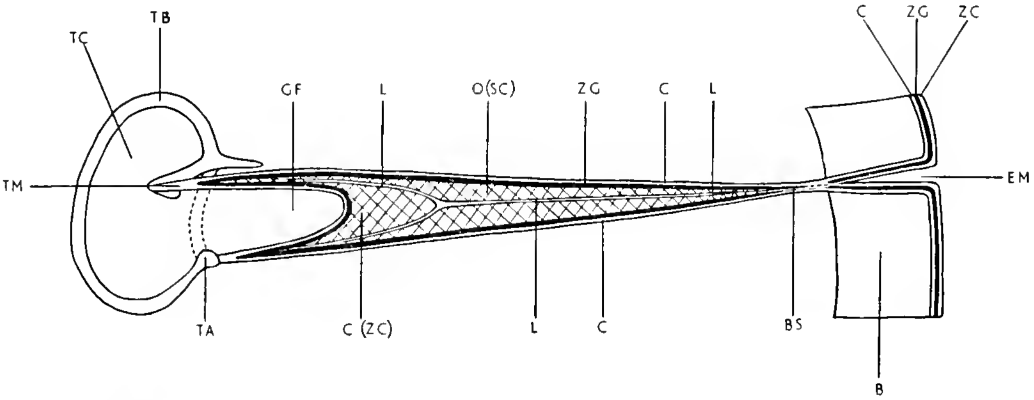
INTRODUCTION

The external auditory meatus of the Cetacea, because of its extreme smallness, seems to have attracted the attention of anatomists since the earliest times, and various descriptions exist of its external form, anatomy and histology. Buchanan (1828), who appears to have been a specialist in the subject of the ceruminous secretions of the ear, discovered in the meatus of *Balaena mysticetus* an 'unctuous cerumen of a greyish blue colour', and Carte and Macalister (1869) stated that the meatus of *Balaenoptera acutorostrata* was 'filled with a dark, greyish sebaceous substance, produced in ceruminous glands, the openings of which were visible on the mucous membrane'. These descriptions seem to indicate that the anatomists just mentioned were concerned only with the soft, pigmented secretion which is to be found abundantly in the distal parts of the meatus of all the larger Cetacea. Lillie (1910) made a detailed study of the whole length of the auditory meatus of several of the larger Cetacea during his researches at the Whaling Station at Inniskea in the west of Ireland, and found that in the 'meatus of all individuals examined there was a solid plug of wax-like substance of fairly definite size and shape, which did not seem to have been hitherto described'. Turner (1913) gave an account of a number of wax plugs from *Megaptera longimana* and *Balaenoptera physalus* which came into his possession, and the descriptions and figures agree very closely with Lillie's original account of the wax plug of the latter species. That Turner wrongly imagined the plug to be secreted by the distal end of the meatus was pointed out by Lillie (1915).

In the course of their investigations on the sense of hearing in the Cetaceans, Fraser and Purves (1954) found it necessary to test the sound conductivity of the external meatus and adjacent structures in the Mysticeti, and were able, through the generosity of the Hector Whaling Company, and the co-operation of the National Institute of Oceanography, to obtain during 1953 and 1954 two large frozen portions of the squamo-mastoid region of *Balaenoptera physalus*. The external meatus was laid open along its entire length, and although the wax plugs of both specimens were badly damaged, sufficient material remained to indicate that Lillie's and Turner's description requires some modification. The sound attenuation of this apparently highly damping substance was found to be less than 1 db. throughout its length, and this surprising result led to a closer examination of the structure as a whole. Microscopic sections were cut from fragments taken from the two specimens of *Balaenoptera physalus*, and two of Lillie's three specimens from this species were radiographed, the remaining specimen being bisected longitudinally at its widest diameter.

LOCATION OF THE WAX PLUG

It has long been supposed that the external meatus of the larger Cetacea is closed for a short distance immediately below the blubber, and that more proximally its lumen opens out again and widens gradually until it terminates in the glove-finger-like structure, which protrudes from the tympanic bulla. That this statement is inaccurate, and that the structure identified by Lillie and others as the epidermis of the meatus is only the corium of the latter, will be seen during the course of the description of the wax plug (see Text-fig. 1). It is not surprising that this part of the meatus has escaped the attention of most Cetacean anatomists since Lillie, for it lies in a deep groove between the squamosal and paroccipital process, and is invested in nearly a foot thickness of tough, fibrous tissue. More distally, near the 'blind' section, the meatus protrudes beyond the lateral limit of the bones, and its lumen is flattened dorso-ventrally so that the dorsal and ventral walls are nearly in apposition. The corium of the superior wall of the proximal part of the meatus conforms with the shape of its adjacent bones, and is sharply convex on its dorsal aspect. Ventrally the corium of this part of the meatus is not covered by bone and is thus, in the living animal, subjected to pressure transmitted through the fibrous tissues. The ventral aspect of the corium is consequently slightly concave and its upper surface bulges towards the lumen of the meatus.



Text-fig. 1. Diagram showing the inter-relationships of the tympanic cavity, external meatus and epidermis in a typical Mysticete. The space occupied by the wax plug is cross-hatched. *TC*, tympanic cavity; *TB*, tympanic bulla; *TM*, tympanic membrane; *TA*, tympanic annulus; *GF*, glove-finger; *C*(*ZC*), core of the wax plug or the zona cornea of the epidermis of the glove-finger; *O*(*SC*), outer covering of the wax plug or the stratum corneum of the epidermis of the external auditory meatus; *L*, lumen of the external auditory meatus; *C*, corium of the dermis; *ZG*, zona germinativa of the epidermis; *ZC*, zona cornea of the epidermis; *EM*, external auditory meatus; *BS*, 'blind' section; *B*, blubber.

The 'glove-finger' has frequently been referred to as the tympanic membrane, but, for reasons which they state, Fraser and Purves (1954) disagree with this interpretation. The homologue of the tympanic membrane is the triangular ligament which is inserted into the manubrium of the malleus. This ligament has a deep but very narrow concavity on its lateral aspect which is continuous with the external meatus, and is thus not fundamentally different from the tympanic membrane of the Odontoceti and other mammals. Between the glove-finger and the tympanic annulus there is another circular concavity which is also continuous with the meatus. The concavity in the tympanic ligament, that which encircles the glove-finger and the whole length of the auditory meatus from the tympanic annulus to the constricted lateral extremity, is filled by the wax plug. A section (Pl. XV, fig. 2) taken near the centre of the so-called blind section in *Balaenoptera acutorostrata* shows that in this species the lumen is not entirely closed, and that it is surrounded by concretions of a waxy consistency. The plug is, therefore, not limited to the dimensions given by Lillie and Turner, but may be a metre or more in length, depending upon the size of the animal. The specimen under examination measured 60 cm. The attenuated distal extremity of the plug is so flattened dorso-ventrally that it is extremely fragile and delicate, and there is little doubt that it had become detached from Lillie's and Turner's specimens before these were described.

The proximal portion of the wax plug takes the form of an elongated, slightly curved and laterally compressed cone, the base of which is deeply concave and drawn out peripherally into a delicate skirt, one side of the latter being longer and more attenuated than the other. One aspect of the external surface is sharply convex and another slightly concave and presenting a fluted appearance. In short, the wax plug is an internal cast of the corium of the external auditory meatus. In addition to the above features the whole surface of the plug is marked by a series of minute grooves running parallel with its long axis which are the external manifestation of the complicated pleating of its internal structure. The concave surface of the base, which is moulded to the glove-finger, presents a coarsely pitted appearance, the significance of which will appear during the description of the histology of the plug.

STRUCTURE AND COMPOSITION

The radiograph, Pl. XIV, fig. 1, and the photograph of the bisected specimen, Pl. XIV, fig. 2, of the wax plug show that its constituent material is differentiated into two distinct components, one of which can be regarded as the outer covering and the other as the core of the plug. The outer covering comprises the whole of the attenuated distal end of the cone as well as the thin, superficial layer which surrounds the base and extends round the outside of the latter's skirt-like margin. The cut face of this component of the plug is marked by a number of coarse striations, which run approximately parallel with the long axis of the cone.

The core is a more bluntly conical structure and forms the greater part of the stout, basal part of the plug, its concave mesial aspect being contiguous with and fitting over the lateral end of the glove-finger. Examination of the cut surface shows that the material of the core is arranged in a series of conspicuous laminations, those nearest the base being concentric with the latter, and approximately semicircular in form. More distally the laminations become thicker and semi-eliptical, and eventually sharply convex to conform in shape with the apex of the cone. The whole series of laminations appears as a number of alternate bands of light- and dark-coloured material, the colours being the macroscopic expression of an alternating histological structure.

Microscopic examination shows that the two components just described are of different origin, the outer covering being derived from the lining of the meatus and the core from the external surface of the glove-finger. Pl. XV, fig. 4, which is a photomicrograph of a transverse section taken from the apex of the outer covering of the plug, shows that the name 'wax plug' is really a misnomer, since the lipoids, which have been dissolved out of the section, occupy only a small part of the total bulk of material. The principal mass consists of a very large number of layers of squamous epithelium arranged in sinuous folds which appear to correspond in position with the longitudinal ridges on the internal wall of the auditory meatus. The squamae of epithelium are all fully keratinized and show none of the earlier stages of cellular change which are normally to be found when this type of epithelium is examined *in situ* on the epidermis.

The photomicrographs, Pl. XVI, figs. 1 and 2, are of transverse and longitudinal sections respectively of the basal part of the core of the plug. The transverse section shows the squamous epithelium arranged not in sinuous folds but in a mosaic of irregularly shaped islets separated from each other by a reticulation of apparently empty spaces. Each islet, Pl. XVII, fig. 4, consists of a central mass of fusiform cells with large degenerate nuclei surrounded by a number of concentrically arranged layers of a homogenous or coarsely striated substance which may contain darkly stained flattened nuclei. Encircling the whole group of islets can be seen the sinuous squamae of the fully keratinized epithelium of the outer covering of the plug. From the macroscopic appearance of the base of the plug it would appear that the spaces between the islets were filled with lipoids and that these have been dissolved out of the section.

The longitudinal section, Pl. XVI, fig. 2, is taken through the first two concentric laminations of that part of the plug which is contiguous with the glove-finger. Comparing the appearance with that of the transverse section described above it will be seen that the islets constitute the cross-section of a series of columns of tissue which are separated from each other by undulating fissures. The first and second laminae are discontinuous, so that two sets of tissue columns appear separated by a space which is partly filled by a layer of keratinized epithelium. The structure of the tissue is markedly different in the two laminae (Pl. XVII, figs. 1 and 2) the first set of columns containing layers of the type of cells which were distinguished in the transverse sections. In the second lamina the curvature of the tissue layers is completely reversed and the spaces between the columns are partly filled by a great number of squamae of keratinized epithelium derived from the central masses of cells which are more degenerate than those of the first lamina.

The general structure of the transverse and longitudinal sections of the core of the plug indicates that the epithelium is generated from the numerous small papillae which are plainly visible on the end of the glove-finger. It is unfortunate that no properly fixed material was available for examination of the soft parts of the meatus and glove-finger, and the sections shown in Pl. XV, fig. 1 and Pl. XVII, fig. 3, show only the corium of these two structures respectively. Ceruminous or sweat glands are virtually absent from the section of the corium of the meatus but very abundant in the section taken through that of one of the papillae on the glove-finger. It is possible that these glands, if present in the meatus, are located in definite areas, although it would not be surprising if they were absent altogether. The ceruminous glands of the glove-finger are even more plentiful in areas other than that shown in the figure.

The homology of the various structures referred to above is not difficult to find when it is remembered that the external meatus and the glove-finger (the pars flaccida of the tympanic membrane) are formed from an involution of the epidermis. Considering first the distal part of the wax plug, it was found that the latter was composed of a great number of layers of keratinized epithelium containing no nuclei and that between the layers there was a series of filamentous interstices which were presumably filled with lipoid. This type of structure is characteristic of the whole of the outer covering of the wax plug and apparently constitutes the stratum corneum of the epidermis of the external auditory meatus. Ranvier, according to Gray (1946), found in the stratum corneum of man granules of a substance which had the characteristics of bees-wax.

Considering next the structure of the core of the plug, it was found that macroscopically the material was divided into a number of discrete concentric laminations and that each lamination consisted of a series of columns of tissue which were presumably generated from papillae on the end of the glove-finger. Each column of tissue in the first lamination consisted of layers of fusiform nucleated cells of a granular appearance followed by homogenous or coarsely striated layers containing darkly stained flattened nuclei, the whole being surmounted by a layer of keratinized epithelium. The entire system of cells gives the appearance of being the strata granulosum, lucidum and corneum, i.e. the zona cornea of the epidermis of the glove-finger. The cells show the characteristic appearance associated with progressive keratinization, the granules probably being the intermediate substance eleidin. The sinuous fissures between the columns of tissue are reminiscent of the spirally coiled ducts of ceruminous or modified sweat glands. The second lamination shows the same type of structure except that the cells are less differentiated, and the granular substance is augmented; a great amount of keratinized squamous epithelium appears between the columns of tissue as well as at their distal extremities.

From the above description it may be concluded that the lumen of the meatus lies on the central axis of the wax plug, but is completely occluded by the stratum corneum of the epidermis of the meatus. The wax plug is, therefore, not merely an amorphous secretion but an intrinsic part of the meatus. The stratum granulosum of the external meatus and the zona germinativa, which is highly vascular and subject to rapid decomposition after the death of the animal, are presumably to be looked for on the outer surface of the plug.

A biochemical analysis of a fragment of the wax plug showed that it contained only 42·5% total lipoid, approximately half the quantity obtained from human ear wax, which contained 88%. The analysis of the lipoids from whale and human ear wax is given below for comparison. The cholesterol and squalene are included in the figures for total unsaponifiable matter. The comparatively large amount of cholesterol is particularly noteworthy, since the figure given above is likely to be much lower than the amount actually present in the wax plug of the living animal. The alcohol in which Lillie's specimens were preserved contained a great number of large triclinic crystals of this substance and the specimens themselves, when removed and partly dried, displayed a glistening surface-covering of small crystals.

	Whale ear wax (%)	Human ear wax (%)
Total fatty acid	32·8	61·3–73·0
Unsaponifiable matter	67·2	27·0–39·7
Total cholesterol	54·4	12·1–17·1
Squalene	Nil	1·0–12·0

DISCUSSION

The above description of the histological and biochemical nature of the wax plug of the Mysticeti shows that it is composed largely of solids with a maximum of 14% soft fatty acids and thus resembles only very slightly and is not homologous with the ear wax of the human subject in which the proportion of fatty acid may be five times as great. The keratinized squamae of epithelium are so closely compacted that the structure can be said to be of a horny rather than waxy consistency, and it would appear that the concentric layers of tissue are more or less continuous from the blind end of the external meatus to the tympanic annulus. Although macroscopically the core of the plug appears to consist of transverse laminations, the microscopic arrangement of the keratin is in the form of columns of tissue in which the squamae of epithelium are predominantly parallel with the long axis of the plug. The matrix, in which the squamae of keratin are embedded, is composed almost entirely of crystalline cholesterol which is known to be able to absorb a considerable amount of water without going into solution, and is well known for the formation of stony concretions in other parts of the body, e.g. gall stones.

In view of the great amount of solid material present, it is not surprising that the wax plug is a good conductor of sound, especially of high-frequency vibrations. During their experiments on the transmission of sound through various organic tissues, Fraser and Purves, found that vibrations conducted along an axis parallel with the direction of longitudinal fibres suffered much less attenuation than those transmitted across the fibres, even though the difference between the acoustic resistances of the fibres and their interstitial substances was very small. This phenomenon was well demonstrated in the case of red muscle, the external meatus, the wax plug and wood, the latter two substances being broadly similar in structure.

Before attempting to give an explanation of the coarse laminations of the core of the plug and their apparent absence from the outer covering, it is necessary to draw attention to certain facts about the rate of growth of the parts of the skull involved in the formation of the auditory region. In the feature most directly concerned, the tympanic bulla (and consequently the tympanic annulus), there is no easily measurable difference in size between that of the newly born juvenile and the most fully grown adult. In view of its association with the tympanic annulus and its importance in regulating the tension of the tympanic ligament, it may be assumed that the glove-finger also remains constant in size throughout the life of the animal. It may further be assumed that the diameter of the bony external meatus, which is directly determined by that of the glove-finger, undergoes no enlargement. Measurement of the mesial distance between the two tympanic bullae in skulls of various ages shows that here too the increase in dimension is very slight. The characteristically great lateral growth of the posterior region of the skull in the Mysticeti is apparently almost wholly associated with the lateral extension of the zygomatic process of the squamosal, the paroccipital process and the mastoid process of the tympano-periotic. During the lateral extension of the above-mentioned bones which are concerned in the formation of the bony external meatus, the wax plug would tend to be drawn away from its contact with the glove-finger, the interval so formed being simultaneously filled up by active formation of squamous epithelium from the former's zona germinativa. The rapidity with which this tissue develops can be judged from the great amount of imperfectly keratinized epithelium in the core of the plug. It would appear that there are regular periods during which lateral extension is either quiescent or very slow and during which a thin continuous layer of fully keratinized epithelium covered externally by cerumen is formed over the end of the glove-finger. The ceruminous layers correspond in position with the thin, dark-coloured bands which are to be seen on the cut face of the plug. The complete reversal of curvature of the epithelium of the second lamina could be explained by the streaming of lipoids between the tissue columns during the quiescent period (see diagrams, Pl. XVI, figs. 3 and 4). The greater thickness of the more distal laminations of the core of the plug is consistent with the greater rate of growth of the juvenile individuals, and although there is a certain degree of irregularity in the amount of tissue formed during each active period, the thickness of the laminations decreases exponentially over the greater part of the series.* In the graph, Text-fig. 2, the length of the core of the plug at each quiescent period is plotted against the lamination number beginning at the distal end. The last two laminations are uncompacted so that a sharp rise appears at the end of the curve. This diminution of compactness must influence the thickness of the laminations near the proximal end of the core, which probably accounts for the fact that this part of the series is not exponential. Since the measurements were obtained from a photographic enlargement (× 10) of the natural size, a small allowance must also be made for spherical aberration at the extremities of the series. If the end of the first lamination corresponds with the time of birth of the animal, the body length would be 6·5 m. (Mackintosh and Wheeler, 1929) and 12 m. at the end of the second lamination, which would represent the nursing period. The third lamination, which is short but very conspicuous, could represent the free feeding period during the animal's first polar season.

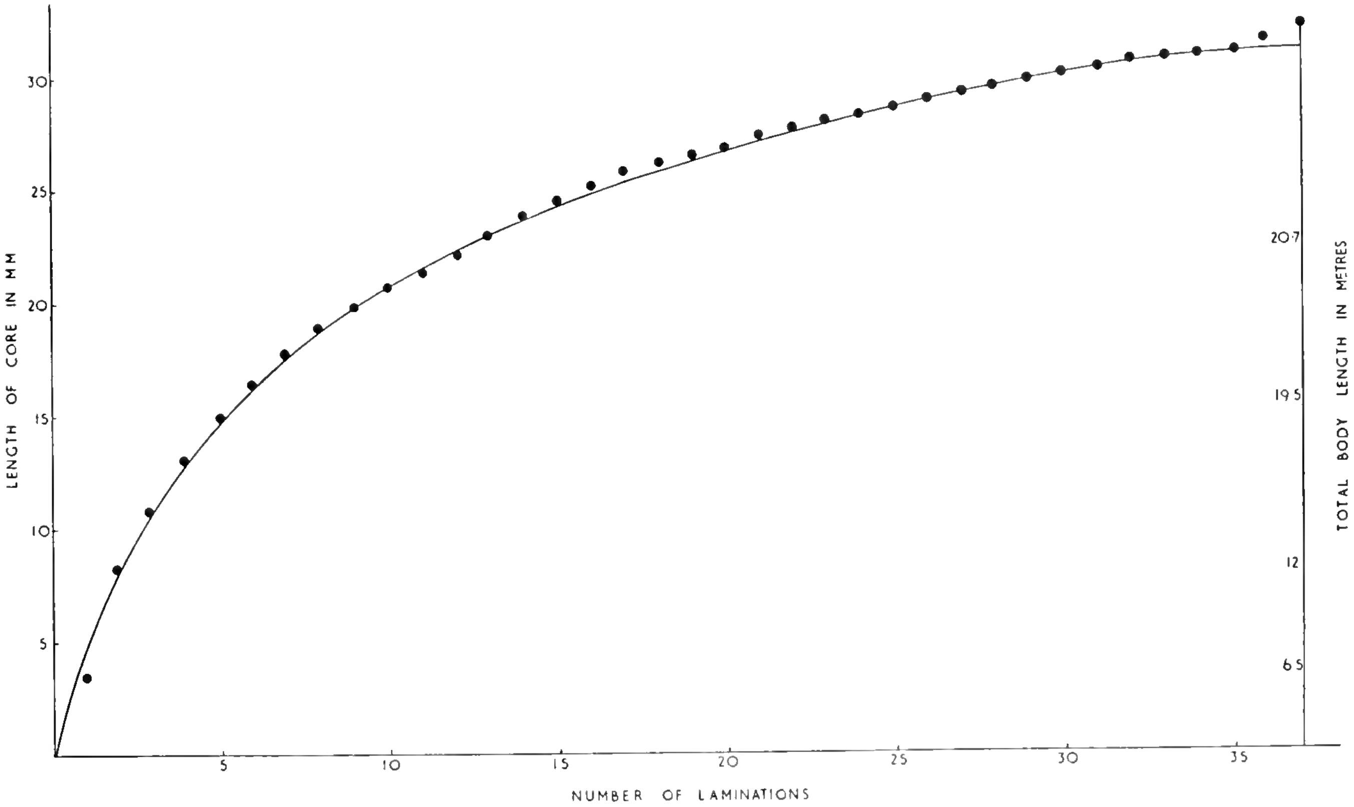
If each subsequent quiescent period (the interlamina space) represents the period of migration north or south, the laminae proximal to the first three would represent five- to six-monthly periods and sexual maturity would occur during the formation of the sixth lamination. The estimated length at sexual maturity in male specimens is 19·5 m., and if this measurement is correlated with those of immature specimens and that of the specimen obtained during 1954, a male of 20·7 m. possessing twelve

---

* The implications of the relation of laminae to physical maturity have not been overlooked. When this is attained it might be expected that increase of the meatal length would cease, but it seems likely that in Cetaceans as in other mammals post-physical maturity increments in extra-cranial processes, involving lateral expansion of the skull as a whole, can continue.

laminations, it will be seen that the length of the core of the plug is not isometric with the body length. This result can be explained by the great disparity between the rate of growth in length of the body and that of the skull width in foetal and juvenile specimens, a feature of growth which is common to all mammals. On the basis of this estimation, a male specimen from the southern hemisphere with the same number of laminations as in Lillie's specimen (Pl. XVIII) would be 18 years old and approximately 22 m. in length.

The radiograph, Pl. XIV, fig. 1, shows two wax plugs from the left and right side of a single specimen of *Balaenoptera physalus*. The number of countable laminations in each specimen as ascertained from the negative was eighteen and the general distribution of light and dark areas indicates that the rate of formation of the plugs is bilaterally symmetrical.



Text-fig. 2. Growth curve of the core of the wax plug in *Balaenoptera physalus*.

It remains to comment upon the outer covering and the distal end of the plug which, as previously stated, appears to be formed from the zona germinativa of the meatus. Since there is no apparent periodic increase in the diameter of the lumen of the meatus, there is no necessity for periodic increased development of its epithelium; indeed, the rate of development would need to be rather slow. The restricted space would also necessitate the inhibition of ceruminous secretion and it will be recalled that no evidence of ceruminous glands could be found.

Whether lamina formation is a six-monthly or an annual event remains to be ascertained, but the evidence obtained from this preliminary examination suggests that it is either one or the other and it seems that further investigation is desirable. The extreme rarity of material is doubtless due to the impracticability of dissecting out the external meatus of whales on the flensing platforms of factory ships, but it should be possible to withdraw the wax plug from the meatus by way of the tympanic cavity after the tympanic bulla has been levered out.

ACKNOWLEDGEMENTS

Grateful acknowledgements are due to the Department of Anatomy of the Medical College of St Bartholomew's Hospital for help in the preparation of microscopic sections and the identification of the histological structures. In this connexion I also wish to thank Dr V. R. Wheatley of the Department of Biochemistry at St Bartholomew's for the chemical analysis shown on p. 299. Acknowledgement is also due to the National Institute of Oceanography, particularly to Dr R. Laws for supervising the collection of the large portion of the skull of *Balaenoptera physalus*, which has been so useful in the general study of the cetacean ear during the preparation of this account. Finally, I wish to thank my colleague Dr F. C. Fraser, Deputy Keeper, Department of Zoology, British Museum (Natural History) for his collaboration.

BIBLIOGRAPHY

Buchanan, T., 1828. *Physiological Illustrations of the Organ of Hearing.* London.

Carte, E. and Macalister, A., 1869. *On the Anatomy of* Balaenoptera rostrata. Phil. Trans. clviii, 201–61, 5 pls.

Fraser, F. C. and Purves, P. E., 1954. *Hearing in Cetaceans.* Bull. Brit. Mus. (Nat. Hist.) Zool. ii, 101–14, 5 pls.

Gray, H., 1946. *Gray's Anatomy.* London.

Lillie, D. G., 1910. *Observations on the Anatomy and General Biology of some members of the Larger Cetacea.* Proc. Zool. Soc. Lond. (1910), 769–92, 1 pl., 10 figs.

Lillie, D. G., 1915. *Cetacea.* Brit. Antarct. ('Terra Nova') Expdn. 1910. Zool. i; 85–124, 8 pls. 13 figs.

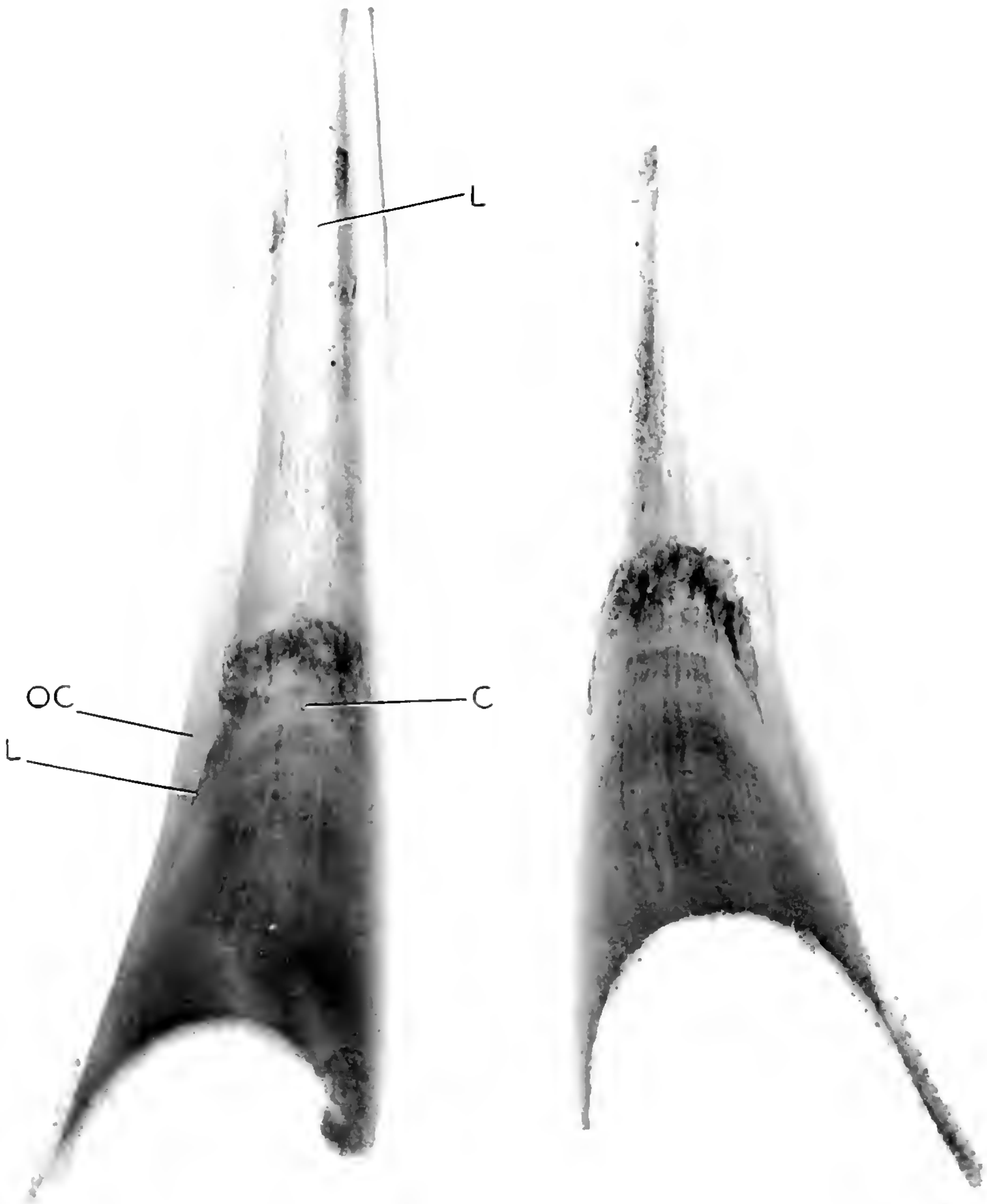
Mackintosh, N. A. and Wheeler, J. F. G., 1929. *Southern Blue and Fin Whales.* Discovery Reports, i, 257–540, 21 pls. 157 figs.

Turner, W., 1913. *Observations on the Auditory Organ in the Cetacea.* Proc. Roy. Soc. Edinb. xxxiv, 10–26, 4 figs.

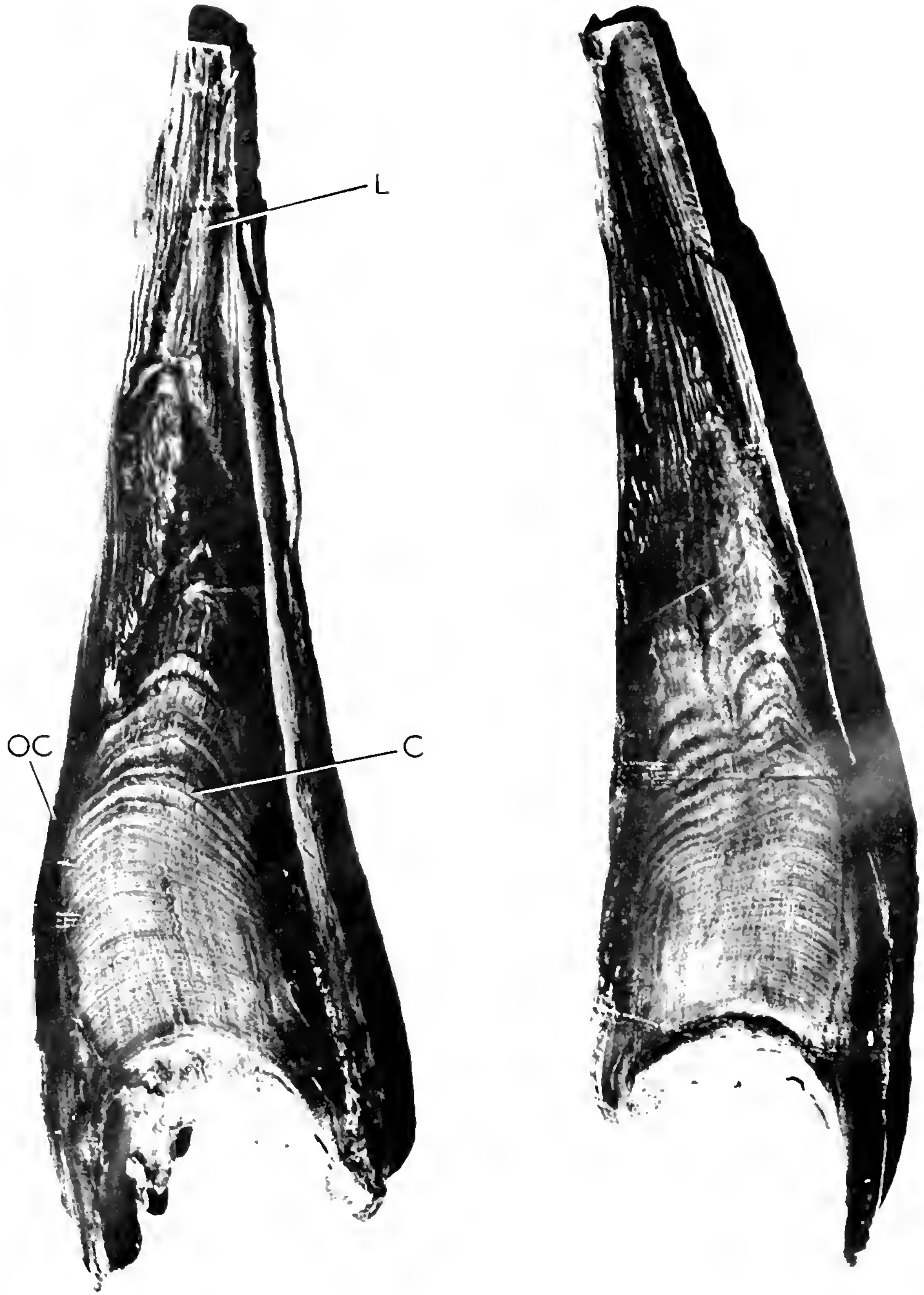
PLATE XIV

Fig. 1. Radiograph of a pair of wax plugs from a specimen of *Balaenoptera physalus*. *OC*, outer covering; *C*, core; L, lumen.

Fig. 2. Bisected specimen of wax plug from *Balaenoptera physalus*. *OC*, outer covering; *C*, core; *L*, lumen.



1



2

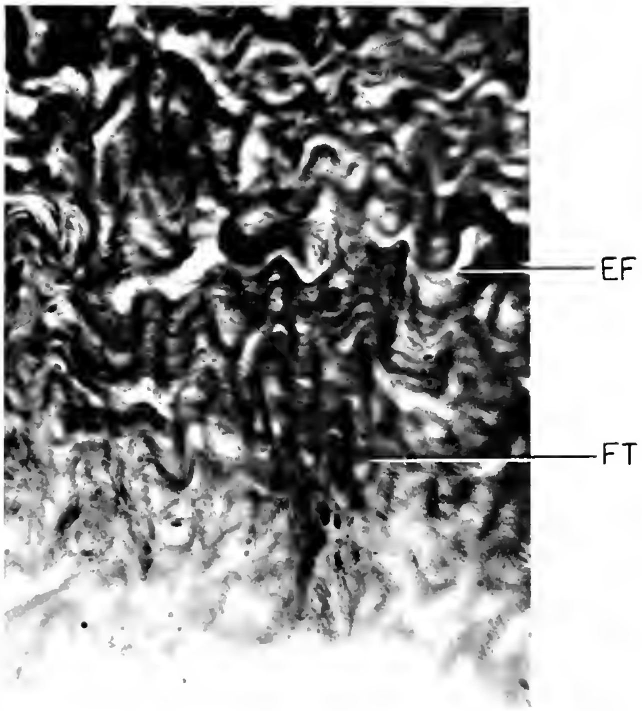
PLATE XV

Fig. 1. Transverse section, × 400, of corium of auditory meatus of *Balaenoptera physalus* showing absence of ceruminous glands. *EF*, elastic fibres; *FT*, fibrous tissue.

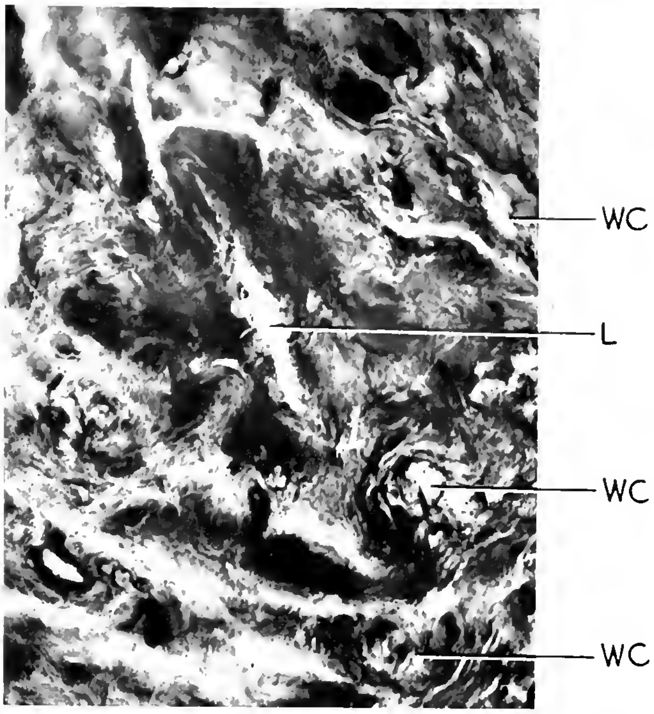
Fig. 2. Transverse section through the 'blind' portion of the external auditory meatus of *Balaenoptera acutorostrata*. *WC*, wax concretions; *L*, lumen of meatus. × 80.

Fig. 3. Transverse section, × 60, of outer covering of wax plug from *Balaenoptera physalus* showing stratum corneum and lumen of meatus (*L*) filled with compacted keratinized epithelium. *KE*, sinuous squamae of keratinized epithelium.

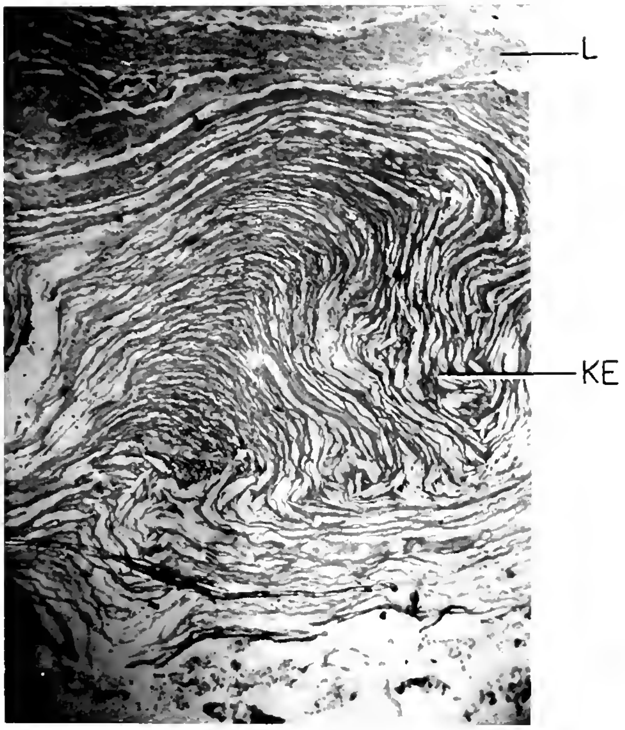
Fig. 4. Transverse section, × 20, of distal end of wax plug from *Balaenoptera physalus*. Lumen of meatus (*L*) filled with compacted keratinized epithelium. *SC*, stratum corneum.



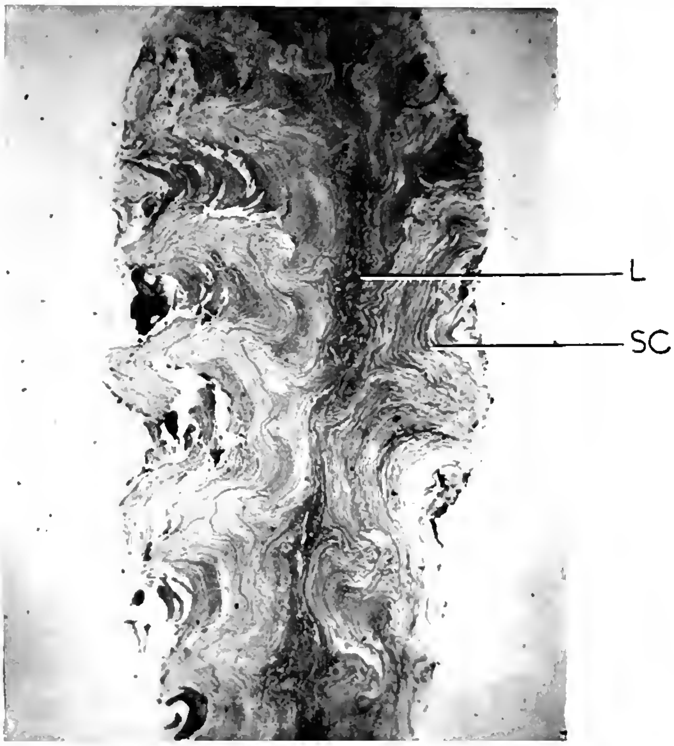
1



2



3



4

PLATE XVI

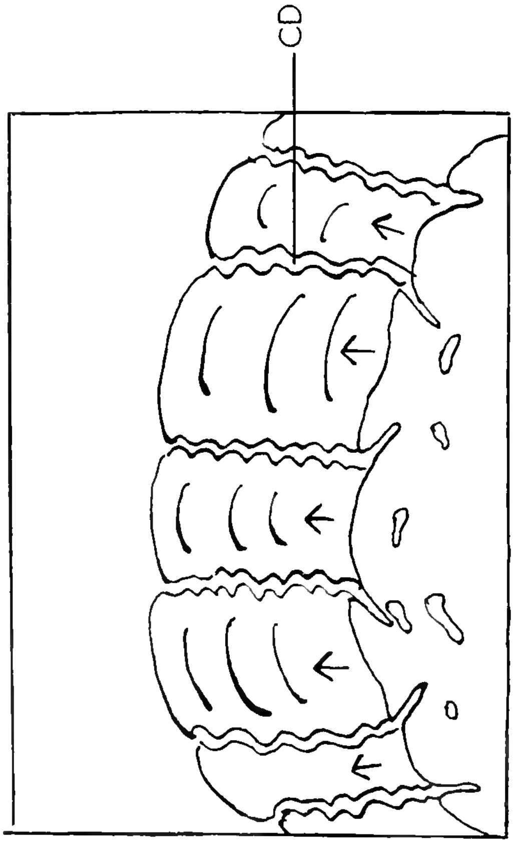
Fig. 1. Transverse section, × 15, of first lamina of wax plug from *Balaenoptera physalus*. *OC*, outer covering; *I*, islet of tissue; *CS*, ceruminous space; *CD*, ceruminous duct.

Fig. 2. Longitudinal section, × 15, of first and second laminae of wax plug from *Balaenoptera physalus*. *KE*, keratinized epithelium; *CL*, ceruminous layer; *CD*, ceruminous duct.

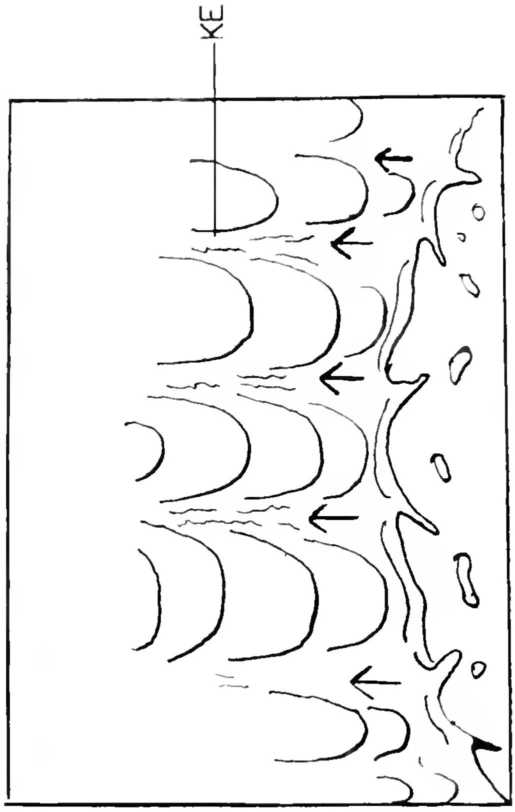
Figs. 3 and 4. Diagrams of longitudinal sections of the first and second laminae of the wax plug from *Balaenoptera physalus* showing the suggested reason for the reversal of curvature of the tissues in the second lamina. Fig. 3, the arrows indicate the pressure points of growth during active formation of the squamous epithelium; Fig. 4, the arrows indicate the pressure points of lipoids during the resting period.

1

2



3



4

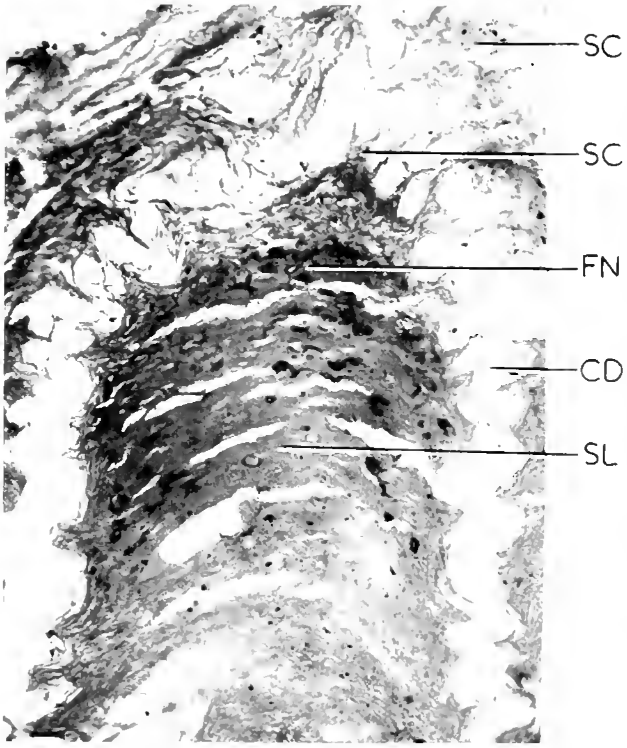
PLATE XVII

Fig. 1. Longitudinal section, × 60, of column of tissue in the first lamina of the wax plug of *Balaenoptera physalus*. *SC*, stratum corneum; *SL*, stratum lucidum (the section is cut off-centre so that the stratum granulosum does not show); *FN*, flattened nuclei; *CD*, ceruminous duct.

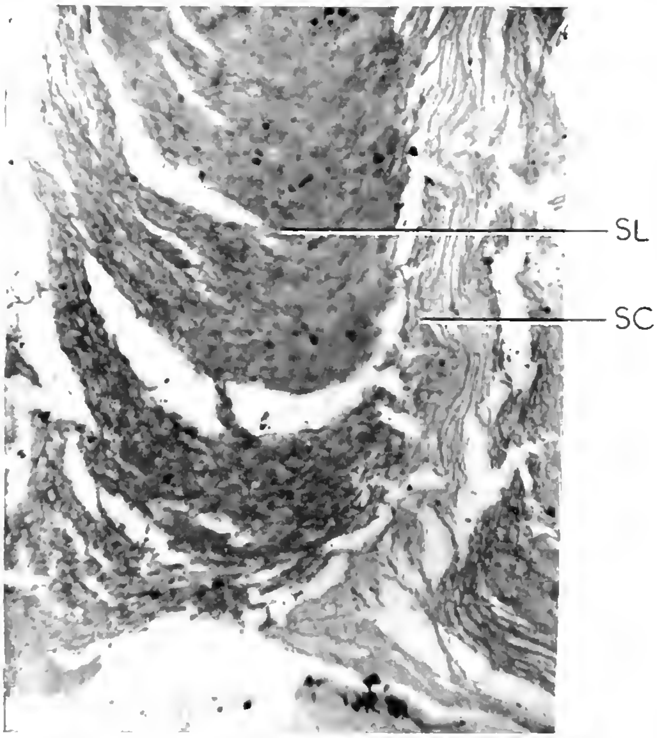
Fig. 2. Longitudinal section, × 60, of column of tissue in the second lamina of wax plug from *Balaenoptera physalus* showing reversal of curvature. *SL*, stratum lucidum; *SC*, stratum corneum.

Fig. 3. Longitudinal section, × 60, of one of the papillae on the corium of the distal end of the glove-finger from *Balaenoptera physalus*. *CD*, ceruminous duct; *CG*, ceruminous gland.

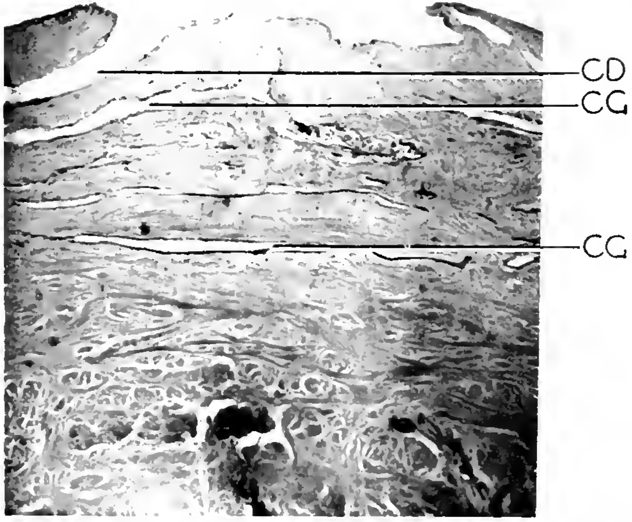
Fig. 4. Longitudinal section, × 60, of one of the columns of tissue of the first lamina of the wax plug of *Balaenoptera physalus*. *SG*, stratum granulosum; *SC*, stratum corneum; *FC*, fusiform cell; *CD*, ceruminous duct; *SL*, stratum lucidum.



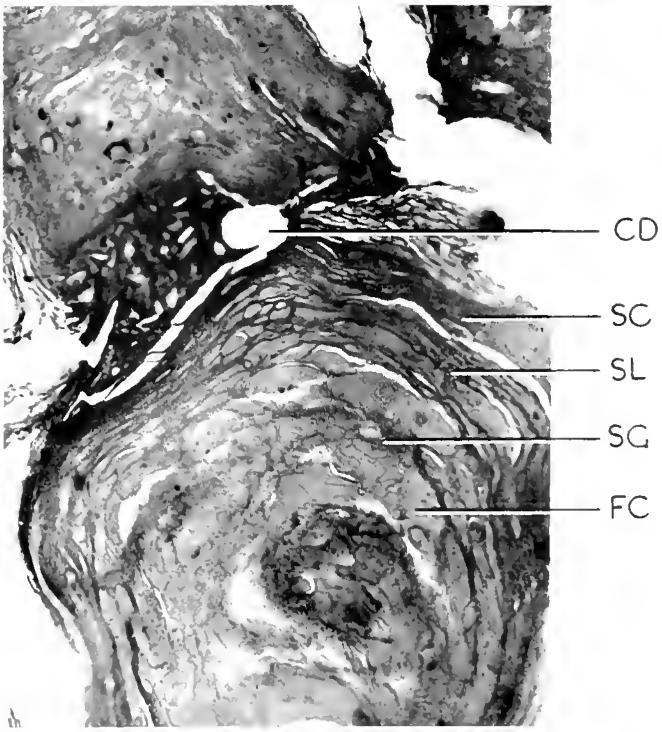
1



2



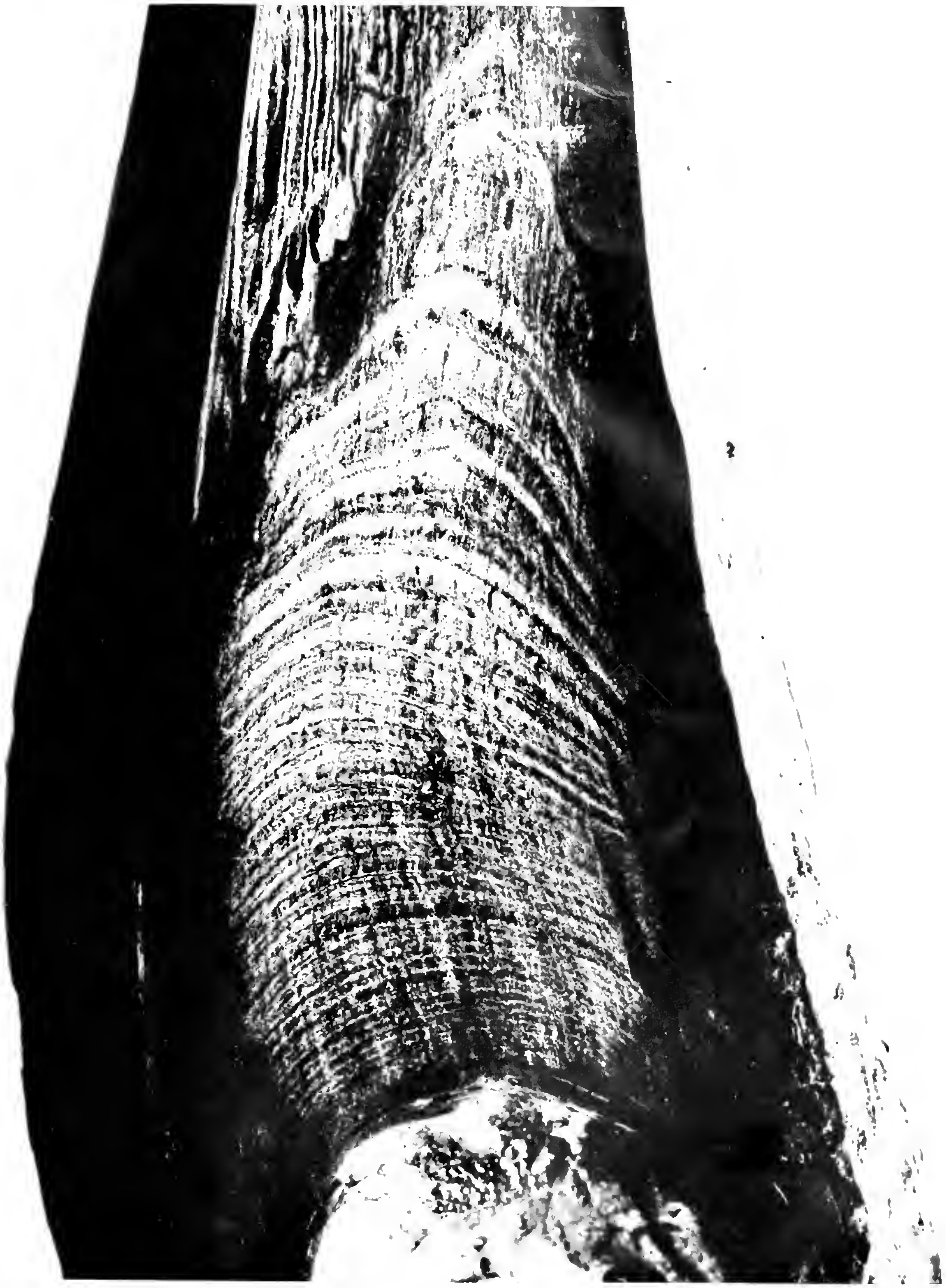
3



4

PLATE XVIII

Enlarged photograph, × 4, of the core of the wax plug from *Balaenoptera physalus*.



[*Discovery Reports. Vol. XXVII, pp.* 303-336, *Plate XIX, August,* 1955.]

STUDIES OF ALEPISAUROID FISHES

By

N. B. MARSHALL

CONTENTS

STUDIES OF ALEPISAUROID FISHES

By N. B. Marshall

(Plate XIX and Text-figs 1–9)

INTRODUCTION

The Alepisauroidea are voracious, bathypelagic fishes which together with the Myctophoidea form the order Iniomi.

Fishes of the order Iniomi are soft-rayed teleosts, which have evolved beyond the level of the Isospondyli in that the premaxillaries exclude the maxillaries from the gape. The pelvic fins are usually abdominal in position, but when they are set close to the pectorals, as in the Aulopidae, there is no association between the pelvic bones and the pectoral girdle. The swim-bladder when present is closed (physoclistous) and the blood supply to the retia mirabilia enters at the anterior end. There are usually 19 principal rays in the caudal fin and 6–11 rays in each pelvic fin. The dorsal fin and anal fin are never opposed and an adipose dorsal fin is usually present. There is no mesocoracoid, nor is a Weberian mechanism present.

The Alepisauroidea can be defined as bathypelagic Iniomi with no swim-bladder or luminescent organs, with a single row of numerous (more than 20) small teeth on each premaxillary, one or two rows of teeth on each palatine, one to three rows of teeth on each dentary and with gill-rakers in the form of spines or teeth. The anal fin has from 12–50 rays and is usually set close to the caudal. Lastly, there are 3–4+4–5 branchiostegal rays.[1]

Compared with most other oceanic, mid-water teleosts, the Alepisauroidea are large, even very large, fishes.[2] Owing to their size and swiftness, our knowledge of this suborder of the Iniomi—at least from catches of mid-water nets—is very incomplete. Almost without exception, the larger known individuals of the larger species have come either from the stomachs of whales or of oceanic fishes, such as tunny, or have been taken on long lines. *Alepisaurus* itself, which is caught on the tunny hooks of Madeiran fishermen, has contained some relatively large paralepidids.

This report is based mainly on specimens from the Discovery Collections. The material contains some new species and is sufficiently extensive to allow of a revision of the Scopelarchidae and a review of the relationships of the alepisauroid fishes.

ACKNOWLEDGEMENTS

My thanks are due to Dr N. A. Mackintosh for putting the material at my disposal and to Dr W. A. Gosline, who has read the manuscript and made some useful critical comments.

---

[1] The plus sign separates the rays on the epihyal and ceratohyal bones.

[2] *Alepisaurus* reaches a standard length of at least 1500 mm.; the largest known *Anotopterus* is 855 mm. in length, while three paralepidids, *Magnisudis barysoma*, *Notolepis coatsi* and *Sudis hyalina*, fall within the standard length range of 400–500 mm. Certain other paralepidids, *Omosudis lowei*, *Evermannella balbo* and *Neoscopelarchoides elongatus*, grow to within the range 150–300 mm.

PART I. CLASSIFICATION OF THE INIOMI

In order to give systematic perspective to these studies, an outline classification of the order Iniomi is given. Those workers mainly responsible for this arrangement will become apparent during the course of this paper.

I. Suborder ALEPISAUROIDEA

Family SCOPELARCHIDAE
  Genera **Scopelarchus** Alcock, **Neoscopelarchoides** Chapman

Family EVERMANNELLIDAE
  Genus **Evermannella** Fowler

Family PARALEPIDIDAE
Subfamily SUDINAE
  Genus **Sudis** Rafinesque Schmaltz
Subfamily PARALEPIDINAE
  Genera **Magnisudis** Harry, **Paralepis** Cuvier, **Notolepis** Dollo, **Lestidium** Gilbert, **Macroparalepis** Ege

Family ANOTOPTERIDAE
  GENUS **Anotopterus** Zugmayer

Family ALEPISAURIDAE
  Genus **Alepisaurus** Lowe

Family OMOSUDIDAE
  Genus **Omosudis** Günther

II. Suborder MYCTOPHOIDEA

Family AULOPIDAE
  Genera **Aulopus** Cuvier, **Hime** Starks and **Latropiscus** Whitley

Family CHLOROPHTHALMIDAE
  Genera **Chlorophthalmus** Bonaparte, **Bathysauropsis** Regan

Family NOTOSUDIDAE[1]
  Genera **Notosudis** Waite, **Luciosudis** Fraser-Brunner

Family BATHYPTEROIDAE
  Genera **Bathypterois** Günther, **Benthosaurus** Goode and Bean

Family IPNOPIDAE
  Genera **Ipnops** Günther, **Bathymicrops** Koefoed

Family NEOSCOPELIDAE
  Genera **Neoscopelus** Johnson, **Solivomer** Miller, **Scopelengys** Alcock

Family MYCTOPHIDAE
  Genera **Electrona** Goode and Bean, **Hygophum** (Tåning) Bolin, **Benthosema** Goode and Bean, **Diogenichthys** Bolin, **Myctophum** Rafinesque, **Ctenoscopelus** Fraser-Brunner, **Loweina** Fowler, **Gonichthys** Gistel, **Ctenobranchus** Fowler, **Tarltonbeania** Eigenmann and Eigenmann, **Diaphus** Eigenmann and Eigenmann, **Notolychnus** Fraser-Brunner, **Lampadena** Goode and Bean, **Lampanyctodes** Fraser-Brunner, **Lampanyctus** Bonaparte, **Ceratoscopelus** Günther, **Gymnoscopelus** Günther, **Lampichthys** Fraser-Brunner, **Notoscopelus** Günther, **Hintonia** Fraser-Brunner, **Scopelopsis** Brauer

---

[1] It would appear that *Scopelosaurus* Bleeker (Act. Soc. Sc. Indo-Neerl, VIII, 1860, Elfde Bijdr. Amboina, p. 13) should be included in this family.

Family HARPADONTIDAE

Genera **Harpadon** Le Sueur, **Bathysaurus** Günther

Family SYNODONTIDAE

Genera **Synodus** (Gronovius) Scopoli, **Trachinocephalus** Gill, **Saurida** Cuvier and Valenciennes, **Xystodus** Ogilby.

The Family SCOPELARCHIDAE

The first known fish of this family was described by Alcock (1896, 1899) under the name *Scopelarchus guentheri*.[1] It was taken by H.M. Indian Marine Survey Steamer 'Investigator' while trawling between depths of 180 and 217 fathoms off Colombo, Ceylon. Observing that the fish '...is a remarkable generalized form of Scopeloid, showing affinities with *Saurus*, *Chlorophthalmus*, *Scopelus*, *Odontostomus* and *Paralepis*', Alcock (1896) placed it in the family Scopelidae, group Scopelarchina.

'Valdivia' took twelve specimens of scopelarchids at various stations in the Atlantic, Indian and Southern Oceans. These were described by Brauer (1902, 1906) as *Dissomma anale* and placed in the family Scopelidae. Roule (1916, 1919), having examined seven scopelarchids taken off the Azores during the cruises of 'Princesse Alice', described them as a new species, *Odontostomus perarmatus*, of the family Odontostomidae. However, *Odontostomus* Cocco (amended to *Evermannella* by Fowler (1901), on account of *Odontostomus* Cocco, 1838, being a homonym of *Odontostomus* Beck, 1837, a molluscan genus) is quite distinct from *Scopelarchus* (see below).

Regan (1911), in setting out the classification of the Iniomi, defined the family Scopelarchidae and placed it in the suborder Alepisauroidea. Then Parr (1928) pointed out that Regan had included both *Evermannella* and *Scopelarchus* (= *Dissomma*) in the Scopelarchidae, and that the diagnosis of the family was based on a study of *Evermannella hyalina*. Parr showed clearly that *Scopelarchus* and *Evermannella* are so distinct as to warrant separation into different families: he was thus able to give the first critical diagnosis of the Scopelarchidae. In a later paper (Parr, 1929), this diagnosis was extended to include findings from osteological studies. Furthermore, in the 1929 paper a new genus and species, *Scopelarchoides nicholsi*, was described, the type and a paratype being taken by 'Pawnee' off the west coast of Mexico. Additions to this description are to be found in a later paper (Parr, 1931 *a*) in which three more specimens are recorded, one from the Gulf of California, one off the west coast of Central America and one from a locality in the Pacific Ocean.

A further new species, *Scopelarchus elongatus*, was described by Norman (1937) from an individual taken north-east of Kerguelen Island by the B.A.N.Z. Antarctic Research Expedition. This was followed by Chapman's (1939) proposal of a new genus and species, *Neoscopelarchoides dentatus*, the holotype coming from the central part of the Gulf of Alaska. Lastly Mead and Böhlke (1953) have described *Scopelarchus linguidens* from three juvenile individuals taken off northern Japan.

The Discovery material contains two new species and a large larval scopelarchid, descriptions of which, together with a fuller account of Norman's species *elongatus*, now follow. But to anticipate a later section, it must be added, that the study of these individuals has led me to conclude that the scopelarchids can be divided into two well-marked genera, *Scopelarchus* Alcock and *Neoscopelarchoides* Chapman. Synonymies will be discussed on p. 312–14.

Scopelarchus cavei sp.n.

(Fig. 1 and Pl. XIX, figs, 5, 6.)

Holotype. A specimen 70 mm. in standard length taken by R.R.S. 'Discovery II' in a young fish trawl, hauled obliquely between 500 m. and the surface, at station 1585: 00° 06′ S, 49° 45·4′ E., Indian Ocean: about 400 miles north-west of the Seychelles.

---

[1] In the 1899 publication Alcock gave the specific name as *güntheri*.

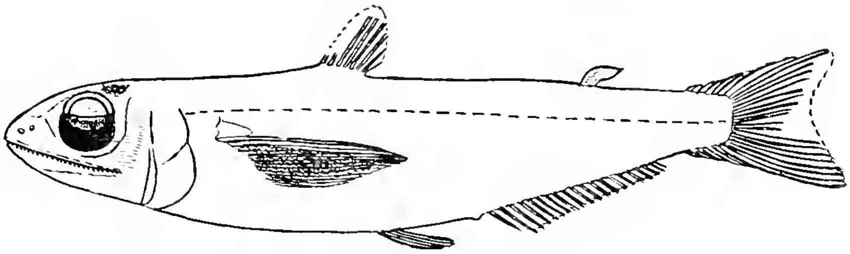
Body proportions in hundredths of the standard length (70 *mm.*). Greatest depth of body 24·3; length of head 25·7; horizontal diameter of eye 8·6; length of snout 7·1; width of bony interorbital 2·6; length of lower jaw 21·4; maxilla 17·8; length from tip of snout to origin of dorsal fin 40; snout to adipose dorsal fin 75·7; snout to pectoral fin 28·6; snout to pelvic fin 47·1; snout to anal fin 61·4; length of pectoral fin 25·7; length of pelvic fin 12·1; length of caudal peduncle 14·3; depth of caudal peduncle 9·3. Body compressed; greatest breadth (at pectoral girdle) 14·3.

Fin-rays. D. 9, A. 21, Pect. 21, Pv. 9.

Scaling. Large cycloid scales on opercula; probably also present on cheeks. Scales over the trunk and tail well ossified, with a shiny, armoured appearance: cycloid. Scale rows between lateral line and origin of dorsal fin 4; between lateral line and origin of anal fin 7. Number of scales along lateral line (to caudal flexure) 43. Lateral line scales only slightly enlarged, about 1·2 times as deep as those immediately adjacent.

Vertebrae. 41.[1]

Dentition. About fifty-five small, pointed retrorse teeth on premaxilla. Dentary with about thirty outer, smallish, pointed teeth and 9–10 inner, larger, and depressible teeth of which the second and third are the largest. The first six of these teeth are barbed. Palatine teeth arranged in two closely adjacent rows, each consisting of 5–6 teeth. Lingual teeth ten, the first longest, the rest gradually decreasing in size.



Text-fig. 1. *Scopelarchus cavei.* Holotype (× 1·3).

Colour (in spirit). General body colour yellowish brown, the dorsal surface darker, with a fairly dense peppering of small melanophores covering the upper half of the flank-area above the lateral line. Immediately behind each eye is a black lunate area. Dorsal, anal, pelvic and caudal fins transparent or whitish. The pectoral fin is black, except for the two uppermost and five of the lowermost fin rays, which are whitish.

Underlying the scales over the lower half of the abdomen is a layer of silvery pigment, which extends from the isthmus to the anus. (Is it possible that luminescent tissue may be associated with such a light-reflecting layer?) Above this silvery area, the black peritoneum of the body cavity shows through the body wall.

This species is most closely related to *Scopelarchus guentheri* Alcock, but has fewer anal rays (21, cf. 26), fewer lateral-line scales (43, cf. *c.* 50) and these scales are not enlarged as in *S. guentheri*. Perhaps there is also a difference in the interorbital width, which in *S. cavei* is relatively broad, whereas in *S. guentheri* Alcock (1899) described the eyes as being separated by a 'mere linear space'.

I have much pleasure in naming this species after A. J. E. Cave, Professor of Anatomy at St Bartholomew's Hospital Medical College.

---

[1] In all counts of vertebral numbers the last, upturned, caudal element has been included.

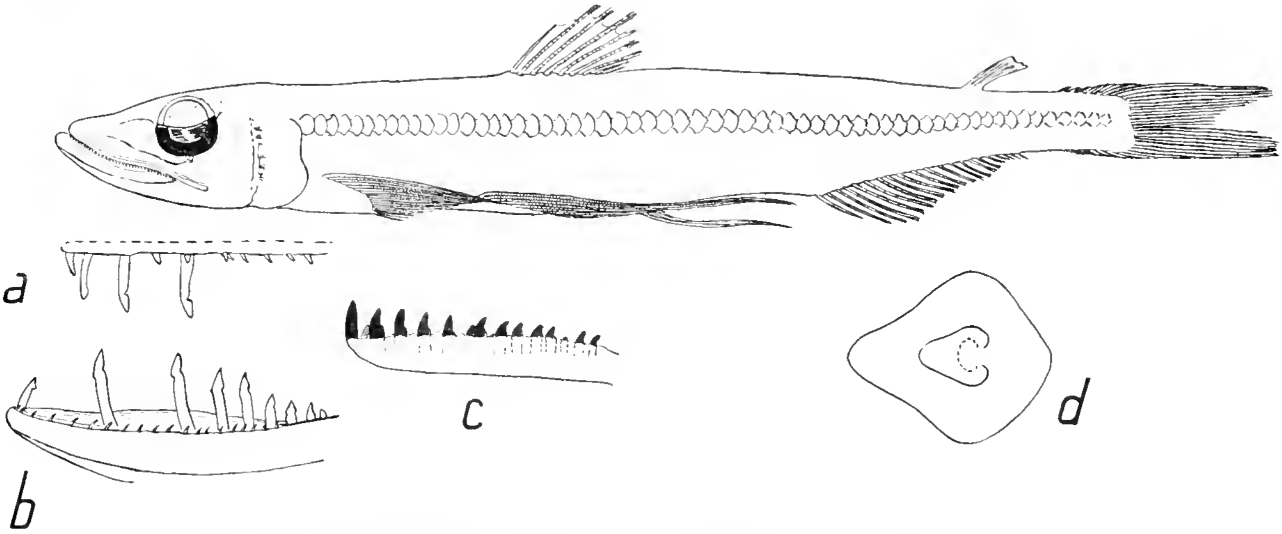
Neoscopelarchoides dubius sp.n.

(Text-fig. 2 and Pl. XIX, figs. 3, 4.)

Holotype. A female, 138 mm. in standard length, taken in a 450 cm. closing net hauled obliquely between 1800 and 1150 m., at station 1759: 31° 54·5′ S, 51° 27·9′ E., Indian Ocean: about 500 miles south-east of Madagascar.

Body proportions in hundredths of the standard length (138 *mm.*). Greatest depth of body 17·5; length of head 22·8; horizontal diameter of eye 5·8; length of snout 8·7; width of bony interorbital 0·7; length of lower jaw 20·3; length of maxilla 15·2; length from tip of snout to origin of dorsal fin 38·4; snout to adipose dorsal fin 81·2; snout to pectoral fin 25·5; snout to pelvic fin 40·9; snout to anal fin 61·5; length of pectoral fin 21·0; length of pelvic fin 29·0; length of caudal peduncle 11·2; depth of caudal peduncle 6·2. Anus situated a little in front of the origin of the anal fin. Trunk not much deeper than wide at mid-point of body.

Fin-rays. D. 9, A. 21, Pect. 27, Pv. 9.



Text-fig. 2. *Neoscopelarchoides dubius.* Holotype (×1): *a*, palatine teeth (×2·5); *b*, mandibular teeth (×2·5); *c*, lingual teeth (×2·5); *d*, lateral line scale (×6).

Scaling. Rather small, thin cycloid scales on cheeks and gill covers and over the body, extending a short way in a B-shaped area over the bases of the principal caudal rays. Scales of lateral line much enlarged. Scales along lateral line 59. Transverse rows of scales between origin of dorsal fin and lateral line 8; between origin of anal fin and lateral line 10–11.

Vertebrae. 57.

Dentition. Premaxilla with about 80 small, pointed, retrorse teeth. Dentary with about thirty outer, smaller pointed teeth and nine inner, long, barbed, depressible teeth, the second and third being the largest. Left palatine with three large, barbed, depressible teeth, these being set somewhat inward from a row of eight small, pointed teeth. Lingual teeth fourteen, moderately compressed, the first the largest, the remainder gradually decreasing in size.

Gill-teeth. The first gill arch bears a series of closely set, small, pointed gill-teeth.

Colour (in spirit). Dark brown above the lateral line, medium brown below, except where the black peritoneum of the body cavity shows through the abdominal walls. The fins are more or less hyaline, except for the caudal, which has a fairly dense covering of small melanophores.

There is a kidney-shaped iridescent area on the outer walls of the optic cup of the eye, close to the lens. This has been regarded as a luminescent organ, but it must be the elliptical mass of fibrous tissue which Brauer (1908) called a 'linsen polster' and which is shown on his pl. 40, figs. 2 and 5, of *Dissomma anale*.

Table 1 shows the number of fin-rays in *Neoscopelarchoides dubius* compared with the other known species of this genus.

N. dubius is also readily distinguishable from the other species by the highly developed pelvic fins. The proportions of the latter expressed in hundredths of the standard length are: *N. dubius*, 29·0; *N. elongatus*, 13·3–14·4; *N. linguidens*, 5·3–5·6; *N. dentatus*, *c.* 17·0 (measured from Chapman's (1939) figure).

NOTE. I have called this species *dubius*, because it is possible that future work may reveal it to be the adult of the larval form, *Benthalbella infans* Zugmayer (see p. 312).

Table 1

Number of fin-rays	Dorsal	Anal	Pectoral	Pelvic
N. dubius sp.n.	9	21	27	9
N. elongatus (Norman)	8–9	26–27	21–22	9
N. dentatus Chapman	6–7	17–21	22–25	9
N. linguidens (Mead and Böhlke)	9–10	28	25–27	9

Neoscopelarchoides elongatus (Norman)

(Text-fig. 3*b*, *b'* and Pl. XIX, figs. 1, 2.)

Scopelarchus elongatus Norman 1937. Rep. B.A.N.Z. Antarct. Res. Exped. 1929–1931 (B), 1 (2), p. 86.

As the original description by Norman (1937) is rather brief, an expanded one is given here. It is based on the type specimen (standard length 198 mm.) which was taken east of Kerguelen Island (45° 53′ S, 84° 33′ E) and on two individuals taken by R.R.S. 'Discovery II'. The first (S.L. 104 mm.) is from station 391 (55° 48½′ S, 52° 35′ W), about 300 miles south-east of the Falkland Islands, in a 450 cm. net hauled between 1200 m. and 1300 m.; date, 18. iv. 30 (Text-fig. 3). The second (S.L. 120 mm.) is from station 725 (53° 23·6′ S, 74° 57·8′ W), about 50 miles south of the western end of the Magellan Strait, in a 100 cm. net hauled obliquely between 250 m. and 196 m.; date 17. xi. 31 (Pl. XIX, figs. 1, 2).

In the following description the data for the type[1] are given first, followed (in parenthesis) by the data for the Discovery specimens, in the above-mentioned order.

Body proportions in hundredths of the standard length 198 *mm.* (104 *and* 120 *mm.*). Greatest depth of body 14·1 (11·1, 10·8); length of head 19·8 (22·1, 22·5); horizontal diameter of eye 5·6 (5·3, 5·8); length of snout 6·1 (7·2, 7·9); width of bony interorbital 1·6 (1·6, 1·5); length of lower jaw (20·2, 20·0); maxilla (17·3, 16·6); length from tip of snout to origin of dorsal fin 39·1 (42·8, 41·7); snout to adipose dorsal fin 79·9 (74·0, 75·0); snout to pectoral fin 21·7 (24·0, 23·3); snout to pelvic fin 37·9 (40·4, 38·3); snout to anal fin 64·6 (65·4, 64·2); length of pectoral fin (14·4, 13·3); length of pelvic fin (14·4, 13·3); depth of caudal peduncle 7·1 (6·2, 6·0); length of caudal peduncle 12·6 (12·5, 12·8).

Fin-rays. D. 9 (9, 8), A. 26 (27, 27) Pect. 22 (21, 21), Pv. 9 (9, 9).

Scaling. (Based on the Discovery specimen from station 725.) Small, thin cycloid scales on cheeks and gill covers and over the rest of the body. Scales of lateral line much enlarged.

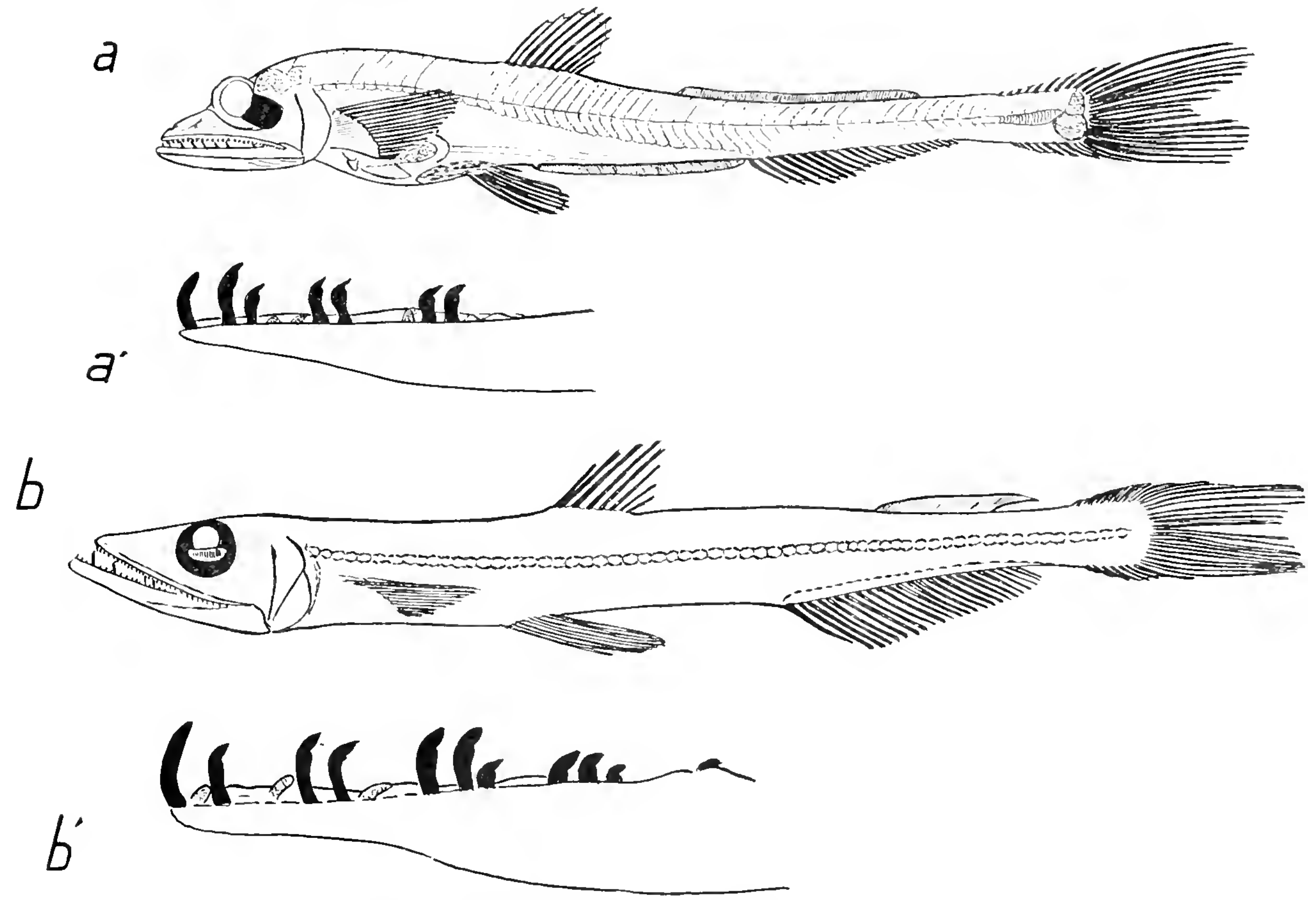
Scales along lateral line 64. Transverse rows of scales between origin of dorsal fin and lateral line 8; between origin of anal fin and lateral line 10–11 (the type specimen has sixty-two scale pockets along the lateral line).

Vertebrae. In the type specimen: 61.

---

[1] Owing to damage, certain measurements for the type specimen had to be omitted.

Dentition (based on Discovery specimens). Premaxillary teeth *c.* 70, pointed, retrorse, small. Dentary with *c.* thirty outer, pointed, retrorse teeth; eleven long, depressible, barbed, inner teeth, the 3rd–5th being the largest. Palatine teeth in two closely adjacent rows, 8–10 smaller, pointed teeth in outer row, 5–6 longer, barbed teeth in inner row. Lingual teeth eleven, barbed, decreasing in size from before backward (see Text-fig. 3*b′*).



Text-fig. 3. *a*, *Neoscopelarchoides* sp. late larval stage (=*Benthalbella infans*) (×2): *a′*, lingual teeth (×9·3); *b*, *Neoscopelarchoides elongatus* (Norman). Specimen from station 391 (×1·3); *b′*, lingual teeth (×9·3).

Neoscopelarchoides sp.

(Text-fig. 3*a*, *a′*.)

This specimen of a late larval stage was taken by R.R.S. 'Discovery II' off the Azores. Station 3051 (lat. 39° 29′ N, long. 9° 50′ W), 26. viii. 52. Net TYF (young fish trawl), hauled obliquely between 700 m. and the surface.

Body proportions in hundredths of the standard length (60·5 *mm.*). Greatest depth of body 13·2; length of head 15·4; diameter of forward lens-containing part of eye 4·1; length of snout 6·6; width of bony interorbital 1·0; length of lower jaw 15·3; length from tip of snout to origin of dorsal fin 38·8; snout to origin of adipose dorsal fin 57·8; snout to anterior ray of pectoral fin 18·2; snout to anterior ray of pelvic fin 33·5; snout to origin of anal fin 64·4; depth of caudal peduncle 4·5; length of caudal peduncle 12·4.

Fin-rays. D. 9, A. 22, Pect. 24, Pv. 9.

As shown in Text-fig. 3*a* the eyes are tubular and are directed forward and upward.

Dentition. About thirty small, pointed, retrorse teeth on premaxilla. Mandible with about twenty outer, small, upright pointed teeth; seven inner, long and slender teeth, all but the first with a tiny barb and all but the first, which is more or less upright, antrorse. Palatine with about twelve smallish, pointed teeth. The lingual teeth (see text-fig. 3*a'*) more than any other feature, show that this must be a young scopelarchid.

When caught the fish was almost transparent, the only colour being the black pigment of the eye tube. The body-wall is quite transparent, the internal organs, gut, liver and mesenteries, showing clearly. The muscles associated with the base of the pelvic fins are moderately dense, but over the rest of the body wall there is but a thin muscle-layer, which becomes less and less easy to distinguish as one works upwards from the pelvics. Along the mid-ventral line from the head to the pelvic fins, there is a sharp hyaline division between the musculature of each side of the body wall.

Relationships. Following on this section, reasons will be given for recognizing two genera of scopelarchids, *Scopelarchus* Alcock and *Neoscopelarchoides* Chapman. One of the features distinguishing them is the relative position of the dorsal and pelvic fins. In the larval specimen from station 3051, the origin of the dorsal fin lies behind that of the pelvic fins, a characteristic of the genus *Neoscopelarchoides*; hence the larva may be presumed to belong to this genus. It also has the full complement of principal caudal and pelvic rays (and presumably of dorsal, anal and pectoral rays), and at this stage there is unlikely to be much shift in the relative positions of the dorsal and pelvic fins. But it cannot be fitted with certainty into any of the four known species. In numbers of fin-rays it is closest to *N. dubius* and it also agrees with this species in the number of body segments before the origin of the anal fin (the remaining myotomes cannot be counted with certainty). The larva has thirty-five pre-anal fin myotomes, and *N. dubius* has thirty-five pre-anal fin lateral line scales and vertebrae. *N. elongatus* has 33–35 pre-anal fin segments but the anal rays (26–27) are more numerous than those of *Benthalbella*.

I have already drawn attention to the fact that *N. dubius* sp.n. may prove to be the adult of a larval form, *Benthalbella infans* described by Zugmayer in 1911. Zugmayer's young fish and the Discovery larva are very similar, the only difference being in the number of anal rays (17 compared with 22). A number of other specimens, previously recorded, also nearly resemble them:

(1) The fish figured in Murray and Hjort (1912) on p. 746 and labelled 'New fish resembling *Dysomma*' (*sic*). The drawing shows nine dorsal and twenty or twenty-one anal rays.

(2) Two *Benthalbella* larvae from the Bay of Cadiz (Schmidt, 1918). Fin-ray formula: D. 9–10, A. 21–22, Pect. 26, Pv. 8–9.

(3) Two *Benthalbella* larvae from Madeira and one from the Azores (Roule and Angel, 1930) which were regarded as young stages of *Omosudis lowei*. Their Plate III, figs. 75 and 76 show a fin-ray complement of D. 8–9, A. 20.

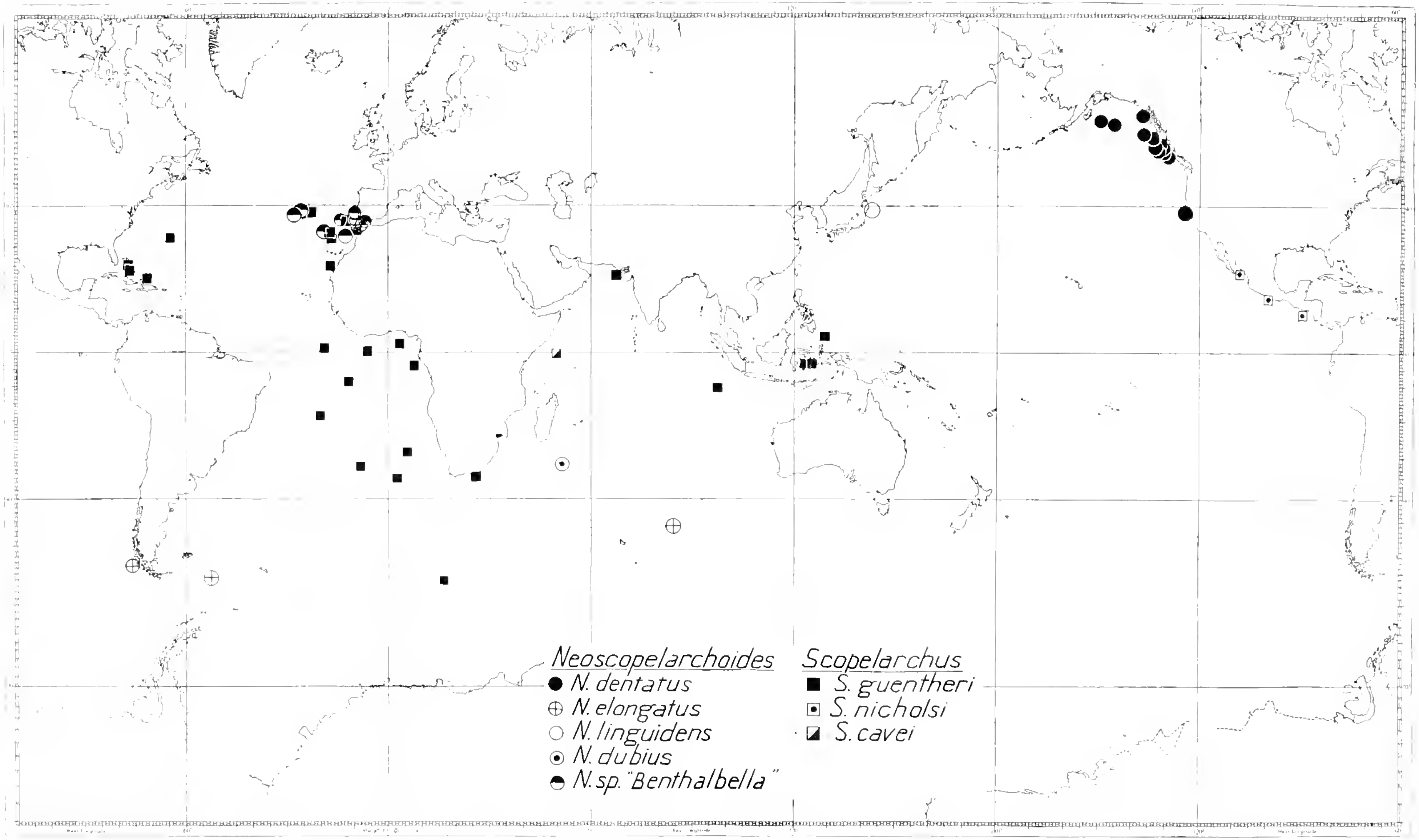
(4) Three post-larval *Benthalbella* from the Strait of Gibraltar (Nybelin, 1948). Fin-ray formula: D. 9–10, A. 20–22, Pect. 27, Pv. 9.

The distribution of these larvae may be seen in the chart, fig. 4.

It would thus seem probable that the Discovery larva and all those listed above belong to one species of *Neoscopelarchoides*. If this is so, the species has a fin-ray complement of D. 9–10, A. 17–22, Pect. 22–27, Pv. 8–9. *N. dubius* comes very close to this; and it may be concluded that either these remarkably large larvae are the young of *N. dubius* or of an unknown, closely-related species.

RELATIONSHIPS AND SYNONYMIES OF THE GENERA

Considering in chronological order the genera that have been included in the Scopelarchidae, *Dissomma* Brauer (1902) is clearly synonymous with *Scopelarchus* Alcock (1896), for *S. guentheri* Alcock and *Dissomma anale* Brauer are either very closely related or belong to the same species.



Text-fig. 4. Distribution of the Scopelarchidae: *Scopelarchus* spp. as square symbols: *Neoscopelarchoides* spp. as round symbols (For elucidation see key at bottom of chart). Data on the distributions have come from the authorities mentioned in the text and from Pappenheim (1914) and Koumans (1953).

Regan (1911) thought that *Neosudis* Castelnau (1873) might be a scopelarchid; but *Neosudis* has a dorsal fin of sixteen rays placed two thirds of the way back along the body, whereas the dorsal fin in the Scopelarchidae has 6–10 rays and is placed about half-way down the body. As Parr (1928) has pointed out, the genus is evidently not related either to the Scopelarchidae or Evermannellidae.

Benthalbella Zugmayer (1911) has already been considered: its status will be discussed below. Turning to *Promacheon* Weber (1913), which was provisionally included by Parr (1928) in the Scopelarchidae, this genus cannot be fitted into this family. The peculiar triangular tooth on each premaxilla, the number, form and arrangement of the other teeth, the absence of teeth on the palatines, the fin-ray formula (D. 14, A. 17–18, Pect. 15, Pv. 10) and the small number of lateral line scales (*c*. 32), show that *Promacheon* has a character complex quite unlike that of the scopelarchids.

Scopelarchoides Parr (1929) is defined has having two areas of abdominal muscles, one surrounding the base of the pelvic fin, the other being an upper lateral musculature with a limited ventral extension. Between these two areas the body-wall is transparent, for the peritoneum is only separated by connective tissue from the outer skin. The division of these muscles is very like that of *Benthalbella* larvae. Chapman (1939) noted that small specimens of *Neoscopelarchoides dentatus* have a translucent abdominal cavity and that the abdominal musculature is fully developed only in the larger individuals. This suggests that the fishes described as *Scopelarchoides nicholsi* were not completely developed. If this is admitted, the differences between *Scopelarchus* and *Scopelarchoides* are clearly no more than differences between different phases of development. The other characters which Parr (1929) has used to define these two genera are nearly all osteological, involving the lesser development of various bones (prootics, opisthotics, preorbitals and subopercula) in *Scopelarchoides*. Evidence from these characters also indicates that *Scopelarchoides* Parr (1929) cannot be retained as a separate genus, and that it is synonymous with *Scopelarchus* Alcock (1896).

It is clear from this study that the scopelarchids can be divided into two genera only: (1) *Scopelarchus* Alcock (1896) comprising the short-bodied species, in which the origin of the dorsal fin is in front of the insertion of the pelvic fins (*S. guentheri* Alcock, *S. nicholsi* (Parr), and *S. cavei* sp.n.). (2) *Neoscopelarchoides*, comprising the long-bodied species having the origin of the dorsal fin behind the insertion of the pelvics (*Scopelarchus elongatus* Norman, *Neoscopelarchoides dentatus* Chapman, *N. dubius* sp.n. *Benthalbella infans* Zugmayer, and *Scopelarchus linguidens* Mead and Böhlke).

Two names are available for the second genus, *Benthalbella* Zugmayer and *Neoscopelarchoides* Chapman. Zugmayer (1911) described *Benthalbella infans* in an Appendix to his report, since he was unable to determine its systematic position, yet he did point out that there were certain resemblances between his fish and Brauer's *Dissomma anale*. Remarking that, 'Ce poisson est très jeune ou plutôt larvaire', he none the less gave it a name because it was then unknown.

Article 30 of the International Rules of Zoological Nomenclature, Section II*e*, β, states that: 'Species which were *species inquirendae* from the standpoint of the author of the generic name at the time of its publication', '. . . are excluded from consideration in determining the types of genera'. In view of Zugmayer's uncertainty as to its systematic position and his admission of its larval character, *Benthalbella infans* cannot be considered as a genotype. *Neoscopelarchoides* Chapman must thus be the name for the second genus, genotype *N. dentatus*.

The characters of the two genera and the main characters of the species are given in the following key. The distribution of the better known species is also given. See also the chart on p. 313.

There is a full description of the family characters in Parr's papers (1928 and 1929).

KEY TO THE SCOPELARCHIDAE

I. Origin of dorsal fin in front of insertions of pelvic fins. **Scopelarchus** Alcock
Other generic characters: Short bodied, greatest height of body from 17 to 25 per cent of standard length; number of vertebrae from 41 to 48 (41 in *S. cavei*; 46 in *S. guentheri* and 48 in *S. nicholsi*); number of scales in lateral line 43–50.[1] Pectoral rays 19–23.

A. Pelvic fins longer than pectorals and extending beyond origin of anal fin. Fin-rays: D. 6–7, A. 21–23, Pect. 20–22. Pv. 9 **S. nicholsi** (Parr)
Distribution. Gulf of California, off west coasts of Mexico and Central America.

B. Pelvic fins shorter than pectorals and not reaching origin of anal fin

b 1. Number of scales along lateral line 43. Fin-rays: D. 9, A. 21, Pect. 21, Pv. 9 **S. cavei** sp.n.

b 2. Number of scales along lateral line 48–50. Fin-rays: D. 7–9, A. 23–26, Pect. 19–21, Pv. 9 **S. guentheri** Alcock

Synonyms:. *Dissomma anale* Brauer (1902 and 1908), *Odontostomus perarmatus* Roule, (1916)
Distribution. Atlantic Ocean, east of Bouvet Island, Indian Ocean, East Indian Archipelago.

II. Origin of dorsal fin behind insertions of pelvic fins. **Neoscopelarchoides** Chapman
Other generic characters: long-bodied, greatest height of body from 10 to 17·5 per cent of standard length (number of vertebrae 57 in *N. dubius*, 61 in *N. elongatus*). Number of scales in lateral line 56–64 (scales not formed in the holotype and two paratypes of *N. linguidens*). Pectoral rays 21–27.

A. Pectoral fins less than half-length of pelvic fins; caudal peduncle from 20 to 25 per cent of standard length. Fin-rays: D. 6–7, A. 17–21, Pect. 22–25, Pv. 9 **N. dentatus** Chapman
Distribution: Gulf of Alaska; off Central California.

B. Pectoral fins equal to, or considerably more than, half the length of pelvic fins (these fins about equal in length in *N. elongatus*, while in *linguidens* and *dubius* the pectorals are about three-quarters the length of the pelvics). Caudal peduncle from 11 to 15 per cent of standard length.

b 1. Length of pelvic fin more than one-quarter of standard length. Fin-rays: D. 9, A. 21, Pect. 27, Pv. 9 **N. dubius** sp.n.

b 2. Length of pelvic fins considerably less than one-quarter of standard length.

(i) Pectoral fins with 21–22 rays. Fin-rays: D. 8–9, A. 26–27, Pect. 21–22, Pv. 9
Distribution. Off Kerguelen Island; Falklands-Magellan Strait region. **N. elongatus** (Norman)

(ii) Pectoral fins with 25–27 rays. Fin-rays: D. 9–10, A. 28, Pect. 25–27, Pv. 9–10 **N. linguidens** (Mead and Böhlke)

The Family PARALEPIDIDAE

Macroparalepis molestus sp.n.

(Text-fig. 5.)

Holotype. An individual 146 mm. in standard length, taken in a 2 m. net during an experimental haul near station 2209 (53° 07·7′ S, 168° 56·4′ E), near Campbell Island, south of New Zealand. 27. i. 38. 2000 m. wire.

Proportions in hundredths of the standard length (146 *mm.*). Greatest depth of body 4·1; length of head 16·1; length of snout 8·2; horizontal diameter of eye 2·7; width of bony interorbital 1·8; length of lower jaw 9·5; length from tip of snout to origin of dorsal fin 63·0; snout to pelvic fin 49·7; snout to anal fin 78·7; length of pectoral fins 7·5; length of pelvic fin 4·8; depth of caudal peduncle 2·0; length of caudal peduncle 5·1.

Fin-rays. D. 12 (last ray bifid), A. 30, Pect. 12, Pv. 9.

---

[1] Counted from upper angle of operculum to caudal flexure.

Scales. Absent, but there are ossifications along the lateral line, which may be modified scales (Harry, 1953*a*) see Text-fig. 5*c* and *d* and below.

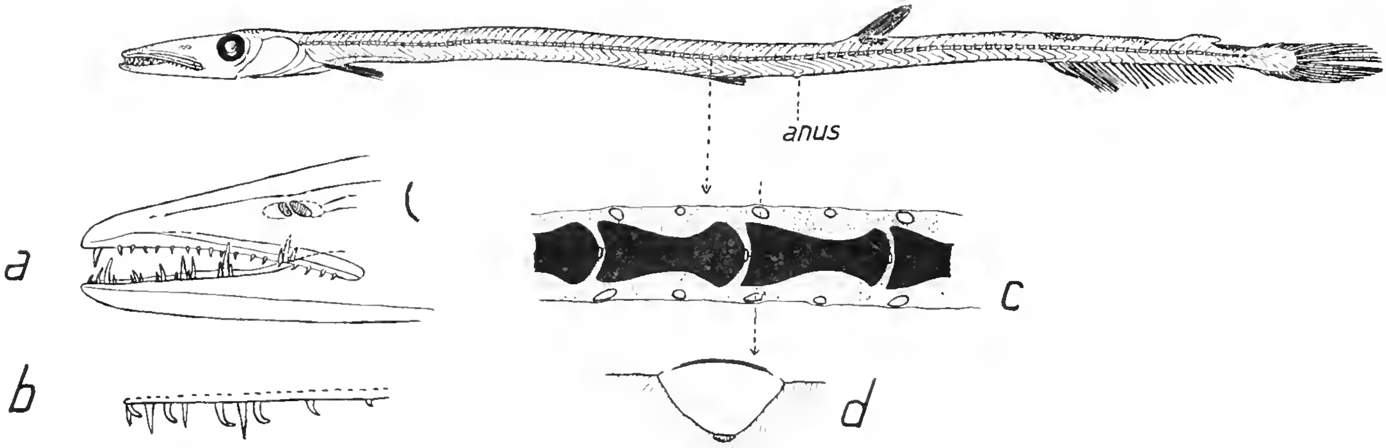
Lateral line. Roofing the gutter-like lateral line along the trunk is a fragile skin in which is set a series of dumb-bell shaped ossifications, one per segment. Above and below each ossification are two pores, the anterior larger than the posterior. Immediately at the end of the ossification comes a small median pore (see Text-fig. 5*c*).

About ninety ossifications occur along the lateral line, the series on the right flank ending opposite the origin of the adipose dorsal fin. The last few, posterior ossifications are not fully developed (presumably the complete series is developed at a later stage).

Number of vertebrae. 101.

Ventral carina. Distinctly developed between the pectoral and pelvic fins.

Dentition. About twenty teeth on the premaxillae, the first being the longest, then come about fourteen retrorse, thorn-like teeth followed by eight or so, small antrorse teeth. Dentary with six long pointed teeth, each of which is flanked by smaller pointed teeth, usually one on each side. Palatines with about 10–12 teeth, these being six hooked outer teeth, and four to six larger, depressible, pointed inner teeth (see Text-fig. 5*b*).



Text-fig. 5. *Macroparalepis molestus* sp.n. Holotype (× 1): *a*, maxillary and mandibular teeth (× 3); *b*, palatine teeth (× 3): *c*, part of lateral line to show pores and bony segments (× 25); *d*, transverse section through lateral line.

Gill-teeth. Rather widely spaced, in a single row, on the upper part of the lower limb of the first gill arch.

Colour (in spirit). Light brown with a peppering of small melanophores along the dorsal surface. Three dorsal 'saddles' of more concentrated pigmentation; the first along the base of the dorsal fin; the second just above the origin of the anal fin, and the third just behind the adipose dorsal fin (see Text-fig. 5).

The study of the above fish has thrown some light on the status of *Macroparalepis* Ege. As a result of his investigations, Harry (1951, 1953*a*) quite reasonably decided to divide *Macroparalepis* Ege into two genera, these corresponding to divisions I and II of Ege's (1933) synopsis of the species. *Macroparalepis* was restricted to division I of the key, while division II was placed under another genus, *Stemonosudis*.

Macroparalepis molestus described above is awkwardly intermediate between these two genera. Like *Macroparalepis*, as defined by Harry (1953), the nostrils of *M. molestus* come before the tip of the maxillary; like *Stemonosudis* the body is slightly compressed and very elongate, the tip of the lower jaw is not elevated and the end of the upper jaw is about 1 orbital diameter from the anterior margin of the eye.

In fin-ray counts *Macroparalepis molestus* is intermediate between the two genera.

	Dorsal	Pectoral	Anal
Macroparalepis	11–14	10–11	24–28
M. molestus	12	12	30
Stemonosudis	9	10–13	37–50

Lastly, in colour pattern *Macroparalepis molestus* partly resembles *Stemonosudis* in having saddles of pigment along the back, but there are no alternating blotches on the base of the anal fin. Furthermore, it is interesting that a pigmentation very similar to that described for *Stemonosudis* has been found by Harry (1953*b*) in a fish that he identifies as a post-larval *Macroparalepis*.

In the present state of our knowledge, it would thus appear advisable to retain *Macroparalepis* as defined by Ege (1933).

The Family ANOTOPTERIDAE

Anotopterus pharao Zugmayer.

Anotopterus pharao Zugmayer, 1911. Result. Camp. sci. Monaco, p. 138, pl. 4, fig. 4 (for a full synonymy see Hubbs, Mead and Wilimovsky (1953)).

During the 1949–50 Antarctic whaling season, the captain of one of the whale-catchers attached to F/F 'Balaena' of United Whalers Limited, obtained a large fish belonging to the genus *Anotopterus*: it was swimming at the surface, the position being approximately lat. 69° S, long. 170° E (Ross Sea area).

Our knowledge of this genus is limited and a search was made through the unnamed Discovery Collections in the hope of finding other specimens. Eventually a small individual of standard length 100 mm. was found: it was taken in the South Atlantic (23° 16′ S, 01° 51·7′ W) in a 450 cm. net hauled obliquely between 600 m. and the surface. The study of these two individuals, as well as of the type of *Eugnathosaurus vorax* Regan and of a specimen of *Anotopterus pharao* from Madeira, forms the basis of this section.

Zugmayer (1911), after examining a fish of total length 165 mm. taken by 'Princesse-Alice' at the North Atlantic station 3028 (36° 54′ 30″ N, 11° 49′ W), described a new genus and species *A. pharao* and furthermore proposed that it should be assigned to a new family, the Anotopteridae. A second fish of 291 mm. taken off Madeira was described by Roule (1927) and compared with the type specimen. Legendre (1934) found five individuals of this species (from 127 mm. to 144 mm.) in the stomachs of *Thunnus alalunga*, caught by fishermen in the Bay of Biscay. These specimens were examined by Roule (1935).

More recently Maul (1946) and Nybelin (1946) have written on *Anotopterus*. Maul obtained specimens of *A. pharao* from the stomachs of *Alepisaurus ferox*, caught off Madeira by local fishermen. Nybelin studied a head (length 150–160 mm.) obtained from the stomach of a halibut (caught by M/S 'Arctica' at 64° 25′ N, 53° 30′ W), and proposed the species *Anotopterus arcticus*. He also examined a complete specimen, of standard length 650 mm., found in the stomach of a fin whale (harpooned in the Weddell Sea at 62° 02′ S, 38° 25′ W) which he regarded as another new species, *A. antarcticus*. Nybelin (1946) also reviewed *Eugnathosaurus vorax*, which was described by Regan (1913) from a head trawled off Coats Land by the Scottish National Antarctic Expedition (station 417 at 71° 22′ S, 16° 34′ W), and he rightly saw that this was a species of *Anotopterus*, but concluded that owing to certain differences in the dentition it was distinct from *A. antarcticus*.

Young *A. pharao* have been recorded from the eastern North Atlantic by Nybelin (1948) and Maul (1952). Nybelin's fish is about 14 mm. long and has 4 palatine teeth: Maul found 14 palatine teeth in a specimen of standard length 47·5 mm.

The foregoing papers were based on fishes from the Atlantic and Antarctic areas, but quite recently Abe (1952) and Hubbs, Mead and Wilimovsky (1953) described specimens from the north-east and north-west Pacific. The latter workers also made a close study of the literature and concluded that there is no good evidence for recognizing more than one species, *pharao*, of the genus *Anotopterus*.

The study of the type of *Eugnathosaurus vorax* and of the two specimens mentioned earlier, together with a specimen from Madeira and published papers, has led me, independently of these ichthyologists, to much the same conclusion. But there is some indication that this one species may be differentiated into a northern and southern form; further material may even show that these 'forms' might better be regarded as separate species. However this may be, my present intention is to bring forward new data on *Anotopterus* and then to point out the differences between fishes from the northern and southern seas. Much of the ground I had intended to cover regarding the status of the species of *Anotopterus* has already been thoroughly dealt with by Hubbs *et al.* (1953).

Comparison of the type specimen of *Eugnathosaurus vorax* Regan (borrowed from the Royal Scottish Museum) with the large Antarctic specimen taken by the whale-catcher has shown them to be closely similar. The measurements in millimetres are given below, those for the type coming first, followed in parentheses by those of the complete fish.

Length of head 150 (147); length of snout 89 (89); horizontal diameter of bony orbit 15·5 (14·5); width of bony interorbital 8·0 (8·0); postorbital length of head 46 (46); length of mandible 111 (108); length of premaxillae 90 (89); length of largest palatine tooth 9·5 (10·5).

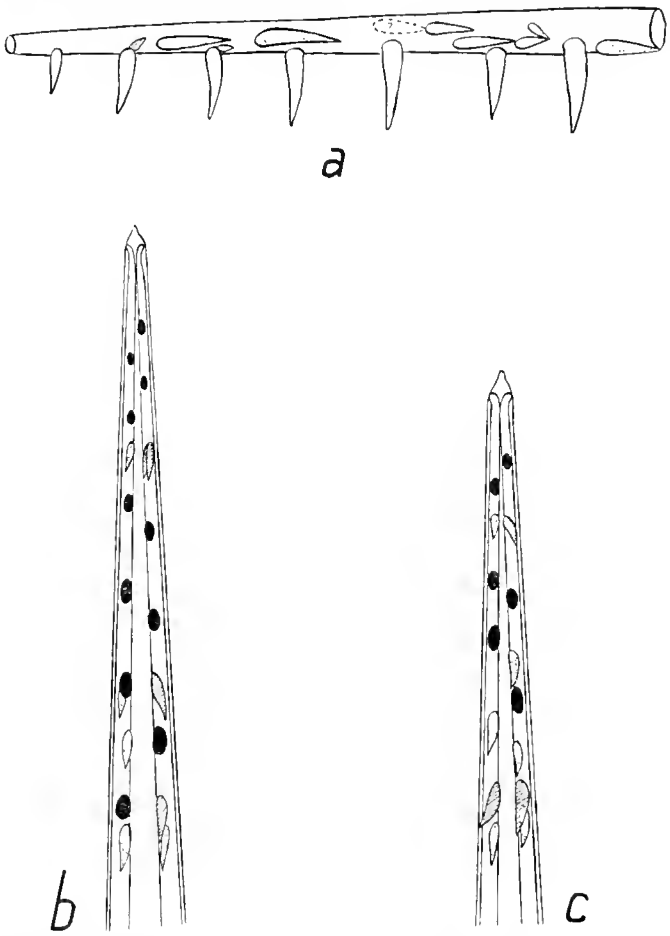
Dentition. The type specimen has no teeth on the first fifth of the length of the left mandible, then come twelve small, pointed and more or less upright teeth, then seven larger teeth inclined backwards and then two squat teeth, shaped rather like a rose thorn. Between the second to fifth mandibular teeth three smaller ones are inserted. In the complete Antarctic specimen, the arrangement of teeth on the left mandible is very similar: there is a short, foremost toothless part, followed by seventeen small, pointed teeth (the first seven of which are inclined forward), then by seven large retrorse teeth and finally by two small thorn-like teeth.

The palatine dentition of the type is well-illustrated in fig. 1 (p. 234) of Regan's (1913) paper. In addition to the teeth shown in this figure, I have found indications of others. There are certainly the remains of a tooth base between the second and third teeth of the right palatine and there are indications of another base in front of the first tooth. On the left palatine there is a tooth base between the second and third teeth; this base is a clear-cut oval with a brownish centre, perhaps an indication of a resorbed tooth. Thus the type had thirteen functional teeth, two of these having been detached at some time.

The palatine dentition of the complete individual is shown in Text-fig. 6*b*. As well as the eleven upright, functional teeth, there are a number of recumbent teeth lying in the dental integument and one obliquely set tooth. The latter is quite hard and is evidently moving upwards into position. The recumbent teeth can be divided into two types: (1) moderately ossified teeth (shown in the figure by cross hatching), and (2) soft teeth (shown dotted). On the right palatine it will be seen that the last two teeth have soft replacement teeth, while on the left palatine two of the moderately ossified recumbent teeth, soon to become functional, are closely associated with what must also be replacement teeth. The tooth pattern suggests that at any time there may be from 11 to 14 palatine teeth in use.

Presumably tooth succession goes on all the time as in *Alepisaurus*. It was of such fishes that Owen (1840–5) wrote: '...the succession of teeth is uninterrupted, the pulps of the new teeth are developed in most of the species in the soft gum or integument covering the dentigerous margins of the bones, and the calcification of the pulp is completed as it lies recumbent and buried loosely in the substance of the gum. The point of the new tooth, which, in this state, is directed backwards, is then exposed by a gradual rotatory movement of the tooth from the horizontal to the vertical position....'

The small individual of standard length 100 mm. taken by R.R.S. 'Discovery II' in the South Atlantic (station 2048, lat. 23° 16′ S, long. 01° 51·7′ W.; 25. iv. 37, N. 450 B: 600–0 m.) has six functional teeth on the left palatine and seven on the right. The dentition of the right palatine is shown in Text-fig. 6*a*. On the right mandible there are seventeen teeth: one retrorse tooth near the symphysis +5 antrorse teeth +11 upright teeth.



Text-fig. 6. Palatine teeth of *Anotopterus pharao*: *a*, right palatine of a specimen 100 mm. in standard length (×6·5); *b* and *c* diagramatic representations of the palatine dentitions of specimens 732 mm. and 278 mm. in standard length (*b*, ×1; *c*, ×1·5). In *b* and *c* the functional teeth are shown in black: the moderately developed replacement teeth are cross hatched; the soft, relatively undeveloped replacement teeth are dotted.

Compared with the type specimen of *Eugnathosaurus vorax*, the proportions of the different parts of the head of the whole fish are as follows. (These figures are in hundredths of the head length, those for the type coming first, followed in brackets by those of the Discovery specimen):

Length of head 150 (24) mm. Proportions per cent: length of snout 59·3 (58·3), width of bony interorbital 5·3 (6·7), horizontal diameter of bony orbit 10·3 (13·3); postorbital length 30·7 (27·1); length of mandible 74·0 (70·8).

The palatine dentition of an individual from Madeira of standard length 278 mm. is shown in Text-fig. 6*c*. There are six completely erect, functional teeth, together with two moderately ossified, obliquely set teeth, one on the left palatine between the first and second upright teeth, the other situated towards the posterior end of the right palatine. Opposite the latter tooth is a fairly well-ossified recumbent tooth, together with a soft replacement tooth. The tooth pattern suggests that, as the fish grows, the complement of these stabbing palatine teeth increases, probably to between eight and ten.

The body proportions and meristic characters of the three complete specimens dealt with above may be seen in Table 2. For other data the reader is referred to Nybelin (1945) and Abe (1952) and the comprehensive tables given by Hubbs, Mead and Wilimovsky (1953).

There are no marked differences in body proportions between all the known individuals of *Anotopterus pharao*. Hubbs *et al.* have remarked that the differences in proportions between *A. pharao* and *A. antarcticus* considered by Nybelin (the pelvic-anal distance, the diameter of the eye, and the depth of the caudal peduncle) are likely to be an expression of age rather than of specific distinctness. Comparison of the 100 mm. and 732 mm. individuals in Table 2 shows them to be closely similar, apart from the relative size of the characters mentioned above. There can be little doubt that these characters are correlated with age. But there seems to be some differentiation within the species in respect of the number of functional palatine teeth and perhaps in the number of vertebrae. (See Table 3.)

Table 2. *Body proportions (expressed in hundredths of the standard length) and meristic features of three individuals of* Anotopterus pharao

Region	Madeira	South Atlantic (23° 16′ S, 01° 51·7′ W)	Antarctic (69° S, 170° E)
Standard length in mm.	278	100	732
Body proportions:			
Head length	20·0	24·0	23·0
Diameter of orbit	2·2	2·8	1·9
Interorbital width	1·25	1·8	1·2
Length of snout	12·2	14·5	12·0
Greatest depth of body	5·3	5·5	3·3
Depth of caudal peduncle	1·6	1·6	1·0
Length of pectoral fin	Damaged	Damaged	7·4
Length of pelvic fin	Damaged	Damaged	3·3
Length between:			
Snout tip—adipose dorsal	91·7	90·0	91·2
Snout—origin of pectoral fin	23·0	23·0	20·2
Origins of pectoral—pelvic fins	38·8	36·0	36·2
Pelvic—anal fins	27·7	25·0	33·1
Pelvic fin—base of caudal fin	38·5	36·0	43·8
Meristic characters:			
Number of palatine teeth	6	13	11
Number of vertebrae	80	—	83
Number of lateral line 'scales'	—	—	83
Number of fin rays:			
Pectoral fin	12	14	14
Pelvic fin	9	9	9
Anal fin	15	15	14

In general the table indicates that fishes from the North Atlantic and North Pacific tend to have fewer (4–10) palatine teeth than those (11–14) in South Atlantic and Antarctic waters, and although there are certain anomalies, the data also suggest that in fishes from northern waters there is a tendency for the number of palatine teeth to increase with age.

The number of vertebrae [($79 \pm 1/2$ to 81) in three northern fishes and 83 in two southern fishes] perhaps lends some support to the suggestion that within this wide-ranging species there is a northern and a southern form. However, Maul's (1952) record from Madeira of a 47·5 mm. fish with 14 palatine teeth has to be considered. All that can be done at present is to draw attention to the possibility considered by Hubbs *et al.* (1953) that *Anotopterus*, like certain ceratoid angler fishes, '...occurs chiefly as young to small adults in the warmer waters and as large adults only in colder waters towards the poles'. Perhaps there is some overlap between the spawning areas of northern and southern forms; perhaps the idea of these two forms is an over-simplification. But these questions must obviously await further data.

Table 3. *Numbers of palatine teeth and vertebrae in* Anotopterus pharao

Authority	Locality	Size of fish (S.L. mm.)	Number of palatine teeth	Number of vertebrae
		NORTH PACIFIC		
Hubbs *et al.* (1953)	Kamchatka	861	10	79 ± 1 or 2 centra
Abe 1952	Kamchatka or Hokkaido	855	10	—
Hubbs *et al.* (1953)	British Columbia	87·3 (head)	5	—
Hubbs *et al.* (1953)	Hokkaido	640·0	10	—
Hubbs *et al.* (1953)	35° 35′ N, 122° 25′ W	299·0	4	—
Hubbs *et al.* (1953)	31° 54·3′ N, 152° 21·6′ W	112·5	8	—
		NORTH ATLANTIC		
Nybelin (1946)	Davis Strait, 64° 25′ N, 53° 30′ W	*c* 150 (head)	10	—
Collett (1896)	Off Cape Finisterre	253 (head)	7	—
Roule (1935)	Bay of Biscay	126–144 (5)	6?	81
Nybelin (1948)	38° 25′ N, 10° 23′ W	14	4	—
Roule (1927)	Madeira	276	6	—
Maul (1946)	Madeira	265–342	6	—
Maul (1952)	Madeira	47·5	14	—
Hubbs *et al.* (1953)	Madeira	247	8	—
Hubbs *et al.* (1953)	Madeira	260	8	—
Marshall	Madeira	278	6	80
		SOUTH ATLANTIC AND ANTARCTIC		
Marshall	23° 16′ S, 01° 51·7′ W	100	13	—
Nyeblin (1946)	Weddell Sea, 62° 02′ S, 38° 25′ W	650	14	83
Marshall	Ross Sea area, 69° S, 170° E.	732	11	83
Regan (1913) and Marshall	Coats Land, 71° 22′ S, 16° 34′ W	150 (head)	11 + 2	—

Lastly, it should be mentioned that the large Antarctic fish bears, on either side of the tail, two basicaudal dermal keels very similar to those described by Hubbs *et al.* (1953) for their large Pacific fishes.

Distribution. It will be apparent from the quotation above, that Hubbs *et al.* (1953) concluded that adult *Anotopterus* probably have an antitropical (bipolar) distribution. The facts presented here—the presence of a young fish in the South Atlantic at latitude 23° S and of a 732 mm. individual in Antarctic waters—does not conflict with this conception.

Concerning the vertical distribution there is definite support for the contention of the foregoing workers that *Anotopterus*, at least when adult, is a surface-dwelling fish.

The fish caught at the surface in the Ross Sea area by the whale-catcher had a very distended abdomen. Soon after capture, this individual vomited up two moderately large *Notolepis coatsi* Dollo of standard lengths 180 mm. and 270 mm. The stomach of each of these fishes was bloated with krill (*Euphausia superba*).

N. coatsi are often to be found in the stomachs of whale-bone whales: in fact nearly all the sizeable specimens in the museum collections have been obtained from whales (see also Clarke, 1950). Examination of the stomach contents of twelve *Notolepis* has invariably shown them to have been eating adult krill. As *Notolepis* feeds on the krill of the surface waters, it is evidently preyed on by *Anotopterus* and in turn both may be fortuitously swallowed by the krill-engulfing whales. It may be concluded that in Antarctic waters *Anotopterus* lives, at least for part of the time, in the upper 100 m. But little is known of the vertical limits of distribution and the possibility of tropical submergence needs to be borne in mind.

PART II. COMPARISON OF ALEPISAUROID AND MYCTOPHOID FISHES

Although the Iniomi have been divided into the suborders Myctophoidea and Alepisauroidea, it is by no means easy to assign clear-cut diagnostic features to these groups. Regan's (1911) definition of the Alepisauroidea was mainly based on the osteology of *Alepisaurus* and *Evermannella*, and he placed the paralepidid fishes and *Sudis* among the Myctophoidea and considered that *Ateleopus* should be put into a third and separate suborder.

Regan's use of the forward attachments of the palatines as a character for separating the alepisauroids and myctophoids cannot be sustained, as a study of Parr's (1929) paper soon shows. The degree of development of the interoperculum (the smallness of this bone in the alepisauroids contrasting with its more normal development in the myctophoids), is a trenchant distinguishing feature, as long as Regan's inclusions within the Alepisauroidea of *Scopelarchus*, *Evermannella*, *Omosudis*, *Alepisaurus* are accepted. But Harry (1951, 1953) has cogently argued that the Paralepididae show a closer relationship to the alepisauroids than to the myctophoids; and in this family the interoperculum is well developed (Parr, 1929). Furthermore, *Anotopterus*, which has many features in common with *Alepisaurus*, differs from the latter in possessing a relatively large interoperculum. Similarly, the preoperculum, which is narrow and almost vertically placed in the Scopelarchidae, Evermannellidae, Omusodidae and Alepisauridae, is broad and boomerang-shaped in the Paralepididae and fairly wide in the Anotopteridae. In both these latter families the preoperculum is obliquely inclined, following the line of the forwardly directed suspensorium.

Regan also based his classification on the design of the pectoral girdle, remarking that in the Myctophoidea the cleithrum is attached to the lower end of the supracleithrum, while in the Alepisauroidea the attachment comes at the upper end of the latter bone. As far as I have been able to extend this observation, it seems true for the myctophoids in which a more 'solid' pectoral girdle is developed, there being a firm join between the supracleithrum and cleithrum. In the myctophoids (*Neoscopelus* and *Lampanyctus crocodilus* were examined) there is a wide area of overlap between these two bones, the cleithrum extending rather beyond the midpoint of the supracleithrum. In the alepisauroids, *Omosudis*, *Evermannella* and *Alepisaurus* the cleithrum is attached to the upper part of the supracleithrum (Regan, 1911; Parr, 1929), but in the paralepidids, although the above attachment is found in *Paralepis speciosa*, Parr (1929) remarks that in *Lestidium intermedium* on the other hand the cleithrum only extends somewhat above the middle of the supracleithrum. Again, in the figure of the pectoral girdle of *Scopelarchus anale* (Parr, 1929), the cleithrum is shown to be attached to the lower end of the supracleithrum. Clearly the type of linkage between these two bones cannot be used as a subordinal diagnostic.

The position of the pectoral fins was also listed as a distinguishing character by Regan, who pointed out that these fins were laterally placed in the myctophoids but were low in position in the alepisauroids. There are a number of exceptions to this generalization and the whole question of the position of the pectoral fins will be more fully discussed in a separate section (pp. 325–28).

Lastly, Regan (1911) said that the Alepisauroidea had '...strong pointed canines in the lower jaw and on the palatines'. This is true for his inclusions, *Scopelarchus*, *Evermannella*, *Omosudis* and *Alepisaurus* and for *Anotopterus*, but this description does not cover certain of the paralepidids, such as *Paralepis* and *Magnisudis* (Harry, 1953). However, there are certain features of dentition possessed by all alepisauroids, namely, the premaxillae each carry a single row of teeth and there are one or two rows of teeth on each palatine and 1–3 rows on each dentary.

Turning now to more recent studies, Harry (1953*a*) stated that the symphysis of the lower jaw is more or less elevated in the Paralepididae, fitting into a corresponding, arched toothless emargination on the upper jaw. As Harry has pointed out elsewhere, the symphysis of the upper jaw is usually toothless in the Alepisauroidea and may be arched. (A specimen of *Evermannella balbo* which I examined had an arched symphysis provided with teeth.) It is also of interest that certain of the Myctophoidea have a bony boss at the symphysis of the lower jaw, which fits into a toothless emargination of the upper jaw (Chlorophthalmidae, Bathypteroidae, *Ipnops*, *Bathymicrops*, *Notosudis*, *Luciosudis* and *Neoscopelus*). In many of the Myctophidae there is certainly a small bony boss at the symphysis of the lower jaw, but this fits against a toothless, slightly depressed area between the two premaxillae, but such close-fitting structures are absent in the jaws of the Aulopidae, Harpadontidae and Synodontidae.

Harry (1953*a*) has also drawn attention to the form of the gill-rakers in the Alepisauroidea. In *Magnisudis* each gill-raker consists of a basal part bearing four long, stiff, depressible, filamentous parts. The rakers of *Alepisaurus ferox* are somewhat similar, each consisting of a basal part supporting a number of spines, of which one to four are longer than the others. Needle-like or spinous gill-rakers are also found in *Paralepis*, *Omosudis* and *Evermannella*.[1] In *Scopelarchus*, *Notolepis*, *Lestidium*, *Macroparalepis* and *Sudis* the rakers are tooth-like. All the gill-arches in *Anotopterus* are without rakers.

More normal lath-like gill-rakers are characteristic of all families of the Myctophoidea, except the Harpadontidae and Synodontidae, these having tooth-like or spinous rakers.

There is therefore much justification for the opening remarks concerning the difficulty of defining the suborders Myctophoidea and Alepisauroidea, but before summarizing this discussion in a section on alepisauroid relationships, there are certain interesting morphological trends within this group which will now be considered. Points of contrast with the myctophoids will then be seen.

The swim-bladder. A survey of the literature and a number of dissections (*Alepisaurus ferox*, *Anotopterus pharao*, *Omosudis lowei*, *Evermannella atrata*, *Scopelarchus guentheri* and *Notolepis coatsi*) show that a swim-bladder is absent in the Alepisauroidea. In the Myctophoidea this organ is only found in the Myctophidae, Marshall (1951 and unpublished) finding a closed swimbladder in twenty-three of the twenty-six species studied. The absence of the swim-bladder in the Aulopidae, Chlorophthalmidae, Synodontidae, Harpadontidae, Ipnopidae and Bathypteroidae was recorded by Günther (1864, 1887).

Correlations between environment and the degree of development of the swim-bladder (including its loss) in teleosts have already been considered by Marshall (1950, 1951) and Jones and Marshall (1953), but in these papers little reference was made to the alepisauroids.

The Alepisauroidea are active, voracious, mid-water fishes, while the Myctophoidea, other than the Myctophidae and Notosudidae seem to be predominantly bottom-dwellers. Many benthic fishes lack a swim-bladder, but the absence of this organ in a mid-water group, such as the Alepisauroidea, is of interest and will be further considered. Marshall (1951 and unpublished) has found a well-developed swim-bladder in many of the bathypelagic fishes, which have centres of abundance in the uppermost 1000 m. of the ocean. But notable exceptions to this rule are found in the Melanostomiatidae, as well as in the Alepisauroidea. (A consideration of the reports by Ege, 1930, Legendre, 1934, and Maul, 1945, supports the view that many paralepidids occur in the uppermost 500 m. and the same would

---

[1] In the specimen of *Evermannella balbo* examined, there are no rakers on the first gill arch but some are present on the second arch.

also appear to be true for *Alepisaurus* and *Anotopterus*. Our knowledge of the vertical distribution of the Scopelarchidae, *Evermannella* and *Omosudis* is less complete.)

Fishes without a swim-bladder are heavier than their environment (Jones and Marshall (1953) have reviewed the data on densities). The only pelagic fish that has been well studied is the mackerel, *Scomber scombrus* with a density of 1·071 and a sinking-factor of 1043.[1]

Very probably other pelagic fishes without a swim-bladder are also heavier than the surrounding water, and, like the mackerel keep their level by unceasing activity. A study of their appearance and food suggests that the Alepisauroidea are active swimmers and their lightly ossified skeletons may point to their having lower sinking-factors than the mackerel. Moreover, Taylor's (1921) work on the density of fish tissues would indicate that the sinking-factor of any alepisauroid is likely to be more than 1000. While there are no observations of swimming in alepisauroids which bear on this problem, it is interesting that Skowron (1928), who studied the luminescence of *Chauliodus sloani*, saw that these fishes at first swam vigorously, but on ceasing active movements sank to the bottom of the container. This, as I have seen in the Red Sea, is also true of *Stomias affinis*. Evidently both fishes are heavier than the surrounding water, and it is significant that, like the alepisauroids, both are without a swim-bladder.

Ossification of the skeleton. Hubbs, Mead and Wilimovsky (1953) found no reason to accept Roule's chimerical hypothesis that *Anotopterus* is a 'monstre normalisé' or 'teratobionte'. Nor is there evidence that this fish or any other alepisauroid is rachitic. Their skeletons are rather delicately but not abnormally built.

A five foot *Alepisaurus ferox* weighs about 4 lb. (Lowe, 1835), a striking indication of its lightly ossified skeleton as well as of its compressed and rather lean-looking body. Harry (1953*a*) has drawn attention to the peculiar cartilaginous development of the jaws in the Paralepididae and Anotopteridae. Certainly, the long time of exposure required to get tolerably clear hard-tube X-ray photographs of these fishes provides further evidence of the lack of calcification in the skeleton; and this is also true of *Omosudis lowei* (S.L. 60 mm.) *Evermannella hyalinus* (S.L. 153 mm.), *Neoscopelarchoides elongatus* (S.L. 198 mm.) and *N. dubius* (S.L. 138 mm.). Only in *Scopelarchus cavei* sp.n. (S.L. 70 mm.) does the degree of ossification of scales and skeleton compare with that, say, in a myctophid.

Moreover, in some of the alepisauroids the calcification of the skeleton seems to be a slow, irregular and protracted process. Beebe (1932) remarks that a post-larval *Omosudis lowei* of total length 11·45 mm. did not have '...a particle of bone in the entire body, fins, fin-rays or appendicular skeleton except for a faint trace in the centre of the supracleithrum'. The head bones, particularly the premaxillae and dentary were well ossified. Similarly, in the large 'Benthalbella' larvae of the scopelarchids, the skeleton, except for the skull, has a soft, cartilaginous texture. In *Anotopterus* the thin, scale-like segments along the lateral line canal (see Text-fig. 7) are only plainly visible in larger individuals. Maul (1946), who studied specimens from 265 mm. to 342 mm. in standard length, remarks that, along the anterior half of one individual, they only became visible after alizarin staining. Lastly, in certain paralepidids (Ege, 1930; Parr, 1931; Harry, 1953*a*), the scaling is not completed until very late in development. I have also found this feature in *Notolepis coatsi*.

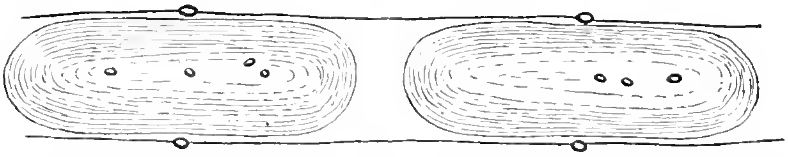
Parr (1937) has suggested that the amount of available vitamin D falls off with increasing depth, and that fishes living at deep levels in the ocean have developed lower requirements for this vitamin, this resulting in less extensive ossification of the skeleton. But assuming vitamin D to be necessary for the normal formation of bone in fishes, *Anotopterus*, *Alepisaurus* and the paralepidids live at levels not very far removed from the phytoplankton-bearing, vitamin D-producing, upper layer of the ocean.

---

[1] $\text{Sinking-factor} = \dfrac{\text{density of fish}}{\text{density of environment}} \times 1000.$

On the other hand, abyssal benthic fishes might be expected to have poorly ossified skeletons, yet in the Bathypteroidae, and Ipnopidae (to consider only the Iniomi), the skeleton is well formed and much denser than in the alepisauroid fishes. (This is well shown in X-ray photographs.) A more solid skeleton is no handicap to a fish which lives on the deep-sea floor, whereas reduced ossification would appear to be an advantage to the bathypelagic Alepisauroidea. This fact compensates these active predacious fishes for the absence of a swim-bladder, for it must result in the lowering of the sinking-factor, and hence less energy is required to maintain the fish at a particular feeding-level in the ocean.

The correlation between the lack of a swim-bladder and the laying-down of less skeletal material in bathypelagic fishes will be considered more fully in a later paper, but one comparison may be made now. *Gonostoma denudatum* has a large, well-developed swim-bladder, while in *G. bathyphilum* there is no trace of this organ. A specimen of *denudatum* (131 mm.) was placed alongside one of *bathyphilum* (122 mm.) and an X-ray photograph obtained. This strikingly confirmed the impression formed by handling these fishes, that *denudatum* had a better ossified skeleton than *bathyphilum*.[1] If this interpretation comes near the truth, more striking corroboration would be hard to find than these structural differences between the two species.



Text-fig. 7. Part of the lateral line (near the origin of the adipose dorsal fin) of *Anotopterus pharao*, showing two of the scale-like ossifications and the lateral line pores (× 6·6).

The setting of the pectoral fins. In defining the two suborders of the Iniomi, Regan (1911) stated that the pectoral fins were lateral in the Myctophoidea, but low in position in the Alepisauroidea. Certainly, the pectorals of *Alepisaurus*, *Anotopterus*, *Omosudis* and *Evermannella* are placed very low on the shoulders, while those of the Aulopidae, Chlorophthalmidae, Synodontidae, Harpadontidae, Ipnopidae and Bathypteroidae are laterally placed. But a number of exceptions to these generalizations are to be found in the Myctophidae, Scopelarchidae and Paralepididae.

Measurements of the angle between the horizontal axis of the body and the axis of the pectoral fin have indicated that such an index comes close to being a diagnostic feature of each suborder. In most alepisauroids this angle is below 45°: in most myctophoids it is above 45°. Data, showing what may be called the pectoral angle, are listed in Table 4.

It is interesting to consider these data in the light of the ideas of Harris (1952) on the function and the evolution of the fins in fishes. Harris contended that, with the evolution of a swim-bladder, there was no longer any tendency for the body to sink or even tilt, because the centres of gravity of the body and the swim-bladder are usually either close together, or else coincident. Pectoral fins set as hydroplanes and an asymmetrical tail, both giving a lift-force (as in sharks) were thus no longer necessary. So the pectorals were freed to become limbs in the Choanichthyes, and brakes (or oars) in the Teleostii, while the caudal fin attained a symmetrical neutral shape, but with a different structural basis, in the Dipnoi, Crossopterygii and Actinopterygii. With increasing specialization of the pectoral fins as brakes, there appears to have been an upward movement of the fins along the sides of the fish and a rotation of the axis of each fin so as to bring the axis near to a vertical position.

Since the Alepisauroidea have no swim-bladder they might be expected to have a specific gravity somewhat greater than their environment (see p. 324). In order to remain at one level, an alepisauroid

---

[1] Fishes of this size may contain well-developed ova, showing that they are nearing, or have attained, the adult phase. Thus the differences in ossification are unlikely to be due to differences in the phase of life.

must presumably make continual compensating movements. Now the setting of the pectoral fins in alepisauroids gives the strong impression that one of their functions is to produce an upward lift during forward motion. Moreover, during the swinging of the tail, the combined caudal and anal fins, which are set close together, may act rather like a heterocercal caudal fin also giving an upward lift. If this is so, the alepisauroids have certain dynamic parallels with the sharks.

Table 4. *Pectoral fin 'angles' in some iniomous fishes.*

ALEPISAUROIDEA			
Scopelarchus guentheri	20°	*Paralepis brevis*	35–40°
S. cavei sp.n.	30°	*P. coregonoides*	25–30°
Neoscopelarchoides elongatus	20°	*P. sphyraenoides*	30°
N. dubius sp.n.	25°	*Anotopterus pharao*	10°
Evermannella balbo	15–20°	*Alepisaurus ferox*	5–10°
Sudis hyalina	45°	*Omosudis lowei*	20–25°
MYCTOPHOIDEA			
Aulopus filamentosus	50°	*Gonichthys cocco*	70°
Chlorophthalmus agassizii	45°	*Ctenobranchus nigro-ocellatus*	75°
Bathysauropsis gracilis	70°	*Diaphus coeruleus*	60°
Bathypterois filifer	70–80°	*D. lutkeni*	55°
Ipnops murrayi	70°	*D. ostenfeldi*	45°
Bathymicrops regis	65°	*D. lucidus*	40°
Harpadon nehereus	40–45°	*D. garmani*	60°
H. squamosus	45°	*Notolychnus valdiviae*	75°
Synodus similis	45°	*Ctenoscopelus phengodes*	45°
Saurida elongata	40°	*Lampadena nitida*	70°
Electrona antarctica	40–45°	*L. chavesi*	60–65°
E. rissoi	60°	*Ceratoscopelus townsendi*	55°
Myctophum affine	55°	*Notoscopelus elongatus*	75°
M. humboldti	50°		

Yet this is to regard the pectorals merely as relatively passive hydroplanes. A study of their structure soon shows that the pectorals of any alepisauroid must have greater mobility than those of a shark. No observations on alepisauroids are available, but Breder and Krumholz (1943) have analysed the functions of the pectoral fins in *Anchoa mitchilli*, which like most clupeids and alepisauroids has low set pectorals, each with an axis making less than 45° with the horizontal axis. (In *A. mitchilli* this angle is about 30°). In spite of a well-developed swim-bladder, an adult *A. mitchilli* is evidently a little heavier than the surrounding water. During swimming there is apparently a slight tendency for the fish to roll, this being counteracted by the constant, irregular beating-down movement of the pectorals. Between these movements, the pectorals also move together in simultaneous down-beats so as to raise the head for swimming. Perhaps the pectorals of the Alepisauroidea have rather similar functions. At all events it is clear that pectorals, with the axis nearer to the horizontal than to the vertical, may act not only as hydroplanes but also as roll-compensating and elevating devices.

But there is another aspect to these considerations. While the evolution of a swim-bladder made possible the evolution of pectoral fins as brakes, the inference that all teleosts with well-developed swim-bladders should have pectorals with this function is only partly true. The remarks above on *A. mitchelli* show this very clearly. When discussing locomotion in the Isospondyli, Breder (1926) remarked that their pectoral fins '...while capable of being folded back do not have the flexibility to be seen in many of the higher teleosts and are not often capable of being used effectively to back water. Their use is more nearly like that of the shark's pectorals...'.

It is significant that the little available evidence suggests that certain isospondylous fishes are somewhat heavier than the environment. This is borne out by the observations of Breder and Krumholz (1943) on *Harengula pensacolae* and *Anchoa mitchilli*, and by measurements of the specific gravity of *Clupea harengus* (Magnan, 1929). Moreover, the studies of the first two authors on *Megalops atlanticus* suggest that the simple, unspecialized type of open swim-bladder, characteristic of most Isospondyli, has a limited function in regulating the specific gravity. After remarking that the pectoral movements of tarpon are not unlike those of *Anchoa mitchilli*, Breder and Krumholz (1943) continue thus: 'Observations in an aquarium of tarpon ranging from 6 cm. to 100 cm. indicate that they seem to become heavier as the time for them to rise for breath approaches. Their pectorals typically work harder and finally with a burst of tail effort they rush to the surface and gulp.... After the ingestion of air they are usually lighter than water and frequently have difficulty descending, until they emit small bubbles by way of the gill clefts, after which they reach a state of approximate balance and from then on become heavier again.'

It would appear therefore, that as far as present knowledge goes, the development of a capacious swim-bladder in the Isospondyli has not always led to a close correspondence between the specific gravity of the body and that of the environment. Correlated with a slight tendency of the fish—at least for part of the time—to sink, the pectorals are set in such a way that they can act as hydroplanes and beat downwards to raise the head. The angle between the axis of the pectoral fin and the horizontal axis of the body in a number of isospondylous fishes is given below.

Elops saurus (40°)
Chanos chanos (15–20°)
Sardinops sagax (30°)
Ilisha filigera (45°)
Odontognathus compressus (45–50°)
Coregonus sp. (45°)
Osmerus eperlanus (40–45°)
Plecoglossus altivelis (25°)
Megalops atlanticus (45°)
Clupea harengus (25°)
Harengula pensacolae (20°)
Pristigaster cayanus (30–35°)
Salmo salar (40°)
Salvelinus alpinus (45°)
Retropinna oameroides (40°)
Galaxias fasciatus (55°)

But not all Isospondyli have an open swim-bladder (see Jones and Marshall (1953)). A closed swim-bladder is commonly found in the Gonostomatidae and Sternoptychidae (Marshall, 1951) and it is of interest to measure the pectoral angle in representatives of these families.

Maurolicus muelleri (60°)
Gonostoma denudatum (45–50°)
Argyropelecus aculeatus (65°)
Polyipnus nuttingi (50°)
Vinciguerria attenuata (40°)
Ichthyococcus ovatus (45°)
Sternoptyx diaphana (60°)

A comparison of the pectoral angle in *Gonostoma denudatum* with that in *G. elongatum* and *G. bathyphilum* (20–25°) is revealing, when considered in the light of the foregoing discussion. *G. denudatum* has a well-developed gas-filled swim-bladder with a powerful gas-secreting complex; *G. elongatum* has a fat-filled swim-bladder with a degenerate complex; *G. bathyphilum* has no swim-bladder. Since the two latter species are probably heavier than their environment, the presence of pectoral fins with a hydroplane-like setting is not surprising. And as *G. denudatum* can presumably bring its weight in water to vanishing point, the possession of pectorals which are beginning to look more like brakes than hydroplanes is more comprehensible.

From these considerations we may return to the Myctophidae, most of which have a swim-bladder. In all investigated species (Marshall, 1951), this swim-bladder is closed and is usually provided with a highly developed gas-secreting complex. Reference to the list of pectoral angles of myctophids (see p. 326) shows that most species have pectorals with a setting more efficient for braking (or paddling) than for hydroplaning.

It would appear therefore that in the Isospondyli and the Iniomi there is some correlation between the possession of a closed swim-bladder and pectorals having angles greater than 45°.[1] But the specialization of pectoral fins as brakes is best seen in the higher groups such as the Percomorphi. It must also be remembered that many of the isospondylous and iniomous fishes with closed swim-bladders undertake considerable diurnal vertical migrations. At the end of a descent, compression of the swim-bladder may leave the fish somewhat heavier than the sea-water, and, until the volume can be restored by gas secretion, the fish will need to make compensating movements. Perhaps this is why the pectorals are not so highly specialized as in the Percomorphi and are set so as to allow some lift-force.

While a closed swim-bladder means that the fish is independent of the surface for replenishing the gases and is able to achieve a finer control of specific gravity, there are certain limitations. Moreover, this discussion does not imply that all fishes with open swim-bladders have only a rough control of their specific gravity. Measurements of their specific gravity (Jones and Marshall, 1953) and observations of their behaviour indicate that cyprinid and esocid fishes are perfectly able to reduce their weight in water to vanishing point. Such fishes are able to manoeuvre more easily than, say, clupeids.

Lastly, the pectorals tend to be lateral and 'brake-set' not only in the Myctophidae but also in other myctophoid fishes, the Aulopidae, Chlorophthalmidae, Synodontidae, Harpadontidae, Ipnopidae and Bathypteroidae. As already mentioned these are predominantly bottom-dwelling fishes and have no swim-bladders, and it is hardly surprising that the pectoral fins should have this setting, for it is a common feature in benthic fishes. Considering only those without a swim-bladder, pectorals with an upright or nearly upright axis are found in the scorpaenids, cottids, nototheniids, gobiids and gobiesocids. Certainly the pectorals in these fishes are used in locomotion and, being so placed, may allow of better control of body movements as the fish grubs for food. The similarity in the setting of these fins in the pelagic Myctophidae on the one hand and the remaining benthic myctophoids on the other is therefore probably an instance of an unusual type of convergence (the independent acquisition of like characters).

The dorsal fin. Except for *Alepisaurus*, the dorsal fin of alepisauroids has 6–15 rays and is set about half-way down the body length. In *Anotopterus* there is no trace of a dorsal fin, while *Alepisaurus* has a long sail-like dorsal, very like that of the sail-fishes (*Istiophorus*). This convergence is, indeed, so striking that it led Dollo (1909) to conclude—on very slender evidence—that *Alepisaurus* uses its dorsal fin as a sail, much in the manner sometimes seen in *Istiophorus*.

In *Alepisaurus ferox* the dorsal fin, which has about 40 rays, originates just behind the head and ends above the origin of the anal fin, i.e. the base of the dorsal extends over more than two-thirds of the standard length. The longest of the anterior rays may measure at least twice the greatest depth of the body.

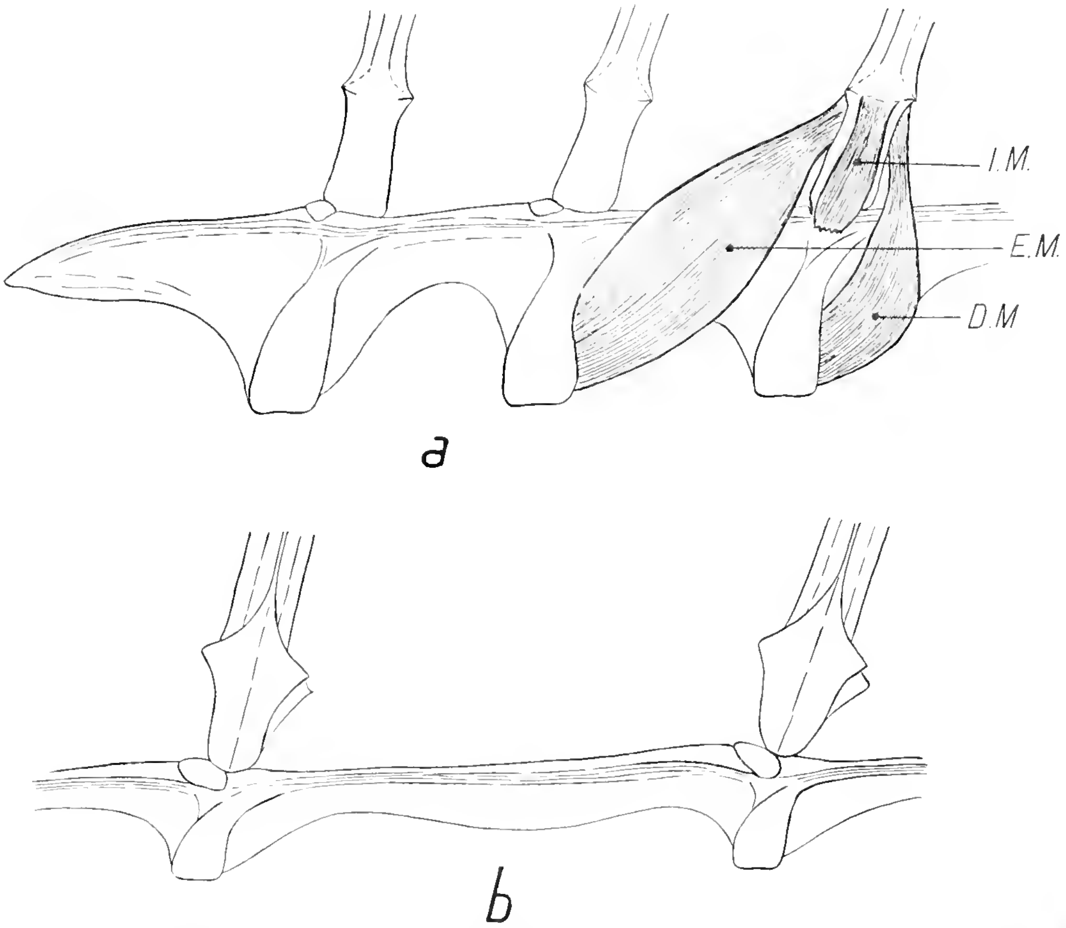
The muscles which move the dorsal fin rays are shown in Text-fig. 8*a*, the upper figure being of the first three rays, the lower of the 14th and 15th rays. It will be seen that the erector muscles are powerfully developed, while the depressors and particularly the inclinators are a good deal smaller.

The basal supports for the dorsal fin are also of interest. At the base of each ray is a distal radial, but it would appear that the intermediate and proximal elements have fused to form a long continuous rod, running the entire length of the dorsal fin, an unusual feature in fishes (Text-fig. 8*a*, *b*). But such a development is hardly surprising in view of the strains imposed on the high dorsal as it is hauled up

---

[1] Two myctophids listed on p. 326, *Gonichthys cocco* and *Ctenobranchus nigro-ocellatus* have no swim-bladder yet have pectoral angles of 70–75°. But both species have a more stream-lined, slender body than other myctophids and both may well keep to a particular level by vigorous swimming movements (rather like *Scomber*). Beebe and Vander Pyl (1944) have remarked on the vigorous unceasing swimming movements of *Gonichthys cocco* as compared with other lantern-fishes.

during active movements. Perhaps the sudden raising of the dorsal gives stability during turns and enables turning to be more rapidly effected, a capacity that may well be important in a fish which preys on such large active fishes as the paralepidids.



Text-fig. 8. Dorsal fin of *Alepisaurus ferox*: *a*, the basal elements supporting the first three dorsal rays. *DM*, *EM*, *IM*, depressor, erector and inclinator muscles of fin-ray (×4·5); *b*, the basal elements supporting the 14th and 15th dorsal rays (×7·5).

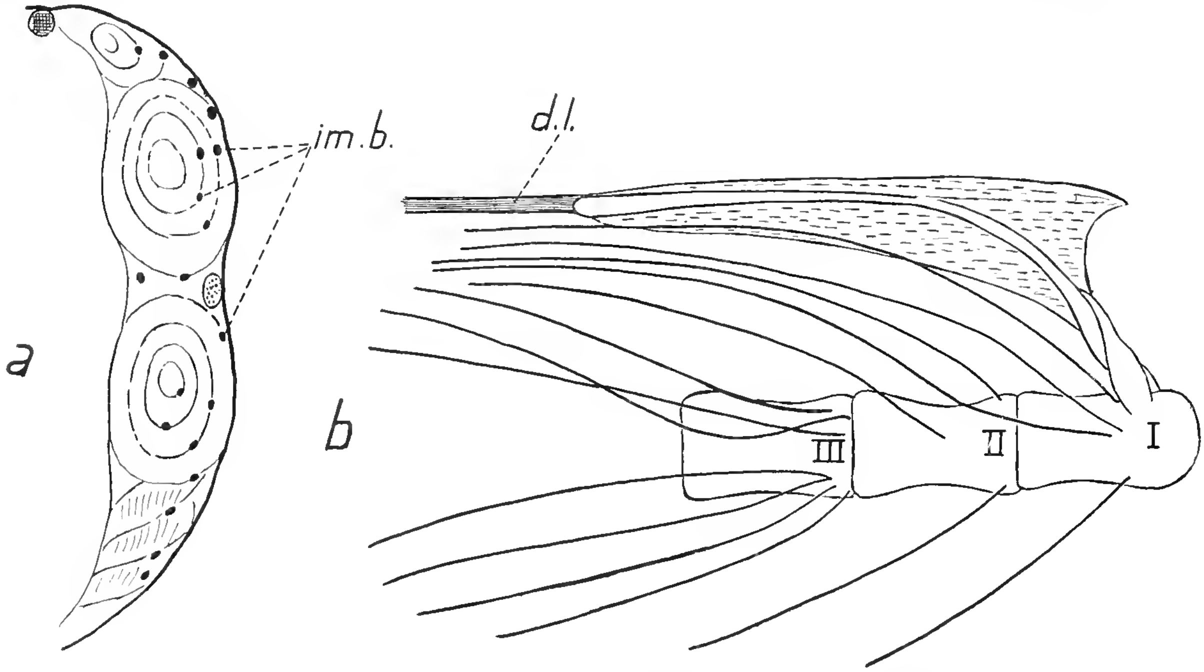
Intermuscular bones

In his *Classification of Fishes*, Berg (1947) remarks that in the lower teleosts true intermuscular bones (epineurals, sometimes also epicentrals) are usually present. In defining the larger groups, Berg states that intermuscular bones are present in the Isospondyli, Haplomi, Ostariophysi (Cyprinoidea) and Apodes. (Definite absence is recorded for the gadoids, Solenichthyes, Microcyprini and Percomorphi.)

Intermuscular bones are also present in certain of the alepisauroid fishes. Hubbs, Mead and Wilimovsky (1953) observed the prominent development of these bones in *Anotopterus* and *Alepisaurus* and described the complex as consisting of a series of thick dorsal elements running horizontally, together with more slender median bones stretching backward and slightly downward. The positions of the intermuscular bones in a transverse section across a medium-sized individual of *Anotopterus pharao* may be seen in Text-fig. 9*a*. The pattern of intermuscular bones in *Alepisaurus* is remarkably similar to that found in *Anotopterus*.

Certain of the Paralepididae and *Omosudis lowei* also have intermuscular bones, which are developed in both the epaxial and hypaxial parts of the myotomes. A drawing of the more conspicuous elements associated with the first three vertebrae of *Omosudis* may be seen in Text-fig. 9*b*. The extraordinary interneural, median, ossified body connected with the first vertebra is also shown. Parr (1929) has already described and figured this ossification, but it may be added that the median dorsal ligament, which runs down the trunk, is attached to its posterior end. In the Paralepididae, I have found intermuscular bones in *Paralepis speciosa*, *P. brevis*, *P. brevirostris* and *P. coregonoides*, but none were found in *Notolepis coatsi*, *N. rissoi kroyeri*, *Lestidium sphyraenoides* and *Sudis hyalina*.

Lastly, X-ray photographs of *Scopelarchus cavei* sp.n., *S. guentheri*, *Neoscopelarchoides dubius* sp.n., *N. elongatus* and *Evermannella balbo* have not revealed the presence of intermuscular bones. (These show up quite clearly in X-ray photographs of paralepidids, *Anotopterus* and *Alepisaurus*.)



Text-fig. 9. *a*, transverse section through the trunk muscles of *Anotopterus pharao*, showing the intermuscular bones (*imb.*) (×9·3); *b*, some of the larger intermuscular bones associated with the first three vertebrae of *Omosudis lowei* (×10·6) *d.l.* = dorsal ligament.

Distensibility of stomach and body-wall

Evermannella, *Omosudis*, *Anotopterus* and *Alepisaurus* are among the alepisauroids capable of swallowing very large prey. Alcock (1899) has a drawing of *Evermannella atrata* very much distended with a large squid, while in the Discovery Collections there is a specimen of *E. indica* with a gonostomatid fish folded up in its stomach, the length of the prey being appreciably longer than the length of the predator's abdomen. The capacity of *Omosudis* for swallowing large prey is well known since Günther's (1887) account of a *Sternoptyx* in the stomach of one individual, victim and predator being equal in bulk. *Anotopterus* also has a highly distensible stomach and body-wall, as the presence of two large *Notolepis coatsi* in the specimen described earlier (p. 321) must indicate. *Alepisaurus* is a highly voracious fish with a comparable capacity for dealing with large prey: in the collections of the Natural History Museum there is an *A. ferox* considerably distended, having swallowed one of its own kind.

There is no record of a scopelarchid or a paralepidid containing large prey (although I have seen many *Notolepis coatsi*, each somewhat distended by a stomach crammed with *Euphausia superba*) and it is interesting that of all the families of alepisauroid fishes, the scopelarchids and paralepidids are the only ones containing species which are fully scaled. Most probably all the scopelarchids are fully scaled, while among the paralepidids this condition obtains in *Magnisudis*, *Paralepis* and *Notolepis* only (Harry, 1953*a*, *b*).

Considering all fishes known to swallow relatively large prey, the striking fact emerges that all are scaleless or have a very reduced squamation. *Omosudis*, *Alepisaurus* and *Evermannella* are completely naked, while *Anotopterus* has scale-like segments only along the lateral line. Other fishes with distensible stomachs and body-walls (the Melanostomiatidae, Idiacanthidae, Astronesthidae, Malacosteidae, Lyomeri, Giganturoidea, *Chiasmodus niger* and *Melanocetus* have no scales). The only known scaled fishes which can engulf large prey are *Stomias* and *Chauliodus*. In *Chauliodus*—and probably in *Stomias*—the scales, which are very thin and do not overlap, lie between the epidermis and the pigmented layer of the corium (Brauer, 1908). Moreover, the scales are not held in pockets, which suggests that fishes cannot have both a normal overlapping scale system and a highly distensible body-wall. Presumably the connective tissue pattern associated with an imbricating squamation sets a limit to the degree of tissue distensibility. However this may be, there is no record of a fish with well-developed, overlapping scales being able to cope with large prey. It is interesting that the scaleless (or virtually scaleless) paralepidids, *Lestidium*, *Macroparalepis* and *Sudis* have relatively larger teeth on the palatines and mandibles than the fully scaled *Magnisudis*, *Paralepis* and *Notolepis*. Is it possible that the larger toothed genera are able to capture (and retain) larger prey and that the loss of scales is an adaptation towards distensibility of the stomach and body wall? On the other hand the scopelarchids with a formidable dentition of stabbing, barbed teeth are completely scaled. A study of the food of these fishes would be of particular interest. (In the stomach of *Scopelarchus guentheri* of standard length 65 mm. I found the remains of copepods and ostracods and a mass of nematocysts, probably of Siphonophora.)

The alepisauroids, which are all pelagic, may be compared and contrasted with the pelagic members of the Myctophoidea, the Myctophidae, *Luciosudis* and *Notosudis*. These latter fishes are fully scaled, the myctophids feeding particularly on copepods and smallish members of the zooplankton (Beebe and Vander Pyl, 1944). There is no evidence that any myctophid fish is able to tackle large prey. *Harpadon*, which of all myctophoid fishes has a dentition most like an alepisauroid, feeds on small fishes and shrimps (Hora, 1934).

To summarize: among the pelagic families of the Iniomi the predominant evolutionary trend in the alepisauroids has been towards adaptations for dealing with nektonic prey, extraordinary elasticity of the tissues of the stomach and body wall being associated with a loss or marked reduction in the scaling. By contrast, the Myctophidae, which feed on planktonic animals, have a complete scaling.

INTERRELATIONSHIPS OF THE ALEPISAUROIDEA

Considerations of the interrelationships within the Alepisauroidea are inseparable from the question whether the suborder represents a natural group, but before attempting to deal with this problem the similarities and differences between the families must be elaborated.

Parr (1929) considered that the Scopelarchidae and Evermannellidae were fairly closely related. Moreover, the other four families, the Alepisauridae, Anotopteridae, Omosudidae and Paralepididae have certain common features.

The characters of these two groups can be listed as follows:

Group 1. Scopelarchidae and Evermannellidae

Intermuscular bones absent: parietals fused with the frontals; anus near to origin of anal fin or midway between pelvic and anal fins;[1] body short to moderately elongate; definite trend towards development of tubular eyes.

---

[1] In larval or juvenile scopelarchids, the anus is closer to the pelvics than to the origin of the anal fin, e.g. in *Neoscopelarchoides linguidens* (Mead and Böhlke, 1953) and in *Benthalbella* larvae.

Group 2. Alepisauridae, Anotopteridae, Omosudidae and Paralepididae

Intermuscular bones present; parietals not fused with frontals (no information on *Anotopterus*); anus much nearer to insertion of pelvic fins than to origin of anal fin; eyes normally formed; definite trend towards development of elongate to very elongate body forms.

It will be noticed that there are certain morphological trends within these two groups. In addition to those listed under the group headings, mention has been made already (pp. 322–31) to others, which can be briefly summarized here. There are tendencies to the development of a lightly ossified skeleton, to the loss of scales, and to the acquisition of means for dealing with very large prey (certain of the mandibular and palatine teeth have become large stabbing canines, and the tissues of the stomach and body wall are distensible). As in the more generalized Isospondyli, the pectoral fins are also set low down on the shoulders and make an angle of less than 45° with the horizontal axis of the body.

These trends lead to more specialized forms, but within each of the two groups there is one family with a more generalized character complex. For example, in Group 1 the Scopelarchidae are fully scaled and have lingual teeth, whereas both these features are absent in the Evermannellidae. In Group 2, some of the Paralepididae are also fully scaled, in contrast to the other three families, the Alepisauridae, Anotopteridae and Omosudidae. In discussing the relationships of the Paralepididae, Harry (1953 *a*) pointed out that *Magnisudis* has many generalized features in common with the Aulopidae and with another myctophoid family, the Chlorophthalmidae. He also considered that the 'Paralepididae are most closely related to the Anotopteridae. They both have the same general proportions, essentially similar osteology, the same peculiar cartilaginous development of the jaws, which is found in these two families alone in the order, and a good number of other similarities.' These two families also show striking resemblances in the development of scale-like ossifications along the lateral line (Text-figs. 5 *c* and 7) and in certain skull features already mentioned on p. 322.

The remaining two families in Group 2, the Alepisauridae and Omosudidae, are perhaps the most nearly related of all. Regan (1911) observed that *Omosudis* has a head, mouth and teeth very much like *Alepisaurus*, and both genera have completely lost the scaling, even along the lateral line.

The alepisauroid fishes are difficult to define, lacking diagnostic characters and it might be argued that they are not a monophyletic group. But Simpson (1953), after expressing his belief that the fissipede carnivores are monophyletic, remarked that he was unable to find a single character that occurred in all fissipedes and in no other mammals. Again, Berg (1940), after defining the Clupeiformes (= Isospondyli), concluded by remarking that 'this order, from which a series of higher orders has arisen, represents an artificial assemblage, its separate members, as may be seen from the diagnosis, greatly differing from one another. In time, the Clupeiformes will doubtless be divided in many orders.'

If the Isospondyli are considered to be merely a convenient grouping of fishes of a 'certain level of organization', then the same may be true of the Iniomi. It has been pointed out on p. 305, that the Iniomi have evolved beyond the 'isospondylous level' mainly in that the premaxillaries exclude the maxillaries from the gape, and it is possible that more than one group of isospondylous—or more likely pre-isospondylous—fishes may 'have tried this experiment' with these jaw-bones. There may well be some parallel with the early evolutionary history of mammals. 'Palaeontologists use an arbitrary criterion that a reptile became a mammal when the dentary-squamosal joint developed and the functional jaw-movement ceased to be on the articular-quadrate joint. This line was probably crossed separately by at least five different lineages...' (Simpson, 1953).

It has also been stressed by Simpson that the development of a higher group of animals seems always to be bound up with definitive adaptive features correlated with a spread into some major living space. 'The adaptive characters involved may be quite broad and varied, as in carnivores and ungulates, or may be quite specific, virtually "single characters" in a taxonomic sense, as in rodents and bats.' As already stated, the alepisauroids are bathypelagic fishes and consideration of the group involves features such as the dentition, type of gill-raker, loss of scales, acquisition of distensible tissues etc., all of which would seem to be correlated with a predacious, large-prey-seizing habit. Such characters remind one more of the broad and varied features of the mammalian carnivores than of those of the bats. (Perhaps in the type of character-complex, the ceratioid angler fishes are the nearest oceanic equivalents to the bats.)

Bearing these theorizings in mind, these studies have done little to dispose of the (partly intuitive) idea that the Iniomi may be no more than an assemblage of lineages, each having attained certain morphological features. When the great differences between, say, a myctophid and *Anotopterus* are considered, the value of keeping the order Iniomi seems questionable. Yet if this is not a compact 'monophyletic' order, it is at the very least a convenient gathering of those 'isospondyloid' fishes with more specialized jaws. Furthermore, there is little reason for discarding the two suborders.

A consideration of the position of the Notosudidae (*Notosudis* Waite, 1916, and *Luciosudis* Fraser-Brunner, 1931), provides something of a test of the usefulness of the classification used in this report (p. 306). The dentition of both genera is somewhat similar to that described for the alepisauroids (p. 305), while the general body-form is reminiscent of certain paralepidids. (Fraser-Brunner, 1931, regarded *Luciosudis* as a paralepidid, while Mead and Taylor, 1953, have listed their new species *Luciosudis harryi* under the Paralepididae.) But the combination of certain features (lath-shaped gill-rakers, anal fins with relatively few rays, lateral pectoral fins with 'axial angles' of more than 45°, pelvic fins set well forward of the mid-standard length and a well-developed scaling) indicates clearly that the Notosudidae have closer affinities with the Myctophoidea.

Similarly there are certain iniomous fishes (not yet described) in the Discovery Collections with no scales and a single row of teeth on the premaxillae, dentaries and palatines—all alepisauroid features—but with an underlying myctophoid character-complex quite like that described for the Notosudidae. But unlike the Notosudidae, one of these new species appears to have a peculiar system of light organs over the flanks. These new fishes must undoubtedly be placed in a new family and if closer examination confirms the presence of light-organs, then the contrast between the Myctophoidea, having three families in which photophores of peculiar structure have arisen, and the Alepisauroidea, in which photophores have not been evolved, will be further emphasized.[1]

But it is also of interest that in number and arrangement of branchiostegal rays (3–4+4–5) the alepisauroids are a more homogeneous suborder than the myctophoids, in which there are three main groups: (1) The Chlorophthalmidae, Ipnopidae, Bathypteroidae, Neoscopelidae and *Luciosudis* most nearly resemble the alepisauroids in having 3–5+4–8 branchiostegal rays. (2) The Myctophidae have 2+5–6+0–2 rays (numbers on the epihyal, ceratohyal and hypohyal). (3) The third group, which consists of the Aulopidae, Synodontidae and Harpadontidae, has more numerous branchiostegal rays. (*Aulopus filamentosus* 8+7, *Hime japonica* 7+7, Synodontidae 12–16; *Synodus lucioceps* 8+10, *Saurida undosquamis* 6+10; Harpadontidae 17–25: *Harpadon nehereus* 9+14. One specimen of each species examined.) Furthermore, the orbitosphenoid bone seems to be consistently absent in the alepisauroids, but may be present or absent in the myctophoids (Regan, 1911; Parr, 1929). However, these aspects of the character-complex of the Myctophoidea will be considered in a later paper.

It is reasonable to conclude that the Myctophoidea and the Alepisauroidea are, at least, useful taxonomic groupings. Each can be adequately defined by a rather loose assemblage of characters and by certain morphological trends. But further discussion of the classification in terms of evolution had

---

[1] Apart from the deep-sea Isospondyli, no predacious, bathypelagic fish has an elaborate system of light-organs.

best be postponed until we know more of the functional morphology and ecology of these fishes. Perhaps study of the Notosudidae and the new fishes mentioned on p. 333 will throw some light on these interesting but somewhat intractable problems.

SUMMARY

This report deals with certain aspects of the classification and functional morphology of the alepisauroid fishes. These are voracious, bathypelagic forms, which, together with the sub-order Myctophoidea form the order Iniomi.

Part I contains a revision of the Scopelarchidae, which are shown to fall into two well-marked genera, *Scopelarchus* Alcock and *Neoscopelarchoides* Chapman. Two new species, *Scopelarchus cavei* and *Neoscopelarchoides dubius* are described and *N. elongatus* (Norman) is redescribed. The remarkably large larval form, *Benthalbella infans* Zugmayer is shown to be a young stage of a species of *Neoscopelarchoides*.

The remainder of the first part is taken up with a description of *Macroparalepis molestus* sp.n. and a review of the family Anotopteridae. While there is no good evidence for regarding *Anotopterus* as consisting of more than one species, *A. pharao* Zugmayer, there is some indication that this species may be differentiated into northern and southern forms.

Some discussion of the classification of the Iniomi, leading to certain considerations of functional morphology, forms the second part of the report. Alepisauroids are compared and contrasted with myctophoids and possible correlations between the presence and absence of a swim-bladder, the degree of ossification of the skeleton and the setting of the pectoral fins are traced. Adaptations for dealing with large prey and the development of intermuscular bones are also reviewed.

In the concluding section, relationships within the Alepisauroidea are considered; and finally there is some discussion on the status of the order Iniomi.

BIBLIOGRAPHY

Abe, T., 1952. *Records of the 'Mizu-uo-Damahi' (New Japanese name),* Anotopterus pharao, *and a record of the 'Etchiopia',* Brama raii, *from near the surface of the North-western Pacific.* Jap. J. Ichth. II (4/5), pp. 230–8.

Alcock, A., 1896. *Natural history notes from H.M. Indian Marine Survey Steamer* 'Investigator', *Series II, No. 23. A supplementary list of the marine fishes of India, with descriptions of 2 new genera and 8 new species.* J. Asiat. Soc. Beng. LXV (2), no. 3, pp. 301–8.

—— 1899. *A descriptive catalogue of the Indian deep-sea fishes in the Indian Museum...collected by the Royal Indian Marine Survey Ship* 'Investigator'. Calcutta.

Beebe, W., 1932. *Nineteen new species and four post-larval deep-sea fish.* Zoologica, N.Y. XIII (4), pp. 47–107.

Beebe, W. and Vander Pyl, M., 1944. *Eastern Pacific Expeditions of the New York Zoological Society.* XXXIII. *Pacific Myctophidae (Fishes).* Zoologica, N.Y. XXIX (2), pp. 59–95.

Berg, L. S. 1947. *Classification of fishes, both recent and fossil.* Trav. Inst. zool. Acad. Sci. U.R.S.S. V (2), pp. 1–517. (Translation in Ann Arbor, Michigan.)

Breder, C. M. 1926. *The locomotion of fishes.* Zoologica, N.Y. IV (5), pp. 159–297.

Breder, C. M. and Krumholz, L. A., 1943. *On the locomotion and feeding behaviour of certain post larval Clupeoidea.* Zoologica, N.Y. XXVIII (2), pp. 61–7.

Brauer, A., 1902. *Diagnosen von neuen Tiefseefischen, welche von der Valdivia-Expedition gesammelt sind.* Zool. Anz. XXV (668), pp. 277–98.

—— 1906. *Die Tiefsee-fische. I. Systematischer Teil.* Wiss. Ergebn. 'Valdivia', XV, pp. 1–420.

—— 1908. *Die Tiefsee-fische. II. Anatomischer Teil.* Wiss. Ergebn. 'Valdivia', XV (2), pp. 1–266.

Castelnau, F. L. de Laparte de, 1873. *Contributions to the ichthyology of Australia.* VII. *Fishes of New Caledonia.* Proc. Zool. Acclim. Soc. Victoria, 1872, pp. 110–22.

Chapman, W. M., 1939. *Eleven new fishes and three new genera of oceanic fishes collected by the International Fisheries Commission from the north-eastern Pacific.* Proc. U.S. nat. Mus. LXXXVI (3062), pp. 501–42.

CLARKE, R., 1950. *The bathypelagic angler fish* Ceratias holbölli *Kröyer.* 'Discovery' Rep. XXVI, pp. 1–32.

COCCO, A., 1838. *Su di alcuni Salmonidi del mare di Messina; lettera al Ch.d. Carlo Luciano Bonaparte.* Nuovi Annali delle Scienze Naturali, Bologna, II, pp. 161–94.

COLLETT, R., 1896. *Poissons provenant des campagnes du yacht* 'l'Hirondelle' (1885–1888). Résult. Camp. sci. Monaco, X, pp. 1–198.

DOLLO, L., 1909. *Les poissons voiliers.* Zool. Jb. XXVII (5), pp. 419–38.

EGE, V., 1930. *The North Atlantic and the Mediterranean species of the genus* Paralepis *Cuv. A systematical and biological investigation.* Reprinted from Rep. Danish oceanogr. Exped. Medit. II, A. 13, pp. 1–201.

—— 1933. *On some new fishes of the families Sudidae and Stomiatidae.* Vidensk. Medd. dansk. naturh. Foren. Kbh. XCIV, pp. 223–36.

FOWLER, H. W., 1901. *Note on the Odontostomidae.* Proc. Acad. nat. Sci. Philad. LIII, pp. 211–12.

FRASER-BRUNNER, A., 1931. *Some interesting West African fishes and descriptions of a new genus and two new species.* Ann. Mag. nat. Hist. Ser. 10, VIII, pp. 217–25.

GÜNTHER, A., 1864. *Catalogue of the fishes in the British Museum,* V, pp. 1–455.

—— 1887. *Report on the deep-sea fishes collected by* H.M.S. 'Challenger' *during the years 1873–1876.* Rep. Sci. Res. Challenger. Zool. XXII, pp. 1–335.

HARRIS, J. E., 1952. *Fin patterns and mode of life of fishes.* Essays in marine biology. Oliver and Boyd, Edinburgh, pp. 17–28.

HARRY, R. R., 1951. *Deep-sea fishes of the Bermuda Oceanographic Expeditions. Family Paralepididae.* Zoologica, N.Y. XXXVI (1), pp. 17–35.

—— 1953*a*. *Studies on the bathypelagic fishes of the family Paralepididae 1. Survey of the Genera.* Pacif. Sci. VII (2), pp. 219–49.

—— 1953*b*. *Studies on the bathypelagic fishes of the family Paralepididae (Order Iniomi). 2. A revision of the North Pacific species.* Proc. Acad. nat. Sci. Philad. CV, pp. 169–230.

HORA, S. L., 1934. *Wanderings of the bombay-duck,* Harpodon nehereus *(Hamilton Buchanan) in Indian waters.* J. Bombay nat. Hist. Soc. XXXVII (3), pp. 640–54.

HUBBS, C. L., MEAD, G. W. and WILIMOVSKY, N. J., 1953. *The widespread, probably antitropical distribution and the relationship of the bathypelagic iniomous fish* Anotopterus pharao. Bull. Scripps. Instn. Oceanogr. tech. VI (5), pp. 173–98.

JONES, F. R. H. and MARSHALL, N. B., 1953. *The structure and functions of the teleostean swimbladder.* Biol. Rev. XXVIII, pp. 16–83.

KOUMANS, F. P., 1953. *Biological results of the Snellius Expedition.* XVI. *The Pisces and Leptocardii of the Snellius Expedition.* Temminckia, IX, pp. 177–275.

LEGENDRE, R., 1934. *La faune pélagique de l'Atlantique au large du Golfe de Gascogne recueillie dans les estomacs de Germons. Première Partie: Poissons.* Ann. Inst. océanogr. Monaco, XIV (6), pp. 249–418.

LOWE, R. T., 1835. *Additional observations on* Alepisaurus ferox. Trans. zool. Soc. Lond. I, pp. 395–400.

MAGNAN, A., 1929. *Les caractéristiques géométriques et physiques des poissons avec contributions à l'étude de leur équilibre statique et dynamique.* Ann. Sci. nat. (Zool.) (10), XII, pp. 1–133.

MARSHALL, N. B., 1950. *Air bladder structure and vertical distribution in deep-sea fishes.* Ann. Rep. Challenger Soc. III, No. 11, p. 26.

—— 1951. *Bathypelagic fishes as sound scatterers in the ocean.* J. Mar. Res. X (1), pp. 1–17.

MAUL, G. E., 1945. *Monografia dos peixes do Museu Municipal do Funchal. Familia Sudidae.* Bol. Mus. Funchal No. 1 (1), pp. 1–37.

—— 1946. *Monografia dos peixes do Museu do Funchal. Ordem. Iniomi.* Bol. Mus. Funchal No. 2 (2), pp. 5–61.

—— 1952. *Additions to previously revised families.* Bol. Mus. Funchal No. 6 (16), pp. 51–62.

MEAD, G. W. and BÖHLKE, J., 1953. Scopelarchus linguidens, *a new bathypelagic fish from off northern Japan.* Jap. J. Ichth. II (6), pp. 241–45.

MEAD, G. W. and TAYLOR, F. H. C., 1953. *A collection of oceanic fishes from off north-eastern Japan.* J. Fish. Res. Bd. Can. X (8), pp. 560–82.

MURRAY, J. and HJORT, J., 1912. *The depths of the ocean.* London: Macmillan.

NORMAN, J. R., 1937. *Fishes.* Rep. B.A.N.Z. Antarct. Res. Exped. 1929–1931, (B) I (2), pp. 49–88.

NYBELIN, O., 1946. *Sur quelques espèces du genre* Anotopterus *Zugmayer et sur la position systématique de la famille des Anotopteridae.* Göteborgs VetenskSamh. Handl. (6) V*b* (1), pp. 3–16.

—— 1948. *Fishes collected by the 'Skagerak' Expedition in the eastern Atlantic 1946.* Göteborgs VetenskSamh. Handl. (6) V*b* (16), pp. 1–95.

OWEN, R., 1840–5. *Odontography; or a treatise on the comparative anatomy of the teeth; their physiological relations, mode of development, and microscopic structure in the vertebrate animals. Vols. I and II.* London: Hippolyte Baillière.

PAPPENHEIM, P., 1914. *Die Fische der deutschen Südpolar-Expedition 1901–1903. II. Die Tiefseefische.* Dtsch. Südpol Exped. 15, Zool. VII, pp. 163–200.

Parr, A. E. 1928. *Deep sea fishes of the order Iniomi from the waters around the Bahama and Bermuda Islands.* Bull. Bingham oceanogr. Coll. III, Art. 3, pp. 1–193.

—— 1929. *A contribution to the osteology and classification of the orders Iniomi and Xenoberyces.* Occ. Pap. Bingham oceanogr. Coll. No. 2, pp. 1–45.

—— 1931 *a. Deep-sea fishes from off the western coast of North and Central America.* Bull. Bingham. oceanogr. Coll. II, Art. 4, pp. 1–53.

—— 1931 *b. On the genera* Paralepis *and* Lestidium *and the taxonomic status of some of their species.* Copeia, No. 4, pp. 152–8.

—— 1937. *Concluding report on fishes.* Bull. Bingham oceanogr. Coll. III, Art. 7, pp. 1–79.

Regan, C. T., 1911. *The anatomy and classification of the teleostean fishes of the order Iniomi.* Ann. Mag. nat. Hist. Ser. 8, VII, pp. 120–33.

—— 1913. *The Antarctic fishes of the Scottish National Antarctic Expedition.* Trans. roy. Soc. Edinb. XLIX, pp. 229–92.

Roule, L., 1916. *Notice préliminaire sur quelques espèces nouvelles ou rares des poissons provenant des croisières de S.A.S. le Prince de Monaco.* Bull. Inst. océanogr. Monaco, No. 320, pp. 1–32.

——1919. *Poissons provenant des campagnes du yacht* 'Princesse Alice' et *du yacht* 'Hirondelle II'. Résult. Camp. sci. Monaco, LII, pp. 1–190.

——1927. *Considérations sur deux espèces abyssales de poissons récemment entrées au Musée Océanographique, et sur la valeur tératologique possible de l'une d'elles.* Bull. Inst. océanogr. Monaco, No. 497, pp. 1–12.

—— 1935. *Nouvelles observations sur un poisson abyssal* (Anotopterus pharao *Zugm.*). Bull. Soc. zool. Fr. LX (3–4), pp. 324–30.

Roule, L. and Angel, F., 1930. *Larves et alevins des poissons provenants des croisières du Prince Albert Ier de Monaco.* Résult. Camp. sci. Monaco, LXXIX, pp. 1–148.

Schmidt, J. 1918. *Argentinidae, Microstomidae, Opisthoproctidae, Mediterranean Odontostomidae.* Rep. Danish oceanogr. Exped. Medit. II, Biol. A 5, pp. 1–40.

Simpson, G. G. 1953. *The major features of evolution.* New York: Columbia University Press.

Skowron, S., 1928. *Über das Leuchten des Tiefseefisches* Chauliodus sloanii. Biol. Zbl. XLVIII, pp. 680–5.

Taylor, H. F., 1921. *Air bladder and specific gravity.* Bull. U.S. Bur. Fish. XXXVIII, pp. 121–6.

Waite, E. R., 1916. *Australian Antarctic Expedition, 1911–1914. Under the leadership of Sir Douglas Mawson,* D.SC. B.E. *Fishes.* Austral. Antarct. Exped. Sci. Rep., Ser. C, III (1), pp. 1–92.

Weber, Max, 1913. *Die Fische der Siboga-Expedition.* Siboga Exped. Monog. 57, Livr. LXV, pp. 1–710. Leiden.

Zugmayer, E., 1911. *Poissons provenant des campagnes du Yacht* 'Princesse-Alice' (1901–1910). Résult. Camp. Sci. Monaco. XXXV, pp. 1–174.

PLATE XIX

Fig. 1. *Neoscopelarchoides elongatus* (Norman), lateral view × 1

Fig. 2. *Neoscopelarchoides elongatus*, dorsal view of head × 1

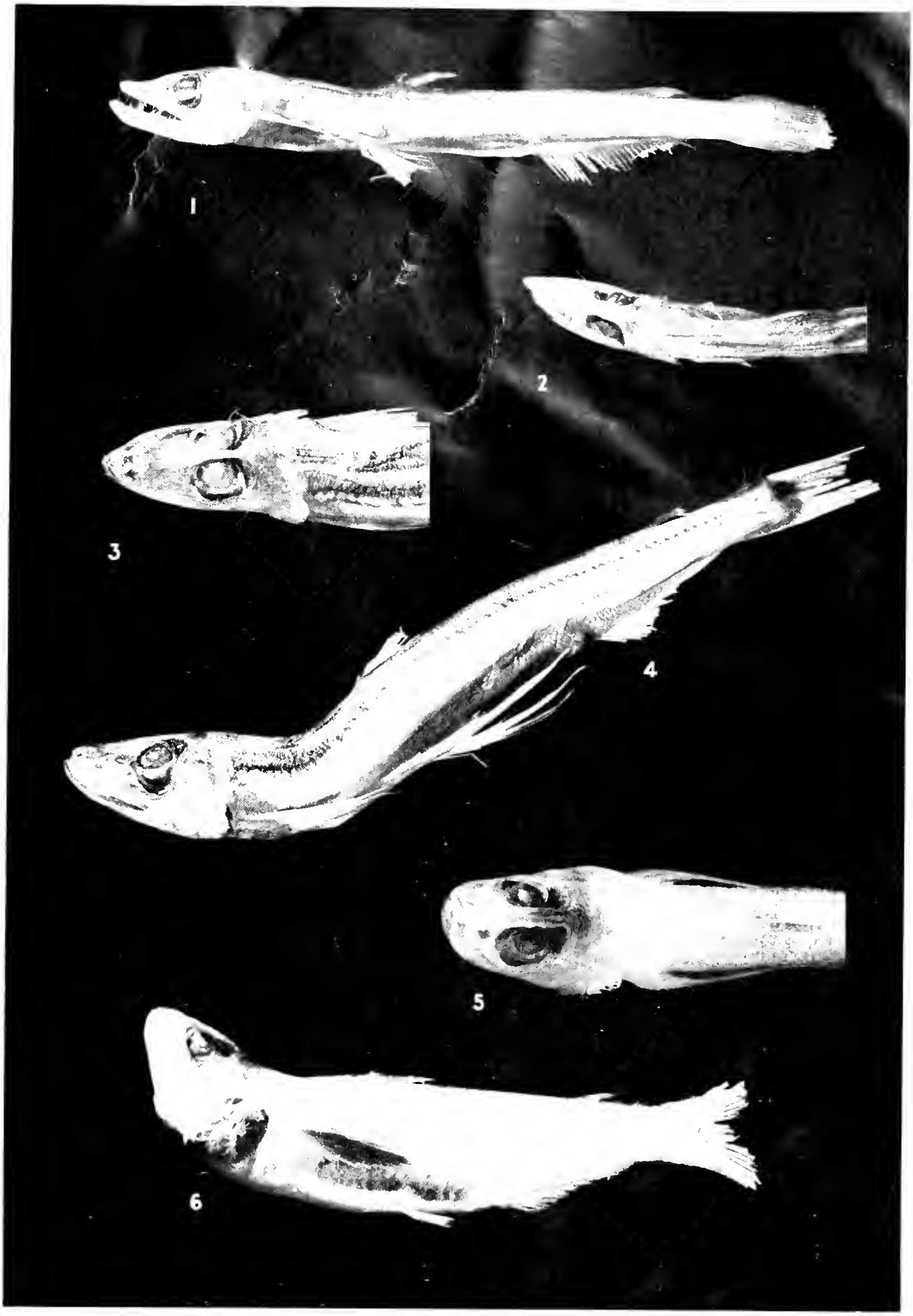
Fig. 3. *Neoscopelarchoides dubius* sp.n., dorsal view of head × 1

Fig. 4. *Neoscopelarchoides dubius* sp.n., lateral view × 1

Fig. 5. *Scopelarchus cavei* sp.n., dorsal view of head × 2

Fig. 6. *Scopelarchus cavei* sp.n., lateral view × 1½.

PLATE XIX



[*Discovery Reports. Vol. XXVII, pp.* 337–376, *August* 1955.]

EUPHAUSIACEA OF THE BENGUELA CURRENT

FIRST SURVEY, R.R.S. 'WILLIAM SCORESBY', MARCH 1950

By

BRIAN P. BODEN

CONTENTS

EUPHAUSIACEA OF THE BENGUELA CURRENT

FIRST SURVEY, R.R.S. 'WILLIAM SCORESBY', MARCH 1950

By Brian P. Boden

(Text-figs. 1–24)

ACKNOWLEDGEMENTS

THIS report was started while I was oceanographer on the staff of the Bermuda Biological Station for Research Inc. My thanks go to the succession of directors the station had during this short period for encouraging me to continue with the work at the expense of station duties.

Dr T. John Hart, National Institute of Oceanography, performed the onerous task of preliminary plankton sorting with his usual skill and patience and sent the euphausiids to me in Bermuda.

I am particularly indebted to several of the staff of the Scripps Institution of Oceanography for their critical reading of the manuscript and their numerous suggestions.

INTRODUCTION

The material upon which this report is based is drawn from the collections made by R.R.S. 'William Scoresby' during her eighth commission and her first survey of the Benguela Current off the coast of South-West Africa.

The stations occupied during this cruise are shown in Fig. 1. The collections were made in March 1950. The hauls were vertical and made with an N 70 closing-net of plankton silk of 70 meshes to the inch and with a mouth diameter of 70 cm.

Fourteen species were represented at these stations; their occurrence is given on pp. 340–45. An overall picture of distribution based on the results of a single cruise may very well be misleading, and therefore the counts are presented simply in tabular form and efforts at interpretation are postponed until the results of the second survey are available. Full station data may be obtained from the *Discovery Reports*, *Station List*, vol. XXVI. Descriptions of the South African species as adults are to be found in Boden (1954).

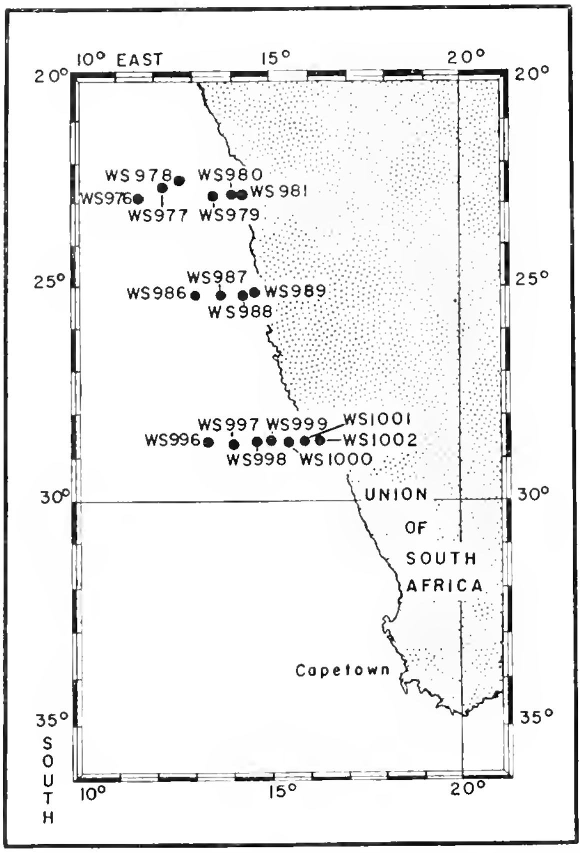


Fig. 1. Plan of stations at which euphausiids were taken during the survey of the Benguela Current by R.R.S. 'William Scoresby', March 1950.

DISTRIBUTION OF THE EUPHAUSIACEA IN THE BENGUELA CURRENT

Thysanopoda microphthalma G. O. Sars

Thysanopoda microphthalma G. O. Sars, 1885, p. 106; *T. distinguenda* Hansen, 1905*a*, p. 17.

One adult female was taken from between 500 m. and 250 m. at station WS 977. Illig (1930) has previously reported the species from the coast of South-West Africa.

Nyctiphanes capensis Hansen

Nyctiphanes capensis Hansen, 1911, p. 19; *N. australis* Stebbing, 1905, p. 113 (*nec* Sars, 1885); *N. australis* Stebbing, 1910, p. 299; *N. africana* Zimmer, 1912, p. 3.

Table 1. *Occurrence of* Nyctiphanes capensis

Station no.	Depth (m.)	Adult males	Adult females	Larvae
WS 979	50–0	6	12	4071
	100–50	4	5	1111
WS 980	50–0	—	2	58
	100–50	1	3	173
WS 981	50–0	—	—	5
WS 988	50–0	—	—	267
	100–50	—	1	452
WS 989	50–0	—	—	454
WS 997	50–0	—	—	—
	100–50	—	—	—
	250–100	—	—	—
	500–250	—	—	—
	750–500	—	—	—
	1000–750	—	—	1
WS 998	50–0	—	—	157
	100–50	—	—	24
	175–100	—	—	7
WS 999	50–0	—	3	952
	100–50	—	—	19
	150–100	—	—	5
WS 1000	50–0	3	13	62
	100–50	—	2	10
	150–100	—	—	52
WS 1001	50–0	9	22	651
	100–50	—	11	17
WS 1002	50–0	—	1	1

The stations at which *N. capensis* was taken are shelf stations. Like other members of the genus, the species is characteristically an inhabitant of shallow, coastal waters. Good collections have been made previously in the Sturrock Dock in Capetown (Boden, 1954).

N. africana Zimmer (1912) is included here as a synonym. Zimmer's rather vague descriptions and drawings of two specimens taken from the stomach contents of the Cape snoek, *Thyrsites atun*, almost certainly refer to *Nyctiphanes capensis* and the fish were taken well within the distribution range of *N. capensis*.

Euphausia lucens Hansen

Euphausia splendens Dana *sens* G. O. Sars, 1885, p. 80; *E. lucens* Hansen, 1905*b*, p. 9; *E. uncinata* Colosi, 1917, p. 186.

Table 2. *Occurrence of* Euphausia lucens

Station no.	Depth (m.)	Adult males	Adult females	Larvae
WS 976	50–0	—	—	—
	100–50	—	—	—
	250–100	—	—	—
	500–250	—	4	5
	750–500	—	5	4
	1000–750	—	—	—
WS 977	50–0	—	1	—
	100–50	—	—	—
	250–100	—	—	—
	500–250	—	—	—
	750–500	—	—	—
	1000–750	—	—	—
WS 978	50–0	—	—	1
	100–50	—	—	—
	250–100	—	—	—
	500–250	—	1	—
	750–500	—	—	—
WS 979	50–0	—	—	14
	100–50	—	—	—
WS 986	50–0	—	—	15
	100–50	—	—	—
	250–100	2	6	1
	500–250	—	2	1
	750–500	—	—	1
	1000–750	—	—	3
WS 996	50–0	—	—	65
	100–50	—	1	6
	250–100	—	—	37
	500–250	—	—	21
	750–500	—	—	5
	1000–750	—	—	8
WS 997	50–0	—	3	14
	100–50	—	—	16
	250–100	—	1	2
	500–250	—	—	—
	750–500	—	—	1
	1000–750	—	—	10
WS 1000	50–0	36	237	—
	100–50	—	5	—
	150–100	—	—	—
WS 1001	50–0	2	18	3
	100–50	—	14	3
WS 1002	50–0	—	6	37

E. lucens is an oceanic species which flourishes in the Pan-Antarctic (Rustadt, 1930) waters. It is probable that in the waters of the Benguela Current it is approaching the limit of its range (John, 1936; Boden, 1954).

Euphausia tenera Hansen

Euphausia gracilis G. O. Sars, 1885, p. 89 (*nec E. gracilis* Dana, 1852, p. 644); *E. tenera* Hansen, 1905*b*, p. 9.

Table 3. *Occurrence of* Euphausia tenera

Station no.	Depth (m.)	Adult males	Adult females	Larvae
WS 996	50–0	—	—	5
	100–50	—	2	2
	250–100	—	—	13
	500–250	—	—	6
	750–500	—	—	1
	1000–750	—	—	6

This tropical to subtropical species occurred at only one station. Since this station is a southern one, it is probable that many of the unidentified pre-furcilia larvae encountered at other stations are really *E. tenera.*

Euphausia recurva Hansen

Euphausia recurva Hansen, 1905*b*, p. 13.

Table 4. *Occurrence of* Euphausia recurva

Station no.	Depth (m.)	Adult males	Adult females	Larvae
WS 976	50–0	—	—	—
	100–50	1	—	—
	250–100	1	2	—
	500–250	6	4	4
	750–500	7	7	—
	1000–750	—	—	—
WS 977	50–0	4	5	—
	100–50	1	—	—
	250–100	—	—	—
	500–250	—	—	—
	750–500	—	—	—
	1000–750	—	—	—
WS 996	50–0	—	—	—
	100–50	1	—	—
	250–100	1	2	—
	500–250	7	9	—
	750–500	—	—	—
	1000–750	—	—	—
WS 997	50–0	7	13	—
	100–50	2	2	—
	250–100	3	2	—
	500–250	—	—	—
	750–500	—	—	—
	1000–750	—	—	—

Evidence of diurnal vertical migration may be discerned in these data. At the day stations WS 976 and WS 996 the animals are absent from the surface layers while at the night stations WS 977 and WS 997 they are concentrated in the upper layers and absent from the lower layers.

Euphausia hanseni Zimmer

Euphausia hanseni Zimmer, 1915, p. 180.

Four adult females of this species were taken, one from station WS 978 and three from station WS 987. All were taken between 250 m. and 100 m.

Euphausia similis var. armata Hansen

Euphausia similis var. *armata* Hansen, 1911, p. 24; *E. similis* var. *lobata* Zimmer, 1914, p. 425.

This species occurred at station WS 997. One adult male was taken between 100 m. and 50 m. and one female between 1000 m. and 750 m.

Nematoscelis megalops G. O. Sars

Nematoscelis megalops G. O. Sars, 1885, p. 127.

Table 5. *Occurrence of* Nematoscelis megalops

Station no.	Depth (m.)	Adult males	Adult females	Larvae
WS 976	50–0	—	—	10
	100–50	—	—	2
	250–100	—	—	2
	500–250	—	—	—
	750–500	—	1	4
	1000–750	—	—	—
WS 977	50–0	1	4	108
	100–50	—	—	—
	250–100	2	2	—
	500–250	—	—	7
	750–500	—	—	—
	1000–750	—	—	—
WS 978	50–0	—	—	—
	100–50	—	—	—
	250–100	—	—	37
	500–250	—	—	350
	500–350	—	—	44
	750–500	—	—	—
WS 986	50–0	—	—	37
	100–50	—	—	37
	250–100	—	—	135
	500–250	—	—	23
	750–500	—	—	—
	1000–750	—	—	2
WS 997	50–0	—	—	1
	100–50	—	—	—
	250–100	—	—	9
	500–250	—	—	—
	750–500	—	—	—
	1000–750	—	—	2

Interesting indications of diurnal vertical migration are evident in these data. Station WS 977 is a night station (21.03–03.45 hr.) and the larvae are concentrated in the upper 50 m. At station WS 978 (10.00–13.04 hr.) a premature closing of the net at 350 m. and subsequent repetition of the 500–250-m. haul reveals a concentration of larvae between 250 m. and 350 m. This, in conjunction with the layering between 250 m. and 100 m. at station WS 986 (08.05–14.07 hr.), indicates that the animals concentrate around 250 m. in the daytime. Evidence of the vertical migration of a very closely allied species, *N. difficilis*, and its possible relation to sonic scattering layers in the Pacific has been presented previously (Boden, 1950*a*).

Thysanoëssa gregaria G. O. Sars

Thysanoëssa gregaria G. O. Sars, 1883, p. 26.

Table 6. *Occurrence of* Thysanoëssa gregaria

Station no.	Depth (m.)	Adult males	Adult females	Larvae
WS 976	50–0	—	—	4
	100–50	—	—	—
	250–100	—	—	—
	500–250	—	—	—
	750–500	—	—	1
	1000–750	—	—	—
WS 996	50–0	—	—	3
	100–50	—	—	—
	250–100	—	—	—
	500–250	—	—	—
	750–500	—	—	—
	1000–750	1	—	—
WS 997	50–0	—	—	1
	100–50	—	—	2
	250–100	1	—	2
	500–250	—	—	—
	750–500	—	—	—
	1000–750	—	—	—

This species is usually quite common in this area (Boden, 1954). Its worldwide distribution is of an antitropical nature (Hubbs, 1950, 1952), although Tattersall (1926) claims that it is common in the deeper waters in the tropical oceanic area. This leads to an attractive speculation that the apparent tropical discontinuity of distribution may be associated with a submergence along temperate isotherms. Actually Tattersall's and Moore's (1952) records are not below 28° N. Brinton (Scripps Inst. of Oceanography—personal communication) finds that the species actually does seek deeper waters toward the tropical limits of its range. The limited number of deep hauls which he has made in the equatorial regions of the Pacific, however, have not yielded any specimens of *T. gregaria* and he is of the opinion that it is a true antitropical species.

Nematobrachion boöpis Calman

Nematodactylus boöpis Calman, 1896, p. 17; *Nematobrachion boöpis* Calman, 1905, p. 153.

Two adult females were captured between 750 m. and 500 m. at station WS 976.

Stylocheiron maximum Hansen

Stylocheiron maximum Hansen, 1908*a*, p. 92.

Two larvae of this species were taken, one at the 250–100-m. level at station WS 976 and the other in the upper 50 m. at station WS 986. At station WS 997 an adult female was taken between 100 m. and 50 m. and another between 500 m. and 250 m.

Stylocheiron elongatum G. O. Sars

Stylocheiron elongatum G. O. Sars, 1883, p. 32.

Eleven larvae were encountered between 1000 m. and 500 m. at station WS 976. One was taken in the upper 50 m. at station WS 997.

Stylocheiron longicorne G. O. Sars

Stylocheiron longicorne G. O. Sars, 1883, p. 32; *S. mastigophorum* (*partim*) Chun, 1887, p 30.

One larva was taken between 500 m. and 250 m. at station WS 997.

Stylocheiron affine Hansen

Stylocheiron affine Hansen, 1910, p. 118.

Five larvae were taken in the upper 250 m. at station WS 976.

A small number of unidentifiable larvae occurred at stations WS 976, 977, 978, 988, 997, 998, 999 and eggs were present in the upper layers at stations WS 976, 977, 978, 986, 996, 997, 998 and 999.

REMARKS

Physical oceanographic conditions in the Benguela Current (Currie, 1953) are somewhat similar to those found in the California Current, and a very close similarity in phytoplankton populations and successions in the two currents has been stressed by Hart (1953).

In general, the distribution of comparable species of euphausiids substantiates this similarity in the two regions. *Nyctiphanes capensis* occupies the same inshore niche in South African waters that *N. simplex* does in Californian waters. *Euphausia lucens*, reaching the northern limit of its range in the Benguela, may be compared with *E. pacifica*, which reaches its southern limit in the California Current. The distribution of *Nyctiphanes megalops* in this survey is very similar to that of *N. difficilis* in California, and that of *Euphausia recurva* and *Thysanoëssa gregaria* is the same in both regions.

Curiously enough, species with comparable distributions in the two currents show remarkable morphological similarities. The appearance of *Nyctiphanes capensis* closely resembles that of *N. simplex*. This is true of all four species of *Nyctiphanes*. These species all occur in areas of upwelling where conditions are roughly the same.

Euphausia lucens and *E. pacifica* are undoubtedly the most closely morphologically allied species in this large genus. Even the copulatory organs of the males show many points of similarity.

Nematoscelis difficilis and *N. megalops* are so closely similar that the females are inseparable. On these grounds Einarsson (1942) cancelled *N. difficilis*. The males are separable on small but consistent differences in the copulatory organs, however, and the species has, therefore, been revived (Boden, 1954).

The distribution of euphausiids in the Pacific is now fairly well understood (Brinton, unpublished) and it may become possible to draw further analogies when the results of the second survey of the Benguela Current have been evaluated.

DEVELOPMENTAL PHASES

It was possible to glean some information on the developmental phases of four of the species encountered. This is presented below.

Nyctiphanes capensis Hansen

Egg. Size range 0·34–0·38 mm. in formalin.

The eggs are carried in two pear-shaped sacs attached by their anterior broad sides to the endopodites of the sixth and seventh cormopods, and by their narrow posterior ends to the exopodites of the eighth cormopods (precisely as in *N. simplex*).

Only one female with intact egg-sacs was found in the collection (Fig. 2). There were fourteen eggs in one sac and sixteen in the other. The perivitelline space of the eggs is small (Fig. 3*a*).

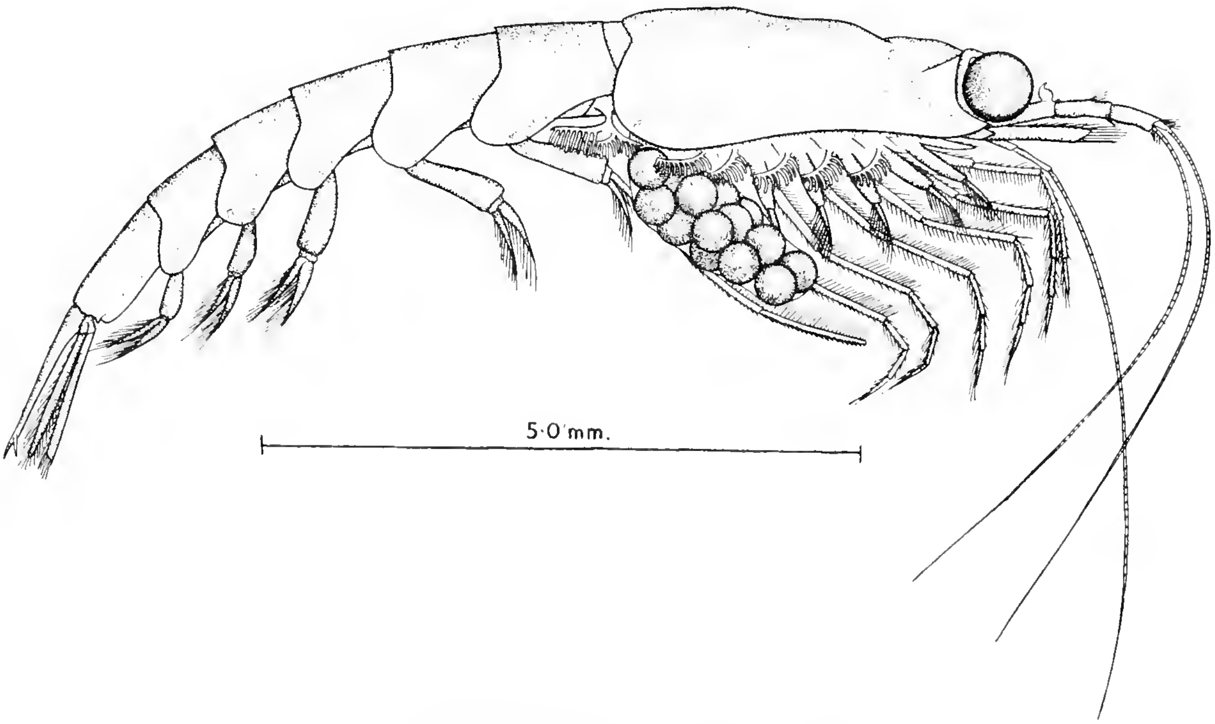


Fig. 2. *Nyctiphanes capensis.* Ovigerous female.

Nauplius. The nauplius stage (Fig. 3*b*, *c*) is passed within the egg-sac. The specimens shown in the figure were removed from the unruptured egg-sac of the female.

The length of the two specimens examined was 0·42 mm. each.

The larva is simple and egg-shaped. It has two small processes at the posterior end, each flanked by one smaller process.

The first antenna is uniramous with three terminal setae. The second antenna is biramous, the rami with four and five terminal setae. The mandible is bud-like and naked.

Pseudometanauplius. Only one specimen of this stage was found (Fig. 3*d*, *e*). It was removed from the ruptured egg-sac of a female. It is probable that the rest had already hatched out.

Length of specimen 0·48 mm. The carapace is oval in dorsal view. The first antenna is unchanged. The second antenna is the same as in the nauplius stage. A median eye has appeared. The anterior lip and buds of three metanaupliar limbs have appeared. There is now a short tail with one pair of postero-lateral and two pairs of terminal spines. The carapace, mandibles, anterior lip, limb-buds and tail are covered by a thin skin.

Metanauplius. No specimens in this stage were encountered. The metanaupliar stage is very transitory and the larva begins to eat only in the next stage. It is probably almost identical with the metanauplii of other species of this genus (cf. Lebour, 1925; Boden, 1951).

First calyptopis. Description based on examination of six specimens (Fig. 4*a–c*). Length range 0·98–1·10 mm.; average length 1·03 mm. Carapace length 0.60–0·63 mm.; average length 0·62 mm.

The carapace is a long, high, narrow dome covering the entire anterior part of the body, and it has no projections of any sort along its inferior margin.

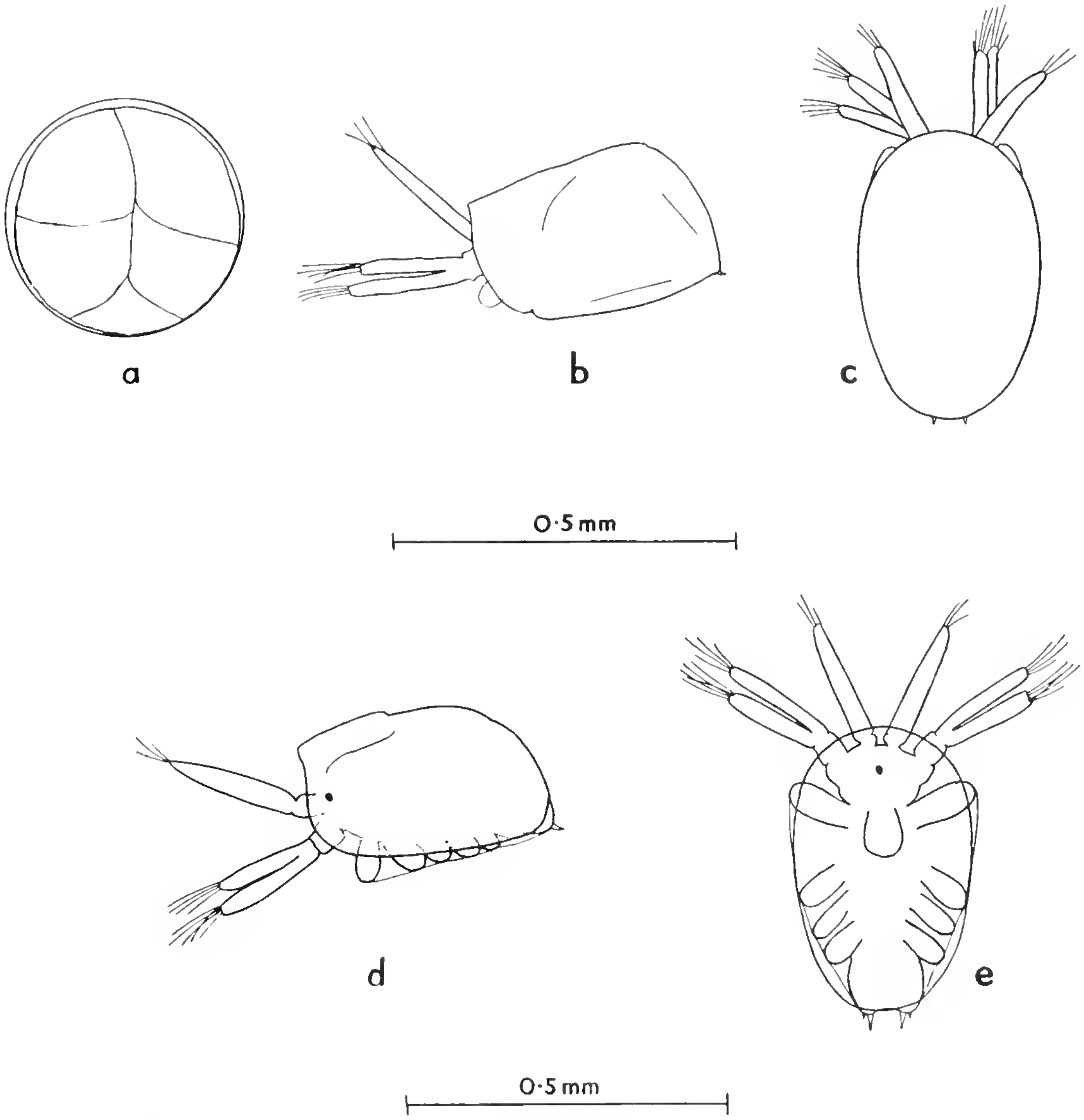


Fig. 3. *Nyctiphanes capensis. a*, egg; *b*, nauplius, lateral view; *c*, nauplius, dorsal view; *d*, pseudometanauplius, lateral view; *e*, pseudometanauplius, ventral view.

The single median eye is visible with the ocular plates on either side of it bearing the rudimentary ocular luminous organ.

The first antennae project forward and downward and are to all intents uniramous. The rudiments of the inner ramus can be seen, however, bearing three setae. The outer ramus carries five terminal setae. The setae are naked.

The second antennae project outward and downward and are carried on a peduncle having two segments. The anterior and longer ramus of the antennae is unsegmented and is armed terminally with four strong setose spines, and laterally with two spines. The second ramus is segmented distally and carries six terminal setose spines.

The mandible is naked and provided with strong biting jaws.

The first and second maxillae and first thoracic limb are present and very strongly resemble the same appendages in *N. australis* as figured by Sars (1885) and in *N. couchii* as figured by Lebour (1924). They are directed forward, are setose, and are used in feeding. The larva first begins eating in this stage. The thoracic segments without limbs are distinct as narrow encircling wrinkles in the integument.

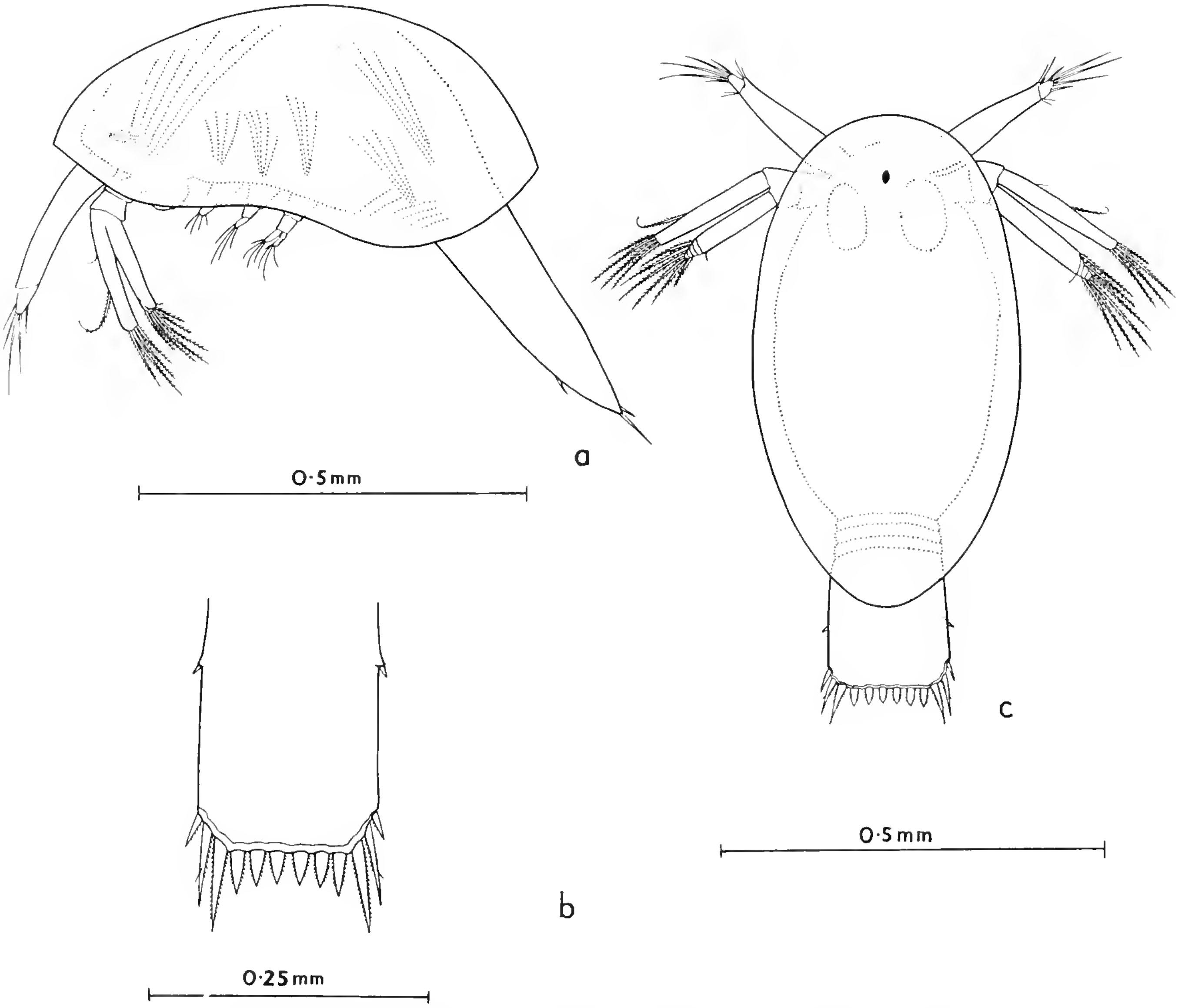


Fig. 4. *Nyctiphanes capensis*. *a*, first calyptopis, lateral view; *b*, telson of same; *c*, first calyptopis, dorsal view.

The abdomen is smooth and unsegmented. The telson has six, serrate, terminal spines decreasing in size from the outer to the inner, three pairs of serrate, postero-lateral spines increasing in size from the outer to the inner, and one pair of small ventro-lateral spines.

Second calyptopis. Six specimens examined (Fig. 5*a*–*c*). Length range 1·40–1·52 mm.; average length 1·46 mm. Carapace length ± 0·85 mm.

The carapace is a little longer than half the total length, and is smooth along the inferior margin (cf. *N. australis*, smooth; *N. simplex*, smooth; and *N. couchii*, denticles).

The median eye is lost and the compound eyes are now well defined but not pigmented. The ocular luminous organ is visible.

There are three segments to the peduncle of the first antenna, which is biramous, the outer ramus carrying four terminal spines and the inner, three.

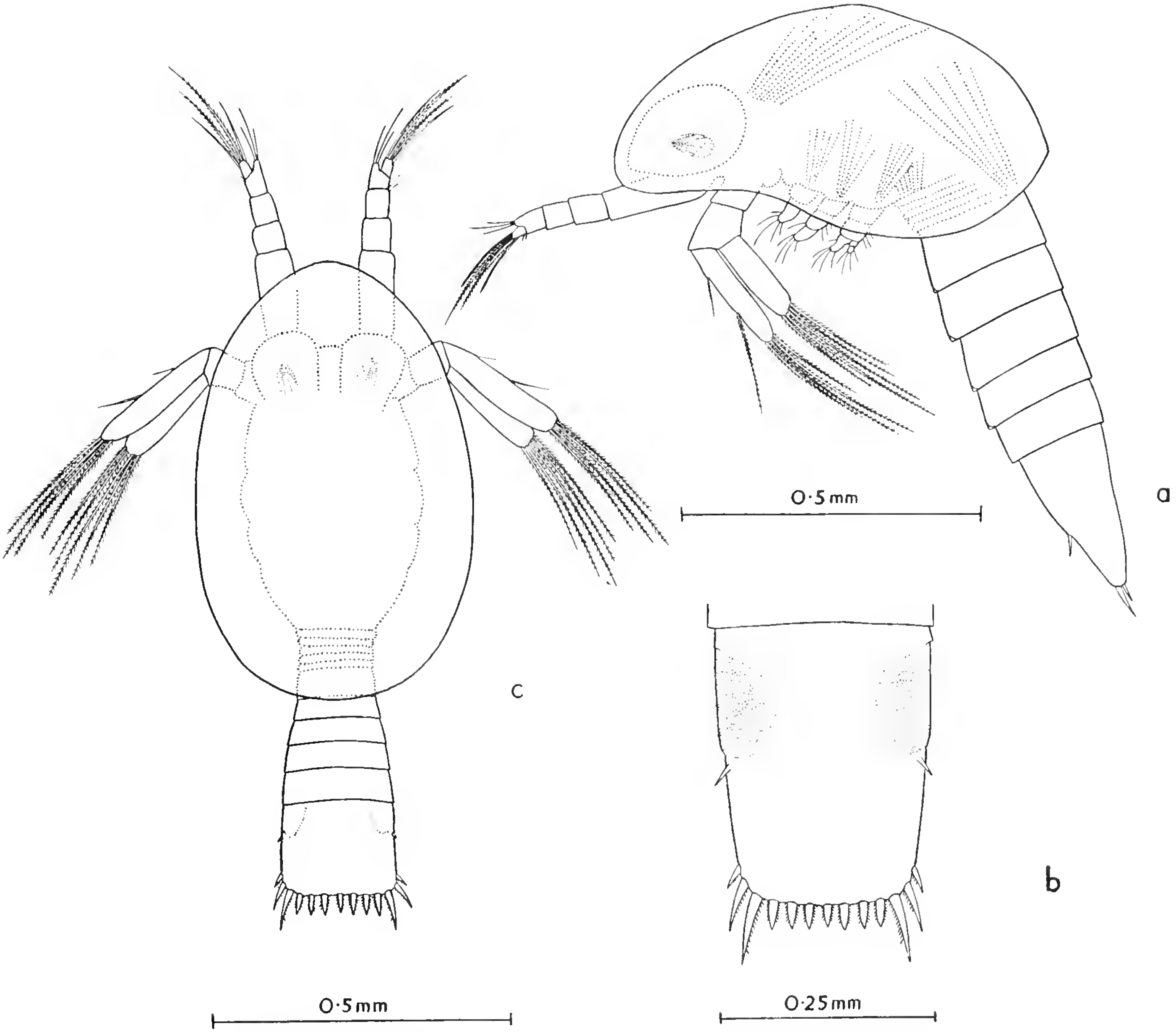


Fig. 5. *Nyctiphanes capensis*. *a*, second calyptopis, lateral view; *b*, telson of same; *c*, second calyptopis, dorsal view.

The remaining thoracic appendages are larger than in the preceding stage but are otherwise unchanged. Occasionally the rudiments of the second thoracic limb may be discerned as a small naked process. The segmentation of the thorax is clearly visible.

The abdomen now has five segments and a telson. The developing uropods can be seen within the integument of the telson. The telson retains the three pairs of postero-lateral and one pair of ventro-lateral spines of the previous stage, but now has seven terminal, serrated spines.

Third calyptopis. Six specimens examined (Fig. 6*a–c*). Length range 1·79–2·22 mm.; average length 1·90 mm. Carapace length ±0·97 mm.

The carapace is a little longer than half the total length of the larva. At this stage a small but distinct tooth appears on the inferior margin of the carapace toward its posterior end. The carapace covers the compound eyes which are now globular and distinctly pigmented.

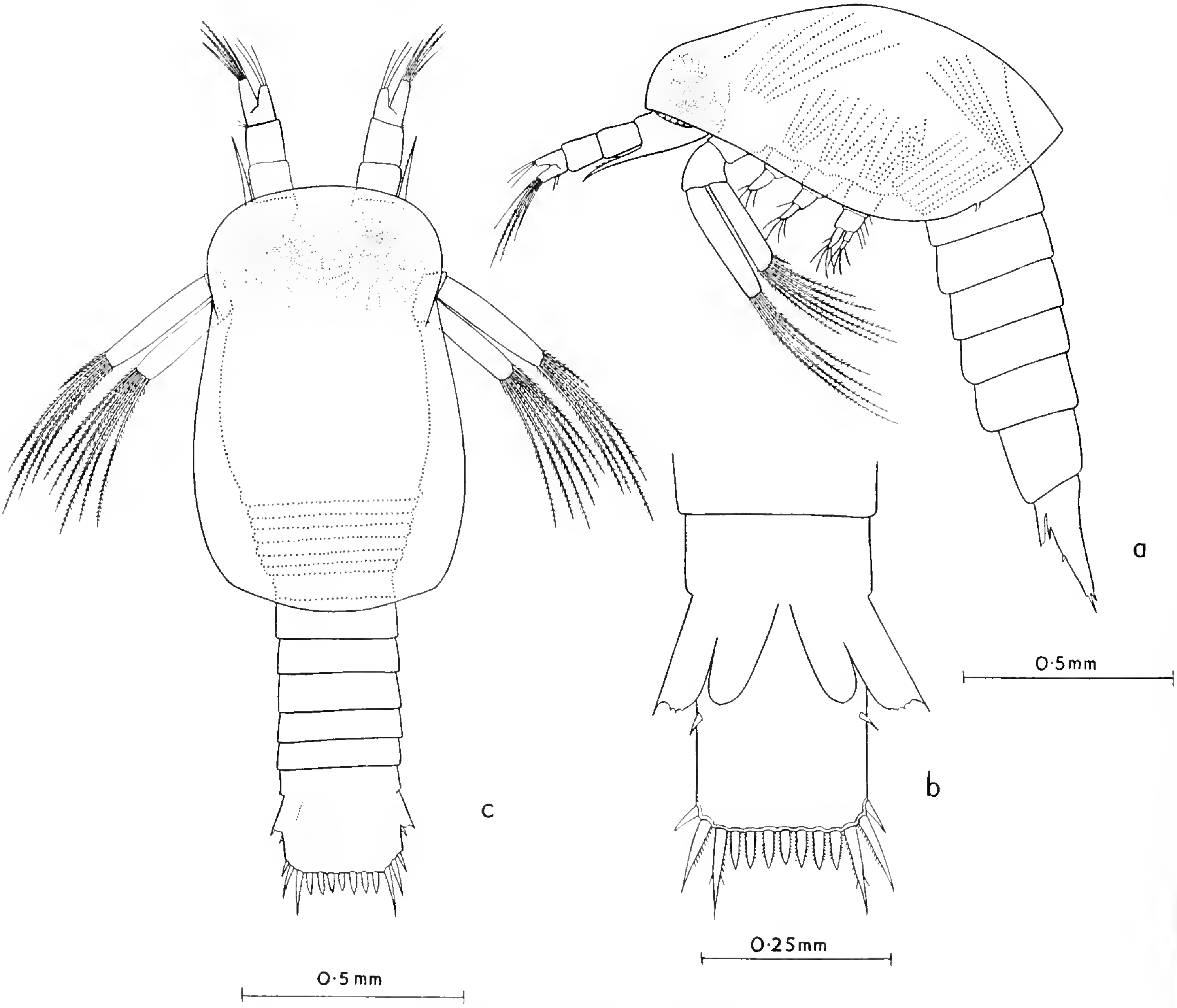


Fig. 6. *Nyctiphanes capensis.* *a*, third calyptopis, lateral view; *b*, telson of same; *c*, third calyptopis, dorsal view.

The outer, distal margin of the basal segment of the first antennal peduncle is produced as a strong, toothed spine which reaches to about the distal end of the third and last segment of the peduncle. The two rami of the first antennae remain unaltered.

The second antennae and the other thoracic appendages are much the same as in the preceding stage.

The abdomen now has six segments and a telson. There are no abdominal appendages. The two rami of the lateral uropods are now visible, the outer ramus being somewhat longer than the inner and having its outer margin produced as a strong spine. The remaining armature of the telson is unchanged.

Dominance in the furcilia stages

For reasons which have been adequately discussed before (Fraser, 1936; John, 1936; Einarsson, 1945; Boden, 1950*b*, 1951) the term 'cyrtopia' for the later larval stages has been discarded, and these stages are now included in the furcilia series. Thus the furcilia stages in this report include all the instars, from the one in which the carapace first withdraws from over the eyes and there are no pleopods at all, to that in which there are five setose pleopods, the second antennal endopod is segmented and there is a single terminal and three pairs of postero-lateral spines on the telson. After one pair of postero-lateral spines has been lost the animal is regarded as 'juvenile' or post-larval, until it reaches adult size. This is done because the ecdyses in the juvenile condition (apparently 9 or 10) are orderly and there is no evidence of dominance in any of the stages. In addition the animal may be sexually mature before attaining fully the adult form.

There are twenty-five possible instars in this series. Six are numerically dominant and are regarded as the actual furcilia stages (Fig. 7). This scheme has been followed by most modern workers since it was first suggested by Fraser (1936). Recently, however, Sheard (1953) has proposed an alternative scheme, based mainly on an exhaustive investigation of *Nyctiphanes australis*, in which the number of furcilia stages is reduced to three and the dominants are disregarded. The stages he proposes are as follows:

Furcilia stage 1 (F I). Eyes developed and free of the carapace, pleopods absent or present as non-setose rudiments. Terminal spines (of telson) generally seven. Lateral spines (postero-lateral of telson) three in number, the central spine always present.

Furcilia stage 2 (F II). Some, or all, pleopods setose. Terminal spines sometimes reduced in number, the central spine always present. The pair of long lateral spines unaltered at the base.

Furcilia stage 3 (F III). All pleopods setose and functional. The pair of long lateral spines are altered at the base. The terminal spines are progressively reduced to one (the median spine). The stage terminates with the end of the phase.

The outer limits of Sheard's series are actually the same as those proposed herein for *N. capensis*, or those of *N. simplex* (Boden, 1951), and his F I and F II stages are the same as the first and second furcilia stages presented here. His F III stage, however, embraces the final four furcilia stages of *N. capensis*. Sheard's F II and F III stages are differentiated mainly on the alteration in the shape of the base of the long lateral spines on the telson. This is a somewhat nebulous character, frequently rather difficult to detect, and is not as reliable an indicator as a definite reduction in the numbers of terminal spines on the telson or the sudden change in both form and function of the second antennal endopod.

Sheard 'lumps' the final furcilia stages into his F III stage and throws considerable doubt on the validity of regarding the dominant instars as actual stages and the remainder as variants, on the grounds that the dominants will change from time to time and from place to place. This concept of the dominance of certain instars he regards as a result of the inadequacy of plankton sampling. His arguments are based almost exclusively on the data he obtained for *N. australis* and are applied in an inferential manner to the other species whose development he describes.

It is perfectly true that most plankton sampling is pitifully inadequate, but this cannot be said of Fraser's (1936) work, in which the concept of the dominants constituting the actual stages was originally expressed. His material was spread adequately through time and space and a very large number of individuals was examined. It is also untrue of Einarsson's (1945) work and most of John's (1936).

While the dominants in *Nyctiphanes* may differ (i.e. the modal position may shift) from time to time or place to place they do not appear to move out of the stage boundaries. For example, in *N. capensis* (Fig. 7) it is possible that F III may at times be expressed as a form having seven terminal spines on the telson instead of five (those with six are abnormalities), but the mode will not be absent altogether. Thus, while a false impression may be registered by dogmatically regarding F III as typified by a form having five terminal spines, this impression will probably be less false than that obtained by disregarding all the modes occurring after F II, and considering all the lateral individuals as belonging to one stage.

Sheard states that it is highly probable that any individual will pass through only a limited number of the many possible instars in the stages he proposes. This is undoubtedly true, and it seems only logical that the modes represent the limited number of instars through which the majority of individuals passes and that they can therefore be expressed as stages, and the remainder as variants.

The fact that in *Nyctiphanes* the modes will shift and that by lumping several series of furcilia taken at different times or places one can hide these modes can, perhaps, be explained without doubting that the dominants may be regarded as valid stages.

The genus *Nyctiphanes* is peculiar among the Euphausiacea in that all four known species are shallow-water, neritic forms with limited geographical ranges. *N. simplex* occurs in Californian waters, *N. couchii* in the North Atlantic, *N. australis* in southern Australian and northern New Zealand waters, and *N. capensis* in South African waters. All these species have a great number of variants in their furcilia series and, therefore, substantiate Frost's (1935) claim that species inhabiting coastal waters regularly exhibit greater larval variation than oceanic species. As Sheard points out, the considerable variation exhibited by *Euphausia superba*, generally regarded as an oceanic species, may not controvert this claim, since it inhabits the region of pack ice, which simulates neritic conditions in some respects. The marked reduction in the number of instars in oceanic species has led to some speculation that the Euphausiacea represent arthropods in which gradual development is giving way to metamorphosis. On this premise, the genus *Nyctiphanes* with its great larval variation could be regarded as somewhat more primitive than other genera. It is probable, however, that the large number of variants is not a primitive, but a secondary feature developed during invasion of coastal waters. The genus has several rather specialized features, including an egg-sac in which the first, more vulnerable, larval stages are passed. This, too, is probably a secondary adaptation to the more varied coastal conditions. Thus the genus, in which variation is most marked and the dominant stages are least 'fixed', is one which is specially adapted to a variety of coastal conditions. The fact that dominant instars do occur in any particular place or time can, perhaps, represent the basis for an argument that these instars are an expression of development under the particular environmental conditions obtaining. In other words, such a genus may have slightly different developmental stages under different environmental conditions.

I agree with Sheard that much experimental work with live animals is desirable before the question can be examined much further, but feel that under the present circumstances it is less useful to 'lump' the furcilia stages than to 'split' them. It is possible, unless one is as careful as Sheard has been in giving full codes and counts for all the variants, that much valuable information on development as an expression of environment may be obscured by disregarding dominance. Full data on geographical position, temperature, salinity, oxygen and phosphate content for the stations at which the species reported on herein were taken are available in the *Discovery Report*, vol. XXVI, pp. 211–58.

Furcilia stages

Twenty-five furcilia instars were encountered. If the same terminology is adopted for all four species of *Nyctiphanes* as for *N. simplex* (Boden, 1951), the total number of furcilia types in each species is as follows: *N. couchii* 15, *N. simplex* 16, *N. australis* 24, *N. capensis* 25. For *N. simplex* it was suspected that three other types may occur. Frequency distributions of the *N. capensis* instars are given in Fig. 7.

In the case of *N. simplex* and *N. capensis* six of these types were dominant and are regarded as stages or successive instars, while the remainder are considered variants. According to Gurney (1942) it seems highly probable that there are six stages in *N. couchii* too. While Sheard recognizes only three stages in *N. australis*, it is possible to interpret his data differently. Table 7 shows the course of development of three species of *Nyctiphanes* and it can be seen that they are fairly similar.

Of very great interest is the fact that two of the species do not conform to the rule first shown by Fraser (1936) that the pleopods first appear as non-setose rudiments and these rudiments become setose at the next moult. *N. capensis* and *N. simplex* develop setose pleopods directly in stage II on somites which bore no non-setose rudiments in stage I.

The six stages of *N. capensis* encountered are as follows:

First furcilia. Pleopods non-setose. Second antennal endopod simple.

Second furcilia. Pleopods mixed. Second antennal endopod simple.

Third furcilia. Pleopods setose. Five terminal spines on telson. Second antennal endopod simple.

Fourth furcilia. Pleopods setose. Three terminal spines on telson. Second antennal endopod simple.

Fifth furcilia. Pleopods setose. Three terminal spines on telson. Second antennal endopod segmented.

Sixth furcilia. Pleopods setose. One terminal spine on telson. Second antennal endopod segmented.

First furcilia. Twenty-two specimens examined. Twelve measured (Fig. 8*a–g*). Length range 2·2–2·8 mm.; average length 2·5 mm.

The following types of furcilia are included in this stage. Those with (*a*) no pleopods, (*b*) one pair, (*c*) two pairs, (*d*) three pairs, (*e*) four pairs of non-setose pleopods. No specimens with five pairs of non-setose pleopods were encountered. The occurrence of the above types was as follows: (*a*) 199, (*b*) 35, (*c*) 34, (*d*) 18, (*e*) 6.

There is no rostrum. The frontal plate is broader than long with a small, distinct, emargination of the anterior border. There is a small, but definite, denticle on the inferior margin of the carapace toward the posterior end. The eyes are heavily pigmented and project beyond the edge of the carapace.

The first antennal peduncle has three segments and the basal segment bears a strong spine, reaching just beyond the middle of the third segment, on its anterior outer margin. The rudiments of the two flagella are present on the third segment.

The second antenna is biramous, natatory, and its endopod is simple.

The usual condition of the thoracic appendages is that the first and second maxillae are clearly visible, the first cormopod is present and bifurcate, and the bud of the second cormopod is free but naked. The remaining cormopods are contained in the integument and difficult to discern. Individuals in which the pleopods are developed frequently have the second cormopod present, bifurcate and with bilobed gill rudiments.

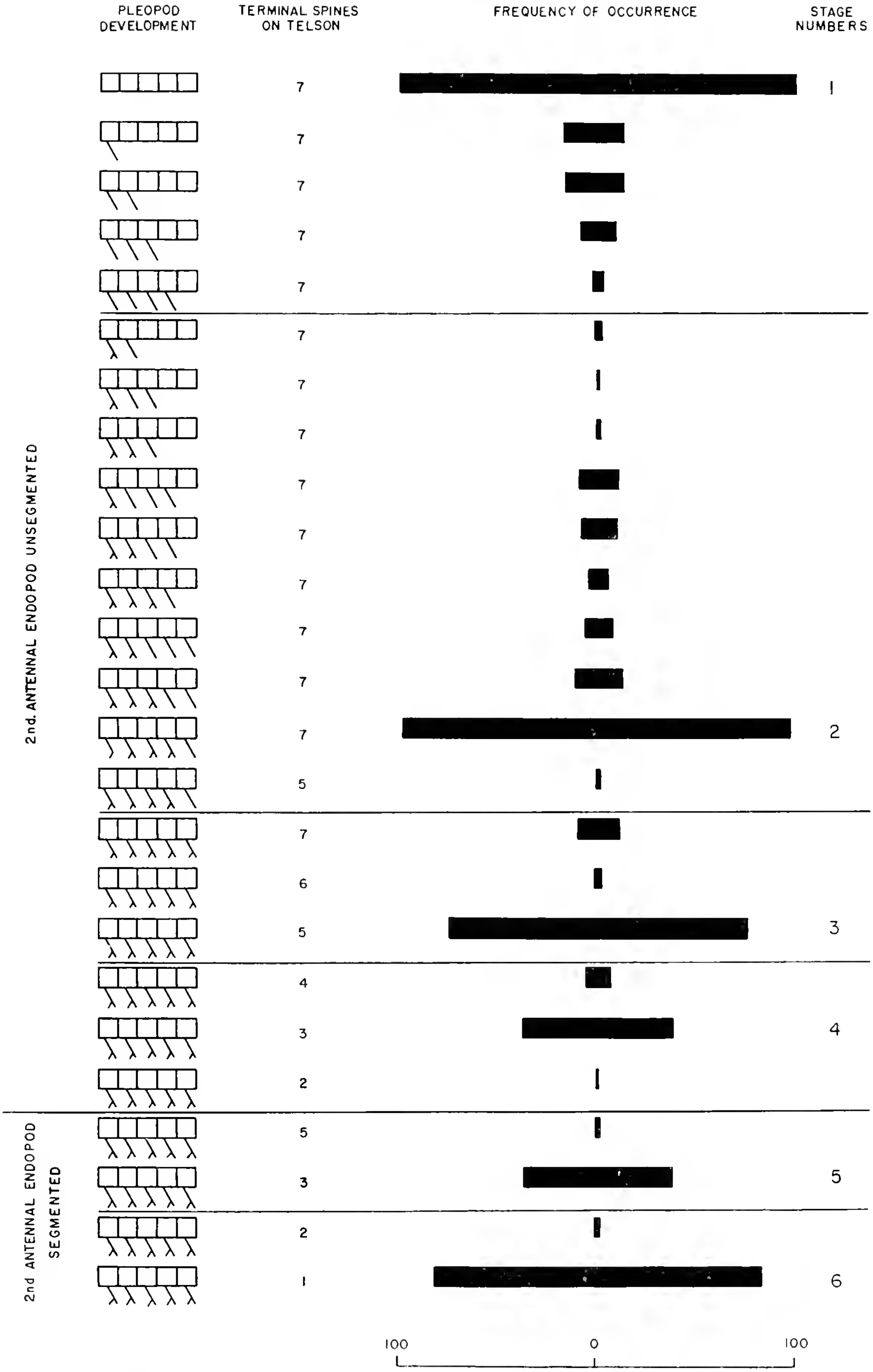


Fig. 7. *Nyctiphanes capensis.* Diagrammatic key to furcilia stages and frequency of occurrence. The rectangles in the left-hand column represent the larval abdomen, each square being an abdominal segment. A simple stroke represents a non-setose pleopod; a feathered stroke represents a setose plopod.

The telson is considerably elongated and the uropods well developed. There is one pair of ventro-lateral spines, three pairs of postero-lateral, and seven terminal spines.

Second furcilia. Nineteen specimens examined (Fig. 8*h*–*k*). Length range 3·7–4·1 mm.; average length 3·9 mm.

In this stage there are four pairs of setose pleopods and one pair of non-setose.

The types encountered with mixed setose and non-setose pleopods were as follows: (*a*) those with four pleopods: one setose, three non-setose; (*b*) those with four pleopods: two setose, two non-setose; (*c*) those with four pleopods: three setose, one non-setose; (*d*) those with five pleopods: two setose, three non-setose; (*e*) those with five pleopods: three setose, two non-setose; (*f*) those with five pleopods: four setose, one non-setose.

Table 7. *Development of three species of* Nyctiphanes

	Stage 1			Stage 2			Stage 3		
	Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines
	N.	S.		N.	S.		N.	S.	
N. capensis	0	0	7	1	4	7	0	5	5
N. simplex	2	0	7	0	5	7	0	5	5
N. couchii	0	0?	7	2	3?	7	0	5?	7

	Stage 4			Stage 5			Stage 6		
	Pleopods		Telson spines	Pelopods		Telson spines	Pleopods		Telson spines
	N.	S.		N.	S.		N.	S.	
N. capensis	0	5	3	0	5	3	0	5	1
N. simplex	0	5	3	0	5	3	0	5	1
N. couchii	0	5	5	0	5	3	0	5	1?

N. = non-setose, S. = setose; stages 5 and 6 have the antennal endopod segmented.
The data for *N. couchii* are taken from Gurney (1942) and those for *N. simplex* from Boden (1951).

Altogether, 286 larvae of this stage were identified in the following numbers: (*a*) 20, (*b*) 19, (*c*) 10, (*d*) 14, (*e*) 28, (*f*) 195. Of these, type (*c*) has previously been reported in the literature only for *Nyctiphanes australis*.

The frontal plate is about as long as it is broad and is somewhat more elongate but still unsegmented.

The second antenna is the same.

The first cormopod is as in the previous stage. The second is bifurcate, segmented, and carries a bilobed gill. The third cormopod is bifurcate, unsegmented, and carries gill rudiments. The remaining cormopods are still bud-like.

The telson has seven terminal spines. The uropods are longer and better developed than in the previous stage.

Third furcilia. Ten specimens examined (Fig. 9*a*–*e*). Length range 4·0–4·4 mm.; average length 4·2 mm.

In this stage there are five setose pleopods, the antennal pleopod is unsegmented and there are (*a*) seven, or (*b*) five terminal spines on the telson. Forty-one specimens of type (*a*) were encountered and one hundred and fifty of type (*b*). Four specimens with six terminal spines were found, each of them abnormal in this respect (Fraser, 1936; John, 1936).

The frontal plate is longer than it is broad and its anterior margin is concave.

The flagella of the first antenna are elongate but unsegmented.

The second antenna is still natatory and both rami are unsegmented.

The endopod of the first cormopod is longer than the exopod and has three segments.

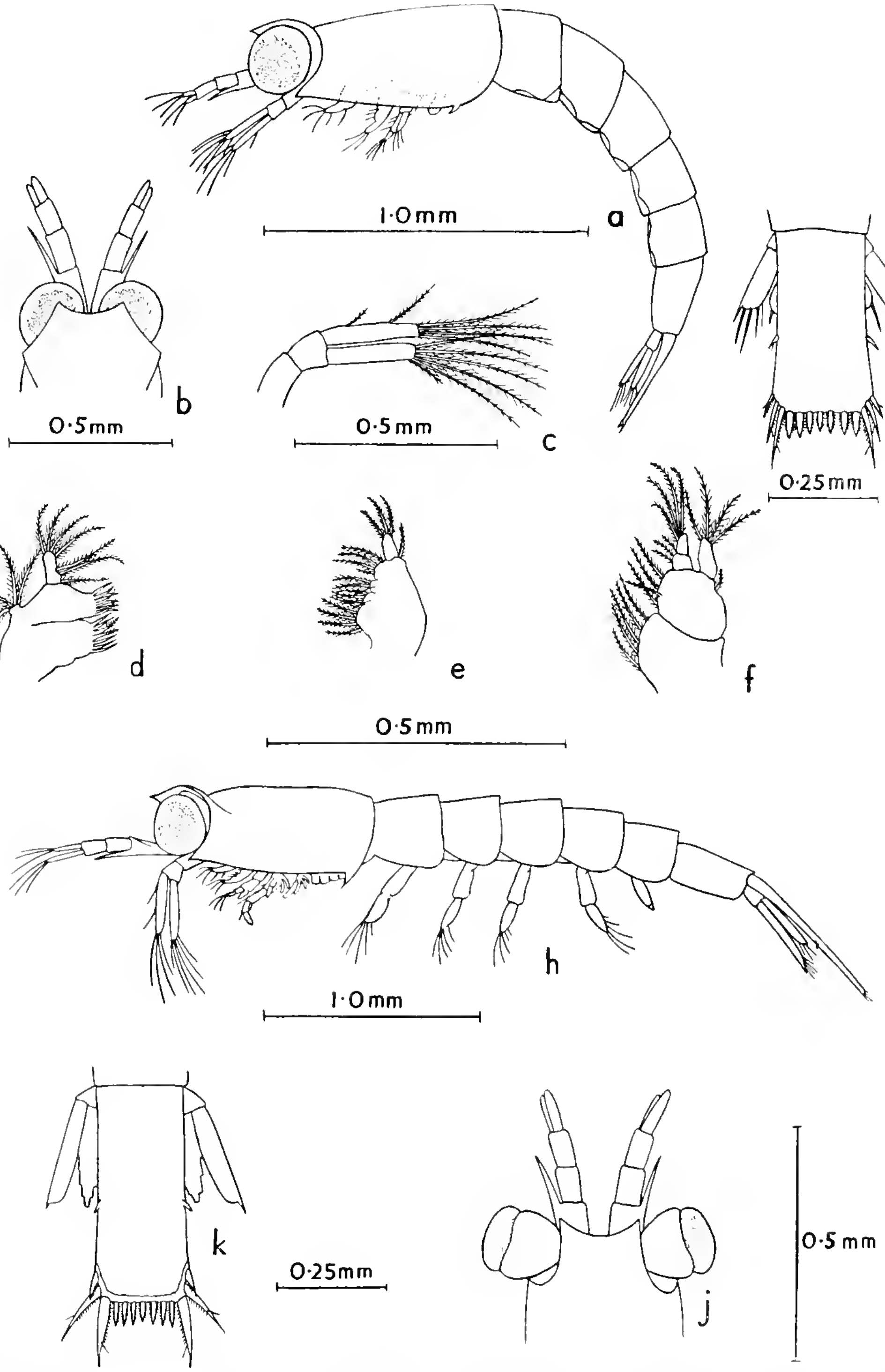


Fig. 8. *Nyctiphanes capensis.* *a*, first furcilia, lateral view; *b*, cephalothorax, dorsal view; *c*, second antenna; *d*, first maxilla; *e*, second maxilla; *f*, first cormopod; *g*, telson of first furcilia; *h*, second furcilia, lateral view; *j*, cephalothorax, dorsal view; *k*, telson of second furcilia.

The second cormopod is well developed; the endopod is long, has five segments, with a strong knee. There is a gill, with two branches, at the base of the exopod.

The endopod of the third cormopod is shorter than the second and is feebly kneed. The gill has two unequal branches. The fourth endopod is shorter than the third, has three segments and is straight. The gill has two branches. The fifth cormopod is short, bifurcate, non-setose with two gill buds.

The remaining cormopods are short, simple buds.

The pleopods are all biramous and setose.

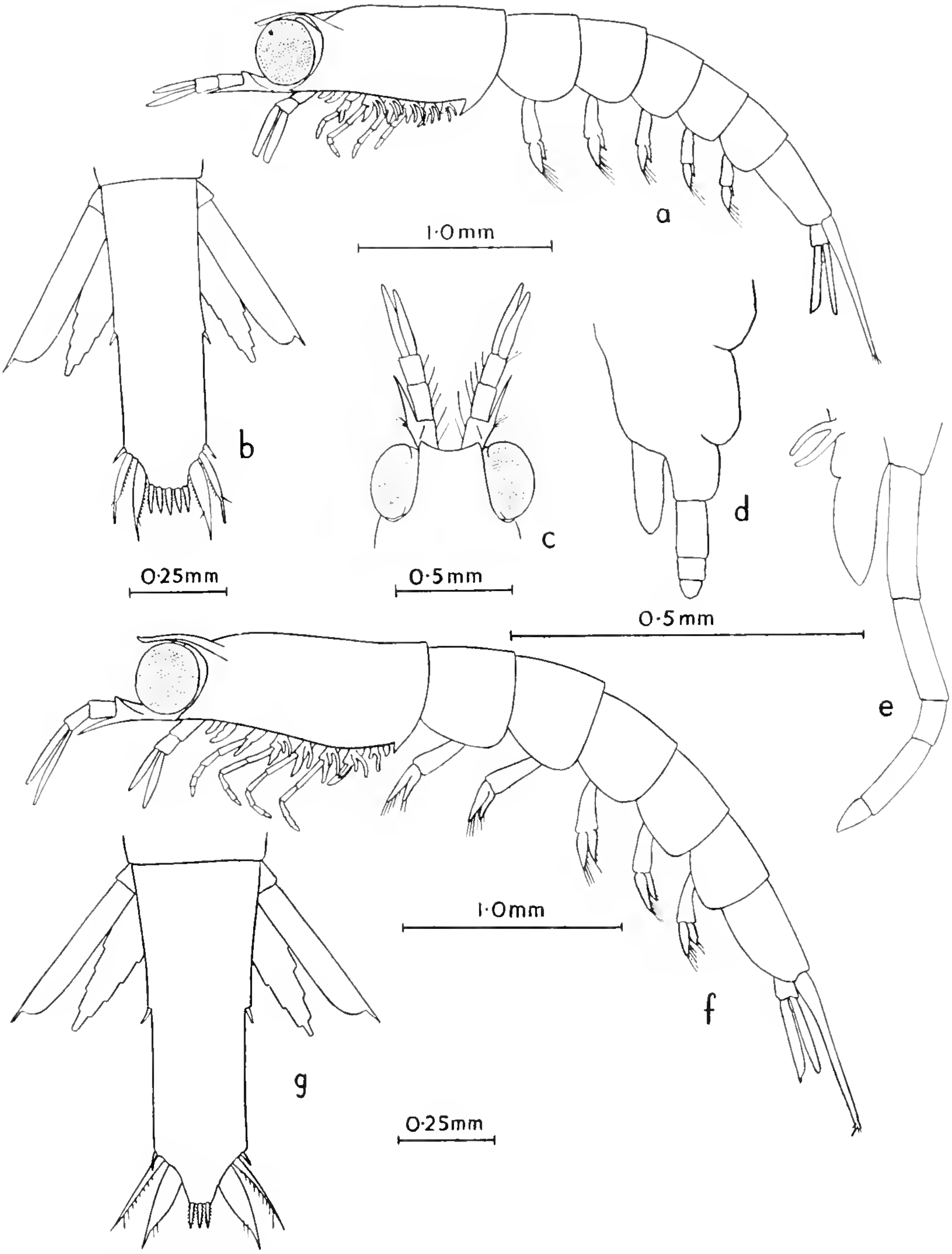


Fig. 9. *Nyctiphanes capensis*. *a*, third furcilia, lateral view; *b*, telson of same; *c*, cephalothorax, dorsal view; *d*, first cormopod; *e*, second cormopod; *f*, fourth furcilia, lateral view; *g*, telson of same.

The number of terminal spines on the telson is reduced to five. The innermost pair of postero-lateral spines is the sturdiest and longest, and has a wide base.

Fourth furcilia. Fifteen specimens examined (Fig. 9*f*, *g*). Length range 4·3–4·6 mm.; average length 4·4 mm.

The second antennal endopod is still simple in this stage but the number of terminal spines on the telson is reduced to three. Twelve with four spines and one with two spines were also found.

The carapace, frontal plate and eyes remain unaltered.

The flagella of the first antenna are still unsegmented and the second antenna remains natatory and unsegmented.

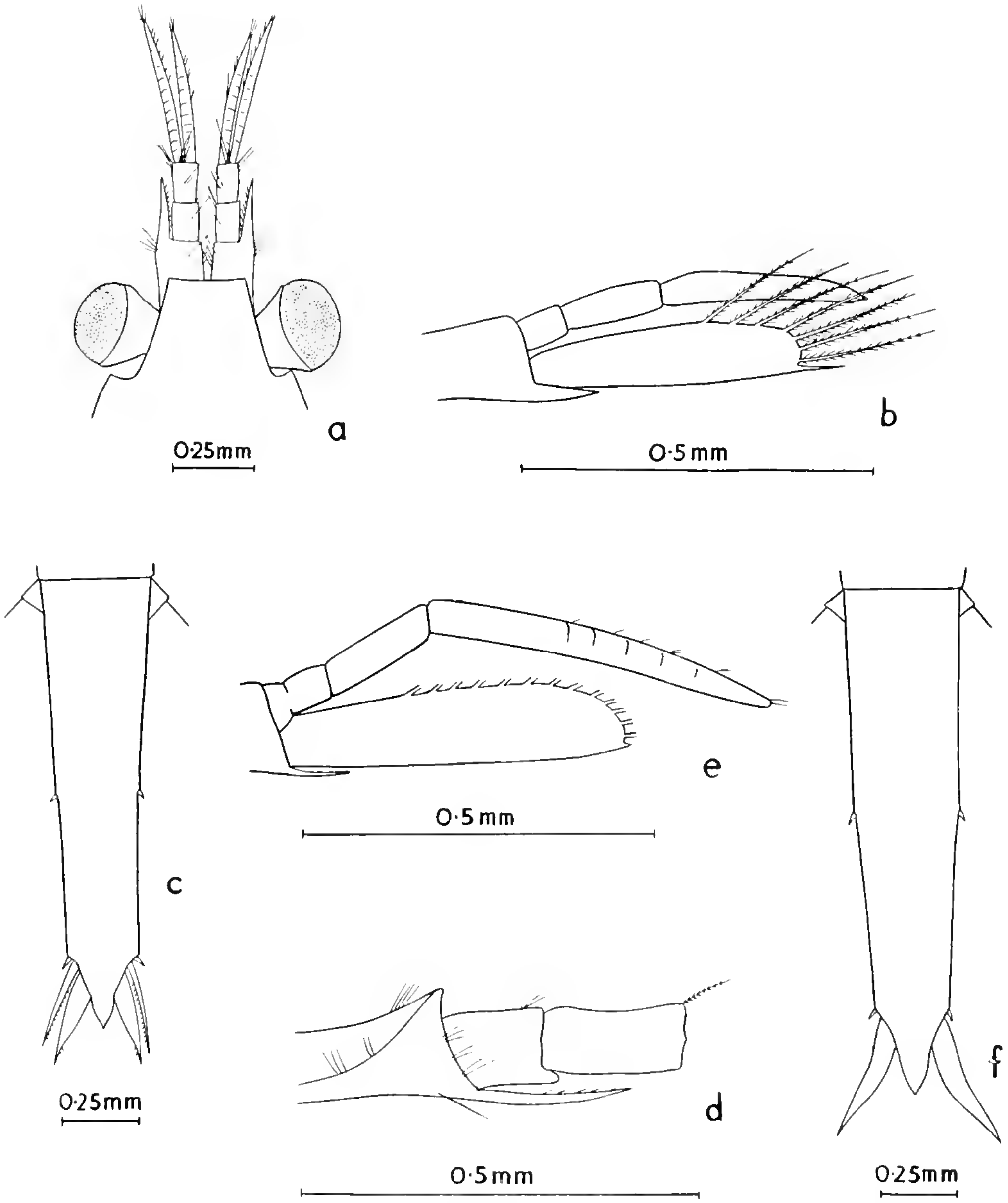


Fig. 10. *Nyctiphanes capensis.* *a*, fifth furcilia, cephalothorax in dorsal view; *b*, second antenna; *c*, telson; *d*, sixth furcilia, peduncle of first antenna; *e*, second antenna; *f*, juvenile telson.

The first four cormopods have their full complement of segments; the first is feebly kneed, the second to the fourth powerfully so. The fifth cormopod is unaltered and the remainder are rudimentary.

The telson still carries three pairs of postero-lateral spines and three terminal spines.

Fifth furcilia. Thirteen specimens examined (Fig. 10*a–c*). Length range 4·5–4·9 mm.; average length 4·7 mm.

The number of terminal spines on the telson remains three, although two specimens were encountered with five terminal spines on the telson.

The carapace retains the lateral denticle and is unaltered except for the frontal plate, which is no longer as concave as formerly. The eyes are the same.

The flagella of the first antenna are setose and segmented.

The second antenna has a segmented non-setose flagellum, and a scale which is setose terminally and along the anterior third of its inner border.

The cormopods are the same as in the previous stage, except that the fifth is now jointed, but still non-setose.

Sixth furcilia. Twenty-one specimens examined (Fig. 10*d*, *e*). Length range 4·8–5·3 mm.; average length 5·1 mm.

The terminal spines on the telson are reduced to one in number. Three abnormal specimens with two terminal spines occurred.

The frontal plate is a trifle narrower than in the previous stage, but the carapace is otherwise unaltered. The tooth on the lateral margin remains. In *N. simplex*, it has disappeared at this stage.

The basal segment of the first antennal peduncle shows the rudiments of the adult reflexed lappet on its upper, distal margin. The spine on its outer margin reaches just beyond the middle of the third segment.

The flagellum of the second antenna has a base with three segments and it reaches beyond the scale for about half its own length. The scale bears setae all along its inner margin and a spine at its base on the outside.

The endopodite of the sixth cormopod is now jointed but that of the seventh is still unjointed. The luminous organ is present at the base of the seventh cormopod.

Juveniles (Fig. 10*f*). Once the outer, long, lateral spines on the telson are lost, the animal is classed as juvenile. It appears to undergo about nine or ten moults before assuming a fully adult form. In the course of this development the cormopods become jointed and geniculate, the frontal plate diminishes and becomes adult in appearance, and the lateral denticle on the carapace disappears. There appears to be considerable individual variation in the development of these characteristics. There is no evidence of dominance in the juvenile series.

Euphausia lucens Hansen

Egg. 0·38–0·40 mm. in formalin (Fig. 11*a*).

Five eggs were found and measured. They appeared to be on the verge of hatching, for all contained well-developed nauplii. The nauplius completely fills the egg-case at this stage.

Nauplius. No free nauplii were found. Those within the egg had three pairs of appendages—uniramous first antennae, biramous second antennae and biramous mandibular palps. The first antenna carries a single terminal spine. Each ramus of the remaining appendages is armed with three spines (Fig. 11*a*).

Pseudometanauplius. This stage was not represented in the material.

Metanauplius. Only one specimen of this stage was found (Fig. 11*b*, *c*).

The length of the carapace is about 0·4 mm. There is a large, elaborately serrated rostral hood.

The first antenna is uniramous and carries three spines.

The second antenna is biramous, the rami being armed with four and five spines respectively. The exopod is segmented distally.

The mandibular palp is reduced to a small papilla.

The unarmed limbs of the metanauplius are partially covered by folds in the carapace.

The telson is differentiated and carries eight spines.

First calyptopis. Five specimens examined (Fig. 12*a*–*c*). Length range 0·98–1·1 mm.; average length 0·99 mm.

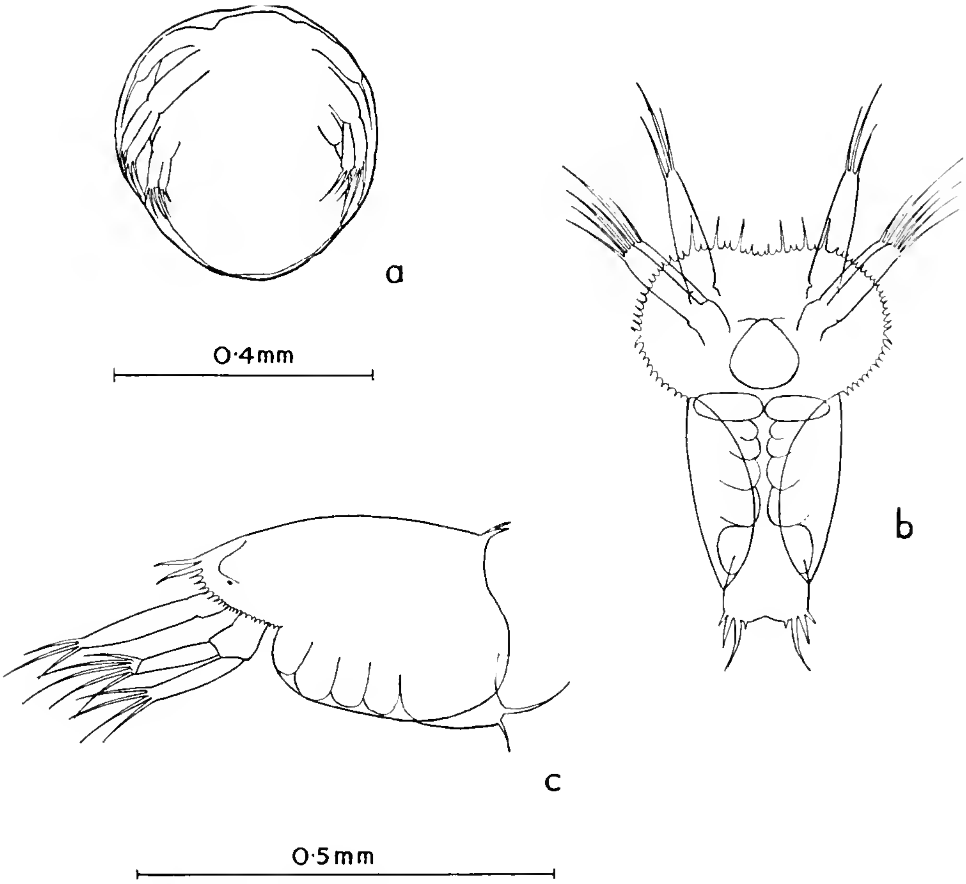


Fig. 11. *Euphausia lucens.* *a*, egg on verge of hatching; *b*, metanauplius in ventral view; *c*, metanauplius in lateral view.

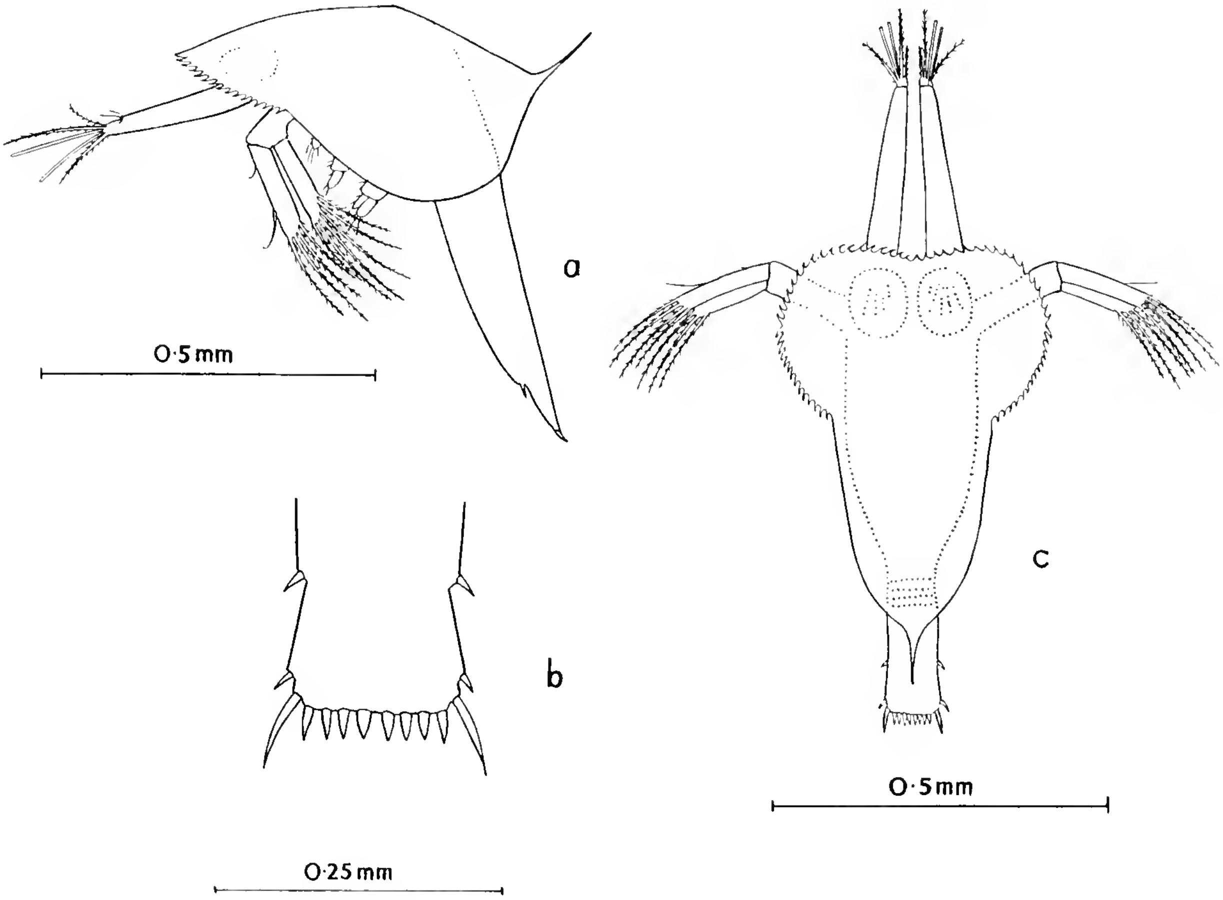


Fig. 12. *Euphausia lucens.* *a*, first calyptopis, lateral view; *b*, distal part of telson; *c*, first calyptopis, dorsal view.

The carapace is domed and the posterior margin is produced as a sharp, upward-pointing spine. The anterior margin of the carapace fans out as a serrated rostral hood. There are no lateral denticles on the inferior margin of the carapace.

The ocular plates can be seen and the median eye is present.

A rudimentary inner ramus, carrying two setae, can be seen on the forward-pointing first antenna. The outer ramus carries four setae, two of which are sensory.

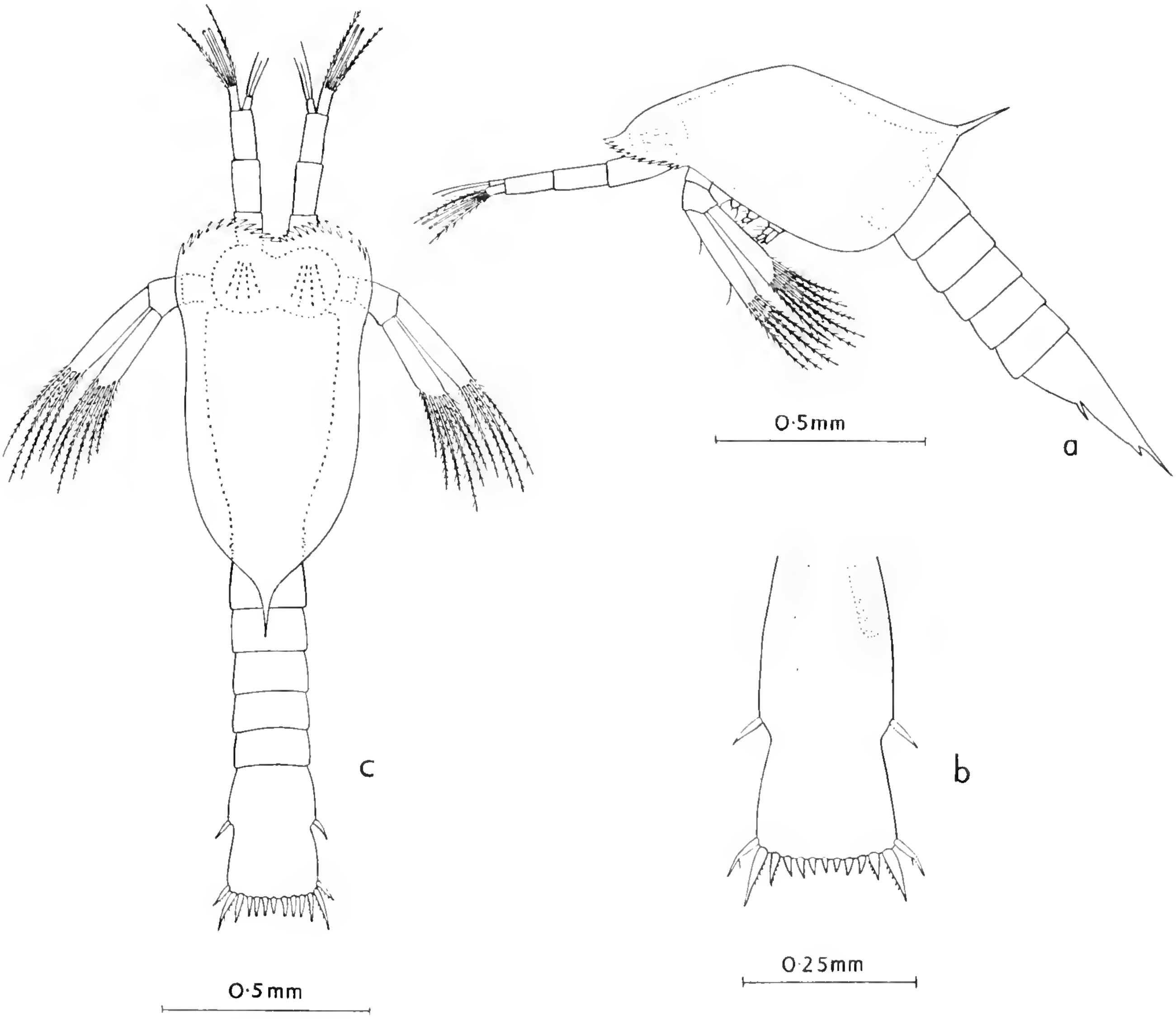


Fig. 13. *Euphausia lucens.* *a*, second calyptopis, lateral view; *b*, telson of same; *c*, second calyptopis, dorsal view.

The second antennal peduncle has two segments, and the antenna is biramous. The anterior ramus carries four setose terminal spines and two lateral spines. The second ramus carries six setose terminal spines.

The first and second maxillae and first thoracic limb are present and setose.

The limbless thoracic segments can be discerned as wrinkles in the integument.

There is no sign of segmentation in the abdomen. The telson is armed with one pair of ventro-lateral spines, three pairs of postero-lateral spines and six terminal spines. The innermost pair of postero-lateral spines resembles the terminal spines more closely than in other euphausiids at this stage, and as a result the telson looks as though it has eight terminal spines.

Second calyptopis. Seven specimens examined (Fig. 13*a–c*). Length range 1·3–1·8 mm.; average length 1·6 mm.

The rostral hood is not as conspicuous as in the preceding stage, although its anterior margin is still serrated. The posterior margin of the carapace is still produced as a sharp spine.

There is no sign of the median eye and the compound eyes are now quite clearly defined.

The biramous first antenna is carried on a peduncle of three segments. The outer ramus carries four setae and the inner three.

The second antenna and remaining thoracic appendages are unchanged.

The thoracic segmentation is clearly visible.

There are now five segments and a telson to the abdomen and the rudimentary uropods can be seen within the integument of the telson. The ventro-lateral and postero-lateral spines of the telson are retained, but there are now seven terminal spines.

Third calyptopis. Five specimens examined (Fig. 14*a–c*). Length range 2·10–2·33 mm.; average length 2·24 mm.

The anterior margin of the rostral hood is serrated and the posterior margin of the carapace is produced as a sharp, dorsal spine. The inferior margin of the carapace has developed a small denticle toward its posterior end.

The globular compound eyes are pigmented and covered by the rostral hood.

On the outer distal margin of the basal segment of the first antennal peduncle is a strong toothed spine reaching nearly to the end of the third segment. The spines on the two rami of the first antennae are unchanged.

There is no alteration in the second antennae or the remaining thoracic appendages.

The abdomen has six segments and a telson. The six segments are naked but the lateral uropods of the telson have developed and are spinose. The outer ramus of the uropod has its outer margin produced as a small tooth. It carries six spines. The inner ramus carries four. There are three pairs of postero-lateral spines and seven terminal spines on the telson. The central terminal spine is much reduced and the remaining three pairs are turned toward it.

Furcilia stages. Six furcilia stages of *E. lucens* were found and they are as follows:

Table 8. *Furcilia stages of* Euphausia lucens

Stage 1			Stage 2			Stage 3			Stage 4			Stage 5			Stage 6		
Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines
N.	S.		N.	S.		N.	S.		N.	S.		N.	S.		N.	S.	
1	—	7	4	1	7	—	5	7	—	5	5	—	5	3	—	5	1

N. = non-setose, S. = setose; stages 5 and 6 have the second antennal endopod segmented.

Specimens found: stage 1 = 6, stage 2 = 3, stage 3 = 5, stage 4 = 2, stage 5 = 6, stage 6 = 8.

While this paper was being prepared it was necessary to move the collection on which it is based from Bermuda to California. This was done by Military Air Transport and despite the most careful packing and rigorous precautions, the tubes containing the furcilia stages of *E. lucens* were broken and most of the contents were lost. Only four of the thirty specimens were salvaged and these belong to the first two stages. For these reasons, descriptions and illustrations of the first two stages only are presented here. It was possible to give the diagnostic characters of the later stages in Table 8 from laboratory notes made at the time of sorting.

First furcilia. Six specimens were found and one was measured and examined (Fig. 15*a–g*). The length was about 3 mm.

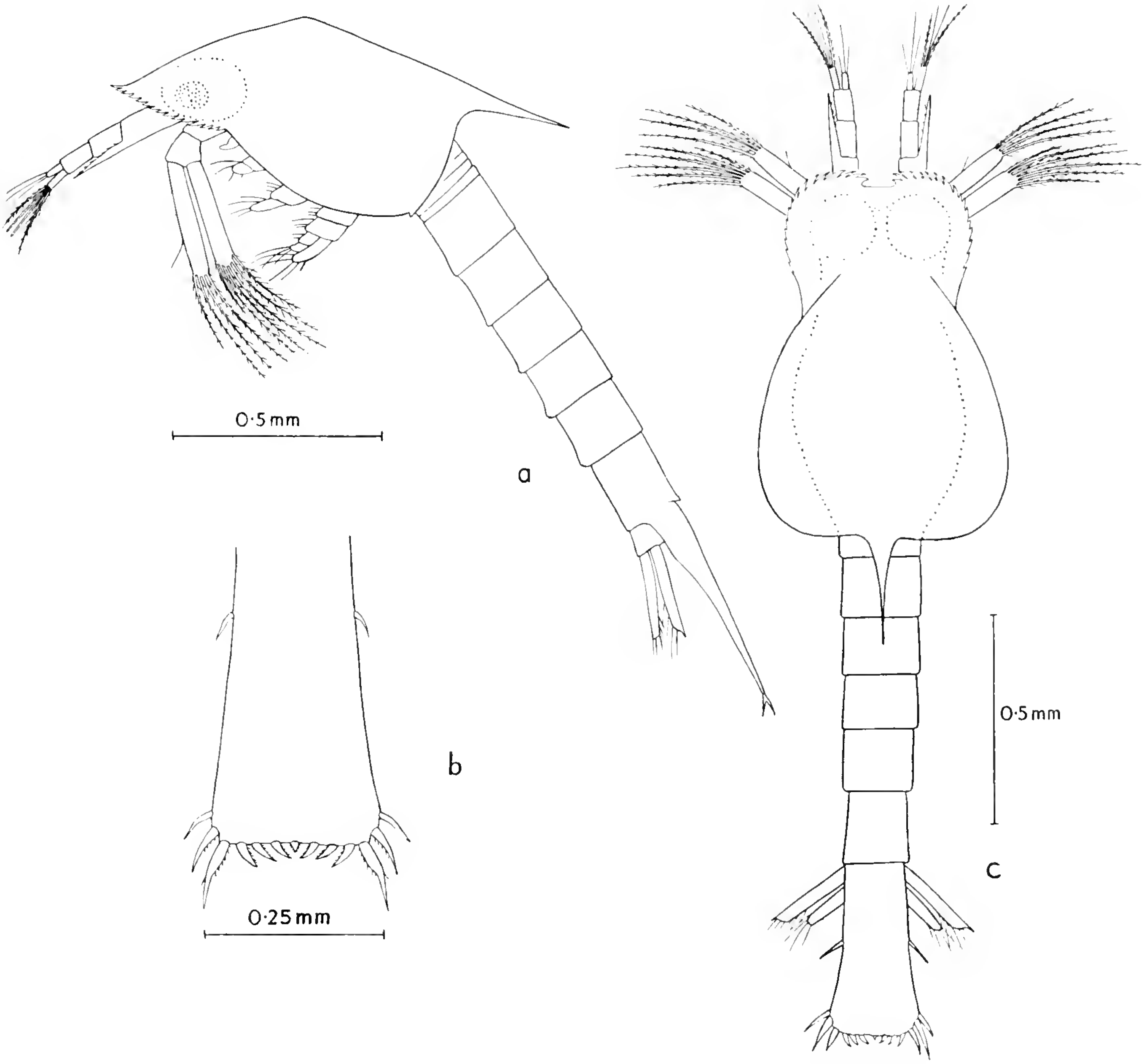


Fig. 14. *Euphausia lucens.* *a*, third calyptopis, lateral view; *b*, telson of same; *c*, third calyptopis, dorsal view.

The anterior margin of the carapace is serrated and the frontal plate is broader than long. The posterior margin of the carapace is slightly produced as a dorsal spine and there is a conspicuous denticle on the inferior margin toward the posterior end.

The pigmented eyes are no longer covered completely by the carapace.

The basal segment of the first antennal peduncle bears, on its outer margin, a strong toothed spine reaching to the end of the third segment. The two rudimentary flagella are present on the third segment and they bear three and four spines respectively.

The natatory, biramous second antenna carries a simple endopod.

The first and second maxillae are visible and the bifurcate first cormopod is present.

The first segment of the abdomen bears one pair of non-setose pleopods.

The telson is elongated and the uropods are well developed. The telson carries seven terminal spines, three pairs of postero-lateral and one pair of ventro-lateral spines.

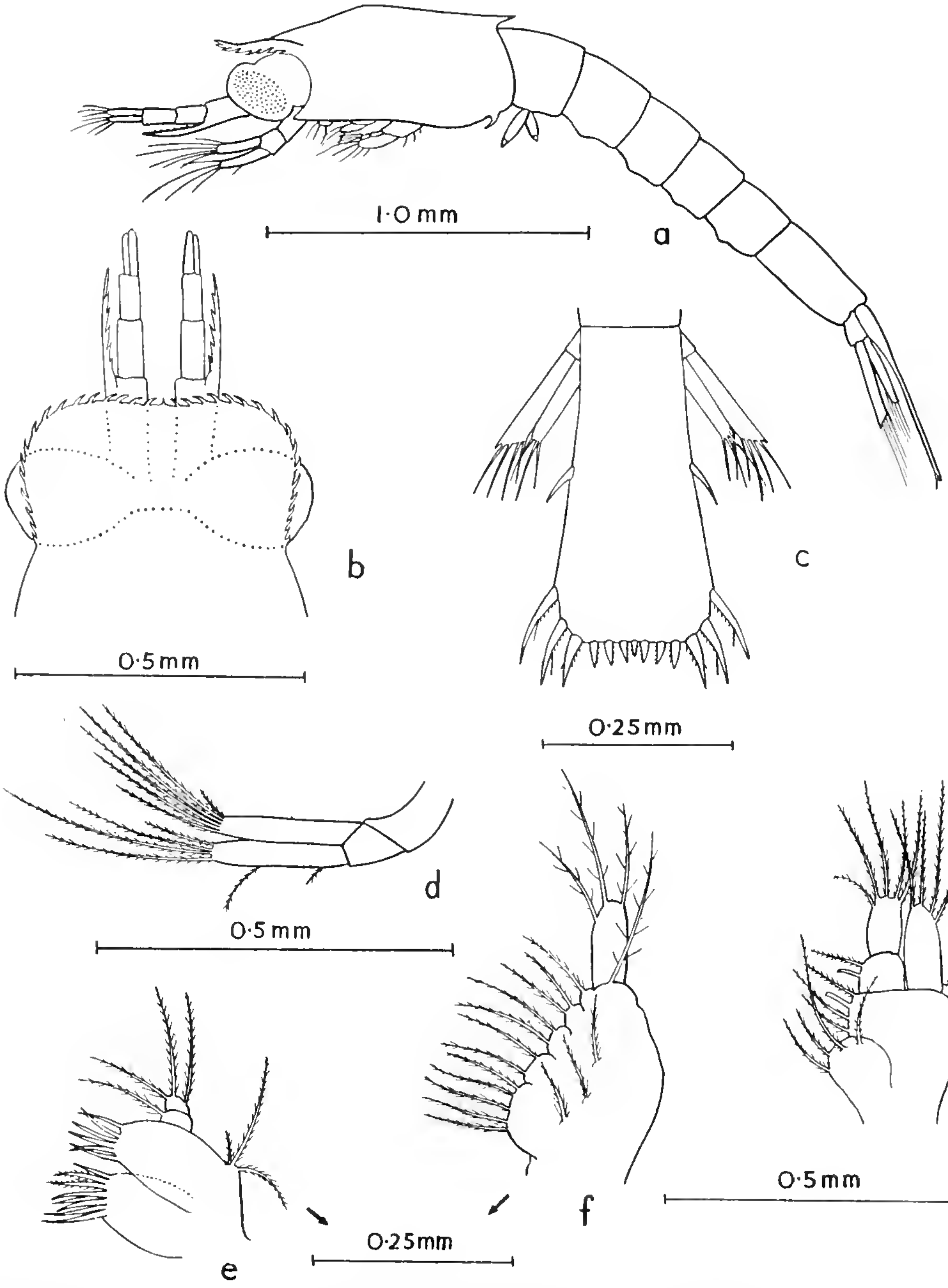


Fig. 15. *Euphausia lucens*. *a*, first furcilia, lateral view; *b*, cephalothorax, dorsal view; *c*, telson and lateral uropods; *d*, second antenna; *e*, first maxilla; *f*, second maxilla; *g*, first cormopod.

Second furcilia. Three specimens were found (Fig. 16*a*, *b*). The average length was 3·5 mm.

The anterior margin of the carapace has narrowed to a finely serrated frontal plate. The posterior margin is no longer produced as a dorsal spine, but the inferior margin retains its denticle.

The rather small eyes project considerably beyond the margins of the frontal plate.

The first and second antennae are unchanged.

The remaining thoracic appendages are the same as in the preceding stage except that the second cormopod has appeared and bears small gill lobes.

The abdomen bears one setose and four non-setose pairs of pleopods.

The condition of the telson remains unchanged.

Remaining stages. The diagnostic characters of the remaining stages are given in Table 8.

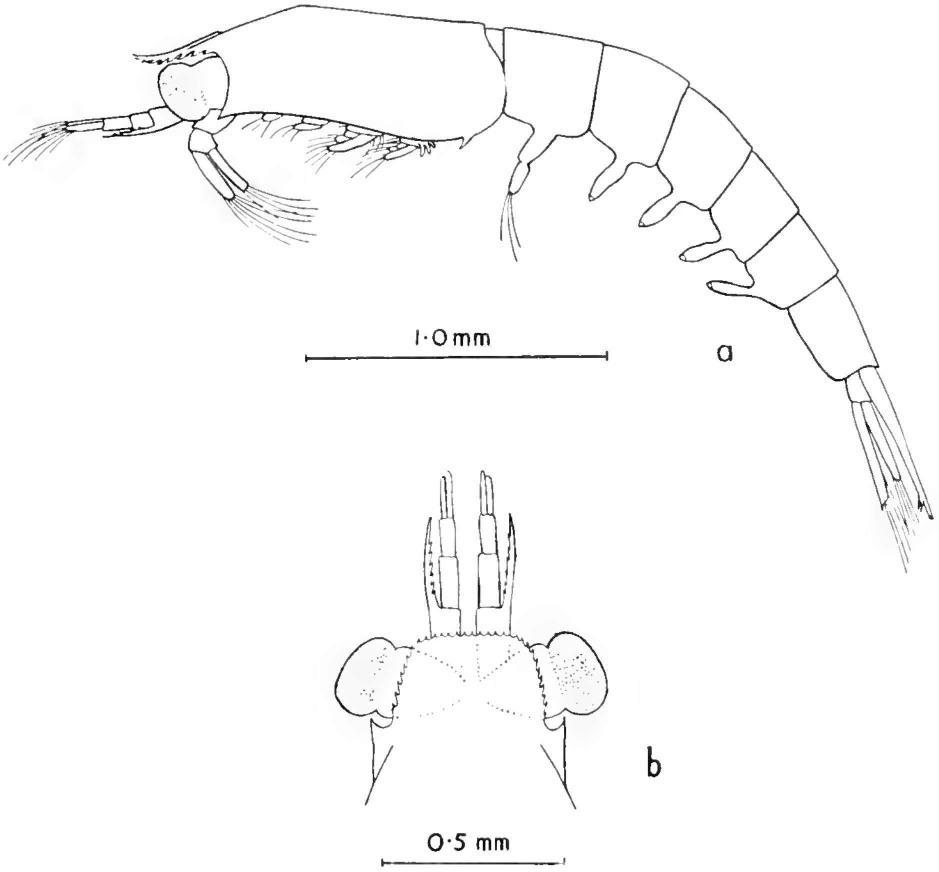


Fig. 16. *Euphausia lucens.* *a*, second furcilia, lateral view; *b*, cephalothorax, dorsal view.

As the animal approaches the adult form the frontal plate becomes smaller and loses its serrations. In the adult phase this plate is a low triangle somewhat broader than long. It may or may not carry a rudimentary rostrum.

The lateral denticle on the carapace moves gradually forward from its posterior position until it reaches about the middle of the inferior margin.

The upper distal margin of the basal segment of the first antennal peduncle becomes progressively more produced until it is an acute, triangular lobe. A keel appears on the upper surface of the third segment.

In the fifth and sixth stages the second antenna loses its natatory function and the endopod becomes segmented.

Euphausia tenera Hansen

It was not possible to identify any pre-furcilia stages of this species.

Five furcilia stages of *E. tenera* were found in the plankton and are presented in Table 9. It seems highly probable that a sixth stage, with only a single terminal spine on the telson, also occurs, although it was not encountered.

Table 9. *Furcilia stages of* Euphausia tenera

Stage 1			Stage 2			Stage 3			Stage 4			Stage 5			Stage 6		
Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines
N.	S.		N.	S.		N.	S.		N.	S.		N.	S.		N.	S.	
3	1	7	1	4	7	—	5	7	—	5	5	—	5	3	—	5	1

N. = non-setose, S. = setose.

Specimens found: stage 1 = 5, stage 2 = 1, stage 3 = 4, stage 4 = 20, stage 5 = 3, stage 6 = 0.

Lebour (1949) has described three stages (the first three) of *E. tenera* from Bermuda. The first of these carries one non-setose pleopod, the second four non-setose and one setose and the third five setose. Only the third of these stages occurred in the series presented here.

The larvae examined during this inquiry were considerably larger than those described by Lebour (*E. tenera* is a small species) and in the first stages the state of development of the cormopods and pleopods was relatively advanced.

My material was preserved, and positive identification was therefore more difficult. However, these larvae occurred in the same tows as adult *E. tenera* and later stages resembled the adult phase of *E. tenera* (particularly in the shape of the rostrum) more closely than that of any other euphausiid present. They conform closely to Lebour's descriptions and illustrations and the similarity in the shape of the rostrum is most marked. The explanation of the discrepancies in the earlier stages may lie in inadequate sampling (only thirty-three specimens were present in this material), and the first two stages described by Lebour are, therefore, the real stages. Another possible explanation of the large size and advanced condition of development may be found in the environmental differences encountered in the Benguela Current and the Bermuda waters. The Benguela Current is a cold, upwelling current with waters rich in nutrient salts, whereas the warm oceanic waters of the north-western Sargasso are notoriously poor in nutriment.

First furcilia. Five specimens examined and measured. Length range 4·0–4·4 mm.; average length 4·2 mm. (Fig. 17*a–j*).

The frontal plate of the carapace is rounded and comes to a sharp point in the centre of the anterior margin. The margin is otherwise quite smooth. The inferior margin of the carapace carries a small denticle toward the posterior end. Its posterior margin lacks a dorsal spine.

There are three segments to the first antennal peduncle and the basal segment carries, on its outer distal margin, a strong-toothed spine which extends to just beyond the distal end of the third segment. The third segment carries two rudimentary flagella.

The second antenna is biramous and natatory. The simple endopod carries four setose spines terminally and the exopod carries seven.

The first and second maxillae are visible. The first and second cormopods are present and bifurcate and the second carries rudimentary gill-lobes. The third is present as a naked, simple bud.

The first abdominal segment carries a pair of setose pleopods and the following three carry non-setose pleopods.

The well-developed telson carries well-developed uropods. It is armed with one pair of ventro-lateral, three pairs of postero-lateral, and seven terminal spines.

Second furcilia. One specimen examined and measured. Length 4·9 mm. (Fig. 18*a*, *b*).

The anterior margin of the frontal plate is somewhat less pointed than in the preceding stage.

The thoracic appendages are unchanged except for the cormopods. The second is now segmented and geniculate. The third is bifurcate and carries rudimentary gills. The fourth is now visible as a simple bud bearing rudimentary gill-lobes.

The abdomen bears four pairs of setose pleopods and one pair of non-setose.

The condition of the telson is unchanged.

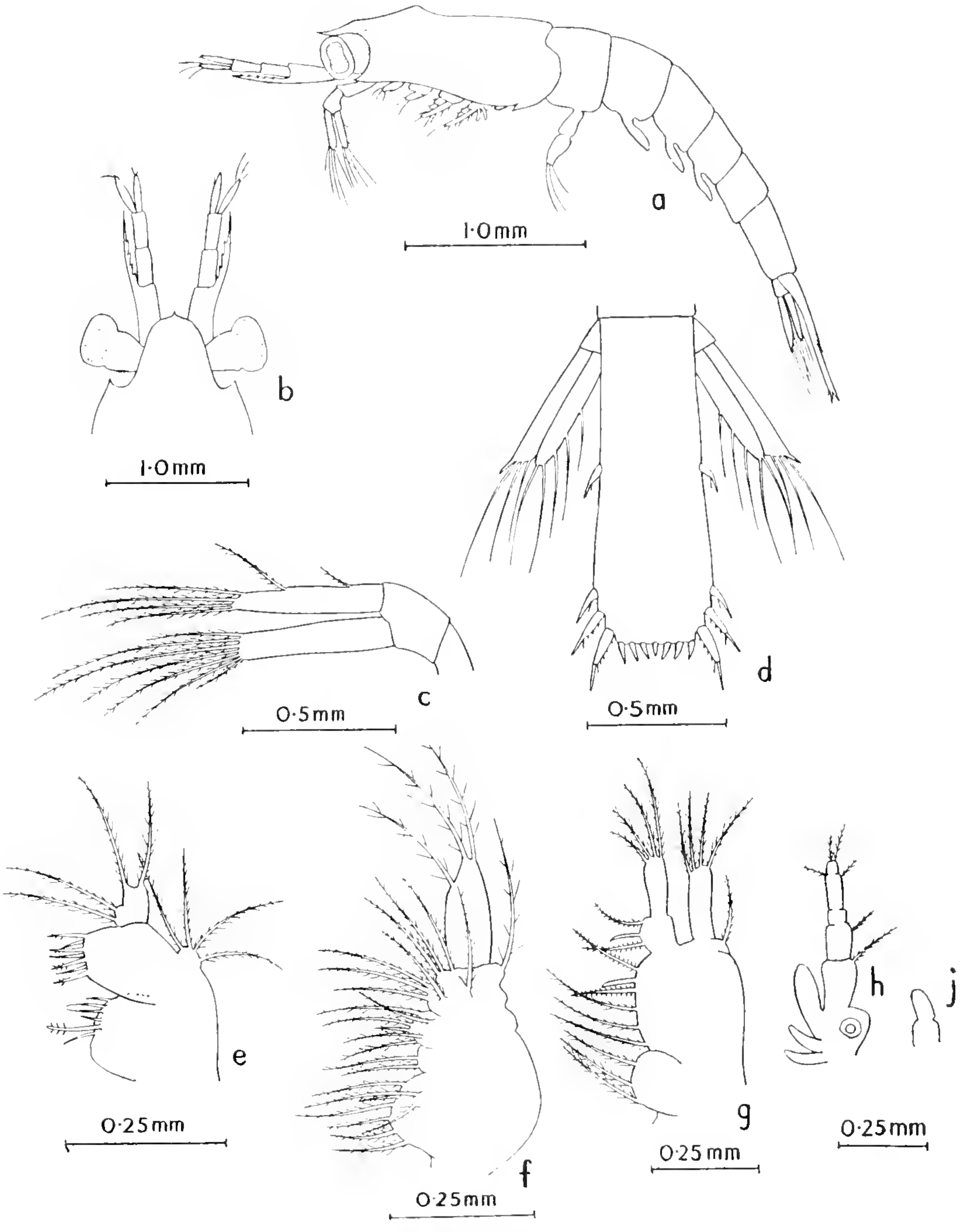


Fig. 17. *Euphausia tenera.* *a*, first furcilia, lateral view; *b*, cephalothorax, dorsal view; *c*, second antenna; *d*, telson and uropods; *e*, first maxilla; *f*, second maxilla; *g*, first cormopod; *h*, second cormopod; *j*, third cormopod.

Third furcilia. Four specimens examined and measured. Length range 5·1–5·3 mm.; average length 5·2 mm. (Fig. 18*c*, *d*).

The anterior margin of the carapace is now produced as a definite, pointed rostrum which extends beyond the eyes.

The endopod of the third cormopod is now segmented and geniculate. The fourth cormopod is bifurcate and the fifth is present as a simple bud. The second to fifth cormopods bear gill-lobes.

All five pairs of pleopods are now setose.

The telson remains the same and still carries seven terminal spines.

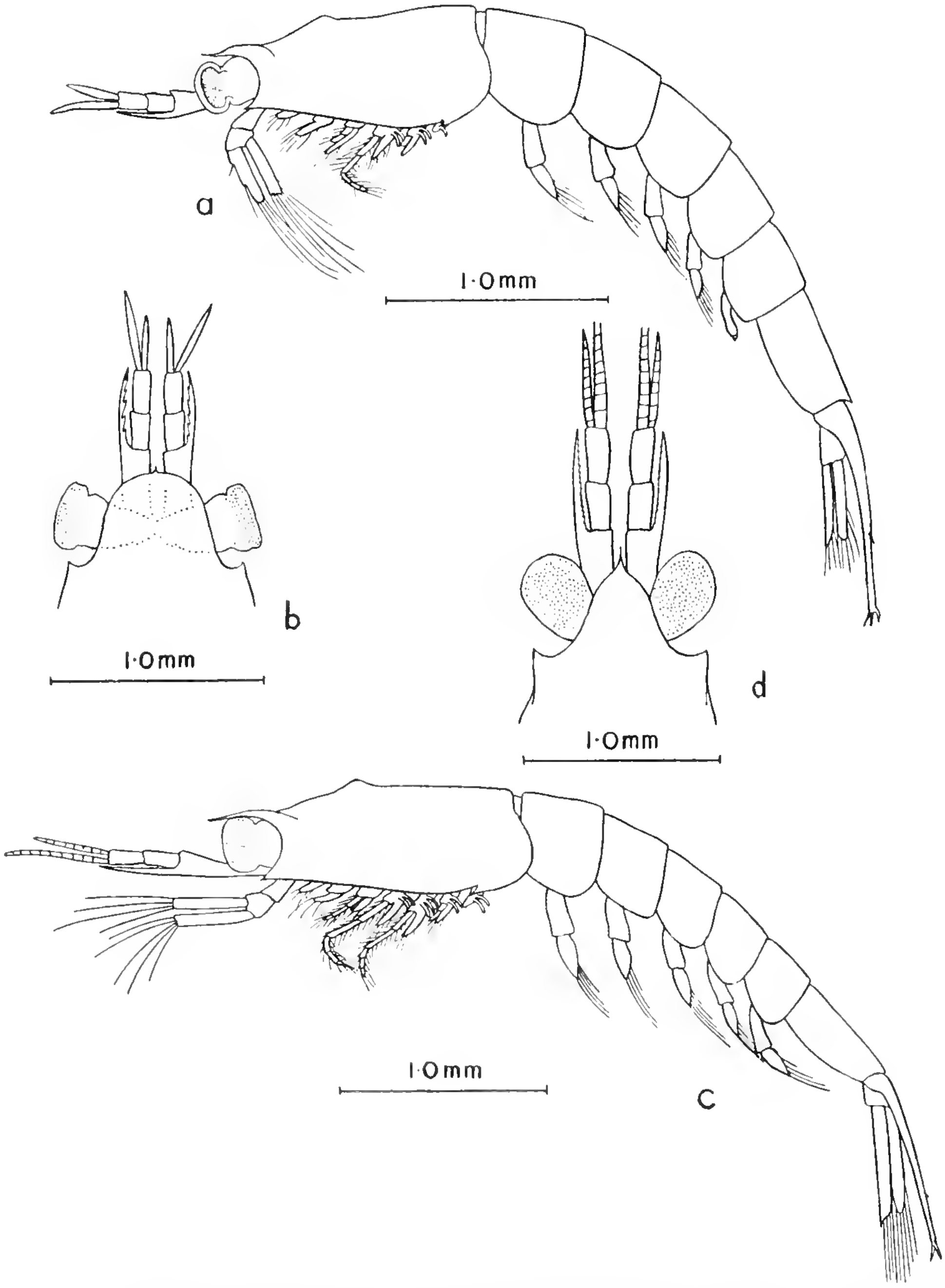


Fig. 18. *Euphausia tenera.* *a*, second furcilia, lateral view; *b*, cephalothorax, dorsal view; *c*, third furcilia, lateral view; *d*, cephalothorax, dorsal view.

Fourth furcilia. Twenty specimens present. Seven examined and measured. Length range 5·3–5·7 mm.; average length 5·5 mm. (Fig. 19*a*, *b*).

The rostrum is a trifle more pronounced, but otherwise unchanged.

The flagella of the first antennae are elongated and segmented.

The endopod of the fourth cormopod is now segmented and geniculate. The fifth is bifurcate and the sixth is present as a simple bud. The second to the sixth bear gill-lobes, those on the sixth being more arborescent than those on the more anterior cormopods.

The pleopods are all setose.

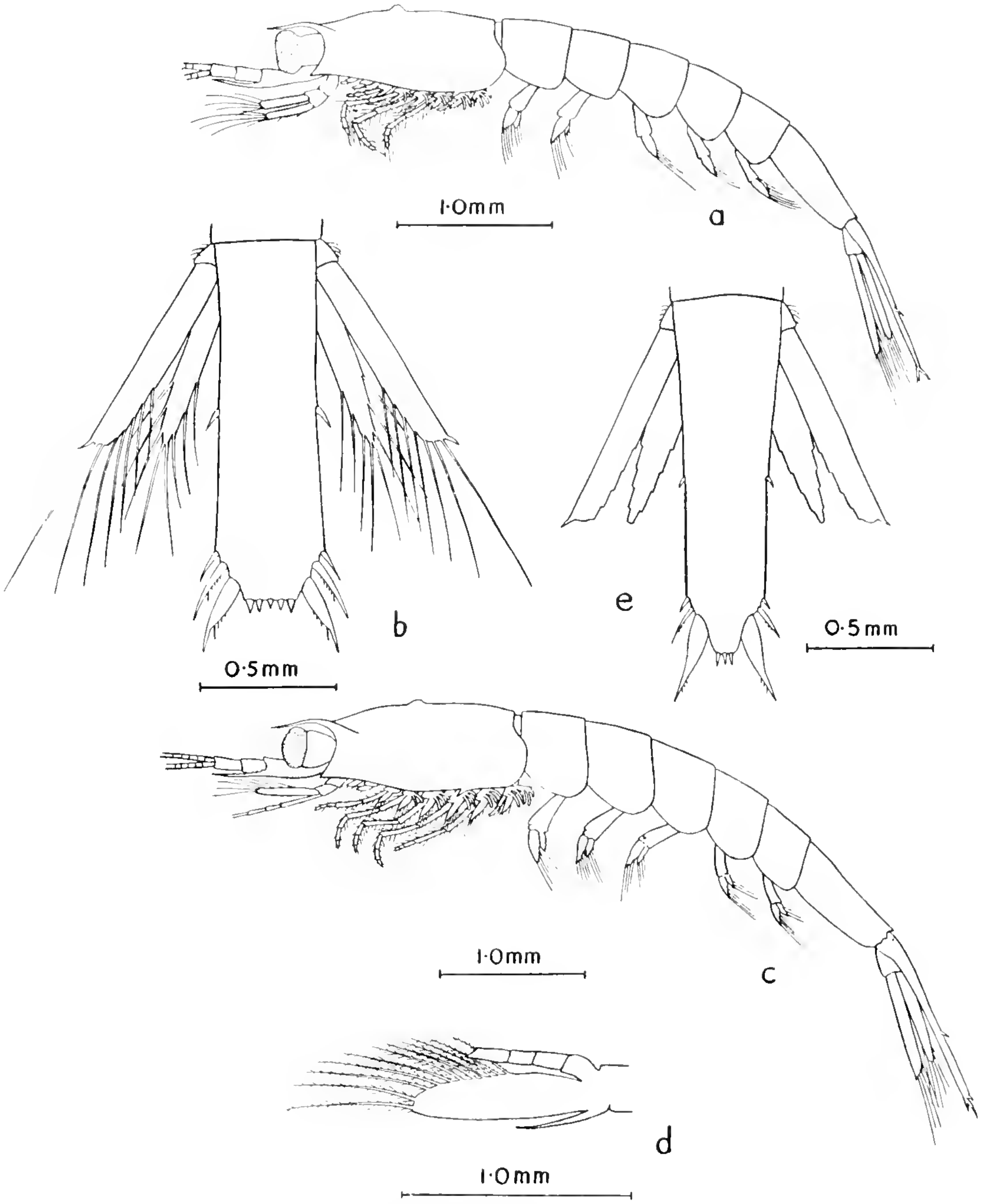


Fig. 19. *Euphausia tenera.* *a*, fourth furcilia, lateral view; *b*, telson and uropods; *c*, fifth furcilia, lateral view; *d*, second antenna; *e*, telson and uropods.

The number of terminal spines on the telson is now reduced to five. There are still three pairs of postero-lateral and one pair of ventro-lateral spines. The lateral uropods are now strongly developed.

Fifth furcilia. Three specimens present. All examined and measured. Length 6·3 mm. (Fig. 19*c*, *d*, *e*).

The second antenna is no longer natatory. The endopod is segmented and the exopod is scale-like with a strong tooth situated proximally at the outer margin.

The sixth cormopod is now bifurcate and carries a complex gill structure.

The two outer pairs of postero-lateral spines on the telson are much reduced while the inner pair has increased considerably in size.

The number of terminal spines has been reduced to three.

Nematoscelis megalops G. O. Sars

Egg. 0·41–0·43 mm. in formalin (Fig. 20*a*, *b*).

There is a moderately large perivitelline space between the egg contents and the thin, transparent membrane. Just before hatching the first nauplius can be clearly seen, and it now completely fills the interior of the egg-capsule.

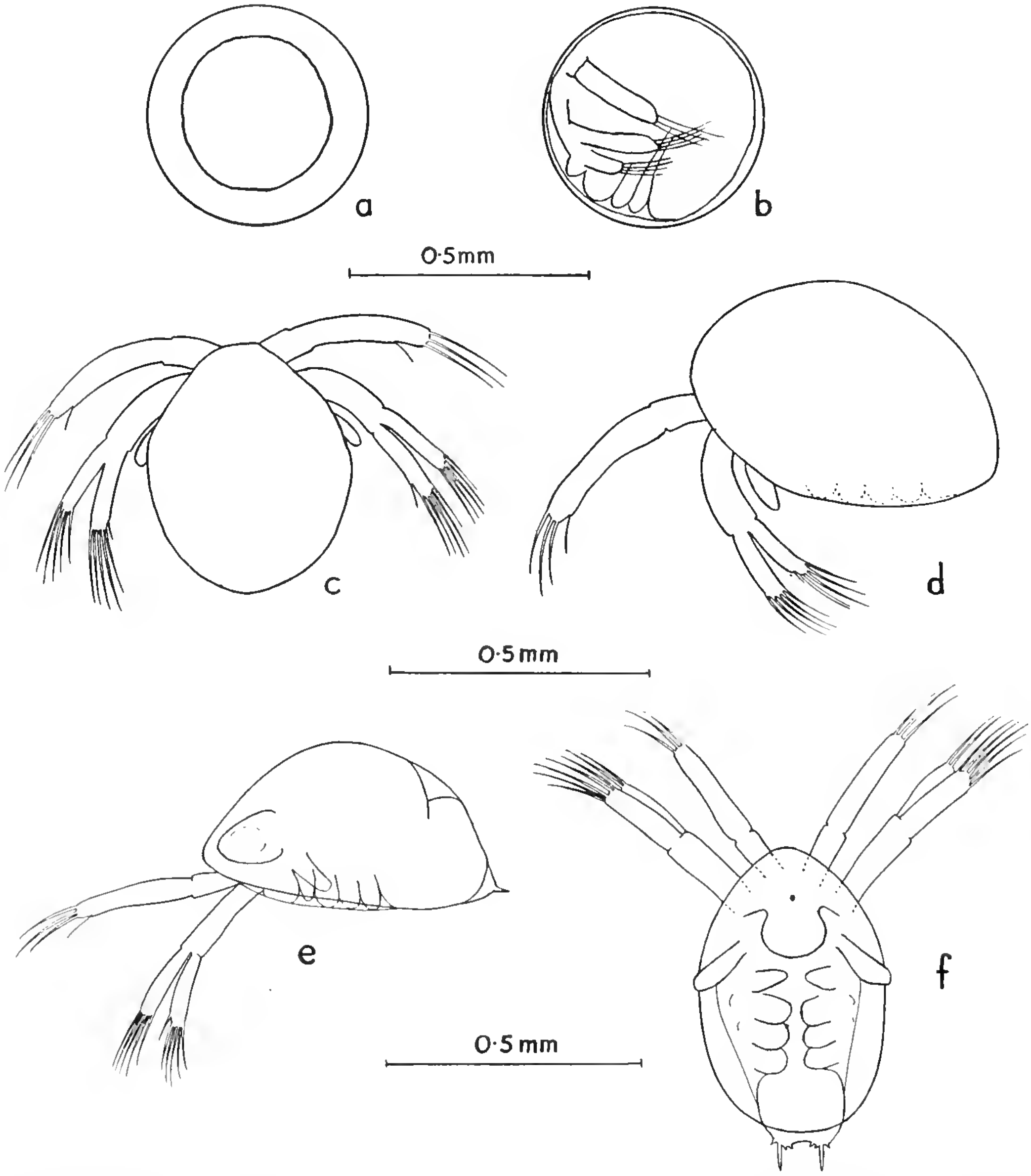


Fig. 20. *Nematoscelis megalops.* *a*, egg; *b*, egg containing nauplius prior to hatching; *c*, nauplius, dorsal view; *d*, nauplius, lateral view; *e*, pseudometanauplius, lateral view; *f*, pseudometanauplius, ventral view.

Nauplius. 0·43–0·53 mm. Six specimens examined (Fig. 20*c*, *d*).

The body is round-oval in dorsal aspect with no appendages or processes at the posterior end.

The first antennae are uniramous, with four setae.

The second antennae are biramous, the branches having five and six setae respectively.

The mandibles are uniramous and naked.

The rudiments of the metanaupliar limbs are discernible through the skin.

Pseudometanauplius. 0·53–0·57 mm. Five specimens examined (Fig. 20*e*, *f*).

The body is more elongated than in the previous stage, oval, and at the posterior end the rudimentary telson can be seen.

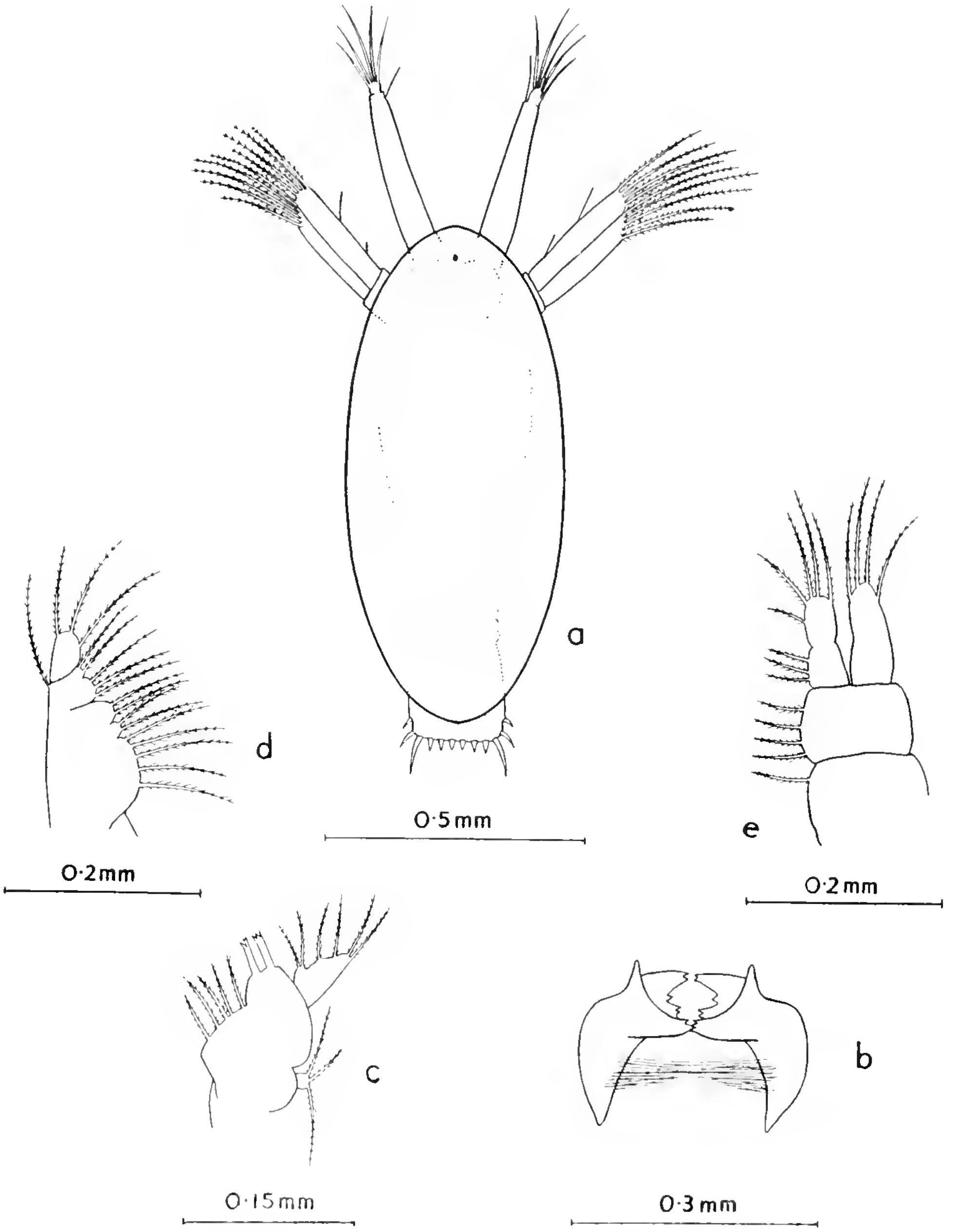


Fig. 21. *Nematoscelis megalops.* *a*, first calyptopis, dorsal view; *b*, mandible; *c*, first maxilla; *d*, second maxilla; *e*, first thoracic limb.

The antennae project forward, but are otherwise unchanged.

The median eye and the rudiments of the ocular plates are visible.

There are two to four pairs of spines at the end of the rudimentary telson.

The carapace, metanaupliar limbs, and telson are encased in an extremely thin, transparent skin.

Metanauplius. No metanaupliar stages were encountered.

First calyptopis. Seven specimens examined (Fig. 21 *a–e*; Fig. 22 *a*, *b*). Length range 0·97–1·0 mm.; average length 0·98 mm.

The carapace is a long, high and very narrow dome which covers the entire anterior part of the body. There are no denticles on the inferior margin.

The ocular plates are visible and the median eye is still present.

The first antennae project forward. The rudiments of an inner ramus can be seen bearing two or three setae. There are five naked terminal setae on the outer ramus.

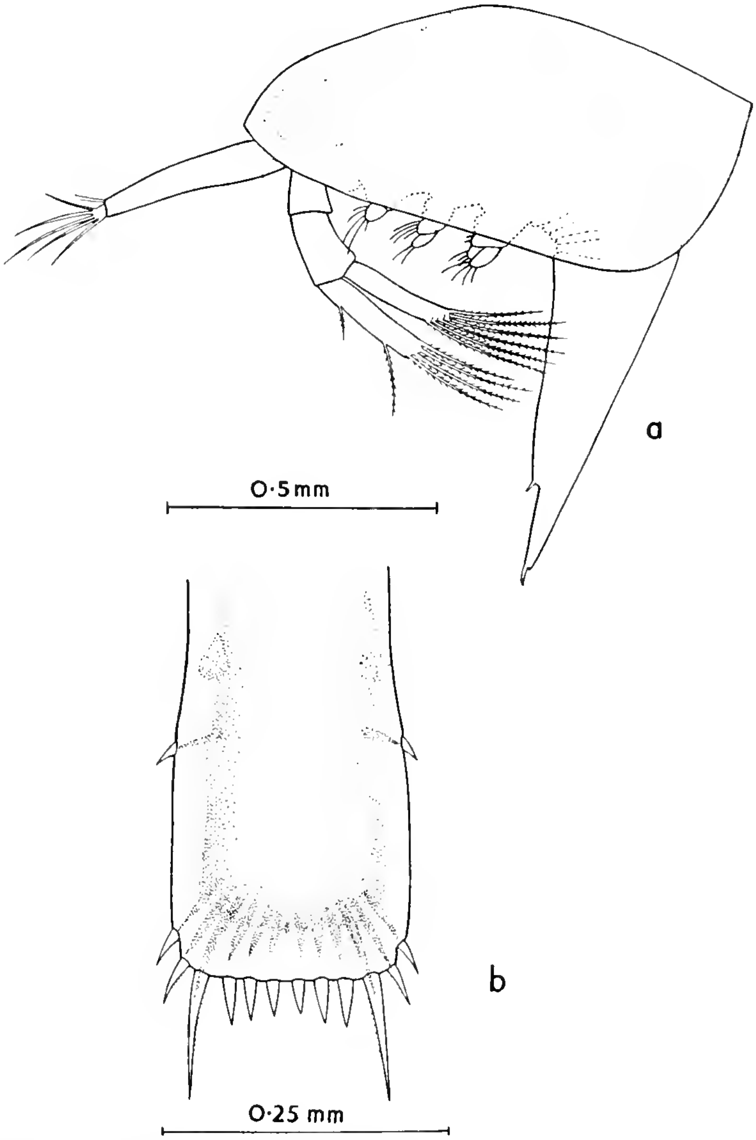


Fig. 22. *Nematoscelis megalops.* *a*, first calyptopis, lateral view; *b*, telson. The form of the telson of the succeeding instar is visible through the skin.

The two rami of the second antennae are carried on a peduncle of two segments. The anterior ramus carries two lateral spines and four setose terminal spines. The second ramus carries six setose terminal spines.

The mandible is naked, and the first and second maxillae and first thoracic limb are present and setose.

The abdomen is unsegmented. The telson carries one pair of ventro-lateral, three pairs of postero-lateral, and six terminal spines.

Second calyptopis. Five specimens examined (Fig. 23*a–c*). Length range 1·6–2·0 mm.; average length 1·7 mm.

The carapace is unchanged except for its posterior margin which has a small, smooth projection in the middle.

The compound eyes and ocular luminous organ are defined, but the median eye is lost.

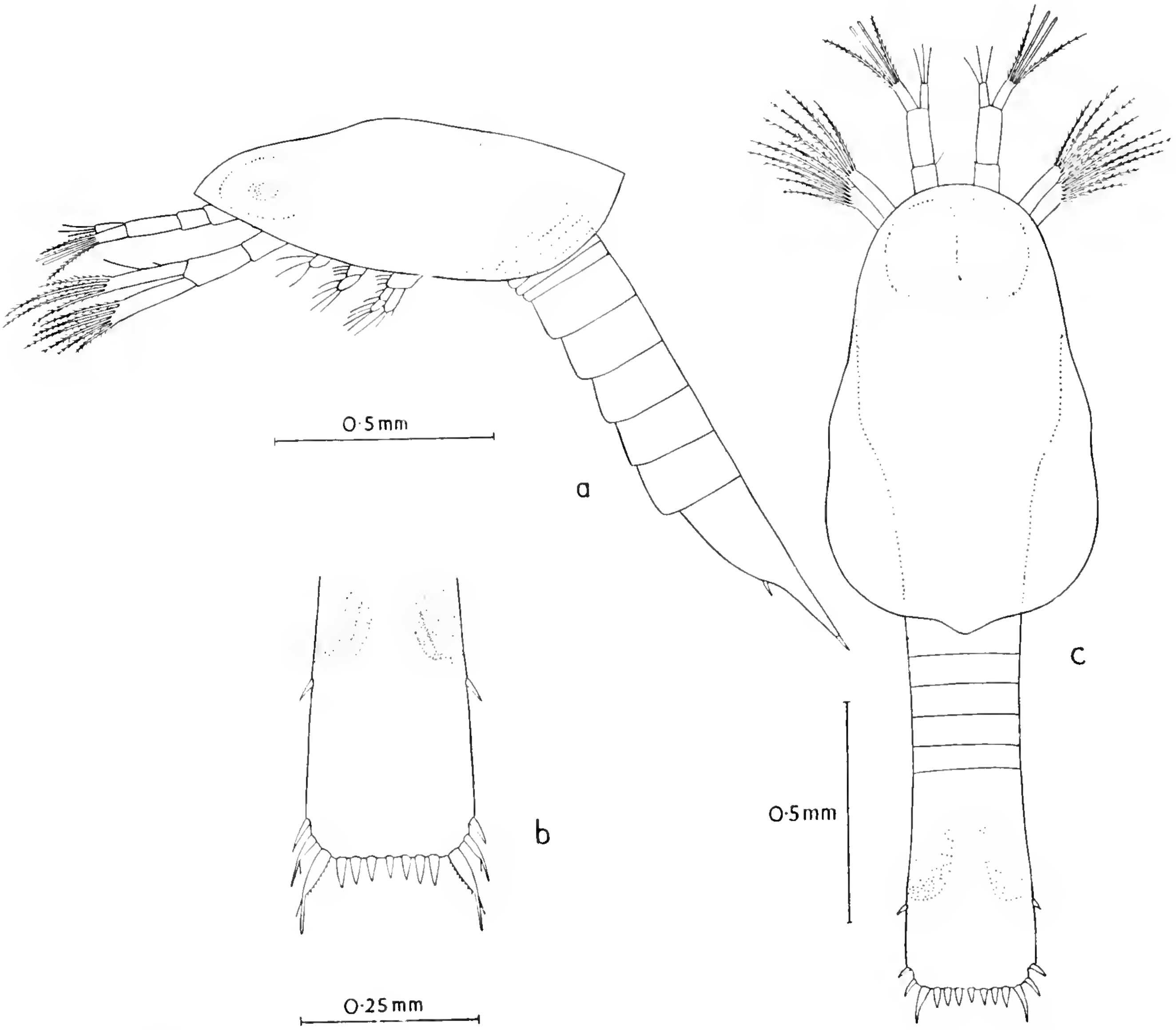


Fig. 23. *Nematoscelis megalops.* *a*, second calyptopis, lateral view; *b*, telson; *c*, second calyptopis, dorsal view.

The first antenna is biramous and has a three-segmented peduncle. The inner ramus carries three terminal setae and the outer ramus four. The second segment of the peduncle carries a small spine on its inner, distal margin.

The remaining thoracic appendages are the same as in the first calyptopis except that the endopodite of the first cormopod now has two segments. In none of the five specimens examined was there any sign of the second thoracic limb. The thorax is clearly segmented.

The abdomen has five segments and a telson. The developing uropods can be very clearly discerned within the integument of the telson. The telson now carries seven terminal spines, three pairs of postero-lateral and one pair of ventro-lateral.

Third calyptopis. Eleven specimens examined (Fig. 24*a*, *b*). Length range 2·4–2·9 mm.; average length 2·7 mm.

The carapace is unchanged except for the appearance of the rudiments of the dorsal crest. The inferior margin is smooth.

The compound eyes are globular and pigmented.

The basal segment of the first antennal peduncle bears a strong toothed spine on its outer, distal margin. This reaches to about the middle of the last peduncular segment.

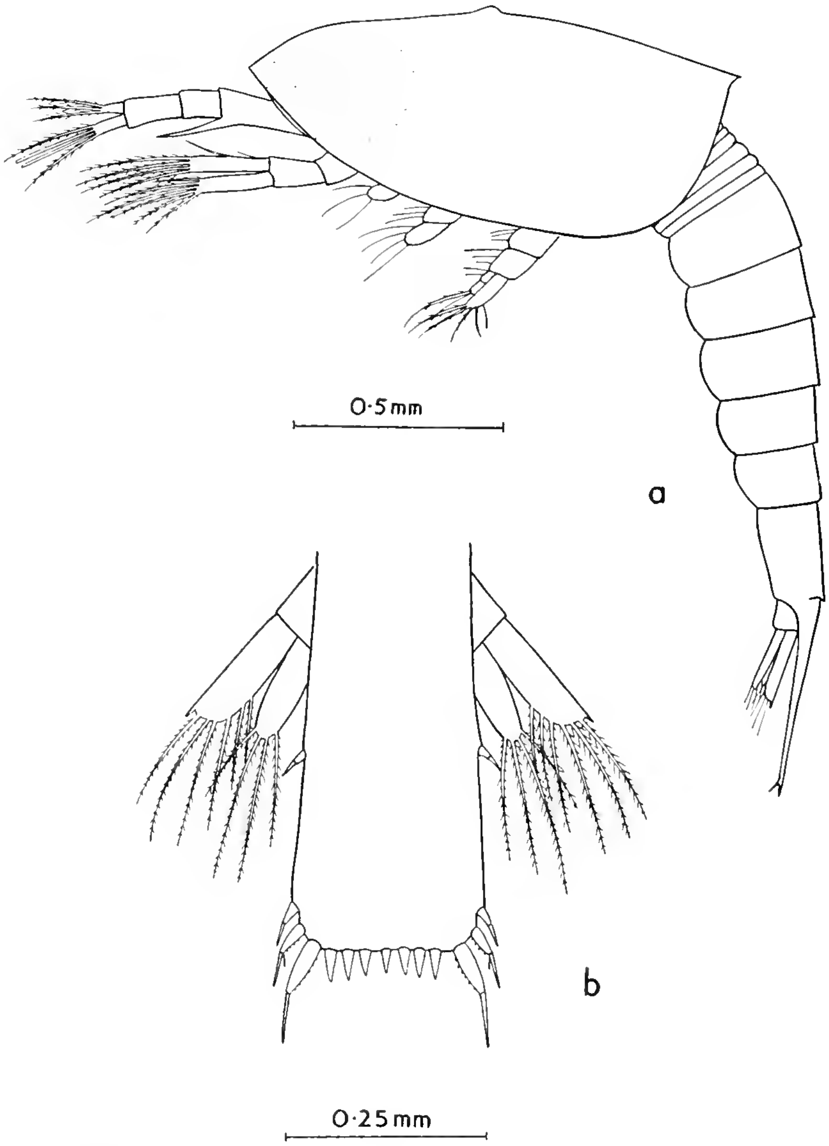


Fig. 24. *Nematoscelis megalops.* *a*, third calyptopis, lateral view; *b*, telson and uropods.

The second antennae and thoracic appendages have not changed.

There are now six abdominal segments and a telson. The abdomen bears no appendages.

The lateral uropods of the telson are now developed and spinose. The outer ramus of the uropod is somewhat longer than the inner and its outer margin is produced as a small, strong tooth. The remaining armature of the telson is unchanged.

A dorsal view of this stage can be seen in Frost (1935), and is, therefore, not figured here. She does not, however, indicate the small, smooth projection on the posterior margin of the carapace. This can be seen even in lateral view.

Furcilia stages. Frost (1935) has already described one calyptopis, three furcilia and four cyrtopia stages for this species. The calyptopis was a third calyptopis and she called the three furcilia the third, eighth and penultimate. The cyrtopia were the first to the fourth inclusive.

Gurney (1942) considers Frost's furcilia stages to be the first, second and third furcilia. Undoubtedly her 'third' and 'eighth' furcilia are in reality the first and second stages respectively, for no preceding or intermediate forms have ever been found. In the present series, however, a form intermediate between Frost's eighth and penultimate furcilia occurs. This form has five setose pleopods and seven terminal spines on the telson. Only one specimen was found, but it is considered here as the third furcilia stage.

Frost's penultimate furcilia had the telson spines reduced to five. This now becomes the fourth furcilia stage. Frost considered that this stage was not the immediate precursor of the first cyrtopia, for in all other cases of euphausiid development there are two stages with only one terminal telson spine; in the first stage the long, outer laterals are present and in the second they are absent. She thought it highly probable that one or more stages exist between her penultimate furcilia and first cyrtopia. In this she was quite right, for one specimen was found in this series having one terminal telson spine and still retaining the long, outer laterals.

I have called this the sixth furcilia, however, rather than the fifth. If it were the fifth the number of terminal spines would have to be reduced from five to one in one stage. This sequence has never been reported in any other euphausiid life-history and it seems justifiable to suspect that there is at least one stage with three terminal spines on the telson. The furcilia stages then are as follows:

Table 10. *Furcilia stages* of Nematoscelis megalops

Stage 1			Stage 2			Stage 3			Stage 4			Stage 5			Stage 6		
Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines	Pleopods		Telson spines
N.	S.		N.	S.		N.	S.		N.	S.		N.	S.		N.	S.	
2	—	7	3	2	7	—	5	7	—	5	5	—	5	3?	—	5	1

N. = non-setose, S. = setose; stages 5 and 6 have the second antennal endopod segmented.

The numbers of specimens in each stage in this series are as follows: stage 1 = 28, stage 2 = 48, stage 3 = 1, stage 4 = 9, stage 5 = 0, stage 6 = 1.

Frost's descriptions and illustrations are accurate and adequate and it is considered unnecessary to elaborate on them.

BIBLIOGRAPHY

BODEN, B. P., 1950*a*. *Plankton organisms in the deep scattering layer.* U.S. Navy Electronics Laboratory Rep., 186, pp. 1–29.

—— 1950*b*. *The post-naupliar larval stages of the crustacean* Euphausia pacifica. Trans. Amer. micro. Soc., **69**, pp. 373–86.

—— 1951. *The egg and larval stages of* Nyctiphanes simplex, *a euphausiid crustacean from California.* Proc. zool. Soc. London, **121** (3), pp. 515–27.

—— 1954. *The euphausiid crustaceans of southern African waters.* Trans. royal Soc. S. Afr. **34** (1), pp. 181–243, 24 figs.

CALMAN, W. T., 1896. *On deep-sea crustacea from the south-west of Ireland.* Trans. royal Irish Acad. **31** (1), pp. 1–21, 2 pls.

—— 1905. *Note on a genus of euphausiid crustacean.* Sci. Invest. Fish. Ireland, 1902–3, **4** (ii), pp. 153–5, 1 pl.

CHUN, C., 1887. *Die pelagische Thierwelt in grösseren Meerestiefen und ihre Beziehungen zu der Oberflächenfauna.* Biblio. Zool. **1**, pp. 1–66, 5 pls.

COLOSI, G., 1917. *Crostacei—Parte II. Eufausiacei.* Racolte planktoniche fatte dalla R. Nave 'Ligura', **2** (7), pp. 165–205, 3 pls.

CURRIE, R., 1953. *Upwelling in the Benguela Current.* Nature, London, **171**, pp. 497–9, 3 figs.

DANA, J. D., 1852. *Conspectus of the crustacea of the exploring expedition under Capt. Wilkes.* Amer. J. Sci. **13** (1), pp. 1–685.

EINARSSON, H., 1942. *Notes on Euphausiacea I–III.* Vidensk. Medd. naturh. ForenKojb. **106**, pp. 263–86.

—— 1945. *Euphausiacea I. Northern Atlantic species.* Dana Rept. 27, pp. 1–185.

FRASER, F. C., 1936. *On the development and distribution of the young stages of krill* (Euphausia superba). Discovery Rept. **14**, pp. 1–192.

FROST, W. E., 1935. *Larval stages of the euphausiids* Nematoscelis megalops (*G. O. S.*) *and* Stylocheiron longicorne (*G. O. S.*) *taken off the south-west coast of Ireland.* Proc. royal Irish Acad. **62** (Sect. B, No. 16), pp. 443–58.

GURNEY, R., 1942. *Larvae of decapod crustacea.* London: Ray Soc. Monog. (no. 129).

HANSEN, H. J., 1905*a*. *Preliminary report on the Schizopoda collected by H.S.H. Prince Albert of Monaco during the cruise of the 'Princesse-Alice' in the year of 1904.* Bull. Mus. Océanog. Monaco, **30**, pp. 1–32.

—— 1905*b*. *Further notes on the Schizopoda.* Bull. Mus. Océanog. Monaco, **42**, pp. 1–32.

—— 1908*a*. *Crustacea Malacostraca I.* Danish Ingolf Exped. **3** (2), pp. 1–20.

—— 1908*b*. *Schizopoda and Cumacea.* Résultats du voyage du S.Y. 'Belgica'. Rapp. Sci., Zool., pp. 1–20, 3 pls.

—— 1910. *The Schizopoda of the Siboga expedition.* Siboga Exped. **37**, pp. 1–123, 16 pls.

—— 1911. *The genera and species of the order Euphausiacea, with an account of remarkable variation.* Bull. Inst. Océanog. Monaco, **210**, pp. 1–54, 18 figs.

HART, T. J., 1953. *Plankton of the Benguela Current.* Nature, London, **171**, pp. 631–3, 2 figs.

HUBBS, C. L., 1950. *On the supposed occurrence in New Zealand of the North Pacific fish genus* Sebastodes. Pacif. Sci. **4**, p. 70.

—— 1952. *Antitropical distribution of fishes and other organisms.* Proc. 7th Pacif. Sci. Congr. **3**, pp. 324–9.

ILLIG, G., 1930. *Die Schizopoden der Deutschen Tief-See Expedition.* Wiss. Ergebn. Deutsch. Tief-See Exped. 'Valdivia', **22** (6) pp. 400–625, figs.

JOHN, D. D., 1936. *The southern species of the genus* Euphausia. Discovery Rept. **14**, p. 193–324, 40 figs.

LEBOUR, M. V., 1924. *The Euphausiidae in the neighbourhood of Plymouth and their importance as herring-food.* J. Mar. Biol. Assoc. Plymouth (n.s.), **13** (2), pp. 402–31.

—— 1925. *The Euphausiidae in the neighbourhood of Plymouth.* II. Nyctiphanes couchii *and* Meganyctiphanes norvegica. J. Mar. Biol. Assoc. Plymouth (n.s.), **13** (4), pp. 810–46.

—— 1949. *Some euphausiids from Bermuda.* Proc. zool. Soc. London, **119** (4), pp. 823–37.

MOORE, H. B., 1952. *Physical factors affecting the distribution of euphausids in the North Atlantic.* Bull. Mar. Sci. Gulf & Caribbean, **1** (4), pp. 278–305.

RUSTADT, D., 1930. *Euphausiacea, with notes on their biogeography and development.* Norske Vid.-Akad. Oslo, **1** (5), pp. 1–83, 5 pls., 51 figs.

SARS, G. O., 1883. *Preliminary notices on the Schizopoda of H.M.S. 'Challenger' Expedition.* Forh. VidenskSelsk., Oslo, **7**, pp. 1–43.

—— 1885. *Report on the Schizopoda collected by H.M.S. 'Challenger' during the years 1873–1876.* Rep. Sci. Res. Voy. H.M.S. 'Challenger'. Zool. **13**, pp. 1–228, 38 pls., 4 figs.

SHEARD, K., 1953. *Taxonomy, distribution and development of the Euphausiacea (Crustacea).* B.A.N.Z.A.R.E. Rept. (Series B), **8** (1), pp. 1–72.

STEBBING, T. R. R., 1905. *General catalogue of South African Crustacea III.* Marine Invest. South Africa, **4** (2), pp. 21–213, 9 pls.

—— 1910. *General catalogue of South African Crustacea V.* Ann. S. Afr. Mus. **6** (6), pp. 281–599, 7 pls.

TATTERSALL, W. M., 1926. *Crustacea of the Order Euphausiacea and Mysidacea from the Western Atlantic.* Proc. U.S. nat. Mus. **69** (8), pp. 1–31.

ZIMMER, C., 1912. *Südwestafrikanische Schizopoden. Schultze, Forschungsreise in Südafrika* 5. Denkschr. med.-naturw. Ges. Jena, **17**, pp. 1–11.

—— 1914. *Die Schizopoden der Deutschen Südpolar Expedition, 1901–3.* Deutsch. Südpol.-Exped. **15**, pp. 377–445, 3 pls.

—— 1915. *Schizopoden des Hamburger Naturhistorischen (Zoologischen) Museums.* Mitt. naturh. Mus., Hamburg, **32**, pp. 159–82, 4 figs.

[*Discovery Reports. Vol. XXVII, pp. 377–395, Plates XX, XXI, September 1955.*]

CESTODES OF WHALES AND DOLPHINS FROM THE DISCOVERY COLLECTIONS

By

S. MARKOWSKI

CONTENTS

CESTODES OF WHALES AND DOLPHINS FROM THE DISCOVERY COLLECTIONS

By S. Markowski

(Plates XX, XXI and Text-figs. 1–45)

MATERIAL AND METHODS

THE material for this study was collected mainly at whaling stations and on board factory ships by various members of the staff of the Discovery Investigations.[1] It consists of eighty-eight samples taken from the intestines and blubber of forty-six Blue Whales (*Balaenoptera musculus*), eight Fin Whales (*B. physalus*), thirteen Sei Whales (*B. borealis*), fourteen Sperm Whales (*Physeter catodon*) and seven dolphins, namely: two *Globicephala edwardi*, two *Lagenorhynchus obscurus*, one *L. australis* and two *Steno bredanensis*. Of these, four samples of *Tetrabothrius affinis* from Blue Whales belong to the collections of the British Museum (Natural History).

The material comprises intestinal forms of cestodes, as well as several examples of larval stages encysted in the blubber. The specimens are on the whole in very good condition, except for a few cases where slight maceration has occurred. In some samples the cestodes have been fixed and preserved attached to portions of the gut.

The bulk of the collection was preserved in 4% formalin, although some of the worms were fixed in Bouin's solution.

About 600 slides of serial sections and whole mounts have been made, stained in Ehrlichs' haematoxylin and counter-stained with erythrosin. The whole mounts, stained in Mayer's paracarmine were cleared in benzyl-alcohol with very good results, even for the larger portions of the strobila. The serial sections have been cut at 10–15 μ thick.

The hosts were caught in South Africa (Saldanha Bay, Durban, Cape Town and Simon's Town), the Azores, the Falkland Islands, South Georgia, the South Shetlands and at various positions in the Southern Ocean. The localities are given with the description of each species.

I have the greatest pleasure in expressing my gratitude to The Royal Society for advancing me a grant from the Browne Research Fund which enabled me to complete this investigation.

I also take this opportunity of expressing my thanks to Dr N. A. Mackintosh, C.B.E., of the National Institute of Oceanography and to Dr H. E. Bargmann of the same Institute for their kind assistance in the course of this work, and to Mr S. Prudhoe of the British Museum (Natural History). My thanks are also extended to Dr Gwendolen Rees who kindly lent whole mounts of *Tetrabothrius* from whales.

ABBREVIATIONS USED IN THE FIGURES

c.s.,	cirrus-sac.	*u.*,	uterus.
e.,	excretory system.	*u.o.*,	uterine opening.
l.m.,	longitudinal muscles.	*v.*,	vagina.
o.v.,	ovary.	*v.d.*,	vas deferens.
t.,	testis.	*v.g.*,	vitelline gland.

---

[1] Now incorporated with the National Institute of Oceanography.

GENERAL DISCUSSION

The cestodes collected represent ten different species belonging to six genera. Of these species, two appear to be new to science and two represent larval stages, the specific identification of which does not seem possible at present, although it can be seen that they belong to two different genera. The list given below shows the names of the cestodes examined and Table 2 (p. 394) their occurrence in particular hosts.

LIST OF CESTODES EXAMINED

1. *Tetrabothrius affinis* (Loennberg, 1891).
2. *T. wilsoni* (Leiper & Atkinson, 1914).
3. *T. ruudi* Nybelin, 1928.
4. *T. schaeferi* sp.n.
5. *Trigonocotyle globicephalae* Baer, 1954.
6. *Tr. prudhoei* sp.n.
7. *Priapocephalus grandis* Nybelin, 1922.
8. *Diplogonoporus balaenopterae* Loennberg, 1892.
9. *Phyllobothrium* larva.
10. Tetraphyllidean larva.

With the exception of the two larval forms and *Diplogonoporus balaenopterae*, the rest of the above mentioned cestodes belong to the family Tetrabothriidae, which appears to contain the bulk of the cestodes found in Cetacean hosts.

Because of their great similarity the identification of certain species presents certain difficulties.

The scolex in the majority of these cestodes bears four suckers, which are variable in shape and size. These suckers are usually provided with modifications called 'epaulettes' or with fleshy protuberances such as occur in the Genus *Trigonocotyle*. The scolex is subject to contraction and consequently its size and shape give no help in specific determination. In the genus *Priapocephalus*, however, this organ is acorn-like and easy to distinguish, though some variations in its contour do occur, as was mentioned by Nybelin (1928) for *P. minor*.

The strobila in the Tetrabothriids is either cylindrical and worm-like, or flattened, as in the other groups of cestodes. The cylindrical strobila appears to be typical of *Tetrabothrius affinis*, though in some cases, a short portion showing flattened segments occurs in the hind part of the body (Pl. XX, fig. 1). In *Trigonocotyle globicephalae* a short anterior portion of the body is cylindrical, while the remainder of the strobila is flattened.

Modifications of the anterior part of the body have also been noticed in the only example of the Pseudophyllidea, present in this collection, namely *Diplogonoporus balaenopterae*, where that portion of the strobila is markedly undulate dorso-ventrally (Pl. XXI, fig. 6). It is difficult to prove at the moment whether these modifications represent natural features or are caused by fixation.

The genital organs in Tetrabothriids are also very similar and uniform in structure. Although there is much variation in the number of the testes in immature proglottids and their size and arrangement in the medullary parenchyma is difficult to determine, in the fully mature segments where egg production has not yet begun, it is possible to ascertain their number and arrangement.

In some forms, as in *Trigonocotyle globicephalae*, the testes, when examined in the cylindrical part of the body, are distributed in many layers. In the flattened portion of the body, however, they are arranged in a single layer.

In the species of *Tetrabothrius* examined during the present work, the testes are situated dorsally, except in *T. affinis*, where they are distributed dorso-ventrally. This arrangement, however, may be altered and affected by the growth of the uterus, particularly when filled with eggs.

The testes seem also to decrease rapidly in number in the gravid segments, being either partially spent or else crowded nearer to the surface of the medullary parenchyma by the uterus. Some differences in the size of the testes in mature segments (measured in transverse sections of the body) are noticeable, and this may be regarded as a valuable feature in specific differentiation (Table 1, p. 387).

The cirrus-sac, although similar in structure, is also subject to much contraction and its size and shape depend greatly on this factor. In some cases, as in *Trigonocotyle globicephalae*, and *Tr. prudhoei* sp.n., some muscular modification occurs in the area of the genital atrium, forming a kind of sucker. This, however, is also met with in other species of Tetrabothriids not found in whales.

In cetacean Tetrabothriids, the ovary and vitelline glands are situated in the ventral half of the segment. In some of the species examined, the ovary contains fairly large egg-cells. The full development of the ovary is reached in the portion of the strobila occupied by the mature proglottids. From this point onwards towards the posterior end, the ovary gradually undergoes a process of deterioration, caused by the overgrowth of the uterus.

In fully gravid segments the uterus is so strongly developed that it practically replaces the rest of the genital system. It is a centrally situated, sac-shaped organ extending laterally and gradually occupying the whole of the medullary parenchyma.

There is no proper uterine pore in cetacean Tetrabothriids. Instead, the uterus opens through the body-wall, when the eggs are ready to be discharged from the segment. The rupture through which the eggs are passed appears on the dorsal surface of the body, at one definite point, and the path in the cortical parenchyma, along which the distending uterus is pushed, is surrounded by a distinct mass of eosinophil tissue. In *Priapocephalus grandis*, however, many such ruptures on the dorsal surface have been observed. No uterine openings or ducts have been found in the two species of *Trigonocotyle* from the present collection.

It seems that a kind of 'cement'[1] protects the newly formed uterine opening from the effects of the gastric juices in the host's intestine and which closes the opening after the eggs have been discharged.

It is well known that the eggs of cestodes lose much of their characteristic structure after fixation and extraction from the uterus. Nevertheless, specific differences seem to occur between the eggs of particular species found in the Discovery Collection. Their size appears to be related to the thickness of the outer and inner membranes in the various species, and in some cases to the number of membranes as well.

The embryos also seem to vary in size with species, and, with the exception of *Tetrabothrius ruudi* (Fig. 15), the three pairs of hooks with which they are all provided exhibit specific differences (Table 1).

The vagina runs ventrally to the cirrus-sac in all examined species of *Tetrabothrius*.

The most striking differences among particular species seem to occur in the structure and arrangement of longitudinal muscles, as seen in transverse section.

In the present material, the longitudinal muscles of Tetrabothriids undergo morphological changes within the individual strobila itself. These changes are associated with the development of the genital organs and it appears that in the immature portion of the strobila, where the genital organs are either non-existent or rudimentary, the longitudinal muscles are differentiated into bundles, but in the mature portion of the strobila, these bundles have taken on a very definite arrangement. As the mature proglottids ripen, and the uterus becomes increasingly distended, the muscle bundles tend to atrophy, although their characteristic arrangement can still be distinguished. This series of changes is shown in sections of *Trigonocotyle globicephalae* (Figs. 24, 25) and *Priapocephalus grandis* (Figs. 34-36).

---

[1] This 'cement' is probably produced by gland-cells in the modified tissue.

SUMMARY OF DISCUSSION

To sum up: Specific differences are to be found in the size and the arrangement of testes, in the size and structure of eggs, embryos and embryonic hooks, and in the arrangement and shape of the longitudinal muscles in the fully mature, but not gravid segments.

SYNONYMY

The history and the nomenclature of some of the Tetrabothriids occurring in Cetacea have been given by Rees (1953).

Recently, Baer (1954) has published a list of synonymous names of Tetrabothriids and their specific classification. From the present work it seems, however, that *Tetrabothrius wilsoni*, which he considers to be synonymous with *T. affinis*, actually represents a distinct species (Table 1, p. 387).

Baer's (1954) criticism of Baylis's (1926) description of *T. affinis* appears to be justified, as the material examined by Baylis seems to represent another species, described in this paper as *T. schaeferi* sp.n. The form mentioned by Rees (1953) as *Tetrabothrius* sp. also appears to represent the same species.

The two new species described in this paper, namely *T. schaeferi* and *Trigonocotyle prudhoei* have been named after Miss F. H. A. Schaefer who, during my recent illness nursed me in hospital, and after my friend Mr S. Prudhoe of the British Museum (Natural History).

SYSTEMATIC NOTES

Genus **Tetrabothrius** Rudolphi, 1819

This genus is represented in the present material by four species. Of these, one seems to be new.

Tetrabothrius affinis (Loennberg, 1892). (Figs. 1–6, Pl. XX, figs. 1–2.)

Diplobothrium affine Loennberg, in Jägerskiöld, 1891.
Tetrabothrium (*Diplobothrium*) *affine*. Loennberg, 1892.

HOSTS: Blue Whale (*Balaenoptera musculus*); Sperm Whale (*Physeter catodon*).
LOCALITIES: Saldanha Bay and Durban (South Africa); South Georgia; and 58° 32′ S, 34° 52′ E.

The specimens examined are about 20 cm. long and about 5 mm. wide. The strobila is cylindrical with very short segments. In some specimens the posterior end of the body is modified into flattened segments, markedly separated from each other (Pl. XX, fig. 1).

This region is the spent part of the body containing the degenerate genital organs.

The scolex, about 2 mm. long and 2 mm. broad, is variable in shape and bears typical 'epaulettes'. A neck does not seem to be present.

The musculature is strongly developed in this species. Cross-sections of the body show that the longitudinal muscles form two distinct rings. The internal ring is composed of strongly developed bundles of a very characteristic shape shown in Fig. 4. The circular and dorso-ventral muscles are also very well developed.

The testes are dorso-ventrally elongate in younger segments and about $90 \times 53\,\mu$ in diameter, but in the more developed segments they are irregularly spherical and seem to be arranged in several layers, which are distributed dorso-ventrally. The thick-walled, coiled vas deferens is well developed. The pear-shaped or rounded cirrus-sac possesses thick muscular walls and a strongly developed cirrus.

The lobate ovary extends transversely in the ventral part of the segment and is composed of distinct egg-cells. The vitelline gland is situated ventrally to the ovary.

Figs. 1–6. *Tetrabothrius affinis* from Blue Whale. 1, cross-section through mature segment; 2, formation of uterine opening and mode of discharging eggs; 3, eggs being discharged from uterus; 4, transverse section of a portion of longitudinal muscle; 5, transverse section of segment showing cirrus-sac and vagina; 6, egg.

The uterus is a well-developed sac. There is no special uterine pore, but dorsally in the central part of the segment, the parenchyma undergoes some modification. Transverse sections of this part of the segment show differentiated tissues which appear to form a cone. Gradually the distending uterus, filled with eggs, breaks through this part of the segment and the eggs are discharged through the rupture in the body-wall. The diameter of the egg is about (66–106 × 33–83)μ with the embryonic membrane measuring 51 × 66μ. The embryo measures about 52 × 26μ and is provided with three pairs of hooks, of which the lateral pairs measure 17μ in length, and the central pair 20μ.

The excretory system, composed of two main canals with transverse vessels, is very well developed. The ventral canal is relatively wider in diameter than the dorsal one, but the latter possesses thick walls.

Tetrabothrius wilsoni (Leiper & Atkinson, 1914). (Figs. 7–10.)

Oriana wilsoni Leiper & Atkinson, 1914.
Tetrabothrius wilsoni Baylis, 1926.
Tetrabothrius affinis Baer, 1954.

HOSTS: Sei Whale (*Balaenoptera borealis*); Blue whale (*B. musculus*).
LOCALITIES: Durban; South Africa; South Georgia.

Of the thirty-four specimens examined several appear to be gravid, a condition not hitherto reported. The length of the worms varies from 6 to 14 cm. and the width from 2 to 3 mm. The body is dorso-ventrally flattened. The scolex bearing four suckers with weakly developed 'epaulettes' is about 3 mm. broad.

The longitudinal muscles are arranged in two very indistinct rings, as shown in Fig. 9. Individual bundles are not well defined and are composed of rather thick muscle fibres. Their arrangement appears diffuse and differs considerably from that found in *Tetrabothrius affinis*. The circular muscles, though present, are poorly developed.

The testes are situated in the dorsal part of the segment, being 99 × 120μ in transverse section. They seem to be arranged in an irregular layer. The vas deferens is not very strongly developed, while the cirrus-sac is pear-shaped or more or less spherical in transverse sections of the strobila.

The ovary is extremely well developed, lobate, extending transversely in the ventral part of the segment, and occupying a considerable area of the proglottid.

The egg-cells are fairly large, being about 15μ in diameter.

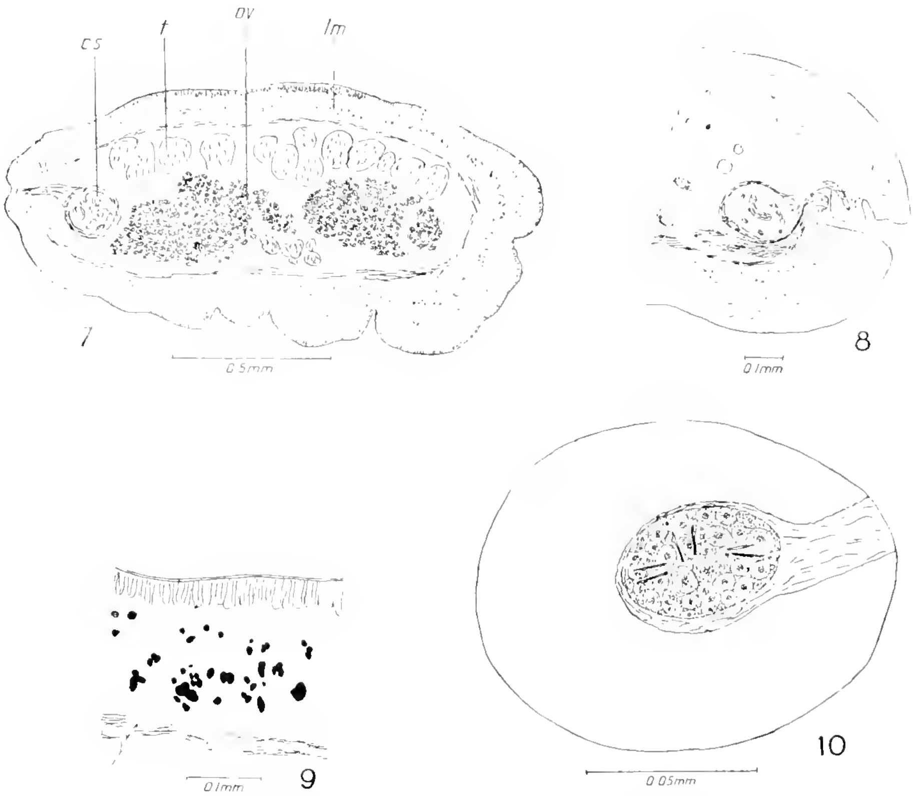
The vitelline gland, situated ventrally beneath the ovary, is well developed.

The uterus, in fully gravid segments, occupies the whole of the medullary parenchyma of the segment, considerably displacing the internal organs. The walls of the segments are much thinner than in *T. affinis*.

The eggs are discharged through a small opening in the dorsal face of the segment. They measure about 90 × 60μ. The embryonic membrane is about 45 × 30μ and the embryo 36 × 21μ in diameter. It seems that the latter is attached by its membrane to the external egg-capsule, as shown in Fig. 10. The external and internal pairs of embryonic hooks are of similar length, i.e. about 12μ.

The excretory system appears to be weakly developed and both the ventral and the dorsal trunks are of similar diameter. In the younger segments, as well as in the gravid, the ventral trunk of the excretory system seems to have a greater diameter. This, however, may be caused by the fixation and contraction of the tissues.

This form, described by Leiper & Atkinson in 1914, by Baylis in 1926 and recently by Baer (1954), represents a valid species, distinguished by differences in the arrangement and structure of the longitudinal muscles, the arrangement of the testes, the development of the ovary, and the structure of the eggs. The above-mentioned authors appear to have dealt only with immature specimens, which of course are not satisfactory for comparative purposes.



Figs. 7–10. *Tetrabothrius wilsoni* from Sei Whale. 7, cross section through mature segment; 8, transverse section of segment showing cirrus-sac and vagina; 9, cross-section through portion of longitudinal muscle; 10, egg.

Tetrabothrius ruudi Nybelin, 1928. (Figs. 11–15.)

HOST: Fin Whale (*Balaenoptera physalus*).

LOCALITY: South Georgia.

The length of the specimens examined is about 9 cm. and the width about 2 mm. The scolex, provided with four suckers and 'epaulettes' is about 2 mm. broad.

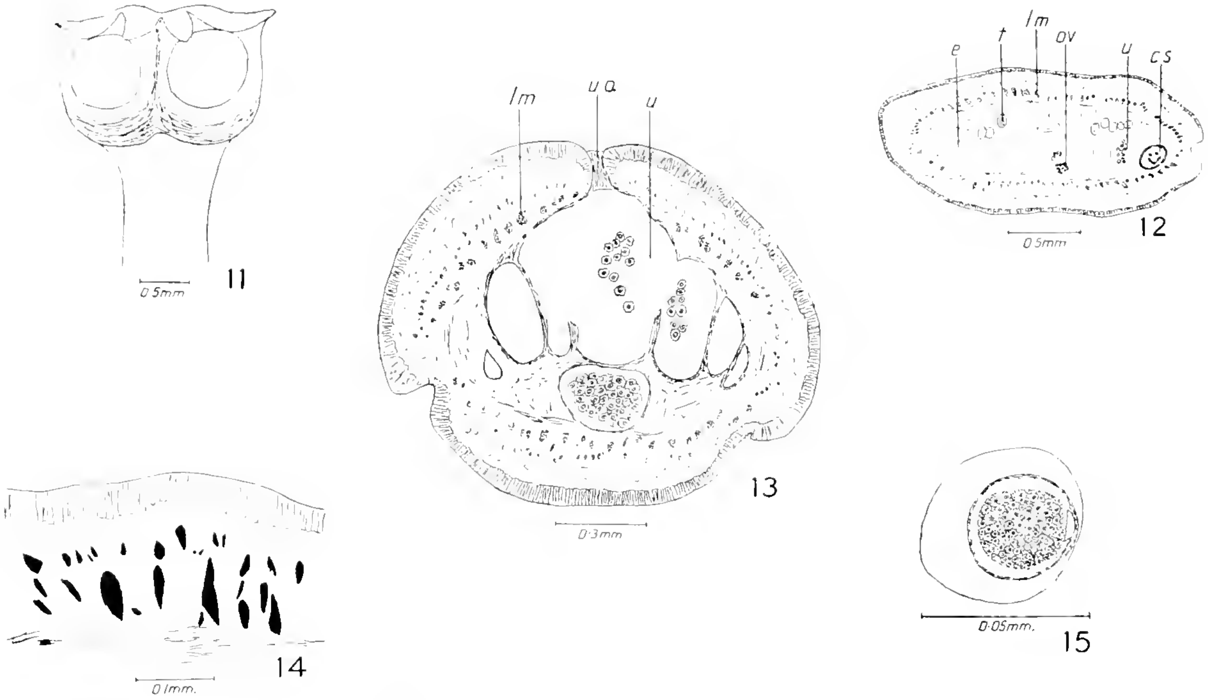
The longitudinal muscles form two more or less distinct rings. The inner one is formed by well accentuated bundles, composed of well developed fibres. The circular muscles are not well developed.

The testes, situated dorsally, are about $42 \times 45\mu$ in transverse section. They are not very numerous. The vas deferens is well developed. The cirrus-sac is pear-shaped, as depicted by Nybelin (1928).

The ovary, extending horizontally in the ventral part of the segment is well developed. The vitelline gland lies ventrally to the ovary.

The very well developed uterus possesses the same kind of opening as in previous forms and similar modified parenchymatous tissue. The formation of the uterine duct commences in the mature segments where the uterus has not yet reached full development. In the early stages the modified tissue surrounding the duct is markedly visible. The eggs are $40–50\mu$ in diameter, the embryonic membrane $30 \times 30\mu$ and the embryo $17 \times 18\mu$. In eggs cleared in glycerine, embryonic hooks have not been observed.

The excretory system shows the ventral vessel to be relatively greater in diameter than the dorsal one, the latter possessing thick muscular walls.



Figs. 11–15. *Tetrabothrius ruudi* from Fin Whale. 11, scolex in lateral view; 12, cross-section of mature segment; 13, cross-section through gravid segment showing uterus and uterine opening situated dorsally; 14, cross-section through portion of longitudinal muscle; 15, egg.

Tetrabothrius schaeferi sp.n. (Figs. 16–20).

Tetrabothrius affine. Baylis, 1926.
Tetrabothrius sp. Rees, 1953.

HOST: Blue Whale (*Balaenoptera musculus*).
LOCALITIES: South Georgia, Southern Ocean.

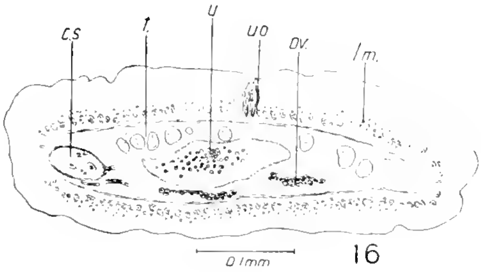
The body is rather slender and flattened, varying from about 7 to 14 cm. in length and about 2 to 3 mm. in breadth. The segmentation is distinct. The scolex, provided with four suckers and 'epaulettes' is 3 mm. broad. A neck is present and well defined.

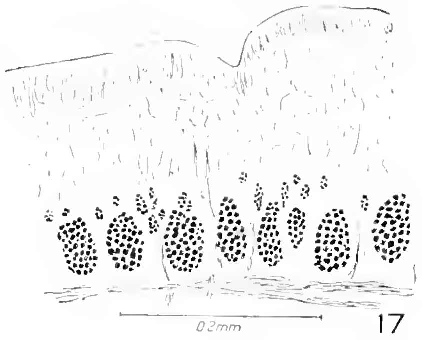
The longitudinal muscles are seen to form two rings, if the segment is examined in cross-section. The inner ring is composed of distinctly separated bundles, irregularly oval in outline and well developed. Immediately, above the inner ring lies the external ring of longitudinal muscles which are weakly developed, as are the circular and dorso-ventral muscles.

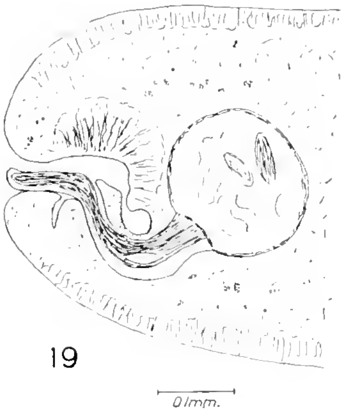
The testes, about fifty in number, are about $90 \times 90\mu$ when measured in transverse section. They occupy the dorsal part of the segment, being arranged in a single or many layers in fields extending laterally and antero-posteriorly. The cirrus-sac, spherical or pear-shaped is about 30μ long and 150μ wide. The vas deferens is a much coiled, fairly well-developed organ. The well-developed ovary lies in the ventral parenchyma. It is lobate and in transverse section more or less oval in outline. The egg-cells are fairly large, about 21μ in diameter. The vitelline gland is ventral to the ovary. The uterus is a sac-like organ which as it matures gradually fills the medullary parenchyma. The uterine duct appears fairly early in the strobila as a differentiation of parenchymatous tissue. The uterine opening is spherical when observed in horizontal section. It is well marked, and surrounded with modified cells which appear to absorb more haematoxylin than the counter-stain erythrosin.

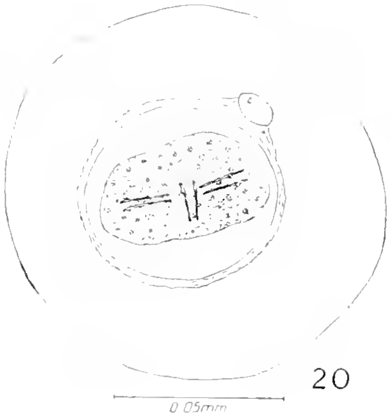
The egg is about $90 \times 75\mu$ in diameter, or more or less spherical. The inner membrane containing an embryo is about 45 × 36μ in diameter, while the embryo is about 24 × 45μ. The lateral pairs of hooks are 12μ in length and the central pair 18μ. The proportions of these hooks is not represented accurately in Fig. 20.

The ventral and dorsal trunks of the excretory system differ in diameter and have rather thin walls. The differences between this new form and *Tetrabothrius affinis* lie in the shape of the body and in the arrangement of the longitudinal muscles. These characters also differ from those found in other species of *Tetrabothrius*. Further differences in structure and in the eggs and the embryos have been given in Table 1.









Figs. 16–20. *Tetrabothrius schaeferi* sp.n. from Blue Whale. 16, Cross-section of semi-gravid segment with eggs; 17, cross-section through longitudinal muscle; 18, cross-section of segment showing cirrus-sac and vagina; 19, cross-section showing cirrus-sac and everted cirrus; 20, egg.

Table 1. *Measurements of Tetrabothriids occurring in the Cetacea from the Discovery Collections*

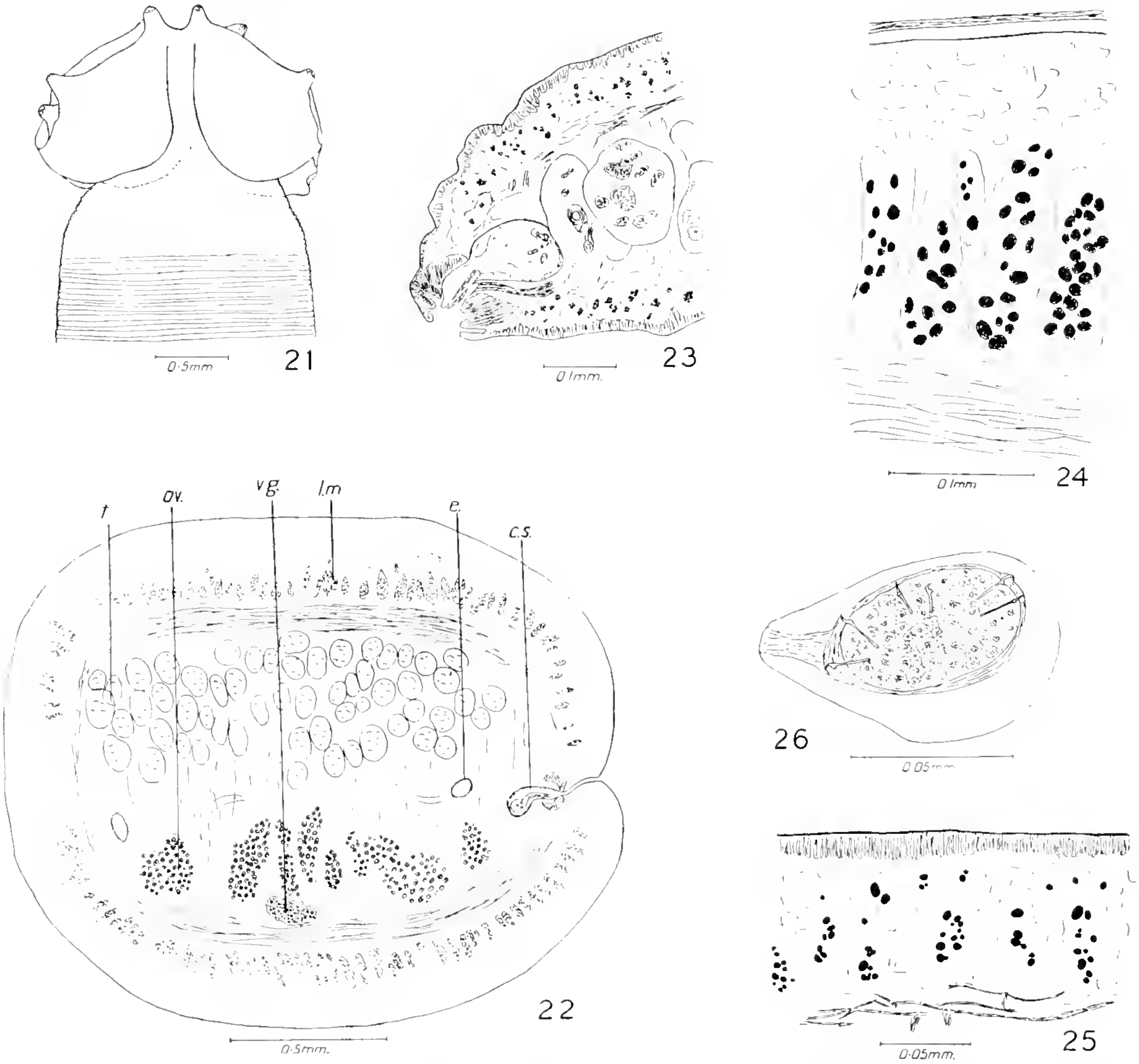
Species	Body length	Body width	Testis diameter	Egg	Embryonic shell	Embryo diameter	Lateral hooks	Central hooks
Tetrabothrius affinis	20 cm.	5 mm.	90 × 53μ	106 × 83μ	51 × 66μ	52 × 26μ	17μ	20μ
T. wilsoni	14 cm.	3 mm.	99 × 120μ	90 × 60μ	45 × 30μ	36 × 21μ	12μ	12μ
T. ruudi	9 cm.	2 mm.	42 × 45μ	40 × 50μ	30 × 30μ	17 × 18μ	—	—
T. schaeferi sp.n.	14 cm.	3 mm.	90 × 90μ	90 × 75μ	45 × 36μ	24 × 45μ	12μ	18μ
Trigonocotyle globicephalae	21 cm.	3·2 mm.	120 × 135μ	75 × 45μ	60 × 40μ	54 × 36μ	18μ	12μ
Tr. prudhoei sp.n.	14·5 cm.	1 mm.	120 × 60μ	60 × 84μ	45 × 30μ	27 × 30μ	9μ	6μ
Priapocephalus grandis	15 m. 24 cm.	12 mm.	68 × 60μ	99 × 66μ	—	33 × 50μ	17μ	17μ

Trigonocotyle Baer, 1932

Trigonocotyle globicephalae Baer, 1954. (Figs. 21–26.)

Prosthecocotyle monticelli Linton 1923; nec Furhmann, 1899.
Trigonocotyle monticelli Linton, 1923; Baer 1932.
Trigonocotyle lintoni Yamaguti, 1942; nec Guiart, 1935.

HOST: *Globicephala edwardi*.
LOCALITY: Off Cape Town (South Africa).



Figs. 21–26. *Trigonocotyle globicephalae* from *Globicephala edwardi*. 21, scolex in lateral view; 22, cross-section through mature segment in anterior cylindrical part of strobila; 23, cross-section through segment in flattened part of strobila, showing cirrus-sac, vagina and longitudinal muscles; 24, cross-section through mature segment in anterior cylindrical part of strobila showing longitudinal muscles; 25, cross-section through gravid, flattened part of strobila showing longitudinal muscles; 26, egg.

The length of the body in the specimens examined is about 21 cm. The strobila appears to be divided into two portions; the anterior part is cylindrical and about 2 cm. in length, composed of very short segments, while the rest of the body is flattened. It seems that the anterior portion, which bears a resemblance to the cylindrical strobila in *Tetrabothrius affinis*, contains mature segments and the flattened part gravid segments with eggs. The scolex, 1·5 mm. broad is provided with four suckers, bearing fleshy protuberances in the form of horns.

The longitudinal muscles are well developed and composed of thick fibres. In transverse section they are collected in elongate bundles, separated from each other by muscular septa. The longitudinal muscles in the cylindrical portion of the strobila are far better developed than those in the gravid segments.

The bundles in the anterior portion are thicker than in the gravid segments as shown in Figs. 24 and 25. This is probably owing to the pressure of the uterus as it becomes distended with eggs. The circular muscles are exceedingly well developed, noticeably in the anterior portion of the body.

The testes are about 120 × 135μ in transverse diameter and arranged in many layers in the cylindrical part of the body. In the flattened portion they seem to be arranged in a single layer. The vas deferens is well developed. The pear-shaped cirrus-sac is about 186 × 90μ in diameter.

The genital atrium possesses a muscular modification in the form of a sucker.

The ovary extends ventrally in the medullary parenchyma and is well developed. The vitelline gland situated ventrally under the ovary is composed of compactly arranged cells. Neither the uterine opening nor the rudiment of its duct has been found. The uterus is very well developed and gradually pushes away other parts of the genital complex. The eggs are 75 × 45μ in diameter and the embryo 54 × 36μ. The lateral hooks measure 18μ and the central 12μ. Yamaguti (1942) could not find any hooks in his material.

The excretory system is well developed and has transverse vessels connecting the two main trunks.

Trigonocotyle prudhoei sp.n. (Figs. 27–32).

HOSTS: *Steno bredanensis*, *Lagenorhynchus obscurus*, *L. australis*.

LOCALITY: 14° 45′ N, 18° 34′ W; East Falkland Islands (southernmost point of Bay of Harbours).

The body is about 14·5 cm. in length and 1 mm. in width and composed of slightly overlapping segments. The scolex, measuring from 1·5–2 mm. in width, is provided with four suckers bearing fleshy protuberances.

The longitudinal muscles are collected into bundles, with some indication of two layers dorsally, when examined in transverse section. They seem to be separated by muscular septa. The circular muscles are well developed. There are also dorso-ventral muscle fibres.

The testes are not very numerous and occur mainly in the dorsal part of the segment. They are about 120 × 60μ in transverse section, the longer axis being in the dorso-ventral plane. The cirrus-sac is flask-shaped, about 32 × 15μ in diameter, with thick muscular walls and a well-developed cirrus. The vas deferens is well developed. Radiate muscles forming a sucker occur in the genital atrium.

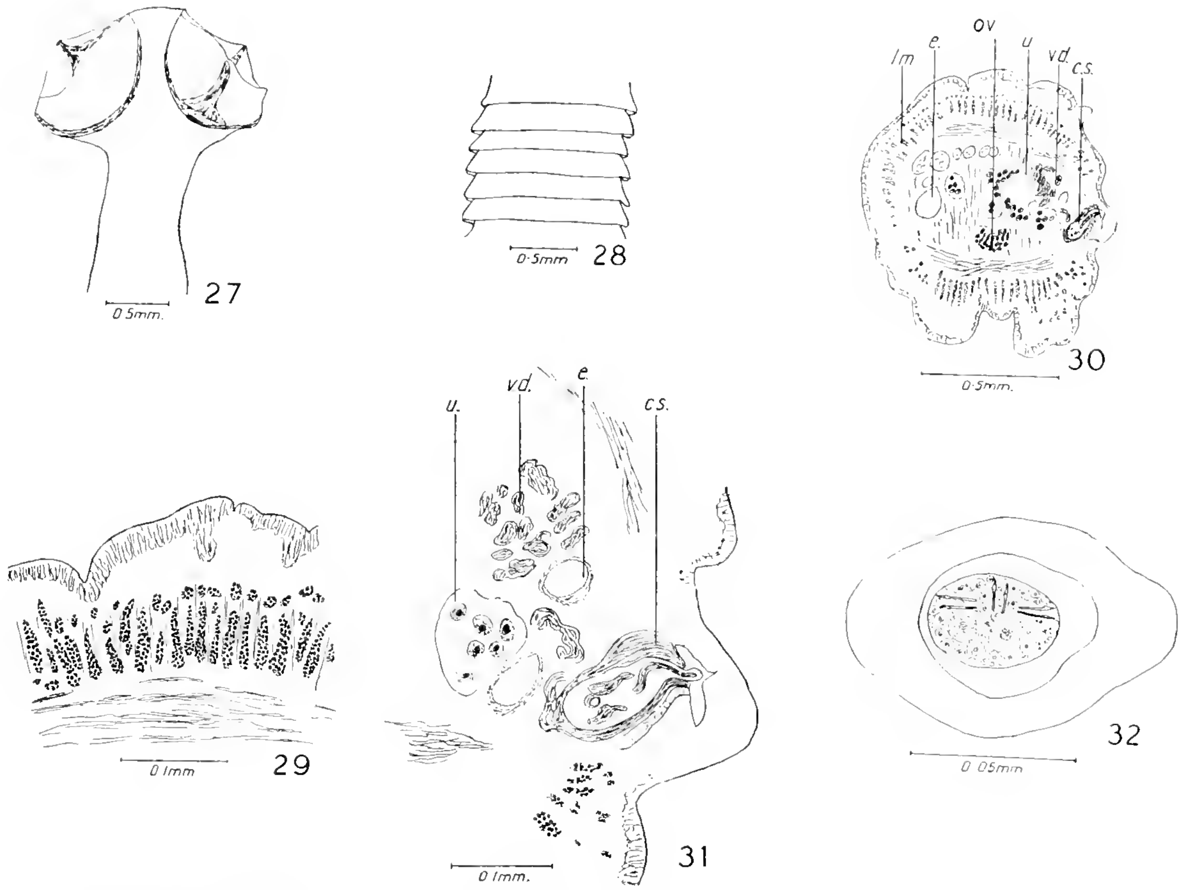
The ovary is situated ventrally and extends laterally on both sides of the median line. The well-developed vitelline gland is situated ventrally beneath the ovary.

Neither a uterine pore nor the rudiment of a uterine duct have been observed.

The eggs are 60 × 84μ. The inner membrane is 45 × 30μ and the embryo 27 × 30μ. The lateral pairs of embryonic hooks measure 9μ and the central 6μ in length.

The excretory system is well developed.

This species differs mainly from other species of *Trigonocotyle* occurring in Cetacea in the form of the serrate strobila and in the arrangement of the longitudinal muscles. It also differs in the number and arrangement of the testes, these being less numerous and distributed dorsally. There are also differences in the size of the eggs and in the length of the embryonic hooks as shown in Table 1.



Figs. 27–32. *Trigonocotyle prudhoei* sp.n. from *Lagenorhynchus obscurus*. 27, the scolex; 28, part of the strobila; 29, cross-section through part of longitudinal muscles; 30, cross-section through mature segment; 31, cross-section showing cirrus-sac and vagina; 32, egg.

Priapocephalus grandis Nybelin, 1922. (Figs. 33–41; Pl. XX, 3–4).

HOSTS: Blue Whale (*Balaenoptera musculus*), Sei Whale (*B. borealis*), Fin Whale (*B. physalus*), Sperm Whale (*Physeter catodon*).

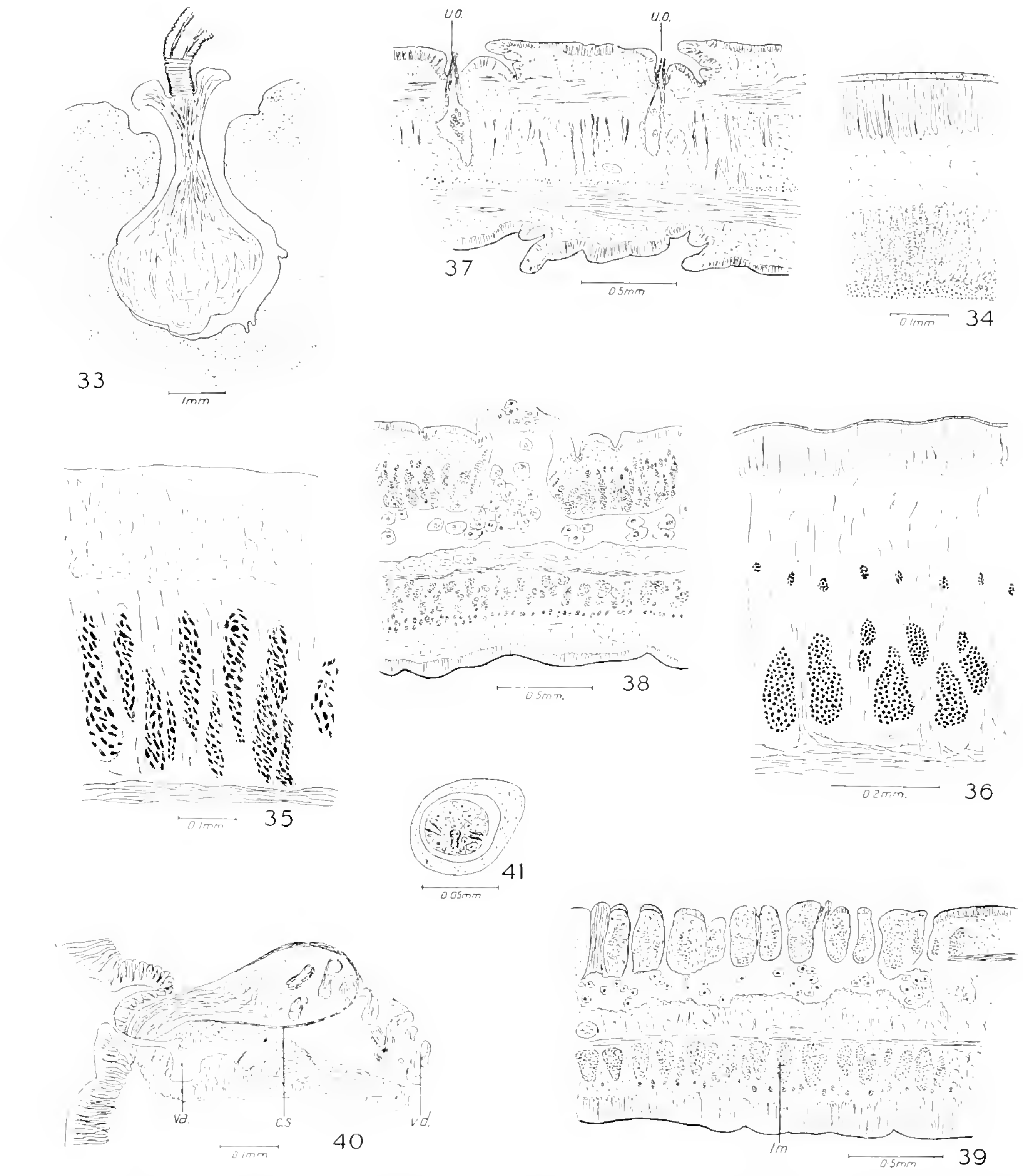
LOCALITIES: Saldanha Bay and Durban (South Africa); South Georgia; Southern Ocean (56° 40′ 32′ S, 24° 33′ W); Porto Pim, Azores.

The size of the specimens examined varies from 4 cm to 15 m. 24 cm. in length with a width varying from 2 to 12 mm. The worms are in various stages of development, from immature to full-grown individuals. There are also fragments of worms, measuring from 12 cm. to 5 m. 75 cm. in length and 2–12 mm. in width; some of these have scolices intact. These are typically acorn-like and are deeply embedded in the mucous which exudes from the gut of the host.

Fig. 33 shows the mode of attachment. It seems that there is a free space between the scolex and the surrounding intestinal tissues of the host. The scolex bears a kind of collar, which possibly serves as a supplementary organ of attachment. The maximum length of the scolex amounts to 7 mm., including the collar; the corresponding width is 4 mm.

The segments are wider than long (the length being about 1·5 mm.), and not craspedote. The body is ivory white or yellowish in preserved specimens.

The longitudinal muscles are very well developed. They are arranged in two rings, the outer one being the less well developed. The inner one is composed of strong bundles, oval in transverse section. The longitudinal muscles are variously developed in the same individual. In the juvenile forms or in



Figs. 33–41. *Priapocephalus grandis* from Blue Whale. 33, longitudinal section through scolex of immature specimen embedded in mucous; 34, cross-section through part of longitudinal muscles; 35, cross-section through part of longitudinal muscles; in segment with rudimentary genital organs; 36, cross-section of longitudinal muscles in mature segment; 37, sagittal section of body showing uterine ducts and openings for discharge of eggs; 38, mode of egg-discharge; 39, cross-section of segment showing uterine pores; 40, cross-section of cirrus-sac and vagina; 41, egg.

the anterior portion of the body the bundles are arranged very densely. They seem to form definitely shaped bundles in the mature and gravid segments. In the young specimens their arrangement is radiate. The differences in the arrangement of the longitudinal muscles in the various segments are shown in Figs. 34–6. The circular muscles are well developed.

The testes are numerous and arranged in many layers. They measure about × 68(53–60)μ in transverse section and about 45 × 53μ in horizontal section. The vas deferens is well developed and arranged in coils. The cirrus-sac is about 135μ long and about 60μ wide.

The fairly large ovary is composed of large egg-cells. The uterus, filled with eggs, occupies most of the medullary parenchyma. The eggs, after the uterus has broken through the cuticle, are discharged by numerous pores situated in the dorsal part of the segment. No specially defined uterine pore is present, as in the species of *Tetrabothrius* described above. There is no difference in the formation of the uterine ducts, but instead of one, several openings are formed. Figs. 37–39 show the mode of discharging the eggs.

The egg is about (83–99 × 66)μ and contains the embryo, 33 × 50μ in diameter. The embryonic hooks are about 17μ in length.

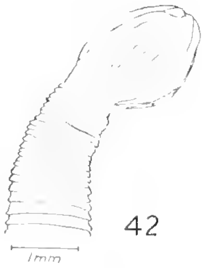
The excretory system is well marked.

GENUS **Diplogonoporus** Loennberg, 1892

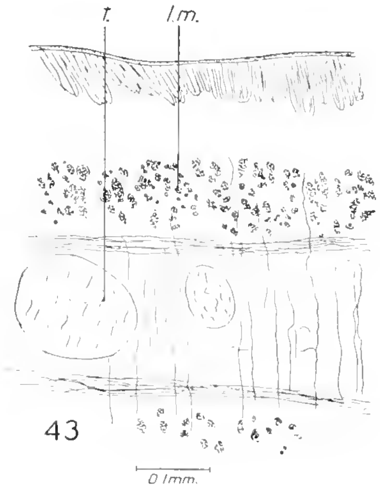
Diplogonoporus balaenopterae Loennberg, 1892. (Figs. 42–43; Pl. XXI, figs. 5–7.)

HOSTS: Blue Whale (*Balaenoptera musculus*); Fin Whale (*B. physalus*); Sei Whale (*B. borealis*).
LOCALITY: South Georgia.

The body is flat and tape-like. In all the specimens with a scolex, irrespective of size, the anterior part of the body is undulate, as shown in Pl. XXI, fig. 6. Though this modification of the body may be caused by fixation, it seems nevertheless to be constant. Although the only complete worms occurring in the collection measure up to about 13 cm. in length, there are many fragments, one of which is over 8 m. long. The scolex is typical, with two grooves from 1 to 1·5 mm. broad and from 1 to 2 mm. long. The bothria are deep and well pronounced. There is no neck.



42



43

Figs. 42, 43. *Diplogonoporus balaenopterae* from Sei Whale. 42, scolex; 43, transverse section showing arrangement of longitudinal muscles.

The longitudinal muscles, as examined in transverse section, form irregular groups of muscle bundles composed of loosely arranged fibres. Individual groups are separated by muscle fibres, running dorso-ventrally. The circular muscles are well developed.

The genital organs occur as separate units in both lateral fields of the segment. In some specimens, however, there are three sets of organs on one side, and two on the other. Two parallel furrows run along the strobila, marking the position of the genital organs. The testes are about $120 \times 150\mu$ in transverse diameter and are arranged in a single layer. Their number between the right and left genital sets seems to be from about thirty-seven to forty. It seems also that the number of testes occurring in each of the genital sets varies greatly when examined in transverse sections, the left-hand side of the segment may possess a few testes or none, while on the right side sixteen or more testes may occur. The cirrus-sac is about $345 \times 300\mu$. The vas deferens is well developed and much coiled. The cirrus is fairly large.

The ovary forms an arch in the ventral half of the segment. The uterus, forming a 'rosette' is filled with operculate eggs of about $66 \times 48\mu$ in diameter. The egg-shell is 3μ thick.

The vitelline glands are situated dorsally and ventrally, in the cortical parenchyma, leaving a free field around the genital organs. They are more or less spherical in transverse section.

LARVAE

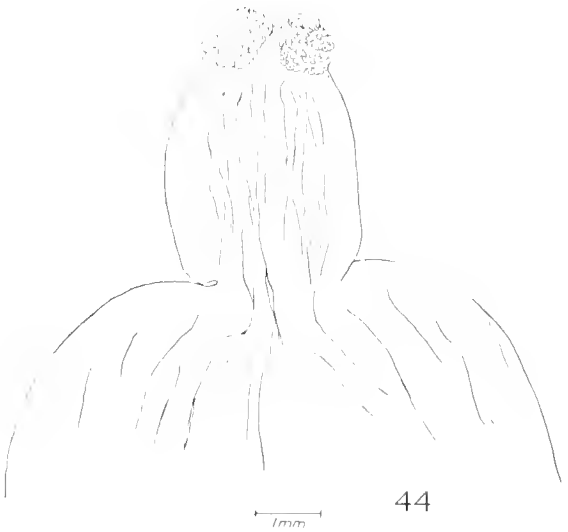
Two types of larval stages have been found in the present material.

All specimens examined seem to belong to the Genus *Phyllobothrium*, except one specimen which probably belongs to the Tetraphyllidea. Specific identification is not possible owing to the complete lack of any morphological characters.

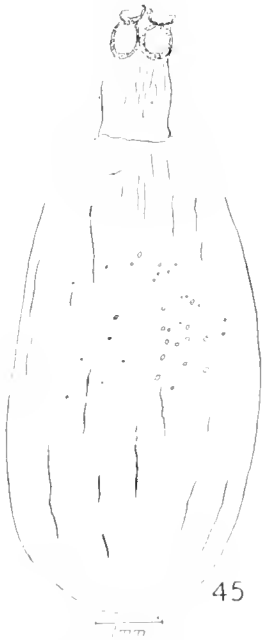
Phyllobothrium (*sensu lato*) sp. larva. (Fig. 44; Pl. XXI, fig. 8.)

HOSTS: Sperm Whale (*Physeter catodon*) and (*Lagenorhynchus obscurus*).
LOCALITIES: Durban, Simon's Town, South Africa and South Georgia.

This larval stage is found in cysts in the blubber and may be regarded as a cysticercus. The body is composed of a bladder with an invaginated scolex and neck. The size of the cyst is variable, measuring from 3–20 × 2–9 mm. The scolex is about 2 mm. broad and is similar to that of *Phyllobothrium*. The evaginated neck is 6 mm. long and 3 mm. wide in the larger specimens.



44



45

Fig. 44. *Phyllobothrium* sp. from Sperm Whale. 44. larval stage extracted from blubber.
Fig. 45. Tetraphyllidean larva from blubber of Sperm Whale.

Tetraphyllidean larva. (Fig. 45.)

Host: Sperm Whale (*Physeter catodon*).
Locality: South Georgia.

Only one specimen has been found; it occurred in the same host together with the previously described form.

The total length of the evaginated cyst is about 9 × 3 mm. The scolex is 1 mm. wide, provided with four discoid suckers, which measure about 420 × 525 μ in diameter.

RELATIONSHIPS BETWEEN THE HOST AND THE PARASITE

From the material examined it seems that host-specificity does not exist. The only exception is *Tetrabothrius ruudi*, which at present has been recorded only in the Fin Whale. This, however, does not mean that this species may not occur in other species of whales, and it is probably a matter of the number of the hosts examined. This appears to be true as far as the present material is concerned.

Table 2. *Infection of hosts with particular species of cestodes*

Host	No. of hosts examined	*Tetrabothrius affinis*	*T. wilsoni*	Species of cestodes		*Trigonocotyle globicephalae*	*T. prudhoei* sp.n.	*Priapocephalus grandis*	*Diplogonoporus balaenopterae*	*Phyllobothrium* sp. larva	Tetraphyllidean larva
				T. ruudi	*T. schaeferi* sp.n.						
Balaenoptera musculus	46	11	2	—	15	—	—	31	1	—	—
B. borealis	13	—	10	—	—	—	—	1	3	—	—
B. physalus	8	—	—	4	—	—	—	2	2	—	—
Physeter catodon	14	1	—	—	—	—	—	1	—	12	—
Lagenorhynchus obscurus	2	—	—	—	—	—	1	—	—	1	1
L. australis	1	—	—	—	—	—	1	—	—	—	—
Steno bredanensis	2	—	—	—	—	—	2	—	—	—	—
Globicephala edwardi	2	—	—	—	—	1	—	—	—	—	—

The Blue Whale has been found to harbour five different species of Cestodes, while in the seven other hosts only one to three different species occurred. Blue Whales formed by far the greater number of the hosts examined (Table 2) and this undoubtedly accounts for the greater variety of worms from this species of whale. Hitherto *Diplogonoporus balaenopterae* has been found only in the Sei Whale. In the present material this cestode has been found in two other hosts, the Fin Whale and the Blue Whale. The latter appears also to be a new host for *Tetrabothrius wilsoni*. The Fin Whale is a new host for *Priapocephalus grandis* and *Tetrabothrius affinis*.

Two species of tapeworms may occur together in the same gut, for in Blue Whale, *Priapocephalus grandis* was found either with *Diplogonoporus balaenopterae* or with *Tetrabothrius affinis*, or with *T. schaeferi* sp.n. Triple infestation has not, however, been noted in any of the hosts examined.

REFERENCES

Baer, J. G., 1932. *Contribution à l'étude des Cestodes de Cétacés.* Rev. Rev. Suisse Zool. xxxix, 3, pp. 195–228.

Baer, J. G., 1954. *Revision taxinomique et étude biologique des Cestodes de la famille des Tetrabothriidae, parasites d'oiseaux de haute mer et de Mammifères marins.* Mém. Univ. Neuchatel, 1, pp. 1–121.

Baylis, H. A., 1926. *Some Tetrabothriid Cestodes from Whales of the genus* Balaenoptera. Journ. Linn. Soc. London, xxxvi, pp. 161–72.

Baylis, H. A., 1932. *A list of Worms parasitic in Cetacea.* Discovery Rep. vi, pp. 395–418.

Fuhrmann, O., 1899. *Das Genus* Prosthecocotyle. Zool. Ang. xxii, pp. 180–3.

Fuhrmann, O., 1903. *Die Tetrabothrien der Säugetiere.* Zbl. Bakt. xxxv, pp. 744–52.

Guiart, J., 1935. *Cestodes parasites provenant des Campagnes scientifiques du Prince Albert* 1$^{\text{er}}$ *de Monaco.* Res. Camp. Sci. Albert 1$^{\text{er}}$, fasc. 91, pp. 68–74.

Jägerskiöld, L. A., 1891. *Einiges über die Schmarotzer der nordatlantischen Balaenopteriden.* Biol. Fören. Förhandl., Stockholm, iii, pp. 127–34.

Leiper, R. T. & Atkinson, E.L., 1914. *Helminths of the British Antarctic Expedition*, 1910–1913. Proc. Zool Soc. Lond. pp. 222–6.

Leiper, R. T. & Atkinson, E. L., 1915. *Parasitic worms with a note on free-living nematoda.* Brit. Antarctic ('Terra Nova') Exped. 1910. Nat. Hist. Rep. Zool. ii (3), pp. 19–60.

Linton, E., 1923. *A new Cetacean Cestode* (Prosthecocotyle monticelli *spec. nov.*) *with a note on the genus* Tetrabothrius Rudolphi. J. Parasit. x, pp. 51–5.

Loennberg, E., 1892. *Anatomische Studien über skandinavische Cestoden*, II Kgl. Sven. Vetensk.-Akad. Handl. xxiv, pp. 1–30.

Nybelin, O., 1922. *Anatomisch-systematische Studien über Pseudophyllideen.* Goteb. Kungl. Vetensk. Handl. xxvi, pp. 1–228.

Nybelin, O., 1928. *Zwei neue Cestoden aus Bartenwalen.* Zool. Anz. lxxviii, pp. 309–14.

Rees, G., 1953. *A record of some parasitic worms from whales in the Ross Sea Area.* Parasit. xliii, 1, pp. 27–34.

Yamaguti, S., 1942. *Studies on the Helminth Fauna of Japan. Part 42. Cestodes of Mammals.* xi, 18 pp. 4 pls. Privately printed, 20 June. Kyoto, Japan.

PLATE XX

Figs. 1–2. *Tetrabothrius affinis* from Blue Whale. 1, cylindrical body with portion of spent segments; 2, strobila.

Figs. 3–4. *Priapocephalus grandis* from Blue Whale. 3, strobila; 4, anterior part of strobila and scolex.


4


1


2

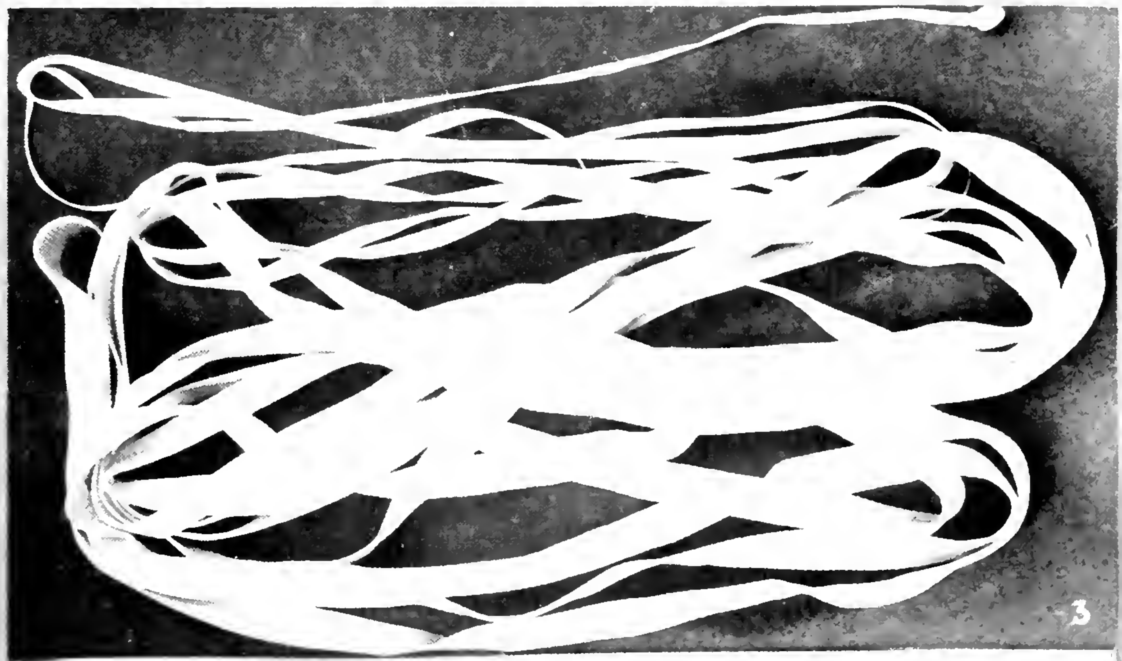
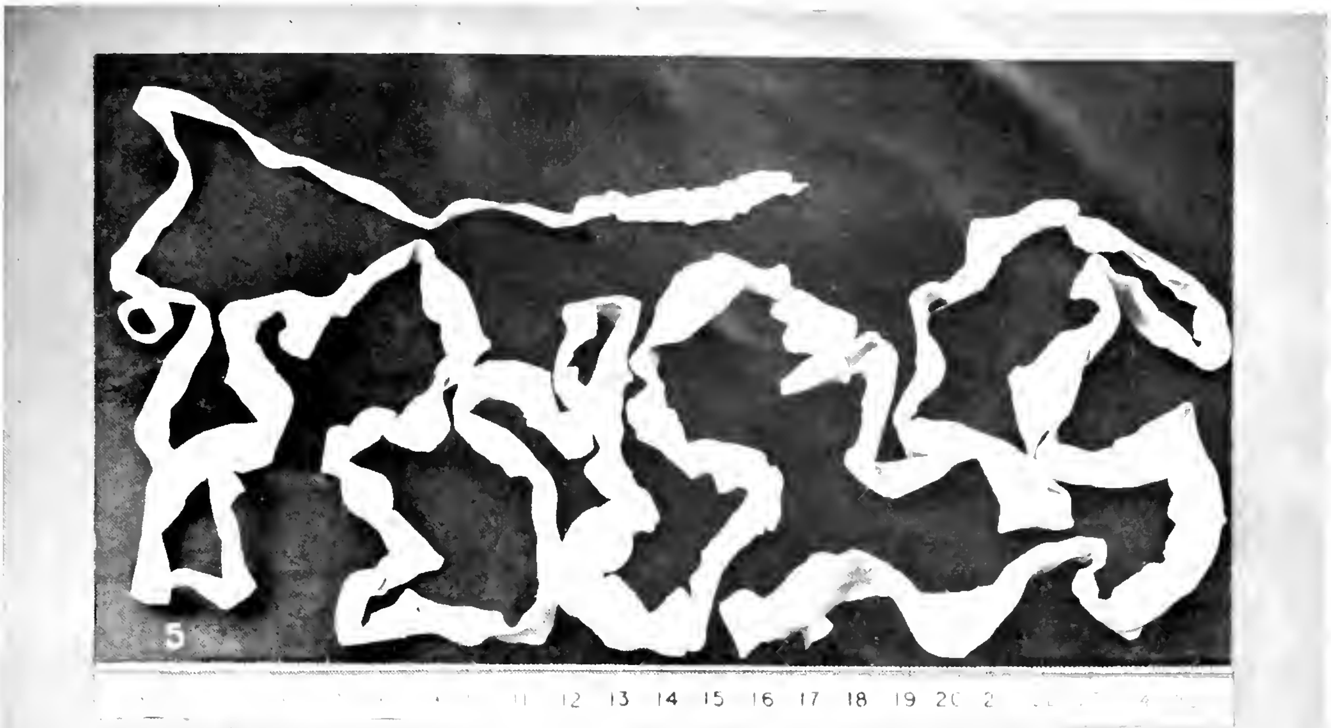

3

PLATE XXI

Figs. 5–7. *Diplogonoporus balaenopterae* from Fin Whale. 5, strobila; 6, anterior part of body; 7, part of the strobila.

Fig. 8. Portion of Sperm Whale blubber infected with *Phyllobothrium* sp.


5


8


6


7

DISCOVERY REPORTS

Vol. XXVII, pp. 1–162, plates I–XII

Issued by the National Institute of Oceanography

SIPHONOPHORA OF THE INDIAN OCEAN

TOGETHER WITH SYSTEMATIC AND BIOLOGICAL NOTES ON RELATED SPECIMENS FROM OTHER OCEANS

by

A. K. Totton

CAMBRIDGE
AT THE UNIVERSITY PRESS
1954

Price sixty shillings net

PUBLISHED BY
THE SYNDICS OF THE CAMBRIDGE UNIVERSITY PRESS
London Office: Bentley House, N.W.1
American Branch: New York
Agents for Canada, India, and Pakistan: Macmillan

Printed in Great Britain at the University Press, Cambridge
(Brooke Crutchley, University Printer)