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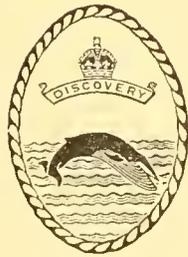
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HYDROMEDUSAE FROM THE DISCOVERY COLLECTIONS

BY

P. L. KRAMP

Zoological Museum, Copenhagen, Denmark



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HYDROMEDUSAE FROM THE DISCOVERY COLLECTIONS

By P. L. Kramp

Zoological Museum, Copenhagen, Denmark

(Plates I-VII, text-figs. 1-19)

INTRODUCTION

THE Discovery collections of Hydromedusae dealt with in the present paper comprise 85 species, namely, 25 Anthomedusae, 19 Leptomedusae, 4 Limnomedusae, 22 Trachymedusae, and 15 Narcomedusae. The following species, the type specimens of which are in the British Museum (Natural History), are described as new:

Euphysora gigantea sp.n.

Ectopleura sacculifera sp.n.

Rathkea africana sp.n.

Merga rubra sp.n.

Leuckartiara annexa sp.n.

Russellia mirabilis g.n., sp.n.

Amphogona apicata sp.n.

Many species are represented by numerous specimens, but these do not represent the total numbers caught in the nets, but only those picked out from the samples and sent to me for examination.

Under each species are given the most important references to the literature, a list of stations where the species was collected, its history (where necessary), some remarks on the morphology (except in the case of very well-known species) and the geographical distribution.

The lists of stations usually comprise all details of date, depth, etc., but in the case of 17 of the most common species these are given in tabular form in Table 1.

The specimens are preserved in formalin, and in comparison with the collections from most other great expeditions the state of preservation is generally very satisfactory, so that it has been possible to make valuable additions to our knowledge of the morphology of several species. Most species of Narcomedusae are, however, extremely fragile, and unfortunately within this group many specimens were indeterminable. However, the collection of Narcomedusae is extensive, and from the material in more or less fair condition and representing several species I have been able to make important progress towards a revision of the species belonging to the genera *Pegantha*, *Solmissus* and *Cunina*, by means of characters to which little attention was paid before. A reliable revision of these medusae, however, requires the study of living specimens.

Vanhöffen's incomplete descriptions are frequently a severe obstacle to our attempts to identify the species established by him. I have been fortunate enough to unravel his species of the genus *Arctapodema* (of the Trachymedusae), three of which are represented in the Discovery collection. Moreover, the extensive material of Halicreidae has convinced me of the correctness of my previous conception of the delimitation of the species of this family, four of which were established by Vanhöffen. Some critical remarks on the tendency by M. E. Thiel to unite several different species are also given.

A comparison of Haeckel's original specimens of *Bougainvillia platygaster* (which are in the Zoological Museum of Copenhagen) with several specimens in the Discovery collections has enabled me to state the position of this species which has been open to question, and its interesting method of asexual propagation is described here for the first time.

A new, most peculiar species is described as *Russellia mirabilis*; it does not merely represent a new genus, but a new family of Anthomedusae.

Four different species of commensal larvae of Narcomedusae of more or less doubtful affinity are also described.

Many species were found in localities far away from their previously known areas of distribution. The Discovery collection, therefore, is of great importance from the point of view of distribution. The systematic account of the species is followed by a zoogeographical discussion.

ABBREVIATIONS

WS: collected by R.R.S. 'William Scoresby'.

MS: collected from the Marine Station on South Georgia.

St. without addition: collected by R.R.S. 'Discovery' and R.R.S. 'Discovery II'.

B oblique haul.

H horizontal haul.

V vertical haul.

SYMBOLS used for nets, etc.

(-o) indicates that the net failed to close at the required depth and was fished to the surface.

Unless specially noted to the contrary, nets N 200 and N 450 were towed horizontally.

BNR Russell's bottom tow-net; a 100 cm. net on a frame attached to skids which raise it clear of the bottom.

BTS Small beam trawl; mesh at cod-end $\frac{1}{2}$ in. (12.5 mm.).

DLH Large dredge; light pattern, 4 ft. in length (1.2 m.).

DRR Rectangular dredge bag bent on to a Russell frame with skids.

$\left. \begin{array}{l} N_{4-T} \\ N_{7-T} \end{array} \right\}$ Nets with mesh of 4 mm. or 7 mm. attached to back of trawl.

N 50 50 cm. tow-net; mouth circular, 50 cm. in diameter; 200 meshes to the linear inch.

N 70 70 cm. tow-net; mouth circular, 70 cm. in diameter; mesh graded, at cod-end 74 to the linear inch.

N 100 1 m. tow-net; mouth circular, 1 m. in diameter; mesh graded, at cod-end 16 to the linear inch. From 1 July 1927 the cod-end made of stramin with 11-12 meshes to the linear inch.

N 200 2 m. tow-net; mouth circular, 2 m. in diameter; mesh graded, at cod-end 4 mm.

N 450 $4\frac{1}{2}$ m. tow-net; mouth circular, $4\frac{1}{2}$ m. in diameter; mesh graded, at cod-end 7 mm.

NCS-D Tow-net of coarse silk, with 16 meshes to the linear inch, attached to dredge.

NCS-T Same attached to back of trawl.

NH Hand net.

NRL Large rectangular net; frame 2.45×0.7 m., with bag of $\frac{1}{2}$ in. mesh (12.5 mm.).

NS Seine net; length 55 m.; mesh at cod-end $1\frac{1}{2}$ in. (3.8 cm.).

OTC Commercial otter trawl; head rope 24.5 m.; mesh at cod-end $1\frac{1}{2}$ in. (3.8 cm.).

RM Mussel rake.

TYF Young-fish trawl; mouth about 20 ft. in circumference (6 m.); bag of stramin with 11-12 meshes to linear inch. Fished until July 1926 with poles and otter-boards, thereafter attached to a circular tow-net frame 2 m. in diameter.

SYSTEMATIC ACCOUNT

ANTHOMEDUSAE

Family CORYNIDAE

Sarsia gracilis Browne 1902

1902 *Sarsia gracilis* Browne, p. 275.

1939 *Sarsia gracilis* Browne & Kramp, p. 271, pl. 14, figs. 1-2, pl. 15, fig. 1.

OCCURRENCE: St. 91. 8. ix. 26. $\frac{1}{2}$ mile off Roman Rock, False Bay, South Africa. Net: NCS-NRL, 35 m. 1 specimen.

The specimen is 6 mm. high, 4.5 mm. in diameter. The manubrium has been artificially stretched to a considerable length, causing the gonad to be divided into two parts separated by an extremely thin thread consisting of the mesosarc layer alone. Apart from this thread-like portion, the manubrium is completely covered by the gonad from its base almost to its extreme end. The four marginal tentacles are characteristic of *Sarsia gracilis* and terminate in a large, oval knob. They are covered throughout the greater part of their length with groups of nematocysts, which towards the distal end of the tentacles are confluent, forming transverse bands or almost complete rings. Therefore I do not hesitate to refer the specimen to *S. gracilis*, in spite of the prolongation of the manubrium which undoubtedly is due to mutilation.

DISTRIBUTION. South Africa, Falkland Islands.

Family TUBULARIIDAE

? *Corymorpha* sp.

(Pl. I, fig. 1)

OCCURRENCE: St. 256. 23. vi. 27. 35° 14' S, 06° 49' E, off South-West Africa. Net: TYF 850-1100(-0) m. 1 specimen.

The specimen is 1.5 mm. high and wide, globular, the gelatinous substance very thick. The four radial canals and the ring-canal are fairly broad; a long apical canal reaches almost to the top of the umbrella. There are no marginal tentacles, not even rudimentary bulbs. The manubrium is carrot-shaped, completely surrounded by the gonad except at the narrow distal end, which reaches a little beyond the level of the velar opening. The musculature of the subumbrella is particularly powerful.

The complete absence of tentacles might indicate that this was a *Pennaria*, but the presence of a well-developed apical canal points rather to the tubulariid medusae formerly named *Amalthaea*, which are abortive medusoids derived from hydroids of the genus *Corymorpha*.

Euphysora furcata Kramp 1948

(Pl. I, fig. 2)

1948a *Euphysora furcata* Kramp, p. 19, figs. 7-8 (Plate).

OCCURRENCE: St. 250. 17. vi. 27. 36° 09' S, 05° 33' W. East of Tristan da Cunha. Net: TYF 300(-0) m. 1 specimen.
St. 1586. 2. v. 35. 02° 39' 24" N, 50° 46' 24" E. Off Somaliland, East Africa. Net: TYFB 550-0 m. 1 specimen.
St. 1604. 29. x. 35. 21° 34' 24" S, 08° 09' 48" E. Off Walvis Bay, South-West Africa. Net: TYFB 182-0 m. 1 specimen.

In the specimens from the two first mentioned localities, the main tentacle is well extended showing the twice dichotomously branched terminal end with its four nematocyst knobs. In one point they differ from the type specimen: there is no indication of perradial divisions of the gonad, which completely encircles the stomach. In both specimens, which are 4-4.5 mm. high, the tentacle opposite the main tentacle is half as long again, thin and unbranched, and the two lateral tentacles are short and conical. In the third specimen, which is 8 mm. high and 6.5 mm. wide (St. 1604), the tentacles are much contracted (Pl. I, fig. 2). This specimen, therefore, resembles *Euphysora valdiviae* Vanhöffen (1911, p. 198). In my original description (1948a) I compared these two species, and I still maintain my previous statement that 'if Vanhöffen's description is not altogether wrong, the two medusae cannot belong to the same species'. From a superficial examination, the present specimen might be mistaken for *E. valdiviae* (as a matter of fact, my footnote (1948a, p. 20) alludes to this specimen), but in contradistinction to *E. valdiviae* the tentacle opposite the main tentacle has a thread-like prolongation, the branches of the main tentacle have nematocyst knobs, and there is no trace of

the hook-like process at the base of the tentacle, emphasized by Vanhöffen as a characteristic structure of his species. The peculiar four perradial and eight adradial nematocyst tracks on the exumbrella, forming anastomoses towards the apex (described by Vanhöffen), are not seen in any of the specimens observed by me. On the other hand, twelve meridional furrows run almost from the base to the summit of the exumbrella; they do not branch, and there are eight adradial and four interradian furrows, but no perradial. There is still the possibility that Vanhöffen's description is misleading and if so *E. valdiviae* must be regarded as an obsolete species.

DISTRIBUTION. The original specimen was taken south of the Newfoundland Bank; I have seen several specimens from other parts of the Atlantic Ocean, and one of the Discovery specimens was taken in the Indian Ocean, off the coast of East Africa.

Euphysora gigantea sp.n.

(Pl. I, figs. 3, 4)

OCCURRENCE: St. 78. 12. vi. 26. 35° 18' 00" S, 19° 01' 10" W. South Atlantic. Net: TYF 1000(-0) m. 1 specimen.
 St. 1972. 28. ii. 37. 52° 11' S, 52° 33' 42" W. East of Falkland Islands. Net: TYFB 2100-1400 m. 1 specimen.
 St. 1995. 13. iii. 37. 61° 21' 06" S, 25° 49' 12" W. South of South Sandwich Islands. Net: TYFB 1800-1300 m. 3 specimens.
 St. 2001. 16. iii. 37. 67° 04' 24" S, 19° 41' W. Weddell Sea. Net: TYFB 1750-1300 m. 2 specimens.
 St. 2006. 19. iii. 37. 66° 16' 42" S, 13° 23' 18" W. Weddell Sea. Net: TYFB 1750-1400 m. 4 specimens.
 St. 2008. 20. iii. 37. 66° 06' 30" S, 06° 45' 36" W. Weddell Sea. Net: TYFB 1500-1300 m. 2 specimens.

Size of the specimens

Station	78	1972	1995			2001		2006			2008	
Height (mm.)	17	20	17	22	23	26	26	11	19	23	8	12
Diam. (mm.)	17	18	17	22	23	28	28	8	19	23	8	12

The specimen, 23 mm. high and wide, from St. 1995 is chosen as the *holotype*.

DESCRIPTION. Umbrella about as high as wide, globular, the gelatinous substance very thick, umbrella-cavity narrow, about half as high as the umbrella. Manubrium cylindrical or slightly barrel-shaped, its length one-half to two-thirds that of the umbrella cavity, surrounded from its base almost to the distal end by a ring-shaped gonad, leaving only a short cylindrical mouth tube. Mouth opening simple, circular, with a slightly everted margin. No apical canal. Four radial canals and ring-canal moderately broad, their endodermal cells not vacuolated. Velum narrow. Only one marginal tentacle, no rudimentary bulbs in the three other perradii. The tentacle has a well-developed conical basal bulb; the tentacle is very long and thin, carrying several bifurcated lateral branches separated by long intervals.

In most of the specimens the tentacle is lost, and even in the best preserved specimen (the type) the distal end is lacking, so that the full length of the tentacle remains unknown. In the type specimen, the number of lateral branches in the existing part of the tentacle is seven, increasing in size from the basal towards the distal part. Each branch consists of a basal trunk and two diverging branches of about the same length as the trunk. The tentacle is hollow with a fairly thick mesogloea. The ectodermal epithelium has entirely disappeared, so that the distribution of the nematocysts cannot be determined. The endodermal cells of the bifurcated branches contain protoplasm and nuclei (Pl. I, fig. 4); presumably they have carried nematocysts, but none of these are left.

According to notes on some of the labels, the colour of the manubrium and the radial canals is a bright, brilliant, deep orange.

DISTRIBUTION. This is evidently an antarctic species. Most of the specimens were taken in deep water south of the Antarctic Convergence, but one specimen was found farther north (St. 78) at a depth of less than 1000 m. in the antarctic intermediate water, which flows northwards below the warmer subantarctic water.

Ectopleura sacculifera sp.n.

(Pl II, figs. 1-3)

OCCURRENCE: St. WS 720. I. viii. 31. $02^{\circ} 52' 18''$ S, $82^{\circ} 19' 30''$ W. Off the Pacific coast of Ecuador. Net: N 50 V, 100-0 m. 1 specimen, the *holotype*.

DESCRIPTION. Umbrella 3 mm. high, slightly conical, diameter in basal part 1.75 mm., jelly thick throughout the length of the umbrella. Exumbrella with eight nematocyst tracks issuing in pairs from the four marginal bulbs, soon divergent and continued at equal distances upward almost to the apex, which is a little depressed. The nematocyst tracks fairly broad below, tapering upward, running along the edges of eight prominent adradial ridges, separated by well-marked perradial and inter-radial grooves. Manubrium half as long as the height of the umbrella-cavity, with a quadrangular base broadly attached to the subumbrella. No gastric peduncle. Mouth tube narrow, mouth a simple circular opening with a slightly thickened rim. Stomach circular in transverse section, completely surrounded by the gonad, which forms four large interradial sac-shaped pouches hanging down from the middle portion of the manubrium almost to the level of the mouth.

No apical canal; four radial canals and ring-canal narrow. Velum narrow. Two opposite moniliform tentacles with large, conical basal bulbs and two rudimentary marginal bulbs.

The most characteristic features of this species are the four large, pendent gonadial sacs on the stomach wall. Similar structures occur in two other medusae (belonging to the same family, but which are in other respects entirely different from *Ectopleura*), namely, the Japanese species *Gotoea typica* Uchida (1927*b*, p. 195) and an undescribed South African species of the genus *Paragotoea* Kramp.

The single specimen of the present species was taken in the tropical East Pacific not far from the coast of Ecuador.

Family CYTAEIDAE

Cytaeis tetrastyla Eschscholtz 1829

OCCURRENCE: St. 282. 12. viii. 27. $01^{\circ} 11' S$, $05^{\circ} 38' E$. Gulf of Guinea. Net: TYF 300(-0) m. 2 specimens.
St. 677. 28. iv. 31. $31^{\circ} 16' 15'' S$, $29^{\circ} 56' 30'' W$. Off southern part of Brazil. Net: TYFB 420-0 m. 1 specimen.
St. 691. 8. v. 31. $00^{\circ} 25' 45'' S$, $29^{\circ} 56' W$. South of St Paul's Rocks. Net: TYFB 400-0 m. 2 specimens.
St. 694. 10. v. 31. $04^{\circ} 05' 30'' N$, $30^{\circ} 00' W$. North of St Paul's Rocks. Net: TYFB 210-0 m. 4 specimens.
St. 701. 16. x. 31. $14^{\circ} 39' 18'' N$, $25^{\circ} 51' 21'' W$. Near Cape Verde Islands. Net: TYFB 242-0 m. 48 specimens.
St. 705. 20. x. 31. $00^{\circ} 03' 24'' N$, $30^{\circ} 36' 48'' W$. North-east of Cape San Roque, Brazil. Net: TYFB 150-0 m. 1 specimen.

St. 707. 22. x. 31. $06^{\circ} 44' S$, $33^{\circ} 33' W$. Off Cape San Roque, Brazil. Net: TYFB 182-0 m. 1 specimen.

The specimens vary in size from 1.5 to 5 mm. in diameter. Those from Stations 677, 691 and 694 (28. iv-10. v. 1931) carry medusa buds on the stomach wall; the specimens from Station 282 (12. viii. 27) and Stations 705 and 707 (20-22. x. 31) have no buds. Among the forty-eight specimens from Station 701 (16. x. 31), 29 have medusa buds.

DISTRIBUTION. Widely distributed in all tropical seas. The localities, where this species was collected by 'Discovery' and 'Discovery II', are scattered over the tropical belt of the Atlantic between Africa and South America.

Family RATHKEIDAE

Rathkea africana sp.n.

(Pl. I, fig. 5)

OCCURRENCE: St. 282. 12. viii. 27. $01^{\circ} 11' S$, $05^{\circ} 38' E$. Gulf of Guinea, near St Thomas. Net: TYF 300(-0) m. 1 specimen, the *holotype*.

DESCRIPTION. Height of umbrella 1.7 mm., diameter 1.2 mm. Umbrella almost cylindrical, evenly vaulted at the top. Jelly very thin (probably shrunk by preservation), no apical projection and no gastric peduncle. Manubrium about one-third as long as the umbrella cavity, cruciform in transverse section. Gonads adradial, smooth, separated by deep grooves in the interradii. Small medusa buds present on the lateral sides of the gonads. Oral lips bifurcated, each with two large and broad terminal clusters of nematocysts; no lateral clusters. Four radial canals and ring-canal very narrow; velum? (crumpled). The eight marginal bulbs small, containing no pigment granules; three or four tentacles in each of the perradial groups, two or three in the interradial. In each group, one of the tentacles, the median one, large and stout, almost as long as the height of the umbrella; the second tentacle about half as long, the third and fourth very small.

In the preserved condition the medusa is colourless, apart from a distinct dark-brown line on either side of the interradial grooves of the manubrium.

This species differs from the northern *Rathkea octopunctata*, as well as from the subantarctic *R. formosissima*, in the absence of an apical projection and a gastric peduncle; in the interradial division of the gonads; in the narrow shape of the marginal bulbs, which are, moreover, destitute of pigmentation; further, in the very uneven size of the tentacles in each group. As far as the oral arms are concerned, they are entirely different from those in *R. formosissima*, and in comparison with *R. octopunctata* the oral arms of the present new species are considerably broader and they have no lateral clusters of nematocysts.

It would be a surprise to find either of these two species in a tropical locality like the Gulf of Guinea. One tropical species of the genus, *R. rubence*, has recently been described from the south-west coast of India by Nair (1951, p. 54, Pl. I, figs. 2-3). It is very similar to *R. octopunctata* except in the shape of the perradial corners of the mouth opening, which are 'developed into swollen lobes' and not drawn out into bifurcated mouth-arms. Thus the medusa from the Gulf of Guinea, *Rathkea africana* sp.n., differs in several respects from all hitherto described species of this genus.

Family BOUGAINVILLIIDAE

Koellikerina maasi (Browne 1910)

1910 *Koellikeria maasi* Browne, p. 22. Pl. 4, figs. 1-5.

1912a *Koellikeria maasi* Vanhöffen, p. 361. Pl. 25, fig. 2.

1939 *Koellikerina maasi* Kramp, p. 512.

OCCURRENCE: St. 1867. 10. xi. 36. $61^{\circ} 37' 36'' S$, $43^{\circ} 56' 06'' W$. Weddell Sea. Net: TYFH 500-450 m. 15 specimens.

Owing to the contraction of the umbrella-margin in the specimens examined by him, Browne was afraid that his figure of the entire medusa (1910, Pl. 4, fig. 2) might not be quite correct; as a matter of fact it is a perfect image of the present better-preserved specimens. I have nothing to add to Browne's thorough description.

DISTRIBUTION. McMurdo Sound (Browne); Gauss Station (Vanhöffen). The occurrence of several specimens in the Weddell Sea confirms the view that this is a truly antarctic species.

Bougainvillia macloviana Lesson 1843

- OCCURRENCE: St. 58. 19. v. 26. Port Stanley, East Falkland Islands. Net: N 70 II, 5-0 m. 200 specimens.
 St. 719. 13. xi. 31. 54° 00' S, 60° 00' W. Net: N 100 B, 109-0 m. 11 specimens.
 St. Sparrow Cove, Falkland Islands. 19. x. 34. 4-6 m. 5 specimens.
 St. 1896. 27. xi. 36. 49° 55' 06" S, 62° 05' W. Net: N 70 B, 128-0 m. 1 specimen.
 St. 1897. 27. xi. 36. 49° 55' S, 63° 09' 24" W. Net: N 100 B, 151-0 m. 5 specimens.
 St. WS. 798. 20. xii. 31. 47° 31' 30" S, 65° 02' W. Net: NCS-T, 49-66 m. 1 specimen.

All these localities are round or near the Falkland Islands.

The specimens taken in October, November and December are 7-16 mm. in diameter. Among the numerous specimens taken in May 1926 (St. 58) a few measure 9 mm. in diameter, but most of them are small, down to 1 mm.

DISTRIBUTION. Widely distributed and very common in subantarctic and antarctic seas, probably circumpolar. Moreover, the medusa has been found in the south-eastern part of the North Sea; this occurrence is undoubtedly due to the transportation of the hydroid by ships.

Bougainvillia platygaster (Haeckel 1879)

(Plate III, figs. 1-6, text-fig. 1)

- 1879 *Hippocrene platygaster* Haeckel, p. 91.
 1910 *Bougainvillia platygaster* Mayer, p. 165.
 1912a *Bougainvillia niobe* Vanhöffen, p. 359.
 1938a *Bougainvillia platygaster* Thiel, p. 299.
 1948b *Bougainvillia niobe* Kramp, p. 4.
 1951a ?*Bougainvillia carolinensis* Vannucci, p. 78; 1951b, pp. 111, 114, 116.

- OCCURRENCE: St. 680. 30. iv. 31. 22° 36' S, 30° 01' 30" W. Net: TYFB 260-0 m. 14 specimens.
 St. 683. 2. v. 31. 16° 48' S, 29° 55' W. Net: TYFB 290-0 m. 1 specimen.
 St. 688. 5. v. 31. 09° 26' 30" S, 29° 50' 30" W. Net: TYFB 450-0 m. 1 specimen.
 St. 708. 23. x. 31. 10° 20' 36" S, 34° 54' 42" W. Net: TYFB 208-0 m. 1 specimen.
 St. 709. 24. x. 31. 14° 01' 24" S, 36° 30' 42" W. Net: TYFB 216-0 m. 5 specimens.
 St. 1374. 24. v. 34. 31° 46' 36" S, 29° 46' 18" E. Net: TYFB 230-0 m. 3 specimens.
 St. 1375. 25. v. 34. 34° 30' 48" S, 26° 19' E. Net: TYFB 210-0 m. 3 specimens.
 St. 1574. 23. iv. 35. 21° 44' 36" S, 40° 33' 42" E. Net: TYFB 600-0 m. 1 specimen.
 St. 1578. 26. iv. 35. 11° 25' 12" S, 42° 03' 06" E. Net: TYFB 500-0 m. 1 specimen.
 St. 1580. 27. iv. 35. 08° 44' 36" S, 41° 50' 18" E. Net: TYFB 450-0 m. 1 specimen.
 St. 1581. 28. iv. 35. 07° 42' 06" S, 44° 14' 06" E. Net: TYFB 600-0 m. 2 specimens.

The distribution of *Bougainvillia platygaster* is shown in Text-fig. 1. Stations 680-709 are off the east coast of Brazil; stations 1374-1581 are off the southern part of the east coast of Africa between Port Elisabeth and Zanzibar. Three of the specimens (Stns 680 and 683) are infested by parasitic narcomedusa-larvae (see p. 90).

The species *Bougainvillia platygaster* has been observed only on few occasions, and its identity has been doubted. Haeckel found it during his stay in 1866 in the Canary Islands. While preparing his monograph *Das System der Medusen* (1879) he borrowed the whole collection of medusae from the Zoological Museum of Copenhagen, together with a detailed list of localities and other information, and this list is still in our possession with Haeckel's hand-written identifications of the species. Many of the specimens are likewise still available in our collections, and among them three specimens of *B. platygaster* from the following two localities, both mentioned in Haeckel's book:

(1) Two specimens collected by Andrea in 1869 at 25° S, 27° W, south of the Brazilian island of Trinidad. In one specimen the manubrium is lost, but the tentacles are retained. The other



Text-fig. 1. Distribution of *Bougainvillia platygaster*. New records = ●, previous records: H=Haeckel, 1879; V=Vanhöffen, 1912a; T=Thiel, 1938; K=Kramp, 1948b.

specimen is well preserved (in alcohol); it is 12 mm. high and wide, with about 12 tentacles in each of the perradial bundles. The stomach has the very flattened shape mentioned in the description, and it carries a great number of medusa buds, although this fact seems to have escaped Haeckel's attention. As Haeckel's original specimen from the Canary Islands has presumably disappeared, I designate this specimen as the *neotype*.

(2) The other locality mentioned by Haeckel as 'in der Nähe der Kap Verden' is about 700 miles north-west of these islands (24° N, 33° W). From this locality we have one specimen collected by Iversen in 1871. It is about 12 mm. high and wide and badly preserved, but it evidently belongs to the same species.

Thiel (1938a) has referred a specimen, taken in the middle of the Atlantic Ocean between the Cape Verde Islands and the West-Indies ($17^{\circ} 53'$ N, $39^{\circ} 19'$ W) to *B. platygaster*. This is the only record of the species since it was described by Haeckel. Medusa buds were not observed by Thiel.

It has generally been supposed that *B. niobe* Mayer was the only species of *Bougainvillia* which propagated by budding. Vanhöffen (1912a) therefore referred a specimen taken in the South Atlantic (about 24° S, 21° W) to *B. niobe*, but evidently from his description it belongs more properly to *B. platygaster*. My previous identification of a specimen with medusa buds (taken by the Swedish Antarctic Expedition off the Brazilian coast in $17^{\circ} 32'$ S, $34^{\circ} 55'$ W) as *B. niobe* must now be corrected to *B. platygaster*, and some young stages recorded from the same region by Vannucci (1951a) as *B. carolinensis* are also possibly the same species.

Before I proceed to a description of the peculiar asexual propagation of the 'Discovery' specimens, some remarks on the general morphology of *B. platygaster* as compared with other species of the genus are necessary.

In *B. platygaster* the umbrella is about as high as wide, with a very thick jelly, somewhat flattened above and with approximately vertical sides. It is not cubical as stated by Haeckel; in cross-section it is almost circular with only a slight indication of flattening of the interradial sides. The specimens taken off the Brazilian coast are 4–11 mm. high and wide, the East-African specimens 5–7 mm. Without exception, in all the specimens the stomach has the very flat shape which is characteristic of this species. In one or two specimens the mouth tube protrudes slightly as a short and narrow prismatic tube, while the stomach itself is quite flat; in all the others the mouth is widely open at the lower level of the stomach.

Almost all the specimens are immature, with the stomach quadrangular in shape with straight or slightly concave sides. Two specimens, a male and a female, have well-developed sexual products, and their gonads are decidedly interradial. In the male (Pl. III, fig. 1) the stomach is slightly, in the female somewhat more concave interradially, but there is no interradial interruption of the gonads. Although the upper surface of the stomach is broad and flat, it is attached to the subumbrella along the arms of a perradial cross. There is no indication of a gastric peduncle.

The oral tentacles branch dichotomously immediately from their points of origin; there is no unbranched basal portion or 'trunk'. In the larger specimens they branch 5–6 times. There are 7–9 marginal tentacles in each of the perradial bundles in specimens less than 7 mm. wide; 9–13 in the larger specimens. The ocelli are crescent-shaped with the concavity turned outwards.

I cannot see any morphological difference between the specimens from the two geographical areas represented in the present collection.

The species of *Bougainvillia* which might possibly be confounded with *B. platygaster* are *B. carolinensis*, *fulva*, and *niobe*.

B. carolinensis (McCrary 1857) occurs along the Atlantic coast of North America, from Woods Hole to Florida, and recently it has been recorded, though with a query, from the Brazilian coast, in

25° S, 47° 51' W, by Vannucci (1951 *a* p. 78, 1951 *b* pp. 111, 114, 116). Only very young stages were observed, less than 1 mm. in diameter; accordingly, the identification seems uncertain; they may be young specimens of *B. platygaster*.¹ The most recent description of *B. carolinensis* was given by Mayer (1910, p. 165, Pl. 16, figs. 7-9, Pl. 17, fig. 7). This is a small medusa, 4 mm. in height. The gonads are interradial as in *B. platygaster*, but the manubrium is long and narrow, and the oral tentacles have a long, undivided shaft. An identity between these two species therefore seems excluded. Recently also recorded from the Gulf of Guinea (Kramp 1955, p. 249).

B. fulva Agassiz & Mayer 1899 is an Indo-Pacific species. In size and general appearance it is very similar to *B. platygaster*, but the stomach is usually longer, about half as long as the height of the bell-cavity, though sometimes shorter (Maas 1905, Pl. I, fig. 8). In young specimens the stomach may be quadrangular (Maas 1905, Pl. II, figs. 10*a*, *b*), but in mature specimens the gonads are distinctly adradial, and widely separated in the interradial spaces (Maas 1905, Pl. II, fig. 10*c*; Kramp 1928, text-fig. 21). In this respect the species differs from *B. platygaster*. Though numerous specimens have been examined by several authors, budding has never been observed.

B. niobe Mayer 1894 occurs off the southern Atlantic coast of North America, from Chesapeake Bay to Florida, and round Bermuda and the Bahama Islands. As mentioned above, the records from the waters off the Brazilian coast are probably all referable to *B. platygaster*. *B. niobe* was well described and figured by Mayer (1910, p. 166, Pl. 18, figs. 1-3, text-fig. 90) and was re-examined by Bigelow (1918, p. 368 and 1938, p. 104). In this species also the stomach is about half as long as the height of the bell-cavity, and the gonads are distinctly adradial. This is especially emphasized by Bigelow, who pointed out the almost complete agreement between *B. niobe* and *B. fulva*; the only difference seems to be the ability of the former to produce medusa buds, which have never been seen in *B. fulva*. Mayer's figures show that *B. niobe* differs further from *platygaster* in the branching of the oral tentacles, which have a fairly long, unbranched, basal trunk before the first bifurcation, whereas in *B. platygaster* they bifurcate immediately after they issue from the mouth tube. Moreover, the ocelli of *B. niobe* seem to be round, not crescent-shaped as in *platygaster*. The medusa buds of *B. niobe* are developed directly on the lateral sides of the stomach, not in clusters.

Thus *B. fulva* and *B. niobe* differ from *B. platygaster* mainly in the distinctly adradial position of their gonads and in the length of the manubrium. Even if the flat shape of the stomach should be due to contraction during preservation, it would be a remarkable coincidence if all the thirty-three specimens collected by 'Discovery II' showed in every case the same mode and degree of contraction. I have come to the conclusion that *Bougainvillia platygaster* is a species distinct from *B. fulva* and *B. niobe*.

Asexual propagation in *Bougainvillia platygaster*

Asexual budding was observed in twelve of the specimens of *Bougainvillia platygaster* collected by 'Discovery II'. It should at once be emphasized that all the specimens were immature. In the largest medusa buds, four long marginal tentacles can be seen curled or doubled up inside the umbrella-cavity and the manubrium carries four small, simple oral tentacles, each with a terminal cluster of nematocysts (Pl. III, figs. 5 and 6). Apparently the buds are produced in three different ways: (1) from pedicels of polypoid hydranths issuing from the corners of the manubrium of the medusa, (2) as outgrowths from stolonial structures, and (3) directly from the walls of the stomach, but investigation shows that there is no fundamental difference between them.

(1) The first method is unique so far among the Hydromedusae. It is seen in five specimens, 5-6 mm. wide, from the south and east coasts of Africa (Stations 1374, 1375 and 1581), and it also

¹ After the above was printed I met Dr M. Vannucci who told me that *B. carolinensis* actually occurs off the east coast of Brazil.

occurs in Haeckel's specimen from the West Atlantic, although Haeckel himself failed to observe it. In each of the four corners of the stomach of the medusa, adjacent to the bases of the radial canals, a typical, well-developed hydranth, mounted on a short pedicel, carries medusa buds as lateral outgrowths with fairly long pedicels (Pl. III, figs. 2-5). The hydranths are fairly broad, each provided with a circle of 10-12 tentacles and a circular mouth opening. They are also able to catch food, as seen in Pl. III, fig. 5, which shows a hydranth grotesquely expanded by a copepod which it has swallowed.

(2) In one of the specimens from St. 1581, off Zanzibar (Pl. III, fig. 6), no hydranths can be observed, but from the corners of the stomach filiform structures have grown outwards, adnate to the epithelium of the subumbrella, exactly like the stolon of a hydroid attached to a solid substratum. They are more or less branched and give rise to pedicels with medusa buds. In the specimen figured, the stolon carries two well-developed medusa buds; the stolon is adnate up to a point a little beyond the origin of the medusa buds, its terminal end being slightly elevated, the internal structure showing that it is in the act of developing into a medusa. The small outgrowth on the right is in a juvenile, unmodified condition; it has no terminal cluster of nematocysts and therefore cannot be regarded as a blastostyle.

(3) Medusa buds situated on the walls of the stomach can be seen in the six specimens from Brazilian waters, three collected in April (St. 680) and three in October (St. 709). Some of the medusa buds are solitary, issuing directly from the stomach wall as in *B. niobe*, but most of them are collected in clusters on branched pedicels. Hydranths are not developed in these clusters, but the very fact that the pedicels of the medusa buds may be branched seems to indicate that they may be regarded as highly reduced stolonial or polypoid structures. This is the only method of budding found in the Brazilian medusae as well as in Haeckel's specimen (described under (1)) in which hydranths are also developed. It also occurs in the medusa from St. 1581, off Zanzibar (described under (2)), in which some of the medusa buds are also borne on stolonial outgrowths from the corners of the stomach.

Although examples of propagation by budding have previously been reported in numerous genera of medusae, the only instances at all comparable with *Bougainvillia platygaster* occur in the limnomedusa, *Proboscidactyla ornata*, and in the leptomedusa, *Phialidium mccradyi*.

Proboscidactyla ornata is a species common to all tropical coasts and in it medusa buds are found on the radial canals. The species has been divided into a number of varieties, or even species and subspecies, based on the position of these buds, which may be either adjacent to the corners of the stomach, or else arise on the first, second or third forking of the radial canals. In every case the medusa buds do not arise directly from the tissues of the radial canals but from a blastostyle, which is a polypoid structure. These buds were first seen by T. Huxley (1877, p. 132, fig. 17) in an unidentified 'Willia' (*Proboscidactyla*). He described them as issuing from small 'stolons', each terminating in a 'knobbed extremity containing many nematocysts'. Huxley's observations were quoted by Browne (1904, p. 727). In a later paper Browne (1916, p. 184) called Huxley's 'stolons' 'blastostyles', a decidedly better term. The occurrence of these structures has been reported subsequently by several other authors, and in 1951, while in the Philippines with the Danish 'Galathea' Expedition, I found numerous specimens of *Proboscidactyla ornata* with medusiferous blastostyles in every possible position on the canals. Pl. III, fig. 7 shows one of these structures which I have observed. It is certainly a blastostyle, a polypoid individual corresponding to the blastostyles on which the gonophores are developed in many hydroid colonies.

In *Phialidium mccradyi* also, medusiferous blastostyles have been found to occur (Brooks, see Mayer, 1910, p. 271, Pl. 34, figs. 2, 3, Pl. 35, figs. 1-3), but in this instance they arise from the immature gonads and are enclosed in gonothecae.

I have already pointed out (p. 13) that the budding structures in *Bougainvillia platygaster* cannot be regarded as blastostyles. Consequently, we have here a method of asexual propagation different from the one met with in the two species just described. Nor can the polyps produced by *B. platygaster* be compared with the actinulae of *Hybocodon* or *Margelopsis* for example. Actinulae are developed from fertilized eggs, which have remained attached to the stomach wall of the medusa, whereas I would emphasize again that in all the budding specimens of *B. platygaster* the gonads were immature.

Although in *B. platygaster* medusa buds arise in three apparently different ways, it must be remembered that an outgrowth on any polypoid structure of a hydrozoan is initially unmodified. Its future is usually predestined by its position on the colony, which indicates whether it will develop into a stolon, a hydranth, a blastostyle or a gonophore. Heteromorphic development, however, often occurs, one of the most frequent results of which leads to the development of a stolon from a bud destined to become a hydranth, and Berrill (1949) has demonstrated that heteromorphism can be due to environmental factors.

In *B. platygaster*, clearly, we have three examples of heteromorphism occurring within a single species. The branched structures described as issuing from the corners of the stomach of the medusa, each carrying a hydranth (sometimes two), are comparable with small hydroid colonies.

In the specimen from St. 1581 (described under (2)) in which no hydranths are developed, the whole 'colony' issuing from the corner of the stomach has been transformed into a creeping stolon adnate to the subumbrella of the medusa. The formation of a terminal hydranth is inhibited and medusa buds issue directly from the stolon. These two structures invariably arise from the corners of the stomach.

Where outgrowths from the lateral walls of the stomach (described under (3)) have no possibility of attachment to a substratum, no stolons and no hydranths are formed but only a cluster of medusa buds on branched pedicels. These may be regarded as completely reduced polypoid colonies.

Although the formation of hydranths by asexual budding from a medusa is contradictory to our usual concept of the normal developmental cycle in hydromedusae, the budding in *Bougainvillia platygaster* forces us to abandon the idea that the asexual offspring of a medusa must always be other medusae.

Family PANDEIDAE

Merga rubra sp.n.

(Pl. II, fig. 4)

OCCURRENCE: St. 661. 2. iv. 31. 57° 36' S, 29° 54' 30" W. North of the South Orkney Islands. Net: TYFV 500-250 m. 1 specimen, the *holotype*.

In spite of the poor condition of the single specimen, it must be described as a new species. The umbrella is 7 mm. high, including the slender and pointed apical projection; the diameter is about 4.5 mm. The walls of the umbrella are fairly thick. The stomach is about three-fifths as long as the height of the bell-cavity and very broad; the perradial edges are attached to the radial canals along more than half the length of the stomach. The oral lips have disappeared. A broad conical apical chamber leads upwards into the gelatinous apical projection. The gonads are mutilated; apparently they are smooth, but their size cannot be gauged; they contain many fairly large eggs. The four radial canals and the ring-canal are fairly narrow. There are two opposite marginal tentacles with very large conical basal bulbs; ocelli not seen. Moreover, there are six rudimentary tentacles, or tenaculæ, slender and tenon-like, solid; two of them are opposite to two of the radial canals, the others are interradial, one in each quadrant. Velum,? Colour: the stomach has a deep reddish brown colour, similar to that of many deep-sea medusae.

Owing to the configuration of the marginal tentacles this medusa might be referred to *Amphinema*, but owing to the very long mesenteries, I think we must place it in the genus *Merga*, at least provisionally. It differs from the other species of this genus by the interradial position of the gonads, by the rudimentary tentacles being developed into tenaculae, and by the possession of an apical chamber above the stomach.

Annatiara affinis (Hartlaub 1913)

1913 *Tiaranna affinis* Hartlaub, p. 269. Text-figs. 220-1.

1920 *Tiaranna affinis* Kramp, p. 6. Pl. 1, fig. 1.

1926 *Tiaranna affinis* Kramp, p. 68. Pl. 1, figs. 15-17.

1934 *Tiaranna affinis* Ranson, p. 436.

1940b *Annatiara affinis* Russell, p. 518.

1953 *Annatiara affinis* Russell, p. 200. Text-figs. 101-3.

OCCURRENCE: St. 89. 28. vi. 26. $34^{\circ} 05' 15''$ S, $16^{\circ} 00' 45''$ E. South Africa. Net: TYF 1000(-0) m. 1 specimen, diam. 19 mm.

St. 69I. 8. v. 31. $00^{\circ} 26' S$, $29^{\circ} 56' W$. Net: TYFB 400-0 m. 1 specimen, diam. 17 mm.

St. 697. 12. v. 31. $09^{\circ} 15' N$, $30^{\circ} 02' W$. Net: TYFB 460-0 m. 2 specimens, diam. 12-13 mm.

DISTRIBUTION. This is an oceanic medusa, occurring mainly in the intermediate water masses. It has been recorded from west of the British Isles and from the Bay of Biscay, and I have seen a specimen taken off Liberia, on the west coast of Africa. The first of the Discovery localities is off the southern part of the west coast of Africa, the two others from the central part of the Atlantic Ocean, between the Cape Verde Islands and Cape St Roque, South America.

Halitholus intermedius (Browne 1902)

1902 *Tiara intermedia* Browne, p. 277.

1939 *Halitholus intermedius* Browne & Kramp, p. 288. Pl. 14, fig. 7, Pl. 16, figs. 1-2.

OCCURRENCE: St 100. 2. x. 26. $33^{\circ} 20' S$, $15^{\circ} 18' E$ to $33^{\circ} 46' S$, $15^{\circ} 08' E$. Net: TYF 475(-0) m. 1 specimen, diam. 5 mm.

St. 1374. 24. v. 34. $31^{\circ} 46' 36'' S$, $29^{\circ} 46' 18'' E$. Net: TYFB 230-0 m. 1 specimen, diam. 4 mm., height 6.5 mm.

I have compared these specimens with specimens from the Falkland Islands and found perfect agreement.

DISTRIBUTION. Previously known only from the Falkland Islands, where this medusa is very common. The two localities mentioned above are off the coast of South Africa, one near Capetown, the other off the south coast. This subantarctic species is thus able to live in the cool water of the Benguela Current.

Leuckartiara octona (Fleming 1823)

1913 *Leuckartiara octona* Hartlaub, p. 285. Text-figs. 239-53.

OCCURRENCE: St. 79. 13. vi. 26. $34^{\circ} 48' S$, $16^{\circ} 36' W$. North-west of Tristan da Cunha. Net: N 450 V 1000-0 m. 1 specimen.

St. 273. 31. vii. 27. $09^{\circ} 38' 00'' S$, $12^{\circ} 42' 30'' E$. Off Angola. Net: TYF 230-200(-0) m. 1 specimen.

St. 276. 5. viii. 27. $05^{\circ} 54' S$, $11^{\circ} 19' E$. Off Congo River. Net: TYF 150(-0) m. 2 specimens.

St. 280. 10. viii. 27. $00^{\circ} 36' S$, $08^{\circ} 28' E$. Off French Congo. Net: TYF 200-100(-0) m. 1 specimen.

St. 701. 16. x. 31. $14^{\circ} 39' 18'' N$, $25^{\circ} 51' 42'' W$. Near Cape Verde Islands. Net: TYFB 242-0 m. 2 specimens.

Dimensions of the specimens

Station	79	273	280	701	701
Height of umbrella (mm.)	10	11	10	10	10
Diam. of umbrella (mm.)	9	9	7	9	10
No. of tentacles	20	19	?	22	22

In some of the specimens there is only one rudimentary tentacle between successive fully developed tentacles, in others there are 1-3. Ocelli are not seen, but for comparison I examined specimens from North European waters and found that the ocelli frequently disappear after prolonged preservation. The agreement between the present specimens and those from northern waters is so perfect that I have no doubt of the correctness of the identification.

DISTRIBUTION. This species has a very extensive distribution. It is abundant in North-West European waters as far north as Iceland. It also occurs in the Mediterranean and on the east coast of North America, and it is further recorded from the coasts of India, Malaya, Japan, the Philippines, and North-East Australia and from Vancouver on the west coast of North America. It has now been found for the first time off the west coast of Africa. The occurrence in the neighbourhood of the island of Tristan da Cunha in the middle of the South Atlantic (St. 79) is of particular interest.

Leuckartiara annexa sp.n.

(Pl. II, figs. 5, 6)

OCCURRENCE: St. 439. 21. ix. 30. 30° 12' S, 32° 24' E. Near Durban, South-East Africa. Net: N 100 B 110-0 m. 1 specimen, the *holotype*.

St. 1576. 25. iv. 35. 14° 42' S, 42° 22' 12" E. Off Mozambique, East Africa. Net: TYFB 400-0 m. 1 specimen. The specimen from St. 439 is chosen as the *holotype*. Umbrella 11 mm. in height, 9 mm. in diameter, regularly dome-shaped with almost perpendicular sides, no apical gelatinous projection, walls fairly thin. Manubrium very large, almost filling the umbrella-cavity, oral lips large and complexly folded, protruding somewhat below the level of the bell margin. The four perradial edges of the stomach are connected with the radial canals along their upper half. The gonads occupy the entire walls of the stomach; they contain numerous ripe eggs. The gonads are interradial, each consisting of two lateral rows of transverse folds, about ten in each row, directed a little upward in the upper half, and downward in the lower half. The two rows of folds are separated by a narrow interradial groove, which is interrupted by the transverse bridge characteristic of *Leuckartiara* and related genera. In the present species the transverse bridge is placed in the middle part of the stomach wall, at an equal distance from the proximal and from the distal end of the stomach. The radial canals are moderately broad with slightly undulated edges. The ring-canal is fairly narrow. Velum narrow.

There are four perradial and four interradial tentacles of about equal size, with large, elongated, somewhat laterally compressed basal bulbs; the base of the bulb clasps the umbrella-margin forming a short abaxial spur. Ocelli are not seen. There are also eight adradial tentacles, much smaller than the others, and of a peculiar shape not seen in any other species of this genus. They have no basal swelling; their proximal part is narrow, adnate to the umbrella-margin and continued rather far upward on the exumbrella, whence a short filiform tentacle projects upward and outward. Alternating with the tentacles are 16 minute rudimentary bulbs.

The other specimen (St. 1576) is small, only 3 mm. high and wide. The manubrium is only half as long as the height of the bell cavity. The four interradial tentacles are somewhat smaller than the perradial. Some of the adradial tentacles are still quite small, the others are similar to those in the adult specimen.

Whereas the perradial and interradial tentacles of this medusa resemble the tentacles of most other species of *Leuckartiara*, the configuration of the adradial tentacles separates it from all other species and justifies the erection of a new species.

Neoturris pileata (Forskål 1775)

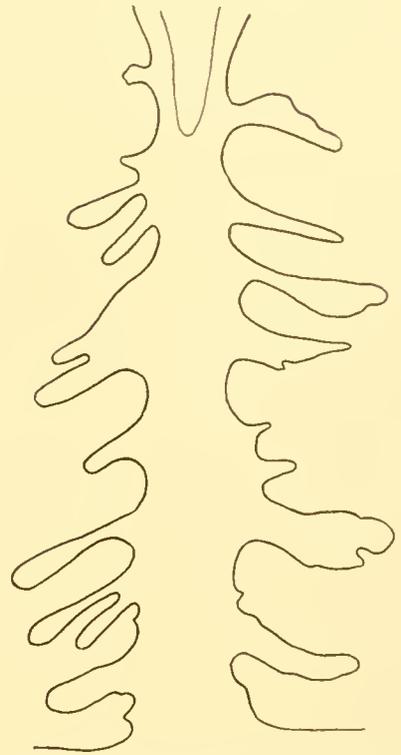
1913 *Neoturris pileata* Hartlaub, p. 326. Text-figs. 270-81.

OCCURRENCE: St. 1606. 31. x. 35. 26° 15' 48" S, 12° 18' E. Off Ichabo Island, South-West Africa. Net: TYFB 190-0 m. 1 specimen.

The specimen is very large, 35 mm. in diameter and 34 mm. in height, the apical projection slightly developed. The free, distal portion of the radial canals is about 19 mm. in length, provided with lateral diverticula of uncommon length, some of them about as long as the width of the canal (text-fig. 2). There are 80 marginal tentacles including a few small ones.

It was a surprise to find this North-Atlantic species so far south in the ocean. I have compared the specimen with several large examples from northern waters; in some of them the lateral diverticula of the radial canals are almost as long as in the present specimen, and in all other respects the agreement is perfect. The considerable length of the diverticula is most probably the consequence of growth beyond the usual size of this species. The structure of the gonads, the length of the 'mesenteries', the shape of the tentacle bulbs, and the number of tentacles are typical of *N. pileata* and leave no doubt of the identification.

DISTRIBUTION. Common in the North-East Atlantic as far north as the south coast of Iceland and in the Mediterranean. Recorded with some doubt from the Philippines and from Vancouver on the west coast of North America. Now found for the first time off the west coast of Africa.



Text-fig. 2. *Neoturris pileata*: radial canal. Specimen from St. 1606.

Pandea conica (Quoy & Gaimard 1824)

1913 *Pandea conica* Hartlaub, p. 338. Text-figs. 286, 287.

OCCURRENCE: 9. xi. 25. 01° 06' N, 13° 05' W. Net: N 200 H 0 m. 1 specimen.

St. 101. 15. x. 26. 33° 50' S, 16° 04' E to 34° 13' S, 15° 49' E. Net: N 450 V 1310-1410 m. 1 specimen.

St. 282. 12. viii. 27. 01° 11' S, 05° 38' E. Net: TYFB 300(-0) m. 6 specimens.

St. 702. 17. x. 31. 10° 59' 18" N, 27° 03' 48" W. Net: TYFB 236-0 m. 6 specimens.

St. 717. 2. xi. 31. 44° 42' S, 53° 32' 12" W. Net: TYFB 212-0 m. 1 specimen.

St. 1600. 25. x. 35. 12° 43' 18" S, 00° 20' 12" E. Net: TYFB 400-330 m. 1 specimen.

St. 1770. 21. v. 36. 33° 49' 06" S, 05° 10' 48" E. Net: N 100 B 100-0 m. 1 specimen.

Young specimens, 2-3 mm. in diameter, were taken in August and October (Stns 282 and 702), larger specimens, 9-13 mm. wide, in October and November.

The occurrence at St. 717, off the southern part of the east coast of South America, is peculiar; the specimen is badly preserved, but careful examination has convinced me of the correctness of the identification.

DISTRIBUTION. Very common in the Mediterranean; twice recorded from the neighbourhood of the Bermuda Islands (Bigelow 1918, p. 373 and 1938, p. 106); and from Japan and the Philippines. A record from the Agulhas Current south of Africa by Vanhöffen (1911, p. 209) seems to be correct. Recently recorded from the Gulf of Guinea (Kramp 1955, p. 251). The present specimens were taken off the west coast of Africa, between the Cape Verde Islands and Capetown. In addition, the specimen

mentioned above from a locality off the coast of Argentina, occurred far away from the other areas of distribution. All the specimens were taken in the upper water-layers, except at St. 101, where the depth of the haul is stated to be 1310–1410 m. The possibility exists that the single specimen was really caught at a higher level; on the other hand, in the Mediterranean the species may sometimes occur in rather deep water.

Pandea rubra Bigelow 1913

1913 *Pandea rubra* Bigelow, p. 14. Pl. 2, figs. 1–7.

1926 *Pandea rubra* Kramp, p. 96. Pl. 2, fig. 15.

1938 *Pandea rubra* Bigelow, p. 107.

OCCURRENCE: St. 107. 4. xi. 26. 45° 03' S, 17° 03' E. South of Africa. Net: N 450 V, 850–950 m. Fragments of one large specimen.

St. 151. 16. i. 27. 53° 25' S, 35° 15' W. North of South Georgia. Net: N 450 V, 1275–1025 m. 1 specimen, diam. c. 80 mm.

St. 1131. 24. ii. 33. 54° 22' 36" S, 34° 08' 24" W. Weddell Sea. Net: N 70 V, 1000–800 m. 1 specimen, diam. 38 mm., height 36 mm.

St. 1989. 10. iii. 37. 55° 53' 12" S, 32° 46' 48" W. Weddell Sea. Net: TYFB, 1500–1200 m. 2 specimens, diam. 64 mm., height 58 mm.; diam. 62 mm., height 63 mm.

The specimens from the Weddell Sea (Stns 1131 and 1989) are in beautiful condition and have retained their deep reddish-brown colour. The exumbrellar jelly is fairly thick and very soft. There are no tracks of nematocysts on the exumbrella. The epithelium of the subumbrella consists of polygonal cells containing a dense mass of pigment granules; no muscular fibres are seen. As stated by Bigelow (1913) the radial canals are 'showing as pale bands'; they are very faintly pigmented except in their lateral notches, which are of a deep brown colour. The ring-canal is likewise pale, but the velum, which is very narrow, is dark. In the tentacles a dark brownish colour is seen in the endoderm. No ocelli are seen. On the label of St. 1989 is written: 'Exterior transparent when fresh, subumbrella deep reddish brown.'

As far as the number of tentacles is concerned, Bigelow (1938, p. 107) has compared specimens from the North-West Pacific with specimens from Bermuda and the North Atlantic. He found an indication that the Atlantic specimens had fewer tentacles than those from the Pacific, but he added: '... larger series might well show that there is actually no regional difference in this respect'. It is interesting to note that in the present specimens from the Weddell Sea the number is comparatively large:

Height of bell (mm.)	36	58	63
No. of tentacles	20	22	24

The largest specimen observed by Bigelow (1913, 75 mm. high) between San Francisco and Unalaska Island had about 20 tentacles.

DISTRIBUTION. This beautiful medusa belongs to the deep and intermediate water-layers and has a very extensive distribution: North-West Pacific (Bigelow 1913); North-East Atlantic (Kramp 1926); Bermuda (Bigelow 1938). Its known area of distribution is thus greatly augmented by the finds mentioned above from the Weddell Sea and South Africa.

Zanclonia weldoni (Browne 1910)

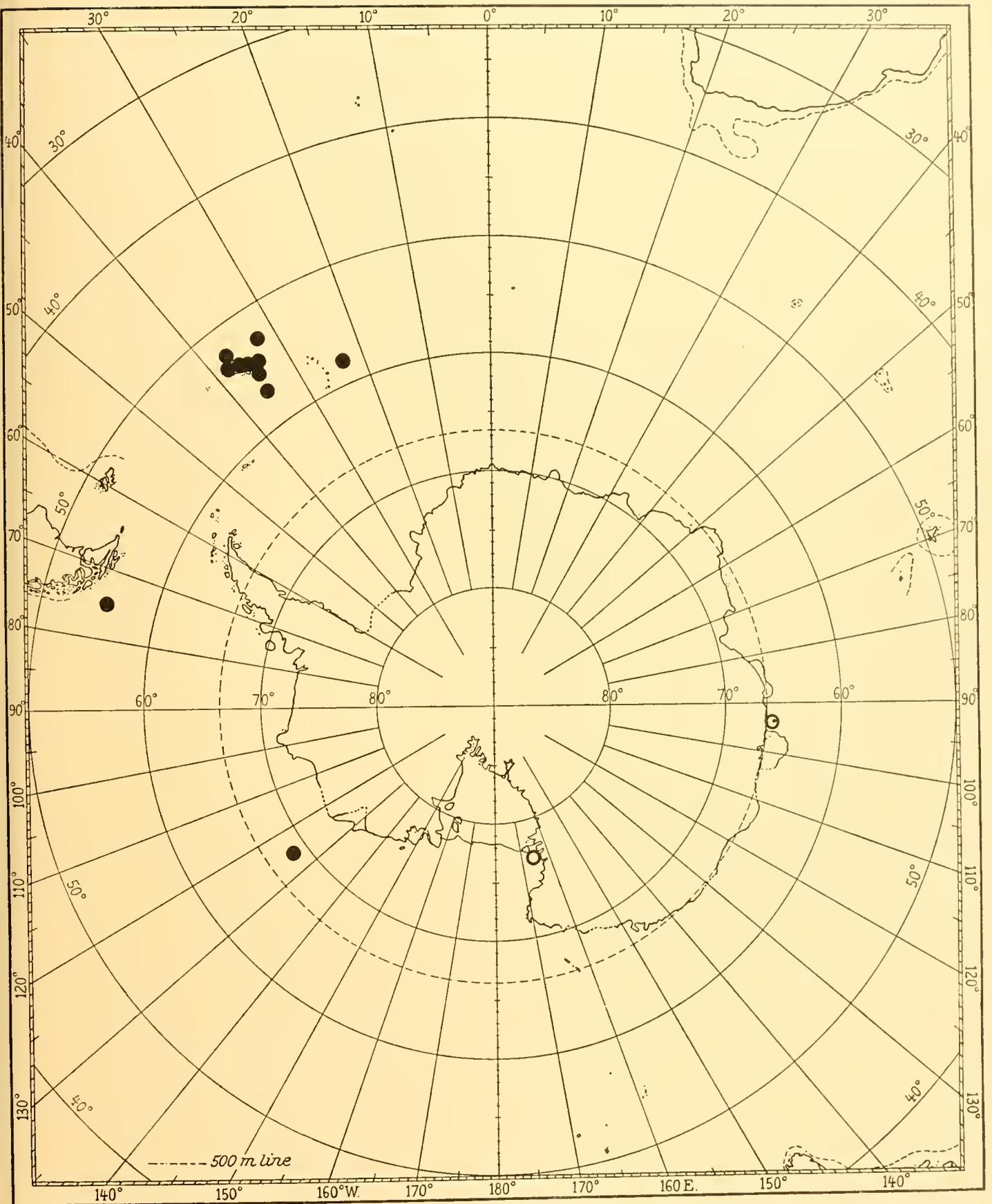
1910 *Catablema weldoni* Browne, p. 13. Pl. 1, figs. 1–5.

1912a *Catablema weldoni* Vanhöffen, p. 362. Pl. 24, fig. 3.

1913 *Zanclonia weldoni* Hartlaub, pp. 313, 348. Text-figs. 261, 262.

OCCURRENCE: (Text-fig. 3) Stns 12, 133, 138, 139, 151, 825, 1050, near South Georgia.

St. 727. South-west of Cape Horn.



Text-fig. 3. Distribution of *Zancloia weldoni*. New records = ●, previous records = ○.

St. 1298. $69^{\circ} 15' 7''$ S, $125^{\circ} 56' 3''$ W.

Stns WS 21, WS 22, WS 29, WS 57, WS 60, WS 61, WS 330, near South Georgia. St. WS 557, east of South Sandwich Islands. (For details, see Table I.)

Most of the 20 specimens are in excellent condition and confirm in every respect Browne's detailed description, except in the regular alternation of large tentacles and small marginal bulbs. These latter are seen in different stages of development into tentacles, and they are irregularly distributed among the fully developed tentacles. Two of the specimens are somewhat larger than any known up to now; they were collected at St. 727, near the south point of South America. One of them is 36 mm. high and 32 mm. in diameter, with 24 large tentacles and no small ones; the other specimen is 37 mm. high and wide, with 32 large tentacles and 10 small ones, irregularly distributed. Both specimens contain numerous eggs. The lateral diverticula of the radial canals are so long that they meet in the interradii, but they never fuse.

In small specimens, 5–6 mm. high, the diameter is about equal to the height; in medium-sized specimens, 8–18 mm. high, the umbrella is usually considerably higher than wide; variations in the ratio may be due to contraction during preservation. Again, in large specimens the diameter increases in proportion to the height; two specimens, 20–21 mm. high, are 23 mm. and 22 mm. wide and, as mentioned above, the two very large specimens from St. 727 are about as wide as high.

The majority of the specimens were collected in the neighbourhood of South Georgia in the summer months of November to February; they vary in size as follows:

Month	Nov.	Dec.	Jan.	Feb.
Height (mm.)	8–9	5–16	10–21	10–20

There is an indication that young specimens appear at the beginning of the summer and increase in size during the succeeding months, but the two very large specimens (St. 727) were taken in November 1931. Two specimens taken at St. 1298 on 2 March 1934 in the Pacific sector of the Antarctic are 14 mm. high and 8–10 mm. wide.

DISTRIBUTION. Previously recorded from McMurdo Sound and Cape Adare (Browne) and from the Gauss Station (Vanhöffen). These records, in conjunction with those of the Discovery collections, indicate that this species has a circumpolar distribution in the antarctic seas.

Pandeidae spp. indeterminatae

OCCURRENCE: St. 208. 7. iv. 27. $62^{\circ} 49' 30''$ S, $60^{\circ} 10' 30''$ W. Off Livingston Island, South Shetland. Net: TYF 800(–0) m. 1 specimen.

St. 707. 22. x. 31. $06^{\circ} 44'$ S, $33^{\circ} 33'$ W. Net: TYFB 182–0 m. 1 specimen.

St. 708. 23. x. 31. $10^{\circ} 20' 36''$ S, $34^{\circ} 54' 42''$ W. Net: TYFB 208–0 m. 1 specimen.

St. 709. 24. x. 31. $14^{\circ} 01' 24''$ S, $36^{\circ} 30' 42''$ W. Net: TYFB 216–0 m. 1 specimen.

St. 1585. 1. v. 35. $00^{\circ} 06'$ S, $49^{\circ} 45' 24''$ E. Net: TYFB 500–0 m. 1 specimen.

Young and more or less mutilated specimens which could not be identified beyond referring them to this family were collected at the above localities.

Family CALYCOPSIDAE

Calycopsis borchgrevinki (Browne 1910)

(Text-fig. 4)

1910 *Sibogita borchgrevinki* Browne, p. 17. Pl. 2, figs. 1–5.

1911 *Calycopsis borchgrevinki* Vanhöffen, p. 215. Pl. 22, fig. 7, text-fig. 10a, b.

1912a *Calycopsis borchgrevinki* Vanhöffen, p. 364.

OCCURRENCE: Stns 114, 115, 120, 151, 382, 395, 454, 662, 663, 666, 958, 1458, 1559. WS 20, WS 37, WS 385.
(For details, see Table 1.)

Altogether 44 specimens of this well-known medusa were preserved. One of the specimens is very small, 3 mm. in diameter, and unfortunately it is badly preserved. The others range in size between 7 mm. and 24 mm. in diameter. As a rule the jelly is very firm.

The sizes of the preserved specimens in the different months of the year are as follows:

Month	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	April
Diam. (mm.)	11-17	12	10-24	7	18	21	9-23

These figures do not show any definite relation between the season and the size of the medusae.

Most of the localities are in the Atlantic sector, fairly evenly distributed between about 22° E and 45° W, in a belt between 48° and 56° S. St. WS 385 and St. 382 are in the neighbourhood of the South Shetlands. Stns 958 and 1458 are in the Pacific sector, between about 62° and 66° S.

DISTRIBUTION. Antarctic and sub-antarctic, circumpolar; previously recorded from Cape Adare (Browne); between Bouvet Island and Enderby Land and north-west of Gauss Station (Vanhöffen).

Calycopsis bigelowi Vanhöffen 1911

(Text-fig. 4)

1911 *Calycopsis bigelowi* Vanhöffen, p. 218. Text-fig. 12.

1918 *Calycopsis bigelowi* Bigelow, p. 377.

1940 *Calycopsis bigelowi* Bigelow, p. 293.

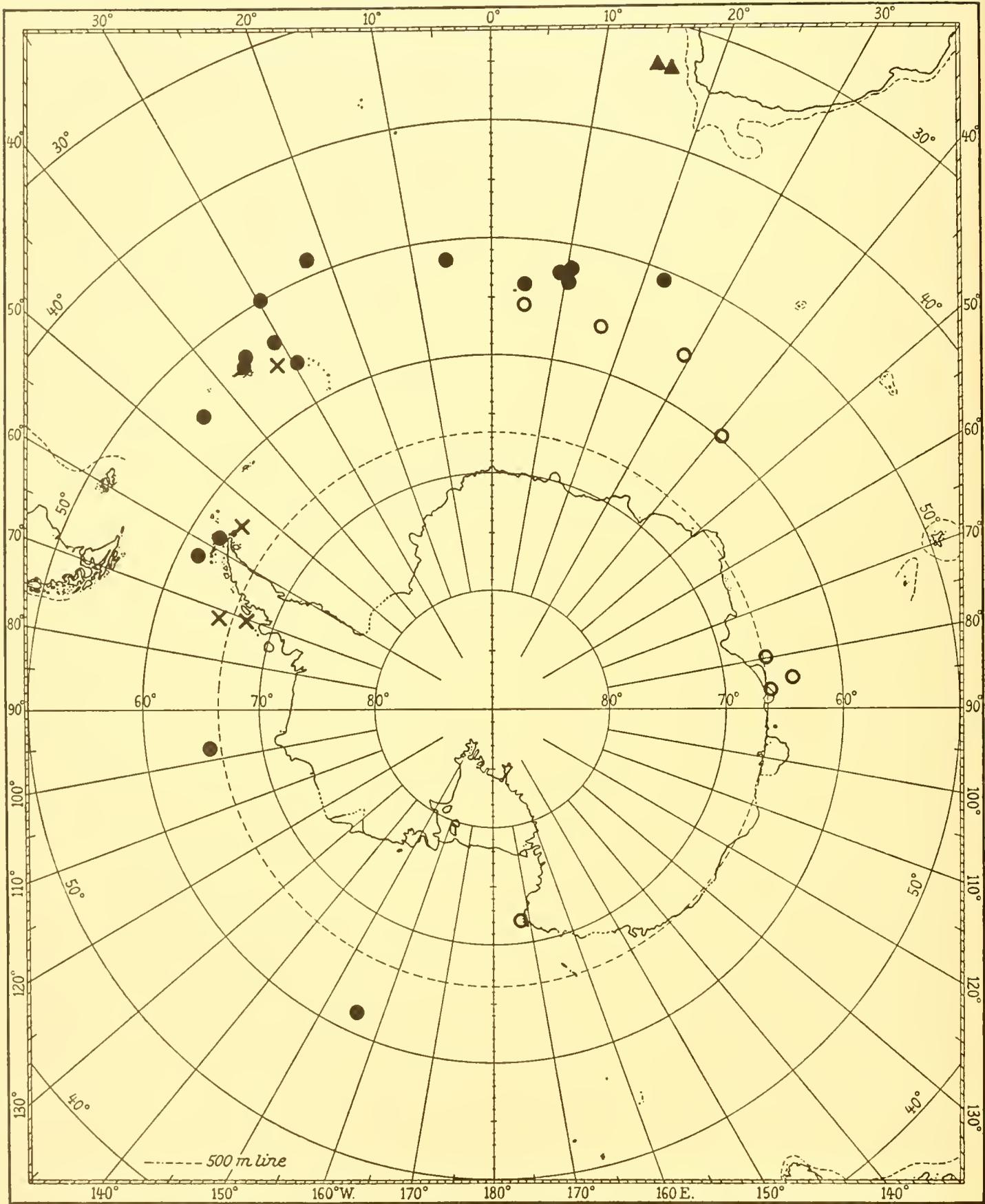
OCCURRENCE: St. 100. 2-4. x. 26. 33° 20' S, 15° 18' E to 33° 46' S, 15° 08' E. Net: TYF 475(-) m. 1 specimen. TYF 2500-2000 m. 1 specimen.

St. 101. 15. x. 26. 33° 50' S, 16° 04' E to 34° 13' S, 15° 49' E. Net: N 450 350-400(-) m. 2 specimens. N 450 V 850-950 m. 1 specimen.

These localities are west of the Cape of Good Hope. A specimen belonging to the same species is labelled as follows: St. 983. 23. x. 32. 55° 10' S, 76° 04' 42'' W. Net: N 100 B 300-80 m. This is very peculiar. The locality is west of the south point of South America, and the haul was made in the upper water-layers, whereas in the other localities the specimens were taken at considerable depths. I cannot suppress a suspicion that some mistake may have taken place.

According to the revision of the genus *Calycopsis* carried out by Bigelow (1913, 1918, 1940), the present specimens must be referred to *C. bigelowi*, and as a matter of fact they agree quite well with the description and figure given by Vanhöffen of this medusa, which was taken in the Gulf of Aden. In spite of the very considerable geographical range, I am convinced that they belong to the same species. At any rate, they are quite different from *C. borchgrevinki*. They vary in diameter from 7 mm. to 16 mm. (Vanhöffen's specimen was 13 mm. wide), the gonads are similar in structure to *C. bigelowi*. A specimen 9 mm. in diameter has about 32 tentacles; the largest specimen, 16 mm. high and wide, has about 48 tentacles of different sizes, some of them quite small; thus, in this respect also, the specimens agree with Vanhöffen's statements. I may add that the jelly is remarkably soft and adhesive, more or less covered by adhering particles of dirt. In all the specimens the gonads have a characteristic yellow-green colour. In some of the specimens, several peculiar projecting lobes are seen between the folds of the gonads, exactly like those observed in *C. typha* by Bigelow (1909, p. 208, *Sibogita nuarchus*); he was able to state after cutting sections that 'such lobes are nothing more than regions of the sexual organ which have made an irregular growth outwards'.

DISTRIBUTION. Previously recorded from the Gulf of Aden, 13° 02.8' N, 46° 41.6' E, in deep water. Now taken west of Cape of Good Hope, also in deep and intermediate water-layers.



Text-fig. 4. Distribution of: *Calycopsis borchgrevinki* = ●, previous records = ○.
C. bigelowi = ▲. *Russellia mirabilis* = ×.

Bythotiara murrayi Günther 1903

1903 *Bythotiara murrayi* Günther, p. 424. Pl. 10, figs. 4, 5.

1953 *Bythotiara murrayi* Russell, p. 215. Pl. 13, fig. 1. Text-figs. 113A, B; 114A, B; 115, 116.

OCCURRENCE: St. 81. 18. vi. 26. 32° 45' S, 08° 47' W. North-east of Tristan da Cunha. Net: N 450 B 650(-0) m. 1 specimen, 17 mm. wide.

St. 1606. 31. x. 35. 26° 15' 48" S, 12° 18' E. Off Ichabo Island, South-West Africa. Net: TYFB 190-0 m. 1 specimen, 26 mm. wide, 21 mm. high.

DISTRIBUTION. Mediterranean. North-East Atlantic as far north as Norway. West coast of Africa off the mouth of the Congo River. Mainly found in deep and intermediate water-layers. Moreover, a specimen taken near Nias Island in the Indian Ocean was referred to this species by Vanhöffen (1911, p. 213, text-fig. 9).

Heterotiara minor Vanhöffen 1911

1911 *Heterotiara minor* Vanhöffen, p. 212. Pl. 22, fig. 5. Text-fig. 8.

1916 *Heterotiara minor* Browne, p. 183.

1919 *Heterotiara minor* Bigelow, p. 287. Pl. 39, fig. 9; Pl 40, figs. 2-4.

1928 *Heterotiara minor* Kramp, p. 58. Text-figs. 27-30.

1953 *Heterotiara minor* Kramp, p. 268.

OCCURRENCE: St. 1371. 19. v. 34. 36° 42' 24" S, 36° 04' 24" E. Net: N 100 B 146-0 m. 2 specimens.

St. 1374. 24. v. 34. 31° 46' 36" S, 29° 46' 18" E. Net: TYFB 230-0 m. 2 specimens.

The localities are off the south-east coast of Africa.

The specimens have the following numbers of tentacles:

Diam. (mm.)	7	9	12	14
No. of tentacles	14	17	19	20

These specimens must therefore be referred to *H. minor* and not to *H. anonyma*, which is a larger medusa with a smaller number of tentacles.

DISTRIBUTION. Widely distributed in the Indian Ocean and the tropical West Pacific. Not previously found farther west than the Chagos Islands, about 72° E.

Family **RUSSELLIDAE** fam.nov.

Anthomedusac with unbranched oral tentacles without terminal cluster of nematocysts, situated above the mouth opening; mouth with simple perradial lips; with groups of hollow, marginal tentacles without basal swellings, partly sunk into narrow fissures of the umbrella margin; with adaxial ocelli.

Russellia gen.n.

Russellidae with an apical projection; with cruciform stomach mounted upon a peduncle; with four pointed oral tentacles; with eight smooth, adradial gonads; with four simple radial canals; with eight groups of marginal tentacles (each group with one large and two small tentacles, the basal part of the large tentacles sunk into a deep furrow of the umbrella margin); with an adaxial ocellus at the base of the free portion of each large tentacle.

Type-species: *Russellia mirabilis* gen.n., sp.n.

The species, which will be described below, is very peculiar and cannot be included in any of the known families of Anthomedusae. It resembles the Calycopsidae in the structure of the basal part of the marginal tentacles, which are of the same type as in *Calycopsis* and *Heterotiara*. In the cross-shaped base of the stomach and the quadrangular mouth it is likewise in accordance with the Calycopsidae and the Pandeidae, and I think that it must be placed in the neighbourhood of these

families. It differs, however, from the Calycopsidae in the possession of a gelatinous apical projection, a well-developed gastric peduncle, four finger-shaped oral tentacles, a pair of small marginal tentacles adjacent to each of the large tentacles, and the presence of an ocellus on each of these latter. Unfortunately the distal parts of the tentacles are missing in all the specimens, so that we do not know whether they have a terminal knob of nematocysts as in the Calycopsidae. In spite of the presence of oral tentacles above the mouth and the grouping of the marginal tentacles, *Russellia* is widely separated from the Bougainvilliidae, in which the corresponding organs have an entirely different structure, and these same features separate it also from any other family of Anthomedusae.

I have great pleasure in naming this genus in honour of the author of many papers on medusae, my friend F. S. Russell.

Russellia mirabilis gen.n., sp.n.

(Plate IV, figs. 1-6, text-fig. 4)

OCCURRENCE: WS 300. 5. x. 28. 55° 07' 30" S, 31° 56' 55" W. Between South Georgia and South Sandwich Islands. Net: N 100 B 100-0 m. 1 specimen.

St. 584. 13. i. 31. 67° 26' 45" S, 69° 35' 15" W. West of Graham Land. Net: N 100 B 165-0 m. 1 specimen.

St. 587. 13. i. 31. 66° 28' 30" S, 71° 16' 15" W. West of Graham Land. Net: N 100 B 400-120 m. 1 specimen.

St. 1871. 12. xi. 36. 64° 04' 24" S, 52° 57' 30" W. East of South Shetland Islands. Net: TYFB 1450-1000 m. 1 specimen.

The specimen from St. 587 is chosen as the *holotype*.

The umbrella (Pl. IV, fig. 1) is 9 mm. in diameter and about 15 mm. in height, of which the broad, dome-shaped apical projection occupies about one-third. Lateral walls moderately thick, the lower margin hanging in lobes somewhat below the level of the ring-canal. The stomach is mounted on a broad, conical peduncle, about 2 mm. in length, which extends partly into the cavity of the stomach. The base of the stomach is cross-shaped; the stomach itself is deeply folded inward in the interradii, and in one of the specimens also in the perradii. In the preserved condition the stomach is slightly wider than long, its length somewhat less than half the height of the bell cavity. The interior surface of the stomach is densely wrinkled transversally, and along each interradius is a narrow, prominent ridge thrown into regular transverse folds (Pl. IV, fig. 2), indicating that in living specimens the stomach may be extended to a greater length. The gonads are adradial, separated in the perradii and interradii by narrow lines. They occupy the entire length of the stomach, and their surface is smooth, without transverse folds.

The mouth tube is very short, the mouth quadrangular with very short and simple perradial lips. The mouth rim is smooth and entire, slightly thickened (Pl. IV, fig. 3); there are no nematocysts in the rim itself, but some few are scattered in the wall above it. At a short distance above the perradial corners of the mouth are four oral tentacles (Pl. IV, fig. 3), finger-shaped, tapering towards their distal end; they have no terminal cluster of nematocysts, but numerous nematocysts are evenly scattered throughout the entire length of the tentacle, no more densely towards the tip than in the basal part.

There are four radial canals. Their ascending part, on the peduncle, is fairly wide, in transverse section like an equilateral triangle; the descending portion on the subumbrella is narrow and flat, with smooth edges. Ring-canal narrow. Velum narrow.

There are eight large tentacles, four perradial and four interradii, of equal size (Pl. IV, figs. 4-6). The basal part of each tentacle, the 'root', is directed upward and outward and is deeply sunk into a narrow fissure between two prominent lobes of the umbrella-margin. In the interradii tentacles the ascending root is directly adnate to the gelatinous tissue of the exumbrella, in the perradii tentacles the root is connected with the terminal part of the corresponding radial canal by a triangular split. The free, filiform parts of the tentacles are only seen in one of the specimens (St. 584); they are very

thin, hollow, up to 5 mm. long, but apparently all of them have lost their terminal portions; it cannot be stated, therefore, whether they have had a terminal knob of nematocysts. Immediately below the point of issue of the filiform tentacles is a red ocellus.

At the base of each of the eight large tentacle roots is a pair of similar tentacular structures, much smaller and diverging on both sides of the large one (Pl. IV, figs. 4-6). Apparently, therefore, this medusa has not merely eight single tentacles, but eight clusters, each consisting of one large and two small tentacles.

The four specimens have the following dimensions:

St. WS 300, diam. 7.5 mm., height 13 mm., male.

St. 584, diam. 7.5 mm., height 12 mm., female.

St. 587, diam. 9 mm., height 14 mm., female (the type specimen).

St. 1871, diam. 9 mm., height 15 mm., male.

The localities where this interesting species was collected are all within the antarctic region. Three of the hauls were made in the upper layers, but at St. 1871, east of South Shetland Islands, the medusa was apparently taken in deep water. If the bathymetric details are correct, this may perhaps be explained by the downward movement of the antarctic surface water in this region.

(Since the above was written, I have seen some specimens of the same species collected by the 'Dana' in West-Indian waters.)

Family TIARANNIDAE

Tiaranna rotunda (Quoy & Gaimard 1824)

(Text-fig. 5)

1910 *Tiara rotunda* Mayer, p. 124.

1913 *Tiaranna rotunda* Hartlaub, p. 266. Text-figs. 218, 219.

1920 *Tiaranna rotunda* Kramp, p. 6. Pl. 1, figs. 2-4.

OCCURRENCE: St. 71. 30. v. 26. 43° 20' S, 46° 02' W. Off Patagonia. Net: N 70 V, 1000-750 m. 1 specimen.

St. 276. 5. viii. 27. 05° 54' S, 11° 19' E. Gulf of Guinea. Net: TYF 150(-0) m. Fragments of two specimens.

St. 1702. 17. iii. 36. 64° 20' 06" S, 139° 54' E. Off Wilkes Land, Antarctica. Net: TYFB 2000-1250 m. 1 specimen.

St. 1723. 28. iii. 36. 60° 06' 42" S, 102° 48' 36" E. Off Queen Mary Land, Antarctica. Net: TYFB 800-500 m.

Fragments of two specimens.

All the specimens are in a very poor condition, but I am so well acquainted with this species that the identification is beyond doubt.

DISTRIBUTION. This species belongs to the deep and intermediate layers; it has been recorded from several localities in the North Atlantic and the western part of the Mediterranean. It might be expected to have a wider distribution, and the above records show that this is so, the area being extended to include the South Atlantic and the antarctic seas to the south of Australia.

Chromatonema rubrum Fewkes 1882

(Text-fig. 5)

1882 *Chromatonema rubrum* Fewkes, p. 305. Pl. 1, fig. 41.

1910 *Thaumantias rubrum* Mayer, p. 199.

1919 *Chromatonema rubrum* Kramp, p. 7. Pl. 1, figs. 1-8. Text-figs. 3, 4a.

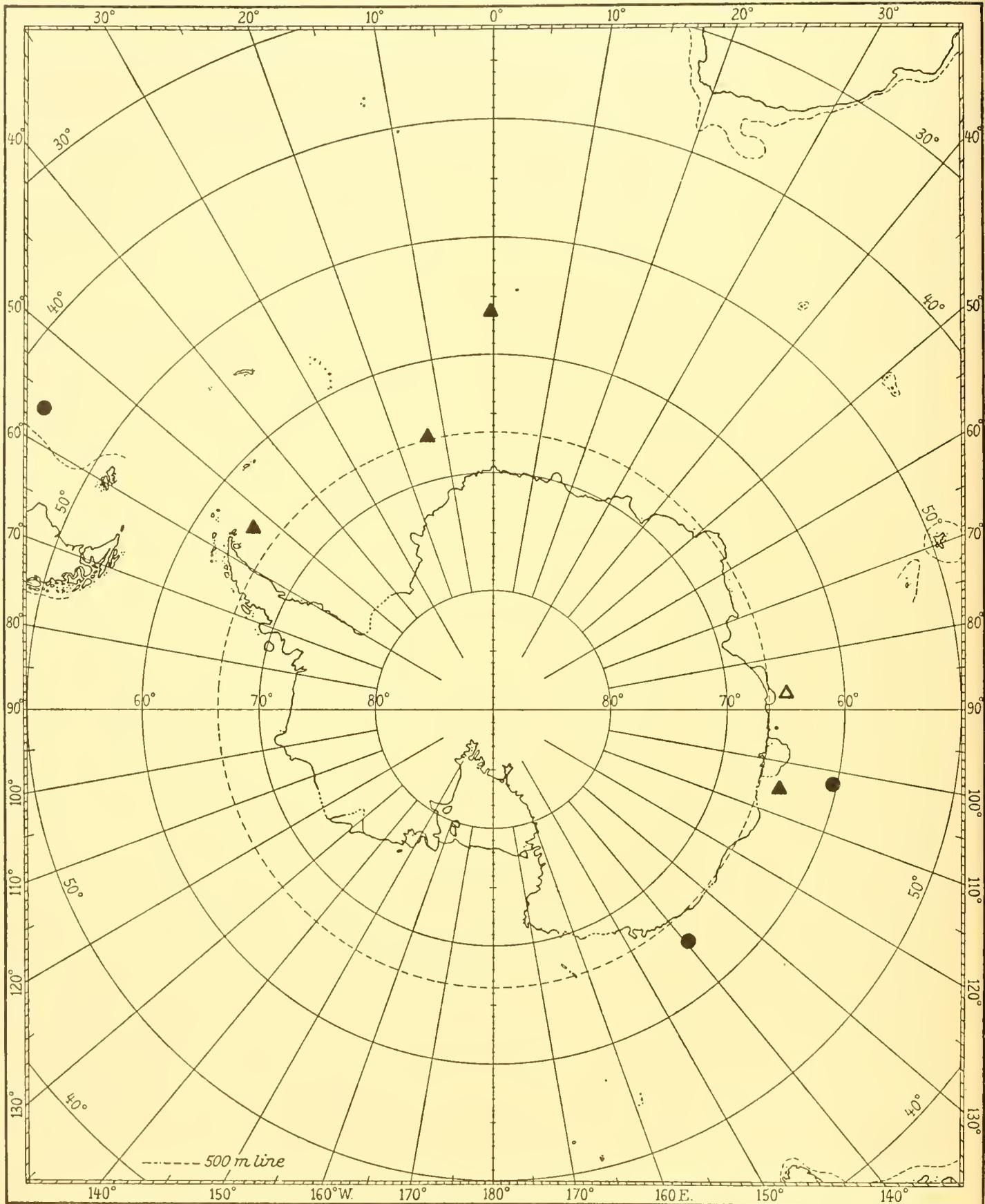
1947 *Chromatonema rubrum* Kramp, p. 52. Pl. 6, fig. 7 (coloured drawing from life).

OCCURRENCE: St. 101. 15. x. 26. 33° 50' S, 16° 04' E to 34° 13' S, 15° 49' E. West of Cape of Good Hope.

Net: N 450 850-950 m. 1 specimen.

St. 1719. 25. iii. 36. 64° 15' 30" S, 104° 03' 24" E. Off Knox Land, Antarctica. Net: TYFB 950-550 m.

1 specimen.



Text-fig. 5. Distribution in the antarctic and adjacent seas of: *Tiaranna rotunda*=●. *Chromatonema rubrum*=▲, previous records=△.

- St. 1780. 2. vi. 36. $56^{\circ} 10' 06''$ S, $00^{\circ} 08' 48''$ W. South-west of Bouvet Island. Net: N 70 B 700-450 m. 1 specimen.
 St. 1871. 12. xi. 36. $64^{\circ} 04' 24''$ S, $52^{\circ} 57' 30''$ W. East of Joinville Island, Graham Land. Net: TYFB 1450-1000 m. 1 specimen.
 St. 2006. 19. iii. 37. $66^{\circ} 16' 42''$ S, $13^{\circ} 23' 18''$ W. Off Coats Land, Antarctica. Net: TYFB 1750-1400 m. 1 specimen.

The specimens are about 15-20 mm. in diameter, more or less damaged.

DISTRIBUTION. This bathypelagic medusa has been found in several localities in the North Atlantic, as far north as the Davis Strait, west of Greenland. It has also been recorded from the neighbourhood of the Bermudas and the Azores. Two other species of *Chromatonema* have been described, *C. erythrogonon* (Bigelow 1909) and *C. hertwigi* (Vanhöffen 1911); the first was found in the tropical east Pacific, the other in the Indian Ocean between Ceylon and the Nicobar Islands. Both of them are probably identical with *C. rubrum*. Moreover, it seems very likely to me that *Ptychogena aurea* Vanhöffen (1912a, p. 366. Pl. 24, fig. 4) belongs to *C. rubrum*. His description, though insufficient, does not contradict this supposition, and the coloured figure shows a considerable resemblance to the specimens collected by 'Discovery II' in other parts of the antarctic seas. Vanhöffen's medusa was found north-west of the Gauss station, and up to now it has been regarded as a doubtful species. The Discovery collections show that *C. rubrum* is widely distributed in the deep sea around half the circumference of the Antarctic Ocean.

LEPTOMEDUSAE

Family LAODICEIDAE

Laodicea undulata (Forbes & Goodsir 1851)

1953 *Laodicea undulata* Russell, p. 230. Pl. 14, figs. 1-3. Text-figs. 123-31.

A survey of the history and nomenclature of this species is given by Russell in the monograph referred to above.

OCCURRENCE: St. 100 C. 1. x. 26. $33^{\circ} 20'$ S, $15^{\circ} 18'$ E to $33^{\circ} 46'$ S, $15^{\circ} 08'$ E. South-west of Cape of Good Hope. Net: TYF 0-5 m. 2 specimens.

St. 708. 23. x. 31. $10^{\circ} 20' 36''$ S, $34^{\circ} 54' 42''$ W. Off Aracaju, Brazil. Net: TYFB 208-0 m. 2 specimens.

The specimens from St. 708 are young stages, about 3 mm. wide; one of the specimens from St. 100 C is 11 mm., the other 31 mm. in diameter. They are typical in every respect, and the occurrence in these two localities confirms the supposition that all forms of *Laodicea* found in the Atlantic area (except *L. pulchra*, see below) belong to *L. undulata*. It has been recorded only once before from the southern Atlantic, namely, from the Patagonian Bank (Thiel 1938b, p. 322). Moreover, I have seen numerous specimens taken in the Gulf of Guinea (Kramp 1955, p. 253).

DISTRIBUTION. Widely distributed in the North Atlantic and the Mediterranean. On the Atlantic coast of America it occurs from the Gulf of Maine to the West Indies, and its American distribution is now augmented southward to the Brazilian coast, besides the record from Patagonia mentioned above. On the European coasts, it occurs from Iceland to Portugal, and on the west coast of Africa it has been recorded from the Cape Verde Islands and the Gulf of Guinea, and now has also been taken near the Cape of Good Hope.

Laodicea pulchra Browne 1902

(Pl. IV, fig. 7)

1902 *Laodicea pulchra* Browne, p. 280.

1939 *Laodicea pulchra* Browne & Kramp, p. 291. Pl. 16, figs. 3-5.

OCCURRENCE: St. 719. 13. xi. 31. $54^{\circ} 00'$ S, $60^{\circ} 00'$ W. South of Falkland Islands. Net: N 100 B 109-0 m. 1 specimen, young stage.

St. 1897. 27. xi. 36. 49° 55' S, 63° 09' 24" W. North-west of Falkland Islands. Net: N 100 B 151-0 m. 2 specimens.

St. WS 832. 1. xi. 32. 50° 49' S, 67° 55' W. Near the coast of southern Patagonia. Net: N 100 B 75-0 m. 2 specimens.

This species was briefly described by Browne in 1902, and its identity was more or less doubted until 1939, when a more thorough description was given and the drawings, previously made by Browne, were reproduced. There is no doubt now that *L. pulchra* is a distinct species. The original collection contained five specimens from the Falkland Islands, and no more have been found up to now. According to a note on the label of St. 1897, this species was a 'common form in this line of stations'; it is deplorable, therefore, that so few specimens were preserved.

The smallest specimen in the original collection was 6 mm. wide and had 17 tentacles. The specimen from St. 719 is in a still younger stage, being 2 mm. wide and 2.5 mm. high; the radial extensions of the stomach are short, but in their lateral walls the gonads are beginning to appear as tiny folds. There are four fully developed perradial tentacles, spirally coiled, and four interradial bulbs which are thick and conical with a small pointed tip. Three cordyli are present between each successive pair of tentacles and bulbs, each of them mounted on a small bulb, the median one somewhat larger than the others. An ocellus is seen on the adaxial side of the tentacular bulbs as well as on the bulb of the median cordylus in each group.

The other specimens are 15-19 mm. in diameter, but it should be remarked that in the specimens from Station 1897 the umbrella margin is much contracted, so that the diameter is only slightly larger than the height of the umbrella. In the preserved condition the specimens have the following dimensions:

Station	WS 832		1897	
Diam. (mm.)	15	19	15	17
Height (mm.)	7	8	11	14
No. of tentacles	38	34	46	52

The radial lobes of the stomach are not quite as long as in the type specimen, reaching along slightly more than the proximal half of the gonads. The transverse folds of the gonads (Pl. IV, fig. 7) are strongly developed and very regular, slowly decreasing in width from the proximal to the distal end of the gonad. The terminal ends of the radial canals between the gonads and the ring-canal are very short. The marginal organs agree with the original description except that the cordyli are less distinctly club-shaped, evenly increasing in width towards their distal end, and, in contradistinction to the statement in the earlier description, they are provided with numerous nematocysts in their outermost parts.

DISTRIBUTION. This species has only been found in the immediate neighbourhood of the Falkland Islands, and between these islands and the coast of Patagonia.

Ptychogena antarctica Browne 1910

(Pl. IV, fig. 8)

1910 *Ptychogena antarctica* Browne, p. 29. Pl. 2, figs. 6-9.

1912a *Ptychogena antarctica* Vanhöffen, p. 365.

OCCURRENCE: St. 1959. 8. ii. 37. Scotia Bay Landing, South Orkney Islands. Found floating on surface very close to the shore. 1 fragmentary specimen.

The few specimens of this medusa observed up to now have all been in a bad and mutilated condition. Browne examined three specimens from Cape Adare and one from McMurdo Sound, and if the identification is correct, Vanhöffen saw a fifth fragmentary specimen from the Gauss Station. The

Discovery specimen has also fallen into several pieces, but some of the isolated parts are in good condition. The gelatinous substance is very thick. Only a small, densely folded piece of the stomach is retained. The gonads (male) are well preserved; each of them is about 28 mm. long and 8 mm. broad, a funnel-shaped prolongation from the stomach encloses their lower surface almost throughout their entire length. The gonads are complexly folded; they have about 15 primary pockets on each side, each of them further divided into two to four or five lamellar folds. The median line, by which the radial canal with the gonads is attached to the subumbrella, is irregularly zigzag, and the lateral diverticula are not attached to the subumbrella. The distance from the gonad to the ring-canal is 12 mm.

The tentacle bulbs are elongated, somewhat laterally compressed, convex on the abaxial side, and very close together. Only a few cordyli are retained, but in one place it can be seen that they alternate with the tentacles. They are club-shaped, but the pedicel is not very thin, exactly as in Browne's figure; their central cavity is very narrow.

If we presume that the stomach has been about 20 mm. wide, the diameter of the entire specimen was probably about 100 mm.

According to a note on the label, the colour of the gonads was 'a very pale dull (or dirty) white pink'.

The description given by Vanhöffen indicates that the Gauss specimen really belonged to this same species, though he stated that the stomach, gonads and tentacles of the living specimen had a dark coffee-brown colour.

DISTRIBUTION. Cape Adare and McMurdo Sound, Victoria Land (Browne); Gauss Station (Vanhöffen). The locality, where the present specimen was taken, off the South Orkney Islands, is on the opposite side of the Antarctic Continent.

Staurophora mertensi Brandt 1838

1908 *Staurophora falklandica* Browne, p. 235. Pl. 1, figs. 1-7.

1919 *Staurophora mertensii* Kramp, p. 39. Pl. 1, fig. 9; Pl. 2, figs. 9-10; Pl. 3, fig. 7. History and synonymy.

1953 *Staurophora mertensi* Russell, p. 239. Text-figs. 132-7.

OCCURRENCE: St. 60. 21. v. 26. 50° 45' S, 56° 33' W. Net: N 100 H 75(-0) m. Fragments.

St. 1895. 26. xi. 36. 49° 55' 12" S, 60° 59' 06" W. Net: N 100 H 0-5 m. 5 specimens.

St. 1896. 7. xi. 36. 49° 55' 06" S, 62° 05' W. Net: N 70 V 140-100 m. Fragments of 2 specimens.

St. 1897. 27. xi. 36. 49° 55' S, 63° 09' 24" W. Net: N 100 B 151-0 m. 5 specimens. 'Common form on this line of stations.'

St. 1959. 8. ii. 37. Scotia Bay Landing, South Orkney Islands. Shore coll., 0 m. 1 specimen.

St. WS 73. 6. iii. 27. 51° 01' S, 58° 54' W. Net: N7-T 121-130 m. 70 specimens and numerous fragments.

St. WS 207. 28. iv. 28. 54° 12' S, 58° 40' W. Net: N 100 B 75-0 m. 3 specimens.

St. WS 865. 29. iii. 32. 50° 03' S, 64° 14' W. Net: NR 126(-0) m. 5 specimens.

With the exception of St. 1959 all these localities are in the surroundings of the Falkland Islands.

Some of the specimens are very large, but most of them are in a fragmentary condition. The specimens collected in November (Stns 1895-7) are 34-60 mm. in diameter; the numerous specimens from St. WS 73, 6 March, vary between 30 and 80 mm., those collected between 29 March and 28 April (Stns WS 207 and WS 865) are 100-120 mm. wide. Unfortunately, the only specimens collected in May (St. 60) cannot be measured.

It is now possible to state with certainty that *Staurophora falklandica* Browne is identical with *S. mertensi*. The description of *S. falklandica* was based on one specimen, and Browne himself pointed out its strong resemblance to the North Atlantic species, from which it was distinguished only by the considerable difference in size between the large and the small tentacles, which alternated almost regularly. An examination of numerous specimens from the northern Atlantic enabled me to

state (Kramp 1919) that the same arrangement was frequently found in the northern form, and now that a large collection of the southern form has become available, I can confirm that in this respect both forms are subject to the same variations. *S. falklandica* has never been observed again since it was described by Browne until now, and in the literature it has usually been mentioned as a doubtful synonym of *S. mertensi*. The Discovery collection has enabled me to compare the two forms side by side, and I have found that they agree in every respect. Unfortunately, very few of the southern specimens are in such a condition that the tentacles can be counted; in four specimens the numbers are as follows:

Diam. (mm.)	34	54	64	115
Approx. no. of tentacles	300	400	700	1400

In this respect also, the Falkland specimens agree with the North Atlantic form.

Staurophora mertensi is thus the only existing species of the genus.

DISTRIBUTION. Arctic-boreal, circumpolar. In the North Pacific it occurs as far south as Akkeshi Bay in northern Japan and Sitka on the south coast of Alaska. In the North Atlantic area it is common from West Greenland to Cape Cod and is occasionally found at Woods Hole. In the eastern part of the North Atlantic it is common round Iceland and along the northern part of the west coast of Norway, occasionally, but not regularly, occurring in the North Sea. Its occurrence in the surroundings of the Falkland Islands and the South Orkney Islands shows that it is a bipolar species.

Family MITROCOMIDAE

Mitrocomella frigida (Browne 1910)

1910 *Cosmetira frigida* Browne, p. 35.

1912a *Cosmetira frigida* Vanhöffen, p. 367. Text-fig. 3.

1932 *Mitrocomella frigida* Kramp, p. 345. Pl. 10, figs. 5-6. Text-figs. 23.

OCCURRENCE: St. 256. 23. vi. 27. 35° 14' S, 6° 49' E. West of Cape of Good Hope. Net: TYF 850-1100(-0) m. 1 specimen. Stns MS 23, MS 26, MS 34, 12. iv, 14. iv and 2. v. 1925. East Cumberland Bay, South Georgia. 1 or 2 specimens on each occasion.

All the specimens are in a poor condition. The description given by me (1932) was based on Browne's original specimens, in the British Museum (Nat. Hist.), London. The number of statocysts then remained uncertain, and in the present specimens from South Georgia their number cannot be counted; but in some other specimens from South Georgia, collected by the Swedish Antarctic Expedition (Kramp 1948b, p. 4), I was able to state that the number is eight. The specimen from St. 256 also has eight statocysts.

DISTRIBUTION. McMurdo Bay, Victoria Land (Browne); Gauss Station (Vanhöffen); South Georgia (Kramp 1948b and the present collection). It is interesting that this antarctic species was also taken at a considerable distance west of the Cape of Good Hope, evidently under the cooling influence of the Benguela Current. The specimen was probably taken in the upper layers (as the net failed to close) where the temperature of the water is given as 17.2° C.

Halopsis ocellata A. Agassiz 1865

1865 *Halopsis ocellata* A. Agassiz, p. 99. Figs. 143-7.

1919 *Halopsis ocellata* Kramp, p. 65. Pl. 4, figs. 1-5. Text-figs. 6-9.

1932 *Halopsis ocellata* Kramp, p. 353. Figs. 6, 12, 19, 28, 32, 43.

1953 *Halopsis ocellata* Russell, p. 273. Pl. 14, fig. 4. Text-figs. 162-6.

OCCURRENCE: St. WS 851. 11. ii. 32. 51° 39' S, 62° 02' 30" W. to 51° 41' S, 62° 00' W. West of the Falkland Islands. Net: N4-T, 221-198 m. 1 specimen.

The occurrence of this North Atlantic medusa near the Falkland Islands is most astonishing. The specimen is, however, typical in every respect, and it is impossible to point out any structure which might justify the erection of a new species distinct from *H. ocellata*. It is 31 mm. in diameter and has 12 radial canals in four groups of three each. Parts of the umbrella margin are mutilated, but from countings in well-preserved portions the number of tentacles may be estimated at about 100, the number of marginal vesicles as between 70 and 80; there is one cirrus between each successive pair of tentacles. Thus also in numerical respects this specimen agrees with the North Atlantic form.

DISTRIBUTION. East coast of North America, north of Cape Cod; west coast of Greenland as far north as Disko Bay; southern and western coasts of Iceland; west of the British Isles; the Faeroes; west coast of Norway from Bergen to Tromsö. In the North Atlantic area this species accordingly may be designated as northern-boreal. The present find in anti-boreal waters shows that it has a bipolar distribution.

Cosmetirella davis (Browne 1902)

(Text-fig. 6)

- 1902 *Tiaropsis davis* Browne, p. 281.
 1910 *Cosmetirella simplex* Browne, p. 34. Pl. 1, figs. 6-8.
 1911 *Phialella falklandica* Vanhöffen, p. 223. Pl. 22, fig. 10.
 1912a *Cosmetirella kerguelensis* + *simplex* Vanhöffen, p. 368.
 1920 *Cosmetirella simplex* Vanhöffen, p. 16.
 1932 *Cosmetirella davis* Kramp, p. 359. Text-figs. 4, 34, 46.
 1938b *Cosmetirella davis* Thiel, p. 327.
 1939 *Cosmetirella davis* Browne & Kramp, p. 293. Pl. 17, fig. 1.
 1949 *Cosmetirella davis* Kramp, p. 3.

OCCURRENCE: Stns 29, 30, 41B, 102, 308, 309, 314, 315, 316, 317, 326, 328, 339, 347, 348, 349, 350, 356, 592, 1719. St. WS 832. Stns MS 1, 2, 7, 9, 11, 19, 20, 22, 23, 26, 32, 62, 65. (For details, see Table 1.)

All these localities are in the neighbourhood of South Georgia, with the exception of the following:

- St. 102. 28. x. 26. 35° 29' 20" S, 18° 33' 40" E. South of Cape of Good Hope. Net: N 100 H 52 m. 1 specimen.
 St. 592. 15. i. 31. 64° 17' S, 75° 31' W. West of Graham Land. Net: N 100 B 124-0 m. 1 specimen.
 St. 1719. 25. iii. 36. 64° 15.5' S, 104° 03.4' E. Off Knox Land, Antarctica. Net: N 100 B 128-0 m. 1 specimen.
 St. WS 832. 1. ii. 32. 50° 49' S, 67° 55' W. Near the coast of southern Patagonia. Net: N 100 B 75-0 m. 1 specimen.

Altogether about 100 specimens of this species were preserved.

As previously pointed out by me (Kramp 1932), the number of tentacles is very variable in this species. Countings of the tentacles in the present collection have given the following results:

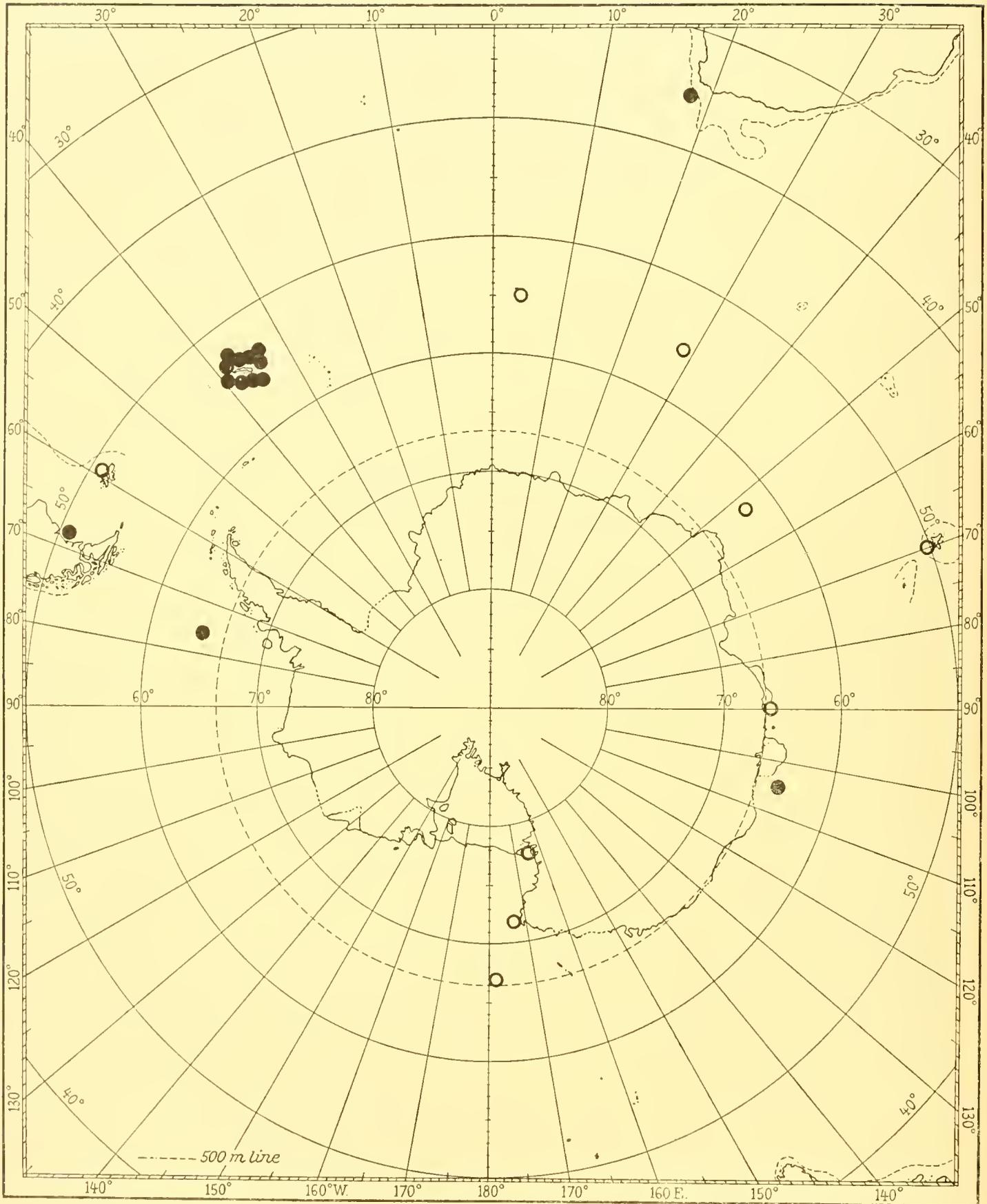
Diam. (mm.)	8-10	10-15	15-20	20-25	25-30	30-35	35-40	50	60
No. of tentacles	42-92	40-92	82-110	140	132-156	152-164	156-172	182	180

Almost all the specimens were collected between January and April, a single one in November, and some fragments in May. Within each of these months the specimens had the following diameters:

Month	Nov.	Jan.	Feb.	Mar.	April
Diam. (mm.)	16	11-35	8-39	11-60	11-20

The specimen taken south of the Cape of Good Hope (St. 102) was 35 mm. in diameter.

DISTRIBUTION. Antarctic and subantarctic, circumpolar (see map of distribution in Kramp 1949). The present record from near the coast of South Africa is not quite isolated, since the species was recorded by Vanhöffen (1920) from a locality off the coast of South-West Africa.



Text-fig. 6. Distribution of *Cosmetirella davisi* = ●, previous records = ○.

Family CAMPANULARIIDAE

Phialidium simplex Browne 1902

1902 *Phialidium simplex* Browne, p. 282.

1939 *Phialidium simplex* Browne & Kramp, p. 299. Pl. 17, figs. 5-9.

1953 *Phialidium simplex* Kramp, p. 272.

OCCURRENCE: St. 1375. 25. v. 34. 34° 30' 8" S, 26° 19' E. Off the south coast of Africa. Net: TYFB 210-0 m. 1 specimen, 12 mm. in diameter with about 48 tentacles.

DISTRIBUTION. Falkland Islands; southern part of the coast of Brazil; north-east coast of Australia.

Phialidium discoïdum (Mayer 1900)

1900 *Oceania discoïda* Mayer, p. 51. Pl. 20, figs. 53-55.

1910 *Phialidium discoïdum* Mayer, p. 272. Pl. 33, figs. 9-11.

OCCURRENCE: St. 708. 23. x. 31. 10° 20' 36" S, 34° 54' 42" W. Off Aracaju, Brazil. Net: TYFB 208-0 m. 5 specimens.

The specimens are almost hemispherical, 3.5-4 mm. in diameter, with 16 tentacles. The stomach is small with somewhat bulging sides; mouth with four simple lips, slightly folded. Two of the specimens have well-developed gonads, one male, and one female with very large eggs; the gonads are thick and cylindrical along the distal one-third to one-half of the radial canals. The 16 tentacles are of about equal size, with short and broad, almost globular basal bulbs. Two or three statocysts between successive tentacles.

These specimens agree so well with Mayer's description and figures of specimens from Tortugas, Florida, that it seems to me very probable that they belong to the same species. On the other hand, all records of this species from the Pacific seem to me very doubtful. It is recorded from several localities in Japan by Maas (1909, p. 25) and Uchida (1925, p. 90; 1927*b*, p. 221; 1938, p. 42) and also from the central Pacific (Uchida 1947*a*, p. 304, text-fig. 6), and from the Pacific coast of Mexico by Bigelow (1909, p. 155. Pl. 6, fig. 8; Pl. 38, figs. 6-7). All these medusae are of larger size and have up to 36 tentacles, and as a rule there is only one statocyst between the tentacles. Bigelow compared his Mexican specimens with specimens from the West Indies, with up to 46 tentacles, and found them indistinguishable from each other. He may be right that they belong to one and the same species, but I am sure that none of them belong to *P. discoïdum* Mayer, which is a small medusa, only 4 mm. wide, with 16 tentacles and usually 3 statocysts between the tentacles. Bigelow is inclined to think that the difference between his specimens and Mayer's was due to the latter being young stages; but according to Mayer's description and figures their gonads were particularly well developed and contained very large eggs, and the same applies to the Brazilian specimens in the Discovery collection.

Another question arises, namely, whether *P. discoïdum* is a valid species. The summer form of *P. hemisphaericum* from North European waters frequently attains a very similar appearance, being mature at a stage with 16 tentacles and then usually with two, sometimes three, statocysts between the tentacles. As a rule, however, its gonads are short and oval and not elongated as in *P. discoïdum*.

DISTRIBUTION. Florida; northern part of the east coast of Brazil.

Obelia sp.

OCCURRENCE: St. 91. 8. ix. 26. False Bay, South Africa. Net: TYF 0-5 m. 3 specimens, c. 3 mm. in diameter.

Family LOVENELLIDAE

Eucheilota sp.

(Pl. V, fig. 1)

OCCURRENCE: St. 91. 8. ix. 26. False Bay, South Africa. Net: TYF 0-5 m. 1 specimen.

I am not inclined to establish a new species for this single specimen, though it does not agree with any of the 14 species of *Eucheilota* described up to now. While on the Danish 'Galathea' Expedition, in the Indian Ocean and western Pacific I saw many medusae belonging to this genus, apparently representing several different species, some of which could not be referred to any known species. A thorough revision is needed before a reliable limitation of these numerous forms can be carried through. Provisionally, therefore, I shall only give a short description and a figure of the little medusa taken in False Bay by R.R.S. 'Discovery'.

The umbrella is almost hemispherical, 2 mm. wide and 1 mm. high, with very thin walls. Manubrium narrow, mouth with an indication of four simple lips. Gonads (male) egg-shaped, about one-third as long as the radial canals, situated a little outside the middle of the canals; one of the gonads is undeveloped. Radial canals and ring-canal very narrow. Velum narrow. There are two well-developed perradial tentacles with broadly conical basal bulbs, and two globular perradial bulbs without tentacles; moreover, four small interradial bulbs and a few very tiny marginal swellings. Eight fairly large adradial marginal vesicles. In each octant about five marginal cirri, typically spiral with a solid endoderm and a terminal knob containing nematocysts. There is no black pigmentation anywhere, neither on the stomach nor on the marginal bulbs.

Family PHIALELLIDAE

Phialella falklandica Browne 1902

1902 *Phialella falklandica* Browne, p. 282.

1909 *Phialella* sp. Benham, p. 307. Pl. 12, figs. 3-6.

1910 *Eucope falklandica* Mayer, p. 237.

1912b *Phialella falklandica* Vanhöffen, p. 21.

1939 *Phialella falklandica* Browne & Kramp, p. 296. Pl. 17, figs. 2-4; Pl. 19, figs. 3-5. Text-fig. 1.

1911 non *Phialella falklandica* Vanhöffen, p. 223. Pl. 22, fig. 10.

OCCURRENCE: St. 58. 19. v. 26. Port Stanley, East Falkland Island. Net: N 70 H 5-0 m. 37 specimens, diam. 4-10 mm.

St. 719. 13. xi. 31. 54° 00' S, 60° 00' W. South of Falkland Islands. Net: N 100 B 109-0 m. 6 specimens, diam. 1-3 mm.

St. WS 832. 1. ii. 32. 50° 49' S, 67° 55' W. Off the coast of southern Patagonia. Net: N 100 B 75-0 m. 1 specimen, diam. 12 mm.

DISTRIBUTION: Common in the neighbourhood of the Falkland Islands (Browne); recorded from the west coast of South America between the Strait of Magellan and Callao in Peru (Vanhöffen); Auckland and Campbell Islands (Benham).

Family PHIALUCIIDAE

Octophialucium medium Kramp 1955

1955 *Octophialucium medium* Kramp, p. 257. Pl. II, fig. 1.

OCCURRENCE: St. 282. 12. vii. 27. 01° 11' S, 05° 38' E. Gulf of Guinea. Net: TYF 300(-0) m. 1 specimen.

The specimen is about 30 mm. in diameter, one of the eight radial canals is bifurcated, the tentacles are lost.

The genus *Octophialucium* was recently established by me to comprise a number of species previously referred to *Octocanna* Haeckel, which must be regarded as an altogether doubtful genus. In the same paper I described a new species, *O. medium*, of which numerous well-preserved specimens were collected by the Danish 'Atlantide' Expedition near the coast of Nigeria. The present specimen was taken somewhat farther south in the Gulf of Guinea.

Octophialucium aphrodite (Bigelow 1906)

1906a *Octocanna polynema* Maas, p. 95. Pl. 3, fig. 10.

1919 *Octocanna aphrodite* Bigelow, p. 307. Pl. 42, figs. 1-2.

1928 *Octocanna aphrodite* Stiasny, p. 212. Text-fig. 2.

1955 *Octophialucium aphrodite* Kramp, p. 259.

OCCURRENCE: St. 1574. 23. iv. 35. 21° 44' 36" S, 40° 33' 42" E. Mozambique Channel. Net: TYFB 600-0 m. 1 specimen.

The specimen is 25 mm. in diameter; the eight radial canals are somewhat irregularly placed. Two of the gonads are retained, they are linear, in the distal one-fifth to one-fourth of the radial canals. The tentacle bulbs are broadly conical, provided with an adaxial papilla, but without an abaxial spur. All the tentacles are of equal size, and there are no rudiments between them. As a rule there is only one marginal vesicle between successive tentacles, rarely two, each with two concretions. Most of the tentacles are lost, but in a considerable portion of the umbrella margin all are retained; the total number of tentacles is estimated as between 80 and 100.

Among the five species of *Octophialucium* known up to now, *O. aphrodite* is the only species to which the present specimen may be referred with some degree of probability. In this species some young bulbs are usually present between the fully developed tentacles, but the Discovery specimen is so similar to the one described and figured by Maas from Amboina that their identity seems to me very probable. The absence of young marginal bulbs may be due to the specimen being fully developed. The largest specimen observed by Maas was likewise 25 mm. in diameter, with about 80 tentacles among which new ones *might* be inserted, but none are shown in his figure. One or two species of this genus occur off the coasts of India; they are quite distinct from *O. aphrodite*.

DISTRIBUTION. Amboina (Maas); Philippines (Bigelow); Java Sea (Stiasny). Now found in the Mozambique Channel between Madagascar and the east coast of Africa.

Family EIRENIDAE

Phialopsis diegensis Torrey 1909

(Text-fig. 7)

1909 *Phialopsis diegensis* Torrey, p. 23. Fig. 9.

1953 *Phialopsis diegensis* Russell, p. 333. Pl. 20, fig. 5. Text-figs. 213-14.

OCCURRENCE: St. 89. 28. vi. 26. 34° 05' 15" S, 16° 00' 45" E. Net: TYF 1000(-0) m. 1 specimen.

St. 100. 2. x. 26. 33° 20' S, 15° 18' E to 33° 46' S, 15° 08' E. Net: TYF 260-310 m. 1 specimen. TYF 475(-0) m. 1 specimen.

St. 256. 23. vi. 27. 35° 14' S, 6° 49' E. Net: TYF 850-1100 (-0) m. 1 specimen.

St. 276. 5. viii. 27. 05° 54' S, 11° 19' E. Net: TYF 150(-0) m. 14 specimens.

St. 282. 12. viii. 27. 01° 11' S, 05° 38' E. Gulf of Guinea. Net: TYF 300(-0) m. 3 specimens.

St. 697. 12. v. 31. 09° 15' 15" N, 30° 01' 45" W. Net: TYFB 460-0 m. 1 specimen.

St. 698. 13. v. 31. 12° 21' 45" N, 30° 07' 30" W. Net: TYFB 470-0 m. 1 specimen.

St. 699. 14. v. 31. 14° 27' 15" N, 30° 02' 15" W. Net: TYFB 370-0 m. 6 specimens.

St. 703. 18. x. 31. 07° 17' N, 28° 01' 54" W. Net: TYFB 358-0 m. 6 specimens.

St. 714. 30. x. 31. 35° 09' 30" S, 47° 00' W. Off Montevideo, Uruguay. Net: TYFB 246-0 m. 4 specimens.

St. 1371. 19. v. 34. 36° 42' 24" S, 36° 04' 24" E. South-east of South Africa. Net: N 100 B 146-0 m. 1 specimen.



Text-fig. 7. Distribution of *Phialopsis diegensis* = ●, previous records = ○.

St. 1568. 11. iv. 35. $34^{\circ} 47' 36''$ S, $34^{\circ} 27' 54''$ E. Net: TYFB 1400-0 m. 4 specimens.

St. 1587. 3. v. 35. $06^{\circ} 05' N$, $52^{\circ} 00' E$. Indian Ocean, off Somaliland. Net: TYFB 450-0 m. 1 specimen.

Stns 89, 100, 256 and 1568 are west and south-west of the Cape of Good Hope; stns 697, 698, 699 and 703 are south-west of the Cape Verde Islands.

This is a leptomedusan with a predominantly oceanic distribution, frequently found at considerable distances from the coasts. It is rarely met with in the uppermost water-layers, and the records of the Discovery collections indicate that it belongs mainly to the deeper parts of the epipelagic region. It was collected at very different seasons, April, May, June, August and October. The diameter of the specimens varies between 6 mm. and 20 mm. with no correlation with the seasons.

DISTRIBUTION. Originally described from San Diego in California (Torrey 1909) and south-west of the Galapagos Islands (Bigelow 1909). Recorded from a few localities in the North Atlantic: Irminger Sea (Maas 1893 as *Irene viridula*), south-west of Ireland (Russell 1940a and 1953) and east of the Newfoundland Bank (Kramp 1948a). Also taken in several localities in the tropical East Atlantic, as far south as the neighbourhood of Ascension Island (Vanhöffen 1911 and 1912a). Some of the localities where it was collected by the 'Discovery' and 'Discovery II' are considerably farther south in the Atlantic, and it has now for the first time been found in the Indian Ocean, off the east coast of Africa.

Family AEQUOREIDAE

Genus Aequorea

Besides some specimens which are too young or too mutilated to be identified with certainty, three species of *Aequorea* were collected, and in spite of the frequently emphasized variability of these medusae and the current uncertainty of the delimitation of the numerous species, I am perfectly sure of the identification of these three species. Two specimens of *A. coerulescens* were taken off the Pacific coast of South America. Of the specimens collected in various parts of the Atlantic Ocean and south-east of Africa, some belong to *A. aequorea* and some to *A. macrodactyla*, two species which are not easily confused when they are tolerably well preserved. None of the other Atlantic species are represented. As mentioned in my paper on the medusae of the Great Barrier Expedition (Kramp 1953, p. 299), I consider *A. macrodactyla* and *A. pensilis* as two distinct species, and in the present collection not a single specimen has given rise to any suspicion of belonging to *A. pensilis*. Measurements and countings were carried out in as many specimens as possible.

Aequorea aequorea (Forskål 1775)

1775 *Medusa aequorea* Forskål.

1809 *Aequorea forskalea* Péron & Lesueur.

1953 *Aequorea forskalea* Russell, p. 342. Pl. 21, fig. 3; Pl. 32, figs. 1, 2. Text-figs. 220A, 221.

OCCURRENCE: St. 446. 9. x. 30. $36^{\circ} 14' S$, $16^{\circ} 09' 45'' E$. South-west of Cape of Good Hope. Net: N 100 B 106-0 m. 2 specimens, diam. 25 mm. and 100 mm.

St. 1230. 23. xii. 33. 6.7 miles north $62^{\circ} W$ of Dungeness Light, Strait of Magellan. Net: BNR 27 m. 6 specimens, diam. 40-125 m.

St. 1889. 23. xi. 36. $45^{\circ} 59' 48'' S$, $66^{\circ} 41' 42'' W$. Net: N 100 B 68-0 m. 1 specimen, diam. 110 mm.

St. WS 2. 13. ix. 26. $22^{\circ} 24' S$, $13^{\circ} 25' E$. Off Walvis Bay, South-West Africa. Net: N 100 H 62 m. 7 specimens, diam. 68-85 mm. and some fragments.

St. WS 95. 17. iv. 27. $48^{\circ} 58' 15'' S$, $64^{\circ} 45' W$. Net: OTC 109-108 m. 1 specimen, diam. 62 mm.

St. WS 106. 24. iv. 27. $48^{\circ} 25' S$, $65^{\circ} 00' W$. Net: N 70 H 0-5 m. 3 specimens, diam. 35-100 mm.

St. WS 749. 18. ix. 31. $52^{\circ} 39' 30'' S$, $69^{\circ} 53' 30'' W$. Net: NR 40(-0) m. 1 specimen, diam. 95 mm.

St. WS 770. 21. x. 31. $46^{\circ} 03' S$, $66^{\circ} 34' W$. Net: N 70 B 57-0 m. 1 specimen, diam. 70 mm.

St. WS 777. 3. xi. 31. $45^{\circ} 56' S$, $66^{\circ} 24' W$ to $45^{\circ} 58' S$, $66^{\circ} 27' W$. Net: OTC 98-99 m. 1 specimen, diam. 80 mm.

With the exception of St. 446 and St. WS 2, the localities are near the coast of southern Patagonia.

Measurements of 13 specimens gave the following results:

Diam. (mm.)	No. of radial canals	No. of tentacles
25	112	c. 35
52	106	c. 50
55	102	c. 45
74	50	c. 100
75	53	c. 106
77	52	?
80	45	c. 75-80
85	49	c. 100
95	c. 125	?
100	125	75
110	140	?
120	160	c. 90
125	112	?

The specimen, 25 mm. wide (St. 446), has an uncommonly large number of radial canals in proportion to its size. The variability is considerable, and it is remarkable that in some specimens the tentacles are much more numerous than the radial canals, whereas in other specimens the opposite is the case. In all the specimens the number of rudimentary bulbs is almost equal to the number of tentacles.

The size of the specimens according to the seasons is as follows:

Month	Sept.	Oct.	Nov.	Dec.	April
Diam. (mm.)	68-95	25-120	80-110	40-125	35-100

Thus, large as well as medium-sized specimens were found at any time within the period between November and April. It must, however, be remembered that the specimens preserved give no adequate impression of the stock actually present at the time. According to a note on the label of St. WS 2 '82 others of this species were thrown away'.

DISTRIBUTION. Owing to confusion with other species, the distribution of *A. aequorea* cannot be stated with certainty. It occurs in the Mediterranean, and it seems to be generally distributed in the coastal waters of the Atlantic Ocean, though apparently it is rare in the tropical belt. On the east coast of North America it occurs as far north as off New York, on the European coasts up to the southern parts of the west coast of Norway. There are two previous records from the west coast of Africa: Senegal (Ranson 1949, p. 128) and the Gulf of Guinea (Kramp 1955, p. 265). The present records from the southern coasts of Africa and South America are considerably farther south than any previously known. I am in doubt as to the correctness of the records from the Pacific coast of North America. On the other hand, I have recently seen some specimens taken in the Persian Gulf.

Aequorea macrodactyla (Brandt 1838)

- 1838 *Mesonema macrodactylum* Brandt, p. 359. Pl. 4.
 1904 *Aequorea maldivensis* Browne, p. 732. Pl. 56, figs. 4-12.
 1905 *Mesonema macrodactylum* Maas, p. 40. Pl. 8, figs. 51, 54.
 1909 *Aequorea macrodactylum* Bigelow, p. 174. Pl. 36, figs. 5-10.
 1910 *Aequorea macrodactyla* Mayer, p. 333.
 1911 *Mesonema coelum pensile* Vanhöffen, p. 230. Text-fig. 21, in part.
 1912a *Mesonema coelum pensile* Vanhöffen, p. 371.
 1938b *Aequorea macrodactyla* Thiel, p. 332. Text-fig. 9.
 1953 *Aequorea macrodactyla* Kramp, p. 294.
 1953 *Aequorea pensilis* Russell, p. 355. Pl. 33, figs. 1-5. Text-figs. 220c, d, 225.

- OCCURRENCE: St. 87. 25. vi. 26. $33^{\circ} 53' 45''$ S, $09^{\circ} 26' 30''$ E. Net: TYF 1000(-0) m. 3 specimens, diam. 10-12 mm.
 St. 89. 28. vi. 26. $34^{\circ} 05' 15''$ S, $16^{\circ} 00' 45''$ E. Net: TYF 1000(-0) m. 25 specimens, diam. 5-20 mm.
 St. 100. 1-4. x. 26. $33^{\circ} 20' S$, $15^{\circ} 18' E$ to $33^{\circ} 46' S$, $15^{\circ} 08' E$. Net: TYF 0-5 m. 15 specimens, diam. 7-42 mm.,
 and several fragments. TYF 475(-0) m. 7 specimens, diam. 6-20 mm. TYF 2500(-0) m. 1 specimen, diam. 12 mm.
 St. 256. 23. vi. 27. $35^{\circ} 14' S$, $06^{\circ} 49' E$. Net: TYF 850-1100(-0) m. 28 specimens, diam. 5-20 mm.
 St. 1370. 18. v. 34. $39^{\circ} 46' 36'' S$, $38^{\circ} 18' 24'' E$. South-east of Africa. Net: N 100 B 113-0 m. 29 specimens,
 diam. 4-21 mm.
 St. 1568. 11. iv. 35. $34^{\circ} 47' 36'' S$, $34^{\circ} 27' 54'' E$. South-east of Africa. Net: TYFB 1400-0 m. 11 specimens,
 diam. 8-29 mm.
 St. 1569. 12. iv. 35. $31^{\circ} 50' 18'' S$, $32^{\circ} 20' 30'' E$. South-east of Africa. Net: TYFB 1200-500 m. 7 specimens,
 diam. 7-20 mm.
 St. 1598. 23. x. 35. $07^{\circ} 10' 48'' S$, $03^{\circ} 31' 18'' W$. Gulf of Guinea. Net: TYFB 460-300 m. 3 specimens, diam.
 11-12 mm.
 St. 1600. 25. x. 35. $12^{\circ} 43' 18'' S$, $00^{\circ} 20' 12'' E$. Net: TYFB 400-330 m. 7 specimens, diam. 10-20 mm.
 St. 1762. 4. v. 36. $31^{\circ} 57' 18'' S$, $44^{\circ} 23' 12'' E$. South-east of Africa. Net: TYF 70 B 850-600 m. 1 specimen,
 diam. 12 mm.
 St. 2035. 7. iv. 37. $33^{\circ} 57' 12'' S$, $16^{\circ} 12' 12'' E$. Net: TYFB 950-750 m. 2 specimens, diam. 14-17 mm.
 St. 2050. 26. iv. 37. $20^{\circ} 26' S$, $02^{\circ} 16' W$. Net: N 450 B 430-0 m. 1 specimen, diam. 14 mm.
 St. WS 90. 7. iv. 27. $52^{\circ} 18' S$, $68^{\circ} 00' W$ to $52^{\circ} 19' 30'' S$, $67^{\circ} 57' W$. Net: N 7-T 82-81 m. 3 specimens, diam.
 27-40 mm.
 St. WS 106. 24. iv. 27. $48^{\circ} 25' S$, $65^{\circ} 00' W$. Net: N 70 H 0-5 m. 1 specimen, diam. 40 mm.
 St. WS 657. 24. vi. 31. $15^{\circ} 38' 18'' S$, $75^{\circ} 53' 24'' W$. On the coast of Peru. Net: N 100 B 67-0 m. 1 specimen,
 diam. 27 mm.
 St. WS 832. 1. ii. 32. $50^{\circ} 49' S$, $67^{\circ} 55' W$. Net: N 100 B 75-0 m. 6 specimens, diam. 22-52 mm.
 Stns 1370, 1568, 1569 and 1762 are south-east of Africa, all the other localities are off the west coast of Africa.
 St. WS 657 is on the Pacific coast of Peru, the other localities are off the southernmost part of the coast of Patagonia.

In all the specimens the tentacle bulbs have the broad base with an abaxial keel clasping the edge of the umbrella margin, which is characteristic of *A. macrodactyla* in contradistinction to *A. pensilis*, and numerically they correspond well with the specimens from the Great Barrier Reef previously examined by me. The specimen from the East Pacific, St. WS 657, has a comparatively small number of radial canals: 46 radial canals, 15 tentacles and about 30 young bulbs. The following table gives the dimensions of the specimens taken in the Atlantic and south-east of Africa. Those from South America are marked with an asterisk; these differ in no essential way from the specimens taken off the coasts of Africa.

Diam. (mm.)	No. of radial canals	No. of tentacles	No. of young bulbs
8	33	6	c. 30
10	32	8	c. 24
11	29	?	?
11	35	5	c. 40
11	46	10	c. 40
11	50	9	c. 40
12	34	?	?
12	42	7	c. 40
14	32	8	40
14	48	8	c. 50
17	43	c. 8	c. 40
*22	70	c. 15	60
*25	76	c. 15	c. 80
*27	84	15	c. 90
*29	84	17	c. 100
*31	88	12-15	c. 120
32	66	c. 14	c. 50
*40	105	c. 25	c. 110
*52	106	15	150-200

Size of the preserved specimens according to the seasons:

Month	Oct.	Feb.	April	May	June
Diam. (mm.)	6-42	22-52	7-40	4-21	5-20

DISTRIBUTION. Widely distributed in the warm parts of the Indian and Pacific Oceans from East Africa to America. Vanhöffen (1911) united several different species under the name *Mesonema coelum pensile*; the specimens recorded by him from near the coasts of South Africa, in the Benguela Current as well as in the Agulhas Current, probably belong to *Aequorea macrodactyla*, as far as can be seen from the accompanying measurements. At least, Vanhöffen's fig. 21 evidently represents a portion of the umbrella-margin of this species. It is likewise probable that the records from Port Natal and west of Ascension Island (Vanhöffen 1912a) apply to the same species. Moreover, *A. macrodactyla* is recorded from Walvis Bay on the West African coast by Thiel (1938b). It may also be met with on the southern parts of the British coasts (Russell 1953). The present records from the neighbourhood of South Africa are not very surprising, but it is interesting that the species was taken as far north as 7° south of the equator. It has not been previously recorded from the Atlantic coast of South America, where 'William Scoresby' found it between Port Deseado and the Strait of Magellan.

Aequorea coerulescens (Brandt 1838)

1838 *Mesonema coerulescens* Brandt, p. 360. Pl. 5.

1909 *Aequorea coerulescens* Bigelow, p. 177. Pl. 4, fig. 4; Pl. 35, figs. 3-8.

1938 *Aequorea coerulescens* Boone, p. 35. Pl. 5 and 6.

OCCURRENCE: St. WS 657. 24. vi. 31. 15° 38' 18" S, 75° 53' 24" W. Off the coast of Peru. Net: N 100 B 67-0 m. 2 specimens.

St. WS 828. 30. i. 32. 50° 51' S, 61° 42' W. Near the Falkland Islands. Net: N 100 B 128-0 m. 1 specimen.

This species is at once conspicuous by its numerous tentacles. One of the specimens from St. WS 657 is 80 mm. in diameter with 82 radial canals, with between 320 and 400 tentacles and numerous small bulbs; the other specimen from the same locality is about 70 mm. wide, but it is badly preserved, and canals and tentacles cannot be counted. The specimen from St. WS 828 is very large, about 145 mm. in diameter; it has 110 radial canals and about 500 tentacles, 3-7 between adjacent radial canals.

DISTRIBUTION. Originally described from the northern Pacific by Brandt. Recorded from two localities off Aguja Point in northern Peru (Bigelow 1909) and Valparaiso, Chile (Boone). Records from Vancouver (Agassiz 1865, p. 108) and from Unalaska Island and San Diego (Torrey 1909, p. 28) are doubtful. Also found in Mutsu Bay and near Shimoda, Japan (Uchida 1947b). The present record from Peru is inside the previously known area of distribution, but the find near the Falkland Islands is of considerable interest. The species has once before been found in the Atlantic, viz. off Luderitz Bay in South-West Africa (Ranson 1949, p. 128).

Aequorea spp. indetermin.

OCCURRENCE: Stns 87, 100, 268, 407, 709, 1374, 1573, 1575, 2053.

Most of these are young stages, as small as 3 mm. in diameter, but there are also some fragments of larger specimens.

Zygocanna vagans Bigelow 1912

1912 *Zygocanna vagans* Bigelow, p. 255.

1919 *Zygocanna vagans* Bigelow, p. 315. Pl. 42, figs. 5-7; Pl. 43, fig. 6.

1940 *Zygocanna vagans* Bigelow, p. 299. Fig. 14.

1905 *Aequoride* juv. Maas, p. 44. Pl. 4, figs. 22, 23.

OCCURRENCE: St. 405. 4. vi. 30. 33° 50' 30" S, 15° 46' E to 34° 16' S, 15° 02' E. West of Cape of Good Hope. Net: TYFB 1200-0 m. 1 specimen.

The specimen is well preserved, 45 mm. in diameter; the stomach is 28 mm. wide; 25 radial canals leave the periphery of the stomach and reach to the ring-canal. There are 30 tentacles situated at somewhat irregular distances from each other; between successive tentacles there are 3-7 rudiments, with long excretory papillae. The statocysts are very numerous. The radial rows of gelatinous papillae on the subumbrella are very conspicuous. The specimen thus agrees perfectly with the descriptions of *Z. vagans*.

DISTRIBUTION. Malayan Archipelago (Maas 1905); the Philippines (Bigelow 1912 and 1919); off Panama and Colombia (Bigelow 1940). Now also found near the Cape of Good Hope, South Africa.

LIMNOMEDUSAE

Family MOERISIIDAE

Tiaricodon coeruleus Browne 1902

1902 *Tiaricodon coeruleus* Browne, p. 276.

1912b *Tiaricodon caeruleus* Vanhöffen, p. 6. Pl. 1, fig. 2; Pl. 2, figs. 2-6.

1939 *Tiaricodon coeruleus* Browne & Kramp, p. 311. Pl. 18, figs. 1-6; Pl. 19, figs. 8-11.

1948b *Tiaricodon coeruleus* Kramp, p. 6.

OCCURRENCE: St. 53. 12. v. 26. Port Stanley, East Falkland Island. Net: RM 0-2 m. 3 specimens.

St. 55. 16. v. 26. Entrance to Port Stanley, East Falkland Island. Net: BTS 10-16 m. 4 specimens.

St. 57. 16. v. 26. Port William, East Falkland Island. Net: BTS 15 m. 4 specimens.

St. 58. 19. v. 26. Port Stanley, East Falkland Island. Net: N 70 H 5-0 m. 47 specimens.

The specimens vary between 3 and 12 mm. in diameter.

DISTRIBUTION. This pretty medusa has previously been found in considerable numbers at the Falkland Islands. Also recorded from a locality south of the South Orkney Islands (Kramp) and from the Strait of Magellan and on the Pacific coast of Peru, off Callao (Vanhöffen).

Family PROBOSCIDACTYLIDAE

Proboscidactyla mutabilis (Browne 1902)

1902 *Willia mutabilis* Browne, p. 280.

1912b ?*Willia mutabilis* Vanhöffen, p. 7. Text-fig. 2.

1938a *Willia mutabilis* Thiel, p. 302.

1939 *Willia mutabilis* Browne & Kramp, p. 302. Pl. 14, figs. 8-9; Pl. 17, figs. 10-12; Pl. 19, fig. 12.

OCCURRENCE: St. 58. 19. v. 26. Port Stanley, East Falkland Island. Net: N 70 H 5-0 m. 24 specimens.

St. WS 832. 1. ii. 32. 50° 49' S, 67° 55' W. Near the coast of southern Patagonia. Net: N 100 B 70-0 m. 1 specimen.

The structure, development and variation of this species was described by Browne & Kramp (1939).

The variation in twelve of the present specimens may be summarized as follows:

No. of specimens	Diam. (mm.)	No. of main radial canals			No. of tentacles + young bulbs	Average no. of tentacles
		6	7	8		
1	3	.	1	.	34	34
8	4	4	1	3	39-50	44
3	5	2	.	1	38-48	44
Total 12		6	2	4		

DISTRIBUTION. Falkland Islands (Browne); Punta Arenas in the Strait of Magellan (Vanhöffen); north-east of Puerto Madryn and on the Patagonian Bank (Thiel). A very peculiar record is recently given by Nair (1951, p. 57), who thinks he has found this species on the Trivandrum Coast in South-West India.

Family OLINDIIDAE

Aglauroopsis conanti Browne 1902

1902 *Aglauroopsis conantii* Browne, p. 283.

1939 *Aglauroopsis conantii* Browne & Kramp, p. 314. Pl. 18, figs. 7-16.

OCCURRENCE: St. 55. 16. v. 26. Entrance to Port Stanley, East Falkland Island. Net: BTS 10-16 m. 1 specimen.

St. 57. 16. v. 26. Port William, East Falkland Island. Net: BTS 15 m. 1 specimen.

St. WS 89. 7. iv. 27. 53° 01' S, 68° 07' W to 52° 59' 30" S, 68° 06' W. Net: N 7-T 23-21 m. 34 specimens. N 4-T 23-21 m. 1 specimen.

St. WS 809. 8. i. 32. 49° 29' S, 66° 27' W. Net: N 4-T 108-104 m. 4 specimens. NCS-T 108-104 m. 4 specimens.

St. WS 812. 10. i. 32. 51° 17' S, 68° 50' W. Net: N 7-T 53-55 m. 50 specimens.

St. WS 832. 1. ii. 32. 50° 49' S, 67° 55' W. Net: N 70 B 75-0 m. 11 specimens. N 100 B 75-0 m. 15 specimens.

St. WS 833. 1. ii. 32. 52° 28' S, 68° 00' W. Net: N 7-T 38-31 m. 4 specimens.

St. WS 847. 9. ii. 32. 50° 15' S, 67° 59' W. Net: NCS-T 51-57 m. 2 specimens.

The localities where this species was collected by 'William Scoresby' are near the coast around the eastern entrance to the Strait of Magellan. 'Discovery' only found it at the Falkland Islands. Most of the specimens of this beautiful and interesting medusa are in an excellent condition. The largest specimens previously observed were 22 mm. in diameter; some of the present specimens are 25 mm. wide. Their size according to the seasons are as follows:

Month	Jan.	Feb.	April	May
Diam. (mm.)	5-25	7-25	8-18	9-12
Specimens	58	32	35	2

The previous records were from November to February.

DISTRIBUTION. Up to now this species has only been observed at the Falkland Islands, where it was found in great abundance. As will be seen from the above records, it is also common in the region of the Strait of Magellan.

Gossea brachymera Bigelow 1909

(Pl. V, figs. 2, 3, text-fig. 8)

1909 *Gossea brachymera* Bigelow, p. 103. Pl. 30, figs. 1-10.

1939 *Gossea brachymera* Russell, p. 707. Pl. 1; text-figs. 1-3.

OCCURRENCE: St. WS 89. 7. iv. 27. 53° 01' S, 68° 07' W to 52° 59' 30" S, 68° 06' W. Net: N 7-T 23-21 m. 1 specimen. N 4-T 23-21 m. 1 specimen.

St. WS 833. 1. ii. 32. 52° 28' S, 68° 00' W. Net: N 7-T 38-31 m. 40 specimens.

Both localities are near the eastern entrance to the Strait of Magellan.

Bigelow described this species from a single small specimen, 5 mm. in diameter, taken in Acapulco Harbour on the Pacific coast of Mexico. A new description was given by Russell, who examined 17 specimens, 4.5-7.5 mm. wide, taken off Grand Island, Louisiana, in the Gulf of Mexico. From a zoogeographical point of view it is very interesting that this same species also occurs off the southernmost part of South America. The specimens collected by 'William Scoresby' are much larger than any seen before, being up to 20 mm. in diameter; they also have a much larger number of tentacles, but in all structural details they agree so well with the previous descriptions that there can be no doubt of their identity. The following remarks are mainly occasioned by the considerable size of the specimens. Some of them are in a very good state of preservation.

The two specimens from St. WS 89 are 14 mm. and 16 mm. wide; the numerous specimens from St. WS 833 vary between 11 mm. and 20 mm. in diameter. The general shape of the medusae agrees

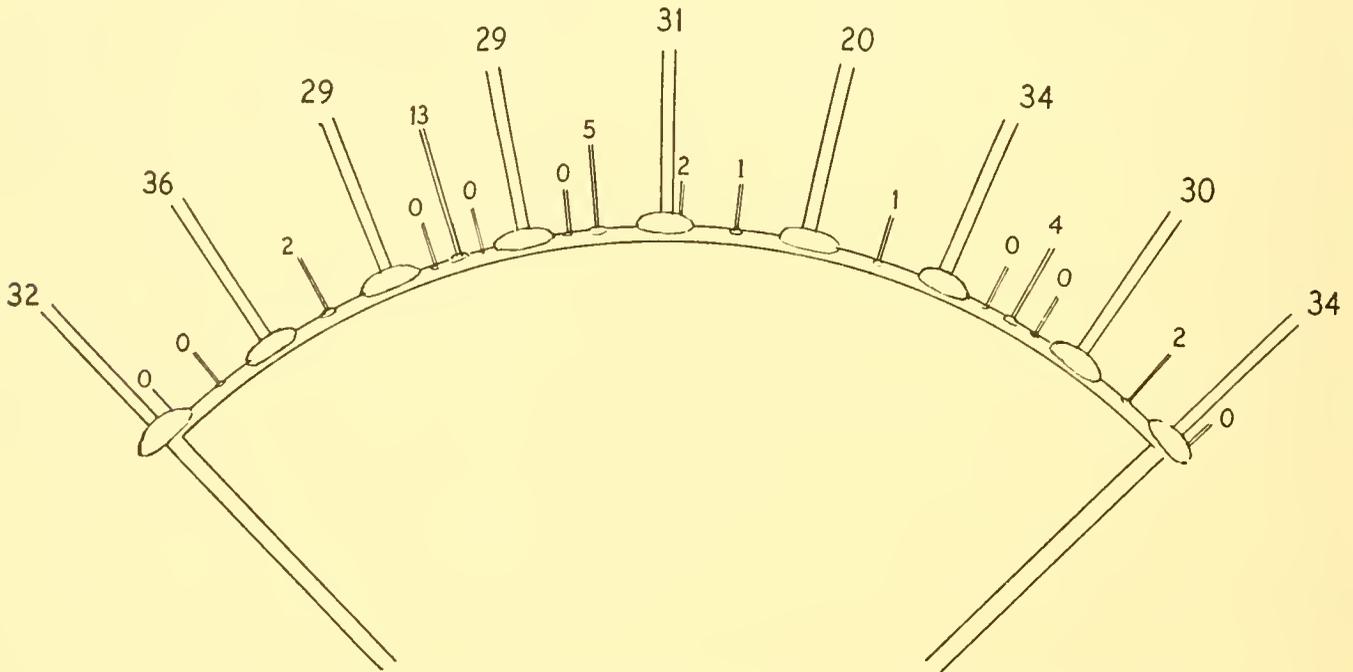
with Russell's figure, though the gelatinous substance of the umbrella is not quite as thick in the present specimens. The gastric peduncle and the nematocyst clusters on the mouth-rim are distinct. In the smaller specimens the gonads are as figured by Russell, being somewhat laterally compressed, wavy, and attached to the subumbrella along the greater part of the radial canals, from the base of the peduncle almost to the ring-canal; but in the larger specimens the gonads are considerably prolonged, terminating in a large, pendent sac, the length of which may be equal to the attached portion.

The structure and arrangement of the marginal tentacles need some additional remarks. Apparently there are two kinds of tentacles; Russell designates them as large tentacles and rudimentary or dwarf tentacles, the latter being regarded as 'true tentacles in an arrested state of development'. The margin of the umbrella is divided into a number of swellings of nematocyst tissue, one at the base of each tentacle, large and oval below the large tentacles, very small below the small tentacles. The relative number of large and small tentacles will be discussed below, sometimes they are almost regularly alternate. According to Russell the tentacles have 'a solid core of endoderm cells arranged in several rows'. The term 'solid tentacles', however, should be used only when the endoderm consists of one row of cells; when there are several rows it means that a central canal is present, though under certain circumstances it may be so tightly compressed that the cavity is obliterated. As a matter of fact, in this species the large tentacles are hollow, even with a distinct and sometimes rather spacious central cavity, especially in the proximal portions. In the smallest 'dwarf' tentacles the endoderm is uniserial in the distal part, multiserial in the proximal part, and during growth the multiserial endoderm extends farther outward towards the tip. Each large tentacle is provided with a terminal knob and several transverse bands of nematocysts encircling the tentacle in its distal part; for most of its length, however, the bands surround only part of the circumference, tapering in width towards the proximal end of the tentacle, the innermost side being destitute of nematocysts. The nematocyst clusters are on the abaxial side of the tentacle. In the largest tentacles the number of nematocyst clusters is frequently about 35, in exceptional cases as many as 40. The basal part of the tentacle is adnate to the exumbrella as described by Russell.

The 'dwarf' tentacles differ slightly from the descriptions by Bigelow and Russell. When quite young they are slender and pointed without indication of a terminal knob, but later on a tiny knob begins to appear, and as the length of the tentacle increases, a small cluster of nematocysts is developed abaxially a little inside the tip, then a second one, and so on. Already in the youngest stage these small tentacles have some nematocysts scattered throughout their length (small ones about 30μ in length), but as soon as the knob and the clusters make their first appearance, they contain nematocysts of a much larger type, about 60μ long. I have seen every transitional stage from tiny 'dwarf' tentacles with a pointed tip to fully developed tentacles with numerous bands of nematocysts.

The small specimen, 5 mm. wide, examined by Bigelow had 16 large tentacles and 8 minute dwarf tentacles, all of which were situated on the marginal swellings below the perradial and interradian tentacles, whereas no dwarf tentacles were attached to the 8 adradial tentacles. In the slightly larger specimens examined by Russell, the large tentacles were likewise 16 in number, each of the perradial and interradian ones flanked by a dwarf tentacle, but there were also 16 small tentacles, one in the middle of the space between every two large tentacles and each with a minute basal swelling of its own. This ideal arrangement may also be seen in larger specimens with a greater number of tentacles; there is always one dwarf tentacle situated on each of the perradial and interradian swellings, whereas all the other small tentacles are situated between the large ones. A regular alternation, however, is rarely seen, because by-and-by small tentacles develop into large tentacles, and the larger the specimen the more irregular is the succession and the relative number of large and small tentacles. When a small tentacle has obtained a certain number of nematocyst clusters, a new small tentacle appears

beside it, or sometimes one on each side of it. The accompanying diagram (text-fig. 8) shows an example of the arrangement of the tentacles in a quadrant of a specimen 14 mm. in diameter; the figures denote the number of nematocyst clusters in each tentacle. The dwarf tentacles on the perradial and interradial swellings are always to the left of the root of the corresponding large tentacle when seen from the exumbrellar side.



Text-fig. 8. *Gossea brachymera*. Diagram of one-quarter of the umbrella margin, showing the arrangement of large and small tentacles. The figures denote the number of nematocyst clusters in each tentacle.

The number of large and small tentacles in specimens of various sizes are shown in the following table:

	Diam. (mm.)	No. of large tentacles	No. of small tentacles	Total no. of tentacles	Ratio of no. of small and large tentacles
Bigelow 1909	5	16	8	24	0.5
Russell 1939	4½-7½	16	24	40	1.5
St. WS 833	11	44	32	76	0.73
	12	36	48	84	1.33
	13	40	?	?	?
	14	40	48	88	1.20
	15	44	44	88	1.00
	17	48	42	90	0.88
	17	52	36	88	0.69
	17	56	32	88	0.57
	17	56	34	90	0.61
	19	52	50	102	0.96
	20	48	40	88	0.83
	20	56	32	88	0.57
	20	60	40	100	0.66

It will be seen that the relative numbers of large and small tentacles are subject to considerable variation, whereas the total numbers are not very variable, being 88-102, average 91, in specimens of more than 13 or 14 mm. in diameter. Apparently, therefore, the final number is attained when the medusa is about 13 mm. wide. It will also be seen that in specimens 12-14 mm. wide there are more

small than large tentacles, whereas in all specimens above 17 mm. in diameter large tentacles are more numerous than small ones.

The statocysts are as described by Russell. They are internal vesicles inside the perradial and interradial marginal swellings immediately at the base of the dwarf tentacle. According to Russell the endodermal root of the dwarf tentacle divides into two; I have found it divided into three branches, one on each side and one in front of the vesicle (Pl. V, figs. 2-3). When seen from the exumbrellar side, these branches may appear as 1-3 small protuberances above the outline of the swelling; this is what Bigelow has seen and figured in Pl. 30, fig. 5.

Evidently the eight small tentacles situated on the perradial and interradial swellings never develop into large tentacles; even in the largest specimens they are very small, usually without nematocyst knobs, though sometimes with a small terminal knob, rarely also with a small cluster of nematocysts inside the terminal knob. Thus these eight small tentacles may really be designated as dwarf tentacles in an arrested stage, whereas all the other small tentacles may develop into large ones. Following Bigelow and Russell, therefore, one may regard each of the large perradial and interradial tentacles with its attendant dwarf tentacle as a 'group', which justifies the reference of this species to the genus *Gossea*.

DISTRIBUTION. Acapulco Harbour, Pacific coast of Mexico (Bigelow); coast of Louisiana, Gulf of Mexico, in brackish water (Russell); eastern entrance to the Strait of Magellan ('William Scoresby').

TRACHYMEDUSAE

Family PTYCHOGASTRIDAE

Ptychogastria polaris Allman 1878

- 1878 *Ptychogastria polaris* Allman, p. 290, 3 figs.
 1881 *Pectyllis arctica* Haeckel, p. 11. Pl. 3, 4.
 1903 *Ptychogastria polaris* Browne, p. 24. Pl. 4, figs. 1, 2; Pl. 5, figs. 6-8.
 1912a *Ptychogastria opposita* Vanhöffen, p. 386. Pl. 25, fig. 6. Text-fig. 20.
 1947 *Ptychogastria polaris* Kramp, p. 4. Pl. 1, figs. 1-4; Pl. 6, figs. 1-2.

OCCURRENCE: St. 177. 5. iii. 27. 63° 17' 30" S, 61° 17' W. Twenty-seven miles south-west of Deception Island, South Shetlands. Net: DLH 1080 m. 6 specimens.

St. 1958. 5. ii. 37. 61° 17' 54" S, 52° 50' 48" W. East of the South Shetland Islands. Net: DRR 830 m. 1 specimen.

Vanhöffen gave a beautiful coloured drawing of the antarctic form of *Ptychogastria* (*P. opposita*), of which six specimens were taken near the Gauss Station. He gave no real description, but only some remarks for comparison between the arctic and the antarctic forms, which he found very similar to each other, and he erected the new species *opposita* mainly on account of its great geographical separation. The Discovery specimens from St. 177 are 8-10 mm. in diameter and much contracted. All the tentacles are lost, but their grouping around the umbrella margin can be distinctly seen. The specimen from St. 1958 is fairly well preserved, though here also most of the tentacles are broken off. It is 12 mm. wide, only slightly contracted, so that the 16 meridional ridges on the exumbrella are faintly indicated. There are about 48 groups of tentacles; the male gonads are well-developed. The umbrella is more transparent than usually seen in this species, and the anatomical details of the medusa can therefore be distinctly observed. According to a note on the label the central part of this specimen was a rich crimson.

I have compared the specimens with specimens from the Arctic, and I cannot see any distinguishing features. I think therefore, that we may safely unite the two forms and designate *Ptychogastria polaris* as a bipolar species. The medusae were taken in dredges hauled along the bottom of the sea, and in the specimens from St. 177 numerous grains of dark sand are found in their subumbrellar cavities;

the specimen from St. 1958 is clean; it was taken in a 'rectangular dredge bag bent on to a Russell frame with skids to raise it clear of deep mud on the sea floor'. In arctic waters also this medusa is most frequently taken at the bottom, though occasionally it may be found swimming in the upper layers.

Another antarctic medusa, *Pectis antarctica* Haeckel, has been referred to this genus; it was found by the 'Challenger' Expedition south-south-east of Kerguelen Island at a depth of 1260 fathoms. Haeckel (1881, p. 15, Pls. 5 and 6, figs. 1-20) gave detailed descriptions and numerous figures of its morphology; but as the same applies to his description of '*Pectyllis arctica*' (= *Ptychogastris polaris*), and as Browne (1903) found 'serious errors' in the description of this latter species, we can regard his description of the former with some scepticism. If Haeckel's account of *P. antarctica* is correct, this species is entirely different from *P. polaris* (including *opposita*), but, unfortunately, the description can never be verified. I have seen the type specimen in the British Museum (Nat. Hist.), and the bottle only contains some tiny fragments, which give no idea of the original appearance of the medusa. As far as I could see, however, the numerous and closely packed tentacles were not arranged in groups as in *P. polaris*. The ring of tentacles seems to be homogenous, equally thick and dense everywhere on the fragments still available. I found no indication of 'höher inserierten einzelnen Saugnäpfen'; the tentacles are all broken near their base and, as already remarked by Browne (1903), the marks left on the exumbrella may well resemble sucking discs. I have previously discussed the relationships of the third Haeckelian species, *P. asteroides*, from the Adriatic Sea and the Straits of Gibraltar (Kramp 1947, p. 5); this seems to be a true *Ptychogastris*, though the tentacles are described by Haeckel as hollow.

DISTRIBUTION. In northern waters, *P. polaris* has a circumpolar distribution in arctic and subarctic areas (see the chart in Kramp 1947). In antarctic seas it has now been found in two widely separated areas: about 90° E and 53-61° W.

Family HALICREIDAE

The Discovery collection comprises four genera and five species of the family Halicreidae, namely: *Halicreas minimum* Fewkes; *Haliscera conica* Vanhöffen; *Haliscera racovitzae* Maas; *Botrynema brucei* Browne; *Halitrephes maasi* Bigelow. Most of these species are represented by numerous specimens, and now that I have been able to examine this extensive material I am more convinced than ever that my earlier conception of the delimitation of these species is correct (Kramp 1947.)

Systematic confusion has occurred mainly because Vanhöffen (1902b), in his 'Valdivia' Report, established five new species of *Halicreas* and *Haliscera*, only one of which, *Halicreas papillosum*, was properly described. This has subsequently been shown to be identical with *Halicreas minimum* Fewkes (1882). The other four species, *Halicreas glabrum* and *rotundatum*, *Haliscera alba* and *conica*, were beautifully figured by the artist of the 'Valdivia' Expedition, but the text gave only some scattered remarks on certain distinguishing features.

Later authors have been much in doubt as to the identities of these species of Vanhöffen's. The confusion was augmented by Thiel (1936) who united three of them, *Halicreas glabrum*, *rotundatum* and *papillosum*, in the single species *H. papillosum*, and combined Vanhöffen's two species, *Haliscera alba* and *conica* with Maas's (1906b) species *Haliscera racovitzae*. Thiel's distribution chart (1936, p. 36) is therefore unreliable.

I have been fortunate in having numerous specimens of Halicreidae to examine from the same areas whence Vanhöffen's species were derived, and I have never seen any resembling *Halicreas rotundatum* and *Haliscera alba*, both of these species being based on very scanty material. I therefore designate *Halicreas rotundatum* and *Haliscera alba* as obsolete species on the ground of inadequate description. Nor can we be sure that the figures in the 'Valdivia' Report are reliable. In the case of the lovely coloured drawing of *Halicreas glabrum*, at any rate, an entirely wrong impression of the

umbrella-margin is given. *Halicreas glabrum*, is probably identical with the species described by Browne (1908) as *Botrynema brucei*. The peculiar arrangement of the tentacles in sixteen groups entirely escaped the notice of the 'Valdivia' artist as well as of Vanhöffen himself.

Apart therefore from *Halicreas papillosum*, which specific name according to the rule of priority gives place to *Halicreas minimum* Fewkes (1882), of Vanhöffen's four remaining species only *Haliscera conica* can be retained as genuine. Vanhöffen recorded two specimens between South Africa and the Antarctic Continent. No proper description was given, but the few remarks in the text together with the two figures enable us to identify this species with certainty. The conical shape of the umbrella as shown in his Pl. 9, fig. 6, is very characteristic, and is retained and perfectly recognizable even in poorly preserved specimens. Moreover, in this case Vanhöffen has given an excellent figure of a section of the umbrella-margin and two of the radial canals with the gonads. I have seen numerous specimens in the Discovery material, as well as in other collections, which agree perfectly in every detail.

Haliscera racovitzae Maas is a distinct species and is represented in the present collection.

Halicreas minimum Fewkes 1882

(Text-fig. 18)

1882 *Halicreas minimum* Fewkes, p. 306.

1902b *Halicreas papillosum* Vanhöffen, p. 68. Pl. 9, figs. 7-8; Pl. 11, fig. 30.

1909 *Halicreas papillosum* Bigelow, p. 138. Pl. 3, fig. 3; Pl. 33, figs. 8, 9; Pl. 34, figs. 1-3, 5, 8, 10, 11.

1938 *Halicreas minimum* Bigelow, p. 122.

1947 *Halicreas minimum* Kramp, p. 7. Pl. 6, fig. 3.

OCCURRENCE: Stns 9, 71, 72, 76, 78, 81, 83, 85, 86, 87, 89, 100, 101, 102, 107, 114, 151, 239, 253, 256, 281, 282, 287, 304, 354, 391, 395, 401, 405, 407, 675, 677, 679, 687, 688, 690, 696, 699, 700, 1554, 1567, 1568, 1569, 1576, 1578, 1581, 1582, 1585, 1587, 1600, 1639, 1707, 1718, 1747, 1749, 1750, 1753, 1754, 1757, 1758, 1762, 1766, 1770, 1808, 1863, 1917, 1919, 1944, 1970, 1972, 1974, 1981, 1989, 1991, 1995, 1999, 2001, 2006, 2008, 2033, 2035, 2038, 2040, 2042, 2044, 2048, 2053, 2055, 2057, 2059, 2061, 2063, 2064, 2066. (For details of station positions, date, etc., see Table 1, p. 110, and text-fig. 18, p. 102.)

All the specimens were taken in hauls through intermediate or deep layers, with the exception of two young specimens, about 6 mm. wide, which were taken in a haul with the young-fish trawl, TYF, 300(-0) m. at St. 282.

Many of these numerous localities are within an area between the west coast of Africa and the east coast of South America, north of 40° S, from which the species was previously known, and the six stations off the east coast of Africa are not far from an area from which it was recorded by Browne (1916, p. 195). On the other hand, the long series of stations at about 32° S, from the south-east coast of Africa eastwards to 83° 36' E, traverses an area whence it has not previously been recorded. Moreover, with two exceptions, it was unknown south of 40° S, and 'Discovery II' has taken it in numerous localities across the Atlantic Ocean south of this latitude and in the area east of the Falkland Islands, around South Georgia and the South Sandwich Islands and farther southwards along the eastern border of the Weddell Sea as far as 66°-67° S (Stns 2001, 2006, 2008). The only previous records from these southern waters were given by Browne (1908, p. 237, 72° 02' S, 23° 40' W) and by Kramp (1948b, p. 7, two localities north-west of South Georgia). 'Discovery II' also found it much farther east in the antarctic region, between 92° 06' E and 129° 25' E, in latitudes between 58° 35' S and 64° 22.6' S (Stns 1639, 1707 and 1718). Thus the Discovery collections have increased the known area of distribution of this species very considerably.

DISTRIBUTION. *Halicreas minimum* seems to be generally distributed in the deep parts of all the oceans, except the Mediterranean and the arctic basins. It is common in the North Atlantic, but it does not cross the submarine ridges between Scotland, Iceland, Greenland and Baffin Land. From

this threshold it is generally distributed southwards into the antarctic region. In the Pacific it has probably a much more extensive distribution than is generally known; it is common in the tropical East Pacific, but it has not yet been taken off the west coast of North America, and there are only a few records from the western Pacific (Bering Sea, Sea of Okhotsk, Japan, North-East Australia). The previous records from the Indian Ocean were likewise few and scattered, until 'Discovery II' found it in numerous localities in the southern parts of this ocean.

Haliscera conica Vanhöffen 1902

(Text-fig. 17)

1902*b* *Haliscera conica* Vanhöffen, p. 72. Pl. 9, fig. 6; Pl. 11, fig. 33.

1910 *Halicreas conica* Mayer, p. 394. Fig. 248.

1912*a* *Haliscera conica* Vanhöffen, p. 381.

1936 *Halicreas album* Thiel, p. 37, in part.

1947 *Haliscera conica* Kramp, p. 6.

OCCURRENCE: Stns 100, 102, 137, 282, 302, 303, 322, 335, 337, 344, 354, 391, 568, 588, 696, 1056. WS 29, WS 30, WS 61, WS 160, WS 190.

Some poorly preserved specimens from Stns 100, 301 and 322 probably also belong to this species. (For details of station positions, date, etc., see Table 1, p. 110, and text-fig. 17, p. 101.)

Stns 100 and 102 are near the Cape of Good Hope, St. 282 is in the Gulf of Guinea, Stns 568 and 588 are west of Graham Land, Antarctic, and St. 696 is south-west of the Cape Verde Islands. The other localities are in the neighbourhood of South Georgia and between this island and the southern point of South America.

Besides the real *Haliscera conica*, Thiel (1936) included under the name of *Halicreas album*, *Haliscera racovitzae* Maas, which is a distinct species, and the doubtful species, *Haliscera alba* Vanhöffen. Most of the specimens collected by the 'Meteor' Expedition and listed by Thiel probably belong to *H. conica*, but some of them may have been *H. racovitzae*.¹

Some of the specimens in the Discovery collections are in a very good state of preservation, and by comparison it has been possible to identify almost all the other specimens. As mentioned on p. 47, the conical shape of the umbrella is very characteristic and resistant even in badly preserved specimens, and as a rule most of the tentacles and radial canals and gonads are retained which, in conjunction with the shape of the umbrella, is sufficient to put the identification beyond any doubt.

The specimens in the present collection vary in diameter between 3 and 16 mm. In adult specimens the height of the umbrella is about two-thirds the diameter; young specimens are only half as high as wide, and the gelatinous substance is thinner than in the adult. The gonads begin to appear when the diameter is 10–12 mm. In the adult the gonads are oval, situated a little nearer to the stomach than to the ring-canal. In a specimen 15 mm. wide the gonads are 2 mm. long, separated from the stomach by 2 mm., from the ring-canal by 2.5 mm. Female gonads contain 7–9 large eggs. The velum is broad, 3 mm. in a specimen 15 mm. wide. The marginal organs agree perfectly with Vanhöffen's Fig. 33. It is characteristic of this species, in contradistinction to *racovitzae* and *bigelowi*, that the thickening of the marginal nematocyst tissue at the base of each tentacle is very broad, forming a broad basal bulb. Vanhöffen's Fig. 33 shows 9 tentacles in the octant, in Fig. 6 there are 11, which may be an artistic exaggeration. In the present collection I have counted the tentacles as follows:

Diam. (mm.)	3	6	7	8	10	11	12	13	14	15
No. of tentacles	16	32	36	48	48	56–60	64	64–70	64–70	c. 72

¹ *Homoeonema alba* from the tropical East Pacific (Bigelow 1909, p. 142) probably belongs to the species which later on was described by me (Kramp 1947, p. 8) as a new species, *Haliscera bigelowi*; it occurs in the North Atlantic.

The number of marginal clubs is 16 in adult specimens, two in each octant, and they are arranged in a characteristic way, which is in accordance with Vanhöffen's figure. One of them is always placed near a radial canal separated from it by one tentacle, usually to the right when seen from the exumbrellar side, exceptionally to the left; the other marginal club is a little to the left of the middle point of the octant. Young specimens up to 7 mm. in diameter have only one marginal club in each octant, always the one developed nearest to a radial canal; the club near the middle of the octant appears later. In all stages of development the tentacles are of different sizes, but of the same structure; they may be about as long as the diameter of the umbrella, but as a rule all or most of them are broken off near their base.

The majority of the specimens were taken in hauls through the intermediate water-layers, mainly in hauls of 500–250 m. and 750–500 m., a few in 250–100 m., very few in vertical hauls from very great depths, and these may have been taken at higher levels during hauling because the nets failed to close.

DISTRIBUTION. Mediterranean (Kramp 1924, p. 29; Ranson 1936, p. 171); several localities between the Canary Islands and the Azores (Ranson 1936); off the west coast of Africa between Cape Verde and the Cape of Good Hope (the Discovery collections); South Atlantic between South Africa and South America (Thiel 1936); subantarctic and antarctic parts of the Atlantic area (Vanhöffen 1902*b*, Thiel 1936, Kramp 1948*b*, p. 6, and the present collection); west of Graham Land in the Pacific sector of the Antarctic (Discovery); also found in the Indian Ocean sector of the Antarctic, near the Gauss Station (Vanhöffen 1912*a*).

Haliscera racovitzae Maas 1906

1906*b* *Homoeonema (Haliscera) racovitzae* Maas, p. 10. Pl. 1, figs. 3, 4; Pl. 2, fig. 13.

1909 *Homoeonema racovitzae* Bigelow, p. 144.

1910 *Halicreas racovitzae* Mayer, p. 393. Fig. 246.

1931 *Halicreas racovitzae* Thiel, p. 328.

1936 ?*Halicreas album* Thiel, p. 37, in part.

1947 *Haliscera racovitzae* Kramp, p. 6.

OCCURRENCE: St. 355. 9. ii. 30. 54° 13' 30" S, 34° 18' 30" W to 54° 10' 30" S, 34° 16' 30" W. East of South Georgia. Net: N 70 V 750–500 m. 1 specimen.

The specimen, which is well preserved, is 7.5 mm. in diameter and 4 mm. in height. The exumbrella is evenly rounded, with no indication of a conical apex, the gelatinous substance being fairly thin and flaccid. Diameter of stomach 3.5 mm., mouth 2 mm. The gonads, male, are broadly egg-shaped, thick (not flat), in the proximal two-fifths of the radial canals close to the stomach. The distal part of the radial canals and the ring-canal are fairly narrow. In each octant there are 6 tentacles, of different sizes, with conical basal bulbs, and two marginal clubs, one separated by one tentacle from the adjacent radial canal to the right (when seen from the exumbrellar side), the other similarly separated from the radial canal to the left by two tentacles. Velum very broad.

This specimen is a perfect image of Maas's beautiful figures, except that it is almost colourless. The species differs distinctly from *H. conica* in the shape of the umbrella, the shape and position of the gonads, the number of tentacles, and their narrow conical bases. I have not the slightest doubt that it is a distinct species. It is not easy to comprehend how Thiel could identify it with *H. alba* Vanhöffen, which has elongated, flat gonads and a much larger number of tentacles. Two specimens from the tropical East Pacific, off Callao, Peru, were referred to *H. racovitzae* by Bigelow (1909) though with some doubt, and it also seems to me the safest course to regard this record as dubious.

Vanhöffen (1912*a*, Pl. 25, fig. 4. Text-fig. 17) has described and figured a medusa taken in the South Atlantic, at about 35° S, and he referred it to *Haliscera racovitzae*, but it cannot possibly belong to this species, nor can it with certainty be referred to any other known species. It was about 10 mm.

wide and had eight very large tentacles opposite to the radial canals and a considerable number of small tentacles in the spaces between the canals.

DISTRIBUTION. *Halicera racovitzae* seems to be a rare medusa; it has only been recorded with certainty from a few localities in the antarctic region: 70° 09' S, 82° 35' W (Maas), the Weddell Sea (Thiel 1931), and east of South Georgia (the present specimen).

Botrynema brucei Browne 1908

(Text-fig. 17)

- 1902b ?*Halicera glabrum* Vanhöffen, p. 70. Pl. 9, fig. 3.
 1908 *Botrynema brucei* Browne, p. 239. Pl. 1, figs. 8-9; Pl. 2, fig. 1.
 1912a *Botrynema brucei* Vanhöffen, p. 382. Pl. 25, fig. 5. Text-figs. 18-19.
 1913 *Botrynema ellinorae* Bigelow, p. 53. Pl. 6, figs. 1-4.
 1942 *Botrynema brucei* Kramp, p. 73.
 1947 *Botrynema brucei* Kramp, p. 11. Pl. 1, fig. 9; Pl. 2, fig. 3; Pl. 4, fig. 4.
 1948a *Botrynema brucei* Kramp, p. 6.
 1953 *Botrynema brucei* Russell, p. 459. Pl. 27, fig. 1. Text-figs. 303-304.
 1936 ?*Halicera papillosum* Thiel, p. 34, in part.

- OCCURRENCE: St. 89. 28. vi. 26. 34° 05' 15" S, 16° 00' 45" E. Net: TYF 1000(-0) m. 1 specimen.
 St. 100. 4. x. 26. 33° 20' S, 15° 18' E to 33° 46' S, 15° 08' E. Net: TYF 2500-2000 m. 1 specimen.
 St. 301. 20-21. i. 30. 52° 36' 30" S, 37° 14' W. Net: N 70 V 750-500 m. 1 specimen.
 St. 391. 18. iv. 30. 55° 48' 30" S, 52° 35' W. Net: N 450 H 1200-1300(-0) m. 1 specimen.
 St. 677. 27. iv. 31. 31° 16' 15" S, 29° 56' 30" W. Net: TYFV 1500-1000 m. 1 specimen.
 St. 1639. 2. xii. 35. 58° 35' S, 92° 06' 12" E. Net: TYFB 2400-1150 m. 1 specimen.
 St. 1702. 17. iii. 36. 64° 20' 06" S, 139° 54' E. Net: TYFB 2000-1250 m. 5 specimens.
 St. 1745. 21. iv. 36. 32° 03' 54" S, 88° 56' 54" E. Net: TYFB 1600-800 m. 1 specimen.
 St. 1750. 25. iv. 36. 32° 12' S, 75° 32' 36" E to 32° 13' 54" S, 75° 21' 30" E. Net: N 450 H 2000-1900 m. 1 specimen.
 St. 1753. 27. iv. 36. 32° 00' 24" S, 68° 50' 54" E. Net: TYFB 2900-1400 m. 1 specimen.
 St. 1825. 5. x. 36. 55° 42' 48" S, 14° 44' 06" W to 55° 44' 12" S, 14° 50' 54" W. Net: TYF 70 B 1150-600 m. 1 specimen.
 St. 1869. 11. xi. 36. 62° 37' 18" S, 48° 05' 12" W. Net: TYFB 1550-1000 m. 1 specimen.
 St. 1871. 12. xi. 36. 64° 04' 24" S, 52° 57' 30" W. Net: TYFB 1450-1000 m. 1 specimen.
 St. 1917. 3. xii. 36. 53° 48' 42" S, 46° 27' 42" W. Net: TYFB 1400-1000 m. 1 specimen.
 St. 1970. 18. ii. 37. 55° 03' S, 54° 04' 12" W. Net: TYFB 1800-1500 m. 1 specimen.
 St. 2033. 6. iv. 37. 33° 54' S, 12° 31' 12" E. Net: TYFB 1350-1250 m. 1 specimen.
 St. WS 38. 22. xii. 26. 54° 01' S, 35° 14' W. Net: N 70 V 1000-750 m. 1 specimen.
 St. WS 63. 20. i. 27. 54° 36' S, 39° 14' W. Net: N 70 V 1000-750 m. 1 specimen.
 St. WS 336. 30. xii. 28. 53° 06' S, 34° 44' W. Net: N 70 V 1000-760 m. 1 specimen.

Stns 89, 100 and 2033 are in the neighbourhood of the Cape of Good Hope; St. 677 is farther west in the Atlantic Ocean; Stns 1639 and 1702 are in the Indian Ocean sector of the Antarctic; Stns 1745, 1750 and 1753 are in the central part of the Indian Ocean, between South Africa and Australia. The other stations are in the Weddell Sea (text-fig. 17, p. 101).

Most of the specimens are about 30 mm. in diameter and 25 mm. in height; some of them, especially those collected by 'William Scoresby', are in very good condition, and even the badly preserved specimens may be identified with certainty by means of the shape of the umbrella with its distinct apical knob and the traces of tentacles which are always more or less retained showing the very characteristic arrangement in groups.

Though it seems to me very probable that *Halicera glabrum* Vanhöffen 1902 is identical with *Botrynema brucei* Browne 1908, I will not use the former name, because that species was not described in a recognizable way, and the figure gave a wrong impression of the appearance of the medusa.

DISTRIBUTION. *Botrynema brucei* is a widely distributed bathypelagic species. It has been found in several localities in the northern Atlantic, south of the submarine ridge between Scotland, Iceland, Greenland and Baffin Land (Kramp 1942, 1947 and 1948a Russell 1953). *H. glabrum* Vanhöffen was taken in seven localities off the west coast of Africa, from the Canary Islands to the Cape of Good Hope and in one locality in the central part of the Indian Ocean. The original specimen of *B. brucei* was found in the Weddell Sea (Browne 1908), and it was recorded under the same name from antarctic waters, north-west of the Gauss Station (Vanhöffen 1912a). In the Pacific it has only been found in the Bering Sea (Bigelow 1913). The localities where it was collected by 'Discovery', 'Discovery II' and 'William Scoresby' are within the same regions from which it was previously known, but they show that the species is much more common in the southern Atlantic and the Antarctic area than was previously known. Some of the specimens recorded as *Halicreas papillosum* by Thiel (1936) may have belonged to *B. brucei*.

Halitrepes maasi Bigelow 1909

(Text-fig. 19)

1909 *Halitrepes maasi* Bigelow, p. 146. Pl. 33, figs. 1-5, 7, 10; Pl. 45, fig. 13.

1912a *Halitrepes valdiviae* Vanhöffen, p. 384, in part.

OCCURRENCE: St. 89. 28. vi. 26. 34° 05' 15" S, 16° 00' 45" E. Net: TYF 1000(-0) m. 1 specimen.

St. 100. 4. x. 26. 33° 20' S, 15° 18' E to 33° 46' S, 15° 08' E. Net: TYFV 2500-2000 m. 1 specimen.

St. 256. 23. vi. 27. 35° 14' S, 06° 49' E. Net: TYF 850-1100(-0) m. 2 specimens.

St. 677. 27. iv. 31. 31° 16' 15" S, 29° 56' 30" W. Net: TYFV 2000-0 m. 1 specimen.

St. 893. 1-2. vi. 32. 49° 37' 30" S, 138° 35' 18" E. Net: N 100 B 260-100 m. 1 specimen.

St. 925. 1. vii. 32. 41° 20' 30" S, 167° 55' 30" E. Net: N 100 B 110-0 m. 2 specimens.

St. 963. 14. ix. 32. 52° 01' 06" S, 139° 13' 12" W. Net: N 100 B 320-128 m. 2 specimens.

St. 1586. 2. v. 35. 02° 39' 24" N, 50° 46' 24" E. Net: TYFB 1650-950 m. 1 specimen.

St. 1606. 31. x. 35. 26° 15' 48" S, 12° 18' E. Net: TYFB 190-0 m. 1 specimen.

St. 1758. 1. v. 36. 31° 55' 36" S, 55° 06' 30" E to 31° 55' S, 55° 05' 06" E. Net: N 450 B 1400-650 m. 2 specimens.

St. 2044. 23. iv. 37. 28° 38' S, 01° 11' 12" W. Net: N 450 B 550-750 m. 2 specimens.

St. 2050. 26. iv. 37. 20° 26' S, 02° 16' W. Net: N 450 B 430-0 m. 1 specimen.

St. 2059. 30. iv. 37. 09° 11' 24" S, 05° 17' 24" W. Net: N 450 B 1900-1400 m. 1 specimen.

St. WS 127. 10. vi. 27. 40° 19' S, 10° 06' W. Net: N 70 V 1000-650 m. 2 specimens.

Moreover, the following specimens may with some doubt be referred to the same species:

St. 401. 22. v. 30. 37° 31' 30" S, 04° 33' E to 37° 29' S, 04° 39' 30" E. Net: TYFH 1200-1300 m. 1 specimen.

St. 702. 17. x. 31. 10° 59' 18" N, 27° 03' 48" W. Net: TYFB 236-0 m. 1 specimen.

Most of the localities are in the Atlantic Ocean, off the southern part of the west coast of Africa. Stns 1586 and 1758 are off the east coast of Africa. St. 893 is south of Australia, St. 925 near New Zealand, St. 963 between New Zealand and South America (text-fig. 19, p. 103).

Almost all the specimens are in a bad state of preservation; the jelly is very soft, the stomach is usually lost, and as a rule only a few of the radial canals can be traced, but in most specimens it was possible to state the approximate number of tentacles.

I have counted the radial canals and tentacles as follows:

Diam. (mm.)	10	15	28	30	30	40	46	47	47	60
Approx. no. of radial canals	16	16	?	20	16	20	?	?	?	?
No. of tentacles	?	32	52	50	54	70	54	64	76	70

The specimen from St. 401 is 55 mm. in diameter and has about 115 tentacles; it is possible, therefore, that it belongs to another species.

The best preserved specimen was taken by 'William Scoresby' at St. WS 127. The margin is bent somewhat inwards, the diameter of the umbrella 40 mm., the stomach 14 mm.; in half the circumference

10 radial canals are retained, they are broad and flat, with female gonads 9 mm. in length, situated about equi-distant from the stomach and the ring-canal, and containing large eggs. There are about 70 tentacles of very different sizes. Some few statocysts are retained.

In a small specimen from St. 925, 10 mm. in diameter, the stomach is 2.5 mm. wide, the mouth opening 1.8 mm.; it has 16 radial canals, but the tentacles could not be counted. In another specimen, from St. 1606, 30 mm. in diameter, the stomach is 9 mm., the mouth opening 5 mm.; there are 16 radial canals and about 54 tentacles.

Bigelow (1909) found three specimens of this species in the tropical East Pacific, but only one of them was in a fairly good condition, 55 mm. wide with 33 radial canals and about 70 tentacles. Two other species have been described: *H. valdiviae* was described, but not figured, by Vanhöffen (1912*a*, p. 384), several specimens being taken in the tropical parts of the Atlantic and Indian Oceans. According to the author, the species is distinguished from *H. maasi* by the number of radial canals which do not exceed 16, in so far as it was possible to count them. As mentioned above, the specimens in the Discovery collection, up to 40 mm. in diameter, have 16–20 radial canals. The number of tentacles in *H. valdiviae* varies as follows:

Diam. (mm.)	9	12	18	20	21	33	34	42	44	70
No. of tentacles	32	32	64	32	32	64	76	96	80	204

Specimens less than 44 mm. wide thus vary approximately within the same limits as the Discovery specimens of corresponding size; I therefore believe that they belong to the same species, and that none of them differ so much from *H. maasi* that a specific separation seems reasonable. The largest specimen observed by Vanhöffen, 70 mm. wide, had 204 tentacles; this very large number may perhaps justify the erection of a separate species. Provisionally, therefore, I think we may retain the name *H. valdiviae* for this single specimen, whereas all the others undoubtedly belong to *H. maasi*.

My description of *H. medius* (Kramp 1948*b*, p. 7, fig. 1) was based on a specimen taken by the Swedish Antarctic Expedition 1901–3, north-west of South Georgia; it was about 100 mm. in diameter with 30 radial canals and about 280 tentacles. There is the possibility, of course, that *H. maasi*, during continued growth, may produce this very large number of tentacles, though such an enormous increase does not seem very probable. Until further evidence is available, it therefore seems to me that we should retain *H. medius* as a separate species.¹

DISTRIBUTION. Tropical and antitropical parts of the Atlantic, Indian and Pacific Oceans, mainly south of the equator, in the deep and intermediate layers.

Family RHOPALONEMATIDAE

Rhopalonema velatum Gegenbaur 1856

OCCURRENCE: Stns 68, 69, 89, 100, 102, 247, 250, 254, 256, 273, 282, 671, 672, 673, 674, 675, 676, 677, 678, 679, 680, 681, 682, 683, 685, 686, 687, 688, 689, 690, 691, 692, 698, 699, 702, 703, 704, 705, 707, 708, 709, 710, 712, 714, 718, 847, 963, 1370, 1371, 1372, 1373, 1374, 1375, 1568, 1571, 1573, 1574, 1575, 1576, 1581, 1585, 1586, 1587, 1749, 1770. (For details of station positions, date, etc., see Table 1, p. 110.)

All the localities are within areas from which the species was known before.

With very few exceptions the medusae were taken in hauls passing through the upper water-layers; the only exceptions are at Stns 847 (N 100 B 270–196 m.) and 1575 (TYFB 800–550 m.).

The following species are synonyms of *R. velatum*: *clavigerum*, *coeruleum* and *polydactylum*, all described by Haeckel 1879, and *R. striatum* Maas 1893. *Rhopalonema funerarium* Vanhöffen 1902*b* is a distinct species.

¹ Since the above was written, I have seen numerous specimens of *Halitrephes* collected by 'Dana', and I am now convinced that *H. maasi* is the only existing species of the genus.

DISTRIBUTION. *Rhopalonema velatum* is widely distributed and very common in the warm parts of all the oceans, including the Mediterranean. Its southern limit of distribution is approximately about 45° S in the Atlantic and Indian Oceans, and about 30° S in the Pacific. In the Atlantic it may occasionally penetrate as far north as off the west coast of Scotland, and it is recorded from the Gulf of Maine on the American coast. It belongs mainly to the upper layers, but may also be met with at considerable depths.

Rhopalonema funerarium Vanhöffen 1902

(Text-fig. 19)

1902b *Rhopalonema funerarium* Vanhöffen, p. 61. Pl. 9, fig. 2; Pl. 10, fig. 17; Pl. 11, fig. 31.

1910 *Rhopalonema coeruleum* Mayer, p. 380, in part.

1947 *Rhopalonema funerarium* Kramp, p. 14. Pl. 2, figs. 4-5.

1953 *Rhopalonema funerarium* Russell, p. 434. Text-figs. 285-6.

OCCURRENCE: St. 100. 2. x. 26. 33° 20' S, 15° 18' E to 33° 46' S, 15° 08' E. Net: TYF 475(-0) m. 3 specimens.

St. 276. 5. viii. 27. 05° 54' S, 11° 19' E. Net: TYF 150(-0) m. 1 specimen.

St. 281. 12. viii. 27. 00° 46' S, 05° 49' 15" E. Net: TYF 850-950(-0) m. 2 specimens.

St. 282. 12. viii. 27. 01° 11' S, 05° 38' E. Net: TYF 300(-0) m. 5 specimens.

St. 285. 16. viii. 27. 02° 43' 30" S, 00° 56' 30" W. Net: N 450 125-175(-0) m. 1 specimen.

St. 698. 13. v. 31. 12° 21' 45" N, 30° 07' 30" W. Net: TYFB 470-0 m. 2 specimens.

St. 700. 18. v. 31. 20° 21' 30" N, 22° 32' 30" W. Net: TYFB 2025-0 m. 1 specimen.

St. 1056. 4. xii. 32. 50° 18' S, 37° 04' 30" W. Net: N 100 B 340-150 m. 1 specimen.

St. 2044. 23. iv. 37. 28° 38' S, 01° 11' 12" W. Net: N 450 B 550-750 m. 2 specimens.

St. 2053. 27. iv. 37. 17° 45' 42" S, 02° 49' 48" W. Net: TYFB 900-550 m. 1 specimen.

St. 2059. 30. iv. 37. 09° 11' 24" S, 05° 17' 24" W. Net: N 750 B 1900-1400 m. 1 specimen.

St. 2061. 1. v. 37. 06° 36' S, 06° 25' 06" W. Net: N 450 B 1900-1500 m. 1 specimen.

St. 2064. 3. v. 37. 00° 46' 54" S, 10° 11' 30" W. Net: N 450 B 1600-1050 m. 1 specimen.

Most of the localities are off the west coast of Africa, between about 20° N and 34° S. St. 1056 is north of South Georgia. Some of the specimens are in fairly good condition. The specimens vary in diameter between 9 and 18 mm. Thiel (1936, p.10) takes it for granted that this species is identical with *R. velatum*, but as demonstrated by me in a previous paper (Kramp 1947, p. 14) it differs from that species in several regards.

DISTRIBUTION. This species is widely distributed in the deep layers of all the oceans, but it seems to be fairly rare. In the Pacific and Indian Oceans it has only been found in tropical waters, in the Atlantic it occurs as far north as west of Scotland and in the Gulf of Maine. It has frequently been recorded from the tropical Atlantic. The occurrence at St. 1056 is considerably farther south than has been known up to now (text-fig. 19, p. 103). It belongs to the deep and intermediate layers, but may occasionally be found at higher levels.

Pantachogon haeckeli Maas 1893

(Text-fig. 18)

1893 *Pantachogon haeckeli* Maas, p. 17. Pl. 1, fig. 2.

1902b *Pantachogon rubrum* Vanhöffen, p. 63. Pl. 9, fig. 9; Pl. 10, figs. 19, 20; Pl. 11, fig. 25.

1947 *Pantachogon haeckeli* Kramp, p. 19. Pl. 2, figs. 7, 8.

1953 *Pantachogon haeckeli* Russell, p. 440. Pl. 25, fig. 2. Text-figs. 290-2.

OCCURRENCE: Stns 9, 68, 71, 76, 78, 85, 86, 87, 89, 100, 101, 114, 117, 138, 151, 256, 298, 300, 301, 304, 305, 313, 320, 325, 335, 344, 358, 391, 395, 407, 661, 666, 668, 671, 673, 675, 677, 696, 699, 700, 769, 1298, 1568, 1569, 1586, 1587, 1606, 1633, 1639, 1707, 1728, 1743, 1745, 1750, 1751, 1753, 1755, 1758, 1761, 1762, 1765, 1784, 1825, 1876, 1917, 1919, 1972, 1989, 1991, 2048, 2063, 2064, 2065. WS 29, WS 36, WS 44, WS 67, WS 110, WS 190. (For details of station positions, date, etc., see Table 1, p. 110, and text-fig. 18, p. 102.)

Many of the localities are in the waters west and east of Africa, from the Cape Verde Islands round the Cape of Good Hope to Somaliland, and in a line along about 32° S from South Africa almost to Australia, within which regions the species was previously known to be of common occurrence. It is also present in numerous localities in the South-West Atlantic, from which region there was only one previous record. A few specimens were taken north and north-west of South Georgia by the Swedish Antarctic Expedition (Kramp 1948*b*, p. 9), but the present collection shows that it is generally distributed and very common in this area. It was taken in numerous hauls round South Georgia and also over the whole area between 30° and 60° W. The southernmost locality was in the Weddell Sea at St. 1876 ($58^{\circ} 37.7' S$, $54^{\circ} 54.4' W$). It also occurred in several localities along 30° W between latitudes 55° S and 30° S.

Of particular interest are the following localities: Stns 114, 117 and 1784 in the neighbourhood of Bouvet Island, St. 1633 south-east of Heard Island, St. 1728 at $53^{\circ} 14.9' S$, $107^{\circ} 02' E$, St. 1707 at $63^{\circ} 36.9' S$, $129^{\circ} 24.7' E$ near the Antarctic Continent, and St. 1298 in the Pacific section of the Antarctic, about 69° S, 126° W. This is the first time this species has been recorded from the South Pacific, and the only reliable previous records from the Indian Ocean sector of the Antarctic ocean are those of Vanhöffen (1902*b*) of *P. rubrum* from between $55^{\circ} 27' S$, $28^{\circ} 59' E$ and $64^{\circ} 14' S$, $53^{\circ} 30' E$. The map given by Thiel (1936, p. 26) is unreliable, because this author has united several different species under the name *P. rubrum*.

DISTRIBUTION. *P. haeckeli* occurs in the deep and intermediate layers, and it is probably generally distributed in the deeper regions of all the oceans, except the arctic basins and the Mediterranean. It is common in the North Atlantic as far as the Wyville Thompson Ridge, and west of Greenland it may occasionally traverse the submarine ridge and penetrate into Baffin Bay. In the North Pacific it is common from Japan to the Bering Sea and off the northern part of the west coast of America between Alaska and Puget Sound, but it has not yet been recorded from the East Pacific farther south.

Colobonema sericeum Vanhöffen 1902

(Text-fig. 19)

1902*b* *Colobonema sericeum* Vanhöffen, p. 57. Pl. 9, fig. 1; Pl. 12, figs. 39-42.

1905 *Colobonema typicum* Maas, p. 53. Pl. 10, figs. 62-5.

1910 *Homoeonema typicum* Mayer, p. 385, in part.

1912*a* *Colobonema sericeum* Vanhöffen, p. 372.

1936 *Colobonema sericeum* Ranson, p. 152. Pl. 2, figs. 14-15.

1953 *Colobonema sericeum* Russell, p. 436. Pl. 25, fig. 1. Text-figs. 287-289.

OCCURRENCE: 2. xi. 25. $6^{\circ} 55' N$, $15^{\circ} 54' W$. 28. x. 25, $13^{\circ} 25' N$, $18^{\circ} 22' W$. Stns 78, 81, 85, 86, 87, 89, 100, 101, 248, 256, 281, 296, 405, 407, 440, 677, 690, 700, 1569, 1575, 1600, 1602, 1604, 1741, 1743, 1747, 1750, 1751, 1753, 1754, 1755, 1757, 1758, 1759, 1762, 1765, 1766, 2031, 2033, 2035, 2036, 2044, 2047, 2057, 2059, 2061, 2063, 2064. (For details of station positions, date, etc., see Table 1, p. 110, and text-fig. 19, p. 103.)

In the Atlantic Ocean, this species was taken in numerous localities off the west coast of Africa, between Cape Verde and the Cape of Good Hope, and farther west towards South America, the southernmost locality was at St. 78, in $35^{\circ} 18' S$, $19^{\circ} 01' W$. It was also taken at most of the stations along latitude about 32° S, from South Africa almost to Australia, and in one locality (St. 1575) in the Mozambique Channel. The species was previously known from about the same regions, with the exception that Stns 677 and 690, about 30° W, are somewhat farther west than any other previous records from the southern Atlantic.

Colobonema sericeum is a bathypelagic medusa, and the majority of the present collections were made in the deep layers; but there are some few exceptions, of which the most remarkable are

Stns 1600 (470-0 m.) and 1602 (175-0 m.), both off the coast of Angola, where an upwelling of cold water from the deep layers takes place. This will be further discussed in the General Section.

DISTRIBUTION. Widely distributed in the deep parts of the great oceans. In the eastern part of the North Atlantic it occurs as far north as off the south and west coasts of Iceland, in the western part off the Newfoundland Bank. It has never been found in the Mediterranean, but it seems to be generally distributed in the Atlantic basin as far south as a little beyond the latitude of the Cape of Good Hope. 'Discovery' found it in 35° S, and by 'Valdivia' it was taken in one locality in 42° S, 14° E, south-west of South Africa. It is also generally distributed in the Indian Ocean north of about 35° S. In the Pacific it has only been recorded from Japan and from the tropical eastern region. In contradistinction to most other bathypelagic medusae, this species does not approach the shelf of the Antarctic Continent; it seems to have a fairly distinct southern limit of distribution in about 35° or 40° S.

Sminthea eurygaster Gegenbaur 1856

1856 *Sminthea eurygaster* Gegenbaur, p. 245. Pl. 9, figs. 14-15.

1879 *Trachynema eurygaster* Haeckel, p. 260.

1879 *Marmanema mammaeforme* Haeckel, p. 262.

1910 *Sminthea eurygaster* Mayer, p. 383. Text-figs. 226-7.

OCCURRENCE: St. 256. 23. vi. 27. 35° 14' S, 06° 49' E. West of Cape of Good Hope. Net: TYF 850-1100(-0) m. 2 specimens.

St. 282. 12. viii. 27. 01° 11' S, 05° 38' E. Gulf of Guinea. Net: TYF 300(-0) m. 1 specimen.

One of the specimens from St. 256 is in a good condition, 6 mm. wide, with well-preserved gonads close to the ring-canal. The specimen from St. 282 is somewhat shrunk, but in this specimen also the gonads are well preserved.

DISTRIBUTION. Mediterranean; Bay of Biscay; near the Azores; Canary Islands; off the north coast of Brazil; in the surroundings of the Amirante and Chagos Islands in the Indian Ocean. Now found in two localities off the west coast of Africa.

Genus *Arctapodema* Dall.

The first two species of this genus were described by Vanhöffen (1902*b*, pp. 65 and 66) as *Homoeonema amplum* and *macrogaster*. Maas (1906*b*, p. 5) gave a new description and numerous figures of *H. amplum* and made it the type of a new genus, *Isonema*. This name being preoccupied, Dall (1907, p. 661) replaced it by *Arctapodema*. Mayer (1910, p. 387), however, retained the name *Homoeonema* (the great confusion concerning this name is discussed in Kramp 1947, pp. 14 *et seq.*).

In 1912*a* Vanhöffen added three new species to the genus: *Isonema antarcticum*, *australe* and *tetragonium*. Ranson (1936, pp. 156 *et seq.*) accepted the generic name *Arctapodema* and provisionally retained all of the five species, whereas Thiel (1936, p. 26) united them all, together with *Pantachogon scotti* Browne, with *Homoeonema platygonon* (*sensu* Browne). A new species, *Isonema najadis*, was described by Pell (1938, p. 926); it is undoubtedly identical with *Arctapodema album*.

With the exception of *A. album*, none of the species have been observed since they were described by Vanhöffen, but three species are represented in the Discovery collection: *amplum*, *antarcticum* and *australe*, and I am able to state that they are distinct species. I am inclined to think that *A. tetragonium* is identical with *amplum* (*sec* below). Vanhöffen's (1902*b*) description of *A. macrogaster* was based on one badly preserved specimen (reconstructed in Pl. 10, fig. 22); it may possibly be identical with *A. australe*, but an identification of these two species is still uncertain.

With a slight alteration of the definition of '*Isonema*' as given by Maas, *Arctapodema* may be characterized as follows: Rhopalonematidae without a gastric peduncle; with urn-shaped stomach;

with gonads adjacent to the stomach; with eight narrow radial canals; with numerous tentacles, all alike, in a single row; with club-shaped marginal statocysts.

As a matter of fact, the position of the gonads is variable. In *A. australe* they are sac-shaped, situated in the proximal parts of the radial canals but distinctly separated from the stomach. In *A. antarcticum* they are restricted to the walls of the upper part of the stomach, whereas no gonads are found on the radial canals. If we knew only these two species, we should probably regard them as belonging to two different genera, but as demonstrated below, *A. amplum* and *tetragonium* may be regarded as transitional forms.

In *Arctapodema* the gonads are radially separated; in *Homoeonema*, which contains only one species, *platygonon* Browne, the gonads form a continuous band around the base of the stomach, extending outwards along the radial canals (see Kramp 1947, p. 17). There is good reason, therefore, to keep these two genera apart.

Arctapodema antarcticum (Vanhöffen 1912)

(Text-fig. 9)

1912a *Isonema antarcticum* Vanhöffen, p. 375. Text-figs. 8-9.

1936 *Arctapodema antarcticum* Ranson, p. 157.

OCCURRENCE: St. 1718. 25. iii. 36. 64° 22' 36" S, 106° 33' 18" E. Off Knox Land, Antarctica. Net: TYFB 900-550 m. 1 specimen.

St. 1749. 24. iv. 36. 32° 04' 06" S, 77° 59' 36" E. Between South Africa and Australia. Net: TYFB 1050-600 m. 1 specimen.

St. 1838. 12. x. 36. 57° 10' 12" S, 30° 42' 30" W. East of the South Sandwich Islands. Net: TYF 70 B 750-250 m. 3 specimens.

St. 1917. 3. xii. 36. 53° 48' 42" S, 46° 27' 42" W. Near Shag Rocks. Net: TYFB 1400-1000 m. 1 specimen.

St. 1919. 4. xii. 36. 54° 02' 54" S, 42° 10' 48" W. West of Shag Rocks. Net: TYFB 1800-1300 m. 1 specimen.

The specimens have the following diameters: St. 1718: 15 mm.; St. 1749: about 13 mm.; St. 1838: 14, 14 and 16 mm.; St. 1917: 11 mm.; St. 1919: 16 mm. The tentacles could only be counted in two of the specimens (Stns 1718 and 1838), both had about 112 tentacles. The manubrium is cylindrical, and the gonads occupy the proximal one-third to one-half of the stomach; they are not ring-shaped as stated by Vanhöffen, they are interrupted in the four perradial corners of the stomach, so that there are four interradian gonads; this applies to female as well as male gonads. In all other regards the specimens agree perfectly with Vanhöffen's description and figure.

DISTRIBUTION. Up to now this species has been known only from the neighbourhood of the Gauss Station, in about 90° E near the Antarctic Continent. It is now seen to have a far more extensive distribution in antarctic waters, and it has also been found in latitude 32° S in the Indian Ocean, about mid-way between South Africa and South Australia (see chart, text-fig. 9). It belongs to the deep water-layers.

Arctapodema amplum (Vanhöffen 1902)

(Pl. V, fig. 4, text-fig. 9)

1902b *Homoeonema amplum* Vanhöffen, p. 65. Pl. 10, fig. 21; Pl. 11, figs. 24, 26, 27.

1906b *Isonema amplum* Maas, p. 5. Pl. 1, figs. 1, 2, 7; Pl. 2, figs. 8-12; Pl. 3, figs. 14-20.

1907 *Arctapodema amplum* Dall, p. 661.

1910 *Homoeonema amplum* Mayer, p. 387. Figs. 236-7.

1912a *Isonema amplum* Vanhöffen, p. 374. Text-figs. 4-7.

1913 *Pantachogon amplum* Bigelow, p. 44.

1936 *Homoeonema platygonon* Thiel, p. 26, in part.

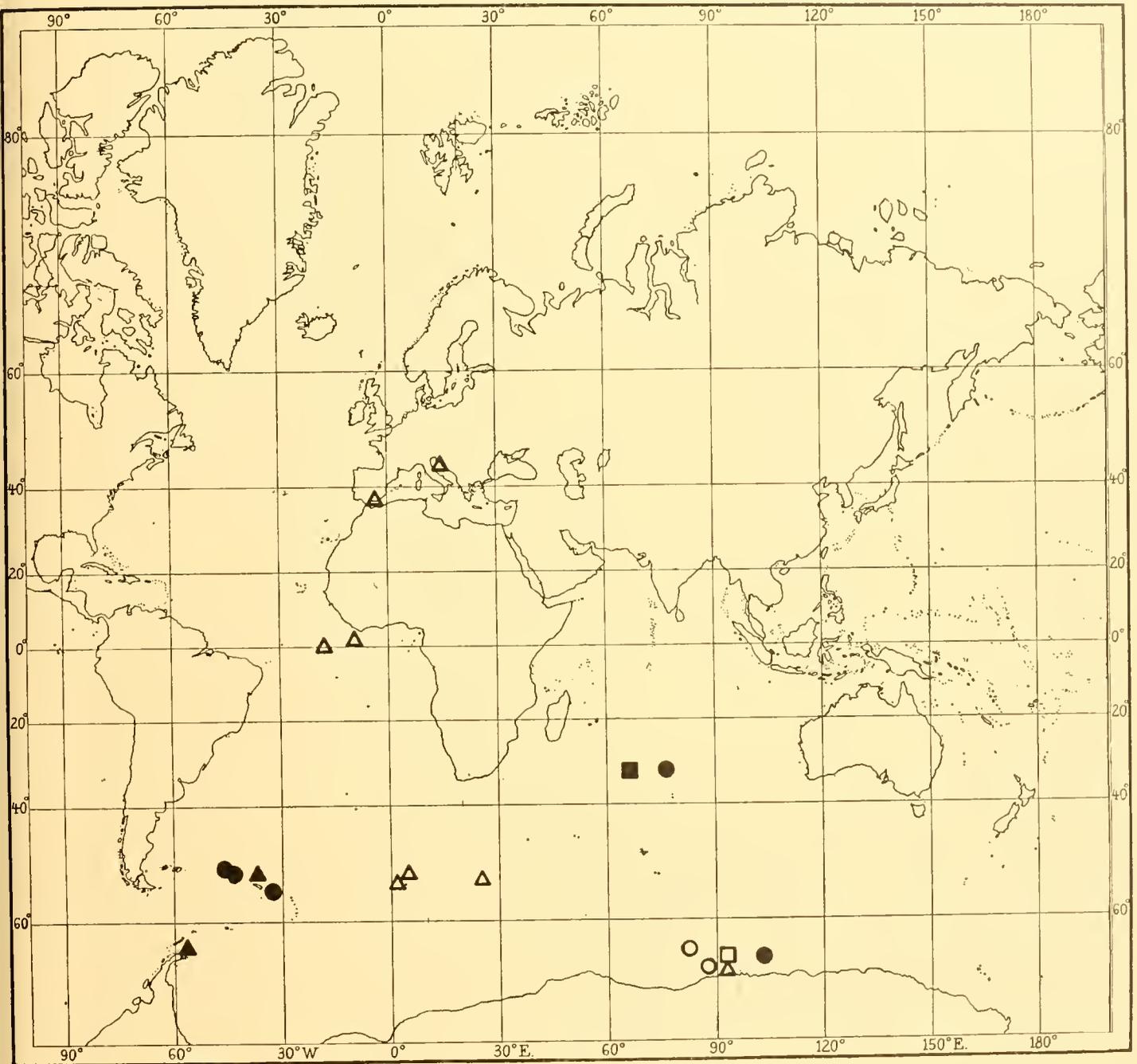
1936 *Arctapodema amplum* Ranson, p. 158. Pl. 2, fig. 17.

1938 *Arctapodema najadis* Pell, p. 926.

1955 *Arctapodema amplum* Kramp, p. 273.

OCCURRENCE: St. WS 160. 27. ii. 28. $53^{\circ} 00' S$, $36^{\circ} 52' W$. North of South Georgia. Net: N 70 V 500-250 m. 2 specimens.

St. WS 388. 16. ii. 29. $62^{\circ} 55' 30'' S$, $57^{\circ} 40' W$. Near the north point of Graham Land. Net: N 70 V 400-250 m. 1 specimen (for distribution see chart, text-fig. 9).



Text-fig. 9. Distribution of: *Arctapodema antarcticum* = ●, previous records = ○.
A. amplum = ▲, previous records = △. *A. australe* = ■, previous records = □.

The specimen from St. 388 is only 4 mm. in diameter. The two specimens from St. 160 are 6 mm. wide, with about 96 tentacles. Their gonads present some features of considerable interest.

The gonads of *A. amplum* have been described and figured in different ways, and evidently their structure is variable. In the first specimen described by Vanhöffen (1902b) the stomach was very small, its base surrounded by eight almost globular gonads. According to Maas (1906b), who

examined several specimens, the young gonads first appear as eight small evaginations on the radial canals close to the stomach; later they are more or less completely divided into two lateral sacs. Their further development may proceed more or less irregularly, and the limits between the gonads and the eight radial diverticula of the upper portion of the stomach may be indistinct. In the largest specimen, 6.5 mm. wide, examined by Vanhöffen (1912*a*) the gonads are divided into two parts, 'von denen die obere der Wurzel der Radialkanäle anliegt, während die untere Partie mit zwei Aussackungen auf dem oberen achtfach gefalteten Teil des Magens ruht'. The accompanying text-figures show that the gonads of Vanhöffen's specimen were at an immature stage. According to Ranson (1936), who examined two specimens from the Mediterranean 7-8 mm. in diameter, the structure and position of the gonads are difficult to state precisely. In his specimens the gonads, issuing from the radial canals close to the stomach, have attained a considerable size; they may touch each other interradially and even fuse together.

In one of the present specimens (St. WS 160, 6 mm. in diameter) the manubrium is short and broad. Gonads (Pl. V, fig. 4) containing numerous large eggs are developed as eleven radial lobes from the upper surface of the stomach, very unequal in size and irregularly distributed, and, moreover, small additional sac-shaped gonads issue from the radial canals at a short distance from the stomach, usually in pairs. No additional gonads are developed on the radial canal above the largest of the gonadial lobes issuing from the stomach.

In the other specimen from the same locality, also 6 mm. wide, the structure is very similar, but the gonads are less developed. The specimen from St. WS 388 is young, 4 mm. wide; the stomach is short, its basal part has 16 radial folds, from which the gonads issue as irregular radial lobes; there are no additional gonads on the radial canals.

The paired, sac-shaped gonads on the proximal part of the radial canals in the specimens from St. WS 160 correspond to those described and figured by Maas in *A. amplum*; the gonadial lobes issuing from the basal wall of the stomach resemble the gonads of *A. tetragonium* (Vanhöffen 1912*a*, p. 377. Text-figs. 12-15). This medusa, which was up to 12.5 mm. wide, had four gonads, kidney-shaped, in the walls of the stomach adjacent to the subumbrella; in other respects the species was similar to *A. amplum*. Considering the irregularities observed in *A. amplum*, it seems very probable to me that *A. tetragonium* is only an aberrant form of *A. amplum*; it was found in the Atlantic Ocean near the equator within the area of distribution of *A. amplum*.

Since gonads may be developed in the stomach wall as well as on the radial canals in *A. amplum*, this species forms a connecting link between *A. antarcticum*, in which the gonads are restricted to the stomach walls, and *A. australe* in which the gonads are situated on the proximal parts of the radial canals. These three species may therefore be regarded as belonging to one genus, *Arctapodema*, in spite of the considerable difference between the two extremes.

DISTRIBUTION. *A. amplum* occurs in the intermediate and deep layers of the Atlantic and Indian sectors of the Antarctic Ocean; in the tropical Atlantic; and in the Mediterranean.

Arctapodema australe (Vanhöffen 1912)

(Pl. V, figs. 5, 6, text-fig. 9)

1912*a* *Isonema australe* Vanhöffen, p. 376. Text-figs. 10-11.

1936 *Arctapodema australe* Ranson, p. 157.

OCCURRENCE: St. 1753. 27. iv. 36. 32° 00' 24" S, 68° 50' 54" E. Between South Africa and Australia. Net: TYFB 2900-1400 m. 1 specimen (for distribution, see chart, text-fig. 9, p. 57).

This species was well described and figured by Vanhöffen. His only specimen was 23 mm. wide and 14 mm. high, with about 112 tentacles. The present specimen is only 7.5 mm. wide and 5 mm. high,

with about 96 tentacles; the jelly is soft and fairly thick; the stomach is short and broad, of a deep violet colour, its upper part with 16 radial folds; it is turned inside out (Pl. V, fig. 5). The eight gonads are almost globular, reddish-brown, of somewhat unequal size, somewhat pendent (Pl. V, fig. 6), but not elongated as in Vanhöffen's much larger specimen; they are placed near the base of the stomach, but distinctly separated from it. Vanhöffen describes the inner surface of the stomach as seen when the mouth is widely open; four ridges run from the four lips of the mouth, and between them are seen short, triangular valves and farther inwards some other similar structures. In the present specimen the stomach is still more widely open, so that the lips cannot be seen from below. The internal surface of the stomach shows eight broad swellings separated by deep, narrow furrows, each of the swellings with a median, flat, longitudinal ridge continued in a pointed, tenon-like prolongation towards the centre of the stomach cavity; these prolongations may correspond to the 'Blättchen' described by Vanhöffen. The swellings and radial folds of the stomach are not gonads; these are only developed on the radial canals. Apart from the minor details in the structure of the stomach wall, this specimen agrees so well with the description of *A. australe* that I do not hesitate to refer it to that species.

DISTRIBUTION. Previously known only from the Gauss Station near the Antarctic Continent, in about 90° E; now also found farther north in the Indian Ocean, about midway between South Africa and South Australia, in the deep and intermediate layers.

Amphogona apicata sp.n.

(Pl. V, fig. 7)

OCCURRENCE: St. 89. 28. vi. 26. 34° 05' 15" S, 16° 00' 45" E. West of Cape of Good Hope. Net: TYF 1000(-0) m. 1 specimen.

St. 102. 28. x. 26. 35° 29' 20" S, 18° 33' 40" E. West of Cape of Good Hope. Net: N 70 V 750-500 m. 2 specimens.

St. 1575. 24. iv. 35. 18° 33' 12" S, 41° 35' 24" E. Mozambique Channel. Net: TYFB 800-550 m. 2 specimens.

St. WS 22. 30. xi. 26. 53° 38' S, 35° 35' W. North of South Georgia. Net: N 70 V 1000-750 m. 2 specimens.

St. WS 70. 23. ii. 27. 51° 58' S, 55° 42' W. East of Falkland Islands. Net: N 70 V 1000-750 m. 2 specimens.

One of the specimens from St. 102, 4.5 mm. in diameter, is chosen as the *holotype*.

DESCRIPTION. Umbrella dome-shaped, as high as wide or slightly higher, diameter up to 7 mm., height up to 8 mm., with a distinct, bluntly conical, gelatinous apical projection, lateral walls thin. Velum broad. The stomach is mounted on a small gelatinous peduncle as long as one-sixth of the height of the bell cavity. Manubrium tubular, length up to one-third of the height of the bell cavity; in the contracted state it may be urn-shaped, almost concealing the peduncle. Mouth with four short, simple lips. Eight narrow radial canals. Gonads sac-shaped, pendent, on the radial canals, in or a little above the middle point of the canals; the gonads are usually of somewhat different size, but large and small gonads are not always regularly alternate. In each of the specimens examined, the gonads are of one sex. Ring-canal narrow. About 64 tentacles. Statocysts? Specimen colourless when preserved in formalin.

Remarks on specimens of different sizes :

Diam. 3 mm., height 4 mm. (St. 102). Only four gonads are developed, and they are not placed crosswise. About 5 tentacles per octant.

Diam. and height 3.5 mm. (St. WS 22). Eight gonads like small dots, a little above the middle of the canals. About 4 tentacles per octant.

Diam. and height 4 mm. (St. WS 22). Gonads in the middle of the canals, all with large eggs. The stomach is strongly contracted, short and broad, concealing the peduncle which is only seen as a small conical prolongation from the apical jelly into the cavity of the stomach. About 4 tentacles per octant. The specimen is well preserved.

Diam. and height 4 mm. (St. WS 70, two specimens). Gonads in the middle of the canals, sac-shaped, of different sizes, large and small not regularly alternate. About 6 tentacles per octant.

Diam. 4.5 mm., height 5.5 mm. (St. 102). Gonads a little above the middle of the canals, two of them, on adjacent canals, fairly large, pendent, with small eggs, the others like small dots. 7-8 tentacles per octant.

Diam. ?, height 5.5 mm. (St. 1575). Gonads in the middle of the canals, mutilated. About 10 tentacles per octant. Bell margin comparatively well preserved, but statocysts lost.

Diam. 7 mm., height 8 mm. (St. 89). Only four of the gonads are developed; they are small, arranged crosswise on the radial canals alternating with the sterile canals. The tentacles cannot be counted.

These details show that the development of the gonads proceeds irregularly; in small as well as large specimens only four gonads may be developed, and when there are eight in different stages of development, they are irregularly arranged.

This species differs from *Amphogona apsteini* by the higher form of the umbrella, the possession of a distinct apical knob, and particularly by the position of the gonads in the middle parts of the radial canals, whereas the gonads of *A. apsteini* are placed very near the ring-canal. *A. pusilla* Hartlaub has only 16 tentacles.

DISTRIBUTION. Bathypelagic in the neighbourhood of the Falkland Islands and South Georgia, west of the Cape of Good Hope, and in the Mozambique Channel.

Tetrorchis erythrogaster Bigelow 1909

1909 *Tetrorchis erythrogaster* Bigelow, p. 124. Pl. 29, figs. 1-3.

1936 *Tetrorchis erythrogaster* Thiel, p. 39.

OCCURRENCE: St. 1598. 23. x. 35. 07° 10' 48" S, 03° 31' 18" W. Gulf of Guinea. Net: TYFB 460-300 m. 1 specimen.
St. 2036. 17. iv. 37. 33° 45' 30" S, 15° 03' 48" E. West of Cape of Good Hope. Net: TYFB 2650-2200 m. 1 specimen.

The specimen from St. 1598 is badly preserved, but the margin is in a fair condition with 4 large and 16 small tentacles. The specimen from St. 2036 is 8 mm. in diameter, 7 mm. in height, and agrees well with Bigelow's description. The four gonads, however, are situated a little higher, in about the middle part of the radial canals. The distal quarter of the manubrium extends beyond the bell cavity. There are 4 large tentacles opposite the fertile radial canals; 16 very small tentacles are arranged at almost equal distances from each other, none of them are situated opposite to the sterile radial canals. According to Bigelow the sterile canals 'can hardly be traced at all as they approach the ring-canal'; in the present specimen they are distinct right out to the ring-canal. Like Bigelow I cannot see the statocysts. According to a note on the label the manubrium was 'a lovely purple red'.

DISTRIBUTION. This characteristic species was originally described from the tropical East Pacific; Thiel records a specimen from the tropical Atlantic near Cape Verde. The present specimens were taken farther south, off the west coast of Africa. The species belongs to the deep and intermediate layers.

Persa incolorata McCrady 1857

1857 *Persa incolorata* McCrady, p. 104. Pl. 12, fig. 3.

1910 *Persa incolorata* Mayer, p. 408. Text-figs. 261-2.

1936 *Persa incolorata* Thiel, p. 43.

1951 *Persa incolorata* Picard, p. 20, fig.

OCCURRENCE: St. 282. 12. viii. 27. 01° 11' S, 05° 38' E. Gulf of Guinea. Net: TYF 300(-0) m. 3 specimens.

The best preserved specimen is 2 mm. in diameter, 2.5 mm. high, with very thin walls and a small apical knob. There is a very short, conical gastric peduncle. The stomach is short, turned inside out, the four short, broadly rounded lips therefore protruding from its upper part. The musculature of the subumbrella is fairly strong. The eight radial canals are very narrow, and each of two opposite canals carries a short, oval gonad in its middle portion. The gonads are connected with the canals

by a very narrow opening; they are female and contain numerous small eggs. There were 6 tentacles per octant, but they are all broken off short. The statocysts are lost. Velum very broad.

The two other specimens are badly preserved. In one of them almost all the tentacles are lost, but some of the sensory clubs are retained. In the other specimen some of the tentacles are retained; they are long and each of them has a distinct terminal knob.

DISTRIBUTION. This peculiar little medusa, which may attain a height of 3 mm., is recorded from North and South Carolina on the Atlantic coast of North America. Mayer (1910) found it at Naples in the Mediterranean, and according to Picard (1951) it is abundant near Marseilles and Villefranche-sur-Mer. It is identical with *P. lucerna* Haeckel from Corfu and *P. dissogonima* Haeckel from the Straits of Gibraltar. Thiel (1936) recorded it from several localities in the central and southern Atlantic between 19° N and 41½° S. The present specimens from the Gulf of Guinea do not increase the known area of distribution.

Crossota brunnea Vanhöffen 1902

(Text-fig. 17)

1902*b* *Crossota brunnea* Vanhöffen, p. 73. Pl. 9, figs. 11-13; Pl. 12, figs. 34-8 and 43-7.

1909 *Crossota brunnea* Bigelow, p. 135. Pl. 2, fig. 7; Pl. 45, fig. 9.

1912*a* *Crossota brunnea* Vanhöffen, p. 385.

1936 *Crossota brunnea* Thiel, p. 20, in part.

OCCURRENCE: Stns 9, 71, 72, 76, 78, 85, 86, 89, 100, 101, 151, 239, 391, 395, 401, 666, 671, 675, 773, 1298, 1574, 1633, 1639, 1707, 1719, 1743, 1745, 1750, 1758, 1776, 1784, 1825, 1917, 1970, 1974, 2042, 2048, 2053, 2061. (For details of position, date, etc., see Table I, p. 110, and text-fig. 17, p. 101.)

The most interesting of these localities is St. 1298 in the South Pacific, in about 69° S, 126° W, this being the first time that the species has been taken in the Pacific outside the tropical region. It is also of considerable interest that it was found in numerous localities in the south-western Atlantic, from which there was only one previous record, when some few specimens were found north-west of South Georgia by the Swedish Antarctic Expedition (Kramp 1948*b*, p. 10); 'Discovery II' even found it in the Weddell Sea. Some of the specimens are in beautiful condition.

I have previously discussed the species of *Crossota* (Kramp 1947, p. 21). It is very deplorable that Thiel (1936) united most of the species under the name *C. brunnea*; his map of distribution is therefore unreliable.

DISTRIBUTION. Common in the deep layers in all the oceans south of the equator; as seen from the present collection it has a circumpolar distribution in the antarctic seas. In the Pacific it had not been found outside a comparatively small area off the coast of Peru (Bigelow 1909) and off southern Japan (Uchida 1947*b*, p. 338), the only record from the northern hemisphere. Now also found in the antarctic part of the Pacific.

Crossota alba Bigelow 1913

1913 *Crossota alba* Bigelow, p. 49. Pl. 3, figs. 9-12.

OCCURRENCE: St. 2059. 30. iv. 37. 09° 11' 24" S, 05° 17' 24" W. Net: N 450 B 1900-1400 m. 1 specimen.

St. 2066. 5. v. 37. 04° 56' 24" N, 14° 46' 42" W. Net: N 450 B 1950-1550 m. 2 specimens.

It was a great surprise to find this medusa in the tropical Atlantic, but I do not hesitate to refer the specimens to this Japanese species, though all of them are destitute of gonads. The exumbrella is furrowed in the characteristic way peculiar to the genus, the structure of the manubrium, the number of tentacles and the colours agree perfectly with the description of *C. alba*.

The specimen from St. 2059 is 16 mm. in diameter and 12 mm. in height; the manubrium is 7 mm. long, tubular; the colour of the stomach is sometimes a deep violet, almost black, but in some lights it appears chocolate-brown; the mouth tube, which is 1 mm. long, is white, and the umbrella

is colourless. The tentacles cannot be counted exactly, their number has probably been about 120. One of the specimens from St. 2066 is 26 mm. wide and badly preserved; the other specimen is much larger, 42 mm. in diameter and 28 mm. in height. The manubrium is narrow, 16 mm. long, 2 mm. of which form the mouth tube. The stomach has the same colour as in the specimen mentioned above, though not quite as dark. Throughout the length of the stomach eight narrow, sharp lines are seen opposite to the eight radial canals, and there are eight fairly broad and flat longitudinal furrows in the intervening spaces. There are about 190 tentacles. The velum is 5 mm. broad. Bigelow's type specimen was about 22 mm. wide with 179 tentacles, 'that is [Bigelow says] only about one-third as many as in *C. brunnea* of about the same size'. The structure of the manubrium is quite different from that in *C. brunnea*.

DISTRIBUTION. Bigelow described two specimens from the east coast of Japan; Uchida (1947*b*, p. 339) gives a doubtful record from the same area, in which one wrecked specimen was found. Now also found in two localities off the west coast of tropical Africa.

Aglaura hemistoma Péron & Lesueur 1809

1910 *Aglaura hemistoma* Mayer, p. 398. Pl. 46, figs. 4-5; Pl. 49, figs. 3-7; Pl. 50, fig. 11. Text-figs. 250-1.

OCCURRENCE: St. 100. 2-4. x. 26. 33° 20' S, 15° 18' E to 33° 46' S, 15° 08' E. Net: TYF 0-5 m. 5 specimens.
TYF 475(-0) m. 3 specimens.

St. 256. 23. vi. 27. 35° 14' S, 06° 49' E. Net: TYF 850-1100(-0) m. 1 specimen.

St. 282. 12. viii. 27. 01° 11' S, 05° 38' E. Net: TYF 300(-0) m. 9 specimens.

St. 690. 7. v. 31. 03° 17' 45" S, 29° 57' 45" W to 03° 20' S, 30° 03' 15" W. Net: TYFV 250-0 m. 2 specimens.
1500(-0) m. 1 specimen.

St. 691. 8. v. 31. 00° 25' 45" S, 29° 56' W. Net: TYFB 400-0 m. 8 specimens.

St. 692. 9. v. 31. 02° 02' 15" N, 30° 08' W. Net: TYFB 350-0 m. 2 specimens.

St. 693. 10. v. 31. 02° 59' 30" N, 29° 59' W to 02° 59' 30" N, 30° 04' 45" W. Net: TYFV 250-0 m. 1 specimen.

St. 701. 16. x. 31. 14° 39' 18" N, 25° 51' 42" W. Net: TYFB 242-0 m. 14 specimens.

St. 703. 18. x. 31. 07° 17' N, 28° 01' 54" W. Net: TYFB 358-0 m. 2 specimens.

St. 704. 19. x. 31. 03° 37' 42" N, 29° 14' W. Net: TYFB 231-0 m. 14 specimens.

St. 705. 20. x. 31. 00° 03' 24" N, 30° 36' 48" W. Net: TYFB 150-0 m. 9 specimens.

St. 842. 3. iii. 32. 36° 04' 48" S, 13° 34' 30" E. Net: N 100 B 155-0 m. 1 specimen.

All these stations are in the Atlantic Ocean between the Cape Verde Islands and the Cape of Good Hope; the southernmost locality is St. 842, in 36° S, 13° E.

DISTRIBUTION. Generally distributed in the warm and temperate parts of all the oceans including the Mediterranean. In the Atlantic it penetrates as far north as the Bay of Biscay and the Gulf of Maine, in the Pacific as far as Japan and California. Its southern limit of distribution is in about 35° S in the Atlantic and Indian Oceans, and in about 20° S in the Pacific.

Family GERYONIDAE

Geryonia proboscidalis (Forskål 1775)

1910 *Geryonia proboscidalis* Mayer, p. 425. Pl. 53, figs. 1-3; Pl. 54, fig. 10. Text-fig. 282.

OCCURRENCE: St. 407. 12. vi. 30. 35° 13' S, 17° 50' 30" E to 34° 57' S, 17° 48' E. Near Cape of Good Hope. Net: TYFB 220-0 m. 1 specimen.

St. 679. 29. iv. 31. 26° 06' 30" S, 30° 06' 15" W. Net: TYFB 300-0 m. 1 specimen.

St. 690. 8. v. 31. 03° 17' 45" S, 29° 57' 45" W to 03° 20' S, 30° 03' 15" W. Net: TYFB 460-0 m. 1 specimen.

St. 692. 9. v. 31. 02° 02' 15" N, 30° 08' W. Net: TYFB 350-0 m. 1 specimen.

St. 1374. 24. v. 34. 31° 46' 36" S, 29° 46' 18" E. South-East Africa. Net: TYFB 230-0 m. 1 specimen.

St. 1586. 2. v. 35. 02° 39' 24" N, 50° 46' 24" E. Net: TYFB 550-0 m. 1 specimen.

St. 2061. 1. v. 37. 06° 36' S, 06° 25' 06" W. Gulf of Guinea. Net: N 450 B 1500-0 m. 1 specimen

The specimens from Stns 679, 1374 and 1586 are young stages, up to 12 mm. wide; the specimens from Stns 407 and 2061 are 38 mm. in diameter.

DISTRIBUTION. Widely distributed in the warm parts of all the oceans including the Mediterranean, approximately between 35° N and 35° S. The present collection adds nothing to the known area of distribution.

Liriope tetraphylla (Chamisso & Eysenhardt 1821)

1953 *Liriope tetraphylla* Russell, p. 419. Pl. 24, fig. 2. Text-figs. 275-82.

OCCURRENCE: Stns 89, 91, 100, 102, 273, 275, 280, 282, 468, 690, 691, 699, 701, 702, 703, 704, 705, 706, 707, 708, 709, 710, 711, 715, 1373, 1374, 1573, 1574, 1580, 1585, 1586, 2033. St. WS 657. (For details of position, date, etc., see Table 1, p. 110.)

Stns 89-102, 1373-4 and 2033 are west of the Cape of Good Hope; Stns 273-82 are off the west coast of tropical Africa; Stns 690-715 are on a line from the Cape Verde Islands along the east coast of South America to south-east of Buenos Ayres; Stns 1573-86 are off the east coast of Africa from the Mozambique Channel to Somaliland. All these localities are within the areas from which the species was known before, but St. 468 is considerably farther south, 54° 48' S, 20° 41' W, north-east of the South Sandwich Islands. St. WS 657 is in the Pacific on the coast of Peru.

DISTRIBUTION. Since it has been realized that all forms of *Liriope* belong to one species, we may state that it is generally distributed in the warm parts of all the oceans, approximately between 40° S and 45° N. Now also found farther south in the Atlantic.

NARCOMEDUSAE

Family AEGINIDAE

Aegina citrea Eschscholtz 1829

1829 *Aegina citrea* Eschscholtz, p. 113. Pl. 11, fig. 4.

1829 *Aegina rosea* Eschscholtz, p. 115. Pl. 10, fig. 3.

1879 *Aegina rhodina* Haeckel, p. 338. Pl. 20, figs. 11-13.

1908 *Aegina lactea* Vanhöffen, p. 50. Pl. 7, fig. 3.

1908 *Aegina brunnea* Vanhöffen, p. 51. Pl. 7, fig. 4.

1909 *Aegina alternans* Bigelow, p. 74. Pl. 17, fig. 1.

1953 *Aegina citrea* Russell, p. 467. Pl. 28, fig. 1. Text-figs. 308-10.

OCCURRENCE: Stns 76, 78, 100, 102, 151, 270, 276, 282, 290, 291, 298, 407, 677, 690, 697, 1370, 1371, 1374, 1575, 1749, 2047, 2053, 2057, 2064, 2070. (For details of position, date, etc., see Table 1, p. 110.)

Most of these localities are in the Atlantic Ocean from the coast of Portugal (St. 2070) to South Georgia (St. 151), but the species was also taken in the area south of Madagascar and farther east in the Indian Ocean (St. 1749). All the localities are inside the regions, from which the species was known before. It was taken at very different depths, e.g. at St. 100, west of the Cape of Good Hope, in hauls from 5-0 m. as well as from 1000-900 m.

The number of tentacles and marginal lappets was counted in 60 specimens with the following results:

No. of tentacles	3	4	5	6
No. of specimens	1	49	9	1

DISTRIBUTION. *Aegina citrea* has its main distribution in the warm and temperate parts of the oceans, but may also occasionally be carried as far north as the south coast of Iceland and southwards to the neighbourhood of South Georgia. In cold areas it only occurs in deep water, but in the warm areas it may be met with at the surface, though there also it frequently occurs in the deep and intermediate layers.

Aeginura grimaldii Maas 1904

1904 *Aeginura grimaldii* Maas, p. 38. Pl. 3, figs. 19-28.

1905 *Aeginura weberi* Maas, p. 77. Pl. 11, fig. 73; Pl. 12, fig. 76; Pl. 14, figs. 90-9.

1936 *Aeginura lauzerotae* Thiel, p. 86. Fig. 18.

1953 *Aeginura grimaldii* Russell, p. 472. Text-figs. 311-12.

OCCURRENCE: St. 287. 19. viii. 27. $02^{\circ} 49' 30''$ S, $09^{\circ} 25' 30''$ W. Net: TYF 800-1000(-0) m. 1 specimen.

St. 298. 29. viii. 27. $13^{\circ} 01' 45''$ N, $21^{\circ} 34' 45''$ W. Net: TYF 900-1200(-0) m. 1 specimen.

St. 1580. 27. iv. 35. $08^{\circ} 44' 36''$ S, $41^{\circ} 50' 18''$ E. Net: TYFB 1300-750 m. 1 specimen.

St. 1585. 1. v. 35. $00^{\circ} 06' S$, $49^{\circ} 45' 24''$ E. Net: TYFB 1400-700 m. 2 specimens.

St. 1587. 3. v. 35. $06^{\circ} 05' N$, $52^{\circ} 00' E$. Net: TYFB 1250-800 m. 2 specimens.

St. 1600. 25. x. 35. $12^{\circ} 43' 18''$ S, $00^{\circ} 20' 12''$ E. Net: TYFB 400-330 m. 2 specimens.

Stns 287, 298 and 1600 are off the west coast of Africa, and Stns 1580, 1585 and 1587 off the east coast between Zanzibar and Somaliland. The species was previously known from the same areas.

DISTRIBUTION. Widely distributed in the deep layers of all the oceans, except in the Mediterranean and in arctic seas.

Solmundella bitentaculata (Quoy & Gaimard 1824)

OCCURRENCE: Stns 17, 100, 102, 107, 151, 270, 275, 276, 282, 303, 304, 305, 306, 311, 313, 319, 320, 321, 323, 325, 334, 335, 336, 337, 342, 343, 344, 353, 354, 355, 356, 357, 358, 589, 661, 690, 1370, 1373, 1606. WS 30, WS 44, WS 54, WS 67, WS 69, WS 139, WS 140, WS 141, WS 151, WS 160. (For details of position, date, etc., see Table 1, p. 110.)

All these localities are south of the equator, several of them are off the west and south coasts of Africa, one (St. 690) is near Cape San Roque in Brazil. Moreover, the species was taken in numerous localities in the area between the South Sandwich Islands and the Falkland Islands, and it was found in one locality west of Graham Land (St. 589). The species has been recorded from all these regions.

This well-known and widely distributed medusa was previously known to occur at very different depths; as far as the present collection is concerned the bathymetrical distribution may be summarized as follows:

Approx. depth of hauls (m.)	100-0	250-100	500-250	750-500	1000-750
No. of hauls	10	15	26	6	3

Accordingly the species may be found everywhere between the surface and depths of about 1000 m., though it seems mainly to occur between 100 and 500 m.

DISTRIBUTION. Widely distributed in all the great oceans, particularly common in the southern hemisphere.

Family SOLMARIDAE *sensu* Bigelow 1909

Narcomedusae without gastric pockets, the genital products being developed either as thickenings or as diverticula in the oral wall of the central stomach; with or without peripheral canals and otoporphae.

This is the definition of the family given by Bigelow (1909, p. 81) as distinct from the Cuninidae and Aeginidae, and I fully agree with this distinction. In a subsequent paper (1918, p. 394) Bigelow referred to the family under the headline: Solmaridae Haeckel, *sensu* Maas 1904, Bigelow 1909, Mayer 1910; but the diagnosis given by Maas ('Narcoméduses à antimères nombreux, sans nombre précis; système entodermique simple, sans canaux périphériques') would exclude the genus *Pegantha*.

The family comprises two genera: *Solmaris* Haeckel and *Pegantha* Haeckel. In 1918 (p. 394) Bigelow was inclined to regard *Polycolpa* Haeckel as a third genus distinct from *Pegantha*; I have recently (Kramp 1955, p. 278) expressed the opinion that the genus *Polycolpa* should be abandoned.

Genus *Pegantha* Haeckel

The diagnosis of this genus given by Bigelow (1909, p. 83) is as follows: 'Solmaridae with canal system and otoporpa; the gonads forming diverticula of the margin of the oral gastric wall. 8-32 tentacles'. Apart from the number of tentacles, which may amount to 40, I agree with this definition. It was slightly altered by Bigelow (1918, p. 394): 'Solmaridae with peripheral canal-system (at least in one generation), and with otoporpa; with gonads localized at the edge of the stomach, as numerous as, and in the radii of, the marginal lappets.' In some cases, however, the interradial sexual pockets are combined with an annular gonad, and in young specimens no interradial pockets are developed.

The genus *Pegantha*, as here defined, conforms with the entire family Peganthidae Haeckel (1879, p. 323): 'Narcomedusen ohne Radial-Canäle und ohne Magentaschen in der Subumbrella; aber mit einem Festoncanal (oder einem Ringkanal, der einen Kranz von getrennten Lappencanälen bildet); mit Otoporpen oder Hörspangen an der Basis der Hörkölbchen.' The family was divided into four genera, exclusively according to the structure of the gonads: *Pegasia* Péron & Lesueur 1809, *Polyxenia* Eschscholtz 1829, *Polycolpa* Haeckel 1879, and *Pegantha* Haeckel 1879. There is no reason whatever to keep these genera apart, and the question then arises, which generic name should be preferred. Bigelow (1940, pp. 303-4) has discussed this; he retained the name *Pegantha*, but with the addition: 'Should it prove, in the future, that the gonads must be discarded here, as a generic character, the name *Pegasia* (or if not *Pegasia*, then *Polyxenia*) will have priority.' It seems to me, however, that Mayer (1910, p. 441) has settled the question by his remark: 'The names *Pegasia* and *Polyxenia* are older than *Pegantha*, but they are so hopelessly confused through vague and inaccurate description that I believe it will be necessary to allow them to lapse into oblivion.' It also seems to me that an identification of Haeckel's three species of *Pericolpa* remains doubtful; none of them have been found again, and though a full description of the only specimen of *P. forskali* is given in the Challenger Report (Haeckel 1881) with several figures, an examination of fresh material is necessary to prove the correctness of his observations. On the other hand, Haeckel's genus *Pegantha* contains a number of well-described species, and I prefer, therefore, to retain the name *Pegantha*.

Haeckel's 'Peganthidae' comprised 16 species. Within each of his four 'genera' the species are characterized by: external shape of the umbrella, number and shape (outline) of the marginal lappets, shape of the gonads, number of marginal sensory clubs and otoporpa; but no attention is paid to the length of the otoporpa, and the conformation and width of the peripheral canals are entirely disregarded.

From time to time no less than 29 species have been referred to *Pegantha*. A provisional revision was attempted by Bigelow (1918, pp. 394 ff.), but, as pointed out by this author himself, larger series of specimens are required to obtain reliable results. The present collection contains a considerable number of specimens, but a satisfactory preservation of these delicate medusae requires very careful handling of each specimen. As a matter of fact, I do not think a successful revision of this and other groups of Narcomedusae will be possible, until a specialist gets an opportunity to study them immediately after they are brought up from the sea and picked out from the mass of crustaceans and pteropods and other animals contained in the plankton samples. The following revision of the species of *Pegantha* should therefore be accepted with due reservations.

Most of the specimens of *Pegantha* in the Discovery collections are in a rather poor condition, but some tolerably well-preserved specimens have enabled me to point out certain distinctive features, which seem to be characteristic of the different species and may be recognized even in fairly young stages and in more or less mutilated specimens. Five species are represented in the collection, and I refer them to five species which have previously been described in a recognizable way, doing away

with all doubtful synonyms. The five species are: *triloba* Haeckel, *martagon* Haeckel, *laevis* H. B. Bigelow, *clara* R. P. Bigelow, and *rubiginosa* Kölliker, which is transferred from the genus *Cumina*. Beside these only two species, '*Polycolpa*' *forskali* Haeckel and *Pegantha magnifica* Haeckel, may possibly be valid species, providing the descriptions are correct, and if so the genus *Pegantha* comprises altogether seven species.

The following forms, which were referred to *Pegantha* by Mayer (1910), are unrecognizable: *Foveolia diadema* Péron & Lesueur 1809 (*Polyxenia diadema* Haeckel), tropical Atlantic; *Aequorea punctata* Quoy & Gaimard 1824 (*Solmaris punctatus* Haeckel), Hawaii Islands; *Polyxenia cyanostylis* Eschscholtz 1829 and Haeckel 1879, Atlantic Ocean; *Polyxenia cyanolina* Haeckel, Indian Ocean; *Solmoneta aureola* Haeckel, Red Sea; *Solmaris godefroyi* Haeckel, Samoa Islands; *Solmaris weberi* Haeckel, tropical Pacific.

Aequorea cyanogramma Quoy & Gaimard 1824 (*Polyxenia cyanogramma* Haeckel) must likewise be abandoned, though attempts have been made to revive it (Vanhöffen 1908, Ranson 1949).

Medusa mollicina Forskål 1775 (Mediterranean), *Pegasia dodecagona* Péron & Lesueur 1809 (South Atlantic), and *Polycolpa zonaria* Haeckel 1879 (Mediterranean) may possibly be identical with *Pegantha martagon* Haeckel as suggested by Bigelow (1918), but it seems very doubtful.

Pegantha biloba Haeckel (Sandwich Islands), *P. quadriloba* Haeckel (tropical Atlantic), *P. pantheon* Haeckel (Philippine Islands), and *Pegasia sieboldii* Haeckel (tropical Atlantic) are probably identical with *P. triloba* Haeckel. *Pegantha dactyletra* Maas 1893 (central Atlantic) is suggested by Bigelow (1918) as possibly identical with *P. laevis*; it rather seems to me to belong to *P. triloba*.

Solmoneta lunulata Haeckel (Canary Islands) is a doubtful synonym of *Pegantha clara* R. P. Bigelow, but too doubtful for a safe identification.

The description of *Solmaris* sp. Browne 1916 (Chagos Archipelago), which is designated by Bigelow (1918) as 'a typical *Polycolpa*', was based on young stages which may have belonged to some species of *Pegantha*.

Undoubted synonyms are: *Pegantha simplex* Bigelow 1904 (= *P. martagon*), *Solmaris insculpta* Mayer 1906 (= *P. triloba*), and *Pegantha smaragdina* H. B. Bigelow 1909 (= *P. clara* R. P. Bigelow 1909).

My studies of the numerous specimens of *Pegantha* in the Discovery collections and additional observations of some fairly well-preserved specimens from the 'Atlantide' Expedition, off the west coast of Africa, have led me to the following conclusions as to the structural features which may serve as characteristics for identification of the species.

UMBRELLA. It may be of specific importance whether the umbrella is highly vaulted or more or less flattened, if the preservation is tolerably good, but frequently the shape cannot be relied on. In *P. triloba* the sculpture of the exumbrella is characteristic, and the gelatinous substance is particularly rigid. In species with a predominantly smooth surface, if the otoporphae seem to be deposited on elevated ridges, it is merely due to casual contraction.

Shape of the MARGINAL LAPPETS. It may be of importance whether the lappets are long or short in proportion to their width. The relation between length and width varies according to the state of contraction and preservation, but in extreme cases it may be a reliable character. The same applies to the outline whether pointed, rectangular, rounded, or pentagonal, etc.

The **GONADS**, which, of course, are undeveloped in young specimens, may sometimes have a characteristic structure (especially in *P. triloba*); but their appearance is not merely dependent on the degree of development, I have also found that a strong contraction in a circular direction may produce foldings which are absent when the umbrella is flatly dilated.

The **NUMBER OF TENTACLES AND LAPPETS** is an important specific character, though it is somewhat

variable in each species. In *P. clara* the number increases considerably with the age of the individual; especially in middle-sized specimens, several of the tentacles are usually smaller than the others, sometimes even almost regularly alternating with the fully developed tentacles. The same applies in a lesser degree to *P. laevis*. In the other species the full number is usually attained in young stages.

The NUMBER OF OTOPORPAE is likewise an important character; it is somewhat variable in each species, but apparently it increases only slightly with age. Their LENGTH is very characteristic, but has been utterly disregarded in the older literature. Unfortunately in badly preserved specimens the otoporpaе are frequently more or less destroyed, so that it is difficult or even impossible to see them. Sometimes the sensory clubs are better preserved than the otoporpaе, but they do not seem to be of use in the identification of species.

The WIDTH OF THE PERIPHERAL CANALS is a character of great importance for distinction between the species; it is rarely mentioned in the descriptions in the literature.

In my attempts to identify the numerous specimens of *Pegantha* in the Discovery collections, I proceeded in the following way. I first looked out for well-preserved specimens, which might serve for a provisional orientation, and then the samples were picked out at random regardless of their geographical origin. In each sample every specimen was measured, the tentacles counted, the number of sensory clubs and length of otoporpaе determined as far as possible, and notes made on the shape of the umbrella, the softness or rigidity of the gelatinous substance, the outline and relative length of the marginal lappets, the width of the peripheral canals, and the conformation of the interradial diverticula and the gonads if they had attained a degree of development which made a description possible. All these observations were written on labels which afterwards were arranged in groups according to the various characters. Some few specimens could immediately be separated as belonging to *P. triloba*, and one agreed perfectly with *P. rubiginosa*. The remaining specimens, by far the most numerous, turned out to represent three well-defined types which could be referred to the three species *martagon*, *laevis* and *clara*, as described in Bigelow's papers after 1909. When in the end I marked the localities on maps, I found that all these three species occurred in tropical and subtropical seas, and that all the specimens taken south of latitude 50° S had been determined as *P. martagon*.

Pegantha martagon Haeckel 1879

(Plate VI, fig. 1, text-fig. 10)

1879 *Pegantha martagon* Haeckel, p. 333. Pl. 19, figs. 4-7.

1904 *Pegantha simplex* Bigelow, p. 260. Pl. 5, figs. 19-20.

1909 *Pegantha martagon* Bigelow, p. 83. Pl. 18, figs. 1-8.

1910 *Pegantha martagon* Mayer, p. 443. Text-figs. 195, 196.

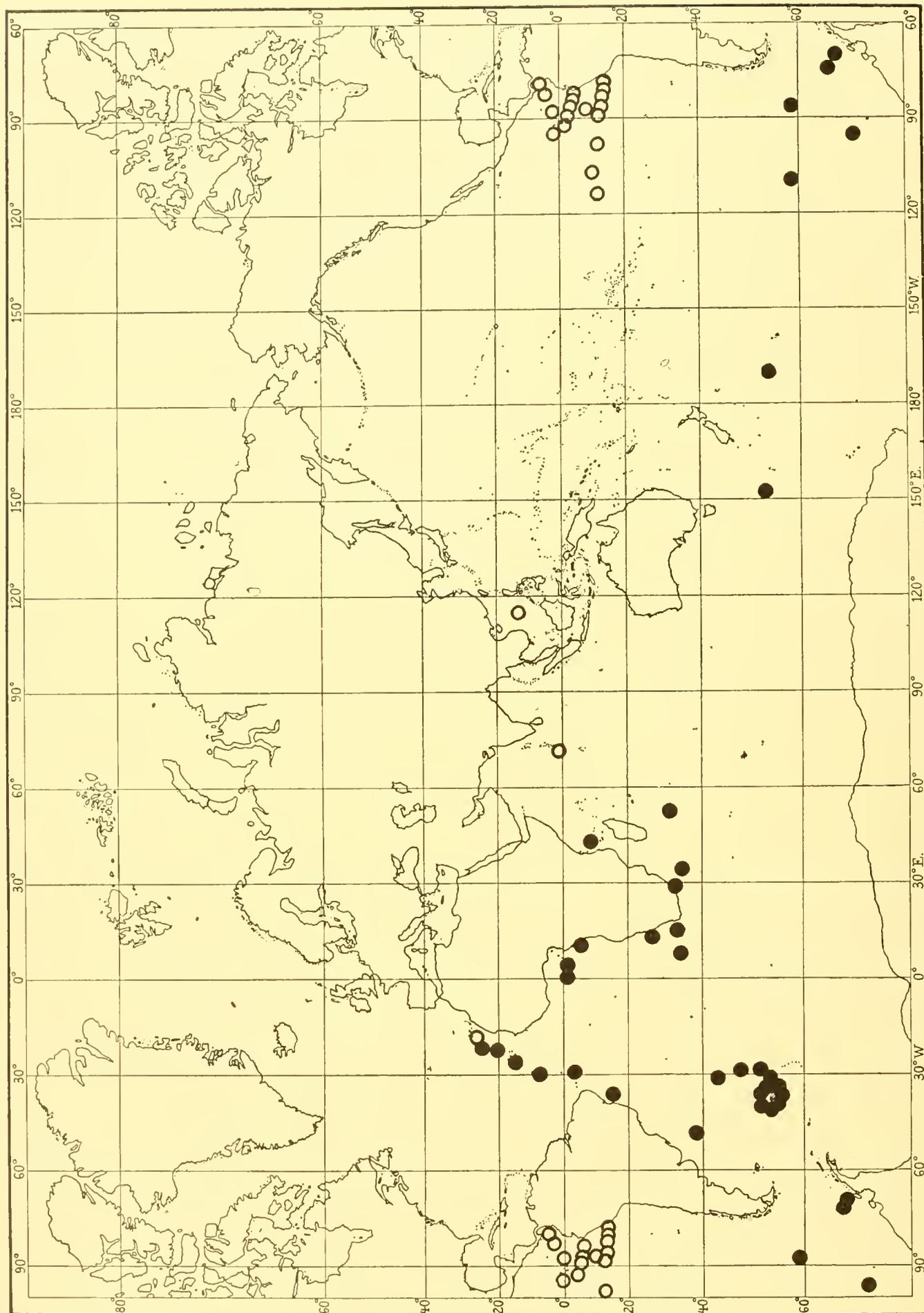
1918 *Pegantha martagon* Bigelow, p. 395.

1940 *Pegantha martagon* Bigelow, p. 308.

1955 *Pegantha martagon* Kramp, p. 277.

OCCURRENCE: Stns 87, 100, 129, 133, 139, 276, 282, 284, 319, 344, 569, 593, 595, 663, 665, 667, 671, 690, 697, 700, 701, 709, 715, 903, 948, 972, 976, 1374, 1568, 1574, 1581, 1606, 1759, 2067. WS 28, WS 35, WS 63, WS 181, WS 186, WS 187, WS 283, WS 286. (For details of position, date, etc., see Table 1, p. 110.)

Stns 903, 948, 972 and 976 are in the South Pacific between 50° S and 60° S; Stns 569, 593 and 595 are in the antarctic area west of Graham Land; Stns 120, 133, 139, 319, 344 and 665 and all the 'William Scoresby' stations are in the neighbourhood of South Georgia, 667 and 671 somewhat farther to the north-east. Stns 1374, 1568, 1574, 1581 and 1759 are off the east coast of Africa between about 35° S and 8° S. The other stations are scattered on both sides of the Atlantic Ocean between about 39° S and 24° N (St. 2067 between the Cape Verde and the Canary Islands) (see chart, text-fig. 10).



Text-fig. 10. Distribution of *Pegantha martagon*. New records = ●, previous records = ○.

The only previous record from the Atlantic was near the Canary Islands, where 32 specimens were taken by the 'Atlantide' Expedition (Kramp 1955).

Apparently the species occurs in the upper layers. On some few occasions (in the South Atlantic and the South Pacific) it was taken in vertical hauls between about 300 m. and 100 m., but the majority of the other hauls were made from various depths to the surface. At St. 100, near the Cape of Good Hope, several specimens were taken in the surface 5 m.

REMARKS ON THE MORPHOLOGY. In well-preserved specimens the central mass of jelly is usually thick and fairly highly vaulted, smooth; an indication of keels may occasionally be present below the otoporpaе, but never continued above these latter. The ventral wall of the stomach is sometimes so strongly contracted that the mouth is a small opening. The interradial pockets, in which the gonads are developed, are usually quite simple, flatly rounded, rarely hemispherical, occasionally slightly folded, forming two or three short lobes. They may sometimes be discerned in specimens only 8–11 mm. in diameter, but frequently no traces of pockets are seen, even in much larger specimens, especially if the state of preservation is bad. When the gonads are particularly well developed, they are not restricted to the interradial pockets, but constitute a continuous folded band along the entire outline of the stomach, comprising the interradial pockets as well as the radial incurvations in the tentacular radii. The marginal lappets are usually about as long as broad, square or evenly rounded, rarely pentagonal or semi-circular. Their relative length is not merely dependent on the state of contraction, but also to some extent on the number of lappets, being somewhat elongated when there are many, short when there are few; in one specimen, 16 mm. in diameter with only seven tentacles, the lappets were only half as long as broad. The number of marginal clubs on the lappets is somewhat variable; sometimes there are only 3, and occasionally I have counted as many as 9 or 10 on each lappet, but as a rule there were 5 or 7, almost always an odd number. The otoporpaе are short and narrow, about twice as long as the width of the transverse portion of the peripheral canal. The number of tentacles varies between 7 and 17 (see below).

The conformation of the peripheral canals is very characteristic and may be recognized even in mutilated specimens (Pl. VI, fig. 1). The transverse portion along the external edge of the lappet is fairly narrow, the lateral portions along the peronia are considerably broader, especially in their proximal parts, tapering in width towards the external margin. When measured mid-way between the basis and the external edge of the lappet, each canal is about one-fifth as wide as the entire lappet. In this respect *P. martagon* differs distinctly from *P. laevis* and *P. clara*.

In the present collection 85 specimens could be measured, varying in diameter between 3 mm. and 30 mm. The number of tentacles in specimens of different sizes will be seen from the following table:

Average diameter (mm.)	No. of tentacles		No. of specimens examined
	Width of variation	Average number	
4.5	8–12	9.5	4
8.3	8–14	11.1	21
13.1	9–17	12.3	24
18.0	7–17	12.1	23
23.7	11–16	12.8	9
27.5	10–16	13.5	4
Total	7–17	11.9	85

It appears from these figures that within each size-group the variation in number of tentacles is rather considerable, but each specimen attains its final number of tentacles at an early stage of development, and only occasionally one or two are added later on. The number of 8 tentacles was found

only in small individuals 3–6 mm. in diameter, 9 were found in specimens up to 19 mm. wide, 10 in specimens between 5 mm. and 27 mm. The smallest specimen with as many as 16 tentacles was 12 mm. wide, and the same number was counted in a particularly large specimen, 30 mm. in diameter. The number of tentacles most frequently met with was 12; it was found in 32 of the 84 specimens examined.

DISTRIBUTION. *Pegantha martagon* was first described from the China Sea; Bigelow records it from the Maldive Islands in the Indian Ocean (1904, as *P. simplex*) and from numerous localities in the tropical East Pacific (1909 and 1940). Recently recorded from the neighbourhood of the Canary Islands (Kramp 1955). In the British Museum (Nat. Hist.), London, I found 5 specimens of *P. martagon*, collected in 35° 00' S, 46° 36' E, south-east of Africa, 29. iv. 1937 by A. Seligman. The Discovery collections show that it is widely distributed in the tropical and subtropical Atlantic and the western part of the Indian Ocean, whence it penetrates southwards into subantarctic seas, where it has a circumpolar distribution.

Pegantha laevis H. B. Bigelow 1909

(Plate VI, fig. 2, text-fig. 11)

- 1909 *Pegantha laevis* Bigelow, p. 97. Pl. 16, fig. 1; Pl. 20, figs. 4–6; Pl. 27, figs. 1–7.
 1910 *Pegantha laevis* Mayer, p. 444.
 1918 *Pegantha laevis* Bigelow, p. 396.
 1949 *Pegantha cyanogramma* Ranson, p. 135.
 1950 *Pegantha laevis* Berrill, p. 301. Fig. 4^{N-L}.
 1955 *Pegantha laevis* Kramp, p. 279.

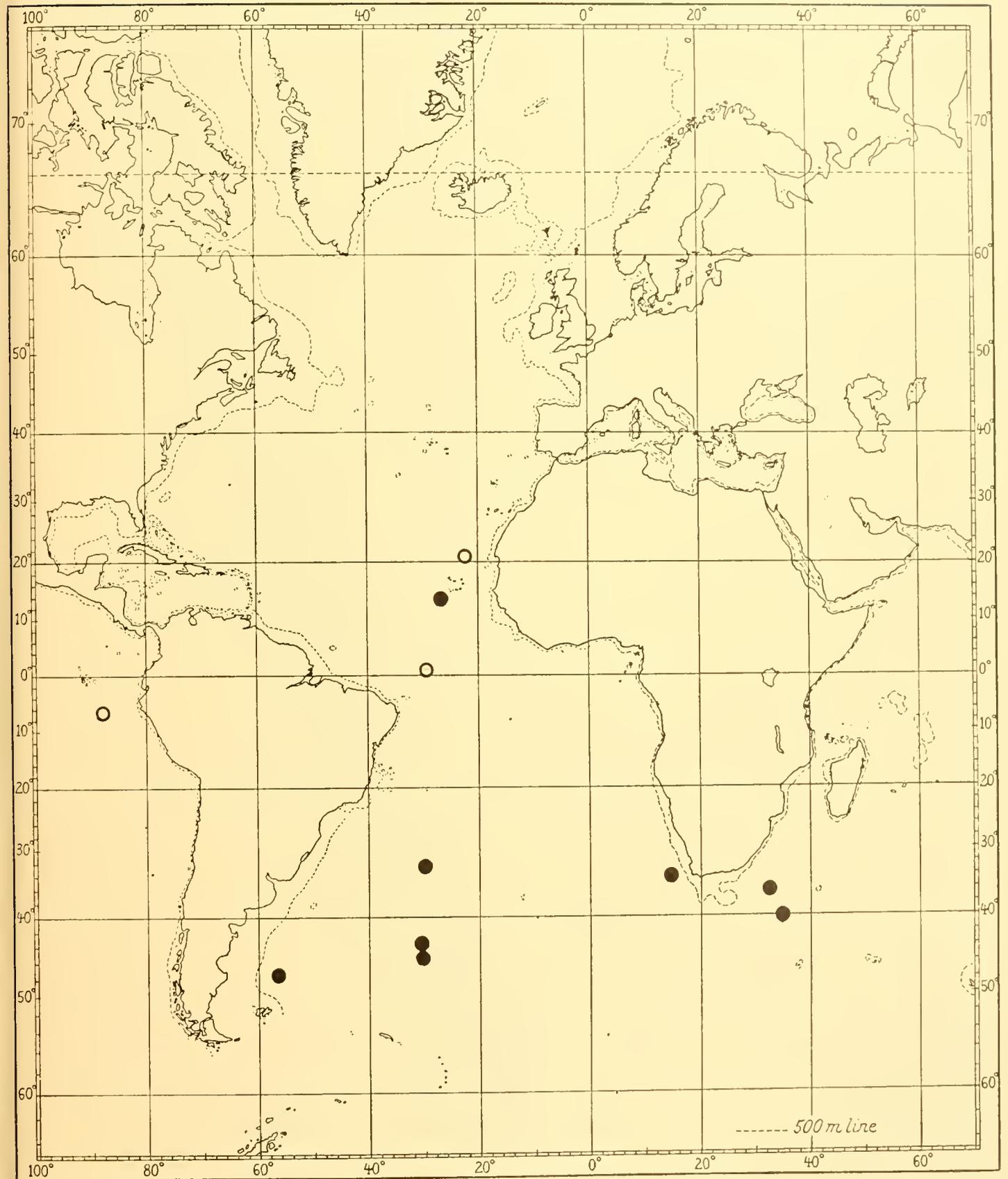
OCCURRENCE: Stns 100, 670, 671, 677, 701, 718, 1370, 1568. (For details of position, date, etc., see Table 1, p. 110.) Stns 1370 and 1568 are off the south-east coast of Africa, St. 701 is near the Cape Verde Islands; the others are in the southern Atlantic between the Cape of Good Hope and Patagonia in the southern part of South America (see chart, text-fig. 11).

The collection gives very little information on the bathymetrical distribution of this species. At St. 100, near the Cape of Good Hope, it was taken partly in the surface 5 metres, partly in hauls 550–450 m. and 2500–0 m. In all the other localities the nets were hauled from more or less deep layers to the surface. All previous finds are from the upper layers.

REMARKS ON THE MORPHOLOGY. One of the most characteristic features of this species is the great width of the peripheral canals. The umbrella is usually somewhat flattened, the surface completely smooth, jelly generally rather soft. The interradial pockets with the gonads may be simple, sac-shaped or bean-shaped, but when further developed they are irregularly lobed; in the largest specimen observed (diam. 44 mm. St. 671) each gonad has 4–5 lobes of different sizes. The marginal lappets are usually almost quadrate with rounded corners, occasionally they are somewhat pointed or pentagonal. Marginal sensory clubs could only be counted in some few specimens and then only in some few of their lappets; the number was sometimes five, sometimes seven. The otoporpaе were usually shorter than the width of the transverse portion of the peripheral canals, but sometimes a little longer.

The peripheral canals are always very broad, especially their lateral portions along the peronia, and of nearly the same width from their base towards the end of the lappet (Pl. VI, fig. 2); as a rule they are more than one-fourth as wide as the entire lappet, and sometimes the space between them is narrower than the canals. Even badly preserved specimens may be specifically identified by this character.

Larvae, as they are described by Bigelow (1909, p. 99), were found in the peripheral canals of two specimens from St. 1568, 17 mm. and 25 mm. in diameter; in these specimens no gonads were developed.



Text-fig. 11. Distribution of *Pegantha laevis*. New records = ●, previous records = ○.

In most of the specimens the marginal lappets are of equal width and the tentacles of equal size, but occasionally two neighbouring lappets are narrow, indicating that they have newly arisen by the longitudinal division of one of normal width, and the tentacle between them is smaller than the others. The smallest specimen observed (St. 718) is only 10 mm. in diameter; it has 17 tentacles, but evidently this number had recently been attained, since several of the tentacles are much smaller than the others; in one specimen (St. 100), 16 mm. wide with 17 tentacles, several of the lappets are broad with a median incurvation carrying a very small tentacle resembling Bigelow's (1909) fig. 4 on Pl. 20. An abnormal development has taken place in a specimen, 28 mm. wide (St. 100); its total number of tentacles cannot be stated, but has exceeded 18; most of the tentacles are of equal size and equally spaced, but in one part of the circumference 8 tentacles of very different sizes are placed more or less closely together separated by narrow lappets.

Among 17 specimens observed, the tentacles could be counted in 13 with the following results:

Diam. (mm.)	No. of tentacles	No. of specimens examined
10	17	1
15-20	14-25, average 17.8	9
21	17	1
30	16	1
33	15	1
40	17	1
44	26	1

These figures show that as a rule the specimens attain their final number of tentacles and lappets at an early stage, but occasionally an additional number is developed during further growth of the individual.

I have been able to examine the specimen collected in the central part of the Atlantic by 'Mercator' and considered by Ranson (1949, p. 135) to belong to *Pegantha cyanogramma* (Q. & G.). It was kindly sent to me by Dr E. Leloup of Brussels. It is a well-preserved and typical specimen of *Pegantha laevis*. The diameter is 22 mm., the height 8 mm., the shape is flattened and the jelly fairly rigid. It has 18 tentacles. The gonads are in an advanced stage of development, very prominent and irregularly lobed as in Bigelow (1909, Pl. 20, fig. 5). Each marginal lappet has 5 short otoporphae. The lappets are bent strongly inwards and accordingly much contracted transversally; the peripheral canals are extraordinarily broad, their lateral portions frequently considerably broader than the space between them. The radiating folds in the ventral wall of the stomach, described by Ranson, are distinct, but not so regularly arranged as one would expect from Ranson's description. Similar foldings may occasionally appear in the stomach wall of other species. The specimen is entirely different from those identified by Vanhöffen (1908) as *Polyxenia cyanogramma*, and which undoubtedly belonged to *P. triloba*.

DISTRIBUTION. Bigelow found this species in the tropical East Pacific, partly off the coast of Peru, partly farther west in about 14° S, 115° W, and near the Hawaiian Islands. In the Atlantic it was taken north of the Cape Verde Islands by the Atlantide Expedition (Kramp 1955), and we may now add the locality where the specimen described above was taken by the Belgian vessel 'Mercator'. The Discovery collections show that it is widely distributed in the tropical and southern parts of the Atlantic and in the western part of the Indian Ocean.

Pegantha clara R. P. Bigelow 1909

(Pl. VI, fig. 3, text-figs. 12, 13)

- 1908 *Polycolpa forskali* Vanhöffen, p. 56 (*non* Haeckel).
 1909 *Pegantha clara* R. P. Bigelow, p. 80. 2 figs.
 1909 *Pegantha smaragdina* H. B. Bigelow, p. 90. Pl. 14, figs. 1-2; Pl. 19, figs. 1-9; Pls. 22-6.
 1912a *Polycolpa forskali* Vanhöffen, p. 391.
 1912b *Polycolpa forskali* Vanhöffen, p. 32.
 1918 *Pegantha clara* H. B. Bigelow, p. 397.
 1938 *Pegantha clara* H. B. Bigelow, p. 134.
 1940 *Pegantha clara* H. B. Bigelow, p. 305. Figs. 15-16.
 1947 *Pegantha clara* Kramp, p. 33. Pl. 4, fig. 7; Pl. 5, figs. 1-10. Text-fig. 12.
 1950 *Pegantha clara* + *smaragdina* Berrill, p. 299. Figs. 4A-E and F-K.

OCCURRENCE: Stns 85, 247, 284, 678, 689, 697, 698, 701, 707, 708, 1370, 1373, 1576, 1585, 1749, 2066, 2068, 2069.
 (For details of position, date, etc., see Table 1, p. 110.)

St. 1749 is in the middle of the Indian Ocean between South Africa and Australia; Stns 1370, 1373, 1576 and 1585 are off the east coast of Africa; the other stations are scattered over the Atlantic Ocean between 30° 46' N. (St. 2069, north of the Canary Islands) and 37° 20' S (St. 247), (see chart, text-fig. 12).

Presumably the species was mainly taken in the upper layers, all of the hauls reaching from various depths to the surface, with the exception of the haul at St. 2066, which is stated to be hauled from 1950 to 1550 m. Previous records, in which the depths are stated, indicate that the species belongs to the upper layers.

REMARKS ON THE MORPHOLOGY. In contradistinction to *P. martagon* and *laevis*, this species is mainly characterized by its long and narrow otoporpa and a continual increase in number of marginal lappets and tentacles during the growth of the individuals. Its peripheral canals are decidedly narrower than in the two other species, but broader than in *P. rubiginosa*.

The shape of the umbrella is usually rather flattened, but occasionally it may be somewhat vaulted, the gelatinous substance thick and moderately rigid, smooth; very young specimens are highly vaulted. Gonads were seen only in some few of the specimens, and they were sac-shaped or half-moon-shaped, simple or somewhat crenulated. When fully developed the marginal lappets are usually tongue-shaped with evenly rounded external edge, rarely slightly pointed, a little longer than broad, frequently one and a half times as long as broad; but owing to the continual addition of new lappets by division of the older ones we almost always find some pairs of lappets of a particularly narrow shape separated by a tentacle of smaller size than the others. Medium-sized specimens have about 21 lappets and tentacles, but the number may amount to 40, possibly even 48. In large specimens with many tentacles the lappets are generally more elongated than in specimens with a smaller number. The otoporpa are long and narrow, usually about as long as the lappets, but in young specimens much longer. In fully developed lappets, their number is most frequently 3 or 5, the median one slightly longer than the others, but sometimes there are 2 or 4. When a lappet with five otoporpa is divided, the new peronium occupies the position of the median otoporpa, and each of the two new lappets then has two otoporpa. Sometimes the otoporpa are mounted on slightly prominent gelatinous keels, but these are never prolonged beyond the ends of the otoporpa.

The peripheral canals (Pl. VI, fig. 3) are of nearly the same width throughout their length, fairly narrow, in fully developed lappets about one-eighth to one-sixth as broad as the lappet; in particularly elongated lappets the canals are proportionately broader, but they never approach the remarkable width as in *P. laevis*.

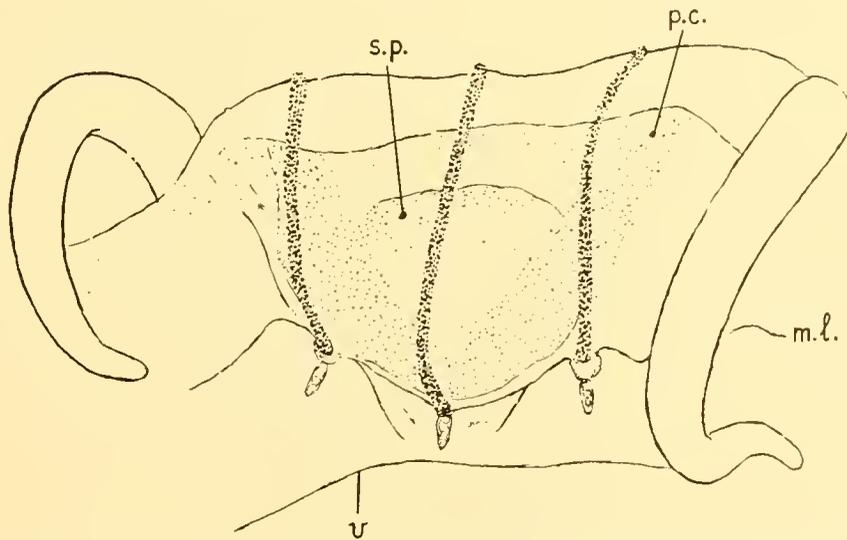


Text-fig. 12. Distribution of *Pegantha clara*. New records=●, previous records=○.

Numerous medusoid larvae were found in the canals in a specimen, 35 mm. wide, from St. 701.

The sample from St. 282 contained three fragments which may possibly have belonged to one specimen of *P. clara*, about 15 mm. in diameter. There are altogether 48 tentacles, many of them small, partly very small, and the lappets are of very different width, most of them more than twice as long as broad and usually with two very long otoporpa. The tentacles and lappets are so densely crowded that the circumference of the medusa may very well have had the great number of 48, and I am inclined to think that the three fragments may really belong to one specimen.

Four very small specimens, 3-4 mm. in diameter, were found at Stations 708 (near the coast of Brazil) and 1585 (East Africa). They have a thick and highly vaulted jelly, and also the marginal lappets are rather thick, with fairly broad canals (text-fig. 13). The lappets are as long as broad or somewhat longer, each of them with three very long otoporpa. In one of the specimens, 4 mm. wide with 10 tentacles, the otoporpa are at least twice as long as the lappets; in the three other specimens, which are 3-3.5 mm. in diameter, with 7, 8 and 9 tentacles respectively, the median otoporpa of each lappet reaches up to the very apex of the umbrella, the two others are about half as long or somewhat more, ending blindly, not connected with the median one.



Text-fig. 13. *Pegantha clara*. A marginal lappet and two tentacles of a young specimen, diameter 3.5 mm., from St. 708. *s.p.* = stomach pouch, *p.c.* = peripheral canal, *m.l.* = margin of lappet, *v.* = velum.

The collection contains 32 specimens, 29 of which could be measured, varying in diameter between 3 mm. and 50 mm. The number of tentacles in proportion to diameter of umbrella is summarized in the following table:

Average diameter (mm.)	No. of tentacles		No. of specimens examined
	Width of variation	Average number	
3.5	7-10	8.5	4
10.0	14-18	15.7	3
12.7	20-23	21.6	7
17.5	18-23	20.8	6
23.0	21	21.0	1
30.2	22-25	23.7	4
45.0	28-40	33.2	4
Total	7-40	20.8	29

The four largest specimens had the following numbers:

Diam. (mm.)	42	43	45	50
No. of tentacles	40	33	32	28

The figures show a rapid increase in the number of tentacles and marginal lappets during the youngest stages from 3 mm. to about 11 mm. or 12 mm. diameter; during the next period the number is fairly constant, but the differences in size between the tentacles and lappets of different age are gradually effaced, and if the growth is continued beyond a diameter of about 30 mm. or 35 mm. a further addition of tentacles and lappets takes place. The result is that in almost all stages of development, lappets of different width and tentacles of different length are present, which is a very characteristic feature of this species. Large and small tentacles may sometimes be almost regularly alternate, but as a rule the sequence is more or less irregular (see Kramp 1947, p. 33).

In 1918 H. B. Bigelow realized that the East Pacific species, *Pegantha smaragdina*, described by him in 1909 was identical with the Atlantic species, *P. clara*, described a few months earlier by R. P. Bigelow. *Solmoneta lunulata* Haeckel from the Canary Islands may possibly be identical with *P. clara*, but, as mentioned on p. 66, this identification seems to me too doubtful to be adopted. I propose, therefore, that the name *Solmoneta lunulata* be regarded as obsolete. According to Bigelow (1938) the specimens identified as *Polycolpa forskali* by Vanhöffen (1908, 1912*a* and 1912*b*) belong to *P. clara*.

DISTRIBUTION. Pacific: off the coast of South America from the Gulf of Panama to about 25° S; between the Hawaiian Islands and the Caroline Islands. Widely distributed in the Atlantic between about 40° S and 50° N. Now for the first time recorded from the Indian Ocean.

Pegantha rubiginosa (Kölliker 1853)

(Pl. VI, fig. 4)

- 1853 *Eurystoma rubiginosum* Kölliker, in Gegenbaur, Kölliker & Müller, p. 322.
 1861 *Aegineta gemmifera* Keferstein & Ehlers, p. 93. Pl. 14, figs. 10-11.
 1879 *Cunina rhododactyla* + *rubiginosa* Haeckel, p. 321.
 1886 *Cunina rhododactyla* Metschnikoff, p. 251.
 1910 *Cunina prolifera* Mayer, p. 480.
 1924 *Cunina rubiginosa* Kramp, p. 37.
 1925*a* *Cunina prolifera* Ranson, p. 91.
 1936 *Cunina rubiginosa* (*pars*) Thiel, p. 77.
 1936 *Cunina rubiginosa* Ranson, p. 199.
 1936 *Cunina lativentris* Damas, pp. 1177-97. Figs. Larvae.
 1940 *Cunina prolifera* Bigelow, p. 303.
 1951*b* *Cunina rubiginosa* Vannucci, pp. 106, 112, 113.
 1955 *Pegantha rubiginosa* Kramp, p. 280.
 1854 *non Cunina prolifera* Gegenbaur.

The specific name *Cunina rubiginosa* was maintained by me in 1924. Bigelow (1940) referred this species to the Solmaridae, genus *Polycolpa* 'if that genus be recognized'. I have recently referred it to the genus *Pegantha*. Thiel (1936) has erroneously identified it with almost all the species of *Cunina*.

OCCURRENCE: St. 697. 12. v. 31. 09° 15' 15" N, 30° 01' 45" W. Net: TYFB 460-0 m. 1 specimen. South-west of the Cape Verde Islands.

The specimen is well preserved, 7 mm. in diameter, with 13 tentacles. The jelly is thick and highly vaulted. Each of the marginal lappets, which are almost semicircular, has two or four otoporpaes; when there are four, two of them are very long, longer than the lappet, flanked by two short ones. The peripheral canals are narrow, of equal width throughout. Gonads are not developed.

The narrow peripheral canals and the evenly rounded outline of the marginal lappets are characteristic of this species. It is also characteristic that as a rule there are two long and two short otoporpaes on each lappet; an odd number is rarely found (see Pl. VI, fig. 4).

DISTRIBUTION. Common in the Mediterranean. First recorded from the Atlantic by Ranson (1925*a*)

in two localities off the coast of Portugal and near the Azores, later by the same author (1936) between the Azores and North America; south of the Canary Islands and in the Gulf of Guinea (Kramp 1955); between the Cape Verde Islands and the north-east coast of Brazil (Vannucci 1951*b* and the present specimen). Damas (1936) found larvae, presumably belonging to this species (under the name of *Cunina lativentris*), parasitic in *Tomopteris* in three localities west of the Strait of Gibraltar and also in the Bay of Biscay. The records by Thiel (1936) with his accompanying map of distribution are unreliable, because he united several different species under the name *Cunina rubiginosa*.

Pegantha triloba Haeckel 1879

- 1879 *Pegantha triloba* Haeckel, p. 333. Pl. 19, figs. 4-7.
 1908 *Polyxenia cyanogramma* Vanhöffen, p. 56. Pl. 2, fig. 8.
 1909 *Pegantha triloba* Bigelow, p. 87. Pl. 14, fig. 3; Pl. 16, fig. 3; Pl. 20, figs. 1-3; Pl. 45, figs. 1-2.
 1910 *Pegantha triloba* Mayer, p. 443. Figs. 293, 294, 297.
 1912*a* *Pegantha triloba* Vanhöffen, p. 389. Fig. 22.
 1912*b* *Pegantha triloba* Vanhöffen, p. 30. Pl. 1, figs. 11-12.
 1918 *Pegantha triloba* Bigelow, p. 395.
 1948*a* *Pegantha triloba* Kramp, p. 15.
 1948*b* *Pegantha triloba* Kramp, p. 11.
 1949 *Pegantha triloba* Ranson, p. 134.

OCCURRENCE: No station number. 29. ix. 25. 25° 47' S, 14° 48' W. Net: HN 0 m. 7 specimens.

St. 291. 24. viii. 27. 03° 46' N, 16° 49' W. Net: TYF 100(-0) m. 1 specimen.

St. 2063. 2. v. 37. 03° 24' 48" S, 07° 51' 12" W. Net: N 450 B 1150-600 m. 1 specimen.

The first of these localities is about mid-way between South America and South Africa, the two others are outside the Gulf of Guinea.

The two specimens from Stns 291 and 2063 are 25 mm. wide with 14 tentacles, and 23 mm. wide with 13 tentacles respectively; they are well preserved and typical specimens, their gonads are well developed and distinctly tripartite with finger-shaped lobes. The seven specimens from the first locality are young stages with the following dimensions:

Diam. (mm.)	5	5	5	6	7	7	15
No. of tentacles	13	13	14	14	12	15	15
Otoporpa per lappet	3	5	5	5	5	6	7

The jelly is thick and rigid; the radiating keels on the exumbrella, typical of this species, are very distinct in the marginal zone, but in the central part they are less pronounced than in the adult specimens. Otoporpa run along the entire length of the gelatinous keels, the median one from each lappet reaching right to the top of the umbrella, meeting in the centre, the others join it at different distances from the marginal zone. Gonads are not developed. These young specimens are very similar to that figured by Vanhöffen (1908, Pl. 8, fig. 8) under the name of *Polyxenia cyanogramma*.

DISTRIBUTION. Widely distributed in the tropical parts of all the great oceans, but apparently not very common in the Atlantic.

Genus *Solmaris* Haeckel

Here again Thiel (1936, pp. 58 ff.) has gone much too far in uniting almost all the species under one name, *S. flavescens* (Kölliker). As the genus is represented in the Discovery collection by one specimen only, I shall abstain from any attempt on a revision of the species for the present.

Solmaris corona (Keferstein & Ehlers 1861)

1910 *Solmaris corona* Mayer, p. 437.

1953 *Solmaris corona* Russell, p. 476. Pl. 28, fig. 2. Text-figs. 313, 314.

OCCURRENCE: St. 100. 30. ix-I. x. 26. 33° 20' S, 15° 18' E to 33° 46' S, 15° 08' E. Net: TYF 0-5 m. 1 specimen.

The locality is near the Cape of Good Hope. The specimen is 8 mm. in diameter with 28 tentacles; it is somewhat mutilated, but sufficient details are retained for certain identification; parts of the gonads are retained.

In the British Museum (Natural History), London, I have seen numerous small specimens, collected in Durban Bay, 26. viii. 1915, labelled by E. T. Browne as *Solmaris*. They evidently belong to *S. corona*.

DISTRIBUTION. Mediterranean. North Atlantic around the British Isles and on the west coast of Norway. Also recorded from the Canary Islands (Haeckel 1881, as *S. coronantha*) and collected by the 'Atlantide' Expedition in two localities in the Gulf of Guinea (Kramp 1955, p. 276); now shown to occur around South Africa. Records from the Indian and Pacific Oceans are more or less doubtful as long as a thorough revision of the different species has not been carried out.

Family CUNINIDAE *sensu* Bigelow 1909

Narcomedusae with undivided radial gastric pouches, equal in number to the tentacles.

The family comprises the genera *Cunina* Eschscholtz 1829 and *Solmissus* Haeckel 1879 and the doubtful genus *Cumissa* Haeckel 1879. As previously stated by me (Kramp 1953, p. 304) there is not sufficient reason to retain the genus *Cunocantha* Haeckel 1879 as distinct from *Cunina*.

Genus *Solmissus* Haeckel

Cuninidae without peripheral canal system or otoporpa.

Among the four species referred to this genus by Haeckel only one, *S. albescens* (Gegenbaur 1856), can be recognized as a valid species, and it is the type species of the genus. It is very common in the Mediterranean and has been found nowhere else. *S. ephesius* Haeckel may be a young stage of the same species. *S. ambiguus* Neppi (1915) from the Adriatic Sea is certainly identical with *S. albescens*. Two other valid species are described: *S. incisa* (Fewkes 1886) and *S. marshalli* Agassiz & Mayer 1902. *S. faberi* and *bleekii* Haeckel are supposed to be identical with *incisa*, but I doubt the correctness of this supposition. In *S. faberi*, which occurred in the South-West Atlantic, the gastric pouches are described as heart-shaped, wider outwardly, and cleft by the insertions of the tentacles, thus very different from the gastric pockets of *incisa*. In *S. bleekii*, from the Atlantic coast of South Africa, the pouches are said to be rectangular, presumably similar to those of *S. marshalli*, but there are twice as many tentacles and marginal lappets, 32 against 14-16, and there is only one marginal club on each of the lappets. The names *faberi* and *bleekii*, therefore, cannot take priority over *incisa* or *marshalli*.

S. albescens and *marshalli* have about the same number of tentacles (up to 16). In *marshalli*, of which numerous specimens are present in the Discovery collection, the gastric pouches are strictly rectangular, about as long as wide; in *albescens* they are more or less rounded, frequently pentagonal. This difference might not be decisive, but *albescens* is also characterized by numerous small warts on the exumbrella, whereas in *marshalli* the exumbrella is smooth. I think we must keep these two species apart.

A new and thorough description with excellent figures of *Solmissus marshalli*, based on living specimens, was given by Bigelow (1909, p. 64), so that no doubt of its structure is left. The description of *S. incisa* in the same paper (p. 67) is less complete; this species is particularly fragile, and the specimens at Bigelow's disposal were more or less damaged. When more than 40 mm. in diameter, they had 20-32 tentacles; a small specimen, 10 mm. wide, had 16 fully developed and 3 small tentacles. As the greatest number observed in *marshalli* was 16, the two species were mainly distinguished from

each other by their numbers of tentacles. As mentioned below, however, I have seen two specimens of *S. marshalli* with as many as 20 tentacles, so that in certain cases specific identification might be doubtful, if no other distinguishing features could be pointed out. A difference seems to exist in the number of statocysts, but these are very readily lost in both species. Apparently, however, the outline of the gastric pouches presents a characteristic difference between the two species. The radial 'elevations' and 'depressions', 24-32 in number, on the subumbrellar side of the disc, mentioned and figured by Fewkes (1886 pp. 954 ff.) in his description of *S. incisa*, evidently mark the outline of the gastric pouches, which themselves had disappeared. According to the figure, these pouches were oval, somewhat elongated and well separated from each other. In 1938 (p. 129) Bigelow likewise described the pouches of *incisa* as 'oval in outline and somewhat longer than broad'. I have been able to note this in several, otherwise much damaged, specimens in the collection from the 'Dana' expeditions. Therefore, in cases of doubt, e.g. in fragmentary specimens, the outline of the gastric pouches provides us with a reliable distinguishing character, and I think we may recognize three distinct species of *Solmissus*: *albescens* in the Mediterranean, and *incisa* and *marshalli*, both of which are widely distributed in the great oceans.

Solmissus marshalli Agassiz & Mayer 1902

(Text-fig. 14)

- 1902 *Solmissus marshalli* Agassiz & Mayer, p. 151. Pl. 5, figs. 23-5.
 1906 *Solmaris punctatus* Mayer, p. 1133.
 1909 *Solmissus marshalli* Bigelow, p. 64. Pl. 16, figs. 5-6; Pl. 21, figs. 4, 6-8.
 1919 *Solmissus marshalli* Bigelow, p. 329.
 1928 *Solmissus marshalli* Uchida, p. 89.
 1940 *Solmissus marshalli* Bigelow, p. 308.

OCCURRENCE: Stns 102, 270, 273, 276, 284, 286, 287, 298, 407, 440, 448, 680, 698, 701, 702, 1371, 1373, 1374, 1568, 1585, 1606, 1768, 2053, 2059, 2061. (For details of position, date, etc., see Table 1, p. 110.)

St. 1585 is off the coast of Somaliland, East Africa; Stns 440, 1371, 1373, 1374 and 1568 are off the south-east coast of Africa; St. 680 is off the Atlantic coast of Brazil; the other localities are scattered over the eastern Atlantic from south-west of the Cape of Good Hope to the Cape Verde Islands (see chart, text-fig. 14).

The bathymetrical range is uncertain. At three of the stations it was apparently taken in deep water, 500-250 m. (St. 102), 900-550 m. (St. 2053), and 1900-1500 m. (St. 2061). In all the other localities it was taken in hauls reaching to the surface, sometimes from deep water, but mainly from depths of less than 300 or 200 m.

Most of the specimens are less than 35 mm. in diameter, but one is 43 mm. (St. 2059). The marginal sensory clubs could only be counted in two specimens and then only in some few of the lappets; in a specimen 31 mm. wide (St. 1371) there are about 10, in a specimen 35 mm. wide (St. 1373) two of the lappets have at least 9.

The number of tentacles in specimens of different size will be seen from the following table:

Diam. (mm.)	Average diam.	No. of tentacles		No. of specimens examined
		Width of variation	Average number	
16-20	19.0	11-12	11.7	3
21-25	25.0	14-16	15.0	2
26-30	27.8	11-20	14.9	12
31-35	32.6	15-20	15.4	5
43	43	16	16.0	1

Almost all the specimens of medium size have 14–16 tentacles. The only specimen with 10 tentacles was taken at St. 1371; it is 31 mm. in diameter, and besides the ten fully developed tentacles a tiny one is situated in the middle of one of the marginal lappets; two other specimens from the same station, both 28 mm. wide, have about 11 tentacles. The large specimen, 43 mm. wide with 16 tentacles, was taken at St. 2059. As a rule the rectangular gastric pouches are as long as broad or a little longer. In the only two specimens with more than 16 tentacles the number is 20, and their gastric pouches are comparatively short and broad and of somewhat different size, some of them almost twice as broad as long, and the corners are slightly rounded. They are, however, quite different from the pouches in *S. incisa*, and in spite of the large number of tentacles in these two specimens I refer them without doubt to *S. marshalli*. They were taken at Stns 284 and 1606, in hauls 300–0 m. and 190–0 m. respectively.

DISTRIBUTION. Most of the previous records of this species are from the tropical Pacific, but under the name *Solmaris flavescens* it was recorded by Vanhöffen (1908, p. 58) from several localities in the tropical Indian and Atlantic Oceans and probably again, under the same name, in 1912a (p. 394) from three localities off the west coast of Africa, between the Cape Verde Islands and 20° S. The record by Ranson (1936, p. 208) from the Mediterranean, near the Balearic Isles, is peculiar, and one cannot but suppose that the only specimen belonged to *S. albescens*. Ranson, it is true, describes the gastric pouches as more pronouncedly rectangular than in *S. albescens*; the pentagonal outline generally seen in this latter species is, however, not quite constant, but may sometimes approach the rectangular shape of the pouches in *S. marshalli*.

Genus *Cunina* Eschscholtz

Cuninidae with otoporpa; with or without peripheral canal system.

Attempts at a revision of the numerous species of *Cunina* (incl. *Cunioctantha*) were made by Bigelow (1909, pp. 51 and 55; 1918, p. 392) and Thiel (1936, pp. 77 and 82). Within the species with more than eight tentacles (*Cunina* sensu stricto), Bigelow recognized 5 species: *globosa* Eschscholtz 1829, *lativentris* Gegenbaur 1856, *proboscidea* Metschnikoff and Metschnikoff 1871, *duplicata* Maas 1893, and *peregrina* Bigelow 1909. I have not seen *lativentris* and *proboscidea* myself, but the three others are represented in the Discovery collections. To Bigelow's revision I shall only add the fact that a gelatinous peduncle, which is emphasized as characteristic of *proboscidea*, was also found in the present specimens of *globosa*, but since this species has a well-developed peripheral canal system, whereas the canal system is degenerate in *proboscidea*, these two species are evidently distinct. Bigelow is inclined to regard *C. duplicata* Maas as identical with *lativentris*; the present collection, however, contains several specimens of a *Cunina* which I believe must be referred to *duplicata*, for it is impossible to identify them with *lativentris* as described and figured by Gegenbaur. On the other hand, there is the possibility that *lativentris* is the same as *globosa* (see below). Provisionally I think we should retain the five species mentioned by Bigelow but no more of this group of *Cunina*, abandoning *mucilaginoso* Chamisso & Eysenhardt 1821, *campanulata* Eschscholtz 1829, *vitrea* Gegenbaur 1856, and *oligotis* Haeckel 1879. According to Bigelow (1914, p. 33), *C. discoides* Fewkes 1881b is probably a young *Solmissus*. *Cunina prolifera* Gegenbaur and *rhododactyla* Haeckel are identical with *rubiginosa* Kölliker and should be transferred to the genus *Pegantha* (see above). I entirely disagree with Thiel (1936) who would reduce the number of species of *Cunina* to one or two (*mucilaginoso* and *rubiginosa*).

Thiel retains the genus *Cunioctantha*, but unites all the species under the name *octonaria*. I think we may state that there are four distinct species, and owing to their variable number of antimeres (usually 8, but varying from 7 to 10 or 11) I refer them all to *Cunina*. *C. octonaria* McCrady 1857 (including *köllikeri* Müller 1861 and *parasitica* Metschnikoff 1881) has no peripheral canals; its

gastric pouches are variable in shape, but always broad and never resembling those of the three other species. *C. fowleri* (Browne 1906) is likewise destitute of peripheral canals, but the spindle-shaped gastric pouches are very characteristic, and its way of developing medusa buds from the gastric pouches, projecting into the bell cavity, is remarkable. I have seen the type specimen in the British Museum (Nat. Hist.). The same asexual propagation occurs in *C. frugifera* Kramp 1948a, a species richly represented in the present collection; it has a well-developed canal system, and its gastric pouches are separated by broad triangular spaces. *C. tenella* (Bigelow 1909), which also has a well-developed peripheral canal system, is distinguished by its triangular, pointed gastric pouches.

Cunina octonaria McCrady 1857

- 1857 *Cunina octonaria* McCrady, p. 109. Pl. 12, figs. 4-5.
 1910 *Cunioctantha octonaria* Mayer, p. 461. Pl. 55, figs. 1-2. Text-figs. 304-5.
 1910 *Cunioctantha octonaria* var. *köllikeri* Mayer, p. 464.
 1910 *Cunioctantha parasitica* Mayer, p. 465.
 1915 *Cunioctantha octonaria* Bigelow, p. 316.
 1932 *Cunioctantha octonaria* Menon, p. 29.
 1935 and 1936 *Cunioctantha octonaria* (*pars*) Thiel, p. 82.
 1951b *Cunioctantha octonaria* Vannucci, pp. 112, 115, 116.
 1951 *Cunioctantha octonaria* Nair, p. 71.
 1953 *Cunina octonaria* Kramp, p. 304.
 1955 *Cunina octonaria* Kramp, p. 284.

OCCURRENCE: St. 282. 12. viii. 27. $01^{\circ} 11' S$, $05^{\circ} 38' E$. Net: TYF 300(-0) m. 1 specimen.
 St. 677. 28. iv. 31. $31^{\circ} 16' 15'' S$, $29^{\circ} 56' 30'' W$. Net: TYFV 2000-0 m. 1 specimen.
 St. 694. 10. v. 31. $04^{\circ} 05' 30'' N$, $30^{\circ} 00' W$. Net: TYFB 210-0 m. 2 specimens.
 St. 701. 16. x. 31. $14^{\circ} 39' 18'' N$, $25^{\circ} 51' 42'' W$. Net: TYFB 242-0 m. 2 specimens.
 St. 1373. 21. v. 34. $31^{\circ} 13' 06'' S$, $31^{\circ} 48' 42'' E$. Net: N 100 B 135-0 m. 2 specimens.

St. 1373 is near the south-east coast of Africa, the others are between the coasts of tropical Africa and South America.

Three of the specimens have seven tentacles, the other five specimens have eight.

DISTRIBUTION. Widely distributed in the warm parts of all the oceans, including the Mediterranean.

I may add that in the British Museum (Nat. Hist.) I have seen the young specimens of *Cunina* from Chagos, mentioned by Browne (1916 p. 201); most of them, but not all, undoubtedly belong to *C. octonaria*.

Cunina frugifera Kramp 1948

- 1948a *Cunina frugifera* Kramp, p. 18. Pl., figs. 1-6.
 1955 *Cunina frugifera* Kramp, p. 285.

OCCURRENCE: St. 100. 30. ix.-2. x. 26. $33^{\circ} 20' S$, $15^{\circ} 18' E$ to $33^{\circ} 46' S$, $15^{\circ} 08' E$. Net: TYF 0-5 m. 7 specimens; 475(-0) m. 1 specimen.
 St. 254. 21. vi. 27. $35^{\circ} 04' S$, $02^{\circ} 59' 30'' E$. Net: TYF 200(-0) m. 1 specimen.
 St. 697. 12. v. 31. $09^{\circ} 15' 15'' N$, $30^{\circ} 01' 45'' W$. Net: TYFB 460-0 m. 1 specimen.
 St. 699. 14. v. 31. $14^{\circ} 27' 15'' N$, $30^{\circ} 02' 15'' W$. Net: TYFV 500-250 m. 1 specimen.
 St. 714. 30. x. 31. $35^{\circ} 09' 30'' S$, $47^{\circ} 00' W$. Net: TYFB 246-0 m. 1 specimen.
 St. 1374. 24. v. 34. $31^{\circ} 46' 36'' S$, $29^{\circ} 46' 18'' E$. Net: TYFB 230-0 m. 1 specimen.
 St. 1568. 11. iv. 35. $34^{\circ} 47' 36'' S$, $34^{\circ} 27' 54'' E$. Net: TYFB 1400-0 m. 3 specimens.
 St. 1585. 1. v. 35. $00^{\circ} 06' S$, $49^{\circ} 45' 24'' E$. Net: TYFB 500-0 m. 1 specimen.

St. 1585 is off the Somaliland coast, East Africa, Stns 1374 and 1568 off the south-east coast of Africa; St. 100 is near the Cape of Good Hope, Stns 697 and 699 are west and south-west of the Cape Verde Islands, St. 714 is off the coast of Uruguay, South America.

The specimens vary in diameter from 4 mm. to 10 mm. The number of tentacles varies between 6 and 9, regardless of the size of the specimens, as follows:

No. of tentacles	Diam. (mm.)							No. of specimens
	4	5	6	7	8	9	10	
6	—	1	—	—	—	—	—	1
7	—	—	—	3	—	—	—	3
8	1	—	3	2	3	—	1	10
9	—	1	—	—	—	1	—	2

In this collection most of the specimens have 8 tentacles; the original specimen described by me in 1948 had 9. Among 15 specimens from the west coast of Africa (Kramp 1955), 11 had 9 tentacles, 2 had 8 and 2 had 7. The number of antimeres is thus rather variable in this species.

Medusa buds are developed on the subumbrellar side of the gastric pockets in ten specimens of all sizes.

In all the specimens the gastric pouches are typical in shape, broad at their base, rapidly tapering outwards and separated by triangular spaces. As mentioned above, this species differs from *C. fowleri* in the possession of well-developed peripheral canals and in the shape of the gastric pouches, which are spindle-shaped in *fowleri*.

DISTRIBUTION. Originally described from the Bay of Cadiz; recently recorded from three localities south of the Canary Islands and in the Gulf of Guinea; the present collection shows that the species is widely distributed in the warm parts of the Atlantic Ocean and off the east coast of Africa as well.

Cunina globosa Eschscholtz 1829

- 1829 *Cunina globosa* Eschscholtz, p. 117. Pl. 9, figs. 3a-c.
 1909 *Cunina globosa* Bigelow, p. 57. Pl. 15, fig. 3; Pl. 17, figs. 3, 8.
 1910 *Cunina globosa* Mayer, p. 476. Text-figs. 311-12.
 1918 *Cunina globosa* Bigelow, p. 393.
 1856 ?*Cunina lativentris* Gegenbaur, p. 260. Pl. 10, fig. 2.
 1904 ?*Cunina lativentris* Maas, p. 31.
 1936 ?*Cunina lativentris* Damas, p. 1177 ff.

OCCURRENCE: St. 100. 1-2. x. 26. 33° 20' S, 15° 18' E to 33° 46' S, 15° 08' E. Net: TYF 0-5 m. 2 specimens; 475(-0) m. 2 specimens.

The locality is near the Cape of Good Hope.

The specimens have the following dimensions:

Diam. (mm.)	12	12	15	18
No. of tentacles	11	12	12	13

These specimens agree so perfectly with Bigelow's description and figures of specimens from the tropical East Pacific, that I refer them to the same species without any doubt. The umbrella is highly vaulted, with a thick jelly; the gastric pouches are square, about as wide as long, and close together, separated by very narrow septa. The marginal lappets are short and broad, with well-developed peripheral canals, each with three very short otoporpa. The specimens are all male, and in two of them the gonads are well developed, following the entire outlines of the gastric pouches as an uninterrupted folded band turning around the interior edges of the septa.

The specimens differ from Bigelow's description in only one respect: they all have a broad, conical gelatinous projection in the central portion of the subumbrella; it is not so large as in *C. proboscidea*, but according to Bigelow a similar gelatinous projection is also present in specimens of *C. lativentris*

from the Mediterranean. This might lead to the supposition that these two species were identical. They are certainly very similar in general appearance, but according to Gegenbaur's description and figure the gastric pouches in *lativentris* are narrow at their base and widening outwards. Apart from the studies on the marginal sense organs by O. & R. Hertwig (1879), no descriptions and no figures of this species have been given since those by Gegenbaur. Owing to the apparent difference in the shape of the gastric pouches I think we should provisionally keep the two species apart, until renewed examination of the Mediterranean medusa has shown whether the characteristic outline of the pouches in *lativentris* is a constant feature. I feel sure that Bigelow was right in referring his specimens to *C. globosa* Eschscholtz, and I feel equally sure that the specimens collected off South Africa by 'Discovery' belong to the same species.

I am not convinced of the correctness of the identification of specimens from the North Atlantic as *C. lativentris* by Damas (1936); they are referred to that species, because they had 8-12 tentacles, broad gastric pouches, and a peripheral canal, but no other details are given.

DISTRIBUTION. Tropical Pacific, about 180° W near the equator (Eschscholtz); Pacific coast of Mexico (Bigelow). Now for the first time recorded from the Atlantic.

Cunina peregrina Bigelow 1909

(Text-fig. 15)

- 1909 *Cunina peregrina* Bigelow, p. 59. Pl. 1, fig. 6; Pl. 15, figs. 1-2; Pl. 28, figs. 1-7; Pl. 45, fig. 8.
 1918 *Cunina peregrina* Bigelow, p. 393.
 1928 *Cunina peregrina* Uchida, p. 87.
 1948a *Cunina peregrina* Kramp, p. 18.
 1955 *Cunina peregrina* Kramp, p. 282.

OCCURRENCE: Stns 677, 697, 699, 701, 707, 1371, 1374, 1576, 1770, 2067. (For details of position, date, etc., see Table 1, p. 110.)

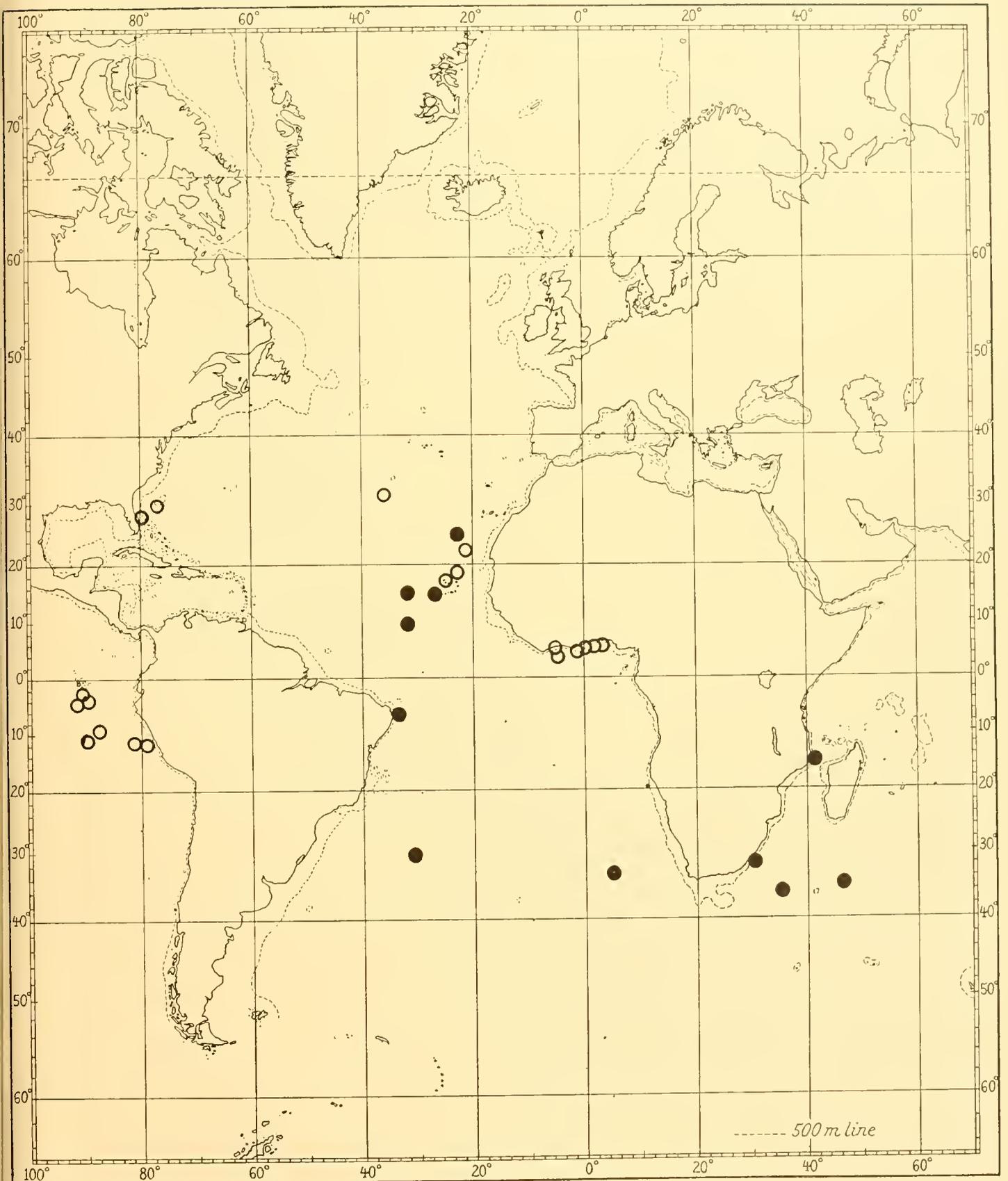
Most of the localities are scattered over the Atlantic Ocean from south-west of the Canary Islands to the latitude of the Cape of Good Hope. Stns 1371 and 1374 are off the south-east coast of Africa, St. 1576 near Mozambique on the east coast of Africa (see chart, Text-fig. 15). Moreover, I have seen a specimen in the British Museum (Nat. Hist.), taken south-east of Africa, in 35° 00' S, 46° 36' E (29. iv. 1937); it was labelled ? *Solmaris* sp.

The collection contains 31 specimens of this characteristic species, which was so well described by Bigelow (1909) that it cannot be mistaken, except when the number of tentacles is particularly small, about 8. I have recently pointed out how, in such cases, it may be distinguished from *C. octonaria*, which is also destitute of peripheral canals.

The number of tentacles and marginal lappets in relation to diameter of the umbrella in the present collection may be summarized as follows:

Average diam. (mm.)	No. of tentacles		No. of specimens examined
	Width of variation	Average number	
4.5	8-12	10.7	6
7.6	7-14	11.2	22
12.0	12	12.0	2
Total	7-14	11.1	30

The smallest specimens are 4 mm. in diameter, one with 8, two with 11 tentacles. The largest specimen is 13 mm. wide with 12 tentacles. Among the specimens 6-10 mm. wide one has 7 tentacles and one has as many as 14, in the others the number varies from 10 to 12, and most of them have 12.



Text-fig. 15. Distribution of *Cunina peregrina*. New records = ●, previous records = ○.

The figures indicate a slight increase in number of tentacles and lappets during growth of the individuals. I noticed this also in the collection from the west coast of Africa taken by the 'Atlantide' Expedition (Kramp 1955). The otoporpaes are narrow; when their number could be ascertained, it varied between 5 and 10 per lappet.

DISTRIBUTION. Pacific coasts of Mexico and Peru; around the Galapagos Islands; Japan. In the Atlantic it has been found north of the Bahamas (Bigelow 1918), south-west of the Azores (Kramp 1948*a*), and in several localities off the west coast of Africa between the Canary Islands and Dahomey in the Gulf of Guinea (Kramp 1955). The present collection shows that it also occurs in the tropical West Atlantic and off the east coast of Africa. There is no record in the literature from the Indian Ocean, but during a visit to the British Museum (Nat. Hist.) in 1954 I saw two specimens, correctly identified as *C. peregrina*, taken near Chagos by 'Sealark', 17. v. 1905; they are 7-7.5 mm. wide with 11-12 tentacles.

Cunina duplicata Maas 1893

(Pl. VI, fig. 5; Pl. VII, figs. 1, 2, text-fig. 16)

1893 *Cunina duplicata* Maas, p. 52. Pl. 5, figs. 9-10.

OCCURRENCE: St. 100. 30. ix-2. x. 26. 33° 20' S, 15° 18' E to 33° 46' S, 15° 08' E. Net: TYF 0-5 m. 12 specimens; TYF 475(-0) m. 1 specimen.

St. 282. 12. viii. 27. 01° 11' S, 05° 38' E. Net: TYF 300(-0) m. 3 specimens.

St. 699. 14. v. 31. 14° 27' 15" N, 30° 02' 15" W. Net: TYFB 370-0 m. 1 specimen.

St. 715. 31. x. 31. 38° 44' 12" S, 49° 18' 42" W. Net: TYFB 230-0 m. 1 specimen.

St. 1370. 18. v. 34. 39° 46' 36" S, 38° 18' 24" E. Net: N 100 B 113-0 m. 5 specimens.

St. 1576. 25. iv. 35. 14° 42' S, 42° 22' 12" E. Net: TYFB 400-0 m. 1 specimen.

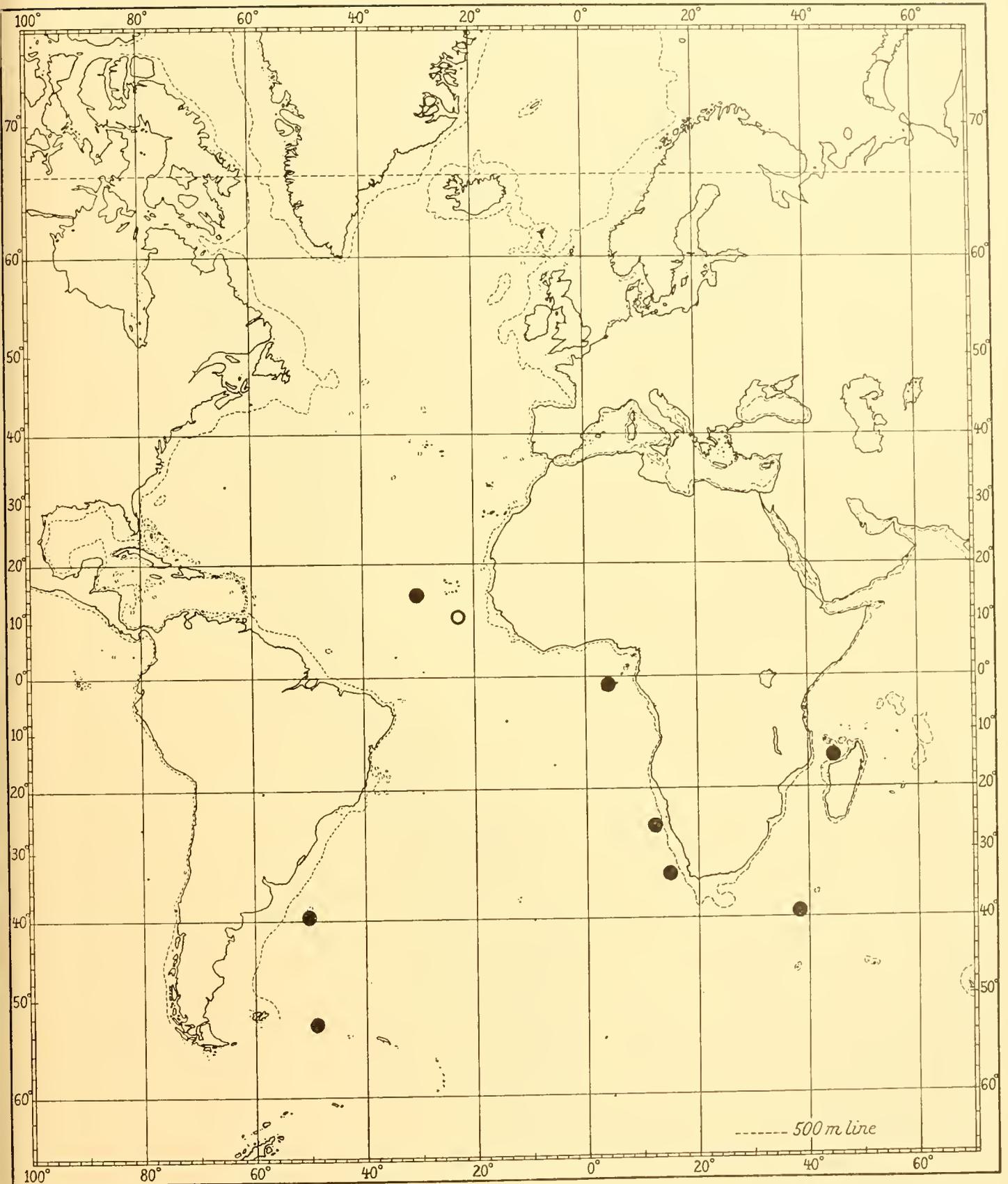
St. 1606. 31. x. 35. 26° 15' 48" S, 12° 18' E. Net: TYFB 190-0 m. 1 specimen.

St. 1974. 1. iii. 37. 52° 58' 24" S, 48° 20' 24" W. Net: TYFB 1600-1000 m. 1 specimen.

Stns 100, 282, 699 and 1606 are off the west coast of Africa between the Cape of Good Hope and the Cape Verde Islands; St. 715 is in the West Atlantic off Cape Corrientes, Argentina; St. 1974 is between South Georgia and the Falkland Islands; St. 1370 is south-east of Africa; St. 1576 in the Mozambique Channel (text-fig. 16).

Cunina duplicata has been observed only once before, when an immature specimen, 20 mm. in diameter with 16 tentacles, was described by Maas from a locality south of the Cape Verde Islands. The most characteristic feature of the species was emphasized as being the regular alternation of eight large and eight small tentacles and large and small gastric pouches. This might simply denote a stage of development lost during further growth, and that is in fact what really happens, as seen in the present specimens. There is, however, a specific character of much greater importance. Among the species of *Cunina* with many tentacles (more than 8 or 10), *duplicata* is the only species in which the gastric pouches are narrow, tongue-shaped, and equal in width to, or even narrower than the spaces between them. This is distinctly seen in Maas's figure and in all the specimens examined by me.

The present collection contains 26 specimens of all sizes, ranging between 4 mm. and 58 mm. in diameter. Some of the young stages are very similar to that described by Maas, large and small gastric pouches and tentacles almost regularly alternate, but later on the development proceeds irregularly; even in the largest specimens new tentacles are developing, and the total number may amount to 27. Another characteristic feature is the considerable width of the lateral parts of the peripheral canals; this is less pronounced in the young stages which, therefore, do not diverge much from Maas's figure, in which the canals are fairly narrow. The present specimens likewise agree with *C. duplicata* in the number and shape of the otoporpaes; there are usually three on each of the marginal lappets, and they are very small. Previous authors (Mayer 1910, p. 481; Bigelow 1909, p. 57 and



Text-fig. 16. Distribution of *Cunina duplicata*. New records = ●, previous record = ○, Maas, 1893.

1918, p. 393) point out the considerable resemblance of *C. duplicata* to *C. lativentris*, but the present specimens are certainly entirely different from *lativentris*, and I think we may safely refer them to the species, *duplicata*, described by Maas.

DESCRIPTION OF AN ADULT SPECIMEN (St. 1974) (Pl. VI, fig. 5): Diameter 50 mm. Umbrella flat, the jelly (as preserved in formalin) rather thin and soft; 27 tentacles in different stages of development. The oral wall of the stomach has almost entirely disappeared, but the outlines of the gastric pouches are undamaged. When fully developed, the gastric pouches are tongue-shaped or rectangular, somewhat longer than broad, with parallel sides, separated by spaces of about the same width. The gonads form a continuous, folded band following the edge of the stomach with its gastric pouches uninterruptedly. The lateral parts of the peripheral canals are very broad, usually broader than the inter-radial spaces between them, of equal width throughout their length, about two-sevenths as long as the radius of the umbrella. The distal, transverse part of the canals is narrow. The fully developed tentacles issue from the terminal ends of the gastric pouches; the endodermal tentacle roots are bent sharply downwards and usually invisible from above. In this specimen all the tentacles are strongly contracted and fairly short, reaching only slightly beyond the margin of the umbrella. Several of the tentacles are small (young) and more or less widely separated from the corresponding gastric pouches, which also are smaller than those corresponding to the fully developed tentacles. The peripheral canals flanking the young tentacles are also narrower than the others. In about one-third of the circumference of this specimen, young and fully developed tentacles alternate regularly. Further remarks on the development of the tentacles and gastric pouches will be given below. There are two or three sensory clubs on each of the marginal lappets, and the otoporpaes are very small. The peronia are very narrow, and in the marginal zone the lappets are separated by very slight indentations. The velum is much torn and mutilated. According to a note on the label, the peripheral canal was milk white in colour, otherwise the specimen was transparent and colourless.

Remarks on other specimens

YOUNG STAGES. Even very small specimens may safely be referred to this species on the basis of the gastric pouches, which are elongated, rectangular with parallel sides, as wide as or somewhat narrower than the interradial spaces between them. The youngest specimen is only 4 mm. wide (St. 699) and has 9 narrow gastric pouches and 9 tentacles of equal size, with no indication of additional tentacles developing. A specimen 5 mm. wide (St. 1370) has 8 fully developed tentacles and 2 or 3 small ones. Three specimens from St. 282 are of particular interest. One of them is 7 mm. wide with 10 tentacles of equal size, each of the ten lappets has a slight median incurvation with a tiny rudiment of a tentacle; in this specimen the oral wall of the stomach is retained and has a small circular mouth opening. The two other specimens from St. 282 are somewhat further developed; one of them is 8 mm. wide with 9 fully developed and 8 very small tentacles, the other is 10 mm. in diameter with 11 fully developed tentacles and 9 small ones, a little larger than in the preceding specimen. In both specimens the gastric pouches correspond in size to the tentacles, and these specimens are very similar to the one described and figured by Maas. In subsequent stages the addition of new tentacles and gastric pouches proceeds irregularly, and the number of small tentacles is always less than that of the fully developed tentacles.

The development of additional antimeres is illustrated in Pl. VII, fig. 1. The specimen (St. 100) is 29 mm. in diameter and has a total number of 23 tentacles. In the marginal lappet between two fully developed tentacles (to the left of the figure), the transverse part of the peripheral canal has formed a small centripetal sling, narrow and pointed; the two parts of the sling are close together, forming a narrow groove which will become the future peronium, and at the end of this groove a

very tiny tentacle is situated; as yet there is no indication of a gastric pouch corresponding to this young tentacle. Between the next two fully developed tentacles, the development has proceeded somewhat further; a small gastric pouch has been formed, the sling of the canal has come into communication with it, the peronium has increased considerably in length, but there is still some distance between the tentacle and the gastric pouch. Presumably each of the two original lappets has had three otoporpa, but the median one has disappeared at the beginning of the formation of the canal sling; when the division is finished and the two new lappets have attained their final width, new sensory clubs and otoporpa will arise, so that there will be two or three of them in each of the fully developed lappets. In this specimen the gonads are in the act of developing, but the folding as seen in larger specimens has not yet appeared; the walls of the gastric pouches are smooth.

The total number of tentacles in specimens of different size are as follows:

Diam. (mm.)	4	5	6	6	7	8	8	8	9	10	17	18	19	22	23	23	29	29	31	33	46	48	50	58
No. of tentacles	9	11	10	14	10	10	13	17	12	20	13	18	20	20	18	19	23	29	20	26	20	19	27	24

In some of the specimens the tentacles are greatly extended, being about as long as the diameter of the umbrella. When sensory clubs are retained (Pl. VII, fig. 2) they are seen to be about 56μ in length and 26μ in width; the statolith, which has been dissolved by the formalin, has been deposited in one fairly large space in the terminal end of the club. The sensory club is situated on a small epithelial cushion. The otoporpa is hardly broader than the club and about three times as long.

In all the present specimens the two canals flanking each of the tentacles are at least as wide as the corresponding gastric pouch. May it not be something like this that Haeckel has seen in his genus *Cunissa*, in which 'jede radiale Magentasche an ihrem Distal-Rande in 2 Lappentaschen sich spaltet'? *C. duplicata*, however, cannot belong to either of the two species of '*Cunissa*', none of which have been found since they were described by Haeckel.

DISTRIBUTION. *Cunina duplicata*, previously known from only one locality south of the Cape Verde Islands, occurs in the central and southern parts of the Atlantic between the Cape Verde Islands and South Georgia, and off the southern part of the east coast of Africa. It apparently belongs to the upper layers, though in the southernmost locality it was taken in a haul between 1600 and 1000 m.

COMMENSAL LARVAE OF NARCOMEDUSAE

Larvae of Narcomedusae were found attached to the subumbrella of the following species of medusae: *Bougainvillia platygaster*, *Rhopalonema velatum*, *Rhopalonema funerarium* and *Pantachogon haeckeli*. The larvae evidently belong to four different species. In all, the development proceeds in a very similar way which, however, differs fundamentally from the development of the other narcomedusa-larvae previously described. Larvae attached to the subumbrella of other medusae and feeding by inserting their prolonged manubrium into the stomach cavity of the host were described by McCrady 1856 and 1857, Brooks 1886, Wilson 1887, and Bigelow 1909, while a general survey of the development of narcomedusa-larvae was given by N. J. Berrill in 1950. In all these cases, it is stated by the authors that the larvae propagate by budding, but the primary individual, as well as all the others, develops into a medusa, so that (as emphasized by Brooks) there is no true alternation of generations. In all the present cases, on the other hand, the development is a true metagenesis, as will be seen from the following description.

The larvae are collected in clusters attached to the subumbrella of the host by means of a number of threads, which are really the tentacles of the primary individual of the cluster. These tentacles are solid, with an endoderm consisting of one row of disc-like cells and terminating in an adhesive, knob-like expansion studded with nematocysts. The body of the primary individual is merely a

tiny knob with no indication of a medusoid structure; it acts as a stolo-prolifer from which other individuals arise by budding, and all these individuals are successively developed into medusae. This is especially clearly seen in young clusters consisting of only few individuals. In their youngest stage the medusoid buds are knob-like, but very soon they develop a long, hollow proboscis, like a trunk, with a terminal mouth-opening. The proboscis usually attains a considerable length, before the umbrella of the future medusa makes its first appearance as an annular dilatation of the proximal part of the bud.

I have observed this in all the present specimens. Further development proceeds in rather different ways in the different species, and at the time of liberation the young medusae, derived from the four different hosts, differ so much from each other that they undoubtedly must belong to four different species of narcomedusae. Presumably the infection takes place in a way similar to that described by Brooks (1886), where an actinula-like larva attaches itself to the subumbrella of the host (a *Turritopsis*) by means of its capitate tentacles and gives rise to a number of medusa buds; but in the specimens observed by him the primary larva itself was transformed into a medusa with a long proboscis and an umbrella, and all the medusa buds were, like the primary individual, liberated at a stage provided with two kinds of tentacles. These consisted of four large capitate tentacles directed upwards and four secondary, still very tiny tentacles, whereas, on the contrary, in all the specimens observed by me all the tentacles of the medusa buds are of equal size and structure, and the primary individual remains in a polypoid stage. Accordingly the development must be regarded as a true metagenesis.

Attached to *Bougainvillia platygaster*

(Pl. VII, figs. 3, 4)

St. 680. 30. iv. 31. 22° 36' S, 30° 01' 30" W. Net: TYFB 260-0 m.

St. 683. 2. v. 31. 16° 48' S, 29° 54' 45" W. Net: TYFB 290-0 m.

These localities are off the east coast of Brazil.

The specimens of infected *Bougainvillia* are all of about the same size, 9 mm. in diameter, and all of them are well preserved; all their organs are retained and undamaged (in contradistinction to the other species, see below), but gonads are not developed. The clusters of narcomedusa larvae are always attached to the subumbrella of the host inside the triangular pouches between the subumbrella and the aboral wall of the square, flattened stomach. As long as the clusters are very young, with only few buds, the medusoid buds are usually also seen inside the periphery of the stomach, but in further stages of development the cluster hangs outside the stomach wall, the buds bending their proboscis towards the mouth of the host. The capitate tentacles of the primary individual maintain their grip above the aboral wall of the stomach (Pl. VII, fig. 3); they vary in number between four and six.

St. 680, two specimens infected. (1) With four very small clusters, one in each interradius. Two of them have only one or two tiny buds still without a proboscis, in the third cluster one of the buds has a short proboscis; in the fourth cluster two buds are provided with a long proboscis and one of them with a small umbrella, scalloped in the margin and with tiny rudiments of 8 tentacles. (2) With five clusters of very numerous medusa buds in different stages of development, two clusters in one of the interradial quadrants, one in each of the others (Pl. VII, fig. 3). The 8 tentacles first appear as tiny knobs, but gradually they become elongated and pointed; in young stages they point upwards, but later on they are directed downwards; long and deep peronia are soon developed.

St. 683, one specimen infected. With four clusters of larvae, interradially situated, two of them consisting of only two buds, both with a long proboscis; a third cluster has three buds, one of them with a small umbrella and tiny rudiments of tentacles; in the fourth cluster four of the buds have a long

proboscis, and the largest of them is a well-developed small medusa, not far from liberation. A fifth cluster has accidentally been detached and was found loose inside the bell cavity of the host. Besides the primary individual the cluster consists of two young buds without an umbrella, but each with a long proboscis, and one medusa in an advanced stage of development (Pl. VII, fig. 4). It is 0.7 mm. in diameter; the jelly is fairly thick in the marginal lappets as well as in the central part of the umbrella. The eight marginal lappets are somewhat longer than broad, ovate in outline and somewhat pointed at the end, the peronia are deep in their proximal part, considerably broadening outwards. A peripheral canal is present. The 8 tentacles are directed downwards, tapering in thickness and reaching a little beyond the bell margin. Each lappet carries three otoporpaes, the two lateral ones are about as long as the lappet, the median one reaches almost to the summit of the exumbrella and runs along an elevated and fairly sharp keel. Only the median sensory club is developed; it is comparatively large. The velum is broad. The proboscis is very long, conical in its basal part.

I am inclined to think that these larvae belong to *Pegantha triloba*; the ovate, pointed outline of the marginal lappets, the very long otoporpaes, and the keels on the exumbrella point in this direction, and apart from the proboscis (which is retained as long as the young medusa is attached to the cluster) they are very like the young medusa, 2.5 mm. wide, of this species, figured by Bigelow (1909, Pl. 16, fig. 3).

Attached to *Rhopalonema velatum*

(Pl. VII, figs. 5-7)

St. 250. 17. vi. 27. 36° 09' S, 05° 33' W. Net: TYF 300(-0) m.

St. 254. 21. vi. 27. 35° 04' S, 02° 59' 30" E. Net: TYF 200(-0) m.

St. 679. 29. iv. 31. 26° 06' 30" S, 30° 06' 15" W. Net: TYFB 300-0 m.

These localities are between South Africa and the southern part of Brazil.

In each of these localities one specimen of *Rhopalonema* was found infected with clusters of narco-medusa larvae, attached to the subumbrella near the base of the manubrium by means of the capitate tentacles of the primary individual of each cluster. The hosts are much degenerated, having lost almost all their organs; in the specimens from Stns 250 and 254 the manubrium is retained; gonads and radial canals have entirely disappeared in all the specimens, but in the specimen from St. 254 the canals are regenerated in a very irregular way. Traces of the marginal tentacles may be discerned.

Each specimen carries one cluster of larvae attached near the base of the manubrium, and one of the medusa buds is always much further developed than the others in the same cluster.

The cluster of larvae from St. 250 (Pl. VII, fig. 5) consists of one well-developed medusa with a long proboscis and with elongated, pointed tentacles; two small buds, each with a long proboscis but with only a slight indication of the future umbrella; and in addition an undetermined number of very small knob-like buds. The primary individual (the stolo-prolifer) has four tentacles.

In the cluster from St. 254 (Pl. VII, fig. 6), one medusa is in an advanced stage of development, the proboscis is fairly short, the tentacles have not yet attained their pointed shape but are knob-like. On the top of the medusa three very small buds are seen without any indication of umbrella, two of them with a short proboscis. The stolo-prolifer has six tentacles of somewhat different size.

The cluster from St. 679 (Pl. VII, fig. 7) is in a very early stage of development. There are only two buds, one much larger than the other, both with a proboscis but no umbrella; the stolo-prolifer has three tentacles, and in this cluster it is clearly seen that the buds, which are destined to become medusae, are derived directly from the stolo-prolifer.

Before the liberation, the medusa has 11 short, pointed tentacles, all of equal size, directed downwards. The eleven marginal lappets are square, separated by fairly deep and narrow peronia; each of

the lappets has two statocysts with very short otoporpaes; no peripheral canal. A narrow velum is present.

The presence of otoporpaes and the absence of peripheral canals indicate that the larvae here described belong to some species of *Cunina*. Bigelow (1909, p. 62, Pl. 45, figs. 3-7) found a stolon attached to the subumbrella of a *Rhopalonema velatum*. From the description, it is not quite clear whether the stolon was attached to the host by means of capitate tentacles or whether the primary individual itself attained a medusoid structure. The cluster of medusa buds consisted of several individuals, many of them of about equal size. When liberated they had 6-8 tentacles, the marginal lappets had two statocysts with otoporpaes and no peripheral canal. They were supposed to belong to *Cunina peregrina*. In spite of the larger number of tentacles and lappets (eleven) I am inclined to think that the present specimens also belong to *C. peregrina* which, among the species of *Cunina* with more than (normally) eight tentacles, is the only species destitute of peripheral canals.

Attached to *Rhopalonema funerarium*

(Pl. VII, figs. 8, 9)

St. 2059. 30. iv. 37. $09^{\circ} 11' 24''$ S, $05^{\circ} 17' 24''$ W. West of Angola, Africa. Net: N 450 B 1900-1400 m.

The specimen of *R. funerarium* is fairly well preserved, though without gonads. On the subumbrella, close to the base of the manubrium, a dense cluster of larvae is attached by means of five capitate tentacles of the primary individual, which acts as a stolon-prolifer. The medusoid larvae are very numerous and densely crowded, many of them (at least 15) with a very long proboscis, and several buds have a small umbrella. There is not, as in the other cases described, one single individual much larger than the others, but a fair number are at an equally advanced stage like the one figured in Pl. VII, fig. 8. They have eight small, pointed tentacles. The eight marginal lappets are separated by well-developed, fairly narrow peronia. Each lappet has two fairly large statocysts with small otoporpaes (Pl. VII, fig. 9). No peripheral canals, but a distinct marginal nettle-ring. Velum well-developed.

These medusae differ from those found in *R. velatum* by the number of tentacles and lappets not exceeding eight and by the larger size of the marginal clubs. They probably likewise belong to the genus *Cunina*, but I do not venture to guess which species they may be referred to, possibly to some unknown deep-sea species.

Attached to *Pantachogon haeckeli*

(Pl. VII, figs. 10, 11)

St. 85. 23. vi. 26. $33^{\circ} 07' 40''$ S, $04^{\circ} 30' 20''$ E. West of Cape of Good Hope. Net: N 450 2000(-0) m.

The specimen of *Pantachogon* is destitute of manubrium and gonads; the margin with its tentacle stumps is partly retained, sufficient to identify the species. A cluster of larvae is situated on the subumbrella near the site of the manubrium, which has been lost. The cluster (Pl. VII, fig. 10) consists of medusoid buds in different stages of development connected with each other and with the primary individual by irregularly branched filiform bridges. The primary individual is attached to the subumbrella of the host by three fairly long and thin, capitate tentacles, its body is very small and shows no indication of a medusoid structure. The youngest buds are destitute of tentacles and proboscis; they soon attain a single tentacle, which is capitate, other tentacles are developed successively, so that the older buds have a number (4-6) of tentacles of different sizes, all terminating in a knob-like cluster of nematocysts. Simultaneously with the tentacles a long proboscis is developed. When the umbrella begins to appear, the tentacles are seen to be directed upwards.

Three young medusae had already been detached from the cluster and were found in the subumbrella cavity of the host, retained by the broad velum. One of them is seen in Pl. VII, fig. 11. They are

about 2 mm. in diameter and 1 mm. in height, and they have 7-8 tentacles, fairly long, capitate, and held in an upright position. In this regard they resemble the young medusa of *Cunina octonaria* figured by Brooks (1886), but the eight tentacles are all of equal size. The eight marginal lappets are broad, the peronia deep and broad. Each of the lappets has two sensory organs; the sensory clubs are not yet fully developed, but a short otoporpa is distinctly seen above each of them. A broad peripheral canal is present. Velum is well developed, but fairly narrow. The larval proboscis is reduced, and the ventral wall of the stomach is flattened, with a central mouth opening.

It is difficult to determine the affinity of these larvae. The number of tentacles and lappets may not remain eight. Capitate tentacles may occur in larvae of *Cunina* (*octonaria*, according to Brooks 1886) as well as in *Pegantha* (*clara*, according to Kramp, 1947). Peripheral canals are present in all species of *Pegantha* and in some species of *Cunina*, but are absent in *Solmaris* and *Solmissus*. The larvae described above probably belong either to *Cunina* or to *Pegantha*, but all known species of these genera have their principal occurrence in the upper layers. The present larvae were found attached to the bathypelagic medusa, *Pantachogon haeckeli*, and I therefore presume that they belong to an unknown deep-sea species.

Tabular view of the appearance of the medusae when liberated:

Host	Tentacles		Statocysts per lappet	Otoporpa	Peripheral canals	Umbrella
	Number	Shape				
<i>Bougainvillia platygaster</i>	8	Filiform	3	Very long	Present	With 8 prominent keels
<i>Rhopalonema velatum</i>	11	Filiform	2	Short	Absent	Smooth
<i>Rhopalonema funerarium</i>	8	Filiform	2	Short	Absent	Smooth
<i>Pantachogon haeckeli</i>	8	Capitate, upright	2	Short	Present	Smooth

ZOOGEOGRAPHICAL REMARKS

The occurrence of medusae may be influenced by various physical factors, but some of these are of importance only under extreme conditions. For example, in coastal waters with a considerable influx of fresh water from the rivers, the salinity of the water is of decisive importance in the distribution of medusae (although its influence may vary with the species), but within the oceanic areas covered by the Discovery Investigations variations in salinity are not great enough to have a significant effect. Oxygen content, nitrates and phosphates may indirectly, through the amount of food animals available, determine the abundance of the specimens, but can hardly alter the specific composition of the fauna. Some species of medusae are morphologically adapted to live in the deep water-layers (where the movements of the water are very slight), and are provided either with a very thick gelatinous mesogloea or with a strong musculature. Frequently, however, it is apparently not the depth itself, but the temperature of the water, which prevents certain species from ascending into the upper layers. Thus in the open ocean a dominant factor in the distribution of medusae is the temperature of the water, and for holopelagic species it is often the only factor of importance, although indeed some of these medusae can tolerate a wide range of temperature. For meropelagic neritic forms the configuration of the sea bottom, to which the fixed polyp stages are attached, may also prevent the penetration of some species into areas where the physical conditions might seem suitable to maintain the medusae.

In a discussion of the distribution of the medusae it is necessary to take into consideration their life-history and their ecological habitat. We must distinguish between meropelagic and holopelagic species, and within each of these groups some species are predominantly epipelagic, others predominantly bathypelagic, although in some cases no sharp line of demarcation can be drawn.

The Leptolina, comprising the Antho-, Lepto- and Limnomedusae, are presumably all meropelagic, and the majority of them are neritic, being derived from hydroids which are attached to objects on the bottom in the coastal regions. In many species the duration of the pelagic life is so short that the medusae cannot possibly be carried far away from the coastal waters by the currents, but in some species the pelagic phase is long enough to allow them to drift into remote regions far from their place of origin, either along the coast, if the current takes that direction, or out into the open sea.

Some few species of Leptolina, however, must be designated as truly oceanic, in so far as they are regularly found far out in the great oceans. Some of them may have littoral hydroids, but an oceanic existence is made possible by the ability of the medusa to propagate by budding, producing several successive generations of medusae. In other instances we know nothing about their propagation, either sexual or asexual; we can only state that they do occur in the open oceans, evidently independent of the coasts.

The Trachylina, comprising the Trachy- and Narcomedusae, are holopelagic, passing their whole life-cycle in a free-swimming condition. Some of them are decidedly bathypelagic, occurring in the deep layers only; others are epipelagic, their occurrence being restricted to the surface waters, down to depths of 100 to 250 m. Again, some species are bathypelagic in tropical and subtropical regions, whereas they may be found nearer the surface in cold areas, indicating that they are more dependent on temperature than on the actual depth of the waters. There are also some species which have their principal habitat in the upper layers, but which occasionally, or under certain conditions, descend to quite considerable depths. In some cases, therefore, the distinction between epipelagic and bathypelagic species is to some degree arbitrary.

DISTRIBUTION OF THE SPECIES OF HYDROMEDUSAE TAKEN BY THE DISCOVERY INVESTIGATIONS

Tables 2-4 give the geographical distribution of the Hydromedusae collected by the Discovery Investigations during the years 1926 to 1937, but in order to complete the picture, records of these species from previous expeditions have also been included. The species have been arranged in the following groups:

- (1) Neritic species of Leptolina (Table 2, p. 124).
- (2) Oceanic species of Leptolina and Trachylina, predominantly epipelagic (Table 3, p. 125).
- (3) Oceanic species of Leptolina and Trachylina predominantly bathypelagic (Table 4, p. 126).

The seven new species, the further distribution of which is not yet known, are not included in the tables. In each table the species are arranged approximately according to their distribution from South to North. This gives a general impression within each group of the penetration of the species away from or into the Antarctic waters, and also indicates which of the species are bipolar.

The regions shown in Tables 2 and 3 and used in the discussion of the distribution of the Hydromedusae are based on the proposals put forward by Ekman in his *Zoogeography of the Sea* (1953). I have made some slight alterations in the names of the regions, for example West-Atlantic for East-American, East-Atlantic-tropical for West-African-tropical etc., and I have separated the East-African-tropical area from the comprehensive Indo-West-Pacific-tropical, region as a distinct region. Each of these large regions may of course be subdivided into minor faunistic provinces, but for the sake of simplification I have refrained from doing this as it would make the discussion unnecessarily complicated. The Antarctic region is, however, divided into three sectors: the Pacific, Atlantic and Indian sectors, because the material available varies very greatly in these three areas.

The regions shown in Tables 2 and 3 may be defined roughly as follows:

Antarctic region. The waters south of the Antarctic Convergence, the mean position of which lies between 50-55° S.

West-Atlantic-antiboreal region. Comprising the south-western part of the Atlantic Ocean between the Antarctic and Subtropical Convergences and off the east coast of South America as far north as Montevideo, between 50-55° S and 35° S.

West-Atlantic-tropical region. Comprising the waters off the American coasts between about 35° S and 35° N. Within this region, Discovery Collections were made as far north as about 10° N, midway between Brazil and West Africa.

West-Atlantic-boreal region. Comprising the waters off the American coast from about 35° N up to Labrador.

Arctic region. Comprising the waters north of the Boreal region.¹

East-Atlantic-boreal region. Comprising the waters of north-western Europe from the English Channel to the north point of Norway.

Mediterranean-Atlantic region. Comprising the Mediterranean Sea and the adjacent Atlantic Ocean between the Bay of Biscay and the Cape Verde Islands. Within this area only four Discovery Collections were made, between about 24° N and 39° N.

East-Atlantic-tropical region. Comprising the waters off the west coast of Africa between about 15° N and Great Fish Bay in 17° S.

South-African region. Comprising the waters off the African coasts between Great Fish Bay on the west coast and Durban, in about 28° S, on the east coast.

East-African-tropical region. Comprising the waters off the east coast of Africa, north of Durban. No collections were made by the Investigations in any other part of the Indo-West-Pacific-tropical region, between the years 1926 and 1937.

Indo-West-Pacific-tropical region. Comprising the waters of the tropical Indian Ocean and the western Pacific from the Polynesian Is. northwards to about 35° N.

Indian-temperate region. Comprising the antiboreal belt north of the Antarctic Convergence and the subtropical tract between South Africa and south-western Australia.

South-Australian-New-Zealand region. Off the Australian coasts, south of about 30° S, and New Zealand.

Pacific-boreal region. Comprising the waters north of 35° N in the western part; 25° N in the eastern part.

East-Pacific-tropical region. Between southern California, about 25° N, and about 8° S, off northern Peru.

Peru-North-Chilensis region. Comprising the waters between 8° S and 42° S.

Of course Ekman's areas mainly apply to the fauna of the continental shelves; his divisions of the oceanic regions are very wide and comprise only a warm-water region and one or two cold-water regions in each of the three great oceans. It seems desirable, however, to distinguish between minor areas also in the distribution of oceanic animals, especially for the epipelagic species, which are partly exposed to the same currents as the neritic forms. Consequently, in Table 3 which shows the distribution of the epipelagic *Leptolina* and *Trachylina*, I have retained the same divisions for the Atlantic Ocean as I have used in Table 2 for the distribution of the neritic forms. But I have condensed the Indian-temperate and the South-Australian-New-Zealand regions into an Indo-West-Pacific-antiboreal region, and have united the Peru-Chilensis region with the East-Pacific-tropical region, because in these areas only such species were found as occur in tropical seas. This arrangement has been adopted here to coincide with the areas covered by the Discovery Investigations; in a general zoogeographical discussion I might proceed otherwise.

Bathypelagic species, which live under quite different conditions, are not limited to regions in the same way, and in Table 4 it will be seen that I have condensed the distributional regions still further.

¹ The deep water-layers in the Davis Strait, west of southern Greenland belong to the boreal region; the deep water-layers in the Norwegian Sea belong to the arctic deep-sea area.



NERITIC SPECIES OF LEPTOLINA (Table 2)

As Table 2 shows, not all the distributional regions are covered by the Discovery collections, and the area most extensively investigated is the Atlantic Ocean, from which by far the most material is available and to which the succeeding remarks mainly apply.

In all, thirty-four species of neritic Leptolina have been taken by the Discovery Investigations—these include the following new species: *Russellia mirabilis* from the Pacific and Atlantic sectors of the Antarctic and later found also in West-Indian waters; *Rathkea africana* from tropical West Africa; *Leuckartiara annexa* from South Africa and tropical East Africa; and *Ectopleura sacculifera* from the Pacific coast of Ecuador.

Among the remaining thirty species, nine occur in Antarctic waters, and it is characteristic that at least six of them are circumpolar. Eighteen species occur in the West-Atlantic-antiboreal region. Two of them are bipolar, *Halopsis ocellata* and *Staurophora mertensi*, both of which are found in the northern boreal region as well as in antiboreal waters near the Falkland Islands. *Staurophora mertensi* also penetrates into the Antarctic as far south as the South Orkney Islands. Apart from *S. mertensi*, only three species are common to both the West-Atlantic-antiboreal and the Antarctic regions, namely: *Cosmetirella davisi*, *Bougainvillia macloviana* and *Tiaricodon coeruleus*. This is very remarkable, since, according to Ekman (1953, p. 349), 'Quite a number of (pelagic) species are common for both this region (the antiboreal) and the antarctic, that is for the whole of the cold-water region of the Southern Ocean.' As examples Ekman mentions some species of copepods, amphipods, and euphausiids; evidently this does not hold good as far as the epipelagic medusae are concerned (see also p. 98 under the epipelagic Trachylina). This impression is confirmed by the other medusae known from the two regions but not collected by the Discovery Investigations; among thirteen of these species seven are purely antarctic, five occur in the West-Atlantic-antiboreal region (mainly at the Falkland Islands), but are not recorded from antarctic waters, and only one is known from both regions.

In the south-western Atlantic, the Antarctic Convergence evidently constitutes a fairly effective barrier between the antarctic and antiboreal faunas of neritic medusae, very few species penetrating from one of these regions to the other. The fauna of the West-Atlantic-antiboreal region, however, is a mixture of different constituents. Several of its inhabitants are characteristic of the area, but there is a considerable admixture of species belonging to tropical waters. Seven of the species shown in Table 2 penetrate into the tropics, but nine are known from southern waters only. The influence of the Brazil Current must account for this admixture of tropical species, some of which are distributed northwards into the boreal parts of the Atlantic. The antiboreal region is thus sharply limited to the south, but not to the north, the Subtropical Convergence (called the antiboreal by Ekman) being a less restricting factor to these animals than is the Antarctic Convergence.

Three of the antiboreal species appear to have a very restricted distribution between the Falkland Islands and the neighbouring coast of South America; they are *Aglauropsis conanti*, *Proboscidactyla mutabilis* and *Laodicea pulchra*. *Bougainvillia macloviana*,¹ *Tiaricodon coeruleus* and *Phialella falklandica* have a scattered occurrence in the southern parts of the Indian and Pacific Oceans also, while of particular interest is the appearance in the South African region (see pp. 4, 15, 30, 31) of the two decidedly southern species, *Sarsia gracilis* and *Halitholus intermedius*, as well as of the two antarctic species, *Mitrocomella frigida* and *Cosmetirella davisi*.

Very few neritic Leptolina were collected by the Discovery Investigations in the tropical Atlantic and they afford evidence of no particular interest, but the material from the South African region on

¹ The occurrence of *B. macloviana* in the East-Atlantic-boreal region (the North Sea) is undoubtedly due to transportation by ships.

the other hand yields important results. Among the eleven neritic species taken there by the Investigations, two were previously known only from the tropical Indian and Pacific Oceans: *Heterotiara minor* has now been taken off the south-east coast of Africa, and *Zygocanna vagans* west of the Cape of Good Hope. *Neoturris pileata*, regarded as a North Atlantic species, has been found considerably farther south than before off the west coast of Africa. All the other species found in the South African region also occur in the West-Atlantic-antiboreal region or in the Antarctic and three of them are widely distributed in the Atlantic Ocean. One of these, *Phialidium simplex*, has a scattered distribution and is known from North-East Australia, Brazil and the Falkland Islands. On the whole, the South African neritic Leptolina evidently do not constitute a local fauna but are a mixture of species, widely distributed and of different origins.

However, in this region the most interesting finds are undoubtedly those of *Sarsia gracilis* and *Halitholus intermedius*, previously known only from the Falkland Islands, and those of the two antarctic circumpolar species, *Mitrocomella frigida* and *Cosmetirella davisii*, the last also occurring in subantarctic waters near the Falkland Islands. All these medusae are so small that presumably their pelagic life is of short duration and they have little chance of being carried long distances by the currents. The nearest shallow-water area is the plateau of Bouvet Island, which is about 1300 miles away from South Africa. We must presume, therefore, that there is an indigenous, local population of these species in South African coastal waters.

In the neighbourhood of South Georgia, *Cosmetirella davisii* was abundant in the surface water at temperatures varying between about 0.5°C . and 3°C .; in subantarctic waters it lives at temperatures of about $5-6^{\circ}\text{C}$., sometimes perhaps as high as 9°C . (e.g. St. WS 832, near Patagonia). At St. 102, a short distance south of the Cape of Good Hope, it was taken in October 1926 in about 54 m. below the surface, where the temperature was about 14°C . *Sarsia gracilis* was taken at St. 91, in False Bay, near Capetown, in September 1936, at 35 m. and in temperatures of about 13.5°C . *Halitholus intermedius* was found in two South African localities, St. 1374 (May 1934) near the south-east coast, and St. 100 (October 1926) west of Capetown, and *Mitrocomella frigida* occurred at St. 256, somewhat farther west of the Cape of Good Hope, in June 1927. Unfortunately we do not know the exact depth of these finds, nor the temperatures, but the medusae were undoubtedly taken in the upper layers in fairly warm water. The hydrographical conditions round the South African coasts are very complicated, and the occurrence of these southern species must presumably be explained as being due to the cooling influence of the Benguela Current.

Very few neritic species of Leptolina were collected in the East-African-tropical region, where *Octophialucium aphrodite* occurred, or in the Peru-Chilensis region where *Aequorea coerulescens* and *A. macrodactyla* were taken. The occurrence of these three species in these regions presents nothing of particular interest.

OCEANIC SPECIES OF LEPTOLINA AND TRACHYLINA PREDOMINANTLY EPIPELAGIC (Table 3)

Of the oceanic Leptolina, predominantly epipelagic, four species were taken by the Discovery Investigations. All of them occur in the warm parts of the oceans, although *Phialopsis diegensis* is also recorded from boreal waters. *Bougainvillia platygaster* and *Euphysora furcata* have so far only been taken in the Atlantic and in the westernmost parts of the Indian Ocean. None of the four species are found in antiboreal or antarctic seas.

Of the oceanic Trachylina, predominantly epipelagic, twenty species were collected by the Discovery Investigations, the majority of them being widely distributed in all the great oceans, mainly in the tropical regions. One species, *Cunina globosa*, was previously known only from the tropical East Pacific

and has now been taken in South African waters. The nineteen other Discovery species all occur in the East-Atlantic-tropical region, and fifteen of these are also found in the Mediterranean-Atlantic region and seventeen in the West-Atlantic-tropical region. Only seven species are distributed farther north into boreal waters in the North Atlantic, all of them as more or less stray visitors from the south; among them *Solmaris corona* which occurs in the eastern Atlantic, from South Africa to Norway.

Of particular interest is the southward distribution of the eighteen species which are more or less generally distributed in the warm parts of the Atlantic, most of them being also known to occur in the Indian and Pacific Oceans. With two exceptions (*Pegantha triloba* and *Pegantha rubiginosa*) they are all found in the South African region. In the western Atlantic eight of the species occur in the antiboreal region; as stated on page 96 this region receives a considerable admixture of neritic medusae from the tropical region. On the other hand, the Antarctic Convergence seems to establish as effective a barrier to the southward distribution of the holopelagic, epipelagic Trachylina as in the case of the neritic Leptolina. According to some diagrams given by Dilwyn John (1936, fig. 6, p. 203 and fig. 29, p. 246) the Antarctic Convergence seems to establish an equally sharp barrier to the distribution of the southern species of *Euphausia*. None of the epipelagic Trachylina are characteristic of the antarctic region, and only two of the species belonging to warmer seas have been found in antarctic waters, *Solmundella bitentaculata* which is circumpolar, and *Pegantha martagon* which was taken in the Pacific as well as in the Atlantic sector of the antarctic region. These two species must accordingly be very eurythermal, whereas none of the other species are able to cross the Antarctic Convergence.

OCEANIC SPECIES OF LEPTOLINA AND TRACHYLINA PREDOMINANTLY BATHYPELAGIC (Table 4)

Most species of bathypelagic medusae have a more or less circumglobal distribution, and several of them also have an extensive distribution from north to south. Submarine barriers may prevent them from penetrating into enclosed deep-sea areas, otherwise they are independent of the coasts. A survey of their geographical distribution may therefore be given by means of comparatively few, wide regions. It is, however, insufficient merely to distinguish between warm-water and cold-water regions, so I have subdivided them in order to give a clearer impression of the distribution of the species, with special regard to the results obtained by the Discovery Investigations.

With the exception of the semibenthic *Ptychogastria polaris*, none of the bathypelagic species collected by the Discovery Investigations occurs in arctic deep-sea areas. It therefore seems best to exclude the Arctic region and to divide the great oceans into boreal, tropical, and antiboreal belts. The Antarctic region with its three sectors must, however, be kept separate. The interesting series of stations off the east coast of Africa also calls for a separate treatment of this region, as do the waters around South Africa, because the latter form a transitional area between the Atlantic and the Indian Oceans, and because extensive collections were made there.

LEPTOLINA predominantly bathypelagic. Besides the new species *Euphysora gigantea*, which was taken in deep water in the Atlantic sector of the antarctic region and in the antiboreal part of the south-western Atlantic, six species belonging to this group were collected, all of them Anthomedusae. *Calycopsis bigelowi* was previously known from the East-African-tropical region only; now it has been taken in deep water west of the Cape of Good Hope. The five other species are widely distributed in the deep parts of the Atlantic Ocean, in tropical as well as boreal regions. With the exception of *Pandea rubra*, which occurs in the northern Pacific, none of these species are recorded with certainty from Indo-Pacific waters; this is remarkable, considering the wide distribution of almost all species

of bathypelagic Trachylina. It is very interesting that three of the species, *Pandea rubra*, *Chromatonema rubrum* and *Tiaranna rotunda*, were taken in the antarctic region (see fig. 5, p. 26) in company with several bathypelagic species of Trachymedusae. They were taken in the deep water below the antarctic surface water at temperatures ranging between about 0° and 1.7° C. Hydrographical observations are not available from all the localities where these species were collected, but from observations at neighbouring stations the temperatures may approximately be stated as follows:

Pandea rubra

- St. 151. North of South Georgia. Jan. 1927. 1025–1275 m. 1–1.5° C.
 St. 1131. East of South Georgia. Feb. 1933. 1000–800 m. 1.6–1.7° C.
 St. 1989. South-east of South Georgia. Mar. 1937. 1500–1200 m. 0.2–0.4° C.

Tiaranna rotunda

- St. 1702. Off Wilkes Land. Mar. 1936. 2000–1250 m. 0° C.
 St. 1723. Off Queen Mary Land. Mar. 1936. 800–500 m. 1.6–1.7° C.

Chromatonema rubrum

- St. 1719. Off Knox Land. Mar. 1936. 950–55 m. 0.3–0.5° C.
 St. 1780. South-west of Bouvet Island. June 1936. 700–450 m. 1.5° C.
 St. 1871. East of Graham Land. Nov. 1936. 1450–1000 m. 0–0.4° C.
 St. 2006. Off Coats Land. Mar. 1937. 1750–1400 m.?

The temperatures in the deep and intermediate layers in the warm seas, where these medusae also occur, are not much higher, usually below 4° or 5° C., and from the North-Atlantic basin *Tiaranna* and *Chromatonema* penetrate far up into the Davis Strait west of Greenland; they may therefore be designated as bathypelagic cold-water species. Apparently *Annatiara affinis* and *Bythotiara murrayi* do not penetrate into the subantarctic or antarctic regions. They are not so strictly bathypelagic as the other species mentioned above, but belong rather to the intermediate layers, about 200–400 m. or so below the surface, where the water-temperatures are somewhat higher than in the deep-sea proper.

TRACHYLINA predominantly bathypelagic. *Ptychogastris polaris* occupies a separate position; it is therefore not included in Table 4. It is partly benthic, for it clings to the sea-bottom by means of the suckers on its tentacles, but may occasionally swim upwards in the water. It has a bipolar distribution, occurring in arctic and northern-boreal as well as in antarctic areas. It was collected by the Discovery Investigations, at the bottom in two localities in the neighbourhood of the South Shetland Islands, St. 177, depth 1080 m. and St. 1958, depth 830 m. We have no information of the bottom-temperatures at these stations; they have presumably been about 0.5–1° C.

The distribution of the two species at the bottom of Table 4, *Crossota alba* and *Tetrorchis erythrogaster*, is imperfectly known and needs no discussion here.

Haliscera racovitzae and the three species of *Arctapodema* have a predominantly antarctic distribution, though *A. amplum* also occurs in the tropical Atlantic and in the Mediterranean; the others were previously known only from antarctic seas, where they occur at intermediate depths, not in the deepest layers. *Haliscera racovitzae* was taken at St. 355, east of South Georgia, in a haul 750–500 m., temperature unknown, probably about 1.7° C., and was previously recorded from the Weddell Sea and near the Antarctic Continent, about 70° S, 82° W. *Arctapodema amplum* was taken at St. WS 160, north of South Georgia, 550–250 m., temperature 2.0–1.9° C., and at St. WS 388, off the South Shetland Islands, 400–250 m., temperature –1.1° to –1.3° C. Since this species occurs in the tropical Atlantic and in

the Mediterranean and is recorded from several localities in the antarctic region (see text-fig. 9, p. 57), it must be very eurythermal. *Arctapodema antarcticum*, previously known only from near the Antarctic Continent in about 90° E, was taken in four localities, St. 1718, off Knox Land, 64° 23' S, 106° 33' E, 900–550 m.; St. 1838, west of the South Sandwich Islands, 700–250 m.; and near the Shag Rocks, at St. 1917, 1400–1000 m., and St. 1919, 1800–1300 m. The temperature of the deep layers was not measured at any of these stations; it probably varied between 0.5° and 2.5° C. Accordingly this species belongs to the 'warm deep water'; but it is not one of the cosmopolitan bathypelagic species penetrating southwards towards the antarctic shelf.

The third species of *Arctapodema*, *A. australe*, was not taken in the antarctic region by the Discovery Investigations, but it was described from the Gauss Station and thus apparently belongs to the antarctic fauna. It is of considerable interest that this species together with *A. antarcticum* was taken much farther north in the Indian Ocean, about 32° S. Both were taken in deep water, *A. antarcticum* at St. 1749, at 1050–600 m., *A. australe* at St. 1753, at 2900–1400 m. These stations are about midway between South Africa and south-west Australia, above the northward continuation of the Kerguelen–Gaussberg Ridge and the water-temperatures are in no way remarkable. In the series of stations along a line in 32° S, the temperatures in the deep layers increased fairly evenly from St. 1738 near Australia to St. 1762 and 1763 south of Madagascar, approximately as follows:

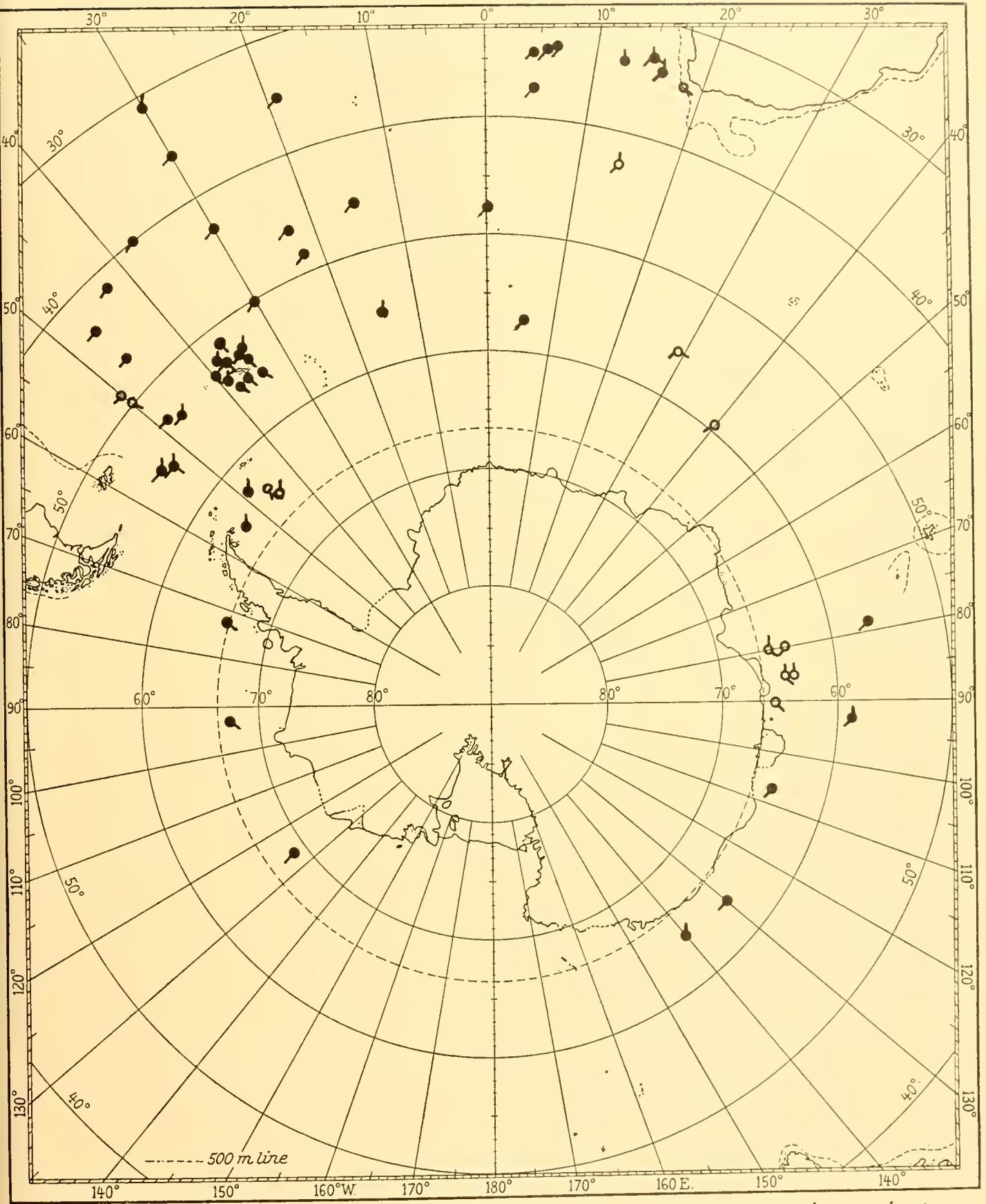
	St. 1738	St. 1750	St. 1752	St. 1762/63
600 m.	8.5° C.	10.7° C.	10.7° C.	12.4° C.
1000 m.	3.9°	6.5°	6.0°	8.1°
1400 m.	2.8°	3.0°	3.1°	3.6°
2900 m.	1.65°	1.6°	1.7°	2.3°

There is no indication of particularly low temperatures at Stns 1750 and 1752 (there are no measurements from Stns 1749 and 1753 where the two species were collected), which might explain why these antarctic medusae were found just here. Nevertheless, their occurrence in this tract of the deep water may indicate that the northward movement of the antarctic bottom water has been especially strong along the ridge (cf. Deacon 1937, p. 97).

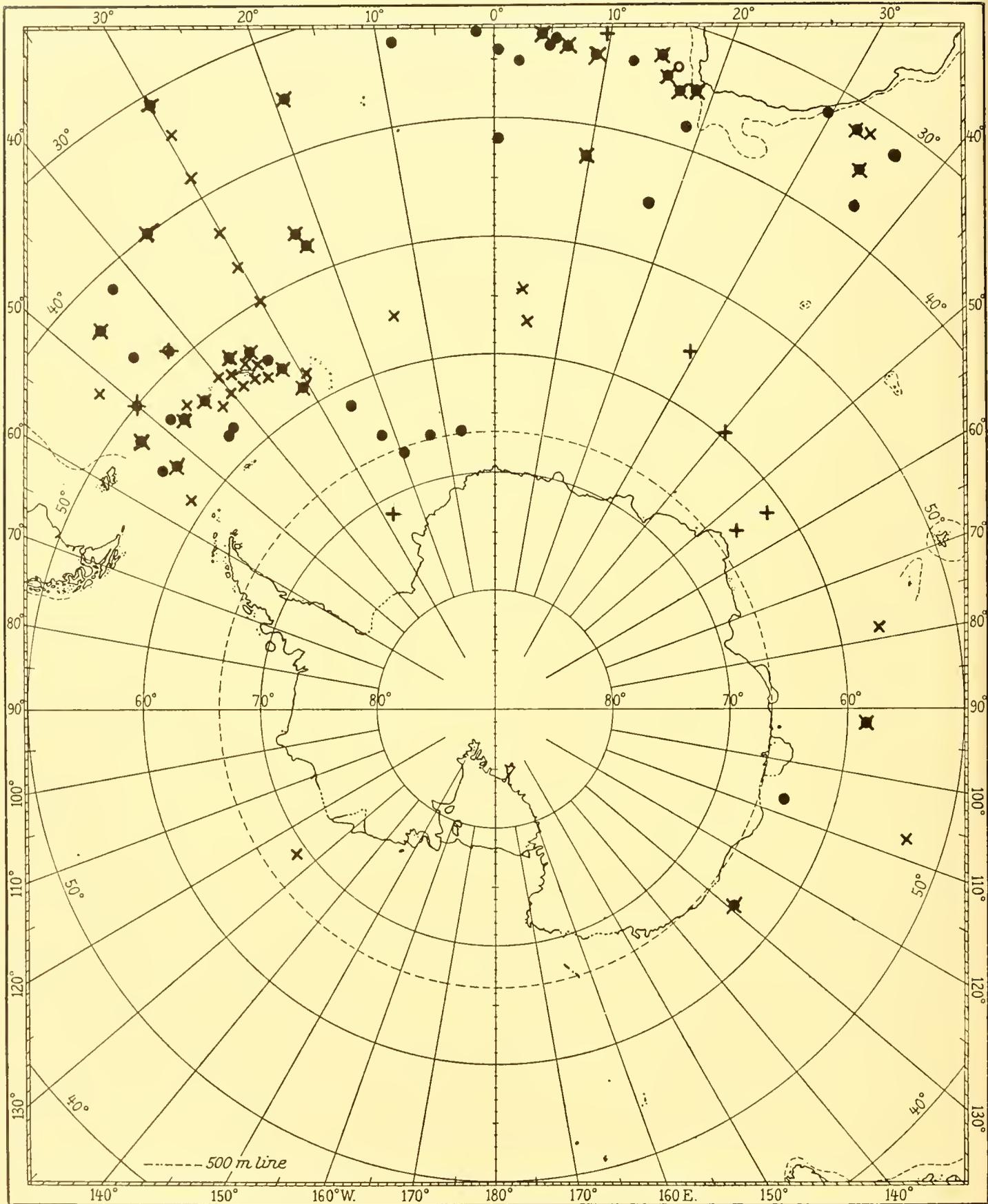
The remaining nine species of bathypelagic Trachylina are widely distributed, most of them are almost cosmopolitan in the deep water of the oceans. *Crossota brunnea*, however, occurs only in the southern hemisphere; *Haliscera conica* occurs somewhat farther north in the Atlantic and in the Mediterranean, but it has not been observed outside the Atlantic area except in the antarctic region, where it is circumpolar.

In contradistinction to the epipelagic Trachylina, most of the widely distributed bathypelagic species penetrate into the antarctic region, but there are also some species which seem to avoid the southern regions. All of them occur in the area around South Africa, most of them extending also into the boreal parts of the Atlantic and Pacific Oceans. Five of these species, *Crossota brunnea*, *Pantachogon haeckeli*, *Haliscera conica*, *Halicreas minimum*, and *Botrynuma brucei*, penetrate into the antarctic region (see Text-figs. 17–18). Probably all of them are circumpolar, but very few collections have been made in the Pacific sector. The depths at which they were taken cannot be stated exactly but ranged between about 700 and 2400 m., though mainly at more than 1000 m. below the surface. Accordingly their occurrence in the antarctic region is restricted to the 'warm deep water'. One might perhaps be inclined to anticipate a difference in their bathymetric distribution according to the distance from the continental slope, but nothing is indicated by the available data. There is not much difference in the southward distribution of the species. The range of temperature was between about 0.2° and 1.8° C.

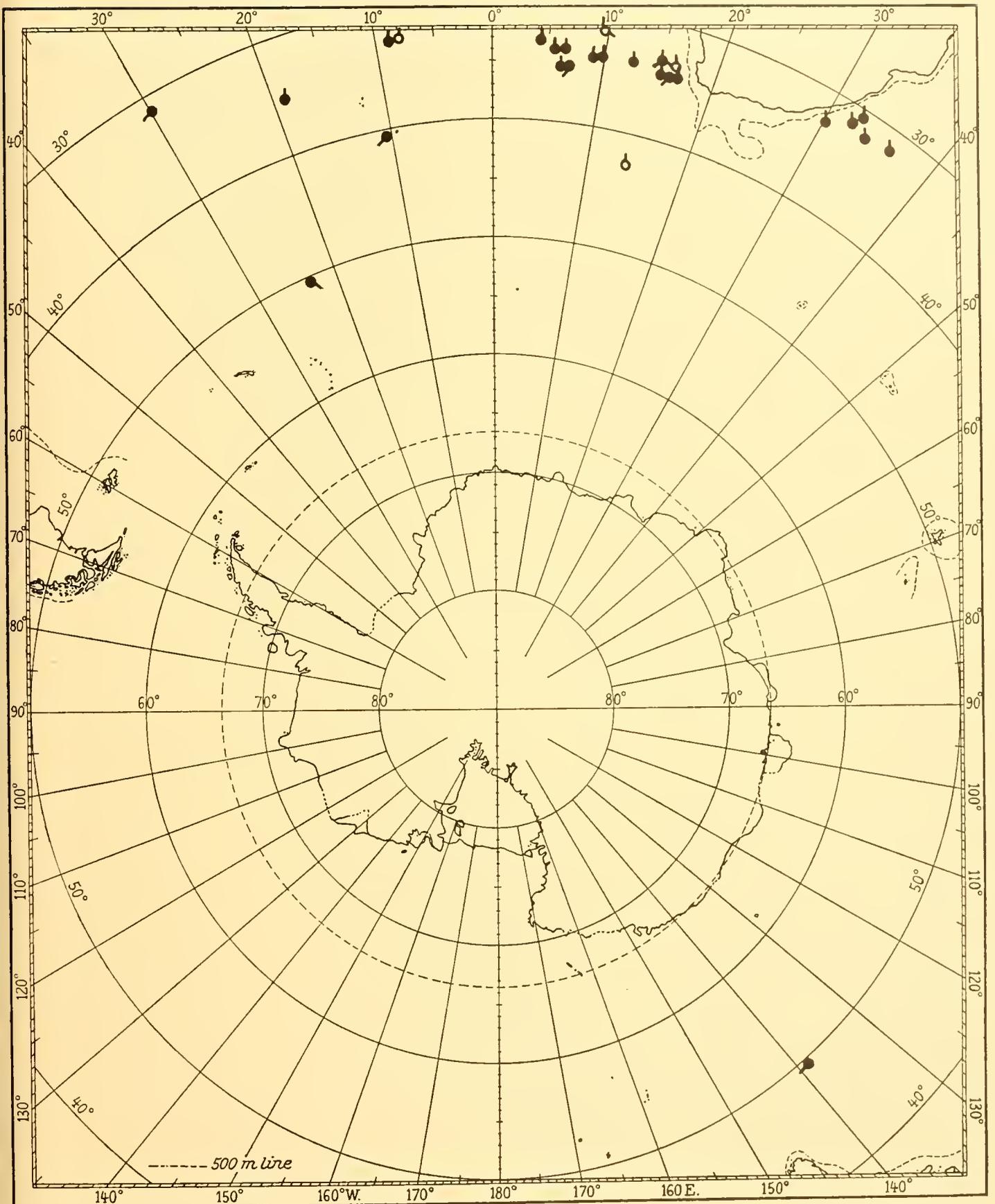
In contradistinction to these preceding five species, *Rhopalonema funerarium*, *Colobonema sericeum*, *Halitrephes maasi* and *Aeginura girmaldii* do not approach the antarctic region (see text-fig. 19). All of



Text-fig. 17. Distribution of: *Botrynema brucei* = ●, previous records = ○. *Crossota brunnea* = ●, previous records = ○. *Haliscera conica* = ●, previous records = ○.



Text-fig. 18. Distribution of: *Halicreas minimum* = ●, previous records = ○. *Pantachogon haeckeli* = ×, previous records = +.



Text-fig. 19. Distribution of: *Colobonema sericeum* = ●, previous records = ○. *Halitrephes maasi* = ●, previous records = ○.
Rhopalonema funerarium = ●, previous records = ○.

them have a circumglobal distribution in the warm and temperate zones, where they generally occur in company with the five species mentioned above. *Rhopalonema funerarium* was taken some distance north of South Georgia, $50^{\circ} 18' S$, in the intermediate layers (340–150 m., temperature $2.5-1.5^{\circ} C.$). It is not strictly bathypelagic, being sometimes taken at less than 200 or 300 m. below the surface, but usually deeper down (e.g. at St. 2064 in a haul 1600–1050 m.). In the waters west of Africa it was taken at temperatures between about 4° and $9^{\circ} C.$ *Halitrephes maasi*, which mainly belongs to the southern hemisphere, may likewise be taken nearer the surface (e.g. at St. 893, south of Australia, in 110–0 m.); but as a rule it occurs at considerable depths. The lowest temperature at which it was found by the Discovery Investigations was about $4^{\circ} C.$, at St. WS 127, south of Gough Island, in 1000–650 m. *Colobonema sericeum* was taken in deep water in numerous localities, partly west of the tropical part of Africa, partly in the Atlantic and Indian Oceans, west and east of South Africa, at temperatures from about $3^{\circ} C.$ upwards. *Aeginura grimaldii* was only found in the tropical regions west and east of Africa. With the exception of *Halitrephes maasi*, these species occur in the northern Atlantic at temperatures similar to those at which they were found near their southern limits of distribution. Though in their principal areas of distribution, horizontal as well as vertical, these species concur with the other bathypelagic Trachylina, they evidently require a slightly higher temperature than species which are able to penetrate into the deep water of the antarctic region.

SUMMARY OF THE ZOOGEOGRAPHICAL RESULTS

The Discovery Investigations have greatly augmented our knowledge of the geographical distribution of the Hydromedusae; in all the areas examined some species were found which had not been observed there before. The numbers are seen in the tables, but it should be noted that the number of species taken in each region is not an index of the variety of the medusan fauna, for the intensity of sampling was very uneven in the different regions. Nevertheless, the figures tell us something about the results obtained.

According to the maps of distribution produced by Thiel (1936), some species of Trachylina might previously have been taken in areas whence in the present paper they are designated as new, but, as already mentioned, Thiel has in several cases united two or more species which makes his maps unreliable.

A number of species are endemic in the antarctic region, most of them neritic species of Leptolina, and we can now state that their distribution is circumpolar (Table 2). Two of them, together with two species previously known only from the Falkland Islands, are found to inhabit the coastal waters of South Africa. Among the bathypelagic Trachylina three species presumably belong to the antarctic seas, but two of them were taken in deep water within a restricted area farther north, $32^{\circ} S$, in the Indian Ocean (Table 4). Altogether ten species were found as new to the antarctic region, four of them are new species, and three of them are bathypelagic Anthomedusae which are widely distributed in the Atlantic Ocean from north to south (Table 4). Most of the species new to antarctic waters were found in the Atlantic sector, which was much more thoroughly investigated than the other sectors.

Our previous knowledge of the fauna of Hydromedusae in the waters off the east coast of South America was deficient. Twenty-eight species were collected in the antiboreal part of the south-western Atlantic, fifteen of them new to the region. The neritic and epipelagic fauna of Hydromedusae in this region is a mixture of species of very different origins; some few of them may be designated as true warm-water species, but most of them occur both in tropical and boreal waters (Tables 2 and 3). There are, however, also a number of neritic Leptolina which are characteristic of this region, though some of them have extended their distribution into the South African region. It is of particular

interest that very few epipelagic species of medusae are common to antarctic and antiboreal waters, the Antarctic Convergence evidently constituting an effective barrier to the distribution of these animals.

The number of species found in the West Atlantic tropical region was twenty-six, of which twelve were new to the area; all of them have an extensive geographical distribution.

Our knowledge of the fauna of medusae off the tropical west coast of Africa was considerably increased by the Danish 'Atlantide' Expedition in 1945-46, twenty-eight species of Hydromedusae being recorded as new to the area (Kramp 1955). Among the few species, which now may be added to the list, only two give occasion for some surprise: *Leuckartiara octona* which is a predominantly northern species, and *Crossota alba* which up to now was only known from the northern Pacific.

The fauna in the waters around South Africa is a mixed fauna; up to now it was very imperfectly known, but now we can state that it is a rich fauna, as far as the Hydromedusae are concerned. Forty-nine species were found by the Discovery Investigations, and among them no less than thirty-three are new to the region. Most of the finds are not astonishing, considering the complicated hydrographical conditions in this area, though several species were found to be distributed considerably farther south than known before. Three species, *Heterotiara minor*, *Zygocanna vagans* and *Cumina globosa*, were previously known only from Indo-Pacific waters. Of very considerable interest is the occurrence of the four antarctic and subantarctic neritic species, *Sarsia gracilis*, *Halitholus intermedius*, *Mitrocomella frigida*, and *Cosmetirella davisii* in the South African coastal area (see, p. 105).

A series of stations off the tropical east coast of Africa was made in April-May 1935. Twenty-one species of Hydromedusae were found, thirteen of them new to the region. Only two neritic species were found, *Leuckartiara annexa*, which is a new species, and *Octophialucium aphrodite*, which was previously known only from the Malayan Archipelago and the Philippines. All the other species found in this series are oceanic, mainly epipelagic, and four of these are now recorded for the first time from outside the Atlantic Ocean (see Table 3).

The twelve species collected in the Indian temperate region, eight of them new to the area, are all oceanic forms, widely distributed except the two species of *Arctapodema*, previously known from antarctic waters only.

The material available from the few hauls in the temperate and warm parts of the Pacific Ocean consists of only six species, one of which is a new species, *Ectopleura sacculifera*, which was taken off the coast of Ecuador. The others are of no great zoogeographical importance.

A comparison between the three tables may be summarized as follows:

Table 2. A considerable number of the neritic species of Leptolina collected by the Discovery Investigations are inhabitants of antarctic or subantarctic seas, where most of them have a circum-polar distribution. A similar number belong to warm or temperate waters; some of these have an extensive distribution from north to south, but only one penetrates into the antarctic region, namely, *Staurophora mertensi* which is bipolar. On the other hand, several of these species have a comparatively narrow distribution from west to east, being restricted either to the Atlantic area or to the Indo-Pacific areas; this also applies to some of the subantarctic species. It may partly be due to deficiency of knowledge, but it seems to be characteristic of the neritic forms that many of them occur within restricted areas and, apart from arctic and antarctic species, few of them have a circum-global distribution. In this respect they differ from the oceanic medusae.

Table 3. The oceanic, epipelagic Leptolina are predominantly warm-water species and do not approach the antarctic waters.

Most of the epipelagic Trachylina are widely distributed in the oceans; only three species are apparently restricted to the Atlantic. On the other hand, among the twenty species collected by the Discovery Investigations only two, which are very eurythermal, penetrate into the antarctic region.

Table 4. The bathypelagic species of *Leptolina* behave in the same manner as the bathypelagic *Trachylina*. The majority of the bathypelagic species are almost cosmopolitan in the deep parts of the oceans, and several species occur in the 'warm deep water' of the antarctic region; but some species require a slightly higher temperature. Ekman (1953, p. 365) calls attention to the interesting fact that 'the comparatively slight difference in temperature between 3° and 0° or 1° seems in this case to be decisive'. This evidently applies to these few species of bathypelagic medusae, whereas a greater number of species may endure the lower temperatures in the deep water below the antarctic surface water.

The distribution of medusae, as of other pelagic animals, affords a multitude of highly interesting problems, and only some few of them are touched upon in the present paper. There are still extensive areas of the sea which are insufficiently investigated, but the comprehensive collections of the Discovery Investigations have contributed greatly towards a better understanding of many problems, the more so because the great majority of the specimens are well preserved. Certain determination of the species was therefore possible, and it should always be borne in mind that this is a necessary condition to every discussion of distributional questions.

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Table 1 (cont.)

'Discovery' Station	Position	Date	Gear	Depth (metres)	Species
		1927 (cont.)			
247	37° 20' 00" S, 12° 47' 30" W	13. vi	TYF	100-115(-0)	<i>Cunina peregrina</i>
248	37° 15' 00" S, 12° 20' 00" W	14. vi	TYF	0-5	<i>Solmissus marshalli</i>
250	36° 09' 00" S, 05° 33' 00" W	17. vi	TYF	300(-0)	<i>Pegantha clara</i>
253	35° 06' 00" S, 02° 19' 00" E	21. vi	TYF	1000-1050	<i>Pegantha laevis</i>
254	35° 04' 00" S, 02° 59' 30" E	21. vi	TYF	200(-0)	<i>Pegantha martagon</i>
256	35° 14' 00" S, 06° 49' 00" E	23. vi	TYF	850-1100(-0)	<i>Solmundella bitentaculata</i>
270	13° 58' 30" S, 11° 43' 30" E	27. vii	TYF	200(-0)	<i>Aegina citrea</i>
270	13° 58' 30" S, 11° 43' 30" E	27. vii	N 70 B	126-0	<i>Liriope tetraphylla</i>
273	09° 38' 00" S, 12° 42' 30" E	31. vii	TYF	200-230(-0)	<i>Crossota brunnea</i>
273	09° 38' 00" S, 12° 42' 30" E	31. vii	N 100 B	118-0	<i>Colobonema sericeum</i>
275	07° 51' 00" S, 12° 42' 00" E	4-5. viii	N 70 H	0-2	<i>Pantachogon laeckeli</i>
276	05° 54' 00" S, 11° 19' 00" E	5 viii	TYF	150(-0)	<i>Rhopalonema velatum</i>
276	05° 54' 00" S, 11° 19' 00" E	5 viii	N 70 B	110-0	<i>Haliscera conica</i>
280	00° 36' 00" S, 08° 28' 00" E	10. viii	TYF	100-200(-0)	<i>Halicreas minimum</i>
281	00° 46' 00" S, 05° 49' 15" E	12. viii	TYF	850-950(-0)	<i>Cosmetirella davisi</i>
282	01° 11' 00" S, 05° 38' 00" E	12. viii	TYF	300(-0)	<i>Calyropsis borchgrevinkii</i>
284	02° 13' 00" S, 01° 52' 00" E	15. viii	N 100 B	71-0	<i>Zanclonia weldoni</i>
286	03° 06' 30" S, 03° 53' 00" W	17. viii	TYF	125(-0)	
287	02° 49' 30" S, 09° 25' 30" W	19. viii	TYF	800-1000(-0)	
290	03° 25' 25" N, 16° 50' 52" W	24. viii	N 70 B	86-0	
291	03° 46' 00" N, 16° 49' 00" W	24. viii	TYF	100(-0)	
296	08° 12' 00" N, 18° 49' 00" W	26. viii	TYF	450-500(-0)	
298	13° 01' 45" N, 21° 34' 45" W	29. viii	TYF	900-1200(-0)	
		1930			
300	52° 26' 30" S, 37° 14' W	20. i	N 70 V	750-500	
301	52° 36' 30" S, 37° 14' W	20-21. i	N 70 V	750-500	
302	52° 46' 30" S, 37° 12' W	21. i	N 70 V	750-500	
303	53° 00' S, 37° 11' W	21. i	N 70 V	500-250	
303	53° 00' S, 37° 11' W	21. i	N 70 V	1000-750	
303	53° 00' S, 37° 11' W	21. i	N 70 V	750-500	
304	53° 06' S, 37° 14' W	21. i	N 70 V	500-250	
304	53° 06' S, 37° 14' W	21. i	N 70 V	750-500	
305	53° 17' S, 37° 10' W	21-22. i	N 70 V	1000-750	

Table I (cont.)

'Discovery' Station	Position	Date 1930 (cont.)	Gear	Depth (metres)	<i>Cunina peregrina</i>	<i>Solmissus marshalli</i>	<i>Pegantha clara</i>	<i>Pegantha laevis</i>	<i>Pegantha martagon</i>	<i>Solmundella bitentaculata</i>	<i>Aegina citrea</i>	<i>Liriope tetraphylla</i>	<i>Crossota brunnea</i>	<i>Colobonema sericeum</i>	<i>Pantachogon haeckeli</i>	<i>Rhopalonema velatum</i>	<i>Haliscera conica</i>	<i>Halicreas minimum</i>	<i>Cosmetirella davisi</i>	<i>Calycopsis borchgrevinkii</i>	<i>Zanclonia weldoni</i>	
335	From 55° 33' S, 36° 49' 30" W to 55° 31' 30" S, 36° 49' 30" W	4-5. ii	N 70 V	750-500
336	From 55° 21' 30" S, 36° 48' 30" W to 55° 20' S, 36° 48' 30" W	5. ii	N 70 V	250-100	.	I	.	.	.	I
336	From 55° 21' 30" S, 36° 48' 30" W to 55° 20' S, 36° 48' 30" W	5. ii	N 70 V	500-250	.	I	.	.	.	I
337	From 55° 09' S, 36° 48' W	5. ii	N 70 V	500-250	8
337	From 55° 09' S, 36° 48' W	5. ii	N 70 V	750-500	I
339	From 54° 51' 30" S, 36° 44' 30" W	5. ii	N 70 V	100-50	I	.	.	.
342	From 55° 47' S, 34° 11' W	7. ii	N 70 V	500-250	7
343	From 55° 40' S, 34° 23' W	7. ii	N 70 V	500-250	6
344	From 55° 33' S, 34° 35' 30" W to 55° 29' 30" S, 34° 32' W	7-8. ii	N 70 V	250-100	6
344	From 55° 33' S, 34° 35' 30" W to 55° 29' 30" S, 34° 32' W	7-8. ii	N 70 V	750-500	I
344	From 55° 33' S, 34° 35' 30" W to 55° 29' 30" S, 34° 32' W	7-8. ii	N 70 V	1000-750	I
347	From 55° 08' S, 35° 14' 30" W	8. ii	N 70 V	100-50	4	.	.	.
348	From 54° 53' 30" S, 35° 41' 30" W	8. ii	N 70 V	90-50	3	.	.	.
349	From 55° 01' S, 35° 27' 30" W	8. ii	N 70 V	50-0	I	.	.	.
349	From 55° 01' S, 35° 27' 30" W	8. ii	N 70 V	100-50	9	.	.	.
350	From 54° 23' S, 36° 00' W	9. ii	N 70 V	100-50	I	.	.	.
353	From 54° 17' 30" S, 35° 06' W	9. ii	N 70 V	500-250
353	From 54° 17' 30" S, 35° 06' W	9. ii	N 70 V	1000-750
354	From 54° 15' 30" S, 34° 47' 30" W to 54° 13' 15" S, 34° 46' W	9. ii	N 70 V	500-250
354	From 54° 15' 30" S, 34° 47' 30" W to 54° 13' 15" S, 34° 46' W	9. ii	N 70 V	750-500
355	From 54° 13' 30" S, 34° 18' 30" W to 54° 10' 30" S, 34° 16' 30" W	9-10. ii	N 70 V	100-50
355	From 54° 13' 30" S, 34° 18' 30" W to 54° 10' 30" S, 34° 16' 30" W	9-10. ii	N 70 V	250-100
356	From 54° 11' S, 33° 49' W to 54° 08' 45" S, 33° 47' 30" W	10. ii	N 70 V	100-50	I	.	.

Table 2. *Geographical distribution of neritic species of Leptolina collected by the Discovery Investigations, 1926-37*

	Antarctic			W. Atlantic-antiboreal	W. Atlantic-tropical	W. Atlantic-boreal	Arctic	E. Atlantic-boreal	Mediterranean-Atlantic	E. Atlantic-tropical	S. African	E. African-tropical	Indo-West Pacific-tropical	Indian temperate	S. Australian-New Zealand	Pacific-boreal	E. Pacific-tropical	Peru-N. Chilensis
	Pacific sector	Atlantic sector	Indian sector															
<i>Koellikerina maasi</i>	○	×	○
<i>Zanclonia weldoni</i>	⊗	×	○
<i>Calycopepis borchgrevinkii</i>	⊗	⊗	○
<i>Ptychogena antarctica</i>	○	×	○
<i>Mitrocomella frigida</i>	○	⊗	○
<i>Cosmetirella davisi</i>	⊗	⊗	⊗	⊗	⊗
<i>Bougainvillia macloviana</i>	.	.	○	⊗	.	.	.	○	○	.	.	.
<i>Tiaricodon coeruleus</i>	.	○	.	⊗	○
<i>Aglauropsis conanti</i>	.	.	.	⊗
<i>Proboscidactyla mutabilis</i>	.	.	.	⊗
<i>Laodicea pulchra</i>	.	.	.	⊗
<i>Phialella falklandica</i>	.	.	.	⊗	○	.	.	.
<i>Sarsia gracilis</i>	.	.	.	○	×
<i>Halitholus intermedius</i>	.	.	.	○	×
<i>Phialidium simplex</i>	.	.	.	○	○	×	.	○
<i>Gossea brachymera</i>	.	.	.	×	○
<i>Aequorea coerulescens</i>	.	.	.	×	○
<i>Pandea conica</i>	.	.	.	×	○	.	.	.	○	⊗	○	.	○
<i>Aequorea macrodactyla</i>	.	.	.	×	.	.	.	○	.	×	⊗	○	.	○
<i>Aequorea aequorea</i>	.	.	.	×	○	○	.	○	○	○	×
<i>Laodicea undulata</i>	.	.	.	○	⊗	○	.	○	○	○	×
<i>Halopsis ocellata</i>	.	.	.	×	.	○	○	○
<i>Staurophora mertensi</i>	.	×	.	⊗	.	○	○	○
<i>Leuckartiara octona</i>	○	.	.	○	○	×	.	.	○
<i>Neoturris pileata</i>	○	○	.	×
<i>Heterotiara minor</i>	○	.	×	.	○
<i>Zygocanna vagans</i>	×	.	○
<i>Phialidium discoïdum</i>	⊗
<i>Octophialucium medium</i>	⊗
<i>Octophialucium aphrodite</i>	×	○
Number of species:																		
× new to the regions	0	4	0	6	0	0	0	0	0	2	9	1	0	0	0	0	0	1
⊗ present + previous records	3	3	1	8	2	0	0	0	0	2	2	0	0	0	0	0	0	1
○ previous records only	3	1	6	4	4	5	2	8	5	2	2	1	7	0	2	3	4	2

Table 3. Geographical distribution of oceanic species of Hydromedusae, predominantly epipelagic, collected by the Discovery Investigations, 1926-37

	Antarctic															
	Pacific sector	Atlantic sector	Indian sector	W. Atlantic-antiboreal	W. Atlantic-tropical	W. Atlantic-boreal	Arctic	E. Atlantic-boreal	Mediterranean-Atlantic	E. Atlantic-tropical	S. African	E. African-tropical	Indo-West Pacific-tropical	Indo-West Pacific-antiboreal	Pacific-boreal	E. Pacific warm-water
LEPTOLINA																
<i>Bougainvillia platygaster</i>	⊗	⊗	×	×
<i>Cytaeis tetrastyla</i>	⊗	.	.	.	○	⊗	.	○	○	.	.	.
<i>Euphysora furcata</i>	○	.	○	.	⊗	×	×
<i>Phialopsis diegensis</i>	×	○	.	○	.	⊗	×	×	.	.	○	○
TRACHYLINA																
<i>Solmundella bitentaculata</i>	⊗	⊗	○	⊗	⊗	.	.	.	○	⊗	⊗	○	○	.	.	○
<i>Pegantha martagon</i>	×	×	.	×	×	.	.	.	×	⊗	×	×	○	.	.	○
<i>Rhopalonema velatum</i>	.	.	.	×	⊗	○	.	○	○	⊗	⊗	⊗	○	⊗	.	○
<i>Aegina citrea</i>	.	.	.	⊗	⊗	○	.	○	⊗	⊗	⊗	○	○	⊗	.	○
<i>Liriope tetrphylla</i>	.	.	.	×	×	○	.	○	○	⊗	⊗	⊗	○	.	.	⊗
<i>Persa incolorata</i>	.	.	.	○	○	.	.	.	○	⊗	○
<i>Cunina duplicata</i>	.	.	.	×	⊗	×
<i>Pegantha laevis</i>	.	.	.	×	×	⊗	×	×
<i>Pegantha clara</i>	⊗	○	.	.	⊗	×	×	×	○	○	.	○
<i>Aglaura hemistoma</i>	⊗	○	.	.	○	⊗	⊗	○	○	.	.	.
<i>Cunina octonaria</i>	⊗	○	.	.	○	⊗	⊗	○	○	.	.	.
<i>Cunina frugifera</i>	×	.	.	.	○	⊗	×	×
<i>Pegantha triloba</i>	○	.	.	.	○	⊗	.	○	○	.	.	○
<i>Pegantha rubiginosa</i>	○	.	.	.	○	⊗
<i>Sminthea eurygaster</i>	○	.	.	.	○	⊗	×	⊗	○	.	.	.
<i>Geryonia proboscidalis</i>	⊗	.	.	.	○	⊗	⊗	⊗	○	.	.	○
<i>Cunina peregrina</i>	⊗	⊗	×	×	○	.	.	.
<i>Solmissus marshalli</i>	×	.	.	.	○	⊗	×	⊗	○	.	.	○
<i>Solmaris corona</i>	○	○	.	.	.	○	.	.	.
<i>Cunina globosa</i>	×	○
Number of species:																
× new to the regions	1	1	0	5	6	0	0	0	1	1	13	8	0	2	0	0
⊗ present + previous records	1	1	0	2	10	0	0	0	2	20	7	4	0	2	0	1
○ previous records only	0	0	1	1	4	8	0	5	13	2	1	6	14	0	3	15

Table 4. *Geographical distribution of oceanic species of Hydromedusae, predominantly bathypelagic, collected by the Discovery Investigations, 1926-37*

	Antarctic			N. Atlantic-boreal	Atlantic warm-water	S.W. Atlantic-antiboreal	S. African	E. African-tropical	Indian warm-water	Indian-temperate	Pacific-boreal	Pacific warm-water
	Pacific sector	Atlantic sector	Indian sector									
LEPTOLINA												
<i>Pandea rubra</i>	.	×	.	○	○	.	×	.	.	.	○	.
<i>Chromatonema rubrum</i>	.	×	×	○	○	.	×
<i>Tiaranna rotunda</i>	.	.	×	○	⊗	×
<i>Amatiara affinis</i>	.	.	.	○	⊗	.	×
<i>Bythotiara murrayi</i>	.	.	.	○	○	.	×
<i>Calycopsis bigelowi</i>	×	○
TRACHYLINA												
<i>Haliscera racovitzae</i>	○	⊗
<i>Arctapodema antarcticum</i>	.	×	⊗	×	.
<i>Arctapodema australe</i>	.	.	○	×	.
<i>Arctapodema amplum</i>	.	⊗	○	.	○
<i>Crossota brunnea</i>	×	⊗	⊗	.	⊗	⊗	⊗	⊗	○	.	×	○
<i>Haliscera conica</i>	×	⊗	○	.	⊗	⊗	⊗
<i>Pantachogon haeckeli</i>	×	×	⊗	○	⊗	⊗	⊗	⊗	○	×	○	○
<i>Halicreas minimum</i>	.	⊗	×	○	⊗	×	⊗	⊗	○	×	○	○
<i>Botrynema brucei</i>	.	⊗	⊗	○	⊗	.	⊗	.	○	⊗	○	.
<i>Rhopalonema funerarium</i>	.	.	.	○	⊗	×	×	.	○	.	.	○
<i>Colobonema sericeum</i>	.	.	.	○	⊗	.	⊗	×	○	⊗	.	○
<i>Aeginura grimaldii</i>	.	.	.	○	⊗	.	○	⊗	○	.	○	○
<i>Halitrephes maasi</i>	⊗	.	⊗	×	○	×	.	○
<i>Crossota alba</i>	×	○	.
<i>Tetrorchis erythrogaster</i>	⊗	.	×	○
Number of species:												
× new to the regions	3	4	3	0	1	3	7	2	0	6	0	0
⊗ present + previous records	0	6	4	0	12	3	7	4	0	2	0	0
○ previous records only	1	0	3	11	4	0	1	1	8	0	6	8

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PLATE I

Fig. 1. *Corymorpha* sp. St. 256. $\times 30$.

Fig. 2. *Euphysora furcata* Kramp. Specimen with contracted tentacle.
St. 1604. $\times 10$.

Figs. 3, 4. *Euphysora gigantea* sp.n.

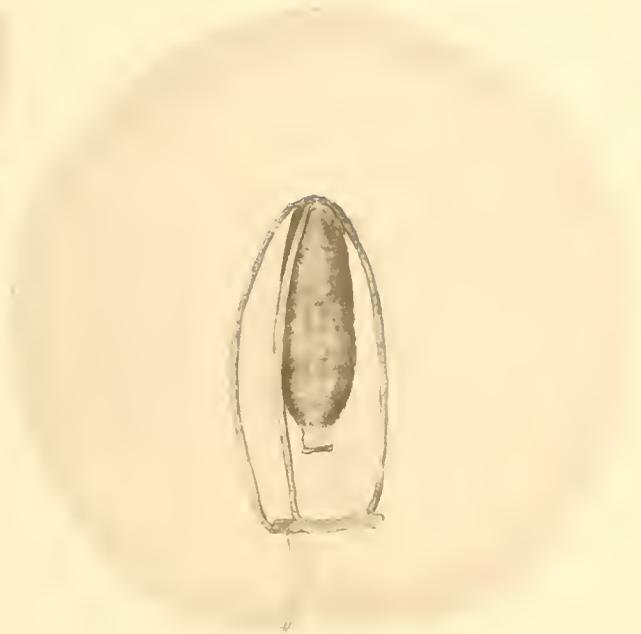
Fig. 3. Type specimen. St. 1995. $\times 4$.

Fig. 4. One of the bifurcated branches of the tentacle.

Fig. 5. *Rathkea africana* sp.n. Type specimen. St. 282. $\times 40$.



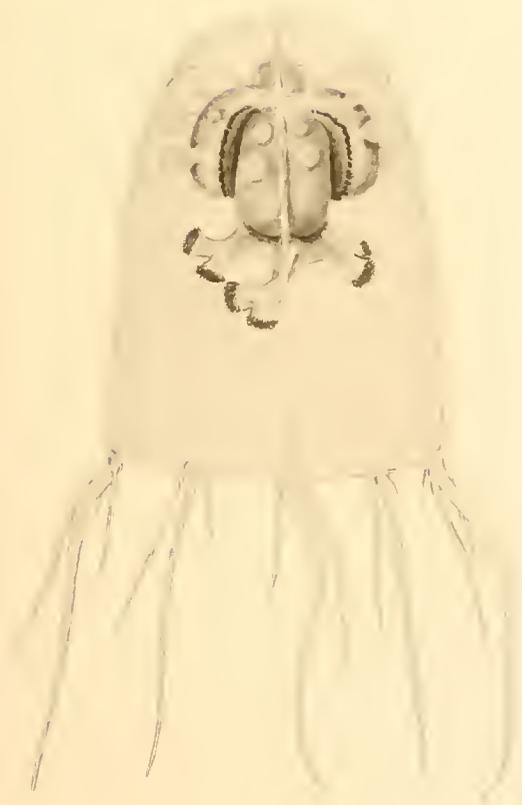
1



3



4



5



2

PLATE II

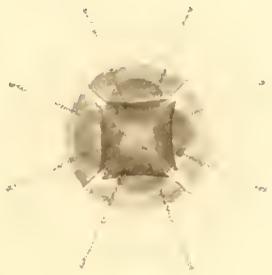
Figs. 1-3. *Ectopleura sacculifera* sp.n. Type specimen. St. WS 720.
× 30. Fig. 1, lateral view. Fig. 2, aboral view. Fig. 3, oral view.

Fig. 4. *Merga rubra* sp.n. Type specimen (the mouth region is
lacking). St. 661. × 10.

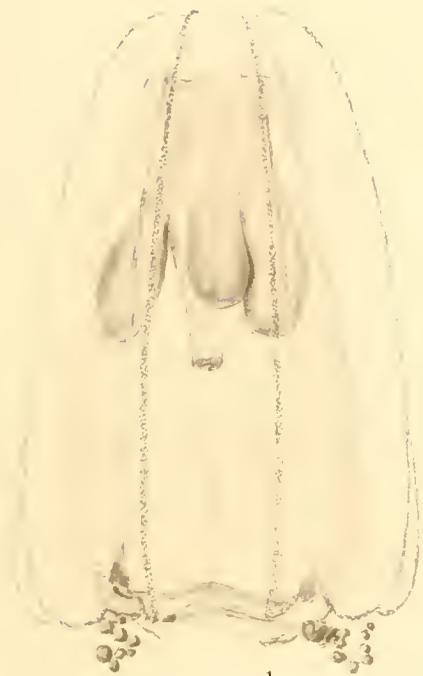
Figs. 5, 6. *Leuckartiara annexa* sp.n.

Fig. 5. Type specimen. St. 439. × 10.

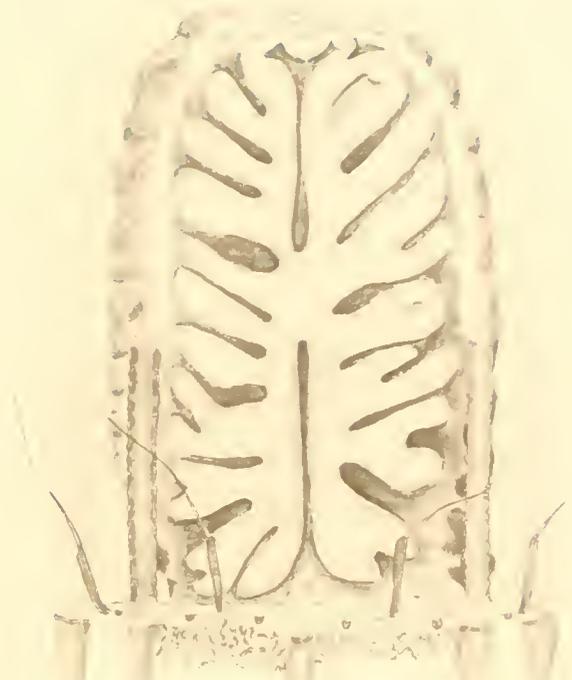
Fig. 6. Adradial tentacle.



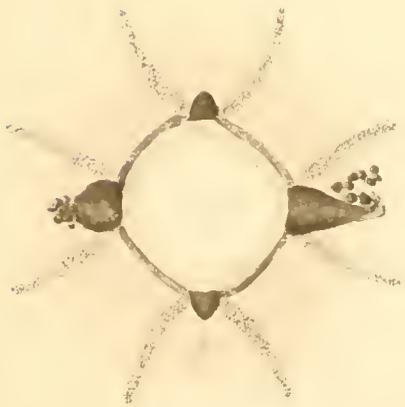
2



1



5



3



6



4

PLATE III

Figs. 1-6. *Bougainvillia platygaster* (Haeckel).

Fig. 1. Aboral view of stomach with male gonads. St. 1374. $\times 30$.

Fig. 2. Aboral view of stomach. Medusa buds are developed on the pedicels of hydranths issuing from the corners of the stomach. St. 1581.

Figs. 3-5. Hydranths developed by budding from the corners of the stomach; medusa buds issuing from the pedicels of the hydranths. The hydranth in fig. 5 has swallowed a copepod. St. 1374. $\times 65$.

Fig. 6. Medusa buds on a stolon without a hydranth. The stolon, issuing from one of the corners of the stomach, was adnate to the subumbrella. St. 1581. $\times 65$.

Fig. 7. *Proboscidactyla ornata* (McCrady). Blastostyle with medusa buds; from a medusa taken in Philippine waters by the 'Galathea' Expedition. $\times 65$.



1



2



3



4



6



5



7

PLATE IV

Figs. 1-6. *Russellia mirabilis* gen.n., sp.n.

Fig. 1. Type specimen. St. 587 (filiform parts of tentacles added from another specimen). $\times 6$.

Fig. 2. Internal view of perradial edge of the stomach. St. 1871.

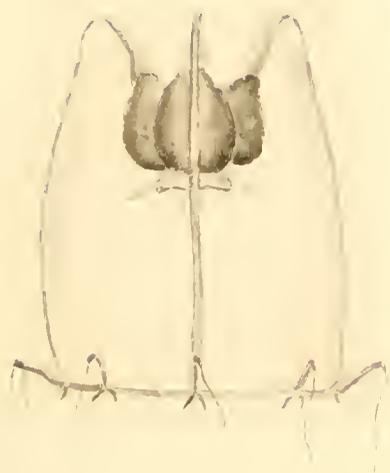
Fig. 3. Oral tentacle and part of mouth rim. St. 1871.

Fig. 4. One-quarter of the umbrella-margin from below, with the roots of three tentacles, each flanked by two dwarf tentacles. St. 1871.

Figs. 5, 6. Tentacle root. St. 1871. Fig. 5, lateral view. Fig. 6, frontal view.

Fig. 7. *Laodicea pulchra* Browne. Gonad and part of the umbrella-margin, aboral view. St. 1897. $\times 10$.

Fig. 8. *Ptychogena antarctica* Browne. Aboral view of gonad; distal end upwards. St. 1959. $\times 4$.



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PLATE V

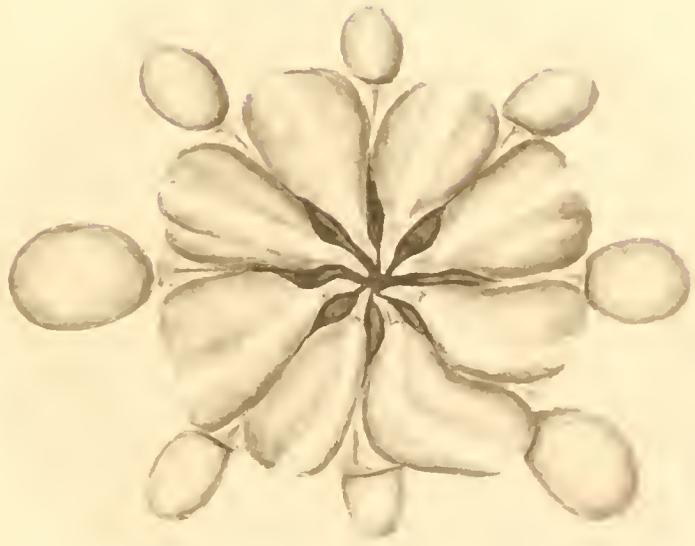
- Fig. 1. *Eucheilota* sp. Oral view. St. 91. $\times 30$.
- Figs. 2, 3. *Gossea brachymera* Bigelow. Interradial marginal swelling with the root of a tentacle, an internal statocyst, and a dwarf tentacle with its three endodermal roots. St. 833. Fig. 2 seen from above through the exumbrellar jelly. Fig. 3, frontal view.
- Fig. 4. *Arctapodema amplum* (Vanhöffen). Aboral view of stomach with large gonads in radial lobes of the stomach and small additional gonads on the radial canals. St. WS 160.
- Figs. 5, 6. *Arctapodema australe* (Vanhöffen). St. 1753.
- Fig. 5. Oral view of stomach turned inside out, showing the internal surface; surrounded by eight gonads on the radial canals.
- Fig. 6. Aboral view of part of the stomach and two gonads hanging below the radial canals.
- Fig. 7. *Amphogona apicata* sp.n. Type specimen. St. 102. (Stomach from another specimen, St. 1575.) $\times 12$.



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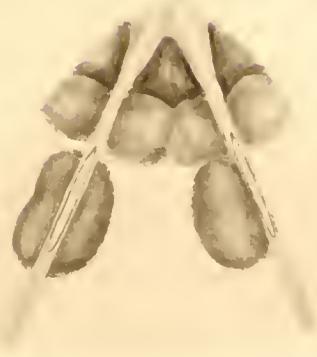
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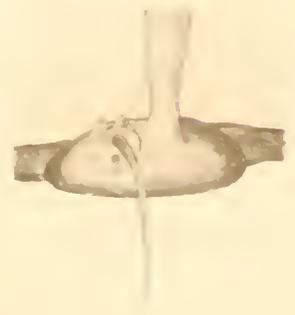
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PLATE VI

Figs. 1-4. Marginal lappets of four species of *Pegantha*, showing the difference in the peripheral canals and the otoporphae.

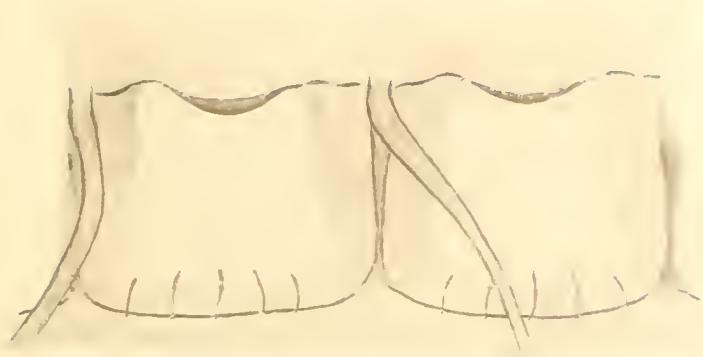
Fig. 1. *Pegantha martagon* Haeckel. St. 129.

Fig. 2. *Pegantha laevis* H. B. Bigelow. St. 1565.

Fig. 3. *Pegantha clara* R. P. Bigelow. St. 697.

Fig. 4. *Pegantha rubiginosa* (Kölliker). 'Atlantide'. St. 83.

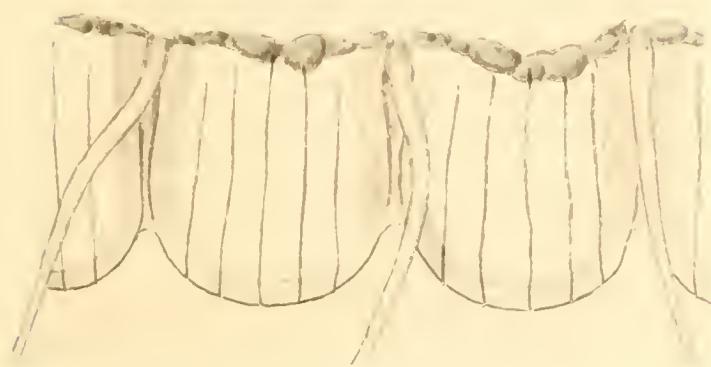
Fig. 5. *Cumina duplicata* Maas. Aboral view of a specimen 50 mm. in diameter. St. 1974.



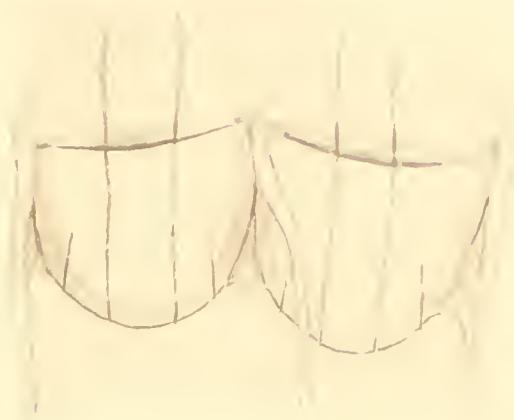
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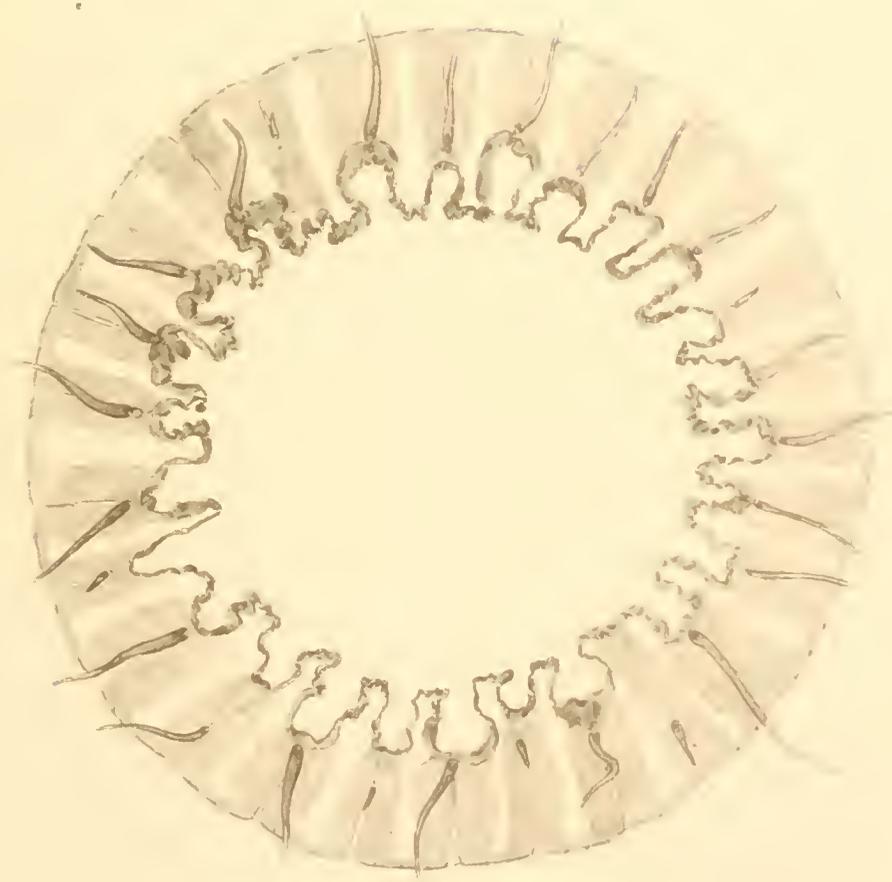
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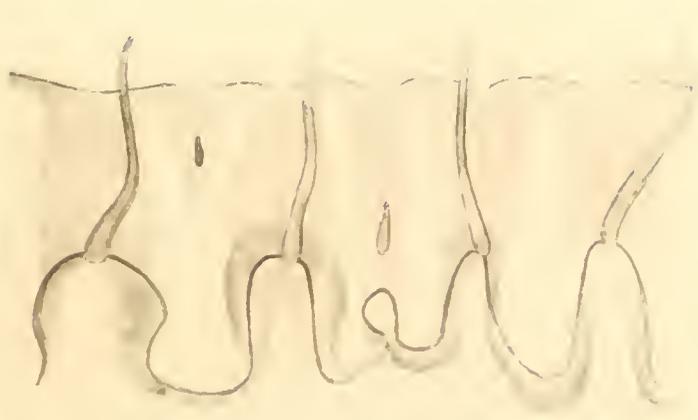
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PLATE VII

- Fig. 1. *Cumina duplicata* Maas. Part of umbrella-margin of a specimen 29 mm. in diameter, showing development of gastric pouches, lappets and tentacles. St. 100. $\times 7$.
- Fig. 2. *Cumina duplicata* Maas. Statocyst with otoporpa. $\times 250$.
- Fig. 3. Two clusters of larvae of ?*Pegantha triloba* Haeckel attached to the subumbrella of *Bougainvillia platygaster* (Haeckel). St. 680. $\times 25$.
- Fig. 4. Larva of ?*Pegantha triloba* shortly before liberation, aboral view, showing radiating edges and otoporpae; from *Bougainvillia platygaster*. St. 683.
- Figs. 5-7. Clusters of larvae, probably of *Cumina peregrina* Bigelow, from *Rhopalonema velatum* Gegenbaur. $\times 35$. Fig. 5, St. 250; fig. 6, St. 254; fig. 7, St. 679.
- Fig. 8. Larva of Narcomedusae in advanced stage of development, from *Rhopalonema funerarium* Vanhöffen. St. 2059. $\times 25$.
- Fig. 9. Part of umbrella margin of the same, showing a peronium and four marginal clubs with otoporpae. $\times 350$.
- Fig. 10. Cluster of larvae of Narcomedusae, from *Pantachogon haeckeli* Maas. St. 85. $\times 25$.
- Fig. 11. Newly liberated medusa of the same. $\times 25$.



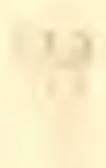
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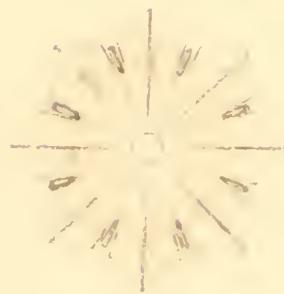
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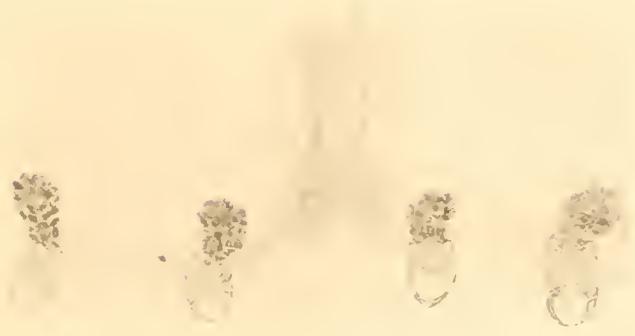
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[*Discovery Reports*. Vol. XXIX, pp. 129-140, February 1957]

NEW OBSERVATIONS ON THE ABERRANT
MEDUSA *TETRAPLATIA VOLITANS* BUSCH

BY

WILLIAM J. REES AND ERNEST WHITE

British Museum (Natural History)

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NEW OBSERVATIONS ON THE ABERRANT MEDUSA *TETRAPLATIA VOLITANS* BUSCH

By William J. Rees and Ernest White

British Museum (Natural History)

(Figs. 1-7)

INTRODUCTION

THE published records of the occurrence of the aberrant medusa *Tetraplatia volitans* Busch indicate that it probably has a cosmopolitan distribution, for it has been found sporadically in all oceans. Until now, however, there were no records of its occurrence in the North Atlantic, except south of Gibraltar and in the Mediterranean. Additional material has come to light which extends its known range northwards along the edge of the continental shelf off the western seaboard of the British Isles. Farther afield too, there are new records of distribution.

Recently and independently, two papers have been published on the occurrence of this medusa in different parts of the world (Beyer, 1955; Hand, 1955), which to some extent present diverging views on the biology of the species. The object of this paper is, therefore, to draw attention to the fact that this species may be found during deep-sea investigations to the south and west of the British Isles, and to draw some conclusions regarding the biology of the species from the additional data.

ACKNOWLEDGEMENTS

We wish to thank Dr N. A. Mackintosh, C.B.E., Dr Helene Bargmann and Mr A. de C. Baker of the National Institute of Oceanography for material in the Discovery collections, and Dr J. H. Fraser, Scottish Home Department, Aberdeen, for a specimen from plankton collected by F.R.V. 'Explorer'.

NEW RECORDS OF *TETRAPLATIA*

The following records of *Tetraplatia* are based on material taken by Dr G. H. Fowler's cruise to the Bay of Biscay in H.M.S. 'Research' in 1900, by R.R.S. 'Discovery II', by 'Carnegie VII' and by 'Explorer'.

The records without an asterisk are new, those denoted by an asterisk have been briefly mentioned by Beyer (1955) and those denoted by an obelus are known only as records in the plankton analysis sheets of the Discovery Investigations.

List of Stations at which *Tetraplatia* was taken:

H.M.S. 'Research', July 1900. Approx. 47° N., 7° W., Bay of Biscay

St. 320, 75-0 fm., 2 specimens.

St. 33*d*, 100-0 fm., 1 specimen.

St. 35*b*, 100-0 fm., 1 specimen.

R.R.S. 'Discovery II'

St. 670, 44° 52' S., 30° 17' W., South Atlantic, 23. iv. 31, TYFB, 470-0 m. 1 specimen.

St. 943, 45° 28.4' S., 179° 06.4' E., South Pacific, S.E. of New Zealand, 1. ix. 32, N 70 V, 500-250 m., 1 specimen.

*St. 1773, 39° 07' S., 00° 15.5' E.-39° 04' S., 00° 12.5' E., South Atlantic, 24. v. 36, N 70 V, 750-500 m., 1 specimen.

- *St. 1775, 44° 40' 3" S., 00° 33' 5" E.—44° 40' S., 00° 37' E., South Atlantic, 27. v. 36, N 70 V, 750–500 m., 2 specimens.
 *†St. 1778, 52° 14' 7" S., 00° 1' W.—52° 12' 8" S., 00° 07' E., South Atlantic, 30. v. 36, N 70 V, 1500–1000 m.
 St. 1913, 53° 55' 2" S., 56° 45' 7" W., South Atlantic, Patagonian Shelf, 1. xii. 36, N 70 B, 250–160 m., 1 specimen.
 *St. 2024, 45° 01' 3" S., 00° 33' 7" E., South Atlantic, 30. iii. 37, N 70 V, 500–250 m., 1 specimen.
 *†St. 2356, 42° 56' 8" S., 00° 21' 2" E., South Atlantic, 7. vii. 38, N 70 V, 750–500 m., 1 specimen.
 *St. 2386, 44° 04' 9" S., 00° 15' 4" E., South Atlantic, 12. viii. 38, N 70 V, 750–500 m., 1 specimen.
 *St. 2496, 50° 20' 7" S., 01° 03' 3" E., South Atlantic, 2. xii. 38, N 70 V, 1000–750 m., 1 specimen.
 St. 2582, 39° 53' 9" S., 00° 39' 1" E., South Atlantic, 20. ii. 39, N 100 B, 1050–750 m., 2 specimens.
 St. 2641, 00° 45' 3" S., 07° 26' 6" W., Equatorial Atlantic, off W. Africa, 16. iv. 39, N 50 V, 100–0 m., 1 specimen.
 St. 3230, 47° 30' N., 07° 35' W., Bay of Biscay, 14. v. 55, N 70 V, 500–250 m., 2 specimens, N 70 V, 750–500 m., 1 specimen.
 St. 3233, 46° 02' N., 09° 19' W., Bay of Biscay, 15. v. 55, N 70 V, 250–100 m., 4 specimens, 500–0 m., 1 specimen.
 St. 3234, 43° 13' N., 12° 04' W., W. of Cape Finisterre, 17. v. 55, N 70 V, 500–250 m., 2 specimens, N 70 V, 750–500 m., 2 specimens, N 70 V, 1000–0 m., 6 specimens.
 St. 3272, 45° 51' N., 08° 43' W., Bay of Biscay, 27. vi. 55, TYFB, 1000–0 m., 8 specimens.
 St. 3273, 46° 27' N., 08° 04' W., Bay of Biscay, 27. vi. 55, N 70 V, 500–250 m., 3 specimens, 750–500 m., 1 specimen.

‘Carnegie VII’

- St. 49/50, 26° 27' S., 115° 21' W., E. South Pacific, 28. xi. 28, surface, 2 specimens.
 St. 93, 14° 41' S., 167° 41' W., South Pacific, between Tahiti and Samoa, 31. iii. 29, surface, 6 specimens.

F.R.V. ‘Explorer’

- St. E 52/1305, 58° 38' N., 8° 21' W., N.W. of Scotland, 24. vi. 52, 500–0 m., 1 specimen.

GEOGRAPHICAL DISTRIBUTION

Earlier records of *Tetraplatia* indicated that it had a world-wide distribution although there were large areas, especially in the Indian Ocean, the North Atlantic and in the Central and South Pacific, where it had not been found. Dantan (1925) gives excellent figures of this species.

The new records of geographical distribution are given in the list of specimens. No new records are available for the Indian Ocean.

Formerly, *Tetraplatia* was not known farther north in the Atlantic Ocean than about the latitude of Gibraltar; now there are several new records of it. In 1900 H.M.S. ‘Research’ took it at three stations in the Bay of Biscay†; recently ‘Discovery II’ took it in 1955 at a neighbouring station, as well as at four other positions to the south-west (Fig. 1). The most northerly recorded position for the species is that of ‘Explorer’ (58° 38' N., 8° 21' W.); these records from the North Atlantic suggest that *Tetraplatia* occurs in deep water along the west coasts of the British Isles.

Farther south, ‘Discovery II’ captured the species off the equatorial West African region (St. 2641), at a series of stations (Sts. 1773, 1775, 1778, 2024, 2356, 2386, 2496, 2582) all approximately along the 0° line, between 38° S. and 52° S. in the South Atlantic, and at two other localities to the west (Sts. 670 and 1913) (Fig. 2).

Three interesting records come from the Pacific. Previously *Tetraplatia* was only known from off Japan (Komai, 1939), off the Californian coast, off equatorial South America (Hand, 1955) and off Chile (Beyer, 1955), but the new localities from the South Pacific (‘Carnegie’ St. 49/50 and St. 93 and ‘Discovery II’ St. 943) indicate that the species must have a wide distribution throughout the greater part of the Pacific (Fig. 2). Consideration of all the records now available implies that the species may occur in all oceans between 52° S. and 58° N.

† For details of stations, see Browne (1906).

So far there are no records either from the Arctic or from the Red Sea. It would be interesting to know whether *Tetraplatia* penetrates into the Arctic basin and also whether it can tolerate the high salinity of the Red Sea.

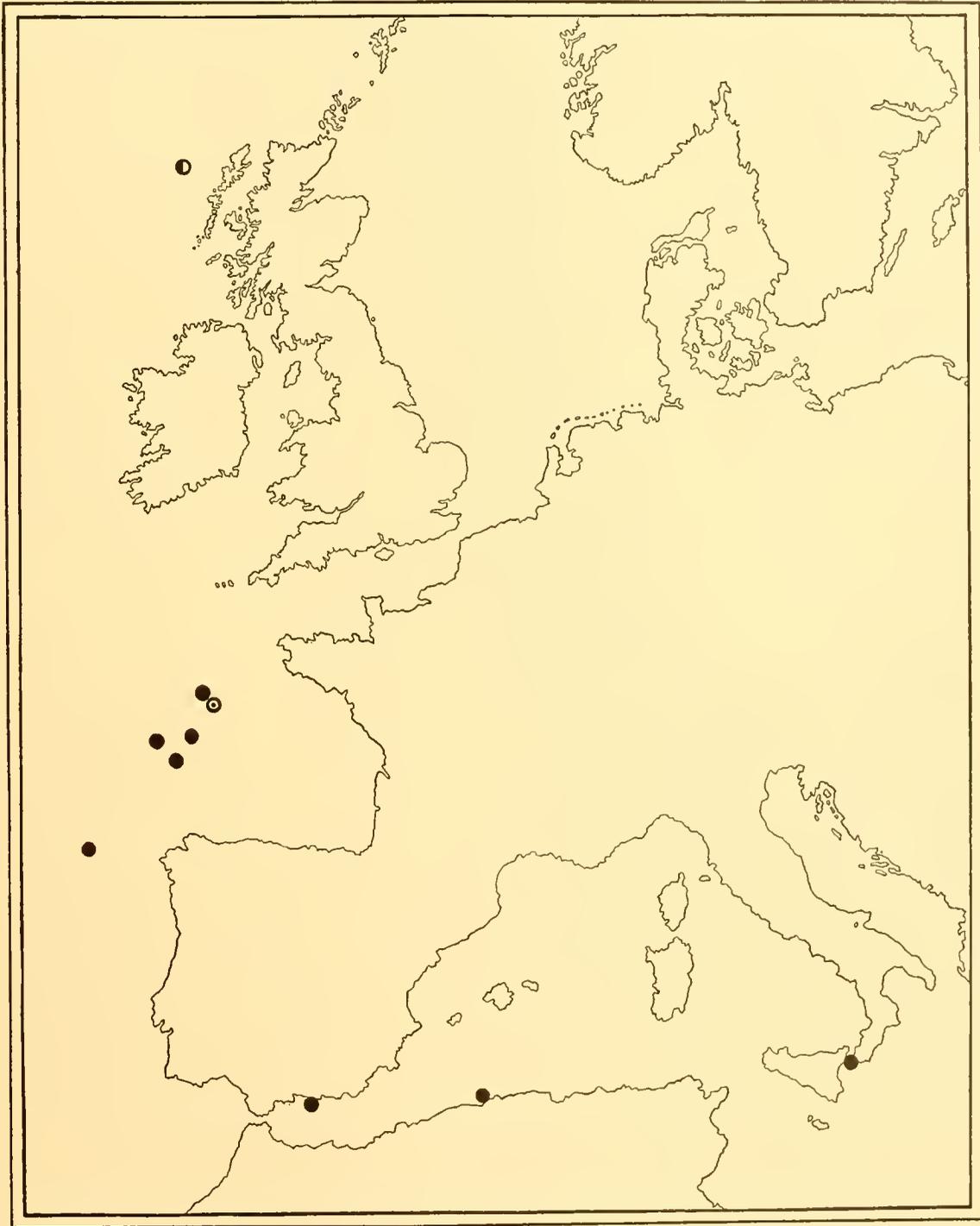


Fig. 1. The distribution of *Tetraplatia volitans* in the North Atlantic. H.M.S. 'Research': open circle with a central dot; R.R.S. 'Discovery II': black circles in Atlantic; F.R.V. 'Explorer': half circle filled-in; previous records in the Mediterranean: black circles.

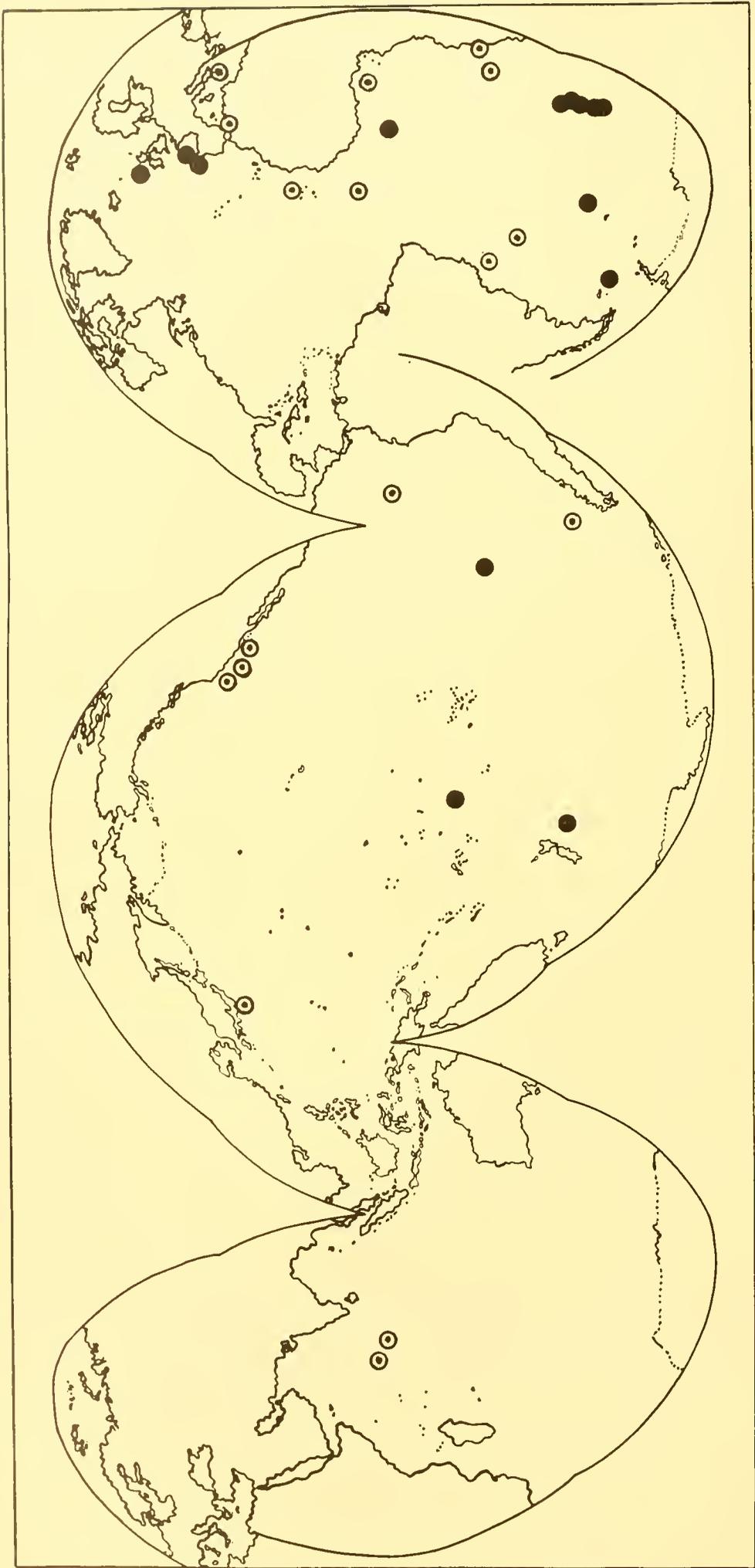


Fig. 2. World-wide distribution of *Tetraplattia volitans*. Previous records: open circles; new records: black circles.

VERTICAL DISTRIBUTION

It is well known that *Tetraplatia volitans* can occur in surface waters in the Mediterranean (Busch, 1851) and elsewhere (Komai, 1939; Hand, 1955). The most recent authors to present some details of vertical distribution have been Hand (1955) and Beyer (1955). From a study of horizontal closing-net hauls taken off the Californian coast, Hand concluded that *Tetraplatia* undergoes vertical migration with centres of population at about 40 m. by night and at about 250 m. or more by day. Hand further concluded from separate open-net hauls that 'in general, the deeper the tow the more specimens were captured'. Concerning this type of fishing (done by the earlier expeditions), we are in agreement with his views that 'little but speculative results can be gleaned from them and no exact information is available on the lower limits of the vertical distribution of *Tetraplatia*'.

Beyer (1955) reported two specimens from the 'Brategg' Expedition in a vertical haul from 1000-550 m.,* this being the first indication that *Tetraplatia* was to be found below 550 m. In an appendix he mentioned briefly other specimens from the closing-net hauls of the Discovery collections. These, together with many additional records (which have subsequently come to light), are discussed here.

The following table (Table 1) summarizes the data on nets, fishing-depth and soundings for catches of *Tetraplatia* in the closing-net hauls of the Discovery collections.

Table 1. Summary of data on type of net, fishing-depth and sounding

Expedition	Station	Type of net	Fishing-depth (m.)	Sounding (m.)
H.M.S. 'Research'	32o	?	75-0	Over 3657
	33 ^d	?	100-0	
	35b	?	100-0	
R.R.S. 'Discovery II'	670	TYFB	470-0	—
	943	N 70 V	500-250	2552
	1773	N 70 V	750-500	5202
	1775	N 70 V	750-500	4166
	1778	N 70 V	1500-1000	3000
	1913	N 70 B	250-160	1628
	2024	N 70 V	500-250	4495
	2356	N 70 V	750-500	1980
	2386	N 70 V	750-500	4089
	2496	N 70 V	1000-750	3482
	2582	N 100 B	1050-750	3897
	2641	N 50 V	100-0	4885
	3230	N 70 V	500-250	1420-1110
		N 70 V	750-500	
	3233	N 70 V	250-100	4817
	3234	N 70 V	500-250	2513
		N 70 V	750-500	
	N 70 V	1000-0		
3272	TYFB	1000-0	4848	
3273	N 70 V	500-250	4707	
	N 70 V	750-500		

This table serves to emphasize that *Tetraplatia* is a pelagic animal frequently occurring far from land and is to be found over very deep water. These results are summarized in Table 2 for the closing-net hauls of 'Discovery II'.

Only a very small percentage of the Discovery collections have been examined for *Tetraplatia*, so that we do not propose to discuss the relative numbers of specimens caught at different depths; what does emerge, however, is that *Tetraplatia* has been taken at all levels from the surface down to the

* Presumably a closing-net.

1000-1500 m. level. When the results are plotted on a chart, many of the records are seen to be from localities where vertical displacement of water masses is likely to take place.

Table 2. Vertical distribution of the specimens from the closing-net hauls of R.R.S. 'Discovery II'

Depth in metres	Number of specimens
0-100	8
100-250	5
250-500	8
500-750	8
750-1000	4
1000-1500	1
1500-2000	—

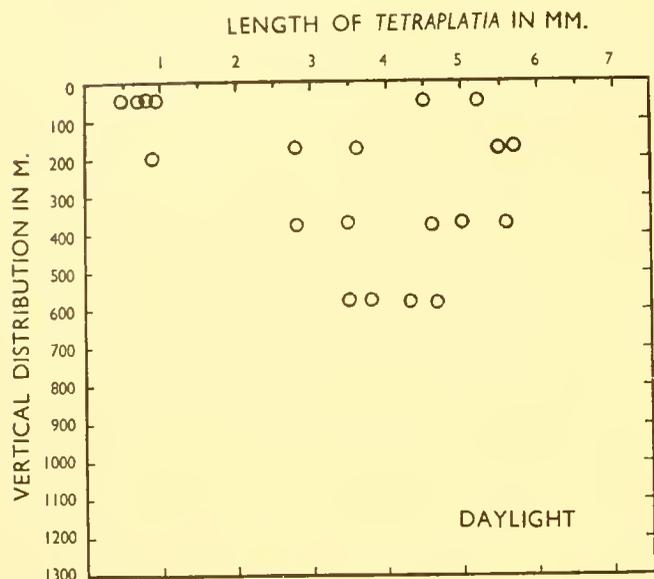


Fig. 3

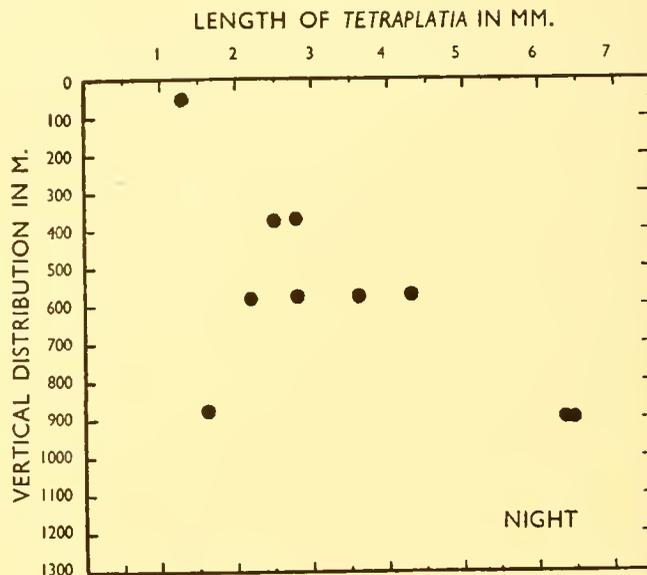


Fig. 4

Figs. 3-4. Vertical distribution of *Tetraplatia volitans*. All records below 100 m. are from the closing-net hauls of R.R.S. 'Discovery II': fig. 3, by day; fig. 4, by night.

The catches of the closing-net hauls have been plotted in Figs. 3 and 4 for any indication of diurnal vertical migration, but it must be remembered that the catches are from different parts of the world and the marked migration reported by Hand from California is perhaps masked by different local conditions. By day *Tetraplatia* was found at the surface down to 500-750 m. with a slight preponderance of young stages in the upper 100 m. At 100-250 m. specimens of 0.9-5.4 mm. in length were found, but below this depth, between 250 and 500 m., only individuals of 2.6-5.7 mm. occurred, and still deeper, at 500-750 m., specimens of 3.5-4.7 mm. were taken. There is no positive indication here (perhaps, as already mentioned, because of the varied localities at which captures were made) that *Tetraplatia* tends to go deeper by day.

Its vertical distribution by night is indicated in Fig. 4. Except for a small specimen (1.6 mm. in length) from St. 2496 (1000-750 m.), there is a suggestion that the larger specimens are to be found at the deeper levels.

SEASONAL OCCURRENCE

In the Mediterranean, *Tetraplatia volitans* was recorded only seasonally by the early investigators. It was found from December to April at Algiers by Viguier (1885) and from January to the end of July at Messina (Carlgren, 1909), and this seasonal appearance is probably due to local changes in hydrographic conditions. In the Bay of Algiers the appearance of *Tetraplatia* in winter is probably related

to the direction of the prevailing winds, which, at this season, blow offshore, displacing surface water and probably causing an upwelling of deeper water.

Elsewhere *Tetraplatia* has been taken in all seasons except in January (Hand, 1955) and 'Discovery II' has taken it all the year round except in January and October.

So long as *Tetraplatia* appeared to be of seasonal occurrence in the plankton, it was thought to have a fixed benthic stage, but since records from several open ocean stations were reported by Leloup (1935), it has been rightly considered to be wholly pelagic. There is a suggestion, as in other wholly planktonic animals, that the young stages of *Tetraplatia* are found in the upper surface layers. 'Carnegie' took six specimens 0.5–0.8 mm. in length in a surface haul at St. 93, and at St. 33d H.M.S. 'Research' took a specimen of 0.9 mm. in the upper 100 m. Another specimen of the same size was taken at 'Discovery II' St. 1913 (250–160 m.), but below this depth no specimen under 1.0 mm. in length was taken in any of the hauls.

HYDROGRAPHIC CORRELATIONS

Fortunately hydrographic observations were made at most of the stations where closing-nets were operated and these are summarized in Table 3. The data are plotted on temperature-salinity charts, similar to those recommended by Pickford (1946) for the analysis of hydrographic correlations (Figs. 5–7).

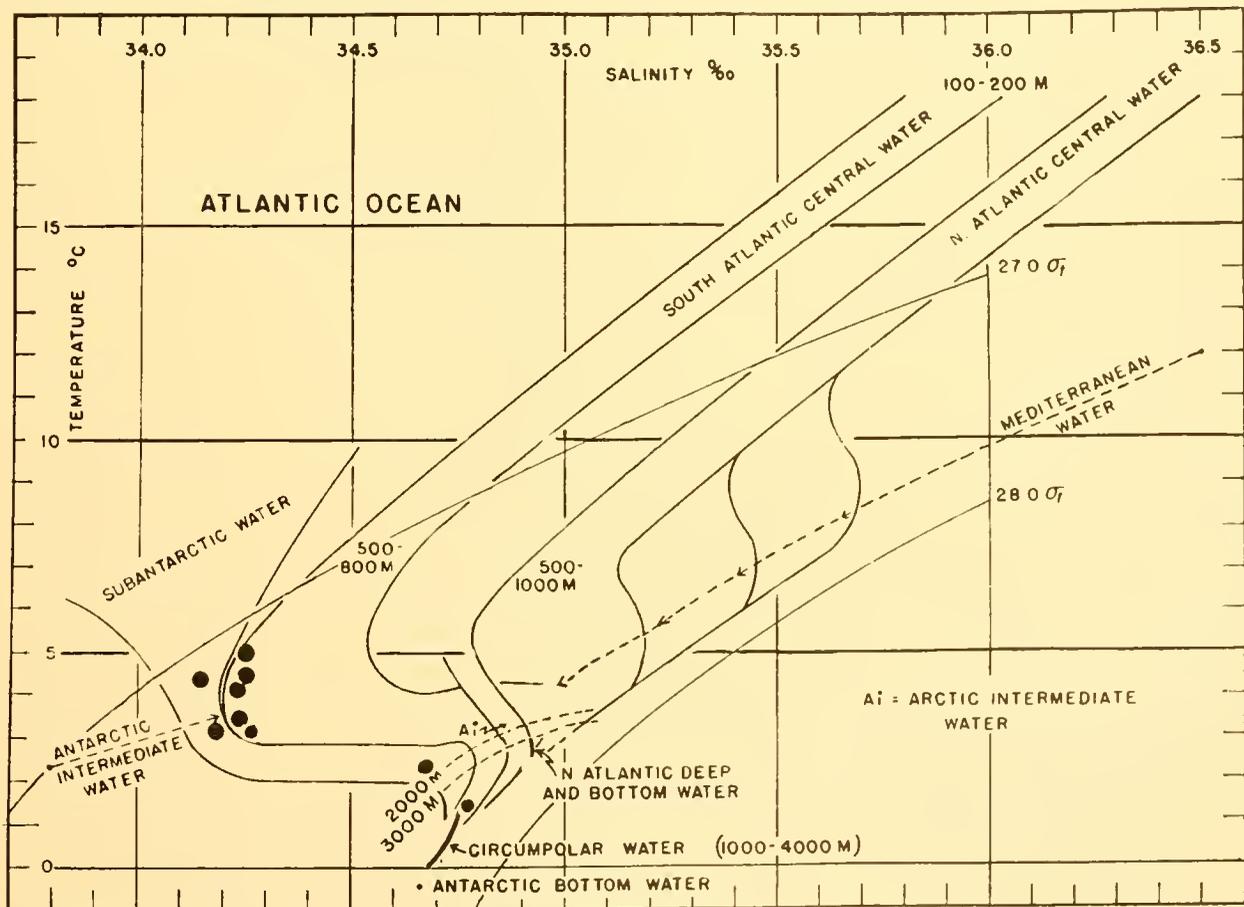


Fig. 5. Distribution of *Tetraplatia volitans* in relation to temperature and salinity in the South Atlantic. Each specimen is plotted according to the recorded salinity and temperature for the depth nearest to the mid-depth of the closing-net at that station. No records of *Tetraplatia* have been used unless temperature and salinity reading have been available for that particular station.

Table 3. Summary of hydrographic data for closing-net stations only

'Discovery II' Station	Depth of capture (m.)	Hydrographic data			
		Depth (m.)	Temperature (° C.)	Salinity (‰)	Density (σ_t)
943	500-250	400	6.08	34.34	27.05
1773	750-500	570	4.50	34.23	27.15
1775	750-500	570	3.56	34.22	27.22
1778	1500-1000	1470	1.39	34.77	27.85
1913	250-160	200	4.34	34.14	27.09
2024	500-250	400	3.35	34.21	27.25
2356	750-500	580	5.07	34.26	27.10
2386	750-500	600	3.15	34.18	27.24
2496	1000-750	930	2.23	34.69	27.72
2582	1050-750	920	3.05	34.27	27.32
2641	100-0	50	22.77	36.08	24.83

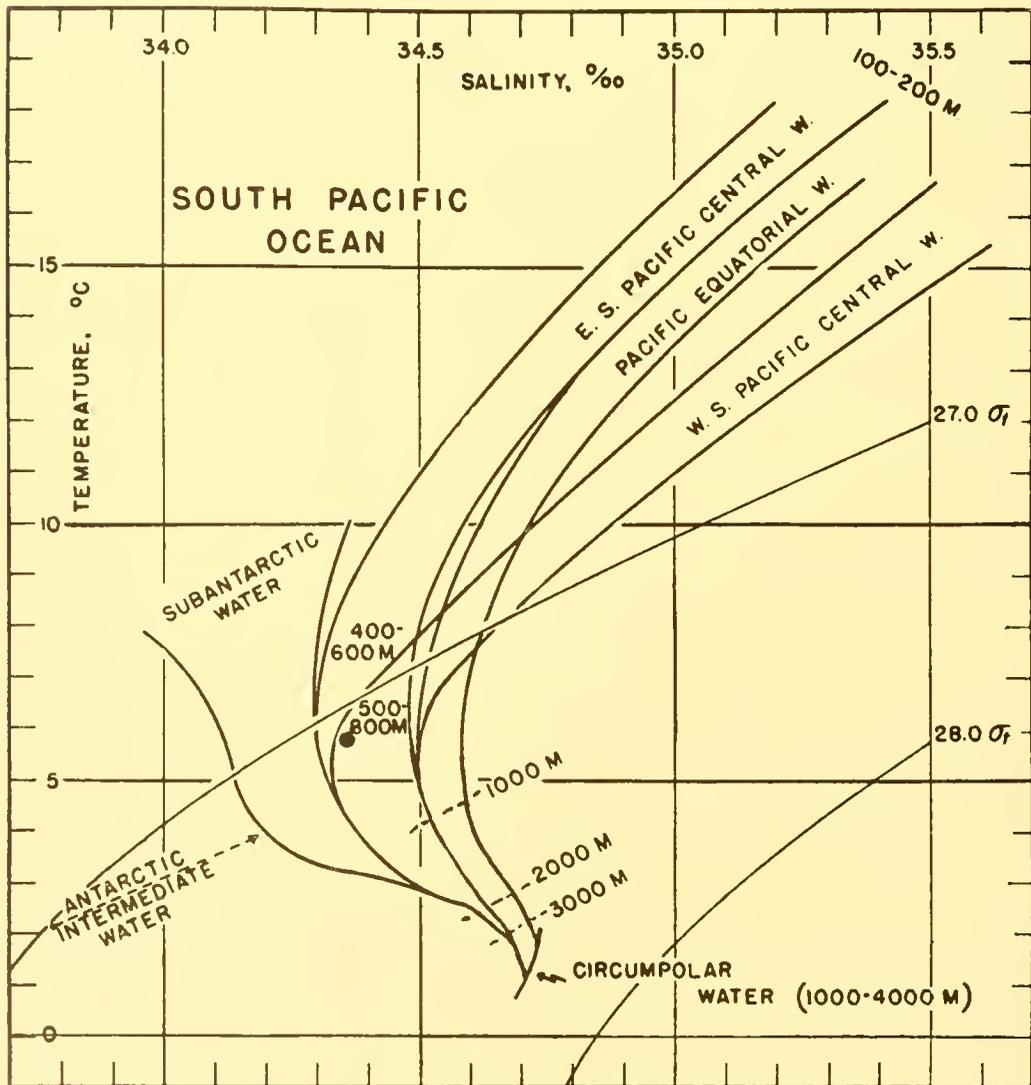


Fig. 6. Distribution of *Tetraplatia volitans* in relation to temperature and salinity in the South Pacific. Details as for Fig. 5.

Detailed hydrographic observations were not made at the North Atlantic stations; those for the South Atlantic are plotted on Fig. 5. Here *Tetraplatia* is an inhabitant of Sub-Antarctic water and of the South Atlantic Central water at temperatures between 1.39°C . and 5.07°C . However, at St. 2641 in the Equatorial Atlantic, *Tetraplatia* was taken in a haul from 100 m. to the surface, where the temperature at 50 m. was 22.77°C . The species must therefore be considered eurythermal.

Hydrographic data are available for only one catch from the Pacific (Fig. 6). This was St. 943 to the south-east of New Zealand where the species was found in W. S. Pacific Central Water.

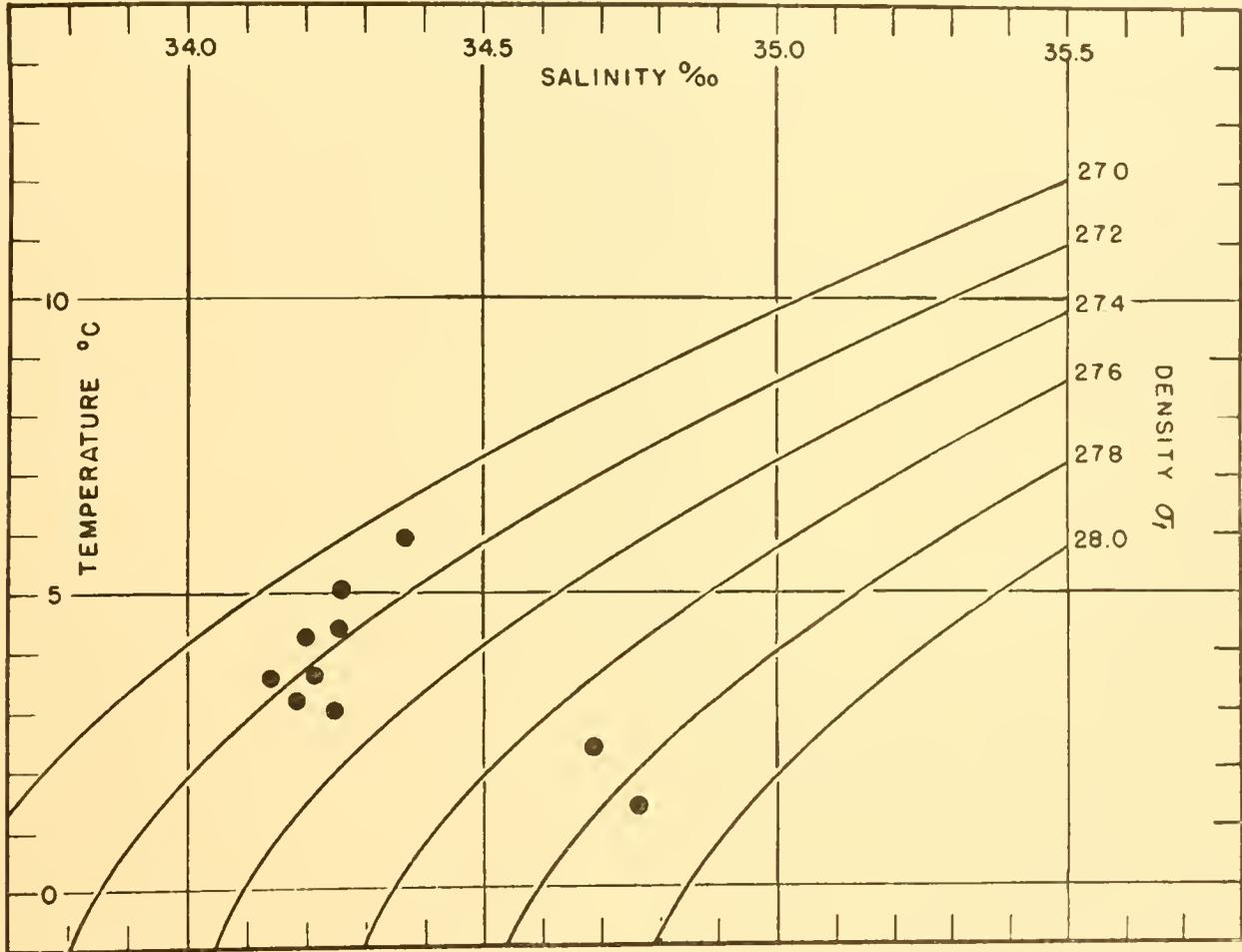


Fig. 7. Distribution of *Tetraplatia volitans* in relation to density layers. Each point represents the probable temperature and salinity at depth of capture as in Fig. 5.

In the South Atlantic, *Tetraplatia* has been found in salinities of 34.14‰ – 34.77‰ and at St. 2641 on the equator where the salinity at 50 m. depth was 36.08‰ . *Tetraplatia* must thus be regarded as a euryhaline species.

The distribution of *Tetraplatia volitans* in relation to salinity, temperature and density is plotted in Fig. 7.*

To conclude, therefore, *Tetraplatia* can exist in temperatures of 1.39°C .– 22.77°C ., salinities of 34.14‰ – 36.08‰ and densities of between (σ_t) 24.83 and 27.85 , so that the species can be regarded

* St. 2641 from the Equatorial Atlantic where the temperature was 22.77°C ., the salinity 36.08‰ and the density 24.83 at 50 m. depth cannot be plotted on this chart. At 100 m. depth the temperature was 16.85°C .; the salinity 35.72‰ and the density 26.12 .

as tolerant of a wide range of conditions. As a bathypelagic planktonic animal *Tetraplatia* could achieve world-wide dispersal through the slow circulation of the water masses in the way envisaged by Coe (1946) for the bathypelagic nemerteans.

SUMMARY

This study of *Tetraplatia volitans* Busch is based on fifty-five specimens from various localities taken by H.M.S. 'Research' (1900), the Discovery collections (1931-54) and the cruises of 'Carnegie VII' and 'Explorer'.

Tetraplatia is recorded for the first time, from the north-east Atlantic in the neighbourhood of the British Isles, from several new localities in the South Atlantic and from three new areas in the South Pacific.

The closing-net hauls of 'Discovery II' show that *Tetraplatia* occurs at all levels from the surface downwards to 1000-1500 m. There is no positive indication of any marked diurnal migration, possibly because of varying local conditions where the specimens were taken, but there is a suggestion that the younger stages are to be found in the upper surface layers. This is in agreement with the conclusions of Leloup (1935) and of Hand (1955) that *Tetraplatia* is wholly pelagic without a bottom benthic phase.

Tetraplatia volitans is found to be a eurythermic, euryhaline pelagic species tolerant of a wide range of conditions.

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ISOPOD CRUSTACEA

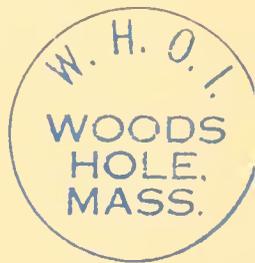
PART II. THE SUB-ORDER VALVIFERA. FAMILIES: IDOTEIDAE,
PSEUDIDOTHEIDAE AND XENARCTURIDAE FAM.N.

WITH A SUPPLEMENT TO ISOPOD CRUSTACEA, PART I. THE FAMILY SEROLIDAE

By

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(Plates VIII and IX; text-figs. 1-22)

INTRODUCTION

THIS paper deals with the Valvifera collected during the years 1925-36 by the Discovery Investigations, with the exception of the family Astacillidae (Arcturidae).

The suborder Valvifera, according to Barnard's (1920, p. 381) analytical key of the principal families, includes the Idoteidae, Pseudidotheidae, Amesopodidae and Astacillidae. Nordenstam (1933, p. 93) pointed out that Barnard did not mention the two families Chaetiliidae and Holognathidae, the former proposed by Dana (1852) to contain his species *Chaetilia ovata*, the latter proposed by Thomson (1904) for his species *Holognathus stewarti* (Filhol). Nordenstam suggested that these two species should be included in the family Idoteidae, the former in his new subfamily Macrochiridotheinae, the latter in the subfamily Idoteinae. To the families included in this suborder must now be added the new family Xenarcturidae, formed to contain the new genus *Xenarcturus* from the Discovery collections.

In the classification of the Valvifera which follows, only those genera have been included to which reference is made in this report:

Suborder Valvifera

Family Idoteidae

Subfamily Idoteinae, Dana, 1852

- Genera *Idotea* Fabricius, 1798
- Paridotea* Stebbing, 1900
- Synidotea* Harger, 1878
- Edotia* Guérin-Méneville, 1844
- Holognathus* Thomson, 1904

Subfamily Mesidoteinae, Racovitza and Sevestos, 1910

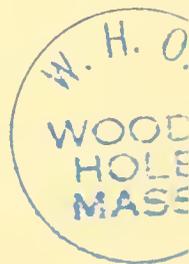
- Genus *Mesidotea* Richardson, 1905

Subfamily Glyptonotinae, Miers, 1881

- Genus *Glyptonotus* Eights, 1852

Subfamily Macrochiridotheinae, Nordenstam, 1933

- Genera *Macrochiridothea* Ohlin, 1901
- Chaetilia* Dana, 1849
- Chiriscus* Richardson, 1911



- Family Pseudidotheidae, Ohlin, 1901
 Genera *Arcturides* Studer, 1882
Pseudidothea Ohlin, 1901
Holidotea Barnard, 1920
- Family Amesopodidae, Stebbing, 1905
 Genus *Amesopous* Stebbing, 1905
- Family Xenarcturidae fam.n.
 Genus *Xenarcturus* g.n.

The Discovery collections contain specimens taken in South African waters as well as from stations in the region of the Patagonian Shelf and from within the Antarctic Convergence. The following species are recorded:

<i>Idotea indica</i> Milne-Edwards, 1840	<i>Glyptonotus antarcticus</i> Eights, 1852
<i>I. metallica</i> Bosc., 1802	<i>Macrochiridothea stebbingi</i> Ohlin, 1901
<i>Paridotea ungulata</i> (Pallas), 1772	<i>M. kruimeli</i> Nierstrasz, 1918
<i>Synidotea hirtipes</i> (Milne-Edwards), 1840	<i>Pseudidothea bonnieri</i> Ohlin, 1901
<i>Edotia bilobata</i> Nordenstam, 1933	<i>P. scutatus</i> sp.n.
<i>E. oculata</i> Ohlin, 1901	<i>Arcturides acuminatus</i> sp.n.
<i>E. oculopetiolata</i> sp.n.	<i>Xenarcturus spinulosus</i> g.n., sp.n.
<i>E. corrugata</i> sp.n.	

The holotypes of the new species are in the British Museum (Natural History).

ACKNOWLEDGEMENT

I should like to record my grateful appreciation and thanks to Dr H. Bargmann who read the first draft of this paper and made many helpful suggestions.

STATION LIST

In the following list of stations those made by R.R.S. 'Discovery' and R.R.S. 'Discovery II' have no letters prefixed to the station number; those made by R.R.S. 'William Scoresby' have the prefix WS and those of the Marine Biological Station the prefix MS. Besides these there are certain localities with no station number; these are grouped together at the end of the list.

St. 5. 31. i. 1926. Tristan da Cunha, Quest Bay, medium rectangular net, frame 4 ft. long and 2½ ft. wide, with bag of 7 mm. each; depth 7-12 m.; several short hauls inside Macrocystis belt.

Paridotea ungulata (Pallas).

St. 123. 15. xii. 26. Off mouth of Cumberland Bay, South Georgia. From 4.1 miles N. 54° E. of Larsen Point, to 1.2 miles S. 62° W. of Merton Rock, large otter trawl, 230-250 m., also net with mesh of 4 mm. attached to trawl 230 m., and tow-net of coarse silk attached to trawl, 220 m., grey mud.

Edotia oculopetiolata sp.n.

St. 140. 23. xii. 26. Stromness Harbour to Larsen Point, South Georgia. From 54° 02' S., 36° 38' W. to 54° 11' 30" S., 36° 29' W., net with mesh of 4 mm. attached to trawl, green mud and stones, 122-136 m.

Edotia oculopetiolata sp.n.

St. 141. 29. xii. 26. East Cumberland Bay, South Georgia, 200 yards from shore, under Mt Duse, small beam trawl, 17-27 m., two short hauls on steeply shelving ground at edge of kelp.

Glyptonotus antarcticus Eights.

St. 144. 5. i. 27. Off mouth of Stromness Harbour, South Georgia. From 54° 04' S., 36° 27' W. to 53° 58' S., 36° 26' W., tow-net of coarse silk attached to trawl, green mud and sand, 155-178 m.

Edotia oculopetiolata sp.n.

- St. 161. 12. iii. 27. Schollaert Channel, Palmer Archipelago, $64^{\circ} 20' 00''$ S., $63^{\circ} 01' 00''$ W., net with mesh of 4 mm. attached to trawl, 335 m.
Edotia oculopetiolata sp.n.
- St. 164. 18. ii. 27. East end of Normanna Strait, South Orkneys, near Cape Hansen, Coronation Island, small beam trawl, 24-36 m.
Glyptonotus antarcticus Eights.
- St. 170. 23. ii. 27. Off Cape Bowles, Clarence Island, $61^{\circ} 25' 30''$ S., $53^{\circ} 46' 00''$ W., large dredge, heavy pattern, 4 ft. in length, 342 m.
Pseudidothea scutatus (Stephensen).
- St. 178. 9-11. iii. 27. Melchior Harbour, Schollaert Channel, Palmer Archipelago, large fish trap, 17 m.
Glyptonotus antarcticus Eights.
- St. 180. 11. iii. 27. 1.7 miles west of north point of Gand Island, Schollaert Channel, Palmer Archipelago, net with mesh of 4 mm. attached to trawl, mud and stones, 160-330 m.
Edotia oculopetiolata sp.n.
- St. 195. 30. iii. 27. Admiralty Bay, King George Island, South Shetlands, $62^{\circ} 07' 00''$ S., $58^{\circ} 28' 30''$ W., net with mesh of 4 mm. attached to trawl (trawl hitched as soon as shot), mud and stones, 391 m.
Edotia oculopetiolata sp.n.
- St. 366. 6. iii. 30. 4 cables south of Cook Island, South Sandwich Islands, large dredge, black sand, 155-322 m., also large otter trawl, 77-152 m.
Glyptonotus antarcticus Eights.
- St. 370. 10. iii. 30. 2 miles north-east of Bristol Island, South Sandwich Islands, large otter trawl, 80-18 m.
Glyptonotus antarcticus Eights.
- St. 371. 14. iii. 30. 1 mile east of Montagu Island, South Sandwich Islands, large otter trawl, 99-161 m., also net with mesh of 4 mm. attached to trawl, 99-161 m.
Glyptonotus antarcticus Eights.
- St. 673. 25. iv. 31. $38^{\circ} 10\frac{1}{2}'$ S., $30^{\circ} 10\frac{1}{4}'$ W. to $38^{\circ} 03\frac{3}{4}'$ S., $29^{\circ} 48'$ W., young fish trawl, oblique haul, 340-0 m.
Idotea metallica Bosc.
- St. 700. 18. v. 31. $20^{\circ} 21\frac{1}{2}'$ N., $22^{\circ} 32\frac{1}{2}'$ W., hand net, at the surface.
Idotea metallica Bosc.
- St. 1489. 17. i. 35. Port Lockroy, Wiencke Island, Palmer Archipelago, found on motor-boat anchor.
Glyptonotus antarcticus Eights.
- St. 1562. 7. iv. 35. $46^{\circ} 51' 7''$ S., $37^{\circ} 56' 5''$ E. to $46^{\circ} 54' 8''$ S., $37^{\circ} 53' 8''$ E., 97-104 m.
Arcturides acuminatus sp.n.
- St. 1564. 7. iv. 35. $46^{\circ} 36' 5''$ S., $38^{\circ} 02' 3''$ E., large dredge, heavy pattern, 4 ft. in length, 110-113 m. (heavy south-west swell).
Arcturides acuminatus sp.n.
- St. 1652. 23. i. 36. $75^{\circ} 56' 2''$ S., $178^{\circ} 35' 5''$ W., rectangular dredge bag bent on a Russell frame with skids to raise it clear of deep mud on the sea floor in the neighbourhood of the Ross Ice Barrier, 567 m.
Glyptonotus antarcticus Eights.
- St. 1941. 29. xii. 36. Leith Harbour, South Georgia, small rectangular dredge, 38 m.
Glyptonotus antarcticus Eights.
- St. WS. 25. 17. xii. 26. Undine Harbour (North), South Georgia, small beam trawl, mud and sand, 18-27 m.
Edotia oculopetiolata sp.n.
- St. WS. 88. 6. iv. 27. $45^{\circ} 00' 00''$ S., $64^{\circ} 57' 30''$ W., from $54^{\circ} 00' 00''$ S., $65^{\circ} 00' 00''$ W. to $54^{\circ} 00' 00''$ S., $64^{\circ} 55' 00''$ W., commercial otter trawl, sand, shells and stones, 118 m.
Macrochiridothea stebbingi Ohlin.
- St. WS. 123. 9. vi. 27. Shore, Gough Island, under stones in rock pools.
Paridotea ungulata (Pallas).
- St. WS. 212. 30. v. 28. $49^{\circ} 22' 00''$ S., $60^{\circ} 10' 00''$ W., tow-net of coarse silk with 16 meshes to the linear inch, attached to trawl, green sand, mud and pebbles, 242-249 m.
Pseudidothea bonnieri Ohlin.

St. WS. 214. 31. v. 28. $48^{\circ} 25' 00''$ S., $60^{\circ} 40' 00''$ W., tow-net of coarse silk with 16 meshes to the linear inch, attached to trawl, fine dark sand, 208-219 m.

Pseudidothea bonnierii Ohlin.

St. WS. 215. 31. v. 28. $47^{\circ} 37' 00''$ S., $60^{\circ} 50' 00''$ W., tow-net of coarse silk (16 meshes to the linear inch) attached to trawl, fine green sand, 219-146 m.

Edotia oculata Ohlin.

St. WS. 219. 3. vi. 28. $47^{\circ} 06' 00''$ S., $62^{\circ} 12' 00''$ W., dark sand, tow-net as above 116-114 m.

Edotia oculata Ohlin.

St. WS. 220. 3. vi. 28. $47^{\circ} 56' 00''$ S., $62^{\circ} 38' 00''$ W., brown sand, tow-net as above, 108-104 m.

St. WS. 222. 8. vi. 28. $48^{\circ} 23' 00''$ S., $65^{\circ} 00' 00''$ W., coarse brown sand and shells, tow-net as above, 100-106 m.

Edotia oculata Ohlin.

St. WS. 237. 7. vii. 28. $46^{\circ} 00' 00''$ S., $60^{\circ} 05' 00''$ W., coarse brown sand and shells, tow-net of coarse silk attached to trawl, 150-256 m.

Xenarcturus spinulosus g.n., sp.n.

St. WS. 245. 18. vii. 28. $52^{\circ} 36' 00''$ S., $63^{\circ} 40' 00''$ W., net with mesh of 4 mm. attached to trawl, dark green sand, madreporic sand, pebbles and shells, 304-290 m.

Edotia bilobata Nordenstam.

St. WS. 756. 10. x. 31. From $50^{\circ} 53' 00''$ S., $60^{\circ} 00' 00''$ W. to $50^{\circ} 56' 30''$ S., $59^{\circ} 56' 00''$ W. to $50^{\circ} 59' 50''$ S., $59^{\circ} 52' 00''$ W., tow-net of coarse silk (16 meshes to the linear inch) attached to trawl, black gravel, green mud and sand, 119 m.

Xenarcturus spinulosus g.n., sp.n., *Pseudidothea bonnierii* Ohlin.

St. WS. 766. 18-19. x. 31. $44^{\circ} 58' 00''$ S., $60^{\circ} 05' 50''$ W., net attached to trawl, fine dark grey sand, 545 m.

Pseudidothea bonnierii Ohlin.

St. WS. 772. 30. x. 31. From $45^{\circ} 13' 00''$ S., $60^{\circ} 00' 00''$ W. to $45^{\circ} 13' 8''$ S., $60^{\circ} 00' 50''$ W., 309-162 m., nets attached to trawl, grey sand; also with nets with mesh of 4 mm. attached to trawl.

Macrochiridothea stebbingi Ohlin.

St. WS. 782. 4. xii. 31. From $50^{\circ} 30' 00''$ S., $58^{\circ} 19' 00''$ W. to $50^{\circ} 27' 00''$ S., $58^{\circ} 31' 00''$ W. (haul B), tow-net of coarse silk (16 meshes to the linear inch) attached to trawl, green sand and rock, 141-146 m.

Xenarcturus spinulosus g.n., sp.n.

St. WS. 787. 7. xii. 31. From $48^{\circ} 44' 00''$ S., $65^{\circ} 24' 50''$ W. to $48^{\circ} 48' 00''$ S., $65^{\circ} 25' 00''$ W., seine net attached to trawl, coarse brown speckled sand, 106-110 m.

Edotia oculata Ohlin.

St. WS. 797. 20. xii. 31. From $47^{\circ} 44' 00''$ S., $64^{\circ} 22' 00''$ W. to $47^{\circ} 45' 20''$ S., $64^{\circ} 18' 00''$ W. (haul B), nets attached to trawl, 115-111 m.

Edotia oculata Ohlin.

St. WS. 806. 7. i. 32. From $49^{\circ} 51' 00''$ S., $65^{\circ} 01' 00''$ W. to $50^{\circ} 03' 00''$ S., $64^{\circ} 23' 00''$ W., seine net attached to trawl, dark green speckled sand and shells, 129-122 m.

Edotia oculata Ohlin.

St. WS. 808. 8. i. 32. From $49^{\circ} 41' 00''$ S., $65^{\circ} 40' 00''$ W. to $49^{\circ} 39' 50''$ S., $65^{\circ} 44' 00''$ W., seine net attached to trawl, brown and green sand, 109-107 m.

Edotia oculata Ohlin.

St. WS. 809. 8. i. 32. From $49^{\circ} 29' 00''$ S., $66^{\circ} 27' 00''$ W. to $49^{\circ} 27' 50''$ S., $66^{\circ} 31' 00''$ W., seine net attached to trawl, brown speckled sand, 107-104 m.

Edotia corrugata sp.n., *Macrochiridothea kruimeli* Nierstrasz.

St. WS. 814. 13. i. 32. From $51^{\circ} 44' 50''$ S., $66^{\circ} 38' 00''$ W. to $51^{\circ} 46' 00''$ S., $66^{\circ} 42' 00''$ W., seine net attached to trawl, coarse dark speckled sand, 111-118 m.

Edotia oculata Ohlin.

St. WS. 816. 14. i. 32. From $52^{\circ} 09' 50''$ S., $64^{\circ} 58' 00''$ W. to $52^{\circ} 10' 00''$ S., $64^{\circ} 54' 00''$ W., net of 4 mm. mesh attached to trawl, shingle, 150 m.

Edotia oculata Ohlin.

St. WS. 818. 17. i. 32. From $52^{\circ} 30' 50''$ S., $63^{\circ} 27' 00''$ W. to $52^{\circ} 32' 00''$ S., $63^{\circ} 23' 00''$ W., commercial otter trawl., haul A, dark speckled sand, from *Cidarid* spines, 272 m.

Pseudidothea bonnierii Ohlin.

St. WS. 825. 28-29. i. 32. From 50° 50' S., 57° 13' W. to 50° 50' S., 57° 17.5' W., net attached to trawl, green sand, mud and shells, 135 m.

Pseudidothea bonnieri Ohlin.

St. WS. 839. 5. ii. 32. From 53° 29.5' S., 63° 31' W. to 53° 31' S., 63° 27' W., commercial otter trawl, fine sand and mud, 503 m.

Pseudidothea bonnieri Ohlin.

St. WS. 871. 1. iv. 32. 53° 16' S., 64° 12' W., small beam trawl, 336-341 m.

Edotia bilobata Nordenstam, *Pseudidothea bonnieri* Ohlin.

St. MS. 25. 13. iv. 25. East Cumberland Bay, South Georgia, 4½ cables north-east to 1½ cables north-west of Hobart Rock, small beam trawl, 36 m.

Glyptonotus antarcticus Eights, *Pseudidothea bonnieri* Ohlin.

St. MS. 71. 9. iii. 26. East Cumberland Bay, South Georgia, 9¼ cables east-by-south to 1.2 miles east-by-south of Sappho Point, small beam trawl and tow-net of coarse silk, 110-60 m.

Edotia oculopetiolata sp.n.

MS. 3. viii. 26. Crawling on female Blue Whale, Saldanha Bay, South Africa.

Paridotea ungulata (Pallas).

9. ix. 26. Walvis Bay, ectoparasitic on *Trigala capensis*.

Idotea indica Milne Edwards.

1927. Brought up on anchor chain S.S. 'Saragossa', Admiralty Bay, King George Island.

Glyptonotus antarcticus Eights.

Jan. 1927. Borge Bay, South Orkneys, fish trap (W. C. Rumbold).

Glyptonotus antarcticus Eights.

28. x. 28. Picked up on beach of King Edward's Point, South Georgia.

Glyptonotus antarcticus Eights.

25. v. 30. At Anchor, Houtjes Point, Saldanha Bay, hand lines, 12 m.

Idotea indica Milne Edwards, *Paridotea ungulata* (Pallas), *Synidotea hirtipes* (Milne Edwards).

1. x. 30. Capetown Docks, on ship's side.

Paridotea ungulata (Pallas).

17. ii. 31. Leith Harbour, South Georgia, hand line, 5 m., from fish stomach, found in boat after fishing with lines, probably *Notothenia rossii*.

Glyptonotus antarcticus Eights (incomplete specimen).

MORPHOLOGY OF THE VALVIFERA

There are several morphological characters in the Valvifera which need further elucidation.

(1) In 1939 I pointed out that in the Isopoda the 'only type of coxal plate so far recognized is one developed on the outer side of the joint and extending to the lateral and even dorsal surfaces of the body. . . . Apart from the development of brood lamellae, the possibility of a corresponding coxal expansion of the inner border of the joint appears to have been overlooked, and yet examination of a number of Isopod types suggests that such a development does occur.'

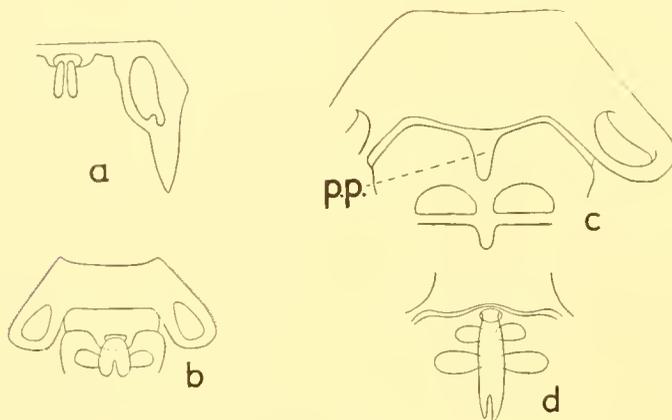
Subsequent work has confirmed and amplified this statement. Ventral coxal plates seem to be characteristic of all the known families of the suborder Valvifera, with the possible exception of the Amesopodidae.* These plates are present in both sexes on the inner ventral side of the coxal joint of each of the thoracic limbs; they extend inwards towards the mid-ventral line, where each meets and may become fused with the corresponding plate from the opposite limb. Their development may be correlated with the typical flattening of the body, the cylindrical shape of the Astacillidae being undoubtedly secondary (Sheppard, 1939, p. 173).

In the breeding females, however, ventral coxal plates as such appear to be absent from the limbs bearing brood lamellae, although a specialized condition is met with in some species of *Edotia* (see

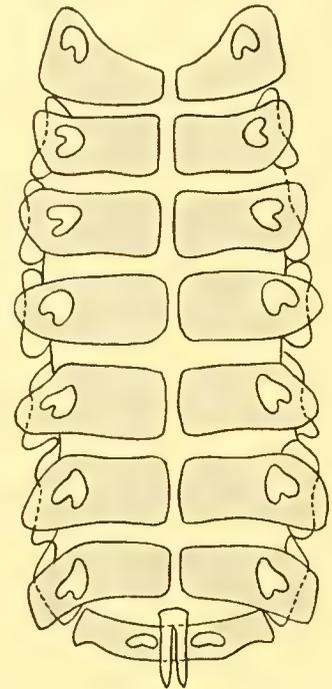
* I have been unable to identify them in *Amesopous richardsonae* Stebbing, the only species of the family, but this may have been due to the small size of the specimen.

pp. 155-157). In the region of the brood-pouch, chitinized rods are present in the ventral integument, but there is also a broad unchitinized central area in the integument, which presumably ensures adequate space for the development of the young. The thoracic limbs not involved in the formation of the brood-pouch carry ventral coxal plates and occasionally accessory supporting plates as well.

(2) Barnard, in the key already referred to, stated that the second ramus of the uropod is absent in the members of the family Idoteidae; this, however, is not the case, for while the absence of this ramus may be a fairly general character among members of the subfamily Idoteinae, it is not universal; it is present, for example, in *Cleantis linearis* Dana and *C. granulosa* (Heller). In the remaining three subfamilies of the Idoteidae, namely, Glyptonotinae, Macrochiridotheinae and Mesidoteinae, its presence, rather than its absence, is characteristic.



Text-fig. 1. Series of diagrams to show the change of position of the penis. (a) *Glyptonotus antarcticus*, $\times 2$. (b) *Edotia oculata*, $\times 13$. (c) *Edotia oculopetiolata*, $\times 17$. (d) *Pseudidothea bonnierii*, $\times 13$. p.p. position of penis.



Text-fig. 2. *Idotea indica* ♂, $\times 6$, ventral view.

(3) A further point must be mentioned in connexion with Barnard's paper, namely, his discussion of the position of the openings of the vasa deferentia in the male. The normal position of these openings in members of the Isopoda is on the ventral surface of the last thoracic somite, either about the middle of the somite, or on its posterior margin. According to Barnard (1920, p. 380), in the members of the Valvifera, the openings have shifted on to the first pleon segment; this certainly seems to be the case in members of the Asticillidae, Pseudidotheidae and Amesopodidae, where the pair of penial filaments are fused to form a single process which, in members of the Pseudidotheidae, are distally cleft (Text-fig. 1, d). But the condition in the family Idoteidae as a whole does not agree with Barnard's statement, for the position of the penial filaments is variable, though it is always posterior to the ventral coxal plates of the last thoracic somite. In *Glyptonotus antarcticus* (Text-fig. 1 a), for example, the penial filaments spring from the articular membrane immediately behind the fused coxal plates of the last thoracic somite; there is, in this species, a slight excavation of the plates in which the bases of the filaments are lodged.

(4) Barnard also made a point of the fact that the penial filaments are separate in the Idoteidae and united into a single process in the Asticillidae. This, however, is not true of all the members of the Idoteidae, for in the species of *Edotia* the basal portions of the two filaments are fused together (Text-fig. 1 b, c).

The following evolutionary series illustrates the way in which the change in form and position of the penis may have occurred.

(i) In *Idotea indica* (Text-fig. 2) the penes are united at their base and spring from the articular membrane between the last thoracic and the first abdominal segments.

(ii) In *Edotia oculata* (Text-fig. 1*b*) the fusion of the penes is more complete, and their base is nearer the abdominal segment, the anterior margin of which is slightly excavated to receive it.

(iii) In *E. oculopetiolata* (Text-fig. 1*c*) the excavation is much deeper and narrower and the fused base of the penes (indicated in the figure) is reduced in size.

(iv) In *Pseudidothea bonnieri* (Text-fig. 1*d*) the penis issues from a median aperture in the sternum of the first abdominal segment, just anterior to the appendages. The double nature of the penis is still indicated by the presence of two ducts and the distal cleft. I have been able to examine a male specimen of *Amesopous richardsonae* Stebbing and find that in this species from another family the penis is single.

(v) In members of the Astacillidae the penis is single though the vasa deferentia remain paired and open separately at its distal extremity.

This series of modifications appears to be due to the narrowing of the body, and, in particular, the narrowing of the abdominal region. A small portion of the articular membrane between the last thoracic and first abdominal segment has gradually become pinched in, and finally cut off by lateral compression of the sternum of the first abdominal segment. This has resulted in a consequent narrowing and fusion of the penial filaments.

SYSTEMATIC ACCOUNT

Family IDOTEIDAE Dana

Subfamily IDOTEINAE, Dana 1852; Miers, 1881

Genus *Idotea* Fabricius, 1798

Idotea indica Milne Edwards, 1840 (Text-figs. 2, 3 *a-d*)

I. indica Milne Edwards, 1840, p. 131.

I. latreillii Guérin Méneville, 1843, p. 32.

I. indica Miers, 1881, p. 50, pl. 2, figs. 4 and 5; Stebbing, 1902, pp. 62-3; Stebbing, 1910, p. 432.

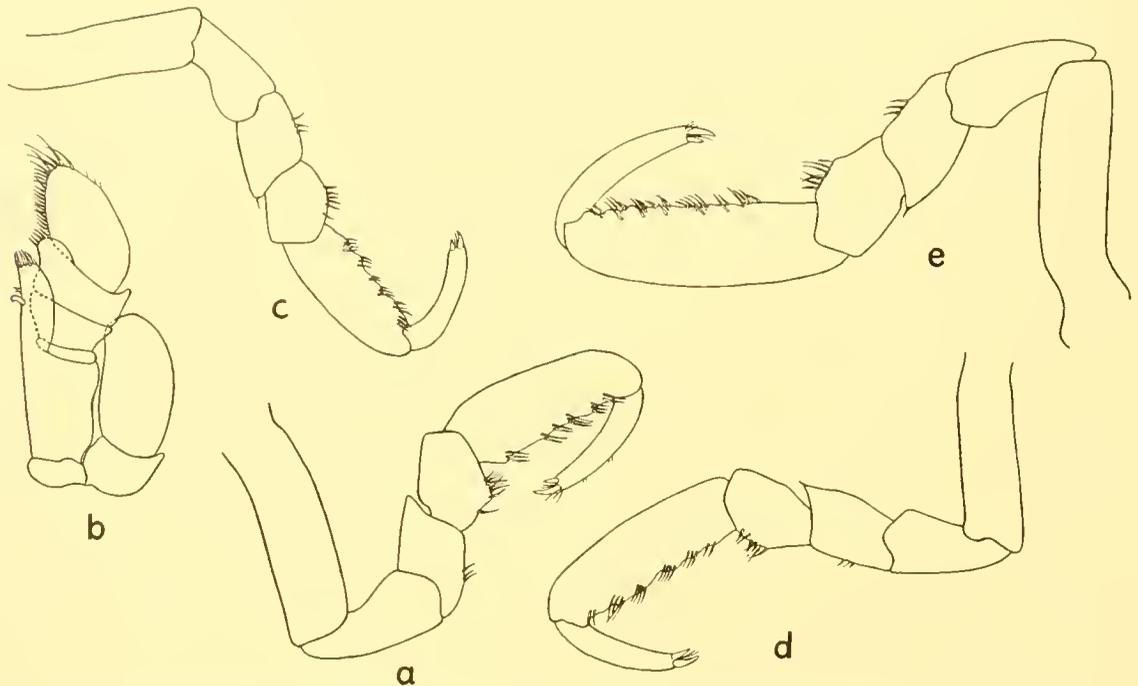
OCCURRENCE. At anchor, Houtjes Point, Saldanha Bay, 25. v. 30, 12 m., 1♂ and 1♀ (non-breeding); ectoparasitic on *Trigla capensis*; Walvis Bay, 9. ix. 26, 1♂.

REMARKS. Judging by the measurements given for this species in Stebbing's paper (1902, p. 63), the specimens in this collection are not full grown; the larger of the two males measures 19 mm. in length and 7 mm. in greatest breadth, the female is considerably larger, being 24 mm. in length and 7.5 mm. in breadth. The female is in the non-breeding condition and bears five pairs of small brood-plates on the coxal plates of the second to the sixth thoracic limbs.

There is little to add to the already published accounts of this species; Miers (1881, p. 50) stated that the last pair of thoracic appendages have 'their penultimate joints thickened and considerably elongated'; Stebbing (1902, p. 63), on the other hand, considered that 'the last peraeopods are not very strikingly larger than the penultimate pair' and suggested that this may be a character of the male sex. My own observations agree with those of Miers, namely, that in both sexes the last pair of thoracic limbs (Text-fig. 3*a, e*) are considerably longer than the penultimate pair (Text-fig. 3*c, d*). The longitudinal medio-dorsal furrow on the metasome mentioned by Guérin-Méneville (1843, p. 32) is present but not very deep.

The form of the coxal plates agrees with Miers's description as far as it goes, but the median ventral extensions (Text-fig. 2), already referred to as a character of the members of the suborder Valvifera, were overlooked by him. The penes are placed on the articular membrane between the last thoracic and first abdominal segment, near the anterior margin of the latter. The palp of the last thoracic (Text-fig. 3*b*) is, according to Stebbing, only very indistinctly four-jointed. On p. 63 (1902) he said: 'the dividing line between its second and third joints is only faintly discernible, except at the edges.' In my preparation this suture is quite well defined.

DISTRIBUTION. This species appears to be a shallow-water form, it has been recorded from depths ranging from 12 to 36 m. With the exception of Milne-Edwards's type specimen collected off the coast of Malabar, all the records are from off the coast of South Africa. Méneville's specimen occurred at the Cape of Good Hope, Stebbing's was collected in Hout Bay, and those of the Discovery collections from Houtjes Point, Saldanha Bay and Walvis Bay.



Text-fig. 3. Appendages of *Idotea indica*. (a) Seventh pereopod, ♂, × 12. (b) Left maxilliped, ♂, × 12. (c) Sixth pereopod, ♂, × 12. (d) Sixth pereopod, ♀, × 12. (e) Seventh pereopod, ♀, × 12.

Idotea metallica Bosc., 1802

I. metallica Bosc. 1802, p. 179, pl. xv, fig. 6; Latreille, 1803, p. 373.

I. peloponesiaca Roux, 1828, pl. xxx, figs. 10-12.

I. atrata Costa, 1838, pl. xl, fig. 3.

I. rugosa Milne-Edwards, 1840, p. 131.

I. robusta Kroyer, 1846, p. 108, pl. xxvi, fig. 3; Harger, 1880, p. 349, pl. 6, figs. 30-32.

I. compacta White, 1847, p. 95.

I. algerica Lucas, 1849, p. 61, pl. vi, fig. 2.

I. argentea Dana, 1852, p. 698, pl. 46, fig. 1.

I. metallica Miers, 1881, p. 35; Dollfus, 1895, p. 8, fig. 24; Norman, 1904, p. 443; Tattersall, 1904, p. 50; Stebbing, 1910, p. 108; Tattersall, 1911, p. 224, fig. 116; Barnard, 1914*a*, p. 203; Vanhoffen, 1914; Collinge, 1917, p. 746.

Idothea metallica Richardson, 1905, p. 362, 3 figs.; Nordenstam, 1933, p. 94; Gurjanowa, 1933, p. 434.

Occurrence. St. 673: 25. vi. 31. 38° 10½' S., 30° 10¼' W. to 38° 03¾' S., 29° 48' W., 340-0 m., 1 ♂. St. 700: 18. v. 31. 20° 21½' N., 22° 32½' W., 0 m., 2 ♂♂, 1 ♀ (breeding).

REMARKS. The Discovery collections contain four specimens of this species, three males and one female; the largest of the males measures 13 mm. in length and 4.5 mm. in greatest breadth; the female, which is in the breeding condition, measures 13.5 mm. in length and 6 mm. in greatest breadth. The female is broader in proportion than the male, the length:breadth ratio of the former being 2.25:1, that of the latter 2.8:1.

There is little to add to the already existing descriptions and figures of this species; Stephensen (1915, p. 13) figured a character also noted in the males of the Discovery collections, namely, the presence of a thick coating of long delicate setae on the inner edge of the 2-5 joints of the second pereopod; this sexual difference does not appear in other descriptions of the species.

Collinge (1917, p. 747) suggested that Stephensen's figure of *I. metallica* is really of a new and allied species, presumably because of the narrowness of the body (length:breadth ratio, 3.17:1). I fail to agree with this suggestion because this is the only character in which Stephensen's *I. metallica* differs from those in the Discovery collections, and Miers (1881, p. 37) had already pointed out that there was 'considerable variation in the degree of prominence of the epimera and in the width of the thoracic segments. In some adult examples the epimera do not project at all, and the serrated appearance of the sides of the thorax is lost. The younger individuals are generally narrower, with the sides more nearly parallel.'

Stephensen (p. 12, fig. 4) did not show the dense fringe of delicate setae which is present on all the peduncular joints of the antennae as well as on the joints of the flagellum, and on the peduncle of the antennule; these setae are exceptionally long in the specimen collected at St. 673.

DISTRIBUTION. This species is apparently cosmopolitan and so far has been recorded from surface waters only. The Discovery specimens were collected some distance off the west coast of Africa.

Genus *Paridotea* Stebbing, 1900

Paridotea ungulata (Pallas), 1772 (Text-fig. 4*a-e*)

Oniscus ungulatus Pallas, 1772, p. 62.

Idotea ungulata Lamarck, 1818, p. 160.

I. edwardsii Guérin-Méneville, 1843, p. 33.

I. lalandii Milne-Edwards, 1840, p. 132.

I. affinis Milne-Edwards, 1840, p. 133.

I. lalandii Krauss, 1843, p. 61.

I. affinis Krauss, 1843, p. 61.

I. nitida Heller, 1861, p. 497.

I. affinis Heller, 1868, p. 130; Miers, 1876*a*, p. 93; Thomson, 1879, p. 232.

I. ungulata Miers, 1881, p. 52.

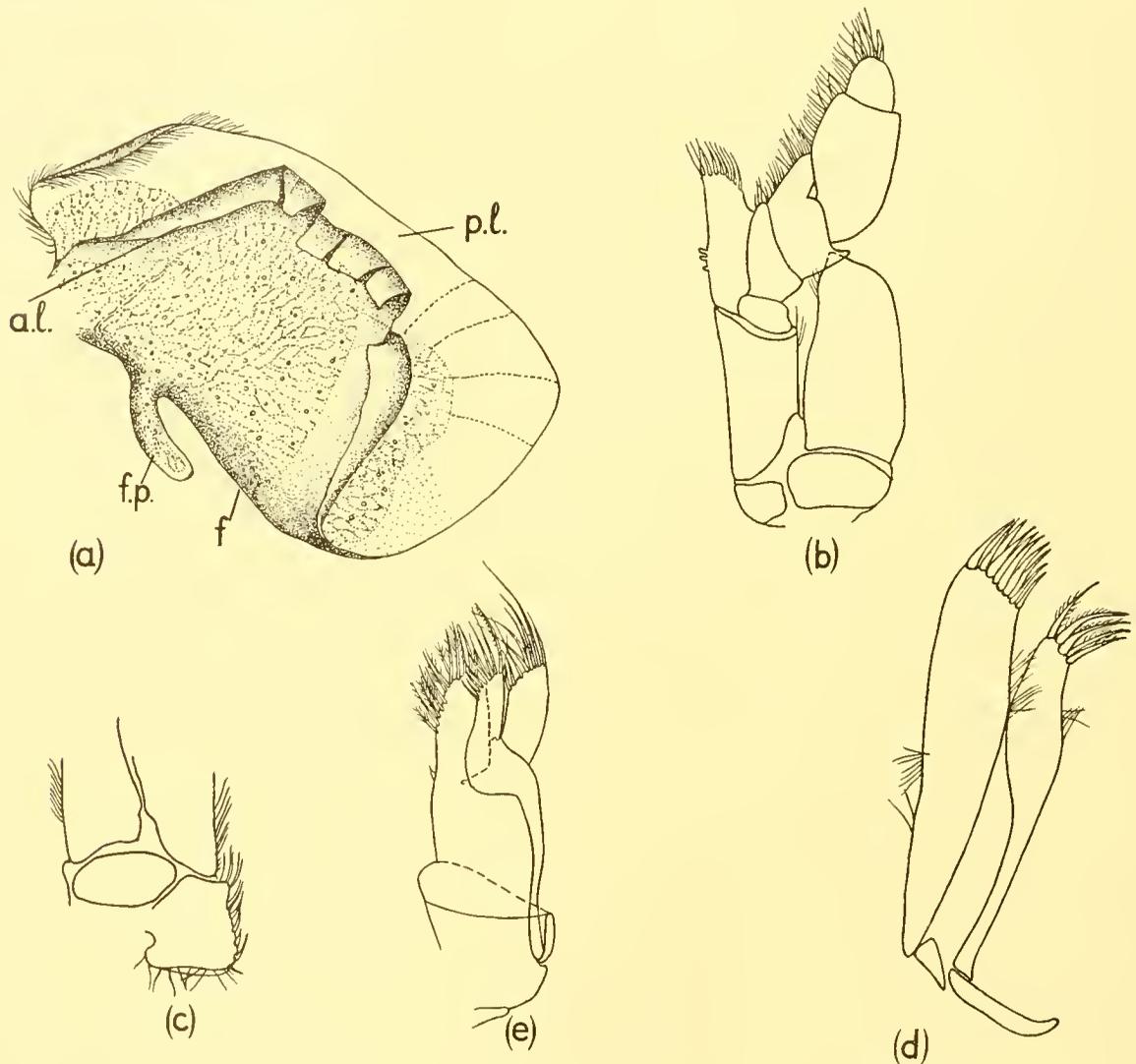
Paridotea ungulata Stebbing, 1900, pp. 53-5; Chilton, 1909, p. 660; Stebbing, 1902, p. 50; Barnard, 1914*b*, pp. 425-6; Nierstrasz, 1917, pp. 113-14, pl. xiv, figs. 43-48; Vanhoffen, 1914, p. 527; Collinge, 1918, pp. 81-2, pl. 8, figs. 24, 25.

Occurrence. St. 5: Tristan da Cunha, Quest Bay, 31. i. 26, 7-12 m., several short hauls inside *Macrocystis* belt, 2 specimens. Crawling on a female Blue Whale, Saldanha Bay; 1 immature specimen. 33° 01' S., 17° 58' E., 5. x. 26, found crawling on shark line; Houtjes Point, 8 m.-0, 1 ♂ and 1 ♀ (breeding); Houtjes Point, 25. v. 30, at anchor, depth 12 m., 1 ♀ (breeding); Capetown Docks, 1. x. 30, on ship's side, 1 ♂. St. WS. 123: 9. vi. 27, shore collection, Gough Island, under stones in rock pools, 3 immature specimens.

REMARKS. The largest male in this material measures 59 mm. in length and 15 mm. in greatest breadth and was collected in Capetown Docks, from the ship's side; the largest female measures 38 mm. in length and 10.5 mm. in greatest breadth; this specimen is in the breeding phase.

There is little to add to the existing descriptions of this species, though it should be pointed out that too much stress seems to be laid on small variations in detail.

The maxillula (Text-fig. 4*d*), for example, was first described by Stebbing (1900, p. 54). He stated there were 'six strongly plumose setae on the narrow inner plate'; in a subsequent paper, published in 1902, he altered this number to five. Nierstrasz (1917, p. 113), discussing this point, said that in his specimens the number of plumose setae varied, some specimens having four and others five. Collinge (1918), not having seen Nierstrasz's paper, disagreed with Stebbing and said (p. 82) that the inner lobe has 'four stout setose spines terminally, and a small setule on the middle of the ventral surface close to the anterior margin'; further, he stated that all his nine specimens were alike in this respect. It is unfortunate that Collinge gave no indication of the size of his specimens; those of Stebbings measured 51 mm. and 48 mm. in length.



Text-fig. 4. *Paridotea ungulata*. (a) First brood lamella (left) of breeding female, $\times 18$. a.l. anterior lobe; p.l. posterior lobe; f, fold; f.p. finger-like projection. (b) Left maxilliped, σ , ventral view, $\times 18$. (c) Base of right maxilliped (breeding f), dorsal view, $\times 18$. (d) Maxillula (right), $\times 21$. (e) Maxilla (left), $\times 21$.

In the Discovery collections the specimens vary considerably in size, and an examination of the maxillula of a large, a medium and a small individual shows that the number of setae is definitely correlated with the size of the individual:

- Large specimen: body length 52 mm. Number of spines 5.
- Medium specimen: body length 22.5 mm. Number of spines 4.
- Small specimen: body length 10 mm. Number of spines 3.

Thus it may be assumed that Collinge's specimens were of a medium size.

A description and figure of the maxilliped was given by Collinge (p. 82 and pl. 8, fig. 25). A figure of this appendage taken from a male specimen is included in the present paper (Text-fig. 4*b*), together with the basal portion of one taken from a breeding female (Text-fig. 4*c*). These figures illustrate a sexual difference in the form of the coxopodite characteristic of many isopods, that is, the development in the breeding female of a coxal 'lobe' which is curved and fringed with setae.

A figure (Text-fig. 4*a*) of the first brood lamella of the left side is also included to show another characteristic isopod feature of the breeding female. This is the folding of the plate, the anterior half of which partially overlies the mouthparts, the posterior half forming the anterior boundary of the marsupium. It also shows the characteristic finger-like projection which extends inwards from near the point of attachment of the lamella on to the coxopodite of the limb.

DISTRIBUTION. This species appears to be a fairly shallow-water form. Its range includes Table Bay, the Cape of Good Hope, the Indian Ocean, South Australia, Auckland, New Zealand, Chile, and Rio de Janeiro.

Genus *Synidotea* Harger, 1878

In the definition of this genus, both Stebbing (1902, p. 60) and Richardson (1905, p. 376) gave the fusion of the epimera of the thoracic somites with their respective somites as a diagnostic character. Stebbing pointed out that the last three thoracic somites were considerably shorter than the rest and the 'demarcation of the side plates was very faint'.

If only the dorsal surface of a species such as *Synidotea hirtipes* (Milne Edwards) is examined, this definition might appear to be correct. Examination of both surfaces, however, shows that the 'epimera' of the last three thoracic somites are coxal in origin, whereas those of the anterior somites are pleural expansions of the terga. In the first four free somites the coxal joints of the limbs are clearly defined, the outer margin of each is ring-like and, except in the first, is clearly marked off from the ventral surface of the pleuron by a suture; the inner margin is produced as a coxal plate which extends to the mid-ventral line.

I have examined specimens of two other species of this genus, *S. nodulosa* (Kroyer) and *S. bicuspidata* (Owen), and in both the form of coxae agrees with the condition found in *S. hirtipes*. It is probable that this character may prove to be common to all members of the genus.

Synidotea hirtipes (Milne-Edwards, 1840)

Idotea hirtipes Milne-Edwards, 1840, p. 134; Krauss, 1843, p. 61.

Edotia hirtipes Miers, 1881, p. 68.

Synidotea hirtipes Benedict, 1897, p. 403; Stebbing, 1902, pp. 59-62; Stebbing, 1910, p. 434; Omer-Cooper, 1926, p. 205.

Occurrence. Houtjes Point, Saldanha Bay, at anchor, 25. v. 30, 12 m., 1 immature specimen.

REMARKS. The Discovery collections contain a single specimen measuring 19 mm. in length and 8.5 mm. in greatest breadth.

The description of this species is already well known; my observations with regard to the second pair of thoracic appendages agree with those of Stebbing (1902, p. 60); he pointed out that they 'are shorter and stouter than the rest and the penultimate joint is considerably expanded to form with the terminal one a prehensile hand'. To a lesser extent an expansion of the penultimate joint is also noticeable on the next three pairs of limbs.

DISTRIBUTION. This species is a shallow-water form recorded from depths varying from 12 to 69 m. The original specimens described by Milne-Edwards were collected from the coast of the Cape of Good Hope; Stebbing's material was collected from the coastal waters around Cape St Blaize

and that of the Discovery collections from Houtjes Point, Saldanha Bay; Omer-Cooper (p. 205) recorded from the Suez Canal specimens which he assigned to this species, though admitting their identification to be doubtful. Except for this last record, the species has only been collected in South African waters.

Genus *Edotia* Guérin-Méneville, 1844

Edotia Guérin-Méneville, 1844, p. 34; Miers, 1881; Nordenstam, 1933, p. 94.

Desmarestia Nicolet, 1849, p. 284.

Epelys Dana, 1849, p. 426; Harger, 1880, p. 357.

Edotea Ohlin, 1901, p. 292; Richardson, 1905, p. 394.

REMARKS. The diagnosis of this genus was given by Richardson (1905, p. 394). She stated that 'epimera of all the segments of the thorax are firmly and perfectly united with the segments'. Richardson used the term 'epimera' to describe the coxal plates which are developed as outgrowths from the coxal joints and which may extend on to the dorsal surface and fuse with the terga of their respective somites. Nordenstam (1933, p. 95), commenting on this statement, said that 'in some species, however, the pereion is traversed by two lateral and parallel grooves on each side; the most laterally situated of these grooves marks off the epimera. This is the case in *E. bilobata* and *E. oculata*. . . . These grooves are indistinct in *E. tuberculata*, and usually they are entirely absent in *E. lilljeborgi*, *acuta*, *triloba*, *montosa*, *magellanica* and *doello-juradoi*.' Further on (p. 100), he said that '*Edotia bilobata* differs from the other species of the genus in having the coxal plates of the last three pereion segments demarcated by very distinct suture-like grooves. These grooves or sutures are not in a line with those grooves which mark off the coxal plates of the anterior segments.' I have examined eight of the eleven species of this genus, four species in the Discovery collections: *E. oculata* Ohlin, *E. bilobata* Nordenstam, *E. oculopetiolata* (Nordenstam's *E. tuberculata*) and *E. corrugata* n.sp.; and four in the British Museum collection, *E. magellanica* Cunningham, *E. montosa* (Stimpson), *E. triloba* (Say) and *E. tuberculata* Guérin-Méneville; none of them conforms to Richardson's diagnostic character, and in none of them do the lateral grooves mentioned by Nordenstam bear any relation to the 'coxal plates of the anterior segments'.

In all these eight species, the coxae of the limbs of the first four free thoracic segments are *not* expanded dorsally into coxal plates. As in *Synidotea*, the outer margin of each coxa is ring-like and (except for the first pair) is clearly marked off from the ventral surface of the pleuron by a suture, *but* ventral coxal plates are present as extensions of the inner margins of the coxae and almost meet in the middle line. In the first pair of limbs, the coxae are fused with the undersurface of the pleura of the first segment.

The coxae of the last three thoracic segments, on the contrary, *are* expanded dorsally into coxal plates and are either fused with or separated by faint sutures from the terga of their respective segments; where fusion has occurred, the position is indicated by a groove. The inner margins of these coxae are also expanded into ventral plates, but these plates are fused in the middle line.

Thus Richardson's diagnostic character is not valid for *Edotia*, while the demarcation of the coxal plates of the last three thoracic segments, regarded by Nordenstam as characteristic only of *E. bilobata*, is common to all eight species and may prove to be present in the remaining three, *lilljeborgi* Ohlin, *acuta* Richardson and *doello-juradoi* Giambiagi. The similar development of coxal plates in the species of *Edotia* and *Synidotea* (see p. 153) emphasizes the close relationship between these two genera; this relationship is indicated by their inclusion previously in the single genus *Edotia*. The coxal joints play an important role in the development of the marsupium or brood pouch. This is formed by overlapping brood lamellae, developed as outgrowths from the coxae of some of the thoracic appendages. In the majority of the Valvifera the marsupium is of the normal isopod type. For example,

in *Idotea emarginata* (Fabr.) the rudiments of the lamellae appear as four pairs of buds on the inner ventral margins of the coxae of the first four free thoracic segments. In the breeding female these buds develop into large, partly chitinized lamellae, lying ventrally to the coxae and overlapping one another to form a complete marsupium (Sheppard, 1939); there are no ventral coxal plates to the coxae of those limbs bearing lamellae, these appear to replace them.

With one exception, the published descriptions of the species of *Edotia* make no mention of any variation from this type of marsupium, but the breeding females of this genus in the Discovery collections all show some modification of the normal form. This modification is most marked in *E. oculata* Ohlin, where a condition is reached, the nearest parallel to which is seen in the Sphaeromidae, where brood pouches are formed by involution of either the ventral or the lateral integument. The single exception just mentioned is found in Nordenstam's (1933) description of *E. tuberculata* Guérin-Méneville (= *E. oculopetiolata* of this paper).

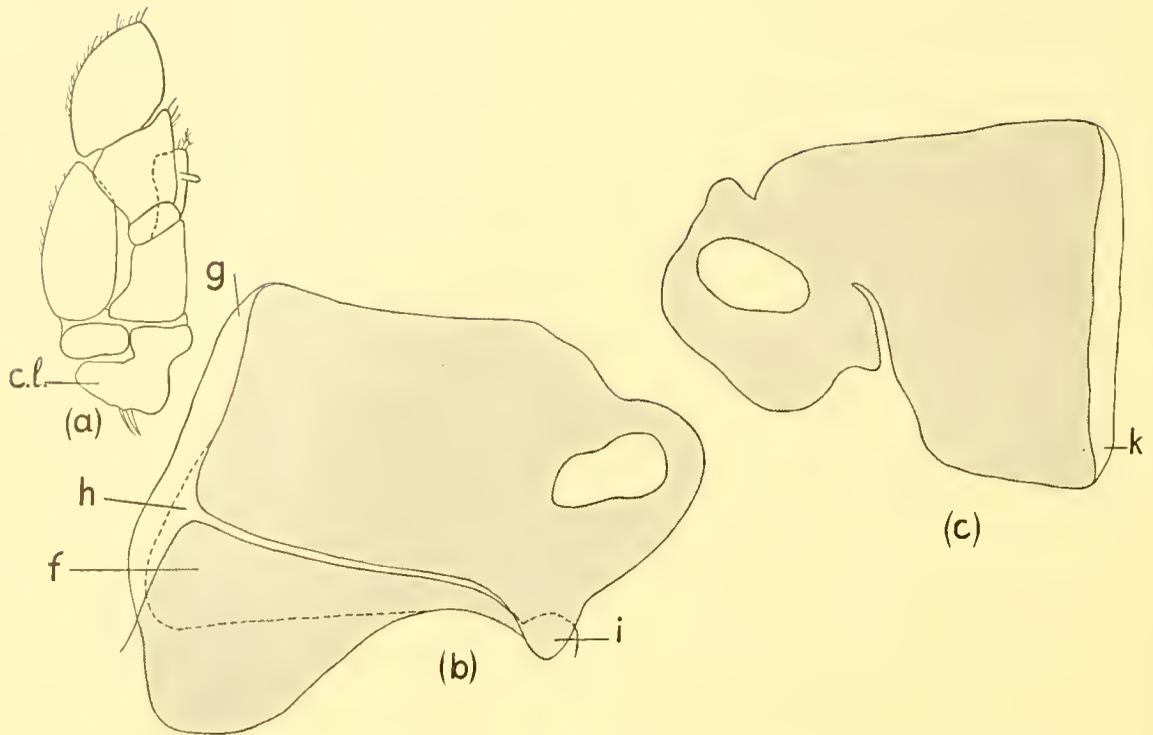
Nordenstam (1933, p. 95), in describing the four pairs of brood lamellae of this species, said: 'they are all fused with each other by a thin chitinous tegument', and 'the anterior margin of the small first pair (belonging to the first pereopods) is not fused anteriorly with the sternum'. Finally, of the fourth pair he said: 'its posterior margin is fastened to the sternum by a thin chitinous tegument.'

From this statement it would appear that the brood pouch, in this species, was a closed pouch communicating with the exterior by a small anterior opening only; this, however, is not the case. I have examined a breeding female of *E. oculopetiolata* and find that contrary to Nordenstam's observations the four pairs of brood lamellae are quite distinct, though modified. They differ from the common isopod type of large overlapping, partially chitinized, lamellae. Each lamella, when viewed from below, can be seen to be highly chitinized and appears to meet its fellow in the mid-ventral line. The posterior chitinized edge of one meets the anterior chitinized edge of the one immediately behind, each of the first three pairs of lamellae possessing, in addition, non-chitinous extensions of the posterior margins, which lie underneath (dorsally to) the chitinous anterior part of the succeeding pair (Text-fig. 5*b*).

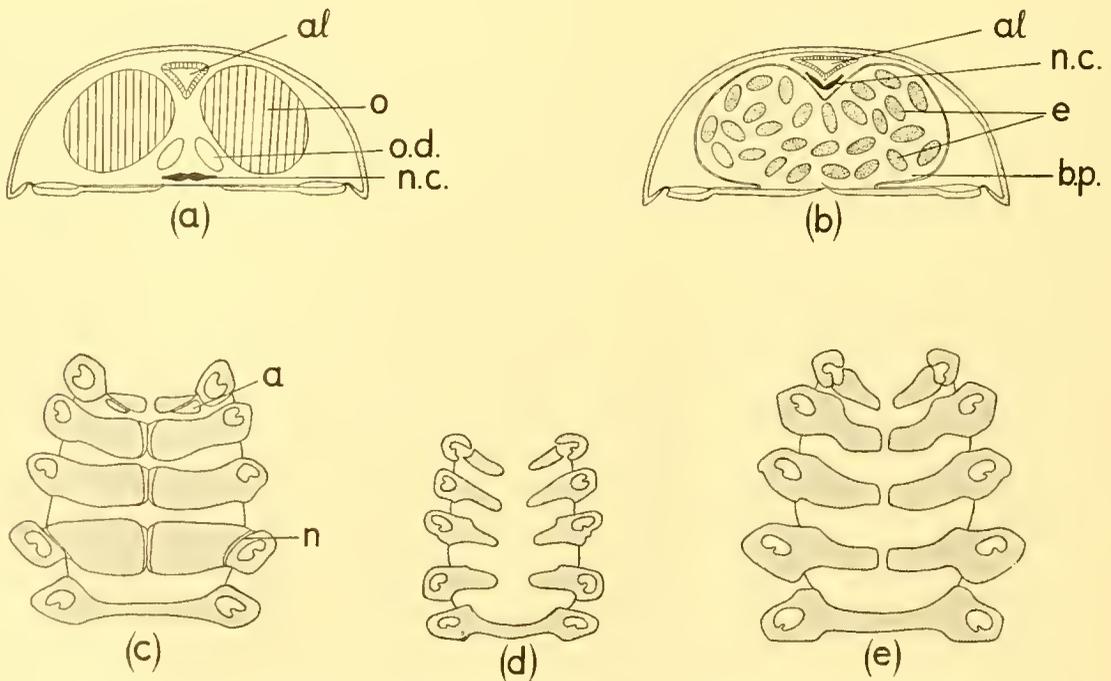
The fourth pair of lamellae are chitinized throughout and are longer than broad (Text-fig. 5*c*). The inner margins of the lamellae also possess non-chitinized extensions, which are short and bent dorsally upwards at right angles. The outer posterior angle (Text-fig. 5*b, i*) in each of the three anterior pairs of lamellae is produced into a strong lobe, which lies over the outer corner of the anterior margin of the lamella immediately behind, and forms an interlocking device. The strongly chitinized lamellae, together with the added rigidity produced by this interlocking, appear to be sufficient to prevent ventral sagging of the pouch and the consequent escape of its contained young, which develop between the lamellae and the ventral body wall. This wall is soft and becomes pushed up dorsally to lie very close to the dorsal body wall, carrying the ventral nerve cord with it into close proximity with the alimentary canal. A similar type of marsupium to that of *E. oculopetiolata* is also found in the breeding female of *E. corrugata* sp.n.

In the females of *E. oculata* Ohlin the modification of the brood pouch is carried farther than in other species of the genus. Among the Discovery specimens of this species there are a number of breeding and non-breeding females. In the breeding females the first four pairs of coxal plates (Text-fig. 6*c*), when viewed from below, very closely resemble those of the male (Text-fig. 6*e*); that is, they are large and nearly meet in the mid-ventral line. As in the male, the outer parts of these plates support the ventral integument, but the inner distal ends take on the function of acting as brood lamellae.

In the non-breeding females on the other hand, the first four pairs of coxal plates are short and comparatively narrow, with a broad unchitinized area of ventral integument between their distal ends



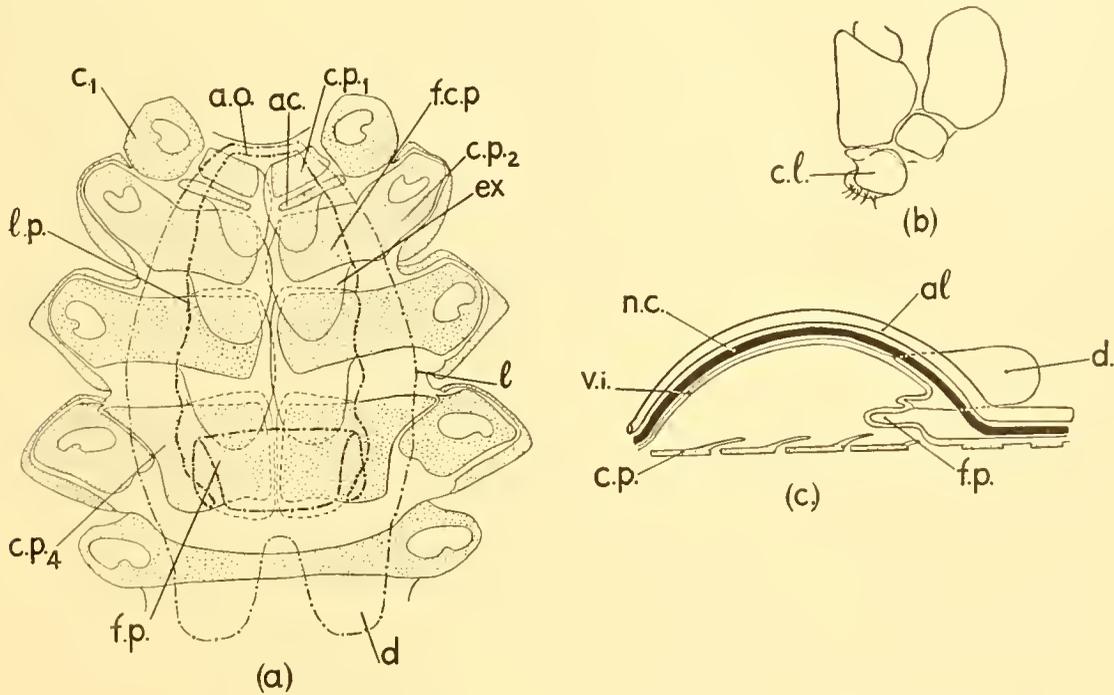
Text-fig. 5. *Edotia oculopetiolata* sp.n. (a) Maxilliped (right) of breeding female, showing coxal lobe, *c.l.*, $\times 30$. (b) Coxa and brood lamella of second free thoracic somite (left), $\times 30$. *f*, anterior part of next lamella; *g*, dorsally directed non-chitinous extension of lamella (extending to dotted line); *h*, non-chitinous area covered by *f*; *i*, projection of lamella fitting over corner of *f*. (c) Coxa and lamella of fourth free thoracic somite (right), $\times 30$. *k*, dorsally directed non-chitinous extension of lamella. Chitinous areas stippled.



Text-fig. 6. *Edotia oculata*. Diagrammatic transverse section of (a) non-breeding female, (b) breeding female. *al.* alimentary canal; *n.c.* nerve cord; *o.* ovary; *o.d.* oviduct; *e.* eggs; *b.p.* brood pouch. Ventral view of (c) breeding female; (d) non-breeding female; (e) male. *a.* accessory plate; *n.* non-chitinous integument between the coxal joint and coxal plate. Chitinous areas stippled.

(Text-fig. 6*d*). Some of the specimens are of full size; it therefore seems reasonable to assume that this is the normal condition in non-breeding females of this species. The wide band of unchitinized integument indicates that the development of these plates proceeds as an inward extension of the coxae and lends support to the view, expressed elsewhere (Sheppard, 1939), that the plates are coxal in origin.

In the fully developed brood pouch in *E. oculata* only the distal inner half of each plate is free; the outer parts are all connected together by the ventral integument, which, at about the middle of the plate, becomes pushed up dorsally to form a large pouch, almost entirely filling the thoracic region of



Text-fig. 7. *Edotia oculata*. (a) Brood pouch from above, dorsal integument removed (diagrammatic). a.c. accessory coxal plate; a.o. anterior opening of brood pouch; c₁, coxa of first pereiopod; c.p.₁, coxal plate of first pereiopod, unfused; c.p.₂, coxal plate of second pereiopod, fused; c.p.₄, coxal plate of fourth pereiopod, unfused; d, diverticulum of brood pouch; ex, soft extension of coxal plate; f.c.p. free part of coxal plate; f.p. fold of posterior wall of brood pouch; l, limit of brood pouch - - - - -; l.p. line showing displacement of ventral integument, - - - - - dorsally and laterally. (b) Base of left maxilliped to show coxal lobe, c.l. (c) Longitudinal section through brood pouch (diagrammatic). al, alimentary canal; c.p. coxal plate; d, diverticulum of brood pouch; f.p. fold of posterior wall of brood pouch; n.c. nerve cord; v.i. ventral integument. Chitinous areas stippled.

the body (Text-fig. 6*b*). The free inner margins of the coxal plates (Text-fig. 7*a*) are produced into membranous extensions; the posterior margins of the first three pairs of plates form large lobes which overlies the plates immediately behind. The extensions of the inner margins are narrow and curved upwards and overlap one another, alternately left over right, and right over left; in the text-figure the plates are slightly pulled apart in the mid-ventral line. The inner edges of the main part of the plates bear microscopic projections, while those of the last two pairs, in addition, are fringed with setae, the whole forming an interlocking device. Thus, a firm ventral wall to the pouch is formed from the distal ends of the coxal (brood) plates. The area of the ventral integument primarily involved in the formation of the rest of the pouch is limited to the region between the free portions of the coxal plates; it extends from just in front of the first pair of plates to the posterior border of the fourth pair. It has become greatly increased in size and is pushed dorsally towards the terga, carrying with it the

nerve cord which may be seen folded below the alimentary canal (Text-fig. 6*b*). All signs of the reproductive system have disappeared except for the posterior ends of the oviducts.

The posterior opening of the pouch, extending transversely immediately behind the free distal portions of the fourth pair of plates, is protected by a fold of the posterior wall of the pouch. This fold is double and is directed forwards to cover about three-quarters of the free surface of the plates; only the middle portion of the wall is involved, resulting in the formation of a pair of lateral diverticula to the pouch (Text-fig. 7*a, c*). The ventral portion of the fold is somewhat thickened and presumably acts as a valve, closing the opening and preventing the escape of eggs and developing young. The anterior opening of the pouch, which is much smaller, is protected by the coxal lobes which are developed on the coxae of the maxillipeds. Some idea of the size of the pouch may be gathered from the fact that a breeding female, measuring only 7 mm. in length, and 4 mm. in greatest breadth, contained 24 young specimens which varied in length from 1.5 to 2 mm.

The significance of these modifications of the brood pouch cannot be discussed without some reference to the habits of the species concerned. The only clue—if it can be called such—lies in the fact that they all appear to live in a 'dirty' environment, their bodies being invariably covered with particles of different types. This mode of life would expose the young, developing in a comparatively soft ventrally directed pouch, to serious damage, either by actual contact with the surroundings, or by infiltration of particles into the marsupium itself. The two kinds of brood pouch met with in *E. oculopetiolata* and *E. oculata* obviously afford greater protection than does the typical form of pouch.

Edotia bilobata Nordenstam, 1933 (Text-fig. 8*a-e*)

Edotia bilobata Nordenstam, 1933, pp. 98–100, pl. 1, fig. 6; text-figs. 23*c*, 24*a-c*.

Occurrence. WS 245: 18. vii. 28, 52° 36' 00" S., 63° 40' 00" W., 304–290 m., 1 ♂. WS 871; 1. iv. 32, 53° 16' 00" S., 64° 12' W., 336–341 m., 1 ♀.

REMARKS. This species was instituted by Nordenstam (1933) from examination of a single immature specimen. The Discovery collections contain two specimens, an adult male measuring 7.8 mm. in length and 3 mm. in greatest breadth, and a breeding female, measuring 10 mm. in length and 3.5 mm. in breadth.

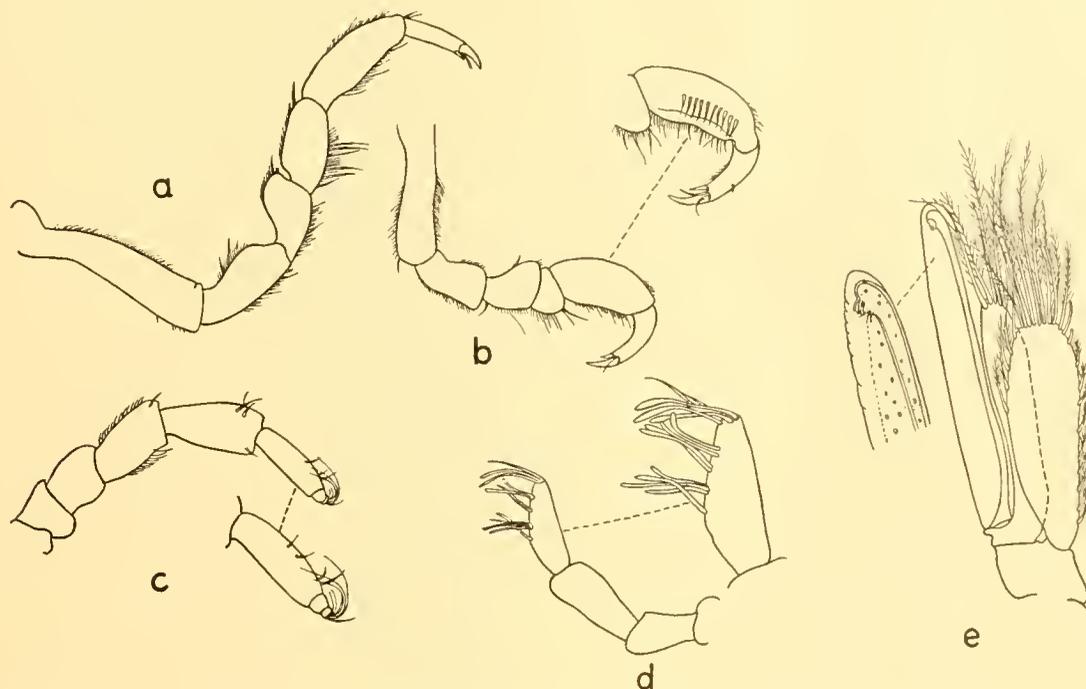
These specimens agree with the description given by Nordenstam except for the coxal plates of the anterior thoracic somites; this point has already been discussed (p. 154) in the introduction to the genus. Before passing on to the consideration of certain details, the general hairiness of the body and its appendages is worth noting. The detailed structure of the antennules and antennae cannot be seen in the figure given by Nordenstam. The sensory setae present on the flagellum of the antennule are more numerous in the male than in the female; in the latter they are six in number and occur near the distal extremity. The arrangement in the male is shown in Text-fig. 8*d*, and the structure of the antenna in Text-fig. 8*c*.

Except for the maxillipeds Nordenstam makes no mention of the form of the thoracic appendages. The second pair of pereopods (Text-fig. 8*b*) is shorter than the remaining ones, but all have the propodus somewhat dilated to form, with the dactylus, a prehensile limb. The remaining six pairs are all very similar in structure (Text-fig. 8*a*).

The brood pouch of the breeding female is of the modified type described in the introduction to the genus (pp. 154–155).

In the male, the penis is single, very broad and distally cleft; its base lies in a shallow depression on the front margin of the first abdominal segment; the form and position of the penis bears a close resemblance to that of *E. oculata* (Text-fig. 1*b*). The appendix masculina is shown in Text-fig. 8*e*.

DISTRIBUTION. The type specimen was collected in shallow water off New Year Island, Falkland Islands; those of the Discovery collections were collected in slightly deeper water (between 341 and 290 m. as compared with 36 m. in practically the same locality).



Text-fig. 8. *Edotia bilobata*, ♂. (a) Third pereopod, $\times 25$. (b) Second pereopod, $\times 25$. (c) Right antenna, $\times 35$. (d) Right antennule, $\times 32$. (e) Second pleopod, $\times 30$.

Edotia oculata Ohlin, 1901

Edotia oculata Ohlin, 1901, pp. 298–301, pl. xxiv, fig. 13; Nordenstam, 1933, p. 93.

Occurrence. WS. 215, 31. v. 28, $47^{\circ} 37' S.$, $60^{\circ} 50' W.$, 219–146 m., 1 ♀. WS. 219, 3. vi. 28, $47^{\circ} 06' S.$, $62^{\circ} 12' W.$, 116–114 m., 3 ♂♂, 9 ♀♀. WS. 220, 3. vi. 28, $47^{\circ} 56' S.$, $62^{\circ} 38' W.$, 108–104 m., 3 specimens. WS 222, 8. vi. 28, $48^{\circ} 23' S.$, $65^{\circ} 00' W.$, 100–106 m., 2 ♀♀. WS 787, 7. xii. 31, $48^{\circ} 44' S.$, $65^{\circ} 24.5' W.$, 106–110 m., 1 ♂, 1 ♀, 3 juv. WS. 797, 20. xii. 31, $47^{\circ} 44' S.$, $64^{\circ} 22' W.$, 115–111 m., 1 ♂. WS 806, 7. i. 32, $49^{\circ} 51' S.$, $65^{\circ} 01' W.$ to $50^{\circ} 03' S.$, $64^{\circ} 23' W.$, 129–122 m., 1 ♂. WS. 808, 8. i. 32, $49^{\circ} 41' S.$, $63^{\circ} 40' W.$, 109–107 m., 3 ♀♀, 2 juv. WS. 814, 13. i. 32, $51^{\circ} 44.5' S.$, $66^{\circ} 38' W.$, 111–118 m., 2 ♀♀. WS. 818, 17. i. 32, $52^{\circ} 09.5' S.$, $64^{\circ} 58' W.$ to $52^{\circ} 10' S.$, $64^{\circ} 54' W.$, 150 m., 1 ♀.

REMARKS. This species has not been recorded since it was first described by Ohlin in 1901 from a single female, measuring 7 mm. in length and 4 mm. in greatest breadth. The Discovery collections contain a number of mature specimens of both sexes; of these, the males are the larger, measuring 9 mm. in length and 5 mm. in greatest breadth; the mature females are approximately the same size as Ohlin's specimen.

Ohlin's estimate of the length of the eye-stalks (p. 298) is too high; they are not 'nearly as long as the peduncle of the antennules' as he suggested, but about the length of the first two joints.

The form of the coxae and of the brood pouch in the breeding female has already been dealt with in the introduction to the genus (pp. 154–158).

The male characters are very like those already described for *E. bilobata*, the flagellum of the antennule bears many more sensory setae than does that of the female. The penis (Text-fig. 1b) is single, broad, rounded and distally cleft; the appendix masculina bears a very close resemblance to that of *E. bilobata* (Text-fig. 8e).

DISTRIBUTION. The Discovery specimens are all recorded from an area between 47° S., 60° W. and 51° S., $66^{\circ} 45'$ W., at depths ranging from 219 to 100 m. Ohlin's specimen came from 38° S., 56° W. at a depth of 52 fathoms (approximately 93.6 m.). Thus the localities from which this species has been collected are all close together and all of them are outside the Antarctic Convergence.

Edotia oculopetiolata sp.n. (Text-fig. 9a-g)

Edotia tuberculata Guérin-Méneville, Nordenstam, 1933, pp. 95-7, figs. 22-23a.

Occurrence. St. 123: 15. xii. 26, off mouth of Cumberland Bay, South Georgia, 230-250 m., 1 ♀; 230 m., 2 immature specimens; 220 m., 1 immature specimen. St. 140: 23. xii. 26, Stromness Harbour, South Georgia, 122-136 m., 1 ♀. St. 144: 5. i. 27, off mouth of Stromness Harbour, South Georgia, 155-178 m., 3 ♀♀ (breeding), 4 ♂♂. St. 180: 11. iii. 27, Schollaert Channel, Palmer Archipelago, 160-330 m., 1 ♂. St. 161: 12. iii. 27, Schollaert Channel, Palmer Archipelago, $64^{\circ} 20' 00''$ S., $63^{\circ} 01' 00''$ W., 335 m., 1 ♂ (damaged). St. 195: 30. iii. 27, Admiralty Bay, King George Island, South Shetlands, 391 m., 1 ♂ and 1 ♀. St. WS 25: 17. xii. 26, Undine Harbour (North), South Georgia, 18-27 m., 1 ♂. St. MS 71: 9. iii. 26, East Cumberland Bay, South Georgia, 110-60 m., 1 ♀.

The holotypes are from St. 195.

REMARKS. Nordenstam (1933, p. 95) identified some specimens from the Swedish Antarctic Expedition as *E. tuberculata*, but he was incorrect in his diagnosis. His specimens differed from Guérin-Méneville's description of the type in a number of characters, and I consider that they should be included in a new species, *E. oculopetiolata*.

Perhaps the most obvious difference between the two forms is that of size. Ohlin (1901, p. 292) gives the length of *E. tuberculata* as 29 mm. and breadth as 11 mm.; Miers (1881, p. 73) gives the length as 30 mm. and breadth also as 11 mm. Nordenstam's specimens, on the other hand, were considerably smaller, a mature male measuring 10 mm. in length and a mature female 9-10 mm. The specimens of the Discovery collections are approximately the same size as those of Nordenstam; the largest male is 11 mm. in length and 4 mm. in greatest breadth. The true *E. tuberculata* is therefore about three times as large as *E. oculopetiolata*.

Apart from size, there are other important differences between the two species. Nordenstam himself (p. 96) noticed that in his specimens 'the eyes are placed on large tubercles, lateral margins of the head are somewhat concave, and dorsal side of head has four tubercles'. The tubercles bearing the eyes (Text-fig. 9f) are so obvious that, if present, they cannot be overlooked, yet none of the descriptions of *E. tuberculata* contains any mention of such a feature; for this reason Nordenstam's identification seems open to doubt.

An examination of the British Museum specimens of *E. tuberculata* has finally settled the point, for in these the eyes are small, lateral in position, and not on tubercles. The apical segment of the uropod in *E. tuberculata* (Miers, 1881, pl. iii, 6) is longer and very much more acute than that of Nordenstam's species (1933, p. 97, fig. 23a). In the introduction to the genus, reference has already been made to the form of coxae and the modification of the brood pouch in this species (p. 155).

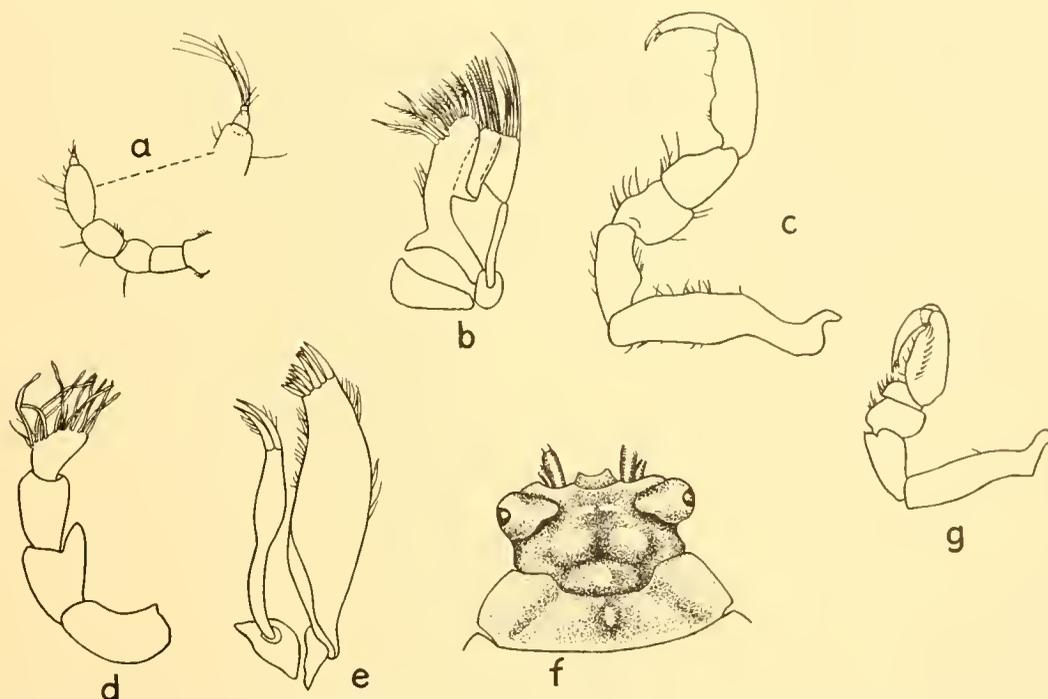
These structural differences are further supported by differences in distribution. The true *E. tuberculata* is found in waters around the south of South America and the shores of the Falkland Islands, that is, in areas outside the Antarctic Convergence; on the other hand, Nordenstam's *E. tuberculata* and the corresponding specimens in the Discovery collections occur in shallow waters off South Georgia, the South Shetland Islands and the Palmer Archipelago—all within the Convergence.

Evidence is accumulating to show that shallow-water species of both isopods and amphipods occur in localities either outside, or inside, the Antarctic Convergence, but that any one species does not occur in both areas. If Nordenstam's identification were correct, then *E. tuberculata* would be an exception to this rule.

The differences listed above appear sufficient to justify the removal of Nordenstam's *E. tuberculata* from the species and to institute a new one, *E. oculopetiolata*, to receive it, together with similar specimens from the Discovery collections.

DESCRIPTION. The *antennule* (Text-fig. 9*d*) is considerably longer and stouter than the antenna (cf. the published figures of *E. tuberculata* of Ohlin, 1901, pl. iii, figs. 10*a*, 2, where the antenna is much longer than the antennule).

The first peduncular joint is slightly longer than the other two, which are of approximately equal length, the inner distal angle of the second joint is produced to form a well-marked projection. The clavate flagellar joint is slightly shorter than the third peduncular joint, and bears, in the male, a number of long sensory setae on its anterior margin. In the female these are fewer in number and are restricted to a small tuft at the distal extremity of the joint.



Text-fig. 9. *Edotia oculopetiolata* sp.n. (a) Antenna, $\times 22$. (b) Left maxilla, $\times 42$. (c) Fifth pereopod, $\times 15$. (d) Antennule, δ , $\times 22$. (e) Left maxilla, $\times 42$. (f) Head and first pereion segment, $\times 12$. (g) First pereopod, $\times 15$.

The *antenna* (Text-fig. 9*a*) consists of a peduncle of five joints and a flagellum of two very short ones (cf. Ohlin, 1901, p. 293 and pl. xxiii, fig. 10*a*2, where the flagellum consists of three joints, the first one of which is of considerable length). The first four peduncular joints are short and subequal, the fifth is nearly twice as long as the fourth. The flagellum is extremely short; the distal joint is much smaller than the basal one, and bears a tuft of long setae.

The *mandibles* are described and figured by Nordenstam (1933, p. 95, fig. 22*a*, *b*).

The outer lobe of the *maxillula* (Text-fig. 9*e*) has ten spines on its obliquely truncated extremity, and a few scattered setae both on its inner and outer borders. The distal extremity of the inner lobe bears two strong, curved, sparsely plumose setae. The outer lobe of the maxilla (Text-fig. 9*b*) bears six long setae on its extremity, the middle lobe bears seven pectinate setae, and the innermost lobe has its rounded distal end fringed with eleven plumose setae, of which the three innermost are much the stronger and are curved inwards.

The palp of the *maxilliped* (Text-fig. 5*a*) is three jointed, the distal joint is broad and bears a fringe of short setae on its outer margin (cf. Ohlin, 1901, for *E. tuberculata*, pl. xxiii, fig. 10*m**xp*, where setae

are present all round this lobe and also on the outer margin of the lamella). The coxopodite bears a coxal lobe in the breeding female.

The second *thoracic appendage* is shown in Text-fig. 9g. It is considerably smaller and shorter than the remaining appendages which increase in length from before backwards. The second, third, fourth and fifth pairs are all subchelate, the last three pairs, which are directed backwards, are ambulatory (Text-fig. 9c of sixth thoracic appendage).

The *pleopods* are of the usual type, the form of the second pleopod of the male is shown by Nordenstam (1933, p. 96, text-fig. 22c, d). Mention has already been made of the form of the uropod.

DISTRIBUTION. Nordenstam's specimens were collected off the coast of South Georgia; those of the Discovery collections from South Georgia; Schollaert Channel, Palmer Archipelago; and Admiralty Bay, King George Island, South Shetlands.

Edotia corrugata n.sp. (Plate VIII, figs. 1, 2; Text-fig. 10a-l)

Occurrence. St. WS 809: 8. i. 32, 49° 29' S., 66° 27' W., 107-104 m., 2 ♂♂ and 2 ♀♀, one breeding and the other non-breeding.

The holotypes are from St. WS. 809.

DESCRIPTION. The *body* of the male (Plate VIII, fig. 1) is longer and narrower than that of the female (Plate VIII, fig. 2), which is compact and strongly arched; the male measures 6.5 mm. in length and 2.6 mm. in greatest breadth; the female 5.5 mm. in length and 2.75 mm. in greatest breadth, the length:breadth ratio of the male is 2.5:1 as compared with a 2:1 ratio in the female.

The *head* (Plate VIII, figs. 1, 2) is almost rectangular, broader than long, with the posterior margin slightly longer than the anterior; the antero-lateral angles are rounded and the anterior margin is excavated for the reception of the antennules. The eyes, which are small and contain little pigment, are situated on either side midway between the anterior and posterior margin of the head, some distance in from the lateral border. The posterior part of the head is raised and separated from the anterior part by a groove; in the middle of the latter is a single large, rounded protuberance, which does not show clearly in the photographs of the entire animal.

The pereion somites in the male are subequal in length, except for the first which is only half the length of the second. They are all supplied with well-developed pleura which, in the first four somites, overhang the bases of the limbs. In the last three they are fused with the dorsal extensions of the coxal plates of their respective limbs. The posterior half of each somite is raised in a pronounced transverse ridge, which extends over the complete width of the somite and its pleura. The crests of the ridges are rounded and give the animal a corrugated appearance when viewed from the side. Each pleuron is broad, being a little over half the width of the tergum from which it is separated by a slight groove; a further groove is present on the pleuron itself. In the hinder three somites these grooves represent the line of fusion of the pleura with the coxal plates.

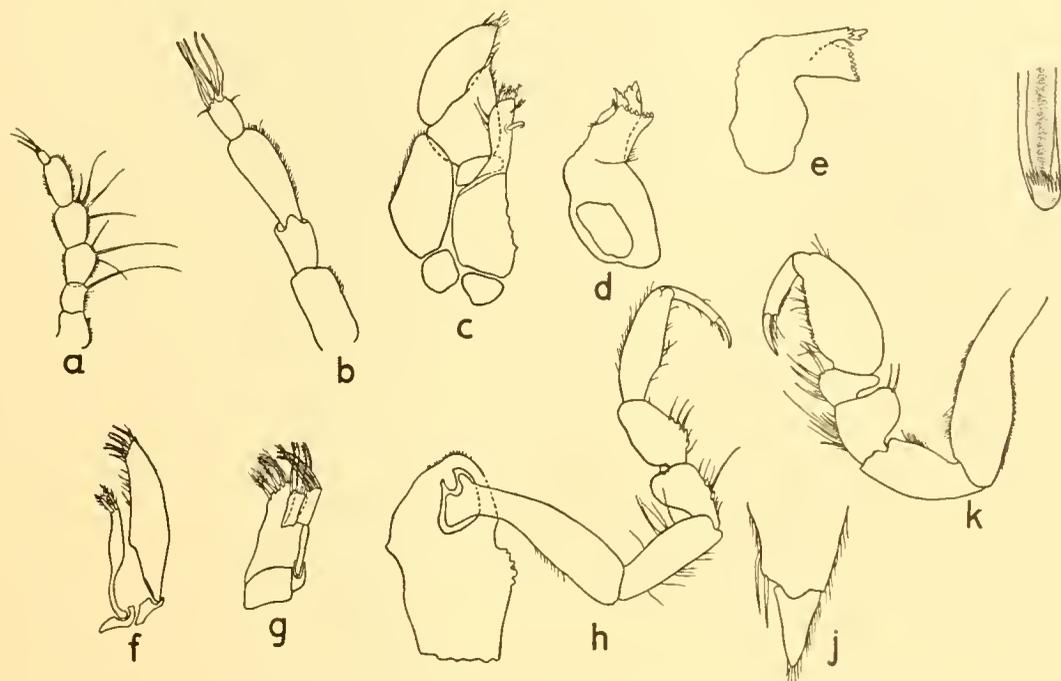
The pleura, the outer margins of which are rounded, are curved slightly forwards on the first three pereion somites, on the fourth they are straight and the posterior three are directed slightly backwards. In the female (Plate VIII, fig. 2) the first five pereion somites are considerably broader than those of the male and are strongly arched, but the arrangement of the ridges and grooves is similar in both sexes. The form of the coxal joint and its outgrowths has been considered in the introduction to the genus (p. 155).

The abdomen, which is somewhat elliptical in shape and slightly broader in the female than in the male, is about a third of the length of the body; its posterior tip is rounded. A small anterior segment is indicated by a transverse groove. Behind this groove the whole of the dorsal surface is elevated, but

the anterior third is separated by a fairly deep groove from the posterior part. In the anterior third the raised area forms a large central protuberance with a smaller one on either side of it.

The *antennules* (Text-fig. 10*b*) are longer than the antennae. The peduncle consists of three joints, the middle one of which is the shortest and the distal one the longest. The flagellum consists of a single joint, about half the length of the third peduncular joint; it bears at its distal extremity five or six sensory setae, three of which arise together from what may be regarded as a minute second joint.

The *antenna* (Text-fig. 10*a*) is extremely short, its five peduncular joints are not much longer than broad; the flagellum, which consists of a single joint, is very small, only about a third of the width of the fifth joint of the peduncle, and less than a third of its length; it bears three long setae at its distal extremity.



Text-fig. 10. *Edotia corrugata* sp.n. (a) Antenna, $\times 50$. (b) Antennule, $\times 50$. (c) Maxilliped (right), $\times 50$. (d) Left mandible, $\times 50$. (e) Right mandible, $\times 50$. (f) Maxillula (left), $\times 50$. (g) Maxilla (left), $\times 50$. (h) Second pereiopod (with coxa), $\times 30$. (j) Distal portion of protopodite and endopodite of uropod, $\times 20$. (k) First pereiopod, $\times 20$. (l) Appendix masculina.

The *maxillula* (Text-fig. 10*f*) is of the usual type; the truncated end of the outer lobe bears six or seven pectinate setae and the delicate inner lobe bears two strong plumose ones. Both the outer and middle lobe of the maxilla (Text-fig. 10*g*) bears five pectinate apical setae; the fixed inner lobe has three delicate and three strong plumose setae on its truncated extremity. The form of the cutting edges of the *mandibles* and the *maxillipeds* can be seen from Text-fig. 10*c, d* and *e*.

All the *pereiopods* are prehensile, the anterior four pairs are directed forwards, the posterior three pairs backwards; the first pair (second thoracic) (Text-fig. 10*f*) is shorter and stouter than the remaining ones, and is subchelate. The propodus is broad and bears, on its inner margin, a double row of short, closely set spines; the dactylus is also armed with a row of short spines. The remaining six pairs are all very similar to each other, both in form and size (Text-fig. 10*h*).

The second pair of *pleopods* is modified in the male, the appendix masculina is long and its distal extremity (Text-fig. 10*l*) is hollowed out on its inner side, the edge being armed with eight or nine spines.

The protopodite of the *uropod* is hollowed out, so that when viewed from the ventral side of the body the uropods together form a convex surface. The inner margin of the protopodite is bent

upwards to form a dorsally directed flange which is continuous with a similar one on the endopodite. The endopodite (Text-fig. 10j) is nearly twice as long as it is broad.

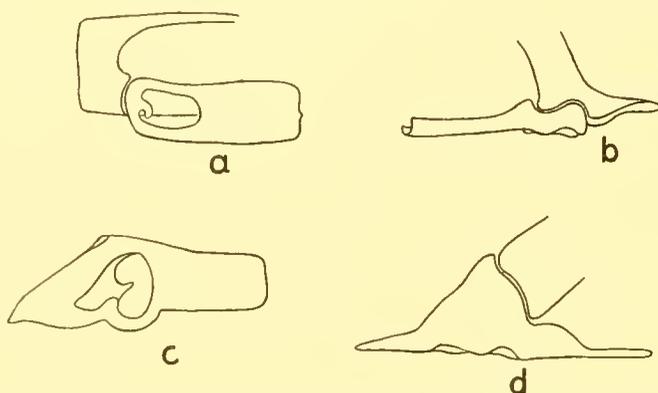
DISTRIBUTION. The specimens were collected at $49^{\circ} 28' 25''$ S., $66^{\circ} 29' 00''$ W., that is to say, in an area of shallow water outside the Antarctic Convergence, off the coast of the southern part of South America.

Subfamily GLYPTONOTINAE Miers, 1881

This subfamily was instituted by Miers (1881) to contain the single genus *Glyptonotus* with its five species: *G. antarcticus* Eights, *G. entomon* Linn., *G. sabini* Kroyer, *G. caecus* Say and *G. tuftsii* Stimpson.

The diagnostic characters of the subfamily were: 'Sides of the head emarginate or cleft and laterally produced beyond the eyes, which thus are situated upon its dorsal surface. The three anterior pairs of legs with the penultimate joint or propodus dilated and forming with the reflexible dactylus a prehensile hand. Species more or less ovate.'

At the present time the only species from the above list remaining in the genus is *G. antarcticus*, but a new species *G. acutus* Richardson was added in 1906, and new genus *Symmius*, with one species *S. caudatus* by Richardson in 1904. The diagnostic character, 'sides of head emarginate or cleft', no longer holds for this subfamily. Although Collinge (1916, p. 114) used this character as diagnostic in separating the two genera, in a later paper (1918, p. 64) he pointed out that the margins are entire both in the existing species of *Glyptonotus* and in *Symmius caudatus*.



Text-fig. 11. *Glyptonotus antarcticus*. (a) Ventral view of coxa and plate of second pereiopod and a portion of the tergum, $\times 2$. (b) Posterior view of (a). (c) Ventral view of sixth coxa and plate, $\times 2$. (d) Posterior view, showing the relationship with the tergum.

Nordenstam (1933, p. 103), in his diagnosis of the subfamily, mentioned that the coxal plates are 'marked off by dorsal sutures on the last three pereion segments'. It is strange that he makes no reference to the coxae of the anterior segments until his discussion on the affinities of the subfamily Macrochiridotheinae; here, on p. 110, he says 'the coxae on these segments are very small in *Glyptonotus*, though distinctly delimited from the segments'. This is an important point, since most authors state that the coxal plates of the anterior thoracic somites are completely fused with their respective somites. Actually, the terga of the second to the fifth thoracic somites inclusive are produced into broad pleura which extend laterally over the bases of the limbs (Text-fig. 11b). On the ventral surface of these somites each coxal joint is clearly defined, its outer margin is ring-like, and except for that of the second, is separated from the ventral surface of the pleuron by a suture. The inner part of the joint is produced as a coxal plate which partly covers the ventral integument and extends almost to the mid-ventral line (Text-fig. 11a). In the hinder three somites the pleura are replaced by coxal plates

which extend on to the dorsal surfaces of their respective somites. As in the anterior somites, coxal plates also extend from the inner borders of the joints to the mid-ventral line; those of the last segment in species of *Glyptonotus* are fused together (Text-fig. 11a).

According to Richardson (1904, pp. 39-40) *Symmius caudatus* has 'epimera present and developed on only the last three segments of the thorax as in *Glyptonotus* Eights, the epimera of the three anterior segments being perfectly united with the segments and with no trace of suture lines'. If this statement were true, there would be an important morphological difference between these two genera, but an examination of the British Museum specimen shows that this statement is incorrect, the form of the coxa is the same in both genera.

Genus *Glyptonotus* Eights, 1852

Glyptonotus antarcticus Eights, 1852 (Plate IX, figs. 1-5; Text-fig. 11a-d)

G. antarcticus Eights, 1852, pp. 331-4, 2 pls.; Miers, 1881, p. 11; Pfeffer, 1887, pp. 115-25, pl. 2, fig. 7; pl. vi, figs. 13-27; Tait, 1917, p. 246, 22 text-figures; Collinge, 1918, p. 65, pls. 1, 2, figs. 1-12; Tattersall, 1921, pp. 232-3; Calabrese, 1931, pp. 323-6, 2 text-figures; Monod, 1931, p. 27; Nordenstam, 1933, pp. 104 and 110.

G. antarcticus var. *acutus* Tattersall, 1921, pp. 233-5, pl. ix, figs. 3, 4; Pesta, 1928, pp. 78 and 81; Calabrese, 1931, pp. 323-6; Nordenstam, 1933, p. 104.

G. acutus Richardson, 1906, p. 10, pl. 1, figs. 2-4; Hodgson, 1910, p. 45, pl. vii; Richardson, 1913, p. 17; Vanhoffen, 1914, p. 527.

Occurrence. St. 141, 29. xii, 26, East Cumberland Bay, South Georgia, 17-27 m., 1 ♂ and 1 ♀ (non-breeding). Jan. 1927, Borge Bay, South Orkneys, fish trap, 1 ♂. St. 164: 18. ii. 27, East end of Normanna Strait, South Orkneys, 24-36 m., 1 ♂, 2 immature. St. 178: 9-11. iii. 27, Melchior Harbour, Schollaert Channel, Palmer Archipelago, 17 m., 1 ♂. 1927, Admiralty Bay, King George Island, South Shetlands, brought up on anchor chain, 1 ♂. 28. x. 28, King Edward's Point, South Georgia, picked up on beach, 1 ♂. St. 366: 6. iii. 20, 4 cables south of Cook Island, South Sandwich Islands, 155-322 m., 1 immature specimen; 77-152 m., 3 immature and 1 immature ♂. St. 370: 10. iii. 30, 2 miles north-east of Bristol Island, South Sandwich Islands, 80-18 m., 1 ♀ (non-breeding). St. 371 14. iii. 30, 1 mile east of Montagu Island, South Sandwich Islands, 99-161 m., 2 immature specimens, 99-161 m.: ♀ (breeding), 1 ♀ (non-breeding) and 2 ♂♂. 17. ii. 31, Leith Harbour, South Georgia, 5 m., from fish stomach, probably from *Notothenia rossii*, 1 incomplete ♂. St. 1489: 17. i. 35, Port Lockroy, Palmer Archipelago, found on motor-boat at anchor. St. 1652: 23. 1. 36, 75° 56' 21" S., 178° 35' 5" W., 567 m., 1 ♀ (non-breeding). St. 1941: 29. xii. 36, Leith Harbour, South Georgia, 38 m., 2 young specimens. St. MS 25: 13. iv. 25, East Cumberland Bay, South Georgia, 36 m., 1 immature ♂.

REMARKS. The only additional points of interest concerning the anatomy of this species have already been dealt with in the general discussion on the characters of the suborder Valvifera and the subfamily Glyptonotinae (pp. 148-164).

The separation of *G. acutus*, even as a variety from *G. antarcticus*, seems to be a matter of great difficulty, if a series of specimens is examined; for it is almost impossible to draw a dividing line between the types, the grading is so complete.

The species *G. acutus* was formed by Richardson (1906) to contain a type which differed from *G. antarcticus* only in proportion. According to Richardson the length of the body of *G. antarcticus* is less than twice as long as it is broad, and the terminal segment is broader than long; on the other hand, the length of *G. acutus* is two and a half times its breadth, and the terminal segment is longer than broad (10-6 mm.). Richardson obtained the proportions given for *G. antarcticus* from the published descriptions and figures of Eights (1852), Miers (1881) and Pfeffer (1887); Miers's description is based on that of Eights, and he gives the size of a specimen as length 90 mm., breadth 45 mm., a ratio of 2:1; a similar ratio is obtained by measuring Pfeffer's figures.

Measurements taken from Richardson's specimen of *G. acutus* show a ratio of length to breadth of 2.1:1 and not 2.5:1, so that the actual difference in the length:breadth ratio of the two species is very small.

The terminal segment of *G. antarcticus* in Eights's figure is certainly slightly broader at the base than it is long, but measurements taken from Pfeffer's figure show a ratio of length to breadth of 1.16:1; in other words, Pfeffer found that the terminal segment was longer than broad. The length to breadth ratio of the terminal segment of Richardson's *C. acutus* is 1.66:1. From these facts it is obvious that the differences between the two species stressed by Richardson are not as marked as she supposed.

The differences between the species have also been discussed at some length by Tattersall (1921) and further by Calabrese (1931), and both authors agree that the two forms represent varieties of a single species and not two distinct species.

Tattersall pointed out the inaccuracy of Miss Richardson's statements of the dimensions of the two species. There is one point in connexion with his remarks which needs correction; in referring to the measurements of Pfeffer's figure, he said (p. 234) that 'the metasome is 1.16 times as long as broad'. 'Metasome' should read 'terminal segment'; the ratio of length to breadth of the metasome is 1.3:1. Tattersall also drew attention to the differences in the proportions of the joints of the posterior limbs of the two varieties, the limbs of *G. antarcticus* being shorter and broader than those of *G. acutus*.

An examination of a number of specimens in the Discovery collections showed that the ratio of body length to breadth, and metasome length to breadth did vary within a comparatively narrow range, and this was most marked in the case of a specimen collected in deeper water (567 m.); the ratio of the most typical 'antarcticus' specimen, however, was linked by a number of intermediate types with the 'acutus' form (Plate IX, fig. 2).

Table I, which includes measurements of specimens described by other authors as well as of some from the Discovery collections, brings out this feature very clearly. In Table I the ratio of carpus length to propodus length is not given, the carpus being either equal to, or slightly longer than, the propodus.

Apart from the localities cited above, *G. antarcticus* has been recorded by Monod (1931) from South Georgia, and Nordenstam from Cumberland Bay, South Georgia (the specimen was dead and found far up the shore).

G. acutus is recorded from South Georgia (Pesta, 1928) from Gauss Station (Vanhoffen, 1917), from Seymour Island, off Graham Land, and off Paulet Island, Graham Land (Nordenstam, 1933) in 100–150 m. The specimens (18 in number) obtained from Seymour Island were living and collected on the ebb-shore.

Table 1 shows:

(1) That a number of specimens described as *G. antarcticus* have the same body ratio as the type *G. acutus*.

(2) That the difference in the body ratio between a typical specimen of *G. antarcticus* and the type specimen of *G. acutus* is considerably less than between the latter and the most 'acute' form.

(3) That the metasome ratio obtained from Eights's figure is probably inaccurate, because measurements taken from other specimens show the length of the terminal segment to be greater than the breadth, indicating that the difference between Richardson's *G. acutus* and a typical specimen of *G. antarcticus* is less than she supposed.

(4) That the limb joints as exemplified by the carpus, propodus and dactylus of the last pair of thoracic limbs are longer and narrower in the more 'acute' forms.

(5) That, excluding Richardson's type specimen, the more 'acute' forms tend to occur in slightly deeper water.

(6) That both 'species' have a similar distribution, both occurring within the Antarctic Convergence; the majority of specimens have been collected between 25 and 65° W.

Table 1

Author	Ratio of body length: breadth	Ratio of metasome length: breadth	Depth at which specimens were obtained	Remarks
Tattersall	2·2:1 (small) to 1·9:1 (large) Length of specimens from 20 to 59 mm.	1·5:1 to 1·2:1	Less than 27 m.	From measurements given. Joints of last thoracic limb. Carpus length to breadth, 2·24:1. Propodus length to dactylus length, 2:1. <i>G. antarcticus</i> , Cumberland Bay, South Georgia
Pfeffer	2:1 Length 62 mm.	1·3:1	?	From figure, <i>G. antarcticus</i> , South Georgia
Collinge	2:1 Length 88 mm. Breadth 43 mm. (♂ specimen)	1·48:1	16-27 m.	From figure, <i>G. antarcticus</i> , Graham Land
Sheppard	1·9:1 Length 89 mm. Breadth 46 mm. (♂ specimen) 2:1 (small) Length 8 mm. Breadth 4 mm. (immature specimen)	1·49:1 1·8:1	24-36 m.	From specimen, <i>G. antarcticus</i> , see Pl. IX, 3. Joints of last thoracic limb. Carpus length to breadth, 2·7:1. Propodus length to dactylus length, 2:1. South Orkneys, near Cape Hansen, Coronation Island
Eights	1·9:1	1·07:1		From figure, <i>G. antarcticus</i> (type). South Shetland Islands
Miers	2:1	—	—	From measurements given, <i>G. antarcticus</i> (Eights)
Sheppard	1·97:1 Length 63 mm. Breadth 32 mm. (♀, non-breeding)	1·5:1	17-27 m.	From specimen, <i>G. antarcticus</i> , see Pl. IX, 1. Joints of last thoracic limb. Carpus length to breadth, 3:1:1. Propodus length to dactylus length, 2:1. East Cumberland Bay, South Georgia
Calabrese	2·1:1	1·5:1	?	From photograph, <i>G. antarcticus</i>
Sheppard	2:1 Length 118 mm. Breadth 58 mm. (♂ specimen)	1·6:1	Fish trap? 17 m.	From specimen, <i>G. antarcticus</i> , see Pl. IX, 5. Joints of last thoracic limb. Carpus length to breadth, 2·5:1 (dactylus missing). Borge Bay, South Orkneys
Richardson	2:1	1·66:1	Shore to 36 m.	From figure, type specimen, <i>G. acutus</i> , Graham Land
Sheppard	2·16:1 Length 91 mm. Breadth 42 mm. (♂ specimen)	1·67:1	77-152 m.	From specimen, <i>G. antarcticus</i> . Joints of last thoracic limb. Carpus length to breadth, 2·57:1. Propodus length to dactylus length, 2:1. Off South Sandwich Islands
Sheppard	2·23:1 Length 105 mm. Breadth 47 mm. (♂ specimen)	1·8:1	99-161 m.	From specimen, <i>G. antarcticus</i> , see Pl. IX, 4. Joints of last thoracic limb. Carpus length to breadth, 3:1. Propodus length to dactylus length, 2:1. East of Montagu Island, South Sandwich Islands
Hodgson	2·27:1 Length 119 mm. Breadth 42 mm. (♂ specimen)	1·8:1	36-225 m.	From figure, <i>G. acutus</i> , Victoria Land
Tattersall	2·45:1 (small) to 2·2:1 (large) Length 20-99 mm. (♂ and ♀ specimen)	2·1:1 to 1·55:1	81-540 m.	From measurements given, <i>G. acutus</i> . Joints of last thoracic limb. Carpus length to breadth, 5·25:1. Propodus length to dactylus length, 1·17:1. McMurdo Sound, etc.
Sheppard	2·4:1 Length 53 mm. Breadth 22 mm. (♀ non-breeding)	1·88:1	567 m.	From specimen, <i>G. antarcticus</i> , see Pl. IX, 2. Joints of last thoracic limb. Carpus length to breadth, 5:1. Propodus length to dactylus length, 1·6:1. 75° 56' 2" S., 178° 35' 5" W.

Note. Sex and measurements not given by authors in some cases.

The most 'acute' forms recorded by Hodgson (1910) and Tattersall (1921) and some in the Discovery collections were obtained from deeper water, between 165 and 175° E.

In reviewing the above facts, including an examination of the series of specimens illustrated on Plate VIII, I have come to the conclusion that it is impossible to separate *G. acutus*, even as a variety, from *G. antarcticus*. The individuals representing the opposite ends of the series appear markedly different in proportion, but when the intermediate forms are introduced, the differences become comparatively small. Apart from these differences in the adult individuals, the young are usually more acute than the adult.

Glyptonotus antarcticus appears to be a species which is in an unstable condition; it is a typical shallow-water form which may be invading deeper water. It is possible that it represents a species which is susceptible to the influence of its environment, and that the two forms, though having the same distribution may live in different habitats, dependent, for example, upon the kind of substratum on which they live; there may be a certain amount of overlapping between the two.

There is one further point to which reference must be made, namely, the *relative* size at which the male reaches maturity. Tattersall (1921, p. 235) states that *G. acutus* appears to mature later than *G. antarcticus*. In a specimen of the latter measuring 58 mm. in length, the appendix masculina on the second pleopod as well as the penial appendages were developed, whereas a male of *G. acutus*, measuring 62 mm. was still without the appendix masculina. The least 'acute' specimen in the Discovery collections, though 10 mm. longer than Tattersall's specimen referred to above, has the penial appendages present, but the second pleopod has no appendix masculina; a more 'acute' form measuring 82 mm. in length was also without an appendix masculina. It is possible that the more acute forms mature later, but there appears to be a certain amount of individual variation.

Subfamily MACROCHIRIDOTHEINAE Nordenstam, 1933 (Text-figs. 12, 13)

This subfamily was instituted by Nordenstam (1933, p. 104) to contain two genera, *Macrochiridothea* Ohlin and *Chiriscus* Richardson, with a possible third genus, *Chaetilia* Dana. A review of the characters on which the diagnosis of the subfamily is based, shows a number of inaccurate observations.

(1) The antennule is said to be longer than the antenna. This is true for *Chiriscus australis* Richardson, but not for the species of *Macrochiridothea*; the antenna is longer in both *M. stebbingi* Ohlin (fig. 12*a, d*), and *M. kruimeli* Nierstrasz (fig. 13*f, g*), and measurements taken from Ohlin's figures show that this is also true for *M. michaelseni* Ohlin.

(2) 'Coxal plates marked off by dorsal sutures on the last three segments of the pereion, those on the second to the fourth segments distinctly delimited from the tergites, but not visible from above.' The first part of this statement is correct, but, as far as the species of *Macrochiridothea* are concerned, there are no coxal plates developed on the outer margins of the coxal joints of the limbs of the second, third and fourth pereion segments; the joints themselves are seen in lateral view.

(3) The abdomen is said to be built up of 'three free abdominal segments anteriorly from the pleotelson'. According to Richardson's description (1911, p. 169) of *Chiriscus australis*, the abdomen consists of three segments only, two short ones anterior to the long terminal one. In both *Macrochiridothea stebbingi* and *M. kruimeli*, a fourth segment is present which is free laterally, but fused in the centre with the pleotelson (Text-fig. 13*a*).

(4) 'Maxillipeds with a three-jointed palp.' This is so in *Chiriscus australis* if Richardson's figure of this appendage is accurate (she shows no endite to the basipodite), but in *Macrochiridothea stebbingi* and *M. kruimeli* four are present (see Text-figs. 12*e, 13e*).

In his discussion on the position of this subfamily amongst the Idoteidae, Nordenstam stresses the systematic value of the morphology of the coxal plate; he points out that the type of plate found in members of the Macrochiridotheinae does not occur in members of the other subfamilies. I cannot agree with this statement, for, in some of the species of *Edotia* belonging to the subfamily Idotheinae, coxal plates are developed on the coxal joints of the last three pairs of thoracic limbs and these extend on to the dorsal surface where they are separated from their respective terga by sutures. The coxal joints of the second, third and fourth pairs of pereopods can be seen in lateral view of *Edotia*, as well as in the species of *Macrochiridothea*. In *Glyptonotus* (subfamily Glyptonotinae), a similar arrangement occurs, but the bases of the limbs of the first four pereion somites are hidden by the development of the pleura. As has already been pointed out, in members of all the subfamilies coxal plates are developed on the inner sides of the coxal joints; these cover the ventral surfaces of their respective somites, and meet and sometimes fuse in the mid-ventral line.

A character peculiar to the species of *Macrochiridothea* is that the coxal joint of the first pereopod is only partially fused with the tergum of its somite; a similar condition can be observed, though to a less extent, in *Pseudidothea bonnieri* Ohlin.

It is difficult to understand why Nordenstam placed the two genera *Chiriscus* and *Macrochiridothea* together in a new subfamily, the only character which they have in common being the 'markedly subchelate (seroliform)' first pereopods. The second and third pairs in the species of *Macrochiridothea* are prehensile, but considerably weaker than the first pair, whereas in *Chiriscus australis* the second and third pairs are not prehensile, and are very similar to the fourth, fifth and seventh pairs. According to Richardson (1911, p. 169), the sixth pair of legs is much longer than the others and is the only pair in which a dactylus is present.

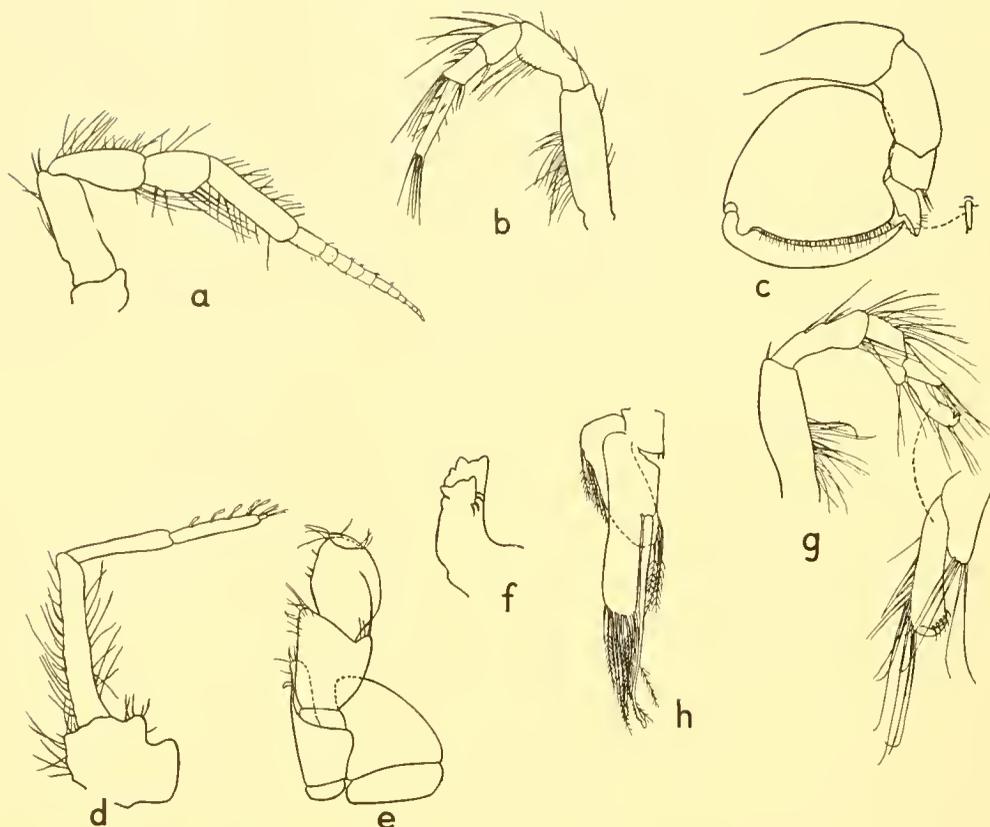
The genus *Macrochiridothea* appears to be more closely allied to *Mesidotea* than to any other form. The two genera have the following characters in common:

- (1) The head is laterally expanded, and the lateral margins are cleft.
- (2) The eyes when present are dorsal and submarginal.
- (3) The antennule is shorter than the antenna and its flagellum consists of one or two joints.
- (4) The first three pairs of pereopods are prehensile. In *Macrochiridothea* the first pair is markedly subchelate (seroliform) and the second and third pairs are considerably weaker, whereas in *Mesidotea* the three pairs are approximately of equal size. The remaining pairs of limbs are ambulatory.
- (5) The abdomen consists of four free segments (fourth partially fused with the pleotelson in *Macrochiridothea*) and a pleotelson.
- (6) Uropods with both an exopod and an endopod; the former in *Mesidotea* is always more or less rudimentary.

The two genera differ from each other in the number of joints to the maxillary palp; this number is five in *Mesidotea* and four in *Macrochiridothea*. They also differ in the coxal joints of the pereopods, which in *Mesidotea*, with the exception of the first, are expanded into coxal plates which extend on to the dorsal surface and are separated from their respective terga by sutures; in *Macrochiridothea* these plates are only developed on the last three pairs of pereopods; they also are separated from their respective terga by sutures.

The family Idoteidae is in much need of revision; its members, taken as a whole, are closely related to each other, consequently it is difficult to select the morphological characters on which a classification should be based.

Whether or not the two genera *Chiriscus* and *Macrochiridothea* should remain together in the subfamily Macrochiridotheinae is doubtful, but it seems wisest to leave them in their present position until a revision of the whole family can be undertaken.



Text-fig. 12. *Macrochiridothea stebbingi*. (a) Antenna, $\times 20$. (b) Third pereiopod, $\times 12$. (c) First pereiopod, $\times 12$. (d) Antennule, $\times 20$. (e) Maxilliped (left), $\times 30$. (f) Cutting edge of left mandible, $\times 30$. (g) Second pereiopod, $\times 12$. (h) Second pereiopod, $\times 17$.

Genus *Macrochiridothea* Ohlin, 1901

Macrochiridothea stebbingi Ohlin, 1901 (Text-fig. 12, a-h)

Macrochiridothea stebbingi Ohlin, 1901, pp. 289-91, pl. xxii, fig. 9.

M. stebbingi var. *multituberculata*, Nordenstam, 1933, pp. 106-8 and 112, pl. 1, fig. 7.

Occurrence. St. WS 88: 6. iv. 27, $54^{\circ} 00' 00''$ S., $64^{\circ} 57' 30''$ W., 118 m., 1 ♀. St. WS 772: 30. x. 31, $45^{\circ} 13' S.$, $60^{\circ} 00' W.$ to $45^{\circ} 13' 8'' S.$, $60^{\circ} 00' 5'' W.$, 309-162 m., 5 specimens, 1 ♀ (non-breeding).

The genus has the characters of the subfamily.

The largest specimen in this collection is a female measuring 9.5 mm. in length and 4 mm. in greatest breadth; the tubercles on the dorsal surface of the body, though similar in distribution, were less pronounced than those on the remaining specimens.

This species was first described by Ohlin (1901, p. 289) from a single female measuring 7 mm. in length. In this description he stated that the head is nearly as long as the first three segments of the mesosome, and that the pereion segments are of 'about the same length', but his figure (pl. xxii, 9a) shows the second pereion somite to be twice as long as the middle of the first, and the lateral margins of the first about three times the length of its centre. Assuming that Ohlin's figure is inaccurate, then the length of the middle of the first pereion somite should be doubled to make it equal to that of the second somite. This would result in a reduction in the ratio, length of the middle of the somite: its lateral margins, i.e. from 1:3 to 1:1.5; this change would bring the proportions more or less into line with those given by Nordenstam for his variety *multituberculata*, and also with the specimens in the Discovery collections. If the length of the central part of the head in Ohlin's figure was shortened to allow for the necessary increase in the length of the first pereion segment, this would lessen the

amount of immersion of the head in that segment and then it would conform to Nordenstam's variety. The general shape of this variety agrees with 'that of the main species', but its posterior part is 'not so deeply immersed into the first segment of the pereion as is the case in the main species'.

The extreme similarity between the main species and the variety *multituberculata* suggests that the above assumption is correct, especially when the remaining differences described by Nordenstam are reviewed:

(1) The eyes of *M. stebbingi* are described as small and black while in Nordenstam's variety they are totally lacking. A very small amount of pigment is present in the eyes of some of the specimens in the Discovery collections, in others it is absent and the eyes are almost invisible. The presence or absence of a small amount of pigment appears to be a variation within the species.

(2) Nordenstam described nine tubercles on each of the first four pereion segments, whereas in the main species there are only seven. In specimens of the Discovery collections, the same arrangement of tubercles is found, but one pair is very small and may easily have been overlooked by Ohlin, especially as his specimen was only 13 mm., a little over half the length of Nordenstam's.

(3) In the variety *multituberculata*, the second peduncular joint of the antennule is longer than the combined length of the third one and the flagellum, whereas, according to Nordenstam (1933, p. 112) in the main species it is only as long as the third peduncular joint plus half the length of the flagellum. Ohlin says that the second joint is nearly equal in length to the combined lengths of the third peduncular joint and the flagellum, but figures it considerably longer. In the specimens of the Discovery collections the length of the second joint is less than that of the third and flagellum together (Text-fig. 12*d*). The flagellum bears an extremely short terminal joint similar to that noted by Nordenstam.

Nordenstam admits that the characters on which he based his new variety may represent individual variations within the species, and I am convinced that this is so. I have therefore included the variety *multituberculata* in the species *M. stebbingi*.

There are certain other points which require clearing up in both Ohlin's and Nordenstam's descriptions; both authors state that the antennule is longer than the antenna, yet measurements of the two appendages show that this is not so (see Text-fig. 12*a, d*). The apparent shortness of the antenna is due to the sharpness of the angle between the second and third peduncular joints.

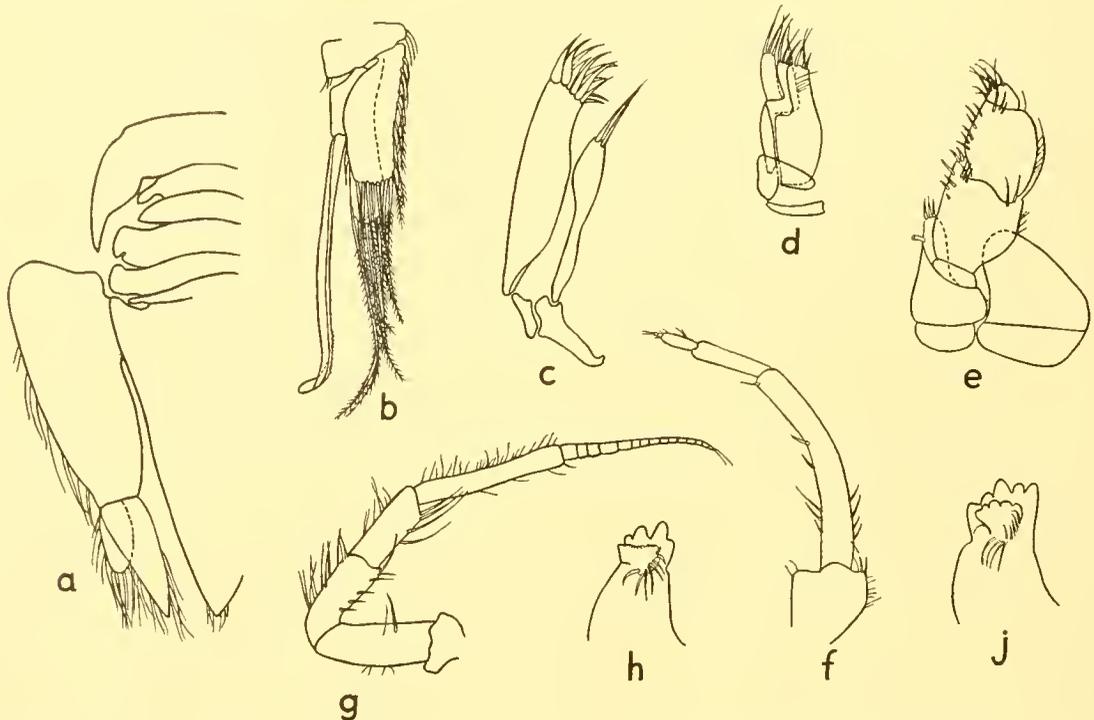
Ohlin gives the number of joints of the palp of the maxilliped as three, and Nordenstam says that the maxillipeds of his variety *multituberculata* are 'as in the main species'. Actually there are four joints to the palp (Text-fig. 12*e*), the first one of which is short.

According to Ohlin the abdomen consists of four free segments and a telson, while Nordenstam describes the abdomen of his variety as being built up of three free segments and a pleotelson. In specimens of the Discovery collections there are four segments and a telson, but the fourth segment is only free laterally (see Text-fig. 13*a* of *M. kruimeli*, in which a similar arrangement occurs). From this figure it can be seen that the last thoracic somite is very small and has much reduced coxal plates; that the first abdominal segment, which is normally hardly visible in a dorsal view of the animal, bears practically no pleural extensions; that these extensions are well developed on the second and third segments, where they are bent downwards laterally at a sharp angle; and that the fourth segment is very narrow, and fused in the mid-dorsal region with the telson, but is free laterally and bears delicate pleural processes.

Nordenstam's statements concerning the abdomen are extremely confused. On p. 111 he says that 'the first two segments are bent downwards laterally in a sharp angle to the dorsal surface. Their posterior angles are pointed and directed backwards. The third segment is enclosed by the second and the pleotelson; laterally, it is not bent downwards, unlike the other two free segments.'

It seems probable that Nordenstam overlooked the presence of the first segment, since his description more or less applies to the second, third and fourth segments; this would explain his statement that the abdomen consists of three free segments and a pleotelson. The form of the limbs have been described by Ohlin (1901, p. 291 and pl. xxii, figs. 9, pl. 1, p. 2, and p. 5); as his figures of these limbs are very small, some have been illustrated in the present paper (Text-fig. 12*b, c* and *g*). The second pair of pleopods is modified in the male (Text-fig. 12*h*).

DISTRIBUTION. Ohlin's specimen was collected from between Isla Neuva and Navarino, in 30 fathoms of water; specimens have also been collected at Port Harriet, Falkland Islands (Stebbing, 1914), and from rocks at Port Williams, Falkland Islands (Nordenstam, 1933). Specimens in the Discovery collections came from some distance north of Le Maire Strait, South America, and also from waters due north of the Falkland Islands.



Text-fig. 13. *Macrochiridothea kruimeli*. (a) Left half of last two pereion somites, abdominal segments, telson and left uropod, $\times 5$. (b) Second pleopod, δ , $\times 17$. (c) Maxillula (right), $\times 30$. (d) Maxilla (right), $\times 60$. (e) Left maxilliped, $\times 30$. (f) Antennule, $\times 25$. (g) Antenna, $\times 25$. (h) Cutting edge of left mandible. (j) Cutting edge of right mandible.

Macrochiridothea kruimeli Nierstrasz, 1918 (Text-fig. 13*a-j*)

M. kruimeli, Nierstrasz, 1918, pp. 130-2, figs. 13, 54-64; Nordenstam, 1933, p. 112.

Occurrence. St WS 809: 8. i. 32, $49^{\circ} 29' S.$, $66^{\circ} 21' W.$, 107-104 mm., 2 $\delta\delta$.

The larger of the two specimens in the Discovery collections is a male measuring 8 mm. in length and 3 mm. in greatest breadth. This is approximately half the size of the female described by Nierstrasz, the length:breadth ratio of which was 5:2. The corresponding ratio of the male is 5:2:2, so that the female is slightly broader in proportion to its length than is the male.

The Discovery specimens agree in most details with the description given by Nierstrasz.

The eyes are very small and contain a little pigment. A few short hairs are present along the anterior margin of the head; these were not present on Nierstrasz's specimen. In the type specimen, the length of the head is said to be as great as that of the second and third thoracic (first and second pereion) somites together, but a measurement taken from Nierstrasz's photograph of this specimen (Plate IX,

fig. 13) shows that the length of the two somites together is undoubtedly the greater, and in this it agrees with the specimens in the Discovery collections.

The form of the coxal joint has already been dealt with under the characteristics of members of the subfamily; the abdomen is illustrated in Text-fig. 13*a*, the only point in which it differs from the description of the type specimen is in having the middle part of the fourth segment fused with that of the telson.

The antenna (Text-fig. 13*g*) is considerably longer than the antennule (Text-fig. 13*f*), and its flagellum consists of fifteen joints, the first of which is the longest. In Nierstrasz's specimen the flagellum, which he says was probably broken, exhibited eight joints. The form of the cutting edges of the mandibles (Text-fig. 13*h, i*) does not agree with Nierstrasz's description. The left mandible has, in addition to the five teeth on the lateral edge and four on the median, nine curved spines. The right mandible is very similar to that of *M. stebbingi*, the median lobe, which is said to be straight in the type specimen, is finely crenulated and eight curved spines are present on its inner side.

The inner lamella of the maxillula (Text-fig. 13*c*) which is missing in the type specimen, is slightly expanded distally and bears two plumose setae; the maxilla (Text-fig. 13*d*) differs from the type specimen in having three instead of five spines at the distal end of the outer lamella.

The maxilliped (Text-fig. 13*e*) is very similar to that of *M. stebbingi*, and has, like that species, four joints to the palp. The modification of the second pleopod in the male is shown in Text-fig. 13*b*, the form of the uropods in Text-fig. 13*a*.

DISTRIBUTION. The type specimen was collected by Dr J. H. Kruiemel from waters off Punta Arenas on the east coast of the southern tip of Chile; the specimens in the Discovery collections come from an area between the Falkland Islands and the mainland of South America, but considerably nearer to the latter.

Family PSEUDIDOTHEIDAE, Ohlin

The members of this family, consisting of three genera *Arcturides* Studer, *Pseudidothea* Ohlin and *Holidotea* Barnard, are intermediate in position between those of the Idoteidae on the one hand and the Astacillidae on the other, that is to say, they possess the idoteid shape and the form of the first four pairs of pereopods with the astacillid uropod and modified first male pleopod.

The diagnostic characters of the family are given by Ohlin (1901, p. 274), and reference is also made to them by Barnard (1920, p. 381), Nordenstam (1933, p. 113) and Hale (1946, p. 168).

Ohlin (1901), in his diagnosis of the family, stated that the peduncle of the antenna consisted of four joints. Studer (1884), in his description of *Arcturides cornutus*, also gave this number; in *Holidotea*, however, there are five (Barnard, 1920). Nordenstam (1933, p. 113) considered that in *Pseudidothea* the peduncle is better described as consisting of five joints, but that the first joint 'is indistinctly marked off on the ventral side from the second' (cf. Ohlin, 1901). I have examined specimens of both *P. bonnieri* Ohlin and *P. scutatus* (Stephensen) and find that five joints are present. Hale (1946) described a new species, *Arcturides tribulis*, which is very similar to *A. cornutus* Studer, and he gave the number of joints of the peduncle as five. In the Discovery collections in another species, *A. acuminatus*, there is a five-jointed peduncle. It would appear that Studer's observation on this point is incorrect, and that a five-jointed peduncle to the antenna is common to all members of the family so far described. According to Hale (1946, p. 168), the only characters separating the genera *Pseudidothea* from *Arcturides* are (1) the number of joints to the flagellum of the antenna which are two in the former and three in the latter genus; (2) the 'secondary ramus' of the uropod is as long as the 'lateral ramus' in *Arcturides*, whereas in *Pseudidothea* the 'secondary ramus' is only about three-quarters the length of the 'lateral ramus'; and (3) the coxae are distinctly marked off on the second to the seventh

pereiopods in *Arcturides*, whereas in *Pseudidothea* they are developed as not very distinct rings around the basis of the second to fifth pereiopods.

Hale's third point requires some amplification. In the species of both *Pseudidothea* and *Arcturides*, the coxal development of the *first* four pairs of pereiopods is exactly similar, the coxal joints of the second, third and fourth pereiopods can be seen in a lateral view of the animal as small rings which, on their inner sides, extend as flat coxal plates over the ventral surface of their respective somites as far as the mid-ventral line. The coxal joint of the first pereiopod is fused with tergum, but its coxal plate does not fuse with that of its fellow in the mid-ventral line.

In the species of *Arcturides* the coxae of the *last* three pairs of pereiopods are fused with the terga of their respective somites, but the suture lines are visible; ventrally the coxal plates of each pair are fused in the mid-ventral line. In the species of *Pseudidothea* the condition has gone a stage further and the suture lines between the coxae and terga are lost and fusion is complete. In neither genus are these posterior coxal joints separate units in contrast to the second, third and fourth pairs of limbs.

In *Holidotea*, the remaining genus of the family, according to Barnard (1920, p. 381) the 'side plates' (presumably coxal in origin) are distinct on all except the first segment; thus, the three genera form a graded series in which the coxae of the last three pairs of pereiopods are free in *Holidotea*, fused to their respective terga but with suture lines distinct in *Arcturides* and completely fused in *Pseudidothea*.

A further character which is common to the three genera is the form of the first pleopod in the male, the modification being similar to that met with in members of the Astacillidae, except that the distal portion of the exopodite is curved outwards as a tapering projection (see figures in descriptions of species). This is less pronounced in *Holidotea* where the endopodite also is reduced in size. In all three the penis is single but bilobed.

Genus *Pseudidothea* Ohlin, 1901

The description of the coxal joint is unsatisfactory in the diagnosis of this genus. Of the species *P. bonnieri*, Ohlin (1901, p. 276) said: 'epimera of all segments visible from above, being small, slightly triangular tubercles'; in his description of the appendages he makes no mention of the first joint. Nordenstam (1933, p. 113) also gave a diagnosis of the genus, and with reference to this point says: 'Coxae developed as incomplete not very distinct rings around the proximal ends of the basipodites of the second to seventh pereiopods.'

The coxal joints of the thoracic limbs of the third, fourth and fifth somites (second to fourth pereiopods) can be seen in a lateral view of the animal, as small rings, which extend as flat coxal plates over the ventral surface of their respective somites up to the mid-ventral line. The coxal joint of the second thoracic limb (first pereiopod) is partially fused with the tergum of its segment, the plate is well developed and extends towards the mid-ventral line where it meets its fellow of the other side.

The coxal joints of the sixth, seventh and eighth pairs of thoracic limbs (5-7 pereiopods) are entirely fused with the lateral parts of the terga of their respective somites. From analogy with other members of the Valvifera it may be assumed that the ventral coxal expansions have fused with one another in the mid-ventral line; this can be correlated with the fact that the posterior part of the body is narrow and more or less cylindrical in shape.

As already noted, the penis in the male is enclosed by the first pleon segment (Text-fig. 1d); it is single, but its double origin may be seen in its bilobed extremity.

Pseudidothea bonnieri Ohlin, 1901 (Text-fig. 14*a-f*)

P. bonnieri, Ohlin, 1901, pp. 276-81, pls. xx and xxi, fig. 6; Barnard, 1920, pp. 380-1; Nordenstam, 1933, p. 114, fig. 27.

Occurrence. St. WS 212: 30. v. 28, 49° 22' 00" S., 60° 10' 00" W., 242-249 m., 1 ♀ (non-breeding). St. WS 214: 31. v. 28, 48° 25' S., 60° 40' W., 208-219 m., 1 ♂. St. WS 756: 10. x. 31, from 50° 53' S., 60° 00' W., to 50° 56.3' S., 59° 56' W., 117 m., 2 ♀♀ (non-breeding), 2 immature. St. WS 766: 18-19. x. 31., 44° 58' 00" S., 60° 05.5' W., 545 m., 2 ♂♂ and 4 immature. St. WS 818: 17. i. 32., 52° 30.5' S., 63° 27' W., 272 m., from Cidaroid spines, 3 immature specimens. St. WS 825: 28-29. i. 32, 50° 50' S., 57° 13' W., 135 m., from Cidaroid spines, 6 ♀♀ (breeding), 3 ♂♂, 8 immature. St. WS 839: 5. ii. 32, 53° 29.5' S., 63° 31' W., 503 m., from Cidaroid spines, 5 ♀♀ (breeding), 6 ♂♂, and a number immature. St. WS 871: i. iv. 32, 53° 16' S., 64° 12' W., 336-341 m., 1 ♂, 1 immature.

REMARKS. The largest specimen in the Discovery collections is a female in the breeding condition, 12 mm. in length and 4 mm. in greatest breadth; the largest male is 9.5 mm. in length and 3 mm. in breadth; the length is the same as that given by Ohlin (1901, p. 281) for the type specimen. My observations on this species differ from those of Ohlin (1901) in the following details:

The antennule (Text-fig. 14*e*) consists of a peduncle of three joints, the second one of which bears on its outer side a rounded tubercle, the apex of which is armed with four short spinules. The flagellum consists of two joints (Text-fig. 12*b*), the first one of which is extremely short. This joint was overlooked by Ohlin. The terminal joint is fairly broad, with a rounded extremity bearing eight sensory setae.

According to Ohlin, the first and second joints of the antennular peduncle are coalescent, so that there is no articulation between them, the suture being visible only from below or *en profile*. Nordenstam (1933, p. 113) said that the peduncle is better described as consisting of five joints, and continues: 'the short proximal joint is indistinctly marked off on the ventral side from the second'. My own observation on this point agrees with Nordenstam as far as the number of joints is concerned, but the proximal one is not 'indistinctly marked off on the ventral side from the second', but is a distinct joint (Text-fig. 14*a*). A tubercle, very similar to that found on the second peduncular joint of the antennule, is present on the second peduncular joint of the antenna. The flagellum consists of two joints with a distal spine which may be regarded as the rudiment of a third, terminal joint.

The details of the cutting edges of the mandible require some amplification. The primary cutting edge of the left mandible (Text-fig. 14*c*) bears four teeth; the secondary one bears three teeth, and between this and the molar tubercle are four spines; the molar tubercle is large, triangular truncated, with a denticulate margin. The primary cutting edge of the right mandible (Text-fig. 14*d*) bears three teeth, the secondary one is more delicate and less chitinized than the corresponding one on the left mandible; it bears six teeth. The molar tubercle is very similar to that of the left side.

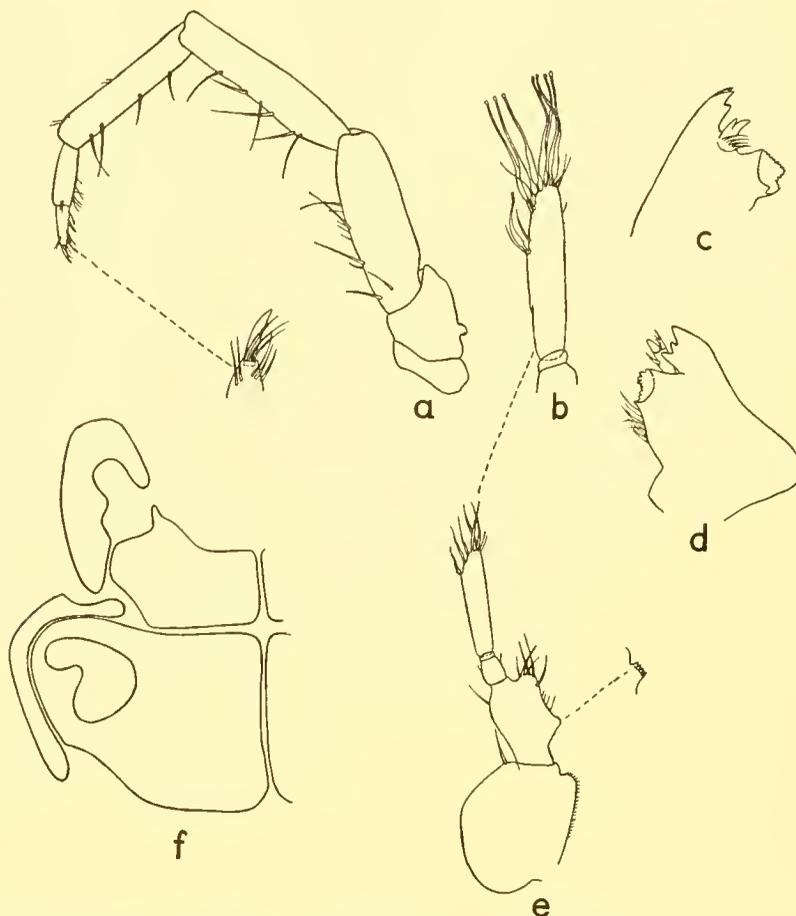
The marsupium of the breeding female consists of four pairs of brood lamellae formed on the coxae of the second, third, fourth and fifth pairs of thoracic appendages; the first pair of these is of the usual isopod type, that is, it is folded and the smaller anterior lobe covers the mouthparts; the larger, posterior lobe forms the anterior boundary to the brood chamber. The maxilliped of the breeding female bears a coxal lobe. The ventral integument in the region of the marsupium is soft and unchitinized (cf. the introduction to the suborder Valvifera, pp. 147-148).

The form of the penial process in the male of this species has already been dealt with in the introduction to this suborder (see p. 149 and Text-fig. 1*d*).

DISTRIBUTION. The species is restricted to an area around the Falkland Islands. Ohlin's specimens were taken in 43° 6' S., long. 60° W.; Nordenstam's specimens were collected south of West Falkland Islands, and those of the Discovery collections were caught between 45° 13' S., 59° 56' 30" W. and

53° 30' 15" S., 63° 29' W. Thus, the species may be said to belong to the shallower waters of the Sub-Antarctic zone.

It seems probable that, as Ohlin suggested, this species is identical with *Idothea miersi* Studer (1884), which was collected in the same locality (47° 1' 6" S., 63° 29' 6" W.).



Text-fig. 14. *Pseudidothea bonnieri*. (a) Antenna, $\times 16$. (b) Flagellum of antennule, $\times 60$. (c) Cutting edge of left mandible, $\times 30$. (d) Right mandible, $\times 30$. (e) Right antennule, $\times 30$. (f) Coxae of first and second pereopods, $\times 32$.

Pseudidothea scutatus sp.n. (Text-figs. 15, 16)

Microarcturus scutatus Stephensen, 1947, pp. 15-17, text-figs. 5 and 6.

Occurrence. St. 170: 23. ii. 27, 61° 25' 30" S., 53° 46' 00" W., 342 m., 4 ♀♀ (breeding), 2 ♂♂, 3 immature.

A male and a female specimen from St. 170 are chosen as holotypes.

DESCRIPTION. The largest male of the Discovery collections was damaged so that measurements cannot be given, the smaller one is 19 mm. in length and 6 mm. in greatest breadth; the breeding female is considerably broader and measures 23.5 mm. in length and 8.75 mm. in greatest breadth.

The *body* is subcylindrical, scarcely depressed (Text-fig. 15a) and characteristically sculptured; all the specimens were thickly coated with fine mud, etc. The anterior margin of the head is deeply excavate, and a median narrow groove extends backwards to unite with the transverse groove which separates the head from the first pereion somite with which it is fused. The eyes, which are small and dorso-lateral in position, are slightly raised. Between the eyes are two raised areas separated from each other by the median groove; immediately behind these, in the mid-line, is a small rounded tubercle. On the first pereion somite, behind the groove separating it from the head, is the first pair of a series of large dorsal protuberances, the flattened surfaces of which are raised 1 mm. above the

general body surface. Each pair is separated by a median space (Text-fig. 15*a*). These protuberances decrease in size and height from the fourth pair backwards; the series is continued on to the pleotelson where it is represented by three pairs of rounded tubercles. A further series of these raised areas occurs in a lateral position above the coxae of the limbs of each pereion somite except the first; a smaller pair is present on the pleotelson in front of the articulation of the uropods. The body surface between the median and lateral protuberances is itself slightly raised and this is more marked on the last three somites. The third pereion somite is the broadest, but this width is much greater in the female than in the male; in the latter there is only a very gradual decrease in width from this somite to the last one.

The *abdominal segments* are fused together to form a pleotelson which forms about one-third of the length of the body. The three pairs of tubercles may possibly indicate the position of three fused segments. The convex surface of the pleotelson slopes away sharply a short distance behind the last pair of tubercles; it ends in a blunt, up-tilted point.

The *antennules* (Text-fig. 15*d*) do not extend to the end of the third peduncular joint of the antennae; each consists of a peduncle of three joints and a flagellum consisting of one large and a terminal minute joint from the extremity of which arises a single sensory seta and a group of three simple ones. The sensory setae on the flagellar joint extend its whole length in the male (Text-fig. 15*d*), but are restricted to the distal half in the female (Text-fig. 15*c*).

The *antenna* (Text-fig. 15*f*) is stout and slightly over half of the length of the body. The peduncle consists of five joints, the first two of which are short, the third joint is broad and longer than the first two together; the fourth and fifth are subequal and about equal to the length of the second and third together. The upper and lateral surfaces of these joints are tuberculate, the ventral margin is fringed with long setae which are directed towards the mouth region. The flagellum consists of two joints which together measure about half the length of the fifth joint of the peduncle; the terminal joint is about half the length of the basal one and is tipped with a stout curved spine.

The *mouthparts* are normal; their form can be seen from Text-fig. 15*b, e* and *g* and Text-fig. 16*k* and *l*.

The coxae of the *first pair of pereiopods* are fused with their somite, but the suture between the ventrally extended coxal plates may be seen in the mid-ventral line. The coxae of the second, third and fourth pairs of pereiopods are just visible in lateral view; they too are expanded into ventral plates, the sutures between which may be seen in the mid-line. The coxae of the last three pairs of pereiopods are completely fused with their respective somites, and the plates of each pair are fused together in the mid-ventral line. This condition of the coxae and their plates agrees with that found in *Pseudidothea bonnieri*.

The first pair of pereiopods (Text-fig. 16*a*) is short, stout and subchelate and is closely applied to the mouthparts. The propodus is broad and armed with modified setae, each of which has a double row of minute rounded serrations; the dactylus ends in one large and two smaller curved spines. The remaining pairs of pereiopods are of approximately the same length except for the last pair which is slightly shorter and more slender. The second, third (Text-fig. 16*j*) and fourth pairs are directed forwards and differ from the remaining three pairs in having the inner margin of the ischium, merus, carpus and propodus sparsely fringed with long setae. The basipodite of each of the last three pairs (Text-fig. 16*f*) bears a well-marked conical projection in about the middle of the length of its posterior surface.

The *brood pouch*, unlike that of *Pseudidothea bonnieri*, consists of five instead of four pairs of lamellae, of these the last pair (Text-fig. 16*g*) is small and forms the posterior limit of the marsupium. The fused ventral coxal plate of the fifth somite in the breeding female is narrow and limited to the

posterior half of the somite and the brood lamellae articulate, one on either side with the anterior region of this plate near the base of each limb. Small coxal lobes are also developed on the coxae of the maxillipeds in the breeding female.

In the male the *penis* (Text-fig. 16*e*) is single but distally cleft.

The protopodite of the *uropod* is long and tapering and bears at its extremity the small pointed endopodite which is tipped with a single seta; the exopodite, like that of *P. bonnieri*, is about three-quarters the length and less than half the breadth of the endopodite, and also bears a single seta at its distal extremity (Text-fig. 16*b*).

The form of the *first pair of pleopods* of the male is shown in Text-fig. 16*d*, that of the female in Text-fig. 16*h*. The basipodite in both sexes is large. Its inner margin bears coupling setae, the structure of which may be seen in Text-fig. 16*d*; there are fourteen of these setae in the male, but only eight in the female. Its outer margin bears a number of minute rounded tubercles which extend along the distal half of its length.

In the female the exopodite and endopodite of the pleopods are of similar structure, rather small, with their distal extremities fringed with a few plumose setae; the endopodite is shorter and narrower than the exopodite. In the male the exopodite is modified, it is traversed by a diagonal groove which extends to the distal extremity which curves outwards and is tipped with a stout spine. The outer margin of the distal third of the exopodite is markedly concave and densely fringed with distally directed setae; the endopodite is considerably narrower and about two-thirds the length of the exopodite, its rounded end is fringed with rather short plumose setae.

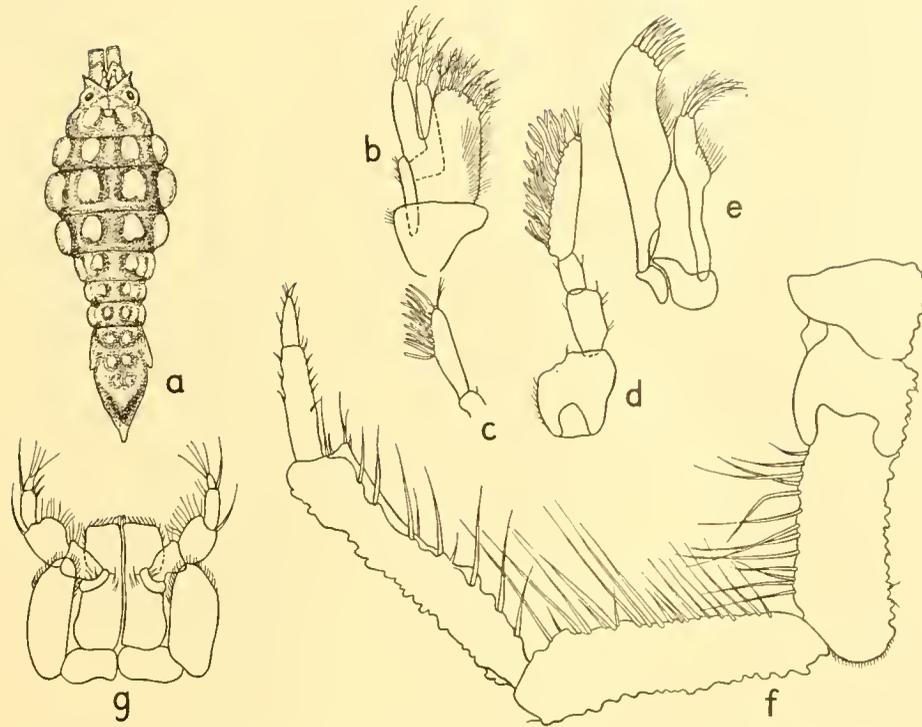
The *appendix masculina* of the second pleopod of the male (Text-fig. 16*c*) is extremely long, it gradually tapers until it has reached three-quarters the length of the endopodite, then suddenly narrows to a whip-like filament; this filament extends back about as far as the tips of the plumose setae which fringe the distal end of the endopodite.

The above description and figures were made before I received Stephensen's paper (1947) in which he described a new species *Microarcturus scutatus*. This species appears to be identical with my specimens, but I cannot agree that it belongs to the genus *Microarcturus*, since the four anterior pairs of pereopods do not markedly differ from the hinder three pairs, that is to say they are *not* of the astacillid type.

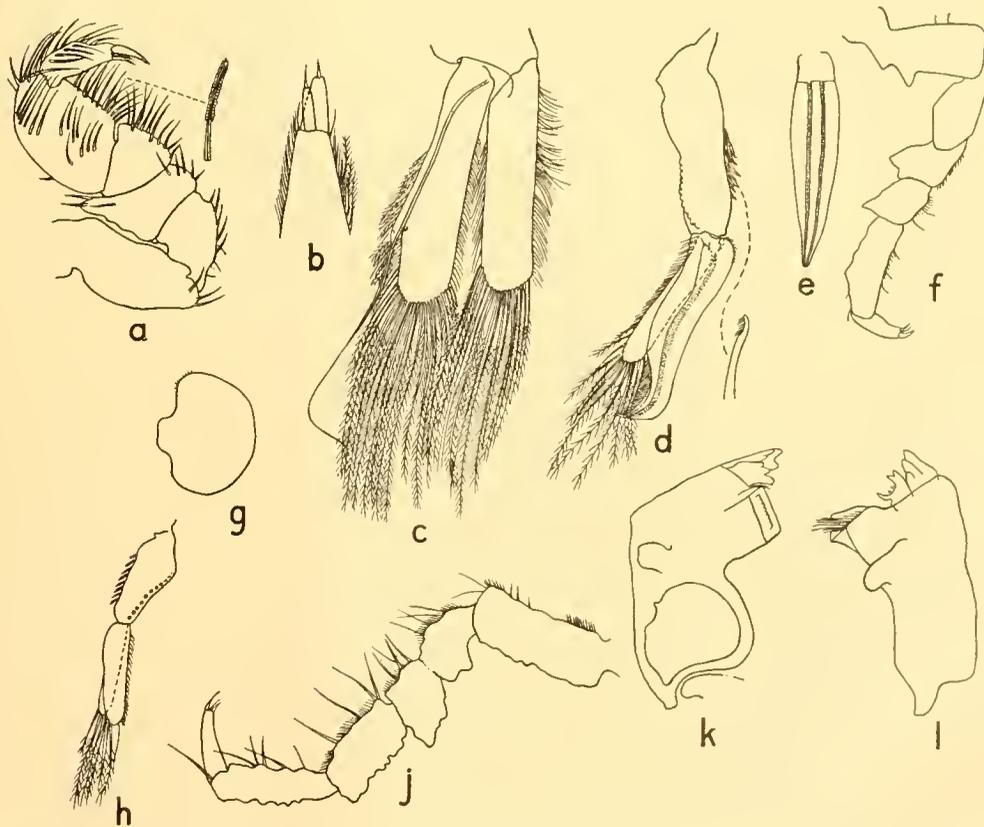
Stephensen's description is based on a single male specimen, 20 mm. in length, and differs only in minor points from that given above. Stephensen (p. 17) states that there are only six or seven coupling setae on the first pair of pleopods (whereas I counted fourteen) in the male and eight in the female.

Large flat tubercles, which form the 'armour' of this species, have also been described for *Antarcturus drygalskii* by Vanhoffen (1914, pp. 521-3 and fig. 53); their arrangement is different, however, and they are absent from the post-thoracic region. Monod (1926, pp. 27-9, figs. 23-25) described a rather similar type of tubercle for *A. belgica*, but again these do not appear on the post-thoracic segments, nor are they present on the last three thoracic segments. The tubercles are not as large or distally so expanded as those of *Pseudidothea scutatus*, and their upper surfaces appear to be toothed at the margin.

DISTRIBUTION. The specimens in the Discovery collections came from a single station, off Cape Bowles, Clarence Island (61° 25' 30" S., 53° 46' 00" W.). Stephensen's specimen was also collected from the South Shetland area off Elephant Island, both of these stations lying within the Antarctic Convergence. The only other species of the genus, *P. bonnieri*, is found farther north, outside the Convergence, in localities around the Falkland Islands; thus, the two species, both shallow-water forms, are separated from each other by the deep waters of the Drake Strait, as well as by the changed hydrographical conditions on either side of the Antarctic Convergence.



Text-fig. 15. *Pseudidothea scutatus* sp.n. (a) Dorsal view of the body, $\times 2$. (b) Right maxilla, $\times 30$. (c) Flagellum of antennule, $\times 12$. (d) Antennule δ , $\times 12$. (e) Right maxillula, $\times 30$. (f) Antenna, $\times 12$. (g) Maxillipeds, $\times 12$.



Text-fig. 16. *Pseudidothea scutatus* sp.n. (a) First pereiopod, $\times 12$. (b) Tip of uropod showing exopodite and endopodite, $\times 12$. (c) Second pleopod δ , $\times 12$. (d) First pleopod (right) δ , $\times 12$. (e) Penis, $\times 12$. (f) Seventh pereiopod, $\times 12$. (g) Last brood lamella (breeding female), $\times 12$. (h) First pleopod (right) f , $\times 12$. (j) Third pereiopod f , $\times 12$. (k) Left mandible, $\times 25$. (l) Right mandible, $\times 25$.

It has already been pointed out in an earlier report (1933, p. 266) that the shallow-water fauna of these two areas is distinct. Each area has its own representative species; it is interesting therefore, that, of the two known species of *Pseudidothea*, one should belong to the group found outside, and the other to the group lying inside the Antarctic Convergence.

Genus *Arcturides* Studer, 1882

The diagnostic characters have been given in the introductory remarks on the family (pp. 173-174).

Arcturides acuminatus sp.n. (Text-figs. 17, 18)

Arcturides cornutus Studer, 1882, p. 57; 1884, pp. 15-17, pl. 1, fig. 4; Beddard, 1886, p. 108.

Occurrence. St. 1562: 17. iv. 35, 46° 51.7' S., 37° 56.5' E. to 46° 54.8' S., 37° 53.8' E., 97-104 m., 1 ♂. St. 1564: 7. iv. 35, 46° 36.5' S., 38° 02.3' E. (off Prince Edward Island), 110-113 m., 1 ♀.

The male holotype is from St. 1562, the female holotype from St. 1564.

DESCRIPTION. The male specimen measures 12.5 mm. in length and 2 mm. in greatest breadth, the female 10 mm. in length and 1.5 mm. in greatest breadth; the *body* is subcylindrical and scarcely depressed (Text-fig. 17*g*). The *head* bears a pair of bluntly pointed, forwardly directed dorsal spines; the antero-lateral angle is rounded; the eyes are large and lateral in position. The first pereion somite which is fused with the head is separated from it by a well-marked groove; it is somewhat deeper than the head and bears a pair of short knob-like dorsal spines and a similar but smaller pair of lateral ones.

The *perion somites* increase in length from the second to the fourth, the fifth and sixth are subequal and about half the length of the fourth, the seventh is considerably shorter. The second, third and fourth somites each bear two pairs of short dorsal spines similar to those on the first segment; a lateral pair, one on either side, placed in a position midway between the dorsal pairs, is also present; the area just above each coxal joint is raised and bears a very small spine. On each of the last three somites a single pair of small dorsal and a pair of lateral spines are present as well as a small one on each coxal area.

The *abdominal segments* are coalesced to form a pleotelson, the shape of which, in dorsal view, may be seen from Text-fig. 17*c*; on the dorsal surface within the anterior third of the pleon are two rows of four very small spines; a number of smaller ones are scattered on the surface behind these rows. Posteriorly the pleotelson is drawn out into a somewhat acute point which extends beyond the extremities of the uropods.

Each *antennule* (Text-fig. 17*f*) extends to about the middle of the third peduncular joint of the antenna; each consists of a peduncle of three joints, the first one of which is very broad, the second is about half the width of the first and the third slightly narrower; the three joints are of approximately equal length; the second joint bears two strong spines on its inner margin. The flagellum consists of a single joint equal in length to the combined length of the two distal joints of the peduncle; it bears three sensory setae and a few simple ones at its distal extremity, and four more sensory setae on the distal half of its margin.

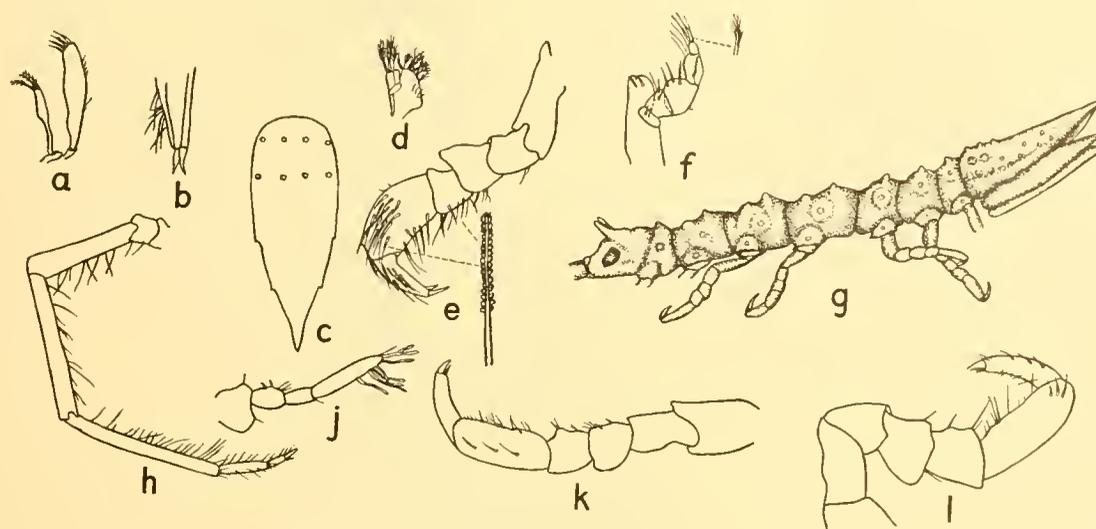
The *antennae* (Text-fig. 17*h*) measure 6.5 mm. in length, each consists of a peduncle of five and a flagellum of three joints. The first segment is very short, the second about twice the length of the first, the third is five times as long as the second, and the fourth and fifth increase in length, the fifth being half as long again as the third. The flagellum is about half the length of the fifth peduncular joint, and its first joint is greater in length than the distal two together. Setae are present on the outer margins of the peduncular joints and scattered on the surface of the joints of the flagellum.

The *mouthparts* are of the usual type, the form of the maxillule and of the maxilla may be seen from Text-fig. 17*a* and *d*. The maxilliped, the distal portion of which is seen in Text-fig. 17*f*, has a five-

jointed palp, the fourth joint of which bears a slightly raised longitudinal region surmounted by a row of very minute rounded projections; the endite is indented and bears two simple setae.

The first, second and last *pereiopods* are shown in Text-fig. 17*e*, *k* and *l*, as well as the setae on the distal three joints of the first pereiopod. Each pereiopod bears, on the margins of the distal half, a series of small rounded tooth-like projections.

The modifications of the first and second *pleopods* of the male and the form of the penis are very similar to those described and figured by Hale (1946, p. 169 and fig. 4, p. 170) for *A. tribulis*. The *penis* (Text-fig. 18*b*) is single but distally cleft. The basipodite of the first pleopod (Text-fig. 18*a*) is about twice as long as broad and has a pronounced curve inwards towards the middle of its outer margin; it bears seven coupling setae on its inner margin (five in *A. tribulis*) and ten very small teeth on its outer margin (these are also present in *A. tribulis*). The form of the exopodite is also very similar in the two species, the oblique furrow terminates in a narrow projection, which is bent



Text-fig. 17. *Arcturides acuminatus* sp.n. (a) Maxillula (left), $\times 25$. (b) Tip of uropod. (c) Dorsal view of pleotelson. (d) Maxilla (right), $\times 15$. (e) First pereiopod, $\times 20$. (f) Maxilliped (left), $\times 25$. (g) Lateral view of female, $\times 7$. (h) Antenna, $\times 12$. (j) Antennule, $\times 18$. (k) Second pereiopod, $\times 20$. (l) Seventh pereiopod, $\times 20$.

outwards and is about a third of the length of the broader part of the exopodite. In *A. acuminatus*, the distal end of the projection is obliquely truncated to form a pointed extremity (Text-fig. 18*a*); the *appendix masculina* of the second pleopod (Text-fig. 18*c*) is about the same length as the endopodite, its distal end is flattened and terminates in a curved pointed projection. The exopodite and endopodite of the *uropod* (Text-fig. 17*b*) are of approximately equal size and each is tipped with a single seta.

A. acuminatus bears a close resemblance to the genotype *A. cornutus* Studer and also to a species, *A. tribulis*, described and figured by Hale in 1946, but differs from them in the following points:

(1) The narrow distal extremity of the pleotelson tapers to a point in *acuminatus* whereas in the other two species it is truncate and notched.

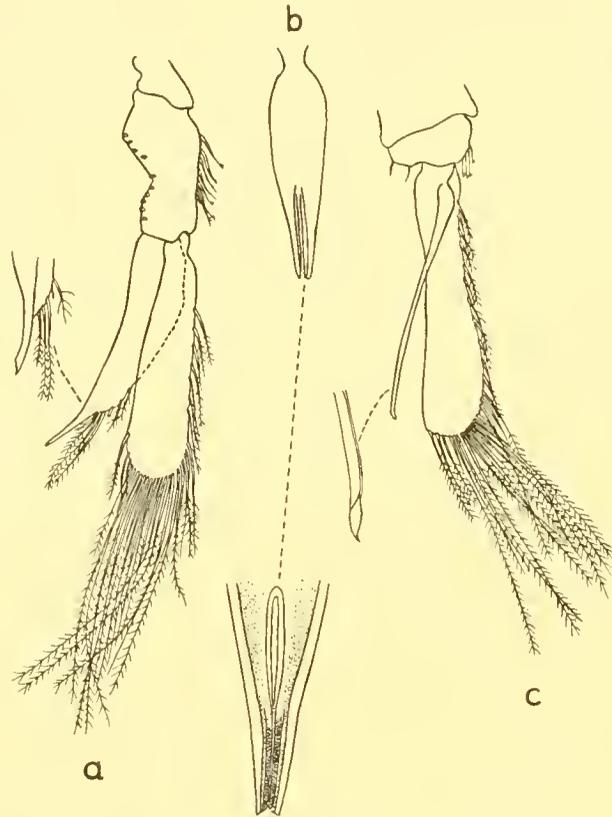
(2) In *acuminatus* the body armature has body spines less well-developed than those of *tribulis*, and the blunt, downwardly directed tooth is not present on the antero-lateral angle of the head.

(3) In *acuminatus* the areas above the insertions of the coxal joints are raised.

(4) The endite of the maxilliped is also different.

Both Studer's and Hale's specimens were obtained from Kerguelen Island, and Hale suggested that in view of their great similarity *tribulis* might be a variety of *cornutus*. Beddard's material of

cornutus, on the other hand, came from Marion Island. I have examined one of his identified specimens in the British Museum (Natural History). The specimen is a male and possesses a pointed pleotelson as in *acuminatus* and therefore differs from Studer's genotype, *cornutus*. Beddard's specimen is slightly larger than the male in the Discovery collections and lacks body spines, except for a pair on the head; the spines on the male specimen in the Discovery collections are less well developed than those of the female. Both Discovery specimens were taken in the neighbourhood of Prince Edward Island, that is, in the same area as Beddard's specimen.



Text-fig. 18. *Arcturides acuminatus* sp.n. (a) First pleopod (right) ♂, ×34. (b) Penis, ×34. (c) Second pleopod ♂ with exopodite removed, ×34.

Prince Edward and Marion Islands are separated by about 1800 miles of deep water from Kerguelen Island; this must almost certainly act as a barrier to the spread of a shallow-water species from one locality to the other. I consider that the specimens collected from these two areas, although very similar, represent two distinct species, and that Beddard's material, recorded as *A. cornutus*, more properly belongs to the new species just described, *A. acuminatus*.

XENARCTURIDAE, fam.n.

DIAGNOSIS. The *body* is dorso-ventrally flattened, without any elongation of the fifth thoracic somite; the second thoracic somite has its middle portion completely fused with the head, but its lateral pleural extensions are free. The tergum of each of the second to the fifth thoracic somites inclusive (first to fourth pereion somites) has on either side a pleural extension which extends laterally over the base of the limb. On the ventral surface of these somites each coxal joint is clearly defined; its outer margin is ring-like and, except for those of the second somite, is separated from the ventral surface of its pleuron by a suture. The inner margins of the coxal joints of these limbs are expanded into coxal plates; each extends over the ventral surface of its somite almost to the mid-line,

where it meets, but does not fuse with, the corresponding plate of the opposite limb. The coxae of the last three pairs of thoracic appendages have plates developed on both their inner and outer margins, the latter extending on to the dorsal surface of the body where they are separated from their respective terga by sutures.

The pleon segments are all coalesced to form a single plate. The *antennule* consists of a peduncle of three joints and a single flagellar joint. The *antenna*, which is setose, is considerably longer than the antennule; it is built up of five peduncular joints and a single one to the flagellum; the distal portion of each antenna is directed towards the mouth. The *maxilliped* has a five-jointed palp; the second pair of *thoracic appendages* is short, setose and carried close to the mouthparts; the third and fourth pairs are long and setose, the remaining four pairs are all alike, and are ambulatory; of these the fifth pair is directed forwards, and the remaining three pairs (6-8) backwards.

The first as well as the second pair of *pleopods* in the male is modified as a copulatory organ; the penis is single. The uropod has a large protopodite, with both endopod and exopod present but of small size.

The *marsupium* of the breeding female is large and formed from four pairs of lamellae carried on the coxae of the second to the fifth pairs of thoracic appendages, its development is similar to that of *Idotea emarginata* (Fabr.) (p. 154).

This family is intermediate in position between the families Pseudidotheidae Ohlin and Astacillidae Stebbing. The broad, dorso-ventrally flattened body of *Xenarcturus* g.n., recalls the body form of the first family, although the breadth of the head and anterior thoracic somites is relatively greater. The fusion of the head with the second thoracic somite is common to all three families; the condition in *Xenarcturus* comes nearest to that of the astacillid genus *Idarcturus* Barnard; in this genus the head is fused with the second thoracic somite, but sutures are distinct laterally, whereas in *Xenarcturus* the pleura of the somite form free lobes.

The fusion of the abdominal segments to form a pleotelson, and the presence of both exopod and endopod on the uropod, are characters shared by members of all three families.

The antennule of *Xenarcturus* has a single joint to the flagellum and this bears sensory setae, which are more numerous in the male than in the female; this character is also found amongst the Astacillidae in the following genera: *Antarcturus* Zur Strassen, *Microarcturus* Nordenstam, *Astacilla* Cordiner and *Neastacilla* Tattersall; it is also a character of *Pseudidothea* Ohlin.

The antenna of *Xenarcturus* differs from that in the other two families in being very setose and directed towards the mouth, and in having a single joint to the flagellum; *Pseudidothea* has two, and the *Astacilla* group three flagellar joints. The palp of the maxilliped is five-jointed like that of *Pseudidothea* and some astacillids; it agrees with *Pseudarcturella chiltoni* Tattersall, in the absence of coupling hooks from the endite of the basipodite.

The form of the thoracic appendages (2-8) is astacillid-like, but with one very important difference, the fifth pair, though directed forwards, resembles the posterior three pairs; that is to say, it is strong and ambulatory, not delicate and setose as in the astacillids. The second pair of thoracic appendages is short and closely applied to the mouth parts, and, like that of the *Arcturus* group, has the dactylus expanded and without a claw. The third and fourth pairs are long and setose.

The modification of the exopod of the first pleopod as a copulatory organ in the male is also present in the astacillid genera *Antarcturus* Zur Strassen, *Dolichiscus* Richardson, and *Neoarcturus* Barnard, as well as in the family Pseudidotheidae.

The diagnosis of the family Astacillidae, as given by Richardson (1905, p. 323), included as a character 'the four anterior pairs of legs *unlike* the three posterior ones, not ambulatory, nor strictly prehensile, directed forward, slender, ciliated', and it is therefore obvious that *Xenarcturus*, with

its four posterior pairs of limbs *alike*, cannot be included in this family. The combination of this limb arrangement with a dorso-ventrally flattened body removes it still further from the Astacillidae.

The fact that the second, third and fourth pairs of thoracic limbs (first, second and third pereopods) are astacillid-like in form excludes the genus from the family Pseudidotheidae; for these reasons the new family Xenarcturidae has been formed to contain it.

Genus *Xenarcturus* g.n.

Xenarcturus spinulosus, g.n., sp.n. (Plate VIII, fig. 3; Text-figs. 19–22)

Occurrence. St. WS 237: 7. vii. 28, 46° 00' 00" S., 60° 05' 00" W., 150–256 m., 1 ♂, 1 ♀ (breeding). St. WS 756: 10. x. 31, from 50° 53' S., 60° 00' W. to 50° 56.3' S., 59° 56' W., 119 m., 2 ♂♂. St. WS 782: 4. xii. 31, from 50° 30' S., 58° 19' W. to 50° 27' S., 58° 31' W., 141–146 m., 1 ♂, 1 ♀.

The male holotype is from St. WS. 756, the female holotype from St. WS. 237. The genus has the characters of the family.

DESCRIPTION. The Discovery collections contain a single breeding and a single non-breeding female, measuring 7.5 mm. in length by 3.5 mm. in greatest breadth, and four mature males of approximately equal size, one of which measures 6.75 mm. in length and 3 mm. in greatest breadth.

The form of the *body* may be seen from Plate VIII, fig. 3; the anterior margin of the head is broad, and the breadth is gradually increased to the fifth thoracic somite, after which it decreases to the extremity of the pleotelson, which ends in an acute point. The dorsal surface of the body is slightly arched in the male, more so in the female; its surface is covered with scattered spinules.

The shape of the head and second thoracic somite, and the position of the eyes are shown in Text-fig. 19*a*; the line of fusion of the head with the second thoracic somite is marked by a shallow groove; the pleural portions of the somite are free and lie partly beneath the lateral margins of the head.

The arrangement of the coxal joints and their plates has already been given in the diagnosis of the family; the pleura of the second to the fifth thoracic somites are separated by grooves from their respective terga; each tergum is raised in the middle, so that the animal when viewed from the side has a slightly corrugated dorsal surface. The form of the pleotelson can be seen from Text-fig. 19*b*.

The *antennule* (Text-fig. 20*a*) is short and broad, the peduncle consists of three joints, the middle one of which is the longest; the flagellum is a single, broad, rounded joint with sensory setae fringing its tip and inner margin; these setae are more numerous in the male than in the female.

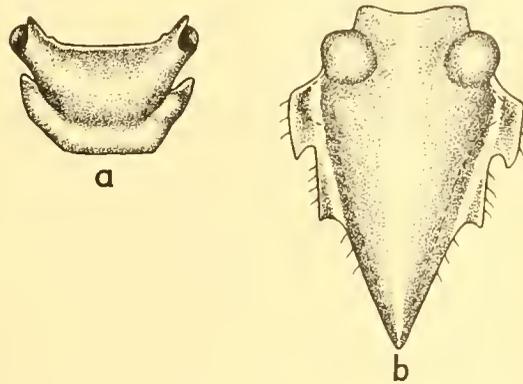
The *antenna* (Text-fig. 20*b*) is very much longer than the antennule; it is bent sharply between the third and fourth peduncular joints so that the flagellum is directed towards the mouth; long setae fringe the inner margins of the second, third and fourth joints. The flagellum consists of a single short joint, tipped with three long setae.

The form of the cutting edge of each *mandible* is shown in Text-fig. 20*c, d*.

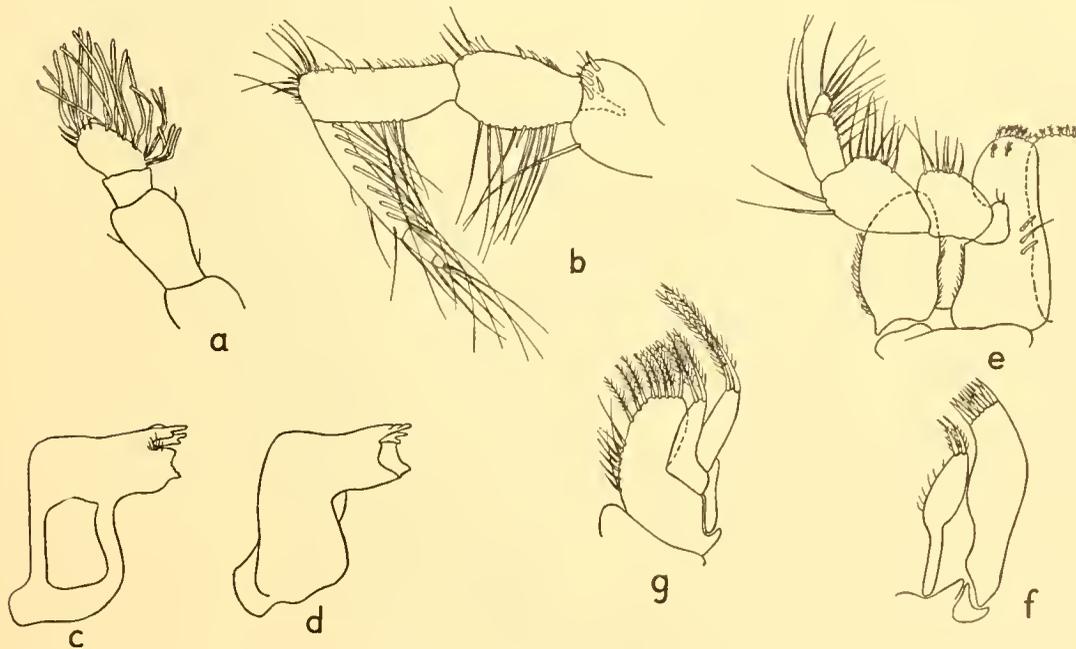
The *maxillula* and *maxilla* (Text-fig. 20*f, g*) show the typical astacillid structure; in the latter, the broad fixed lobe has its rounded extremity fringed with plumose setae; each of the two outer lobes bears two plumose setae on its truncate distal extremity; those of the outer lobe are the longer. The palp of the *maxilliped* (Text-fig. 20*e*) is five-jointed, the inner margin of each joint, except the first, is fringed with long setae; no coupling hooks are present on either the basipodite or its endite, but the edges of these appear to interlock with those of the opposite maxilliped; as in other isopods, a coxal lobe is developed on the coxal joint of the breeding female.

The second thoracic appendage (*first pereopod*) (Text-fig. 21*a*) is shorter and broader in proportion than the succeeding appendages, and the dactylus is broad, with its rounded distal end fringed with long setae; similar setae are also present on the inner margins of the ischium, merus, carpus and

propodus. The third and fourth *thoracic appendages* (Text-fig. 21*b*) are both alike, and are directed forwards and curved towards the mouth; each is about one and a half times the length of the second thoracic appendage and is considerably stouter. The inner margins of the merus, carpus and propodus bear long setae; the dactylus ends in a curved claw. The remaining four pairs of thoracic appendages are all very similar; they are stout and ambulatory in function (Text-fig. 21*c*) and the dactylus of



Text-fig. 19. *Xenarcturus spinulosus* g.n., sp.n. (a) Head and first pereion (second thoracic) somite, $\times 12$. (b) Dorsal view of pleotelson. $\times 7$.



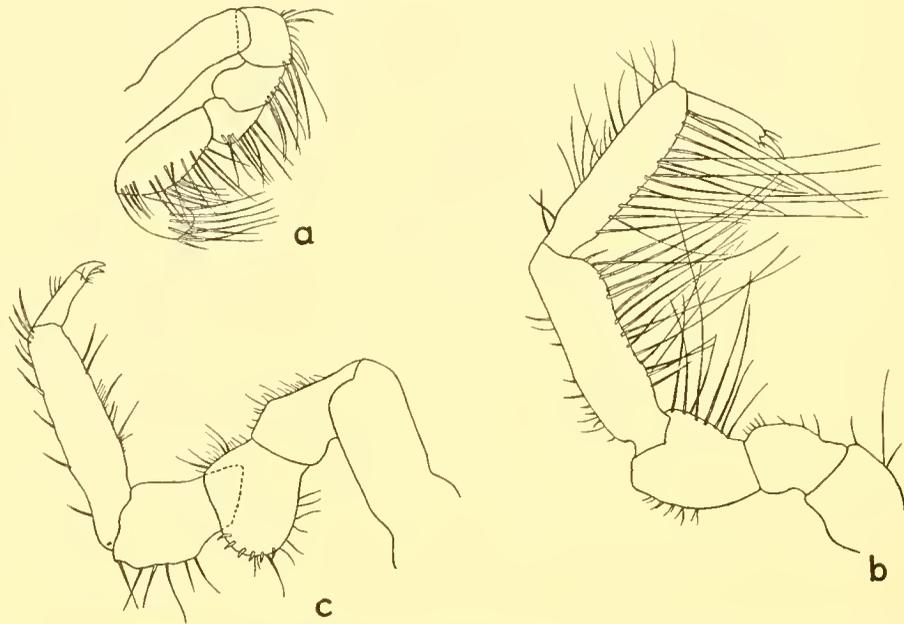
Text-fig. 20. *Xenarcturus spinulosus* g.n., sp.n. (a) Antennule, $\times 32$. (b) Antenna, $\times 32$. (c) Left mandible (dorsal view), $\times 50$. (d) Right mandible (ventral view), $\times 50$. (e) Right maxilliped (ventral view), $\times 50$. (f) Left maxillula, $\times 60$. (g) Left maxilla, $\times 60$.

each ends in a curved claw. The distal end of the merus of the last thoracic appendage has its inner angle produced to form a subacute projection. The surface of the joints is covered with scattered spinules similar to those covering the body surface.

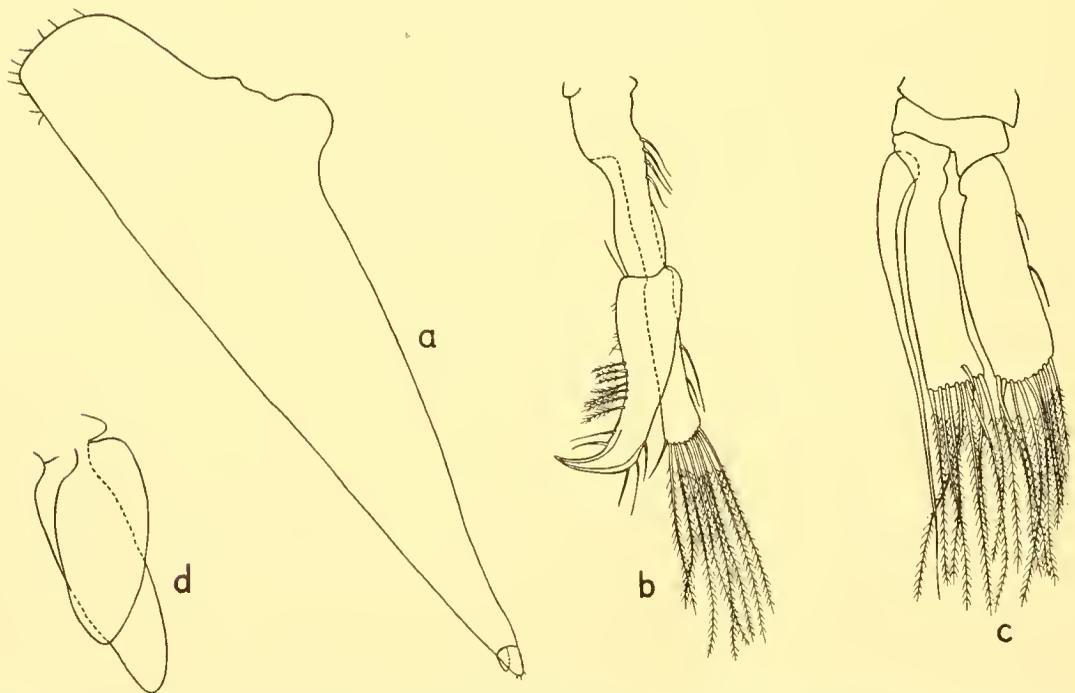
In the breeding female, *brood lamellae* are developed on each of the second to the fifth pairs of thoracic appendages inclusive.

The first *pleopod of the male* (Text-fig. 22*b*) has the exopod modified as a copulatory organ; it is longer than the endopod and has its distal portion bent almost at right angles and drawn out into an acute point. Its outer concave margin bears a number of plumose setae; a similar modification is seen

in the first pleopod of the male of *Pseudidothea bonnieri* Ohlin. The form of the *appendix musculina* on the second pleopod of the male is also very similar to that of *P. bonnieri*; it is considerably longer than endopod (Text-fig. 22*a*), nearly straight, but decreasing in thickness so that its distal portion



Text-fig. 21. *Xenarcturus spinulosus* g.n., sp.n. (a) First pereopod, $\times 32$. (b) Second pereopod, $\times 32$. (c) Fourth pereopod, $\times 32$.



Text-fig. 22. *Xenarcturus spinulosus* g.n., sp.n. (a) Uropod (dorsal view), $\times 32$. (b) First pleopod (right) δ , $\times 32$. (c) Second pleopod (left) δ , $\times 32$. (d) Third pleopod, δ , $\times 32$.

forms an acute point. The *penis* is single, it is rather long and tapers to a rounded extremity. The remaining pleopods (Text-fig. 22*d*) are all similar. The protopodite of the uropod (Text-fig. 22*a*) is large and carries at its tip a small exopod and an endopod which is slightly larger.

DISTRIBUTION. The three stations at which this species was collected are all on the Patagonian Shelf. St. WS. 237 (46° 00' S., 60° 05' W.) lies some distance farther north than the other two, towards the edge of the shelf. Sts. WS. 756 and WS. 783 are both a little north of the Falkland Islands.

SUMMARY

1. The paper deals with fifteen species in the Discovery collections, 1925-36, belonging to the families Idoteidae, Pseudidotheidae and Xenarcturidae fam.n.
2. One new genus and five new species are described: *Xenarcturus spinulosus*, *Edotia oculopetiolata*, *E. corrugata*, *Pseudidothea scutatus* (= *Microarcturus scutatus* Stephensen, 1947) and *Arcturides acuminatus*.
3. Points of morphological interest, including modifications in the form of the brood pouch of *Edotia*, are discussed.

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SUPPLEMENT TO ISOPOD CRUSTACEA, PART I:

THE FAMILY SEROLIDAE (Text-figs. 23-29)

Since the publication of the Discovery Report, *The Family Serolidae*, vol. VII, 1933, pp. 253-362, three new species have been erected. One, *Serolis johnstoni* Hale, was collected by the B.A.N.Z. Antarctic Research Expedition, 1929-31, and is described in volume VI of the reports (Hale, 1952, pp. 32-5); the other two, *S. acuminata* sp.n. and *S. ovata* sp.n., occurred amongst the specimens collected by R.R.S. 'Discovery II' between 1928 and 1937 and are described below. The type specimens of *S. acuminata* and *S. ovata* are deposited in the British Museum (Nat. Hist.).

According to Hale (1952, p. 35), *S. johnstoni* comes nearest to *S. gerlachei* Monod (1925, p. 299 and 1926, p. 36, figs. 35-7), but the latter differs in having (1) no transverse lateral ridges on the dorsum of second peraeon somite; (2) no median dorsal spine at the hinder margin of the first two free peraeon somites; (3) the coxal plates of the seventh peraeon somite shorter; (4) an additional longitudinal carina on each side of the median carina of the telsonic somite; (5) a small jointlet at the distal end of the third joint of the palp of the maxilliped; (6) the posterior spines on inner edge of the propodus of the first peraeopod broader' (cf. Hale, 1952, p. 33, fig. 4 sp. and Monod, 1926, fig. 36c).

In *S. johnstoni* the coxal plates of the seventh thoracic somite are figured by Hale (fig. 4, pin. ♂) as being incomplete (i.e. broken) in the adult male, but are shown complete on one side of a young male (fig. 4, juv. ♂) and extending back beyond the tips of the pleural plates of the second and third abdominal segments. If Hale's figure of the adult male is correct, the broken part of the coxal plate must have been very delicate. Presumably, when complete it extends backwards over the pleural plates as far as in the young specimen, for I know of no example in which the young differ from the adult in this respect.

Hale states on p. 32 that the pleural plates of the second abdominal segment are produced beyond those of the third; this is shown in his figure of the adult male, whereas in his figure of the young male the plates of the third segment are shown as extending beyond those of the second. Normally, the comparative lengths of these plates do not change with age, so that the arrangement shown in the figure of the young male is either abnormal or represented incorrectly.

S. johnstoni can be placed in the key to the species of the genus (Sheppard, 1933, pp. 278–82) in Section BI, CII, b1 α (p. 280) together with *S. gerlachei* Monod, for both species have the median dorsal portion of the cephalosome produced backwards into a spine.

There is one point which needs correction in the published Discovery report on this family (Sheppard, 1933). On p. 273, fig. 2, showing the form of the maxilliped in various species of *Serolis*, *S. discoverii* sp.n. should read *S. exigua* Nordenstam. The error arose because a form already named and described as a new species proved to be identical with Nordenstam's new species *S. exigua* which appeared before the publication of my report; owing to an oversight the name in this figure was not altered to read *S. exigua* Nordenstam.

STATION LIST

Further records of species of *Serolis* collected between 1928 and 1937.

St. WS 213: 30. v. 28, 49° 22' 00" S., 60° 10' 00" W., net of 7 mm. mesh attached to trawl, green sand, mud and pebbles, 49–239 m.

Serolis neaera Beddard, 1 ♀ (breeding), 1 ♂.

St. WS 772: 30. x. 31, from 45° 13' S., 60° 00' W. to 45° 13.8' S., 60° 00.5' W., tow-net of coarse silk attached to back of trawl, grey sand, 309–163 m.

Serolis schythei Lütken, 2 ♀♀ (breeding), 1 (non-breeding), 5 ♂♂, and a number of immature.

St. WS 783: haul A, 5. xii. 31, 50° 03.5' S., 60° 08' W., net of 7 mm. mesh attached to trawl, rock, stones and shells, 157–159 m.

Serolis schythei Lütken, 3 ♀♀ (breeding).

St. WS 836: 2. ii. 32, 53° 05.5' S., 67° 38' W., small beam trawl, 14–16 m.

Serolis convexa Cunningham, 1 ♂.

St. WS 821: 18. i. 32, from 52° 55' S., 60° 57' W. to 52° 56.5' S., 60° 53' W., net of 4 mm. mesh attached to trawl, fine green grey sand and mud, 461–468 m.

Serolis neaera Beddard, 1 ♀ (breeding), 2 damaged and 1 immature specimen.

St. 1230: 23. xii. 33, 6.7 miles N. 62° W. from Dungeness Light, Magellan Strait, Russell's bottom tow-net, 29 m.

Serolis orbiculata sp.n., 1 ♀ (non-breeding).

St. 1562: 7. iv. 35, 46° 51.7' S., 37° 56.5' E. to 46° 54.8' S., 37° 53.8' E., Russells' bottom tow-net, 97–104 m.

Serolis septemcarinata Miers, 4 ♀♀ (breeding), 9 ♂♂, and a number of immature specimens.

St. 1562: 7. iv. 35, 46° 51.7' S., 37° 56.5' E. to 46° 54.8' S., 37° 53.8' E., large rectangular net, 90–97 m.

Serolis septemcarinata Miers, 1 ♀ (breeding), 2 ♂♂, 1 immature.

St. 1564: 46° 36.5' S., 38° 02.3' E., 7. iv. 35, large dredge, 108–118 m.

Serolis septemcarinata Miers, 1 ♀ (breeding), 4 ♂♂, 2 immature.

St. 1660: 27. i. 36, 74° 46.4' S., 178° 23.4' E., large otter trawl, 351 m. (taken from jar of unsorted bottom fauna).

Serolis acuminata sp.n., 8 ♀♀ (breeding), 2 ♀♀ (non-breeding), 10 ♂♂, and a number of immature specimens.

St. 1873: 13. xi. 36, 61° 20.8' S., 54° 04.2' W., rectangular dredge bag bent on to a Russell frame, etc., 210–180 m.

Serolis trilobitoides, 1 ♀ (non-breeding), *Serolis ovata* sp.n., 1 ♀ (non-breeding).

St. 1902: 49° 48' S., 67° 39.5' W., 4 miles S. 32° E. of Cape San Francisco de Paula Light, large otter trawl, 50–80–50 m.

Serolis schythei Lütken, 1 ♀.

St. 1941: 29. xii. 36, Leith Harbour, South Georgia, small rectangular dredge. 38 m.

Serolis pagenstecheri Pfeffer, 1 ♂, 1 ♀ (non-breeding); 55–22 m. *Serolis pagenstecheri* Pfeffer, 3 ♂♂, 2 ♀♀ (non-breeding).

St. 1948: 60° 49.4' S., 52° 40' W., 4. i. 37, rectangular dredge bag bent on to a Russell frame, etc., 490–610 m.

Serolis trilobitoides Eights, 1 ♂, 1 ♀ (non-breeding). *Note on colour*: centre brown with dark brown lines and shadings, pleurae pale brown shades and spotted with dark brown; limbs pale brown.

Serolis bouveri Richardson, 2 ♂♂. *Note on colour*: dark brown with cream margins to pleura, limbs pale brown.

St. 1955: 29. i. 37, 61° 35.1' S., 57° 23.2' W., rectangular dredge bag bent on to a Russell frame, etc., 440–410 m.

Serolis trilobitoides Eights, 1 ♀ (breeding), 2 ♀♀ (non-breeding), 2 ♂♂.

St. 1957: 3. ii. 37, off south side of Clarence island, 7 miles east of Cape Bowles, South Shetlands, large dredge, heavy pattern, 4 ft. long (1.2 m.), 785–810 m.

Serolis meridionalis Hodgson, 1 ♀ (breeding), 1 ♀ (non-breeding) incomplete.

Serolis acuminata sp.n. (Text-figs. 23–26)

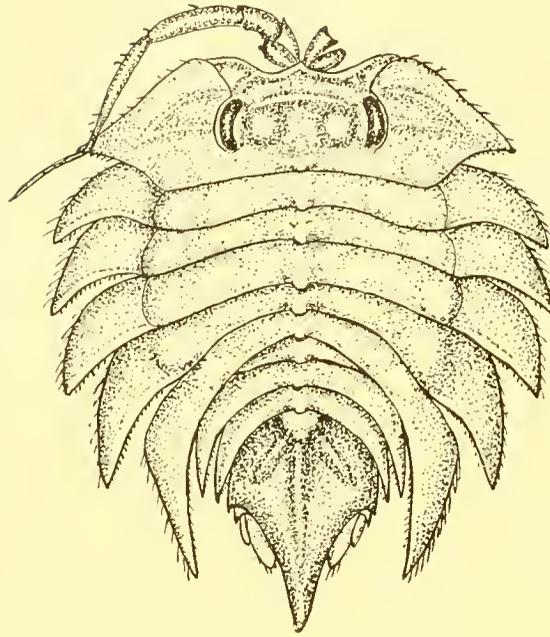
Occurrence. St. 1660: 27. i. 36, 74° 46.4' S., 178° 23.4' E., 351 m., 8 ♀♀ (breeding), 10 ♂♂, 2 ♀♀ (non-breeding) and a number of immature specimens.

One male and one female specimen from St. 1660 are chosen as holotypes.

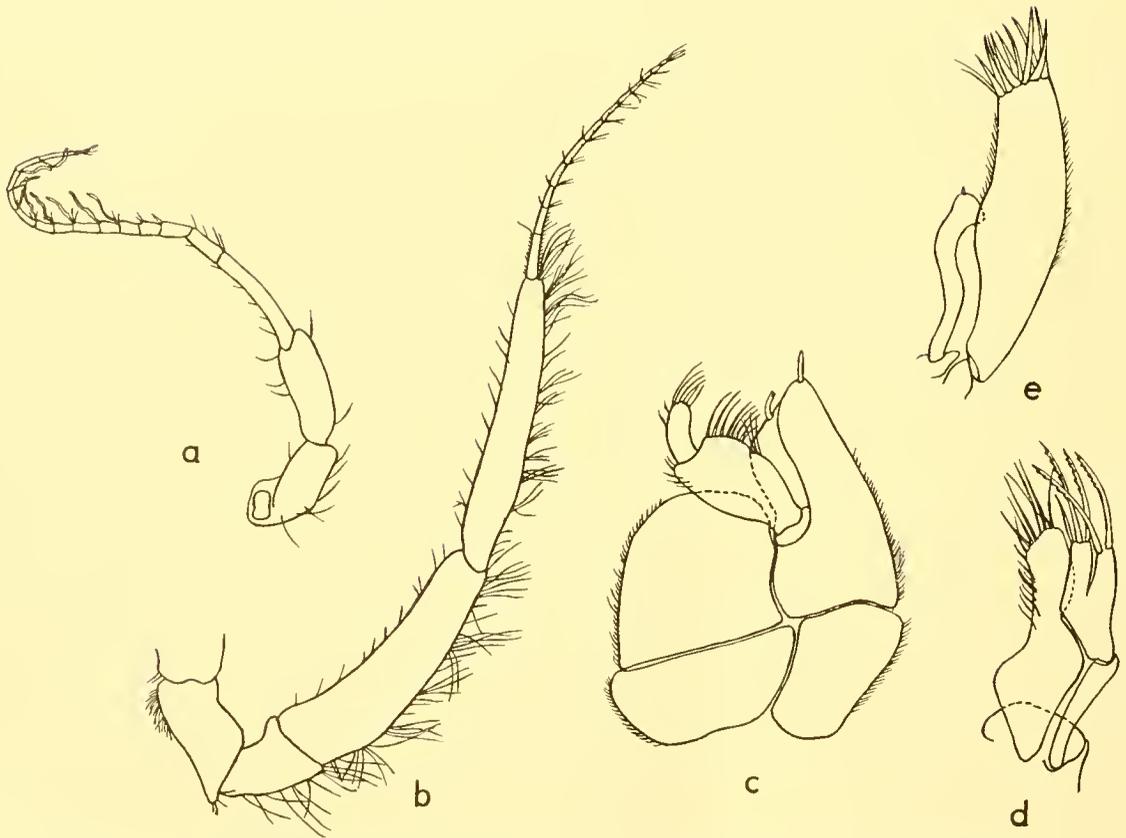
DESCRIPTION. The size of the largest male (Text-fig. 23) is 11 mm. in length and 10 mm. in greatest breadth; the female, which is in the breeding condition, is 10 mm. in length and 8 mm. in greatest breadth. The male is proportionately slightly broader than the female with a length:breadth ratio of 1.1:1 as compared with the female ratio of 1.25:1. The head is twice as broad as long and broadest anteriorly. The anterior margin shows two shallow excavations one on either side of a small pointed rostrum; behind the latter, running parallel with it, is a slight transverse ridge. A second ridge extends between the anterior extremity of the eyes and the area of the head between the eyes is raised into two rounded prominences; between these two, posteriorly, is a small median one.

The suture line separating the head from the second thoracic (first pereion) somite extends to just behind the eyes, which are about half the length of the head, reniform in shape and contain black pigment. The lateral or coxal portion of the second thoracic somite on either side of the head is marked by two low transverse ridges, one, extending outwards from just in front of the eye, curves backwards to meet the second ridge which extends outwards from the middle region of the eye (Text-fig. 23); the resulting single ridge curves slightly backwards and disappears. The median portion of the somite, which is completely fused with the head, is narrow and bears a small backwardly projecting median spine. On either side of the junction of the tergal with the coxal region is a low rounded eminence. The second, third and fourth pereion somites are subequal; each is produced backwards in the mid-dorsal line into a small spiniform process, which increases in size from before backwards. A low prominence occurs just within the lateral margins of all the pereion somites. The sixth and seventh thoracic somites (fifth and sixth pereion) are slightly narrower than preceding somites. Well-developed coxal plates are present on each of the second to the sixth pereion somites; those of the first three are separated by distinct sutures from their respective somites. The coxal plates are not closely applied together and each is fringed with delicate hairs, which are longer on their lateral than their posterior margins; the plates of the last two segments are longer than the preceding ones, and those of the last extend backwards to beyond the tip of the uropods. The posterior margin of each of the three free abdominal segments is produced into a median spiniform process similar to, but slightly smaller than, those of the thoracic somites. The pleural plates of the third abdominal segment extend backwards slightly farther than those of the second, but not quite as far as the level of the base of the uropods. A short lateral carina is present on either side of the median one. The terminal segment narrows considerably between the uropods and extends for some distance beyond the tip of these, as a pointed process; the dorsal surface has a small low eminence in the median line from which a median carina extends backwards disappearing at the level of the tip of the uropods.

The *antennule* (Text-fig. 24a) has a peduncle of four joints, the first one of which is broad and geniculate, with a few scattered hairs; the second joint is about equal in length and breadth to the first; the third is the same length as the second, but narrower and three times as long as the fourth. The flagellum consists of twelve joints and a minute terminal one; a single sensory seta is found at the distal end of all except the first three joints.



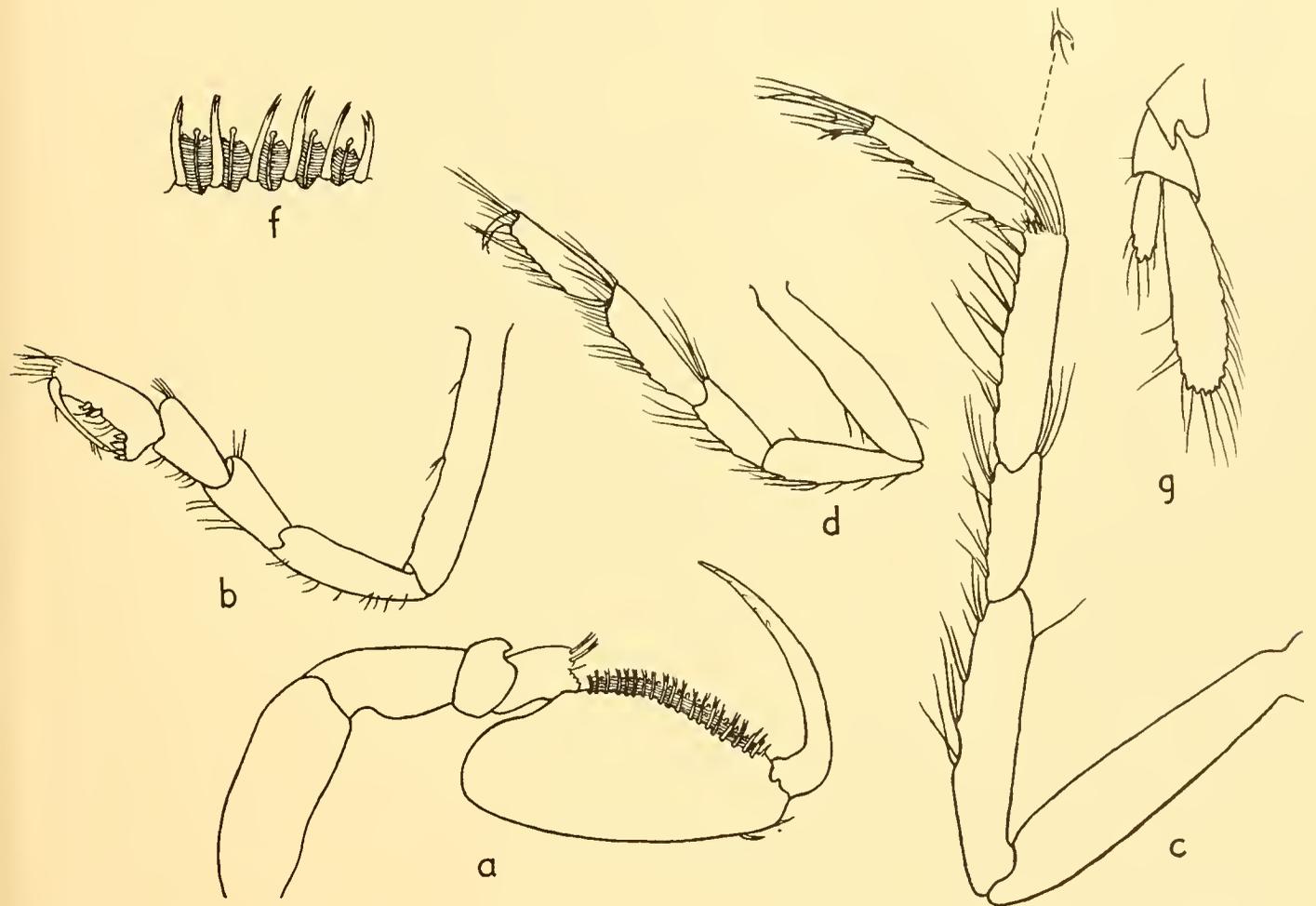
Text-fig. 23. *Serolis acuminata* sp.n., $\times 7$.



Text-fig. 24. *Serolis acuminata* sp.n. (a) Antennule, $\times 16$. (b) Antenna, $\times 16$. (c) Maxilliped, $\times 50$. (d) Maxilla, $\times 50$. (e) Maxillula, $\times 50$.

The form of the *antenna* may be seen from Text-fig. 24*b*, the peduncle consists of five joints, and the flagellum of twelve, of which the terminal three are small. The first three joints are fringed with very short hairs, the next six joints each bear a longitudinal row of minute spiniform processes.

The *mouthparts* are of the usual type, the maxilliped (Text-fig. 24*c*) is broad, with the basipodite separated from its lamella by a suture; the maxilla (Text-fig. 24*d*) has its two outer lobes each bearing two long setae with delicate pectinations along their inner edges; the truncate distal end of the fixed lobe is fringed with delicate setae; the outer lobe of the maxillula (Text-fig. 24*e*) is stout and bears ten



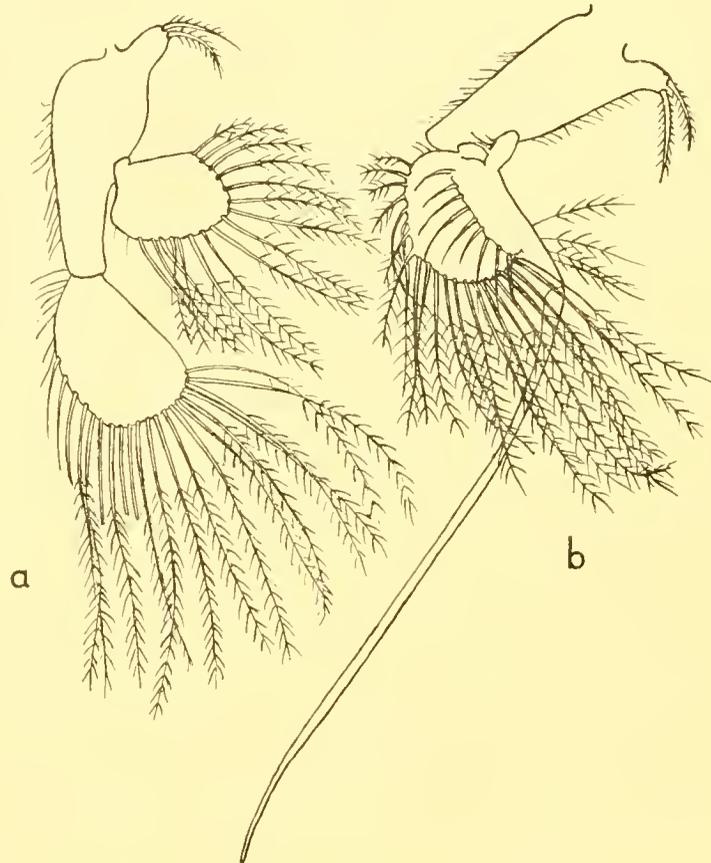
Text-fig. 25. *Serolis acuminata* sp.n. (a) First pereiopod, $\times 30$. (b) Second pereiopod, $\times 30$. (c) Sixth pereiopod, $\times 30$. (d) Seventh pereiopod, $\times 30$. (e) Spines on propodus of first pereiopod, enlarged. (f) Uropod, $\times 30$.

spines and two delicate setae on the inner angle of its distal truncate extremity; the inner lobe is considerably shorter than the outer and is broadest at its distal extremity which is rounded and bears a single minute spine.

The first, second, sixth and last *pereiopods* are shown in Text-figs. 25*a*, *b*, *c* and *d*. The propodus of the first is greatly expanded, with its inner edge armed with a row of about twenty-two broad processes alternating with modified spines (Text-fig. 25*f*); the dactylus bears five flattened spines in its distal region and the distal end of the carpus is crenulate and bears two modified spines similar to those on the propodus. The second pereiopod (Text-fig. 25*b*) is much smaller than the first, with the propodus expanded and its inner margin armed with stout spines, a pair of which occurs at about the middle of its length and a group of four at its broadened proximal end. The remaining pereiopods,

except for the last, are more or less alike (Text-fig. 25 *c*); the last pair (Text-fig. 25 *d*) are considerably smaller, with the propodus proportionately broader and the dactylus shorter and curved.

The first and second *pleopods* of the male are shown in Text-fig. 26 *a* and *b*; the *appendix masculina* of the second pleopod reaches to the level of the tips of the uropods. The uropods (Text-fig. 25 *g*), as already noted, do not extend beyond about two-thirds of the length of the terminal segment; the exopod is about half the length of the endopod, both have notched margins from which spring delicate setae, these are restricted to the distal region of the exopod.



Text-fig. 26. *Serolis acuminata* sp.n. (a) First pleopod ♂, × 36. (b) Second pleopod ♂, × 36.

This species fits into the key of the species of *Serolis* (Sheppard, 1933, pp. 278–82) in the section containing *S. cornuta* Studer and *S. trilobitoides* (Eights) (p. 280, BI, CIIb2). The species can be readily distinguished from these by its smaller size and by the shape of the terminal segment.

DISTRIBUTION. Ross Sea.

Serolis ovata sp.n. (Text-figs. 27–29)

Occurrence. St. 1873: 13. xi. 36, 61° 20'8" S., 54° 04' 2" W., 210–180 m., 1 ♀ (non-breeding), the holotype.

DESCRIPTION. The single specimen (Text-fig. 27) on which this species is based is a female in the non-breeding phase, measuring 13 mm. in length and slightly over 10 mm. in greatest breadth; it is broadly ovate in outline and compact in form. The head is broadest anteriorly where the width is twice that of the length; a very small median rostral process is present, on either side of which the anterior margin is slightly excavated in the region of the base of the antennule. A curved transverse ridge extends from just behind the rostral process and dies out on the coxal area of the second thoracic somite; behind this, and in front of the eyes, the head is raised into a somewhat pitted area which is

separated from the hinder part of the head by a second transverse ridge which extends between the anterior limit of the eyes. The hinder part of the head, between the eyes, is raised into two low, rounded prominences and between these, in the posterior median position, is a very small rounded projection. The region between the sutures separating the head from the second thoracic somite is marked by a shallow groove. The eyes are reniform in shape and contain black pigment.

As in all the members of the Serolidae, the second thoracic (first pereion) somite is fused with the head, the limits of which may be seen laterally by the presence of sutures. The median portion of the tergum of this and the succeeding somites, both thoracic and abdominal, is raised in a slight keel. The coxal plates of all the segments are somewhat thickened at their lateral margins; in this character the species resembles *S. bouvieri* Richardson (1906, pp. 7-10), where a similar but much greater thickening occurs. The third, fourth and fifth thoracic (second-fourth pereion) somites are subequal and their terga are separated from their respective coxal plates by sutures; the terga of the sixth and seventh thoracic somites together have a length less than one of the preceding ones; that of the seventh is about half the length of the sixth; the tergum and coxal plates of the last thoracic somite, as in most species of *Serolis*, are absent.

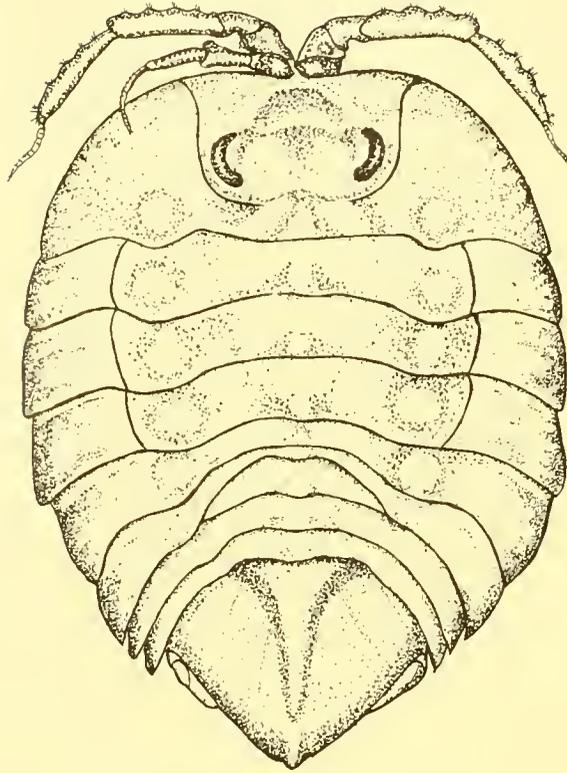
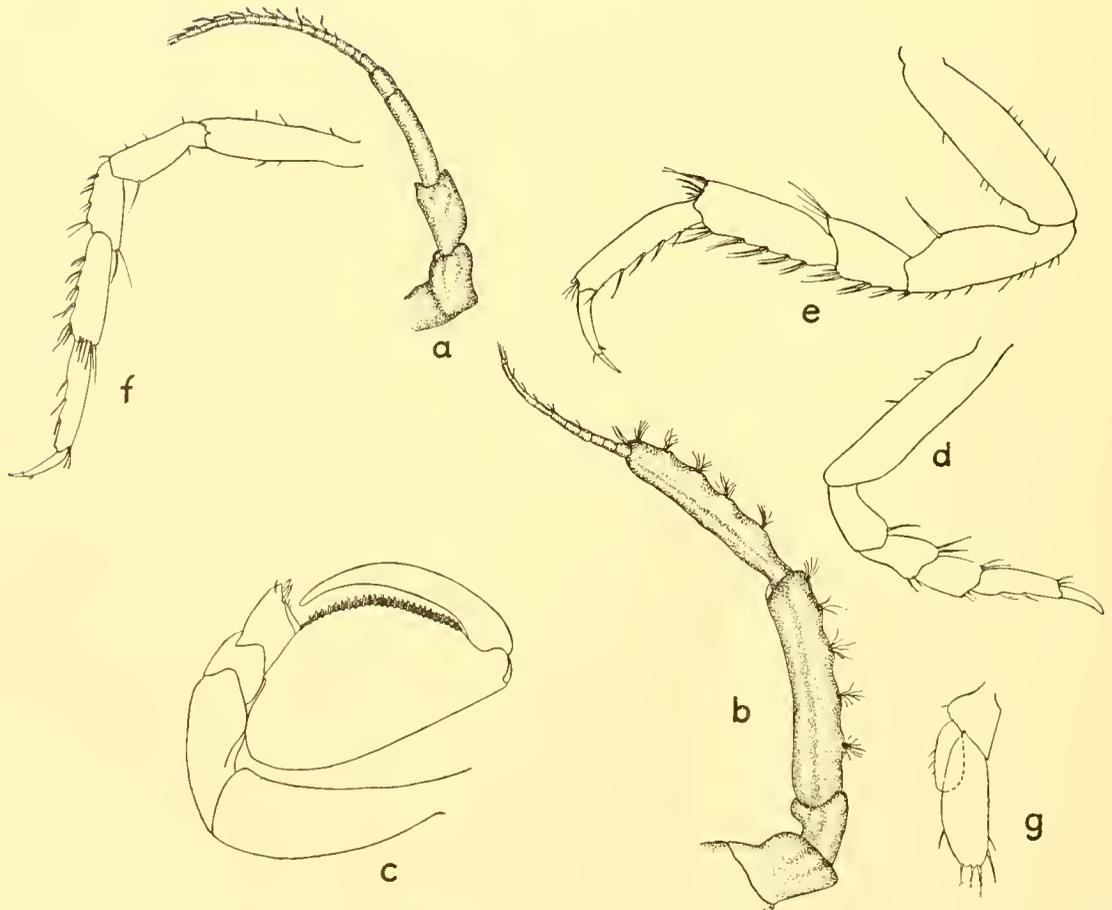
The terga of the three free abdominal segments are subequal and each is equal to the combined length of the sixth and seventh thoracic somites; the pleural plates of the second and third segments extend back beyond the coxal plates of the seventh thoracic somite, those of the third are slightly longer than the second, and reach to the level of the distal extremity of the protopodite of the uropods. The terminal segment is broader than long, somewhat pentagonal in outline, with thickened margins and a raised central area, the latter forming a broad keel, which narrows towards the posterior extremity of the segment and disappears a little distance from the tip of the segment, which is rounded and slightly keeled; arising from the broader portion of the keel, on either side, is a series of three delicate ridges (Text-fig. 27) which curve outwards and backwards and disappear some distance from the margins of the segment.

The peduncle of the *antennule* (Text-fig. 28*a*) consists of four joints, the first one of which is broad and geniculate, with a raised, rounded longitudinal ridge extending from the middle of its distal upper margin to a point a little short of the geniculation; a similar ridge is present on the second joint which is broadest at its distal end and is about two-thirds the length of the first; the third joint is a little longer but about half the width of the second, and the fourth is a third of the length of the third: the flagellum consists of seventeen joints, the distal one of which is very small; a single sensory seta is present at the distal end of each joint except the first four.

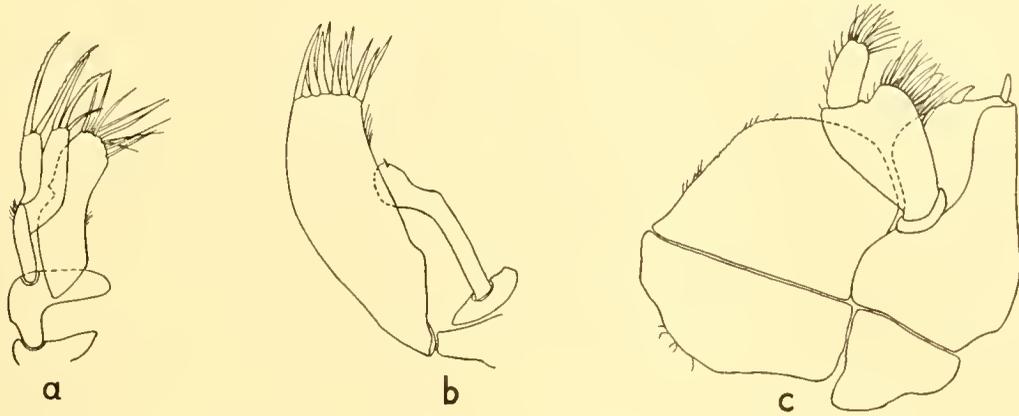
The *antenna* is shown in Text-fig. 28*b*; the first joint of the peduncle is short; the second and third are subequal, but the second is broader than the third which is narrower at its proximal end; the fourth and fifth are subequal and three times as long as the third; the fifth is narrower than the fourth; these two last-mentioned joints each possess five groups of delicate hairs which are found on raised areas along their anterior margins; a longitudinal ridge is present on all except the first joint of the peduncle; the flagellum is shorter and narrower than the fifth joint of the peduncle and consists of eleven joints, the distal one of which is small.

The *mouthparts* are of the usual type, the form of the maxillula, maxilla and maxilliped may be seen in the Text-fig. 27*a, b* and *c*.

The first, second, sixth and seventh *pereiopods* are shown in Text-fig. 28*c, d, e* and *f*. The first pereiopod, as usual, is of a stout build, with the propodus greatly expanded and with its inner margin armed with a row of about thirty-three broadly oval processes alternating with modified spines similar to those illustrated for *S. acuminata* (Text-fig. 25*f*). The distal edge of the carpus is crenulate and bears two spines similar to those on the propodus.

Text-fig. 27. *Serolis ovata* sp.n., ×7.Text-fig. 28. *Serolis ovata* sp.n. (a) Antennule, ×12. (b) Antenna, ×12. (c) First pereopod, ×12. (d) Second pereopod, ×12. (e) Sixth pereopod, ×12. (f) Seventh pereopod, ×12. (g) Uropod, ×12.

The protopodite of each of the first three pairs of *pleopods* is triangular in shape, and like those of *S. acuminata* bear plumose setae (Text-fig. 26*a*); the exopodite of the fourth pleopod is divided, near its distal end, by a transverse suture at right angles to its long axis: the uropods (Text-fig. 28*g*) extend half way along the lateral margins of the terminal segment; the protopodite of each is triangular in shape; the exopodite is half the length of the endopodite, and both have rounded distal extremities, that of the former bears two or three short plumose setae, and a few simple ones.



Text-fig. 29. *Serolis ovata* sp.n. (a) Maxilla, $\times 32$. (b) Maxillula, $\times 32$. (c) Maxilliped, $\times 32$.

This species can be placed in the key to the species of *Serolis* (Sheppard, 1933, pp. 279–82), in section BIC1*b* (pleural plates on third abdominal segment extend beyond those of second) and in this group in 2β (ii) (Uropods *not* broad and extending beyond the posterior extremity of the terminal segment). Thus, in general characters *S. ovata* sp.n. comes nearest to *S. exigua* Nordenstam (1933, pp. 70–5), but can be readily distinguished from that species by the compact form of its body with its somewhat thickened coxal plates, and by the absence of a median backwardly projecting spine to the cephalosome.

DISTRIBUTION. Scotia Sea, $61^{\circ} 20.8' S.$, $54.04^{\circ} 2' W.$

SUMMARY

1. The supplement records additional species of the family Serolidae from the Discovery collections made between 1928–37.
2. Two new species *Serolis acuminata* and *Serolis ovata* are described.

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PLATE VIII

Fig. 1. *Edotia corrugata*, sp.n. ♂, × 8.

Fig. 2. *Edotia corrugata*, sp.n., ♀, × 8.

Fig. 3. *Xenarcturus spinulosus*, g.n., sp.n., ♂, × 8.



1



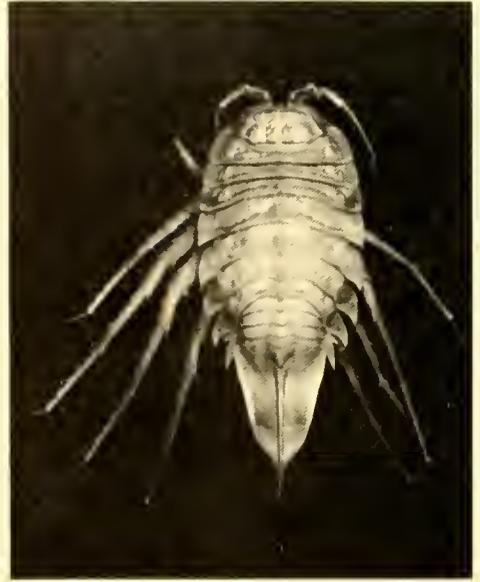
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PLATE IX

Glyptonotus antarcticus

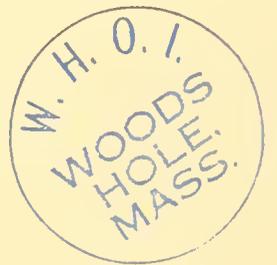
- Fig. 1. Non-breeding ♀ from 17-27 m. depth. Length 63 mm., breadth 32 mm.
- Fig. 2. Non-breeding ♀ from 567 m. depth. Length 53 mm., breadth 22 mm.
- Fig. 3. ♂ from 24-36 m. depth. Length 89 mm., breadth 46 mm.
- Fig. 4. ♂ from 99-161 m. depth. Length 105 mm., breadth 47 mm.
- Fig. 5. ♂ from a fish-trap. Length, 118 mm., breadth 58 mm.

[*Discovery Reports. Vol. XXIX, pp. 199-228, Plate X, April, 1958.*]

THE DISTRIBUTION OF THE CHAETOGNATHA
OF THE SOUTHERN OCEAN

By

P. M. DAVID



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THE DISTRIBUTION OF THE CHAETOGNATHA OF THE SOUTHERN OCEAN

By P. M. David

(Plate X; Figs. 1-13)

INTRODUCTION

A NUMBER of reports on antarctic Chaetognatha have been already published (Steinhaus, 1900; Fowler, 1907; Ritter-Zahony, 1909, 1911; Germain, 1913; Jameson, 1914; Johnston and Taylor, 1921; Burfield, 1930; Bollmann, 1934; Thiel, 1938; Ghirardelli, 1953), but in most cases the collections reported on were small and restricted both in horizontal and in seasonal range.

The Discovery collections cover nearly all areas of the Southern Ocean in all seasons of the year, and from this material it is possible not only to compile a complete list of species present, but also to discover quite a lot about their distribution and something of their life histories. The approach to the subject adopted here is essentially distributional rather than systematic.

While working on *Sagitta gazellae* I also assembled data on the other species in the collections, and was struck by the very consistent pattern of vertical distribution of the commoner chaetognath species. This pattern was not clearly demonstrated in the earlier reports on antarctic chaetognaths, and it seemed worth while to attempt to show it in the present paper.

Throughout this paper the name 'Southern Ocean' has been employed to describe all that ocean which lies between the subtropical convergence and the Antarctic continent. This area is divided into two zones, the subantarctic and the antarctic, which are separated by the antarctic convergence. While it has been held by some authorities that the Southern Ocean is not a geographical entity, there is no doubt that it has at least a faunistic unity and is therefore a term of considerable value to those working on the distribution of animals in the southern hemisphere.

ACKNOWLEDGEMENTS

I am greatly indebted to Mr J. W. S. Marr for advice and for the loan of his notes on chaetognaths from the second and fourth commissions of Discovery II (1931-3 and 1935-7). These have enabled me to check many points arising from the work and have considerably lightened the task of searching through the collections for stray exotic species. I am also grateful to Mr A. Styles for preparing the diagrams for publication.

MATERIAL AND METHODS

All the material used for this study has been taken from the collections made by ships of the Discovery Committee and subsequently of the National Institute of Oceanography. It would, of course, be best if all the chaetognaths in the collections could be used for this work, but the immense labour involved in sorting and identifying them from the large number of samples available would not be repaid by the results, and therefore an attempt has been made to manage on a limited number of stations chosen from many radiating lines and many other scattered stations. For a start it was desirable to find a line of stations which extended from the subtropics southwards to as near the Antarctic continent as the ice conditions would permit. The line chosen was that worked in March 1937 on the Greenwich meridian (0°) (see Fig. 1). This gives a close approximation to typical summer conditions. In order to

verify that the pattern of distribution found in that line was not peculiar to one area, a line in 80° W (in the Pacific Ocean sector) and another in 90° E (in the Indian Ocean sector) were also examined. The line in 80° W was also worked in March, and that in 90° E in February, so seasonal differences should not affect the comparison greatly. In addition to these summer lines it was obviously desirable to find out if the pattern of distribution altered much in winter, and for this purpose a line of stations in 0° worked in August 1938 was chosen, and by analogy with the consistent pattern of distribution shown by the three summer lines it was considered that the winter pattern of distribution in 0° could be taken as circumpolar. There were two lines of stations worked in August in the Indian Ocean sector

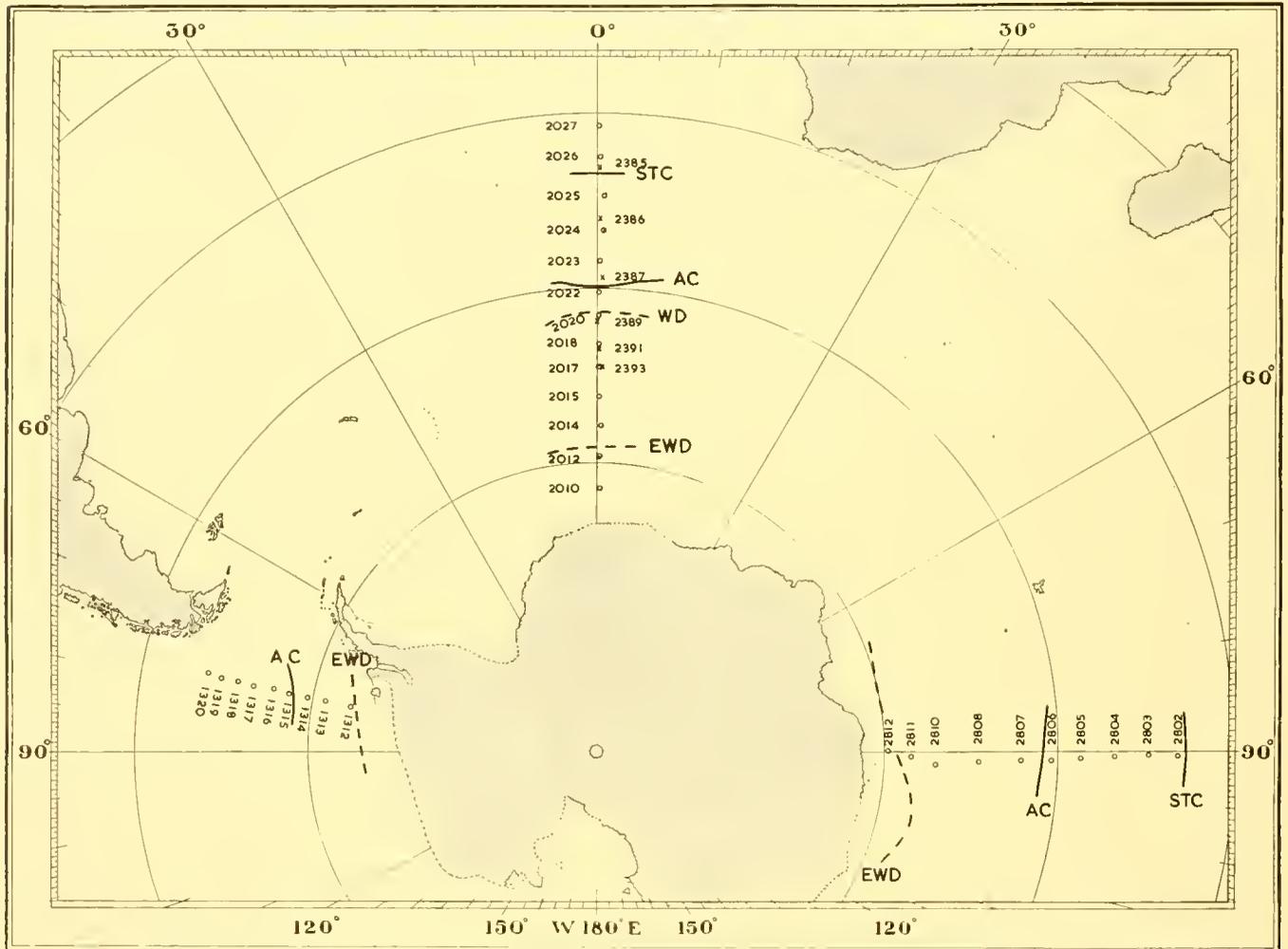


Fig. 1. The positions of the stations used for the sections (Figs. 3, 5, 7, 8, 10, 11 and 13), the positions of the convergences and the approximate northern boundaries of the Weddell and East Wind Drifts. STC=Subtropical Convergence. AC=Antarctic Convergence. WD=Weddell Drift. EWD=East Wind Drift. O=Summer Stations. X=Winter Stations.

(though none in the Pacific in that month) which could have been used for comparison, but owing to the bad weather so prevalent in the Antarctic at that time of year neither of them was complete, and a precise comparison would have been unsatisfactory. Inspection of the samples, however, shows that the winter distribution of the Chaetognatha there is quite in line with what is found in 0° .

The data used are those from the 70 cm. vertical closing nets (N 70 V) fished through horizons from 1500 m. to the surface (the horizons being 1500-1000, 1000-750, 750-500, 500-250, 250-100, 100-50 and 50-0 m.). While these nets do not sample adequately the larger zooplankton, there is no doubt that the medium- and small-sized animals are taken satisfactorily, and the advantages of having nets which have fished accurately known depths, which have been closed before being

brought to the surface, and which do not catch anything while being lowered, far outweigh the slightly erratic manner in which the larger animals are caught. In so far as the Chaetognatha are concerned it is only the large specimens of *Sagitta gazellae* and *S. maxima* which are to some extent missed by the nets, the other species being small enough to be adequately sampled.

The results, corrected to represent numbers per 250 m. haul (Mackintosh, 1937, p. 377), have been plotted by contours of density of numbers in the manner of a physical section for temperature, salinity, etc. This method of plotting has many limitations; the stations may be widely spaced and one may question the legitimacy of presuming that any population of animals is continuous over the hundred miles or so between stations. When there are small numbers of animals, this objection is probably valid; yet the consistency of the pattern of distribution shown by the sections (Figs. 3-8) is surely evidence that the method of presenting the data is not badly at fault; for if the populations consisted of randomly spread, small patches of animals, it is unlikely that such patches would be found at two or three stations in such similar numbers that they could be plotted by the contour method with the results shown, and further, even if the populations were patchy but not randomly spread, as is quite likely, then the contour section will show the area of abundance of such patches, which is, after all, what is required. One disadvantage of the use of nets, such as the N 70 V, which fish through relatively wide horizons, is brought into prominence by the use of the contour-plotting method; that is, that a haul containing a large number of two or more species has to be plotted as if both species occupied the same place in the water column, yet it is quite likely that on occasions when the net has passed through two (or more) water masses in one haul the plankton populations are as separate as the water masses themselves.

No subsampling has been done except possibly in the 80° W line where the numbers given by Mackintosh (1937) have been used. In this line, however, the northernmost stations have been re-examined for subtropical species which might have been missed in the original sorting which was done in conditions unfavourable for the careful microscopical examination required to identify, for example, very young specimens of *Sagitta serratodentata*. The fact that some of these have now been found does not in any way affect the conclusions reached in that paper.

In addition to these lines of vertical nets, consideration of other vertical and oblique net data has been necessary to describe the distribution of the rare and the exotic species which are sometimes found in the Southern Ocean but which did not happen to occur in the four lines of stations used to describe the distribution of the commoner species.

A SUMMARY OF THE SPECIES OF CHAETOGNATHA FOUND IN THE SOUTHERN OCEAN

The chaetognath fauna can be conveniently considered as composed of three elements: (i) 'endemic' species, (ii) species common to other regions which maintain themselves in the Southern Ocean, and (iii) exotic species which probably do not maintain themselves in the area but which are carried in presumably by water movements from other regions. In addition there are a few species reported by various authors as occurring in the area, but which have not been found in the extensive Discovery collections and which are probably the result of misidentification or mistakes in labelling.

I. 'ENDEMIC' SPECIES

(a) *Sagitta gazellae*

Sagitta gazellae Ritter-Zahony, 1909. *Die Chätognathen der Gazelle-expedition*. Zool. Anz. xxxiv, pp. 787-93.
S. gazellae Ritter-Zahony, 1911; Germain, 1913; Jameson, 1914; Burfield, 1930; Bollmann, 1934; David, 1955.
S. hexaptera Steinhaus, 1900; Fowler, 1907; Germain, 1913.

Sagitta innom. Fowler, 1908.

S. lyra Johnston & Taylor, 1921; Bollmann, 1934 (part); Thomson, 1947 (part).

S. maxima group Thiel, 1938 (part).

I have discussed the validity of this species in a previous report (David, 1955) and have shown that it is separate from *S. lyra* with which it has been frequently considered synonymous. In the Southern Ocean it exists in two main forms or races. One is predominantly subantarctic and the other is predominantly antarctic. These two forms can be distinguished at all stages, except perhaps at the very youngest ones. It is possible that they should be regarded as subspecifically, or even specifically distinct.

HORIZONTAL DISTRIBUTION. Circumpolar, limited in the north by the subtropical convergence, and in the south by the antarctic continental slope. Its maximum abundance is in the subantarctic.

It should be noted here that very large specimens (up to 64 mm.) of *S. lyra* have been reported by Tchindonova (1955) from the Kurile-Kamchatka trench, and from her Table 1 (p. 300) it looks as if these specimens closely resemble *S. gazellae*, especially in the tail-segment percentages (10-15.4). However, on p. 299 she records that many of these specimens had fully developed ovaries 'reaching as far as the ventral ganglion, in some cases indeed nearly to the region of the head'; it is therefore apparent that these specimens cannot be *S. gazellae*, for, at maturity stage III¹ and beyond, all the posterior teeth are lost in that species (David, 1955, pp. 243, 259), whereas the smallest number of posterior teeth in the Kurile-Kamchatka specimens is 6 (at 47 mm.). It seems unlikely that these specimens are *S. lyra* either, for the smallest number of hooks is 4-5 (at 64 mm.) and is more usually 6 or 7, whereas at maturity stages III and IV *S. lyra* has 3 or even less (Tokioka, 1939; Hamon, 1952; David, 1955). It seems probable that these specimens are *S. maxima*, despite the very small tail percentage given, for the head armature numbers fit that species well, as does the size range and the fact that *S. maxima* is found in a similar environment in the North Atlantic. Examination of the paths taken by the nerve cords from the ventral ganglion would have settled the question had the specimens been figured, for in *S. maxima* the two posterior cords run down the inner margins of the fins on the ventral side giving off branches to the fins at intervals, whereas in *S. lyra* and *S. gazellae* these cords run direct to the anterior insertion of the fins where they divide to run down the inner margins of the fins on both the ventral and dorsal sides.

(b) *Sagitta marri*

Sagitta marri David, 1956. *Sagitta planctonis and related forms*. Bull. Brit. Mus. (Nat. Hist.), Zool. iv, 8, pp. 435-51.

S. zetesios Fowler, 1907.

S. planctonis (non Steinhaus) Ritter-Zahony, 1911 (part); Jameson, 1914; Johnston & Taylor, 1921; Burfield, 1930 (part); Bollmann, 1934 (part); Mackintosh, 1937; Thiel, 1938 (part).

S. planktonis (non Steinhaus) Hardy and Gunther, 1936.

Ritter-Zahony recognized that this antarctic form differed from its close relations in warmer oceans, but, for reasons which I have discussed elsewhere (David, 1956), regarded it as an intermediate form between *S. zetesios* Fowler and *S. planctonis* Steinhaus. It is shown to be a separate species by the shape and position of the seminal vesicles, and by other anatomical features.

HORIZONTAL DISTRIBUTION. Circumpolar; its maximum abundance is in the Antarctic.

¹ Following Kramp (1939) I distinguish five stages of maturity numbered I-V for the common antarctic chaetognaths, stage I being the immature forms and stage V the spent animals. At stage III the seminal vesicles are full and the ovaries somewhat enlarged. At stage IV the ovaries are fully developed and breeding takes place. From most points of view the distinction between stages III and IV is slight, and animals in both stages may be regarded as fully mature.

(c) *Eukrohnia* sp.

E. fowleri Ritter-Zahony, 1911 (part).

This form, which was considered to be *E. fowleri* by Ritter-Zahony, appears on careful examination to be a species in its own right. The number of teeth, the absence of eye pigment, and other points separate it from *E. fowleri*. It will be described and named in a separate publication.

HORIZONTAL DISTRIBUTION. Circumpolar, northern limits not known, but it has not been found in the Discovery collections north of the subtropical convergence. It is possible that it may be found in other oceans, but it seems at present to be an endemic form.

II. SPECIES COMMON TO OTHER REGIONS

(a) *Sagitta maxima*

Sagitta maxima (Conant) 1896.

Spadella maxima Conant, 1896, Johns Hopkins Univ. Circ. 15, p. 84.

Sagitta whartoni Fowler, 1896.

S. gigantea Broch, 1906.

S. maxima Ritter-Zahony, 1911; Germain, 1913; Jameson, 1914; Huntsman, 1919; Burfield, 1930; Bollmann, 1934; Thiel, 1938 (part); Fraser, 1952.

S. lyra Michael, 1911 (part).

Doubts have been expressed about the validity of this species, notably by Michael (1911, 1919) and Thomson (1947), but it is in fact an easily recognizable form which can be differentiated from its near relatives *S. lyra* and *S. gazellae* by its greater tail-segment percentage, the position of the commencement of the anterior fins, and the position of the seminal vesicles.

The Southern Ocean form of this species is considerably smaller than its arctic counterpart (see Plate X). The latter has been reported at more than 90 mm. in length (Fraser, 1952), whereas 55 mm. appears to be the maximum length of the southern form. It can be seen from Plate X that the arctic specimen is, apart from its much greater length, a far more massive creature than the southern specimen. It seems quite possible that a careful study of these two forms would reveal, at the least, sub-specific differences between them.

HORIZONTAL DISTRIBUTION. Circumpolar in the West Wind Drift, most abundant in the subantarctic zone. It is apparently absent from the more tropical parts of the Indian Ocean, as it was not found in the two series of stations in 90° E made between 30° S and the equator, where nets were fished to 1500 m. (stations 2683-91 and 2886-96). It occurs in the Benguela Current as far north as 22° 48' S, Station W.S. 976 (Station List 'William Scoresby' 1950, 1953), and Thiel may have found it further north in the Atlantic, though his records may well have been of *S. lyra* which he failed to distinguish from *S. maxima*. In the Peru Current it occurs as far north as 04° 20.4' S, Stations W.S. 701 and 722, though three of the specimens taken in this area were far from typical of either the arctic or antarctic forms, resembling *S. lyra* in many features. Table 1 shows a comparison of the Peru Current specimens with two subarctic specimens and a series from the Southern Ocean. Whereas the arctic and Southern Ocean forms have very similar armature formulae at the same stage of maturity (though at very different lengths), the Peru Current specimens show a very considerable reduction of head armature with advancing maturity. It seems possible that a study of the Peru Current population of *S. maxima* might shed considerable light on the phylogenetic relationships of the group of chaetognaths composed of *S. lyra*, *S. gazellae*, and *S. maxima*.

(b) *Sagitta macrocephala*

Sagitta macrocephala Fowler, 1905, *The Biscayan Plankton of H.M.S. Research*. Trans. Linn. Soc. London, Ser. 2, vol. x, p. 65.

S. macrocephala Fowler, 1906; Ritter-Zahony, 1911, 1914; Germain & Joubin, 1916; Michael, 1919; Bollmann, 1934; Thiel, 1938; Tokioka, 1939; Fraser, 1952.

An easily recognized species. The antarctic specimens appear to be identical with those from other oceans.

HORIZONTAL DISTRIBUTION. Widespread in all deep oceans, circumpolar, but always in small numbers.

Table I. Comparison of the length and head armature of specimens of *S. maxima* at Stages III and IV of maturity, from the Arctic, Antarctic and Peru Current

Length	Tail segment	%	Hooks	Anterior teeth	Posterior teeth	Ovary	%	Seminal vesicles	Station no.	Depth
Arctic										
84	17	20.3	5/5	5/5	6/6	26	31.0	pres.	3227	1000-750
73	15	20.6	6/6	5/5	7/7	13	17.8	pres.	3227	1500-1000
Antarctic										
55	12	21.8	5/6	4/5	6/7	12	21.8	pres.	1729	1500-1000
46.5	11	23.7	7/6	?	6/6	19/17	41.0	pres.	2584	1500-1000
46	11	24.0	5/5	4/4	7/7	16/8	34.4	pres.	2849	1000-750
44	10	22.8	5/5	4/5	6/5	5	11.4	pres.	993	1000-750
44	11	25.0	5/5	6/6	?	7	15.9	pres.	666	1000-750
43	10.5	24.5	6/5	4/4	6/6	10	23.1	pres.	2451	1000-750
Peru Current										
38	7.5	19.7	3/3	2/2	3/3	8.5	22.5	—	WS 612	1000-750
35	8	22.8	3/4	2/2	2/1	15.5	44.5	—	WS 701	1000-750
35	8	22.8	3/3	2/2	3/1	5	14.3	—	WS 606	1000-750

(c) *Eukrohnia hamata*

Eukrohnia hamata (Möbius), 1875.

*E. hamata*¹ Ritter-Zahony, 1909, 1911; Jameson, 1914; Johnston & Taylor, 1921; Burfield, 1930; Bollmann, 1934;

Hardy & Gunther, 1936; Mackintosh, 1937; Thiel, 1938; Ghirardelli, 1953.

Spadella hamata Grassi, 1883; Fowler, 1896.

Krohnia foliacea Aida, 1897.

K. hamata + *K. hamata* var. *borealis* Moltschanoff, 1907.

K. hamata Hertwig, 1880; Langerhans, 1880; Conant, 1896; Krumbach, 1903; Fowler, 1905, 1906.

This well-known species exhibits a great deal of variation in size. In the Southern Ocean there are two clearly defined races more or less separated by the antarctic convergence; and the specimens from subtropical waters seem to belong to a smaller race also. *E. hamata* var. *antarctica* Johnston & Taylor is the spent form which seems able to live for a while after spawning.

HORIZONTAL DISTRIBUTION. Cosmopolitan in the deep oceans, circumpolar, maximum abundance (in the Southern Ocean) in the vicinity of the antarctic convergence.

(d) *Heterokrohnia mirabilis*

Heterokrohnia mirabilis Ritter-Zahony, 1911, *Revision der Chaetognathen*. Deutsche Sudpolar Exped. Bd. XIII (5), p. 42.

H. mirabilis Tchindonova, 1955.

¹ Only those authors who have examined antarctic material have been included in the synonymy under *E. hamata*.

This remarkable species was first described from eight specimens in the Gauss collections which were taken in deep hauls (3423–2000 m.) from far south in the antarctic zone. Only one further specimen has been reported, that found by the Russian expedition to the Kuriles trench which was taken between 5000 m. and the surface (Tchindonova, 1955). The specimen reported as *H. mirabilis* by Jameson (1914) seems, from its head armature, to have been a damaged specimen of *E. hamata*.

Two specimens have been found in Discovery collections (Station 661, 3000–2000 m.), but neither of them is in good enough condition to determine the precise shape of the fins, and it seems worth while considering whether these specimens could be distorted examples of some better-known form. The presence of transverse musculature on the tail segment was regarded by Ritter-Zahony as a point of great importance ('the tail has no homologue in any hitherto known chaetognaths'), but Tokioka (1952, p. 312), referring to *Zahonyia cestoda* van Oye (an enigmatic deep-living chaetognath), remarks: 'It is a noteworthy fact that some species with strongly developed musculature assume an appearance when they are in a strongly contracted state, as if they were provided with a transverse musculature along the whole body.' This appearance can occasionally be observed in specimens of *E. hamata*. The Discovery specimens of *H. mirabilis* do show transverse musculature in the tail, but they do not appear to be at all strongly contracted. The number of anterior teeth in this species (see Table 2) is strikingly large in comparison with other antarctic deep-water forms (15, as compared with 10 in *S. macrocephala*, and 8 in *S. marri*), and, as Ritter-Zahony has pointed out, only *S. helenae* (a tropical epiplanktonic species) has comparable numbers. Ritter-Zahony records that the gut of the largest of his specimens was brick red when fresh, and although the colour has faded from the Discovery specimens the appearance of the gut is the same as that in specimens of *S. macrocephala* and *E. fowleri*, both of which have a red gut when fresh.

Ritter-Zahony was unable to find any eyes in his specimens, and both Discovery specimens are also apparently without eyes. Neither of the Discovery specimens has ripe seminal vesicles, but the smaller animal has rudiments of them in the same position as those figured by Ritter-Zahony in his fig. 46. From the tail-segment percentage and general appearance the most likely species which could be confused with *H. mirabilis* is *S. macrocephala*, but the vestibular organ in these two species is quite different, being quite smooth in *H. mirabilis* (see Fig. 2) and distinctly papillated in *S. macrocephala*, and although Ritter-Zahony stated that in young specimens of *H. mirabilis* small papillae were present, they are present in *S. macrocephala* at all sizes. Ritter-Zahony did not record *S. macrocephala* from the Antarctic, yet it is not an uncommon species in the Discovery collections and this would lead one to suspect that *H. mirabilis* was indeed a damaged specimen of that species. Nevertheless, bearing all these possibilities in mind I am convinced that *H. mirabilis* is a valid species, though I feel that really perfect specimens might show that it should belong to the genus *Sagitta*.

HORIZONTAL DISTRIBUTION. Antarctic, between 64° 29' S—65° 18' S and 80° 00' E—85° 27' E (Gauss), Discovery Station 661, 57° 36' S 29° 54' W. North Pacific.

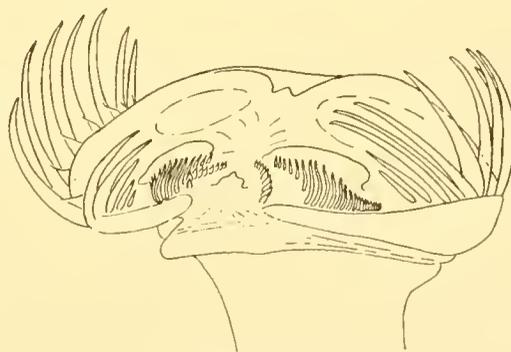


Fig. 2. The head of *H. mirabilis* seen from an antero-dorsal direction.

III. EXOTIC SPECIES

This group is composed of seven species which will not be discussed in detail as they are all subtropical or tropical forms which almost certainly do not maintain themselves in the Southern Ocean.

(a) *Sagitta hexaptera* (d'Orbigny)

A widespread species in subtropical and tropical seas with a considerable tolerance for the colder parts of those areas; mainly an inhabitant of the surface 100 m.

(b) *Sagitta lyra* (Krohn)

A widespread species in subtropical and tropical seas, having a slightly greater tolerance than *S. hexaptera* to cold water. Normally an inhabitant of the water layers below 100 m. though infrequent below 500 m.

(c) *Sagitta decipiens* (Fowler)

A widely distributed form typical of the water layers below 100 m. in the tropics and subtropics.

Table 2. *Length and head armature of all specimens of H. mirabilis so far reported*

Length	Tail %	Hooks	Anterior teeth	Posterior teeth	Depth (m.)		
19	32.7	11/11	14/15	33/?	3423	Ritter-Zahony, 1911	
18.6	32.3	10/9	15/15	29/30	3000		
12	33.3	?/10	10/11	25/?	3000		
10	35	11/11	?/5	6/6	3000		
10	35	—	—	—	2000		
9.4	40	9/9	—	1/1	3000		
9	35.5	8/9	?/4	2/1	3000		
8	37.5	9/9	4/4	1/1	3000		
36	44.4	14/14	13/13	14/16	5000-0		Tchindonova, 1955
33	39.5	11/12	10/9	29/22	3000-2000		Discovery collections
10.2	36.3	8/8	3/?	1/1	3000-2000		

(d) *Sagitta minima* (Conant)

The distribution of this species is not at all well known, but it is common in the subtropics of the southern hemisphere.

(e) *Sagitta serratodentata* Krohn

A very widely distributed form which exhibits considerable, possibly specific, variation. The most cold-tolerant of the exotic species considered here, it normally inhabits the surface water.

(f) *Sagitta zetesios* Fowler.

An inhabitant of deep water, usually below 750 m., in tropical and subtropical waters.

(g) *Krohmitta subtilis* (Grassi)

This is a common subtropical species usually in the 250-100 m. layer, but it is occasionally found in surface hauls.

(h) *Pterosagitta draco* (Krohn)

A common surface form in warm latitudes.

None of these species is common in the Southern Ocean, but all have been found, usually as single specimens but occasionally as several together, at some time in the Discovery collections made south of the subtropical convergence. None of these species has been found in Discovery collections made south of the antarctic convergence, and usually they are not found more than two or three degrees south of the subtropical convergence. Previous authors have recorded some of them in the Antarctic

and in view of the absence of Discovery records to confirm them it seems probable that most of these anomalous records can be regarded as misidentifications of badly preserved material. For example, *S. hexaptera* has been reported from the Antarctic by Fowler (1907), Ritter-Zahony (1911), Germain (1913), and Johnston & Taylor (1921). In all these cases, except that of Ritter-Zahony, confusion with specimens of *S. gazellae* on which the fins were damaged seems to be the most likely explanation; after 1921 the same confusion does not seem to have arisen, although, surprisingly enough, very recently three large specimens of *S. hexaptera* were reported from the Mediterranean as specimens of *S. gazellae* (Furnestin, 1953, 1955). In the case of Ritter-Zahony (1911) there can be little doubt that the specimens reputedly from $66^{\circ} 2' S 89^{\circ} 38' E$ were *S. hexaptera*, since he was very familiar with that species and with *S. gazellae*, but it is significant that in the same haul he found *K. subtilis*, another subtropical species, and it is possible that there may have been confusion with a haul made on the same date (22nd November) in 1901 (not 1902 as reported) when the ship's noon position was $34^{\circ} 9' S 17^{\circ} 26' E$ in the vicinity of Cape Town where one would expect to find these two subtropical species. *S. serratodentata* has been reported by Burfield (1930) from the Ross Sea. Only one specimen was taken, and the only explanation I can suggest is contamination from a more northerly sample. It is quite easy for a specimen to be caught inside the lid of a sample jar and the lid to be put on to another jar, or for a single specimen to be left under the rim of a petri dish while sorting. Several authors have recorded the species from the northern part of the Subantarctic where its presence can be confirmed by Discovery records.

IV. DOUBTFUL SPECIES

S. neglecta. This tropical species was reported by Johnston & Taylor (1921) from $64^{\circ} 34' S 117^{\circ} 1' E$, and must be regarded as a case of mistaken identification. The species is rare even in subtropical waters and certainly does not occur in Discovery collections from the Southern Ocean.

VERTICAL DISTRIBUTION

The vertical distribution of the relative density of the populations of chaetognaths is shown in Figs. 3, 5, 7, 8, 10, 11, 12 and 13 on three lines of stations, one in the Atlantic sector (meridian of 0°), one in the Indian Ocean sector (meridian of $90^{\circ} E$) and one in the Pacific Ocean sector (meridian of $80^{\circ} W$).

Before comparing the results from these sections it is necessary to indicate that there are certain obvious physical differences involved. The line in $90^{\circ} E$ is perhaps the most simple; it is relatively long and the subantarctic zone extends from about $40^{\circ} S$ to about $52^{\circ} S$, both convergences being rather indistinct. The antarctic zone was accessible from about $52^{\circ} S$ to the ice edge in $65^{\circ} S$. Only Station 2812 in this line is within the area of the East Wind Drift. The line in 0° is rather longer than that in $90^{\circ} E$, and it has some rather peculiar physical characteristics. The subantarctic zone extends from a fairly sharp subtropical convergence in $39^{\circ} S$ to a rather diffuse antarctic convergence in about $50^{\circ} S$. The antarctic zone was accessible thence to nearly $70^{\circ} S$. This zone is, however, complicated by the presence of the Weddell Drift, a broad tongue of cold water originating in the Weddell Sea and deflected by the coast of Grahamland in a north and easterly direction. Deacon (1936) shows its northern limit to be in about $52^{\circ} S$ in 0° and its southern boundary is probably in about $61^{\circ} S$, though it is difficult to define accurately, and both limits indeed are no doubt to be taken as tentative and subject to variation. Stations 2010 and probably 2012 lie within the influence of the East Wind Drift, and it is possible that there may be swirls or eddies between the East Wind Drift and the Weddell Current (Marr, personal communication). The line in $80^{\circ} W$ is the shortest of the three, and the surface isotherms show that considerable north/south compression of the water masses takes place in this area. The width of the subantarctic zone is not known, since the position of the subtropical convergence has

never been determined in that part of the eastern Pacific. The presence of a few specimens of *S. serratodentata* at the northernmost station of the line (1320) suggests that the subtropical convergence might be within 200 miles or so of that position, for the species is found elsewhere in the subantarctic only within that distance of the subtropical convergence. The isotherms off the coast of southern Chile run parallel to the coast (Gunther, 1936) and this suggests that there may be a southward loop of the convergence lying from about 45° S 90° W to about 53° S 80° W and thence northward in the meridian of about 77° W (see Fig. 1), but there is no hydrological information other than that mentioned to back up this view. In 80° W the subantarctic zone extends to a fairly sharp convergence in $63^{\circ} 30'$ S and the antarctic zone was accessible thence to $68^{\circ} 18'$ S.

In view of the differing length of the three lines, the antarctic convergence has been used as a point of reference in the diagrams.

For making the sections shown in Figs 3, 5, 7, 8, 10, 11, 13 the data given in Tables 4 a-c (p. 225) were used. The contours adopted indicate the following quantities in terms of numbers per 250 m. haul:

	Summer	Winter
<i>S. gazellae</i>	1-5-10-20-40	1-5-10-20
<i>S. marri</i>	5-10-20	1-5
<i>S. maxima</i>	4-10-30	1-5-10
<i>S. serratodentata</i>	2-20-400	
<i>S. decipiens</i>	1-10-20	
<i>E. hamata</i>	1-20-100-200	1-15-50-100

It will be seen that the contours are not the same for all the species, and this is due to the very large differences in total numbers of the species present. Originally the contours were chosen by a simple progression, e.g. 5-10-20-40, but it was found that in certain species strict adherence to this method produced rather confused-looking sections, and a certain amount of allowance had to be made. In *S. maxima* and *S. marri*, for example, it was not felt necessary to indicate occasional stray specimens obviously separated from the main population, and as a result the contours for these two species begin at 4 and 5 respectively. In *S. maxima*, examination of the data showed that contours at 20 and at 40 would be an additional complication which would show nothing more than a single contour at 30. It should perhaps be pointed out that more contours tend to emphasize the separateness of the species shown in the maximum density sections in Fig. 12, but the extra amount of lines and shading tend to make the figures look confused. *S. serratodentata* has a relatively compact population and when it is present in large numbers they are really large, e.g. 620 and 715 for single hauls in 0° and 90° E, and it was not thought necessary to indicate any more than the contours given. *S. decipiens* also shows a similar compactness with smaller numbers. *E. hamata* is often present in large numbers, and it was not thought that contours between 20 and 100 would show anything better than the two at those densities.

For the winter sections where the numbers of all species were lower, lower contours were used and these have followed the simple progression except in the case of *E. hamata*, where again the intermediate contours seemed to be unnecessary.

S. gazellae (Fig. 3). The northern limit of the species is shown to be just north of the subtropical convergence in 0° at a depth of 200 m. and probably it is at a similar point in 90° E though at less depth, but in this line there is no negative station north of 2802 to prove it, though there is little doubt that the northern limit is near the convergence (David, 1955). In 80° W it is evident that the species extends well north beyond Station 1320 which is well south of the subtropical convergence. The southern limit in 0° is probably just at the continental slope, though there is not a negative station at the southern end of this line. In 90° E the species does not extend nearly so far south but ceases in

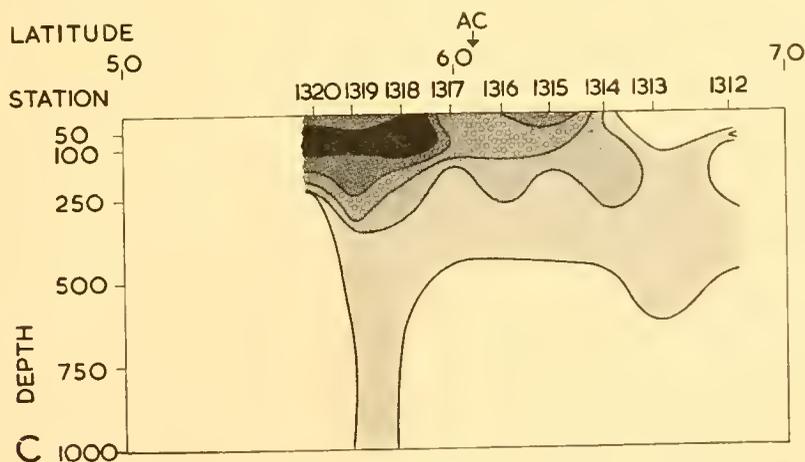
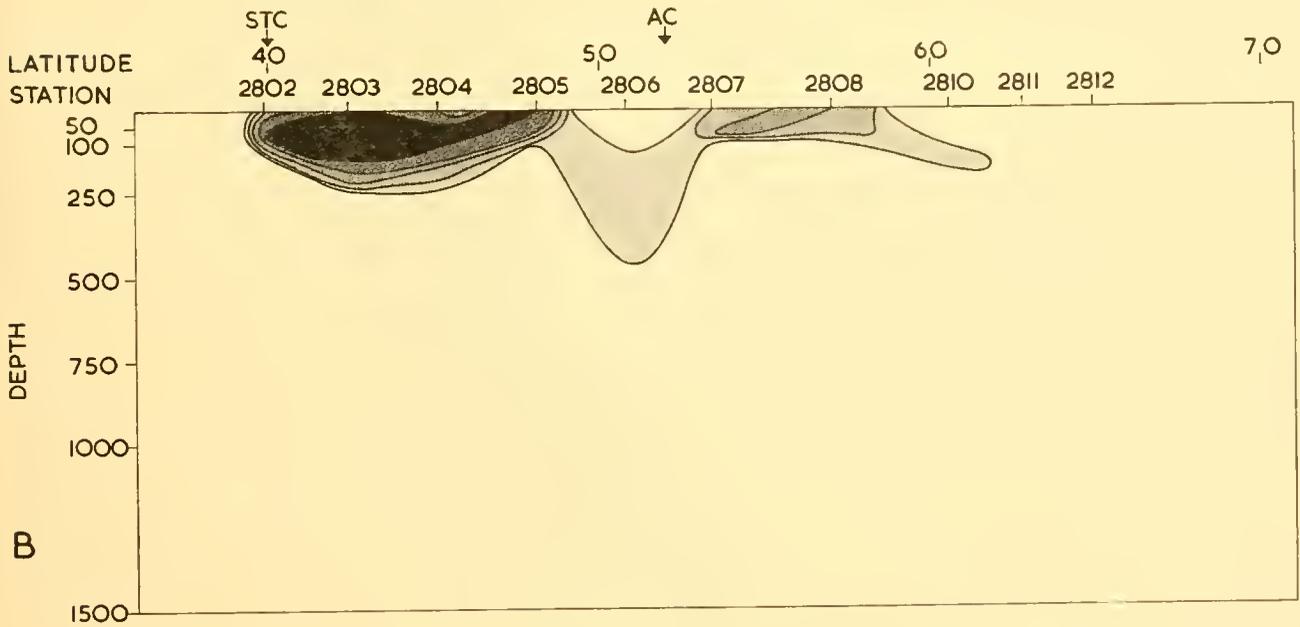
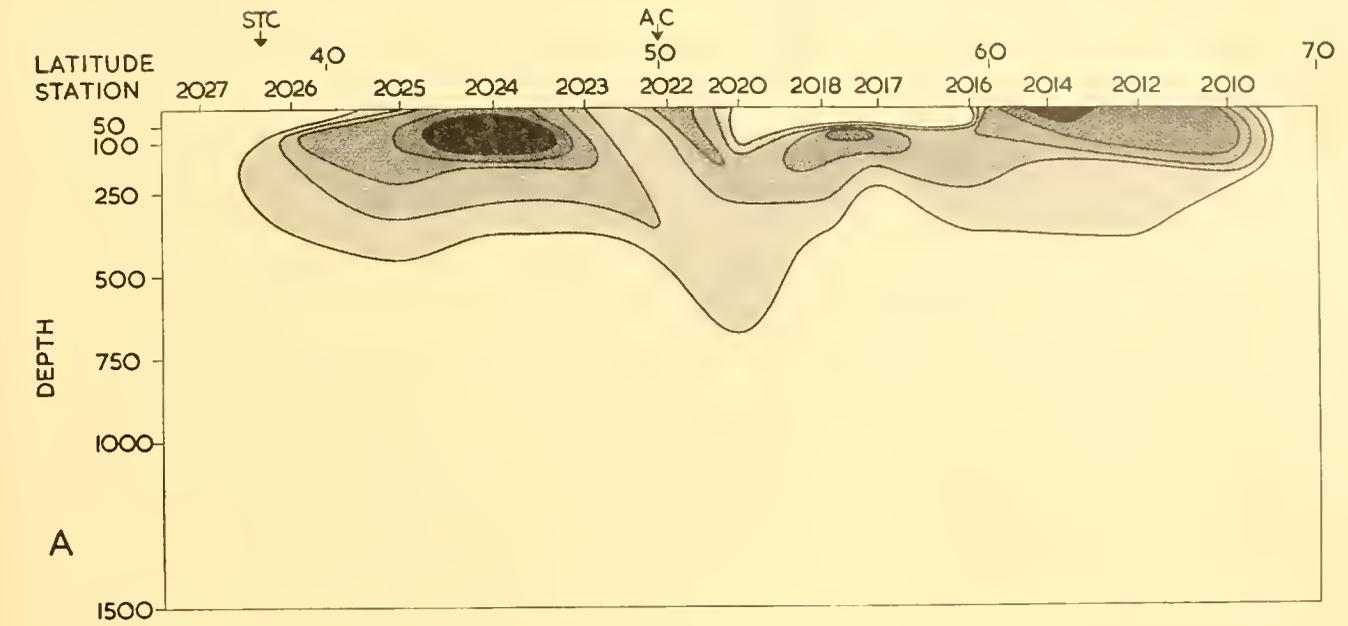


Fig. 3. The vertical distribution in summer of *S. gazellae* in 0° (A), 90° E (B) and 80° W (C). For the numbers taken in each net see tables 4 a-c (p. 225).

62° S some 180 miles short of the ice edge (Station 2812). In 80° W the species extends, in small numbers at least, right to the ice edge (Station 1312). In all the sections for the summer months it can be seen that this species is not common below 250 m. but Table 4 shows that it does extend in small numbers to 1000 m. In each section there is an extension into deeper water in the region of the antarctic convergence, and the same phenomenon has been noticed in other sections not figured here. It may be due to the sinking of the surface waters in this region.

The main concentration of the species in each line is in the subantarctic, but in 0° there is another concentration south of 60° which is not paralleled in either 90° E or 80° W, though there is a lesser concentration in about 55° S in 90° E and in 63–64° S in 80° W, which is probably comparable with a small concentration between 100 and 50 m. in 55–56° S in 0°. Possibly the presence of the Weddell Current in 0° prevents this concentration from being a surface one as are those in 90° E and 80° W. It seems likely that the large antarctic concentration in 0° is a feature unique to that particular area and it is tentatively suggested that its presence is in some way caused by the eddies or swirls between the East Wind and Weddell Drifts which have been already mentioned (p. 209).

Fig. 4 shows the catches of *S. gazellae* in 0° plotted against temperature and salinity and indicates how wide a tolerance the species has, though it can be seen that the largest concentrations are restricted to a narrow range of salinity. The concentrations above 20 per 250 m. haul are found between 33.94 and 34.46‰ with a temperature range of -0.18° to 11°.

Much of this information, together with further details, is given in a separate paper on *S. gazellae* (David, 1955).

S. marri (Fig. 5). The northern limit of this species is rather variable, since occasional specimens get carried north by the antarctic intermediate water, but the northern limits of the main concentrations are clearly south of the antarctic convergence. The southern limit appears to be the antarctic continental slope. From the three sections shown, the extreme northern limits are found to be 43½° S in 0°, 48° S in 90° E and 63½° S in 80° W. This wide latitudinal difference is explicable partly by variations in the latitude of the antarctic convergence, and partly by the exceptional absence of any considerable numbers of the species in the subantarctic in the 80° W line. It will be seen that the northernmost part of the main concentration in each line is 180 miles from the convergence in 80° W, 240 miles from it in 90° E, and 330 miles from it in 0°. The species is commonest between 200 and 600 m. but extends in smaller numbers to 1500 m. and occasionally more. The subantarctic specimens are never found in the surface layers, that is above 150 m., but they may extend to 1500 m. though always in small numbers. In the Antarctic the species is not at all uncommon in the surface 100 m., that is, in the antarctic surface water, but this shows only in one of the vertical sections, that in 80° W. However, Baker (1955) records *S. planctonis* (= *S. marri*) in 39% of the N 100 B nets fished in the antarctic surface layers.

The main concentrations of *S. marri* are in the warm deep water, as reference to the temperature/

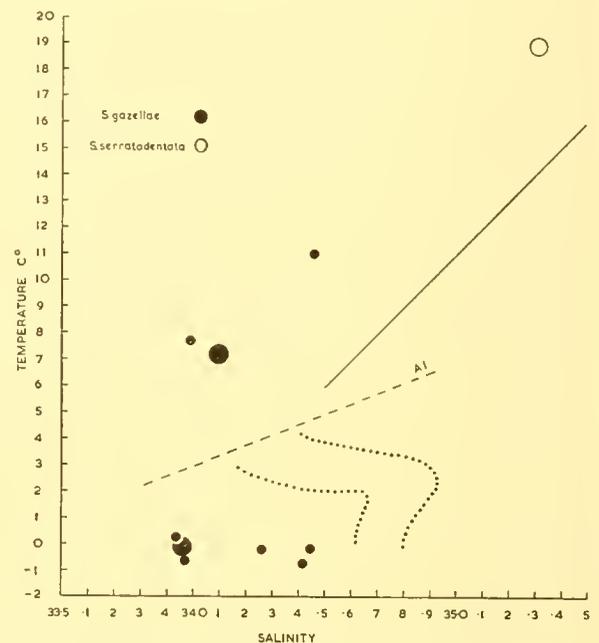


Fig. 4. The relative distribution of the two highest orders of abundance of *S. gazellae* and *S. serratodentata* in the 0° meridian in March plotted against temperature and salinity. The line A1 represents the core of the antarctic intermediate water, the two broken lines the approximate boundaries of the warm deep water, and the solid line the core of the South Atlantic central water.

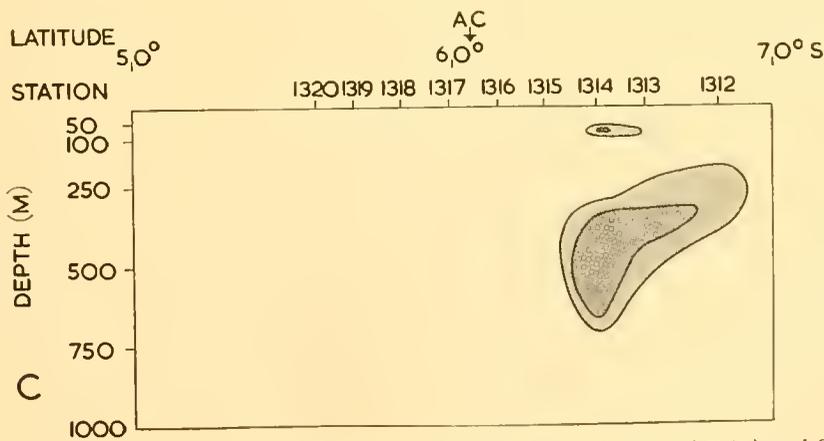
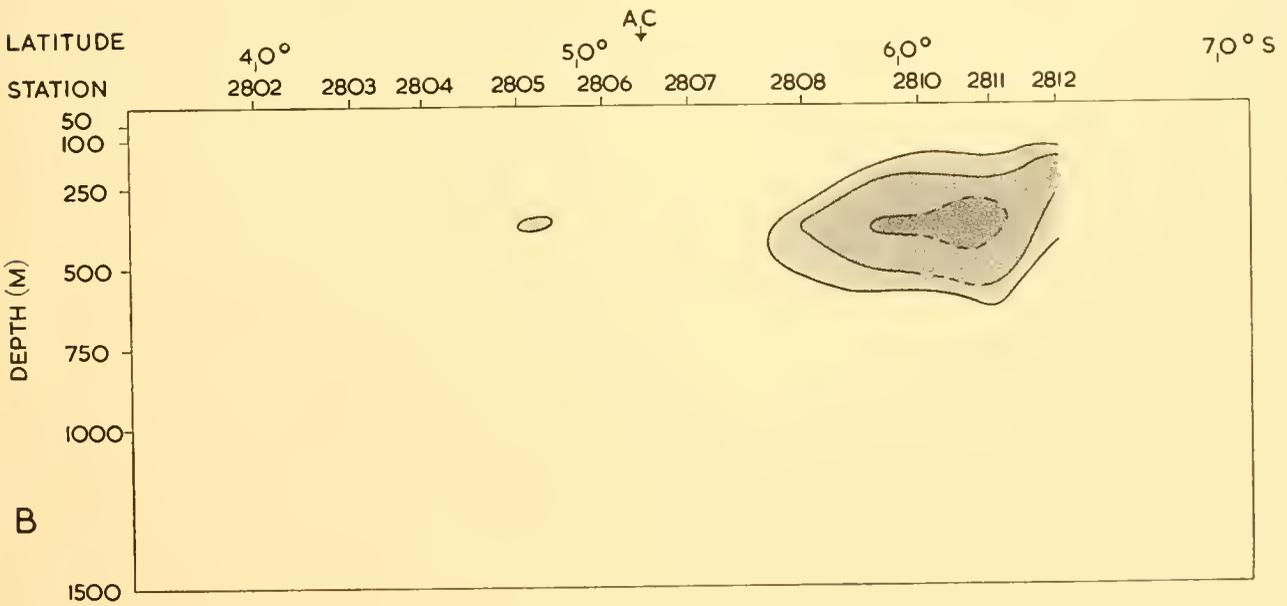
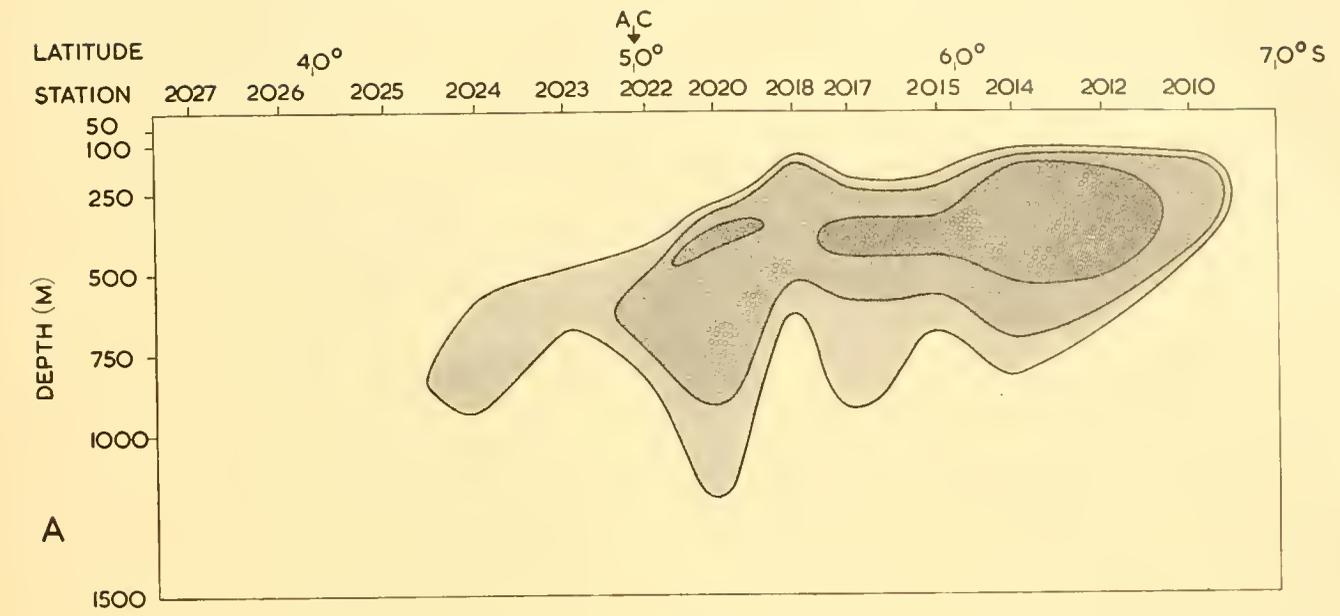


Fig. 5. The vertical distribution of *S. marri* in 0° (A), 90° E (B) and 80° W (C).
 For numbers taken in each net see tables 4 a-c (p. 225).

salinity diagram (Fig. 6) shows. The very narrow tolerance range of the maximum concentrations of the species, 34.67–34.71 ‰ and 0.1 to 1° C, suggests a restricted distribution, but within these limits is a very large mass of water, and the section in 0° (Fig. 6) shows indirectly how extensive this water mass is. The temperature/salinity diagram also shows clearly how parts of the population are 'lost' by being carried north to the antarctic intermediate water. These 'sterile expatriates' (Ekman, 1953) are probably lost mainly by the movement of the antarctic surface water at the convergence where it sinks to form the intermediate layer.

The numbers in each line vary greatly, those in 0° being much higher than in the other two lines. In 90° E the 500–250 m. sample at Station 2811 was spilt during sorting aboard ship, and a large part of it was lost. It would evidently have been a key sample, and the contours from the other samples suggest that there would have been quite a large concentration there. I have indicated this by a dotted line in Fig. 5B.

S. marri is perhaps the most characteristic antarctic chaetognath of all, for although it lives in a water mass whose origins are found in the subtropics of the southern hemisphere, it only inhabits it when mixing and cooling have reduced it to the very precise conditions of temperature and salinity found in the warm deep water of the antarctic zone.

Eukrohnia sp. This species occurs very sparsely in the vertical sections, always below 1000 m. Its northern and southern limits are not yet known. It occurs in the antarctic zone as the commonest chaetognath below 1500 m.

S. maxima (Fig. 7). This species is the subantarctic counterpart of *S. marri*. Its northern limit appears to be just within the subtropical zone at a depth of about 500 m., though it must extend considerably further north in some places as it has been found in both the Peru and Benguela currents. In the main, however, it is characteristically a subantarctic species. Its southern limit is usually not far south of the antarctic convergence, but it occurs in small numbers further south than this; in 80° W, for example, it occurs to the ice edge. These southerly records must be regarded as losses of population such as occur in *S. marri* to the north of its normal habitat, and in the case of *S. maxima* are probably due to mixing of the antarctic intermediate water with the warm deep water in the vicinity of the convergence.

The species is most numerous between 150 and 500 m. but extends in smaller numbers to 1500 m. It occurs very exceptionally in the subantarctic surface waters, but apparently never in the antarctic surface waters.

The main concentration of *S. maxima* is in the antarctic intermediate water, as reference to the temperature/salinity diagram (Fig. 6) shows, but it is also found on either side of this water mass. The salinity range for the larger concentrations is from 33.98 to 34.5 ‰ and the temperature range is from 0.3 to 7.3° C, a much wider tolerance than that of *S. marri*, reflecting perhaps the more varied conditions found in the moderate depths in the subantarctic zone.

The sections (Fig. 7) show that in 80° W the species extends in considerable numbers south of the antarctic convergence, while the other lines show the main concentrations ceasing well to the north

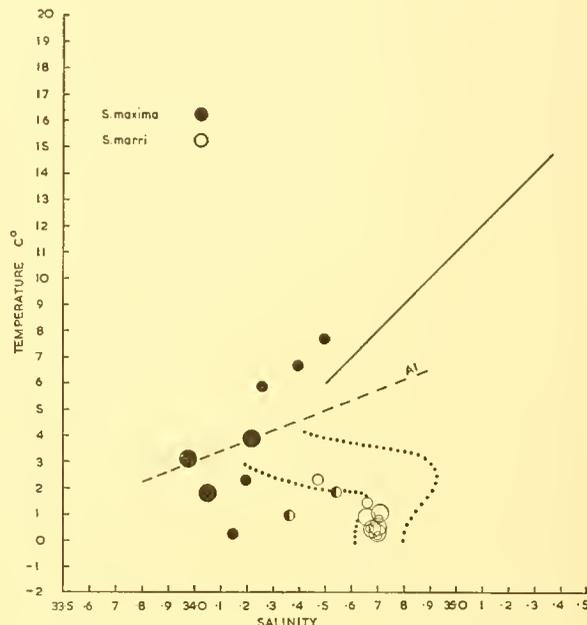


Fig. 6. The relative distribution of the two highest orders of abundance of *S. marri* and *S. maxima* in the 0° meridian in March, plotted against temperature and salinity. For explanation of the lines on the figure see legend to Fig. 4.

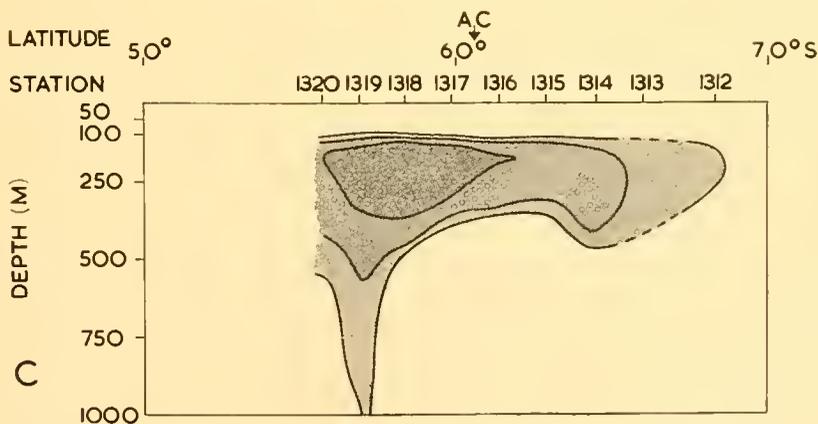
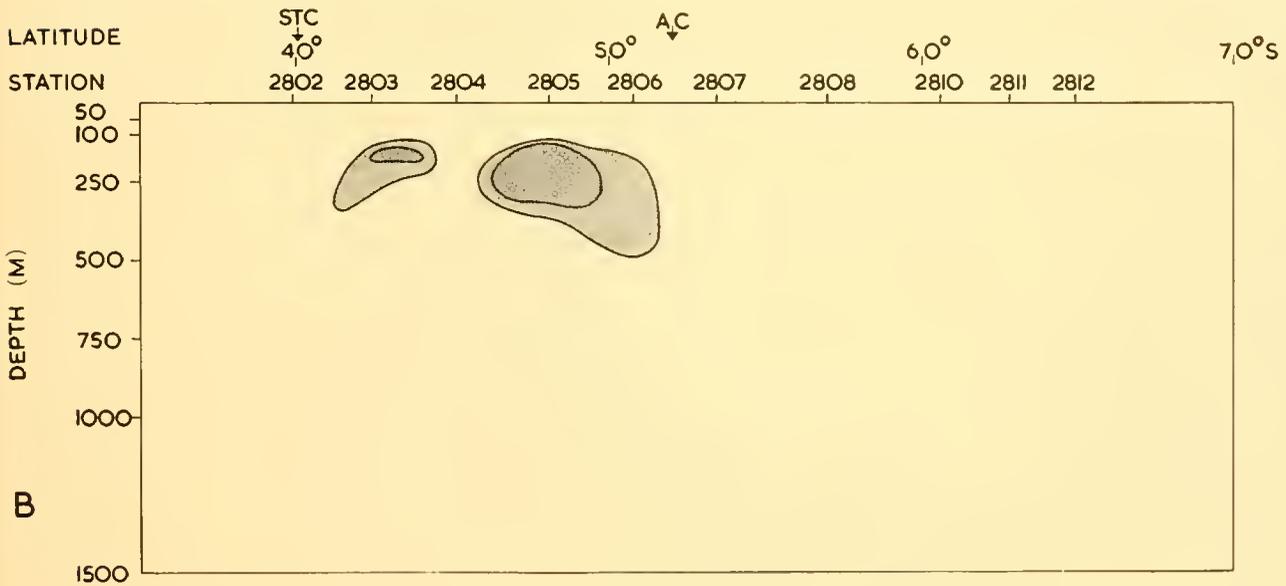
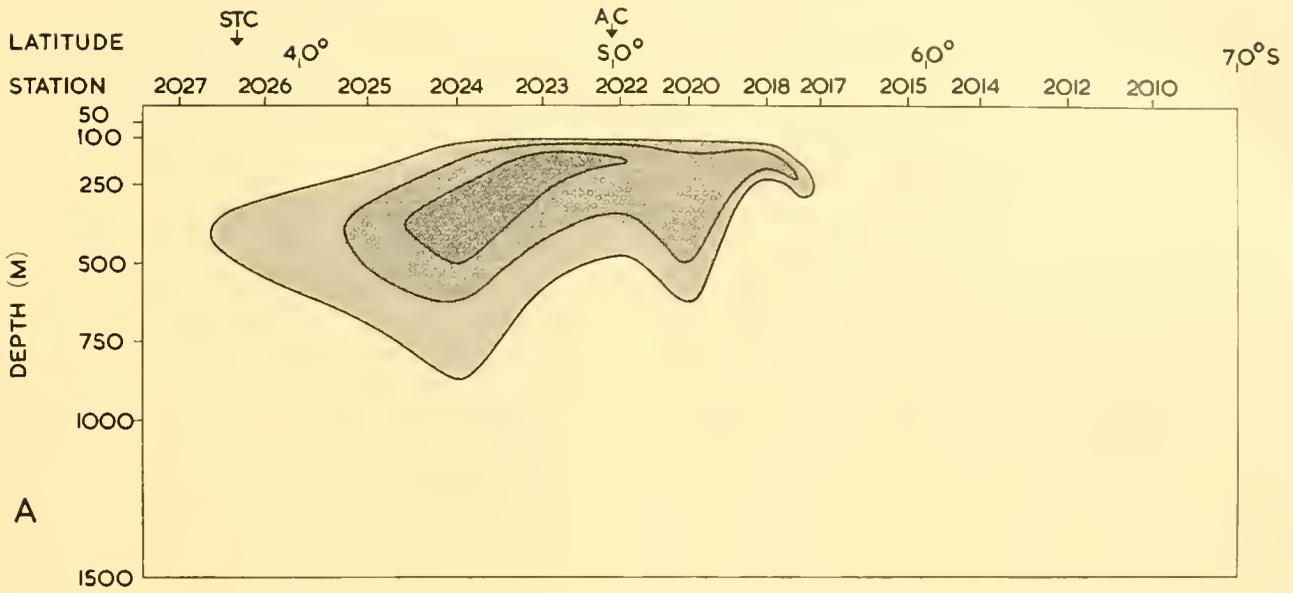


Fig. 7. The vertical distribution of *S. maxima* in 0° (A), 90° E (B) and 80° W (C).
For numbers taken in each net see tables 4 a-c (p. 225).

of the convergence. The numbers vary considerably, those in 80° W being very much higher than those in 0° , while those in 90° E were very small indeed. It will be seen that the population in 90° E appears to be split into two parts, but it is doubtful if this is of any great significance as the numbers are relatively small, and if the species is patchy in distribution then the net at Station 2804, 250–100 m. may have missed the patch which would have linked the populations.

Table 3. *The occurrence of S. macrocephala in the lines of stations 0° , 90° E and 80° W*

Line	Station	Depth	Number of specimens
0°	2022	1500–1000	1
	2025	1000–750	2
90° E	2802	1000–750	1
		1500–1000	1
	2803	1000–750	2
		1500–1000	1
	2804	1000–750	3
80° W	2806	1500–1000	1
	—	—	—

S. macrocephala. This species does not occur in numbers suitable for giving a contoured section, but in the lines under consideration it occurred at the stations shown in Table 3. It was not recorded from 80° W (possibly it was not recognized), but it has been taken by 'Discovery II' in the Western Pacific (Stations 2736, 2738, 2825, 2826) and from the South Atlantic sector (Stations 1771, 1772, 1773, 1775, 1776, 1777, 1805, 1807, 1808), so it seems likely that it also occurs in the Eastern Pacific. The species occurs in the tropics and subtropics and extends to the region of the West Wind Drift, though it is never present except in very small numbers in the Southern Ocean. It is rather more frequent in the Subantarctic than in the Antarctic.

The shallowest depth horizon at which it has been taken is 750–500 m., but this is exceptional. Johnston & Taylor recorded two specimens from a depth of 100 fms. ($64^{\circ} 34' S$ $117^{\circ} 1' E$), but this must be regarded as a mistake in identification as no other specimens have been taken at such a shallow depth. The species has been taken in nets down to 2400 m. but even in large (2 m.) nets at depths below 1000 m. the numbers caught have been very small, and one must conclude that it is an uncommon form in the Southern Ocean.

E. hamata (Fig. 8). It is not possible to define the northern limits of the distribution of this species, as it is one of the classic examples of bipolar distribution with tropical submergence. Its southern limit is the Antarctic continent. Its upper limit in the Southern Ocean is the surface, though immediately north of the subtropical convergence it is only found in deeper water. Its lower limit is below 1500 m. though it becomes less frequent in deeper water than it is in the top 500 m.

This species is by far the most abundant chaetognath in the Southern Ocean, and in all three sections it is very numerous. The section in 80° W, however, shows the greatest numbers with as many as 1275 specimens per 250 m. haul. The numbers in 0° are slightly less and those in 90° E least of all.

If this disparity in numbers is considered then it can be seen from fig. 8 that the pattern of distribution is essentially similar in all three lines. The maximum concentrations in each line are in the top 500 m, and the species is abundant to this depth in both the subantarctic and antarctic zones. The numbers decrease sharply at the subtropical convergence in 0° , and, although this decrease is not evident from fig. 8 B, in 90° E the actual numbers taken (see Table 4b, p. 227) fall off considerably at Station 2802 which was evidently just south of the convergence in that meridian. There is no fall off in numbers evident in 80° W but then the northernmost Station (1320) was probably 200 miles or more south of the convergence.

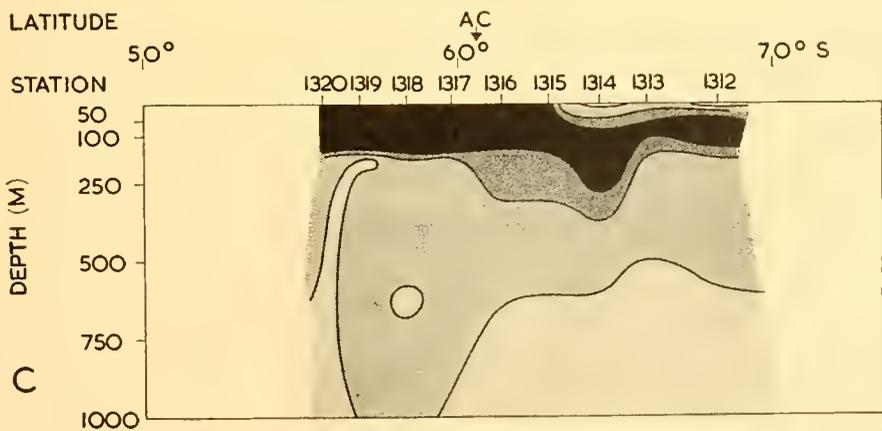
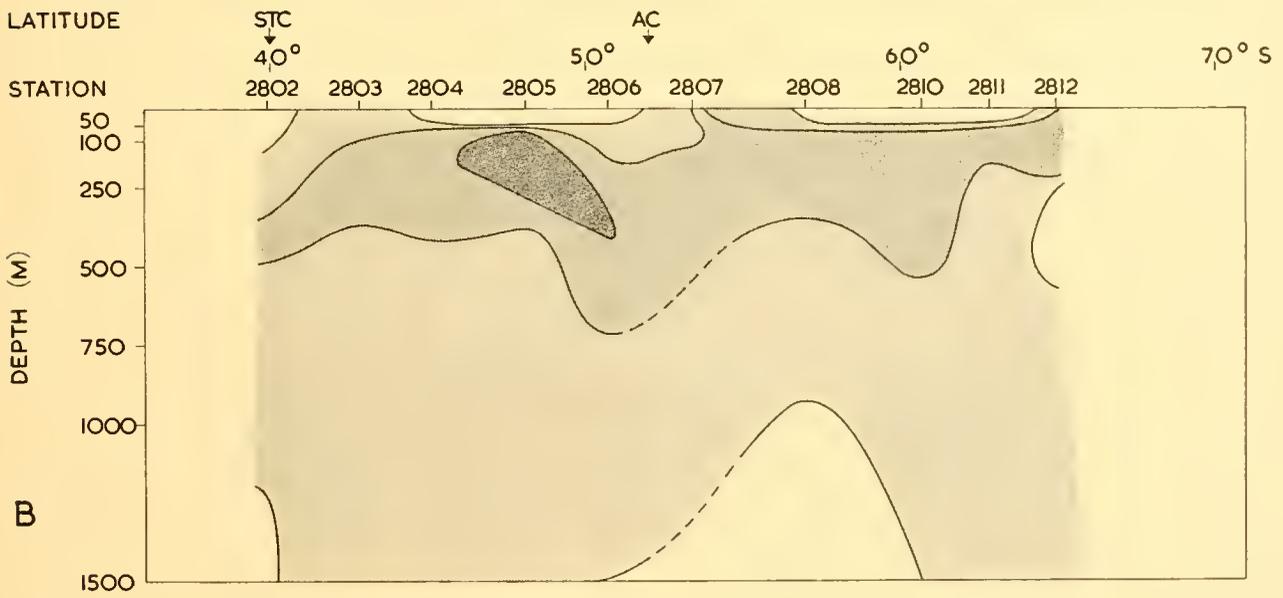
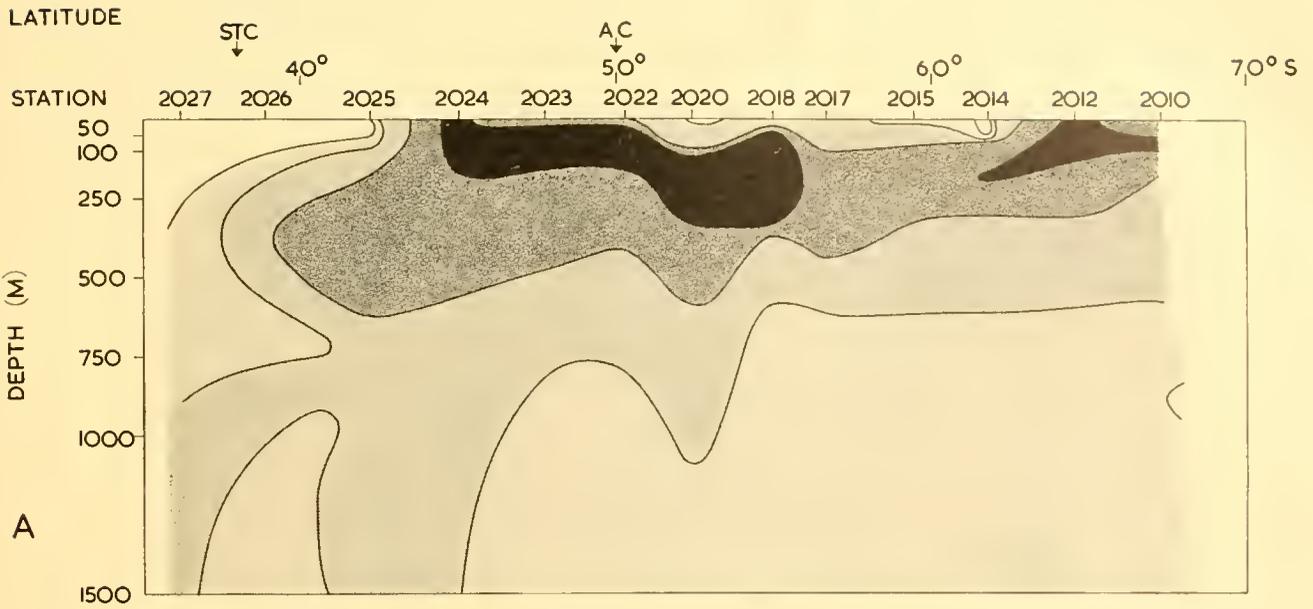


Fig. 8. The vertical distribution of *E. hamata* in 0° (A), 90° E (B) and 80° W (C).
For the numbers taken in each net see tables 4 a-c (p. 225).

The temperature/salinity diagram (Fig. 9) shows that *E. hamata* can tolerate a wide range of temperature and salinity, as would be expected from such a cosmopolitan species. Nevertheless, I believe this wide degree of tolerance is more apparent than real, for in the Southern Ocean there are two forms or races of *E. hamata* analogous to the small northern and large southern races of *S. gazellae*, and I think that a careful study of the populations of *E. hamata* in the subtropics and tropics would show that there also the species consists of several ecologically separate races, all of which would be found to have much more precise physical and chemical requirements than would appear at present.

In unpublished informal reports Mr J. W. S. Marr, who made observations on this species for many years, has shown that mixing of the two Southern Ocean forms occurs seldom, but that where it does occur, as for example in the Falkland Island sector of the Antarctic, the mixing is indicative of similar mixing of the surface waters, and that the numbers of the 'foreign' race fall off sharply on each side of the convergence, showing that each race is intolerant of physical conditions on the 'other' side of the convergence. The variation, distribution and life history of *E. hamata* in the Southern Ocean might well form the substance for a separate report on its own and may one day be thus treated.

S. serratodentata and *S. decipiens*. In the addition to the typical Southern Ocean species whose distribution is dealt with above there are two subtropical species, *S. decipiens* and *S. serratodentata* which occur in sufficient numbers south of the subtropical convergence to justify the sections shown in Figs. 10 and 11. *S. serratodentata* (Fig. 10) is often very numerous but almost completely restricted to the surface layers. *S. decipiens* (Fig. 11) is usually only present in smaller numbers and is restricted, at least in its main concentrations to the 500–250 m layer. Neither species extends more than 200 or 300 miles south of the Subtropical convergence.

H. mirabilis. This species does not figure on the vertical sections and there is little to add to Ritter-Zahony's description of its distribution. It is found below 2000 m., and in the Antarctic it probably inhabits the cold bottom water.

THE SEGREGATION OF SPECIES

In Fig. 12 the summer distribution of all the common southern chaetognath species is indicated. Inspection of Figs. 3, 5, 7, 8, 10 and 11 shows that the ranges of most of the species overlap extensively, but if only the maximum density of each species is considered, then it will be seen that there is no overlap. To show this point more clearly Fig. 12 has been constructed in which the contours of the two highest densities of each species of *Sagitta* have been superimposed upon one another in each section. In 0° and 90° E five species are shown, but in 80° W only three, since two species of subtropical origin are absent. It will be noticed that the main concentrations of the species do not overlap. Sometimes the second highest densities overlap, but not the highest. If *Eukrohnia hamata* (Fig. 8) is compared with these sections, it will be seen that it does overlap the highest concentrations of some of the other

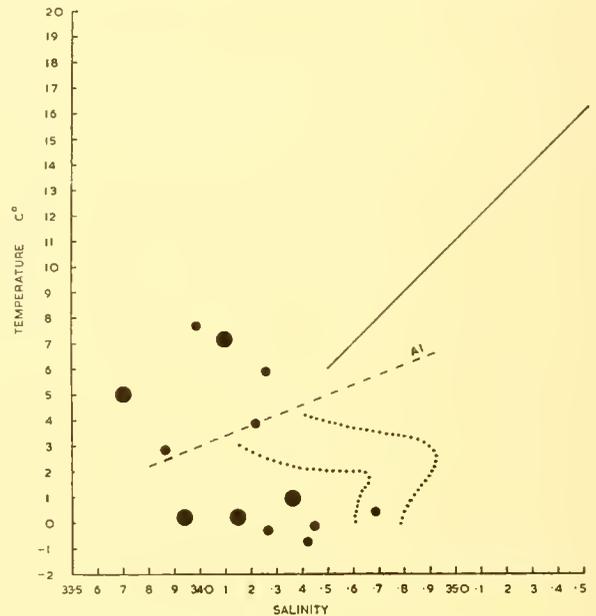


Fig. 9. The distribution of the two highest orders of abundance of *E. hamata* in the 0° meridian in March, plotted against temperature and salinity. For explanation of the significance of the lines on the figure see legend to Fig. 4.

species. It can also be seen from these sections that there are two populations of *S. gazellae*, representing the two races which occupy respectively the antarctic and subantarctic surface waters, while to the north *S. serratodentata* (see Fig. 10) occupies a similar habitat in the subtropical zone. In the deeper layers *S. marri*, *S. maxima* and *S. decipiens* (see Fig. 11) are distributionally analogous in the three zones.

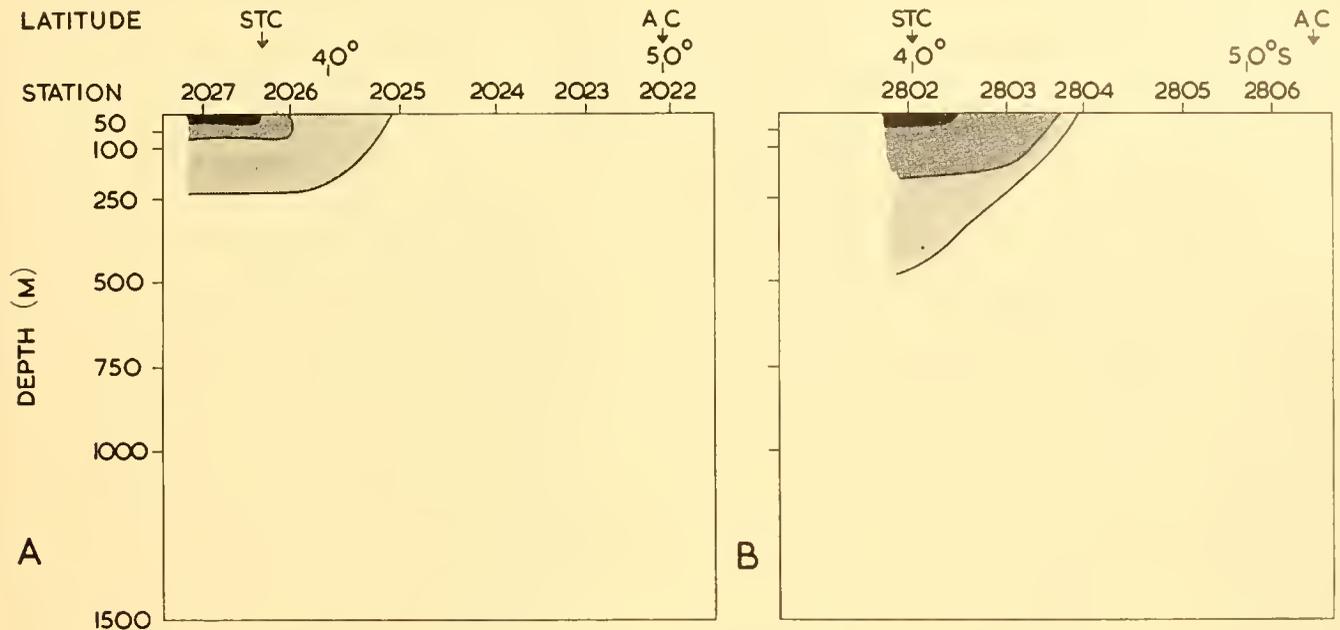


Fig. 10. The vertical distribution of *S. serratodentata* in 0° (A) and 90° E (B).

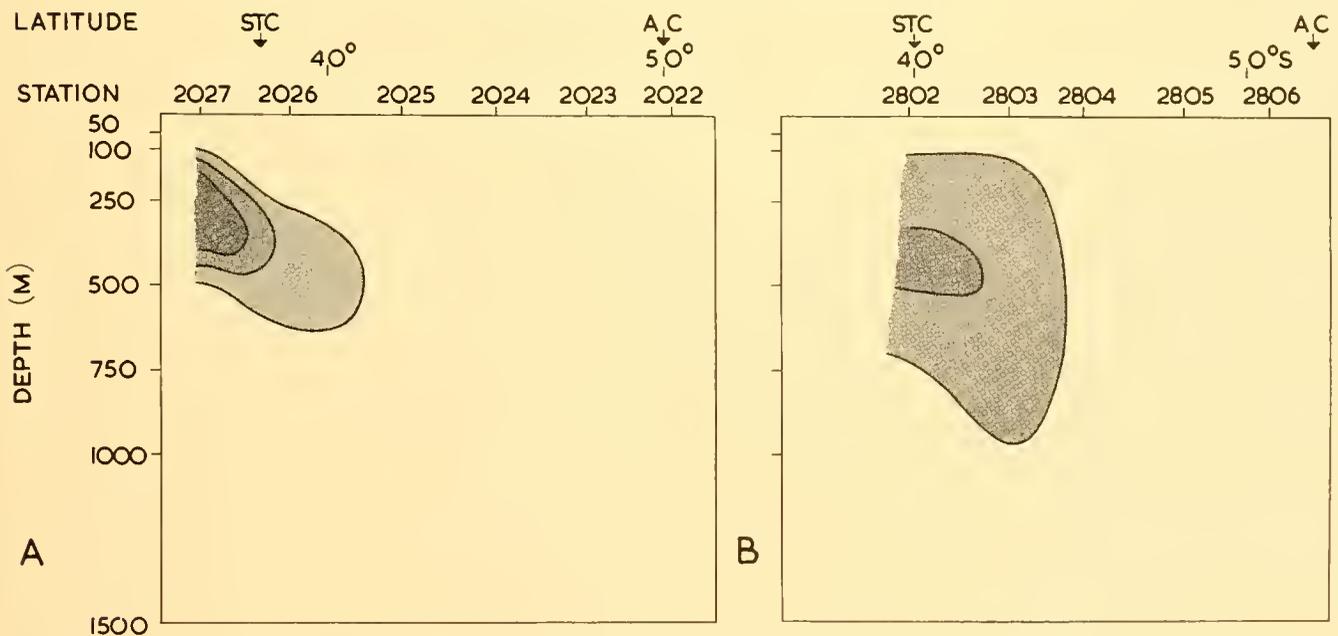


Fig. 11. The vertical distribution of *S. decipiens* in 0° (A) and 90° E (B).

This rather striking segregation of the species of *Sagitta* is of considerable interest, for although mixing does take place, there is no doubt that each species is concentrated in a particular area to the relative exclusion of the others, and it must be presumed that minor differences in the physical characteristics of these water masses are responsible for the segregation of the species, for reference to the temperature/salinity diagrams shows that most of the species can tolerate a greater range than that in which they are most abundant. This segregation must have been of considerable importance in

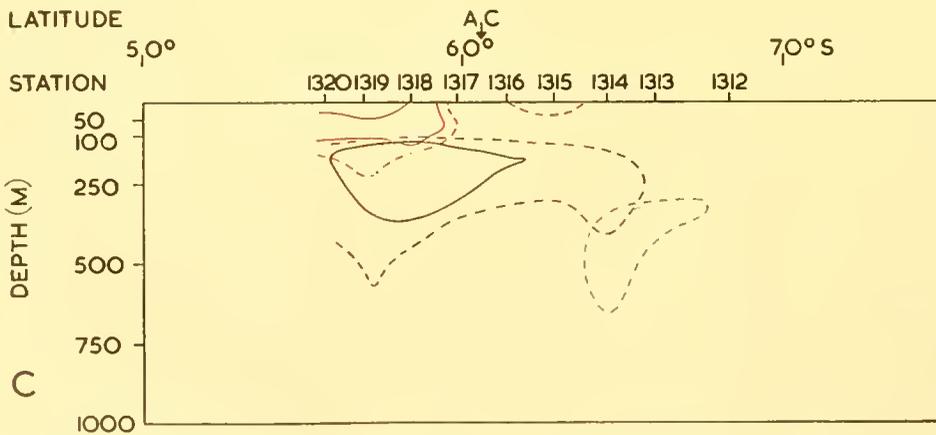
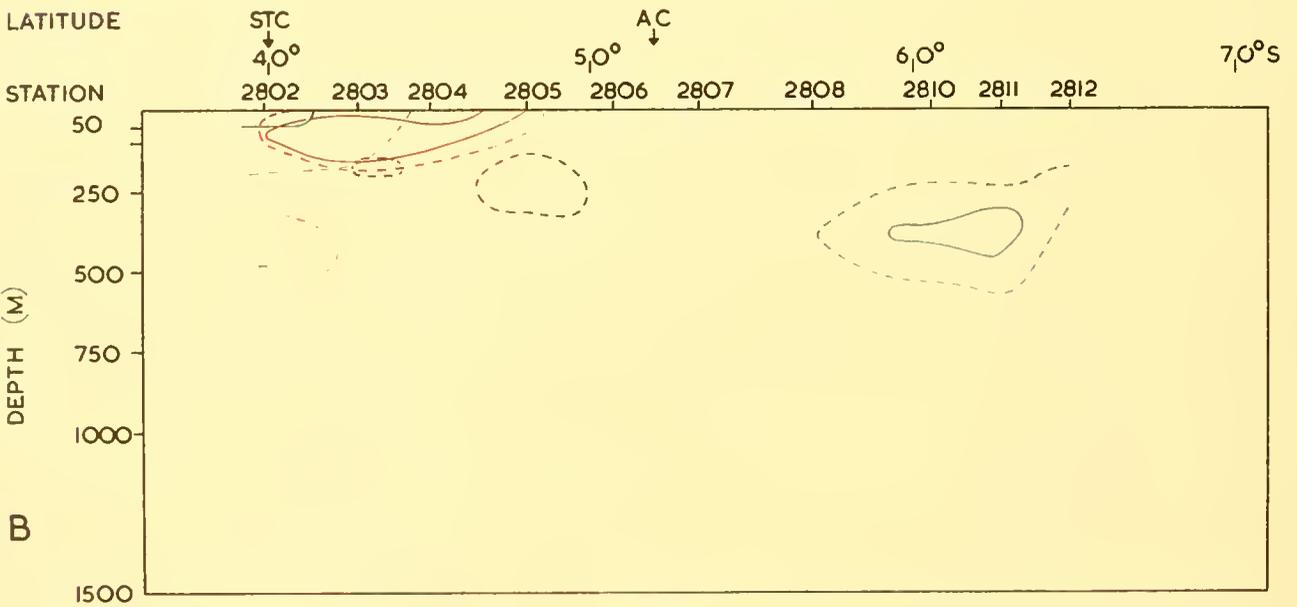
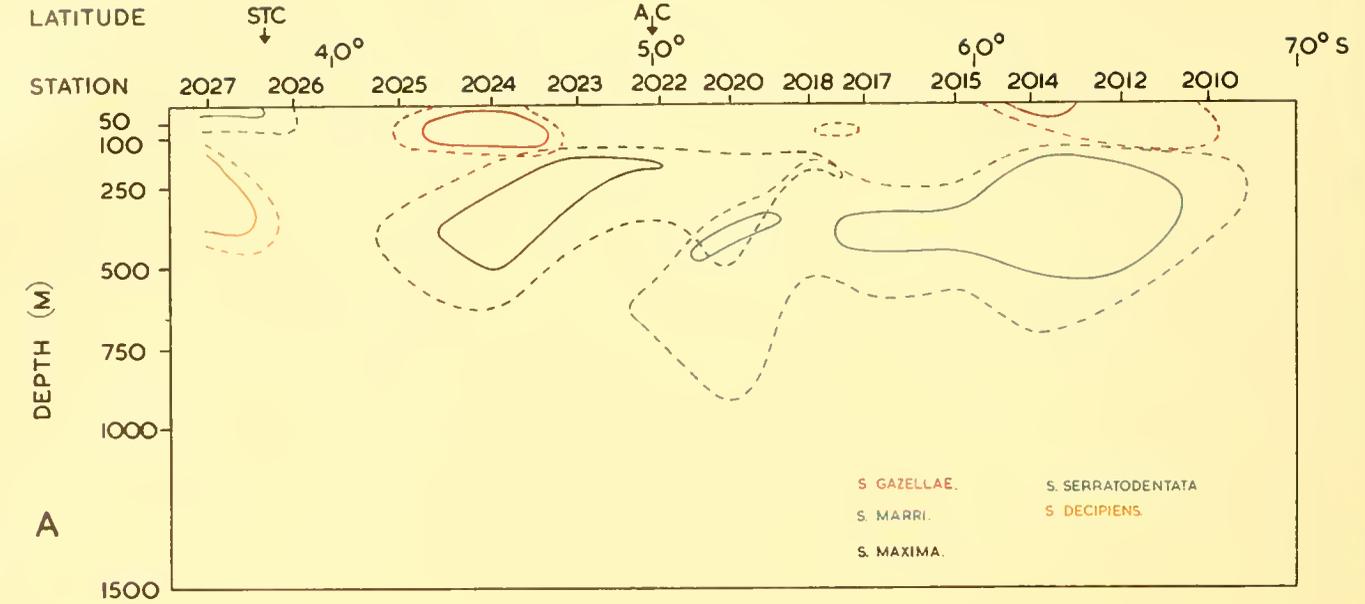


Fig. 12. The relative distribution of the two highest contours of density of *S. gazellae*, *S. marri*, *S. maxima*, *S. serratodentata* and *S. decipiens* in 0° (A), 90° E (B) and 80° W (C) (*S. serratodentata* and *S. decipiens* are not present in 80° W). The coloured contours should be compared with figs. 3, 5, 7, 8, 10 and 11.

originating and maintaining the species found in the Southern Ocean, and in this connexion it is not therefore surprising to find that when overlapping does take place it is between species of two separate genera, *Eukrohnia* and *Sagitta*, and not between species of the one genus.

WINTER DISTRIBUTION

Fig. 13 shows the vertical distribution of the four common species in 0° in August. At that time of the year the ice edge was in about 57° S, so that only a small part of the antarctic zone could be sampled.

S. gazellae. The main subantarctic concentration has moved from the surface layer down to the 250–100 m. horizon, but is still in the same latitudes. A small antarctic maximum appears in about 56° S which seems to be analogous with the March concentration (see Fig. 3) in the same latitude. This concentration also has descended from 100–50 m. to 250–100 m.

S. marri. The section does not go far enough south to sample the main part of the population of the species, and is therefore based on very small numbers which are not very informative. There is, however, a suggestion of a deeper winter distribution as found by Mackintosh (1937) for the 80° W line. An interesting feature of this section is the extension of part of the population into the Sub-antarctic in the 1500–1000 m. layer.

S. maxima. The main concentration is a little deeper in this line than it is in the summer one, and extends rather further south.

E. hamata. This species shows a clear movement to deeper water in the winter and possibly a slight southward extension of the main concentration.

Other species (not shown in the section). The August line in 0° does not commence so far north as the March one, so it is difficult to draw any conclusions about the subtropical species. *S. serratodentata* was present in very small numbers at Station 2385 at 250–100 m. and *S. decipiens* at the same station at 500–250 m. An August line (2867–2875) in the western Indian Ocean sector, which began just north of the subtropical convergence showed *S. serratodentata* present in the 50–0 m. haul in quite considerable numbers (465 per 250 m. haul) and *S. decipiens* present in the 500–250 m. horizon.

THE DISTRIBUTION OF THE MATURE STAGES

An interesting feature which is apparently common to all the most abundant Southern Ocean chaetognaths is the habit of descending into deep water to breed. This has been clearly shown for *S. gazellae* (David, 1955, p. 270). In *E. hamata* animals at stages III and IV (Krampe, 1939) (see footnote, p. 204) are only found below 750 m., though animals at stage V ('var. *antarctica*') are sometimes found at the surface as well as in deep water. Specimens of *S. maxima* at stages III and IV are also found below 750 m. Very few specimens of *S. marri* at stage IV have been taken, but specimens at stage III are also only found below 750 m. These three latter species differ from *S. gazellae* in that the very young stages are found throughout the top 1000 m. of water, whereas very young *S. gazellae* are found only in the top 250 m.

It is difficult to imagine anything advantageous to the animals in this performance of deep spawning, which is also a habit of *S. lyra* and *S. planctonis* in the subtropics, but it is possibly a behavioural relic of some deep-living ancestral form. Since there are relatively fewer barriers to the spread of animals in deep water than there are to the spread of those at the surface, it seems quite likely that radiation in the group may have been via deep-living forms.

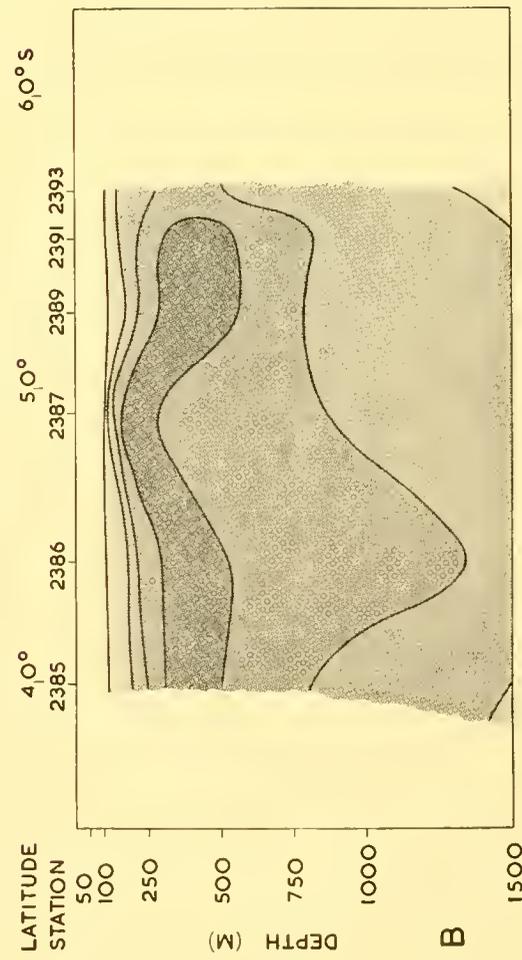
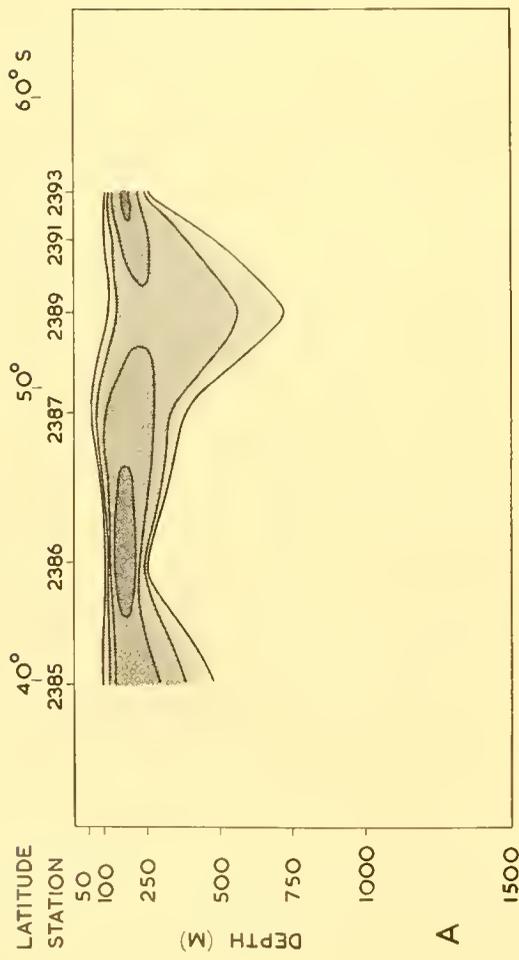
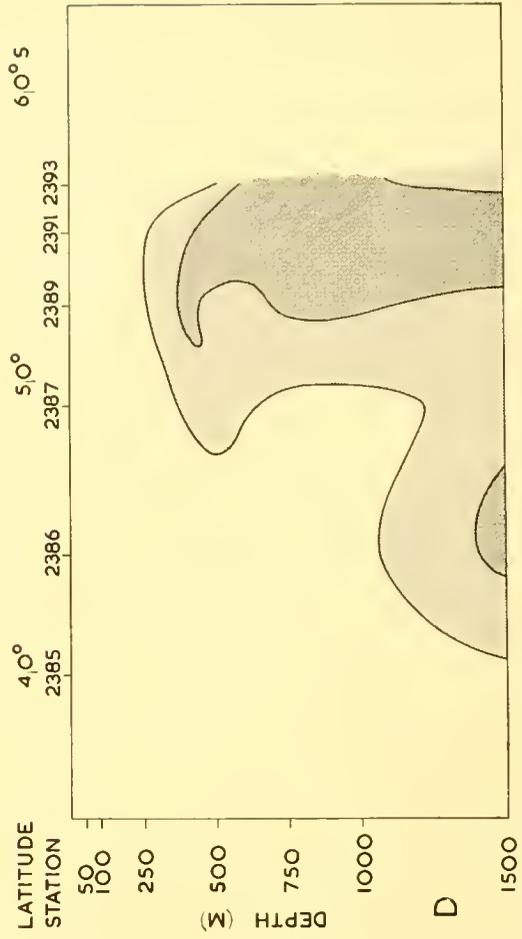
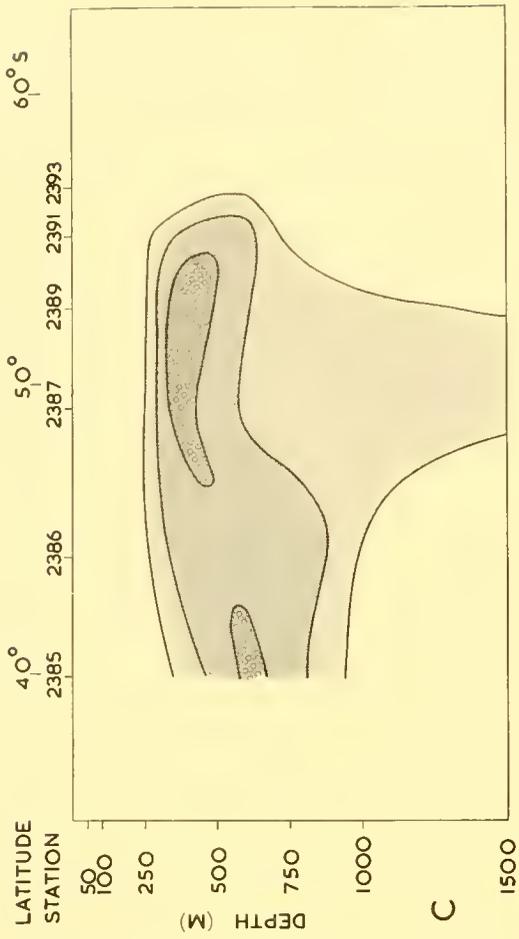


Fig. 13. The vertical distribution of (A) *S. gazellae*, (B) *E. hamata*, (C) *S. marri* and (D) *S. maxima* in the 0° meridian in August.

THE PATTERN OF DISTRIBUTION

The chaetognath fauna of the Southern Ocean is remarkable in the very small numbers of species present, seven only, living and maintaining themselves beneath a surface area of about 21 million square miles of sea, in comparison, for example, with the subtropical zone of the southern hemisphere which has not nearly so great a surface area yet contains at least sixteen species if not more.¹ This is, however, in keeping with the well-known principle that cold waters support fewer species than warm, though usually in larger numbers.

Among other points which emerge from this study is the fairly high proportion of endemic species—three out of seven. The antarctic benthic fauna is characterized by its high proportion of endemic species, which would be expected by virtue of its isolation, geographic and physical (covering temperature, salinity and other features), from the benthic fauna of the southern continents. The planktonic fauna would not be expected to be so subject to isolation, yet evidently from the data presented here it must be. The boundaries between water masses in the open ocean however are not usually clear cut and distinct, and large-scale swirls or eddies are probably produced where water masses meet. Salients of one water mass may from time to time be pinched off by another in the boundary region, and gradually absorbed. Thus the fauna carried in such a salient may be found outside its normal habitat; but such stray records should not be regarded as typical of the range of a species.

It is evident that barriers exist which limit the habitat of each species, and it seems likely that the convergence areas can be regarded as effective in this respect; nevertheless, there must also be other factors involved, and although temperature or salinity considered separately indicates that there is considerable overlap of tolerance in the various populations, the two factors in combination seem to have a considerable effect (see Figs. 4, 6 and 9). It is probable that if other physical factors were also considered in combination, the actual tolerance of each species would be circumscribed within precise and narrow boundaries; but it must be remembered that this would probably only mean that a particular species lived in a particular water mass, and that while the combination of physical factors identified the water mass, they might not necessarily be the factors governing the distribution of the species. Biological differences, as yet imperfectly understood, between various water masses, such as those which are being investigated by Wilson (1953, 1954) and Wilson & Armstrong (1954), may well play an important part in limiting the distribution of the plankton.

SUMMARY

The Chaetognatha of the antarctic and subantarctic zones can be classified broadly into three groups: (a) 'endemic' species, (b) species common to other regions, and (c) exotic species which do not maintain themselves in the area. There are three species in group (a), four in group (b) and eight in group (c). The horizontal distribution of these is discussed, and the vertical distribution of the seven species in groups (a) and (b) and two species of group (c) is shown by sections based on data from vertical closing nets worked in the Atlantic, Indian and Pacific Ocean sectors of the Southern Ocean. The results show that the distribution pattern is distinctive for each species, that the areas of maximum abundance of species of the genus *Sagitta* are mutually exclusive, and that despite the relative uniformity of the environment, these species are influenced by quite effective isolating factors.

¹ It is interesting to note that Tchindonova (1955, p. 307), commenting on the same phenomenon in the north Pacific, says: 'While there are 23 different species known for the Yellow Sea and the Sea of Japan out of which 16 are warm, and only two are cold water species, in the region of the Kurile-Kamchatka trench only seven species altogether have been found by us.'

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APPENDIX: TABLE 4

Table 4 (a-c)

Note: In this table the numbers of each species are corrected for a 250 m. haul (see p. 203). A horizontal dash indicates that a sample was missing and not examined, or that the weather prevented the haul from being made.

Table 4 a. *The March line in 0°*

Station no. ...	2027	2026	2025	2024	2023	2022	2020	2018	2017	2015	2014	2012	2010
<i>S. gazellae</i>													
50-0	0	0	5	30	5	15	0	0	0	0	55	30	10
100-50	0	10	25	90	10	5	0	20	20	10	15	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	—	0	1	0	0	—	0	0	—	0	0
<i>S. marri</i>													
50-0	0	0	0	0	0	0	0	0	0	0	0	0	0
100-50	0	0	0	0	0	0	0	0	0	0	0	0	0
250-100	0	0	0	0	0	0	0	15	3	3	25	20	15
500-250	0	0	0	0	2	3	22	17	25	26	30	33	18
750-500	0	0	0	8	8	16	12	5	7	6	14	10	0
1000-750	0	0	1	10	1	2	11	0	7	2	3	1	1
1500-1000	0	0	—	1	0	4	7	—	1	1	—	2	0
<i>S. maxima</i>													
50-0	0	0	0	0	0	0	0	0	0	0	0	0	0
100-50	0	0	0	0	0	0	0	0	0	0	0	0	0
250-100	0	0	2	10	50	31	15	16	2	0	0	0	0
500-250	1	10	14	55	12	6	16	0	1	0	0	0	0
750-500	0	1	7	7	2	2	4	0	1	0	0	0	0
1000-750	0	0	0	4	2	0	2	2	0	1	1	0	1
1500-1000	0	1	—	0	3	1	2	—	0	0	—	0	0
<i>E. hamata</i>													
50-0	0	0	0	240	110	175	10	40	?	10	0	235	110
100-50	0	0	10	445	440	275	60	465	75	85	110	250	245
250-100	0	12	65	190	170	180	375	710	165	160	215	145	90
500-250	13	101	180	201	137	113	164	70	127	74	53	79	52
750-500	19	8	101	56	41	42	85	12	16	17	17	11	11
1000-750	18	29	37	38	10	11	28	13	8	5	8	10	20
1500-1000	36	6	—	16	17	12	15	—	7	5	—	0	3

Table 4a (cont.)

Station no. ...	2027	2026	2025	2024	2023	2022	2020	2018	2017	2015	2014	2012	2010
<i>S. serratodentata</i>													
50-0	620	20	0	0	0	0	0	0	0	0	0	0	0
100-50	15	20	0	0	0	0	0	0	0	0	0	0	0
250-100	5	8	0	0	0	0	0	0	0	0	0	0	0
500-250	0	0	0	0	0	0	0	0	0	0	0	0	0
750-500	0	0	0	0	0	0	0	0	0	0	0	0	0
1000-750	0	0	0	0	0	0	0	0	0	0	0	0	0
1500-1000	0	0	—	0	0	0	0	—	0	0	—	0	0
<i>S. decipiens</i>													
50-0	0	0	0	0	0	0	0	0	0	0	0	0	0
100-50	0	0	0	0	0	0	0	0	0	0	0	0	0
250-100	20	0	0	0	0	0	0	0	0	0	0	0	0
500-250	25	4	3	0	0	0	0	0	0	0	0	0	0
750-500	0	1	0	0	0	0	0	0	0	0	0	0	0
1000-750	0	0	0	0	0	0	0	0	0	0	0	0	0
1500-1000	0	0	—	0	0	0	0	—	0	0	—	0	0
<i>S. lyra</i>													
50-0	0	0	0	0	0	0	0	0	0	0	0	0	0
100-50	15	0	0	0	0	0	0	0	0	0	0	0	0
250-100	3	2	0	0	0	0	0	0	0	0	0	0	0
500-250	4	4	1	0	0	0	0	0	0	0	0	0	0
750-500	4	0	0	0	0	0	0	0	0	0	0	0	0
1000-750	3	2	0	0	0	0	0	0	0	0	0	0	0
1500-1000	12	0	—	0	0	0	0	—	0	0	—	0	0
<i>S. macrocephala</i>													
50-0	0	0	0	0	0	0	0	0	0	0	0	0	0
100-50	0	0	0	0	0	0	0	0	0	0	0	0	0
250-100	0	0	0	0	0	0	0	0	0	0	0	0	0
500-250	0	0	0	0	0	0	0	0	0	0	0	0	0
750-500	0	0	0	0	0	0	0	0	0	0	0	0	0
1000-750	0	0	2	0	0	0	0	0	0	0	0	0	0
1500-1000	0	0	—	0	0	1	0	—	0	0	—	0	0
<i>S. zetesios</i>													
50-0	0	0	0	0	0	0	0	0	0	0	0	0	0
100-50	0	0	0	0	0	0	0	0	0	0	0	0	0
250-100	0	0	0	0	0	0	0	0	0	0	0	0	0
500-250	0	0	0	0	0	0	0	0	0	0	0	0	0
750-500	1	0	0	0	0	0	0	0	0	0	0	0	0
1000-750	1	0	0	0	0	0	0	0	0	0	0	0	0
1500-1000	2	0	—	0	0	0	0	—	0	0	—	0	0

Table 4b. The February line in 90° E

Station no. ...	2802	2803	2804	2805	2806	2807	2808	2810	2811	2812
<i>S. gazellae</i>										
50-0	10	35	20	40	0	5	10	0	0	0
100-50	45	95	55	25	0	10	5	0	0	0
250-100	0	24	9	0	2	0	0	2	0	0
500-250	0	0	0	0	4	—	0	0	0?	0
750-500	0	0	0	0	1	—	0	1	0	0
1000-750	0	1	0	1	0	—	0	0	0	1
1500-1000	0	0	0	—	0	—	—	0	0	0

Table 4b (cont.)

Station no. ...	2802	2803	2804	2805	2806	2807	2808	2810	2811	2812
<i>S. marri</i>										
50-0	0	0	0	0	0	0	0	0	0	0
100-50	0	0	0	0	0	0	0	0	0	0
250-100	0	0	0	0	0	0	0	7	2	12
500-250	0	0	0	5	1	—	11	22	0?	8
750-500	0	0	0	2	0	—	1	2	5	0
1000-750	0	0	0	3	3	—	1	1	1	4
1500-1000	0	0	0	—	0	—	—	2	1	0
<i>S. maxima</i>										
50-0	0	0	0	0	0	0	0	0	0	0
100-50	0	0	0	0	0	0	0	0	0	0
250-100	0	10	2	27	5	0	0	2	0	0
500-250	3	1	3	3	7	—	0	0	2?	0
750-500	2	0	0	1	3	—	0	0	0	0
1000-750	2	2	0	1	2	—	0	0	0	0
1500-1000	0	1	0	—	0	—	—	0	0	0
<i>E. hamata</i>										
50-0	0	5	0	0	0	20	0	0	0	5
100-50	0	5	45	125	10	15	40	15	70	50
250-100	4	72	40	180	20	27	70	90	17	50
500-250	25	16	24	19	114	—	11	39	3?	0
750-500	13	24	3	13	21	—	2	10	9	3
1000-750	3	14	4	15	18	—	3	7	2	5
1500-1000	1	13	3	—	1	—	—	7	3	5
<i>S. serratodentata</i>										
50-0	715	65	0	0	0	0	0	0	0	0
100-50	115	10	0	0	0	0	0	0	0	0
250-100	24	0	0	0	0	0	0	0	0	0
500-250	4	0	0	0	0	—	0	0	0?	0
750-500	0	0	0	0	0	—	0	0	0	0
1000-750	0	0	0	0	0	—	0	0	0	0
1500-1000	0	0	0	—	0	—	—	0	0	0
<i>S. decipiens</i>										
50-0	0	0	0	0	0	0	0	0	0	0
100-50	0	0	0	0	0	0	0	0	0	0
250-100	2	3	0	0	0	0	0	0	0	0
500-250	13	4	0	0	0	—	0	0	0?	0
750-500	8	1	0	0	0	—	0	0	0	0
1000-750	0	3	0	0	0	—	0	0	0	0
1500-1000	0	0	0	—	0	—	—	0	0	0
<i>S. lyra</i>										
50-0	0	0	0	0	0	0	0	0	0	0
100-50	0	0	0	0	0	0	0	0	0	0
250-100	15	0	0	0	0	0	0	0	0	0
500-250	7	0	0	0	0	—	0	0	0	0
750-500	0	1	0	0	0	—	0	0	0?	0
1000-750	2	1	0	0	0	—	0	0	0	0
1500-1000	0	0	0	—	0	—	—	0	0	0
<i>S. macrocephala</i>										
50-0	0	0	0	0	0	0	0	0	0	0
100-50	0	0	0	0	0	0	0	0	0	0
250-100	0	0	0	0	0	0	0	0	0	0
500-250	0	0	0	0	0	—	0	0	0?	0
750-500	0	0	0	0	0	—	0	0	0	0
1000-750	1	2	3	0	0	—	0	0	0	0
1500-1000	1	1	0	—	1	—	—	0	0	0

Table 4c. *The August line in 0°*

Station no.	2385	2386	2387	2389	2391	2393
<i>S. gazellae</i>						
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
<i>S. marri</i>						
50-0	0	0	0	0	0	0
100-50	0	0	0	0	0	0
250-100	0	0	0	0	0	0
500-250	0	1	1	5	4	0
750-500	0	0	1	4	8	7
1000-750	0	0	0	7	9	7
1500-1000	0	6	2	4	9	2
<i>S. maxima</i>						
50-0	0	0	0	0	0	0
100-50	0	0	0	0	0	0
250-100	0	0	0	0	0	0
500-250	1	7	12	14	6	1
750-500	12	7	3	5	6	0
1000-750	3	6	1	1	0	1
1500-1000	0	0	2	2	1	0
<i>E. hamata</i>						
50-0	0	0	0	0	0	0
100-50	0	0	0	0	0	0
250-100	4	10	160	8	25	27
500-250	134	196	82	207	197	73
750-500	106	73	78	87	89	28
1000-750	26	110	48	31	40	16
1500-1000	15	29	22	10	18	14
<i>S. serratodentata</i>						
50-0	0	0	0	0	0	0
100-50	0	0	0	0	0	0
250-100	10	0	0	0	0	0
500-250	0	0	0	0	0	0
750-500	0	0	0	0	0	0
1000-750	0	0	0	0	0	0
1500-1000	0	0	0	0	0	0
<i>S. decipiens</i>						
50-0	0	0	0	0	0	0
100-50	0	0	0	0	0	0
250-100	0	0	0	0	0	0
500-250	7	2	0	0	0	0
750-500	0	0	0	0	0	0
1000-750	3	0	0	0	0	0
1500-1000	2	0	0	0	0	0
<i>S. macrocephala</i>						
50-0	0	0	0	0	0	0
100-50	0	0	0	0	0	0
250-100	0	0	0	0	0	0
500-250	0	0	0	0	0	0
750-500	0	0	0	0	0	0
1000-750	0	1	1	0	0	0
1500-1000	0	2	0	0	0	0

PLATE X

An antarctic and an arctic specimen of *S. maxima* at the same stage of maturity. $\times 2\frac{1}{4}$ approx.



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THE RELIABILITY OF DEEP-SEA REVERSING THERMOMETERS

By

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AND

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THE RELIABILITY OF DEEP-SEA REVERSING THERMOMETERS

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(Figs. 1-7)

INTRODUCTION

WITH the advance of our knowledge of oceanography little remains to be written about the construction and methods of using deep-sea reversing thermometers; they have, in fact, become standard equipment and, in general, the performance of any individual thermometer over a period of years appears to be taken very much for granted. This uncritical attitude is no doubt associated with the more universal use of this instrument. Until fairly recent times the use of deep-sea reversing thermometers was confined largely to the few major oceanic expeditions where, on the return of the ship, the bulk of the equipment was generally sold, or stored away in some unlikely place, and forgotten. Even when sold the only information usually available to the new owners was the original certificate of calibration. Periodic checks on the zero point of all the 'Meteor' deep-sea thermometers were, however, made by Böhnecke and Wüst (Wüst, 1932) during the Expedition of 1925-7, and a critical survey of the accuracy of the reversing thermometers used in the 'Carnegie' in 1928-9 was published fifteen years later (Sverdrup, Fleming, Soule and Ennis, 1944). Wüst's check was made to determine any change in zero point during the period of the Expedition whereas the examination of the 'Carnegie' temperature readings was made to assess the reliability of the deep-sea thermometers, especially with regard to minor differences in the temperatures recorded by each pair of thermometers.* So far as we have been able to find out, no other published data exist—except for a very brief reference in the 'Carnegie' report—concerning any possible change in the characteristics, or in the behaviour generally, after their use, or storage, over a number of years. Nor has there been any comparison between thermometers by different makers. Although not specifically referring to the behaviour of deep-sea thermometers with regard to their continued use, a recent note by Whitney (1955) should perhaps be mentioned. Doubts have been expressed at the Woods Hole Oceanographic Institution about certain aspects of the behaviour of unprotected reversing thermometers, mainly in respect of the determination of the mean pressure coefficient (m.p.c. or 'Q'), and in his paper Whitney describes the re-examination, after a period of three years, of a group of such thermometers. Results of the tests were largely negative but, nevertheless, are extremely valuable in that they emphasize the individuality of these instruments and so the difficulty of attempting to codify their characteristics.

At the last check (1953-4) by the National Physical Laboratory (N.P.L.) of nearly all the deep-sea thermometers now held by the National Institute of Oceanography (N.I.O.), some eighty of these instruments were examined. Of these, thirty-six protected and two unprotected deep-sea reversing thermometers had been the property of the Discovery Committee, and had been in use or, when not

* Mostly two protected thermometers were used by the 'Carnegie' at each depth—a practice adopted for all depths by the Discovery Committee and, in turn, by the National Institute of Oceanography.

in use, had always been kept in an upright position, over periods varying between fifteen and twenty-nine years. The records of these thermometers over such exceptionally long periods are probably unique. In this paper, therefore, after a review of the errors and eccentricities to which deep-sea thermometers are liable, we can examine the general question whether or not they change or deteriorate with age. We hope to show that most thermometers, at least of certain British and German makes, can continue to give good service for very long periods, provided they are properly cared for; and that there is little change with age apart from a tendency for the zero point to rise.

All the thirty-eight thermometers had previously been re-certified at least once, after the issue of the original certificate of test. Sixteen of the thirty-six protected thermometers were made in Germany prior to 1926 (by Richter and Weise, of Berlin); the remainder were made at various times between 1934 and 1938 by Negretti and Zambra, of London. The scale range varies considerably, but all are divided to $1/10^{\circ}$ C. In 1953-4 certificates were issued in respect of thirty-three protected thermometers only, as the mercury column of each of the remaining three (of German origin) consistently refused to break at the constriction or appendix when the thermometer was reversed unless the thermometer was tapped. The action of these thermometers had, however, been satisfactory when they were previously examined by the N.P.L. in 1949. It is unfortunate that only two unprotected thermometers of any considerable age have survived for comparison but, in view of their extreme vulnerability, this is not, perhaps, surprising.

ERRORS AND ECCENTRICITIES

Although the zero point of a reversing thermometer* is dependent on the 'break-off' action of the mercury column at the constriction or appendix peculiar to this type of thermometer, there is a characteristic rise (of the order of a few hundredths of a degree) of zero with age very similar to that which commonly takes place in ordinary mercury-in-glass thermometers; except for this rise of zero the majority of deep-sea thermometers appear to maintain their accuracy remarkably well for many years—whether in store or frequent use—provided that they are properly cared for. That a few become erratic in their habits after repeated use, is not surprising; for instance, those used for observations at the greater depths may, if used in tropical waters, be cooled rapidly from 28° to 1° C. between the surface and a depth of 5000 m., and as quickly heated again when returning to the surface.

Erratic readings from deep-sea thermometers usually result from only a few basic causes, the commonest of which is the presence of a minute bubble of gas in the column of mercury, somewhere in the capillary of the thermometer. On reversal the mercury column breaks at the point where the bubble is then situated. Rough handling of a thermometer is usually the reason for the occurrence of this condition which, nevertheless can occur in normal use even when the greatest care is taken to protect the instrument from shock.

One eccentricity, however, for which it is difficult to find a satisfactory explanation is the failure of the column of mercury to break at all, unless the thermometer is tapped. With very low temperatures this is perhaps understandable, since the amount of mercury concerned is small and, if reversal is unusually slow, the weight of mercury involved might not be sufficient to overcome the surface tension and bring the constriction into action. (We revert to this point below, p. 238, when considering the histories of the various thermometers.) There is no evidence, however, that the amount of mercury reversed determines whether the thread breaks or not. This eccentricity can occur at all

* Deep-sea reversing thermometers comprise two thermometers—main and auxiliary. Since the latter is a conventional, or standard type of thermometer it has not been considered in this paper, and any reference to a reversing thermometer should be taken as referring to the main thermometer only.

depths, and over the whole range of ocean temperatures, and it may be that with repeated use some physical change of a purely temporary nature takes place in the structure of the glass; such a change may affect a particular constriction or appendix (in themselves a tribute to the glassblower's skill) sufficiently to upset the normal action of the thermometer. If, however, a thermometer which behaves erratically in this manner is 'rested' for some months—in an upright position—it will usually behave normally when returned to service. This recovery of normal accuracy after 'resting', and without 'manipulation' of the thermometer,* seems to be strong evidence for a temporary change in the structure of the glass.

CALIBRATION AND CERTIFICATION OF DEEP-SEA REVERSING THERMOMETERS

The original certificates of scale correction for the thirteen German thermometers under review were issued in 1924 and 1925 by the Physikalisch-Technische Reichsanstalt (P.T.R.) of Berlin, who also re-examined some of them in 1933 and 1935. Unfortunately, the N.I.O. does not now possess the original (1924–5) certificates for the three thermometers (nos. 1008, 1011 and 1257) re-examined by the P.T.R. in 1933, nor for those re-examined in 1935 (nos. 863, 883 and 1019). An attempt was made to obtain copies of these German certificates, but this was not possible since all pre-war thermometric records of the P.T.R. were lost during the bombing of Berlin.† All checks on the German thermometers, subsequent to 1935, have been made at the N.P.L. The original calibration of the British thermometers now under review, and all subsequent checks, were also made at the N.P.L.

The limits of accuracy of the P.T.R. calibrations of the main thermometer, as given on their certificates, were $\pm 0.01^\circ \text{C.}$; the limits quoted by the N.P.L. were, up to and including the year 1938, also $\pm 0.01^\circ \text{C.}$; in 1949 and 1953 they were $\pm 0.02^\circ \text{C.}$ This change was actually made in 1939 but it is of interest to note that in 1929, in connection with tests on a protected deep-sea thermometer (of the range -2° to $+16^\circ \text{C.}$) made by Richter and Weise, the N.P.L. would only give a certificate of corrections to $\pm 0.02^\circ \text{C.}$ Messrs Negretti and Zambra, in commenting on this,‡ wrote as follows: '... they (the N.P.L.) report to us that, a number of tests having been carried out, the reproductivity of the readings does not admit giving the corrections closer than 0.02°C. , and we must say that we rather agree with them when $1^\circ = 8 \text{ mms.}$...' Of the thermometers now under review those of German make, with one exception, differ only slightly in range and, apart from this exception, the length of 1° on the scale of the main thermometers of the remainder varies between 8.1 and 9.1 mm. The thickness of the graduation line is approximately 0.05 mm. The range of the British thermometers is the same throughout (-2° to 12°C.), with the length of one scale degree varying between 9.6 and 11.3 mm. The average is 10.5 mm. The thickness of the graduation line is, approximately, 0.1 mm. This slightly more open scale is, no doubt, a help towards more accurate readings but still does not warrant corrections being determined to a greater degree of accuracy than $\pm 0.02^\circ$. That it is possible in field-work to read these thermometers to a greater degree of accuracy cannot be gainsaid. Any experienced observer expects to obtain readings accurate to $\pm 0.01^\circ \text{C.}$

* 'Manipulation' is the comprehensive term used to describe all aspects of the corrective treatment used when trying to restore a temporarily erratic thermometer to its normal action (Whitney, 1952).

† Personal communication to one of the authors (H.F.P.H.).

‡ Letter from Messrs Negretti and Zambra, dated 29 October 1929, to the Director of Research, Discovery Committee. This extract is published by permission of Messrs Negretti and Zambra.

Table 1. *Protected deep-sea thermometers*

(1) Ships and commissions: D.—R.R.S. 'Discovery', 1925-7; D. II—R.R.S. Discovery II', 1929-31, 1933-5, 1937-9 and 1950-1; WS.—R.R.S. 'William Scoresby', 1928-9, 1929-31, 1931 and 1950.
 (2) The figures in parentheses after the commissions of the various ships are the number of times the thermometer concerned was used on that commission.
 (3) An assessment of the reliability is available only for the following commissions: R.R.S. 'Discovery', 1925-7; R.R.S. 'Discovery II', 1929-31, 1933-5, 1937-9 and 1950-1; R.R.S. 'William Scoresby', 1950.
 (4) When the expression 'no comments' is used in connection with thermometers whose reliability has been assessed, it may be assumed that the action was entirely satisfactory.

Thermometer no.	Range (° C.)	Vol. (°)	Zero error (° C.)										No. of times used	Ships and commissions on which used	Reliability	
			1924†	1925†	1933†	1934	1935†	1937	1938	1949	1953	1953				
854	-2/19.3	152	-0.01	—	—	—	—	—	—	—	—	0.02	0.02	—	D. II 35/37 (66), 37/39 (44) and 50/51 (2)	Apparently not used
863	-2/19	154	*	—	—	-0.04	—	—	-0.01	-0.02	112	—	—	—	D. II 35/37 (66), 37/39 (44) and 50/51 (2)	Mercury stuck in expansion chamber once (37/39)
869	-2/17.9	166	-0.66	—	—	—	—	—	Nil	0.01	12	—	—	—	D. II 50/51 (2†)	Two completely erroneous readings (50/51)†
871	-2/18.8	265	Nil	—	—	—	—	—	0.01	0.02†	5	—	—	—	D. 25/27	No comments
876	-2/18.2	209	-0.01	—	—	—	—	—	0.01	0.01	11	—	—	—	D. 25/27	No comments
883	-2/17.3	238	*	—	—	—	—	0.02	—	—	1	—	—	—	D. II 37/39	Completely erroneous reading (37/39)
971	-2/25	97	—	0.05	—	—	—	—	0.01	0.01	3	—	—	—	D. II 50/51	No comments
1008	-2/18.5	127	*	—	0.02	—	—	—	0.02	0.05	27	—	—	—	D. 25/27 (5); D. II 31/33 (6), 35/37 (4) and 37/39 (12)	Twice failed to 'break' (37/39)
1011	-2/18.1	93	*	—	0.01	—	—	—	0.03	0.03	116	—	—	—	D. II 35/37 (63), 37/39 (37) and 50/51 (16)	In collision (37/39). Twice failed to 'break' (50/51)
1019	-2/19.5	150	*	—	—	—	—	Nil	0.02	0.01	51	—	—	—	D. 25/27 (9); D. II 37/39 (42); WS. 50 (1†)	Mercury stuck in expansion chamber once (50)†
1023	-2/18.5	155	—	Nil	—	—	—	—	0.03	0.04	38	—	—	—	D. 25/27 (13); WS. 50 (25)	Two completely erroneous readings (25/27) and (50)
1025	-2/18.7	156	—	Nil	—	—	—	—	0.02	0.03	68	—	—	—	D. II 29/31 (29), 31/33 (2), 37/39 (24) and 50/51 (13)	No comments
1257	-1.3/17.3	114	—	-0.03	—	—	—	—	-0.01	Nil	459	—	—	—	WS. 28/29 (101), 29/31 (38) and 31 (46); D. II 35/37 (193) and 37/39 (81)	No comments
CD 5556	-2/12	55	—	—	-0.01	—	—	—	Nil	0.01	49	—	—	—	D. II 33/35 (29), 35/37 (4), 37/39 (15) and 50/51 (1)	Erratic at times (33/35, 37/39 and 50/51)

Table I (cont.)

Thermometer no.	Range (° C.)	Vol. (°)	Zero error (° C.)										No. of times used	Ships and commissions on which used	Reliability
			1924†	1925†	1933†	1934	1935†	1937	1938	1949	1953	1954			
CD 5559	-2/12	61	1924†	1925†	1933†	1934	1935†	1937	1938	1949	1953	1954	297	D. II 37/39 (240) and 50/51 (57)	Two impossible readings and once stuck (37/39). No comments (50/51)
CD 5563	-2/12	55		-0.03						0.01	Nil	271	D. II 33/35 (172), 35/37 (2), 37/39 (66) and 50/51 (31)	Erratic (33/35). Two impossible readings, and once stuck (37/39). No comments (50/51)	
CG 11309	-2.5/12	70			Nil					0.02	0.04	216	D. II 37/39 (209) and 50/51 (7)	Four erroneous readings and once stuck (37/39). Erratic over a period (50/51)	
CG 15243	-2.5/12	104			-0.01					-0.03	-0.01	259	D. II 37/39 (252), WS. 50 (7)	Stuck once (50)	
CH 17798	-2.5/12	49			0.01					0.04	0.05	169	D. II 37/39 (168), WS. 50 (1)	Irregular action (50)	
CH 17799	-2.5/12	55			0.01					0.01	0.04	2	WS. 50	Stuck once (50)	
CH 17800	-2.5/12	49			0.01					0.02	0.04	179	D. II 37/39 (155), WS. 50 (24)	One impossible reading (37/39)	
CH 17801	-2.5/12	64			Nil					0.01	0.03	72	D. II 37/39 (48), WS. 50 (24)	One impossible reading (37/39). Twice failed to break (50)	
CH 17803	-2.5/12	61			Nil					0.02	0.04	191	D. II 37/39 (168), WS. 50 (23)	One impossible reading (37/39)	
CH 17804	-2.8/12	70			Nil					0.02	0.05	90	D. II 37/39 (68), WS. 50 (22)	No comments	
CH 17805	-2.5/12	58			0.01					0.03	0.06	8	WS. 50	Stuck once (50)	
CH 17808	-2.5/12	58			Nil					0.01	0.03	176	D. II 37/39	No comments	
CH 22676	-2.5/12	61			Nil					0.07	0.08	104	D. II 50/51	One erroneous reading (50/51)	
CH 22677	-2.5/12	67			Nil					Nil	0.03	55	D. II 50/51	No comments	
CH 22678	-2.5/12	61			Nil					0.03	0.04	108	D. II 50/51	One erroneous reading (50/51)	
CH 22679	-2.5/12	70			Nil					0.04	0.07	111	D. II 50/51	No comments	
CH 22680	-2.5/12	58			Nil					0.01	0.03	77	D. II 50/51	No comments	
CH 22681	-2.5/12	61			Nil					0.04	0.04	—	—	Not used	
CH 22683	-2.5/12	73			Nil					0.05	0.07	102	D. II 50/51	No comments	

* The original certificates for these thermometers cannot now be found. It is, however, virtually certain that the original certificates were issued in 1924 or 1925.

† Thermometers in these years checked by Physikalisches Technische Reichsanstalt. Remainder of certificates by National Physical Laboratory.

‡ In 1953 a statement of examination only was issued by the N.P.L. in respect of this thermometer. Since the refusal of a certificate was solely on account of the large corrections required to the auxiliary thermometer the particulars relating to the main thermometer have been included in this table.

PROTECTED THERMOMETERS

CHANGE WITH AGE IN THE ZERO POINT AND SCALE CORRECTIONS

Most of the information concerning the thermometers under review is best given in tabular form. In Table 1 we have, therefore, listed the physical particulars for the protected deep-sea thermometers, i.e. range, volume of mercury reversed at 0° (usually referred to as V_0) and the periodic zero error, together with data regarding the thermometers when actually in use. Unfortunately these data are not as complete as we would wish; for certain thermometers they are, however, considered sufficient to give a reasonable indication of the reliability to be expected from that instrument.

The table shows that the zero point generally rises with increasing age. This is a normal characteristic of all conventional, or standard type thermometers and, as already mentioned, reversing thermometers do not seem to provide any exception to this rule. Generally any major shift of zero occurs in the early years of the life of a thermometer, a fact seemingly borne out by the figures available for our protected deep-sea instruments. If we consider the various age groups in order, the following facts concerning the zero point appear.

29-group (1924-53). Four thermometers—nos. 854, 869, 871 and 876. Only one thermometer (869) shows a zero drift of more than 0.03° and, for all thermometers, the greater part of the drift took place between the years 1924 and 1949. Between checks in 1949 and 1953 two thermometers registered nil drift and the other two only 0.01° . All of Richter and Wiese's make. First check at P.T.R., remainder by N.P.L.

28-group (1925-53). Three thermometers—nos. 971, 1023 and 1025. Drift of zero point for all three thermometers very similar. Maximum drift 0.04° , minimum 0.03° , with the major change again occurring before 1949. Between 1949 and 1953 no change for one thermometer, 0.01° for the others. First check at P.T.R., remainder by N.P.L. All of Richter and Wiese's make.

20-group (1933-53). Three thermometers—nos. 1008, 1011 and 1257. Little change in period under review. Maximum shift of zero was 0.03° , minimum 0.02° . Two thermometers showed major drift between 1933 and 1949; the zero of the remaining one was constant between these dates but shifted 0.03° between 1949 and 1953. Of Richter and Wiese's make and it is virtually certain that they were made, and originally calibrated by the P.T.R., before 1925. This information cannot now be checked (see p. 233). One known check by P.T.R., two by N.P.L.; thermometers nos. 1011 and 1257 extensively used, especially the latter.

19-group (1934-53). Three thermometers—nos. CD 5556, 5559 and 5563. All from one batch of twelve made by Negretti and Zambra. Maximum drift of zero, 0.05° , minimum 0.02° . One thermometer normal, with rise of zero point over whole period; the remaining two, after a rise between 1934 and 1949, showed a fall of zero between 1949 and 1953. All checks by N.P.L. Although extensively used, the behaviour of the whole batch was generally erratic. It is only fair to say, however, that after a lapse of many years Negretti and Zambra had not long begun again to make reversing thermometers.

18-group (1935-53). Three thermometers—nos. 863, 883 and 1019. Zero points remarkably constant over period but, as in the 20-year group, it is virtually certain that the calibration by the P.T.R. in 1935 was a re-calibration, and that the thermometers were originally calibrated there in 1924 or 1925. All made by Richter and Wiese. One check by P.T.R., two by N.P.L.

16-group (1937-53). Two thermometers—nos. CG 11309 and CG 15243. Sole survivors of two separate batches of six instruments each. Zero of no. 11309 shows a steady rise over the whole period; that of no. 15243 fluctuates. Of Negretti and Zambra's manufacture. All calibrations by N.P.L. Both thermometers used extensively but CG 11309 was, at times, rather erratic.

15-group (1938-53). Fifteen thermometers—nos. CH 17798 etc., and CH 22676 etc. comprising eight and seven thermometers respectively from two batches of twelve made in 1938 by Negretti and Zambra. First batch shows in general a much more regular drift of zero than the second batch, of which all now under review had a nil correction to zero at first calibration. No obvious reason for this difference is apparent; both batches were made by the same, and at that time the senior, operative on this work. All checks by N.P.L. Extensive use generally, with only a few minor and unimportant failures.

Normally, a shift of zero point should be reflected equally in the scale corrections throughout the whole range of a conventional thermometer, and this holds good also for protected reversing thermometers. Correction graphs for each calibration of all the thermometers listed in Table 1 have been drawn and, with only a few exceptions, there is a considerable similarity in the general trend of the correction curve at each calibration of individual thermometers. Those made by Richter and Wiese show, in general, less variation in the scale corrections required over the whole range, and over the years but, despite the larger and sometimes more irregular scale corrections required to a number of the thermometers made by Negretti and Zambra (possibly because of a slightly more irregular bore in the glass tubing), there is a more marked similarity in the trend of the various calibration curves for each instrument. Since it is easier to demonstrate the change of zero and scale corrections graphically,

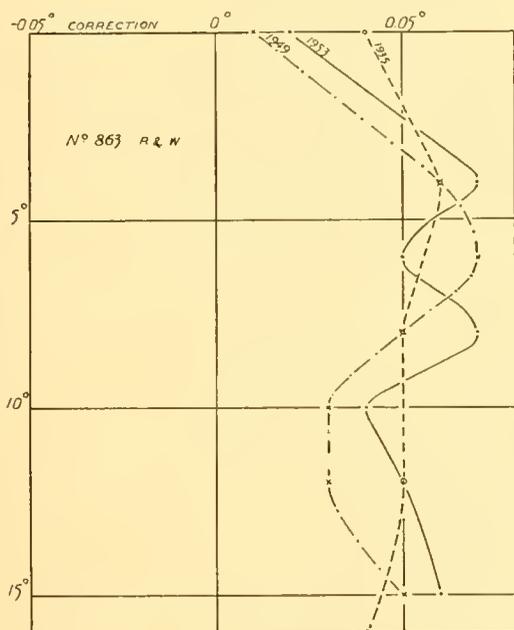


Fig. 1

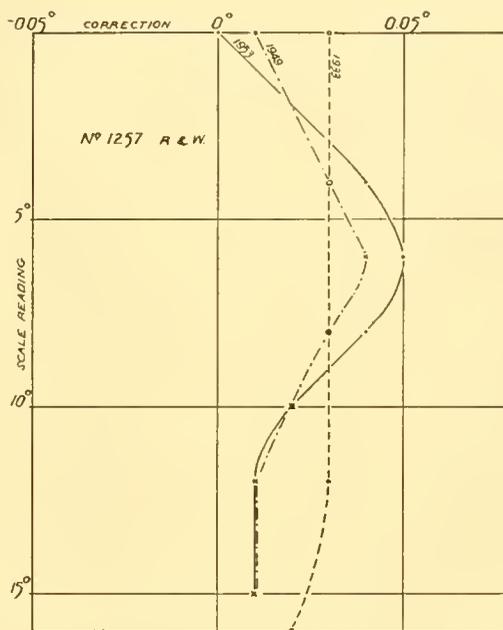


Fig. 2

typical correction graphs for two German and three British thermometers have been selected and appear as Figs. 1-5. Each comprises the correction curves for the various calibrations, with the actual scale correction plotted against the scale range.

EFFECT OF THE VOLUME OF MERCURY (V_0)*

Of the thirteen German-made thermometers listed in Table 1 three (nos. 863, 1011 and 1257) have been extensively used, especially no. 1257 with which 459 observations were made between 1928 and 1939. Four others were used to a lesser degree, whereas the remaining six appear to have had little or no use. Unfortunately the early history of these thermometers is obscure as notes on their performance were not regularly kept. We cannot say, therefore, whether they are reliable, or whether they had been used and found erratic.

On the other hand the stock of reversing thermometers carried in the ships has always been well in excess of immediate demands. Once in use a good working set of thermometers remained so until individual instruments were lost, or broken, or became erratic in their action. In these circumstances

* V_0 is the volume of mercury, in degrees, reversed at 0° C. It is determined for each thermometer by the maker. It is not, so far as we are aware, re-determined at any subsequent re-calibration.

it was quite possible for a thermometer only to have been brought into use for a few stations at the end of a commission (normally twenty months), or not to have been used at all.

Nevertheless, it is perhaps significant that the constant V_0 for three of the German thermometers least used is $>200^\circ$ (max. 265°). This large value for V_0 inevitably entails a large and often badly shaped expansion chamber at the top of the bore, and so to a tendency for the mercury to stick in this

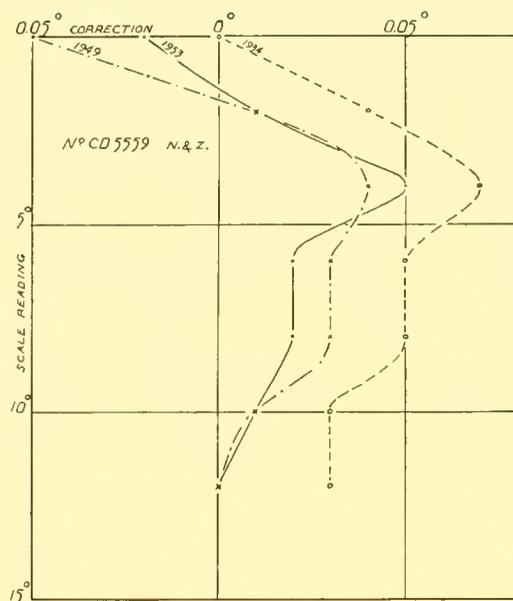


Fig. 3

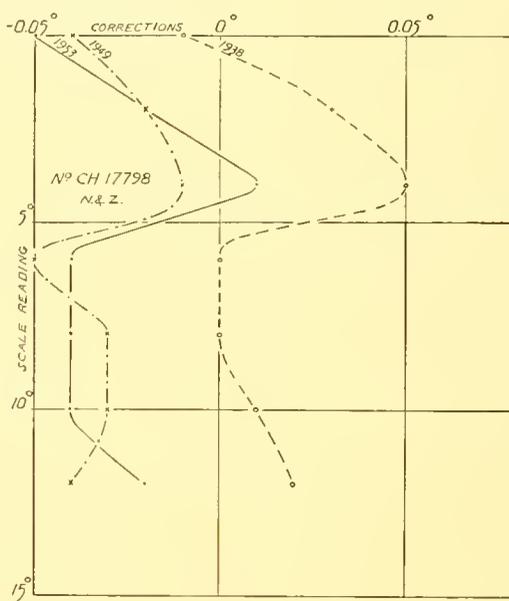


Fig. 4

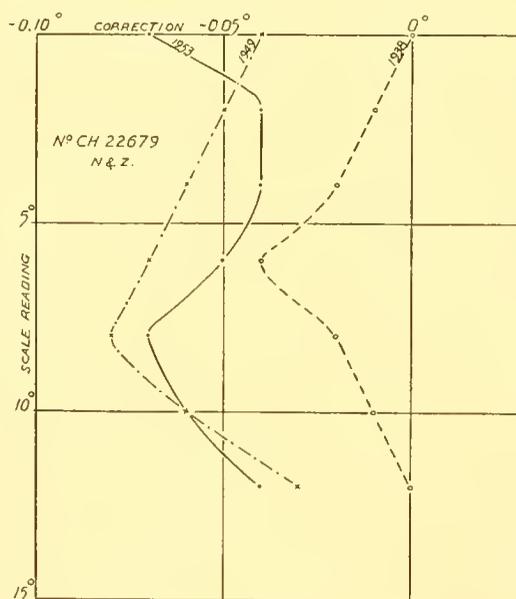


Fig. 5

chamber, instead of running back to the main bulb, when the thermometer is reset. It has already been mentioned that at the N.P.L. check in 1953-4 three other German-made thermometers of the earlier age groups (24, 22 and 20 years) failed to meet the requirements for a certificate. All were condemned for the same failure, i.e. the mercury column did not break at the constriction unless the thermometer was tapped. For these instruments the value for V_0 was less than half the figure mentioned above, but was still considerably larger than that of present day thermometers.

V_0 differs from thermometer to thermometer. Some years ago its value varied widely (reference to Table 1 shows a variation between 49° and 265°) but it has now been stabilized—at any rate in British instruments—within what appear to be reasonable limits, though the size of the expansion chamber is still determined to some extent by convenience of construction, and no two manufacturers are likely to agree on an ideal size. It is, however, generally agreed that high volumes should be avoided. It might perhaps be thought that the different weights of mercury below the constriction with different values of V_0 would be reflected in the performance of individual thermometers; this, as mentioned above, does not appear to be borne out in practice. So far as we can see there is no connection between V_0 and the performance of a thermometer, other than the tendency of those with a high V_0 for the mercury to stick in the expansion chamber.

INCIDENCE OF FAILURES

In Table 2 the number of successful temperature observations is related to the number of failures. It is based on (a) the scientific log-books kept in the ship for each voyage since 1925 which record all deep-sea temperatures taken, together with the thermometer numbers; (b) the temperature correction

Table 2. *Number of observations and incidence of failures in German and British thermometers*

Ship	Commission	Make of thermometer and number of observations		Failures			
		German	British	German		British	
				No.	Age (%)	No.	Age (%)
Discovery	1925-7	678	—	24	3.5	—	—
William Scoresby	1926-7	150	—	18*	12	—	—
William Scoresby	1928-9	926	—	26	2.8	—	—
Discovery II	1929-31	1777	137	38	2.1	4	2.9
William Scoresby	1929-31	363	—	11	3.0	—	—
William Scoresby	1931	941	—	13	1.4	—	—
Discovery II	1931-3	2275	1780	55	2.4	14	0.8
Discovery II	1933-5	2486	901	53	2.1	40†	4.4
Discovery II	1935-7	2921	129	45	1.5	10‡	7.7
Discovery II	1937-9	762	3334	25	3.3	37	1.1
William Scoresby	1950	84	111	2	2.4	6	5.4
Discovery II	1950-1	242	1861	5	2.1	21	1.1

* Mostly one erratic thermometer.

† Mainly one poor batch of thermometers.

‡ Mostly due to one erratic thermometer from 1933/5 batch.

Table 3 summarizes the figures in Table 2 for the whole period 1925-51.

Table 3. *Summary of Table 2*

Make of thermometer	No. of observations	Failures	
		No.	Age (%)
German (R. and W.)	13,605	315	2.31
British (N. and Z.)	8,253	132	1.60
Totals	21,858	447	2.04

books kept from 1933 onwards; and (c) a thermometer log kept personally by one of the writers of this paper. Separate figures are shown for British and German thermometers and failures have only been classified as such when due to one or other of the following: mercury failing to break at the constriction, mercury sticking in the expansion chamber when the thermometer is reset, and uncertain causes of anomalous temperatures. No account has been taken of the erratic behaviour of thermometers after

being in collision, or suffering shock of any other kind, nor have losses on station, or accidental breakages, been included. When a thermometer suspected of giving anomalous readings was checked several times against a reliable thermometer only one 'failure' was recorded for the whole series of comparisons.

In view of the difficulty of making reversing thermometers, and the unavoidably rough usage which they receive at times in bad weather at sea we think it is remarkable that the overall percentage of failure—just over 2%—is so low. Ignoring the continued use by the 'William Scoresby', in 1926–7, of one erratic thermometer, the percentage failure of German-made thermometers for the period 1925–51 averaged 2.25 and, in general the performance of these instruments was remarkably steady. The earliest figure of 3.5% failures, in 1925–7, was on the first occasion of their use, and before we had experience in spotting idiosyncrasies. Later, in 1931 in the 'William Scoresby', and in 1935–7 in the 'Discovery II', almost the same set of reliable German thermometers was in use throughout each period, with a consequent and marked reduction in the number of failures. For the 'William Scoresby' the percentage of failure was 1.38 for 941 observations, and for 'Discovery II' 1.54 for 2921 observations.

Except for the commissions of 1933–5 and 1935–7 of 'Discovery II', when the number of failures was increased considerably by the use of one rather erratic batch of thermometers (of which three, nos. CD 5556, 5559 and 5563 remain in use), the British-made deep-sea reversing thermometers have been equally, if not more, satisfactory. They have maintained their accuracy well and for all other commissions of 'Discovery II' they were extensively used (for 7112 temperature observations out of a total of 8142), with a percentage of failure of only 1.07. Even if the figures for the 'William Scoresby's' commission of 1950 are included, this percentage failure is increased only to 1.17.

UNPROTECTED DEEP-SEA REVERSING THERMOMETERS

Earlier in this paper it was mentioned that only two pre-war unprotected reversing thermometers had survived for comparison with each other. Actually, four such instruments remain but of these the history of two is obscure. They do not appear to have been used, nor to have been re-calibrated more than once, and their characteristics have not therefore been considered. In addition, fifteen post-war unprotected thermometers remain from a batch made in 1949; some of these were fairly extensively used in 'Discovery II' in 1950–1 and all have since been re-calibrated once. The scale limits of both pre- and post-war instruments is -2° to $+60^{\circ}$ C.

ZERO POINT

One of the pre-war thermometers (no. CC 14318) was calibrated by the N.P.L. in 1933, 1950 and 1954. A normal rise of zero point ($+0.04^{\circ}$ C.) was observed over this period but there is little resemblance between the trend of the scale corrections in 1933, and those of later years, though closer agreement exists between these last determinations. The scale corrections for thermometer no. CG 15290 (determined in 1937, 1949 and 1954) show no agreement whatsoever between the various calibrations. A correction graph for each thermometer comprising the various scale corrections at each calibration has been drawn. These appear as Figs. 6 and 7. On the other hand, the scale corrections for the fifteen post-war instruments show a remarkable similarity in their trend at their re-calibration in 1954. Only in three instances has there been no shift of zero point since the original check in 1950; for the remainder there is the normal rise, which is reflected equally throughout the scale.

MEAN PRESSURE COEFFICIENT ('Q')

The mean pressure coefficient (m.p.c.) used in calculating the depth from the reading obtained upon reversal of an unprotected deep-sea thermometer, and referred to in the depth equation as 'Q', is defined as the increase in apparent temperature, in ° C., due to a pressure of 1 kg. per sq. cm. The determination of this coefficient is made at the N.P.L. by supporting the thermometer in a stout steel cylinder, containing a light oil. The cylinder is immersed in melting ice (0° C.), and pressure is applied and maintained constant for a suitable time to establish thermal equilibrium. The cylinder containing the thermometer is then reversed, and the thermometer is removed and immersed in ice to the reading.

Prior to 1950 the m.p.c. given on all certificates issued by the N.P.L., in respect of this type of thermometer, was determined at three points on the scale; since 1950, however, determination has been made at only two points. The average pressures applied at the original calibration and the limits of the scale reading (for existing N.I.O. thermometers) are shown in Table 4 below.

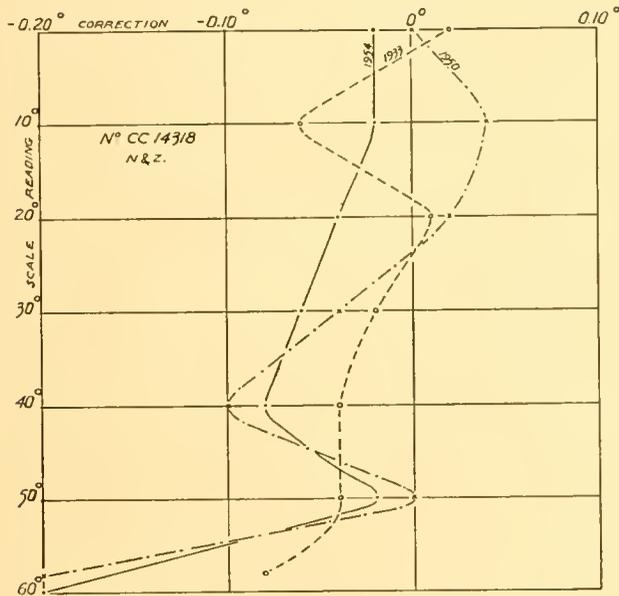


Fig. 6

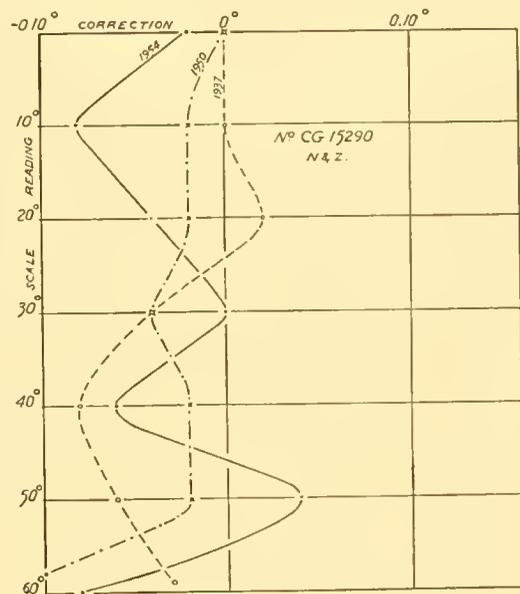


Fig. 7

Table 4. Limits of accuracy of mean pressure coefficient

Average test pressures in kg./cm. ²		Range of increased thermometer reading in ° C. (approx.)*	Estimated accuracy of m.p.c. (° C. per kg./cm. ²)
3-point determination	2-point determination		
157.5	—	13-17	± 0.0005
283.5	284.74	24-30	± 0.0002
525.2	537.20	45-56	± 0.0001

* Different for each thermometer, as it is dependent on the diameter of the capillary and thickness of the walls of the bulb.

In most unprotected thermometers the m.p.c. is remarkably constant over the range of pressure covered by the calibration and is about 0.1° C. per kg./cm.². Reference to Wüst (1932) shows that out of forty-seven thermometers of this type carried by the 'Meteor' only in one instance was there any difference greater than 0.0010° C. kg./cm.² in the m.p.c. at the original calibration, over the whole test range. On the return of the 'Meteor' the surviving thermometers were re-calibrated and the change in the average m.p.c. noted. Differences varied between nil and 0.0013, with an average for

eighteen thermometers of 0.0004. After the sixth commission of the 'Discovery II' (1950-1) nineteen unprotected thermometers—all of British make—remained available for use. Four of these were of pre-war origin; the remainder were made in 1949. Seventeen were re-calibrated in 1954 and, for reasons which will be explained later, a more detailed check of the m.p.c. has been made in respect of four of these. So that comparison can easily be made with the 'Meteor' thermometers, the particulars relating to the 'Discovery II's' thermometers have been similarly arranged in Table 5, but without the full particulars of the detailed check.

With one exception the figures in Table 5 show a marked stability in the m.p.c. Not only is there close agreement between the values at different points on the range of individual thermometers but, as in the German-made thermometers of the 'Meteor' Expedition, little change has occurred over periods varying between four and seventeen years. These figures, in fact, indicate that determination of the m.p.c. from observations at atmospheric pressure and at two elevated pressures is probably sufficient, and that an average of the values thus obtained is sufficiently accurate for all depth calculations in dynamical oceanography. It is interesting to note that certificates issued by the P.T.R., between 1925 and 1931, in respect of unprotected thermometers made by Richter and Wiese, and held by the Discovery Committee, gave only one value for the m.p.c. to cover the whole scale range. In view of the information available from Wüst's critical examination (1932) it is virtually certain that this value for the m.p.c. was an average of two or more determinations at different points on the scale.

As we have already shown (Table 4) the lowest range on the scale over which the m.p.c. for the N.I.O. thermometers was determined was 0° to about 13° C., for determinations at three elevated pressures. For 2-point determination the lowest range was 0° to about 24°. Recently, one fishery research laboratory has found it necessary to use unprotected thermometers at much shallower depths than hitherto considered necessary. All thermometers of this type then held by them had been certified by the N.P.L. for m.p.c. at the usual three points, and they inquired whether it would be correct to assume that, if these values were plotted, a value for the m.p.c. at a lower point on the scale could be obtained by extrapolation. At the time of this query all the unprotected thermometers listed in Table 5 were with the N.P.L. for re-certification. It was arranged that some of them, instead of being checked only at the now-customary two points, should be checked over the whole range. Four thermometers, nos. CC 14318, DI 18225-6 and DI 18232 were chosen and observations made at seven elevated pressures. The estimated accuracy of the measurement of increase of thermometer reading after the application of pressure was $\pm 0.05^\circ$ C. This uncertainty affects the computed value of the m.p.c. by an amount which varies with the pressure range used. For example, at a pressure of 34.80 kg./cm.², the estimated accuracy of the m.p.c. was ± 0.0015 while at 536.41 kg./cm.² the value was ± 0.0001 . From the figures obtained it seemed at first sight that extrapolation of the m.p.c. for scale points below the normal test points would be difficult but, when the increase of the thermometer reading was examined arithmetically, and graphically, it was found that this increase was linear within the limits imposed by the uncertainty of the actual measurements. Taking into consideration the other errors which may occur in field-work, it is unlikely therefore that any additional small error due to taking a mean m.p.c. over the whole pressure range will have a significant effect on the computation of depth, the limit of accuracy of which is approximately ± 1 m. for each 1000 m. of depth.

Table 5. Calibration of unprotected thermometers for mean pressure coefficient

Thermo- meter no.	Date	Original calibration			Average	Re-calibration 1949-50 (average m.p.c.)	Re-calibration 1954 (average m.p.c.)	m.p.c. Difference between first and last check	Number of times used (total for all commissions)
		Test pressure (kg./cm. ²)	m.p.c.						
CC 14316	1933	157.5	0.0990	} 0.0988	0.0990	—	0.0002	161	
		283.5	0.0988						
		551.2	0.0987						
CC 14318	1933	157.5	0.1004	} 0.1005	0.1005	*0.1012 (0.1007)	*0.0007 (0.0002)	243	
		283.5	0.1005						
		551.2	0.1006						
CG 15290	1937	157.5	0.1066	} 0.1072	0.1078	0.1078	0.0006	67	
		283.5	0.1071						
		519.5	0.1079						
CG 15291	1937	157.5	0.1086	} 0.1097	Not tested	0.1106	0.0009	—	
		283.5	0.1098						
		519.5	0.1107						
DI 18225	1950	284.74 537.20	0.0955 0.0953	} 0.0954	—	*0.0955 (0.0954)	0.0001	104	
DI 18226	1950	284.74 537.20	0.0946 0.0948	} 0.0947	—	*0.0945 (0.0946)	*0.0002 (0.0001)	108	
DI 18227	1950	284.74 537.20	0.0956 0.0957	} 0.0956	—	0.0956	Nil	79	
DI 18228	1950	284.74 537.20	0.1043 0.1045	} 0.1044	—	0.1045	0.0001	68	
DI 18229	1950	284.74 537.20	0.0948 0.0949	} 0.0948	—	0.0949	0.0001	81	
DI 18230	1950	284.74 537.20	0.0942 0.0942	} 0.0942	—	0.0944	0.0002	17	
DI 18231	1950	284.74 537.20	0.0956 0.0958	} 0.0957	—	0.0956	0.0001	13	
DI 18232	1950	284.74 537.20	0.1047 0.1050	} 0.1048	—	*0.1046 (0.1047)	*0.0002 (0.0001)	—	
DI 18233	1950	284.74 537.20	0.0958 0.0960	} 0.0959	—	0.0962	0.0003	—	
DI 18234	1950	284.74 536.88	0.0950 0.0953	} 0.0951	—	0.0949	0.0002	—	
DI 18235	1950	284.74 536.88	0.0950 0.0950	} 0.0950	—	0.0950	Nil	—	
DI 18236	1950	284.74 537.20	0.0956 0.0956	} 0.0956	—	0.0958	0.0002	—	
DI 18237	1950	284.74 537.20	0.0951 0.0950	} 0.0950	—	0.0950	Nil	—	
DI 18238	1950	284.74 537.20	0.0960 0.0962	} 0.0961	—	0.0962	0.0001	—	
DI 18239	1950	284.74 537.20	0.0953 0.0953	} 0.0953	—	0.0953	Nil	—	

* Average of seven determinations. The figure in parentheses below is the average of the three, or two, test points corresponding to those of the original calibration.

SUMMARY

1. Observations over many years leave little doubt that deep-sea reversing thermometers, both of the protected and unprotected types, remain, with few exceptions, very reliable.
2. Failures to show an accurate temperature are few, only 447 being noted out of a total of 21,858 observations.
3. It is suggested that the reason for one type of erratic behaviour, hitherto not understood, may be due to some temporary physical change in the glass.
4. There is little difficulty in the field in reading temperatures to $\pm 0.01^{\circ}$ C.
5. The use of a series of unprotected reversing thermometers on a cast of water-bottles to measure the depth at which the bottles closed will record these depths within a limit of approximately ± 1 m. for each 1000 m. of depth.

This paper has been read in manuscript by Dr G. E. R. Deacon, C.B.E., F.R.S., and Dr N. A. Mackintosh, C.B.E.; to them we are indebted for encouragement and advice. We should also like to thank Mr R. Harrison, lately of Messrs Negretti and Zambra, for his valuable help in respect of some of the technical aspects of the manufacture of deep-sea thermometers.

Mention should also be made of the valuable work of the late Mr J. G. Durham of the N.P.L., who for many years calibrated and re-calibrated a large proportion of the deep-sea thermometers now under review.

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OCTOCORALS
PART I. PENNATULARIANS

By

HJALMAR BROCH

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OCTOCORALS

PART I. PENNATULARIANS

By Hjalmar Broch

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(Plates XI and XII, text-figures 1-5)

INTRODUCTION

THE Discovery collections of pennatularians are not very extensive. This is not especially surprising, because the structure of the species living at greater depths and their mode of life on the muddy bottom enable them to escape most collecting gear, a fact emphasized on an earlier occasion (Broch 1957).

The collections include the following species:

Cavernularia elegans (Herklots)

Veretillum cynomorium (Pallas)

Actinoptilum molle Kükenthal

Renilla mülleri Kölliker

Umbellula lindahli Kölliker

Pennatula rubra Ellis

Pteroëides griseum (Bohadsch)

With the exception of *Umbellula lindahli*, all the species belong to the coastal shelf waters and mostly to shallow depths above some 100 m. *Renilla mülleri* is an American species, whereas the others belong to the Atlanto-African fauna, *Actinoptilum molle* being known only from the coastal waters of South Africa.

The genus *Umbellula* was represented by comparatively rich material from Antarctic waters, and I therefore seized the opportunity to make a critical study of the much disputed species of this genus. An introduction to such a revision has recently been published in the report on the pennatularians of the Swedish Deep-Sea Expedition (Broch 1957). A broader survey on the other hand, necessitated both material from different areas as well as a re-examination of types described from earlier expeditions: especially those from the 'Challenger' Expedition. This work was made possible by a grant from the National Institute of Oceanography; I am greatly indebted to Dr N. A. Mackintosh who arranged this for me, thus allowing me to extend the scope of my study beyond the strict limits of the Discovery collections.

Prior to 1939, Mrs L. M. I. MacFadyen (née Dean) worked on these collections at the British Museum, but for various reasons she was unable to write an account. After the war the whole collection was sent to me for report, together with her valuable notes. By agreement with Mrs MacFadyen I have made full use of these notes as indicated in the text.

My work at the British Museum (Natural History) was facilitated in every way by Miss Helene E. Bargmann of the staff of the National Institute of Oceanography, and by Dr W. J. Rees and Mr Ernest White of the Museum. I wish to express my gratitude for their never-ceasing aid and counsel on all occasions.

VERETILLIDAE

SOME GENERAL REMARKS ON THE FAMILY

Hickson (1916) emended the definition of this family to include the genus *Actinoptilum*, which Kükenthal and Broch (1911) had united with *Echinoptilum* in the family Echinoptilidae, the zooids having more or less distinctly developed calices. Hickson maintained that the 'calices' mentioned by Kükenthal and Broch in *Actinoptilum* were verrucae not calices. It is not clear, where we ought to draw the line between a calix and a verruca; in *Actinoptilum* these structures are quite rudimentary and consist only of two rather small, low teeth. Two corresponding teeth have been developed in *Echinoptilum*; indeed in *E. echinatum* they are remarkably large, and in this species Hickson did acknowledge them to be part of a calix. But it is impossible to tell whether the smaller teeth of *Actinoptilum* are a commencement (oriment) or the remnants (rudiments) of a calix or a verruca.

Much more stress must be laid on the external symmetry. Hickson quite correctly pointed out that the external features of *Actinoptilum* show no hint of bilateral symmetry and that accordingly the right place for the genus was among the Veretillidae. He also maintained that the Veretillidae are 'sea-pens in which the autozooids and siphonozooids are distributed without any definite arrangement in horizontal or longitudinal rows'. This statement, however, cannot be accepted. Both in *Veretillum* and in *Actinoptilum* longitudinal furrows divide the surface of the rachis into obvious longitudinal ribbon-like fields, each of which generally shows a single row of autozooids placed at somewhat varying intervals, so that they do not form regular transverse rows. Drawings of living specimens of *Veretillum cynomorium* (Kükenthal and Broch 1911, pl. XIII, fig. 1) show that in this species the siphonozooids form a single longitudinal row in the middle of the ribbon-like field, whereas in *Actinoptilum molle* they are irregularly placed, crowded on the 'ribbon', and generally arranged side by side.

Hickson (1916) agreed with Kükenthal and Broch (1911) that the Veretillidae probably stand near the ancestral sea-pens. After examination of specimens from the 'John Murray Expedition' and comparison with specimens from other collections, Hickson (1937) wrote: 'The consideration of these specimens confirms the view that I ventured to put forward in 1918 (p. 131) that in these radially symmetrical Veretillidae we have the most primitive forms of the Pennatulacea.' However, it is not clear, whether in this case he was referring to the genus *Cavernularia*, or the Veretillidae as a whole.

It is impossible to tell which form of spicules is the most primitive. But it is obvious that the spicules of the radially symmetrical Veretillidae in general are much more variable than those of the externally bilateral sea-pens. The development of the spicules has not yet been determined in the Veretillidae; nevertheless, there is much to be said for regarding the flat biscuit-shaped spicules as the most primitive. They occur in *Veretillum* and *Actinoptilum*, where an axis is wanting, as well as in the axiferous genus *Lituarina*. In *Actinoptilum*, however, the biscuit-shaped spicules are restricted to the stalk, whereas the rachis has three-flanged, rod- or needle-shaped spicules similar to the dominant type in the bilaterally symmetrical groups. The genus *Cavernularia*, in the wide sense of Hickson (1937), on the other hand, displays a great variation both in form and disposition of the spicules. In some species they are restricted to the surface layer, in others they also occur in great numbers in the inner tissues of the stalk. The spicules may be of uniform shape throughout, or they may have one shape in the surface tissues and another in the interior of the specimen. In one species the spicules are knobbed or branched at their ends, in others oval, slender spindles or needle-shaped. A revision of this genus is indeed needed, but must be based on extensive investigation of the variations and behaviour in living specimens.

Cavernularia elegans (Herklots 1858)

(Synonymy before 1910, see Kükenthal and Broch 1911.)

Cavernularia elegans + *C. madeirensis* + *C. pusilla*, Kükenthal 1915, pp. 15-17, figs. 19, 20.

St. 274. Off Angola, W. Africa, 65 m. 1 specimen (identified by Mrs MacFadyen).

In a note Mrs MacFadyen gives the following data concerning the specimen: 'A small club-shaped colony very similar in appearance to Kükenthal and Broch's photograph (1911, Pl. 18, fig. 29) shows

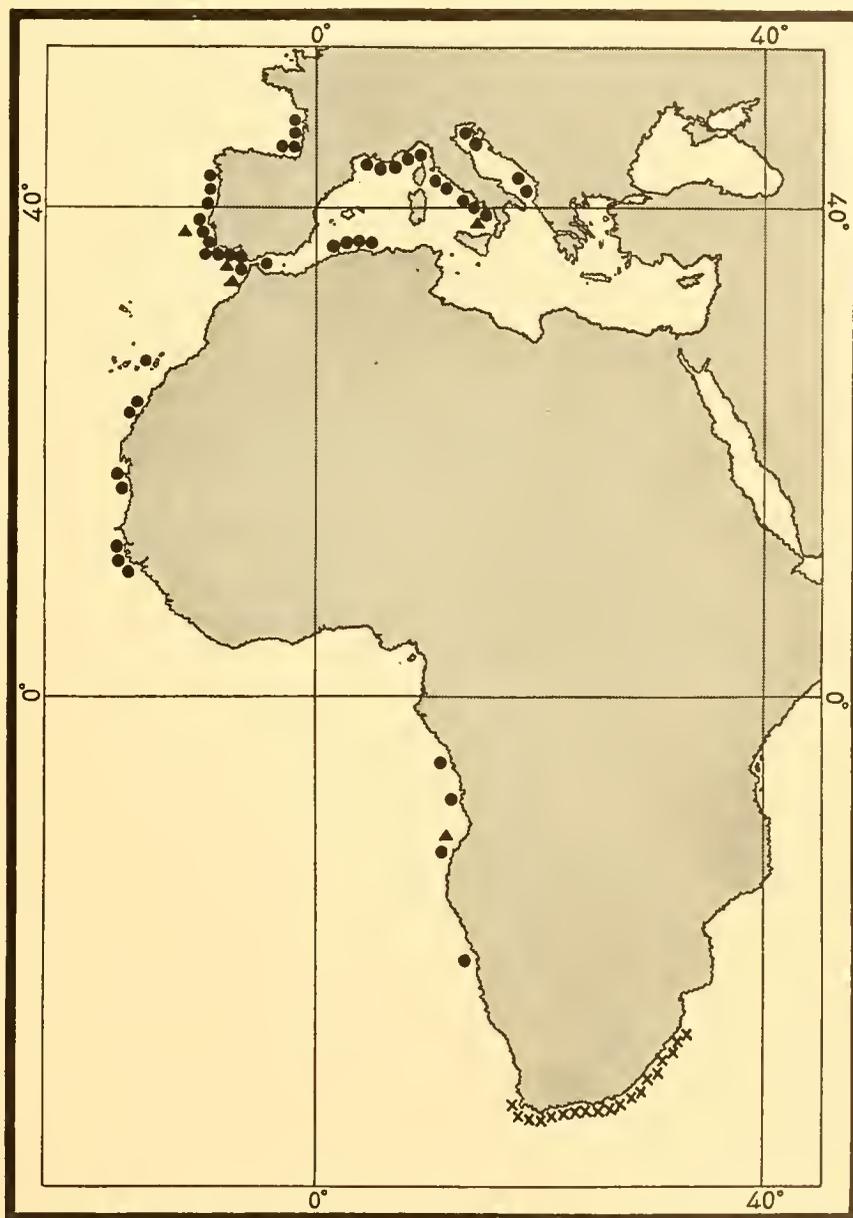


Fig. 1. Chart showing the distribution of *Veretillum cynomorium*, *Actinoptilum molle*, and *Pennatula rubra*. ● *Veretillum cynomorium* (mainly after Pax and Müller, 1954). × *Actinoptilum molle*. ▲ *Pennatula rubra*.

a head [rachis] 2.3 cm. long and 1.2 cm. broad and a stalk, 2.7 cm. long and 4 mm. broad at the top, 7 mm. broad near the base. The autozooids are up to 4 mm. long (excluding the tentacles) and 3 mm. in diameter. The siphonozooids are numerous, scattered between the autozooids on the head. There is no axis. The spicules are of the usual needle-like *Cavernularia* type. Small groups of minute almost rounded spicules ['calcareous concretions' Broch 1957] are formed in the inside of the stalk, a point

in which the species differs from *C. obesa* (also without an axis) which has larger and more numerous spicules inside the stalk.

'The colour of the colony is creamy with a dark brownish ring on the polyp just below where the tentacles arise.'

The species has been recorded both from the Indian Ocean and Japan, but Kükenthal (1915) queried these localities. Evidently these records need confirmation. The habitat of *C. elegans* almost coincides with that of *Veretillum cynomorium* (text-fig. 1), but exact positions along the West African coast are remarkably scanty, although the species is said to be a shallow-water form. *Cavernularia madeirensis* Studer 1878 is certainly a synonym, and the Mediterranean *C. pusilla* (Philippi 1835) also is based on a small specimen of *C. elegans*. Consideration of Kükenthal's (1915) definitions does not reveal any distinguishing characters of importance between all these three species.

It is correct to say that the Discovery specimen represents the first exact location of the species on the West African coast, all earlier statements being given in general terms. Studer (1878) was a little more precise in describing *C. madeirensis* from 90 m. depth on the west coast of Madeira, and Roule (1905) recorded the same species from the Atlantic Ocean near Morocco in 99 m. Kükenthal and Broch (1911) reported that *C. pusilla* was found at Palermo and Sicily, and Kölliker (1872) also queried a record from the Adriatic.

Veretillum cynomorium (Pallas 1766)

(Synonymy before 1910, see Kükenthal and Broch 1911.)

V. cynomorium Kükenthal 1915, p. 12, figs. 12, 13.

V. cynomorium Stuart Thomson 1923, p. 59.

V. cynomorium J. A. Thomson 1927, p. 63.

V. cynomorium J. A. Thomson 1929, p. 10.

V. cynomorium Nobre 1931, p. 34.

V. cynomorium Broch 1953, p. 10.

V. cynomorium Pax & Müller 1954.

V. cynomorium Pax & Müller 1955, p. 90.

St. 272. Off Elephant Bay, Angola, W. Africa, 43-91 m. 2 specimens (identified by Mrs MacFadyen).

In a note Mrs MacFadyen writes: 'The larger has a total height of 8.5 cm. and a stalk of 1.7 cm. They are both quite typical specimens of this radially symmetrical Pennatulid. The colour is pale cream.'

Pax and Müller (1954) have recently given a review of the distribution of *V. cynomorium*, a species characteristic of the tropical and temperate eastern Atlantic and Mediterranean (text-fig. 1). The northern limit of its habitat is evidently the Bay of Biscay, and its southern border lies somewhere south of the great Bay of Whales, South Africa, where Kükenthal and Broch (1911) reported its occurrence. According to Stuart Thomson (1923) the species has not been found on the South African coast south and east of Saldanha Bay. Probably the colder currents check its advance just south of the Bay of Whales.

The species is limited to the shallower shelf-waters above some 100 m. If the identification of the specimen from 540 m. depth near the Canaries (28° 47' N, 13° 44' 45" W, J. A. Thomson 1927) is proved to be correct, this occurrence probably depends on an erratic specimen which has managed to grow up and continue to live, in spite of having sunk to the bottom far below its normal habitat. Similar cases have been observed in other benthic animals; it is necessary to regard them with caution and not immediately to deduce an extended normal habitat from these probably sporadic occurrences.

Actinoptilum molle Kükenthal 1910

Cavernularia obesa + *C. elegans* Hickson 1900, Part I, p. 89, Pl. 3, A, B.

Actinoptilum molle Kükenthal 1910, p. 51.

Actinoptilum molle Kükenthal & Broch 1911, p. 201, Pl. 13, figs. 3, 4; Pl. 18, fig. 37.

A. molle Kükenthal 1915, p. 20, fig. 22.

A. molle J. Stuart Thomson 1915, p. 3, Pl. 1, figs. 3, 4.

A. molle Hickson 1916, p. 41.

A. molle J. Stuart Thomson 1923, p. 81.

St. 91. False Bay, South Africa, 35 m. 4 specimens (identified by Mrs MacFadyen).

In a note Mrs MacFadyen writes: 'The largest 20.5 cm. in length of which 6.5 cm. consist of the rachis. In our specimens the colour of the stalk is pale yellow, of the rachis very pale pink, the polyp-tentacles are pale yellow, the polyp anthocodiae with deep red spicules. The vertical lines in the rachis as figured by Kükenthal and Broch are clearly seen.'

In the British Museum 5 additional specimens were examined: (1) 'South Africa', J. Stuart Thomson (S. J. Hickson coll.); (2) Gilchrist coll., St. 145, 29° 40' 30" S, 31° 20' 00" E, 42 fm. 12 July 1920; (3) Gilchrist coll., St. 188, 29° 36' 30" S, 31° 16' 30" E, 33 fm. 12 August 1920 (2 specimens); (4) Gilchrist coll., St. 453, 33° 34' 30" S, 27° 09' 05" E, 40 fm. 1 September 1920.

Stuart Thomson (1915) pointed out that *Actinoptilum molle* 'is probably the most common Penatulid in South African Seas'. Later on he (1923) emphasized 'that it occurs in the colder water of Table Bay as well as in the warmer of Algoa Bay and False Bay'. The depth of the habitat ranges from 35 m. (Discovery St. 91) and down to 183 m. ('Pieter Faure' 1902).

The remarkably restricted habitat of *A. molle* (text-fig. 1) is rather astonishing, especially when we consider Stuart Thomson's words which indicate considerable tolerance to changes in temperature; one might therefore expect the species to penetrate farther northwards from Table Bay along the western coast of South Africa, although east of False Bay and as far as the east coast of Natal it is found living in warmer water. A limiting factor must exist, but with the data available it cannot be determined at present. The species may be found to disappear where the cold Benguela Current impinges on the coast.

RENILLIDAE

Renilla mülleri Kölliker 1872

(A complete synonymy of this American species was given by E. Deichmann 1936.)

St. W.S. 742. Off the southern coast of Chile, 38° 22' S, 73° 41' W, 58-47 m. 5 specimens.

The specimens are large and of a light violet colour. Deichmann writes that the species is distributed over 'Gulf of Mexico, Venezuela, Brazil—coast of Chile, west coast of Central America'. It seems unknown, whether the distribution along the South American coast is continuous, or if a gap exists southwards from Brazil along the Patagonian coast round the southern Chilean coast to the locality at which the species was taken by 'William Scoresby'.

UMBELLULIDAE

REVISION OF THE GENUS *UMBELLULA*

In a recent paper (1957) I have given some comments on the taxonomy of *Umbellula*, beginning with the remark that 'certainly too many species have been described within this genus'. Both Kükenthal and Broch (1911), Kükenthal (1915) and Hickson (1916) gave extensive reviews of the genus, but a thorough critical revision of the species is needed and can to a large extent only be achieved by examination of the type specimens kept in museums all over the world.

As emphasized in my paper (1957) I agree with Hickson (1916) that the *Umbellula* species fall into two main groups, viz. those with spicules, and those without. On the other hand, I cannot share Hickson's opinion that the shape of the axis (especially above the hold-fast), whether quadrangular or round in section, is only of subordinate value taxonomically. To a marked degree, this shape is correlated with calcification: round axes generally being rather poorly or almost uncalcified, whereas quadrangular axes are as a whole heavily encrusted with lime. This character is doubtless constant in and characteristic of a species. It is necessary to emphasize that we are speaking of the axis, and not of the stem or the stalk with its cover of soft tissues (cf. the remark about Marshall's description of *U. gracilis*, p. 255).

Before going into details concerning the species of *Umbellula* and their synonymy, the following key may clarify the important taxonomic characters:

KEY TO THE SPECIES OF *UMBELLULA*

I. With spicules.

A. Axis round, only feebly encrusted with carbonate of lime and very flexible. Two kinds of spicules, large and small, all round in transverse section, feebly fusiform or rod-shaped, often the larger with somewhat knobbed ends, and sprinkled with granulations. *Umbellula durissima* Köll.

B. Axis quadrangular, rather rigid and strongly encrusted with carbonate of lime. Spicules rod- or needle-shaped with three longitudinal ridges or flanges, sprinkled all over with small spines or warts.

U. thomsonii Köll.

II. Without spicules.

A. Axis round, almost devoid of lime, thin and extraordinarily flexible.

(1) Cluster with rather small autozooids concentrated in a pompon on the distal end of the rachis.

U. huxleyi Köll.

(2) Clusters with large autozooids irregularly placed on a rather long rachis forming a tassel.

U. spicata Kükenthal

B. Axis quadrangular, richly encrusted with carbonate of lime.

(1) Axis thin but rigid and rather brittle. Autozooids numerous and small, packed in a pompon on the short distal end of rachis. Specimens at most some 35 cm. high. *U. pellucida* Kükenthal

(2) Axis variable, but generally rather thick and flexible. Autozooids large, in colder waters generally very large and often very numerous in the tassels and not especially crowded. Full-grown specimens seldom as small as 40 cm. *U. lindahli* Köll.

(The arctic *U. encrinus* L. is more robust in its entire construction. Its axis is thicker than that of *U. lindahli* which does not seem to exceed 2 mm. in its thinnest part just below the polypiferous rachis. The autozooids are larger than those of *U. lindahli*. Possibly only an extreme form of this species, see p. 270.)

SPICULATE SPECIES OF *UMBELLULA*

The rich collection of *Umbellula* from the Swedish Deep-Sea Expedition indicated that as yet only two species with spicules can be distinguished with certainty. These species are above all characterized by the shape and structure of their spicules and by the construction of the axis.

Umbellula durissima Kölliker 1880

U. durissima Kölliker 1880, p. 16, Pl. 8, figs. 32, 33.

U. durissima + *U. dura* J. A. Thomson & W. D. Henderson 1906, pp. 92, 93, Pl. 8, fig. 9.

U. durissima + *U. dura* J. A. Thomson & J. Ritchie 1906, p. 859, Pl. 1, fig. 5.

U. eloisia Nutting 1912, p. 43, Pl. 6, figs. 3, 3a.

U. durissima + *U. dura* + *U. eloisia* Kükenthal 1915, p. 56.

U. durissima Hickson 1916, p. 126.

U. durissima Broch 1957, pp. 360, 363, text-fig. 7, Pl. 1, fig. 5.

This very characteristic species has dimorphic spicules: (1) Spicules up to 3 mm. long form a narrow band along the aboral side of the pinnulae adjoining the strong band of similar large spicules along the aboral side of the tentacle stem, a short way below its base on the anthocodia. (2) Small fusiform spicules crowded in the surface tissues of autozooids and rachis. All the spicules are round in section, they are never three-flanged. The axis is round in section and remarkably feebly calcified in contrast to the heavy armoured autozooids with their calcareous spicules.

(Holotype: British Museum (Nat. Hist.). Reg. No. 1881. 2. 11. 21.)

Umbellula thomsonii Kölliker 1874

U. thomsonii Kölliker 1874a, p. 13.

U. thomsonii Kölliker 1874b, p. 10, Pl. 1, figs. 1-5.

U. thomsonii + *U. Güntheri* + *U. leptocaulis* + *U. simplex* Kölliker 1880, pp. 18-20, Pl. 9, figs. 34-36.

Non-*U. Güntheri* A. Agassiz 1888, p. 314.

Non-*U. Güntheri* Studer 1894, p. 57.

U. crassiflora Roule 1905, p. 456.

U. intermedia + *U. rosea* + *U. Köllikeri* Thomson & Henderson 1906, pp. 94, 95, 97, Pl. 5, fig. 5.

U. Hendersoni Balss 1910, p. 68, footnote.

U. Güntheri Broch 1913, p. 3, Pl. 1, fig. 1.

U. thomsonii + *U. Güntheri* + *U. rosea* + *U. crassiflora* + *U. intermedia* + *U. simplex* Kükenthal 1915, pp. 52, 54, 56-58.

U. aciculifera J. Stuart Thomson 1915, p. 20, Pl. 2, fig. 2, text-fig. (on p. 21).

U. Güntheri Hickson 1916, pp. 120 *et seq.*

U. aciculifera J. Stuart Thomson 1923, pp. 49 *et seq.*

U. Güntheri + *U. thomsonii* Deichmann 1936, pp. 268, 269.

U. Güntheri Broch 1957, p. 351, Pl. 1, fig. 1, text-figs. 1-3.

This very characteristic species is easily identified by its three-flanged spicules (Broch 1913) and its strongly calcified, quadrangular rigid axis.

Discussing the synonymy of *U. Güntheri* Kölliker 1880, I (Broch 1957) suggested the possibility that both *U. leptocaulis* Kölliker and *U. simplex* Kölliker (1880) had been founded on young specimens of *U. Güntheri*. An examination of the original specimens in the British Museum has fully corroborated the suggestion.

In the same place (1957, p. 357) the position of *U. thomsonii* Kölliker 1874 was also touched upon, but owing to discrepancies in the different papers of Kölliker (1874a, 1874b, 1880) and the interpretations of Kükenthal (1915), I found the problem so confused that it was impossible to solve it without a study of Kölliker's types, although most statements indicated *U. Güntheri* to be a synonym of *U. thomsonii*.

Kölliker based his descriptions of *U. thomsonii* on two specimens from the 'Challenger' Expedition (1880, p. 19, specimens A and B). The smaller specimen B could not be found in the collections of the British Museum;* according to Kölliker its height was 270 mm., but the specimen was defective. Specimen A has accordingly been selected as the lectotype of *U. thomsonii*. Kölliker wrote that the specimen was 895 mm. high and complete. However, the upper part with the autozoid cluster has now been broken off just below the swollen rachis. The upper limit of the holdfast cannot be ascertained with certainty, and the basal 'bulb' is contracted and not discernible.

Text-fig. 2 shows the position of the autozooids; it is a little at variance with the descriptions both of Kölliker (1874a, 1874b, 1880) and Kükenthal (1915). Originally there was one primary polyp (hatched in text-fig. 2) and twelve secondary autozooids, but two of the latter (stippled in text-fig. 2) had been cut away. The primary polyp and nine secondary autozooids are arranged in a whorl, and can be regarded as a direct continuation of the developmental sequence demonstrated by me (1957,

* Presumably the specimen was kept by Kölliker as a reward for working out the collection.

text-fig. 1) in *U. güntneri*. In addition to the autozooids forming the whorl, three fullgrown autozooids are found on the inner side of the ring, evidently displaced or pushed to the inner side of the whorl at intervals between autozooids of the outer circle. This displacement may possibly be due in part to a contraction of the rachis, especially in the case of the single displaced autozooid (unstippled in text-fig. 2). But the two inner autozooids on the other side are more likely to have budded inside the whorl. As far as we can judge from the literature, this specimen is the largest *U. thomsonii* examined up till now. This may explain the 'irregular' arrangement of the autozooids as compared with Broch's (1957) specimens. Probably very large clusters will be found to exhibit a more or less complete inner whorl of autozooids.

The re-examination of Kölliker's type thus confirms the synonymy of *U. thomsonii* and *U. güntneri*, and the first name must therefore have the priority.

(Lectotype: British Museum (Nat. Hist.) Reg. No. 1881. 2. 11. 23. Kölliker's Specimen A designated on p. 253, paragraph 4 as the lectotype).

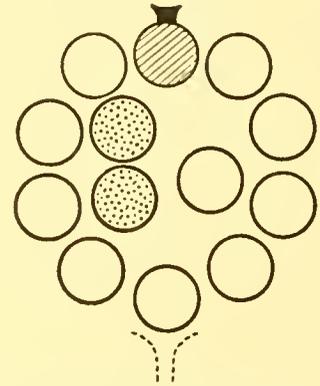


Fig. 2. *Umbellula thomsonii* Köll. (Specimen A, lectotype). Diagram of the arrangement of the autozooids in ventral aspect. The primary polyp hatched, the two autozooids which have been cut away stippled.

NON-SPICULATE SPECIES OF *UMBELLULA*

In this second group of *Umbellula*, variations in, and contraction of specimens make the limitation of species exceedingly difficult, and specialists have wavered in their interpretations between a couple of species only, or a vast number, describing practically every new specimen as a new species. Here, of course, degrees of contraction have been welcomed as 'specific criteria'.

In these non-spiculate forms also, the shape of the axis is a comparatively reliable character, but again it is necessary to study the naked axis and not to judge by a superficial survey when the axis is enveloped in its more or less fleshy, inflated or contracted coverings.

Apparently nobody has studied the axis of the *Umbellula* species with the aim of determining the role of the calcareous incrustation. In taxonomic literature, among the specific characters often given is the possession of either a 'rigid', or a very flexible, stem. (It should be mentioned here that living pennatularians and their axes are throughout much more flexible than preserved specimens.) Where the calcareous incrustation of the axis is very scanty or almost wanting, the horny structure in some cases is rather more spongy than fibrous, and in such cases compression may distort it to a certain degree. The anatomical structure of the surrounding sheaths of the holdfast (or stalk) and their system of canals may then give the false impression that the axis was approximately quadrangular, and it is essential to make a critical study of the axis itself, its structure and the degree of calcareous incrustation.

The non-spiculate species fall into two groups: A, with a round axis, only very little if at all incrustated with lime, and B, with a quadrangular axis rather heavily incrustated with calcareous matter.

Group A

Axis round, devoid of lime, very flexible.

Umbellula huxleyi Kölliker 1880 (Pl. 1, Figs. 1a, b)

U. huxleyi pars Kölliker 1880, p. 21, Pl. 9, figs. 37a, b.

U. gracilis A. M. Marshall 1883, p. 142, Pl. 25, figs. 29-35.

U. huxleyi Nutting 1909, p. 711.

U. huxleyi Kükenthal & Broch 1911, p. 290, Pl. 21, fig. 54.

U. gracilis Broch 1913, p. 6, Pl. 1, figs. 2, 3.

U. huxleyi + *U. gracilis* Kükenthal 1915, p. 53.

U. huxleyi Hickson 1916, pp. 122 seq.

Non-*U. huxleyi* Hickson 1937, p. 119.

This species was described by Kölliker from the 'Challenger' Expedition. In his report he mentions four specimens (A–D), one of which (C) is missing,* whereas the other three are in the collections of the British Museum (Nat. Hist.). The specimens, which according to their size and structure must be his A and B, have quadrangular axes; they are evidently young specimens of *U. lindahli*; they are discussed under this species on page 264. It is, however, quite clear that Kölliker really based his work on the largest specimen D, which he carefully described and figured. Specimen D has accordingly been selected as lectotype of *U. huxleyi*.

Kölliker wrote: 'Axis indistinctly quadrangular', evidently basing his definition on specimens A and B, caught in the same haul and assigned to the same species as D. (As mentioned above, these two specimens have now been assigned to *U. lindahli*.) The axis of the lectotype D is round throughout in section; the holdfast ('stalk'), which according to Kölliker is 34 mm. long, is also round. The axis is only very little thicker than the 'stem' and without any hint of quadrangularity. The thickening of the 'stalk' is due to greater development of the coenosarcal tissues which show some longitudinal wrinkles, suggesting a more or less angular section in the part shortly above the 'bulb'.

Kölliker assumed that the species was 'indistinctly bilateral in the fully developed stage'. Kükenthal (1915) on the other hand wrote: 'Die Zooide . . . stehen . . . am Schopfkessel dichter und nur ein dorsales Feld freilassend, gehen aber nicht auf das von den Polypen umschlossene innere Feld über'. In young specimens also this seems to be partly the case. Kölliker's type specimen D has no naked field dorsally between the siphonozooids on the swollen rachis below the autozoooid cluster, and although siphonozooids are apparently absent between the bases of the autozoooids in the lectotype, they have been observed in this position in larger specimens than those from the 'Challenger' and 'Valdivia' Expeditions. These two specimens are of about the same size, 180 and 193 mm., respectively, but the polyp clusters differ markedly in the development of their autozoooids. The lectotype has 18 autozoooids, ranging from mere buds to fully developed polyps; but a primary polyp is not distinguishable, and it is impossible to describe any arrangement in whorls. The 'Valdivia' specimen had only 6 autozoooids. The dorsal one, which was a little smaller and placed a trifle above the circle, was considered to be the primary polyp; the autozoooid to the left of the primary polyp was also a little smaller than the other four secondary autozoooids. Nevertheless, the 'Valdivia' specimen evidently belongs to the same species as the 'Challenger' lectotype of *U. huxleyi*.

U. gracilis Marshall, from the 'Triton' Expedition, is also probably synonymous with this species although two of Marshall's statements might seem contradictory. He says (1883, p. 143): 'Stem cylindrical along the greater part of its length, becoming quadrangular in the terminal dilated part.' A glance at his drawing (1883, Pl. 25, fig. 29) shows at once that Marshall does not refer to the axis but to the entire stem and holdfast, and that he is really describing the longitudinal furrows caused by contraction of the ample tissues surrounding the lower and somewhat thickened part of the (round) axis. Marshall does not especially confine himself to the axis but uses the confusing phrase 'the stem or calcareous axis'. Here, however, we must remember that the four longitudinal main canals of the stalk-tissues (when contracted) always cause the thicker holdfast to appear more or less distinctly square, independently of the shape of the axis, whether round or square.

* See footnote, p. 253.

The other discrepancy lies in Marshall's introductory words, where he summed up the specific characteristics as 'distinctly bilateral'. However, his drawings (1883, Pl. 25, figs. 29, 30) clearly show that the bilateral arrangement of autozooids in the cluster is also quite rudimentary in his rather small specimen, and that, to cite his own words, 'it is difficult to make out any definite plan of arrangement of the polyps'.

Kölliker's specimen from the 'Challenger' and the statements of Kükenthal and Broch (1911) all indicate a similar rudimentary bilateral arrangement in young specimens of *U. huxleyi*, and Marshall evidently had a young stage of this species.

The large specimen of '*U. gracilis*' described from the 'Michael Sars' Expedition (Broch 1913) with a total length of 547 mm. had no less than 25 autozooids crowded together in the cluster which was almost globose (a pompon) because the polypiferous distal part of the rachis was extremely short. No bilateral arrangement of the autozooids could be traced, nor was it possible to point out any primary polyp because the axis did not run into the wall of any autozoid, but terminated in the swollen rachis.

In 1955 Dr A. R. Longhurst collected no less than 17 specimens of *huxleyi* in one haul with an otter trawl off Bissagos I. (Port Guiana) on a muddy bottom in 600 m. depth. This collection was generously placed at my disposal, and Dr Longhurst informed me that the comparatively large holdfasts ('stalks') of the specimens were rather strongly inflated and pulsating, when they came on deck. This is the first time apparently that pulsation has been observed in an *Umbellula*, and confirms the view that the lower part of the stem is, and also ought to be termed, a holdfast for digging into the mud.

Most of Longhurst's specimens measure about 27–28 cm. in length, three or four are a little shorter, as small as 18 cm. The specimens with two exceptions were stowed together and crushed into a container, so that it is impossible to count the autozooids in the clusters. Nevertheless, it can be seen that these agree with the polyp clusters described by Marshall (1883) and Broch (1913). Two specimens (Pl. 1, fig. 1a, b) had been picked out and preserved in a special glass container; they give an excellent impression of the specific characteristics.

The smaller specimen (b) has 14 fully developed autozooids and a 15th bud in the central part of the cluster. Eight of the autozooids constitute an outer (basal), somewhat irregular whorl, the others are crowded within this whorl and rather irregularly arranged. No primary polyp can be traced with any certainty, and with exception of the bud, the autozooids are of all but equal size. In the larger specimen (a), 10 autozooids constitute the outer (basal), very irregular whorl, and eight other autozooids of the same size are irregularly crowded within it showing no bilateral arrangement. It is impossible to trace a primary polyp. The largest autozooids of the outer whorl (excluding the tentacles) measure 17 mm. in length with a breadth of 3.5 mm. The autozooids of this specimen contain numerous eggs, whereas no eggs were observed in the smaller specimen.

Although of subordinate importance, it should be noted here that the tentacles of the preserved specimens are comparatively short in most adult autozooids, measuring $\frac{1}{3}$ to $\frac{1}{2}$ of the body length. In a few polyps the tentacles are more extended, being as long as or even longer than the body. The largest autozooids were found in the basal whorl. The dimensions are the same whether the specimens were filled with eggs or were sterile adult autozooids.

Symmetrical features are displayed with varying distinctness. In a few cases there is a strip without autozooids along the dorsal side of the swollen rachis, where it is possible to discern the almost hair-thin terminal part of the axis ending in the basi-dorsal wall of one of the autozooids, which is probably the primary polyp, although not differing in any way from the other autozooids. In every richer cluster, however, the upper part of the axis has been completely buried in the tissues of the rachis, and the polyp-free dorsal strip has disappeared completely; every trace of bilateral arrangement has

also been obscured by the larger clusters, the tightly packed autozooids being grouped on an extremely short terminal part of the rachis.

In these two best preserved specimens, siphonozooids were observed everywhere on the rachis, both between the autozooids and on the rapidly tapering part below the cluster. It was impossible to find any siphonozooids on the extremely thin upper part of the stem as well as on the holdfast.

The axis is extremely thin. In its upper part, immediately below the cluster, its diameter is scarcely 0.5 mm., nor does it increase until the middle of the stem is reached; from here downwards the axis slowly grows stouter and attains its greatest diameter—about 1 mm.—in the middle of the holdfast, tapering again towards the basal end. This entirely agrees with Marshall's observations, and with his remark that 'for the greater part of its length the stalk is extremely flexible, so much so that it can readily be coiled in circles of 5 mm. diameter without the slightest danger of breaking'. Although in live specimens the flexibility of the axis in most other deep-living, slender pennatularians is also great, such an extreme flexibility like that of *U. huxleyi* is very seldom encountered. It must be correlated with the extraordinarily scanty calcareous incrustation. On the other hand, the species has a very efficient holdfast, as shown by the photographs (Pl. 1, fig. 1). These two characters explain why the species has been reported from remarkably few localities, although its habitat, as collections show, is very extended and shallower than those of most other species of the genus.

Hickson's (1937) *U. huxleyi* with its rigid and quadrangular axis belongs to *U. pellucida* (see p. 261).

U. huxleyi is characterized by its obviously concentrated, pompon-like cluster, whereas the second spicule-free species *spicata* with a round axis is distinguished by the long, spaced tassel of very slender, long autozooids.

(Lectotype: British Museum (Nat. Hist.). Reg. No. 1881. 2. 11. 25. Specimen D of K lliker, 1880.)

Umbellula spicata K kenthal 1902 (Pl. 1, fig. 2)

U. spicata + *U. valdiviae* K kenthal 1902, p. 594.

?*U. elongata* + *U. radiata* + *U. pendula* Thomson & Henderson 1906, pp. 96, 98, 99, Pl. 7, fig. 6.

U. spicata + *U. valdiviae* K kenthal & Broch 1911, pp. 294, 295, Pl. 16, figs. 17-19, Pl. 20, fig. 51a, b; Pl. 21, figs. 52, 53.

U. spicata + *U. valdiviae* + *U. elongata* (?) + *U. radiata* (?) + *U. pendula* (?) K kenthal 1915, pp. 53, 55, 57, fig. 60.

According to K kenthal and Broch (1911), *U. spicata* and *U. valdiviae* differ as follows: *U. valdiviae* has a weak, more slender stem (this is not perceivable in the excellent figures). The rachis is not so contracted ('viel dicker') in *U. valdiviae* as in *U. spicata*. In *U. valdiviae*, the tentacle pinnulae alternate in size, whereas they increase successively in length towards the end of the tentacle in *U. spicata*. Neither of these features, which obviously are results of contraction, nor the differences in the arrangement of the siphonozooids mentioned in the detailed description, furnish a sufficient *fundamentum divisionis*. It must also be emphasized here that none of the specimens from the 'Valdivia' Expedition were adult.

In the collections at the British Museum (Nat. Hist.), an unrecorded specimen is labelled '1914. 1. 27. 1. Between Aden & Bombay, 13° N, 76° E, 600-700 fthms. J. E. Purton.' The specimen is broken, the lower part of the stem with the holdfast is in three pieces, whereas the upper part of the stem with the rachis and the large autozoid-tassel is comparatively very well preserved (Pl. 1, fig. 2). If these four fragments represent the entire specimen, its total length was about 55 cm., including the 9.5 cm. long rachis with its cluster of autozooids. In the lower part of the rachis the autozooids are placed in a couple of very indistinct whorls round the stem, but in the upper two-thirds or more, no regularity in the arrangement of the autozooids can be traced. These are separated by

comparatively large interspaces, especially on the lower part of the rachis, whereas all interspaces, as well as the tapering part of the rachis below the autozooids, are packed with comparatively prominent siphonozooids.

The autozooids are remarkably slender and long, in spite of the basal halves being filled with eggs. The length of the polyp body is up to 35 mm., but the breadth never exceeds 3 mm. The pinnulae do not show any features of taxonomic importance, their lengths evidently varying with the degree of contraction.

The salient feature of *U. spicata* as compared with *U. huxleyi* is the remarkable length of its rachis. This is very obvious on comparison of specimens in the photographs on Pl. 1, the autozooids of which are filled with eggs or larvae. The photographs also show that the reticulation of the surface of an autozooid does not depend on its being ripe, as was maintained by Hickson (1937, p. 120).

In the British Museum specimen the rachis occupies about 17% of the entire height, but in other specimens found hitherto it does not seem to be more than 10%. This long and slender rachis is thus a specific character, which however does not appear until, with growth, more autozooids have developed (cf. Kükenthal and Broch 1911, Pl. 16, fig. 19, and Pl. 20, fig. 51). In quite young specimens the autozooids show a bilateral arrangement, which however very soon disappears with the irregular budding of secondary autozooids on all sides of the rachis.

The British Museum specimen also presents other features which are of special interest. The upper part of the axis is round in section, but about the middle, or a little lower down, the axis is almost square, and this continues till the upper limit of the holdfast, whence the circular section continues to its lower end. It is remarkable that in the region with the square section the axis has an obviously loose structure and that calcareous incrustation seems to be completely wanting. This structure strongly recalls that of *U. huxleyi* and is evidently connected with the great flexibility of these specimens compared with species whose axes are rich in lime incrustation. The central core also of the axis in *U. spicata* is much looser in structure than the surface layer, and in some places below the middle length the axis even seems to have a central lumen. It is probable that such axes may become partially compressed into a square shape, by strong contractions of the sheath, e.g. when irritated by the unusual environment in the trawl, net, or when placed in preservative. This distortion has probably led some investigators to disregard the value of the normal shape of the axis as a taxonomic character. In *U. spicata* the British Museum mature specimen shows that a round axis with an extraordinarily loose or almost spongy structure in part, or even with a central lumen, is one of the specific characteristics.

It is probable that *U. elongata*, *U. radiata* and *U. pendula* Thomson and Henderson (1906) must be included among the synonyms of *U. spicata*, but the descriptions are so incomplete and expressed in such general terms, and the drawing of *U. elongata* is so schematic, that it is impossible to determine their identity without examination of the original material.

Group B

Axis quadrangular, encrusted with lime.

In the second group of *Umbellula* without spicules the axis is quadrangular and strongly encrusted with calcareous matter. A long series of species has been described from all waters, together with the type species of the genus, the arctic *U. encrinus* (L. 1758), which seems to be confined to the deep waters of the Arctic Ocean, north of the ridges separating them from the Atlantic. *U. lindahli* Kölliker 1874 has been reported from the Atlantic Ocean, southwards from Greenland; *U. ambigua* Fischer 1889 (Marion 1906) from the central Atlantic; and more recently, *U. carpenteri* Kölliker 1880 has been shown to have a circumglobal habitat (Broch 1957). Kölliker described *carpenteri* from

Antarctic waters together with *U. magniflora* Kölliker 1880, and the 'Valdivia' Expedition brought back a third species, *U. antarctica* Kükenthal 1902, from the same area. Two species from the Indian Ocean were also erected in 1902 by Kükenthal, *U. rigida* and *U. pellucida*, and several other species have been added since that date.

Both Jungersen (1907) and Hickson (1907) expressed their doubts as to the validity of the three antarctic species *carpenteri*, *magniflora* and *antarctica*. Jungersen who gave careful details concerning *U. carpenteri*, wrote (1907, p. 9): 'es kommt mir deshalb als sehr möglich vor, dass diese Art nicht nur noch grösser wachsen, sondern höchst wahrscheinlich die Zahl der Polypen bedeutend vermehren und die ganze Form des Schopfes ändern mag, mit anderen Worten sich den Typus der *U. encrinus* (oder deren antarktischen Vertreters der *U. magniflora*=*U. encrinus* var. *antarctica* Kkth.) mehr nähern kann'. In 1937 Hickson was inclined to go yet a step further, and discard the shape of the axis as a specific criterion, considering all spicule-free Umbellulae as one species.

It is appropriate to consider here the distinguishing characters which have been used in this group. In his key Kükenthal (1915) gave them as follows:

1.	{ Polypenträger kurz, Polypen annähernd in konzentrischen Kreisen stehend.	2
	{ Polypenträger lang, Polypen bilateral angeordnet.	11
2.	Achse vierkantig.	3
3.	Polypen ohne Spicula.	4
4.	{ Tentakel ebenso lang oder länger als der Polypenkörper.	5
	{ Tentakel kürzer als der Polypenkörper.	8
5.	{ Stock elastisch.	6
	{ Stock starr.	7
6.	{ Kiel äusserst dünn.	<i>U. lindahli</i>
	{ Kiel relativ dick.	<i>U. encrinus</i>
7.	{ Schopfkkelch lateral abgeplattet.	<i>U. carpenteri</i>
	{ Schopfkkelch dorsoventral abgeplattet.	<i>U. rigida</i>
8.	{ Polypen zahlreich in mehreren konzentrischen Kreisen	9
	{ Polypen in geringer Zahl in einem Kreise.	<i>U. magniflora</i>
9.	{ Polypen schlank und sehr gross.	<i>U. antarctica</i>
	{ Polypen dick, tonnenförmig und klein.	<i>U. pellucida</i>
11.	Achse vierkantig.	12
12.	Polypen ohne Spicula.	13
13.	{ Tentakel lang.	<i>U. purpurea</i>
	{ Tentakel kurz.	<i>U. köllikeri</i>

A glance at this key immediately raises the question: how to distinguish between the terms 'short' and 'long'? None of the species mentioned in it has a rachis comparable with that of *U. spicata*, the only one which can be characterized as 'long'. It is also questionable whether a difference exists between arrangement in approximately concentric whorls and bilateral arrangement. The young specimens in most species are more or less bilateral; the older specimens generally have fairly distinct whorls, concentrically arranged, sometimes indistinctly bilateral.

The other characters of the key in most cases are questions of degree or gradation, or are due to different stages of contraction. Some (e.g. point 5, whether the stem is rigid or elastic) might seem legitimate; however, the more specimens we investigate, the more difficult are the cases we run up against. Specimens are always more flexible when first caught than later on, and, of course, dry they are always much more rigid and brittle than if wet; in formalin or spirit their condition is intermediate between these two extremes. Rigidity is correlated to a certain degree with calcareous encrustation, with size of the specimens, etc. It must also be emphasized that flexibility evidently increases to some extent with the thickness of the sheathing tissue, as can be observed in typical colonies of

'*U. antarctica*'. To a great extent development of these covering tissues seems to depend on ecological conditions.

Characters like 'thin' as opposed to 'relatively thick' must be said to intergrade, and lateral or dorso-ventral compression is doubtless due to contraction; on the other hand in *U. pellucida* the shape of the autozooids is to some extent characteristic.

Hickson (1916) also discussed the question of distinguishing between the many species of this group. In general terms he gives his view as follows:

- I. With a large number of autozooids (i.e. 40-50 in specimens of from 400-500 mm. in length) the autozooids being 20 mm. or more in body length.
 - A. Tentacles much shorter. *U. antarctica*
- II. With an intermediate number of autozooids (i.e. 15-40 in specimens 400-500 mm. in length).
 - B. With a quadrangular axis. *U. encrinus, U. Weberi*
- III. With a small number of autozooids (i.e. 8-15 in specimens 400-500 mm. in length).
 - A. With tentacles longer than the bodies. *U. Carpenteri, U. Lindahli, U. loma*
 - B. With tentacles shorter than the bodies. *U. Jordani, U. magniflora, U. pellucida*

It is evident that Hickson was of the opinion that the number of autozooids is comparatively constant in any single species of a certain length. Even allowing for the fact that as yet no specimen of e.g. *U. pellucida* as long as 400 mm. has been observed, the idea of a specific, characteristic, constant proportion between the length of the specimen and its number of autozooids is clearly disproved in my last paper (Broch, 1957 text-fig. 5), by the table of growth in *U. güntheri*, and again by the collections brought home by the Discovery Investigations.

In his key, Hickson only emphasizes in one place (II, B) the fact that the axis is quadrangular in two species of the group. Nevertheless, it is quadrangular in all species noted here in his table. The other character, the comparative length of body and tentacles in the autozooids, is of very little value because of the degree of contraction.*

Later on Hickson (1937) examined a great number of *Umbellula* from the Indian Ocean, which in spite of the quadrangular axis he named *U. huxleyi* Kölliker. Special attention was paid to the degree of contraction in relation to the sexual development of the autozooids, and Hickson came to the conclusion that 'it is obvious that pregnancy offers a physical impediment to contraction'.

It is usually quite easy to recognize the ripe from the barren autozooids without dissection, because the gonads in the former are clearly indicated by rectangular areas on the surface of the body wall. Such markings are clearly shown in Kölliker's figure (1880, pl. IX, fig. 37a) of *U. huxleyi*, and in Kükenthal and Broch's figure (1911, pl. XVI, fig. 17) of *U. spicata*. In the picture of *U. pellucida* (pl. XVI, fig. 20) by the authors of the 'Valdivia' Report the autozooids are strongly contracted, and there are no quadrangular markings on the body wall. No mention is made of the sexual condition of any of the species, but there can be little doubt that the two species, *U. spicata* and *U. pellucida*, are only ripe and barren forms of the same species, (according to Hickson).

It will suffice to point out that Kölliker's type specimen of *U. huxleyi* is a quite young, unripe *U. spicata* like Kükenthal and Broch's specimens of this species. The first known ripe specimen of *U. spicata* is figured in Pl. I, fig. 2; its surface is devoid of rectangular areas in the autozooids. The ripe specimen of *U. huxleyi* figured in Pl. I, fig. 1a also has smooth autozooids. Several specimens of '*U. huxleyi*' from the John Murray Expedition (re-examined by me in the British Museum (Nat.

* It might seem questionable, whether *U. loma* belongs to this group, because Nutting (1909) wrote that it has a few spicules on the swollen part of rachis below the polyp cluster, and one ought possibly to query it here. However, all other features suggest that the specimen is in its right place.

Hist.)) have autozooids packed with eggs, easily observable through the semi-pellucid, smooth body wall.

The examination of a very great number of spicule-free specimens shows that the proliferation and arrangement of the autozooids on the rachis afford specific characteristics, as indicated by Kükenthal and Broch in 1911. Later collections now give grounds for some further systematic regrouping.

In *U. spicata* as mentioned above, the rachis is remarkably long, and the autozooids bud irregularly. Siphonozooids of rather large size are crowded in the interspaces all over the rachis. Development results in a long, spaced tassel (Pl. I, fig. 2). Another more common developmental series is illustrated by *U. lindahli*. We might call it the *carpenteri-magniflora-antarctica* line. In the first stages the budding of autozooids shows a more or less distinctly bilateral arrangement, resulting in a ventral whorl lying distally on the rachis. Gradually the primary polyp is pushed into the central field of the whorl (or the upper part of the whorl dorsally encircles the primary polyp). During this 'magniflora phase' the short proximal part of the rachis beneath the autozooid whorl generally takes the shape of a bowl on the top of the stem, and in the inner (upper) central field additional autozooids are budded in more or less indistinct whorls. At the same time the distal part of the rachis develops into a short spigot covered all over by autozooids, the bases of which are surrounded by large siphonozooids. This cluster can be regarded as a tassel, although much more concentrated than the *spicata* type. This *antarctica* (or *encrinus*) type is furnished with a distinct, generally rather regular, basal whorl of long autozooids (cf. Pl. II, fig. 6).

In some species, however, the budding of autozooids is restricted to the short distal end of the rachis, and so concentrated that the cluster is more correctly regarded as an almost globose pompon as in *U. huxleyi* (Pl. I, fig. 1) or *U. pellucida* (Pl. II, fig. 3). Here the autozooids often seem so crowded that no room is left between them for siphonozooids.

Umbellula pellucida Kükenthal 1902 (Pl. II, fig. 3a, b)

U. pellucida Kükenthal 1902, p. 593.

U. purpurea pars Thomson & Henderson 1906, p. 95.

U. pellucida Kükenthal & Broch 1911, p. 300, Pl. 16, fig. 20; Pl. 20, fig. 50a-c.

U. pellucida Hickson 1916, p. 134, Pl. 4, figs. 25, 26.

U. huxleyi Hickson 1937, p. 119.

This species is one of the small *Umbellulae*, none of the specimens (about 250) examined attaining a length of 350 mm. and only quite exceptionally exceeding 300 mm. The species is evidently comparatively common in the Indian Ocean, and prefers lesser depths than most other species of the genus, seemingly above 1600 m., although a single specimen has been caught at 2001 m. depth by the John Murray Expedition.

'The axis in all the specimens is quadrangular in section: that is to say, it is marked by four shallow longitudinal grooves with four prominent rounded ridges. At the stalk end the ridges become shallower, and for a considerable distance the axis becomes almost circular in section. The greatest width of the axis of a large specimen is 1 mm.', wrote Hickson (1937) who had at his disposal 249 specimens.

These words at once tell us that the specimens do not belong to *U. huxleyi*, and examination of these specimens in the British Museum (Nat. Hist.) at once confirmed that they belong to *U. pellucida*. The structure of the axis is quite different from *U. huxleyi*; it is abundantly incrustated with lime and compact throughout; the stem is therefore only slightly flexible, and in preserved specimens rather rigid and brittle like other species with square axes.

Kükenthal and Broch (1911) described the autozooids in *pellucida* as barrel-shaped. This will depend in part upon the degree of contraction, and Hickson's (1916) drawings show funnel-shaped

autozooids which are evidently much more extended than those of Kükenthal and Broch (again reproduced by Kükenthal 1915), which were drawn on board the 'Valdivia' from living specimens. The autozoid cluster strongly recalls that of *U. huxleyi*. The autozooids are small and crowded on to the short distal part of the rachis, and as Hickson (1937) pointed out, their arrangement varies so much from specimen to specimen, that in most cases it is impossible to trace any regularity. In larger clusters the numbers of autozooids commonly amount to some 25 to 30. In several specimens a naked narrow dorsal field along the axis gives an impression of certain bilaterality in the pompon.

The specimens from the German 'Valdivia' Expedition had a somewhat thicker basal holdfast, the length of which according to Kükenthal (1915) measured one-sixth to one-quarter of the entire stem. In most of the specimens from the John Murray Expedition, this part is so contracted transversely that it is impossible to trace an upper limit of the holdfast.

Young specimens of *U. pellucida* are probably difficult to distinguish from those of *U. lindahli* in some cases, but developmental stages of *U. pellucida* have hitherto escaped the collectors; probably their dimensions will be very tiny.

In his review Kükenthal (1915) stated that there were no siphonozooids between the autozooids of the cluster, but that they only occurred on the swollen part of the rachis below the cluster and in small numbers on the thin stem. External examination of some of the specimens from the John Murray Expedition, the siphonozooids of which are very obvious on the rachis below the cluster, showed that no siphonozooids could be detected between the autozooids. This feature seems to be constant and therefore *pellucida* differs from the following species, *lindahli*, where comparatively large siphonozooids are present between the autozooids of the cluster.

Thomson and Henderson (1906) described an *U. purpurea* with round axis from the Indian Ocean. A 'cotype' of it had been deposited in the British Museum (Nat. Hist.). This specimen has evidently been regarded as a younger stage of *purpurea*, described from a type specimen with no less than 53 autozooids arranged in 4 whorls + 7 'at the tip that had no definite arrangement'. The cluster of the 'cotype' has only 11 autozooids, which measure some 5-6 mm. in length (without the tentacles). Eight of them, including the primary, largest polyp, are placed in one whorl, the last three in the central upper field within this whorl. All the autozooids are directed towards the ventral side of the specimen and give the entire cluster a decidedly bilateral appearance. The polyps are semi-pellucid and in all characters including the quadrangular axis recall *U. pellucida*; the axis obviously differs from the description of Thomson and Henderson. This cotype is evidently not *purpurea* but a rather young stage of *U. pellucida*. A renewed investigation of the type specimen of *purpurea* is needed to settle its identity.

Umbellula lindahli Kölliker 1874 (Pl. I, fig. 3, Pl. II, figs. 5, 6)

U. miniacea + *U. pallida* Lindahl 1875, pp. 12, 13, Pls. 1-3.

U. lindahli Kölliker 1874b, p. 11.

U. carpenteri + *U. magniflora* Kölliker 1880, pp. 23, 24, Pl. 10, figs. 38-40; Pl. 11, figs. 41, 42.

U. Bairdii Verrill 1884, p. 219.

U. Bairdii Verrill 1885, p. 509, Pl. 1, figs. 1, 2.

U. ambigua Fischer 1889, p. 37.

U. encrinus var. *antarctica* + *U. Köllikeri* + *U. rigida* Kükenthal 1902, pp. 595, 596.

U. lindahli Jungersen 1904, p. 75, Pl. 3, figs. 37-46.

U. ambigua Marion 1906, p. 146, Pl. 15, fig. 22.

U. carpenteri Hickson 1907, p. 12, Pl. 1, figs. 1-7.

U. carpenteri Jungersen 1907, p. 5, Pl. 1, figs. 1-10.

U. encrinus var. *ambigua* Stephens 1907, p. 21.

U. Jordani Nutting 1908, p. 564, Pl. 42, fig. 3.

U. loma + *U. magniflora* Nutting 1909, p. 710, 712, Pl. 87, fig. 9.

U. antarctica + *U. rigida* + *U. köllikeri* Kükenthal & Broch 1911, pp. 286, 292, Pl. 15, fig. 15; Pl. 26, fig. 16.

U. magniflora + *U. carpenteri* Nutting 1912, pp. 42, 43.

U. carpenteri Kükenthal 1912, p. 345, Pl. 23, fig. 22.

U. lindahli + *U. encrinus ambigua* + *U. carpenteri* + *U. rigida* + *U. antarctica* + *U. köllikeri* + *U. jordani* + *U. loma* Kükenthal 1915, pp. 48–50, 54, figs. 55–7.

U. antarctica + *U. Weberi* + *U. Jordani* Hickson 1916, pp. 128, 131, 133, Pl. 3, fig. 20; Pl. 4, fig. 24; text-fig. 29B, D, G.

U. encrinus var. *lindahli* Jungersen 1916b, p. 500.

U. encrinus var. *lindahli* Jungersen 1919, p. 1158.

U. encrinus var. *lindahli* Broch 1929, p. 149.

U. lindahli Deichmann 1936, p. 268.

U. encrinus Madsen 1948, p. 17.

U. carpenteri Broch 1957, p. 357, Pl. 1, figs. 2–4, text-figs. 4–6.

Under the name of *Umbellula carpenteri*, Kölliker (1880) gave a description of 5 specimens (A–E) from the ‘Challenger’ stations 156 and 157. Unfortunately, he did not say precisely from which station each specimen originated, and all of them have been merged in the same container. However, he mentioned that the specimens A–E exhibit ‘a very interesting gradation from a bilateral to an apparently irregular arrangement of the polyps’. Kölliker probably used the largest specimen E as the main base for his description. Specimen C is lost, but the specimens A, B, D and E are in the British Museum (Nat. Hist.). All are figured in Kölliker’s paper.

According to Kölliker, the type specimen E has eight polyps, arranged in the form of a rosette, and surrounding a ninth middle polyp like a cup; the axis terminated not in the ninth, but in one of the eight. It is, however, not possible to tell with certainty where the axis terminates if specimen E is examined. It does not end in the (dorsal) wall of the upper autozoid (see text-fig. 3, 1), but is bent inwards below its base, disappearing into the tissues of the rachis below the autozooids. This is the condition met with in *U. magniflora* (see below). Dissection would be necessary to determine whether the central, or the dorsal autozoid of the cluster is the primary polyp. In appearance the specimens resemble those from the Discovery collections which are intermediate between typical *carpenteri* and *magniflora* specimens.

In specimen D (Kölliker 1880, Pl. 10, fig. 39) all autozooids have contracted tentacles. In the same way as in *Cornularia* (Broch 1935) and *Solenopodium* (Broch and Horridge 1957) the tentacles seem to be laid together, stretched upwards and contracted like those of a slug by inverting the distal (oral) part of the body wall. It is interesting to note in this connexion that polyps with contracted tentacles have very seldom been found among over a hundred specimens of *Umbellula* which have passed through my hands. The specimen D (text-fig. 3, 2) has eight autozooids in one slightly irregular whorl. The conspicuously smaller, primary polyp is distinctly characterized by the terminal part of the axis running up to about the middle of its (dorsal) wall. The primary polyp has, on the other hand, been displaced a little to the inner side of the whorl, evidently by the outgrowth of the two adjacent secondary autozooids.

Specimen B (length 105 mm.) figured by Kölliker (1880, Pl. 10, fig. 39a) has 3 autozooids, the median of which is the primary polyp, the axis continuing in its (dorsal) wall till about one-third below the tentacle bases; there is a small knob where it terminates, but there seems to have been no free end of the rachis. The specimen differs a little from the youngest developmental stages from the Swedish Deep-Sea Expedition (Broch 1957), but corresponds with two small specimens from Discovery St. 181.

Specimen A which is only 51.5 mm. long, also has been figured by Kölliker (1880, Pl. 10, fig. 39*b*). His description runs: 'Four polyps, all lateral with a free end of the rachis, are visible in fig. 39, C.' The letter C must be due to a slip of the pen. The specimen is figured in dorsal (in Kölliker's terminology 'ventral') view. It seems to have escaped Kölliker's attention that a small but undeniable autozoid bud is placed ventrally between the two figured median autozooids (Pl. I, fig. 3); the cluster thus has 5, not 4 autozooids. This, however, does not alter Kölliker's implication in the text that no primary polyp can be traced. On the other hand, the obvious, free end of the rachis strongly recalls the young stages from the Swedish Deep-Sea Expedition, although in these a primary polyp is clearly to be seen (Broch 1957).

The Challenger collection in the British Museum (Nat. Hist.) also contains two more young stages of the species *lindahli*, viz. the two smaller specimens assigned by Kölliker to *U. huxleyi* (see p. 255). Their quadrangular axes differ from this species, and also their other features show that they belong to the same species which Kölliker thoroughly described under the name of *U. carpenteri*.

Kölliker (1880, p. 24) instituted another, new species, *U. magniflora*. Here the rachis is bowl-shaped, and as far as can be discerned in the type specimen, which is in a rather bad state, the axis enters from below centrally. It is impossible to see where it terminates, and it is also not possible to tell which of the autozooids might be the primary polyp. The arrangement of the autozooids (text-fig. 3, 3) is very like that in a specimen from 'Discovery' St. 371 with a total length of 46 cm. (Table, p. 266 no. 5). Kölliker's type has an outer whorl of 9 autozooids along the brim of the 'bowl' and in the centre, within it, one central autozoid of the same size as the marginal autozooids; finally, there is also one polyp bud below it as indicated in text-fig. 3, 3. Because of the brittleness of the specimen I did not venture upon a more thorough investigation. This specimen is without doubt only an individual variant, or growth form, of '*U. carpenteri*', a variant rather common among the specimens from subantarctic-antarctic waters, which are a little larger than those examined and mentioned by Hickson (1907) and Jungersen (1907) under the name of *U. carpenteri*. The size of Kölliker's specimen (740 mm. total length) corresponds with the smaller specimens of the '*magniflora*' stage from the Discovery collections.

A third antarctic *Umbellula* was announced in a preliminary paper by Kükenthal (1902) as *U. encrinus* var. *antarctica*. In his paper on *U. carpenteri* from the Belgian Antarctic Expedition, Jungersen (1907) hints at the possibility of all three antarctic *Umbellula* species being synonyms: 'es kommt mir deshalb als sehr möglich vor, dass diese Art nicht nur noch grösser wachsen, sondern höchst wahrscheinlich die Zahl der Polypen bedeutend vermehren und die ganze Form des Schopfes ändern mag, mit anderen Worten sich den Typus der *U. encrinus* (oder deren antarktischen Vertreters der *U. magniflora* = *U. encrinus* var. *antarctica* Kkth.) mehr nähern kann.' Kükenthal and Broch (1911), and Kükenthal (1915) raised the variety to a separate species *U. antarctica*, and Kükenthal distinguished between three antarctic species, viz. *U. carpenteri*, *U. magniflora* and *U. antarctica*.

The following table gives a list of the specimens from the Discovery collections:

Station	Depth (m.)	Remarks on the specimens
180	160	One specimen: total height 67 cm.
11 March 1927 Palmer Archipelago		3-4 irregular whorls of autozooids. The axis enters the centre of the bowl-shaped basal part of the rachis. Siphonozooids in all intervals between the autozooids, some of them with half extended tentacles. In spite of a very thin stem it is a typical <i>antarctica</i> specimen.
181	160-335	6 specimens.
12 March 1927 Palmer Archipelago		1 and 2, total height 7.5 cm. Both have only one pair of fully developed secondary autozooids, but whereas 1 only shows the first traces of a lower pair, in 2 this is seen as small buds (text-fig. 3, 4). The

Station	Depth (m.)	Remarks on the specimens
181 12 March 1927 Palmer Archipelago (cont.)	160-335	<p>terminal part of the axis ends in the dorsal wall of the primary autozooid, but does not project spine-like (cf. Broch 1957). The axis is very thin but distinctly quadrangular. 3, total length 47 cm.</p> <p>The primary polyp has been pushed to the inner side of the whorl by the dorsal secondary autozooids (text-fig. 3, 5). Siphonozooids distinct between the autozooids, a few with extended tentacles. Autozooids: body up to 2 cm., tentacles 1-2 cm. (In spite of the much greater size, the cluster of the specimen has only one autozooid more than the 14.8 cm. specimen figured by Jungersen (1907, Pl. I, figs. 1, 2), with which it otherwise agrees except in size of bodies of the autozooids which, according to Jungersen, measure only up to 8 mm.).</p> <p>4, total length 90 cm.; 5, total length 93 cm.</p> <p>The specimens were labelled <i>U. magniflora</i> by Mrs MacFadyen; they are in a bad state of preservation, but evidently showed the same features as specimen 6.</p> <p>6, total length 98 cm.</p> <p>In its upper part the axis is only 1.5 mm. thick and enters the centre of the bowl-shaped 'bottom' of the rachis, but from here it runs along the outer wall of the rachis to its brim, terminating at the base of an autozooid seated on the inner side of a whorl of 15 secondary autozooids. Inside this whorl the rachis is crowded by siphonozooids and seems hirsute because of the extended tentacles. Some of the siphonozooids of the lower side of the rachis also have extended tentacles. Typical <i>magniflora</i>.</p>
182 14 March 1927 Palmer Archipelago	278-530	<p>One specimen: total length 105 cm.</p> <p>Lower part of rachis bowl-shaped, axis entering its centre from below and disappearing. A few of the external siphonozooids have extended tentacles. 12 autozooids form a whorl along the brim, 3 more autozooids in the central upper field of the 'bowl'; the field is covered with hair-like tentacles of otherwise invisible siphonozooids. A primary polyp cannot be located. Some of the autozooids show the following lengths of body + tentacles in mm.: 4 + 4; 4 + 3.5; 3.5 + 4; 3.5 + 2.5; 3 + 2.5. Typical <i>magniflora</i>.</p>
366 6 March 1930 S. Sandwich Is.	77-152	<p>7 specimens.</p> <p>1, total length 24 cm.</p> <p>The axis enters the centre of the broadly obconic basal part of rachis from below and disappears. 10 large autozooids (body up to 17 mm., tentacles to 22 mm. long) constitute a basal whorl, and within it there are two additional irregular whorls of large autozooids. The basal whorl recalls <i>magniflora</i>, but the additional autozooid whorls transform the cluster into <i>antarctica</i>.</p> <p>2, total length 43 cm.</p> <p>Both autozooid bodies and tentacles up to 25 mm. long. Basal part of rachis bowl-shaped, axis entering centrally and disappearing. One lower (marginal) whorl of 11 autozooids, within it on a short spigot 3 irregular whorls. All interspaces between the autozooids crowded with rather prominent siphonozooids with withdrawn tentacles. Typical <i>antarctica</i> with the basal part of rachis like that of <i>magniflora</i>.</p> <p>3, total length 45 cm.</p> <p>Strongly twisted just below the cluster. Both autozooid bodies and tentacles up to 3 cm. Axis entering centrally from below, thence following the (dorsal) wall to disappear in an interspace between two autozooids of the basal whorl. This consists of 11 polyps. Within and above it, numerous crowded autozooids in 3-4 indistinct, very irregular whorls. Siphonozooids in all interspaces between the autozooids, always with retracted tentacles. Typical <i>antarctica</i>.</p> <p>4, total length 73 cm.</p> <p>Axis diameter about 2 mm. just above the holdfast, only 1 mm. near the cluster. Basal part of rachis bowl-shaped, axis entering the centre from below and disappearing. 9 fully developed autozooids along the brim of the 'bowl' in a single whorl, a tenth indicated by a bud. Diametrically opposite the bud one fully developed autozooid (the primary polyp?) is seated on the inner side of the whorl. Autozooid bodies 1.5-2 cm. long. Siphonozooids on the 'bowl' below the autozooids seemingly crowded into radial fields, no siphonozooids visible inside the autozooid whorl. Typical <i>magniflora</i>.</p> <p>5, total length 86 cm.</p> <p>Axis as in 4, entering the bowl-shaped basal part of rachis in the centre from below, but abruptly making a bend to one (the dorsal?) side and following the wall to the brim. There are 10 autozooids in a whorl round the brim of the 'bowl', and the axis lies in a narrow,</p>

Station	Depth (m.)	Remarks on the specimens
366 6 March 1930 S. Sandwich Is. (cont.)	77-152	<p>deep furrow between the two (dorsal) secondary autozooids, then again it bends a little inwards to end in the basal wall of an eleventh autozooid (the primary polyp), which has been displaced to the inner side of the whorl (text-fig. 3, 7). Autozooid bodies 2-2.5 cm., tentacles 1.5-2 cm. long. Siphonozooids evidently placed like those of 4, but all but invisible. Typical <i>magniflora</i>.</p> <p>6, total length about 100 cm. Rachis bowl-shaped with 11 marginal autozooids and one a little smaller (primary polyp?) near the centre of the whorl. The axis enters the centre from below and disappears. Siphonozooids numerous on the lower side of rachis, not visible within the whorl of autozooids. Tentacles retracted.</p> <p>7, total length about 107 cm. Rachis like that of 6, surrounded by a whorl of 10 autozooids. In the central field there are two additional autozooids of the same size. Siphonozooids only visible on the lower part of rachis, some of them with extended tentacles. Both in 6 and 7 the stem is exceedingly slender and flexible, the upper part of the axis just below the rachis does not attain a diameter of 1 mm., and shortly above the holdfast it is only 1.5 mm. thick.</p>
371 14 March 1930 S. Sandwich Is.	99-161	<p>6 specimens.</p> <p>1, total length 31 cm. Specimen rather 'fleshy', but with a thin axis, measuring just below the cluster 0.7 mm., shortly above the holdfast about 1 mm. thick. Rachis basally laterally compressed by contraction. Autozooids in 3-4 quite irregular whorls, young and small autozooids budding irregularly between the large ones. Although rather strongly contracted the larger autozooids with body lengths up to 20 mm. and tentacles 8-10 mm. long. Siphonozooids in all interspaces between the autozooids, with retracted tentacles.</p> <p>2 and 3, total length in both about 37 cm. Both specimens rather fleshy. Axis just above the holdfast about 2 mm., below the rachis 1 mm. thick. Autozooids with body lengths up to 4 cm., tentacles to 2 cm. Both the tissues of the polyps and those of the wrinkled and folded stem and holdfast are not distinctly contracted but are remarkably flaccid. 2, has some 37 autozooids, the 9 lowermost of which constitute a whorl round the bowl-shaped basal part of rachis. 3, has 12 autozooids in the basal whorl of the ample tassel. Both specimens link <i>antarctica</i> together with <i>rigida</i> (cf. Kükenthal and Broch 1911, Pl. 26, fig. 16).</p> <p>4, total length 43 cm. The specimen is fleshy, the coenenchyma wrinkled and folded although seemingly not very contracted. Axis 3 mm. thick just above the holdfast, 1.8 below the cluster. Rachis was bowl-shaped below the cluster, but is now (by preservation?) strongly wrinkled. The axis enters the rachis in the centre from below and disappears. The cluster has more than 40 autozooids with bodies up to 4 cm. and tentacles mostly 1.5-2 cm. long. Young polyps and new buds irregularly scattered among the fully developed autozooids. Siphonozooids crowded in all interspaces between the autozooids as well as on rachis below the cluster, none with extended tentacles.</p> <p>5, total length 46 cm. Rather slender, axis just above the holdfast 1-1.5 mm., just below the cluster $\frac{3}{4}$ mm. thick. The basal part of rachis is nearly bowl-shaped. The axis enters it centrally from below, but here it bends and follows one (dorsal) side ending in the basi-dorsal wall of one (primary) autozooid. There are 8 fully developed secondary autozooids in one simple whorl along the brim of the bowl-shaped rachis; a small ninth bud diametrically opposite the primary polyp. This has been pushed to the inner side of the whorl (the cluster almost coincides with text-fig. 3, 7). The autozooids are rather inflated and show body lengths up to 3 cm., whereas the rather contracted tentacles at most are 1.2 cm. long. Siphonozooids indistinctly observed in all spaces between the autozooids. Typical <i>magniflora</i>.</p> <p>6, total length 88 cm. Very slender, axis near the holdfast 1.5 mm., just below the cluster $\frac{3}{4}$ mm. thick. Autozooids contracted but not externally wrinkled, body up to 2 cm., tentacles up to 5 mm. long. Siphonozooids in all interspaces between the autozooids, almost invisible, also crowded on the under side of the bowl-shaped rachis. 10 autozooids in a simple whorl and an eleventh displaced to the inner side on one (the dorsal?) side. The cluster agrees with 5 from St. 366 (text-fig. 3, 7) but the terminal part of the axis is buried in the tissues of the rachis.</p>

Station	Depth (m.)	Remarks on the specimens
1644 16 January 1936 Ross Sea	645	1 specimen, total length 15.5 cm. The cluster has 5 large autozooids and 4 equal buds, the positions of which are evident from text-fig. 3, 6. The arrangement is obviously bilateral, but the displacement of the primary polyp by the budding of the two dorsal autozooids indicates the development of a bowl-shaped rachis. Siphonozooids are crowded in all interspaces between the autozooids as well as on the tapering basal part of rachis below the cluster, many with tentacles extended.
1645 17 January 1936 Ross Sea	435	1 specimen, total length 55 cm. The lower part of rachis is bowl-shaped with 11 fully developed autozooids along the brim. Inside the whorl one fully developed autozooid is seated near one side, and evidently two buds are developing near the other side. The central field appears covered by hairs because of the extended tentacles of the siphonozooids, which also give the part of the rachis below the autozooid whorl a shaggy look. Between the autozooids of the whorl no siphonozooids were visible.
1652 23 January 1936 Ross Sea	567	1 specimen, total length 36 cm. Axis just above the holdfast 1 mm. thick, just below the cluster $\frac{3}{4}$ mm. thick. Autozooids with bodies up to 3 cm., tentacles up to 2.2 cm. long. One whorl consisting of 7 full-grown autozooids and one small bud; in the inner field one excentric, large autozooid. Siphonozooids all over the rachis, tentacles retracted. Typical <i>magniflora</i> .
1948 4 January 1937 S. Shetland Is.	490-610	3 specimens. 1, total length 36 cm. The comparatively distinct holdfast is about 6.5 cm. long and rather fleshy like the stem. Axis just above the holdfast 2 mm. thick, just below rachis 1 mm. thick. It enters the centre of the broad obconical basal part of rachis and disappears in the tissues. Autozooids moderately contracted, body up to 2 cm., tentacles up to 1.7 cm. long. Five full-grown individuals and one bud make up a basal whorl of autozooids. Within and above it 3-4 quite irregular crowded 'whorls' of autozooids are developed, and in all interspaces between them and on rachis below the tassel, siphonozooids are thickly placed, some of them with extended tentacles. Typical <i>antarctica</i> . 2, total length 37 cm. Holdfast about 8.5 cm. long, with dimensions as in 1. Holdfast and stem fleshy. Autozooids moderately contracted, body length up to 2.5 cm., tentacles to 2 cm. There is a basal whorl of 11 autozooids, and 4-5 quite indistinct and irregular 'whorls' on a short spigot within the basal whorl. Here as in 1 the autozooids of the inner 'whorls' are a little smaller than those of the base. Siphonozooids, often with extended tentacles, are crowded between the autozooids and all over the rachis. Here as in the following 3 the basal part is that of a typical <i>magniflora</i> , but the upper 'whorls' of the tassel have changed the specimen into a typical <i>antarctica</i> . 3, total length 38.5 cm. Holdfast contracted, about 9 cm. long, axis dimensions agreeing with 1 and 2. Specimen fleshy. The upper part of the stem just below the cluster is strongly curved owing to contractions of the coenenchyma. The basal whorl of the tassel consists of 11 flaccid autozooids with bodies up to 3 cm. and tentacles up to 2 cm. long. The distal part of the tassel is packed with irregularly placed, somewhat smaller autozooids, and all interspaces between them are crowded with siphonozooids, some of them with extended tentacles. Between the autozooids several new buds are observed.

The Discovery collections contain no less than 26 specimens of different sizes from antarctic waters which furnish a good basis for a discussion of the problem (Table, pp. 264 to 267).

The smallest specimens (St. 181) are only 7.5 cm. long and besides the primary polyp they have one pair of fully developed secondary autozooids and below them a pair of autozooid buds (text-fig. 3, 4). Thus they correspond to Broch's (1957) text-fig. 4, III, and text-fig. 5, no. 5 (*Umbellula carpenteri*), although the rachis does not jut out above the primary polyp and the buds are placed a little below the first pair of secondary autozooids. This probably is the 'normal' case.

In a third specimen from St. 181 (text-fig. 3, 5) with a total length of 47 cm., a third pair of autozooids has evidently been developed at the dorso-lateral sides of the primary polyp, or the rachis has been thickened a little at the same time as a lower (more ventral) pair has pushed the upper pair more

to the dorsal side of the primary polyp. A specimen from St. 1644 (total length 15.5 cm., text-fig. 3, 6) shows that new buds may also arise on the dorso-lateral sides of the primary polyp (i.e. also on the axis), ventrally between, or a little below, the lowermost pair of secondary autozooids.

This development leads to the formation of a cluster like that figured in text-fig. 3, 7 from a specimen with total length 86 cm. (St. 366, no. 5 of the table). Here the lower part of the rachis has a bowl-like shape, and the secondary autozooids are situated along its brim. The axis enters the centre of the bowl at the bottom, but from here it follows the dorsal side of the rachis in a deep and narrow furrow to the brim between two dorsal secondary autozooids, bends inwards and ends in the basidorsal wall of the primary polyp, which has been displaced into the central field by the growth of the whorl of secondary autozooids.

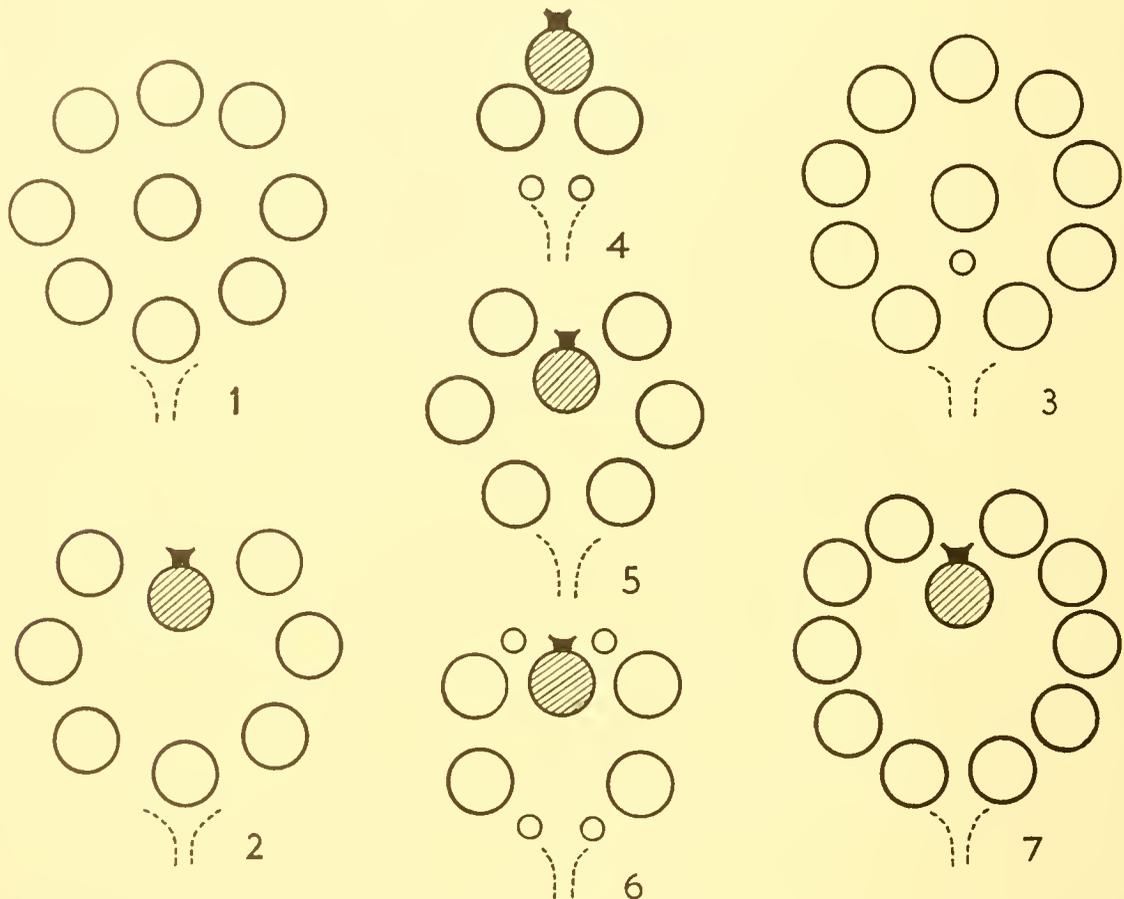


Fig. 3. *Umbellula lindahli*. Diagrams showing the arrangements of autozooids in clusters with comparatively few polyps. Where distinguishable the primary polyp is hatched. 1. Type specimen E of *Umbellula carpenteri* Kölliker, 1880. 2. Kölliker's specimen D of the same species. 3. Type specimen of *Umbellula magniflora* Kölliker, 1880. 4. Two small specimens from *Discovery* St. 181 (nos. 1 and 2 of the table, p. 264). 5. *Discovery* St. 181, no. 3 (p. 265). 6. The specimen from *Discovery* St. 1644 (p. 267). 7. *Discovery* St. 366, specimen no. 5 (p. 265).

In other specimens this dorsal furrow has disappeared because of the growth of the rachis-tissues and can only be made out by dissection. Here we might speak of typical *magniflora* specimens, when only some few further autozooids have developed in the central field. The type specimen of Kölliker's (1880) *magniflora* (text-fig. 3, 3) evidently shows the commencement of the development of such clusters.

On the other hand, we cannot look on this development of the cluster as absolutely characteristic of the species. In several cases the primary polyp and the axis retain their peripheral dorsal position, and the entire cluster in the main keeps its predominantly ventral position on the rachis, with generally

also a more or less distinct bilateral structure. In these specimens the rachis below the autozooids generally retains a more slender and obconical shape in preserved specimens, although we also find stages, where the rachis is more fleshy, or less strongly contracted. This development leads to the formation of polyp-clusters like those of the largest specimens from the Swedish Deep-Sea Expedition (Broch 1957, text-fig. 4, VII). In that paper the possibility was indicated, that such clusters with two whorls of autozooids may give the final and normal arrangement of the species, as found in specimens with total heights of 105 and 119 cm. This, however, is not the case in antarctic waters. In the *magniflora* type especially, there is a tendency for several autozooids to develop in the central field within the first whorl of secondary autozooids. Great crowding results and arrangement in whorls is soon lost. At the same time the inner part of the 'bowl' develops into a spigot carrying autozooids on all sides. In typical *antarctica* forms, like those from St. 1948 (see also Pl. 2, fig. 6), these features are distinct, and in the largest of them (total height 38.5 cm.) new autozooids are budded everywhere between the old ones. Evidently the number of autozooids in the cluster in some way or other depends on local conditions rather than on hereditary fixed characters. On the other hand, collections like those from Stns. 366 and 371 indicate that specimens may develop divergently in one locality. Great individual variations can occur under apparently uniform conditions.

No correlation exists between total length and number of autozooids in the specimens, when they have passed their first stages of development. The specimen described by Kükenthal and Broch (1911) as the type of *U. antarctica* was rather short (total length 465 mm., a cotype 460 mm.); on the other hand, its 'stalk' (both holdfast and stem) is remarkably fleshy. Although this is the case in many specimens of typical *antarctica* forms, comparatively slender specimens with very thin coenosarc on stem and holdfast, but with typical *antarctica* clusters, also occur fairly frequently. In most cases such slender specimens have fewer autozooids in their clusters, which vary from the bilateral *carpenteri* to the radial *magniflora* type. The collections corroborate the suggestion of Hickson (1907) and of Jungersen (1907) that all antarctic *Umbellulae* with square axes and without spicules (apart from the calcareous concretions in the inner tissues of the terminal part of the holdfast) belong to one very variable species.

A study of the descriptions of other non-spiculate species of *Umbellula* with square axes shows that it is exceedingly difficult to trace differences, which might serve as reliable *fundamenta divisionis*. Many so-called characters are due to contraction; others to a certain degree are apparently dependent on local conditions. Polyp clusters have a tendency to develop more autozooids in subantarctic-antarctic as well as in subarctic-arctic seas, i.e. in colder areas, than in temperate and tropical waters. One might suggest that this is not only due to lower temperature, but also to an admixture of water from melting ice, i.e. to variations in salinity. In these colder seas, *Umbellula* is also found at much shallower depths than elsewhere. It is accordingly necessary to be most cautious in using the numbers of autozooids in the clusters for specific determination, because these numbers show no correlation with the length of the specimens (Broch 1957).

It has been mentioned earlier that Kükenthal was at first inclined to look on *U. antarctica* as a variety of *U. encrinus*. Later on he (1915) reduced *U. ambigua* Fischer (also retained by Marion (1906) as a separate species) to a variety of *U. encrinus*. This course was already indicated by Jane Stephens (1907), who had no less than 17 specimens at her disposal, the stems of which (from the clusters downwards) ranged from 112 to 420 mm. (Marion's specimen measured in the same way was about 350 mm.). The numbers of autozooids in the clusters varied from 6 to 43, and the polyp bodies from 8 to 30 mm. Marion's drawings (1906, Pl. 15, fig. 22, and 22A) might well have been made from a typical specimen of *U. magniflora* Kölliker, and in his text Marion (1906, p. 146) writes: 'L'*Umbellula ambigua* se rapproche intiment de l'*Umbellula grandiflora* Kölliker prise dans l'Extrême-Sud, aux îles

Kerguelen. Cette curieuse affinité mérite d'être remarquée.' (By a slip of the pen Marion has written *grandiflora* instead of *magniflora* as his particulars prove.) There are no differences between Marion's and Kölliker's descriptions, and the Discovery specimens also coincide with them. It might be objected that Marion's specimen has a much shorter stem than the 'Challenger' specimen (measured in the same way as Stephens's specimens, the stem of Kölliker's specimen is some 690 mm.). Stephens, however, in her table gave measurements of a variation of 'ambigua' quite parallel to that of *U. thomsonii* (Broch 1957 '*U. güntneri*'), additional evidence against the use of length of the stem (or total length of the specimen) as compared with the numbers of autozooids in the clusters for specific identification.

Finally, it is impossible to trace any distinct limit or difference between the typical *U. carpenteri* and the species *U. lindahli* (comp. Kölliker 1880, Jungersen 1904, 1907, and Broch 1957).

It is also necessary to discuss the relations between *U. lindahli* Kölliker (1874) and *U. encrinus* (L. 1758). Jungersen (1904, 1907) dealt partly with the question but although he considered them to be different species, he omitted to define their characteristic differences precisely and only hinted at their varying dimensions.

Summing up the characters stated by Kükenthal (1915) the following differences appear: (1) *U. lindahli* has a very long and thin stem, whereas the stem of *U. encrinus* is not especially thin. (2) The autozooids of *U. lindahli* are gathered in a slender cluster and occur in smaller numbers than in the much more robust clusters of *U. encrinus*, but the arrangement of the polyps otherwise agrees. (3) The tentacles of the autozooids of *U. lindahli* are twice as long as the polyp body, in *U. encrinus* of about the same length as the body. (4) In *U. lindahli* siphonozooids constitute two longitudinal rows along the thin part of the stem, in *U. encrinus* they are arranged all round it, and the coenosarc is thicker and more fleshy than in *U. lindahli*. The differences under (2) and (3) can at once be discarded as being due to contraction; (4) is correlated with a more or less copious individual development of the coenosarc, a fact clearly evident in the specimens from the Discovery collections.

Jungersen (1904) in his first paper came to the conclusion that *U. encrinus* must be regarded as a distinct species apart from *U. lindahli*, although differentiation was difficult. After the examination of new supplementary collections (1916*b*, 1919) he decided that *lindahli* and *encrinus* represent two varieties of one species, the older, Linnean name, *encrinus* having priority. This view was also accepted by myself (Broch 1929) in my review of the Arctic Octocorals where I mentioned the two groups as *U. encrinus* forma *typica* and forma *lindahli*.

Although there are no definite limits between the other 'species' amalgamated here under the name of *U. lindahli*, a somewhat greater gap apparently separates *U. encrinus* from the rest. It is of course necessary to make reservations when dealing with characters which may be correlated with the dimensions of the coenosarc, or which are largely due to contraction. The obvious parallel development in both cold-water areas must be considered: in extreme cases theoretically this should lead up to *U. encrinus* from *U. lindahli*. It would then be correct to consider *encrinus* as an ecologically distinct geographical form of *lindahli*. However, although at present it is difficult to define the limits exactly, I prefer to treat *encrinus* as a separate species. Probably the gap between the two 'species' emphasized by Jungersen (1904) is due to the limits and differences between the Atlantic and the Arctic deep-sea areas. Their size differs so greatly that it is generally easy to distinguish between specimens of the two 'species'.

ZOOGEOGRAPHICAL REMARKS ON *UMBELLULA*

As an introduction to the distribution of the species, all known localities are listed in the following table:

Umbellula durissima Kölliker

Pacific Ocean

34° 07' N, 138° 00' E, 1030 m., bottom temp. 2.3° C. Shio Misaki Light, Japan, N 82° E, 12.5 miles, 1092 m. (Kölliker 1880, type locality) (*eloisa* Nutting)

Indian Ocean

10° 06' N, 92° 29' E, 1300 m. (*dura* Thomson & Henderson) 03° 27' S, 131° 00' E, 567 m. Off the Laccadive Is, 2070 m.

Atlantic Ocean

02° 26'–02° 24' N, 39° 26'–39° 12' W, 4474–4430 m. 48° 06' S, 10° 5' W, 3188 m.

Antarctic

68° 06' S, 10° 05' E, 3185 m.

Umbellula thomsonii Kölliker

Atlantic Ocean

35° 20' N, 13° 04' W, 3768 m. (Kölliker 1880, type locality) 01° 47' N, 26° 46' W, 3380 m.
Off Morocco, 2000 and 2125 m. Guadeloupe ('Blake' St. 162) 1336 m.
29° 08' N, 22° 53' W, 5160 m. 28° 54' N, 26° 46' W, (?)
30° 19'–30° 30' N, 55° 56'–56° 19' W, 5600–5340 m. 24° 12'–24° 28' N, 63° 23'–63° 18' W, 5850–5860 m.
12° 22'–12° 13' N, 52° 00'–51° 44' W, 5044–5033 m. 01° 03'–00° 58' N, 18° 40'–18° 37' W, 5250–5300 m.
Cape Point NE by E ¼ E, 46 miles, 183–1647 m. (*aciculifera* St Thomson)

Indian Ocean

11° 58' N, 88° 52' E, 3190 m. (*rosea* Thomson & Henderson) 12° 20' N, 85° 08' E, 3290 m. (*hendersoni* Balss)
06° 52' N, 81° 11' E, 3500 m. (*intermedia* Thomson & Henderson) 04° 56' N, 80° 52' 30" E, 3240 m.

Pacific Ocean

13° 50' S, 151° 49' E, 4460 m. (*leptocaulis* Kölliker) 36° 10' N, 178° 00' E, 3750 m. (*simplex* Kölliker)

Umbellula huxleyi Kölliker

Pacific Ocean

34° 71' N, 135° 39' E, S. of Yeddo (Japan), 1034 m., bottom temp. 3.3° C. (Kölliker 1880, type locality) 32° 50' 20" N, 118° 03' 30" W, 915 m.

Indian Ocean

S.W. of Great Nicobar, 296 m.

Atlantic Ocean

59° 29' 30" N, 07° 13' W, 1032 m. 28° 08' N, 13° 35' W, 1365 m.
Off Bissagos I. (Port Guiana), 600 m.

Umbellula spicata Kükenthal

Indian Ocean

06° 24' 01" N, 49° 43.8' E, east coast of Africa, 741 m. 03° 07' 00" S, 40° 45.8' E, 748 m. (*valdiviae* Kükenthal)
(Kükenthal 1902, type locality) 09° 29' 34" N, 75° 38' E, 659 m. (*elongata* Thomson & Henderson)
00° 27' 04" S, 42° 47.3' E, 638 m. (*valdiviae* Kükenthal) Andaman Is, 344–403 m. (*pendula* Thomson & Henderson)
Andaman Is., 897 m. (*radiata* Thomson & Henderson) 13° N, 76° E, 1281–1098 m.

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Umbellula pellucida Kükenthal

Indian Ocean

- 06° 24' 01" N, 49° 31.6' E, 628 m. (Kükenthal 1902, type locality) 10° 48' S, 123° 23' E, near Rotti, 918 m.
 05° 15' 48"-05° 13' 42" N, 73° 22' 48"-73° 23' 36" E, 797 m. 13° 48' 05"-13° 48' 36" N, 49° 16' 48"-49° 16' 24" E, 2000 m.
 (huxleyi Hickson) Andaman Is. (no other dates) (*purpurea* pars, Thomson & Henderson)
 13° 16' 00"-13° 16' 36" N, 46° 20' 24"-46° 14' 00" E, 220 m. (huxleyi Hickson)

Umbellula lindahli Kölliker

Atlantic Ocean

- 71° 27' N, 53° 58' W, 223 m. and 70° 43' N, 52° 03' W, 752 m. (type localities of Lindahl's *miniacea* and *pallida*) 64° 45' N, 29° 06' W, 1039 m.
 59° 29' N, 07° 51' W, 1061-1114 m. 61° 50' N, 56° 21' W, 2626 m.
 52° 00' N, 12° 06' W, 846-934 m. (*ambigua* Stephens) Gulf of Gascogne 896 m. (*ambigua* Marion)
 51° 58' N, 12° 25' W, 975-1007 m. (*ambigua* Stephens) 51° 59' N, 12° 32' W, 846-934 m. (*ambigua* Stephens)
 51° 36' N, 11° 57' W, 988-1208 m. (*ambigua* Stephens) 51° 54' N, 11° 57' W, 641 m. (*ambigua* Stephens)
 40° 33'-40° 34' N, 35° 24'-35° 52' W, 4600-4540 m. (*carpenteri* Broch) 50° 42' N, 11° 18' W, 1148-1333 m. (*ambigua* Stephens)
 Off Yucatan, 2869 m. 38° 30' 30"-38° 53' N, 69° 08' 25"-69° 24' 40" W, 3168-3720 m. (*Bairdii* Verrill)
 01° 03'-00° 58' N, 18° 40'-18° 37' W, 5250-5300 m. (*carpenteri* Broch) Off Dominica, 2070 m.

Indian Ocean

- 01° 47' 08" S, 41° 58' 08" E, 1670 m. (*köllikeri* Kükenthal) 01° 57' S, 73° 19.1' E, 2919 m. (*rigida* Kükenthal)
 05° 40' S, 132° 26' E, near Kei Is., 310 m. (*antarctica* Hickson) 05° 40' S, 120° 45' E, off South Celebes, 1158 m. (*Jordani* Hickson)
 05° 40' S, 120° 45' E, near Saleyer, 1158 m. (*antarctica* Hickson) 07° 28' S, 115° 24' E, near Bali, 1018 m. (*Weberi* Hickson)
 07° 28' S, 115° 24' E, E. Bali Sea, 1060 m. (*antarctica* Hickson)

Pacific Ocean

- Off Kauai (near Hawaii) in four places, 705-2405 m. (*Jordani* and *Gilberti* Nutting) Near San Clemente I. (California), 604 m. (*loma* Nutting)
 32° 44' 50" N, 117° 48' 45" W, 448 m. (*magniflora* Nutting) South-east point Santa Catalina I. 19° 30' E, 3.2 miles (California), 611 m. (*magniflora* Nutting)
 North-east point Santa Barbara I. N 89 W, 4.7 miles (California), 802 m. (*magniflora* Nutting) East point San Nicholas I. S, 7.6 miles (California), 395-620 m. (*magniflora* Nutting)
 46° 44' N, 144° 02' E, 928 m. Off Omar Saki Light, Japan, 919 m.
 Shio Misaki Light N 49° E, 7 miles (Japan), 997-1303 m. (*magniflora* Nutting) 34° 71' N, 135° 39' E, S. of Yeddo (Japan), 1034 m., bottom temp. 3.3° C. (*huxleyi* Kölliker)

Antarctic

- 46° 16' S, 48° 97' E (east of Kerguelen I.), 2938 m., bottom temp. 0.8° C. (*magniflora* Kölliker 1880, type) 53° 55' S, 108° 55' E, 5310 m., and 62° 26' S, 95° 44' E, 3560 m. (type localities of *carpenteri* Kölliker 1880)
 70° 40' S, 102° 15' W, 2800 m. 78° S, 174° E, 540 m.
 Near Gauss-Berg, 2450 and 2725 m. East of Bouvet Is., 457 m. (*antarctica* Kükenthal, type locality)

Discovery localities

- St. 180. 11. iii. 27. 1.7 miles W of N point of Gand I., Schollaert Channel, Palmer Archipelago, 160-330 m. (150 m., 0.00° C.).
 St. 181. 12. iii. 27. Schollaert Channel, Palmer Archipelago, 64° 21' 00" S, 63° 01' 00" W, 335 m. (0.40° C.).
 St. 182. 14. iii. 27. Schollaert Channel, Palmer Archipelago, 64° 21' 00" S, 62° 58' 00" W, 278 m. (0.12° C.).
 St. 366. 6. iii. 30. 4 cables south of Cook I., South Sandwich Is., 77-152 m.
 St. 371. 14. iii. 30. 1 mile east of Montagu I., South Sandwich Is., 90-161 m. (150 m. 0.44° C.).
 St. 1644. 16. i. 36. 78° 24.8' S, 164° 10.3' W (Bay of Whales), 645 m. (585 m. ÷ 1.85° C.).
 St. 1645. 17. i. 36. 77° 43.3' S, 166° 18.2' W, 475 m. (450 m. ÷ 1.85° C.).
 St. 1652. 23. i. 36. 75° 56.2' S, 178° 35.5' W, 567 m. (541 m. ÷ 1.90° C.).
 St. 1948. 4. i. 37. 60° 49.4' S, 52° 40' W, 490-610 m.

Although Pennatularians are rather scarce in oceanic collections, it is questionable whether the picture thus presented of their distribution and numerical occurrence on the sea-bottom is a true one. I have touched on this problem in a recent paper (Broch 1957). It is obvious that the catch depends to a great extent on the gear used, and unfortunately there is at present no gear able to catch more than a small percentage of all the specimens available. Mooring in the mud, flexibility, contractility, and strong holdfasts especially in the larger specimens, all combine to keep the Pennatularians anchored *in situ*. Some casual catches, nevertheless, show that some species at all events are patchy in occurrence. This is well known of shallow-water species like *Pennatula phosphorea*, *Virgularia* and *Stylatula* among others, and latterly it has been observed in some species of *Umbellula*; for example, about 240 specimens of *U. pellucida* were taken at St. 194 by the 'John Murray' Expedition (Hickson 1937), 45 *U. thomsonii* at Discovery Station 342, and 157 specimens at St. 362 by the Swedish Deep-Sea Expedition.

In this connexion, it should be noted that bottom samplers (grabs) do not catch Pennatularians even at localities where other gear proves them to be comparatively numerous. It is most probable that the larger, slender, very flexible, deeper-living sea-pens cannot be caught by the grabs, which therefore only give a fragmentary picture of the momentary balance in populations of the *medium-sized* bottom animals.

In spite of these negative results, however, a review of the many scattered localities (text-fig. 4) gives us a few hints as to the environmental requirements of *Umbellula* and the distribution of the species.

U. durissima has only been captured singly at depths from 1012 to 4474 m. The stem is very flexible, and most specimens evidently escape the usual fishing gear. Curiously enough one of the first specimens was captured in antarctic waters, where the species has never since been observed. All other records are from intermediate depths in the tropical and subtropical regions of the Atlantic, Indian and Pacific Oceans.

U. thomsonii appears to be plentiful in the deeper waters of the Atlantic and Indian Oceans (from 1336 down to 5860 m., mostly below 3000 m.), but from Pacific waters only two young specimens have been recorded from 3750 and 4460 m. The largest catches to date were made by the Swedish Deep-Sea Expedition in the Atlantic Ocean, where at St. 342 (5033 m.) the prawn otter-trawl caught 45 specimens, and at St. 363 (5300 m.) 157 specimens. The species appears to avoid territories where arctic or antarctic waters influence the bottom conditions, although low temperatures may not necessarily be the main factor.

U. huxleyi has been found in a few, very scattered places in the Atlantic, Indian and Pacific Oceans, generally in tropical and subtropical areas at depths between 296 and 1365 m. The widely spread localities and the records only of single specimens were even more conspicuous than in *U. durissima*, until the remarkable catch made by Dr A. R. Longhurst in 1955 off Bissago I. (Port Guiana), where one haul of the otter-trawl yielded no less than 17 specimens at 600 m. depth. Not only had a 'patch' been found, but by good fortune the gear also chanced to detach all these specimens from the mud. (Whether this was just a stroke of luck in sampling the elusive benthos is another question.) The catch may indicate that optimum conditions existed here at about 600 m. depth, though on comparison with other records, with one exception situated at greater depths and at lower temperatures, this appears very remarkable.

Only two very characteristic *Umbellula* species have so far been located in the Indian Ocean alone. Several 'species' have been described from the Indo-Malayan region, but most of them must be reduced to synonyms. Hickson (1937) touched on the problem in his own way saying: 'It is very improbable that a larger number of specimens belonging to the same genus, and all in approximately

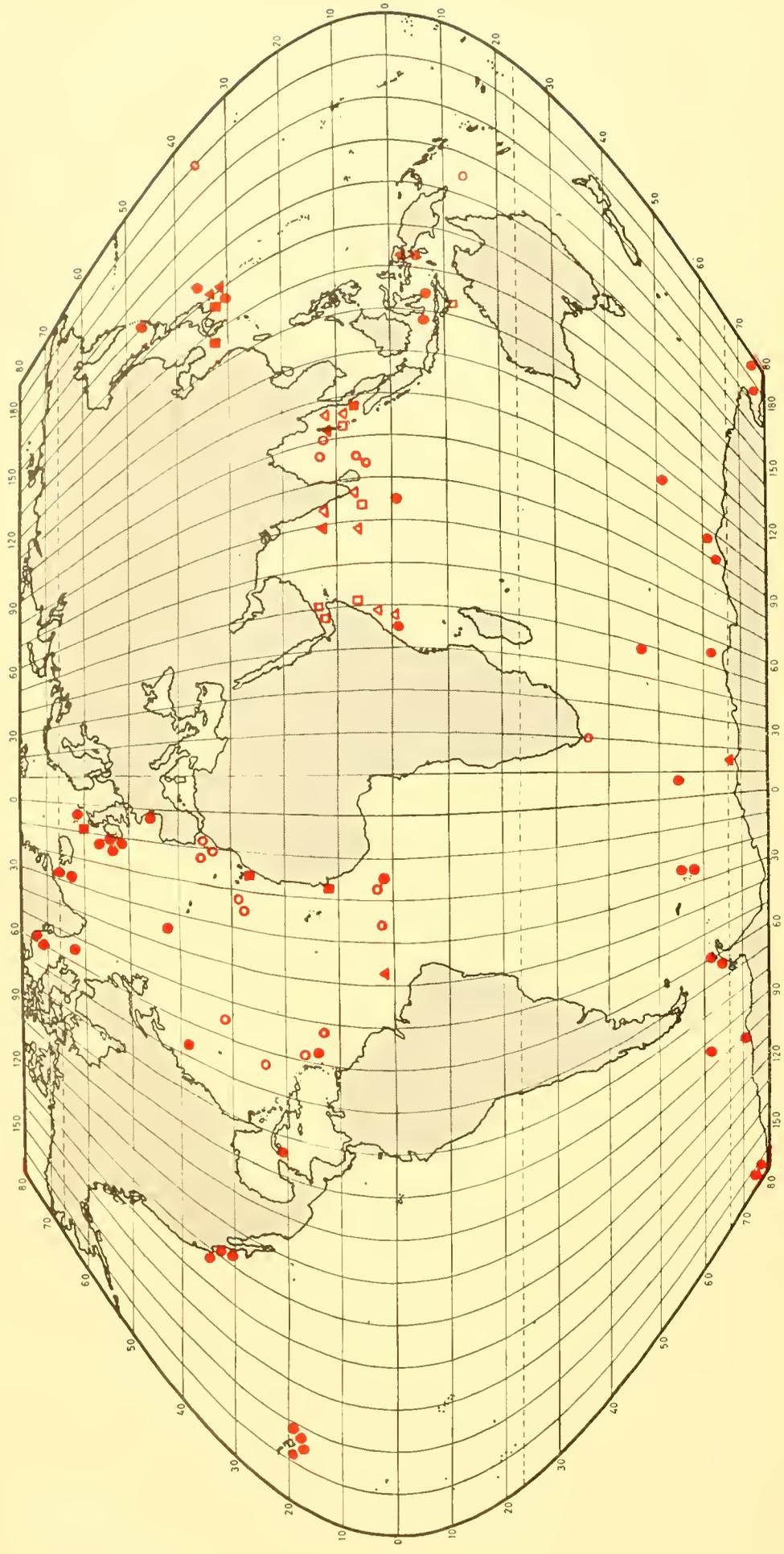


Fig. 4. Records of *Umbellula* (North Polar Sea with *U. encrinus* excluded: see fig. 5). *U. durissima* ▲; *U. thomsonii* ○; *U. huxleyi* ■; *U. spicata* △; *U. pelucida* □; *U. lindahli* ●.

the same sexual condition, living in the same locality in deep water, should belong to more than one species. Any cross-fertilization that might occur would soon swamp any specific distinctions.' This of course to a great extent depends on what we consider as specific characters. Nearly related species may according to the laws of heredity live and propagate side by side and nevertheless keep their specific identities intact, and so far as we know this is as true for the deep sea as for every other domain. The Indian Ocean contains an extraordinarily rich fauna in its deeper regions, but at present we do not know, which factors, or combination of factors, make this ocean especially favourable for *Umbellula* and for the moment it must suffice to record the known facts.

U. spicata appears to be confined to the Indian Ocean and at the same time has a remarkably narrow bathymetrical range between 344 and 1281 m. Different growth stages have been interpreted as distinct species, and because of the great flexibility of the stem, adult specimens had not been caught and described hitherto.

U. pellucida also seems to be restricted to the Indian Ocean. Its known bathymetric range is from 220 to 2001 m. It is noteworthy that the deepest haul only gave one specimen, whereas the haul in 220 m. resulted in some 240 specimens; also one haul in 625 m. depth gave 8 specimens, all other catches consist of 1 or 2 specimens. This may be taken as an indication that the upper part of the habitat offers the optimum conditions, and that the deepest locality, separated widely from the next record, shows an erratic individual which has grown up below the normal habitat of the species.

U. lindahli is the most widespread species of the genus, and if *U. encrinurus* turns out to be an ecologically distinct form, the species inhabits all oceans. At the same time the bathymetric range—77–5310 m.—is much greater than in the other species. Most of the earlier records in the Antarctic region were from great depths, from 2450 to 5310 m., and only two localities showed depths as shallow as 540 and 457 m. It was therefore surprising that all the nine Discovery Stations lie between 645 and 77 m.

It has been rather usual to regard temperature as the deciding factor, when deeper living bottom animals ascend in higher latitudes to lesser depths than elsewhere. *U. lindahli*, on the other hand, is remarkable in that both the deepest locality (5310 m.), and the shallowest (77 m.) are situated in Antarctica, and that the deepest record here almost coincides with depths in the Atlantic near the equator.

One may say that generally the more robust and better developed specimens have been observed in Antarctica, the slenderer specimens in deeper waters of the tropical seas. However, there are exceptions, e.g. the comparatively short and fleshy '*antarctica*' specimens are common both in the Antarctic and in the tropical part of the Indian Ocean. The question of geographically distinct varieties in *U. lindahli* must also be considered.

In spite of comparatively numerous localities (cf. text-fig. 4, 49 records, 16 of which are in Antarctic waters) the evidence is scanty, and it is not astonishing that *U. lindahli* has been described under several names, which in some cases might seem to indicate local races. The Discovery collections have proved that the three 'species' only described from Antarctic waters represent either developmental phases, or more or less luxuriant individuals. '*U. carpenteri*' doubtless represents younger stages in most cases and larger specimens cannot be distinguished from '*U. magniflora (ambigua)*'. Nothing indicates that these forms are restricted to special geographical areas. A more luxuriant development of the cluster leads from *U. magniflora* to *U. antarctica*; from the specific name one might assume that the latter represented a special Antarctic variety, but typical *U. antarctica* are also comparatively frequent in tropical Indian waters.

The accessible data do not yet indicate geographical races, or varieties, in *U. lindahli*. On the

contrary, we can say that the more extensive our material has become, the more indefinite are the limits which earlier seemed to point in the direction of local 'species'.

Nevertheless, we must make one reservation as to the high-arctic *U. encrinus* already mentioned on page 270. A study of its occurrence (text-fig. 5) indicates that it must have penetrated into the Polar deep and into the cold bottom water of the Davis Strait and Baffin Bay from the Atlantic Ocean. In the Polar Sea it has been found in water as shallow as 180 m., and it is therefore astonishing that the species apparently has not been able to pass beyond the submarine Lomonosov mountain range into the western part of the Polar Basin.

Geographical distribution seems to indicate that *U. encrinus* in reality is an ecologically distinct group. It must have invaded its two distinct habitats from the more temperate Atlantic bottom waters. The western habitat in Davis Strait and Baffin Bay is barred to the north by shallow thresholds from the central (both eastern and western) Polar Deep, and communication with the eastern north Atlantic-Arctic deep sea, north of the Scotland-Iceland-Greenland ridges, round the southern part of Greenland seems unlikely in the present state of our knowledge. It is, therefore, natural to assume that penetration was originally via the Atlantic bottom water into the Davis Strait, and that a secondary invasion occurred over the submarine ridge in the Faroe Channel. This double origin in Arctic waters of *U. encrinus* favours considering it as an ecologically distinct, geographical variety, and not as a genetically separate species.

A study of Jungersen's (1916, 1919) papers indicates that the morphological differences between *U. lindahli* and *U. encrinus* are more fluid in the Davis Strait, where no prominent submarine ridges accentuate the biophysical border lines as do the submarine ridges from Scotland past the Faroes and Iceland to East Greenland. But in spite of this the gap between the Arctic and the Atlantic groups is so conspicuous that at present it is more convenient to treat *U. lindahli* and *U. encrinus* as separate species.

It is striking that *U. encrinus* is much more coarse and luxuriant than the largest Antarctic specimens of *U. lindahli* hitherto captured. If the first is an extreme geographical race, the question again arises, why the Antarctic specimens do not attain such large dimensions as the Arctic. Are conditions of life subjected to greater fluctuations and, therefore, less favourable in Antarctic waters, than in the much more sharply circumscribed Arctic deep sea?

PENNATULIDAE

Pennatula rubra Ellis 1764

(Synonymy before 1910, see Kükenthal and Broch 1911)

P. rubra Kükenthal & Broch 1911, p. 382, text-figs. 182-7.

P. rubra Kükenthal 1915, p. 91, figs. 98, 99.

P. rubra Hickson 1916, p. 183.

St. 272. Off Elephant Bay, Angola, 200-230 m. 9 specimens (three of them identified by Mrs MacFadyen) from 13 to 25 cm. length.

St. 2633. 13° 11.5' S, 12° 44.1' E (off mouth of Elephant Bay, Angola) 104-? (sounding 91-104 m., but a note states that the net was fishing clear of the bottom at the end of the haul). 1 specimen, length 11 cm.

The specimens from St. 272 vary much in length, and so does the length of the stalk, which generally measures one-half to one-quarter of the entire specimen. It is of interest to note that the larger specimens are much more inflated than the smaller ones, which are rather contracted, although not so strongly as the specimen from St. 2633, which has a total length of 11 cm. only. Evidently the length of the specimen depends to a certain degree on the degree of contraction, and a living *Pennatula rubra* doubtless shows a great faculty of inflation by imbibing water. This influences the colours also. The



Fig. 5. The distribution of *Umbellula encrinus* in the North Polar Sea (after Broch, 1956). The submarine Lomonosov Ridge from Greenland to the New Siberian Islands is indicated

spicules generally are dark, almost blood red, and the more inflated the specimen is, the more pinkish it becomes, whereas strongly contracted specimens like that from St. 2633 are dark red, especially on its leaves and rachis. In such specimens, however, the longitudinal dorsal white band along the rachis is extraordinarily obvious and comparatively broad. In the specimen from St. 2633 the 5 cm. long stalk is yellowish white.

At a first glance this strongly contracted specimen recalls *P. phosphorea* f. *variegata*. Earlier authors like Kükenthal and Broch (1911) have generally emphasized the spongy tissues of *P. rubra*, which enables it to extend markedly, but nobody seems on the other hand to have hinted at its strikingly great faculty of contraction. This power is comparable with that of *Pteroëides griseum* (comp. Niedermayer 1911). In *Pennatula* the colour is confined to the spicules, and the shade of the colour of a specimen will therefore depend to a great extent upon its state of dilation or contraction. This was easily seen in the 10 specimens from the Discovery collections, the specimens of which were very differently expanded.

P. rubra is characterized in the literature as a Mediterranean species. Looking at the few localities which are sufficiently precise to plot on a chart (fig. 1, p. 249), the species, like *Cavernularia elegans*, (p. 250) seems to belong zoogeographically to the same group as *Veretillum cynomorium*; more localities are recorded from the Atlantic Ocean than from the Mediterranean. Like *V. cynomorium* also, *Pennatula rubra* seems to have its eastern border in the Mediterranean off southern Italy; along the eastern coasts of the Atlantic, it is distributed from Portugal and southwards to Angola, and its bathymetric range lies between 60 and 230 m. depth.

P'TEROËIDIDAE

Pteroëides griseum (Bohadsch 1761)

(Synonymy before 1910, see Kükenthal and Broch, 1911)

P. griseum Kükenthal 1915, p. 98, figs. 104-7.

P. griseum Hickson 1916, pp. 219 et seq.

P. spinosum Pax & Müller 1953, p. 31.

P. griseum Broch 1953, p. 15.

P. spinosum Pax 1956, p. 59.

St. 2634, 12° 17.4' S, 13° 31.3' E, 80-91 m. 1 specimen, total length 20 cm.

The specimen is rather strongly contracted, although its total length is 20 cm. However, the total length (or height) of a specimen of *Pteroëides* is rather problematical, because of its enormous faculty of inflation and contraction. This is easily observed in aquaria. By night I have observed specimens of *P. griseum*, the raches of which have expanded to about 1 ft. in height above the mud with a breadth of 4-5 in., whereas by day the same specimens had contracted to a length of 4-5 in., only a couple of inches broad, and all but entirely buried in the muddy bottom; in this case the leaves were moreover packed against each other along the stem.

Most authors have admitted two varieties of *P. griseum*, var. *longispinosum* and var. *brevispinosum* (see Kükenthal 1915, p. 99). The Discovery specimen is of special interest in this connexion. Most of its leaves belong to the *brevispinosum* type, but some of them are decidedly of the *longispinosum* type. This supports Kükenthal's (1915) words, that the two varieties instituted by Kölliker 'nicht scharf getrennt sind'.

Hickson (1916) was of the opinion that the numbers of rays in the leaves in the middle of the rachis must be looked upon as the most important specific character. This character, however, is only of mediocre value, being useful only in adult specimens. Thus Hickson placed *P. lusitanicum* Broch in

a different group of the genus to *P. griseum*, whereas the first-named species is based most probably on a young specimen of the latter. To solve this question very extensive material is necessary.

According to the literature, *P. griseum* seems to be comparatively common in the Mediterranean, at all events as far east as the Adriatic. In the Atlantic Ocean it has been reported from the European coasts as far northwards as the Faroes (Kükenthal 1915), but up till now it does not seem to have been reported from the coast of Africa. The species lives in tolerably shallow water, but when we consider its biotope with the soft muddy bottom, and its mode of life in daylight almost entirely burrowed in the mud, it is easily understood that it had hitherto escaped the investigators. The Discovery record seems to indicate that *P. griseum* almost coincides zoogeographically with *Cavernularia elegans*, *Veretillum cynomorium* and *Pennatula rubra*.

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* Quoted from Pax and Müller 1954.

PLATE XI

- Fig. 1. *Umbellula huxleyi* Kölliker. Two specimens from off Bissagos I. (Port Guiana), 600 m. (natural size). (a) the smaller specimen, autozooids not ripe, devoid of eggs; (b) the larger specimen, autozooids filled with eggs.
- Fig. 2. *Umbellula spicata* Kükenthal. The polyp tassel of the specimen from 13° N, 76° E, 600–700 fthms (natural size). The basal parts of the autozooids are crammed with eggs.
- Fig. 3. *Umbellula carpenteri* Kölliker 1880, specimen A. Cluster in ventral view ($\times 2$). The budding fifth autozoid is distinctly seen in the middle below the acute top of the rachis. The specimen is a juvenile stage of *Umbellula lindahlia*.

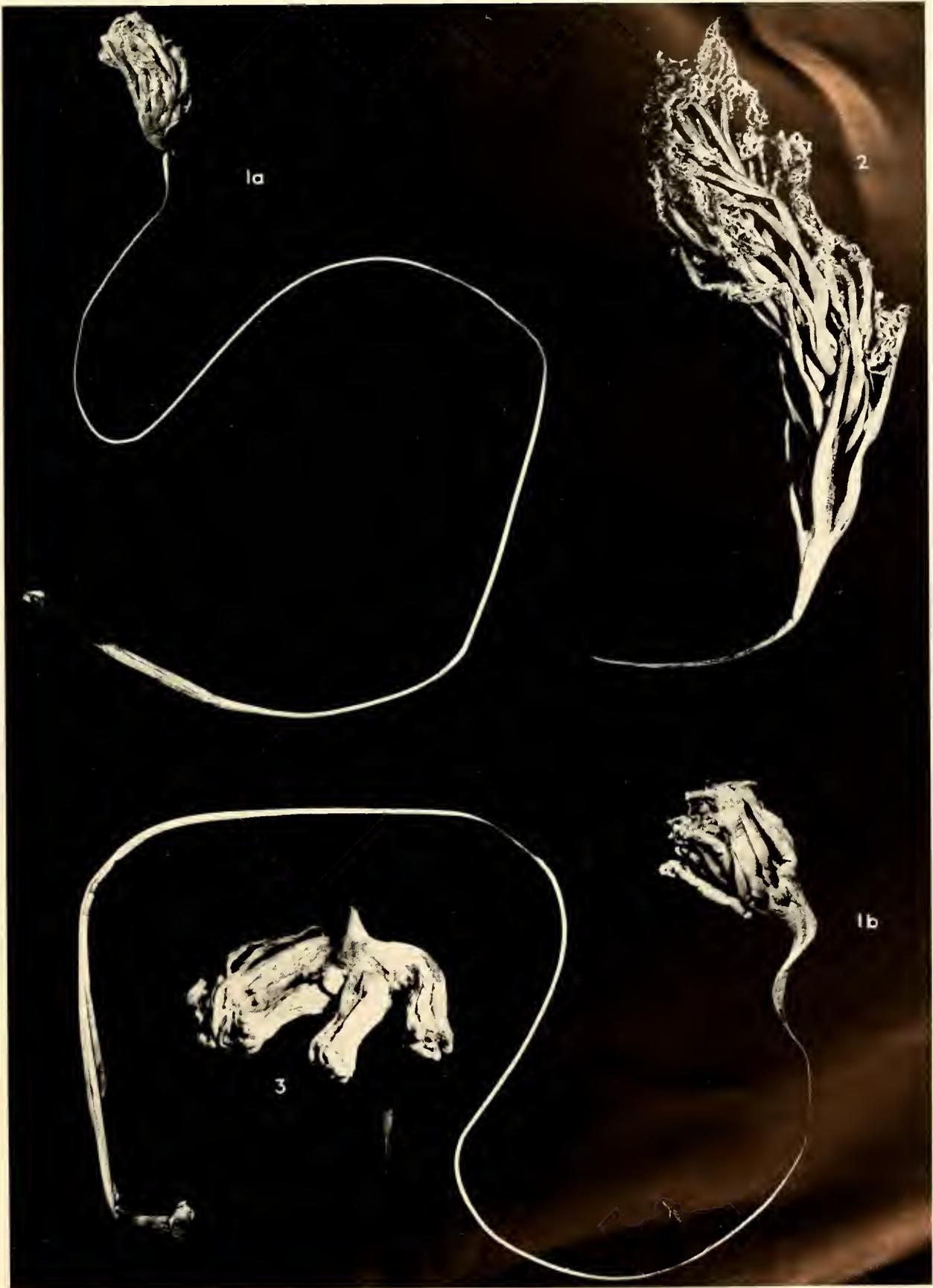
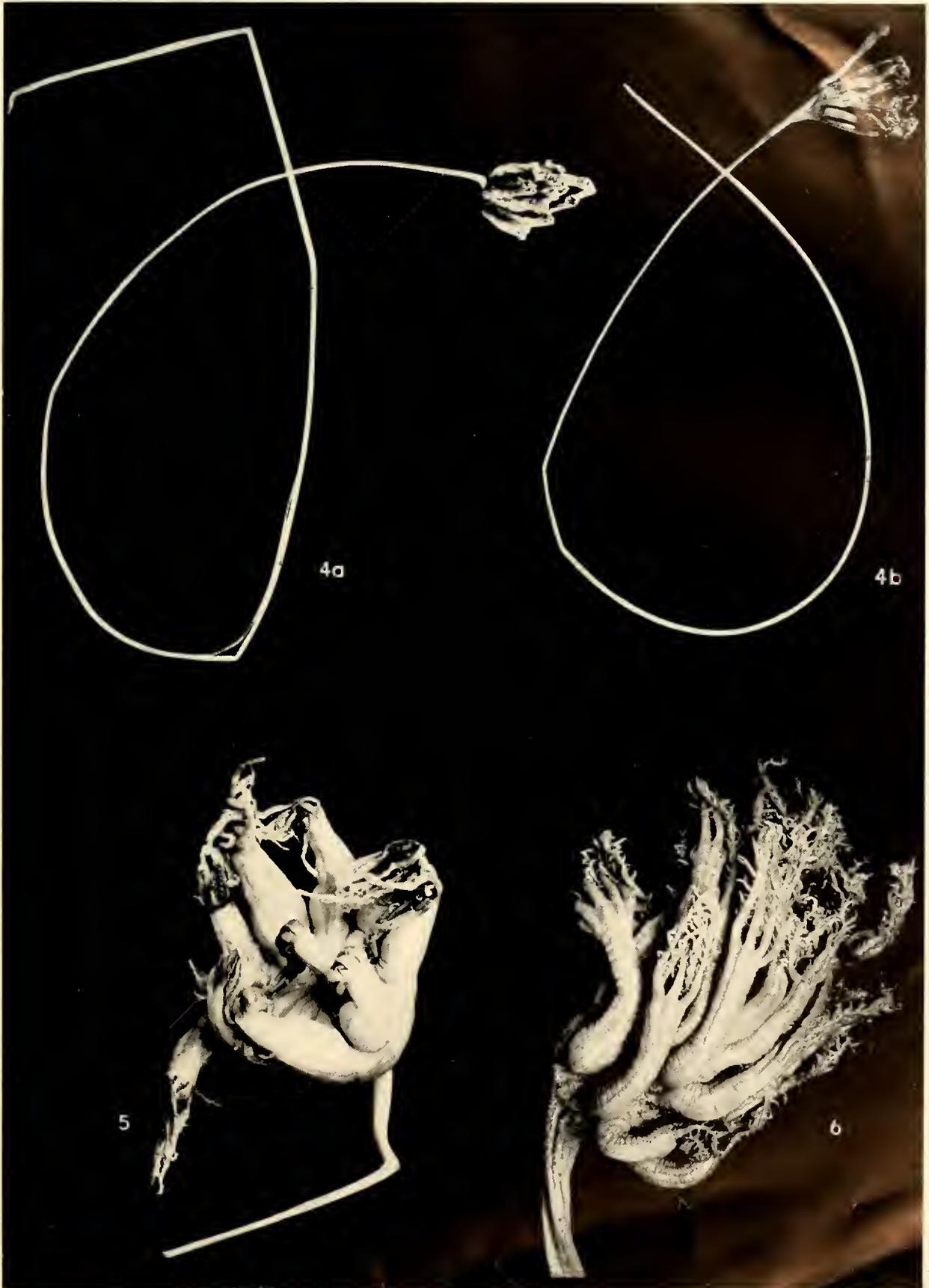


PLATE XII

- Fig. 4. *Umbellula pellucida* Kükenthal. Two specimens from the John Murray Expedition Station 194. The stalk is rigid and straight, but has been artificially coiled when photographed; it is easily seen in the figures that the axis was thereby fractured in some places (natural size). *a*, an unripe specimen without eggs in the autozooids. *b*, a ripe specimen with autozooids crammed with eggs.
- Fig. 5. *Umbellula lindahli* Kölliker. Cluster of a typical *magniflora* specimen from 'Discovery' St. 366, No. 4 of the table (natural size).
- Fig. 6. *Umbellula lindahli* Kölliker. Tassel of an *antarctica* specimen from 'Discovery' St. 366, No. 1 of the table (natural size).



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THE FOETAL GROWTH RATES OF WHALES
WITH SPECIAL REFERENCE TO THE FIN
WHALE, *BALAENOPTERA PHYSALUS* LINN.

BY

R. M. LAWS

National Institute of Oceanography



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THE FOETAL GROWTH RATES OF WHALES WITH SPECIAL REFERENCE TO THE FIN WHALE, *BALAENOPTERA PHYSALUS* LINN.

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(Plate XIII, text-figures 1-13)

INTRODUCTION

IN the course of an investigation of the reproductive cycle of the southern hemisphere fin whale, *Balaenoptera physalus* Linn., it was necessary to obtain an accurate mean curve of foetal growth in length. It is usual to describe foetal growth in terms of weight, but there are relatively few records of foetal weights of whales owing to the practical difficulties. For present purposes length is therefore much more suitable than weight and as there is a constant relation between length and weight (Text-fig. 13), the curve of growth in length may later be converted to a weight-growth curve by reference to the relatively small number of foetal weight records.

This is an interesting problem quite apart from any indirect use which may be made of the results. The main stimulus for this study was the need to obtain accurate information about the mating season, length of pregnancy and the calving season in the fin whale. It is not possible in this species to study any of these problems directly and in fact the humpback whale, *Megaptera novaeangliae* Borowski, is the only species in which the length of the gestation period and progress of the pairing and calving seasons have been fixed accurately (Chittleborough, 1954, 1958) because this is the only species in which the breeding population has been studied directly in the breeding season. It can therefore be used as a comparative check on the conclusions about other species.

In the fin whale and most other species an indirect approach is necessary because it has not been possible to study the animals in the breeding area.

The most profitable approach to this problem in the fin whale was thought to be a comparison with other species of Mysticetes and with Odontocetes, together with a detailed examination of the data accumulated by 'Discovery' Investigations since 1925 and in recent years by the National Institute of Oceanography. These comprise records of foetal length (snout—notch of flukes) of 956 fin whales and 1112 blue whales (*Balaenoptera musculus* Linn.), together with some records of other species. In addition there are 115 records of foetal weight. These lengths and weights were all measured by biologists or specially trained observers; length records accumulated since 1954 have not been included, but the weight data include records up to the 1957/58 whaling season.

The records of foetal lengths of a number of species given in the International Whaling Statistics from 1932 onwards have not been used. It is well known that these measurements are not accurate, though this in itself will probably not affect an average growth curve. More serious is the fact that small foetuses are almost invariably missed, and as pointed out by Brinkmann (1948), this has the effect of altering the slope of the growth curve.

I am indebted to Dr N. A. Mackintosh, C.B.E. and Mr S. G. Brown for their helpful suggestions and to the biologists, too numerous to name here, who collected the original data for the 'Discovery' Committee and the National Institute of Oceanography. Mr A. Style drew most of the figures.

PREVIOUS WORK

Guldberg (1886), from an examination of the lengths of foetuses of balcen whales in the North Atlantic, was able to show that there is a definite pairing season. Subsequently, more data were collected and reported on by Cocks (a series of papers 1886-90 referred to by Mackintosh and Wheeler, 1929), Grieg (1889), Guldberg (1894), True (1904), Collett (1911), Hamilton (1915), Barrett-Hamilton (Hinton, 1925), and others. An important paper by Risting (1928) was the first attempt at statistical treatment of a large body of data; he gives average growth curves and calculates the standard deviations of the monthly samples.

Hinton (1925) believed that in the southern fin whale, after an initial 61-day period of slow development, growth was probably linear from 30 cm. to birth at 610 cm. and that this regular growth occupied a period of 9 months. By a simple calculation he obtained the dates of pairing from individual foetuses, and made similar calculations for other species. Risting (1928), Zenkovic (1935) and Zemskiy (1950*a*) also adopted this method. The main points of interest are, first, that initial growth was assumed to be very slow, and secondly, that subsequent growth was assumed to proceed at a uniform rate.

Mackintosh and Wheeler (1929) reviewed the position at that time and came to some important conclusions about the breeding season and foetal growth in blue and fin whales. They first considered the more direct evidence concerning the time of the breeding season. This included information about the seasonal change in the condition of the reproductive organs of both sexes and suggested that the breeding season begins in the earlier part of the southern winter, i.e. in April and May. Examination of foetal length records confirmed this and they concluded that the frequency of pairings is at a maximum in June-July, that gestation lasts for a little less than a year and that 2 years is probably the usual interval between successive pregnancies.

In view of the fact that most later workers on foetal growth of whales have adopted the methods used by Mackintosh and Wheeler (1929), a further brief explanation is called for here. Their own material consisted of eighty-one fin whale and fifty blue whale foetuses, which they plotted graphically according to lengths and the dates on which they were found. The average monthly lengths were also plotted and a 'mean curve of growth' was drawn in by eye 'to represent as well as possible the general trend in the mass of plotted points, regard also being paid to the monthly average lengths' (p. 422). This curve shows a rate of growth which is slow initially and gradually increases throughout pregnancy. The main weakness in this method lies in the uncertainty of the rate of growth in the earliest stages, but this was partly overcome by these authors by fixing the time of the pairing season, as described above, from other sources. They concluded that the gestation periods of blue and fin whales are about $10\frac{1}{4}$ and $11\frac{1}{2}$ months. The former is in fairly close agreement with the conclusions reached in the present paper and the latter estimate is almost identical with them. These methods were applied by Matthews to the humpback whale (1937), the sperm whale, *Physeter catodon* Linn. (1938*a*) and the sei whale, *Balaenoptera borealis* Lesson (1938*b*). His conclusions about the length of gestation and the pairing season in the humpback whale are very close to those of Chittleborough (1958) based on more direct evidence. Matthews's figures (figs. 53, 54) in fact show a gestation period of almost 12 months, though he states in the text that gestation takes about 11 months (p. 58). For the sperm whale Matthews shows that growth is linear, which suggests a fundamental difference between this species and the balcen whales. Later authors appear to have overlooked, or ignored, this (Mizue and Jimbo, 1950; Clarke, 1956), and have drawn in a freehand curve.

Paulsen (1939) reviewed Risting's (1928) work and collected information about the occurrence of twinning and multiple foetuses. The next important paper is that by Brinkmann (1948) which

included a section on foetal growth, based on 580 fin whale foetuses and 276 blue whale foetuses whose lengths were recorded by trained Norwegian observers in the Antarctic season 1939/40. This author's conclusions were in very close agreement with those of Mackintosh and Wheeler (1929) concerning the shape of the growth curve for the 4 months, December to March. He showed that for the first 2 months the figures given by the International Whaling Statistics and by Risting (1928) are higher, probably because small foetuses have been overlooked.

Zemskiy (1950*b*) studied the relation of length to weight in 100 antarctic fin whale embryos and concluded that there were two distinct stages of development characterized by differences in the ratio of length to weight. He also showed that there is no change in body proportions over a range of lengths from 50 to 565 cm. This work will be discussed below.

Jonsgård (1951) discussed the foetal length records available to him for the minke whale (*B. acutorostrata* Lacépède) and drew attention to the probable effects of differential migration of pregnant females on the apparent curve of foetal growth.

Post-war observations by Japanese workers are recorded in several papers which deal in aggregate with some thousands of foetal lengths (Mizue and Jimbo, 1950; Nishiwaki and Hayashi, 1950; Nishiwaki and Oye, 1951; Mizue and Murata, 1951; Ohno and Fujino, 1952; Omura, 1953; Sakiura, Ozaki and Fujino, 1953; Kakuwa, Kawakami and Iguchi, 1953; Omura and Sakiura, 1956). The results of this work endorsed previous conclusions, particularly the work of Mackintosh and Wheeler (1929) on blue and fin whales. All these authors were content to draw in curves by eye, without attempting to obtain a mathematical fit to the points. Another important paper on twinning and multiple foetuses in southern fin whales, dealing in part with foetal growth, was contributed by Kimura (1957).

Reference must be made to a short paper by Frazer and Huggett (1958), based on foetal lengths included in the International Whaling Statistics. They conclude that the gestation periods of sperm, humpback, fin and blue whales are respectively 15-16, 12, 9-10 and 9 months. They state that other data suggest that the pilot whale, *Globicephala melaena* Traill, has a gestation period of 16 months.

So far we have been concerned mainly with the baleen whales (*Mysticeti*). The material available for a study of foetal growth in the toothed whales (*Odontoceti*) is much less abundant. The principal papers are those by Guldberg (1894) on four species of odontocetes, by Matthews (1938*a*), Mizue and Jimbo (1950) and Clarke (1956) on the sperm whale; papers by Degerbol and Nielsen (1930), Vladykov (1944) and Doan and Douglas (1953) on the white whale (*Delphinapterus leucas* Pallas); and an important work by Möhl-Hansen (1954) on the porpoise (*Phocaena phocoena* Linn.). The full results of recent work on the pilot whale (*Globicephala melaena* Traill) are not yet available (Frazer and Huggett, 1958; Sergeant, unpublished; Ann. Rep. Fish. Res. Bd Can., 1954). There are other papers which give less complete information about the course of foetal growth, and estimates of the length of gestation, size at birth, etc., for several species.

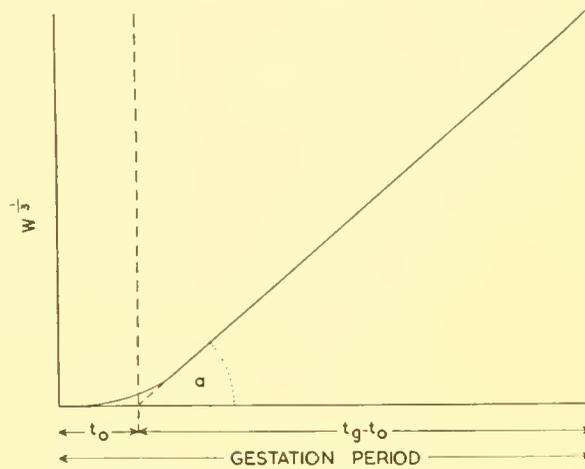
Finally, it should be mentioned that Scott (1949) has shown that for ten cetacean species the average neonatal length is directly correlated with adult length (which he defines as an estimate of the maximum length generally attained).

METHODS

Most of the data which are available for different species are sufficient to fix the rates of foetal growth for only part of the gestation period. For the southern fin whale in particular the bulk of the records cover the 6 months October to March, the first two of these months being poorly represented (Text-fig. 9). For some other species the data are perhaps rather more widely spread in time, or cover an earlier part of gestation; for example, the humpback whale, the minke whale, the sperm whale and

the porpoise. These limited curves may be extrapolated forwards to birth and backwards to conception. It is usually possible to estimate the average neonatal length with some accuracy, but the effect of extrapolation on the estimated time of birth can be greatly influenced by uneven sampling caused by differential migration of pregnant females (see below). The difficulty about finding the average date of conception by this method is that the rate of growth in the first 2 months is very slow. One approach is to take a species such as the humpback whale for which the average dates of conception and calving have been established, as well as the growth of the foetus over part of gestation. Then by analogy the growth rate in the early months can be estimated for other species. Freehand extrapolation and analogy do not provide a very firm basis, and the detailed conclusions drawn from growth curves constructed in this way may be greatly in error.

A better approach is to see whether it is possible to make any mathematical generalizations about foetal growth by combining the data which are available from all sources, for a variety of species, concerning foetal lengths, and mating and calving seasons.



Text-fig. 1. Diagram illustrating relation between foetal weight (or length), gestation period, t_0 and a (after Huggett and Widdas, 1951).

In this respect the work of Huggett and Widdas (1951) provides a starting point. These authors showed that for a variety of mammals of widely different mammalian orders the cube root of the foetal weight gave a linear plot with age for all except the first part of pregnancy. They suggested that the beginning of this steady state of growth might be correlated with the full establishment of the placental circulation. Previously to this work they had shown that foetal length increases linearly with age.

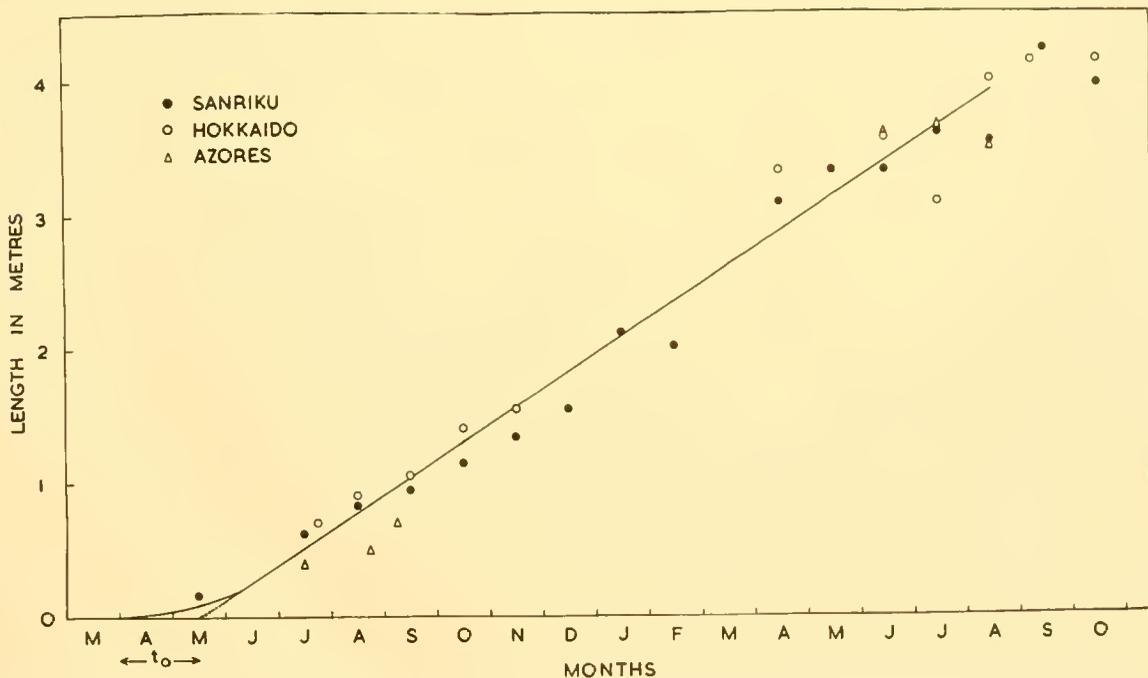
Their hypothesis is expressed in the general formula $W^{1/3} = a(t - t_0)$ and since $W \propto L^3$ it follows that $L = a(t - t_0)$. The term a is constant in respect of any particular species and is called by them the 'specific foetal growth velocity'. It is the slope of the line relating foetal weight, $W^{1/3}$ (or foetal length, L) to the age after conception (t) in that segment of the growth curve where the relationship is linear. The term t_0 'is the intercept where the linear part of the plot, if produced backwards, cuts the time axis' (see Text-fig. 1). This term has 'no clear biological significance in foetal development, but if the numerical value of t_0 can be estimated by analogy with other mammals. . . then one known weight (W) and time from conception (t) would be sufficient to determine the value of a for the mammal concerned'. Their estimate of t_0 for different animals is based on the observation that t_0 increases as the gestation time lengthens but forms a decreasing fraction of the total gestation time. Huggett and Widdas use arbitrary estimates of t_0 : for gestation times from 0 to 50 days $t_0 \approx 0.4 \times$ (gestation time); 50-100 days, $t_0 \approx 0.3 \times$ (gestation time); 100-400 days $t_0 \approx 0.2 \times$ (gestation time); and over 400 days $t_0 \approx 0.1 \times$ (gestation time). These estimates of t_0 apply to weight data and for length t_0 is slightly less.

For example, in the sheep $Wt_0=38.6$ days and $Lt_0=34$ days. In the present paper Lt_0 is assumed to be $0.9 \times Wt_0$, and Huggett and Widdas's scale of estimates of Wt_0 is converted by this factor.

Huggett and Widdas state that the growth velocity found by their method for blue and fin whales is 'at least $2\frac{1}{2}$ times greater than the highest rate found for all other mammals, and about 10 times greater than the rate for Primates'. They remark that it 'would be interesting to see if these high rates are peculiar to the large whales or are the same in related species of smaller size'. It is generally considered that the Odontocetes are on average on a lower grade than Mysticetes (Simpson, 1945) and in general they are smaller, so they will now be discussed in this order. Conspicuous modifications in the shape as well as the magnitude of the foetal growth curves of the Mysticetes as compared with the Odontocetes then become apparent.

TOOTHED WHALES (*ODONTOCETI*)

Data on the foetal growth of the sperm whale given by Matthews (1938*a*), Mizue and Jimbo (1950), and Clarke (1956) have been used. As the full original data are not given the mean monthly foetal lengths have been taken from the graphs and the Japanese measurements have been converted from



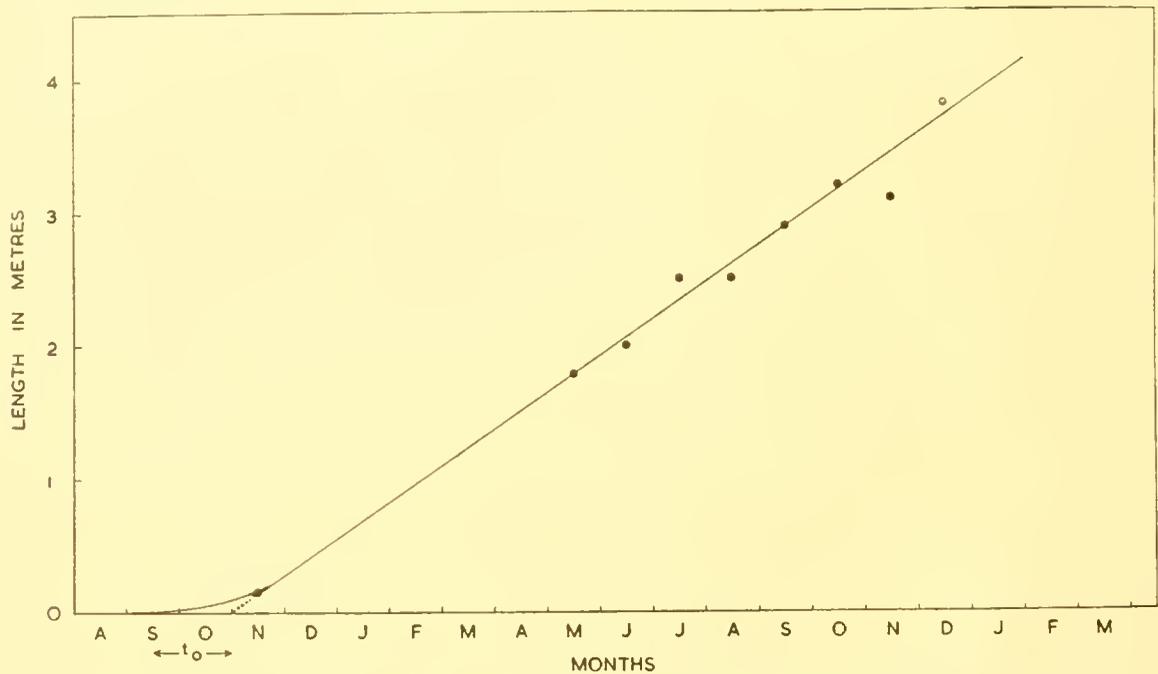
Text-fig. 2. Foetal growth in length of northern hemisphere sperm whale, *Physeter catodon* (points represent monthly means). In drawing the average growth curve only the North Pacific data have been used.

feet to metres in the interests of uniformity. Although great care was exercised, some small errors may have resulted from this treatment, but it is thought that they do not affect the conclusions drawn.

These data are set out graphically for northern and southern hemisphere sperm whales in Text-figs. 2 and 3. The average neonatal lengths are taken to be 3.92 m. in the northern hemisphere (Clarke, 1956) and 4.15 m. in the southern hemisphere (Matthews, 1938*a*, p. 138, '4 metres or a little more'). Lines representing the average rate of growth have been fitted by inspection, slightly weighted to allow for the variation in size of the monthly samples. Both northern and southern hemisphere data suggest that growth is linear for most of gestation. For the northern data the length of the period ($t_g - t_0$) is 15 months, or 457 days. If the neonatal length of southern hemisphere sperm whales is

assumed to be 4.15 m. then this part of gestation is again 15 months. For foetal weight data Huggett and Widdas's (1951) arbitrary scale suggests that Wt_0 is about $0.08 \times$ (gestation time) for gestation periods of 450–500 days and converting, $Lt_0 \approx 0.07 \times$ (gestation time). Then $Lt_0 \approx (0.07 \times 457)/0.93 \approx 34$ days and the total gestation period is 491 days or 16 months. This agrees well with previous estimates (16–17 months) which have taken account of other evidence of the pairing and calving season, and also the bimodal frequency distribution of foetal lengths.

The steeper growth curve of the foetal sperm whale in the southern hemisphere, and also the larger neonatal size of the southern animals, is in line with work on other cetaceans showing that southern hemisphere adults are larger than those in the north (e.g. Jonsgård, 1952; Pike, 1953). Clarke (1956, p. 289) has already suggested that both male and female sperm whales attain larger sizes in the southern hemisphere.



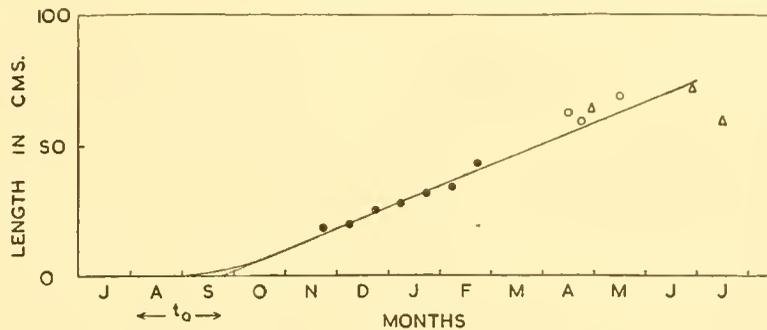
Text-fig. 3. Foetal growth in length of southern hemisphere sperm whale, *Physeter catodon* (points represent monthly means).

For the porpoise, Möhl-Hansen (1954) gives data on the length of 119 foetuses from the Baltic. Of the females judged to be sexually mature 84% were pregnant; there were not two foetal length groups, and this together with other data gives striking evidence that the gestation period is under a year. He estimates that pairing occurs in July and August and that the duration of pregnancy 'should be 11, or at least 10–11, months, instead of 9–10 as usually assumed' (p. 389). The average neonatal length is approximately 75 cm. These data are presented graphically in Text-fig. 4, in which Möhl-Hansen's mean monthly values for November to February are shown; also three individual length records from the Zoological Museum, Copenhagen, and three individual records from Holland (Van Deirse, 1946). The Norwegian material for the porpoise (Grieg, 1898; Möhl-Hansen, 1954, fig. 7) shows a higher growth rate than the material from Denmark and Holland; it is not used here. The line fitted by inspection attains 75 cm. at the end of June and intersects the abscissa in the second half of September giving an estimate of $9\frac{1}{4}$ months (or 282 days) for $(t_g - t_0)$. For gestation periods of a little over 300 days, using Huggett and Widdas's estimate converted for length, $Lt_0 \approx 0.15 \times$ (gestation time) and therefore $Lt_0 \approx (0.15 \times 282)/0.85 \approx 50$ days.

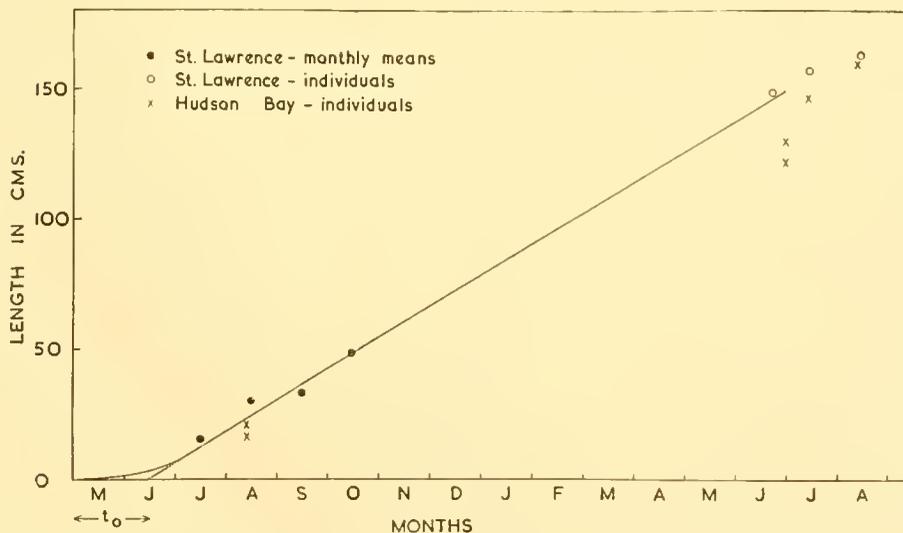
The total gestation period estimated in this way is therefore 332 days or nearly 11 months, which is in close agreement with Möhl-Hansen's (1954) estimate. The peak time of conceptions is the beginning

of August, which also agrees very well with this author's conclusions; peak calving is estimated as the end of June and does not seriously conflict with the information given by him.

Limited data are published by Vladykov (1944) and Doan and Douglas (1953) from studies of the white whale in the Saint Lawrence area and Hudson Bay, respectively. These are set out in Text-fig. 5 from which it appears that in this species also foetal growth can be described by a linear plot, with parturition at the end of June and Lt_0 in the middle of June, so that the estimate of $(t_\sigma - t_0)$ is $12\frac{1}{2}$ months, or 380 days. For gestation periods of this magnitude Lt_0 is estimated to be $0.1 \times$ (gestation time). Then $Lt_0 \approx (0.1 \times 380)/0.9 \approx 42$ days. The gestation period is therefore estimated to be 422 days,



Text-fig. 4. Foetal growth in length of the porpoise, *Phocaena phocoena*. Black circles, monthly means, Denmark; white circles, single records, Denmark; white triangles, single records, Holland.



Text-fig. 5. Foetal growth in length of the white whale, *Delphinapterus leucas*.

or just under 14 months, with the majority of conceptions in April and May and birth at an average length of 1.5 m. taking place about the end of June. This is not in close agreement with the tentative conclusions of Vladykov (1944) and Doan and Douglas (1953).

In the Greenland area this species has been studied by Degerbol and Nielsen (1930) who give lengths of 131 foetuses measured in the 6 months, November to April. Their data also suggest that after the initial period growth is linear, but the slope of their growth curve is steeper, and the neonatal length evidently greater, than in the Canadian populations. It is not possible to estimate the gestation period from these data.

For these three species of toothed whales the foetal growth in length can be described by a linear plot over most of the period of gestation and the estimates of the length of the gestation period by means of Huggett and Widdas's (1951) method are in fairly close agreement with previously published

estimates. The assumption (from rather sparse data) that Lt_0 is 90% of Wt_0 appears to be justified and the length of the estimated period Lt_0 varies from 34 days in *Physeter* to 50 days in *Phocaena*.

Huggett and Widdas (1951, p. 413) remark that 'among mammals in the intermediate range of [their] Fig. 8, the period of linear growth is determined by the size of the foetus at birth. Thus, as the birth weight of the young is increased the mammal does not grow its young quicker, along a steeper slope, but must grow its foetus for a longer time.' This is now seen not to be entirely true of the toothed whales in which the slope of linear growth may be steeper and also continued for a longer time, as for instance in the sperm whale compared with the porpoise. This answers the question put by Huggett and Widdas (1951) (see p. 287), and shows that Rubner's finding (1908) that, in all species except man, the birth weight is proportional to the gestation time, is not true of the toothed whales. As will be apparent when the position in baleen whales has been established, it is even less applicable to whales in general.

BALEEN WHALES (*MYSTICETI*)

The only group of whalebone whales in which foetal growth has been studied in any detail are the Balaenopterids. The principal papers are listed in an earlier section of this paper.

In all species of Balaenopterids and in the grey whale, *Eschrichtius gibbosus* Erxleben (Hubbs, 1958), the gestation period has been fixed at a year or less. Records of mean monthly foetal lengths, evidence of the pairing season from examination of male and female reproductive tracts, of the occurrence of calves, and of the proportion of mature females which are pregnant, all point to this conclusion. Indeed, it is evident that in some species females commonly undergo two pregnancies in 2 years (Jonsgård, 1951; Omura and Sakiura, 1956) and in others it is not uncommon (Chittleborough, 1958; Laws, 1958; Hubbs, 1958).

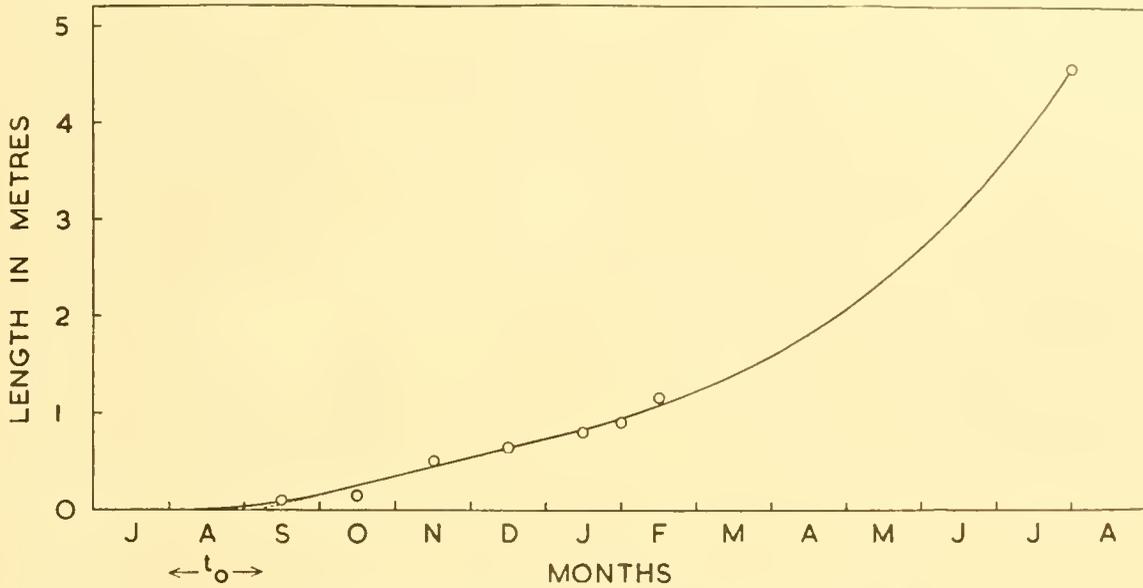
The neonatal lengths are known fairly accurately for most species and adequate foetal length records cover several months of the gestation period in these species (Text-fig. 12). When the mean monthly foetal lengths and the neonatal lengths are plotted, it is immediately apparent that if the gestation period for these species is a year or less, foetal growth in length cannot be described by a straight line as in the *Odontocetes* discussed above. Instead it appears that the slope of the growth curve, 'gradually increases throughout pregnancy' as Mackintosh and Wheeler (1929) showed for blue and fin whales. It should be pointed out that even in these two species, which are the fastest growing whales, more than two straight lines are necessary in order to fit the points and at the same time to give a gestation period of a year or less.

A number of trial plots were made at first and these suggested that the first half of foetal growth was linear (as in the toothed whales), while the data for the second part agreed quite well with an exponential growth rate.

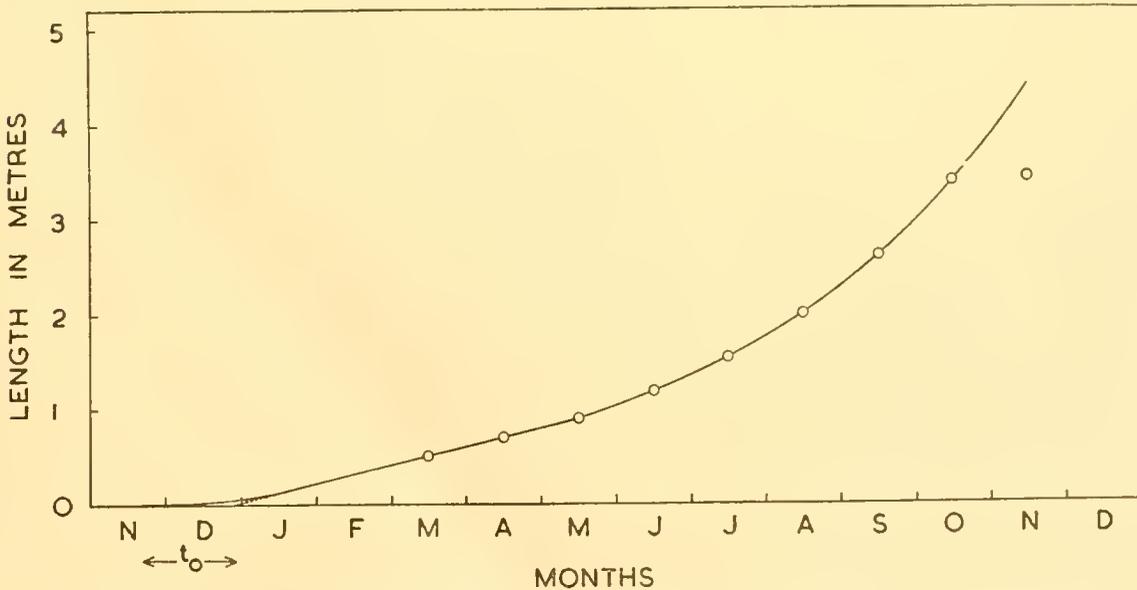
The humpback whale is the species in which the duration of pregnancy has been fixed with most precision (Chittleborough, 1954, 1958). In Text-fig. 6 a curve of foetal growth in length has been constructed for this species. The method has been to take the mean dates of conception and calving as early August, so that the gestation period is 12 months, and the neonatal length given by Chittleborough (1954, 1958) has been plotted accordingly. The mean monthly foetal lengths given by Matthews (1937) have been used and also the mean foetal length for a sample taken in the first week in February, given by Symons and Weston (1958). The monthly means from March onwards are based on very small samples and have not been plotted. A linear plot has been fitted to the foetal length values for September to January and has been continued as an exponential curve up to the neonatal point. The linear part of the curve intersects the abscissa at the end of the first week in September, giving a value for Lt_0 of approximately 38 days. The slope of the linear segment of the

curve is slightly less than the slope of the sperm whale curve (Text-fig. 12) and Lt_0 is very close to this value for the sperm whale in which $Lt_0 \approx 34$ days.

This suggests that it is correct to interpret the middle phase of foetal growth as linear in the humpback whale at least and probably this also holds good for other baleen whales. The exponential fit to the second part does not rest on a firm foundation and, as will be seen in the more detailed



Text-fig. 6. Foetal growth in length of southern hemisphere humpback whale, *Megaptera novaeangliae*. Points are mean values. See text for explanation.



Text-fig. 7. Foetal growth in length of northern hemisphere sei whale, *Balaenoptera borealis*. Points represent monthly means.

discussion of blue and fin whales, the variability in the monthly foetal lengths is such that foetal growth could be described by a series of linear phases of different slope, or by a more complicated general formula. The logarithmic plot has been accepted as the most simple fit for all the species considered.

As foetal growth of baleen whales cannot be described by a linear plot of foetal length throughout gestation, the values of Lt_0 cannot be derived by reference to the length of gestation. However, it is

found that for the four species considered so far (in which Lt_0 has been estimated from the length of gestation (toothed whales), or by reference to an accurately fixed conception date (humpback whale)), the slope of linear growth is closely correlated with Lt_0 (Table 1). As the correlation is so close the values of Lt_0 for other species in which a is known have been obtained by extrapolation (blue and fin whale) or interpolation (northern sei whale, minke whale). These values are bracketed in Table 1.

For the northern sei whale (*Balaenoptera borealis* Lesson), the mean monthly foetal length values given by Mizue and Jimbo (1950) fit almost exactly a linear/log growth curve. The three points for March, April and May fall on a straight line intersecting the abscissa at the end of December, and the five means for the succeeding months, June to October, fall on a logarithmic curve (Text-fig. 7). Moreover, the neonatal length given by Mizue and Jimbo (1950) for this species (14-15 ft., or about 4.4 m.) is very close to the length of the humpback whale at birth and the fitted curves of these two species are almost identical (Text-fig. 12). If Lt_0 can be taken to be 39 days (Table 1) then the average date of conception is in the third week in November. By extrapolation of the exponential growth

Table 1. *Values of Lt_0 and a for eight cetacean species*

<i>Species</i>	Lt_0	a
<i>Physeter catodon</i>	34	0.84
<i>Delphinapterus leucas</i>	42	0.47
<i>Phocaena phocaena</i>	50	0.25
<i>Megaptera novaeangliae</i>	38	0.70
<i>Balaenoptera musculus</i>	(30)	1.00
<i>B. physalus</i>	(33)	0.88
<i>B. borealis</i>	(39)	0.66
<i>B. acutorostrata</i>	(43)	0.49

curve in the second half of pregnancy the birth length is reached in mid-November, so the gestation period estimated in this way is almost 12 months. Mizue and Jimbo (1950) also assume that the end of November is the average time of birth, but that the time of pairing is in January, giving a gestation period of less than 11 months. It should, however, be noted that these authors fix the time of conception by freehand extrapolation.

Since the work of Mizue and Jimbo (1950), Omura and Fujino (1954) have shown that the northern and southern types of sei whale in the western Pacific Ocean are the species *B. borealis* Lesson, and *B. brydei* Olsen, respectively. These two species are similar in size, the former being apparently slightly larger. The main differences are in the quality and shape of the baleen plates, the shape of the palate, and the extent of the ventral grooves. The catch at the Bonin Islands is now composed of Bryde's whales, but formerly, when the material in Mizue and Jimbo's (1950) paper was collected, the whaling season was earlier and the catch was almost entirely composed of sei whales. According to Omura and Fujino (1954) sei whales are taken at the Bonin Islands from November to April and in May and June the catch is composed of Bryde's whales; at Sanriku and Hokkaido the catch is almost entirely sei whales.

It seems reasonable, therefore, to conclude that the data presented in Text-figure 7 apply to the sei whale, *B. borealis*. In view of the similarity in the size of *B. borealis* and *B. brydei* it is probable that the average neonatal lengths and foetal growth curves are similar, though the breeding season may be different.

The mean monthly foetal lengths for July to October of the northern fin whale given by Mizue and Jimbo (1950) also lie on an exponential curve.

The foetal growth of the minke whale has been discussed by Jonsgård (1951) and Omura and Sakiura (1956). There is no reliable information on the length of gestation but Jonsgård found that only

4.5% of the adult females examined were non-pregnant, and all lactating females were pregnant. This strongly suggests that the gestation period is less than 12 months (as there are not two foetal length groups) and Jonsgård concluded that 'the majority of mature females bring forth young once a year'. His material covers too short a period to allow for an estimate of the duration of gestation. Nor is an estimate of the length of gestation possible from the data available to Omura and Sakiura (1956). Earlier estimates of the duration of gestation as 10 months, made by Eschricht and Guldberg are referred to by Jonsgård (1951), who concludes that pairing occurs from about January to the end of May, with a maximum frequency probably in March. For reasons which Jonsgård discusses, Grieg's (1889) material has not been used in the present paper. Although Jonsgård has concluded that, owing to differential migration, the foetal measurements available are not truly representative of the stock of whales, his mean lengths for the 4 months April to July are very similar to those given by Omura and Sakiura (1956, fig. 23, curve A).

The growth curve for these months appears to be linear as in other species (Text-fig. 12) and intersects the abscissa at L_{t_0} in mid-March. By analogy with other species the period from conception to L_{t_0} is probably about 43 days (i.e. intermediate between the humpback whale and the porpoise) which gives an estimated average date of conception at the beginning of February. It is not possible to come to any conclusions about the later part of pregnancy, but with a neonatal length of 2.46 m. (Jonsgård, 1951) or even 2.8 m. (Omura and Sakiura, 1956) the rate of growth must increase markedly if pregnancy is to occupy no more than 12 months.

The evidence presented so far strongly suggests that, in a baleen whale species foetal growth in length may be represented by a curve, increasing very slowly at first, then linearly for about 4 months, and finally increasing exponentially until parturition. Although the strong measure of agreement between the different species, and particularly between the estimated and observed conception dates for the humpback whale, is very suggestive, it must not be forgotten that mean values of small samples may differ considerably from the true mean value in the population sampled, and the evidence for a phase of exponential growth is not conclusive.

FIN AND BLUE WHALES

The foregoing parts of this paper have been concerned with published data, and without the full original records it was not possible to calculate the extent of variation within the monthly samples.

For 956 southern hemisphere fin whales and 1112 blue whales the original data on foetal lengths are available and will now be used in a more detailed study of foetal growth in these species in order to test the hypothesis put forward above.

Of the fin whale records, five are from Saldanha Bay, South Africa, 268 are from South Georgia and 683 are from the pelagic whaling grounds. The South Georgia sample extends by 2 months the period of foetal growth covered by the pelagic data. Of the blue whale records, seven are from Saldanha Bay, and ninety are from South Georgia. As they do not extend the period for which data are available they are not used in calculating the monthly means.

All these measurements were made either by biologists or by specially trained observers, and the sources of error may therefore be considered to be minimal¹. The foetal length records are summarized in Tables 2 and 3; conclusions about the growth curves are presented in Tables 4 and 5 and Text-fig. 8.

The variability of the length records is indicated by the mean plus or minus two standard errors. There is a 95% probability that the true mean of the population as a whole, in any one month, assuming the sample is not biased, will lie within this range. For the fin whale the value of four

¹ For example, the uterus is searched for a small foetus if a functional corpus luteum is seen in the ovaries.

Table 2. Records of foetal lengths of southern hemisphere fin whales (Antarctic pelagic and South Georgia). Length groups are given to the first decimal place and, for example, group 1.0-1.2 is to be taken as 1.01-1.20.

Length (m.)	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total
0.0-0.2	1	3	3	2	—	—	—	9
0.2-0.4	3	5	9	14	2	—	—	33
0.4-0.6	2	1	10	10	4	—	—	27
0.6-0.8	5	9	13	18	7	4	—	56
0.8-1.0	4	5	21	20	6	4	—	60
1.0-1.2	3	14	8	14	8	3	—	50
1.2-1.4	3	5	15	24	19	6	—	72
1.4-1.6	1	10	2	22	13	6	—	54
1.6-1.8	—	4	14	20	14	9	—	61
1.8-2.0	—	1	15	23	15	5	—	59
2.0-2.2	—	1	10	19	10	6	1	47
2.2-2.4	—	1	10	14	20	7	—	52
2.4-2.6	—	—	4	18	19	10	—	51
2.6-2.8	—	—	6	9	26	5	1	47
2.8-3.0	—	—	2	16	20	13	—	51
3.0-3.2	—	—	—	11	16	10	1	38
3.2-3.4	—	—	—	4	7	5	—	16
3.4-3.6	—	—	—	1	13	14	—	28
3.6-3.8	—	—	—	4	18	10	—	32
3.8-4.0	—	—	—	3	14	10	—	27
4.0-4.2	—	—	—	1	14	8	—	23
4.2-4.4	1	—	—	3	5	10	—	19
4.4-4.6	—	—	—	—	8	3	1	12
4.6-4.8	—	—	—	—	4	5	1	10
4.8-5.0	—	—	—	—	1	4	—	5
5.0-5.2	—	—	—	—	—	3	—	3
5.2-5.4	—	—	—	—	1	2	—	3
5.4-5.6	—	—	—	—	—	1	—	1
5.6-5.8	—	—	—	—	—	—	1	1
5.8-6.0	—	—	—	—	—	2	—	2
6.0-6.2	—	—	—	—	—	—	1	1
6.2-6.4	—	—	—	1	—	—	—	1
Total	23	59	142	271	284	165	7	951

Table 3. Records of foetal lengths of southern hemisphere blue whales (Antarctic pelagic only). Length groups as in Table 2

Length (m.)	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total
0.0-0.2	—	—	1	—	—	—	—	1
0.2-0.4	—	3	2	1	—	—	—	6
0.4-0.6	—	3	7	3	—	—	—	13
0.6-0.8	—	2	5	4	1	—	—	12
0.8-1.0	—	1	17	12	4	—	—	34
1.0-1.2	1	2	7	6	—	—	—	16
1.2-1.4	—	8	30	24	8	2	—	72
1.4-1.6	—	3	32	28	6	2	—	71
1.6-1.8	1	4	11	5	1	—	—	22
1.8-2.0	—	4	32	34	9	1	—	80
2.0-2.2	—	2	17	22	13	1	—	55
2.2-2.4	—	—	7	15	2	—	—	24
2.4-2.6	—	1	25	37	16	5	—	84
2.6-2.8	—	—	15	33	20	3	—	71
2.8-3.0	—	—	1	1	2	1	—	5
3.0-3.2	—	—	13	40	13	6	—	72
3.2-3.4	—	—	7	30	13	7	—	57
3.4-3.6	—	—	1	4	1	1	—	7
3.6-3.8	—	—	4	29	27	4	—	64
3.8-4.0	—	—	1	14	22	9	1	47
4.0-4.2	—	—	—	1	5	1	—	7
4.2-4.4	—	—	1	19	16	7	1	44
4.4-4.6	—	—	1	11	19	11	—	42
4.6-4.8	—	—	—	1	3	2	—	6
4.8-5.0	—	—	—	8	10	8	—	26
5.0-5.2	—	—	—	3	11	9	—	23
5.2-5.4	—	—	—	—	—	—	—	—
5.4-5.6	—	—	—	1	15	9	—	25
5.6-5.8	—	—	—	1	4	2	—	7
5.8-6.0	—	—	—	—	1	—	—	1
6.0-6.2	—	—	—	—	1	5	—	6
6.2-6.4	—	—	—	—	—	1	3	4
6.4-6.6	—	—	—	—	—	—	—	—
6.6-6.8	—	—	—	—	1	2	—	3
6.8-7.0	—	—	—	—	1	—	—	1
7.0-7.2	—	—	—	—	1	—	—	1
7.2-7.4	—	—	—	—	1	—	—	1
Total	2	33	237	387	248	101	2	1010

Table 4. Growth in length of southern hemisphere fin whale embryos. See text for explanation

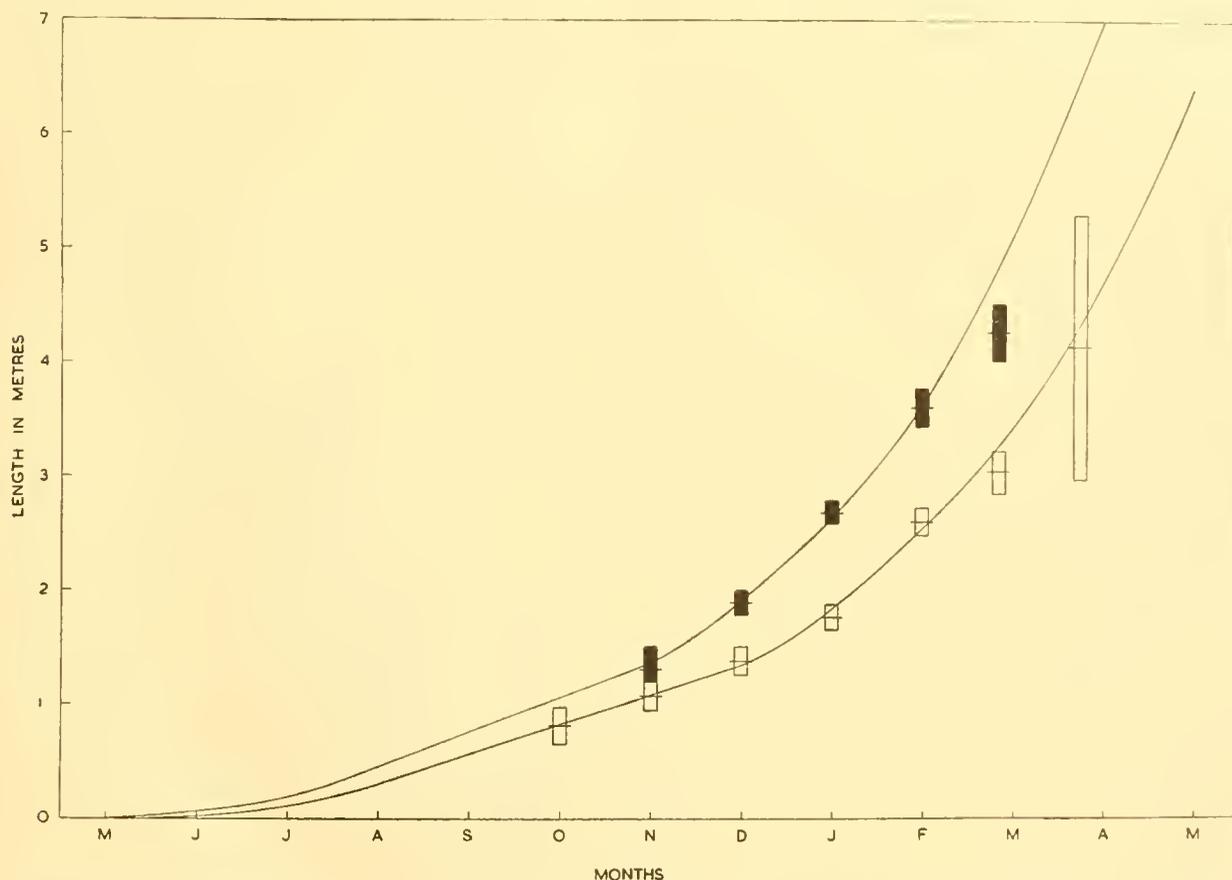
Month	Size of sample	Mean length (m.)	2 S.E.	Fitted curve
Early June	—	—	—	0.00
Mid-July	—	—	—	0.10
Mid-August	3	—	—	0.30
Mid-September	2	—	—	0.55
Mid-October	23	0.809	0.158	0.80
Mid-November	59	1.069	0.128	1.07
Mid-December	142	1.377	0.121	1.33
Mid-January	271	1.775	0.112	1.82
Mid-February	284	2.620	0.128	2.55
Mid-March	165	3.056	0.188	3.40
Mid-April	7	4.128	1.154	4.70
Mid-May	—	—	—	6.40
Total	956	—	—	—

Table 5. Growth in length of southern hemisphere blue whale embryos. See text for explanation

Month	Size of sample	Mean length (m.)	2 S.E.	Fitted curve
Mid-May	—	—	—	0.00
Mid-June	—	—	—	0.06
Mid-July	2	—	—	0.18
Mid-August	2	—	—	0.45
Mid-September	2	—	—	0.75
Mid-October	6	1.153	—	1.05
Mid-November	33	1.300	0.199	1.35
Mid-December	237	1.896	0.104	1.90
Mid-January	387	2.682	0.109	2.63
Mid-February	248	3.597	0.168	3.60
Mid-March	101	4.258	0.246	5.10
Mid-April	2	—	—	7.00
Total	1022	—	—	—

standard errors is about 0.26 m. Even in January and February, in which the sample sizes are large, the variation is of this order. The explanation of this relatively large variation is undoubtedly that the pairing season extends over several months, thus increasing the length variation within the monthly samples. Comparison of Tables 4 and 5 shows that a similar variation occurs in the blue whale.

Symons (1955) compared foetal length data for fin whales taken in area IV in 1954 and in areas III and IV in 1955¹, and suggested that those in the second year were 'some 1 to 2 weeks late in their peak period of conception'. He then put forward a hypothesis based on this supposed difference.



Text-fig. 8. Foetal growth in length of southern hemisphere blue whale, *Balaenoptera musculus*, and fin whale, *B. physalus*. Rectangles represent monthly means, plus or minus two standard errors. (Black—blue whale; white—fin whale).

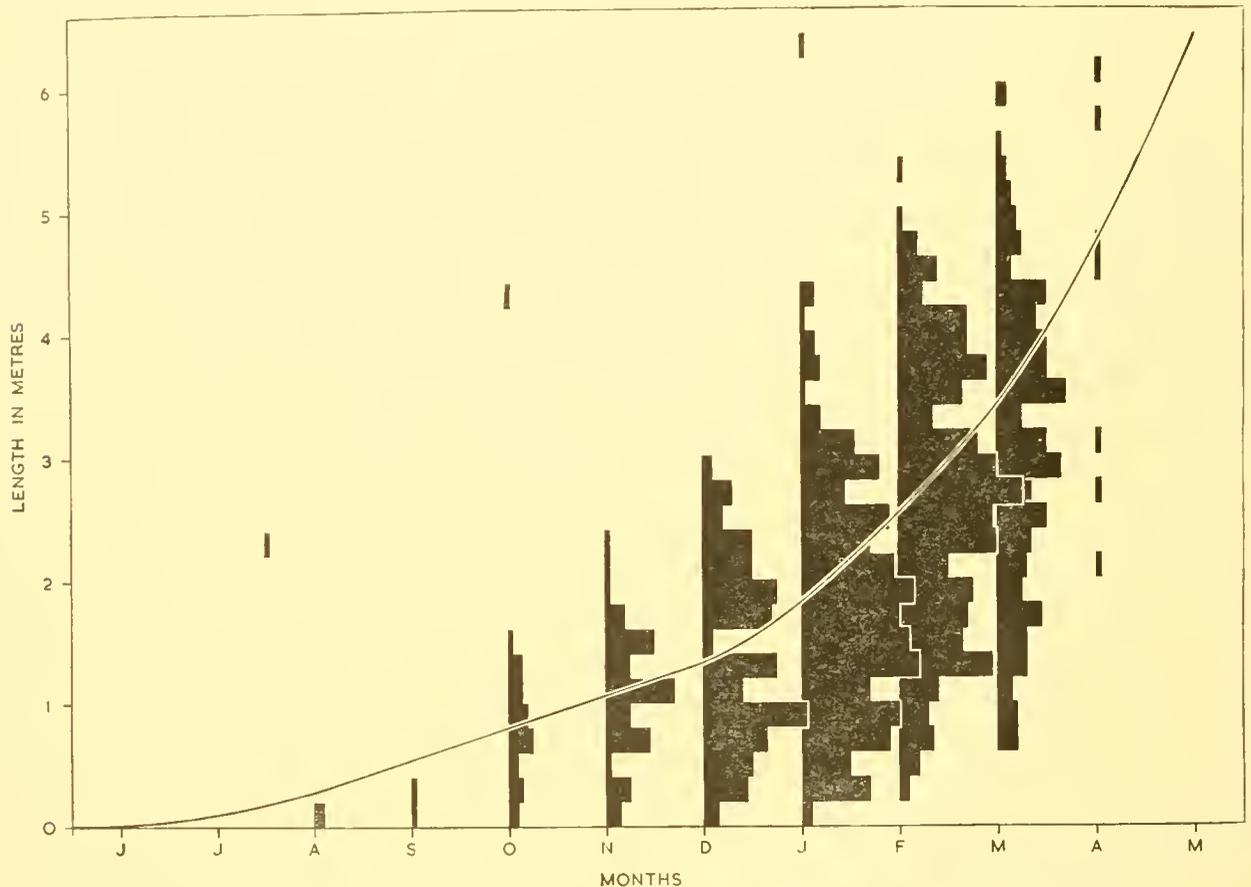
In fact the greatest differences between his mean lengths are almost within the range of four standard errors (about 0.26 m. or 10 in.) calculated for the present material and certainly well within plus or minus two standard errors of the means for his very much smaller samples. The supposed difference between these two years is therefore unlikely to be significant.

The average growth curve for the fin whale has been fitted as follows. The mean foetal lengths of the samples for October, November and December are thought to be very close to the true mean lengths for these months; they lie on a straight line which cuts the abscissa, when extrapolated, in mid-July. The slope of this line is very similar to that calculated for the sperm whale (Text-fig. 12) and the period from conception to Lt_0 is estimated to be 33 days in the fin whale (Table 1). This gives the second week in June as a mean conception date for the southern hemisphere fin whale, which agrees very well with independent conclusions from other data. (These include the follicular cycle of females at puberty, and the histological cycle of testis activity and of testis tubule diameters,

¹ There are six Antarctic whaling 'areas'. Areas III and IV are south of the Indian Ocean.

which will be described in a later paper.) It should be noted that this conclusion is in agreement with that reached by Mackintosh and Wheeler (1929) on similar grounds.

A second straight line of different slope can be drawn through the blocks marking the means plus or minus two standard errors shown for January, February, March and April in Text-fig. 8. When extrapolated this gives an impossibly long gestation period. In any case the true monthly means of the population are probably well within the range of four standard errors, and in addition it can be shown that the samples for March and April are biased towards lower values, owing to differential migration of females from the area (discussed below). A logarithmic curve has therefore been fitted to the mean lengths for December, January and February. When extrapolated this attains the mean



Text-fig. 9. Monthly foetal length frequencies of southern hemisphere fin whales, *Balaenoptera physalus*; class interval 0.2 m. The estimated mean growth curve is taken from Text-fig. 8.

birth length (6.4 m., Mackintosh and Wheeler, 1929) in mid-May, giving a gestation period of just over 11 months. It is considered that this estimate is as accurate as the data permit and that it is unlikely to be more than plus or minus 15 days in error.

The reasons for concluding that the fin whale foetal length samples for March and April are biased, must now be presented.

First, it should be noted that almost all the material comes from antarctic waters. In Text-fig. 9 the monthly foetal length frequency distributions are set out in 0.2 m. groups. This figure gives a better idea of the individual variation than the same data presented in Table 2, and it will be noticed that the shape of the frequency distributions changes from month to month and that the relative numbers of larger foetuses appear to be reduced in March. The April sample is really too small to show such a tendency.

In Text-fig. 10 these monthly length frequencies have been smoothed (in groups of three), converted to percentages, and smooth curves drawn through the points thus allowing a more direct comparison to be made. It can be seen that the monthly length frequencies show a normal unskewed distribution, which is compatible with linear growth, in the early months (October and November). The later curves (December and January) are negatively skewed, suggesting an increasing growth rate. On this assumption the curves for February and March should also be negatively skewed, but the February sample shows an almost normal distribution and the March curve is positively skewed, that is to say the trend is reversed. This suggests either that the slope of the foetal growth curve has greatly decreased again (which would result in the extension of the gestation period over more than 12 months), or that some large foetuses are missing from the February sample and more are missed in March and April. The first explanation is ruled out by other considerations discussed above, and we are left with the second possibility.

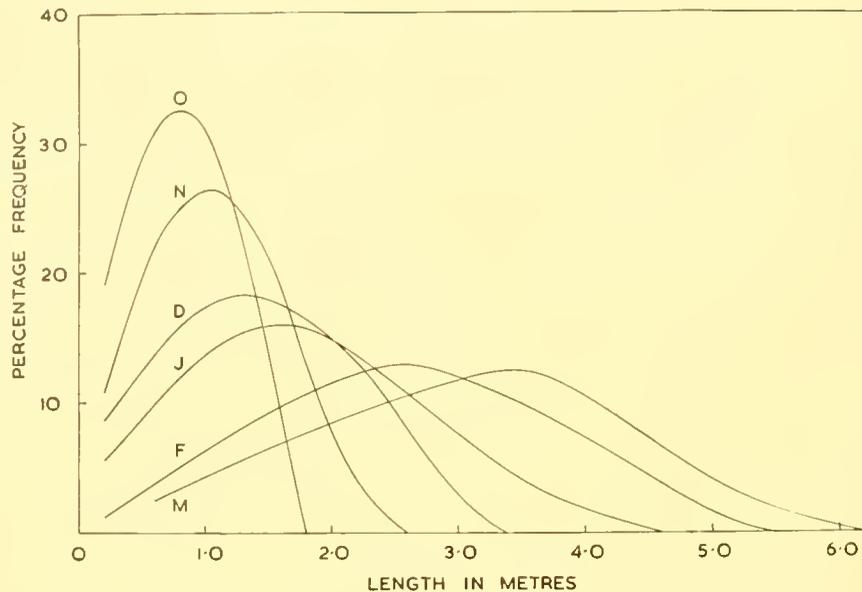
Text-fig. 11 has been constructed to demonstrate the changes which may be expected in the foetal length frequency curves during the year. It has been assumed, for the purpose of discussion, that the frequency of conceptions is described by a normal curve extending over, say, 6 months (shown in the figure as an inset), that the average curve of growth in length is that given in Table 4 and Text-fig. 8, and that there is no variation in the growth rates of individual foetuses. The diagram has been constructed by plotting the average growth curve (thick line) and drawing in six similar growth curves displaced by intervals of 1 month (dotted lines). The space between these curves then extends over 6 months. This follows the practice of Mackintosh and Wheeler (1929, fig. 146). The frequency curve of foetal length has then been drawn in for each month by plotting the assumed conception frequencies against the average foetal lengths taken from the curves for each of the 6 months of conception (see inset). The frequency curves of foetal lengths constructed in this way for different sampling months demonstrate the transformation of the *shape* of the monthly length frequency curves, though not their magnitude.

The curve of conception frequencies used here is an arbitrary one and there are reasons for supposing that in the fin whale it does not show a normal distribution but is negatively skewed, i.e. the mode is earlier in time. This would have the effect of shifting the modes in the estimated foetal length frequencies for monthly samples to slightly higher values. The skewness of the curves of, for example, December, January and February would be slightly less in a more realistic model.

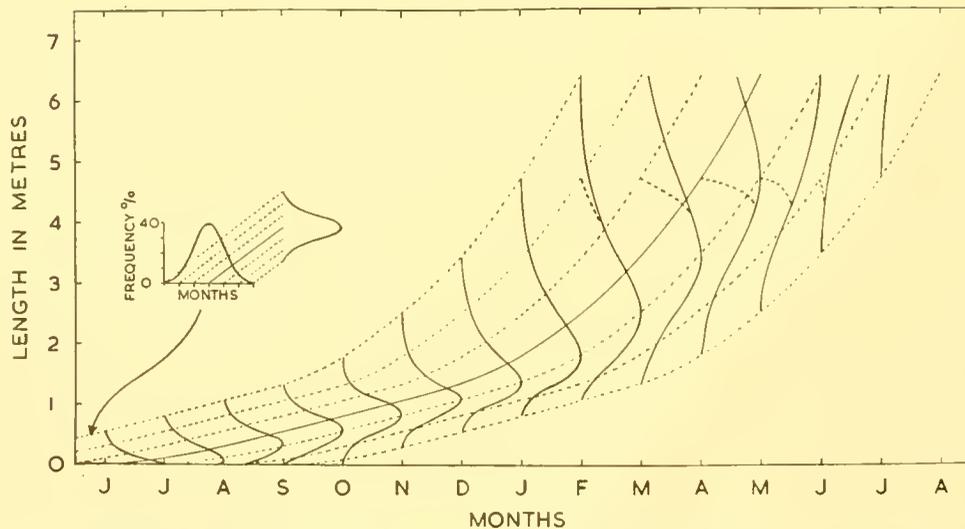
The shapes of these model curves are very similar to the sample length frequency curves for October, November, December, January and February (Text-fig. 10), and follow the same trend of increasing skewness and increased length range. The length frequency curve for the March sample shows a reversal of this trend and there are insufficient observations for April.

It has been suggested above that from March onwards the larger foetuses are missing from samples because females approaching full term migrate out of the Antarctic area, so as to arrive in the breeding area for parturition. Let us assume that the adult fin whale travels some 3000 nautical miles from the Antarctic feeding grounds to the subtropical breeding areas (from about 65° S. to about 15° S.); unfortunately we have no direct information on the duration of this migration. A fin whale and a blue whale each recovered some 2000 miles from the place of marking had travelled, in the Antarctic, at minimum average speeds of about 1.3 and 1.7 knots, respectively (Brown, 1957), but these speeds are undoubtedly well below the average speeds on migration. There is more useful information about the humpback whale, which is, however, a slower animal than the fin whale. Aerial observation of six migrating adults which were followed for distances of 3–20 miles showed that they travelled at speeds of 3.6–6.5 knots, averaging about 5 knots (Chittleborough, 1953). One 43 ft. male humpback marked (no. A137) on 7 July 1953 off East Australia (*ca.* 35° 10' S., 150° 35' E.) was recovered

7 days later 525 miles to the north (27° S., 153° 26' E.) having maintained an average speed of 3.6 knots in its northward migration. If the migrating near-term fin whales travel at 4-6 knots they will take 21-31 days to cover the distance from the Antarctic to sub-tropical breeding areas. We may therefore assume that about a month will elapse between the time of leaving the Antarctic whaling grounds and giving birth to the calf.



Text-fig. 10. Monthly foetal length frequencies of southern hemisphere fin whales, *Balaenoptera physalus*, smoothed and converted into percentages.



Text-fig. 11. Diagram to show expected changes in the shapes of the monthly foetal length frequencies for the fin whale. See text for explanation.

Referring now to the average foetal growth curve for fin whales, this means that foetuses above about 4.75 m. in length should be under-represented in the Antarctic samples. The probable effect of this on the shape of the monthly length frequency curves is indicated in Text-fig. 11 by the broken lines. The February sample should be only slightly affected, but from March onwards the effect on the frequency distribution should be considerable. Thus the model frequency curve for March becomes skewed in the reverse direction to those for December and January. This is precisely what the actual length frequencies of the monthly samples show (Text-fig. 10).

This is undoubtedly an over-simplified picture. Conceptions probably extend over a longer period than 6 months and are not normally distributed, and there is no doubt that the individual variation in growth rates may be quite large. Kimura (1957) has shown that the differences in the body lengths of a pair of twin fin whales increases with time and suggests that at birth it will average about 2 ft. (0.62 m.). The average neonatal length of the blue whale is estimated to be 7.0 m. (Mackintosh and Wheeler, 1929), but one foetus examined at South Georgia measured 7.46 m. (Pl. XIII, fig. 2). Such variation should have no effect on the calculated average growth curves, but would explain the presence of some 7% of fin whale foetuses in the March sample which are above 5 m. in length.

Zemskiy (1950a) claimed that female embryos are larger than male embryos. He gives the mean length of sixty-six females as 247.6 cm. and of sixty-seven males as 221.1 cm. Reference to Table 4 (in the present paper) where the values of two standard errors are shown to be 12 to 19 cm. for much larger samples suggests that this supposed sex difference in growth rate is not statistically significant. Kimura (1957, p. 113) studied the lengths of pairs of twins of different sex and concluded that there is no sex difference in the rate of foetal growth.

It appears then, that foetal growth in length in the fin whale can best be described by a growth curve of the shape given in Table 4, and drawn in Text-fig. 8. It is possible that growth in the second half of pregnancy is not exponential, but if pregnancy is to occupy less than 12 months (required by the high percentage of adult females which are pregnant), then at least two more periods of differing linear growth rates are required making three in all, or the growth curve must be similar to but more complicated than an exponential curve. While this is not impossible there is no evidence for it and exponential growth appears to provide a simpler explanation. The samples taken in the Antarctic in the 5 months from October to February may be considered to be representative of the progress of foetal growth, but differential migration out of the area affects the validity of the samples from March onwards.

Four of the five foetal length records from August and September (from Saldanha Bay, South Africa) are below the calculated average lengths for these months (Text-fig. 9). In view of the small number of records, the largest of which is undoubtedly aberrant (and will be discussed later) this is statistically insignificant, but there are reasons for supposing that there is a differential migration southwards from the breeding grounds (complementary to the northward migration of near-term females from the Antarctic feeding grounds in March) so that samples from Saldanha Bay (33° S.) are likely to be biased towards small foetuses. In general, females with larger foetuses might be expected to have moved further south. It is relevant that Chittleborough (1954, 1958) found only two early embryos among several hundred recently pregnant females examined on the west coast of Australia, which suggests migration out of the area shortly after conception. Jonsgård (1951) reached similar conclusions about the minke whale on the west coast of Norway.

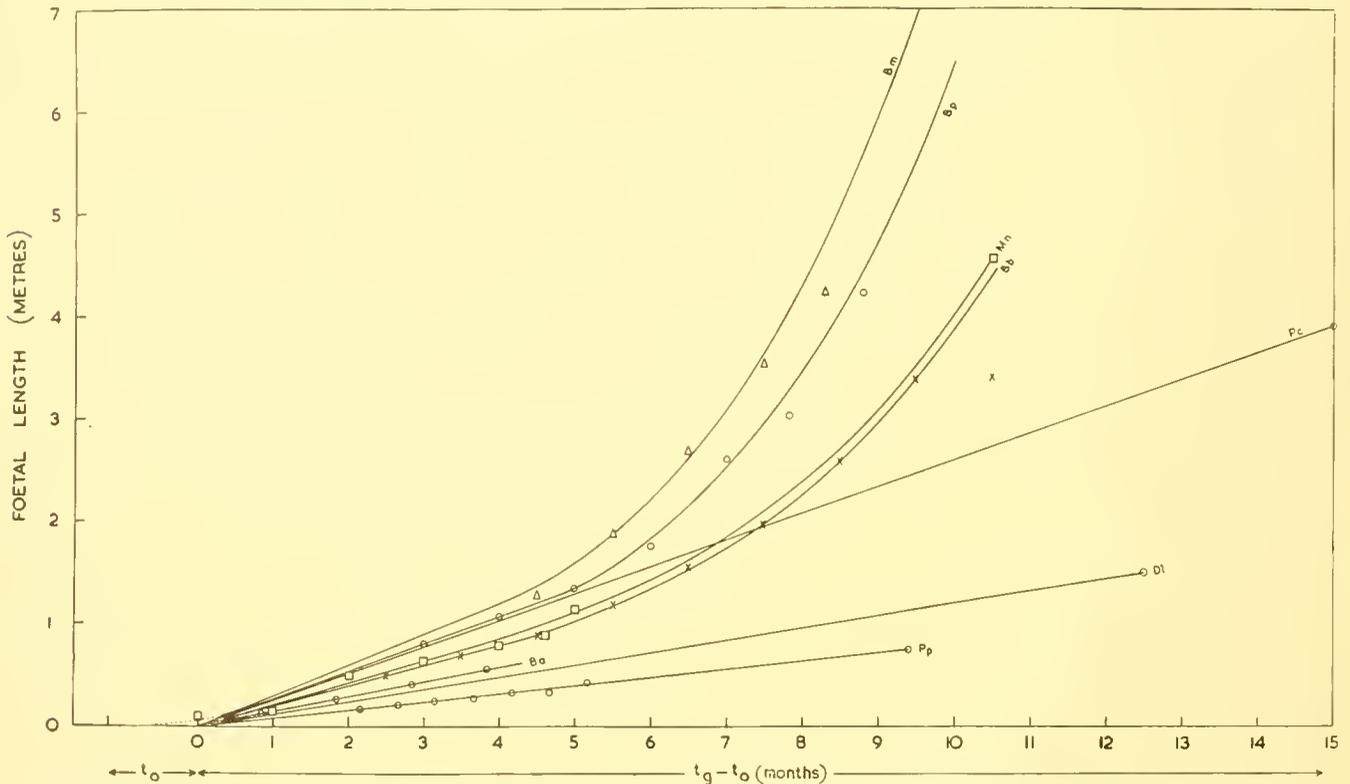
It is also to be expected that very early embryos (i.e. less than one month post-conception) will be absent in Antarctic samples. The effect of this on the mean foetal length would be most marked in the earlier months prior to November, for which in any case very few length records are available.

There are three foetuses in Text-fig. 9 which are conspicuously out of phase with the rest. These three foetuses are displaced by 4, $5\frac{3}{4}$ and 6 months from the average growth curve and it is thought that they represent foetuses conceived following supplementary ovulations in November to December (Laws, 1956, 1958). It is also likely that some of the smallest embryos from December onwards are the products of matings at this time. This question will be considered in more detail in a later paper, but is mentioned here for the sake of completeness and to draw attention to the wide spread of months in which conception may occur in this species.

The data for the blue whale have been examined in the same way as those for the fin whale, but it is not possible to reach such firm conclusions. Although there are more records of blue whale foetal lengths than there are for fin whales, they are spread over a shorter period (Tables 3, 5, Text-fig. 8).

It will be seen from Text-fig. 8 that a straight line could be fitted to the monthly mean values of foetal length for the blue whale which would intersect the abscissa in September, would attain 7 m. in June, and would be very much steeper than any other linear plot of foetal growth in mammalia.

Analysis of the monthly foetal length frequencies by the method used for the fin whale gives a similar picture of foetal growth to that in the fin whale, showing that growth is not linear in the second half of pregnancy. The length frequency curve for November is slightly skewed (corresponding to the December frequency distribution in the fin whale); the curves for December and January show



Text-fig. 12. Diagram showing estimated mean foetal growth curves of five Balaenopterids and three Odontocetes. For comparative purposes the origin of the curves is taken as t_0 . (Bm=*Balaenoptera musculus*; Bp=*B. physalus*; Bb=*B. borealis*; Ba=*B. acutorostrata*; Mn=*Megaptera novaeangliae*; Pc=*Physeter catodon*; Dl=*Delphinapterus leucas*; Pp=*Phocaena phocoena*).

increased skewness, and the distributions for February and March show a reversal of this trend. The same inferences are drawn from the shapes of these monthly length-frequency distributions as for the fin whale frequency distributions, and an exponential curve has been fitted to the mean foetal lengths for November, December, January and February. This curve attains the average neonatal length (7.0 m.) in mid-April.

The slope of the linear segment of the blue whale growth curve is based on very sparse data. It has been plotted with reference to six records for October, two for September, two for August and two for July. It cuts the abscissa at the end of June and the period from conception to Lt_0 is estimated to be 30 days, slightly shorter than the similar period in the fin whale (33 days) because the slope of the linear segment of the growth curve is steeper (Table 1). This gives an estimated mean date of conception in the fourth week in May, which fits quite well with inferences made from other evidence. The estimated gestation period of the blue whale is therefore $10\frac{3}{4}$ months and although less confidence

is attached to this figure than for the fin whale estimate, it is very unlikely to be greatly in error.

The average growth curves now obtained for different species are compared in Text-fig. 12, by taking Lt_0 as the origin of the curves. For the four Balaenopterids the slopes of the linear segments of the growth curves have also been plotted against the slope of the logarithmic parts and are found to be closely correlated; the steeper the linear segment, the steeper is the logarithmic segment.

THE LENGTH/WEIGHT RELATIONSHIP

It has been shown that in the baleen whales growth in length is extremely rapid, probably following an exponential curve in the second half of pregnancy. In general, $W \propto L^3$ so the growth in weight will be even more rapid and it is therefore instructive to examine the data on the weights of whale foetuses. Zemskiy (1950b) gave records of foetal length and weight for sixty-five fin whale foetuses. Nishiwaki and Hayashi (1950) plotted weight against length for forty-three fin and blue whale foetuses, but their records were not given in tabular form and have not been used. Nishiwaki and Oye (1951) gave full information on the weights and lengths of thirty-nine fin whale, and twenty-three blue whale foetuses, and Symons (1955) gives the weight and length of one large blue whale foetus. The National Institute of Oceanography has records of foetal weights for ninety-six fin whale, seven blue whale, nine humpback whale and three sei whale foetuses making, together with published records, a total of 243 baleen whale foetuses for which length/weight records are available. All data have been converted to metric units for comparison, and the 115 previously unpublished records of foetal weight obtained by the National Institute of Oceanography are set out in Table 6. In addition Möhl-Hansen (1954) gives records of weight and length for ninety-three porpoise foetuses.

In Text-fig. 13 this material is presented graphically. The records for blue, fin and sei whales were originally plotted separately but showed no specific differences and have not therefore been distinguished. The three rather lighter than average records are fin whales. The humpback whale foetuses appear to be consistently heavier than blue, fin and sei whale foetuses of similar lengths and have therefore been given separate symbols. The plotted points for the porpoise are monthly means.

It is apparent that there is little scatter; the greater scatter at lower values is at least partly due to the limits of accuracy of the methods of weighing, how much of the umbilical cord is included, etc. For the genus *Balaenoptera* the range of variation in length between individuals of the same weight is about 20% of the mean length.

Zemskiy (1950b) examined the relationship between foetal length and weight for 100 fin whale foetuses (details of only sixty-five are given in his paper). He plotted weight against length on arithmetic scales and concluded that 'the intra-uterine development of the fin whale embryo may be divided into two stages having different features. The first period is characterized by an intensive growth in the linear dimensions of the embryo while its mass increases relatively slowly. The rapid growth in length continues until the embryo is approximately 90 cm long. The second period is characterized by an intensive growth in weight whilst the linear growth of the embryo is relatively slow' (translation). Adoption of logarithmic scales (Text-fig. 13) shows, however, that there is a *constant* relation between weight and length at least from about 30 cm onwards. The decrease in the embryonic length/weight ratio, K , used by Zemskiy is presumably only another way of expressing the known fact that $W \propto L^3$, so that weight naturally increases more rapidly than length.

The mean lengths at birth for southern blue and fin and for northern sei whales are estimated to be 7.0, 6.4 and about 4.4 m., respectively. From the regression line fitted by inspection in Text-fig. 13, these lengths correspond to birth weights of 2500 kg. (2.46 tons), 1900 kg. (1.86 tons) and 650 kg.

(0.64 tons). A regression line has also been drawn for the small series of humpback whale records which suggests a mean birth weight (at a length of 4.56 m.) of about 1300 kg (1.28 tons).

Almost all of this growth takes place in the last part of pregnancy. Mackintosh and Wheeler (1929, p. 426) pointed out that a 0.5 m. foetus 'differs very little in appearance and bodily proportions from the adult and so far as the internal structures are concerned the organs are probably all laid down by the time the foetus has reached 0.1 m. It is therefore natural to suppose that the actual linear rate

Table 6. *Length and weight data for 115 baleen whale foetuses*

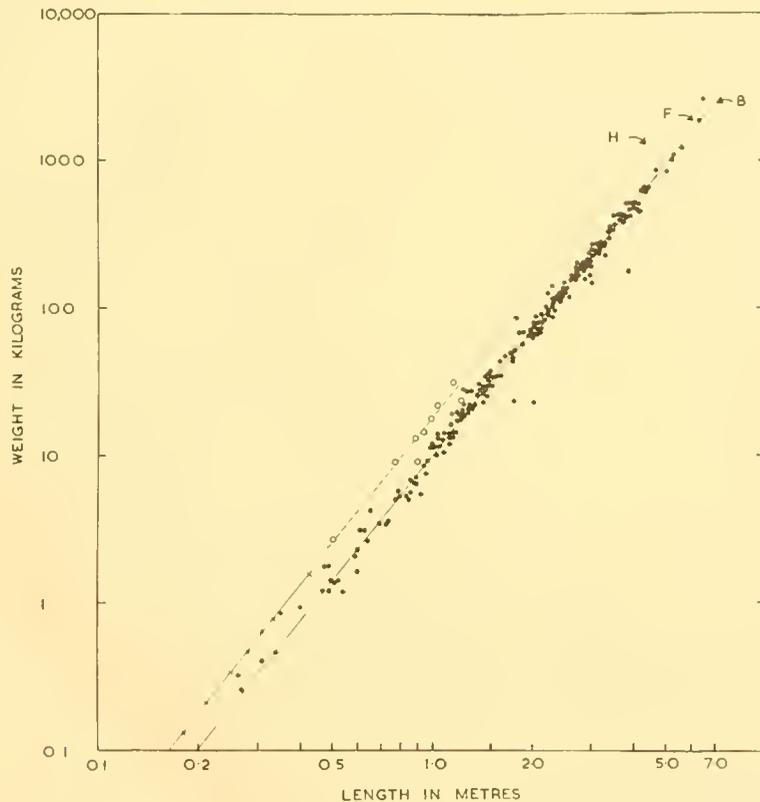
<i>Fin whale foetuses</i>							
<i>Length</i>	<i>Weight</i>	<i>Length</i>	<i>Weight</i>	<i>Length</i>	<i>Weight</i>	<i>Length</i>	<i>Weight</i>
<i>(m.)</i>	<i>(kg.)</i>	<i>(m.)</i>	<i>(kg.)</i>	<i>(m.)</i>	<i>(kg.)</i>	<i>(m.)</i>	<i>(kg.)</i>
0.26	0.32	0.9	6.4	1.42	29.0	2.76	167
0.27	0.25	0.94	5.5	1.44	26.0	2.79	200
0.31	0.4	0.95	8.5	1.45	28.5	2.83	178
0.34	0.45	0.96	9.0	1.46	29.0	2.87	190
0.35	0.85	0.96	7.5	1.48	31.0	2.9	192
0.4	0.93	1.0	11.5	1.5	29.0	2.92	191
0.47	1.2	1.0	12.0	1.5	36.5	2.95	203
0.48	1.8	1.02	11.5	1.53	33.0	2.95	203
0.48	1.76	1.04	10.0	1.59	33.5	3.03	168
0.51	1.36	1.06	11.5	1.62	43.0	3.08	228
0.52	1.4	1.08	13.0	1.78	23.0	3.13	243
0.54	1.15	1.14	14.0	1.98	64.5	3.15	234
0.59	2.04	1.15	11.4	2.03	22.5	3.22	254
0.6	1.6	1.16	14.0	2.05	79.5	3.28	279
0.6	2.3	1.16	15.5	2.12	71.0	3.35	228
0.62	3.06	1.18	17.0	2.13	91.0	3.74	433
0.62	3.05	1.24	19.0	2.15	79.5	3.86	382
0.64	2.6	1.25	19.0	2.15	79.5	4.0	471
0.66	4.3	1.27	28.0	2.24	86.5	4.05	471
0.7	3.35	1.3	19.0	2.34	97.0	4.06	509
0.75	3.6	1.3	21.5	2.43	126.0	4.23	611
0.85	5.3	1.3	27.5	2.52	147	4.3	455
0.86	5.0	1.32	19.8	2.56	137	4.48	611
0.87	5.5	1.32	27.0	2.66	153	5.4	1089

<i>Blue whale</i>		<i>Humpback whale</i>		<i>Sei whale</i>	
<i>Length</i>	<i>Weight</i>	<i>Length</i>	<i>Weight</i>	<i>Length</i>	<i>Weight</i>
<i>(m.)</i>	<i>(kg.)</i>	<i>(m.)</i>	<i>(kg.)</i>	<i>(m.)</i>	<i>(kg.)</i>
1.17	15.5	0.51	2.65	1.05	13.0
1.25	22.0	0.78	9.0	2.12	88.5
1.42	28.0	0.9	9.0	2.28	102
1.7	46.5	0.9	13.0		
2.22	100	0.95	14.5		
3.14	272	1.0	17.6		
3.5	365	1.05	21.8		
		1.17	31.0		
		1.24	23.5		

of growth is extremely slow while the foetus grows from zero to about 0.1 m. compared with its subsequent growth up to the end of gestation, for from between 0.1 and 0.5 m. up to birth at 6-7 m. development consists mainly in increase in size.' Comparison of Pl. XIII, figs. 1 and 2, illustrates this point. 'The 18.5 cm. foetus shown in fig. 1 is already typically cetacean in appearance (2 months after conception) and even at this age does not differ very markedly in bodily proportions from the 7.46 m. foetus illustrated in fig. 2.

Zemskiy (1950*b*, figs. 2, 3) demonstrated this by means of detailed measurements of sixty-six fin whale embryos between 49.5 and 569 cm. in length. He took five series of measurements (snout-umbilicus; snout-anus; head length; pectoral girth; anal girth) and showed that the ratio of these measurements to body length (expressed as percentages) remained more or less constant within this range of foetal lengths. The smaller series of foetal measurements given by Mackintosh and Wheeler (1929, pp. 324-29) are in very close agreement. These authors also give the results of similar measurements on over 600 post-natal fin whales. Their mean percentage values for these three linear proportions in adults are very close to the mean values for foetuses and well within the foetal ranges.

Zemskiy states that the throat grooves (a special feature of the rorquals) first become apparent at a length of 1.0 m., and become distinct and similar in appearance to those of the adult at a length of 1.5 m. The baleen is first discernible externally in embryos of about 3.0-4.0 m. (Mackintosh and Wheeler, 1929, fig. 96; Zemskiy, 1950).



Text-fig. 13. Plot of foetal weight against length for 234 blue, fin and sei whales (black circles), nine humpback whales (white circles), and ninety-three porpoises (crosses=monthly mean values). Regression lines have been fitted by eye and the neonatal values for blue, fin and humpback whales are indicated.

In the last 5 months of pregnancy the blue whale foetus grows in length from 1.3 to 7.0 m., corresponding to an increase in weight of 2480 kg. (from 20 to 2500 kg.) or 2.44 tons. In the last *two* months of pregnancy the average gain in weight is over 2 tons (420-2500 kg). The growth rate of the fin whale is of the same order of magnitude. In some individual blue whales the growth rate is probably even greater; the largest blue whale foetus (Pl. XIII, fig. 2) measured 7.46 m. and must have weighed about 2800 kg. (2.75 tons).

Expressed in this way the foetal growth rate of the baleen whales is seen to be phenomenally rapid, and without parallel.

CONCLUSIONS

Previous papers dealing with foetal growth of whales and with the breeding season and the gestation period have attacked the problem by plotting the mean monthly foetal lengths and then drawing in a curve by eye. The method developed by Huggett and Widdas (1951) for dealing with foetal length and weight data appears to hold good for the three species of toothed whales considered in this paper and to a limited extent for the five Balaenopterid species which have been studied. In particular this method provides for an objective estimate of the length of the initial period of very slow growth before the placental circulation is fully established. This is impossible by means of freehand extrapolation.

Huggett and Widdas (1951, p. 314) remark that in 'mammals in the intermediate range of [their] fig. 8, the period of linear growth is determined by the size of the foetus at birth. Thus, as the birth weight of the young is increased the mammal does not grow its young quicker, along a steeper slope, but must grow its foetus for a longer time. This will offer an explanation of Rubner's finding in 1908 that in all species except man the birth weight is proportional to the gestation time.'

It will be apparent that this is not true of the marine mammals which have been studied. In most species of seals the period of foetal growth is of more or less equal duration, but the birth weight of the largest species is ten times that of the smallest species. Increased size at birth is attained by increasing the growth rate, rather than by extending the gestation period. In the toothed whales which have been studied, increased size at birth appears to be attained both by increasing the rate of growth and by extending the period of gestation, as in the sperm whale.

The growth velocities of the species of toothed whales studied fall within the ranges $a \approx 0.05$ and $a \approx 0.02$ (for weight) as do all the species of mammals considered by Huggett and Widdas (1951, fig. 8), with the conspicuous exception of the fin and blue whales. In the Balaenopterids, the evidence discussed in this paper shows that for the first part of gestation the growth velocity is within this range, but the growth rate (for L or $W^{\frac{1}{3}}$) probably increases exponentially after the fifth month of pregnancy. In all Balaenopterid species the gestation period is 12 months or less and the very large neonatal sizes are attained by this phenomenal burst of growth in the second half of pregnancy, not as in the sperm whale by extending the gestation period. In fact, it appears that in the genus *Balaenoptera* there is a tendency to shorten the gestation period in association with this increased growth.

Huggett and Widdas (1951) were unable from their data to suggest any biochemical or physiological reason why growth should conform to a cube root law, and it is even more difficult to see why baleen whale foetuses should follow an exponential cube root law.

For some fundamental reason the gestation period of the rorquals does not exceed 12 months whereas in the sperm whale it is possible for gestation to occupy 16 months. One of the most conspicuous differences in the behaviour of baleen whales as compared with the toothed whales is the very discontinuous feeding cycle of the former. Almost all baleen whales must enter polar waters to feed at a time when their planktonic food is available in suitable quantity; when not feeding it is probable that they must seek warmer waters where energy loss due to heat radiation is less. The period when food is available in amounts large enough to make its collection economical for the whales is limited in the Southern Ocean to a period of 3 or 4 months (Marr, 1956) although some animals move south before this period and others stay in polar waters later (see Mackintosh and Brown, 1956, fig. 2). During the feeding period the baleen whales lay down thick reserves of blubber (Ash, 1956) on which they draw for the remainder of the year.

Most Balaenopterid species have a 2-year sexual cycle, comprising a gestation period of less than a year, lactation occupying about 6 months and the remaining 6 or 7 months in anoestrus. Conception

and calving take place in winter in low latitudes and the annual feeding migrations occur in mid-pregnancy and at the end of lactation or beginning of the anoestrus period.

If the initial linear phase of growth were to persist it can be shown by extrapolation that the gestation periods would have to be approximately doubled in order to attain the present neonatal sizes. One effect of this would be to reduce the reproductive rate very greatly. Conversely, if gestation were limited to 12 months and the present linear growth persisted throughout, the birth sizes would be only half the present sizes. If the gestation periods, or the neonatal sizes, were intermediate between these extremes, then it seems probable that the reproductive cycle would be out of step with the feeding cycle. For instance, with a gestation period of 18 months, other things being equal, parturition would occur in the Antarctic and the chances of survival of the calf might well be affected.

With regard to feeding habits, the difference in the nature of the food is also perhaps significant and it is interesting that in the blue, fin, sei and humpback whales the beginning of the great burst of growth is associated with the arrival of these species on the polar feeding grounds. Little or nothing is known of foetal growth in a temperate zone species like *B. brydei*, which is presumably subject to rather different feeding conditions.

The evidence for a period of exponential growth is by no means conclusive and it may be that growth could be described by a series of successive growth cycles. It should be noted that if exponential growth is adopted as a means of increasing neonatal size, the duration of the growth period must be kept relatively short, because a small increase in the length of the growth period will entail a disproportionately great increase in the neonatal size, which is of course limited by the size of the mother. Similarly, an increase in the slope of the curve of exponential growth may cause a very large increase in the final size. In the blue whale, for instance, it is estimated that an increase of half a month in the length of the gestation period to bring it into line with that of the fin whale would, if growth is exponential, result in a neonatal length of 8.4 m., corresponding to a weight of about 4000 kg. or 3.93 tons; that is an increase of 60% in the birth weight for a gestation period only half a month longer. In the larger baleen whales a shortening of the gestation period is seen to be essential if the slope of the growth curve is further increased and on the evidence at present available this appears to be the general trend in the large Balaenopterids.

SUMMARY

1. The literature on foetal growth in whales is reviewed.
2. It is shown that foetal growth in three species of toothed whales can be described by a linear plot of length. The method of Huggett and Widdas (1951) is used to estimate the duration of the non-linear early part of pregnancy and so to estimate mean conception dates and gestation periods.
3. In the toothed whales studied larger neonatal sizes are attained by increased rates of growth and by extension of the gestation period.
4. In the baleen whales the first half of pregnancy follows this law, but thereafter growth can best be described by a logarithmic plot of length or of the cube root of weight. So far as is known this is unique among mammals.
5. Original foetal length data for 956 southern fin whales and 1022 blue whales are presented, examined and discussed. Mean foetal growth curves (length) are given for southern hemisphere fin and blue whales.
6. The average duration of gestation is estimated to be $11\frac{1}{4}$ months (early June to mid-May) in the southern fin whale; $10\frac{3}{4}$ months (end of May to mid-April) in the southern blue whale.
7. The length/weight relationship of foetal baleen whales is examined, the data comprising 243 records of foetal length and weight. The mean lengths at birth for southern hemisphere blue,

fin and humpback whales and for the northern sei whale are estimated to be 7.0, 6.4, 4.56 and about 4.4 m. The corresponding birth weights are 2500 kg. (2.46 tons), 1900 kg. (1.86 tons), 1300 kg. (1.28 tons) and 650 kg. (0.64 tons).

8. Most of this growth takes place in the last 2 months of pregnancy. In the blue whale the average gain in foetal weight during this period is over two tons.

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PLATE XIII

Fig. 1. An 18.5 cm. fin whale foetus (male).

Fig. 2. A 7.46 m. blue whale foetus (male), estimated weight 2.75 tons.

(photo: N. A. Mackintosh)

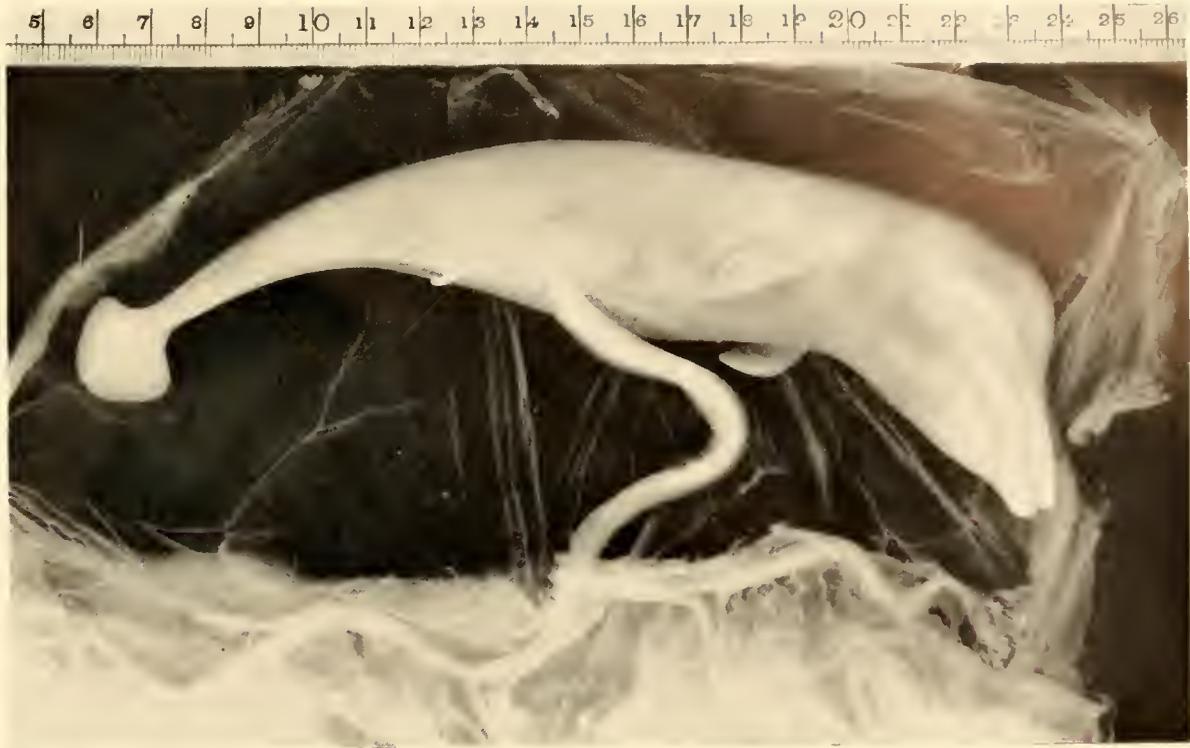


Fig. 1



Fig. 2



THE DISTRIBUTION AND LIFE HISTORY
OF *EUPHAUSIA TRIACANTHA*
HOLT AND TATTERSALL

BY

A. DE C. BAKER

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THE DISTRIBUTION AND LIFE HISTORY OF *EUPHAUSIA TRIACANTHA* HOLT AND TATTERSALL

By A. de C. Baker

(Text-figs. 1-16)



INTRODUCTION

ONE approach to the problem of revealing the basic principles governing the distribution of planktonic organisms is to make special studies of selected representative species. Detailed examination and comparison of species with different distributional, reproductive and feeding habits should help to elucidate the factors controlling these habits.

David (1955) has already made such a study of the carnivore, *Sagitta gazellae* Ritter-Zahony, 1909, from the Discovery collections and Mr J. W. S. Marr, who is working on *Euphausia superba* Dana, 1852, has published a preliminary account of the broad features of its distribution (1956). The present paper on *E. triacantha* Holt and Tattersall, 1906, is intended as a further contribution to this work.

There are several reasons for selecting *E. triacantha* as a species for detailed examination. John (1936) has shown that the distribution of the southern members of the genus *Euphausia* is such that they occur in more or less overlapping concentric zones round the Antarctic continent. *E. superba* occurs in the East Wind drift and Weddell Sea regions of the Southern Ocean (Marr, 1956) and *E. triacantha* is found to the north of this in the West Wind drift (John, 1936); thus a useful comparison can be drawn between the two species. Also *E. triacantha* displays little or none of the shoaling habit found in *E. superba*. That *E. triacantha* performs a marked diurnal vertical migration, a character not found in *Sagitta gazellae* (David, 1955) nor in *E. superba* (Mr Marr, personal communication), is of additional interest for purposes of comparison. It is also easily identified in the samples, a point of some considerable importance where much material has to be examined.

ACKNOWLEDGEMENTS

This study was undertaken at the suggestion of Dr N. A. Mackintosh, C.B.E., who has given me much helpful advice and criticism.

I would also like to express my thanks to those of my colleagues who have given me help and advice from time to time, particularly to Mr J. W. S. Marr for allowing me to use his data for the section concerning *E. superba* and also for reading and criticizing the draft of that section; to Dr H. E. Bargmann for her assistance during the study of the reproductive system; to Mr P. M. David for reading and criticizing the typescript and to Mr P. Foxton for allowing me to make use of the data he collected during the sixth Antarctic commission (1950-1) of R.R.S. 'Discovery II'.

I would also like to thank Mr A. E. Fisher who helped me in the early stages of this work by sorting many samples, and Mr A. Style who prepared several of the figures for publication.

PREVIOUS WORK ON THE SPECIES

Since the original description by Holt and Tattersall (1906), based on a single male specimen taken by the National Antarctic Expedition, *E. triacantha* has been described from the material taken by many of the major expeditions to the Southern Ocean. In 1902 the Swedish Antarctic Expedition took this species at four stations in the eastern south Atlantic. At one station in June Hansen (1913, p. 34) records 'numerous specimens' and also that the stages of development at another station in April ranged 'from very young to full grown'. Hansen gives a fuller description than was possible from the type specimen and includes an account of the copulatory organs. Zimmer (1914) records five specimens taken by the Deutsche Sudpolar-Expedition in the Indian Ocean, and Illig (1930) records four specimens taken by the Deutsche Tiefsee-Expedition. Tattersall (1924), in a survey of the Subantarctic and Antarctic euphausiids, considered that *E. triacantha* was entirely a Subantarctic species. The 'Norvegia' Expedition 1927-8 and 1928-9 took six specimens, five females and one larva. This larva, a second furcilia, was the first that had been taken and Rustad (1930) describes it in some detail. The later 'Norvegia' Expeditions, 1929-30 and 1930-1, took fewer adults but provided material for the description of the first, second and third calyptopes (Rustad, 1934). Ruud (1932), in an account of the Euphausiidae taken on the whaling expedition of S.S. 'Vikingen' in 1929-30, mentions fifteen specimens that were taken, and suggests that the species belongs to the warm deep water. He also describes two metanauplii which he believes 'very probably belong to one of the two species, *E. frigida* or *E. triacantha*'.

Subsequent work has mainly been based upon material from the 'Discovery' collections. Mackintosh (1934), in his account of the distribution of the macroplankton in the neighbourhood of the Falkland Island Dependencies, includes *E. triacantha* in the species which probably belong only to the Antarctic water but which occasionally stray into Subantarctic water. He also points out that the numbers taken in the surface show a marked diurnal variation. This diurnal variation was also observed by Hardy and Gunther (1935) who note the almost complete absence of the species from the upper 200 m. during daylight hours and conclude that this is due to a diurnal vertical migration. They also note that at times it was 'moderately abundant' off the north and north-eastern coast of South Georgia and that it was present at only one station in the region to the south and south-west of the island.

In his account of the southern species of the genus *Euphausia* John (1936) gives a full description of the adults and of the larvae from the second calyptopis upwards. He distinguishes seven furcilia stages and gives length ranges for these and the calyptopis stages. From the examination of the characteristics, mainly of the copulatory organs, of Hansens Group *d* (1911), he shows this to be a natural group and suggests that the four species, *E. hanseni* Zimmer, 1915, *E. spinifera* Sars, 1885, *E. longirostris* Hansen, 1908 and *E. triacantha*, represent stages in the colonization of the cold southern water, *E. hanseni* being the most northern and *E. triacantha* the most southern species of the group. Regarding the distribution he shows that *E. triacantha* occurs to the north of the northern limit of the pack-ice and in a narrow belt of the Subantarctic. He also suggests that breeding takes place in this narrower, Subantarctic, part of its range.

While considering the vertical distribution of the Antarctic macroplankton Mackintosh (1937) suggests that, in spite of the rather scanty material taken by the 70 cm. vertical nets, *E. triacantha* can be included among those species that perform an energetic daily migration but no extensive annual migration. He also points out that the limits of distribution of a species may be controlled by migration between the northward moving surface water and the southward moving deep water.

Other descriptions and references to the distribution of *E. triacantha* are included in Tattersall (1908, 1913) and Hansen (1911); keys are to be found in Tattersall (1925), Rustad (1930) and Sheard (1953).

MATERIAL AND METHODS

This paper is based upon material contained in the plankton samples of the Discovery Collections. The samples used were largely those collected by means of oblique hauls with the 100 cm. diameter net (N 100B) but, for the purpose of studying vertical distribution, samples obtained from vertical hauls with the 70 cm. closing net (N 70 V) have also been used and a number of samples from oblique hauls with the young fish trawl (TYFB) have been examined where it was necessary to fill in gaps in the distribution chart.

The N 100B was fished for 20 min. from approximately 100 m. to the surface and, at some stations, also from 250 to 100 m. and 500 to 250 m. During these deeper hauls the net was closed at the upper horizon before being brought to the surface. At the majority of stations the N 70 V was fished at six depths: 50-0, 100-50, 250-100, 500-250, 750-500, and 1000-750 m.; an additional haul from 1500-1000 m. was also fished at a good many stations. Details of the construction and the methods employed in working these nets can be found in Kemp, Hardy and Mackintosh (1929).

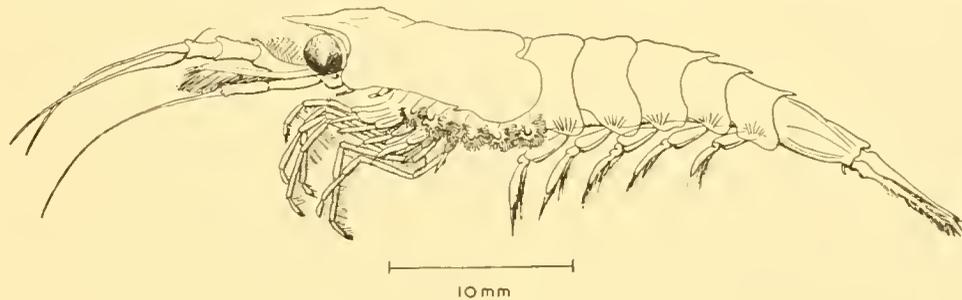


Fig. 1. Adult female *E. triacantha*.

By no means all the available material has been used for this study. The samples have been chosen largely from certain lines or groups of stations in order to give adequate coverage of the Southern Ocean at different times of year and to represent the principal features of the distribution of the species. It is very unlikely that the method of selection has introduced any accidental bias which affects the results. A great many samples had already been analysed by other workers for different purposes before this present work was started, and these analyses, which consist of counts, or both counts and measurements, have been used where possible.

Where a large number of samples have to be examined the time involved depends to a great extent on the ease with which the species can be identified. Adult *E. triacantha* can usually be picked out quite readily on its general appearance alone, but in cases of doubt it can be distinguished from the other related species with mid-dorsal spines on the third to fifth abdominal segments, i.e. *E. hanseni*, *E. spinifera* and *E. longirostris*, by the absence of post-ocular spines (Fig. 1). The larvae are also fairly easily identified, either by the strong median spine on the posterior margin of the carapace in the first calyptopis to first furcilia, or by the presence, in the later stages, of the mid-dorsal abdominal spines. They can be distinguished from the larvae of *E. spinifera* and *E. longirostris* in all these stages by the absence of denticles on the margin of the frontal plate.

The lengths given in this paper have been measured from the anterior margin of the eyes to the tip of the telson.

Except for those specimens collected during the earlier years of the Discovery Investigations, when crustacea picked out of samples were preserved in alcohol, all the material is preserved in neutralized sea-water formalin.

HORIZONTAL DISTRIBUTION OF ADOLESCENTS AND ADULTS RANGE IN ANTARCTIC AND SUBANTARCTIC WATER

In the preparation of the chart (Fig. 2) and other figures showing the horizontal distribution of adolescent and adult *E. triacantha* the data used have been limited to oblique hauls made at night between approximately 100 m. and the surface with the 100 cm. diameter net. There are two reasons for this limitation of the data. First, although the N70V hauls provide valuable information on the vertical distribution of larval stages, the numbers of adolescents and adults taken in these nets are small where a comparison of the populations of different regions is required. Secondly, as mentioned above, *E. triacantha* performs a marked diurnal vertical migration and consequently hauls are strictly comparable only when taken through the same depth range at the same hour of the day or night. In selecting the stations for plotting in Fig. 2 it was considered sufficient if they had been worked during the hours of darkness. However, owing to the routine adopted for station work, over 75% of the hauls were, in fact, taken between 2100 and 0100 hrs.

In Fig. 2 the number of *E. triacantha* at each station is shown according to the scale on the chart. North of 50° S between 30° W and 60° W no N100B hauls are available. In this area, therefore, oblique hauls with the young fish trawl (TYF) have been examined, but only to determine the presence or absence of *E. triacantha*, since the quantities sampled by this larger net are not comparable with those from the 1 m. net. Presence at these stations is indicated by a cross. Absence is shown by an open circle in the usual manner.

The Southern Ocean consists of a continuous circumpolar belt of deep water in which the environment is more or less uniform from east to west and in which changes take place from north to south. Broadly speaking this results in the distribution of the planktonic species in circumpolar belts of greater or lesser width. It has been shown (Baker, 1954) that within these belts there is no longitude in which the commoner macroplankton species, including *E. triacantha*, may not be found (Fig. 2).

While considering the distribution of *E. triacantha*, John (1936, p. 232) states that 'it occurs throughout the ice-free water of the Antarctic Zone'. The present more detailed study shows this to be true, as will be seen from the distribution chart. However, there is a very marked concentration in the region of the Antarctic convergence, and where it has been taken in the higher latitudes the catches tend to be small. It also occurs consistently to the north of the Antarctic convergence and this southern zone of the Subantarctic water must be considered as part of the normal habitat.

Except possibly in the south-western Atlantic, *E. triacantha* shows a close association with the Antarctic convergence throughout its circumpolar range. Because of this association the latitudinal distribution in relation to the convergence can be examined by using it as a datum line.

In Fig. 3, six meridional lines of stations are plotted according to the distance of the stations north or south of the Antarctic convergence. The positions of the convergence shown in the figure are from observations made at the time of crossing, and have been taken from Mackintosh (1946, Table 9). The number of animals taken at each station is shown as a percentage of the total number of animals taken along each line of stations. The lines have been selected so that different longitudes and months are represented. It will be seen from this diagram that, although the total range of *E. triacantha* may extend from 450 miles to the north of the convergence to 650 miles to the south, in all these lines of stations at least 60% of the population in the surface waters at night occurs in the region 150 miles north to 200 miles south of the convergence.

It is generally accepted that the Antarctic convergence can act as an important faunistic boundary (Mackintosh, 1934, p. 83; Ommaney, 1936, pp. 298-9). David (1955) found that, although the

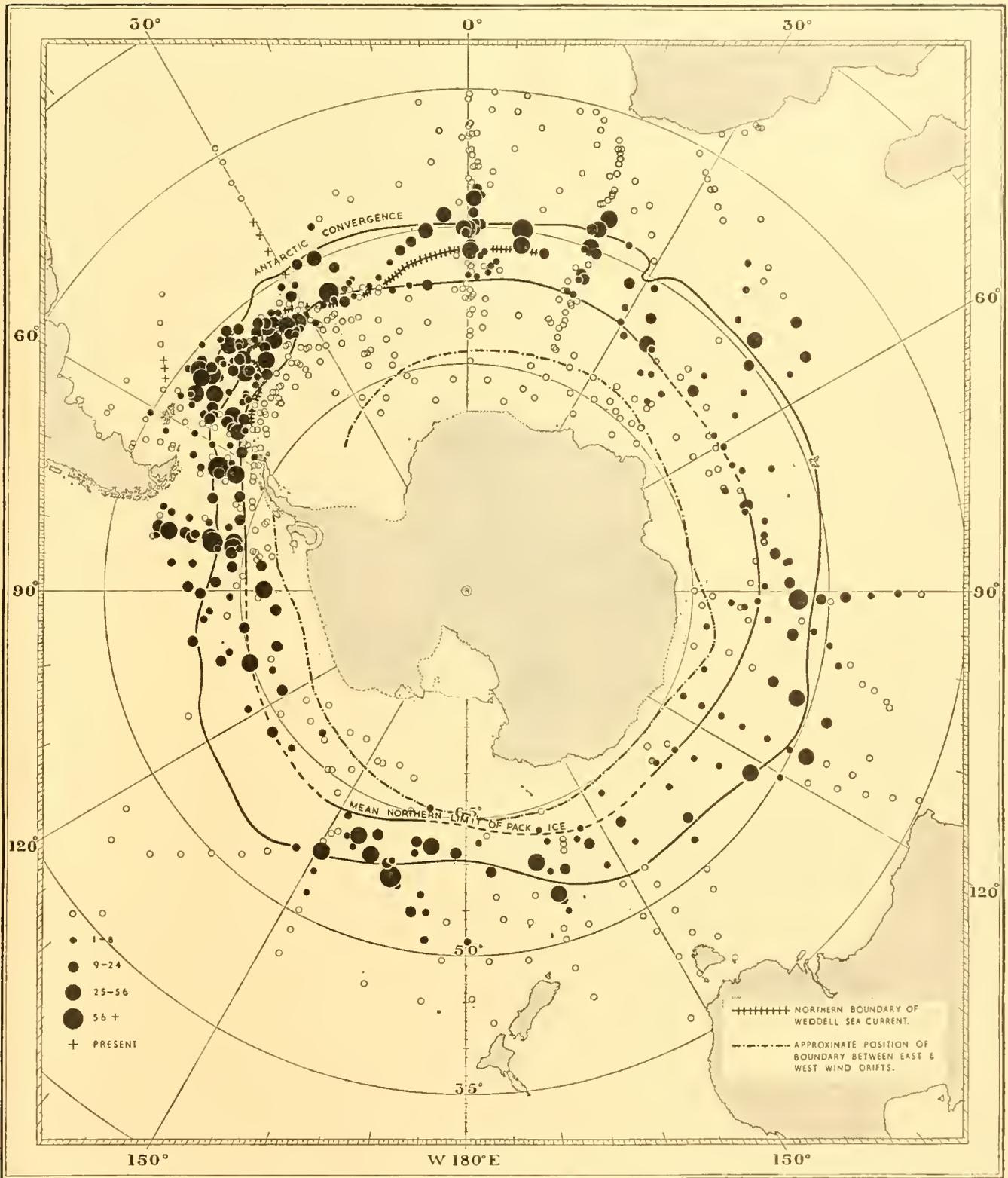


Fig. 2. The horizontal distribution of adolescent and adult *E. triacantha* in the upper 100 m. of water at night based upon shallow oblique hauls with the 1 m. net. The mean position of the Antarctic convergence and the mean northern limit of the pack-ice are shown.

chaetognath *Sagitta gazellae* was present in both Antarctic and Subantarctic waters the catches were extremely small in a region 100 miles north to 200 miles south of the convergence and he distinguished separate races in the population to the north and south of it. It will be clear from Fig. 3 that the pattern of distribution for *E. triacantha* is the reverse of that for *S. gazellae* and that the catches in fact reach a maximum in the vicinity of the convergence. David suggests that it is likely that the sudden changes in physical conditions, brought about by the fluctuations in the position of the Antarctic convergence, are unfavourable to *S. gazellae*. In the case of *E. triacantha*, however, such conditions are evidently favourable.

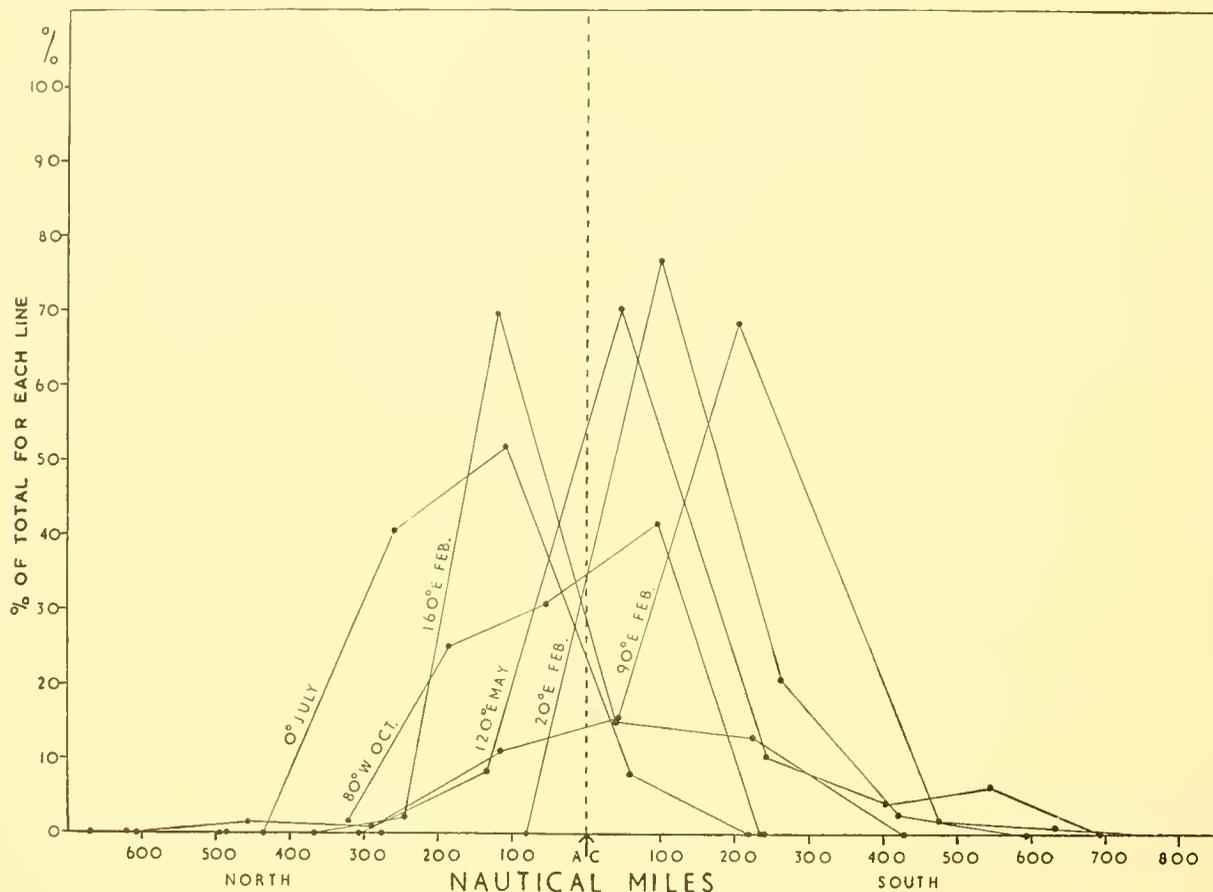


Fig. 3. The number of adolescent and adult *E. triacantha* in a series of shallow oblique night hauls with the 1 m. net from north-south lines of stations plotted according to the distance in nautical miles from the Antarctic convergence. The number per 20 min. haul is expressed as a percentage of the total catch for each line. The position of the convergence has been taken from Mackintosh (1946, Table 9).

SEASONAL VARIATION

In Fig. 4 the distribution of adolescent and adult *E. triacantha* in relation to the Antarctic convergence is shown for each season of the year. The mean catch per 20 min. haul has been plotted at intervals of 50 miles north and south of the convergence. The crosses indicate the intervals for which no data are available. In order to obtain sufficient observations lines of stations from several different regions of the Southern Ocean have been used; the number taken from each sector in each season is shown in Table 1. The exact position of the convergence was indeterminate for a line of stations (2311-2320) along the Greenwich meridian in April and the mean position of $49^{\circ} 50' S$, based on nine other lines along the same meridian, has been used as an approximation. This is unlikely to fall more than 20 miles from the actual position and as the observations are in 50-mile groups no significant error

is involved. The year has been divided into seasons as follows: summer, December–February; autumn, March–May; winter, June–August; spring, September–November.

It will be seen from Fig. 4 that, except for the large number taken between 300 and 350 miles north of the convergence in summer, the region of maximum abundance, at least in the upper 100 m., bears very much the same relationship to the convergence throughout the year. The number of observations in each 50-mile interval varies considerably and where these are very low the value

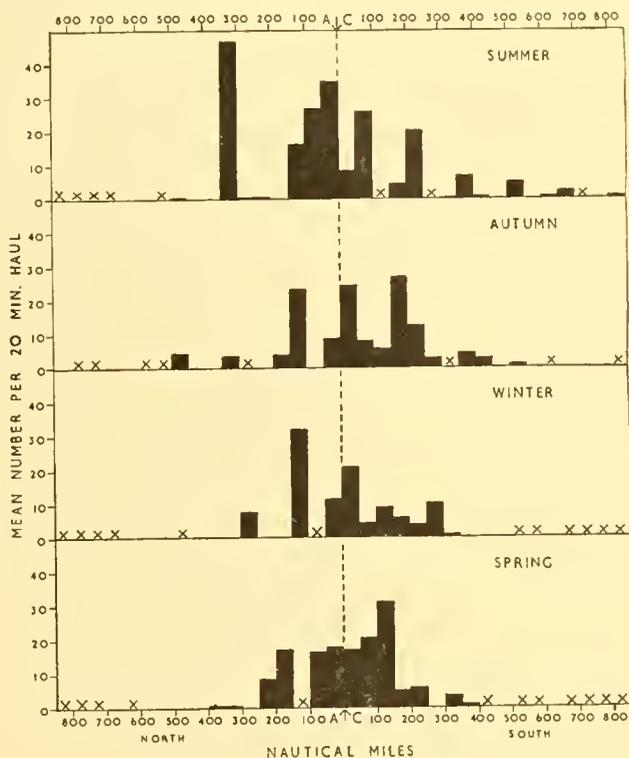


Fig. 4. The seasonal variation in horizontal distribution of adolescent and adult *E. triacantha* in relation to the Antarctic convergence. The mean number of specimens per 20 min. haul has been calculated for each 50-mile belt north and south of the convergence. Belts in which no observations are available are indicated by crosses.

Table 1. The lines of stations used for Fig. 4, showing the sectors in which they were worked. The figures in brackets indicate the number of stations used in each line

Sector	Season			
	Summer	Autumn	Winter	Spring
0°–90° E	2492–2500 (5)	1361–1369 (9)	1788–1801 (9)	1806–1813 (6)
	2531–2541 (6)	1772–1781 (8)	2355–2362 (7)	2425–2430 (4)
	2565–2576 (8)	2311–2320 (5)	2378–2380 (3)	2446–2453 (6)
	2582–2592 (8)	2340–2350 (5)	2385–2393 (4)	2459–2465 (5)
	—	2612–2625 (9)	2411–2419 (6)	—
90° E–180°	1675–1682 (6)	879– 887 (9)	898– 906 (7)	—
	2155–2168 (9)	1723–1733 (6)	913– 923 (8)	—
	2204–2212 (5)	—	—	—
	2802–2811 (9)	—	—	—
180°–90° W	—	—	—	946– 951 (6)
	—	—	—	2736–2745 (8)
90° W–0°	1222–1228 (4)	1312–1320 (5)	—	1027–1035 (5)
	—	—	—	1415–1421 (4)
	—	—	—	1442–1450 (5)

obtained for the mean number per 20 min. haul gives only a very approximate indication of the level of abundance. This applies particularly to the high figure 300 miles north of the convergence in summer which is based on only one observation, St. 1228, in December, at which a large catch of post larval specimens were taken.

The diagram shows the spread to the south as being greater in summer than during the rest of the year. This is due to the inclusion of four lines of stations worked in the 90° E– 180° region where, as will be shown below, the total range is considerably greater than in other sectors.

REGIONAL VARIATION

In Fig. 5 mean numbers per 20 min. haul from a series of observations made along the Greenwich meridian are compared with those from a similar series made between 90° E and 170° E. The data have been treated in the same manner as in Fig. 4.

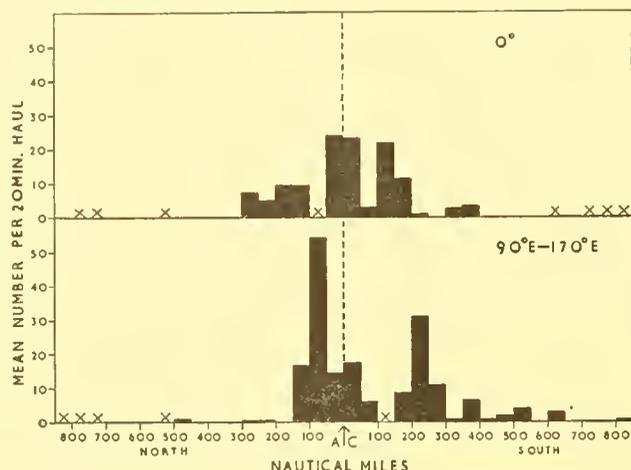


Fig. 5. The distribution of adolescent and adult *E. triacantha* in relation to the Antarctic convergence in the Greenwich meridian compared with that in the sector 90° E– 170° E (see Fig. 4 for explanation).

It will be seen that the total north–south range is considerably greater between 90° E and 170° E than on the 0° line; it extends over 1350 miles in the former and only 700 miles in the latter. The range over which *E. triacantha* is abundant is, however, similar in both regions, though in the Greenwich meridian the northern and southern limits are some 150–200 miles further north.

There is little doubt that the southward spread of *E. triacantha* in the South Atlantic (0°) is restricted, at least to some extent, by the Weddell drift, the core of which crosses the Greenwich meridian in about 60° S (Deacon, 1937, p. 28). The northern limit of the Weddell drift is not clearly defined, but Deacon (p. 25) records two occasions in the mid-South Atlantic when a marked temperature change has indicated a convergence between Antarctic water coming from the north of Graham Land through Drake Passage and that from the Weddell Sea. One occurred in approximately 55° S, 22° W and the other, less clearly marked, between $51^{\circ} 20'$ S, 07° E and 52° S, 06° E. The boundary, being further south to the west of these last two positions, is likely, in 0° , to occur between 53° S and 54° S. This corresponds to a position some 130–250 miles south of the mean position of the Antarctic convergence in 0° and it will be seen from Fig. 5 that the number of *E. triacantha* fall off considerably in this region. Ommaney (1936, p. 297) found a similar distribution in *Rhincalanus gigas* Brady, 1883, that is a falling off in numbers to a level of comparative scarcity in the Weddell Sea water.

In the Indian Ocean (Fig. 5, 90° E– 170° E), although the numbers are small beyond 400 miles south of the Antarctic convergence, the total range extends as far south as the boundary between the East and West Wind drifts.

DISTRIBUTION IN RELATION TO SURFACE TEMPERATURE

The extreme range of surface temperature over which *E. triacantha* has been found is -1.80°C . (St. 463) to 11.88°C . (St. 2803); two specimens only were taken at each of these stations. The 100-0 m. N100B night hauls have been grouped according to the season and the surface temperature, using 2°C . intervals, and the mean catch per 20 min. haul calculated for each group. These means are shown in Table 2. At two stations, 2807 in summer and 452 in spring, unusually large catches have raised the mean considerably and the values obtained when these catches are omitted are shown in brackets. It can be seen that, except during the spring, the greater part of the population lives in a zone in which the surface temperatures are between 2 and 8°C .

E. triacantha is an inhabitant of the West Wind drift and is virtually excluded from the Weddell Sea water and the East Wind drift. It is clear from the surface temperature range mentioned above and from the moderately large catches taken in the West Wind drift in spring that the exclusion from the Weddell Sea and East Wind drift cannot only be due to an intolerance of low surface temperatures.

Table 2. Seasonal variation with surface temperature of the mean number of adolescent and adult *Euphausia triacantha* per 20 min. haul. Means calculated for 2°C intervals (see text for explanation of figures in brackets)

Surface temperature ($^{\circ}\text{C}$.)	Summer		Autumn		Winter		Spring	
	Mean	No. obs.	Mean	No. obs.	Mean	No. obs.	Mean	No. obs.
-2.00-0.01	0.74	19	1.13	16	4.40	35	7.30	69
0.00-1.99	1.61	36	6.20	46	10.68	18	13.09 (9.22)	33
2.00-3.99	9.70 (7.58)	37	14.08	36	12.36	11	11.37	19
4.00-5.99	16.69	16	10.88	17	15.70	10	5.21	24
6.00-7.99	19.11	9	4.07	15	3.00	8	0.36	11
8.00-9.99	0.25	8	0.67	6	0.00	7	0.00	8
10.00-11.99	0.43	7	0.00	4	0.00	4	0.00	1
12.00-13.99	0.00	1	0.00	3	0.00	3	0.00	4

Referring back to Fig. 2 (circumpolar chart) it will be seen that in the east and mid-south Atlantic the southern limit of distribution corresponds very closely with the mean northern position of the pack-ice, and it is possible that the pack-ice has some influence on the southward spread of the species. That this correlation does not occur to the same extent in the Pacific and Indian Oceans suggests that the pack-ice is not the sole limiting factor.

It is possible, in a species such as *E. triacantha* which performs an extensive diurnal migration, that the temperature at the lower level of the vertical range may have a controlling influence on the horizontal distribution. It has been found that the southern limit of distribution of *E. triacantha* falls close to the position of the 1°C . isotherm at 600 m. but it is impossible at present to examine this correlation more closely.

Moore (1952) has suggested that the limits of distribution, both horizontal and vertical, of diurnally migrating euphausiid species may be controlled by a balance between temperature and illumination, but to study this balance in the case of *E. triacantha* a great deal of information would be required on the illumination at different depths in the Antarctic.

EUPHAUSIA TRIACANTHA AND *E. SUPERBA*

In Fig. 6 the distribution of adolescent and adult *E. triacantha* is plotted with that of *E. superba* over 20 mm. long. The data are derived from both day and night hauls from 100 m. to the surface with the N100B. Mr J. W. S. Marr has kindly allowed me to use his unpublished data on *E. superba* for

this figure. (The data from horizontal surface hauls with the 1 m. net (N 100H) have been published in Marr, 1956, Fig. 1.) The sizes of the symbols used in Fig. 6 to indicate the numbers per 20 min. haul are the same for both species; for the sake of clarity negative stations have been omitted.

The figure shows the great difference between the numbers of *E. triacantha* and those of *E. superba*;

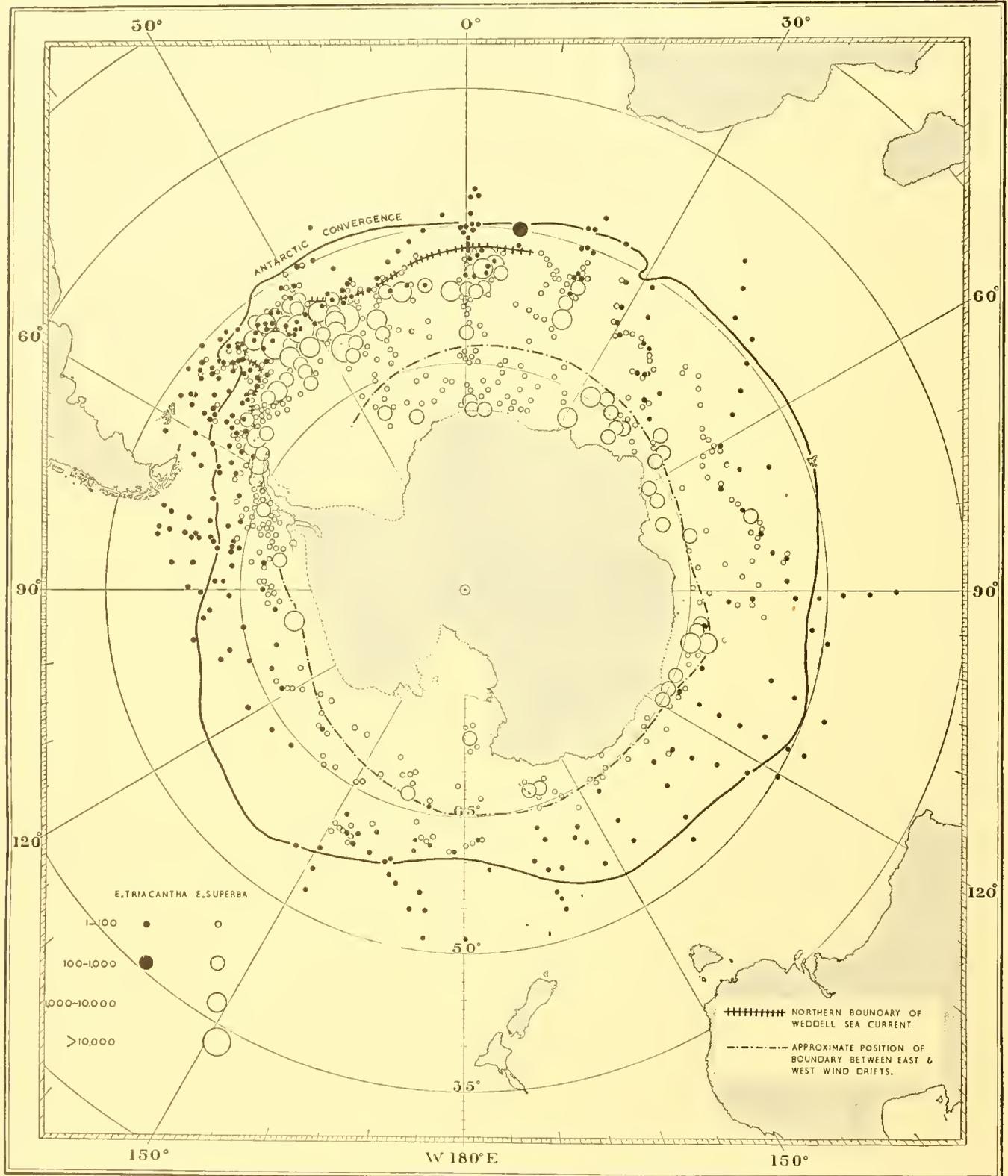


Fig. 6. The horizontal distribution of adolescent and adult *E. triacantha* taken in shallow oblique hauls with the 1 m. net during the day and night compared with the distribution of *E. superba* over 20 mm. long from similar hauls.

except at one station (St. 452) *E. triacantha* has not exceeded 100 per 20 min. haul, whereas *E. superba*, even when only those over 20 mm. are considered, exceeded 10,000 at four stations. It also shows that, although mixing of these species does occur, in general they are confined to different water masses, *E. triacantha* to the West-Wind drift and *E. superba* to the East Wind and Weddell drifts. The mixing is only found at the junction of these water masses and is most marked in the region of South Georgia where, as pointed out by Hardy and Gunther (1935), hydrological conditions are complex.

HORIZONTAL DISTRIBUTION OF LARVAE

The larvae considered here include the first, second and third calyptopis stages and the seven furcilia stages described by John (1936, p. 278). The data presented in Fig. 7 are based upon night hauls

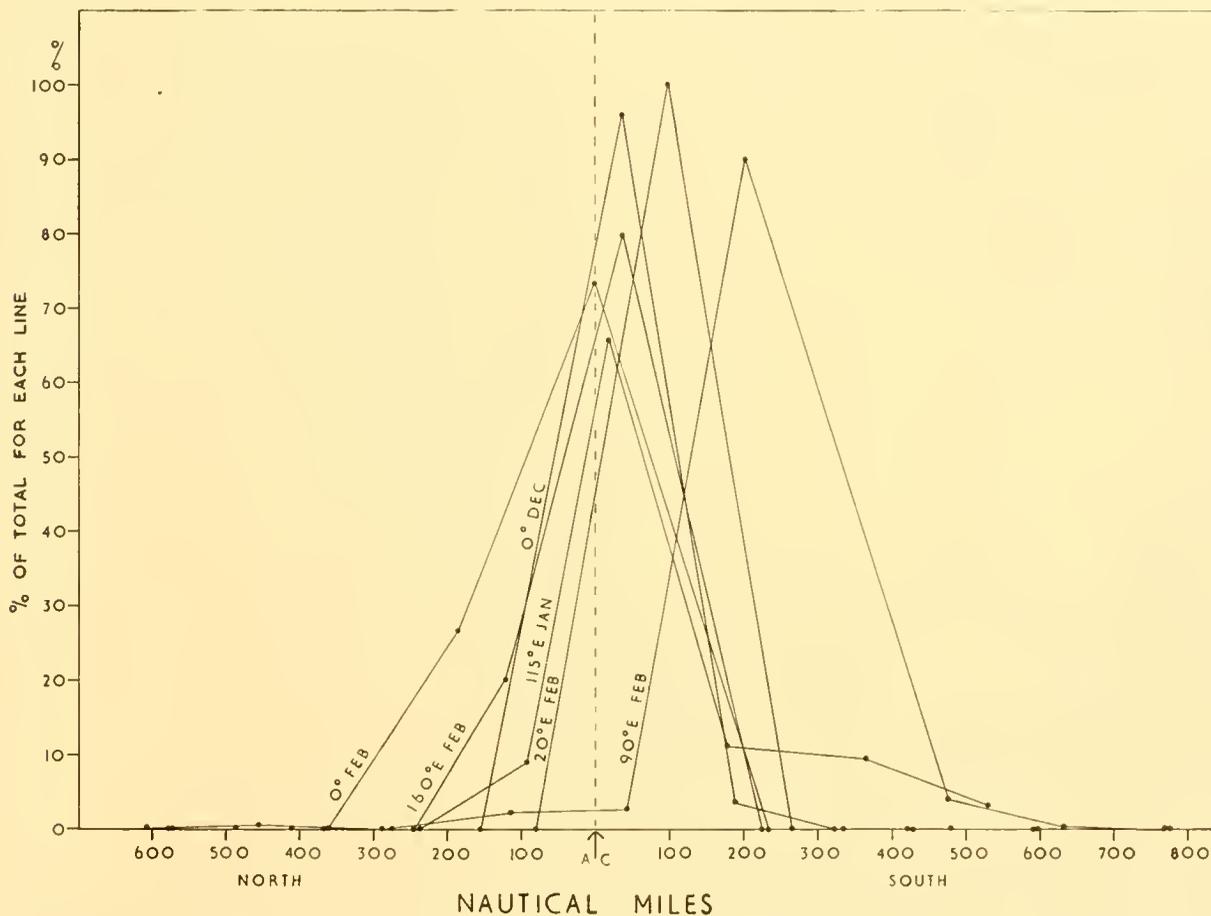


Fig. 7. The number of larval *E. triacantha* in a series of shallow oblique night hauls with the 1 m. net from north-south lines of stations plotted according to the distance in nautical miles from the Antarctic convergence. The number per haul is expressed as a percentage of the total catch for each line. The position of the convergence has been taken from Mackintosh (1946, Table 9).

between 100 m. and the surface with N 100B and it is possible that the mesh of this net is not small enough to take representative samples of the first and second calyptopis stages. However, the meridional lines of stations used in preparing this figure were worked in December, January and February, during which months the predominant larval stages, as will be shown later (p. 334), are the second to seventh furcilia. The data for the larvae have been treated in the same manner as those for the adolescents and adults, that is, the number of larvae taken at each station is shown as a percentage of the total number of larvae taken along each line.

The total north to south range of the larvae, as shown in this figure, is approximately the same as

that of the adults but, in general, the region of abundance is a belt extending for 200 miles south of the Antarctic convergence. This, however, is not always so; in the Falkland sector the region of abundance extends for about 200 miles to the north of the convergence and at Station 1880 (Fig. 8) in $45^{\circ} 53' 8''$ S, some 650 miles north of the mean position of the convergence, moderately large numbers (93) of third calyptopes and first, second and third furciliars were taken in an N 100 B. This station, at which the temperature was 7.47° C. at the surface and 3.95° C. at 100 m. lies in the path

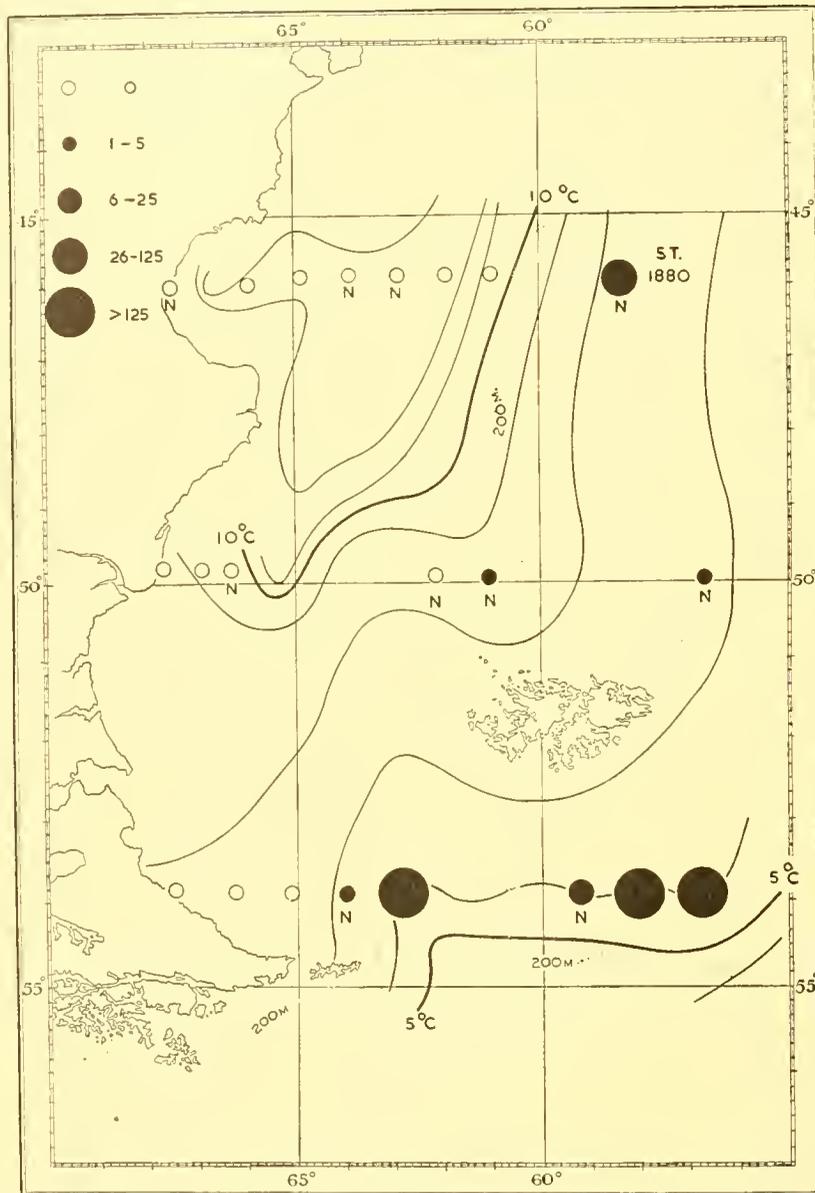


Fig. 8. The distribution of larval *E. triacantha* on the Patagonian shelf and slope from shallow oblique hauls with the 1 m. net. Night stations marked N. Isotherms taken from an unpublished internal report.

of the relatively cold Falkland current which runs northwards from Cape Horn and extends over the Patagonian continental shelf and slope (Deacon, 1937, p. 51). As shown in Fig. 8 a concentration of larvae was found in the Subantarctic water east of Cape Horn and some of these were probably carried north in this current.

Fig. 8 shows three east-west lines of stations which started in oceanic water and ran in towards the Patagonian coast over the slope and shelf. These have been used to determine whether or not *E. triacantha* larvae are present in shelf water. Many of these stations were worked during daylight

hours when the 100-0 m. N100B would not normally be expected to take a representative sample of the species owing to its diurnal vertical movements. However, at several day stations on the shelf nearly the whole water column was sampled, the net fishing to within 20 m. of the bottom, so unless the larvae were lying either on or very close to the bottom, for which there is no evidence one way or the other, these stations can be used as evidence of the presence or absence of *E. triacantha*. Night stations are indicated in the figure by the letter N.

It can be seen that, although moderately large catches of larvae were taken off the edge of the shelf even in daylight, they were only taken at two stations inside the 200 m. contour and there was only one larva at each of these.

VERTICAL DISTRIBUTION OF ADOLESCENTS AND ADULTS

In considering the vertical distribution of *E. triacantha* it is necessary to take into account the diurnal vertical migration, the existence of which was shown by Mackintosh (1934, 1937) and Hardy and Gunther (1935). Mackintosh, while studying the effect of diurnal variations upon the catches in the

Table 3. *Diurnal variation in the numbers of adolescent and adult Euphausia triacantha taken at stations within its normal horizontal range by the 100-0 m. N100B*

Day	Total no. of hauls	No. of positive hauls	% of positive hauls	Total no. of <i>E. triacantha</i>	Mean no. <i>E. triacantha</i> per haul.	
					All hauls	Positive hauls only
Day	379	6	1.6	17	0.045	2.8
Night	430	292	67.9	4016	9.340	13.8

100-0 m. N100B, found that *E. triacantha* was taken in only three out of 127 hauls made between 0600 and 1759 hrs. This diurnal variation in the numbers in the upper 100 m. is confirmed and shown to be even more marked by the present data. It will be seen from Table 3 that of 379 hauls taken during daylight hours within the horizontal range of adolescent and adult *E. triacantha* (see Table 4)

Table 4. *The approximate northern and southern limits of Euphausia triacantha in each 10° of longitude. Only stations falling within these limits have been used in assessing diurnal migration*

Sector	East longitude		West longitude	
	Northern limit (° S)	Southern limit (° S)	Northern limit (° S)	Southern limit (° S)
0°-10°	46	54	47	54
10°-20°	47	54	48.5	54.5
20°-30°	47	54.5	46	54.5
30°-40°	47	57	50	55.5
40°-50°	47	57	50	58.5
50°-60°	47	55.5	50	60
60°-70°	50	58	55	61
70°-80°	51	58	55	65
80°-90°	51	58	55	69
90°-100°	49	60	58	69
100°-110°	49	60	58	65
110°-120°	49	60	58	65
120°-130°	50.5	60	58	65
130°-140°	52	60	58	65
140°-150°	52	60	56	65
150°-160°	54	60	56	62.5
160°-170°	54	62	56	62.5
170°-180°	57	64	53.5	62.5

it was present in only 1·6%, whereas it was present in 67·9% of similar hauls taken during the night. It is also clear from Table 3 that on the few occasions it has been taken in the upper 100 m. during the day it has only been present in small numbers, the mean number per haul, considering positive hauls, only being 2·8; the corresponding figure for night hauls is 13·8.

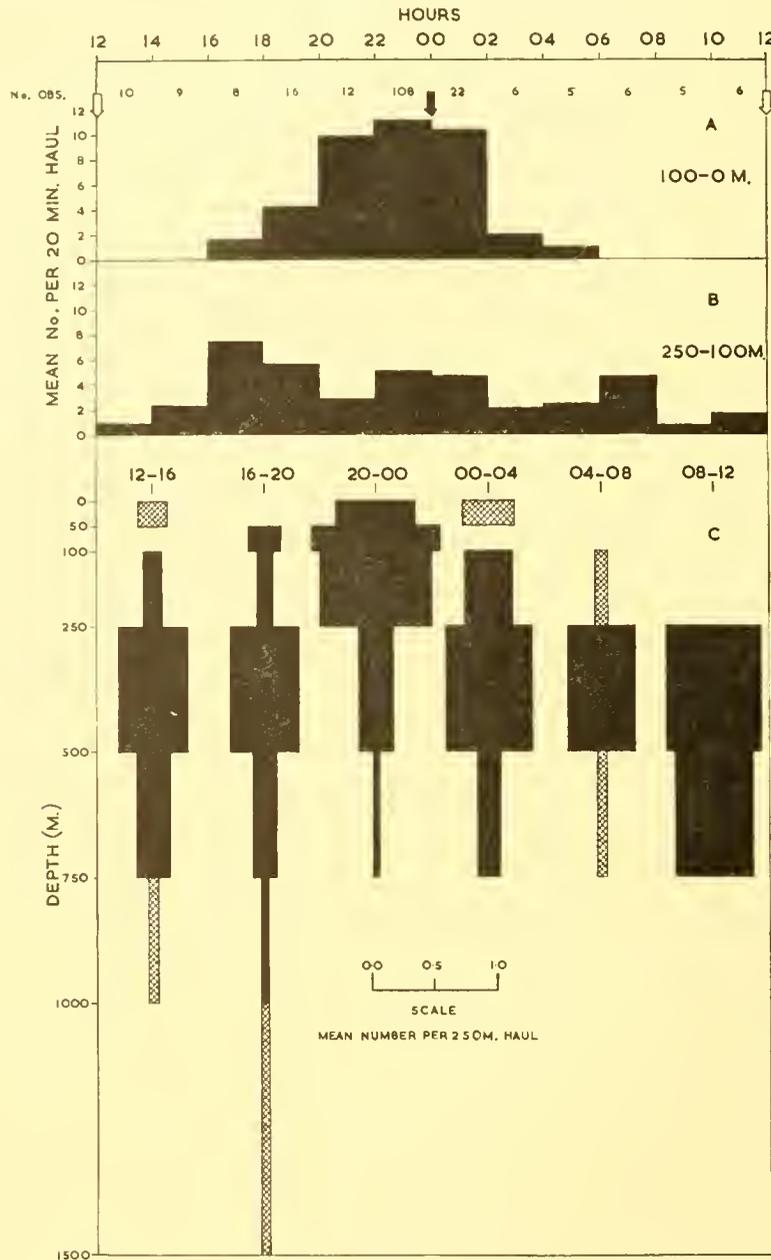


Fig. 9. The daily vertical distribution of adolescent and adult *E. triacantha*. A, the mean number per 20 min. N100B haul in the upper 100 m. for each 2-hourly period. B, the mean number per 20 min. N100B haul between 250-100 m. for each 2-hourly period. C, the mean number per 250 m. N70V haul for each 4-hourly period. Cross-hatching indicates means based on only one specimen. (See Table 5 for the number of observations on which this figure is based.)

The diurnal variation in the numbers in the surface water could be caused by a diurnal variation in avoidance of the net. However, it is shown below (p. 328) that there is no such difference between day and night avoidance, and consequently this must be a real variation in the population and not just an apparent one due to the sampling methods.

Fig. 9A and B shows the mean number of adolescent and adult *E. triacantha* per 20 min. 100-0 m. and 250-100 m. hauls, respectively, for each 2-hourly period. Only those stations have been used at

which simultaneous observations were made through each depth horizon. The 250–100 m. haul takes 30 min. and the numbers taken in these nets have been corrected for a 20 min. haul for comparison with the upper net. Although the two layers sampled are usually approximately 100–0 m. and 250–100 m., in some instances the upper net fished from 150–0 m. and the lower net started fishing as deep as 500 m.; no allowance has been made for this variation. The number of observations in each 2-hourly period varies greatly owing to the routine adopted for working stations.

It will be seen that between 0600 and 1600 hrs. adolescent and adult *E. triacantha* are absent from the upper 100 m. From 1600 to 2000 hrs. the numbers increase rather slowly, between 2000 and 2200 hrs. there is a more rapid increase and the maximum is reached between 2200 and midnight. The descent in the early morning follows a similar but slightly steeper curve. The pattern of distribution in the 250–100 m. layer is not so clear. Between 0800 and 1600 hrs. the numbers are low and the major part of the population must be below 250 m. Between 1600 and 0800 hrs. there is a considerable variation but there are two slight peaks between 1600 and 1800 hrs. and 0600 and 0800 hrs. and these probably represent part of the population passing through the layer during their ascent and descent. It is clear from this diagram that part of the population migrates upwards from a depth below 250 m. but does not continue up into the 100–0 m. layer.

Table 5. *The number of observations in each 4-hourly period and at each depth used in preparing Fig. 9C.*

Depth (m.)	Time (hr.)					
	12–16	16–20	20–00	00–04	04–08	08–12
50–0	21	37	149	12	13	39
100–50	21	37	149	13	13	39
250–100	21	36	149	12	14	38
500–250	18	36	148	13	13	38
750–500	15	36	140	11	13	37
1000–750	13	34	134	7	13	36
1500–1000	1	7	43	0	0	2

There are not enough samples from 1 m. nets hauled below 250 m. to give helpful data, and, as has been stated above, the vertical hauls with the 70 cm. diameter net do not provide adequate data concerning the distribution of adult euphausiids of the size and comparative scarceness of *E. triacantha*. In spite of this it was felt that some measure of the population below 250 m. was necessary, however poor it might be, and these N70V data are presented in Fig. 9C. The observations have been divided into six 4-hourly groups and the width of each block represents the mean catch per 250 m. haul. The number of observations at each depth and in each 4-hourly period are shown in Table 5. Before discussing this diagram it should be stressed that only the gross changes in vertical distribution can be considered. To emphasize this point cross-hatching has been used where, before correction for a 250 m. haul, the total for the particular time and depth is only one individual.

The gross daily changes in vertical distribution shown by this figure agree well enough with those seen in the N100B data. In addition it is evident that, for 16 out of the 24 hrs., a large proportion of the population is to be found between 750 and 250 m. There is, however, one anomaly. From 2000 hrs. to midnight the proportion of the population between 250 and 100 m. does not agree with that shown by the N100B; on the basis of Fig. 9C a peak would be expected between these hours in Fig. 9B. This may be partly due to the oblique nets sampling the water between 500 and 250 m., in which the population is reduced at this time.

Thus it appears that during the day the majority of the population of adolescent and adult *E. triacantha* is to be found between 500 and 250 m., part sinking below 500 m. for a short time around

midday, and that towards dusk there is a fairly rapid rise into the upper 250 m. of water, followed by a descent again in the early morning.

It seems probable, though by no means certain, that those animals which in daytime are between 500 and 750 m., do not migrate into the upper 100 m. during the night but remain within the 250-100 m. level, whereas those animals that spend the day between 500 and 250 m. probably enter the top 100 m.

There is no evidence from these data of the midnight sinking displayed by many other diurnal migrants. It may well occur, however, for it is unlikely to be detected with time intervals as widely spaced as these.

Various authors have shown that the extent of diurnal migration varies in some animals with their age, size and sex. Russell (1931) found that the smaller specimens of *Sagitta elegans* Verrill, 1873, rose to the surface before the larger ones at dusk and were later in leaving the surface at dawn; Southern

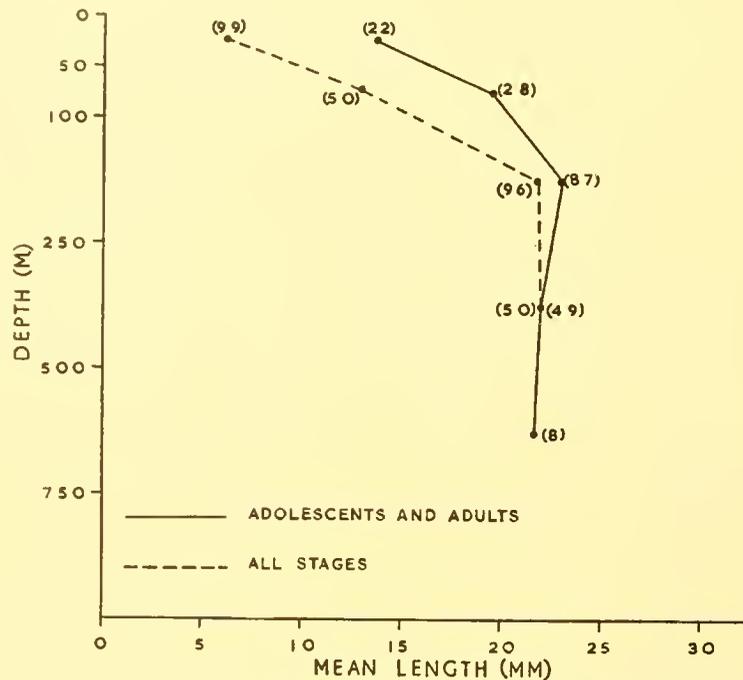


Fig. 10. Variation of the mean length with depth of all stages and of adolescents and adults only taken in the N70V between 2000 hrs. and midnight. The numbers of specimens upon which the means are based are shown in brackets.

and Gardiner (1932) showed that the reverse applied to *Daphnia longispina* O. F. Muller (1785) in Lough Derg. Motoda (1953), working at Lake Shikotsu in Japan, found that at midday the copepodites of *Acanthodiaptomus yumanacensis* (Brehm) were nearer to the surface than the adults. He also observed that the males of this species showed a greater sensitivity to light than the females. Cushing (1951) suggests that 'some animals become more sensitive to light as they grow older and others become less so'.

In Fig. 10 the mean lengths of adolescents and adults taken by the N70V between 2000 hrs. and midnight on the Greenwich meridian, have been plotted against depth. We are only concerned here with the relative lengths at different depths, the actual lengths are dependent upon the time of year the hauls were made. There is little doubt that there is a definite tendency for the smaller individuals to inhabit the upper 100 m. during this period whereas the larger ones are found below this level. It does not follow that the larger animals are never found in the upper layers, for specimens of over 35 mm. have frequently been taken in the 100-0 m. N100B at night; nor does it mean that the

smaller specimens are never found in deeper water. It would be interesting to compare the mean lengths at different depths between 0800 and midday but unfortunately the data are insufficient. There is an even more marked variation in the mean lengths when the larvae are included with these figures (pecked line) showing that there is a very strong tendency for them to inhabit the upper layers during the night. There is probably little or no significance in the reduction of mean length below 250 m. in this figure.

Although illumination is probably not the only factor involved in diurnal vertical migration, it is reasonable to assume that it plays the major part, and that any variation in length of daylight would influence the time spent at a particular depth. At 50° S there are approximately 8 hrs. more darkness

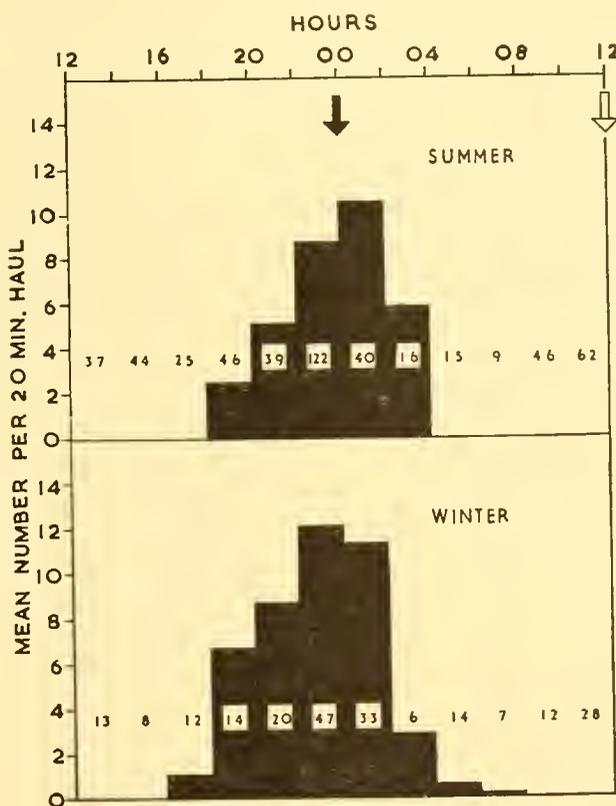


Fig. 11. The diurnal variation of the numbers of adolescent and adult *E. triacantha* in the upper 100 m. in winter and summer. The number of observations for each 2-hourly period are shown.

in winter than in summer, and it could be expected that this would affect the time spent in the upper 100 m. by *E. triacantha*. In Fig. 11 the mean numbers per 20 min. 100–0 m. N 100 B haul are plotted for summer and winter at 2-hourly intervals. As illumination is the primary consideration in this case summer has been taken as mid-September to mid-March and winter as mid-March to mid-September. This allows approximately three months either side of the longest and shortest days. From the figure there is not a great deal of difference in the time spent in the surface water by the majority of the animals, but the period during which no adolescent and adult *E. triacantha* are found in the surface at all is 6 hrs. shorter in winter than in summer. If there were sufficient data to compare winter and summer observations in the Bellingshausen Sea region it would probably be found that there was a greater difference, for the horizontal range of *E. triacantha* lies very much further south—between about 58° S and 69° S—where there is a difference of more than 13 hrs. between winter and summer darkness.

Most workers on plankton have at some time been faced by the problem of whether their results are affected by the organisms avoiding the net, in particular whether there is a greater degree of

avoidance during the day than during the night (Holt and Tattersall, 1905; Frost, 1932; Gardiner, 1934). Southern and Gardiner (1932) found that when they arranged a number of species in the order of the difference between day and night catches they were also in order of size. They concluded that the larger animals were more successful in avoiding the net and that this was a factor of some importance when considering the variation between day and night hauls. Hardy and Gunther (1935), when considering the vertical migration of the larvae of *E. frigida* Hansen, 1911, and *Thysanoessa* spp., found that there was no significant difference between the relative populations in the upper 1000 m. as shown by the nets by day and by night. The same seems to apply to adolescent and adult *E. triacantha*. In Table 6 the same data as were used in preparing Fig. 9C are given, except the mean catches for each depth range are based upon the actual catches and not those corrected for a 250 haul. The totals of these means can be taken as a measure of the total population, as shown by the N70 V, in each 4-hourly period. Although these totals show a variation they do not indicate any significant increase in the amount of avoidance during the day. This does not mean that the animals do not avoid the N70 V, it just shows that there is no appreciable diurnal variation in the amount of avoidance, and consequently reasonable comparisons can be made of day and night hauls. It should be pointed

Table 6. *The mean catch with the N70 V in each depth range, uncorrected for a 250 m. haul and divided into 4-hourly periods. The totals represent the relative total population for each period. (These figures, corrected for a 250 m. haul have been used in preparing Fig. 9C. The numbers of hauls in each interval are given in Table 5)*

Depth (m.)	Time (hr.)					
	12-16	16-20	20-00	00-04	04-08	08-12
50-0	0.05	0.00	0.13	0.08	0.00	0.00
100-50	0.00	0.05	0.21	0.00	0.00	0.00
250-100	0.10	0.08	0.56	0.25	0.07	0.00
500-250	0.56	0.56	0.28	0.69	0.54	0.76
750-500	0.27	0.19	0.05	0.18	0.08	0.62
1000-750	0.08	0.06	0.00	0.00	0.00	0.00
Total	1.06	0.94	1.23	1.20	0.69	1.38

out that here we may be dealing with a special case and that this does not apply to all species. It has been shown above that the larger *E. triacantha*, i.e. those that would be more successful in avoiding the net, tend to inhabit deeper water where the increase in illumination during the day is not very great, and that in the upper waters, where the diurnal variation in illumination might be expected to have an effect, the animals are smaller and consequently less successful in avoiding the net. Mr Marr (personal communication) has found that in the case of adult *E. superba*, which inhabits the surface water and displays no diurnal migration, illumination has a very marked effect on the amount of avoidance, so much so that daylight hauls with the N70 V very rarely take any adult *E. superba* at all.

Both Hardy and Gunther (1935) and Mackintosh (1937) have shown that the horizontal distribution of planktonic animals may be influenced by variations in their vertical distribution. Mackintosh suggested that populations, at least of certain common species in the Antarctic, could maintain their particular horizontal ranges by means of seasonal or diurnal vertical movements between water masses moving in different directions. To the south of the Antarctic convergence the directions of movement of the water masses are fairly well known (for details see Deacon, 1937). North of about 65° S the Antarctic surface water, a layer of cold water 100-250 m. in thickness, is moving to the east and north and below this lies the warm deep water which generally has a strong southerly component. We have seen above that the diurnal vertical movements of *E. triacantha* are sufficient for the animals to alternate between the two currents and it follows that, provided the relative speeds of the currents

are such that they counterbalance any difference in the times spent in each, the population would tend to be maintained in the same latitude. This does not imply, however, north and south movements in the same longitude, for the animals will always be moving towards the east during the night under the influence of the easterly component of the Antarctic surface water. The water movements to the north of the Antarctic convergence are not so well known as those to the south and it is difficult to say what effect vertical movements of animals might have on their horizontal distribution.

VERTICAL DISTRIBUTION OF LARVAE

The vertical distribution of the larval stages of *E. triacantha* has not been examined in great detail, since the material available is necessarily more limited than that for the adolescents and adults. This is partly due to the restricted breeding period and partly to the narrow latitudinal range of the larvae.

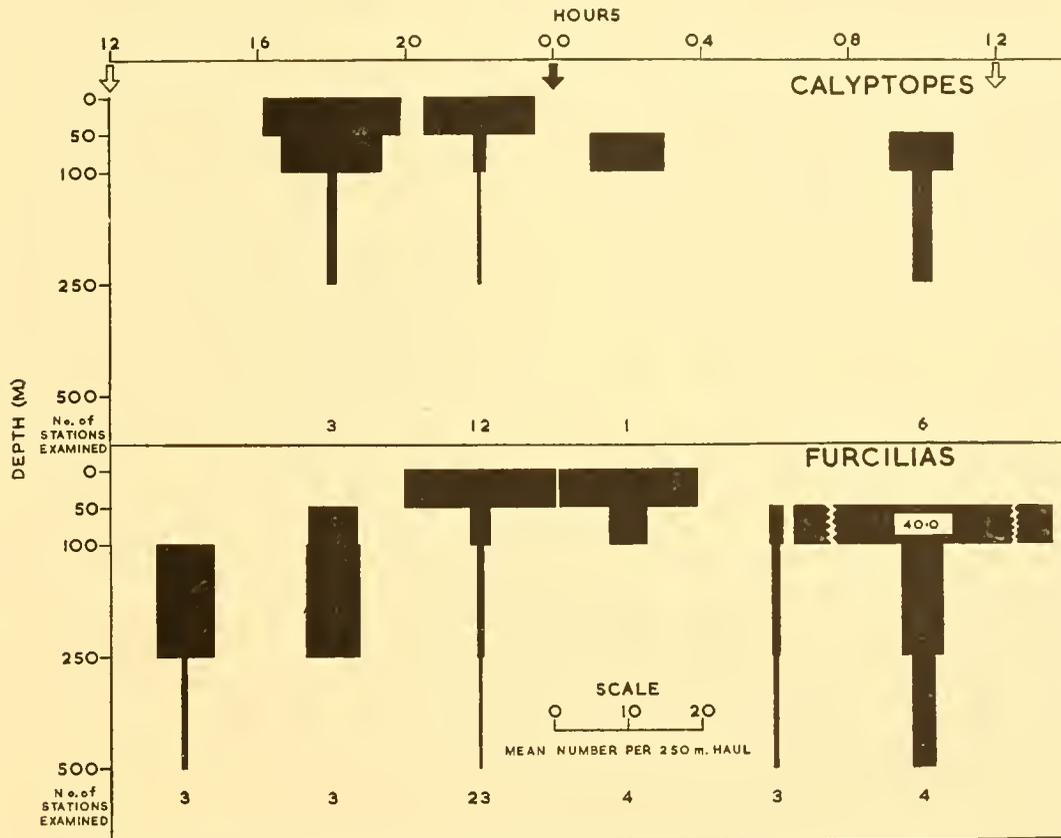


Fig. 12. The daily vertical distribution of calyptopes and furciliars from the N70V hauls. Only stations at which the larvae occurred have been used in calculating the mean number per 250 m. haul.

The data obtained from the material that has been examined are presented in Fig. 12. As in Fig. 9C the day has been divided in six 4-hourly periods and the mean catch per 250 m. haul calculated for each depth range in these periods. In calculating these means only stations at which calyptopes or furciliars occurred have been taken into account.

This figure suggests that, although the calyptopis stages probably perform a diurnal migration, it is confined mainly to the upper 100 m. The furciliars, however, show a more pronounced migration that extends between 250 m. and the surface. No calyptopes have been taken from below 250 m. and no furciliars from below 500 m. It has been mentioned above that some animals become sensitive to light with increasing age (Cushing, 1951) and the fact that the calyptopes do not descend below 250 m. during the day may be due to the lack of sensitivity to light or it may be due to a lack of

swimming power. Whatever the cause, there is little doubt that the depth attained during migrations increases with age.

To the south of the Antarctic convergence the larval stages are thus confined mainly to the north-easterly moving Antarctic surface water and the effect of this can be seen in their concentration in the region of the convergence.

SWARMING

There are no records of *E. triacantha* forming shoals on the same scale as *E. superba* (Mackintosh and Wheeler, 1929; Hardy and Gunther, 1935; Marr, 1956) or such as are sometimes seen in *Meganyctiphanes norvegica* (M. Sars), 1857 (Macdonald, 1927). On the contrary, the adults are generally rather sparsely but evenly distributed. Out of 292 night hauls between 100 m. and the surface with the N 100B only ten contained more than fifty adolescents and adults. In nine of these the majority were juveniles in the post larval stage and in the tenth over 90% were under 20 mm. Thus, although swarming does not occur in the adults, occasionally hauls have been taken which contain numbers of the younger stages that are significantly larger than average. Two of these are of particular interest—at St. 1936E, one of a series of stations repeated at approximately 3-hourly intervals, and at St. 2807. At St. 1936E a flight of five 1 m. nets were towed horizontally at the following depths: 5, 22, 44, 86 and 133 m. The upper three nets contained 0, 517 and 8 larvae, respectively. These larvae must have been confined to a layer not more than 40 m. in thickness and very probably much less since the smaller number of larvae in the 44 m. net does not necessarily indicate a continuation of the concentration of larvae down to this level, since this net fished for a short time at 22 m. while the net above was being attached to the warp. It is not possible to determine the horizontal spread of this group of larvae owing to their diurnal vertical movements, but at St. 1936D worked half a mile to the south two hours previously a similar flight of five nets fished at intervals down to 155 m. took a total of only forty-eight larvae.

At St. 2807 an N 100B was fished from only 33 m. to the surface owing to bad weather, but even in this shallow haul 248 larvae were taken—a relatively dense swarm, at least for *E. triacantha*.

Marr (1956) finds that the older stages of *E. superba* accumulate in thin plate-like shoals and, although there is no evidence to show the horizontal extent of the patches of *E. triacantha* larvae that have been found, it seems probable that they too only occupy a comparatively narrow vertical range.

DEVELOPMENT AND GROWTH

LARVAL STAGES

The most comprehensive account of the larval stages of *Euphausia triacantha* is that by John (1936, p. 278). In this he describes and figures the second and third calyptopes and the seven furcilia. The first calyptopis is described by Rustad (1934, p. 19). Up to the present time no larval stage earlier than the first calyptopis has been found which can be referred with certainty to *E. triacantha*. Ruud (1932, p. 55) describes a metanauplius with a denticulate margin to the carapace which he suggests probably belongs to either *E. frigida* or *E. triacantha*; many metanauplii similar to this have been found in the 'Discovery' material, but as these have been taken not only within the range of *E. triacantha* but also to the north and south it seems certain that this type of metanauplius occurs in more than one of the southern species of *Euphausia*.

Table 7 shows the range and mean lengths of the ten larval stages examined; these data are plotted in Fig. 13. Measurements are from the anterior margin of the eyes to the tip of the telson. The mean length of the seventh furcilia is probably rather low, for there is tendency for the second pair of posterior-

lateral spines, the presence of which distinguishes this furcilia from the immediately post-larval forms, to break off in those furcilia which are shortly due to moult, and this results in their inclusion with the post-larvae. Although there is general agreement with John's results, the mean lengths of the fifth and sixth furcilia suggest that the latter stage may frequently be omitted. In the last four furcilia stages there is a gradual reduction in the number of terminal spines on the telson, from seven in the fourth furcilia to five in the fifth, three in the sixth and one in the seventh and all subsequent

Table 7. Mean lengths and ranges of length of the larval stages from first calyptopis to seventh furcilia

Stage	No. measured	Range (mm.)	Mean length (mm.)
C1	24	0.9-1.1	1.0
C2	27	1.6-2.3	1.9
C3	82	2.5-3.6	2.9
F1	110	3.4-4.8	4.4
F2	152	5.0-6.3	5.7
F3	171	6.0-7.4	6.9
F4	130	7.0-9.0	8.1
F5	73	8.0-10.5	9.6
F6	71	8.1-11.0	9.6
F7	59	8.2-11.3	10.0

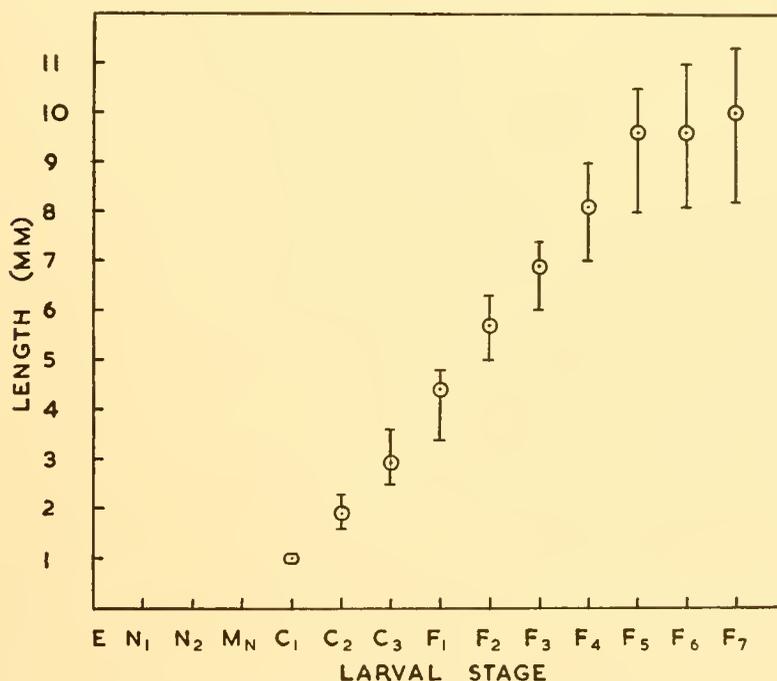


Fig. 13. The mean lengths (circles) and total range of length (vertical lines) of the larval stages from first calyptopis to seventh furcilia.

stages. In furcilia which are about to moult it is sometimes possible to see through the exoskeleton and to determine the number of terminal spines that will be present in the next stage (Lebour, 1926; Fraser, 1936; John, 1936). It has been possible to do this for a total of 141 fourth furcilia and 99 fifth furcilia. Table 8 shows the number and percentage of these fourth furcilia that were going to moult to fifth furcilia and the number and percentage that were going to moult directly to sixth furcilia omitting the five-spined stage. Similarly, the 99 fifth furcilia have been divided according to whether they were going to moult into sixth or directly into seventh furcilia. The percentages in Table 8 have been used in Fig. 14 to trace the developmental paths taken by one hundred fourth furcilia. Of the original hundred, nine moult to sixth furcilia and ninety-one to fifth furcilia by

the loss of four and two spines, respectively. Of these ninety-one fifth furcilia ten moult to sixth furcilia, whereas eighty-one miss out this three-spined stage and moult directly to the one-spined seventh furcilia. The nineteen sixth furcilia that have moulted from both fourth and fifth furcilia also moult to seventh furcilia. There are, then, three alternative routes from fourth to seventh furcilia, 4-5-6-7; 4-6-7; 4-5-7, and it is the last of these that the majority of larvae follow.

Table 8. *Variation in the number of terminal spines on the telson lost during ecdysis of the fourth and fifth furciliae*

<i>Furcilia stage</i>	<i>No. of terminal spines</i>	<i>No. of terminal spines in next stage</i>	<i>No. specimens examined</i>	<i>%</i>
4	7	5	129	91.4
4	7	3	12	8.6
		Total	141	100.0
5	5	3	11	11.1
5	5	1	88	88.9
		Total	99	100.0

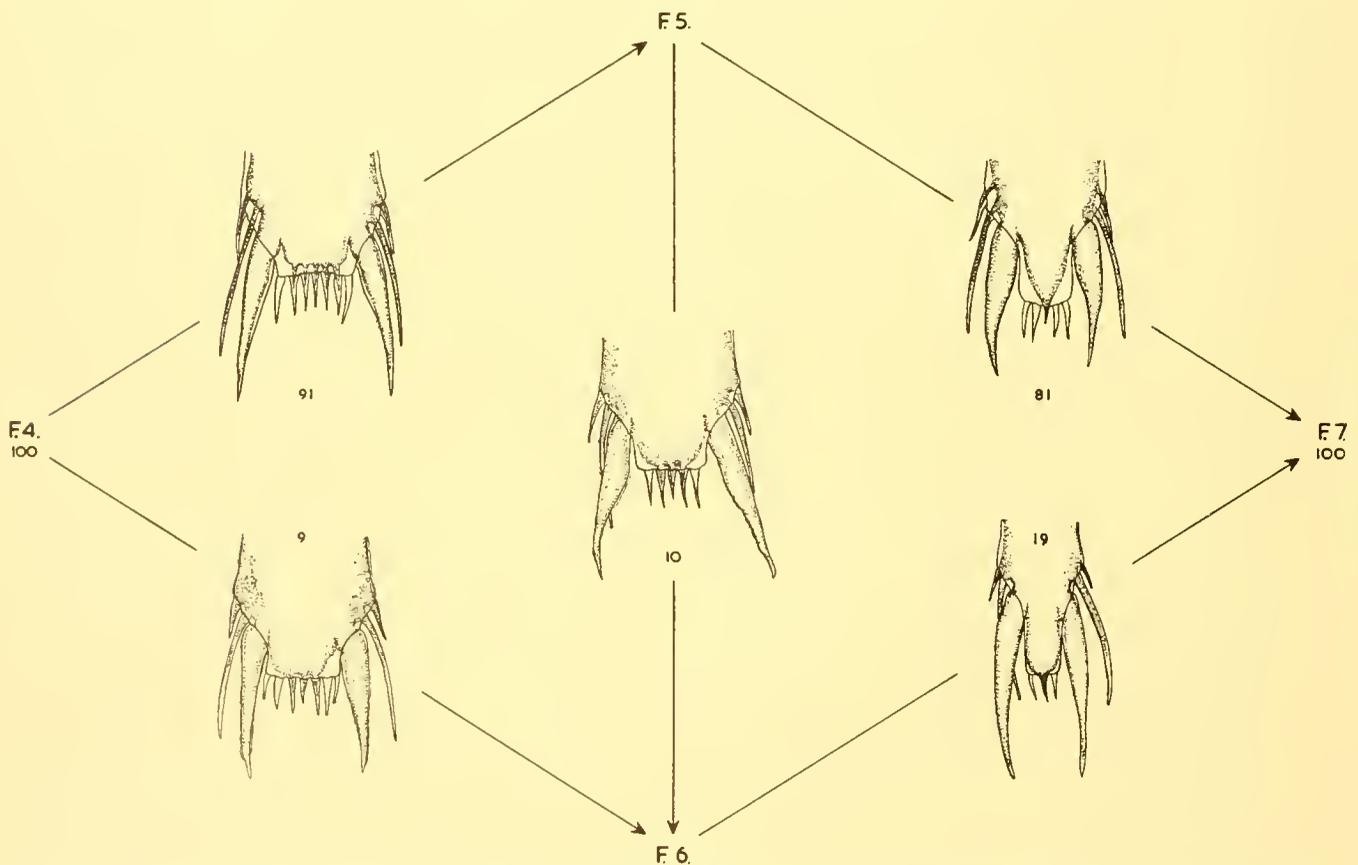


Fig. 14. The paths of development of one hundred fourth furciliae calculated from the percentages of fourth furciliae moulting to fifth or sixth furciliae and the percentages of fifth furciliae moulting to sixth or seventh furciliae (see Table 8). The figures show the arrangements of the spines on the telson in each stage and it can be seen how the number of terminal spines in the succeeding stage is determined.

Although it is now accepted that, within one species, larvae with certain combinations of setose and non-setose pleopods tend to be dominant and that the few other combinations that occur can be considered as variants, it is unusual for any of the furciliae which are recognized by the number of terminal spines on the telson, to be omitted. This point is emphasized by Boden (1955, p. 375) who,

writing of a furcilia of *Nematoscelis megalops* G. O. Sars, 1885, which bears one terminal spine, states '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 life history and it seems justifiable to suspect that there is at least one stage with three terminal spines on the telson'. John (1936, p. 257) does record two larvae of *E. vallentini* in which seven spines are followed by three but this sequence does not occur in the majority of the larvae. Lebour (1926, p. 786), on the other hand, shows that this is the usual developmental sequence in *Nematoscelis microps* G. O. Sars, 1883 from the Mediterranean and it is confirmed by Gurney (1947, p. 60) from his Bermuda material.

In view of this and of the results obtained in the case of *E. triacantha* it is possible that when the larval development of more species is known it will be found that the omission of some of the later furcilia stages is more common than has previously been thought.

It is not intended to suggest that this necessarily applies in the case of *Nematoscelis megalops* but, as both Boden, who had, however, only a few late furcilia, and Frost (1935) failed to find larvae with three terminal spines, it is a point that will bear further consideration when more material is available.

SPAWNING

Both the time and the place of spawning can only be inferred from the presence of young larvae since neither eggs which can be identified as those of *E. triacantha*, nor gravid females have been found in the plankton. The earliest date at which first calyptopes have been found is 23 September and the latest 16 December. In order to obtain some indication of the time of spawning it is necessary to know the period required for development from the egg to the first calyptopis. The only estimate available is that from Lebour's (1924, p. 408) laboratory experiments on *Nyctiphanes couchii* (Bell), 1853, which gave a period of 8-9 days for development from nauplii free in the egg-sacs to the first calyptopes. If the assumption is made that a similar period is required in *E. triacantha*, spawning could be expected to occur from mid-September to early December, although it must occasionally take place later than this, for a few third calyptopes (a total of eighteen from five stations) have been taken in January and early February. However, the maximum number of calyptopes are found in late October and November and the main spawning almost certainly takes place during these months.

It is probably reasonable to assume that spawning takes place in the region of maximum abundance of larvae, that is in a belt 200 miles wide south of the Antarctic convergence. There is, however, no evidence regarding the depth at which it occurs.

ADOLESCENTS AND ADULTS

Prior to the development of the external reproductive organs, the petasma in the male and the thelycum in the female, the only external character distinguishing the sexes in *E. triacantha* is the presence of setae on the coxopodite of the sixth thoracic limb of the male and their absence in the female. Thus *E. triacantha* differs from *E. superba* in which the male has a narrower and more shallow carapace than the female and in which there are also differences in the shape of the rostrum and of the spine at the anterior lateral corner of the carapace (Bargmann, 1937, p. 328). However, the sex of nearly all post-larval *E. triacantha* can be determined by examination of the reproductive system.

The development of the reproductive systems follows very closely the patterns described by Bargmann (1937) for *E. superba* and it is not proposed to describe it in detail here. In the male the only differences appear to be the number of lobes of the testis—twelve in *E. triacantha* as compared with fifteen in *E. superba*—and, in *E. triacantha*, the lesser degree of coiling of the vasa deferentia between the anterior and posterior flexures.

In the immediately post-larval female the ovary is unlobed and saddle-shaped. Growth takes place steadily, the ovary becoming lobed and extending ventrally on to the thoracic muscles and posteriorly into the abdominal region. Development of the thelycum takes place simultaneously with the growth of the ovary and by the time the thelycum reaches the adult shape and is heavily chitinized the ovary is usually touching or overlapping the thoracic muscles and the shell gland is just starting to develop.

Eggs were measured under a low power binocular microscope in 108 *E. triacantha* at various stages of maturity, the smallest female in which this was possible being 20 mm. in length and in which the eggs were 0.05 mm. in diameter. The smallest female *E. superba* in which Bargmann (1945, p. 115) found eggs of this size was 27 mm. When they can first be measured all the eggs on the dorsal surface of the ovary are of uniform size, but as the ovary matures the eggs in the region of the oviduct increase in size more rapidly than the others and it is in this region that the largest eggs are always found. At a slightly later stage the eggs near the tips of the lobes enlarge and a graded series is formed from the median part of the ovary where the eggs are small to the outer edges of the lobes where they are large. However, even in the most mature female examined, in which the largest eggs measured 0.44 mm. and were opaque and yolky in appearance, there still remained a narrow border of small eggs (0.05 mm. diameter) round each of the lobes, and it is probable that these eggs never develop any further. Only two females have been taken which give the appearance of having spawned. However, in one of these the thelycum contained two full spermatophores and in the other, one full and one damaged spermatophore. In both these the ovary had the original saddle-shape described by Bargmann (1937, p. 348) for spawned *E. superba* and the oviducts could be seen as wide flat bands whereas in the young stages with this type of ovary they are narrow.

Out of eighty-five female *E. triacantha* carrying spermatophores fifty-three were full, ten half-full and fourteen empty. The remaining eight carried one full spermatophore, the other having been broken off, and these can probably be included with those with full spermatophores. Although these numbers are small this suggests that the sperm-mass remains in the spermatophore for some considerable time before migrating into the thelycum. It is interesting to compare this with Bargmann's observation (1945, p. 117) that 'of 556 females (*E. superba*) carrying spermatophores, only 102 were full, showing that the migration of the sperm-mass into the thelycum must be a rapid process'.

GROWTH RATE

The life cycle of *E. triacantha* takes two years to complete as in *E. superba* (Ruud, 1932; Bargmann, 1945). This is shown in Fig. 15 in which the data from hauls down to 500 m. with the N100B and N70V have been used to plot the length frequencies for each month of the year. The animals have been divided into two-millimetre groups and the number in each group expressed as a percentage of the total number measured in each month. These totals are shown at the top of the figure. In calculating the larval frequencies measurements have not been made; instead it has been considered sufficient to use the mean length for each stage shown in Fig. 13 (p. 331). In view of the fact that the data have been taken from many different localities in different years the results presented in Fig. 15 are remarkably consistent, and this suggests that there is little variation in the rate of growth from region to region and from year to year.

In September three distinct size groups can be seen: the larvae, which result from a recent spawning, the adolescents, which were spawned in the previous year, and the adults, spawned two years previously and now due to spawn themselves. The larvae in September consist entirely of first calyp-topes. In the succeeding months the young stock is gradually built up, the predominant stages being first and second furcilia in November (about 4-6 mm.), second and third furcilia in December and fourth to seventh furcilia in January and February. By April nearly all the 0-year group have become

post larval. From December onwards there are, in Fig. 15, still slight indications of three size groups and it is possible that a small part of the population does not spawn in the third spring but lives to spawn in the spring of the fourth year. The males of over 30 mm. in December carry ripe spermatophores, and in the next two months an increasing number of undoubted 1-year group males attain sexual maturity until, by March, practically all those over 25 mm. have reached the mature condition. On the other hand, during these months all females, including those over 30 mm. in length, have immature ovaries. Thus it is not possible to be certain whether these larger size groups are made up of animals that have grown more rapidly and the males have become sexually mature rather early, or whether they represent a small part of the population having a three-year cycle.

Considering only those males which clearly belong to either the 0-year group or 1-year group the time taken to reach various degrees of maturity can be determined. The period of adolescence, that is the period during which the reproductive system is still developing (Bargmann's stages 1-5), lasts

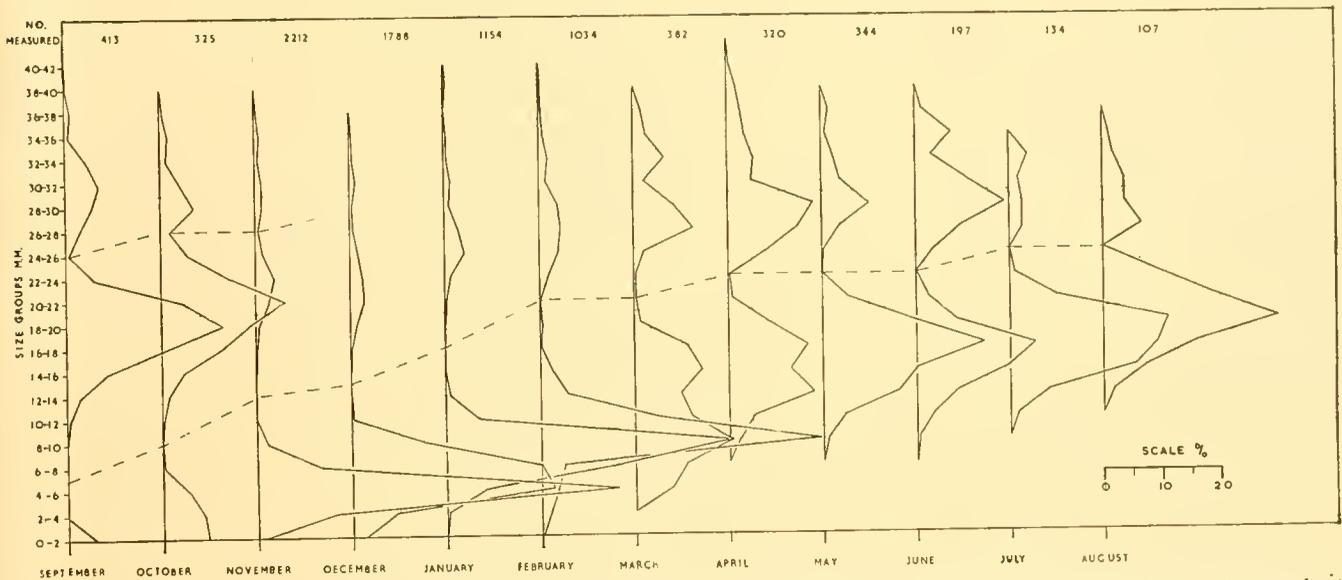


Fig. 15. Monthly percentage length frequencies of *E. triacantha*. The number of specimens measured in each month is shown at the top. The pecked lines divide the population into year groups. These groups have been used in preparing the growth curve, Fig. 16.

from April to about the following November. During this and the next month an increasing number of males are found with imperfect spermatophores in the spermatophore sacs or ejaculatory ducts, and, using Bargmann's criteria, these can be considered as having entered the adult phase. During January and February a large proportion are found with mature spermatophores in both the spermatophore sacs and the ejaculatory ducts, and by March nearly all have reached this fully adult condition and are presumably ready for pairing. It seems probable, however, that pairing is generally delayed, because, although from January onwards a few females are found carrying spermatophores, it is not until June that the majority do so.

A complete analysis of egg sizes has not been made, but it is apparent from those that have been measured that eggs of over 0.3 mm. in diameter begin to appear in the ovaries about May, and that the number of females with such eggs and the number of eggs of this size present in each ovary increases until, in August very nearly all the adult females have ovaries with at least some large eggs. The two females, mentioned above, with the appearance of having spawned, were taken in late September.

The growth rate during the two years of the life cycle can best be seen by separating the year groups

and calculating the mean length for each month. The 0- and 1-year groups are readily distinguished and the points at which they have been separated are indicated in Fig. 15 by the lower pecked line.

The 1- and 2-year groups can also be separated in September, October and November as all the males above the upper pecked line have fully developed spermatophores and nearly all the females have well-developed ovaries with large eggs scattered about the surface, whereas these characters are

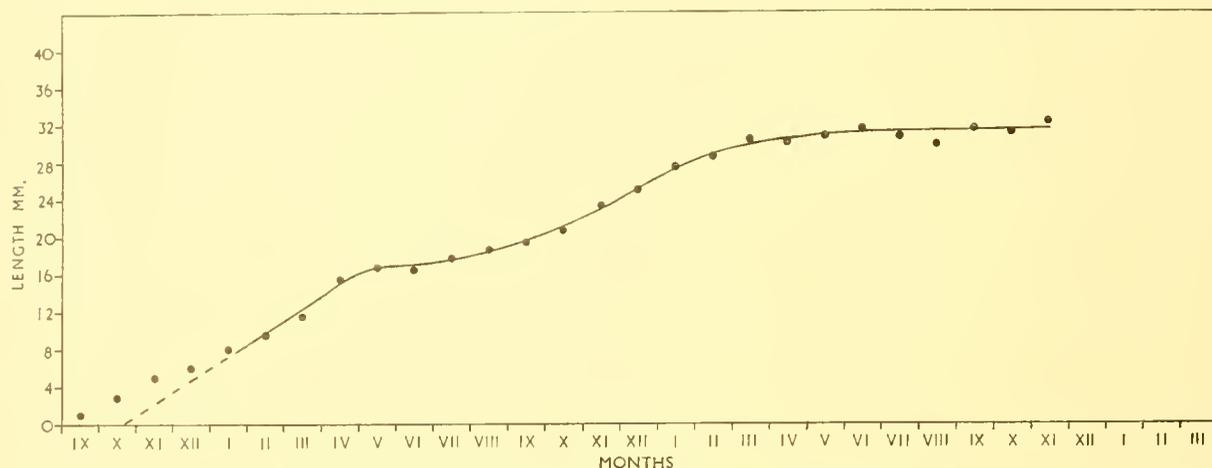


Fig. 16. Growth curve for *E. triacantha* taken from Fig. 15.

Table 9. Mean monthly lengths of *Euphausia triacantha*

Months	Mean length (mm.)	No. of obs.	Mean length (mm.)	No. of obs.	Mean length (mm.)	No. of obs.
September	1.0	20	19.3	319	31.5	74
October	2.8	64	20.6	221	31.1	40
November	5.0	1954	23.2	176	32.2	82
December	6.0	1620	24.9	168	—	—
January	8.1	1052	27.5	105	—	—
February	9.6	880	28.5	154	—	—
March	11.5	270	30.2	112	—	—
April	15.5	166	30.0	154	—	—
May	16.7	281	30.7	63	—	—
June	16.4	110	31.4	87	—	—
July	17.7	122	30.7	12	—	—
August	18.5	89	29.8	18	—	—

absent in the smaller size groups. For the purposes of calculating the mean monthly lengths for Fig. 16 it has been assumed that after the end of November all those animals in size groups above the pecked line in Fig. 15 belong to the 1-year group. The mean lengths and the number of observations on which they are based are shown in Table 9. The mean lengths for September to December do not take account of larvae not yet hatched and the estimated curve for these months is shown in Fig. 16 as a pecked line which starts at the estimated mean time of hatching (see p. 333) and joins the rest of the curve in January when no more larvae are being hatched.

During the first six and a half months after hatching, that is from mid-October to the end of April, *E. triacantha* grows fairly steadily at a rate of about 2.5 mm. per month. With the onset of winter the rate of growth slows down to less than half this, the curve giving an average of 1 mm. per month for May to August. From September to February of the second year the rate is again increased though

it does not reach that of the first summer, the average being 1.7 mm. per month, and after March little or no further growth takes place. The two periods of rapid growth during the life cycle correspond with the periods of phytoplankton abundance described by Hart (1942) for his 'Northern Region'.

A comparison of this growth curve with Bargmann's curve for *E. superba* (1945, p. 129), shows that, whereas *E. triacantha* stops growing in the first half of the second year of life, *E. superba* is still growing during the early part of the third year. Thus it appears that the larger size of *E. superba* is reached by a longer period of growth rather than by a faster average rate.

SUMMARY

1. The material upon which this paper is based was contained in samples taken during oblique hauls with the 1 m. net and vertical hauls with the 70 cm. closing net.

2. The horizontal range of the adolescents and adults extends from Subantarctic water southwards to the northern limits of the East Wind and Weddell drifts. The region of maximum abundance is a circumpolar belt extending from 150 miles north to 200 miles south of the Antarctic convergence and there is little or no seasonal variation in this distribution. The extreme range of surface temperature is $-1.80-11.88^{\circ}$ C., the greater part of the population living between 2 and 8° C. for most of the year.

3. The distribution of *E. triacantha* is compared with that of *E. superba*, and it is shown that the southern limit of the former roughly coincides with the northern limit of the latter.

4. The region of maximum abundance of larvae is a belt extending for 200 miles south of the Antarctic convergence.

5. All stages from first calyptopis upwards perform a diurnal migration which becomes more marked with increasing age. The lower limit of the vertical range does not normally extend below 750 m.

6. Adolescent and adult *E. triacantha* do not form swarms and indeed are rather evenly distributed, but there is evidence of occasional small-scale swarming in the larvae.

7. The mean lengths of the larval stages have been calculated and it is shown that the furcilia stage with three terminal spines on the telson is usually omitted.

8. Spawning takes place mainly in October and November and it is presumed to occur in the region of maximum abundance of larvae.

9. The development of both the male and female reproductive systems is similar to that of *E. superba*.

10. Monthly length frequencies show distinct year groups. The normal life cycle takes two years from hatching to breeding. Growth is slower in winter than in summer and ceases earlier than in *E. superba*.

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