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ASCIDIACEA

by

R. H. Millar

CAMBRIDGE
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By A. K. Totton

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ASCIDIACEA

By

R. H. MILLAR

Marine Station, Millport

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ASCIDIACEA

By R. H. Millar

Marine Station, Millport

(Plates I–VI, text-figs. 1–72)

INTRODUCTION

The ascidians which this report describes were collected during the years 1925–37 by R.R.S. 'Discovery', R.R.S. 'Discovery II', R.R.S. 'William Scoresby', and the staff of the Marine Biological Station at South Georgia. A large part of the material is from the Falkland Islands and Patagonian shelf in the Subantarctic, and much was also collected from the vicinity of Graham Land, South Georgia and the South Shetland, South Orkney, and South Sandwich Islands in the Weddell Sea sector of the Antarctic. Of the many other localities represented, one of the most interesting is the Three Kings district at the northern end of New Zealand.

There are altogether about 2500 specimens, representing seventy-eight identifiable species. Of these, thirteen are described as new and there are three new *forms* of known species. The type specimens are deposited in the British Museum (Nat. Hist.).

LIST OF NEW GENERA, SPECIES AND FORMS

Aplidium falklandicum sp.n.
A. stanleyi sp.n.
A. quadrisulcatum sp.n.
A. seeligeri sp.n.
Aplidiopsis discoveryi sp.n.
Protopolyclinum gen.n.
P. pedunculatum sp.n.
Ritterella vestita sp.n.
Didemnum trivolutum sp.n.
Podoclavella kottae sp.n.
Sycozoa anomala sp.n.
Cnemidocarpa tricostata sp.n.
Styela schmitti f. *simplex* n.
Molgula setigera f. *georgiana* n.
,, ,, f. *marioni* n.
Eugyra brewinae sp.n.
E. ärnbäckae sp.n.

The task of working through the material was greatly eased by the fact that Dr A. Ärnbäck-Christie-Linde had completed the process of sorting the collection before her death. She also made preliminary identifications of a number of the specimens and left notes on some of them. Her notes, which were made available to me, have been very valuable. Nevertheless, I have had to re-examine all the material, and this report represents my own views, which differ in many points from those which Dr Ärnbäck-Christie-Linde would have expressed had she lived to write the account of the Ascidiacea from the 'Discovery' collections.

CLASSIFICATION

I have adopted the classification used by Huus (1937–40) in Kükenthal and Krumbach's *Handbuch der Zoologie*, with the following modifications:

In the order Enterogona, suborder Phlebobranchiata I have recognized the family Diazonidae Garstang, 1891, as distinct from the family Cionidae Lahille, 1887, using these groups as defined by Berrill (1950). *Ciona* occupies a somewhat isolated and probably primitive position, indicated especially by the failure of the two epicardia to fuse and by the position of the gut (Berrill, 1936), and therefore merits a family to distinguish it from the diazonids (*Diazona*, *Tylobranchion*, *Rhopalea*).

In the order Pleurogona, suborder Stolidobranchiata, I have again followed Berrill (1950), who gave convincing reasons for dividing the family Styelidae Sluiter, 1895, into two subfamilies only, Botryllinae Adams, 1858, and Styelinae Herdman, 1881, although Huus and others have recognized a third subfamily Polyzoinae Hartmeyer 1903.

Two minor points in which the present classification differs from that of Huus concern the genera *Herdmania* Lahille, 1887, and *Bathypera* Michaelsen, 1904. I have used the generic name *Herdmania* for the species *H. momus* (Savigny), although Huus used it for a polyclinid species generally referred to as *Euherdmania claviformis* (Ritter). The generic name *Herdmania* was preoccupied when Ritter (1903) proposed it, as he himself later recognized (Ritter, 1904).

The position of *Bathypera* is still doubtful, and although Huus placed this genus in the family Molgulidae, I believe that a number of characters show it to be better placed in the family Pyuridae.

SYSTEMATIC LIST OF SPECIES IN THE COLLECTION

Order *ENTEROGONA* Perrier, 1898

Suborder APLOUSOBRANCHIATA Lahille, 1886

Family POLYCLINIDAE Verrill, 1871

Subfamily Polycliniinae Adams, 1858

Genus **Aplidium** Savigny, 1816

A. circumvolutum (Sluiter)
A. fuegiense Cunningham
A. variabile (Herdman)
A. falklandicum sp.n.
A. radiatum (Sluiter)
A. caeruleum (Sluiter)
A. stanleyi sp.n.
A. quadrisulcatum sp.n.
A. seeligeri sp.n.

Genus **Synoicum** Phipps, 1774

S. adareanum (Herdman)
S. georgianum Sluiter
S. giardi (Herdman)
S. kuranui Brewin

Genus **Aplidiopsis** Lahille, 1890

A. discoveryi sp.n.

Genus **Protopolyclinum** gen.n.

P. pedunculatum sp.n.

Subfamily Euherdmaniinae Seeliger, 1906

Genus **Ritterella** Harant, 1931

R. vestita sp.n.

Family DIDEMNIDAE Giard, 1872

Genus **Didemnum** Savigny, 1816

D. studeri Hartmeyer
D. biglans (Sluiter)
D. trivolutum sp.n.

Genus **Leptoclinides** Bjerkan, 1905

L. diemenensis Michaelsen

Genus **Trididemnum** Della Valle, 1881

T. auriculatum Michaelsen

Family CLAVELINIDAE Forbes & Hanley, 1848

Subfamily CLAVELININAE Seeliger, 1906

Genus **Podoclavella** Herdman, 1890

P. cylindrica (Quoy & Gaimard)
P. kottae sp.n.

Genus **Clavelina** Savigny, 1816

C. claviformis (Herdman)

Subfamily POLYCITORINAE Michaelsen, 1904

Genus **Sycozoa** Lesson, 1830

S. sigillinoides Lesson
S. georgiana (Michaelsen)
S. anomala sp.n.

Genus **Distaplia** Della Valle, 1881

D. colligans Sluiter
D. cylindrica (Lesson)

Genus **Hypsistozoa** Brewin, 1953

H. fasmeriana (Michaelsen)

Genus **Cystodytes** van Drasche, 1883

C. dellechiajei (Della Valle)
C. dellechiajei f. *antarctica* (Sluiter)

Genus **Atapozoa** Brewin, 1956

A. marshi Brewin

Suborder PHLEBOBRANCHIATA Lahille, 1886

Family DIAZONIDAE Garstang, 1891

Genus **Tylobranchion** Herdman, 1886

T. speciosum Herdman

Family ASCIDIIDAE Adams, 1858

Genus **Ascidia** Linnaeus, 1767

A. translucida Herdman
A. challengeri Herdman
A. interrupta Heller
A. sydneiensis Stimpson

Family AGNESIIDAE Huntsman, 1912

Genus **Agnesia** Michaelsen, 1898

A. glaciata Michaelsen

Genus **Caenagnesia** Ärnbäck, 1938

C. bocki Ärnbäck

Family CORELLIDAE Lahille, 1887

Subfamily CORELLINAE Herdman, 1882

Genus **Corella** Alder & Hancock, 1870

C. eumyota Traustedt

Order *PLEUROGONA* Perrier, 1898

Suborder STOLIDOBRANCHIATA Lahille, 1886

Family STYELIDAE Sluiter, 1895

Subfamily Botryllinae Adams, 1858

Genus **Botryllus** Gaertner, 1774

?*B. separatus* Sluiter

Genus **Polyzoa** Lesson, 1830

P. opuntia Lesson

P. reticulata (Herdman)

Genus **Alloeocarpa** Michaelsen, 1900

A. incrustans (Herdman)

Genus **Amphicarpa** Michaelsen, 1922

A. diptycha (Hartmeyer)

Subfamily Styelinae Herdman, 1881

Genus **Cnemidocarpa** Huntsman, 1912

C. pfefferi (Michaelsen)
C. nordenskjöldi (Michaelsen)
C. drygalskii (Hartmeyer)
C. verrucosa (Lesson)
C. tricostata sp.n.

Genus **Styela** Fleming, 1822

S. schmitti van Name f. *simplex* n.
S. insinuosa (Sluiter)
S. magalhaensis Michaelsen
S. paessleri Michaelsen
S. partita (Stimpson)

Family PYURIDAE Hartmeyer, 1908

Genus **Pyura** Molina, 1782

P. stolonifera (Heller)
P. setosa (Sluiter)
P. discoveryi (Herdman)
P. squamata Hartmeyer
P. legumen (Lesson)
P. georgiana (Michaelsen)
P. bouvetensis (Michaelsen)
P. jacatrensis (Sluiter)
P. vittata (Stimpson)

Genus **Herdmania** Lahille, 1887

H. momus (Savigny)

Genus **Bathypera** Michaelsen, 1904

B. splendens Michaelsen

Family MOLGULIDAE Lacaze-Duthiers, 1877

Genus **Molgula** Forbes & Hanley, 1848

M. pedunculata Herdman
M. falsensis Millar
M. platei Hartmeyer
M. malvinensis Ärnbäck
M. bacca Herdman
M. setigera Ärnbäck f. *georgiana* n.
M. setigera Ärnbäck f. *marioni* n.
M. sabulosa (Quoy & Gaimard)

Genus **Ascopera** Herdman, 1881
A. gigantea Herdman

Genus **Paramolgula** Traustedt, 1885
P. gregaria (Lesson)

Genus **Eugyra** Alder & Hancock, 1870
E. kerguelenensis Herdman
E. brewinae sp.n.
E. ärnbäckae sp.n.

LIST OF STATIONS AND SPECIES COLLECTED AT EACH

R.R.S. 'DISCOVERY'

Station 1. 16. xi. 25. Clarence Bay, Ascension Island, 7° 55′ 15″ S., 14° 25′ W. Medium rectangular net, coralline, sand and shells, 16–27 m.

Pyura vittata (Stimpson). 1 specimen.

Station 2. 17. xi. 25. Clarence Bay, Ascension Island, St Catherine's Pt. and Collyer Pt. Shore collection.

Styela partita (Stimpson). 2 specimens.

Station 27. 15. iii. 26. West Cumberland Bay, South Georgia; 3·3 miles S. 44° E. of Jason Lt. Large dredge, mud and rock, 110 m.

?*Aplidium fuegiense* Cunningham. 1 specimen.
A. radiatum (Sluiter). 2 specimens.
Cnemidocarpa tricostata sp.n. 1 specimen.
Pyura discoveryi (Herdman). 29 specimens.
Molgula pedunculata Herdman. 23 specimens.

Station 39. 25. iii. 26. East Cumberland Bay, South Georgia. From 8 cables S. 81° W. of Merton Rock to 1·3 miles N. 7° E. of Macmahon Rock. Large otter trawl, grey mud, 179–235 m.

Aplidium circumvolutum (Sluiter). 1 specimen.
Sycozoa georgiana (Michaelsen). 5 specimens.
Distaplia cylindrica (Lesson). 2 specimens.
Ascidia translucida Herdman. 1 specimen.
Cnemidocarpa verrucosa (Lesson). 4 specimens.
Pyura georgiana Michaelsen. 2 specimens.
Molgula pedunculata Herdman. 7 specimens.
Ascopera gigantea Herdman. 2 specimens.

Station 42. 1. iv. 26. Off mouth of Cumberland Bay, South Georgia. From 6·3 miles N. 89° E. to 4 miles N. 39° E. of Jason Lt. Large otter trawl, mud, 120–204 m.

Caenagnesia bocki Ärnbäck. 1 specimen.
Polyzoa reticulata (Herdman). 1 specimen.
Cnemidocarpa pfefferi (Michaelsen). 1 specimen.
C. verrucosa (Lesson). 1 specimen.
Pyura discoveryi (Herdman). 44 specimens.
P. georgiana Michaelsen. 4 specimens.
Molgula pedunculata Herdman. 2 specimens.
Ascopera gigantea Herdman. 8 specimens.

Station 45. 6. iv. 26. 2·7 miles S. 85° E. of Jason Lt., South Georgia. Large otter trawl, grey mud, 238–270 m.

Sycozoa sigillinoides Lesson. 3 specimens.
Distaplia cylindrica (Lesson). 1 specimen.
Cnemidocarpa verrucosa (Lesson). 7 specimens.
Molgula pedunculata Herdman. 10 specimens.
Ascopera gigantea Herdman. 24 specimens.

Station 48. 3. v. 26. 8·3 miles N. 53° E. of William Pt. Beacon, Port William, Falkland Islands. Large otter trawl, sand and shell, 105–115 m.

Alloeocarpa incrustans (Herdman). 1 specimen.

Station 51. 4. v. 26. Off Eddystone Rock, East Falkland Island. From 7 miles N. 50° E. to 7·6 miles N. 63° E. of Eddystone Rock. Large otter trawl, fine sand, 105–115 and 115 m.

Aplidium fuegiense Cunningham. 1 specimen.
A. falklandicum sp.n. 2 specimens.
Sycozoa sigillinoides Lesson. 7 specimens.
Cnemidocarpa verrucosa (Lesson). 1 specimen.
Polyzoa reticulata (Herdman). 1 specimen.
Alloeocarpa incrustans (Herdman). 2 specimens.
Paramolgula gregaria (Lesson). 1 specimen.

Station 52. 5. v. 26. Port William, East Falkland Island, 7·4 cables N. 17° E. of Navy Pt. Hand lines, 17 m.

Alloeocarpa incrustans (Herdman). 1 specimen.
Pyura legumen (Lesson). 4 specimens.
Paramolgula gregaria (Lesson). 1 specimen.

Station 53. 12. v. 26. Port Stanley, East Falkland Island. Hulk of 'Great Britain'. Mussel rake, 0–2 m.

Aplidium falklandicum sp.n. 1 specimen.
Sycozoa sigillinoides Lesson. 28 specimens.
Cnemidocarpa nordenskjöldi (Michaelsen). 4 specimens.
C. verrucosa (Lesson). 7 specimens.
Styela paessleri Michaelsen. 4 specimens.
Pyura legumen (Lesson). 1 specimen.
Paramolgula gregaria (Lesson). 9 specimens.

Station 55. 16. v. 26. Entrance to Port Stanley, East Falkland Island, 2 cables S. 24° E. of Navy Pt. Small beam trawl, 10–16 m.

Corella eumyota Traustedt. 4 specimens.
Cnemidocarpa verrucosa (Lesson). 4 specimens.
Alloeocarpa incrustans (Herdman). 1 specimen.
Pyura legumen (Lesson). 1 specimen.
Paramolgula gregaria (Lesson). 2 specimens.

Station 56. 16. v. 26. Sparrow Cove, Port William, East Falkland Island, 1·5 cables N. 50° E. of Sparrow Pt. Small beam trawl, 10·5–16 m.

Didemnum studeri Hartmeyer. 2 specimens.
Alloeocarpa incrustans (Herdman). 3 specimens.
Pyura legumen (Lesson). 7 specimens.
Paramolgula gregaria (Lesson). 1 specimen.

Station 57. 16. v. 26. Port William, East Falkland Island, 5·5 cables S. 20° W. of Sparrow Pt. Small beam trawl, 15 m.

Pyura legumen (Lesson). 2 specimens.
Paramolgula gregaria (Lesson).

Station 58. 19. v. 26. Port Stanley, East Falkland Island. Mussel rake, 1–2 m.

Polyzoa reticulata (Herdman). 13 specimens.
Alloeocarpa incrustans (Herdman). 1 specimen.
Cnemidocarpa verrucosa (Lesson). 32 specimens.
Paramolgula gregaria (Lesson). 3 specimens.

Station 90. 10. vii. 26. Simon's Town, False Bay, South Africa. Basin of H.M. Dockyard. Hand net, 0–2 m.

Ascidia sydneiensis Stimpson. 1 specimen.
Pyura stolonifera (Heller). 2 specimens.

Station 91. 8. ix. 26. 0·5 mile off Roman Rock, False Bay, South Africa. Small rectangular net, sand, 35 m.

Agnesia glaciata Michaelsen. 1 specimen.
Molgula falsensis Millar. 6 specimens.

Station 123. 15. xii. 26. Off mouth of Cumberland Bay, South Georgia. From 4·1 miles N. 54° E. of Larsen Pt. to 1·2 miles S. 62° W. of Merton Rock. Large otter trawl, grey mud, 230–250 m.

Distaplia cylindrica (Lesson). 4 specimens.
Tylobranchion speciosum Herdman. 1 specimen.
Cnemidocarpa pfefferi (Michaelsen). 1 specimen.
C. verrucosa (Lesson). 1 specimen.
?*Styela magalhaensis* Michaelsen. 2 specimens.
Pyura georgiana Michaelsen. 8 specimens.
Molgula pedunculata Herdman. 20 specimens.
Ascopera gigantea Herdman. 5 specimens.

Station 140. 23. xii. 26. Stromness Harbour to Larsen Pt., South Georgia. From 54° 02′ S., 36° 38′ W. to 54° 11′ 30″ S., 36° 29′ W. Large otter trawl, green mud and stones, 122–136 m.

Synoicum georgianum Sluiter. 1 specimen.
Sycozoa georgiana (Michaelsen). 1 specimen.
Distaplia cylindrica (Lesson). 1 specimen.
Polyzoa reticulata (Herdman). 1 specimen.
Cnemidocarpa verrucosa (Lesson). 1 specimen.
Pyura discoveryi (Herdman). 42 specimens.
P. georgiana Michaelsen. 5 specimens.
Molgula pedunculata Herdman. 5 specimens.
Ascopera gigantea Herdman. 2 specimens.

Station 141. 29. xii. 26. East Cumberland Bay, South Georgia, 200 yards from shore, under Mt. Druse. Small beam trawl, mud, 17–27 m.

Polyzoa reticulata (Herdman). 2 specimens.
Alloeocarpa incrustans (Herdman). 1 specimen.

Station 142. 30. xii. 26. East Cumberland Bay, South Georgia. From 54° 11′ 30″ S., 36° 35′ W. to 54° 12′ S., 36° 29′ 30″ W. Large otter trawl, mud, 88–273 m.

Distaplia cylindrica (Lesson). 1 specimen.

Station 143. East Cumberland Bay, South Georgia. 54° 12′ S., 36° 29′ 30″ W. Large otter trawl, mud, 273 m.

Cnemidocarpa verrucosa (Lesson). 1 specimen.

Station 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. Large otter trawl, green mud and sand, 155–178 m.

Synoicum georgianum Sluiter. 3 specimens.
Tylobranchion speciosum Herdman. 5 specimens.
Pyura discoveryi (Herdman). 25 specimens.
P. georgiana Michaelsen. 5 specimens.
Molgula pedunculata Herdman. 7 specimens.

Station 145. 7. i. 27. Stromness Harbour, South Georgia. Between Grass Island and Tonsberg Pt. Small beam trawl, 26–35 m.

Sycozoa sigillinoides Lesson. 8 specimens.
Ascidia challengeri Herdman. 1 specimen.
Polyzoa opuntia Lesson. 1 specimen.
Alloeocarpa incrustans (Herdman). 2 specimens.
Pyura georgiana Michaelsen. 1 specimen.

Station 148. 9. i. 27. Off Cape Saunders, South Georgia. From 54° 03′ S., 36° 39′ W. to 54° 05′ S., 36° 36′ 30″ W. Large otter trawl, grey mud and stones, 132–148 m.

Distaplia cylindrica (Lesson). 4 specimens.
Polyzoa reticulata (Herdman). 1 specimen.
Cnemidocarpa verrucosa (Lesson). 2 specimens.
Pyura discoveryi (Herdman). 10 specimens.
P. georgiana Michaelsen. 1 specimen.

Station 149. 10. i. 27. Mouth of East Cumberland Bay, South Georgia. From 1·15 miles N. 76½° W. to 2·62 miles S. 11° W. of Merton Rock. Large otter trawl, mud, 200–234 m.

Synoicum georgianum Sluiter. 1 specimen.
Sycozoa georgiana (Michaelsen). 3 specimens.
Distaplia cylindrica (Lesson). 1 specimen.

Station 152. 17. i. 27. 53° 51′ 30″ S., 36° 18′ 30″ W. Large dredge, rock, 245 m.

Pyura discoveryi (Herdman). 3 specimens.
P. georgiana Michaelsen. 1 specimen.
Ascopera gigantea Herdman. 1 specimen.

Station 156. 20. i. 27. 53° 51′ S., 36° 21′ 30″ W. Large dredge, rock, 200–236 m.

Ascidia challengeri Herdman. 3 specimens.
Styela insinuosa (Sluiter). 1 specimen.
Pyura georgiana Michaelsen. 1 specimen.
Ascopera gigantea Herdman. 1 specimen.

Station 159. 21. i. 27. 53° 52′ 30″ S., 36° 08′ W. Large dredge, rock, 160 m.

Cnemidocarpa pfefferi (Michaelsen). 1 specimen.
C. verrucosa (Lesson). 4 specimens.
Pyura discoveryi (Herdman). 10 specimens.
Molgula malvinensis Ärnbäck. 3 specimens.
M. setigera Ärnbäck f. *georgiana* n. 4 specimens.
Ascopera gigantea Herdman. 1 specimen.

Station 160. 7. ii. 27. Near Shag Rocks, 53° 43′ 40″ S., 40° 57′ W. Large dredge, stones and rock, 177 m.

Aplidium variabile (Herdman). 21 specimens.
Tylobranchion speciosum Herdman. 2 specimens.
Ascidia challengeri Herdman. 2 specimens.
Cnemidocarpa verrucosa (Lesson). 1 specimen.
Pyura discoveryi (Herdman). 2 specimens.
Molgula pedunculata Herdman. 1 specimen.

Station 164. 18. ii. 27. East end of Normanna Strait, South Orkneys, near C. Hansen, Coronation Island. Small beam trawl, 24–36 m.

Aplidium radiatum (Sluiter). 1 specimen.
A. falklandicum sp.n. 7 specimens.
Distaplia colligans Sluiter. 1 specimen.
Ascidia challengeri Herdman. 2 specimens.

Station 170. 23. ii. 27. Off Cape Bowles, Clarence Island, 61° 25′ 30″ S., 53° 46′ W. Large dredge, rock, 342 m.

Aplidium circumvolutum (Sluiter). 4 specimens.
Pyura discoveryi (Herdman). 1 specimen.
P. bouvetensis (Michaelsen). 8 specimens.

Station 175. 2. iii. 27. Bransfield Strait, South Shetlands, 63° 17′ 20″ S., 59° 48′ 15″ W. Large dredge, mud, stones and gravel, 200 m.

Aplidium circumvolutum (Sluiter). 1 specimen.
Synoicum adareanum (Herdman). 2 specimens.
Pyura setosa (Sluiter). 1 specimen.
Molgula bacca Herdman. 1 specimen.

Station 177. 5. iii. 27. 27 miles south-west of Deception I., South Shetlands. 63° 17′ 30″ S., 61° 17′ W. Large dredge, mud, coarse sand and stones, 1080 m.

Pyura discoveryi (Herdman). 1 specimen.

Station 181. 12. iii. 27. Schollaert Channel, Palmer Archipelago, 64° 20′ S., 63° 01′ W. Large otter trawl, mud, 160–335 m.

Aplidium radiatum (Sluiter). 6 specimens.
Cystodytes dellechiajei f. *antarctica* (Sluiter). 1 specimen.
Caenagnesia bocki Ärnbäck. 1 specimen.
Pyura bouvetensis (Michaelsen). 2 specimens.
Bathypera splendens Michaelsen. 1 specimen.

Station 182. 14. iii. 27. Schollaert Channel, Palmer Archipelago, 64° 21′ S., 62° 58′ W. Large otter trawl, mud, 278–500 m.

Didemnum biglans (Sluiter). 1 specimen.
Caenagnesia bocki Ärnbäck. 4 specimens.

Station 186. 16. iii. 27. Fournier Bay, Anvers Island, Palmer Archipelago, 64° 25′ 30″ S., 63° 02′ W. Large dredge, mud, 295 m.

Aplidium radiatum (Sluiter). 1 specimen.

Station 187. 18. iii. 27. Neumayr Channel, Palmer Archipelago, 64° 48′ 30″ S., 63° 31′ 30″ W. Large otter trawl, mud, 259–354 m.

Didemnum biglans (Sluiter). 1 specimen.
Cnemidocarpa drygalskii (Hartmeyer). 3 specimens.
Pyura discoveryi (Herdman). 1 specimen.
P. squamata Hartmeyer. 1 specimen.
P. bouvetensis (Michaelsen). 49 specimens.

Station 189. 23. iii. 27. Port Lockroy, Wienke Island, Palmer Archipelago. Hand net, 0 m.

Distaplia cylindrica (Lesson). 1 specimen.

Station 190. 24. iii. 27. Bismarck Strait, Palmer Archipelago, 64° 56′ S., 65° 35′ W. Large dredge, stones, mud and rock, 93–126, and 315 m.

Aplidium circumvolutum (Sluiter). 3 specimens.
A. radiatum (Sluiter). 3 specimens.
A. caeruleum (Sluiter). 1 specimen.
Cystodytes dellechiajei f. *antarctica* (Sluiter). 1 specimen.
Cnemidocarpa verrucosa (Lesson). 1 specimen.
Pyura discoveryi (Herdman). 1 specimen.
P. bouvetensis (Michaelsen). 8 specimens.
Molgula pedunculata Herdman. 1 specimen.

Station 195. 30. iii. 27. Admiralty Bay, King George Island, South Shetlands, 62° 07′ S., 58° 28′ 30″ W. Medium otter trawl, mud and stones, 391 m.

Ascidia challengeri Herdman. 6 specimens.
Pyura bouvetensis (Michaelsen). 3 specimens.
Ascopera gigantea Herdman. 1 specimen.

Station 279. 10. vii. 27. Off Cape Lopez, French Congo. From 8·5 miles N. 71° E. to 15 miles N. 24° E. of Cape Lopez Lt. Large otter trawl, mud and fine sand, 58–67 m.

Ascidia interrupta Heller. 3 specimens.

Station 363. 26. ii. 30. 2·5 miles S. 80° E. of S.E. point of Zavodovski Island, South Sandwich Islands. Large dredge, 329–278 m.

?*Sycozoa georgiana* (Michaelsen). 7 specimens.

Station 366. 6. iii. 30. 4 cables south of Cook Island, South Sandwich Islands. Large dredge, black sand, 155–322 m.

Distaplia cylindrica (Lesson). 7 specimens.
Cnemidocarpa verrucosa (Lesson). 10 specimens.
Ascopera gigantea Herdman. 27 specimens.
Eugyra ärnbäckae sp.n. 46 specimens.

Station 370. 10. iii. 30. 2 miles north-east of Bristol Island, South Sandwich Islands. Large otter trawl, 18–80 m.

Cnemidocarpa verrucosa (Lesson). 1 specimen.

Station 371. 14. iii. 30. 1 mile east of Montagu Island, South Sandwich Islands. Large otter trawl, 99–161 m.

Tylobranchion speciosum Herdman. 2 specimens.
Cnemidocarpa verrucosa (Lesson). 1 specimen.
Ascopera gigantea Herdman. 5 specimens.

Station 388. 16. iv. 30. 56° 19′ 30″ S., 67° 09′ 45″ W. Large dredge, 121 m.

Styela schmitti van Name f. *simplex* n. 6 specimens.
Alloeocarpa incrustans (Herdman). 35 specimens.

Station 399. 18. v. 30. 1 mile S.E. of S.W. point of Gough Island. Large dredge, 141–102 m.

Didemnum studeri Hartmeyer. 1 specimen.

Station 474. 12. xi. 30. 1 mile west of Shag Rocks, South Georgia. Large dredge, 199 m.

Synoicum georgianum Sluiter. 1 specimen.
Polyzoa reticulata (Herdman). 1 specimen.
Alloeocarpa incrustans (Herdman). 2 specimens.
Cnemidocarpa verrucosa (Lesson). 1 specimen.
Styela insinuosa (Sluiter). 2 specimens.
Pyura discoveryi (Herdman). 11 specimens.
Molgula malvinensis Ärnbäck. 2 specimens.
M. setigera Ärnbäck f. *georgiana* n. 1 specimen.

Station 476. 12. xi. 30. 1 mile north of Shag Rocks, South Georgia. 1 m. tow-net, 165–0 m. (net touched bottom).

Distaplia colligans Sluiter. 1 specimen.

Station 599. 17. i. 31. 67° 08′ S., 69° 06′ 30″ W. Large dredge, 203 m.

Cnemidocarpa verrucosa (Lesson). 1 specimen.
Pyura bouvetensis (Michaelsen). 1 specimen.
Molgula pedunculata Herdman. 1 specimen.

Station 600. 17. i. 31. 67° 09′ S., 69° 27′ W. Large otter trawl, 501–527 m.

Pyura bouvetensis (Michaelsen). 3 specimens.

Station 652. 14. iii. 31. Burdwood Bank, 54° 04′ S., 61° 40′ W. Large otter trawl, 171–169 m. Large dredge, 164 m.

Aplidium fuegiense Cunningham. 1 specimen.
A. falklandicum sp.n. 3 specimens.
Sycozoa sigillinoides Lesson. 1 specimen.

Station 929. 16. viii. 32. 34° 21′ S., 172° 48′ E. to 34° 22′ S., 172° 49′ 48″ E. Large otter trawl, 58–55 m.

Sycozoa anomala sp.n. 4 specimens.
Clavelina claviformis (Herdman). 2 specimens.

Station 934. 17. vii. 32. 34° 11′ 36″ S., 172° 10′ 54″ E. to 34° 11′ 24″ S., 172° 10′ 18″ E. Large otter trawl, 98–92 m.

Protopolyclinum pedunculatum gen.n., sp.n. 4 specimens.
Ritterella vestita sp.n. 1 specimen.
Podoclavella kottae sp.n. 1 specimen.
Cystodytes dellechiajei (Della Valle). 4 specimens.
?*Botryllus separatus* Sluiter. 1 specimen.

Station 935. 17. viii. 32. 34° 11′ 30″ S., 172° 08′ 30″ E. to 34° 11′ 54″ S., 172° 08′ 30″ E. Large dredge, 84 m.

?*Aplidium quadrisulcatum* sp.n. 4 specimens.
A. seeligeri sp.n. 1 specimen.
Synoicum kuranui Brewin. 6 specimens.
Leptoclinides diemenensis Michaelsen. 1 specimen.
Hypsistozoa fasmeriana (Michaelsen). 1 specimen.
Atapozoa marshi Brewin. 2 specimens.
Cystodytes dellechiajei (Della Valle). 3 specimens.

Station 936. 18. viii. 32. 35° 03′ 30″ S., 172° 58′ 12″ E. to 35° 05′ 24″ S., 172° 58′ 42″ E. Large otter trawl, 50–57 m.

Eugyra brewinae sp.n. 17 specimens.

Station 939. 18. viii. 32. 35° 49′ 36″ S., 173° 27′ E. to 35° 51′ 36″ S., 173° 28′ 54″ E. Large otter trawl, 87 m.

Aplidium quadrisulcatum sp.n. 5 specimens.
Agnesia glaciata Michaelsen. 4 specimens.

Station 941. 20. viii. 32. 40° 51′ 24″ S., 174° 48′ 12″ E. to 40° 55′ 48″ S., 174° 46′ 42″ E. Large dredge, 128 m.

Aplidium seeligeri sp.n. 1 specimen.
Aplidiopsis discoveryi sp.n. 1 specimen.

Station 1113. 5. ii. 33. 63° 04′ 30″ S., 62° 15′ W. Tow-net, 275–130 m.

Distaplia colligans Sluiter. 1 specimen.

Station 1159. 17. iii. 33. 55° 48′ 42″ S., 14° 45′ 12″ E. Tow-net, 230–0 m.

Cnemidocarpa verrucosa (Lesson). 1 specimen.

Station 1230. 23. xii. 33. 6·7 miles N. 62° W. from Dungeness Lt., Magellan Strait. Russell's bottom tow-net, 27 m.

Sycozoa sigillinoides Lesson. 5 specimens.
Polyzoa opuntia Lesson. 13 specimens.
P. reticulata (Herdman). 1 specimen.
Alloeocarpa incrustans (Herdman). 1 specimen.
Paramolgula gregaria (Lesson). 4 specimens.

Station 1563. 7. iv. 35. 46° 48′ 24″ S., 37° 49′ 12″ E. Large dredge, 113–99 m. and 101–106 m.

?*Aplidium caeruleum* (Sluiter). 1 specimen.
Pyura jacatrensis (Sluiter). 1 specimen.
Molgula setigera Ärnbäck f. *marioni* n. 1 specimen.

Station 1652. 23. i. 36. 75° 56′ 12″ S., 178° 35′ 30″ W. Harvey's phytoplankton net, 567 m.

Ascidia challengeri Herdman. 3 specimens.
Corella eumyota Traustedt. 2 specimens.

Station 1660. 27. i. 36. 74° 46′ 24″ S., 178° 23′ 24″ E. Large otter trawl, 351 m.

Synoicum adareanum (Herdman). 5 specimens.
Ascidia challengeri Herdman. 1 specimen.

Station 1686. 4. iii. 36. 38° 16′ 6″ S., 144° 40′ 12″ E. Queenscliffe Jetty, Port Philip, Victoria, Australia. Mussel rake, 0 m.

Podoclavella cylindrica (Quoy & Gaimard). 1 specimen.
Ascidia sydneiensis Stimpson. 1 specimen.
Amphicarpa diptycha (Hartmeyer). 1 specimen.
Herdmania momus (Savigny). 1 specimen.
Molgula sabulosa (Quoy & Gaimard). 1 specimen.

Station 1873. 13. xi. 36. 61° 20′ 48″ S., 54° 04′ 12″ W. Russell rectangular dredge, 210–180 m.

Ascopera gigantea Herdman. 1 specimen.

Station 1900. 27–28. xi. 36. 49° 49′ 30″ S., 66° 14′ 24″ W. to 49° 49′ 24″ S., 66° 14′ 48″ W. 1 m. tow-net, 0–5 m.

Distaplia cylindrica (Lesson). 1 specimen.

Station 1902. 28. xi. 36. 49° 48′ S., 67° 39′ 30″ W. 4 miles S. 32° E. of Cape San Fransisco de Paula Lt. Large otter trawl, 50–80 m.

Aplidium falklandicum sp.n. 4 specimens.
Polyzoa opuntia Lesson. 13 specimens.
Paramolgula gregaria (Lesson). 4 specimens.

Station 1906. 29–30. xi. 36. 53° 54′ 36″ S., 63° 58′ 6″ W. 1 m. tow-net, 0–5 m.

Distaplia cylindrica (Lesson). 2 specimens.

Station 1941. 29. xii. 36. Leith Harbour, South Georgia. Small dredge, 38 and 55–22 m.

Synoicum georgianum Sluiter. 1 specimen.
Alloeocarpa incrustans (Herdman). 2 specimens.
Eugyra kerguelenensis Herdman. 77 specimens.

Station 1948. 4. i. 37. 60° 49′ 24″ S., 52° 40′ W. Russell rectangular dredge, 490–610 m.

Pyura discoveryi (Herdman). 1 specimen.

Station 1952. 11. i. 37. Between Penguin Island and Lion's Rump, King George Island, South Shetlands. Russell rectangular dredge, 367–383 m.

Aplidium caeruleum Sluiter. 2 specimens.
Cnemidocarpa pfefferi (Michaelsen). 1 specimen.
C. verrucosa (Lesson). 1 specimen.
Pyura bouvetensis (Michaelsen). 3 specimens.

Station 1955. 29. i. 37. 61° 35′ 6″ S., 57° 23′ 18″ W. Russell rectangular dredge, 440–410 m.

Pyura bouvetensis (Michaelsen). 1 specimen.

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Station WS 25. 17. xii. 26. Undine Harbour (North), South Georgia. Small beam trawl, mud and sand, 18–27 m.

Aplidium falklandicum sp.n. 1 specimen.
Ascidia translucida Herdman. 2 specimens.
Cnemidocarpa verrucosa (Lesson). 1 specimen.
Polyzoa reticulata (Herdman). 1 specimen.

Station WS 27. 19. xii. 26. 53° 55′ S., 38° 01′ W. 1 m. tow-net, gravel, 104 and 107 m.

Aplidium falklandicum sp.n. 1 specimen.
Synoicum giardi (Herdman). 1 specimen.
Tylobranchion speciosum Herdman. 18 specimens.
Ascidia challengeri Herdman. 1 specimen.
Polyzoa reticulata (Herdman). 1 specimen.
Molgula pedunculata Herdman. 1 specimen.

Station WS 33. 21. xii. 26. 54° 59′ S., 35° 24′ W. 1 m. horizontal tow-net 0–5 m., 1 m. horizontal tow-net, grey mud and stones, 130 m.

Synoicum adareanum (Herdman). 1 specimen.
?*Sycozoa georgiana* (Michaelsen). 1 specimen.
Distaplia cylindrica (Lesson). 1 specimen.

Station WS 62. 19. i. 27. Wilson Harbour, South Georgia. Small beam trawl, 26–83 m.

Pyura georgiana Michaelsen. 3 specimens.

Station WS 65. 21. i. 27. Undine Harbour (North), South Georgia. Shore collection.

Alloeocarpa incrustans (Herdman). 1 specimen.

Station WS 71. 23. ii. 27. 6 miles N. 60° E. of Cape Pembroke Lt., East Falkland Island. Commercial otter trawl, 82–80 m.

Aplidium fuegiense Cunningham. 4 specimens.
Polyzoa opuntia Lesson. 6 specimens.
P. reticulata (Herdman). 1 specimen.
Alloeocarpa incrustans (Herdman). 7 specimens.
Cnemidocarpa nordenskjöldi (Michaelsen). 5 specimens.
C. verrucosa (Lesson). 10 specimens.
Pyura legumen (Lesson). 3 specimens.
Paramolgula gregaria (Lesson). 6 specimens.

Station WS 72. 5. iii. 27. 51° 07′ S., 57° 34′ W. Commercial otter trawl, 95 m.

Aplidium variabile (Herdman). 3 specimens.
A. falklandicum sp.n. 3 specimens.
Paramolgula gregaria (Lesson). 6 specimens.

Station WS 73. 6. iii. 27. From 51° 02′ S., 58° 55′ W. to 51° S., 58° 53′ W. Commercial otter trawl, 121–130 m.

Aplidium fuegiense Cunningham. 26 specimens.
A. falklandicum sp.n. 1 specimen.
Paramolgula gregaria (Lesson). 9 specimens.

Station WS 75. 10. iii. 27. From 51° S., 60° 30′ W. to 51° 02′ 42″ S., 60° 31′ 42″ W. Commercial otter trawl, 64–104 m.

Polyzoa opuntia Lesson. 1 specimen.

Station WS 76. 11. iii. 27. From 51° S., 62° W. to 51° S., 62° 04′ 36″ W. Commercial otter trawl, fine dark sand, 205–207 m.

Aplidium fuegiense Cunningham. 4 specimens.

Station WS 79. 13. iii. 27. From 51° S., 65° W. to 51° 03′ S., 64° 59′ W. Commercial otter trawl, fine dark sand, 132–131 m.

Aplidium fuegiense Cunningham. 2 specimens.
A. falklandicum sp.n. 4 specimens.
Paramolgula gregaria (Lesson). 5 specimens.

Station WS 80. 14. iii. 27. From 50° 58′ S., 63° 39′ W. to 50° 55′ 30″ S., 63° 36′ W. Commercial otter trawl, fine dark sand, 152–156 m.

Aplidium fuegiense Cunningham. 1 specimen.

Station WS 81. 19. iii. 27. 8 miles N. 11° W. of North Island, Falkland Islands. From 51° 03 ′S., 61° 15′ W. to 51° 30′ 30″ S., 61° 10′ W. Commercial otter trawl, sand, 81–82 m.

Aplidium falklandicum sp.n. 4 specimens.
Cnemidocarpa verrucosa (Lesson). 11 specimens.

Station WS 82. 21. iii. 27. From 54° 05′ S., 57° 45′ W. to 54° 07′ S., 57° 47′ 30″ W. Commercial otter trawl, 140–144 m.

Polyzoa reticulata (Herdman). 1 specimen.

Station WS 83. 24. iii. 27. 14 miles S. 64° W. of George Island, East Falkland Island. From 52° 28′ S., 60° 06′ W. to 52° 30′ S., 60° 09′ 30″ W. Commercial otter trawl, fine green sand and shells, 137–129 m.

Aplidium fuegiense Cunningham. 4 specimens.

Station WS 84. 24. iii. 27. 7½ miles S. 9° W. of Sea Lion Island, East Falkland Island. From 52° 33′ S., 59° 08′ W. to 52° 34′ 30″ S., 59° 11′ W. Commercial otter trawl, coarse sand, shells and stones, 75–74 m.

Aplidium fuegiense Cunningham. 3 specimens.
A. falklandicum sp.n. 3 specimens.
Trididemnum auriculatum Michaelsen. 1 specimen.
Sycozoa sigillinoides Lesson. 1 specimen.
Alloeocarpa incrustans (Herdman). 1 specimen.
Pyura legumen (Lesson). 1 specimen.

Station WS 85. 25. iii. 27. 8 miles S. 66° E. of Lively Island, East Falkland Island. From 52° 09′ S., 58° 14′ W. to 52° 08′ S., 58° 09′ W. Commercial otter trawl, sand and shells, 79 m.

Aplidium fuegiense Cunningham. 2 specimens.
Sycozoa sigillinoides Lesson. 1 specimen.
Polyzoa reticulata (Herdman). 13 specimens.
Cnemidocarpa verrucosa (Lesson). 1 specimen.

Station WS 86. 3. iv. 27. From 53° 53′ S., 60° 37′ W. to 53° 54′ S., 60° 30′ W. Commercial otter trawl, sand, shells and stones, 151–147 m.

Aplidium fuegiense Cunningham. 3 specimens.
A. falklandicum sp.n. 1 specimen.
Polyzoa opuntia Lesson. 1 specimen.
Alloeocarpa incrustans (Herdman). 1 specimen.

Station WS 88. 6. iv. 27. From 54° 00′ S., 65° 00′ W. to 54° 00′ S., 64° 55′ W. Commercial otter trawl, 118 m.

Paramolgula gregaria (Lesson). 1 specimen.

Station WS 89. 7. iv. 27. 9 miles N. 21° E. of Arenas Pt. Lt., Tierra del Fuego. From 53° 01′ S., 68° 07′ W. to 52° 59′ 30″ S., 68° 06′ W. Commercial otter trawl, mud, gravel and stones, 23–21 m.

Pyura legumen (Lesson). 1 specimen.
Paramolgula gregaria (Lesson). 5 specimens.

Station WS 90. 7. iv. 27. 13 miles N. 83° E. of Cape Virgins Lt., Argentine Republic. From 52° 18′ S., 68° W. to 52° 19′ 30″ S., 67° 57′ W. Commercial otter trawl, fine dark sand, 82–81 m.

Aplidium fuegiense Cunningham. 4 specimens.
A. falklandicum sp.n. 3 specimens.
Sycozoa sigillinoides Lesson. 1 specimen.
Distaplia cylindrica (Lesson). 1 specimen.
Pyura legumen (Lesson). 1 specimen.

Station WS 91. 8. iv. 27. From 52° 54′ 30″ S., 64° 39′ W. to 52° 53′ S., 64° 36′ W. Commercial otter trawl, fine dark sand and shells, 191–205 m.

Aplidium fuegiense Cunningham. 2 specimens.
A. variabile (Herdman). 15 specimens.
A. falklandicum sp.n. 4 specimens.

Station WS 92. 8. iv. 27. From 52° S., 65° W. to 51° 57′ S., 65° 02′ W. Commercial otter trawl, fine dark sand and stones, 145–143 m.

Aplidium fuegiense Cunningham. 1 specimen.
Sycozoa sigillinoides Lesson. 11 specimens.

Station WS 93. 9. iv. 27. 7 miles S. 80° W. of Beaver Island, West Falkland Island. From 51° 51′ S., 61° 30′ W. to 51° 54′ S., 61° 30′ W. Commercial otter trawl, grey sand, 133–130 m.

Aplidium circumvolutum (Sluiter). 1 specimen.
A. fuegiense Cunningham. 3 specimens.
A. variabile (Herdman). 1 specimen.
A. falklandicum sp.n. 1 specimen.

Station WS 94. 16. iv. 27. From 50° S., 65° W. to 50° S., 64° 55′ 30″ W. Commercial otter trawl, fine dark sand, 110–126 m.

Aplidium fuegiense Cunningham. 2 specimens.
Cnemidocarpa nordenskjöldi (Michaelsen). 2 specimens.

Station WS 95. 17. iv. 27. From 48° 57′ S., 64° 45′ W. to 48° 59′ 30″ S., 64° 45′ W. Commercial otter trawl, fine dark sand, stones and shells, 109–108 m.

Aplidium fuegiense Cunningham. 2 specimens.
Sycozoa sigillinoides Lesson. 1 specimen.
Polyzoa opuntia Lesson. 1 specimen.

Station WS 99. 19. iv. 27. From 49° 41′ S., 59° 14′ W. to 49° 43′ S., 59° 15′ W. Commercial otter trawl, fine dark sand, 251–225 m.

Didemnum trivolutum sp.n. 3 specimens.

Station WS 108. 25. iv. 27. From 48° 30′ S., 63° 36′ W. to 48° 31′ 30″ S., 63° 31′ 30″ W. Commercial otter trawl, fine dark sand, 118–120 m.

Aplidium fuegiense Cunningham. 7 specimens.
A. falklandicum sp.n. 5 specimens.

Station WS 154. 26. ii. 28. 54° S., 36° 52′ W. Tow-net, 115–0 m.

Aplidium falklandicum sp.n. 1 specimen.

Station WS 182. 8. iii. 28. 55° 30′ S., 34° 50′ W. Tow-net, 750–520 m.

Aplidium falklandicum sp.n. 1 specimen.

Station WS 210. 29. v. 28. 50° 17′ S., 60° 06′ W. Commercial otter trawl, green sand, 161 m.

Paramolgula gregaria (Lesson). 2 specimens.

Station WS 214. 31. v. 28. 48° 25′ S., 60° 40′ W. Commercial otter trawl, fine dark sand, 208–219 m.

Sycozoa sigillinoides Lesson. 2 specimens.

Station WS 215. 31. v. 28. 47° 37′ S., 60° 50′ W. Commercial otter trawl, fine green sand, 219–146 m.

Sycozoa sigillinoides Lesson. 2 specimens.

Station WS 216. 1. vi. 28. 47° 37′ S., 60° 50′ W. Commercial otter trawl, fine sand, 219–133 m.

Alloeocarpa incrustans (Herdman). 1 specimen.

Station WS 219. 3. vi. 28. 47° 06′ S., 62° 12′ W. Commercial otter trawl, dark sand, 116–114 m.

Aplidium fuegiense Cunningham. 4 specimens.
A. variabile (Herdman). 5 specimens.
A. falklandicum sp.n. 11 specimens.

Station WS 220. 3. vi. 28. 47° 56′ S., 62° 38′ W. Commercial otter trawl, brown sand, 108–104 m.

Aplidium fuegiense Cunningham. 1 specimen.
A. variabile (Herdman). 1 specimen.
A. falklandicum sp.n. 2 specimens.
Sycozoa sigillinoides Lesson. 2 specimens.

Station WS 221. 4. vi. 28. 48° 23′ S., 65° 15′ W. Commercial otter trawl, brown sand, mud, pebbles, large stones and shells, 76–91 m.

Polyzoa opuntia Lesson. 2 specimens.
Cnemidocarpa nordenskjöldi (Michaelsen). 1 specimen.

Station WS 222. 8. vi. 28. 48° 23′ S., 65° W. Commercial otter trawl, coarse brown sand and shells, 100–106 m.

Aplidium falklandicum sp.n. 6 specimens.
Paramolgula gregaria (Lesson). 1 specimen.

Station WS 226. 10. vi. 28. 49° 20′ S., 62° 30′ W. Commercial otter trawl, green sand, 144–152 m.

Sycozoa sigillinoides Lesson. 14 specimens.

Station WS 229. 1. vii. 28. 50° 35′ S., 57° 20′ W. Commercial otter trawl, fine green sand, 210–271 m.

Aplidium stanleyi sp.n. 11 specimens.

Station WS 233. 5. vii. 28. 49° 25′ S., 59° 45′ W. Commercial otter trawl, fine green sand, 185–175 m.

Aplidium fuegiense Cunningham. 1 specimen.

Station WS 235. 6. vii. 28. 47° 56′ S., 61° 10′ W. Commercial otter trawl, dark green sand, 155 m.

Aplidium variabile (Herdman). 1 specimen.

Station WS 237. 7. vii. 28. 46° S., 60° 05′ W. Commercial otter trawl, coarse brown sand and shells, 150–256 m.

Aplidium variabile (Herdman). 1 specimen.
Sycozoa sigillinoides Lesson. 1 specimen.

Station WS 239. 15. vii. 28. 51° 10′ S., 62° 10′ W. Commercial otter trawl, coarse dark sand, 196–193 m.

Aplidium falklandicum sp.n. 2 specimens.
Sycozoa sigillinoides Lesson. 1 specimen.

Station WS 243. 17. vii. 28. 51° 06′ S., 64° 30′ W. Commercial otter trawl, coarse dark sand, 144–141 m.

Aplidium falklandicum sp.n. 5 specimens.
Sycozoa sigillinoides Lesson. 2 specimens.
Tylobranchion speciosum Herdman. 1 specimen.
Cnemidocarpa nordenskjöldi (Michaelsen). 7 specimens.
Paramolgula gregaria (Lesson). 4 specimens.

Station WS 244. 18. vii. 28. 52° S., 62° 40′ W. Commercial otter trawl, fine dark sand and mud, 253–247 m.

Aplidium circumvolutum (Sluiter). 13 specimens.
A. falklandicum sp.n. 6 specimens.
Sycozoa sigillinoides Lesson. 8 specimens.

Station WS 245. 18. vii. 28. 52° 36′ S., 63° 40′ W. Commercial otter trawl, dark green sand, 304–290 m.

Sycozoa sigillinoides Lesson. 28 specimens.

Station WS 246. 19. vii. 28. 52° 25′ S., 61° W. Commercial otter trawl, coarse green sand and pebbles, 267–208 m.

Didemnum studeri Hartmeyer. 2 specimens.

Station WS 247. 19. vii. 28. 52° 40′ S., 60° 05′ W. Large heavy dredge, rocks, 172 m.

Aplidium fuegiense Cunningham. 1 specimen.
Alloeocarpa incrustans (Herdman). 1 specimen.
Cnemidocarpa nordenskjöldi (Michaelsen). 11 specimens.

Station WS 249. 20. vii. 28. 52° 10′ S., 57° 30′ W. Large heavy dredge, fine brown and green sand, shells and stones, 166 m.

Aplidium fuegiense Cunningham. 1 specimen.

Station WS 567. 6. iii. 31. 53° 54′ 15″ S., 37° 05′ 30″ W. 70 cm. tow-net, 145 m.

Pyura georgiana Michaelsen. 1 specimen.

Station WS 582. 30. iv. 31. 53° 42′ 30″ S., 70° 55′ W. Hand lines, 12 m.

Cnemidocarpa nordenskjöldi (Michaelsen). 1 specimen.

Station WS 583. 2. v. 31. 53° 39′ S., 70° 54′ 30″ W., Magellan Strait. Small beam trawl, 14–78 m.

Aplidium fuegiense Cunningham. 2 specimens.
Cnemidocarpa nordenskjöldi (Michaelsen). 2 specimens.

Station WS 742. 5. ix. 31. 38° 22′ S., 73° 41′ W. Small beam trawl, 47–35 m.

Molgula platei Hartmeyer. 27 specimens.

Station WS 756. 10. x. 31. From 50° 53′ S., 60° W. to 50° 56′ 18″ S., 59° 56′ W., to 50° 59′ 30″ S., 59° 52′ W. Commercial otter trawl, black gravel, green mud and sand, 104–119 m.

Paramolgula gregaria (Lesson). 1 specimen.

Station WS 764. 17. x. 31. From 44° 40′ S., 62° W. to 44° 36′ 30″ S., 61° 57′ W., to 44° 41′ S., 61° 52′ W. Commercial otter trawl, fine green sand, 110–104 m.

Aplidium fuegiense Cunningham. 6 specimens.
A. falklandicum sp.n. 7 specimens.

Station WS 765. 17. x. 31. From 45° 06′ S., 60° 30′ W., to 45° 08′ S., 60° 26′ 30″ W. Commercial otter trawl, brown and green mud and sand, 113–119 m.

Aplidium falklandicum sp.n. 2 specimens.
Sycozoa sigillinoides Lesson. 24 specimens.
Distaplia cylindrica (Lesson). 1 specimen.
Alloeocarpa incrustans (Herdman). 2 specimens.

Station WS 771. 29. x. 31. From 42° 40′ S., 60° 32′ W. to 42° 43′ 30″ S., 60° 30′ W. Commercial otter trawl, dark green sand, 90 m.

Aplidium fuegiense Cunningham. 1 specimen.
A. variabile (Herdman). 1 specimen.
A. falklandicum sp.n. 1 specimen.

Station WS 772. 30. x. 31. From 45° 13′ S., 60° W. to 45° 13′ 48″ S., 60° 00′ 30″ W. Commercial otter trawl, grey sand, 309–163 m.

Aplidium variabile (Herdman). 2 specimens.
Sycozoa sigillinoides Lesson. 9 specimens.

Station WS 774. 1. xi. 31. From 47° 09′ S., 62° W. to 47° 07′ S., 62° 04′ W. Commercial otter trawl, dark green sand and mud, 139–144 m.

Aplidium falklandicum sp.n. 2 specimens.

Station WS 775. 2. xi. 31. From 46° 44′ 30″ S., 63° 30′ W. to 46° 45′ S., 63° 36′ W. Commercial otter trawl, gravel and fine grey sand, 115–110 m.

Aplidium circumvolutum (Sluiter). 3 specimens.
A. fuegiense Cunningham. 1 specimen.
A. falklandicum sp.n. 1 specimen.
Sycozoa sigillinoides Lesson. 3 specimens.
Agnesia glaciata Michaelsen. 3 specimens.

Station WS 776. 3. xi. 31. From 46° 19′ S., 65° W. to 46° 17′ 30″ S., 65° 04′ 30″ W. Commercial otter trawl, grey mud and sand, 110–99 m.

Aplidium fuegiense Cunningham. 1 specimen.
Styela magalhaensis Michaelsen. 1 specimen.
Paramolgula gregaria (Lesson). 1 specimen.

Station WS 781. 6. xi. 31. From 50° 29′ S., 58° 52′ W. to 50° 31′ S., 58° 48′ W. Commercial otter trawl, dark green sand and mud, 148 m.

Aplidium fuegiense Cunningham. 7 specimens.
A. variabile (Herdman). 6 specimens.
Paramolgula gregaria (Lesson). 2 specimens.

Station WS 782. 4. xii. 31. From 50° 30′ S., 58° 19′ W. to 50° 28′ 30″ S., 58° 23′ 30″ W. to 50° 27′ S., 58° 31′ W. Commercial otter trawl, green sand and rocks, 141–146 m.

Aplidium circumvolutum (Sluiter). 1 specimen.
A. variabile (Herdman). 6 specimens.
A. falklandicum sp.n. 1 specimen.
Paramolgula gregaria (Lesson). 3 specimens.

Station WS 783. 5. xii. 31. From 50° 03′ 30″ S., 60° 08′ W. to 50° 02′ S., 60° 12′ W. to 50° 03′ 30″ S., 60° 16′ W. Commercial otter trawl, 165–0 m. Conical dredge, 157 m.

Aplidium circumvolutum (Sluiter). 26 specimens.
A. variabile (Herdman). 2 specimens.

Station WS 784. 5. xii. 31. From 49° 48′ 30″ S., 61° 03′ W. to 49° 47′ S., 61° 07′ W. Commercial otter trawl, dark green sand and rocks, 170–164 m.

Aplidium circumvolutum (Sluiter). 1 specimen.
Sycozoa sigillinoides Lesson. 1 specimen.
Cnemidocarpa nordenskjöldi (Michaelsen). 5 specimens.
Paramolgula gregaria (Lesson). 2 specimens.

Station WS 785. 6. xii. 31. From 49° 27′ S., 62° 32′ W. to 49° 26′ S., 62° 36′ W. to 49° 24′ 30″ S., 62° 39′ W. to 49° 23′ S., 62° 43′ 30″ W. Commercial otter trawl, dark green sand, 150–147 m.

Sycozoa sigillinoides Lesson. 7 specimens.

Station WS 787. 7. xii. 31. From 48° 44′ S., 65° 24′ 30″ W. to 48° 48′ S., 65° 25′ W. Commercial otter trawl, coarse brown speckled sand, 106–110 m.

Aplidium fuegiense Cunningham. 15 specimens.
A. variabile (Herdman). 1 specimen.
A. falklandicum sp.n. 5 specimens.
Distaplia cylindrica (Lesson). 3 specimens.

Station WS 788. 13. xii. 31. From 45° 06′ 30″ S., 64° 56′ W. to 45° 07′ 30″ S., 64° 52′ W. Commercial otter trawl, speckled grey mud, sand and gravel, 82–88 m.

Polyzoa opuntia Lesson. 1 specimen.
Pyura legumen (Lesson). 1 specimen.

Station WS 791. 14. xii. 31. From 45° 38′ S., 62° 57′ W. to 45° 39′ 30″ S., 62° 53′ W. to 45° 44′ S., 62° 37′ W. Commercial otter trawl, green sand, 97–95 m., 95–101 m.

Aplidium fuegiense Cunningham. 15 specimens.
A. variabile (Herdman). 3 specimens.
A. falklandicum sp.n. 12 specimens.
Paramolgula gregaria (Lesson). 1 specimen.

Station WS 792. 15. xii. 31. From 45° 49′ S., 62° 23′ W. to 45° 50′ S., 62° 18′ 30″ W. to 45° 54′ 30″ S., 62° 04′ W. Commercial otter trawl, dark green sand and rocks, 102–106 m.

Aplidium fuegiense Cunningham. 7 specimens.
A. falklandicum sp.n. 8 specimens.

Station WS 793. 15. xii. 31. From 45° 52′ 18″ S., 61° 37′ W. to 45° 53′ 48″ S., 61° 33′ W. Commercial otter trawl, rocks, 108–111 m.

Aplidium variabile (Herdman). 8 specimens.
A. falklandicum sp.n. 4 specimens.

Station WS 794. 17. xii. 31. From 46° 11′ 48″ S., 61° 01′ W. to 46° 13′ 30″ S., 60° 57′ 30″ W. Commercial otter trawl, 123–126 m.

Aplidium variabile (Herdman). 1 specimen.
Synoicum georgianum Sluiter. 2 specimens.

Station WS 796. 21. xii. 31. From 47° 51′ S., 63° 43′ W. to 47° 56′ S., 63° 22′ W. Commercial otter trawl, 106–113 and 108–112 m.

Aplidium variabile (Herdman). 2 specimens.
A. falklandicum sp.n. 1 specimen.
Paramolgula gregaria (Lesson). 8 specimens.

Station WS 797. 20. xii. 31. From 47° 44′ S., 64° 22′ W. to 47° 45′ 12″ S., 64° 18′ W. to 47° 50′ 18″ S., 63° 57′ W. Commercial otter trawl, 115–111 m.

Aplidium fuegiense Cunningham. 9 specimens.
A. variabile (Herdman). 6 specimens.
Paramolgula gregaria (Lesson). 3 specimens.

Station WS 798. 20. xii. 31. From 47° 31′ 30″ S., 62° 05′ W. to 47° 32′ 30″ S., 64° 58′ W. Commercial otter trawl, pebbles, shells and sand, 49–66 m.

Polyzoa opuntia Lesson. 7 specimens.
Paramolgula gregaria (Lesson). 3 specimens.

Station WS 799. 21. xii. 31. From 48° 03′ 30″ S., 62° 50′ 18″ W. to 48° 05′ S., 62° 46′ W. to 48° 10′ S., 62° 31′ W. (*a*) Hand net, 0 m.; (*b*) commercial otter trawl, dark green sand, 141–137 m.

Aplidium variabile (Herdman). 1 specimen.
Sycozoa sigillinoides Lesson. 6 specimens.

Station WS 800. 21–22. xii. 31. From 48° 15′ S., 62° 11′ 48″ W. to 48° 16′ 30″ S., 62° 08′ W. to 48° 21′ 30″ S., 61° 48′ W. Commercial otter trawl, dark sand and shells, 137–139 m.

Aplidium fuegiense Cunningham. 3 specimens.
Sycozoa sigillinoides Lesson. 2 specimens.

Station WS 801. 22. xii. 31. From 48° 25′ 30″ S., 61° 30′ W. to 48° 27′ S., 61° 26′ W. Commercial otter trawl, dark sand, 165 m.

Aplidium fuegiense Cunningham. 1 specimen.

Station WS 805. 6. i. 32. From 50° 11′ S., 63° 37′ W. to 50° 09′ 30″ S., 63° 31′ W. Commercial otter trawl, coarse dark speckled sand, 148–150 m.

Cnemidocarpa nordenskjöldi (Michaelsen). 11 specimens.

Station WS 807. 7. i. 32. From 49° 51′ S., 65° 01′ W. to 49° 50′ S., 65° 05′ W. Commercial otter trawl, dark sand, 124–126 m.

Aplidium fuegiense Cunningham. 2 specimens.
A. falklandicum sp.n. 1 specimen.

Station WS 808. 8. i. 32. From 49° 41′ S., 65° 40′ W. to 49° 39′ 30″ S., 65° 44′ W. Commercial otter trawl, brown and green sand, 110–106 m.

Aplidium fuegiense Cunningham. 6 specimens.
A. variabile (Herdman). 3 specimens.
Paramolgula gregaria (Lesson). 1 specimen.

Station WS 809. 8. i. 32. From 49° 29′ S., 62° 27′ W. to 49° 27′ 30″ S., 66° 31′ W. to 49° 32′ 30″S., 66° 51′ 30″ W. Commercial otter trawl, brown speckled sand, 104–101 m.

Aplidium fuegiense Cunningham. 1 specimen.

Station WS 811. 10. i. 32. From 51° 22′ S., 68° 03′ W. to 51° 27′ 30″ S., 67° 43′ W. Commercial otter trawl, 99 m.

Aplidium fuegiense Cunningham. 1 specimen.
A. variabile (Herdman). 2 specimens.
Didemnum trivolutum sp.n. 1 specimen.
Pyura legumen (Lesson). 2 specimens.

Station WS 813. 13. i. 32. From 51° 34′ 30″ S., 67° 18′ 30″ W. to 51° 36′ S., 67° 14′ W. Commercial otter trawl, dark speckled sand, 106–102 m.

Aplidium fuegiense Cunningham. 1 specimen.
A. variabile (Herdman). 107 specimens.
A. falklandicum sp.n. 2 specimens.

Station WS 814. 13. i. 32. From 51° 44′ 30″ S., 66° 38′ W. to 51° 46′ S., 66° 42′ W. Commercial otter trawl, speckled sand, 112–119 m.

Sycozoa sigillinoides Lesson. 2 specimens.

Station WS 816. 14. i. 32. From 52° 09′ 30″ S., 64° 58′ W. to 52° 10′ S., 64° 54′ W. Commercial otter trawl, shingle, 150 m.

Aplidium variabile (Herdman). 3 specimens.
Sycozoa sigillinoides Lesson. 2 specimens.

Station WS 818. 17. i. 32. From 52° 30′ 30″ S., 63° 27′ W. to 52° 32′ S., 63° 23′ W. to 52° 37′ S., 63° 02′ W. Commercial otter trawl, dark speckled sand, 272–278 m.

Sycozoa sigillinoides Lesson. 5 specimens.

Station WS 819. 17. i. 32. From 52° 41′ 18″ S., 62° 41′ W. to 52° 42′ 30″ S., 62° 38′ W. to 52° 47′ 30″ S., 62° 17′ W. Commercial otter trawl, dark speckled sand, 313–329 m.

Sycozoa sigillinoides Lesson. 1 specimen.

Station WS 823. 19. i. 32. From 52° 12′ 30″ S., 60° 02′ W. to 52° 16′ 30″ S., 60° W. Commercial otter trawl, green grey fine sand, 80–95 m.

Polyzoa reticulata (Herdman). 1 specimen.
Cnemidocarpa verrucosa (Lesson). 1 specimen.
Paramolgula gregaria (Lesson). 1 specimen.

Station WS 824. 19. i. 32. From 52° 31′ S., 58° 29′ W. to 52° 27′ 30″ S., 58° 28′ 30″ W. Commercial otter trawl, green speckled sand and shells, 146–137 m.

Aplidium circumvolutum (Sluiter). 11 specimens.
A. variabile (Herdman). 5 specimens.

Station WS 833. 1. ii. 32. From 52° 28′ S., 68° W. to 52° 32′ S., 68° W. Commercial otter trawl, brown and grey mud and fine sand, 38–31 m.

Sycozoa sigillinoides Lesson. 3 specimens.

Station WS 834. 2. ii. 32. From 52° 57′ S., 68° 07′ W. to 52° 58′ 30″ S., 68° 09′ 30″ W. Commercial otter trawl, dark brown grey shingle and stones, 27–38 m.

Sycozoa sigillinoides Lesson. 50 specimens.
Polyzoa opuntia Lesson. 2 specimens.
Pyura legumen (Lesson). 1 specimen.
Paramolgula gregaria (Lesson). 8 specimens.

Station WS 837. 3. ii. 32. From 52° 48′ 30″ S., 66° 30′ W. to 52° 50′ S., 66° 26′ W. Commercial otter trawl, coarse dark green sand and pebbles, 102 m.

Aplidium fuegiense Cunningham. 10 specimens.
Polyzoa opuntia Lesson. 2 specimens.

Station WS 838. 5. ii. 32. From 53° 11′ S., 65° 02′ W. to 53° 12′ 30″ S., 64° 58′ W. Commercial otter trawl, 149–159 m.

Aplidium variabile (Herdman). 2 specimens.

Station WS 839. 5. ii. 32. From 53° 29′ 30″ S., 63° 31′ W. to 53° 31′ S., 63° 27′ W. Commercial otter trawl, 503–534 m.

Sycozoa sigillinoides Lesson. 1 specimen.

Station WS 841. 6. ii. 32. From 54° 11′ S., 60° 23′ W. to 54° 12′ 30″ S., 60° 20′ W. Commercial otter trawl, shingle and shells, 110–121 m.

Aplidium fuegiense Cunningham. 1 specimen.
Sycozoa sigillinoides Lesson. 3 specimens.
Tylobranchion speciosum Herdman. 1 specimen.
Styela paessleri Michaelsen. 1 specimen.

Station WS 847. 9. ii. 32. From 50° 15′ S., 67° 59′ W. to 50° 16′ 30″ S., 67° 55′ W. to 50° 21′ S., 67° 33′ W. Commercial otter trawl, 57–84 m. and 51–57 m.

Aplidium fuegiense Cunningham. 6 specimens.
A. variabile (Herdman). 3 specimens.
A. falklandicum sp.n. 2 specimens.
Sycozoa sigillinoides Lesson. 5 specimens.
Cnemidocarpa nordenskjöldi (Michaelsen). 1 specimen.
Paramolgula gregaria (Lesson). 4 specimens.

Station WS 849. 10. ii. 32. From 50° 56′ 30″ S., 65° W. to 50° 57′ S., 66° 22′ W. Commercial otter trawl, dark sand, 137 m.

Paramolgula gregaria (Lesson). 1 specimen.

Station WS 852. 21. iii. 32. 44° 12′ 30″ S., 64° 13′ W. Small beam trawl, 86–88 m.

Pyura legumen (Lesson). 1 specimen.

Station WS 854. 22. iii. 32. 45° 16′ S., 64° 25′ W. Small beam trawl, 97 m.

Eugyra kerguelenensis Herdman. 8 specimens.

Station WS 856. 23. iii. 32. 46° 35′ S., 64° 11′ W. Small beam trawl, 104 m.

Aplidium circumvolutum (Sluiter). 30 specimens.
Eugyra kerguelenensis Herdman. 1 specimen.

Station WS 857. 23. iii. 32. From 47° 11′ S., 64° 15′ W. to 47° 12′ S., 64° 09′ W. Commercial otter trawl, 123–124 m.

Aplidium variabile (Herdman). 2 specimens.

Station WS 858. 24. iii. 32. From 45° 42′ S., 60° 30′ W. to 45° 40′ 30″ S., 60° 33′ W. Commercial otter trawl, 132–123 m.

Aplidium falklandicum sp.n. 1 specimen.

Station WS 861. 27. iii. 32. 47° 40′ S., 64° 12′ W. Small beam trawl, 117–124 m.

Paramolgula gregaria (Lesson). 4 specimens.

Station WS 863. 28. iii. 32. 49° 05′ S., 64° 09′ W. Small beam trawl, 121–117 m.

Paramolgula gregaria (Lesson). 2 specimens.

Station WS 864. 28. iii. 32. From 49° 32′ S., 64° 15′ W. to 49° 35′ S., 64° 17′ W. Commercial otter trawl, 128–126 m.

Paramolgula gregaria (Lesson). 4 specimens.

Station WS 865. 29. iii. 32. 50° 03′ S., 64° 14′ W. Small beam trawl, 126–128 m.

Aplidium variabile (Herdman). 3 specimens.

A. falklandicum sp.n. 2 specimens.

Station WS 869. 31. iii. 32. 52° 15′ 30″ S., 64° 13′ 48″ W. Small beam trawl, 187–201 m.

Aplidium variabile (Herdman). 10 specimens.

Station WS 871. 1. iv. 32. 53° 16′ S., 64° 12′ W. Small beam trawl, 336–342 m.

Aplidium fuegiense Cunningham. 2 specimens.

Cystodytes dellechiajei Della Valle. 11 specimens.

MARINE BIOLOGICAL STATION

Station MS 6. 12. ii. 25. East Cumberland Bay, South Georgia. $\frac{1}{4}$ mile south of Hope Pt. to $1\frac{1}{4}$ cables south by east of King Edward Pt. Lt. Small beam trawl, 24–30 m.

Alloeocarpa incrustans (Herdman). 1 specimen.

Station MS 10. 14. ii. 25. East Cumberland Bay, South Georgia. $\frac{1}{4}$ mile S.E. of Hope Pt. to $\frac{1}{4}$ mile S. of Government Flagstaff. Small beam trawl, 26–18 m.

Synoicum georgianum Sluiter. 2 specimens.
Ascidia translucida Herdman. 2 specimens.
Polyzoa reticulata (Herdman). 1 specimen.
Alloeocarpa incrustans (Herdman). 1 specimen.

Station MS 14. 17. ii. 25. From 1·5 miles S.E. by S. to 1·5 miles S. $\frac{1}{2}$ W. of Sappho Pt., East Cumberland Bay, South Georgia. Small dredge, 190–110 m.

Sycozoa georgiana (Michaelsen). 4 specimens.
Polyzoa reticulata (Herdman). 1 specimen.
Pyura georgiana Michaelsen. 4 specimens.

Station MS 33. 1. v. 25. 1 cable E. of Hobart Rock, East Cumberland Bay, South Georgia. Small beam trawl, 40 m.

Polyzoa opuntia Lesson. 1 specimen.

Alloeocarpa incrustans (Herdman). 1 specimen.

Station MS 62. 24. ii. 26. East Cumberland Bay, South Georgia. $\frac{1}{2}$ cable E. to $3\frac{3}{4}$ cables S. of Hobart Pt. Small beam trawl, 31 m.

Polyzoa reticulata (Herdman). 1 specimen.

Station MS 63. 24. ii. 26. East Cumberland Bay, South Georgia. 1·3 miles S. by E. to 1·6 miles S.E. by S. of Hope Pt. Small beam trawl, 23 m.

Distaplia colligans Sluiter. 2 specimens.

Station MS 64. 24. ii. 26. East Cumberland Bay, South Georgia. 1·8 miles S.E. by S. of King Edward Pt. Lt. Small dredge, 7–15 m.

Aplidium variabile (Herdman). 3 specimens.
Synoicum giardi (Herdman). 1 specimen.
Polyzoa opuntia. Lesson 1 specimen.
Alloeocarpa incrustans (Herdman). 2 specimens.

Station MS 65. 28. ii. 26. East Cumberland Bay, South Georgia. 1·6 miles S.E. of Hobart Rock to 1 cable N. of Dartmouth Pt. Small beam trawl, 39 m.

Aplidium circumvolutum (Sluiter). 1 specimen.
Ascidia translucida Herdman. 1 specimen.

Station MS 67. 28. ii. 26. East Cumberland Bay, South Georgia. 3 cables N.E. of Hobart Rock to ½ cable W. of Hope Pt. Small beam trawl, 38 m.

Alloeocarpa incrustans (Herdman). 1 specimen.

Station MS 68. 2. iii. 26. East Cumberland Bay, South Georgia. 1·7 miles S. ½ E. to 8½ cables S.E. by E. of Sappho Pt. Large rectangular net, 220–247 m.

Sycozoa georgiana (Michaelsen). 4 specimens.
Distaplia cylindrica (Lesson). 7 specimens.
Ascidia translucida Herdman. 2 specimens.
Cnemidocarpa verrucosa (Lesson). 2 specimens.
Pyura georgiana Michaelsen. 6 specimens.
Molgula pedunculata Herdman. 1 specimen.
Ascopera gigantea Herdman. 39 specimens.

Station MS 71. 9. iii. 26. East Cumberland Bay, South Georgia. 9¼ cables E. by S. to 1·2 miles E. by S. of Sappho Pt. Small beam trawl, 110–60 m.

?*Aplidium fuegiense* Cunningham. 3 specimens.
?*A. variabile* (Herdman). 22 specimens.
Synoicum adareanum (Herdman). 1 specimen.
S. giardi (Herdman). 1 specimen.
Didemnum studeri Hartmeyer. 1 specimen.
Ascidia challengeri Herdman. 1 specimen.
Polyzoa reticulata (Herdman). 1 specimen.
Cnemidocarpa verrucosa (Lesson). 3 specimens.
Paramolgula gregaria (Lesson). 3 specimens.

Station MS 74. 17. iii. 26. East Cumberland Bay, South Georgia. 1 cable S.E. by E. of Hope Pt. to 3·1 miles S.W. of Merton Rock. Small beam trawl, 22–40 m.

Synoicum georgianum Sluiter. 1 specimen.
Distaplia colligans Sluiter. 2 specimens.
Polyzoa reticulata (Herdman). 1 specimen.
Alloeocarpa incrustans (Herdman). 8 specimens.

British Graham Land Expedition, 1934–7

Stella Creek (6. v. 35)	*Ascidia challengeri* Herdman. 3 specimens. *Cnemidocarpa verrucosa* (Lesson). 14 specimens.
Stella Creek. (5. x. 35)	*Distaplia cylindrica* (Lesson). 1 specimen.
Port Lockroy. (23. i. 35)	*Distaplia cylindrica* (Lesson). 1 specimen.

Deception Island, South Shetlands

3. i. 24. 25–30 m.	*Ascopera gigantea* Herdman. 6 specimens.

Port Stanley, Falkland Islands

9. iii. 26. Shore collection	*Polyzoa opuntia* Lesson. 1 specimen.
17. vi. 28. Shore collection	*Polyzoa opuntia* Lesson. 1 specimen.

ABBREVIATIONS USED IN TEXT-FIGURES

a.	anus
a.l.	atrial languet
amp.	ampulla
a.o.	atrial opening
a.p.	ampulla of pyloric gland
a.s.	atrial siphon
a.sw.	ampullary swelling
b.c.	blood channels
b.f.	branchial fold
b.p.	branchial papilla
br.p.	brood pouch
c.cl.c.	common cloacal chamber
d.f.	dorsal fold
d.l.	dorsal languet
d.la.	dorsal lamina
d.p.	dorsal papilla
d.t.	dorsal tubercle
e.	endostyle
emb.	embryo
en.	endocarp
ep.c.	epicardiac cavity
ep.s.	suture of epicardium and body wall
fl.	flange
g.	gonad
ga.	ganglion
h.	heart
i.	intestine
inf.	infundibulum
l.a.	lateral ampulla
l.b.	longitudinal bar
lg.	ligament
l.m.	longitudinal muscles
l.t.o.	lateral thoracic organ
m.a	median ampulla
m.i.	mid-intestine
mus.	muscle
oe.	oesophagus
od.	oviduct
o.o.	oral opening
o.s.	oral siphon
ov.	ovary
p.	papilla
p.a.	post-abdomen
p.b.	parastigmatic bar
p.bd.	peripharyngeal band
pc.	pericardium
py.c.	pyloric caecum
p.st.	post-stomach
r.	rectum
rb.	rib of oral tentacle
res.	reserve material
r.s.	renal sac
r.v.	radial vessels
s.d.	sperm duct
s.d.c.	sperm duct convolutions
sk.	stalk
sn.	stolon
st.	stomach
st.c.	stomach caecum
t.	testis
th.	thorax
t.m.	transverse muscles
tn.	tentacle
t.p.	transverse-bar papilla
tri.	thoracic triangle
t.t.	test teeth
t.z.	terminal zooid
v.	vesicle
v.c.	vacuolated cell
v.p.	ventral papilla
v.pr.	vascular process
v.pr.o.	origin of vascular process

DESCRIPTION OF SPECIES

Order *ENTEROGONA* Perrier, 1898

Suborder APLOUSOBRANCHIATA Lahille, 1886

Family POLYCLINIDAE Verrill, 1871

Subfamily Polyclininae Adams, 1858

Genus **Aplidium** Savigny, 1816

The genera *Aplidium* Savigny, 1816, and *Amaroucium* Milne Edwards, 1842, are not readily distinguishable and recently there has been a tendency to regard them as synonymous.

A varying number of diagnostic characters (Table 1) has been used by different authorities to separate the two genera.

Van Name (1945), using six diagnostic characters, noted that, even on this basis, 'there are intermediate forms that may be assigned to either genus'. (p. 28). He stated that *Amaroucium* 'hardly merits recognition as anything more than a rather indefinitely distinguished subgenus or section of *Aplidium* Savigny', although it is 'universally adopted in all books on ascidians' (p. 30).

Berrill (1950) pointed out the difficulties involved in using van Name's list of diagnostic characters, and concluded that 'the situation is clearly absurd'. He adopted *Aplidium* as the comprehensive genus, with *Amaroucium* as a subgenus.

Using van Name's list of characters, I have compared forty species variously assigned to *Aplidium* and *Amaroucium*, taking details from published accounts. An additional character included in the comparison was the position of the anus relative to the rows of stigmata (Tokioka, 1953). With regard to this last character I find that, although in some species the anus is situated opposite the 4th row of stigmata, and in others opposite the 7th to 10th, yet the ratio of rows of stigmata anterior to anus to rows of stigmata posterior to anus gives no clear separation of species into two groups. The two characters which might be used to separate *Aplidium* and *Amaroucium* are (1) the arrangement of the testes, and (2) the length of the post-abdomen. The first of these characters is undoubtedly influenced by the second, a short post-abdomen tending to produce a bunching of the testis follicles, but the length of the post-abdomen is itself an unsatisfactory character for generic distinction, as it varies greatly during the annual cycle of the zooids.

Table 1

	Aplidium	*Amaroucium*
Hartmeyer (1923–4)	Atrial siphon with or without languet	Atrial siphon always with languet
	Testis follicles in a bunch	Testis follicles more or less regularly arranged along sperm duct
Harant & Vernières (1933)	Atrial languet absent	Atrial languet present
Huus (1937)	Atrial opening with or without languet	Atrial opening with long languet
	Stomach longitudinally folded	Stomach longitudinally folded
	Post-abdomen relatively short	Post-abdomen long
	Testes in a bunch or cluster	Testis follicles biserially arranged along sperm duct
van Name (1945)	Colony sessile by a broad base	Colony massive or capitate
	Zooids rather stout, with few rows of stigmata	Zooids large with many rows of stigmata
	Short post-abdomen	Long post-abdomen
	Stomach with a few deep longitudinal folds	Stomach with distinct longitudinal plications
	Atrial opening well back on dorsal side	Atrial opening well forward
	Testes in a compact mass	Testes serially arranged along the sperm duct

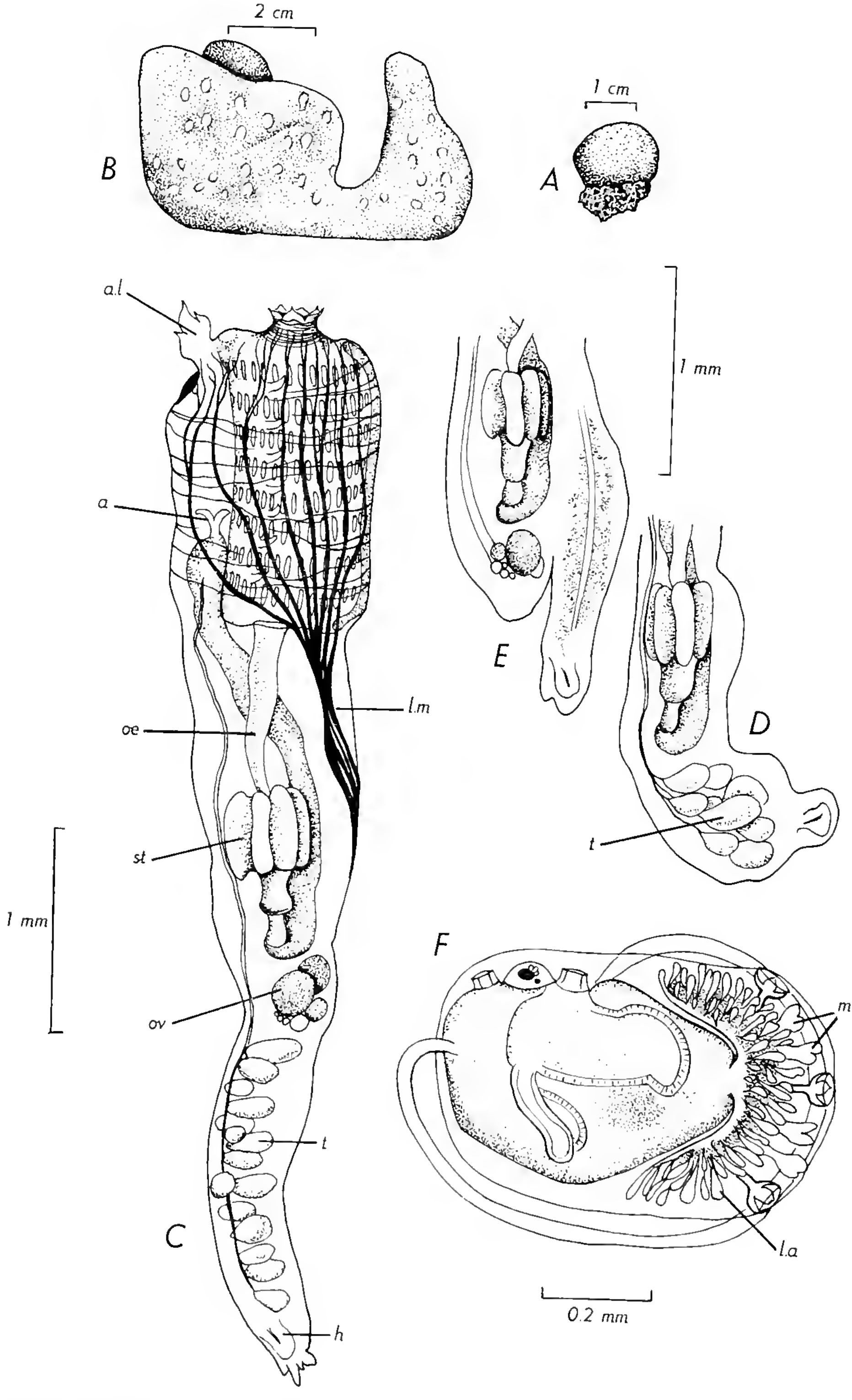
Another result of the shortening of the post-abdomen has been the development in *Aplidium pallidum* (Verrill) of a type of budding shown by Brien (1925) to involve division of the stomach. Should this feature be found to occur in other species, it might serve as a diagnostic character of *Aplidium*, but as so far it has been studied only in *A. pallidum*, such a course is not at present practicable.

The above considerations lead me to believe that there is no generic distinction to be made within the group, and I therefore agree with Berrill (1950) and Kott (1954) in adopting for all species the generic name *Aplidium*, which has priority over *Amaroucium*.

Aplidium circumvolutum (Sluiter) (Text-fig. 1; Pl. I, fig. 1)

Psammaplidium circumvolutum Sluiter, 1900, p. 14, pl. 1, fig. 7; pl. 3, fig. 1.
Amaroucium circumvolutum Michaelsen, 1924, p. 383.
Amaroucium circumvolutum var. *kerguelenense* Pérès, 1952, pp. 213–15, figs. 1, 2.

Occurrence. St. 39: S. Georgia, 179–235 m. St. 170: S. Shetlands, 342 m. St. 175: S. Shetlands, 200 m. St. 190: Palmer Archipelago, 93–126 m. St. WS 93: Falkland Islands, 133–130 m. St. WS 244: Patagonian Shelf, 253–247 m. St. WS 775: Patagonian Shelf, 115–110 m. St. WS 782: Patagonian Shelf, 141–146 m. St. WS 783: Patagonian Shelf, 157 m. St. WS 784: Falkland Islands,



Text-fig. 1. *Aplidium circumvolutum* (Sluiter): A, colony from Patagonian Shelf (St. WS 783); B, colony from S. Georgia (St. 39); C, zooid (St. WS 783); D, abdomen and post-abdomen of zooid with testis (St. WS 824); E, abdomen and post-abdomen of zooid with ovary but no testis (St. WS 256); F, larva (St. 856).

170–164 m. St. WS 824: Patagonian Shelf, 146–137 m. St. WS 856: Patagonian Shelf, 104 m. St. MS 65: S. Georgia, 39 m.

COLONY. Most of the colonies collected from the region of the Falkland Islands and the Patagonian Shelf were rather small, forming rounded or pillow-shaped masses with a flattened lower surface, and were generally under 2 cm. in diameter (Text-fig. 1 A). Sand was present on the surface and also within the colony. The test matrix was clear, rather sparse, and not very tough. The specimens from farther south tended to be larger, attaining a diameter of 7–9 cm., and generally contained less sand (Text-fig. 1 B). There is no obvious arrangement of the zooids in systems, a feature noted also by Pérès (1952), and common cloacal openings could not be seen.

ZOOID (Fig. 1 C). Contracted zooids measured 2–5 mm. in length, but must have been longer than this in life.

THORAX. The atrial opening has a characteristic languet (*a.l.*) which is wide and divided into three pointed lobes, of which the central is longest. Another feature which distinguishes the species is the very strong coat of longitudinal thoracic muscles which continue into the abdomen as a narrowing ventral band. (*l.m.*). Transverse muscles are also well developed. There are seven to eleven rows of stigmata, and a series of short languets on the left branchial wall.

GUT. The oesophagus (*oe.*) is narrow and long, and the stomach (*st.*) short, wide, and provided with five or six folds which are usually distinct but sometimes shallow. This number of folds is characteristic of the species, and was noted by Michaelsen (1924), although Sluiter (1900) described a smooth stomach in the type specimen. The remainder of the gut has no distinctive features. Two rounded lobes are present on the anus (*a*), which is situated opposite the 5th row of stigmata in zooids with 8–10 rows.

GONADS. The ovary (*ov.*) is small and placed close below the loop of the intestine, and the testis (*t*) consists of an irregular series of block-like or pear-shaped follicles below the ovary. In some zooids the follicles are condensed to form a compact group (Text-fig. 1 D, *t*) in others (Text-fig. 1 C, *t*) they are extended as usual in the genus and a few zooids show no testes (Text-fig. 1 E). The compact arrangement of the follicles has been regarded as a characteristic of the species (Michaelsen, 1924), but Pérès (1952) noted that in some zooids follicles were also present farther back in the post-abdomen. There is, in fact, variation according to the stage of the reproductive cycle.

LARVA (Text-fig. 1 F). Larvae vary from 0·5 to 0·8 mm. in length, measured from the end of the papillae to the base of the tail. There are three rather widely spaced papillae, and between each two, a pair of notched median ampullae (*m.a.*) occur. In most species of *Aplidium* the larva has a single ampulla between each two papillae, but in this species each has evidently divided. The most characteristic feature of the larva is the great development of fringing lateral ampullae (*l.a.*) round the anterior end of the trunk; this fringe clearly distinguishes the larva of *circumvolutum* from all others found in the 'Discovery' collections. Both ocellus and otolith are present. Larvae from subantarctic and antarctic colonies differ only in size (see below).

COMPARISON OF SPECIMENS FROM THE FALKLAND-PATAGONIAN REGION WITH ANTARCTIC SPECIMENS. Table 2 shows the constant differences between specimens from the Falkland Islands and Patagonian Shelf and those from South Georgia and the Palmer Archipelago.

Table 2

	Subantarctic	*Antarctic*
Colony	Small, with rather soft test	Large with firm test
Zooid	Mean length 3 mm., 7 or 8 rows of stigmata	Mean length 5 mm., 10 or 11 rows of stigmata
Larvae	2 or 3 per breeding zooid. Mean length 0·6 mm.	Up to 11 per breeding zooid. Mean length 0·8 mm.

Biology. Table 2 suggests that in its Antarctic range this species has larger colonies, larger zooids with a better developed branchial sac, and larger and more numerous larvae. The inference is that the centre of distribution is in the Antarctic rather than the Subantarctic.

Examination of many specimens showed that all the zooids of a colony keep in phase in their sexual cycle, but that different colonies taken from the same station at the same time differ widely in their sexual state. Thus colonies collected from St. WS 856, on 23 March 1932 varied sexually, as follows:

	No. of colonies
No gonads present	8
Zooids in male phase	3
Zooids in female phase	3
Zooids with embryos	1

The occasional occurrence, in other samples, of zooids with both ovary and testis shows that the sexes are not separate; it is likely that the species is protandrous, as usual in *Aplidium*. The comparative rarity of such zooids, however, suggests that the regression of the testis is rapid after the zooid has functioned as a male. The relatively large number of colonies with zoiods lacking gonads and the absence of gonads in zooids carrying embryos further indicates that the ovary also regresses rapidly after functioning.

Embryos or larvae were present only in colonies collected as follows:

South Georgia	*Falkland Islands*
28. ii. 1926	5. xii. 1931
25. iii. 1926	19. i. 1932
	23. iii. 1932

As the species did not occur in collections made in other months, however, no more can be said than that breeding takes place in the southern summer, with an indication of an earlier start in the Subantarctic than in the Antarctic region.

Remarks. This is a species which shows slight anatomical differences in different parts of its range. A variety described by Pérès (1952) from Kerguelen (var. *kerguelenense*), has each of the oral lobes bifid, and a very wide atrial languet. The differences which I have noted above between the subantarctic and the antarctic specimens in the 'Discovery' collections do not seem to merit systematic distinction.

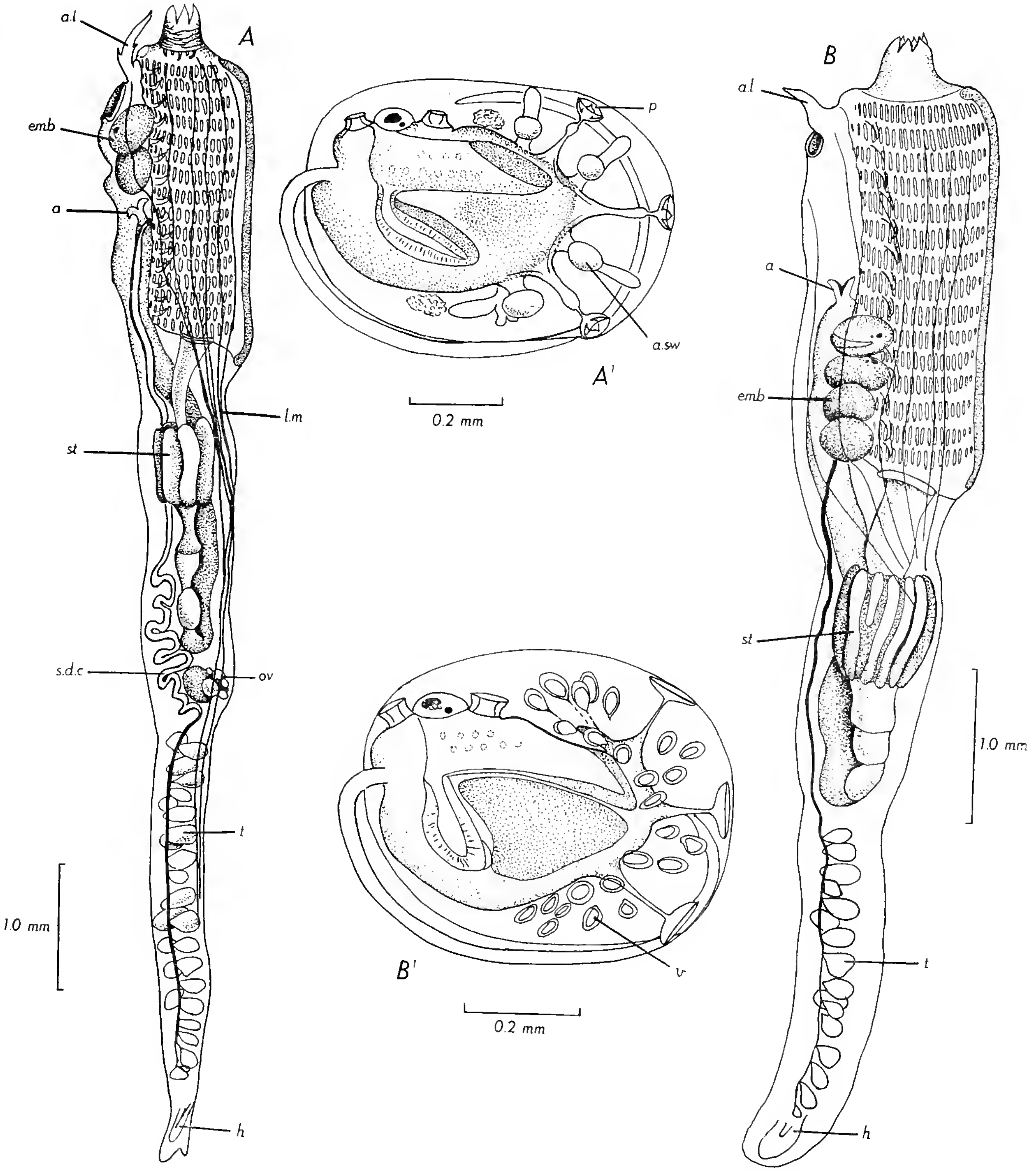
Distribution. New Zealand; Chatham Islands; Subantarctic (Kerguelen, Patagonian Shelf), Antarctic (Graham Land, S. Georgia).

Aplidium fuegiense Cunningham (Text-fig. 2A; Pl. I, fig. 2)

Aplidium fuegiense Cunningham, 1871, p. 66.
For synonymy see van Name, 1945, p. 43.

Occurrence. ?St. 27: S. Georgia, 110 m. St. 51: Falkland Islands, 105–115 m. St. 652: Burdwood Bank, 171–169 m. St. WS 71: Falkland Islands, 82–80 m. St. WS 73: Falkland Islands, 121–130 m. St. WS 76: Patagonian Shelf, 207–205 m. St. WS 79: Patagonian Shelf, 132–131 m. St. WS 80: Patagonian Shelf, 152–156 m. St. WS 83, Falkland Islands, 137–129 m. St. WS 84: Falkland Islands, 75–74 m. St. WS 85: Falkland Islands, 79 m. St. WS 86: Patagonian Shelf, 151–147 m. St. WS 90: Patagonian Shelf, 82–81 m. St. WS 91: Patagonian Shelf, 191–205 m. St. WS 92: Patagonian Shelf, 145–143 m. St. WS 93: Falkland Islands, 133–130 m. St. WS 94: Patagonian Shelf, 110–126 m. St. WS 95: Patagonian Shelf, 109–108 m. St. WS 108: Falkland Islands, 118–120 m. St. WS 219: Patagonian Shelf, 116–114 m. St. WS 220: Patagonian Shelf, 108–104 m. St. WS 233: Falkland Islands, 185–175 m. St. WS 247: Patagonian Shelf, 172 m. St. WS 249:

Patagonian Shelf, 166 m. St. WS 583: Magellan Strait, 14–78 m. St. WS 764: Patagonian Shelf, 110–104 m. St. WS 771: Patagonian Shelf, 90 m. St. WS 775: Patagonian Shelf, 115–110 m. St. WS 776: Patagonian Shelf, 110–99 m. St. WS 781: Patagonian Shelf, 148 m. St. WS 787: Patagonian Shelf, 106–110 m. St. WS 791: Patagonian Shelf, 97–95 m. St. WS 792: Patagonian Shelf, 102–106 m. St. WS 797: Patagonian Shelf, 115–111 m. St. WS 800: Patagonian Shelf,



Text-fig. 2. *Aplidium fuegiense* Cunningham: A, zooid; A^1, larva (St. WS 84). *Aplidium variabile* (Herdman): B, zooid; B^1, larva (St. WS 824).

137–139 m. St. WS 801: Patagonian Shelf, 165 m. St. WS 807: Patagonian Shelf, 124–126 m. St. WS 808: Patagonian Shelf, 110–106 m. St. WS 809: Patagonian Shelf, 104–101 m. St. WS 811: Patagonian Shelf, 99 m. St. WS 813: Patagonian Shelf, 106–102 m. St. WS 837: Patagonian Shelf, 102 m. St. WS 841: Patagonian Shelf, 110–121 m. St. WS 847: Patagonian Shelf, 57–84 m. St. WS 871: Patagonian Shelf, 336–342 m. ?St. MS 71: S. Georgia, 110–60 m.

COLONY. As van Name (1945) has said, this species is so variable that 'an attempt to describe the colonies in respect to form and size is impossible to fulfill'. Some colonies in the 'Discovery' collections are relatively short and rounded, but many have a very characteristic long form tapering gradually to a fine point at the free end (Pl. I, fig. 2). These long colonies were apparently attached by the lower rounded end to a bottom of sand. The colour of the preserved colonies is usually some shade of orange, yellow or brown, and the zooids sometimes show through the test, but not always. Generally there are no obvious systems of zooids, but in a few cases the zooids could be seen to be arranged in double rows, probably representing narrow oval systems. The surface is usually smooth and without encrusting sand, but the interior of the colony may have a good deal of embedded sand. Some of the long narrow colonies appear to have lain horizontally on the sand during life, as sand is adhering to the test at several places along the length of the colony (St. WS 808). In most of the specimens, the surface-layer of the test has a characteristic appearance owing to the presence of many small round pale yellow or orange-coloured vesicles. When the colony is cut open the zooids are seen to be closely spaced. The longest colony in this collection is one of 63 cm. from the Patagonian Shelf (St. WS 808), but one specimen from the same region is recorded as forming a 'portion of a colony weighing 300 g.'.

Table 3

Maximum diameter of colony (cm.)	*Mean no. of rows of stigmata*	*Mean no. of folds on stomach*
0·5	18	5
1·5	18	5
2·0	16	5
3·0	17	5
7·0	21	6
7·0	21	5
8·0	22	5
8·0	20	5
9·0	17	5
10·0	18	5
15·0	16	5
28·0	15	5

ZOOID (Text-fig. 2A). The length of the zooids in the 'Discovery' material varies a good deal, from about 6 to 18 mm., and depends largely on the development of the post-abdomen. The most characteristic features of the zooid are: (1) the moderately developed and forwardly directed atrial languet; (2) the small atrial opening placed a short distance back along the dorsal side of the thorax; (3) the large branchial sac with ten to twenty-two rows of stigmata; and (4) the stomach with five or six sharply defined undivided longitudinal folds. The number of rows of stigmata and the number of folds on the stomach do not show any clear correlation with the size of the colony, as shown in Table 3.

GUT. Van Name (1945) states that the stomach has usually four to six folds, but sometimes at least eight or ten. Having examined several zooids from each of many colonies in the 'Discovery' collection, I have found the number of folds on the stomach to be always five or six, which I conclude to be the normal number at least in specimens from the Patagonian Shelf. The rest of the gut shows no diagnostic features. The anus is placed about half way along the branchial sac, opposite the 8th or 9th row of stigmata in zooids with 16 rows. It has two lobes.

GONADS. Mature zooids generally have both ovary (*ov.*) and testis (*t.*). The ovary has a few ova of various sizes and is situated immediately below the intestinal loop. The testis follicles form a long series extending down the post-abdomen. In several colonies, mature zooids had the sperm duct convoluted opposite and just below the intestinal loop (*s.d.c.*). This is not the result of abdominal contraction and the increased length of sperm duct may serve as a reservoir for sperm.

LARVA (Text-fig. 2 A¹). The variations in length of the larvae are shown in Table 4.

Table 4

Date	3. ii. 32	6. iii. 27	13. iii. 27	14. iii. 27	14. iii. 31	24. iii. 27	24. iii. 27	1. iv. 32	7. iv. 27
Length (mm.)	0·86	0·70–0·88	0·70	0·70	0·86	0·86	0·70	0·88–0·90	0·66–0·72

All the colonies with these larvae were obtained from the Falkland Islands and the Patagonian Shelf. There is no correlation between length of the larva and the month of the year. The larva is characterized by the rather rounded and robust appearance of the trunk, the widely spaced papillae (*p.*), and the four lateral ampullae on each side, each with a rounded swelling near the base (Fig. 2 A¹, *a.sw.*).

BIOLOGY. The breeding season is indicated in Table 5 which shows the number of colonies examined in each month in which the species was taken, and also the number of these colonies containing larvae.

Table 5

Month	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
No. of colonies examined	3	3	3	0	0	4	7	36	12	8	14	15
No. of colonies with larvae	0	0	0	0	0	0	0	0	0	1	10	3

When allowance is made for the small number of colonies collected between May and September owing to the difficulty of working during the winter months, it is still evident that the breeding season is limited to a short period in the southern summer and autumn, mainly the months of February, March and April.

Between one and seven larvae were found in the atrial cavity of zooids in different colonies. The zooids with only one larva were smaller than those with several larvae.

An examination of the colonies gives some picture of the annual cycle of growth and reproduction in the species. In December most colonies have well-developed zooids but few have acquired gonads. During the next three months the development of gonads takes place and few colonies were then found which lacked gonads. Breeding follows with the greatest production of larvae in March. Subsequently, the gonads disappear and all the colonies collected in July had de-differentiated zooids representing the normal post-breeding or overwintering condition in species of *Aplidium.*

REMARKS. It is difficult to be certain that all the suggested synonyms for this species are reliable, and that all records under the name *A. fuegiense* refer to the same species. Of the reported occurrences in the West Antarctic, those from MacRobertson Land and Enderby Land (Kott, 1954) may not refer to the present species. The colony and zooid described by Kott agree quite well with the specimens from the Magellan region, but the number of folds on the wall of the stomach (8) is rather high. The main difference, however, is the size of the larva, which Kott says is twice that of *A. caeruleum* (Sluiter). The larva of the latter species is, according to Kott's scale drawing, about 1 mm. from the end of the papillae to the base of the tail, which means that the larvae from MacRobertson Land and Enderby Land were about 2 mm. in length. This is a very large larva indeed, and is between two and three times the size of the larvae of *A. fuegiense* in the 'Discovery' collections, placing it beyond the probable range of variation of that species.

A. fuegiense is, I think, typically a subantarctic species, the 'Discovery' collections providing very many specimens from the Patagonian Shelf and the neighbourhood of the Falkland Islands, and only two doubtful records from elsewhere (South Georgia). The specimens from South Georgia were in a state of de-differentiation, the zooids being reduced to post-abdomens, and the identification is therefore uncertain.

I disagree with van Name (1945) when he says that *A. variable* (Herdman, 1886) is 'very likely synonymous' with *A. fuegiense*. A comparison of the two species is given on p. 33.

DISTRIBUTION. Subantarctic (Falkland Islands, Patagonian Shelf, Magellan region, coast of Argentina to La Plata); ?Antarctic (South Georgia).

Aplidium variabile (Herdman) (Text-fig. 2 B)

Amaroucium variabile Herdman, 1886, p. 216, pl. 29, figs. 7–12, text-fig. 9.
For synonymy see Kott (1954), p. 174.

OCCURRENCE. St. 160: Shag Rocks, 117 m. St. WS 72: Falkland Islands, 95 m. St. WS 91: Patagonian Shelf, 191–205 m. St. WS 93: Falkland Islands, 133–130 m. St. WS 219: Patagonian Shelf, 116–114 m. St. WS 220: Patagonian Shelf, 108–104 m. St. WS 235: Patagonian Shelf, 155 m. St. WS 237: Patagonian Shelf, 150–256 m. St. WS 771: Patagonian Shelf, 90 m. St. WS 772: Patagonian Shelf, 309–163 m. St. WS 781: Patagonian Shelf, 148 m. St. WS 782: Patagonian Shelf, 141–146 m. St. WS 783: Patagonian Shelf, 165–0 m. St. WS 787: Patagonian Shelf, 106–110 m. St. WS 791: Patagonian Shelf, 95–101 m. St. WS 793: Patagonian Shelf, 108–111 m. St. WS 794: Patagonian Shelf, 123–126 m. St. WS 796: Patagonian Shelf, 108–113 m. St. WS 797: Patagonian Shelf, 115–111 m. St. WS 799: Patagonian Shelf, 141–137 m. St. WS 808: Patagonian Shelf, 110–106 m. St. WS 811: Patagonian Shelf, 99 m. St. WS 813: Patagonian Shelf, 106–102 m. St. WS 816: Patagonian Shelf, 150 m. St. WS 824: Patagonian Shelf, 146–137 m. St. WS 838: Patagonian Shelf, 149–159 m. St. WS 847: Patagonian Shelf, 57–84 m. St. WS 857: Patagonian Shelf, 123–124 m. St. WS 865: Patagonian Shelf, 126–128 m. St. WS 869: Patagonian Shelf, 187–201 m. St. MS 64: S. Georgia, 7–15 m. ?St. MS 71: S. Georgia, 110–60 m.

COLONY. Colonies of many shapes are present in the collection, the shape depending to some extent on the object to which the colony is attached. The colonies which have been growing on the stems of hydroids tend to be long and narrow and often laterally flattened. Other colonies have apparently been on a sandy bottom and these are usually more globular with a short irregular stalk. Some specimens are slightly lobed. A few colonies have the long narrow finger-like form commonly found in *A. fuegiense*.

The colour in preserved specimens is generally pale buff-yellow, buff, or buff-grey. In most cases the surface is smooth and the colony without sand; although some specimens have a light coating of sand all over, sand, when present, is more often confined to the stalk or basal part of the colony. Usually the zooids show through the test quite distinctly. Definite arrangement of the zooids is seldom apparent, but sometimes they are grouped into small indistinct systems. Usually the zooids lie obliquely to the surface of the colony and not at right angles as in Kott's (1954) specimens. The colonies may reach a length of 12 cm. but are generally under 4 cm. in their greatest dimension.

ZOOID (Text-fig. 2 B). The length of the zooids varies from 1·5 to 8·0 mm. according to the degree of contraction and the development of the post-abdomen. In large zooids the thorax may attain 3·5 mm. and the abdomen 2·0 mm. Herdman (1886), in his original account, gave 2·5 mm. as the usual measurement of the thorax and abdomen together, but one of the colonies from the 'Challenger' collection which I have examined has well-expanded zooids with thorax 3·5 mm., abdomen 2·0 mm. and post-abdomen 4·0 mm.

THORAX. The oral siphon is 6-lobed and the atrial siphon has a simple or 3-cleft languet. The branchial sac has from nine to fifteen rows of stigmata.

GUT. The stomach has from ten to sixteen longitudinal folds, generally from twelve to fifteen. One or two of the folds often extend only part of the length of the stomach. The anus has two distinct lips. It is situated opposite the 8th row of stigmata in zooids with fifteen or sixteen rows.

LARVA (Text-fig. 2B^1). The larva of this species has not been described. It ranges from 0·58 to 0·70 mm. in length, measured from the end of the papillae to the base of the tail. The trunk is rather deep and stout. The most characteristic feature of the larva is the presence of many small apparently isolated vesicles (*v.*) arranged in a semicircle round the anterior end of the trunk. The three anterior papillae are rather widely spaced and have slender stalks. There are no paired or median ampullae, a feature unusual in species of *Aplidium*. Both ocellus and otolith are present. There are up to ten larvae in the atrial cavity of breeding zooids.

REMARKS. Herdman (1886) pointed out that this species somewhat resembles *A. fuegiense* in external appearance, and Hartmeyer (1911, 1912) also regarded the species as similar. Van Name (1945) stated that they are 'very likely synonymous'. I have examined many specimens of both species, including thirteen colonies of Herdman's type material of *A. variabile*, kindly lent by the British Museum (Natural History). In my opinion the species are certainly separate, and reliable distinctions are found in both zooids and larvae, as shown in Table 6.

Table 6

	Stomach	*Larva*
A. fuegiense	5 or 6 undivided folds	Trunk 0·66–0·90 mm.; paired club-like anterior ampullae; no small isolated vesicles
A. variabile	Usually 10–15 folds, a few of them divided or incomplete	Trunk 0·58–70 mm.; no club-like anterior ampullae; many small isolated vesicles

With regard to these features, the stomach of *A. fuegiense* is very characteristic and I find that the number of folds does not exceed six, even in the largest colonies with fully mature zooids. The 'Discovery' material, therefore, gives no confirmation of van Name's (1945) statement that the folds on the stomach sometimes number at least eight or ten. In the type specimens of *A. variabile* the zooids which I have examined show thirteen to fifteen folds, thus agreeing with Herdman's statement and illustration. Hartmeyer (1911) found fourteen folds, sometimes fewer, and later (1912) stated that the number may be as low as six; he may have been confusing the two species. There is little doubt, however, that the number is generally at least twelve, and Kott (1954) always found fourteen or fifteen folds.

Although there were embryos in one of the type specimens, no fully developed larvae were present, and the larval description is based on 'Discovery' specimens from the Patagonian Shelf. The larvae of *A. variabile* and *A. fuegiense* cannot be confused.

Apart from one record for the Chatham Islands (New Zealand) by Sluiter (1900), *A. variabile* has previously been taken only from Kerguelen, where it seems to be fairly common. Michaelsen (1924) was in some doubt whether to accept the record from New Zealand, and if we ignore it, the previous records were confined to Kerguelen. The wide geographical separation of the previous and the new localities is perhaps not surprising, when it is remembered that the latitude of Kerguelen Island and the Falkland Islands is almost the same and that many Subantarctic and Antarctic species have a very wide distribution.

Distribution. Subantarctic (Kerguelen; Patagonian Shelf; Falkland Islands); Antarctic (Shag Rocks; South Georgia).

Aplidium falklandicum sp.n. (Text-fig. 3, A-H; Pl. I, figs. 3, 4)

Holotype. St. WS 73, 121–130 m. Length of colony: 19·0 cm.

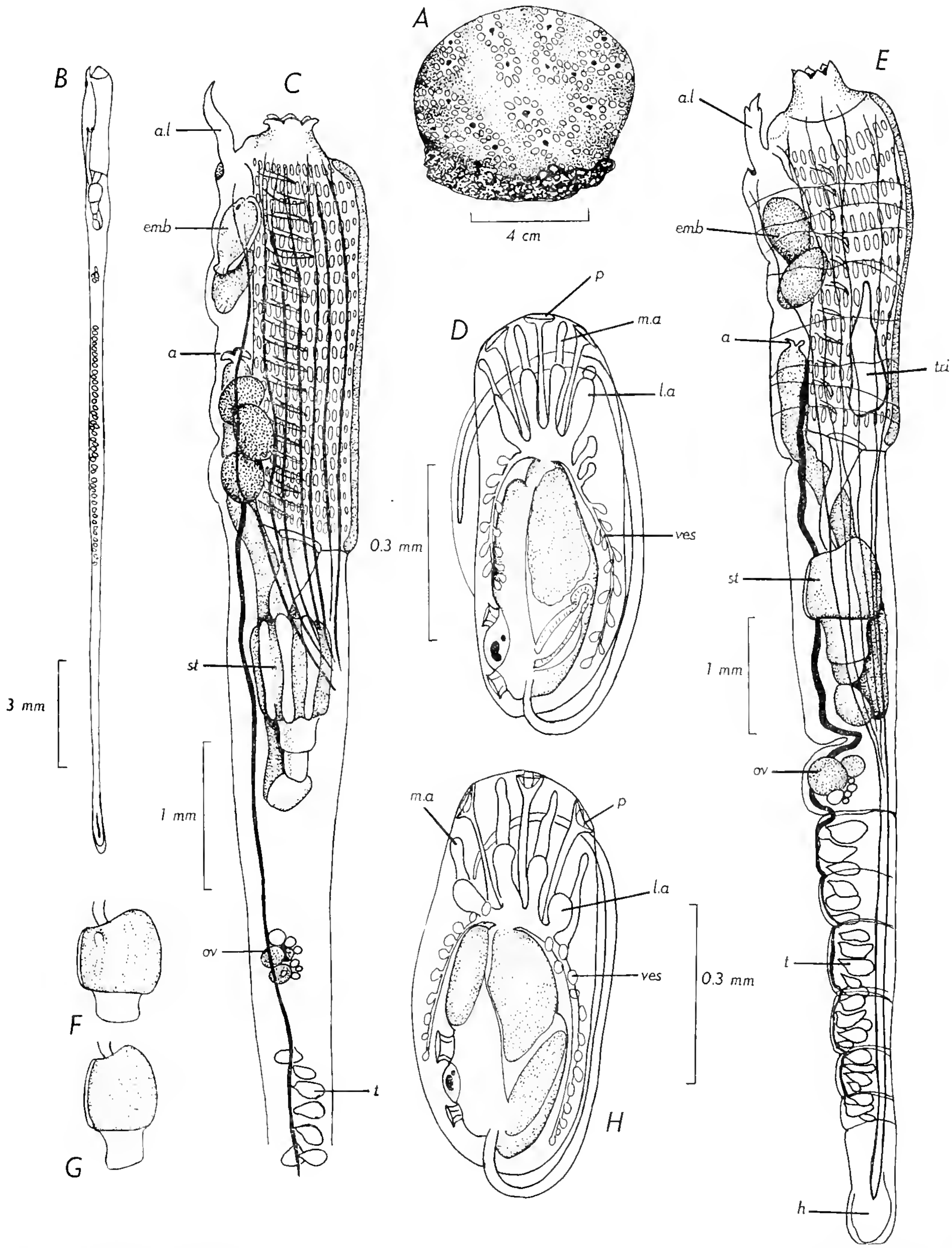
Diagnosis of species. Colonies low, pillow-shaped, globular, or elongate. Systems of zooids oval or elongate. Zooid with atrial languet simple and triangular, or slightly trifid; about seven moderately strong longitudinal muscles; ten to twenty-three rows of stigmata; stomach with five to seven shallow longitudinal folds, or a few indistinct marks or quite smooth. Larva with trunk 0·40–0·70 mm. long; papillae closely spaced, with slender stalks; four narrow median ampullae; about four pairs of lateral ampullae; a dorsal and a ventral lateral series of small vesicles.

Occurrence. St. 51: Falkland Islands, 105–115 m. St. 53: Falkland Islands, 0–2 m. St. 164: S. Orkneys, 24–36 m. St. 652: Burdwood Bank, 171–169 m. St. 1902: Patagonian Shelf, 50–80 m. St. WS 25: S. Georgia, 18–27 m. St. WS 27: S. Georgia, 107 m. St. WS 72: Falkland Islands, 95 m. St. WS 73: Falkland Islands 121–130 m. St. WS 79: Patagonian Shelf, 132–131 m. St. WS 81: Falkland Islands, 81–82 m. St. WS 84: Falkland Islands, 75–74 m. St. WS 86: Falkland Islands, 151–147m. St. WS 90: Patagonian Shelf, 82–81 m. St. WS 91: Patagonian Shelf, 191–205 m. St. WS 93: Falkland Islands, 133–130 m. St. WS 108: Falkland Islands, 118–120 m. St. WS 154: S. Georgia, 115–0 m. St. WS 182: Palmer Archipelago, 750–520 m. St. WS 219: Patagonian Shelf, 116–114 m. St. WS 220: Patagonian Shelf, 108–104 m. St. WS 222: Patagonian Shelf, 100–106 m. St. WS 239: Falkland Islands, 196–193 m. St. WS 243: Patagonian Shelf, 144–141 m. St. WS 244: Patagonian Shelf, 253–247 m. St. WS 764: Patagonian Shelf, 110–104 m. St. WS 765: Patagonian Shelf, 113–119 m. St. WS 771: Patagonian Shelf, 90 m. St. WS 774: Patagonian Shelf, 139–144 m. St. WS 775: Patagonian Shelf, 115–110 m. St. WS 782: Patagonian Shelf, 141–146 m. St. WS 787: Patagonian Shelf, 106–110 m. St. WS 791: Patagonian Shelf, 97–95 m. St. WS 792: Patagonian Shelf, 102–106 m. St. WS 793: Patagonian Shelf, 108–111 m. St. WS 796: Patagonian Shelf, 106–113 m. St. WS 807: Patagonian Shelf, 124–126 m. St. WS 813: Patagonian Shelf, 106–102 m. St. WS 847: Patagonian Shelf, 57–84 m. St. WS 858: Patagonian Shelf, 132–123 m. St WS 865: Patagonian Shelf, 126–128 m.

Colony. (Text-fig. 3A; Pl. I, figs. 3, 4.) Colonies vary from low dome-shaped or globular, to ovoid, long or tongue-like masses and often attain a diameter of 6–8 cm. Generally the colony is simple but is occasionally divided into a few lobes. Attachment is sometimes by a broad base, but often by a narrow area, and occasionally a short pedicel is formed. The surface is usually smooth, but sand is sometimes present, especially at the base. Preserved specimens are pale yellow-grey to buff, and a pattern may be formed by the systems of zooids showing through the semi-transparent test. The common cloacal openings are many, small and round. The largest colonies in the collection are about 20 cm. long. In a few specimens there is no apparent place of attachment, and these colonies may have rested freely on the bottom, but most specimens were attached to shells or small stones.

Zooid (Text-figs. 3B, C, E). In well-developed and expanded zooids the thorax is 1·8–3·0 mm. in length. The abdomen is about the same length or slightly shorter. The post-abdomen varies greatly in length, often exceeds 6 mm. and sometimes reaches 20 mm. (Text-fig. 3B). The thorax is the widest part of the zooid and the post-abdomen the narrowest but the differences in width are slight.

Thorax. There are six pointed oral lobes, and the atrial opening, which lies opposite the first or second row of stigmata, is surmounted by a short triangular simple, or slightly trifid languet (*a.l.*). Six to eight moderately strong longitudinal muscles are present on each side of the thorax. Zooids from different colonies vary a good deal in the development of the branchial sac, which may have from ten to twenty-three rows of stigmata. Each row generally has twelve to fifteen stigmata. The dorsal languets are quite large. In about half of the specimens the zooids have a conspicuous triangular



Text-fig. 3. *Aplidium falklandicum* sp.n.: A, colony; B, zooid; C, anterior part of zooid with no thoracic triangles; *D*, larva (St. WS 793); E, zooid with thoracic triangles; F, G, stomach of zooids showing indistinct markings; H, larva (St. WS 72).

white area on each side of the body wall near the base of the ventral part of the thorax (Fig. 3E, *tri.*). Other specimens have no trace of this (Fig. 3C).

GUT. The oesophagus is usually longer than the stomach and is widest at its branchial end. There is much variation in the stomach. The zooids of some colonies have a stomach with five to seven shallow but distinct longitudinal folds (Text-fig. 3C), but in other specimens (Text-fig. 3E, F, G) the folds are reduced to a variable degree, or broken up into a few indistinct swellings or completely absent. In the last case the stomach is like that of *Synoicum*. The intestine and rectum are of the type usual in *Aplidium*. The anus has two small diverging lips; it is situated opposite the 9th row of stigmata when twelve rows are present and opposite the 12th row in zooids with twenty-one rows.

GONADS. The ovary is either close behind the intestinal loop (Text-fig. 3E, *ov.*) or at some distance from it (Text-fig. 3C, *ov.*). A long series of small testis follicles (*t*) occupies much of the length of the post-abdomen.

LARVA (Text-figs. 3D, H). The trunk of the larva ranges in length from 0·40 to 0·70 mm. The three papillae are closely spaced and are borne on slender stalks. There are four long narrow median ampullae and four pairs of shorter stouter lateral ampullae. On each side of the dorsal and ventral part of the trunk there is a slender strand of tissue bearing a series of small rounded vesicles (*ves.*). Both ocellus and otolith are present.

Table 7

	Colony	*Stomach*	*Larva*
A. falklandicum	Variable; low to elongate	5–7 shallow folds, or reduction of folds, or smooth	Slender. Trunk 0·40–0·70 mm. Papillae close. Lateral series of dorsal and ventral vesicles
A. fuegiense	Variable; low to elongate	5–7 deep folds	Stout. Trunk 0·6—0·90 mm. Papillae distant. No series of vesicles

BIOLOGY. Colonies were collected in all months of the year except August and September, and larvae were found in the subantarctic material in January, February, March, April, June, July, October, November and December. There were no larvae in the antarctic specimens. It appears that the species breeds throughout the year, and in this respect resembles *A. caeruleum* as described by Hartmeyer (1911). The larvae in each breeding zooid number from four to nine.

None of the colonies showed the accumulation of reserve material in the post-abdomen which is commonly found during the post-breeding and overwintering period in many species of polyclinid ascidians. It may be that in species which breed almost continuously throughout the year the de-differentiation of zooids and the accompanying resting phase have been reduced.

REMARKS. I have been surprised that this species, which is apparently common round the Falkland Islands and on the Patagonian Shelf, could not be identified with any known species, and I suspect that hitherto it has been confused with *A. fuegiense*, with which it is often collected. A comparison of the two species is shown in Table 7.

It is evident from the table that the larva affords the best characters for distinguishing the species, as will be seen also by comparing Text-figs. 2A^1 and 3D, H.

The larva also indicates that specimens possessing white thoracic triangles and those lacking them are both of *A. falklandicum* (see Text-figs. 3D, H). It unites, too, a whole series of specimens showing structural differences in the stomach, which might otherwise have been thought to indicate specific differences.

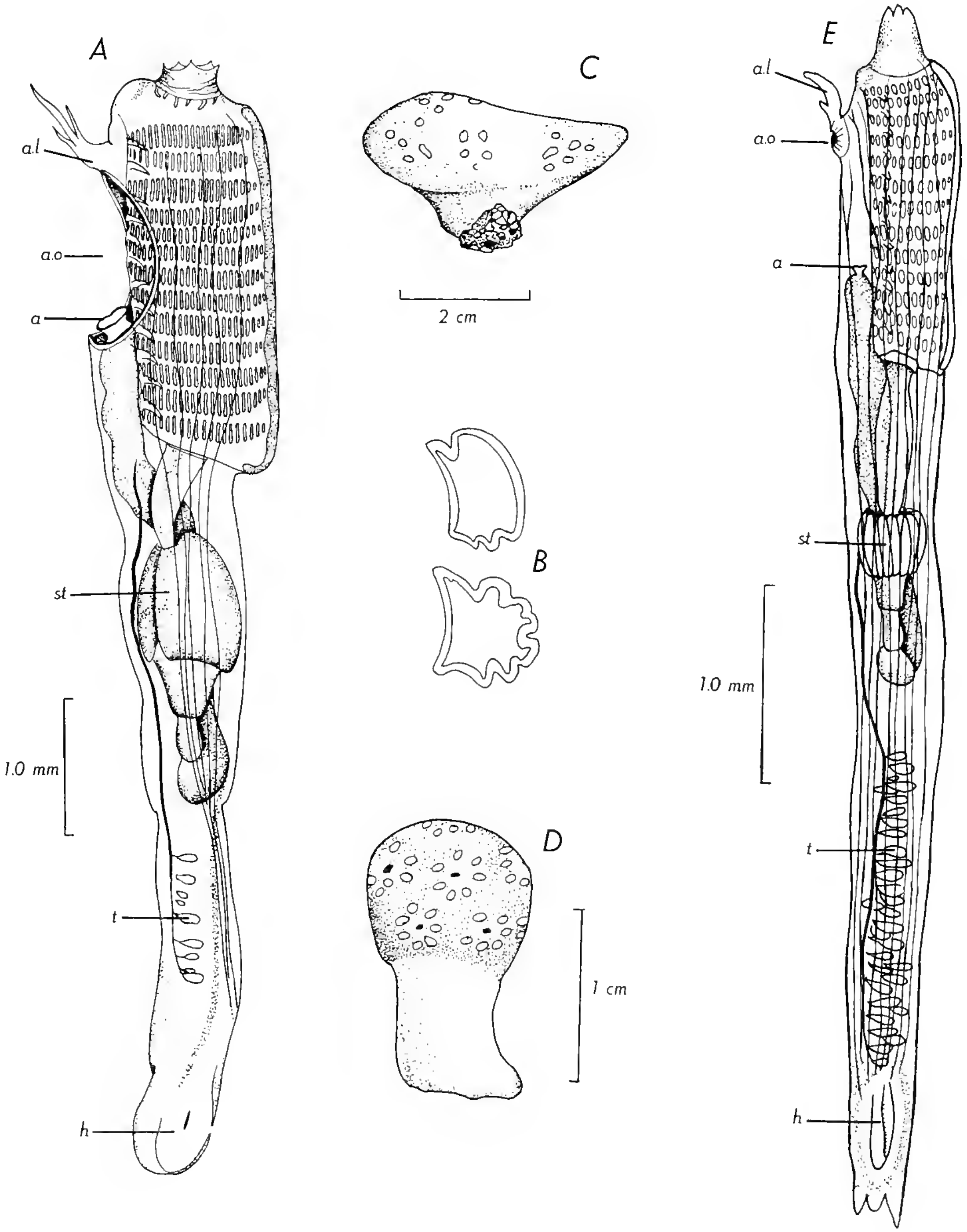
DISTRIBUTION. Subantarctic (Falkland Islands, Patagonian Shelf); Antarctic (Graham Land, S. Orkneys, S. Georgia).

Aplidium radiatum (Sluiter) (Text-fig. 4A, B; Pl. I, fig. 5)

Psammaplidium radiatum Sluiter, 1906, p. 25, pl. 2, figs. 23, 24; pl. 4, fig. 52.
Amaroucium radiatum Hartmeyer, 1909–11, p. 1471.
Aplidium radiatum Kott, 1954, p. 173.

OCCURRENCE. St. 27: S. Georgia, 110 m. St. 164: S. Orkneys, 24–36 m. St. 181: Palmer Archipelago, 160–335 m. St. 186: Palmer Archipelago, 295 m. St. 190: Palmer Archipelago, 93–126 m.

COLONY (Pl. I, fig. 5). Most colonies have a stalk which, in the 'Discovery' material, is always shorter than the head, although sometimes only slightly shorter. In a few colonies there is no stalk,



Text-fig. 4. *Aplidium radiatum* (Sluiter): A, zooid; B, transverse sections of stomach of two zooids (St. 186). *Aplidium seeligeri* sp.n.: C, D, two colonies (Sts. 935, 941); E, zooid (St. 941).

the lower end of the colony merely being flat. The head of the stalked colonies is almost spherical, or ovoid or cylindrical. The general colour of the preserved colony is grey, patterned by the regular double rows of zooids, converging at the apex of the colony, which constitute one of the most characteristic features of the species. The double rows are produced by the adjacent long narrow oval systems of zooids. Each of the systems has a long central cloacal canal, and the canals of most of the systems open into a common depression at the apex of the colony. Although this is the condition generally found in the species, some colonies have, in addition, other cloacal openings scattered over the surface, as observed by Kott (1954). Sand is almost always present within the common test, especially in the superficial layers, but the test material itself is transparent. The largest and smallest specimens in the collection are 6·4 and 1·5 cm. in total length.

ZOOID (Text-fig. 4A). The zooid is large and stout, the thorax being about 3 mm. long and the abdomen about the same length; the post-abdomen is variable, and often exceeds the combined length of the thorax and abdomen.

THORAX. The three narrow pointed lobes of the atrial languet (*a.l.*) are always present. Sluiter (1906) noted that the atrial opening is placed a short distance back on the dorsal side of the thorax. The 'Discovery' specimens not only confirm this as a constant feature of the species, but also show that in all well-expanded zooids the opening is of a size unusually great in *Aplidium*, and exposes a large part of the dorsal side of the thorax (*a.o.*). There are thirteen to nineteen rows of stigmata, the number being independent of the size of the colony, at least in the 'Discovery' specimens, all of which are well grown.

GUT. The oesophagus varies in length. According to Sluiter (1906) and Kott (1954) the stomach has four longitudinal folds, but I find a considerable variation in the appearance of the stomach in zooids even from the same colony. In many there are six to eight folds (Text-fig. 4B), but other zooids have a stomach showing no true folds. One or other of these conditions is probably an artifact. The folds, when present, are rather shallow in the 'Discovery' specimens. The undivided anus lies between the 8th and 9th rows of stigmata in zooids with 13 rows.

GONADS. In some colonies zooids were seen with an ovary and in others there was a very slightly developed testis (*t*) in the form of a row of small pear-shaped follicles.

BIOLOGY. There is not enough material to give much information on this subject. One specimen taken in March (St. 190) had large eggs in the oviduct and one specimen in the same month (St. 27) had embryos in the atrial cavity, but larvae were not found in any colony. Kott (1954) recorded embryos in January in her specimens from the neighbourhood of Enderby Land, but unfortunately they too were not fully developed. The embryos are very large, according to Kott.

REMARKS. Some of the 'Discovery' specimens were taken from near the type locality in the Palmer Archipelago, but others extend the known range of the species to the South Orkneys and South Georgia.

This species has two features unusual in the genus: (1) sharp division of the colony into a head which carries the oral and cloacal openings and a stalk which lacks them; and (2) the openings of cloacal canals from several systems into a common apical depression.

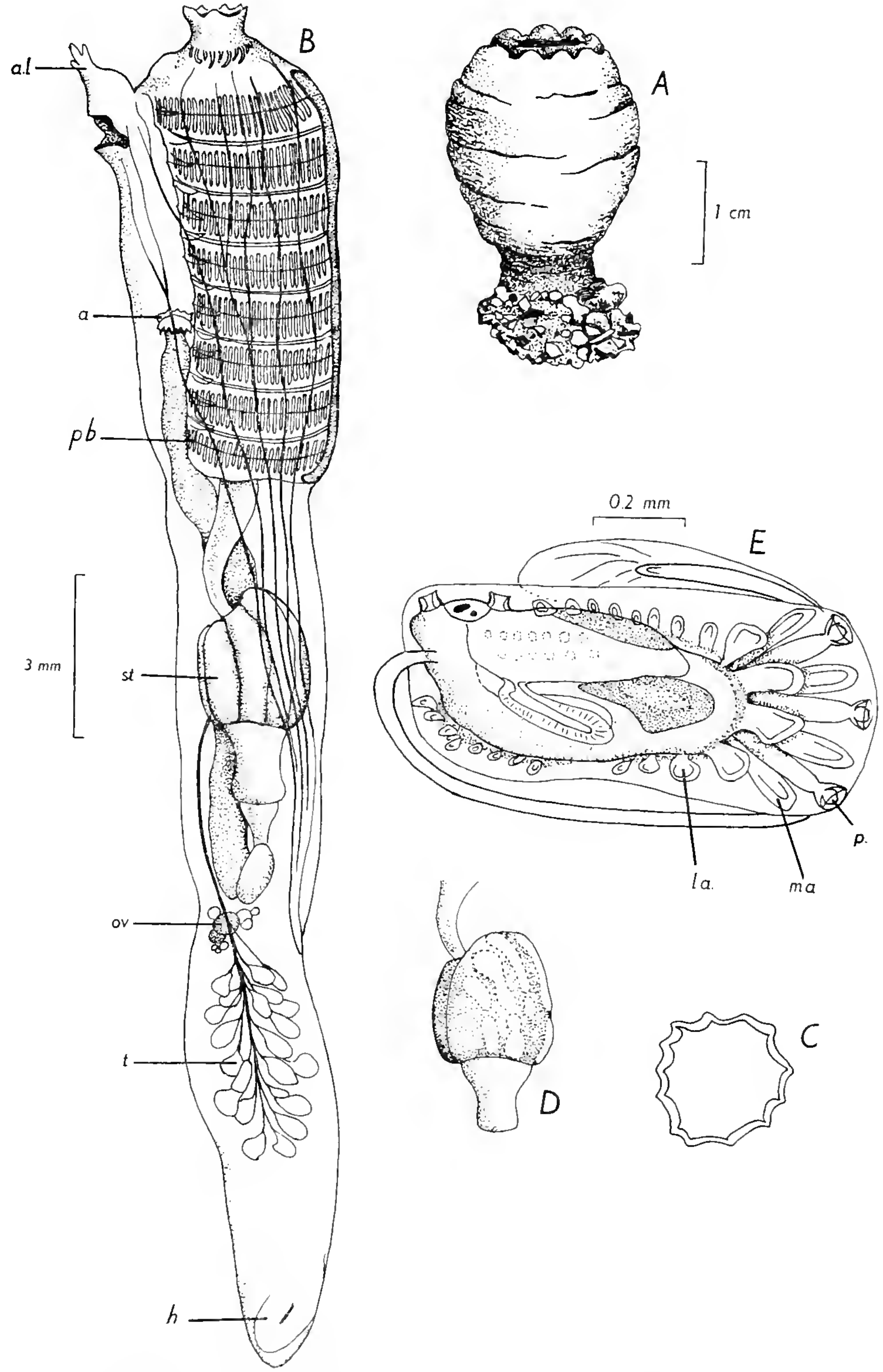
These are both characters found elsewhere principally in species of *Sycozoa*.

DISTRIBUTION. Western Antarctic (Graham Land, South Orkneys, South Georgia), Eastern Antarctic (Enderby Land).

Aplidium caeruleum (Sluiter) (Text-fig. 5)

Amaroucium caeruleum Sluiter, 1906, p. 16, pl. 1, figs. 13–16; pl. 4, fig. 49.
Aplidium caeruleum Kott, 1954, p. 172, fig. 66.

OCCURRENCE. St. 190: Palmer Archipelago, 93–126 m. ?St. 1563: Marion Island, 113–99 m. St. 1952: S. Shetlands, 376–383 m.



Text-fig. 5. *Aplidium caeruleum* (Sluiter): A, colony; B, zooid; C, transverse section of stomach; D, stomach with low broken folds (St. 1952); E, larva (St. 190).

COLONY (Text-fig. 5A). Most of the colonies in the collection show the characteristic shape of a stout club or cone attached by the narrow end. They reach a height of 4 cm. The specimens do not show the blue coloration which gives the species its name; Hartmeyer (1911) also found that much of his material was not blue, but van Name (1945) mentions the colour as being characteristic of most material. The superficial layer of the common test is firm and is impregnated with sand grains, but the test within the colony has no sand and is soft and clear, this being the usual condition in the species. Sand is also lacking immediately round the oral openings of the zooids and round the margin of the common cloacal opening. The zooids are arranged in a single peripheral layer with their oral openings forming a ring round the upper part of the colony, slight swellings marking the position of the zooids. The zooids number up to fifteen in a colony.

ZOOID (Text-fig. 5B). Table 8 shows the principle characters of the zooids of the 'Discovery' specimens compared with those described by Sluiter (1906), Hartmeyer (1911) and Kott (1954).

Table 8

	'Discovery'	*Sluiter*	*Hartmeyer*	*Kott*
Atrial languet	3-lobed	Toothed	3-lobed	3-lobed
Oral tentacles	20–30	20	?	?
Stigmata	8 rows, each crossed by a parastigmatic transverse bar; or 16 rows without bars	10 rows	?	16–20 rows, the anterior rows with parastigmatic transverse bars
Stomach	10–13 low folds sometimes broken	8 entire folds and a few short ones	No true folds; instead pigmented lines	Smooth externally; internally with papillae sometimes arranged in rows
Larva	Trunk 1·0 mm. long	Trunk 1·2 mm. long	?	Trunk 1·0 mm. long (measurement taken from fig. 66, Kott)
No. of larvae per breeding zooid	1–11	4 or 5	4 or 5	?

THORAX. The branchial sac is of a kind unusual in *Aplidium* in that parastigmatic transverse bars (*p.b.*) are often present. These cross all the rows of stigmata in some of the 'Discovery' specimens, but in others are entirely absent. As specimens with parastigmatic bars have only half the number of rows possessed by specimens lacking the bars, it is evident that each row crossed by a bar is later divided into two rows. This accounts for the large range in the number of rows. It may also explain the fact that Sluiter noted ten rows of stigmata but eighteen dorsal languets, the additional languets presumably corresponding in position to parastigmatic transverse bars which may have been present in parts of the branchial sac.

GUT. The true structure of the stomach is by no means certain. Deep and well-developed folds are apparently rarely or never present, and are sometimes represented by pigmented lines or rows of internal papillae. In the 'Discovery' specimens the folds are usually undivided (Text-fig. 5B, *st.*), but sometimes broken up (Text-fig. 5D). The anus is opposite the 5th row of stigmata.

GONADS. The gonads have the position usual in *Aplidium*, but the testis follicles (*t.*) are crowded together instead of being biserially arranged.

LARVA (Text-fig. 5E). The larva, with a trunk 1 mm. long, is unusually large for species of *Aplidium*. The papillae are not very widely spaced, and have stout stems. Four median ampullae (*m.a.*) are present, and on each side lies a series of lateral ampullae (*l.a.*) which number six according to Kott (1954), but are much more numerous in the 'Discovery' specimens. The lateral ampullae are attached to a ridge which extends on each side along the dorsal and ventral parts of the trunk. This arrangement is like that described by Carlisle (1952) in *Polyclinum aurantium* Milne Edwards.

The only colonies in the collection with larvae were two taken in March (St. 190); all the larvae from one colony have both ocellus and otolith (Text-fig. 5E), but all those from the other colony lack an ocellus. This is a very curious fact, but as the larvae and the zooids from which they come are identical in all other respects, I cannot doubt that both colonies are of *A. caeruleum*.

According to Sluiter (1906) and Kott (1954) the larvae are contained in a brood pouch, but Hartmeyer (1911) doubted the existence of a special pouch. In the 'Discovery' specimens the larvae were lying in the atrial cavity, as they normally do in species of *Aplidium*.

BIOLOGY. It is not possible to add anything regarding the general biology of the species from the scanty material available. Hartmeyer (1911), however, from a study of his rich material, found all stages of male and female ripeness at all seasons, the larvae not being confined to any one period. They were present, for instance, both in January and in July. This is a remarkable case of independence of temperature in the breeding cycle of an antarctic ascidian.

REMARKS. The identification of the specimens in the collection is not in doubt, except the single colony from Marion Island (St. 1563). In this colony all the zooids are degenerate and identification rests on the shape and texture of the colony, which closely agree with typical colonies of the species. There must remain considerable doubt, however, especially in view of the more northern latitude of the station.

DISTRIBUTION. Western Antarctic (Graham Land, South Shetlands), Eastern Antarctic (Kaiser Wilhelm II Land, MacRobertson Land, Enderby Land). (?Marion Island.)

Aplidium stanleyi sp.n. (Text-fig. 6A, B, C)

DIAGNOSIS OF SPECIES. Colony consisting of low heads arising from a sandy base. Zooids with the atrial opening a little way back along the dorsal side of the thorax. Twelve to fifteen rows of stigmata. Post-abdomen narrow, even with fully developed gonads. Stomach with twenty to twenty-four longitudinal folds. Testis a long series of small follicles.

OCCURRENCE. St. WS 229: Falkland Islands, 210–271 m.

HOLOTYPE. St. WS 229: size—12 mm. wide at base, 11 mm. high.

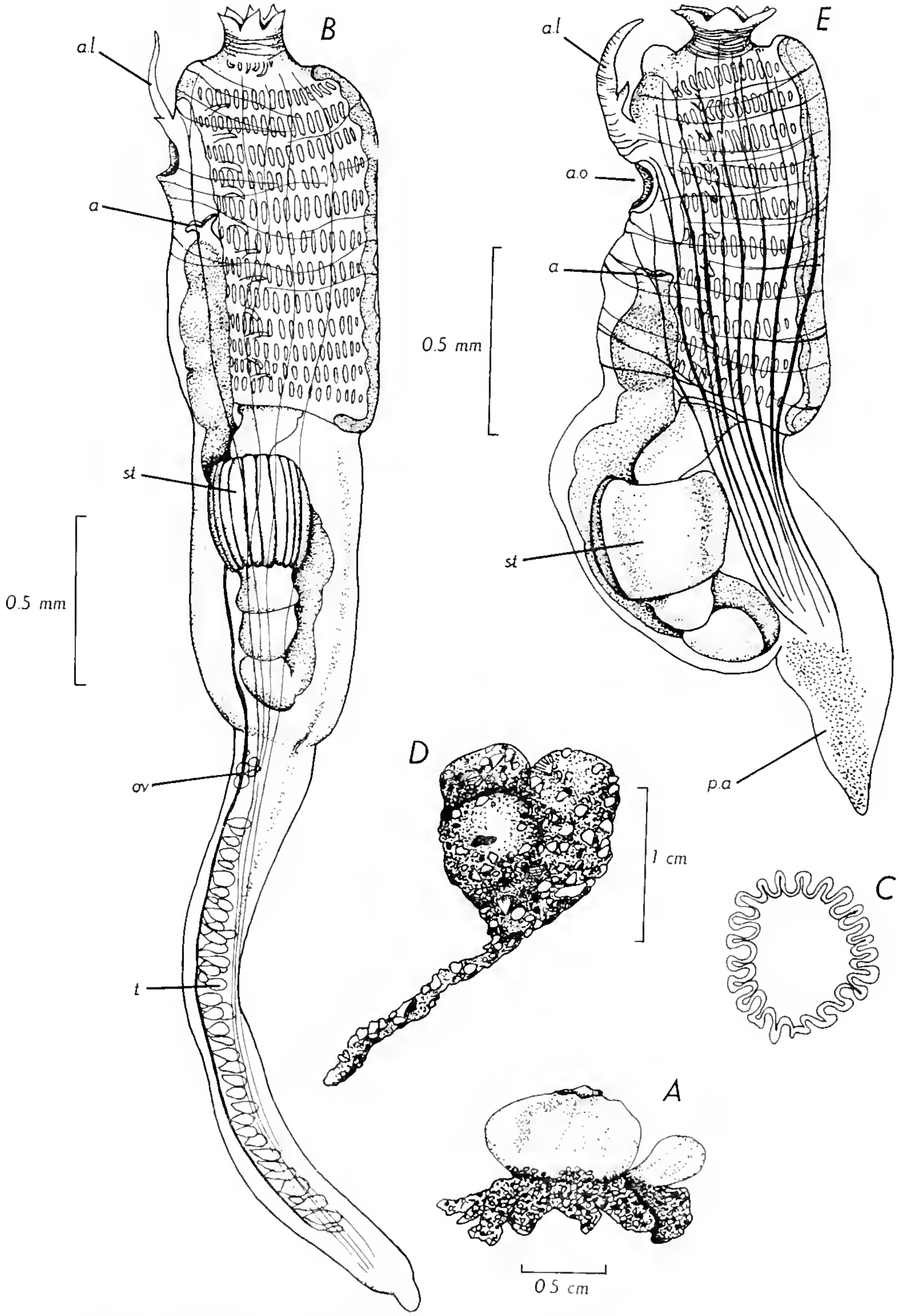
COLONY (Text-fig. 6A). This species is represented by many colonies taken in a single haul from the continental shelf round the Falkland Islands. The largest colony is 1·4 cm. high and 1·4 cm. wide. Typically each colony consists of one head or a few heads joined basally, where there is an expansion of the common test which is here heavily impregnated with sand. At its junction with this base, the head is narrowed and the upper part is expanded with a rather flattened or slightly dome-shaped apical end. The test material is sufficiently clear to allow the zooids to show through. They are arranged in a single system in each head, no head having been found with more than one common cloacal opening. The basal sandy test is often produced into a number of finger-like processes or broad lobes, and the colonies appear to have been loosely attached to the sandy substratum.

ZOOID (Text-fig. 6B). The zooids are small, averaging about 5 mm. in length, of which the thorax and abdomen account for about 2 mm.

THORAX. The oral siphon has six pointed lobes. The atrial opening is placed a short distance back along the dorsal side of the thorax, opposite to the 3rd row of stigmata, and is a simple round hole, bearing on its dorsal margin a languet (*a.l.*). The languet is sometimes simple and triangular, but more often is divided into a long narrow median lobe and a short pointed lobe at its base on each side. The muscles on the thorax are only moderately well developed. There are from twelve to fifteen rows of stigmata in the branchial sac, each row with about fifteen stigmata.

GUT. The oesophagus is short in all zooids examined, and the stomach (*st.*) barrel-shaped with from twenty to twenty-four narrow close longitudinal folds. The intestinal loop is usually rather short. The anus has two shallow lobes and is situated opposite the 5th or 6th row of stigmata in zooids with twelve rows.

POST-ABDOMEN. In some zooids the post-abdomen is short but when fully grown it is very long and narrow, extending far down into the basal sand-covered test. It is typically very slender, being only half the width of the abdomen.



Text-fig. 6. *Aplidium stanleyi* sp.n. (St. WS 229): A, colony; B, zooid; C, transverse section of stomach. *Aplidium quadrisulcatum* sp.n. (St. 939): D, colony; E, zooid.

GONADS. The ovary is represented in some zooids by a small group of ova in the upper part of the post-abdomen (*ov.*). The testis consists of a long narrow series of many small pear-shaped follicles occupying much of the length of the post-abdomen (*t*). No larvae were found.

REMARKS. This species is distinguished from all species of *Aplidium* described from South America, the Subantarctic, and the Antarctic by the following combination of characters: (1) colony small and loosely attached to a sandy substratum; (2) stomach with twenty to twenty-four folds; (3) post-abdomen conspicuously narrower than abdomen.

It most resembles three species from New Zealand: *A. phortax* (Michaelsen, 1924), *A. benhami* Brewin, 1946, and *A. adamsi* Brewin, 1946. From these species it is distinguished by characters (1) and (3).

DISTRIBUTION. Falkland Islands.

Aplidium quadrisulcatum sp.n. (fig. 6D, E)

HOLOTYPE. St. 939: size of colony 1 cm. in diameter.

DIAGNOSIS OF SPECIES. Colony of variable shape, with sand embedded in the test. Zooids small; oral siphon with six shallow or deep lobes; atrial opening about one-third of the length of the thorax from the base of the oral siphon; atrial languet with 1 median and 2 short lateral lobes; nine to eleven strong longitudinal muscles; 10 rows of stigmata; stomach with four or five indistinct folds.

OCCURRENCE. ?St. 935: North Island, New Zealand, 84 m. St. 939: North Island, New Zealand, 87 m.

COLONY (Text-fig. 6D). The colonies from St. 939 are small, the largest being 1·3 cm. in diameter. These colonies vary in shape from flat cushion-like masses to single or lobed ovate heads with a narrow stalk. Sand is present on the surface and throughout the common test, rendering the colonies very firm. Systems of zooids are not visible, but a single common cloacal opening is present in each small colony and on each lobe of the larger colonies. A few specimens from St. 935, which probably belong to this species, reach a diameter of 2·3 cm., and completely lack sand.

Table 9

	Colony	*Longitudinal muscles*	*Rows of stigmata*	*Stomach folds*
A. quadrisulcatum sp.n.	With sand	9–11	10	4 or 5
A. scabellum (Michaelsen)	With sand	1 strong dorsal muscle	20	6
A. nottii (Brewin)	No sand	10–12	14–16	4 or 5
A. novae-zealandae Brewin	With sand	14	14 or 15	4 or 5
A. oamaruensis (Brewin)	With sand	10	16–18	4
A. thomsoni Brewin	With sand	Concentrated on ventral side of post-abdomen	5	5 or 6

ZOOID (Text-fig. 6E). The zooid is small, not exceeding 2·0 mm. in length. In most zooids there is no post-abdomen, or a very short one, probably owing to the specimens having been collected out of the breeding season.

THORAX. The short wide oral siphon is divided into six broad, pointed lobes, and the oval atrial opening (*a.o.*), is situated opposite the 3rd and 4th rows of stigmata, that is about one-third of the length of the thorax from its anterior end. There is a triangular pointed atrial languet (*a.l.*) of variable length, with two short pointed lateral lobes near its base. Nine to eleven longitudinal muscles converge on the sides of the abdomen. Ten rows of short stigmata are usually present, with twelve to fifteen in each row.

GUT. The oesophagus is quite wide, and the squat stomach has four or five rather indistinct longitudinal folds. The divisions of the intestine are short. The wide rectum ends in the plain-edged anus opposite the 7th row of stigmata.

Gonads. None of the zooids examined showed any trace of gonads, and no embryos or larvae were found.

Remarks. The characters of *A. quadrisulcatum* are given in Table 9 for comparison with those of species from New Zealand and the Chatham Islands with which it is most likely to be confused. These species all have a small number of folds on the stomach, but can be separated by other characters.

Distribution. North end of North Island, New Zealand.

Aplidium seeligeri sp.n. (Text-fig. 4, C, D, E)

Holotype. St. 935. Size of colony 4 by 1·5 by 2·5 cm.

Diagnosis of species. Colony consisting of a head of variable shape borne on a short stalk. Zooids arranged in small round systems with central common cloacal openings. Zooids with six-lobed oral iphon and a very short atrial siphon surmounted by a triangular languet with two lateral lobes; ten to twelve equally spaced longitudinal muscles; thirteen to sixteen rows of stigmata; oesophagus quite long; stomach with nineteen to twenty-two folds.

Occurrence. St. 935: North Island, New Zealand, 84 m. St. 941: North Island, New Zealand, 128 m.

Colony (Text-fig. 4C, D). The larger of the two specimens (Text-fig. 4C) is a somewhat flattened mass, 4 cm. long, 2·5 cm. across, and 1·5 cm. in height; the lower part is narrowed to form a short tapering stalk apparently attached to the substratum by a small area. This specimen is buff-coloured in the preserved state, smooth and soft, with the zooids showing through as brown spots. The other colony (St. 941) (Text-fig. 4D) has an almost spherical head and a short stalk rather more than half the diameter of the head. This specimen is 1·5 cm. in total length. The surface is smooth and rather soft, and of a pale dirty buff colour through which the zooids can be faintly seen. In both colonies the zooids are arranged in small round systems of six to twelve zooids, with a small central cloacal opening.

Zooid (Text-fig. 4E). In well-expanded zooids the thorax and abdomen each measures about 1·8 mm., and the post-abdomen up to 5 mm.

Thorax. Six shallow lobes are present on the oral siphon, and the atrial opening (*a.o.*) is at the end of a very short siphon opposite the 3rd and 4th row of stigmata. There is a short triangular atrial languet with two small lateral lobes near the base. Ten to twelve slender longitudinal muscles are equally spaced round the thorax and continue along the sides of the abdomen and post-abdomen without appreciably converging in the post-abdomen. There are thirteen to sixteen rows of short oval stigmata, with about twelve stigmata in each row.

Table 10

	Colony	*Longitudinal muscles*	*Atrial opening*	*Stigmata*	*Oesophagus*	*Stomach*
A. seeligeri	Stalked	10–12	Short siphon	13–16 rows	Long	19–22 folds
A. phortax	Sessile	13 or 14	Sessile	10–13 rows	Short	23–26 folds

Gut. The oesophagus is more than twice as long as the stomach and narrows at both its upper and lower ends. The stomach is barrel-shaped with nineteen to twenty-two narrow continuous folds. The rectum is wide and ends in a simple anus at the level of the 10th row of stigmata.

Gonads. The post-abdomen of some zooids contains a series of small testis follicles (*t*), with a straight common sperm-duct. No ovary was present, but a few zooids had a single brown egg or developing embryo in the atrial cavity. In these embryos the rudiment of the trunk measured 0·52 mm. in length.

Remarks. *A. seeligeri* bears more resemblance to *A. phortax* (Michaelsen), a species also found in

New Zealand, than to any other species. The principle characters serving to distinguish these species are shown in Table 10.

Distribution. North end of North Island, New Zealand.

The genera *Synoicum* Phipps, *Aplidiopsis* Lahille, and *Polyclinum* Savigny differ from *Aplidium* in having the stomach without longitudinal folds. Their main distinguishing characters are shown in Table 11.

Aplidiopsis is intermediate between *Synoicum* and *Polyclinum*, but is apparently closer to *Synoicum* from which it differs only in having a constriction at the junction of abdomen and post-abdomen. It may be doubted whether this is a character of generic value but I retain *Aplidiopsis* because *A. discoveryi* sp.n. (see p. 51) confirms the generic characters.

Table 11

	Branchial papillae	*Stomach wall*	*Gut loop*	*Post-abdomen*	*Gonads*
Synoicum	Absent	Areolated or smooth	Not twisted	Not narrowed to form a pedicel joining abdomen	Testis compact, sometimes partially surrounding ovary
Aplidiopsis	Absent	Smooth	Not twisted	Narrowed to form a pedicel joining abdomen	Testis compact partially surrounding ovary
Polyclinium	Present	Smooth	Twisted	Narrowed to form a pedicel joining abdomen	Testis compact partially surrounding ovary

Genus Synoicum Phipps, 1774

Synoicum adareanum (Herdman) (Text-fig. 7E; Pl. I, fig. 6)

Polyclinum adareanum Herdman, 1902, p. 195, pl. 22, figs. 1–9.
For synonymy see van Name 1945, p. 59.

Occurrence. St. 175: S. Shetlands, 200 m. St. 1660: Ross Sea, 351 m. St. WS 33: S. Georgia, 130 m. St. MS 71: S. Georgia, 110–60 m.

Colony. The numerous colonies from St. 1660, in the Ross Sea, are very typical of this species. There is a stalk of variable length with diameter always less than that of the head, but sometimes only slightly less. The stalk is brown, tough, and transversely wrinkled. The head is ovate or roughly conical, smoother than the stalk, grey or pale pink-grey. Systems of zooids are circular and not very large. Kott's (1954) statement that the systems in her specimens were from 20 to 80 mm. in diameter is difficult to understand, as the diameter of the whole head rarely exceeds 100 mm. Sluiter (1906) records a specimen 180 mm. long and 120 mm. in diameter. A large specimen in the 'Discovery' material has the head 70 mm. long and the stalk 30 mm., and another specimen has a total length of 130 mm. This material is therefore among the largest yet recorded. The colonies may be single, but often two stalks arise from a common base. There is an error (possibly typographical) in van Name's statement that Sluiter's (1906) illustration was of a specimen 10 cm. high and 65 cm. in diameter; the diameter should have been 6·5 cm.

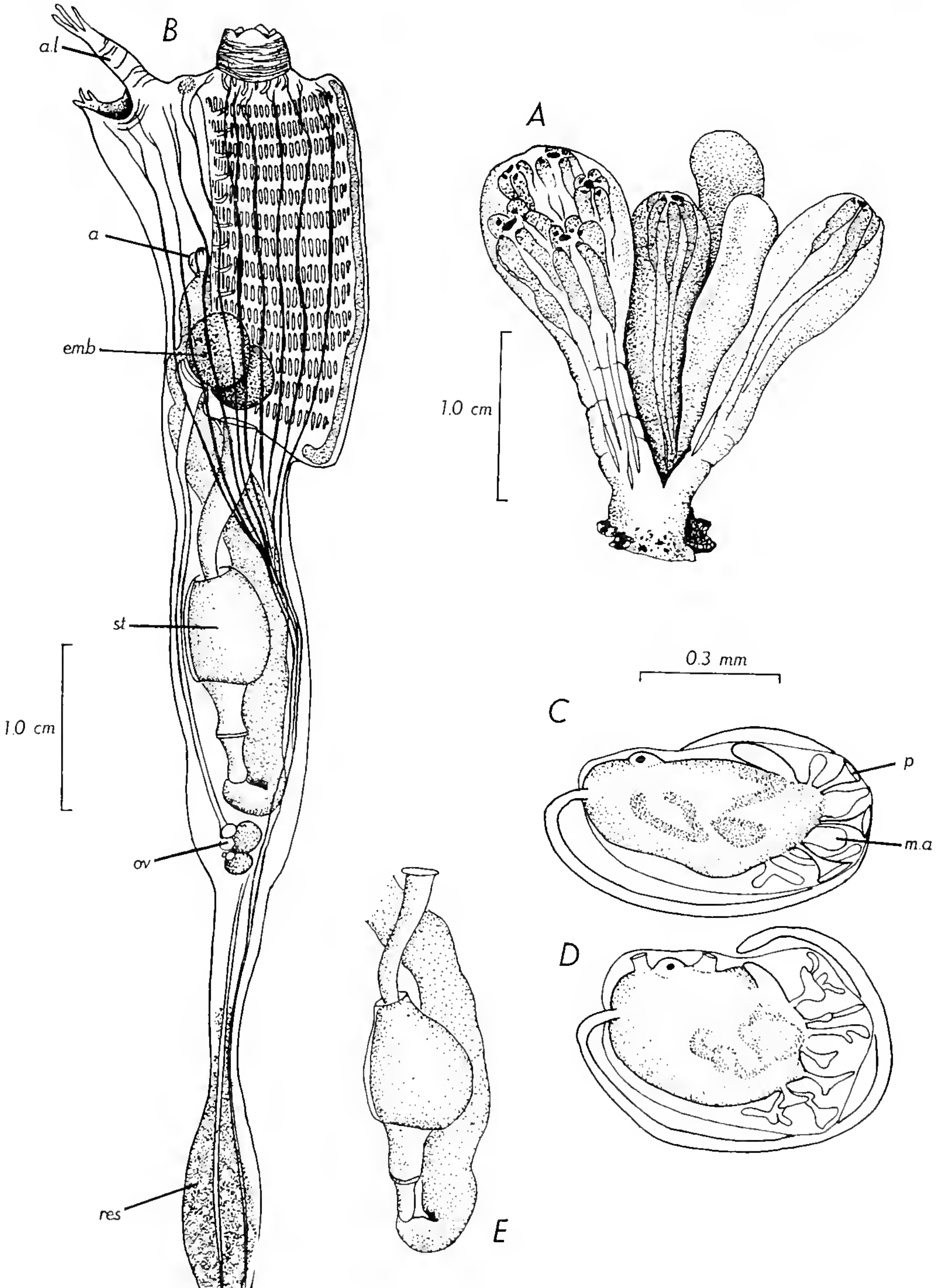
Several small colonies from South Georgia, which I place in this species, also have a short stalk and rounded head with distinct circular systems of zooids. The largest of these colonies is 18 mm. high.

Zooid. The zooids may attain 12 mm. in length, of which the thorax and abdomen commonly occupy about 4 mm.

Thorax. The number of oral tentacles in several zooids examined varied between sixteen and twenty-four, a number considerably greater than that given by van Name (1945) who recorded about twelve. All zooids examined had eighteen to twenty rows of stigmata, each row with thirty, or a few more, stigmata. Van Name (1945) states that there are 'a dozen or more' stigmata in a row but Kott (1954) found twenty to thirty.

GUT. In uncontracted zooids the stomach (Text-fig. 7E) has a narrow anterior end, is widest just behind the middle and somewhat narrowed posteriorly. The anteroventral margin is slightly concave. In the 'Discovery' specimens the stomach is quite sharply marked off from both the oesophagus and the intestine, although Kott (1954) did not find this in her material. The anus is situated opposite the 13th or 14th row of stigmata and has two lips which are usually reflected.

REMARKS. The synonymy of this species is still obscure. According to van Name (1945), *S. georgianum* Sluiter and *S. kohli* Sluiter should probably both be referred to *S. adareanum*, but I believe that



Text-fig. 7. *Synoicum georgianum* Sluiter (St. 149): A, colony; B, zooid; C, fully developed larva; D, larva showing break-up of papillae and ampullae. *Synoicum adareanum* (Herdman) (St. 1660): E, gut this is not so (see below). If *S. adareanum* extends to South Georgia, and I have here accepted several specimens from that area as *S. adareanum*, the small size of these specimens might be explained by less favourable conditions prevailing on the boundary of the geographical range.

DISTRIBUTION. Antarctic (Graham Land, South Shetlands, South Georgia, Ross Sea, Kaiser Wilhelm II Land, Enderby Land, Adélie Land, MacRobertson Land), Subantarctic (Kerguelen).

Synoicum georgianum Sluiter (Text-fig. 7 A, B, C, D; Pl. I, fig. 7)

Synoicum georgianum Sluiter, 1932, p. 11, figs. 9, 10.

OCCURRENCE. St. 140: S. Georgia, 122–136 m. St. 144: S. Georgia, 155–178 m. St. 149: S. Georgia, 200–234 m. St. 474: S. Georgia, 199 m. St. 1941: S. Georgia, 55–22 m. St. WS 794: Patagonian Shelf, 123–126 m. St. MS 10: S. Georgia, 26–18 m. St. MS 74: S. Georgia, 22–40 m.

COLONY (Text-fig. 7A; Pl. I, fig. 7). The colonies are all small, never exceeding 2·5 cm. in length. Two, three or four heads generally arise from a common base, are narrow in their lower part and gradually widen towards the distal end. Some colonies consist of many small heads attached to a mass of basal, somewhat root-like processes, a condition approaching that described by Sluiter for the type colonies, and in these colonies the individual heads constitute single systems each with an apical common cloacal opening, as described by Sluiter. In other, larger, heads there are up to five round systems of zooids. Usually the surface of the colony is bare, but sometimes there is a coating of sand or broken shell which is confined to the outer layer of the test. The test material is very clear, soft and flexible.

ZOOID (Text-fig. 7B). The size and proportions of the zooid are variable, but often the thorax is about 2 mm. long and the abdomen 2 or 3 mm. The post-abdomen is narrow and may be longer than the thorax and abdomen combined. In some zooids the post-abdomen contains reserve material (*res.*) similar to that often stored in the post-abdomen of other polyclinid species.

THORAX. The oral siphon has six lobes, which are sometimes very shallow. The anterior margin of the atrial siphon is elongated into a languet (*a.l.*) almost always provided with three narrow teeth. On the posterior margin there are generally three short teeth.

BRANCHIAL SAC. Thirteen to fifteen rows of stigmata are present, each with about thirty stigmata.

GUT. The gut is indistinguishable from that of *S. adareanum*, except that the stomach is not pear-shaped, but this is a slight difference. The anus lies opposite the 8th row of stigmata, and is provided with two lips.

GONADS. In two of the specimens collected in December gonads are present. The ovary (*ov.*) is small and compact, with few ova, and lies a short distance below the loop of the intestine, not, as in Sluiter's specimen, overlapping the lower part of the loop. In a few zooids there is a long series of testis follicles below the ovary.

LARVA (Text-fig. 7C, D). One colony (St. 144, 5. i. 1927) had fully developed larvae in the atrial cavities of the zooids. These varied from 0·54 to 0·64 mm. in length from the end of the papillae to the base of the tail. In the earlier stages of development (Text-fig. 7C) the three anterior papillae and the four median ampullae were seen together with a few large dorsal and ventral (lateral?) ampullae. In later stages the gut and siphons could be seen and the sensory vesicle containing only a spherical otolith and no trace of the ocellus. Still more advanced larvae (Text-fig. 7D) showed a breaking-up of the papillae and ampullae: this stage may represent the early metamorphosis of larvae retained beyond the normal period in the atrial cavity.

REMARKS. In dealing with *S. adareanum* I have already mentioned that *S. georgianum* has been regarded as a synonym (van Name, 1945). Sluiter pointed out, however, in his original description, that the formation of the colony in *S. georgianum* was different, and the colonies described above confirm this. As these colonies contain mature zooids, they are not to be regarded as young specimens. Corresponding differences in the zooids are more difficult to find, but Table 12 lists the constant distinctions shown by the colony and zooids of the specimens in the 'Discovery' collections.

Table 12

	S. adareanum	*S. georgianum*
Colony	Stalk firm, opaque, wrinkled and sharply marked off from head. Colony massive	Stalk and head not sharply marked off from each other; both transparent. Colony slender
Zooid	18–20 rows of stigmata	13–15 rows of stigmata
	Anus opposite 13th row	Anus opposite 7th or 8th row
	Stomach pear-shaped	Stomach not pear-shaped

Previous accounts do not always bear out these distinctions. Thus the number of rows of stigmata in *S. adareanum* is variously given as ten to twelve (Sluiter, 1906), fifteen to twenty (Kott, 1954), fourteen or fewer up to twenty (van Name, 1945), and about twenty (Herdman, 1902). The relative position of the anus is not clear in previous descriptions, and the stomach has been variously described but was often stated to be contracted. The most reliable distinction appears to be the form and habit of the colony, and accounts of *S. adareanum* agree with most of the characters listed above.

DISTRIBUTION. Antarctic (South Georgia), Subantarctic (Patagonian Shelf).

Synoicum giardi (Herdman) (Text-fig. 8A; Pl. I, fig. 8)

Morchellium giardi Herdman, 1886, vol. 14, p. 181, pl. 25, figs. 1–3.
Synoicum giardi Hartmeyer, 1911, p. 550, pl. 47, fig. 7, pl. 56, figs. 1–3; Kott, 1954, p. 169, fig. 62.
For other references see Kott, 1954, p. 169.

OCCURRENCE. St. WS 27: S. Georgia, 107 m. St. MS 64: S. Georgia, 7–15 m. St. MS 71: S. Georgia, 110–60 m.

COLONY (Pl. I, fig. 8). One colony measures 2·7 by 1·6 cm. in diameter, and about 0·5 cm. in thickness, and is thus rather flatter than the colonies of this species already described by Herdman (1886), Hartmeyer (1911) and Kott (1954). Another colony is 3 cm. long and 1·5 cm. in thickness, being of a low-dome-like shape. The surface of the colonies is smooth, and the colour grey to buff, with star-shaped markings produced by the regular arrangement of the zooids in circular systems. No sand is present on the surface or within the colonies, and the common test is semi-cartilaginous in texture.

ZOOID (Text-fig. 8A). The thorax and abdomen together measure about 3 mm. and the post-abdomen is at least as long. Some reserve material (*res.*) was present in the lower part of the post-abdomen of a few zooids, and this part was frequently bent so as to lie almost parallel to the base of the colony.

THORAX. There are six moderately developed lobes on the oral siphon, and the atrial siphon has a simple languet. Twelve to fourteen rows, each with about twelve stigmata, are present in the branchial sac, compared with fourteen to sixteen rows in Hartmeyer's and eighteen in Kott's specimens.

GUT. The gut is typical of the species, with an ovoid stomach having conspicuous areolations which, however, do not project so much as in the specimens described by previous authors. The anus is level with the 8th or 9th row of stigmata.

GONADS. In a few zooids a small ovary (*ov.*) was present at some distance below the end of the intestinal loop, and a few poorly developed testis follicles (*t.*) occurred in a series posterior to the ovary.

REMARKS. All the previous records of this species are from the region of Kerguelen, and the 'Discovery' specimens therefore extend the range to South Georgia and suggest that the species may have a wider distribution in the Antarctic.

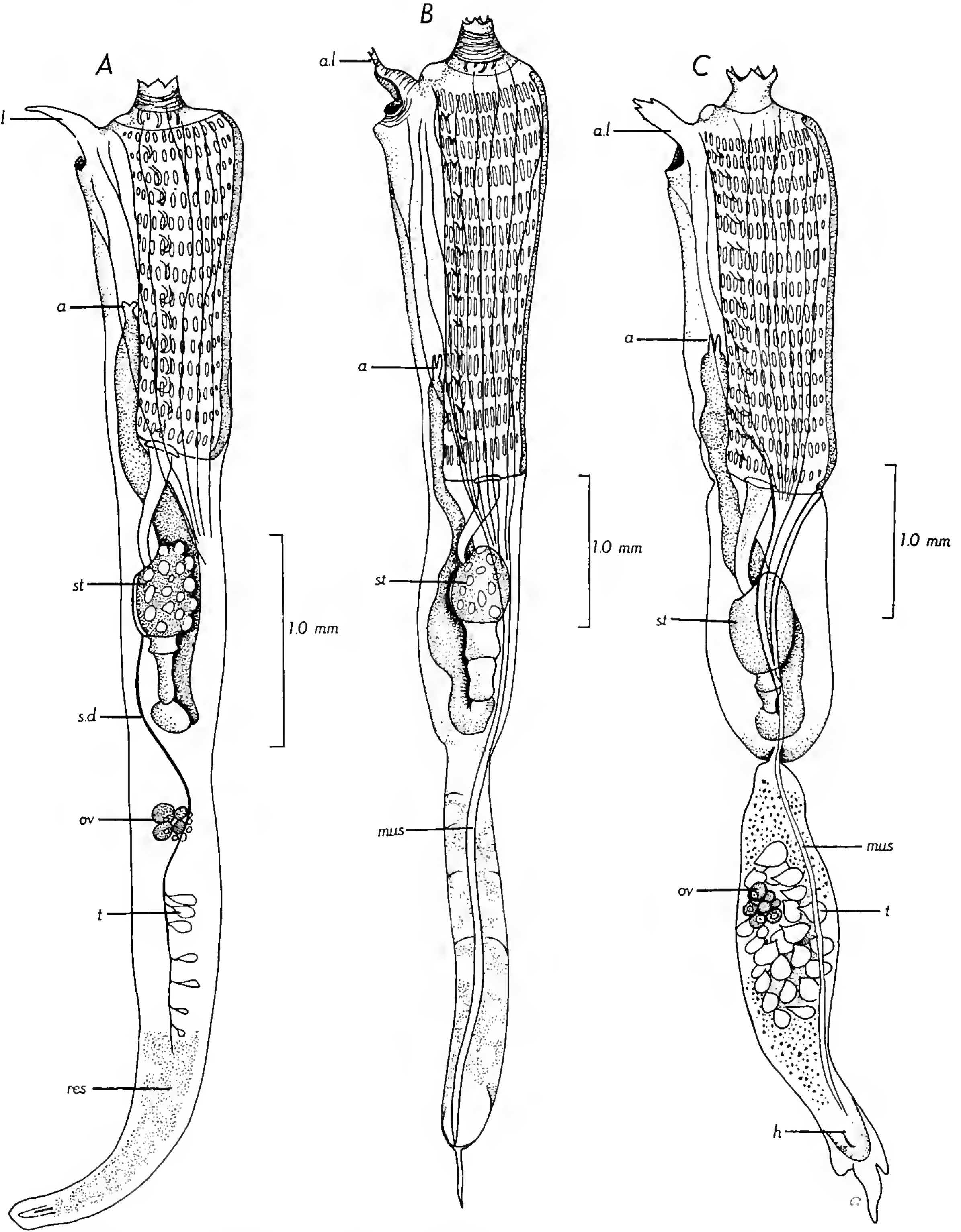
DISTRIBUTION. Antarctic (South Georgia), Subantarctic (Kerguelen).

Synoicum kuranui Brewin (Text-fig. 8 B, Pl. I, fig. 9)

Synoicum kuranui Brewin, 1950, p. 355, text-fig. 1.

OCCURRENCE. St. 935: North Island, New Zealand, 84 m.

COLONY (Pl. I, fig. 9). A number of stalked heads are present in the collection, but it is uncertain whether these represent the heads of a single colony or are distinct colonies. The longest of these



Text-fig. 8. *Synoicum giardi* (Herdman) (St. MS 71): A, zooid. *Synoicum kuranui* Brewin (St. 935): B, zooid. *Aplidiopsis discoveryi* sp.n. (St. 941): C, zooid.

pieces is 4·5 cm., of which the head occupies about 1 cm. The average lengths are about 1·0 cm. for the head and 2·5 cm. for the stalk. The head is conical, ovoid, or inverted conical, and has a greatest diameter about twice that of the stalk. The stalk is of uniform diameter except where it expands on joining the head. Both head and stalk have a coating of sand and broken shell, but the coating is thicker on the stalk. The head is fairly soft and the stalk hard. The zooids are arranged roughly at right angles to the surface of the head of the colony. A longitudinal section of the colony shows that the thorax and abdomen of the zooids form a uniform peripheral layer and that the post-abdomens are contained in the core. Sand is relatively scarce in the peripheral layer and densely packed in the core where it occupies most of the space between the post-abdomens. Sand is also abundant within the stalk.

ZOOID (Text-fig. 8B). The thorax averages 3 mm. and the abdomen 1·5 mm. in length; the post-abdomen varies greatly and often extends for many millimetres down into the stalk. When preserved in alcohol the zooids are brown.

THORAX. The oral siphon is moderately wide and its rim scarcely lobed. The short atrial siphon is far forward, with a small simple opening, and a strap-like bifid languet (*a.l.*). There may be a small tooth on the posterior margin of the atrial opening. Nine or ten thin longitudinal muscles pass down the sides of the thorax and condense into a strong band (*mus.*) which extends to the end of the post-abdomen. The oral tentacles are slender and few, apparently about eight in number. Fourteen rows of stigmata are usual, each with sixteen to eighteen stigmata. The dorsal languets are short and curved.

GUT. The oesophagus is narrow and curved so that it enters the antero-dorsal side of the stomach. The walls of the stomach are marked by rather few and not very prominent round areolations. Sometimes these are reduced to little more than superficial marks. The anus, which lies opposite the 11th row of stigmata, has two distinct lobes.

GONADS. In none of the zooids was any trace of gonads found, nor were larvae found.

Table 13

	S. kuranui (type material)	*S. kuranui* ('Discovery' material)	*S. arenaceum*
Colony	Capitate heads united by basal mass	Capitate heads, possibly originally united at the base	Cylindrical heads united by basal mass
Atrial languet	Moderate length, with 3–5 short apical lobes	Moderate length with 2 short apical teeth	Long, with 2 or 3 apical teeth
Longitudinal muscles	10–13, slender	9 or 10, slender	About 5, wide
Stigmata	10 rows, each with 14 or 15 stigmata	14 rows, each with 16–18 stigmata	15 rows, each with 12 stigmata
Stomach	Low areolations	Low areolations	Smooth or with faint irregular marks
Gonads	Ovary distant from intestinal loop	Not developed	Ovary distant from intestinal loop

REMARKS. Brewin (1950) pointed out the resemblance between this species and *S. arenaceum* (Michaelsen, 1924), but maintained that the zooids differ specifically. Table 13 gives a comparison between Brewin's type material, the 'Discovery' specimens, and *S. arenaceum*.

The similarities between the type specimens and those in the 'Discovery' collection indicate that they are of the same species. It is difficult, with the limited material, to decide whether *S. arenaceum* is a separate species, especially as the 'Discovery' specimens are in some respects intermediate between the type specimens of *S. kuranui* and *S. arenaceum*, e.g. in the number of rows of stigmata.

With the present evidence it seems best to recognize *S. kuranui* and *S. arenaceum* as separate species, while admitting that they may have to be united if more specimens become available.

DISTRIBUTION. Northern part of North Island, New Zealand.

Genus **Aplidiopsis** Lahille, 1890

Aplidiopsis discoveryi sp.n. (Text-fig. 8C)

HOLOTYPE. St. 941. Size of colony 1·5 × 1·2 × 0·7 cm.

DIAGNOSIS OF SPECIES. Colony of irregular shape, with several common cloacal openings. Zooids with six pointed oral lobes and a wide simple or toothed atrial languet. About fourteen rows of stigmata; no papillae on transverse bars. Stomach smooth; intestinal loop not twisted. Post-abdomen arising from abdomen by a narrow pedicel. Testis follicles in an ovoid or elongated mass but not serially arranged; ovary embedded amongst testis follicles.

OCCURRENCE. St. 941: North Island, New Zealand, 128 m.

COLONY. The colony is an irregular simple mass, not divided into lobes, and broadly attached to a barnacle shell. The common test is semi-transparent, and, there being no sand on or within the test, the zooids are visible. They are arranged in several small systems each with an oval or slit-like common cloacal opening.

ZOOID (Text-fig. 8C). Zooids vary from 4·5 to 7·5 mm. in total length. The thorax is 2–3 mm. long, slightly wider than the abdomen which measures 1·5–2·5 mm. in length; the post-abdomen is generally at least as long as the abdomen. The size of the post-abdomen, however, varies according to the degree of development of the gonads; it is narrow and attached to the abdomen by a short and slender pedicel. Pigment, which in the preserved state is orange in colour, is present on much of the body wall, especially in the post-abdomen.

THORAX. The oral siphon has six pointed lobes, and the round atrial opening, which is opposite the first or second row of stigmata, is surmounted by a fairly wide simple or distally toothed languet (*a.l.*). Eight to ten narrow longitudinal muscles run down each side of the thorax. At the posterior end of the thorax the muscles condense to form a single band on each side, and the left band passes over to the right ventral side of the abdomen where it unites with the right band. The single muscle (*mus.*) thus formed continues into the post-abdomen and ends at its posterior end.

Fourteen or fifteen rows of stigmata are present, each with fifteen to twenty stigmata. The transverse bars bear the pointed triangular dorsal languets, but no papillae.

GUT. The oesophagus is quite long and narrow, and enters the stomach on its oblique antero-dorsal face. The stomach is ovoid, with the anterior end generally wider than the posterior. Two short narrow chambers constitute the post-stomach. The intestine makes a simple loop. The rectum extends to the level of the 10th row of stigmata and ends in a two-lipped anus (*a*).

GONADS. Much of the post-abdomen is occupied by the bulky testis (*t*) composed of numerous pear-shaped follicles. The follicles, instead of being serially arranged as in *Aplidium*, are grouped into an ovoid or somewhat elongated mass as in *Polyclinum*. As in that genus also, the ovary (*ov.*) is a small body embedded amongst the testis follicles. Neither sperm duct nor oviduct could be distinguished in the 'Discovery' specimen.

REMARKS. No other species of *Aplidiopsis* is known from New Zealand. *A. discoveryi* is not likely to be confused with any other species hitherto described.

DISTRIBUTION. North end of North Island, New Zealand.

Genus Protopolyclinum gen.n.

DIAGNOSIS OF THE GENUS. A genus of the family Polyclinidae with the atrial siphon opening directly on the surface of the colony, not into a common cloacal cavity; the zooids divided into thorax, abdomen and post-abdomen, the post-abdomen joined to the abdomen by a narrow neck, and containing the gonads and heart, and having muscles in its body wall; the branchial sac with papillae on the transverse bars, and the intestine not twisted as in *Polyclinum*.

Protopolyclinum pedunculatum gen.n., sp.n. (Text-fig. 9, Pl. I, fig. 10)

HOLOTYPE. Size: stalk, 12·6 cm.; head, 1·4 cm.

OCCURRENCE. St. 934: North Island, New Zealand, 92–98 m.

COLONY (Pl. I, fig. 10). There are four specimens, measuring, including the stalk, 10, 12, 13 and 14 cm. The heads have respectively the following measurements:

Length (mm.)	6, 10, 14, 14
Greatest diameter (mm.)	5, 7, 10, 10

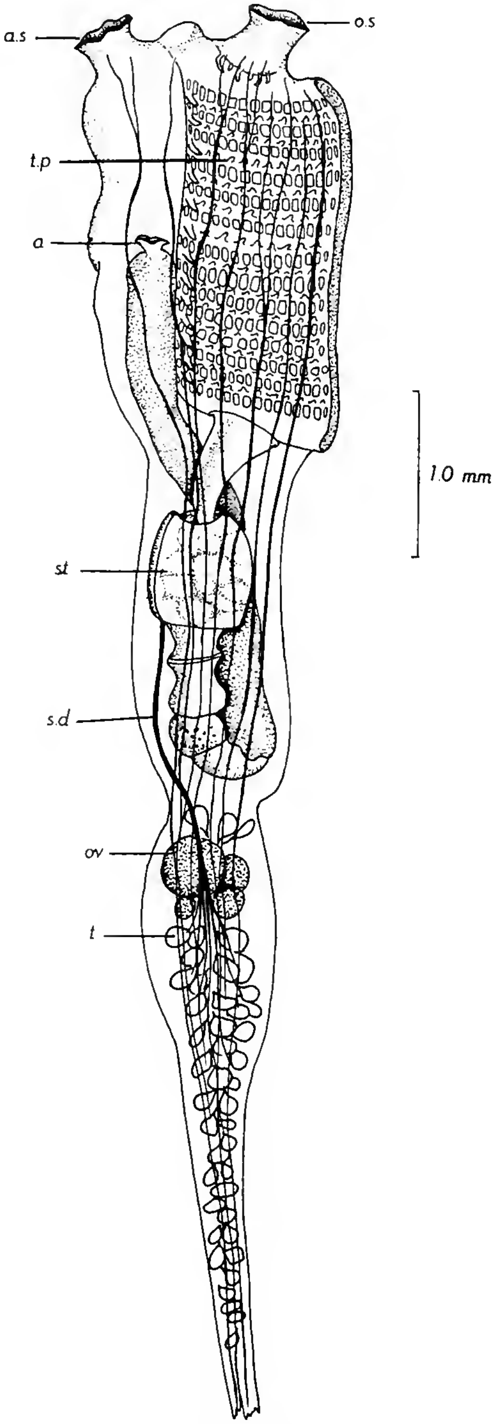
The head of the colony is ovoid, and usually slightly narrower towards the point where it joins the stalk. In the preserved state it is pale yellow grey, and of a soft consistency. In most of the specimens the stalk is widest at its junction with the head, but in the two smallest colonies the greatest width is a little way below the head. The lower half or quarter of the stalk becomes gradually narrower, so that near the point of attachment it has a diameter of only 1 mm. At its widest it may reach a diameter of 4 mm. Immediately below the narrowest part, the stalk expands to form a wider base by which the colony is attached to the substratum. The two smallest heads arise from a single expanded basal mass of test and, although the other two are separate, it is possible that originally all four specimens were members of a single complex colony. The stalk is firmer than the head, especially in its lower half. In its upper part it has the same colour as the head, but the lower part becomes gradually darker and more orange coloured. A series of dark rings round the stalk gives it an annulated appearance.

The zooids are not arranged in systems, and have no apparent order in the head.

ZOOID (Text-fig. 9). The zooid is divided into thorax, abdomen and post-abdomen. In a specimen of average size these measure respectively about 2·7, 2·0 and 4·0 mm.; these lengths do not include the long post-abdominal process which extends for several centimetres down inside the stalk.

THORAX. The thorax is wider than the other two divisions of the zooid. The oral (*o.s.*) and atrial (*a.s.*) siphons are both short and wide, and show no lobes or only very shallow ones. The siphons are placed close together at the anterior end of the thorax. The atrial siphon opens directly on the surface of the colony and not into a common cloacal cavity as in other members of the family Polyclinidae. On each side of the thorax there are about six longitudinal muscles, divided into a few branches at their upper end, and converging as they approach the abdomen. Longitudinal muscles are present not only on the abdomen, but also down the whole length of the post-abdominal process. There are about twelve simple oral tentacles arranged in a single circle at the base of the siphon. The dorsal tubercle is a small ovoid body, with a simple longitudinal slit. The branchial sac has about thirteen rows of stigmata which are rather wide and rectangular and number about sixteen in a row. On the transverse bars of the branchial sac there are small papillae similar to those in the genus *Polyclinum*. The dorsal languets are short and curved.

GUT. The oesophagus is of moderate length and width. The stomach is wide and roughly barrel-shaped, with the walls almost smooth, but showing large, faint areolations or ovoid markings. In some zooids these are outlined by little more than slight irregular transverse ridges. The post-stomach is divided into two chambers by an expanded ring, and the mid-gut also has two chambers, the first of which has a granulation on the walls. At its junction with the mid-gut the rectum has a pair of small lobes as in other members of the family. The loop of the intestine is not twisted as in *Polyclinum*, and the post-stomach and mid-gut lie on the right side of the rectum as in *Aplidium*. The anus has two lips, and lies about halfway along the length of the branchial sac opposite the 7th row of stigmata.



Text-fig. 9. *Protopolyclinum pedunculatum* gen.n., sp.n. (St. 934): Zooid.

Post-abdomen. A narrow and very short neck joins the post-abdomen to the abdomen. Below this neck the post-abdomen swells to accommodate the gonads. The ovary (*ov.*) lies near the anterior end of the post-abdomen and has a few ova of various sizes. A few testis follicles lie anterior to the ovary, but most of them are posterior to it (*t*). They are not arranged in a single or double series as they commonly are in *Aplidium*, but instead form, immediately below the ovary, a wide mass which gradually decreases in thickness and passes into the narrow posterior part of the post-abdomen as a single series of follicles. The sperm-duct (*s.d.*) as it passes back over the ovary divides into several smaller ducts which spread out to the testis follicles. Below the level of the testis the post-abdomen continues as a slender process which passes downwards inside the stalk of the colony for a distance of several centimetres. This lower process is divided by a central septum separating the two blood channels. The walls of the process are provided with thin longitudinal muscles. Near the lower end of the post-abdominal process there is often seen an accumulation of cells containing reserve material. At its extreme lower end is the heart, a simple U-shaped tube.

Larva. Some zooids in one colony contained a few larvae which unfortunately were not, I believe, fully developed. The most advanced of these larvae measures about 0·7 mm. from the end of the papillae to the base of the tail. There are three anterior papillae, flanked on each side by a row of four rounded ampullae. No epidermal vesicles are present at the stage of development represented by these larvae. There is an ocellus and an otolith. The tail when coiled round the larva reaches to about the sensory vesicle.

Remarks. With the exception of the atrial siphon which opens directly to the exterior, all the characters of this interesting genus indicate that it should be placed in the subfamily Polyclininae. The existence of branchial papillae and the form of the post-abdomen suggest a systematic position closer to *Polyclinum* than to *Aplidium*. But it is separated from *Polyclinum*, not only by the absence of common cloacal cavities, but also by the presence of muscles on the wall of the post-abdomen. *Protopolyclinum* probably branched off from the primitive *Polyclinum* stock after that stock had acquired its main characters, but before all of them had been fixed as we know them in recent species. Thus the loss of post-abdominal muscles had not occurred and probably the arrangement of zooids in systems with common cloacal cavities had not yet been acquired. It is possible, however, that common cloacal cavities were originally present and subsequently lost, but this seems unlikely for the possession of these structures must be assumed to be useful as they are a common feature in several unrelated groups of compound ascidians. If these assumptions about the origin of *Protopolyclinum* are correct, the two main lines of the Polyclininae typified by *Polyclinum* and *Aplidium* respectively must have acquired common cloacal cavities independently of each other, an interesting case of convergent evolution.

The presence of a stalk shows a degree of specialization which finds a parallel not in the Polyclinidae but in the Polycitoridae, where *Sycozoa* has a similar form.

DISTRIBUTION. North end of North Island, New Zealand.

Subfamily EUHERDMANIINAE Seeliger, 1906

Genus **Ritterella** Harant, 1931

Harant (1931) created the genus *Ritterella* for a species described and named by Ritter & Forsyth (1917) as *Amaroucium aequali-siphonalis*. This genus differs from *Aplidium* (syn. *Amaroucium*) only in having the two siphons equal and both opening directly on the surface of the colony. Oka (1933) created the genus *Sigillinaria* for a species *S. clavata*, the genus being distinguished from *Aplidium* by the same single character. *Sigillinaria* is therefore a synonym of *Ritterella*. This is not always recognized, and some authors use the name *Sigillinaria* (van Name, 1945; Brewin, 1950), while others use *Ritterella* (Huus, 1933, Tokioka, 1953).

Ritterella vestita sp.n. (Text-fig. 10)

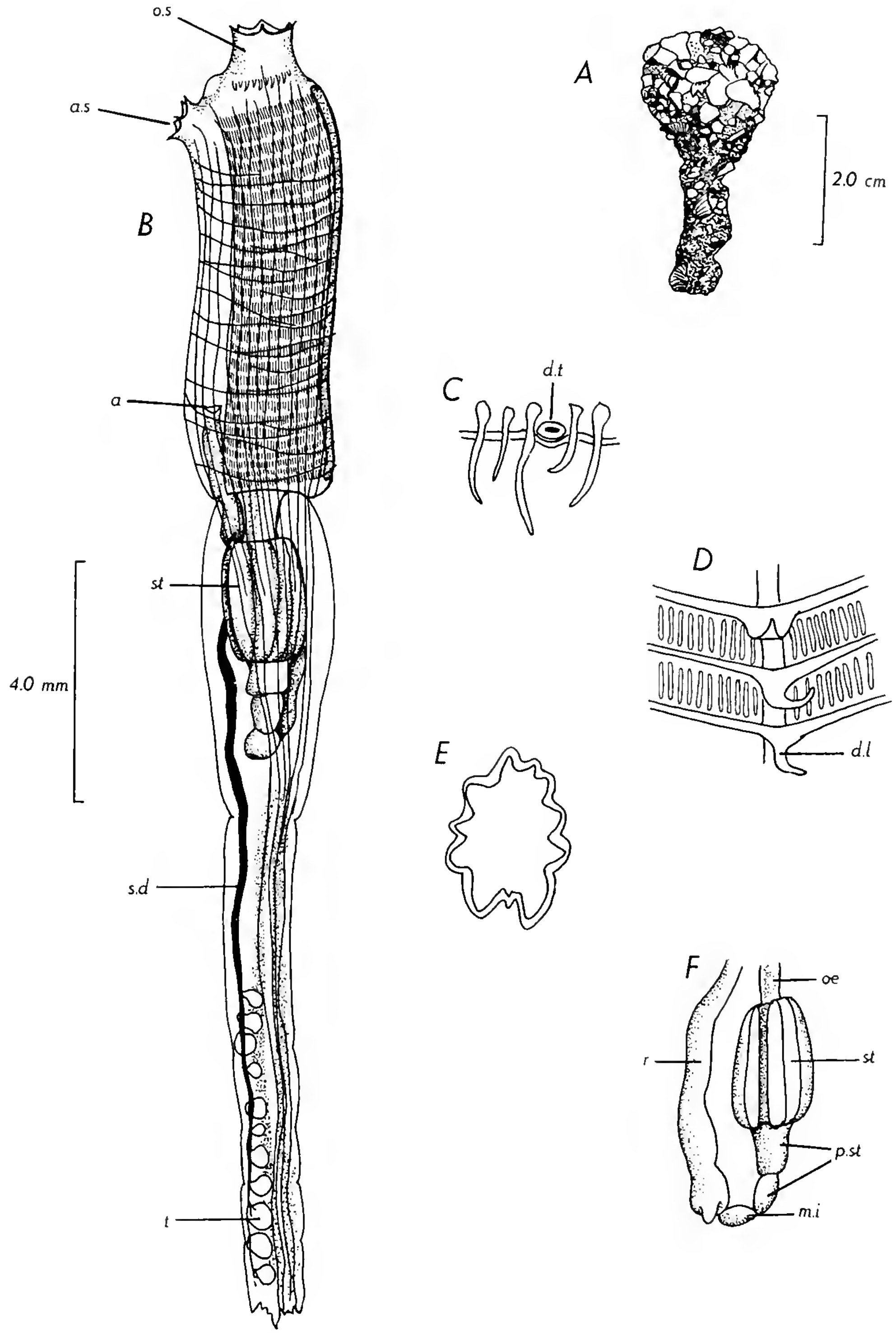
DIAGNOSIS OF SPECIES. Zooids completely embedded; oral and atrial siphons each with six shallow pointed lobes and both opening directly on the surface; about twenty-four simple oral tentacles; dorsal tubercle with a simple transverse opening; twenty-seven to thirty-four rows of stigmata; stomach with eight to ten longitudinal folds; testis follicles in a long series in the post-abdomen.

OCCURRENCE. St. 934: North Island, New Zealand, 98–92 m.

COLONY (Text-fig. 10A). The single specimen, the holotype, which is probably incomplete, consists of a stalk 2 cm. long and about 0·4 cm. in diameter, from the end of which a triangular, expanded head arises, about 2 cm. long and 2·4 cm. wide at the distal end, where the width is greatest. The whole specimen is rough and mottled grey, its appearance being due to the heavy layer of encrusting broken shell which completely covers the test. The common test itself is clear and the shell is confined to the surface.

ZOOID (Text-fig. 10B). The zooids are entirely embedded in the common test and show no arrangement in systems. When exceptionally well expanded the thorax measures about 8 mm., but in most zooids it is more or less contracted and may then measure less than 4 mm. in length. The abdomen is between 2 and 4 mm. long, and the post-abdomen may exceed 10 mm. In the preserved state the zooids are dull orange in colour. The wide oral siphon (*o.s.*) is terminal, of moderate length, and has six shallow pointed lobes. The atrial siphon (*a.s.*) lies a short distance back along the dorsal side of the thorax; it also opens on the surface, is short and wide, and has six pointed lobes. The body wall is rather thick and opaque, with up to twenty-five slender longitudinal muscles and many slender circular muscles. The longitudinal muscles converge in the sides of the abdomen and continue along the whole length of the post-abdomen.

Branchial sac. There are about twenty-four simple oral tentacles of alternating sizes (Text-fig. 10C). The dorsal tubercle is very simple and has an oval transverse slit (Text-fig. 10C, *d.t.*). Twenty-seven to thirty-four rows of narrow stigmata are present, each row usually containing forty to fifty stigmata. There are no parastigmatic transverse bars. The hooked dorsal languets (Text-fig. 10D, *d.l.*) are wide at the base and taper rapidly to a point. The languets towards the posterior end of the branchial sac become progressively larger.



Text-fig. 10. *Ritterella vestita* sp.n. (St. 934): A, colony; B, zooid; C, oral tentacles and dorsal tubercle; D, part of roof of branchial sac, showing dorsal languets; E, transverse section of stomach; F, part of gut.

GUT (Text-fig. 10F). The oesophagus is wide, and shorter than the stomach. The stomach is longer than wide, slightly laterally compressed, and has eight to ten uninterrupted longitudinal folds. There are two divisions of the post-stomach (*p.st.*) which together are shorter than the stomach. The mid-intestine (*m.i.*) is a short chamber lying horizontally at the lowest part of the gut loop. At its junction with the mid-intestine the rectum (*r*) bears a pair of caeca. The rectum passes directly up to the base of the thorax where it ends in a simple anus situated opposite the 22nd row of stigmata in zooids with twenty-eight rows.

GONADS. No zooid examined had an ovary. A testis was present in a few zooids and constituted a series of rounded follicles (*t*) occupying much of the length of the post-abdomen. The sperm duct (*s.d.*) leads straight forward towards the base of the thorax, but its terminal part could not be seen.

REMARKS. Four species of *Ritterella* have been described from the waters surrounding New Zealand and as Table 14 shows, these are all clearly different from the present species.

Table 14

	No. rows stigmata	*Oesophagus*	*Stomach*
R. novae-zealandiae (Brewin)	3, each of 21–25	Much longer than stomach	Smoooth
R. opaca (Brewin)	3, each of 9 or 10	Much longer than stomach	4 folds
R. aurea (Brewin)	3, each of 15–17	Much longer than stomach	3 or 4 folds
R. arenosa (Brewin)	9 or 10, each of 20–24	Short	Smooth
R. vestita sp.n.	27–34, each of 40–50	Shorter than stomach	8–10 folds

Other species of *Ritterella* are known from Kamchatka and Sakhalin (*R. clavata* (Oka)), from Japan (*R. pedunculata* Tokioka, *R. yamazi* Tokioka) and from the west coast of North America (*R. pulchra* (Ritter), *R. aequali-siphonalis* (Ritter & Forsyth)). All of these species, however, are quite distinct from *R. vestita*.

The genus, as known at present, is confined to the Pacific Ocean.

DISTRIBUTION. North Island, New Zealand.

Family DIDEMNIDAE Giard, 1872

Genus **Didemnum** Savigny, 1816

Didemnum studeri Hartmeyer

Didemnum studeri Hartmeyer, 1911, p. 538.

OCCURRENCE. St. 56: Falkland Islands, 10·5–16 m. St. 399: Gough Island, 142–102 m. St. WS 246: Falkland Islands, 267–208 m. St. MS 71: S. Georgia, 110–60 m.

COLONY. The preserved specimens are dirty white or pale buff grey. They are thin encrusting sheets, some of them investing the tubes of worms, and may reach 7 cm. in greatest diameter. There are a few inconspicuous common cloacal openings. The spicules range from 10 to 40 μ in diameter and most are under 20 μ. The rays are irregular and short, and some spicules are almost spherical in outline.

ZOOID. The zooid has a rather larger atrial opening than has been described in previous accounts; there is no atrial languet or at most a small upper lip over the opening. A long slender retractor process extends downwards from the lower end of the thorax.

GONADS. No ovaries are developed in these specimens. The structure of the testis in the 'Discovery' material is, in Table 15, compared with previous accounts.

DISTRIBUTION. Subantarctic (Kerguelen, Magellanic region, Chatham Islands, Aukland, Stewart Island, Macquarie Island, Tasmania, Gough Island, Falkland Islands), Antarctic (South Georgia).

REMARKS. In spite of certain differences in detail, particularly in the testis and sperm duct, the

'Discovery' specimens belong, without much doubt, to *D. studeri*. The nearest existing records of the species are from Tierra del Fuego and the Strait of Magellan. It is not surprising to find it at the Falkland Islands, but the record from Gough Island is considerably farther north, where the temperature at 150 m. is about 4° C. higher.

Table 15

	'Discovery'	*Hartmeyer* 1911	*Michaelsen* 1919	*Kott* 1954
No. of follicles	2–4	3	2–3	3
No. of spiral turns	4–7	At least 7	7–8	7–10

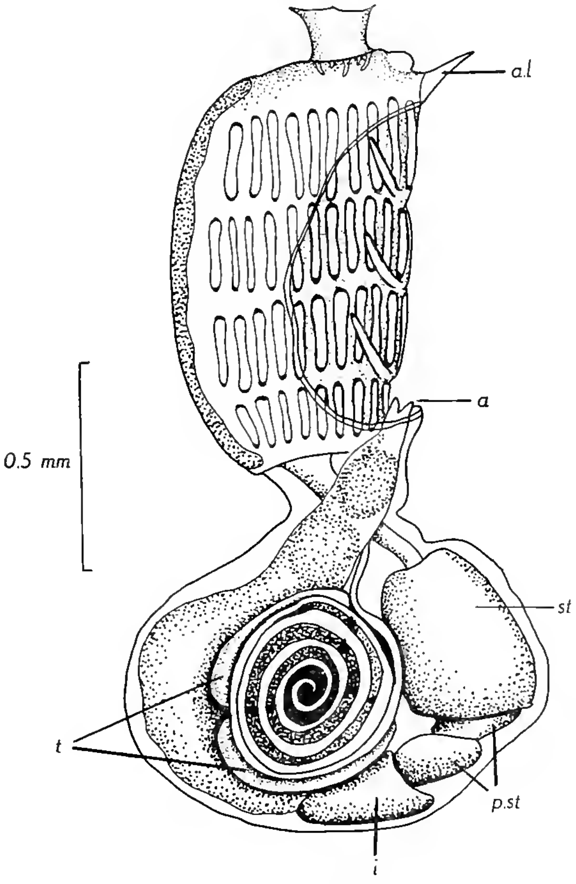
Didemnum biglans (Sluiter) (Text-fig. 11)

Leptoclinum biglans Sluiter, 1906, p. 29, pl. 2, figs. 27, 28.
For synonymy see Kott, 1954, p. 159.

Occurrence. St. 182: Palmer Archipelago, 273–500 m. St. 187: Palmer Archipelago, 259–354 m.

Colony. The colony from St. 182 is attached to the sandy tube of a worm, and measures about 5 cm. in length. It is thick and fleshy, and, preserved, is of a pale buff-grey colour, the zooids forming paler spots on the surface. Four round or oval common cloacal openings are found scattered over the surface of this colony. Although the zooids are grouped there is no very obvious arrangement in systems. No spicules whatever are present in the common test, but the superficial layer has round empty spaces very like the cavities occupied by spicules in other didemnids, and I am inclined to believe that this colony may originally have had a layer of spicules near the surface and that these have been destroyed after the specimen was collected, possibly by acid in the preserving liquid. This explanation of the superficial empty spaces is supported by Sluiter's (1906) statement that no vesicular cells are present in this species. On the other hand, it may be that the colony had no spicules in life. Within the colony there are very large cavities, especially in the upper half of the test, the thoraces of the zooids being contained in strands of test which pass from the upper layer down to the basal layer of common test, a condition very like that found in *Diplosoma*.

The specimen from St. 187 is in all essentials like that from St. 182, but is smaller and was growing on the test of a specimen of *Pyura discoveryi*.



Text-fig. 11. *Didemnum biglans* (Sluiter) (St. 182): Zooid.

Zooid (Text-fig. 11). The zooids are small, having an average length of 2 mm. The oral siphon is short with six indistinct lobes. Much of the dorsal surface of the branchial sac is exposed by the large atrial opening which extends, in well-expanded zooids, from the 1st to the 4th row of stigmata. The opening is surmounted by a short triangular atrial languet (*a.l.*). There is no trace of lateral thoracic organs.

Branchial sac. Ten to twelve long stigmata are present in each of the four rows. The stigmata are generally of the width shown in Text-fig. 11, but in a few exceptionally well expanded zooids they are much wider and rectangular in shape. The three dorsal languets are long, and usually forwardly directed.

Gut. The oesophagus is narrow and about as long as the stomach, which is a wide barrel-shaped organ. The post-stomach is about equal in length to the intestine, and the wide rectum ends in a two-lipped anus situated at the base of the thorax, opposite the 4th row of stigmata.

Gonads. In most zooids the ovary is not developed, and when present it is represented by one large ovum, and a group of smaller ova. The testis consists of two or three rounded follicles (*t.*) on the surface of which the sperm-duct makes four to six spiral turns.

Developing embryos were present in the common test below several of the zooids, but none had reached the larval stage.

Remarks. I have had some difficulty in deciding the identity of these specimens, mainly owing to the complete absence of spicules. This feature may be an artifact, as suggested above, or may represent the extreme reduction of spicules which previous authors (van Name, 1945; Kott, 1954) have noted as being scarce in some colonies which they examined. It is relevant that considerable variation is known in the abundance of spicules in other species of Didemnidae (e.g. *Trididemnum tenerum* (Verrill), van Name, 1945, Berrill, 1950; *T. opacum* (Ritter), van Name, 1945; *Didemnum helgolandicum* Michaelsen, unpublished personal observation).

Table 16

	'Discovery'	*Sluiter*	*Hartmeyer*	*van Name*	*Kott*
Spicules	Absent	Common only in upper layer	As Sluiter's description	Usually common in upper layer, sometimes very few	Mainly in upper layer, nowhere dense
Atrial opening	Large	?	Small	?	?
Lateral thoracic organs	Absent	Present	Present	Present	Present
No. of stigmata per row	10–12	?	?	10–12	?
No. of testis follicles	2 or 3	1	2	?	2
No. of turns of sperm duct	4–6	3	3–4	?	4–5

A comparison of the 'Discovery' specimens with the descriptions given by Sluiter (1906), Hartmeyer (1911), van Name (1945) and Kott (1954) is given in Table 16.

The differences shown above seem less important than the similarities, especially considering the doubtful nature of the absence of spicules, and I conclude that the colonies are within the probable range of variation of *D. biglans*.

Distribution. Antarctic (Graham Land, Enderby Land, Kaiser Wilhelm II Land).

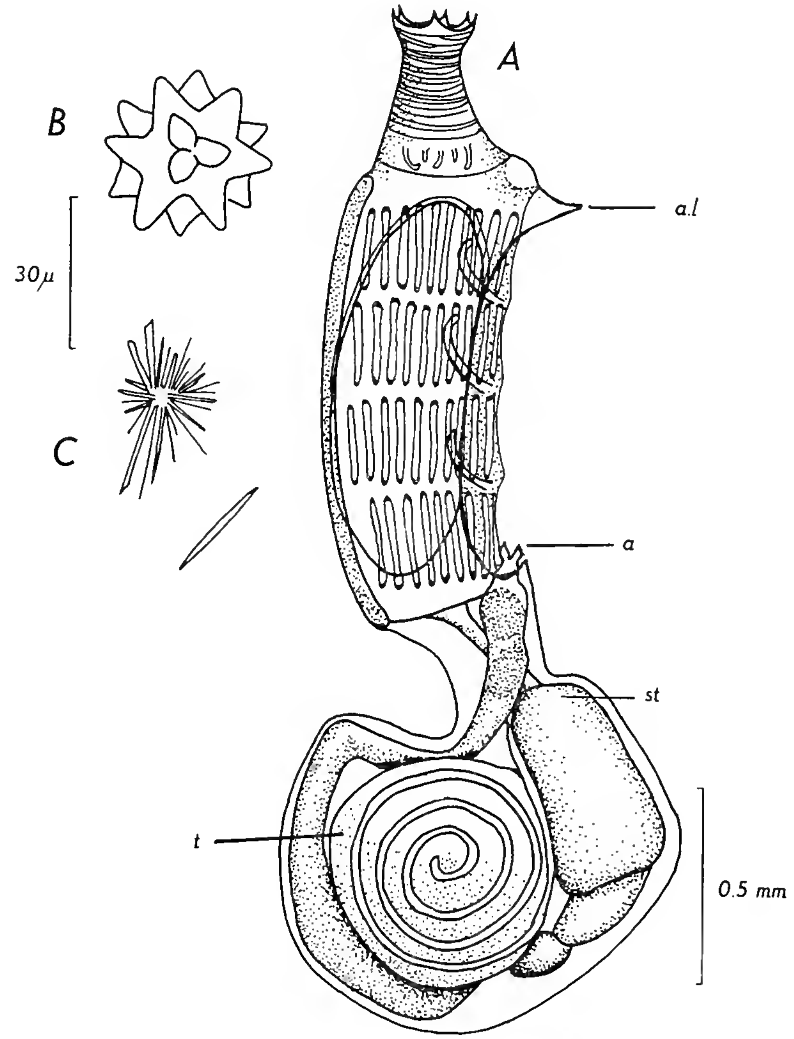
Didemnum trivolutum sp.n. (Text-fig. 12)

Holotype. St. WS 811.

Diagnosis of species. Colony thin and encrusting, with spicules densely packed throughout the whole depth of the test. Spicules of a regular stellate shape, 20 to 40 μ in diameter with eight to twelve rays in optical section; also some spicules with very thin needle-like rays. Zooid with wide, long atrial opening, surmounted by a languet; lateral thoracic organs large; stomach rather rectangular; testis undivided, with sperm-duct making three spiral turns.

Occurrence. St. WS 99: Falkland Islands, 251–225 m. St. WS 811: Patagonian Shelf, 99 m.

Colony. The specimens consist of large sheeting masses, sometimes growing round the tubes of worms, and reaching a length of 10 cm. The average thickness of the colony is 3 mm. In colour the preserved colonies are generally pale grey or almost white, with a pattern of darker spots marking the positions of the zooids. A few slit-like common cloacal openings are present on the surface. All parts of the common test are crowded with spicules, which are present even in the most superficial layer, there being no bladder cells such as are often found in the uppermost layer of the test in didemnids. The spicules are mostly of a regular stellate form, reaching 40 μ in diameter and having from eight to twelve pointed conical rays in optical section (Text-fig. 12 B). A few spicules were also seen consisting of bundles of very thin needle-like rays arranged in a stellate pattern, these spicules also being 30–40 μ in diameter (Text-fig. 12 C). A system of common cloacal canals lies a little above the middle level of the colony.



Text-fig. 12. *Didemnum trivolutum* sp.n. (St. WS 811): A, zooid; B, C, spicules.

Zooid (Text-fig. 12A). The thorax is about 1·6 mm. long and the abdomen about 1·0 mm. The prominent oral siphon has six pointed lobes. A large part of the dorsal side of the thorax is exposed by the atrial opening which extends at least half the length of the thorax and often extends almost the whole length. On the anterior border the opening bears a short triangular languet (*a.l.*). There are large oval lateral thoracic organs with associated masses of small spicules. These organs occupy most of each side of the thorax.

Branchial sac. There are about eleven long narrow stigmata in each of the four rows. The three dorsal languets are long, curved, and directed anteriorly.

GUT. The oesophagus is narrow and the stomach (*st.*) large with a somewhat rectangular outline. The post-stomach is generally quite long and conical, but is sometimes short. The intestine is short and narrow. The rectum is wide at its lower end but soon narrows. The narrow part is bent into an S-shaped curve. The anus, which is situated at the base of the thorax, opposite the 4th row of stigmata, has two shallow lips.

GONADS. The testis (*t*) is undivided and the sperm duct makes three spiral turns round it. In some colonies only the ovary was developed.

REMARKS. *D. trivolutum* somewhat resembles two other species from South American waters, *D. tenue* (Herdman) and *D. chilense* Ärnbäck. The characters which most readily separate *D. trivolutum* are listed in Table 17. In this comparison the characters of *D. chilense* were taken from Ärnbäck (1929, fig. 5), and the diameter of the spicules of *D. tenue* was measured in specimens of Herdman's original material kindly lent by the British Museum (Natural History).

It will be seen that *D. tenue* and *D. chilense* are not distinguished from each other by the characters listed. But Ärnbäck, having compared material of the two species, was satisfied that, in spite of similarities 'the differences are more essential, lying in the form of the zooids, which are not very elongated but larger in the species *tenue*, having a short atrial languet, a longer and more sharply curved intestinal loop'.

Table 17

	D. trivolutum	*D. tenue*	*D. chilense*
Spicules	Up to 40μ in diameter	Up to 25μ in diameter	Up to 26 in μ diameter
Lateral thoracic organs	Large; placed half-way along thorax	Small; placed at posterior end of thorax	Not described
Sperm duct	3 spiral turns	Unknown	6–7 spiral turns

Genus **Leptoclinides** Bjerkan, 1905

This genus was characterized by Bjerkan as having four rows of stigmata and a backwardly directed funnel-like atrial siphon. Van Name (1945) suggested that it should be no more than a subgenus of *Didemnum*, and Carlisle & Carlisle (1954) gave reasons for dividing the species hitherto assigned to *Leptoclinides* among other genera of the Didemnidae, while retaining *Leptoclinides* as a subgenus of *Didemnum*. I believe, however, that the well-developed funnel-like atrial siphon clearly distinguishes *Leptoclinides* from *Didemnum*, no species of which shows any tendency towards the production of an atrial siphon.

Leptoclinides diemenensis Michaelsen (Text-fig. 13)

Leptoclinides diemenensis Michaelsen, 1924, p. 331, fig. 12.

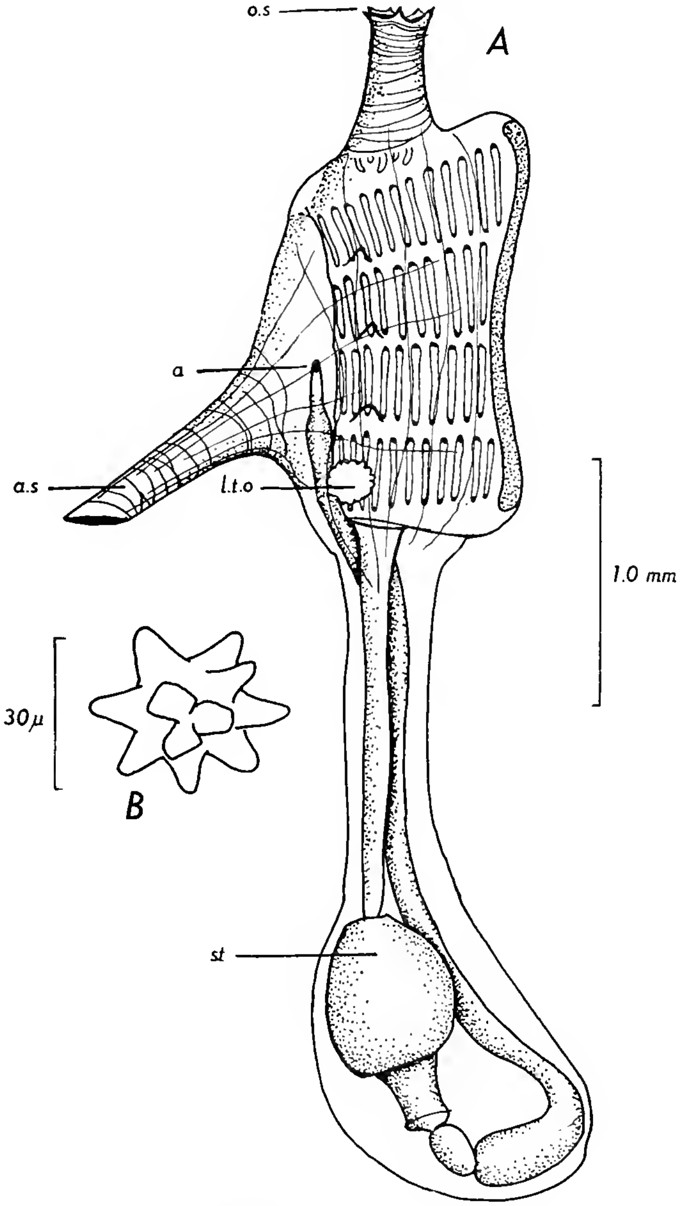
OCCURRENCE. St. 935: North Island, New Zealand, 84 m.

COLONY. The colony is about 3 cm. long and 0·7 cm. in thickness. It is pale orange brown in colour. The upper surface has a number of low rounded swellings, each with a common cloacal opening at its centre. These openings are less than 1 mm. in diameter and are spaced about 5 mm. apart. Around each opening is an irregular system of closely spaced zooids. The colony is firm and its surface smooth.

Sections show that the uppermost layer of the common test is composed largely of closely pressed bladder cells, each about 70–80 μ in diameter and extending to about five cells in depth. Below these is a layer of densely packed spicules. Spicules are also present in the deeper parts of the common test, but are more scattered. The spicules are generally 20–35 μ in diameter, only a few reaching 40 μ.

They are of a regular stellate shape, with about eight rays in optical section (Text-fig. 13 B). Small spindle-shaped and irregular cells are also present in the test, but no pigment cells.

Zooid (Text-fig. 13 A). The thorax often reaches 2 mm. in length. The abdomen, including the long waist, is about the same length, or slightly more. These zooids are larger than Michaelsen's (1924), which had a total length of 2·5 mm. In most zooids the oral siphon (*o.s.*) is quite long, tubular to conical, and muscular, with six shallow pointed lobes. The base of the atrial siphon (*a.s.*) is at or slightly posterior to the middle of the branchial sac. The siphon varies in length in different zooids, but often is longer than the oral siphon. It is frequently, but not always, backwardly directed. Five or six slender longitudinal muscles pass along each side of the thorax. Near the posterior end of the thorax there is a conspicuous lateral thoracic organ (*l.t.o.*) on each side. The mass of spicules occupying the cavity of the organ is about 125 μ in diameter.



Text-fig. 13. *Leptoclinides diemenensis* Michaelsen (St. 935): A, zooid; B, spicule.

Branchial sac. There are twelve to fourteen long narrow stigmata in each of the four rows. The dorsal languets are short, triangular, and blunt.

Gut. This agrees well with Michaelsen's account, except that in the 'Discovery' material the anus (*a*) is rather farther forward, and lies opposite the 3rd row of stigmata instead of the 4th.

Gonads. There is no trace of gonads in any of the specimens.

Remarks. Five species of *Leptoclinides* have been described from New Zealand and Chatham Islands: *L. diemenensis* Michaelsen, *L. sparsus* Michaelsen, *L. sluiteri* Brewin, *L. marmoreus* Brewin, and *L. auranticus* Brewin. *L. sparsus* is similar to *L. diemenensis* from which it differs in having stellate pigment cells in the test. The characters which separate the remaining species are given in Table 18. Some of these characters are not very satisfactory for distinguishing the species, but as the variation within each species is not known at present, it is best to maintain them.

Table 18

	Diameter of spicules (μ)	*Length of zooids* (mm.)	*No. of stigmata per row*	*Abdomen*	*Oesophagus*	*Sperm duct*
L. diemenensis	20–35	Up to 4	12–14	Not wider than thorax	Longer than stomach	6–7 turns
L. sluiteri	12–25	Up to 1	9 or 10	Wider than thorax	Equal in length to stomach	9 or 10 turns
L. marmoreus	10–45	Up to 1·6	10	Not wider than thorax	Shorter than stomach	9 turns
L. auranticus	10–60	Up to 1	11 or 12	Equals thorax in width	Equal in length to stomach	7 turns

Sluiter (1909) has described, under the name *Polysyncraton*, a number of species from the Indonesian region evidently belonging to *Leptoclinides*. It is a little doubtful if these are all different species, and I should not be surprised if a proper revision of the group, as represented in Australasian waters, showed that the same species has been described under several names. This view is also expressed by Tokioka (1949) in dealing with *L. rufus* (Sluiter) from Japanese waters.

Distribution. North of North Island, New Zealand.

Genus **Trididemnum** Della Valle, 1881

Trididemnum auriculatum Michaelsen (Text-fig. 14)

Trididemnum auriculatum Michaelsen, 1919, p. 38, text-fig. 3.

Occurrence. St. WS 84: Falkland Islands, 75–74 m.

Colony. The specimen is a large sheeting colony, varying from 2 to 4 mm. in thickness, of a dirty white colour. Two or three common cloacal openings are visible on the surface. Regular stellate spicules are densely packed in all layers of the test, and range from 37 to 66 μ in diameter.

Zooid (Text-fig. 14A). The zooid agrees closely with the description given by Michaelsen (1919), except that the 'Discovery' specimen has about seven spiral turns of the sperm duct. (*s.d.*), instead of only five in the type specimen. The lateral thoracic organs are large and conspicuous, as in Michaelsen's material.

Larva (Text-fig. 14B). The larva is of the usual didemnid type, with three vertically arranged papillae (*p.*) and four pairs of anterior ampullae (*amp.*). Both ocellus and otolith are present. The larvae measure from 0·5 to 0·6 mm. in length from the end of the papillae to the base of the tail.

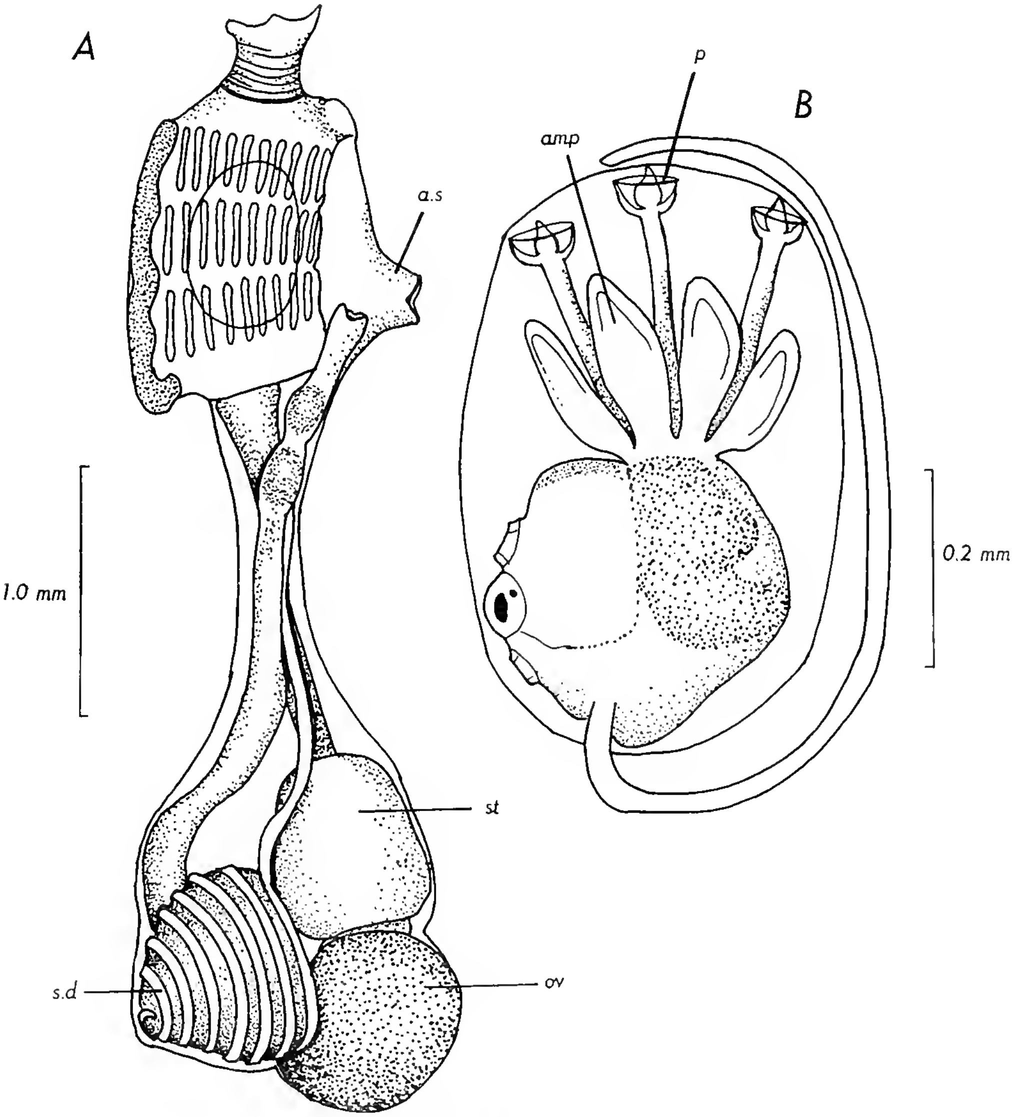
Remarks. Van Name (1945) suggested that perhaps this species was not distinct from *T. propinquum* (Herdman), but Ärnbäck (1929) stated that a comparison of the species 'shows at once that they are not identical'. The distinguishing characters particularly mentioned by Ärnbäck are given in Table 19.

These do not seem to be entirely satisfactory distinctions, and the difficulty arises from the incomplete description of *T. propinquum* given by Herdman (1886). Ärnbäck, however, was convinced that the two species are distinct, and there is no doubt that the 'Discovery' specimen belongs to *T. auriculatum*.

DISTRIBUTION. Subantarctic (Strait of Magellan; Guaitecas Islands, Chile; Falkland Islands).

Table 19

	T. propinquum	*T. auriculatum*
Zooids	Short	Long and slender
Abdomen	About same length as thorax	Twice as long as thorax
Stigmata	Short	Long and narrow



Text-fig. 14. *Trididemnum auriculatum* Michaelsen (St. WS 84): A, zooid; B, larva.

There are also in the collections several colonies of didemnid ascidians which I am unable to place, even in their correct genus, because the zooids have no gonads. It would be very unwise to try to name these specimens using other characters, because with few exceptions the nature of the testis and sperm duct is almost essential for the determination of genera and species in this family.

Family CLAVELINIDAE Forbes & Hanley, 1848

Sub-family Clavelininae Seeliger, 1906

Genus **Podoclavella** Herdman, 1890

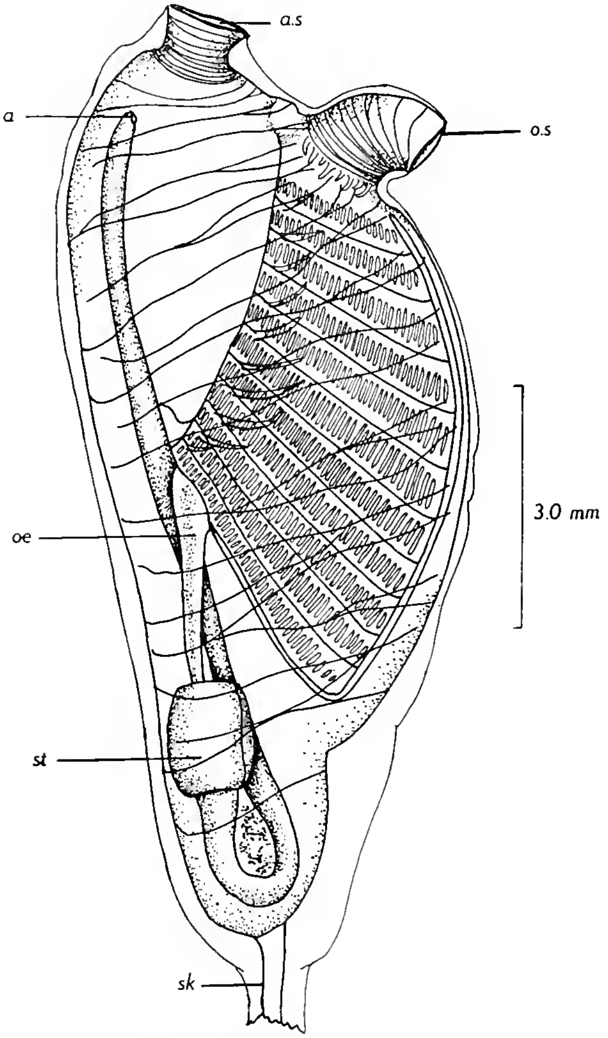
Podoclavella cylindrica (Quoy & Gaimard) (Text-fig. 15)

Polyclinum cylindricum Quoy & Gaimard, 1834, p. 618.

For synonymy see Michaelsen, 1930, p. 475.

Occurrence. St. 1686: Victoria, Australia, 0 m.

Colony. The colony consists of a bunch of zooids united only at their lower ends where a narrow stalk joins a stouter cylindrical stem. This is attached to the substratum by an expanded base.



Text-fig. 15. *Podoclavella cylindrica* (Quoy & Gaimard) (St. 1686): Zooid.

Zooid (Text-fig. 15). Large zooids reach a length of 11 mm. but many of the zooids in the colony are much shorter. The body is widest anterior to the middle and tapers towards the base, where it abruptly narrows to join the stalk.

Thorax. The oral siphon (*o.s.*) does not occupy the extreme anterior end of the thorax, being instead displaced slightly down the ventral border. This siphon is also curious in being sharply bent in a ventral direction. The atrial siphon (*a.s.*) is terminal. Both siphons have numerous circular muscles. Fifteen to twenty slender muscles pass obliquely across the thorax and abdomen.

BRANCHIAL SAC. In large zooids there are up to twenty-eight simple oral tentacles of alternating sizes. The very small dorsal tubercle lies transversely and has a simple slit-like opening. Eleven or twelve rows of narrow stigmata are present, the rows being separated by prominent raised bars. In large zooids there may be as many as forty-five stigmata in a row. The dorsal languets are long and slender. The branchial sac lies obliquely in the body and the rows of stigmata lie in a correspondingly oblique position.

ABDOMEN. The abdomen is much shorter and narrower than the thorax.

GUT. The oesophagus (*oes.*) is long and narrow, and passes straight back to the stomach (*st.*), which is ovoid and has smooth walls. Below the stomach the intestinal loop is short, but the rectum is very long and in its anterior half diverges from the dorsal side of the branchial sac. The simple anus (*a*) lies near the base of the atrial siphon.

REMARKS. This species has been described under a number of generic names, but it certainly belongs to *Podoclavella* where Kott (1957) placed it, and not to *Clavelina* to which it was assigned by Michaelsen (1930).

The 'Discovery' material shows some differences from that described by Kott (1957), and is in certain respects intermediate between *P. cylindrica* and *P. australis* (Herdman). But *P. australis* is very probably a synonym of *P. cylindrica*, or at most a geographical form, as suggested by Kott. The comparison of the only marked differences that is given in Table 20 shows the intermediate position of the 'Discovery' material, and strongly suggests that only one species is involved, *P. cylindrica*.

Table 20

	P. cylindrica (Kott, 1957)	*P. australis* (Kott, 1957)	'Discovery' specimen
No. of muscles	About 25	12	15–20
No. of rows of stigmata	21	10	11 or 12

DISTRIBUTION. West and south coast of Australia; Bass Strait.

Podoclavella kottae sp.n. (Text-figs. 16, 17; Pl. II, fig. 1)

HOLOTYPE. Size, largest zooid 12 cm. long. St. 934.

DIAGNOSIS OF SPECIES. Zooids united only at base. Thorax short and ovoid; abdomen stalk-like and many times larger than thorax. Atrial opening terminal; oral opening in basal half of thorax; both openings with strong wide sphincter muscles. Branchial sac with up to twenty-seven rows of stigmata, the anterior and posterior rows much shorter than the middle rows. Oesophagus and intestine very long and narrow; stomach ovoid and situated in a basal swelling of the stalk; anus close to oesophageal mouth.

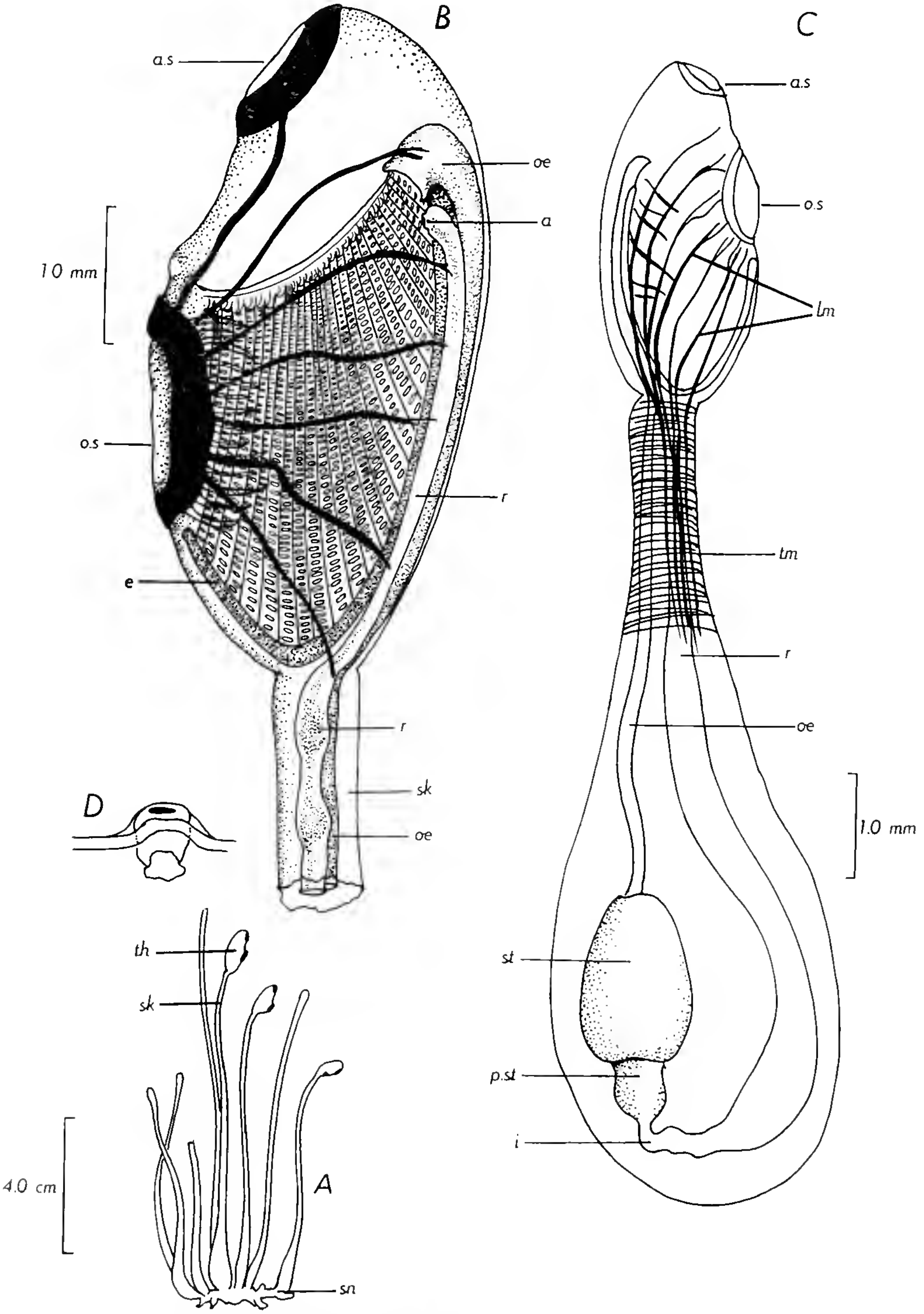
OCCURRENCE. St. 934: North Island, New Zealand, 98–92 m.

COLONY (Text-fig. 16A; Pl. II, fig. 1). The specimen has eight zooids, the largest being 12 cm. long. Fully developed zooids consist of a short thorax (*th.*) borne on a long slender stalk (*sk.*) which constitutes the abdomen. The stalks have a basal swelling the lower part of which is united to a short compact creeping stolon (*sn.*). The stalks are buff-coloured and the thoraces clear.

ZOOID (Text-fig. 16B, C).

THORAX. The thorax of a well-developed zooid is 5–6 mm. long and 3–4 mm. wide. It is ovoid, narrowest at its junction with the stalk and widest about one-third to one-half of its length up from the stalk. The atrial siphon (*a.s.*) is terminal or almost so, and the oral siphon (*o.s.*) slightly behind the middle of the thorax. Each opening is sessile and wide, the oral being the wider of the two. A wide and conspicuous band of circular muscle surrounds each opening. About fourteen muscles radiate across the thorax from the margin of the oral opening, seven on each side. Anatomically these are longitudinal muscles, although in fully developed zooids they lie transversely to the longitudinal axis of the zooid. Their origin as longitudinal muscles is, however, shown by their position in young developing zooids (Text-fig. 16C, *l.m.*). A few narrow and irregular transverse strands are present on the thorax. Only the young developing stages of the zooid have transverse muscles in the abdomen (*t.m.*) and they are confined to the upper part of it.

Branchial sac. The large oral tentacles number twenty-six to twenty-eight and are arranged in a single circle. The dorsal tubercle (Text-fig. 16D) is small, with a simple transverse oval slit.

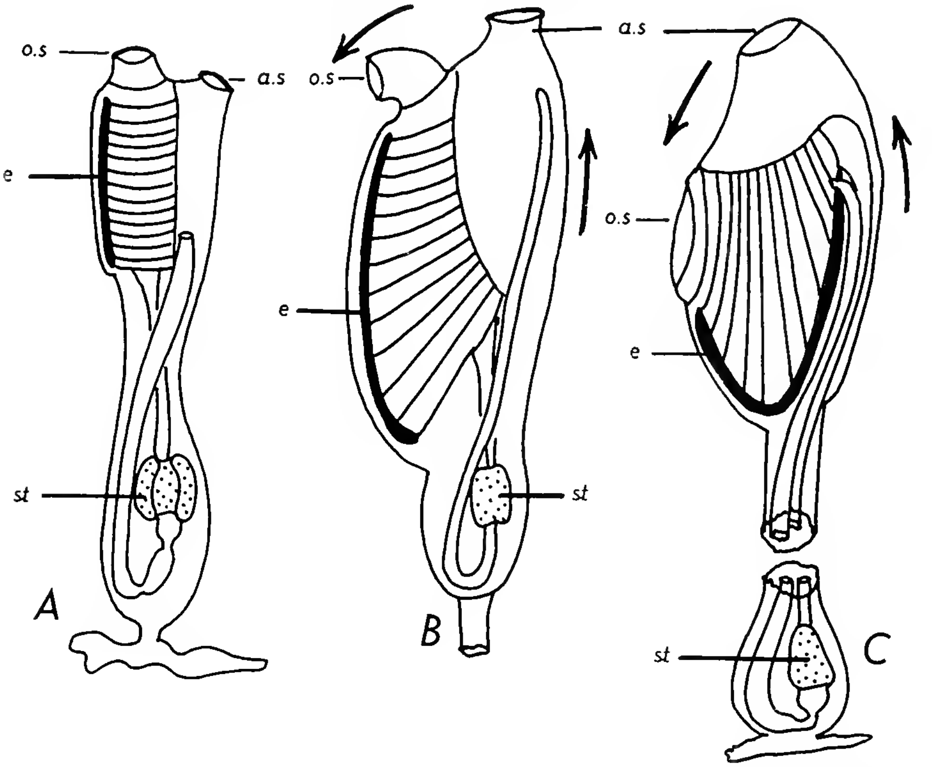


Text-fig. 16. *Podoclavella kottae* sp.n. (St. 934): A, colony; B, thorax of zooid; C, abdomen with regenerating thorax; D, dorsal tubercle.

A row of pointed triangular languets occupies the mid-dorsal line of the branchial sac. The transverse rows of stigmata number thirteen to twenty-seven, according to the size of the zooid, and the rows lie in line with the long axis of the stalk. The anterior and posterior rows are shorter than the middle ones, and the shortest rows have less than twenty stigmata, whereas at least sixty are present in the longest. The endostyle (*e*) is conspicuous and strongly curved.

Table 21

	P. detorta	*P. kottae*
Number of rows of stigmata	'Apparently 6' (van Name, 1918)	Up to 27
Lower end of intestinal loop	Some distance up from base of stalk	At base of stalk
Anus	Far anterior to oesophageal mouth; lobed (Sluiter, 1904)	Beside oesophageal mouth; without lobes



Text-fig. 17. *Podoclavella kottae* sp.n. Suggested stages in its evolution from A, the unmodified form illustrated by *Clavelina*, through B, the modified form illustrated by *Podoclavella cylindrica* to C, *P. kottae*.

ABDOMEN. The abdomen lies within the stalk, occupying the whole length. It is much narrower than the thorax, except at the lower end which is enlarged and accommodates the stomach and intestinal loop.

GUT. The oesophageal mouth is at the postero-dorsal corner of the branchial sac and lies within the anterior one-third of the thorax. From there the oesophagus (*oe.*) passes back behind the postero-ventral border of the branchial sac and into the stalk, within which it runs down to the basal swelling. The stomach (*st.*) is ovoid and has smooth walls. Behind it is a short conical post-stomach and a short horizontal intestine (*i*) not clearly marked off from the rectum. The rectum is wide at its lower end but narrows as it passes up within the stalk. In both stalk and thorax it lies close to the oesophagus. The anus (*a.*) is situated to the left of the oesophageal mouth and is small and simple without lobes.

GONADS. Neither ovary nor testis was present in any of the zooids.

REMARKS. This species most resembles *P. detorta* Sluiter, but is distinguished as shown in Table 21.

Other characters might help to distinguish the two species, but the accounts of *P. detorta* by Sluiter (1904) and van Name (1918) differ with regard to these characters. Thus the very wide and strong sphincters on the oral and atrial openings of *P. kottae* are characteristic. According to van Name (1918) the corresponding muscles of *P. detorta* are slender, but Sluiter (1904) describes them as strong, although his figure gives no suggestion of this.

The orientation of the thorax and the great development of the abdomen in *P. detorta* and *P. kottae* are features deserving notice. The structure of *P. kottae* can be derived from the unspecialized type of *Clavelina* through a stage like that represented by *Podoclavella cylindrica*. In this series (Text-fig. 17) two processes have been involved: (1) the formation of a stalk, and (2) unequal growth of the dorsal and ventral sides of the thorax. The former process led finally to the enclosure of the abdomen within a very long narrow stalk with the consequent elongation of the oesophagus and rectum. The latter process has shifted the oral siphon down towards the stalk and at the same time drawn the oesophageal mouth up towards the still terminal atrial siphon.

Distribution. North Island, New Zealand.

Genus **Clavelina** Savigny, 1816

Clavelina claviformis (Herdman) (Text-fig. 18; Pl. II, fig. 2)

Colella claviformis Herdman, 1899, p. 67, pl. Dist. 3, figs. 1–15.
Clavelina sigillaria Michaelsen, 1924, p. 269, figs. 1–4.
Clavelina claviformis Kott, 1957, p. 88, fig. 22.

Occurrence. St. 929: North Island, New Zealand, 58–55 m.

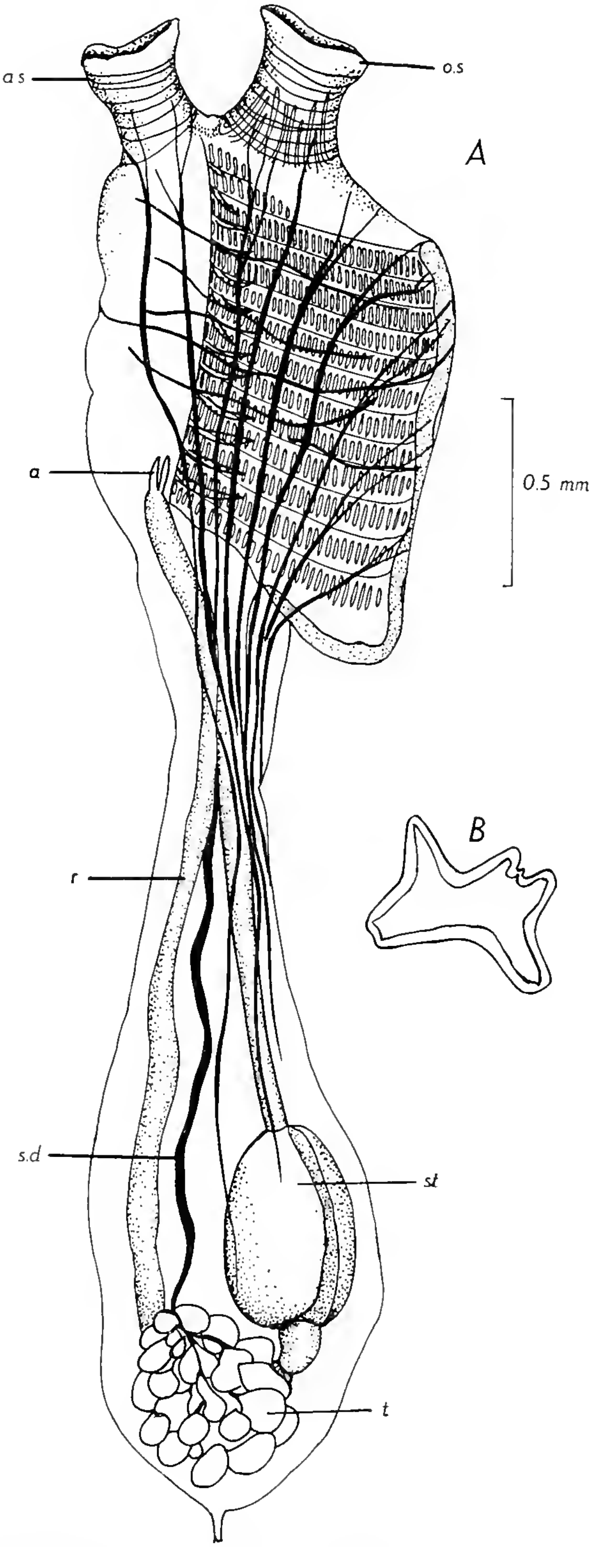
Colony (Pl. II, fig. 2). Two examples are present in the 'Discovery' collections, from the same station and probably derived from the same group of colonies. One specimen is a single stalked head, and the other consists of a group of about twelve stalked heads attached to a common base. The largest of these has a head 11 cm. long on a stalk of 8 cm., and the smallest is less than half that size. In outline the head is ovate to lanceolate, and is sometimes slightly compressed, but this may be an artifact. The stalk is narrower than the head and is of uniform diameter down to the base. Both the head and the stalk are semi-transparent or pale grey, smooth and without any encrusting matter. The common test is tough and cartilaginous, but the surface has a slimy consistency. The zooids show through the test quite clearly.

Zooid (Text-fig. 18A). The thorax is shorter and usually wider than the abdomen, especially when contracted. One typical zooid had a thorax 1·7 mm. and an abdomen 3·0 mm. long. The two siphons are of almost equal length, and are close together at the anterior end of the thorax. They have circular openings with lobes scarcely marked or entirely wanting. The body wall of the thorax has a series of nine to eleven prominent longitudinal muscles which, passing up from the abdomen, diverge as they approach the anterior part of the thorax, where they generally divide into a few branches. The more ventral muscles of the series diverge towards the ventral margin of the thorax, recalling the course of the muscles in *Tylobranchion*.

Branchial sac. From twelve to twenty long slender simple oral tentacles are present in a single circle. The dorsal tubercle is small, with a narrow transverse oval slit. In some zooids the branchial sac has nine rows of stigmata, but more often there are ten to twelve complete rows and two or three short anterior rows, each consisting of a few stigmata in the dorsal part of the branchial sac and none in the ventral part. There are up to forty-five stigmata in the complete rows. The dorsal languets are pointed and moderately long, those at the posterior end being the longest.

Gut. The long narrow oesophagus passes down to the stomach which lies in the posterior third of the abdomen. The stomach (*st.*) is ovoid or in some zooids nearly globular. There are four folds on the walls, best seen in a transverse section (Text-fig. 18B). The intestine is short and the rectum (*r*) long and narrow. The anus (*a*) lies far back in the thorax, opposite the last or second last row of stigmata; it has two deep rounded lobes.

GONADS. Some of the zooids have a well-developed testis (*t.*) consisting of a large group of many small pear-shaped follicles, lying on the right side of the zooid near the lower part of the intestinal



Text-fig. 18. *Clavelina claviformis* (Herdman) (St. 929): A, zooid; B, transverse section of stomach.

loop. The sperm duct passes almost straight forward beside the rectum. No ovary was found in any zooid examined, but the zooids are known to be hermaphrodite.

Distribution. Eastern Australia; North Island, New Zealand.

Subfamily Polycitorinae Michaelsen, 1904

Berrill (1950) proposed the subfamily Holozoinae for the three genera, *Distaplia* Della Valle, 1881, *Holozoa* Lesson, 1830, and *Sycozoa* Lesson, 1830, and pointed out that these genera formed a very natural group of closely related forms. Many authors have had difficulty in deciding whether these three genera are in fact separate. Thus Hartmeyer (1909, in Bronn) regarded *Distaplia* as a synonym of *Holozoa*, but maintained *Sycozoa*. Van Name (1945) allowed the separation of *Holozoa* mainly on the grounds of the shape of the colony and the alleged pelagic phase in its adult life, but was evidently not entirely satisfied that it is distinct from *Distaplia*. Brewin (1953) united the two genera under the *nomen conservandum Distaplia*, at the same time maintaining the separation of *Sycozoa*, and establishing a new genus *Hypsistozoa*. I agree with Brewin's decision to unite *Holozoa* and *Distaplia*, but the position of *Sycozoa* is more difficult to determine.

Before Brewin's (1953) paper, the colony of *Sycozoa* had been described as typically having one terminal common cloacal opening, but she found in living material from New Zealand waters a 'very regular arrangement of the common cloacal apertures around the periphery of the distal part of the head, a region entirely free of zooids...'. As I shall show below, this is certainly not the case in the 'Discovery' specimens, in which examination of many well-preserved colonies, both of *S. sigillinoides* and *S. georgiana*, showed one terminal common cloacal opening. Brewin emended the generic description to agree with her New Zealand material, and acceptance of the emended diagnosis would exclude both the type species *S. sigillinoides* and also *S. georgiana*. This seems to be unjustified, and I suggest that the arrangement of the common cloacal openings be disregarded.

The question is further complicated by the structure of a new species, *Sycozoa anomala*, in the 'Discovery' collections, from north of New Zealand. The main reason for separating *Sycozoa* from *Distaplia* has hitherto been the unisexual nature of the colonies of *Sycozoa* and their hermaphrodite nature in *Distaplia*. But the new species, *S. anomala*, from the 'Discovery' collections, which in all other respects agrees well with other species of *Sycozoa*, has hermaphrodite colonies as well as unisexual ones. The distinction between the two genera thus seems to break down. In *S. anomala* the position of the ovary also is somewhat intermediate between the genera, and the logical course might be to unite *Sycozoa* with *Distaplia*, the name *Sycozoa* having priority. But as there are many well-known species bearing the name *Distaplia*, this course would undoubtedly lead to great confusion, and I have retained both *Distaplia* and *Sycozoa*.

Genus Sycozoa Lesson, 1830

There are several reasons why separation of species of *Sycozoa* is difficult, one of the more important being ignorance of the changing forms of the colony during its normal annual cycle, and under different conditions of environment. Thus *S. ramulosa* (Herdman) and *S. umbellata* (Michaelsen) may be two forms of *S. sigillinoides*. The characters of *S. ramulosa* which Ärnbäck (1950) used to distinguish it from *S. sigillinoides* are: (1) its longer body and especially the branchial sac; (2) the extension of the testis beyond the intestinal loop; (3) the small number (one to three) of eggs in each brood pouch.

The shape of the body depends greatly on its state of contraction and is rather a difficult character to determine. The size of the testis varies according to the degree of sexual development of the zooid and is therefore also unreliable. It may be noted that, among the 'Discovery' material, there are colonies combining character (2) of *S. ramulosa* with character (3) of *S. sigillinoides* (e.g. St. 1230). Moreover, Michaelsen (1924) found brood pouches in *S. sigillinoides* containing from one to three larvae, and I have found from two to fourteen in different specimens of the same species. I therefore agree with van Name (1945) and Kott (1954) that *S. ramulosa* is a synonym of *S. sigillinoides.*

Regarding *S. umbellata* (Michaelsen) both Michaelsen (1924) himself and Ärnbäck (1950) are inclined to regard this also as a synonym of *S. sigillinoides.*

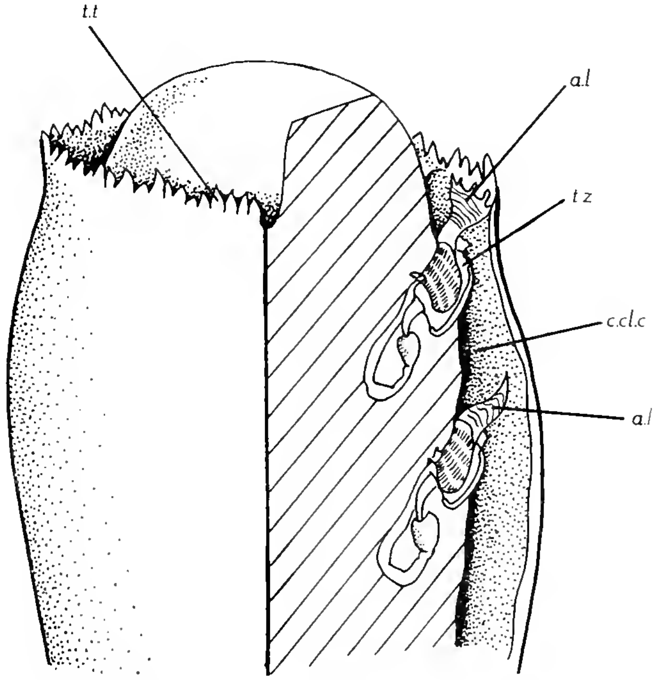
S. georgiana (Michaelsen) is another form which some authors think might be *S. sigillinoides* (Brewin, 1953). But I believe that the speciess hould be maintained (see p. 74), although I am not altogether sure that it is distinct from *S. gaimardi* (Herdman), an insufficiently known form.

Herdman (1886) described *S. quoyi* from Kerguelen, but his description did not sufficiently distinguish it from *S. sigillinoides.* Kott (1954) maintains their separation on the grounds of slight anatomical distinctions in the gut and the much larger size of the larva. In view of the variations in larval size which can occur within one species I am still doubtful about the validity of *S. quoyi.*

Sycozoa sigillinoides Lesson (Text-fig. 19, Pl. II, figs. 3–8)

Sycozoa sigillinoides Lesson, 1830, p. 436, pl. Moll. 13, fig. 15, 15b.
Non *Sycozoa sigillinoides* Brewin, 1952, p. 190, text-fig. 2.
For synonymy see van Name, 1945.

OCCURRENCE. St. 45: S. Georgia, 238–270 m. St. 51: Falkland Islands, 105–115 m. St. 53: Falkland Islands, 0–2 m. St. 145: S. Georgia, 26–35 m. St. 652: Burdwood Bank, 164 m. St. 1230: Magellan Strait, 27 m. St. WS 84: Falkland Islands, 75–74 m. St. WS 85: Falkland Islands, 79 m. St. WS 90: Patagonian Shelf, 82–81 m. St. WS 92: Patagonian Shelf, 145–143 m. St. WS 95: Patagonian Shelf, 109–108 m. St. WS 214: Patagonian Shelf, 208–219 m. St. WS 215: Patagonian Shelf, 219–146 m. St. WS 220: Patagonian Shelf, 108–104 m. St. WS 226: Patagonian Shelf, 144–152 m. St. WS 237: Patagonian Shelf, 150–256 m. St. WS 239: Patagonian Shelf, 196–193 m. St. WS 243: Patagonian Shelf, 144–141 m. St. WS 244: Patagonian Shelf, 253–247 m. St. WS 245: Patagonian Shelf, 304–290 m. St. WS 765: Patagonian Shelf, 113–119 m. St. WS 772: Patagonian Shelf, 309–163 m. St. WS 775: Patagonian Shelf, 115–110 m. St. WS 784: Patagonian Shelf, 170–



Text-fig. 19. *Sycozoa sigillinoides* Lesson. Cut-away section of the upper part of the head.

164 m. St. WS 785: Patagonian Shelf, 150–147 m. St. WS 799: Patagonian Shelf, 0 m. St. WS 800: Patagonian Shelf, 137–139 m. St. WS 814: Patagonian Shelf, 112–119 m. St. WS 816: Patagonian Shelf, 150 m. St. WS 818: Patagonian Shelf, 272–278 m. St. WS 819: Patagonian Shelf, 313–329 m. St. WS 833: Patagonian Shelf, 38–31 m. St. WS 834: Patagonian Shelf, 27–38 m. St. WS 839: Patagonian Shelf, 503–534 m. St. WS 841: Patagonian Shelf, 110–121 m. St. WS 847: Patagonian Shelf, 51–57 m.

COLONY. The shape of the colony varies greatly but the causes of variation are only partly known. In many specimens which are fully developed and more or less intact there is a stout main stem which in life appears to have lain on the sandy bottom either free or loosely fixed. This stem fulfils the function of a creeping stolon and gives rise to one or a few bunches of upright stalks, each stalk bearing a single head (Pl. II, figs. 3, 4). A true rooting system does not seem to be developed, but in other respects the habit is very like that of the Australian species *S. tenuicaulis* (Herdman) (see Herdman, 1899, pl. Dist. 1, fig. 2; Brewin, 1953. Text-fig. 1 B).

Many specimens, however, have a single stalk bearing one head (e.g. St. WS 90); these are perhaps broken pieces of complex colonies, for they have the same characters of stalk and head.

A third type of colony consists of a simple or slightly branched stalk attached basally to a solid object (e.g. St. WS 95).

Many unattached heads were also taken in the collections, and these will be referred to later (see p. 73).

Finally there is the headless condition represented either by isolated hard orange-coloured stalks or by whole complex colonies completely lacking zooids (e.g. St. WS 800) (Pl. II, fig. 5).

In well-developed complex colonies the stalks reach 6 cm. in length, occasionally more, and the heads up to 2·5 cm. long and 1·0 cm. wide.

Two groups of specimens from South Georgia (St. 45, St. 145) have a short fleshy stalk attached to an alga, and a head at least twice as long as the stalk (Pl. II, fig. 8). As the structure of the head, the zooids and their arrangement, and the larvae all agree closely with the other examples of *S. sigillinoides* in the collection, I am including these specimens within that species, although not entirely satisfied with this course. They are very like the specimens also from South Georgia figured by Ärnbäck (1950, fig. 26) as *S. sigillinoides*, and like Herdman's (1886) type of his species *S. quoyi* from Kerguelen, and also like Michaelsen's (1907) specimens from South Georgia, which he named *S. quoyi* var. *zschaui*. I regard *S. quoyi* as a synonym of *S. sigillinoides*.

In the 'Discovery' colonies, which are preserved in alcohol, the head is soft and usually yellow-grey. It is almost cylindrical, and rounded or tapered at each end. The stalk, although wide at the upper end, is sometimes constricted where it joins the head, and is narrowest at the base. It is firm, buff or dull orange in colour, and typically marked with fine annular ridges. The basal stem is similar to the stalk but is stouter and usually shorter.

As I have already remarked, I disagree with Brewin (1953) in her description of the common cloacal openings in the genus. In well-preserved specimens of *S. sigillinoides* which I have examined, the apex of the head has a single common cloacal opening, all the more clearly marked because the test bears a series of teeth round its border (Text-fig. 19, *t.t.*). The opening is ring-shaped as viewed from the apex of the colony owing to the projection of the central core of common test of the head. The individual cloacal canals, each serving a double row of zooids, lead into the terminal opening, and not directly to the surface of the colony.

ZOOID. The atrial languet has been described as 'of varying length' (van Name, 1945), and 'sometimes fringed with a number of lobes' (Kott, 1954). I have found that differences in the atrial languet are related to the position of the zooid in the colony. All zooids except the terminal one in each row have a pointed triangular languet. In the terminal zooids only, that is those immediately round the common cloacal opening, the end of the atrial languet is wide and straight with a row of pointed or leaf-like teeth. These teeth correspond to the teeth present on the test round the common cloacal opening, already mentioned, and doubtless are responsible for their formation.

The intestine only occasionally shows the subdivisions which Kott (1954) used to distinguish *S. sigillinoides* from *S. quoyi*.

LARVA. The larvae from different colonies vary in size from 0·40 to 0·76 mm., measured from the end of the papillae to the base of the tail, the majority being between 0·50 and 0·60 mm. Caullery (1909), Salfi (1925) and Kott (1954) have already described the larva. The sensory vesicle contains only one black pigment spot, the spherical otolith, 22–26 μ in diameter.

BIOLOGY. Breeding probably does not occur in the southern winter, yet as shown by the figures in Table 22 it is not restricted to a short period of the year.

Table 22

Month	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
No. of colonies examined	3	3	6	—	—	5	1	6	4	6	9	3
No. of colonies with embryos	1	1	0	—	—	2	0	1	1	2	4	1

In different colonies the embryos in the brood pouches numbered from two to fourteen.

The heads and zooids are unisexual, but all zooids in a head are not at the same stage of development. In a single head buds and young non-functional zooids may be found at the base; then a zone of functional but sexually unripe zooids occurs; and finally the distal part of the head is devoid of zooids but contains many isolated brood pouches with embryos and larvae. The brood pouches disappear finally, having presumably been set free by the disintegration of the common test. Whether the larvae escape before or after this is unknown.

It has long been known that heads occur free in the water, and indeed the first record of the species (Lesson, 1830) was of an isolated pelagic head. Free heads were frequent amongst the 'Discovery' material, having been taken in various years in January, February, October and December, i.e. in the southern spring and summer. Brewin (1953) suggests that the breaking off of heads is caused by rough weather, but van Name (1945) considers it as probably a normal event in the life of the species. Headless stalks, at any rate, seem to be a part of the annual cycle (Pl. II, fig. 5); they occur in the 'Discovery' collections sometimes in December, but most often in May, June and July, i.e. in the southern winter. At the depths from which these headless stalks were collected (137–304 m.) storm action could not account for the loss of the heads, and I conclude that they were lost in the normal course of events. But headless stalks do not necessarily imply free pelagic heads, as heads disintegrate after breeding. Whether intact heads also break off, except by storm or other accidental damage, is still doubtful.

The headless stalks do not die, and Pl. II, fig. 7, illustrates the growth of new heads. The old stalk consists of a firm outer layer with a sharply defined upper margin, and a softer central core of test material containing many small rounded orange bodies and perhaps a few remaining vascular processes from the zooids which formerly occupied the head. Caullery (1909) and Salfi (1925, 1926) have shown that these rounded bodies are buds formed by multiple constriction of the vascular processes of the zooids. The reduced state of the colonies, containing the buds but no zooids, recalls the overwintering condition of colonies of the Family Polyclinidae, but I do not know if the colony of *Sycozoa* also has a period of quiescence. When the buds develop they produce new zooids within the central test near the upper end of the old stalk, and at the same time new central test material begins to bulge out from the end of the stalk. As the new test continues to grow it forms a new head containing the developing zooids. Regenerating heads on old stalks were taken in December, March and May, but most often in June and July. We may conclude that loss of the head follows breeding and is in turn followed by regeneration of a new head, the speed of regeneration perhaps depending on water temperature, as in colonies of *Aplidium* in northern temperate waters.

In the related genus *Hypsistozoa*, Brewin (1956*a*) has shown that, accompanying and following the production of larvae, the distal part of the head of the colony is resorbed. Meanwhile, new zooids at the junction of the stalk and the old head are forming a new head. This is a process very similar to that occurring in *Sycozoa*.

It seems curious that one species should show two habits so different as the single stalk and the branched complex form. Perhaps some of the apparently simple forms are stalks broken off from more complex colonies, but it is also possible that the simple and the complex forms represent different phases of the life cycle. This is suggested by the growth of several young heads instead of one, from the end of the old stalks, a process seen in several specimens (Pl. II, fig. 7). Perhaps the colonies which develop from settled larvae have single stalks, which, after breeding and loss of the head, may develop a group of new heads from the original stalk, thus giving rise to a complex colony, the original stalk becoming the stout basal stem of the new colony.

DISTRIBUTION. Owing to the confusion regarding species it is difficult to state exactly the distribution of *S. sigillinoides*, but it is certainly widely spread in both western and eastern parts of southern and Subantarctic waters (Falkland Islands, Patagonian Shelf, Tierra del Fuego, Kerguelen, Macquarie Island, Tasmania, South Australia) and the Antarctic (South Georgia, Graham Land, Kaiser Wilhelm II Land, Enderby Land, MacRobertson Land).

Sycozoa georgiana (Michaelsen) (Pl. III, fig. 5)

Colella georgiana Michaelsen, 1907, p. 62, pl. 1, fig. 6; pl. 3, fig. 15.

For synonymy see van Name, 1945, pp. 154–5.

OCCURRENCE. St. 39: S. Georgia, 179–235 m. St. 140: S. Georgia, 122–136 m. St. 149: S. Georgia, 200–234 m. ?St. 363: S. Sandwich Islands, 329–278 m. ?St. WS 33: S. Georgia, 130 m. St. MS 14: S. Georgia, 190–110 m. St. MS 68: S. Georgia, 220–247 m.

COLONY (Pl. III, fig. 5). The form of the colony and the shape of the head are the main features which distinguish this species from *S. sigillinoides*. Colonies are attached to some solid object over which spreads a system of creeping branched stolons giving rise at intervals to single or grouped stalks. Each stalk bears a characteristic head which is pear-shaped or almost globular, and never, in the specimens examined, long as in *S. sigillinoides*. The heads in the 'Discovery' material are not laterally compressed as in Michaelsen's (1907) description. Usually the head is as wide as long, and sometimes is wider. One of the largest specimens has a stalk of 4·7 cm. and a head 0·7 cm. long by 0·9 cm. wide. The stalk and the head are of the same pale grey colour and the same smooth rather soft consistency, whereas in *S. sigillinoides* the head and stalk differ from each other. Zooids are generally absent from the lower part of the head, and the oral openings are confined to a wide zone round the single terminal common cloacal opening. Sluiter (1932) found that the zooids were not arranged in rows, and Michaelsen (1907) did not mention any regular arrangement. At first sight this also seems to be the case in the 'Discovery' specimens, but careful examination shows that the zooids are in short rows each with a few zooids.

ZOOID. The zooid seems to present no characters by which it can be distinguished from *S. sigillinoides*. Certainly it cannot be separated by the number of branchial stigmata in a row, as Kott (1954, p. 155) has done in her key. Sluiter (1932) stated that in *young zooids* the stigmata number ten to twelve in each half row, but in fully developed zooids there are up to twenty, and in the 'Discovery' material I have counted eighteen stigmata in a half row. This is the same number as in many zooids of *S. sigillinoides*. As in *S. sigillinoides* the zooids immediately surrounding the common cloacal opening have a broad-ended atrial languet, but in other zooids it is pointed. The brood pouches are long, narrow and coiled at the lower end.

LARVA. Embryos and larvae together numbering from ten to twenty-eight in a brood pouch are present in some colonies collected in March. The larvae measure from 0·60 to 0·65 mm. from the end of the papillae to base of the tail, and could not be distinguished from larvae of *S. sigillinoides*, unless by a somewhat longer tail, but this is a variable character.

REMARKS. In spite of its resemblance to *S. sigillinoides*, I do not doubt that *S. georgiana* is a valid species. Its known range is confined to South Georgia and perhaps the South Sandwich Islands (St. 363). It is not a form that has often occurred in any collections, and owing to its scarcity, little is known of its biology.

One colony from South Georgia (St. WS 33) has a shape very like that described for *S. gaimardi* (Herdman, 1886). But as no characters other than the mushroom-shaped head and the large number of embryos in the brood pouch seem reliable in that species, and the 'Discovery' colony is without embryos, I have included the specimen in *S. georgiana*.

DISTRIBUTION. Antarctic (South Georgia, ?South Sandwich Islands).

Sycozoa anomala sp.n. (Text-fig. 20; Pl. III, fig. 6)

HOLOTYPE. Size: head 1·8 cm., stalk 2·0 cm. long. St. 929.

DIAGNOSIS OF SPECIES. Colonies hermaphrodite or unisexual. Zooids unisexual; female with coiled brood pouch; branchial sac with no parastigmatic transverse bars; stomach smooth externally; ovary somewhat projecting below the abdomen. Larva with otolith but no ocellus.

OCCURRENCE. St. 929: North Island, New Zealand, 55–58 m.

COLONY (Pl. III, fig. 6). The material consists of three single colonies and a compound colony with four stalked heads. The largest of the single heads has a length of 1·8 cm. and a breadth of 1·3 cm., and is carried on a stalk of 2·0 cm. The compound colony has a basal stem of 1·3 cm. at the end of which is a group of four stalks, the longest 1·3 cm. The heads of the isolated colonies are a little flattened but the compound colony has round heads. The head is smooth and pale translucent buff-grey, the zooids being visible as double rows of paler spots. Longitudinal furrows separate the adjacent double rows. The stalk is rather paler than the head, widest at its attachment to the head, and tapering towards the base. The compound colony has a certain amount of sand sticking to the basal stem, but the other colonies are quite free of sand. At the apex of each head there is a single simple common cloacal opening, through the centre of which the terminal common test may project slightly.

ZOOID (Text-fig. 20A). The zooid is about 2 mm. in length, seldom more, and the thorax and abdomen are of about equal length, except when the gonads are highly developed and projecting. The oral siphon (*o.s.*) has six short pointed lobes and the atrial opening is large with a triangular atrial languet (*a.l.*). The zooids surrounding the common cloacal opening have a wide languet with a few small teeth; the remaining zooids have a narrower triangular languet without teeth.

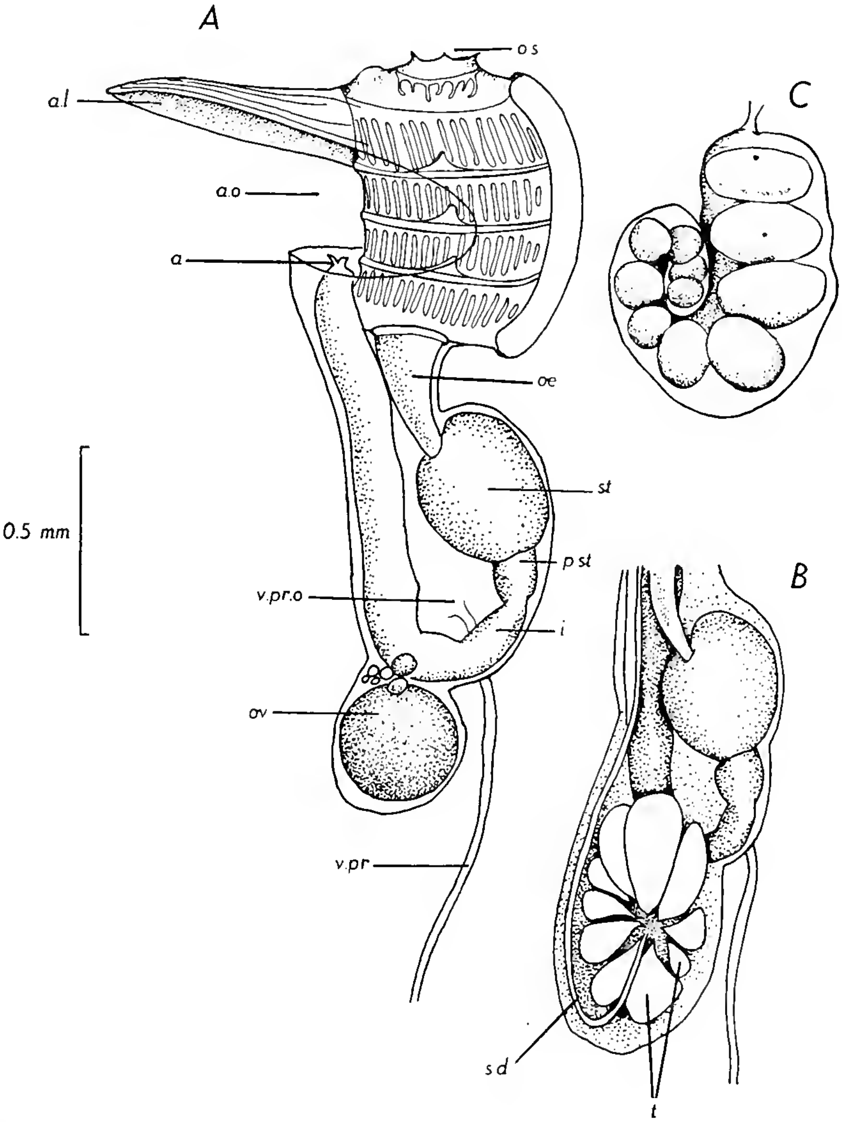
BRANCHIAL SAC. There are about sixteen long slender oral tentacles of varying length. The four rows of stigmata have no parastigmatic transverse bars. A short blunt languet is present on each transverse bar of the left side. The stigmata are long and narrow, and number at least fifteen in each row. The endostyle is wide.

GUT. The oesophagus (*oe.*) is of moderate length, narrow and curved ventrally. The ovoid or pear-shaped stomach (*st.*) has walls which are smooth externally, but internally are provided with minute papillae. White pigment spots are scattered on the surface of the stomach. A short post-stomach (*p.st.*)

leads to the intestine (*i*) which forms a short loop. The rectum is straight and ends with a two-lipped anus lying level with the transverse bar separating the third and fourth rows of stigmata.

Vascular process. A slender vascular process (*v.pr.*) arises from the left side of the abdomen and passes down below the zooid into the common test of the colony. Some of these processes, but not all, extend down into the stalk of the colony.

Gonads. In the compound colony all the zooids were male, but two of the single colonies had both male and female zooids; the third single colony was in degeneration.



Text-fig. 20. *Sycozoa anomala* sp.n. (St. 929): A, female zooid; B, abdomen of male zooid; C, brood pouch with embryos.

The ovary (*ov.*) lies slightly behind the intestinal loop, but in contact with it, and bulges out from the abdomen to form a small sac-like projection recalling the condition in *Distaplia*. The ovaries examined contained a group of ova of various sizes.

In male zooids the testis (*t*) is a rosette of six to ten wedge-shaped follicles contained in a projection from the abdomen similar to that accommodating the ovary in female zooids, but generally larger. The sperm duct (*s.d.*), arising from the centre of the rosette, loops back before passing forward beside the rectum (Text-fig. 20B).

Many of the female zooids had well-developed brood pouches (Text-fig. 20C). These are rather short, strongly coiled, and usually contained from nine to eleven embryos.

None of the zooids showed any sign of hermaphroditism, and the youngest buds in which any gonad was visible were clearly either male or female.

Larva. The larva could not be distinguished from that of *S. sigillinoides* except by its rather smaller size, 0·44–0·48 mm. from the end of the papillae to the base of the tail. This size, however, falls within the range of the larva of *S. sigillinoides*.

Remarks. In most respects this species is a quite typical *Sycozoa*, but the hermaphrodite nature of the colonies is exceptional.

The species seems to come closest to *S. pulchra* (Herdman) from the Torres Strait between Australia and New Guinea, and *S. kanzasi* (Oka) from Japanese waters. *S. pulchra* has hermaphrodite zooids and is therefore clearly different. *S. kanzasi* is more difficult to distinguish, but the species can be separated as shown in Table 23.

Table 23

	S. kanzasi	*S. anomala*
Oral siphon	Usually with plain margin	With 6 short pointed lobes
Oral tentacles	12	16
Knob-like structure over stomach	Present	Absent
Anus	With plain margin	With 2 lips

There is little doubt that the two species are very nearly related. Unfortunately the gonads of the specimens seen by Oka (1930) and Tokioka (1953) were not well developed. The knob-like process over the stomach is perhaps an unsatisfactory character for separating the species, because it is interpreted by Tokioka as a rudimentary bud and is therefore liable to be present or absent according to the phase of asexual development at which the zooid is examined.

Distribution. North end of North Island, New Zealand.

Genus **Distaplia** Della Valle, 1881

Distaplia colligans Sluiter (Text-fig. 21; Pl. III, fig. 3)

Distaplia colligans Sluiter, 1932, p. 7, figs. 5–8.

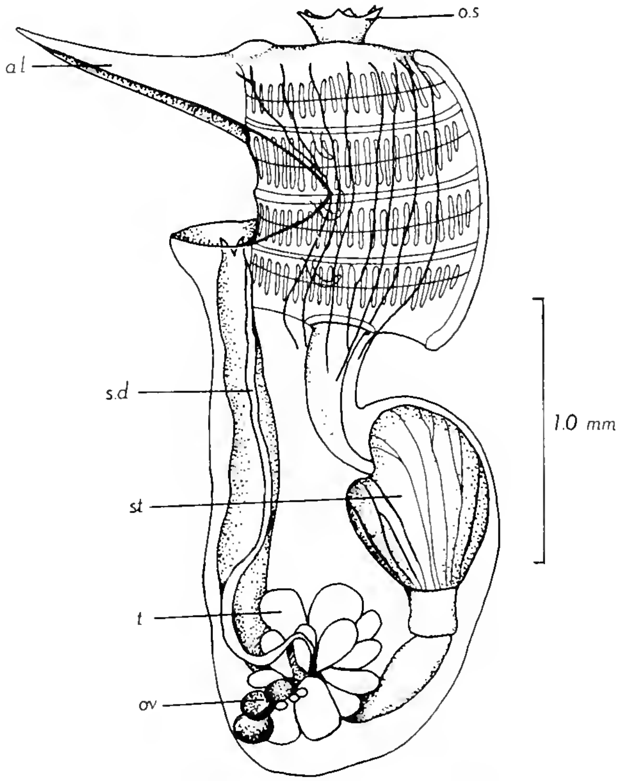
Occurrence. St. 164: S. Orkneys, 24–36 m. St. 476: S. Georgia, 165–0 m. St. 1113: Bransfield Strait, 275–130 m. St. MS 63: S. Georgia, 23 m. St. MS 74: S. Georgia, 22–40 m.

Colony. The colonies from stations 164, MS 63 and MS 74 are all very similar. The largest of these specimens is 1·2 cm. long and 0·3 cm. thick (St. MS 63). The preserved colour is a dull purple brown, marked with paler spots where the zooids show through the test. Generally the colonies are rather low and flattened or pillow shaped, not subdivided or lobed. No common cloacal openings are apparent on the surface, and usually no regular arrangement of the zooids can be made out, although in parts of one of the colonies from St. MS 63 there is an appearance of linear arrangement. In one of Sluiter's specimens there was a regular alignment of the zooids in double rows, but in the other this was apparently not conspicuous. The common test is soft and pliable, and semi-transparent but with a slightly cloudy appearance owing to the presence of many small pale cells, especially in the surface layer.

Zooid (Text-fig. 21). The zooids generally measure about 3 mm. in length, but their length in life was probably rather more, as the thorax in most colonies is much contracted, except in the specimens from St. 476 and St. 1113, which will be discussed later (p. 78). The oral siphon (*o.s.*) is short, sometimes quite distinctly six-lobed, but more often almost without lobes. Narrow but fairly strong thoracic muscles are present. A triangular and moderately long atrial languet (*a.l.*) is found in all zooids. I could find no trace of a vascular process from the posterior end of the zooids.

GUT. The oesophagus is narrow and of moderate length. In some colonies the wall of the stomach (*st.*) is distinctly marked with many fine ridges, but in others the wall is almost smooth externally. Sluiter does not describe any markings on the stomach of his type specimens, and his figure shows none.

GONADS. The gonads in Sluiter's specimens were evidently not very well developed, only a group of small testis follicles being present, and no trace of an ovary. Sluiter concluded that the colonies were unisexual. 'Discovery' specimens collected in February and March show a variety of sexual stages. In one colony some zooids are seen with a group of about twelve testis follicles (*t*) and a few small ova (*ov.*), and other zooids have a testis and quite large ova. The colony from the South Orkney Islands has zooids with only the ovary present and no testis. It is likely that Sluiter's two specimens were in the early male phase. The gonads are situated beside the loop of the intestine and scarcely project from the body except when at the height of their development. Only in some colonies from South Georgia and the South Orkney Islands is there any sign of a brood pouch; the zooids have a small sac-like projection from the dorsal body wall behind the atrial opening, evidently in the early stages of development.



Text-fig. 21. *Distaplia colligans* Sluiter (St. MS 63): Zooid.

REMARKS. All these colonies, with the possible exception of the ones from St. 476 and St. 1113, are in good agreement with Sluiter's type specimens of *D. colligans*, although the new specimens differ slightly in having markings on the wall of the stomach, and in the larger size of the zooids.

The single colonies from St. 476 and St. 1113 (Pl. III, fig. 3) are larger (2 cm. in diameter and 7 cm. long respectively) and paler than those already described. The zooids also are much larger, reaching 8 mm. in length when fully expanded. In other respects, however, they are similar and I am inclined to think that the differences may be due to the stage of the annual cycle at which the colonies have arrived.

D. colligans must be considered rather scarce or at least hard to find, and it may prove to have a wider distribution in the Antarctic than at present appears.

DISTRIBUTION. Antarctic (South Georgia; South Orkney Islands; Bransfield Strait).

Distaplia cylindrica (Lesson) (Pl. III, fig. 4)

Holozoa cylindrica Lesson, 1830, p. 439.
For synonymy see van Name (1945), p. 143.

OCCURRENCE. St. 39: S. Georgia, 179–235 m. St. 45: S. Georgia, 238–270 m. St. 123: S. Georgia, 230–250 m. St. 140: S. Georgia, 122–136 m. St. 142: S. Georgia, 88–273 m. St. 148: S. Georgia, 132–148 m. St. 149: S. Georgia, 200–234 m. St. 189: Palmer Archipelago, 0 m. St. 366: S. Sandwich Islands, 155–322 m. St. 1900: Patagonian Shelf, 0–5 m. St. 1906: Patagonian Shelf, 0–5 m. St. WS 33: S. Georgia, 0–5 m. St. WS 90: Patagonian Shelf, 82–81 m. St. WS 765: Patagonian Shelf, 113–119 m. St. WS 787: Patagonian Shelf, 106–110 m. St. MS 68: S. Georgia, 220–247 m. B.G.L.E., Stella Creek. B.G.L.E., Port Lockroy, 0–5 m.

COLONY. Many of the specimens in the collection are only parts of colonies, but there are also a few intact specimens, in which the base is attached, generally to a few small stones or pebbles. This basal area is sometimes wider than the rest of the colony, and in other cases the colony widens towards the base but narrows again at the immediate area of attachment. The largest colony (St. 148), measures, in the preserved state, 460 cm., but a label with the specimen showed that an earlier measurement, probably in the fresh state, was 485 cm. Even this colony was not intact. Another specimen was part of a 'strip floating on the surface', 20–25 ft. long. This floating fragment, over 7 m. in length, represents one of the longest specimens ever recorded.

In alcohol the colony is usually a dull greyish green, but the collector of the large floating strip has given the following description of the fresh colony: 'general colour pale yellow white; details of colour: background pale indeterminate, zooids bright creamy white'.

ZOOID. Ärnbäck (1949, 1950) has shown that, contrary to the belief of previous workers, the zooids are hermaphrodite, with the testis maturing before the ovary. The material on which she worked was part of the 'Discovery' collection (St. 149), which I have been able to re-examine. This and other specimens show that the zooid in the fully developed female condition has two large eggs. Two embryos, or occasionally three, are found in the brood pouch.

BIOLOGY. (*a*) *Breeding*. The breeding condition of all colonies in the 'Discovery' collection is shown in Table 24. The zooids are classed as 'well developed male', in which the testis is moderate or large; 'well developed female', with moderate or large eggs in the ovary; and 'with embryos', in which the brood pouch contains one, two, or three developing embryos. No colonies were collected in the winter months of May to September, but enough material was taken during the rest of the year to show that zooids were already well advanced as males in October and that the testis was present from then on until January when it began to regress. In October and November the ovary had not yet started to develop, in December and January it was large, and thereafter decreased. The presence of eggs or embryos in the samples of December, March and April indicates a breeding season confined to the southern summer. No fully developed larvae were seen in any of the zooids during that period, perhaps owing to a long period of incubation. If this is so larval settlement is not likely to take place before April.

Zooids in different parts of a colony are in different sexual conditions. One large colony of 130 cm. illustrates this (St. 366). Zooids are absent from the basal 6 cm. of the colony. Zooids at 10 cm. from the base have no gonads, no brood pouch, and no embryos. Some zooids at 20 cm. from the base have an ovary and others have not, and some zooids have a spherical brood pouch, but without embryos.

At 30 cm. the gonad has disappeared but many of the zooids have two embryos in the brood pouch, and this is the usual condition throughout the rest of the colony, with some variations in the state of the ovary.

This grading of sexual development in the zooids indicates that towards the base of the colony the zooids are younger than those higher up the colony, and is to be expected in forms with a linear arrangement of the zooids (e.g. *Sycozoa*) but not necessarily in *D. cylindrica* which has small oval systems. In some at least of the colonies which have embryos the zooids contain very little or no food in the gut, and it is likely that the zooids become moribund once the eggs are passed into the brood pouches. Specimens collected in April and containing embryos had non-functional zooids and some colonies lacked zooids altogether. None of the colonies in the collection showed any sign of the accumulation of reserve materials or other provision for overwintering and how the species passes through the winter is not known.

Table 24

Month	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*
Well-developed male	—	—	—	—	—	2	3	3	1	—	0	0
Well-developed female	—	—	—	—	—	0	0	4	3	—	1	0
With embryos	—	—	—	—	—	0	0	1	0	—	3	1

(*b*) *Feeding*. The contents of the gut show one or two interesting features. In the branchial sac of zooids in several colonies there was much coarse sand as well as organic matter (Pl. VI, figs. 4, 5), but the stomach and intestine showed no large sand grains, (Pl. VI, fig. 3). Unless this is an artifact produced in some way during collection or handling of the specimens, there seems to be some kind of sorting mechanism at work between the branchial sac and the stomach, a feature noticed in other and unrelated species (see p. 146). Coarse matter is present in the branchial sac right up to the mouth of the oesophagus, but none enters the oesophagus. That the mechanism is not simply one which excludes large particles is indicated by the presence of some diatoms in the intestine, equal in size to the sand grains which are excluded. The oesophagus perhaps accepts mainly organic matter, or particles with a smooth surface, but I do not know which of these characters is the important one or how the selection mechanism works. There must be an accumulation of sand particles in the branchial sac which is presumably cleaned at intervals by thoracic contractions expelling the whole contents of the branchial sac.

DISTRIBUTION. Antarctic (Graham Land, Kaiser Wilhelm II Land, MacRobertson Land, South Georgia, South Sandwich Islands), Subantarctic (Patagonian Shelf, Strait of Magellan).

Genus **Hypsistozoa** Brewin, 1953

Hypsistozoa fasmeriana (Michaelsen) (Text-fig. 22, Pl. III, fig. 2)

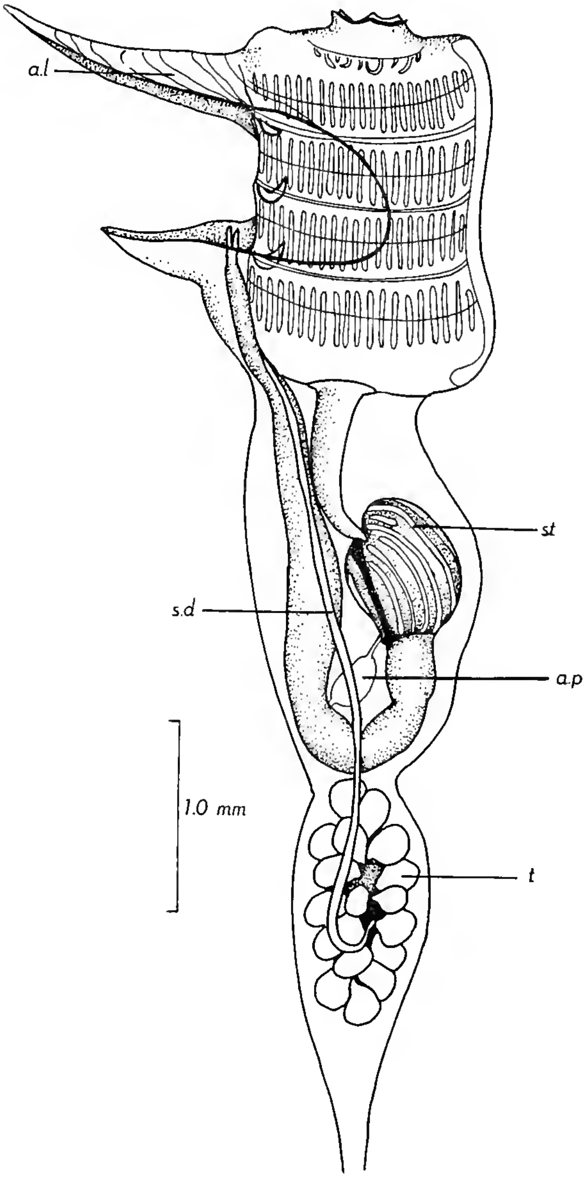
Distaplia fasmeriana Michaelsen, 1924.
Hypsistozoa fasmeriana Brewin, 1953, p. 56.

OCCURRENCE. St. 935: North Island, New Zealand, 84 m.

COLONY (Pl. III, fig. 2). The single specimen of this interesting species is a colony with head 1·3 cm. long and 1·1 cm. wide, borne on a stalk 1·6 cm. long and 0·7 cm. wide. The head is greyish brown and the stalk dull pale orange; both are smooth and without any encrusting matter. Rows of zooids are visible through the test; the systems are in fact long narrow elipses, but so narrow that the zooids have the appearance of being arranged in double rows. The common cloacal openings, of which there are several, are scattered on the surface of the colony, but are largely confined to the distal part. Each opening is round or oval and is bordered by a projecting rim of test.

Zooid (Text-fig. 22). The zooids agree closely with Michaelsen's (1924) detailed description, except that the stomach (*st.*) of the 'Discovery' specimens has rather more folds, there being up to twenty instead of fifteen as noted by Michaelsen.

Gonads. Many of the zooids in the 'Discovery' colony have no trace of gonads, but in a few there is a large testis (*t.*), consisting of many closely packed small orange-coloured follicles forming a long body situated entirely behind the loop of the intestine. The sperm duct (*s.d.*) is sinuous or hooked at its origin. No female gonads were seen, although, as Brewin (1946) has shown, the zooids are hermaphrodite. There were also no brood pouches.



Text-fig. 22. *Hypsistozoa fasmeriana* (Michaelsen) (St. 935): Zooid.

Remarks. The species was very carefully described by Michaelsen (1924) who, in the absence of gonads in his specimens, put it in the genus *Distaplia*. But Brewin (1946) found specimens with gonads which projected into the right anterior part of the vascular process, and she later erected a new genus *Hypsistozoa* for the species (Brewin, 1953).

The annual cycle and the complex and interesting embryonic development have been described in detail by Brewin (1956*a*).

DISTRIBUTION. *H. fasmeriana* has been previously recorded from Stewart Island, to the south of South Island, New Zealand (Michaelsen, 1924) and from Christchurch, South Island, New Zealand, and East Cape, North Island, New Zealand (Brewin, 1946, 1950, 1951, 1953). The 'Discovery' record considerably extends the range northwards. The species seems to be confined to the New Zealand region, but within that region it exists in the different temperature conditions which prevail at the extreme south and extreme north of these islands.

Genus **Cystodytes** von Drasche, 1884

Cystodytes dellechiajei (Della Valle)

Distoma dellechiajei Della Valle, 1877, p. 40.
For synonymy see van Name (1945), p. 133.

OCCURRENCE. St. 934: North Island, New Zealand, 98 m. St. 935: North Island, New Zealand, 84 m. St. WS 871: Patagonian Shelf, 336–342 m.

COLONY. The several colonies collected from St. 935 are ovoid rather than flat and encrusting; the largest is 3·0 cm. in length. The colony from St. 934 has its outline broken by a number of projecting lobes.

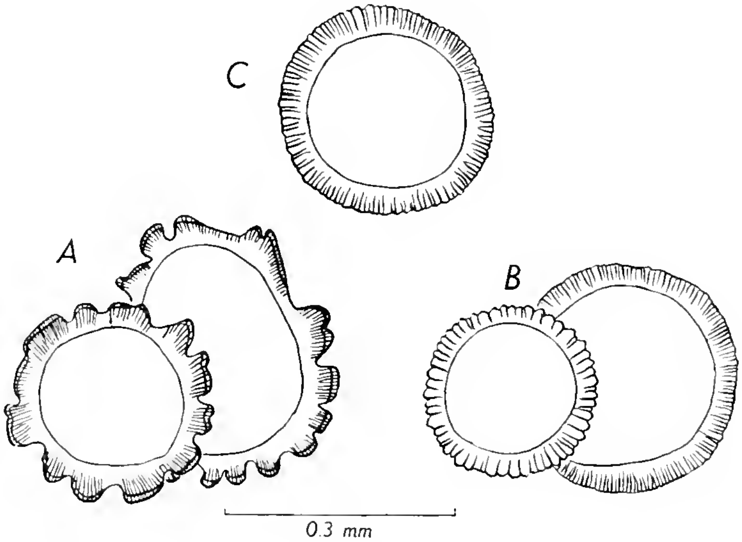
DISTRIBUTION. This species is very widely distributed, mainly in tropical and subtropical waters. It also extends to the more temperate waters of New Zealand and the Chatham Islands (Brewin, 1948, 1951, 1952, 1956*b*).

C. dellechiajei f. antarctica (Sluiter) (Text-fig. 23)

Cystodytes antarcticus, Sluiter, 1912, p. 460; 1914, p. 27; Ärnbäck, 1950, p. 26, pl. 5, fig. 25, text-figs. 6–8.

OCCURRENCE. St. 181: Palmer Archipelago, 160–335 m. St. 190: Palmer Archipelago, 93–126 m.

COLONY. Several colonies were collected from the Palmer Archipelago, and the largest of these measures 6 cm. long by 1·5 cm. wide and about 1·5 cm. thick. This colony is considerably larger than any collected by the second Charcot Expedition or the Swedish Antarctic Expedition of 1901–3, the only two expeditions which have hitherto taken the form.



Text-fig. 23. *Cystodytes dellechiajei* (Della Valle): A, spicules of f. *antarctica* (St. 190); B, spicules of typical form (St. 934); C, spicules of typical form (St. WS 871)

The disc-shaped spicules (Text-fig. 23 A), which reach 0·3 mm. in diameter, have a crenelated margin, as described by Ärnbäck (1950).

ZOOID. The zooid is much as described by Ärnbäck, but there is only a relatively short waist joining the thorax and abdomen. This condition may have resulted from contraction.

LARVA. No fully developed larvae were found in any of the colonies, but the large colony from St. 190 had some advanced embryos with the tail differentiated. These embryos had a length of 1·1 to 1·2 mm.

REMARKS. Sluiter (1912) described a species *C. antarcticus*, which Ärnbäck (1950) retained, but thought would very probably prove to be a form of *C. dellechiajei*, if more material could be studied.

The only way of distinguishing *C. dellechiajei* and *C. antarcticus*, other than by their distribution, is by the shape of the spicules. All antarctic specimens so far examined, including the 'Discovery' ones, have spicules with a distinctly crenelated margin (Text-fig. 23A). Specimens from other regions have the margin smooth or minutely notched (Text-fig. 23B, C), but there is sufficient variation in the size and distinctness of the notches to render doubtful the value of this character for separating species. I therefore propose that the present specimens, together with those previously called *C. antarcticus*, should be recognized as a form *antarctica* nom.nov. of *C. dellechiajei*.

DISTRIBUTION. The form *antarctica* is recorded only from the vicinity of Graham Land.

Subfamily ATAPOZOINAE Brewin, 1956

Genus **Atapozoa** Brewin, 1956

Atapozoa marshi Brewin (Text-fig. 24)

Atapozoa marshi Brewin, 1956*c*, p. 31, fig. 1.

OCCURRENCE. St. 935: North Island, New Zealand, 84 m.

COLONY (Text-fig. 24A, B). There are two specimens. The larger has a cylindrical stalk 1·3 cm. long and an ovoid head 1·0 cm. long. In the smaller specimen the stalk is only 0·3 cm. in length and the head is globular, with a diameter of about 1·0 cm. In each the stalk is encrusted with white shelly debris but the head is bare. The zooids, which are confined to the head, are seen through the test as orange-brown bodies. The test is semi-transparent and firm, but contains no 'kotballen' (masses of foreign matter) which Brewin found in her specimens.

ZOOID (Text-fig. 24C). Large zooids in which the abdomen is well developed reach a total length of 3·4 mm.; zooids with a short abdomen are little more than half that length. The siphons are both provided with six distinct lobes. Eighteen to twenty longitudinal muscles are present on each side of the thorax, and converge to form a more compact band of muscle which extends down the whole length of each side of the abdomen. Some zooids have a short vascular process (*v.pr.*) at the lower end of the abdomen. A small thin-walled projection from the base of the dorsal side of the thorax (*b.p.*) is present in some zooids and may represent the brood pouch described by Brewin. The whole body is of an orange-brown colour when preserved in alcohol.

BRANCHIAL SAC. Details are difficult to distinguish owing to the contraction of the thorax. The oral tentacles are closely spaced and number at least twenty. There are three rows of stigmata but the number in each row could not be determined; they probably exceed twenty. The hooked dorsal languets on the two transverse bars are quite prominent.

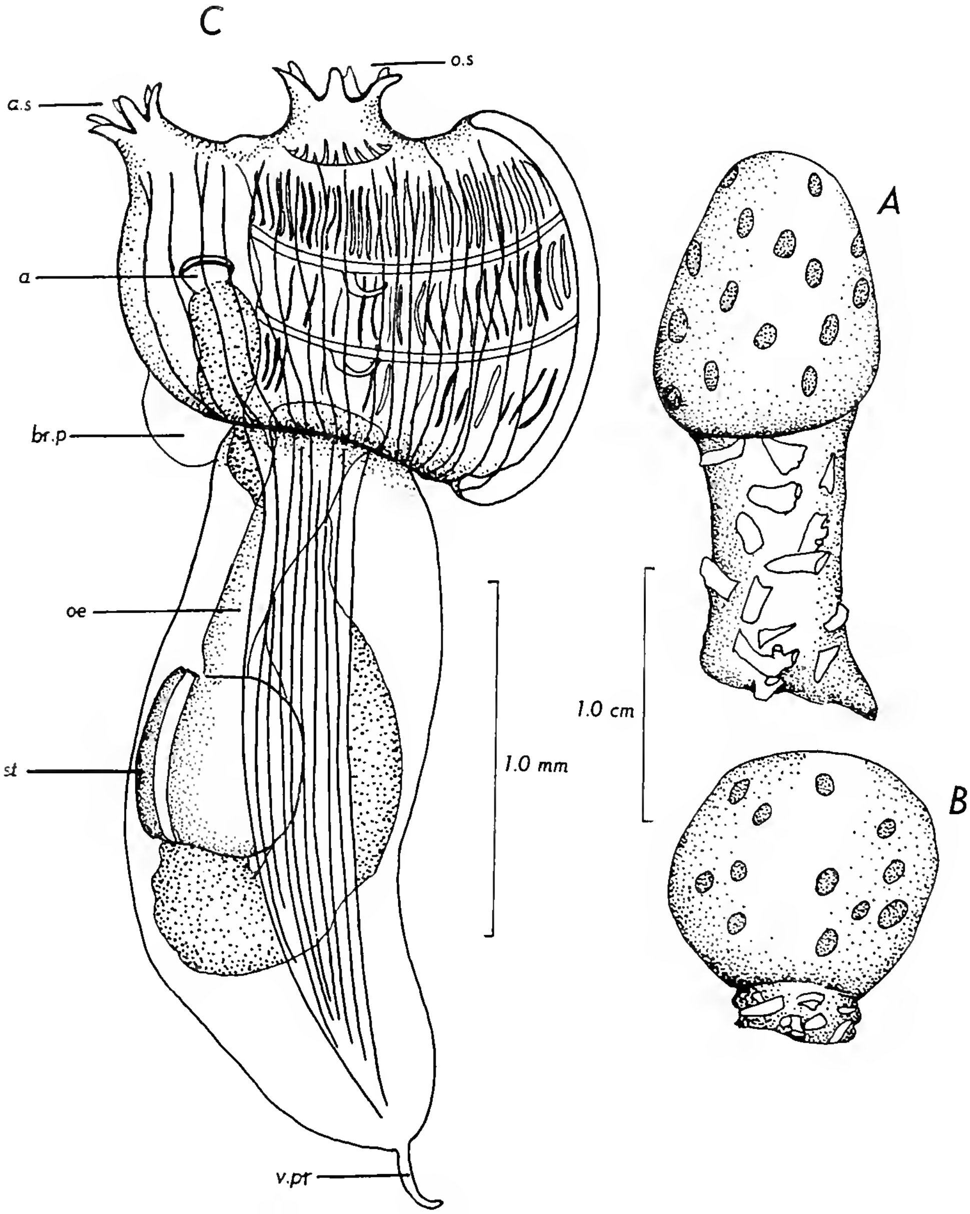
GUT. The oesophagus (*oe.*) is nearly twice as long as the stomach, and in this respect differs from Brewin's type specimens most zooids of which had a short oesophagus. The stomach (*st.*) is smooth-walled and the intestinal loop short, without any apparent divisions. In the type specimens the anus was smooth-edged; in the 'Discovery' material the anus (*a*), which lies opposite the second row of stigmata, has two lips.

GONADS. Gonads were not developed in the present specimens.

REMARKS. The genus *Atapozoa* was erected by Brewin (1956*c*) for a species found at Trigg Island, near Perth, Western Australia. *Atapozoa* differs from *Eudistoma* in having a stalked brood pouch, and only two anterior papillae in the larva instead of three.

There were no larvae in the 'Discovery' specimens, and the brood pouch, if present at all, was in a rudimentary state. The identification therefore rests on the other characters of the zooid and on the structure of the colony, in all of which features there is close agreement with the type specimens.

DISTRIBUTION. Western Australia; North Island, New Zealand.



Text-fig. 24. *Atapozoa marshi* Brewin (St. 935): A, B, two colonies; C, zooid.

Suborder PHLEBOBRANCHIATA Lahille, 1886

Family DIAZONIDAE Garstang, 1891

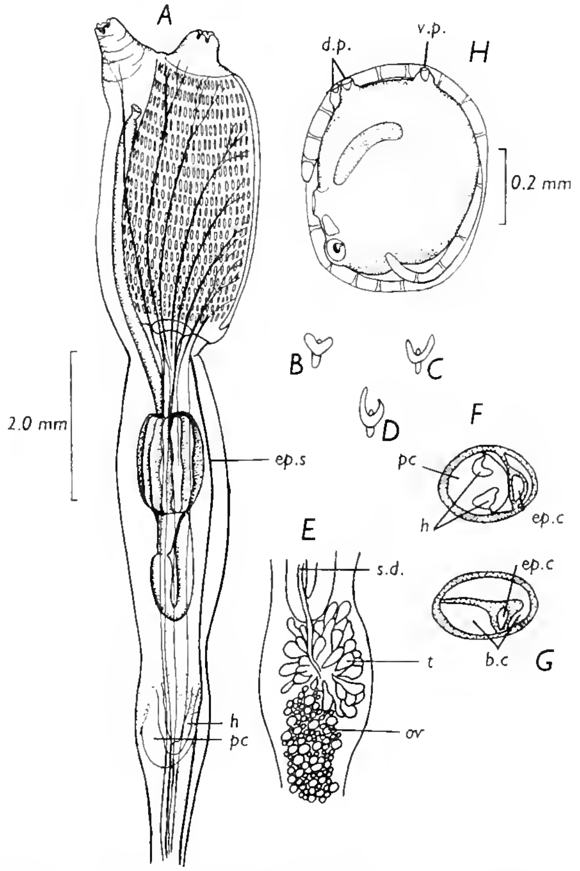
Genus **Tylobranchion** Herdman, 1886

Tylobranchion speciosum Herdman (Text-fig. 25; Pl. III, fig. 1)

Tylobranchion speciosum Herdman, 1886, p. 157, pl. 22, figs. 1–17.
For synonymy see Kott (1954), p. 152.

Occurrence. St. 123: S. Georgia, 230–250 m. St. 144: S. Georgia, 155–178 m. St. 160: Shag Rocks, 177 m. St. 371: S. Sandwich Islands, 99–161 m. St. WS 27: S. Georgia, 104 m. St. WS 243: Patagonian Shelf, 144–141 m. St. WS 841: Patagonian Shelf, 110–121 m.

Colony. The largest specimen in the collection is one from the Patagonian Shelf (St. WS 841), measuring 9 cm. tall, 1·5 cm. thick, and 7 cm. long. The original colony must have been still larger, as the specimen is only a portion. In form the colonies (Pl. III, fig. 1) are generally pillar-like, wedge-shaped, or club-shaped and are often markedly flattened from side to side. The test is firm but not hard, sometimes almost clear and occasionally nearly opaque. Some of the colonies from South Georgia and the Patagonian Shelf are reddish brown in colour. In most specimens the zooids are readily visible through the test. Attachment of the colony is usually to a small group of pebbles embedded in the basal test.



Text-fig. 25. *Tylobranchion speciosum* Herdman: A, zooid (St. WS 27); B, C, D, branchial papillae from different specimens (Sts. WS 27, 371, WS 243); E, gonads; F, transverse section of zooid at level of heart; and G, below level of heart; H, larva (St. 144).

Zooid (Text-fig. 25A). The general structure of the zooid is already known, and the principal variations in the 'Discovery' specimens are tabulated on page 86. Certain points regarding the lower part of the zooid, however, have remained doubtful. Berrill (1935) described a true post-abdomen containing the heart and gonads, but Ärnbäck (1927, 1950) showed that the heart is much farther forward than Berrill's figure indicated. A careful examination of the 'Discovery' specimens allows me not only to confirm Ärnbäck's findings, but also to add details concerning the epicardium and the nature of the posterior part of the zooid. The epicardium is a flattened tube forming a partition across the abdomen. Extending from just below the base of the thorax, it reaches the pericardium (*pc.*) but instead of ending there it continues into the lower, narrow part of the zooid where it forms a partition separating the two blood channels (Text-fig. 25G, *b.c.*). This part of the zooid behind the heart also contains muscles of the body wall and is not homologous with the vascular process which occupies a similar position in the related *Diazona*. In *Diazona* the vascular process has a mesenchymatous septum and no extension of the epicardium.

GONADS (Text-fig. 25E). Specimens collected in July (St. WS 243, Patagonian Shelf), and March (St. 371, South Sandwich Islands) had well-developed gonads consisting of bunched testis follicles (*t.*) at the lower end of the intestinal loop, and an elongated ovary (*ov.*) below the testis.

LARVA (Text-fig. 25H). Two of the specimens carry larvae. One colony from the Patagonian Shelf (St. WS 243), collected in July, has only three larvae in the zooids, and one colony from South Georgia (St. 144) collected in January, has many larvae in each breeding zooid. Only the latter specimen has fully developed larvae. These measured about 0·55 mm. from the end of the papillae to the base of the tail. There are two short dorsal papillae (*d.p.*) placed close together, and one short ventral papilla (*v.p.*), the three arranged to form a triangle. The trunk is deep and rounded. Within the cerebral vesicle the black otolith projects from the floor, but there is no trace of a pigmented ocellus.

Table 25

Species or material	*Height of colony (cm.)*	*Length of zooids (mm.)*	*Thoracic muscles*	*Branchial papillae*	*Stomach folds*	*Distribution or occurrence*
T. antarcticum	Up to 2	Thorax 2, abdomen 2·75	7 or 8	Tall; processes long	Sinuous and narrow	E. and W. Antarctic
T. speciosum	—	Thorax 4–5, abdomen 7–8	Numerous (about 11?)	Flattened; processes short	About 17, slightly sinuous	Kerguelen
T. weddelli	—	Thorax 7–8, abdomen 7	9 or 10	Flattened; processes short	14, straight	W. Antarctic
'Discovery' St. 144 (4 colonies)	1·6–2·7	Thorax 3·5–5·0, abdomen 3·0–5·5	6–8	Short; processes quite long	17–19; mostly straight	S. Georgia
'Discovery' St. WS 27 (18 colonies)	1·6–5·0	Thorax 2·0–6·0, abdomen 3·0–7·0	7–12	Short with short processes or long with long processes	12–18, mostly straight, but some sinuous in some zooids	S. Georgia
'Discovery' St. 371 (2 colonies)	3·0, 3·5	Thorax 6–7, abdomen 7–9	8–11	Long; processes long	12–16, straight	S. Sandwich Is.
'Discovery' St. WS 243 (1 colony)	4·5	Thorax 4, abdomen 5	7	Long; processes long	Apparently smooth	Patagonian Shelf
'Discovery' St. WS 841 (piece of 1 colony)	Piece, 7 by 9	Thorax 3, abdomen 3	7–10	Short; processes short	10–12	Patagonian Shelf
'Discovery' St. 160 (2 colonies)	4·5, 4·0	Thorax 5–6, abdomen 3–5	6–8	Short; processes short	15 or 16	Shag Rocks

REMARKS. Three species of *Tylobranchion* have been described from southern waters, *T. speciosum*, Herdman, *T. antarcticum* Herdman, and *T. weddelli* Ärnbäck. Van Name (1945) doubted whether they are distinct, and Kott (1954), after examining material from the B.A.N.Z. Antarctic Research Expedition of 1929–31 decided that they all represent one species. But Ärnbäck (1950) still maintained their separation. I have to record, however, that in her personal notes, to which I have had access, she seemed to have found less clear distinctions between the species represented in the 'Discovery' collections. The characters shown in Table 25 include those used by Ärnbäck to separate the three species. They show such a degree of overlapping that I am accepting Kott's (1954) view of the identity of the species, the name *T. speciosum* having priority.

The systematic position of the genus has been much discussed. Originally placed in the family Polyclinidae by Herdman (1886), it is now generally regarded as a phlebobranchiate ascidian, related to, or actually within, the family Diazonidae. The larva, with its triangular arrangement of the papillae, also shows that the genus should be removed from the Polyclinidae.

The 'Discovery' records are of special interest as they extend the known range northwards to the edge of the Antarctic and beyond into the Subantarctic (Patagonian Shelf). Ärnbäck (1950) had already recorded the species (as *T. antarcticum*) from South Georgia, at that time the most northern locality.

Distribution. Antarctic (Cape Adare, MacRobertson Land, Kaiser Wilhelm II Land, Graham Land, South Georgia, South Shetland Islands, South Sandwich Islands), Subantarctic (Patagonian Shelf).

Family ASCIDIIDAE Adams, 1858

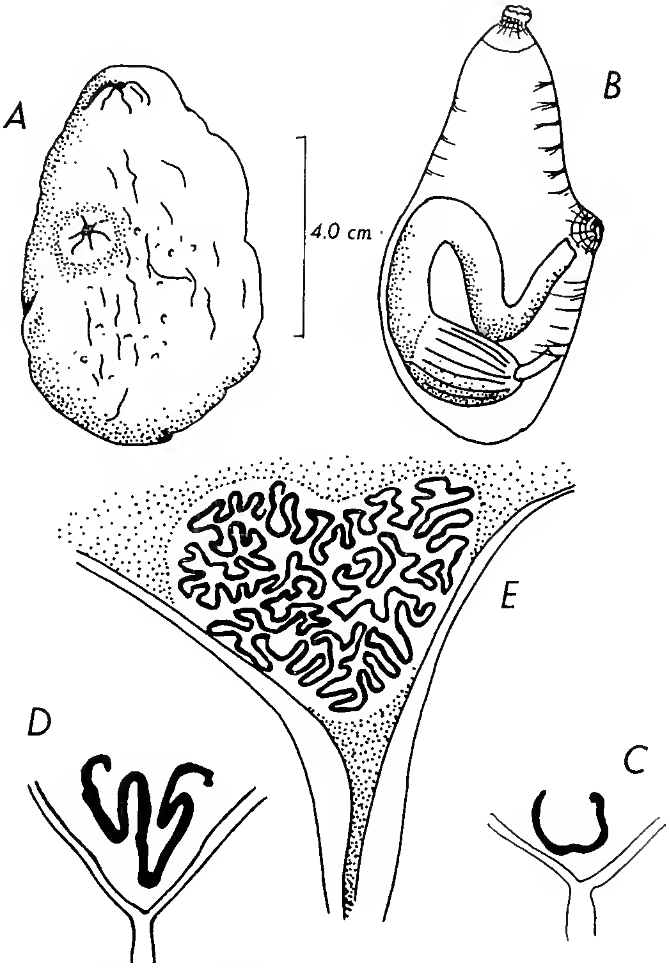
Genus **Ascidia** Linnaeus, 1767

Ascidia translucida Herdman (Text-fig. 26)

Ascidia translucida Herdman, 1880, p. 466.
?*Ascidia plicata* Kott, 1954, p. 150, fig. 31.

Occurrence. St. 39: S. Georgia, 179–235 m. St. WS 25: S. Georgia, 18–27 m. St. MS 10: S. Georgia, 26–18 m. St. MS 65: S. Georgia, 39 m. St. MS 68: S. Georgia, 220–247 m.

External appearance (Text-fig. 26A). The largest of the six specimens is 19·0 cm. long and the



Text-fig. 26. *Ascidia translucida* Herdman (St. MS 68): A, external appearance; B, specimen with test removed; C, D, E, dorsal tubercles of small, medium and large specimens, respectively.

smallest 1·5 cm. long. The size of the largest animal is greater than any yet recorded for this species, unless we accept *A. plicata* Kott as a synonym, Kott having recorded specimens of that species up to 29 cm. in length (see below for a discussion of *A. plicata*).

DORSAL TUBERCLE. The species is distinguished mainly by the very complex form of the opening of the dorsal tubercle. The large specimens in the 'Discovery' collection show this feature but in smaller ones the opening is much simpler, and a series of increasing complexity can be seen (Text-fig. 26C–E).

ORAL TENTACLES AND BRANCHIAL BARS. The numbers of oral tentacles and of longitudinal branchial bars are given in Table 26, for specimens of different sizes.

Table 26

Length of body (cm.)	*No. of tentacles*	*No. of longitudinal bars*
19·0	18	39
8·5	16	36
8·2	21	25
7·5	25	40
2·9	36	27
1·5	19	20

These figures give the total numbers of tentacles, including the smallest visible ones. If the larger and more conspicuous tentacles only are counted, the numbers would be reduced by one-third to one half. The number of tentacles does not increase steadily with growth of the body; in fact there is a tendency for large animals to lose tentacles.

BRANCHIAL SAC. The wall of the branchial sac is plicate, as noted by Herdman (1882). I have found that in large specimens the plication is complex, as the walls of each fold are thrown into a series of lesser folds, as described by Kott (1954) in her species *A. plicata*. Correlated with this folding there has developed immediately external to the perforated wall, a flat sheet of tissue extending over the whole outer surface of the wall. This sheet represents an expansion of the outer part of the transverse bars, and serves to support the folded stigmatic wall. The sheet is pierced by transverse rows of slit-like openings by which alone the water may escape from the branchial cavity to the surrounding peribranchial cavities.

The papillae of the branchial sac are large, and in some places intermediate papillae may be seen, but these seem usually to be associated with the growth of new transverse bars.

REMARKS. *A. translucida* is readily distinguished by its dorsal tubercle from other Antarctic and Subantarctic species except *A. plicata* Kott (1954) in which a similar tubercle has been described. Kott states that this species is distinguished from *A. translucida* by (1) the branchial wall with primary and secondary folds, (2) the atrial siphon one-third to one half of the body length from the oral siphon, and (3) the absence of secondary branchial papillae.

I believe that the branchial wall of *A. translucida* is essentially the same as that described for *A. plicata*. The type specimen of *A. translucida*, which Herdman described and illustrated, was only 2·2 cm. in length, and a specimen of this small size might be expected to have a simple type of folding in the branchial sac. The 'Discovery' specimen of 2·9 cm. length has only slight folding of the wall, and the smallest specimen available, of length 1·5 cm., shows no folding at all. There is, therefore, a gradual increase in complexity with increasing age and size.

The second feature used to distinguish *A. plicata*, the distance of the atrial siphon from the anterior end of the body, does not in fact separate the two species, in each of which the distance is between one-third and one half of the body length.

The third criterion, the presence or absence of intermediate papillae in the branchial sac, is also an unreliable character. In *A. translucida*, Hartmeyer (1912) found that secondary papillae were present in older specimens but not in younger ones. Ärnbäck (1938) also noted that in *A. translucida* these papillae exist in some parts of the branchial sac but not in others.

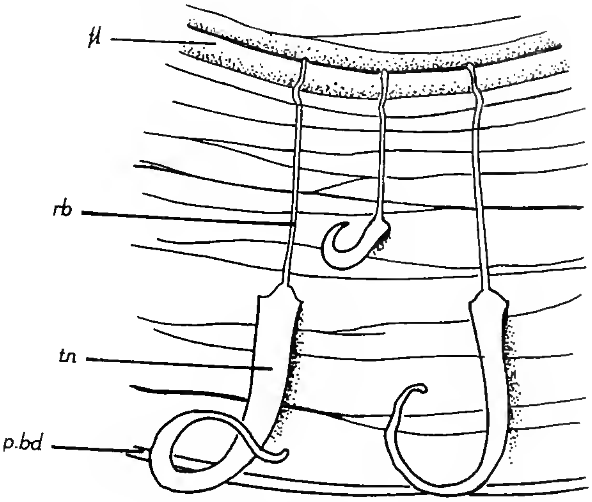
For these reasons I regard *A. plicata* as very probably a synonym of *A. translucida*.

Distribution. Antarctic (South Georgia), Subantarctic (Kerguelen).

Ascidia challengeri Herdman (Text-fig. 27)

Ascidia challengeri Herdman, 1882, p. 102, pl. 30.
Ascidia charcoti Sluiter, 1905, p. 471.
Ascidia dispar Ärnbäck, 1938, p. 48; text-fig. 11.

Occurrence. St. 145: S. Georgia, 26–35 m. St. 156: S. Georgia, 200–236 m. St. 160: Shag Rocks (S. Georgia), 177 m. St. 164: S. Orkneys, 24–36 m. St. 195: S. Shetlands, 391 m. St. 1652: Ross Sea, 567 m. St. 1660: Ross Sea, 351 m. St. WS 27: S. Georgia, 107 m. St. MS 71: S. Georgia, 110–60 m. B.G.L.E., 1934–7, Stella Creek.



Text-fig. 27. *Ascidia challengeri* Herdman (St. 145): Oral tentacles.

External appearance. The specimens range in length from 1·3 cm. to 11·0 cm., the largest being from the Ross Sea. They vary from a regular oval and laterally flattened form to an irregular pear-shaped form. The siphons are generally, but not always, inconspicuous, the oral one terminal and the atrial about one-third of the body length from it.

Table 27

	A. dispar	*A. challengeri*
No. of tentacles	About 50	Few, usually up to 20
Dorsal lamina	Extends far beyond oesophageal mouth	Scarcely extends beyond oesophageal mouth
No. of longitudinal branchial bars per side	40–50	30–32
Intermediate branchial papillae	Absent	Usually present
Branchial stigmata	Short and irregular	Long and regular

Remarks. Ärnbäck (1938) described a new species *A. dispar*, based on a single specimen from South Georgia. She recognized the strong similarity to *A. challengeri*, but gave as main distinctions those shown in Table 27.

Of these characters the ones which, judging by distinctions between other species of *Ascidia*, are likely to be the most reliable are (1) the number of tentacles, (2) the number of longitudinal branchial bars, and (3) the presence or absence of intermediate branchial papillae. In Table 28 I have shown the variation in the 'Discovery' specimens in respect of these three characters. A fourth character which I have added is the presence or absence of a rib running forward along the inner siphonal wall from the base of each tentacle (Text-fig. 27, *rb.*). This is a feature which I noticed in some specimens and which is illustrated but not mentioned by Herdman (1923, pl. 13, fig. 1) in *A. challengeri.* Inspection of the way in which these characters are distributed among the specimens shows that it is impossible to maintain the distinctions made by Ärnbäck in establishing *A. dispar*, which I therefore regard as a synonym of *A. challengeri.*

Table 28

Station	156	160	*WS* 27	156	*MS* 71	145
Locality	*S. Georgia*	*Shag Rocks*	*S. Georgia*	*S. Georgia*	*S. Georgia*	*S. Georgia*
No. of tentacles	40–43	30	48–50	26	50–55	29
No. of longitudinal branchial bars	50–53	60	About 39	28	About 40	32
Intermediate branchial papillae	Present	Present	?	Absent	Present in places	Absent
Tentacle ribs	Absent	Absent	?	?	Present	Present

Station	164	1652	1660	195	*B.G.L.E.*
Locality	*S. Orkneys*	*Ross Sea*	*Ross Sea*	*S. Shetlands*	*Stella Creek*
No. of tentacles	18	12–15	26	11–16	12–14
No. of longitudinal branchial bars	38–40	54–58	36	33	27–32
Intermediate branchial papillae	Present	Present	Present	Present	Present in places
Tentacle ribs	Absent	Present	?	?	Present or absent

Two other species seem to be closely related, if distinct: *A. placenta* Herdman, and *A. meridionalis* Herdman. Herdman (1923) himself suggested that *A. meridionalis* might prove to be the same as *A. challengeri.*

DISTRIBUTION. Antarctic (South Georgia, Graham Land, South Orkneys, South Shetlands, Kaiser Wilhelm II Land, Wilkes Land, King George V Land, Ross Sea), Subantarctic (Kerguelen).

Ascidia interrupta Heller (Text-fig. 28)

Ascidia interrupta Heller, 1878, p. 89, pl. 2, fig. 9.
For synonymy see van Name, 1945, p. 182.

OCCURRENCE. St. 279: French Congo, West Africa, 58–67 m.

EXTERNAL APPEARANCE (Text-fig. 28A). The three specimens are 7·3 cm. long by 3·0 cm. wide, 7·4 by 5·0 cm., and 7·6 by 2·8 cm. The shape is long and rather narrow, but the outline is irregular and the surface of the body has swellings and depressions. At the anterior end the body is slightly narrowed towards the oral siphon (*o.s.*). The atrial siphon (*a.s.*) is scarcely marked externally. It is situated between one half and two-thirds of the body length from the anterior end.

TEST. The test is fairly thick, hyaline and cartilaginous in appearance, and is semi-transparent.

BODY WALL. The left side of the body has few muscles, and on the right side the muscles form a loose irregular, but mainly transverse, mesh of slender strands. When the test has been removed, the oral siphon is seen to be a narrow, but not very long tube, and the atrial siphon a short conical tube projecting almost at right angles to the long axis of the body.

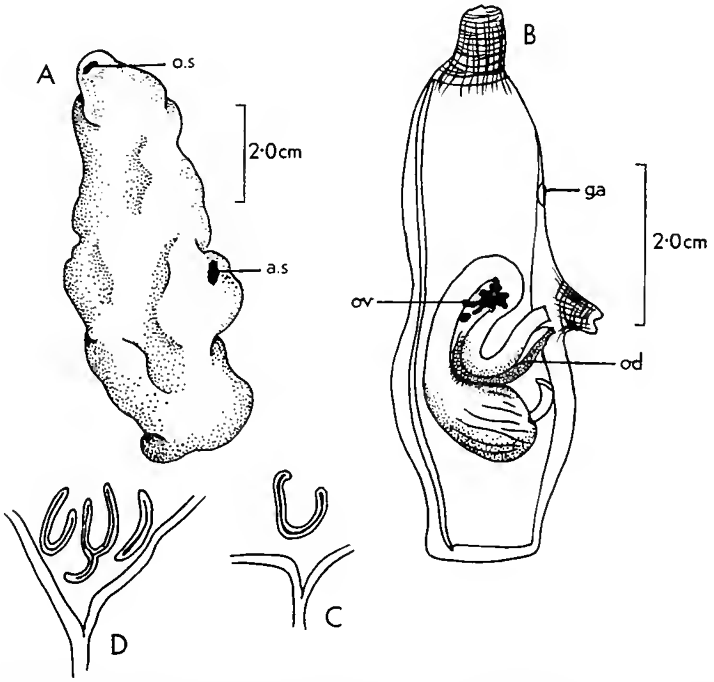
TENTACLES. There are from eighty to 110 oral tentacles in the 'Discovery' specimens. They are slender and closely crowded.

Dorsal tubercle. In one of the specimens examined, the dorsal tubercle is of a simple U-shape, with the right limb a little turned inwards (Text-fig. 28C). In another specimen the opening is broken up into a number of irregular pieces, but is still basically U-shaped (Text-fig. 28D).

Branchial sac. There are fifty to sixty longitudinal bars on each side of the branchial sac.

Gut. The gut (Fig. 28B) is very like that illustrated by van Name (1945, fig. 97).

Gonads. In all three specimens the testis is poorly developed, and the ovary is a small slightly lobed body lying within the intestinal loop (Text-fig. 28B, *ov.*).



Text-fig. 28. *Ascidia interrupta* Heller (St. 279): A, external appearance; B, specimen with test removed; C, D, dorsal tubercles of two specimens.

Remarks. These animals from the French Congo, West Africa agree very closely with the detailed description given by van Name (1945) of the species as it occurs on the tropical coasts of the American side of the Atlantic. So far as I am aware, it has not been recorded hitherto from the African coast and the 'Discovery' specimens are from deeper water than previous records. This is a further example of the distribution of a tropical species on both sides of the Atlantic.

Distribution. East coast of tropical America; French Congo, West Africa.

Ascidia sydneiensis Stimpson (Text-fig. 29)

Ascidia sydneiensis Stimpson 1855, p. 387.

For synonymy see van Name 1945, p. 189.

Occurrence. St. 90: False Bay, S. Africa, 0–2 m. St. 1686: Victoria, Australia, 0 m.

External appearance. The specimen from False Bay, South Africa is 5·0 cm. long and 3·0 cm. wide. The specimen from Victoria, Australia is 9·2 cm. long and 6·9 cm. wide.

Internal structure. Both specimens are quite typical of this species. Each shows the characteristic bands of muscles on the right side (Text-fig. 29B), the large number of oral tentacles (150–200), and the complex dorsal tubercle.

Remarks. In the South African individual the gut is full of food, consisting largely of algal cells, diatoms and peridineans with a certain amount of coarser inorganic matter.

Distribution. Widely distributed throughout the warmer and temperate waters of the world.

Family AGNESIIDAE Huntsman, 1912

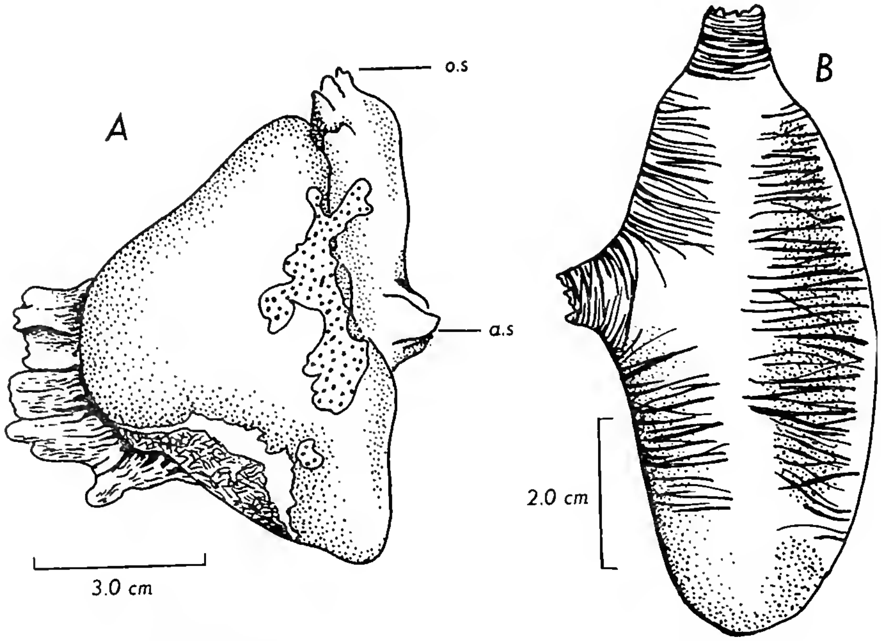
Genus **Agnesia** Michaelsen, 1898

Agnesia glaciata Michaelsen (Text-fig. 30)

Agnesia glaciata Michaelsen 1898, p. 370.
Agnesia krausei Michaelsen, 1912, p. 181, figs. 24, 25.
Agnesia capensis Millar, 1955, p. 191, fig. 19.

Occurrence. St. 91: False Bay, S. Africa, 35 m. St. 939: N. Island, New Zealand, 87 m. St. WS 775: Patagonian Shelf, 115–110 m.

External appearance. The two specimens from the Patagonian Shelf have lengths of 17 and 10 mm. The single specimen from False Bay, South Africa, is 9 mm. long and the largest of those from north of New Zealand is 12 mm. long. In most cases the body is rectangular in outline. In all specimens the test is thin and very transparent, but is hidden to a variable degree by the sand or broken shell which adheres to it. This coating of sand is most complete in the specimens from New Zealand and least in those from the Patagonian Shelf. Test hairs are sparsely developed in the specimens from the Patagonian Shelf and South Africa, but appear to be absent in the New Zealand specimens.

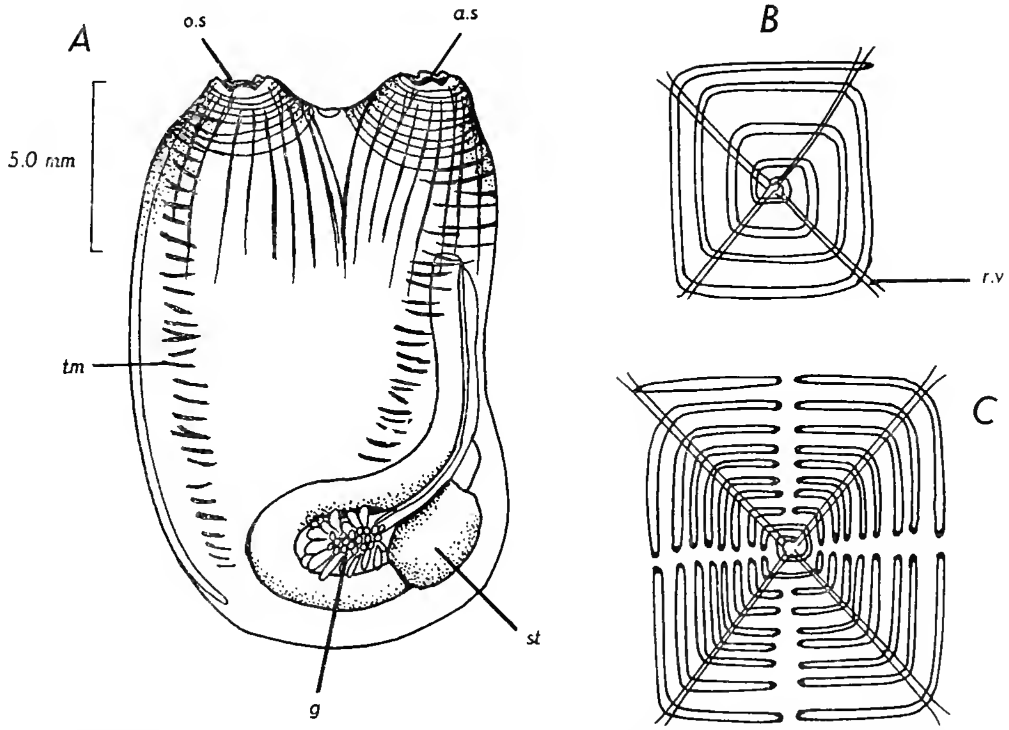


Text-fig. 29. *Ascidia sydneiensis* Stimpson (St. 1686): A, external appearance of specimen; B, same specimen with test removed.

Musculature (Text-fig. 30A). The same arrangement of muscles is found in all the specimens, but the degree of development varies. Longitudinal muscles radiate out from the two siphons and pass downwards across the upper part of the body. Strong circular muscles are present on both siphons, round which they form complete rings. Posterior to the siphons the circular muscles are represented by four longitudinal series of short transverse bands (*t.m.*), one series near the dorsal and one near the ventral margin of each side of the body. When the body is contracted these short transverse bands are inconspicuous, and this may possibly account for the omission of any reference to them by Michaelsen (1898, 1900) in his descriptions of *A. glaciata* and *A. krausei*.

Remarks. *A. glaciata*, the type species of the genus, was found off Tierra del Fuego and described by Michaelsen (1898, 1900); he subsequently described another species, *A. krausei*, from the Patagonian Shelf. A single specimen from Table Bay, South Africa, was made the type of a third species, *A. capensis* (Millar, 1955). The three descriptions are very similar, as may be seen by the comparison of the diagnostic characters given in Table 29. Details of the 'Discovery' specimens are included.

It is evident from the table below that both the number of turns of the stigmata, and whether the stigmata are undivided (Text-fig. 30B) or divided (Text-fig. 30C) depend on the size of the specimen. The distinctions between *A. krausei* and *A. glaciata* therefore break down. As van Name (1945) pointed out *A. krausei* is to be regarded as a young stage of *A. glaciata*, because division of the stigmata is likely to occur in older specimens. Having now been able to examine a second specimen of *Agnesia* from Table Bay, South Africa, I find that this one possesses radial vessels across the stigmata (Text-fig. 30B, *r.v.*), and conclude that my earlier observation (Millar, 1955) was incorrect or based on poor material. The distinction between *A. capensis* and *A. glaciata* also disappears, and one species, *A. glaciata*, remains. All specimens of *Agnesia* in the 'Discovery' collection can be referred to *A. glaciata*, which appears to be a species of wide distribution in southern waters.



Text-fig. 30. *Agnesia glaciata* Michaelsen: A, specimen from Patagonian Shelf (St. WS 775); B, stigma of specimen from False Bay, S. Africa (St. 91); C, stigma of specimen from St. WS 775.

Table 29

	A. krausei	*A. glaciata*	*A. capensis* (type specimen)	'Discovery' St. 91 (S. Africa)	'Discovery' St. WS 775 (Patagonian Shelf) Specimen 1	'Discovery' St. WS 775 (Patagonian Shelf) Specimen 2	'Discovery' St. 939 (New Zealand)
Length of body (mm.)	Up to 9	Up to 18	11	9	10	17	12
No. of turns of stigmata	4–5	7–9	3–5	4	5	9	5
Nature of stigmata	Undivided	Divided	Divided	Undivided	Divided	Divided	Undivided
Radial stigmatic vessels	Present	Present	Absent	Present	Present	Present	Present

Distribution. Subantarctic (Magellan region); South Africa; north of New Zealand.

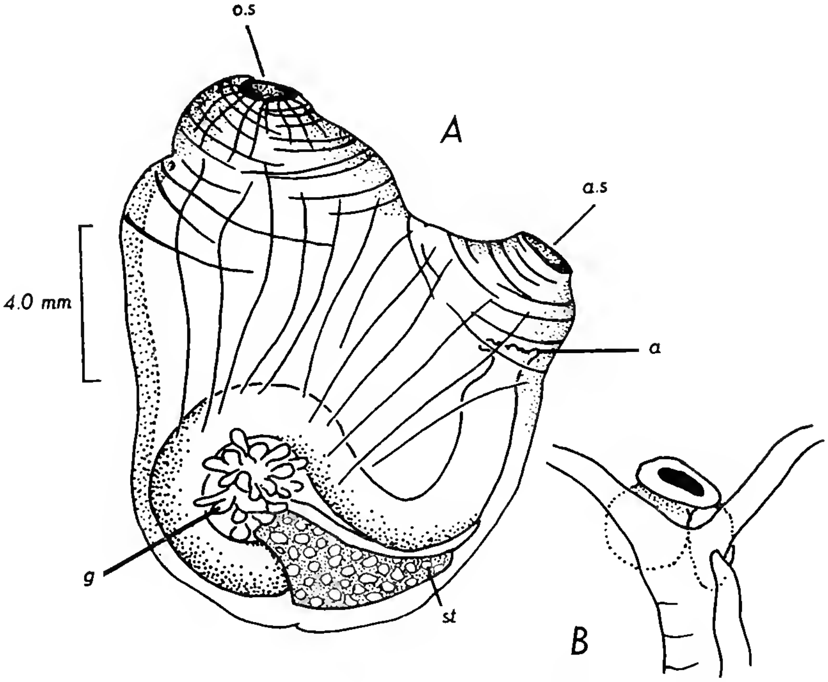
Genus **Caenagnesia** Ärnbäck, 1938

Caenagnesia bocki Ärnbäck (Text-fig. 31)

Caenagnesia bocki Ärnbäck, 1938, p. 41, pl. 2, figs. 20–22.
Agnesia complicata Kott, 1954, p. 151, figs. 32, 33.

Occurrence. St. 42: S. Georgia, 120–204 m. St. 181: Palmer Archipelago, 160–335 m. St. 182: Palmer Archipelago, 278–500 m.

External appearance. The shape of these specimens is very much as described by Ärnbäck (1938). In some of them there is a coating of fine sand or mud on most of the test. One specimen (St. 182) has fine test processes arising from the lower part of the body, as in the type specimen. The largest specimen is only 15 mm. in length, as compared with 20 mm. in Ärnbäck's material, and 30 mm. in Kott's material.



Text-fig. 31. *Caenagnesia bocki* Ärnbäck (St. 42): A, specimen with test removed; B, dorsal tubercle.

Internal structure. The 'Discovery' specimens show remarkable agreement with Ärnbäck's detailed account. The numerous oral tentacles are arranged in five distinct circles. The rectum appears to be a little shorter than that shown in Ärnbäck's fig. 20.

Remarks. This species has been recorded only twice before; off Graham Land (Ärnbäck, 1938), and off Enderby Land (Kott, 1954) if we accept *Agnesia complicata* Kott as a synonym of *C. bocki*. Kott's description of the specimens which she examined from near Enderby Land agrees very closely with Ärnbäck's description of the type specimens, except in having a better developed branchial sac. In *A. complicata* there were twenty-four transverse rows of infundibula each with seventeen infundibula, as compared with twelve rows each with thirteen or fourteen infundibula in *C. bocki*. This difference can be accounted for by the larger size of the specimens from Enderby Land.

Kott mentioned 'bifid languets' alternating with each transverse row of infundibula and not with each two rows (cf. *A. septentrionalis* Huntsman, *A. glaciata* Michaelsen, van Name, 1945, p. 201). These 'bifid languets' are in fact the bifid papillae which are present on the transverse vessels. True languets, to which Huntsman referred in *A. septentrionalis*, are present only along the roof of the branchial sac. *Caenagnesia*, having a continuous dorsal lamina, has no languets.

Distribution. Antarctic (Graham Land, South Georgia, Enderby Land).

Family CORELLIDAE Lahille, 1887

Subfamily CORELLINAE Herdman, 1882

Genus **Corella** Alder & Hancock, 1870

Corella eumyota Traustedt

Corella eumyota Traustedt, 1882, pp. 271, 273, pl. 4, figs. 2, 3; pl. 5, figs. 13, 14.
For synonymy see van Name, 1945, p. 212.

OCCURRENCE. St. 55: Falkland Islands, 10–16 m. St. 1652: Ross Sea, 567 m.

REMARKS. I have nothing to add to the descriptions already existing of this well-known species. Van Name (1945) discusses the problems involved in determining the probable synonyms of the species.

DISTRIBUTION. Antarctic (Graham Land, Kaiser Wilhelm II Land, Ross Sea, ?Wilkes Land), Subantarctic (Falkland Islands, coast of Chile, Magellan region, Auckland Islands, Macquarie Islands), South Africa, St Paul (Indian Ocean), New Zealand (North and South Islands), south and west Australia, Tasmania.

Order *PLEUROGONA* Perrier, 1898

Suborder STOLIDOBRANCHIATA Lahille, 1886

Family STYELIDAE Sluiter, 1895

Subfamily BOTRYLLINAE Adams, 1858

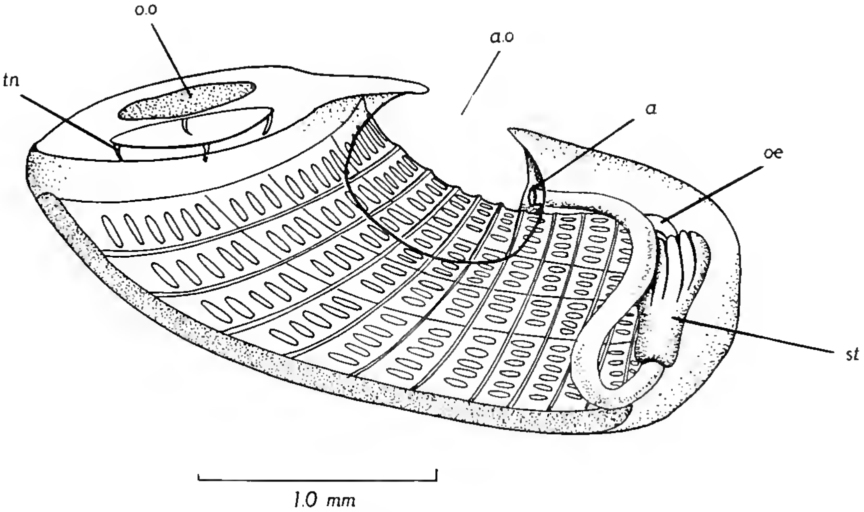
Genus **Botryllus** Gaertner (in Pallas), 1774

?**Botryllus separatus** Sluiter (Text-fig. 32)

Botryllus separatus Sluiter, 1904, p. 100, pl. 15, fig. 22.

OCCURRENCE. St. 934: North Island, New Zealand, 98–92 m.

EXTERNAL APPEARANCE. The single example is a brown colony approximately 8·0 by 4·5 cm., soft and thick. There are numerous round, oval or somewhat elongated systems of zooids. Groups of vascular ampullae lie between the systems and also form a fringe round the margin of the colony.



Text-fig. 32. ? *Botryllus separatus* Sluiter (St. 934): Zooid.

ZOOID (Text-fig. 32). The zooids attain a maximum length of 3 mm. and are golden-brown in colour in the preserved state. The oral opening (*o.o.*) is sessile and without lobes, and the atrial opening (*a.o.*) is large, exposing part of the dorsal surface of the branchial sac.

TENTACLES. Only four tentacles (*tn.*) were seen, although Sluiter noted eight.

BRANCHIAL SAC. There are twelve rows of stigmata in most zooids examined, each row with about eighteen stigmata. The three longitudinal branchial bars customary in the genus are present. The dorsal lamina is a narrow membrane.

GUT. The gut is confined to the posterior part of the zooid. It consists of a short curved oesophagus (*oe.*), a conical stomach (*st.*) with nine folds but completely lacking a pyloric caecum, and an S-shaped intestine and rectum. The anus (*a*), which lies opposite the 7th row of stigmata, has a plain margin.

GONADS. No gonads were present in any of the zooids examined.

REMARKS. Few species of either *Botryllus* or *Botrylloides* have been described from the North Island of New Zealand or the Australian coasts, and the present specimen does not agree well with any of them. The main points on which I base identification are the absence of a pyloric caecum and the presence of nine folds on the stomach. But there must remain some doubt about this identification because reliable characters are few in the botryllids, and the nearest record of *B. separatus* is from the vicinity of Borneo.

DISTRIBUTION. Indonesia; North Island, New Zealand.

Genus **Polyzoa** Lesson, 1830

Polyzoa opuntia Lesson (Text-fig. 33A; Pl. V, fig. 1)

Polyzoa opuntia Lesson, 1830, p. 437.
For synonymy see van Name 1945, p. 236.

OCCURRENCE. St. 145: S. Georgia, 26–35 m. St. 1230: Magellan Strait, 27 m. St. 1902: Patagonian Shelf, 50–80 m. St. WS 71: Falkland Islands, 82–80 m. St. WS 75: Falkland Islands, 64–104 m. St. WS 86: Patagonian Shelf, 151–147 m. St. WS 95: Patagonian Shelf, 109–108 m. St. WS 221: Patagonian Shelf, 76–91 m. St. WS 788: Patagonian Shelf: 82–88 m. St. WS 798: Patagonian Shelf, 49–66 m. St. WS 834: Patagonian Shelf, 27–38 m. St. WS 837: Patagonian Shelf, 95–102 m. St. MS 33: S. Georgia, 40 m. St. MS 64: S. Georgia, 7–15 m. St. Port Stanley, Falkland Islands, on shore.

EXTERNAL APPEARANCE (Pl. V, fig. 1). The colony of this species, although variable, is well known and characteristic, and needs no further description.

LARVA (Text-fig. 33A). The larva has an ovoid trunk measuring about 0·8 mm. from the anterior end of the papillae to the base of the tail. Behind the three papillae is a number of ampullae forming a complete ring round the anterior end of the trunk. There is a single black sense organ. The tail is about 1·5 mm. long, excluding the fin of test which projects about 0·6 mm. beyond the end of the tail.

BIOLOGY. Larvae were found in colonies from the Patagonian Shelf and Falkland Islands in December, February, March and June, and in colonies from the Magellan Strait in December. No larvae were present in the colonies from S. Georgia.

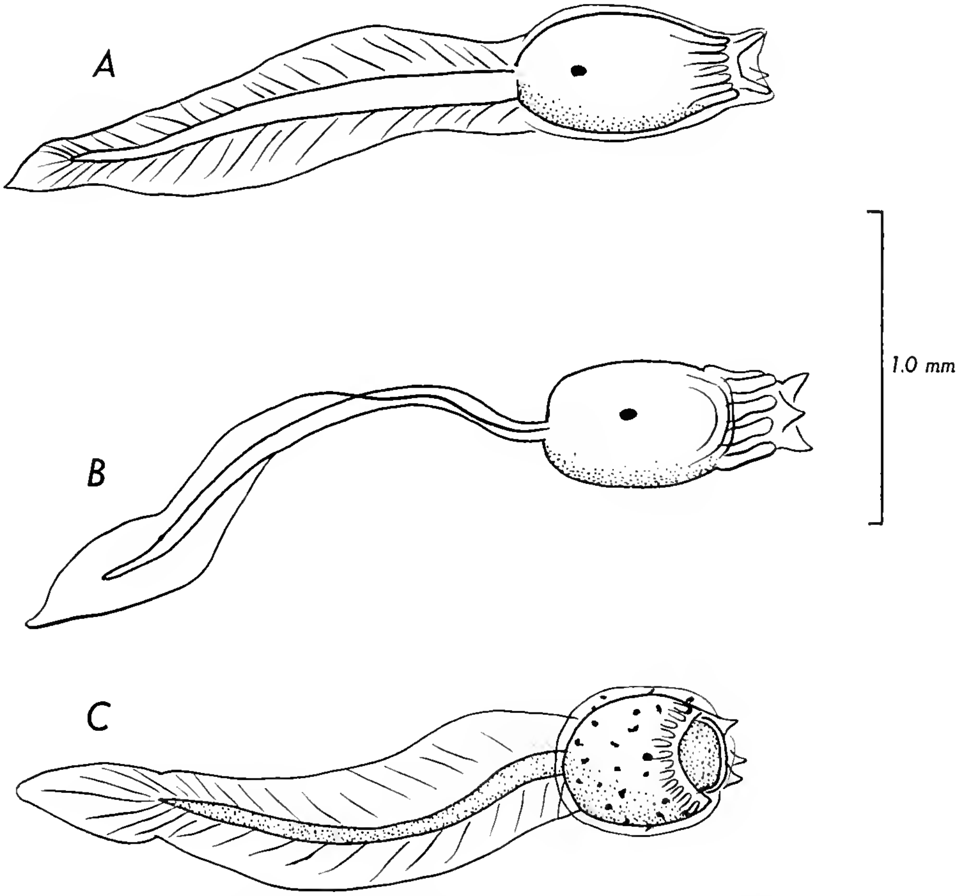
REMARKS. Ärnbäck (1950) separated *P. opuntia* Lesson and *P. coccinea* Cunningham, which van Name (1945) regarded as synonymous species. The distinctions which Ärnbäck proposed are: (1) the difference between seven longitudinal bars (*P. opuntia*) and eight bars (*P. coccinea*) on the left branchial wall; and (2) differences in the form of the colony. The colony is very variable and I doubt whether these distinctions are sufficiently great or constant in the genus to justify this course.

DISTRIBUTION. Subantarctic (coast of Argentine, Falkland Islands, Kerguelen, Tierra del Fuego), Antarctic (South Georgia, Heard Island).

Polyzoa reticulata (Herdman) (Text-fig. 33B; Pl. V, fig. 6)

Chorizocormus reticulatus Herdman, 1886, p. 346, pl. 46, figs. 1–8.
For synonymy see van Name 1945, p. 237.

OCCURRENCE. St. 42: S. Georgia, 120–204 m. St. 51: Falkland Islands, 105–115 m. St. 58: Falkland Islands, 1–2 m. St. 140: S. Georgia, 122–136 m. St. 141: S. Georgia, 17–27 m. St. 148: S. Georgia, 132–148 m. St. 474: S. Georgia, 199 m. St. 1230: Magellan Strait, 27 m. St. WS 25: S. Georgia, 18–27 m. St. WS 27: S. Georgia, 107 m. St. WS 71: Falkland Islands, 80–82 m. St. WS 82: Falkland Islands, 140–144 m. St. WS 85: Falkland Islands, 79 m. St. WS 823: Patagonian Shelf, 80–95 m. St. MS 10: S. Georgia, 26–18 m. St. MS 14: S. Georgia, 190–110 m. St. MS 62: S. Georgia, 31 m. St. MS 71: S. Georgia, 110–60 m. St. MS 74: S. Georgia, 22–40 m.



Text-fig. 33. Larvae of A, *Polyzoa opuntia* Lesson (St. WS 221), B, *P. reticulata* (Herdman) (St. MS 74), and C, *Alloeocarpa incrustans* (Herdman) (St. 388).

EXTERNAL APPEARANCE (Pl. V, fig. 6). The colonies vary in form, some having closely united zooids with little or no stolon, and in others the zooids are widely separated with long narrow stolons.

LARVA (Text-fig. 33B). In form this is very like the larva of *P. opuntia*. The trunk is from 0·72 to 0·90 mm. long, and the tail from 1·0 to 1·5 mm. excluding the projecting fin of test material. There are three papillae, about fourteen ampullae in a ring round the anterior end of the trunk, and a single black sense organ.

BIOLOGY. Larvae were present in colonies collected at Falkland Islands in February and March, and at South Georgia in November, December, February and March.

DISTRIBUTION. Subantarctic (Falkland Islands, Patagonian Shelf, Magellan Strait, Kerguelen, Campbell Islands, Macquarie Islands), Antarctic (South Georgia).

Genus Alloeocarpa Michaelsen, 1900

Alloeocarpa incrustans (Herdman) (Text-fig. 33C; Pl. V, fig. 8)

Synstyela incrustans Herdman 1886 (in part; not Philippine specimens), p. 342, pl. 46, figs. 9–14.
For synonymy see van Name 1945, p. 239

OCCURRENCE. St. 48: Falkland Islands, 105–115 m. St. 51: Falkland Islands, 105–115 m. St. 52: Falkland Islands, 17 m. St. 55: Falkland Islands, 10–16 m. St. 56: Falkland Islands, 10·5–16 m. St. 58: Falkland Islands, 1–2 m. St. 141: S. Georgia, 17–27 m. St. 145: S. Georgia, 26–35 m. St. 388: Cape Horn, 121 m. St. 474: S. Georgia, 199 m. St. 1230: Magellan Strait, 27 m. St. 1941: S. Georgia, 55–22 m. St. WS 65: S. Georgia, shore collection. St. WS 71: Falkland Islands, 82–80 m. St. WS 84: Falkland Islands, 75–74 m. St. WS 86: Patagonian Shelf, 151–147 m. St. WS 216: Patagonian Shelf, 219–133 m. St. WS 247: Falkland Islands, 172 m. St. WS 765: Patagonian Shelf, 113–119 m. St. MS 6: S. Georgia, 24–30 m. St. MS 10: S. Georgia, 26–18 m. St. MS 33: S. Georgia, 40 m. St. MS 64: S. Georgia, 7–15 m. St. MS 67: S. Georgia, 38 m. St. MS 74: S. Georgia, 22–40 m.

EXTERNAL APPEARANCE (Pl. V, fig. 8). Colonies vary from solid fleshy masses with no free space between zooids to forms in which the zooids are separate and united only by a thin basal membrane of test. In the preserved state the colour is brown or grey, but according to the collector's note accompanying colonies from St. WS 765 they may be 'brick red' or 'lemon yellow' in life.

BRANCHIAL SAC. A number of species, subspecies and forms have been described by various authors, differing mainly in the number of longitudinal branchial bars, and the number and shape of the gonads. After examining many colonies from the 'Discovery' collections I have not found any consistent differences in these characters. For example, Michaelsen (1904) separated two species, *A. zschaui* and *A. incrustans*, by the former having sixteen or seventeen branchial bars and the oviducts wider than long, and the latter having twelve to fourteen bars and the oviducts longer than wide. But in the 'Discovery' collections specimens are found with sixteen bars and the oviducts longer than wide (St. 1941), thus combining characters of both species, and other specimens (St. 58) have an even greater number of bars (twenty-two) together with similar oviducts. There is therefore no reason to separate colonies on the basis of these characters. Van Name (1945) regards *A. zschaui* as identical with *A. incrustans*, but Ärnbäck (1950) allows it the rank of a *form* of *A. incrustans*. A few of the colonies approach Ärnbäck's subspecies, *A. incrustans rugosa*, but in this case also I doubt whether the points of distinction merit the status of a subspecies.

GONADS. In nearly all specimens the testes are confined to the left and the ovaries to the right of the body, but I have found a few in which two or three ovaries are present on the left side, immediately in front of the testes.

LARVA (Text-fig. 33C). In shape the larva is very similar to that of *Polyzoa opuntia* and *P. reticulata*. The trunk varies a great deal in size, from 0·34 up to 0·8 mm. and the tail is from 0·9 to 1·2 mm., excluding the fin of test. The great variation in size of the trunk is surprising, but no accompanying differences were found in structure of either the larva or the adult, so the character seems to have little systematic importance in this species. There are the usual three papillae, single black sense organ (only visible on dissection) and ring of anterior ampullae (eighteen to twenty-six in number). The larva is red-brown in the preserved state. In some larvae there are distinct pigment spots on the surface of the trunk, and these appear to be produced by pigment cells within the test.

BIOLOGY. The presence or absence of larvae in the colonies of the collection is shown in Table 30. The numbers are small, but it is evident that breeding is not confined to a short season, although it probably occurs chiefly in the months of January to May, i.e. southern summer and autumn.

Larvae were found in the colonies from the Patagonian Shelf and Falkland Islands in February, March, April, May and June, and in colonies from South Georgia in November, January and February.

Distribution. Subantarctic (Falkland Islands to Tierra del Fuego), Antarctic (South Georgia).

Table 30

	V	*VI*	*VII*	*VIII*	*IX*	*X*	*XI*	*XII*	*I*	*II*	*III*	*IV*
No. of colonies with larvae	3	1	0	—	—	0	1	0	2	1	1	2
No. of colonies without larvae	4	0	1	—	—	1	0	2	1	4	1	0

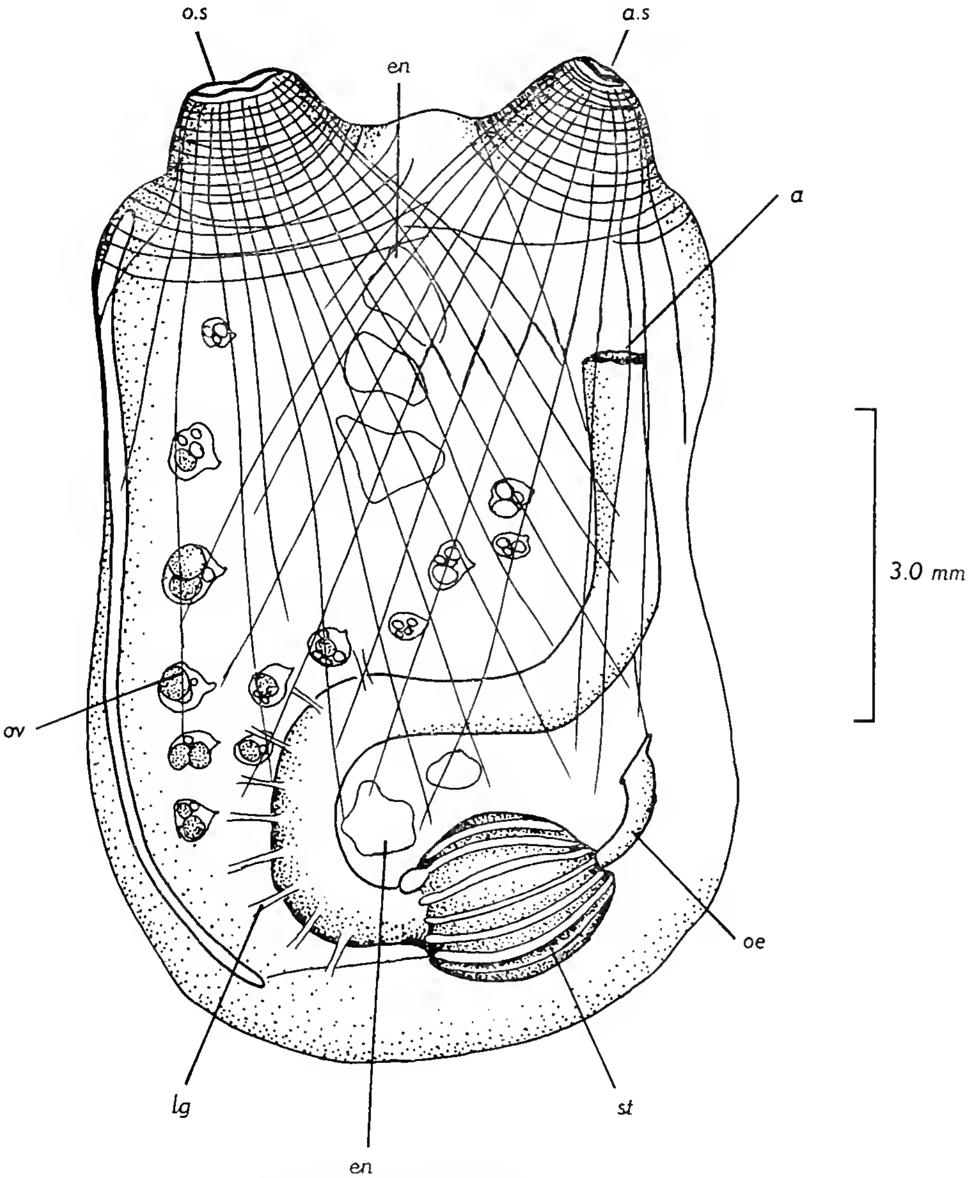
Genus **Amphicarpa** Michaelsen, 1922

Amphicarpa diptycha (Hartmeyer) (Text-fig. 34, Pl. V, fig. 3)

Distomus diptychos Hartmeyer, 1919, p. 87, pl. 2, fig. 48.

Occurrence. St. 1686: Victoria, Australia, 0 m.

External appearance (Pl. V, fig. 3). The colony, which is about 5 cm. long, and rather less in width, had been growing on the shell of a living mussel. For the most part the zooids are close



Text-fig. 34. *Amphicarpa diptycha* (Hartmeyer) (St. 1686): Zooid.

together, only those on the margins of the colony lying some distance apart. Where the zooids are separated the narrow basal stolons which unite them can be seen. Sand almost completely covers both zooids and stolons. The zooids are ovoid, upright, may be slightly narrowed at the base, and bear the two inconspicuous siphons at the upper end. The largest zooids are about 1 cm. long.

TENTACLES. The oral tentacles, although closely spaced, number only about 50, whereas Kott (1952) found about 100.

DORSAL TUBERCLE. The opening of the dorsal tubercle is a simple longitudinal slit.

BRANCHIAL SAC. In a large zooid the longitudinal branchial bars have the following arrangement: dorsal line 0 (12) 5 (9) 6 endostyle.

GUT. The gut is just as Kott described it, including the series of ligaments (Text-fig. 34, *lg.*) attached to the intestine.

GONADS. Only the ovaries are present in zooids of the 'Discovery' colony, there being no trace of testes. On the right side there is a slightly curved row of about eight very small ovaries; on the left side two rows diverge from the postero-ventral part of the body wall, one parallel to the endostyle and the other following the course of the intestine (*ov.*).

ENDOCARPS. Large and small endocarps (*en.*) are scattered over much of the body wall.

DISTRIBUTION. Western and southern coasts of Australia; Tasmania.

Subfamily STYELINAE Herdman, 1881

Genus **Cnemidocarpa** Huntsman, 1913

Cnemidocarpa pfefferi (Michaelsen) (Text-figs. 35 A–C)

Styela pfefferi Michaelsen, 1898, p. 367.

OCCURRENCE. St. 42: S. Georgia, 120–204 m. St. 123: S. Georgia, 230–250 m. St. 159: S. Georgia, 160 m. St. 1952: S. Shetlands, 367–383 m.

EXTERNAL APPEARANCE. The largest specimen is 5·2 cm. high and 2·5 cm. wide, and the smallest one 2·2 by 2·2 cm. The body is generally upright with the two quite prominent siphons a little distance apart at the upper end. Shallow furrows divide the surface into large irregular areas. All the examples in the 'Discovery' collection are pale grey in the preserved state, with a fairly smooth surface which is almost free of encrusting matter.

TENTACLES. These vary from ten to thirty-two according to the size of the specimen.

DORSAL TUBERCLE. The dorsal tubercle of the 'Discovery' specimens is constant in form, having a C-shaped slit with inrolled horns and the open interval facing forward.

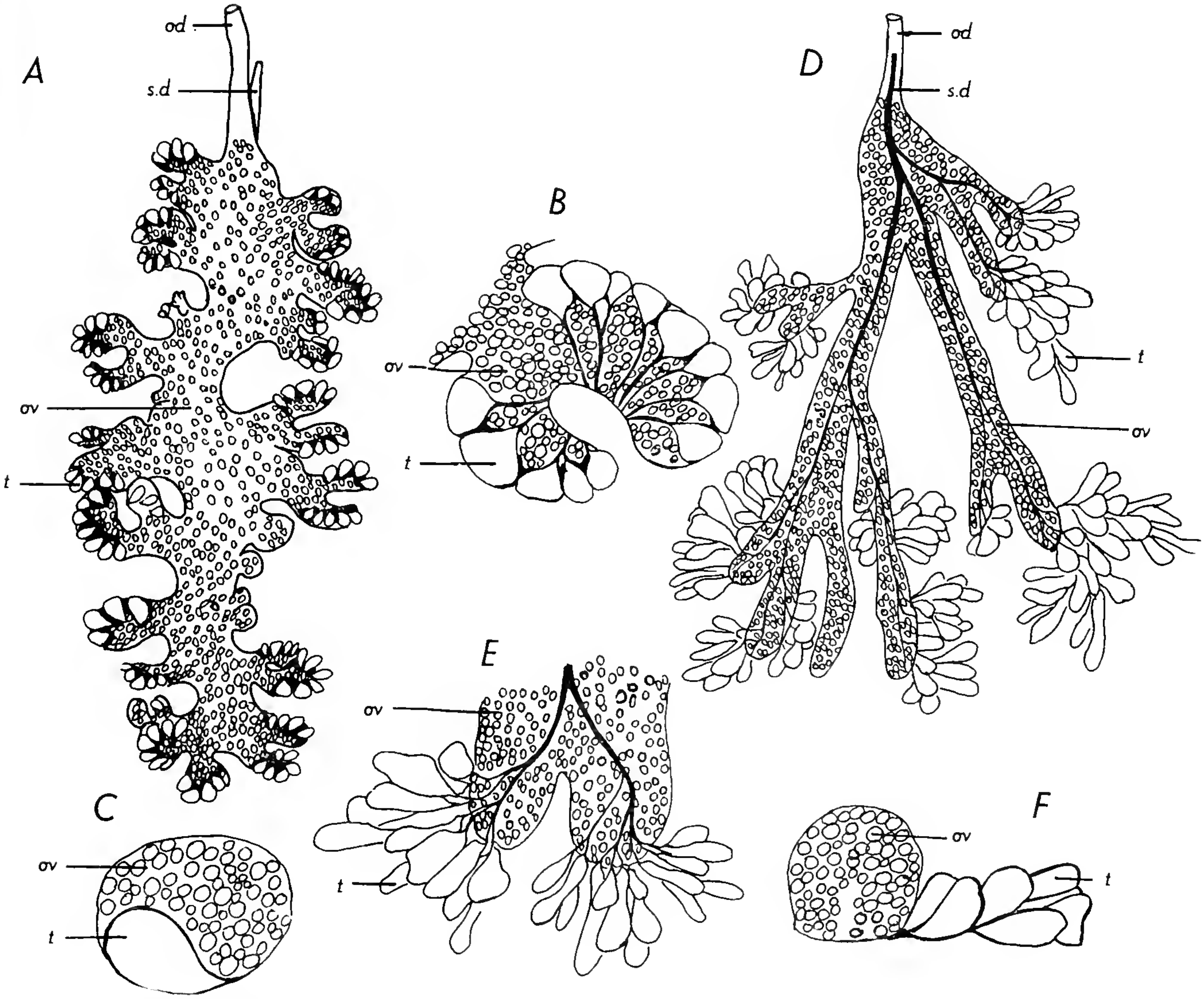
GUT. The stomach has twenty-four to thirty-one complete folds.

GONADS (Text-figs. 35 A, B, C). In all specimens dissected there were two gonads on each side. Each consists of a sinuous ovary (*ov.*), the sides of which have swellings, knobs, or short branches. These short lateral branches are generally in pairs with the two limbs curved in towards each other. The testis follicles (*t*) are arranged on the sides of the branches in a very characteristic manner (see Text-fig. 35 B) and are closely united to the ovarian branches from the sides of which they scarcely project even when well developed. The gonad is therefore of the *Cnemidocarpa* type, in which the testis is bound closely to the ovary, within a common membrane.

REMARKS. This species has been confused with *Styela paessleri*, and van Name (1945) considered them to be probably identical. The structure of the gonads is, however, quite different, although when *S. paessleri* is at full maturity the testis is so large that it presses closely round the sides of the ovary (see p. 115). The difference in the gonads of the two species will be best understood by reference to

Text-figs. 35 A–C and D–F which show the close union of testis and ovary in *C. pfefferi* and their separation in *S. paessleri*.

Distribution. Antarctic (South Georgia, South Shetland Islands).



Text-fig. 35. *Cnemidocarpa pfefferi* (Michaelsen) (St. 123): A, gonad; B, lobe of gonad enlarged; C, transverse section of lobe of gonad. *Styela paessleri* Michaelsen (St. 53): D, gonad; E, part of gonad enlarged; F, transverse section of part of gonad.

Cnemidocarpa nordenskjöldi (Michaelsen) (Text-figs. 36 A, C, D)

Styela nordenskjöldi Michaelsen, 1898, p. 365.

Occurrence. St. 53: Falkland Islands, 0–2 m. St. WS 71: Falkland Islands, 82–80 m. St. WS 94: Patagonian Shelf, 110–126 m. St. WS 221: Patagonian Shelf, 76–91 m. St. WS 243: Patagonian Shelf, 144–141 m. St. WS 247: Falkland Islands, 172 m. St. WS 582: Magellan Strait, 12 m. St. WS 583: Magellan Strait, 14–78 m. St. WS 784: Patagonian Shelf, 170–164 m. St. WS 805: Patagonian Shelf, 148–150 m. St. WS 847: Patagonian Shelf, 51–57 m.

External appearance. The many specimens range from very young ones, little over 1 mm. in length, to a large one 5 cm. long and 2·6 cm. high. They are variable in shape, either ovoid, almost globular or low with an expanded base. The siphons are not very far apart and may be quite prominent or rather small. Small mammillations break up the surface of the test, giving it a slightly rough appearance. Although preserved specimens are brown, a collector's note describes one specimen as 'orange' in life.

INTERNAL STRUCTURE. The anatomy of the species has already been described in detail, particularly by Michaelsen (1900), van Name (1945) and Ärnbäck (1950). The specimens in the 'Discovery' collections are in close agreement with these accounts. But three specimens from the Palmer Archipelago which I have assigned to the closely related *C. drygalskii* (Hartmeyer) require that these species be compared, particularly as van Name (1945) considered them to be possibly synonymous. In Table 31 I have shown their main characters, including those of 'Discovery' specimens.

Table 31

	C. nordenskjöldi		*C. drygalskii*	
	Michaelsen (1900)	'Discovery' specimens	Hartmeyer (1911)	'Discovery' specimens
Tentacles	About 44	28–36	30–40	26–35
Dorsal tubercle	C-shaped or closed ring	C-shaped	Half-moon or ring-shaped	C-shaped
Branchial folds	10–12 bars per fold; 4–6 bars between folds	10–20 bars per fold; 4–14 bars between folds	8–20 or more bars per fold; 4–6 bars between folds	5–20 bars per fold; 3–10 bars between folds
Parastigmatic bars	Present in places	Present	Present	Present
Dorsal lamina	A few irregular teeth	Smooth	Smooth	Smooth
Stomach folds	About 21	20–26	About 14	12–15
Intestinal loop	Crosses endostyle	Crosses endostyle, except in very small specimens	Does not cross endostyle	Does not cross endostyle
Anus	3 lips each subdivided	2 or 3 lips, more or less subdivided	2 lips; smooth margin	2 or 3 lips, more or less subdivided
Gonads	One on each side; testis follicles closely bound to ovary	One on each side; testis follicles closely bound to ovary	One on right, one or two on left; testis follicles closely bound to ovary	One on each side; testis follicles closely bound to ovary

It appears from the comparison that only two characters separate the species: (1) the number of folds on the wall of the stomach; and (2) whether or not the intestinal loops cross the endostyle into the right half of the body (Text-fig. 36A, B).

The number of folds on the stomach seems to be a valid distinguishing character, as shown by the following comparison of 'Discovery' specimens of approximately the same size:

	C. nordenskjöldi			*C. drygalskii*		
Body length (cm.)	1·3	1·8	2·1	1·5	2·3	2·5
No. of folds on stomach	20	24	26	12	12	15

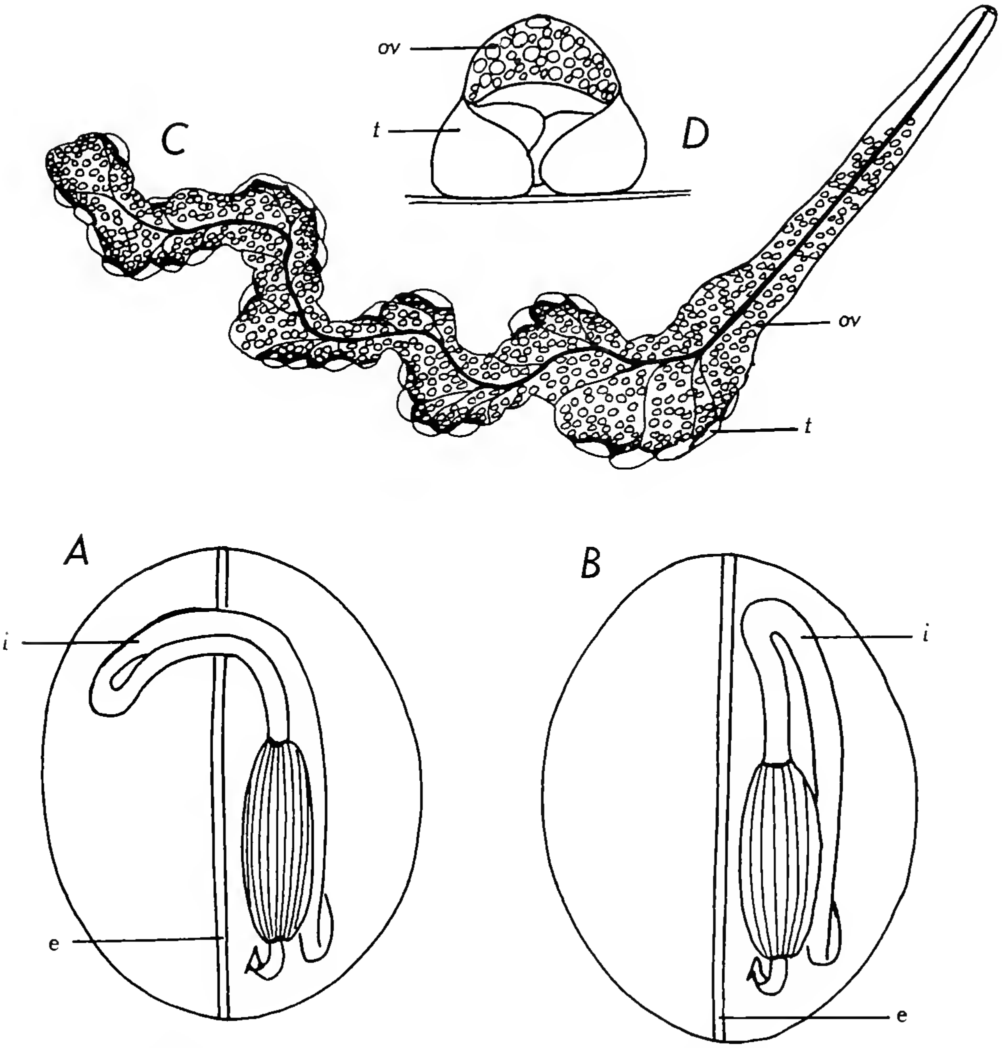
The course of the intestinal loop is also generally a reliable character and only breaks down in young specimens of *C. nordenskjöldi*, in which the loop has not yet grown across the endostyle to the right side of the body.

The two species also differ in distribution, *C. nordenskjöldi* being confined to the Subantarctic and *C. drygalskii* to the Antarctic.

GONADS. *Cnemidocarpa* and *Styela* are distinguished from each other mainly by differences in the structure of their gonads. That these distinctions are not entirely satisfactory is shown by *C. nordenskjöldi*. In this species the testis follicles are closely applied to the sides and parietal surface of the gonad and are enclosed along with the ovary within a common membrane (Fig. 36C, D), thus agreeing with the condition in *Cnemidocarpa* (see van Name, 1945, pp. 262–3). When the testis is fully developed, however, the follicles project slightly from the sides of the gonad, which then approaches the condition typical of *Styela*. In fact van Name (1945) placed the species in *Styela*, but pointed out that 'the gonads approach the *Cnemidocarpa* type'. Ärnbäck (1950), however, suggested that the species should be placed in her genus *Ypsilocarpa*, which, she says, 'agrees with the genus *Cnemidocarpa* as regards the general structure of the reproductive organs, the ovary and testis not being separated'.

The genus *Ypsilocarpa* (Ärnbäck, 1921) was characterized as follows:

'*Branchial sac.* Four folds on each side; three are well developed, and one—the second—is in a rudimentary state.



Text-fig. 36. *Cnemidocarpa nordenskjöldi* (Michaelsen) and *C. drygalskii* (Hartmeyer): A, B, comparison of the intestinal loop, ventral view; C, gonad of *C. nordenskjöldi* (St. WS 805); D, transverse section of the same.

Gonads. One elongate cylindrical gonad on each side, bent into the shape of the letter U, and made up of both ovary and testis.

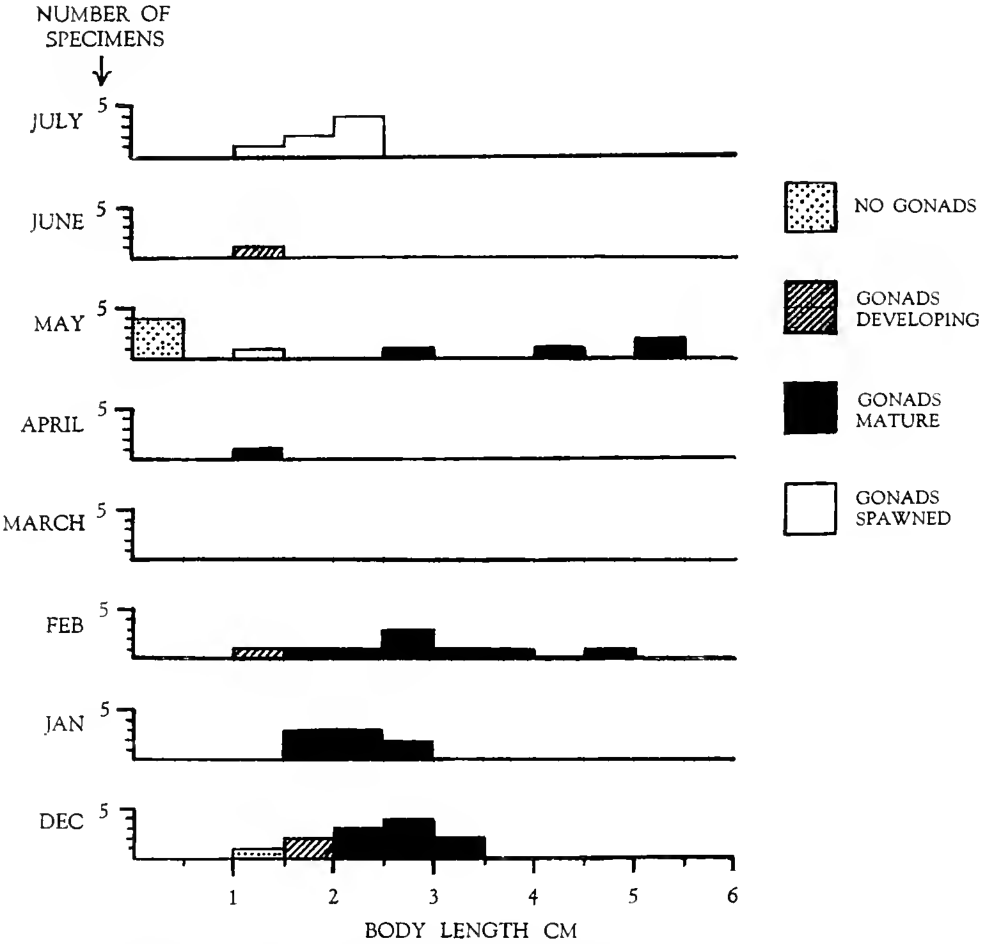
Atrial tentacles. The atrial tentacles are thickly scattered over the narrow velum.'

Ärnbäck evidently regarded the gonads and the atrial tentacles as the best characters for separating *Ypsilocarpa* from *Cnemidocarpa*, but as mentioned above found the structure of the gonad basically similar. There remains only the number of the gonads, their considerable length, and their shape, together with the distribution of the atrial tentacles, to distinguish the two genera, but I do not consider that these characters, even in combination, are of generic value. The proper genus for *nordenskjöldi* is therefore thought to be *Cnemidocarpa*.

Biology. In Text-fig. 37 are shown the size-distribution and state of the gonads in all specimens, adding together all material from different years.

Only large specimens were present in December, January, February and April. Material collected in May shows a number of very small specimens representing the new generation. The breeding season probably occurs between the end of February and the beginning of May. This is confirmed by the state of the gonads which are full from December until February in those animals large enough to be mature. In July animals of a similar size have empty gonads, showing that these animals have spawned.

Distribution. Subantarctic (Falkland Islands to Tierra del Fuego).



Text-fig. 37. *Cnemidocarpa nordenskjöldi* (Michaelsen): Size distribution and condition of the gonads of specimens collected in different months.

Cnemidocarpa drygalskii (Hartmeyer) (Text-fig. 36B)

Styela drygalskii Hartmeyer, 1911, p. 452, pl. 45, fig. 6, pl. 50, figs. 6–10.

Occurrence. St. 187: Palmer Archipelago, 259–354 m.

External appearance. The body is dorso-ventrally flattened into a low dome-shape, with a broad base of attachment. A roughened surface is produced by the presence of many small raised plates on the test. The colour is pale brown.

Internal structure. The diagnostic characters of the species, and details of the 'Discovery' specimens, have been given in the comparison with *Cnemidocarpa nordenskjöldi* (see Table 31).

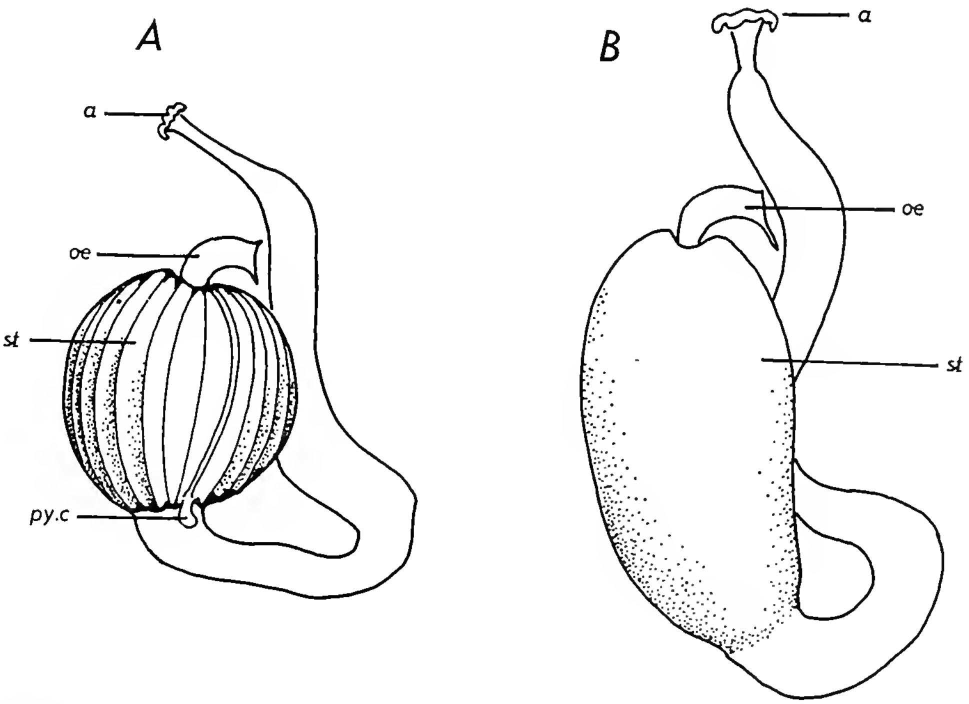
Remarks. I believe that this species, like the previous one, is best placed in the genus *Cnemidocarpa*, and for the same reasons relating to the structure of the gonad which is similar in both species (see p. 102).

DISTRIBUTION. Antarctic (Graham Land; Kaiser Wilhelm II Land).

Cnemidocarpa verrucosa (Lesson) (Text-fig. 38; Pl. V, fig. 5)

Cynthia verrucosa Lesson, 1830, p. 151, pl. 53, fig. 2.
For synonymy see van Name 1945, p. 272.

OCCURRENCE. St. 39: S. Georgia, 179–235 m. St. 42: S. Georgia, 120–204 m. St. 45: S. Georgia, 238–270 m. St. 51: Falkland Islands, 105–115 m. St. 53: Falkland Islands, 0–2 m. St. 55: Falkland Islands, 10–16 m. St. 58: Falkland Islands, 1–2 m. St. 123: S. Georgia, 230–250 m. St. 140: S. Georgia, 122–136 m. St. 143: S. Georgia, 273 m. St. 148: S. Georgia, 132–148 m. St. 159: S. Georgia, 160 m. St. 160: S. Georgia, 177 m. St. 190: Palmer Archipelago, 93–126 m. and 315 m. St. 366: S. Sandwich Islands, 332–155 m. St. 370: S. Sandwich Islands, 80–18 m. St. 371: S. Sandwich Islands, 99–161 m. St. 474: S. Georgia, 199 m. St. 599: S. Shetlands, 203 m. St. 1159: between Bouvet Island and Crozet Island, 230–0 m. St. 1952: S. Shetlands, 367–383 m. St. WS 25: S. Georgia, 18–27 m. St. WS 71: Falkland Islands, 82–80 m. St. WS 81: Falkland Islands, 81–82 m. St. WS 85: Falkland Islands, 79 m. St. WS 823: Patagonian Shelf, 80–95 m. St. MS 68: S. Georgia, 220–247 m. St. MS 71: S. Georgia, 110–60 m. British Graham Land Expedition, 1934–7: St. Stella Creek, 10 m.



Text-fig. 38. *Cnemidocarpa verrucosa* (Lesson) (St. 366): A, gut of specimen 0·4 cm. long; B, gut of specimen 4·0 cm. long.

EXTERNAL APPEARANCE (Pl. V, fig. 5). The appearance of this species is well known and characteristic (see van Name, 1945, p. 272). The largest specimen in the collection has a length of 16 cm. and a breadth of 6·7 cm.

BRANCHIAL SAC. In large individuals the wall of the branchial sac is minutely plicate with the folds running parallel to the longitudinal bars.

GUT. Hartmeyer (1911) found a small pyloric caecum in young specimens, although there is none in large ones. This is confirmed by examination of the 'Discovery' material; specimens of greatest diameter about 0·4 cm. possess a small caecum (Text-fig. 38A, *p.c.*), but all specimens over about 2·0 cm. in diameter lack a caecum (Text-fig. 38B). There are about twenty-four folds on the wall of the stomach, but they are internal and are visible from the outside only in small specimens (see Text-fig. 38A, B).

BIOLOGY. Text-fig. 39 shows the size-distribution, in different months, of the specimens from two collecting areas: (1) the Falkland Islands and Patagonian Shelf; and (2) South Georgia, the South Shetland Islands, the South Sandwich Islands and Graham Land. In both populations breeding had probably started before March, as indicated by the presence of young individuals in that month. In the more southerly localities no very young specimens were taken in April, but it must be pointed out that the total numbers collected at this time were very small. The samples from the Falkland Islands and Patagonian Shelf, taken in May, include quite a high proportion of young individuals, suggesting a breeding season extending farther into the southern autumn in the Subantarctic population, than in the Antarctic population.

The histograms for March (Antarctic) and May (Subantarctic) point to the presence of at least two year-classes, and the animals may possibly live for two years or more. These are only very tentative suggestions, however, as the numbers of specimens are small and the months of collection limited.

DISTRIBUTION. Subantarctic (Falkland Islands, Patagonian Shelf, Kerguelen); Antarctic (Graham Land, Kaiser Wilhelm II Land, South Georgia, South Shetland Islands, South Sandwich Islands, Enderby Land, Queen Mary Land, MacRobertson Land).

Cnemidocarpa tricostata sp.n. (Text-fig. 40)

DIAGNOSIS OF SPECIES. Ventral half of body with a thick coat of test hairs, dorsal half without hairs. About twenty-two oral tentacles, and a single circle of atrial tentacles. Dorsal tubercle with a straight opening. Branchial sac without folds, but with three longitudinal bars on each side. Stomach with about thirteen folds. One gonad on the left side and none on the right.

OCCURRENCE. St. 27: S. Georgia, 110 m.

EXTERNAL APPEARANCE (Text-fig. 40A). The single specimen is 1·2 cm. high and 0·9 cm. across at the widest point. In the preserved state it is pear-shaped with a swollen base which apparently rested on a soft substratum. The upper part of the body narrows towards the siphons which are close together and project as short tubular papillae with 4-cleft openings. The test on the upper half of the body is broken up into rounded wart-like swellings, which in some places have the appearance of being arranged in circles passing round the body. No test hairs or foreign particles are present on the upper part of the body, which is yellowish grey in colour. The lower half bears a thick coat of test hairs to which a few sand grains adhere. These hairs are unbranched and not very long. They arise either singly or in groups of two or three.

TEST. The test is rather thin but tough.

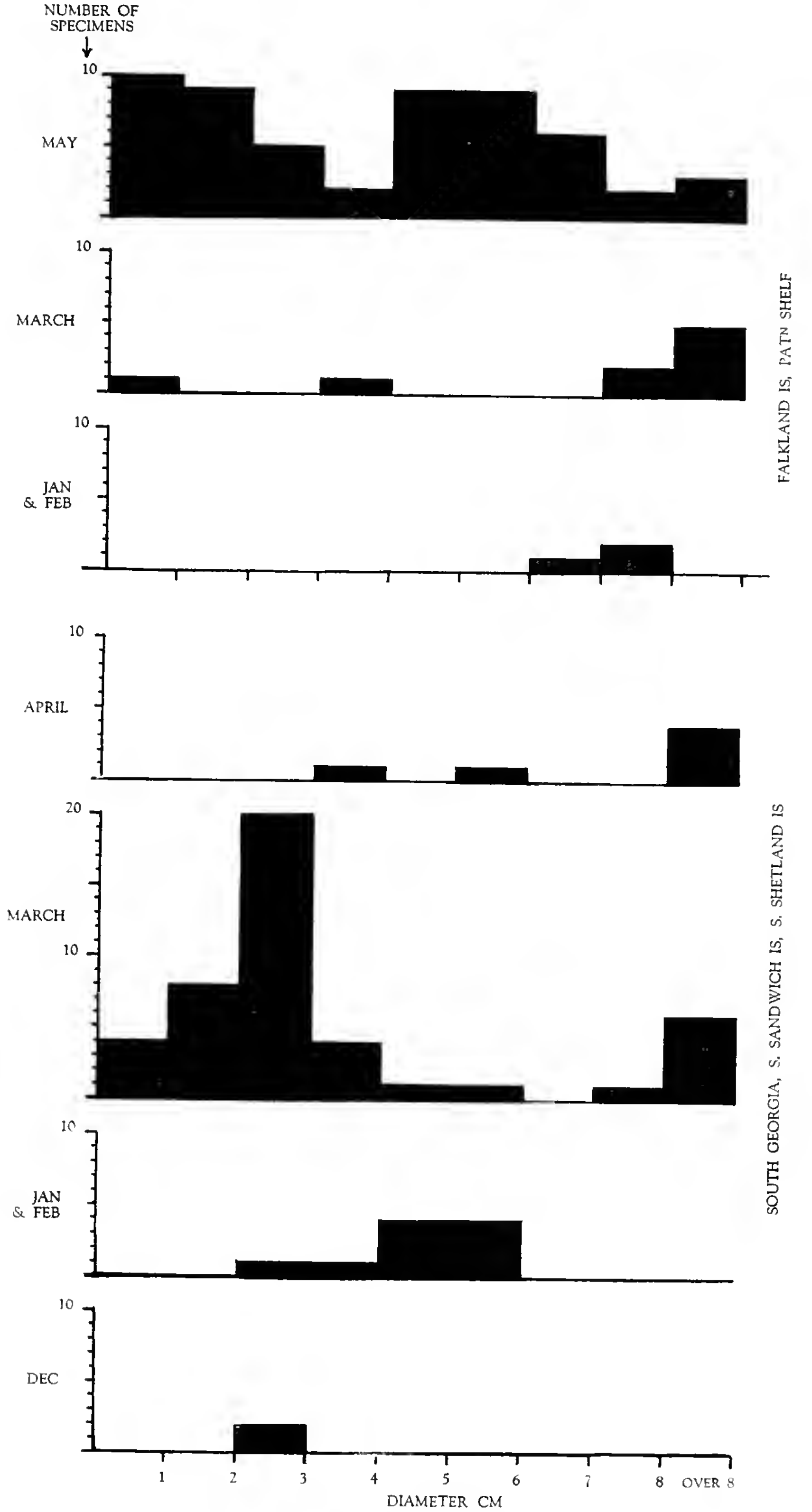
BODY WALL. The muscles of the body wall are arranged in two layers, an external one of weak circular muscles and an internal one of strong longitudinal muscles. A few large clear endocarps are attached to the inner surface of the body wall.

TENTACLES. There are about twenty-two simple oral tentacles and a single circle of many slender atrial tentacles.

DORSAL TUBERCLE. The dorsal tubercle is rather small, with a simple oval transverse opening (Text-fig. 40D).

BRANCHIAL SAC. There are no folds on the branchial walls, each side having only three tall longitudinal bars (Text-fig. 40C, *l.b.*). The meshes are therefore long, and each accommodates up to thirty stigmata (Text-fig. 40E). Slender parastigmatic transverse bars pass across the centres of the rows of stigmata. At the anterior end of the branchial sac the dorsal lamina (*d.la.*) is narrow, and it increases gradually in width towards the oesophageal mouth; the margin is plain and slightly rolled in.

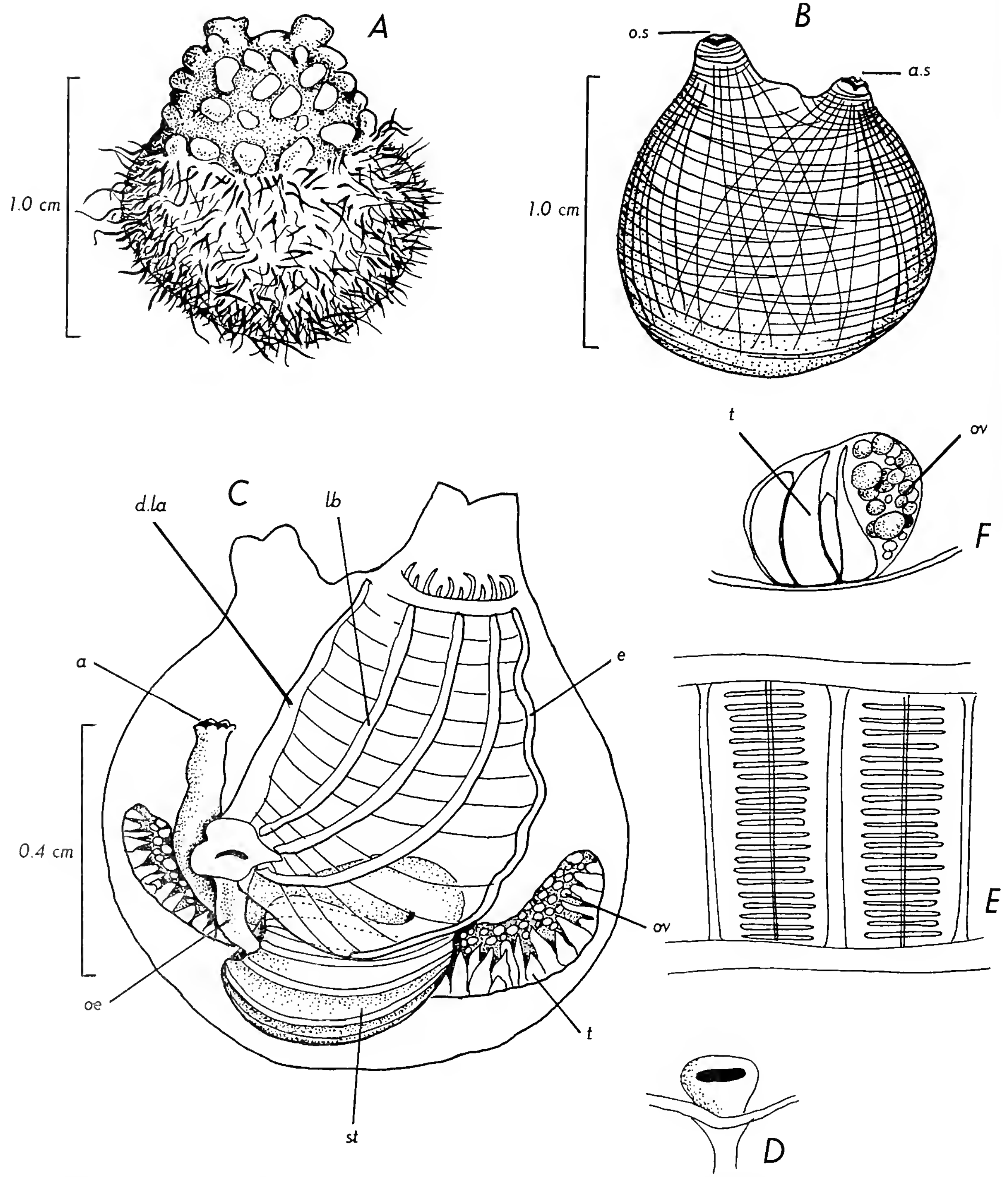
GUT. The oesophagus (*oe.*) is short, curved and rather wide. About thirteen longitudinal folds mark the walls of the large ovoid stomach (*st.*). A very small straight pyloric caecum is hidden in the bend



Text-fig. 39. *Cnemidocarpa verrucosa* (Lesson): Size-distribution of specimens collected from different areas and in different months.

between the stomach and the intestine. The intestine bends sharply back after leaving the stomach, lies close to the left side of the stomach, then bends forwards near the oesophagus. The rectum is of moderate length and ends in a wide anus (*a.*) with about twelve shallow lobes.

Gonad (Text-fig. 40C, F). Only a single gonad was found in this specimen, and that is on the



Text-fig. 40. *Cnemidocarpa tricostata* sp.n. (St. 27): A, external appearance; B, specimen with test removed; C, specimen with right half of the body removed seen from the right; D, dorsal tubercle; E, part of branchial wall; F, transverse section of gonad.

left side. The gonad starts ventrally a little to the right of the endostyle, and curves across the posterior half of the left side of the body to end rather far back in the atrial cavity. In structure the gonad is of the typical *Cnemidocarpa*-type, with the testis (*t*) occupying that part of the gonad which is attached to the body wall, and the ovary (*ov.*) on the free or mesial side. The testis consists of long narrow follicles arranged in a series along the length of the gonad. The ovary occupies the superficial part of the gonad and shows oocytes of various sizes. No oviduct could be seen. Two short slender sperm ducts were found along the length of the gonad, projecting from its free (ovarian) surface.

REMARKS. This is a very distinctive species not readily confused with any *Cnemidocarpa* yet described. In the formation of the branchial sac it is most like *Styela insinuosa* (Sluiter), but in having only three bars on each side shows a still greater simplification. A few species of *Cnemidocarpa* and *Styela* have a reduced number of branchial folds. Thus in *C. mortenseni* (Hartmeyer) there is only one on each side, and in the deep-sea species *S. sericata* Herdman there are no folds but twenty to thirty longitudinal bars on each side.

The presence of only one gonad in *C. tricostata* is also a remarkable case of simplification.

DISTRIBUTION. Antarctic (South Georgia).

Genus **Styela** Fleming, 1822

Styela schmitti van Name f. **simplex** n. (Text-fig. 41)

Styela schmitti van Name, 1945, p. 298, text-fig. 195.

DIAGNOSIS OF FORM *SIMPLEX*. Characters as in the species but with about eight tentacles, a simple slit-like opening of the dorsal tubercle, and only one well-developed fold and a rudimentary one on each side of the branchial sac.

OCCURRENCE. St. 388: off Cape Horn, Tierra del Fuego, 121 m.

EXTERNAL APPEARANCE (Fig. 41 A–C). The shape of the body is much as described by van Name (1945) except that it is generally rather narrower and more nearly cylindrical. The sizes of the body and stalk in the 'Discovery' specimens are:

Body length (mm.)	7	7	5	5	5	5
Stalk length (mm.)	4	3	3	3	2	1

A light coating of sand and broken shell covers the body of all the specimens, but does not extend to the stalk. Two small projections close together at the upper end of the body mark the scarcely visible siphons.

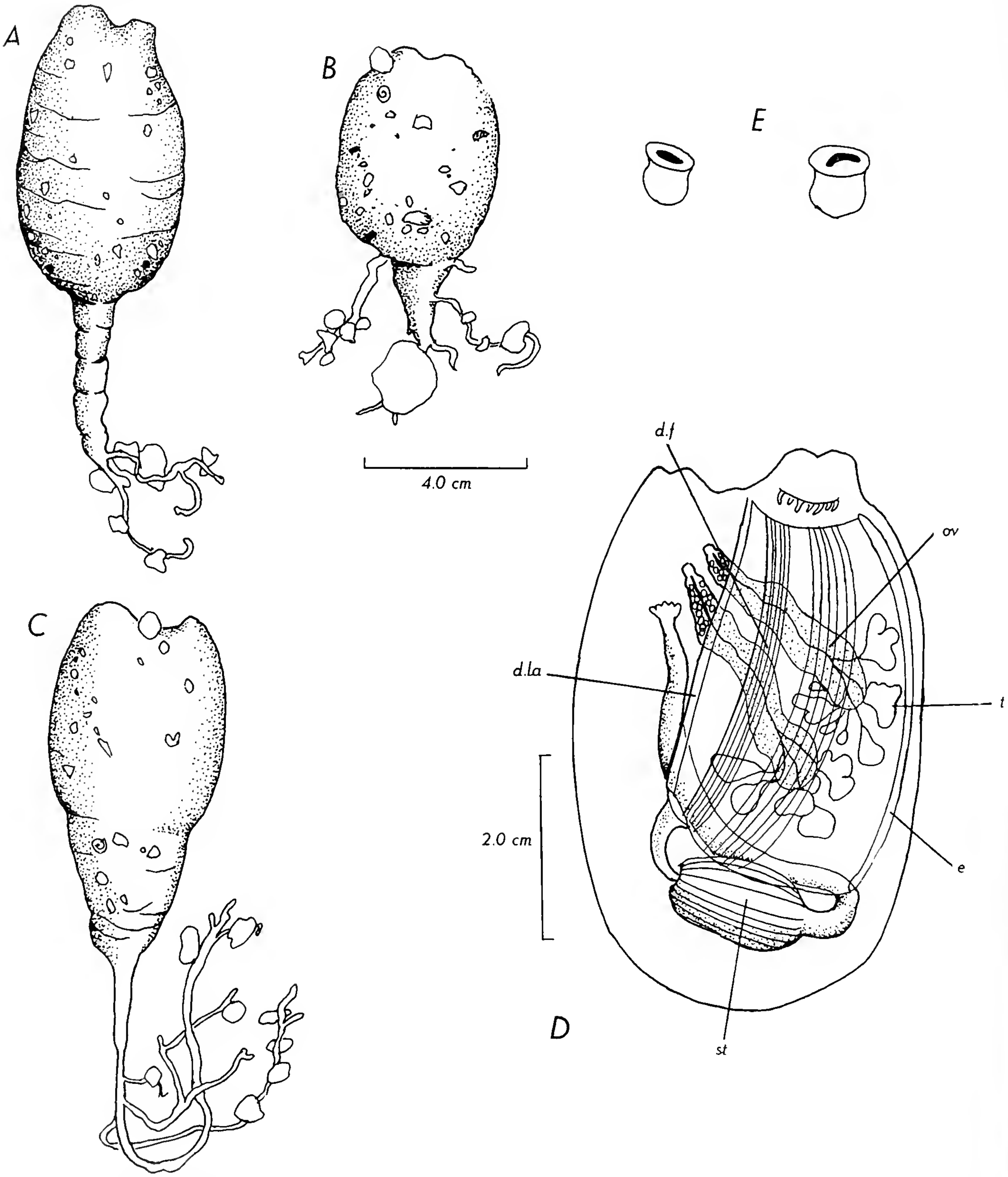
INTERNAL STRUCTURE (Text-fig. 41 D). The main internal characters of the form *simplex* are shown in Table 32 along with those of van Name's type material of the species.

Table 32

	S. schmitti f. *simplex* ('Discovery' material)	*S. schmitti* (type material, van Name)
Body-wall muscles	External circular and internal longitudinal muscles forming sheets of fine strands	Diffuse
Tentacles	8–16; short	Probably 35–40
Dorsal tubercle	Simple transverse slit	Modified C-shaped slit, with open interval to left
Branchial folds	Well-developed dorsal fold, rudimentary second fold, other folds absent	4 folds, dorsal one highest, ventral one sometimes reduced
No. of stomach folds	About 20	About 20
Anus	2 simple or slightly frilled lobes	A number of deep rounded lobes
Gonads	2 each side; ovaries tubular; testes grouped round blind ends of ovaries	Normally 2 each side; ovaries elongate sinuous; testes along both sides and round blind ends of ovaries
Occurrence	Off Tierra del Fuego; 121 m.	Off Montevideo, Uruguay; about 21 m.

In the branchial sac only the dorsal fold is present on each side and a second one is represented merely by the closer spacing of some of the longitudinal bars. The arrangement of the bars on one side in a large specimen was: dorsal line 4 (6) 3 (6) 3 endostyle.

It will be seen from the above table that f. *simplex* is principally distinguished from the type material



Text-fig. 41. *Styela schmitti* van Name f. *simplex* n. (St. 388): A, B, C, external appearance of three specimens; D, specimen with right side of the body removed, seen from the right; E, dorsal tubercle of two specimens.

by: (1) the smaller number of tentacles; (2) the simpler dorsal tubercle; and (3) the greater reduction of the branchial folds.

The similarities between the 'Discovery' specimens and those described by van Name are too great to justify specific distinction. The degree of distinctness is best indicated, I believe, by a separate form, f. *simplex*, the name referring to the tendency towards simplification in several organs.

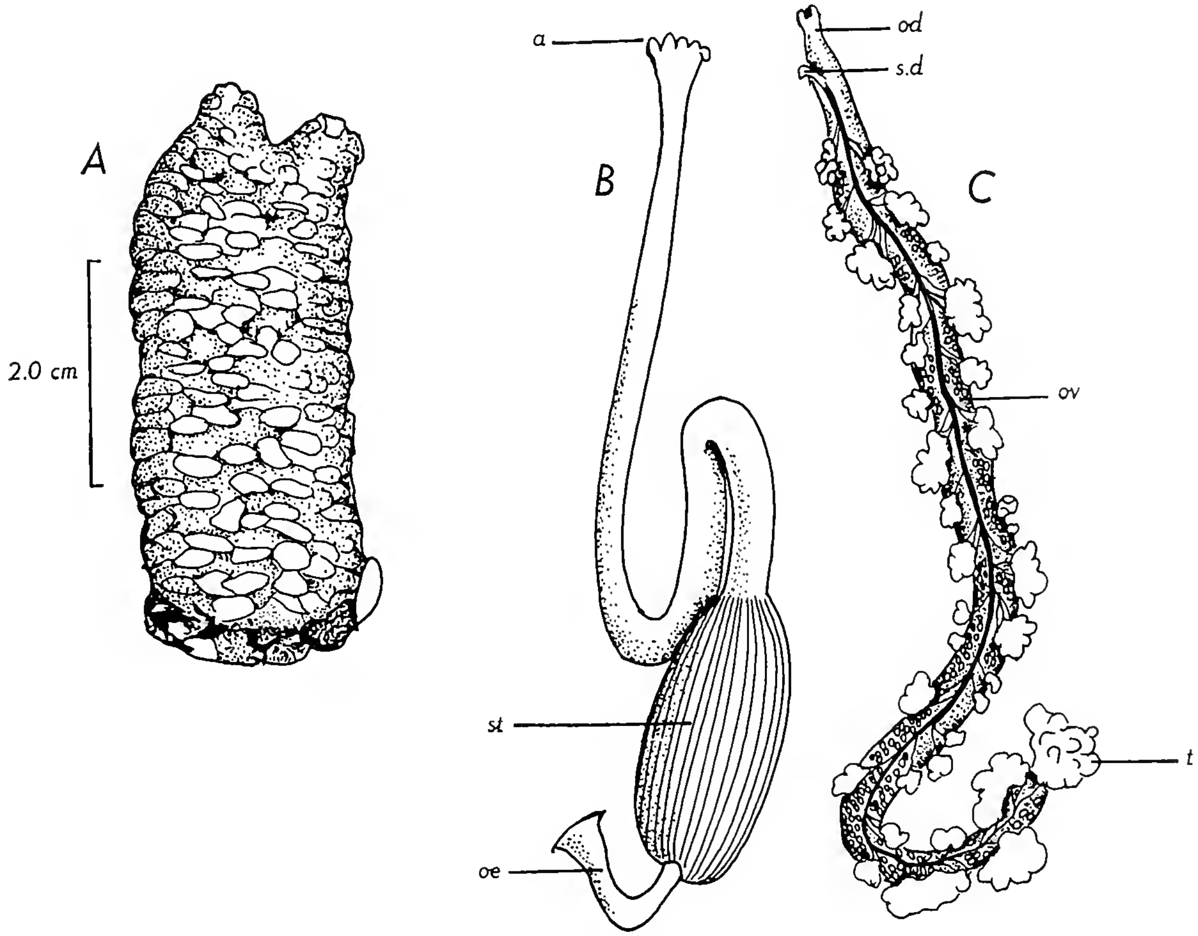
DISTRIBUTION. Off Uruguay (typical form); off Cape Horn, Tierra del Fuego (f. *simplex*).

Styela insinuosa (Sluiter) (Text-fig. 42)

Tethyum insinuosum Sluiter, 1912, p. 24, pl. 2, figs. 28–32; pl. 3, figs. 33–35; pl. 4, fig. 44.

OCCURRENCE. St. 156: S. Georgia, 200–236 m. St. 474: S. Georgia, 199 m.

EXTERNAL APPEARANCE (Text-fig. 42A). The specimens are all more or less cylindrical, with the siphons fairly close together at the upper end. The whole surface is covered with low wart-like swellings, and the colour in the preserved state is brown. The largest specimen is 5·3 cm. high by 2·0 cm. wide, and the smallest is 2·2 cm. by 1·5 cm.



Text-fig. 42. *Styela insinuosa* (Sluiter) (St. 474): A, external appearance; B, gut; C, left gonad.

BODY WALL. The body wall is quite thick, owing to the existence of powerful muscles which constitute an inner longitudinal, a middle circular, and an outer longitudinal layer.

TENTACLES. There are twenty-four oral tentacles in the largest animal and about sixteen in the smallest; Sluiter (1914) found up to thirty-two. The atrial tentacles are numerous and stand in a single circle on the margin of a low velum within the atrial siphon.

DORSAL TUBERCLE. The slit of the dorsal tubercle is C-shaped with inrolled horns, the open interval facing forward.

BRANCHIAL SAC. The complete absence of branchial folds constitutes the most remarkable and characteristic feature of the species. There are only four large longitudinal bars on each side of the branchial sac. Plication of the branchial wall increases the surface area, as it does in several species of *Ascidia*.

GUT (Text-fig. 42B). Sluiter has already described the course of the gut, noting the longitudinal position of the stomach and double intestinal loop. All the 'Discovery' specimens confirm his description, but I find more folds on the wall of the stomach, about thirty-five even in a small specimen instead of the twenty which he found, and the stomach sometimes lies obliquely or almost vertically. The margin of the anus has about twelve distinct lobes.

GONADS. In the type specimens Sluiter described one gonad on the left and two on the right, but Kott (1954) found only one on each side. In the 'Discovery' material also there is a single gonad on each side. The anterior part of each ovary (Text-fig. 42C, *ov.*) is straight and the posterior part variously bent. In the largest specimen the right gonad is distinctly curved upwards to form a U with unequal limbs. Groups of testis follicles (*t*) are situated along the length of the ovaries, but are more plentiful at their posterior ends and are sometimes confined to this region.

REMARKS. This is a species which has seldom been taken by expeditions, only Sluiter and Kott having examined material so far as I know.

Very few styelid ascidians, other than compound forms, have carried the reduction of branchial folds, and even branchial bars, so far. I would point to the similarity between the present species and the Arctic styelid species *Pelonaia corrugata* Goodsir & Forbes, which also has flat branchial walls. The form of the gonads is another point of similarity, particularly in the specimen of *S. insinuosa* with a U-shaped gonad. Both are aberrant species of the family Styelidae, but it is doubtful whether the resemblance is due to convergence or to close relationship.

DISTRIBUTION. Antarctic (South Shetlands, King George V Land; South Georgia).

Styela magalhaensis Michaelsen (Text-fig. 43)

Styela canopus var. *magalhaensis* Michaelsen, 1898, p. 367.
?*S. melincae* Ärnbäck, 1929, p. 2.

OCCURRENCE. ?St. 123: S. Georgia, 230–250 m. St. WS 776: Patagonian Shelf, 110–99 m.

EXTERNAL APPEARANCE. The single specimen from St. WS 776 is of a squat conical shape with the siphons forming low projections close together on the upper narrow side. Irregular rounded swellings are present on the surface. The general colour is creamy grey. The length and height are both 1·1 cm.

TEST. The test, although tough, is not very thick. It is raised in irregular wart-like swellings.

BODY WALL. Longitudinal and circular muscles are evenly spread over the rather thin body wall, which is brown in the preserved state.

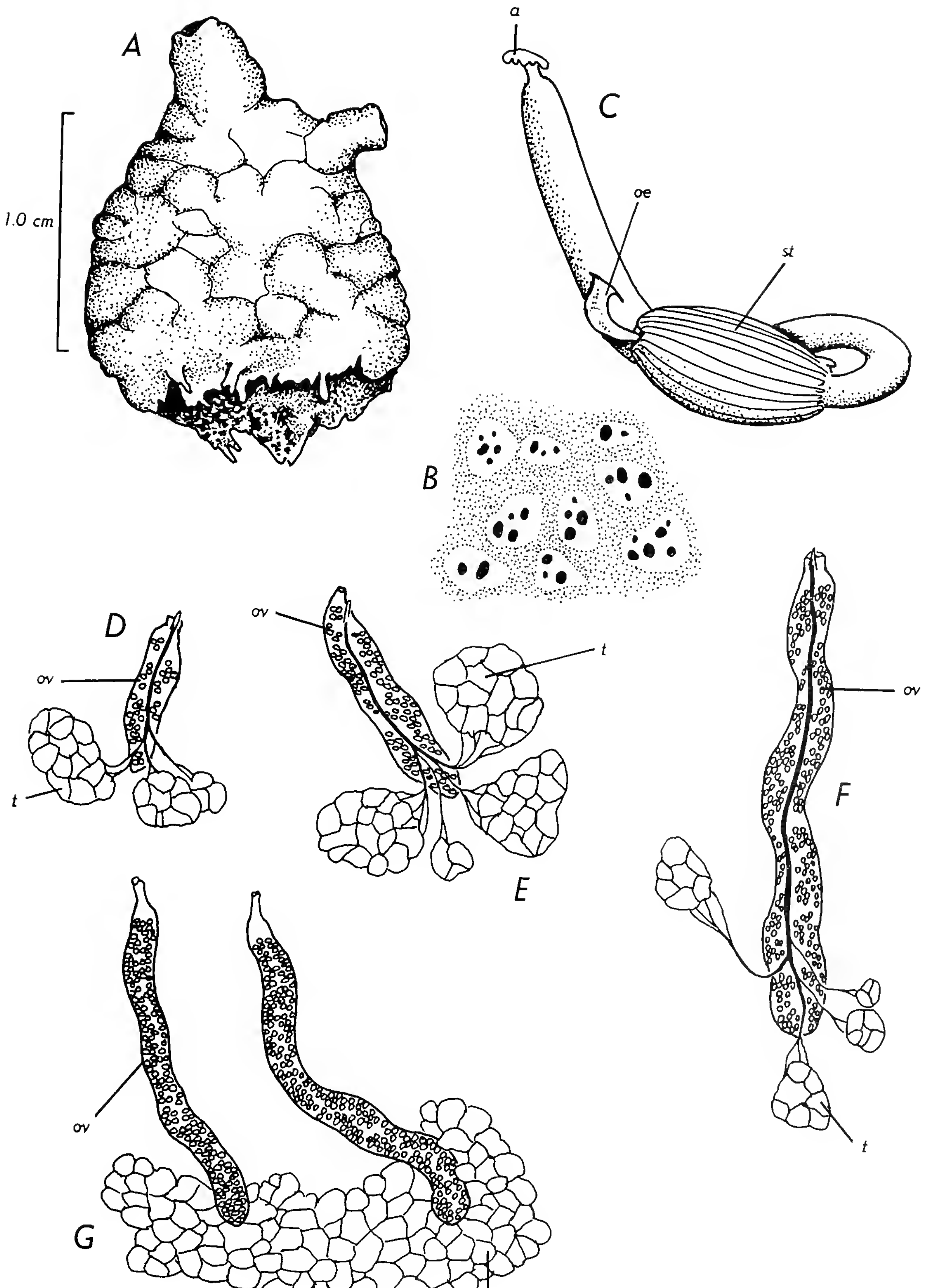
TENTACLES. There are about sixty-four of various sizes.

DORSAL TUBERCLE. The dorsal tubercle has a simple U-shaped opening facing forward.

BRANCHIAL SAC. Each side of the branchial sac is thrown into four quite distinct folds, with the following distribution of longitudinal bars: dorsal line 4 (14) 4 (15) 6 (12) 5 (13) 4 endostyle. The dorsal lamina is a simple membrane with a plain inrolled edge.

GUT. Most of the gut lies in the lower part of the body. The oesophagus is curved, and the walls of the long stomach have about twenty-four longitudinal folds. There is a very small pyloric caecum. The first part of the intestine lies parallel to the stomach, and the rectum bends upwards towards the atrial siphon.

GONADS. One of the most characteristic features of this species is the form of the gonads (Text-fig. 43G). In ripe specimens these constitute two long tubular sinuous ovaries (*ov.*) on each side, with



Text-fig. 43. ? *Styela magalhaensis* Michaelsen (St. 123): A, external appearance; B part of test; C, gut; D, E, F, gonads. *Styela magalhaensis* Michaelsen (St. WS 776): G, gonads.

a compact mass of testis follicles (*t*) at their lower ends; this is the condition in the 'Discovery' specimen from St. WS 776. Van Name (1945) is a little doubtful if these gonads are sufficiently different from those of *S. paessleri* to justify specific distinction, but on the whole thinks that they are. From a study of the 'Discovery' specimens of *S. paessleri* (see p. 115), and the present specimen I have no hesitation in regarding these as separate species.

There are two specimens from South Georgia (St. 123) which I include in *S. magalhaensis* with some hesitation. Details are as follows.

EXTERNAL APPEARANCE. The larger specimen (Text-fig. 43A) is 1·6 cm. high and 0·9 cm. wide, and the smaller one is 1·2 by 0·8 cm. The body is ovoid to conical in shape with the siphons fairly close together at the upper end. Small tag-like processes are present on the lower part of the body. Elsewhere the surface of the test is divided indistinctly into polygonal plates, each of which has a few brown pigment spots (Text-fig. 43B).

BODY WALL. This is thin and semi-transparent, with weak muscles. A few finger-like endocarps are scattered on the inner surface of the body wall.

TENTACLES. There are about thirty-three simple curved oral tentacles, which are quite long and alternate in length. Long fine thread-like atrial tentacles are present scattered over a wide area at the base of the atrial siphon.

DORSAL TUBERCLE. The opening of the dorsal tubercle is crescentic and faces forward.

BRANCHIAL SAC. The longitudinal bars on the four folds are arranged as follows in the larger specimen: dorsal line 3 (14) 4 (12) 5 (13) 8 (11) 8 endostyle.

GUT (Text-fig. 43C). The oesophagus (*oe.*) is curved. The stomach (*st.*) which lies horizontally, near the base of the body, is oval to diamond-shaped in outline, and has about twenty-four longitudinal folds. Both the intestine and rectum are wide, but immediately before the anus (*a.*) the rectum abruptly narrows. About twelve reflected lobes subdivide the margin of the anus.

GONADS (Text-fig. 43D–F). Both specimens have two gonads on each side. The ovaries (*ov.*) vary from rather short and straight to quite long and sinuous. At the lower end of each ovary are two, three, or four rounded masses of testis follicles (*t.*), lying at some distance from the ovary.

REMARKS. Although I have provisionally included these two specimens in *S. magalhaensis*, the pigmentation and sculpturing of the test, and the failure of the testicular masses to coalesce, are differences which might indicate some systematic distinction. But at present there is too little material, and the similarities to typical specimens of *S. magalhaensis* are too great, to permit separating those two specimens from that species.

A number of other species have been described from the southern part of the South American coast, which are sufficiently like *S. magalhaensis* to raise some doubts regarding their validity. The characters of these species are shown in Table 33 for comparison with the present species.

Conclusions regarding the validity of Herdman's three species must be cautious, as the descriptions are not sufficiently detailed. It does seem, however, that *S. oblonga* differs sufficiently from *S. magalhaensis* to avoid confusion. As nothing is known regarding the gonads or gut of *S. flava*, the species must remain of uncertain value. *S. glans* appears to be very like *S. magalhaensis*, especially in the structure of its gonads. Here again details of the gut are wanting, but *S. glans* might well prove to be a synonym of *S. magalhaensis*. Van Name (1945) has argued that *S. melincae* is identical with *S. magalhaensis*, and the above comparison shows the similarities on which his conclusion rests. Only the numbers of tentacles and of branchial bars on the folds differ markedly and these are both characters varying with body size; Michaelsen's specimens were larger than Ärnbäck's specimens.

DISTRIBUTION. Subantarctic (southern part of Argentine coast; Magellan region; ?Guaitecas Islands, Chile); Antarctic (MacRobertson Land, South Georgia).

Table 33

	S. magalhaensis Michaelsen	*S. melincae* Ärnbäck	*S. glans* Herdman	*S. oblonga* Herdman	*S. flava* Herdman
Tentacles	About 60	About 24	'Few'	12	About 60
Dorsal tubercle	Arc-shaped, facing forward	C-shaped, facing forward	'Simple'	'Cup-shaped'	'Irregular'
Branchial sac	Well developed. About 20 bars per fold; 4 between	Well developed. 5–9 bars per fold; 2–5 between	Rudimentary. 5 bars per fold; 5 between	Rudimentary. 6–9 bars per fold; 3 between	Low. 10 bars per fold; 10 between
Stomach folds	About 24	About 25	?	?	?
Gonads	2 each side (sometimes only one); testis masses fused near proximal end of ovary	2 each side; testis masses fused near proximal end of ovary	2 each side; testis masses fused near proximal end of ovary	One each side; testis masses in clusters near proximal end of ovary	?

Styela paessleri Michaelsen (Text-fig. 35 D–F)

Styela paessleri Michaelsen, 1898, p. 368.

Occurrence. St. 53: Falkland Islands, 0–2 m. St. WS 841: Patagonian Shelf, 110–121 m.

External appearance. The largest specimen in this collection is 4·0 cm. high and 2·2 cm. wide, and the smallest one 2·5 by 1·4 cm. The body is irregular, varying from dome-shaped to tall and columnar, with the siphons close together at the upper end. The test is wrinkled, leathery and generally some shade of brown.

Tentacles. The oral tentacles are numerous, and I have counted thirty-five and fifty-eight respectively in two specimens of moderate size; Michaelsen (1898) noted about sixty tentacles.

Dorsal tubercle. In two specimens examined the dorsal tubercle was C-shaped with the open interval posterior, and in a third specimen it was in the form of a horizontal S. According to Michaelsen the opening is either a straight slit or a slit with the left end turned back.

Gonads (Text-fig. 35 D–F). The gonads are very characteristic in this species. There are two on each side, each consisting of a branched ovary (*ov.*) and many round or pear-shaped testis follicles (*t*) grouped round the ends of the ovarian branches. The gonads are of the *Styela* type, in which the testis follicles are separate from the ovary instead of being closely united to it within a common membrane as in *Cnemidocarpa*. When fully developed the testis follicles of *S. paessleri* may become closely crowded together to form large irregular masses pressed against the sides of the ovary and to some extent overlapping it. In this way the basic structure of the gonads is to some extent obscured.

Remarks. Kott (1954) records the species from Kerguelen but is a little doubtful about the identification.

Van Name (1945) considered that *S. paessleri* probably includes Michaelsen's species *S. pfefferi*, but as I have pointed out (see p. 100) the latter species is clearly distinguished by its gonads and is in fact a *Cnemidocarpa*.

Distribution. Subantarctic (Falkland Islands to Tierra del Fuego; ?Kerguelen).

Styela partita (Stimpson) (Text-fig. 44)

Cynthia partita Stimpson, 1852, p. 231.

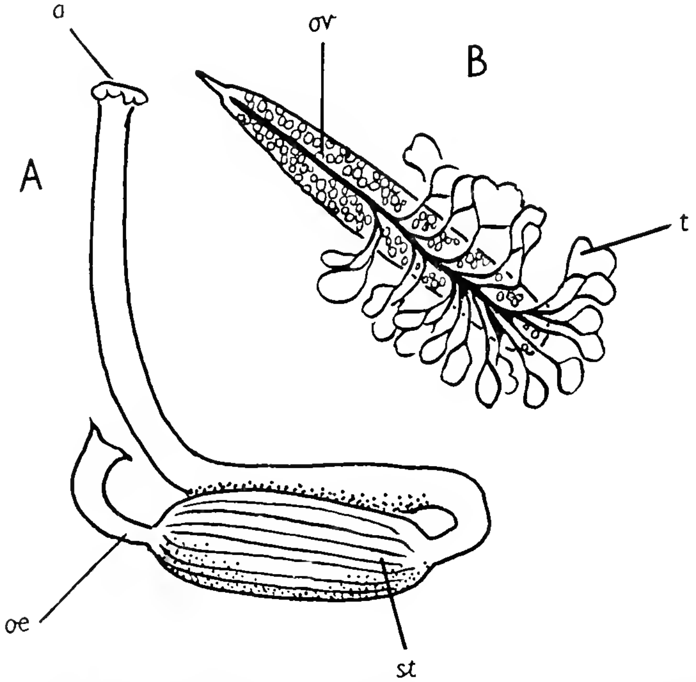
For synonymy see van Name 1945, p. 290, and Tokioka, 1953, p. 262.

Occurrence. St. 2: Ascension Island, 0 m.

External appearance. The larger of the two specimens has a height of 1·1 cm. and a greatest width of 0·6 cm., and the smaller specimen is 0·4 cm. high and 0·5 cm. wide. The surface is smooth, shining and slightly wrinkled.

INTERNAL STRUCTURE. This is a well-known species and I shall merely summarize the main characters of the larger of our two specimens. Oral tentacles thirty; atrial tentacles many, short, resembling papillae, and spread over a narrow belt at the base of the atrial siphon. Dorsal tubercle very small with an indistinct opening. Branchial sac—dorsal line 2 (10) 2 (7) 3 (8) 3 (5) 3 endostyle. Stomach with twenty-one folds; anus with six lobes. Gonads two on each side, of the shape shown in Text-fig. 44B.

DISTRIBUTION. Warm waters of Atlantic American coast; English Channel to West Africa; Mediterranean; Japan.



Text-fig. 44. *Styela partita* (Stimpson) (St. 2): A, gut; B, left gonad.

Family PYURIDAE Hartmeyer, 1908

Genus **Pyura** Molina, 1782

Pyura stolonifera (Heller)

Cynthia stolonifera Heller, 1878, p. 10, pl. 2, fig. 10.
For synonymy see Kott, 1952, p. 274.

OCCURRENCE. St. 90: False Bay, S. Africa, 0–2 m.

EXTERNAL APPEARANCE. The larger of the two specimens is 5·5 cm. high, including a basal extension of test, and 5·0 cm. wide. On the upper side the siphons are close together and prominent. The surface of the body bears some knob-like swellings.

INTERNAL STRUCTURE. In one specimen there are eight and in the other about fourteen dorsal languets. The dorsal tubercle has a complex and much convoluted slit which is basically C-shaped with the open interval directed back to the left. The complex dorsal tubercle, and the shortening of the dorsal side of the branchial sac with consequent reduction in the number of dorsal languets are two characteristic features of the species.

DISTRIBUTION. South Africa; western, southern and eastern Australia; Tahiti.

Pyura setosa (Sluiter) (Pl. IV, fig. 2)

Halocynthia setosa Sluiter, 1905, p. 472.
For synonymy and references see Kott (1954), p. 126.

OCCURRENCE. St. 175: S. Shetlands.

EXTERNAL APPEARANCE (Pl. IV, fig. 2). The single specimen is ovoid, 3·5 cm. long and 2·6 cm. high, and almost completely covered with a thick coat of long stiff bristles. These bristles, which reach 13 mm. in length, bear many short pointed spines.

TENTACLES. There are about twenty-one compound tentacles of various sizes and a few small almost unbranched ones.

DORSAL TUBERCLE. The dorsal tubercle is C-shaped with the open interval facing forward and a little to the right.

BRANCHIAL SAC. The anterior part of the dorsal lamina is a toothed membrane, and for most of its length the lamina is represented by long pointed closely crowded languets united basally by a narrow membrane. The longitudinal bars on the six branchial folds are arranged thus: dorsal line 3 (31) 3 (16) 3 (15) 5 (26) 5 (29) 2 (30) 2 endostyle.

GONADS. The left gonad is within the intestinal loop, and the right gonad is a long horizontal sac. The sperm duct and oviduct are short and turned upwards towards the atrial siphon.

Table 34

	P. setosa	*P. stubenrauchi*	*P. echinops*
Test spines	Up to 21 mm. long	Up to 5 mm.	'Short'
Tentacles	About 16	About 30	About 38
Dorsal tubercle	Horse-shoe with inrolled horns; facing forward	Horse-shoe; facing forward	Horse-shoe, inrolled horns, facing forward
Dorsal lamina	Series of languets, anterior ones small, posterior large	A membrane toothed at posterior end	A membrane toothed except at anterior end
Branchial folds	6 each side	4 each side	4 each side
Occurrence	Western and eastern Antarctic	Strait of Magellan	North coast Argentine

REMARKS. *P. setosa* is a very distinctive species, but two other species *P. stubenrauchi* (Michaelsen) and *P. echinops* Ärnbäck have been described with similar characters, and the important features of the three are shown in Table 34.

It appears from this comparison that *P. stubenrauchi* and *P. echinops* are the same species as suggested by van Name (1945); the name *P. stubenrauchi* has priority.

P. setosa is distinguished from *P. stubenrauchi* by several characters, but principally the subdivision of the dorsal lamina into languets and the presence of six branchial folds on each side. The two species are nevertheless obviously closely related, having been derived from a common ancestor by geographical speciation.

DISTRIBUTION. Antarctic (Graham Land, South Orkney Islands, Kaiser Wilhelm II Land, McMurdo Bay, Adelie Land, Enderby Land, MacRobertson Land).

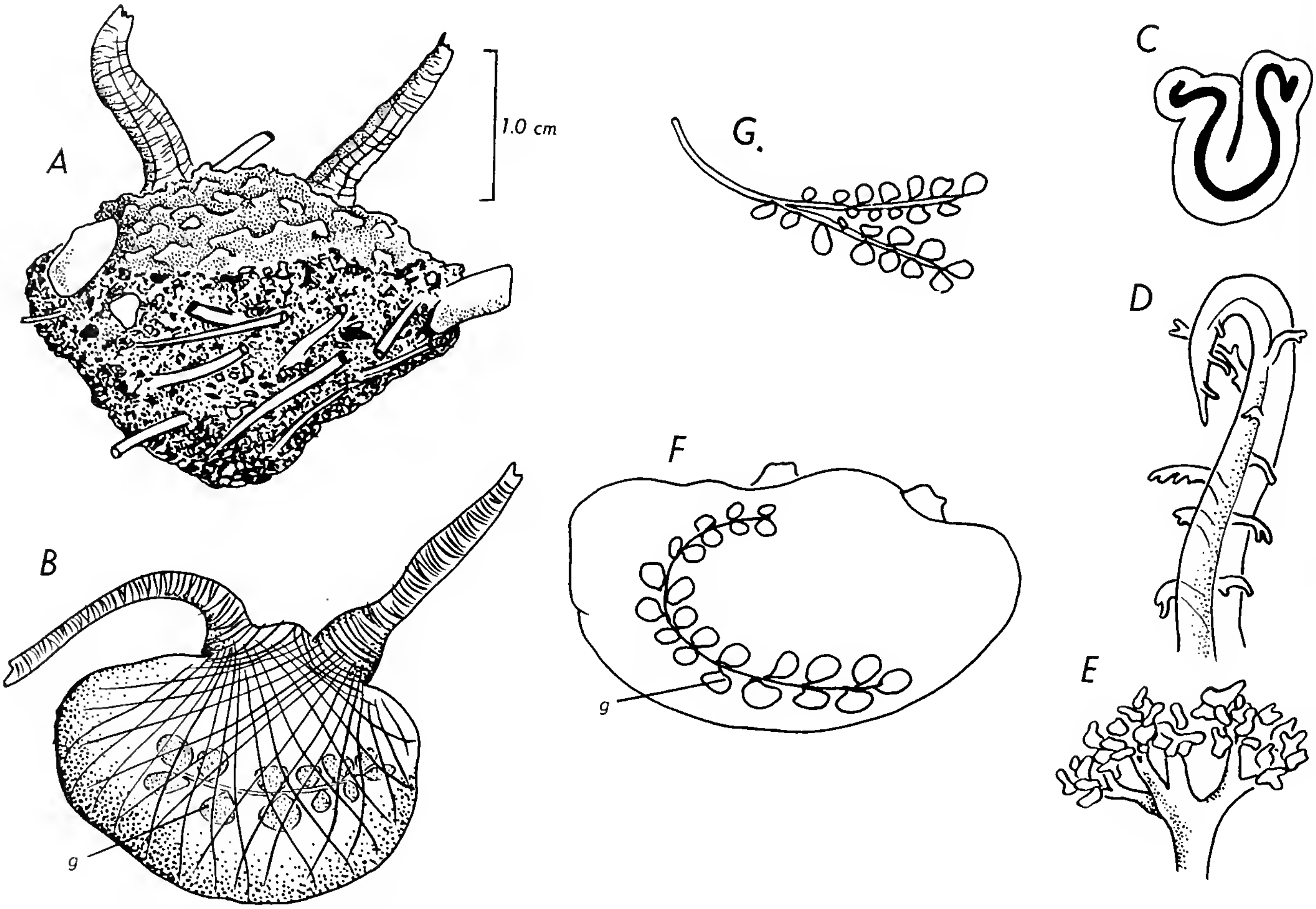
Pyura discoveryi (Herdman) (Text-fig. 45; Pl. IV, fig. 1)

Halocynthia discoveryi Herdman, 1910, p. 9, pl. 4, figs. 6–12.

OCCURRENCE. St. 27: S. Georgia, 110 m. St. 42: S. Georgia, 120–204 m. St. 140: S. Georgia, 122–136 m. St. 144: S. Georgia, 155–178 m. St. 148: S. Georgia, 132–148 m. St. 152: S. Georgia, 245 m. St. 159: S. Georgia, 160 m. St. 160: S. Georgia, 177 m. St. 170: S. Shetlands, 342 m.

St. 177: S. Shetlands, 1080 m. St. 187: Palmer Archipelago, 259–354 m. St. 190: Palmer Archipelago, 93–126 m. St. 474: S. Georgia, 199 m. St. 1948: S. Shetlands, 490–610 m.

EXTERNAL APPEARANCE (Text-fig. 45 A). This species is generally found in groups of several individuals growing together, attached basally to bottom material, and to each other by irregular areas of their sides. In some cases there is little or no encrusting matter on the test, but in others the whole body except the siphons is covered with sand, small stones and broken shell. The shape is variable, often upright and sometimes rather squat, and the siphons may be short or remarkably long (Text-fig. 45 A).



Text-fig. 45. *Pyura discoveryi* (Herdman) (St. 474): A, specimen with long siphons; B, the same with test removed; C, dorsal tubercle; D, oral tentacle; E, hepatic tubules; F, showing position of left gonad (St. 1948); G, right gonad of same specimen.

SIPHONS. According to Kott (1954) there are no spines in the lining of the siphons, and I also can find none.

TENTACLES. The tentacles number sixteen to twenty and are only slightly branched (Text-fig. 45 D).

DORSAL TUBERCLE. The opening of the dorsal tubercle is basically U-shaped with the ends of the limbs variously bent; usually both are turned outwards, or the left one outwards and the right one inwards, or one or other may point forward (Text-fig. 45 C).

BRANCHIAL SAC. Some authors have said that there are six branchial folds on each side (Herdman, 1910; Hartmeyer, 1911; Kott, 1954) and others that there are seven (Sluiter, 1914; Ärnbäck, 1938; van Name, 1945). In all the specimens from the 'Discovery' collection that I have examined there are seven folds, and although the ventral fold is lower than the others, it is unmistakably present. This finding agrees with Ärnbäck's careful review of the question (see Ärnbäck, 1938, pp. 30–2). In a specimen of length 3·4 cm. the longitudinal bars have the following arrangement: dorsal line 4 (16) 2 (16) 2 (22) 2 (24) 2 (17) 2 (13) 3 (8) 1 endostyle. There is, in some specimens, a slight tendency for the longitudinal bars to project at the posterior ends of the branchial folds, as in *P. jacatrensis*.

Gonads. I have nothing to add to the existing accounts of the gonads, except to note that in one specimen (St. 1948) the right gonad is Y-shaped, having two branches (Text-fig. 45 G).

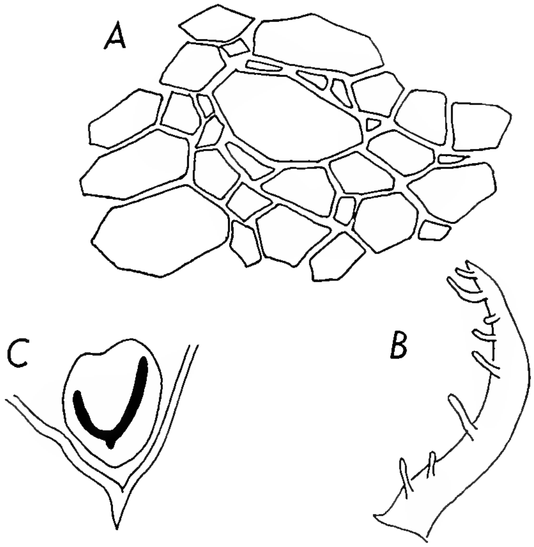
Distribution. Antarctic (McMurdo Bay, Kaiser Wilhelm II Land, Alexander I Land, Graham Land, South Shetlands, Wilkes Land, South Georgia, near Shag Rocks).

Pyura squamata Hartmeyer (Text-fig. 46)

Pyura squamata Hartmeyer, 1909–11, p. 1337 (nomen nudem); 1911, p. 439, pl. 45, fig. 12, pl. 50, figs. 1–5.

Occurrence. St. 187: Palmer Archipelago, 259 m.

External appearance. The single specimen is 1·7 cm. long, 1·0 cm. broad and 0·5 cm. in height. It is yellow-grey in colour and patterned all over with small, mainly hexagonal plates into which the test is divided (Text-fig. 46 A).



Text-fig. 46. *Pyura squamata* Hartmeyer (St. 187): A, part of test; B, oral tentacle; C, dorsal tubercle.

Internal structure. Owing to the damaged condition of the specimen certain details of structure could not be seen. But the form of the tentacles (Text-fig. 46 B) and dorsal tubercle (Text-fig. 46 C), the arrangement of branchial bars, and the shape of the gonads all conform closely to Hartmeyer's description of the type specimen. The anus is divided into seven rounded lobes; in the type specimen the anus was destroyed.

Remarks. This species is characterized principally by the polygonal plates of the test, and the presence of only five well-developed branchial folds, with a rudimentary 6th fold.

In spite of the damaged state of the only specimen in the 'Discovery' collection I have no hesitation in assigning it to *P. squamata*.

Distribution. Antarctic (Kaiser Wilhelm II Land, Charcot Land, Palmer Archipelago).

Pyura legumen (Lesson) (Text-figs. 47 A, B, C; 48; Pl. IV, fig. 6)

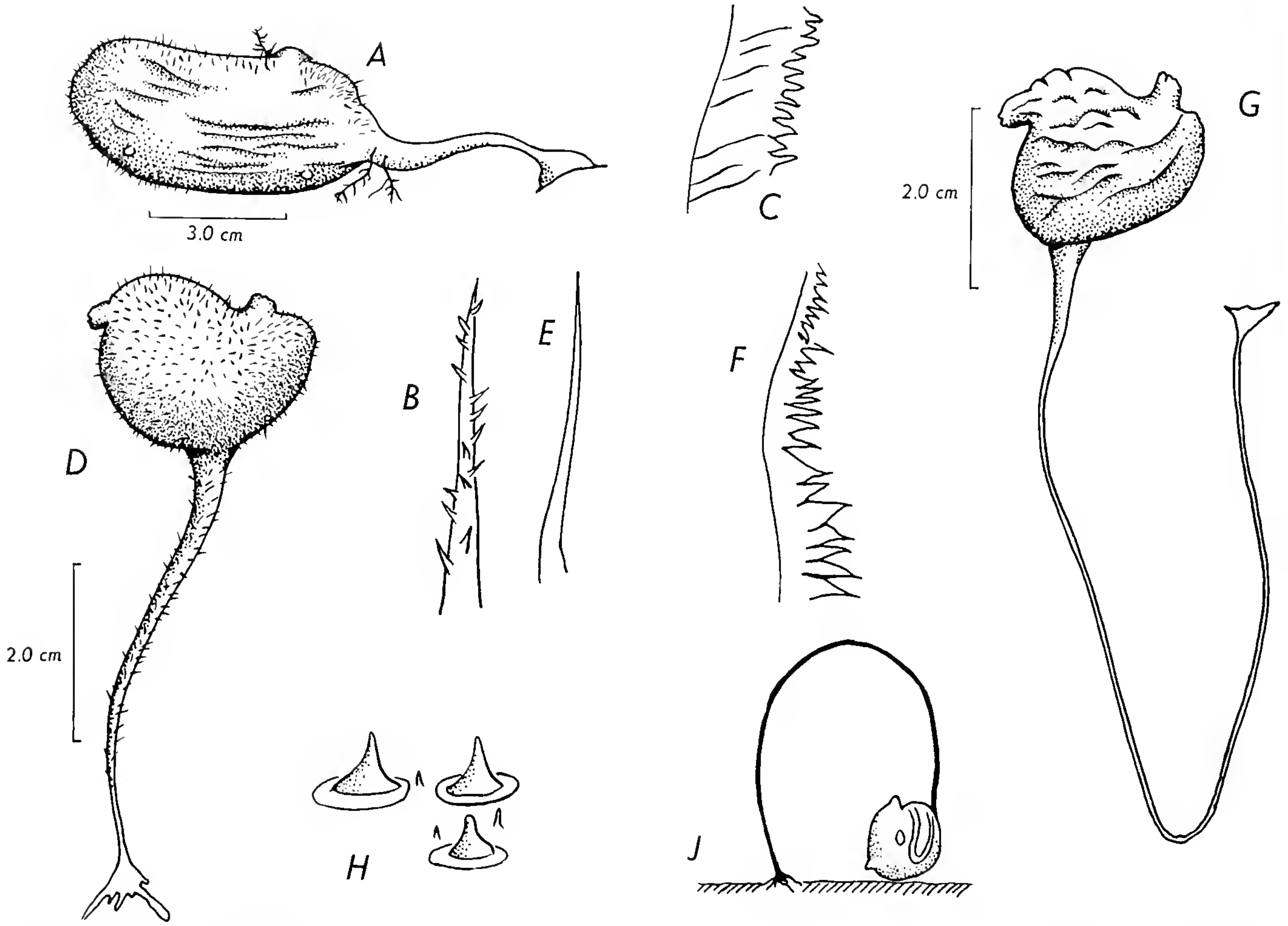
Boltenia legumen Lesson, 1830, p. 149, pl. 53, fig. 1.

For synonymy see van Name, 1945, p. 326.

Occurrence. St. 52: Falkland Islands, 17 m. St. 53: Falkland Islands, 0–2 m. St. 55: Falkland Islands, 10–16 m. St. 56: Falkland Islands, 10·5–10 m. St. 57: Falkland Islands, 15 m. St. WS 71:

Falkland Islands, 82–80 m. St. WS 84: Falkland Islands, 75–74 m. St. WS 89: Tierra del Fuego, 23–21 m. St. WS 90: Patagonian Shelf, 82–81 m. St. WS 788: Patagonian Shelf, 82–88 m. St. WS 811: Patagonian Shelf, 99 m. St. WS 834: Patagonian Shelf, 27–28 m. St. WS 852: Patagonian Shelf, 86–88 m.

External appearance (Text-fig. 47A; Pl. IV, fig. 6). The general appearance of this species is already well known. In almost all the 'Discovery' specimens the point of origin of the stalk is at the anterior ventral part of the body, but in some small ones it is mid-ventral. The proportion of body length to stalk length bears no direct relation to the total size of the animal, that is, to its age (see Text-fig. 48). Irregular longitudinal furrows mark the surface, and in some animals these break the test into rectangular or polygonal areas each bearing a group of spines. The degree to which spines are developed is very variable. They may be numerous and short, forming a kind of fur, or few and scattered. When well developed the spines reach 2 mm. in length, are sharply pointed, and bear small thorn-like processes (Text-fig. 47B).



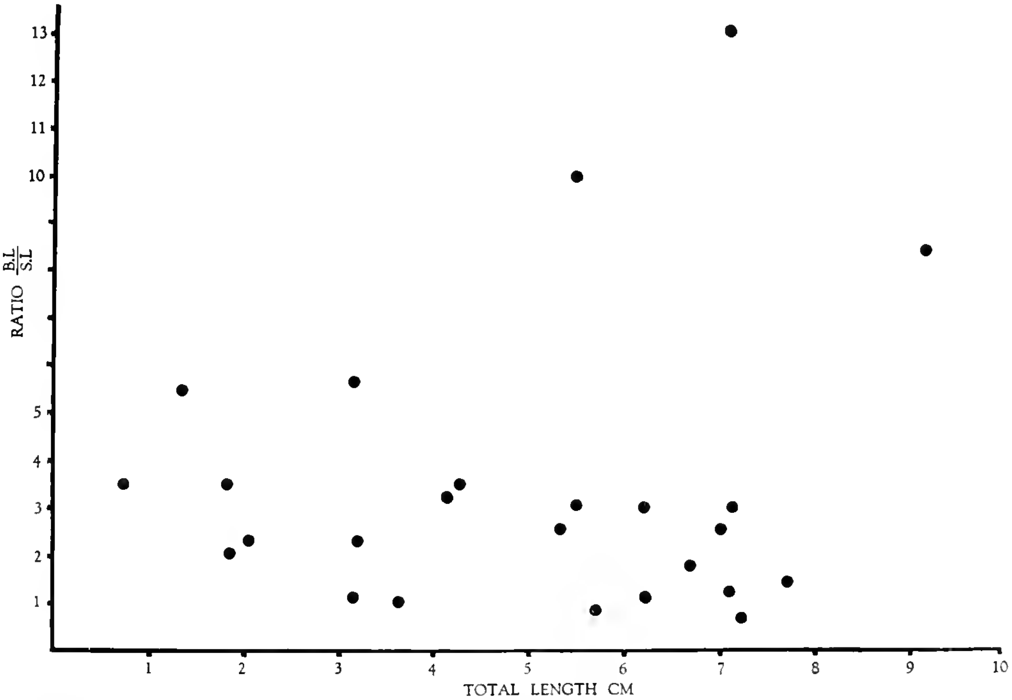
Text-fig. 47. *Pyura legumen* (Lesson) (St. 57): A, intact specimen; B, test-spine; C, part of dorsal lamina. *Pyura georgiana* Michaelsen (St. MS 14): D, intact specimen; E, test-spine; F, part of dorsal lamina. *Pyura bouvetensis* (Michaelsen) (St. 181): G, intact specimen; H, test-spines; J, probable attitude in life with body resting lightly on the bottom.

Atrial organs. The three pads, called atrial organs, which lie within the atrial siphon, at its base, have been noticed by several workers, especially Michaelsen (1900) and Ärnbäck (1938). The structure and function of the organs, however, have never been clarified. Sections show that the atrial organs are thick pads of test substance richly provided with blood spaces. As these spaces are lined with epidermis they are to be regarded as specially developed test vessels. Great numbers of blood cells, many of them phagocytes, lie in the test matrix. The function of the atrial organs is still unknown.

Parietal organs. Michaelsen (1900) noted the existence of other enigmatic structures which have become known as the parietal organs. These were described as a pair of swellings of the body wall, one on each side, and containing vacuolated cells. I have examined many specimens of *P. legumen* without finding parietal organs, although they are easily seen in related species (see p. 122), and I can only conclude that they are not always present or recognizable in *P. legumen*.

Branchial sac. In a specimen with body 3·9 cm. and stalk 3·2 cm. the branchial sac has the following arrangement of longitudinal bars: dorsal line 2 (22) 2 (13) 3 (20) 3 (20) 3 (15) 4 (12) 1 (3) 1 endostyle.

Biology. There are not enough specimens to indicate the breeding season of this species.



Text-fig. 48. *Pyura legumen* (Lesson). Relation between the ratio body-length/stalk-length and the total length.

In some animals the intestine is filled with plankton organisms, mainly small algal cells and *Globigerina* sp. together with diatoms.

Remarks. I discuss this and the two related species *P. georgiana* and *P. bouvetensis* on p. 124.

Distribution. Subantarctic (Falkland Islands, Patagonian Shelf, Magellen region).

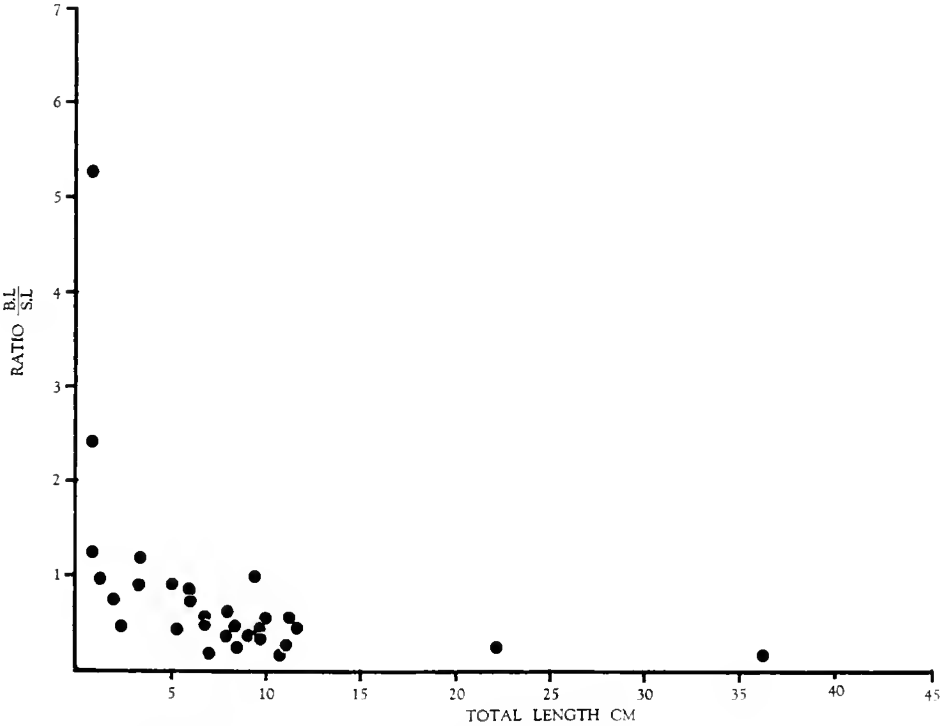
Pyura georgiana (Michelsen) (Text-figs. 47D–F; 49; 50; Pl. IV, fig. 7)

Boltenia georgiana Michaelsen, 1898, p. 364.

Occurrence. St. 39: S. Georgia, 179–235 m. St. 42: S. Georgia, 120–204 m. St. 123: S. Georgia, 230–250 m. St. 140: S. Georgia, 122–136 m. St. 144: S. Georgia, 155–178 m. St. 145: S. Georgia, 26–35 m. St. 148: S. Georgia, 132–148 m. St. 152: S. Georgia, 245 m. St. 156: S. Georgia, 200–236 m. St. WS 62: S. Georgia, 26–83 m. St. WS 567: S. Georgia, 145 m. St. MS 14: S. Georgia, 190–110 m. St. MS 68: S. Georgia, 220–247 m.

External appearance (Text-fig. 47D; Pl. IV, fig. 7). This species differs from *P. legumen* in having the stalk originating from near the middle, or somewhat towards the anterior end, of the ventral side, instead of at the extreme anterior end of that side, and passing down ventrally from the body and not as an oblique continuation of the long axis of the body, as in *P. legumen*. If the ratio of the height (i.e. dorso-ventral diameter) of the body to the length of the stalk is plotted against the total length of the specimen, it is seen that this ratio decreases with increase of total length, that is presumably with age (Text-fig. 49). Old animals may have a stalk from three to eight times the dorso-ventral diameter of the body, whereas in young animals the stalk may barely equal the diameter of the body. As in *P. legumen* the surface of the body bears a sparse but variable coating of spines (Text-fig. 47E). In *P. georgiana* however, the spines usually lack the secondary thorn-like processes commonly found in *P. legumen*.

PARIETAL ORGANS. This species has no atrial organs within the base of the atrial siphon, but in every specimen dissected a parietal organ was found on the middle of each side of the body. Sections show that the parietal organs consist of a number of closely packed rounded vesicles (Text-fig. 50A, *v.*), each vesicle being composed of many vacuolated cells (Text-fig. 50B, *v.c.*). It is not clear whether these cells remain separate although crowded together, or whether they form a syncytium. In fixed and sectioned material the vacuoles of the cells are empty, and it is not possible to say whether the parietal organs may be stores of reserve material, or, as Kott (1954) suggests, renal organs.



Text-fig. 49. *Pyura georgiana* Michaelsen. Relation between the ratio body-length/stalk-length and the total length.

Årnbäck (1938) has well described the remaining internal organs of the species.

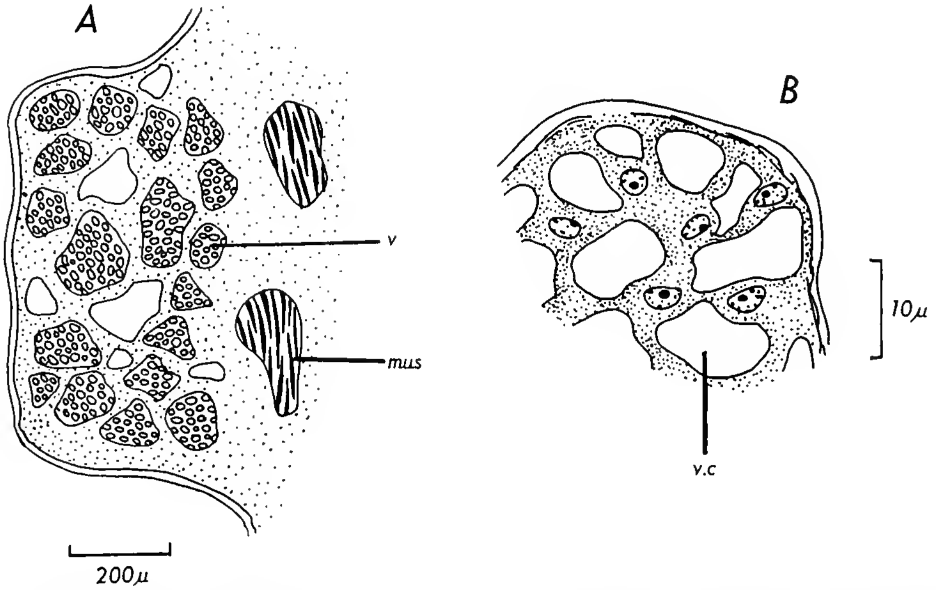
BIOLOGY. One large animal from St. 123, collected on 15 December 1926, has several small specimens of the same species attached to its test. These young ones had a body ranging from 0·25 to 0·70 cm. in diameter and apparently represented a settlement from one breeding season. Without knowing the rate of growth, however, it is not possible to say when breeding took place but it may have been within the previous month, that is in late November or early December.

REMARKS. The range of depth given by van Name (1945) suggests that this is a shallow water species, but in fact it has generally been taken from depths of 100–200 m., although Michaelsen's (1900) original record was from water of 16–25 m. Most of the 'Discovery' material is from depths of more than 100 m.

Ärnbäck (1938, p. 37) discusses the possibility that *P. scotti* Herdman and *P. antarctica* van Beneden are identical with *P. georgiana*.

There is a single record of two specimens from the northern part of the Argentine coast, 37° 50′ S., 56° 11′ W., by Ärnbäck (1938). This is a locality far north of all others from which *P. georgiana* has been taken and were it not given on Ärnbäck's authority the record would require confirmation.

Distribution. Antarctic (South Georgia), Subantarctic (north coast of Argentine).



Text-fig. 50. *Pyura georgiana* Michaelsen: A, section through the parietal organ to show vesicles (*v.*); B, part of a vesicle, at higher magnification, to show vacuolated cells (*v.c.*).

Pyura bouvetensis (Michaelsen) (Text-fig. 47 G, H, J; Pl. IV, figs. 4, 5)

Boltenia bouvetensis Michaelsen, 1904, p. 216, pl. 10, fig. 6; pl. 11, figs. 23, 24.
Boltenia salebrosa Sluiter, 1905, p. 474; 1906, p. 45; 1906*a*, p. 554.
Boltenia turqueti Sluiter, 1905, p. 474.
Boltenia turqueti Hartmeyer, 1909–11, p. 1342; Sluiter, 1914, p. 11; Ärnbäck, 1938, p. 37; van Name, 1945, p. 331.
?*Pyura legumen* Kott, 1954, p. 124.

Occurrence. St. 170: S. Shetlands, 342 m. St. 181: Palmer Archipelago, 160–335 m. St. 187: Palmer Archipelago, 259–354 m. St. 190: Palmer Archipelago, 93–126 m. and 315 m. St. 195; S. Shetlands, 391 m. St. 599: S. Shetlands, 203 m. St. 600: S. Shetlands, 501–527 m. St. 1952: S. Shetlands, 367–383 m. St. 1955: S. Shetlands, 440–410 m.

External appearance (Text-fig. 47 G; Pl. IV, figs. 4, 5). The largest of the many specimens has a stalk of 21·0 cm. and a body of 3·0 cm. long (antero-posteriorly) by 2·3 cm. high (dorso-ventrally). In the smallest complete specimen the stalk is 3·0 cm. and the body 1·2 cm. long by 1·1 cm. high. The stalk originates from the antero-ventral part of the body, is moderately thick here, and becomes gradually thinner towards the lower end. A stalk so slender and flexible could not support the body which may in fact rest on the bottom (Text-fig. 47 J). In appearance and texture the surface of the body varies from brown, wrinkled and fairly tough to pale ochre, smooth and so thin as to be semi-transparent. In the latter case the parietal organs, gut and branchial folds can be seen through the test. A slight swelling, small disc, or group of root-like processes serve to attach the stalk to the substratum. The surface of the test is beset with short conical spines each standing on a circular disc-shaped area of test (Text-fig. 47 H). These spines are very different from those of either *P. legumen* or *P. georgiana*.

Body wall. The body wall is thin, with narrow but distinct circular muscles round the siphons and narrow longitudinal muscles radiating across the body from the siphons. The siphons are small and wart-like.

Parietal organs. About the centre of the left side of the body above the intestinal loop, there is a small ovoid parietal organ and another at a corresponding point on the right side. This species has no atrial organs.

Tentacles. In large specimens there are about twelve large compound tentacles and a few very small ones between them.

Dorsal tubercle. The dorsal tubercle has a C-shaped slit with the horns turned inwards or spirally coiled.

Branchial sac. On the margin of the wide dorsal lamina there is a series of distinct teeth. The longitudinal bars of a large specimen are arranged as follows: dorsal line 5 (22) 3 (21) 2 (23) 3 (24) 6 (18) 3 (22) 2 (17) 7 endostyle.

Gut. The gut is bent into a long flat U-shaped loop lying far down in the ventral half of the left side. At the posterior end of the body is the curved oesophagus, which leads to the short pear-shaped stomach with walls bearing twenty or more narrow folds. The intestine and rectum are narrow, and bent so that the anus lies close to the oesophagus.

Gonads. The gonads are long and narrow, the left one within the intestinal loop and the right one at a corresponding position on the opposite side. In each gonad the ovary is long and continuous, and the testis is developed as a series of about four swellings along the length of the gonad.

Remarks. I agree with van Name (1945) that there is no reason for separating *P. bouvetensis*, which Michaelsen (1904) described from the neighbourhood of Bouvet Island, from the much better-known *P. turqueti* of the Graham Land region. Owing to an error of Michaelsen's it was originally thought that the gonads of *P. bouvetensis* differed from those of related species, but now that this mistake has been put right, *P. bouvetensis* and *P. turqueti* are indistinguishable.

Distribution. Antarctic (Bouvet Island, Graham Land region, South Shetland Islands, ?Victoria Land as *P. scotti* Herdman, 1910, ?Enderby Land, ?MacRobertson Land as *P. legumen* Kott, 1954).

The relationship of P. legumen, P. georgiana *and* P. bouvetensis

These three species constitute a natural and closely related group, but their validity as separate species has been questioned. Of recent authors, Ärnbäck (1938) and van Name (1945) have both maintained the three species, although van Name was a little doubtful whether *P. legumen* and *P. georgiana* should be separated. Kott (1954), however, definitely identifies *P. turqueti* with *P. legumen*, after examining material from Enderby Land and MacRobertson Land, which apparently showed a great variety of external form. I cannot agree with this, as the presence of atrial organs readily distinguishes *P. legumen* and from *P. bouvetensis* (syn. *P. turqueti*). Moreover, the locality of the specimens which she identified as *P. legumen* was in the high Antarctic, very different from the well-localized area of distribution of *P. legumen* in the Subantarctic.

The rich 'Discovery' material shows, I think, that the three forms are best regarded as three separate species. One of these, *P. legumen*, is confined to the Subantarctic waters of the Falkland Islands, Patagonian Shelf and Magellan region. The other two are Antarctic species: *P. georgiana*, probably with a very local distribution round South Georgia, and *P. bouvetensis*, which is circumpolar. The two latter species are more closely related to one another than to *P. legumen*. This close relationship is shown by both having parietal organs but no atrial organs, and by the relatively long stalk.

The forms that we have been considering present a case of the breaking up of a population into species which, at their present stage of evolution, still show their close relationship.

Pyura jacatrensis (Sluiter) (Text-fig. 51)

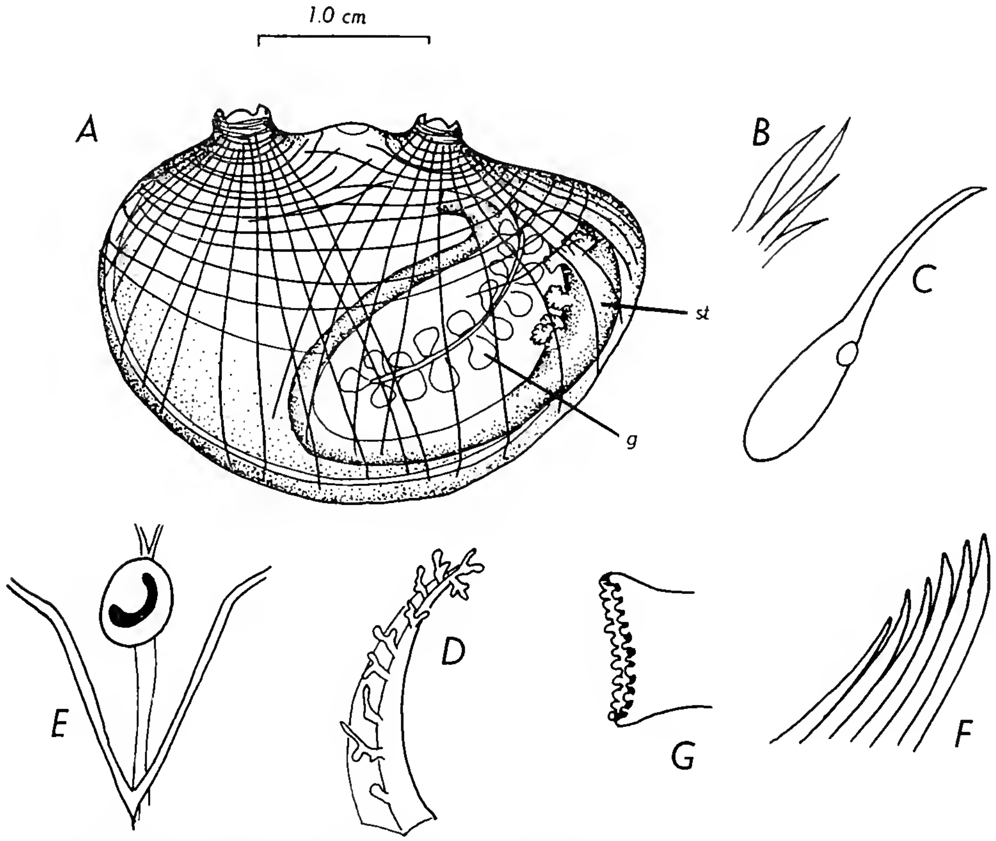
Cynthia jacatrensis Sluiter, 1890, p. 331, pl. 1, figs. 8, 9.
For synonymy see Kott 1954, p. 127.

Occurrence. St. 1563: Marion Island, S. Indian Ocean. 113–99 m.

External appearance. The single specimen is 3·2 cm. long and 2·2 cm. high, of an ovoid shape and almost completely covered by sand, shell and debris. The siphons are visible externally as short wide tubes more or less free of encrusting matter.

Test. The test is not very thick, but is tough. Its inner surface is pale grey. On the lining of the siphons there are slender pointed spines (Text-fig. 51 B, C) agreeing with those found by Kott (1954).

Body wall. On the body wall the muscles which radiate from the siphons are quite numerous, and regularly arranged (Text-fig. 51 A). The circular muscles are not numerous, except on and near the siphons.



Text-fig. 51. *Pyura jacatrensis* (Sluiter) (St. 1563): A, specimen with test removed; B, spines from lining of oral siphon; C, one of the spines at higher magnification; D, oral tentacle; E, dorsal tubercle; F, posterior end of a branchial fold; G, anus.

Tentacles. There are sixteen oral tentacles (Text-fig. 51 D) of alternating sizes. The primary branches are short and only very slightly divided.

Dorsal tubercle. The opening of the dorsal tubercle is a small crescentic slit with the open interval facing obliquely to the right and forward (Text-fig. 51 E).

Branchial sac. Six sharply defined folds are present on each side of the branchial sac, with longitudinal bars thus arranged: dorsal line 1 (14) 3 (16) 3 (16) 2 (17) 2 (15) 3 (11) 3 endostyle.

There are about thirteen stigmata to each mesh on the flat parts between folds. The dorsal lamina is represented by about forty narrow pointed languets. At the posterior end of each branchial fold the longitudinal bars are prolonged as groups of slender processes (Text-fig. 51 F).

Gut. A number of branched hepatic lobes are given off from the surface of the stomach (*st.*) but as they are few, most of the stomach is exposed. The primary loop of the gut is rather widely open. Kott (1952) has described the anal border in this species as 'smooth' in her Australian specimens, and as 'gently indented, but not divided into distinct lobes', in a later publication (Kott, 1954) dealing with material from Macquarie Island, Kerguelen and Tasmania. The 'Discovery' specimen from Marion Island has the anal border minutely cut into about thirty very short lobes (Text-fig. 51 G).

Gonads. One curved gonad (*g*) lies on each side of the body and comprises about twelve pairs of sac-like lobes arranged along the gonoducts.

Remarks. Apart from the subdivision of the anal border, this specimen is in good agreement with Kott's (1952, 1954) accounts of *P. jacatrensis*. It appears doubtful, however, whether this species is sufficiently distinct from *P. vittata* (Stimpson). In her key to the species of *Pyura*, Kott (1952, pp. 260–3) separates *P. jacatrensis* from *P. vittata* by the smooth anal border of the former and the lobed border of the latter. But there are differences in the published descriptions of the anal border in *P. vittata*. Thus according to van Name (1945) the border is 'usually with rounded lobes', and it is variously described by Tokioka as indistinctly lobed (1949), 'not lobed' (1950) and 'plainly margined' (1952). In spite of the unsatisfactory nature of the distinctions, it is unlikely that the two species are the same, since *P. vittata* is known chiefly from the tropical and subtropical waters of eastern America and West Africa, and from Japanese waters, whereas *P. jacatrensis* has been recorded from Indonesia, Western Australia, Tasmania, Kerguelen and Macquarie Island. Further evidence might show that the records from warm waters refer to *P. vittata*, and those from Kerguelen, Marion Island, Macquarie Island and perhaps Tasmania refer to a different species. But there is not yet enough information to make a decision possible.

Distribution. Indonesia, Western Australia, Tasmania, Subantarctic (Macquarie Island, Marion Island), Antarctic (Kerguelen).

Pyura vittata (Stimpson)

Cynthia vittata Stimpson, 1852, p. 230.
For synonymy see van Name, 1945, p. 321.

Occurrence. St. 1: Ascension Island, S. Atlantic Ocean, 16–27 m.

External appearance. The single specimen measures 2·0 by 1·5 cm., has a very irregular outline owing to the presence of rounded swellings on the surface, and is dirty pale grey in colour.

Internal structure. The specimen was somewhat damaged but all details which were seen are typical of the species, and may be summarized as follows: Tentacles 32. Dorsal tubercle with C-shaped slit having inrolled horns. Thirty slender dorsal languets. Six branchial folds with bars arranged thus: dorsal line 3 (13) 5 (17) 3 (17) 4 (20) 8 (15) 6 (12) 7 endostyle. Stomach with large branched liver. Endocarps along dorsal side of intestine. Gonads not present. The only point needing special mention is the two-lipped anus. This does not agree with van Name's (1945) description of the species as found in tropical American waters, the nearest locality with adequately described specimens. But the apparently variable form of the anal margin (see remarks under *P. jacatrensis*) shows that it is not an important diagnostic character.

Distribution. Warm waters of the Atlantic coast of America; west Africa, Ascension Island, Japan.

Genus **Herdmania** Lahille, 1887

Herdmania momus (Savigny) (Text-fig. 52)

Cynthia momus Savigny, 1816, p. 143, pl. 1, fig. 2; pl. 4, fig. 1.
For synonymy see Kott, 1952, p. 279 (var. *grandis*), p. 281 (var. *galei*), p. 282 (var. *curvata*).

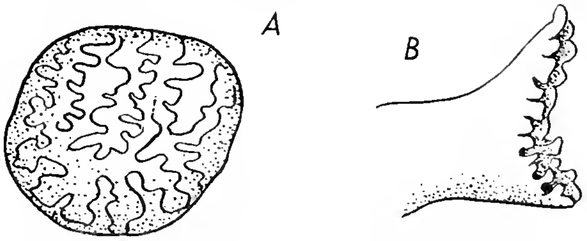
Occurrence. St. 1686: Victoria, Australia, 0 m.

External appearance. The single specimen measures 11 cm. long by 7 cm. high, and is heavily encrusted with hydroids and other organisms. The short wide siphons are visible externally.

Internal structure. As the species has been described in detail by several authors (see particularly van Name, 1945; Kott, 1952; and Tokioka, 1953) I shall mention only a few important features of this specimen.

Dorsal tubercle. The tubercle is a large conspicuous cushion with a complicated sinuous slit (Text-fig. 52A), similar to that illustrated by Kott (1952, fig. 124), for var. *grandis*.

Branchial sac. There are fourteen folds on one side of the branchial sac, with up to thirty longitudinal bars on the larger folds, and several between folds.



Text-fig. 52. *Herdmania momus* (Savigny) (St. 1686): A, dorsal tubercle; B, anus.

Gut. About twenty-four lobes surround the anal opening (Text-fig. 52B).

Remarks. This is a very variable species, but is always readily identified by the spicules in the body wall and branchial sac, and by the large number of branchial folds.

Several varieties and forms (see Michaelsen, 1919; Kott, 1952) have been described and for a discussion of these van Name (1945) and Tokioka (1953) should be consulted. Both of these latter authors suggest that the subdivisions of the species have little systematic value, but nothing can be added to the argument here on evidence from one specimen. This specimen agrees closely with the description of var. *grandis*, which is characterized specially by (1) the large size, (2) the large number of branchial folds (ten to thirteen on each side), and (3) the large and complex dorsal tubercle.

Distribution. Widely spread in warm waters of the world.

Genus **Bathypera** Michaelsen, 1904

Bathypera splendens Michaelsen (Text-fig. 53)

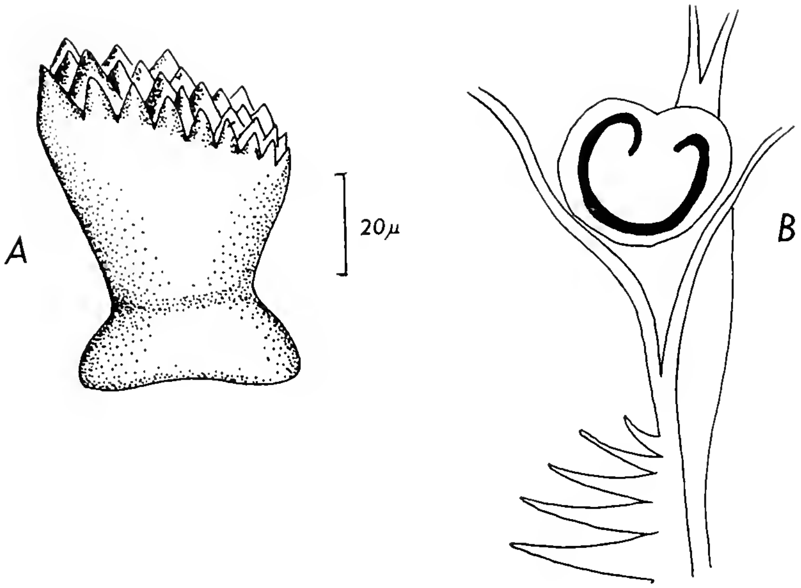
Bathypera splendens Michaelsen, 1904, p. 192, pl. 10, fig. 9; pl. 11, figs. 15–19.
Pyura liouvillia Sluiter, 1912, p.. 543

Occurrence. St. 181: Palmer Archipelago, 160–335 m.

External appearance. The body of the single specimen is roughly spherical, approximately 2 cm. in diameter and slightly flattened on the dorsal side, where the siphons make two small, widely separated, conical projections. The general colour is grey, paler on the siphons, and the surface feels rough to the touch owing to the presence of the characteristic test spicules (Text-fig. 53A) arranged at right angles to the surface.

Internal structure. Several detailed descriptions (Michaelsen, 1904; Hartmeyer, 1911; Herdman, 1923; Kott, 1954) leave little to be added. In the 'Discovery' specimen the dorsal tubercle has a complete C-shaped slit (Text-fig. 53B), not broken into two parts as in Kott's description. Michaelsen described and illustrated a short oviduct and sperm duct, but in Kott's specimens these were much longer. The present specimen shows only moderately long ducts.

Distribution. Antarctic (Graham Land, Enderby Land, Kaiser Wilhelm II Land, Adelie Land, Wilkes Land, MacRobertson Land).



Text-fig. 53. *Bathypera splendens* Michaelsen (St. 181): A, spicule from test; B, dorsal tubercle.

Family MOLGULIDAE Lacaze-Duthiers, 1877

Genus **Molgula** Forbes & Hanley, 1848

Molgula pedunculata Herdman (Text-fig. 54; Pl. V, fig. 4)

Molgula pedunculata Herdman, 1881, p. 234.
For synonymy see van Name (1945).

Occurrence. St. 27: S. Georgia, 110 m. St. 39: S. Georgia, 179–235 m. St. 42: S. Georgia, 120–204 m. St. 45: S. Georgia, 238–270 m. St. 123: S. Georgia, 230–250 m. St. 140: S. Georgia, 122–136 m. St. 144: S. Georgia, 155–178 m. St. 160: Shag Rocks, 177 m. St. 190: Palmer Archipelago, 93–126 m. St. 599: Graham Land, 203 m. St. WS 27: S. Georgia, 107 m. St. MS 68: S. Georgia, 220–247 m.

External appearance. The largest of the many specimens in the collection is 2·6 cm. long. Almost all of them show some degree of the development of tag-like processes or short hairs on the test. The body is longer than wide, and is generally ovoid or somewhat rectangular, with the siphons symmetrically placed on the upper border. In some specimens, more often the small ones, the lower part of the body is produced into a narrow stalk, which is occasionally almost as long as the body, but is generally much shorter.

Internal structure. The variation in the internal structure of the 'Discovery' specimens will be discussed in relation to Ärnbäck's (1938) account of her species *M. angulata*, to which, in her preliminary notes, she assigned a number of specimens in the 'Discovery' collection. Table 35 gives the main characters of *M. angulata*, and of the 'Discovery' specimens which I identify as *M. pedunculata*.

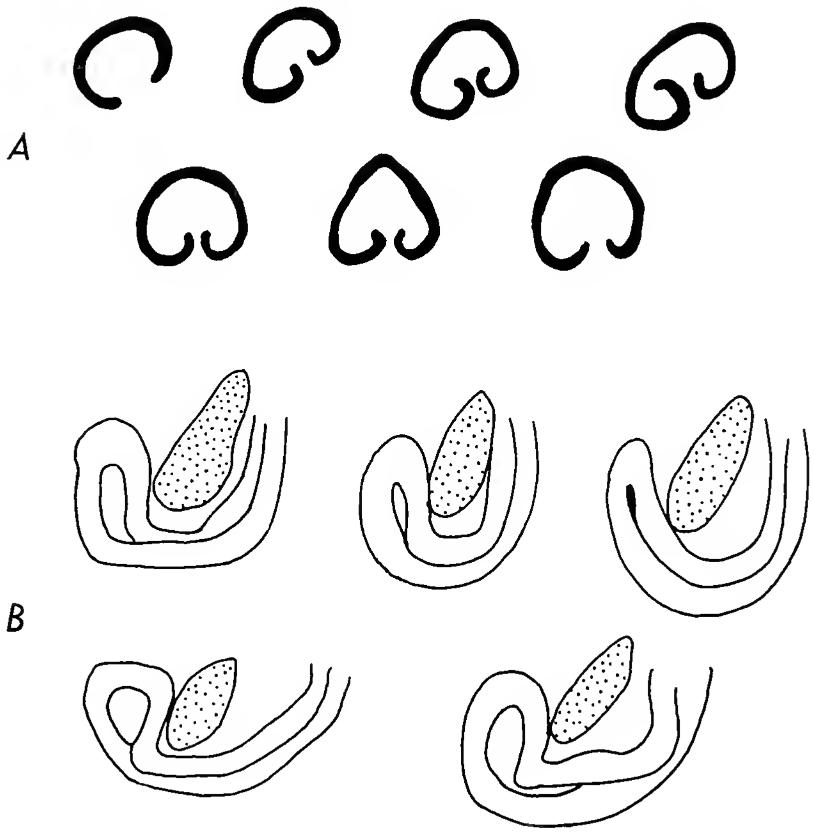
Table 35

	M. angulata	*M. pedunculata* ('Discovery' specimens)
Tentacles	At least 20; the largest bipinnate	Usually 12–16; the largest tri-pinnate
Dorsal tubercle	Transversely elongated; horns inturned; faces back left	Sometimes transversely, sometimes longitudinally elongated; horns usually inrolled; usually faces back left (see Text-fig. 54A)
Branchial sac	7 folds; about 11 bars per fold; 1 or 2 bars between folds	7 folds; 6–13 bars per fold; 1–4 bars between folds
Gut	Sharp bend in intestine	Intestine variously curved, sometimes with sharp bend (see Text-fig. 54B)

Text-fig. 54 supplements the information in Table 35 by showing some forms of dorsal tubercle and intestine in the present specimens. These comparisons show that the type and only specimen of Ärnbäck's *M. angulata* lies within the range of variation of the much more abundant 'Discovery' material, which is readily identifiable as *M. pedunculata*. *M. angulata* must therefore be regarded as a synonym of *M. pedunculata*, as suggested by van Name (1945).

Remarks. See p. 137 for notes on the differences between this species and *M. sabulosa* (Quoy & Gaimard) which Kott (1952, 1954) believes to be identical.

Distribution. Antarctic (Graham Land, Kaiser Wilhelm II Land, South Georgia, Kerguelen).



Text-fig. 54. *Molgula pedunculata* Herdman: A, different forms of opening of the dorsal tubercle; B, different forms of gut (clear) and left gonad (stippled).

Molgula falsensis Millar (Text-fig. 55)

Molgula falsensis Millar, 1955, pp. 217–9, fig. 40.

Occurrence. St. 91: False Bay, S. Africa, 35 m.

External appearance (Text-fig. 55 A). The six specimens range from 8 by 8 mm. up to 13 by 7 mm. All of them are covered with adhering fragments of shell and grains of sand.

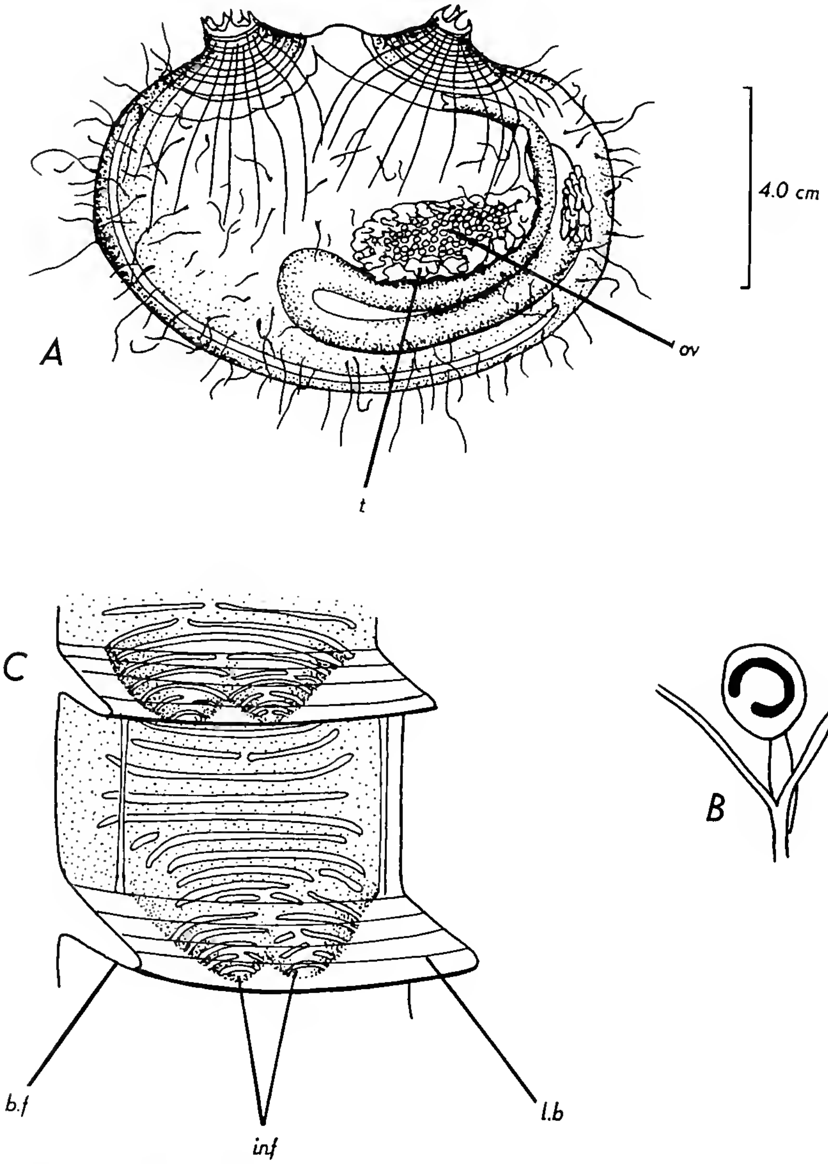
Test. The test is thin, flexible and transparent and has a sparse coating of very fine hairs.

Body wall. Muscles which radiate from the siphons extend only a short distance across the sides of the body; other muscles, oblique and circular, are very few, except round the siphons.

Tentacles. There are about twenty-one oral tentacles, of which four or five are large and tripinnate. Only eight to ten tentacles were present in the type specimens (Millar, 1955).

Dorsal tubercle. The C-shaped opening of the dorsal tubercle faces backwards and to the right (Text-fig. 55 B).

Branchial sac. There are seven tall narrow branchial folds, with the following arrangement of longitudinal bars in a large specimen: dorsal line o (6) o (7) o (8) o (8) o (6) o (6) o (5) o endostyle. The absence of bars between folds was also noted in the type specimens. The infundibula are very regular (Text-fig. 55 C, *inf*.).



Text-fig. 55. *Molgula falsensis* Millar (St. 91): A, intact specimen; B, dorsal tubercle; C, part of branchial wall.

Gut. The primary loop of the intestine is almost closed, and the secondary loop very open.

Gonads. The left gonad occupies the secondary gut loop and the right gonad lies immediately above the renal sac. The sac-like ovary (*ov.*) has an upturned oviduct with crescentic opening, and is fringed by numerous testis follicles (*t*).

Distribution. False Bay, South Africa.

Molgula platei Hartmeyer (Text-fig. 56; Pl. V, fig. 7)

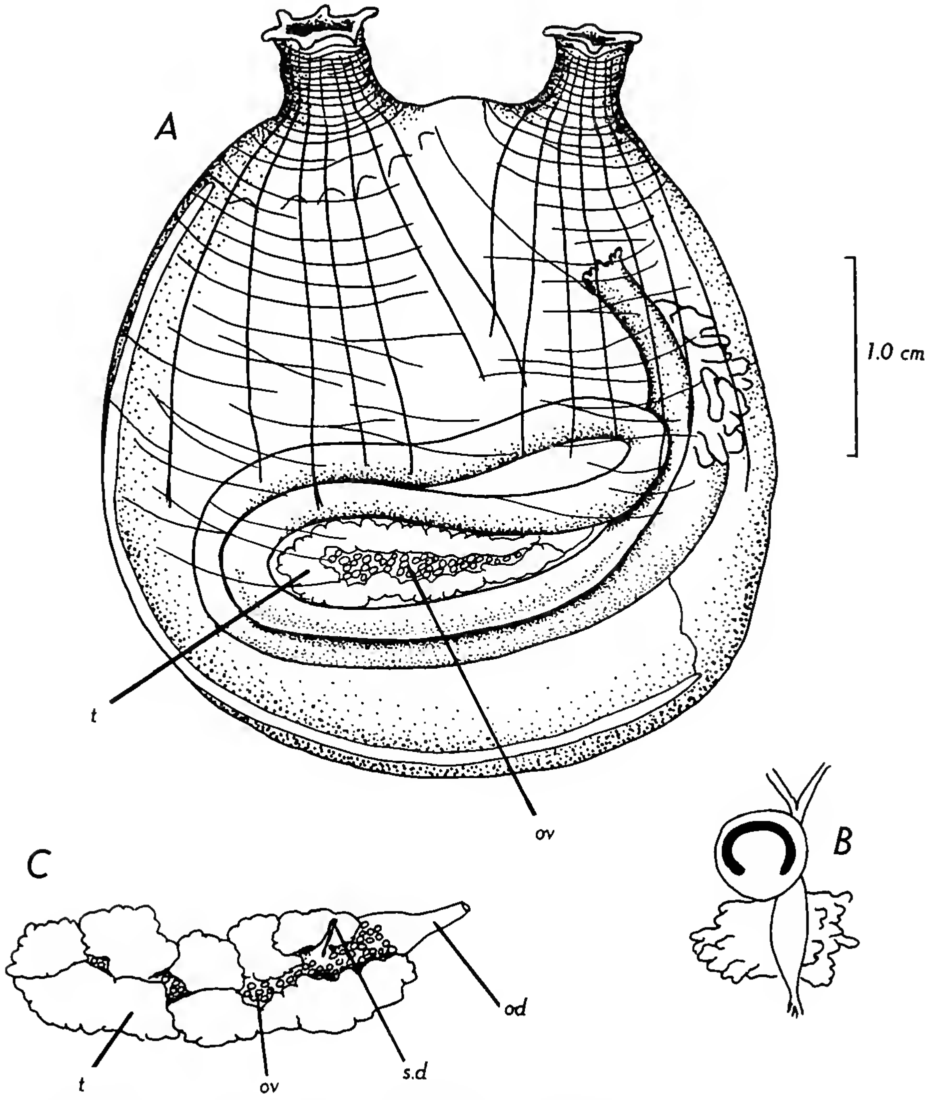
Molgula platei Hartmeyer, 1914, p. 8, figs. 2, 3.

For synonymy and remarks see van Name 1945, p. 413.

Occurrence. St. WS 742: off coast of Chile, 47–35 m.

External appearance (Pl. V, fig. 7). Many specimens are present in the collection, all taken in a single haul. They range from 0·6 to 3·6 cm. in greatest diameter. The body is ovoid and upright, generally somewhat broader at the base, and narrower at the upper end where the siphons form two low conical papillae. But in some specimens the base is narrowed. The colour is pale grey and the surface smooth and quite soft, being free of encrusting matter, except for some at the base of the body. The animals had evidently been lying free or slightly embedded in soft bottom material. A number of animals were joined together by fusion of the test of the lower part of the body.

TEST. The test is thin and flexible, but quite tough, and is almost transparent.



Text-fig. 56. *Molgula platei* Hartmeyer (St. WS 742): A, specimen removed from test; B, dorsal tubercle, with ganglion and neural gland; C, gonad.

BODY WALL. The body wall is also thin. Narrow but quite conspicuous longitudinal muscles pass from the siphons to about half way across the body. Circular and irregular oblique muscles are not very conspicuous or numerous on the body itself, but circular muscles are well developed round the siphons.

TENTACLES. Thirteen or fourteen much branched tentacles alternate in size. Hartmeyer (1914) noted thirty-two tentacles of three sizes. The larger tentacles have four orders of branching.

DORSAL TUBERCLE. The opening of the dorsal tubercle is C-shaped with the open interval turned backwards or back to the left (Text-fig. 56 B).

Branchial sac. On each side of the branchial sac are six folds, with the following arrangement of longitudinal bars as seen in a moderate sized animal: dorsal line 0 (5) 0 (6) 0 (8) 0 (7) 0 (6) 0 (5) 0 endostyle. Van Name (1945) wrongly quotes Hartmeyer (1914) as giving the number of bars on the folds as from two to four, whereas Hartmeyer in describing the type specimen stated that there were from two to four bars on one side of the folds. The total number would thus correspond to the number found in the 'Discovery' specimens.

Gut. The shape of the gut seems to be characteristic and affords the best means of distinguishing between this species and *M. manhattensis* (De Kay). In *M. platei* the primary loop is closed for most of its extent, as it is in the other species, but the secondary loop also is almost completely closed. About half of the intestinal loop is bent at a sharp angle to lie almost horizontally over its lower half (see Text-fig. 56A), bringing the bend of the primary loop in contact with the rectum. In *M. manhattensis* the curvature of the secondary loop is typically the arc of a circle with the opening of the loop dorsal, contrasted with the flattened horizontal secondary loop with the opening posterior, in *M. platei*.

Gonads. The left gonad lies in the secondary intestinal loop and the right gonad lies obliquely above the renal sac. (Text-fig. 56A). The central ovary (*ov.*) and fringing testis (*t*) are much as described by Hartmeyer. The oviduct (*od.*) is terminal and the sperm duct (*s.d.*) a short distance from it.

Remarks. This species has previously been known only by a single specimen from the coastal waters of Chile near Chiloe Island. Van Name (1945), while allowing the species to stand, was in some doubt whether it differed sufficiently from *M. manhattensis* to justify separation, but the plentiful material of the 'Discovery' collection confirms Hartmeyer's view that the two species are distinct.

Distribution. Coastal waters of Chile (about 38° S. to 44° S.).

Molgula malvinensis Ärnbäck (Text-fig. 57)

Molgula malvinensis Ärnbäck, 1938, p. 5, pl. 1, figs. 1–3; text-fig. 1.

Occurrence. St. 159: S. Georgia, 160 m. St. 474: S. Georgia, 199 m.

External appearance. The largest specimen measures 4·3 cm. long (antero-posteriorly) by 3·0 cm. high (dorso-ventrally) by 2·0 cm. wide and is considerably larger than specimens hitherto obtained; the smallest is 2·7 by 1·7 by 1·5 cm. The body is almost completely hidden by adhering sand and small stones, the contracted siphons alone being visible on the upper surface. Ärnbäck (1938) states that the test bears irregular hair-like processes. The test processes of the specimens in the 'Discovery' collection are either grouped together in small bunches or are compound, several hairs arising from a short common stem. At their outer ends these hairs are usually expanded, where they are attached to the small stones covering the body.

Tentacles (Text-fig. 57B). The tentacles differ somewhat from those illustrated by Ärnbäck (1938, text-fig. 1) who shows them as bi-pinnate. Van Name (1945) states that the tentacles are like those of *M. occidentalis* Traustedt, which are at least tri-pinnate. In the 'Discovery' specimens there are about eight large tentacles and the same number of very small ones. Even the large tentacles are only once pinnate and the branches, which number four or five on each side, are very short.

Dorsal tubercle (Text-fig. 57C). The dorsal tubercle has a C-shaped slit with the horns inrolled; the opening of the C faces right in one of the specimens examined and left in the other.

Branchial sac. There are, as reported by Ärnbäck, seven folds on the right side of the branchial sac and six on the left side. Longitudinal bars are distributed as follows in the largest specimen:

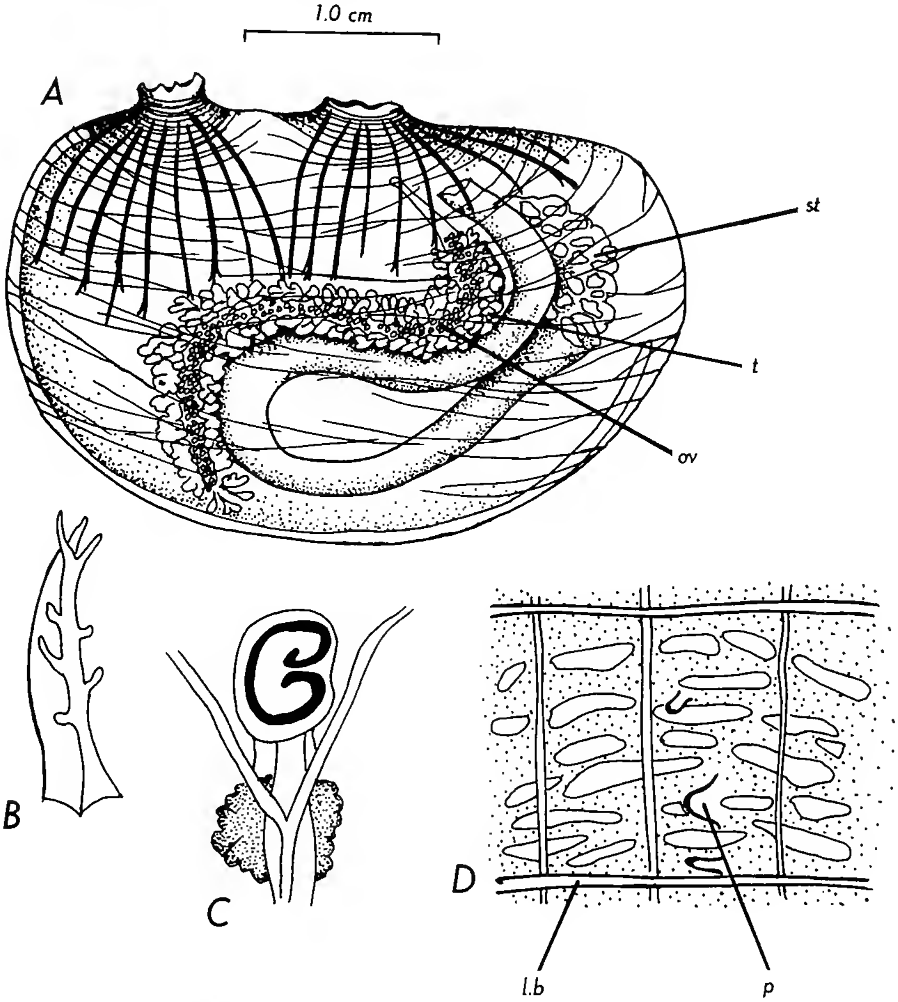
Left—dorsal line 1 (18) 1 (22) 1 (21) 2 (20) 2 (20) 1 (14) 0 endostyle.

Right—dorsal line 2 (14) 1 (21) 1 (26) 1 (22) 1 (22) 1 (20) 1 (16) 0 endostyle.

In this specimen there are twice as many bars on the folds as in Ärnbäck's specimens, a fact corresponding to the greater body size. In the type specimen the edge of the dorsal lamina was toothed, but van Name (1945) noted that it is sometimes almost smooth. In the 'Discovery' animals dissected, the lamina is distinctly toothed throughout its whole length. Small papillae were present on the branchial wall of the type specimens and a few were also seen in the 'Discovery' material (Text-fig. 57 D, *p*). They are probably the rudiments of new transverse bars.

GUT. The curvature of the secondary loop is rather less than in the type specimens.

GONADS. The position of the gonads is characteristic of the species, the left one bent round the intestinal loop (Text-fig. 57 A), and the right one bent round the renal sac. The ovary (*ov.*) is narrow and tubular, and is bordered by lobed testis follicles (*t*) along its whole length. Both oviduct and sperm duct are long and straight, and are embedded in the body wall.



Text-fig. 57. *Molgula malvinensis* Ärnbäck (St. 159): A, specimen removed from test; B, oral tentacle; C, dorsal tubercle, with ganglion and neural gland; D, part of branchial wall.

REMARKS. As pointed out by van Name (1945) this species resembles *M. occidentalis* Traustedt. It is even more like *M. pyriformis* Herdman. From these two species it can be distinguished as shown in Table 36.

M. pyriformis rests on a single specimen and as the differences separating it from *M. malvinensis* are not great it might be possible to unite it with that species if more specimens could be examined from the area from which the type of *M. pyriformis* was obtained. In the meantime, however, the two species must be recognized.

DISTRIBUTION. Antarctic (South Georgia, Shag Rocks; Kerguelen), Subantarctic (Falkland Islands; Macquarie Island).

Molgula bacca Herdman

Molgula bacca Herdman, 1910, p. 13, pl. 4, figs. 1–5.

Occurrence. St. 175: S. Shetlands, 200 m.

External appearance. The single specimen has a body 2·0 cm. long and stalk 0·7 cm. As in Ärnbäck's specimen from the Graham Land region the surface of the test bears very small scattered tag-like processes, which are most numerous on the siphons; they are coated with sand. The test is thin and transparent, allowing the branchial folds and the gut to be seen from the outside. The shape of the specimen is almost identical to those illustrated by Herdman (1910, pl. 4, figs. 1, 2) and by Ärnbäck (1938, text-fig. 4). It seems to be constant in the species which is characterized by (1) the pear-shaped body, (2) the short basal stalk, (3) the asymmetrically placed short siphons, and (4) the transparent test.

Body wall. The muscles of the body wall are slender and run almost entirely in a transverse direction. They are best developed on the dorsal and ventral areas of the body, and absent from the area overlying the gut.

Table 36

	M. malvinensis	*M. occidentalis*	*M. pyriformis*
Dorsal tubercle opening	C-shaped	C-shaped	Simple funnel-shaped
Primary intestinal loop	Open	Nearly closed	Widely open
Secondary intestinal loop	Bent to less than ½ circle	Bent to ¾ circle	Bent to about ½ circle
Left gonad	Extending beyond distal bend of primary intestinal loop	Barely reaching distal bend of primary intestinal loop	Extending to distal bend of primary intestinal loop
Distribution	Antarctic and Subantarctic	Warm Atlantic America and tropical W. Africa	Off Buenos Aires

Tentacles. Fourteen tentacles were counted, of which four were very large, occupying the dorsal, ventral and mid-lateral positions. The larger tentacles are much branched and at least three times pinnate.

Dorsal tubercle. The dorsal tubercle faces obliquely to the left and rear and has the horns turned inwards.

Branchial sac. Longitudinal branchial bars are arranged as follows on the left side: dorsal line 5 (12) 1 (18) 2 (18) 2 (16) 3 (13) 3 (13) 1 (12) 2 endostyle. The bars on the ventral faces of the folds are stouter than those on the dorsal faces.

I have nothing to add regarding the gut and there were no gonads in this specimen.

Distribution. Antarctic (Graham Land region, McMurdo Bay, Kaiser Wilhelm II Land).

Molgula setigera Ärnbäck f. georgiana n. (Text-fig. 58 A–D)

Diagnosis of form. Differs from the typical form of the species in (1) opening of dorsal tubercle a simple longitudinal slit, (2) long bristle-like hairs of test confined to region of siphons, and (3) several sperm ducts.

Occurrence. St. 159: S. Georgia, 160 m. St. 474: S. Georgia, 199 m.

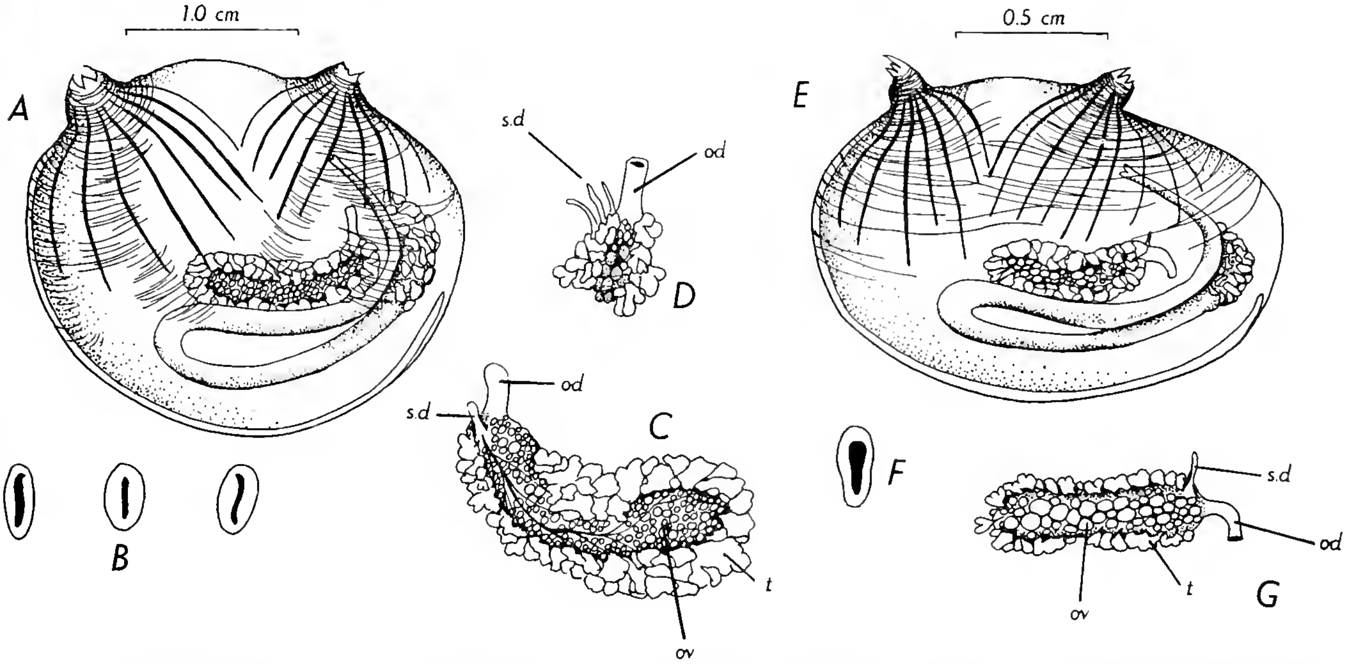
External appearance. There are five specimens of this form, varying in length from 2·5 to 2·8 cm. The shape of the body is roughly ovoid, but its outline is very irregular owing to the great amount of small stones and sand sticking to the test. Only the siphons are free of this covering. The most noticeable feature is a tuft of long stiff bristles round the opening of each siphon. In one of the type specimens of the species described by Ärnbäck (1938), bristles covered almost all the body except the ventral side, but in the others they were sparsely arranged on the sides and dense only on the siphons. In the 'Discovery' specimens the bristles are even more strictly limited to the siphons.

Tentacles. There are twenty-two tentacles in one specimen examined. They have short branches and are at most bi-pinnate.

Dorsal tubercle. The dorsal tubercle in each of four animals has a narrow longitudinal slit-like opening, either straight, slightly sinuous, or very slightly curved (Text-fig. 58 B). This is quite distinct from the C-shaped opening described by Ärnbäck in the typical form of the species.

Branchial sac. The number of branchial folds varies; in one animal there are seven on each side and in another seven on the left and six on the right. There are six to fourteen longitudinal bars on the folds and either one bar or none, between folds.

Gut. In general shape the gut conforms to Ärnbäck's description and figure, but the upwards bend of the rectum is less acute, in the 'Discovery' specimens.



Text-fig. 58. *Molgula setigera* Ärnbäck f. *georgiana* (St. 474): A, specimen with test removed; B, dorsal tubercle; C, gonad with one sperm duct; D, part of gonad with three sperm ducts. *Molgula setigera* f. *marioni* (St. 1563): E, specimen with test removed; F, dorsal tubercle; G, gonad.

Gonads. The form of the gonads (Text-fig. 58 C, D) is fairly constant, resembling that of the type specimens, but the gonoducts are variable. Usually the oviduct (*od.*) is moderately long, but in at least one specimen is quite short; it is always directed up towards the atrial siphon. The sperm ducts (*s.d.*) vary in number and position. There may be from one to five short narrow sperm ducts near the base of the oviduct.

Remarks. These specimens from South Georgia have certain slight but constant differences from Ärnbäck's types of *M. setigera*, and I have hesitated whether to include them in that species or to regard them as a new species. The presence of bristles only on the siphons, and the existence of several sperm ducts are perhaps minor differences, but the condition of the dorsal tubercle is a more important character. There is little doubt that the 'Discovery' material from South Georgia is taken from a genetically different population than that from the Falkland Islands on which the species was founded. However, the remarkable similarities which all the specimens have suggest a very close relationship which is perhaps best denoted by calling the South Georgia population a new form, f. *georgiana*. Should more specimens become available from either Falkland Islands or South Georgia, or from places between, it may be possible to revise the systematic position.

Molgula setigera Ärnbäck f. **marioni** n. (Text-fig. 58 E–G)

Diagnosis of form. Differs from the typical form of the species in (1) opening of dorsal tubercle a simple longitudinal oval slit, (2) long bristle-like hairs of test confined to region of siphons, and (3) oviduct turned down ventrally.

Occurrence. St. 1563: Marion Island, 101–106 m.

External appearance. The single specimen which is almost completely covered with sand and fragments of shell is about 1·6 cm. long. Two prominent groups of bristles, up to 6 mm. long, mark the positions of the siphons. Elsewhere the body has a covering of very much more slender and flexible test hairs.

Tentacles. There are sixteen bi-pinnate tentacles of various sizes.

Dorsal tubercle. The dorsal tubercle has a longitudinal oval opening (Text-fig. 58 F), quite unlike that of the type specimens of *M. setigera*.

Branchial sac. The seven folds on each side of the branchial sac have each from three to ten longitudinal bars, the smallest number being on the most ventral fold. There are no bars between folds.

Gut. No differences were seen between the gut of f. *marioni* and f. *georgiana*.

Gonads. The gonads have the same structure as in the typical form but differ in the downward bend of the short oviduct, which is directed ventrally away from the atrial siphon (Text-fig. 58 G, *od.*).

Remarks. This specimen is clearly related to the specimens from South Georgia representing f. *georgiana* and the typical form of the species from Falkland Islands. But just as clearly it differs, and the degree of difference is best recognized by placing the specimen in a separate form, f. *marioni*.

If my interpretation of the 'Discovery' material is right *M. setigera* presents an interesting case of a species breaking up into separate populations, each inhabiting its own restricted area, and each having slight but constant anatomical differences. Working with preserved material, it is impossible to say whether these isolated populations, in the areas of Falkland Islands, South Georgia and Marion Island respectively, have yet attained complete genetic, as well as geographical, isolation. If it could be shown that they have, then the populations would have to be recognized as separate species, instead of forms.

M. setigera, it has been suggested (van Name, 1945), might prove to be synonymous with *M. kophameli* Michaelsen, from the Strait of Magellan. The two species are similar but the complete absence of bristles in *M. kophameli* does not support the suggestion.

I believe that Kott's (1954) record of *M. setigera* from Enderby Land probably refers to a different species. These Antarctic specimens have, judging from Kott's account, certain features which do not agree with *M. setigera*. The position of the gonads seems to be different, since they diverge from the intestinal loop and the renal sac, whereas in *M. setigera* they are close and parallel to those organs. Also it is not clear if stiff bristles are present on the test.

Distribution (of species including forms). Subantarctic (Falkland Islands, Marion Island), Antarctic (South Georgia).

Molgula sabulosa (Quoy & Gaimard) (Text-fig. 59)

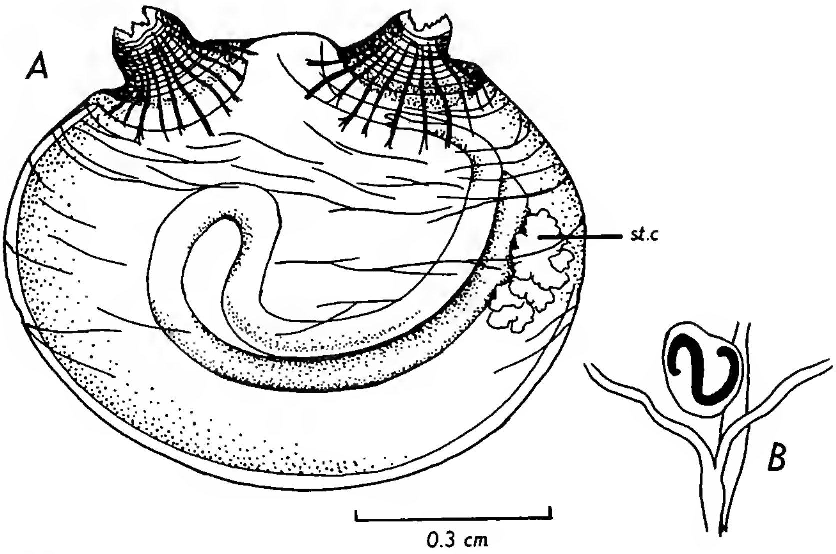
Ascidia sabulosa Quoy & Gaimard, 1834, p. 613, pl. 91, figs. 19–22.
Molgula forbesi Herdman, 1881, p. 236.
Molgula sabulosa Kott, 1952, p. 298, figs. 166–8.

Occurrence. St. 1686: Victoria, Australia, 0 m.

External appearance. There is only one specimen, and this measures 1 by 1 cm. The body is roughly ovoid with the upper surface slightly flattened, and the two short conical siphons situated fairly close together on the flat portion. The sides of the body are also flattened. Short processes of the test are present on the dorsal flattened area, and also along the mid-ventral line. A light coat of sand covers the whole surface of the body.

BODY WALL. Both the test and body wall are quite thin. The internal siphons are conical with toothed borders and prominent radial muscles. Radial longitudinal muscles also pass across the sides of the body, and generally are fewer on the left side than on the right.

TENTACLES. There are twelve quite large pinnate tentacles and, alternating with them, about the same number of very small tentacles.



Text-fig. 59. *Molgula sabulosa* (Quoy and Gaimard): A, specimen with test removed; B, dorsal tubercle.

DORSAL TUBERCLE. The dorsal tubercle has a characteristic horizontal S-shaped slit (Text-fig. 59B) as described by Herdman (1882) and Kott (1952).

BRANCHIAL SAC. In the branchial sac there are seven folds on each side, each fold with about six longitudinal bars. There are no bars between the folds.

GUT. The oesophagus is short and the stomach has a group of short rounded caeca (*st.c.*). The primary intestinal loop is almost closed except at its anterior bend where the limbs are slightly separated. The secondary loop is a flat horizontal semicircle or crescent, with the opening dorsal.

GONADS. No gonads were found in this specimen.

RENAL SAC. The renal sac is gently curved and is not very large.

REMARKS. Kott (1952, 1954) united *M. sabulosa* with *M. pedunculata*, but in spite of certain similarities the species are distinct, as shown in Table 37.

Table 37

	M. sabulosa	*M. pedunculata*
Test processes	Present	Present
Tentacles	12 large and 12 small	12–20
Dorsal tubercle opening	Horizontal S	C-shaped, facing backwards; both horns inrolled
Branchial sac	7 folds; 3–6 bars per fold; 0–1 bar between folds	7 folds; 6–13 bars per fold; 1–4 bars between folds
Gonads	Testis massed at lower, blind, end of ovary	Testis along whole length of ovary
Distribution	S. Australia–Indonesia	Antarctic

Of these characters the shape of the opening on the dorsal tubercle in itself is enough to separate the two species.

The specimen from Enderby Land, which Kott (1954) provisionally identified as *M. sabulosa* does not seem to be this species, but may be *M. pedunculata.*

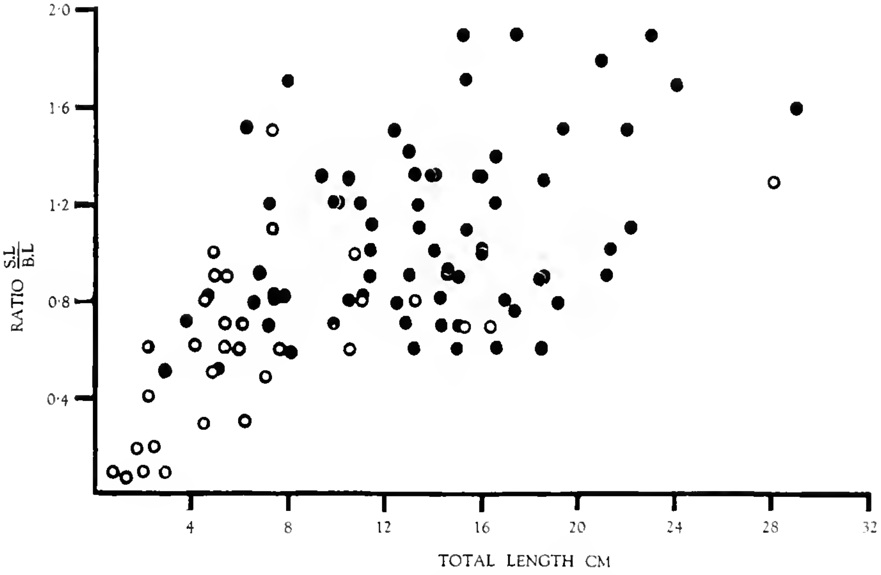
Distribution. Southern Australia; Indonesia.

Genus Ascopera Herdman, 1881

Ascopera gigantea Herdman (Text-figs. 60–62; Pl. VI, figs. 1, 2)

Ascopera gigantea Herdman, 1881, p. 238.
Ascopera pedunculata Herdman, 1881, p. 239.
?*Ascopera bouvetensis* Michaelsen, 1904, p. 188.

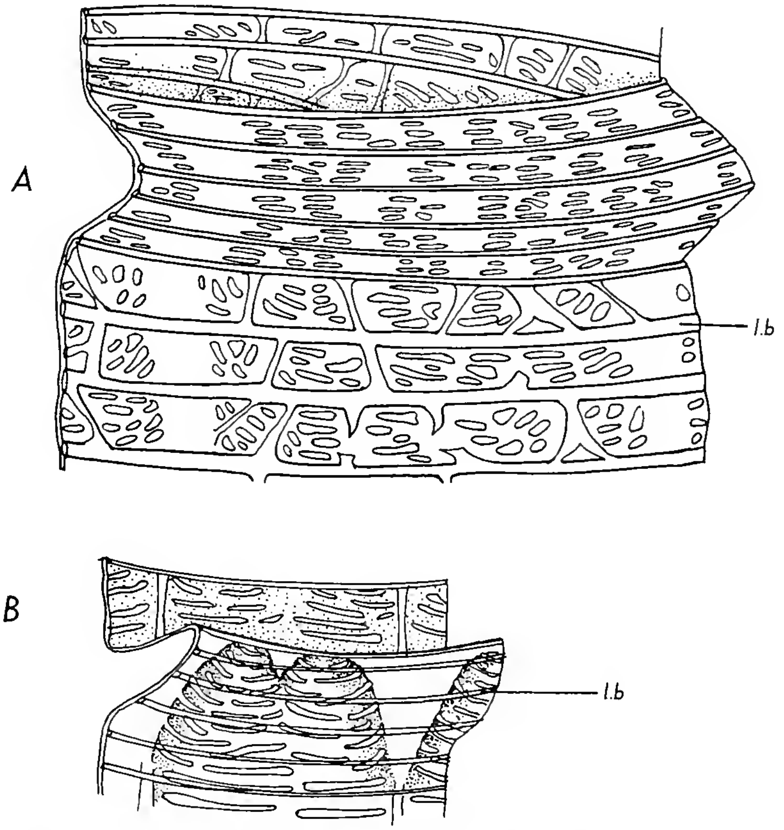
Occurrence. St. 39: S. Georgia, 179–235 m. St. 42: S. Georgia, 120–204 m. St. 45: S. Georgia, 238–270 m. St. 123: S. Georgia, 230–250 m. St. 140: S. Georgia, 122–136 m. St. 152: S. Georgia, 245 m. St. 156: S. Georgia, 200–236 m. St. 159: S. Georgia, 160 m. St. 195: S. Shetlands, 391 m. St. 366: S. Sandwich Islands, 155–322 m. St. 371: S. Sandwich Islands, 99–161 m. St. 1873: Scotia Sea, 210–180 m. St. MS 68: S. Georgia, 220–247 m. St. Deception Islands, S. Shetlands, 25–30 m.



Text-fig. 60. *Ascopera gigantea* Herdman. Relation between the ratio stalk-length/body-length and the total length, in specimens from the S. Sandwich Islands (○) and from S. Georgia (●).

External appearance and the possible separation of *A. gigantea* and *A. pedunculata*. The smallest specimen has a total length of 0·9 cm. and the largest one 28·0 cm. The shape of the body has already been well described (Herdman, 1882; Hartmeyer, 1911; Ärnbäck, 1938), but as it was the main reason for originally separating the species *A. gigantea* and *A. pedunculata*, I shall deal with it in some detail. According to Herdman (1882) the ratio length of stalk to length of body in *A. gigantea* was 1:2 and in *A. pedunculata* about 2·4:1. Text-fig. 60 shows the ratio of stalk length to body length plotted against total length, for all specimens in the 'Discovery' collection from the two areas which yielded most of the material: South Sandwich Islands, and South Georgia. There is a tendency for the smallest specimens to have a relatively shorter stalk, but in specimens over 4 or 5 cm. the correlation between total length and the ratio of stalk to body is weak. Inspection of Text-fig. 60 suggests that the populations from the South Sandwich Islands and South Georgia cannot be separated by a difference in the ratio of stalk to body. This is confirmed by using the coefficient of difference (Mayr, Linsley & Usinger, 1953) to determine how far this character overlaps in the two populations. The level of distinctness of the populations is much below that conventionally recognized as subspecific.[1] It is therefore clear that *Ascopera*, as represented in the rich 'Discovery' material, cannot be separated into two species or even geographical forms. I therefore agree with van Name (1945) that *A. pedunculata* is a synonym of *A. gigantea*.

BRANCHIAL SAC. The irregularity of the stigmata and transverse vessels (Text-fig. 61 A) has been stressed in descriptions of *Ascopera*, but in some specimens, especially young ones, the typical molgulid arrangement of spiral stigmata is readily seen (Text-fig. 61 B). There is also, in small animals, less irregularity in the vessels, many of which are still transverse and unbranched. As in other molgulids, too, the stigmata form infundibula, which rise into the branchial folds to form pouches. Longitudinal bars have the following arrangement in two specimens of moderate size:



Text-fig. 61. *Ascopera gigantea* Herdman (St. 371): A, part of the branchial wall of a large specimen; B, of a small specimen.

(1) dorsal line—5 (12) 3 (8) 7 (7) 4 (9) 6 (9) 8 (5) 6 (9) 3 endostyle.
(2) dorsal line—4 (9) 1 (16) 4 (14) 3 (11) 6 (13) 6 (7) 2 (8) 2 endostyle.

GUT. Yellow glandular tissue on the surface of the stomach extends down each side of the intestine for some distance (Text-fig. 62 A, *gl.*).

GONADS (Text-fig. 62 B). The gonads are long sausage-shaped bodies, each with a central ovary (*ov.*) extending the whole length of the gonad, and a series of testis lobes (*t*) arranged along the sides of the ovary. One terminal oviduct (*od.*) is normally present, pointing towards the atrial siphon, but

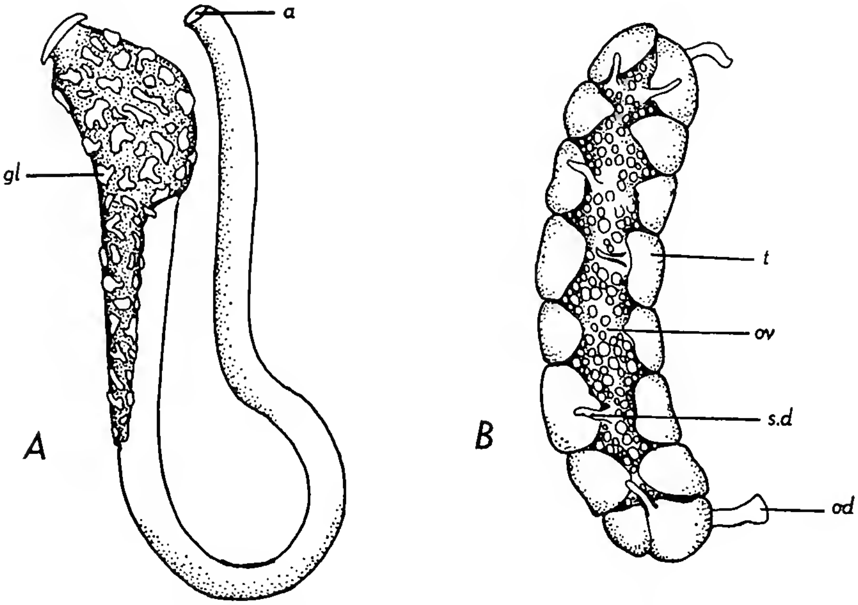
---

[1] Coefficient of distinctness of two populations A and $B = \dfrac{\text{mean}_A - \text{mean}_B}{\text{standard deviation}_A - \text{standard deviation}_B}$. Here the coefficient of distinctness $= \dfrac{1{\cdot}1 - 0{\cdot}6}{0{\cdot}3742 + 0{\cdot}3755} = 0{\cdot}667$, which is much below the conventional level for subspecific distinctness (1·28).

occasionally there is an additional oviduct, at the other end of the gonad. About six short sperm ducts (*s.d.*) are scattered along the mesial surface of the gonad.

Remarks. As I have stated above I see no reason to distinguish between Herdman's two species of *Ascopera*, and the name *A. gigantea* has priority. Michaelsen (1904) described a new species *A. bouvetensis* from three small specimens collected at Bouvet Island. It is very likely that this species should also be referred to *A. gigantea*, from which it seems to differ in nothing but size.

Distribution. Antarctic (Kaiser Wilhelm II Land, Graham region, South Sandwich Islands, South Shetlands, South Georgia, Kerguelen, ?Bouvet Island).



Text-fig. 62. *Ascopera gigantea* Herdman (St. 371): A, gut; B, gonad.

Genus **Paramolgula** Traustedt, 1885

Paramolgula gregaria (Lesson) (Text-fig. 63, Pl. V fig. 2)

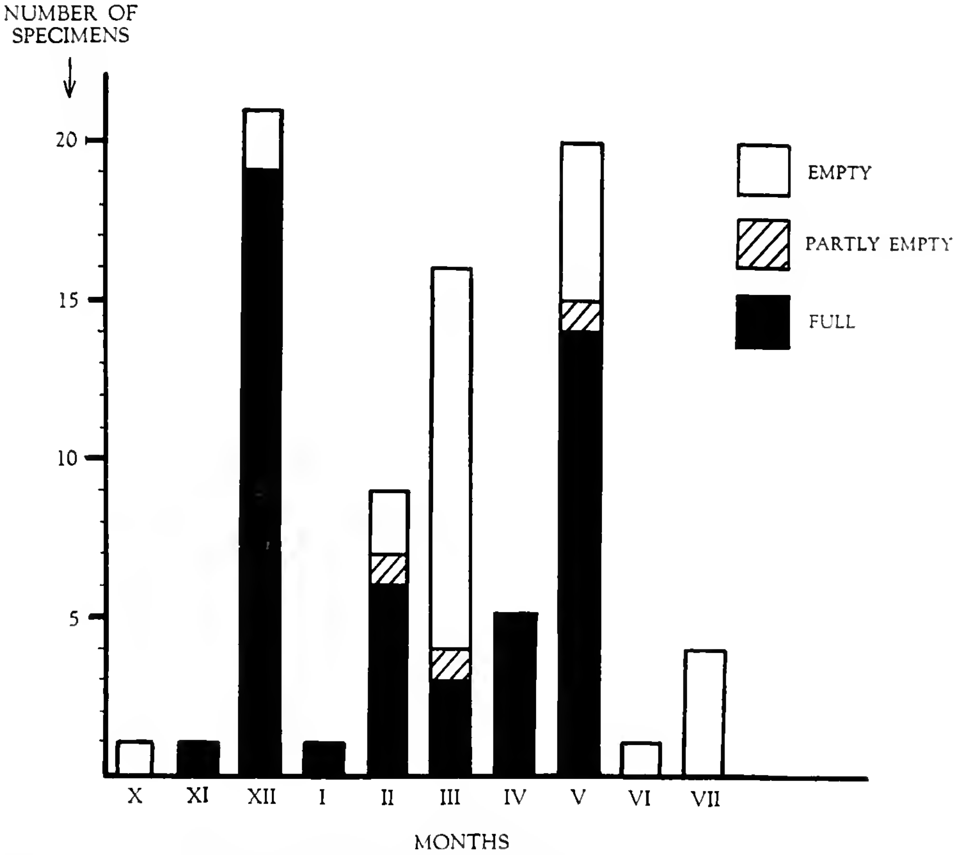
Cynthia gregaria Lesson, 1830, p. 157, pl. 52, fig. 3.
For synonymy see van Name (1945), p. 428.

Occurrence. St. 51: Falkland Islands, 115 m. St. 52: Falkland Islands, 17 m. St. 53: Falkland Islands, 0–2 m. St. 55: Falkland Islands, 10–16 m. St. 56: Falkland Islands, 10·5–10 m. St. 57: Falkland Islands, 15 m. St. 58: Falkland Islands, 1–2 m. St. 1230: Magellan Strait, 27 m. St. 1902: Patagonian Shelf, 50–80 m. St. WS 71: Falkland Islands, 82–80 m. St. WS 72: Falkland Islands, 95 m. St. WS 73: Falkland Islands, 121–130 m. St. WS 79: Patagonian Shelf, 132–131 m. St. WS 88: Patagonian Shelf, 118 m. St. WS 89: Patagonian Shelf, 23–21 m. St. WS 210: Falkland Islands, 161 m. St. WS 222: Patagonian Shelf, 100–106 m. St. WS 243: Patagonian Shelf, 144–141 m. St. WS 756: Falkland Islands, 119–104 m. St. WS 776: Patagonian Shelf, 110–99 m. St. WS 781: Patagonian Shelf, 148 m. St. WS 782: Patagonian Shelf, 141–146 m. St. WS 784: Patagonian Shelf, 170–164 m. St. WS 791: Patagonian Shelf, 97–95 m. St. WS 796: Patagonian Shelf, 108–112 m. St. WS 797: Patagonian Shelf, 115–111 m. St. WS 798: Patagonian Shelf, 49–66 m. St. WS 808: Patagonian Shelf, 110–106 m. St. WS 823: Patagonian Shelf, 80–95 m. St. WS 834: Patagonian Shelf, 27–38 m. St. WS 847: Patagonian Shelf, 57–84 m. St. WS 849: Patagonian Shelf, 137 m. St. WS 861: Patagonian Shelf, 117–124 m. St. WS 863: Patagonian Shelf, 121–117 m. St. WS 864: Patagonian Shelf, 128–126 m. St. MS 71: S. Georgia, 110–60 m.

External appearance. This well-known species requires little additional description as regards external form. The smallest specimen in the collection is 1·1 cm. long and the largest 23·0 cm. Several specimens give no evidence of attachment other than the presence of sand on the test, but in some a number of small pebbles are embedded in the test of the lower part of the body, suggesting that in life these animals were thus anchored to the bottom.

Internal structure. This also has been well described by a number of authors (see especially van Name, 1945). The individual variation in the branchial sac, intestinal curvature, and position of the left gonad in the species are such as to include the characteristics of form *capax* Ärnbäck (1938).

Biology. (*a*) *Breeding.* The annual breeding cycle has been determined by examining all specimens and estimating the state of the gonad, which has been classified as 'full', 'spawning' or 'empty'. These groupings refer to the ovary; 'spawning' means that an appreciable quantity of eggs has been shed from the ovary and the specimen has evidently been taken during its female-spawning period. Animals under about 3 cm. have not been included as they had not yet attained sexual maturity. Text-fig. 63 shows the reproductive state of all animals over 3 cm. long. It seems that most of the spawning takes place in the months of February to May, that the animals are spent during the southern winter, and that the gonad becomes active again in November. No material was available from the months of August and September.



Text-fig. 63. *Paramolgula gregaria* Traustedt. State of the gonad in all specimens, in all years, in relation to the month of the year.

(*b*) *Food.* Specimens were examined from material collected at different times of the year. In all of these there was food in the gut, and at all seasons the food consisted largely of unicellular planktonic algae, mainly under 20 μ in diameter. Diatoms were also present, but less abundant. Occasionally parts of crustacea (amphipods and copepods) were found, and it seemed that these were either alive or recently dead when ingested by the ascidian as the guts of the crustaceans contained recognizable food particles. Inorganic particles, mainly sand grains, were found in only a few specimens and never in great quantity. The food of this ascidian can therefore be said to be principally live plankton rather than organic debris.

REMARKS. The record from St. MS 71 is interesting as it extends the known range of the species as far as South Georgia.

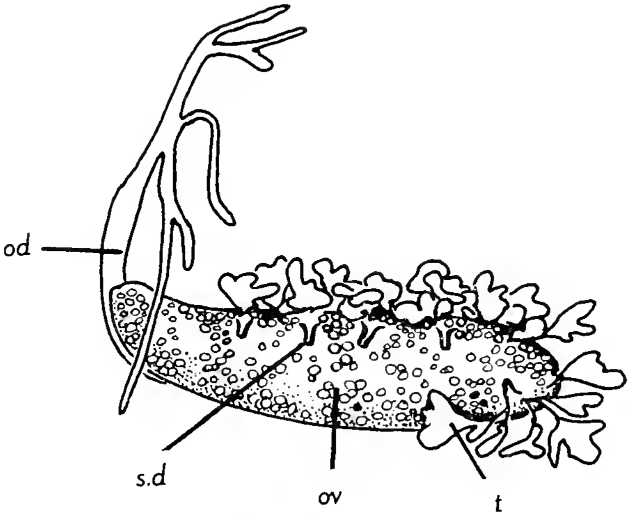
DISTRIBUTION. Antarctic (South Georgia), Subantarctic (Falkland Islands, Patagonian Shelf, Magellan region, coast of Chile).

Genus **Eugyra** Alder & Hancock, 1870

Eugyra kerguelenensis Herdman (Text-fig. 64)

Eugyra kerguelenensis Herdman, 1881, p. 237.
For synonymy see Kott (1954), p. 139.

OCCURRENCE. St. 1941: S. Georgia, 38 m. St. WS 854: Patagonian Shelf, 97 m. St. WS 856: Patagonian Shelf, 104 m.



Text-fig. 64. *Eugyra kerguelenensis* Herdman (St. 1941): Gonad.

EXTERNAL APPEARANCE. The largest specimens are those from the Patagonian Shelf, which reach a greatest diameter of 20 mm. These equal in size the largest yet found, which were described from Kerguelen by Kott (1954). The specimens from South Georgia in the 'Discovery' collections range from 8 to 18 mm. In all specimens the surface of the body has a coat, sometimes not very thick, of moderately long, unbranched hairs to which sand and mud adheres. The body is ovoid to globular. There is generally a sunken area round the siphons, sometimes with four grooves running from its corners as described by van Name (1945).

BODY WALL. Muscles, both longitudinal and circular, are best developed on and near the siphons. There is, in addition, a narrow row of transverse fibres overlying the endostyle, as already described by other authors, but I have found this band to continue in some specimens across the dorsal part of the body and down its posterior surface.

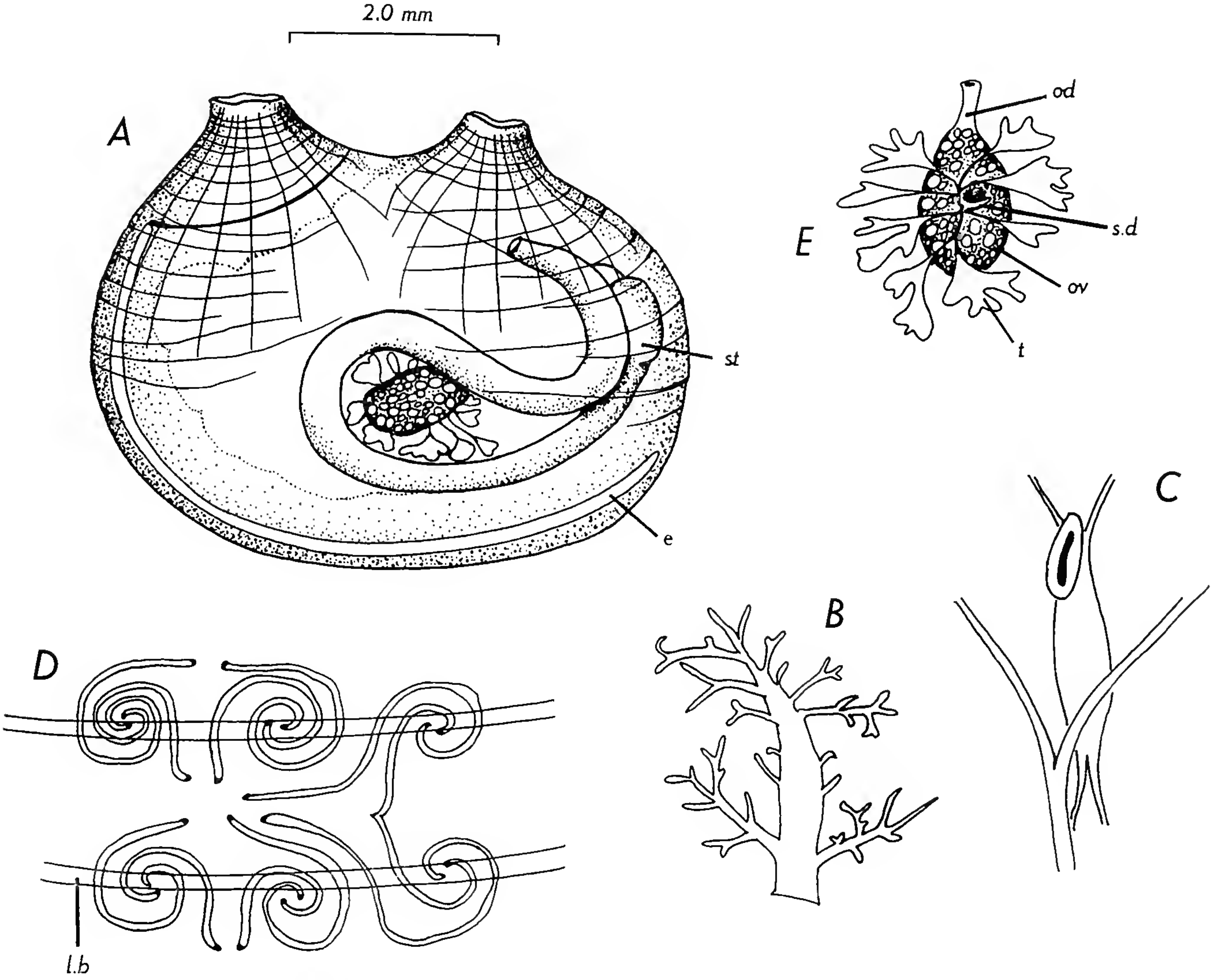
TENTACLES. The oral tentacles usually number only ten to thirteen, even in quite large specimens.

DORSAL TUBERCLE. Van Name (1945) shows and describes the dorsal tubercle as having an 'almost completely closed ring-like opening', but the 'Discovery' animals have a more nearly C-shaped or crescentic slit.

BRANCHIAL SAC. The branchial sac does not differ from previous accounts.

GONADS. The form of the gonads is not exactly that described by Hartmeyer (1912), who stated that the testis follicles are arranged in a complete ring round the ovary. Instead I find that the testis follicles (Text-fig. 64, *t*) are generally confined to the dorsal side and the anterior end of the ovary (*ov.*). In some specimens the oviduct is simple, short and terminal, but in a few of those from South Georgia it is branched in an antler-like fashion (*od.*). I do not know if all the branches have openings. The male openings are on about five small sperm ducts (*s.d.*) arranged along the dorsal margin of the gonad.

DISTRIBUTION. Antarctic (Kerguelen, South Georgia), Subantarctic (off coast of Argentina).



Text-fig. 65. *Eugyra brewinae* sp.n. (St. 936): A, specimen with test removed; B, oral tentacle; C, dorsal tubercle and ganglion; D, part of branchial wall; E, gonad.

Eugyra brewinae sp.n. (Text-fig. 65)

HOLOTYPE. Size: 5 mm. diameter.

DIAGNOSIS OF SPECIES. Body small and covered with sand. Test and body wall very thin and transparent. Dorsal tubercle a simple longitudinal slit. Branchial sac with six longitudinal bars on each side. Stigmata in regular double spirals. Gonad on left side only, within primary intestinal loop, consisting of central ovary and radially arranged, branched testis-lobes. Renal sac small, close to stomach.

Occurrence. St. 936: North Island, New Zealand, 50–57 m.

External appearance. The specimens are ovoid, and have a greatest diameter ranging from 3 to 6 mm. A complete covering of sand conceals the body, and, at least in the preserved state, no siphons are visible externally.

Test. The test is very thin, flexible and transparent, when the coat of sand grains has been removed.

Body wall. The body wall also is thin and has narrow muscles, consisting of circular strands mainly on the upper half of the body, and longitudinal strands radiating from the siphons and extending about half way across the body.

Tentacles. There are ten to twelve tentacles of at least two sizes, the larger ones being tri-pinnate and quite bushy (Text-fig. 65B).

Dorsal tubercle. The dorsal tubercle, which lies below the anterior end of the ganglion, is small with a simple longitudinal slit, either straight or very slightly curved (Text-fig. 65C).

Branchial sac. In the branchial sac there are six longitudinal bars, more closely spaced in the dorsal part of the sac, but no folds. Below each bar lies a longitudinal row of infundibula, and in addition there are a few infundibula between the dorsal bar and the dorsal lamina, and a few between the ventral bar and the endostyle, in each case at the antrior end of the branchial sac. The infundibula project only very slightly from the surface of the branchial wall. Each infundibulum consists of two parallel spiral stigmata (Text-fig. 65D). The dorsal lamina is a plain narrow membrane.

Gut. The oesophagus is short and leads to the small barrel-shaped stomach (Text-fig. 65A, *st.*) which is scarcely wider than the intestine. The proximal part of the intestine is horizontal, and the distal part together with the rectum make an S-shaped bend, leaving an open area at the bend of the primary loop in which the single gonad is accommodated. The anus has a plain margin.

Gonad. The gonad consists of a central sac-shaped ovary (Text-fig. 65E, *ov.*) with, applied to its mesial side, a radially arranged group of eight to eleven testis lobes (*t*). These lobes are slightly branched and may project far enough from the sides of the ovary to lie against the surface of the intestine. The oviduct (*od.*) is short and projects upwards towards the atrial siphon. A single short sperm duct (*s.d.*) is placed centrally within the rosette of testis lobes.

Renal sac. The renal sac is small but quite conspicuous owing to its almost white colour. It lies close against the stomach, on its postero-ventral side.

Remarks. This small sand-covered species, which could easily be overlooked, does not seem to have been found or recognized in previous collections.

Distribution. North end of North Island, New Zealand.

Eugyra ärnbäckae sp.n. (Text-fig. 66; Pl. IV, fig. 3, Pl. VI, fig. 6, 7)

Holotype. Size: body 12 mm., stalk, 100 mm.

Diagnosis of species. Body with a long slender stalk, arising near the oral siphon. Tentacles about sixteen, slightly branched. Dorsal tubercle with a simple longitudinal or oblique opening. Branchial sac with seven longitudinal bars on each side. Stigmata in double spirals. Right gonad above renal sac; left gonad in secondary intestinal loop.

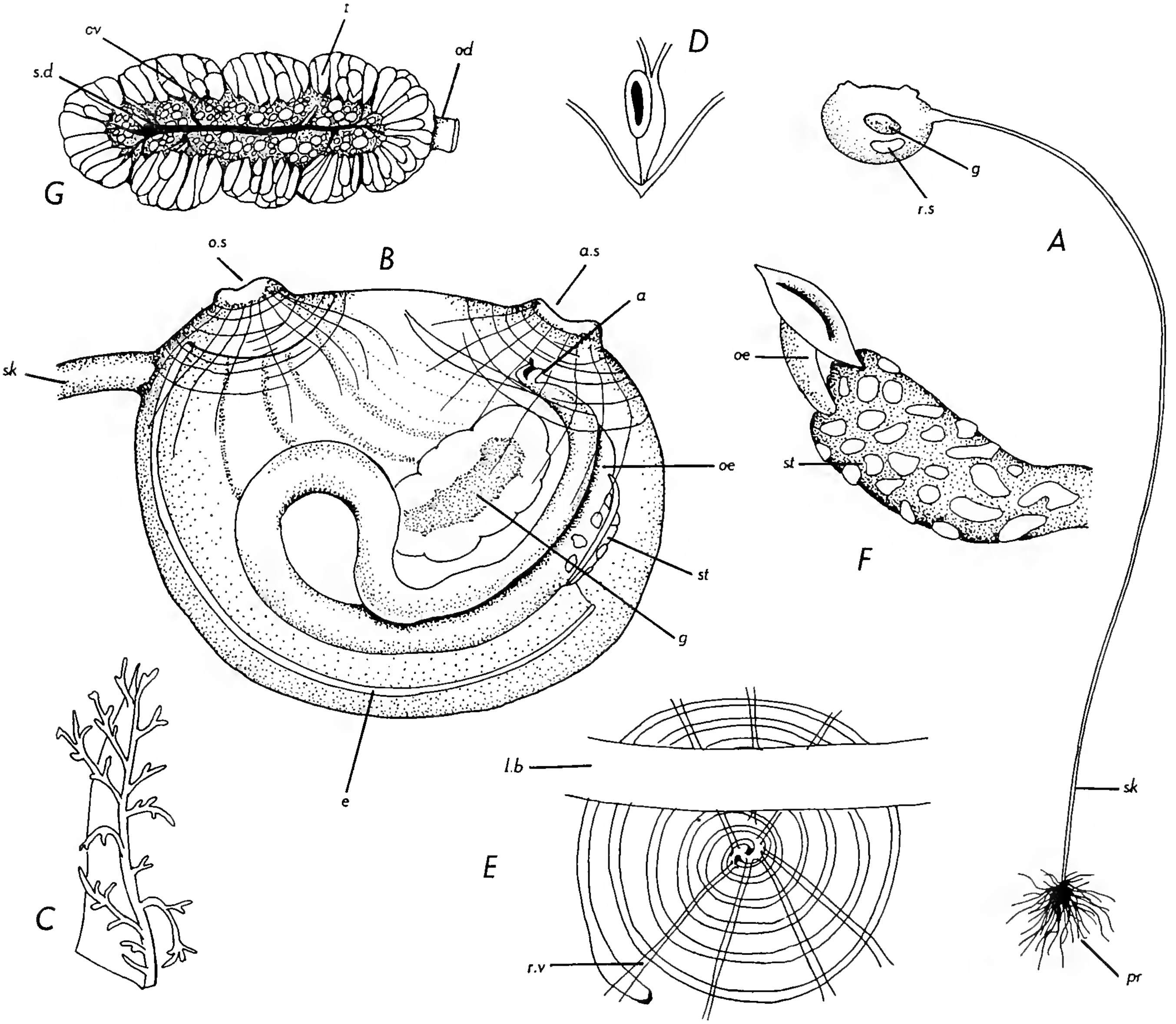
Occurrence. St. 366: S. Sandwich Islands, 155–322 m.

External appearance (Text-fig. 66A, B; Pl. IV, fig. 3). The body is small and ovoid with the low conical siphons situated far apart on the dorsal side. A long and very slender stalk (Text-fig. 66B, *sk.*) arises from the anterior end of the body, a little below the oral siphon (*o.s.*). The lengths of body and stalk of six specimens are:

Body length (mm.)	12	10	9	8	8	7
Stalk length (mm.)	95	75	92	87	65	62

The stalk is of nearly uniform diameter down to its lower end, where it bears a dense tuft of hair-like processes. A few sand particles adhere to the body and to the basal test-hairs of the stalk. The test of the body is very thin and almost completely transparent.

Body wall. The body wall is very thin, with slender muscles, which are mainly circular strands concentrated round the siphons. A few longitudinal strands radiate from the siphons across the sides of the body.



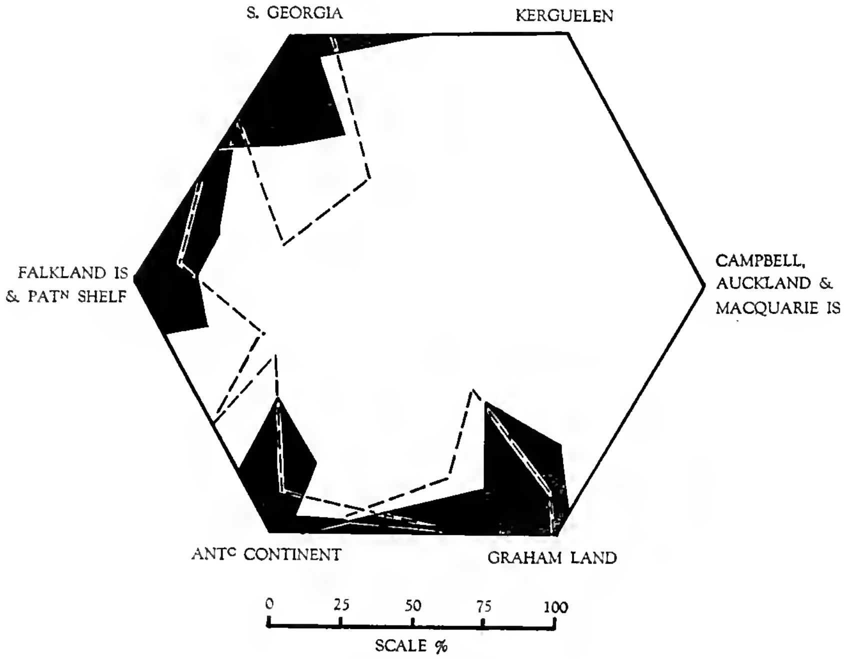
Text-fig. 66. *Eugyra ärnbäckae* sp.n. (St. 366): A, intact specimen from the right; B, body from the left; C, oral tentacle; D, dorsal tubercle; E, a stigma; F, stomach; G, gonad.

Tentacles. There are eight large oral tentacles (Text-fig. 66C) and eight smaller ones alternating with them, and sometimes a few still smaller ones can be seen. The tentacles have a stout tapering stem, a few primary branches and some short secondary branches.

Dorsal tubercle. The dorsal tubercle is small with a straight or slightly curved slit placed in a longitudinal or oblique direction (Text-fig. 66D). The dorsal tubercle covers the anterior part of the small ganglion.

Branchial sac. There are no folds in the branchial sac, which has on each side seven tall longitudinal bars. Under each longitudinal bar is a row of flat stigmata (Text-fig. 66E). The stigmata are arranged in double spirals meeting at the centre, the total number of turns being six or seven in large stigmata. Some stigmata form unbroken spirals but others are broken at intervals. Radial vessels (*r.v.*) numbering up to about twelve originate at the centre of each stigma, some of them passing dorsally and some ventrally to join the corresponding vessels of the adjacent stigmata. The dorsal lamina has an undivided border and becomes gradually wider towards the posterior end of the branchial sac.

GUT. The oesophagus is short and curved (Text-fig. 66B, F, *oe.*), and the stomach (*st.*) wider than the rest of the gut and about twice as long as wide. Its surface is marked with many low rounded swellings. The intestinal loop is open only at its distal part. The rectum bends upwards and forwards to end below the atrial siphon. The anus (*a.*) has a two-lipped opening.



Text-fig. 67. Affinities of ascidian faunas in the Discovery Collections. Four of the corners of the figure represent the four faunal areas: 1, Antarctic Continent; 2, Graham Land; 3, S. Georgia and 4, the Falkland Islands and the Patagonian Shelf. In each area the percentage of species found also in the other areas is indicated by the height of the peak pointing to the other area. Black polygons represent ascidian species. Clear polygons enclosed by broken lines represent sponge species and are based on figures given by Burton (1932).

GONADS. There is one gonad on each side of the body, that of the left side lying a little dorsal to the gut, in the secondary intestinal loop. The right gonad (Text-fig. 66A, *g*) lies dorsal to the renal sac. Each gonad (Text-fig. 66G) is sausage-shaped or ovoid and consists of the ovary (*ov.*) extending the whole length of the gonad, and the testis (*t.*) in the form of groups of follicles arranged round the sides and ends of the ovary. There is a single short terminal oviduct (*od.*) and usually two male openings on short tubes (*s.d.*), arising from the mesial face of the gonad.

RENAL SAC. The renal sac is a short slightly curved body on the lower half of the right side (Text-fig. 66A, *r.s.*).

FEEDING MECHANISM. The branchial sac contains a mixture of sand grains, small inorganic particles, whole and broken diatoms and small algal cells (Pl. VI, fig. 6). Sand grains and most of the other inorganic particles are, however, absent from the stomach and intestine (Pl. VI, fig. 7) indicating that there is some sorting mechanism. The mechanism is probably in the oesophagus which appears to accept food particles and reject sand grains and other particles not of food value. The nature of this mechanism is unknown, and its operation does not seem to depend solely on the size of the particles, because diatoms are accepted which are as large as the sand grains that are rejected. Possibly the angular outline or the inorganic nature of the sand grains allows them to be detected and prevented from passing to the stomach.

REMARKS. This new species does not fit readily into any of the existing genera of the Molgulidae. It is, however, in fairly good agreement with *Eugyra* as defined by Michaelsen (1915), Hartmeyer (1923) and van Name (1945) differing principally in (1) the flat instead of conical stigmata, and (2) the position of the left gonad in the secondary instead of the primary gut-loop. The structure of the branchial sac is in general that of a *Eugyra*. Characteristically *Eugyra* has the left gonad within the primary gut loop, but in some species it is only partially within the loop. The condition in *E. ärnbäckae* therefore represents a further stage in the shifting of the gonad out of the primary loop. The possession of a stalk, while not common in the genus, is known also in the Arctic species *E. pedunculata* Traustedt.

DISTRIBUTION. Antarctic (South Sandwich Islands).

GEOGRAPHICAL DISTRIBUTION

The ascidians have certain biological similarities to the sponges, particularly the sessile habit of the adult, and the short pelagic life of the larva which lasts for about a day in both groups. These are two characters greatly influencing the geographical spread of species, and it is therefore of interest to analyse the distribution of the ascidians in the same way as Burton (1932) has done for the Antarctic sponges. Table 38 gives the geographical distribution of all the ascidian species identified in the 'Discovery' collections.

The three main Antarctic and Subantarctic areas in which ascidians were collected are (1) the Graham Land region, (2) South Georgia, and (3) the Falkland Islands and Patagonian Shelf. For each of these areas and also for the remaining part of the Antarctic continent, I have shown below the numbers of species which are also found in the other principal Antarctic and Subantarctic regions:

Antarctic continent, excluding Graham Land region, number of species		23
Of these, number also at	Graham Land	20
	S. Georgia	11
	Falkland Islands and Patagonian Shelf	5
	Kerguelen	6
	Campbell, Auckland and Macquarie Islands	2
Graham Land region, number of species		23
Of these, number also at	Antarctic continent excluding Graham Land region	20
	South Georgia	12
	Falkland Islands and Patagonian Shelf	7
	Kerguelen	7
	Campbell, Auckland and Macquarie Islands	2
South Georgia, number of species		32
Of these, number also at	Antarctic continent excluding Graham Land	12
	Graham Land	12
	Falkland Islands and Patagonian Shelf	15
	Kerguelen	14
	Campbell, Auckland and Macquarie Islands	3
Falkland Islands and *Patagonian Shelf*, number of species		24
Of these, number also at	Antarctic continent excluding Graham Land region	5
	Graham Land	7
	South Georgia	15
	Kerguelen	8
	Campbell, Auckland and Macquarie Islands	5

Table 38. *Distribution of species*

Species	*Antarctic Continent (excluding Graham Land)*	*Graham Land*	*South Shetlands*	*South Orkneys*	*South Georgia and Shag Rocks*	*South Sandwich Islands*	*Falkland Islands and Patagonian Shelf*	*Magellan region and Tierra del Fuego*	*Kerguelen*	*Campbell, Auckland and Macquarie Islands*	*New Zealand*	*Further distribution*
Aplidium circumvolutum	.	+	+	.	?+	.	+	.	+	.	+	.
A. fuegiense	.	.	.	.	+	.	+	+	.	.	.	.
A. variabile	.	.	.	.	+	.	+	.	+	.	.	.
A. falklandicum sp.n.	.	+	.	+	+	.	+	.	.	.	.	.
A. radiatum	+	+	.	+	+	.	.	.	.	.	.	.
A. caeruleum	+	+	+	.	.	.	.	.	.	.	.	?Marion Island
A. stanleyi sp.n.	.	.	.	.	.	.	+	.	.	.	.	.
A. quadrisculcatum sp.n.	.	.	.	.	.	.	.	.	.	.	+	.
A. seeligeri sp.n.	.	.	.	.	.	.	.	.	.	.	+	.
Synoicum adareanum	+	+	+	.	+	.	.	.	+	.	.	.
S. georgianum	.	.	.	.	+	.	+	.	.	.	.	.
S. giardi	.	.	.	.	+	.	.	.	+	.	.	.
S. kuranui	.	.	.	.	.	.	.	.	.	.	+	.
Aplidiopsis discoveryi sp.n.	.	.	.	.	.	.	.	.	.	.	+	.
Protopolyclinum pedunculatum sp.n.	.	.	.	.	.	.	.	.	.	.	+	.
Ritterella vestita sp.n.	.	.	.	.	.	.	.	.	.	.	+	.
Didemnum studeri	.	.	.	.	+	.	+	+	+	+	.	Stewart Island, Tasmania, Gough Island
D. biglans	+	+	.	.	.	.	.	.	.	.	.	.
D. trivolutum sp.n.	.	.	.	.	.	.	+	.	.	.	.	.
Leptoclinides diemenensis	.	.	.	.	.	.	.	.	.	.	+	.
Trididemnum auriculatum	.	.	.	.	.	.	+	+	.	.	.	Chile
Podoclavella cylindrica	.		.	.	.	.	.	.	.	.	.	W. and S. Australia
P. kottae sp.n.	.	.	.	.	.	.	.	.	.	.	+	.
Clavelina claviformis	.	.	.	.	.	.	.	.	.	.	+	E. Australia
Sycozoa sigillinoides	+	+	.	+	.	.	+	+	+	+	.	Southern Australia
S. georgiana	.	.	.	.	+	?+	.	.	.	.	.	.
S. anomala sp.n.	.	.	.	.	.	.	.	.	.	.	+	.
Distaplia colligans	.	.	.	+	+	.	.	.	.	.	.	.
D. cylindrica	+	+	.	.	+	+	+	+	.	.	.	.
Hypsistozoa fasmeriana	.	.	.	.	.	.	.	.	.	.	+	.
Cystodytes dellechiajei	.	.	.	.	.	.	+	.	.	.	+	Widely distributed in warm waters of the world
C. dellechiajei f. *antarctica*	.	+	.	.	.	.	.	.	.	.	.	.
Atapozoa marshi	.	.	.	.	.	.	.	.	.	.	+	Western Australia
Tylobranchion speciosum	+	+	+	.	+	+	+	.	.	.	.	.
Ascidia translucida	.	.	.	.	+	.	.	.	+	.	.	.
A. challengeri	+	+	+	+	+	.	.	.	+	.	.	Bass Strait
A. interrupta	.	.	.	.	.	.	.	.	.	.	.	East coast tropical America; West Africa

Table 38 (*cont.*)

Species	*Antarctic Continent (excluding Graham Land)*	*Graham Land*	*South Shetlands*	*South Orkneys*	*South Georgia and Shag Rocks*	*South Sandwich Islands*	*Falkland Islands and Patagonian Shelf*	*Magellan region and Tierra del Fuego*	*Kerguelen*	*Campbell, Auckland and Macquarie Islands*	*New Zealand*	*Further distribution*
A. sydneiensis	.	.	.	.	.	.	.	.	.	.	.	Widely distributed; warm and temperate waters of the world
Agnesia glaciata	.	.	.	.	.	.	.	+	.	.	+	South Africa
Caenagnesia bocki	+	+	.	.	+	.	.	.	.	.	.	.
Corella eumyota	+	+	.	.	.	.	+	+	.	+	+	South Africa; St. Paul; South West Australia; Tasmania
?Botryllus separatus	.	.	.	.	.	.	.	.	.	.	+	Indonesia
Polyzoa opuntia	.	.	.	.	+	.	+	+	+	.	.	Heard Island
P. reticulata	.	.	.	.	+	.	+	+	+	+	.	.
Alloeocarpa incrustans	.	.	.	.	+	.	+	+	.	.	.	.
Amphicarpa diptycha	.	.	.	.	.	.	.	.	.	.	.	Western and Southern Australia; Tasmania
Cnemidocarpa pfefferi	.	.	+	.	+	.	.	.	.	.	.	.
C. nordenskjöldi	.	.	.	.	.	.	+	+	.	.	.	.
C. drygalskii	+	+	.	.	.	.	.	.	.	.	.	.
C. verrucosa	+	+	+	.	+	+	+	.	+	.	.	.
C. tricostata sp.n.	.	.	.	.	+	.	.	.	.	.	.	.
Styela schmitti (including f. *simplex*)	.	.	.	.	.	.	.	+	.	.	.	Off Uruguay, South America
S. insinuosa	+	.	+	.	+	.	.	.	.	.	.	.
S. magalhaensis	+	.	.	.	+	.	.	+	.	.	.	?South coast Chile; south coast Argentine
S. paessleri	.	.	.	.	.	.	+	+	.	.	.	.
S. partita	.	.	.	.	.	.	.	.	.	.	.	Warm Atlantic American coast; English Channel to West Africa; Mediterranean; Ascension Island; Japan
Pyura stolonifera	.	.	.	.	.	.	.	.	.	.	.	South Africa; South Australia; Tahiti
P. setosa	+	+	.	+	.	.	.	.	.	.	.	.
P. discoveryi	+	+	+	.	+	.	.	.	.	.	.	.
P. squamata	+	+	.	.	.	.	.	.	.	.	.	.
P. legumen	.	.	.	.	.	.	+	+	.	.	.	.
P. georgiana	.	.	.	.	+	.	.	.	.	.	.	North coast Argentine
P. bouvetensis	?+	+	+	.	.	.	.	.	.	.	.	Bouvet Island
P. jacatrensis	.	.	.	.	.	.	.	.	+	+	.	Indonesia; West Australia; Tasmania; Marion Island
P. vittata	.	.	.	.	.	.	.	.	.	.	.	Warm East Atlantic coast America; West Africa; Japan; Ascension Island
Herdmania momus	.	.	.	.	.	.	.	.	.	.	.	Widely spread in warm waters of the world

Table 38 (*cont.*)

Species	*Antarctic Continent (excluding Graham Land)*	*Graham Land*	*South Shetlands*	*South Orkneys*	*South Georgia and Shag Rocks*	*South Sandwich Islands*	*Falkland Islands and Patagonian Shelf*	*Magellan region and Tierra del Fuego*	*Kerguelen*	*Campbell, Auckland and Macquarie Islands*	*New Zealand*	*Further distribution*
Bathypera splendens	+	+	.	.	.	.	.	.	.	.	.	.
Molgula pedunculata	+	+	.	.	+	.	.	.	+	.	.	.
M. falsensis	.	.	.	.	.	.	.	.	.	.	.	South Africa
M. platei	.	.	.	.	.	.	.	.	.	.	.	Coastal waters of Chile
M. malvinensis	.	.	.	.	+	.	+	.	+	+	.	.
M. bacca	+	+	.	.	.	.	.	.	.	.	.	.
M. setigera (including forms)	.	.	.	.	+	.	+	.	.	.	.	Marion Island
M. sabulosa	.	.	.	.	.	.	.	.	.	.	.	South Australia; Indonesia
Ascopera gigantea	+	+	.	.	+	+	.	.	+	.	.	?Bouvet Island
Paramolgula gregaria	.	.	.	.	+	.	+	+	.	.	.	Coast of Chile
Eugyra kerguelenensis	.	.	.	.	+	.	.	.	+	.	.	Off coast of Argentine
E. brewinae sp.n.	.	.	.	.	.	.	.	.	.	.	+	.
E. ärnbäckae sp.n.	.	.	.	.	.	+	.	.	.	.	.	.

Text-fig. 67 presents the affinities of the ascidian faunas as shown by the species in the 'Discovery' collection, and for comparison the sponge faunas of the same areas based on Burton's (1932) figures.

Most of the species of ascidians found round the main part of the Antarctic continent also occur in the Graham Land region, but progressively fewer in South Georgia, Kerguelen, the Falkland–Patagonian region, and the Campbell–Auckland–Macquarie Islands region.

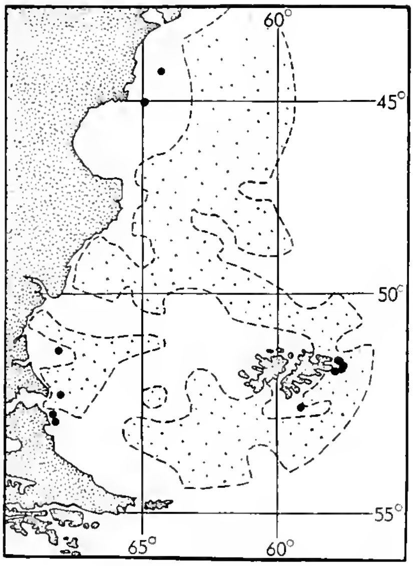
Similarly, amongst the species of the Graham Land region, a high proportion is also known from the rest of the Antarctic continent, and fewer from the remaining regions.

Of the South Georgia species nearly half are also known from the Falkland–Patagonian region and also from Kerguelen, and smaller proportions from elsewhere.

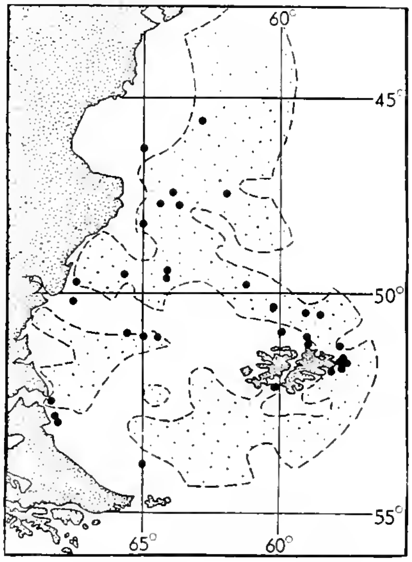
Amongst the species from the Falkland–Patagonian region more than half also occur in South Georgia.

The ascidian faunas therefore show the following affinities. In the high Antarctic the closest ties are between the main part of the continent and the Graham Land region, which is no more than a peninsula projecting into somewhat lower latitudes, but still well south of the Antarctic convergence. The Antarctic continent including Graham Land, shows its closest affinity with South Georgia. The latter region, however, has more species in common with the Subantarctic Falkland–Patagonian region. So far as ascidians are concerned South Georgia occupies a position intermediate between the true Antarctic and the true Subantarctic, a fact probably resulting from the colonization of South Georgia from South America and the Falkland Islands via Burdwood Bank on the one hand and from Graham Land via the South Orkney Islands on the other hand. South Georgia lies in the path of material carried by the West Wind Drift from the southern end of South America and from the northern end of the Graham peninsula.

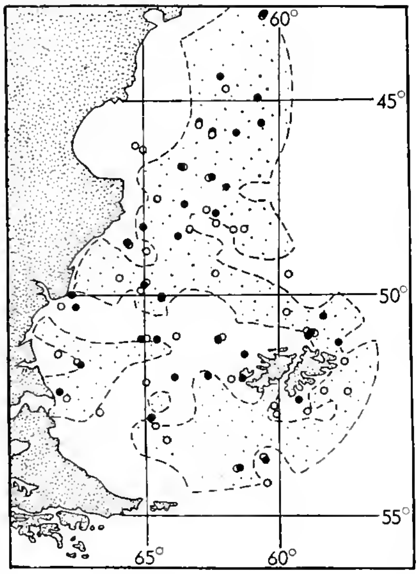
The affinities of the sponge faunas (Text-fig. 67) agree quite well with those shown by the ascidian faunas. But the sponge faunas of South Georgia and the Falkland–Patagonian region have more in common with those of the Antarctic continent (including Graham Land) than is the case in ascidians.



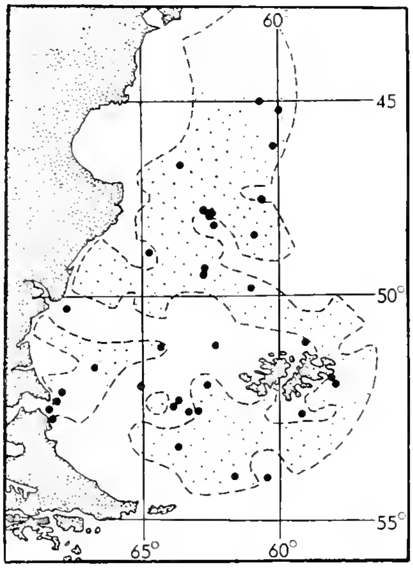
Text-fig. 68



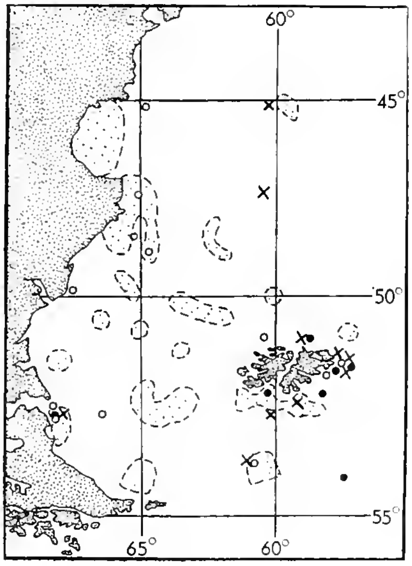
Text-fig. 69



Text-fig. 70



Text-fig. 71



Text-fig. 72

Text-fig. 68. *Pyura legumen* ●. Occurrence on the Patagonian Shelf. Stippled areas indicate the nature of the bottom (after Matthews, 1934), 76–98% fine sand.

Text-fig. 69. *Paramolgula gregaria* ●. Occurrence on the Patagonian Shelf. Stippled areas indicate the nature of the bottom (after Matthews, 1934), 76–98% fine sand.

Text-fig. 70. *Aplidium fuegiense* ○ and *A. falklandicum* ●. Occurrence on the Patagonian Shelf. Stippled areas indicate the nature of the bottom (after Matthews, 1934), 76–98% fine sand.

Text-fig. 71. *Sycozoa sigillinoides* ●. Occurrence on the Patagonian Shelf. Stippled areas indicate the nature of the bottom (after Matthews, 1934), 76–98% fine sand.

Text-fig. 72. *Polyzoa opuntia* ○, *P. reticulata* ● and *Alloeocarpa incrustans* ×. Occurrence on the Patagonian Shelf. Stippled areas indicate the nature of the bottom (after Matthews, 1934), 'large fragments, 15 mm. and over'.

LOCAL DISTRIBUTION

The abundance of some species on the Patagonian Shelf and round the Falkland Islands allows closer investigation of the factors which control their local distribution.

Pyura legumen and *Paramolgula gregaria* are two species of simple ascidian commonly collected in the area. Text-figs. 68 and 69 show the stations at which they were taken. *P. legumen* occurred close to the coast of South America and of the Falkland Islands, but not on the main part of the Patagonian Shelf. *P. gregaria* was found to be widely distributed on the Shelf, occupying not only the main part but also the inshore areas where *P. legumen* occurred.

P. legumen has a stalk and requires for its attachment firm solid objects. Matthews (1934) has shown that such objects are common only in certain areas and are absent over most of the main part of the Shelf, from which we have seen *P. legumen* also to be absent.

P. gregaria is a stalkless species with a broad base and is able to live on a substratum of fine deposits; its presence over a large part of the shelf corresponds to the wide distribution of fine deposits. This explanation of the different occurrence of these two species seems more satisfactory than any based on differences in depth, temperature or water currents.

Most species of the family Polyclinidae live attached to hard substrata, but on the Patagonian Shelf there are species which lie on the surface of the sand only lightly attached or quite free. *Aplidium fuegiense* and *A. falklandicum* may be taken as typical of these, and their wide distribution on the shelf is shown in Text-fig. 70. Most of the records are from stations where the bottom material consists largely of fine sand. *A. fuegiense* is a particularly successful species in the area, to judge from its abundance, and it has a shape modified to suit its habitat. The colony is long and narrow, the expanded base lying slightly embedded in the sand and the tapering distal part floating freely in the water. *A. falklandicum*, with a similar local distribution, sometimes has a similarly shaped colony, but is at least occasionally solidly attached.

In the family Clavelinidae *Sycozoa sigillinoides* has a distribution on the Patagonian Shelf (Text-fig. 71) similar to that of the two polyclinid species. The form of its colony is quite different, however, the heads, which alone contain the zooids, being borne on stalks, but the result is the same, namely the zooids are kept free of the sandy bottom.

Three compound species of the family Styelidae occur in the Patagonian region: *Polyzoa opuntia*, *P. reticulata* and *Alloeocarpa incrustans* (Text-fig. 72). All three species need solid firm objects for attachment and tend to be restricted to coastal waters where such objects are common, or to other areas with gravel and large fragments. *P. opuntia* in particular, which has large heavy colonies of upright habit, and a small basal area, requires a firm substratum. The fact that this species and *Pyura legumen* have similar local distributions may be related to their similar needs in this respect. *Polyzoa reticulata*, unlike *P. opuntia*, forms colonies spreading horizontally over flat surfaces, and the two species, which are closely related, occupy slightly different ecological niches.

GEOGRAPHICAL SPECIATION

Among Antarctic and Subantarctic ascidians there are several instances of geographical speciation. In some cases the process has led to the complete separation of species, each species occupying a different region. An example of this is the group of closely related species *Pyura legumen*, *P. georgiana* and *P. bouvetensis*. Anatomical features show *P. georgiana* and *P. bouvetensis* to be a pair of closely related species and *P. legumen* to be more distantly related to both. The common ancestor of all three species probably first split into a Subantarctic population which became *P. legumen* and an Antarctic population which later divided into *P. georgiana* and *P. bouvetensis*. The geographical separation of the three species now seems to be complete, although they occupy adjacent areas. Ecological differences also exist and the percentage distribution of the 'Discovery' specimens at different depths is given in Table 39, showing that the more southern species inhabit progressively greater depths.

Table 39

	Depth (metres)			
	0–100	100–200	*More than* 200	
P. legumen	100	0	0	Percentage distribution
P. georgiana	18	64	18	
P. bouvetensis	0	12	88	

The same family provides another example of geographical speciation. *Pyura stubenrauchi* and *P. setosa* appear to represent respectively the Subantarctic and Antarctic species derived from a common stock, and their geographical ranges do not overlap.

In the family Styelidae there are also instances of the same process. The little-known species *Styela schmitti* shows slight but apparently constant structural differences in specimens from Montevideo and from Cape Horn, which I believe to represent geographical forms. As the species has been collected only twice, however, it is not possible to say with certainty whether its distribution is continuous, with the observed anatomical differences representing different points of a cline, or whether it is discontinuous with separate geographical subspecies.

I have already mentioned the difficulty of deciding if *Cnemidocarpa nordenskjöldi* and *C. drygalskii* are different species. If they are, and I have given reasons for thinking them to be separate, they constitute a pair of very closely related species, one species occurring only in the Subantarctic and the other only in the Antarctic.

The family Molgulidae, as represented in the 'Discovery' collections, gives one example of populations of a species from different areas showing structural differences. This is *Molgula setigera*, with distinct forms from South Georgia and Marion Island and the typical form from the Falkland Islands.

Conditions in the Antarctic and Subantarctic seem to have favoured the geographical speciation of ascidians. The same has been found in other groups (see Ekman, 1953), and has been explained by the long geological isolation of the Antarctic Continent. The position of the Antarctic Convergence, coinciding as it does with the barrier formed by deep water, must have been effective in maintaining the separation of populations upon which geographical speciation depends.

The presence of isolated islands near the Antarctic Convergence also encourages the breaking up of populations into groups which become genetically isolated as subspecies or species.

THE SIZE OF SOUTH POLAR ASCIDIANS

The size attained by an ascidian depends mainly on the water temperature and the food supply. In a species adapted to cold water it is the food supply which limits growth. Ascidians feed largely on plankton, which is abundant in Antarctic waters, so it is probable that the rich phytoplankton is the primary cause of the large size which certain south polar species attain.

A survey of the 'Discovery' material gives little evidence of an increase in the size of specimens of one species from areas nearer the south pole. In fact not many species cross the Antarctic Convergence so it is difficult to find species in which this tendency might appear. *Aplidium circumvolutum*, however, does increase in size towards the pole. But in *Distaplia cylindrica*, which occurs in both the Subantarctic and the Antarctic, almost equally large specimens were taken from South Georgia and the Patagonian Shelf.

Closely related species inhabiting the Subantarctic and the Antarctic also show no clear case of greater size in more southern species. *Cnemidocarpa nordenskjöldi* and *C. drygalskii*, for example, attain about the same size.

Pyura legumen, *P. georgiana* and *P. bouvetensis* inhabit progressively more southern waters but also fail to show any corresponding increase in body size, although there is a striking increase in the length of the stalk.

It is true, however, that the Subantarctic and Antarctic species of a family are often considerably larger than the temperate and tropical species of the same family. This is particularly noticeable in *Distaplia cylindrica* and in the molgulids *Paramolgula gregaria* and *Ascopera gigantea.*

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INDEX TO GENERA AND SPECIES

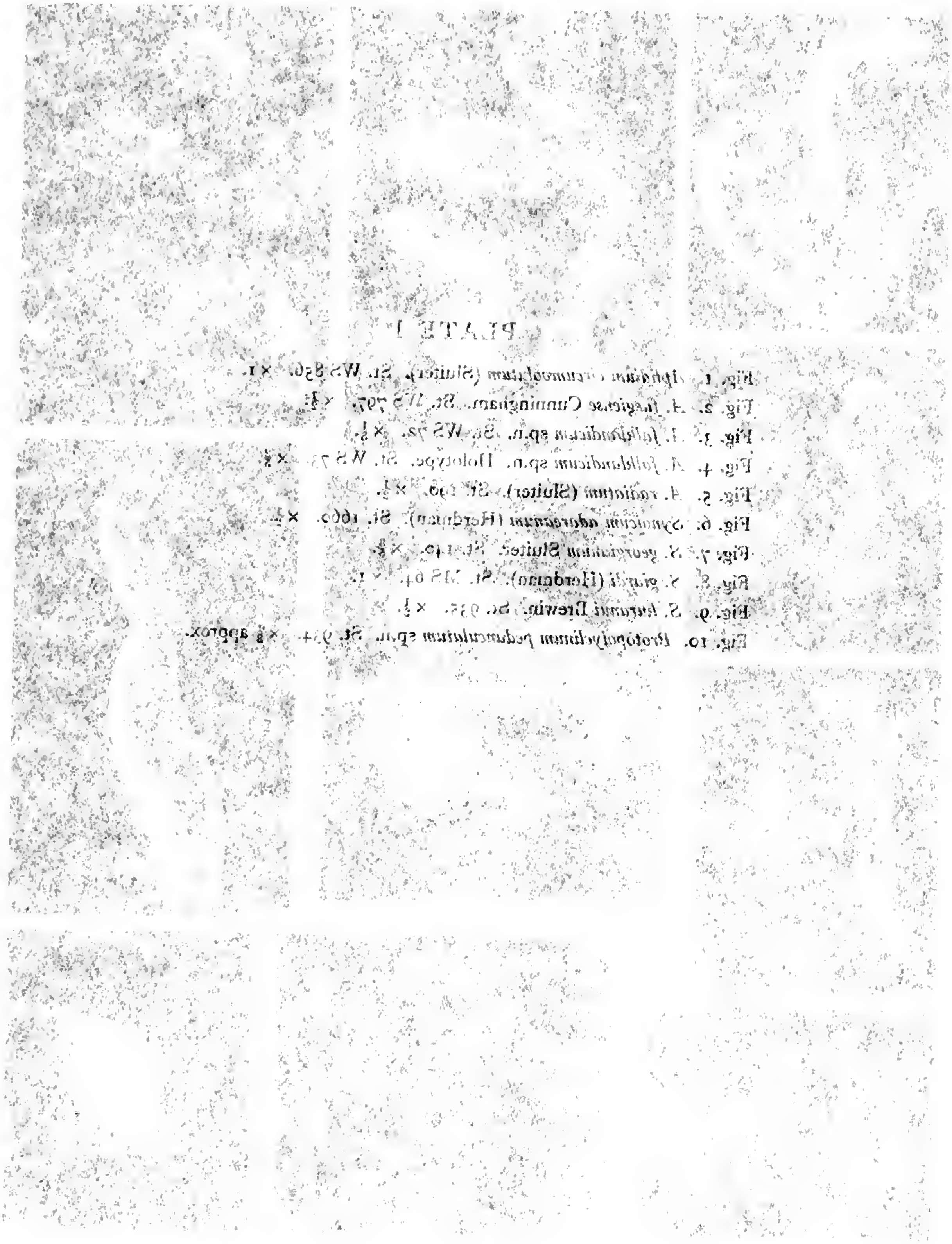


PLATE I

Fig. 1. *Aplidium circumvolutum* (Sluiter). St. WS 856. × 1.

Fig. 2. *A. fuegiense* Cunningham. St. WS 797. × ½.

Fig. 3. *A. falklandicum* sp.n. St. WS 72. × ⅓.

Fig. 4. *A. falklandicum* sp.n. Holotype. St. WS 73. × ⅖.

Fig. 5. *A. radiatum* (Sluiter). St. 190. × ½.

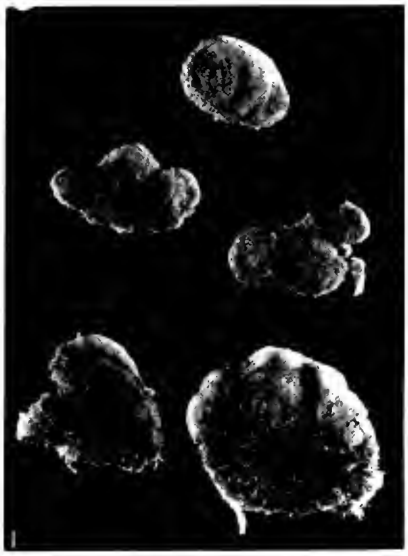
Fig. 6. *Synoicum adareanum* (Herdman). St. 1660. × ½.

Fig. 7. *S. georgianum* Sluiter. St. 140. × ⅗.

Fig. 8. *S. giardi* (Herdman). St. MS 64. × 1.

Fig. 9. *S. kuranui* Brewin. St. 935. × ½.

Fig. 10. *Protopolyclinum pedunculatum* sp.n. St. 934. × ⅓ approx.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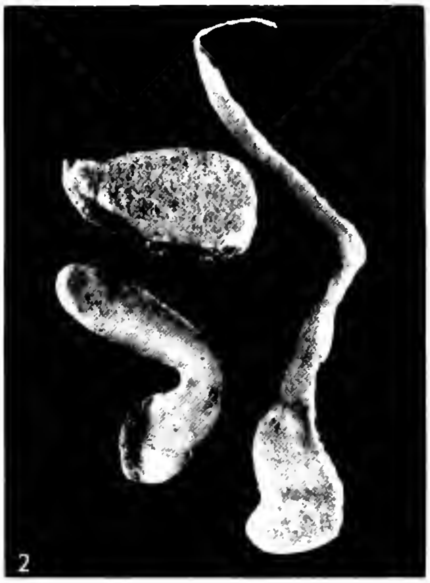
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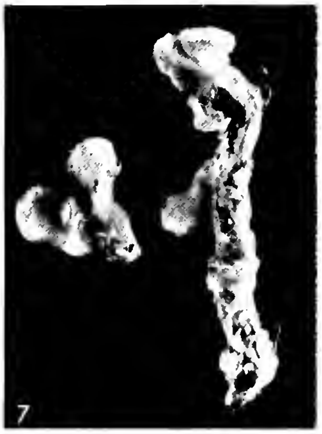
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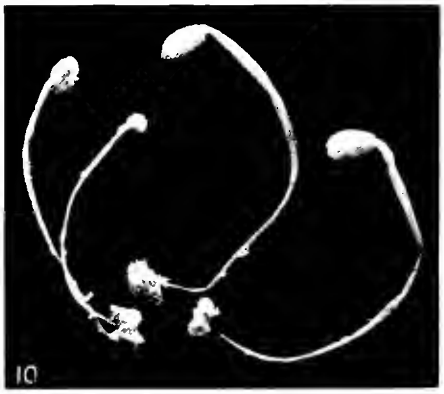
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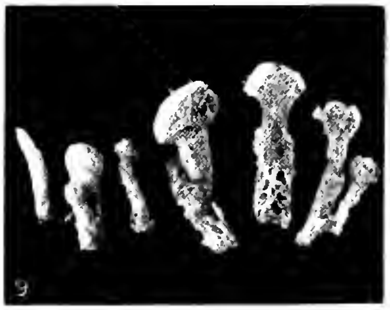
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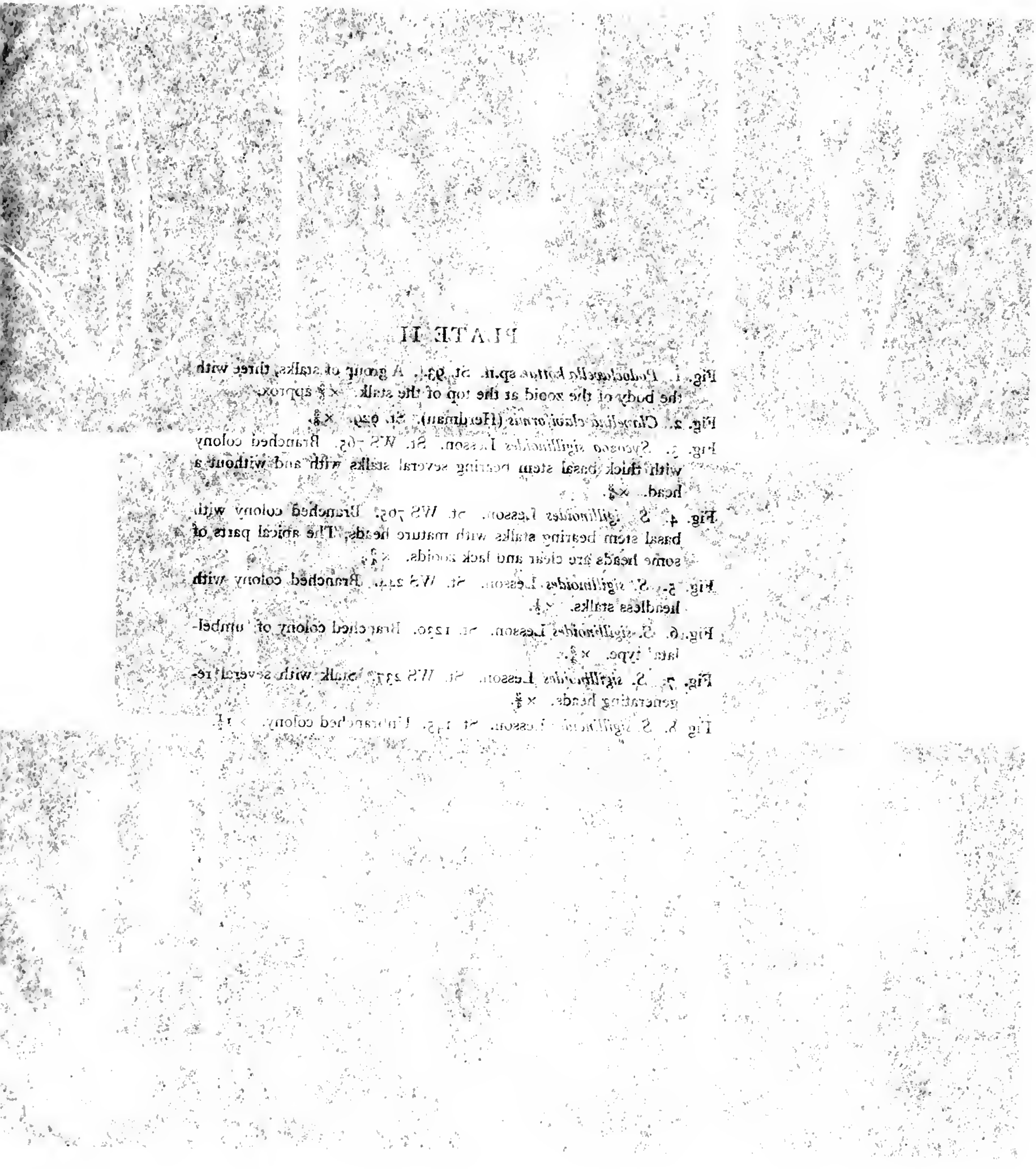

PLATE II

Fig. 1. *Podoclavella kottae* sp.n. St. 934. A group of stalks, three with the body of the zooid at the top of the stalk. × $\frac{3}{5}$ approx.

Fig. 2. *Clavelina claviformis* (Herdman). St. 929. × $\frac{3}{8}$.

Fig. 3. *Sycozoa sigillinoides* Lesson. St. WS 765. Branched colony with thick basal stem bearing several stalks with and without a head. × $\frac{3}{4}$.

Fig. 4. *S. sigillinoides* Lesson. St. WS 765. Branched colony with basal stem bearing stalks with mature heads. The apical parts of some heads are clear and lack zooids. × $\frac{3}{4}$.

Fig. 5. *S. sigillinoides* Lesson. St. WS 244. Branched colony with headless stalks. × $\frac{1}{2}$.

Fig. 6. *S. sigillinoides* Lesson. St. 1230. Branched colony of 'umbellata' type. × $\frac{3}{4}$.

Fig. 7. *S. sigillinoides* Lesson. St. WS 237. Stalk with several regenerating heads. × $\frac{3}{4}$.

Fig. 8. *S. sigillinoides* Lesson. St. 145. Unbranched colony. × $1\frac{1}{2}$.


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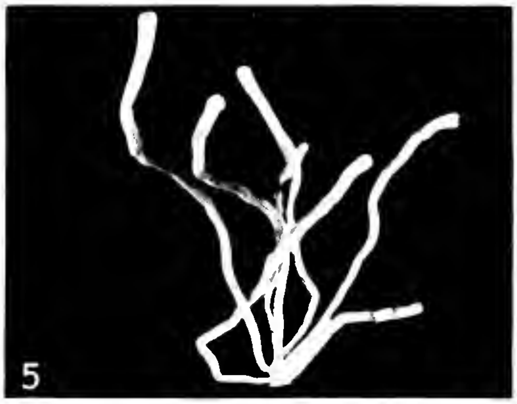
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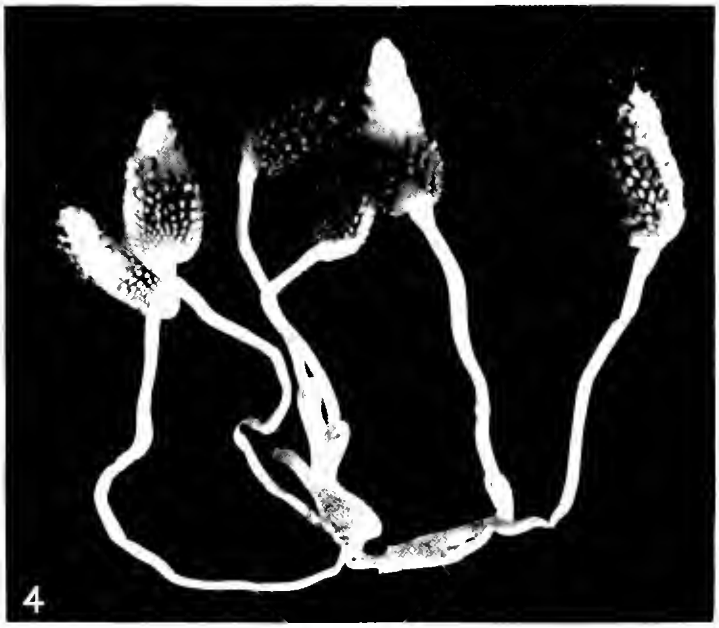
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PLATE III

Fig. 1. *Tylobranchion speciosum* Herdman. St. 144. Two colonies. × $1\frac{1}{2}$.

Fig. 2. *Hypsistozoa fasmeriana* (Michaelsen). St. 935. Colony. × $\frac{33}{20}$.

Fig. 3. *Distaplia colligans* Sluiter. St. 1113. × $\frac{3}{4}$.

Fig. 4. *D. cylindrica* (Lesson). St. 366. (Scale in cm.)

Fig. 5. *Sycozoa georgiana* (Michaelsen). St. MS 68. × $1\frac{1}{2}$.

Fig. 6. *S. anomala* sp.n. St. 929. × $1\frac{1}{8}$.


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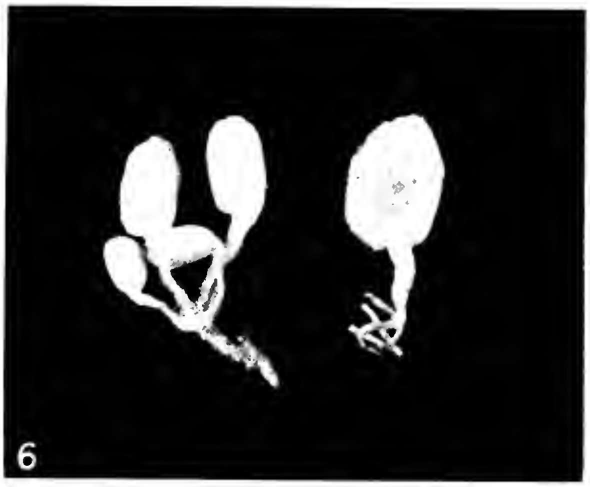
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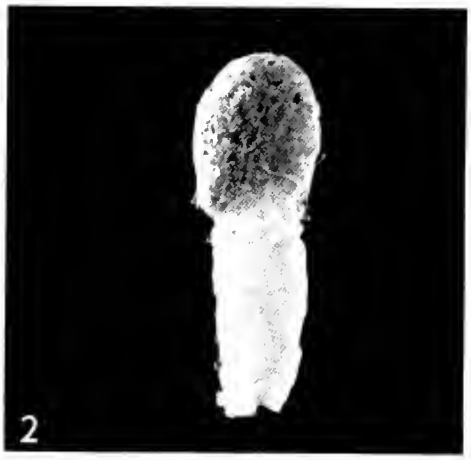
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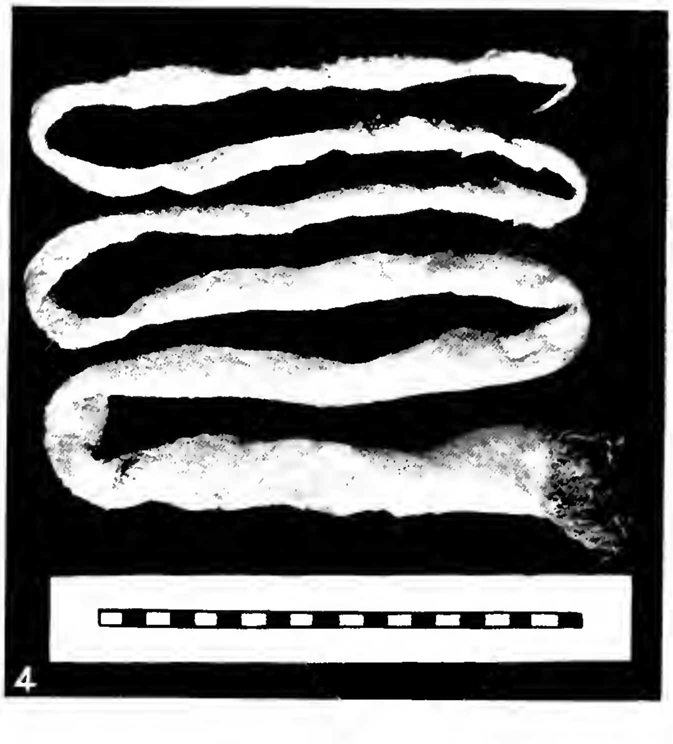
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PLATE IV

Fig. 1. *Pyura discoveryi* (Herdman). St. 27. Right: a single specimen. Left: two specimens growing together. $\times 1\frac{1}{2}$.

Fig. 2. *P. setosa* (Sluiter). St. 175. Specimen growing on a stone; the test has been damaged at one place. $\times \frac{6}{7}$.

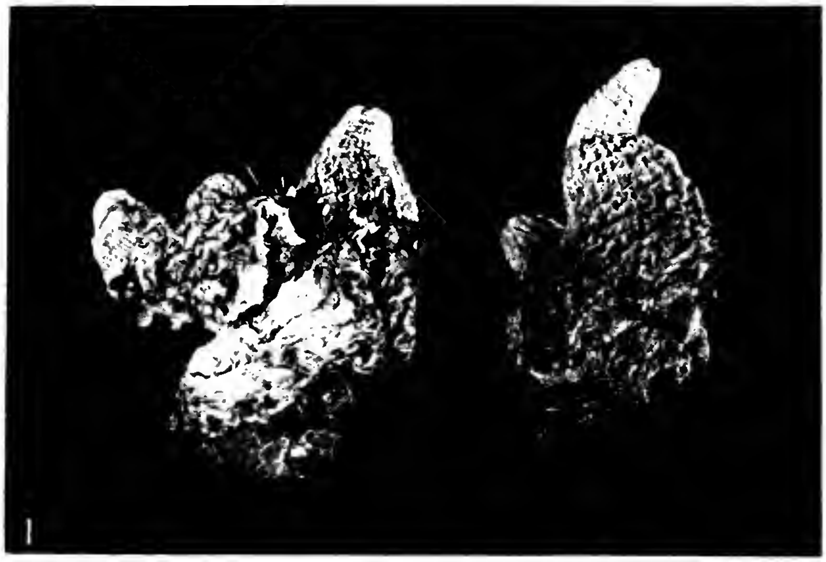
Fig. 3. *Eugyra ärnbäckae* sp.n. St. 366. Intact specimens. $\times \frac{3}{4}$.

Fig. 4. *Pyura bouvetensis* (Michaelsen). St. 1952. Specimen with thin papery test. $\times \frac{3}{4}$.

Fig. 5. *P. bouvetensis* (Michaelsen). St. 181. Specimen with leathery wrinkled test. $\times \frac{3}{4}$.

Fig. 6. *P. legumen* (Lesson). St. 52. $\times \frac{3}{4}$ approx.

Fig. 7. *P. georgiana* Michaelsen. St. 123. $\times \frac{3}{4}$.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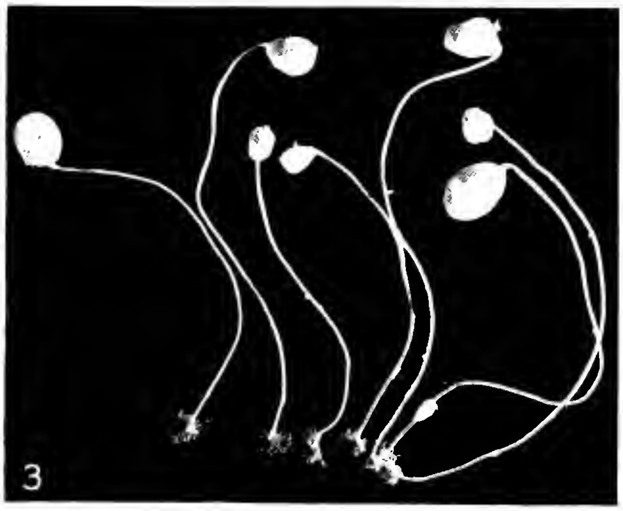
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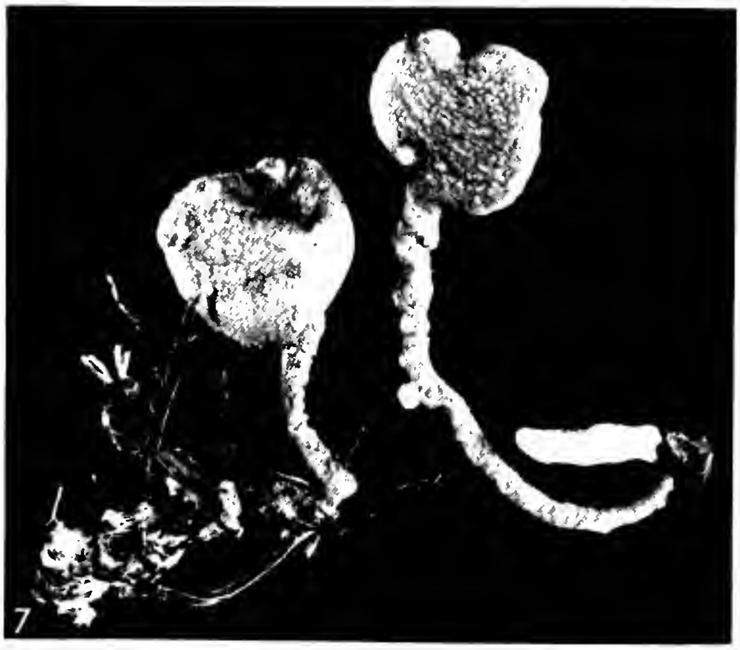
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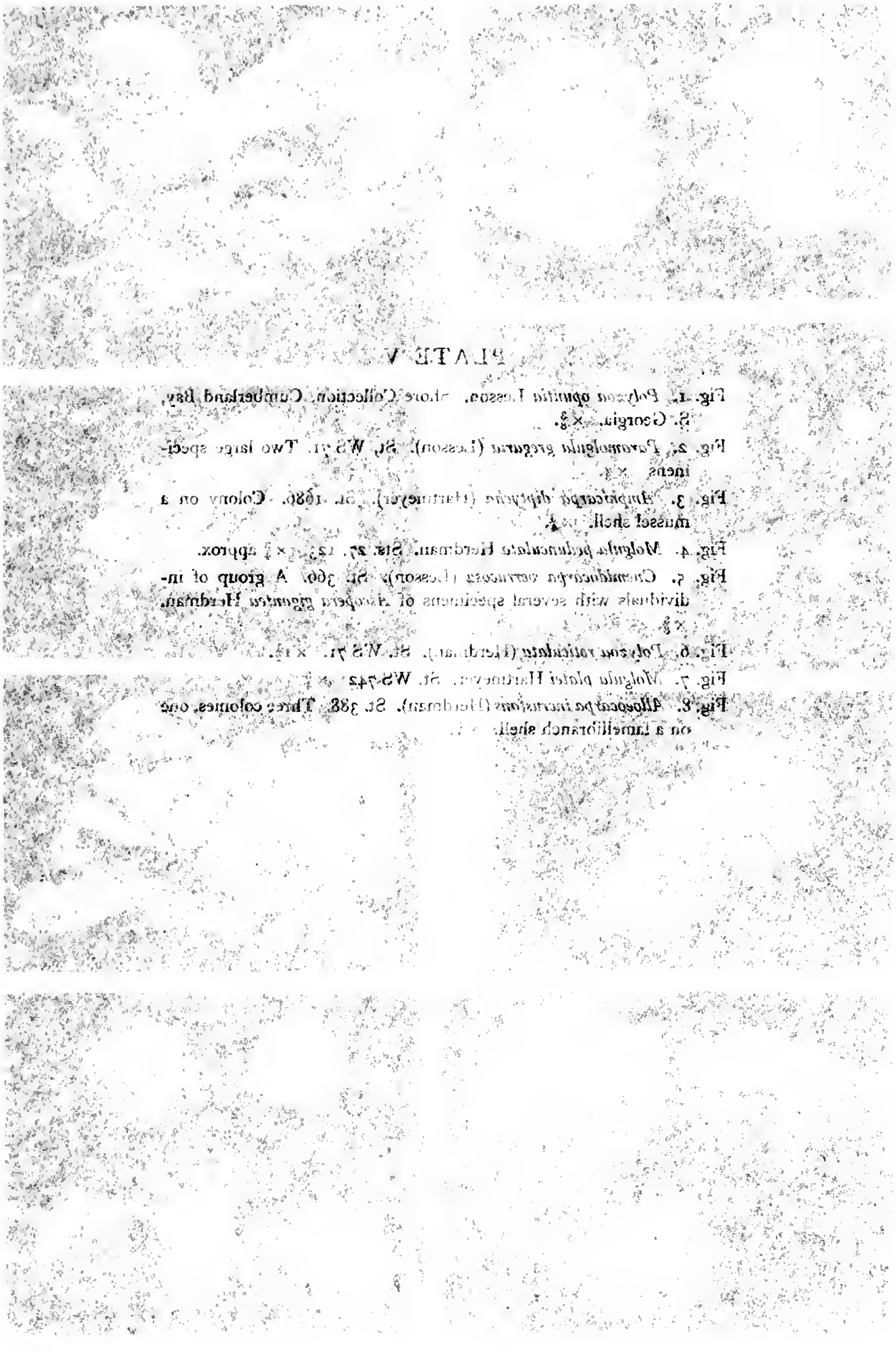


PLATE V

Fig. 1. *Polyzoa opuntia* Lesson. Shore Collection, Cumberland Bay, S. Georgia. $\times \frac{3}{8}$.

Fig. 2. *Paramolgula gregaria* (Lesson). St. WS 71. Two large specimens. $\times \frac{3}{8}$.

Fig. 3. *Amphicarpa diptycha* (Hartmeyer). St. 1686. Colony on a mussel shell. $\times \frac{3}{4}$.

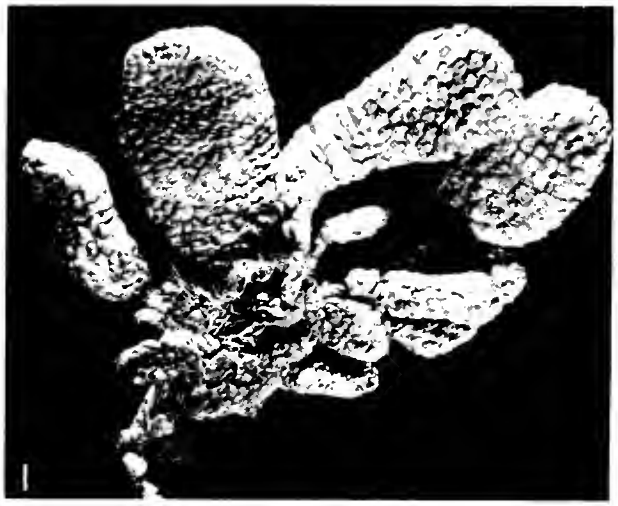
Fig. 4. *Molgula pedunculata* Herdman. Sts. 27, 123. $\times \frac{3}{4}$ approx.

Fig. 5. *Cnemidocarpa verrucosa* (Lesson). St. 366. A group of individuals with several specimens of *Ascopera gigantea* Herdman. $\times \frac{3}{8}$.

Fig. 6. *Polyzoa reticulata* (Herdman). St. WS 71. $\times 1\frac{1}{2}$.

Fig. 7. *Molgula platei* Hartmeyer. St. WS 742. $\times \frac{3}{4}$

Fig. 8. *Alloeocarpa incrustans* (Herdman). St. 388. Three colonies, one on a lamellibranch shell. $\times \frac{3}{4}$.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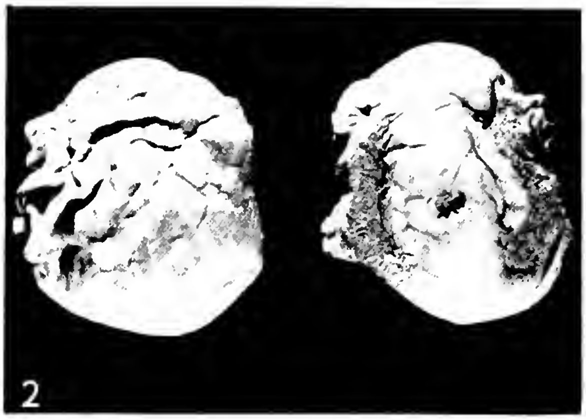
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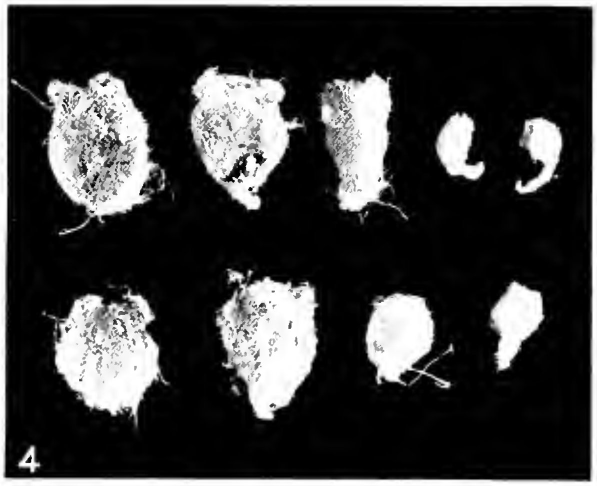
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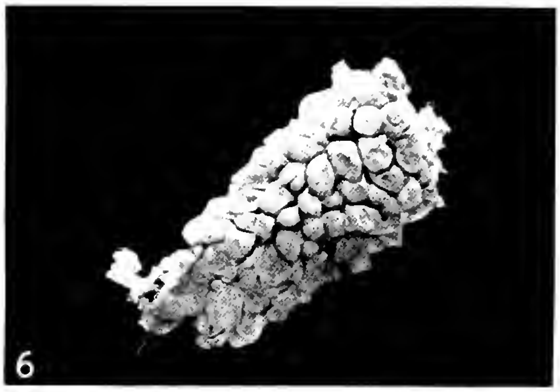
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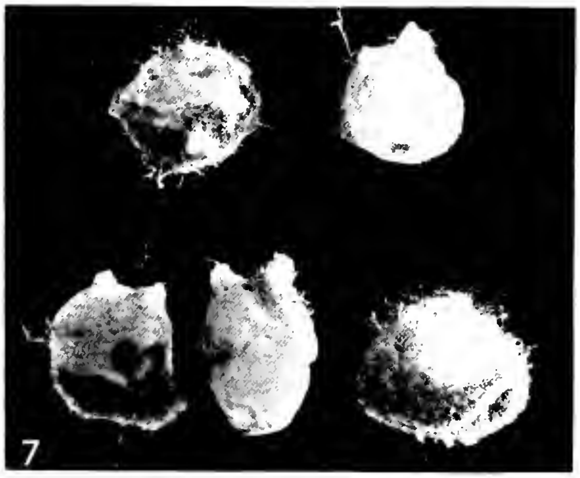
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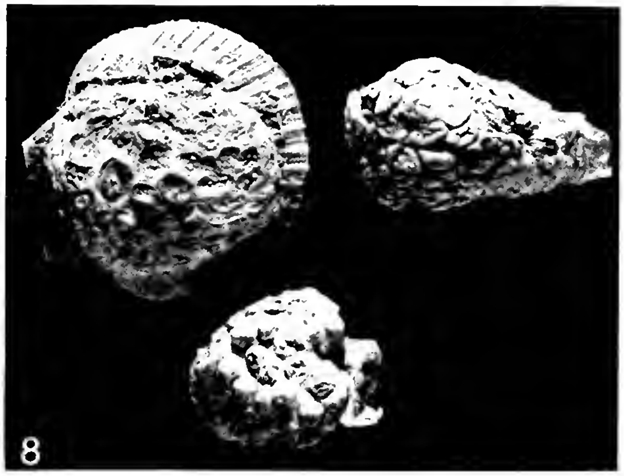
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PLATE VI

Fig. 1. *Ascopera gigantea* Herdman. St. MS 68. Long-stalked specimens from S. Georgia. × $\frac{3}{8}$.

Fig. 2. *A. gigantea* Herdman. Deception Island. Short-stalked specimens. × $\frac{3}{8}$.

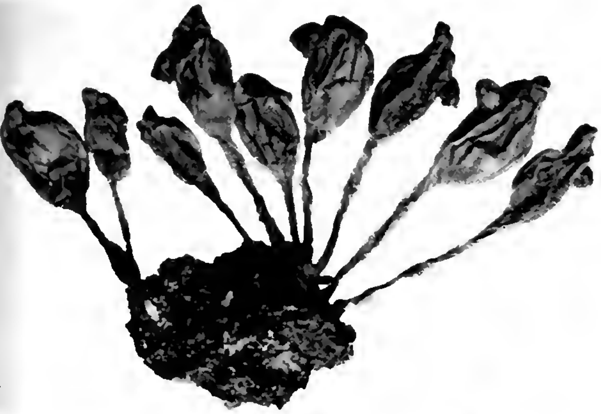
Fig. 3. *Distaplia cylindrica* (Lesson). Photomicrograph × 60. Contents of intestine, with a few small sand grains and many small food particles.

Fig. 4. *D. cylindrica* (Lesson). Photomicrograph × 25·5. Zooid stained in eosin and cleared to show large sand grains in branchial sac but none in oesophagus, stomach, intestine or rectum. The dark mass in the intestine is an accumulation of small food particles.

Fig. 5. *D. cylindrica* (Lesson). Photomicrograph × 60. Contents of branchial sac with many large sand grains.

Fig. 6. *Eugyra ärnbäckae* sp.n. Photomicrograph × 45. Contents of branchial sac with many large sand grains.

Fig. 7. *E. ärnbäckae* sp.n. Photomicrograph × 45. Contents of stomach with many food particles, some quite large, but no large sand grains.



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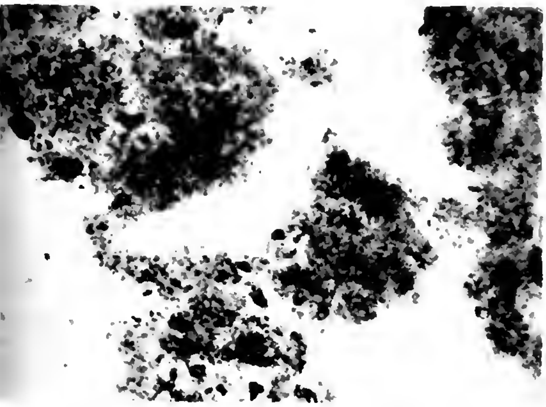

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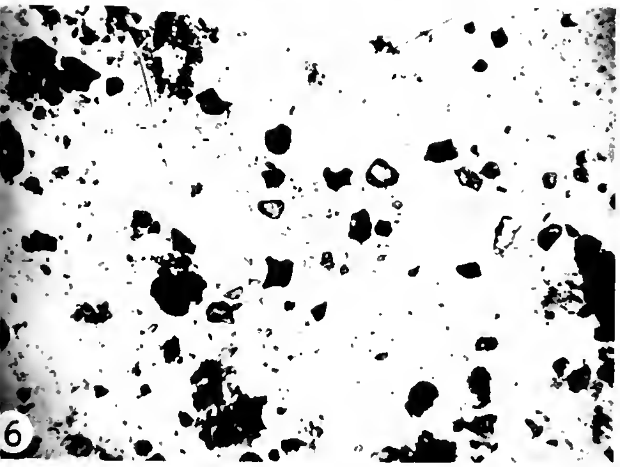

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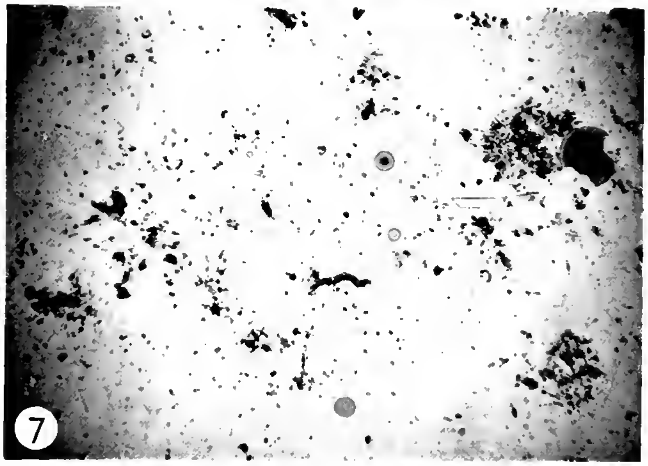

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[*Discovery Reports*, *Vol. XXX*, *pp.* 161–300, *April* 1960.]

THE DISTRIBUTION OF PELAGIC POLYCHAETES IN THE SOUTH ATLANTIC OCEAN

By

NORMAN TEBBLE
British Museum (Natural History)

CONTENTS

THE DISTRIBUTION OF PELAGIC POLYCHAETES IN THE SOUTH ATLANTIC OCEAN

By Norman Tebble
British Museum (Natural History)

(Text-figs. 1–52)

INTRODUCTION

The object of this report is to investigate the distribution of pelagic polychaetes in the South Atlantic Ocean in relation to their environment. It is a contribution to the work on the distribution and dispersal of plankton in the Southern Oceans formerly directed by the Discovery Committee and now continued by the National Institute of Oceanography. As a zoogeographical study it is also intended to be an extension of C. C. A. Monro's (1930, 1936) systematic analyses of the polychaete fauna of the Southern Oceans.

The report is in two main parts: SYSTEMATIC ACCOUNT and ZOOGEOGRAPHY. It is fundamental in a zoogeographical survey to define the units involved—the species—and the Systematic Account forms an integral part of this paper. The principal water masses have been found to influence the distribution of many pelagic polychaetes in the South Atlantic Ocean; the zoogeographical account has been separated therefore into two sections, *Hydrological Environment* and *Distribution of Species*. In the former the characteristics of the water masses are described and in the latter the distribution of species is considered in relation to these. Details of the number of specimens and species collected at each station are tabulated in the tables and appendices.

The treatment of some species from the South Atlantic Ocean is necessarily incomplete, because the distribution of endemic antarctic species and of antarctic and sub-antarctic cosmopolitan populations is more properly a circumpolar study. However in the present state of our knowledge it was felt that a study of the group as a whole was necessary; it is hoped to make circumpolar distribution the subject of a future report.

It has not been possible to examine all the very numerous plankton samples collected by the Discovery Investigations in the South Atlantic Ocean. The material first examined, principally from South Georgia and along the Greenwich Meridian, was sorted by the staff of the N.I.O. and included also the specimens reported by Monro (1930, 1936); subsequently many more hauls were examined in order to extend the work over as wide an area as possible.

The complete development of pelagic polychaetes from the fertilized egg to sexual maturity is unknown, but development is probably direct without metamorphosis. Age groups are almost impossible to define in the present state of our knowledge, and the majority of the specimens described in this report are therefore at indeterminate stages of development.

ACKNOWLEDGEMENTS

I would like to take this opportunity of thanking Dr N. A. Mackintosh, C.B.E., for permitting me to work on Discovery collections and for advice during the preparation of this report. My thanks are due also to Dr G. R. Deacon, F.R.S. and my colleague, Mr N. B. Marshall for helpful criticism. In addition Miss A. C. Edwards has been very helpful in many ways, particularly in the preparation of charts and hydrological sections.

MATERIAL AND METHODS

The plankton samples examined for this report are a selection from material collected by the Royal Research ships 'Discovery', 'Discovery II' and 'William Scoresby', between the years 1925 and 1939, on cruises in the Atlantic Ocean from the Ice Edge in 70° S. to just north of the Equator. Selection was necessary because there is a greater concentration, particularly during the summer months, of Discovery stations in the Antarctic region than elsewhere in the Atlantic. It was accordingly decided (1) to examine material from as wide an area as possible, and (2) to use certain lines of stations for this purpose. The positions of the stations from which samples were used are shown in Text-figs. 1–5; the approximate positions of the major surface hydrological boundaries are indicated in Text-figs. 1, 4*a* and *b*. These boundaries fluctuate and are therefore shown nearest to their actual location when the stations were worked.

Station data are given in the text, in tables, charts, hydrological sections and the appendices, but should further information be required the reader is referred to the Discovery Station Lists (*Discovery Reports*, vols. I, III, IV, XXI, XXII, XXIV). Full descriptions of the plankton nets and hydrological methods are given in Kemp, Hardy and Mackintosh (1929) and in the respective Station Lists; the nets used are briefly given below:

(1) N 50: hauled vertically (V) only. With its very fine mesh this net is primarily designed to capture phytoplankton; the NC 50 net (attached to larger nets) was used to a small extent.

(2) N 70: hauled vertically (V), towed obliquely (B) or horizontally (H); designed to capture medium and smaller size macroplankton.

(3) N 100: hauled vertically (V) and towed obliquely (B) or horizontally (H); designed to collect the larger macroplankton.

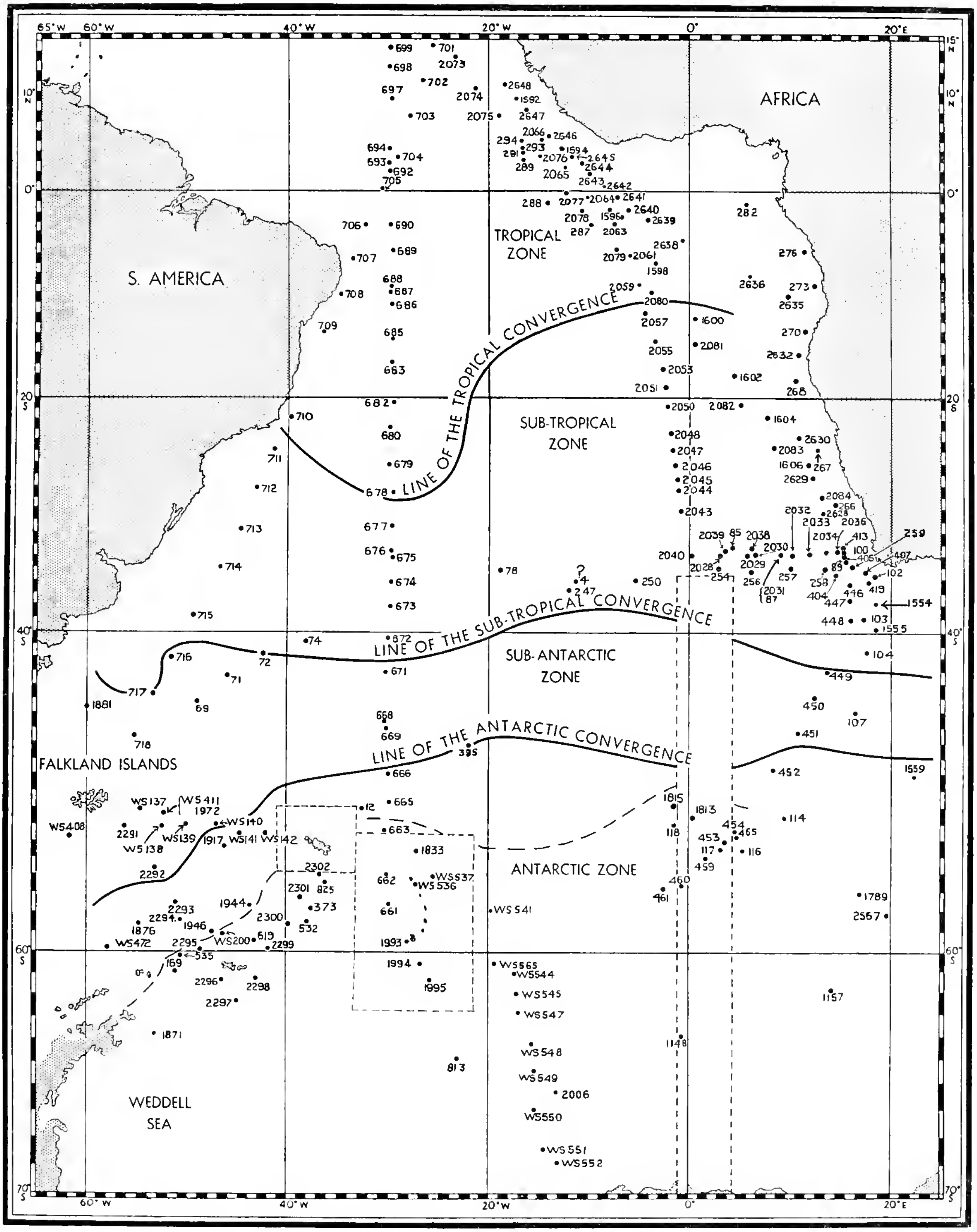
(4) TYF: hauled vertically (V), towed obliquely (B) or horizontally (H); designed to catch macroplankton.

(5) N 450: for macroplankton.

The N 50 and N 70 nets when used vertically were hauled at a constant speed through a known depth range, but the speed and depth of the towed nets were subject to some variation depending on weather conditions and regulation of the speed of the ship. The vertical nets are therefore of greater value for quantitative analysis.

Unless otherwise stated, all station numbers used in this report refer to those made by the Discovery Investigations. When made by 'Discovery' (Sts. 1–299) or 'Discovery II' (Sts. 300–2648), these are not prefixed, but when made by 'William Scoresby', the letters WS precede each; for the South Sandwich Survey the letters SS are used, and for the Marine Biological Station on South Georgia, the letters MS.

Details of areas from which samples have been examined are given here: these are considered either as 'Surveys', where a comparatively small area was made the object of intensive collecting, or as 'Lines' when the ships made collections in set directions.



Text-fig. 1. Chart showing all stations at which specimens were obtained, except round South Georgia, South Sandwich Islands and in the region of the Greenwich Meridian (0° Line). For these see Text-figs. 2, 3, 4*a*, 4*b* and 5.

(1) *The South Georgia Surveys* (Text-figs. 2 and 3).

Collections from two surveys have been examined; closing (N 70 V) nets were used on both, at depths down to 1000 m.; 50–0 m., 100–50 m., 250–100 m., 750–500 m., 1000–750 m.:

(*a*) February to March 1928, Sts. WS 137 to WS 195.[1]

(*b*) January to February 1930, Sts. 300–358.

Material collected at Sts. MS 11, MS 22, MS 25, MS 31, MS 32, MS 34A and MS 62, and most of that reported by Hardy and Gunther (1935) from the Survey of December to January 1926–7 has also been available. Additional samples from the following stations within the South Georgia area have also been examined: Sts. 17, 26, 41, 130, 150, 151, 527, 1079, 1201, 1935, 1936, WS 53, WS 59, WS 60, WS 61, WS 351, WS 372.

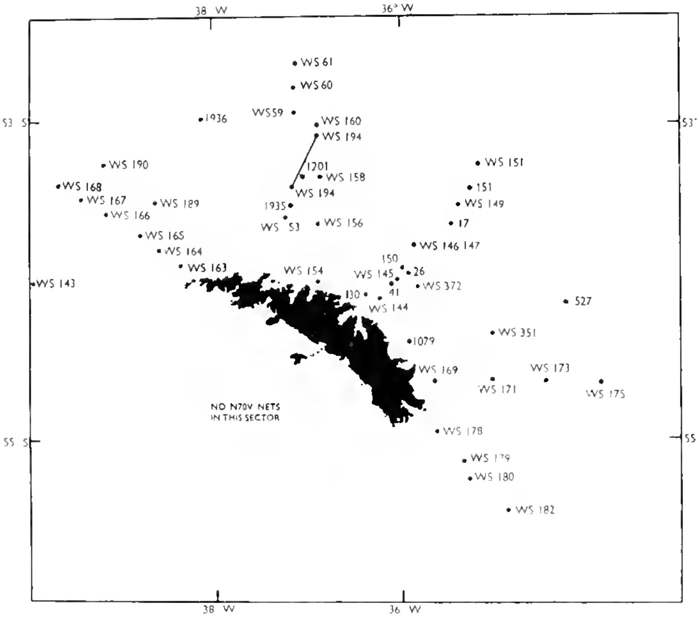


Fig. 2

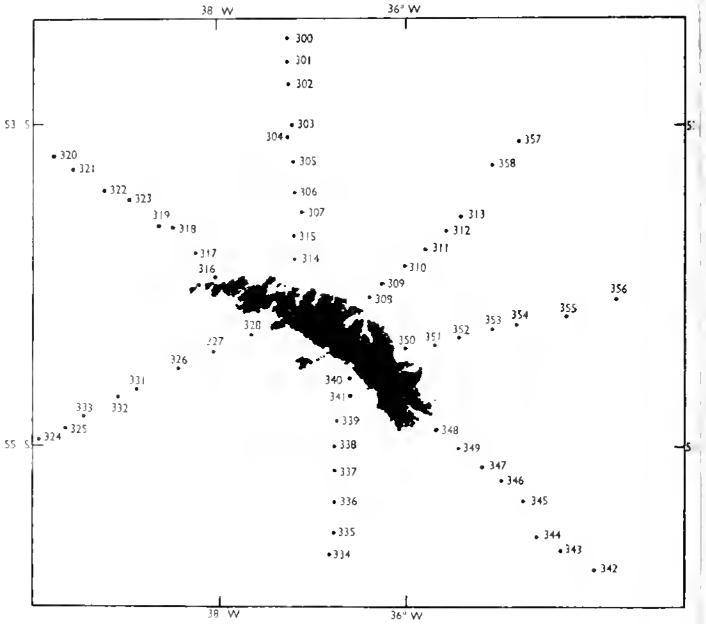


Fig. 3

Text-figs. 2 and 3. South Georgia Surveys. Fig. 2, Sts. WS 144–WS 194, February–March 1928; also some miscellaneous stations in the area; fig. 3, Sts. 300–358, January-February 1930.

(2) *The 0° Line* (Text-figs. 4*a* and *b*).

Collections were made within a few degrees of the Greenwich Meridian in the Antarctic, Sub-Antarctic and Sub-Tropical zones between latitude 70° S. and 36° S. Samples from N 70 V nets were examined from all the following stations (the most southerly station is given first in each case, its position depending generally on the location of the pack-ice).

(*a*) November to December 1938, Sts. 2501, 2498, 2496, 2494, 2492.

(*b*) January 1939, Sts. 2547, 2545, 2543, 2541, 2538, 2535, 2533–2530.

(*c*) March to April 1937, Sts. 2010, 2012, 2014, 2017, 2018, 2020, 2022–2027.

(*d*) April 1938, Sts. 2322, 2320, 2318, 2316, 2313, 2311.

(*e*) May to June 1936, Sts. 1782, 1781, 1779–1772.

The following stations do not form a continuous line, but have been grouped together for convenience:

(*f*) July 1938, Sts. 2361, 2358–2355.
August 1938, Sts. 2392, 2391, 2389, 2387, 2386, 2385.
September 1938, Sts. 2425, 2424.

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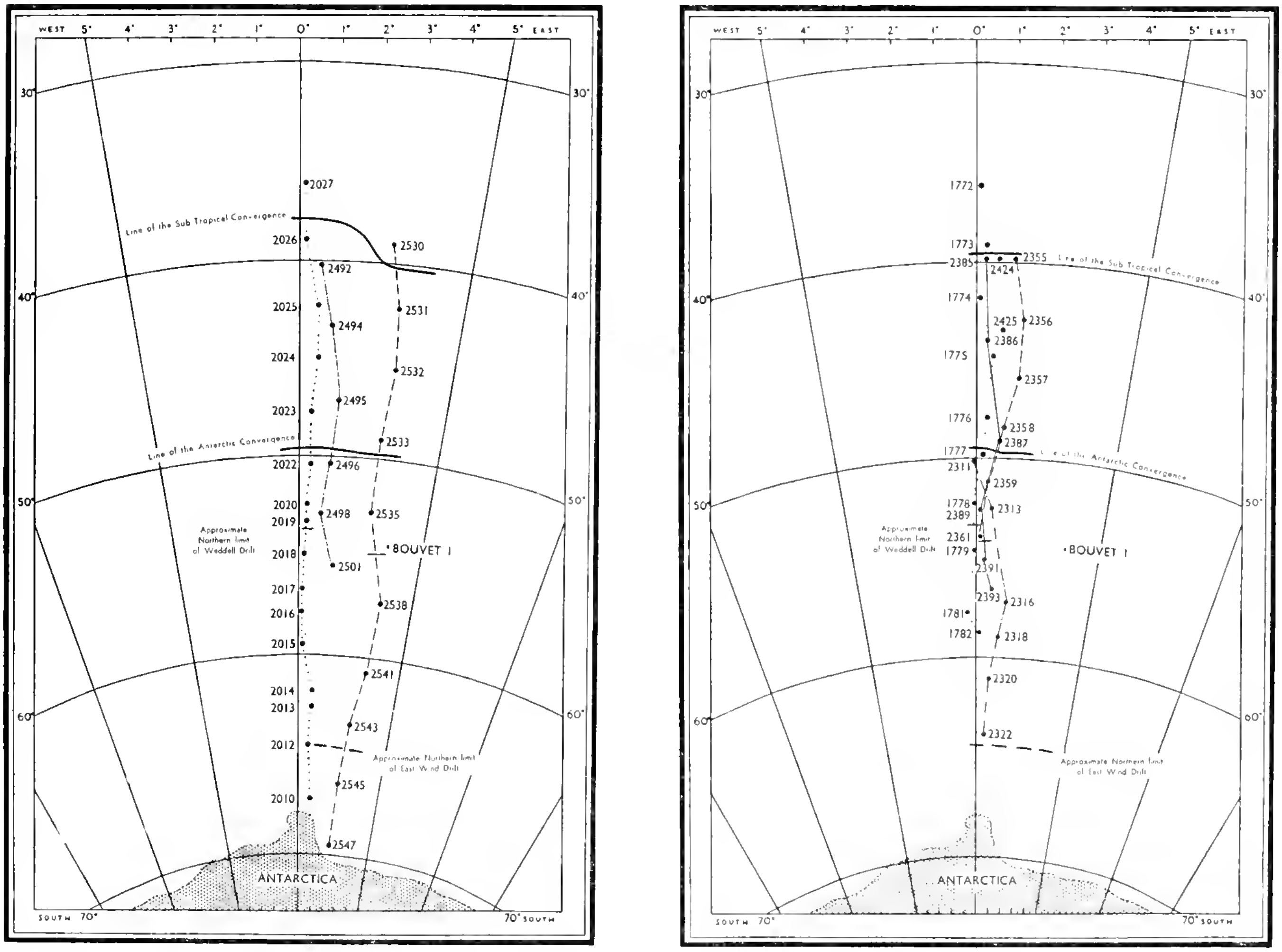
[1] Sts. WS 137 to WS 142 are actually some distance from South Georgia and are listed here for convenience only.

Normally seven hauls were made at all these stations, from 50–0 m., 100–50 m., 250–100 m., 500–250 m., 750–500 m., 1000–750 m. and 1500–1000 m. Allowance has been made for these varying lengths of haul in the vertical distribution charts for three species collected along the 0° Line. A haul of 250 m. has been taken as the standard, and the number of specimens collected in the 50–0 m. and 100–50 m. hauls multiplied by 5, in the 250–100 m. hauls by 5/3, and in the 1500–1000 m. hauls by ½.



(*a*) (*b*)

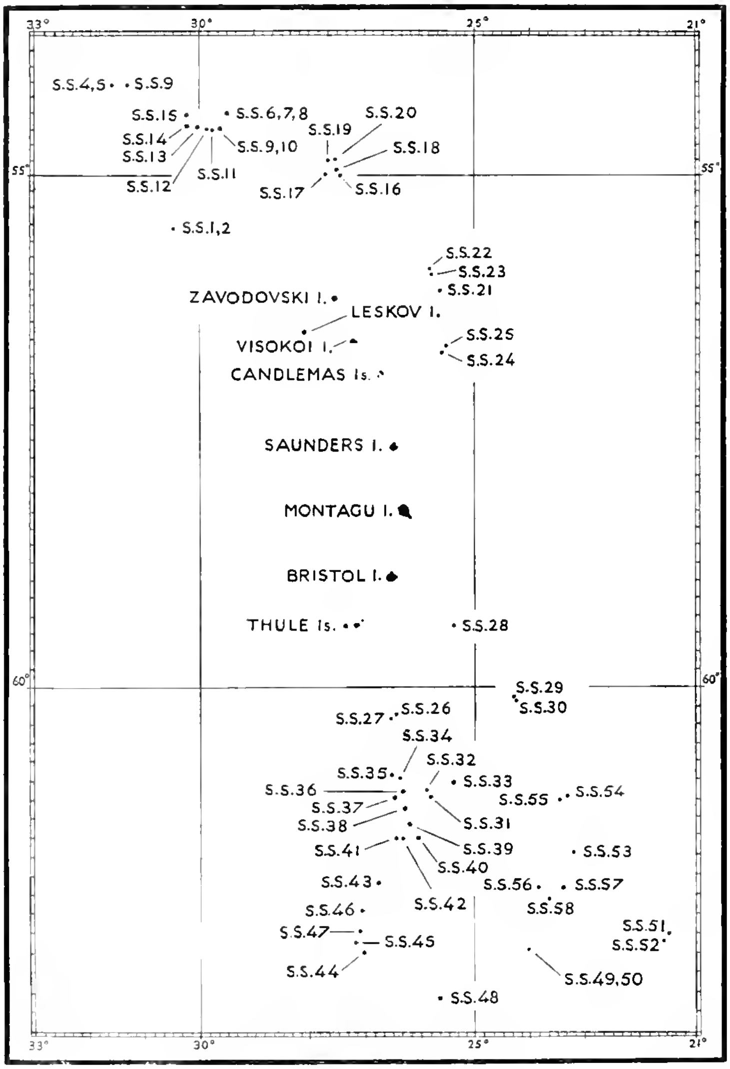
Text-fig. 4. Greenwich Meridian (0° Line). (*a*) Sts. 2010–27, March-April 1937; Sts. 2492–2501, November–December 1938; Sts. 2530–47, January 1939. (*b*) Sts. 1772–82, May–June 1936; Sts. 2311–22, April 1938; Sts. 2355–61, 2385–93, 2424 and 2425, July–September 1938.

Each amended number is plotted in the mean position of depth for each particular haul. The effect is that the plotted numbers represent the relative density of the population per unit volume of water in that part of the column sampled in each haul. The actual numbers of specimens caught by each net are given in Appendix I. The N 70 V samples from the 0° Line collections were taken in three hydrological zones over a distance of approximately 2160 nautical miles and provide quantitative information on the distribution of the smaller polychaetes.

In addition to the above samples material collected by N 100 B or N 70 B nets was examined from the following stations on the 0° Line: 1148, 1772, 2010–2027; 1813, 1815, 2322 (see Appendix II).

(3) *The South Sandwich Survey* (Text-fig. 5).

Collections were made around the South Sandwich Islands from November 1927, to February 1928, at Sts. SS 1–SS 58, with N 50 V, N 70 V, N 70 B and N 100 B nets. No samples were collected below 250 m., so that the results obtained are restricted in value, but they do provide limited confirmation of other more complete data.



Text-fig. 5. South Sandwich Survey. Sts. SS 1–SS 58, November–January 1927–8.

(4) *South Sandwich Islands to the Ice Edge in 68° 53′ S.* (Text-fig. 1).

In January and February 1931, collections were made at Sts. WS 536, WS 537, WS 541, WS 544 to WS 552 and WS 555, of which the N 70 B and N 100 B samples have been studied.

(5) *Falkland Islands to the Ice Edge in the Weddell Sea and to South Georgia* (Text-fig. 1).

In March 1938, collections were made down to 750 m. at twelve stations, 2291–2302, from which samples from N 70 B, N 100 B and N 100 H nets have been examined.

(6) *Cape Town to Bouvet Island* (Text-fig. 1).

In October and November 1926, collections in the Sub-Antarctic and Sub-Tropical zones were made at Sts. 100, 102, 103, 104, 107, 114, 116, 117 and 118, from which the N 70 V samples have been examined. This line of stations was repeated in June and August 1930, Sts. 404, 405, 407, 413, 419, and in October, Sts. 446–61, from which TYFB and N 100 B samples have been examined.

(7) *The 30° Line* (Text-fig. 1).

During March, April and May of 1931 collections were made along the meridian of 30° W., from 57° 36′ S. to 14° 27¼ N., in four hydrological zones, at Sts. 661–99. Catches were made at various depths down to 3000 m. with the TYFB and TYFV nets.

(8) *Falkland Islands to Cape Town* (Text-fig. 1).

In May and June 1926 collections near the Sub-Tropical Convergence were made at Sts. 71, 72, 74, 78, 85, 87 and 89 with the N 70 V and TYF nets. Part of this line, from Tristan da Cunha to Cape Town, was repeated in June 1927 (Sts. 250, 254, 256, 257, 258 and 259), with shallow TYF nets.

(9) *Cape Verde Islands to and from Cape Town* (Text-fig. 1).

Some of these stations extend the lines noted above.

(*a*) July to August 1927: Sts. 266, 267, 268, 270, 273, 276, 282, 287, 288, 289, 291 and 294; only samples from TYF nets, towed near the surface, examined.

(*b*) October to November 1935, Sts. 1592, 1594, 1596, 1598, 1600, 1602, 1604, 1606; samples from TYFB nets towed at various depths between 700 m. and the surface.

(*c*) April to May 1937, Sts. 2028–66; samples from N 70 B, N 100 H, TYFB, N 450 B and N 450 H nets towed at various depths.

(*d*) October to November 1937, Sts. 2073–84; samples from TYFB nets towed at the surface and at depth.

(*e*) March to April 1939, Sts. 2627–48; samples from N 50 V and TYFB nets fished through the surface layers and TYFB nets towed at depth.

All these samples provide information on the distribution of species within the Sub-Tropical and Tropical zones.

(10) *Cape Verde Islands to Falkland Islands* (Text-fig. 1).

During October and November 1931 collections were made at Sts. 701–18, from depths varying between 358 and 150 m. to the surface with the TYFB nets used once at each station. This is the only line of stations in the western area of the South Atlantic.

Specimens from the following miscellaneous stations have also been examined (Text-figs. 1 and 2).

(11) *Antarctic Zone.*

Sts. 12, 169, 373, 395, 461, 532, 535, 619, 813, 825, 1148, 1157, 1559, 1789, 1813, 1815, 1833, 1871, 1876, 1917, 1944, 1946, 1993, 1994, 1995, 2006, 2567, WS 200, WS 472.

(12) *Sub-Antarctic Zone.*

Sts. 1881, WS 408, WS 411.

(13) *Sub-Tropical Zone.*

Sts. 4, 1554, 1555.

At the majority of these miscellaneous stations, single specimens of some of the larger species had frequently been picked out of the samples and were preserved separately (Appendix II, Table *j*). In addition some stations are from localities from which Monro (1930, 1936) reported material.

Full use has been made of the Plankton Analysis Sheets prepared by the staff of the N.I.O., when sorting the samples. These sheets summarize all the major phyto- and zooplankton groups collected. As noted in the appendices, the nil-results for complete samples are taken directly from these Analyses except when I did the sorting, for the negative results of which I am responsible. All these negative results have been considered when discussing the distribution of individual species. The charts showing distribution do not, however, show the negative stations (except Text-figs. 23 and 24 and Tables 14–19) although it is highly desirable to indicate the regions from which a species is absent. The reason for this omission is the difficulty of defining a negative station. Many species are taken mostly, but not exclusively, in certain nets and all nets were not always used at all stations. Moreover the same number of samples was not collected at every station. Thus, although a species may not have been collected at a particular station, this station may not necessarily be a negative one. The species-distribution charts should therefore be compared with the charts for all the stations examined (Text-figs. 1–5); in this way a fair idea is obtained of presence and absence in the area covered.

SYSTEMATIC ACCOUNT

A considerable literature exists on the systematics of pelagic polychaetes, of which the most comprehensive is the report by Stop-Bowitz (1948) on the 'Michael Sars' North Atlantic Deep-Sea Expedition in which many nomenclatorial problems are clarified. These include the replacing of numerous long-established names by others which have priority but which for various reasons have been overlooked. I have accepted most of the conclusions reached by Stop-Bowitz and reference can be made to his paper for greater detail. Lists of synonyms preceding the descriptions of species have been restricted to works important to distribution in the Atlantic Ocean, and to references of systematic value; the spelling of specific names in these lists follows that used in each particular reference.

The remoteness of the regions in which many pelagic polychaetes occur has resulted in our having little or no knowledge of the living animal. Minute morphological differences therefore have frequently been accepted as specific characters, when they may in fact indicate geographical variants or different stages in life cycles. It is emphasized below that this is particularly true of the Alciopidae.

All specimens recorded for the first time in this report have been deposited in the British Museum (Natural History) Collections (Registered numbers, 1955:6:1:1 to 2849, 1955:6:2:1 to 2291 and 1955:6:3:1 to 2507).

Family TOMOPTERIDAE

All species in this family are exclusively pelagic in habitat and aberrant in form, never having more than two pairs of chaetigate processes and having over most of the body achaetous parapodia with paddle-shaped pinnules.

Prostomium with a pair of laterally directed antennae, which together form its anterior border, a pair of nuchal organs and normally a pair of eyes. There may be two pairs of lateral chaetigate processes just behind the eyes—of which the anterior and smaller pair is often missing (the first pair of chaetigers), whereas the posterior pair is always present (the second pair of chaetigers). Parapodia are biramous and achaetous with notopodia and neuropodia modified into paddle-shaped pinnules; these pinnules may carry glands of unknown function which have been given the following names: (*a*) chromophil glands; these are large glands which appear only in neuropodia and stain deeply with haematoxylin; (*b*) hyaline glands; very small glands which occur in either notopodia or neuropodia, they may be pigmented or appear only as crystalline spots; they do not stain with haematoxylin; (*c*) rosette glands; very small glands which occur on the trunks of the parapodia or on notopodia and neuropodia; they do not stain with haematoxylin; (*d*) spur glands; these are small, normally subsidiary to the chromophil glands, and occur only on neuropodia; they stain with haematoxylin. The spur gland is so called because it projects from the normally entire surface of the pinnule. Posteriorly the body may be prolonged into a tail bearing rudimentary parapodia. Throughout his work on

Tomopteridae, Stop-Bowitz (1948) used indentation of the aciculae in the second pair of chaetigers as a character of specific importance. In no specimen examined by me have I found support for such use.

Two genera are known in this family, *Enapteris* Rosa, 1908*b* with pinnules which do not border the inner edge of parapodia-rami and *Tomopteris* Eschscholtz, 1825, in which the pinnules surround the rami. No specimens of *Enapteris*, a monospecific genus, have been seen in the plankton samples examined here.

Genus Tomopteris Eschscholtz, 1825

Notopodial and neuropodial pinnules always completely surrounding the parapodial trunk.

Type species. Tomopteris onisciformis Eschscholtz, 1825.

Type locality. South Seas (Pacific).

It has long been the practice of many, but not all, authors to split this genus into two subgenera, *Tomopteris sensu stricto*, almost always with hyaline glands, always without rosette glands and normally, but not always, without a first pair of chaetigers and a tail, and *Johnstonella* Gosse, 1853, always with rosette glands, normally but not always, without hyaline glands and normally, but not always, with a first pair of chaetigers and a tail. I have always had the greatest difficulty in separating rosettes and highly pigmented hyaline glands, and have retained the former only where it is clearly comparable with common usage. I can, however, see no point in retaining this subgeneric division when it neither separates the genus into natural groups nor represents a practical method of separating groups of species.

Table 1. *In this table the presence (×) or absence (–) of the more important diagnostic characters in the species described below is indicated*

		Hyaline glands					*Chromophil glands*				
	First chaetigers	*Apical*	*Dorsal*	*On most feet*	*On 3rd and 4th feet only*	*Rosette glands*	*Compact*	*Diffuse*	*With spur*	*Pinnules extend to body wall*	*Tail*
T. planktonis	–	×	–	×	–	–	×	–	–	–	–
T. carpenteri	–	–	×	×	–	–	×	–	–	–	–
T. septentrionalis	–	–	×	×	–	–	–	×	–	–	–
T. ligulata	–	–	×	×	–	–	×	–	–	×	–
T. elegans	×	–	×	–	×	–	×	–	–	–	–
T. nisseni	–	×	–	×	–	–	×	–	–	–	×
T. krampi	×	×	–	×	–	–	×	–	–	–	×
T. kempi	–	–	–	–	–	×	×	–	–	–	×
T. apsteini	×	–	–	–	–	×	×	–	×	–	×

Tomopteris planktonis Apstein, 1900

Original localities. In the Atlantic Ocean between Ascension Island and Brazil, Ascension Island and Cape Verde Islands and between Newfoundland and Iceland.

Tomopteris planktonis Apstein, 1900, p. 42, pl. 11, figs. 21, 22, and pl. 12.
Tomopteris planktonis Reibisch, 1905, pp. 9–10, figs. 14, 15.
Tomopteris (*Tomopteris*) *planktonis* Rosa, 1908*b*, pp. 301–2.
Tomopteris (*Tomopteris*) *planktonis* Malaquin and Carin, 1911, pp. 14–15.
Tomopteris ligulata Ehlers, 1917, pp. 232–33 (in part).
Tomopteris (*Tomopteris*) *planktonis* Malaquin and Carin, 1922, p. 22, p. 27, pp. 39–40; pl. 10, figs. 1, 2 (in part).
Tomopteris (*Tomopteris*) *planktonis* Fauvel, 1923, pp. 224–5, fig. 84*d*.
Tomopteris (*Tomopteris*) *planktonis* Augener, 1929, pp. 303–4.
Tomopteris (*Tomopteris*) *carpenteri* Monro, 1930, pp. 84–6 (in part).
Tomopteris planktonis Fauvel, 1932*a*, p. 18.

Tomopteris (*Tomopteris*) *planktonis* Caroli, 1933, pp. 378–9.
Tomopteris (*Tomopteris*) *cavalli* Monro, 1936, p. 121.
Tomopteris (*Tomopteris*) *planktonis* Monro, 1936, p. 121 (in part).
Tomopteris (*Tomopteris*) *septentrionalis* Monro, 1936, pp. 121–2 (in part).
Tomopteris planktonis Monro, 1937, p. 270.
Tomopteris (*Tomopteris*) *planktonis* Terio, 1947, pp. 356–7.
Tomopteris (*Tomopteris*) *planktonis* Stop-Bowitz, 1948, pp. 52–4 (in part), fig. 39.
Tomopteris (*Tomopteris*) *planktonis* Stop-Bowitz, 1949, pp. 13–16.
Tomopteris planktonis Wesenburg-Lund, 1950*b*, pp. 43–4.
Tomopteris (*Tomopteris*) *planktonis* Stop-Bowitz, 1951, p. 9.

Description. In Table 2 measurements of a selection of specimens from various stations and depths have been listed according to size.

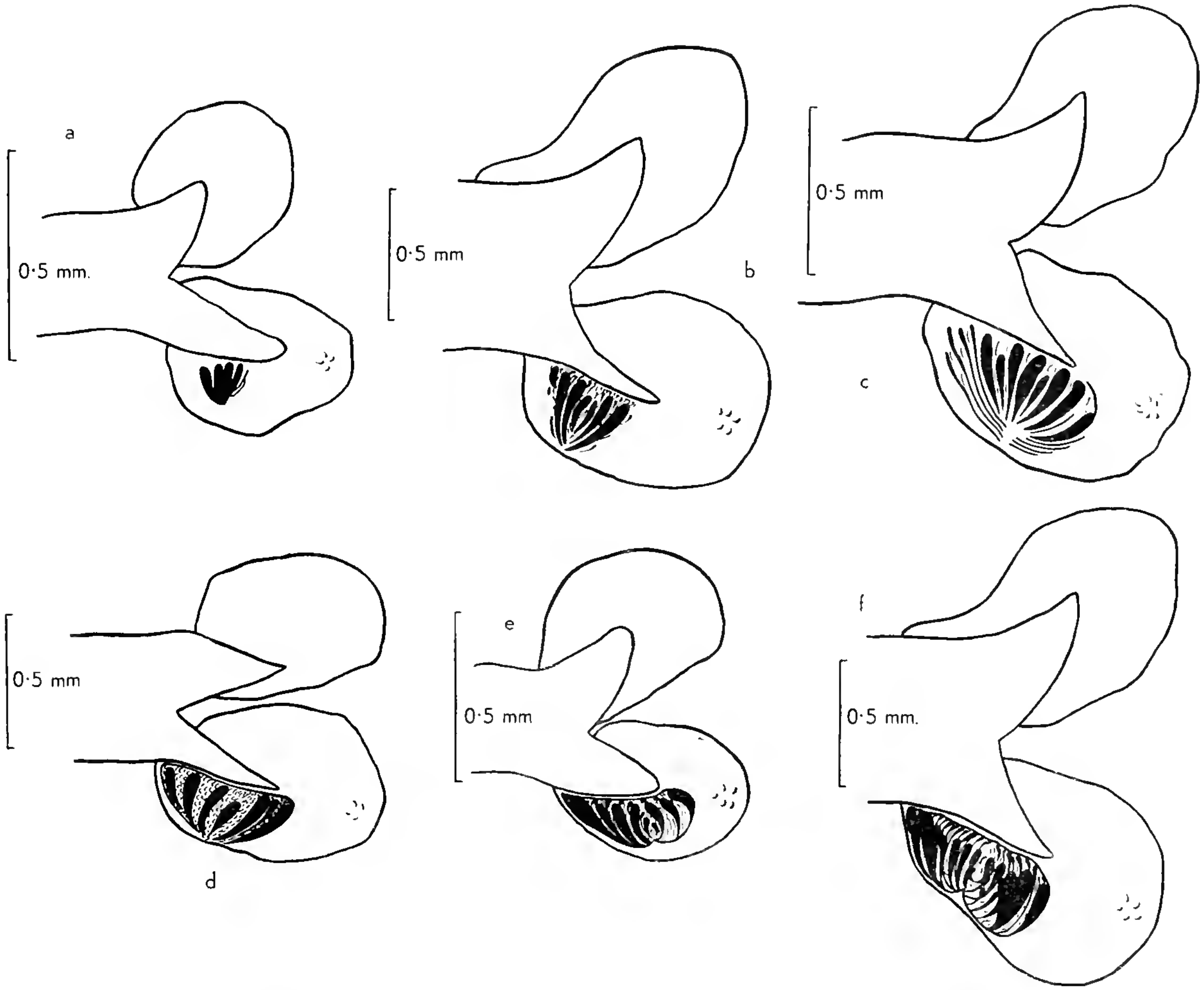
Table 2. *Measurements of* Tomopteris planktonis

Station no.	*Net*	*Depth (m.)*	*Length (mm.)*	*Greatest width (mm.)*	*No. of parapodia*
2024	N 70 V	100–50	2·0	0·5	10
2023	N 70 V	500–250	2·5	1·0	13
2393	N 70 V	750–500	3·0	1·5	12
2084	TYFB	240–0	3·5	2·0	14
2028	N 70 B	118–0	3·5	2·0	15
2034	N 100 B	162–0	4·0	1·5	14
259	TYF	450–370	5·0	2·0	15
2014	N 70 V	250–100	5·0	2·0	15
2027	N 70 V	250–100	5·0	2·0	16
1781	N 70 V	750–500	5·0	2·5	16
1779	N 70 V	750–500	6·0	2·5	16
661	TYFV	500–250	6·5	2·5	15
686	TYFB	400–0	7·0	3·0	17
672	TYFB	200–0	7·5	3·0	17
254	TYF	200(–0)*	8·0	3·0	15
674	TYFB	280–0	9·0	3·0	17
2040	TYFB	600–0	10·5	3·0	17

* When the symbol (–0) is used it means that the net was hauled open to the surface because of failure in the closing mechanism.

The anterior border of the antennae is entire, and there is a pair of prominent eyes on the prostomium. The first pair of chaetigers is never present in this species; the second pair reach normally to about two-thirds the length of the body; occasionally they are longer, but never more than the body length. Hyaline glands appear apically on the neuropodial pinnule of all feet, but they are frequently indistinct. The chromophil glands appear first on the inferior border of the neuropodial pinnules of the fourth parapodia, and vary slightly in position and development according to the size of the specimen. In the smallest, and almost certainly youngest forms (Text-fig. 6*a*), the gland is not fully developed, but consists of a group of small tubules some distance away from the junction of the corner of the pinnule with the parapodial trunk. In the largest and more mature specimens, the gland consists of numerous tubules and projects right into this corner (Text-fig. 6*f*). Stages between these two extremes are shown in Text-figs. 6*b–e* but the glands are not always developed to the same extent on all feet in the same specimen. In a specimen from St. 1776 the gland on the fourth foot was developed as in Text-fig. 6*a*, but on the seventh was similar to that illustrated in Text-fig. 6*e*. From St. 254 there are a number of specimens with fully-developed chromophil glands on the fourth to seventh feet but with no development of the gland from the eighth foot up to the end of the body. A tail is never present in this species.

Discussion. In Apstein's original description of *T. planktonis* he particularly noted the absence of a first pair of chaetigers but some later authors (Malaquin and Carin, 1922, and Stop-Bowitz, 1948) have noticed their presence in supposedly young forms. From Apstein's illustration it is clear that his specimen, 5 mm. long for thirteen pairs of parapodia, was not fully developed, the chromophil gland being some distance from the pinnule. It is in fact of that size and stage of development in which one would expect a first pair of chaetigers to be present, if they are present at all. In the present survey, even in the smallest specimens, 2 mm. long for ten pairs of parapodia, there is no sign of a first pair of chaetigers, and I must conclude that the particular specimens to which Malaquin and Carin (1922) and Stop-Bowitz (1948) referred are not *T. planktonis*; it is possible that they were dealing with young specimens of *T. elegans* (see pp. 179–180).



Text-fig. 6. *Tomopteris planktonis*: parapodia of specimens from (*a*) St. 1782, (*b*) St. 254, (*c*) St. 2316, (*d*) St. 2393, (*e*) St. 1776, (*f*) St. 254.

In the course of this work I have re-examined the following material:

(*a*) Monro, 1930, p. 87, as *T. cavalli*, from 'Discovery', St. 89, 1000–0 m. Monro reported four specimens, three of which are present in the B.M.(N.H.), (Reg. no. 1930, 10.8.848–850) all of them in a state of bad preservation; two have a first pair of chaetigers, the larger, 15 mm. long for twenty-three parapodia, has a tail, and the other, 11 mm. long for twenty-one parapodia has hyaline glands. Neither of these can be *T. cavalli*, which was first described by Rosa (1907) without hyaline glands, or a tail, or a first pair of chaetigers. I think they are *T. krampi* Wesenburg-Lund (1936) (see below, pp. 181–182). The third specimen, 9 mm. long for twenty parapodia, is too macerated to allow of specific determination.

(*b*) Monro, 1936, p. 121, as *T. cavalli* from 'Discovery', St. 451, 170–0 m. Monro reported five specimens, nine are present in the B.M.(N.H.), (Reg. no. 1936.2.8.1000–6). All these specimens are small, between 3 and 6 mm. long for twelve to sixteen pairs of parapodia, and have apical hyaline glands on neuropodial pinnules. Not even in the smallest, 3 mm. long for twelve parapodia, is there a first pair of chaetigers. I consider all these specimens are *T. planktonis.*

One of the original localities from which specimens of *T. cavalli* were first described was in the South Atlantic, off Buenos Aires Province (Rosa, 1907) and I had expected to find it in the present survey. It is, however, very close to *T. planktonis*, differing only in being without hyaline glands, and in having a mid-ventral chromophil gland. This latter character has been shown (p. 172) to be characteristic of development of *T. planktonis* and of specimens of *T. planktonis* which also have fully developed chromophil glands on other feet (Text-fig. 6, p. 173). Moreover all species of *Tomopteris* normally possessing hyaline glands have a proportion of them pigmented, but occasionally specimens occur with some of these glands on a few parapodia lacking pigment and therefore are difficult to see. In *T. planktonis* the hyaline glands are often unpigmented and staining of the pinnule is necessary to show up the glands. A negative characteristic of this kind can be very confusing and I doubt whether *T. cavalli* is a valid species.

(*c*) In re-examining Monro's (1936) material of *T. septentrionalis* from 'Discovery', St. 41 A (B.M.(N.H.), Reg. no. 1936.2.8.1038) I find it to be *T. planktonis.*

General distribution. T. planktonis has been widely reported from the Atlantic at all explored depths: it is circumpolar in Antarctic waters and almost certainly cosmopolitan (see pp. 228–231).

Tomopteris carpenteri Quatrefages, 1865

Type locality. The Southern Ocean; 60° 3′ S., 0° 6′ E.

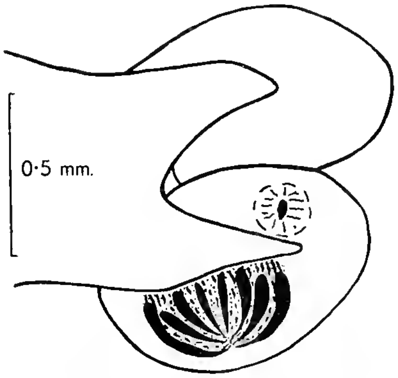
Tomopteris carpenteri Quatrefages, 1865, pp. 227–9, pl. 20, figs. 1, 2.
Tomopteris carpenteri Ehlers, 1917, pp. 229–31, pl. 12, figs. 9–12 (in part).
nec Tomopteris carpenteri McIntosh, 1925,pp. 29–32.
Tomopteris carpenteri Augener, 1929, pp. 304–7.
Tomopteris carpenteri Benham, 1929, pp. 191–5, pl. 11, figs. 18–23.
Tomopteris (*Tomopteris*) *carpenteri* Monro, 1930, pp. 84–6 (in part).
Tomopteris carpenteri Hardy and Gunther, 1935, p. 115.
Tomopteris (*Tomopteris*) *Carpenteri* Stop-Bowitz, 1949, pp. 16–17, figs. 6–7.
Tomopteris (*Tomopteris*) *Carpenteri*, Stop-Bowitz, 1951, p. 9.
Tomopteris carpenteri, Fauvel, 1953*b*, pp. 4–5.

Description. This is the largest of all known Tomopteridae, measuring up to 90 mm. long by 18 mm. wide for thirty-five pairs of parapodia; normally, however, it is about 55 mm. long by 15 mm. wide for thirty-three pairs. In the present survey a larger number of young specimens of this species have been examined and the measurements for a number of these are listed according to size in Table 3. Within the size ranges of these juvenile specimens confusion can arise when separating *T. carpenteri* from *T. planktonis.*

The anterior border of the antennae is entire. In young forms the eyes are always visible on the dorsal surface of the prostomium, but are much less distinct in the adult. A first pair of chaetigers is never present; the second pair may reach back to three-quarters of the length of the body. The hyaline gland is deeply pigmented and first appears in both young and adult specimens on the third neuropodial pinnule, dorsal to the parapodial trunk; it is always conspicuous and is present on each foot up to the end of the body. Chromophil glands appear on the neuropodial pinnule, ventral to the parapodial trunk on all feet from the fourth backwards (Text-fig. 7). They are much bigger in the adult than in the young forms but apart from size there is no structural difference. There is no tail in this species.

Table 3. *Measurements of* Tomopteris carpenteri (*juveniles*)

Station no.	*Net*	*Depth (m.)*	*Length (mm.)*	*Greatest width (mm.)*	*No. of parapodia*
353	N 70 V	250–100	3·5	1·0	13
WS 146	N 70 V	500–250	4·0	1·0	13
301	N 70 V	500–250	4·0	1·5	13
355	N 70 V	500–100	4·0	1·5	14
WS 137	N 70 V	100–50	4·0	1·5	14
MS 25	NC 50 H	10	5·0	2·5	17
WS 143	N 70 V	750–470	5·0	2·0	16
MS 22	NC 50 V	40–0	6·0	2·5	18
WS 141	N 70 V	750–500	8·0	3·0	17
MS 11	NC 50 H	9	9·0	3·0	18
WS 143	N 70 V	750–470	10·0	4·5	18



Text-fig. 7. *Tomopteris carpenteri*: parapodium of specimen from St. MS 11.

Discussion. In his Discovery report of 1930, Monro suggested that *T. planktonis* was probably the young form of *T. carpenteri*, but Augener (1929) had clearly demonstrated that this is not correct. Large numbers of young forms of *T. carpenteri* from the South Georgia surveys in the present material of the same size range as *T. planktonis* (compare the tables on p. 172 and p. 175) support Augener's conclusion. In *T. planktonis* the hyaline gland is normally unpigmented and apical on the neuropodium, whereas in *T. carpenteri* it is dorsal and always distinctly pigmented even in the very smallest specimens (compare Text-fig. 6, p. 173 and Text-fig. 7). Monro was able to see a copy of Augener's work before his report was published and he added a note to the effect that, if *T. carpenteri* and *T. planktonis* are separate species, his material from Sts. MS 11, MS 19, MS 22, MS 25, MS 31, MS 32, MS 34A, MS 62 and SS 21 would be *T. planktonis*. I have re-examined all these, except the specimen from St. MS 19 which is not in the B.M.(N.H.) collections, and find that in fact they are all young *T. carpenteri*, except the specimen from SS 21 which is *T. planktonis*. Monro noted also that all these are coastal stations (actually SS 21 is not), the suggestion being that the specimens might represent an inshore breeding species. This note will be discussed later (pp. 224–228), but it can be stated here that in the present work the smallest specimens of *T. carpenteri* have been found only in the neighbourhood of South Georgia.

In 1925 McIntosh reported *T. carpenteri* from off the Cape of Good Hope, 33° 46′ 00 S., 17° 13′ 00 E. It is unfortunate that this specimen is not available for examination, but it is described with a tail, with frilled margins to the pinnules, and is figured with a deep indentation in the anterior border of the antennae: it is clearly *T. nisseni* (see pp. 180–181).

General distribution. *T. carpenteri* is known only from the Antarctic Zone where the adult has been recorded from all explored depths; the smallest specimens of this species were found only around South Georgia (see pp. 224–228).

Tomopteris septentrionalis Quatrefages, 1865

Type locality. '...les mers du Danemark.'

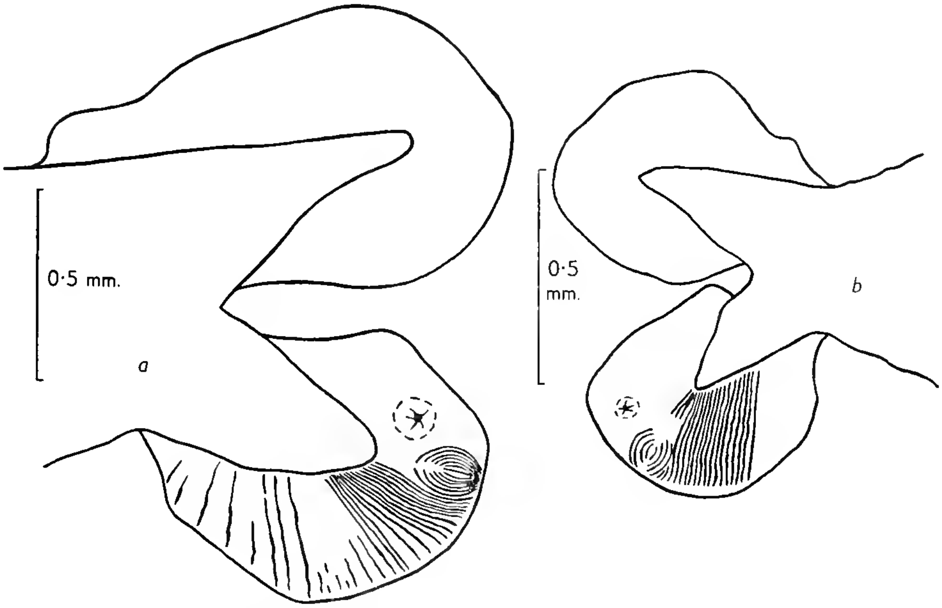
Tomopteris septentrionalis Steenstrup, 1849, p. iv (*nomen nudum*).
Tomopteris septentrionalis Quatrefages, 1865, p. 229.
Tomopteris Eschscholtzii Greeff, 1879*a*, pp. 276–7, pl. 15, figs. 42, 48, 51.
Tomopteris septentrionalis Levinsen, 1883, p. 245.
Tomopteris Eschscholtzii Apstein, 1900, p. 42.
Tomopteris septentrionalis Apstein, 1900, pp. 41–2, pl. 11, figs. 16–17.
Tomopteris septentrionalis Reibisch, 1905, p. 9, fig. 13.
Tomopteris (*Tomopteris*) *septentrionalis* Rosa, 1908*b*, pp. 297–301, pl. 12, fig. 17.
Tomopteris (*Johnstonella*) *septentrionalis* Gravier, 1911*b*, pp. 72–3.
Tomopteris septentrionalis Southern, 1911, pp. 20–8.
Tomopteris septentrionalis Ehlers, 1917, p. 229.
Tomopteris septentrionalis Saemundson, 1918, pp. 191–2.
Tomopteris (*Tomopteris*) *septentrionalis* Fauvel, 1923, p. 224, fig. 84*d*.
Tomopteris septentrionalis McIntosh, 1925, pp. 24–6, pl. 5, fig. 3, pl. 1, fig. 6.
Tomopteris septentrionalis Wesenburg-Lund, 1928, pp. 137–8.
Tomopteris (*Tomopteris*) *septentrionalis* Augener, 1929, pp. 301–2.
Tomopteris (*Tomopteris*) *septentrionalis* Monro, 1930, pp. 86–7.
Tomopteris septentrionalis Fauvel, 1932*a*, p. 18.
Tomopteris septentrionalis Hardy and Gunther, 1935, p. 115.
Tomopteris septentrionalis Wesenburg-Lund, 1935, pp. 9–12, text-fig. 2, pl. 1, figs. 7, 8, 9.
Tomopteris (*Tomopteris*) *septentrionalis* Monro, 1936, pp. 121–2 (in part).
Tomopteris septentrionalis Wesenburg-Lund, 1936, pp. 4–7, fig. 6.
Tomopteris septentrionalis Monro, 1939*b*, p. 108.
Tomopteris (*Tomopteris*) *septentrionalis* Stop-Bowitz, 1948, pp. 49–51, figs. 36–7.
Tomopteris (*Tomopteris*) *septentrionalis* Stop-Bowitz, 1949, pp. 12–13.

Description. In Table 4 the measurements of a selection of specimens from various stations and depths have been listed according to size.

Table 4. *Measurements of* Tomopteris septentrionalis

Station no.	*Net*	*Depth (m.)*	*Length (mm.)*	*Greatest width (mm.)*	*No. of parapodia*
2543	N 70 V	50–0	4·0	1·5	14
2638	TYFB	150–0	5·5	2·0	14
2080	TYFB	400–0	6·0	2·0	16
266	TYF	200–0	6·0	2·5	15
2020	N 70 V	1000–1500	8·0	3·0	16
661	TYFV	500–250	8·0	2·5	18
2630	TYFB	1050–550	8·5	3·0	20
266	TYF	200–0	9·0	3·0	21
SS 24	N 100 B	81–0	9·0	3·5	19
1555	TYFB	1000–0	10·0	4·0	19
671	TYFB	360–0	11·0	3·0	21
514	N 100 B	155–0	11·0	3·5	19
2083	TYFB	330–0	12·0	4·0	20
1606	TYFB	190–0	12·5	3·5	21
100	TYF	475–0	12·5	4·0	21
SS 24	N 70 B	81–0	14·0	3·5	19
SS 35	N 100 B	119–0	15·0	4·0	19

The anterior border of the antennae has a prominent central indentation and there is a pair of eyes on the prostomium. The first pair of chaetigers is never present; the second pair reach to about three-quarters the length of the body. Hyaline glands may appear on the first parapodia in the dorsal part of the neuropodial pinnule (Text-fig. 8), but are always present from the third foot up to the end of the body; they are frequently pigmented but may be difficult to see. The chromophil glands appear first on the neuropodia of the third pair of parapodia and subsequently on all feet; they are not compact but consist of a series of ramifying tubules which are situated between the ventral and apical surfaces (Text-fig. 8). A tail is never present.



Text-fig. 8. *Tomopteris septentrionalis*: parapodia of specimens from (*a*) St. 250, (*b*) St. 2017.

Discussion. The diffuse chromophil gland in *T. septentrionalis* might cause it to be confused with both *T. planktonis* and *T. elegans*. *T. planktonis* however has a compact chromophil gland in the adult and it is only in young specimens that any similarity between the two exists; as noted above (p. 174) Monro's (1936) specimen of *T. septentrionalis* from St. 41 A, is *T. planktonis*. The presence of the first pair of chaetigers in *T. elegans* serves to separate it from *T. septentrionalis*.

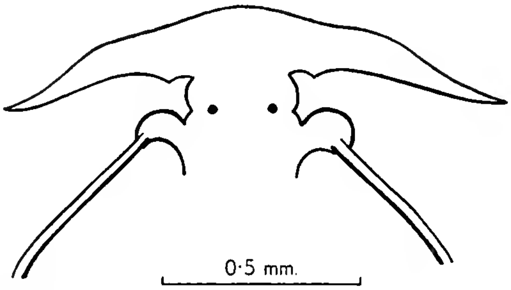
General distribution. Cosmopolitan at all explored depths (see pp. 228–231).

Tomopteris ligulata Rosa, 1908

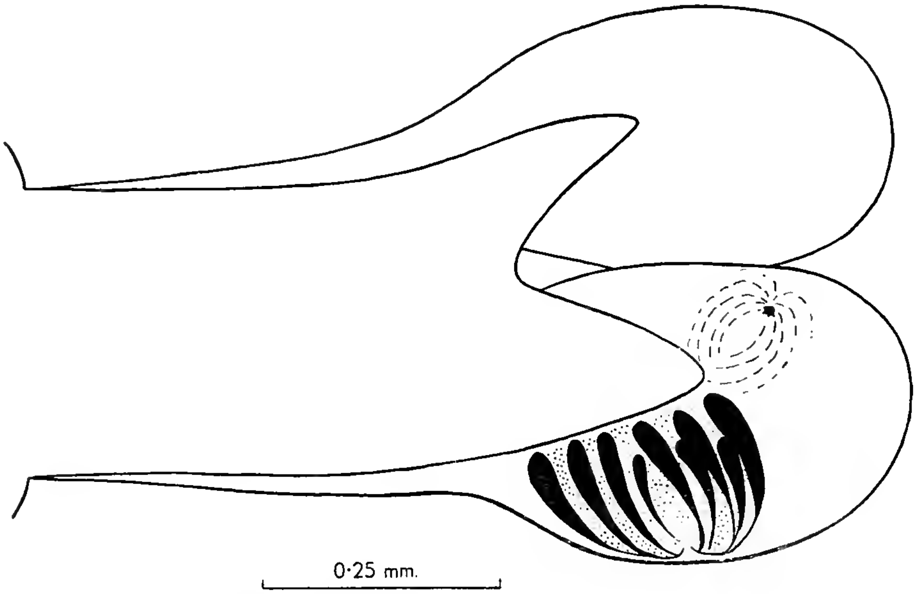
Original localities. Atlantic Ocean, 22° N., 35° W., 33° S., 30° W., Pacific Ocean, 31° S., 84° W.

Tomopteris ligulata Rosa, 1908*a*, p. 1.
Tomopteris (*Tomopteris*) *ligulata* Rosa, 1908*b*, pp. 302–4, pl. 12, figs. 18, 19.
Tomopteris (*Tomopteris*) *ligulata* Malaquin and Carin, 1911, pp. 15–16.
Tomopteris ligulata Ehlers, 1917, pp. 232–3 (in part).
Tomopteris ligulata Malaquin and Carin, 1922, p. 22, p. 28, pp. 41–2, pl. 6, fig. 3, pl. 10, figs. 3–5.
Tomopteris (*Tomopteris*) *ligulata* Fauvel, 1923, p. 224, fig. 84*e*.
Tomopteris (*Tomopteris*) *ligulata* Caroli, 1928*a*, pp. 4–5.
Tomopteris (*Tomopteris*) *ligulata* Caroli, 1928*b*, pp. 7–8, fig. 3.
Tomopteris (*Tomopteris*) *ligulata* Caroli, 1933, p. 379.
Tomopteris planktonis Monro, 1936, p. 121 (in part).
Tomopteris ligulata Monro, 1939*a*, p. 348.
Tomopteris (*Tomopteris*) *ligulata* Stop-Bowitz, 1948, p. 52, fig. 38.

Description. Fifteen specimens of this species have been examined, of which the largest measures 10·5 mm. long for twenty-two pairs of parapodia and the smallest 4 mm. long for sixteen pairs: the others vary between these limits. The anterior border of the antennae is entire and there is a pair of prominent eyes on the prostomium (Text-fig. 9). There is no first pair of chaetigers; the second pair reach to about two-thirds of the length of the body. The hyaline gland is normally distinct (Text-fig. 10) and appears in a dorsal position from the third neuropodial pinnule to the end of the body and the chromophil gland appears ventrally from the fourth neuropodial pinnule. The pinnules border the parapodia almost to the junction with the body wall (Text-fig. 10): this is a characteristic of the species. In preservative the pinnules frequently become bent concavely backwards, possibly because of the torsion exerted by their long line of contact with the parapodia. There is no tail.



Text-fig. 9. *Tomopteris ligulata*: prostomium and 2nd pair of chaetigers of specimen from St. 2028.



Text-fig. 10. *Tomopteris ligulata*: parapodium of specimen from St. 2028.

Discussion. Through the courtesy of Professor Stresemann and Dr Hartwich, I have been able to examine two specimens of *T. ligulata* Rosa, identified by Ehlers, and described by him in the Deutsche Süd-Polar Expedition's report, 1917, pp. 232–3. The specimens are from the Zoology Museum, University of Berlin (Kat. no. 5857), locality, 63° 42′ S., 82° 0′ E., collected 17. iii. 1903. One specimen is very fragile, 4–5 mm. long, with seventeen pairs of parapodia, with the pinnules not continued close to the body wall, but rounded and typical of the *T. planktonis* condition shown in Text-fig. 6*a–f*, p. 173; the chromophil glands are ventral and the hyaline glands indistinct. The second specimen, not so fragile as the first, is 4–5 mm. long with sixteen pairs of parapodia. Again the parapodial pinnules are not continued close to the body wall and are similar in shape to those of *T. planktonis*; the chromophil gland is ventral and the hyaline gland indistinct. In neither of the specimens is there a first pair of chaetigers; I consider both of them to be *T. planktonis*. On re-examination of the four specimens reported by Monro (1936) from 'Discovery', St. 714 as *T. planktonis*, I find that three of them (B.M.(N.H.) Reg. no. 1936.2.8.1010–1012) are *T. ligulata*.

General distribution. *T. ligulata* has been frequently recorded from the Atlantic where it has its southern limit of distribution at the Sub-Tropical Convergence (see p. 248).

Tomopteris elegans Chun, 1887

Type locality. Canary Islands, 500–1300 m.

Tomopteris elegans Chun, 1887, pp. 18–19, pl. 3, figs. 4–9.
Tomopteris Kefersteinii Apstein, 1900, p. 41, pl. 11, fig. 15 (*nec T. Kefersteinii* Greeff).
Tomopteris (*Tomopteris*) *elegans* Rosa, 1908*b*, pp. 294–7, pl. 12, fig. 16.
Tomopteris elegans Ehlers, 1917, p. 227.
Tomopteris (*Tomopteris*) *elegans* Malaquin and Carin, 1922, pp. 37–8, pl. 5, figs. 1–6, pl. 8, figs. 3–5, pl. 9, figs. 1–3.
Tomopteris (*Tomopteris*) *elegans* Fauvel, 1923, p. 223, figs. 84*b*, *c*.
Tomopteris elegans Benham, 1929, pp. 196–7, pl. 2, figs. 24–6.
Tomopteris (*Tomopteris*) *elegans* Terio, 1947, pp. 353–4, fig. 18.
Tomopteris (*Tomopteris*) *elegans* Stop-Bowitz, 1948, pp. 46–8, fig. 33*a–b*.

Description. Twenty-six specimens of this species have been examined, and in Table 5 measurements of nine of them are listed as typical of their size range.

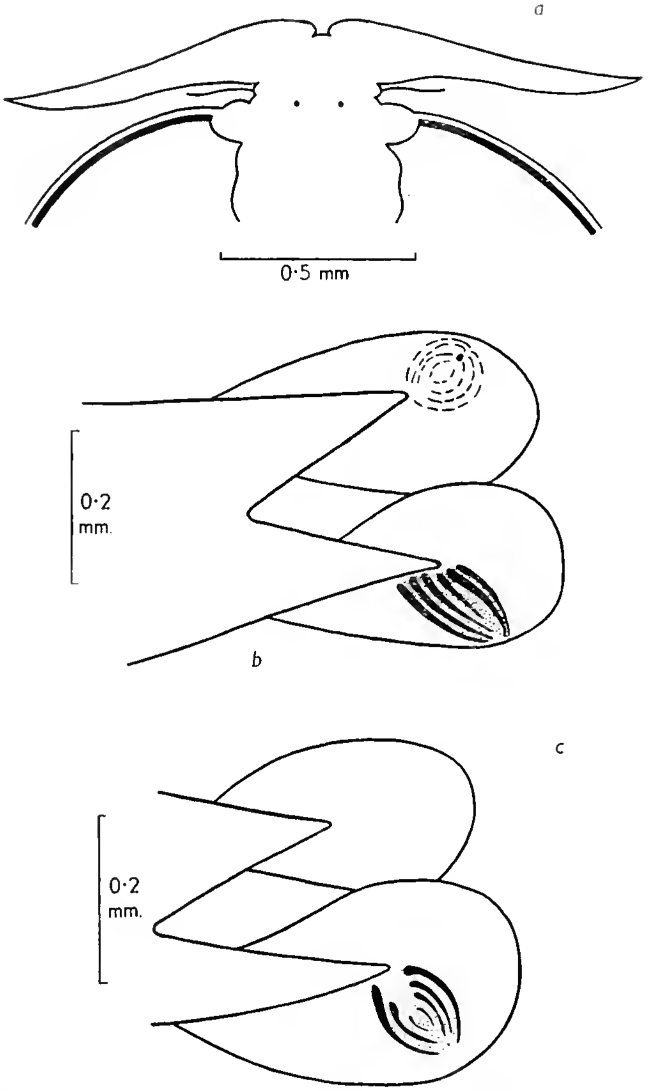
Table 5. *Measurements of* Tomopteris elegans

Station no.	*Net*	*Depth (m.)*	*Length (mm.)*	*Greatest width (mm.)*	*No. of parapodia*
2632	TYFB	1800–0	4·0	1·5	14
2030	N 70 B	250–0	4·5	2·0	15
2028	TYFB	118–0	5·0	2·5	13
2040	TYFB	600–0	5·0	2·0	14
690	TYFB	1500–0	5·0	2·0	14
2028	TYFB	118–0	5·5	2·5	14
2040	TYFB	600–0	6·5	3·0	14
			6·5	3·0	14
2079	TYFB	250–0	7·0	2·5	15

The anterior border of the antennae has a pronounced central indentation (Text-fig. 11*a*). A pair of eyes is present, frequently indistinct in small specimens. The first pair of chaetigers is always present (Text-fig. 11*a*) and the second pair reach to two-thirds the length of the body. Pigmented hyaline glands are present on the notopodial pinnules of the third and fourth feet only (Text-fig. 11*b*), elsewhere they are absent. Chromophil glands appear from the fourth neuropodial pinnule on all feet up to the end of the body; they are ventral in position just below the apex of the parapodial trunk (Text-fig. 11*c*). There is no tail.

Discussion. It is possible that in some very young specimens of *T. elegans* the hyaline glands are not pigmented; such specimens could have been confused with *T. planktonis* and have given rise to the idea that *T. planktonis* has a first pair of chaetigers.

General distribution. *T. elegans* is widely distributed in the warmer waters of all seas: it has its southern limit of distribution in the Atlantic Ocean at the Sub-Tropical Convergence (see pp. 250–252).



Text-fig. 11. *Tomopteris elegans*: (*a*) prostomium and 1st and 2nd pair of chaetigers of specimen from St. 2028, (*b*) 4th parapodium of specimen from St. 2028, (*c*) 5th parapodium of specimen from St. 2632.

Tomopteris nisseni Rosa, 1908

Type locality. Atlantic Ocean, 20° S., 27° W.

Tomopteris Nisseni Rosa, 1908*a*, p. 1.
Tomopteris (*Tomopteris*) *Nisseni* Rosa, 1908*b*, pp. 292–4.
Tomopteris (*Tomopteris*) *Nisseni* Malaquin and Carin, 1911, pp. 11–12.
Tomopteris Nisseni Southern, 1911, pp. 17–20, pl. 1, figs. 1–2.
Tomopteris Nisseni Malaquin and Carin, 1922, pl. 4, figs. 1–4, pl. 8, figs. 1–2.
Tomopteris (*Tomopteris*) *Nisseni* Fauvel, 1923, p. 222, fig. 83*e*, *g*.
Tomopteris carpenteri McIntosh, 1925, pp. 29–31.
Tomopteris nisseni McIntosh, 1925, pp. 26–7.
Tomopteris (*Tomopteris*) *nisseni* Monro, 1930, pp. 87–8.
Tomopteris Nisseni Fauvel, 1932*a*, pp. 17–18.
Tomopteris nisseni Wesenburg-Lund, 1935, pp. 6–9, figs. 13–15.
Tomopteris (*Tomopteris*) *Nisseni* Terio, 1947, pp. 351–3, figs. 16–17.
Tomopteris (*Tomopteris*) *Nisseni* Stop-Bowitz, 1948, pp. 44–6, figs. 29–30.
Tomopteris nisseni Wesenburg-Lund, 1950*b*, p. 42.
Tomopteris nisseni Wesenburg-Lund, 1951, pp. 32–3.

Description. This is a large species which may measure up to 60 mm. long in the adult, but it appears to be very difficult to catch and preserve in good condition, so that for the majority of specimens it is not possible to give accurate measurements or parapodial counts. Among the largest specimens is one from St. 1555, measuring 49 mm. in length by 11 mm. wide for twenty-five parapodia with another four rudimentary feet on the broken tail. At St. 2646 one of the smaller specimens occurred, measuring 7·5 mm. long by 3 mm. wide for nineteen parapodia. There is a deep indentation in the middle of the anterior border of the antennae, and two prominent eyes are set close together on the prostomium. The first pair of chaetigers is missing; the second pair is very long and in the smaller specimens may be four or five times as long as the body, but in the adult it is normally only twice the body length. Parapodial pinnules are reduced to a fringe bordering the feet. Apical hyaline glands normally appear first on the neuropodial pinnules of the third parapodia and on the notopodia of the eighth feet, and on all subsequent rami to the end of the body. They are frequently indistinct and in the smaller specimens are difficult to see. Prominent chromophil glands appear first in the ventral part of the fourth neuropodial pinnule in the adult, and are present on all parapodia up to the pygidium. In the small specimens, the chromophil gland may not appear until the tenth foot or later. The notopodial hyaline gland seems to vary a great deal in position, Rosa (1908*b*) reporting it from the third, Fauvel (1923) from the eighth or ninth, Wesenburg-Lund (1935) from the fifth and Stop-Bowitz (1948) from the fourth pair of parapodia: in the specimens examined here it does not vary to this extent, but in small specimens it is frequently so indistinct that it cannot be seen on some anterior feet. A prominent tail is present with rudimentary parapodia, but it is almost always incomplete.

Discussion. As noted on page 175 the *T. carpenteri* described by McIntosh (1925) from off South Africa is almost certainly *T. nisseni*. The relationship of *T. nisseni* to other species is discussed on page 182.

General distribution. T. nisseni is widely reported from the Atlantic Ocean in which its southern distribution is limited by the Sub-Tropical Convergence (see pp. 246–248).

Tomopteris krampi Wesenburg-Lund, 1936

Type locality. North Atlantic Ocean, 36° 19′ N., 26° 50′ W.

Tomopteris (*Tomopteris*) *cavallii* Monro, 1930, p. 87 (in part ?).
Tomopteris Krampi Wesenburg-Lund, 1936, pp. 8–11, figs. 1–3.
Tomopteris (*Tomopteris*) *Krampi* Stop-Bowitz, 1948, pp. 48–9, fig. 34.

Description. The measurements of all specimens of this species examined in the present survey are listed in Table 6, except Monro's 1930 material from 'Discovery', St. 89, which are on p. 173.

Table 6. *Measurements of* Tomopteris krampi

Station no.	*Net*	*Depth (m.)*	*Length (mm.)*	*Greatest width (mm.)*	*No. of parapodia*
2081	TYFB	950–500	9·0	3·0	22
*2083	TYFB	330–0	13·0	4·0	21
256	TYF	1100–800(–0)	19·0	5·0	22
			19·0	5·5	23
*1604	TYFB	620–500	19·0	5·0	22
673	TYFV	1000–750	21·0	7·0	23
*1606	TYFB	600–300	26·0	9·0	22

Specimens indicated by an asterisk have a tail and this is included in the measurement of length. The anterior border of the first pair of chaetigers is entire with a slight fold in the central portion; there is a pair of eyes on the prostomium. The first pair of chaetigers is present and the second pair extend a little beyond the body length. Hyaline glands appear on all notopodial and neuropodial pinnules from the third feet. They are distinct in most specimens and apical in position near the apex of the parapodial rami. Chromophil glands occur ventrally on the neuropodial pinnule of all feet from the third backwards, except in the specimen from St. 2081 where they appear first on the fourth foot. A tail is normally present but is frequently broken off.

Discussion. As noted on p. 173, I think it possible that two of the specimens reported by Monro (1930) as *T. cavallii* are *T. krampi*. Most of the Discovery material examined here is larger than the original specimens recorded by Wesenburg-Lund (1936), who gave a size range of 10–15 mm. in length by 4–5 mm. wide, or by Stop-Bowitz (1948) who reported one of the larger of his specimens as 10 mm. long by 4 mm. wide. Both these authors noted that the chromophil gland began on the fourth foot, whereas in my material this is the case in only the smallest specimen. It is probable that as development proceeds, the chromophil gland appears on the third foot. Both Wesenburg-Lund (1936) and Stop-Bowitz (1948) regarded *T. krampi* as closely related to *T. elegans*, but I think it is much closer to *T. nisseni* or *T. kempi*. *T. nisseni* is normally much bigger than *krampi*, but apart from size differs only in lacking a first pair of chaetigers and in the arrangement of the hyaline glands; *T. kempi* also differs in being without a first pair of chaetigers, but has rosette glands instead of hyaline glands (p. 183). The size range of Monro's smaller specimens of *T. kempi* (p. 182) covers that found here for *T. krampi*, otherwise I would have suggested that the material above represents the young stages of *T. kempi* which possibly lose the first pair of chaetigers on becoming adult.

General distribution. Known only from the Atlantic, off south-west Iceland, Southern Greenland (Wesenburg-Lund, 1936) between the Canaries and the Azores and between Newfoundland and Ireland (Støp-Bowitz, 1948) *T. krampi* is reported here for the first time from the South Atlantic, probably having the southern limit of its distribution at the Sub-Tropical Convergence (see p. 250).

Tomopteris kempi Monro, 1930

Type locality. 'Discovery', St. 4, off Tristan da Cunha, 36° 55′ 00″ S., 12° 12′ 00″ W., 0–10 m. B.M.(N.H.) Reg. no. 1930.10.8.3076–3080, 7 specimens.

Tomopteris (*Johnstonella*) *kempi* Monro, 1930, pp. 88–9, fig. 27.

Description. Measurements of all seven specimens reported by Monro are listed in Table 7.

Table 7. *Measurements of* Tomopteris kempi

Length (mm.)	*Greatest width (mm.)*	*No. of parapodia up to tail*	*No. of rudimentary parapodia on tail*
9	3·0	14	3
12	4·0	15	2
13	4·0	15	1
18	6·0	15	3
38	10·0	16	2
55	12·0	16	4
55	20·0	16	3

There is a small indentation in the middle of the antennae and a pair of indistinct eyes on the prostomium. The first pair of chaetigers is missing; the second pair about two-thirds the body length in the larger specimens, but in the small ones the chaetigers are a third as long again. On the third parapodia and all subsequent feet there is a black spot on the notopodial and neuropodial pinnules, where they meet the apex of the parapodial trunks. These black spots Monro called rosette glands. From the third foot backwards, there is a ventral chromophil gland in the neuropodia. There is a prominent tail carrying rudimentary feet.

Discussion. The black spot described by Monro as a rosette gland bears no resemblance to described rosettes, nor does it have any of the fine tubules normally associated with hyaline glands. It is probably advisable to separate it from the hyaline organ, but to call it a rosette over-emphasizes the difference, and tends to hide the close relationship of *T. kempi* to *T. nisseni* and *T. krampi.*

Tomopteris apsteini Rosa, 1908

Type locality. Messina, Mediterranean Sea.

Tomopteris (*Tomopteris*) *Apsteini* Rosa, 1908*b*, pp. 288–92, pl. 13, figs. 10–13.
Tomopteris rosaea Ehlers, 1917, pp. 224–7, pl. 11, figs. 2–8.
Tomopteris (*Johnstonella*) *apsteini* Malaquin and Carin, 1922, pp. 31–4, pl. 2, figs. 1–4; pl. 3, figs. 1–7, pl. 7, figs. 1–3.
Tomopteris (*Johnstonella*) *Apsteini* Fauvel, 1923, pp. 220–1, fig. 83*a–d*.
Tomopteris (*Johnstonella*) *Apsteini* Støp-Bowitz, 1948, pp. 39–42, figs. 26–7.

Description. In Table 8 measurements for ten of the twenty-five specimens examined have been listed, including the smallest and largest.

Table 8. *Measurements of* Tomopteris apsteini

Station no.	*Net*	*Depth (m.)*	*Length (mm.)*	*Greatest width (mm.)*	*No. of parapodia*
679	TYFV	250–0	8	3·5	22
679	TYFB	300–0	9	2·5	21
676	TYFB	290–0	10	3·0	22
682	TYFB	375–0	13	4·0	21
678	TYFB	360–0	15	4·5	21
1555	TYFB	1000–0	18	7·5	19
2083	TYFB	330–0	20	7·0	19
247	TYF	115–100(–0)	22	6·0	19
674	TYFB	280–0	43	13·0	30
677	TYFV	2000–0	47	10·0	30

There is a small indentation in the middle of the anterior border of the antennae. A pair of eyes is present on the prostomium but the eyes are rarely distinct. The first pair of chaetigers is small, the second pair extend to about two-thirds the length of the body. One rosette is present near the ventral surface of the parapodia of each of the first two feet; thereafter one is present on all notopodial and neuropodial pinnules where they meet the apex of the parapodial trunk. The characteristic 'spur' glands of the species may appear on the first neuropodia, projecting prominently from the ventral border of the pinnules; they are always present from the second feet onwards and from the third are associated with the large chromophil glands. In the larger specimens, both spur and chromophil glands are so close together that they appear as one, with the spur represented as an outgrowth breaking the ventral surface of the pinnule. A prominent tail is always present and with it are normally associated rudimentary parapodia.

General distribution. T. apsteini has its southern limit of distribution in the Atlantic Ocean at the Sub-Tropical Convergence (see p. 252).

Family ALCIOPIDAE

Exclusively pelagic. Body elongate with numerous segments; exceptionally short and wide. Prostomium small with two very large eyes, and normally with five antennae. Three or five pairs of tentacular cirri. Proboscis eversible, sometimes with two long anterior cirriform appendages, always with papillae, rarely with chitinous teeth. Parapodia uniramous with dorsal and ventral cirri, pedal lobe, simple and/or compound chaetae, and normally with pigmented segmental glands. In the female, anterior dorsal cirri may be modified into seminal pouches. Anal cirri present.

Genus NAIADES Delle Chiaje, 1830

Body elongate with the prostomium carrying five antennae. There are three pairs of tentacular cirri and the first three pairs of parapodia are reduced. Proboscis bell-shaped with two short anterior cirriform lobes, between which are small papillae. Parapodia with simple chaetae only; the pedal lobe is without an appendage.

Type species. Naiades cantrainii Delle Chiaje, 1830.

Type locality. Naples.

Stop-Bowitz (1948) has demonstrated the necessity for replacing the long accepted generic name *Alciopa* with *Naiades.*

Naiades cantrainii Delle Chiaje, 1830

Naiades cantrainii Delle Chiaje, 1830, pl. 82, figs. 14, 18, 21.
Alciopa Reynaudi Krohn, 1845, pp. 172–3, pl. vi, figs. 1–6, *nec* Aud. and M. Edwards.
Alciopa Edwardsii Krohn, 1847, pp. 39–40.
Alciope Edwardsii Grube, 1850, p. 305.
Krohnia Edwardsii Quatrefages, 1865, p. 158.
Alciopa Edwardsii Ehlers, 1868, p. 176.
Alciopa Cantrainii Claparède, 1870, pp. 469–71, pl. 10, fig. 2.
Alciopa Cantrainii Greeff, 1876, pp. 57–60.
Alciope cantrainii Viguier, 1886, p. 404.
Alciope microcephala Viguier, 1886, pp. 404–5, pl. 26, figs. 1–5.
Alciopa cantrainii Apstein, 1891, p. 128.
Alciopa Cantrainii Apstein, 1900, p. 7, pl. 5, fig. 53.
Alciope cantrainii Ehlers, 1913, p. 464.
Alciope Cantrainii Fauvel, 1916, pp. 64–5.
Alciopa Cantrainii Fauvel, 1923, pp. 203–4, fig. 76.
Alciopa cantrainii Monro, 1930, p. 84.
Alciopa cantrainii Monro, 1936, p. 115.
Alciopa cantrainii Wesenburg-Lund, 1939, pp. 25–8, fig. 19.
Naiades Cantrainii Stop-Bowitz, 1948, pp. 24–5, figs. 15–16.

Description. This species may measure up to 110 mm. in length by 8 mm. wide across the tips of chaetae, but complete specimens are not common. The body is sharply terminated anteriorly with the eyes projecting prominently forward with the small prostomium between them. There are two pairs of small anterior antennae and one small unpaired median antenna on the dorsal surface between the eyes. The first pair of tentacular cirri are long, the remaining two very small. The first three pairs of parapodia are much reduced with small lobes and no chaetae but with aciculae; in the female the dorsal and ventral cirri of the second pair are modified as seminal pouches. Subsequent parapodia up to the end of the body each have a large foliaceous dorsal cirrus, a smaller ventral cirrus, a prominent projecting acicula, long simple chaetae and a strongly pigmented dorsal segmental gland.

General distribution. N. cantrainii is widely reported from the South Atlantic where it has its southern limit of distribution at the Sub-Tropical Convergence (see p. 257).

Genus Vanadis Claparède, 1870

Body elongate. Prostomium with two pairs of small antennae on the anterior border and one single, dorsal, and posterior to these. There are three to five pairs of tentacular cirri. Parapodia with long compound chaetae and pedal lobe with terminal appendage. Proboscis sometimes with two long cirriform appendages and always with small terminal papillae.

Type species. Vanadis formosa Claparède, 1870.

Type locality. Gulf of Naples.

Vanadis formosa Claparède, 1870

Vanadis formosa Claparède, 1870, pp. 480–4, pl. 10, fig. 3.
Vanadis pelagica Greeff, 1876, p. 67, pl. 3, figs. 33–4.
Alciopa longirhyncha Greeff, 1885, pp. 453–5, pl. 14, fig. 37.
Alciopa Krohnii Hering, 1892, p. 738, pl. 4, figs. 1–13.
Vanadis formosa Apstein, 1900, pp. 8–10, pl. 1, fig. 1–6.
Vanadis formosa Lo Bianco, 1904, p. 50, pl. 29, fig. 113.
Vanadis formosa Southern, 1911, pp. 2–3.
Vanadis formosa Fauvel, 1916, pp. 65–6.
Vanadis formosa McIntosh, 1922, p. 13.
Vanadis formosa Fauvel, 1923, pp. 205–6, fig. 77*a–c*.
Vanadis formosa McIntosh, 1923, pp. 440–1.
Vanadis formosa Monro, 1930, p. 81 (in part).
Vanadis formosa Fauvel, 1932*a*, pp. 16–17.
Vanadis formosa Augener, 1934, pp. 217–19.
Vanadis formosa Monro, 1936, p. 116.
Vanadis formosa Monro, 1937, p. 268.
Vanadis formosa Monro, 1939*a*, p. 348.
Vanadis formosa Wesenburg-Lund, 1939, pp. 28–32, figs. 20–21, chart 15.
Vanadis formosa Støp-Bowitz, 1948, pp. 25–6, fig. 17, chart 18.
Vanadis formosa Støp-Bowitz, 1951, p. 7.

Description. This species may measure up to 300 mm. in length by 4–5 mm. wide across the bases of parapodia and 12 mm. across the tips of chaetae, but complete specimens are rare. The two pairs of anterior antennae are digitiform: the single antenna is between the large eyes. The proboscis has two long terminal processes, each carrying a pair of basal ailerons. These ailerons are continuous with dorsal and ventral circlets of papillae; there are six papillae in each of the dorsal and ventral groups and they form a coronet terminal on the proboscis. There are three pairs of tentacular cirri on each of successive segments behind the prostomium, of which the first pair are the longest and are joined to each other by a large basal ceratophore across the ventral surface behind the prostomium. The first two pairs of parapodia are reduced or modified in the mature female, the dorsal cirri becoming voluminous seminal pouches. In the male there is no modification of anterior parapodia but the first two pairs are reduced. In both sexes from the third foot onwards, parapodia are well developed with large foliaceous dorsal and smaller ventral cirri; each foot has a pedal mamelon with a projecting acicula, a cirriform appendage and compound chaetae with short terminal articles. Darkly pigmented segmental glands appear on each foot after the first three, except in the mature females when they appear on the first two modified parapodia. In some specimens which have no seminal pouches on anterior feet, there are well-developed white ventral glands appearing at the twenty-fifth parapodia and continuing up to the end of the body. Støp-Bowitz (1948) has associated this gland with the male.

Discussion. In re-examining Monro's (1930) material of *V. formosa* I find the specimens from 'Discovery' Sts. 85 and 287 are *V. crystallina* (below) and those from Sts. 270 and 282 are *V. longissima* (p. 187).

General distribution. V. formosa is widely reported from the South Atlantic where it has its southern limit of distribution at the Sub-Tropical Convergence (see pp. 252–255).

Vanadis crystallina Greeff, 1876

Type locality. Gulf of Naples.

Vanadis crystallina Greeff, 1876, pp. 68–9, pl. 4, figs. 35–9.
Alciopa candida Hering, 1892, p. 732, pl. 3.
Vanadis crystallina Apstein, 1900, pp. 10–11, pl. 1, fig. 7.
Vanadis cristallina Lo Bianco, 1904, p. 50, fig. 112.
Vanadis crystallina Granata, 1911, p. 56.
Vanadis crystallina Ehlers, 1913, p. 466.
Vanadis crystallina Fauvel, 1916, p. 66.
Vanadis crystallina Fauvel, 1923, pp. 206–7, fig. 77*d, e*.
Vanadis augeneri Benham, 1929, pp. 187–8, pl. 1, figs. 1–7.
Vanadis formosa Monro, 1930, p. 81 (in part).
Vanadis crystallina Fauvel, 1932*a*, p. 17.
Vanadis Augeneri Fauvel, 1935, pp. 295–6.
Vanadis crystallina Monro, 1936, pp. 116–17.
Vanadis formosa Monro, 1937, p. 268.
Vanadis crystallina Wesenburg-Lund, 1939, pp. 32–4, fig. 22, chart 16.
Vanadis Augeneri Fauvel, 1951, p. 292.
Vanadis crystallina Stop-Bowitz, 1951, p. 7.

Description. V. crystallina may measure up to 145 mm. in length by 0·6 mm. wide across the parapodial bases and 3·0 mm. wide across the tips of chaetae, but complete specimens are rare. The antennae are small and conical. The proboscis carries two long terminal processes with two pairs of basal ailerons continuous with dorsal and ventral circlets of four to six papillae. Three pairs of tentacular cirri are present on successive segments behind the prostomium, of which the first are the longest and are joined ventrally by basal ceratophores. The first seven to ten pairs of parapodia are rudimentary; they have no chaetae and only very small parapodial cirri of which the dorsal are the largest and tend to be ovate. In the mature female the first and second of these parapodia have dorsal cirri modified as voluminous seminal pouches; well-developed parapodia appear after the first seven to ten feet, each with a broadly foliaceous dorsal cirrus, a smaller ventral foliaceous cirrus and a long pedal lobe with projecting acicula, cirriform appendage and long compound chaetae with short terminal articles. There is some variation in the position of the pigmented segmental glands on the body. In all mature females and in most other specimens they begin at the fourth foot and continue up to the end of the body, but in a number of specimens they appear first between the seventh and twelfth foot. There appears to be no pattern in this variation, specimens from the same station showing both conditions, and it is probably due to the strength of the pigment in particular glands surviving preservation.

Discussion. Most modern authors describe this species with four pairs of tentacular cirri, although Hering (1892, as *Alciopa candida*) clearly demonstrated that it has only three. Fauvel (1935) first drew attention to this possibility of error, in describing *Vanadis augeneri* Benham, from Annam, and this has been substantiated in recent studies (Stop-Bowitz, 1948). I have re-examined the type specimens of *V. augeneri* (Benham 1929, (B.M.(N.H.), Reg. no. 1929.9.20.1) from 'Terra Nova', Sts. 123–213 and they are identical with the above description of *V. crystallina*. Neither of them are mature females.

Monro (1930) reported specimens from 'Discovery', Sts. 85 and 287 as *V. formosa* (B.M.(N.H.), Reg. no. 1930.10.8.907/958), apparently because the two anterior dorsal cirri of each are modified as seminal pouches; in all respects, however, the specimens are identical with *V. crystallina* and I refer them to this species. Similarly I consider Monro's (1937) specimen of *V. formosa*, from 'John Murray', St. 131 D (not 13 D as printed) (B.M.(N.H.), Reg. no. 1937.9.2.91) to be *V. crystallina*. The specimen from St. 100 (p. 254) has a bifurcate median antenna.

The descriptions of *V. formosa* and *V. crystallina* indicate how closely related they are, and because they both occupy the same zoogeographical areas it is possible that they represent stages in the complex life cycle of a single species. This, of course, can only be elucidated through observation of the living animals.

General distribution. *V. crystallina* is widely reported from the South Atlantic where it has its southern limit of distribution at the Sub-Tropical Convergence (see pp. 252–255).

Vanadis longissima (Levinsen), 1885

Type locality. 26° 0′ N., 26° 0′ W.

Rhynchonerella longissima Levinsen, 1885, pp. 330–1, figs. 7–10.
Vanadis longissima Fauvel, 1916, pp. 66–7.
Vanadis longissima Fauvel, 1923, p. 207, fig. 77*f–g*.
Vanadis longissima Monro, 1930, pp. 79–91, fig. 24*a–c*.
Vanadis formosa Monro, 1930, p. 81 (in part).
Vanadis antarctica Monro, 1930, p. 116 (in part).

Description. No complete specimens of this species have been examined but the longest piece is 80 mm. in length by 9 mm. wide across the tips of chaetae. The dorsal unpaired antenna lies immediately behind the paired anterior group. The proboscis is terminated by twelve separate small papillae. There are three pairs of conical tentacular cirri, all of equal length, of which the first are joined ventrally. The first pair of parapodia are achaetous and have small but broadly foliaceous dorsal cirri; ventral cirri are minute. In the mature female the dorsal cirri of the second and third parapodia are converted into very large, darkly pigmented, seminal pouches, ventral cirri are small and conical; between the two cirri a single compound chaeta projects. The pigment on the seminal pouches appears to originate from the pigmented segmental glands on the second and third feet. From the fourth foot parapodia have foliaceous dorsal cirri, conical pedal and ventral cirri and long compound chaetae; all parapodia gradually increase in size to a constant width at about the eleventh foot. On specimens other than mature females the second and third feet are poorly developed with small foliaceous dorsal cirri and short ventral cirri. The occurrence of the pigmented segmental glands does not follow a particular pattern; this is indicated in Table 9 where the position of the glands up to the forty-third feet has been tabulated from four specimens with more than one hundred chaetigers. After the forty-third parapodia the glands appear at intervals of one, two or three feet up the end of the body. Although no complete specimens have been examined, all the material listed has at least one hundred pairs of parapodia. Normally the pigment is confined to the gland or the dorsal surface of the gland-bearing segment but it may also cover the dorsal and ventral surfaces giving a striped appearance to the specimens.

Discussion. I have re-examined Monro's (1930) specimens of *V. formosa* from 'Discovery', Sts. 270 and 282 (B.M.(N.H.), Reg. no. 1930.10.8.942/904) and his 1936 material of *V. antarctica* from 'William Scoresby', Sts. WS 408, WS 411 (B.M.(N.H.), Reg. no. 1936.2.8.866/867) and consider them to be *V. longissima*.

General distribution. *V. longissima* has been widely reported from the Atlantic Ocean where it probably has its southern limit of distribution at the Antarctic Convergence (see p. 224).

Table 9. *Variation in the position of pigmented segmental glands in* Vanadis longissima (× *indicates the gland is present; L.=left-hand side, R.=right-hand side*)

Parapodia no.	*St. WS* 411 ♀		*St.* 680		*St.* 1972		*St.* 2291	
	L.	*R.*	*L.*	*R.*	*L.*	*R.*	*L.*	*R.*
1	.	.	.	.	.	.	.	.
2	×	×	.	.	×	×	×	×
3	×	×	.	.	×	×	×	×
4	×	×	×	×	×	×	×	×
5	×	×	×	×	×	×	×	×
6	×	×	×	×	.	.	×	×
7	×	×	.	.	×	×	×	×
8	×	×	.	.	×	×	×	×
9	×	×	.	.	×	×	×	×
10	.	.	×	×	.	.	×	×
11	.	.	×	×	.	.	.	.
12	.	.	.	.	.	.	.	.
13	×	×	.	.	×	×	×	×
14	×	×	.	.	×	×	×	×
15	×	×	.	.	×	×	×	×
16	.	.	×	×	.	.	.	.
17	.	.	.	.	×	×	.	.
18	.	.	.	.	.	.	.	.
19	×	×	.	.	.	.	×	×
20	×	×	×	×	×	×	.	×
21	×	×	×	×	.	.	.	.
22	.	.	.	.	.	×	.	.
23	.	.	.	.	.	.	.	.
24	.	.	.	.	.	.	×	×
25	×	×	×	×	×	×	.	.
26	×	×	.	.	.	.	.	.
27	.	.	.	.	.	.	.	.
28	.	.	×	×	×	×	×	×
29	.	.	×	×	.	.	.	.
30	×	×	.	.	×	×	×	.
31	.	.	.	.	.	.	.	.
32	.	.	.	.	×	×	×	×
33	.	.	×	×	×	×	.	.
34	.	.	.	.	.	.	.	×
35	×	×	.	.	×	×	×	×
36	.	.	.	.	.	.	×	.
37	.	.	×	×	.	.	.	.
38	.	.	×	×	×	×	×	×
39	.	.	.	.	.	.	×	.
40	×	×	.	.	.	.	×	.
41	.	.	.	.	.	.	×	.
42	.	.	.	.	×	×	.	×
43	×	×	×	.	.	.	.	.

Vanadis antarctica (McIntosh), 1885

Type locality. At the surface of the Southern Ocean between 'Challenger', Sts. 154, 64° 37′ S., 85° 49′ E., and 155, 64° 18′ S., 94° 47′ E.

Alciopa antarctica McIntosh, 1885, pp. 175–6, pl. 28, figs. 2–4, pl. 32, fig. 12.
Vanadis antarctica Apstein, 1900, p. 11.
Vanadis antarctica Willey, 1902, pp. 271–3, pl. 44, fig. 8, pi. 46, figs. 1 and 2.
Alciopa antarctica Gravier, 1911*b*, pp. 65–70, pl. 2, fig. 26, pl. 3, figs. 28–9, pl. 4, fig. 38.
Vanadis antarctica Ehlers, 1913, p. 466 (in part).

Vanadis antarctica Benham, 1921, pp. 58–61, pl. 8, figs. 61–2.
Vanadis antarctica Augener, 1932, pp. 27–8.
Vanadis antarctica Fauvel, 1936*a*, pp. 17–18.
Vanadis antarctica Mønro, 1936, p. 116 (in part).
Vanadis antarctica Støp-Bowitz, 1948, p. 30.
Vanadis antarctica Støp-Bowitz, 1949, pp. 5–9.
Vanadis antarctica Støp-Bowitz, 1951, p. 7.
Vanadis antarctica Baker, 1954, pp. 208–17.

Description. One of the only two complete specimens of this species examined measures 230 mm. long for 5 mm. wide across the bases of parapodia, and 15 mm. wide across the tips of chaetae. The two pairs of anterior antennae are ovate; the single posterior antenna, between the large eyes, is digitiform. A circlet of twelve separate papillae terminates the proboscis; the papillae are normally equal in length, but sometimes a few of them are slightly longer than the others. There are three pairs of long, slender tentacular cirri on each of successive segments behind the prostomium, of which the first are joined ventrally by basal ceratophores. The first pair of parapodia have prominent foliaceous cirri (which have frequently been mistaken for a fourth pair of tentacular cirri) and tiny ventral cirri, which are always difficult to see. In the female, the dorsal cirri of the next two parapodia are modified as seminal pouches. Subsequently, there is a group of from seven to ten parapodia, which are small though fully developed, each with a pedal lobe and appendage, compound chaetae and dorsal and ventral cirri. Thereafter the parapodia are much larger with the pedal lobes very much longer than the foliaceous cirri and with exceedingly long chaetae. Segmental glands are strongly pigmented, and in the region of the first group of small parapodia (and sometimes including the most anterior of the larger parapodia) the pigment extends over the dorsal surface of the body. This gives the species the appearance of having a pigmented neck and although the degree of pigmentation varies from light to heavy it is always present. The occurrence of the pigmented segmental glands in four specimens is given in Table 10. Although the glands are always present anteriorly they may be absent in the middle body-region, but beyond a certain point on the body, varying between the twenty-third and fiftieth parapodia, the glands are present on every segment, in contrast to *V. longissima* where beyond the fiftieth segment glands are still missing from some chaetigers.

Discussion. I have examined the type specimen in the B.M.(N.H.) (Reg. no. 1885.12.1.131 A), of *Alciopa antarctica* McIntosh, 1885. Unfortunately this specimen is without its head, and efforts to find it, including inquiries at the University of St Andrews, where McIntosh did his work, have been unsuccessful. However the anterior seminal pouches of the left-hand side are present and indicate the specimen is female. As noted on page 187 the specimens reported by Monro (1936) from Sts. WS 408 and 411 as *V. antarctica* are *V. longissima*.

The descriptions of *V. antarctica* and *V. longissima* show the close relation of these two species, and the possibility of their being geographical races of one species is discussed on page 224.

General distribution. V. antarctica is confined to the Antarctic Zone (see p. 224).

Vanadis violacea Apstein, 1893

Type locality. Unknown.

Vanadis violacea Apstein, 1893, p. 143.
Vanadis violacea Monro, 1936, p. 117.

Monro reported two specimens of this species, one each from 'Discovery', Sts. 413 and 419 (B.M.(N.H.), Reg. no. 1936.2.8.900/901), but neither specimen permits of an adequate description of the species, which may represent another race of the *V. longissima-V. antarctica* complex.

Table 10. *Variation in the position of the pigmented segmental glands in* Vanadis antarctica (× *indicates the gland is present; L. = left-hand side, R. = right-hand side)*

Parapodia no.	*Type* ♀		*St.* 1789		*St.* 2006		*St.* 2012 ♀	
	L.	*R.*	*L.*	*R.*	*L.*	*R.*	*L.*	*R.*
1	.	*	.	.	.	.	.	.
2	×	*	×	×	×	×	×	×
3	×	*	×	×	×	×	×	×
4	×	*	×	×	×	×	.	.
5	×	×	×	×	×	×	×	×
6	×	×	×	×	×	×	×	×
7	×	×	×	×	×	×	×	×
8	×	×	×	×	×	×	×	×
9	×	×	×	×	×	×	×	×
10	.	.	.	.	.	.	.	.
11	.	.	.	×	.	.	.	.
12	.	.	×	.	.	.	.	.
13	×	×	×	×	×	×	.	.
14	×	×	×	×	×	×	×	.
15	×	×	×	×	×	×	×	×
16	.	×	.	.	.	.	×	.
17	.	.	.	×	.	.	.	.
18	×	×	.	.	.	.	.	.
19	×	×	×	.	×	×	×	.
20	×	.	×	×	×	×	.	×
21	.	.	×	.	×	×	.	×
22	×	×	.	×	.	.	.	.
23	×	×	×	×	×	.	.	.
24	.	.	×	×	×	×	×	×
25	×	×	×	×	×	×	.	.
26	×	×	×	×	×	×	×	.
27	×	×	.	×	×	×	×	.
28	×	×	×	×	×	×	.	×
29	×	×	×	×	×	×	.	.
30	×	×	×	×	×	×	×	×
31	×	×	×	×	×	×	.	.
32	Present on all succeeding parapodia						×	×
33							.	.
34							×	×
35							.	.
36							.	.
37							×	×
38							×	.
39							.	×
40							×	×
41							.	.
42							×	.
43							×	×
44							.	.
45							×	×
46							×	×
47							.	×
48							×	×
49							.	×
50							×	×
51							×	×
52							×	×
53							×	×
54							×	×
							Present on all succeeding parapodia	

* Segments missing.

Genus RHYNCHONERELLA Costa, 1862

(Emended Claparède, 1868, *pro Rhynchonereella* Costa, 1862)

Prostomium extending beyond the eyes and carrying five antennae. Five pairs of tentacular cirri. Parapodia with a cirriform appendage on the pedal lobe; with simple and/or compound chaetae.

Type species. Rhynchonerella gracilis Costa, 1862.

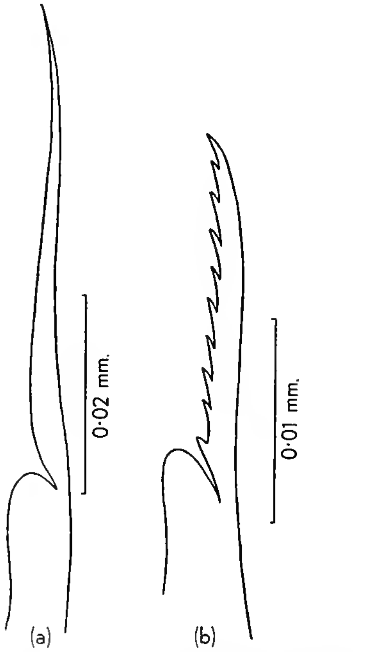
Type locality. Gulf of Naples.

Rhynchonerella bongraini (Gravier), 1911, *n.comb.*

Type locality. Pelagic haul off the Ice Edge, 69° 15′ S., 108° 5′ W., brought from 950 m. to the surface.

Callizona Bongraini Gravier, 1911*a*, p. 312.
Callizona Bongraini Gravier, 1911*b*, p. 70, pl. 4, figs. 39–43.
Callizona Bongraini Gravier, 1911*c*, p. 694.
Callizonella bongraini Augener, 1929, pp. 294–300, fig. 2*a–g*.
Callizona bongraini Benham, 1929, pp. 189–90, pl. 1, figs. 11–12.
Rhynchonerella fulgens Monro, 1930, p. 83, fig. 26.
Alciopid larvae Hardy and Gunther, 1935, p. 117.
Callizonella Bongraini Fauvel, 1936*a*, pp. 18–19.
Callizonella bongraini Monro, 1936, p. 119.
Krohnia Bongraini Stop-Bowitz, 1948, p. 33.
Krohnia Bongraini Stop-Bowitz, 1949, pp. 9–12, figs. 3–4.
Krohnia Bongraini Stop-Bowitz, 1951, p. 8.

Description. The majority of specimens are not complete, except one which measures 13 mm. in length for fifty-one chaetigers with a width across the tips of chaetae of 3·5 mm. Of the incomplete specimens one measures 15 mm. long for fifty-nine chaetigers, and another 11 mm. for forty chaetigers. There are two pairs of short, foliaceous antennae set close together on the anterior border of the prostomium and a median, single, subulate antenna set in the middle of the dorsal surface in the groove between the two enormous spherical eyes. These eyes have a diameter of approximately 0·3 mm. each and cover about 90% of the prostomial surface. The five pairs of tentacular cirri are arranged thus $1+\frac{1}{1}+\frac{1}{1}$; the unpaired anterior is medium in length, the dorsal pair long (posterior longest, about 0·5 mm.), and the ventral pair short. Parapodia have large foliaceous dorsal cirri and smaller ventral foliaceous cirri; the cirriform appendage on the pedal lobe is very small. Characteristic compound chaetae with smooth or denticulated terminal articles (Text-fig. 12*a–b*) appear on the first seven or eight chaetigers. The chaetae with smooth articles are two to three times longer than the others but not so numerous. On the last two feet carrying compound chaetae, very much longer simple chaetae appear and gradually replace the former completely. Aciculae appear on all feet. Segmental glands are present, but rarely before the tenth foot; they are seldom pigmented. The proboscis is terminated by twelve blunt papillae.



Text-fig. 12. *Rhynchonerella bongraini*: compound chaetae with (*a*) smooth terminal articles, (*b*) denticulate terminal articles.

Discussion. No one has ever reported specimens of the species originally described as *Callizona bongraini* without compound chaetae on the anterior feet. Stop-Bowitz (1948, 1949 and 1951), however, placed it in *Krohnia* Quatrefages, 1865, which genus has only simple chaetae. Clearly the species must be included in *Rhynchonerella*, which it approaches in having compound chaetae, in its cephalic appendages and in having an appendage on the pedal lobe. I have re-examined the specimens described by Monro (1930) as *R. fulgens* (B.M.(N.H.), Reg. no. 1930.10.8.905/906:912), from Sts. SS 33 and SS 53, and consider them to be *R. bongraini*. This misinterpretation was clearly due to the small size in *R. bongraini* of the pedal appendage, which is exceedingly difficult to see, because it can be hidden behind the large pedal lobe. All the material reported by Hardy and Gunther (1935) as alciopid larvae is not available for examination, but it is almost certain that they were dealing entirely with *R. bongraini*.

General distribution. *R. bongraini* is known only from the Antarctic Zone where it appears to be confined to the Antarctic Surface Water and the upper layers of the Warm Deep Water (see pp. 218–223).

Rhynchonerella angelini (Kinberg) 1866

Type locality. China Sea, 20° S., 107° E.

Krohnia Angelini Kinberg, 1866, p. 242.
Rhynchonerella Angelini Greeff, 1876, p. 57.
Callizona Grubei Greeff, 1876, pp. 72–3, pl. 5, figs. 63–6, pl. 6, figs. 69–88.
Callizona Grubei Levinsen, 1885, p. 333, fig. 13.
Callizona Angelini Apstein, 1900, pp. 18–19, pl. 4, figs. 33–8.
Callizona Angelini Reibisch, 1905, pp. 4–5, figs. 7–8.
Callizona Angelini Southern, 1911, pp. 4–5.
Callizona Angelini Fauvel, 1916, pp. 68–9.
Callizona Angelini Fauvel, 1923, p. 215, fig. 81 *d–i*.
Callizona angelini Monro, 1930, p. 82.
Callizona Angelini Fauvel, 1932*a*, p. 17.
Callizona angelini Monro, 1936, p. 118.
Callizona angelini Wesenburg-Lund, 1939, pp. 41–2.
Rhynchonerella Angelini Stop-Bowitz, 1948, pp. 34–6.

Description. The largest specimen examined measures 67 mm. in length by 6 mm. wide across the tips of chaetae. Two pairs of very short but broad, almost dumpy, antennae are situated on a prostomial extension in front of the eyes; a single unpaired cirriform antenna occurs dorsally between the eyes. The five pairs of tentacular cirri are arranged thus $1+\frac{1}{1}+\frac{1}{1}$; the unpaired and two ventrals are short, the two dorsals long and conical. Over the anterior three-quarters of the body the parapodia have broadly foliaceous dorsal cirri which become elongate posteriorly; smaller, but still large, foliaceous ventral cirri; pedal lobes, each with a prominent cirriform appendage carrying two types of compound chaetae, an inferior group, short stout acicular bristles with short smooth terminal articles and a superior group with long smooth articles: the acicular bristles decrease in number posteriorly. In the last one-quarter of the body the overall width is gradually reduced to a minimum of 0·25 mm., and the body assumes an appearance which Wesenberg-Lund (1939) described as a 'whip-cord like tail'. Parapodial cirri are here considerably reduced in size but never entirely disappear, and chaetae though smaller are still present. Pigmented segmental glands are present on all feet. The proboscis is terminated by twelve small tubercles.

General distribution. *R. angelini* is widely reported from the Atlantic Ocean in which it probably has its southern limit of distribution at the Sub-Tropical Convergence (see p. 255).

Genus Krohnia Quatrefages, 1865

Prostomium with five antennae. Five pairs of tentacular cirri. Parapodia with a cirriform appendage on the pedal lobe and with simple chaetae only.

Type species. Alciopa lepidota Krohn, 1845.

Type locality. Messina, Mediterranean.

Krohnia lepidota (Krohn), 1845

Alciopa lepidota Krohn, 1845, p. 175.
Krohnia lepidota Quatrefages, 1865, pp. 158–9.
Alciopa lepidota Langerhans, 1880, p. 312.
Callizonella lepidota Apstein, 1891, p. 133.
Callizonella lepidota Apstein, 1900, p. 12, pl. 11, figs. 11–13.
Callizonella lepidota Fauvel, 1916, p. 67.
Callizonella lepidota Fauvel, 1923, pp. 211–12, fig. 79*e–h*.
Callizonella lepidota Wesenburg-Lund, 1939, pp. 38–40, fig. 25, chart 19.
Krohnia lepidota Stop-Bowitz, 1948, p. 33.

Description. All the specimens examined are fragments of which the longest is 50 mm. in length by 4 mm. wide across the tips of chaetae. Two pairs of small conical antennae are situated on the anterior border of the prostomium in front of the eyes and an unpaired cirriform antenna occurs dorsally between the eyes. The five pairs of tentacular cirri are arranged thus: $1+\frac{1}{1}+\frac{1}{1}$, of which the posterior dorsal is very much longer than the others, all of which are subequal. Parapodia have foliaceous dorsal cirri with an acuminate tip, small lanceolate ventral cirri, very long pedal lobes, each with a conspicuous appendage, and prominent simple chaetae. These last are of two types: stout acicular chaetae, more numerous anteriorly, and long fine chaetae which gradually replace the former posteriorly. The whole body surface is sprinkled with black spots, which run in lines along the antennae and tentacular cirri and are scattered over the eyes and prostomium; they are arranged in a linear series at the dorsal edge of the parapodia and ventrally at the base of the feet and in the mid-ventral line; the anterior surface of each pedal lobe has a single black spot in its centre. These spots show clearly only in well-preserved specimens, but in all material they are present and even when some have disappeared, an overall pattern similar to that described can be visualized.

General distribution. K. lepidota is known from the Atlantic but not in large numbers; it is possible that it has its southern limit of distribution at the Sub-Tropical Convergence (see p. 255).

Genus Alciopa Audouin and Milne-Edwards, 1829

Body comparatively short and wide with a smaller number of segments than found elsewhere in the family. Prostomium with five antennae. Three pairs of tentacular cirri. Proboscis with two long cirriform appendages. Parapodia with foliaceous cirri; pedal lobe with two cirri and compound chaetae; no rudimentary parapodia present.

Type species. Alciopa reynaudii Audouin and Milne-Edwards, 1829.

Type locality. The Atlantic Ocean.

Alciopa reynaudii Audouin and Milne-Edwards, 1829

Alciopa Reynaudii Audouin and Milne-Edwards, 1829, p. 202.
Alciopa Reynaudii Audouin and Milne-Edwards, 1833, p. 35.
Nauphanta celox Greeff, 1876, pp. 69–71, pl. 3, figs. 40–2, pl. 4, figs. 43–55.
Nauphanta celox Levinsen, 1882, p. 214, pl. 7, fig. 9.

Greeffia oahuensis McIntosh, 1885, pp. 182–3, pl. 28, figs. 5–7.
Nauphanta celox, Levinsen, 1885, pp. 331–2, figs. 11–12.
Greeffia celox Apstein, 1891, pp. 131–2, figs. 12–15.
Greeffia celox Apstein, 1900, p. 12, pl. 2, fig. 10.
Greeffia celox Reibisch, 1905, pp. 5–6, fig. 9.
Greeffia celox Southern, 1911, p. 3.
Greeffia celox Fauvel, 1916, p. 67.
Greeffia celox Fauvel, 1923, p. 208, figs. 78*a–c*.
Greeffia oahuensis Monro, 1930, pp. 82–3, fig. 25.
Greeffia oahuensis Monro, 1936, p. 118.
Greeffia oahuensis Wesenburg-Lund, 1939, pp. 35–6, fig. 23.
Alciopa Reynaudii Stop-Bowitz, 1948, p. 30, fig. 21.

Description. The longest complete specimen of *Alciopa reynaudii* measures 46 mm. long by 10 mm. wide across the tips of chaetae. One pair of short conical antennae is directed forward from the anterior border of the prostomium, and the other pair directed laterally from the side; the single antenna is dorsal between the eyes and is merely a knob-like structure on a pale surface area. There are three pairs of tentacular cirri, all small but the middle one longer than the others. All parapodia are well developed with large imbricated cordiform dorsal cirri, ventral foliaceous cirri, two cirriform appendages on the pedal lobe, long compound slender capillary chaetae and pigmented segmental glands. Each segment carries dorsally and ventrally dark brown lateral markings which may disappear after long periods in preservative fluid. The body tapers to a fine point at the pygidium and carries a long unpaired anal cirrus. The whole aspect of this species is one of massiveness when compared with the elongate fragile species in other genera of the family.

General distribution. *A. reynaudii* has been frequently recorded from the South Atlantic, where it has its southern limit of distribution at the Sub-Tropical Convergence (see p. 257).

Genus Torrea Quatrefages, 1865

Type species. Torrea candida (Delle Chiaje), 1841.
Type locality. Sicily.

Torrea candida (Delle Chiaje), 1841

Alcyopa candida Delle Chiaje, 1841, p. 98.
Torrea candida Monro, 1930, p. 82.
Torrea candida Monro, 1936, p. 119.

Monro (1930) reported this species from 'Discovery' Sts. 102, N 100 H, 104 m. (1) and 294, TYF, 100–150(–0) m. (1), and in 1936 from St. 714 TYFB, 246–0 m. (1) but all these specimens are fragmentary and not identifiable with accuracy.

Family TYPHLOSCOLECIDAE

Exclusively pelagic. Body spindle-shaped or cylindrical. Prostomium not distinctly marked off from the rest of the body, terminated with a palpode, without eyes. Projecting nuchal organs present. Peristomium indistinct, bearing one pair of large foliaceous cirri. The two succeeding segments also bear only one pair, but thereafter there are two representing the dorsal and ventral cirri of the parapodia. Pedal mamelon reduced, with an acicula and a few small acicular chaetae visible. Two foliaceous anal cirri.

Genus Typhloscolex Busch, 1851

Body short and spindle-shaped. Prostomium with dorsal and ventral ciliated epaulettes, the dorsal epaulette carrying two small wings. Chaetae begin on the fifth parapodia.

Type species. Typhloscolex mülleri Busch, 1851.

Type locality. Trieste.

Typhloscolex mülleri Busch, 1851

Typhloscolex Mülleri Busch, 1851, pp. 115–16, pl. 11, figs. 1–6.
Sagitella Bobretzkii Wagner, 1872, p. 347, 2 figs.
Sagitella barbata Uljanin, 1878, pp. 6–8, pl. 1, fig. 2.
Sagitella praecox Uljanin, 1878, pp. 8–9, pl. 1, fig. 3.
Acicularia Virchowii Greeff, 1879*a*, pp. 237–45, pl. 13, figs. 1–18.
Typhloscolex Mülleri Greeff, 1879*b*, pp. 661–71.
Typhloscolex Mülleri Reibisch, 1895, pp. 52–3, figs. 7–14.
Typhloscolex Mülleri Reibisch, 1905, pp. 6–7, fig. 10.
Typhloscolex mülleri Ehlers, 1913, p. 530.
Typhloscolex Mülleri Fauvel, 1923, pp. 226–7, fig. 85*f–h*.
Typhloscolex mülleri Augener, 1929, pp. 307–8.
Typhloscolex Mülleri Monro, 1930, p. 90.
Typhloscolex Mülleri Fauvel, 1932*a*, p. 19
Typhloscolex mülleri Hardy and Gunther, 1935, p. 116.
Typhloscolex sp. Hardy and Gunther, 1935, p. 116.
Sagitella cornuta Hardy and Gunther, 1935, p. 116.
Typhloscolex Mülleri Fauvel, 1936*a*, p. 19.
Typhloscolex Mülleri Fauvel, 1939, p. 279.
Typhloscolex Mülleri Stop-Bowitz, 1948, p. 55.
Typhloscolex Mülleri Stop-Bowitz, 1949, pp. 17–18, fig. 8.
Typhloscolex Mülleri Støp-Bowitz, 1951, p. 10.

Description. Measurements of a selection of specimens are listed in Table 11 and indicate the size range found in this species.

Table 11. *Measurements of* Typhloscolex mülleri

Station no.	*Net*	*Depth (m.)*	*Length (mm.)*	*Greatest width (mm.)*	*No. of parapodia*
2530	N 70 V	500–250	2·0	0·5	20
1775	N 70 V	1000–750	2·5	1·0	20
103	N 70 V	500–250	2·8	0·5	17
1773	N 70 V	1500–1000	3·0	1·5	25
2531	N 70 V	750–500	3·0	1·5	24
		750–500	3·0	0·5	25
2532	N 70 V	500–250	3·0	0·5	20
			3·0	0·5	24
666	TYFV	1000–750	3·5	2·0	21
1775	N 70 V	1000–750	5·0	1·0	26
2532	N 70 V	500–250	6·5	0·7	30
117	N 70 V	750–500	7·0	1·0	24

The ciliated epaulettes are approximately as wide as the body and arranged perpendicularly to its long axis; between them the finely pointed palpode projects forwards. At the base of the dorsal epaulette there are two small oval wings. On each side of the peristomium are the first cirri, large and kidney-shaped, covering the epaulettes laterally. On each of the next two segments there is a pair of oval cirri, and thereafter foliaceous dorsal and ventral cirri are present on all segments up to the end of the body. In some specimens these are very distended and may contain sexual products. Simple chaetae and aciculae appear on the fifth parapodia. Two small elliptical anal papillae terminate the body posteriorly.

Discussion. I have re-examined the following specimens from Hardy and Gunther (1935, p. 116), *Sagitella cornuta* from Sts. WS 26, WS 30, WS 70, and *Typhloscolex* sp., from Sts. 137, WS 38 and WS 63, and consider them to be *T. mülleri*. Unfortunately all the material reported by Hardy and Gunther is not available for examination.

T. mülleri is closely related to *T. phyllodes* Reibisch, 1895 and *T. leuckarti* Reibisch, 1895 and all three have been reported from the same areas in the South Atlantic. *T. phyllodes* differs from *T. mülleri* in having ciliated epaulettes smaller than the body width, whereas in *T. leuckarti* the same organs are greater than the body width. Reibisch did not give measurements for the width of his specimens, but it is clear from his drawings that in both *T. phyllodes* and *T. leuckarti* the greatest width is about half the length. His drawings of *T. mülleri* show specimens about seven times as long as wide. In the material I have examined there are specimens from the same stations and depths covering these size ranges, yet in all of them the ciliated epaulettes are neither smaller nor larger than the body width.

In some of the widest of my specimens (possibly corresponding to *T. phyllodes* and *T. leuckarti* of Reibisch) sexual products are present in the cirri. I suggest, therefore, that *phyllodes* and *leuckarti* may represent the sexually maturing members of the population, and further that Reibisch's two species may be shown, when observations on the living animal have been made, to be synonymous with *T. mülleri*.

General distribution. *T. mülleri* is cosmopolitan and has been widely reported from the Atlantic (see pp. 231–236).

Genus TRAVISIOPSIS Levinsen, 1885

Body cylindrical or spindle-shaped, prostomium with nuchal organs flanking a caruncle but without ciliated epaulettes. Otherwise similar to *Typhloscolex* except that it is much larger in the adult.

Type species. *Travisiopsis lobifera* Levinsen, 1885.

Type locality. 42° 50′ N., 46° 10′ W.

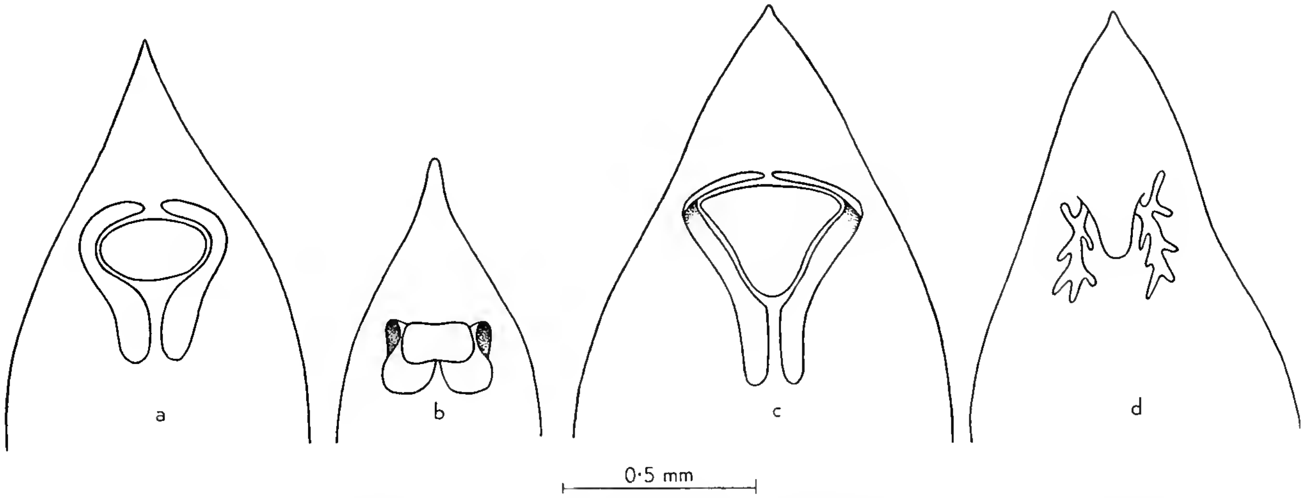
Travisiopsis lobifera Levinsen, 1885

Travisiopsis lobifera Levinsen, 1885, pp. 336–40, figs. 17–20.
Travisiopsis lobifera Reibisch, 1895, p. 57.
Travisiopsis lobifera Southern, 1911, p. 31, pl. 1, fig. 4.
Travisiopsis lobifera Fauvel, 1916, pp. 73–4.
Travisiopsis lobifera Fauvel, 1923, p. 229, fig. 86*a–d*.
Sagitella kowalewskii Benham, 1929, p. 191 *nec Sagitella kowalewskii* Benham, 1927, pp. 80–1, pl. 2, figs. 33–4 (see *Travisiopsis levinseni*).
Travisiopsis lobifera Fauvel, 1932*a*, p. 19.
Travisiopsis lobifera Fauvel, 1932*b*, pp. 66–7.
Travisiopsis lobifera Støp-Bowitz, 1948, pp. 57–8, fig. 44.
Travisiopsis lobifera Friedrich, 1950*a*, pp. 315–19.
Travisiopsis lobifera Støp-Bowitz, 1951, p. 10.

Description. This cylindrical-shaped species may measure up to 25 mm. long by 4–6 mm. wide for a constant twenty-one segments. The median dorsal caruncle, situated between the peristomium and the first parapodia, is characteristically oval and wholly attached (Text-fig. 13*a*). Paired nuchal lobes surround the caruncle in the form of fixed processes anteriorly and laterally, with free projecting lobes posteriorly which reach as far as the single cirri of the second parapodia. The single cirri of the peristomium and the first two feet are circular, thereafter the parapodial cirri are heart-shaped. A group of the three acicular chaetae project from between the parapodial cirri from the sixth to seventh segment backwards. Anal cirri are variable in form from elongate oval to rectangular.

Discussion. I have re-examined Benham's 1929 specimens of *Sagitella kowalewskii* from the 'Terra Nova' Expedition, in the B.M.(N.H.) (Reg. no. 1929.9.20.3/4, Sts. 92 and 130), and find them to be *Travisiopsis lobifera* (the specimen from St. 282 is not in the B.M. collections). It will be noted from the synonymy that Benham's 1927 *Sagitella kowalewskii* material is not *Travisiopsis lobifera*, but *T. levinseni* (see below).

General distribution. T. lobifera is not common in the South Atlantic, but has been found to the north of the Sub-Tropical Convergence only (see p. 245).



Text-fig. 13. Prostomia of (*a*) *Travisiopsis lobifera*, (*b*) *T. levinseni*, (*c*) *T. lanceolata*, (*d*) *T. coniceps*, all with all lateral cirri removed but showing nuchal organs and lobes.

Travisiopsis levinseni Southern, 1910

Type locality. 53° 7′ N., 15° 9′ W., 650–750 fathoms (1188·7–1371·6 m.).

Travisiopsis levinseni Southern, 1910, p. 429.
Travisiopsis levinseni Southern, 1911, pp. 32–3, pl. 2, figs. 7–10.
Sagitella Kowalewskii Gravier, ? 1911*b*, pp. 74–6, pl. 3, figs. 30–2, *nec* Wagner.
Sagittella cornuta Ehlers, 1912, p. 25 (in part) *nec Sagittella cornuta* Ehlers, 1913, pp. 527–9, pl. 39, figs. 8–14 (see *Travisiopsis lanceolata*).
Sagittella opaca Ehlers, 1913, p. 529, pl. 39, figs. 16–17.
Travisiopsis Levinseni Fauvel, 1916, p. 76.
Travisiopsis Levinseni Fauvel, 1923, pp. 229–30, fig. 86*h*, *i* and *k*.
Sagitella Kowalewskii Benham, 1927, pp. 80–1, pl. 2, figs. 33–4, *nec Sagitella Kowalewskii* Benham, 1929, p. 191 (see *Travisiopsis lobifera*).
Sagitella Kowalewskii Monro, 1930, pp. 89–90.
Travisiopsis sp. Monro, 1930, pp. 90–1.
Travisiopsis Levinseni Wesenburg-Lund, 1935, pp. 14–15.
Travisiopsis benhami Monro, 1936, pp. 123–4, fig. 17*a–c*.
Travisiopsis Levinseni Monro, 1939*a*, p. 346.
Travisiopsis levinseni Stop-Bowitz, 1948, pp. 59–60, fig. 46, fig. 47*a–b*.
Travisiopsis levinseni Stop-Bowitz, 1949, p. 19.
Travisiopsis levinseni Friedrich, 1950*a*, pp. 315–19.
Travisiopsis benhami Friedrich, 1950*a*, pp. 315–19.
Travisiopsis benhami Friedrich, 1950*c*, p. 15.
Travisiopsis levinseni Wesenburg-Lund, 1950*a*, p. 13.
Travisiopsis Levinseni Wesenburg-Lund, 1950*b*, p. 44.
Travisiopsis Levinseni Stop-Bowitz, 1951, p. 11.
Travisiopsis levinseni Wesenburg-Lund, 1951, p. 33.

Description. This species normally measures between 13–25 mm. in length by 4–6 mm. wide, though exceptionally specimens up to 34 mm. long have been found (for example, Monro, 1930, as *Travisiopsis* sp.). The body is spindle-shaped and there are twenty-five segments. Between the peristomium and the first parapodium is the rectangular caruncle with semi-circular nuchal lobes directed backwards from its posterior border (Text-fig. 13*b*). The lobes are continuous with, and part of, fixed nuchal processes which border the caruncle laterally. Cirri of the peristomium and first two parapodia are foliaceous; thereafter the paired parapodial cirri are rectangular becoming lanceolate posteriorly. A small group of three aciculae project from between the parapodial cirri; these are always variable in position and may begin anywhere between the sixth and thirteenth foot and continue up to the penultimate segment. Anal cirri are long and oval, supported by a central rib.

Discussion. I have examined the specimens listed below and consider them all to be *Travisiopsis levinseni*.

(*a*) From Monro, 1930, as *Sagitella kowalewskii*, 'Discovery', Sts. 17, 78, 85, 89, 116, B.M.(N.H.), Reg. no. 1930.10.8.793:805/6:902/3.

(*b*) From Monro, 1930, as *Travisiopsis* sp., 'Discovery', St. 100, B.M.(N.H.), Reg. no. 1930.10.8.1017.

(*c*) From Monro, 1936 as *Travisiopsis benhami* (Types) 'Discovery', Sts. 151, 575, 588 and 'William Scoresby', Sts. 35, 549, 55, 716 B.M.(N.H.), Reg. no. 1936.2.8.1192–1199.

(*d*) From Benham, 1927 as *Sagitella kowalewskii* 'Terra Nova', St. 275, B.M.(N.H.), Reg. no. 1928.2.29.10.

It will be noted from the synonymy that Benham's 1929, *Sagitella kowalewskii*, material is *Travisiopsis lobifera* (p. 196).

In 1912 Ehlers first described a species which he called *Sagittella cornuta* (*sic*), the two type specimens of which are in the B.M.(N.H.). One of these (Reg. no. 1911.11.1.61) is *Travisiopsis levinseni*, although small for the species (5 mm. long for twenty-five parapodia), and the other (Reg. no. 1911.11.1.62) although in a poor state of preservation appears to be *Sagitella kowalewskii* Wagner (1872). These specimens must not be confused with Ehlers 1913 material from the *Deutsche Südpolar-Expedition*, which is identical with *Travisiopsis lanceolata* (see below).

General distribution. *T. levinseni* has been reported from the Atlantic Ocean in all explored water masses (see pp. 236–237).

Travisiopsis lanceolata Southern, 1910

Type locality. 51° 12′ N., 11° 55′ W., 500 fathoms (914·4 m.).

Travisiopsis lanceolata Southern, 1910, p. 429.
Travisiopsis lanceolata Southern, 1911, pp. 30–2, pl. 1, figs. 3, 5, 6.
Sagittella cornuta Ehlers, 1913, pp. 527–9, pl. 39, figs. 8–14 (in part), *nec* Ehlers 1912.
Travisiopsis lanceolata Fauvel, 1916, pp. 75–6.
Travisiopsis lanceolata Fauvel, 1923, p. 229, figs. 86*e–g*.
Sagitella cornuta Monro, 1930, p. 90, *nec* Ehlers, 1912.
Travisiopsis lanceolata Fauvel, 1932*a*, p. 20.
Travisiopsis Lanceolata (*sic*), Wesenburg-Lund, 1935, p. 13.
Travisiopsis atlantica Treadwell, 1936, pp. 62–3, figs. 30–3.
Travisiopsis lanceolata Monro, 1939*a*, p. 348.
Travisiopsis lanceolata Wesenburg-Lund, 1939, pp. 20–1.
Travisiopsis atlantica Treadwell, 1941, p. 22.
Travisiopsis lanceolata Stop-Bowitz, 1948, pp. 58–9, figs. 45–6.
Travisiopsis lanceolata Friedrich, 1950*a*, pp. 315–19.
Travisiopsis lanceolata Wesenburg-Lund, 1950*a*, p. 13.
Travisiopsis lanceolata Hartman, 1956, p. 277.

Description. This spindle-shaped species measures up to 31 mm. in length by 4–6 mm. wide for twenty-two segments. The median dorsal caruncle, situated between the peristomium and the first parapodia, is in the shape of a ∇ with the posterior portion not attached to the body surface, and with two long characteristic finger-shaped nuchal processes on either side, directed posteriorly (Text-fig. 13*c*, p. 197). These nuchal lobes curl around the caruncle anteriorly and almost meet; posteriorly they may reach to the fourth parapodia. Cirri on the first three segments are reniform; on succeeding parapodia they are almost square becoming lanceolate posteriorly. Anal cirri are lanceolate with a supporting central rib.

Discussion. I have re-examined Monro's (1930) specimen of *Sagitella cornuta*, from 'Discovery', St 258 (B.M.(N.H.), Reg. no. 1930.10.8.1067) and consider it to be *Travisiopsis lanceolata.* Some of Ehlers's 1913 material of *Sagitella cornuta* is clearly *Travisiopsis lanceolata* but his 1912 material, named *S. cornuta*, is *T. lobifera.*

General distribution. T. lanceolata is well known from the Atlantic Ocean where it probably has its southern limit of distribution at the Sub-Tropical Convergence (see p. 246).

Travisiopsis coniceps (Chamberlin), 1919

Type locality. 5° 11′ S., 98° 56′ W., off Galapagos Islands.

Sagittella lobifera Ehlers, 1912, pp. 24–5, pl. 3, figs. 1–4.
Plotobia coniceps Chamberlin, 1919, pp. 156–7, pl. 66, figs. 2–4.
Nuchubranchia palmata Treadwell, 1928, pp. 481–2, figs. 66–8.
Sagitella lobifera Monro, 1930, p. 90.
Sagitella lobifera Monro, 1936, pp. 122–3.
Sagitella lobifera Monro, 1939*b*, p. 108.
Travisiopsis coniceps Stop-Bowitz, 1948, p. 61.
Travisiopsis coniceps Stop-Bowitz, 1951, pp. 11–12.
Travisiopsis coniceps Hartman, 1956, p. 277.

Description. This species is cylindrical in shape and measures between 18 and 30 mm. in length by 4–6 mm. wide, for twenty-two segments. In the median dorsal line, between the peristomium and the first parapodium, is the backwardly directed, tongue-shaped caruncle with characteristic pinnate nuchal lobes on either side (Text-fig. 13*d*, p. 197). The single cirri on the first three segments are heart-shaped, thereafter parapodial cirri are broadly foliaceous. Two or three aciculae project from between the parapodial lobes from the sixth foot posteriorly. Anal cirri are long and spatulate with a central rib.

Discussion. As Stop-Bowitz (1948) has pointed out the name *lobifera* is preoccupied in the genus *Travisiopsis* by Levinsen's species; the next name available is *coniceps.* I have re-examined the holotype of *Sagittella lobifera* (*sic*) Ehlers, 1912 (B.M.(N.H.), Reg. no. 1911.11.1.87) from 68° 52′ S., 178° 15′ E., and it is identical with *Travisiopsis coniceps.* In addition, I have examined the following specimens and consider them all to be *T. coniceps*:

(*a*) From Treadwell, 1928, as *Nuchubranchia palmata*, in the collection of the New York Zoological Society, by courtesy of Dr Beebe.

(*b*) From Monro, 1930, as *Sagitella lobifera*, 'Discovery', Sts. 78, 85, 100 (B.M.(N.H.), Reg. no. 1930.10.8.1018:1162:1177, respectively).

(*c*) From Monro, 1936 as *S. lobifera*, 'Discovery', Sts. 395, 590 (B.M.(N.H.), Reg. no. 1936.2.8. 1182–1189 and 1190–1191 respectively).

(*d*) From Monro, 1939*b*, as *S. lobifera*, B.A.N.Z.A.R.E., Sts. 27, 45, 96 (B.M.(N.H.), Reg. no. 1941.3.3.3948/53.

General distribution. Travisiopsis coniceps has been widely reported from the South Atlantic Ocean but never in large numbers (see p. 245).

Family PHYLLODOCIDAE

Not exclusively pelagic. Body normally long and slender with numerous segments, except in the pelagic genera where it is short and wide and the number of segments is small and fixed within narrow limits. Prostomium normally with eyes and four or five antennae. First two or three segments with tentacular cirri. Parapodia uniramous or biramous with simple and/or compound chaetae; cirri normally present. Proboscis protrusible, usually with papillae, exceptionally with chitinous jaws. Anal cirri normally present.

Subfamily *Lopadorhynchinae*

Exclusively pelagic. Prostomium with four antennae. Compound chaetae always present, simple chaetae may be absent. Anal cirri sometimes present.

Genus Lopadorhynchus Grube, 1855

(Emended Malaquin and Dehorne, 1907 *pro Lopadorrhynchus* Grube, 1855)

Two dorsal antennae appear as extensions of the anterior lateral border of the prostomium and two ventral antennae are close to the mouth. Normally three pairs of tentacular cirri, exceptionally two. Parapodia uniramous and modified anteriorly so that the body is divided into two distinct regions: simple and compound chaetae are present supported by a prominent pedal lobe with acicula. Dorsal cirri present on all parapodia, ventral cirri may be absent on anterior feet, always present elsewhere. Proboscis smooth or papillate. Anal cirri absent.

Type species. Lopadorhynchus brevis Grube, 1855.

Type locality. Mediterranean.

In 1914 Bergström founded the genus *Prolopadorhynchus* to include species of *Lopadorhynchus* with ventral cirri on the first two parapodia. Most authors have adopted *Prolopadorhynchus* as a subgenus on this basis, but I see no purpose served by this division. The genus is not large enough to warrant artificial separation purely for convenience and the modifications, which have been ascribed by most authorities to anterior ventral cirri, make it difficult to define their presence or absence in several species, confusing rather than clarifying the situation.

Lopadorhynchus brevis Grube, 1855

Lopadorrhynchus brevis Grube, 1855, p. 100, pl. 3, fig. 15.
Lopadorhynchus brevis Kleinenburg, 1886, p. 21.
Lopadorhynchus brevis Reibisch, 1895, p. 35.
Lopadorhynchus brevis Lo Bianco, 1904, p. 52, pl. 24, fig. 121.
Lopadorhynchus brevis Ehlers, 1913, p. 463.
Lopadorhynchus brevis Bergström, 1914, p. 181.
Lopadorrhynchus parvum Chamberlin, 1919, pp. 114–16, pl. 17, figs. 6, 7.
Lopadorrhynchus nans Chamberlin, 1919, pp. 116–19, pl. 17, figs. 1–5.
Lopadorhynchus brevis Fauvel, 1923, p. 184, fig. 69K.
Lopadorhynchus brevis Monro, 1930, p. 78.
Lopadorhynchus brevis Monro, 1937, pp. 266–7.
Lopadorhynchus brevis Monro, 1939*a*, p. 347.
Lopadorhynchus brevis Wesenburg-Lund, 1939, pp. 12–15, figs. 8–10, chart 7.
Lopadorhynchus brevis Stop-Bowitz, 1948, p. 18.

Description. This species may measure 20 mm. long by 7 mm. wide, across the tips of chaetae for twenty-seven chaetigers, but normally specimens measure between 8–9 mm. by 4 mm. wide for twenty-two to twenty-four chaetigers. The body is divided into two separate regions at the posterior border of the third chaetiger. The prostomium is wider than long, with a straight anterior border with two long dorsal and two short ventral antennae. Two eyes are present, but may not be visible in specimens preserved in alcohol. Three pairs of tentacular cirri are present, one dorsal and one ventral just behind the antennae and the third very small almost an appendage of the lower of these. The first three parapodia have no ventral cirri but a linear series of stout simple chaetae thicker than those from the fourth foot posteriorly; these have both compound and simple chaetae, grouped fan-wise about a spatulate pedal lobe, and ventral cirri. The compound chaetae have a heterogomph articulation and smooth, ovate terminal pieces. Dorsal cirri are long on the first three parapodia, thereafter they are lanceolate; ventral cirri are small and subulate.

Discussion. In 1919 Chamberlin described two new species, *Lopadorhynchus nans*, differing from *L. brevis* in the arrangement of simple chaetae, and *L. parvum* which is without eyes. Neither of these characters warrants specific separation. All species of *Lopadorhynchus* reported to have eyes lose the ocular pigment when preserved in alcohol, and the arrangement of chaetae in the parapodia varies from specimen to specimen within the same species. In describing *L. nans*, Chamberlin also referred to ventral cirri which, however, are clearly post-setal lobes.

General distribution. L. brevis has not been reported in large numbers from the South Atlantic and appears only to the north of the Sub-Tropical Convergence (see pp. 259–261).

Lopadorhynchus uncinatus Fauvel, 1915

Original localities. From off the Azores and Monaco.

Lopadorhynchus uncinatus Fauvel, 1915, p. 3, fig. 2.
Lopadorhynchus uncinatus Fauvel, 1916, pp. 57–61, pl. 1, figs. 2, 3, pl. 4, figs. 4–14.
Lopadorhynchus uncinatus Fauvel, 1923, pp. 184–5, figs. 67*a–g*.
Lopadorhynchus uncinatus Fauvel, 1932*b*, p. 75.
Lopadorhynchus uncinatus Monro, 1936, pp. 113–14.
Lopadorhynchus uncinatus Monro, 1937, p. 266.
Lopadorhynchus uncinatus Wesenburg-Lund, 1939, pp. 10–12, figs. 6–7, chart 6.
Lopadorhynchus uncinatus Treadwell, 1939, pp. 207–8, fig. 35.

Description. This species measures up to 24 mm. long by 6 mm. wide, across the tips of chaetae, for a maximum of thirty-two chaetigers. The body is divided into two distinct regions at the posterior border of the second chaetiger. The prostomium is wider than long, pointed anteriorly with two long dorsal and two short ventral antennae. Two eyes may be present but the ocular pigment frequently disappears in alcohol; Monro (1936) for example, reported a specimen from 'Discovery', St. 714 with eyes, but these are not visible now. The first two pairs of tentacular cirri are long and subulate, lying dorsally and ventrally, just behind the antennae, the third is rudimentary at the base of the ventral pair. Parapodia of the first two chaetigers are much more prominent than the rest, they are large and stout, with up to seven strong unidentate hooks, grouped terminally, surrounded by a ruff or collar (possibly the modified ventral cirrus) and have a small dorsal cirrus: the whole foot is directed laterally. The succeeding feet are directed backwards and are thin and paddle-shaped with stout dorsal cirri and smaller ventral cirri with chaetae grouped fan-wise about the pedal lobe; both simple and compound chaetae are present in the first of these chaetigers, but gradually the latter replace the former entirely. The terminal article of the compound bristles is ovate with serrations on one side and the articulation is heterogomph. Dorsal cirri are short and conical, ventral cirri smaller than these and subulate.

General distribution. L. uncinatus has frequently been recorded from the South Atlantic where it has its southern limit of distribution at the Sub-Tropical Convergence (see pp. 259–261).

Lopadorhynchus krohnii (Claparède), 1870

Type locality. Naples.

Hydrophanes Krohnii Claparède, 1870, pp. 464–6, pl. 11, fig. 2.
Hydrophanes Krohnii Viguier, 1886, pp. 385–7, pl. 22, figs. 1–10.
Lopadorhynchus Viguieri Reibisch, 1893, p. 253.
Lopadorhynchus Viguieri Reibisch, 1895, pp. 37–8, pl. 4, fig. 4.
Lopadorhynchus viguieri Ehlers, 1913, p. 463.
Lopadorhynchus Krohnii Bergström, 1914, pp. 180–2, fig. 68.
Lopadorhynchus Krohnii Fauvel, 1923, pp. 185–6, fig. 69*a–d*.
Lopadorhynchus Krohnii var. *simplex* Monro, 1930, p. 72, fig. 23.
Lopadorhynchus Krohnii var. *simplex* Monro, 1936, p. 113.
Lopadorhynchus Krohnii Wesenburg-Lund, 1939, pp. 15–16, fig. 11.

Description. A large specimen of this species may measure 10·5 mm. long by 3 mm. wide for twenty-three chaetigers, but normally the length varies between 5 and 7 mm. and the width is 2 mm. for twenty to twenty-two chaetigers. The body is divided into two distinct regions at the posterior border of the second chaetiger. The prostomium is twice as wide as long, with a rounded anterior border and two long dorsal and two very short ventral antennae. No eyes have been seen in the specimens examined. There are two pairs of elongate tentacular cirri. The first two chaetigers are directed laterally and are shorter and stouter than the rest; they have simple hooked chaetae and a dorsal cirrus but no ventral cirrus. The remaining parapodia are directed posteriorly and are thin and lanceolate with small dorsal cirri and short ventral cirri; chaetae are compound, with heterogomph articulation and serrated ovate terminal pieces, grouped fan-wise about the large lanceolate pedal lobe.

Discussion. In the specimens examined no simple chaetae were present posterior to the first two parapodia and in this respect the material differs from that widely reported from the Mediterranean (Wesenburg-Lund, 1939). I do not consider, however, that this warrants the erection of a new variety as Monro (1930) did in naming his material *L. krohnii* var. *simplex*. I find it identical with *L. krohnii*. It may be significant, all my material and Monro's being larger than the European, that simple chaetae may disappear with age and approaching sexual maturity, but clearly more material than at present available is required to confirm this.

General distribution. L. krohnii has been found at a number of stations in the South Atlantic where it has its southern limit of distribution at the Sub-Tropical Convergence (see pp. 259–261).

Genus PELAGOBIA Greff, 1879

Prostomium with four antennae. Two pairs of tentacular cirri on the first chaetiger. Parapodia uniramous with dorsal and ventral cirri cylindrical (dorsal cirrus reduced or absent on the second chaetiger), with a chaetigerous mamelon, aciculae, and compound chaetae with denticulate terminal pieces. Proboscis smooth, pygidium with two anal cirri.

Type species. Pelagobia longicirrata Greeff, 1879.

Type locality. Arrecife, Canary Islands.

Pelagobia longicirrata Greeff, 1879

Pelagobia longicirrata Greeff, 1879*a*, pp. 247–9, pl. 14, figs. 23–5.
Pelagobia longocirrata Viguier, 1886, pp. 377–82, pl. 21, figs. 1–13.
Pelagobia longecirrata Reibisch, 1895, pp. 21–4, pl. 2, figs. 1–9.
Pelagobia longecirrata Reibisch, 1905, pp. 3–4, figs. 4–6.
Pelagobia longecirrata Southern, 1909, p. 2, pl. 1, fig. 1.
Pelagobia Viguieri Gravier, 1911*a*, p. 311.

Pelagobia Viguieri Gravier, 1911*b*, pp. 62–5, pl. 2, figs. 22–5.
Pelagobia longicirrata Ehlers, 1912, p. 14.
Pelagobia longicirrata Ehlers, 1913, pp. 460–2 and p. 591.
Pelagobia longicirrata Bergström, 1914, pp. 186–7, fig. 70.
Pelagobia longicirrata Ditlevsen, 1914, p. 690.
Pelagobia longicirrata Fauvel, 1916, pp. 61–2, pl. 1, figs. 6, 7.
Pelagobia viguieri Chamberlin, 1919, pp. 122–5.
Pelagobia longicirrata McIntosh, 1921, p. 294.
Pelagobia viguieri Benham, 1921, pp. 57–8, pl. 7, figs. 58–60.
Pelagobia longicirrata Fauvel, 1923, p. 192, fig. 72*a–c*.
Pelagobia longicirrata McIntosh, 1923, pp. 435–7, pl. 134, figs. 4 and 4*a*.
Pelagobia viguieri Benham, 1927, p. 78 (in part).
Pelagobia longicirrata Augener, 1929, pp. 291–4.
Pelagobia longicirrata Hardy and Gunther, 1935, p. 113, fig. 52.
Pelagobia longicirrata Fauvel, 1936*a*, pp. 16–17.
Pelagobia longicirrata Monro, 1936, p. 114.
Pelagobia longecirrata Nolte, 1938, pp. 274–8, figs. 217–23.
Pelagobia erinensis Nolte, 1938, pp. 278–81, figs. 224–5.
Pelagobia longicirrata Fauvel, 1939, p. 276.
Pelagobia viguieri Treadwell, 1943, p. 33.
Pelagobia longicirrata Stop-Bowitz, 1948, p. 21.
Pelagobia longicirrata Friedrich, 1950*c*, pp. 14, 20.
Pelagobia longicirrata Wesenburg-Lund, 1950*b*, pp. 37–8, chart 9.
Pelagobia longicirrata Fauvel, 1951, p. 292.
Pelagobia longicirrata Støp-Bowitz, 1951, p. 6.
Pelagobia viguieri Uschakov, 1952, pp. 103–4, fig. 1.
Pelagobia longicirrata Fauvel, 1953*a*, p. 131, fig. 63*a–d*.
Pelagobia viguieri Uschakov, 1955, pp. 105–6, fig. 11.

Description. Normally measuring between 2 and 8 mm. in length for fifteen to twenty-five chaetigers, a large specimen of this species may be 12 mm. long. The body is slightly flattened dorsoventrally and chaetae and cirri project far out from the body wall, so that the width of the body across the parapodial bases averages 0·8 mm. and the distance between the tips of chaetae is 3 mm. The prostomium is approximately cone-shaped, truncated anteriorly, carrying two eyes and four small antennae, two dorsal and two ventral. The two pairs of tentacular cirri are long and subulate and between each pair is a pedal mamelon with short chaetae. Each parapodium from the third chaetiger onwards (counting the segment carrying the tentacular cirri as the first chaetiger) is well developed, with pedal mamelon, acicula, compound chaetae and long dorsal and ventral cirri. The main shafts of the chaetae are smooth and without denticulation, the terminal articles are long and denticulated along one edge. The anal cirri are short and blunt.

Discussion. Some authors, Southern (1909), Chamberlin (1919) and Fauvel (1923), have described denticulations on the shaft of the chaetae in *P. longicirrata*, and this has caused confusion in the status of *P. serrata* Southern, 1909, and *P. viguieri* Gravier, 1911. Originally, *P. longicirrata* was described with the terminal article of the chaetae denticulated and the shaft smooth. This was accepted until Southern (1909), in describing a new species, *P. serrata*, with denticulations on the shaft, described similar, but less clear, denticulations on the shafts of chaetae of specimens he assigned to *P. longicirrata*. I have examined the specimens described by Southern (1909) as *P. longicirrata*, in the Dublin Museum and the B.M.(N.H.) collections (Reg. no. 1909.11.29.1), and their chaetae have completely smooth shafts. Furthermore, being able to examine the original specimens of *P. serrata* in the Dublin and the B.M. (N.H.) collections (Reg. no. 1909.11.29.2), I have been able to compare the shafts of the chaetae in these two species. The only species with serrations on the shaft is *P. serrata*; *P. longicirrata* has smooth shafts. Chamberlin (1919) and Fauvel (1923) appear to have followed Southern in recording that *P. longicirrata* has a denticulated shaft without having specimens illustrating it. On the other hand, Fauvel (1916), Monro (1936) and Stop-Bowitz (1948 and 1949) in reporting *P. longicirrata* all made particular reference to the presence of smooth shafts on the compound chaetae. The lack of denticulations was attributed either to inferior microscopic magnification, or regarded as being only of varietal importance. When Gravier (1911 *a*) first described *P. viguieri*, he assigned to it characters which, compared with those of *P. longicirrata*, are due only to differences in growth (large cirri, number of segments, extent of the nuchal organs) except for the shape of the chaetae. His description of the chaetae is similar to mine above for *P. longicirrata*, but he was clearly influenced by Southern's diagnosis and probably felt that because the shafts of the chaetae in his specimens were smooth, they must be separated from a species which had denticulated shafts. Benham (1921 and 1929) assigned specimens to *P. viguieri* without considering *P. longicirrata*, which he probably overlooked; some of this material is in the B.M.(N.H.) collections (Reg. no. 1928.2.29.14/18:20), and it is identical with my Discovery material.[1] Treadwell (1943) and Uschakov (1952 and 1955) appear to have followed Chamberlin (1919) and Fauvel (1923), in describing specimens as *P. viguieri*.

In submitting, therefore, that *P. viguieri* is a synonym of *P. longicirrata*, I have purposely not considered the status of *P. serrata*. This species has been reported by Southern (1909) from off the Irish Coast and by Fauvel (1916) from the Azores and Monaco. It is clearly different from *P. longicirrata*, but whether or not this difference warrants specific status depends on an examination of many more specimens than are now available.

General distribution. *P. longicirrata* is cosmopolitan, but exhibits important geographical and seasonal patterns of distribution within the Antarctic and Sub-Antarctic Zones (see pp. 237–242).

Genus MAUPASIA Viguier, 1886

Prostomium with four antennae. Three pairs of tentacular cirri. Parapodia uniramous with dorsal and ventral cirri, and compound chaetae only. Proboscis smooth. Anal cirri rudimentary.

Type species. *Maupasia caeca* Viguier, 1886.

Type locality. Bay of Algiers.

Maupasia caeca Viguier, 1886

Maupasia coeca Viguier, 1886, pp. 382–5, pl. 21, figs. 14–20.
Maupasia caeca var. *atlantica* Southern, 1909, pp. 4–5, pl. 1.
Maupasia caeca Ehlers, 1912, p. 15.
Maupasia caeca Ehlers, 1913, p. 462.
Maupasia caeca Fauvel, 1916, p. 63.
Maupasia caeca Fauvel, 1923, pp. 190–1, fig. 71 *a–d*.
Maupasia caeca Hardy and Gunther, 1935, p. 115.
Maupasia coeca Wesenburg-Lund, 1939, pp. 19–20, fig. 15, chart 11.

Description. This species measures up to 6 mm. long by 1 mm. wide across the bases of parapodia and up to 3 mm. wide across the tips of chaetae; the number of chaetigers varies between fifteen and eighteen. The small prostomium is approximately circular in shape, with two dorsal and two ventral antennae, equal in length, on the outer anterior margins. Two pairs of long tentacular cirri are situated immediately behind the prostomium on each successive segment, not clearly separated from each other but distinctly marked off from the segment behind. Each pair of tentacular cirri have

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[1] These specimens are from 'Terra Nova', Sts. 275 and 288 respectively, the specimen from St. 343 (B.M.(N.H.), Reg. no. 1928.2.29.19) is *Maupasia caeca* (see Benham, 1921).

compound chaetae between them. The following segments bear parapodia with characteristic foliaceous dorsal and lanceolate ventral cirri. In the larger specimens the dorsal cirri contain genital products. All chaetae are heterogomph spingers with straight smooth terminal pieces. Anal appendages are very small circular cirri.

General distribution. The few records indicate a wide distribution in the S. Atlantic (see p. 242).

Phalocrophorus pictus Greeff, 1879

This phyllodocid belongs to the subfamily Iospilinae. One specimen was reported by Hardy and Gunther (1935) from St. WS 63 on the December to January 1926–7, South Georgia Survey. Ehlers (1913) previously recorded it from the Indian Ocean sector of the Antarctic Zone; Augener (1929) reported it from the Weddell Sea and Fauvel (1936*a*) records it from the 'Belgica' collections in the Pacific Antarctic sector. North of the Sub-Tropical Convergence in the South Atlantic Ocean *P. pictus* was reported by Reibisch (1895), Friedrich (1950*c*) and Stop-Bowitz (1951). This species has not been found in the present surveys and is known from too few records to permit an adequate analysis of its distribution.

Family APHRODITIDAE

Not exclusively pelagic. Prostomium normally with four sessile or pedunculate eyes, one to three antennae and two palps. Protrusible proboscis crowned with papillae and frequently with chitinous jaws. A feature of this family is the possession of elytra on the dorsal surface of the parapodia, of which the first pairs are always attached to segments 2, 4, 5 and 7, thereafter the arrangement varies. Parapodia biramous, exceptionally reduced.

Subfamily *POLYNOINAE*

Not exclusively pelagic. Twelve or more pairs of elytra, inserted on segments 2, 4, 5, 7, 9–23, thence sometimes on every third segment up to the end of the body.

Genus LAGISCA Malmgren, 1865

Not exclusively pelagic. Fifteen pairs of elytra, normally covering the greater part of the body except the posterior extremity. Proboscis with chitinous jaws. Parapodia biramous.

Type species. Lagisca extenuata (Grube), 1840.

Type locality. Mediterranean—not pelagic.

Lagisca hubrechti (McIntosh), 1900

Original localities. From the North-west Atlantic.

Evarne Hubrechti McIntosh, 1900, pp. 360–3, pl. 28, fig. 6, pl. 30, fig. 10, pl. 33, fig. 1, pl. 40, figs. 1–4
Lagisca Hubrechti Fauvel, 1914*a*, pp. 67–8, pl. 4, figs. 11–17.
Lagisca Hubrechti Fauvel, 1914*b*, pp. 3–4.
Lagisca Hubrechti Fauvel, 1916, pp. 28–32, pl. 1, fig. 1, pl. 3, figs. 1–5, 9–14.
Lagisca Hubrechti Fauvel, 1923, pp. 78–80, fig. 29*a–k*.
Lagisca hubrechti Monro, 1930, p. 45.
Lagisca Hubrechti Fauvel, 1932*a*, pp. 10–11.
Lagisca hubrechti Wesenburg-Lund, 1939, pp. 6–7, fig. 3, chart 3.
Lagisca Hubrechti Stop-Bowitz, 1948, pp. 11, fig. 8.

Description. The largest specimen of *Lagisca hubrechti* examined was reported from St. 100 by Monro (1930) and is 22 mm. long by 13 mm. wide across the tips of chaetae, having the full complement of fifteen elytrophores. Other specimens are smaller than this and range from 5 mm. long by 4 mm. wide for twelve elytrophores. Notopodial chaetae are stout, transparent and unidentate with a serration along one edge; neuropodial chaetae are transparent and unidentate, beset with very small spines; occasionally a superior chaeta in the neuropodial group may be bidentate. There is a characteristic large caudal appendage terminating the body posteriorly.

General distribution. Only one record of this species is known south of the Sub-Tropical Convergence in the South Atlantic (see p. 259).

The following species of Polynoinae were reported from the collections of 'Discovery' by Monro (1930) but have not been found in the present work.

Nectochaeta caroli Fauvel, 1914

Nectochaeta caroli Monro, 1930, p. 46, from St. 273, TYF, 200–230(–0), 3 specimens; St. 276, N 100, 100(–0) m., 29 specimens.

Podarmus atlanticus Monro, 1930

Podarmus atlanticus Monro, 1930, pp. 42–3, from St. 282 TYF, 300(–0) m., 1 specimen.

Stop-Bowitz (1948) reports this species from the North Atlantic and considers that Monro's material could not have the forty-five segments described, if it had the fourteen pairs of elytra of the original generic diagnosis by Chamberlin (1919). In fact, Monro's type (B.M.(N.H.), Reg. no. 1930.10.8.236), has forty-five chaetigers and eighteen pairs of elytrophores, as originally described. Clearly the species is too little known to warrant accurate assessment, but it may represent the pelagic phase of a benthic species.

Sheila bathypelagica Monro, 1930

Sheila bathypelagica Monro, 1930, pp. 43–5, fig. 8, from St. 256, TYF, 850–1100 m., 1 specimen.

Antinoë pelagica Monro, 1930

Antinoë pelagica Monro, 1930, pp. 63–5, fig. 16, from St. 45, NCS-T, 238–270 m., 1 specimen, and St. SS 18, N 70 V, 50–0 m., 1 specimen.

Macellicephala McIntosh, 1885

Macellicephala sp. Monro, 1930, St. 144, NCS-T, 155–178 m., 1 specimen.

In 1936 Monro reported the following species from the collection of 'Discovery II':

Harmothoë benthophila Ehlers, 1913

Harmothoë benthophila Monro, 1936, pp. 87–8, from St. 702, TYFB, 236–0 m., 1 specimen. I have not found this species in the present survey.

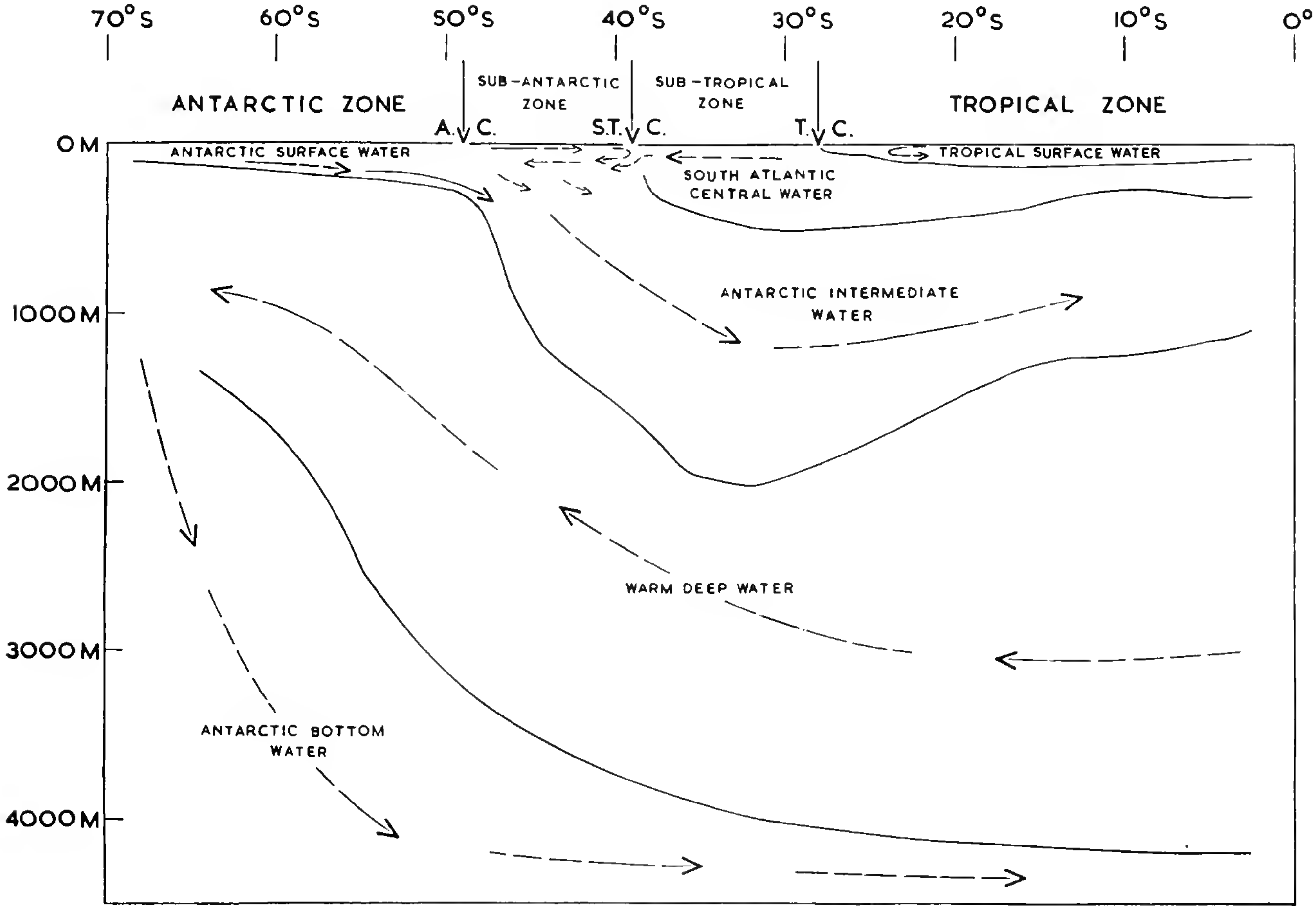
ZOOGEOGRAPHY

1. HYDROLOGICAL ENVIRONMENT

In the South Atlantic Ocean four hydrological zones can be recognized, the Antarctic, Sub-Antarctic, Sub-Tropical and Tropical (Text-fig. 1, p. 165). Each zone has a characteristic surface water mass beneath which are intermediate, deep and bottom water masses not confined by any surface zonation (Text-fig. 14).

It cannot be over-emphasized that neither the zones nor the water masses can be rigidly defined; they are subject to continual fluctuation and considerable intermixing. In the distribution maps, therefore, their positions correspond as nearly as possible with conditions existing when the samples were collected at the stations shown; in consequence these positions depart a little from the average estimated from all available data by Deacon (1933, 1937) and Mackintosh (1946).

Text-figs. (15–22[1]) of temperature and salinity sections on the Greenwich Meridian have been prepared from data in the Discovery Station Lists. They indicate the seasonal and depth fluctuations in hydrological conditions and the movements of the principal water masses. I have drawn freely from the work of Deacon (1933, 1937) on the hydrology of the Antarctic Sector of the South Atlantic and along the meridian of 30° W., and from Mackintosh (1946) on the varying positions of the Antarctic Convergence.



Text-fig. 14. Diagram indicating the circulation of water approximately along the meridian of 30° W. The arrows indicate the general movement of the water masses. A.C. = Antarctic Convergence, S.T.C. = Sub-Tropical Convergence, T.C. = Tropical Convergence.

(i) SURFACE WATER MASSES

(*a*) *Antarctic Surface Water* is found around Antarctica as a cold poorly saline layer lying in the surface 100–250 m. above warmer water of higher salinity. In the South Atlantic Ocean, three main sources of water contribute to its composition: (1) Water from the Bellingshausen Sea which flows in along the southern side of the Drake Strait, (2) water flowing out of the Weddell Sea in a north-easterly direction, and (3) water from the East Wind Drift which flows in a westerly direction from the southern Indian Ocean into the Weddell Sea. Of these three components the Weddell Sea Water (Weddell Drift) probably exerts the greatest influence because in winter it carries the main body of pack-ice across the South Atlantic.

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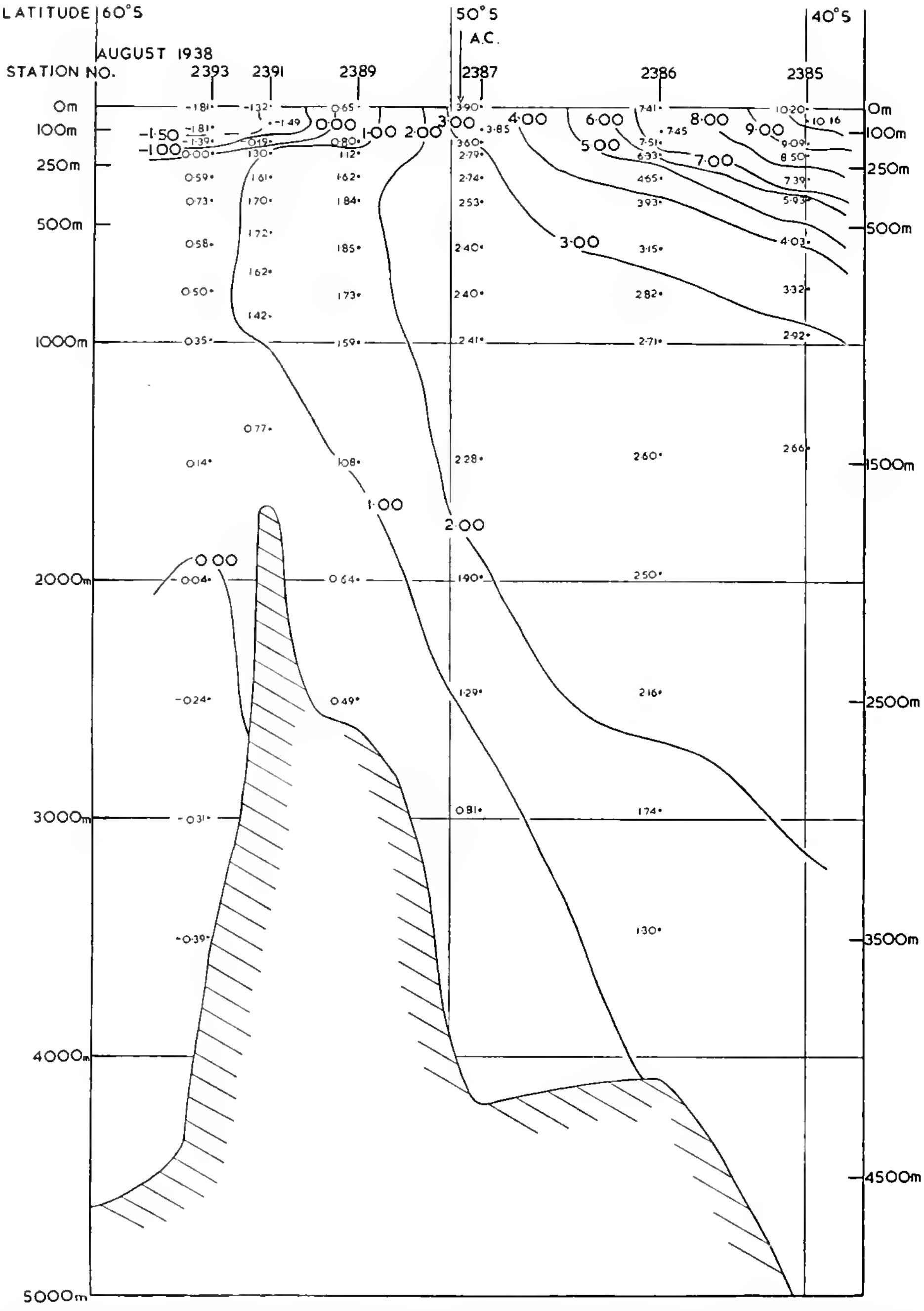
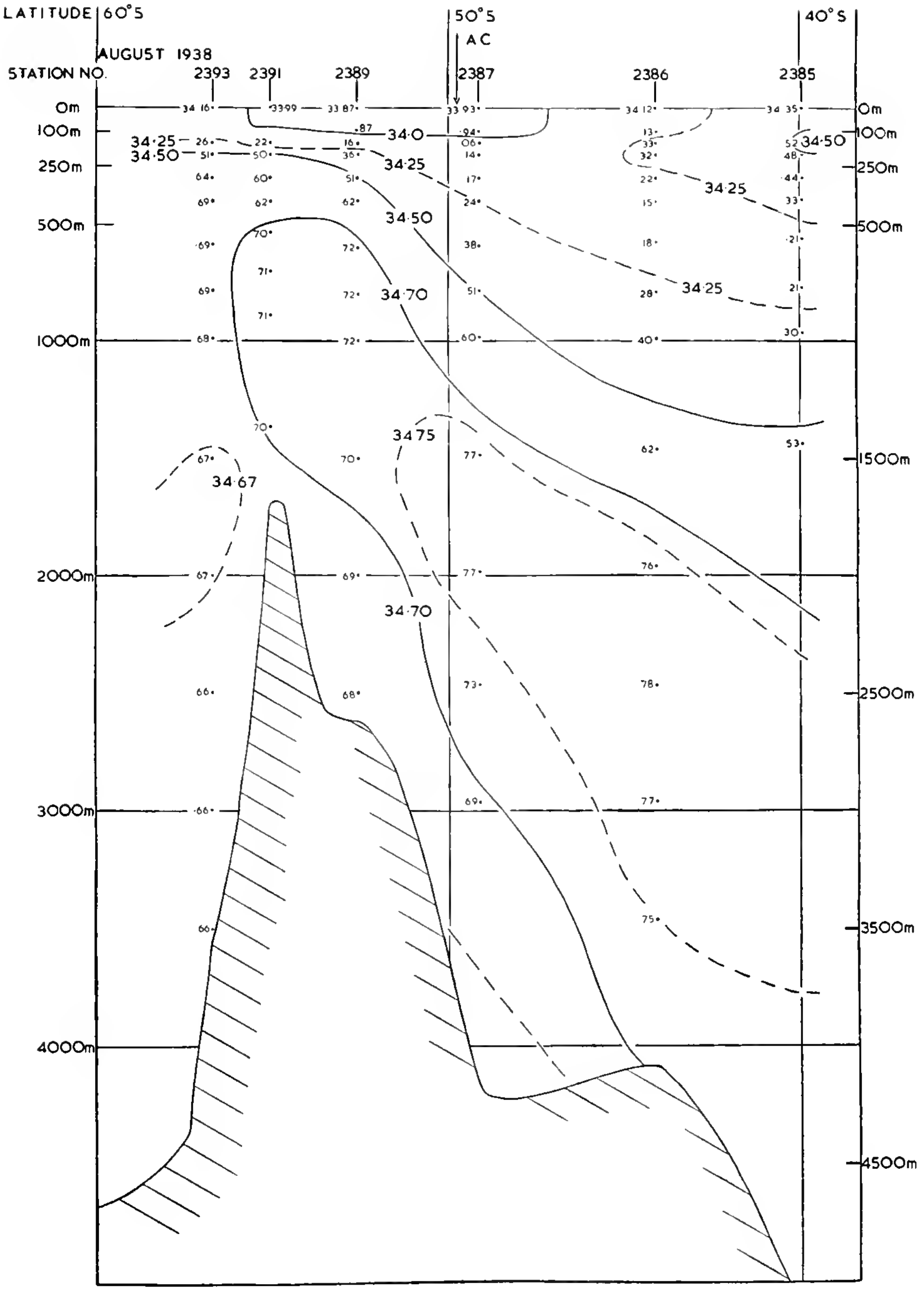
[1] The vertical scale in these sections has been much exaggerated, and to avoid confusion all the readings have not been included on the figures but they have all been taken into account in drawing the isotherms and isohalines. It is not considered that temperature and salinity are more, or less, important than other hydrological features but they are more easily interpreted and for this reason have been more widely used.



Text-fig. 15. Distribution of temperature (° C.) between 60° S. and 40° S. in the region of the Greenwich Meridian, August 1938 (see Text-fig. 4*b* for station positions).

The distribution of the pack-ice has a marked effect on the salinity and temperature of Antarctic Surface Water, and varies from season to season. During the winter months of June to August, the pack-ice extends to about 55–56° S. (Mackintosh and Herdman, 1940); surface temperatures are very low with a minimum of −1·81° C. (Text-fig. 15) and the open water has a salinity of about 34·00‰ (Text-fig. 16). In summer the pack-ice melts, causing dilution of the upper layers; at the same time absorption of radiation brings about an increase of surface temperature. As mixing proceeds well-marked discontinuity layers are set up. These effects are shown in the hydrological sections for January 1939, in which the surface temperatures are all above 0·0° C. (Text-fig. 17), and a belt of poorly saline water, with a salinity of less than 34‰, covers the surface to about 50–20 m. depth and extends from the higher latitudes as far north as about 55° S. (Text-fig. 18).

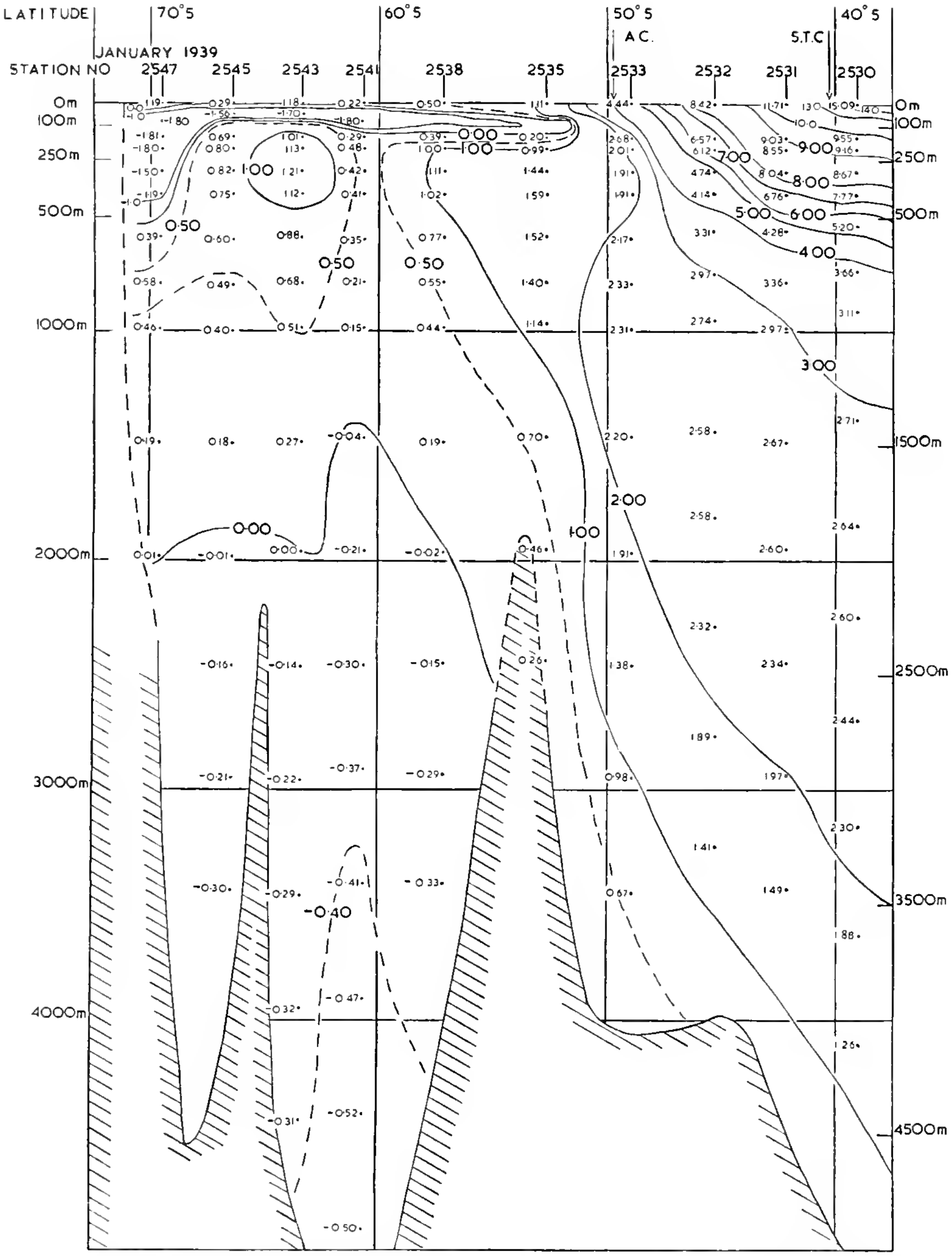


Text-fig. 16. Distribution of salinity (‰) between 60° S. and 40° S. in the region of the Greenwich Meridian, August 1938.

The Bellingshausen Sea Current is slightly warmer than the Weddell Drift; consequently, where these two currents meet, the colder Weddell water sinks below the lighter Bellingshausen water. The resulting convergence is normally marked by a mean temperature difference in the top 100 m. of 1° to 1·5° C. In Text-figs. 4*a* and 4*b* (p. 167) the position of this boundary is shown for stations made about the Greenwich Meridian; details are given in Table 12 for the stations in the hydrological sections (Text-figs. 15, 17, 19, 21).

The two types of water can be traced across the Scotia Sea, around South Georgia, and as far east as the longitude of Bouvet Island (Deacon, 1937, p. 25).

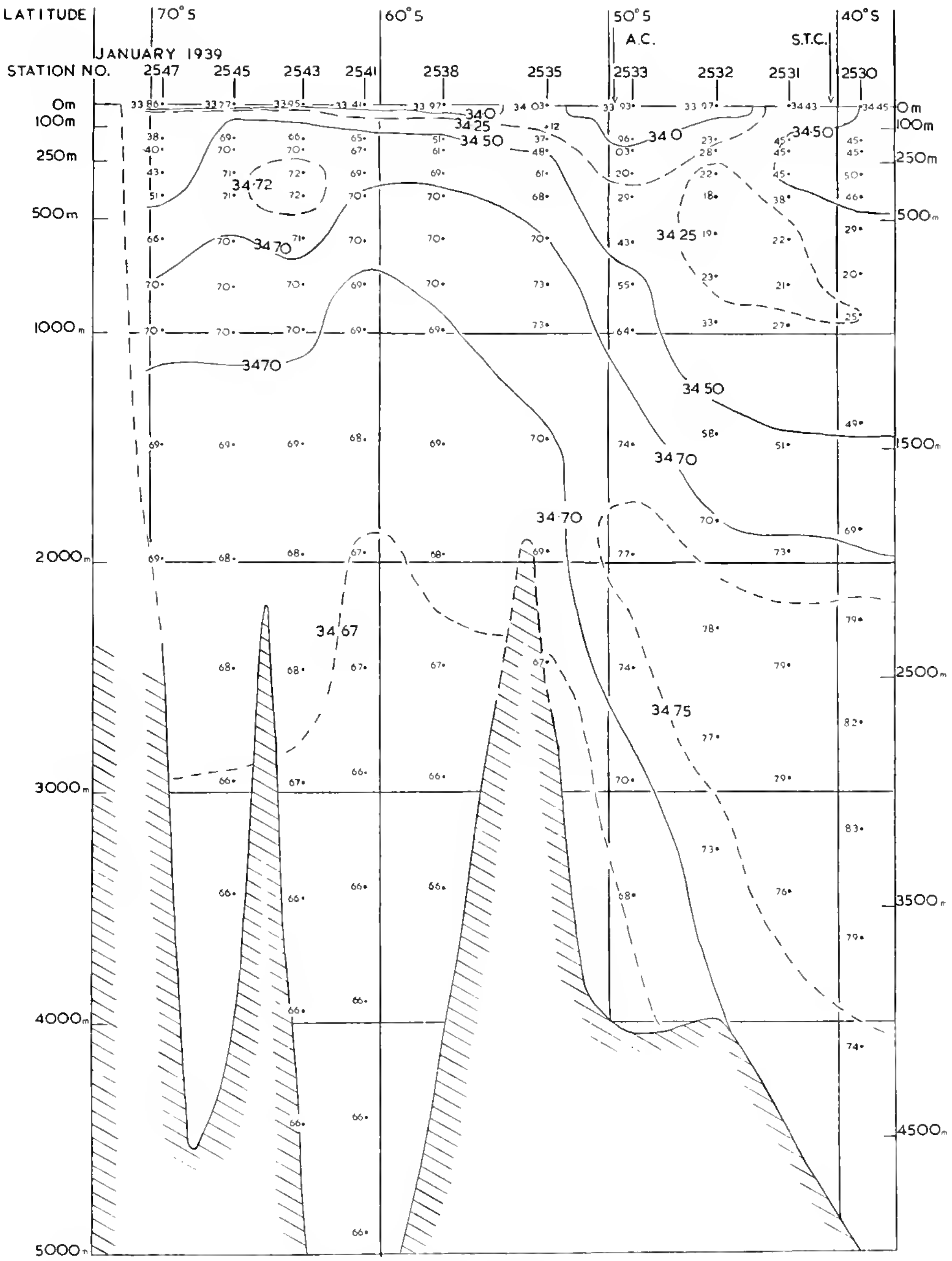
The main direction of movement of the Antarctic Surface Water is north-eastward across the South Atlantic Ocean, with an occasional swing to north or south. To the west of South Georgia there is



Text-fig. 17. Distribution of temperature (° C.) between 70° S. and 40° S. in the region of the Greenwich Meridian, January 1939 (see Text-fig. 4*a* for station positions).

Table 12

Date	*Station no.*		*Mean temperature ° C., in top 100 m.*		*Temperature difference (° C.)*
	Weddell water	*Bellingshausen water*	*Weddell water*	*Bellingshausen water*	
June 1936	1779	1778	−0·81	+0·68	1·49
March 1937	2018	2020	+0·41	+1·60	1·19
August 1938	2391	2389	−1·37	+0·61	1·97
January 1939	2538	2535	−0·36	+0·75	1·11



Text-fig. 18. Distribution of salinity (‰) between 70° S. and 40° S. in the region of the Greenwich Meridian, January 1939.

'a small southward movement', which 'causes the south-west coast of the island to be bathed with water from the Bellingshausen sea current whilst the Weddell Current is held off shore' (Deacon, 1937, p. 32). North-east of South Georgia, movement is more to the north and the Weddell Current normally has an important influence off this coast of the island. East of the Greenwich Meridian in the higher latitudes, the East Wind Drift flows westward along the Antarctic continent into the Weddell Sea.

Antarctic Surface Water extends northwards until it meets and mixes with the warmer, lighter Sub-Antarctic Surface layer, and sinks below it along a well-marked line, the ANTARCTIC CONVERGENCE. The position of the convergence can normally be recognized by a sharp change in surface temperature. In summer, when the convergence is crossed from south to north, an increase from 3°

to 5·5° C. is normal; in winter a rise from 1° to 3·5° C. occurs. The salinity in this region is about 33·93‰. When the surface temperature change is not sharply marked, the position of the Antarctic Convergence is indicated by the sinking of the coldest part of Antarctic Surface Water below 200 m. For example, in March 1937 'Discovery II', crossed the convergence in 49° 50′ S. north of St. 2022, and although no very sharp change in the surface temperatures between Sts. 2022 and 2023 is apparent, experience shows that the prominent northerly bend of the 2·00° C. isotherm between 200 and 300 m. in this area (Text-fig. 19) indicates the position of the convergence.

In August 1938, January 1939 and May 1936 the Antarctic Convergence lay in the positions indicated in the temperature and salinity sections for these months (Text-figs. 15–16, 17–18, 21–22). In April 1931, Deacon (1933) found it to occur along the meridian of 30° W., just north of St. 666; in March 1938 its position lay between Sts. 2292 and 2293 (Mackintosh, 1946).

(*b*) *Sub-Antarctic Surface Water* extends to greater depths than the Antarctic Surface layer. From south to north, the surface temperatures increase from approximately 3° to 11·5° C. in winter, and from 5·5° to 15·0° C. in summer; the salinity is low varying between 33·85 to 34·65‰. No discontinuity layers are set up and vertical mixing takes place. In consequence, it is not possible to define any boundary between the Sub-Antarctic Surface Water and the underlying Antarctic Intermediate layer.

In the upper layer of Sub-Antarctic Surface Water movement is a little to the north of east continuously around the continent. In the middle layers the principal component of movement is to the south, and below this to the north again (Text-fig. 14). Between the Falkland Islands and South Georgia the position of the Antarctic Convergence is less sharply defined than elsewhere because Sub-Antarctic Surface water moves southwards and rather confused conditions exist. South and west of the Cape of Good Hope also, confused conditions are found because of an admixture of sub-tropical water from the opposed Agulhas current. Böhnecke (1938) distinguished a secondary polar front in the Sub-Antarctic Zone, which Deacon (1945) has confirmed from Discovery observations south of the Agulhas current. Along the Greenwich Meridian this boundary lies approximately in latitude 45° S. and separates water of mixed origin in the southern half of the Sub-Antarctic Zone from more stably stratified water in the northern half. It has a marked effect on the distribution of *Pelagobia longicirrata*.

The northern boundary of the Sub-Antarctic Zone is at the *Sub-Tropical Convergence* where Sub-Antarctic Surface Water sinks but does not move to the north. It either mixes with Sub-Tropical Water moving south or wells up to the surface. At the Sub-Tropical Convergence a much sharper change of temperature and salinity takes place than at the Antarctic Convergence and it has a much greater influence on the distribution of pelagic polychaetes. In Table 13, the hydrological details and positions of the stations adjacent to the Sub-Tropical Convergence have been listed.

Deacon (1933) has given an analysis of the conditions prevailing in April 1931 and further details of the lines of stations made since 1936 are shown in Text-figs. 17–22.

In the vicinity of Tristan da Cunha a variation of 6° of latitude in the position of the Sub-Tropical Convergence is possible (Deacon, 1945), and St. 4, made in January 1925, with a surface temperature of 14·59° C. and a salinity of 34·85‰, very close to the Sub-Tropical Convergence, is of uncertain hydrological position. No details are available for St. 247 also near Tristan da Cunha, but at St. 254, about 10° to the west and slightly south, the surface temperature was 13·5° C. and salinity 35·14‰, which in June, when these readings were made, indicates the station is north of the Sub-Tropical Convergence.

It will be noted from these hydrological readings that increase in temperature is the best indicator of the position of the Sub-Tropical Convergence, salinity increase not always being marked.

(*c*) *South Atlantic Central Water*[1] is much warmer and more saline than Sub-Antarctic Surface Water. Its surface temperature increases from approximately 11·5° C. in winter and 14·5° C. in summer just north of the Sub-Tropical Convergence to 23° C. at the Tropical Convergence, under which it sinks along a line of discontinuity marked by the 23° C. isotherm. Its surface salinity maximum is 36‰. The maximum depth of South Atlantic Central Water is rarely more than 500 m. and is marked by a line of discontinuity with the Antarctic Intermediate layer, where the temperature is about 10·5° C. and the salinity varies between 34·85 to 35‰.

Table 13. *Stations adjacent to the Sub-Tropical Convergence*

Date	*Station no.*	*Temperature (° C.)*	*Salinity (‰)*	*Hydrological position*
3. vi. 26	74	13·61	34·86	Sub-Tropical
1. vi. 26	72	12·65	34·67	Close to the Sub-Tropical Convergence
30. v. 26	71	10·16	34·37	Sub-Antarctic
30. x. 26	103	18·92	35·52	Sub-Tropical
4. xi. 26	107	5·91	34·02	Sub-Antarctic
10. x. 30	448	14·35	34·85	Sub-Tropical
11/12. x. 30	449	9·45	34·39	Sub-Antarctic
23. iv. 31	672	15·65	34·93	Sub-Tropical
22/23. iv. 31	671	9·70	34·32	Sub-Antarctic
31. x. 31	715	15·76	34·29	Sub-Tropical
1. xi. 31	716	10·52	34·31	Sub-Antarctic
2. xi. 31	717	13·28	35·50	Close to the Sub-Tropical Convergence
3. xi. 31	718	8·00	34·65	Sub-Antarctic
24. v. 36	1773	13·11	34·57	Sub-Tropical
25. v. 36	1774	9·40	34·29	Sub-Antarctic
2. iv. 37	2027	19·14	35·37	Sub-Tropical
1. iv. 37	2026	14·09	34·61	Sub-Antarctic
11/12. i. 39	2530	13·40	34·45	Sub-Tropical
12. i. 39	2531	11·71	33·43	Sub-Antarctic

The general movement of South Atlantic Central Water is southwards under the influence of the prevailing northerly winds. This is particularly marked in the western part of the South Atlantic where the water flows in the Brazil current. The water is deflected eastwards when the region of the West Winds is reached, and here its direction of flow is similar to that of the Sub-Antarctic Surface Water, but owing to their very different properties the two types of water remain distinct to a large extent. There is some evidence that part of the South Atlantic Central Water 'is possibly deflected southwards near the Cape of Good Hope to mix with water which turns back from the Agulhas current in an easterly direction across the Indian Ocean' (Deacon, 1937, p. 74).

The 23° C. surface isotherm on the line between the Cape Verde Islands and the Falkland Islands is situated between Sts. 710 and 711, and on the 30° W. Line between Sts. 677 and 678. Between Cape Town and the Cape Verde Islands hydrological readings were not made at all stations, and in Text-fig. 1 and all the distribution charts of species in this report, the position of the 23° C. isotherm from the 'Meteor' results (Böhnecke, 1936) has been used to indicate the location of the Tropical Convergence in the eastern Atlantic.

(*d*) *Tropical Surface Water* rarely exceeds 145 m. in depth. It has a temperature range of 23° to 29° C. from south to north, and a salinity maximum of 37‰. As noted above, it forms a marked

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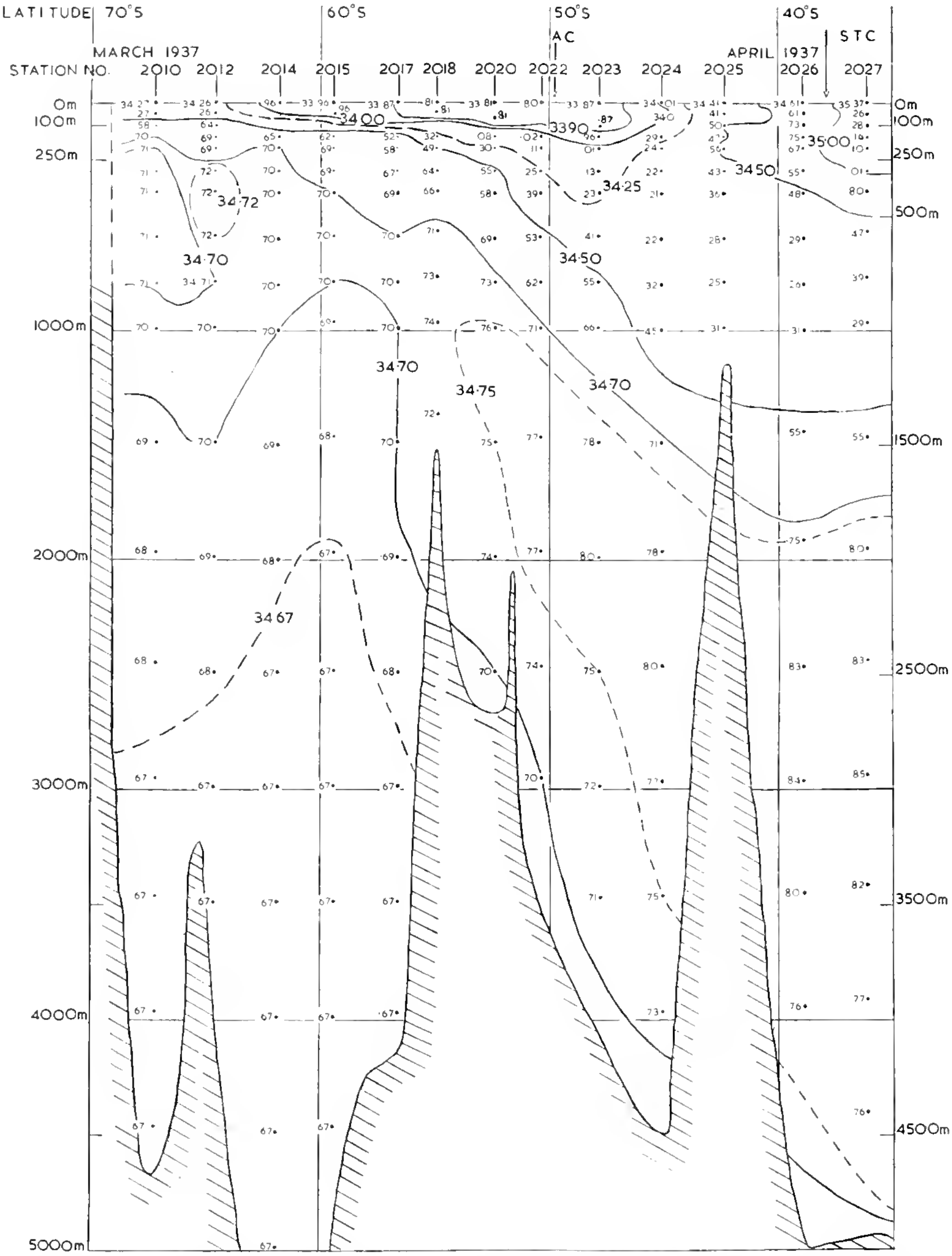
[1] The term 'South Atlantic Central Water', is taken from Sverdrup, Johnson and Fleming (1946); it is synonymous with Deacon's (1933) Sub-Tropical Surface Water and Sub-Tropical Under Water.

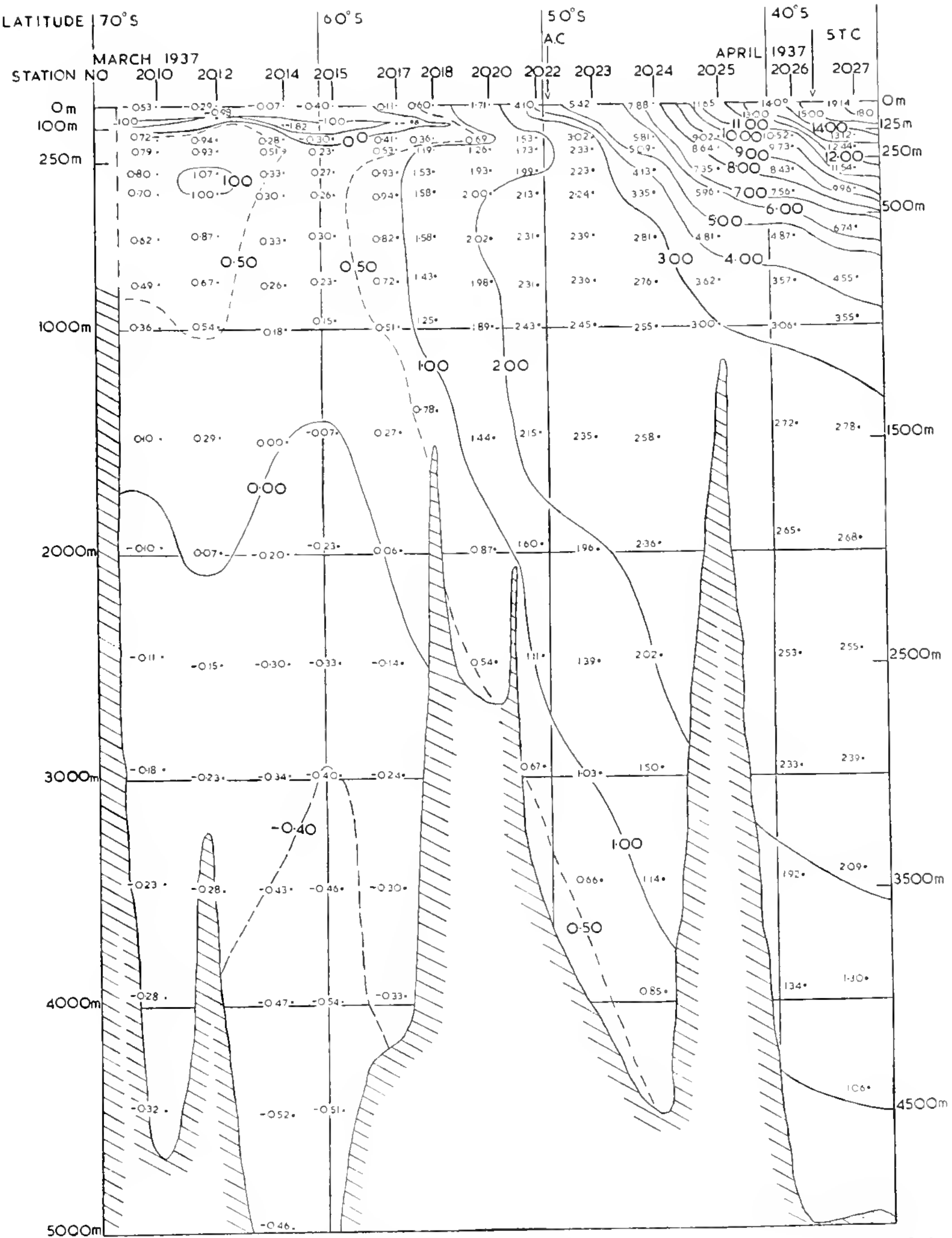


Text-fig. 19. Distribution of temperature (° C.) between 70° S. and 35° S. in the region of the Greenwich Meridian, March–April 1937 (see Text-fig. 4*a* for station positions).

discontinuity (indicated by the 23° C. isotherm) with the South Atlantic Central Water. The Tropical Convergence does not appear to have as much influence on the distribution of pelagic polychaetes as either the Antarctic or Sub-Tropical Convergences.

(ii) INTERMEDIATE AND DEEP WATER MASSES

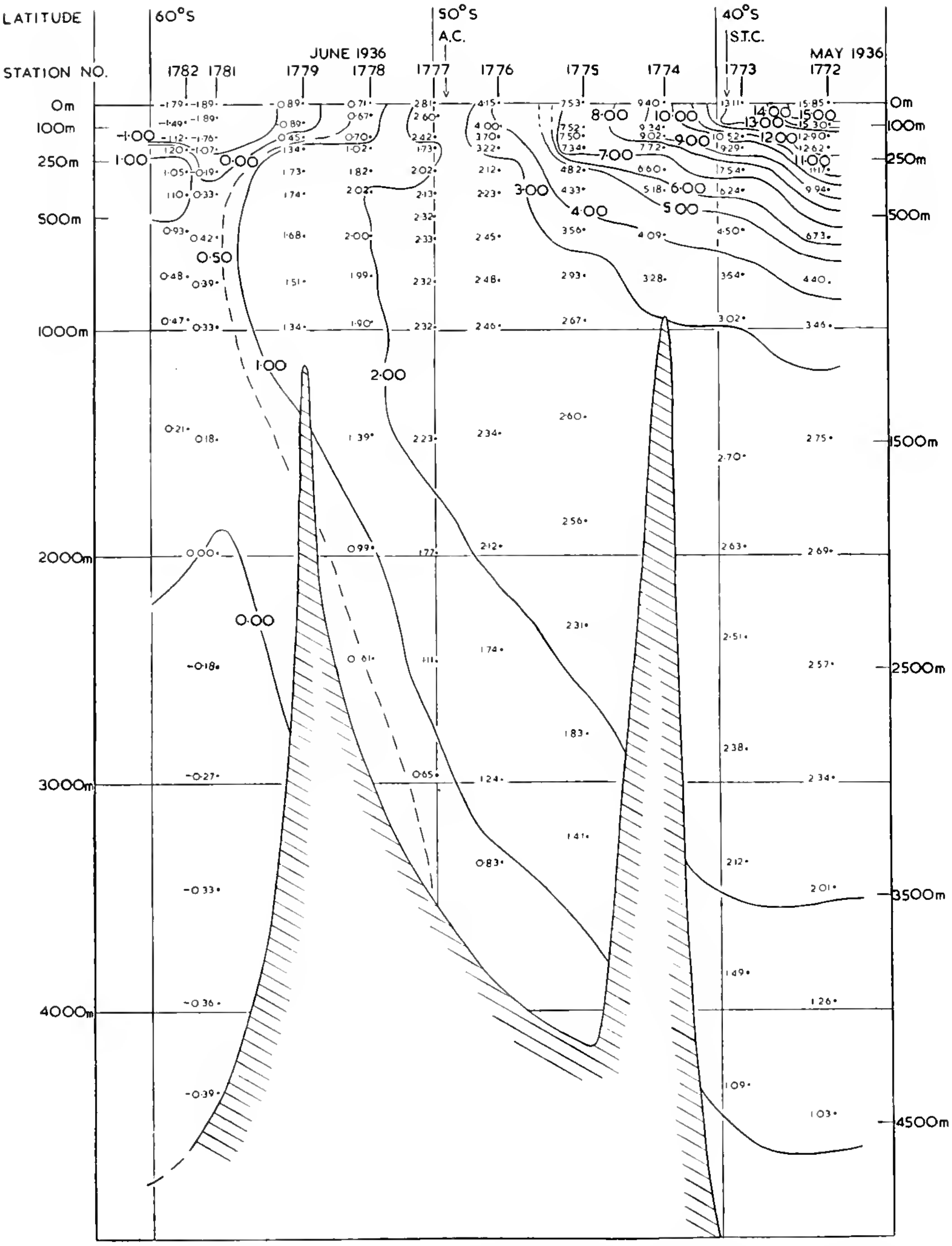
When the Antarctic Surface Water sinks at the Antarctic Convergence it mixes with water of Sub-Antarctic origin, and together with this gives rise to the north-flowing Antarctic Intermediate Water. Below the Antarctic Surface Water and Antarctic Intermediate Water throughout the South Atlantic is the Warm Deep Water with a southerly component in its movement, and beneath it the heavy Antarctic Bottom Water.



Text-fig. 20. Distribution of salinity (‰) between 70° S. and 35° S. in the region of the Greenwich Meridian, March–April 1937.

(*a*) *Antarctic Intermediate Water* has been shown by Deacon (1933) to reach a depth of about 1100 m. in latitude 45° S. increasing to 2000 m. in 30° S. and decreasing again to about 1200 m. in 5° S. along the meridian of 30° W. It is characterized by its low salinity, which at the level of minimum salinity increases from 34·15 to 34·65 ‰ between 47° S. and the Equator; the temperature increase over this distance is from 3·2° to 4·85° C.

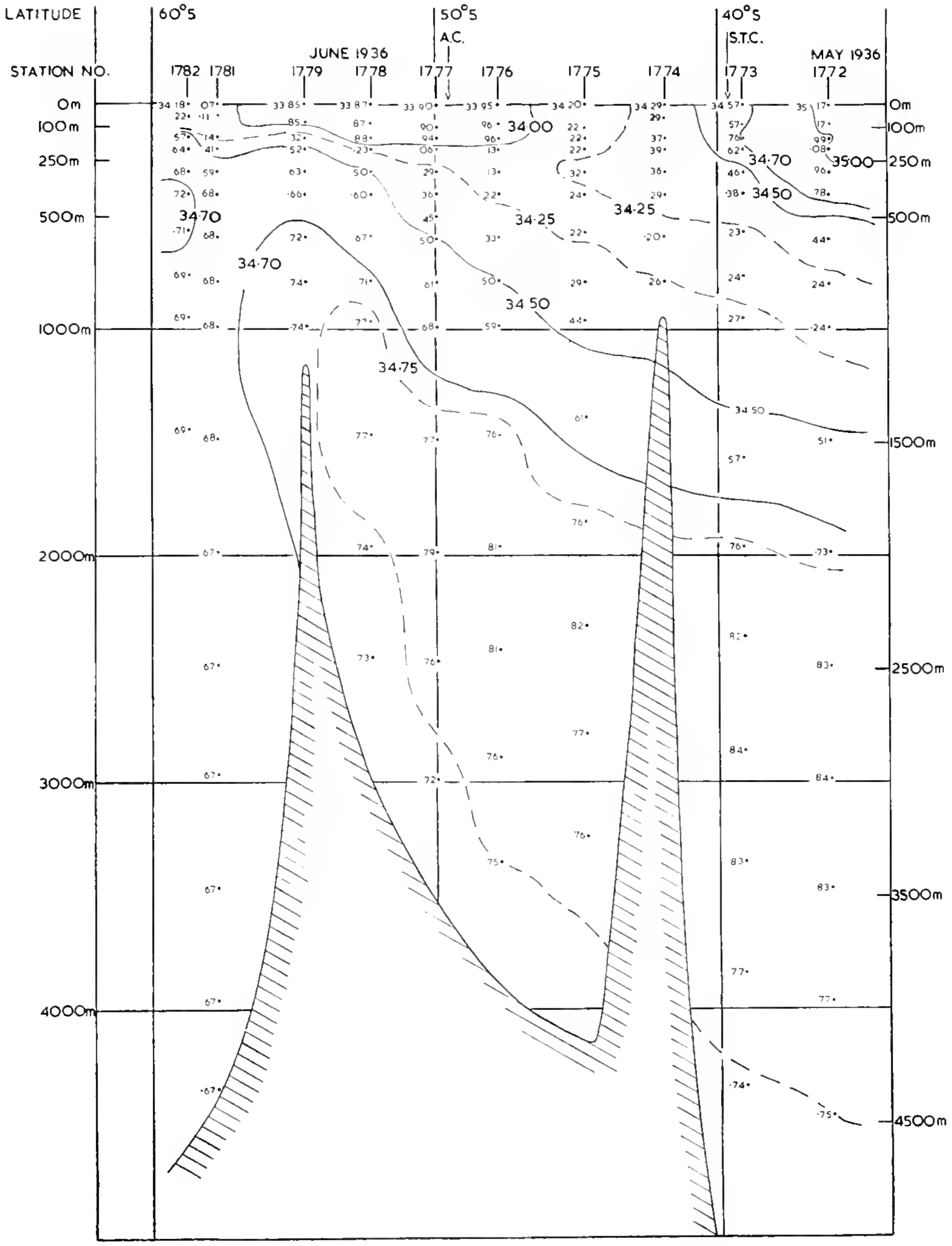
The principal direction of movement of Antarctic Intermediate Water can be seen in the temperature sections (Text-figs. 15, 17, 19, 21), in the sinking of Antarctic Surface Water at the Antarctic Convergence, where the isotherms for 2° and 3° C. between 150 and 500 m. swing markedly north. The depth of the layer has been estimated from these sections, at stations where samples were collected near the boundary between it and the Warm Deep Water. The temperature in Antarctic Intermediate



Text-fig. 21. Distribution of temperature (° C.) between 60° S. and 35° S. in the region of the Greenwich Meridian, May–June 1936 (see Text-fig. 4*b* for station positions).

Water decreases with depth to a minimum value increasing again to a maximum in the Warm Deep. The boundary between them can be taken to lie midway between these two depths (Deacon, 1933). At St. 2533 the minimum temperature in the Antarctic Intermediate water was 1·91° C. at 400 m. and the maximum temperature in the Warm Deep Layer 2·33° C. at 790 m.; the boundary at this station is therefore about 600 m. At other stations on the 0° Line the depth of the Antarctic Intermediate water was estimated in the same way and found to lie at 1620 m. at St. 2532; 900 m. at St. 2023; 1250 m. at St. 2024; 800 m. (?) at St. 1776; 1400 m. at St. 1775; 900 m. at St. 2387 and at approximately 1500 m. at St. 2386.

(*b*) *Warm Deep Water*, with its principal component of movement directed south lies below the Antarctic Intermediate Water at considerable depths in the Tropical, Sub-Tropical and Sub-Antarctic



Text-fig. 22. Distribution of salinity (‰) between 70° S. and 35° S. in the region of the Greenwich Meridian, May–June 1936.

Zones, but in the Antarctic Zone it rises steeply to within 250–100 m. of the surface. The position of its upper boundary with the Antarctic Surface and Antarctic Intermediate water has been discussed already; its lower boundary with Antarctic Bottom Water lies at depths beyond the range of any of the nets fished at the stations from which samples have been examined here.

The temperature of the Warm Deep Water decreases with depth, but its salinity increases until a maximum is reached at the core of the layer. The rise of this water close to the surface within the Antarctic Zone is very well indicated in Text-figs. 15, 17, 19, 21, by the sharp southern bend in the 2° C. isotherm between 500 and 1000 m. and in the 1° C. isotherm between 250 and 1000 m. The isohaline for 34·70‰ (Text-figs. 16, 18, 20 and 22) indicates the depth at which the core of the layer occurs and shows the sharp rise of the warm deep water to near the surface south of the Antarctic Convergence.

(*c*) *Antarctic Bottom Water* is not separated by a discontinuity layer from the Warm Deep Water and the position of the boundary between the two is difficult to estimate. None of the samples examined here was collected in this water mass.

2. Distribution of Species

Only the distribution of the species described in the Systematic Account is discussed in this section. This excludes a very few species inadequately described or known only from a few records. Taxonomic sequence has been retained only where this is of zoogeographical significance. The species are arranged in order of occurrence from south to north, that is from the ice-edge to the equator. Endemic antarctic polychaetes are considered first, then the cosmopolitan forms and finally the sub-tropical and tropical species.

Previous work on pelagic polychaetes in the South Atlantic Ocean has been mainly confined to material from particular zones, except for the reports by Monro (1930, 1936) on some of the Discovery Collections, and Friedrich (1950*c*) on the 'Meteor' material, both of which covered the whole area. The Deutsche Südpolar Expedition (Ehlers, 1913, 1917) and the Swedish Antarctic Expedition (Støp-Bowitz, 1951) made collections in the Antarctic and occasionally elsewhere, but other expeditions referred to in this section worked either in the Antarctic, or in the Sub-Tropical and Tropical Zones.

The wide area and numerous stations in the South Atlantic, from which I have examined material from the Discovery Collections, are shown in Text-figs. 1–4, pp. 165–7. The extensive hydrological work also carried out by the Discovery Investigations is summarized in the previous section of this report; it has enabled me to indicate, to a certain degree, the effect of variation in the hydrological environment on the distribution of the pelagic polychaetes of this area.

Rhynchonerella bongraini

(Text-figs. 23–6, Tables 14 and 15, Appendices I and II)

The endemic antarctic *R. bongraini* was collected only in the top 500 m. of water, that is in Antarctic Surface Water and in the upper layers of the Warm Deep Water. The specimens varied between 4–15 mm. in length and occurred mainly in samples collected by the N 70 V net; on rare occasions it was caught by the N 100 net.

The occurrence of *R. bongraini* in the region of the Greenwich Meridian is shown both in Text-figs. 23 and 24 and in Tables 14 and 15. The temperature and salinity characteristics of the top 500 m. of water in which it occurs are shown in Text-figs. 15–21.

In this region *R. bongraini* is absent from stations immediately south of the Antarctic Convergence and its distribution in the Antarctic Surface Water seems to be controlled more by the influence of the Weddell Drift than by the position of the convergence. The existence of a boundary between Bellingshausen Sea Water and Weddell Drift has already been noted (p. 209), and *R. bongraini* was never collected to the north of this boundary.

The records of *R. bongraini* from the South Sandwich Survey have been plotted in Text-fig. 25 and listed in Appendix II, Table *b*. Nets were not fished below 250 m., so that only the Antarctic Surface Water was sampled. All the South Sandwich stations lie well within the Weddell Drift (Deacon, 1937) so that it is not surprising to find *R. bongraini* at thirty-two out of the fifty-eight stations.

The distribution of *R. bongraini* in the South Georgia area is shown in Text-fig. 26, which includes the following records:

1. The Alciopid larvae of Hardy and Gunther (1935): December–January Survey 1926–7, Sts. 124, 210–100 m. (1), WS 35, 51 m. (1), WS 36, 250–100 m. (1) and WS 112, 160–50 m. (1). Of these, I

have been able to examine only the specimen from St. 124 which is definitely *R. bongraini* but the other specimens are almost certainly the same.

2. February–March Survey 1928, Sts. WS 145, 275–100 m., (1), WS 146, 500–250 m. (1), WS 149, 250–100 m. (1), WS 190, 750–0 m. (2), and 1000–0 m. (4).
3. January–February Survey 1930, one specimen from St. 323, 250–100 m.

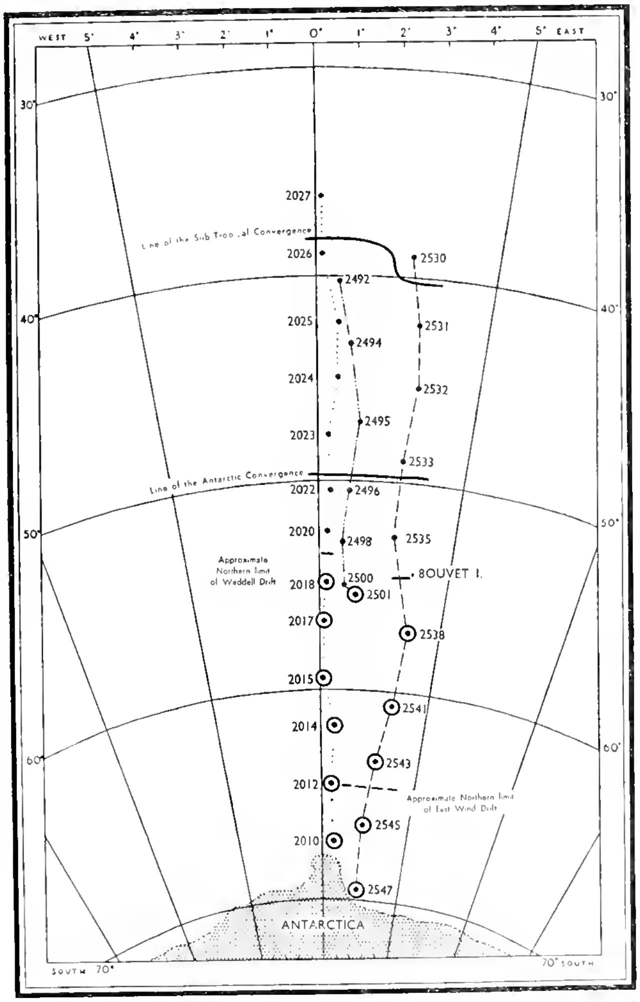


Fig. 23

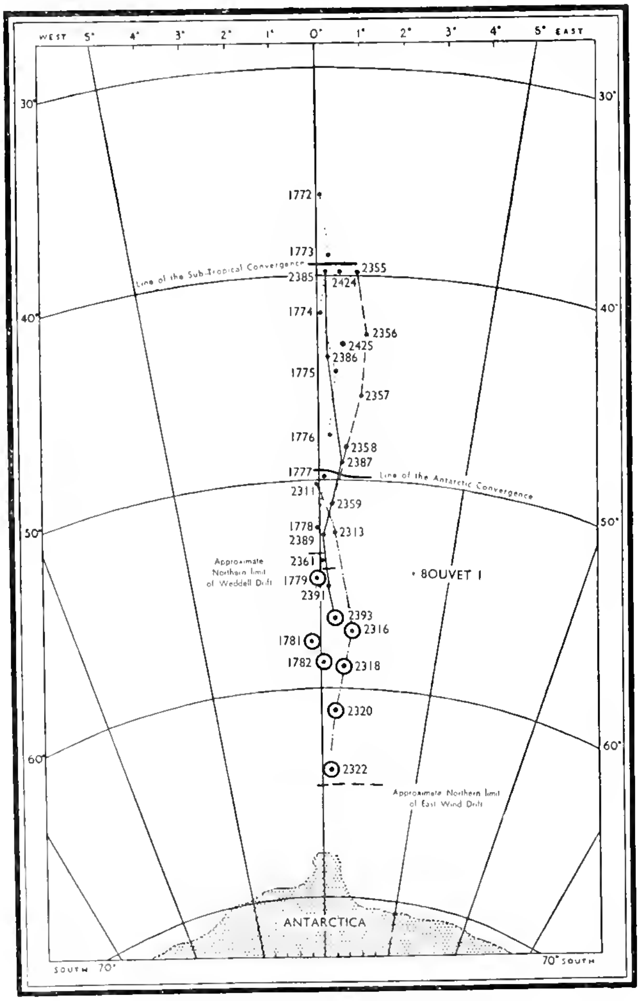


Fig. 24

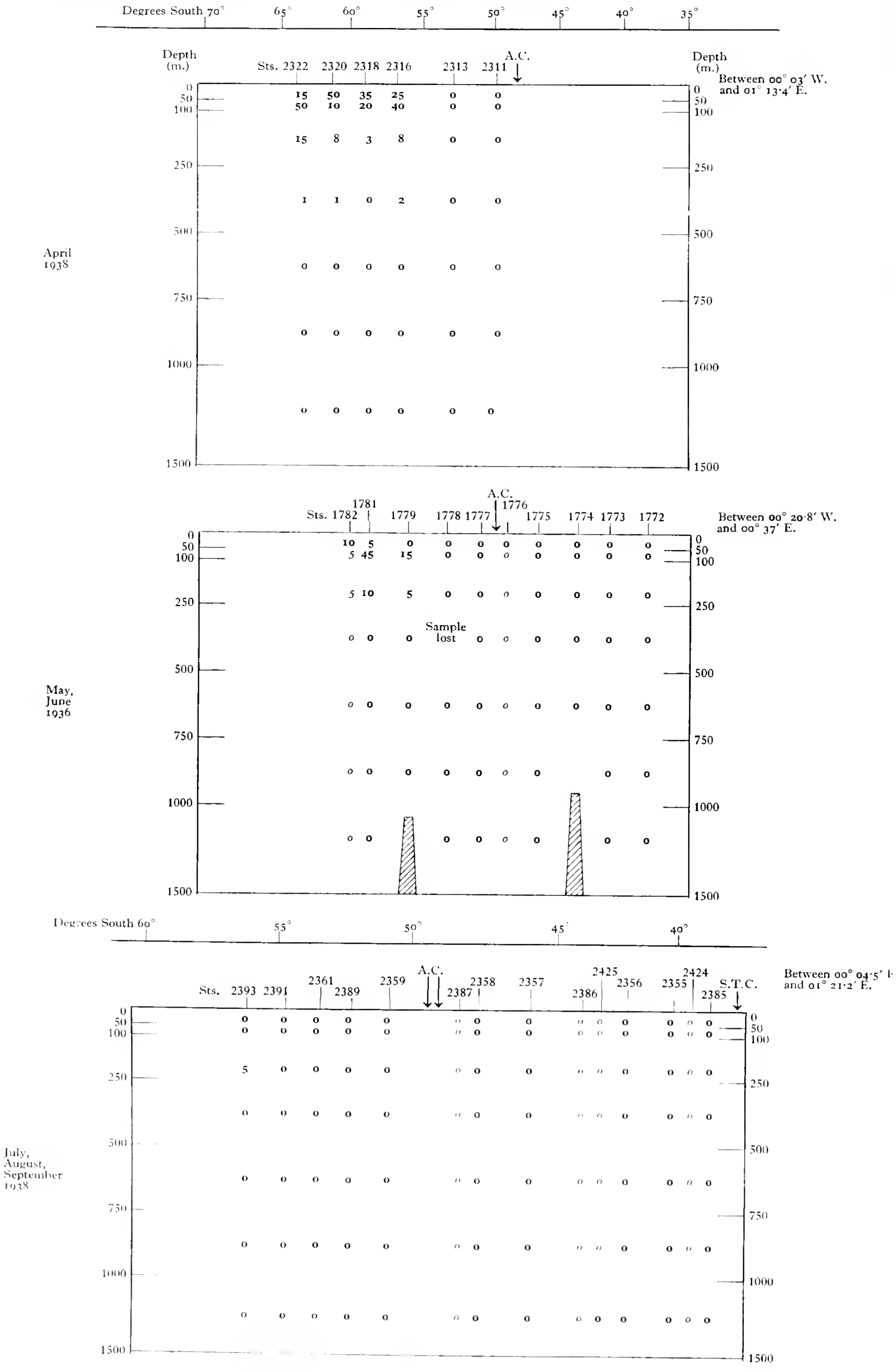
Text-fig. 23. Occurrence of *Rhynchonerella bongraini* ⊙ in the region of the Greenwich Meridian. Sts. 2010–27, March–April 1937; Sts. 2492–2501, November–December 1938; Sts. 2530–47, January 1939, N 70 V nets.

Text-fig. 24. Occurrence of *Rhynchonerella bongraini* ⊙ in the region of the Greenwich Meridian. Sts. 1772–82, May–June 1936; Sts. 2311–22, April 1938; Sts. 2355–61, 2385–93, 2424 and 2425, July–September 1938, N 70 V nets.

The sparseness of this distribution is in marked contrast to that found on the Greenwich Meridian and around the South Sandwich Islands; this is particularly true of the top 50 m. of water. Disregarding the catches at St. WS 190, where the nets were hauled from 1000 and 750 m. to the surface, there is no record from 50–0 m., and only one specimen was caught by a net hauled between 100 and 50 m., at St. WS 35, which, as shown by Hardy and Gunther (1935, fig. 41) fished in Weddell Sea Water. At St. WS 112 (160–50 m.), the specimen may have been taken in Warm Deep Water at the lowest part of the haul, but if it was collected at the top of the haul, it would also have been taken in Weddell Sea Water.

The remaining records of *R. bongraini* from the South Georgia Survey are from the upper layers of Warm Deep Water, some of them north of the northern limit of Weddell Drift, and it is not unlikely that this species inhabits this layer to the north, as far as the Antarctic Convergence.

Table 14. Rhynchonerella bongraini. *Distribution in the region of the Greenwich Meridian, between 64° S. and 35° S. (N 70 V nets only.) Italic light type indicates hauls made between sunrise and sunset. A.C. = Antarctic Convergence, S.T.C. = Sub-Tropical Convergence.*



April 1938

Between 00° 03′ W. and 01° 13·4′ E.

Depth (m.)	Sts. 2322	2320	2318	2316	2313	2311
0–50	15	50	35	25	0	0
50–100	50	10	20	40	0	0
100–250	15	8	3	8	0	0
250–500	1	1	0	2	0	0
500–750	0	0	0	0	0	0
750–1000	0	0	0	0	0	0
1000–1500	0	0	0	0	0	0

May, June 1936

Between 00° 20·8′ W. and 00° 37′ E.

Depth (m.)	Sts. 1782	1781	1779	1778	1777	1776	1775	1774	1773	1772
0–50	10	5	0	0	0	0	0	0	0	0
50–100	*5*	45	15	0	0	*0*	0	0	0	0
100–250	*5*	10	5	0	0	*0*	0	0	0	0
250–500	*0*	0	0	Sample lost	0	*0*	0	0	0	0
500–750	*0*	0	0	0	0	*0*	0	0	0	0
750–1000	*0*	0	0	0	0	*0*	0		0	0
1000–1500	*0*	0		0	0	*0*	0		0	0

July, August, September 1938

Between 00° 04·5′ and 01° 21·2′ E.

Depth (m.)	Sts. 2393	2391	2361	2389	2359	2387	2358	2357	2386	2425	2356	2355	2424	2385
0–50	0	0	0	0	0	*0*	0	0	*0*	*0*	0	0	*0*	0
50–100	0	0	0	0	0	*0*	0	0	*0*	*0*	0	0	*0*	0
100–250	5	0	0	0	0	*0*	0	0	*0*	*0*	0	0	*0*	0
250–500	0	0	0	0	0	*0*	0	0	*0*	*0*	0	0	*0*	0
500–750	0	0	0	0	0	*0*	0	0	*0*	*0*	0	0	*0*	0
750–1000	0	0	0	0	0	*0*	0	0	*0*	*0*	0	0	*0*	0
1000–1500	0	0	0	0	0	*0*	0	0	*0*	0	0	0	*0*	0

Table 15. Rhynchonerella bongraini. *Distribution in the region of the Greenwich Meridian, between 70° S. and 35° S. (N 70 V nets only.) Italic light type indicates hauls made between sunrise and sunset. A.C. = Antarctic Convergence, S.T.C. = Sub-Tropical Convergence.*

Degrees South 70° 65° 60° 55° 50° 45 40° 35°

November, December 1938

Between 00° 37·6′ E. and 01° 23·7′ E.

Depth (m.)	2501	2498	2496	A.C. ↓	2495	2494	2492
0–50	*0*	0	0		*0*	*0*	*0*
50–100	*30*	0	0		*0*	*0*	*0*
100–250	*3*	0	0		*0*	*0*	*0*
250–500	*1*	0	0		*0*	*0*	*0*
500–750	*0*	0	0		*0*	*0*	*0*
750–1000	*0*	0	0		*0*	*0*	*0*
1000–1500	No net	0	Sample lost		*0*	*0*	*0*

January 1939

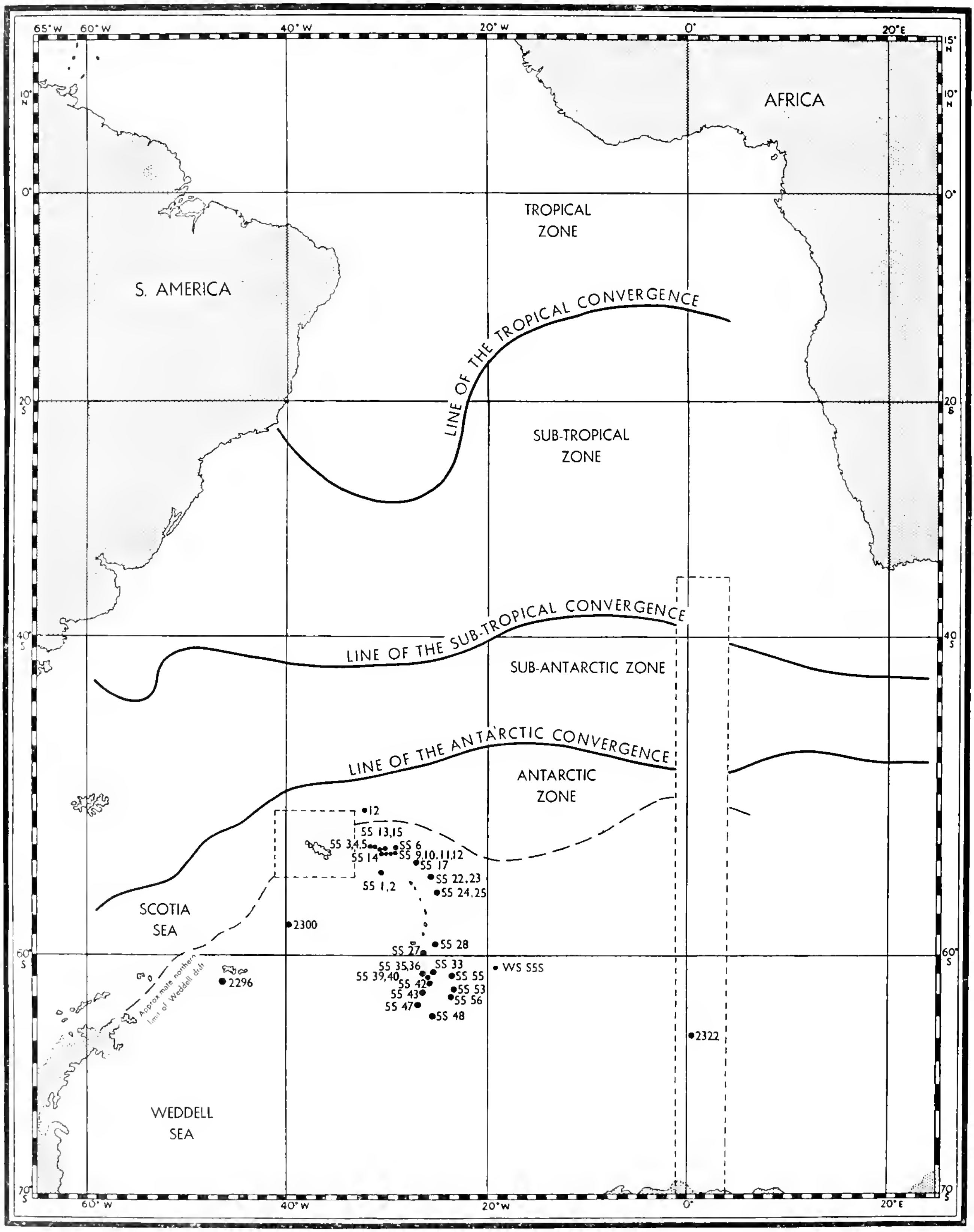
Between 02° 04·7 E. and 03° 33·7′ E.

Depth (m.)	2547	2545	2543	2541	2538	2535	A.C. ↓	2533	2532	2531	S.T.C. ↓	2530
0–50	*0*	*5*	*20*	*45*	*0*	*0*		*0*	0	0		0
50–100	*0*	*5*	*0*	*20*	*25*	*0*		*0*	0	0		0
100–250	*3*	*7*	*2*	*3*	*7*	*0*		*0*	0	0		0
250–500	*0*	*0*	*0*	*0*	*1*	*0*		*0*	0	0		0
500–750	*0*	*0*	*0*	*0*	*0*	*0*		*0*	0	0		0
750–1000	*0*	*0*	*0*	*0*	*0*	*0*		*0*	0	0		0
1000–1500	*0*	0	*0*	0	No net	0		*0*	No net	0		0

March, April 1937

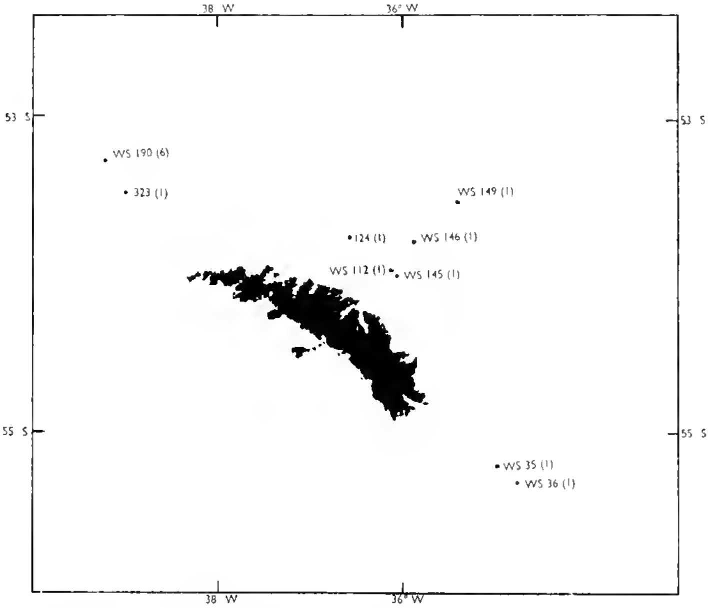
Between 00° 6·7′ E. and 00° 39·7′ E.

Depth (m.)	2010	2012	2014	2015	2017	2018	2020	2022	A.C. ↓	2023	2024	2025	2026	S.T.C. ↓	2027
0–50	15	5	20	*0*	*0*	5	0	0		0	0	0	0		*0*
50–100	*25*	15	10	*20*	*15*	0	0	0		0	0	0	0		*0*
100–250	*5*	0	0	*13*	*2*	2	0	0		0	0	0	0		*0*
250–500	*2*	0	6	*11*	*1*	0	0	0		0	0	0	0		*0*
500–750	*0*	0	0	*0*	*0*	0	0	0		0	0	0	0		*0*
750–1000	*0*	*0*	0	*0*	*0*	0	0	0		0	0	0	0		*0*
1000–1500	*0*	*0*	No net	*0*	*0*	No net	0	0		0	0	▨	0		0



Text-fig. 25. Occurrence of *Rhynchonerella bongraini* round the South Sandwich Islands and in the Weddell Sea (see also Text-figs. 23, 24 and 26, Tables 14, 15).

Samples from N 70 V nets, other than those along the 0° Line and around South Georgia and the South Sandwich Islands, were not extensively examined. Only four miscellaneous records of *R. bongraini* are reported here. These are from St. 12, N 70 V, 500–250 m. (1); St. 2296, N 70 B, 240–110 m. (3); St. 2300, N 100 B, 350–200 m. (1); St. 2322, N 100 H, 5–0 m. (1), and have been plotted in Text-fig. 25. They confirm the suggestions made above. At St. 2322 the species was collected in the Weddell Drift and the other records are from the upper layers of the Warm Deep Water. The surface position of St. 12 was outside the influence of Weddell Drift and the net which collected *R. bongraini* there fished in the Warm Deep Water.



Text-fig. 26. Occurrence of *Rhynchonerella bongraini* round South Georgia, December–January 1926–7, February–March 1928, and January–February 1930, N 70 V nets. Number of specimens at each station in brackets.

Previous records. The only published records of *R. bongraini* from about the Greenwich Meridian are those made between 1927 and 1931 by the Norwegian Antarctic Expedition (Støp-Bowitz, 1949), which collected the species at twelve stations, all south of the northern limit of Weddell Drift, from hauls made between 400 m. and the surface.

In 1930 Monro reported *R. bongraini* from around the South Sandwich Islands at Sts. SS 33 and SS 53, as *R. fulgens*, and in 1936 from St. WS 555 as *Callizonella bongraini*. Stop-Bowitz (1949) reported this species (as *Krohnia bongraini*) from 57° 48′ S., 26° 25′ W., in a net hauled between 400 and 300 m.

Apart from Hardy and Gunther's (1935) records of *Rhynchonerella bongraini* as 'Alciopid larvae' discussed on page 192, this species has previously been reported from South Georgia only by the Swedish Antarctic Expedition, 1901–3 (Stop-Bowitz, 1951). No details of depth are given for this record.

Augener (1929) reported *R. bongraini* (as *Callizonella bongraini*) from fifteen stations made in the Weddell Sea, between 450 m. and the surface, by the Deutsche Südpolar Expedition, 1911–12. On the Norwegian Antarctic Expedition of 1927–31 it was collected at 59° 59′ S., 45° 18′ W. between 100–200 m., and at 58° 09′ S., 37° 38′ W. between 300 and 200 m. (Stop-Bowitz, 1949), apart from the records already noted. The Swedish Antarctic Expedition, 1901–3, also collected this species at four other stations in the Antarctic zone, with nets fishing between 700 m. and the surface (Støp-Bowitz, 1951). These records support my suggestions on the distribution of *R. bongraini* as far as the information given with them allows.

Vanadis antarctica and *Vanadis longissima*

(Text-fig. 27, Appendix II)

V. antarctica, collected only to the south of the Antarctic Convergence, and *V. longissima*, collected only to the north of this boundary, are considered here together, because they may represent geographical races of one species. Both species are large and were collected only by the N 100 and TYF nets.

Of the *V. antarctica* hauls, all but two were made in the Antarctic Surface Water and only the specimen, from St. 1936, was collected north of the influence of Weddell Drift. *V. longissima* also occurred mainly in the top layers of water, but at St. 2636 one specimen was probably taken in the Antarctic Intermediate Current.

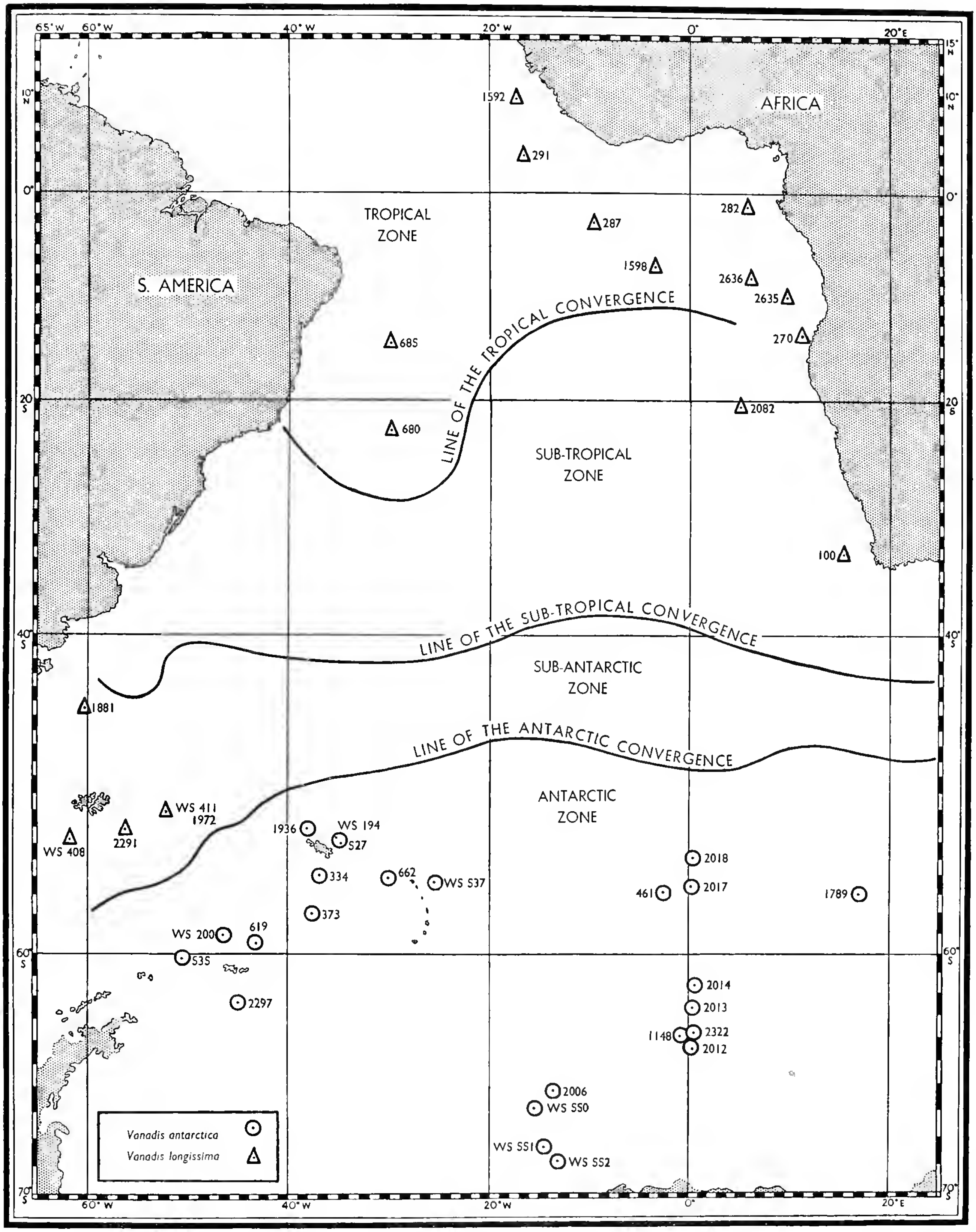
The very close morphological similarity between *V. antarctica* and *V. longissima* and the possibility that they are separated in distribution at the surface by the Antarctic Convergence makes it tenable that they are cold and warm water forms of one species, the cold form inhabiting the Antarctic Zone and the warm the Sub-Antarctic, Sub-Tropical and Tropical Zones. Moreover it is possible that they are not isolated from one another in the deeper Antarctic Intermediate Layer or in the Warm Deep Water, but mix freely in the region of the Antarctic Convergence and are carried to their respective surface habitats by the movements of the water masses. Both species could be carried south in the Warm Deep Water, *V. antarctica* could circulate northwards in the Antarctic Surface Water and *V. longissima* northwards in the Antarctic Intermediate Water (Text-fig. 14, p. 207). Clearly, however, not only are more records required from depth in the Antarctic and Sub-Antarctic Zones to indicate the relative densities of the circumpolar populations of both, but the reproductive habits of the species must be investigated before the many problems of the *V. longissima*-*V. antarctica* complex can be satisfactorily solved.

Previous records. Within the Atlantic sector of the Antarctic the only records of *V. antarctica* north of the Antarctic Convergence are from Monro (1936), from Sts. WS 408 and WS 411. I have re-examined these specimens and consider them to be *V. longissima*. The Swedish Antarctic Expedition collected one specimen of *V. antarctica* at 69° 51′ S., 49° 37′ W., from a net hauled to the surface from 200 m. (Stop-Bowitz, 1951). Baker (1954) reported numerous specimens of *V. antarctica* from the 100–0 m. 'Discovery' samples within the Atlantic sector of the Antarctic and also demonstrated the circumpolar continuity of the species between these depths. *V. longissima* was reported by Apstein (1900) from the South Atlantic at three stations between 3° S., 13° W., and 2° S., 26° W., and by Monro (1930) from Sts. 287 and 291.

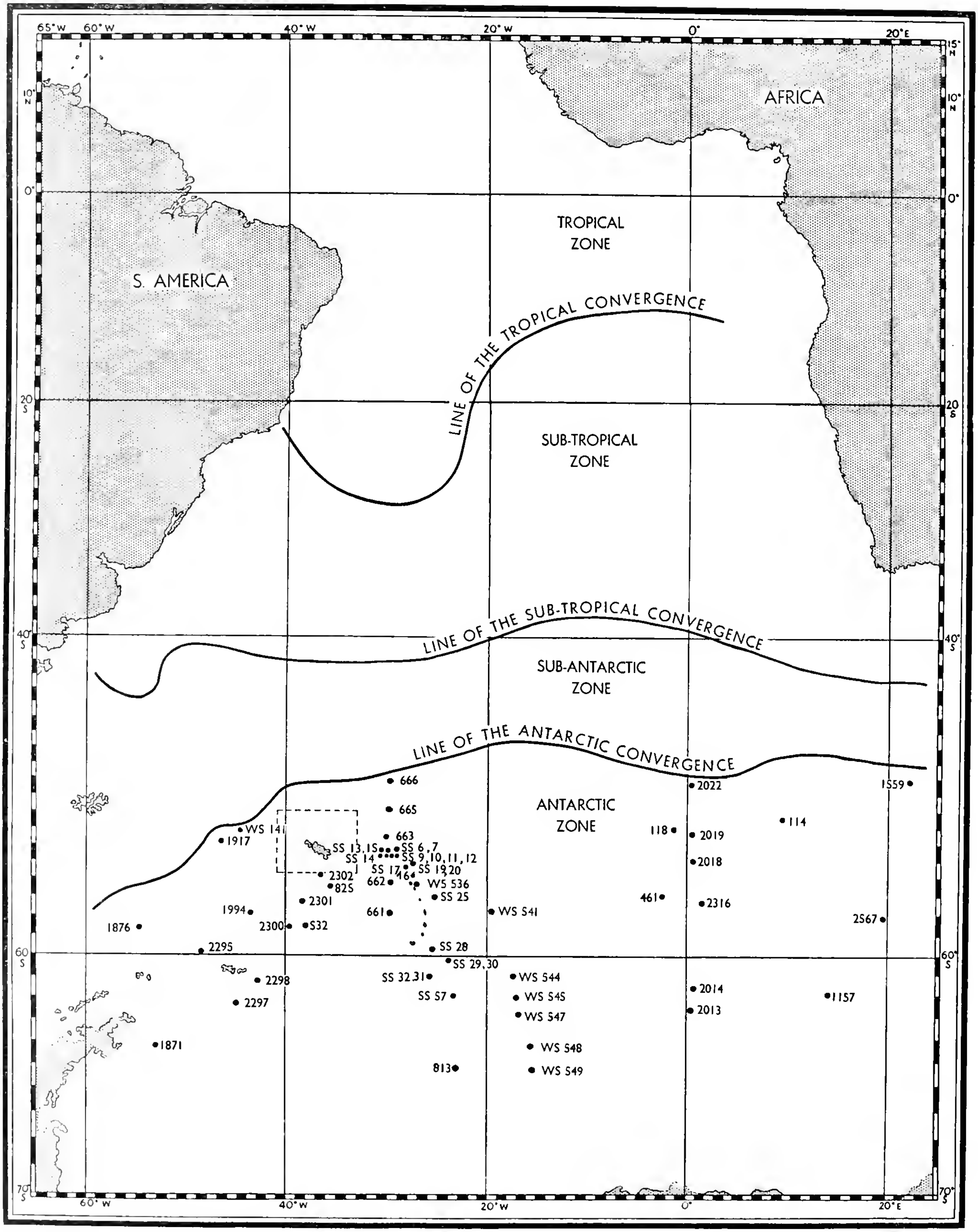
Tomopteris carpenteri

(Text-figs. 28–30, Appendices I and II)

The endemic antarctic *T. carpenteri* was collected in all water masses at all explored depths within the Antarctic Zone. This species measures up to 70 mm. in length and occurred mainly in the larger nets. However, in N 70 V samples from the South Georgia Surveys, there were numerous small specimens of *T. carpenteri* less than 12 mm. in length. These include the smallest specimens of the species ever collected, and I refer to them here as *juveniles*. All other specimens, none of which measures less than 15 mm., I have defined as *adult*. This purely arbitrary definition serves to separate the material into two groups. Recognition of maturity in the Tomopteridae depends on the presence of sexual products in the parapodial pinnules, and unfortunately in many of the largest preserved specimens of *T. carpenteri* these are not visible.



Text-fig. 27. Occurrence of *Vanadis antarctica* and *V. longissima*.



Text-fig. 28. Occurrence of *Tomopteris carpenteri*. All specimens adult except at St. WS 141 (see also Text-figs. 29, 30.)

The records of adult *T. carpenteri* [Text-figs. 28 (except St. WS 141) and 29] confirm the known distribution of the species; it has never been reported north of the Antarctic Convergence,[1] and is widely distributed in the Antarctic Surface Water and occurs also in the Warm Deep Water.

Juvenile specimens of *T. carpenteri* were collected only around South Georgia [Text-fig. 28 at St. WS 141 and Text-fig. 30, Appendix I (Tables *a* and *b*)] in January, February and March, at all depths from 750 m. to the surface. Although the N 70 nets were hauled extensively on the Greenwich Meridian and in the South Sandwich Surveys, juvenile *T. carpenteri* were never collected in either area. There can be little doubt that if juvenile *T. carpenteri* had occurred about the Greenwich Meridian, they would have been picked up by the N 70 V nets, because specimens of *T. planktonis* and *T. septentrionalis* within the same size range were collected there and also round South Georgia. However, the numerous records of '*Tomopteris* unidentifiable' listed in Appendix I from South Georgia and the 0° Line must be considered. I do not regard any of these as young *T. carpenteri*, but they are listed as unidentifiable because I cannot decide if they are *T. septentrionalis* or *T. planktonis*.[2] The principal diagnostic characters of these last two species (the diffuse chromophil and hyaline glands), have been destroyed in all the specimens not identified. In juvenile *T. carpenteri* however, the hyaline gland is dorsal on the parapodial pinnule and has escaped destruction affecting the apical region. I suggest that *T. carpenteri* may breed around South Georgia but not in the open ocean.

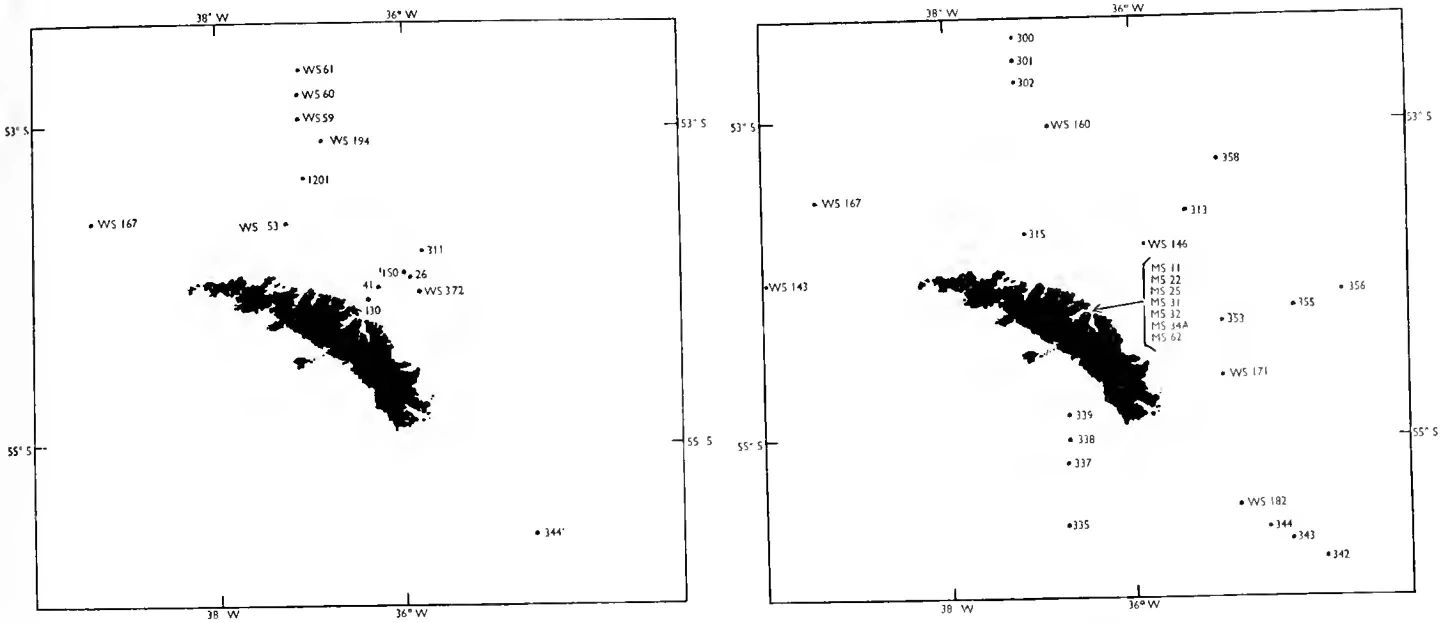


Fig. 29

Fig. 30

Text-figs. 29 and 30. Occurrence of *Tomopteris carpenteri* round South Georgia. Fig. 29. Adults. Fig. 30. Juveniles.

Previous records. Juvenile specimens of *T. carpenteri* have previously been collected only by the 'Norwegica' but not from the Atlantic Ocean, Stop-Bowitz (1949) reporting three specimens from the Pacific at 67° 30′ S., 91° 33′ W., 50–0 m., and 66° 48′ S., 79° 56′ W., 100–50 m. Monro (1930) recorded eleven juvenile specimens from seven Marine Station shallow hauls made in Cumberland Bay, South Georgia, as either *T. carpenteri* or *T. planktonis*. I have examined them and find them all to be *carpenteri*. Considering the large collections which have been made in the Antarctic Zone of

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[1] Except by McIntosh (1925); as noted on p. 175 this record is probably *T. nisseni*.

[2] Theoretically it is possible that there are also several other species of the same size range including *T. cavalli* (see pp. 173–174).

the Southern Oceans this distribution is very sparse and it will be of interest to note how future collecting will contribute to our knowledge of the distribution of juvenile *T. carpenteri*.

The original record of *T. carpenteri* (adult) was made by Quatrefages (1865) from 60° 3′ S., 0° 6′ E. Since then the adult has frequently been reported from the Atlantic sector of the Antarctic. In earlier Discovery reports Monro (1930, 1936) recorded it from South Georgia, the South Sandwich Islands and numerous localities scattered throughout the area, and Hardy and Gunther (1935) also reported it from South Georgia. The 'Norwegica' collected the species near Bouvet Island and the South Sandwich Islands (Stop-Bowitz, 1949) and the Swedish Antarctic Expedition collected it near the South Orkneys (Stop-Bowitz, 1951).

Tomopteris planktonis and *Tomopteris septentrionalis*

(Text-figs. 31–3, Appendices I and II)

T. planktonis and *T. septentrionalis* are the only known cosmopolitan tomopterids and have been found in all explored water masses in the South Atlantic Ocean. *T. planktonis* (size range 2–10 mm.) was collected principally by the N 70 net but occurred also in all other nets except the N 450. *T. septentrionalis* measures up to 15 mm. in length and was caught frequently by all the nets.

T. septentrionalis was caught more often by the larger nets than *T. planktonis*, therefore some points about their distribution must be emphasized or they may be misinterpreted. In addition the larger number of '*Tomopteris unidentifiable*' listed in Appendix I, which, as noted on p. 227 are probably either *T. planktonis* or *T. septentrionalis*, must also be considered.

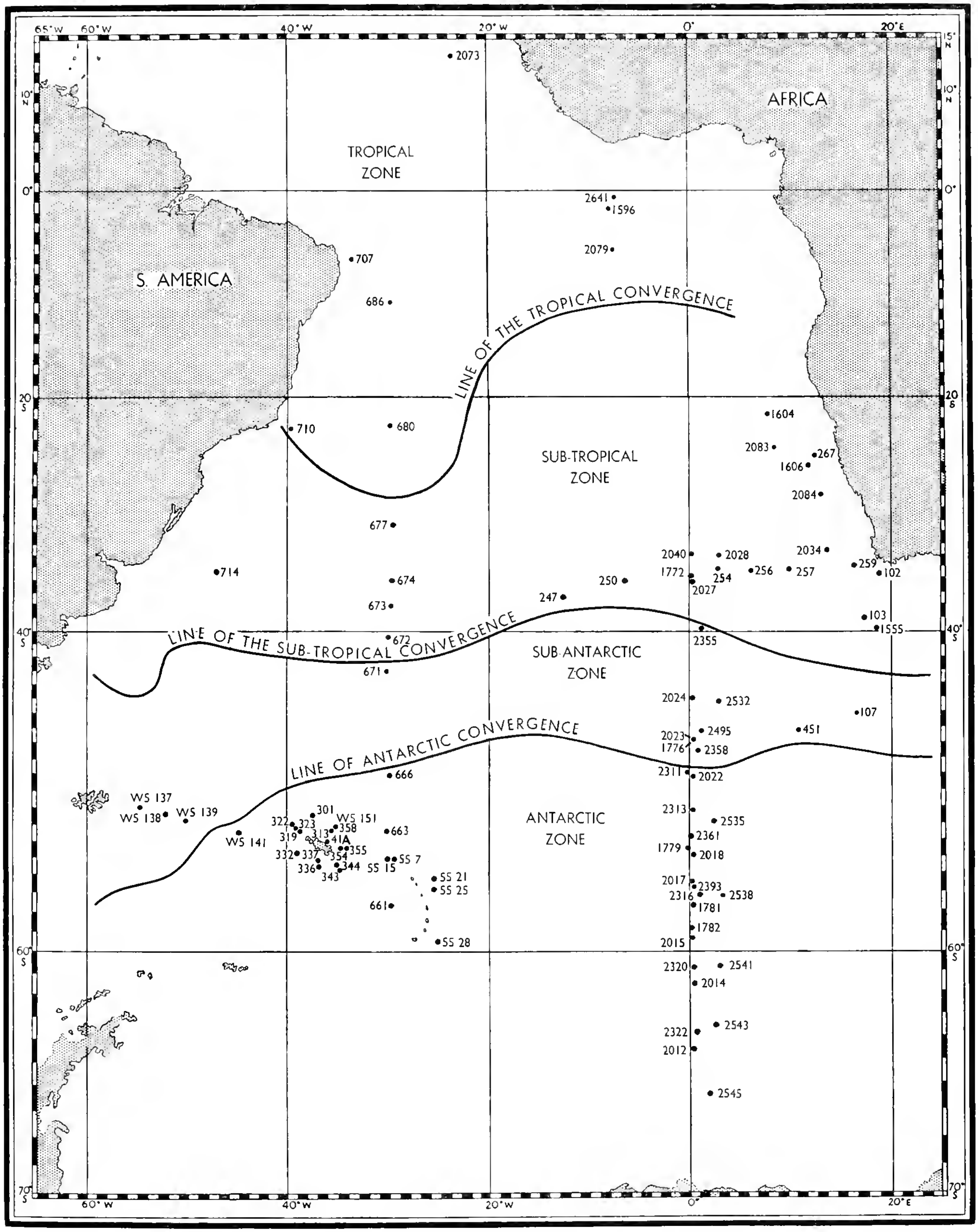
(*a*) Around South Georgia both species were frequently taken in the Warm Deep Water, but a few exceptions (five of *T. planktonis* and one of *T. septentrionalis*), together with the fourteen '*Tomopteris unidentifiable*', were collected outside this water mass. Additional samples around South Georgia may show either that both species inhabit Antarctic Surface Water and Warm Deep Water, or that one of them inhabits the Warm Deep layer only.

(*b*) In the vicinity of the Greenwich Meridian, *T. septentrionalis* was caught more often by the N 100 B nets than *T. planktonis* which, however, appears to be equally well distributed there, because it was caught more often by the N 70 V nets, which explored a greater depth range.

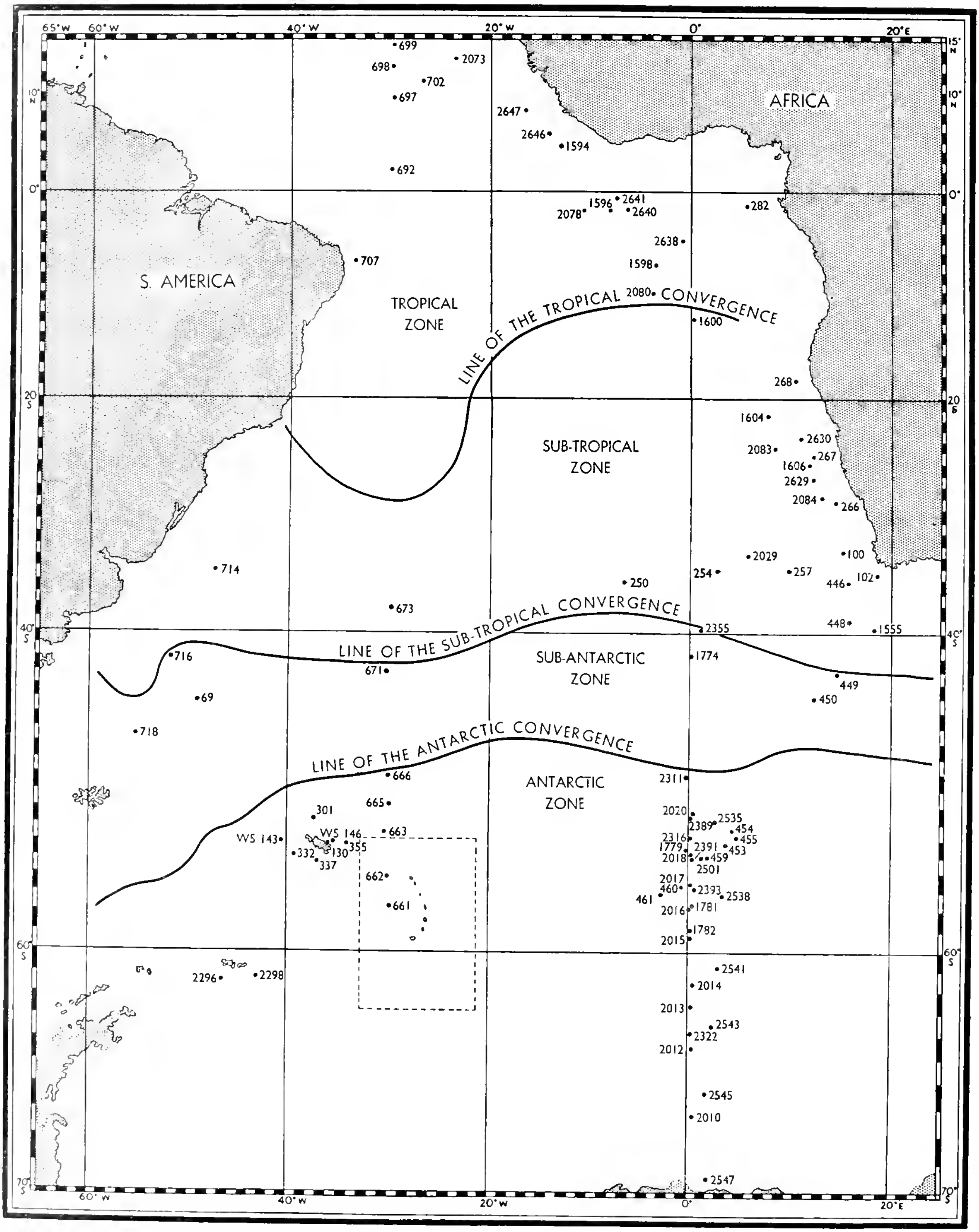
(*c*) In the South Sandwich survey *T. septentrionalis* was collected fifty-five times, of which forty-five were by the towed nets (Text-fig. 33), but *T. planktonis* was caught only on five occasions, of which three were with towed nets (Text-fig. 31). *T. septentrionalis* is not necessarily more abundant than *T. planktonis* in this region, but the type of net may not have been so favourable for catching the latter species.

Previous records. *T. planktonis* has been widely reported from the South Atlantic Ocean. In the Antarctic Zone it was reported by Augener (1929) from the Weddell Sea, by Monro (1930, as *T. carpenteri*) from St. SS 21, and by Stop-Bowitz (1949, 1951) from Bouvet Island, the South Sandwich Islands and South Georgia. The records of *T. planktonis* in the present work appear to be the first from the Sub-Antarctic Zone. In the Sub-Tropical and Tropical Zones, Apstein (1900) reported it west and north of Ascension Island, and Monro (1936) from 'Discovery' stations between the Cape Verde Islands and the Falkland Islands.

T. septentrionalis was reported by Augener (1929) from the Weddell Sea, by Monro (1930) from South Georgia and the South Sandwich Islands, by Hardy and Gunther (1935) from South Georgia, by Monro (1936) from 'Discovery' stations scattered throughout the Antarctic Zone and by Stop-Bowitz (1949, 1951) at numerous localities between 10° E. and South Georgia. There appear to be



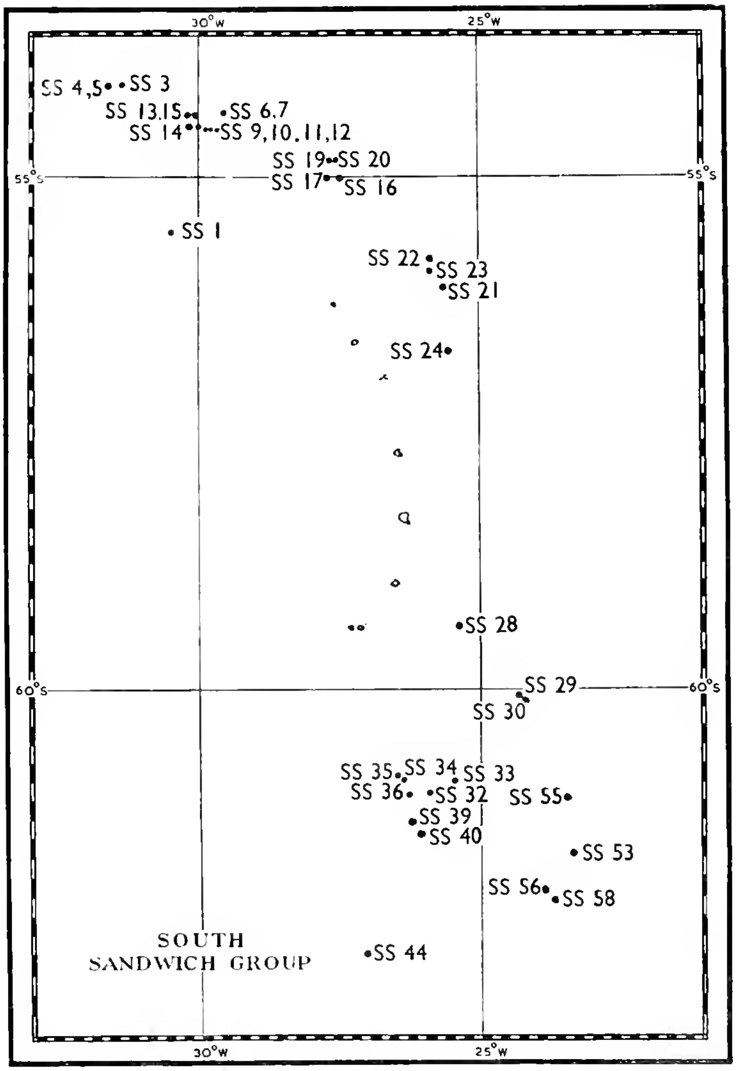
Text-fig. 31. Occurrence of *Tomopteris planktonis*.



Text-fig. 32. Occurrence of *Tomopteris septentrionalis* (see also Text-fig. 33).

no previous records of *T. septentrionalis* from the Sub-Antarctic, other than those reported by Monro (1936) from 'Discovery' Sts. 450 and 449, and he also recorded it in abundance from the Sub-Tropical and Tropical Zones. Stop-Bowitz (1951) reported it off the coast of Brazil.

Both *T. planktonis* and *T. septentrionalis* were probably present in the 'Meteor' collections from the South Atlantic, reported by Friedrich (1950*c*) as Tomopteridae.



Text-fig. 33. Occurrence of *Tomopteris septentrionalis* round the South Sandwich Islands.

Typhloscolex mülleri

(Text-figs. 34, 35, 36; Tables 16 and 17, Appendices I and II)

The cosmopolitan *T. mülleri* was collected in all explored water masses of the South Atlantic except in the Antarctic Zone where it appears mainly in the Warm Deep Water; it occurs in Antarctic Surface Water only south of the northern limit of Weddell Drift. This species is small, rarely measuring more than 7 mm. in length and was caught mainly by the N 70 nets.

In the South Georgia Surveys, *T. mülleri* was caught by eleven nets in February–March 1928, nine times between 1000 and 250 m. and once in each of the 250–100 and 100–50 m. nets[1] (Text-fig. 34). In January–February 1930, no catches were made above 100 m., but six were made by nets

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[1] Disregarding the catches made at St. WS 190 where the nets from 1000 and 750 m. did not close.

Table 16. Typhloscolex mülleri. *Distribution in the region of the Greenwich Meridian, between 64° S. and 35° S. (N 70 V nets only.) Italic light type indicates hauls made between sunrise and sunset. A.C. = Antarctic Convergence, S.T.C. = Sub-Tropical Convergence.*

Degrees South 70° 65° 60° 55° 50° 45° 40° 35°

April 1938

Between 00° 03′ W. and 01° 13·4′ E.

A.C. (after Stn. 2311)

Depth (m.)	Stns. 2322	2320	2318	2316	2313	2311
0–50	0	5	15	0	0	0
50–100	0	0	0	0	0	0
100–250	2	0	0	0	0	2
250–500	1	6	5	9	2	0
500–750	6	1	0	0	0	0
750–1000	0	1	0	0	0	0
1000–1500	0	1	0	0	0	1

May, June 1936

Between 00° 20·8′ W. and 00° 37′ E.

A.C. (between Stns. 1777 and 1776); S.T.C. (between Stns. 1774 and 1773)

Depth (m.)	Sts. 1782	1781	1779	1778	1777	1776	1775	1774	1773	1772
0–50	0	0	0	0	0	0	0	0	0	0
50–100	*0*	0	0	0	0	*0*	0	0	0	0
100–250	*2*	7	0	0	0	*0*	0	3	0	2
250–500	*14*	6	1	Sample lost	1	*0*	4	4	1	1
500–750	*0*	0	0	1	3	*1*	4	3	7	1
750–1000	*0*	0	0	5	0	*1*	2		2	0
1000–1500	*1*	0		0	0	*0*	0		2	0

Degrees South 60° 55° 50° 45° 40°

July, August, September 1938

Between 00° 04·5′ E. and 01° 21·2′ E.

A.C. (between Stns. 2359 and 2387); S.T.C. (after Stn. 2385)

Depth (m.)	Sts. 2393	2391	2361	2389	2359	2387	2358	2357	2386	2425	2356	2355	2424	2385
0–50	0	0	0	0	0	*0*	0	0	*0*	*0*	0	0	*0*	0
50–100	0	0	0	0	0	*0*	0	0	*0*	*0*	0	0	*0*	0
100–250	0	0	0	0	0	*0*	0	0	*0*	*0*	0	0	*0*	2
250–500	0	2	2	2	0	*0*	4	3	*0*	*3*	1	3	*4*	0
500–750	6	0	1	1	0	*1*	3	4	*0*	*2*	4	4	*4*	0
750–1000	1	0	2	1	0	*1*	3	1	*1*	*1*	1	1	*1*	0
1000–1500	1	0	3	1	1	0	1	0	0	0	2	1	*1*	1

Table 17. Typhloscolex mülleri. *Distribution in the region of the Greenwich Meridian, between 70° S. and 35° S. (N 70 V nets only.) Italic light type indicates hauls made between sunrise and sunset. A.C. = Antarctic Convergence, S.T.C. = Sub-Tropical Convergence.*

Degrees South 70° 65° 60° 55° 50° 45° 40° 35°

November, December 1938

Between 00° 37·6' E and 01° 23·7' E.

Depth (m.)	Sts. 2501	2498	2496	A.C. ↓	2495	2494	2492
0–50	*0*	0	0		*0*	*0*	*0*
50–100	*10*	0	0		*0*	*0*	*0*
100–250	*2*	0	0		*0*	0	*0*
250–500	*1*	4	5		*1*	*0*	*4*
500–750	*0*	0	0		*0*	*0*	*3*
750–1000	*0*	0	0		*0*	*3*	*0*
1000–1500	No net	0	Sample lost		*1*	*0*	*0*

January 1939

Between 02° 04·7' E. and 03° 33·7' E.

Depth (m.)	Sts. 2547	2545	2543	2541	2538	2535	A.C. ↓	2533	2532	2531	S.T.C. ↓	2530
0–50	*0*	*0*	*0*	*5*	*0*	*0*		*0*	0	0		0
50–100	*0*	*5*	*5*	0	*0*	*0*		*0*	5	0		0
100–250	*0*	*5*	*2*	*2*	*2*	*3*		*0*	2	2		0
250–500	*9*	*5*	*1*	*7*	*8*	*3*		*2*	3	4		5
500–750	*2*	*6*	*3*	*4*	*3*	*1*		*1*	4	3		1
750–1000	*0*	*0*	*1*	*0*	*1*	*0*		*0*	0	0		2
1000–1500	*0*	0	*0*	0	No net	0		*0*	No net	0		0

March, April 1937

Between 00° 6·7' E and 00° 39·7' E.

Depth (m.)	Sts. 2010	2012	2014	2015	2017	2018	2020	2022	A.C. ↓	2023	2024	2025	2026	S.T.C. ↓	2027
0–50	5	5	0	*0*	*0*	0	0	0		0	0	0	0		0
50–100	*0*	0	0	*0*	*0*	0	0	0		0	0	0	0		*0*
100–250	*3*	0	3	*2*	*7*	2	0	0		0	0	0	0		*0*
250–500	*1*	3	6	*8*	*1*	0	3	1		0	2	5	1		*0*
500–750	*0*	0	2	*1*	*1*	1	1	0		1	2	6	0		*0*
750–1000	*0*	*0*	1	0	*0*	0	0	0		0	3	0	0		*0*
1000–1500	*0*	*0*	No net	*0*	0	No net	0	0		0	0	▨	0		0

hauled between 250–100 m. and twenty-two from nets hauled between 1000 and 250 m. (Text-fig. 35). Hardy and Gunther (1935) reported it altogether nineteen times from the December–January Survey, 1926–7, in sixteen nets hauled between 1000 and 250 m. and the remainder from nets closing at 100 m.

The combined results of these three surveys show that the species was collected once in Antarctic Surface Water, in the 100–50 m. nets, nine times in the nets hauled between 250 and 100 m. which fished in Antarctic Surface Water and Warm Deep Water, and thirty-one times by the nets which were hauled in the Warm Deep Water between 1000 and 250 m. These suggest that around South Georgia, *T. mülleri* is essentially a Warm Deep Water species.

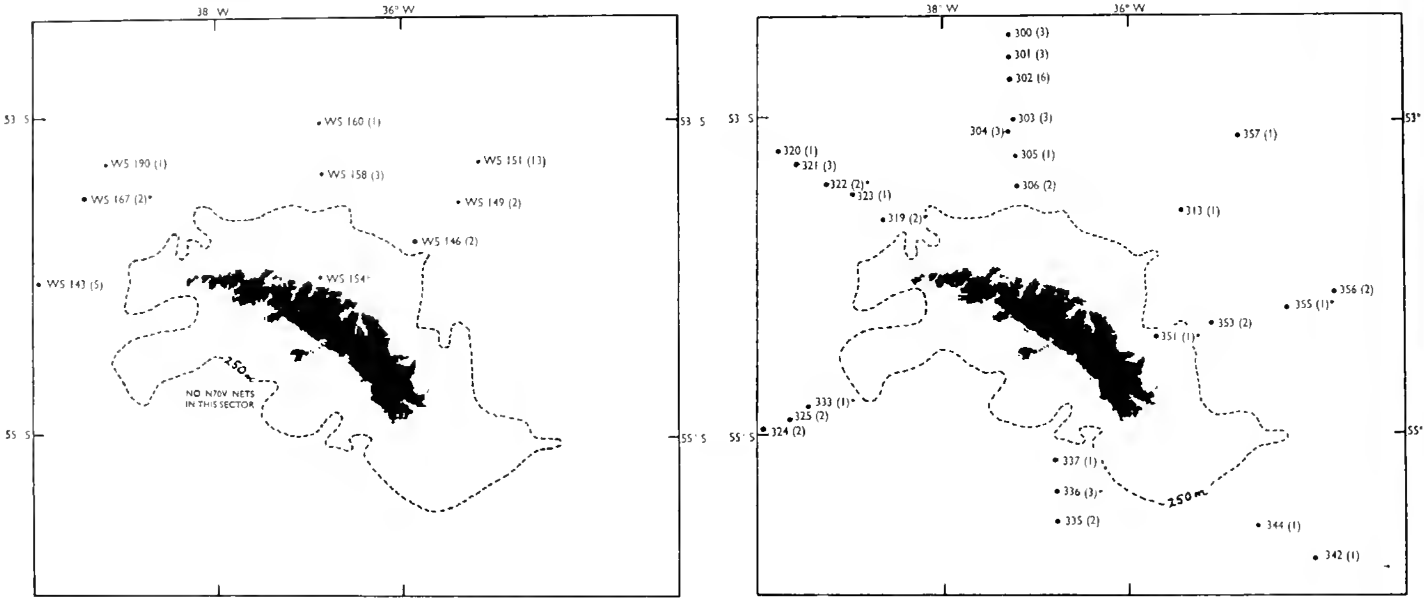
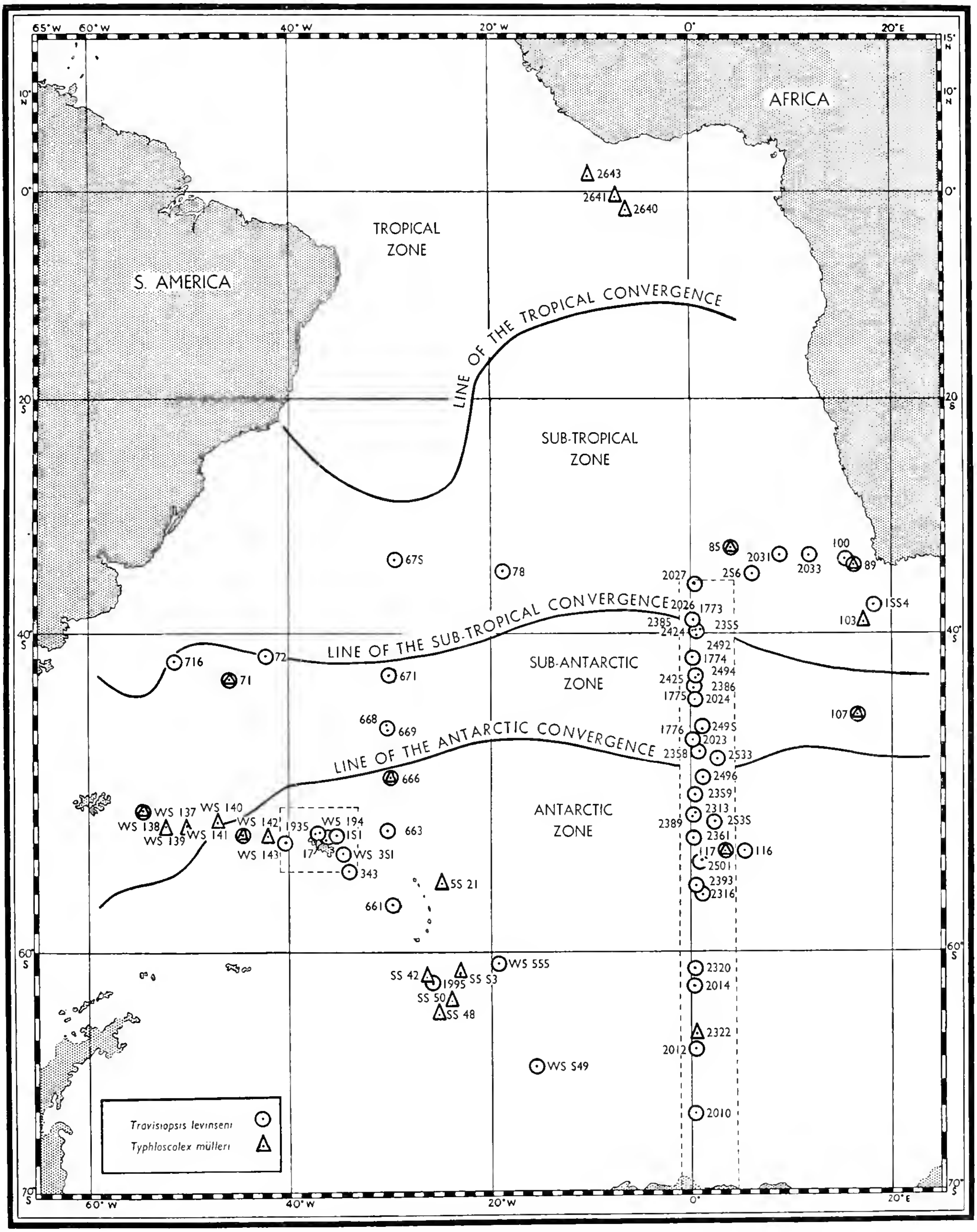


Fig. 34 Fig. 35

Text-figs. 34 and 35. Occurrence of *Typhloscolex mülleri* round South Georgia. N 70 V nets, 1000–250 m. Number of specimens at each station in brackets. * = one at 100–50 m. † = two at 100–250 m. Fig. 34. February–March 1928. Fig. 35. January–February 1930.

The occurrence of *T. mülleri* in the region of the Greenwich Meridian is shown both in Text-figs. 4*a* and *b* (p. 167) and in Tables 17 and 18. It occurred at all stations made in this area, except St. 2027.

T. mülleri was never caught in very large numbers about the Greenwich Meridian, but nevertheless it was collected with marked regularity at certain depths, particularly between 1000 and 250 m. In January 1939, it occurred in all nets fished between 750 and 250 m. and in general at stations in the Antarctic Zone it was taken fairly regularly in the Warm Deep Water. In contrast to the South Georgia area where it was largely confined to the Warm Deep Water, on the Greenwich Meridian it occasionally occurred in the summer months in some number in the surface layer. Nine catches of *T. mülleri* were made in Antarctic Surface Water, south of the northern limit of Weddell Drift, indicating that possibly the species migrates upwards into Weddell Sea Water at this season. In winter, on the contrary, the collections along the Greenwich Meridian indicate that *T. mülleri* leaves the top 250 m. of water and is more concentrated between 500 and 1500 m. than in the summer. Between November and April, for example, thirteen successful hauls out of twenty-three were made between 250–100 m. and seven successful hauls out of forty-one hauled between 1500–750 m. In the May–September collections, however, the situation is reversed with one successful haul out of nine between 250–100 m., but with eight out of seventeen collections in between 1500 and 750 m.



Text-fig. 36. Occurrence of *Typhloscolex mülleri* and *Travisiopsis levinseni* (see also Text-figs. 34, 35; and Tables 16, 17).

In the Sub-Antarctic Zone, *T. mülleri* is concentrated along the Greenwich Meridian between 100 and 750 m. in summer, but is found in the deeper layers, between 250 and 1500 m. in winter, within Sub-Antarctic Surface Water, Antarctic Intermediate Water and Warm Deep Water.

T. mülleri was collected at five stations in the South Sandwich Survey (Text-fig. 36, Appendix II, Table *b*); at three of these stations the nets fished in the Warm Deep Water and at the other two in Weddell Sea Water.

Miscellaneous records of *Typhloscolex mülleri* (Text-fig. 36), include no catches from Antarctic Surface Water, north of the northern limit of Weddell Drift, but elsewhere there are records from all explored water masses. The absence of *T. mülleri* to the west of, and between Sts. 85 and 2640 is probably of no significance, because few fine mesh nets were hauled there.

Previous records. Apart from Hardy and Gunther's records (1935) of *T. mülleri* noted above, the species has not previously been reported from the South Georgia area.

Stop-Bowitz (1949) reported *T. mülleri* from the Antarctic Zone at five stations made by the 'Norwegica', in the summers of 1927–8 and 1928–9 about the Greenwich Meridian. These records are from stations south of 56° 53′ S. and from between 50–19, 100–49, 100–50, 200–98, 400–201 and 400–202 m., of which those hauled above 100 m. are presumably from the Weddell Drift and the others from the Warm Deep Layer. Although small in number these catches provide additional evidence for the suggestion that *T. mülleri* invades the Antarctic Surface Water south of the northern limit of Weddell Drift only.

Monro (1930) reported *T. mülleri* from St. SS 53 but no other references in literature from the South Sandwich area have been noted.

Other records of *T. mülleri* from the Antarctic Zone have been reported by Augener (1929) from the Weddell Sea (0° 23′ S., 200–0 m., and 72° 20′ S., 600–0 m.). From the 'Meteor' expedition Friedrich (1950*c*) reported *Typhloscolex* (probably including *mülleri*) in the Sub-Antarctic and Antarctic Zones as far south as latitude 65° S.

T. mülleri has been frequently reported from the Sub-Tropical and Tropical Zones. Reibisch (1895) recorded it in large numbers from 200 m. to the surface, north of 10° S. between Ascension Island and the mouth of the Amazon, and to the Cape Verde Islands. Ehlers (1913) reported it from 12° 11′ S., 6° 16′ W., 2000 m., 10° 45′ S., 6° 32′ W., 400 m., 8° 43′ S., 11° 55′ W., 3000 m. and 0° 52′ S., 16° W., 400 m. Friedrich (1950*c*, fig. 4) may have referred to it in the many *Typhloscolex* records he noted between 40° S. and the Equator. Stop-Bowitz (1951) reported it from Tropical Surface Water.

Travisiopsis levinseni

(Text-fig. 36, Appendices I and II)

T. levinseni is a cosmopolitan species normally measuring between 13 and 18 mm. in length; it was caught by all nets used by the Discovery Investigations except the N 50. Although widely distributed in all explored water masses of the South Atlantic, *T. levinseni* was never caught in abundance. In the majority of cases, only a single specimen was taken (the largest catch consisting of three specimens), but there is a possibility that it was accidentally missed by the nets. *T. levinseni* was collected around South Georgia in the Warm Deep Water only; in the South Sandwich Survey, where the majority of nets fished in the Antarctic Surface Water, it was never collected; along the 0° Line it was caught by nineteen nets hauled in the Warm Deep Water and by only three nets in the surface water; elsewhere in the Antarctic Zone it was collected six times in the Warm Deep Water and twice by nets which may have traversed this layer into Antarctic Surface Water. These results suggest that in the Antarctic Zone, *T. levinseni* is probably a Warm Deep Water species.

Previous records. *T. levinseni* was collected by 'Discovery' Investigations in the Antarctic and Sub-Tropical Zones (Monro, 1930, as *Sagitella kowalewskii* and *Travisiopsis* sp., and Monro, 1936 as *T. benhami*), and Stop-Bowitz (1949, 1951) reported it from six localities in the Antarctic Zone. The 'Meteor' Expedition collected it in the South Atlantic but no details are available (Friedrich, 1950*c*).

Pelagobia longicirrata

(Text-figs. 37–44, Tables 18 and 19, Appendices I and II)

The cosmopolitan *P. longicirrata* was collected in all explored water masses of the South Atlantic except in the top 100 m. of Sub-Antarctic Surface Water between 45° S. and the Sub-Tropical Convergence in the region of the Greenwich Meridian. This species rarely measures more than 12 mm. in length and was collected mainly by the N 50 and N 70 nets.

In the surveys made about the Greenwich Meridian, *P. longicirrata* was found at all the stations except two, Sts. 1774 and 1777 (Text-figs. 4*a* and *b*); its distribution is shown in Tables 18 and 19, and shows a concentration in the surface layers in summer and migration to depth in winter. It was absent during July and August 1938 from hauls between 100 m. and the surface, and specimens were only collected in this layer in June 1936 at St. 1782. From November to April, however, large numbers of *P. longicirrata* occurred at almost every station between 100 m. and the surface. Below 100 m. the species was present at all depths throughout the year. This seasonal migration to depth is similar to that which Mackintosh (1937) found in 80° W. for the copepods *Rhincalanus gigas* and *Calanus acutus* and the chaetognath *Eukrohnia hamata.*

In the Sub-Antarctic Zone between the Antarctic Convergence and 45° S., *P. longicirrata* appeared abundantly during the summer in the 100–0 m. nets, but north of 45° S. it was absent. Between 45° S. and the Sub-Tropical Convergence, ten nets were hauled in the November–April surveys through 100–50 and 50–0 m. (two each at Sts. 2494, 2592, 2531, 2025 and 2026) and no specimens were taken. Immediately south of Sts. 2494, 2531 and 2025, however, large numbers were collected (forty at Sts. 2495, 470 at St. 2532 and fifteen at St. 2024). The salinity records at these stations show that there is a difference of 0·52 ‰ in the mean salinity of the top 100 m. of water between Sts. 2495 and 2494; that between Sts. 2531 and 2532 a difference of 0·42 ‰ exists and between Sts. 2025 and 2024, 0·39 ‰. Each of these differences represents a greater change in salinity than that found in crossing the Antarctic Convergence on the respective lines, the differences between Sts. 2496–2495 and 2535–2533 being 0·02 ‰ and between Sts. 2022–2023, 0·04 ‰. Two of these changes in salinity are indicated in Text-figs. 18 and 19 (pp. 211, 214) in which the isohalines in the region of the Antarctic Convergence are almost horizontal, whereas at about 45° S. they rise almost vertically to the surface. It is possible therefore, that, although the Antarctic Convergence does not restrict the surface distribution of *P. longicirrata*, a minor convergence may affect it in the Sub-Antarctic Zone, in latitude 45° S., and although cosmopolitan it may have a partially segregated summer population gathering in the surface waters south of 45° S. for feeding and breeding purposes.

The few records of *P. longicirrata* from the surface 50 m. of water around South Georgia (Text-fig. 37) is in direct contrast to its abundance in this layer during the summer months on the Greenwich Meridian. The species was not taken by any of the twenty-five nets hauled between 50–0 m. in February–March 1928, and only eleven specimens were caught at three stations (309 (8), 338 (2), and 334 (1)) in January–February 1930, although fifty-seven nets were hauled through the same depth.

Hardy and Gunther (1935, p. 116) tabulated 459 specimens of *P. longicirrata* as being taken in eighty nets from 50–0 m. At first sight this appears to indicate a widespread distribution of the species in the surface layer; but reference to the basic data, given in Appendix II of their report,

Table 18. Pelagobia longicirrata. *Distribution in the region of the Greenwich Meridian, between 64° S. and 35° S. (N 70 V nets only.) Italic light type indicates hauls made between sunrise and sunset. A.C. = Antarctic Convergence, S.T.C. = Sub-Tropical Convergence.*

Degrees South 70° 65° 60° 55° 50° 45° 40° 35°

April 1938. Between 00° 03′ W. and 01° 13·4′ E.

Depth (m.)	Sts. 2322	2320	2318	2316	2313	2311	A.C.
0–50	10	20	225	25	0	0	
50–100	40	40	25	15	0	0	
100–250	17	20	27	13	2	2	
250–500	14	3	8	7	0	0	
500–750	14	1	2	3	0	1	
750–1000	3	1	0	4	0	3	
1000–1500	1	1	1	1	2	1	

May, June 1936. Between 00° 20·8′ W and 00° 37′ E.

Depth (m.)	Sts. 1782	1781	1779	1778	1777	A.C.	1776	1775	1774	S.T.C.	1773	1772
0–50	5	0	0	0	0		0	0	0		0	0
50–100	*85*	0	0	0	0		*0*	0	0		0	0
100–250	*13*	17	3	0	0		*0*	0	0		0	0
250–500	*14*	9	2	Sample lost	0		*0*	0	0		0	1
500–750	*5*	2	5	1	0		*0*	0	0		0	0
750–1000	*0*	0	6	5	0		*1*	2			1	1
1000–1500	*3*	2		2	0		*1*	0			0	0

Degrees South 60° 55° 50° 45° 40°

July, August, September 1938. Between 00° 04·5′ E. and 01° 21·2′ E.

Depth (m.)	Sts. 2393	2391	2361	2389	2359	A.C.	2387	2358	2357	2386	2425	2356	2355	2424	2385	S.T.C.
0–50	0	0	0	0	0		*0*	0	0	*0*	*0*	0	0	*0*	0	
50–100	0	0	0	0	0		*0*	0	0	*0*	*0*	0	0	*0*	0	
100–250	2	0	2	0	0		*0*	0	0	*0*	*0*	0	0	*0*	0	
250–500	8	2	18	0	0		*0*	0	0	*0*	*0*	0	0	*0*	0	
500–750	7	4	8	1	1		*0*	1	2	*1*	*3*	2	0	*0*	2	
750–1000	7	1	7	2	1		*2*	4	7	*1*	*4*	1	0	*1*	0	
1000–1500	3	1	3	3	1		*1*	5	5	*1*	3	1	1	*2*	0	

Table 19. Pelagobia longicirrata. *Distribution in the region of the Greenwich Meridian, between 70° S. and 35° S. (N 70 V nets only.) Italic light type indicates hauls made between sunrise and sunset. A.C. = Antarctic Convergence, S.T.C. = Sub-Tropical Convergence.*

Degrees South 70° 65° 60° 55° 50° 45° 40° 35°

November, December 1938

Between 00° 37°·6′ E. and 01° 23·7′ E.

Depth (m.)	Sts. 2501	2498	2496	A.C. ↓	2495	2494	2492
0–50	*20*	150	0		*0*	*0*	*0*
50–100	*30*	70	0		*40*	*0*	*0*
100–250	*2*	0	10		*53*	*0*	*0*
250–500	*1*	1	1		*0*	*1*	*0*
500–750	*3*	5	1		*2*	*0*	*0*
750–1000		5	1		*0*	*0*	0
1000–1500	No net	3	Sample lost		*1*	*2*	*0*

January 1939

Between 02° 04·7′ E. and 03° 33·7′ E.

Depth (m.)	Sts. 2547	2545	2543	2541	2538	2535	A.C. ↓	2533	2532	2531	S.T.C. ↓	2530
0–50	*0*	*40*	*100*	*20*	*0*	*40*		*0*	350	0		0
50–100	*40*	*15*	*55*	*60*	*0*	*720*		*110*	120	0		0
100–250	*117*	*15*	*5*	*8*	*42*	*98*		*2*	42	3		0
250–500	*28*	*8*	*12*	*10*	*40*	*10*		*5*	24	3		8
500–750	*5*	*6*	*18*	*0*	*9*	*10*		*8*	5	4		2
750–1000	*8*	*4*	*3*	*5*	*9*	*3*		*0*	0	2		3
1000–1500	*3*	4	*2*	2	No net	2		*3*	No net	5		1

March, April 1937

Between 00° 6·7′ E. and 00° 39·7′ E.

Depth (m.)	Sts. 2010	2012	2014	2015	2017	2018	2020	2022	A.C. ↓	2023	2024	2025	2026	S.T.C. ↓	2027
0–50	0	165	25	*0*	*60*	70	0	0		30	0	0	0		10
50–100	*5*	25	210	*15*	*55*	0	0	15		5	15	0	0		*5*
100–250	*2*	35	32	*20*	*47*	3	0	0		0	0	0	0		0
250–500	*4*	24	1	*4*	*11*	3	0	0		1	0	0	1		*0*
500–750	*2*	4	8	*10*	*4*	3	0	3		1	2	1	0		*0*
750–1000	*2*	*1*	0	*3*	*7*	4	1	4		0	1	0	0		*4*
1000–1500	*0*	*3*	No net	*1*	*1*	No net	5	1		1	1		1		1

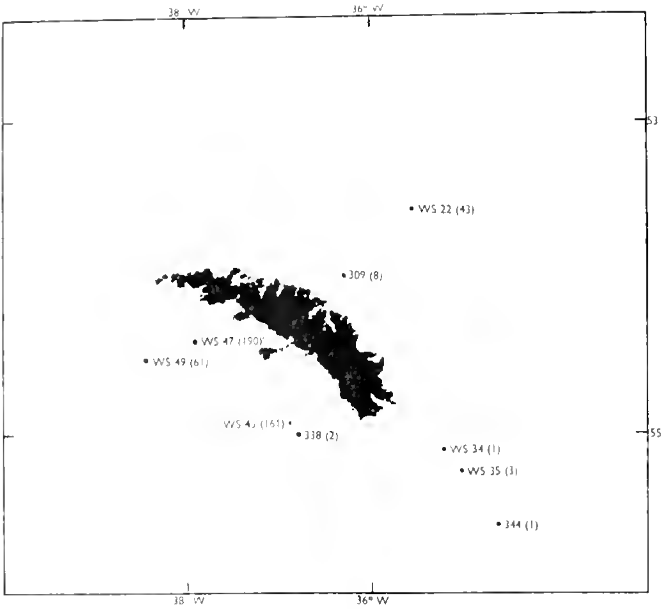


Fig. 37

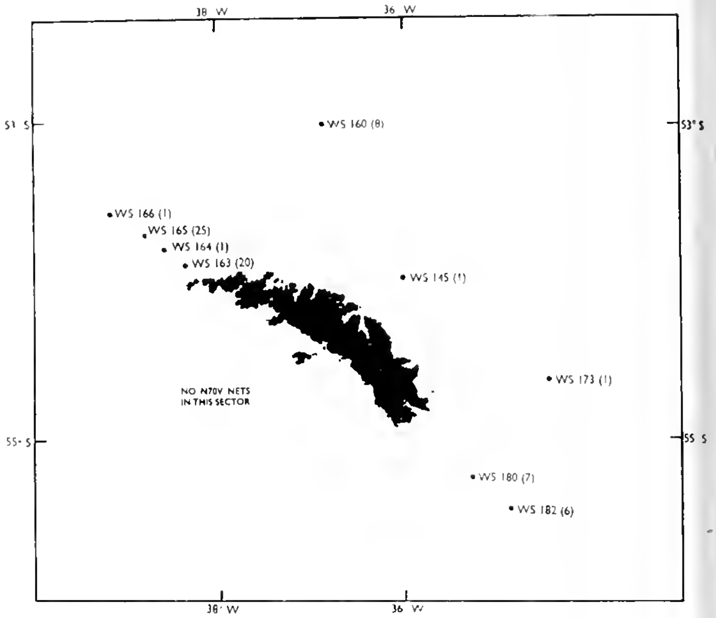


Fig. 38

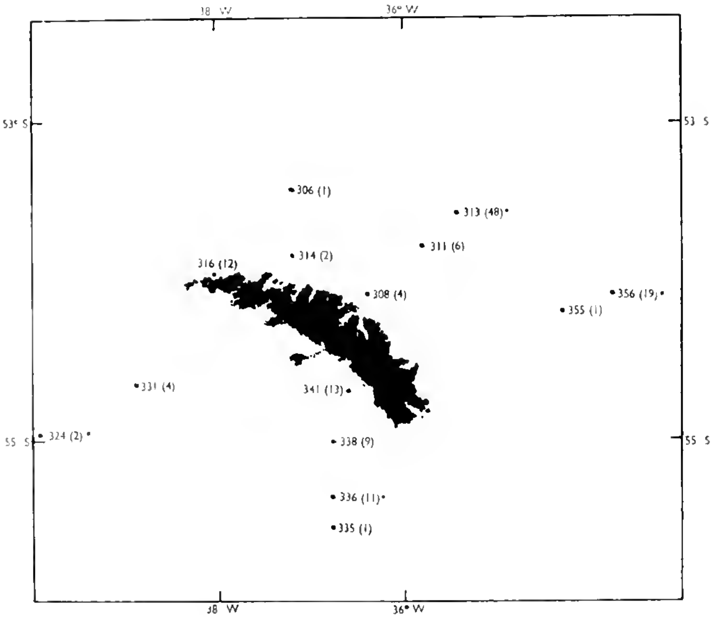


Fig. 39

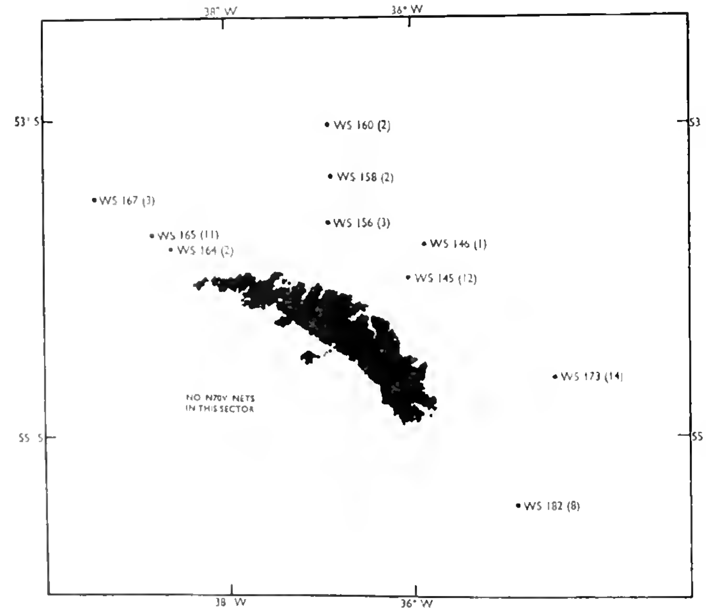


Fig. 40

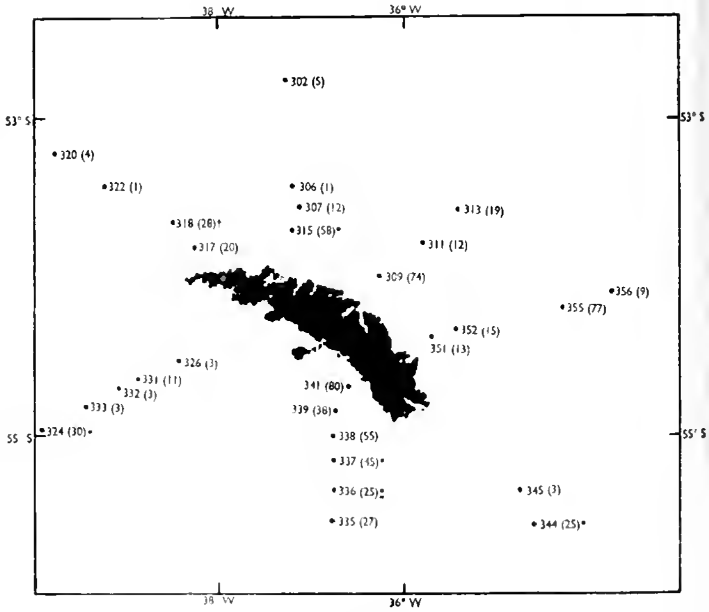


Fig. 41

Text-figs. 37–41. Occurrence of *Pelagobia longicirrata* round South Georgia. N 70 V nets. Number of specimens at each station in brackets. Fig. 37. 50–0 m. Sts. WS 22–49, November–January 1926–7; Sts. 309–44, January–February 1930. Fig. 38. 100–50 m. February–March 1928. Fig. 39. 100–50 m. February–March 1930. Fig. 40. 250–100 m. February–March 1928. Fig. 41. 250–100 m. January–February 1930. * = $\frac{1}{5}$ sample sorted; ** = $\frac{2}{5}$ sample sorted; † = $\frac{3}{10}$ sample sorted.

shows that these 459 specimens occurred at six stations only, two nets containing four specimens and the others 43, 161, 190 and 61 specimens respectively. Of these last, 351 specimens were caught between sunset and sunrise, consequently this sparse, patchy distribution may be due in part to diurnal migration. The positions of these surface stations are also shown in Text-fig. 37.

At depths between 250–50 m., *P. longicirrata* was much more abundant, particularly in the deeper layers of the Antarctic Surface Water (Text-figs. 38–41), and was more generally distributed around the island. Hardy and Gunther recorded a similar picture.

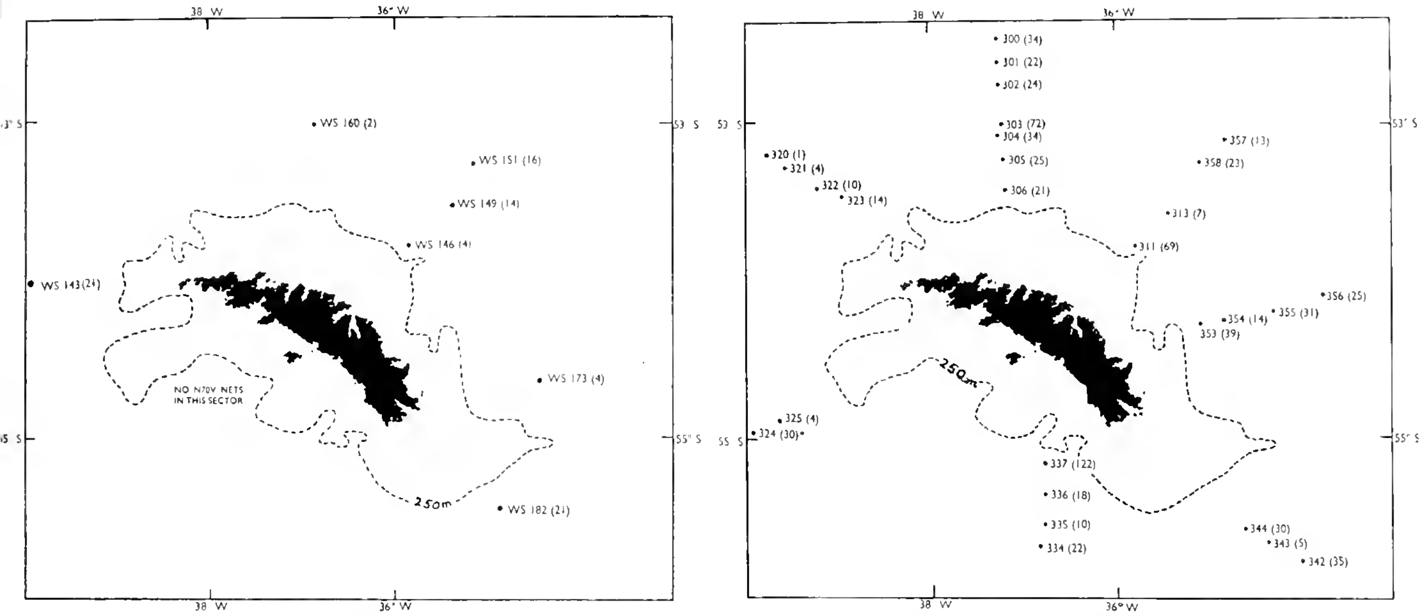


Fig. 42 Fig. 43

Text-figs. 42–43. Occurrence of *Pelagobia longicirrata* round South Georgia. N 70 V nets. Number of specimens at each station in brackets. Fig. 42. 1000–250 m. February–March 1928. Fig. 43. 1000–250 m. January–February 1930. * = $\frac{1}{5}$ sample sorted.

P. longicirrata was fairly evenly distributed around South Georgia at depths between 250–1000 m., below which nets were not used (Text-figs. 42, 43). In the summer months, its occurrence in the deeper layers gives much the same picture of vertical distribution as that shown for the 0° Line, but I have no evidence of its migration to depth in winter in the South Georgia area.

P. longicirrata was also collected around South Georgia at Sts. 17 and 41 (Monro, 1936), and St. 1079; these records have been plotted on Text-fig. 44 and details are listed in Appendix II, Table *j*; they conform to the general pattern already found.

The records of *P. longicirrata* from the South Sandwich Survey are plotted in Text-fig. 44 and listed in Appendix II, Table *b*. It was collected at only sixteen of the fifty-eight stations and never in large numbers, which is surprising because the collections were made during the summer and both N 50 and N 70 nets were used frequently. However, the records are only of restricted value, because nets did not fish below 250 m.

P. longicirrata was also collected at numerous miscellaneous stations (Text-fig. 44 and Appendix II) throughout the South Atlantic Ocean.

Previous records. Stop-Bowitz (1948) reported *P. longicirrata* from the area about the Greenwich Meridian in twenty-six nets hauled by the 'Norwegica', from depths down to 400 m.; and of these twelve were south of 59° 53′ S. and hauled between 100 m. and the surface.

Apart from the Hardy and Gunther (1935) and Monro (1936) records already noted, only Støp-Bowitz (1949, 1951) has previously reported *P. longicirrata* from South Georgia from collections made by the Norwegian and Swedish Antarctic Expeditions in East Cumberland Bay, from 160 to 72 m. (one specimen) and 150 to 0 m. (one specimen) respectively.

Monro (1936) previously reported *P. longicirrata* from around the South Sandwich Islands, at St. WS 555 and Stop-Bowitz (1949) reported it from two 'Norwegica' Stations at 57° 48′ S., 26° 25′ W., from 400 to 300 m., and 55° 33′ S., 26° 26′ W., from 100 m.

Other records from the Antarctic Zone include Augener (1929) from seventeen stations in the Weddell Sea from 600 m. to the surface. The farthest south of these is in 77° 40′ S. close in to the Filchner shelf ice, the most southerly record for *P. longicirrata* or any adult pelagic polychaete in the Atlantic. The 'Norwegica' (Stop-Bowitz, 1949) collected it at four stations other than those already mentioned, from 59° 53′ S., 8° 40′ W., 400–500 m., 59° 09′ S., 9° 58′ W., 300–100 m., 57° 37′ S., 19° 16′ W., 200–50 m., and 58° 09′ S., 37° 38′ W., 300–200 m., and the Swedish Antarctic Expedition, 1901–3, found it at the following positions, 52° 43′ S., 58° 52′ W., 61° 29′ S., 58° 0′ W. and 63° 33′ S., 44° 26′ W. (Stop-Bowitz, 1951).

North of the Antarctic Convergence Reibisch (1895) reported *P. longicirrata* from Ascension Island north-west to the mouth of the Amazon and north to the Equator, in regular abundance from the surface to 200 m., once at 400 m. and again at 1000 m.; Stop-Bowitz (1951) reported it once off the coast of Brazil at 4° 26′ N., 28° 59′ W., from 750–500 m. Friedrich (1950) noted its abundance throughout the South Atlantic in the 'Meteor' collections but gave no details.

Maupasia caeca

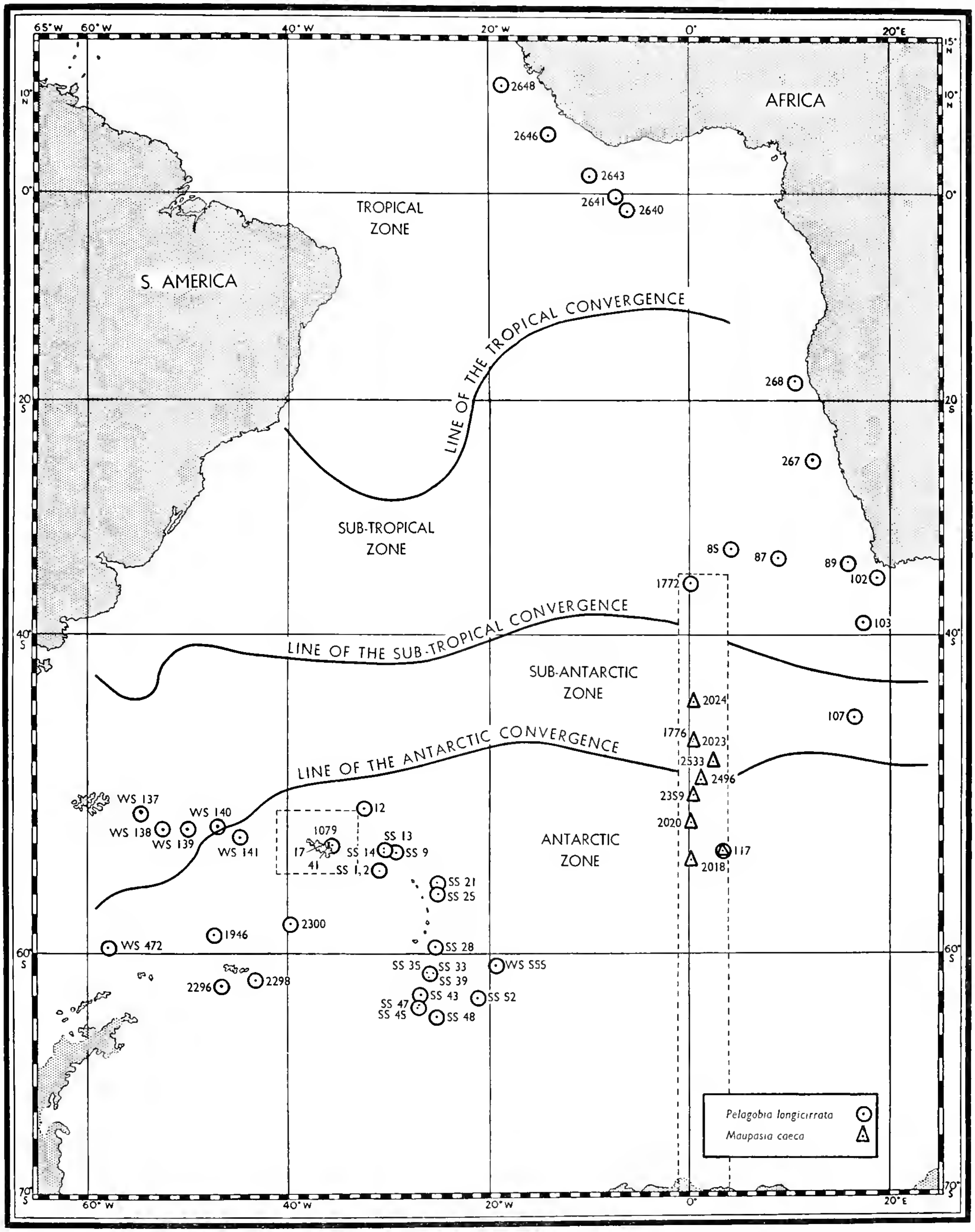
(Text-fig. 44)

M. caeca is a widely, though sparsely, distributed species in the South Atlantic Ocean and does not appear to be restricted in its range by surface hydrological boundaries. It rarely measures more than 6 mm. long and was caught only by N 70 nets.

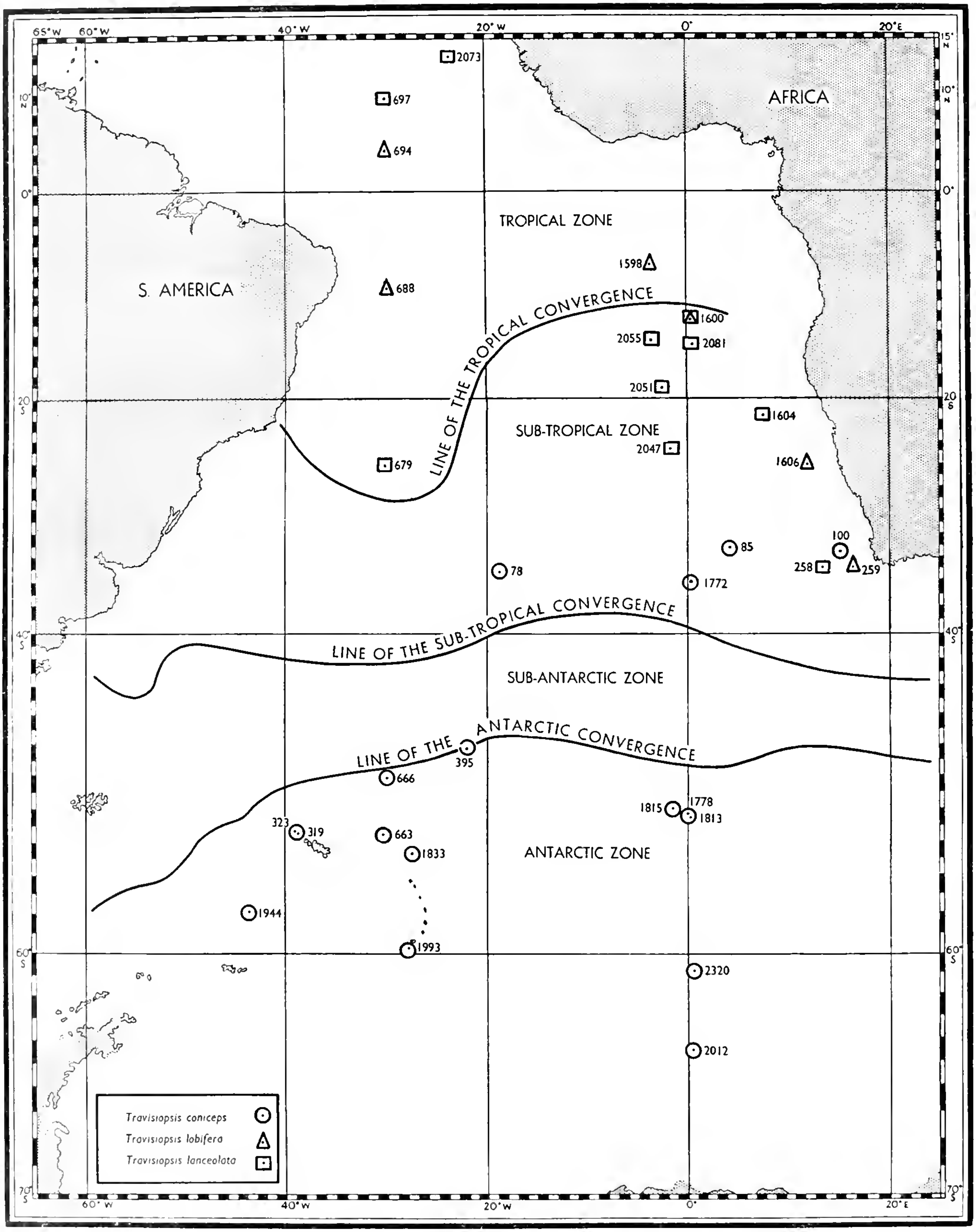
At each of the following stations and depths, one specimen was collected: St. 117, 250–100 and 750–500 m.; St. 1776, 1000–750 m.; St. 2018, 500–250 m.; St. 2020, 1000–750 m.; St. 2023, 750–500 m.; St. 2024, 750–500 m.; St. 2359, 750–500 m.; St. 2496, 500–250 m.; and St. 2533, 1500–1000 m.

These stations include the first records of *M. caeca* in the Antarctic Zone of the South Atlantic Ocean. It was collected in the Warm Deep Water at Sts. 117, 2018, 2020, 2359 and 2496. In the Sub-Antarctic Zone this species occurred in the Antarctic Intermediate Water, at Sts. 1776, 2023 and 2024, and in the Warm Deep Water at St. 2533. There are no records of *M. caeca* in Discovery material from Tropical and Sub-Tropical Zones although it has been reported from there by other workers.

Previous records. M. caeca was originally described from specimens collected in the Mediterranean (Bay of Algiers) by Viguier (1886); Ehlers (1912) first reported it in the Antarctic Zone from the collections of the National Antarctic Expedition 1901–4 in McMurdo Sound, and from the Deutsche Südpolar-Expedition 1901–3, off Kaiser Wilhelm II Land (Ehlers, 1913). In this latter work, Ehlers also recorded it from 00° 52′ S., 16° 00′ W., in the Tropical Zone of the South Atlantic. Southern (1909) reported this species as *M. caeca* var. *atlantica* from 51° 54′ N., 11° 57′ W.; Fauvel (1916) reported *M. caeca* off Cape Finisterre; Hardy and Gunther (1935) found it at St. WS 70 in the Sub-Antarctic Zone of the South Atlantic, and Wesenburg-Lund (1939) recorded it from the Mediterranean. Friedrich (1950*c*) reported *Maupasia* from the 'Meteor' collections in the Sub-Antarctic Sub-Tropical and Tropical Zones.



Text-fig. 44. Occurrence of *Pelagobia longicirrata* and *Maupasia caeca*. (See also Text-figs. 37–43, and Tables 18, 19).



Text-fig. 45. Occurrence of *Travisiopsis coniceps*, *T. lobifera* and *T. lanceolata*.

Travisiopsis coniceps

(Text-fig. 45, Table 20)

T. coniceps is widely distributed throughout the South Atlantic, and, measuring 18–30 mm. in length, could have been collected by all nets used in Discovery Investigations.

In the Antarctic Zone *T. coniceps* was collected in the Warm Deep Water only. In the Sub-Tropical Zone it was caught in South Atlantic Central Water at St. 1772 and at Sts. 78, 85 and 100, where the nets were hauled open to the surface; it may also have been collected in Antarctic Intermediate Water or Warm Deep Water. It is probable that this species normally inhabits the deeper water masses and this may explain the absence of records from the Sub-Antarctic Zone and the Sub-Tropical Zone, north of St. 100, from which regions comparatively few samples have been examined from depth.

Table 20. *Occurrence of* Travisiopsis coniceps

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Antarctic	319	**1000–750***	N 70 V	2	Antarctic	1944	1500–1200	TYFB	2
	323	750–500	N 70 V	1		1993	950–650	TYFB	2
	395	1600–1500	N 450 H	11		2012	**750–500**	N 70 V	1
	663	1500–1000	TYFV	1		2320	**1000–750**	N 70 V	1
	666	3000–2000	TYFV	1	Sub-Tropical	78	1000(–0)†	TYF	2
	1778	**1500–1000**	N 70 V	1		85	**2000(–0)**	N 450	1
	1813	1500–1000	N 70 V	1		100	2000(–0)	TYF	1
	1815	1000–750	N 70 V	1		1772	440–150	N 70 B	1
	1833	1000–750	N 70 V	1					

* Heavy type indicates a night haul. † (–0) indicates that the net failed to close and fished open to the surface.

Previous records. Monro (1930, 1936) reported *T. coniceps* as *Sagitella lobifera* from the Antarctic Zone at St. 395, and in the Sub-Tropical Zone from Sts. 78, 85 and 100; these records are listed above. Stop-Bowitz (1951) reported it from 49° 56′ S., 49° 56′ W.

Travisiopsis lobifera

(Text-fig. 45, Table 21)

T. lobifera was collected only in the Sub-Tropical and Tropical Zones, and, although the records for it are few, its absence from all stations south of the Sub-Tropical Convergence provides some evidence that it is restricted in its southerly distribution at this boundary. This species measures up to 25 mm. in length and could have been caught by most of the nets used in Discovery Investigations.

In the Sub-Tropical Zone, *T. lobifera* was caught in South Atlantic Central Water at Sts. 259 and 1600 and in Antarctic Intermediate Water at St. 1606. In the Tropical Zone it was collected in Tropical Surface Water or South Atlantic Central Water.

Table 21. *Occurrence of* Travisiopsis lobifera

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	259	**450–370**	TYF	1	Tropical	688	**450–0**	TYFB	1
	1600	**151–0**	TYFB	5		694	**210–0**	TYFB	1
		400–330	TYFB	1		1598	**180–0**	TYFB	4
	1606	**600–500**	TYFB	1					

Previous records. Levinsen (1885) reported *T. lobifera* from the Tropical Zone in 11° 50′ S., 8° 10′ W., and 15° 6′ S., 6° W.

Travisiopsis lanceolata

(Text-fig. 45, Table 22)

The records for *T. lanceolata* are not numerous but they indicate that it has its southern limit of distribution at the Sub-Tropical Convergence. Measuring up to 31 mm. in length *T. lanceolata* could have been caught by all the nets used by Discovery Investigations, in all hydrological zones.

In the Sub-Tropical Zone *T. lanceolata* was taken in the Antarctic Intermediate Water (Sts. 2051, 2047, 2081, 1604) and possibly in the South Atlantic Central Water (Sts. 1600 and 258) also. At St. 2055 it may have penetrated into the Warm Deep Water as well. In the Tropical Zone (Sts. 697 and 2073) *T. lanceolata* was caught in either Tropical Surface Water or South Atlantic Central Water and at St. 679 it occurred either in the Warm Deep Water or the Antarctic Intermediate Water.

Table 22. *Occurrence of* Travisiopsis lanceolata

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	258	**450–320**	TYF	1	Sub-Tropical	2055	1400–2000	TYFB	1
	1600	**400–330**	TYFB	2		2081	950–500	TYFB	2
	1604	**620–500**	TYFB	1	Tropical	679	**1500–1000**	TYFV	1
	2047	1300–900	TYFB	3		697	**460–0**	TYFB	1
	2051	990–600	TYFB	1		2073	**375–0**	TYFB	1

Previous records. *T. lanceolata* was collected by the Deutsche Südpolar-Expedition in the Tropical and Sub-Tropical Zones of the South Atlantic (Ehlers, 1913, as *Sagittella cornuta* (*sic*)), but in the Indian and Pacific Ocean sectors of the Antarctic this expedition collected it south of the Sub-Tropical Convergence. These anomalous records may be the result of confusion with *T. levinseni.* Monro (1930) reported *T. lanceolata* from the Sub-Tropical Zone as *Sagitella cornuta* and from the Tropical Zone (1939*a* as *T. lanceolata*); Friedrich (1950*c*) reported it from the 'Meteor', collections but gave no details.

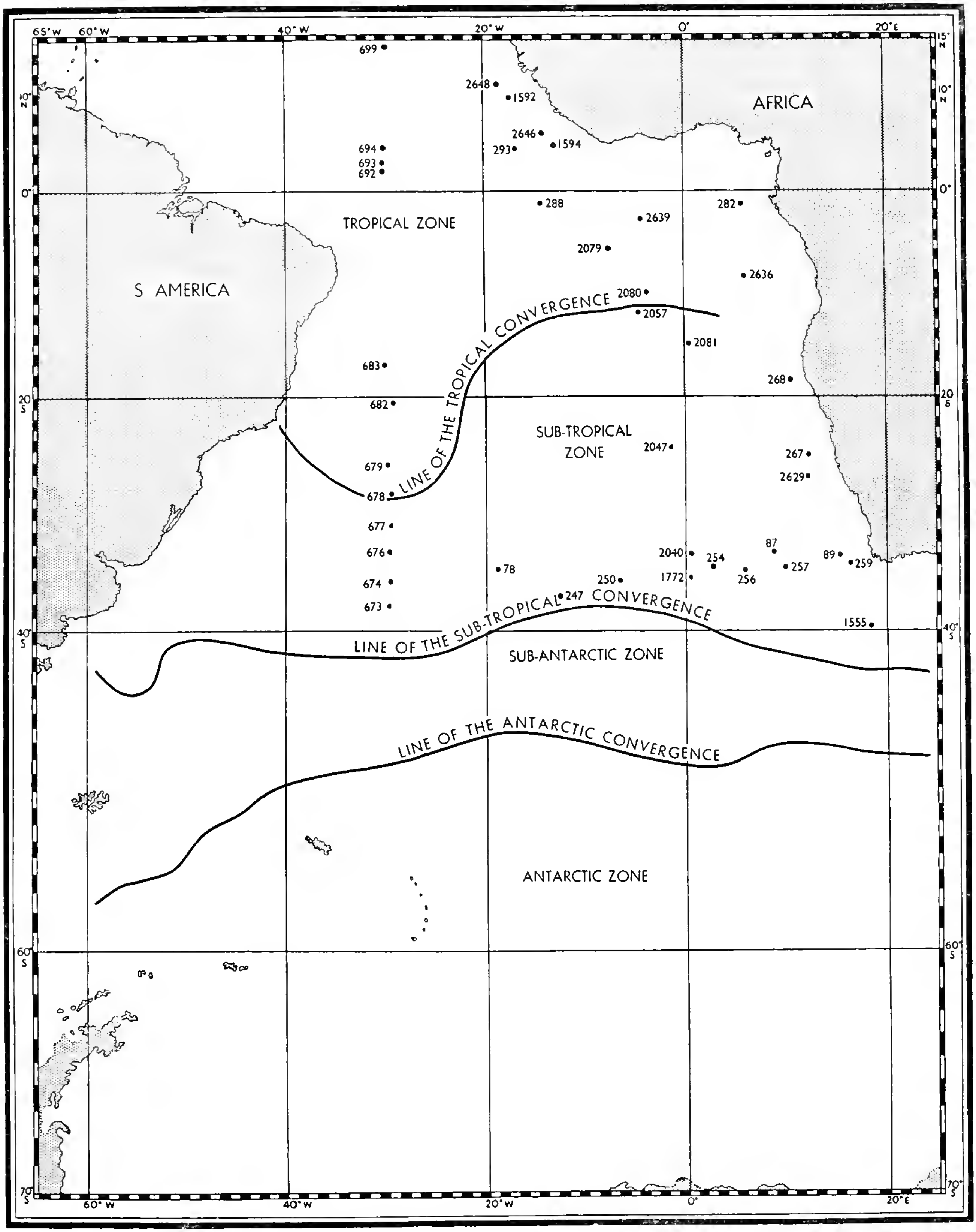
Tomopteris nisseni

(Text-fig. 46, Table 23)

T. nisseni was collected in the Sub-Tropical and Tropical Zones only, and its absence from all nets in the Antarctic and Sub-Antarctic Zones indicates that it has its southern limit of distribution at the Sub-Tropical Convergence. The species measures between 8 and 60 mm. long and could have been caught by all nets used in Discovery Expeditions.

In the Sub-Tropical Zone *T. nisseni* was caught in South Atlantic Central Water at Sts. 674, 676, 247, 2040, 254, and in Antarctic Intermediate Water at Sts. 673, 677, 2057, 2047, 2081 and 2629. At the other Stations in this zone the nets crossed the boundaries between these two waters and *T. nisseni* could have been caught in either. In the Tropical Zone it was taken in Antarctic Intermediate water at Sts. 693, 699, 1592, 1594 (1750–950 m.), 2648 (1450–950 m.) 2646 (1500–800 m.) 2639, 2636 and in South Atlantic Central Water at St. 1594 (430–300 m.). At Sts. 678, 679, 682, 683, 692, 2648, 288, 2079, 2080 (400–0 m.), 2646 (250–0 m.), 1594 (144–0 m.) and 282, *T. nisseni* was collected by nets towed in both Tropical Surface and South Atlantic Central Water.

Previous records. *T. nisseni* has been reported from the South Atlantic by Rosa (1908*b*) from 20° S., 27° W. and McIntosh (1925) in recording *T. carpenteri* from off South Africa probably also referred to this species. Monro (1930) recorded it from Discovery collections in the Tropical and Sub-Tropical Zones.



Text-fig. 46. Occurrence of *Tomopteris nisseni*.

Table 23. *Occurrence of* Tomopteris nisseni

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	78	1000–0	TYF	1	Tropical	282	**300(–0)**	TYF	1
	87	1000–0	TYF	4		288	**250(–0)**	TYF	1
	89	1000–0	TYF	3		293	**120–100(–0)**	TYF	1
	247	**115–100(–0)**	TYF	1		678	**360–0**	TYFB	1
	250	**300(–0)**	TYF	3		679	**300–0**	TYFB	3
	254	200–0	TYF	5		682	**375–0**	TYFB	1
	256	1100–850(–0)	TYF	1		683	**290–0**	TYFB	3
	257	250–0	TYF	3		692	**350–0**	TYFB	1
	259	**450–370**	TYF	3		693	500–250	TYFV	1
	267	**550–450(–0)**	TYF	1		694	210–0	TYFB	2
	268	**150–100(–0)**	TYF	1		699	750–500	TYFV	1
	673	**2000–1500**	TYFV	1		1592	**700–450**	TYFB	1
	674	**280–0**	TYFB	2		1594	**144–0**	TYFB	1
	676	**290–0**	TYFB	2			**430–300**	TYFB	1
	677	750–500	TYFV	1		2079	**250–0**	TYFB	2
	1555	**1000–0**	TYFB	1		2080	400–0	TYFB	1
	1772	750–450	N 70 B	1			1750–950	TYFB	1
	2040	600–0	TYFB	1		2636	**950–550**	TYFB	1
	2047	1300–900	TYFB	1		2639	**1200–600**	TYFB	1
	2057	1450–700	N 450 H	1		2646	**250–0**	TYFB	3
	2081	950–500	TYFB	1			**1500–800**	TYFB	1
	2629	**1800–1300**	TYFB	1		2648	**500–0**	TYFB	1
							1450–950	TYFB	1

Tomopteris ligulata

(Text-fig. 47, Table 24)

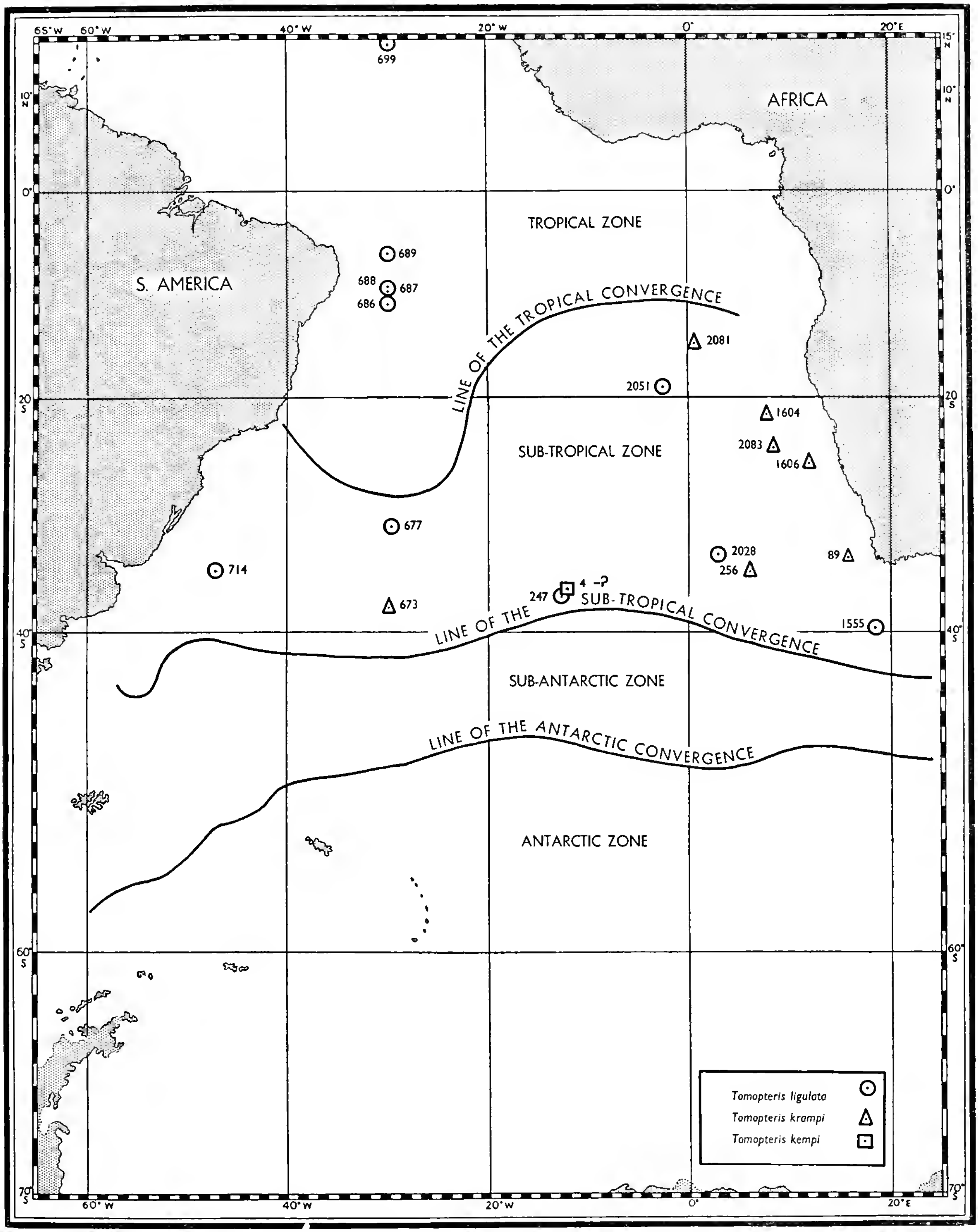
T. ligulata was collected only to the north of the Sub-Tropical Convergence and the records obtained indicate that it is restricted in the South Atlantic to the Sub-Tropical and Tropical Zones. *T. ligulata* rarely measures more than 11 mm. in length but it appears to have been missed by the N 50 and N 70 nets and was caught only by the larger N 100 and TYF and it is possible that it is more abundantly distributed than the records suggest.

In the Sub-Tropical Zone *T. ligulata* was collected in South Atlantic Central Water at Sts. 714, 677, 247 and 2028, in Antarctic Intermediate Water at St. 2051, and one or other of these water masses at St. 1555. In the Tropical Zone this species was taken in Tropical Surface Water or South Atlantic Central Water at Sts. 686, 688 and 689, and in Antarctic Intermediate Water at St. 687; at St 699 it was collected in either South Atlantic Central or Antarctic Intermediate Water.

Table 24. *Occurrence of* Tomopteris ligulata

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	247	**115–100(–0)**	TYF	1	Tropical	686	**400–0**	TYFB	1
	677	**420–0**	TYFB	1		687	750–500	TYFV	1
	714	**246–0**	TYFB	3		688	**450–0**	TYFB	2
	1555	**1000–0**	TYFB	1		689	**410–0**	TYFB	1
	2028	**5–0**	N 100 H	2		699	500–250	TYFV	1
	2051	990–600	TYFB	1					

Previous records. Rosa's (1908*b*) original records of *T. ligulata* included one from the South Atlantic in 33° S., 30′ W., and Monro (1936) reported it (as *T. planktonis*) from St. 714. I have re-examined the specimens reported by Ehlers (1917) as *T. ligulata* from 62° 42′ S., 82° 0′ E. in the Antarctic Zone, and consider them to be *T. planktonis*. Friedrich (1950*c*) probably included this species in his Tomopteridae, reported from the South Atlantic 'Meteor' collections.



Text-fig. 47. Occurrence of *Tomopteris ligulata*, *T. krampi* and *T. kempi*.

Tomopteris krampi

(Text-fig. 47, Table 25)

T. krampi has not previously been reported from the South Atlantic Ocean. It varies in length from 9 to 26 mm. and all nets could normally catch it. The few records may be due to the small number of N 70 nets hauled north of the Sub-Tropical Convergence. The species is evidently restricted in its distribution in the South Atlantic by this boundary; none of numerous nets fished to the south collected it.

In the Sub-Tropical Zone, *T. krampi* was collected in South Atlantic Central Water at St. 2083, in Antarctic Intermediate Water at Sts. 673, 2081 and 1604 and in either of these waters at Sts. 89 and 1606.

Table 25. *Occurrence of* Tomopteris krampi

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	89	1000–0	TYF	2
	256	1100–800(–0)	TYF	2
	673	**1000–750**	TYFV	1
	1604	**620–500**	TYFB	1
	1606	**600–500**	TYFB	1
	2081	950–500	TYFB	1
	2083	**330–0**	TYFB	1

Previous records. Wesenberg-Lund (1936) and Stop-Bowitz (1948) reported *T. krampi* from the North Atlantic. Friedrich (1950*c*) reports *T. krampi* from the 'Meteor' Expedition, but gives no details of locality and it may have been collected at stations in the North Atlantic Ocean.

Tomopteris kempi

(Text-fig. 47)

The only locality in the world at which *T. kempi* has been collected is 'Discovery' St. 4, from 10 to 0 m. with an N 100 H net, seven specimens (Monro, 1930). The hydrological position of St. 4 is uncertain because it was made very close to the Sub-Tropical Convergence.

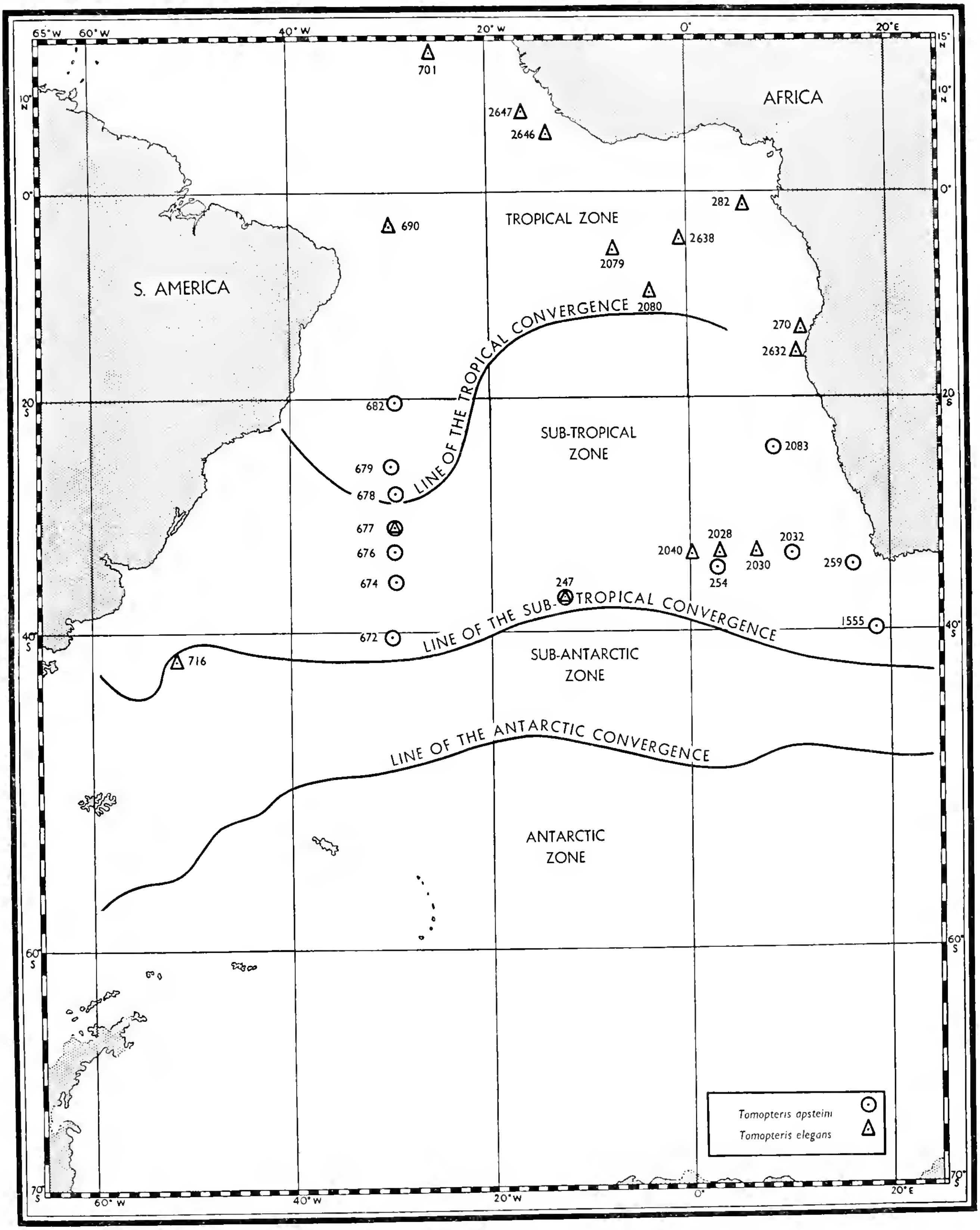
It is remarkable that *T. kempi* has not been found again; it may either have been missed by expeditions and is really widespread in distribution, or is an isolated species.

Tomopteris elegans

(Text-fig. 48, Table 26)

T. elegans was collected at sixteen stations north of the Sub-Tropical Convergence and is evidently restricted in its southerly distribution at this boundary. Although this species rarely measures more than 7 mm. long it was collected only twice by an N 70 net whereas the larger TYF caught it fourteen times. It is possible, therefore, that although often missed by the smaller nets, it occurs in sufficient abundance for the larger nets to collect it and the records obtained may not reflect the real intensity of its distribution. The specimen from St. 716 is the only one collected south of this boundary and because no others were caught there I presume this to be an anomaly.

In the Sub-Tropical Zone *T. elegans* was caught in South Atlantic Central Water at Sts. 247, 270, 2028 and 2030, and in either South Atlantic Central Water or Antarctic Intermediate Water at St. 2040. At Sts. 677 and 2632 the nets were hauled from considerable depths and the water masses in which the specimens were collected are uncertain.



Text-fig. 48. Occurrence of *Tomopteris apsteini* and *T. elegans*.

In the Tropical Zone this species was caught in either Tropical Surface Water or South Atlantic Central Water at all stations except 690, in which the net may have also collected it in Antarctic Intermediate Water.

Table 26. *Occurrence of* Tomopteris elegans

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Antarctic	716	**212–0**	TYFB	1	Tropical	282	**300(–0)**	TYF	1
Sub-Tropical	247	**115–100(–0)**	TYF	1		690	**1500–0**	TYFV	2
	270	**200–0**	TYF	1		701	**242–0**	TYFB	1
	677	**2000–0**	TYFV	1		2079	**250–0**	TYFB	3
	2028	**118–0**	N 70 B	6		2080	400–0	TYFB	1
	2030	**168–0**	N 70 B	1		2638	150–0	TYFB	2
	2040	600–0	TYFB	3		2646	**250–0**	TYFB	2
	2632	**1800–?**	TYFB	1		2647	**310–0**	TYFB	1

Previous records. Ehlers (1917) recorded *T. elegans* from several localities in the Tropical and Sub-Tropical Zones of the South Atlantic all from nets fished through the surface waters. Friedrich (1950*c*) may have included this species in the Tomopteridae of the 'Meteor' collections which he reported from the South Atlantic.

Tomopteris apsteini

(Text-fig. 48, Table 27)

T. apsteini was collected only in the Sub-Tropical and Tropical Zones and it is evident that it is restricted in its southerly distribution by the Sub-Tropical Convergence. This species measures from 8 to 47 mm. in length and could have been caught by all the nets used in Discovery Investigations.

In the Sub-Tropical Zone *T. apsteini* was collected in South Atlantic Central Water at Sts. 247, 254, 259, 672, 674, 676, 677 (420–0 m.) and 2032. At St. 1555 it may have been caught also in Antarctic Intermediate Water and at St. 677 (2000–0 m.) also in the Warm Deep Water. In the Tropical Zone, where *T. apsteini* was collected only at stations made along the 30° Line, it was caught by nets which fished in both Tropical Surface Water and South Atlantic Central Water.

Table 27. *Occurrence of* Tomopteris apsteini

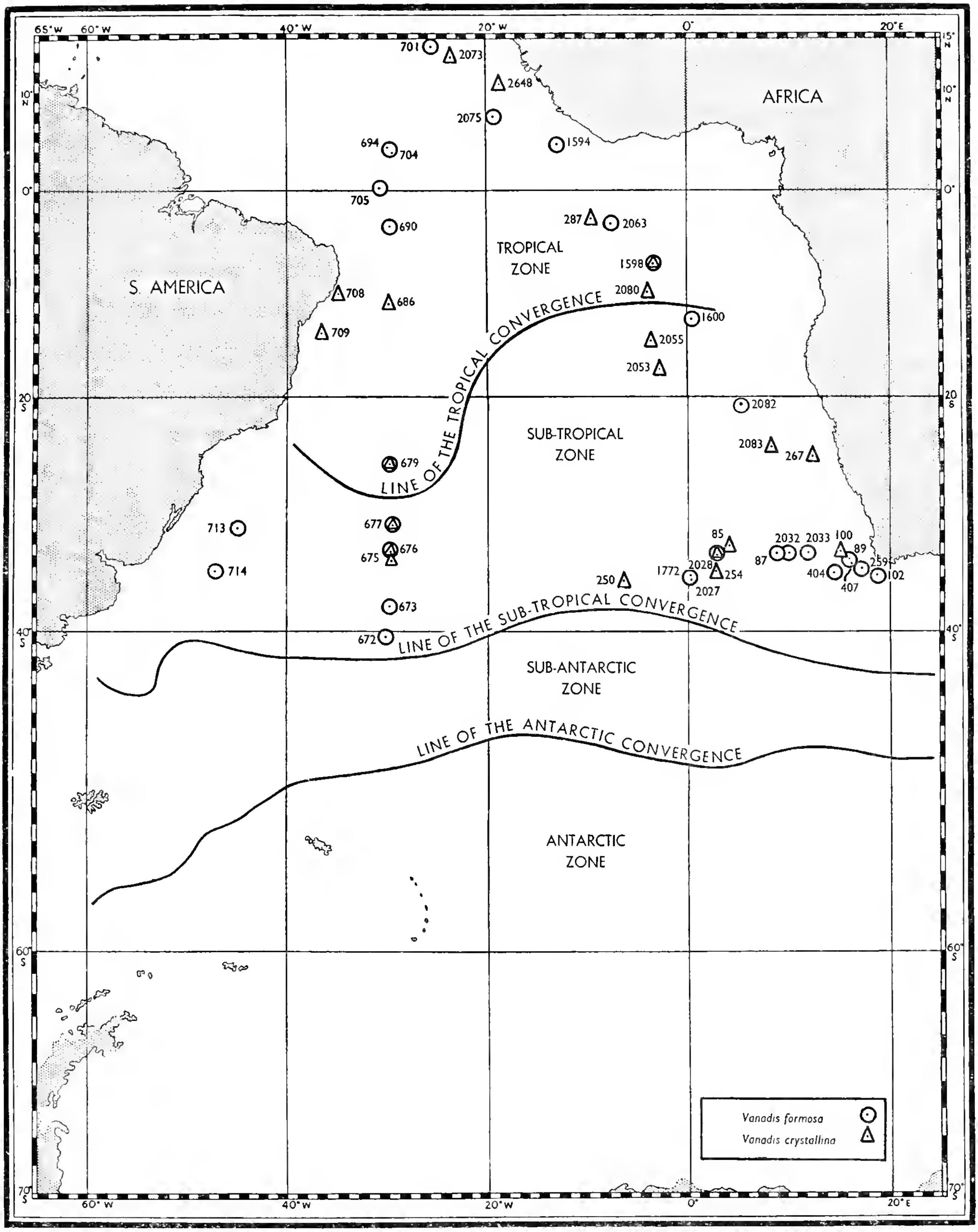
Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	247	**115–100(–0)**	TYF	2	Sub-Tropical	1555	**1000–0**	TYFB	2
	254	**200–0**	TYF	1		2032	**5–0**	N 100 H	1
	259	**450–370**	TYF	1		2083	**330–0**	TYFB	4
	672	200–0	TYFB	2	Tropical	678	**360–0**	TYFB	1
	674	**280–0**	TYFB	2		679	250–0	TYFV	1
	676	**290–0**	TYFB	2			**300–0**	TYFB	1
	677	**420–0**	TYFB	1		682	**375–0**	TYFB	1
		2000–0	TYFV	1					

Previous records. *T. apsteini* was collected in the South Atlantic by the Deutsche Südpolar-Expedition (Ehlers, 1917, as *T. rosaea*) and possibly also by the 'Meteor' expedition (Friedrich, 1950*c*, as Tomopteridae).

Vanadis formosa and *Vanadis crystallina*

(Text-fig. 49, Tables 28 and 29)

V. formosa and *V. crystallina* are closely related and are therefore considered together. Both species inhabit the Sub-Tropical and Tropical Zones and are restricted in their southerly distribution by the Sub-Tropical Convergence. Each is a large species, *V. formosa* measuring up to 300 mm. in length



Text-fig. 49. Occurrence of *Vanadis formosa* and *V. crystallina*.

and *V. crystallina* up to 145 mm., so that they might occur in all samples from the N 100, TYF and N 450 nets.

V. formosa was collected in the Sub-Tropical Zone in South Atlantic Central Water at Sts. 102, 259, 404, 407 (220–0 m.) 672, 673, 676, 677, 713, 714, 1600, 1772, 2027, 2032, 2082 and in Antarctic Intermediate Water at Sts. 407 and 2033. At Sts. 87 and 89 in the Sub-Tropical Zone it was caught by nets which fished in both South Atlantic Central and Antarctic Intermediate Water.

Table 28. *Occurrence of* Vanadis formosa

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	87	1000–0	TYF	1	Sub-Tropical	2027	310–150	N 100 B	1
	89	1000–0	TYF	1		2028	118–0	N 70 B	1
	102	52	N 100 H	1		2032	111–0	N 100 B	3
	259	450–370	TYF	2		2033	1350–1250	TYFB	1
	404	100–0	N 100 B	2		2082	330–0	TYFB	1
	407	220–0	TYFB	1	Tropical	679	300–0	TYFB	2
		900–800	N 450 H	1		690	460–0	TYFB	3
	672	200–0	TYFB	1			1500–0	TYFB	3
	673	340–0	TYFB	1		694	210–0	TYFB	1
	676	290–0	TYFB	1		701	242–0	TYFB	2
	677	250–0	TYFV	1		704	231–0	TYFB	1
		420–0	TYFB	6		705	150–0	TYFB	1
	713	200–0	TYFB	2		1594	144–0	TYFB	1
	714	246–0	TYFB	3		1598	180–0	TYFB	2
	1600	151–0	TYFB	1		2063	1150–600	TYFB	1
	1772	113–0	N 100 B	1		2075	1200–950	TYFB	1

In the Tropical Zone *V. formosa* was collected in either Tropical Surface or Antarctic Intermediate Water at Sts. 690 (460–0 m.), 694, 701, 705, 704, 1594, 1598 and in Antarctic Intermediate Water at Sts. 2063 and 2075. The net which collected this species at St. 690 (1500–0 m.) fished in Tropical Surface, South Atlantic Central, Antarctic Intermediate or Warm Deep Water.

V. crystallina was caught in the Sub-Tropical Zone in South Atlantic Central Water at Sts. 250, 254, 675, 676, 677, 2028 and 2083, in Antarctic Intermediate Water at St. 2053 and in Warm Deep Water at Sts. 100 and 2055. The net which collected this species at St. 85 fished in South Atlantic Central, Antarctic Intermediate and Warm Deep Water.

In the Tropical Zone *V. crystallina* was collected in Tropical Surface or South Atlantic Central Water at Sts. 708, 709, 1598 (180–0 m.), 2073, 2080 and 2648 and in the South Atlantic Central Water or Antarctic Intermediate Water at St. 1598 (460–300 m.).

Table 29. *Occurrence of* Vanadis crystallina

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	85	2000(–0)	N 450 H	1	Sub-Tropical	2055	2000–1400	TYFB	1
	100C	2000–2500	TYF	1		2083	330–0	TYFB	1
	250	300(–0)	TYF	4	Tropical	679	300–0	TYFB	2
	254	200–0	TYF	2		686	400–0	TYFB	1
	267	550–450(–0)	TYF	1		708	208–0	TYFB	2
	287	1000–800(–0)	TYF	1		709	216–0	TYFB	1
	675	250–0	TYFV	1		1598	180–0	TYFB	2
	676	290–0	TYFB	1			460–300	TYFB	1
	677	420–0	TYFB	3		2073	375–0	TYFB	1
	2028	118–0	N 70 B	4		2080	400–0	TYFB	1
		118–0	N 100 B	1		2648	500–0	TYFB	1
	2053	900–500	TYFB	1					

Previous records. V. formosa was reported by Greeff (1885 as *Alciopa longirhyncha*) from off islands in the Gulf of Guinea. Apstein (1900) reported *Vanadis formosa* and *V. crystallina* from numerous localities in the South Atlantic between Ascension Island and the Equator and Ascension Island and the mouth of the Amazon. Monro (1930, 1936) recorded *V. formosa* from several stations made by 'Discovery' Investigations in the Tropical and Sub-Tropical Zones, and he also reported *V. crystallina* in 1936 from the Cape Verde to Falkland Islands line of stations. From the 'Meteor' collections, Friedrich (1950*c*), reported *V. crystallina* but he gave no details.

Rhynchonerella angelini

(Text-fig. 50)

R. angelini is known from few records, all from the Sub-Tropical Zone, and it is possible that it is limited in its southerly distribution at the Sub-Tropical Convergence. This species may measure up to 67 mm. in length and would normally only be caught by the larger nets.

The following records of *R. angelini*, except that from St. 74, are taken from Monro's 1930[1] and 1936 Discovery Reports; all these specimens have been re-examined: St. 74, N 70 V, 1000–0 (1); St. 250, TYF, 300–0 (2); St. 257, TYF, 250–0 (1); St. 268, TYF, 150–100–0 (1); St. 405, TYFB, 1200–0 (1). *R. angelini* was caught in South Atlantic Central Water at Sts. 250, 257 and 260; at Sts. 74 and 405 it could have been collected in either South Atlantic Central Water or Antarctic Intermediate Water.

Previous records. Records of *R. angelini* from the South Atlantic were made by Greeff (1876, as *Callizona grubei*) and Levinsen (1885, as *Callizona grubei*) all north of the Sub-Tropical Convergence. Friedrich (1950*c*) reported it from the 'Meteor' collections (as *Callizona angelini*) but gave no details.

Krohnia lepidota

(Text-fig. 50, Table 30)

K. lepidota is known from few records all north of the Sub-Tropical Convergence and it is possible that this boundary restricts its southerly distribution. Measuring up to 50 mm. long *K. lepidota* was normally only collected by the larger nets but a fragment was caught by the N 50 V at St. 2641.

In the Sub-Tropical Zone *K. lepidota* was caught in South Atlantic Central Water at St. 254 and in this water mass, or Antarctic Intermediate or Warm Deep Water at St. 2632. In the Tropical Zone *K. lepidota* was collected at all stations in either Tropical Surface Water or South Atlantic Central Water.

Table 30. *Occurrence of* Krohnia lepidota

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	254	200(–0)	TYF	2	Tropical	1598	**180–0**	TYFB	1
	2632	**1800–0** ?	TYFB	1		2073	**375–0**	TYFB	1
Tropical	282	**300(–0)**	TYF	1		2080	400–0	TYFB	2
	693	250–0	TYFV	2		2641	**100–0**	N 50 V	1

Previous records. K. lepidota was reported by Apstein (1900, as *Callizonella lepidota*), from four stations between the Equator and Ascension Island, and at three between Ascension Island and the mouth of the Amazon. Under this name also, Friedrich (1950*c*) reported *K. lepidota* from the 'Meteor' collections in the South Atlantic but he gave no details.

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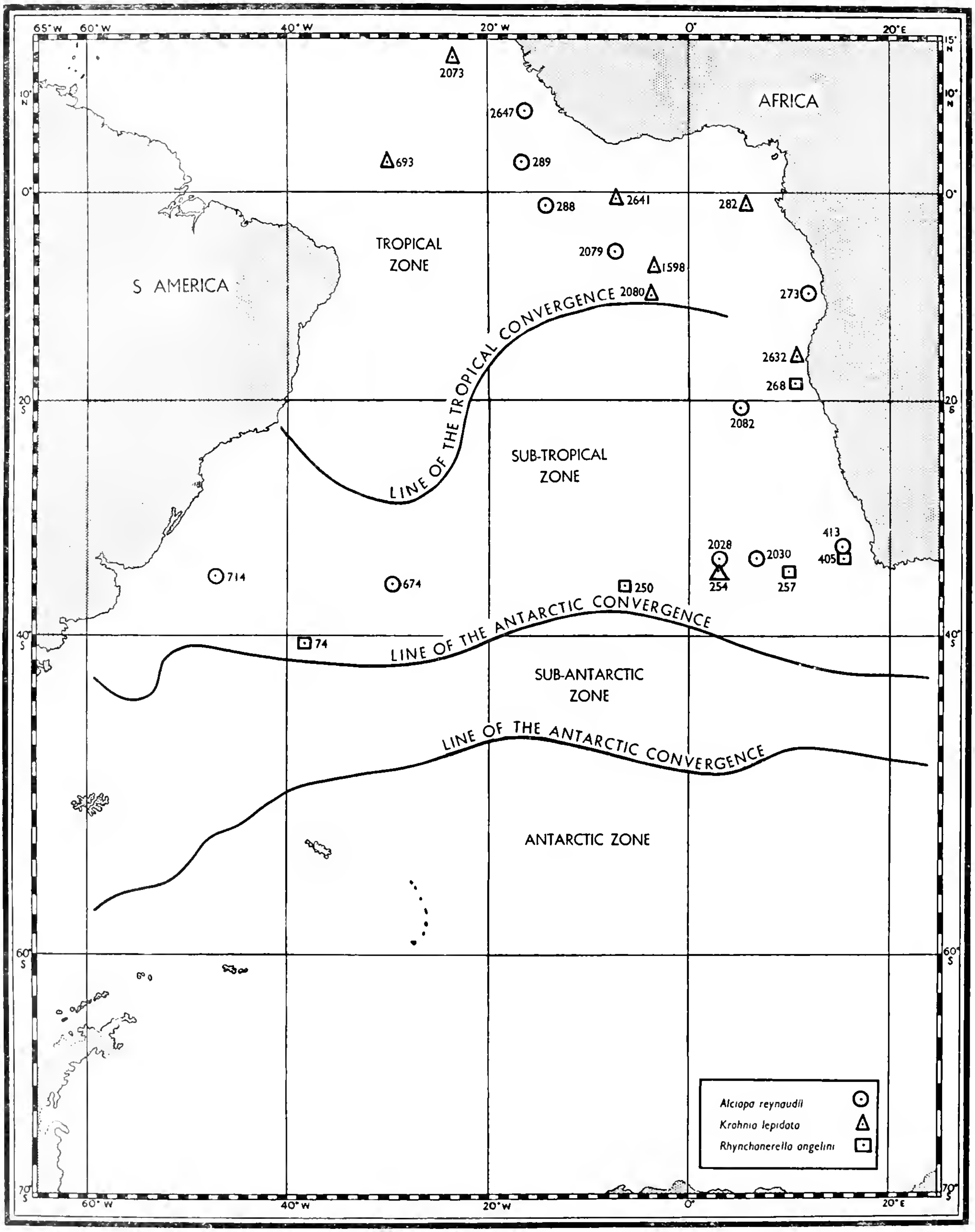
[1] Monro's specimen from 'Discovery', St. 245, was not deposited in the British Museum (N.H.) collections.



Text-fig. 50. Occurrence of *Rhynchonerella angelini*, *Krohnia lepidota* and *Alciopa reynaudii*.

Alciopa reynaudii

(Text-fig. 50, Table 31)

A. reynaudii was collected only to the north of the Sub-Tropical Convergence and is restricted in its distribution in the South Atlantic to the Sub-Tropical and Tropical Zones. Measuring between 30 and 40 mm. in length this species was normally collected only by the larger nets.

In the Sub-Tropical Zone *A. reynaudii* was collected in South Atlantic Central Water and in the Tropical Zone in South Atlantic Central or Tropical Surface Water.

Table 31. *Occurrence of* Alciopa reynaudii

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	413	350–0	TYFB	1
	674	**280–0**	TYFB	1
	714	246–0	TYFB	1
	2028	**5–0** **118–0**	N 100 H N 70 B	2 1
	2030	168–0	N 100 B	1
Sub-Tropical	2082	330–0	TYFB	1
Tropical	273	**200–230(–0)**	TYF	1
	288	**250(–0)**	TYF	1
	289	**225–125(–0)**	TYF	1
	2079	**250–0**	TYFB	1
	2647	**310–0**	TYFB	1

Previous records. *A. reynaudii* has been reported from the Tropical Zone in the South Atlantic by Greeff (1876, as *Nauphanta celox*) and Wesenberg-Lund (1939, as *Greefia oahuensis*) and from the Tropical and Sub-Tropical Zones by Levinsen (1885, as *Nauphanta celox*) and Monro (1930, 1936, as *Greefia oahuensis*).

Naiades cantrainii

(Text-fig. 51, Table 32)

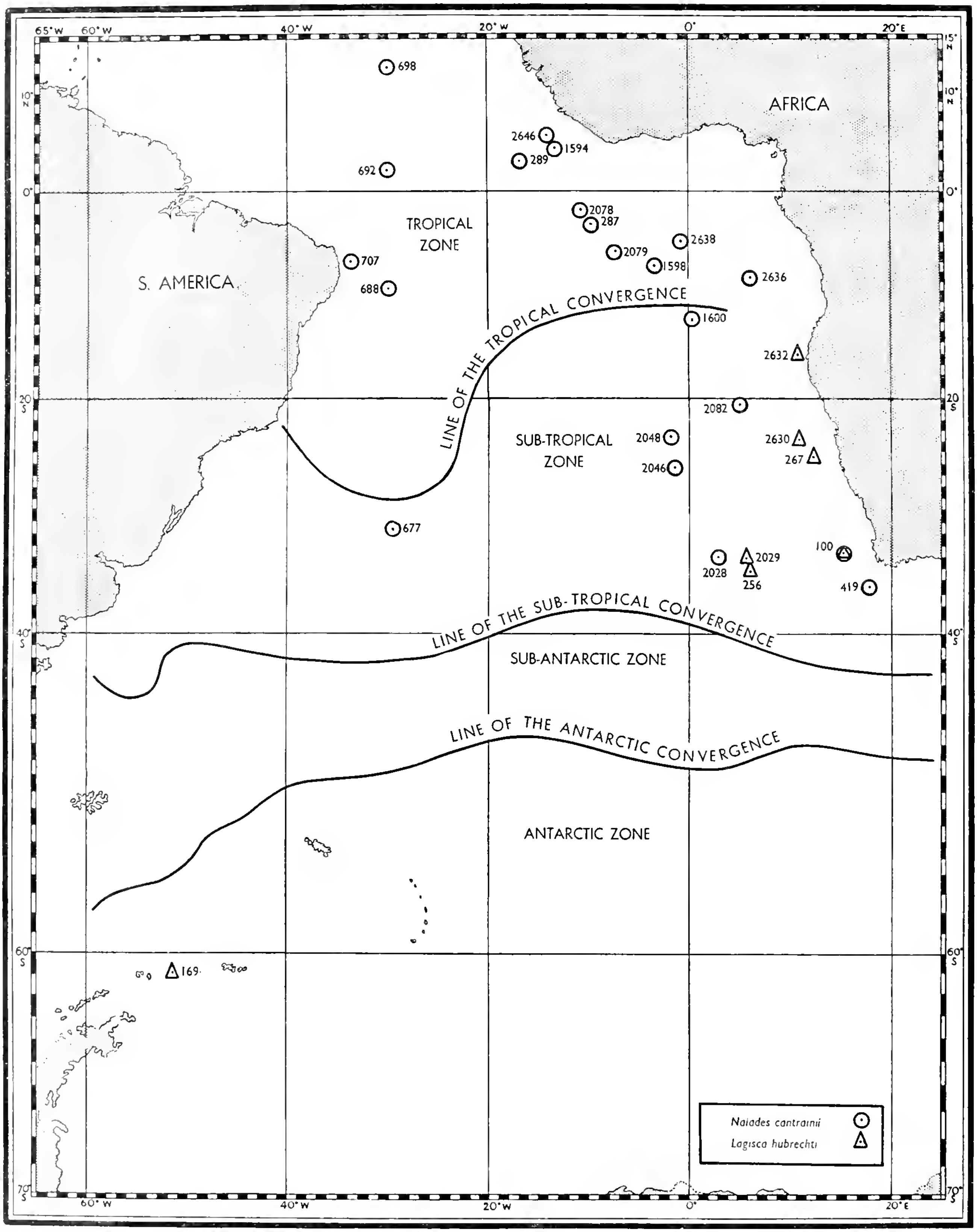
N. cantrainii occurs in abundance in the South Atlantic where it is clearly limited in its southerly distribution at the Sub-Tropical Convergence. Measuring up to 110 mm. in length this species was normally collected only by the larger nets.

In the Sub-Tropical Zone *N. cantrainii* was collected in South Atlantic Central Water at Sts. 677, 1600, 2028, 2082, 419 and 100 and in South Atlantic Central Water or Antarctic Intermediate Water at Sts. 2048 and 2046. In the Tropical Zone the collections at Sts. 289 and 2646 were made in South Atlantic Central Water and in this water mass or Tropical Surface Water at Sts. 707, 688, 692, 1594, 2079 (250–0 m.), 1598 and 2638. The specimen collected at St. 2078 was taken from Warm Deep Water and those from Sts. 2079 (555–250 m.) and 2636 from the Antarctic Intermediate layer or South Atlantic Central Water.

Table 32. *Occurrence of* Naiades cantrainii

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	100	475(–0)	TYF	1
	419	50–0	N 70 V	1
	677	250–0	TYFV	2
	1600	**151–0**	TYFB	1
		400–330	TYFB	1
	2028	**118–0**	N 70 B	1
	2046	500–0	N 450 B	1
	2048	600–0	N 450 B	1
	2082	330–0	TYFB	2
Tropical	287	**1000–800(–0)**	TYF	2
	289	**225–125(–0)**	TYF	1
	688	450–0	TYFB	2
Tropical	692	350–0	TYFB	1
	698	470–0	TYFB	1
	707	**182–0**	TYFB	1
	1594	**144–0**	TYFB	2
	1598	**180–0**	TYFB	6
	2078	2600–1400	TYFB	1
	2079	**250–0** **555–250**	TYFB TYFB	1 1
	2636	**950–550**	TYFB	1
	2638	**150–0**	TYFB	2
	2646	**250–100**	TYFB	1

Previous records. *N. cantrainii* was reported from a station on the Equator by Apstein (1900, as *Alciopa cantrainii*) and Monro (1930, 1936) reported it from the Tropical Zone in the South Atlantic.



Text-fig. 51. Occurrence of *Naiades cantrainii* and *Lagisca hubrechti*.

Lagisca hubrechti

(Text-fig. 51, Table 33)

L. hubrechti was found in thirteen samples from six stations in the Sub-Tropical Zone and in one sample in the Antarctic Zone. This species varies in length between 5–22 mm. and could have been caught by most nets.

At St. 100, *L. hubrechti* was collected in South Atlantic Central Water, Antarctic Intermediate Water and also in the Warm Deep Layer, and it occurs more frequently in the deeper waters at the other stations made in the Sub-Tropical Zone. The single record of *L. hubrechti* from the Antarctic Zone cannot be considered an anomaly because our knowledge of the pelagic Polynoinae is limited to comparatively few records of several species which may represent pelagic phases of bottom living forms and it is possible that *L. hubrechti* is one of these. More information on the life cycle of this species is necessary before its distribution can be analysed.

Table 33. *Occurrence of* Lagisca hubrechti

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Antarctic	169	1100–1000	TYF	1	Sub-Tropical	100	2500–2000	TYF	15
Sub-Tropical	100	225	TYF	6			2500(–0)	TYF	11
		475(–0)	TYF	3		256	1100–850(–0)	TYF	3
		550–450	TYF	5		267	**550–450(–0)**	TYF	1
		675–625	TYF	6		2029	2900–2600	TYFB	1
		1000–300	TYF	1		2630	**1050–550**	TYFB	1
		1000–900	TYF	1		2632	**1800–0** ?	TYFB	1

Previous records. Monro (1930) reported *L. hubrechti* from 'Discovery' collections in the Antarctic Zone (St. 169, as above) and in the Sub-Tropical Zone.

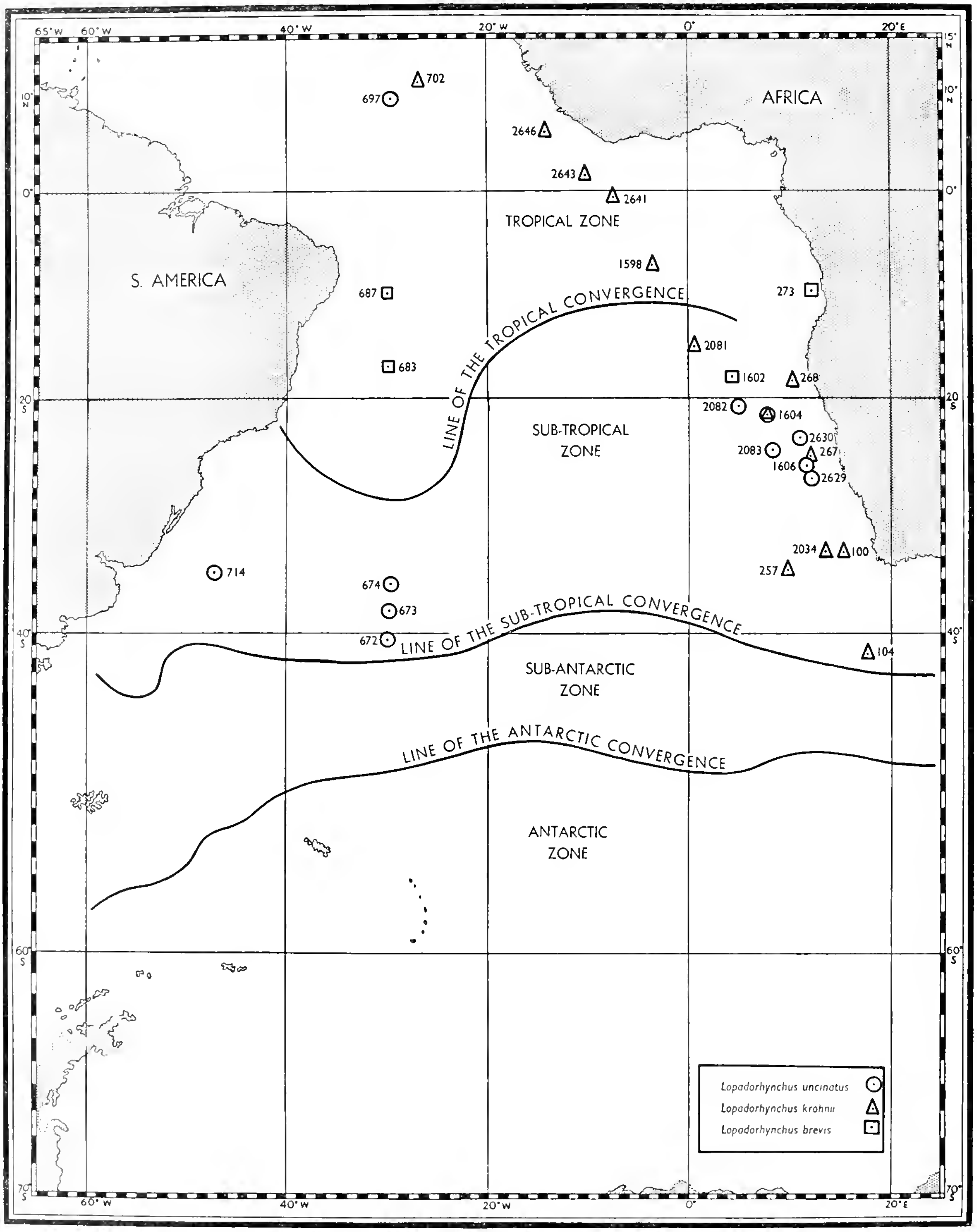
Lopadorhynchus uncinatus, *Lopadorhynchus krohnii* and *Lopadorhynchus brevis*

(Text-fig. 52, Table 34)

L. uncinatus and *L. krohnii* were collected at numerous stations north of the Sub-Tropical Convergence and it is evident that they are limited in their southerly distribution by this barrier; *L. brevis* was collected at only four stations, all north of the Sub-Tropical Convergence and it is possible that this species also is limited by this barrier, but the records are too few to warrant drawing firm conclusions about its distribution. *L. uncinatus* measures between 13–24 mm. in length, *L. krohnii* between 5–10·5 mm. and *L. brevis* 7–20 mm.; normally all three could be caught by the N 70 nets and *L. uncinatus* and *L. brevis* could also be collected by the N 100 and TYF.

In the Sub-Tropical Zone *L. uncinatus* was collected in either the South Atlantic Central Water or Antarctic Intermediate Water at Sts. 714, 672, 673, 674, 1604, 2083 and 1606; in Antarctic Intermediate Water at Sts. 2082 and 2630; and in this layer or in the Warm Deep Water at St. 2629. In the Tropical Zone the net which caught it at St. 697, fished in both Tropical Surface Water and South Atlantic Central Water.

L. krohnii was collected in the Sub-Tropical Zone in South Atlantic Central Water at Sts. 104, 257, 268, 2034, 1604 and 2081 and in Warm Deep Water at Sts. 100 (2500–2000 m.). At St. 100 (475–0 m.) it was caught in either South Atlantic Central Water or Antarctic Intermediate Water. In the Tropical Zone *L. krohnii* was collected in Tropical Surface Water or South Atlantic Central



Text-fig. 52. Occurrence of *Lopadorhynchus uncinatus*, *L. krohnii* and *L. brevis*.

Water at Sts. 702, 2643 and 2641, in Antarctic Intermediate Water or South Atlantic Central Water at St. 1598, and in Warm Deep Water or Antarctic Intermediate Water at St. 2646.

L. brevis was collected in South Atlantic Central Water at St. 1602 in the Sub-Tropical Zone and at Sts. 273 and 687 in the Tropical Zone. At St. 683 it was collected in either Tropical Surface Water or South Atlantic Central Water.

Table 34. *Occurrence of* Lopadorhynchus uncinatus, krohnii *and* brevis

Occurrence of Lopadorhynchus uncinatus

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	672	200–0	TYFB	1	Sub-Tropical	2082	1100–800	TYFB	1
	673	340–0	TYFB	1		2083	**330–0**	TYFB	7
	674	**280–0**	TYFB	1		2629	**1800–1300**	TYFB	1
	714	**246–0**	TYFB	1		2630	**1050–550**	TYFB	1
	1604	**182–0**	TYFB	2	Tropical	697	**460–0**	TYFB	1
	1606	**190–0**	TYFB	3					

Occurrence of Lopadorhynchus krohnii

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*	*Zone*	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	100	475(–0)	TYFB	1	Sub-Tropical	2034	**5–0**	N 100 H	1
		2500–2000	TYFB	1		2081	950–500	TYFB	1
	104	5–0	N 100 H	1	Tropical	702	**236–0**	TYFB	1
	257	**250(–0)**	TYF	1		1598	**460–300**	TYFB	6
	267	**550–450(0)**	TYF	3		2641	**100–0**	N 50 V	1
	268	**150–100(–0)**	TYF	2		2643	**100–0**	N 50 V	1
	1604	**620–500**	TYFB	1		2646	**1500–800**	TYFB	1

Occurrence of Lopadorhynchus brevis

Zone	*Station no.*	*Depth (m.)*	*Net*	*No. of specimens*
Sub-Tropical	1602	**175–0**	TYFB	1
Tropical	273	**230–200(–0)**	TYF	1
	683	**290–0**	TYFB	1
	687	500–250	TYFV	1

Previous records. L. uncinatus was reported by Monro (1936) from St. 714 as listed above, and he also records *L. krohnii* in the same paper from St. 702 as *L. krohnii* var. *simplex*. Reibisch (1895) records *L. krohnii* as *L. viguieri* from near the Equator, and Friedrich (1950*c*) notes its presence in the 'Meteor' collections; *L. brevis* was collected by the Deutsche Südpolar Expedition in the Tropical Zone of the South Atlantic (Ehlers, 1913) and Monro (1930) recorded it from St. 273.

ZOOGEOGRAPHICAL REVIEW

It has long been known that the total plankton production is greater in higher latitudes than in the tropics and successive expeditions have established that this is especially true of the South Atlantic (Friedrich, 1950*b*; Foxton, 1956). Except off the south-west coast of Africa where the effect of the cold Benguela current is dominant, the total number of plankton organisms in the top 50 m. of water is at least ten times greater in the Antarctic Zone than in the Sub-Tropical and Tropical Zones [Hentschel (1933); Sverdrup, Johnson and Fleming (1946)]. The total plankton collected in summer between 1000–0 m. by seven expeditions has been compared by Foxton (1956) who found the ratio of the amount collected in the higher latitudes to that in the lower to vary between 14:1 (Meteor) to 4·5:1 (Discovery). Only a few species, occurring in large numbers, make up the abundant plankton in the upper 150 m. of water in the Antarctic Zone (Hardy and Gunther, 1935), whereas in the Sub-Tropical and Tropical Zones many species form the small standing crop (Sverdrup, Johnson and Fleming, 1946).

The twenty-nine polychaetes examined in this report conform to this general pattern of plankton distribution. The most abundant is the cosmopolitan *Pelagobia longicirrata* which occurs in large numbers in the Antarctic Zone. This species is particularly abundant along the Greenwich Meridian in the top 100 m. of water and around South Georgia between 250–50 m. The endemic antarctic *Rhynchonerella bongraini* is also abundant but being more restricted in its distribution than *Pelagobia longicirrata* has not been collected so extensively. The nine other species inhabiting the Antarctic Zone do not appear in large numbers; seven of them are cosmopolitan or widely distributed. Sixteen species appear to be limited in their southerly distribution by the Sub-Tropical Convergence but none of them occurs in abundance. Only the cosmopolitan *Tomopteris septentrionalis* and *T. planktonis* have been collected in large numbers in the Sub-Tropical Zone off South Africa in a region where intensive collections were made.

The following points of interest have emerged from the present survey:

1. There are no families of pelagic Polychaeta endemic to any hydrological zone in the South Atlantic Ocean.

2. There are no endemic genera of pelagic Polychaeta in the Antarctic Zone.

3. The following three species of pelagic Polychaeta are endemic to the Antarctic Zone:[1]

Rhynchonerella bongraini, *Vanadis antarctica*, *Tomopteris carpenteri*.

Rhynchonerella bongraini was collected only in the top 500 m. of water in the Antarctic Zone within the Weddell Drift, East Wind Drift and the upper layers of the Warm Deep Water.

Vanadis antarctica probably occurs in all water masses in the Antarctic Zone. It is very similar, morphologically, to *V. longissima* and with it may represent two geographical races of one species.

Adult *Tomopteris carpenteri* were found in all explored water masses of the Antarctic Zone. The smallest specimens of this species, however, were collected only around South Georgia.

4. In addition to *Tomopteris carpenteri*, two other species of tomopterids are known from the Antarctic Zone; *T. planktonis* and *T. septentrionalis*. All three species are very closely related and it is possible that the endemic *T. carpenteri* has evolved from one of the others (both cosmopolitan) as an isolated antarctic form. None of these species has a first pair of chaetigers, rosette glands, spur glands or a tail.

5. There are no endemic species of pelagic Polychaeta in the Sub-Antarctic Zone[2], and no species appears to have its northern limit of distribution at the Sub-Tropical Convergence.

6. *Vanadis longissima* is the only species (or geographical race of a species) of pelagic Polychaeta with its southern limit of distribution at the Antarctic Convergence; it was collected only in the Sub-Antarctic, Sub-Tropical and Tropical Zones.

7. The genera *Krohnia*, *Alciopa*, *Naiades* and *Lopadorhynchus* have not been collected south of the Sub-Tropical Convergence; they may be confined to warmer waters.

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[1] *Antinoë pelagica* Monro, 1930, is known only from two records in the Antarctic Zone; these are insufficient to warrant listing this species as endemic.

[2] *Tomopteris kempi* was collected only at St. 4 very close to the Sub-Tropical Convergence, either in the Sub-Tropical or Sub-Antarctic Zone. If future collections show it to be confined to the latter it will be the only known endemic Sub-Antarctic pelagic polychaete.

8. The following species have been found only to the north of the Sub-Tropical Convergence. It is evident that most of them, and probable that all of them, are limited to the south by this boundary though the evidence is not conclusive for some of the scarcer species: *Tomopteris ligulata*, *T. krampi*, *T. elegans*, *T. apsteini*, *T. nisseni*, *Vanadis formosa*, *V. crystallina*, *Rhynchonerella angelini*, *Krohnia lepidota*, *Alciopa reynaudii*, *Naiades cantrainii*, *Travisiopsis lobifera*, *T. lanceolata*, *Lopadorhynchus brevis*, *L. uncinatus*, *L. krohnii*.

All these species have also been reported from the North Atlantic Ocean, where the majority of them appear to be restricted in their northerly distribution by a surface hydrological boundary, the Secondary Polar Front or Labrador Front (Böhnecke, 1938), approximating to the Sub-Tropical Convergence in the South Atlantic. Böhnecke distinguished the Secondary Polar Front by a temperature of 15° C. in summer and 9° C. in winter, extending along the cold-wall region in the left bank of the Gulf Stream to approximately 53° N. in 30° W. To the east of this position, around the British Isles and North-west Europe, the disposition of the land masses makes it difficult to distinguish a convergence.[1]

Collections from the North Atlantic Ocean have not been available in quantity for examination, but in addition to the material in the British Museum (Nat. Hist.) reported by Monro (1939*a*), I have consulted the work of the following authors, who have recorded pelagic polychaetes from near the Secondary Polar Front and/or north of it about the Polar Front: Reibisch (1895), Apstein (1900), Huntsman (1921), Wesenberg-Lund (1935, 1936), Treadwell (1943, 1948), Stop-Bowitz (1948), Wesenberg-Lund (1950*b*, 1953), Grainger (1954).

In these references I can find no record of the following species from north of the Secondary Polar Front in the North Atlantic Ocean: *Tomopteris ligulata*, *T. elegans*, *T. apsteini*, *Vanadis formosa*, *V. crystallina*, *Krohnia lepidota*, *Alciopa reynaudii*, *Naiades cantrainii*, *Travisiopsis lobifera*, *Lopadorhynchus uncinatus*, *L. brevis*, *L. krohnii*.

The water circulation in the North Atlantic Ocean is much more complicated than south of the Equator, but although I have made no attempt to interpret distribution in depth, it is significant that these species are restricted by somewhat similar surface hydrological conditions to those which limit their movement in the South Atlantic Ocean.

The remaining species, *Tomopteris nisseni*, *T. krampi*, *Rhynchonerella angelini*, and *Travisiopsis lanceolata* range northwards beyond the Secondary Polar Front in the North Atlantic Ocean—in brief this front is no barrier to them. No endemic pelagic polychaetes are known from arctic waters, which implies that there is a constant influx of more southerly populations maintaining the homogeneity of the species over a wide area and preventing the evolution of endemic forms. It is possible therefore that the endemic antarctic *Tomopteris carpenteri* may be represented in the arctic fauna by *T. nisseni* and *T. krampi*. Similarly the endemic antarctic *Rhynchonerella bongraini* corresponds to *R. angelini*. Likewise, although the genus *Travisiopsis* is not represented by an endemic species in the Antarctic Zone the species *T. coniceps* occurs only in southern waters and its corresponding species in arctic waters is *T. lanceolata*.

9. The following species were collected in all hydrological zones in the South Atlantic Ocean: *Tomopteris planktonis*, *T. septentrionalis*, *Typhloscolex mülleri*, *Travisiopsis levinseni*, *Pelagobia longicirrata*.

Of these, *Tomopteris planktonis*, *T. septentrionalis* and *Travisiopsis levinseni* were collected in all explored water masses but never in abundance. Many more samples are needed before their distribution can be accurately analysed.

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[1] East of 53° N., 30° W., where no clear boundary can be distinguished, Southern (1911) has reported *Vanadis formosa* from stations with surface temperatures between 12° and 16·3° C. and *Alciopa reynaudii* as *Greefia celox* from stations with surface temperatures between 10·5 to 11·15° C.

Typhloscolex mülleri was collected throughout the year in the Antarctic Deep Water, migrating to depth in winter. A few records from the surface layers in summer suggest that at this season this species may also inhabit the Weddell Drift. In the Sub-Antarctic Zone *T. mülleri* was collected in Antarctic Intermediate Water and Warm Deep Water; and in the Sub-Tropical and Tropical Zones in South Atlantic Central Water, Antarctic Intermediate Water and possibly in Tropical Surface Water.

Pelagobia longicirrata was collected in all explored water masses of the South Atlantic, except in Sub-Antarctic Surface Water north of 45° S. on the Greenwich Meridian. In the Antarctic and Sub-Antarctic Zones, this species was collected in abundance in summer, from depths of 100 m. to the surface, between the Ice Edge and 45° S., where a minor boundary seems to limit its northerly movement. Deacon (1945) has suggested that this boundary separates well-mixed water in the southern half of the Sub-Antarctic Zone from more stably stratified water in the northern half; it may segregate a southern population of *Pelagobia longicirrata* which inhabits the surface layers for feeding (and/or breeding) purposes. In the Antarctic and Sub-Antarctic Zones, *P. longicirrata* migrates to depth in winter.

10. The following species are widespread in distribution, but were never collected in abundance. More collections are required before their distribution can be comprehensively analysed: *Maupasia caeca*, *Travisiopsis coniceps*, *Lagisca hubrechti*.

11. *Circulation*. It has been repeatedly found throughout this work that species which occur at depth are limited in their distribution by surface hydrological boundaries. Restriction in range may be maintained by migration between water masses moving in opposite directions. Throughout the Sub-Tropical and Tropical Zones, species which were not collected south of the Sub-Tropical Convergence could remain in this environment by migrating between southerly flowing South Atlantic Central Water, northerly flowing Antarctic Intermediate Water and/or southerly moving Warm Deep Water. Observations on the life histories of these species would help in understanding their distribution. Surface currents throughout these zones set up an anti-clockwise circulation which would also restrict the southerly movement of the species.

It is probable that most cosmopolitan pelagic polychaetes enter the Antarctic and Sub-Antarctic Zones in the southerly moving Warm Deep Water. Vertical migration in the Antarctic Zone to Antarctic Surface Water together with movement within this layer, until it sinks to form the northerly flowing Antarctic Intermediate Water, would allow these species to circulate throughout the South Atlantic. Within the Antarctic Zone a closed circulation between Antarctic Surface Water and Warm Deep Water is the simplest explanation of zonal movement, but endemic antarctic species and antarctic populations of cosmopolitan species are undoubtedly affected by much more complex circumpolar influences.

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APPENDIX I

VERTICAL N 70 V NETS ONLY

N.B. Depths in heavy type indicate hauls made between sunset and sunrise. Samples sorted by the staff of the N.I.O. and recorded on the Plankton Analysis Sheets. The tables include all the species collected except *Maupasia caeca* (see p. 242) and *Travisiopsis coniceps* (see p. 245).

Table *a*. R.R.S. 'William Scoresby'. Sts. WS 137–143, Falkland Islands to South Georgia. Sts. WS 144–190, South Georgia Survey, February–March 1928.

Table *b*. R.R.S. 'Discovery II'. Sts. 300–358, South Georgia Survey, January–February 1930.

Table *c*. R.R.S. 'Discovery II'. 0° Line: Sts. 1772–1782, May–June 1936. Sts. 2010–2027, March–April 1937. Sts. 2311–2322, April 1938. Sts. 2355–2501, July–December 1938. Sts. 2530–2547, January 1939.

Table *a*. *R.R.S. 'William Scoresby'. Sts. WS 137–143, Falkland Island to South Georgia. Sts. WS 144–190, South Georgia survey, February–March 1928*

Station no., date and position	*Depth* (*m.*)	Rhynchonella bongraini	Pelagobia longicirrata	Tomopteris carpenteri (*juvenile*)	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiable*)	Typhloscolex mülleri	Travisiopsis levinseni
St. WS 137, 8–9. ii. 28	**50–0**	—	3	—	—	—	—	—	—
52° 08′ 00″ S., 54° 55′ 00″ W.	**100–50**	—	9	—	—	—	14	—	—
	250–90	—	6	—	—	—	18	—	—
	500–250	—	—	—	3	—	—	—	—
	750–500	—	—	—	—	—	—	—	—
	1000–750	—	4	—	—	—	2	2	1
St. WS 138, 9. ii. 28	50–0	—	—	—	—	—	—	—	—
52° 36′ 00″ S., 52° 16′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	5	—	2	—	—	—	—
	500–250	—	12	—	—	—	7	—	—
	750–390	—	—	—	—	—	—	—	—
	1000–710	—	8	—	1	—	—	3	—
St. WS 139, 10. ii. 28	50–0	—	1	—	—	—	—	—	—
53° 00′ 00″ S., 49° 50′ 00″ W.	100–50	—	13	—	1	—	—	1	—
	250–100	—	5	—	1	—	—	—	—
	500–200	—	10	—	—	—	—	3	—
	750–500	—	2	—	—	—	—	1	—
St. WS 140, 11. ii. 28	50–0	—	3	—	—	—	—	—	—
53° 17′ 00″ S., 47° 02′ 00″ W.	100–50	—	39	—	—	—	—	1	—
	250–90	—	—	—	—	—	—	—	—
	500–250	—	7	—	—	—	—	—	—
	750–460	—	—	—	—	—	—	1	—
	1000–750	—	9	—	—	—	—	2	—
St. WS 141, 13. ii. 28	50–0	—	—	—	—	—	—	—	—
53° 32′ 00″ S., 44° 52′ 00″ W.	100–50	—	11	—	—	—	—	—	—
	250–100	—	149	—	—	—	—	—	—
	500–250	—	60	3	1	—	—	—	—
	750–490	—	3	1	—	—	—	7	—
	1000–750	—	30	—	—	—	3	—	1
St. WS 142, 14. ii. 28	50–0	—	—	—	—	—	—	—	—
53° 33′ 00″ S., 42° 03′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	210–100	—	—	—	—	—	—	—	—
St. WS 143, 14–15. ii. 28	**50–0**	—	—	—	—	—	—	—	—
53° 58′ 00″ S., 40° 30′ 00″ W.	**100–50**	—	—	—	—	—	—	—	—
[Sts. WS 137 to WS 142 are	**250–100**	—	19	—	—	—	—	—	—
between the Falkland Islands	**500–240**	—	10	—	—	—	—	—	—
and South Georgia]	**750–470**	—	6	5	—	—	—	4	2
	1000–710	—	5	—	—	1	1	1	—

Table *a* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris carpenteri (*juvenile*)	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiable*)	Typhloscolex mülleri	Travisiopsis levinseni
St. WS 144, 19. ii. 28	50–0	—	—	—	—	—	—	—	—
54° 08′ 00″ S., 36° 10′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	270–100	—	—	—	—	—	—	—	—
St. WS 145, 19. ii. 28	50–0	—	—	—	—	—	—	—	—
54° 00′ 00″ S., 36° 00′ 00″ W.	100–50	—	1	—	—	—	—	—	—
	275–100	1	12	—	—	—	—	—	—
St. WS 146, 19. ii. 28	50–0	—	—	—	—	—	—	—	—
53° 50′ 00″ S., 35° 50′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	1	1	—	—	—	—	—
	500–250	1	—	—	—	—	—	—	—
	750–500	—	1	—	—	1	2	2	—
	1000–750	—	3	—	—	—	1	—	—
St. WS 147, 21. ii. 28	**50–0**	—	—	—	—	—	—	—	—
53° 50′ 00″ S., 35° 50′ 00″ W.	**100–50**	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
St. WS 149, 22. ii. 28	50–0	—	—	—	—	—	—	—	—
53° 32′ 00″ S., 35° 22′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	1	—	—	—	—	—	—	—
	500–250	—	2	—	—	—	—	—	—
	750–500	—	3	—	—	—	1	2	—
	1000–750	—	9	—	—	—	—	—	—
St. WS 151, 22. ii. 28	50–0	—	—	—	—	—	—	—	—
53° 17′ 00″ S., 35° 08′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	—	—	—
	750–450	—	10	—	1	—	—	13	—
	1000–750	—	6	—	—	—	1	—	—
St. WS 154, 26. ii. 28	50–0	—	—	—	—	—	—	—	—
54° 00′ 00″ S., 36° 52′ 00″ W.	100–50	—	—	—	—	—	—	2	—
St. WS 156, 26. ii. 28	**50–0**	—	—	—	—	—	—	—	—
53° 40′ 00″ S., 36° 52′ 00″ W.	**100–50**	—	—	—	—	—	—	—	—
	200–100	—	3	—	—	—	—	—	—
St. WS 158, 27. ii. 28	50–0	—	—	—	—	—	—	—	—
53° 20′ 00″ S., 36° 52′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	2	—	—	—	—	—	—
	500–250	—	—	—	—	—	—	3	—
St. WS 160, 27. ii. 28	50–0	—	—	—	—	—	—	—	—
53° 00′ 00″ S., 36° 52′ 00″ W.	100–50	—	8	—	—	—	—	—	—
	250–100	—	2	1	—	—	—	—	—
	500–250	—	2	—	—	—	—	1	—
St. WS 163, 29. ii. 28	50–0	—	—	—	—	—	—	—	—
53° 54′ 00″ S., 38° 18′ 00″ W.	80–50	—	20	—	—	—	—	—	—
St. WS 164, 29. ii. 28	**50–0**	—	—	—	—	—	—	—	—
53° 49′ 00″ S., 38° 32′ 00″ W.	**100–50**	—	1	—	—	—	—	—	—
	140–100	—	2	—	—	—	—	—	—
St. WS 165, 1. iii. 28	**50–0**	—	—	—	—	—	—	—	—
53° 44′ 00″ S., 38° 46′ 00″ W.	**100–50**	—	25	—	—	—	—	—	—
	150–100	—	11	—	—	—	—	—	—
St. WS 166, 1. iii. 28	50–0	—	—	—	—	—	—	—	—
53° 36′ 00″ S., 39° 08′ 00″ W.	100–50	—	1	—	—	—	—	—	—
	140–100	—	—	—	—	—	—	—	—

Table *a* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris carpenteri (*juvenile*)	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiable*)	Typhloscolex mülleri	Travisiopsis levinseni
St. WS 167, 1. iii. 28	50–0	—	—	—	—	—	—	—	—
53° 31′ 00″ S., 39° 22′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	3	1	—	—	—	1	—
	460–250*	—	—	—	—	—	—	1	—
St. WS 168, 1. iii. 28	50–0	—	—	—	—	—	—	—	—
53° 26′ 00″ S., 39° 36′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
St. WS 169, 6. iii. 28	50–0	—	—	—	—	—	—	—	—
54° 36′ 00″ S., 35° 40′ 00″ W.	100–50	—	—	—	—	—	—	—	—
St. WS 171, 6. iii. 28	50–0	—	—	—	—	—	—	—	—
54° 36′ 00″ S., 35° 00′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	1	—	—	—	—	—
St. WS 173, 6–7. iii. 28	50–0	—	—	—	—	—	—	—	—
54° 36′ 00″ S., 34° 25′ 00″ W.	100–50	—	1	—	—	—	—	—	—
	250–100	—	14	—	—	—	—	—	—
	500–250	—	4	—	—	—	—	—	—
St. WS 175, 7. iii. 28	50–0	—	—	—	—	—	—	—	—
54° 36′ 00″ S., 33° 50′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	—	—	—
St. WS 178, 7. iii. 28	50–0	—	—	—	—	—	—	—	—
10 miles S.E., of Cooper Island	100–50	—	—	—	—	—	—	—	—
St. WS 179, 7. iii. 28	50–0	—	—	—	—	—	—	—	—
55° 08′ 00″ S., 35° 20′ 00″ W.	100–50	—	—	—	—	—	—	—	—
St. WS 180, 7. iii. 28	50–0	—	—	—	—	—	—	—	—
55° 18′ 00″ S., 35° 10′ 00″ W.	100–50	—	7	—	—	—	—	—	—
St. WS 182, 8. iii. 28	50–0	—	—	—	—	—	—	—	—
55° 30′ 00″ S., 34° 50′ 00″ W.	100–50	—	6	—	—	—	—	—	—
	250–100	—	8	—	—	—	—	—	—
	500–250	—	1	1	—	—	—	—	—
	750–520	—	—	—	—	—	—	—	—
	1000–750	—	20	—	—	—	2	—	—
St. WS 189, 9. iii. 28	50–0	—	—	—	—	—	—	—	—
53° 30′ 00″ S., 38° 35′ 00″ W.									
St. WS 190, 10. iii. 28	50–0	—	—	—	—	—	—	—	—
55 miles N.W. of Bird Island	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	—	—	—
	750–500	—	—	—	—	—	—	1	—
	750–0†	2	—	—	—	—	—	3	—
	1000–0†	4	—	—	—	—	—	1	—

* One adult *T. carpenteri.*

† Depths from Plankton Analysis Sheets, not from Station Lists.

Table *b*. *R.R.S. 'Discovery II'. Sts. 300–358, South Georgia survey, January–February 1930*

Station no., date and position	*Depth (m.)*	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris carpenteri (*juvenile*)	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiable*)	Typhloscolex mülleri	Travisiopsis levinseni
St. 300, 20. i. 30	50–0	—	—	—	—	—	—	—	—
52° 26′ 30″ S., 37° 14′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	13	1	—	—	2	1	—
	750–500	—	14	—	—	—	—	2	—
	1000–750	—	7	—	—	—	—	—	—
St. 301, 20–21. i. 30	**50–0**	—	—	—	—	—	—	—	—
52° 36′ 30″ S., 37° 14′ 00″ W.	**100–50**	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	5	1	—	1	5	2	—
	750–500	—	12	—	1	—	3	—	—
	1000–750	—	5	—	—	1	—	1	—
St. 302, 21. i. 30	50–0	—	—	—	—	—	—	—	—
52° 46′ 30″ S., 37° 12′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	5	1	—	—	—	—	—
	500–250	—	6	—	—	—	3	1	—
	750–500	—	10	—	—	—	5	4	—
	1000–750	—	8	—	—	—	2	1	—
St. 303, 21. i. 30	50–0	—	—	—	—	—	—	—	—
53° 00′ 00″ S., 37° 11′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	7	—	—	—	3	1	—
	750–500	—	39	—	—	—	—	2	—
	1000–750	—	26	—	—	—	1	—	—
St. 304, 21. i. 30	50–0	—	—	—	—	—	—	—	—
53° 06′ 00″ S., 37° 14′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	2	—	—	—	—	1	—
	750–500	—	11	—	—	—	2	2	—
	1000–750	—	21	—	—	—	—	—	—
St. 305, 21–22. i. 30	**50–0**	—	—	—	—	—	—	—	—
53° 17′ 00″ S., 37° 10′ 00″ W.	**100–50**	—	—	—	—	—	1	—	—
	250–100	—	—	—	—	—	1	—	—
	500–250	—	8	—	—	—	1	1	—
	750–500	—	9	—	—	—	2	—	—
	1000–750	—	8	—	—	—	2	—	—
St. 306, 22. i. 30	**50–0**	—	—	—	—	—	—	—	—
53° 28′ 00″ S., 37° 07′ 00″ W.	**100–50**	—	1	—	—	—	—	—	—
	250–100	—	1	—	—	—	—	—	—
	500–250	—	5	—	—	—	—	1	—
	750–500	—	16	—	—	—	1	1	—
St. 307, 22. i. 30	50–0	—	—	—	—	—	—	—	—
53° 36′ 00″ S., 37° 04′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	180–100	—	12	—	—	—	—	—	—
St. 308, 24. i. 30	50–0	—	—	—	—	—	—	—	—
54° 07′ 15″ S., 36° 24′ 30″ W.	100–50	—	4	—	—	—	—	—	—
St. 309, 24. i. 30	50–0	—	8	—	—	—	—	—	—
54° 00′ 30″ S., 36° 12′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	240–100	—	74	—	—	—	—	—	—
St. 310, 24. i. 30	50–0	—	—	—	—	—	—	—	—
53° 53′ 30″ S., 36° 00′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	145–100	—	—	—	—	—	—	—	—

Table *b* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris carpenteri (*juvenile*)	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiable*)	Typhloscolex mülleri	Traviopsis levinseni
St. 311, 24. i. 30	50–0	—	—	—	—	—	—	—	—
53° 47′ 00″ S., 35° 48′ 30″ W.	100–50	—	6	—	—	—	—	—	—
	250–100	—	12	—	—	—	—	—	—
	500–250*	—	—	—	—	—	—	—	—
	690–500	—	69	—	—	—	—	—	—
St. 312, 24–25. i. 30	**50–0**	—	—	—	—	—	—	—	—
53° 39′ 45″ S., 35° 37′ 30″ W.	**100–50**	—	—	—	—	—	—	—	—
	220–100	—	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	—	—	—
St. 313, 25. i. 30	50–0	—	—	—	—	—	—	—	—
53° 32′ 30″ S., 35° 24′ 30″ W.	100–50	—	48†	1†	—	—	2†	—	—
	250–100	—	19	1	1	—	3	—	—
	500–250	—	4	—	—	—	—	1	—
	750–500	—	2	—	1	—	—	—	—
	1000–750	—	1	—	—	—	—	—	—
St. 314, 29. i. 30	50–0	—	—	—	—	—	—	—	—
53° 56′ 00″ S., 37° 14′ 00″ W.	100–50	—	2	—	—	—	—	—	—
St. 315, 29. i. 30	50–0	—	—	—	—	—	—	—	—
53° 46′ 00″ S., 37° 14′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	150–100	—	58†	1†	—	—	—	—	—
St. 316, 29. i. 30	50–0	—	—	—	—	—	—	—	—
53° 54′ 30″ S., 38° 01′ 00″ W.	100–50	—	12	—	—	—	—	—	—
St. 317, 29. i. 30	50–0	—	—	—	—	—	—	—	—
53° 47′ 15″ S., 38° 12′ 30″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	20	—	—	—	—	—	—
St. 318, 29. i. 30	50–0	—	—	—	—	—	—	—	—
53° 39′ 00″ S., 38° 24′ 30″ W.	100–50	—	—	—	—	—	—	—	—
	150–100	—	28‡	—	—	—	—	—	—
St. 319, 29–30. i. 30	**50–0**	—	—	—	—	—	—	—	—
53° 37′ 00″ S., 38° 39′ 30″ W. to	**100–50**	—	—	—	—	—	—	—	—
53° 33′ 30″ S., 38° 37′ 00″ W.	**250–100**	—	—	—	—	—	—	1	—
	500–250	—	—	—	—	—	9	1	—
	750–500	—	—	—	—	—	—	—	—
	1000–750	—	—	—	1	—	—	—	—
St. 320, 30. i. 30	50–0	—	—	—	—	—	—	—	—
53° 10′ 30″ S., 39° 44′ 30″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	4	—	—	—	—	—	—
	500–250	—	—	—	—	—	—	1	—
	750–500	—	1	—	—	—	—	—	—
	1000–750	—	—	—	—	—	—	—	—
St. 321, 30–31. i. 30	**50–0**	—	—	—	—	—	—	—	—
53° 17′ 00″ S., 39° 31′ 00″ W.	**100–50**	—	—	—	—	—	1	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	—	2	—
	750–500	—	3	—	—	—	1	1	—
	1000–750	—	1	—	—	—	—	—	—
St. 322, 31. i. 30	50–0	—	—	—	—	—	—	—	—
53° 24′ 30″ S., 39° 17′ 30″ W. to	100–50	—	—	—	—	—	—	—	—
53° 27′ 00″ S., 29° 22′ 00″ W.	250–100	—	1	—	—	—	—	1	—
	500–250	—	—	—	—	—	1	1	—
	750–500	—	7	—	1	—	—	—	—
	1000–750	—	3	—	—	—	—	—	—

Table *b* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris carpenteri (*juvenile*)	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiable*)	Typhloscolex mülleri	Traviosiopsis levinseni
St. 323, 31. i. 30	50–0	—	—	—	—	—	—	—	—
53° 28′ 00″ S., 38° 55′ 00″ W. to	100–50	—	—	—	—	—	—	—	—
53° 29′ 00″ S., 38° 55′ 30″ W.	250–100	1	—	—	—	—	1	—	—
	500–250	—	3	—	1	—	1	1	—
	750–500	—	10	—	—	—	—	—	—
	1000–750	—	1	—	—	—	1	—	—
St. 324, 1. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 56′ 00″ S., 39° 57′ 00″ W. to	100–50	—	2†	—	—	—	—	—	—
54° 56′ 00″ S., 40° 01′ 00″ W.	250–100	—	3†	—	—	—	—	—	—
	500–250	—	14†	—	—	—	1†	1†	—
	750–500	—	2†	—	—	—	1†	—	—
	1000–750	—	14†	—	—	—	1†	1†	—
St. 325, 1. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 53′ 00″ S., 39° 40′ 00″ W. to	100–50	—	—	—	—	—	—	—	—
54° 51′ 00″ S., 39° 37′ 00″ W.	250–100	—	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	1	1	—
	750–500	—	2	—	—	—	—	1	—
	1000–750	—	2	—	—	—	1	—	—
St. 326, 2. ii. 30	**50–0**	—	—	—	—	—	—	—	—
54° 33′ 00″ S., 38° 29′ 30″ W. to	**100–50**	—	—	—	—	—	—	—	—
54° 32′ 30″ S., 38° 21′ 00″ W.	**200–100**	—	3	—	—	—	—	—	—
St. 327, 2. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 26′ 30″ S., 38° 06′ 00″ W. to	100–50	—	—	—	—	—	—	—	—
54° 25′ 00″ S., 38° 03′ 00″ W.	200–100	—	—	—	—	—	—	—	—
St. 328, 2. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 20′ 30″ S., 37° 42′ 30″ W.	100–50	—	—	—	—	—	—	—	—
St. 331, 2. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 40′ 00″ S., 38° 52′ 30″ W.	100–50	—	4	—	—	—	—	—	—
	200–100	—	11†	—	—	—	1†	—	—
St. 332, 2–3. ii. 30	**50–0**	—	—	—	—	—	—	—	—
54° 44′ 30″ S., 39° 09′ 00″ W.	**100–50**	—	—	—	—	—	—	—	—
	250–100	—	3	—	1	2	—	—	—
St. 333, 3. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 48′ 30″ S., 38° 24′ 30″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	3†	—	—	—	2†	1†	—
St. 334, 4. ii. 30	50–0	—	—	—	—	—	—	—	—
55° 43′ 00″ S., 36° 51′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	6	—	—	—	—	—	—
	750–500	—	11	—	—	—	1	—	—
	1000–750	—	5	—	—	—	—	—	—
St. 335, 4–5. ii. 30	**50–0**	—	—	—	—	—	—	—	—
55° 33′ 00″ S., 36° 49′ 30″ W.	**100–50**	—	1	—	—	—	1	—	—
	250–100	—	27	1	—	—	—	—	—
	500–250	—	9	—	—	—	—	2	—
	750–500	—	1	—	—	—	—	—	—
	1000–0	—	14†	—	—	—	—	—	—
St. 336, 5. ii. 30	50–0	—	—	—	—	—	—	—	—
55° 21′ 30″ S., 36° 48′ 30″ W. to	100–50	—	11†	—	—	—	—	—	—
55° 20′ 00″ S., 36° 48′ 30″ W.	250–100	—	25§	—	—	—	2§	1§	—
	500–250	—	7	—	—	—	2	2	—
	750–500	—	11	—	1	—	—	—	—

Table *b* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris carpenteri (*juvenile*)	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiable*)	Typhloscolex mülleri	Traviopsis levinseni
St. 337, 5. ii. 30	50–0	—	—	1	—	—	—	—	—
55° 09′ 00″ S., 36° 48′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	45†	—	1†	—	—	—	—
	500–250	—	74	—	—	1	3	1	—
	750–500	—	7	—	—	—	1	—	—
	1000–750	—	41	—	—	—	—	—	—
St. 338, 5. ii. 30	50–0	—	2	—	—	—	1	—	—
55° 00′ 30″ S., 36° 46′ 00″ W.	100–50	—	9	—	—	—	1	—	—
	225–100	—	55	1	—	—	—	—	—
St. 339, 5. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 51′ 30″ S., 36° 44′ 30″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	38	1	—	—	—	—	—
St. 340, 5. ii. 30	**50–0**	—	—	—	—	—	—	—	—
54° 36′ 00″ S., 36° 40′ 30″ W.	**100–50**	—	—	—	—	—	—	—	—
St. 341, 5–6. ii. 30	**50–0**	—	—	—	—	—	—	—	—
54° 43′ 00″ S., 36° 42′ 30″ W.	**100–50**	—	13	—	—	—	—	—	—
	230–100	—	80	—	—	—	—	—	—
St. 342, 7. ii. 30	50–0	—	—	—	—	—	—	—	—
55° 47′ 00″ S., 34° 11′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	24	1	—	—	—	—	—
	750–500	—	11	—	—	—	—	1	—
St. 343, 7. ii. 30	50–0	—	—	—	—	—	—	—	—
55° 40′ 00″ S., 34° 23′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—	—
	500–250	—	5	1	1	—	1	—	1
St. 344, 7–8. ii. 30	**50–0**	—	1	—	—	—	—	—	—
55° 33′ 00″ S., 34° 35′ 30″ W. to	**100–50**	—	—	—	—	—	—	—	—
55° 29′ 30″ S., 34° 32′ 00″ W.	**250–100**	—	25†	1†	—	—	—	—	—
	500–250	—	7	—	1	—	—	—	—
	750–500	—	15	—	—	—	—	1	—
	1000–750	—	8	—	—	—	—	—	—
St. 345, 8. ii. 30	50–0	—	—	—	—	—	—	—	—
55° 20′ 00″ S., 34° 47′ 30″ W.	100–50	—	—	—	—	—	—	—	—
	180–100	—	3	—	—	—	2	—	—
St. 346, 8. ii. 30	50–0	—	—	—	—	—	—	—	—
55° 14′ 00″ S., 35° 02′ 00″ W.	100–50	—	—	—	—	—	—	—	—
St. 347, 8. ii. 30	50–0	—	—	—	—	—	—	—	—
55° 08′ 00″ S., 35° 14′ 30″ W.	100–50	—	—	—	—	—	—	—	—
St. 348, 8. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 53′ 30″ S., 35° 41′ 30″ W.	90–50	—	—	—	—	—	—	—	—
St. 349, 8. ii. 30	**50–0**	—	—	—	—	—	—	—	—
55° 01′ 00″ S., 35° 27′ 30″ W.	**100–50**	—	—	—	—	—	—	—	—
St. 350, 9. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 23′ 00″ S., 36° 00′ 00″ W.	100–50	—	—	—	—	—	—	—	—
St. 351, 9. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 21′ 30″ S., 35° 42′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	210–100	—	13	—	—	—	—	1	—
St. 352, 9. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 19′ 00″ S., 35° 24′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	190–100	—	15	—	—	—	—	—	—

Table *b* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris carpenteri (*juvenile*)	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiable*)	Typhloscolex mülleri	Travisiopsis levinseni
St. 353, 9. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 17′ 30″ S., 35° 06′ 00″ W.	100–50	—	—	—	—	—	—	—	—
	250–100	—	—	1	—	—	—	—	—
	500–250	—	3	1	—	—	—	1	—
	750–500	—	23	—	—	—	—	1	—
	1000–750	—	13	—	—	—	2	—	—
St. 354, 9. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 15′ 30″ S., 34° 47′ 30″ W. to	100–50	—	—	—	—	—	—	—	—
54° 13′ 15″ S., 34° 46′ 00″ W.	250–100	—	—	—	—	—	—	—	—
	500–250	—	—	—	1	—	—	—	—
	750–500	—	10	—	—	—	—	—	—
	1000–750	—	4	—	—	—	—	—	—
St. 355, 9–10. ii. 30	**50–0**	—	—	—	—	—	1	—	—
54° 13′ 30″ S., 34° 18′ 30″ W. to	**100–50**	—	1	—	1	—	—	—	—
54° 10′ 30″ S., 34° 16′ 30″ W.	**250–100**	—	77	1	2	—	—	1	—
	500–250	—	9	—	1	—	—	—	—
	750–500	—	16	—	—	1	—	—	—
	1000–750	—	6	—	—	—	—	—	—
St. 356, 10. ii. 30	50–0	—	—	—	—	—	—	—	—
54° 11′ 00″ S., 33° 49′ 00″ W. to	100–50	—	19†	—	—	—	—	—	—
54° 08′ 45″ S., 33° 47′ 30″ W.	250–100	—	9	4	—	—	3	—	—
	500–250	—	14	—	—	—	—	1	—
	750–500	—	11	—	—	—	—	1	—
	1000–750	—	—	—	—	—	—	—	—
St. 357, 10. ii. 30	50–0	—	—	—	—	—	—	—	—
53° 07′ 00″ S., 34° 48′ 00″ W. to	100–50	—	—	—	—	—	—	—	—
53° 07′ 30″ S., 34° 45′ 30″ W.	250–100	—	—	—	—	—	1	—	—
	500–250	—	2	—	—	—	—	1	—
	750–500	—	11	—	—	—	—	—	—
St. 358, 11. ii. 30	**50–0**	—	—	—	—	—	—	—	—
53° 16′ 30″ S., 35° 02′ 30″ W. to	**100–50**	—	—	—	—	—	—	—	—
53° 17′ 00″ S., 34° 58′ 00″ W.	**250–100**	—	—	—	—	—	—	—	—
	500–250	—	2	1	4	—	—	—	—
	750–500	—	7	—	1	—	—	—	—
	1000–750	—	14	—	—	—	1	—	—

* One adult *Tomopteris carpenteri*.

‡ Three-tenths of total sample.

† One-fifth of total sample.

§ Two-fifths of total sample.

Table *c*. *R.R.S. 'Discovery II'. Sts. 1772–1782, May–June 1936. Sts. 2010–2027, March–April 1937. Sts. 2311–2322, April 1938. Sts. 2355–2501, July–December 1938. Sts. 2530–2547, January 1939*

Station no., date and position	*Depth (m.)*	Rhyncho-nerella bongraini	Pelagobia longi-cirrata	Tomo-pteris planktonis	Tomo-pteris septen-trionalis	Tomo-pteris (*unidenti-fiable*)	Typhlo-scolex mülleri	Travi-siopsis levinseni
St. 1772, 23. v. 36	**50–0**	—	—	—	—	—	—	—
36° 01·8′ S., 00° 04·3′ E. to	**100–50**	—	—	—	—	—	—	—
36° 06·8′ S., 00° 05·4′ E.	**250–100**	—	—	—	—	—	1	—
	500–250	—	1	—	—	1	1	—
	750–500	—	—	—	—	2	1	—
	1000–750	—	1	—	—	—	—	—
	1500–1000	—	—	—	—	—	—	—
St. 1773, 24. v. 36	**50–0**	—	—	—	—	—	—	—
39° 07′ S., 00° 15·5′ E. to	**100–50**	—	—	—	—	—	—	—
39° 04′ S., 00° 12·5′ E.	**250–100**	—	1	—	—	—	—	—
	500–250	—	—	—	—	1	1	—
	750–500	—	—	—	—	—	7	—
	1000–750	—	1	—	—	—	2	—
	1500–1000	—	—	—	—	1	4	1
St. 1774, 25. v. 36	**50–0**	—	—	—	—	—	—	—
41° 50′ S., 00° 01·7′ E. to	**100–50**	—	—	—	—	—	—	—
41° 54·3′ S., 00° 03·3′ E.	**250–100**	—	—	—	1	—	2	1
	500–250	—	—	—	—	1	4	1
	750–500	—	—	—	—	1	3	3
St. 1775, 27. v. 36	**50–0**	—	—	—	—	—	—	—
44° 40·3′ S., 00° 33·5′ E. to	**100–50**	—	—	—	—	—	—	—
44° 40′ S., 00° 37′ E.	**250–100**	—	—	—	—	—	—	—
	500–250	—	—	—	—	1	4	1
	750–500	—	—	—	—	—	4	—
	1000–750	—	2	—	—	—	2	—
	1500–1000	—	—	—	—	—	—	—
St. 1776, 28. v. 36	**50–0**	—	—	—	—	—	—	—
47° 43′ S., 00° 25·5′ E. to	100–50	—	—	—	—	—	—	—
47° 48′ S., 00° 23·6′ E.	250–100	—	—	—	—	—	—	1
	500–250	—	—	—	—	1	—	2
	750–500	—	—	7	—	—	1	—
	1000–750	—	1	1	—	—	1	—
	1500–1000	—	2	—	—	—	—	1
St. 1777, 29. v. 36	**50–0**	—	—	—	—	—	—	—
49° 58·9′ S., 00° 07·1′ E. to	**100–50**	—	—	—	—	—	—	—
50° 02·1′ S., 00° 02·6′ E.	**250–100**	—	—	—	—	—	—	—
	500–250	—	—	—	—	4	1	—
	750–500	—	—	—	—	—	3	—
	1000–750	—	—	—	—	—	—	—
	1500–1000	—	—	—	—	—	—	—
St. 1778, 30. v. 36	**50–0**	—	—	—	—	—	—	—
52° 14·7′ S., 00° 1′ W. to	**100–50**	—	—	—	—	—	—	—
52° 12·8′ S., 00° 0·7′ E.	**250–100**	—	—	—	—	—	—	—
	500–250*	—	—	—	—	—	—	—
	750–500	—	1	—	—	—	1	—
	1000–750	—	5	—	—	—	5	—
	1500–1000	—	4	—	—	1	—	—
St. 1779, 1. vi. 36	**50–0**	—	—	—	—	—	—	—
54° 36·2′ S., 00° 05·1′ W. to	**100–50**	3	—	—	—	—	—	—
54° 34·8′ S., 00° 04·9′ W.	**250–100**	3	2	—	2	—	—	—
	500–250	—	2	—	—	—	1	—
	750–500	—	5	1	—	—	—	—
	950–750	—	6	—	—	—	—	—

Table *c* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhyncho-nerella bongraini	Pelagobia longi-cirrata	Tomo-pteris planktonis	Tomo-pteris septen-trionalis	Tomo-pteris (*unidenti-fiable*)	Typhlo-scolex müllei	Travi-siopsis levinseni
St. 1781, 2. vi. 36	**50–0**	1	—	—	5	—	—	—
57° 41·8′ S., 00° 19·8′ W. to	**100–50**	9	—	—	11	—	—	—
57° 44·9′ S., 00° 20·8′ W.	**250–100**	6	10	—	—	—	4	—
	500–250	—	9	2	1	—	6	—
	750–500	—	2	2	—	—	—	—
	1000–750	—	—	—	—	—	—	—
	1500–1000	—	4	—	—	—	—	—
St. 1782, 3. vi. 36	**50–0**	2	1	—	1	—	—	—
58° 44·6′ S., 00° 01·5′ E. to	100–50	1	17	—	—	—	—	—
58° 47·9′ S., 00° 00·7′ E.	250–100	3	8	2	1	—	1	—
	500–250	—	14	—	—	—	14	—
	750–500	—	5	—	—	—	—	—
	1000–750	—	—	—	—	—	—	—
	1500–1000	—	6	—	—	—	2	—
St. 2010, 21. iii. 37	**50–0**	3	—	—	3	—	1	—
67° 14·3′ S., 00° 39·7′ E.	100–50	5	1	—	—	1	—	—
	250–100	3	1	—	7	—	2	—
	500–250	2	4	—	3	—	1	1
	750–500	—	2	—	—	2	—	—
	1000–750	—	2	—	—	—	—	—
	1500–1000	—	—	—	—	—	—	—
St. 2012, 22. iii. 37	**50–0**	1	33	—	3	—	1	—
64° 31·9′ S., 00° 28·59′ E.	**100–50**	3	5	—	—	—	—	1
	250–100	—	21	—	—	1	—	2
	500–250	—	24	1	—	1	3	—
	750–500	—	4	—	—	1	—	1
	1000–750	—	1	—	—	—	—	—
	1500–1000	—	6	—	—	—	—	—
St. 2014, 23. iii. 37	**50–0**	4	5	—	—	—	—	—
61° 46·5′ S., 00° 35·1′ E.	**100–50**	2	42	—	2	—	—	—
	250–100	—	19	1	—	—	2	—
	500–250	6	1	—	—	2	6	—
	750–500	—	8	—	—	2	2	—
	1000–750	—	—	—	—	—	1	—
St. 2015, 25. iii. 37	50–0	—	—	—	1	—	—	—
59° 23·8′ S., 00° 09·3′ E.	100–50	4	3	—	3	—	—	—
	250–100	8	12	—	—	—	1	—
	500–250	11	4	—	—	—	8	—
	750–500	—	10	—	—	—	1	—
	1000–750	—	3	—	—	—	—	—
	1500–1000	—	2	—	—	—	—	—
St. 2017, 26. iii. 37	50–0	—	12	—	3	—	—	—
56° 34·3′ S., 00° 06·7′ E.	100–50	3	11	—	—	—	—	—
	250–100	1	28	—	1	—	4	—
	500–250	1	11	3	1	—	1	—
	750–500	—	4	—	—	—	1	—
	1000–750	—	7	—	—	—	—	—
	1500–1000	—	2	—	—	—	—	—
St. 2018, 26. iii. 37	**50–0**	7	14	—	10	—	—	—
54° 55·3′ S., 00° 11·8′ E.	**100–50**	4	—	1	—	—	—	—
	250–100	2	2	—	1	—	1	—
	500–250	—	3	—	—	—	—	—
	750–500	—	3	—	—	—	1	—
	1000–750	—	4	—	—	—	—	—

Table *c* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiable*)	Typhloscolex mülleri	Travisiopsis levinseni
St. 2020, 27. iii. 37	**50–0**	—	—	—	—	—	—	—
52° 25·6′ S., 00° 18·5′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	2	—	3	—
	750–500	—	—	—	—	—	1	—
	1000–750	—	1	—	—	—	—	—
	1500–1000	—	10	—	1	—	—	—
St. 2022, 28. iii. 37	**50–0**	—	—	—	—	—	—	—
50° 17·7′ S., 00° 23·1′ E.	**100–50**	—	3	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	1	—
	750–500	—	3	2	—	—	—	—
	1000–750	—	4	—	—	—	—	—
	1500–1000	—	2	—	—	—	—	—
St. 2023, 29. iii. 37	**50–0**	—	6	3	—	—	—	—
47° 46′ S., 00° 20·6′ E.	**100–50**	—	1	1	—	—	—	—
	250–100	—	—	2	—	—	—	—
	500–250	—	1	5	—	—	—	—
	750–500	—	1	8	—	—	1	—
	1000–750	—	—	—	—	—	—	—
	1500–1000	—	2	—	—	—	—	—
St. 2024, 30. iii. 37	**50–0**	—	—	—	—	—	—	—
45° 01·3′ S., 00° 33·7′ E.	**100–50**	—	3	4	—	—	—	—
	250–100	—	—	2	—	—	—	—
	500–250	—	—	—	—	—	2	—
	750–500	—	2	1	—	—	2	—
	1000–750	—	1	2	—	—	3	1
	1500–1000	—	2	—	—	—	—	—
St. 2025, 31. iii. 37	**50–0**	—	—	—	—	—	—	—
42° 10·6′ S., 00° 34·2′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	5	—
	750–500	—	1	—	—	—	6	—
	1000–750	—	—	—	—	—	—	—
St. 2026, 1. iv. 37	**50–0**	—	—	—	—	—	—	—
38° 56′ S., 00° 10·2′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	1	—	—	—	1	1
	750–500	—	—	—	—	—	—	—
	1000–750	—	—	—	—	—	—	—
	1500–1000	—	2	—	—	—	—	—
St. 2027, 2. iv. 37	50–0	—	2	—	—	—	—	—
36° 07·3′ S., 00° 07′ E.	100–50	—	1	—	—	1	—	—
	250–100	—	—	2	—	—	—	—
	500–250	—	—	—	—	—	—	—
	750–500	—	—	—	—	—	—	—
	1000–750	—	4	1	—	—	—	—
	1500–1000	—	2	2	—	—	—	2
St. 2311, 11–12. iv. 38	**50–0**	—	—	—	—	—	—	—
50° 05·2′ S., 00° 03′ W.	**100–50**	—	—	—	—	—	—	—
	250–100	—	1	—	1	3	1	—
	500–250	—	—	1	—	—	—	—
	750–500	—	1	—	—	1	—	—
	1000–750	—	3	—	—	—	—	—
	1500–1000	—	2	—	—	1	2	—

Table *c* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhyncho-nerella bongraini	Pelagobia longi-cirrata	Tomo-pteris planktonis	Tomo-pteris septen-trionalis	Tomo-pteris (*unidenti-fiable*)	Typhlo-scolex mülleri	Travi-siopsis levinseni
St. 2313, 12. iv. 38	**50–0**	—	—	—	—	—	—	—
52° 27′ S., 00° 29·2′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	1	—	—	—	—	—
	500–250	—	—	1	—	—	2	1
	750–500	—	—	—	—	—	—	1
	1000–750	—	—	—	—	—	—	—
	1500–1000	—	4	—	—	—	—	—
St. 2316, 14–15. iv. 38	**50–0**	—	5	—	3	—	—	—
57° 15·5′ S., 01° 13·4′ E.	**100–50**	—	3	—	—	—	—	1
	250–100†	—	8	—	—	1	—	1
	500–250	—	7	1	—	2	9	—
	750–500	—	3	—	—	1	—	—
	1000–750	—	4	—	—	—	—	—
	1500–1000	—	2	—	—	—	—	—
St. 2318, 15–16. iv. 38	**50–0**	—	45	—	—	1	3	—
58° 58·7′ S., 01° 00′ E.	**100–50**	—	5	—	—	—	—	—
	250–100	—	14	—	—	2	—	—
	500–250	—	8	—	—	—	5	—
	750–500	—	2	—	—	—	—	—
	1000–750	—	—	—	—	—	—	—
	1500–1000	—	2	—	—	—	—	—
St. 2320, 16–17. iv. 38	**50–0**	10	4	—	—	—	1	—
61° 10·6′ S., 00° 43·7′ E.	**100–50**	2	8	—	—	—	—	—
	250–100	5	12	—	—	—	—	—
	500–250	1	3	3	—	—	6	1
	750–500	—	1	1	—	1	1	—
	1000–750	—	1	—	—	—	1	—
	1500–1000	—	2	—	—	—	2	—
St. 2322, 17–18. iv. 38	**50–0**	3	2	—	—	—	—	—
63° 53′ S., 00° 24·4′ E.	**100–50**	10	8	—	1	—	—	—
	250–100	9	10	—	—	—	1	—
	500–250	1	14	—	—	3	1	—
	750–500	—	14	—	—	—	6	—
	1000–750	—	3	—	—	—	—	—
	1500–1000	—	2	—	—	—	—	—
St. 2355, 6–7. vii. 38	**50–0**	—	—	—	1	—	—	—
39° 51·4′ S., 01° 06·8′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	4	—	—	3	—
	750–500	—	—	—	—	—	4	—
	1000–750	—	—	—	—	—	1	—
	1500–1000	—	2	—	—	1	2	—
St. 2356, 7. vii. 38	**50–0**	—	—	—	—	—	—	—
42° 56·8′ S., 01° 21·2′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	1	—
	750–500	—	2	—	—	—	4	—
	1000–750	—	1	—	—	—	1	—
	1500–1000	—	2	—	—	—	4	—
St. 2357, 8–9. vii. 38	**50–0**	—	—	—	—	—	—	—
45° 51·4′ S., 01° 18·2′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	—	2	3	—
	750–500	—	2	—	—	—	4	—
	1000–750	—	7	—	—	—	1	—
	1500–1000	—	10	—	—	—	—	—

Table *c* (*cont*).

Station no., date and position	*Depth (m.)*	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiabie*)	Typhloscolex mülleri	Travisiopsis levinseni
St. 2358, 9. vii. 38	**50–0**	—	—	—	—	—	—	—
48° 24·6′ S., 00° 51′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	1	—	—	4	—
	750–500	—	1	—	—	1	3	—
	1000–750	—	4	—	—	—	3	—
	1500–1000	—	10	—	—	—	2	1
St. 2359, 10. vii. 38	**50–0**	—	—	—	—	—	—	—
51° 11·4′ S., 00° 25·2′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	—	—
	750–500	—	1	—	—	—	—	1
	1000–750	—	1	—	—	—	—	—
	1500–1000	—	2	—	—	1	2	—
St. 2361, 11. vii. 38	**50–0**	—	—	—	—	—	—	—
53° 50·6′ S., 00° 00·8′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	1	—	—	—	—	—
	500–250	—	18	6	—	—	2	—
	750–500	—	8	1	—	2	1	1
	1000–750	—	7	—	—	—	2	—
	1500–1000	—	6	1	—	—	6	—
St. 2385, 10. viii. 38	**50–0**	—	—	—	—	—	—	—
39° 56·9′ S., 00° 14·1′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	—	—	—	1	1	—
	500–250	—	—	—	—	1	—	2
	750–500	—	2	—	—	—	—	—
	1000–750	—	—	—	—	1	—	—
	1500–1000	—	—	—	—	1	2	—
St. 2386, 12. viii. 38	50–0	—	—	—	—	—	—	—
44° 04·9′ S., 00° 15·4′ E.	100–50	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	—	—
	750–500	—	1	—	—	—	—	1
	1000–750	—	1	—	—	—	1	—
	1500–1000	—	2	—	—	—	—	—
St. 2387, 14. viii. 38	50–0	—	—	—	—	—	—	—
49° 08·2′ S., 00° 41·5′ E.	100–50	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	—	1	—	—
	750–500	—	—	—	—	1	1	—
	1000–750	—	2	—	—	—	1	—
	1500–1000	—	2	—	—	1	—	—
St. 2389, 15. viii. 38	**50–0**	—	—	—	—	—	—	—
52° 35·3′ S., 00° 04·5′ E.	**100–50**	—	—	—	1	—	—	—
	250–100	—	—	—	—	—	—	1
	500–250	—	—	—	—	—	2	—
	750–500	—	1	—	—	—	1	—
	1000–750	—	2	—	—	—	1	—
	1500–1000	—	6	—	—	—	2	—
St. 2391, 16. viii. 38	**50–0**	—	—	—	—	—	—	—
55° 03·3′ S., 00° 19·1′ E.	**100–50**	—	—	—	1	—	—	—
	250–100	—	—	—	1	—	—	—
	500–250	—	2	—	—	—	2	—
	750–500	—	4	—	—	—	—	—
	1000–750	—	1	—	—	—	—	—
	1500–1000	—	2	—	—	—	—	—

Table *c* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris planktonis	Tomopteris septentrionalis	Tomopteris (*unidentifiable*)	Typhloscolex müller	Travisiopsis levinseni
St. 2393, 17. viii. 38 56° 42·3′ S., 00° 38·3′ E.	**50–0**	—	—	—	—	—	—	—
	100–50	—	—	—	6	—	—	—
	250–100	3	1	—	1	2	—	—
	500–250	—	8	1	—	2	—	—
	750–500	—	7	2	—	3	6	1
	1000–750	—	7	—	—	—	1	—
	1500–1000	—	6	—	—	—	2	1
St. 2424, 19. ix. 38 39° 53·7′ S., 00° 38·9′ E.	50–0	—	—	—	—	—	—	—
	100–50	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	4	3
	750–500	—	—	—	—	—	4	1
	1000–750	—	1	—	—	—	1	—
	1500–1000	—	4	—	—	—	2	—
St. 2425, 20. ix. 38 43° 28·4′ S., 00° 41·1′ E.	50–0	—	—	—	—	—	—	—
	100–50	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	3	1
	750–500	—	3	—	—	—	2	—
	1000–750	—	4	—	—	—	1	—
	1500–1000	—	6	—	—	—	—	—
St. 2492, 28. xi. 38 40° 12·8′ S., 00° 37·6′ E.	50–0	—	—	—	—	—	—	—
	100–50	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	—	—	—	—	4	2
	750–500	—	—	—	—	—	3	—
	1000–750	—	—	—	—	—	—	—
	1500–1000	—	—	—	—	—	—	1
St. 2494, 30. xi. 38 43° 18·1′ S., 00° 54·6′ E.	50–0	—	—	—	—	—	—	—
	100–50	—	—	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	1	—	—	—	—	1
	750–500	—	—	—	—	—	—	—
	1000–750	—	—	—	—	—	3	—
	1500–1000	—	4	—	—	—	—	—
St. 2495, 1. xii. 38 47° 11·2′ S., 01° 17·5′ E.	50–0	—	—	—	—	—	—	—
	100–50	—	8	3	—	—	—	—
	250–100	—	32	2	—	—	—	—
	500–250	—	—	—	—	—	1	—
	750–500	—	2	—	—	—	—	1
	1000–750	—	—	—	—	—	—	—
	1500–1000	—	2	—	—	—	1	—
St. 2496, 2. xii. 38 50° 20·7′ S., 01° 03·3′ E.	**50–0**	—	—	—	—	1	—	—
	100–50	—	—	—	—	—	—	—
	250–100	—	6	—	—	—	—	—
	500–250	—	1	—	—	—	5	—
	750–500	—	1	—	—	—	—	1
	1000–750	—	1	—	—	—	—	—
	1500–1000*	—	—	—	—	—	—	—
St. 2498, 3. xii. 38 52° 53·5′ S., 00° 50·3′ E.	**50–0**	—	30	—	—	—	—	—
	100–50	—	14	—	—	—	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	1	—	—	—	4	—
	750–500	—	5	—	—	—	—	—
	1000–750	—	5	—	—	—	—	—
	1500–1000	—	6	—	—	—	—	—

Table *c* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhyncho-nerella bongraini	Pelagobia longi-cirrata	Tomo-pteris planktonis	Tomo-pteris septen-trionalis	Tomo-pteris (*unidenti-fiable*)	Typhlo-scolex mülleri	Travi-siopsis levinseni
St. 2501, 5. xii. 38	50–0	—	4	—	—	—	—	—
55° 30·2′ S., 01° 23·7′ E.	100–50	6	6	—	—	1	2	—
	250–100	2	1	—	—	—	1	—
	500–250	1	1	—	—	—	1	1
	750–500	—	3	—	—	1	—	—
	1000–750	—	3	—	1	1	—	—
St. 2530, 11–12. i. 39	**50–0**	—	—	—	—	—	—	—
39° 03′ S., 02° 35′ E.	**100–50**	—	—	—	—	2	—	—
	250–100	—	—	—	—	—	—	—
	500–250	—	8	—	—	—	5	—
	750–500	—	2	—	—	—	1	—
	1000–750	—	3	—	—	—	2	—
	1500–900	—	2	—	—	—	—	—
St. 2531, 12. i. 39	**50–0**	—	—	—	—	—	—	—
42° 07·9′ S., 02° 50·9′ E.	**100–50**	—	—	—	—	—	—	—
	250–100	—	2	—	—	2	1	—
	500–250	—	3	—	—	2	4	—
	750–500	—	4	—	—	—	3	—
	1000–750	—	2	—	—	1	—	—
	1500–1000	—	10	—	—	—	—	—
St. 2532, 13–14. i. 39	**50–0**	—	70	—	—	—	—	—
45° 18·9′ S., 03° 09·8′ E.	**100–50**	—	24	1	—	—	1	—
	250–100	—	25	—	—	—	1	—
	500–250	—	24	—	—	—	3	—
	750–500	—	5	—	—	—	4	—
	1000–750	—	—	—	—	—	—	—
St. 2533, 15. i. 39	50–0	—	—	—	—	—	—	—
48° 58·4′ S., 02° 47·1′ E.	100–50	—	22	—	—	—	—	—
	250–100	—	1	—	—	—	—	—
	500–250	—	5	—	—	—	2	1
	750–500	—	8	—	—	1	1	—
	1000–750	—	—	—	—	—	—	—
	1500–1000	—	6	—	—	—	—	—
St. 2535, 16. i. 39	50–0	—	8	—	—	1	—	—
52° 40·8′ S., 02° 45·4′ E.	100–50	—	144	—	1	—	—	—
	250–100	—	59	—	—	—	2	—
	500–250	—	10	—	—	—	3	1
	750–500	—	10	2	1	—	1	—
	1000–750	—	3	—	—	—	—	—
	1500–1000	—	4	—	—	—	—	—
St. 2538, 18. i. 39	50–0	—	—	—	—	—	—	—
57° 11·9′ S., 03° 33·7′ E.	100–50	5	—	—	4	—	—	—
	250–100	4	25	—	—	2	1	—
	500–250	1	40	—	1	—	8	—
	750–500	—	9	—	—	2	3	—
	1000–750	—	9	1	—	—	1	—
St. 2541, 19–20. i. 39	50–0	9	4	—	6	—	1	—
60° 41·7′ S., 03° 13·9′ E.	100–50	4	12	—	—	2	—	—
	250–100	2	5	1	—	—	1	—
	500–250	—	10	—	—	—	7	—
	750–500	—	9	—	—	—	4	—
	1000–750	—	5	—	—	—	—	—
	1500–1000	—	4	—	—	—	—	—

Table *c* (*cont.*)

Station no., date and position	*Depth* (*m.*)	Rhyncho-nerella bongraini	Pelagobia longi-cirrata	Tomo-pteris planktonis	Tomo-pteris septen-trionalis	Tomo-pteris (*unidenti-fiable*)	Typhlo-scolex mülleri	Travi-siopsis levinseni
St. 2543, 20. i. 39 63° 24·7′ S., 02° 44·7′ E.	50–0	4	20	1	1	—	4	—
	100–50	—	11	—	—	—	1	—
	250–100	1	3	2	3	—	1	—
	500–250	—	12	—	1	—	1	—
	750–500	—	18	—	—	—	3	—
	1000–750	—	3	1	—	1	1	—
	1500–1000	—	4	—	—	—	—	—
St. 2545, 21. i. 39 66° 23·7′ S., 02° 16·2′ E.	50–0	1	8	—	1	—	—	—
	100–50	1	3	—	—	—	1	—
	250–100	4	9	—	—	4	3	—
	500–250	—	8	1	2	—	5	—
	750–500	—	6	1	—	—	6	—
	1000–750	—	4	1	1	—	—	—
	1500–1000	—	8	—	—	1	—	—
St. 2547, 22. i. 39 69° 30·2′ S., 02° 04·7′ E.	50–0	—	—	—	—	—	—	—
	100–50	—	8	—	—	—	—	—
	250–100	2	70	—	—	1	—	—
	500–250	—	28	—	5	—	9	—
	750–500	—	5	—	—	—	2	—
	1000–750	—	8	—	—	—	—	—
	1500–1000	—	6	—	—	—	—	—

* Sample lost. † One adult *Tomopteris carpenteri*

APPENDIX II

MISCELLANEOUS NETS

Note. Not all the hauls at all the stations listed were examined. Depths in heavy type indicate hauls made between sunset and sunrise.

Table *a*. R.R.S. 'Discovery II': 0° Line. Sts. 2010–2027, March–April 1937, N 100 B nets.

Table *b*. South Sandwich Islands Survey. Sts. SS 1–SS 58, November–February 1927–28, N 50, N 70 and N 100 nets.

Table *c*. R.R.S. 'William Scoresby'. South Sandwich Islands to Ice Edge to South Georgia. Sts. WS 536, WS 537, WS 541, WS 544, WS 545, WS 547, WS 552 and WS 555, N 70 and N 100 nets.

Table *d*. R.R.S. 'Discovery II'. Falkland Islands to Ice Edge to South Georgia. Sts. 2291–2302, N 70 B, N 100 nets.

Table *e*. R.R.S. 'Discovery', R.R.S. 'Discovery II'. Cape Town to Bouvet Island. Sts. 100, 102–104, 107, 114, 116–118, 404, 405, 407, 413, 419, 446, 448–455, 459–461, 463–466, N 70, N 100 and TYF nets.

Table *f*. R.R.S. 'Discovery II'. 30° W. line. Sts. 661–699, TYF nets.

Table *g*. R.R.S. 'Discovery'. Falkland Islands to Cape Town. Sts. 69, 71, 72, 74, 78, 85, 87, 89, 247, 250, 254, 256, 257–259, N 70 and TYF nets.

Table *h*. R.R.S. 'Discovery', R.R.S. 'Discovery II'. Cape Verde Islands to and from Cape Town. Sts. 266–268, 270, 273, 276, 282, 287–289, 291, 294, N 100 and TYF nets; Sts. 1592, 1594, 1596, 1598, 1600, 1602, 1604, 1606, TYF nets; Sts. 2028–2040, 2042, 2044–2048, 2050, 2051, 2053, 2055, 2057, 2059, 2061, 2063–2066, N 100, TYF and N 450 nets; Sts. 2073–2084, TYF nets; Sts. 2627–2630, 2632, 2635, 2636, 2638, 2639–2648, N 50 and TYF nets.

Table *j*. R.R.S. 'Discovery II'. Cape Verde Islands to Falkland Islands. Sts. 701–718, TYF nets.

Table *k*. Miscellaneous stations, all nets.

N.B. All negative results for complete samples in Tables *b*, *c*, *e*, *g*, *h* (Sts. 266–94) and *j* are taken from the Plankton Analysis Sheets prepared by the staff of the Discovery Investigations. Samples in Tables *a*, *d* and *h* (except Sts. 266–294) were sorted by the author. Specimens from Sts. 701–18 picked out on board the ship. Specimens in Tables *j* and *k* preserved separately except where noted. Reference to Tables 20–34 in the text should also be made for some of the species collected.

Table *a*. *0° Line, St. 2010–2027, N 100 B nets only*

Station no., date and position	*Depth (m.)*	Tomopteris carpenteri (*adult*)	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis antarctica	Travisiopsis levinseni
St. 2010, 21. iii. 37	105–0	—	—	—	—	—
67° 14·3′ S., 00° 39·7′ E.	420–150	—	—	18	—	2
	700–400	—	—	1	—	2
St. 2011, 22. iii. 37	102–0	—	—	—	—	—
65° 14·3′ S., 00° 29·7′ E.						
St. 2012, 22. iii. 37	106–0	—	—	10	6	—
64° 31·9′ S., 00° 28·59′ E.	420–150	—	—	—	—	—
	700–400	—	—	—	—	1
St. 2013, 23. iii. 37	118–0	1	—	1	2	—
62° 43·3′ S., 00° 34·2′ E.						
St. 2014, 23. iii. 37	**97–0**	1	4	17	—	1
61° 46·5′ S., 00° 35·1′ E.	**400–150**	1	—	—	1	—
	700–450(–0)	1	—	1	—	—
St. 2015, 25. iii. 37	119–0	—	—	—	—	
59° 23·8′ S., 00° 09·3′ E.	450–150	—	2	2	—	—
	800–400	—	—	1	—	—
St. 2016, 25. iii. 37	**128–0**	—	—	7	—	—
57° 45·9′ S., 00° 04′ E.						
St. 2017, 26. iii. 37	130–0	—	—	1	1	—
56° 34·3′ S., 00° 06·7′ E.	500–150	—	—	1	—	—
	850–500	—	—	—	—	—
St. 2018, 26. iii. 37	**130–0**	1	—	63	1	—
54° 55·3′ S., 00° 11·8′ E.						
St. 2019, 27. iii. 37	118–0	—	—	—	—	—
53° 15·4′ S., 00° 16·1′ E.	450–150	—	—	—	—	—
	700–400(–0)	1	—	—	—	—
St. 2020, 27. iii. 37	**123–0**	—	—	—	—	—
52° 25·6′ S., 00° 18·5′ E.	**450–150**	—	—	—	—	—
	750–450	—	—	—	—	—
St. 2021, 28. iii. 37	153–0	—	—	—	—	—
51° 01·7′ S., 00° 24·4′ E.						
St. 2022, 28. iii. 37	**118–0**	—	—	—	—	—
50° 17·7′ S., 00° 23·1′ E.	**450–150**	1	—	—	—	—
	700–400	—	—	—	—	—
St. 2023, 29. iii. 37	**120–0**	—	—	—	—	—
47° 46′ S., 00° 20·6′ E.	**450–150**	—	—	—	—	2
	750–400	—	—	—	—	—
St. 2024, 30. iii. 37	**100–0**	—	—	—	—	—
45° 01·3′ S., 00° 33·7′ E.	**450–150**	—	—	—	—	1
	650–400	—	—	—	—	—
St. 2025, 31. iii. 37	**109–0**	—	—	—	—	—
42° 10·6′ S., 00° 34·2′ E.	**440–150**	—	—	—	—	—
	750–400	—	—	—	—	—
St. 2026, 1. iv. 37	**130–0**	—	—	—	—	—
38° 56′ S., 00° 10·2′ E.	**450–150**	—	—	—	—	—
	750–400	—	—	—	—	—
St. 2027, 2. iv. 37	78–0	—	—	—	—	—
36° 07·3′ S., 00° 07′ E.	310–150	—	—	—	—	—
	600–400	—	—	—	—	—

Table *b*. *South Sandwich Survey*

Station no., date and position	*Net*	*Depth* (*m.*)	Rhyncho-nerella bongraini	Pelagobia longi-cirrata	Tomopteris carpenteri (*adult*)	Tomopteris planktonis	Tomopteris septen-trionalis	Typhlo-scolex mülleri
St. SS 1, 18. xi. 27	N 70 B	83–0	3	2	—	—	8	—
55° 35′ 00″ S., 30° 30′ 00″ W.	N 100 B	83–0	—	—	—	—	2	—
St. SS 2, 20. xi. 27	N 70 B	50–0	—	—	—	—	—	—
55° 36′ 00″ S., 30° 33′ 00″ W.	N 70 B	100–0	—	—	—	—	—	—
	N 70 B	250–0	1	1	—	—	—	—
St. SS 3, 24. xi. 27	N 50 V	100–0	—	—	—	—	—	—
54° 02′ 00″ S., 31° 22′ 00″ W.	N 70 V	50–0	—	—	—	—	—	—
	N 70 V	100–50	1	—	—	—	3	—
	N 70 V	250–100	—	—	—	—	—	—
St. SS 4, 25. xi. 27	N 70 B	**102–0**	5	—	—	—	6	—
54° 03′ 00″ S., 31° 38′ 00″ W.	N 100 B	**102–0**	1	—	—	—	1	—
St. SS 5, 25. xi. 27	N 70 B	**98–0**	6	—	—	—	—	—
54° 02′ 00″ S., 31° 40′ 00″ W.	N 100 B	**98–0**	—	—	—	—	5	—
St. SS 6, 29. xi. 27	N 70 B	**137–0**	7	—	1	—	5	—
54° 20′ 00″ S., 29° 31′ 00″ W.	N 100 B	**137–0**	—	—	2*	—	3*	—
St. SS 7, 29. xi. 27	N 70 B	**150–0**	—	—	—	1	3	—
54° 19′ 20″ S., 29° 32′ 40″ W.	N 100 B	**150–0**	—	—	1	—	—	—
St. SS 8, 30. xi. 27	N 50 V	100–0	—	—	—	—	—	—
54° 20′ 00″ S., 29° 31′ 00″ W.	N 70 V	50–0	—	—	—	—	—	—
	N 70 V	100–50	—	—	—	—	—	—
	N 70 V	250–100	—	—	—	—	—	—
St. SS 9, 2. xii. 27	N 70 B	58–0	1	1	—	—	18	—
54° 31′ 00″ S., 29° 40′ 00″ W.	N 100 B	58–0	—	—	3	—	14	—
St. SS 10, 2. xii. 27	N 70 B	100–0	1	—	1	—	3*	—
54° 30′ 20″ S., 29° 38′ 45″ W.	N 100 B	100–0	—	—	1*	—	6*	—
St. SS 11, 6. xii. 27	N 70 B	**84–0**	6	—	—	—	2	—
54° 31′ 00″ S., 29° 48′ 00″ W.	N 100 B	**84–0**	2	—	1	—	6	—
St. SS 12, 6. xii. 27	N 70 B	**123–0**	4	—	1	—	8	—
54° 30′ 20″ S., 29° 50′ 20″ W.	N 100 B	**123–0**	—	—	1*	—	—	—
St. SS 13, 8. xii. 27	N 50 V	100–0	—	—	—	—	—	—
54° 22′ 00″ S., 30° 00′ 00″ W.	N 70 V	50–0	—	—	—	—	—	—
	N 70 V	100–50	—	1	1	—	2	—
	N 70 V	250–100	1	3	—	—	1	—
St. SS 14, 11. xii. 27	N 70 B	55–0	3	1	—	—	—	—
54° 30′ 00″ S., 30° 11′ 00″ W.	N 100 B	55–0	1	—	1	—	7	—
St. SS 15, 11. xii. 27	N 70 B	**104–0**	5	—	—	1	3	—
54° 22′ 00″ S., 30° 11′ 00″ W.	N 100 B	**104–0**	5	—	2	—	9	—
St. SS 16, 14. xii. 27	N 70 B	**104–0**	—	—	—	—	1*	—
55° 00′ 00″ S., 27° 29′ 00″ W.	N 100 B	**104–0**	—	—	1*	—	3*	—
St. SS 17, 14. xii. 27	N 70 B	**99–0**	1	—	1*	—	—	—
55° 00′ 00″ S., 27° 43′ 00″ W.	N 100 B	**99–0**	—	—	1*	—	4*	—
St. SS 18, 15. xii. 27	N 50 V	100–0	—	—	—	—	—	—
54° 58′ 00″ S., 27° 32′ 00″ W.	N 70 V	50–0	—	—	—	—	—	—
	N 70 V	100–50	—	—	—	—	—	—
	N 70 V	250–100	—	—	—	—	—	—
St. SS 19, 19. xii. 27	N 70 B	137–0	—	—	1*	—	—	—
54° 51′ 30″ S., 27° 38′ 00″ W.	N 100 B	137–0	—	—	—	—	2*	—
St. SS 20, 19. xii. 27	N 70 B	100–0	—	—	—	—	3	—
54° 52′ 30″ S., 27° 36′ 30″ W.	N 100 B	100–0	—	—	1	—	1*	—
St. SS 21, 21. xii. 27	N 50 V	100–0	—	—	—	—	—	—
56° 21′ 00″ S., 25° 40′ 00″ W.	N 70 V	50–0	—	—	—	—	—	—
	N 70 V	100–50	—	—	—	—	2*	—
	N 70 V	250–100	—	3	—	1†	2*	1
St. SS 22, 22. xii. 27	N 70 B	**95–0**	4	—	—	—	2	—
55° 56′ 00″ S., 25° 56′ 00″ W.	N 100 B	**95–0**	—	—	—	—	1	—
St. SS 23, 22. xii. 27	N 70 B	**124–0**	5	—	—	—	7	—
55° 59′ 00″ S., 25° 56′ 00″ W.	N 100 B	**124–0**	—	—	—	—	—	—

Table *b* (*cont.*)

Station no., date and position	*Net*	*Depth* (*m.*)	Rhyncho-nerella bongraini	Pelagobia longi-cirrata	Tomopteris carpenteri (*adults*)	Tomopteris planktonis	Tomopteris septen-trionalis	Typhlo-scolex mülleri
St. SS 24, 24. xii. 27	N 70 B	81–0	1	—	—	—	10	—
56° 49′ 00″ S., 25° 35′ 00″ W.	N 100 B	81–0	—	—	—	—	15*	—
St. SS 25, 24. xii. 27	N 70 B	62–0	3	1	1	2	—	—
56° 47′ 50″ S., 25° 33′ 00″ W.	N 100 B	62–0	—	—	1	—	—	—
St. SS 26, 4. i. 28	N 70 B	79–0	—	—	—	—	—	—
60° 14′ 00″ S., 26° 27′ 00″ W.	N 100 B	79–0	—	—	—	—	—	—
St. SS 27, 4. i. 28	N 70 B	104–0	1	—	—	—	—	—
60° 15′ 00″ S., 26° 33′ 00″ W.	N 100 B	104–0	—	—	—	—	—	—
St. SS 28, 11. i. 28	N 50 V	100–0	—	—	—	1	—	—
59° 26′ 00″ S., 25° 24′ 00″ W.	N 70 V	50–0	2	—	—	—	1	—
	N 70 V	**100–(0)**	1	1	1	—	1	—
	N 70 V	**250–(0)**	2	—	—	—	—	—
St. SS 29, 13. i. 28	N 70 B	97–0	—	—	2	—	1	—
60° 05′ 30″ S., 24° 19′ 00″ W.	N 100 B	97–0	—	—	—	—	2	—
St. SS 30, 13. i. 28	N 70 B	119–0	—	—	1	—	1	—
60° 08′ 30″ S., 24° 19′ 00″ W.	N 100 B	119–0	—	—	4	—	7	—
St. SS 31, 18. i. 28	N 70 B	135–0	—	—	—	—	—	—
60° 59′ 00″ S., 25° 55′ 30″ W.	N 100 B	135–0	—	—	1	—	—	—
St. SS 32, 18. i. 28	N 70 B	115–0	—	—	1*	—	1*	—
60° 57′ 00″ S., 25° 57′ 30″ W.	N 100 B	115–0	—	—	1*	—	1*	—
St. SS 33, 20. i. 28	N 50 V	100–0	—	—	—	—	—	—
60° 52′ 00″ S., 25° 29′ 00″ W.	N 70 V	50–0	—	—	—	—	1*	—
	N 70 V	**100–(0)**	—	1	—	—	—	—
	N 70 V	**250–100**	3‡	—	—	—	2*	—
St. SS 34, 21. i. 28	N 70 B	141–0	—	—	—	—	1	—
60° 51′ 00″ S., 26° 25′ 00″ W.	N 100 B	141–0	—	—	—	—	3	—
St. SS 35, 21. i. 28	N 70 B	**119–0**	3	1	—	—	—	—
60° 49′ 00″ S., 26° 32′ 00″ W.	N 100 B	**119–0**	—	—	—	—	1*	—
St. SS 36, 24. i. 28	N 70 B	128–0	1	—	—	—	2	—
60° 58′ 00″ S., 26° 20′ 00″ W.	N 100 B	128–0	—	—	—	—	—	—
St. SS 37, 24. i. 28	N 70 B	130–0	—	—	—	—	—	—
61° 00′ 20″ S., 26° 26′ 00″ W.	N 100 B	130–0	—	—	—	—	—	—
St. SS 38, 27. i. 28	N 50 V	100–0	—	—	—	—	—	—
61° 05′ 00″ S., 26° 20′ 00″ W.	N 70 V	50–0	—	—	—	—	—	—
	N 70 V	100–50	—	—	—	—	—	—
	N 70 V	250–100	—	—	—	—	—	—
St. SS 39, 28. i. 28	N 70 B	69–0	1	10	—	—	2	—
61° 14′ 00″ S., 26° 16′ 30″ W.	N 100 B	69–0	—	—	—	—	4	—
St. SS 40, 28. i. 28	N 70 B	97–0	1	—	—	—	3	—
61° 19′ 00″ S., 26° 06′ 00″ W.	N 100 B	97–0	—	—	—	—	3	—
St. SS 41, 1. ii. 28	N 70 B	137–0	—	—	—	—	—	—
61° 21′ 30″ S., 26° 25′ 00″ W.	N 100 B	137–0	—	—	—	—	—	—
St. SS 42, 1. ii. 28	N 70 B	119–0	1	—	—	—	—	1
61° 21′ 30″ S., 26° 20′ 30″ W.	N 100 B	119–0	—	—	—	—	—	—
St. SS 43, 2. ii. 28	N 50 V	100–0	—	—	—	—	—	—
61° 45′ 00″ S., 26° 50′ 00″ W.	N 70 V	50–0	—	—	—	—	—	—
	N 70 V	100–50	—	1	—	—	—	—
	N 70 V	250–100	1	—	—	—	—	—
St. SS 44, 3. ii. 28	N 70 B	110–0	—	—	—	—	—	—
62° 23′ 00″ S., 27° 04′ 00″ W.	N 100 B	110–0	—	—	—	—	1*	—
St. SS 45, 3. ii. 28	N 70 B	99–0	—	1	—	—	—	—
62° 17′ 45″ S., 27° 15′ 45″ W.	N 100 B	99–0	—	—	—	—	—	—
St. SS 46, 7. ii. 28	N 70 B	119–0	—	—	—	—	—	—
62° 00′ 20″ S., 27° 05′ 00″ W.	N 100 B	119–0	—	—	—	—	—	—
St. SS 47, 7. ii. 28	N 70 B	**141–0**	2	2	—	—	—	—
62° 13′ 00″ S., 27° 10′ 00″ W.	N 100 B	**141–0**	—	—	—	—	—	—

Table *b* (*cont.*)

Station no., date and position	*Net*	*Depth (m.)*	Rhynchonerella bongraini	Pelagobia longicirrata	Tomopteris carpenteri (*adults*)	Tomopteris planktonis	Tomopteris septentrionalis	Typhloscolex mülleri
St. SS 48, 11. ii. 28	N 50 V	100–0	—	—	—	—	—	—
62° 45′ 00″ S., 25 42′ 00″ W.	N 70 V	50–0	—	—	—	—	—	—
	N 70 V	100–50	—	—	—	—	—	—
	N 70 V	250–100	1	1	—	—	—	1
St. SS 49, 12. ii. 28	N 70 B	141–0	—	—	—	—	—	—
62° 21′ 30″ S., 24° 02′ 30″ W.	N 100 B	141–0	—	—	—	—	—	—
St. SS 50, 12. ii. 28	N 70 B	95–0	—	—	—	—	—	1
62° 19′ 20″ S., 24° 02′ 00″ W.	N 100 B	95–0	—	—	—	—	—	—
St. SS 51, 15. ii. 28	N 70 B	110–0	—	—	—	—	—	—
62° 11′ 30″ S., 21° 30′ 00″ W.	N 100 B	110–0	—	—	—	—	—	—
St. SS 52, 15. ii. 28	N 70 B	146–0	—	1	—	—	—	—
62° 15′ 00″ S., 21° 36′ 20″ W.	N 100 B	146–0	—	—	—	—	—	—
St. SS 53, 16. ii. 28	N 50 V	100–0	—	—	—	—	—	—
61° 30′ 00″ S., 23° 20′ 00″ W.	N 70 V	50–0	—	—	—	—	—	—
	N 70 V	100–0	—	—	—	—	2	—
	N 70 V	250–100	1‡	—	—	—	—	1*
St. SS 54, 20. ii. 28	N 70 B	**95–0**	—	—	—	—	—	—
60° 59′ 20″ S., 23° 21′ 50″ W.	N 100 B	**95–0**	—	—	—	—	—	—
St. SS 55, 20. ii. 28	N 70 B	155–0	1	—	—	—	1	—
61° 01′ 00″ S., 23° 30′ 00″ W.	N 100 B	155–0	—	—	—	—	—	—
St. SS 56, 22. ii. 28	N 50 V	100–0	1	—	—	—	1*	—
61° 49′ 00″ S., 23° 54′ 00″ W.	N 70 V	50–0	—	—	—	—	—	—
	N 70 V	**100–50**	2	—	—	—	—	—
	N 70 V	**250–100**	3	—	—	—	—	—
St. SS 57, 23. ii. 28	N 70 B	95–0	—	—	1*	—	—	—
61° 49′ 30″ S., 23° 28′ 00″ W.	N 100 B	95–0	—	—	1*	—	—	—
St. SS 58, 23. ii. 28	N 70 B	**104–0**	—	—	—	—	1	—
61° 55′ 00″ S., 23° 40′ 00″ W.	N 100 B	**104–0**	—	—	—	—	—	—

* Monro, 1930. † As *Tomopteris carpenteri* or *T. planktonis*. ‡ As *Rhynchonerella fulgens*.

Table *c*. *South Sandwich Islands to Ice Edge in 68° 53′ S.*

Station no., date and position	*Net*	*Depth (m.)*	Tomopteris carpenteri (*adult*)	Vanadis antarctica	Rhynchonerella bongraini	Pelagobia longicirrata	Travisiopsis levinseni
St. WS 536, 24. i. 31 56° 28′ S., 27° 21′ W.	N 100 B	**102–0**	5	—	—	—	—
St. WS 537, 25–26. i. 31 56° 10′ S., 25° 35′ W.	N 70 B	**67–0**	—	1	—	—	—
St. WS 541, 28. i. 31 57° 51′ 30″ S., 19° 51′ 30″ W.	N 100 B	102–0	2	—	—	—	—
St. WS 544, 29. i. 31 60° 59′ S., 17° 50′ W.	N 100 B	**146–0**	3	—	—	—	—
St. WS 545, 30. i. 31 61° 51′ S., 17° 15′ W.	N 100 B	124–0	1	—	—	—	—
St. WS 547, 30. i. 31 62° 40′ S., 17° 02′ W.	N 100 B	**154–0**	1	—	—	—	—
St. WS 548, 31. i. 31 64° 07′ S., 15° 38′ W.	N 100 B	106–0	1	—	—	—	—
St. WS 549, 31. i. 31 65° 17′ S., 15° 33′ W.	N 100 B	**128–0**	2	—	—	—	2
St. WS 550, 1. ii. 31 66° 51′ 30″ S., 15° 24′ W.	N 70 B	121–0	—	1	—	—	—
St. WS 551, 1. ii. 31 68° 17′ 30″ S., 14° 26′ 30″ W.	N 70 B	121–0	—	2	—	—	—
St. WS 552, 2. ii. 31 68° 53′ S., 13° 03′ W. to 68° 50′ S., 13° 03′ W.	N 100 B	?	—	1	—	—	—
St. WS 555, 6. ii. 31 60° 27′ S., 19° 36′ W.	N 100 B	174–0	—	—	3*	3	1†

These specimens were reported by Monro, 1936: * As *Callizonella bongraini*, † As *Travisiopsis benhami*.

Table *d*. *Falkland Islands to Ice Edge to South Georgia*

Station no., date and position	*Net*	*Depth* (*m*.)	Rhynchonerella bongraini	Vanadis antarctica	Vanadis longissima	Pelagobia longicirrata	Tomopteris carpenteri (*adult*)	Tomopteris septentrionalis
St. 2291, 20. iii. 38	N 100 B	104–0	—	—	1	—	—	—
53° 02·3′ S., 56° 20·9′ W.	N 70 B	380–275	—	—	—	—	—	—
	N 100 B	380–275	—	—	—	—	—	—
St. 2292, 21–22. iii. 38	N 100 B	119–0	—	—	—	—	—	—
55° 41·2′ S., 53° 31·6′ W.	N 100 B	375–225	—	—	—	—	—	—
St. 2293, 22. iii. 38	N 100 B	53–0	—	—	—	—	—	—
57° 34·9′ S., 51° 06·2′ W.								
St. 2294, 23. iii. 38	N 70 B	180–0	—	—	—	—	—	—
58° 44·8′ S., 49° 47·8′ W.	N 100 B	180–0	—	—	—	—	—	—
St. 2295, 23. iii. 38	N 100 H	5–0	—	—	—	—	2	—
59° 58′ S., 48° 28·1′ W.	N 70 B	93–0	—	—	—	—	1	—
	N 100 B	93–0	—	—	—	—	—	—
	N 70 B	310–160	—	—	—	—	1	—
	N 100 B	310–160	—	—	—	—	—	—
St. 2296, 24. iii. 38	N 100 H	5–0	—	—	—	—	—	1
61° 22·7′ S., 46° 43·1′ W.	N 100 B	134–0	—	—	—	—	—	3
	N 70 B	240–110	3	—	—	236*	—	—
	N 100 B	240–110	—	—	—	—	—	5
St. 2297, 25. iii. 38	N 100 H	5–0	—	—	—	—	—	—
62° 21·2′ S., 45° 05·3′ W.	N 70 B	94–0	—	—	—	—	—	—
	N 100 B	94–0	—	—	—	—	3	—
	N 100 B	490–230	—	1	—	—	1	—
	N 100 B	750–0	—	—	—	—	—	—
St. 2298, 25. iii. 38	N 100 H	5–0	—	—	—	—	2	—
61° 09·6′ S., 43° 15·6′ W.	N 70 B	97–0	—	—	—	—	2	—
	N 100 B	97–0	—	—	—	—	1	—
	N 70 B	340–170	—	—	—	8	—	—
	N 100 B	340–170	—	—	—	—	—	1
St. 2299, 26. iii. 38	N 100 H	5–0	—	—	—	—	—	—
59° 52·6′ S., 41° 40·4′ W.	N 70 B	170–0	—	—	—	—	—	—
	N 100 B	170–0	—	—	—	—	—	—
St. 2300, 26. iii. 38	N 100 H	5–0	—	—	—	—	14	—
58° 33′ S., 39° 54·7′ W.	N 70 B	106–0	—	—	—	—	8	—
	N 100 B	106–0	—	—	—	—	12	—
	N 70 B	350–200	—	—	—	—	—	—
	N 100 B	350–200	1	—	—	7	—	—
St. 2301, 27. iii. 38	N 100 H	5–0	—	—	—	—	2	—
57° 14′ S., 38° 13·5′ W.	N 70 B	135–0	—	—	—	—	—	—
	N 100 B	135–0	—	—	—	—	—	—
St. 2302, 27. iii. 38	N 100 H	5–0	—	—	—	—	—	—
55° 56·3′ S., 36° 42·9′ W.	N 70 B	103–0	—	—	—	—	1	—
	N 100 B	103–0	—	—	—	—	—	—
	N 70 B	360–130	—	—	—	—	—	—
	N 100 B	360–130	—	—	—	—	—	—

* One-fifth of sample.

Table *e*. *Cape Town to Bouvet Island*

Station no., date and position	*Net*	*Depth (m.)*	Tomopteris carpenteri (*adult*)	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis antarctica	Vanadis longissima	Typhloscolex müller i	Travisiopsis levinseni	Pelagobi longicirrata
St. 100, 1–4. x. 26 33° 20′ 00″ S. 15° 18′ 00″ W. to 33° 46′ 00″ S. 15° 08′ 00″ E.	TYF	5–0	—	—	38	—	1	—	—	—
	TYF	225	—	—	—	—	—	—	—	—
	TYF	310–260	—	—	65	—	—	—	—	—
	TYF	475(–0)	—	—	116	—	—	—	—	—
	TYF	550–450	—	—	15	—	—	—	1	—
	TYF	675–625	—	—	—	—	—	—	—	—
	TYF	1000–300	—	—	—	—	—	—	—	—
	TYF	**1000–900**	—	—	—	—	—	—	—	—
	TYF	2000(–0)	—	—	—	—	—	—	—	—
	TYF	2500(–0)	—	—	137	—	—	—	—	—
	TYF	2500–2000	—	—	32	—	—	—	3†	—
St. 102, 28. x. 26 35° 29′ 20″ S., 18° 33′ 40″ E.	N 70 V	250–100	—	—	—	—	—	—	—	1
	N 70 V	500–250	—	—	1	—	—	—	—	12
	N 70 V	750–500	—	2	—	—	—	—	—	4
	N 70 V	1000–750	—	—	4	—	—	—	—	1
	N 100 H	52	—	—	—	—	—	—	—	—
	N 100 H	104	—	—	—	—	—	—	—	—
St. 103, 30. x. 26 39° 04′ 00″ S., 17° 38′ 00″ E.	N 70 V	50–0	—	—	—	—	—	—	—	1
	N 70 V	250–100	—	1	—	—	—	1	—	—
	N 70 V	500–250	—	—	—	—	—	—	—	1
St. 104, 31. x. 26 41° 33′ 30″ S., 17° 58′ 00″ W.	N 100 H	56(–0)	—	—	—	—	—	—	—	—
St. 107, 4. xi. 26 45° 03′ 00″ S., 17° 03′ 00″ E.	N 70 V	250–80	—	—	—	—	—	—	—	2
	N 70 V	500–250	—	1	—	—	—	2	1	1
	N 70 V	750–500	—	—	—	—	—	4	2	2
	N 70 V	1000–750	—	—	—	—	—	2	—	2
St. 114, 12. xi. 26 52° 25′ S., 9° 50′ E.	N 100 H	90	5*	—	—	—	—	—	—	—
St. 116, 14. xi. 26 54° 30′ 00″ S., 5° 34′ 00″ E.	N 100 H	110(–0)	—	—	—	—	—	—	2‡	—
St. 117, 17. xi. 26 About 5 miles N. 72° E. of Bouvet Island, 54° 20′ 40″ S., 3° 48′ 45″ E.	N 70 V	100–50	—	—	—	—	—	—	—	2
	N 70 V	250–100	—	—	—	—	—	—	—	6
	N 70 V	500–300	—	—	—	—	—	—	1	—
	N 70 V	750–500	—	—	—	—	—	1	1	6
St. 118, 19. xi. 26 53° 07′ S., 1° 26′ W.	N 100 H	100	3*	—	—	—	—	—	—	—
St. 404, 4. vi. 30 35° 34′ S., 15° 00½′ E.	N 100 B	100–0	—	—	—	—	—	—	—	—
St. 405, 4. vi. 30 33° 50′ 30″ S., 15° 46′ 00″ E. to 34° 16′ 00″ S., 15° 02′ 00″ E.	TYFB	1200–0	—	—	—	—	—	—	—	—
St. 407, 12. vi. 30 35° 13′ S., 17° 50½′ E. to 34° 57′ S., 17° 48′ E.	TYFB	220–0	—	—	—	—	—	—	—	—
	N 450 H	900–800	—	—	—	—	—	—	—	—
St. 413, 21. viii. 30 33° 13′ 00″ S., 15° 46′ 30″ E.	TYFB	350–0	—	—	—	—	—	—	—	—
St. 419, 30 viii. 30 36° 29′ 00″ S., 18° 16′ 15″ E. to 36° 29′ 00″ S., 18° 15′ 15″ E.	N 70 V§	50–0	—	—	—	—	—	—	—	—
	N 100 B§	84–0	—	—	—	—	—	—	—	—
St. 446, 9. x. 30 36° 14′ 00″ S., 16° 09′ 45″ E.	N 100 B	106–0	—	—	15¶	—	—	—	—	—
St. 448, 10. x. 30 39° 03′ 00″ S., 16° 11′ 45″ E.	N 100 B	161–0	—	—	4¶	—	—	—	—	—
St. 449, 11–12. x. 30 42° 30′ 30″ S., 15° 14′ 15″ E.	N 100 B	150–0	—	—	7¶	—	—	—	—	—

Table *e* (*cont.*)

Station no., date and position	*Net*	*Depth* (*m.*)	Tomopteris carpenteri (*adult*)	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis antarctica	Vanadis longissima	Typhloscolex mülleri	Travisiopsis levinseni	Pelagobia longicirrata
t. 450, 12–13. x. 30 44° 57′ 45″ S., 12° 57′ 15″ E. to 44° 56′ 30″ S., 12° 54′ 00″ E.	N 100 B	150–0	—	—	25¶	—	—	—	—	—
t. 451, 13–14. x. 30 47° 19′ 45″ S., 11° 05′ 00″ E.	N 100 B	170–0	—	9**	—	—	—	—	—	—
t. 452, 14. x. 30 49° 50′ 00″ S., 08° 32′ 30″ E.	N 100 B	91–0	—	—	—	—	—	—	—	—
t. 453, 16–17. x. 30 54° 05′ 30″ S., 03° 57′ 15″ E. to 54° 07′ 00″ S., 04° 03′ 00″ E.	N 100 B	165–0	—	—	20¶	—	—	—	—	—
t. 454, 17. x. 30 53° 42′ 00″ S., 04° 42′ 00″ E.	N 100 B	192–0	—	—	4¶	—	—	—	—	—
t. 455, 18. x. 30 53° 55′ 30″ S., 04° 47′ 00″ E.	N 100 B	116–0	—	—	3¶	—	—	—	—	—
t. 459, 19. x. 30 55° 09′ 15″ S., 02° 00′ 00″ E.	N 100 B	183–0	—	—	5¶	—	—	—	—	—
t. 460, 20–21. x. 30 56° 46′ 00″ S., 00° 41′ 45″ W.	N 100 B	155–0	—	—	8¶	—	—	—	—	—
t. 461 C, 21–22. x. 30 56° 44′ 00″ S., 02° 22′ 00″ W.	N 100 B	**95–0**	1	—	1	1	—	—	—	—
St. 463, 24. x. 30 55° 42′ 00″ S., 10° 54′ 00″ W.	N 100 B	132–0	—	—	—	—	—	—	—	—
St. 464, 26. x. 30 56° 03′ 00″ S., 12° 18′ 00″ W.	N 100 H	67(–0)	—	—	—	—	—	—	—	—
St. 465, 26. x. 30 55° 49′ 00″ S., 14° 02′ 15″ W.	N 100 B	113–0	—	—	—	—	—	—	—	—
St. 466, 27. x. 30 55° 35′ 00″ S., 16° 31′ 30″ W.	N 100 B	79–0	—	—	—	—	—	—	—	—

* Monro, 1930. † Reported by Monro, 1930, as *Travisiopsis* sp. ‡ Reported by Monro, 1930 as *Sagitella kowalewskii*. § One specimen of *Vanadis violacea* from each of these nets, not now identifiable. ¶ Monro, 1936. ** Reported by Monro, 1936, as *Tomopteris cavallii*.

Table *f*. *30° W. Line*

Station no., date and position	*Net*	*Depth* (*m.*)	Tomopteris carpenteri (*adult*)	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis antarctica	Vanadis longissima	Typhloscolex mülleri	Travisiopsis levinseni
St. 661, 2. iv. 31 57° 36′ S., 29° 54′ 30″ W. to 57° 36′ S., 29° 35′ W.	TYFB	**360–0**	5	—	3	—	—	—	—
	TYFV	500–250	—	1	5	—	—	—	1
	TYFV	750–500	2	—	—	—	—	—	—
St. 662, 3. iv. 31 55° 56′ S., 29° 57′ W.	TYFB	**460–0**	1	—	4	1	—	—	—
St. 663, 4. iv. 31 53° 34′ 30″ S., 30° 25′ 45″ W. to 53° 32′ 15″ S., 30° 20′ W.	TYFB	**380–0**	4	3	5	—	—	—	—
	TYFV	500–250	—	—	—	—	—	—	1
	TYFV	1500–1000	—	—	—	—	—	—	—
St. 665, 17. iv. 31 51° 41′ 30″ S., 29° 58′ 45″ W.	TYFB	**250–0**	1	—	1	—	—	—	—
St. 666, 17–18. iv. 31 49° 58′ 45″ S., 29° 52′ 30″ W. to 49° 58′ 45″ S., 30° 13′ W.	TYFB	**320–0**	1	1	5	—	—	—	—
	TYFV	750–500	1	—	—	—	—	—	1
	TYFV	1000–750	—	1	1	—	—	1	2
	TYFV	3000–2000	—	—	—	—	—	—	1
St. 668, 19. iv. 31 46° 42′ 30″ S., 30° 22′ W. to 46° 43′ 30″ S., 30° 22′ W.	TYFB	**375–0**	—	—	—	—	—	—	1
	TYFV	500–250	—	—	—	—	—	—	1
	TYFV	**1500–1000**	—	—	—	—	—	—	2
St. 669, 21. iv. 31 47° 04′ S., 30° 17′ W.	TYFV	2000–0	—	—	—	—	—	—	3

Table *f* (*cont.*)

Station no., date and position	*Net*	*Depth (m.)*	Tomopteris carpenteri (*adult*)	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis antarctica	Vanadis longissima	Typhloscolex mülleri	Travisiopsis levinseni
St. 671, 22–23. iv. 31	TYFB	**360–0**	—	—	1	—	—	—	—
43° 08′ S., 30° 15′ 45″ W.	TYFV	1000–0	—	5	—	—	—	—	1
	TYFV	1000–750	—	—	—	—	—	—	1
	TYFV	**1500–1000**	—	—	—	—	—	—	1
	TYFV	**2000–1500**	—	—	—	—	—	—	3
St. 672, 23. iv. 31	TYFB	200–0	—	2	—	—	—	—	—
40° 25′ S., 30° 06′ W.									
St. 673, 24–25. iv. 31	TYFB	340–0	—	—	—	—	—	—	—
38° 10′ 30″ S., 30° 10′ 15″ W. to	TYFV	250–0	—	—	2	—	—	—	—
38° 03′ 45″ S., 29° 48′ W.	TYFV	**500–250**	—	1	—	—	—	—	—
	TYFV	**1000–750**	—	—	—	—	—	—	—
	TYFV	**2000–1500**	—	—	—	—	—	—	—
St. 674, 25. iv. 31	TYFB	**280–0**	—	2	—	—	—	—	—
35° 58′ 30″ S., 29° 56′ W.									
St. 675, 26. iv. 31	TYFV	250–0	—	—	—	—	—	—	—
34° 08′ S., 29° 50′ 30″ W.	TYFV	1000–750	—	—	—	—	—	—	1
St. 676, 26. iv. 31	TYFB	**290–0**	—	—	—	—	—	—	—
33° 43′ 45″ S., 29° 52′ 45″ W.									
St. 677, 27–28. iv. 31	TYFB	**420–0**	—	—	—	—	—	—	—
31° 16′ 15″ S., 29° 56′ 30″ W.	TYFV	250–0	—	—	—	—	—	—	—
	TYFV	750–500	—	—	—	—	—	—	—
	TYFV	**2000–0**	—	2	—	—	—	—	—
St. 678, 28. iv. 31	TYFB	**360–0**	—	—	—	—	—	—	—
28° 30′ S., 29° 58′ W.									
St. 679, 29. iv. 31	TYFB	**300–0**	—	—	—	—	—	—	—
26° 06′ 30″ S., 30° 06′ 15″ W.	TYFV	250–0	—	—	—	—	—	—	—
	TYFV	**1500–1000**	—	—	—	—	—	—	—
St. 680, 3. iv. 31	TYFB	**260–0**	—	1	—	—	1	—	—
22° 36′ S., 30′ 01′ 30″ W.									
St. 682, 1. v. 31	TYFB	**375–0**	—	—	—	—	—	—	—
20° 11′ S., 29° 57′ 15″ W.									
St. 683, 2. v. 31	TYFB	**290–0**	—	—	—	—	—	—	—
16° 48′ S., 29° 54′ 45″ W.									
St. 685, 3. v. 31	TYFB	**350–0**	—	—	—	—	2	—	—
14° 28′ 45″ S., 29° 48′ 45″ W.									
St. 686, 4. v. 31	TYFB	**400–0**	—	1	—	—	—	—	—
11° 02′ 30″ S., 29° 51′ W.									
St. 687, 5. v. 31	TYFV	500–250	—	—	—	—	—	—	—
09° 47′ S., 29° 51′ W.	TYFV	750–500	—	—	—	—	—	—	—
St. 688, 5. v. 31	TYFB	**450–0**	—	—	—	—	—	—	—
09° 26′ 30″ S., 29° 50′ 30″ W.									
St. 689, 6. v. 31	TYFB	**410–0**	—	—	—	—	—	—	—
05° 59′ 45″ S., 29° 49′ 30″ W.									
St. 690, 7–8. v. 31	TYFB	**460–0**	—	—	—	—	—	—	—
03° 17′ 45″ S., 29° 57′ 45″ W. to	TYFV	**1500–0**	—	—	—	—	—	—	—
03° 20′ S., 30° 03′ 15″ W.									
St. 692, 9. v. 31	TYFB	**350–0**	—	—	2	—	—	—	—
02° 02′ 15″ N., 30° 08′ W.									
St. 693, 10. v. 31	TYFV	250–0	—	—	—	—	—	—	—
02° 59′ 30″ N., 29° 59′ W. to	TYFV	500–250	—	—	—	—	—	—	—
02° 59′ 30″ N., 30° 04′ 45″ W.									
St. 694, 10. v. 31	TYFB	**210–0**	—	—	—	—	—	—	—
04° 05′ 30″ N., 30° 00′ W.									
St. 697, 12. v. 31	TYFB	**460–0**	—	—	6	—	—	—	—
09° 15′ 15″ N., 30° 01′ 45″ W.									
St. 698, 13. v. 31	TYFB	**470–0**	—	—	2	—	—	—	—
12° 21′ 45″ N., 30° 07′ 30″ W.									
St. 699, 14. v. 31	TYFB	**370–0**	—	—	1	—	—	—	—
14° 27′ 15″ N., 30° 02′ 15″ W.	TYFV	500–250	—	—	—	—	—	—	—
	TYFV	750–500	—	—	—	—	—	—	—

Table g. *Falkland Islands to Cape Town*

Station no., date and position	*Net*	*Depth (m.)*	Tomopteris planktonis	Tomopteris septentrionalis	Travisiopsis levinseni	Typhloscolex mülleri	Pelagobia longicirrata
St. 69, 25. v. 26 45° 06′ 00″ S., 49° 00′ 00″ W.	N 70 H	**45(–0)**	—	7	—	—	—
St. 71, 30. v. 26	TYF	2000–0	—	—	—	—	—
43° 20′ 00″ S., 46° 02′ 00″ W.	N 70 V	500–250	—	—	—	2	—
	N 70 V	750–500	—	—	—	2	—
	N 70 V	1000–750	—	—	1	1	—
St. 72, 1. vi. 26 41° 43′ 20″ S., 42° 20′ 40″ W.	N 70 V	500–250	—	—	1	—	—
St. 74, 3. vi. 26 40° 30′ 40″ S., 38° 14′ 50″ W.	N 70 V	1000–0	—	—	—	—	—
St. 78, 12. vi. 26 35° 18′ 00″ S., 19° 01′ 10″ W.	TYF	1000(–0)	—	—	1	—	—
St. 85, 23. vi. 26	N 450	**2000(–0)**	—	—	1	—	—
33° 07′ 40″ S., 4° 30′ 20″ E.	N 70 V	1000–750	—	—	—	1	1
St. 87, 25. vi. 26	TYF	1000–0	—	—	—	—	—
33° 53′ 45″ S., 9° 26′ 30″ E.	N 70 V	1000–0	—	—	—	—	2
St. 89, 28. vi. 26	TYF	1000(–0)	—	—	1	—	—
34° 05′ 15″ S., 16° 00′ 45″ E.	N 70 V	100–50	—	—	—	—	1
	N 70 V	250–100	—	—	—	—	2
	N 70 V	750–500(–0)	—	—	—	1	2
St. 247, 16. vi. 27 37° 20′ 00″ S., 12° 47′ 30″ W.	TYF	**115–100**	2	—	—	—	—
St. 250, 17. vi. 27 36° 09′ 00″ S., 5° 33′ 00″ W.	TYF	**300(–0)**	13	3	—	—	—
St. 254, 21. vi. 27 35° 04′ 00″ S., 2° 59′ 30″ E.	TYF	**200–0**	39	1	—	—	—
St. 256, 23. vi. 27 35° 14′ 00″ S., 6° 49′ 00″ E.	TYF	1100–850(–0)	2	—	3	—	—
St. 257, 24. vi. 27 35° 01′ 00″ S., 10° 18′ 00″ E.	TYF	**250(–0)**	20	13	—	—	—
St. 258, 25. vi. 27 35° 03′ 30″ S., 13° 55′ 00″ E.	TYF	**450–320**	—	—	—	—	—
St. 259, 26. vi. 27 34° 59′ 00″ S., 16° 39′ 00″ E.	TYF	**450–370**	1	—	—	—	—

Table *h*. *Cape Verde Islands to and from Cape Town*

Station no., date and position	*Net*	*Depth (m.)*	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis longissima	Travisiopsis levinseni	Typhloscolex mülleri	Pelagobia longicirrata
St. 266, 21. vii. 27	TYF	**200–0**	—	11	—	—	—	—
29° 34′ 00″ S., 12° 24′ 00″ E.								
St. 267, 23. vii. 27	TYF	**550–450(–0)**	113	113	—	—	—	1
24° 31′ 00″ S., 12° 15′ 30″ E.								
St. 268, 25. vii. 27	TYF	**150–100(–0)**	—	73	—	—	—	1
18° 37′ 00″ S., 10° 46′ 00″ E.	N 100 B	73–0	—	10	—	—	—	—
St. 270, 27. vii. 27	TYF	**200–0**	—	—	1	—	—	—
13° 58′ 30″ S., 11° 43′ 30″ E.								
St. 273, 31. vii. 27	TYF	**230–200(–0)**	—	—	—	—	—	—
9° 38′ 00″ S., 12° 42′ 30″ E.								
St. 276, 5. viii. 27	TYF	**150(–0)**	—	—	—	—	—	—
5° 54′ 00″ S., 11° 19′ 00″ E.								
St. 282, 12. viii. 27	TYF	**300(–0)**	—	3	1	—	—	—
1° 11′ 00″ S., 5° 38′ 00″ E.								
St. 287, 19. viii. 27	TYF	**1000–800(–0)**	—	—	1	—	—	—
2° 49′ 30″ S., 9° 25′ 30″ W.								
St. 288, 21. viii. 27	TYF	**250(–0)**	—	—	—	—	—	—
00° 56′ 00″ S., 14° 08′ 30″ W.								
St. 289, 23–24. viii. 27	TYF	**225–125(–0)**	—	—	—	—	—	—
3° 04′ 45″ N., 16° 52′ 00″ W.								
St. 291, 24. viii. 27	TYF	100(–0)	—	—	1	—	—	—
3° 46′ 00″ N., 16° 49′ 00″ W.								
St. 294, 25. viii. 27	TYF	**115–100(–0)**	—	—	—	—	—	—
4° 33′ 15″ N., 16° 52′ 45″ W.								
St. 1592, 17. x. 35	TYFB	**200–0**	—	—	1	—	—	—
09° 31·4′ N., 18° 05·2′ W.	TYFB	**700–450**	—	—	—	—	—	—
St. 1594, 19. x. 35	TYFB	**144–0**	—	2	—	—	—	—
04° 15·9′ N., 12° 58·2′ W.	TYFB	**490–300**	—	—	—	—	—	—
St. 1596, 21. x. 35	TYFB	**170–0**	2	2	—	—	—	—
01° 40·3′ S., 07° 46·9′ W.	TYFB	**450–310**	—	—	—	—	—	—
St. 1598, 23. x. 35	TYFB	**180–0**	—	1	3	—	—	—
07° 10·8′ S., 02° 06·9′ W.	TYFB	**460–300**	—	1	—	—	—	—
St. 1600, 25. x. 35	TYFB	**151–0**	—	12	—	—	—	—
12° 43·3′ S., 00° 20·2′ E.	TYFB	**400–330**	—	3	—	—	—	—
St. 1602, 27. x. 35	TYFB	**175–0**	—	—	—	—	—	—
17° 59·9′ S., 04° 27·1′ E.	TYFB	**470–300**	—	—	—	—	—	—
St. 1604, 29. x. 35	TYFB	**182–0**	1	—	—	—	—	—
21° 34·4′ S., 08° 09·8′ E.	TYFB	**620–500**	—	1	—	—	—	—
St. 1606, 31. x. 35	TYFB	**190–0**	1	9	—	—	—	—
26° 15·8′ S., 12° 18′ E.	TYFB	**600–500**	—	—	—	—	—	—
St. 2028, 3. iv. 37	N 100 H	**5–0**	—	—	—	—	—	—
33° 57′ S., 03° 02·4′ E.	N 70 B	**118–0**	1	—	—	—	—	—
	N 100 B	**118–0**	2	—	—	—	—	—
St. 2029, 3. iv. 37	TYFB	2900–2600	—	1	—	—	—	—
33° 57′ S., 03° 02·4′ E.								
St. 2030, 4. iv. 37	N 100 H	**0–5**	—	—	—	—	—	—
33° 58·1′ S., 06° 47′ E.	N 70 B	**168–0**	—	—	—	—	—	—
	N 100 B	**168–0**	—	—	—	—	—	—
St. 2031, 5. iv. 37	TYFB	1800–1550	—	—	—	1	—	—
33° 57·2′ S., 09° 22·2′ E.								
St. 2032, 5. iv. 37	N 100 H	**0–5**	—	—	—	—	—	—
33° 57·5′ S., 10° 24·1′ E. to	N 70 B	**111–0**	—	—	—	—	—	—
33° 59·6′ S., 10° 24·6′ E.	N 100 B	**111–0**	—	—	—	—	—	—
St. 2033, 6. iv. 37	N 100 H	0–5	—	—	—	—	—	—
33° 54′ S., 12° 31·2′ E.	TYFB	1350–1250	—	—	—	1	—	—

Table *h* (*cont.*)

Station no., date and position	*Net*	*Depth* (*m.*)	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis longissima	Travisiopsis levinseni	Typhloscolex mülleri	Pelagobia longicirrata
St. 2034, 6. iv. 37	N 100 H	**0–5**	—	—	—	—	—	—
33° 46·6′ S., 14° 01·6′ E.	N 70 B	**162–0**	1	—	—	—	—	—
	N 100 B	**162–0**	3	—	—	—	—	—
St. 2035, 7. iv. 37	N 100 H	0–5	—	—	—	—	—	—
33° 57·2′ S., 16° 12·2′ E.	TYFB	950–750	—	—	—	—	—	—
St. 2036, 17. iv. 37	N 100 H	0–5	—	—	—	—	—	—
33° 45·5′ S., 15° 03·8′ E.	TYFB	2650–2200	—	—	—	—	—	—
St. 2037, 18. iv. 37	N 100 H	0–5	—	—	—	—	—	—
33° 29·4′ S., 10° 43′ E.	TYFB	2050–1800	—	—	—	—	—	—
St. 2038, 19. iv. 37	TYFB	1200–850	—	—	—	—	—	—
33° 29·2′ S., 06° 37·9′ E.								
St. 2039, 20. iv. 37	N 100 H	0–5	—	—	—	—	—	—
33° 38·5′ S., 3° 58·5′ E.	TYFB	1500–1200	—	—	—	—	—	—
St. 2040, 21. iv. 37	TYFB	600–0	1	—	—	—	—	—
33° 54·1′ S., 00° 08·8′ E.								
St. 2042, 22. iv. 37	TYFB	2800–2300	—	—	—	—	—	—
31° 40·5′ S., 00° 28·4′ W.								
St. 2044, 23. iv. 37	N 100 H	0–5	—	—	—	—	—	—
28° 38′ S., 01° 11·2′ W.	N 450 H	550–750	—	—	—	—	—	—
	N 450 B	750–0	—	—	—	—	—	—
St. 2045, 23. iv. 37	N 100 H	**0–5**	—	—	—	—	—	—
27° 27·1′ S., 01° 18·6′ W.								
St. 2046, 24. iv. 37	N 450 B	500–0	—	—	—	—	—	—
26° 06·9′ S., 01° 33·6′ W.								
St. 2047, 24. iv. 37	N 100 H	0–5	—	—	—	—	—	—
24° 53·9′ S., 01° 43·5′ W.	TYFB	1300–900	—	—	—	—	—	—
St. 2048, 25. iv. 37	N 450 B	1400–600	—	—	—	—	—	—
23° 16′ S., 01° 51·7′ W.	N 450 B	600–0	—	—	—	—	—	—
St. 2050, 26. iv. 37	N 450 B	430–0	—	—	—	—	—	—
20° 26′ S., 02° 16′ W.								
St. 2051, 26. iv. 37	TYFB	990–600	—	—	—	—	—	—
19° 10′ S., 02° 30·9′ W.								
St. 2053, 27. iv. 37	N 450 B	500–0	—	—	—	—	—	—
17° 45·7′ S., 02° 49·8′ W.	TYFB	900–550	—	—	—	—	—	—
St. 2055, 28. iv. 37	TYFB	2000–1400	—	—	—	—	—	—
14° 55·8′ S., 03° 39·7′ W.								
St. 2057, 29. iv. 37	N 450 B	1450–700	—	—	—	—	—	—
12° 09′ S., 04° 28·2′ W.	N 450 B	700–0	—	—	—	—	—	—
St. 2059, 30. iv. 37	N 450 B	1900–1400	—	—	—	—	—	—
09° 11·4′ S., 05° 17·4′ W.	N 450 B	1400–0	—	—	—	—	—	—
St. 2061, 1. v. 37	N 450 B	1900–1500	—	—	—	—	—	—
06° 36′ S., 06° 25·1′ W.	N 450 B	1500–0	—	—	—	—	—	—
St. 2063, 2. v. 37	N 450 B	1150–600	—	—	—	—	—	—
03° 24·8′ S., 07° 51·2′ W.	N 450 B	600–0	—	—	—	—	—	—
St. 2064, 3. v. 37	N 450 B	1600–1050	—	—	—	—	—	—
00° 46·9′ S., 10° 11·5′ W.	N 450 B	1050–0	—	—	—	—	—	—
St. 2065, 4. v. 37	N 450 B	1600–1400	—	—	—	—	—	—
02° 07·9′ N., 12° 30·5′ W.	N 450 B	1400–0	—	—	—	—	—	—
St. 2066, 5. v. 37	N 450 B	1950–1550	—	—	—	—	—	—
04° 56·4′ N., 14° 46·7′ W.	N 450 B	1550–0	—	—	—	—	—	—
St. 2073, 20. x. 37	TYFB	**375–0**	1	1	—	—	—	—
13° 12·2′ N., 23° 44′ W.								
St. 2074, 21. x. 37	TYFB	**875–400**	—	—	—	—	—	—
10° 10·9′ N., 21° 13·6′ W.								
St. 2075, 22. x. 37	TYFB	**1200–950**	—	—	—	—	—	—
07° 30·6′ N., 19° 03·3′ W.								

Table *h* (*cont.*)

Station no., date and position	*Net*	*Depth* (*m.*)	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis longissima	Travisiopsis levinseni	Typhloscolex müllerі	Pelagobia longicirrata
St. 2076, 24. x. 37 03° 05·4′ N., 15° 14·5′ W.	TYFB	1400–1050	—	—	—	—	—	—
St. 2077, 25. x. 37 00° 04·2′ S., 12° 22·1′ W.	TYFB	1300–1000	—	—	—	—	—	—
St. 2078, 26. x. 37 01° 53·2′ S., 10° 53·8′ W.	TYFB	2600–1400	—	1	—	—	—	—
St. 2079, 27. x. 37	TYFB	**250–0**	1	—	—	—	—	—
05° 51′ S., 07° 44·3′ W.	TYFB	**550–250**	—	—	—	—	—	—
St. 2080, 29. x. 37	TYFB	400–0	—	1	—	—	—	—
10° 12·7′ S., 04° 02′ W.	TYFB	1750–950	—	—	—	—	—	—
St. 2081, 31. x. 37 15° 25·2′ S., 00° 28·9′ E.	TYFB	950–500	—	—	—	—	—	—
St. 2082, 2. xi. 37	TYFB	330–0	—	—	1	—	—	—
20° 53·4′ S., 05° 23·6′ E.	TYFB	1100–800	—	—	—	—	—	—
St. 2083, 3. xi. 37 24° 43·9′ S., 08° 58·7′ E.	TYFB	**330–0**	1	4	—	—	—	—
St. 2084, 5. xi. 37	TYFB	240–0	1	—	—	—	—	—
28° 52·9′ S., 13° 20·4′ E.	TYFB	1500–800	—	5	—	—	—	—
St. 2627, 29. iii. 39 33° 11·5′ S., 17° 14·7′ E.	TYFB	**310–40**	—	—	—	—	—	—
St. 2628, 30. iii. 39 30° 54·1′ S., 13° 14·1′ E.	TYFB	**1300–650**	—	—	—	—	—	—
St. 2629, 31. iii. 39 27° 17·1′ S., 12° 04′ E.	TYFB	**1800–1300**	—	1	—	—	—	—
St. 2630, 1. iv. 39 23° 39·2′ S., 10° 53·6′ E.	TYFB	**1050–550**	—	8	—	—	—	—
St. 2632, 3. iv. 39 15° 56·3′ S., 10° 49′ E.	TYFB	**1800–?**	—	—	—	—	—	—
St. 2635, 11. iv. 39 10° 19′ S., 09° 36·4′ E.	TYFB	**280–0**	—	—	1	—	—	—
St. 2636, 12. iv. 39 08° 26·5′ S., 05° 59·4′ E.	TYFB	**950–550**	—	—	1	—	—	—
St. 2638, 14. iv. 39 04° 50·3′ S., 00° 47·3′ W.	TYFB	**150–0**	—	1	—	—	—	—
St. 2639, 15. iv. 39 02° 53·2′ S., 04° 21·5′ W.	TYFB	**1200–600**	—	—	—	—	—	—
St. 2640, 16. iv. 39 01° 47′ S., 06° 13′ W.	N 50 V	100–0	—	1	—	—	1	1
St. 2641, 16–17. iv. 39 00° 45·3′ S., 07° 26·6′ W.	N 50 V	**100–0**	2	1	—	—	2	3
St. 2642, 17. iv. 39 00° 18·7′ N., 08° 39·4′ W.	N 50 V	100–0	—	—	—	—	—	—
St. 2643, 18. iv. 39 01° 27·4′ N., 09° 53·5′ W.	N 50 V	**100–0**	—	—	—	—	1	1
St. 2644, 18. iv. 39 02° 35·8′ N., 10° 58·5′ W.	N 50 V	100–0	—	—	—	—	—	—
St. 2645, 19. iv. 39 03° 39·2′ N., 12° 09·6′ W.	N 50 V	**100–0**	—	—	—	—	—	—
St. 2646, 19. iv. 39	TYFB	**250–0**	—	3	—	—	—	—
05° 38·7′ N., 14° 03·1′ W.	TYFB	**1500–800**	—	—	—	—	—	2
St. 2647, 20. iv. 39 07° 58′ N., 16° 36·3′ W.	TYFB	**310–0**	—	3	—	—	—	—
St. 2648, 21. iv. 39	TYFB	**500–0**	—	—	—	—	—	—
10° 29·8′ N., 18° 46·1′ W.	TYFB	**1450–950**	—	—	—	—	—	2

Table *j*. *Cape Verde Islands to Falkland Islands*

Station no., date and position	*Net*	*Depth (m.)*	Tomopteris planktonis	Tomopteris septentrionalis	Travisiopsis levinseni
St. 701, 16. x. 31 14° 39·3′ N., 25° 51·7′ W.	TYFB	**242–0***	—	—	—
St. 702, 17. x. 31 10° 59·3′ N., 27° 03·8′ W.	TYFB	**236–0***	—	1	—
St. 703, 18. x. 31 07° 17′ N., 28° 01·9′ W.	TYFB	**358–0**	—	—	—
St. 704, 19. x. 31 03° 37·7′ N., 29° 14′ W.	TYFB	**231–0***	—	—	—
St. 705, 20. x. 31 00° 03·4′ N., 30° 36·8′ W.	TYFB	**150–0***	—	—	—
St. 706, 21. x. 31 03° 26·2′ S., 32° 08·3′ W.	TYFB	**354–0***	—	—	—
St. 707, 22. x. 31 06° 44′ S., 33° 33′ W.	TYFB	**182–0***	4†	2†	—
St. 708, 23. x. 31 10° 20·6′ S., 34° 54·7′ W.	TYFB	**208–0***	—	—	—
St. 709, 24. x. 31 14° 01·4′ S., 36° 30·7′ W.	TYFB	**216–0***	—	—	—
St. 710, 26. x. 31 21° 45′ S., 39° 50′ W.	TYFB	**294–0**	1†	—	—
St. 711, 27. x. 31 24° 40·7′ S., 41° 30·8′ W.	TYFB	**290–0***	—	—	—
St. 712, 28. x. 31 28° 02·1′ S., 43° 09·5′ W.	TYFB	**224–0***	—	—	—
St. 713, 29. x. 31 31° 37·1′ S., 45° 00′ W.	TYFB	**200–0***	—	—	—
St. 714, 30. x. 31 35° 09·5′ S., 47° 00′ W.	TYFB	**246–0***	1†	4†	—
St. 715, 31. x. 31 38° 44·2′ S., 49° 18·7′ W.	TYFB	**230–0***	—	—	—
St. 716, 1. xi. 31 42° 08·8′ S., 51° 35′ W.	TYFB	**212–0**	—	2†	1
St. 717, 2. xi. 31 44° 42′ S., 53° 32·2′ W.	TYFB	**212–0**	—	—	—
St. 718, 3. xi. 31 47° 27·2′ S., 55° 10·2′ W.	TYFB	**262–0**	—	12†	—

* Numerous polychaetes which I have not seen are reported on the Analyses Sheets from these stations.

† Reported by Monro, 1936, as *Tomopteris planktonis.*

Table *k*. *Miscellaneous Stations*

Station no., date and position	*Net*	*Depth (m.)*	Tomopteris carpenteri *(adult)*	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis antarctica	Vanadis longissima	Rhynchonerella bongraini	Typhloscolex mülleri	Travisiopsis levinseni	Pelagobia longicirrata
St. 4, 30. i. 26 36° 55′ 00″ S., 12° 12′ 00″ W.	N 100 H	10–0*	—	—	—	—	—	—	—	—	—
St. 12, 18. ii. 26 51° 55′ 00″ S., 32° 27′ 30″ W.	N 70 V	500–250*	—	—	—	—	—	1	—	—	2
St. 17, 4. iii. 26 46 miles N. 46° E. of Jason Light, South Georgia	N 70 V	500–250*	—	—	—	—	—	—	—	1	6†
St. 26, 14. iii. 26 26·5 miles N. 54° E. of Jason Light, South Georgia	N 100 H	60(–0)	1	—	—	—	—	—	—	—	—

Table *k* (*cont.*)

Station no., date and position		*Net*	*Depth* (*m.*)	Tomopteris carpenteri (*adult*)	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis antarctica	Vanadis longissima	Rhynchonerella bongraini	Typhloscolex mülleri	Travisiopsis levinseni	Pelagobia longicirrata
St. 41, 28. iii. 26	*A*	N 70 V	265–150*	—	1**	—	—	—	—	—	—	3‡
16·5 miles N. 39° E. of	*B*	N 70 V	265–150*	—	—	—	—	—	—	—	—	6‡
Barff Point	*D*	N 70 V	**240–150***	—	—	—	—	—	—	—	—	5‡
South Georgia	*E*	N 70 V	**150–100***	—	—	—	—	—	—	—	—	4‡
St. 45, 6. iv. 26 2·7 miles S. 85° E. of Jason Light, South Georgia		NCS-T	270–238	—	—	—	—	—	—	—	—	—
St. 130, 20. xii. 26 54° 06′ 00″ S., 36° 23′ 00″ W.		N 70 H	5–0*	3	—	1†	—	—	—	—	—	—
St. 150, 15–16. i. 27 53° 52′ 30″ S., 36° 00′ W. to 53° 31° S., 35° 24′ 30″ W.		N 100 H	5–0*	38	—	—	—	—	—	—	—	—
St. 151, 16. i. 27 53° 25′ 00″ S., 35° 15′ 00″ W.		N 70 V	1000–750	—	—	—	—	—	—	—	1§	—
St. 169, 22. ii. 27 60° 48′ 50″ S., 51° 00′ 20″ W.		TYF	1100–1000	—	—	—	—	—	—	—	—	—
St. 334, 4. ii. 30 53° 43′ S., 36° 51′ W.		N 70 B	110–0	—	—	—	1‡	—	—	—	—	—
St. 373, 19. iii. 30 58° 00′ S., 33° 44′ W.		TYFB	**275–0**	—	—	—	1‡	—	—	—	—	—
St. 395, 13. v. 30 48° 26¾′ S., 22° 10′ W. to 48° 26½′ S., 22° 06½′ W.		N 450 H	1600–1500	—	—	—	—	—	—	—	—	—
St. 461, 21–22. x. 30												
56° 44′ S., 02° 23′ W.	*B*	N 100 B	?	1	—	—	—	—	—	—	—	—
56° 44′ S., 02° 22′ W.	*C*	N 100 B	95–0*	—	—	—	1‡	—	—	—	—	—
St. 527, 11. xii. 30 54° 09¼′ S., 34° 29½′ W.		N 450 H	**122(–0)**	—	—	—	3‡	—	—	—	—	—
St. 532, 15. xii. 30 58° 29′ S., 37° 44′ W.		N 100 B	150–0	3	—	—	—	—	—	—	—	—
St. 535, 18. xii. 30 60° 13¼′ S., 50° 51½′ W.		N 100 B	155–0	—	—	—	1	—	—	—	—	—
St. 619, 19. ii. 31 59° 33′ S., 43° 07¼′ W.		N 70 B	114–0	—	—	—	1‡	—	—	—	—	—
St. 813, 16. i. 32 64° 55·9′ S., 23° 13′ W.		N 100 B	**135–0**	1	—	—	—	—	—	—	—	—
St. 825, 28. i. 32 56° 31·2′ S., 36° 00·5′ W.		N 70 B	**117–0**	1	—	—	—	—	—	—	—	—
St. 1079, 14. xii. 32 54° 24′ S., 35° 54·5′ W.		N 50 V	100–0	—	—	—	—	—	—	—	—	7
St. 1148, 9. iii. 33 63° 52′ S., 00° 54·9′ W.		N 100 H	**5–0**	—	—	—	1‡	—	—	—	—	—
St. 1157, 15. iii. 33 61° 51′ 5″ S., 14° 31′ 3″ E.		TYFB	240–0	2	—	—	—	—	—	—	—	—
St. 1201, 27. xi. 33 53° 19·9′ S., 37° 07·4′ W.		N 100 B	93–0	1	—	—	—	—	—	—	—	—
St. 1554, 28. iii. 35 38° 02·9′ S., 18° 39·7′ E.		TYFB	1500–0*	—	—	—	—	—	—	—	1	—
St. 1555, 29. iii. 35 39° 51·6′ S., 18° 41·8′ E.		TYFB	**1000–0***	—	2	1	—	—	—	—	—	—
St. 1559, 2. iv. 35 50° 07·2′ S., 22° 16·8′ E.		N 450 H	500(–0)*	12	—	—	—	—	—	—	—	—
St. 1772, 23. v. 36		N 70 B	**440–150***	—	—	—	—	—	—	—	—	3
36° 01·8′ S., 00° 04·3′ E.		N 70 B	**750–450***	—	2	—	—	—	—	—	—	—
St. 1789, 8. vi. 36 57° 11·4′ S., 17° 12·6′ E.		N 70 B	120–0	—	—	—	1	—	—	—	—	—
St. 1871, 12. xi. 36 64° 04·4′ S., 52° 57·5′ W.		TYFB	1450–1000	1	—	—	—	—	—	—	—	—

Table *k* (*cont.*)

Station no., date and position		*Net*	*Depth (m.)*	Tomopteris carpenteri (*adult*)	Tomopteris planktonis	Tomopteris septentrionalis	Vanadis antarctica	Vanadis longissima	Rhynchonerella bongraini	Typhloscolex mülleri	Travisiopsis levinseni	Pelagobia longicirrata
St. 1876, 14. xi. 36 58° 37·7′ S., 54° 54·4′ W.		TYFB	1550–1100	1	—	—	—	—	—	—	—	—
St. 1881, 22. xi. 36 45° 49·5′ S., 60° 01·8′ W.		N 100 B	173–0*	—	—	—	—	1	—	—	—	—
St. 1917, 3. xii. 36 53° 48·7′ S., 46° 27·7′ W.		TYFB	1400–1000	1	—	—	—	—	—	—	—	—
St. 1935, 11. xii. 36												
53° 31·9′ S., 37° 22·4′ W.	*F*	N 100 H	200	—	—	—	—	—	—	—	3	—
53° 32′ S., 37° 25·2′ W.	*H*	N 100 H	170	—	—	—	—	—	—	—	2	—
St. 1936, 15. xii. 36 52° 58·8′ S., 37° 59·8′ W.	*H*	N 100 H	109	—	—	—	1	—	—	—	—	—
St. 1946, 3. i. 37 59° 09·2′ S., 48° 26·6′ W.		TYFB	1700–1300	—	—	—	—	—	—	—	—	1
St. 1972, 28. ii. 37 52° 11′ S., 52° 33·7′ W.		N 70 B	139–0*	—	—	—	—	1	—	—	—	—
St. 1993, 12. iii. 37 59° 37·7′ S., 27° 52·8′ W.		TYFB	950–650	—	—	—	—	—	—	—	—	—
St. 1994, 12. iii. 37 60° 35·6′ S., 26° 40·4′ W.		N 100 B	**254–166(–0)**	1	—	—	—	—	—	—	—	—
St. 1995, 13. iii. 37 61° 21·1′ S., 25° 49·2′ W.		TYFB	1800–1300	—	—	—	—	—	—	—	1	—
St. 2006, 19. iii. 37 66° 16·7′ S., 13° 23·3′ W.		N 100 B	131–0	—	—	—	1	—	—	—	—	—
St. 2322, 17–18. iv. 38		N 100 B	5–0*	—	—	—	1	—	1	—	—	—
65° 53′ S., 00° 24·4′ E.		N 100 B	106–0*	—	—	1	3	—	—	—	—	—
		N 100 B	670–420*	—	1	1	—	—	—	1	1	—
St. 2567, 30. i. 39 58° 12′ S., 19° 46′ E.		N 100 H	5–0	13	—	—	—	—	—	—	—	—
St. WS 53, 11–12. i. 27	*B*	N 100 H	**5–0**	1‡	—	—	—	—	—	—	—	—
54° 03′ 30″ S., 38° 35′ W.	*L*	N 100 H	**5–0**	1	—	—	—	—	—	—	—	—
to	*M*	N 100 H	**5–0**	1	—	—	—	—	—	—	—	—
53° 29′ 00″ S, 37° 13′ 45″ W.	*O*	N 100 H	**5–0**	1	—	—	—	—	—	—	—	—
	P	N 100 H	**5–0**	7	—	—	—	—	—	—	—	—
	T	N 100 H	**5–0**	2	—	—	—	—	—	—	—	—
	U	N 100 H	**5–0**	2	—	—	—	—	—	—	—	—
	V	N 100 H	**5–0**	1	—	—	—	—	—	—	—	—
St. WS 59, 17. i. 27 52° 57′ S., 37° 06′ 30″ W.		N 100 H	113	2	—	—	—	—	—	—	—	—
St. WS 60, 17. i. 27 52° 47′ S., 37° 06′ 30″ W.		N 100 H	**146**	2	—	—	—	—	—	—	—	—
St. WS 61, 18. i. 27		N 100 H	**5–0**	1	—	—	—	—	—	—	—	—
53° 37′ 30″ S., 37° 06′ 30″ W.		N 100 H	**132**	3	—	—	—	—	—	—	—	—
St. WS 194, 11–12. iii. 28 53° 23′ S., 37° 10′ W. to 53° 03′ S., 36′ 52′ W.		N 100 B	88–0*	1	—	—	1	—	—	—	—	—
St. WS 200, 21. iv. 28 59° 05′ S., 46° 32′ W.		N 100 B	93–0	—	—	—	3	—	—	—	—	—
St. WS 351, 11. i. 29 54° 21′ 30″ S., 34° 59′ W.		N 70 V	**1000–750**	—	—	—	—	—	—	1	—	—
St. WS 372, 21. i. 29 54° 08′ 30″ S., 35° 42′ W.		N 100 B	150–0	2	—	—	—	—	—	—	—	—
St. WS 408, 26. ii. 29 53° 50′ S., 62° 10′ W.		N 70 B	112–0*	—	—	—	—	1‖	—	—	—	—
St. WS 411, 14. iii. 29 52° 08′ S., 52° 35′ W.		N 70 B	100–0*	—	—	—	—	1‖	—	—	—	—
St. WS 472, 12. xi. 29 59° 42½′ S., 58° 01′ W.		N 100 B	125–0	—	—	—	—	—	—	—	—	3

* These samples were sorted. Other records in this table are for specimens picked out at random. † Monro, 1930. ‡ Monro, 1936. § Reported by Monro, 1936, as *Travisiopsis benhami*. ‖ Reported by Monro, 1936, as *Vanadis antarctica*. ** Reported by Munro, 1936, as *Tomopteris septentrionalis*.

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STUDIES ON *PHYSALIA PHYSALIS* (L.)

PART 1. NATURAL HISTORY AND MORPHOLOGY

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STUDIES ON *PHYSALIA PHYSALIS* (L.)

PART 1. NATURAL HISTORY AND MORPHOLOGY

By A. K. Totton

British Museum (Natural History)

(Plates VII to XXV, text-figures 1–31)

INTRODUCTION

Although much of this story is technical, it is hoped that it may be of interest to laymen, seafarers and voyagers as well as professional zoologists. So it will be as well to explain that the Portuguese man-of-war is a sort of jelly-fish. People often ask 'why Portuguese?' It was the Portuguese, in the time of Henry the Navigator, who had fleets of the then curious, new, light ships called caravels. Between 1420 and 1552 they were exploring half the maritime world, and their characteristic fore-and-aft lateen sails were well known to all seamen. I think it must have been the possession of a fore-and-aft sail or crest, and the way in which *Physalia** heads into the wind, a fact which no sailorman could fail to notice, but one which is certainly not observed in these days, that led seamen in the latter part of the fifteenth century to call these animals 'caravels' or 'Portuguese men-of-war'.† The seamen who took Sloane to Jamaica in 1687 were still doing so; but in these days of steam and diesel engines the name seems to be half-forgotten. Australians call the animals 'Bluebottles', and the Spaniards of the Canary Islands 'agua viva'.

ACKNOWLEDGEMENTS

I have to thank the Trustees of the Percy Sladen Trust for a grant which made my work at Arrecife possible. It was entirely due to the kindness and hospitality of the Administrator of the Parador Nacional, Señor Don José Juaréz Sanchez-Herrera, who showed keen interest in the work and went out of his way to satisfy every want, that a laboratory was arranged on his very convenient premises. It was one of the few places on the island where running water, hot and cold, and easy access to sea-water were available. Suitable boats were difficult to find, but Señor Don C. Martinez Cabrero was kind enough to lend his dinghy fitted with an outboard motor.

I also wish to thank Dr G. O. Mackie for his valuable co-operation in the field, and Dr Helene Bargmann for help in the arrangement of this report.

MATERIAL AND METHODS

The specimens, on which the morphological facts described in this memoir are based, derive partly from the Discovery Collections, but chiefly from those collected, anaesthetized and preserved in

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* *Physalia* must not be confused with a smaller blue, floating, crested polyp *Vellela*, also very well known to seafarers, which is only two or three inches long.

† When I was trying to get permission to take some official photographs of the Portuguese man-of-war, so unfamiliar to the layman was this popular English name, that it was necessary to explain to the authorities that the object was of a zoological and not of a nautical nature.

formalin during a three-months' visit that I made in the spring of 1955 to Arrecife, Canary Islands. During part of this time I was fortunate enough to have the co-operation of Dr G. O. Mackie.

After having worked on these specimens, which range in size from 11 to 180 mm. in float-length, for two and a half years at the British Museum (Natural History), I heard that Miss Eleanor Dodge was preparing to work at Miami, Florida on the toxin of *Physalia*. I wrote to ask if she would be kind enough to secure me some larvae should they be available. On 14 January 1958 I received from her a most welcome series of young specimens measuring from 4 to 15 mm. in length. Miss Dodge was also kind enough to send me from Crandon Park Beach, Biscayne Key, off Miami, a second valuable collection of younger larvae measuring from 1·2 to 5 mm. in length, collected on 20 January 1958, which I received on 14 February 1958. I was thus able to figure and insert into the typescript, which I had already completed, information on those stages of development at which budding begins. In this way I have been able to complete the picture of the origin and pattern of budding in *Physalia*.

It is almost impossible to examine specimens fully until the air in the float has been displaced by fluid, or the float cut off. My most rewarding work has been done by combining successive dissections with photography. The methods employed had to be purely exploratory to begin with, because previous accounts of the arrangement of the groups of buds in *Physalia* were too superficial and illustrated either not at all (Schneider, 1896) or so inadequately (Steche, 1910; Okada, 1932, 1935) that they could not be checked and built upon. In fact it was necessary to start *de novo*. Now that some kind of pattern has been recognized it may be thought that the exploratory phase of the work was unduly long. The results must be published now before further refinements of the analysis can be made. But it is hoped that someone in the future will be able more quickly to examine a series of specimens (comparable with the young specimens to which I devoted much attention), and will find out to what extent there is variation of the pattern observed and illustrated in this memoir.

It is regretted that a better photographic technique was not available, but it was not possible to make repeated dissections in the photographic studio of the Museum. Also, the carrying of such dissections in dishes of formalin over long distances from laboratory to studio was found to cause too much disarray of the specimens through swirling motions of the liquid. Recourse was therefore made to dissection on the stage of a Bausch and Lomb binocular dissecting microscope set up on the base of an old Leica photocopier. The arm carrying the viewer, a Leica camera and lamps was swung to one side. When the dissection had been displayed, the body of the microscope was slid out and camera and viewer were moved into position.

A method of dissection that I would recommend to anyone wishing to examine the structure of *Physalia* for the first time is as follows: First remove the float, leaving the primary polyp and appendages of both oral and main zone attached to a narrow strip of the bladder-wall. Secondly, sever the oral zone at the basal internode from the main zone. Thirdly, sever the first two cormidia by a cut with fine scissors just to the oral side of the main tentacle. Then make a similar cut a little to the oral side of the chief tentacle of cormidium V. This will leave the three most representative cormidia attached to a strip of the bladder-wall, which can be turned about and folded to reveal the internodes between the three cormidia. A well-relaxed specimen about 4–5 in. in float-length would probably not be too complexly branched for recognition of the basic pattern of arrangement of branches, polyps, tentacles, and gonodendra. This basic pattern is described on page 328.

The structure of contracted specimens is exceedingly difficult, if not impossible, to analyse satisfactorily, so live specimens to be examined in this way should be carefully anaesthetized in magnesium chloride ($7\frac{1}{2}\%$ in fresh water) and fixed in formalin. It was found that expansion was aided by injecting with a fine needle both the magnesium chloride and the formalin into the gastrovascular space near the base of the chief tentacle. The muscular walls were found to be self-sealing. Air can be drawn out from the float for sampling in the same way without loss, though it is better to cut out the complete air-sac.

The pneumatocyst can be quickly removed from a living specimen by making an incision with scissors down the wall of the pneumatocodon, while it is held by the crest in the air. Contraction of the outer muscular wall soon frees the sac, which can be tied off for safety short of the aboral valve before cutting off the remains of the pneumatocodon. Pressure can then be applied to the immersed sac (which of course floats) to dilate the dorsal processes until fixation is complete.

Physalia, it was found, could be handled by the float without fear of stinging, but a pair of plastic salad-servers, kept scrupulously clean, was used for handling the numerous laboratory specimens, and particularly for lifting them in a breeze from the sea into buckets. In this operation it was found imperative to avoid allowing the tentacles to touch either oars, gunwale or thwarts of the boat; tentacles adhere tightly to wooden objects and are almost impossible to remove. When lifted from the sea the tentacles may hang down for 5 or 6 ft. and need careful handling in a breeze.

The authorities at the Victoria Hospital at Las Palmas, where hundreds of stung patients are treated, advised the taking of an anti-histamine if badly stung, but there was no occasion to do so because the precautions outlined above were taken.

From my rough diary I see that specimens of *Physalia* were available at Arrecife, where we arrived on 18 February 1955, as follows:

4 March	First specimens brought in by Senor Don Jorgé from Graciosa I.
10	Three right-handed specimens drifted in.
15	Wind S.E. all day, but dropping. At 5 p.m. numerous left-handed *Physalia* taken. Later when wind was S.W., many right-handed specimens taken.
20	Calculated that with present wind *Physalia* would pass 1 or 2 km. south of Arrecife, where in fact none came ashore. Drove to Caletta on north coast and picked up thirty-two.
4 April	Many young specimens drifted on to beach on east side of Islote de los Ingleses.
9	One specimen, 4·5 in. float-length.
13	Strong N.E. trades. Many left-handed *Physalia*. First experiments on drifting.
15	A few *Physalia*. Second set of drifting experiments.
16	Sixty-five specimens brought in by boys. Third set of drifting experiments.
18	One young specimen.
21	A large sea-area covered by specimens, spotted through binoculars at 6.30 p.m. half-a-mile south of laboratory. Two dozen brought in.
6 May	One young specimen from east side of Islote.
10	One young specimen.
12	Small specimens.
13	Three small specimens.
24	Departure.

I could get no reliable information in the Canaries as to periodicity of appearance of *Physalia*, except that at Las Palmas they were most noticeable up to June, after which they decreased in numbers. There was a common belief that they bred on a reef protecting El Canteras beach on the north side, and were washed off the reef into the bathing-area.

The Arrecife boys soon came to know that we were interested in 'agua viva' as they called *Physalia*, and I used to issue buckets and a pair of plastic salad-servers to the best collectors, with a warning that only really fresh specimens, and particularly very tiny ones were needed. If specimens are to be kept in good condition for more than a day or so, very large vessels are required, such as the hatching-tanks used by Brooks and Conklin (1891).

The electricity supply at Arrecife used to be cut off at 1 a.m., after three warning flicks given a quarter of an hour previously. So it was always a race against time at the end of a busy day to transfer specimens to buckets and plastic bowls of fresh seawater; to get rid of stale water and moribund specimens, which I always deflated with a pair of scissors to avoid re-collection; and to reach one's bedroom and light a candle before the lights went out.

NON-TECHNICAL DESCRIPTION OF THE PORTUGUESE MAN-OF-WAR

For the benefit of the reader who does not wish to examine minutely the structure of *Physalia*, I will attempt to give in plain language a short account of its significant features with the least assumption of previous knowledge.

The conventional idea of a marine animal must be forgotten. *Physalia* is very simply organized, without head, tail, limbs, skeleton, mouth, alimentary canal, anus, gills, blood-vessels, body-cavity, kidneys, brain or one-way-traffic nerves. It is really an overgrown polyp-like* larva, belonging to the Cnidaria, the group which includes jelly-fish, corals and sea-anemones. It floats on its side and, without growing-up into a sexually mature animal itself, produces underneath as buds, innumerable similar daughter polyps—these too are really in the larval phase—which bud again and produce thousands of minute and not fully formed adults, having the essential structure of a jelly-fish or medusa, and which are called gonophores.† Though not fully formed like the usual jelly-fish, the gonophores represent the adult, sexual phase; and in any one specimen are all either male or female. The daughter polyps also bud off non-sexual simplified adults for propelling the broken-off branchlets which bear the true sexual adults.

So, in *Physalia*, we have two components to think of:

(1) The original polyp, hatched from the egg, which becomes a sort of nurse carrying about the innumerable buds to which it gives rise. An asexual larva itself, it not only buds off other larvae, but adults as well, both asexual and sexual. The larva is a hollow sac with a mouth at one end and only a single tentacle (Pl. VII, fig. 2); it develops from a fertilized egg and becomes very much enlarged and continues to float. The much enlarged original polyp itself extends from one end of the specimen to the other. One end is free of buds and has near its tip a pore communicating with the enormous air-sac, which as a small depression during the early development becomes pushed inside the float-end of the polyp. At the other end, the mouth, stomach and tiny tentacle of the original polyp soon become nearly hidden by all the daughter buds (Pl. VIII).

(2) We must consider these daughter buds: some of them take in and digest the food, some consist chiefly of a long stinging tentacle, others, the palpons, appear to be protective and sensory, and the remainder are the little imperfect sexual adults (the gonophores) and the asexual medusoids (the swimming bells or nectophores).

In no other cnidarian do we find such prolific budding as in *Physalia* (Pl. IX). After the original polyp has hatched from the egg and has assumed the horizontal position characteristic of the species, and the aboral float has begun to enlarge, the first buds begin to appear on the under-surface in the middle part of the polyp. Later buds arise in turn from the bases of the first buds which soon elongate, so that subsequent series of buds are borne on stalks or peduncles. The first series of buds is arranged in two major zones: an oral zone of at least five small peduncles separated by a gap, the basal internode, from a larger main zone of six or seven peduncles. As series after series of buds appear, each laterally

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* A polyp has the shape of an elongated cylinder fastened at one end, with a mouth and one or more tentacles at the free end. The name is derived from the French word 'poulpe' meaning octopus with its mobile tentacles.

† I find that Leuckart (1851) had long ago come to the same conclusion.

on the peduncle of its predecessor, they gradually appear changed in character from the long feeding polyps (gastrozooids) to smaller protective palpons. The gastrozooids differ from those of related species in becoming separated from their tentacles. Each stinging tentacle itself is borne on an enlarged base (ampulla), which supplies stinging-cells (nematoblasts) to the long stinging tentacle. The palpons protect the even smaller, reduced, sexual medusoids or gonophores, which are the true adults. Probably the palpons have an anal function as well. There are intermediate stages between the first and last kinds of polyps.

The float is at first relatively small (Pl. VII), occupying the aboral end of the animal, but later on, greatly enlarged the float appears on top. On the inner wall of the air-sac of the float is a round pellucid patch, the gas-gland (Pl. VIII, fig. 5), which secretes air from the water into the air-sac. There is one common digestive and circulatory space, stretching also round the air-sac, with which all the daughter polyps and gonophores communicate, so that the products of digestion can reach all parts. Waste products can diffuse out through the fine tissues, through which oxygen also can be taken up from the sea; undigested refuse like fish-bones and scales can be got rid of again through the mouths of the gastrozooids.

The details of reproduction are still unknown, but probably terminal branches bearing the gonophores break off and are kept on the move by the asexual medusoids (swimming-bells). Fertilization probably takes place in the sea.

It was realized long ago that the long axis of *Physalia* takes up early in life a peculiar orientation in the water. Whereas most siphonophores have the oral-aboral axis vertical, the overgrown air-sac of *Physalia* topples over so to speak so that the long axis is horizontal. Circular and longitudinal sheets of muscle are developed everywhere, so that the animal can turn and twist about, lengthen and shorten its polyps and tentacles, and open wide and close its many mouths.

Physalia appears to be very successful in avoiding being eaten except in the juvenile stage. It needs no sense-organs to find food. Fishes as large as mackerel and flying fish bump into its tentacles and provide much more food than *Physalia* can digest. When the surplus is jettisoned, many of the attached feeding gastrozooids are lost, but this loss is quickly made good by the great proliferation of buds, a faculty which may have arisen in consequence of the abundant food.

Physalia is indeed an unusual sort of animal, an association of larval and adult individuals or persons—as opposed to organs—which have been budded from the parent larva but which have not become separated from it, the parent larva itself having developed a giant float to carry all these individuals at the surface of the sea.

APPEARANCE AND HABITS

Physalia's sky-blue, or light green, air-filled bladder with carmine-edged crest floats at the surface and the animal drifts in the wind. The float may reach a length of 10 or 12 in. and its deep-blue trailing tentacles, difficult to see when fully extended, can reach a length of 50 m. or more. The tentacles carry enormous numbers of stinging-cells or nematocysts.

The smallest specimens from Miami (Pl. VII) measured 1·25 mm. in length. This is less than the smallest, previously recorded by Huxley (1859), figured by him and probably taken in the spring of 1847 in the South Atlantic; it measured one-tenth of an inch (2·5 mm.) in length, though he gave it as measuring one-fifth of an inch. The Miami collection of about 100 larval individuals (1·25–5 mm.) was made on 20 January 1958 and reached me (in formalin) on 14 February. When the vial was opened the animals were a beautiful turquoise-blue all over and were uniformly covered with nematocysts. They were transferred to dishes of stock formalin neutralized with hexamine and covered with black paper after being examined with a tungsten ribbon lamp. But next morning little colour remained.

After another day there was practically none left. Agassiz and Mayer (1902) recorded traces of this blue colour in their figures of young individuals and also a plum-coloured pigment at the pore end. I have seen traces of this pigment too.

The first occasion when larvae were collected at Miami was on 21 October 1957. No more were seen until 8 November, and thereafter on 11, 13, 15 and 21 November; on the last date the first large accumulation of *Physalia* specimens was found. Further collections were made on 9, 12, 16 and 17 December and the last and most valuable, already mentioned, on 20 January 1958. The lengths of the larvae are given in Table 1.

Table 1

Date	*Larval length* (*mm.*)
8 November 1957	Under 30
11 November 1957	From 5 to 8, but mostly between 20–40
13 November 1957	From 19 to 59, but mostly between 30–50
21 November 1957	From 23 to 150, but mostly between 23–150
17 December 1957	Probably less than 15, mostly between 60–80
20 January 1958	From 1·25 to 5

Miss Dodge informed me that, though the large forms seemed more prevalent, the small ones could be found on certain (not all) days, and in large numbers if at all.

Physalia feeds on flying fish, mackerel and other surface-swimming fishes which collide with the tentacles, become immobilized by the nematocysts and are drawn up to the hundreds of feeding polyps, which lie on one side of the under-surface of the float. R. P. Bigelow has described (1891) how he was able to keep alive in large 'hatching-tanks', and study for a week or more, numbers of *Physalia* taken in the summer of 1889 in Vineyard Sound. His short paper is well worth reading. He reported that the pull of a live fish on a tentacle caused retraction, but contact—except by the mouth of a gastrozooid—with food or its close proximity caused no response. He noted the contrast between the erected crests—relaxed only for a short time—of animals seen in the Gulf Stream and the relaxed crests of specimens kept in the Woods Hole tanks. By directing a stream of air from a bellows on to relaxed specimens he obtained a general contraction of muscles and erection of the crest. He noted the shedding of gonodendra in the tanks and the detachment of gorged animals from the remains of the fish on which they were feeding. He also noticed that the palmar surface of the hand was not sensitive to the sting of nematocysts, which he likened to that of a bee when touched by the back of a finger.

In 1942 E. W. Gudger gave a résumé of recorded observations on the feeding habits of *Physalia*, from the time of Quoy and Gaimard's 1824 report on the voyage of 'Uranie' and 'Physicienne' onwards. In 1947 D. P. Wilson published photographs of a 5·5 cm. wrasse, *Ctenolabrus rupestris* (L.), in the process of being digested by a *Physalia* about 23 cm. in length.

Much light is thrown on the mechanisms in coelenterates by a recent paper by W. F. Loomis (1955) on feeding-reactions in *Hydra*, which are initiated and controlled by a hormone, reduced glutathione, released from the prey itself after penetration by nematocysts. If, as seems possible, the feeding-mechanisms of coelenterates generally is under some such hormone control, it becomes more easy to understand the method in *Physalia*. Very vast numbers of nematocysts would produce the discharge from the prey of large quantities of hormone and the feeding-mechanism would operate effectively. It may be that the often observed dropping of a half-digested fish is not a sign of repletion but of the autoxidation of the hormone, which, in *Hydra*, Loomis noted took place rather sluggishly. Since this report went to press, Lenhoff and Schneiderman* (1959) have published the results of experiments showing that reduced glutathione does induce a feeding response in *Physalia*.

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* Tentacles are not lacking, as they state, but are partly separated from the fully grown gastrozooids.

Association with *Nomeus*

The association with *Physalia* of the little purplish-barred stomateoid, the rudder-fish, *Nomeus gronovii* is interesting. It has long been known to shelter under *Physalia*, although I never saw one in the Canaries, and it was thought to lure other fishes into the reach of the tentacles; it was also considered to be immune from their stings. But Garman (1896) reported partially digested *Nomeus* attached to the tentacles, and an 18 cm. long specimen of a male *Physalia* taken by 'Discovery II' between stations when testing gear, on 29 December 1929, in a position 3° 22′ S., 32° 25′ W., is accompanied by a label in the handwriting of Dr Stanley Kemp, recording that 'twenty or more small *Nomeus* were seen swimming below the *Physalia* and in one dip the latter was caught as well as several of the fish. In the net the fish came into contact with the tentacles of the siphonophore and were immediately killed.' Kojiro Kato (1933) observed that *Nomeus* vigorously attacked *Physalia* from below, eating parts of it, including the tentacles. On opening the stomach of one fish as a check, he found unmistakable *Physalia* tissues inside.

I am indebted to Mr J. C. Natzio for a note on another stomateoid fish-associate. Natzio, a senior boy of Charterhouse School, sailed aboard R.R.S. 'Discovery II' to assist in the biological work of the spring cruise of 1958, and referred to the fish as *Lirus maculatus*. I understand that it is better known as *Schedophilus maculatus* (Günther), but I have found no reference to this association in the *Physalia* literature. On a few days following 17 March, when the ship was frequently stopped on station, the fishes were often seen to swim around and beneath tentacles of medium sized *Physalia*, and both animals were often taken together in hand-nets. On several occasions *Schedophilus* was noticed to swim from one *Physalia* to another. In an aquarium one of the fishes escaped after being entangled for about 10 min., and continued to swim around with apparently no ill effects. Mr Foxton, who was also on board, told me that another specimen of *Schedophilus* after being stung by *Physalia* towed the *Physalia* along the surface of a tank, later escaped, rolled on its side, but eventually appeared to recover. This fish, like *Nomeus*, is banded with blue, though the colour is not very conspicuous.

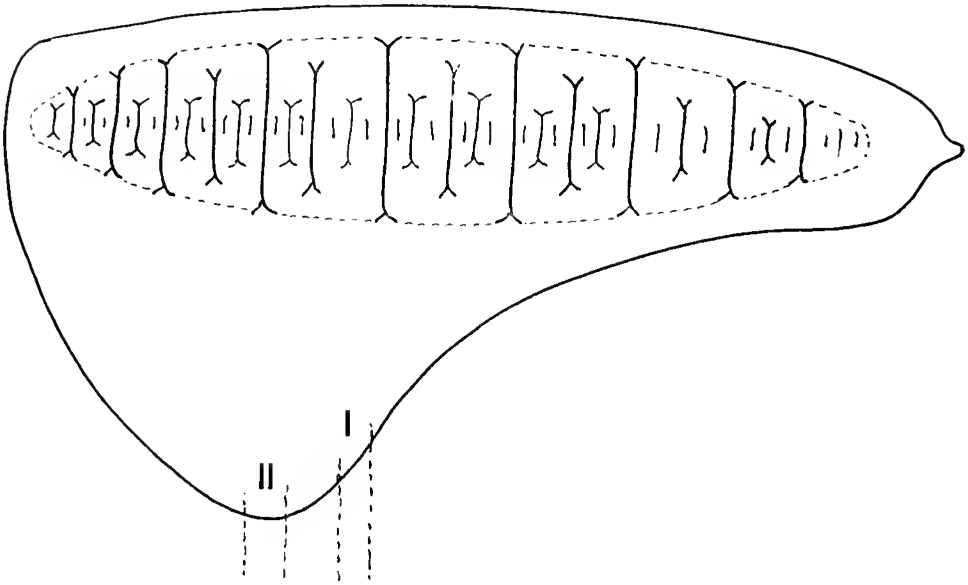
Rolling- or Somersaulting-Behaviour (Pl. X, figs. 1–6)

Much time was mistakenly spent at Arrecife watching rolling-behaviour, filming it and taking still photographs in the laboratory. It was only much later on, when the specimens were no longer available, that I realized that rolling takes place much more frequently in the still air of the laboratory than at sea in a good breeze. My tentative conclusion is that *Physalia*, when in a state of muscular tonus with crest erect, is in unstable equilibrium and is unable to remain upright without the aid of the force exerted by the wind. In the relaxed position, assumed after some time in the laboratory, it does remain upright but with the crest deflated, and the overall length increases, and the width decreases. In a note on sailing-experiment 3 (see page 318) I mention that specimen 1 fell over into the wind when the breeze dropped.

The older naturalists interpreted rolling-movements as change of 'tack', but the reason for it seems to be as follows: in the contracted, inflated condition with crest erect, *Physalia* is asymmetrical because most of the large tentacles, gastrozooids and gonodendra lie well out on the windward side, so that the heeling force thus set up prevents the animal from capsizing in a breeze. When the wind drops, the animal falls into the wind, and complicated muscular contortions are then needed to get back into the sailing position. This of course needs confirmation under conditions open to the wind, but I have certainly observed at sea in winds of force 3 or 4, a number of animals steadily drifting along without rolling; on the other hand I have not had an opportunity to watch them in a calm except under laboratory conditions. It is significant that Huxley (1859) in commenting on this somersaulting-behaviour said, '...I have over and over again watched the operation going on with great vigour in a dead calm'.

FLOATATION: PNEUMATOCYST OR AIR-SAC

I was surprised, when I first dissected a live *Physalia* by making a vertical cut with scissors down the outer pneumatocodon wall, to see how quickly this muscular coat retracted and freed the pneumatocyst; and particularly to see the branching digitiform processes of the latter which fit into the pockets of the crest. Because little attention seems to have been paid to them, I give a photograph (Pl. X, fig. 7) of a fixed specimen. To obtain fixation of the extended air-sac, which is covered inside, except for the area of the gas-gland, by a thin chitinous layer, it is necessary to maintain pressure for some time on the sac while it is in the fixative. The raising and lowering of the crest evidently depends on muscular compression and relaxation of the float and the air-sac, as described by Leuckart (1851). Lesson (1843) gave a crude figure (*M*, pl. 11).



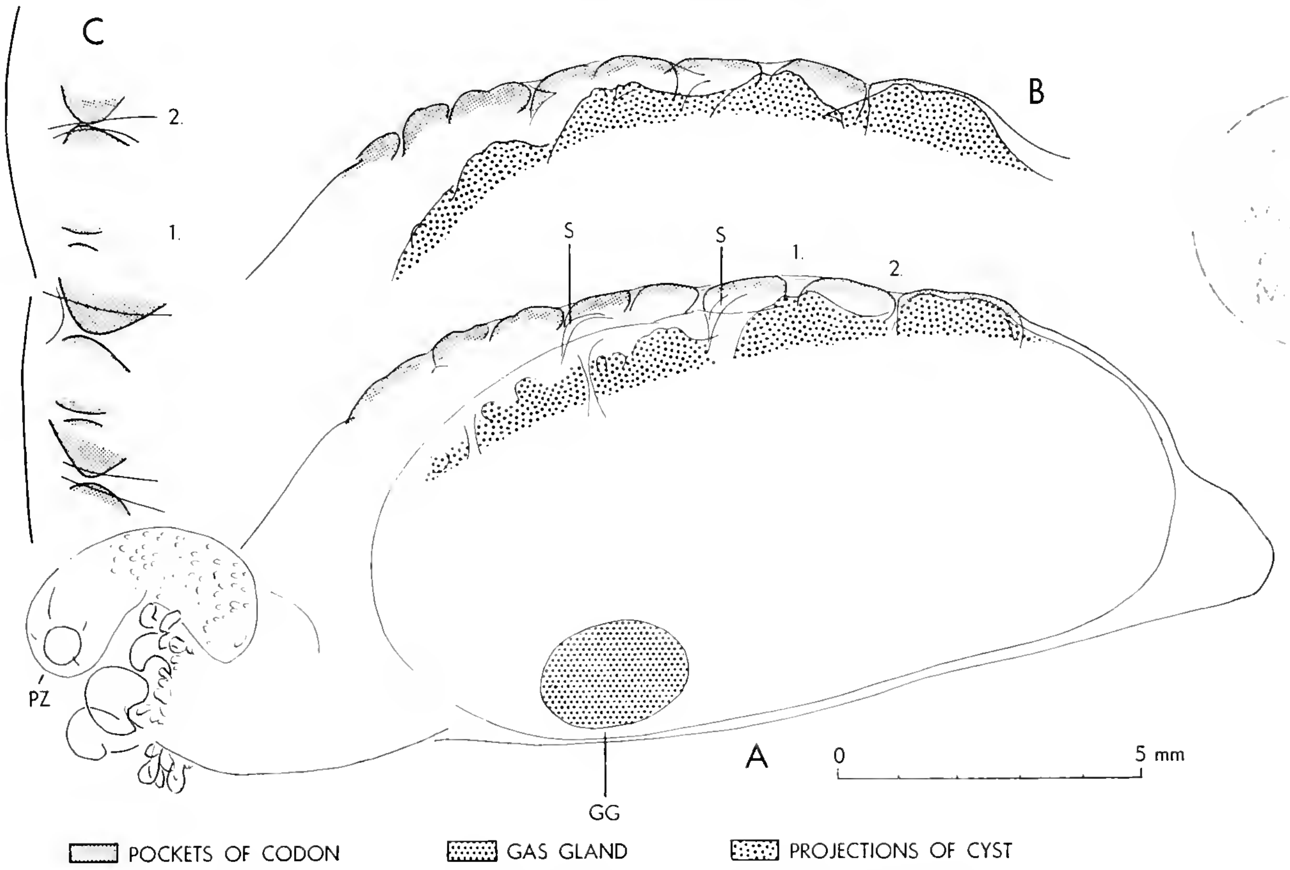
Text-fig. 1. *Physalia physalis*. A right-handed specimen, number 58, × $\frac{5}{6}$ (Discovery St. 3255). Plan-view from above to show the septa of the crest. I, II = cormidia I and II (main zone).

The textbook account of *Physalia* by Delage and Hérouard (1901) contains statements—no authority quoted—about crest-structure which need correction. First of all I have never seen any sign of an internal longitudinal septum in the crest. Secondly there is no perforated septum joining the edges of the primary and secondary septa, and partially enclosing the outer pockets of the pneumatocodon. In consequence it is untrue to say that the finger-like processes of the saccus form horizontal pairs, one on each side of a longitudinal septum. The authors also wrongly describe the gas-gland as strip-shaped: it is nearly circular. Their diagram of the relationship between crest-pockets and saccus, shown in their pl. 28, fig. 4, is useful.

Here is a description of the crest of a specimen well preserved in an extended condition—specimen no. 58, taken by R.R.S. 'Discovery II' at St. 3255 on 13 June 1955 (in 41° 08′ N., 14° 32′ W.), right-handed, of floatlength 16 cm., gas-gland diameter 45 cm. and pneumatocyst-capacity about 300 c.c. The first developed set of septa, ten in number, hang down some 3 cm. in the central region. The major pockets are subdivided three times, and rudiments of a fourth series are visible at the crest-margin. The secondary septa are 2·5 cm. deep, the tertiaries 1 cm. and the fourth series 0·5 cm. A view of the float and crest from above is given in Text-fig. 1.

From this figure it will be seen that the crest is of considerable thickness, and that there are depressions where the lower edges of the septa meet the sides of the float at the sites of the original fusion of pockets. For this reason the sides of the crest have not got plane surfaces.

The method of formation of the transverse septa which hang down inside the crest of the float can be deduced by seriating growth-stages. In a young specimen, No. Juv. 5 (Text-fig. 2), which has a float-length of 19 mm. (artificially stretched some 3 mm. by injection of fluids into the pericystic space), the upper surface of the pneumatocyst itself, now withdrawn from the crest, shows the beginnings of six dome-shaped pockets. At the apex of each pocket are the collapsed rudiments of later-developed twin pockets, themselves showing the beginnings of subdivision. Development of the crest is less marked at the ends than in the centre of the float.



Text-fig. 2. *Physalia physalis*. Young left-handed specimen, number 5, × 8. Float-length 19 mm. To show origin of the crest as a fusion of crest-pockets. *A*, *B* from to windward, *C*, from above. *PZ* = protozooid at oral end, *GG* = gas-gland, *S* = septum, 1 = before fusion, 2 = after fusion.

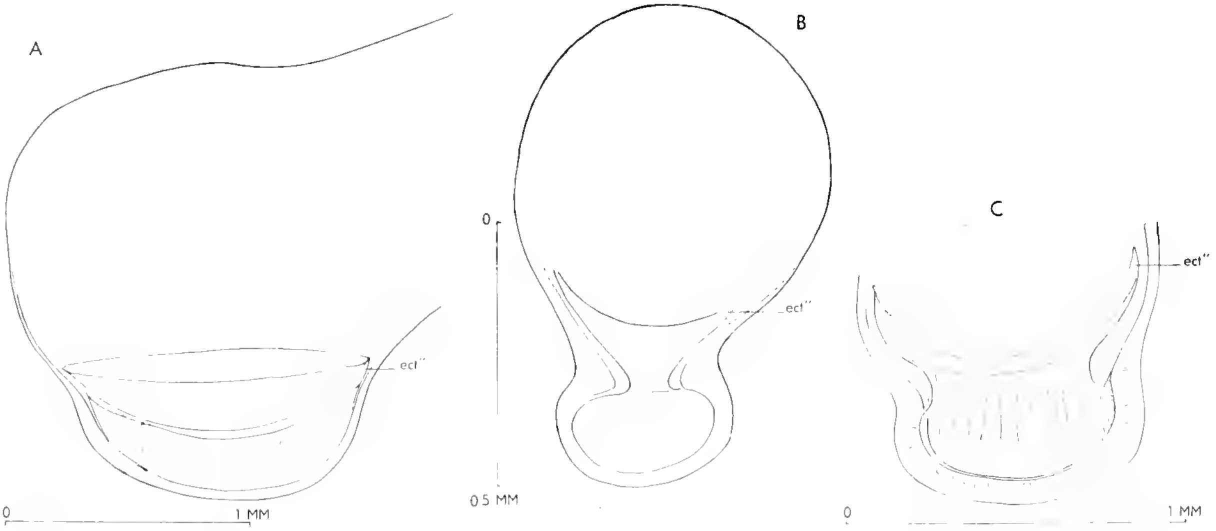
Part of the upper wall of the float is pushed out by the expanding muscular projections of the pneumatocyst, and the anterior wall of each pocket gradually fuses with the posterior wall of the adjacent pocket, forming a septum (Text-fig. 2), which grows deeper as the fusion-process proceeds with age. The secondary, tertiary and subsequent septa develop in a similar way as the finger-like projections of the pneumatocyst divide and push out smaller pockets at a higher level (Pl. X, fig. 7). The outer longitudinal muscles seem not to be involved in the fusion-process. A section of a septum shows a core of structureless lamella covered with gastrodermis. Leuckart (1851) stated that the septa were formed by the inner (gastrodermic) layer of circular muscles.

To obtain accurate data on the relationship between float-length, saccus-capacity and area of gas-gland it would be necessary and far more easy to work on living material. However I have arrived at some rough conclusions after measuring material fixed in formalin. The relationship between float-length and capacity of a number of specimens was noted and a graph made.* Judging by the way in which the capacity-curve flattens out at the higher values, it might be supposed that the maximum float-length would not be more than about 23 cm. (9 in.), though Quatrefages's famous specimen (1854) measured 25 by 10 cm., or nearly 10 in. in length. I am indebted to Mr B. S. Kisch for a record of a 12-in. specimen washed ashore on 15 September 1957, at Erromardi, Bay of Biscay, at about the same time as the Channel swarm noted on page 315, but I have no data as to capacity in this specimen. When measuring the float-capacity of fixed specimens I withdrew and pumped back air several times with a hypodermic needle and syringe, but this method cannot be as satisfactory as working on living specimens. Even the measurement of float-length of fixed specimens cannot be made satisfactorily owing to frequent distortion due to preservation.

The relationship between the area of the gas-gland and the capacity of the air-sac appears to be roughly as shown in Table 2:

Table 2

Area of gas-gland (*mm.*^{2})	*Capacity of air-sac* (*c.c.*)
17	0·5
300	50
1000	150
1500	250–300



Text-fig. 3. *Physalia physalis*. Gas-glands of three larvae seen in optical section through the float-wall. *A*, × 32, *B*, × 70, *C*, × 45. *ect''* = secondary ectoderm.

In the early stages the gas-gland and the air-sac itself resemble those of physonect siphonophores. The secondary ectoderm forms a very deep layer which projects well into the air-sac itself as a solid plug (Text-fig. 3). A section of an 11 mm.-long specimen at this stage was published by Okada (1935).

It is remarkable that a simple epithelium can build up a gas-pressure. But *Physalia* is not alone in its ability to do this, for although in most fishes with a closed swim-bladder this build-up against a pressure-gradient is achieved by a counter-current capillary system—the *rete mirabile*—it has been shown by Sundnes, Enns and Scholander (1958), in at least three species of salmonid fish, that the pressure build-up of oxygen and nitrogen does not take place in the blood but is a function of the epithelium lining the swim-bladder.

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* The data and graph, unfortunately, have since been mislaid.

After this larval stage has been passed through (Text-fig. 3) the gas-gland becomes a flattened disk on the lower part of the enlarged section of the float (Pl. VIII, figs. 1, 5). I made the following rough measurements, under one and the same set of conditions, of fourteen live specimens, whose horizontal length overall, omitting appendages, ranged from 35 to 60 mm. (see Table 3).

Table 3

Float-length (*mm.*)	*Gas-gland diameter* (*mm.*)	*Float-length* (*mm.*)	*Gas-gland diameter* (*mm.*)
35	10	50	10
40	8	50	10
40	9	50	15
40	10	55	12
40	10	60	10
45	7	60	11
45	8	60	13

Measurement of other specimens from various localities after fixation in formalin, some with and some without relaxation in magnesium chloride, are given in Table 4.

Table 4

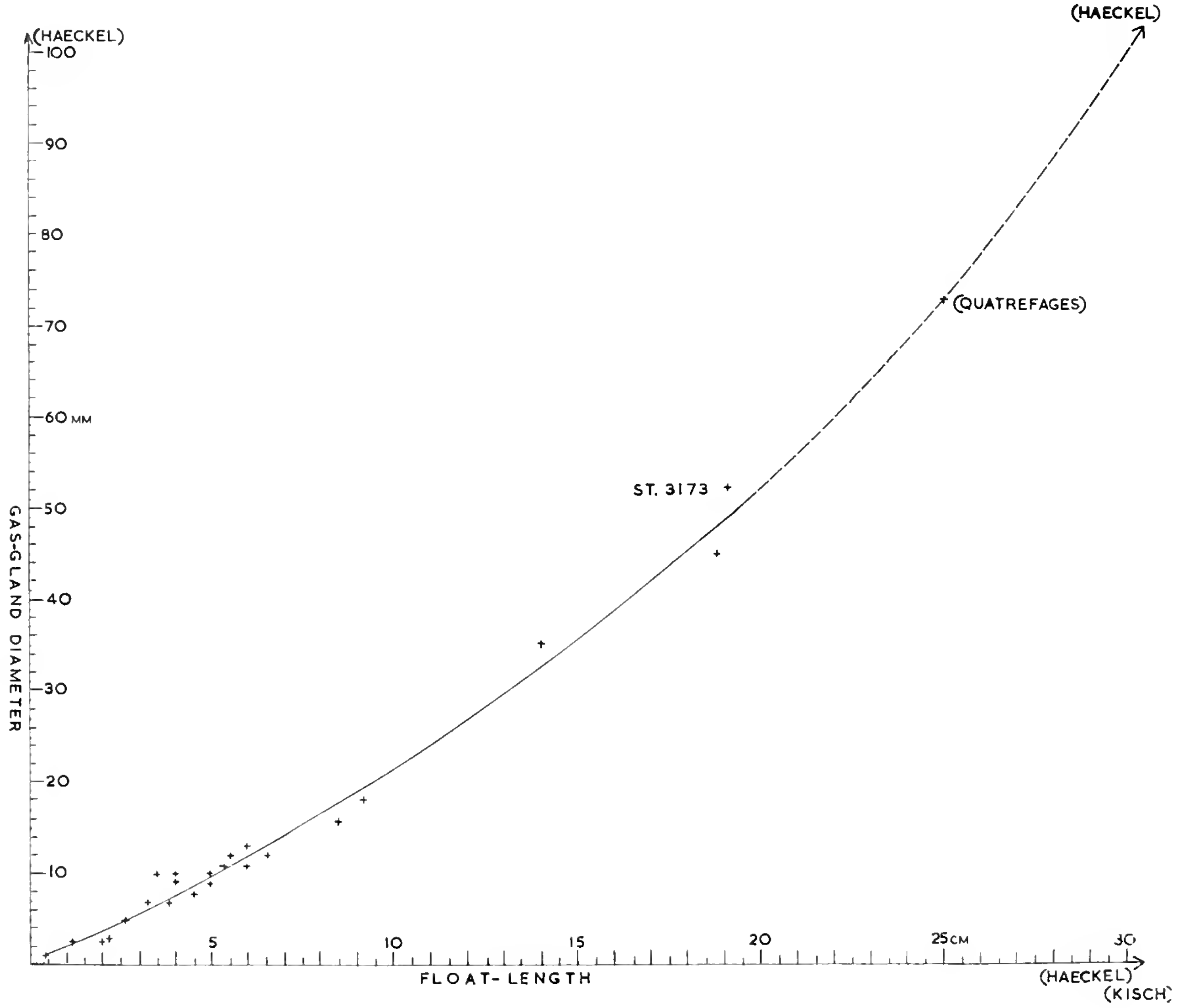
Float-length (*mm.*)	*Gas-gland diameter* (*mm.*)	*Float-length* (*mm.*)	*Gas-gland diameter* (*mm.*)
2	0·8	50	9
4	1·0	53	11
11·5	2·5	65	12
20	2·5	85	16
22	3·0	92	18
26	5·0	140	35
32	7·0	188	45
38	7		

These data are shown in the form of a graph in Text-fig. 4, from which it can be concluded that Quatrefages's huge specimen may have had a gas-gland of diameter exceeding 70 mm. The largest known to me is that of a 'Discovery' specimen from St. 3173 (42° 35′ N., 11° 35′ W.), whose gas-gland measures 52·5 mm. Haeckel (1888) thought the gas-gland could reach a diameter of 100 or 200 mm.

Quatrefages (1854) described how a *Physalia* (right-handed and about 25 cm. in length) that he had been investigating at La Rochelle suddenly lost all its air and collapsed; and, having chanced to glance at it again a quarter of an hour afterwards, he was surprised to see it distended again, although a little smaller than before. He concluded that it must have taken in air through the pore. Haeckel (1888) stated that, by compressing the float voluntarily, the animal could extrude the included air through the apical stigma and sink down. After a short time had elapsed, he said it could rise again, secreting a great mass of air by the pneumadenia and refilling the float. He said he had often observed this process repeated in December 1866 off the Canary Islands.

I saw no sign of this behaviour at Lanzarote, nor did I succeed in squeezing the air out, owing to the slipperiness of the animal. Louis Agassiz (1862) who had observed thousands of *Physalia* alive recorded that he had never seen them emptying their air-sac and sinking under the surface of the water, even in stormy weather.

On the other hand, young specimens appear to act differently. Eschscholtz (1829) found, on irritating a *Physalia* five lines long (15–16 mm.), that it suddenly expelled all the air from its bladder and sank. Agassiz and Mayer (1902), who studied a number of young animals between 2 and 4 mm. in length taken by 'Albatross' in the autumn and winter of 1899, among the Paumotus and Society Islands, related that 'unlike the adult, these young individuals possess the ability to sink below the surface; a feat which they accomplish by extruding a bubble of air through the pore of the float. In a few minutes the gas regenerates and then the animals rise to the surface'. A. Agassiz (1883) had already observed a young specimen of about 6 mm. 'swimming at various levels in the jar in which it was kept'. Miss Eleanor Dodge, writing from Miami, has kindly informed me that she has talked with people who have caught *Physalia* in plankton nets with their floats empty, but she did not refer to their size; it looks as if they must have been small, perhaps larval stages.



Text-fig. 4. *Physalia physalis*. The relation between the diameter of the gas-gland and the length of the float.

My companion at Lanzarote, George Mackie, made some experiments by withdrawing measured quantities of air from the pneumatocyst with a hypodermic syringe, but there was little subsequent change of volume.

Quatrefages seems to have been the first to have analysed the contents of the pneumatocyst; his results are given in Table 5:

Table 5

		Percentage of		
Specimen	*Gas (c.c.)*	O	N	CO_2
1	45	17·7	82·2	0
2	72	17·2	82·7	0

On 25 September 1957 I removed the air-sac from a moribund, 7-in., right-handed specimen at Hastings—the last specimen of a swarm that began to come ashore in westerly winds on 10 September. About the same time, specimens were coming ashore also at St Jean de Luz, Bay of Biscay, and at Almunecar Granada in the Mediterranean. I took the excised air-sac, which I had placed unfixed in a jar of medicinal paraffin, to the Government Chemist's department on 26 September. On the next day, 27 September, Mr D. Green made the following analysis of the contents, whose cubic capacity he estimated at 200 c.c. The gas was liberated from the sac under brine and was found to contain carbon dioxide 0·5% by volume, oxygen 19·9% and nitrogen (by difference) 79·6%,* as compared with the average composition of atmospheric air: CO_2, 0·04%; O, 20·99%, and N plus inert gases 78·98%.

Schloesing and Richard (1896) gave the following analysis of float-gases shown in Table 6:

Table 6

Gas (c.c.)	*Percentage of* O	N	A	CO_2
410	15·1	82·02	1·18	1·7

Wittenberg (1958) has recently reported finding, in specimens taken at Woods Hole, a fifth component, carbon monoxide (traces to 8%). The majority of specimens contained from 1 to 5% CO, which accounted for all the combustible gas present.

MOTION RELATIVE TO WIND AND WATER

Physalia has a characteristic orientation relative to the wind. The aboral† half is free of appendages and the animal floats with its long axis at an angle of about 45° from the down-wind direction. The tentacles and appendages are borne on a bulge on the oral half of the animal, the tentacles streaming out on the windward side and acting as a drogue or sea-anchor. The bulge is situated either on the left or right side of the float (Text-fig. 5), and I think that left or right-handedness in a particular individual must be established on the first windy day that the larva keeps to the surface. The larval tentacle would cause a drag on the windward side, so that the float would be blown (so to speak) to leeward. As the new tentacles grow—and we know that their development is very precocious—this drag would be increased, and the part of the float from which they are budded would become bowed-out to windward as a bulge, resulting fortuitously in a left- or right-handed individual.

We may liken the steadily drifting *Physalia* to a sailing vessel hove-to on either the port or starboard tack. In life the oral end heads up to the wind, an important point to remember when observing the behaviour of living specimens in a breeze. Right-handed individuals appear to be on the port tack and left-handed ones on the starboard tack.

The animal, being asymmetrical, does not drift straight downwind. I have to thank Dr Henry Charnock, Reader in Oceanography at Imperial College, London, for a tentative explanation of its direction of drift. Suppose we consider a grossly simplified model of a left-handed animal seen from above, with a crest AB and the point of attachment of the appendages (the bulge) at C (Text-fig. 6a). In a given wind a force is exerted at X. This force has two components, one normal to the crest AB and the other along the crest; their resultant is R (Text-fig. 6b). After resting in this position during a

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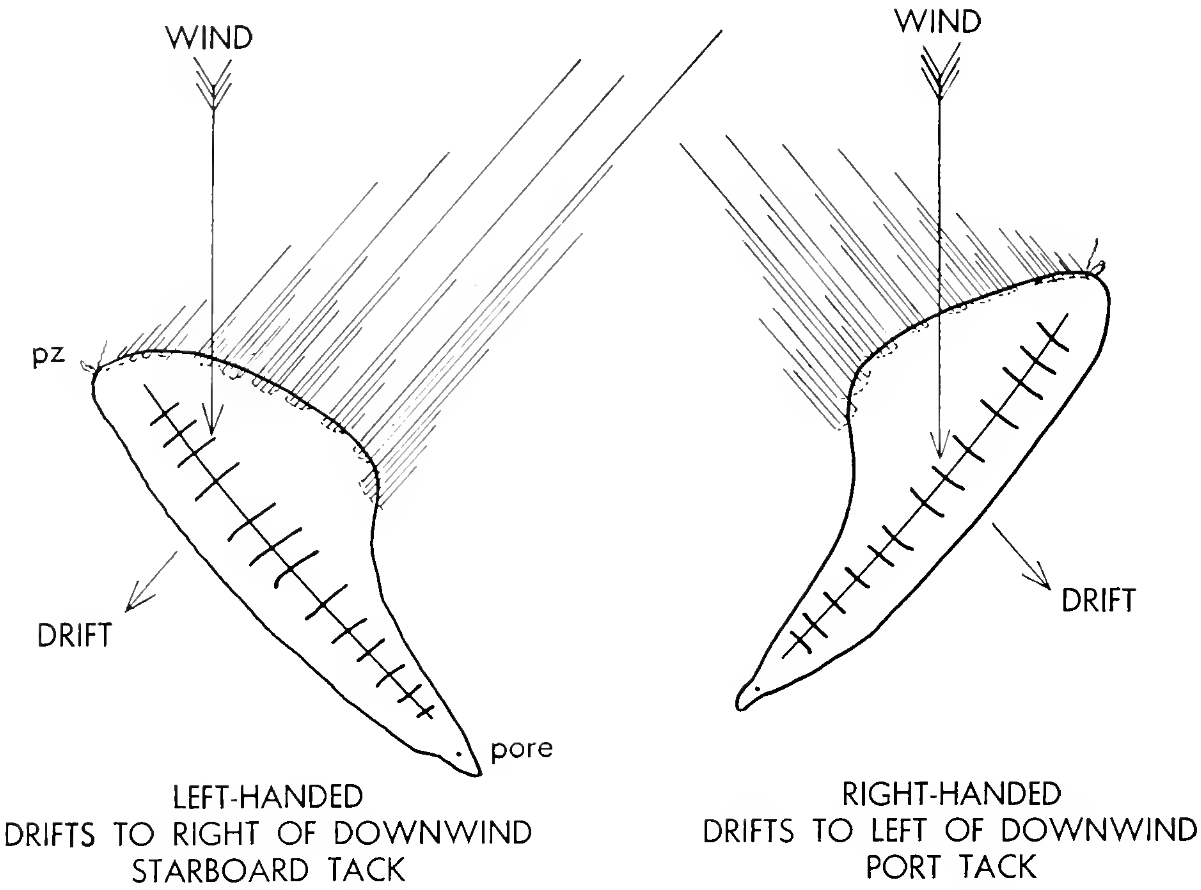
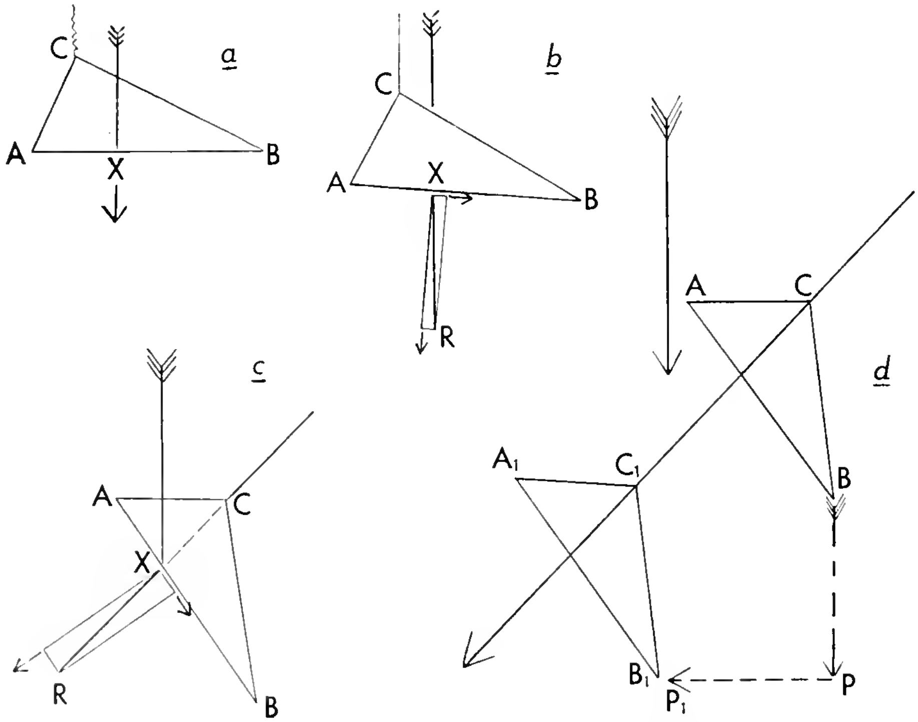
* Presumably this figure includes the inert gases.

† Huxley (1859), Haeckel (1888), Schneider (1898) and Okada (1932) all regarded, mistakenly I feel, the aboral (pore) end as anterior and the oral (protozooid) end as posterior.



Text-fig. 5. *Physalia physalis.* Angle of drift from the windward direction of left- and right-handed specimens. *PZ* = protozooid.



Text-fig. 6. *Physalia physalis.* Direction of drift. *a*, *b*, *c*, to show why the drift is not normally straight down-wind. *d*, to show an apparent movement into the wind caused by drift of the surface water to leeward.

calm, if caught by the wind the animal will be seen to rotate until *R* comes into line with *C* (Text-fig. 6*c*); it then drifts steadily, along a course at an angle of about 45° with the down-wind direction—to the right in this case because the specimen is left-handed. Rotation is very rapid, because the aboral half of the animal *X–B*, being free of appendages, only rests lightly on the surface.

The slight drift along the axis *AB*, which theory shows to be inevitable, I could not detect at sea. On the other hand there appeared to be a marked progression in the opposite direction, that is from *B* to *A*. No doubt this is accounted for by movement of the surface layer of water past *B* in the direction *BP*, and by a visual impression of movement of the animal across the wind from *P* to P_1 (Text-fig. 6*d*). The direction of drift of both right- and left-handed specimens is shown diagrammatically in Text-fig. 5.

Woodcock (1944) was the first to draw attention to the motion of *Physalia* relative to wind and water. He cited observations on the asymmetry of 421 specimens in the North Atlantic and the Gulf of Mexico, and put forward a hypothesis to explain the advantages to specimens in the northern hemisphere of being driven consistently about 45° to the left of the down-wind direction. He also cited twenty-two preserved specimens from the southern hemisphere, most of which were mirror-images of the northern ones, and which would have been driven to the right according to his theory. But Fontaine (1954) noticed that forms driven ashore on the southern coast of Jamaica by prevailing east winds were left-handed, that is, they would have been driven to the right of the down-wind direction. I will not refer in detail to Woodcock's hypothesis because it need never, I think, have been postulated. My companion, Dr G. O. Mackie, and I (1956) found at Arrecife and off the island of Allegranza to the north of Lanzarote that both right- and left-handed specimens appear to be common in the North Atlantic. Chun (1887) had already recorded finding on the same day and in the same place in the Pacific Ocean thirty-two young specimens, of which eighteen were right- and fourteen left-handed. He also mentioned that both Eschscholtz and Leukart had referred to what he called this 'inversion'. We found that the type which comes ashore at any particular spot depends on the local wind. Indeed, on one particular day, 15 March 1955, a south-east wind had blown at Arrecife and was falling off at 18.00 hr., when I collected specimens that would have been driven to the left of the wind. An hour or two later, when the wind had shifted to the south-west, specimens of the other other hand were taken. Winds from these two quarters were less likely to have driven in *Physalia* of the opposite hands, as can be seen from Text-fig. 7. Dr Mackie suggested to me that this disymmetry may have survival value, in that it obviates the stranding of the whole mixed population of *Physalia* in any one set of circumstances. No doubt it also ensures optimum density of the population in the most favourable environment. Woodcock had already suggested that motion either to the right or left of the wind would make it possible for *Physalia* to avoid remaining in the convergent zone caused by parallel, wind-induced surface vortices; as for example in the North Atlantic, where it could be fatally trapped by sargasso weed in those areas where the weed is common.

Wilson (1947) had accepted, as a working hypothesis, Woodcock's contention that movement will always be to the left of the wind-direction in the northern hemisphere, and suggested that though a fair breeze might give the full 45° inclination, a storm might tend to drive *Physalia* more directly before it.* His table VI assumed this last suggestion. He also thought that shoals of *Physalia* blown on to our coasts may have bred in latitudes higher than usual. If that were the case, one would expect the specimens to be small instead of exceptionally large.

After the preliminary experiments and observations on drifting *Physalia* made on 14 April 1955, at Arrecife, I carried out some further crude experiments on 15 and 16 April off the shore and inside

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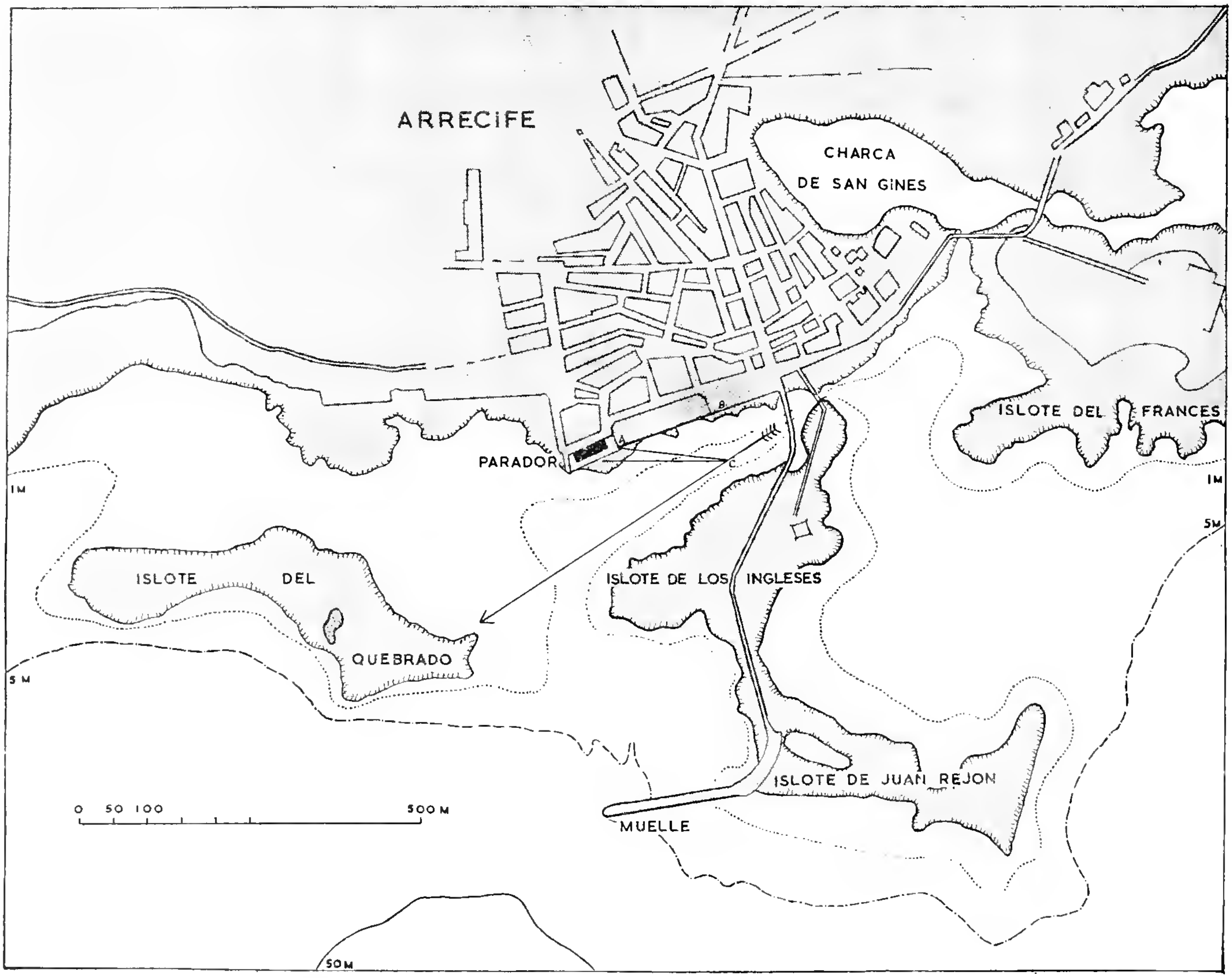
* Natzio's observations (see p. 322) tend to confirm this.

the mole and reefs, between the Parador and the bridge with specimens of float-length 18 cm. approx. Running in the direction of the wind was a measured distance of 150 m. between the wall *A* of the Parador forecourt and a second wall, *B* to the eastward near the bandstand (Text-fig. 7). The boat was taken up to a point marked *C* in Text-fig. 7 in line with wall *B*. A cross-bearing kept the outer or



Text-fig. 7. *Physalia physalis*. Chart of Arrecife, Canary Islands, showing position of drifting experiments.

Table 7

Run	*Specimen*	*Time of start at* C (*hr.*)	*Time of finish at* A (*hr.*)	*Notes on* 15 *April*
1	1	11.11	11.24	Not much crest up. A few minutes lost in 'rolling' at the start
2	2	11.33	11.41	Crest well up. Came right in to Parador wall
3	1	11.48	11.59	Crest well up at 11.50. At 11.58 breeze fell off and *Physalia* fell over into the wind. Arrived 50 m. out from wall *A*
4	3	12.25	12.30	No. 3 was used on 14 April. Crest was good but tentacles deteriorating. Arrived 30–40 m. from wall *A*
5	4	12.35	12.44	Another of yesterday's specimens, in similar condition. Arrived 20 m. out from wall

southernmost pier of the bridge in line with the pylon of the old drawbridge to the eastward of it. This conveniently gave the wind direction as well. Times of arrival of specimens opposite the Parador forecourt wall *A* were taken. Near here they were generally driven ashore. A spherical glass-float, which had been put over the side at *C* with the specimens, then had to be sighted, chased and its position approximately fixed by cross-bearings on shore marks. It consistently travelled down-wind. Five runs were made on 15 April towards the end of flood-tide between 11.11 and 12.35 hr. The times taken for *Physalia* to be driven from the starting-point *C* to the end of wall *A* were as shown in Table 7.

On this day, 15 April, the wind-velocity (? at Airport) was given by the kindness of the Meteorological Office, London, as 19 knots at 12.00 hr., direction 070°.

A second series of experiments was carried out on 16 April, at slack-water (low tide), when the velocity of the wind was less than on 15 April, perhaps 8 knots. No data could be given by the Meteorological Office, except that at 09.00 hr. the wind velocity was 8 knots, direction 120°. The results were as shown in Table 8:

Table 8

Run	*Specimen*	*Start at* C (*hr.*)	*Finish at* A (*hr.*)	*Notes on* 16 *April*
6	5	14.05½	14.11	A 'roll' at the start
7	6	15.23	15.32	Arrived 20 m. out from wall *A*
8	(4 together) 7, 8, 9, 10	15.40		
	7		15.49	Arrived close to wall *A*.
	8, 9			Picked up again (between extremes)
	10			Arrived 50 m. to east of wall *A*. Time lost through bad discipline of crew (2 boys)

No further opportunities for similar experiments occurred before I left Arrecife on 24 May.

The direction taken by the long axis of *Physalia* relative to the wind is about 40°, estimated by holding close above the specimens a long pennant attached to the end of a bamboo.* It was not easy to have the boat manœuvred into the right position for close observation without blanketing the specimen or impeding its progress, and my notes were more than once blown into the water.

In order to get some idea of the angle of drift from down-wind direction at slack-water in a light breeze, I select the experiments on specimens 7–10. The course taken by no. 7 forms the hypotenuse of a right-angled triangle, of which the other sides are formed by (*a*) the distance (100 m.) from the end of the Parador wall *A* to the line-of-sight formed by the piers of the two bridges (direction of wind), and (*b*) the distance along the direction of the wind from the starting-point *C* to a point opposite the Parador wall *A*. This distance is almost the same as that between the two walls *A* and *B*. Measurement on paper of this triangle gives the angle of drift from the down-wind direction taken by no. 7 as 34° (Text-fig. 8); for no. 10 the angle was 42°.

Plotting the result of the experiment on specimen 4 in the same way, I find that it drifted about 180 m. in 9 min., a speed of 20 m. a minute or 0·75 knots in a breeze of velocity rather less than 19 knots over the end of a flood-tide that can be ignored.† Specimens 6 and 7 made similar speeds, and specimens 2 and 5 were driven rather faster. These last four experiments were made under slightly different conditions. In Table 9 I suggest a comparison between boat performances and *Physalia* in 10–15-knot wind (see Text-fig. 9).

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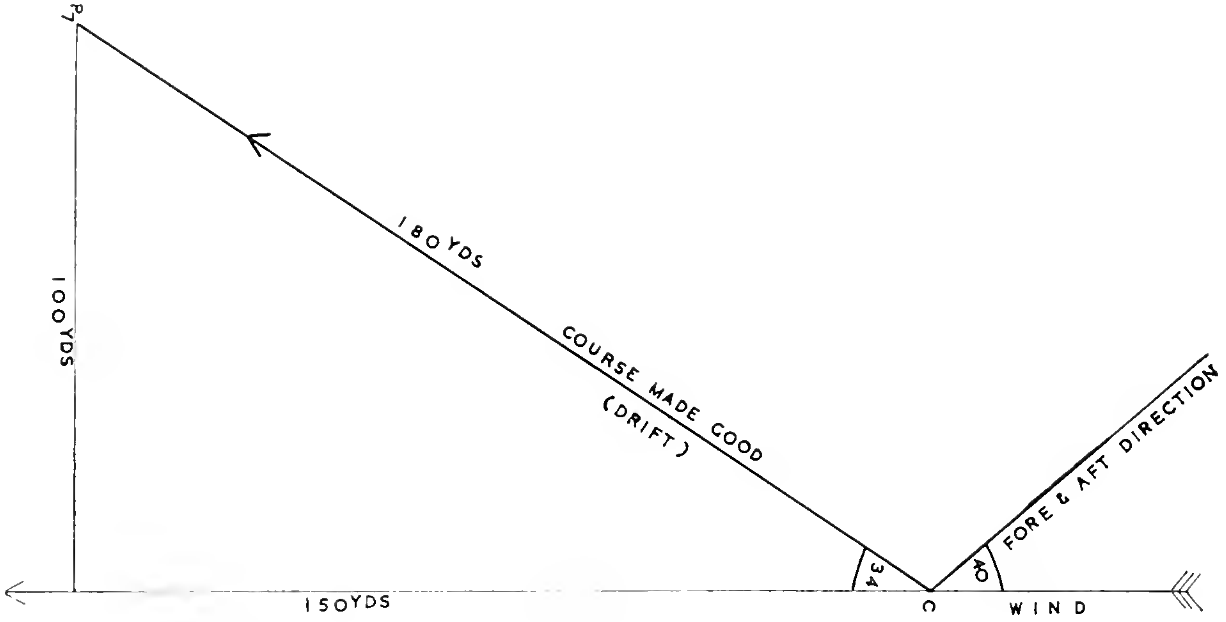
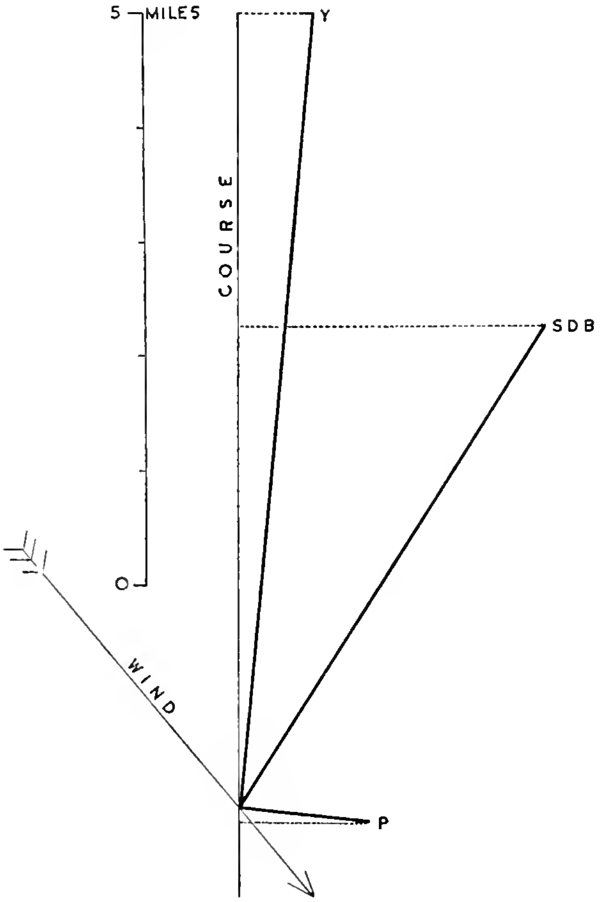
* The protozooid faces up-wind, the pore down-wind (see Text-fig. 5).

† Compare this with the estimate of Woodcock (1956) of 15·6 m. per minute in a breeze of 13 knots for a specimen of 17 cm. in length.



Text-fig. 8. *Physalia physalis.* Angle of drift in experiment number 7.



Text-fig. 9. *Physalia physalis.* Comparison between courses-made-good by a deep-keeled fast sailing yacht, *Y*, a shallow draft sailing boat, *SDB* and *Physalia*, *P*.

Table 9

	Yacht, 50 ft., with much lateral resistance	*Boat, shallow draft, 24 ft. × 8 ft. × 1 ft., canvas, 160 sq. ft.*	Physalia
Angle of fore-and-aft-line from the wind	40°	40°	40°
Course made good	45°	70°	146°
Leeway	5°	32°	95°
Forward speed, knots	7	5	−0·13
Sideways speed, knots	1	2·8	0·75

(It may be of interest to record here some observations that I made in May 1956 at Villefranche on the sailing-behaviour of *Velella*, about which little seems to be known. The observations were made from the causeway that links Le Port with La Darse. Small numbers of *Velella* were drifting slowly in the light breeze close into the rocks, so that I could look down on them at range of about 15 yards. After watching several individuals closely for 2 hr. or so, I came to the following tentative conclusions: *Velella* orientates its long axis to the wind in much the same way as *Physalia*. Having a rather short axis, it appears to be not very stable so that now and then it turns slowly, but eventually takes up its original orientation again at an angle of about 40° to the wind. Right- and left-handed forms occur as in *Physalia*, but no further opportunities arose, as I hoped they would, to continue a study of *Velella*.)

Since this report was begun, Woodcock (1956) published an interesting short article on 'Dimorphism in the Portuguese man-of-war', partly to give further details in support of his contention that, in the North Atlantic, the animal is consistently driven by the wind to the left of the down-wind direction. Whether Woodcock's figures would satisfy a statistician that left-handed individuals predominate there, and if so to what extent, it is not for me to say, but in view of the large population which must exist there I feel doubtful. I would agree that, supposing roughly equal numbers of the two kinds started off on their drifting-voyages round the average cyclonic wind-system of the North Atlantic, left-sailing *Physalia* might tend to sail away from the centre of the system, often in the direction of coastal waters. This was pointed out to me previously by Dr Mackie, but it would be a very big task to collect evidence of this. I have already started to fix the positions and tack of a few specimens observed at sea, in the hope that one day a meteorologist might be induced to work out the estimated positions of the same animals on a few days both before and after the time of observation. It is only in this way that I think we shall obtain data on their circulatory movements. It seems to me very improbable that ecological factors can act selectively for tack on each generation, or that dimorphism can be due to genetic differences. That anything like a 'tack'-change can be caused by 'migration of the tentacles on the pneumatophore' seems to me quite out of the question, although as the animal grows older, small branches of the cormidia do grow out to leeward. I very much like Woodcock's chart of the Kaiwi channel, which shows clearly the effect of a change of wind on the landfall of *Physalia*. His statement that off Deewhy Beach, Sidney, the right-sailers outnumber the others is interesting; but I doubt whether it will be confirmed, as Woodcock seems to hope, that most *Physalia* in the southermost hemisphere sail to the right.

But I can give him one more record of southern hemisphere specimens—sixty-seven 4-cm.-long *Physalia** collected by Prof. T. A. Stephenson at Muizenberg Beach, False Bay, S. Africa (prevailing winds in summer, south-east). Only one of these was right-handed.

For statistical purposes it is useless just to count animals of either tack from the southern hemisphere. Woodcock (1944) said 'of twenty-two south latitude animals preserved at the Museum of Comparative Zoology, Harvard University, and at the U.S. National Museum in Washington,

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* B.M. Reg. No. 1934, 3.14.1.

nineteen were left-handed and three were right-handed, that is 86% of them were mirror-images of the animals from the northern hemisphere'. We must know whether and how frequently animals of either tack can in theory come ashore with winds that occur on beaches for which records are available.

Once more I have pleasure in acknowledging my indebtedness to Mr J. C. Natzio for reporting to me observations made aboard R.R.S. 'Discovery II' in the vicinity of 38° 35′ N., 20° 13′ W. in the middle of March 1958. The ship was frequently stopped and it was possible to keep *Physalia* individuals in view for some time. On a typical occasion the ship was lying-to with the wind north-west, force 2, on the port beam. The ship was drifting to leeward at about $\frac{1}{2}$ a knot and the speed of drift of *Physalia* specimens was estimated at about $\frac{1}{4}$ of a knot in a direction to the left of down-wind. The angle between the animals' course (drift) and the direction of this force 2 wind was about 40°, the maximum observed. In winds stronger than force 4 the line of the floats' crests was parallel to the wind's direction and the animals drifted straight down-wind. Natzio doubted whether *Physalia* drifted any faster under these conditions. *Physalia*, he said, is quite easily blown by a slight gust so that the blunter, oval end is temporarily ahead, and the animal may sail in this way for some little distance. He also reported that rolling appeared to be slow and deliberate in calm weather, while in a wind the animals seemed to be suddenly blown straight over until the crest was horizontal on the surface of the water. He got the impression that capsizing was caused by a sudden gust upsetting the stability of the float, and not as I suggested by a lull, for he observed a float to be blown apparently straight over on the water where it would remain for some seconds, after which it would flick back suddenly into the upright position again. In my opinion this behaviour does not constitute the rolling phenomenon. Natzio likened the appearance of *Physalia* to that of a buoy with a tide running past it, the tentacles functioning as the buoy's mooring cables; they have the same retarding effect as that of a sea-anchor.

During this spring cruise of 'Discovery II', Natzio reported, *Physalia* was seldom absent from view south of about 38° 30′ N. As a rule one specimen was not out of sight before others came into view. The maximum float-length observed would have been about 7–8 in. A swarm might consist of more than a hundred in an area of as many square yards, and the individuals in a swarm varied in size from the maximum down to as little as an inch or so. The average length was perhaps about 4–5 in. Very small ones could easily have escaped observation. Apart from the swarms, Natzio's impression was that *Physalia* was quite widely scattered.

Stinging-powers and Toxicology

It appears from various published accounts that there is a complex mixture of pharmacologically active substances in the tentacles of the Cnidaria, not all of them necessarily confined to the stinging-capsules or nematocysts. It is not surprising, therefore, that the effects of being stung by these animals, or of injecting extracts, are varied. In addition some nematocysts have greater powers of penetration than others. Lane and Dodge (1958) report that tentacle-nematocysts of living *Physalia* may occasionally penetrate heavy-gauge surgical gloves. Attempts have been made to identify the substances which produce the stinging sensation and other effects, but until quite recently all the cnidarian substances used for experimental work have been obtained from crude tentacle-extracts. Fortunately new techniques are now available (Phillips, 1956; Lane and Dodge, 1958) for obtaining pure capsular contents.

As to the effects of being stung by *Physalia* I know of no records of fatalities, but as Elizabeth Pope (1953) has pointed out there has been some confusion in Queensland between *Physalia*, to which the name Portuguese man-of-war should be strictly confined, and a very dangerous Charybdeid jelly-fish of the genus *Chiropsalmus*, to which some Queensland people have applied the same name. There is very good evidence that *Chiropsalmus* has caused the death of a healthy man aged 21 years within 3 min. of stinging, as well as a boy of 11 years in the Cairns swimming-bath. The toxin concerned must be far more deadly than the fastest-acting snake-venom. Very recently, Southcott (1958) has reviewed the subject of lethal stingings by cubomedusan jelly-fish and has pointed out that it is still uncertain whether the cubomedusan responsibile for deaths in northern Australian waters belongs to the genus *Chiropsalmus* Haeckel or *Chironex* Southcott. But Halstead (1958), who a month or two earlier discussed the subject of jelly-fish stings and their medical management, suggested that the species *Chironex fleckeri* Southcott might be identical with *Chiropsalmus quadrigatus*.

I have myself witnessed the effects of *Physalia* stings at Las Palmas, Canary Islands, where hundreds of bathers are treated at the Victoria Hospital. In one particular case I saw a girl being helped out of the water and up the beach with extensive urticarial weals all over her legs. She seemed in great pain. And yet I was told by a visitor to the Cape Verde Islands, that in one bay, João Devora, where he constantly met with *Physalia*, though it was absent in Bahia des Gates at Matiota, everyone was quite used to being stung and made no fuss about it. Again, I was told by an Australian that on the eastern beaches where *Physalia* is common, boys often pick up a specimen and creeping up behind a victim slap him on the back with the tentacles.

The obvious treatment for stings is the application of an anti-histamine cream or taking an anti-histamine by the mouth. First-aid treatment commonly given is the application of urine, picric acid or ammonia to the skin, and rubbing the skin with sand, though it is difficult to see how such methods could be effective.

Lane and Dodge (1958) report that nematocysts on laboratory surfaces or clothing retain their reactivity for at least two weeks, and that surfaces, clothing and skin can be decontaminated by the application of 95% ethanol. Although this treatment of the skin does not reduce the pain of the stings already received, Lane and Dodge consider that the local application of alcohol to the skin of a stung swimmer is an effective palliative measure, because the toxicity of the capsule contents of *Physalia* is reduced by such an organic solvent, which also inactivates adherent nematocysts.

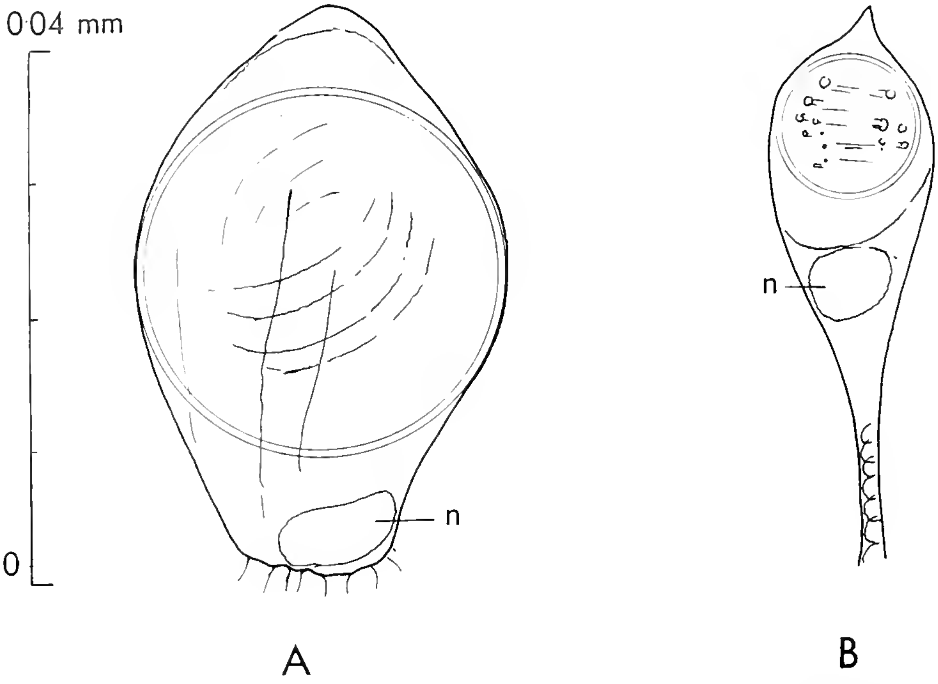
Some of the reactions to the injection of crude tentacle-extracts of Cnidaria in laboratory animals are: somnolence, paralysis, anaesthesia, digestive disturbances, prostration, respiratory interference, anaphylactic shock, and in small animals even death. But a distinction must be made between the injection of the crude extracts and being stung by the contents of the stinging capsules themselves. The effects of the latter are usually burning pain of varying degrees of severity at the site of contact, urticarial weals, pain in the lymphatic glands of groin or armpit, and perhaps shock.

Lane and Dodge (1958) have made a new and very different approach to the toxin problem, and one which pharmacologists appear to think is very promising, though perhaps it has not gone very far yet. They say that the nematocyst content appears to be a highly labile protein-complex. When tested in fish, frogs or mice it appeared to affect the nervous system, particularly the respiratory centres, before involving the voluntary muscles. The toxin elicited responses in the isolated heart of the clam which were similar to those caused by acetylcholine.

After intraperitoneal injection of mice with an appropriate toxin sample of pure *Physalia* capsule-content, Lane and Dodge report the following symptoms: increased activity and tremors probably due to local irritation. After 10 min. there were ataxia, decreased muscle-tone, flaccid paralysis, slowed and laboured breathing, defecation, aphrodisia, marked myosis, cyanosis, anoxic convulsions and death. Survival time was 1–48 hr. depending on the dose administered.

NEMATOCYSTS

We do not yet know the whole story of the development, transport and thread-devagination of the nematocysts of *Physalia*. There are two distinct types of nematocyst. Those found in the tentacles have globular capsules and tapering threads or filaments (Pl. XXV, fig. 4). The capsules are of two mean sizes, 26·8 μ and 11·3 μ in diameter (Lane and Dodge, 1958). That the threads taper can be seen both in optical section of the coiled-up threads and in devaginated ones. Pl. XXV, fig. 5 shows pads of these isorhizas round the mouth of a gastrozooid. Having no butt or hampe they should be referred to as isorhizas. Developmental stages can be found in the walls of the ampullae, from which they migrate not to the earliest formed pads or heads of the tentacle, but to those that have grown a little They can be seen during passage in the ectoderm of the tentacle-tube or lamella. Will (1909) figured the cnidoblasts of this type of nematocyst, and although I could not resolve all the details of those I have examined, I can confirm his account of them in general (Text-fig. 10). The nucleus and nucleolus of the cnidoblast or mother-cell are clearly visible at the inner end. In immature cnidocysts there is a large, central, homogeneous, hyaline mass at the circumference of which the thread can later be seen developing. Surrounding this central mass is a clearer, transparent substance which presumably forms the capsule wall. In 1926 Will published, without figures, an interpretation of what he thought to be the earliest developmental stages, but there still remains doubt about the details.* Chun (1892) had published figures of immature, tentacular cnidoblasts which show the 'tube externe', a feature that was puzzling until Weill (1934) showed that it was only the prematurely devaginated thread of an immature nematocyst. In many immature cnidoblasts I have seen the thread of the nematocyst partially devaginated in coils in the body of the cnidoblast as figured by Chun. The thread of the nematocyst is frequently found in preserved material to be devaginated while



Text-fig. 10. *Physalia physalis*. Nematoblasts. *A*, from the ampulla, capsule diameter 27 μ. *B*, from the ampulla, capsule diameter 11 μ. *n* = nucleus.

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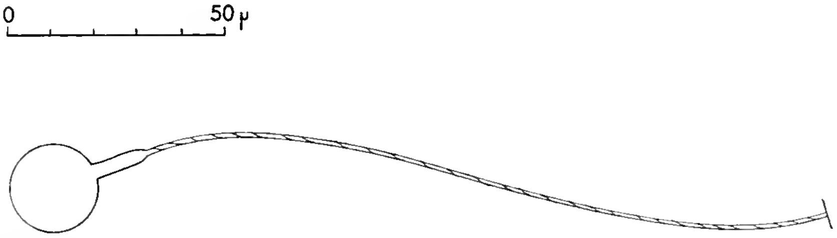
* In my opinion nothing is known yet about normal nematogenesis in any Cnidarian, except that the nematocyst originates as a homogeneous secretion-mass in an ectodermal mother-cell (nematoblast).

the capsule of the nematocyst is still retained by the cnidoblast. It is under these circumstances that fibrils of the cnidoblast-wall can best be seen.

The nematocysts of the tentacle of the protozooid appear to migrate into the tentacular heads from the ectoderm around its base. In mature specimens it is only in this region of the protozooid that any nematocysts can be seen, though the larvae are uniformly covered. It is a point of great interest that because the protozooid possesses only a relatively small tentacle, this never reaches that later stage in evolution found in secondary tentacles, where the much greater demand by these enormous tentacles for nematocysts has led to the development of hypertrophied basigasters called ampullae (see p. 355). In most siphonophores the basigaster of the protozooid is indeed smaller than those of the secondary gastrozooids, but in none of the other siphonophores is the contrast in size so great as in *Physalia*.

Neither my colleagues, Dr Evans and Mr Macfarlane, nor myself have been able to resolve the finer details of the threads of the nematocysts. There were certainly no spines as large as those indicated by Hardy (1956, fig. 24F) in any threads which we have examined. I was disappointed in an offer that was made to obtain pictures with an electron-microscope—the only satisfactory way of clearing up this point.



Text-fig. 11. *Physalia physalis.* Nematocyst discharged from a palpon, to show butt or hampe. The spiral bands are not correctly represented. No spines were visible. × 575.

The nematocysts of the palpons of *Physalia* appear to differ slightly from those found on the tentacles. I am again indebted to Miss Eleanor Dodge for a sample of nematocysts which she isolated from palpons. With the assistance of Dr Evans and Mr Macfarlane, I was able to measure and make a drawing (Text-fig. 11) of a representative capsule. It has a diameter of 20 μ and, unlike those of the tentacles, possessed a butt or hampe at the base of the thread, the diameter of the butt measuring 3 μ and its length 15 μ. Although we examined nematocysts with a twelfth-inch objective in ordinary light as well as with phase-contrast and dark-ground illumination, none of us could resolve the finer details of the spiral bands on the everted thread. However it was quite clear that there were no large spines on the butt as illustrated by Weill (1934) in his fig. 343*b*. Weill was not very precise about the place of occurrence of his 'sténotèles': he said that they came from the 'stolons gonozooidiques supportant les médusoides', but I can only suppose that he meant the palpons. I estimate that it would take nearly 80,000 of these capsules to inject 1 mg. of toxin into the prey, and about 24,000 of the tentacular capsules. The defensive role of the palpons in *Physalia* may be important because of the predatory habit of the associated fish, *Nomeus gronovii*.*

Lane and Dodge found that nematocysts were still reactive after isolation from the tentacle-tissues and 20 weeks of frozen storage. They estimated that 1 g. of packed, wet, 'purified' nematocysts contained approximately 1,058,000 nematocysts.

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* An article by Professor C. E. Lane (*Sci. Amer.* 202, 1960, p. 158) on nematocysts and their toxin, and on feeding reactions, contains some good photographs and a sketch of gastrozooids stimulated by glutathione. Unfortunately the article repeats some old morphological errors. Professor Lane demonstrates the relative immunity of the loggerhead turtle and of *Nomeus gronovii*.

MORPHOLOGY OF *PHYSALIA*

HISTORICAL

So much has been written about *Physalia* that useful observations are likely to be overlooked. Many of the accounts are travellers' tales which have been shown to have no foundation. It would take too long and be too unprofitable to make a new summary, especially as five previous ones exist, namely those of Lesson (1843), Quatrefages (1854), Huxley (1859), Haeckel (1888), and Chun (1897*b*). Lesson, who had frequent opportunities to make observations on *Physalia* during the long voyage of 'Coquille' (1822/5) published an account of them in 1827 and 1838, and repeated these more fully with a survey of past observations in 1843.

I have come across no satisfactorily complete account of *Physalia's* complicated morphology. Chun (1887) did once promise to deal with it thoroughly in a monograph on the Siphonophora but the work never materialized. Olfers (1832) gave a useful list of early references and names and figured the gonodendra. He mistook discharged nematocysts for Vorticellids attached to the tentacles. Olfers was of course writing before Wagner (1835) had published the first figures of nematocysts.* Trembley (1744) has figured what were probably the undischarged nematoblasts of *Hydra*, but it was Sir Joseph Banks's observations on *Physalia*, contained in his journal in an entry dated 12 April 1770 and seemingly entirely overlooked by Weill (1934), author of the first monograph on the subject, which provide our first knowledge of any nematocysts. I have to thank Dr A. M. Lysaght for drawing my attention to this entry: '. . .if touched by any substance they immediately exsert millions of exceedingly fine white threads about a line in length which pierce the skin and adhere to it giving very acute pain[.] When the animal exserts them out of any of the little knobbs or beads which are not in contact with some substance into which they can pierce they appear very visibly to the naked eye like small fibres of snow-white cotton.' Hooker published a shortened, rather dull and unscholarly version of Banks's Journal in 1896.†

On both 11 and 12 April, Banks noted that he had seen undoubted proof that the Albatross eat *Physalia*: 'April 11th. . . .an Albatross that I had shot dischar[ge]d a large quantity[,] incredible as it may appear that any animal should feed upon this blubber whose stings innumerable give a much more acute pain to a hand which touches them than nettles.'

Banks also observed the 'kind of sail which he erects or depresses at pleasure'. But his other notes on trimming the sail and being able to sail 'in any direction he pleases' are not so trustworthy. The description of making it 'concave on one side and convex on the other varying the concavity or the convexity to which ever side he pleases for the convenience of catching the wind' is more likely a description of righting behaviour.

In the British Museum (Natural History) is a specimen, still well-preserved in alcohol, which must be one of Banks's (B.M. Reg. no. 1925.8.13.2). The label on the old 'surgeon's round' bears the names *Holothuria physalis* in much-faded ink. Its style, with a ruled line at top and bottom, and the handwriting corresponds well with that of labels on three bottles of fishes, *Serranus atricaudatus*, *Anthias sacer* and *Sebastes kuhlii*, all known I am told to be Banksian specimens. The Banksian *Physalia* has a float measuring about 7 cm. in length. It bears seven major tentacles and a number of gonodendra

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* Wagner mistook the discharged nematocysts from the acontial threads of *Actinia holsatica* from Heligoland for sperms. Soon afterwards Ehrenberg (1838) published a large coloured plate of *Hydra vulgaris*, showing a number of irregularly discharged stenoteles, all with the tip of the thread still within the nematoblast, and the capsule at the outer end. He was under the impression that the capsules could be shot out and withdrawn again.

† The original is now in the Mitchell Library, New South Wales. A complete edition is to be published shortly under the editorship of J. C. Beaglehole.

which carry male gonophores. The specimen is right-handed and would have sailed to the left of the down-wind direction. It must be the specimen caught during Cook's first voyage, on 7 October 1768, south of the Cape Verde Islands, in latitude 9° 42′ N., and figured by Parkinson.

Huxley's (1859) observations, repeated from his 1855 communication, and his review of previous work are most useful. He longed for a Caliph Omar to straighten out the systematics, which, he complained, gave him an unpleasant vertigo. He made no proper distinction between palpons ('hydrocysts') and gastrozooids, and did not adequately describe the gonodendra ('gonoblastidia'), but to Huxley we are indebted for the first figure of a larva of *Physalia*.

Haeckel (1888) in his famous 'Challenger' report had to admit that physalids required a far more accurate anatomical examination than had been employed hitherto. He listed four genera and eleven species. He thought that there were four groups of species of *Physalia*, two with crested and two with non-crested floats. In each of these divisions there was a group with one and a group with several large main tentacles. I believe that all *Physalia* are crested in life, and that when fully grown they all have seven or more large tentacles. I have examined hundreds of living specimens of all growth stages in the Canary Islands, as well as preserved specimens from all oceans. I see no grounds for suspecting that there may be more than one species, which should bear the name *Physalia physalis* (L.). My field studies of Atlantic forms have provided answers to the two questions, which needed answering, before coming to this conclusion; (1) Are some of these animals crested throughout life while others are not, or is this only a matter of age and of degree of temporary inflation or deflation of the pneumatocyst? (2) Do successive growth-stages show (*a*) differing numbers of large (main) tentacles, and (*b*) a filling-up of the gap between the oral and main series of cormidia? The facts are that all *Physalia* are crested, that the number of large tentacles increases with age, and that the gap in question becomes relatively smaller and less conspicuous as growth proceeds.

Chun (1897*b*) and Bigelow (1911) both held the view that there were two and only two species, an Atlantic and an Indo-Pacific. But Bigelow assumed that, because up to that time none of the Pacific specimens examined had more than one large tentacle, it was evident that this was the final stage of development and that therefore the fully grown Pacific forms resembled an immature stage of the Atlantic *Physalia*. This argument has since been shown by Kawamura (1910) not to hold good. He found in fact later stages of development with more than one large tentacle.

The figures of *Physalia* drawn by Haeckel (1888) for pl. XXVI of his 'Challenger' report give no hint of the great complexity of budding. The only one of these figures which appears reliable is number 4. It is not a lateral view as stated, but a view from above of a right-handed specimen.* It shows very well the general shape of a relaxed specimen, although the basal internode is hardly visible, and the dorsal apical pore and ventral gas-gland cannot be seen. The protozooid is really in a terminal position (Pl. XI, figs. 1–3) and not in the subterminal one shown by Haeckel. Fig. 3 of Haeckel's plate showing a young specimen is misleading, because it shows the protozooid as having an ampulla and a gonodendron, structures never found in that position at any stage, and does not show the oral zone of appendages (see page 337). In fig. 3 (to which I refer again on page 339) and in fig. 6, Haeckel has simplified the structure of the gonodendron. Also the ampulla is always united along most of one side to the tentacle by the muscular fold which runs down the length of the tentacle. Haeckel's fig. 7 is valueless and fig. 8 is not at all accurate; fig. 5 is typical of a rather moribund specimen. I mention these points not to detract from the great value of Haeckel's pioneer work, but to help those who are not familiar with *Physalia*. Haeckel made the most of the specimens of the relatively few good species

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* Brandt's generic name *Alophota*, used by Haeckel in explanation of the figure, refers to his idea that there were species of *Physalia* with no crest.

of siphonophores (thirty) which he included in his monograph, by making idealized coloured drawings, even when he was not sure of the details. It is greatly to his credit that he undertook the formidable task of making coloured sketches of living animals in the field, a task which would be quite impossible for me.

In 1932 G. H. Parker made some interesting experiments at Key West, Florida, on the neuromuscular activities of the tentacles. He also recorded the measured length of an extended tentacle as a little over 9 m., and stated that the tentacles can shorten to one-seventieth of their maximum length.

POLYMORPHISM

In *Physalia* there are three types of medusoid individuals all found on the gonodendra: (1) the reduced male and female gonophores, (2) the peculiar asexual nectophores, and (3) the jelly-polyps, which are probably vestigial nectophores.

Of polypoid individuals there are four types, as well as the unique protozooid with its small moniliform tentacle: (1) the feeding gastrozooids which become separated from their tentacles, (2) the gastrozooids of group 1 of cormidia II–VII of the main zone and of all the cormidia of the oral zone, (3) the secondary and tertiary gonozooids, which like those of (2) give rise by budding to the branches of the gonodendra; none of these have tentacles, and (4) the gonopalpons, which have no tentacles.

PATTERN OF BUDDING IN THE CORMIDIA

In spite of the large number of papers on *Physalia*, there is no good account of its gross morphology, especially of the cormidial groups of appendages and their development.

Anyone who tries to decide on the number and structure of these groups of buds will not be surprised to learn, I think, that so far no one has had sufficient patience to pursue the subject to a satisfactory conclusion. Without properly relaxed specimens, it was in the past a hopeless task; even today with better material to study, my conclusions must be of a tentative nature. In order to reach more definite results in the future, efforts should be made to anaesthetize and preserve in a thoroughly relaxed state the oldest as well as the very youngest stages of development. From a morphological point of view, the potential value of well-preserved, young specimens increases greatly for every millimetre below ten in float-length.

Previous workers on *Physalia* have tended, I feel sure, to simplify the problem by ignoring all except the largest branches of the cormidia. Accordingly, having had a great number of living specimens to deal with at Arrecife, on my return in 1955 I decided to make a completely fresh study of the structure and developmental sequence of the cormidia. My analysis is based upon detailed examination of some two dozen younger and three dozen older specimens, including those taken by R.R.S. 'Discovery', and has since been confirmed by examination of the lovely series of larvae, so kindly sent me from Miami by Miss Eleanor Dodge. Three years of laborious observation, dissection and photography have established a basic pattern of budding in the cormidia, a pattern which would have been less clear but for this opportunity of studying the early larval stages. The complexity of this pattern is illustrated by the series of growth stages shown on Pls. VII–IX. In some of the larvae examined (Pl. VII) very early indications of budding can be seen; others already carry several buds. The juvenile specimens shown on Pl. VIII vary in length between 12 mm. and 80 mm., and exhibit ever increasing budding, which culminates in the branching mass of cormidia typical of the adult *Physalia* (Pl. IX).

The cormidia are budded from a narrow tract of tissue lying along the under and windward side of the float extending from the protozooid (Pl. VIII, fig. 2) to a point half-way to the pore. This tract is divided by a gap—Haeckel's 'basal internode'—into two (Pl. XI, fig. 5), an oral zone and a main, aboral zone. The gap is particularly well marked in young stages. Specimens with float-lengths of two or three centimetres show this division clearly. For study of the cormidia, I found it best to dissect off the whole of the budding-tract from the float and to examine the inner side first of all. In a well preserved, relaxed specimen a series of depressed openings, about a dozen in number, can be seen. Five or more in the oral zone are separated by the basal internode from the main series of seven in the aboral zone (Pl. XIII, fig. 1). The isolated first group of Cormidium I* opens separately into the pericystic space, as can be seen in specimen Lanzarote Juv B (Pl. XIII, fig. 4), so that although there are definitely only six cormidia in the aboral zone of this specimen, there are seven main openings into the pericystic space of the float, including two such openings in Cormidium I: they are the openings of the peduncles of the chief tentacles of each cormidium. Once the position of these peduncles has been found (Pl. XIII, fig. 1) it is possible, even in large specimens, to cut off each cormidial complex entire. The openings are clearly shown in the plate. Before cutting off the cormidia, it is essential to note their orientation, both with regard to the oral (protozooid) end of the float and to the leeward side, otherwise analysis of the pattern of branching becomes very difficult.

Steche (1910) and Okada (1932) numbered the cormidia of the main aboral zone starting from the aboral end; I have followed this method, both for the oral and aboral zones. In Pl. XI, figs. 4, 5, the ventral budding-tract removed from a specimen of float-length 10–11 cm. is shown with the cormidia clearly numbered. In this specimen there are at least six oral and six aboral groups; the seventh main aboral group is not developed. Seven is the maximum number of primary main-zone cormidia that I have found.

The branching-system of typical cormidia (III and VI of the main aboral zone, and 1 and 2 of the oral zone) of a specimen, number 25 from Lanzarote, were very carefully analysed. The results are shown in schematic drawings (Text-fig. 12), which not only give the correct proportions of the cormidia, but the exact number of groups on the related branches. Tables 10 and 11 (p. 338) give similar accurate analyses of the groups and branches of all the cormidia of both main and oral zones of specimen 25. This is the first time that such an analysis has been attempted.

Comparison of the four drawings of Text-fig. 12 will at once make clear the main pattern of arrangement of groups in cormidia both from the oral and the main zone.

Main aboral zone (Pls. XII–XVIII)

In the main zone, the definitive number of cormidia cannot be determined in early stages; in specimens of from 1 to 2 cm. float-length there are often only five; in specimens of from 3 to 4 cm. float-length there may be six; even in a specimen with float-length of 17 cm., taken by R.R.S. 'Discovery II' in 3° 22′ S., 32° 25′ W., there are still only six cormidia in the main zone, although (as already mentioned) seven is the number usually found in the largest specimens. As in the oral zone, the smallest and presumably the youngest (VI or VII) lies at the oral end of the main zone.

Careful examination of seven of the best preserved of my collection of younger specimens, measuring from 1·7 to 2·1 cm. in float-length, served to illustrate the early essential pattern of growth in the cormidia of the main zone (Table 10). There are three chief components of each cormidium: (1) a reduced group at the oral end consisting only of a gastrozooid with a peculiar gonodendron at its base, (2) a first tripartite group, or first lateral group, consisting of gastrozooid, tentacle and ampulla, and a gonodendron at the base of the gastrozooid, and (3) a further series of similar lateral tripartite groups, each growing from the base of its predecessor. This is the essential arrangement which visual analysis brings to light and which I have been able to record photographically. It is obscured only too soon by the development of (4) secondary series of branches (leeward, oral and aboral) from the bases of some of the lateral groups, bearing more tripartite groups (Text-fig. 12).

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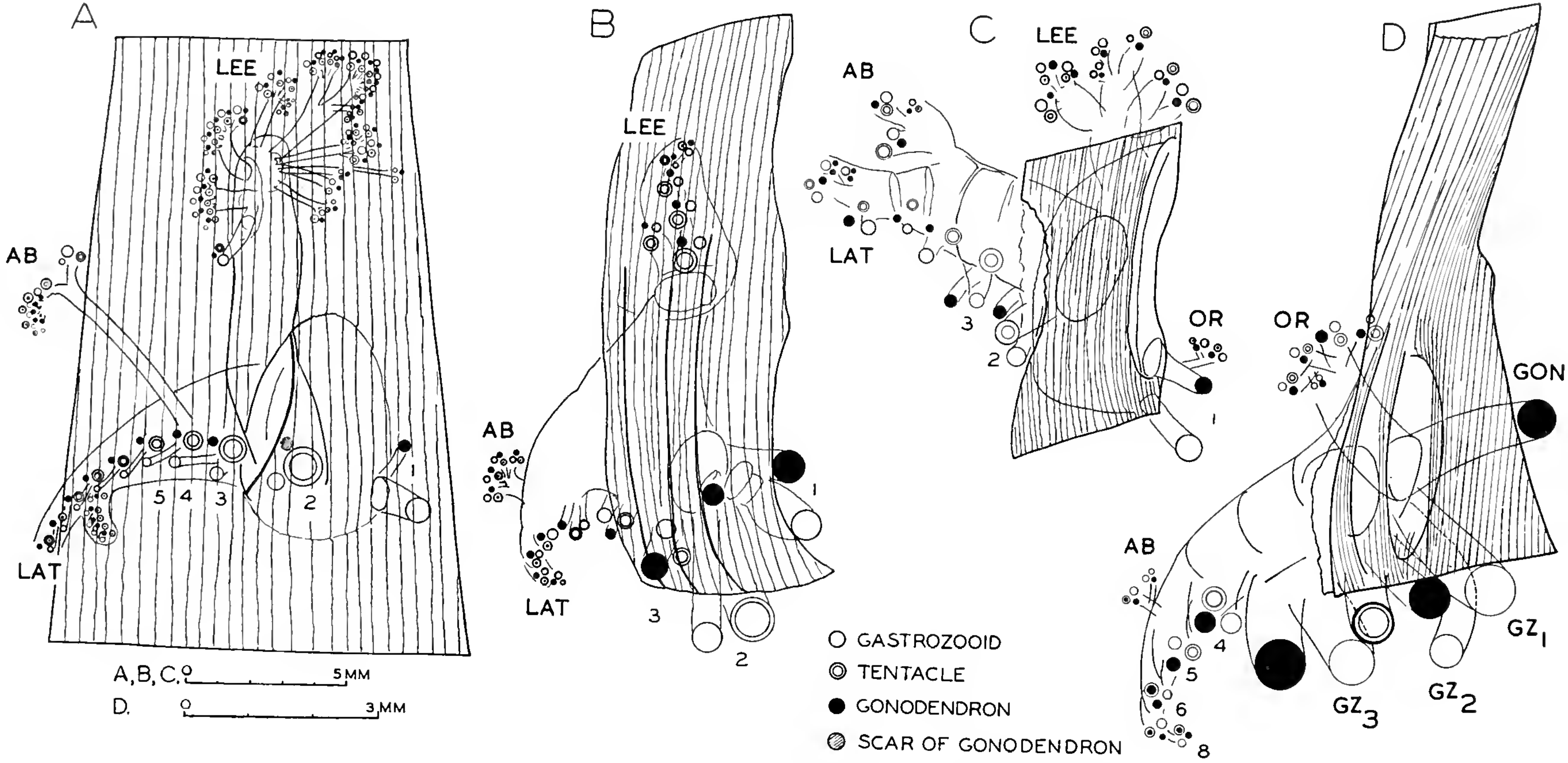
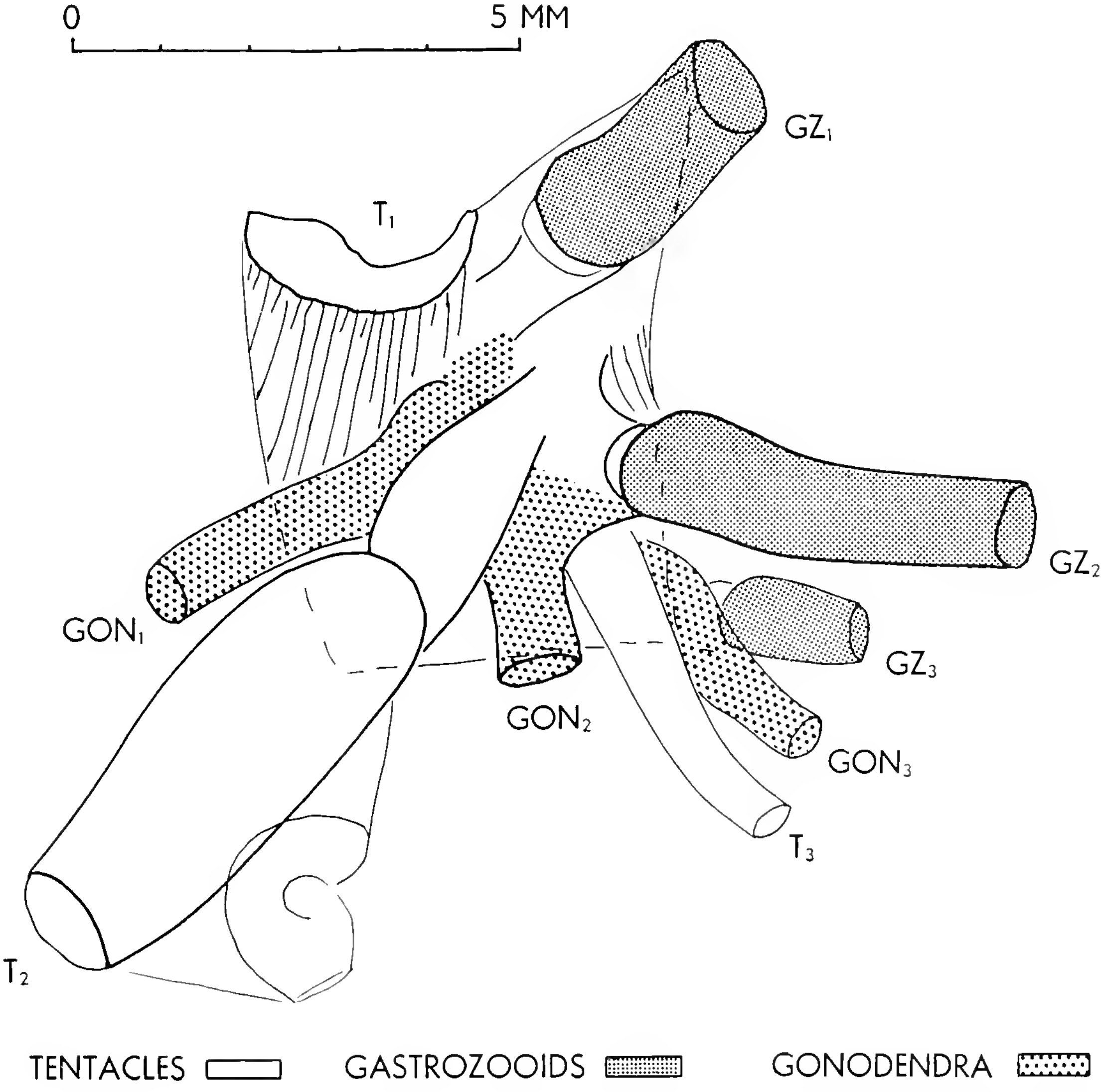
* Arabic numerals will be used for the cormidia of the oral zone and Roman for those of the aboral zone.



Text-fig. 12. *Physalia physalis.* Schematic drawings of separated cormidia of a left-handed specimen, number Lanzarote 25, cut from the lower part of the outer wall of the float. Float-length 18 cm., gas-gland diameter 2·5 cm., to show pattern of budding common to all cormidia. *A*, cormidium III (main zone) from above, ×4·5. *B*, cormidium VI (main zone) from above, ×4·5. *C*, cormidium 1 (oral zone) from above, ×4·5. *D*, cormidium 2 (oral zone) from above, ×9. *AB* = aboral branch, *Lat* = lateral branch, *Lee* = lee-branch, *Or* = oral branch. Tripartite groups numbered 1–8. *Gz* = gastrozooids of groups 1, 2, 3. *GON* = gonodendron of group 1. Note the common peduncle formed by the bases of groups 2 *et seq.*

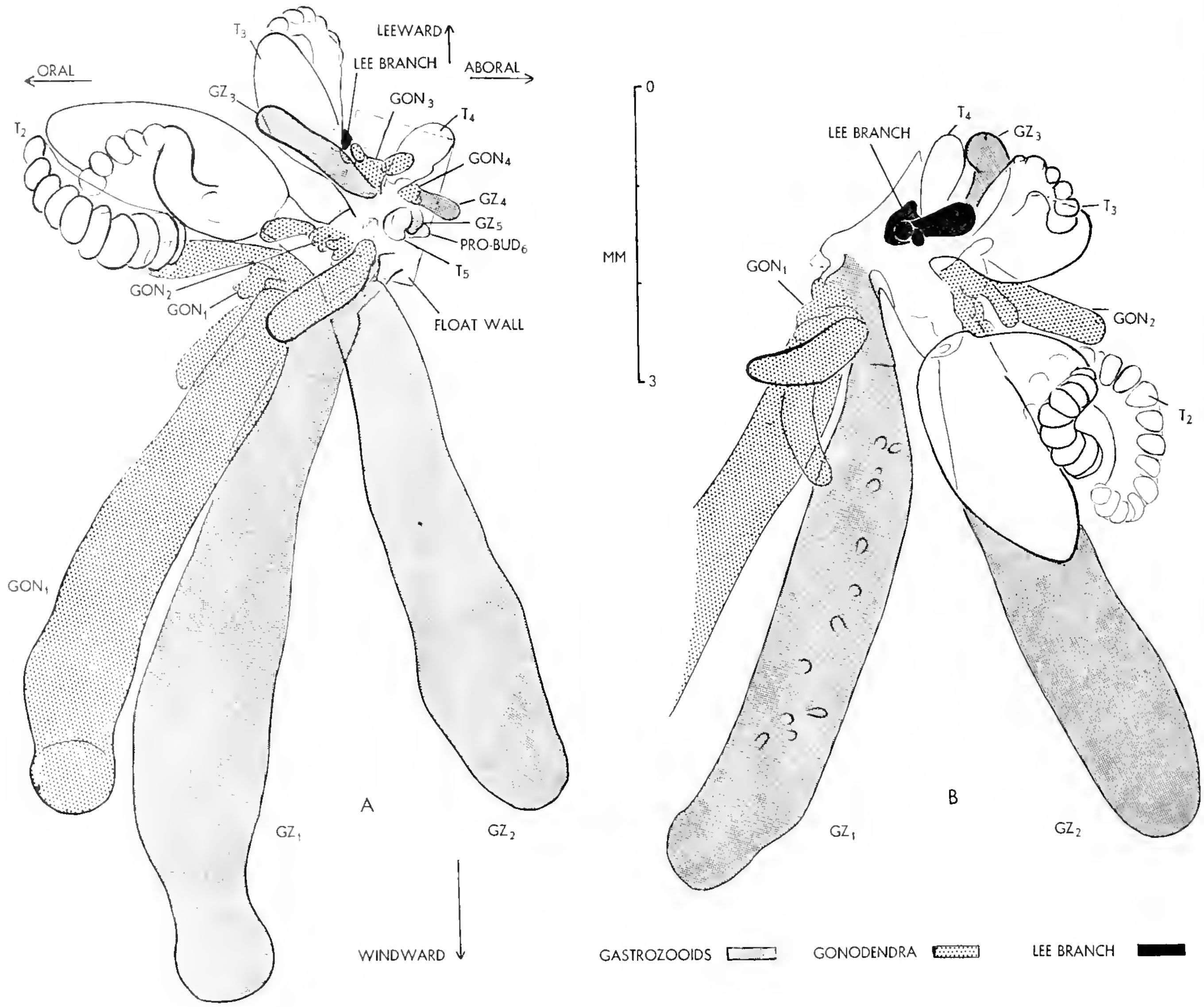
(1) *Reduced group.* In cormidia III–VII prominent gastrozooids are found at the oral end of the cormidia, associated each with a characteristic, but atypical gonodendron (Pl. XII, fig. 4). In cormidia I and II on the other hand, each equally noticeable gastrozooid is linked both with a gonodendron and with a tentacle (Pl. XIII, figs. 3, 4), and lies on the aboral side of the tentacle. Thus in cormidia I and II the reduced group is missing and the first one is tripartite like all the other components of the cormidia (Text-fig. 13), whereas in cormidia III–VII the tripartite pattern of the first group has been lost by the non-development of its tentacle. This pattern can generally be recognized even in old specimens when viewing them from the windward side. All seven cormidia open separately into the pericystic space. Both the gastrozooid and the gonodendron of the first groups (group 1) of cormidia III–VII appear to retain separate openings into the common atrium, or enlarged and subdivided base of each cormidium (Text-fig. 12B). But if early stages of their development are examined (Text-fig. 14A) it can be seen that the gonodendron is budded from the base of the gastrozooid as usual. It is only because of the subsequent broadening of its base and incorporation into the



Text-fig. 13. *Physalia physalis.* Base of cormidium II (main zone) of a right-handed specimen, float-length 5 cm., from St. 403, to show the tripartite nature of the first three groups. In cormidium II, all the groups including group 1 are tripartite. × 11·5.

growing and thickening wall of the float that the first gastrozooid's relationships become obscured in later growth stages (Text-fig. 12). The main foramen is that of the peduncle of the tentacle of group 2.

(2) and (3) *Tripartite groups,* first and laterals.* The general pattern of arrangement of the tripartite groups is easy to recognize once it becomes familiar (Pl. XIV, figs. 1–4). These groups were first described by Schneider (1898), who had only two specimens to work on, under the name of 'Urgruppen', and although his account is difficult to follow without figures, it is a sound analysis of the tripartite groups and their subsidiary lateral branches. Each 'Urgruppe' (Text-fig. 15) consists of one polyp (gastrozooid), one tentacle and one genital cluster (gonodendron), all borne on a single peduncle (Pl. XIV, fig. 1). These simple 'Urgruppen' very soon become complicated, said Schneider, by the development of second, third and fourth 'Urgruppen' on similar peduncles, each arranged on one side of a thickened peduncle and separated from one another by lateral peduncles. Here he was probably referring to the relationship between the first tripartite group of a cormidium and the series (3) which



Text-fig. 14. *Physalia physalis.* Two views of cormidium VI (main zone) of a young left-handed specimen, number 11, to show stages in the growth of the lateral groups and lee-branches. *A* = oral view; *B* = aboral view. ×9·5. 1st group without a tentacle, *GZ* 1 and *GON* 1; lateral groups, gastrozooids *GZ* 2–5, gonodendra *GON* 2–5, tentacles *T* 2–5.

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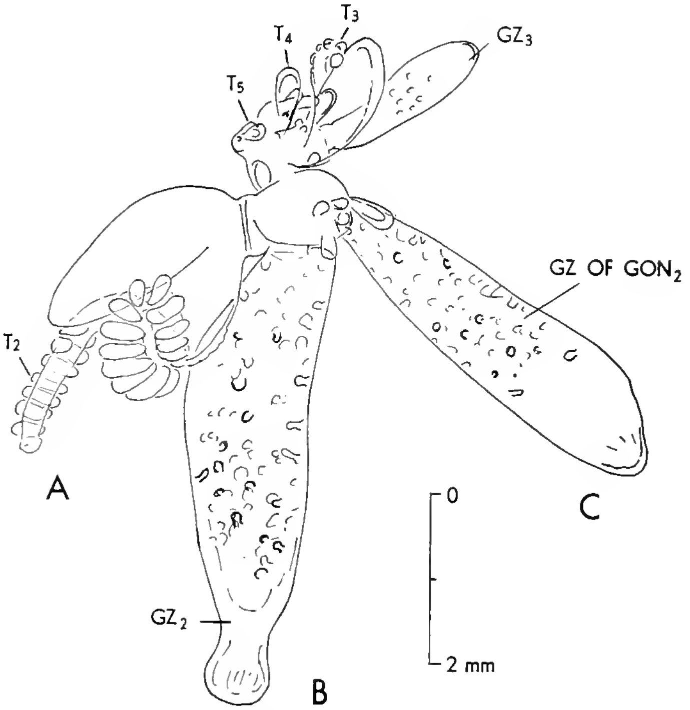
* The significance of these is explained on page 361.

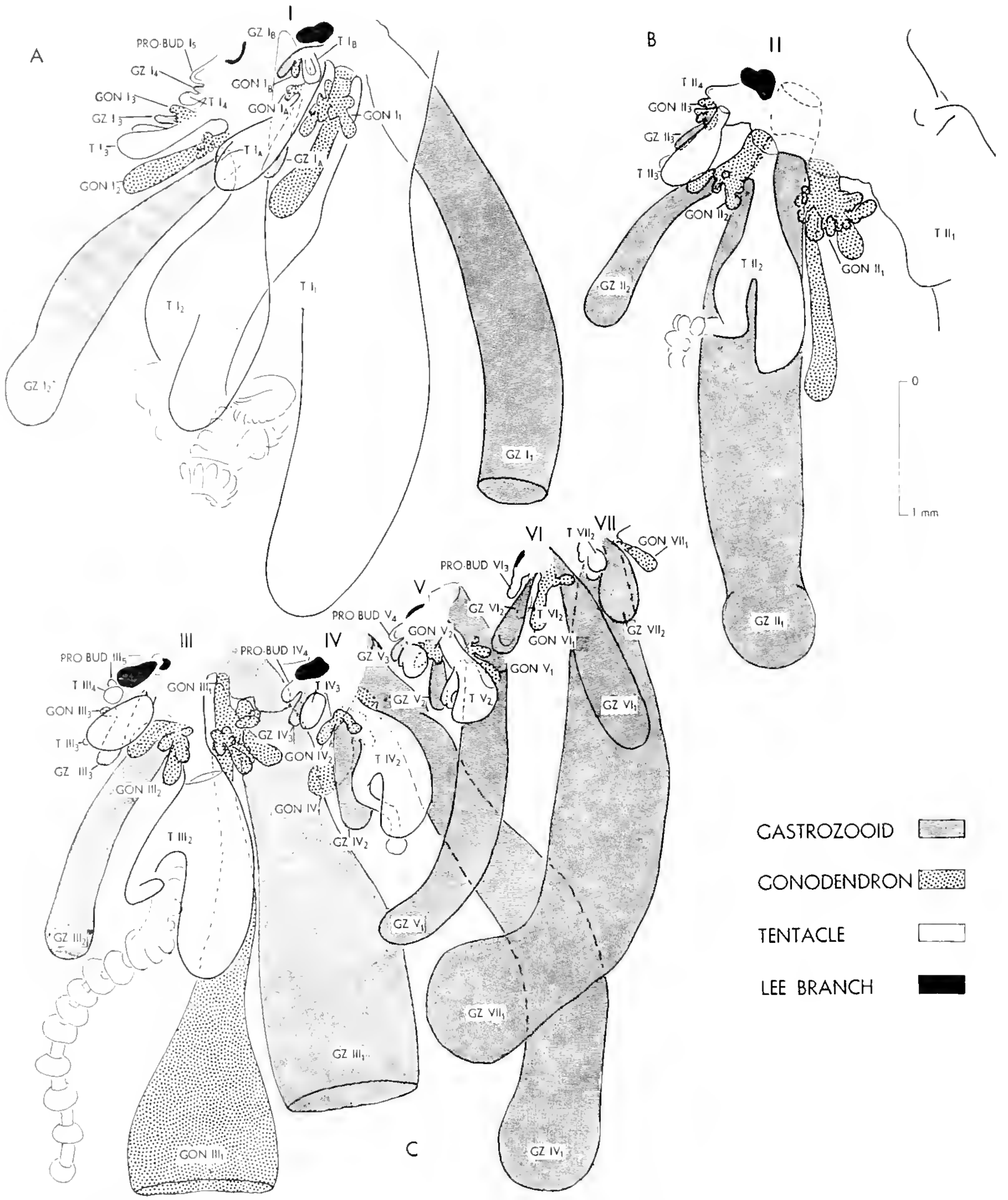
I call lateral groups. Whether he was also referring to the series (4) arising from the bases of the lateral groups is not clear.

The development of group 2 and the subsequent lateral tripartite groups can best be seen in the aboral region of the main zone by examining cormidium I of a young specimen (Pl. XIV, figs. 2–3). This region looks very complicated in older stages (Pl. XIV, fig. 4); when mature it is almost impossible to analyse this first cormidium without knowledge of the younger stages. Cormidium I has room to expand because it lies at the aboral end of the main series, consequently the primary and lateral groups, especially the first, are better developed and more widely separated than those of the other cormidia. Its aboral end forms a projection (Pl. XIV, fig. 3) on which the youngest groups can be seen. Two beautiful young specimens, measuring 2·9 and 8 cm. in float-length, show clearly that at this stage there are at least eight lateral groups in cormidium I. They decrease in size according to youth, so that the one at the aboral end is a very small bud (Pl. XIV, fig. 3). Each group consists of a gastrozooid, a gonodendron and a tentacle. They look as if they might be, and indeed at one time I thought they were, beginnings of new cormidia, but in each of the other cormidia of the main zone there is a counterpart of this series of lateral groups. As previously stated, there is evidence that the latest (youngest) cormidia to appear do so at the *oral* end of the budding-zone, whereas in the lateral groups the pattern of development is reversed, the youngest groups appearing at the *aboral* end of each cormidium. When fully developed, there may be from ten to twelve fan-shaped lateral groups (Pl. XV, fig. 4) in each main zone cormidium. They bud successively (Pl. XVII, fig. 4) each from the base of its predecessor and as growth proceeds they curl round (Pl. XV, fig. 6) so that the last small lateral of one cormidium can be seen lying to the oral side of the first and largest tentacle of the cormidium that lies at its aboral end.



Text-fig. 15. *Physalia physalis.* Cormidium 5 (oral zone) of a young specimen number 11, less group 1, to show the three parts, *A*, *B*, *C*, of an 'Urgruppe'. Note the endodermal villi. *GZ* of *GON*$_2$ = gonozooid mentioned on p. 347. × 11.

(4) *Secondary basal branches.* These tend to occur wherever there is room for further growth and expansion, that is, on the *leeward* side of the float, at the *aboral* ends of the cormidia, and, in the case



Text-fig. 16. *Physalia physalis.* The cormidia of the main zone of a well-preserved, young, right-handed specimen K2, float-length 11 mm., taken by Miss Dodge near Miami, to show the pattern of budding. *A* = cormidium I, *B* = cormidium II, *C* = cormidia III–VII. Group 1 of cormidium I is atypical in having lateral (1_A) and basal (1_B) buds. The arrangement of the parts for this drawing differs slightly from that in the specimen as photographed in Pl. VIII, fig. 5. ×20. (From below, see Text-fig. 21 E.)

of cormidium VII, at the *oral* end of the cormidium. These secondary branches form a regular pattern and consist of later developed tripartite groups of appendages (Text-fig. 12). To *leeward* (Pl. XV, fig. 3) they arise from the base of the *second group*, which becomes incorporated into the ventral wall of each cormidial section of the float; *aborally* (Pl. XVI, fig. 3) they can spring from the peduncles of the *fourth* lateral group *et seq.* The branch at the oral end, when present, springs from the base of the gonodendron of the first group.

Some differences, not very great, exist between the seven cormidia of the main zone. It has already been pointed out that cormidium I is the most expanded (Pl. XV, fig. 4); cormidium II (Pl. XVI, fig. 4) is atypical because of the predominance of its main tentacle and in the absence of the reduced first group (see page 331) so characteristic of cormidia III–VII; cormidia III–V are the typical ones (Pl. XII, figs. 3, 4). In cormidium VII there is a secondary *oral* branch of groups at the base of group 1 as just mentioned. It is next to the basal internode between the two zones, where again there is room for the cormidium to expand, and it seems homologous with the regular series of secondary branches, met with in all mature cormidia (described under (4)), which spring normally from the bases of the peduncles of the second or third and fourth or fifth lateral groups. All these secondary branches of groups are shown in Text-fig. 12.

The degree of complexity which is brought about through the budding of secondary and subsequent series of *basal* buds is illustrated in Pl. XVI, figs. 1–4 of cormidium II of a left-handed 10-in. specimen, number Lanzarote 2. Figures 2, 4 are views from the aboral end. In figure 3 a black bristle indicates the position from which were cut the terminal, lateral groups 5–12, which curled over from left to right of the picture. Figure 1 is a view from the oro-lateral side of the cormidium. Before this photograph was taken a complex *basal* branch (Text-fig. 17A) had been cut off. This branch *A* consisted of six branchlets (Text-fig. 18). The first five of these were single tripartite groups, of which only the gonodendra remained. From the base of the fifth was budded a tertiary branch of five groups. The sixth branchlet (Pl. XVII, fig. 1) consisted of six groups. So that from this one *basal* branch *A* had been budded seventeen tripartite groups. After the photograph (Pl. XVI, fig. 1) had been taken a second basal branch was cut off (Text-fig. 17B). This branch *B* consisted of thirteen groups. Another branch *C* (Text-fig. 17) was left intact and bore nine groups. At the base of group 2 of the main series of laterals of this cormidium II (Text-fig. 17D) is another complex *basal* branch *D*, whose number of groups is at least 16; and from the base of group 4 of the same main series of laterals of cormidium II is a still further branch carrying six groups. Both group 4 and its basal branch are shown in Pl. XVI, fig. 3 to the left of the bristle, and lying on a small rectangular piece of black paper. The *basal* branch is the uppermost of the two.

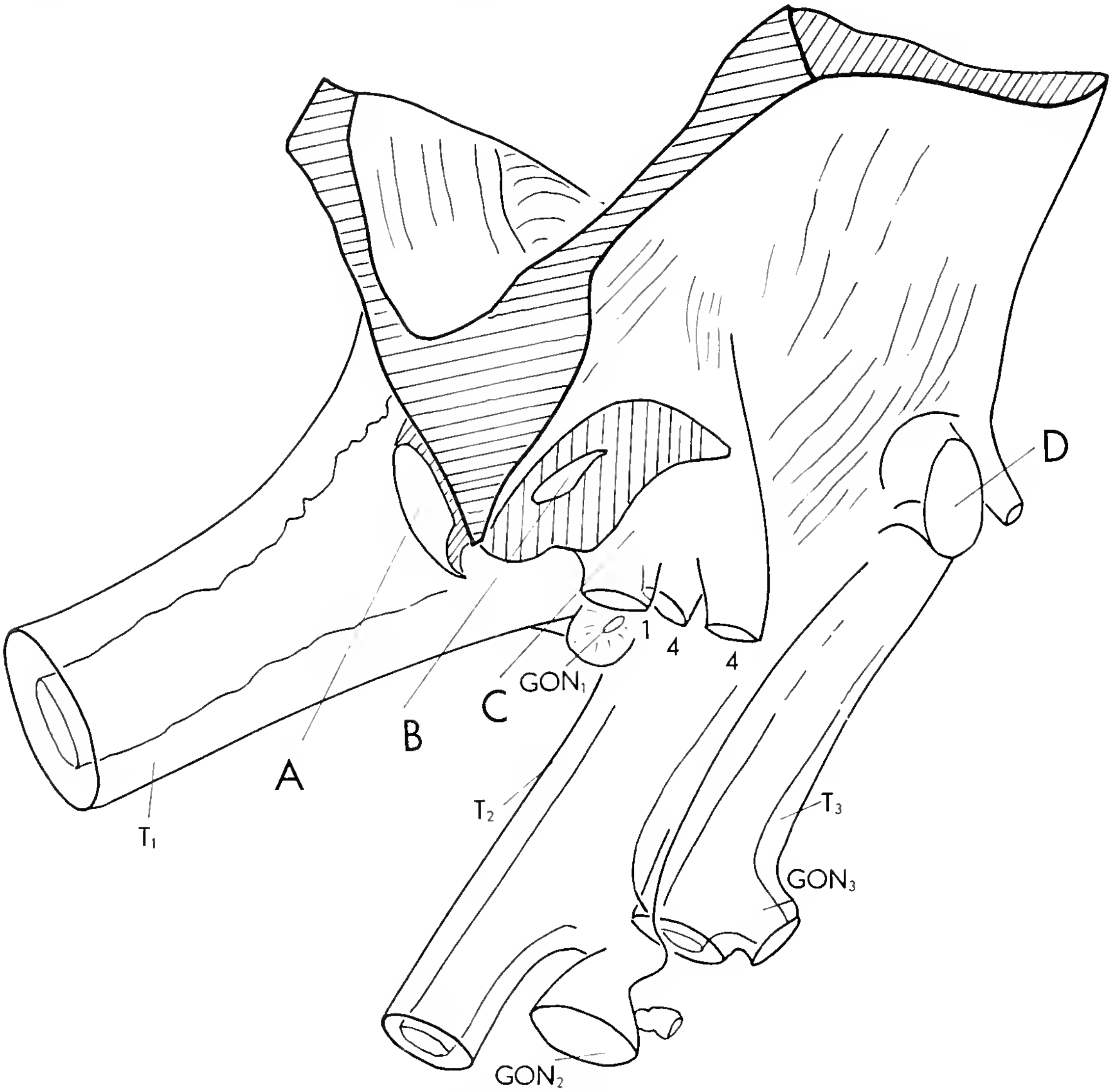
So the secondary and subsequent *basal* branches of cormidium II, which lie to *leeward*, had given rise by budding to at least sixty-one tripartite groups.

Further illustrations of this complex secondary cormidial budding will be found in the figures of cormidium III of the same specimen, Lanzarote 2 (Pls. XVII, XVIII). The first two (Pl. XVIII) show the cormidium viewed from opposite ends, and the rest show the severed branches, with indications of the positions from which they were cut. Figures 2 and 4 show the severed aboral branch and Pl. XVII, figure 3 shows the branches remaining *in situ* more clearly displayed. This photograph was taken after severing the terminal laterals 5–11, further magnified in figure 4.

A final re-examination was made of the two dozen young specimens measuring from 1 to 9 cm. float-length. They included a fine series of fifteen of the specimens sent me by Miss Dodge from Miami. The object of the re-examination was to make sure of the number of cormidia at the aboral end of the main zone. Some doubt had arisen whether there were two or only one anterior to the cormidium bearing the main tentacle, cormidium II, because of the condition found in one of Miss Dodge's specimens, number K 2 (Pl. VIII, figs. 5, 6, Text-fig. 19).

In every specimen of *Physalia* that I have examined, with the exception of K 2 just mentioned, it could be seen quite clearly that anterior to cormidium II there is a series of distinct tripartite groups, numbering in later stages a dozen or more, and that they obviously form a single cormidium, number I. The criterion is whether the first group of cormidium I is a simple tripartite, or whether it buds off a series of lateral groups.

In specimen K 2, which has a float-length of 12 mm. and is very well preserved, it appeared that there were lateral groups present in the first group of cormidium I. I therefore made camera-lucida sketches of both cormidium II and of group 1 of cormidium I of K 2. These are reproduced in Text-fig. 16. They show that group 1 has developed, beside a bud of basal leeward groups, at least two lateral groups, 1_A and 1_B. This condition is very exceptional.



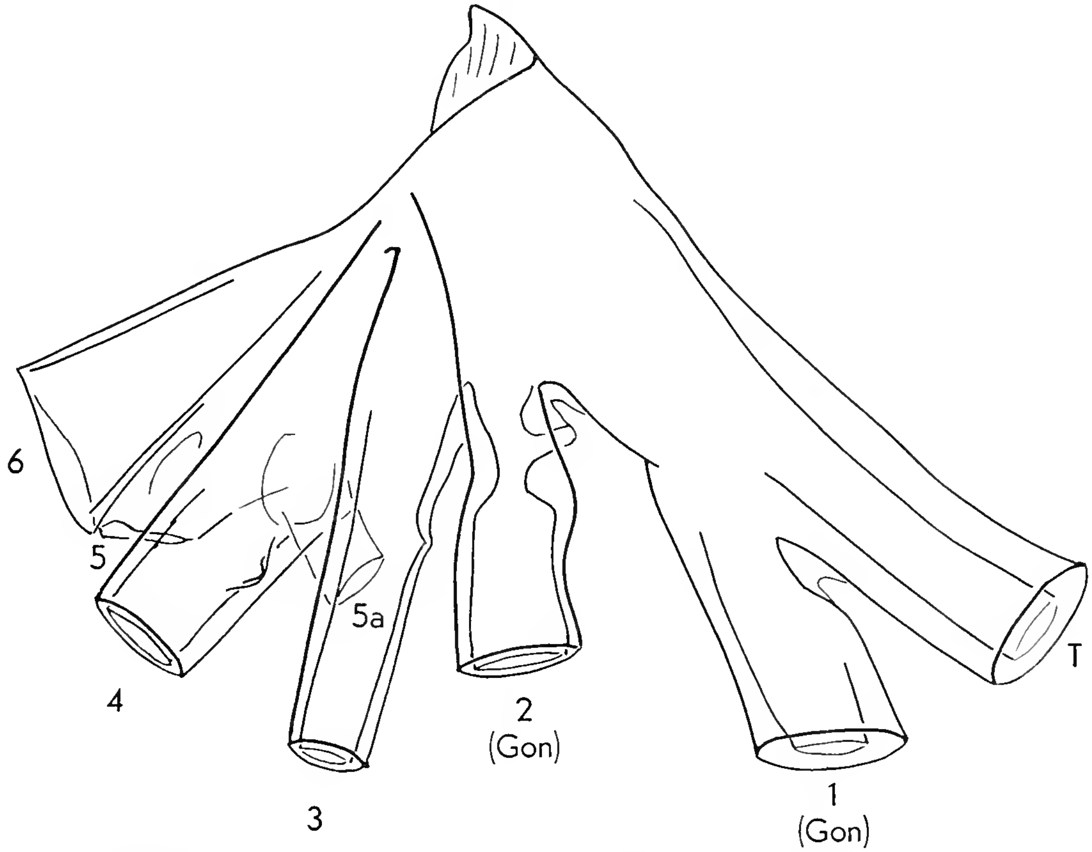
Text-fig. 17. *Physalia physalis.* Oro-lateral view of the base of cormidium II, specimen number Lanzarote 2, to show positions from which complex, secondary, basal branches were budded. Branch *A* was cut off and is shown in Pl. XVII, fig. 2. Branch *B* was cut off. Only the bases of branches *C* and *D* are shown. These four branches gave rise to 54 tripartite groups. A scar between the bases of tentacles 1 and 2 marks the position from which the gonodendron of group 1 was detached. The bases of gonodendra 2 and 3 are indicated, groups 4–11 are not shown; they would curl round to the left behind. $C_{1, 4, 4}$ = number of end-sections of branch *C* on three separate branchlets.

In the course of re-examination I confirmed that, in all other specimens, these branches of cormidium I originate from the compound joint pedicels of group 2 *et seq.*, and that group 1 is a simple, isolated tripartite group (see page 329). In K 2 on the other hand, group 1, though isolated, is exceptional in having rudiments of leeward groups and lateral groups. In all the other thirteen specimens of about the same age sent me by Miss Dodge this isolation of group 1 of cormidium I can be clearly seen. It was this isolation which led me to suspect the presence of two cormidia anterior to cormidium II bearing the main tentacle.

Oral zone (Pls. XI, XIX)

The oral end of the float carries the protozooid (the primary gastrozooid) and ventrally five or more groups of cormidia arranged in oblique rows. The youngest cormidium lies nearest the protozooid (Pl. XIX, fig. 1).

Previous authors have mentioned the complexity of budding in the oral zone cormidia, but I know of no detailed analysis of their structure and development. In unrelaxed specimens, such analysis is well-nigh impossible, but among the few mature specimens that I have handled, specimen number 25 from Lanzarote, which had been specially relaxed in magnesium chloride, showed after dissection that the pattern of budding is essentially the same as in the main zone, except that the first two groups of a cormidium, and sometimes the lee-branches as well, appear to open separately into the pericystic space. This multiplicity of openings makes it less easy to separate the oral cormidia from one another for individual examination. Five cormidia can be distinguished with certainty (Pl. XI, fig. 4), but my analysis of specimen number 25 (Table 11) (based on a unique well-relaxed animal, the only one ever examined) shows that most probably seven oral zone cormidia are present in fully grown *Physalia*. This will have to be confirmed by examination of additional relaxed specimens.



Text-fig. 18. *Physalia physalis*. Proximal part of basal branch *A* (see Text-fig. 17) to show bases of six branchlets described in the text. Scars could be seen at the bases of 2, 3 and 4 from which tentacles have been lost.

The whole *oral* zone appears to be somewhat reduced and growth is less profuse. None of the *oral* cormidia of specimen Lanzarote 25 has a tripartite group 1, and only two have a tripartite group 2. With the exception of cormidium 1, neither are lee branches present in group 2; on the other hand in group 1, *oral* branches occur more frequently in this group than in the main zone (cf. Tables 10 and 11).

The gastrozooids of the *oral* zone are definitely gastrozooids, not palpons, but they seem to develop slowly and in the early stages are not easily recognizable (Pl. XI, figs 1–3).

Table 10. *Analysis of branching of cormidia of main zone of specimen Lanzarote no. 25*

Aboral End *Oral End*

Cormidia	I	II	III	IV	V	VI	VII
Group 1	Tripartite	Tripartite	Gz., Gon. (no tentacle)	Gz., Gon. (2 brs.) (no tentacle)	Gz., Gon. (of 7 sectns. Gz. and palpons, each from base of last). (No tentacle)	Gz., Gon. (no tentacle)	Gz., Gon. (no tentacle) [Oral br. of 6 groups]
2	Tripartite 5 Lee branches (1) 5 grps. (2) 4 grps. basal br. of 2 grps. (3) 5 grps. (4) 5 grps. (5) 1 grp.	Tripartite 3 Lee branches (1) 5 grps. and bud (2) 3 branchlets of 3, 4, 1 grps. (3) 1 grp.	Tripartite 3 Lee branches (1) 5 branchlets of 1, 5, 5, 3, 2 grps. (2) 3 branchlets of 4, 6, 2 grps. (3) 4 branchlets of 5, 1, 2, 2 grps.	Tripartite 1 Lee branch of 6 grps. from base of grp. 1 3 branchlets of 1, 4, 3 grps. From base of grp. 2 1 branchlet of 3 grps.	Tripartite 1 Lee branch of 7 grps.	Tripartite 1 Lee branch of 5 grps. from base of grp. 1 1 branchlet of 5 grps.	Tripartite 1 Lee branch of 5 grps. from base of grp. 1 1 branchlet of 1 grp.
3	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite
4	Tripartite (T. lost) [Aboral br. of 6 grps., 1 branchlet of 4 grps.]	Tripartite [Aboral br. of 1, 4 grps.]	Tripartite [Aboral br. of 6 grps.]	Tripartite [Aboral br. of 4, 2 grps.]	Tripartite [Aboral br. of 6 grps.]	Tripartite	Tripartite
5	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite [Aboral br. of 4 grps.]	Tripartite
6	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite
7	Tripartite	Tripartite	Tripartite Aboral branchlet of 5 grps. from base	Tripartite	Tripartite	Tripartite	Tripartite
8	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	End of branching
9	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	—
10	Tripartite	End of branching	Tripartite	Tripartite	Tripartite	End of branching	—
11	Tripartite	—	End of branching	Tripartite	End of branching	—	—
12	Tripartite	—	—	Tripartite	—	—	—
13	End of branching	—	—	Tripartite	—	—	—

Br., Branch; Gon., Gonodendron; Grp., Group; Gz., Gastrozooid; T. Tentacle

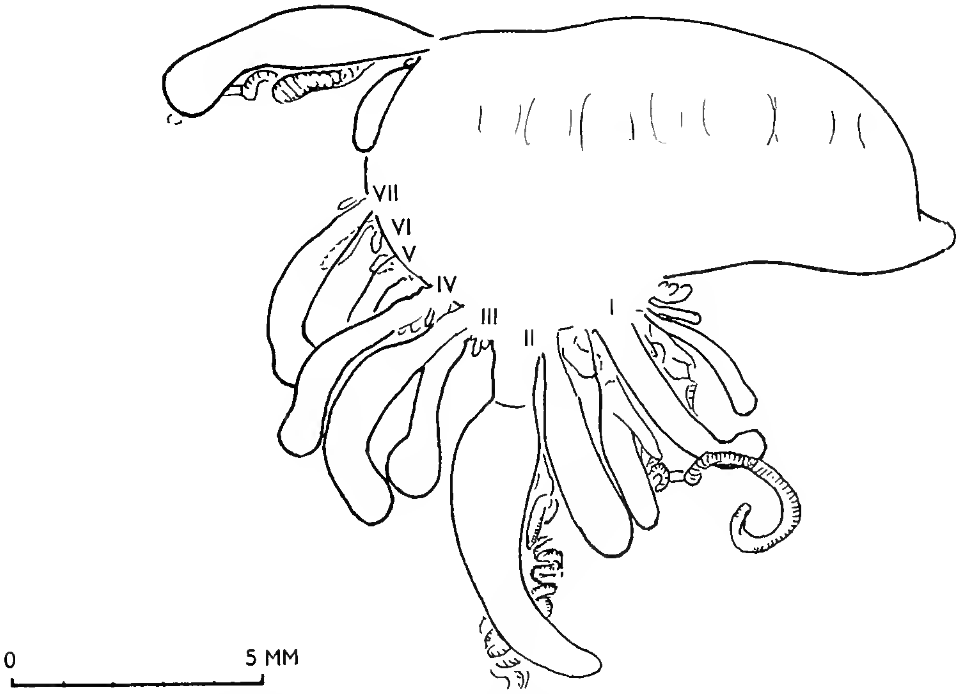
Table 11. *Analysis of branching of cormidia of oral zone of specimen, Lanzarote no. 25*

Aboral End *Oral End*

Cormidia	1	2	3	4	5	6	7
Group 1	Gz., Gon. (no T.) [oral br. 3 grps.]	Gz., Gon. (no. T.) [oral br. 4 grps.]	Gz., Gon. (no T.) [oral br. 2 grps.]	Gz., Gon. (no T.) [oral br. 4 grps.]	Gz., Gon. (no T.) (no oral br.)	Gz., Gon. (no T.) (no oral br.)	Gz., Gon. (no T.) [oral br. 2 grps.]
2	Tripartite Lee br. of 5 grps. From grp. 3, 1 branchlet of 3 grps.	Gz., Gon. (no T.) (No Lee br.)	Gz., Gon. (no T.) (No Lee br.)	Gz., Gon. (no T.) (No Lee br.)	Tripartite (No Lee br.)	Gz., Gon. (no T.) (No Lee br.)	Gz., Gon. (no T.) (No Lee br.)
3	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite
4	Tripartite	Tripartite	Tripartite Aboral br. of 1 grp.	Tripartite	Tripartite (No aboral br.)	Tripartite	Tripartite
5	Tripartite Aboral br. of 3 grps.	Tripartite	Tripartite	Tripartite (No aboral br.)	End of branching	Tripartite (No aboral br.)	Bud (No aboral br.)
6	Tripartite	Tripartite Aboral br. of 2 grps.	Tripartite	Tripartite	—	End of branching	End of branching
7	Tripartite	Tripartite	Tripartite	Tripartite	—	—	—
8	Tripartite	(Bud)	(Bud)	(Bud)	—	—	—
9	Tripartite	End of branching	End of branching	End of branching	—	—	—
10	(Bud)	—	—	—	—	—	—

Br., Branch; Gon., Gonodendron; Grp., Group; Gz., Gastrozooid; T., Tentacle.

The second groups of all the main zone cormidia were tripartite, whereas this condition was found only in the first and fifth cormidia of the oral zone. Lee-branches were found only in cormidium 1 of the oral zone, the best developed, whereas they occurred in all the main zone cormidia. Aboral branches were absent from cormidia 4, 5, 6 and 7 of the oral zone, but all the cormidia except VII of the main zone had an aboral branch. Fewer lateral groups occurred in the oral zone than in the main zone. All the main zone cormidia consisted of at least seven groups, and one of them (I) had thirteen. In the oral zone all the cormidia had four groups at least and one of them (1) had ten.



Text-fig. 19. *Physalia physalis.* Young right-handed specimen, K2, viewed from above, showing the positions of the seven main zone cormidia.

Now that I have made a fresh study of *Physalia* I can in general confirm the facts given by Steche (1910, p. 361) about the main zone of cormidia in young specimens except that I find seven cormidia. This is the most valuable part of his paper, being an analysis of young specimens collected by 'Vettor Pisani' in the Pacific, Indian and Atlantic Oceans. The earlier part of the same paper dealing with still younger developmental stages was based on deductions made from figures by Huxley and Haeckel. This part, in my view, is not of much value because these figures themselves are not all of sufficient accuracy to be reliable. Haeckel's (1888) figures in particular are obviously simplified, idealized and, in some respects, erroneous as Steche suspected.* There is a further useful criticism I must make of

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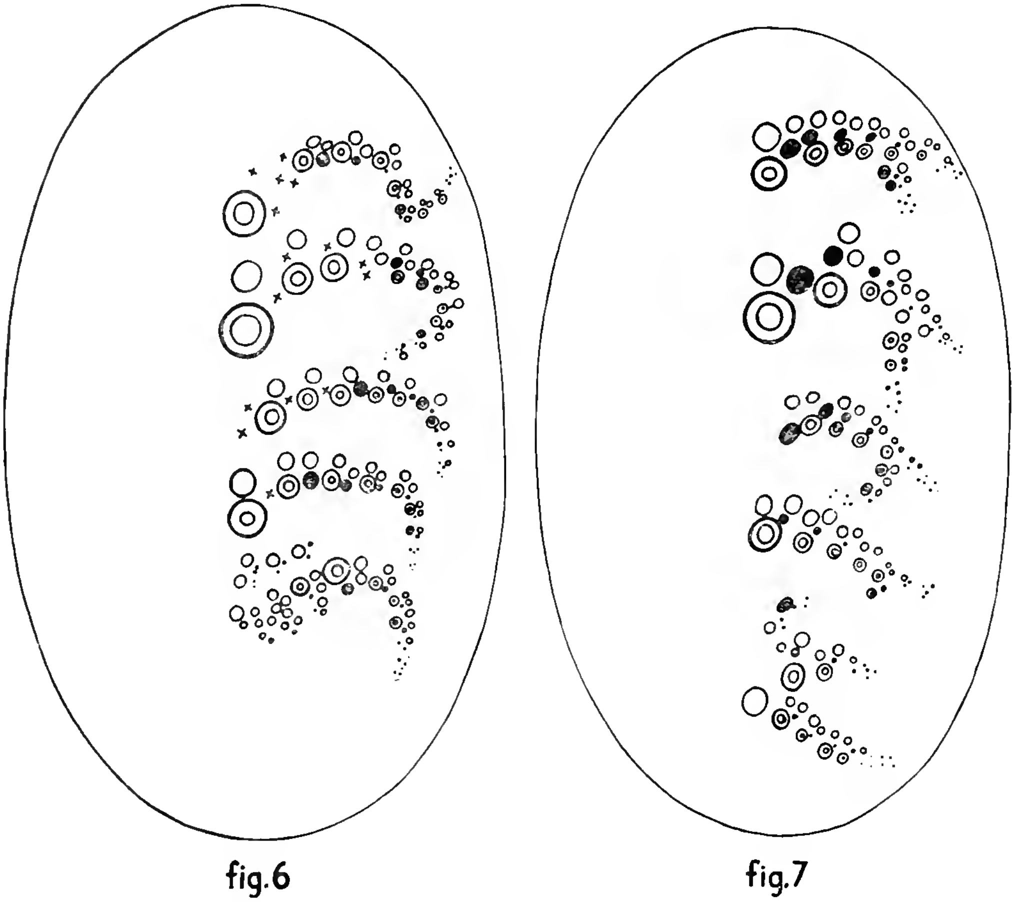
* For instance Haeckel's fig. 3 of a specimen purporting to be about 17 mm. in float-length was probably finished from a wrongly interpreted sketch. It shows a large ampulla at the base of the primary polyp where one never develops. In the original sketch, no doubt this was correctly meant to represent the oral end of the float, but in the finished drawing, a gap has appeared between this end of the float and the oral zone of cormidia which is labelled as a tentacle. The tiny tentacle so characteristic of the primary polyp can just be recognized at its base. It is shown clearly in Haeckel's fig. 4. His fig. 3 does show what might be taken to be five cormidia in the main zone as one would expect, but the gonodendra have been represented as too far advanced in development, and the ampulla of the cormidium at the oral end of the main zone appears to be unusually large. The muscular lamella uniting the ampulla to the base of the tentacle has been omitted, and the extent of the remains of the deflated crest is not properly indicated. All these points show that deductions made from this sort of figure are unreliable, although the figure does show correctly the first three large secondary gastrozooids to appear. I am a great admirer of Haeckel's industry and artistic ability and generally speaking his figures are a great advance on anything available in his day.

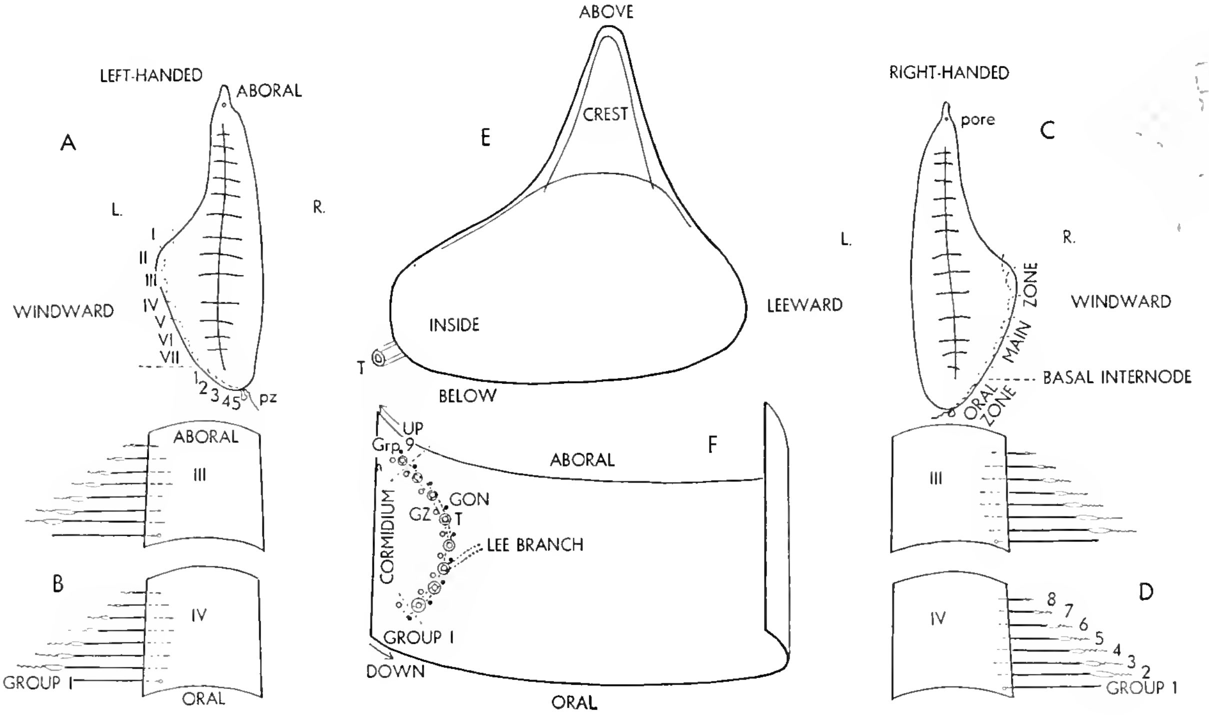
Steche's account. In explanation of his figs. 6 and 7 (reproduced as Text-fig. 20 here) the reader is not told whether the specimens were right- or left-handed, nor whether the viewpoint was from below or from inside the float (above). But by comparing Steche's figures with my diagrams (Text-fig. 21)—I dislike this form of representation but am obliged to use it for this purpose—it will be seen that Steche must have been representing left-handed forms from below. In my view, Steche lost his sense of orientation (a very easy thing to do when examining parts of *Physalia* under a lens), for he appears to have misrepresented the direction of the line of budding of the successive lateral groups of the cormidium. As already stated, these bud from the base of the first or main group in any one cormidium, and subsequently from each other. Steche showed the line as extending first of all almost at right-angles to the main axis of the float, and then as curling round in the oral direction. Thus he represented the last lateral group of cormidium III for example as approaching the chief tentacle of cormidium IV, whereas in fact I find that it lies next to the chief tentacle of cormidium II. The budding line also does not run in the early part of its course as far down towards the lower part of the float as Steche showed it. Okada (1932) too has commented on this error of Steche's. Okada also correctly described the line of 'insertion' of the lateral groups as extending first obliquely downwards, and then upwards. These terms apply when looking down on to the animal as it floats on the water (Text-fig. 21).



Text-fig. 20. *Physalia physalis*. Steche's (1910) schematic representation of the pattern of budding. Fig. 6 shows lateral groups (Gruppen, 2. Ordnung). Fig. 7 shows branches from laterals (Reihen, 3. Ordnung). Aboral end above. ⊙ = tentacle, ○ = gastrozooid, ● = gonodendron, × = lost appendage scar.

Steche's elaborate diagrams of a two-dimensional arrangement of the cormidia do not in my view give at all an adequate idea of the complicated sequence, which is three-dimensional. At any rate I failed to understand the later parts of his account.

Moser (1925), who had sixty specimens of *Physalia* taken by the 'Gauss' expedition to deal with, said that she had wanted to find an answer to the question whether certain alleged differences in origin and arrangement of the groups of appendages described by Steche had the significance given to them by him, or whether they were the expression of unending variation. But she had to confess that their study was so irksome and time-consuming that finally, without coming to any conclusion, she had contented herself with confirming the fact that there was great variation, and only exceptionally was there the regularity of arrangement found by Steche. I, like Steche, found a regular pattern of arrangement.



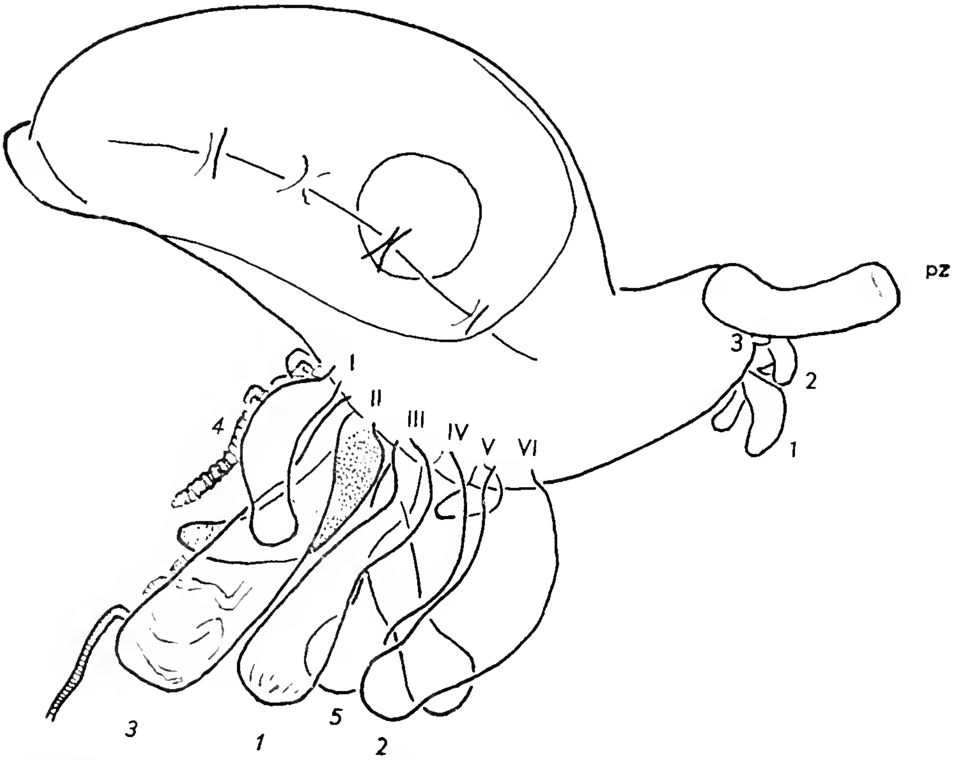
Text-fig. 21. *Physalia physalis.* Orientation of specimens, left-handed *A, B, E* and *F*, right-handed *C* and *D*. *B* and *D* = separated cormidia of left- and right-handed specimens: group 1 at the oral end is the oldest. Outline of *A* drawn from life at Arrecife. Other diagrams, schematic. *F* = part of a lower wall of a left-handed specimen showing a single cormidium and lee-branch.

In 1932 Okada repeated Steche's scheme of diagrammatic representation of the arrangement of cormidia, again with little success. Okada, who must have seen more of the very early developmental stages than anyone before him, said (1935) that a fairly large number occurred in the plankton taken at the Sete Marine Laboratory of Kyoto University in the spring of 1934, and that by comparing them with one another he could deduce the order in which the polyps and tentacles were budded. Unfortunately he did not enlarge on the subject in his short communication. The figures *b*, *c* and *d* of his fig. 1 are all labelled to show that gastrozooid number 1, the earliest to appear, lies on the oral side of the main tentacle, and gastrozooid number 2 on the oral side again of number 1. Okada's figures *c* and *d* both show gastrozooid number 3 on the aboral side of the main tentacle. In his 1932 paper Okada had indicated the same order of appearance, based on the degree of development of gastrozooids in a young specimen whose float-length was 2·5 mm. In addition, he indicated that gastrozooid number 4 appeared aborally to number 3, and that number 5 appeared between numbers 1 and 2.

The specimen shown (1935) in Okada's fig. 1 *d* with a float-length of about 5·25 mm. still shows only the first three of the secondary gastrozooids of the main zone. Until January 1958, I was unable to add any further evidence on this point because my specimens were too far developed, but since receiving Miss Dodge's material I have been able to clear up the sequence of the appearance and identity of these early buds.

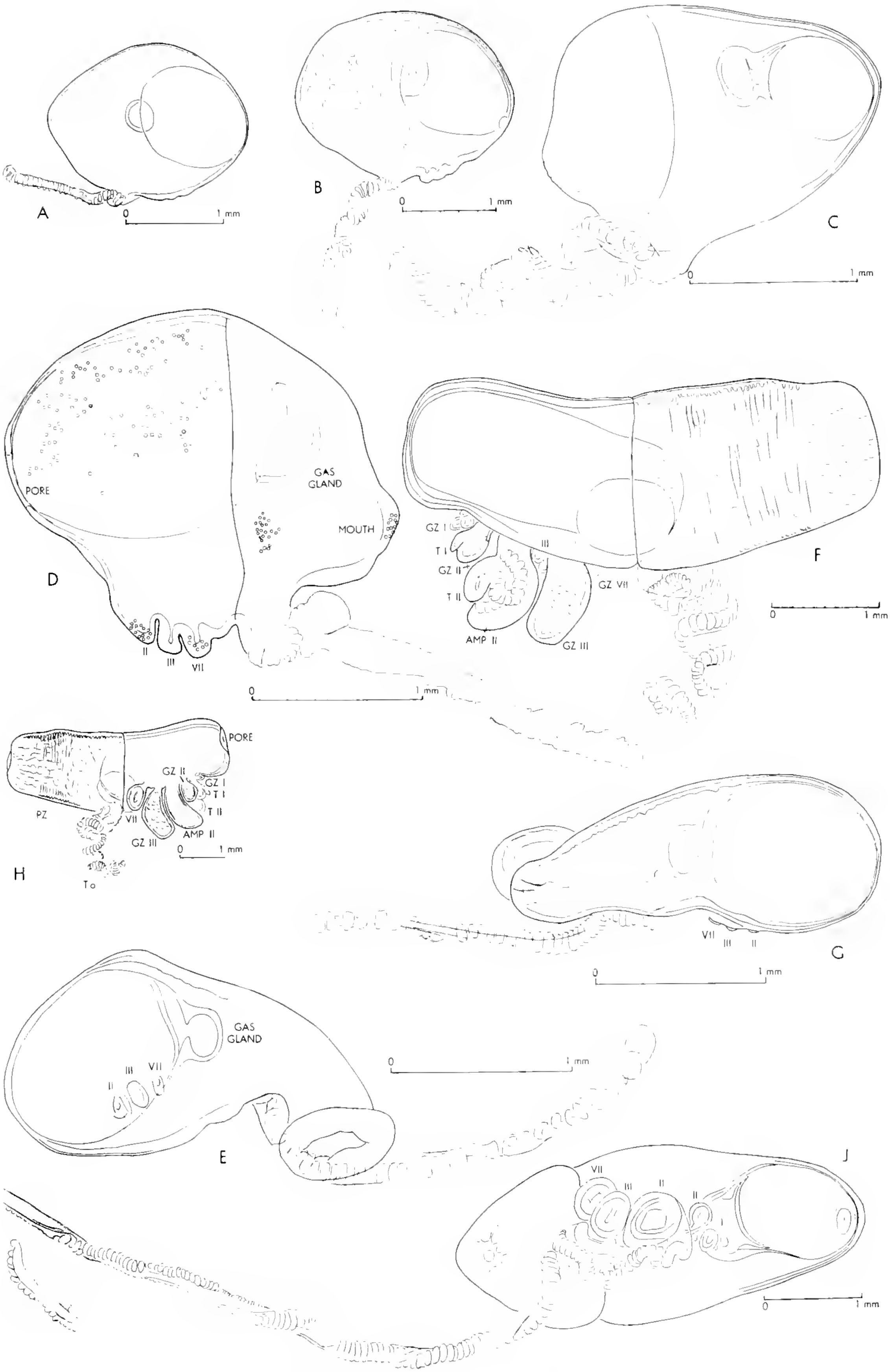
Early Larvae (Pl. VII, Text-figs. 23–4)

Huxley (1859) was the first to figure the early larva of *Physalia*. He gave a figure of an individual taken probably in the spring of 1847 in the South Atlantic. It measures one-tenth of an inch (2·5 mm.), though he recorded it as one-fifth of an inch, in length. There is no sign in this figured specimen of secondary buds. Haeckel followed with one of his idealized figures (1888) and then Alexander Agassiz and A. G. Mayer (1902) gave two more interesting and convincing ones. Their specimens measured 2 mm. and 4 mm. in length and were found by 'Albatross' at the Fiji Islands, 1897–8, and on 5 and 7 September, and 4 November, 1899 and 22 January 1900, among the Paumotus and Society Islands. The smaller specimen was reported as having two very small evaginated protuberances from the ventral floor of the float.

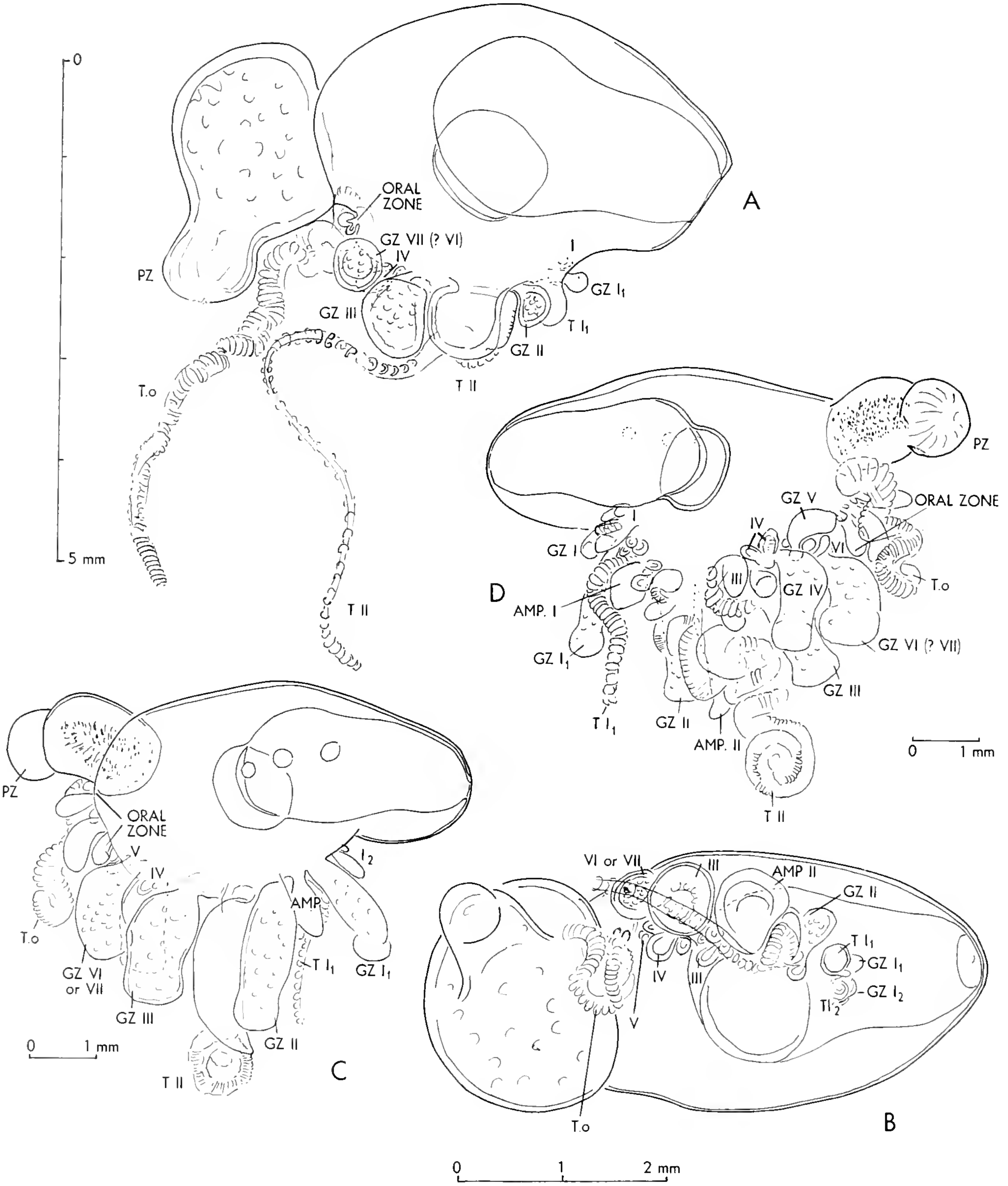


Text-fig. 22. *Physalia physalis*. Young left-handed specimen from Arrecife seen from above (overall length 22 mm.). Italic arabic numerals below show order of appearance of the first five gastrozooids. Six cormidia are shown in the main zone and three in the oral.

The first of the secondary buds to appear in *Physalia* are those of the gastrozooids of group number one of cormidia III and VII (or VI if only six cormidia are present) (Pl. VII, fig. 3, Text-figs. 23 and 24). These are closely followed by the bud for the ampulla of the main tentacle of cormidium II. Its gastrozooid follows a little later from the same very short peduncle. Even at much later stages the first two precocious gastrozooids (III and VII) are very noticeable and rather isolated (Pl. XIII, fig. 5). In Okada's (1932, 1935) notation they are P 1 and P 2 respectively, and the ampulla is *ph* ('phyllomeride').



Text-fig. 23. *Physalia physalis.* Larvae collected by Miss Dodge near Miami. All except *D* are right-handed. *A*, 2 mm. long, × 16. *B*, 2·2 mm. long, × 15·5. *C*, 2·05 mm. long, × 28. *D*, 2·3 mm. long, × 28·5. *E*, 2·25 mm. long, seen from below, × 30. *F*, 4·75 mm. long, × 18. *G* (larva *E* seen from above), × 28. *H* (larva *F* seen from above), × 7·5. *J*, 4 mm. long, seen from below, × 11. *AMP* = ampulla of tentacle, *GZ* = gastrozooid, *PZ* = protozooid, *T* = tentacle.



Text-fig. 24. *Physalia physalis.* Older right-handed larvae collected by Miss Dodge near Miami. *A*, larva no. 24, 5·25 mm. long, seen from above, × 17. *B*, no. 24 seen from to windward, × 18. *C*, 7 mm. long, float-length 5·5 mm., seen from above, × 12. *D*, the same, seen from below, × 12. *To* = tentacle of protozooid. Other lettering as in Text-fig. 23.

The first three buds appear in surface view as short transverse folds (Text-fig. 23 A, B, D, E). On the sloping aboral side of the ampulla of II (Text-fig. 23, D) arises the gastrozooid of cormidium II (P 3 in Okada's notation). From now on, the rate of growth of cormidium I is speeded up relatively, the gastrozooid of its first group becoming Okada's P 4.

The identity of Okada's polyps, therefore appears to be:

P 1	Gastrozooid of cormidium III
P 2	Gastrozooid of cormidium VII or VI
P 3	Gastrozooid of cormidium II
P 4	Gastrozooid of cormidium I
P 5	Gastrozooid of cormidium IV (or V)

The points of interest that have come out of my examination of Dr. Dodge's larvae are as follows:

(1) The final main pattern found in, say, a 10-in. specimen of *Physalia*, namely of buds arranged in seven main and five or more oral cormidia, each consisting of repeated triple groups of gastrozooid, tentacle and gonodendron, does not arise regularly in orderly progression. As in other suborders of siphonophores certain buds develop precociously.

The first of these secondary buds to appear are three in number: the gastrozooids of the main zone cormidia III and VII, and the ampulla of the tentacle of cormidium II, which forms the main tentacle.

(2) The fact that the oral zone of cormidia does not appear at first is due, probably to the fact that the first three precocious buds leave no room for it, so that its five, somewhat reduced, cormidia appear as an after-thought.

(3) Right- or left-handedness appears almost as soon as the first three buds, which are formed in the same longitudinal meridian as the larval (protozooid) tentacle. This larval tentacle must stream out to one side or the other as soon as the larva surfaces, and the three buds lie just below the surface on that same side (Text-fig. 23 A, B). The tentacles of early formed cormidia such as I and II, which soon follow, appear on the under side of the cormidial primordia, and the gas-gland very early takes up an asymmetrical position towards the under side. These two phenomena enable the observer to see whether an individual larva will become a left- or right-handed specimen, even where it measures only a couple of millimetres in length, and before there is any sign of the future crest.

(4) The first indication of the future crest is the appearance of two or three little dome-shaped projections from the upper surface of the air-sac (Text-fig. 24 C).

(5) The secondary buds can soon be seen to form an oblique line, the aboral one rather lower in the water than the oral one. The gastrozooids of III and VII lie above the rudiments of cormidia IV and V. These are formed a little later and are not so easy to see because of being crowded out by the precocious ones III and VII (Text-fig. 24 A, B).

(6) The gastrozooids of cormidia I and II can be seen quite clearly to develop on the aboral sides of their respective tentacles, whose formation tends to precede them (Text-fig. 24 C).

(7) There is often a quantity of dark pigment-granules in the endoderm of the air-sac. It surrounds the pore, but not symmetrically, and assuming that this pigmented area must be uppermost as in other siphonophores, it would seem that when the pigment is first formed the larva is orientated with its long axis neither vertical nor horizontal in the water, but at an acute angle to the surface. My belief is that this pigmented area round the pore of a siphonophore *saccus* in some way utilizes the light energy to control the contraction of the sphincter-muscle controlling the exit of gas according to the intensity of the light and the depth from the surface. The extent of the sphincter-muscle can be judged by its freedom from nematocysts which cover the rest of the larval body. In most of the specimens examined the pore was closed.

(8) I have examined early stages of the gas-gland only in optical section and as seen through the (cleared) pneumatocodon, so that I cannot add much to what Okada (1935, figs. 2 and 3) showed of it.

(9) It will be realized that because the oral half of the larva seems to be very muscular, the shape of the specimens varies a good deal with the state of contraction and content of food. The extent of the *saccus* too must vary with the content of gas at any particular time.

Physalia is distinguished from almost every other siphonophore by this complexity of branching by budding of the cormidia. Whereas in two sub-orders of siphonophores these cormidia bear bracts, and in one of them the terminal cormidia break off to lead a free existence and perform the function of reproduction, in the sub-order Cystonecta to which *Physalia* belongs there are no bracts and only the gonodendra break off. The most striking feature of the budding-pattern that distinguishes *Physalia* from its nearest allies, the cystonects *Rhizophysa*, *Bathyphysa* and *Pterophysa*, is that in them there is a single linear axial arrangement of successive tripartite groups (Urgruppen), namely gastrozooid, tentacle and gonodendron, the youngest group being nearest the float, whereas in *Physalia* each of the original tripartite groups gives rise to a series of up to a dozen lateral groups of the same kind, while still younger groups are budded from the bases of these.

In spite of the great complexity of growth, and in spite of the fact that, owing to varying stages of growth and states of contraction in the twenty young specimens from Lanzarote examined by me, no two look exactly alike, I have seen nothing in specimens from all oceans to make me suspect that I have been dealing with more than one species of *Physalia*. The view expressed by Steche (1910, p. 361) that there is one pattern of budding-characteristic of a species *utriculus* and another of a species *physalis* is not acceptable to me, particularly since Okada (1932) has demonstrated that the supposed characteristics of a Pacific *utriculus* are those of a juvenile specimen of *physalis*.

The only other siphonophore at all like *Physalia* is a remarkable specimen, now lost, taken by H.M.S. 'Challenger' and described by Haeckel (1888) as *Salacia polygastrica*. It was later renamed *Salacella* by Delage and Hérouard (1901) because the name *Salacia* was preoccupied. Haeckel not only named this delicate specimen—the stem measured only half a millimetre in diameter—which was 'much contracted in the spirit bottle', but he softened 'it gradually with water to make it so elastic that it could be extended to that degree which is figured in (his) plate xxv, fig. 1'. Haeckel's idealized figure shows a truly remarkable animal. No other specimen has ever been seen, but if such animals do exist they have many features in common with *Physalia*, from which they differ strikingly in the nature of their air-sac and by the fact that the cormidia are borne on a long stem. The existence of *Salacella*, if confirmed, would demonstrate conclusively that *Physalia* retains characteristics of larval forms such as are also found in physonect genera.

There is one striking morphological feature of *Physalia* which remains a puzzle, namely the arrangement of the cormidia in two zones, oral and main. It may be that one original complete series has become interrupted for some functional reason connected with the dynamics of orientation to the wind, but more probably precocious growth in some main cormidia left little space for the oral ones and so led to retardation in growth and reduction in complexity.

Structure and Development of the Gonodendra

(Pls. XX–XXIII, Text-figs. 25–27)

Whereas in the cystonects, *Rhizophysa* spp. and *Pterophysa conifera*, a single gonodendron is budded out between neighbouring gastrozooids as a simple ovoid sac, which only subsequently develops terminal side-branches, in *Physalia* the gonodendra are much more diffuse structures.

In my completely fresh study of *Physalia*, the task of finding out how the gonodendra were constructed and developed was started in an exploratory way by examining the oldest and youngest stages that could be found. At Arrecife, I collected as many as possible of the large gonodendra dropped by live specimens in the laboratory tanks. Scars are often seen in places were there should be, but is not, a gonodendron (Text-fig. 17): this suggests that the dropping of a gonodendron occurs naturally. I soon found that the egg-shaped gonophores, hitherto supposed to be all male, were in any single gonodendron either all male or all female, and that the stalked medusoids, generally supposed to be female gonophores, were asexual nectophores and not gonophores at all, thus confirming Steche's view (1907).

Microscopical preparations were made of the young stages of the terminal branchlets of the genital clusters (which Schneider called 'Genitaltrauben'), and the growth-stages were seriated. Finally an attempt was made to work back from the oldest stages and forward from the youngest to a meeting-point which could be interpreted in terms of younger growth-stages and of mature structure.

Every primary gastrozooid develops a gonodendron at its base,* and the whole complex—gastrozooid, tentacle and ampulla, and gonodendron—is referred to in this report as a tripartite group.

A gonodendron develops when a main gastrozooid buds-off a number, varying from five to seven, of gonozooids (secondary gastrozooids) budding from one another and *lacking the characteristic type of tentacle*. The gonozooids bud from the base of a primary gastrozooid (Pl. XIV, figs. 1, 2) and the common base elongates to form a peduncle (Text-fig. 15), and the peduncles of the gonozooids elongate to form branches of the gonodendron (Text-fig. 25). The whole structure, somewhat resembling the wrist, palm and fingers of the hand, curls up as when the thumb and little finger are opposed, and eventually forms the globular gonodendron shown in Pl. XX, figs. 2, 6. The bases of the gonozooids give rise to the genital clusters, consisting of successively smaller palpons, and of gonophores, jelly-polyps, and nectophores (Pl. XX, figs. 3, 4). The gonophores represent the original, now much reduced, adult sexual phase of *Physalia*. The clusters branch and rebranch (Text-figs. 25, 26) and come to form the ultimate branchlets of the gonodendra (Pl. XX, fig. 5). At first they are short (Pl. XX, fig. 3), but they grow very much longer than the gonozooids, which finally appear to arise from the basal branches of a mature gonodendron (Pl. XVII, fig. 2).

The largest of the gonodendra which I preserved, a female one, was a globular mass of palpons and gonophores measuring 4 or 5 cm. in diameter (6 or 7 cm. when flattened in a dish), and consisted of seven main branches radiating out from its stem. Each main branch rebranched at least five times, so that there would be about 224 (7×2^5) terminal branchlets carrying 448 gonopalpons (two per branchlet), 224 medusoid nectophores and 2400 gonophores (ten per branchlet). Very many gonodendra were present in all but the very youngest stages of development, often five or more well-developed ones at a time. The potential number of gonodendra (Pl. XX, fig. 1) formed on the main zone of cormidia alone, based on an analysis of cormidium II of specimen no. Lanzarote 2, is about 500, and the number of gonophores, or adults, that they might bear would be at least a million.

The muscular peduncle, or stem, and the branches of the gonodendra are highly contractile, but I have not noticed much sign of movement of the nectophores and palpons. I think it probable that whole gonodendra and perhaps later the terminal parts of the branchlets also become detached in the sea. Generally five or six gonozooids, from the bases of which the genital clusters grow, are found at the bases of the branches of these dropped gonodendra, but (as expected) never any tentacles.

Analysis of the complexity of the gonodendra had been attempted in 1908 by Lens and van

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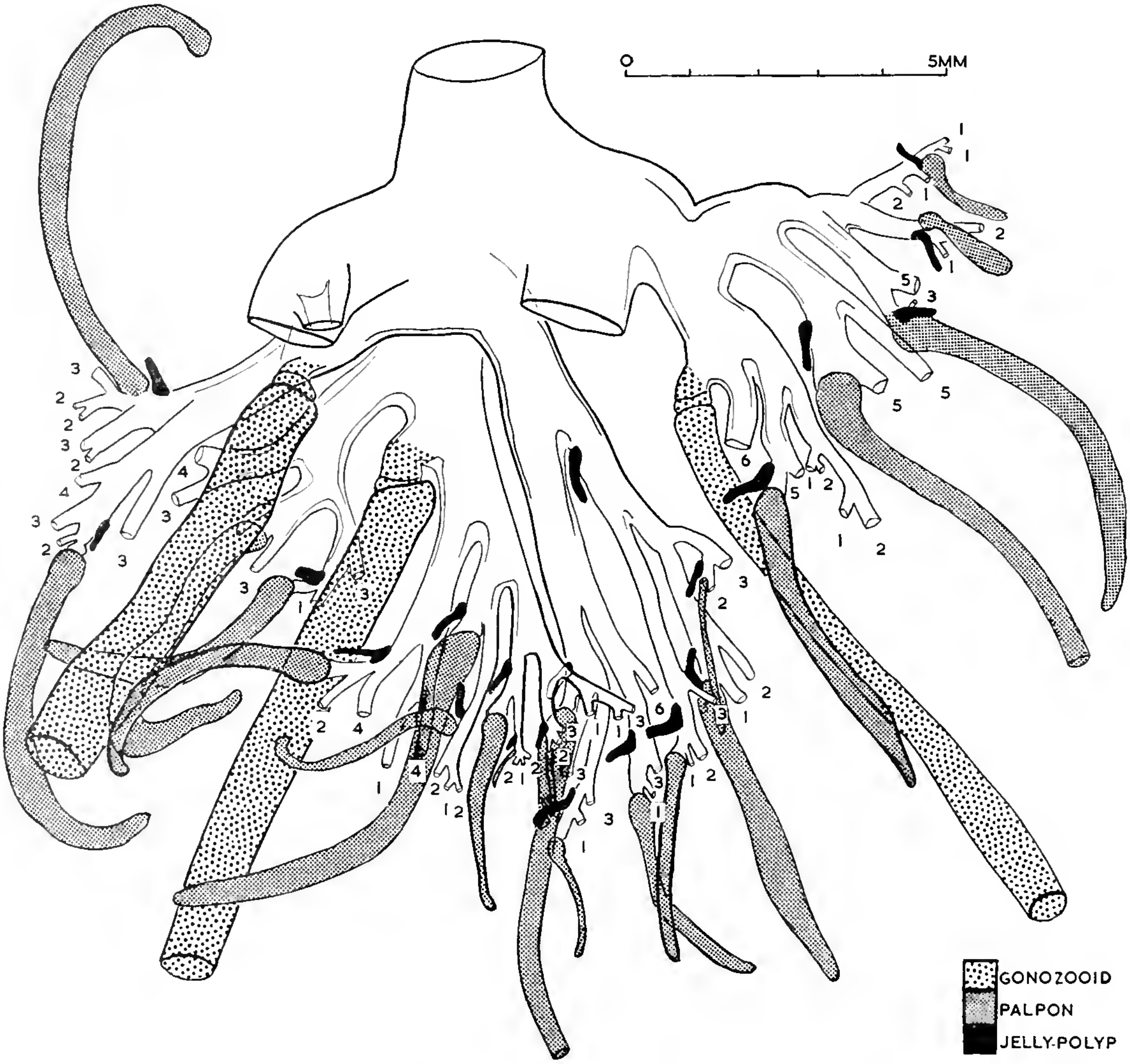
* Delage and Hérouard (1901) show the gonodendron as arising from the pedicel of the ampulla—this is not correct.

Riemsdijk. They found that the ultimate branchlets consisted of two divisions, one bearing a jelly-polyp* and palpon, and the other a nectophore and palpon, and both bearing gonophores.

My study of the morphology and development of the gonodendra of *Physalia* substantiates the work of Lens and van Riemsdijk and amplifies it. I find that each normal final branchlet of the fully formed gonodendra consists of two sections, which are very likely homologous, each carrying one palpon and numerous gonophores (reduced sexual medusoids). The two sections can be distinguished from one another because the terminal one has a jelly-polyp (*jp*) at the base of the palpon (*pt*), whereas the sub-terminal section has a long-stalked nectophore (*n*) in this position. The terminal palpons with their jelly-polyps are visible in the earliest growth-stages of the gonodendra (Pl. XXII, fig. 4); in well-developed specimens the oldest terminal palpons at the bases of the larger gonodendral branches reach a considerable size (Text-fig. 25).



Text-fig. 25. *Physalia physalis*. A young gonodendron after removal of three branches. Specimen, Lanzarote no. 2. The numerals refer to the number of subterminal, nectophore-bearing sections (not shown) on each end branch. ×9.

No further budding occurs from a terminal section. Growth of the gonodendra proceeds by buds which develop on the sub-terminal sections and which give rise by dichotomy to a successive series of

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* The jelly-polyp was called by Chun (1897*a*) and Steche (1907) the 'Gallert-polypoid'. It develops characters closely resembling in some ways those of the nectophore or asexual medusoid (see page 351).

terminal (final) sections and budding sub-terminal ones. The whole process was studied in the developmental stages now described and illustrated on Pls. XXI–XXIII.

I examined first the youngest stages found at the bases of the smallest gonodendra (Pl. XXII, figs. 1–3). These genital clusters arise opposite the basal jelly-polyps as innumerable small, laterally flattened, subdivided lobes, the pro-buds, arranged in many planes, and often look at first sight like trefoils. They bud and rebud several times to form the ultimate branchlets of the gonodendron (Pl. XXI, fig. 1), as distinct from its main branches, which are formed by the elongated peduncles of the gonozooids and first palpons, as described on page 347. The pro-buds of the genital clusters grow rapidly in length in an apical direction and produce sub-terminal buds on one side, so that the apex becomes bent to the other side. Each of these little lobes thus comes to appear bi-lobed (Text-fig. 27A and B). These two stages have not been specially identified, and are hypothetical. One half, really the faster growing terminal end, can soon be recognized as the rudiment of a palpon and a jelly-polyp; the sub-terminal part is a new pro-bud, *B* (Text-fig. 27B). As a result of further budding, pro-bud *B* develops secondary dichotomies, and the new pro-buds B_1, B_2, (Text-fig. 27D) each become transformed into replicas (Text-fig. 27E) of the previous stage, shown in Text-fig. 27C. The terminal part of each successive pro-bud grows faster than the sub-terminal part to form a new terminal palpon and jelly-polyp, while the sub-terminal section can either end by becoming the palpon and nectophore, or go on developing and dividing into another terminal and sub-terminal section. We are now at stage *D* (Text-fig. 27) where there is a major dichotomy between the left '*B*'-side bearing pro-buds B_1 and B_2 and the right '*A*'-side bearing the terminal palpon and pro-bud A_2. The two halves are essentially alike, but one is farther advanced in growth than the other, for on the '*A*'-side we can soon recognize the rudiment of another palpon and jelly-polyp pro-bud A_2^{1A} (Text-fig. 27F). As a result of repeated sub-terminal budding and dichotomy we get a series of terminal sections—palpon and jelly-polyp—alternating with sub-terminal pro-buds. These developmental processes which I have postulated would account for the origin of the final branchlets of the whole gonodendron (Text-fig. 26). Having followed the development of one of the branchlets as far as the last dichotomy, we can see what is the destiny of the final sub-terminal pro-buds:* they divide for the last time to form the rudiments of the sub-terminal nectophore and palpon of the sub-terminal section (Pl. XXI, fig. 3).

In some cases a final sub-terminal pro-bud is not developed: that is, the final palpon and nectophore are not budded off, then the branchlet ends in a terminal section only, consisting of a palpon and jelly-polyp. Pl. XXI, fig. 7 shows a pair of final branchlets, the right with two terminal sections and the left with two terminal and a final sub-terminal section. Normally there is a matching pair of final branchlets with sub-terminal sections.

I must now describe in greater detail how the middle growth-stages of the genital clusters (Schneider's 'Genitaltrauben') develop into the final branches of the fully grown gonodendra. I have not determined whether there is a definite number of new buddings and dichotomies which might fix the amount of branching. But if we take the hypothetical stage shown in Text-fig. 27F as the starting-point of the next stage, it can be seen at once, on comparison with Pl. XXII, fig. 4, that the whole of the right side of Text-fig. 27F as well as the whole of the left side—the major dichotomy is between pro-buds A_2 and B_1—can develop into something similar to what is shown in Pl. XXII, fig. 5. In both figures the larger palpon (*p.st*) and the jelly-polyp (*jp*) form a terminal section; and the sub-terminal pro-bud (*pr.* A_2^2) above it in Text-fig. 27F has given rise in Pl. XXII, fig. 5 to a smaller terminal section and a new sub-terminal one. From the latter arise (1) the nectophore (*nect*), and (2) the palpon of a

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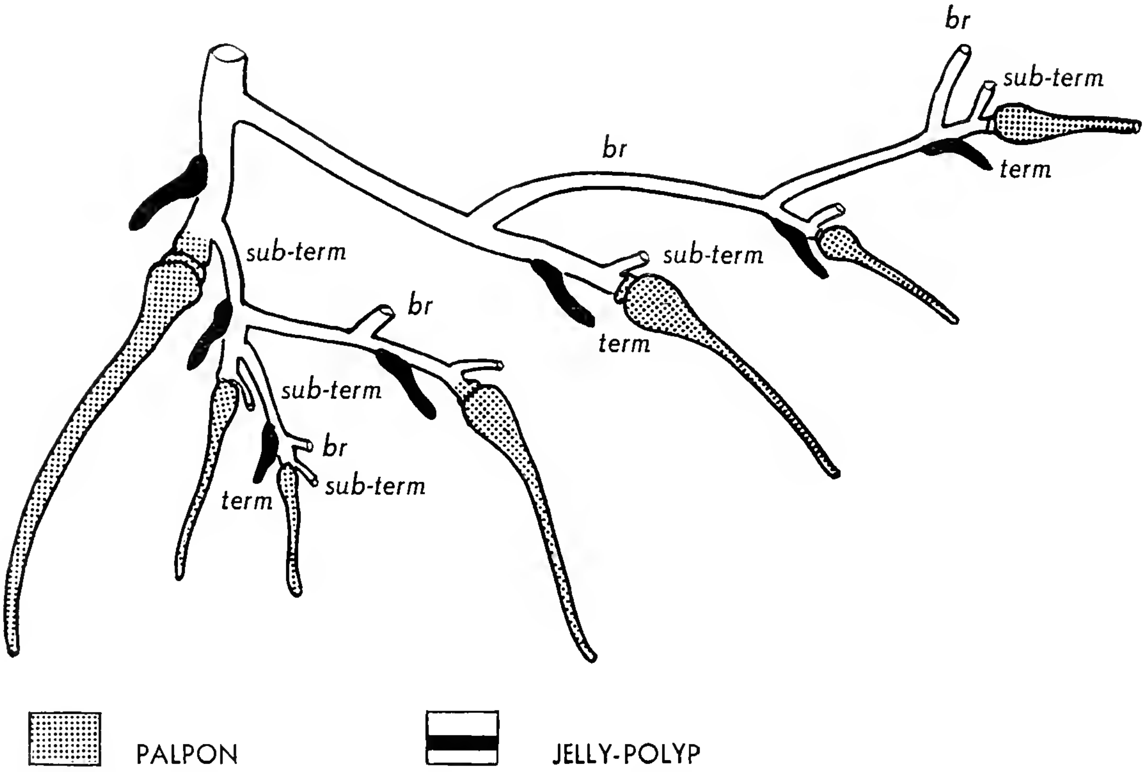
* Such as A_2^2, Text-fig. 27F. Pl. XXII, fig. 4 is the equivalent of the '*B*'-side of Text-fig. 27F.

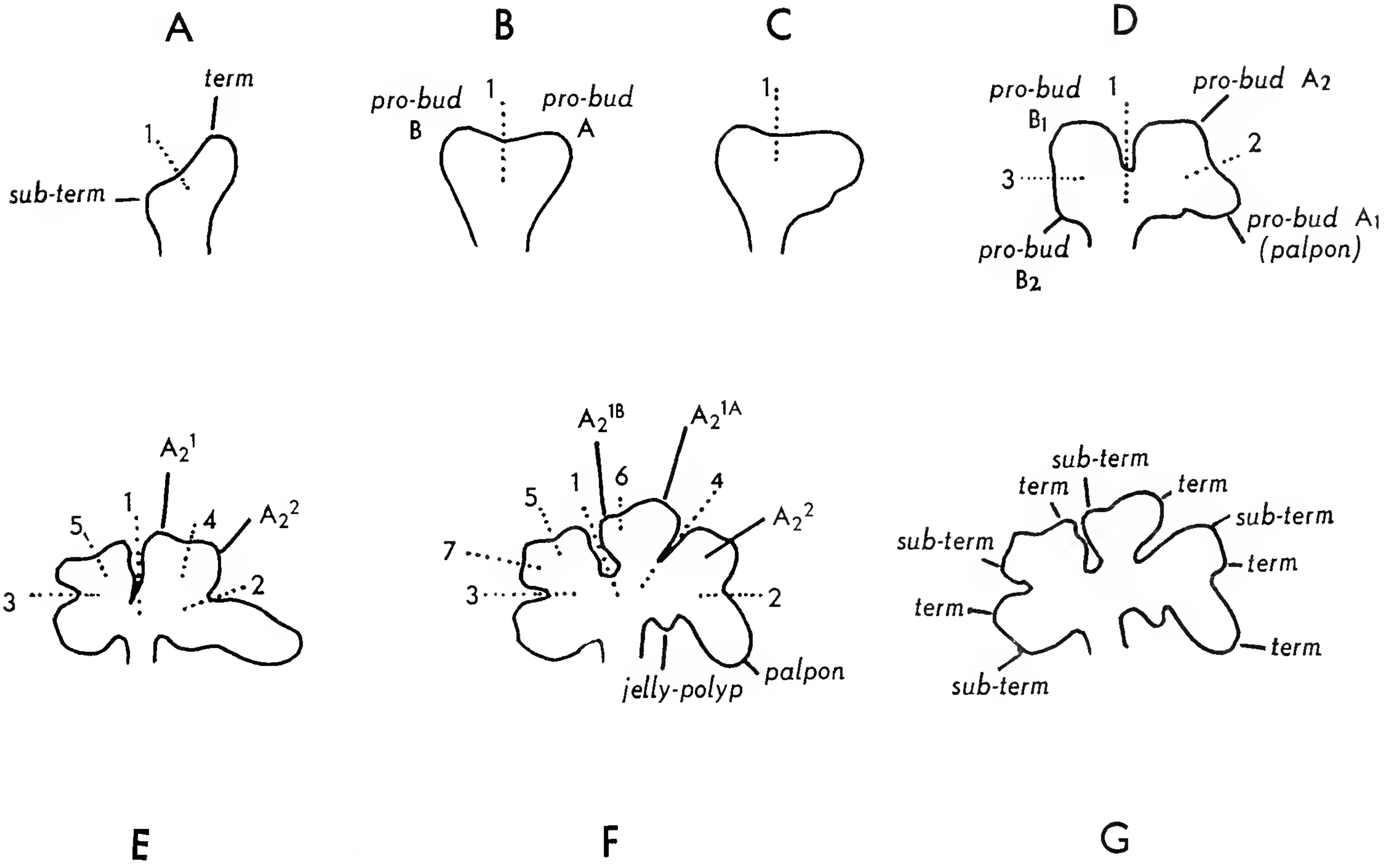
final branchlet. In Text-fig. 27F the second pro-bud A_2 of fig. D has developed into similar terminal and sub-terminal sections ($A_2{}^{1B}$, $A_2{}^{1A}$).

New pro-buds always arise sub-terminally, and as a rule at a point opposite a jelly-polyp. Sometimes they form terminal-type, sometimes sub-terminal-type sections. Pl. XXII, figs. 6 and 8 show slightly later stages of development that might have been reached later on by the specimen shown in Text-fig. 27F. The first palpon, which is morphologically the terminal part of the branchlet, has grown very much more rapidly than the sub-terminal parts. Pl. XXII, fig. 11 shows how complicated the young genital clusters look when the branchlets lie side by side. Those shown in Pl. XXII, fig. 8 have been separated, flattened out and mounted on a microscope slide.



Text-fig. 26. *Physalia physalis.* Schematic drawing of a branch of a gonodendron to show repetitive pattern of growth. *br* = branch, *sub-term* = sub-terminal section, *term* = terminal section.

It will be noticed at this stage, which I call the Key-stage from a fancied resemblance to the lever-steps of a simple key, that the buds of both terminal and sub-terminal sections stand out more or less at right-angles to the long axes. In the next stage (Pl. XXIII, fig. 2) they are more or less parallel to one another and stand at an angle of 45° to the common axis. The jelly-polyps are no longer little conical projections but have become more cylindrical; and the nectophore bud shows its medusoid nature. The gonophores are now conspicuous objects. Pl. XXIII, fig. 2 (right) may usefully be compared with its earlier counterpart shown on the right-hand of Pl. XXII, fig. 4. Stages of growth intermediate between those shown in Pl. XXIII, figs. 1 and 2 may be seen in Pl. XXII, figs. 10, 11 . The most mature stage of growth of branchlets of the gonodendron that I have seen is shown in Pl. XXI, fig. 3, which shows clearly (1) the jelly-polyp (*jp*) of the palpon (*pt*) of the terminal section, (2) the asexual nectophore (*n*) and palpon (*ps.t*) of the sub-terminal section, and (3) a number of female gonophores. A rather less mature stage is shown in Pl. XXI, fig. 2, where the mesogloea of the stalks of both nectophore and jelly-polyp is less well-developed, and their endodermal canals are relatively larger in diameter and still open. Pl. XXI, fig. 4 shows the last four dichotomies of part of an immature gonodendron spread out on a microscope slide.



Text-fig. 27. *Physalia physalis.* Early growth stages (hypothetical) of branches of a gonodendron. A later growth stage of fig. *F* (cf. Pl. XXII, fig. 2) is shown in Pl. XXII, fig. 5. *sub-term* = sub-terminal section, *term* = terminal section, 1, 2, 3 etc. = successive dichotomies, A_1, A_2, A_2^1, A_2^{1A}, etc. = successive buddings.

JELLY-POLYPS

(Pl. XXI)

As stated on page 348 there is at the base of each terminal branchlet a palpon which has at its base a jelly-polyp. These are well shown in Pl. XXI, figs. 1, 2, 6, 7. It is necessary to understand the regular type of branching just described in the gonodendra in order to demonstrate that the jelly-polyps are not vestigial stalks left after the nectophores have dropped off, an erroneous interpretation put forward by Huxley, Haeckel and Chun.

In the older growth-stages, both jelly-polyp and nectophore-stalk look much alike (Pl. XXI, fig. 3). This resemblance of the oldest known growth-stage of these two buds is due to the fact that in each the endodermal lumen becomes relatively reduced at the same time as the mesogloea becomes very much thicker (Pl. XXI, fig. 3). In both cases the endodermal canal—now almost occluded—comes to lie on the abaxial side, next to the ectodermal fold (Pl. XXI, fig. 6) except sub-terminally, where it lies centrally to link up with the sub-umbrella of the nectophore and the tip of the jelly-polyp. This structural resemblance between the basal parts of these two kinds of buds—one a medusoid and the other, once thought to be a polyp, but now shown to be a reduced nectophore—was for long inexplicable. No wonder that the jelly-polyp was mistaken for the stem of a broken-off 'female medusoid'. The jelly-polyp seems to be in fact a reduced nectophore. Both have the frenum-like longitudinal muscular lamella referred to above as the ectodermal fold.

One morphological feature of the gonodendra, common to those cystonects whose gonodendra are well enough known to me for comparison, namely *Physalia physalis*, *Rhizophysa eysenhardti*, *R. filiformis* and *Pterophysa conifera*, is that in all of them the final sections of the branchlets consist of a group of three kinds of bud: (1) a terminal gonopalpon without a palpacle (reduced tentacle), (2) a sub-terminal nectophore (asexual medusoid bud) [(1) and (2) together forming what I have described, in *Physalia*, as the sub-terminal section] and (3) male or female gonophores. But in *Physalia* alone there is, proximal to these three structures, another palpon with a jelly-polyp (a reduced nectophore), these two structures forming the terminal section, which is developed first and which gives rise by budding to the sub-terminal section (carrying the nectophore and palpon). The sub-terminal section is budded out (Pl. XXI, fig. 3) from the base of the palpon at a point opposite to its jelly-polyp.

The difference between the gonodendra of *Physalia* and those of the other cystonects is that in *Physalia* there are multiple-terminal as well as sub-terminal sections, whereas in the other cystonects there is a single sac-like terminal section from which the multiple ones are budded. The sub-terminal sections in all cystonects are clearly homologous. The arrangement in *Physalia* is the most complex and so is probably the most highly evolved. These comparative morphological details form a key to understanding the relationships between the various cystonects.

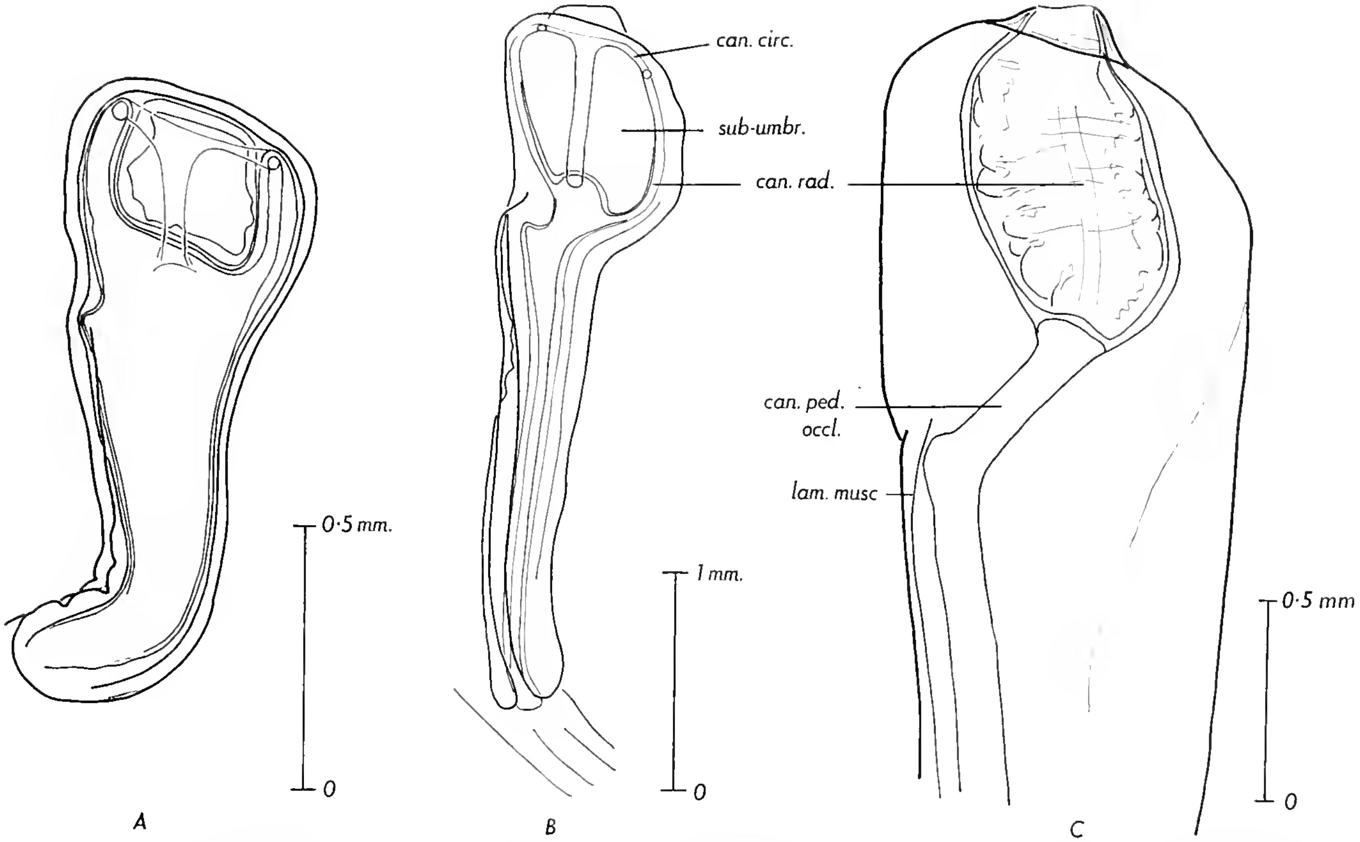
Long ago, sketches of a terminal branchlet of a young gonodendron were published by Chun (1897*a*, fig. 26*b*), and of an old as well as of a very young stage of the same by Richter (1907, figs. 7 and 8). Richter referred to four types of buds: (1) palpon, (2) male medusoid, (3) female medusoid (i.e. nectophore), and (4) 'Gallertpolypoid' (that is, jelly-polyp, interpreted by Haeckel as the 'pedicels' of detached female medusoids). Richter's figures, though incorrectly labelled, are basically sound and may be compared with my photographs. Libbie Hyman (1940) in her indispensable book of reference gave a figure of part of a gonodendron (fig. 155 B) which is unfortunately misleading. She seems to have mistaken palpons for jelly-polyps in both this and fig. 155 A. The latter figure in other respects gives a good representation of an early stage of development of three gonodendra; but the characteristic arrangement of palpons, gonophores, jelly-polyps and nectophores is not correctly shown in her fig. 155 B.

NECTOPHORES

(Pl. XXIV)

The best criterion for judging the degree of development of a gonodendron is the state of development of the nectophores (Pl. XXIV, figs. 5–7). In early stages I find that the coelenteron of the nectophore pedicel is spacious and the mesogloea thin. In the most advanced stages I have seen the mesogloea is very thick and the coelenteron of the pedicel occluded (Text-fig. 28). Huxley (1859), Haeckel (1888) and Chun (1897*b*) all regarded the nectophores as female medusoids, which they thought probably became detached and produced ova as free-swimming Anthomedusae. Chun even suggested that they might develop into the *Amalthaea amoebigera* of Haeckel (1879) (a doubtful synonym of *A. sarsi* Allman, *fide* Kramp).

The nectophore of *Physalia* has no manubrium and no germ-cells have been seen at any stage of its development. Moreover, the occlusion of the endodermal canal in the nectophore-stalk would probably prevent later entry of ova in any way similar to that described by Brooks and Conklin (1891) for *Rhodalia*. The secondary ectoderm of the sub-umbrella is peculiar in having folds of the mesogloea supporting it, figured by Goto (1897, figs. 8 and 9). What Goto called the manubrium is in my



Text-fig. 28. *Physalia physalis.* Three nectophores at different growth-stages. In *A* the gastrovascular space is wide open; in *C* occluded. *A*, ×70, *B*, ×29, *C*, ×53. *can.circ.* = circular canal, *can.ped.occl* = pedicular canal (occluded), *can.rad* = radial canal, *lam.musc* = muscular lamella.

view nothing more than the irregular folding of these tissues at the point where the radial canals arise from the pedicel in the most advanced growth-stages that we know. It seems probable that the nectophores must function as swimming-bells.

Judging by the undoubted breaking-loose of the terminal branchlets, consisting of terminal gonopalpon, nectophore and sexual medusoids, of *Rhizophysa*, I think it likely that the equivalent sections in *Physalia* may do the same thing. In *Rhizophysa*, nectophore and palpon are orientated in a peculiar way, axes in line, as if to balance each other when detached and swimming. In *Physalia* I have seen some very expanded gonodendra in which the stalk separating this part of the branch from the basal section—gonopalpon and jelly-polyp—is very fine. These terminal sections of the gonodendra, when detached, are probably kept on the move by pulsations of the nectophores. It may be that the final branchlets become freed at some particular stage of growth, or at a certain season of the year, but I must say that I have seen no specimens in which the nectophores are missing from the normal position in which they first appear as very small buds very early in the development of the gonodendron.

PALPONS

(Pls. XX, XXV)

Besides the gonophores and nectophores, the final parts of the gonodendra in *Physalia* are made up of palpons (Pl. XX, fig. 4). The normal sub-terminal ones have at their base an asexual nectophore; the palpons of the terminal sections have at their base a jelly-polyp ('Gallertpolypoid' of Chun, a reduced nectophore). None of the palpons have palpacles (simple tentacles).

There appears to be no recent summing-up of our knowledge of the homology and functional morphology of palpons and it will not be out of place to consider the subject briefly here. We have to go back to Haeckel's great 'Challenger' report (1888) to find anything of the sort. Haeckel set great store on allowing the empirical and speculative methods of research to converge. Nevertheless, while I am a sincere admirer of his prodigious pioneering work, I always regret that Haeckel allowed so much hypothetical interpretation and terminology to colour his observational records, because a great deal of it now seems to be quite mistaken. It is a pity also that he should have idealized his finished figures in order to make his preliminary sketches complete and attractive. But these are trivial criticisms of his painstaking work in general.

What he has to say about palpons is contained in four sections of his general introduction, under the headings: (1) palpons or 'tasters', (2) cystons or anal vesicles, (3) palpacles or 'tasting' filaments (the German word 'tasten' meaning to touch) and (4) gonostyles or reproductive stalks. Haeckel, while agreeing that palpacles were only the tentacles of palpons and not a separate sort of bud, contrasted palpons with cystons, saying that palpons were mouthless and had no glandular villi, whereas cystons could empty fluid and excretions from the canal system through a terminal opening which was to be regarded as an anus. He used Allman's term 'gonostyles' or 'blastostyles' for what he called the 'sexual palpons', frequently branched, whose sole function was to produce gonophores. A subsidiary title for his section 4 is 'Blastostyles, Gonoblastidia, Gonodendra, Klinozooids'. The term gonodendra he specifically applied to large clustered masses of gonophores attached to branched gonostyles, which last he regarded as secondary polypoid individuals. He mentioned that palpons are found generally distributed in the physonects and cystonects, but not in the calycophores.

As a result of my own observations on living and preserved material of physonects and cystonects, I conclude that there is no real distinction between palpons and cystons. Terminal openings may suddenly appear where there has been no previous indication that such a thing is possible. I cannot now find my field notes on the subject, but I think that it was in *Nanomia bijuga* that I first observed (at Villefranche) the flattening-out of palpons in a progressive peristalsis followed by an opening-wide of the tip of the palpon and the ejection of particles. In some species of *Forskalia*, for example, the Mediterranean species with the lemon-coloured spot on the velum that I call *edwardsi*, I have often observed the well-known ejection of an orange-coloured liquid from the tip of a palpon. I have observed palpons opening in other species too. In one particular preserved specimen of *Physalia physalis* many of the palpons were fixed in the act of opening (Pl. XXV, figs. 2, 3) and in others there is a collection of dark matter, usually distributed over the villi, near the tip as if about to be ejected. It appears to me that the palpons are to be regarded primarily as reduced secondary polyps budded from the bases of replicated gonozooids. Secondarily, they may become separated from the gonophores and gonodendra. This can be very clearly seen in a small specimen of *Athorybia rosacea*, taken by 'Discovery II' in September 1955, off Lanzarote at St. 3308, and brought to me by Dr Kramp. It can also be clearly seen in *Forskalia edwardsi*, and I have illustrated it in a figure of *Marrus antarcticus* (Totton, 1954, fig. 21). In *Physophora hydrostatica*, where the palpons are very large, this relationship is not apparent in mature specimens, which represent the condition found in the post-larva developed to a higher degree. In the physonect *Nanomia bijuga* a bunch of male and a bunch of female gonophores is budded from the pedicel of each palpon. I think it probable that some palpons have come to act as food-reservoirs for the growing gonodendra—in *Pyrostephos antarcticus* they are usually full of liquid fat or oil—as well as organs of defaecation. In *Physophora*, *Forskalia* and *Athorybia* they are particularly active sensory organs. In *Apolemia uvaria* there is a kind of palpon, few in number, that is brown and heavily armed with nematocysts. The palpons of *Physalia physalis* have a beautiful pad of nematocysts on one side of the tip and on the tip itself. In this species all stages of regression from gastrozooid to gonopalpon (non-feeding gonozooid) can be seen when tracing the development of a gonodendron by successive budding or replication.

All palpons, it would seem, are reduced secondary gastrozooids (gonozooids), specialized for purposes other than feeding. It is in *Apolemia uvaria* that they most nearly resemble gastrozooids, because in this species the tentacle of the gastrozooid is unbranched and looks like a palpacle. The repeated sac-like protuberances from the stem of *Rhizophysa*—the buds of the gonodendra—show little similarity to palpons, though the side branches terminate in palpons; but the intricately branched gonodendra of *Physalia* clearly originate from the peduncles of secondary gastrozooids.

It has always been a puzzle to understand the appearance of a partial ring of palpons round the base of the protozooid at an early post-larval stage in the development of physonects. But in the light of what has now been learned about the branching system in *Physalia*, it has become easier to homologize the process of budding of successively more reduced daughter polyps from the bases of the gastrozooids in *Physalia* with the phenomenon to which I have just referred, namely the budding of a partial ring of palpons. In *Forskalia* the whole gonodendron buds from a basal palpon; in *Marrus* it probably does so as well; in *Athorybia** there is a palmate arrangement of eight or nine palpons arising from the pedicels of the gonodendron, but it would be necessary to study growth-stages to determine the minute structure.

AMPULLAE

Haeckel (1888)—to whose account of *Physalia* most students hitherto have been likely to refer—used the same term for true palpons and for the basal ampullae of the tentacles. For a long time I have held the view that these ampullae, containing as they do in their walls innumerable nematoblasts, were homologous with basigasters or nematoblast-nurseries—otherwise missing in *Physalia*, except in the protozooid—which have become separated from the gastrozooids, just as the tentacles have. Schneider (1898), I find, came to the same conclusion. But for a time I had to modify my interpretation because on two occasions I found young growth-stages of ampullae with papillae inside, and a terminal part that resembles a gastrozooid instead of the tip of an ampulla. My final conclusion is that an ampulla is simply the hypertrophied basigaster of a gastrozooid. This is the sort of condition found normally in the young growth-stages of gastrozooids of all siphonophores, where the basigaster is relatively enormous, and the as yet undeveloped terminal part appears only as a slight projection from it.

At the proximal end of a tentacle, particularly a young one, it can be seen that the last few nematocyst-'heads' budded contain no nematocysts. In this region, nematocysts can be seen in the ectoderm of the muscular lamella where it connects the ampulla to the tentacle: these nematocysts appear to be migrating to the 'heads'. There is in this region a sudden transition between 'heads' devoid of nematocysts and 'heads' well armed with them. As the ampulla and tentacle increase in size the 'heads' become bigger. Migration of nematocysts into the 'heads' takes place only in the restricted area already described. The original tip of a tentacle has, naturally, small 'heads'.

A fact of great evolutionary interest is that the protozooid which has only a small tentacle, has no ampulla, but instead a very inconspicuous basigaster of a generalized type. We have here then an evolutionary phenomenon, found also in physonects like *Agalma elegans*, where the protozooid and its basigaster remain at an earlier phylogenetic level, while the basigasters in the secondary gastrozooids are more highly evolved. Instead of being able to deduce the evolutionary steps from a study of fossils, we can do so, in bud-colonies of this sort, from a study of successively produced buds.

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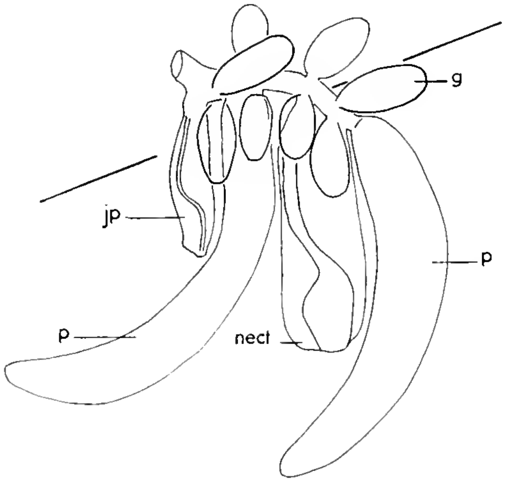
* These palpons do not open directly as stated by Haeckel into the common stem cavity. It is necessary to anaesthetize the delicate creatures to cause relaxation of the muscles before one can really observe their structure. Even so, the air in the float, which always rises to the surface, makes it almost impossible to observe the under-surface until the air has been replaced by liquid. Today of course we have what Haeckel had not—binocular dissecting microscopes.

GONOPHORES

(Pls. XX–XXIV, Text-fig. 29)

Two of those who in the past have done the most detailed work on the gonodendra are Richter (1907) and Steche (1907). By one of those strange but not infrequent coincidences, these two men appear to have been working simultaneously but unknown to each other, the one at Leipzig and the other at Strassburg.



Text-fig. 29. *Physalia physalis.* End branchlet of a mature gonodendron shown in section in Pl. XXIV, fig. 3. The plane of section is indicated by a line. Two gonophores that lie on the underside and appear in the plate are not shown in the drawing. *g* = gonophore, *jp* = jelly-polyp, *nect* = nectophore, *p* = palpon.

Prior to the work of Steche, Huxley (1851, 1859), Haeckel (1888), Brooks and Conklin (1891) and Goto (1897) all regarded the gonophores as male organs. Huxley and Haeckel thought that the ova developed later on the stalked 'female medusoids' (now known to be nectophores) after becoming freed from the gonodendra.

Richter (1907) also regarded the gonophores as being male organs and his whole account of their development is most unusual, as he himself admitted, and is in my view unacceptable. In fact I think that Richter reversed the proper sequence of events in the various growth-stages.

Steche (1907) demonstrated for the first time the existence in *Physalia* of two kinds of gonophores, female as well as male, and stated that each gonodendron was wholly of one sex only. Even now Steche's work is not well known, and this is the first occasion on which his observations have been confirmed. Curiously enough Steche himself stumbled quite accidentally across the fact that some of the gonophores were female, when he was investigating the 'Glockenkern' (entocodon) of various hydroids and siphonophores during the winter of 1905. In some sections of the nectophore of *Physalia* he had fortunately included a large specimen of the real female gonophore growing from its base. He recorded how surprised he was to find a single layer of unripe germ-cells instead of the thick spermarium he had expected to see. He described and figured in longitudinal section a developmental phase in some ovoid medusoids, in which the spadix of giant 'multinucleate' cells was capped by a single layer of what he called female germ-cells (Taf. X, fig. 26). I have a section which confirms his figure (Pl. XXIV, fig. 3). Text-fig. 29 shows the plane in which the section was cut.

Richter wrote an addendum to his paper in which he commented on Steche's work published while his own manuscript was in the printer's hands. Most of the addendum is concerned with relatively unimportant differences in their two papers, but Richter also remarked that 'Steche made some very interesting observations on older examples of *Rhizophysa* and *Physalia* which apparently lead to an explanation of the place of origin, previously unknown, of the female germ-cells. According to him the structures previously regarded as male gonophores are undifferentiated germ-tissue, which only later, and in different specimens, develop into male and female germ-cells. In my oldest examples these transformations minutely described by Steche were not observed'. Actually, Richter figured (Taf. XXVIII, fig. 25) what is obviously a section of one of these female gonophores, that he took to be a stage in the development of a male gonophore. Richter rather ungraciously added that Steche had made no new contribution to the subject of the gonodendron and its appendages.

Perez (1929) published good figures of the endodermal cells of the spadix of the male gonophore, and drew particular attention to the division of many of the nuclei into two, three or more parts, and to the physiological significance of this phenomenon, namely the control of a 'flux metabolique' between the coelenteron and the developing germ-cells. He gathered together many other instances of this phenomenon, of which the multilobate nuclei of the *rete* on the ventral radial canal of the young nectophore of Hippopodiids is another.

Although the complete story of the method of reproduction in *Physalia* is not yet and perhaps never will be known, some progress has been made, and I have been able to substantiate Steche's work and to extend it. Having cut sections of gonodendra to elucidate morphological points, I found two quite distinct types of gonophores, which matched those sectioned and figured by Steche in 1907. I then examined dozens of gonodendra of all sizes which had been dropped by my laboratory specimens at Lanzarote. I found that I could soon distinguish these two types of gonophores, very often without clearing and mounting stained specimens, and from surface inspection in the light of a tungsten-ribbon lamp, or in optical section only.

One type (Pl. XXIII, fig. 5), evidently the male, had a thick cap of germ-cells borne by a relatively less capacious endodermal spadix. The walls of this spadix were relatively thin and not at all or only a little lobulated. The cap of germ-cells, situated as usual in the secondary ectoderm formed by the entocodon ('Glockenkern') and covering the spadix, consists of very numerous small cells which presumably are spermatogonia. I have not made a cytological study of them.

The other type of gonophore, which can be recognized at all stages of growth, is presumably the female (Pl. XXIV, fig. 3). Its endodermal spadix has much larger cells than those of the male type, about 7000 in number, and the whole ectoderm of the spadix becomes lobulated. In place of the thick cap of spermatogonia there is a very thin layer of germ-cells in the secondary ectoderm. Selecting one of the largest female gonodendra, I managed to cut one of the small gonophores in half transversely and then, after removing the outer membranes, to dissect out the endodermal spadix, leaving the mesogloea and the thin layer of secondary ectoderm with its germ-cells intact. When stained with Ehrlich's haematoxylin and cleared, I found to my astonishment that the germ-cells formed a continuous, narrow, sinuous band, one cell thick and two cells broad, running over the surface (Pl. XXIII, fig. 4). Rapid inspection of a whole mount showed that the cells had large nuclei containing stained chromatin particles. The polygonal cells measure about 13–14 μ in diameter and contain vacuoles. The nuclei are about 11–12 μ in diameter. The female gonophores measure up to 1·7 mm. in length and 0·85 mm. in diameter.

In the latest stage of development, in both male and female gonophores, I find that the whole manubrium (with the exception of the outer membranes with the pair of linked and branched radial canals) may be drawn out, often inside out, into the lumen of the branchlet (Pl. XXIII, fig. 6). These masses, curious to relate, circulate freely in the branches and the cavities of the palpons. I have observed this in living gonodendra.* It was this sequence of events that Richter misinterpreted, reversing the

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* I have already mentioned (page 354) that the palpons can open their tips.

order in which they occur; nor did he state how he deduced his sequence. In the legend to his text-fig. 7, he stated that in the *youngest* stage of development of the male gonophore, the germ-cells lie inside the branchlets and he indicated schematically certain opaque bodies filling the lumen of the branchlets. The pedicels of the nectophores shown in Richter's fig. 7 have little mesogloea, and on this criterion alone (see page 352), apart from my observations on living material just described, I believe that this figure represents an advanced but not final stage in the development of the male gonophore. Richter described a complicated sequence of developmental events. In the youngest stage of the male gonophore he showed the conventional medusoid bud, an outgrowth of ectoderm, mesogloea and endoderm with a small 'Glockenkern' (entocodon). He described how the growth of the 'Glockenkern' downwards pushes the endoderm, ectoderm and 'Glockenkern' into the lumen of the branch, and subsequently, how the lower ectodermal layer of the 'Glockenkern' pushes up again into the half-emptied gonophore. This he appears to have thought resulted in the condition shown in his fig. 25, Taf. XXVIII, which he regarded as the *penultimate* stage of development of male germ-cells, but which I regard as an early stage.

Examination of several of my specimens that bore at least ten large gonodendra showed that all the gonodendra of one specimen were either all male or all female. Ripe eggs have never been seen. Haeckel said that *Physalia* specimens which he observed in the Bay of Algeciras on his way home from the Canaries in March 1867 bore ripe sperm, but he did not state whether the sperms were motile. Because we find ripe eggs neither on the bud-colony nor shed in surface waters, it is probable as Steche (1907) said that they undergo development in the depths, as in *Velella*.

ORIGIN OF *PHYSALIA* AND THE SIPHONOPHORA: THE PAEDOPHORE HYPOTHESIS

The evolution of *Physalia* and the other siphonophores seems to be linked with that of certain corymorphine, myriotheline and margelopsine hydroids; with *Pelagohydra* and with the so-called Disconantha (*Velella*, *Porpema*, *Porpita*).

Hadži* (1918), like Chun (1897*a*) before him, suggested the derivation of physonect siphonophores from the floating hydroid *Margelopsis gibbesi* (fig. 8 and legend); also of the Chondrophora (Disconantha) from corymorphine hydroids (fig. 9 and legend) and of both physonect and calycaphore siphonophores from simple hydroid corms of the *Myriothela*-type (fig. 10). Garstang (1946), who I think cannot have known of Hadži's paper, also drew attention to the similarity between disconanths and corymorphines, and between physonects and myriothelines. A review of work on the phylogeny of siphonophores and disconanths may be found in a paper by Leloup (1954).

I suggest that all these comparable forms, corymorphine, myriotheline and margelopsine† hydroids as well as *Pelagohydra* and the disconanths and siphonophores, are themselves derivatives of comparatively lately evolved and new types of animal organization—tentaculate actinula larvae, and that it is through the adaptive radiation of such larvae that these neotenic groups have arisen. The new tentaculate actinula larva must not be confused with the conception of the actinula of Brooks's (1886) hypothesis. Brooks's hypothesis satisfactorily accounts for the origin of the Hydroida, from which stock the precursors of the paedophores must have arisen in the following way: Certain early hydroids tended to retain their larvae which hitherto had been released early as eggs or free-swimming ciliated planulae. We can see this sort of trend in some bougainvillid hydroids today. These retained larvae must have been comparable on release with the actinulae of present-day myriotheline hydroids.

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* So far I have only a translation of some of the figure subscripts in this paper, which is in Serbo-Croat.

† These subfamily names have been used by evolutionists in a general way and are so used without precise restriction here.

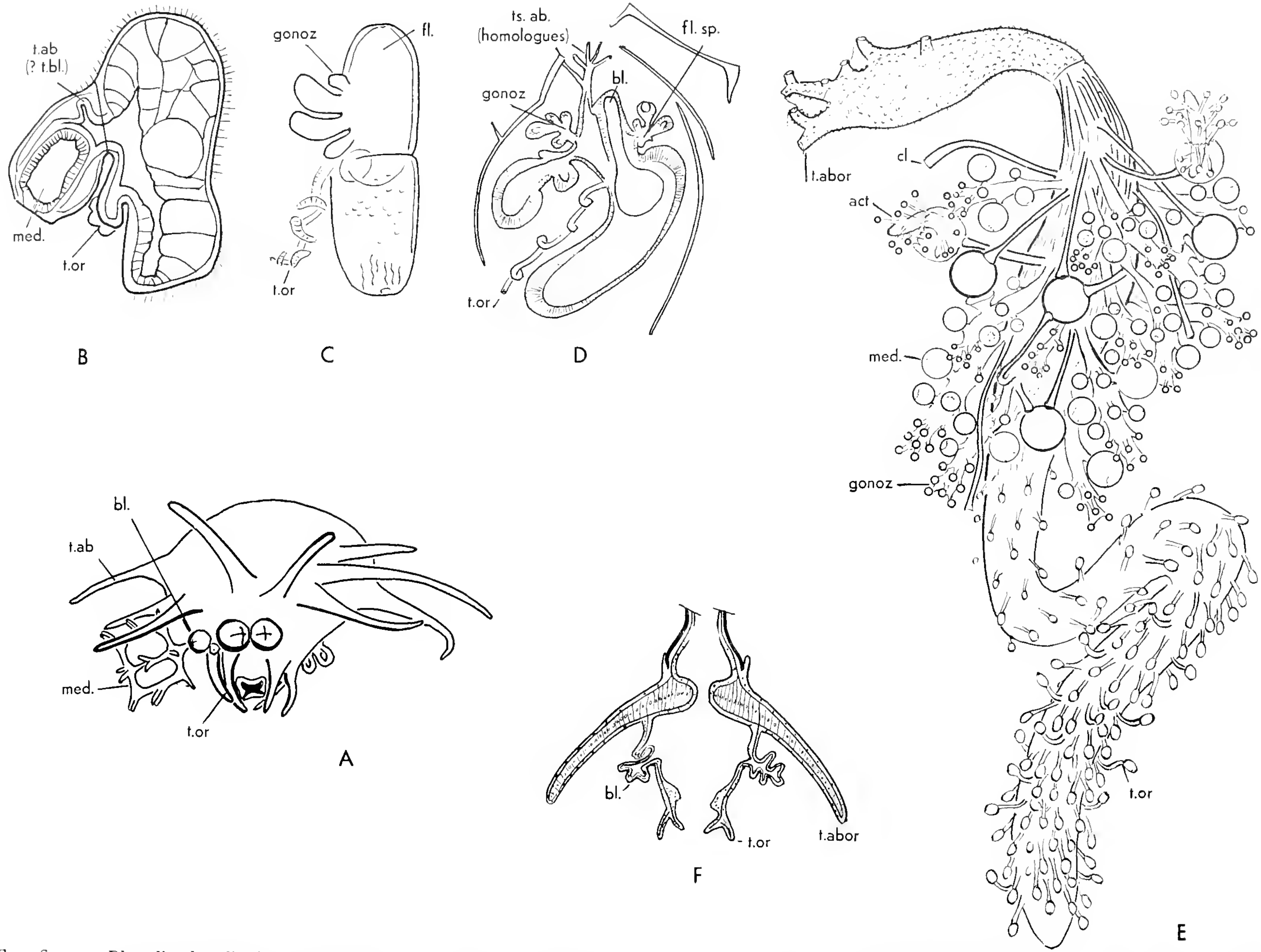
At first, no doubt, the actinulae swam by means of tentacles, as suggested by Garstang (1946), before settling down on the substratum and budding-off the sexually mature medusae. Soon asexual reproduction or budding took place during the prolonged, free-swimming larval phase, and finally the sexual adult stage was budded from the daughter polyps (gonozooids) of the still free-swimming actinula, originally a larva but now a neotenic, mature animal of a new type. So now the parent zygote (oozoid) has become an asexual carrier of the offspring (gonozooids) that I call a *paedophore*.

I do not propose to try to suggest all the detailed steps that must have followed one another in the course of the origin and adaptive radiation of this new type of organism, the paedophore. But some of the animals evidently remained entirely free-swimming and emerged as disconanths, *Pelagohydra* and some of the margelopsines, while others took to the bottom and emerged as loosely attached myriotheline and corymorphine hydroids. The great interest of *Margelopsis haeckeli* (Werner, 1954) is that it is planktonic for most of the year. During this time the larvae are retained until they develop into actinulae, which are then set free to become free-swimming hydroids; but the autumnal eggs develop into stereoblastulae, which pass the winter on the sea-bed. This life-cycle indicates how an entirely free-swimming hydroid may have arisen from a fixed precursor as a neotenous larva.

The essential structural organization of the new type of actinula is the possession of two sets of larval tentacles, oral and aboral, together with daughter polyps in the region between. These daughter polyps either have functional mouths and are called gonozooids, as in the disconanths, or the mouths are lacking although the polyps have tentacles and are obviously reduced polyps, as in *Myriothela penola* Manton. Again, the daughter polyps may be so reduced as to form scarcely recognizable stalks which bear the medusae, as in *Margelopsis haeckeli* Hartlaub.

In siphonophores generally, these reduced gonozooids are difficult to identify because often there is a replication accompanied by successive reduction. This can be seen in *Physalia*, where each gastrozooid except the protozooid may be regarded as the first of a series of groups (cormidia) of gonozooids, the last gonophores and nectophores being produced on the last few of the series of replicates called palpons.

Garstang agreed with Schneider who, in 1896, expressed the view that the siphonophore somatocyst was homologous with a bracteal canal. These canals Garstang showed to be homologues of tentacles. Leloup in 1954 suggested that a siphonophore tentacle was homologous with an oral tentacle of an actinula. Neither of these zoologists pursued the subject to the conclusion at which I myself have arrived. In fact Garstang still thought that the nectophore of a siphonophore represented the cauline gonophores of a stalked hydroid, and not those of hydroids like the corymorphines that bear them on the hydranth. In my view it is with the gonophores of the hydranths that the nectophores are to be homologized. We can in fact put the figure of a swimming margelopsine hydroid, *Climacocodon* or *M. gibbesi*, which is really a neotenous actinuloid nurse-carrier, side by side with that of either a calyconula or a physonect larva of a siphonophore and show correspondence of essentials (Text-fig. 30). Although *Climacocodon* has radial symmetry and many tentacles arranged in two groups, oral and aboral, and produces sexual medusae, while the calyconula has only one of each group of tentacles and a single asexual medusa arranged on a single meridian, Garstang has provided an explanation for this difference in symmetry. Bilateral symmetry in the calyconula was due, he pointed out, to the presence of a great deal of yolk which restricted the delamination of tissues to a single meridian. The calyconula, no doubt, is not very like the larva of the ancestral siphonophore, which probably had a float as does the larva of the cystonects, the group which includes *Physalia*. Garstang showed how the calycophores had lost this float. Like the larva of the physonects, the calyconula has a precocious nectophore, which the cystonula larva of *Physalia* has not.



Text-fig. 30. *Physalia physalis.* Some siphonophoran and other Paedophores, to demonstrate homologies. *A*, *Climacocodon ikarii* Uchida (after Uchida 1924), ×37. *B*, Calyconula larva of *Sulculeolaria quadrivalvi* Blainville (after Metchnikoff, 1874), ×20. *C*, larva of *Physalia physalis*, ×9·5. *D*, larva of *Agalma elegans* (Sars) in section (after Totton, 1956), ×43. *E*, *Myriothela purpurea* (Gosse) (after Allman, 1876), ×4. (There are difficulties in determining the prior name of this intertidal species from the Dorset coast. '*Arum cocksii* Vigurs' (Cocks, Ann. Rept R. Corn. Poly. Soc. for 1849, p. 90 (published 1850)) is a *nomen nudum*. The same name on p. 34 of the Report for 1853 of the same society (published 1854) is antedated by *Spadix purpurea* Gosse (Ann. Mag. nat. Hist. Vol. XII, p. 125) published in July 1853. The prior generic name is *Myriothela* Sars 1849, if *Lucernaria* Fabricius 1780 is excluded.) *F*, *Tubularia larynx* (after Leloup, 1954), ×10. *bl* = position of blastostyle (hidden), *bl.sp* = special blastostyle (nectosome), *fl* = float, *gonod* = gonodendron, *gonoz* = gonozooids (homologues), *med* = medusoid, ***t.ab*** = **aboral tentacles,** ***t.bl*** = **tentacle of blastostyle,** ***t.or*** = **oral tentacle.**

It is in this context that we may look for the meaning of the tripartite groups of *Physalia*, about which I said so much earlier on when describing the pattern of budding in the cormidia (pages 328 ff.). Each tripartite group is the homologue of an asexual replicated gonozooid of *Velella* and of a blastostyle* of *Climacocodon*, with which I have just compared a siphonophore actinula larva. The difference is that the *Physalia* polyp, or gastrozooid, is very much elongated, the aboral tentatcles of the *Physalia* nurse-carrier are absent, and its oral tentacles reduced to a single one, and the single gonozooid complex, the gondendron, has replaced the simple gonozooid or blastostyle.

If early larvae of *Physalia* are compared with those of the other two groups of siphonophores, namely the calyconulae of Calycophora and the physonulae of Physonectae, both resemblances and differences will be noticed at once; the large air-sac and tentacle in *Physalia*, the large nectophore and small tentacle in the calyconula, and the air-sac, tentacle and bracts of the physonula (Text-fig. 30).

Had it not been for comparison of the cystonect cystonula larva of *Physalia* with the physonect larva and with the calycophore calyconula, it would have been more difficult to speculate about the ancestry of *Physalia*. As it is, it seems possible that *Physalia's* ancestor arose by neoteny after the first appearance of actinula larvae in hydroids, and that it proved advantageous to develop an enormous float, to bud extravagantly and precociously, and to develop bigger and better tentacles with very numerous nematocysts for the capture of the comparatively large fish with which the animal came into contact so effortlessly.

Thus evolution for *Physalia* has consisted, I think, partly in its ability through the ages to improve its adaptation to catch and devour fishes at the surface of the sea and to live in a stormy environment. In this respect it may be contrasted with the deep-sea calycophore species of *Chuniphyes* which have particularly small polyps and no floats. On the other hand the floats of even deep-sea cystonects are large. *Physalia* is also obviously adapted to drift at an angle of about 45° to the right or left of the down-wind direction. Because this angle increases† as the waterline lengthens, it looks as if this adaptation has evolutionary value. If the process of being drifted on to a lee-shore is the analogue of being captured by a predator, the future of *Physalia* may lie in the direction of improvement in this adaptation. Herein may be part of the significance of the great size of the float in *Physalia*, and a rapid growth-rate would help in this respect. The apparent neotenic character of *Physalia* lends cogency to these considerations.

We do not know that right- or left-handedness is affected by natural selection, and it is difficult to see how one tack can be more advantageous than the other. I do not think that Woodcock's suggestion of advantages to be gained by one tack in feeding is a good one, though the theory of wind-induced vortices no doubt is sound. But it is quite certain that the tack of an individual is fixed from a very early phase of its life-history. The future tack of any individual larva can be recognized already when only the rudiments of secondary buds are becoming visible and the length of the larva is still less than 1·5 mm. The gas-gland itself, even at that age, does not lie symmetrically in the axial line. Because, by custom, we call the meridian in which the tentacle and secondary buds lie ventral, the dorso-ventral plane early comes to lie almost parallel to the surface of the water. The gas-gland itself, while still located at the oral end of the air-sac, then lies asymmetrically, somewhat on the underside. I am of the opinion that right- and left-handedness arises fortuitously when the larva surfaces. Perhaps there is a slight bias of which we know nothing, but the tentacle must come to lie either to the right or to the left, and henceforward the tack is fixed.

I think the predominance of one tack would be disadvantageous because the maintenance of both

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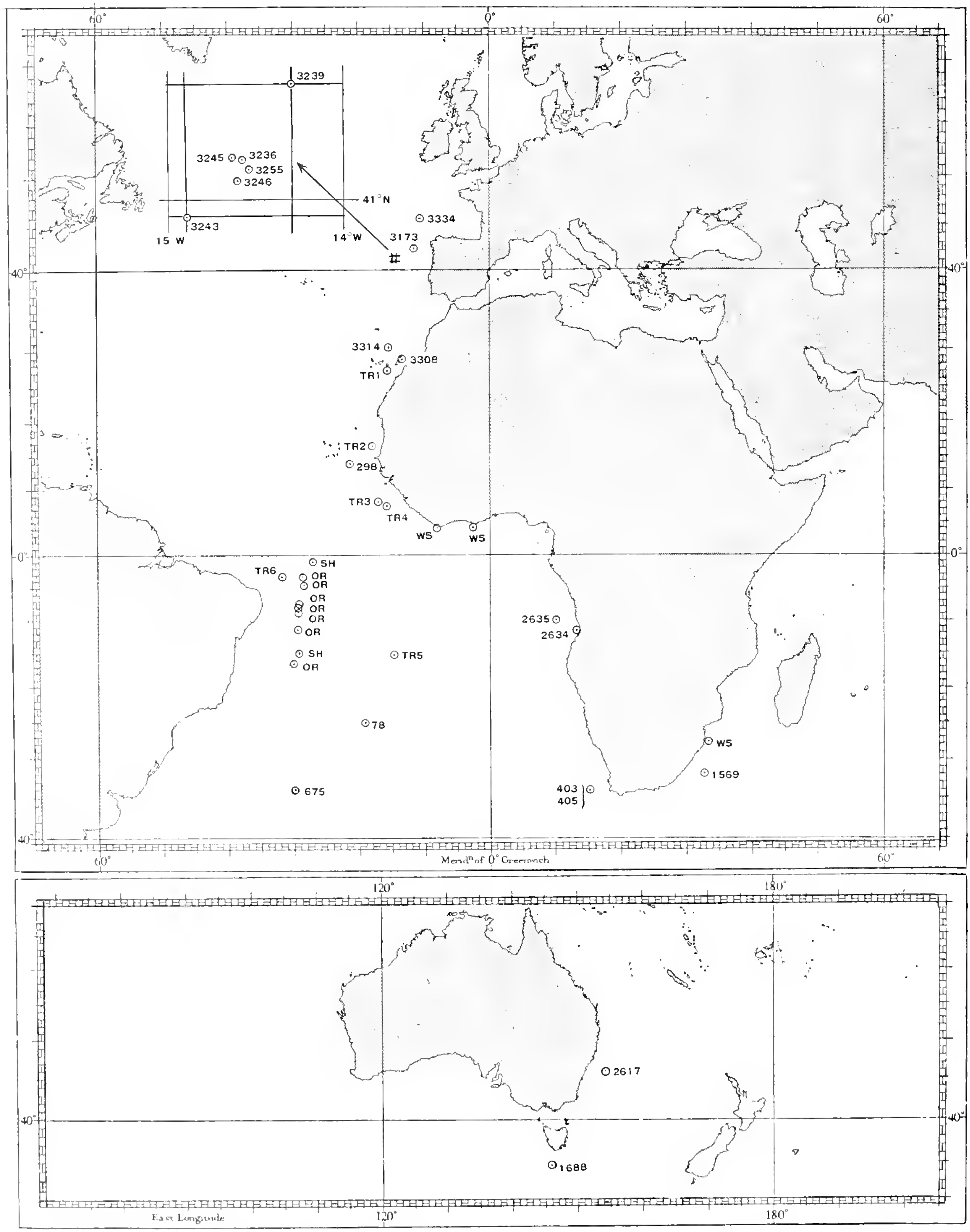
* Present but not shown in the original figure.

† Woodcock (1956) stated that the young specimens drifted at a smaller angle. I can well believe this, but have not checked it.



Text-fig. 31. *Physalia physalis.* Chart to show the distribution of specimens recorded by members of the staff of the National Institute of Oceanography in the Atlantic, and in Australian waters.

forms obviates the danger of the population being swept out of its optimum environment by the wind. The mere fact of being drifted by the wind at 20–30 m. per minute must be of great value in food capture and must aid maximum distribution.

DISTRIBUTION

It does not seem an adequate treatment of this subject to deal merely with such observations as may be recorded in the literature. It is hoped to make a special study of the question later on, basing it on replies to a questionnaire circulated through appropriate channels to seafarers.

The potential value of ships' logs is shown by the following extracts provided by the Marine Superintendent of the Meteorological Office from meteorological log-books of various ships:

> (1) *M.V. San Veronico* (Eagle Oil and Shipping Co.)
> Captain S. Miller, O.B.E. Curaçao to Rotterdam.
> 13 May 1957, at 12.00 G.M.T. in 36° 30′ N., 36° 24′ W. While the ship was stopped for engine repairs many Portuguese Men-o'-War were observed. They consisted of....The bladder size varied up to about 8 in. in length. On puncturing the bladder of one caught in a bucket (see photograph) it was observed....[A note on 'deflation' and subsequent 're-inflation' follows, but is not precise enough for evaluation at present.]
>
> (2) *S.S. Loch Garth* (Royal Mail Lines)
> Captain G. S. Grant. West coast of North America.
> 30 May 1957, at 39° 50′ N., 124° 32′ W.
> At 17.40 G.M.T. the ship passed through a line of small Portuguese Men O'War formed in a direction N.E.–S.W. The line approximately a quarter of a mile in length and 50 ft. in width, was of a dark green appearance. [Query: were these *Velella*?]
>
> (3) *S.S. Tekoa* (New Zealand Shipping Co.)
> Captain F. C. Taylor. Curaçao to London.
> (*a*) 15 June 1957, at 19.00 G.M.T. in 36° N. 43° 20′ W. passed through numerous Portuguese Men O' War (*Physalia*) and By-the-Wind Sailors (*Velella*). These siphonophores are usually seen when entering the Gulf Stream, but they have been sighted this time without the usual accompanying rise in sea temperature which generally ushers you into the Gulf Stream.
> (*b*) 16 June 1957. Vessel still passing many of the above....
>
> (4) *S.S. Orion* (Orient Line)
> Captain J. O. Birch, D.S.C., R.D. Honolulu to Vancouver.
> 25 August 1957 in 44° 18′ N., 132° 06′ W. The sea was observed to be thickly speckled with transparent colourless jellyfish, circular in shape and about 2–4 in. in diameter. When viewed through binoculars a dark centre could be seen and also what appeared to be a small vertical fin. No tentacles or feelers however could be seen and the observer therefore is not definitely sure as to whether they were Portuguese Men O' War or not. The sea continued to be speckled with these jellyfish until dusk, sometimes lying in bands down-wind. The vessel therefore has passed through a field of these marine creatures at least 164 miles wide. Wind N. × W. Force 3. Ship's course 048°, speed 17·8 knots. [Internal evidence seems to indicate that what Captain Birch saw were specimens of *Velella*.]
>
> (5) A note headed *Physalia* appeared in *The Marine Observer's Log*, vol. IX, 1932. It was an extract from the Meteorological Log of *S.S. Niagara*, Captain T. V. Hill. Auckland, New Zealand to Victoria, B.C. 'At 4.0 p.m. 19 May 1931, large numbers of *Physalia*....' [Once more the evidence pointed to a mis-identification, but similar logs must contain a wealth of useful information.]

To the Hydrographer of the Navy, Rear-Admiral K. St B. Collins, O.B.E., D.S.C., I am indebted for supplying the following information in response to a request for observations to be made if possible by ships of the Fleet during a cruise in the West Indies at the beginning of the year 1958.

> Portuguese Men-o-war were sighted from *H.M.S. Delight* between 13.00 and 15.30 on 5 February 1958, off Havana, Cuba. The ship was steering course 260° speed 14 knots, and the men-o-war could be

> seen at ranges up to three hundred yards. Density: individuals over 500 yards apart from 13.00 to 14.00 (i.e. dispersed over 14 miles). Large shoal at 15.00, extending for 3 miles with individuals about 200 yards apart. Type: all appeared to be left-handed on starboard tack. Meteorological conditions: Wind from 120°, 10 knots; sea temperature 79° F. The Gulf Stream in this locality was flowing at two knots.

This must be the first recorded occasion on which the tack of specimens has been noted at sea.

Observations or collections made by 'Discovery' and 'Discovery II' or members of the staff travelling in other ships are recorded in Table 12.

Table 12

Position	*Station*	*Date*	*Tack of specimen*
	R.R.S. 'Discovery' and 'Discovery II'		
27° 15′ N., 15° 32′ W.	Testing gear	21 October 1925	1 R
16° 19′ N., 18° 24′ W.		26 October 1925	1 R
8° 06′ N., 17° 06′ W.		1 November 1925	2 L
7° 17′ N., 16° 19′ W.		2 November 1925	1 L (2)
25° 5′, S., 15° 17′ W.		28 November 1925	1 L
25° 47′ S., 14° 48′ W.		29 November 1925	1 L
3° 22′ S., 32° 25′ W.		29 December 1929	1 L (2)
35° 18′ S., 19° 01′ 10″ W.	78	12 June 1926	1 L
13° 01′ 45″ N., 21° 34′ 45″ W.	298	29 August 1927	1
34° 14′ S., 15° 01′ E.	403	24 May 1930	1 R
34° 16′ S., 15° 02′ E.	405	4 June 1930	1
34° 08′ S., 29° 50·2′ W.	675	26 April 1931	3 R
31° 50·3′ S., 32° 20·5′ E.	1569	12 April 1935	—
45° 10·8′ S., 146° 04·6′ E.	1688	6 March 1936	1 L
12° 17·4′ S., 13° 31·3′ E.	2634	10 April 1939	1 L
10° 19′ S., 09° 36·4′ E.	2635	11 April 1939	—
34° 02′ S., 154° 16′ E.	2717	8 October 1950	2 L, 1 R
42° 35′ N., 11° 35′ W.	3173	22 November 1954	1 R
42° 02′ N., 13° 16′ W.	3235	18 May 1955	—
41° 11′ N., 14° 34′ W.	3236	19 May 1955	1
41° 30′ N., 14° 17′ W.	3239	24 May 1955	1 R
40° 56′ N., 14° 53′ W.	3243	26 May 1955	2
41° 10½′ N., 14° 38′ W.	3245	27/28 May 1955	2 R (3)
41° 05′ N., 14° 36′ W.	3246	30 May 1955	1 R
41° 08′ N., 14° 32′ W.	3255	11/13 June 1955	2 R
28° 49½′ N., 13° 40¼′ W. 28° 49¾′ N., 13° 37¾′ W.	3308	19 September 1955	1
30° 08′ N., 15° 53′ W.	3314	21 September 1955	—
45° 44½′ N., 10° 48′ W.	3334	13 October 1955	1 R
	R.S.S. 'William Scoresby'		
27° 52′ S., 33° 05′ E.	—	8 August 1950	1
04° 25′ N., 02° 46′ W.	—	27 October 1950	2
04° 26′ N., 08° 17′ W.	—	27 October 1950	1
	'Southern Harvester'		
15° 05′ S., 29° 22′ W.	—	5 May 1948	1
01° 11′ S., 27° 17′ W.	—	8 May 1948	1
	'Orwell'		
16° 12′ S., 30° 11′ W.	—	25 January 1954	1
11° 37′ S., 29° 40′ W.	—	26 January 1954	1
09° 03′ S., 29° 22′ W.	—	27 January 1954	1
08° 18′ S., 29° 15′ W.	—	27 January 1954	1
07° 40′ S., 29° 07′ W.	—	27 January 1954	1
04° 21′ S., 28° 44′ W.	—	28 January 1954	2
03° 47′ S., 28° 35′ W.	—	28 January 1954	2

All these positions are shown in Text-fig. 31.

Information is required on the following points.

(1) Where is the animal most commonly met with?

(2) Does it occur at sea in vast shoals or isolated or both, and under what meteorological conditions?

(3) *Physalia* occurs in two forms, right- and left-handed: are both forms equally common and do they occur together?

(4) Is it difficult for an observer on shipboard who is familiar with boat-sailing to distinguish the right- from the left-hander by the way it is orientated to the wind? (The right-hander appears to be hove-to on the port-tack and drifts to the left of the down-wind direction, and vice versa, the tentacles acting as a drogue.)

(5) Fixes are required for animals definitely observed to be right- or left-handers with a record of wind-force.

(6) In a wind does the animal drift along steadily? In a sudden lull does it fall over into the wind? Subsequently, and in a flat calm, does the animal roll about and somersault to right itself?

(7) Is *Physalia* ever observed in long parallel wind-rows?

(8) Records of recollection of previous observations on *Physalia* in any oceans are needed.

(9) Precise records are needed of the effects of stinging by *Physalia* (identified as having a bladder that rests on the surface).

SUMMARY

1. There is only one species of Portuguese man-of-war, *Physalia physalis* (L.), though it occurs everywhere in two forms, the so-called right-handed and left-handed. Both forms were found together in the Canary Islands. The question of right- and left-handedness is discussed.

2. Observations from a boat were made at close quarters on left-handed specimens drifting in a moderate breeze at slack tide. The angle of drift from down-wind direction was measured, and the rate of drift determined.

3. The well-known somersaulting phenomena were studied in open water. They were seen generally in a calm and followed loss of equilibrium in the absence of a breeze.

4. Specimens ranging in float-length from 11 to 180 mm. were anaesthetized and fixed for morphological study.

5. The animal is shown to consist of a hypertrophied asexual larva acting as nurse-carrier for other larvae, the polyps, and adults, the medusoid gonophores.

6. The pattern of budding has been determined. There are two budding-zones on the under and windward side of the oral half of the float, separated by a gap into a main zone and a reduced oral zone. The budding system is basically the same in both.

7. The single cormidia of a number of specimens, both young and old, have been compared with one another on the same specimen and from specimen to specimen, and photographic records made from several angles.

8. The general pattern of budding in a single cormidium shows a series of about a dozen tripartite groups, consisting each of a single gastrozooid and its associated tentacle and nematocyst nursery (the ampulla) together with a complex gonodendron, each group budded from the base of its predecessor with the youngest group formed at the aboral end. Secondary branches and branchlets carrying still more series of tripartite groups are produced from the bases of certain groups of the first series, and tertiary ones from the bases of some groups of the secondary series. A well-marked series of these branches is formed to leeward of the main series.

9. Full details of sexual reproduction are unknown and ripe ova have never been observed. *Physalia* is dioecious. Some of the so-called 'male' gonophores are female.

10. There is no evidence that the so-called 'female' medusoids are shed and that the jelly-polyps (Gallertpolypoide) represent their stalks, as has been suggested. The 'female' medusoids are nectophores, not concerned with sexual reproduction.

11. The jelly-polyps, the 'Gallertpolypoide' of Chun, found on the branches of the gonodendra, are vestigial nectophores. In the early stages of their development there is no sign of a 'Glockenkern'.

12. The basal ampullae of the tentacles are homologous with the basigasters of gastrozooids of other siphonophores. Their walls are filled with nematoblasts.

13. The gonodendra and tentacles are more complex and so probably more highly evolved than in other cystonects. Their growth-stages and the structure of their asexual nectophores and jelly-polyps were studied. Early egg-cells were located in bands in the ectoderm of female gonophores. Photomicrographs of early growth-stages of the gonophores are given.

14. A brief review of the literature, including the pharmacology of stinging is given.

15. A list is given of points upon which further information about the living animal is desired.

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STUDIES ON *PHYSALIA PHYSALIS* (L.)

PART 2. BEHAVIOUR AND HISTOLOGY

BY G. O. MACKIE

(Dept. of Zoology, University of Alberta)

CONTENTS

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(Plates XXVI to XXVIII, text-figures 1–6)

INTRODUCTION

THE morphological complexity of the siphonophores is well known. It has engaged the attention of a great number of distinguished biologists, and it is only comparatively recently that the true interrelationships of the group have been satisfactorily established. However, preoccupation with gross morphology has led most workers to neglect certain important aspects of siphonophore organization, particularly in the fields of physiology and behaviour.

The group is unique amongst the Coelenterata in the capacity shown by some of its species to secrete gas into a float and to regulate density (and hence to achieve vertical migration) by adjusting the amount of enclosed gas; and yet, in recent times only one worker (Jacobs, 1937) has investigated this phenomenon. The small size and delicacy of most siphonophores makes them exceptionally difficult animals to handle, but, if the various technical difficulties could be overcome, the rewards of a thorough physiological investigation would certainly be rich. Certain members of the Calycophora, such as *Hippopodius*, can perform density regulation *without* the aid of a gas-filled float. The mechanism for this is completely unknown. Furthermore, there is virtually no published information on the extent of nervous co-ordination between the different parts of a siphonophore colony. These are but two of the outstanding problems in the realm of functional organization.

An investigation of the behaviour and reactions of the siphonophores was begun by the author in 1954, but it soon became clear that the significance of the behavioural findings would be hard to establish unless more was known of the histology. Although we are still far from achieving a full understanding of the structural and functional organization of the siphonophores, it has been possible to make some progress by means of this twofold method of investigation. In the following account, an attempt will be made to describe the chief activities of one siphonophore, *Physalia*, together with the extent of co-ordination between the different parts and the microscopic structure of the component tissues.

The material used in the investigation came from three sources. The bulk of it was collected at Lanzarote in the Canary Islands during the spring of 1955, and the behavioural observations were made at that time. Some material was fixed for the author by Miss Elaine Robson from a specimen captured near Plymouth in November 1954. Finally, some material from the 'Discovery' collections was examined.

The author wishes to acknowledge his particular debt to Mr A. K. Totton, who conceived the idea of a joint expedition to the Canary Islands and whose advice has been a great help, both then and since. Certain of the results reported here were incorporated in the author's Doctor's thesis, which was presented, under the supervision of Dr W. Holmes, at Oxford in 1956. It is a pleasure to acknowledge the help of Professor Hardy, Dr Holmes and others at Oxford, and of the late Professor R. B. Miller in whose department at Edmonton the work was completed. The expenses of the project were met by a Research and Maintenance grant from the Department of Scientific and Industrial Research (which included an additional sum of money for the Canary trip) and by grants from the General Research Fund of the University of Alberta, and from the National Research Council of Canada.

BEHAVIOUR

1. INTRODUCTION: INDIVIDUALITY IN SIPHONOPHORES

It is customary to speak of siphonophores as colonies consisting of modified polypoid and medusoid individuals, all attached to a common stem.

This simple picture is satisfactory enough where the medusoid individuals are concerned. In the colonial Hydrozoa nectophores and gonophores are always easy to recognize as medusoids, both in their manner of development and in their mature structure. The remaining parts of a colony are not always so easy to classify. For example, in both the sessile *Corymorpha* and its pelagic relative *Velella*, the sexual medusoids are borne upon protuberances from the body-wall which are alike and homologous in every respect, except that in *Corymorpha* they are mouthless, while in *Velella* they have mouths and ingest food. In *Velella* they are known as 'gonozooids'. Taking a rigid view of the concepts of the colony and the individual, two interpretations are possible for this state of affairs. Either the gonozooids represent true individuals (as their name implies) and function as such in *Velella* while becoming reduced in *Corymorpha*; or they have originated in phylogeny from hydranth outgrowths, and such individuality as they have acquired is secondary. If the first interpretation is correct, then *Corymorpha* must be regarded as a reduced colony. If the second is correct, then the structures in question should not be called gono*zooids*, unless it is made clear that they have acquired their individual status secondarily. The latter interpretation is preferable and it leads to the conclusion that individuality can be complete or partial; that it can probably also be lost or gained; that it is, in fact, an unreliable concept.

If the siphonophores are considered from the functional point of view, the distinction between the colony and the individual becomes even harder to define. In many siphonophores, one must recognize that a new, communal individuality has emerged from the ancestral assemblage. The organism acts like a well-integrated individual. Whatever their origins, the component parts have now achieved the status of organs in an individual. In a certain sense, the siphonophores represent a method of escaping from the limitations of the diploblastic pattern. Another more successful method of escape involved the development of a third germ layer. In the Triploblastica, organ systems develop within the individual. In the Siphonophora, individuals become organs.

The problem now to be considered concerns the extent to which *Physalia* has progressed beyond the condition of an assemblage of autonomous individuals toward the status of a new individuality.

2. BEHAVIOUR OF THE FLOAT

The outline of the float (seen from above) is shown in Text-fig. 1. The main groups of appendages are situated around the bulge (*b*). When the float is being driven before the wind the drag is concentrated in this region and, as a result, the float automatically assumes the orientation shown. The shape of the float is such that when orientated for sailing it does not move directly down-wind, but to one or other side of the down-wind direction, according to the mirror-image dimorphism (Woodcock, 1944, 1956; Totton and Mackie, 1956).*

In adopting a sailing posture the float responds actively by erection of the crest or sail (*s*); at the same time the apical pore-end (*a*) curves round toward the windward side. Bigelow (1891) found that

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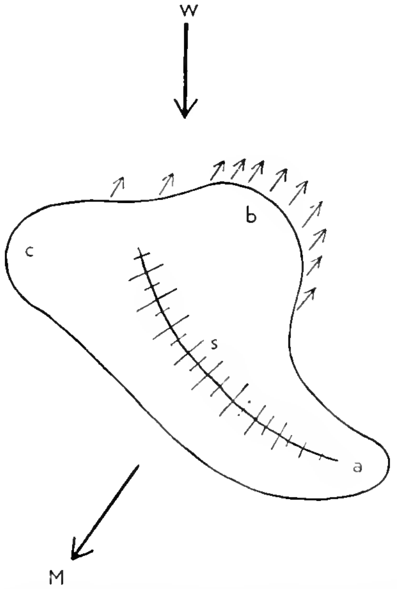
* In my thesis (submitted July, 1956, at Oxford) I suggested that the advantages inherent in dimorphism are not to be explained by reference to local phenomena such as distribution of Sargasso weed, islands, etc., but should be thought of in terms of world distribution. In any given ocean one dimorphic form will presumably be better fitted to survive than the other, but it will not always be the same form, and, for the species as a whole, it is not important which form has the advantage. The important thing must be that by virtue of the dimorphism the species is fitted for life in *any* ocean. Woodcock (publ. August, 1956) adopts a rather similar view.

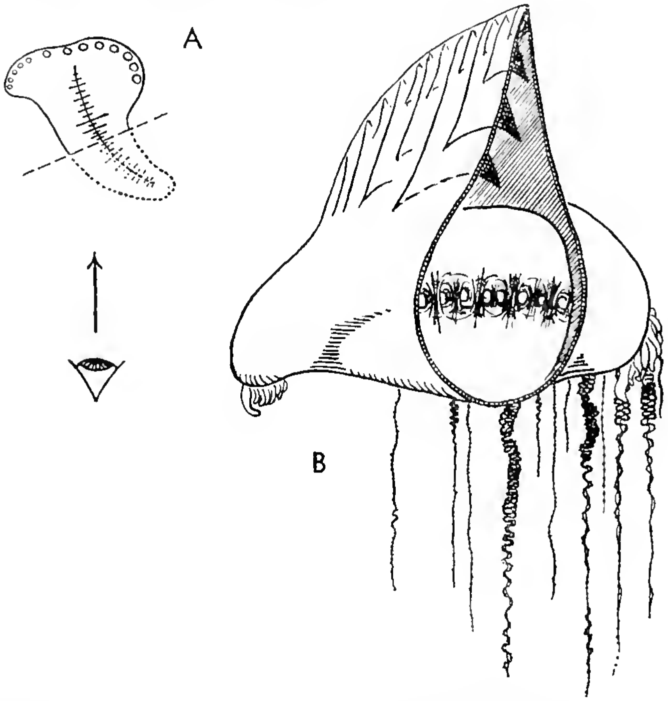
erection of the crest took place when air was blown against the float with bellows. Wilson (1947) found that splashing seawater on the float was also effective, although according to Bigelow only rain-water elicits the response. In the Canary Islands it was observed that in specimens brought into the calm of the laboratory, the crest usually collapsed and the float became flaccid. In specimens exposed to the wind, on the other hand, the crest became erect. The erect condition of the crest is shown in Pl. XXVI, fig. 1.



Text-fig. 1. Diagram of *Physalia*, seen from above, to show the sailing posture. *M* = direction of movement, *W* = wind direction, *a* = apical pore end of float, *b* = bulge, *c* = oral end, *s* = sail (crest). The arrows around the bulge (*b*) represent the forces of drag caused by the tentacles.

The way in which the wind acts has not been determined. Nerve-cells equipped with sense-hairs (to be described below) occur in the ectoderm of the float, and may be concerned in the reception of wind stimuli. Alternatively the buffeting and agitation caused by the wind or spray, or a combination of such factors may evoke direct responses in the float musculature, leading to crest erection. It should be explained that erection of the crest occurs automatically whenever the float musculature achieves a certain degree of tension. Any stimulus evoking an overall tightening of the float musculature will therefore normally lead to crest erection. The mechanism is surprisingly simple. The float consists of two containers: an outer muscular case, the codon (strictly: 'pneumatocodon') and an inner air bladder, the saccus ('pneumatosaccus'). The saccus lies free in the coelenteron, being surrounded by the codon and attached to it only in the region of the apical pore. The saccus is an inert, pliable structure whose shape is determined by that of the enclosing codon. Electric shocks applied to its wall were found to evoke no visible response, either local or general. Along its upper side it bears a row of thin-walled outpushings which become inflated whenever the air in the saccus as a whole is sufficiently compressed. At other times, the outpushings are collapsed and inconspicuous. This can be demonstrated experimentally by removing a saccus intact from a specimen, ligaturing its apical connection with the codon as a precaution against loss of air, and placing it under pressure by means of weights. In Pl. XXVI, fig. 2 a saccus is shown under pressure, with the outpushings inflated. In Pl. XXVI, fig. 3 the same saccus is shown without the weights. In normal circumstances, the necessary pressure is engendered by contraction of the enclosing codon. The dorsal processes of the saccus fit into pockets (Text-fig. 2) in the roof of the codon causing them to fill out, and stand erect. The arrangement is reminiscent of a pneumatic tyre, with inflatable inner tube. The enclosed air functions, indeed, as a 'pneumatic skeleton', comparable in some ways to the 'hydrostatic skeleton' of actinians (Chapman, 1949).

Many observers have commented on the strange rolling-activity and somersaulting performed by the float of *Physalia* in calm weather. Wilson (1947) suggests that this activity serves to keep the float moist. This would be particularly important in calm conditions in tropical waters. Perhaps a better interpretation of the activity is that proposed by Totton (personal communication). The upright position of the float, with sail 'trimmed to the wind' is inherently unstable, and can only be maintained when the wind is exerting a certain pressure against the side of the float. If there is little wind, the instability of the float in the sailing posture becomes manifest, and the float collapses on to its side. The float responds to collapse by movements which have the effect of restoring the upright position. In the upright position again, a new attempt at the sailing posture takes place, which, if the wind is still insufficient, results in another collapse.



Text-fig. 2. *A*, View of the float from above, to show the angle from which *B* is seen. The apical pore end (dotted) has been removed at the level indicated by the broken line. The openings around the bulge region and the side lead into the groups of appendages. *B*, View into the interior of a float from which the apical pore end and the whole saccus has been removed. For convenience, the float and crest are drawn as if they were still supported from within by the saccus, but if an animal were actually opened in this way, the float would collapse completely. Note the vaulting in the roof, forming pockets into which the saccus outpushings would normally fit.

The author's observations, considered in retrospect, support Totton's interpretation. It was several times observed that a sudden drop in the wind would cause sailing specimens of *Physalia* to fall over on to the windward side. Specimens were much less apt to fall on to their leeward sides; to do so would mean hauling a considerable weight of tentacles up out of the water. Bigelow (1891) was the first to draw attention to this fact. The float is precariously balanced, and slight local contractions of the muscular wall can bring about shifting in the centre of gravity and consequent rolling into a new orientation. Rolling occurs mainly about the *a–b* axis (Text-fig. 1), sometimes about the *b–c* axis. In the latter case, the apical pore end may rear up high in the air, and a complete somersault take place. These variations are understandable when one considers that all three sides of the float are contractile and that contraction can be localized in particular areas. A considerable range of body form can be assumed, in all of which the pattern of rolling will be different. It was found possible, by electrical stimulation of appropriate regions of the float wall, to evoke local contractions of sufficient power to bring about shifting of the centre of gravity and various kinds of rolling.

In the laboratory, the animals' own efforts are not always sufficient to achieve righting; in the natural environment, however, wave action may assist the process as in *Porpita* (Mackie, 1959). One laboratory specimen made unsuccessful attempts at righting for more than 10 min. The attempts occurred at intervals of 25–35 sec.

The righting activity, whether successful or not, consists of leeward side contractions. The repeated performance of righting movements may be of assistance in developing the asymmetry of the young animal. It is not known how the primary asymmetry arises, but it is a reasonable assumption that once a leeward side and a windward side have been established, however tentatively, the normal activity of the float will tend to fix and even to enhance it.

The contraction of the codon musculature during the righting movements is not a smooth, steady increase in tension; it is a succession of jerks, sometimes barely perceptible, which follow one another at intervals of 1½–2 sec. After each jerk there is some slight relaxation of the muscle, but this is more than made good by the next jerk. In most specimens where rolling-behaviour was studied, five or six jerks were sufficient to bring about the necessary degree of contraction for righting to take place. In the specimen referred to above, which had difficulty in righting, ten or fifteen jerks were observed in each unsuccessful attempt. If a kymograph record of the reaction could be obtained, the tracing would be a 'staircase'. We are probably dealing with a phenomenon in the same class as the stepped contraction of the sphincter-muscle of *Calliactis*, or of the circular swimming-musculature of *Aurelia*. Such responses are explained on a basis of neuromuscular facilitation (Pantin, 1935).

3. BEHAVIOUR OF THE TENTACLES

In a medium-sized *Physalia* (gas-gland diameter = 1·4 cm.) observed when sailing freely outside the harbour at Arrecife, the longer tentacles were found to extend to distances of 8–10 m. Following stimulation of the float, the tentacles were drawn in, achieving what appeared to be full contraction after about 1 min. The tentacles then measured 12–15 cm. These findings accord with Parker's statement that a tentacle may contract to 1/70 its full length (Parker, 1932).

As it contracts, a tentacle is thrown into lateral loops and then into primary and secondary coils. The coiling seems to be a straightforward mechanical accompaniment of shortening, and is not to be thought of as a device for ensnaring prey. The tentacles cannot 'writhe' or wrap themselves actively round objects. The prey is secured to them solely by the nematocyst-filaments, acting as harpoons.

The process of fish-capture has never been closely observed in natural conditions, although specimens holding prey in their tentacles have been studied in the laboratory (Wilson, 1947). Under normal environmental conditions, contact of a tentacle with any solid object such as a fish will presumably evoke nematocyst discharge. The object, if animate, will suffer a temporary paralysis from the action of the toxic substance in the nematocysts. It will be held against the tentacle by the nematocysts, and its weight, or the increased drag it causes, will stretch the tentacle and thus evoke contraction. Gradually the fish will be brought up to the region of the gastrozooids which will apply themselves to it, and begin to digest it.

Laboratory observations made in the Canary Islands suggest that any abrupt mechanical stimulation applied to the tentacles, whether causing stretching or not, will evoke contraction. For instance, it was observed that a captured fish would be held passively in the tentacles for quite a long time unless it became active, and struggled to escape. If this happened, the tentacles would begin to shorten again. Any tactile stimulus, such as pinching with forceps, or striking with a glass rod caused some degree of contraction either local or general. Bigelow (1891) found that there was little, if any, sensitivity to food substances in solution.

The most characteristic activity of the tentacles is a rhythmic shortening and lengthening. On the other hand, tentacles, whatever their rate of contraction, can remain completely motionless for long periods. Bigelow was the first to describe the shortening and lengthening of the tentacles. He did not regard it as sufficiently regular to be called 'rhythmic'. Parker (1932), however, found evidence for rhythmicity in the movements, the interval between successive performances being 30–75 sec. In the present investigation a definite rhythm was observed. It was sometimes a very loose one as in the cases studied by Parker, but in many examples, particularly where fresh healthy specimens were under observation, a much more regular rhythm was in evidence. It was found that the rhythm was slower in small tentacles than in large ones, but that in all tentacles, whatever their size, the frequency depended on the general degree of contraction of the tentacle within which the smaller rhythmic changes in length were taking place. In one case a small moderately extended tentacle was timed over 23 min. The contractions followed one another every 10–17 sec. The specimen was then transferred to another tank and, as invariably happens following such disturbance, the tentacles shortened considerably. When the rhythmic activity emerged again in the original tentacle studied, the contractions were coming at 5–10-sec. intervals. Gradually the overall length of the tentacles increased again, and the frequency of the rhythm declined.

Rhythmic shortening and lengthening seems as a rule to accompany gradual changes in overall length and it may, in fact, be the basis for such changes. In this there is a superficial resemblance to the rhythm in *Metridium* (Batham and Pantin, 1950). However, in *Metridium* the rhythm is slow, sigmoid and distinct from the facilitated responses evoked by mechanical stimulation, while in *Physalia* the contraction phase of the cycle is rapid, 'stepped', and indistinguishable from a mechanically evoked contraction. The 'steps' are much more noticeable in the contraction of the tentacles than in contraction of the float because the amplitude of the contractions is much greater. Each 'step' may shorten the tentacle by several inches. Not more than three or four 'steps' are distinguishable in the contraction phase of the rhythmic movements. The elongation of the tentacle following one of these stepped contractions is smooth and gradual. It is probably passive, being caused by gravity or drag. Endodermal circular muscle is present in the tentacles, but there is no evidence that it assists elongation. It is more likely that it serves for movement of fluids in the coelenteron.

Rhythmic shortening and lengthening is carried on independently by individual tentacles, its rate depending on their sizes, and states of contraction. We are evidently dealing with a well-developed local action-system, such as frequently characterizes structures with a high degree of autonomy (Pantin, 1952). It was observed in the laboratory that rhythmic movements had the effect of unravelling any tangles which had occurred among the tentacles. This, however, may be no more than an incidental occurrence.

4. The Behaviour of the remaining appendages

The gastrozooids show a considerable amount of activity in some specimens. This consists of random 'searching' movements. On touching a solid object they apply themselves to it, the mouths spreading out over any area up to 1 cm. in diameter. Although Bigelow (1891) stated that attachment to inorganic objects was of brief duration, it was observed in the Canary Islands that gastrozooids sometimes remained attached to the polythene wall of the tank for periods of more than an hour. It is, however, too early to say whether or not the feeding response involves chemical as well as tactile stimuli, as in *Hydra* (Semal, 1954*b*).*

The appearance of a fish enshrouded by feeding gastrozooids is well-known from Wilson's account (*op. cit.*). The edges of the zooid-mouths spread out until they touch and then press up against one

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* It does (see footnote on p. 308).

another forming a seam. Thus the whole fish, or a large part of it, becomes enclosed in an improvised stomach, or extension of the coelenteron. Fish in various stages of digestion were collected and preserved on the Canary expedition. The largest, which was an unidentifiable specimen 9 cm. long, had been caught by a fairly small *Physalia* (gas-gland diameter = 1 cm.). Another specimen collected by the author is the shapeless lump figured by Hardy (1956, page 120). It is not known how much of a fish is usually digested and how much rejected. A partially decomposed fish might serve as bait to lure other fish into the tentacles, but this is a matter for speculation.

No original observations were made on the remaining appendages. According to Brooks (cited by Steche, 1907), the nectophores can perform pumping-movements. The author has observed nectophores in *Forskalia* pulsating while little more than bell-buds. Like immature heart muscle, the subumbrellar muscle of medusae is active long before its activity is required. Steche's suggestion that the nectophores come into their own only when the whole gonodendron is shed is therefore still tenable. The function of the nectophores, according to Steche, would be to keep the detached gonodendron in motion and well-oxygenated. It is certainly hard to see what function they could have while the gonodendra are still attached to the parent colony.

5. CO-ORDINATION

For the most part, the appendages behave independently. The capture of prey by one tentacle does not visibly affect the activities of other tentacles or of the gastrozooids. Although the gastrozooids apply themselves eagerly to any object they encounter, the presence of a fish struggling in the tentacles a few centimetres away causes not the slightest alteration in their random movements. Whether this is still true when some of the gastrozooids have begun to digest the fish, is not known. The rolling behaviour of the float is not affected by the activities of the tentacles or gastrozooids. It continues without interruption during feeding. In fact, *Physalia* usually acts like an assemblage of autonomous individuals. The behaviour of the individuals is linked in terms of functional significance but not in terms of direct nervous integration.

There is, however, one response in which nervous integration can be seen. When an unusually strong stimulus, such as firm pinching with forceps, is applied to the float, a general contraction follows immediately, or so quickly that no time lag is visible to the naked eye. This contraction involves a sudden shortening of all or a proportion of the appendages. Appendages near to and remote from the site of stimulation are affected equally and, as far as can be seen, simultaneously. The stems of the gonodendra also shorten. The contraction is brief, and the appendages soon fall back into their autonomous activities again.

This response has the appearance of a nervous through-conduction reaction. Parker (1932), in his valuable physiological study of the nervous system, overlooked this reaction. He also overlooked the earlier account of Bigelow (1891). In it, Bigelow describes how squeezing the float or applying some strong stimulus to the base of the tentacles may evoke a general contraction of the colony. In natural conditions, it would seem likely that very turbulent surface conditions or abrupt collision with any floating object, such as a clump of Sargasso weed or another *Physalia* would evoke this response. This might be of value in preventing tangling of the tentacles.

The co-ordination observed is of a most elementary type. It is interesting in that it points to the existence of nervous communication between the different members of the organism. A somewhat similar response takes place in *Alcyonium* (Horridge, 1956*b*), where, likewise, the response is apparently protective in nature. In the physonectid siphonophore, *Forskalia*, the author has observed similar violent overall contractions of the siphosome appendages following abrupt stimulation of the stem, a closely comparable situation to that found in *Physalia*. Here, however, a more elaborate form of integration (which has still to be fully analysed) is in evidence. It appears that *Forskalia* can swim forwards or backwards by altering the shape of the mouths of the swimming bells; the shape of the bell mouth in *Forskalia* appears to depend on the degree of contraction in two groups of radial muscle fibres in the velum, an arrangement unique to this group. Phases of activity or inactivity are common to the whole assemblage of swimming bells, but when active the bells beat at different frequencies after the first one or two beats. Certain observations point to the possibility of inhibition as a co-ordinating mechanism in the activities of the swimming-bells (Mackie, cited by Hardy, 1956). The observations in question were, however, made on a few, rather imperfect specimens, at a time when the author was not fully aware of the issues involved, and it would be of great interest to repeat the work.

In the case of certain Calycophora (for example, *Hippopodius*, *Chelophyes*), histological study provides clear evidence that in contrast to the arrangement in *Forskalia*, where two median exumbrellar nerve tracts connect the marginal rings of the bell with the stem, there is in these genera no direct nervous connection between the stem and bells. What is remarkable, however, is that in spite of the histological absence of nerve connectives, observations on living calycophores suggest that some sort of integration does, nevertheless, exist.

The problems of nervous co-ordination in the siphonophores are therefore considerably more complex than study of a simple form like *Physalia* would tend to suggest.

HISTOLOGY

1. INTRODUCTION: THE SIPHONOPHORA COMPARED WITH OTHER HYDROZOA

The main features in the histology of the siphonophores were established by the end of the nineteenth century. Good comparative accounts were given by Chun (1897, 1902) and Schneider (1902), the two workers who contributed most to the actual investigations. There has been little subsequent work of importance.

In their basic microscopic structure, the siphonophores bear a close similarity to other Hydrozoa. However, the tissues are often brought to a higher degree of elaboration and histological perfection than elsewhere in the Class. This is true of the striated muscle in the swimming-bells of certain Calycophora, where Q, J and H bands are clearly distinguishable; of the nervous system in the bells of Physonectae, where exumbrellar tracts are developed; and of the mesogloea in genera such as *Hippopodius*, *Chelophyes* and *Diphyes*, where the exquisite moulding of the swimming bells is achieved by means of an elaborately orientated system of mesogloeal fibrils. One must also mention the complicated mechanism of the nematocyst batteries in such forms as *Praya* sp.n.* (Korotneff, 1884), which is without parallel in the entire Phylum.

In addition to the tissues common to all hydrozoans, the siphonophores (except for the Calycophora) possess gas-secreting tissue, for which the only known counterpart in the Class is the basal disk in *Hydra* (Kepner and Miller, 1928; Kepner and Thomas, 1928). The Calycophora show two tissue regions for which no counterpart is known: the capillary network in the radial canal system of the swimming bells, and the sack-like 'somatocyst', whose cells show a great capacity for changes in volume. The functions of these regions are unknown.

There is one other striking feature in the histology of the siphonophores which should be mentioned. Although the two marginal nerve-rings are present, the swimming bells lack a subumbrellar nerve-plexus. Conduction across the muscle-sheet must therefore be myoid. This and certain other evidence suggest the possibility that, in hydrozoan medusae generally, the swimming beat, though

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* Identified by Totton as *Stephanophyes superba* Chun.

originating in the marginal nerve rings, may be conducted across the muscle-sheet independently of the nervous system, the latter serving simply to negotiate radial responses between the margin and the manubrium. The absence of the subumbrellar plexus in swimming-bells and in such forms as *Eucopella* (Lendenfeld, 1883), may be correlated with the absence of a manubrium. A nerve-plexus has never been found in the velum of a hydrozoan, and here too the muscle must presumably conduct the impulse for its own contraction. Horridge (1955) has found that in *Geryonia* radial responses involving movements of the proboscis can take place at the same time as rhythmic pulsation of the circular swimming muscle, which suggests that one or other of the responses is independent of the nervous system. The histological study of Krasińska (1914) indicates that the nerve-plexus is connected not with the circular muscle but with the radial. Thus, a variety of evidence points to the independent myoid conduction of the rhythmic swimming impulses in certain, if not in all, Hydrozoa. In the Scyphozoan medusae, where two nerve-plexuses are present (Horridge, 1956*a*), the situation is probably different.

Physalia, by virtue of its large size and sturdy construction, is a good object for histological study. All other common siphonophores are extremely delicate, and it is with justice that Bolles Lee (1900) wrote of them: 'This group contains some of the most difficult forms to preserve that are to be found in the whole range of the animal kingdom.' The tendency toward fragmentation is often a severe handicap to the investigator. In *Physalia*, the gonodendra tend to break off when the animal is fixed, but otherwise the parts remain intact.

In the account which follows, reference will be made to the work of previous authors where appropriate, but it may be stated at this point that the basic work on *Physalia* is Chun's section in Bronn's *Thier-Reich* (Chun, 1897, 1902). The present account is, in the main, supplementary to it.

2. HISTOLOGICAL TECHNIQUES

Specimens of *Physalia* quickly deteriorate in the laboratory, unless the water in which they are kept is well oxygenated. Only freshly caught specimens were used in this investigation.

Pieces of tissue were removed, washed briefly in distilled water, and placed in one or other of the following fixatives: Flemming's fluid without acetic acid ('F.W.A.'), Baker's formaldehyde-calcium (Ca-formaldehyde), both made isotonic with the seawater (Pantin, 1948); Zenker's and Helly's Fluids (Baker, 1950); Bouin's and Carnoy's Fluids (Pantin, *op. cit.*), formaldehyde-sublimate-seawater, being a mixture of ten parts formaldehyde with ninety parts saturated mercuric chloride in seawater.

If the float was to be fixed, the fixing-fluid was injected directly into the coelenteron between the codon and saccus, the whole float being immersed in the fixative at the same time. The intact float can be fixed with virtually no shrinkage or distortion by this method, so long as the air inside is not allowed to escape. When injecting the fixative care is therefore needed to avoid puncturing the saccus. The fixative was injected with a hypodermic syringe, or in the case of fixatives containing mercuric chloride, with a fine glass pipette.

Wherever possible, whole strips of material were examined. Paraffin sections are hard to make, more subject to distortion and altogether less revealing than thin strips of intact epithelium. In certain cases, as in the study of the nervous system, sections were found to be almost useless. The strips were prepared from fixed material under a binocular dissecting microscope, the tissue being lightly stained beforehand in some dye, such as gentian violet, which could be washed out afterwards in alcohol. The special staining techniques will be referred to where particular tissues are described. Unless otherwise stated, Heidenhain's iron haematoxylin (Pantin, 1948) was used. This method was found to be most generally useful, giving incomparably the best results with Flemming material, as other students of the Coelenterata have found.

Stained preparations were mounted in Canada balsam or in some other alcohol- or xylene-miscible medium. As a check on the amount of shrinkage caused by dehydration and clearing, control strips or gelatin sections were mounted in an aqueous medium (usually Farrant's) where shrinkage is negligible. Measurements of cellular and epithelial dimensions were made on preparations which had never been subjected to alcohol higher than 70%.

3. THE MUSCULAR SYSTEM

In the tentacles, gastrozooids, palpons and float of *Physalia*, both ectodermal and endodermal muscle fibres are present. As in *Hydra*, the endodermal fibres run in a circular direction, the ectodermal in a longitudinal.

In the tentacles and codon, the ectodermal muscle is very strongly developed. The ridges of mesogloea which support the muscle fibres are thrown into deep folds, particularly when the organism as a whole is contracted. There appear to be no radially orientated muscle fibres in any region. The endodermal system is less well-developed than the ectodermal, except in the codon. There is no endodermal muscle in the medusoid members, and the ectodermal system is only properly developed in the asexual nectophores. The subumbrellar muscle of these members has been examined in several specimens, but no striations are visible. This probably indicates that the medusoids examined, though the most advanced specimens obtainable from attached gonodendra, were not yet mature when fixed.

The musculature of the float has been studied in greater detail than that of other regions because it is technically easier to prepare. However, muscle throughout the animal shows the same histological characteristics.

A longitudinal section through a young *Physalia* is given by Okada (fig. 156D in Hyman, 1940). The inner chamber of the float (the saccus) develops as an invagination, the region of invagination becoming almost occluded in later life; the only trace of it is the apical pore. Okada's section does not go directly through the apical pore but slightly to one side of it, so that the opening from the inside of the saccus to the exterior is not shown. In actual fact, the tissues never grow together in this region, and the pore is not obliterated. It is sometimes possible to squeeze out a bubble of air, but only by vigorous pressure. Normally the pore is tightly constricted and it is unlikely that in natural conditions any leakage of air takes place. There is no other opening out of the float chamber, such as occurs in forms like *Physophora* (Leloup, 1941).

The saccus, being an invagination of the codon, has the same tissue layers as the latter, but they are 'inside out'. The ectoderm of the saccus is the innermost layer of the float. Like the ectoderm of the codon, it secretes a chitinous cuticle, but this has the special title of 'pneumatocyst'. It was first described by Schneider (1898).

The cross-section through the float-wall given by Chun (1902, fig. 79) correctly shows the relative thicknesses of the codon and saccus, and their general structure. The figure omits certain features, the chief of which are: the cuticle, the pneumatocyst, the nerve-plexus in the codon-ectoderm, the muscle fibres of the codon-endoderm and of the saccus-ectoderm. These omissions have been corrected in Text-fig. 3 accompanying this text. The ectodermal fibres run along the length of the float, parallel to the crest. The endodermal fibres run round the float, in a circular direction. Thus in Text-fig. 3, which represents a section at right angles to the longitudinal axis, only the cut ends of the ectodermal fibres (*m.ec*) are shown, while the endodermal fibres (*m.en*) appear in side view. The septa which divide up the roof of the codon into pockets (Text-fig. 2) are folds of endodermal tissue and mesogloea drawn out from the body-wall. The inflatable processes of the saccus, described on page 373, fit into these pockets. As the animal grows, a regular subdivision of the pockets proceeds, new septa appearing between those already formed.

Throughout the animal, the muscle tissue shows uniformity in its fine structure, although there are marked regional differences in fibre density, and in the degree of flattening of the layers. The flattened regions are particularly easy to examine in whole-strip preparations.

For showing the nuclei and cell membranes as well as the muscle fibres, iron haematoxylin is to be recommended; to stain the nuclei against a clear background, thionin and toluidin blue are suitable; and for staining the fibres, leaving the interfibrillar substance and cell membranes clear, Newton's crystal violet gives good results. The latter stain is often used for chromosomes, but in coelenterate material, where muscle fibres are ubiquitously present, it is not to be recommended. Thionin gives sharp and precise chromosome staining in F.W.A. and Zenker material. Chromosomes can also be studied 'in negative', that is they show up as light bodies against a darkly staining nuclear sap in silver preparations of Ca-formaldehyde material.

The float musculature consists of simple undifferentiated sheets, one cell thick. There are no special muscle groups. The fibres run parallel to one another in either a longitudinal or a circular direction, except at certain angles where the muscle sheet is 'tailored' into a triangular pattern, similar to that described and figured for the subumbrellar muscle sheet of *Forskalia* swimming-bells (Schaeppi, 1898, p. 536). In the region of the gas-gland the saccus-ectoderm is almost devoid of muscle fibres.

In cross-section the muscle layer can be seen to consist of a cell body layer containing the nuclei and a fibre layer in contact with the mesogloea (Text-fig. 3). The cell boundaries are not usually visible in sections, and are omitted from the figure. Seen in surface view (in strip-preparations) the cellular outlines can be made out (Pl. XXVI, fig. 4). The cells are usually five- or six-sided, the nucleus (or nuclei) lying towards the centre. Binucleate cells occur in all four muscle sheets of the float, but without regularity. Polyploid cells also occur, and there is reason to believe that they arise from binucleate cells by metaphase combination of the chromosomes, as in certain mammalian tissues such as the liver (Beams and King, 1942). The data obtained on polyploidy and the cytology of *Physalia* in general will be presented in more detail elsewhere. The cells shown in Pl. XXVI, fig. 4, with the exception of a probable tetraploid on the extreme right, are diploids.

The chromosome number most commonly encountered in diploid float-cells is twenty (Pl. XXVII, fig. 1). There are no constrictions visible along the length of the chromosomes which would correspond to centromeres or to nucleolar organizer regions. The chromosomes are simple rods, three pairs of which are particularly long ($4{\cdot}5\,\mu$ in a typical late prophase), the remaining seven pairs grading down in length (from $3{\cdot}0\,\mu$ to about $1{\cdot}8\,\mu$ in such a case). Because of the flattening of the layer in which they lie, the chromosomes of the saccus epithelia are spread out in prophase, as if they had been treated by a squash-technique. If the prophase chromosomes lie on their flat sides, that is with both chromatids in the plane of the muscle sheet, they show little lateral curvature. If, however, they lie on their narrow edges, vertical to the plane of flattening, they are usually bent. Examples of both these conditions are shown. None of the chromosomes is intrinsically V-shaped, although all are susceptible to distortion in the flattened epithelia.

The nuclei contain a variable number of nucleoli, as can be seen in Pl. XXVI, fig. 4, but if there are many of them, the individual nucleoli are small. Planimeter estimations, using camera lucida tracings of 112 nuclei and their nucleoli, have been carried out, and it has been found that whatever the ploidy of a cell (which may be up to $32n$), the total of the surface areas of the nucleoli is between 1/12 and 1/19 the surface area of the nucleus in which they occur. The tissue used was the saccus-endoderm, which is fairly evenly flattened over wide areas. A similar finding is reported for *Rana* by Beatty (1949).

The nuclei in the more flattened regions, particularly in the saccus-ectoderm which may be less than $2\,\mu$ thick, are often so compressed within the narrow confines of the layer that they assume very irregular shapes, frequently becoming elongated in the grooves between the muscle fibres. Under these conditions fragmentation appears to take place. Pieces of nuclear matter become lodged on either side of a muscle ridge and, though sometimes remaining connected by tenuous tubes of nuclear membrane, they frequently separate completely. This phenomenon is to be regarded as a cytological accident rather than as a regular, significant process that could be dignified by the title 'amitosis'. Chromosomes lodge in the troughs between muscle-fibres and fail to reach the spindle at metaphase; the daughters of such divisions are therefore deficient. Chromosomes break transversely but, in some cases at least, the fragments take their place on the spindle and divide normally. This is interesting as it suggests that the spindle attachment is not a single, localized one, but is of the diffuse or polycentric type. There is evidence too that the nucleoli, like the nuclei, can be squeezed out and caused to divide if subjected to exceptional mechanical stress.

The occurrence of mitosis in the nuclear layer has no visible effect on the underlying fibre layer of the epithelium. This is also the case in the *Hydra* ectoderm, although in the endoderm the fibres are said to be absorbed during mitosis and resecreted following its completion (McConnell, 1932). Electron-microscope studies by Hess, Cohen and Robson (1957) show that in *Hydra* (both in the ectoderm and endoderm) the muscle fibres are contained within basal outgrowths of the epithelial cells and that the fibres do not fuse with one another, although they may come into close proximity. There is no evidence therefore in *Hydra* for true anastomosis in the fibre sheet; and the fact that fibres are not affected by the mitosis of their nuclei cannot serve as a demonstration of any breakdown in the simple cell-fibre relationship.

In *Physalia* the fibres form what at first sight appears to be an anastomosing network. Individual fibres can be traced for distances of over 300 μ without interconnections. Few fibres end freely; they may vary in thickness, becoming thin and inconspicuous, but usually they can be traced back into the 'net' again. Where two fibres come together, the *appearance* is one of direct fusion (Pl. XXVI, fig. 5). In actual fact true anastomosis (that is, direct confluence of fibre material) may never occur. Instances have been found where what appears to be a single fibre in the net has become bent or buckled at some point, revealing itself as two closely applied fibres (Pl. XXVI, fig. 6). The 'anastomosing net' may be no more than an array of discrete but closely juxtaposed fibres, as in *Hydra*.

Although in many preparations the nuclear layer appears syncytial, staining with iron haematoxylin invariably shows up the cellular boundaries. A typical cell of the saccus-endoderm may have ten or fifteen fibres running under it, some of which can be followed beneath six or eight other cells. Attempts to relate particular fibres to particular cells have not been successful, even in regions where the fibres are strongly contracted (Pl. XXVI, fig. 7). Although we cannot at this stage determine in any case which fibres 'belong' to particular cells, we have no definite grounds for abandoning the classical view of the muscle sheet as divisible into territories referable to individual cells.

4. THE NERVOUS SYSTEM

Chun (1882) was the first to identify nerves in *Physalia*, in the ectoderm of the gastrozooids. In the related *Rhizophysa*, but not in *Physalia* itself, Chun discovered nerves in the float. With the exception of Parker (1932) whose studies revealed that conduction in the tentacles is neuromuscular, not simply muscular, no other workers on *Physalia* refer to the nervous system. Nerves have never been identified histologically in the tentacles.

An attempt to stain the nerves in *Physalia* was made in the present investigation. It is possible to make out the general distribution of the nerves in lightly stained carmalum and haemalum preparations, and Sudan-black staining of Ca-formaldehyde material sometimes colours the fibres fairly well. However, the author's main efforts have been directed towards making silver preparations, since these, when successful, are much the most revealing. Holmes's method (1947), which has been used successfully on a variety of coelenterate material, was used to stain paraffin sections and whole strips of tissue taken from *Physalia*. Results have been only partially successful. In many preparations, the nerves show up quite well, but there is generally too much background staining (particularly in the region of the muscle-mesogloea interface) for the nerves to stand out in fine detail. This fault could probably be rectified by further trial and error adjustment of the staining schedule. In paraffin sections, nerves have not been positively identified, partly because the formaldehyde-sublimate fixative recommended for the sharpest nerve staining is rough in its action on the tissue generally, and partly because the imbedding technique further distorts the tissue relationships, where much muscle and collagenous mesogloea are present. Nerves have been found only in the strip preparations.

Chun's finding of nerves in the ectoderm of gastrozooids has been confirmed. A continuous ectodermal plexus extends throughout gastrozooids, codon, palpons and gonophores. In Pl. XXVII, fig. 2, a portion of the nerve-plexus from the codon-ectoderm is shown. A tripolar neuron (centre) and a bipolar (lower right) can be seen. The dark bands crossing the field from top to bottom are the longitudinal muscle-ridges of the ectoderm. In the codon-ectoderm there were estimated to be about 140 nerve-cells per sq. mm. In the gastrozooids, there appear to be about half this number. Tripolar neurons predominate; out of fifty studied in a particular area, thirty-two were probably tripolar, the remainder being bipolar. A few multipolar cells (4- and 5-polar) were also seen.

Bi-nucleate neurons also occur sparsely in the float. This is not a unique finding; Hertwig and Hertwig (1878*a*) found bi-nucleate neurons in *Cunina*. Nervous tissue in coelenterates is evidently post-mitotic in the main but, where bi-nucleate neurons occur, it may be that mitosis has taken place in the nucleus of a young neuron after differentiation has proceeded too far for the cytoplasm also to divide.

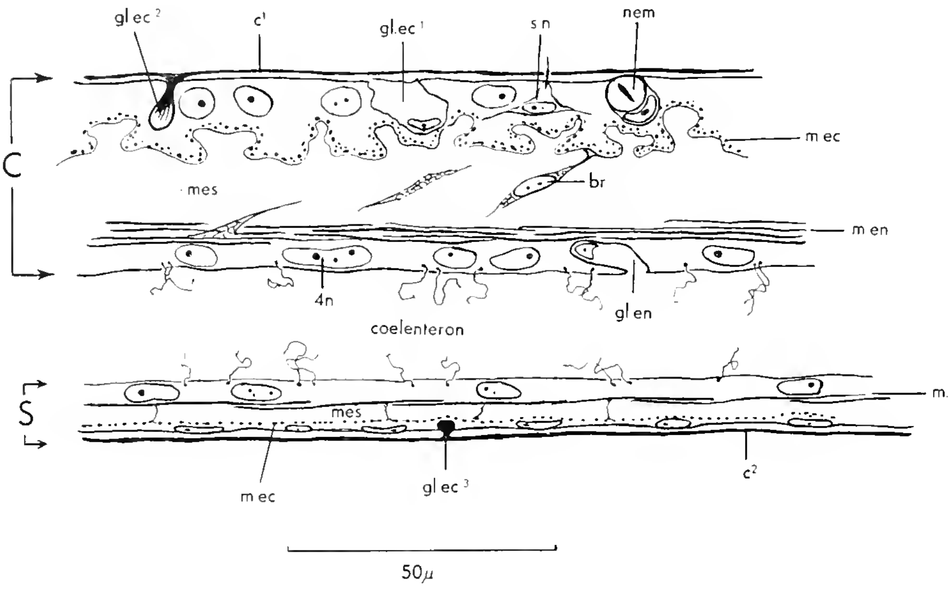
The exact character of the inter-neural associations has not been determined. It is often difficult to decide where a fibre from one nerve ends and another begins, but the preparations are not stained sufficiently precisely for accurate observations on the fine structure to be possible. Fibres have been found to run for distances of up to 100 μ without branching or associating with processes from other nerves.

In no region examined was there any hint of an elaboration of the plexus into orientated tracts. Pieces of tissue were examined from several regions of the float, and it is unlikely that tracts, such as those which occur in the stem-bladder of *Physophora* (Korotneff, 1884, Taf. 15, fig. 26) would have escaped observation. The plexus is distributed evenly in all regions examined.

In some of the preparations, sense-hairs (in groups of two or more) can be seen emerging from the surface of the ectoderm (Text-fig. 3). In most such cases, a nerve-cell (*s.n*) can be found in the region underlying these sense-hairs. In a few cases a conical projection of the nerve-cell can be seen passing up to the superficial region, the sense-hairs being embedded in it. Around the roots of the sense-hairs, the cytoplasm of the conical projections shows a dense aggregation of very fine granules. Thus, although the evidence is incomplete, it is probably true to say that the sense-hairs belong to the nerve-cells, not to the surrounding muscle-cells, and that the majority of the nerve-cells possess sense-hairs. Where one or other component is apparently absent, this can usually be attributed to vagaries in the staining technique. It was found that some gastrozooids fixed in Ca-formaldehyde showed the sense-hairs and their relationships with the nerve-cells quite clearly, when Peter's glycine developer (Peters, 1955) was used. It is not quite clear whether the sense-hairs penetrate the cuticle, but it would seem reasonable to suppose that they do.

Attempts to demonstrate nerves in the tentacles have so far been unsuccessful. It is highly probable that nerves do exist here, particularly in view of Parker's physiological findings (Parker, 1932). The exceptionally muscular nature of the tentacles makes them very difficult to examine histologically.

Thin strips of ectoderm are hard to obtain because of the deep folding of the layer. It would be of great interest to obtain histological data about the nerves in these regions, because Parker's finding of a high conduction rate (120 cm./sec. at 26° C.) makes it probable that the neurons would show a longitudinal orientation as they do in the mesenteries of *Calliactis* (Pantin, 1952).



Text-fig. 3. Transverse section through adjacent portions of the codon (*C*) and saccus (*S*). *br* = bridge cell, c^1 = cuticle of codon, c^2 = pneumatocyst, *gl.ec*^{1} = ectodermal gland cell, *gl.ec*^{2} = root-like cuticular body believed to represent site of extinct gland cell, *gl.ec*^{3} = similar body attaching pneumatocyst, *gl.en* = endodermal gland cell opening into the coelenteron, *mes* = mesogloea, *m.ec*, *m.en* = muscle fibres of ectoderm and endoderm respectively, *nem* = nematocyst, 4*n* = tetraploid nucleus, *s.n* = nerve-cell with sense hair.

An examination of the sexual medusoids (gonophores) from formol-fixed 'Discovery' material revealed the presence of nerves in the ectoderm of both ex- and subumbrellar surfaces. These nerves have been overlooked by previous workers using the sectioning technique (for example Steche, 1907). In the present investigation, they were studied in strips of tissue peeled off from the mesogloea, and stained in Hansen's trioxyhaematein. The nerve-cells are distributed sparsely but evenly. A point of interest is that there is no differentiation of the plexus into marginal nerve-rings. In medusae and swimming-bells where rhythmic pulsations take place, two marginal nerve-rings, one subumbrellar and one exumbrellar, are found in the ectoderm at the base of the velum. In *Physalia* the development of the gonophore is halted in the stage known as 'eumedusoid' (Hyman, 1940); the gonophore probably has no capacity for movement, judging from the almost complete absence of muscle fibres from the subumbrellar. One assumes that the ancestor of *Physalia* had free-swimming gonophores and that the captive, reduced condition is a secondary one. But it is not easy to say whether the diffuse, undifferentiated arrangement of the nervous system is degenerate, or whether it represents the ancestral pattern, or only a stage in the development from the ancestral pattern. At all events, it represents a *hypothetical* ancestral condition, from which the nervous systems of all hydrozoan medusae and medusoids can be held to derive. The chief specialization of the original diffuse plexus has, of course, been the development of the marginal rings, but evolution has led also to the complete loss of the plexus from certain regions (for example, the subumbrella of swimming-bells) and its elaboration into exumbrellar tracts (for example, in the swimming-bells of certain Physonectae). It may one day become possible to give a complete and coherent explanation for these developments, in terms both of form and function.

The arrangement of the nervous system in the asexual medusoids (nectophores) of *Physalia* has not been ascertained. The epithelia are hard to peel off for examination as strip preparations. No well-fixed examples of larger medusoids were available for study, and sections of specimens fixed in museum formalin have revealed nothing definite.

Certain regions of *Physalia* show no trace of nervous tissue. Intensive studies have been made, prompted by a feeling that nerves 'ought' to be present throughout the animal, but the only result has been to fortify the author's opinion that they are frequently absent. One of these regions is the saccus-ectoderm, a tissue extending over an area of several square inches in medium-sized specimens. As noted earlier, it appears to be inert, and incapable of active movements. It is so thin that nerves, if present, would stand out clearly. Indeed, if nerves were present, this would be an ideal situation in which to study their fine structure. In the codon-ectoderm, which is much thicker, and consequently more difficult to treat, nerves can nevertheless be identified by a variety of staining methods. Thus their absence from the saccus is all the more striking. It is possible to imagine a situation where very long, fine nerve processes, sparsely distributed, proceed across the saccus from cell-bodies located in the codon, but the improbability of such an arrangement will be apparent to anyone familiar with the histology of the coelenterates.

Nerves have not been found in the endoderm of any part of *Physalia.* It is possible, but not likely, that they could have escaped observation in the gastrozooids, palpons and tentacles, for these regions (particularly the last) are hard to examine by the strip technique. But in the endoderm of the codon and saccus, where conditions for observing nerves would be nearly ideal, their absence can be vouched for. It is worth noting that only rarely have students of the Hydrozoa found clear evidence for the existence of endodermal nerves. They seem to be present in *Hydra* (Semal, 1952*b* and earlier workers), but this is something of an exception.

5. THE MESOGLOEA

The mesogloea in most regions of *Physalia* functions as a *Stützlamelle*, that is, as a support for the muscle fibres. When the fibres contract the mesogloea falls into folds; when they lengthen the folds are smoothed out (though they may not completely disappear). The mesogloea is noticeably thickest where the musculature is most powerful (that is, in the tentacles and codon), and in such regions permanent folds develop. It was at one time held that this folding of the mesogloea in coelenterates was simply and solely the result of muscle activity in regions of high fibre density but Krasińska (1914) argues convincingly against this view.

In the float, tentacles, and gastrozooids, and in the stems of the gonodendra, strands of cytoplasm stretch across the mesogloea from endoderm to ectoderm. In the codon and tentacles (where the mesogloea is thick) these cytoplasmic bridges are often nucleated, and consist of complete cells (bridge cells). Some are shown in Text-fig. 3 (*br*) and Pl. XXVII, fig. 4. In older specimens the bridges are thick, and contain several nuclei. Cell boundaries are hard to distinguish here, and the bridges often look syncytial; polyploid cells are common in them. The cytoplasmic bridges crossing the mesogloea elsewhere are not nucleated.

The bridges probably originate from the endoderm. Their exact limits are hard to define, as they emerge from among a mass of muscle fibres on one side of the mesogloea and disappear into another mass of muscle fibres on the other. Of all structures tending to obscure cellular relationships, muscle is the chief offender. A sufficient number of cases has been observed, however, where cytoplasmic bridges seem to arise directly from the endoderm, for the arrangement to be depicted as in Text-fig. 3. Chun (1902) was also of the opinion that the bridges were endodermal.

The bridges are often drawn out into long, thin strands crossing the mesogloea at very acute angles (down to 10°). The oblique orientation of the bridges is constant over wide areas, and may, in part, represent tensions in the mesogloea set up by contraction in the two muscle sheets.

In the tentacles and codon (and possibly elsewhere), the endodermal bridges have little blind projections which pierce the mesogloea on either side. In the tentacles these projections form a cluster around each bridge-cell where it leaves the endoderm. In the codon the projections occur along the whole length of the bridge-cell. It is not known whether these outgrowths have pseudopodial properties, but they look like pseudopodia. As to their function, that is a matter for speculation. No amoebocytes have been observed and the bridge-cells may fulfil the function of transporting nutritive substances across the mesogloea; their outgrowths could serve to distribute the substances to the mesogloea. On the other hand they might serve to collect metabolic waste, like the outgrowths from the flame-cells which penetrate the parenchyma of planarians. It is not intended to suggest that the bridge-cells are homologous with flame-cells; on the contrary, the presence of 'pseudopodial' outgrowths may indicate that they represent amoebocytes which have become fixed in permanent positions.

Large pieces of mesogloea, freed from muscle-fibres, can be prepared from the codon and saccus by careful dissection. The tissue is first briefly immersed in gentian violet; then it is placed in a petri-dish of distilled water under a low-power binocular microscope and the muscle fibres are stripped away with watch-maker's forceps. The sheet of mesogloea (pure, except for the bridge-cells) is then washed in 70% alcohol to remove the stain. It can be restained in any way desired. In the present investigation, iron haematoxylin was found to show up the fine structure well, if differentiation was not carried too far.

Study of stained sheets of mesogloea, both by teasing in glycerine and by examination intact at high magnifications, reveals that the mesogloea has a laminated structure. The laminae are broad, flat sheets which cross one another at a variety of oblique angles, without any apparent regularity in orientation. The mesogloeal substance is finely fibrillated. This, and the laminated structure, can be seen in Pl. XXVII, fig. 3. The laminae do not appear to be regularly interwoven. In *Calliactis* and other actinians, on the other hand, the mesogloea has a lattice-like structure of 'undulating sheets' as in a woven fabric (Chapman, 1953), and the warp-and-weft arrangement is regular in character, with a definite orientation in particular regions. It is thus more highly organized than the mesogloea of the float in *Physalia*.

The periodic acid-Schiff technique has been applied to sections of *Physalia* material. The mesogloea in all regions gives a strong positive reaction (indicating abundant polysaccharide), particularly near the muscle interface. This can be seen in the transverse section of a palpon (Pl. XXVII, fig. 6), where the mesogloea forming the central core of the villus has a definite, dark outer ring. X-ray diffraction analysis of strips of mesogloea (prepared by the method described above) was carried out by Dr K. M. Rudall. Collagen, as recognized by its wide-angle diffraction pattern was found in abundance in the thick mesogloea of the codon. It was also found, but less abundantly in the mesogloea of the saccus. For a survey of the distribution of collagen and chitin in coelenterates, Rudall (1955) should be consulted.

The mesogloea in the nectophores and jelly-polyps ('Gallertpolypoide') is of the gelatinous, distended type characteristic of medusae and medusoid members. Such mesogloea seems to serve primarily for buoyancy (Jacobs, 1937). In many medusae it is fortified by a system of orientated fibrils (Alvarado, 1932) and this is true of the swimming-bells in siphonophores such as *Hippopodius* (Mackie, unpublished). However, the nectophores and jelly-polypoids of *Physalia* have not been investigated from this point of view. The functional significance of the jelly-polypoids remains problematical. One is at a loss to know whether they serve for flotation or food storage or whether indeed they have a function at all, or are merely vestigial.

The cuticle and pneumatocyst

The pneumatocyst is the lining of the saccus cavity. It can be regarded as an internal cuticle, for it is secreted by invaginated ectoderm and remains continuous with the rest of the cuticle via the apical pore, which is the site of invagination. It is a regular feature of the float in Cystonectae and Physonectae. Usually, as in *Physophora* (Leloup, 1941), it is a thick conspicuous structure, evidently having a skeletal function, whereas the external cuticle is either absent or so thin that it escapes observation. In *Physalia* the pneumatocyst (first described by Schneider, 1898) is a transparent membrane about $\frac{1}{4}\mu$ thick in a young specimen. The external cuticle is probably much thinner.

It seems possible to distinguish two clear types of cuticle in the Hydrozoa. The first type of cuticle, found in *Hydra fusca* (Schulze, 1871) and *Cunina* (Hertwig and Hertwig, 1878*b*) is apparently not secreted by specialized gland-cells. It is a very thin membrane attached to the ectoderm by means of numerous small bulbous protuberances, many of which are found embedded in each ectodermal cell. Such a cuticle is probably secreted by the whole ectoderm. In the second type, seen in *Eucopella* (Lendenfeld, 1883), the cuticle is secreted by specialized gland cells distributed throughout the ectoderm. This type of cuticle is often very thick and may be laid down in layers as the perisarc or theca. The cuticle of *Physalia* is here considered to belong to the second type, for the evidence strongly suggests that it is associated with special gland-cells.

In dealing with cuticles of the second type, particularly where a perisarc is formed, it should be noted that the concepts of the production of the perisarcal substance as a viscous secretion from ectodermal gland cells containing refringent inclusions, its subsequent hardening, and its reabsorption in budding regions are at least seventy years old, inherent in the writings of Weismann, von Lendenfeld and other workers of that period. Berrill (1949), in his studies on *Obelia*, appears to have arrived more or less independently at the same conclusions. The term 'polymerization' is now used to describe the process of hardening in the cuticular substance (Hammett, 1943).

Weismann's work has been criticized by Berrill (1949, p. 235) on the grounds that his illustrations, though beautiful and accurate 'were interpreted in an extremely static manner remote from any concept of a living organism'. This may be true to some extent of the particular publication that Berrill refers to, but in justice to Weismann we should note that he also provided us with a detailed account (Weismann, 1881) of active processes in living hydroids somewhat along the lines of Berrill's own studies. Again, in the particular case where Berrill (p. 245) finds it necessary to interpret 'at face value' some illustrations which seem to show that the perisarc can be laid down and dissolved 'under certain more or less obscure conditions', it would be more appropriate to consult Weismann's account of the process in *Plumularia* (Weismann, 1880).

The distribution of the cuticle in *Physalia* has been investigated by teasing fixed material under the dissecting microscope. The earlier workers, for instance, Schulze (1871), used maceration techniques on fresh material. After fixation in Bouin, the cuticle can be lifted or scraped away with fine needles and its distribution can thus be determined. By means of this technique the cuticle has been found to extend over the float, gastrozooids, tentacles, ampullae, palpons and gonodendra. It has not been found in the gonophores, nectophores or in the jelly-polyps, but in these regions, a very thin cuticle might escape detection by the method used. For studying the fine structure of the cuticle, it was found that certain silver preparations served the purpose. These preparations were some of the numerous 'failures' from attempts to stain the nervous system, and the exact conditions under which the cuticle becomes impregnated have not been worked out. No other methods proved to be of any use; the cuticle is normally transparent, and shows no particular affinity for acidic or basic coal-tar dyes, carmine or haematoxylin. No greenish coloration was produced by treatment with chlorazolblack such as occurs in the arthropod cuticle; however, the value of the latter stain in the histochemical identification of chitin is doubtful.

The main value of the silver preparations has been to show how the cuticle is attached to the underlying epithelium. In certain of the silver preparations of whole strips of codon-ectoderm, the cuticle shows up well as a dark sheet of granular material, split in places and flaking away, revealing the ectoderm underneath. Around the edges where the cuticle is damaged, one can see dark strands of cuticular substance passing down into the ectoderm. In places where the cuticle has disintegrated more completely, these strands are often all that remains of the cuticle. They are funnel-like structures, rooted in the epithelium by means of a basal swelling. They may run almost perpendicularly from the cuticle proper down into the ectoderm, but more often they run obliquely. In such cases, they can be seen to good advantage in surface view, that is to say in the strip-preparations. Pl. XXVII, fig. 5 shows two of these funnel-like cuticular tubes running down into the ectoderm, where their swollen basal parts are rooted. The details of the ectoderm cells are not shown in this photograph, as the silver has precipitated heavily and coarsely over the whole exposed surface. The basal swellings are light in colour, and appear to be hollow. Sometimes the stalk or funnel region is also hollow in appearance.

These structures appear to consist of solidified streams of cuticular substance running from extinct gland cells (represented in outline by the swollen bases) up into the cuticular sheet. This was also von Lendenfeld's interpretation of a closely similar histological picture in *Eucopella* (Lendenfeld, 1883). Apart from these structures, no connections between the cuticle and ectoderm have been found.

In the case of the pneumatocyst, or cuticle of the saccus, the means of attachment to the ectoderm again appears to consist solely of swollen portions of the cuticle embedded in the ectoderm, and again it is probably fair to say that these represent the sites of extinct gland-cells. The globular thickenings are black in unstained preparations, and can be seen without difficulty. They proceed directly from the underside of the cuticular sheet, and there is no stem or funnel region as in the codon. The only part of the saccus not lined by the pneumatocyst is the gas-gland. This becomes explicable if it is assumed that the pneumatocyst has the properties of an insulator against gaseous diffusion; in the main part of the saccus its function would be to prevent loss of gases by diffusion, but in the region of the gas-gland, where gases enter the float-chamber, its absence is a functional necessity. Certain other findings support the view that the pneumatocyst may function as an insulator (see page 389).

The chemical composition of the cuticle or pneumatocyst in the Siphonophora has never been satisfactorily determined. In *Velella*, which is not a true siphonophore (see Totton, 1954), it is clear that the substance lining the concentric float-chambers is chitin (Leuckart, 1852; Henze, 1908; Rudall, 1955), but apart from some unsatisfactory early work by Leuckart on *Physalia*, nothing has been done on the siphonophores. We know from an earlier paper (1851) that Leuckart thought the saccus to be a homogeneous, 'structureless' substance, like the chitinous skeleton of *Velella*, whereas, in fact, it is living tissue, composed of ectoderm, endoderm and mesogloea, with only a thin membrane of what might be and, as we shall see, actually is chitin. Thus when Leuckart (1852) reported that the saccus consisted of chitin, we cannot place much value on his finding. Nearly all the saccus dissolves in caustic potash, as he would surely have noticed if, as he claimed, he used this reagent.

In the present investigation a modification of Campbell's chitosan method (Richards, 1951) was employed to test for the presence of chitin in the pneumatocyst. A whole saccus was used in one test, and the dissected pneumatocyst in another.

The tests gave a positive result. It was necessary to shorten the period in caustic alkali to 2 min., as after this the membrane tended to disintegrate (but not to dissolve) at 160° C. This curtailed treatment has a precedent in Richards's method for butterfly wing scales, which are also thin and fragile. In the test where a whole saccus was used, all the tissue dissolved, except for the pneumatocyst. Subsequent treatment with iodine and then with sulphuric acid gave results consistent with the other evidence that the material is chitinous.

A further investigation of the chemical nature of the cuticular material of the float has been carried out by Dr K. M. Rudall, using the X-ray diffraction technique. A characteristic chitin pattern was obtained. The pattern could not be defined as typically α- or typically β-chitin. In addition to the chitin, another substance soluble in benzene was found to be present; it is probably lipid in nature. No other coelenterate cuticle has yet been shown to contain lipid material. No trace of it was found in *Velella* by Rudall (1955) using the X-ray diffraction technique.

It is too early to say much on the significance of the lipid-like material, but if we are looking for some substance which would provide the cuticle with a capacity to resist diffusion (chitin alone being useless from this point of view) then a lipid would certainly meet our needs. In *Velella*, where the stigmata, float-chambers and tracheae are believed to serve as a route for gaseous exchange (Chun, 1888), diffusion taking place directly through the walls of the tracheae, it would be surprising indeed to find lipids associated with the chitin, for what is needed here is permeability to gases rather than impermeability. Thus the presence of the lipid in the one case and its absence in the other accords well with the presumed functional requirements.

With regard to the secretion of the cuticular substances, the evidence is very circumstantial and incomplete. Gland-cells occur in the ectoderm, and their distribution corresponds to a large extent with the distribution of the cuticle. The gland-cells show many features in common with gland-cells which, in other hydrozoans, are believed to secrete the cuticle (see, for instance, Berrill on *Obelia*). However, it is a regrettable fact that none of the author's preparations simultaneously show both distinct and recognizable gland-cells and an intact, unmistakable cuticle. The bulbous swellings at the bases of the cuticular funnels (Pl. XXVII, fig. 5) probably represent the sites of gland-cells, and the tattered fragments of material overlying the ectodermal gland-cells in sections of a palpon (Pl. XXVII, fig. 6) probably represent the cuticle, but in neither case are the relationships well-enough shown to be regarded as conclusive. The gland-cells *might* have another function, or only a proportion of them might be concerned in cuticle secretion, or some might secrete chitin and others lipid. We do not yet know. A thorough cytological and cytochemical examination is needed.

Ectodermal gland-cells occur in the codon, tentacles, ampullae, gastrozooids, palpons (where they are very abundant) and stems of the gonodendra. Steche (1907), referred to similar gland-cells in the palpons of *Rhizophysa*, and figured one (Taf. XI, fig. 4). He stated that they are also present in *Physalia* but did not say where; they do not appear in his drawings of the medusoids of *Physalia*, but this is in accord with the present finding that gland-cells are absent from these members, and from the jelly-polyps. The cuticle is also absent from these regions, as far as we can tell.

The absence of gland-cells from the ectoderm of the saccus is puzzling, when it is considered that the cuticle here (pneumatocyst) is fairly thick. The author's tentative explanation is that like the cuticle elsewhere in the animal, the pneumatocyst is secreted by gland-cells, but that secretion stops at a fairly early stage; the sites of the extinct gland cells would be shown by the knob-like thickenings referred to above. Possibly, by virtue of its completely protected situation inside the air bladder, the pneumtocyst is not subject to erosion or damage, and a continuous supply of the material is not needed; the exposed parts of the cuticle on the other hand, would need replenishment from time to time. If this is true, the pneumatocyst would keep pace with growth of the float not by uptake of new material but by stretching to cover a wider area.

Although a detailed study of the gland-cells and their secretion (or secretions) has not been undertaken, certain information is nevertheless available. The gland-cells give a strong P.A.S. reaction

(Pl. XXVII, fig. 6). The reaction appears to take place both in the granules and in the matter interspersed among them. The secretion generally shows considerable tenacity towards haematoxylin, as noted by Berrill (1949) in the case of similar cells in *Obelia*. There appears to be little if any metachromasia with toluidin blue. In some gelatin sections of Ca-formaldehyde material a diffuse background coloration was obtained with Sudan black. This is of interest in view of the finding that a lipid-like material occurs in the cuticle.

The gland-cells present a fairly uniform appearance throughout the animal and it has not been possible to distinguish more than one type of cell. It is of interest in this connection to note the discovery by Mettey and Hamon (1949) of two types of gland-cell in the ectoderm of *Abylopsis tetragona* (Calycophora). No hint is given of their functional significance, but one of them ('cellule à substance hyaline') has histological features in common with the gland-cells in *Physalia*. In *Physalia*, if secretion of substances other than those of the cuticle were involved, mucus would merit consideration. Specimens kept in captivity sometimes produce a glutinous substance, but this seems to come from the endodermal gland-cells of the gastrozooids.

Not only in the Siphonophora, but in the Hydrozoa generally, cuticle secretion presents many problems. Bonner (1955) found that, in the planula of *Phialidium*, gland cells giving a positive P.A.S. reaction are concentrated in the anterior pole, where a chitinous secretion appears at the time when the larva fixes itself. As with *Physalia*, the chitinous secretion has not been definitely traced to the gland-cells. Bonner further found that the gland-cells disappear after fixation, although the perisarc continues to form around the column of the young hydroid. Although this might suggest that the gland-cells are only needed when a copious amount of chitin is to be produced (that is, for attachment), it might also mean that the cells produce some substance which mixes with the chitin at the time of attachment but is not produced at other times. In the actinula larva of *Tubularia larynx* Pyefinch and Downing (1949) found evidence for an 'extra-chitinous cement' substance in the attachment region. However, a cuticular sheath is also present in this region, and Ciamician (1879) reported that in *T. mesembryanthemum* such a sheath (early perisarc) is produced by gland cells in the aboral ectoderm.

Thus, although there is a possibility that the gland-cells, which are found in the aboral ectoderm of planula and actinula larvae, produce something other than chitin, this is unlikely. Bonner's description of the gland-cells in *Phialidium* accords with the present writer's findings on *Physalia*; in both cases the major part of the evidence points toward chitin as the substance secreted.

6. The gas-gland

The gas-gland occupies a circular thickened area on the lower surface of the pneumatosaccus, toward the side *b–c* (Text-fig. 1) of the float.

The length, breadth and depth of the float may vary considerably according to the posture of the animal, but the diameter of the gas-gland (g) is less variable, and can be used as a rough index of the size (and, perhaps, age) of the specimen. Collapse of the float leads to very little alteration in g. It would be of interest to calibrate degrees of morphological complexity in the budding pattern against g values.

According to Haeckel (1888) the gas-gland of the largest specimens of *Physalia* may measure 10–15 cm. across. In a large 'Discovery' specimen in the University Museum, Oxford, $g=5\cdot25$ cm.; in the largest 'Discovery' specimen in the British Museum, $g=4\cdot0$ cm. Compared with these, the specimens collected in the Canary Islands were small: in the largest $g=2\cdot5$ cm., and, in the smallest, $g=0\cdot35$ cm.

The histology of the gas-gland in *Physalia* has been studied by Dahlgren and Kepner (1908). A section through the gas-gland of a very young specimen is given by Okada (reproduced by Hyman, 1940). In the present investigation gas-glands from seven specimens of *Physalia* were examined, either in sections or in whole mount preparations. Some new observations have been made, but interpretation has been difficult, and a further analysis is needed. The appearance of the cells in the gas-gland varies markedly from one specimen to the next, and it is not clear to what extent this variability is due to differing ages of the specimens, differing physiological states at the time of fixation or to differing methods of fixation. A new investigation should take account of all these factors.

In a young specimen ($g = 0{\cdot}6$ cm.) the gas-gland achieves a thickness of 60 μ. The surrounding saccus has a thickness of about 10 μ. The gas-gland consists of ectoderm, mesogloea and endoderm, all of which are continuous with but clearly distinguishable from the the corresponding layers of the surrounding tissue. Ectoderm and endoderm consist of tall columnar cells. They are separated by a thick mesogloea; elsewhere in the saccus the mesogloea is thin, and the cells flat. Muscle fibres are present in both ecto- and endoderm, but are infrequent in the ectoderm. They run for the most part circularly in the ectoderm and radially in the endoderm. Cytoplasmic processes cross the mesogloea here, as elsewhere in the saccus. No nerves are present.

The endoderm of the gas-gland consists of cells of one type, resembling the cells of the surrounding regions in size, number of nucleoli and staining properties of nucleus and cytoplasm, but they are unflattened and closely packed together forming a columnar epithelium. They each bear about 4–10 flagellae arising from basal bodies located in their distal tips. Around the edge of the gas-gland the endoderm merges into the flattened cells characteristic of the remainder of the saccus. The endoderm of the gas-gland, then, appears to be an unspecialized tissue, differing only from the general endoderm of the float in being columnar, rather than squamous. There is no reason to suppose that it functions actively in gas secretion.

The ectoderm of the gas-gland shows a greater degree of specialization than the endoderm. This is also the case in the other Siphonophora which have been examined. The cells of the gas-gland ectoderm are sharply delimited from those of the surrounding regions. At least three types of cell have been identified, each with cytological characteristics distinct from those of the remaining saccus ectoderm cells. The cuticle (pneumatocyst) is absent over the gas-gland ectoderm, and the musculature reduced.

The three types of cell occurring in the gas-gland ectoderm are: (*a*) tall columnar cells forming the bulk of the tissue; (*b*) giant cells, scattered sparsely throughout the tissue, being particularly evident in younger specimens; (*c*) a third type ('islet cells') occurring in clusters of three and upwards, characterized by their denser cytoplasm and darkly staining, deep-lying nuclei. Of these three types, only the first has hitherto been described in *Physalia*. Giant cells have been described in various Physonectae and in other Cystonectae. Islets cells have no known counterpart in other Siphonophora.

(*a*) *The columnar cells*

Dahlgren and Kepner's description of gas-secreting cells in *Physalia* refers to cells of this type. According to these authors a gaseous secretion develops in the region of a 'chromatic vacuole' distad of the nucleus, originating from granules which swell and become filled with gas. Gas-bubbles rupture the cell-wall and break into the gas-chamber.

A study of the Canary material has revealed the existence of chromatic vacuoles in only one specimen, a young one ($g = 0{\cdot}8$ cm.) fixed in Ca-formaldehyde. The gland was post-chromed for 36 hr., sectioned in paraffin and stained in iron haematoxylin. The chromatic vacuoles are not as regular in size and shape as those figured by Dahlgren and Kepner, but they are recognizably the same structures.

They are present in the large majority of interphase cells, but appear to be absent in cells undergoing mitosis, where the nucleus or spindle lies up near the free end of the cell. The chromatic vacuole consists of blobs or crescents of darkly staining matter deposited irregularly around the walls of a clear vacuole. Fixation and subsequent treatment were compatible with the preservation of lipoid. It is, however, too early to say what relation, if any, these structures bear to the Golgi element.

The chromatic vacuole has not been identified in the remaining specimens, which were fixed in Zenker, Helly and F.W.A. (without post-osmification). Whether this is because the fixatives were unsuitable, or because the gas-glands were older or inactive at the time of fixation has yet to be determined. Dahlgren and Kepner did not give the size of their specimens, nor did they mention the histological techniques they employed.

With regard to the secretory activity described by Dahlgren and Kepner, bubbles or vacuoles have from time to time been observed in the distal part of these cells. Such cases are rare in the author's material. Granules have not been seen, and the distal region typically shows a homogeneous or finely fibrillar content, representing normal fixed cytoplasm. However, the histological picture would be expected to vary according to the physiological state of the gland when fixed, and Dahlgren and Kepner's material may have been in a more active secretory state than the author's. The fact that bubbles were found in the Canary material, however infrequently, does constitute evidence in support of Dahlgren and Kepner's general hypothesis.

Dahlgren and Kepner figured and described bundles of mesogloeal matter interspersed amongst the bases of the gas-gland cells. Such bodies have not been observed in the author's material.

Groups of columnar cells have been found which, from the size of their nuclei, would appear to be tetra- or octoploids. The cells are in other respects indistinguishable from the remaining columnar cells. This condition has already been encountered in the general ectoderm and endoderm of the float, and no particular significance need be attached to it. It appears to be fortuitous, and the result of metaphase fusion in binucleate cells.

(*b*) *Giant cells*

In all of the specimens examined, isolated giant cells occur in the gas-gland ectoderm. They occupy a sub-epithelial position, being covered by slanting columnar cells. In young gas-glands they are fairly evenly distributed; their nuclei are rounded and compact, and stain densely in Feulgen preparations (Pl. XXVIII, fig. 1). In older specimens, the giant cells are separated from one another by wide expanses of columnar epithelium. Evidently, while the latter multiply by regular mitosis, causing expansion of the gas-gland, the giant cells do not divide. Even in the most mature examples studied, the majority of the giant cells occur singly. In the older gas-glands, the giant cells show considerable lobulation and distortion of the nucleus. There is no sign, however, that they are degenerate or pycnotic. A similar distortion characterizes normal muscle nuclei in young, healthy specimens, and this too increases with age. A large number of nucleoli may be present, and the cells vary considerably in size, the larger ones having the greater numbers of nucleoli. It has not yet been possible to establish clear polyploid groupings on a basis either of nuclear volume or number of nucleoli, but it seems very probable that we are dealing with a case of 'endoploidy' ('*endomitotische Polyploidisierung*', Geitler, 1953). It is interesting to find that in the salmonoid genus *Argentina* the gas gland also contains giant cells with deformed, fragmented nuclei (Fänge, 1958).

(*c*) *Islet cells* (Pl. XXVIII, fig. 2)

Cells of this type have been found only in one specimen ($g = 0{\cdot}8$ cm.). The specimen was fixed in F.W.A., which gives a most faithful and delicate fixation, well-suited to the detection of fine cytological detail. The islet cells show up well in iron haematoxylin, thionin and Feulgen preparations.

The cells have been found to occur in clusters (islets) of from three to eighteen; in some cases, they are distributed around a narrow but well-defined intercellular space. Like the giant cells, they occupy a sub-epithelial position. They have sharp outlines, by virtue of their condensed and fibrous cytoplasm, and a small, densely staining nucleus near the base of the islet. The nuclei show varying degrees of staining intensity with iron haematoxylin. Some are so dark that the nucleolus (which normally stains much more deeply than the rest of the nucleus) is not separately distinguishable. In Feulgen preparations, the nuclei stain brilliantly. This is sometimes a sign of pycnosis (Alfert, 1955), but there are no other symptoms of degeneration in the islets.

The islets occur without apparent regularity throughout the gland. They are frequently, but not in the example shown in Pl. XXVIII, fig. 2, associated with the giant cells, clustering around the latter. Mitosis has not been observed in them. From their frequent association with the giant cells, it might be thought that they contribute in some way to the latter's formation, but there is no direct evidence for this.

With regard to the physiological aspects of gas-secretion in the Siphonophora, very little is known. In certain forms, such as *Physophora*, there is abundant evidence that gas-bubbles can be emitted from the float, causing the animal to sink in the water. The gas can be regenerated in a few minutes (Keferstein and Ehlers, 1861, and subsequent workers). Jacobs (1937), in an important paper, described a similar process in *Stephanomia* (=*Nanomia*) *bijuga*. Gas-secretion was observed by this worker in an isolated float after some of the contents had been discharged; it involved the appearance of small bubbles in the region of the gas-gland, their rapid increase in size and fusion together, and their final merging with the air already in the float.

It has yet to be shown which of the various cells of the gas-gland are actually responsible for the secretion. Schneider (1902) maintains that the giant cells in *Rhizophysa* and *Physophora* are responsible, but Dahlgren and Kepner's observations on *Physalia* point to the columnar epithelium as the source. The present investigation has given some support to the latter view. The chemistry of gas secretion, and the character of the stimulus or stimuli evoking it or inhibiting it are completely unknown.

Some workers have held that in *Physalia*, as in *Rhizophysa*, etc., gas may be emitted from the float causing the animal to sink below the surface. Observations in the Canary Islands in no way support this view. Specimens were never observed to liberate gas spontaneously. It is very difficult to squeeze even a few small bubbles out through the apical pore by manual pressure. Nothing in the structure of *Physalia* suggests that it is adapted for submarine existence. It is a robustly built animal adapted for sailing on the surface, and there is no shred of evidence to show that it ever leaves the surface during its adult life.

The float probably loses gases slowly by diffusion in spite of its insulation (the pneumatocyst), and as the animal grows the volume of gas in the float must steadily increase. A steady demand for gas is therefore to be expected, but there is no reason why sudden demands for large quantities of gas need normally occur. The persistence of the gas-gland in the adult, and its growth with the rest of the float tissues, as well as its small size relative to the float as a whole are just about what one would expect to find.

A series of experiments was undertaken to test the capacity for gas-secretion. The volume of the float was estimated by water displacement in a measuring cylinder. Known values of gas were then withdrawn with a syringe, and the volume of the float measured again at intervals. However, this rather clumsy technique failed to yield any significant data. It was found, moreover, that the specimens deteriorated quickly in the laboratory, and both controls and experimental animals tended to

Table 1. *Analysis of the gases filling the float in* Physalia
(*previous work summarized from Winterstein*, 1921)

	Oxygen (%)	*Carbon dioxide* (%)	*Nitrogen and other gases* (%)
De Quatrefages	17·22–17·78	—	The remainder
Schloessing and Richard			
(*a*)	12·2	—	The remainder
(*b*)	15·1	1·7	The remainder, of which 1·18 is argon
This paper			
Sample (*a*)	17·24 ±0·1	0·071 ±0·01	The remainder
Sample (*b*)	17·71	0·033	The remainder
Normal air	20·95	0·03	The remainder, of which about 1 % is argon

lose volume after a few hours. Large tanks with circulating water are needed to keep *Physalia* in good condition. Bigelow kept specimens in this way for up to a week at Woods Hole. Frequent changing of the water in a small tank is laborious and has the disadvantage of disturbing the animals. An attempt to keep specimens in a plastic cage anchored in the bay at Arrecife was unsuccessful as the wave motion battered the animals against the walls of the cage, and damaged their appendages.

Two samples of gas were collected in tubes by displacement of liquid paraffin, the gas being withdrawn from the float with a syringe and injected into the tubes (capacity about 30 c.c.) equipped with self-sealing rubber diaphragms. The results of the analysis, made two months later by Miss Ann Sweeney of the Department of Physiology, Oxford, together with some earlier records, are given in the accompanying table (Table 1).

7. NEMATOCYSTS

Weill (1934) describes two sorts of nematocyst in *Physalia*: atrichous isorhizas in the tentacles, stenoteles in a certain (not clearly specified) region of the gonodendra. The present study has confirmed the existence of two types of nematocyst, and it is now possible to add some further details on their structure and distribution.

First, with regard to structure, examination of the discharged filaments of the isorhizas, both large and small types, reveals the presence of small teeth on three spiral ridges. An early illustration by Murbach (cited and reproduced by Will (1915)) hints at this feature. Hardy (1956, fig. 24E, F) in a drawing based on a preparation by the present author shows the teeth and ridges. Thus it is clear that Weill's description of the isorhizas as 'atrichous' should be amended to 'holotrichous'. Pl. XXVIII, figs. 5, 6 show the appearance of the teeth under phase contrast.

In this investigation a convenient technique for preparing isolated nematocysts from fixed tissue was found to be as follows: The tissue is washed well to remove the fixative. Then it is placed in 1 % solution of pepsin in 0·1 N-HCl at 37° C. After an hour or more the tissue is removed and without washing is dabbed gently on a slide. Nematocysts come loose forming a smear. When the smear is nearly dry it is exposed to the vapour of 40% formaldehyde for 5 min. Then it is transferred to 90% alcohol. Staining can be carried out in Unna's orcein or the smear may be carried through to absolute alcohol, cleared and mounted and examined under phase contrast. In the latter case a mounting medium with a low refractive index such as G. Gurr's XAM (R.I. = 1·491) offers certain advantages.

In many tentacular preparations isorhizas with incompletely discharged filaments were found (Pl. XXVIII, fig. 5). Picken (1953) and Robson (1953) should be consulted for a detailed analysis of the process of discharge and the structure of the filament in *Corynactis* which, like *Physalia*, has large holotrichous isorhizas.

An interesting feature of the isorhizas in *Physalia* is the elaborate fibrillar 'basket' occurring in the surrounding cnidoblasts. The general appearance of this fibril-complex is well known from Will (1909).

Reproductions of two illustrations showing the fibrils in large and small cnidoblasts are given by Will (1915) and of the small type only by Hyman (1940). The peptic digestion technique has the notable advantage of dissolving away the cnidoblast completely except for these fibrils. Where a pepsin smear is allowed to dry before being placed in the alcohol, violent surface-tension forces accompanying the last moments of evaporation draw the nematocysts together in clumps, often removing them from their 'baskets'. In the mounted preparation intact isolated 'baskets' can thus be studied. The appearance of such a 'basket', originally surrounding a large isorhiza, is shown in Pl. XXVIII, fig. 7. It will be seen that the fibrils, far from tailing-off towards the apex as Will suggests, continue and form an elaborate fibrillar reticulum around a hole through which, in the intact cell, the nematocyst would discharge. The fibrillar 'basket' in the cnidoblast containing the small type of isorhiza has a similar reticular structure at its apex and resembles the large type except that, as Will shows, the fibrils intertwine in the basal region forming a single, helically wound stalk.

The fibrils are thought to be contractile. The effect of magnesium salts and chloretone in preventing nematocyst discharge in an electrical field was attributed by earlier workers (and more recently by Parker and Van Alstyne, 1932) to anaesthesia of these fibrils. The fibrils stain strongly with iron haematoxylin after coagulant fixation in a way similar to muscle fibres. Like fixed muscle, they resist peptic digestion. Whereas chitin and collagen are laid down extracellularly in Coelenterata, muscle is probably always intracellular, like these fibrils. However, if muscular, these fibrils are unique in certain respects, chiefly in their tendency to intertwine in a helical fashion. Attempts to stain the fibrils with Unna's orcein, known to colour elastic tissue, failed completely, though the nematocyst capsules took the stain. While it is possible that the fibrils are indeed muscular and assist discharge in some way, another possible function is worth mentioning: that they serve to strengthen the wall of the cnidoblast and to retain the capsule *after* discharge has occurred. 'Harpooned' fish have been seen to struggle violently but unsuccessfully after capture by the tentacles. The discharged nematocysts are the only means by which the fish is secured to the tentacles. The fibrils in the cnidoblasts are rooted in the mesogloea and may thus prevent the nematocysts (which they enclose) from tearing loose while a captured fish is being carried up to the digestive organs.

With regard to distribution, Weill correctly states that the tentacles contain numerous large and small isorhizas. They do not form an even series from large to small; the intermediate sizes are rare. The range of variation in capsule diameters in the material studied was 9–30 μ (Weill gives 15–40 μ).

Nematocysts also occur in the gastrozooids (as Huxley, 1859, pl. x, fig. 4, discovered). They tend to occur in groups arranged at regular intervals around the lip region. These nematocysts resemble the small isorhizas of the tentacles and like them lie in cnidoblasts with long basal stalks. In addition to isorhizas, stenoteles occur in the gastrozooids; they are scattered sparsely over the organ. The butt region (Weill's *hampe*) can be clearly seen in the undischarged capsule. For some reason only one discharged stenotele has been found in the author's material. The everted butt is 14 μ long and lacks lateral spikes or barbs. Measurements of stenoteles from a gastrozooid give typical diameters of 17–19 μ. The isorhizas in this preparation are 11–15 μ.

In the codon-ectoderm, stenoteles occur sparsely, either independently or in small groups. However, in very young specimens of *Physalia*, this region appears to be much more generously equipped with nematocysts.

In mentioning the occurrence of stenoteles in the gonodendra Weill was probably referring to the palpons as the specific site. Stenoteles are very abundant in the distal region of the palpons and spread back along one side for a distance of about one-third the length of the whole organ. They are evenly matched for size and achieve diameters of 21–25 μ (Weill gives 35–40 μ).

It will be noted that Weill's micron-estimations are higher than those given here both for stenoteles and isorhizas. This may reflect true variation between individuals or populations of *Physalia*. Semal (1954*a*) found such variation between different populations of *Hydra*. Even in an individual *Physalia* the typical capsule diameter of the large isorhizas may differ by as much as 5 μ between two tentacles.

Developing stages can easily be obtained by peptic digestion from the ampullae connected with the bases of the tentacles. The young nematocysts nearly always exhibit what Weill has shown to be the prematurely discharged condition. Earlier interpreters of nematocyst development have been hampered by failing to appreciate this fact. In the present study, using only fixed material, the author has not attempted to reinterpret the development picture. The most recent account referring to the process in *Physalia* is that of Will (1929).

Developing nematocysts are found in the float, gastrozooids and palpons as well as in the ampullae. In silver preparations the capsules and discharged tube (Will's '*zuführender Kanal*') stain heavily in silver preparation (Pl. XXVIII, fig. 4). The group shown is typical in that it consists of a small, even number of developing stages. Groups of two, four and eight are so common that one can probably assume that such groups derive from one or two primordial cnidoblasts which divide *in situ* by mitosis before capsule secretion begins. The close grouping of the cnidoblasts can often be attributed to the presence of bridges of cytoplasm holding the cells together. Such bridges have been described in the older literature (for example, in *Physalia* by Goto, 1895) and more recently in *Hydra* (Hess, Cohen and Robson, 1957). In silver preparations one can often make out, especially in the younger stages, a strand of fibrous material running between the two nuclei within the cytoplasmic bridge (Pl. XXVIII, fig. 3). This fibre strand is in all probability a mitotic spindle relic—the 'fusom' of J. Hirschler (1935). In certain 'fusoms' chromatin material lodging in the interchromosomal connectives during anaphase gives to the persistent 'fusom' a nuclear reaction. Such cases have been interpreted as stages in amitotic division. Some earlier students of cnidoblast development appear to have been misled by this 'pseudoamitosis'.

In the more mature cnidoblast groups the 'fusom' appears to degenerate but the cytoplasmic bridges persist longer, and are sometimes seen in the fully mature groups. Hirschler (1955) describes a case (egg nurse-cell complexes in the Arthropod ovary) where the 'fusom' provides a means whereby physiological co-operation between members of the group can take place. It would be interesting to ascertain whether any such co-operation were possible within the cnidoblast groups in *Physalia*. In cases where the group remains interconnected in maturity one might look, for instance, for some capacity for synchronized development or simultaneous discharge. A 'fusom'-like structure also occurs in interstitial cells of *Hydra* (McConnell, 1937). In *Physalia*, the 'fusom' is not confined to the cnidoblast groups. It occasionally occurs in the float musculature but is only easily detectable where it contains Feulgen-positive material. This is probably matrical matter from the chromosomes which has become lodged in the interzonal connectives during anaphase. Examples of such anaphases also occur in the float.

Some simple experiments were carried out on living material in the Canary Islands to determine some of the factors influencing nematocyst discharge.

Parker and Van Alstyne (1932) mention that the tentacle nematocysts in *Physalia* discharge in an electrical field, and that discharge is inhibited by magnesium anaesthesia. The author independently arrived at the same results. An attempt was made, by controlling the 'electrical field', to compare discharge thresholds in different regions and under various conditions. The electrodes were placed at a fixed distance from the tentacles, and the strength of the shock was increased until the nematocysts discharged *en masse*. A 2 V. accumulator was used, giving make-and-break shocks through an induction coil. The distance between tentacles and electrodes was selected arbitrarily, but was kept as constant as possible throughout the experiments. The results may be summarized as follows:

(1) Nematocysts from large and small tentacles, from all animals tested, discharged at approximately the same threshold.

(2) The threshold appeared to be unaffected by the state of contraction in the tentacle.

(3) Nematocysts from the basal growing region of the tentacles required strong shocks to discharge, or were undischargeable.

(4) Weak solutions of chloretone, chloral hydrate and magnesium sulphate all inhibited discharge partially or completely, depending on their concentration. Solutions too weak to produce total anaesthesia produced definite *levels* of anaesthesia, which were quickly reached and were maintained with little perceptible change over periods of hours.

(5) Strong solutions of many chemical substances, including anaesthetics, had an irritant effect, and caused discharge, along with contraction of the tentacles.

(6) Elevation and depression of the temperature caused depression and elevation respectively of the threshold.

(7) Following anaesthesia, the normal discharge level was restored when the tentacle was transferred to fresh seawater.

(8) Segregated nematocysts (teased on a slide) failed to discharge in the electrical field.

In all these experiments seawater controls were maintained. The method was too rough and ready to be used for absolute determinations, but for comparative studies of the type carried out it gave consistent results.

The reaction to anaesthesia and to cold resembles that of muscle and, as the cnidoblasts contain fibrils similar in appearance to muscle fibres, Parker and Van Alstyne's suggestion that it is these fibrils whose reactivity determines the discharge level is a reasonable one (see, however, p. 395, para. 2).

The high threshold of discharge in the basal regions of the tentacles indicates that the nematocysts or their cnidoblasts are immature here. Histological examination confirms this. The immature region extends a few centimetres below the tip of the ampulla in large tentacles; exact data were not obtained.

It is interesting to consider the case of the fish *Nomeus* which lives in commensal association with *Physalia* and appears to escape injury from the nematocysts. The author has not observed *Nomeus*, and the records do not clearly show whether the fish survives because it avoids being stung, or because, when stung, it is immune to the poison. To the author it seems likely that the fish avoids being stung and has innate or acquired behaviour patterns directed to this end. The situation in which it lives is not really so hazardous as it might appear. The tentacles are only dangerous if contact is made with them. No searching or exploratory movements of the sort performed by the tentacles of *Velella* take place. To escape injury, all that a fish will require is small size, agility and an avoidance reaction.*

The toxic and distressing nature of the sting to human beings has been the subject of frequent comment (see particularly Phisalix, 1922). In the present study, the matter was not deliberately investigated, although the author was frequently stung. The pain and shock produced are evidently strictly proportional to the number of nematocysts discharged. Probably several hundred need to penetrate the skin to produce really severe discomfort in a human.†

8. HISTOLOGY OF THE DIGESTIVE REGIONS

Our knowledge of digestion in the siphonophores is rather scanty. Most of the information available is reviewed by Yonge (1930, 1931) in discussions of digestion in the Coelenterata generally. In those species which have been most thoroughly investigated, the evidence shows that a preliminary extracellular digestion, of proteins only, takes place in the enteron, this being followed by intracellular

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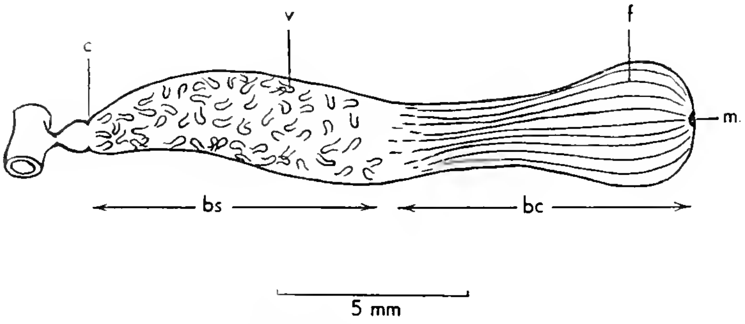
* See Totton, Part I, p. 309.

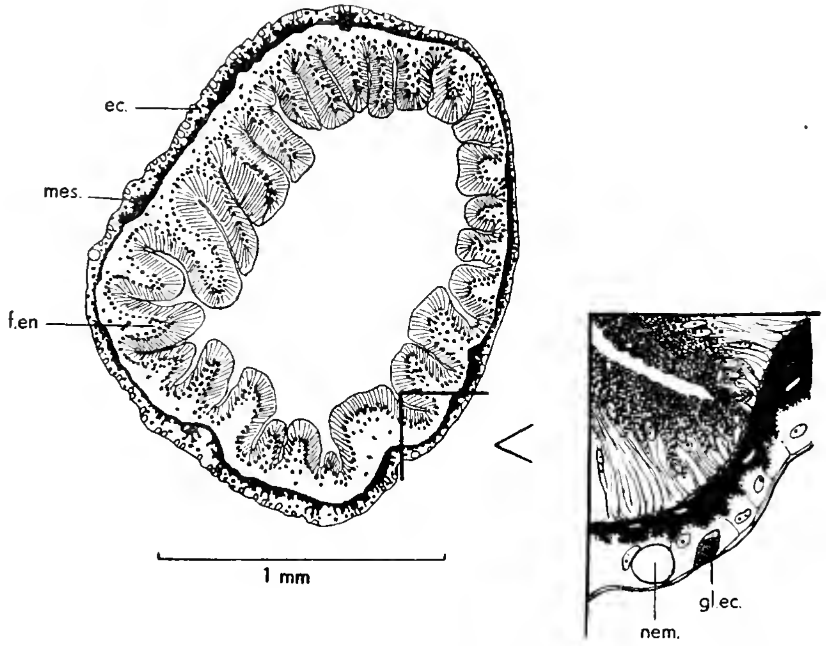
† Investigation of the Loggerhead turtle, which feeds on *Physalia*, reveals no immune bodies in the blood (Dodge and Lane, 1960. Nature 185, pp. 330–331). Probably the nematocysts cannot penetrate the reptile's thick hide.

digestion by the endoderm cells of proteins, fats, and, to a lesser degree, of some carbohydrates. Whether this is true of the Siphonophora in general has yet to be shown, but there are good reasons for supposing that the two phases of digestion, extra- and intracellular, take place in *Physalia*.

The gastrozooids are, of course, the main digestive units. They spread out over the body of a fish, and the surface of the fish dissolves; this can only be the result of extracellular digestion. A partially digested broth then passes into the enteron. In a later stage of digestion, gastrozooids are found with their mouths constricted, and their interiors filled with food matter. For reasons given below, intracellular digestion can be stated to take place at this stage. We know from Bodansky and Rose (1922) that various enzymes are produced in the gastrozooids, but we are still far from knowing which cells produce which enzymes. In addition to the gastrozooids, we have to consider the palpons, which, from their structure, are clearly concerned in digestion at some stage in the life-cycle, even though they may not play an important role while the gonodendra are still attached to the parent colony.



Text-fig. 4. Sketch of a gastrozooid showing the main regions. *bc* = buccal region, *bs* = basal region, *c* = valve-like constriction near base, *f* = fold, *m* = mouth, *v* = villus. The endodermal folds and villi are seen through the transparent wall of the zooid.



Text-fig. 5. Transverse section through a gastrozooid in the buccal region. Inset: an enlarged region. *ec* = ectoderm, *f.en* = folded endoderm (secretory cells), *gl.ec* = ectodermal gland cell, *mes* = mesogloea, *nem* = nematocyst.

The gastrozooid of *Physalia* consists of two well-defined regions (Text-fig. 4) which will be referred to as the 'buccal' and 'basal' regions. The buccal region, consisting of the whole distal half of the zooid, can be spread out as a flat disk in feeding. The basal half is characterized by conspicuous projections of the endoderm into the enteron known as 'villi', which have often been described in the earlier literature (for example, Huxley, 1859). In young gastrozooids the basal region is longer than the buccal, but in mature examples the two regions are approximately the same length when the zooid is relaxed. The gastrozooid has considerable powers of expansion and contraction, tending to elongate during exploratory activity.

The buccal region (Text-fig. 5) in a relaxed zooid shows a regular folding of the endoderm into longitudinal ridges. These ridges are visible to the naked eye in ordinary preserved material. In zooids where the buccal region was fixed in an expanded state, the ridges are inconspicuous or absent, and it may be concluded that the folding is a mechanical device making possible the accommodation of the bulky endoderm cells when contraction takes place.

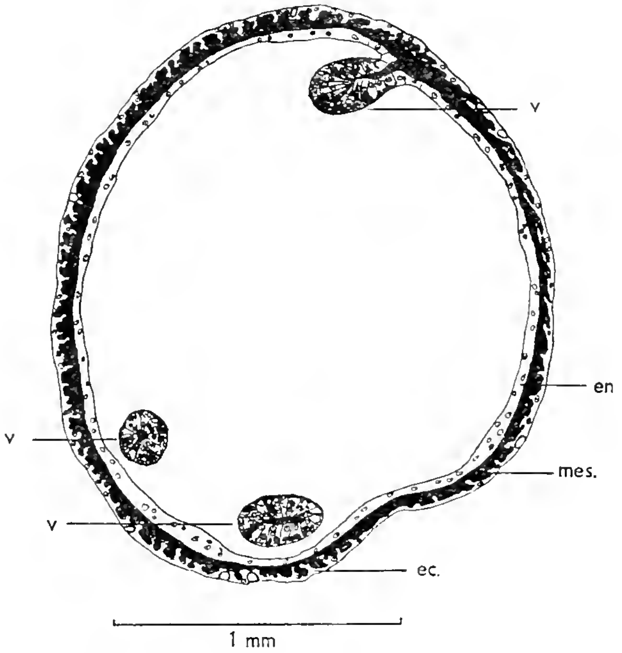
The cells of the buccal region are secretory. The secretory matter fills the distal part of the cells and takes the form of rounded droplets, or, in some cases, of a finer, more diffuse substance. The droplets may measure $10\,\mu$ in diameter. They are well seen in unstained F.W.A. material, where they show an amber coloration. In gelatin sections of Ca-formaldehyde material, stained in Sudan black, the droplets show little if any darkening, and can therefore be said to contain little lipid material. They stain strongly with eosin in Zenker material, and with iron haematoxylin in Helly. The P.A.S. reaction is strong in the region of the secretion, but the secretion droplets do not stain any more strongly than the matter surrounding them. Protein tests have not been carried out, but are clearly indicated for any future study, in view of the probably enzymatic character of the secretion. Where the secretion is more diffuse, we may be dealing with cells in the process of elaborating their product, this not yet having coalesced to form the droplets. Alternatively, the cells with the diffuse secretion might constitute a distinct type, like the '*cellules spumeuses*' in *Hydra*, while the cells with the droplets would correspond to the '*cellules sphéruleuses*' (Semal-van Gansen, 1954*b*). A further investigation along the lines of Semal-van Gansen's beautiful study is required.

In gastrozooids fixed when not feeding, the buccal cells are packed with secretory matter. In one specimen, fixed while actually attached to a captured fish, many of the cells appear empty, although it is difficult to compare the appearance of cells in the expanded, flattened specimens and in the folded, contracted ones. If correct, however, this observation would indicate that the buccal cells tend to discharge their product during feeding, and it would seem likely therefore that the secretory matter consists of the enzymes responsible for the preliminary extracellular digestion. It was mentioned above (page 390) that a glutinous substance produced by captive specimens of *Physalia* seems to originate from the gastrozooids, and the author is inclined to suppose that this substance may derive from the buccal gland cells by degenerative breakdown in conditions of oxygen shortage. However, Mettey and Hamon (1949) hold that the buccal gland-cells in the gastrozooid of *Abylopsis* secrete a viscous substance as their normal product, and that it serves for the agglutination of prey.

In *Hydra*, the cells concerned in the production of proteolytic enzymes undergo a series of secretory cycles, discharging their product when food is ingested, and resecreting it again rapidly, until they reach a stage of senescence, when they quit the endoderm and drift out into the enteron. It is too early to say whether, in *Physalia*, the buccal cells undergo cycles of secretion or, if they do, how many cycles can take place, but there is evidence that cells or large portions of cytoplasm containing secretion-droplets are shed from the endoderm and mix with the food matter undergoing digestion. Such objects, sometimes apparently consisting of whole buccal endoderm cells, have been found free in the enteric fluid. Loose droplets are also found, and these sometimes appear to have fused together into large globules, or to have formed aggregates. Parallels to these observations are recorded by Semal-van Gansen for *Hydra*.

In *Hydra* the gland-cells usually have two flagella projecting into the enteron from their free edge.

In *Physalia* two sorts of flagellum occur, and they are found in large numbers. They are best seen in gastrozooids fixed while feeding, the buccal endoderm being spread out as a flat sheet (Pl. XXVII, fig. 7). They occur in rows. The shorter flagella (about 10 μ in length) occur in groups of about a dozen. The long flagella (about 25 μ in length) are more closely bunched together, and occur in groups of about half a dozen. These numbers are rather variable. The short flagella seem to arise from the centre of the cells, the larger from the sides. Both sorts of flagellum can probably occur in one and the same cell, but this is not always the case, and groups of the longer sort are in a minority. The blepharoplast in both types is single, not double as in *Hydra*. The endoderm throughout *Physalia* is flagellated, but the bunches of long flagella are confined to the buccal cells of the gastrozooids.



Text-fig. 6. Transverse section through a gastrozooid in the basal region. *ec* = ectoderm, *en* = endoderm, *mes* = mesogloea, *v* = villi, cut at various angles.

Turning now to the basal region of the gastrozooid, we find a more complicated organization of the endoderm. The most conspicuous features are the villi. These are finger-like projections from the lining of the zooid, consisting of endoderm cells covering a central core of mesogloea (Text-fig. 6; Pl. XXVII, fig. 6); the ectoderm is not involved. The villi can be seen through the transparent wall of the zooid (Text-fig. 4).

The endodermal cells of the villi are probably all of one type; they are quite clearly active in intracellular digestion. In certain specimens, which had been feeding shortly before fixation, the enteron is filled with a mixture of partly-digested flesh, pigment, both dispersed and in aggregates, and nematocysts, discharged and undischarged. The same objects have been identified in vacuoles in the endoderm cells of the villi, and it may therefore be stated with confidence that these cells engulf whole particles of food, and enclose them in digestive vacuoles. A variety of stages in the breakdown of food can be found amongst the vacuoles.

The pigment in the food is probably melanin, guanin or some other pigment originating from the dermal chromatophores and iridocytes of the captured fish. Part of it may, however, derive from broken down haemoglobin originating in the blood of the fish. The pigment evidently resists digestion in the vacuoles fairly successfully, for the cells of the villi nearly always contain some, whether feeding has taken place recently or not. Presumably it is eventually ejected, and some of the dispersed pigment found in the enteron may have been excreted in this way; the aggregates of pigment, however, are clearly derived directly from the food, and are sometimes surrounded by tissues from the fish. The pigment found in the endoderm of *Hydra* is also probably melanin derived directly from the food, and in this case originating in the eyes of the *Daphnia* on which *Hydra* preys (Semal-van Gansen, 1954*b*). It was earlier supposed to derive from the chromatin of broken-down nuclei (Schlottke, 1930).

The occurrence of nematocysts in the cells of the endoderm and in the enteric contents is at first rather surprising, although a similar finding has been recorded for *Halistemma* (Claus, 1878). The nematocysts are clearly undergoing digestion, for they have no surrounding cnidoblasts. In the villi irregular, amber-coloured lumps are sometimes found which probably represent nematocysts in advanced stages of digestion, but more often intact, spherical nematocysts are seen, and these may lie in vacuoles situated well down towards the base of the cells.

It might be supposed that these nematocysts are senile ones which have been removed from the ectoderm, crossed the mesogloea to the endoderm and have then passed to the gastrozooids for digestion. If this were so, one would expect to find nematocysts in stages of migration across the mesogloea. However, study of numerous sections from various parts of many specimens has revealed no evidence, direct or indirect, that this takes place. The nematocysts in question are the large and small isorhizas characteristic of the tentacles. What probably happens is that the gastrozooids apply themselves to the captured fish while some of the tentacles are still attached to it, and tentacular matter is ingested together with the tissues of the fish. Only in this way does it seem possible to account for the presence of undischarged capsules in the enteric contents, and, later on, the villi. It is interesting to note that the cells of the villi can engulf objects such as the largest nematocysts, whose diameter is typically about 25 μ.

In the general endoderm of the basal region of the gastrozooid (that is, in the parts lying between the villi) three main cell types are distinguishable. The first type, which is in a majority, is apparently non-glandular, and is probably simply absorptive. Cells of the second type are closely similar to the buccal gland-cells, and may even be identical to them. Cells of the third type are evidently glandular, but they differ from the cells of the buccal region. They resemble more the '*cellules glandulaires moyennes*' which Mettey and Hamon (1949) described in *Abylopsis*. In the latter form, these cells have a region of very basophil, sudanophil cytoplasm ('chromatoplasm') around the nucleus: they are believed to produce a diastase. In *Physalia* the cells thought to be comparable have a similar region of basophil cytoplasm around the nucleus; this area also stains strongly in P.A.S. preparations. The cytology of these regions has not yet been investigated in detail, and no further observations can be added.

The palpons, as stated above, probably do not play an important role in digestion while the gonodendra are still attached to the parent colony; indeed, the younger animals manage without them. In the structure of their endoderm they resemble young gastrozooids. The villi are well developed, but the buccal region lacks the heavy concentration of glandular cells found in the gastrozooids and, probably as a result of this, is not thrown into folds. In the distal extremity, where the mouth 'should' be, an indentation can sometimes be seen, but sections have not revealed an actual opening here. If tightly constricted however, a mouth or incipient mouth, might not be easy to detect.*

The villi in a number of cases have been found to contain food vacuoles, with nematocysts and pigment matter in them, but palpons have not been observed feeding, and it seems unlikely that they do feed at this stage; the food matter could reach them from the general enteron, having been taken in via the gastrozooids in the first place. Bits of semi-digested food and pigment have been found elsewhere in the enteron, for instance in such remote regions as the ampulla of a large tentacle.

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* Totton (Part I, p. 354 and Plate XXV, figs. 2, 3) shows that openings do exist.

Throughout the Siphonophora, palpons show a perplexing array of possible functions. In *Apolemia* (Willem, 1894) and *Forskalia* (Neppi, 1921) they seem able to eject waste matter through a terminal orifice. In *Physophora*, however, they are sensitive, prehensile effector organs (Totton, 1954). In *Physalia*, their precise function is not known, but it seems probable that they are concerned with the feeding or defence of the gonodendra, particularly if the latter drop away into deep water, as Steche (1907) suggests. Alternatively, they may be vestigial structures.

Only two clearly distinct cell types have been found in the endoderm in regions other than the palpons and gastrozooids. The first of the two types is a gland cell (Text-fig. 3, *gl.en*); its nucleus is a thin curved disk pushed away to one side of the cell by the pressure of the secretory mass. The secretion apparently consists not of granules or globules (although fixation may sometimes give the cytoplasm a reticular appearance), but of a homogeneous substance. It is P.A.S. positive. In whole pieces of codon-endoderm fixed in F.W.A. and stained in iron haematoxylin a clear area, evidently an opening, can be seen at the free surface of each of these gland cells. The gland cells usually occur singly, and mitosis has not been observed in them. Their function is not known for certain, but from their structure it would seem reasonable to suppose that they are mucus-secreting ('goblet') cells. They very closely resemble goblet cells of the type shown in fig. 64 of Hertwig (1895).

The second cell-type from the general endoderm shows no secretory inclusions and no digestive vacuoles. It is probably simply absorptive. Mitosis takes place in these cells with approximately the same frequency as in the ectoderm; the descriptions of polysomaty, the binucleate condition, and nuclear fragmentation under stress, etc. (see under 'Muscle') apply to both ecto- and endoderm.

In the spadix of the gonophores, the endoderm cells are exceptionally tall and columnar; they show a multinucleate condition, the nuclei undergoing amitosis (Perez, 1929). The significance of this is not clear. In the ampullae, the endoderm also shows regional specialization, the cells along one side being very small and closely packed together; again, we cannot suggest an explanation.

The probable sequence of events in feeding and digestion may be reconstructed as follows. On making contact with a fish, the gastrozooids apply themselves to it, spreading out the whole buccal region as a flat disk. The buccal gland-cells then discharge their contents (?proteolytic enzymes), whose powerful corrosive action dissolves away the surface of the fish. Detached particles of food and dissolved substances are then swept back by the rows of long and short flagella towards the basal region of the zooid, where they accumulate. After an unknown time the gastrozooids detach, their mouths close, and the matter in the enteron is subjected to further digestion, under the action of secretions from cells of the buccal type, and from another type of cell located in the basal region. At the same time, solid particles of food are engulfed phagocytically by the cells of the villi, and digested in vacuoles. Further steps in the process are less clear. The gastrozooids have a valve-like structure near the base (Text-fig. 4*c*) and this is presumably shut during digestion. After a time, it would probably open, allowing the digested matter to disperse throughout the enteron, where dissolved substances would be absorbed by the general endoderm. The bulk of the solid matter which resists extracellular digestion in the enteron of the gastrozooids would be dealt with intracellularly by the cells of the villi. Whether the products of digestion in the villi are set free again, or are used locally we do not know.

Ejection of waste matter has not been observed, and nothing is known about the time necessary for various stages of digestion nor about the variations in pH during digestion. If a further investigation should become possible, feeding experiments with pH indicators and with substances in suspension like carmine, indian ink, etc., would be of value in solving many of these problems.

DISCUSSION

From what has been said on the structure and activities of *Physalia*, it will be seen that the outstanding need is for further physiological and experimental work on living animals. This need is very apparent where the functions of gas-secretion and digestion are concerned, but I would like to comment particularly on the organization of the nervous and muscular systems.

We know from observation of living specimens that a rapid, probably through-conducted, contractile response takes place throughout the organism following strong tactile stimulation, and that at other times the members behave independently, but histological study reveals no differentiation of the nerve plexus into two systems, one of which could serve for through-conduction, the other for local conduction. Even more puzzling is the absence of nerves from three of the four float epithelia. In the case of the ectoderm and endoderm of the saccus, the histological absence of nerves fits in well with the apparent incapacity for active response, but in the case of the codon endoderm, where the musculature must contract and relax in harmony with that of the ectoderm to produce the characteristic postural changes, the absence of nerves is surprising. One can only suppose that the muscle response here is a direct one, possibly to tensions set up in the mesogloea by contraction in the ectoderm, possibly to forces negotiated via the 'pneumatic skeleton'.

It is easy to make the mistake of attributing to siphonophores more refined physiological mechanisms than their basically simple structure can allow. It must be borne in mind that there are few structures here which could be called organs, that there are no muscles in the sense of groups of fibres or fibre bundles having localized origins and insertions, and that there are no ganglionic aggregations of nerve elements which could function as centres of direction and co-ordination. To think of the integration of the organism in terms of motor versus sensory pathways, reflexes, pacemakers etc., is fraught with danger. The nervous system is dispensed with completely in many regions, for example, the gas-gland, which by analogy with vertebrates one would expect to be well innervated.

One other topic calls for comment. In studying the histology of *Physalia*, one finds signs that the large size of the animal sometimes places demands upon the component tissue elements which can be met only with difficulty and with deleterious side effects. One recalls particularly the cytological aberrations referred to on pp. 381, 382, some of which appear to be caused by excessive flattening of the epithelia and mechanical stress. If the epithelia were able to proliferate in depth and to differentiate into further cell types, such mechanical difficulties would not arise, but this ability would require the existence of a third germ layer, that is a mesoderm. Some writers deny that the distinction between mesoderm and mesogloea is a valid or significant one. However, mesoderm, as a source of cells, can relieve the ectoderm and endoderm of many functions and allow an overall increase in tissue specialization. Mesogloea, however elaborate, provides no such benefits.

SUMMARY

A. BEHAVIOUR

(1) The float of *Physalia* responds actively to wind by adoption of a characteristic 'sailing posture' together with erection of the crest. Crest erection results automatically from an increased pressure on the enclosed air ('pneumatic skeleton') whether caused by a general increase in muscular tone, as in natural conditions, or by experimental manipulation. Observations on rolling behaviour support the view that these movements represent attempts to adopt the sailing posture in conditions of calm.

(2) Muscular contraction, both in the float and tentacles, is stepped.

(3) The tentacles show an inherent rhythmic shortening and lengthening behaviour. The frequency depends on the general degree of contraction within which the rhythmic movements take place, being more rapid when the tentacle is contracted than when extended. Tentacles perform rhythmic behaviour independently.

(4) When extended, the larger tentacles of a medium-sized *Physalia* were estimated to measure 8–10 m.; following stimulation they contracted within a minute to 12–15 cm.

(5) The gastrozooids perform random, searching movements. The presence of food in the tentacles does not appear to affect this behaviour. Gastrozooids respond to physical contact by spreading out their buccal regions over the object encountered.

(6) Strong stimulation applied to the float results in general contraction of all appendages. This reaction is very rapid and, unlike the other reactions, appears to be through-conducted.

B. Histology

(1) Muscle is present in all four epithelia of the float but nerves are present only in the codon ectoderm.

(2) Polyploid cells, probably deriving from binucleate cells by combination of the two sets of chromosomes during mitosis, are found throughout the float epithelia. Their distribution is random.

(3) The diploid chromosome number is 20, but mitotic aberrations are common and may lead to the production of cells with abnormal chromosome complements.

(4) Fragmentation of nuclei is demonstrable in the saccus-ectoderm and is attributable to the excessive flattening and stretching of the layer.

(5) Muscle-fibres are not visibly affected during mitosis in the nuclear layer.

(6) The nerve-plexus has been demonstrated throughout the ectoderm except in the tentacles, where technical difficulties have prevented effective study, and in the saccus where nerves are absent. Nerves have not been located in the endoderm of any region.

(7) The plexus is a diffuse one. Tripolar neurons predominate over bipolar. Many (possibly all) nerve cells bear conical projections extending to the surface from which emerge two or more hairs, presumed to be sensory.

(8) Cellular processes or whole cells cross the mesogloea of *Physalia* from endoderm to ectoderm. In certain regions they have short lateral diverticula.

(9) The mesogloea has a laminated structure. Broad flat sheets cross one another. X-ray diffraction tests point to the collagenous nature of the mesogloea.

(10) A thin cuticle has been identified covering the ectoderm in many parts of *Physalia*. Evidence is given for the secretion of this material from ectodermal gland-cells.

(11) The chitosan test identifies the cuticular material as chitinous. X-ray diffraction tests agree and, in addition, reveal the presence of a benzene soluble material, possibly lipid, in the cuticle lining the air-sac.

(12) In the ectoderm of the gas-gland three types of cell have been found. Results from an analysis of the gaseous contents of the air-sac are given.

(13) The large and small nematocysts occurring on the tentacles are holotrichous isorhizas. Small isorhizas also occur in groups round the gastrozooid lip-region. Stenoteles occur in gastrozooids, palpons and float.

(14) Details are given concerning the fibrillar system found in cnidoblasts containing isorhizas.

(15) Cnidoblasts with developing nematocysts are found in the tentacular ampullae, and over other regions of the ectoderm. In the gastrozooids they tend to occur in small groups of even numbers,

pairs of them being interconnected by cytoplasmic bridges, some of which surround fibrillar strands thought to represent Hirschler's 'fusom'.

(16) Isorhizas discharge in an electrical field while *in situ*, but not when isolated. Discharge is inhibited by anaesthetics, either partially or completely depending on their strength. Cold acts in the same way.

(17) Endodermal glandular cells, presumed to produce proteolytic enzymes, occur in the distal part of the gastrozooids. Certain cells in the proximal region are also of a glandular character. The cells of the villi are phagocytic. The dark matter in them appears to derive from dermal pigments of captured fish. Nematocysts, apparently taken in with the food, also occur together with other matter undergoing digestion in the villus cells. The histology of the endoderm of palpons resembles that of gastrozooids except that the buccal gland cells are relatively less well developed.

(18) Non glandular absorptive cells occur throughout the endoderm in non-digestive regions, together with 'goblet' cells. All endoderm cells are flagellated but exceptionally long flagellae (25 μ) are associated with the buccal endoderm of the gastrozooids.

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PLATE VII

Post-larvae of *Physalia physalis* collected by Miss Dodge near Miami, Florida.

Fig. 1. Early stages showing the formation of cormidia II, III and VII are seen in the lowermost two larvae (cf. Text-fig. 23 *D*). Cormidia I and IV can be seen as buds in the top right specimen (cf. Text-figs. 23 *J* and 24, *A* and *B*). × 7·3.

Fig. 2. Two of the earliest stages of development of cormidia II, III and VII (cf. Text-fig. 23 *B*, *D*, *E* and *G*). × 16 approx.

Fig. 3. The lowermost specimen shows buds of cormidia I, II, III and VII. The square-shaped bud is the ampulla of II group$_1$, and is separated by its tentacle from the gastrozooid of II group$_1$. The uppermost specimen shows the extent of the pneumatocyst (cf. Text-figs. 23 *J* and 24 *A* and *B*). × 11·4 approx.

Fig. 4. The four buds seen clearly in the centre and lower right specimens are those of gastrozooid II, ampulla II, gastrozooids III$_1$ and VII$_1$ (cf. Text-figs. 23 *J* and 24 *A* and *B*). × 7·3.

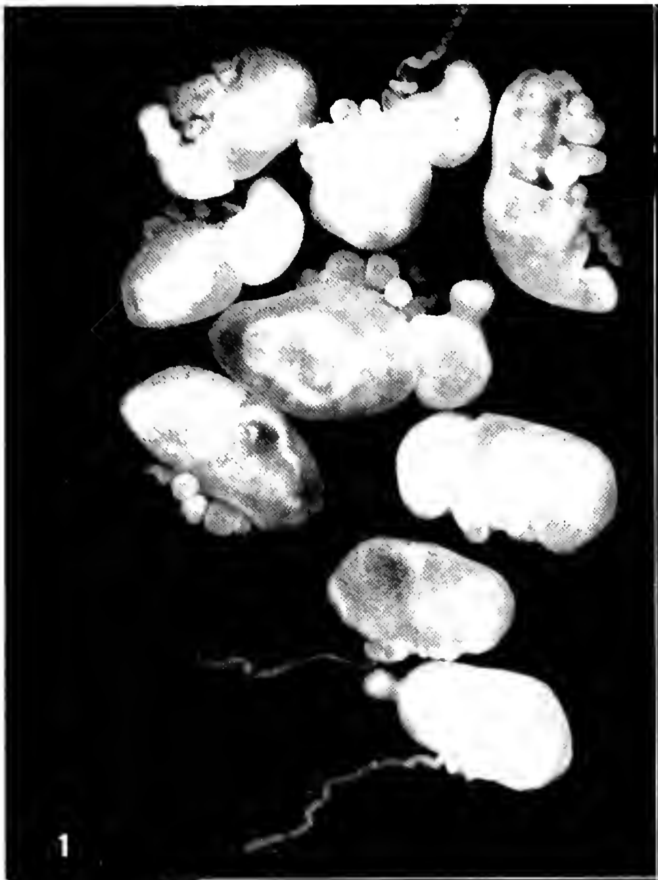

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PLATE VIII

Fig. 1. A young left-handed *Physalia* from Arrecife, specimen Juv. 12, float-length 2·9 cm., showing crest, gas-gland, basal internode, main tentacle (cormidium II) and individual groups of cormidium I. × 1·9.

Fig. 2. A young right-handed *Physalia* from Arrecife, specimen Juv. 8, float-length 3 cm., viewed from above, showing early stages of crest-development, oral zone and main zone of six cormidia separated by the basal internode. The limits of cormidium III can be seen extending from the oral side of the main tentacle (II) to the large gastrozooid of its group 1 on the other side. × 2.

Fig. 3. A left-handed young specimen from Arrecife, Juv. 5, float-length 19 mm., viewed from the leeward (under) side. There are six cormidia in the main zone and five in the oral. × 4·7.

Fig. 4. The same from the windward (upper) side. At this stage some main zone cormidia bear a larger windward gastrozooid (group 1) and a smaller leeward one. In the oral zone two gastrozooids of groups 1 and 2 predominate (cf. Text-fig. 22). × 4·7.

Fig. 5. A young right-handed *Physalia*, K2, float-length 12 mm., gas-gland diameter 2·5 mm., taken by Miss Dodge near Miami, Florida, viewed from the leeward (under) side. There are seven cormidia in the main zone. × 5. (For details see Text-fig. 16.)

Fig. 6. The same specimen from the windward (upper) side. Cormidium VI is partly hidden by VII (cf. Text-fig. 19).


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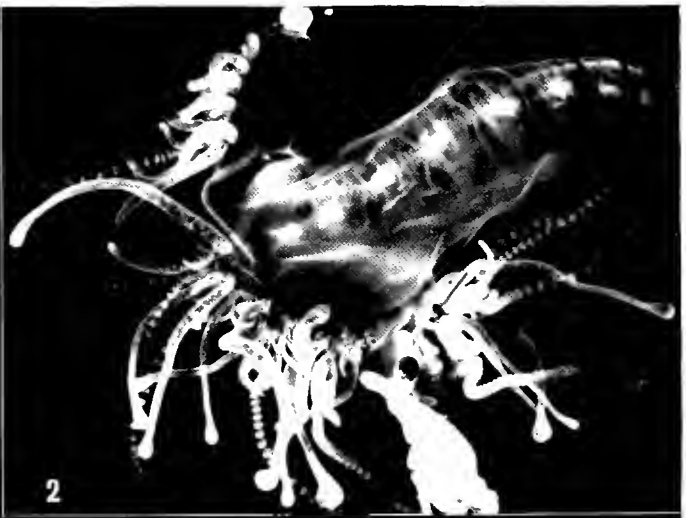
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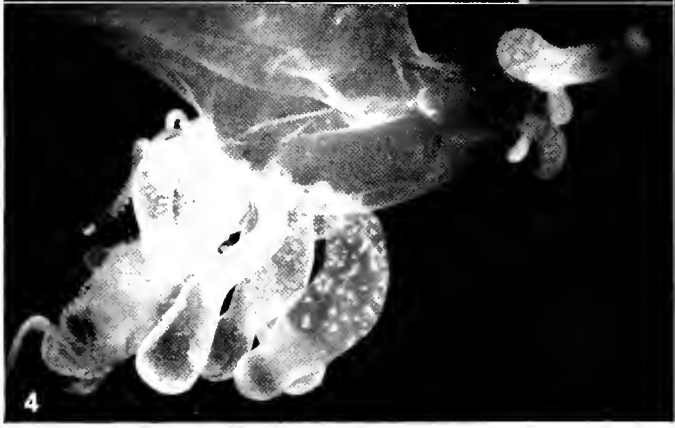
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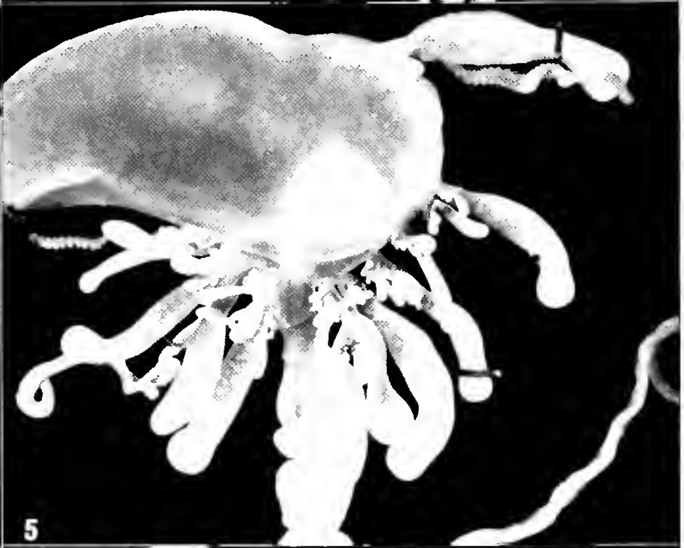
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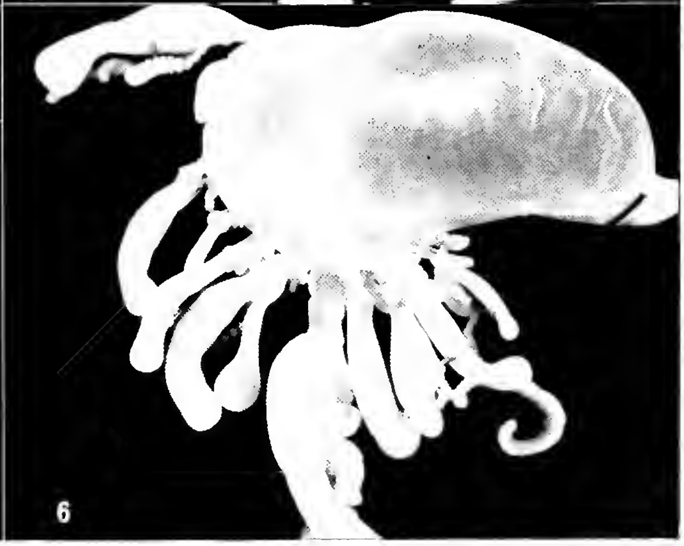
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PLATE IX

Fig. 1. A medium sized, right-handed, living specimen in a tank at Miami Marine Laboratory. By courtesy of Dr Charles E. Lane.

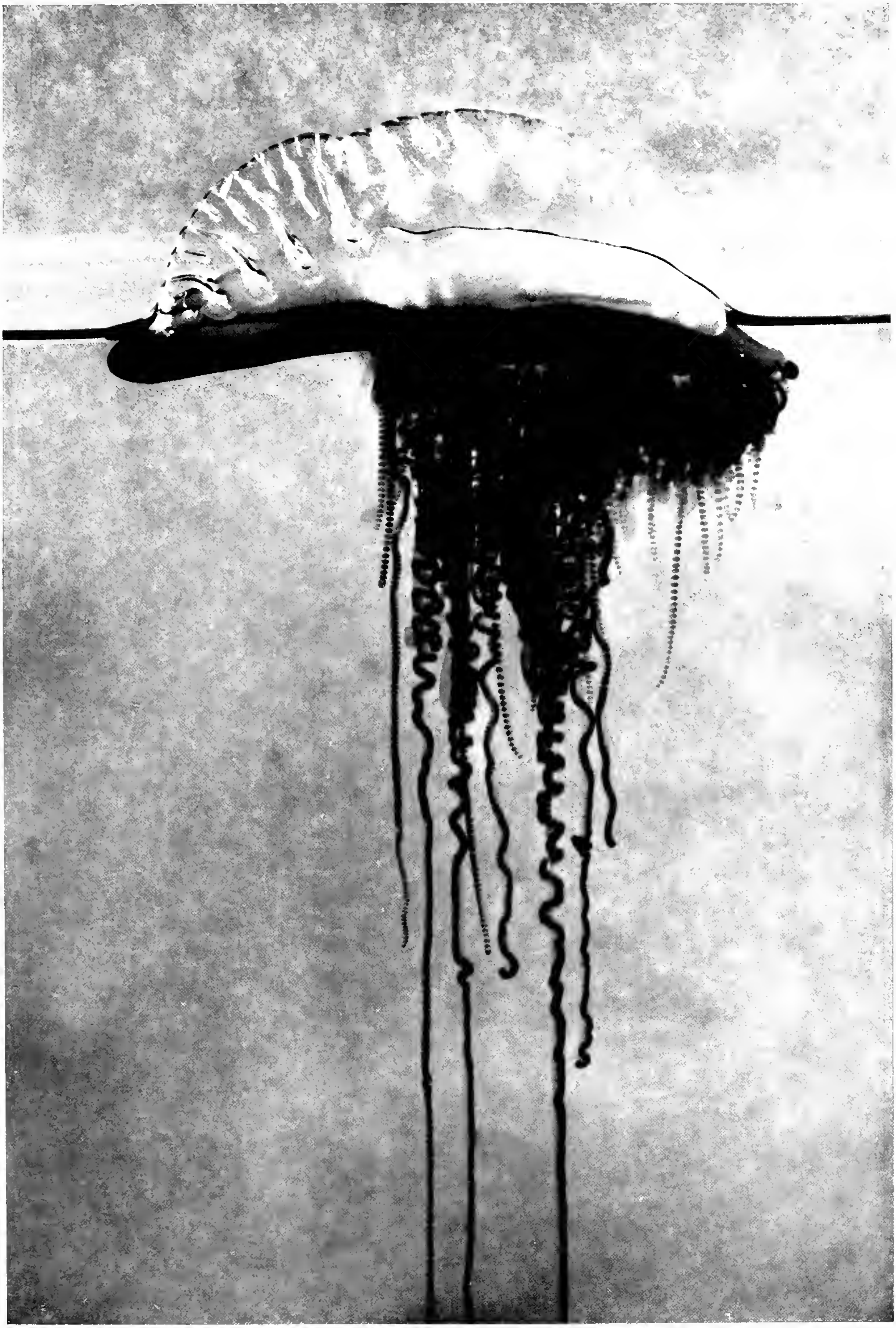

PLATE X

Figs. 1–6. Living *Physalia* rolling in a laboratory tank at Arrecife. Figs. 2, 3 and 5 show phases of the righting motion. The aboral end is raised as in figs. 2 and 3, and after twisting movements falls over as in figs. 4 and 6. The gas-gland can be seen in figs. 1 and 3.

Fig. 7. Air-sac of *Physalia* dissected out and fixed in a state of artificial compression (tied off near pore) to show partially inflated dorsal processes, and the disk-shaped gas-gland. × 1·25.


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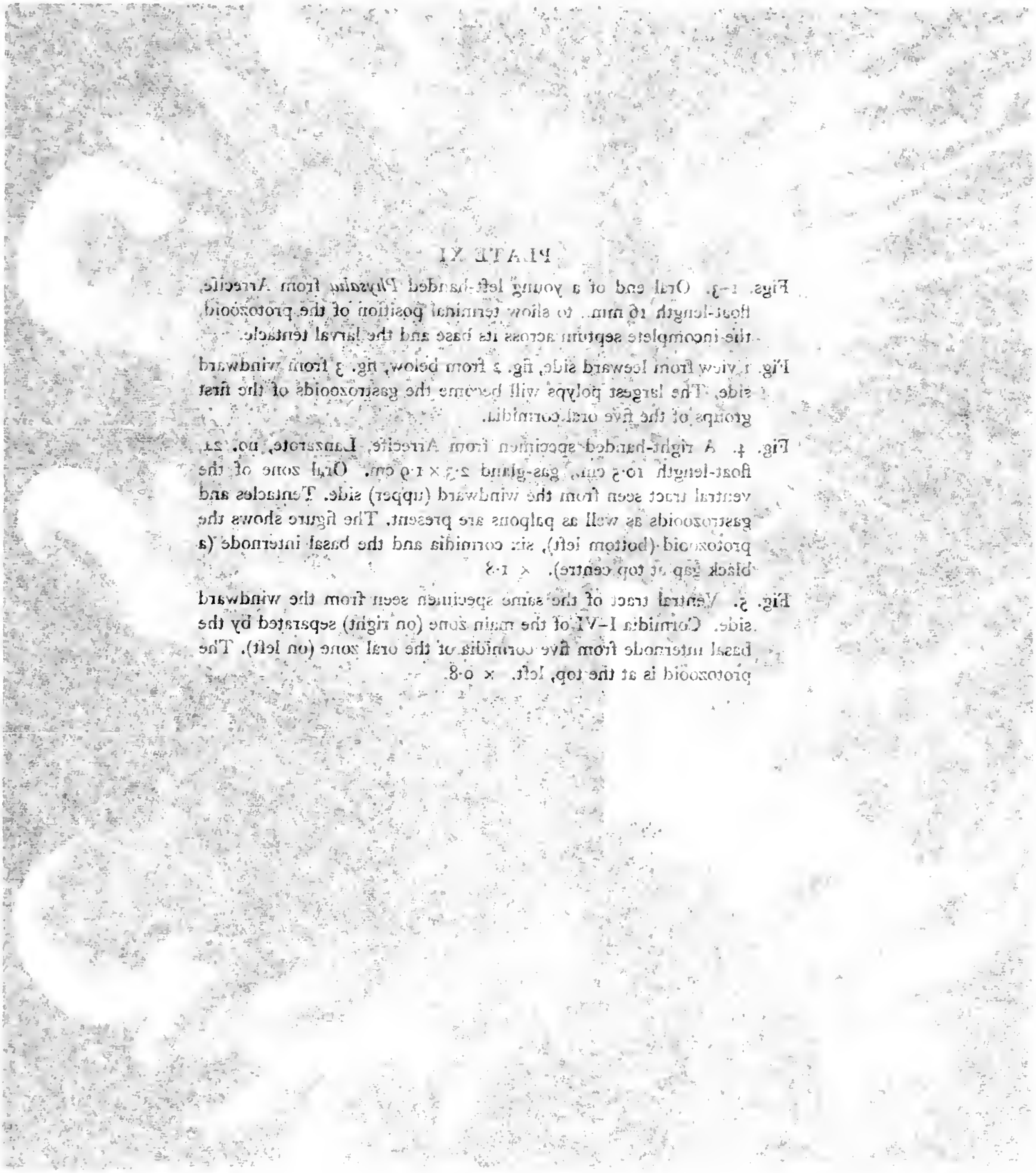


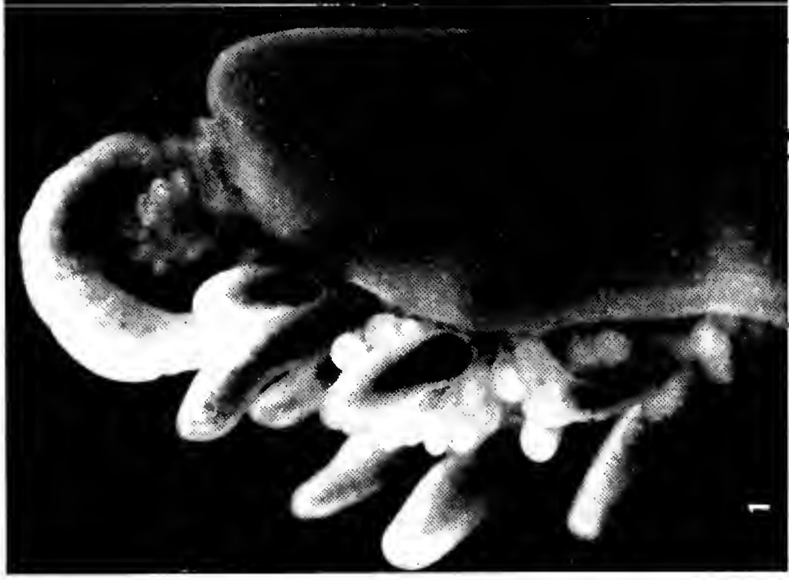
PLATE XI

Figs. 1–3. Oral end of a young left-handed *Physalia* from Arrecife, float-length 16 mm., to show terminal position of the protozooid, the incomplete septum across its base and the larval tentacle.

Fig. 1 view from leeward side, fig. 2 from below, fig. 3 from windward side. The largest polyps will become the gastrozooids of the first groups of the five oral cormidia.

Fig. 4. A right-handed specimen from Arrecife, Lanzarote, no. 24, float-length 10·5 cm., gas-gland 2·3 × 1·9 cm. Oral zone of the ventral tract seen from the windward (upper) side. Tentacles and gastrozooids as well as palpons are present. The figure shows the protozooid (bottom left), six cormidia and the basal internode (a black gap at top centre). × 1·8

Fig. 5. Ventral tract of the same specimen seen from the windward side. Cormidia I–VI of the main zone (on right) separated by the basal internode from five cormidia of the oral zone (on left). The protozooid is at the top, left. × 0·8.



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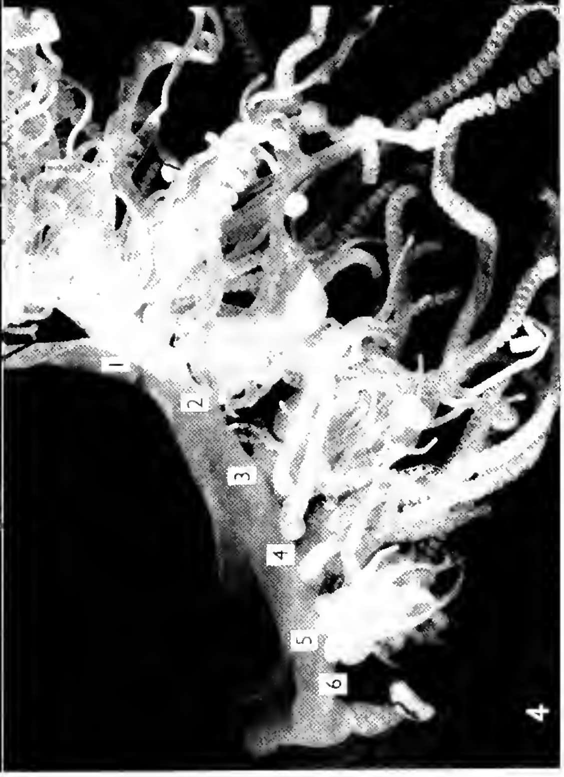

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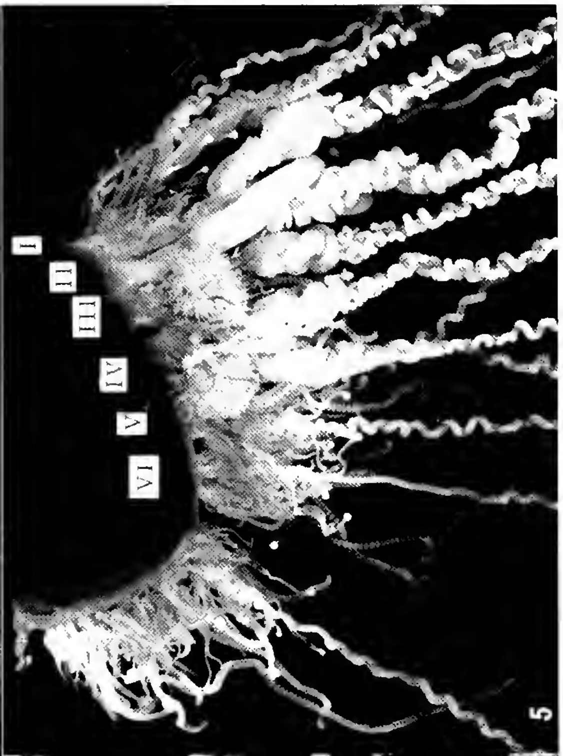

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PLATE XII

Figs. 1–3. A left-handed specimen from Lanzarote, no. 3, float-length 9 cm., gas-gland diameter 2·3 cm. Cormidia IV, III, and II seen from the aboral end to show similarity of pattern of all cormidia, and acceleration of growth in those at the aboral end. Terminal lateral groups at top right, lee-branches on left and aboral branch in centre. × 1·3.

Fig. 4. The same specimen as in figs 1-3. Cormidium IV seen from the oral end to show the characteristic gastrozooid and gonophore of group 1 (black background). × 2·2.

Fig. 5. The same specimen as in figs. 1–3. Cormidium II seen from the aboral end to show lee-branches (top left), terminal lateral groups (top right), aboral branch (centre, black background) and gonodendron of group 1 (main). × 2·6.

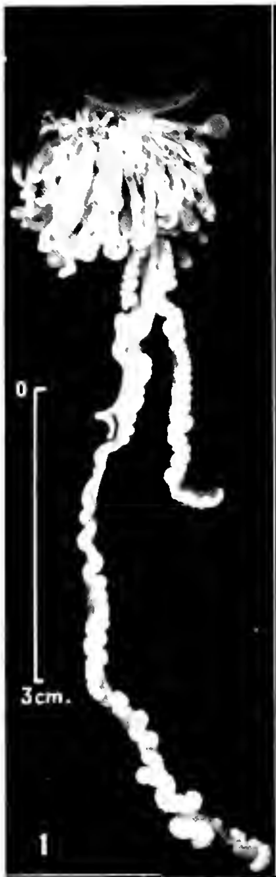

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PLATE XIII

Fig. 1. A left-handed specimen from Lanzarote, no. 25. Ventral tract seen from inside the float (above), oral end to the right after injection of black gelatine into cormidia (except I). × 1·3.

Fig. 2. A young left-handed specimen from Lanzarote, no. Juv. B, float-length 8 cm., seen from above or windward side. The distinctness of the groups of cormidium I can be seen at the aboral end (left). The largest ampulla is that of group 2 of cormidium II. Parts of cormidium I and II are obscured by the black background inserted under the groups of cormidium I. The other side is shown in fig. 4. × 2.

Fig. 3. The same specimen. Cormidium II from the windward side. At top left (aboral end) appears the precocious gastrozooid of group 1, and below its point of attachment is the slender peduncle of its gonodendron. Its (main) tentacle and ampulla lie to the right. × 5·7.

Fig. 4. The same specimen. Cormidium I seen from below or the leeward side. The other side is shown in fig. 2. The tentacle of group 1 is on the left. × 5.

Fig. 5. The same specimen. Cormidia III, IV, V and VI. Main tentacle of II on the left. Note the four prominent gastrozooids of the first groups (which do not bear tentacles) that grow directly from the bladder-wall, and are some of the earliest buds to appear. The large horizontal gastrozooid is part of group 1 of cormidium III. The vertical two gastrozooids at a lower level are parts of groups 1 of cormidia IV and V. The horizontal gastrozooid at a higher level (right) is part of group 1 of cormidium VI. × 5.7.

Fig. 6. The same specimen. Cormidium III seen from the windward side (oral end to the right). Gastrozooid and gonodendron of group 1 on the right. Terminal lateral groups on the left. This stage of development is rather later than that shown in the figures of specimen K2. × 5·7.

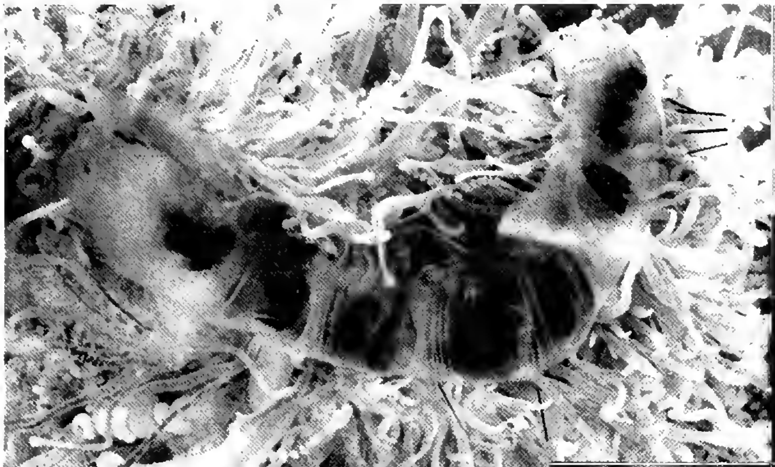


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PLATE XIV

Fig. 1. Cormidium IV of a young left-handed specimen from Lanzarote, no. Juv. 11, to show stages in the growth of the tripartite groups. Group 1 (bottom) has a gastrozooid and gonodendron, but no tentacle. Group 2 (right and centre) is tripartite, but the gastrozooid has been lost. Group 3 (top, left and right) is tripartite. Group 4 (left and across to top right) is tripartite. × 8. For drawing of a comparable cormidium of the oral zone see Text-fig. 15.

Fig. 2. Part of cormidium I of specimen no. 5 from Lanzarote to show an early growth stage of a tripartite group (black background below) gastrozooid, tentacle and ampulla, and gonodendron. × 6·5.

Fig. 3. A young left-handed specimen from Lanzarote, no. Juv. 12 (cf. Pl. VIII, fig. 1), float-length 2·9 cm., gas-gland diameter 7 mm., seen from the upper or windward side to show eight individual groups of cormidium I, on the left; main tentacle (cormidium II) on the right, with lateral groups on its left; tentacle (ampulla) and gastrozooid of groups 1 of cormidium I (gonodendron underneath) in centre; tentacle (gonodendron lying over it, gastrozooid missing) of group 2 of cormidium I; groups 4–8 of cormidium I at top left. There are no nematocyst heads yet developed on the tentacles of groups 5–8 (see Pl. XV, fig. 5 for more mature state of the projection carrying the terminal laterals of cormidium I). × 5·5.

Fig. 4. A right-handed specimen from Lanzarote, no. 5, float-length 11·5 cm. Cormidium I viewed from windward and slightly above to show: main series of groups (eleven), oldest on the left, youngest curling back almost to meet it; lee-branches at top left and right; aboral branch just under a horizontal tentacle of lee-branch at right indicated by a white pointer; scar of gastrozooid of main group at right base of its peduncle; gonodendron of main tentacle to left of its peduncle. Tentacles of groups 6, 7, 8, and 9 lie on the top of those of 2 and 3. × 2·3.


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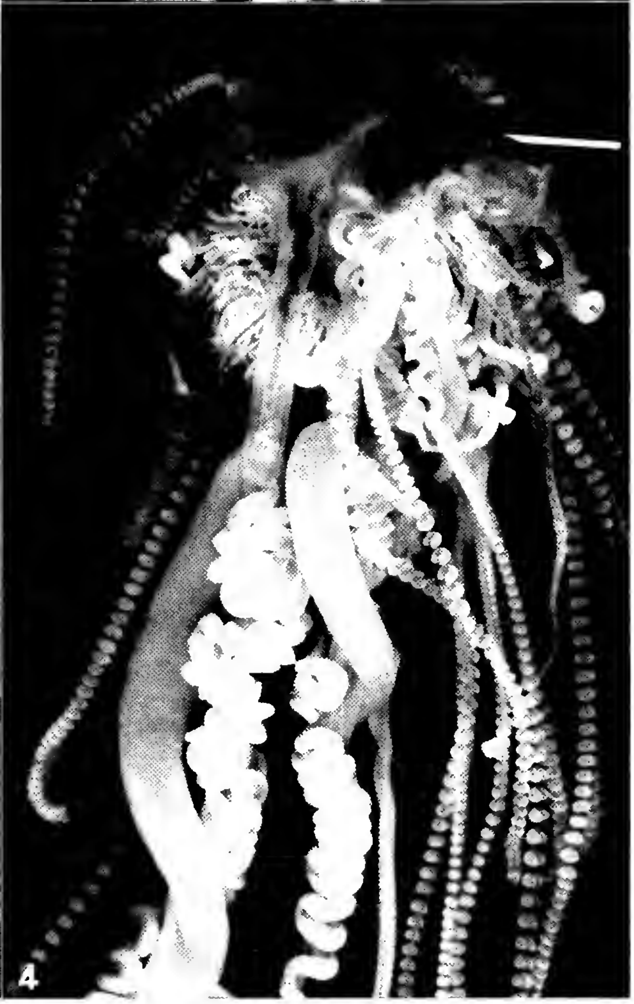
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PLATE XV

Fig. 1. A young left-handed specimen from Lanzarote, no. Juv. 12, float-length 2·9 cm., gas-gland diameter 7 mm., seen from leeward (under) side to show early growth stages of lee-branches (on black background) at base of cormidium III (five groups to the left, two to the right). All three parts of a young group can be seen in the left-hand branch (oral end) of group 1 at base of cormidium III (on right-hand black background), tentacle, gastrozooid and gonodendron (reading from right to left). × 4.

Fig. 2. Specimen Juv. B. Cormidia V and VI before separation (oral end to the right) seen from to windward. Cormidium VI is seen partly from the aboral end. The figure shows the conspicuous, precocious gastrozooid of group 1 of V and of VI (right), and the peculiar gonodendron; the lateral groups of VI (bottom centre); on the left, the gastrozooid and gonodendron of group 1 of VI (above), and lateral groups (below). × 5·3.

Fig. 3. A left-handed specimen from Lanzarote, no. 25. Cormidium III seen from above (inside float) to show lee-branches (top right). The main series of lateral groups is at the bottom, group 1 to the right. × 1·6.

Fig. 4. A left-handed specimen from Lanzarote, no. 2, float-length 10 cm., Cormidium I to show individual groups (sixteen). The gastrozooid is on the aboral side of each group; the gonodendron is hidden underneath (except that of group 2). The bases of the peduncles were cut in dissection. × 1·5.

Fig. 5. A right-handed specimen, B.M. Register no. 26.3.6.1, float-length 18·5 cm., taken by R.R.S. 'Discovery' on 21 October, 1925, in 27° 15′ N., 15° 32′ W. Cormidium I viewed from aboro-windward side to show the projection formed by the younger lateral groups of I (to which all these tentacles belong). For an earlier stage of development of this area, see Pl. XIV, fig. 3. × 1·4.

Fig. 6. A left-handed specimen form Lanzarote, no. 16, float-length 12 cm. Cormidium I to show curled-up terminal, lateral groups, fourteen in number. × 5.


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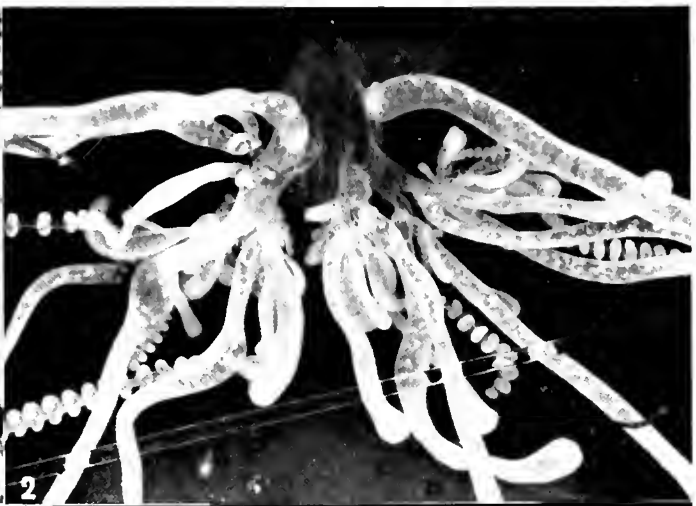
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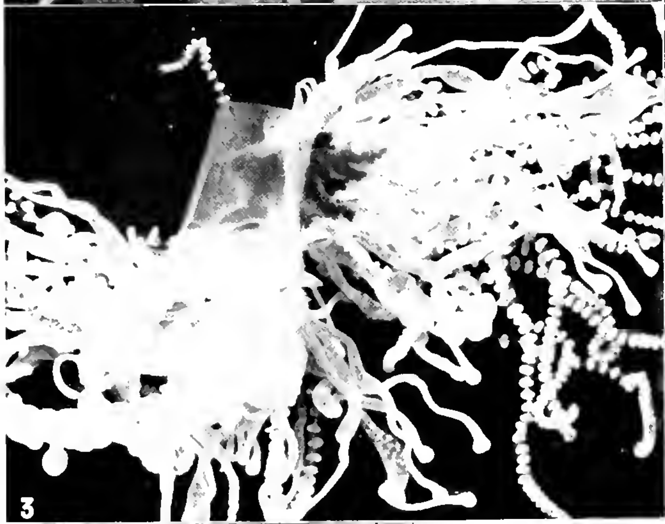
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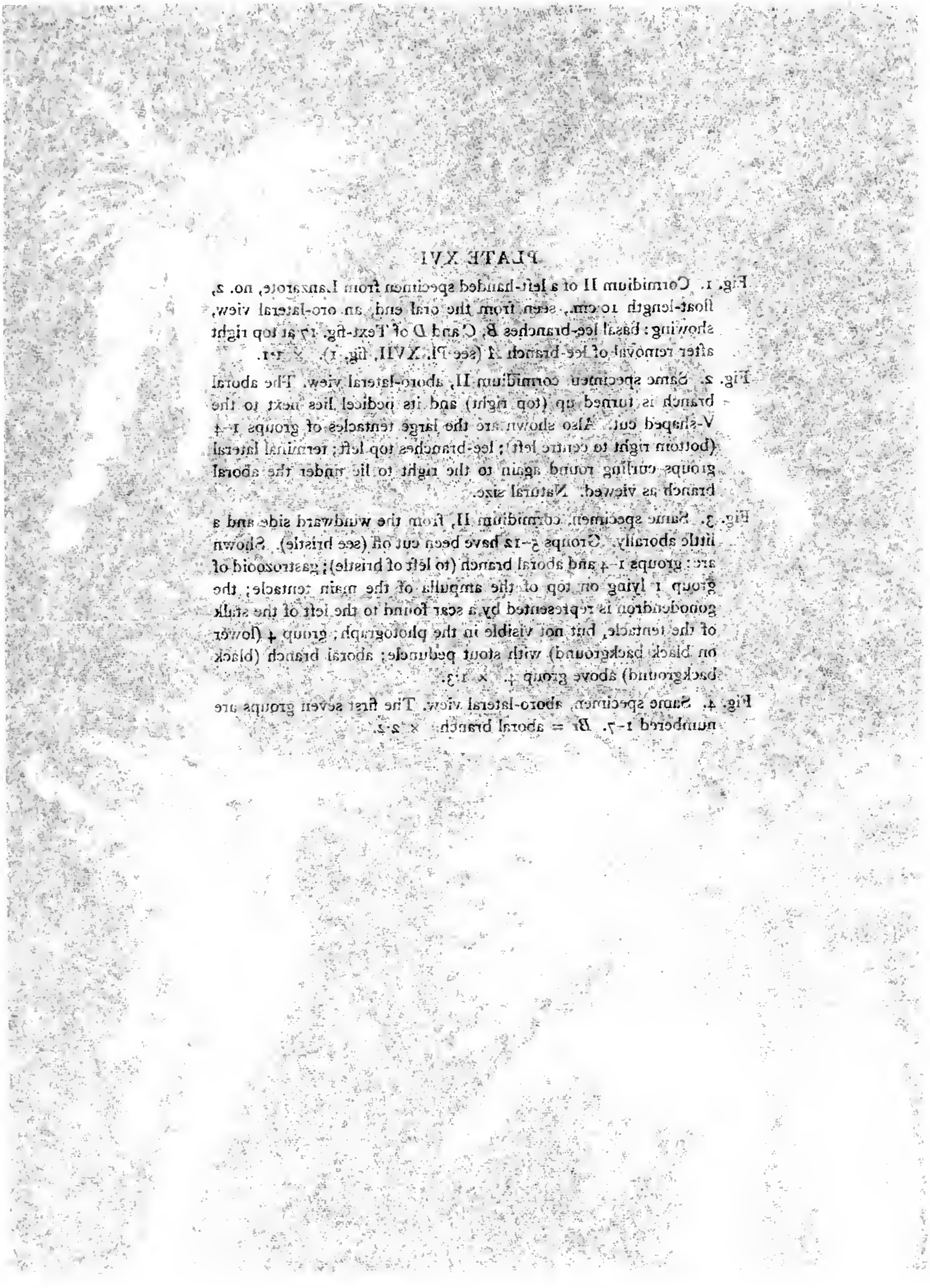

PLATE XVI

Fig. 1. Cormidium II of a left-handed specimen from Lanzarote, no. 2, float-length 10 cm., seen from the oral end, an oro-lateral view, showing: basal lee-branches *B*, *C* and *D* of Text-fig. 17 at top right after removal of lee-branch *A* (see Pl. XVII, fig. 1). × 1·1.

Fig. 2. Same specimen, cormidium II, aboro-lateral view. The aboral branch is turned up (top right) and its pedicel lies next to the V-shaped cut. Also shown are the large tentacles of groups 1–4 (bottom right to centre left); lee-branches top left; terminal lateral groups curling round again to the right to lie under the aboral branch as viewed. Natural size.

Fig. 3. Same specimen, cormidium II, from the windward side and a little aborally. Groups 5–12 have been cut off (see bristle). Shown are: groups 1–4 and aboral branch (to left of bristle); gastrozooid of group 1 lying on top of the ampulla of the main tentacle; the gonodendron is represented by a scar found to the left of the stalk of the tentacle, but not visible in the photograph; group 4 (lower on black background) with stout peduncle; aboral branch (black background) above group 4. × 1·3.

Fig. 4. Same specimen, aboro-lateral view. The first seven groups are numbered 1–7. *Br* = aboral branch. × 2·2.


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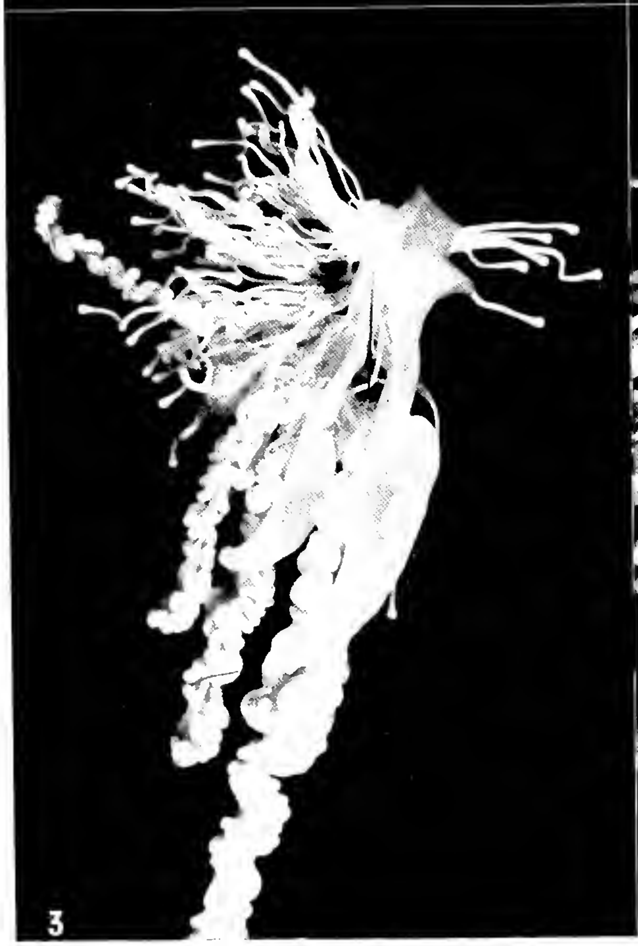
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PLATE XVII

Fig. 1. Part of cormidium II of specimen Lanzarote no. 2. Separated branchlet 6 of the lee-branch figured in fig. 2. × 2·6.

Fig. 2. One of the basal lee-branches (see Text-fig. 17*A*) cut from cormidium II, consisting of six branchlets representing the remains of tripartite groups 1–5, or subsidiary basal branches, 5*a* and 6. Branchlet 1 has lost its gastrozooid; branchlets 2–5 are gonodendra only; 5*a* and 6 consist of five and six groups respectively (for branchlet 6, see fig. 1). × 1·3

Fig. 3. Cormidium III of specimen, Lanzarote, no. 2, seen from the aboral end after cutting off the terminal lateral groups 5–11 which are pinned out to the right (top). Shown are: lee-branches, top left; tentacle and gonodendron of group 1 (largest); tentacle and gonodendron of group 2, between T_1 and GON_1; gastrozooid$_4$, tentacle$_4$ and gonodendron$_4$ between T_1 and several laterals; T_3 and GON_3 between lee-branch and GON_1; bristle marks the spot from which lateral groups were cut. × 1·8.

Fig. 4. The same cormidium showing terminal laterals 5–11, group 5 on the left (group 11 is very small) and a subsidiary basal branch of two groups from the base of group 6 at the top. The divisions between the groups, except 9 and 10, are marked. × 5·4.

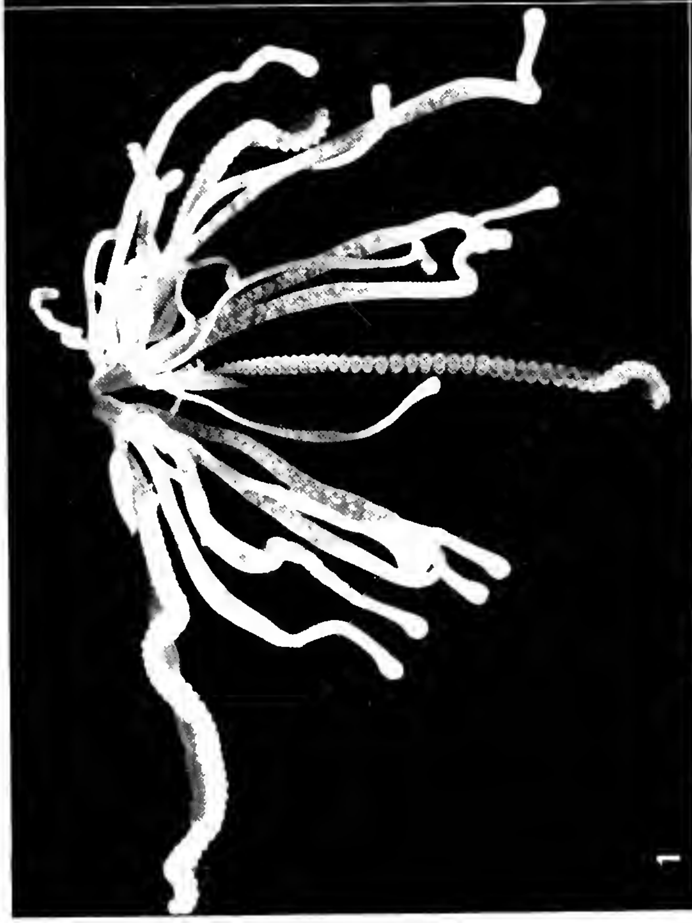
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PLATE XVIII

Fig. 1. Lanzarote specimen, no. 2. Cormidium III (less group 1) seen from the oral end to show: *GZ*, *T* (main tentacle) and ampulla, and *GON* of group 2; lee-branch, top right; and the series of lateral groups, bottom left. × 1·8.

Fig. 2. The same cormidium seen from the aboral end to show: lee-branches top left; terminal lateral groups right; middle lateral groups centre; aboral branch severed, on black background, after lowering from base of laterals. × 3.

Fig. 3. The same before cutting off branches. Lee-branches are shown at top left. × 1·8.

Fig. 4. The aboral branch from the base of group 5 of cormidium III of the same specimen to show: three groups, the largest, no. 1, on the right, smallest at top left; subsidiary basal branchlet of two groups from base of 1/2. The first has a light ampulla, the second is small (top right). × 3.

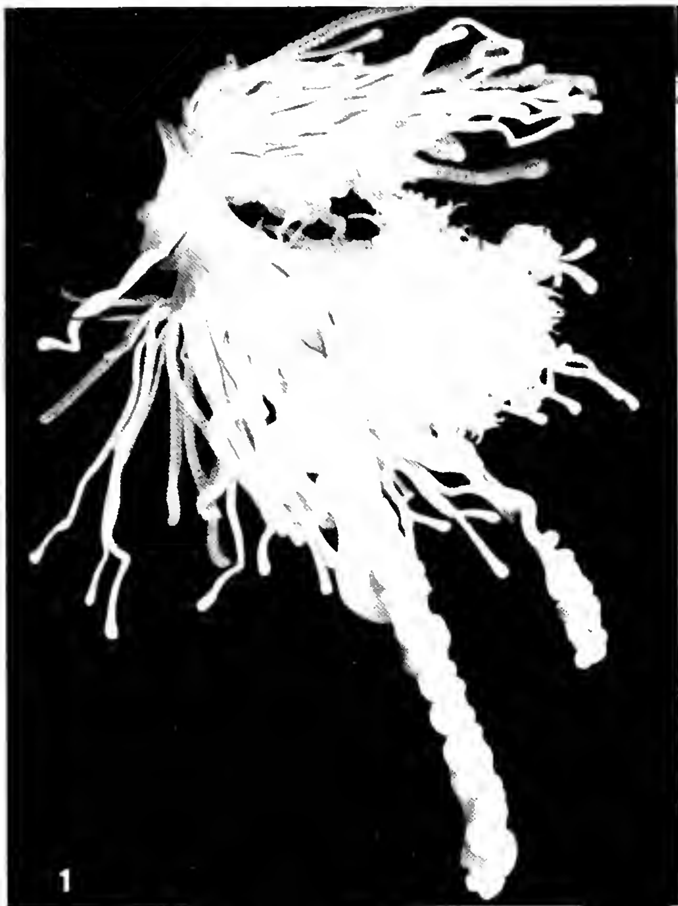
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PLATE XIX

Fig. 1. A young right-handed specimen from Arrecife, no. Juv. 8, float-length 30 mm., gas-gland diameter 5 mm., to show: oral zone with five cormidia; the basal internode between the oral and main zones; the large gastrozooid of group 1 of cormidium VII; and the protozooid and larval tentacle. × 3·8.

Fig. 2. Part of the oral zone of a left-handed specimen, Lanzarote, no. 25. Cormidia 1 and 2 seen from above. The finger-shaped projection (left centre) is the main series of lateral groups (axis filled with black gelatine). See schematic drawing, Text-fig. 12*C*, *D*. × 1·8.

Fig. 3. The same specimen seen, tilted back, from the aboral end and windward side to show: main series of lateral groups of cormidium 1, filled with black gelatine; lee-branch of cormidium 1 top left; aboral branch of cormidium 1; the peculiar gonodendron of group 1 of cormidium 1 top right; gastrozooid of group 2 of cormidium 1 overlying large ampulla of tentacle 2; gastrozooids of groups 3–6 of cormidium 1, bases filled with black gelatine; tentacle$_8$ of cormidium 1, just left of GZ_6; ampulla of tentacle$_7$, just to left of T_8. × 1·8. See schematic drawing, Text-fig. 12*C*.

Fig. 4. Specimen Lanzarote, no. 25. Oral zone of cormidium 1 seen from the aboral end, showing: GZ_1 top right; series of lateral groups, right top centre to left centre foreground; lee-branch top left; aboral branch left centre. × 5·4. See schematic drawing, Text-fig. 12*C*.

Fig. 5. The same cormidium seen from the oral end to show: GZ_1 top left; GON_1 left; lee-side of lateral groups centre; lee-branch right. × 5·4.


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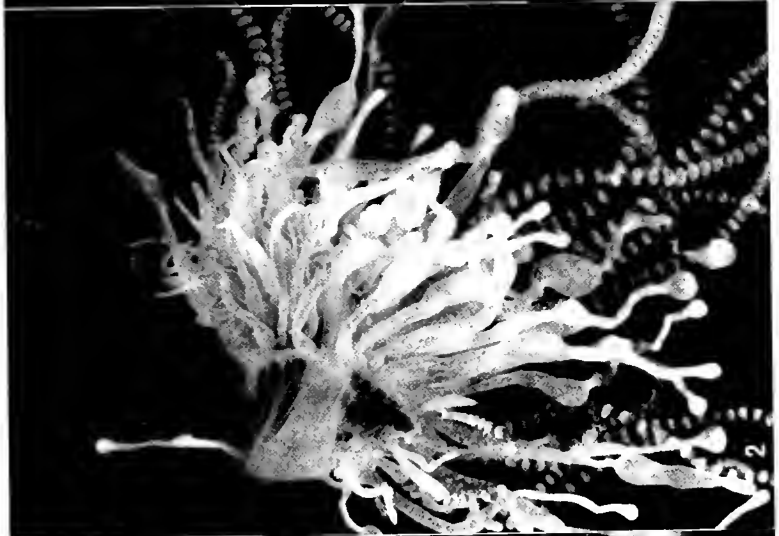
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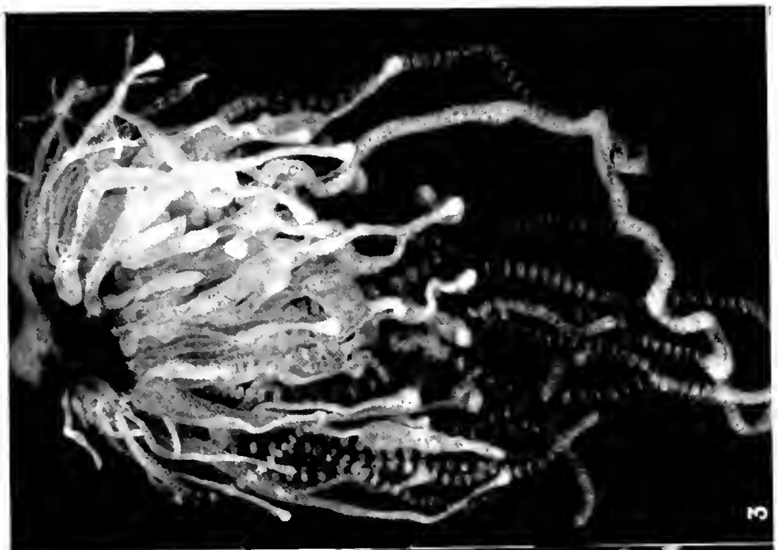
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PLATE XX

Fig. 1. A large, preserved right-handed *Physalia*, float-length 20 cm., from Villefranche, Mediterranean, by permission of Dr G. Tregouboff, Museum, Station Zoologique, to show gonodendra of a mature specimen. Cormidium 1 on the right. × 0·6.

Fig. 2. A mature gonodendron dropped by a living specimen in a laboratory tank at Arrecife. Photographed (as in life) after anaesthetization in $MgCl_2$ and fixation in formalin, and seen from above. × 1·3.

Fig. 3. One tripartite group of a cormidium of specimen Lanzarote, no. 2. Of the eight gastrozooids, number 3 with a prominent kink is probably the original one of the whole group, associated with the tentacle; numbers 2, 5, 7 and 8, which are gonozooids without tentacles, were budded from its base. The genital tufts (palpons, nectophores, gonophores and jelly-polyps) are budded from the bases of the gonozooids. For details, after removal of three branches, see Text-fig. 25. × 1·1.

Fig. 4. A young gonodendron from specimen Lanzarote, no. 2 from basal branch *A* (branchlet 3) of cormidium II. The polyps whose tips can be clearly seen are palpons; the long polyps are gonozooids (with no tentacles). × 4.

Fig. 5. A gonodendron not fully developed. × 8.

Fig. 6. A mature gonodendron dropped by the same living specimen shown in fig. 2, seen from the side. × 1·5.


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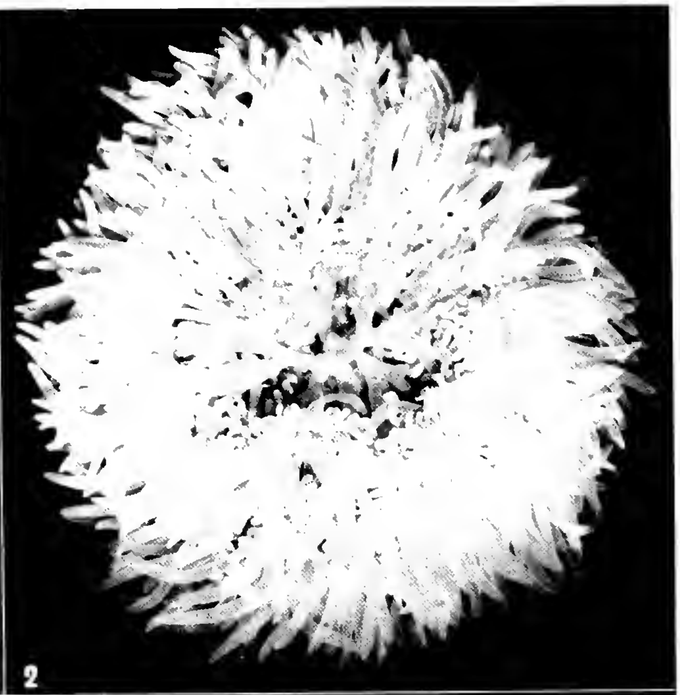
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PLATE XXI

Fig. 1. End branchlets of an immature gonodendron to show the pattern of arrangement and the open endodermal canals in the stalks of the nectophores. × 5.

Fig. 2. One end-branchlet of an immature gonodendron, enlarged. × 8·7.

Fig. 3. Part of a gonodendron to show a fully developed end-branchlet consisting of a terminal section (jelly-polyp and terminal palpon) and a sub-terminal section (nectophore and palpon). Several female gonophores are visible. The endodermal canal of the nectophore is now occluded and the mesogloea hypertrophied both in the nectophore and jelly-polyp. *p.st* = sub-terminal palpon, *n* = nectophore, *p.t* = terminal palpon, *jp* = jelly-polyp. × 7.

Fig. 4. Part of an immature gonodendron of a female specimen from the Scilly Isles, kept for a time in a tank in the Laboratory, Plymouth, in November 1954. There are two end-branchlets lying partly on top of each other, so that the jelly-polyp of the right-hand branchlet is almost hidden by the shorter, central palpon. The proximal gonophores are more fully developed than the distal ones. The lumen of the endodermal canal of the stalk of the nectophore is still open. × 16.

Fig. 5. An end-branchlet of a gonodendron in a middle stage of development. The jelly-polyp is seen as a hollow, finger-shaped process next to the palpon of the terminal section. At this stage of development the endodermal canal of the stalk of the nectophore is wide open. × 31.

Fig. 6. Part of a branchlet of an immature gonodendron which has lost the sub-terminal palpon and most of the gonophores. Jelly-polyp on the left, terminal palpon at the bottom, nectophore and gonophore. The radial and circular canals of the nectophore can be seen in optical section, and also the muscular lamella on the stalk of the nectophore. × 25.

Fig. 7. The Plymouth specimen (see fig. 4), showing a pair of end-branchlets of a maturing gonodendron. That on the right differs rom the usual type (on the left) in having two terminal sections nstead of one terminal and a sub-terminal section, and so in being vithout a nectophore. Each section on the right has a jelly-polyp, erminal palpon and gonophores. × 10·3.

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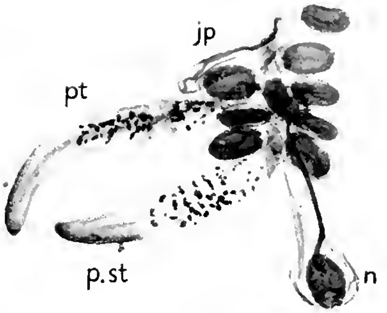

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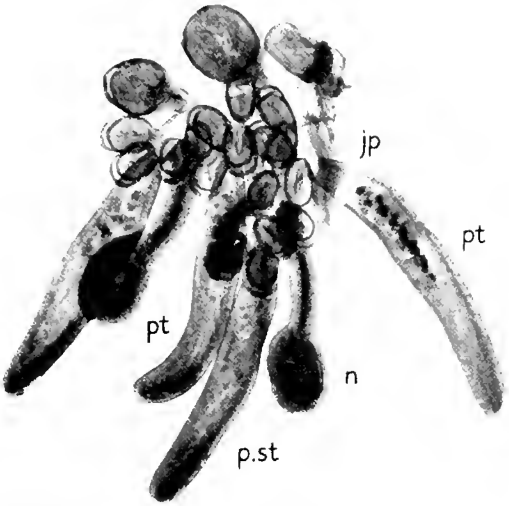

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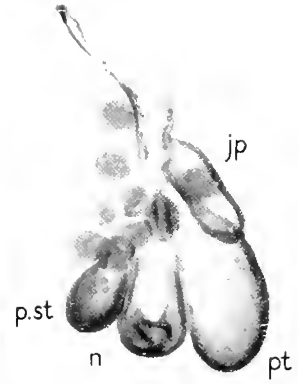

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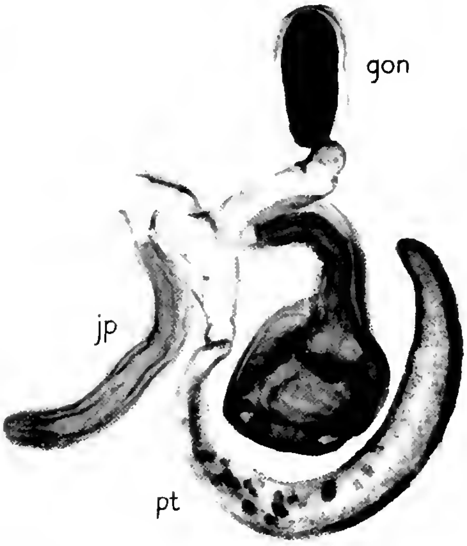

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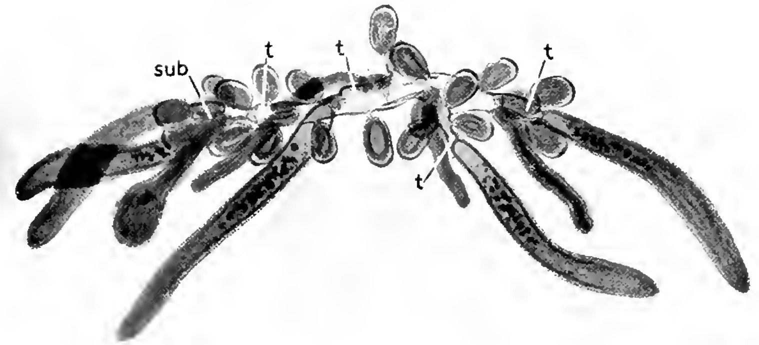

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PLATE XXII

Genital tufts of gonodendra

Figs. 1, 2, 3 and 7. Early growth stages (cf. fig. 2 with Text-fig. 27 *G*).

Fig. 1 × 36, fig. 2 × 70, fig. 3 × 76, fig. 7 × 65.

Fig. 4. Terminal and sub-terminal sections of end-branchlets. × 60.

Fig. 5. Middle stage of development of an end-branchlet (cf. Text-fig. 27 *G* for an earlier stage of the same). × 55.

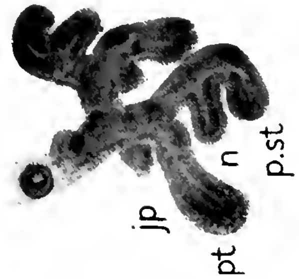
Fig. 6. (In the 'key' stage of development) showing two branchlets growing out sub-terminally from the large palpon. The smaller one consists of only the usual two end sections, terminal and sub-terminal; the second itself bears a similar branchlet growing out sub-terminally opposite its larger terminal palpon. The left-hand part of this specimen was removed for the sake of clarity. × 40.

Fig. 8. (Cf. with fig. 6) showing rapid growth of the terminal palpon, on the tip of which can be seen a heavy armature of nematocysts. Its jelly-polyp can be seen below the palpon. × 30.

Fig. 9. A 'key' stage showing how a sub-terminal section buds from a terminal one. × 79.

Fig. 10. Showing a branchlet 'dividing' three times; three end sections on the right, three on the left and numerous gonophores. The tips of the palpons are heavily armed with nematocysts. The right side is comparable with fig. 8. × 36.

Fig. 11. Showing how complicated the genital tufts look when lying side by side. Here two tufts, partially separated, have been flattened in one plane on a microscopical slide. × 37.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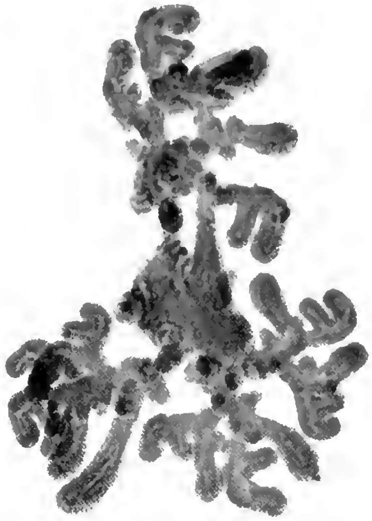

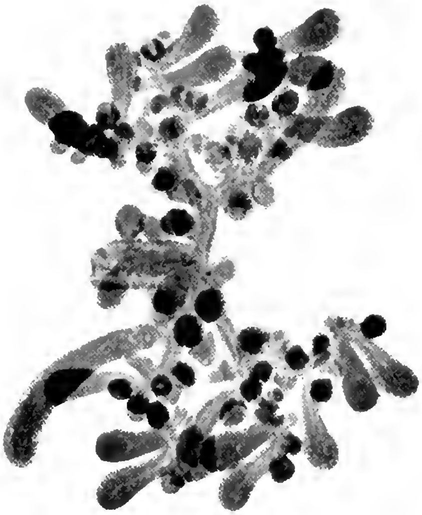

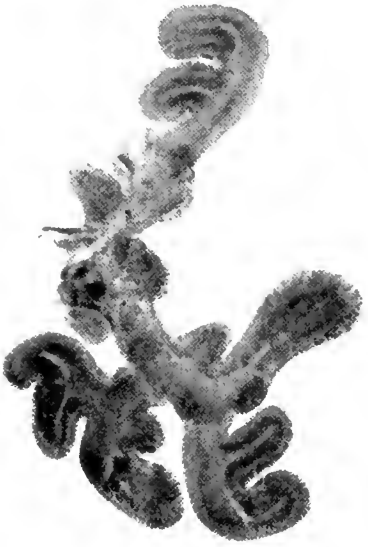

PLATE XXIII

Fig. 1. Young stage of development of a genital tuft of a gonodendron of the Plymouth specimen. × 55.

Fig. 2. Part of an immature male gonodendron, middle stage of development of an end-branchlet, showing its origin as a sub-terminal bud growing out opposite a jelly-polyp of a terminal palpon. The terminal section on the left (jelly-polyp and palpon) has not developed a sub-terminal pro-bud, which might have given rise to a pair of similar end-branchlets. × 40.

Fig. 3. Part of an immature gonodendron of the Plymouth specimen. Passing from below round to the top right three typical end-branchlets at an early stage of development can be seen. Each consists of a terminal section (appearing to be basal and consisting of jelly-polyp and terminal palpon) and a sub-terminal section (top right) consisting of nectophore and sub-terminal palpon. Rudiments of gonophores are visible. One gonophore always appears at the base of the terminal palpon. × 55.

Fig. 4. Part of the ectoderm of a female gonophore freed from the endoderm and the covering exumbrella of the medusoid, to show the sinuous band of oogonia. × 15, further magnified on the right.

Fig. 5. Fully grown male gonophores. Inside the thin outer membranes can be seen the cap of spermatocytes, completely surrounding the spadix. × 17.

Fig. 6. Part of a female gonodendron from specimen Lanzarote, no. 25, dropped in the laboratory, to show the endoderm of the gonophores drawn inside out into the lumen of the branch of the gonodendron. × 15.

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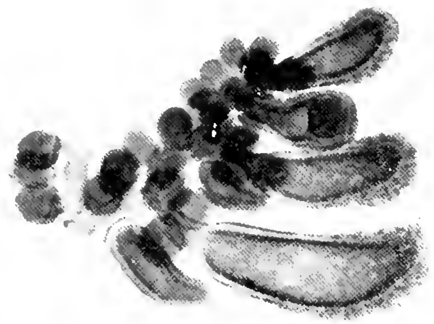

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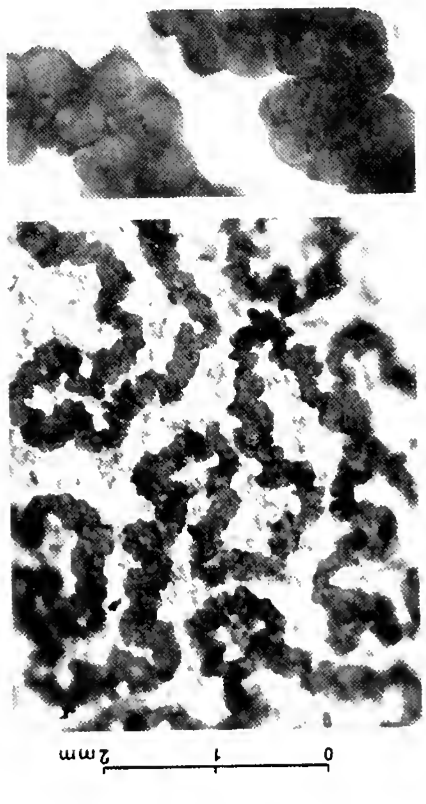

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PLATE XXIV

Female gonophores

Figs. 1 and 2. Young growth stages in transverse section. The radial canals are visible in the endoderm of the outer wall and the oogonia in the ectoderm of the spadix. × 242.

Fig. 3. Transverse and longitudinal sections in an end-branchlet of a gonodendron. The section passes through the bases of a nectophore and jelly-polyp (left and right centre), but below the bases of the two palpons of the terminal and sub-terminal sections of the branchlet. A terminal palpon is visible, bottom right. Similarity in structure is shown in the nectophore and jelly-polyp—type of ectoderm hypertrophied mesogloea, occlusion of canal and muscular lamella. × 38. (See Text-fig. 29.)

Figs. 4–7. Growth of the nectophores (seen in optical section). In fig. 5 the perforation of the velum is visible; in fig. 6 the endodermal canal is occluded; in fig. 7 the gastrovascular space of the stalk is wide open, and the ectoderm can be seen cupped in the endoderm. Radial and circular canals are visible in optical section. Fig. 4 × 50, fig. 5 × 55, fig. 6 × 50, fig. 7 × 219.

Figs. 8–15. Young male gonophores (seen in optical section). Photomicrographs to show stages in the growth of the entocodon which gives rise to the cup-shaped mass of spermatocytes that later covers the spadix. The smaller gonophore (fig. 13) shows the earliest stage, comparable with the entocodon of the much larger nectophore that grew alongside it (fig. 7) and measures 0·1 mm. in diameter. In the larger gonophore (fig. 13) the base of the entocodon has started to grow over the spadix, and the primary endoderm has become reduced in thickness though it contains vestiges of two or three radial canals. × 270.

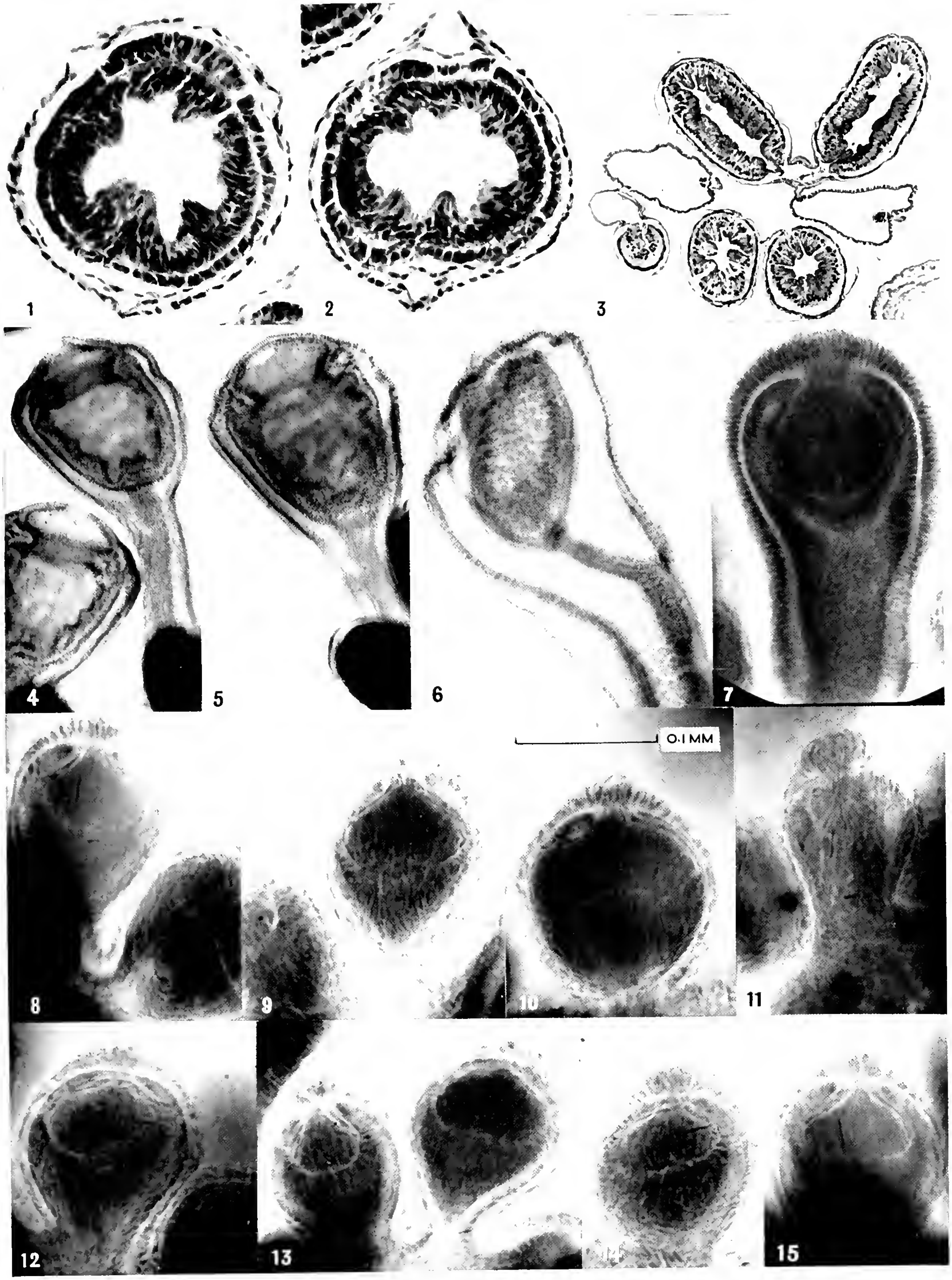
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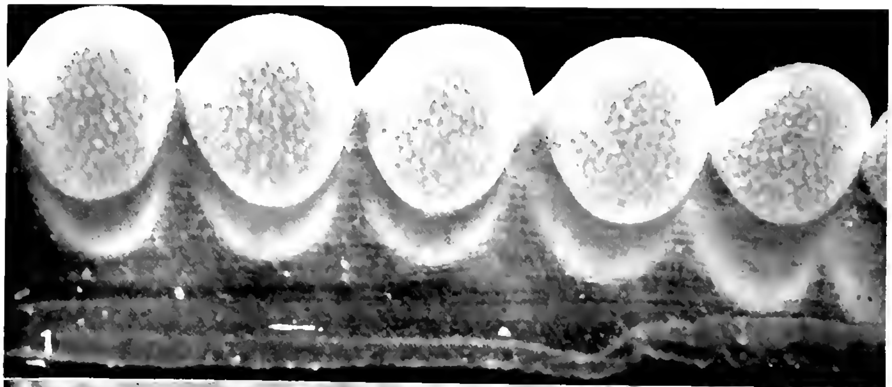
PLATE XXV

Fig. 1. Part of a small tentacle from a basal branch of cormidium II of specimen Lanzarote, no. 2, to show the longitudinal muscular lamella and nematocyst heads, each containing about 600 nematocysts (0·027 mm. or $\frac{1}{1000}$ inch in diameter). × 30.

Figs. 2 and 3. Palpons of a specimen from Chesil Beach, Dorset, B.M. Register no. 1954.10.9.1, to show apical opening of palpons, analogous to an anus. Fig. 2 × 29, fig. 3 × 25.

Fig. 4. Living and still reactive tentacular nematocysts of *Physalia* (by courtesy of Dr Charles E. Lane, University of Miami). The two size groups average 11·5 μ and 26·8 μ in diameter. Optical sections of the coiled-up threads show that the threads taper towards the tip (anisorhizas). The point of emergence (*P*) to which the base of the thread is attached is indicated in this photograph by a dark prominence. × 1500.

Fig. 5. Oral end of a gastrozooid to show apical pads of nematocysts and meridional striae. Both of these features are absent in the palpons. × 32.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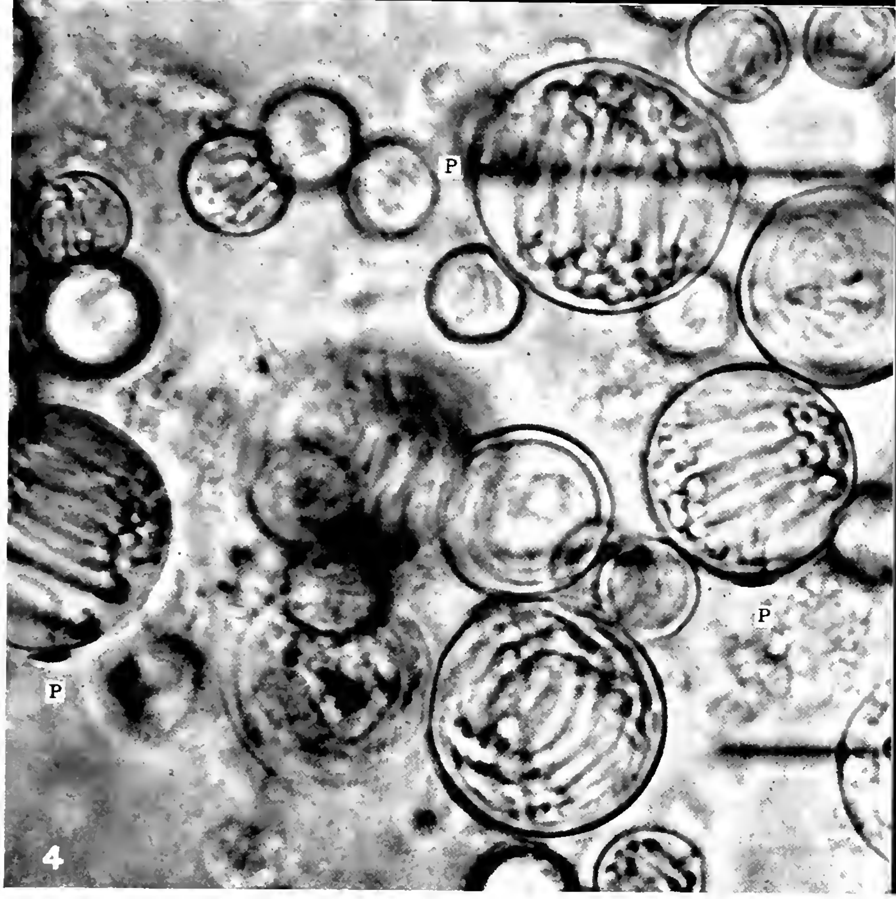
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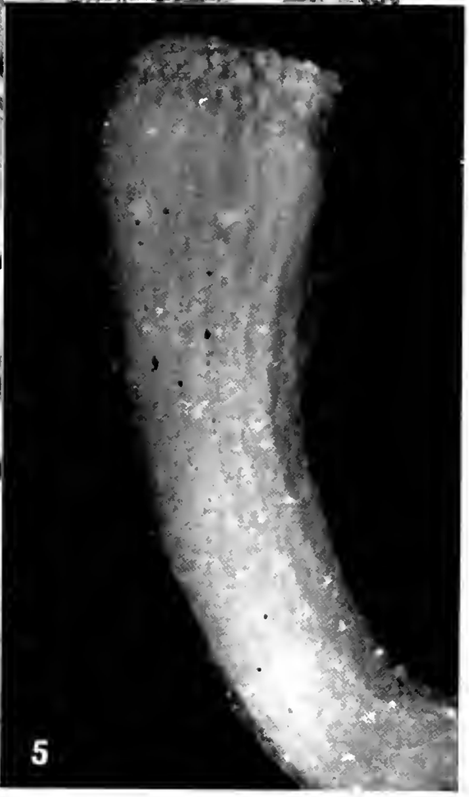
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PLATE XXVI

Fig. 1. A freshly caught specimen of *Physalia*, with the crest erect.

Fig. 2. The saccus, removed from a living specimen, photographed from beneath.

Fig. 3. The same saccus as in fig. 2, but with a 50 g. weight resting on it.

Fig. 4. The endodermal muscle sheet of the saccus, showing cell outlines and muscle fibres (F.W.A., iron haematoxylin).

Fig. 5. Detail of saccus muscle fibres, showing 'anastomoses' (F.W.A., iron haematoxylin).

Fig. 6. Another region of the muscle sheet, where some fibres have buckled, revealing their double nature (F.W.A., iron haematoxylin).

Fig. 7. Contracted muscle fibres from the dorsal outpushings of the saccus (Bouin, iron haematoxylin).


1


2


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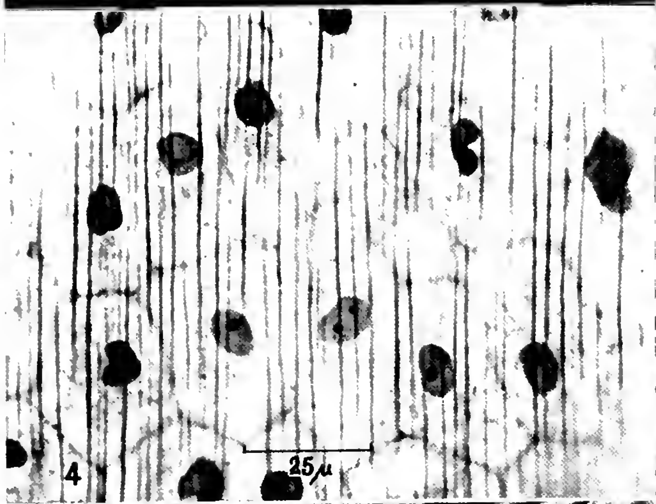
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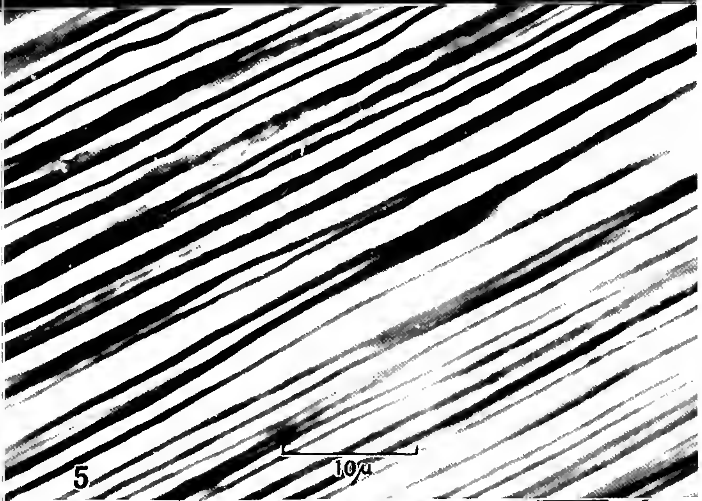
25μ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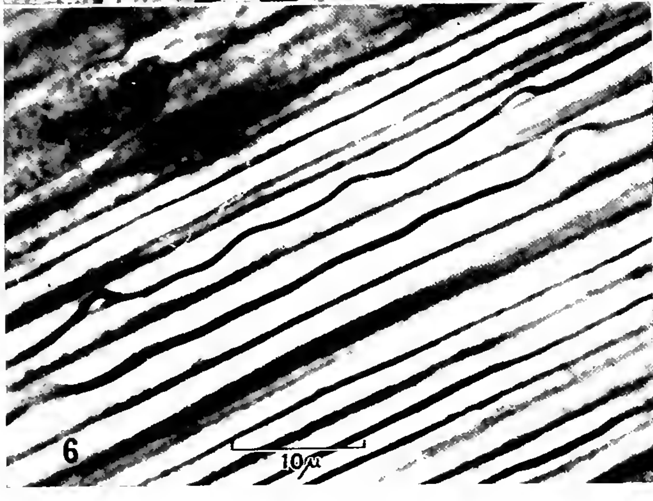
10μ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10μ


7

PLATE XXVII

Fig. 1. The diploid set of chromosomes from the saccus ectoderm. Late prophase. F.W.A., thionin. Scale 5 μ

Fig. 2. The codon ectoderm of *Physalia*, showing part of the nerve plexus. Formaldehyde-sublimate, Holmes's silver method. Scale 25 μ

Fig. 3. Frayed edge of mesogloea from the saccus, showing criss-cross laminae. Helly, iron haematoxylin. Scale 100 μ

Fig. 4. Gelatin section through the codon, near the base of some appendages. 'Bridge cells' cross the mesogloea from the endoderm (bottom) to the ectoderm (top right). F.W.A., Mayer's haemalum. Scale 50 μ

Fig. 5. Surface view of the codon ectoderm, in a region where the cuticle is partly disintegrated. Strands of cuticular material are seen running obliquely down from the underside of the fragments of cuticle, their swollen bases being embedded in the ectoderm. Bouin, silver (see too, Text-fig. 3, *gl.ec*^{2}). Scale 20 μ

Fig. 6. Paraffin section through the wall of a palpon (top) with a portion of a villus cut transversely (bottom). Zenker, P.A.S. Scale 50 μ

Fig. 7. Surface view of expanded buccal endoderm from a feeding gastrozooid, showing rows of short cilia, and a bunch of long ones. Formaldehyde-sublimate, silver. Scale 10 μ

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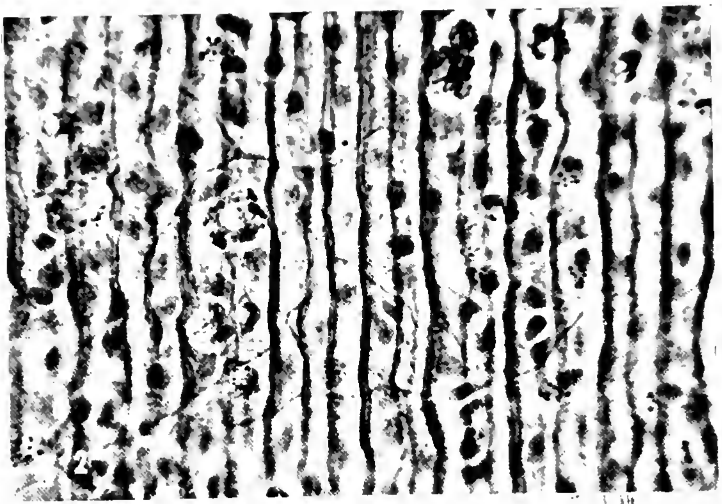

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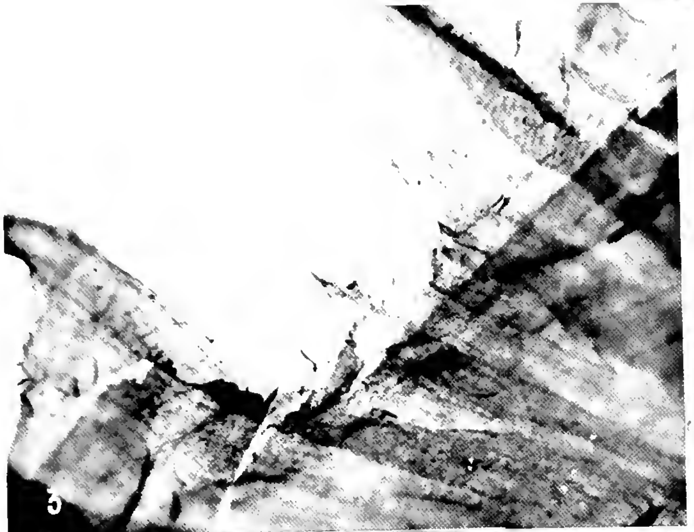

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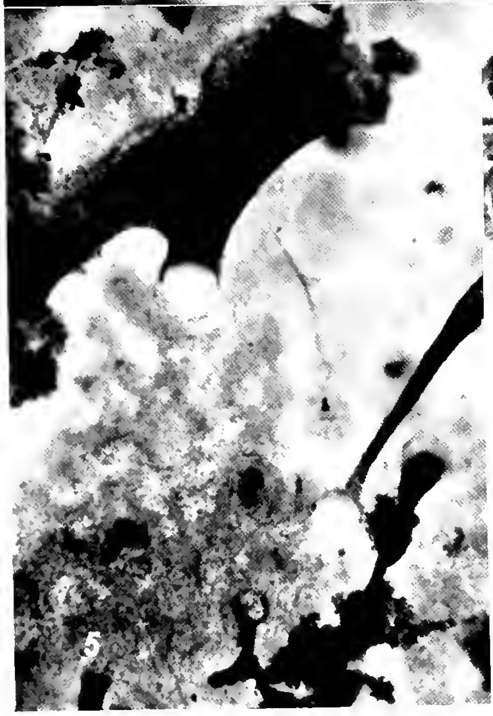

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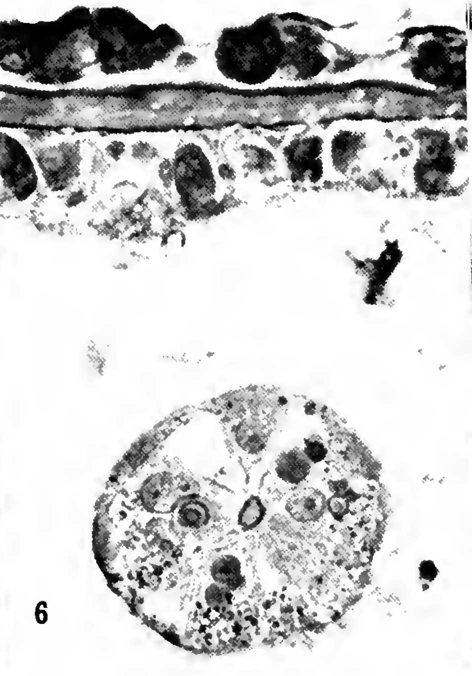

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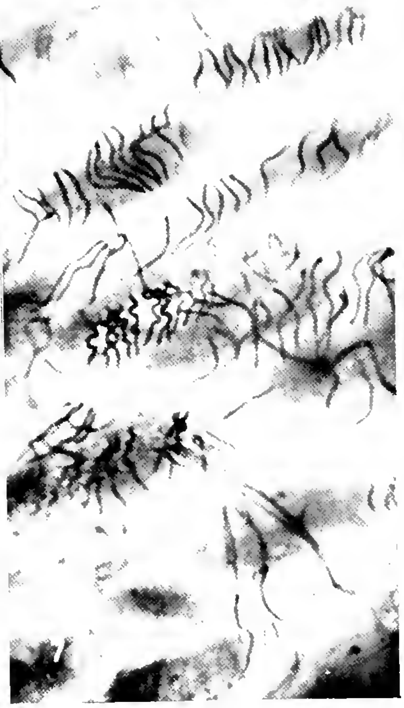

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PLATE XXVIII

Fig. 1. Gas-gland ectoderm from a young *Physalia*. The nuclei only are stained (Helly, Feulgen).

Fig. 2. Gas-gland ectoderm from another specimen, showing an 'islet' of six cells. The dark dots in the surrounding tissue are the nucleoli of the columnar cells. Some exceptionally large nucleoli to the right of the 'islet' belong to polyploid cells (F.W.A., iron haematoxylin).

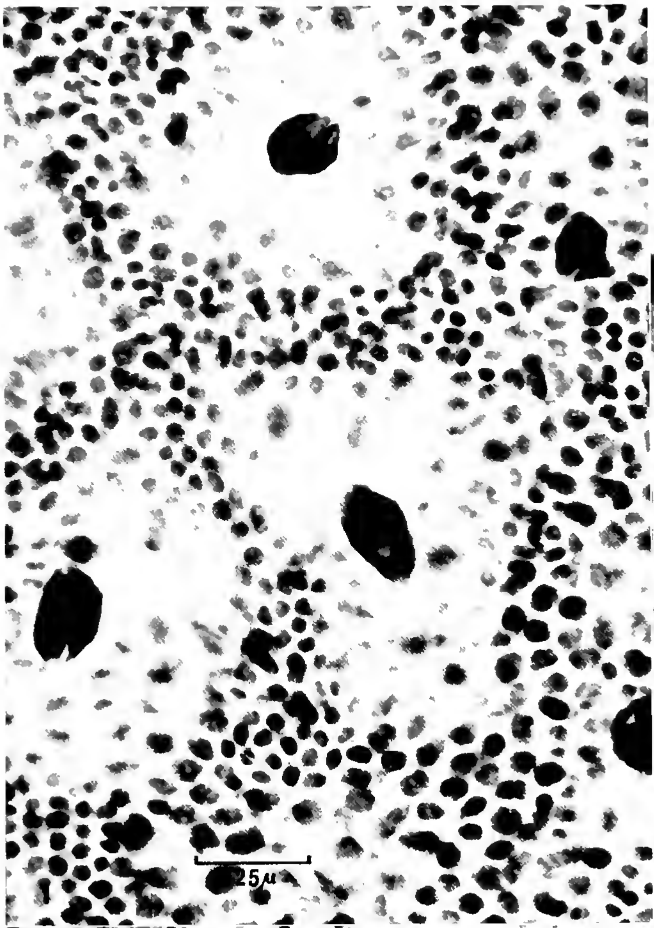
Fig. 3. A pair of young cnidoblasts from the ectoderm of a gastrozooid, showing Hirschler's 'fusom' (Ca-formaldehyde, silver).

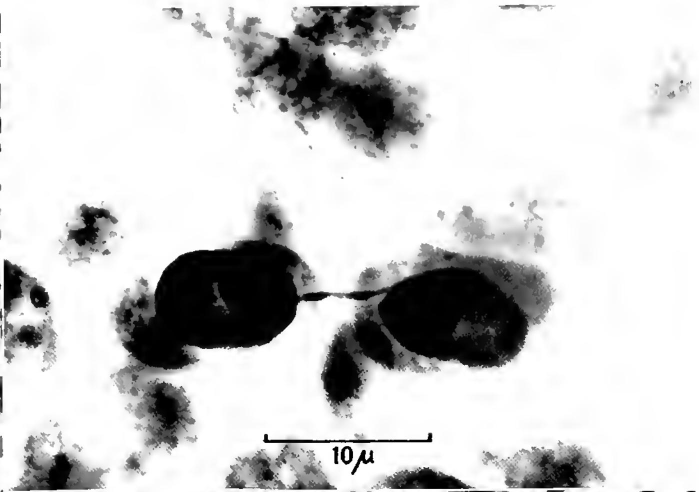
Fig. 4. A group of four prematurely discharged developing nematocysts from a gastrozooid. The cnidoblasts are not stained (formaldehyde-sublimate, silver).

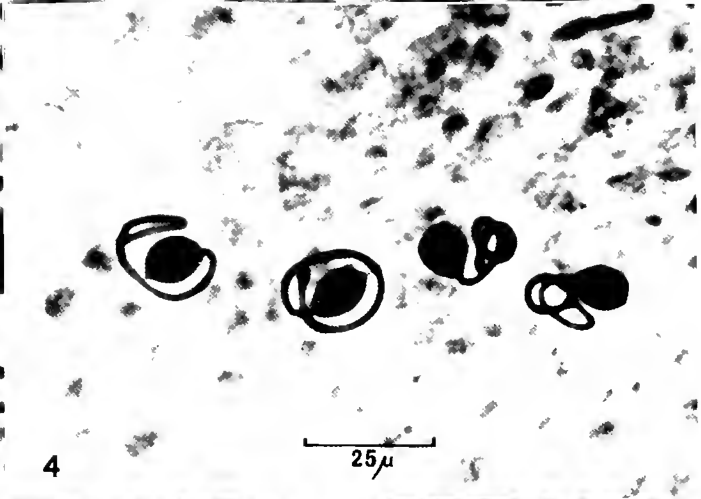
Fig. 5. Part of the incompletely discharged filament of a large isorhiza. The undischarged part is seen coiled within the discharged part (phase contrast).

Fig. 6. Group of large isorhizas from a tentacle. The arrow indicates part of a discharged filament showing the three spiral ridges beset with teeth (phase contrast).

Fig. 7. Fibrillar 'basket' from a cnidoblast, isolated by peptic digestion. The nematocyst (a large isorhiza) has escaped from the 'basket' leaving it somewhat distorted. The reticular association of fine fibrils around the apical opening is shown (phase contrast).







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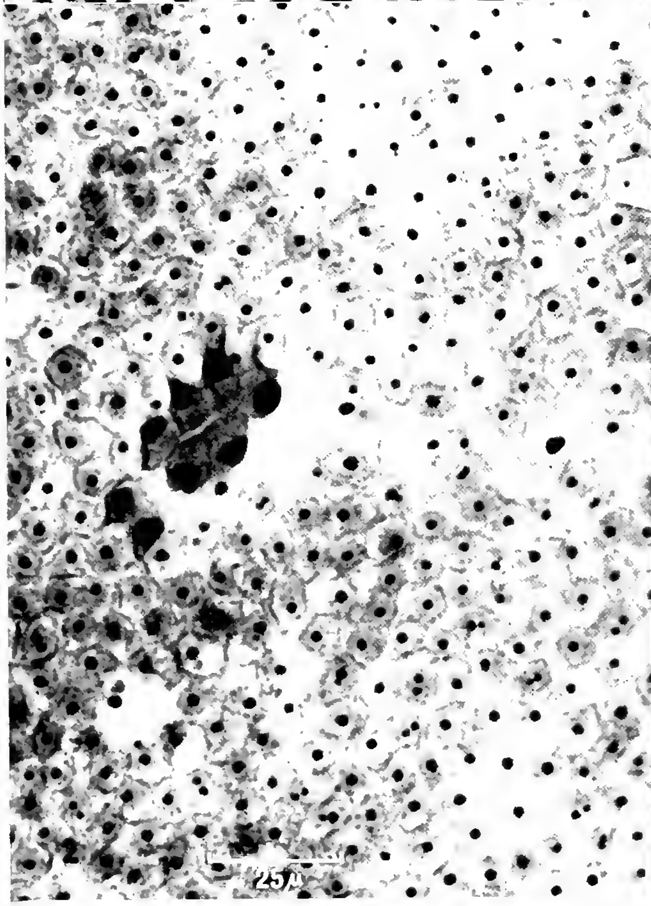

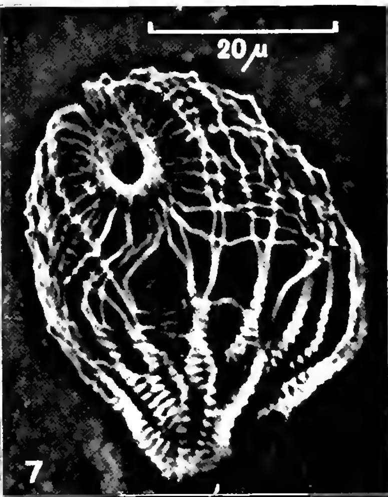

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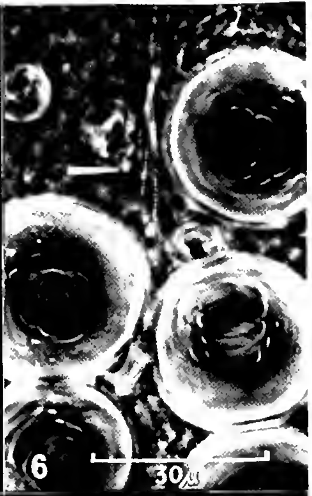

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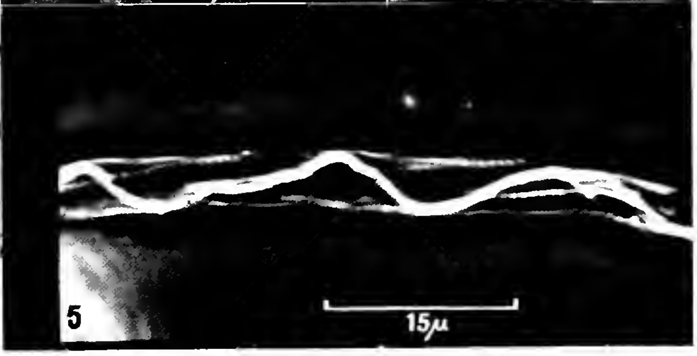

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